The Distribution and Ecophysiology of *Acacia* Species in the South Western Zone of Saudi Arabia

by

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DECLARATION

This thesis and the work presented herein is my own work except where otherwise indicated, and no part of it has been presented for higher degree.

Aref February 1996.

DEDICATION

To my mother, brothers, sisters and wife with love, respect and appreciation

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ABSTRACT

The thesis is a description of the patterns and distribution of *Acacia* trees in Saudi Arabia and an evaluation of the morphological and physiological responses of seedlings to limitation in soil water availability. Species examined were *Acacia ehrnbergiana* Hayne, *Acacia asak* (Forssk.) Willd, and *Acacia negrii* Pinchi-Sermoli. The objective was to investigate the environmental factors controlling the distribution of these species in natural communities in south western Saudi Arabia.

Fifteen major community types constitute the major part of the natural vegetation of the study area and are dominated by the *Acacia* species: *A. negrii*, *A. gerradii*, *A. asak*, *A. seyal*, *A. nubica*, *A. homulosa*, *A. ehrnbergiana*, *A. laeta*, and *A. tortilis*. Also present are *Ziziphus spina-christi, Juniperus procera, Tamarix aphylla, Hyphaen thebaica, Olea europea* and *Ficus salicifolia*. The form of trees in the region is controlled by rainfall and by factors affecting the distribution and the availability of water, such as topography and soil texture. *Acacia* species showed clear differences along these environmental gradients. *Juniperus procera* has the highest number of trees per site whilst *Tamarix aphylla* has the lowest density.

In the laboratory, seeds may be treated to enhance germination. Seed scarified by abrasion or acid treatment, and seed exposed to a heat shock showed stimulated germination. The duration of exposure to moist conditions required to make the testa permeable and to initiate germination of the seeds was ranked as follows: *A. ehrnbergiana* > *A. tortilis* > *A. seyal* > *A. asak* > *A. negrii*.

The effect of drought on water relations was studied on plants grown in long soil columns for *Acacia negrii*, *A. ehrnbergiana* and *A. asak*. Water deficit resulted in active osmotic adjustment in leaves, with decreases in osmotic potential at full and zero turgor, and increased bulk elastic modulus and leaf dry weight to turgid weight ratio. Stomatal conductance was correlated with soil water status.

The effects of different water regimes on the root growth development of three *Acacia* species was studied. This showed they had the ability to grow tap roots which penetrate deep into the water table. The total weight of the root for the dry and intermediate treatments were higher than for the wet treatment (control), and both had greater root lengths than the wet treatment. The increase in root weight was mainly due to a substantial shift in assimilates allocated in favour of roots with total biomass being unaffected.

Photosynthetic rates in *Acacia negrii* and *Acacia ehrnbergiana* seedlings decreased with declining soil water content. Photosynthesis was reduced by 60% and 55% for *Acacia negrii* and *Acacia ehrnbergiana* respectively after 8 days of the drought period. The more mesic *Acacia negrii* exhibited higher water use efficiency

(WUE) whereas the more drought tolerant *Acacia ehrnbergiana* had a lower WUE. The rapid recovery in photosynthesis following rewatering after a period of stress suggests that *Acacia negrii* should be able to take advantage of summer rainfall by rapidly increasing photosynthesis. After rewatering, the net photosynthesis of the *Acacia negrii* seedlings recovered from 2.9 μmol $m^{-2} s^{-1}$ to 7.0 μmol $m^{-2} s^{-1}$ over 24 hours. After four days reaching pre-treatment values. However, photosynthesis for *Acacia ehrnbergiana* recovered slowly and to a level below the control seedlings.

The results of this study provide important information for the improvement of current silvicultural techniques. They suggest utilising the native species' responses in planning and management of forests to obtain the greatest benefits in Saudi Arabia.

CONTENTS

LIST OF TABLES

List of tables continued

LIST OF FIGURES

List of figures continued

List of figures continued

List of figures continued

List of figures continued

List of figures continued

CHAPTER 1

General Introduction and a Review of literature

1.1 Introduction

Saudi Arabia covers an area of nearly 2,300,000 km^2. Of this, arable land covers 500,000 km^2 (Migahid, 1978). Natural rangeland covers a total of more than 1,500,000 km^2 and about 16,000 km^2 are covered with forests. The characteristic hot climate with low relative humidity, except in the coastal areas, prevails throughout most of Saudi Arabia. The rainfall in the upper two thirds of the Kingdom is scant and irregular (Al-Jerash, 1985). The annual average rainfall varies from 30 to 50 mm in the north west, while it is 40 to 90 mm in the north east. However, in the mountains of the south-western region it exceeds 300 mm (El-khatib, 1974; Al-Jerash, 1985). While a large part of the kingdom is a plateau of base-rich rock with a well developed soil layer, other parts are vast deserts as in Rub Al-khali and Nafud. These physiographic features result in mostly saline and alkaline soils (El-khatib, 1974 and Al-Mafarij, 1985).

The south western part of the Hijaze and Asir (Fig 1.1) have the richest and most varied flora in Saudi Arabia. They contain mountain, escarpments, deep valleys, rolling land, rocky hills, wadis, waterfalls and pools (Vesey-Fitzgerald, 1957). Such topography along with a mild climate and relatively high amount of rainfall creates a diversity of habitats for plants such as *Acacia, Juniperus* and *Hyphaene thebaica* (Abo-Hassan *et al.*, 1984). However in Hijaze and Asir there is degradation of the plant communities and this is due to several reasons, the most important of which are overgrazing, land clearance for construction and agriculture, and tree cutting for charcoal and other purposes. In addition there has been a reduction in rainfall which has lead to drought (Ministry of Agriculture and Water, 1984). It has become clear that the future long-term development in this region depends on the conservation of its natural resources particularly forest, trees and shrubs as well as on the restoration and reforestation of the degraded lands.

Beside the natural dry forests growing in the south western mountain covering 16,000 km^2, afforestation plantations are established in a few parts of the country (Abo-Hassan *et al.*, 1984). During the past two decades, along with the economic rise in the Kingdom, afforestation activities have increased tremendously. Indigenous

(*Acacia* species and *Tamarix* species) and exotic species such as *Casuarina* and *Eucalyptus* have been planted (Abo-Hassan, 1976 and Aref, 1987). The main problem of establishing seedlings in an arid region such as Saudi Arabia are :

1. Low and erratic supply of moisture and low relative humidity
2. Desiccating wind, often abrasive, containing dust and sand
3. Extremes of temperature

The important role of afforestation in the arid zone necessitates the proper selection of the planting stock (Abo-Hassan, 1976). Usually fast growing species are used in irrigated or unirrigated plantations to achieve that task. Thus, species selection in the afforestation projects is of major importance (Aref, 1987). Adaptability of the selected species to the prevailing environmental conditions of the afforestion site in arid regions is of vital importance (Abo-Hassan, 1976). This is due to the expensive activities included in establishing tree plantations in arid regions beside the highly important role of trees under these environments. *Acacia* species are most suitable for afforestation under adverse conditions in the arid zone. *Acacia* species are especially important because they are legumes and so can fix nitrogen (Stock *et al.*, 1995). There are many other benefits from *Acacia* species, including the provision of fuel in the form of wood and charcoal, medicines, tannins, gum, building material, rope and fiber, honey and shade (Maydell, 1990 and Chaudhary, 1983). In addition to these uses, for many nomadic and pastoralist people in arid areas, *Acacia* species represent the major source of food for their livestock at certain time of the year.

The composition and structure of the vegetation is influenced directly by environmental gradients. The character and intensity of these influences may vary between different regions characterised by distinctive vegetation, climate soil and physiography (Whittaker, 1975; Peet, 1981; Willims *et al.*, 1992). The composition and structure of the forest differs not only with time but also in space. Both the site (including both climate and soil) and the geographical distribution of forest species help to determine the nature of a given forest stand. The study of interactions between forests and their environment is of great importance for water and soil conservation (Whittaker, 1965; Wesser and Armbruster, 1991). There are many important factors, including the amount of rainfall, air temperature, high altitude and drought, but drought seems to be the major factor limiting survival and growth of tree seedlings (Kramer, 1983).

Very few studies have been done in Saudi Arabia to assess the ecology of the natural forest. Little is known about the response of *Acacia* species seedlings to the low soil moisture conditions that prevail during the dry season and in particular their ability to acclimate to environmental changes. An understanding is needed of the morphological and physiological changes that are induced by the limitation in soil water availability. This study is a description of the patterns and distribution of *Acacia* trees and an evaluation of the morphological and physiological response of *Acacia ehrnbergiana*, *A. negrii* and *A. asak* seedlings to the limitation in soil water availability.

The results of this study will enable specialists to improve the silviculture. The study will also explore the possibilities of planning the management of forest to obtain the greatest benefits. Thus, the next sections of this introduction will serve to briefly review the literature.

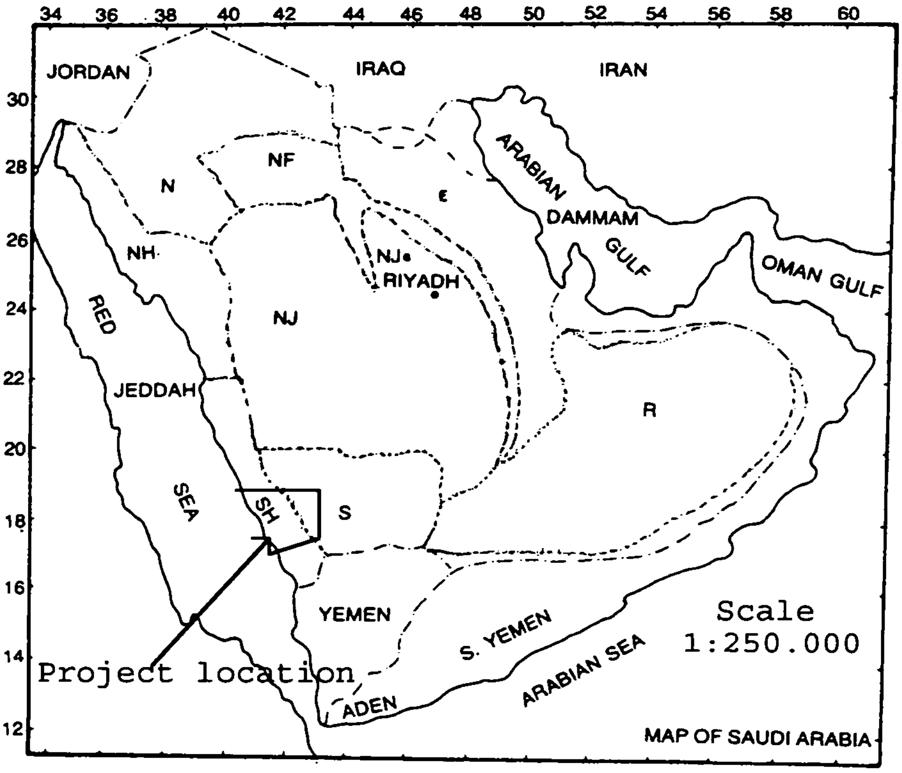

Figure 1.1: Phytogeographical regions of the Kingdom of Saudi Arabia (Migahid 1978). Scale 1: 250,000

N. North region, including Tabuk, Al Jaef and Sakakah area

NF. Nefud region, include the great northern Nufud area, Dahna' and Al-Qassim area

NH. North Hijaz, representing the western part of Saudi Arabia the extends along the Red Sea coast north of Jeddah.

SH. South Hijaz, representing the southern part of the western region exending south of Jeddah to the Yemen boundaries. It includes Alshugayg

S. Southern region, lying to the east of South Hijaz, to the south of Najd and to the north of Yemen. It include Abha, Al soudah, Bisha and Najran areas.

NJw. Western Najd

NJe. Eastern Najd.

E. Eastern region, between Dahina' and Arabian Gulf.

R. Al Rub' Al Khali, representing most of southern and south-eastern parts of Saudi Arabia.

1.2 Review of literature

1.2.1 The adaptability of vegetation to arid desert conditions

The climate of the Kingdom of Saudi Arabia is extremely arid, with a strong solar radiation during the dry season. The summer is long, hot and dry, and winter is short with little rainfall (Al-Jerash, 1985). Consequently, the vegetation which survives these arid conditions develops a number of features which enables it to grow and flourish. These main components of the vegetation are as follows:

1) Most importantly there is a high proportion of ephemeral annuals. These constitute between 50% and 60% of the species found in the desert areas of the Kingdom (Migahid, 1978). Such herbaceous plants are able to complete their life cycle within 6 to 8 weeks on average (Kramer, 1983). They germinate in the short rainy season and spend the dry period, which may extend to the remainder of the year or to a number of years, in the form of dormant seeds. These plants survive the arid period by completing their growth life cycle during the wet period of the year when the seeds are formed (Evenari *et al.*, 1971). Morphologically, these ephemeral annuals are small in size and shallow rooted, but their roots have the capacity to spread horizontally and cover a large area of soil, thus enabling them to exploit rainfall no matter how sparse (Evenari *et al.*, 1971; Migahid *et al.*, 1974). Furthermore, the seeds of these herbaceous plants are characteristically ephemeral in that they possess mechanisms which enable them to remain dormant, curbing premature development and thus avoiding abortive attempts at growth (Evenari *et al.*, 1971).

2) Other longer-living species. These continue to grow during the arid season, adopting a variety of forms depending on the particular species (Fischer and Turner 1978). These plants are called xerophytes and are of two kinds; succulents eg *Aloe vera*, and sclerophytes eg *Acacia* species (Maydell, 1990; Migahid, 1978). Xerophytic plants have the ability to resist drought by morphological and physiological adaptations which enable them to cope with arid environments. These include:

1. An extensive root. Most of these plants possess a highly extensive root system which spreads both vertically and horizontally. Vertically, the roots reach great depths, sometimes 10 to 15 metres (Evenari *et al.*, 1971). This enables them to absorb

any water available in the deepest layers of the soil (Migahid *et al.*, 1974 and Kramer, 1983).

2. Small leaf size, thought to be particularly related to a decrease in the area of the transpiring surface (Kramer, 1983). In general, it can be said that plants with smaller leaves predominate in arid regions (Evenari *et al.*, 1971; El-Amin, 1976).

3. The leaves of some of the plants are covered by thick hairs which reflect part of the rays of the sun and together retain humidity at the surface which reduces transpiration, as is the case with *Pergularia tomentosa* and *Abutilon* species (Migahid *et al.*, 1974).

4. Branches of some of the plants are reduced to thorns, as is the case with *Alhagi maurorum* and *Zilla spinosa* (Migahid, 1978).

5. Decreasing water loss through the cuticle. Most of the plants growing in arid regions possess thick cuticles which help both to decrease water loss and to protect the plant from the rays of the sun by reflection (El-Amin, 1976). However, the decrease in cuticular transpiration is primarily ascribable to the deposition of lipids and wax (Skoss, 1955).

6. One of the most important adaptive mechanisms to drought is osmotic adjustment, that is the net accumulation of solutes in response to declining water potential. Adjustment in osmotic potential during drought may promote turgor and limit desiccation (Turner and Jones, 1980; Turner, 1986 and Abrams, 1988). There are several sets of experimental data for both herbaceous and woody plant that demonstrate this in both leaves and roots (Morgan, 1984). Stomeman *et al.* (1994) reported a significant osmotic adjustment in water stressed *Eucalyptus marginata* seedlings, Bahari *et al.* (1985) reported significant osmotic adjustment during drought in six woody species of oak. In these studies osmotic adjustment was associated with partial or turgor maintenance. This may act to maintain a favourable gradient for water uptake from drying soil, without given rise to a large tissue water deficit (Stomeman *et al.*, 1994).

1.2.2 Germination of seed in species of the arid zone

The regulation of the process of germination requires mechanisms that keep the seed dormant in unconducive conditions (Clements *et al.*, 1977). For example, the non-dormant seeds of *Artemisia abyssinica* germinate quickly when exposed to fluctuating temperatures equivalent to those which prevail in the rainy season (December to April) (Mahmoud *et al.*, 1982). Seeds which do not germinate then, go into a state of dormancy when exposed to high temperatures equivalent to those which prevail in May, the beginning of the drought season. These dormant seeds are also able to germinate when exposed to temperatures equivalent to those which prevail in one of the months of the rainy season. This clearly shows that temperature is a factor which prompts the seeds to germinate in the season that is most conducive (Mahmoud *et al.*, 1982). Chemical mechanisms involving inhibition of metabolism obstruct the gas and make impermeable testa also prevents the onset of the germination. Thus together with the non-permeable seed germ, the process of germination is spread over successive periods, over years. This preserves a number of seeds as 'seed bank' in the soil which are enable subsequently to germinate when conditions are right.

The vegetation in the arid region has several strategies for survival in the spatially and temporally variable environment. For example, the *Acacias*, the dominant perennial in many arid areas of Africa and the Middle East such as Saudi Arabia, produce substantial quantities of seeds to overcome the high rate of infestation by Bruchid beetles (*Bruchidius* spp) and the unpredictable environment (Sabiiti and Wein, 1987). The average annual seed production of *Acacia saligna* and *Acacia cyclops* is 10,000 and 3,000 seeds per square metre of canopy cover respectively (Holmes *et al.*, 1987). Also *Acacia albida*, in a good year, can produce more than 143,000 seeds per tree (Wickens, 1969). Another general survival strategy adopted by *Acacia* species, is the ability to accumulate large quantities of viable seed in the soil (Cole, 1986; Holmes *et al.*, 1987; Sabiiti and Wein, 1987). For example, *Acacia melanoxylon* produces seeds which can remain viable in the soil for at least 50 years (Farrel and Ashton, 1978). Milton and Hall, (1981) in South Africa reported the existence of a large quantity of viable *Acacia* seeds, 125-250 million seeds per hectare in the top 10 cm of soil. The long viability of *Acacia* seeds is achieved by the water-impermeable testa of the seed, which exerts a physical exogenous dormancy (Holmes *et al.*, 1987). Other advantages of the impermeable seed testa are the ability to withstand fire, and recolonize burnt sites after a fire, as well as to survive ingestion by animals and birds, thereby allowing dispersal (Rolston, 1978). Fire is another factor to which *Acacia* species are adapted. Fire stimulates the regeneration of many *Acacia* species by heat rupture of the lens (Tran and Cavanagh, 1984). Omer (1975) studied the effect of fire on the regeneration of five *Acacias* in the Sudan. He found the germination of four of them was either enhanced or not affected by light or heavy fire. The germination of the fifth species was inhibited only by heavy fire. Farrel and Ashton (1978) reported that, although the natural regeneration of *Acacia melanoxylon* in Australia can occur without fire, even-aged regeneration of considerable density follows catastrophic fires. Additional support was provided by Sabiiti and Wein, (1987) who found that high fire intensity in natural forest stimulates high seedling emergence of *Acacia siberiana*. Also Jianmin and Sinclair (1993) reported that the *Acacia myrtifolia* was killed by fire and subsequently regenerated from seed.

The hard impermeable seed testa of *Acacia* species permits long-distance dispersion of the seeds and enables the *Acacias* to survive in the patchy and unpredictable environment of the arid regions (Rolston, 1978). Domestic and wild animals consume large quantities of *Acacia* seeds (Coughenour and Detling, 1986; Milton and Hall, 1981; Pellow, 1983). Large proportions of the seeds eaten by animals are returned to the soil without being damaged. For example, Wickens (1969) reported that up to 66% of *Acacia albida* seeds eaten by animals were returned to the soil and they were viable. The passage of *Acacia* seeds through animal's, digestive tracts has a positive effect on the germination of *Acacia* seeds which has been attributed to scarification of seeds by digestive fluids (Pellow, 1983; Ahmed, 1986; Coughenour and Detling, 1986). Ahmed (1986) reported that the germination of *Acacia tortilis* subspecies *spriocarpa* increased from an average of 19.6% without ingestion to 54.2% after animal ingestion. Also, Coughenour and Detling (1986) reported that in Turkana, Kenya, a dense population of *Acacia tortilis* occurs from the seeds defecated in goat and camel corrals. Not only does animal ingestion enhance the germination of *Acacia* seeds, but also the digestive fluids of herbivores kill the larvae of the Bruchid beetles (Southgate, 1977; Pellow, 1983; Ahmed, 1986; Coughenour and Detling, 1986). The dung also provides the seeds with nutrients and reduces the rate of drying by mulching (Ahmed, 1986; Coughenour and Detling, 1986).

1.2.3 Vegetation composition in the arid zone

The vegetation composition in the arid region depends largely on rainfall and on factors affecting the availability and distribution of water (Noy Mier, 1974; Yair and Danin, 1980; Shmida and Wilson, 1985; Blesky, 1989). At regional levels the diversity and species richness of species increases with increasing rainfall (Noy-Mier, 1974; Geerling, 1985). On a smaller scale the factors of topography, soil texture and soil depth become more important in determining vegetation composition and density (Noy-Mier, 1974). Sandy soil in arid regions was found to support denser vegetation than silty or clay soils because of its lower water holding capacity (Noy-Mier, 1974; Shmida and Wilson, 1985; Choudhari, 1988). Also, many workers reported that vegetation composition was determined by its topographical position relative to the runoff or run-on of surface water (Noy-Mier, 1974; Yair and Danin, 1980; Shmida and Wilson, 1985; LeHouerou *et al.*, 1988). Other factors which have been found to contribute to control of the vegetation composition are the proportion of exchangeable calcium, salinity, and the available phosphate (Noy-Mier, 1974).

At the temporal level, the composition of the regeneration at any given site varies with the amount of water received at that site for that particular year (Kassas, 1957; Mahmoud,1977; Shmida and Wilson, 1985). Kassas (1957) reported that vegetation of the semi-arid region in the north Sudan showed a remarkable difference between seasons and fluctuated greatly from one year to another. He recorded the number of species within a known plot on four occasions. In the wettest year, the rainfall was 244 mm. He recorded seventy species (fifty-eight ephemeral and twenty perennial). In the driest year, the rainfall was 178 mm. He recorded forty-four species. Thirty-four of the species which were recorded in the wettest year did not appear in the dry year. Shmida and Wilson (1985) reported evidence that re generation of different species are favoured in different years. Agnew and Wterman (1989) reported that the establishment of some species in a dry area of Kenya occurs intermittently and he suggested that those species require a run of good rainfall years. Agnew's results were similar to the results reported by Chesterfield and Parsons (1985) in Australia.

1.2.4 Competition in the arid zone

The importance of competition in the arid regions has been debated and Went (1955); Weins, (1977) have even denied the existence of competition in arid regions. Neither of them provided evidence to support his statement (Fowler, 1986).

The importance of competition in shaping the community in arid regions has also been debated. One group suggested that the high environmental fluctuations control the vegetation to the extent that competition rarely occurs and its effect on the community is therefore minimal (Weins, 1977). The.second group assumes that competition for the scarce resource (water) in the arid region is intense and important in shaping the community's structure (Noy-Mier, 1974; Fowler, 1986; Penridge and Walker, 1986; Smith *et al.* 1986). Evidence supporting the existence and importance of competition exists. For example, Smith and Goodman (1986) reported a positive correlation between the nearest-neighbour distance and the combined canopy cover for both within and between *Acacia* species in South Africa. Similar results were reported by Penridge *et al.* (1986) in Australia. Belsky (1994) provided other evidence by reporting that mature shrubs inhibit shrub seedling establishment to a distance of five times their canopy radius. Also growth of *Acacia tortilis* (tree) for the first three years by *Cenchrus ciliaris* (grass) is as a result of competition for water in the upper soil layer (Belsky, 1994). In both cases the correlation was attributed to the existence of competition. Another example is Obied's and Seif El Din (1970) study in the Sudan reporting the absence of *Acacia senegal* seedling establishment under the canopy of established trees. Their findings were supported by Smith and Goodman (1986) for *Acacia nilotica* and *Acacia tortilis* in South Africa.

The failure of *Acacia* seedlings to establish under other woody vegetation suggest that disturbance is very important in order for *Acacia* to maintain their dominance in the arid and semiarid regions. Smith and Goodman (1986) reported that the elimination of elephants from the Mruzi Game Reserve in South Africa was followed by an increase in the density of *Acacia* followed in turn by an increase in the establishment of *Euclea*, an evergreen shrub. In conclusion, despite the debate over the importance or even sometimes the existence of competition in arid regions several studies suggest that competition in arid regions does exist and is very important.

1.2.5 The primary production in arid regions

The primary production, the rate of dry matter accumulation, in the arid regions is low due to the limited water availability (LeHouerou *et al.*, 1988). Several studies have been carried out to estimate the net primary productivity in arid regions. Noy-Mier (1974) estimated the annual above ground net primary production to range from 3 to 300 g m^{-2} $year^{-1}$. Turner and Randall (1989) estimated the net above ground production for annual vegetation to be from less than 0.1 g m^{-2} to 64 g m^{-2} for perennials the productivity ranged from 20 g m^{-2} to 68 g m^{-2}. Whittaker and Likens,

1973) suggested a mean annual primary productivity for desert scrub of 70 g m^{-2} $year^{-1}$. The net primary productivity in the arid region is highly variable (Noy-Mier, 1974). This variability of the primary production is closely linked to rainfall and to factors affecting the distribution and the availability of water (Whittaker and Likens, 1973; Turner and Randall (1989). At the regional scale, the net primary productivity increases with increasing rainfall (Geerling, 1985; Murphy and Lugo, 1986), while the variability of net primary productivity decreases with increasing rainfall (Allen, 1986). On local scale, the net primary productivity is determined by the site position relative to the pattern of water runoff and run-in (Allen, 1986). LeHouerou *et al.*, (1988) reported that variability of net primary production in arid regions decreases with run-on and increases with run-off. Also the net primary productivity is greater in coarse-textured top soil than in fine-textured top soils (Noy-Mier, 1974; Shmida and Wilson, 1985). Le Houerou *et al.* (1988) reported that variability of primary production is higher in fine-textured soils compared to coarse-textured soils.

1.2.6 Development of water stress in plants

Water is essential for growth, and it is needed in much larger quantities than are the plant nutrients (Boyer, 1985). Plants require a reserve of water to maintain their metabolic and other biologic functions (Kramer, 1969). Vascular plants have evolved intricate systems to maintain and regulate water within their systems, such as roots and stomatal controls (Turner, 1986). A water potential gradient from the soil to the atmosphere provides the driving force to move water through the conducting channels of the plant (Boyer, 1985). Actively growing plants have a continuous liquid water phase from the soil water through to the liquid/gas phase in the cell/air environment within a leaf. Evaporation creates a vapour pressure deficit that serves as the driving force to move water in the plant (Wilkins, 1979). As much as the entire volume of water within a plant may be lost during one day under favourable conditions of transpiration (Passioura, 1982). The continuity of water in the conducting system provides an essential communication network between roots and shoots that keeps the rate of absorption and transpiration in balance (Boyer, 1985). Thus, when transpiration increases, if the water supply to the leaves is insufficient, then the leaf water potential will decline (Wilkins, 1979; Passioura, 1988). If soil water content is low the root to soil water potential (Ψ soil root) will decline, and this stimulates synthesis of ABA (abscissic acid) Zhang and Davies (1989). This is translocated to the leaves in the xylem (transpiration) stream and cause stomatal closure. This can be demonstrated in artificial circumstances (e.g. Khalil and Grace, 1993) using the split root system. The transpiration rate usually depends on how much water can be absorbed by the roots and on the surface area of the leaves (Boyer, 1985). When the roots cannot supply enough water to meet the needs of the evaporating surface a deficiency will result and the plant will respond by closing the stomata to control wilting (Kramer, 1969). A high root/shoot ratio is desirable to provide adequate water for high transpiration and to forage for water under conditions of low water supply.

The lower water potential in the leaves provides a driving force for water movement out of adjacent organs, resulting in subsequent loss of water from the stem followed by the roots (Boyer, 1985). Such a decline of water potential can lead to the development of water stress (Hsiao, 1973). Water stress refers to a deleterious effect on the growth rate and physiological performance of a plant caused by the decline in the chemical potential or by a change in water content (Turner, 1986). Leaf water potential is defined as the difference between the free energy status of water in the plant tissue and that of pure water at the same temperature and normal atmospheric pressure (Kramer, 1983). At zero water potential the plant's tissues are fully turgid and as more water is lost than absorbed the water potential becomes negative and decreases (Hsiao, 1973). The turgor pressure of the cell also decreases, and when the water potential reaches the level at which cell turgor pressure is zero, the cell is flaccid and severely stressed (Kramer, 1969). The value of total water potential at which the turgor potential appreciably declines varies from species to species and may also vary with the conditions to which the plant has been exposed previously (Newman, 1976).

When the soil dries, there is an increase in resistance to water flow through the soil to the plant roots (Passioura, 1982 and Boyer, 1985). The resistance may be due to shrinkage of soil away from the roots as the soil dries or contraction of the stressed roots from the soil (Kramer, 1988). Both effects will result in formation of vapour gaps between the root and soil thus reducing the effective area of contact between the root and soil water, which will increase the flow resistance at the root-soil interface (Passioura, 1988). Kramer (1988) asserted that shoot water stress usually develops before any significant stress occurs in the roots; the dehydrating effect of maize plants growing in drying soil (Sharp and Davies, 1979) supports these ideas. Boyer (1985) postulated that, as soil dries, the roots communicate the soil condition to the shoot as a change in xylem water potential thus altering the rate of delivery of solutes to the shoot. Thus, the development of water stress in leaves is caused by the inevitable decline of leaf water potential as a result of transpiration. In contrast, during soil drying leaf and shoot functioning is not always related to shoot water potential, because plants may develop active control of shoot water status (Kramer, 1988). Schulze and Hall (1981) pointed out that the same leaf water potential may be reached, either by strongly transpiring well watered plants or water stressed plants with low transpiration rates. Moreover, it is possible for water stressed plants to exhibit higher shoot water potentials than well watered plants (Jones, 1985) once the stomata have closed. Khalil and Grace (1992) who found that the bulk leaf water potential of the water stressed seedlings (*Acer pseudoplatanus*) showed no response to water stress until day 23, after which water potential fell significantly by day 28.

1.2.7 Response of stomata to water stress

Stomata provide a highly regulated system to restrict water loss to the atmosphere and provide an avenue for the uptake of CO_2 , an essential prerequisite for the production of biomass (Whitehead, 1980). Stomatal closure by plants growing in water stress has been well established (Hsiao, 1973). In drought situations stomata may close either in response to internal factors (including leaf water status, leaf temperature and CO_2 concentration) or external factors (including ambient CO_2 concentration, ambient temperature and humidity) (Kramer, 1883). Closure as a response to an internal signal results when water deficit within the leaf causes a loss of turgor which then affects the guard cells (Crawford, 1989). However, water stress within the plant can also cause stomatal closure without the delay that is necessary for loss of turgor. Sobrado and Turner (1983) reported that the relationship between leaf conductance and leaf water potential of *Helianthus annuus* and *Helianthus petiolaris* was not affected by the rate of stress development

Differences among other tree species in sensitivity of stomata to water deficits have been reported (Hsiao, 1973; Federer and Gee,1976; Ackerson,1981). An earlier view of this response was that as soil dries down the water uptake by the plant is reduced and this results in a reduction in water potential which in turn causes a decline in turgor potential of stomatal guard cells. As a result, stomatal conductance is reduced (Hsiao, 1973). However, under limited soil water supply, a poor correlation has been reported between stomatal conductance and leaf water potential and turgor potential in response to a change in saturation deficit in both herbaceous and woody species (Slatyer, 1967 and Tuner *et al.*, 1978). Some studies showed an almost linear decrease in conductance with declining leaf water potential (Ficher and Turner, 1978; Jones and Rawson, 1979). However water potential of leaves can vary over a considerable range without a marked effect on stomatal aperture (Jarvis 1980).

A number of plant species, especially Legumes, close stomata in dry soil even though the plant's internal water status has not changed (Bates and Hall, 1981). Stomatal conductance in five *Alnus glutinosa* clones decreased after irrigation was withheld (Hennessey and Lorenzi, 1987). There was a close correlation between stomatal conductance and soil water status (Turner *et al.*, 1978; Gollan *et al.*, 1985). However decreases in stomatal conductance were not accompanied by a particular decline in bulk leaf water potentials. Blackman and Davies (1985) reported that stomatal conductance decreased even though the leaf potential was similar to those of well-watered in maize. This indicates that leaf water relations were not the variable controlling the stomatal behaviour. Other authors have shown that stomatal conductance decreases with low soil water availability (Brown *et al.*, 1976; Kelliher *et al.*, 1980; Ullmann, 1989; Gwoing *et al.*, 1990 and Zhang and Davies, 1989). Schulze (1986) reported that stomata respond to a signal from the roots when the soil dries before the leaves wilt. Several recent studies by Turner (1986) and by Schulze (1986) have presented evidence indicating that stomatal conductance is more closly correlated with soil water status than with plant water status. Khalil and Grace (1992) found that reduction in stomatal conductance of sycamore seedlings (*Acer pesudoplatanus*) was strongly correlated with the changes in soil water status

1.2.8 Effects of water stress on photosynthesis

When a terrestrial plant is subjected to a drought stress, the leaf net CO_2 uptake declines as a result of the stomatal closure (Brix 1962,; Melzack *et al.*, 1985,; Kaiser, 1987; Chaves, 1991; Cornic *et al.*, 1992). Plants in xeric sites exhibited higher rates of photosynthesis than plants in moist sites under water stress (Bahari *et al.*, 1985; Abrams and Kubiske 1990; Ni and Pallardy, 1991, 1992; Owens and Schreiber, 1992 and Barton and James, 1993). The higher photosynthetic capacities in several species may be related to resource availability and enable successful exploitation of regions with unpredictable weather (Davies and Kozlowski, 1977; Ehleringer and Mooney, 1983; Medina and Francisco, 1994). Abrams *et al.* (1989) found the seedlings of *Fraxinus pennsylvanica* March from the most xeric habitat, maintained the highest net photosynthesis during 17 days drought. Barton and James (1993) found carbon dioxide uptake of three higher elevation species decreased to 25% of well watered controls by day 16 of drought and zero CO_2 uptake by day 29. In contrast the lower altitude species showed levels above 50 % of the control on day 16 and still exhibited positive CO_2 uptake on day 29. The capacity to limit water loss and the ability to sustain stomatal opening at low water potentials appear to promote the success of the plant growth in dry site. Also Bahari *et al.*, (1985) found *Quercus* species (from xeric site) exhibiting higher photosynthesis under drought compared with *Acer saccharum* and *Cornus florida* (from moist site).

There are many sets of experimental data demonstrating that carbon assimilation can be limited by stomatal closure either in response to a decrease in plant water potential or to an increase in the water vapour pressure difference between the leaf and air (Chaves, 1991). Brix (1962) who found that the net photosynthesis for tomato and loblolly pine seedlings was affected by water stress because of decreased stomatal conductance. Seiler and Johnson (1988) found that photosynthesis decreased greatly with needle water potential for loblolly pine (*Pinus taeda* L.). Franco *et al.*, 1994 reported that the desert shrub *Larrea tridentata* exhibited a net photosynthetic rate of 18.8 and 21.3 μmol m^{-2}s^{-1} for small and large leaves respectively. This 15% higher net photosynthesis of the large leaves was accompanied by 42% higher stomatal conductance. Henso *et al.*, 1989 found the effects of a progressive increase in soil water deficit on the leaf conductance and gas exchange of lupin (*Lupinus cosentinii*) and wheat (*Triticum aestivum*). Chartzoulakis *et al.*, (1993) found water stress reduced the rate of photosynthesis by 53 to 64% in Kiwifruit seedlings (Kiwifruit cv Hayward), in relation to the control. This decline was attributed to stomatal closure. Weber and Gates (1990) found there was a linear relationship between gas exchange with leaf conductance. Eastman *et al.*, (1995) reported that both photosynthetic rate and stomatal conductance declined in response to water stress in an experiment on seedlings of spruce (*Picea glauca* (Moench)) Voss × *P. engelmanni* Parry hybrid complex). This may be because of the relationship between stomatal conductance and water potential. As drought develops the stomata close and consequently photosynthesis and transpiration decrease. However, at the whole plant level water deficit not only reduces photosynthesis by a. stomatal and non-stomatal effect but also by a reduction in leaf area (Chaves, 1991; Cornic *et al.*, 1992. Reduction in leaf area by water stress is an important cause of reduced crop yield because the reduced photosynthetic surface persists if the stress is relieved (Kramer, 1983). The seasonal pattern of gas exchange (Farquhar and Sharkey, 1982; Abrams and Kubiske, 1990; Owens *et al.*, 1992) is influenced by an array of morphological and physiological adaptations. A combination of specific morphological and physiological adaptations allows xerophytic trees to be particularly well-adapted to regions with an unpredictable summer drought pattern (Tenhunen *et al.*, 1990).

Seiler and Cazell (1990) reported that red spruce (*Picea rubens* Sarg) seedlings maintained photosynthesis at water potentials as low -3 MPa. Within twenty four hours after rehydration, the water stressed seedlings had photosynthetic rates as high as the control seedlings. Stoneman *et al.* (1994) found plants of *Eucalyptus marginata* Donn ex Sm. were very sensitive to water deficit, although this species naturally grows in a drought-prone environment. However they were fully recovered by the second day after rewatering. It is postulated that the restriction of CO_2 due to stomatal closure was a major constraint to photosynthesis (Chaves, 1991).

1.2.9 Effects of water stress on root growth and dry matter /production

Water stress treatments cause large differences in growth rate, leading to substantial differences in dry matter produced. Often, shifts in the allocation of assimilate have been observed (Khalil and Grace, 1992). Bradbury (1990) found two species, *Sesbania sesban* and *Acacia nilotica* increased the distribution of dry matter to the stem at the expense of root and leaf biomass under water stress. Becker *et al.*, 1987 found water stress reduced red pine (*Pinus resinosa*) seedling survival and growth. Also Hallgren and Helms (1992) found drought reduced internode elongation in red fir and white fir. Many workers have reported a decreased stem dry weight of tree species as a consequence of water stress, for example Khalil and Grace, (1992) in sycamore. Water stress reduces leaf area per plant through inhibiting or reducing leaf initiation, restricting final leaf size and accelerating leaf senescence and shedding, all result in reducing (Kramer, 1983). Many workers report a decreased leaf dry weight under water stress, for example Khalil and Grace, (1992) in sycamore. Leaf shedding during water deficit is another adaptation by which certain plants avoid injurious or lethal desiccation (Pallardly and Rhoads, 1993). Leafless plants drop some of their branches thus reducing the total transpiring surface. Herbaceous perennials, on the other hand, lose almost all of their green leaves and cease photosynthetic activity, which is then resumed with the onset of the rainy season when new green branches develop from latent buds (Fisher and Turner, 1978).

It has been stated that water deficits reduce the rate of root growth, root branching and cambial growth (Kramer 1969) but more normally we see that root growth is reduced less than shoot growth.. Root elongation and radial expansion must be restricted through restricted cell division, cell enlargement, and tissue differentiation just as are shoot extension and cambial activity in the stem and branches. Asakawa and Makino (1989) reported that *Acacia albida* seedlings always had a high dry matter weight of root compared to shoot regardless soil moisture condition. Newman (1965) who found reduction in root growth at -0.7 MPa bars total water potential in *Linum usitatatissimum*. At -1.5 MPa, root growth was 20% or less of the rate before drying, but some root growth occurred in soil drier than -2.0 MPa. This result means that the root growth was not influenced by water potential. The failure of roots to grow into dry soil is probably more the result of physical impedance than soil water stress (Passioura, 1988) because soil strength increases sharply as soil dries resulting in physical resistance to penetration by a root tip. Wright *et al.*, (1992) found that Jack pine (*Pinus banksiana* Lamb) under water stress inhibited secondary and tertiary but not primary root growth. This suggests evasion of surface drought through primary root exploration of deeper soil. Similarly Phillips and Riha (1994) reported that the shift in partitioning of biomass to roots in a dry treatment resulted in root growth rates above those for the wet treatment for *Eucalyptus viminalis.*

Growth of the root is decreased or stopped by severe soil water stress and roots tend to become suberized to their tips, reducing their capacity to absorb water (Kramer, 1983). The root systems in some species show a high degree of morphological plasticity that enables them to cope with varying soil moisture content (Reader *et al.*, 1992; Belsky 1994). However, because of the time lag in transmission of water stress from leaves to roots, the roots are the last tissues to be stressed (Kozlowski *et al.*, 1991). Although most findings showed decreased root growth as a result of water stress, Khalil and Grace (1992) in their study with *Acer pseudoplatanus* seedlings found soil drying altered the root distribution profile and increased root growth in water stress treatments relative to well-watered plants. Similarly Sharp and Davies (1985) showed that increases in density and depth of rooting can result in maintenance of a high rate of water extraction in dry soil with a beneficial effect on shoot water status.

1.3 Description of *Acacia* Mill.

The name *Acacia* is derived from the Greek for 'thorn' (El Amin, 1990). The genus of *Acacia* Miller is estimated to comprise 1100-1200 tree and shrub species in the world (El Amin, 1990; Kennenni, 1991). Most *Acacia* species grow in arid and semiarid regions, where the temperature is 40 to 45 °C in the summer and less than 5 °C in the winter (Al Zaghath, 1989).

Acacia is represented in Saudi Arabia by trees and scrambling shrubs, mostly heavily armed with spines or thorns. The leaflets are mostly very small, under 3mm long in many cases, numerous and densely crowded. The flowers are borne in small globose heads at the ends of shoots or occasionally in terminal much branched panicles or they may be crowded in spikes (Chaudhary, 1983). *Acacia* species in Saudi Arabia carry different names, sometimes specifically for individual species, sometimes as regional names and often as a broadly used name for all of a group of species. Commonly used names are Salam, Talh, Samer, Sant, Kidaad, Kittad, Dhahi, Satteha, Wawaat, and Orfot or Aarfot (Chaudhary, 1983). Five species from different elevation, *Acacia negrii* (2200 m), *Acacia asak* and *seyal* (500 m), *Acacia ehrnbergiana* and *Acacia tortilis* (Sea level) have been used in the glasshouse experiments which are reported here: Notes on these species follow.

Acacia negrii Pichi-Sermoli

A widespread species in the high mountain in Saudi Arabia and also distributed throughout much of Africa such as Ethiopia, Somalia and Nigeria (El Amin, 1976;Chaudhary, 1983; El Amin, 1990 and Al Zaghath, 1989). It may be recognized by its flat-topped crown, white flowers and grey bark (Chaudhary, 1983). The substrate is often sand-loam where the roots are effective in binding the soil. It forms a tree to 5-7 m; the leaflets are mostly very large with from 14-34 pairs (ZAl Zaghath, 1989).

Acacia asak (Forssk.) Wild.

A widespread species in Sudan (El Amin, 1976) and south west Saudia Arabia (Al Zaghath, 1989). It may be recognized by its flat-topped crown, bright yellow flowers and brown bark (March-April). It forms a tree to 4-6 m high, the leaf is mostly 3-6 leaflet pairs, leaflets from 6-12 pairs to reach 20 pairs. Substrate, sand to sand-loam (Chaudhary, 1983).

Acacia seyal Del.

A widespread species in Africa south and north of the Sahara (El Amin, 1976; Maydell, 1990) and in north and south west Saudi Arabia (Al Zaghath, 1989). It may be recognized by its flat-topped crown, bright yellow flowers and powdery bark. Tree to 12 m high and 60 cm in girth, usually with spreading branches and a flat-topped crown. Bark varying from pale yellow to reddish, conspicuously powdery, the bark of branchlets reddish-brown (Al Zaghath, 1989). Flowering December-April, flowers appearing shortly before the new leaves and very conspicuous, the yellow heads about

12 mm across on stout stalks up to 3.5 cm long with a whorl of bracts towards the base (Chaudhary, 1983).

Acacia tortilis (Forsk) Hayne.

A widespread species in Australia, Africa south and north of Sahara (El Amin, 1976 and 1990; Maydell, 1990) and in Saudi Arabia (Al Zaghath, 1989). Habitat, in sandy areas where the roots are effective in binding the soil. Tree to 5-10 m, often irregular and stunted as a result of cropping by livestock (Maydell, 1990). Bark reddish brown, slightly fissured (Chaudhary, 1983). Branchlets glabrous or very finely hair. Spines up to 5 cm long sometimes shortly hairy, with a slender stalk 2.5-3.5 cm long; 2-5 pairs of pinnae about 12 mm long with 6-15 pairs of narrow leaflets rounded at apex. Flowers appear from May to June (Al Zaghath, 1989).

Acacia ehrnbergiana Hayne

A widespread species in Africa south and north of Sahara (El Amin, 1976 and1990; Maydell, 1990) and in Saudi Arabia (Al Zaghath, 1989). The species may be recognized by its bark peeling into yellow flakes exposing pinkish new bark; older stems grey, rough. Leaflets 10-12 pairs. Flower (December-May), Fruits (Feb-May), (El Amin, 1990). Habitat, dry sand plain with a rainfall less than 100 mm in low land (Maydell, 1990 and Al Zaghath, 1989).

1.4 The Aim of the study

The vegetation cover in Saudi Arabia has been affected by severe drought periods during the last two decades, Moreover, the rapid population growth in the area of study and the resultant activities have led to depletion of the vegetation cover to the point of diminishing its ability to regenerate. Consequently, many valuable plant species are endangered, with some already extinct. The general objective of this study is to examine the environmental factors controlling the distribution of the natural communities in south western Saudi Arabia. The outcome of the research should provide important ecological and ecophysiological foundations for forest management and silviculture in Saudi Arabia. The specific questions and objectives to be addressed are:

Question A: Does tree species richness increase with increased elevation in South-western in Saudi Arabia?

Question B: What are the major factors affecting the distribution of the dominant tree species and germination and early establishment of the dominant *Acacia* species?

The specific objectives are:

1. To describe species distributions on an altitudinal transect in the south western part of Saudi Arabia

2. To investgate seed germination of *Acacia negrii*, *A. hernbergiana*, *A.asak*, *A. seyal* and *A. tortilis.*

3. To assess the effect of water stress on seedlings of *Acacia negrii*, *A. asak* and *A. ehrnbergiana*.

4. To assess the effect of water regimes on the root development for *Acacia negrii*, *A. asak* and *A. ehrnbergiana*.

5. To make a comparative study of the impact of soil drying on the gas exchange of *Acacia negrii and A. ehrnbergiana*

CHAPTER TWO

Species Distribution along an Altitudinal Gradient in South Western Saudi Arabia

2.1 Introduction

The Kingdom of Saudi Arabia is host to some 16,000 species of plant (Migahid, 1978), distributed primarily within two phytogeographic regions. By phytogeographic region is meant an area distinguished from the neighbouring regions by its characteristic flora, its plant cover and climate (Brown, 1970; El-khatib, 1974; Al-Jerash, 1985). The Kingdom of Saudi Arabia falls within two distinct regions, these being: (1) the Sahara-Arabian region, and (2) the Sudanian region (see Zohary, 1973). The vegetation of Saudi Arabia has been affected by severe drought during the last two decades. The rapid increase in population and consequent human activities (grazing, firewood, and charcoal production) has led to poor natural regeneration of many important trees. It is probable that many plant species are endangered and some have become extinct over the last few decades.

The first serious study of the plant ecology of Saudi Arabia was carried out by Vesey-Fitzgerald (1955, 1957 a, b) who worked on the Red Sea coast, North and South of Jeddha. He argued that plant distribution was largely determined by rainfall, topography and by drainage. He divided the vegetation into eight main association, namely: (a) the *Olea-Tarchononthus* association (b) the *Acacia mellifera* associations (c) the *Acacia asak* associations (d) the *Acacia tortilis* associations (e) the *Reama* raetam association (f) the associations of the coastal plain (g) the association of the beach (h) the association of halophytes. He also described the vegetation in central and Eastern Arabia and there categorized the types into six associations namely: (a) the vegetation of the central sands, characterised by a few species of perennials and of annuals (b) the *Rhanterium* steppe (c) the *Stipa* steppe (d) dwarf shrubs and salt bushes in the drainage lines (e) coastal white-sand associations (f) coastal salt bush associations.

Vegetation of a certain physiognomy usually occurs over a certain range of environmental condition to which the dominant growth forms are adapted (Whittaker, 1975, 1978; Allen and Peet, 1990). Physiogonomically similar communities occur in different situations where similar environmental conditions exist (Allen and Peet, 1990; Willams-Linera, 1990). This physiognomic convergence of vegetation in widely separated regions is one the major phenomena of plant geography and a major justification of the physiognomic approach to vegetation classification (Whittaker, 1975; Fatchen and Barker, 1979; Willams-Linera, 1990).

Many of the essential factors which affect plant growth and reproduction may be thought of as existing in the form of continuous gradients for example, temperature, water availability or the concentration of particular nutrients in the soil (Whittaker, 1978; Kramer, 1983; Gaston, 1990; Allen and Barker, 1991). Each plant species is expected to have a distinct optimum and range of tolerance for each factor manifested in its productivity or some other growth attribute (Whittaker, 1978). The relationship a particular species has to a particular gradient may be expressed in terms of relative favourability by means of a distribution curve (Austin and Smith, 1989).

The distribution of plants along gradients has been extensively studied (Curtis, 1955; Whittaker, 1965). Variation in species composition and structure of the vegetation is often interpreted in the context of complex gradients of elevation and topographic position (Whittaker, 1965; Peet, 1981). Increase in elevation is generally associated with decrease in temperature and evapotranspiration, and increase in precipitation. The modern argument for the existence of the continuum is presented graphically for a single environmental gradient (Whittaker, 1978). However, the originator of the idea, Gleason (1920) made almost no mention of competition as a determinant of species distribution. Whittaker, (1978) suggested that where species are dominant, few in number, and the close ecological equivalent to each other, they may be regularly distributed along an environmental gradient. He quoted an example of a replacement series for coniferous tree species in relation to elevation on north-facing slopes in the Santa Catalina and Pinaleno Mountains, Arizona. Another example is described by Margules *et al.* (1987) who studied changes in species diversity (*Eucalyptus* sp.) in south eastern Australia. They found three environmental variables, mean annual rainfall, mean annual temperature and solar radiation, to be the important factors in controlling distribution of the vegetation. The effects of rainfall and temperature were highly significant and solar radiation was less significant. Austin and Smith, (1989) recognised three types of environmental gradient: (1) indirect environmental gradients which are composed of a complex combination of factors, such as latitude which may be correlated with such factors as temperature or rainfall which do have a direct effect on plant growth (Peet, 1981); (2) a gradient of essential resources such as mineral, water, and oxygen; (3) direct environmental gradients of factors such as soil pH which is directly related to nutrient availability and hence plant growth. Allen and Barker, (1991) describe an example from the Southern Rocky mountains - a mountainous region with low rainfall, where vegetation distribution can be attributed to differences in site moisture status and evapotranspiration. On the other hand, vegetation in high rainfall regions often varies with topographic position because geomorphic features are correlated with soil chemical and physical properties (Reif and Allen, 1988). Hughes, (1949) has classified soils within elevation zones into suites, each related to a specific parent rock. Each soil suite has a specific and characteristic set of plant communities and the whole can be looked upon as a soil suit-plant community complex.

The vegetation in the arid environment is controlled by abiotic factors mainly through the variability of rainfall. During drought periods the primary production decreases (Ellis and Swift, 1988; LeHouerou, *et al.*, 1988) and the number of animals supported by the system may decrease by 50 % or more (Ellis and Swift, 1988). To counteract the effect of drought, nomads, the main utilizers of the system, increased the spatial scale of their exploitation of the system. This was achieved by dividing herds into smaller more mobile units and spreading the grazing pressure over a larger area thus reducing the possibilities of the degradation (Ellis and Swift, 1988). Another benefit of frequent movement during drought periods is that it ensures the spread of seeds over a much larger area (Amed, 1986). In disturbed sites, only the species adapted to the amount of water received at any particular site will be able to regenerate and establish themselves (Kassas, 1957; Mohmoud, 1977). Therefore, if drought continues for two or three years, only species whose zone of abundance is on xeric sites relative to the disturbed sites will be able to establish themselves (Ellis and Swift, 1988). Similarly after drought periods, with average and above average rainfall, the disturbed sites will be occupied by abundant species in the area or by species adapted to mesic sites relative to disturbed sites (Mohmoud, 1977). Olson (1985) reported increase in biomass and improvements in the vegetation composition after drought in the semiarid region in the Sudan.

Saudi Arabia has a unique flora with many eco-physiological adaptations to the arid environment. It is only recently that an understanding of its taxonomic diversity has begun to emerge and already many species and whole communities are threatened by unacceptable pressures of use.

My objective in this chapter is to characterize the forest types over an altitudinal range within a limited area of Saudi Arabia. This requires the observation and description of the patterns within tree communities, including both an assessment of the species present and the ecological factors which may be important in determining distribution of the species.

2.2 Material and Methods

2.2.2 Study Area Description

The South western region of Saudi Arabia extends from the Jazain in the west to Najed in the east, and from Abha in the north to Najrin in the south (Fig 2 .1). Over 300 km in length and 90 km wide, it contains mountain, escarpments, deep valleys, rolling land, rocky hills, wadis, waterfalls and pools. Such topography along with a relatively mild climate and high relatively rainfall create a diversity of habitats for plants such as *Acacia*, *Juniperus* and *Hyphaene thebiaca*. (Al -Arifi, 1992).

2.2.3 Climate

The climate of South western Saudi Arabia is arid and semi-arid. The arid portion is the plain (Tama sea level) and the semi-arid is a higher elevation region (Al Sudah 2600 m). An important feature of the climate is that it is essentially elevation-dependent. Representative data on temperature, humidity, precipitation and vapour pressure deficit are shown Fig 2.3, 2.4, 2.5 and 2.6. Table 2.1. a generalised summary of the precipitation pattern in the mountains would suggest a maximum precipitation at the highest elevation (2600 m, a.s.l) of perhaps 350 mm a year. Moving down the west slopes to the mountain valleys and plains, at nearly sea level elevations, rainfall decreases rapidly to an average of only about 55 mm a year. The rainfall occurs only in spring and summer in the mountains and in the winter and spring on the plain. The average annual temperatures vary also with elevation. At around sea level, the temperature is 35 °C in the summer, and 15 °C in the winter. The rate of decline with elevation is about 6 °C km^{-1}. In contrast, at high elevation the annual temperature is 25 °C in the summer, and 0 °C in the winter. The average relative humidity does not show much dependence on elevation. Variation in relative humidity are inconsistent with elevation and with a certain direction. The relative humidity is generally high (60%) (Abdel Rahman and Balegh, 1974; Ministry of Agriculture and Water, 1984). The vapour pressure deficit (δe) was calculated from temperature and relative humidity as:

$$\delta e = e_s\ (T_a)\text{-}e$$

where $e_s\ (T_a)$ = saturation vapour pressure (kPa) at T_a, and e = the vapour pressure (kPa) at T_d air temperature. The values for $e_s\ (T_a)$ was obtained from the Table in Pearcy *et al.* (1989). (see Fig 2.6).

Figure 2.1: Map showing the south western region of Saudi Arabia.

Table: 2.1 Climatological data of a representative stations in South Western of Saudi Arabia.

	Station Abha	Station Al Sudah	Station Al shugayg
Latitude	18° 12′	18° 14′	18° 9′
Longitude	40° 39′	42° 29′	42° 6′
Elevation (m)	2200	2600	8
Temperature ° C	0-25	0-20	15-35
Relative humidity (%)	50	55	66
Rainfall (mm)	290	350	55

Maximal wind velocities of 60 and 50 km/hr were recorded in Al shugayg and Abha respectively. There are three dominant weather regimes: (1) summer weather beginning each day at noon, becoming cool and wet from the west then becoming dry and hot when reaching the desert; (2) winter weather, with storms coming from west and south west winds as cold wet air masses coming from India through the Arabian Sea; (3) weather associated with east winds, which are hot in spring and autumn and cold in winter (Abdel Rahman and Balegh, 1974; Ministry of Agriculture and Water, 1984).

2.2.4 Geology

The Arabian Peninsula is an ancient massif composed of stable rock whose present geological structure was developed at the same time as the formation of the Alps (Chapman, 1978; Bayer, 1984). Geological movements caused the mass to tilt eastward and the western and southern edges to tilt upward. In the valley formed by the fault, called the Great Rift, the Red Sea was formed. A second but lower escarpment, the Jabal Tuwaig, runs approximately North and South through the area of Najid (Power *et al.*, 1966). The Arabian shield, a large area of igneous and metamorphic rock in Saudi Arabia is the most promising for mineral resources. Copper, zinc and gold have been found (Bayer, 1984).The northern part of the Red Sea escarpment is called the Hejaze and the Southern half is known as the Asir. The Tihama, or coastal lowland, rises gradually from the Red Sea to the mountains. Here intermittent rivers from the mountains disappear in the sand before reaching the Sea (Bayer, 1984). The Asir region extends south to the borders of Yemen. The central plateau, the Najid, extends eastward to Tuwaig and beyond. North of Najid a large sand desert, the Nafud, separates the rest of the peninsula from the steppes of Northern Arabia. South of the Najid is the greatest sand desert in the word, the Rub al khai (Alsayari *et al.*, 1987). The sedimentary rocks consist mainly of limestone, sandstone, and shale, having an aggregate thickness as great as 5,500 metres, thinning toward the west as the basement rocks become shallower Power *et al.,* 1966 (Fig 2.2).

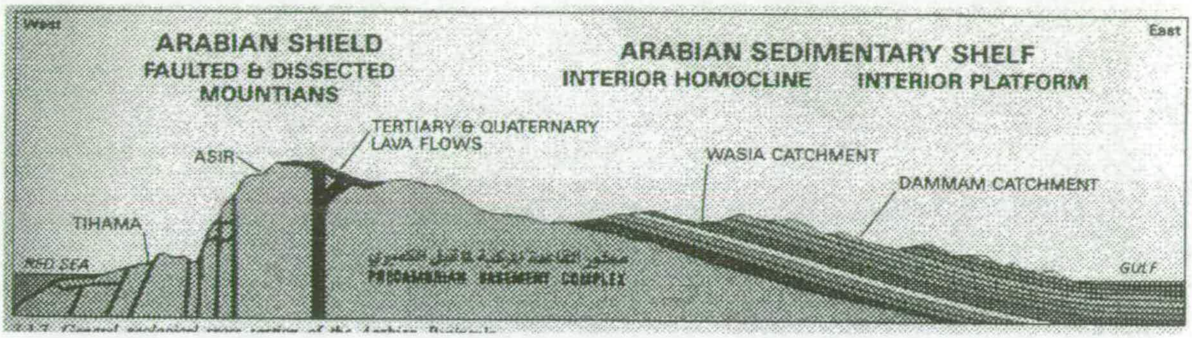

Fig 2.2: General geological cross section of the Arabian Peninsula (Ministry of Agriculture and Water, 1984).

2.2.5 Soil

Alkaline formation (pH 7.0 to 8.2) allows some agricultural production in certain portions of the country (Aba-husayn and Sayegh, 1977; Aba-husayn *et al.*, 1980). Sand-covered areas are suitable for agriculture if there is sufficient irrigation and drainage. This is the case in some places in the eastern province, and generally in the highlands of the Najed (El-Katib, 1974). Wadis and wadi banks contain the richest soils and are cultivated for cereals and tree plantations (Ministry Agriculture and Water, 1984).

Studies concerned with soils of the south western region are recent and very few. They are for the most part, very specific and of local nature (Aba-husayn *et al.*, 1980). Some of these studies, however, give general information about the characteristics of soil in parts of the region in relation to elevation, topography and rainfall (El-khatib, 1974; Al-Souli *et al*, 1980).

Studies for parts of the region, reveal that soil on the steep slopes of the mountains and hills are shallow, rocky, and greyish brown to yellowish red in colour. Deeper soils occurring at the foot of slopes, and other soils with the same medium texture, are fertile and suitable for cultivation (Al-Souli *et al.*, 1980). Differences in soil characteristics with elevation were also noticed by other workers (Aba Husayn *et al.*, 1980). Soil developed on stable landscapes at elevation higher than 2000 meters were found to have well-developed profiles and near neutral pH values (El-khatib, 1974). Alluvial terraces near wadi banks at lower elevations (1000 to 1500 m), are characterised by deep soils with low developed profiles, and pH slightly exceeds neutral, with noticeable amounts of carbonates (Al-Arifi, 1992).

Soils developed on basaltic volcanic rocks at Al-Bassam, approximately 2000 metres elevation near Khamis Mushayt were characterized by Dixon and Viani (1980). The area receives a relatively high rainfall (300-400 mm a year as reported by Schyfsma, 1978). The soils have a well-developed solum and a calcium carbonate enriched B horizon of reddish colour and fine texture. Mineralogical analysis of the <0.002 mm fraction reveals smectite dominance with lesser amounts of chlorite and kaolinite. Traces of goethite, mica and quartz are also present (Al-Arifi, 1992).

2.2.1 Data collection

Vegetation at ten elevations (six sites per elevation) was sampled during the summer of 1991 (May to August). Forest stands are represented at a range of physiographic positions typical of the Asir mountain in South western Saudi Arabia, on valley ravines, valley floor sites, mountain slopes and ridge tops. Mountain slopes were predominantly west and east facing, reflecting the general topography of the region. In order to delineate an area for measurement, a random spot in the site was first selected. From there a distance of twenty metres was measured and then a distance of twenty five metres at right angles to the original line. The start and end point were connected by coloured rope. Then a mirror image was made to form a rectangle (20 m×25 m). Tree stands were selected based on the following criteria : (i) representative of the physiographic position, (ii) free from any recent disturbance and (iii) homogeneous units of vegetation. The number of individuals of each species, their crown cover, number of species and the stem diameter at ground level were measured. The percentage cover of the shrubs and herbs were measured in 5 m × 5 m, quadrats on along line transects. Field procedures followed methods of Whittaker, (1965); Beatley, (1975); Woodward, (1975); Peet, (1980) and Burke *et al.*, (1989), and equipment used include a cloth metre tape, clippers, altimeter, callipers and plastic bags.

The soils were sampled in each plot. Six samples were taken from each plot at 0-15 cm depths then mixed, and from this mixture one sample was taken. Assuming it to be representative of the plot. The soil samples were analysed for pH, organic matter and texture, by the soil department at King Saud University as explained in Table 2.2 .

The rainfall, temperature and humidity were obtained from the nearest meteorological stations (Fig 2.3, 4 and 5). One of these stations is located in Abha, 2200 m a.s.l.. The second is located in Al Sudah, 2600 m a.s.l., about 30 km from Abha. The third is located in Al Shugayg, sea level, about 90 km from Al sudah. The main rock type from geological maps (Ministry of Agriculture and Water, 1984) was also noted.

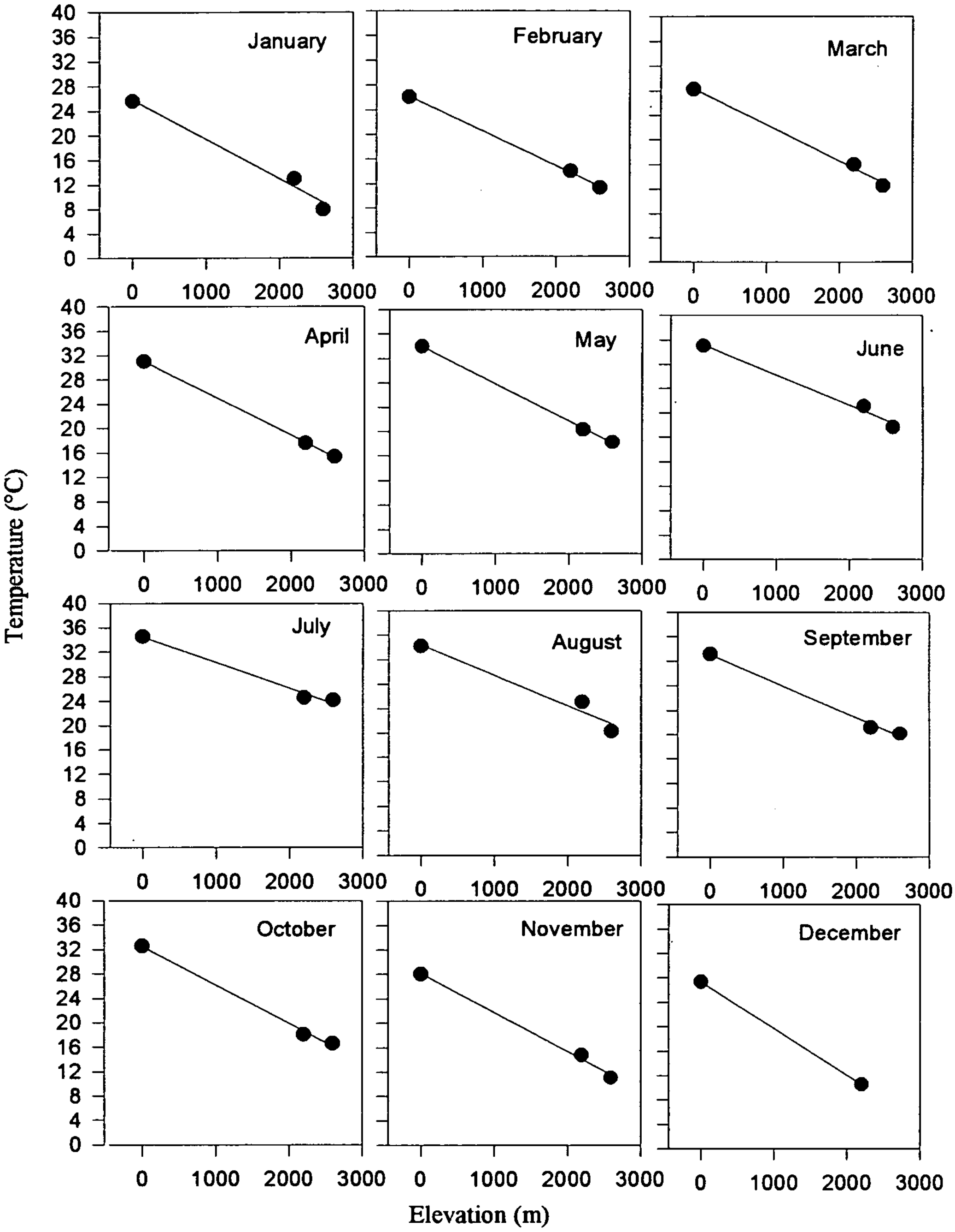

Figure 2.3: The plot of the mean temperature for three stations Alshugayg (sea level m a.s.l.), Abha (2200 m a.s.l) and Al soudah (2600 m a.s.l) versus the altitude in south western Saudi Arabia. Monthly means from 1974 to 1991. Means ± SE.

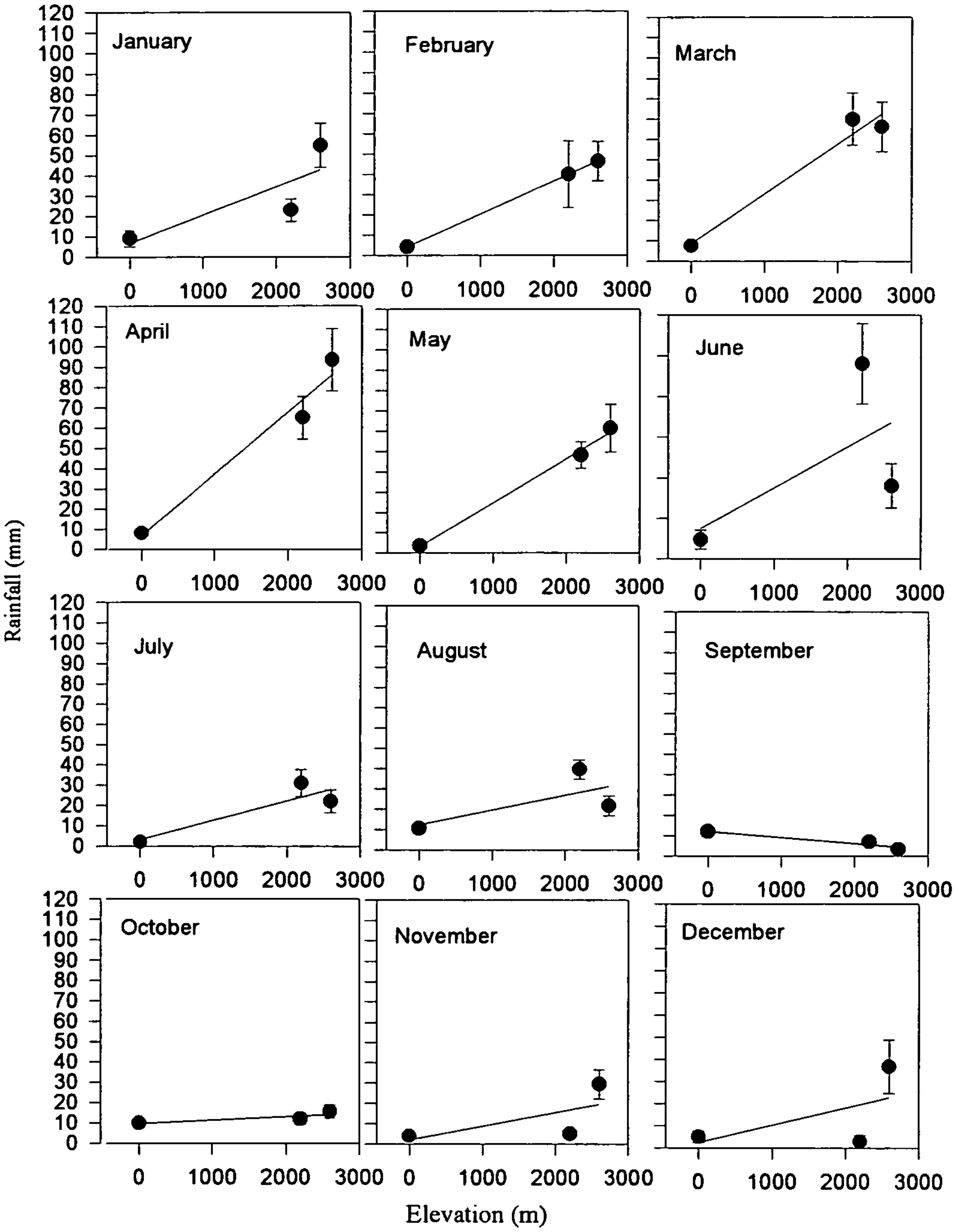

Figure 2.4: The plot of the mean rainfall for three stations Alshugayg (sea level m a.s.l), Abha (2200 ma.s.l) and Alsoudah (2600) versus the altitude in south western Saudi Arabia. Monthly means from 1974 to 1991. Means ± SE.

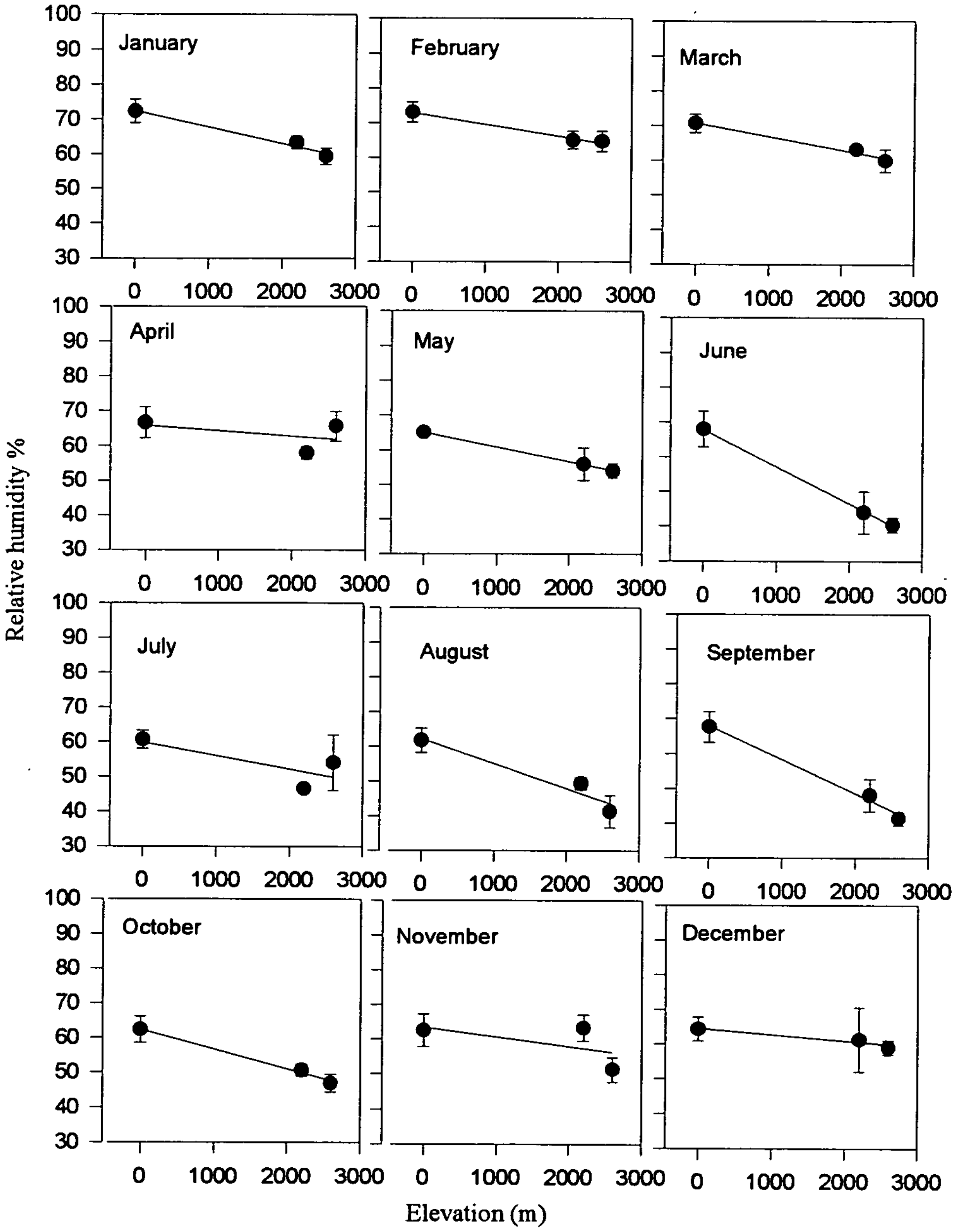

Figure 2.5: The plot of the mean relative humidity for three stations Alshugayg (sea level m a.s.l.), Abha (2200 m a.s.l) and Al soudah (2600 m a.s.l) versus the altitude in south western Saudi Arabia. Monthly means from 1974 to 1991. Means ± SE.

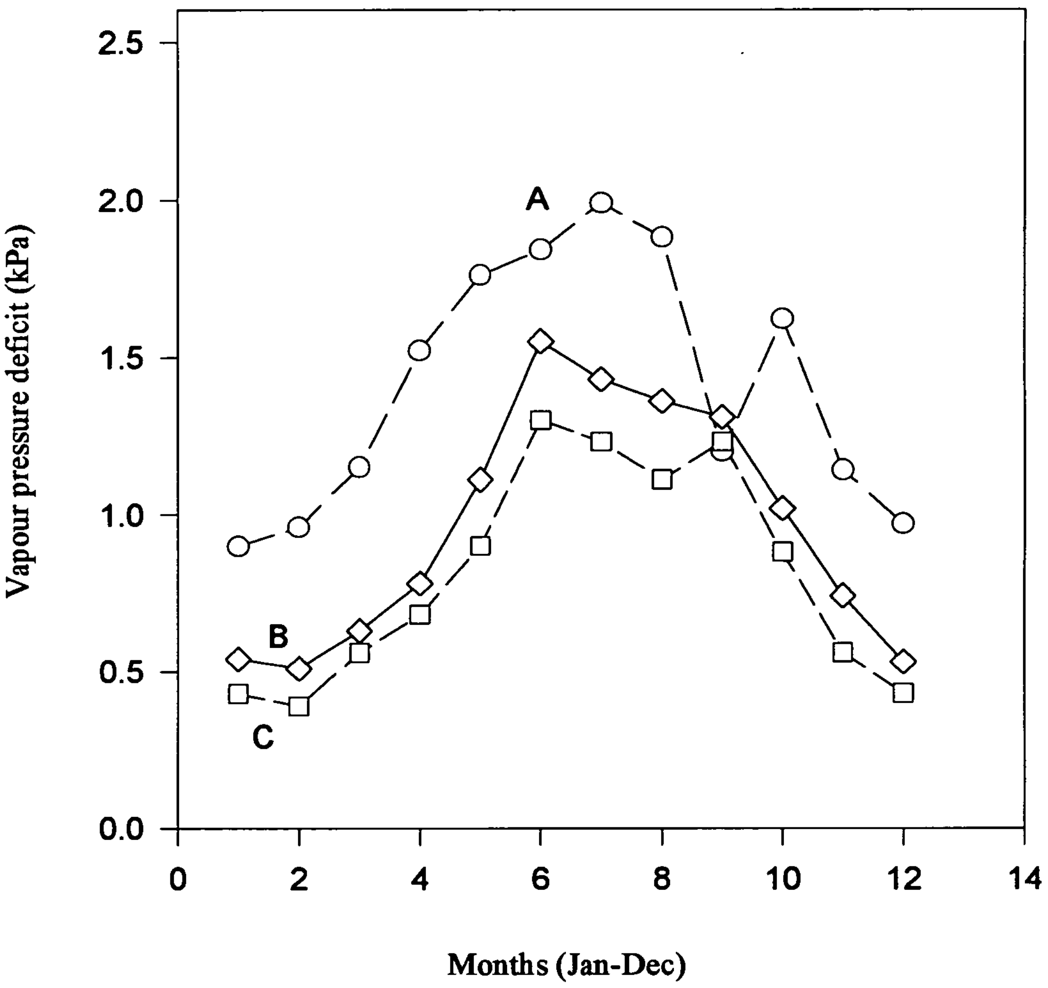

Figure 2.6: Vapour pressure deficit for Alshugayg (A; sea level m a.s.l.) Abha (B; 2200 m a.s.l.), Al soudah (C ; 2600 m a.s.l.) in the south west of Saudi Arabia. Monthly means from 1974 to 1991.

2.3 Results

2.3. 1 Soil

A general summary of the analysis of the soil in all sites would suggest maximum organic matter and minimum pH value at highest elevation. Soil degradation was very high and this was associated with very low organic matter and high pH in all sites. (Table 2.2 and Fig 2.7 and 2.8).

Table 2.2 : Summary of the physical and chemical properties of the soil

Site	Elevation (m)	Texture	pH*	OM %**
1	Sea level (0)	loam sand	7.4±0.20	0.85±0.1
2	500	sand	7.8±0.15	0.78±0.08
3	1000	sand loam	8.2±.0.19	0.23±0.02
4	1500	loam sand	8.1±0.18	0.45±0.05
5	2100	sand loam	7.9±0.16	0.54±0.04
6	2200	sand loam	8.6±0.06	0.78±0.08
6	2300	sand loam	7.6±0.2	0.78±0.04
8	2400	sand loam	7.4±0.11	0.16±0.02
9	2500	sand loam	7.3±0.12	0.65±0.1
10	2600	sand loam	7.2±0.19	3.15±0.2

* pH was determined in 1: 2.5 soil / water ratio.

* * Organic matter (OM) was determined by Walkey and Black methods using potassium dichromate (Richards, 1954).

2.3.2 Vegetation and habitat features

Fifteen communities were recognised in the area surveyed. The distribution of the main species of these communities indicated an interesting difference between the two slopes (Table 2.3). For instance, most of the tree species (12) were found on the western slope whilst only 3 species were found on the eastern slope. Those species found on the eastern slope were not found on the western slope (Table 2.4). For instance *Acacia gerradii* was found with an average 25% shrubs whilst *Acacia tortilis* and *A. ehrnbergiana* were found without any shrubs. *Olea europea* was found with 10 % herbs whilst *Zizphus spina-christi* was without any herbs. The cover of shrubs was between of 0% and 25% . The percentage herbs was between 1% and 18% (Fig 2.11). It is probable that some herbs were seasonally absent, because the study was in the summer. The number of the tree species in each site was between two and four (Fig 2.9). The total number of individual trees varied from site to site, the minimum number being 15 trees and the maximum number 130 (Fig 2.10).

Table 2.3: Characteristics of the species and their parameters at each elevation. (MT) mean trees per site (20m*25m), (MSH) mean stem height (m), (MSD) mean stem diameter (cm) and (MC) mean crown width(m^2). The number limits refer to standard deviations.

Species	Aspect	MT	MSH (m)	MSD (cm)	MC(m^2)
Hyphaene thebaica	West slope	34±14	4.8±0.21	7.54±2.6	7.3±1.08
Tamarix aphylla	West slope	6±3.5	5.43±0.37	7.89±1.34	7.18±0.7
Acacia tortilis	West slope	23±2.3	3.76±0.22	11.45±1.2	6.9±0.68
Acacia ehrnbergiana	West slope	41±0.95	4.2±0.14	7.9±0.50	5.1±0.50
Ziziphus spina-christi	West slope	14±1.8	6.1±0.76	13.5±0.32	9.9±0.70
Ficus salicifolia	West slope	13±4.09	3.8±0.13	13.0±1.09	5.4±1.05
Acacia seyal	West slope	14±2.75	3.0±0.21	8.0±0.90	6.34±1.30
Acacia asak	West slope	30±2.80	3.8±0.19	8.4±0.48	6.4±0.46
Acacia nubica	West slope	10±1.34	2.3±0.11	6.0±0.30	3.4±0.20
Acacia homulosa	West slope	13±0.50	2.6±0.09	6.0±1.05	4.1±1.03
Acacia laeta	West slope	13±1.50	3.3±1.61	5.9±5.51	9.1±4.50
Olea europea	West slope	15±2.64	2.8±0.22	8±1.09	3.2±.66
Acacia gerradii	East slope	10±1.50	2.8±0.11	5.1±.19	3.4±0.14
Acacia negrii	East slope	25±2.01	3.13±0.51	7.2±1.71	3.1±0.66
Juniperus procera	East slope	60±6.62	5.6±0.22	11±0.56	4.1±0.28

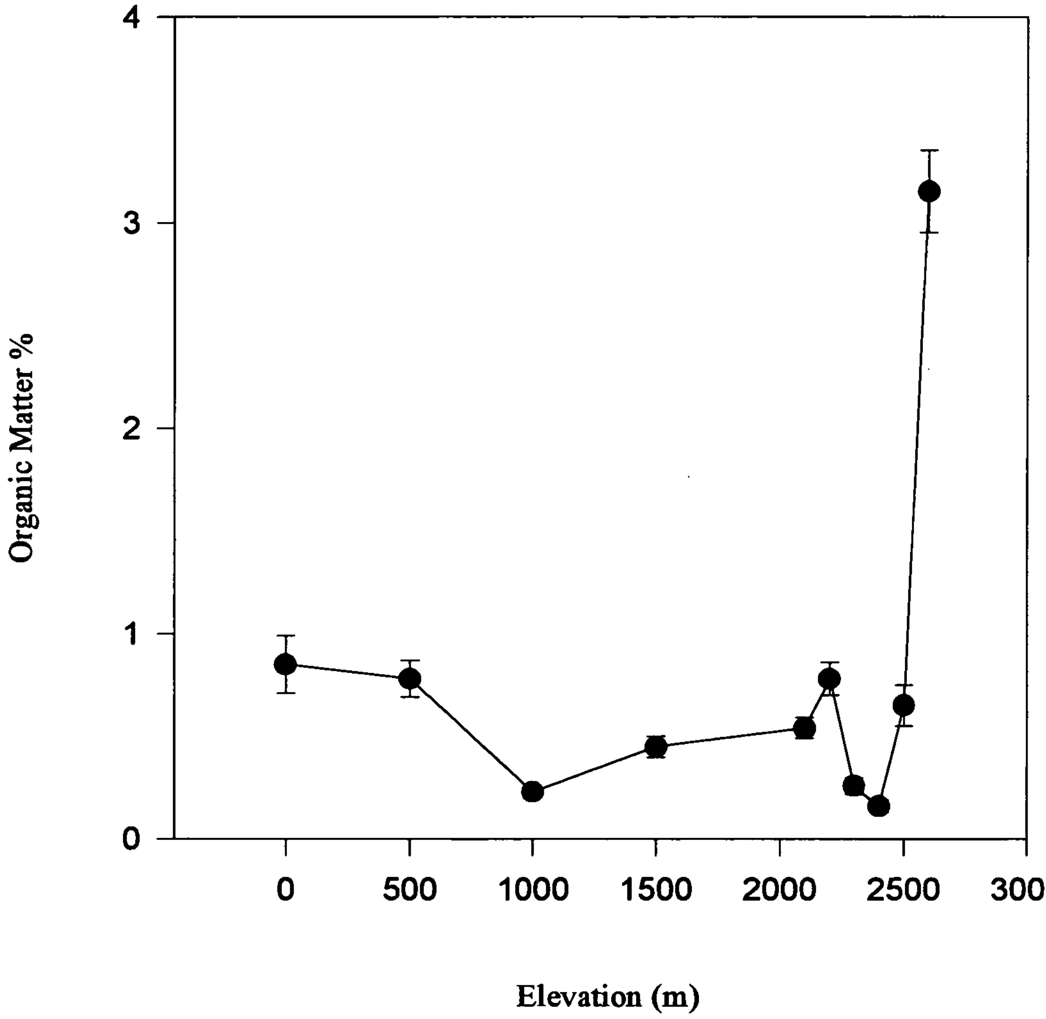

Figure 2.7: Change in organic matter % for each site along the Asir mountains from sea level to an elevation of 2600 m a.s.l. Points are means of six sites determination ± standard error.

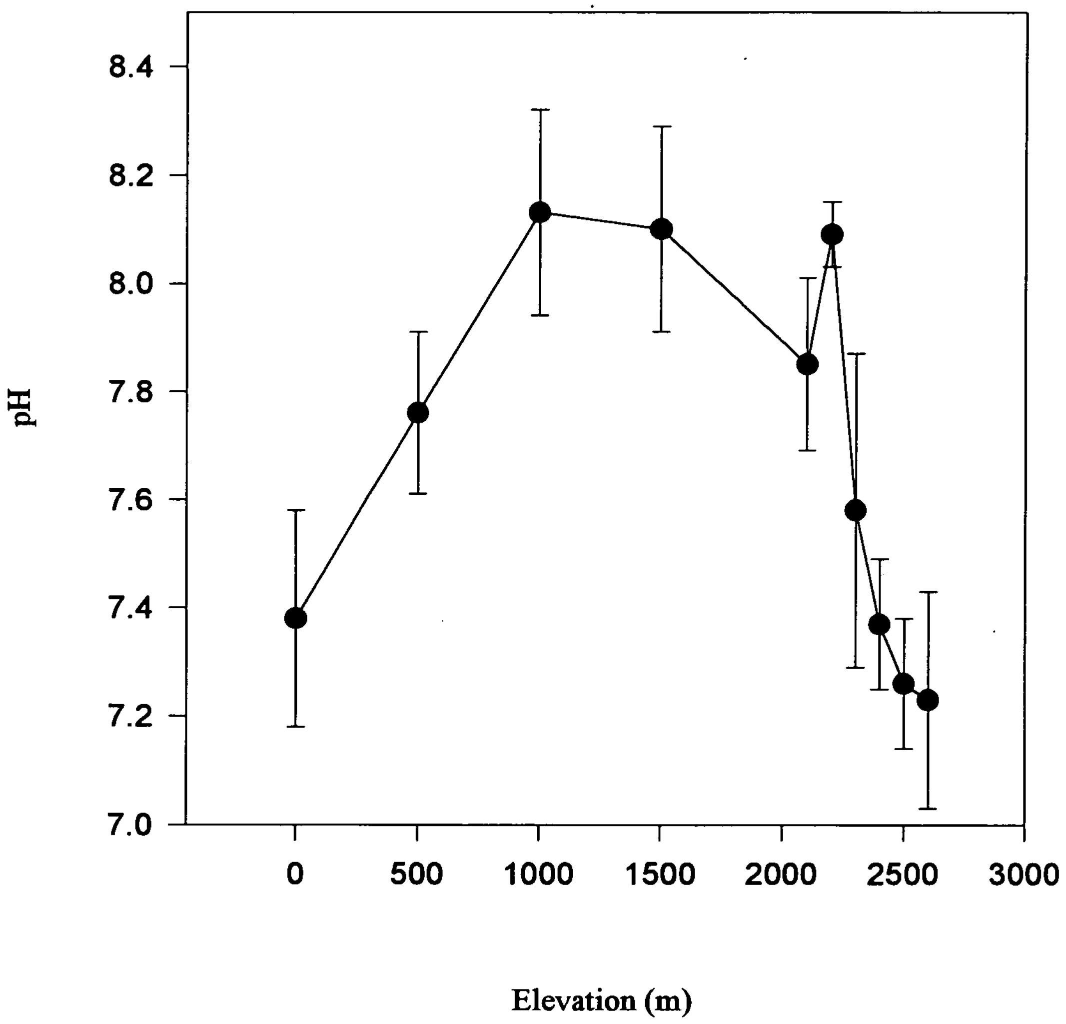

Figure 2.8: Change soil pH for each site along Asir mountains from sea level to an elevation of 2600 mm a.s.l. Points are the means of six sites determinations ± standard error.

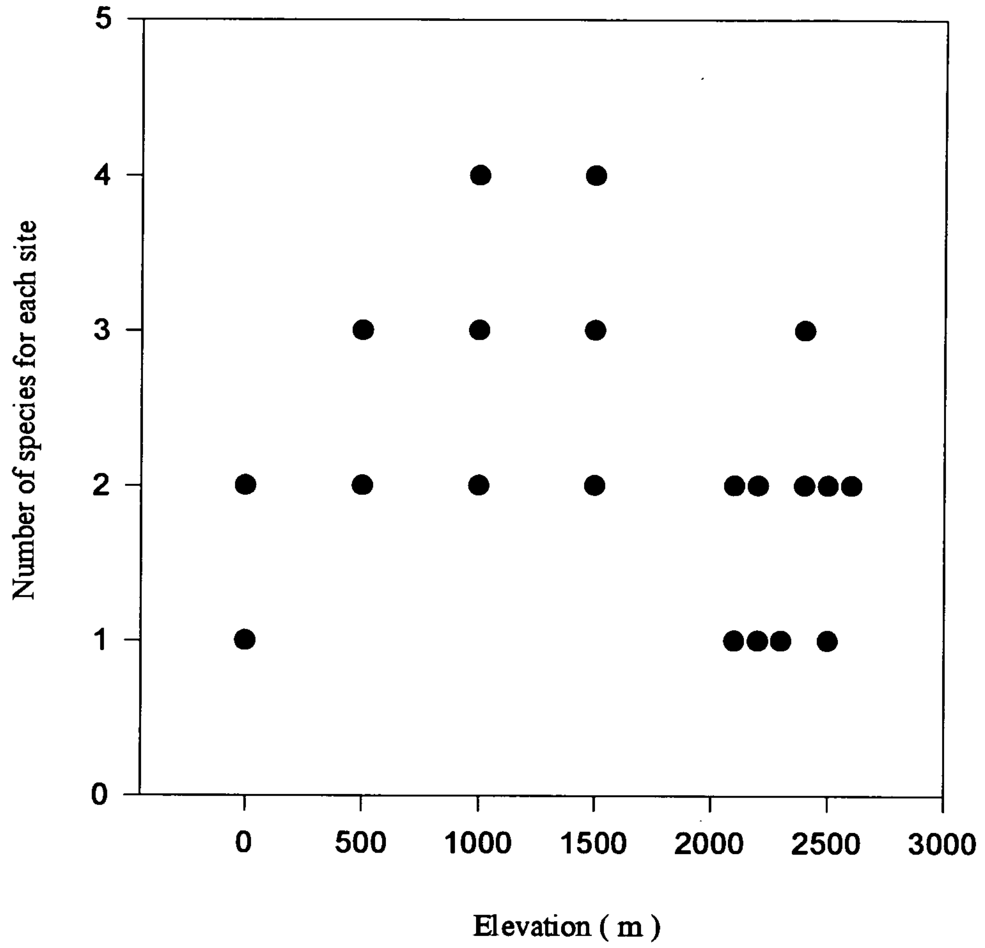

Figure 2.9: The number of tree species for each site along the Asir mountains from sea level to an elevation of 2600 m.

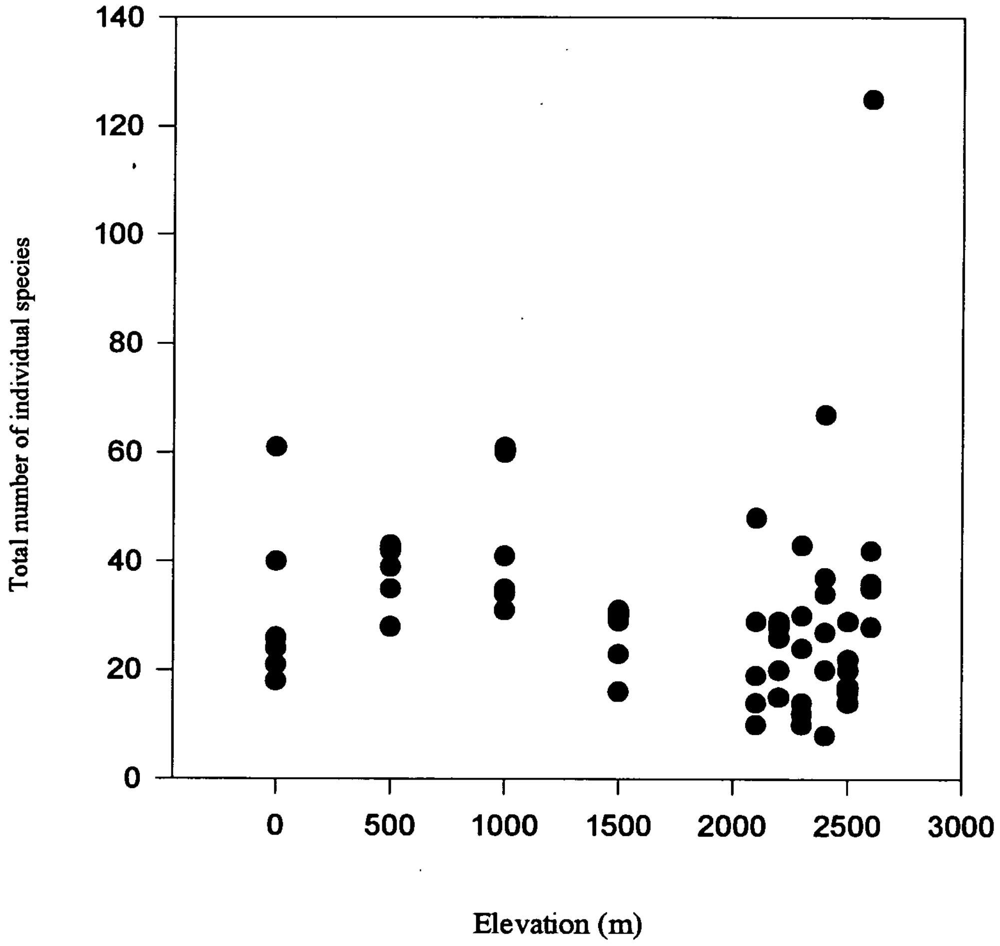

Figure 2.10: The total number individual trees for each site along the Asir mountains from sea level to an elevation of 2600 m.

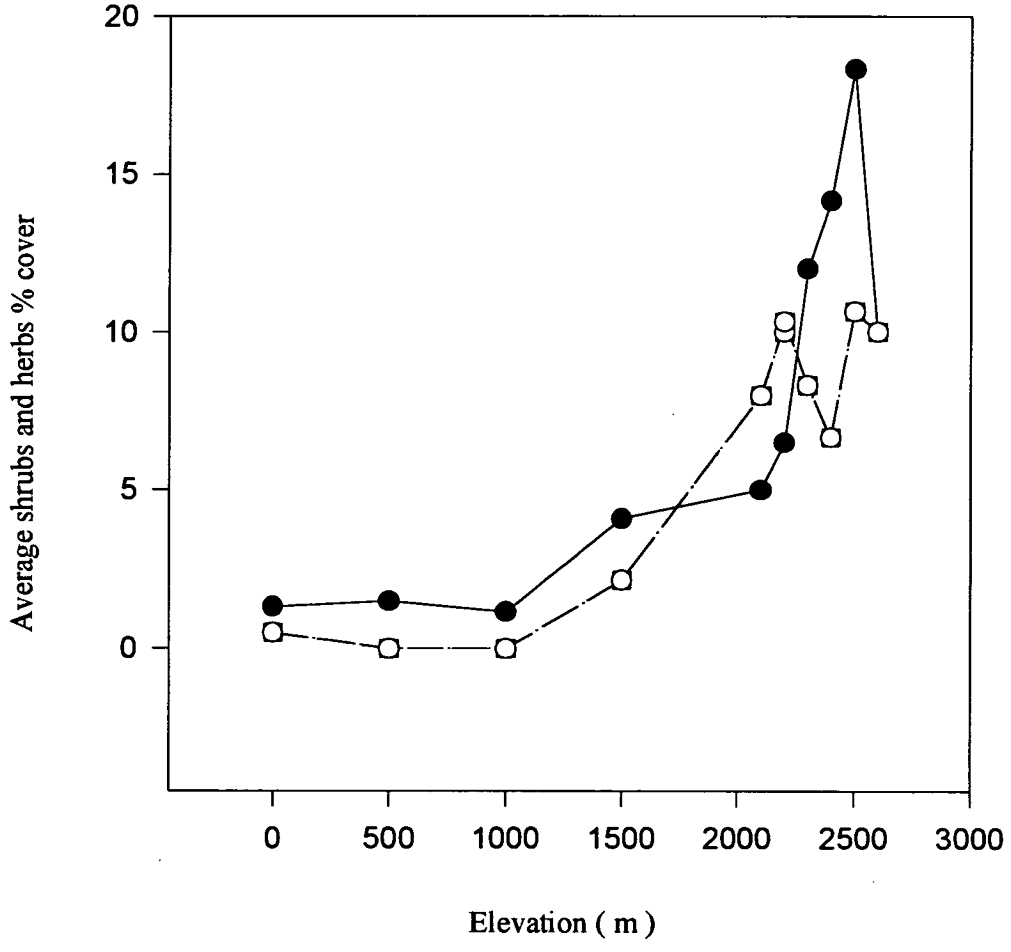

Figure 2.11: The percentage cover of shrubs (O) and herbs (●) for each site along Asir mountains from sea level of an elevation of 2600 m. Points are means of six sites.

The following section gives details about each species as observed from sea level to high elevation. Most of the information as recorded at the sites (see method), but supplementary information was obtained from the Department of Agriculture and local people.

1. Palmae *Hyphaene thebaica* (L.) Mart.

The coastal plain presents habitats favourable for vegetation dominated by *Hyphaene thebaica* (Fig 2.12). The site was from 10 to 15 km east of the Red Sea. This community was found on deep (15 to 20 cm) sandy soil, with a pH of 7.3 to 7.4. The height was 9-14 m. The bole of *Hyphane thebaica* was fairly smooth but showing the scars of the fallen leaves. The leaves are in tufts at the ends of the branches. The leaves are about 1.2 m long fan-shaped, with the blade divided into segments nearly to the markedly asymmetrical base; segments about 60 cm long armed with curved thorns. Stem diameters are (7.5 to 12.5 cm) and crown diameters are (7.3 to 10.5 m) Table 2.3. The trunk commonly branches dichotomously, and often each branch is itself divided dichotomously giving a very distinctive appearance. It flowers in March with males and females on separate trees. The inflorescence is similar in both sexes, up to 1.2 m long, with short branches at irregular intervals and 2-3 spikes arising from each branch; the male flowers are stalked (Migahid, 1978). In many instances, the dominant plant forms almost pure stands. Associated species are poorly represented (Fig 2.16), but include *Tamarix aphylla* and *Acacia tortilis.* It is neither grazed by animals nor cut for fuel.

2. Tamaricaceae *Tamarix aphylla* (L.) Karst.

According to Migahid (1978) there are five species of *Tamarix* in Saudi Arabia. At this site on the coastal plain *Tamarix aphylla* was recorded (Fig 2.12) . The plant cover ranges from 30 to 40 per cent. This community type occurs in deep sandy and often saline habitats (Fig 2.16). The height is 3-10 m, the pole green, leaves alternate, reduced to 1-2 mm scales, which are more or less triangular, acuminate and glandulous (Al-Mafirij, 1985). The diameter and crown are represented Stem diameters are (7.89 to 11.5 cm) and crown diameters are (7.18 to 13.5 m) Table 2.3. Associates include *Acacia tortilis* and *Hyphaene thebaica.* This community has been degraded by human activity

3. Leguminosae (Mimosaceae) *Acacia tortilis* (Forssk) Hayne.

This plant is widespread, but continuous destruction of the dominant species has restricted the area occupied by its growth. Associates include the *Acacia hernbergiana* community. The community of which this is a prominent member occurs on rocky and gravely slopes (Fig 2.17). The tree height is 3-6 m, often irregular and stunted as a result of cropping by livestock. The bark is reddish brown, slightly fissured. The branchlets are glabrous or very finely hairy. Spines are up to 5 cm long; there are 2-5 pairs of pinnae about 12 mm long with 6-15 pairs of narrow leaflets with a rounded at apex (Al-Zaghath, 1989; Chaudhary, 1983 and Migihid, 1978). Stem diameters are (11.5 to 15.6 cm) and crown diameters are (7.0 to 7.11 m) Table 2.3. The plant distribution ranges from sea level to 500 m a.s.l (Fig 2.12).

4. Leguminosae (Mimosaceae) *Acacia ehrnbergiana* Hayne.

This community has a wide ecological and sociological range. The distribution ranges from sea level to 1000 m (Fig 2.12). It is found mainly on the beds of watercourses (Fig 2.17). Associated species include *Acacia tortilis*, *Ficus salicifolia* and *Ziziphus spina-christi*. The plant is browsed by camels and cut for fuel. The height is 3-9 m, it has bark peeling into yellow flakes exposing pinkish new bark, older stems are grey rough. Leaflets are 10-12 pairs. Stem diameters are (7.5 to 11.5 cm) and crown diameters are (7.7 to 8.5 m) Table 2.3. Habitat, dry sand plain with a rainfall less than 100 mm (Al-Zaghath, 1989, Chaudhary, 1983 and Migihid, 1978).

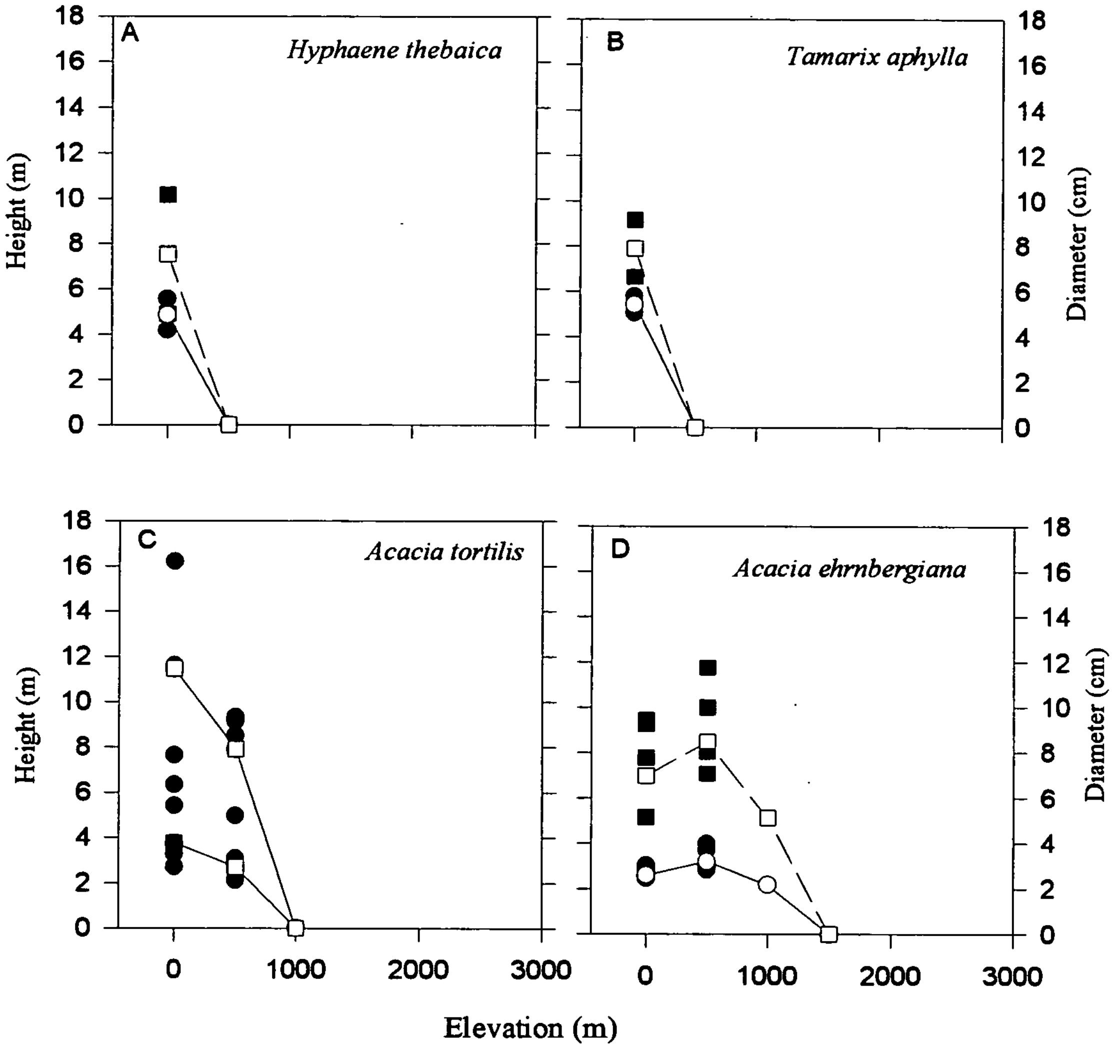

Figure 2.12: The plot of the mean height for each plot (●) and the overall mean height (O) and the mean diameter for each plot (■) and the overall mean diameter (□) of (A) *Hyphaene thebaica* , (B) *Tamarix aphylla* , (C) *Acacia tortilis* , and (D) *A. ehrnbergiana* versus the altitude south western Saudi Arabia.

Figure 2.16: Pictures of (A) dom palms (*Hyphaena thebaica*) and (B) *Tamarix aphylla* sea level.

Figure 2. 17: Pictures of (A) *Acacia tortilis* and (B) *Acacia ehrnbergiana* at 500 m a.s.l.

5. Moraceae *Ficus salicifolia* Vahl.

This species occurs at an elevation 500 m (Fig 2.13), and is uncommon. It occupies sandy loam habitats with a rainfall 100-120 mm, and *Ficus salicifolia* forms almost a pure stand. The associated species are poorly represented (Fig 2.18). The average height is 13 m. The branchlets are grey tomentose (Migihid, 1978), the bark light brown. Leaves are alternate, 4 to 8 cm, petioles are 3 cm long. Stem diameters are (13.8 to 16.8 cm) and crown diameters are (9.9 to 10.5 m) Table 2.3.

6. Rhamnaceae *Ziziphus spina-christi* (L.) Willd.

Ziziphus is a large widespread genus, of which most species grow in dry conditions and are conspicuously thorny, often with thorns in pairs, one being straight and the other curved. *Ziziphus spina-christi* (L) is 8 to 6 m high and 0.5-1.0 m in girth. Branching occurs low on the trunk, forming a tangled crown. The bark is grey, deeply fissured, flaking off in large patches; the slash is reddish (Migihid, 1978). Leaves are 2.5 to 6 cm long. It is represented in a majority of the community types in the area surveyed ranging from 500 to 1000 m a.s.l (Fig 2.13). The associated species include *Acacia tortilis* and *Acacia ehrnbergiana* (Fig 2.18). The community type occurs on deep sandy soil. The average stem height 13.5 m . Stem diameters are (13.4 to 13.8 cm) and crown diameters are (6.3 to 7.5 m) Table 2.3.

7. Leguminosae (Mimosaceae) *Acacia seyal* Del.

This species is widespread and abundant and may be recognized by its flat-topped crown, bright yellow flowers and powdery bark (Al-Zaghath 1989, Chaudhary 1983). Distribution ranges from 500 to 1500 m a.s.l (Fig 2.15). The ground surface is covered by gravel, and the water is scarce. Flower (Des-Apr), appearing shortly before the new leave and very conspicuous. The leaf is mostly 8-12 pairs. Associated species include *Acacia asak, A. nubica* and *A. homulosa* (Fig 2.19). The soil is sandy loam. Stem diameters are (8.0to 9.4 cm) and crown diameters are (6.2 to 6.9 m) Table 2.3.

8. Leguminosae (Mimosaceae) *Acacia asak* (Forssk.) Willd.

This species forms a community with a wide ecological range from 500 to 1500 m a.s.l (Fig 2.13), and occurs on rocky and gravely slopes. Associated species include, *Acacia seyal, A. nubica* and *homulosa*. The plant cover ranges from 50 to 70 per cent, and the dominant contributes the major part of this cover. The tree is up to 2.3-4.2 m high (Fig 2.19). The leaf is mostly 3-6 pairs. leaflets from 6-12 pairs to reach 20 pairs (Al- Zaghath, 1989 Chaudhary, 1983). Stem diameters are (8.3 to 9.8 cm) and crown diameters are (6.4 to 6.8 m) Table 2.3.

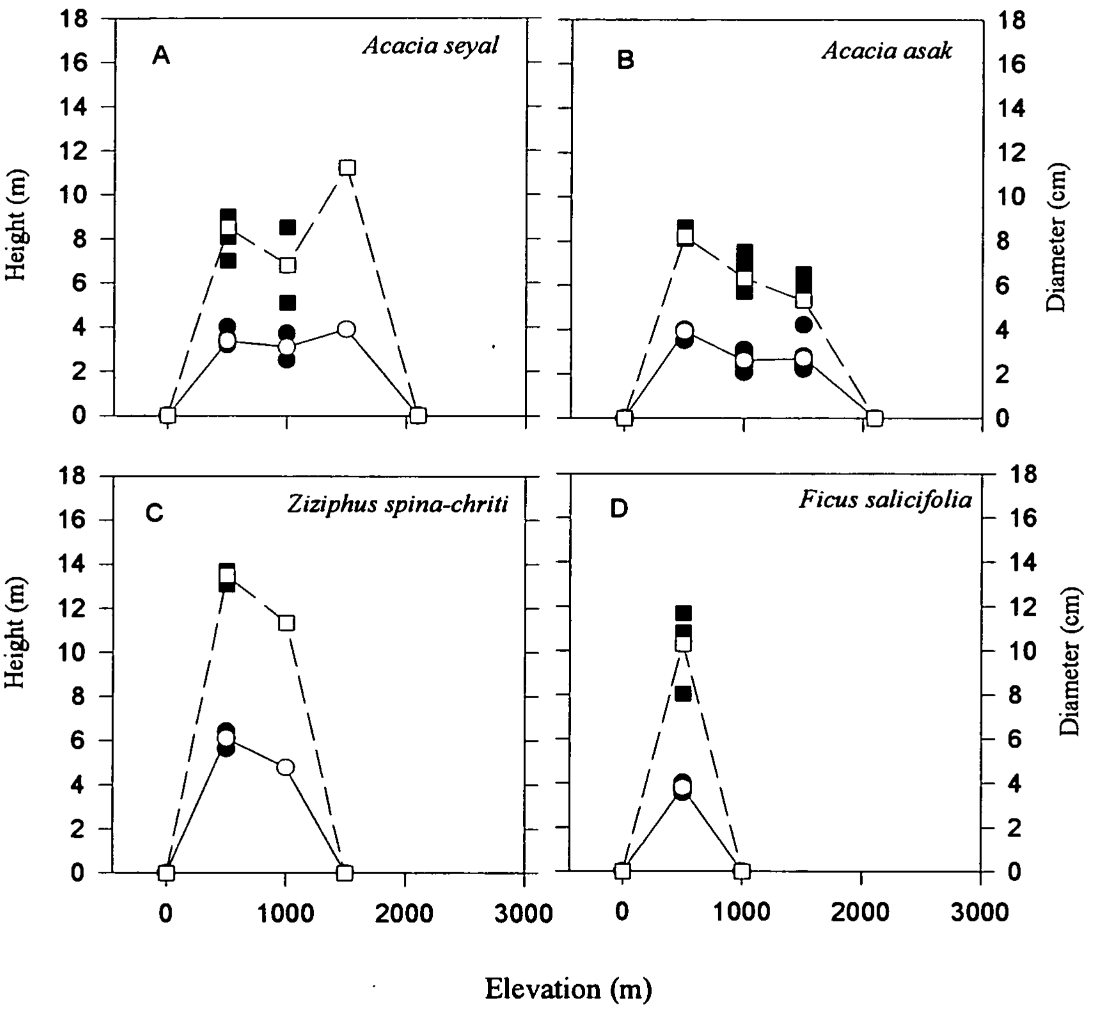

Figure 2.13: The plot of the mean height for each plot (●) and the overall mean height (O) and the mean diameter for each plot (■) and the overall mean diameter (□) of (A) *Acacia seyal*, (B) *A. asak*, (C) *Ziziphus spina-christi*, and (D) *Ficus salicifolia* versus the altitude south western Saudi Arabia

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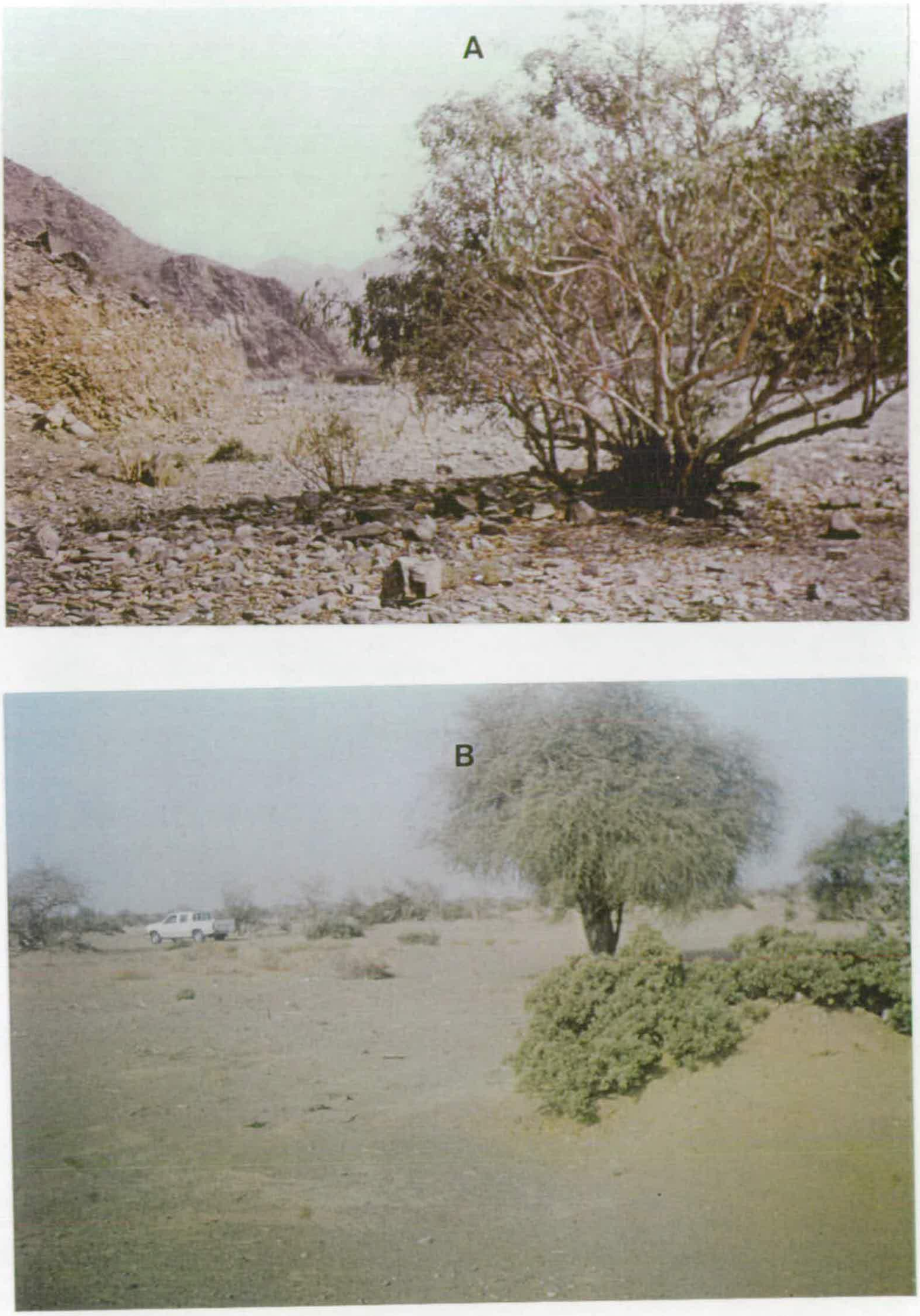


Figure 2.18: Pictures of (A) *Ficus salicifolia* at 500 m a.s. l. and (B) *Ziziphus spini-christi* at 1000 m a. s. l.

Figure 2.19: Pictures of (A) *Acacia sayel* and (B) *Acacia asak* at 500 to 1500 m a. s. l.

9. Leguminosae (Mimosaceae) *Acacia nubica* Benth.

These are small *Acacia* trees up 3 m high with basal branching occurring on the dry stony ground. The species occurs at an elevation 1000 m a.s.l (Fig 2.14). The bark is smooth, green-grey. Leaves are 1.5-5.5 cm; pinnae 5-11 pairs. The distance between trees is from 10 to 15 m (Al- Zaghath, 1989; Chaudhary, 1983). Stem diameters are (5.5 to 6.2 cm) and crown diameters are (4.2 to 5 m) Table 2.3. Associated species: *Acacia asak* and *A. homulosa* (Fig 2.20).

10. Leguminosae (Mimosaceae) *Acacia homulosa* Benth.

The *Acacia homulosa* community is found at 1000 m elevation (Fig 2.14). *A. homulosa* is very scarce in the area surveyed. Associated species: *Acacia laeta, A. nubica and A. asak* (Fig 2.20). This community occurs on the rocky and gravelly slope with a rainfall 150-170 mm.. The tree height is up to 3 m. The leaves are in 2-3 pairs, leaflets 5-8 pairs (Al- Zaghath, 1989; Chaudhary, 1983). Stem diameters are (6.0 to 8.4 cm) and crown diameters are (4.0 to 5.2 m) Table 2.3.

11. Leguminosae (Mimosaceae) *Acacia laeta* R. Br. Ex. Benth.

The *Acacia laeta* community is very scarce, but it occupies a wide area on rocky sites and usually on sandy loam from 1000 m to 1500 m (Fig 2.14). Associated species include *Acacia nubica*, *A. asak*, and *A. homulosa*. *A. laeta* is a small tree with grey-green bark which appears black where seen from afar (Fig 2.21). Leaves are bipinnate with 2-3 pairs of fairly large pinnate leaflets and 3-5 pairs of pinnae. The leaflets are clearly sparated from each other and are asymmetric (Al- Zaghath, 1989; Chaudhary, 1983). Stem diameters are (6.0 to 6.5 cm) and crown diameters are (8.5 to 9 m) Table 2.3.

12. Oleaceae *Olea europea* L.

The olive community is found mainly at an elevation of 1500 m a.s.l (Fig 2.14). *Olea europea* is an evergreen tree with coriaceous leaves. It is the characteristic and usually dominant species. A typical tree is 4-14 m high, and the stem is much branched (Migihid, 1978). Leaves are lanceolate to ovate. The plant forms almost pure stands covering a wide area (Fig 2.21). This community occurs on the rocky sites rainfall 150 to 200 mm and gravely slopes. Stem diameters are (8.0 to 12.5 cm) and crown diameters are (3.5o 6.4 m) Table 2.3.

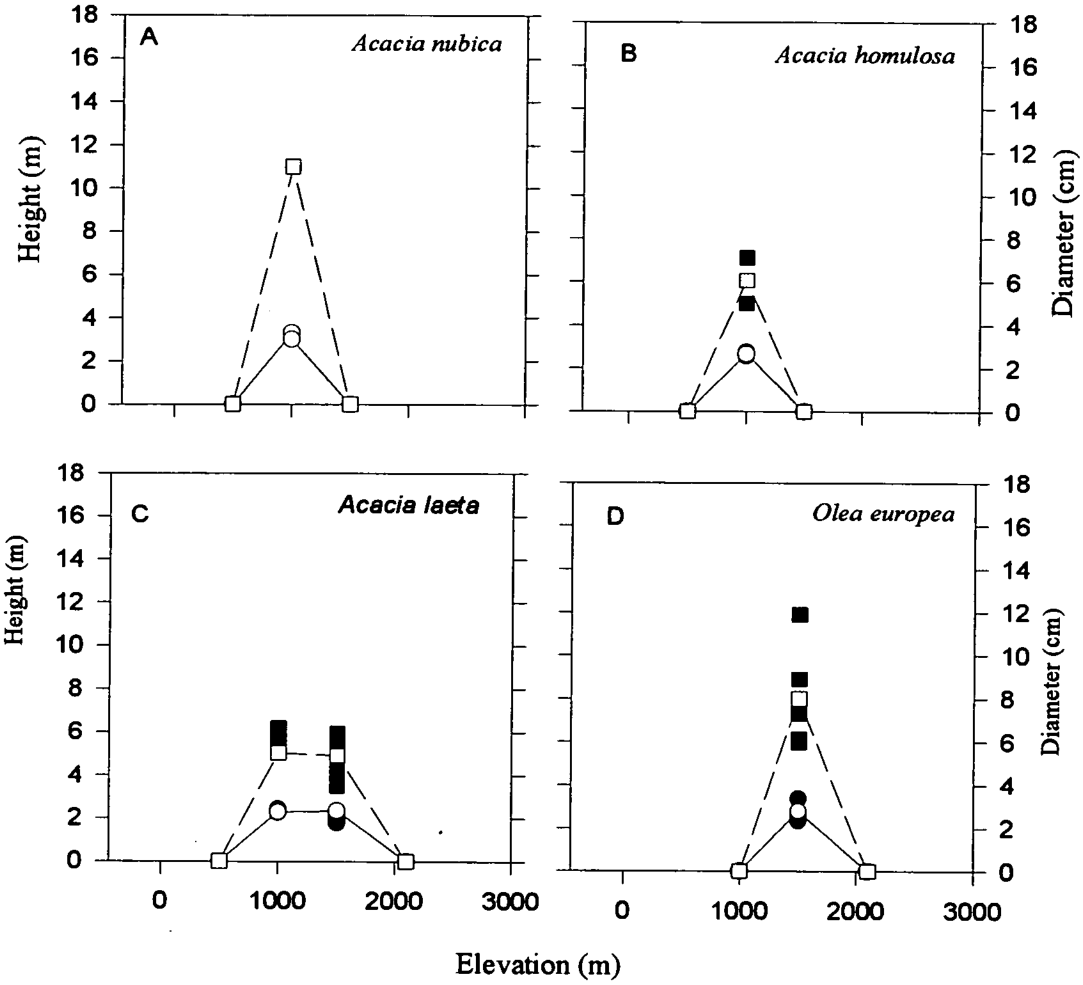


Figure 2.14: The plot of the mean height for each plot (●) and the overall mean height (O) and the mean diameter for each plot (■) and the overall mean diameter (□) of (A) *Acacia nubica*, (B) *Acacai homulosa*, (C) *Acacia laeta*, and (D) *Olea europea* versus the altitude south western Saudi Arabia.

Figure 2.20: Pictures of (A) *Acacia nubica* and (B) *Acacia homulosa* at 1000 m a.s.l.

Figure 2.21: Pictures of (A) *Acacia laeta* and (B) *Olea europea* at 1500 m a. s. l.

13. Leguminosae (Mimosaceae) *Acacia gerradii* Zoh.

The *Acacia gerradii* community is widespread in the eastern slope of the Asir mountains, at elevation above about 2100 to 2400 m (Fig 2.15). The community type occurs on sandy loam and rocky sites rainfall 200 to 250 mm, and the average temperature is 25 °C (Al-Zaghath, 1989; Chaudhary, 1983). Associated species are *Acacia negrii and J. procera* (Fig 2.22). The leaf is mostly 3-6 pairs. The leaflets are mostly very large from 10-18 pairs. Stem diameters are (6.5 to 8.0 cm) and crown diameters are (4.4 to 6.0 m) Table 2.3.

14. Leguminosae (Mimosaceae) *Acacia negrii* Pinchi-Sermoli

This species forms the second community in the eastern slope of the Asir mountains, at elevations above about 2100 to 2600 m a.s.l (Fig 2.15). The dominant species is widespread in the area surveyed. *Acacia negrii* contributes the major part of this cover. Associated species are *Acacia gerradii,* and *Juniperus procera* (Fig 2.23). This community occupies sandy loam habitats. It apparently prefers a high (200 to 300 mm per year) rainfall, and an average temperature of 25 °C (Al-Zaghath, 1989; Chaudhary, 1983). The leaf is mostly 2-5 pairs. The leaflets are mostly very large from 14-34 pairs. The height is 3-7 m. Stem diameters are (7.2 to 8.5 cm) and crown diameters are (4.3 to 4.8 m) Table 2.3.

15. Cupressaceae *Juniperus procera* Hochst. ex Endl.

J. procera forms the third community in the eastern slope of the Asir mountains, at an elevation above about 2100 to 2600 m a.s.l (Fig 15). The community is thickest along the lip of the main precipice where the species forms a pure stand, contributing the major part of the cover. It is a tree with two kinds of leaf, spreading needle-like and imbricated scale-like. Cones are fleshy and berry-like when young. Fruit is glossy, reddish brown. Needle leaves and branches becme reddish when they dry (Abo-Hasan, 1984; Migahid, 1978). Associated species include *Acacia negrii* (Fig 2.23) .The soil is usually sandy loam, pH 7.2-7.3. Stem diameters are (11.5 to 16.9 cm) and crown diameters are (4.0 to 8.8 m) Table 2.3.

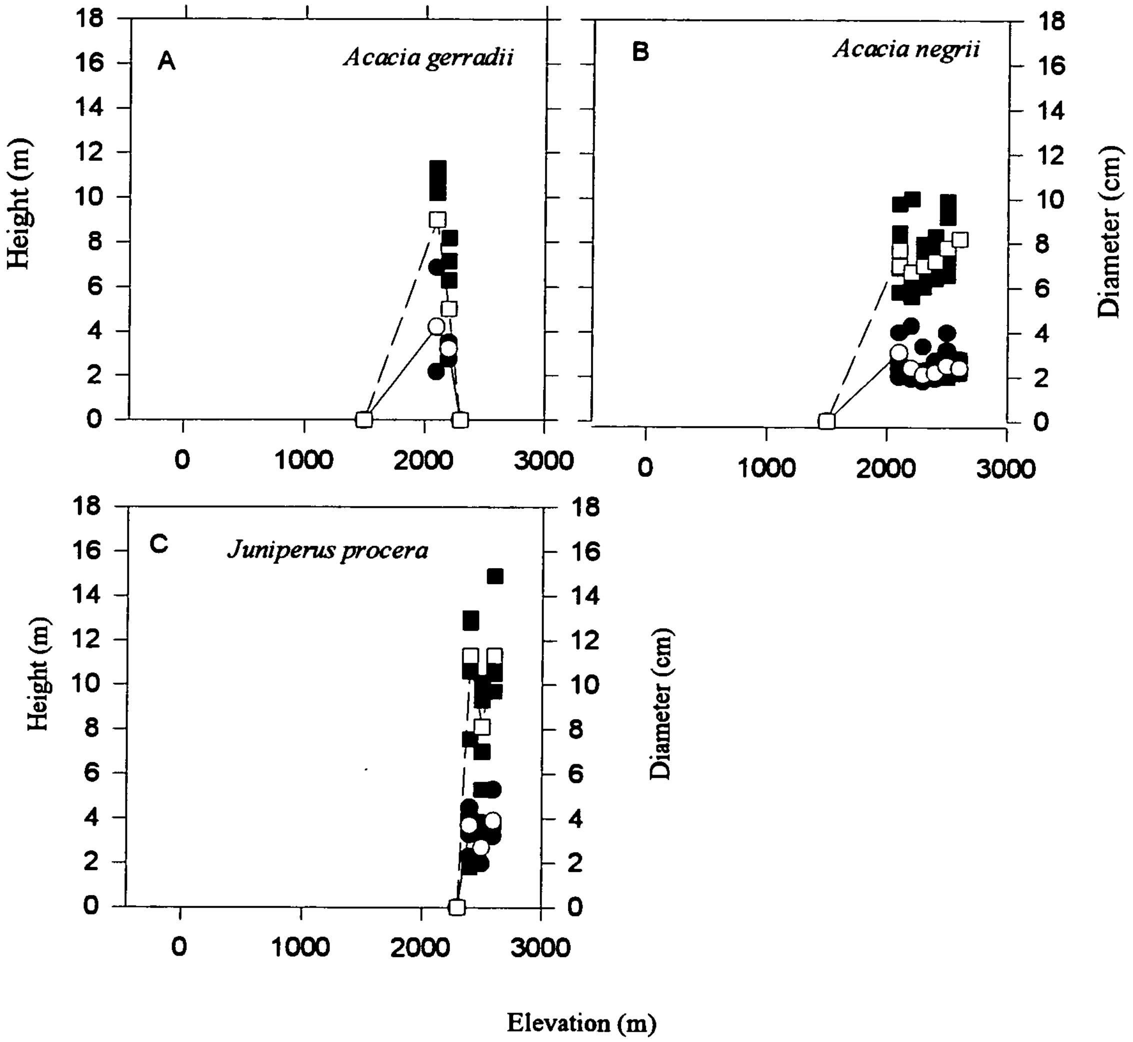


Figure 2.15: The plot of the mean height for each plot (●) and the overall mean height (O) and the mean diameter for each plot (■) and the overall mean diameter (□) of (A) *Acacia gerradi*, (B) *Acacia negrii* and (C) *Juniperus procera* versus the altitude south western Saudi Arabia.

Figure 2.22: Pictures of (A) *Acacia gerradii* at 2300 m a. s. l.

Figure 2.23: Pictures of (A) *Acacia negrii* at 2400 m a. s. l. and (B) *Juniperus procera* at 2600 m a. s. l.

2.4 Discussion

The aim of this part of the present study was to characterize the forest types over an altitudinal range within the area of south western Saudi Arabia. Tree species, type of the soil, amount of rainfall, temperature and humidity were investigated in order to indicate some relations between distribution of the vegetation and the topography.

The distribution of the recognised types of vegetation in the area surveyed is related mainly to its physiographic features and soil attributes. Studies of the desert vegetation in Iraq (Batanouny and Sheikh, 1972) and in Egypt (Batanounyand Abdel Wahab, 1973) are in agreement with this conclusion. Controlling variables relate mainly to an influence on the amount, availability and continuity of the water supply (Peet, 1981; Barton, 1993). Kramer and Kozlowski (1979) reported that the distribution of forests, their species composition and productively are controlled chiefly by too little or too much water. Water deficit reduces plant growth and crop yield more than all other stresses combined, because of its ubiquitous nature (Kramer, 1983).

In low areas, temperatures are usually high throughout the year and can reach up to 35 °C in the summer. Rain falls in the spring, and the annual average is 55 mm which is a very small amount, hardly enough to sustain the vegetation for a month let alone for a whole year. Variability of rainfall is a common character of the arid land climate (Abdel Rahman and Balegh, 1974; Al-Jerash, 1985). Danin (1989), reported similar conditions in the coastal plain, foothills and wadis of the gulf of Elat and demonstrated that theses communities tolerate lower annual temperature (23-26 °C) and receive higher annual rainfall (5-30 mm).

The vegetation's ability to tolerate such conditions is a strong indication of its resilience (Barton, 1993). The vegetation may be assisted by roots which grow deep in the soil for moisture. Climate and plant life have an intimate relationship. This has been studied by many geographers and ecologists. Oliver (1973) states "The fact that early climatic classification used vegetation as an index of climate and that it has been suggested that the easiest way to recognise a climatic region is through its effect upon the predominant grouping of plants that grow on the earth's surface". Rapid changes in mean temperature, mean rainfall, and consequently growth season with elevation in the mountains of Western Saudi Arabia are clearly demonstrated. These changes are obviously responsible of the vegetation transformation with the climatically controlled vertical zones (Gaston, 1990). Thus, variable bioclimatic factors with elevation should be expected in the mountains of this region. The effect of elevation on temperature and rainfall is profound, and likely to exert a strong influence on the germination, phenology and growth of species. The temperature lapse rate (about - 6.5 °C per km) is similar to that reported for mountainous sites in other parts of the world (Grace, 1977). The rate of change in rainfall varies, but it is clear that much more water is supplied at the upper stations than lower ones. The dryness of the atmosphere, which is best experessed as saturation deficit, shows a marked seasonality and a greater dryness at the lower sites.

On a smaller scale the factors of topography, soil texture, soil depth become more important in determining vegetation composition and density (Noy-Mier, 1974; Parker, 1990). The results of the analysis show that the pH value decreases as we move from upland to low land (Table 2.2). This indicates that the soil has been swept down by the rain as it flows from hill tops downwards. Yair and Danin (1980) showed that the runoff generated by rainfall in the arid region of Negev in Israel is spatially non-uniform. And the amount of carbon increases with the rise in temperature. This leads to an increase in the decomposition of materials especially organic matter. In certain elevated area the increase in organic matter is not so noticeable because of the spare of vegetation (Fig 2.7). Wild (1994) reported that organic matter is not an essential component of soils but it has important effects on soil structure and is a source of nutrients, particularly nitrogen, phosphorus and sulphur. The spatial and temporal variability of water often imposes heterogeneity of other factors, such as redistribution of nutrients, minerals, and organic matter Yair and Danin (1980). Safriel *et al.* (1989) suggested that the spatial and temporal distribution of water may be responsible for the observed fluctuation in nitrogen availability in arid regions. Also, Danin (1989) reported a pronounced difference in soil salinity in Judean deserts, resulting from efficient leaching of south-west facing slopes by incident rainfall.

The results obtained pertain to fifteen types of vegetation spread throughout the area under study: three types on the eastern side of the hills (the eastern slope is not that steepy and drain into the inland plateau) and twelve on the western side (the western slope is very steep). As has already been mentioned the environmental conditions have led to the distribution of vegetation throughout the sites and in various proportions. It was observed that the vegetation of the type *Acacia negrii* and *Acacia gerradii* exist in the elevated cold areas which also contain vegetation of the type *Juniperus procera*. However, *Juniperus procera* grows more densely in some areas because of the abundance of rain and the low temperature. This kind of forest also occurs in Eritrea, Somalia and Ethiopia at the same height (Zohary, 1973 and Sharew, 1994).

In the lower levels, *Juniperus* trees disappear, presumably due to increase in temperature and decreases in available water. As to the other vegetational types (*Olea europea, Acacia asak, A. nubica, A. seyal, A. homulosa, A. laeta, A. ehrnbergiana, A.tortilis, Hyphaen thebica, Tamarix aphylla, Ficus salicifolia* and *Ziziphus spina-christi.*) which grow on the western side, they vary in density, growth and distribution. Elmin (1990) reported similar distribution of *Acacia* species in north Sudan where the conditions are similar. Halevy (1972) reported *Acacia tortilis* as a Sudanian trees dominating the more arid places of the southern coast of Sinai. Waisel (1972) reported that *Ziziphus spina-christi* grows in a diffused pattern on the Mediterranean coastal plain and Jordan Valley, and that *Tamarix aphylla* has a very wide range of distribution in North and South Africa and Western Asia. In tropical regions, Vetaas (1992), detected some similar communities on an arid mountain plateau in Sudan and concluded that the species composition, at all spatial scales is directly or indirectly related to variation in temperature and moisture. In certain sites the species can be found either concentrated or spread out, because they are out of the range of their geographic distribution or because they require very specific types of environment in contrast to the common species which were found in various types of habitats and sustained a wide range of environmental factors. Distribution may also be determined by felling and pasturing for long periods of time without replacement through plantation. Human factors contribute to the disruption of the natural equilibrium among the components of the ecosystem, thus causing its deterioration (Batanouny, 1975). It may also be due to the absence of conditions conducive to growth.

The results of measurement of length, diameter, density or otherwise of vegetation indicates a disparity in the conditions conducive to growth which have lead to variations in growth. The vegetation is mostly short and has many branches at a height of fifty centimetres above the soil especially in the case of *Acacia*. The general sparsity of trees also causes the crowns of the trees to develop strongly and appear as a dome, ball, or umbrella shape. The crown was generally broad and in many case their width was equal to their height. Lower branches of many trees had the tendency to grow horizontally and even pressed to the ground, but grazing by camels, goats, sheep and harvesting by man have caused the lower branches to disappear in quite a few cases. This is in agreement with Agnew and Waterman (1989) who reported the virtual disappearance of *Acacia-Commiphora* woodland from southern Kenya by heavy browsing. The vegetation starts to grow sideways when the conditions are good and the rain is plentiful (Agnew and Waterman, 1989). Shrubs and herbs are distributed in patches in the various sites because of the same conditions which affect the growth of trees. It has been observed that they become denser as we move upwards. As to the scarcity of grass, this is due to the fact that the study was conducted in the summer when the period of growth is very short (lasting for two months or less). Grass grows in the spring when the rain is plentiful. Noy-Mier (1974), Yair and Danin (1980); Belsky (1989) have reported that the vegetation composition in the arid and semi-arid regions depends largely on rainfall and factors affecting the availability and distribution of water. The main explanation for the persistence of woody species of the south western Saudi Arabia is that ecosystems are robust, with aridity being dominating factor. This tends to override even such strong influences as man and livestock The shifts in climatic zones may also have eliminated species which were not able to shift with them. The species which survive in such environments are likely to be the most robust.

2.5 Conclusion

There are two facing slopes, one is the eastern (Abah and Alsoudah), where the temperatures range from 22-26 °C the elevation is around 2200 to 2600 m a.s.l, and precipitation is 300 mm per year. The most common trees are *Acacia* species and *Juniperus procera*. The second is in the western plain (Ash shugayg), where the temperature is between 35-37 °C and the elevation is from sea level to 1500 m a.s.l and precipitation is only 55 mm per year. The most abundant species in the vegetation are *Hyphaen thebica*, *Ziziphus spina christi*,, *Acacia tortilis*, and *A. ehrnbergiana*.

The result of this study show that *Acacia species* occurred along a unique environmental gradient. The species cover was not uniform in all the zone, because of the variation in topography and moisture (Table 2.4). Suggest, there are two factors appear to

Table 2.4 : Distribution of the species along the environmental gradient in the South of Saudi Arabi

Elevation (m)

Species	Sea level	500 m	1000 m	1500 m	2000 m	3000 m
Hyphaene thebaica	-----					
Tamarix aphylla	-----					
Acacia tortilis	------------	--------				
Acacia ehrnbergiana	-----------	---------	----------			
Ficus salicifolia		---------				
Ziziphus spina-christi		---------	----------			
Acacia sayel		---------	----------	----------		
Acacia asak		---------	----------	----------		
Acacia nubica			---------			
Acacia homulosa			----------			
Acacia laeta			----------	---------		
Olea europea				----------		
Acacia gerradii					---------	
Acacia negrii					---------	-------
Juniperus procera					---------	--------

play a key role in the distribution of the species studied. There is a lack of natural regeneration and many valuable plant species are endangered with some already extinct.

There is a need for an effective management programme aimed at conservation of the existing vegetation covers as well as re introduction of the extinct species. Evidently, however, this cannot be carried out without thorough understanding of the key factors that affect the growth and the distribution of these species. Therefore, the main objective of the glasshouse experiments is as follows: *Evaluation and assessment of the key environmental factors influencing the growth and physiology and the investigation of optimum conditions required for propagation and growth of the selected species.*

CHAPTER 3

Effect of Pre-germination Treatment on Seed Germination of *Acacia negrii*, *A. asak*, *A. ehrnbergiana*, *A. seyal* and *A. tortilis*.

3. 1. Introduction

Regeneration from seed in most plant communities is dependent upon the occurrence of gaps in the vegetation, and as discussed in the previous chapter, these are plentiful at all the sites. Planting trees like *Tamarix aphylla* or *Ziziphus spina-christi* and *Hypheane thebaica,* is usually combined with species of *Acacia*, which have the ability to reproduce by seeds and fix nitrogen. However the central problem encountered when using *Acacia* species is the poor germination of the seed when harvested directly from the parent plant (Clement *et al.*, 1977; Bebawi and Mohamed, 1985). *Acacia* species are especially important because they are used widely in afforestation and agroforestry in Saudi Arabia. *Acacia negrii, A. asak, A. ehrnbergiana, A. seyal and A.tortilis* have a low percentage and rate of germination under natural conditions (Mahmoud, 1977), and appropriate pregermination treatments are not well documented in Saudi Arabia.

The seed of a number of species often germinate slowly or fail to germinate at all after sowing, even though they are viable. There are two main causes of this phenomenon, referred to as dormancy (Barton, 1969; Spurny, 1973; Edwards, 1973 and Singh *et al.*, 1985). First, there may be internal dormancy, a condition ordinarily resulting from incomplete digestion of the fats, protein, and other complex insoluble substances stored in the seed. Second, dormancy may be imposed by a hard and impervious coat (Clements *et al.*, 1977). Most *Acacia* species have a hard coat, which can be broken by mechanical or chemical softening or etching of the seed coat (Edwards, 1973; Clement *et al.*, 1977; Sadhu and Kaul, 1989; Danthu *et al.*, 1992).

In the arid environment, short favourable growing seasons are separated by a long very unfavourable dry period, and the success and survival of *Acacia* species depends not only on successful resistance to adverse condition, but also on the ability to synchronise the life-cycle with the changing seasons (Went, 1949). Since seed germination and establishment is the most critical time in the life-cycle, some method of controlling the time of germination is essential if the species is to survive (Went, 1949; 1955; Mahmoud *et al.*, 1982). The pattern of the germination response to temperature, which appears to be correlated with the geographical distribution of the species, allows seedling establishment to occur at the most favourable time of the year for the particular climatic area (Thompson, 1970). Thus it synchronises the species to its environment and must be of considerable selective importance (Went, 1949; Mahmoud *et al.*, 1982).

Several artificial methods are used to break the hard impermeable seed coats of the Leguminosae (Mimosoideae), and other families, and so release them from dormancy. These include treatments with concentrated sulphuric acid, mechanical scarification, and heating (Bewley, 1985; Bell *et al.*, 1987; Corral and Pérez-garac, 1990; Tesfaye, 1992, and Singh *et al.*, 1990). Larsen (1962) found that seeds of 43 *Acacia* species when placed in boiling water and immediately removed from the source of heat and left to cool, germinated faster and more completely than untreated seeds. Rana and Nautiyal, (1990) found mechanical and chemical scarification proved most effective while temperature treatments were not so effective. These methods are used to soften the seed coat in the laboratory, but the natural means are not well understood. The best known natural factors are those of high temperature and temperature fluctuation (Whittaker and Gimingham, 1962; Corral and Pérez-garac, 1990 and Shea *et al.*, 1979).

To obtain rapid and synchronous germination artificially, the seeds must be subjected to some physical or chemical treatment which will quickly destroy the integrity of the impermeable cover and permit the imbibition of the embryo. The most commonly recommended procedures are treatment with sulphuric acid (acid scarifiction), immersion in hot or even boiling water and mechanical injury of the impermeable cover by chipping or abrasion (mechanical scarification), Table 1.1.

Table 3.1 Example of the effects of different treatments on various impermeable seeds.

Treatment	Species	Untreated	Treated	Time (period)	Authors	(years)
Sulphuric acid 80% (H_2SO_4)	*A. acuminata*	20%	70%-88 %	3,5,10,15 min	Singh and *et al.*	1990
	A. adshrgens	20%	80%-90%	3,5,10,15 min		
Scarification	*A. arabica A. cateh*	10% 18%	45.5% 48%		Misra & Singh	1981
Boiling water	*A. extensa*	11.5%	80%-90%	1,3,5 min	Shea *et al.*	1979
	A. pulchella	18.7%	79%-80%	1,3,5 min		
Temperature						
40, 80 °C	*A. constricta*	10%	90%	10, 40 min	Washitani	1988
80, 90 °C	*A. pulchella*	10, 20%	57%-74%	20, 30 min	Shea *et al.*	1979

There are many different methods to test germination. The easiest and simplest method is to determine how many seeds will actually germinate during a given period in the glasshouse. A more critical measure of success is the percentage of seeds which produce plantable seedlings.

The objective of this Chapter is to explore the effect of pre-germination treatment on five native Saudi Arabian *Acacia* species (*Acacia negrii, A. ehrnbergiana, A. asak, A. seyal* and *A. tortilis*) by dry heating, treatment with sulphuric acid and boiling water. The result of recommended methods of pretreatment will help to define a strategy for large scale application in reforestation, conservation and development projects in Saudi Arabia.

3.2 Material and Methods

3.2.1 Experimental material

Ripe fruit of *Acacia negrii, A. asak, A. ehrnbergiana, A. seyal* and *A.tortilis* were collected from healthy mature trees in April 1994, from three different ecological zones, sea level, 500 m above sea level and 2200 m above sea level in South western Saudi Arabia. The seeds were extracted from the fruits by hand. Empty seeds were removed by floating.

A considerable proportion of the floating seeds had insect holes and deep surface wrinkles, which suggested they were not viable (Fig 3.1). Dry seeds were packed in cotton cloth bags and stored in room temperature until the study began in May and June 1994.

Figure 3.1: This figure shows (A) seeds of *Acacia negrii*, *A. asak*,*A. seyal*, *A. ehrnbergiana* and *A. tortilis* which have been attacked by Bruchid beetles (*Bruchidius* spp) (B).

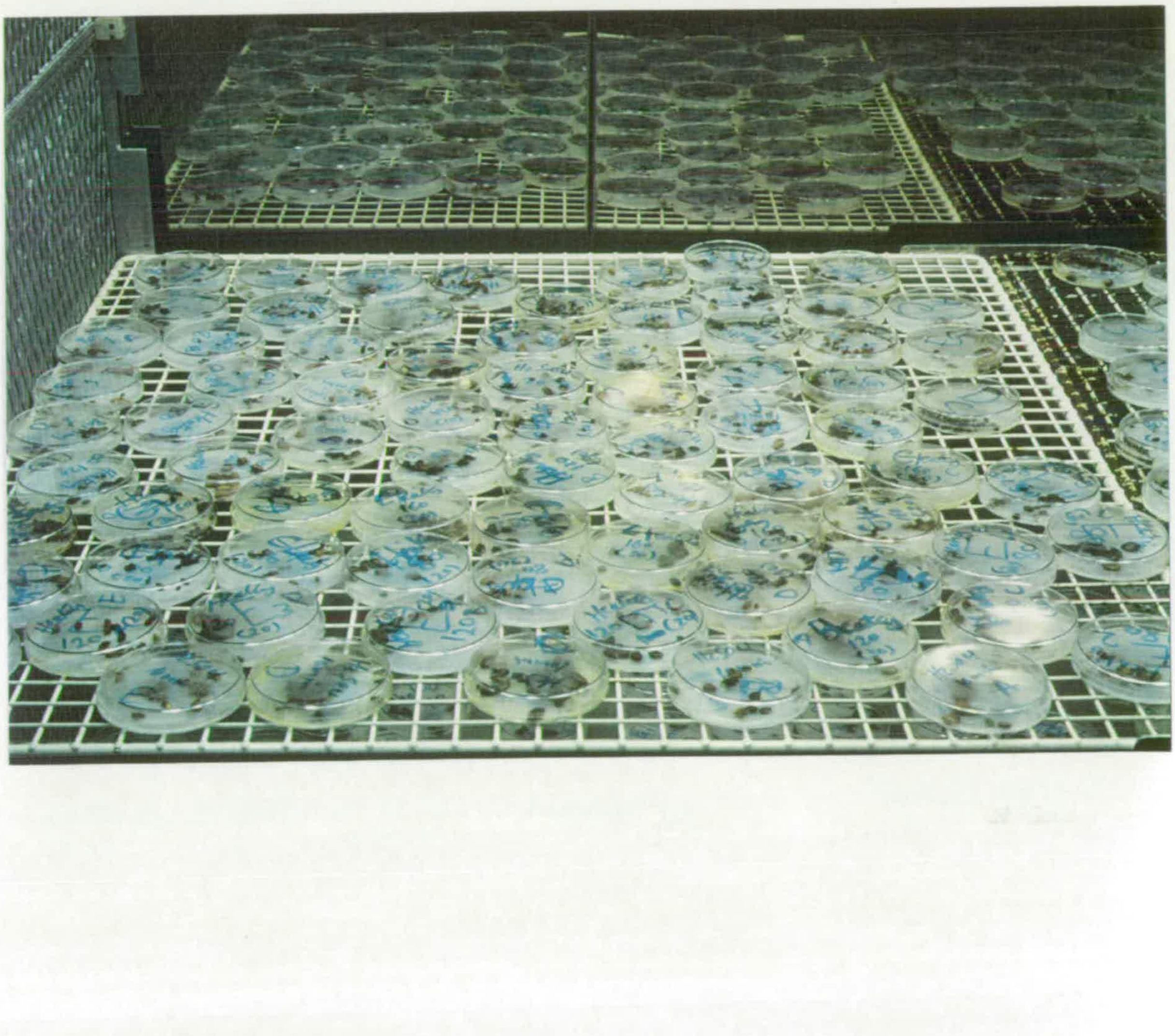


Figure 3.2: This figure shows the experiment of *Acacia seeds* (*A. negrii*, *A. asak*, *A. seyal*, *A. ehrnbergiana* and *A. tortilis*) in growth chamber (seed in Petri-dishes) after treatment by dry heating, sulphuric acid and boiling water.

Figure 3.3: Pattern of seedlings devlopment from different *Acacia* species: (A) *A. negrii*, (B) *A. asak*, (C) *A. seyal*, (D) *A. ehrnbergiana* and (E) *A. tortilis*.

3.2.2 Experimental design and treatment

The study was carried out at the Institute of Ecology and Resource Management, University of Edinburgh. The design adopted was a randomised block with four replications. In each treatment 100 seeds (25 seed each replication) were used. The effects of hot water, sulphuric acid and dry heating on the germination of all the species involved the following treatments:

1. Control - One hundred seeds of each species were soaked in distilled water.

2. Hot water treatment- Seeds were immersed boiling water (about 300 ml distilled water pre treatment) maintained at 100 °C for 1, 5 and 10 minutes.

3. Acid treatment- Seeds were immersed in a beaker containing 300 ml of concentrated sulphuric acid (H_2SO_4) for 10, 20 and 40 minutes. These seeds were stirred vigorously every two minutes with a glass rod to prevent the deposition of carbon on the seed surface which might interfere with the action of acid on the testa. The seeds, after being soaked for the appropriate time in the acid, were washed thoroughly with tap water and rinsed in distilled water.

4. Heat-shock treatment- dry seeds were placed in an oven at 80 °C for 10, 20, and 30 minutes.

3.2.3 Germination conditions

After a pre-germination treatment, seeds were placed in 5.5 cm Petri-dishes containing a double layer of Whatman No.1 filter papers (Fig 3.2). Care was taken to maintain the filter paper moist; distilled water was added when necessary. Covered Petri-dishes were placed in the incubator. Constant temperature (25 °C) and relative humidity (about 70 %) were maintained inside the incubator. Seeds were illuminated at all times by fluorescent tubes (21 × 150 watt HQI-R metal halide lamps. 12 × 100 watt incandescent lamps) and photon flux density at seed level was about 20 μmol $m^{-2}s^{-1}$. Four Petri-dishes (25 seeds each) were used for each treatment, for each species.

3.3 Data collection and analysis

Observations on the germinating seeds were made daily. Those seeds which had germinated were counted and discarded. Decayed seeds were also removed to avoid contamination. The criterion for germination was the protruding epicotyl had reached contamination. The criterion for germination was that the protruding epicotyl had reached a length of at least 10 mm (Fig 3.3). At the end of three weeks, germination was expressed as percent of all seeds sown, and the mean was calculated. After arcsine transformation of the percentage figures, the data were subjected to analysis variance (ANOVA).

3.4 Results

3.4.1 The average weight and size seeds.

The average weight and size of 100 seeds were measured. The seed of *Acacia negrii* is greenish, the funicle twisted. The seed *A. asak* is light to light green, and the funicle is lateral and deciduous. The seed *A. ehrnbergiana* is dull-green, with a reddish sub-terminal funicle. The seed *A. seyal* is greenish, the funicle twisted. Seed of *A. tortilis* is reddish-brown, and the funicle sub-terminal, twisted (Hassan and A-Farraj, 1989). The species have a different seed shape index calculated as length/width, and also differ in length and weight (Table 3.2).

Table 3.2 Average weight and size of *Acacia* seeds. Mean ±SE n =100

Species	Weight (g)	Length (mm)	Width (mm)	Shape index (length/width, ratio)
Acacia negrii	0.08±0.02	7.34±0.10	4.74±0.10	1.55
A. asak	0.04±0.01	6.77±0.10	5.71±0.10	1.19
A. seyal	0.09±0.10	9.23±0.08	5.19±0.08	1.77
A. ehrnbergiana	0.03±0.04	5.41±0..07	2.96±0.05	1.83
A. tortilis	0.02±0.03	4.77±0.06	2.98±0.04	1.60

3.4.2 Viability of the embryo

Tests to determine viability of the seeds were carried out using 2,3,5 tri-phenyl tetrazolium chloride (ISTA, 1985; Moor, 1973). The viability was between 90 to 94 % for all species.

3.4.3 Effects of seed pre-germination treatment on germination

The experiment investigated the effect of pre-germination treatment. There were highly significant differences (P<0.0001) between the species and between treatments. In all cases the control treatment had the lowest percentage germination (Fig 3.4. 3.5, 3.6, 3.7 and 3.8).

In *Acacia negrii* (2200 m a.s.l), germination was enhanced by pre-treatment in sulphuric acid for 10 minutes, boiling water for 5 minutes and dry heat for 20 minute at 80 °C. However dry heating for 30 minutes, sulphuric acid for 40 minutes and boiling water for 10 minutes diminshed germination (Tables 3.3, 3.4 and 3.4).

In the case of *Acacia asak* (500 m a.s.l), germination was enhanced by pre-treatment in sulphuric acid for 10 or 20 minutes, boiling water for 5 minutes and dry heat for 10 minutes at 80 °C. In contrast, seed treated by dry heating for 30 minutes, sulphuric acid for 40 minutes and boiling water for 10 minutes had the lowest germination (Tables 3.3, 3.4 and 3.4).

For *Acacia seyal* (500 m a.s.l), pre-treatment by sulphuric acid for 10 minutes, dry heating for 10 minutes at 80 °C and boiling water for 10 minutes all stimulated germination. In contrast, boiling water for 1 minute, sulphuric acid for 40 minutes and dry heat for 30 minutes reduced germination (Tables 3.3, 3.4 and 3.4).

In *Acacia ehrnbergiana* (Sea level), pre-treatment by sulphuric acid for 40 minutes, boiling water for 10 minutes and 5 minutes all stimulated germination. In contrast, dry heating for 30 minutes at 80 °C, and boiling water for 1 minute and sulphuric acid for 10 minutes reduced germination (Tables 3.3, 3.4 and 3.4).

For *Acacia tortilis* (Sea level), pre-treatment by sulphuric acid for 40 minutes, boiling water for 5 minutes and 10 minutes stimulated germination. In contrast, seed treated by dry heating for 30 minutes at 80 °C, and boiling water for 1 minute and dry heating for 10 minutes at 80 °C gave the lowest germination (Tables 3.3, 3.4 and 3.5).

Table 3.3: Effect of pre-germination boiling water treatment on the seed germination of *Acacia* species after 18 days. Mean angle after arcsine transformation of % germination ±SE

Variable	control	boiling (1 min)	boiling (5 min)	boiling (10 min)
Acacia negrii	30.8±0.75	49.5±6.8	59.0±3.9	36.2±2.5
A. asak	33.2±1.6	56.9±4.4	58.9±2.9	46.0±5.6
A. seyal	30.5±2.6	38.6±2.3	48.8±7.1	50.9±3.5
A. ehrnbergiana	32.5±2.2	46.7±3.5	60.1±4.6	66.1±8.1
A. tortilis	29.9±0.65	35.1±0.6	50.2±2.4	55.0±2.3

Pre-germination treatment by sulphuric acid, boiling water and dry heating accelerated the germination of *Acacia asak* and *A. negrii* seeds over 24 to 48 hours. However, the untreated seeds took more that four days to germinate. Overall the greatest germination response of 90 % and 85 % was obtained by sulphuric acid (40 min) for *Acacia tortilis* and *Acacia ehrnbergiana* respectively (Fig 3.9). The second best germination response of 80 % was obtained by dry heating (20 min) and boiling (10 min) water for *Acacia ehrnbergiana* (Fig 3.10 and 3.11).

Table 3.4: Effect of pre-germination sulphuric acid treatment on the seed germination of *Acacia* species after 18 days. Mean angle after arcsine transformation of % germination ±SE

Variable	control	sulphuric acid (10 min)	sulphuric acid (20 min)	sulphuric acid (40 min)
Acacia negrii	30.8±0.7	62.9±2.6	45.0±2.7	34.4±1.0
A. asak	33.2±1.6	63.5±6.1	65.4±9.5	40.3±4.1
A. seyal	30.5±2.6	58.4±3.5	48.5±1.9	43.8±2.5
A. ehrnbergiana	32.5±2.2	52.6±2.1	62.1±1.4	71.9±2.2
A. tortilis	29.9±0.6	53.8±1.1	54.1±4.6	82.1±1.9

Table 3.5: Effect of pre-germination dry heating treatment on the seed germination of *Acacia* species after 18 days. Mean angle after arcsine transformation of % germination ±SE

Variable	control	dry heating 80°C (10 min)	dry heating 80°C (20 min)	dry heating 80°C (30 min)
Acacia negrii	30.8±0.75	42.1±4.1	53.4±4.1	33.8±1.8
A. asak	33.2±1.6	60.6±10.1	51.4±2.6	37.3±3.4
A. seyal	30.5±2.6	54.4±5.5	47.3±2.8	34.8±3.7
A. ehrnbergiana	32.5±2.2	54.7±4.3	53.9±3.9	33.4±4.8
A. tortilis	29.9±0.65	46.6±6.9	41.5±2.9	29.9±1.9

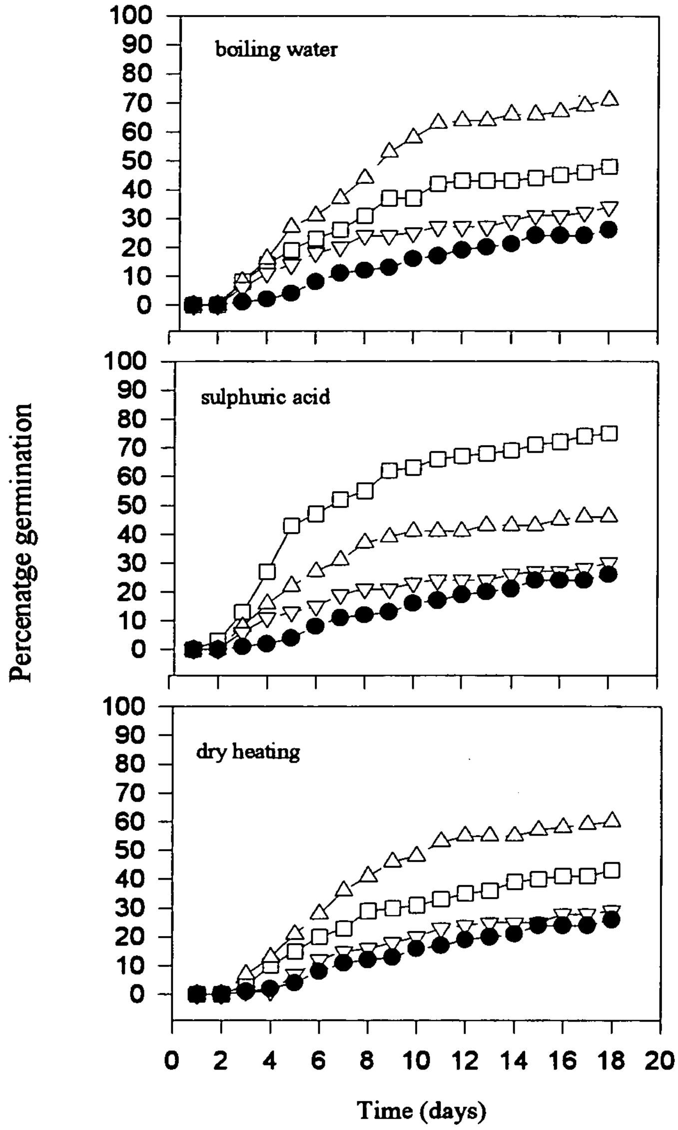


Figure 3.1: Percentage germination of *Acacia negrii* under the three treatments with control: in boiling water (□) 1 minute, (Δ) 5 minutes, (∇) 10 minutes and control (O). Sulphuric acid (□) 10 minutes, (Δ) 20 minutes, (∇) 40 minutes and control (O). Dry heating (□) 10 minutes, (Δ) 20 minutes, (∇) 40 minutes and control (●).

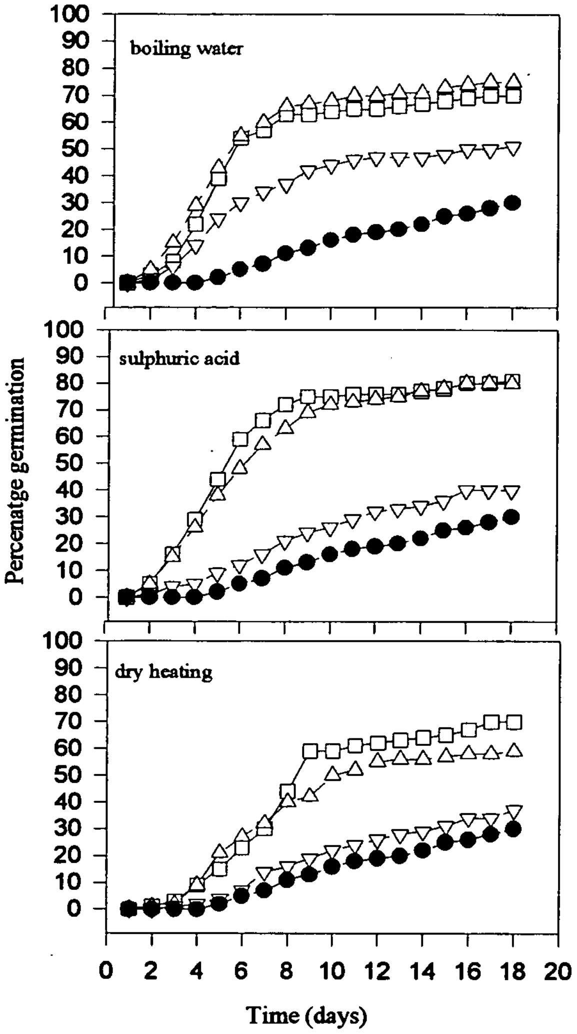


Figure 3.2: Percentage germination of *Acacia asak* under the three treatments with control: in boiling water (□) 1 minute, (Δ) 5 minutes, (∇) 10 minutes and control (O). Sulphuric acid (□) 10 minutes, (Δ) 20 minutes, (∇) 40 minutes and control (O). Dry heating (□) 10 minutes, (Δ) 20 minutes, (∇) 40 minutes and control (●).

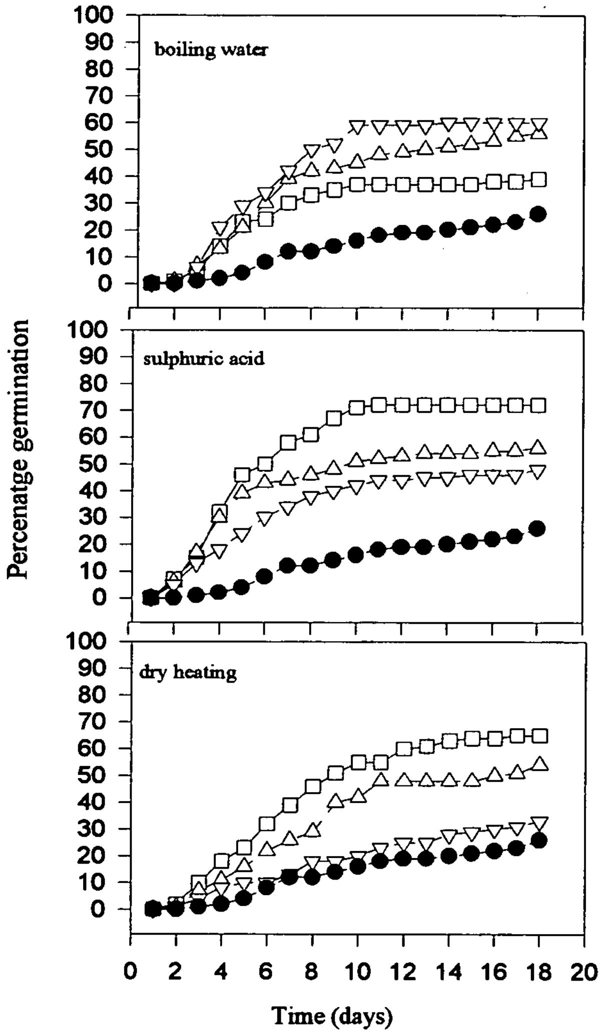


Figure 3.6: Percentage germination of *Acacia seyal* under the three treatments with control: in boiling water (□) 1 minute, (Δ) 5 minutes, (∇) 10 minutes and control (O). Sulphuric acid (□) 10 minutes, (Δ) 20 minutes, (∇) 40 minutes and control (O). Dry heating (□) 10 minutes, (Δ) 20 minutes, (∇) 30 minutes and control (●).

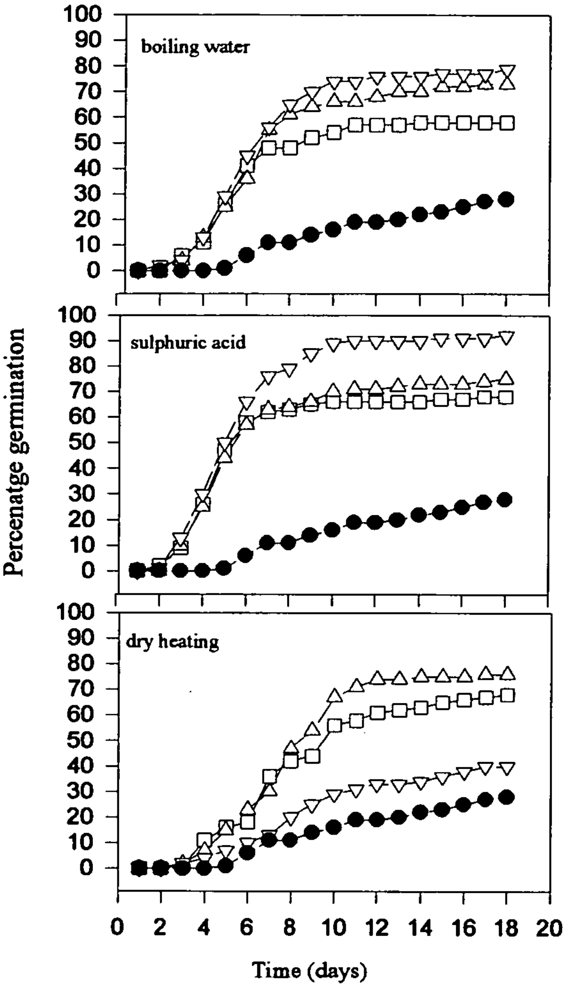


Figure 3.7: Percentage germination of *Acacia ehrnbergiana* under the three treatments with control: in boiling water (□) 1 minute, (Δ) 5 minutes, (∇) 10 minutes and control (O). Sulphuric acid (□) 10 minutes, (Δ) 20 minutes, (∇) 40 minutes and control (O). Dry heating (□) 10 minutes, (Δ) 20 minutes, (∇) 30 minutes and control (●).

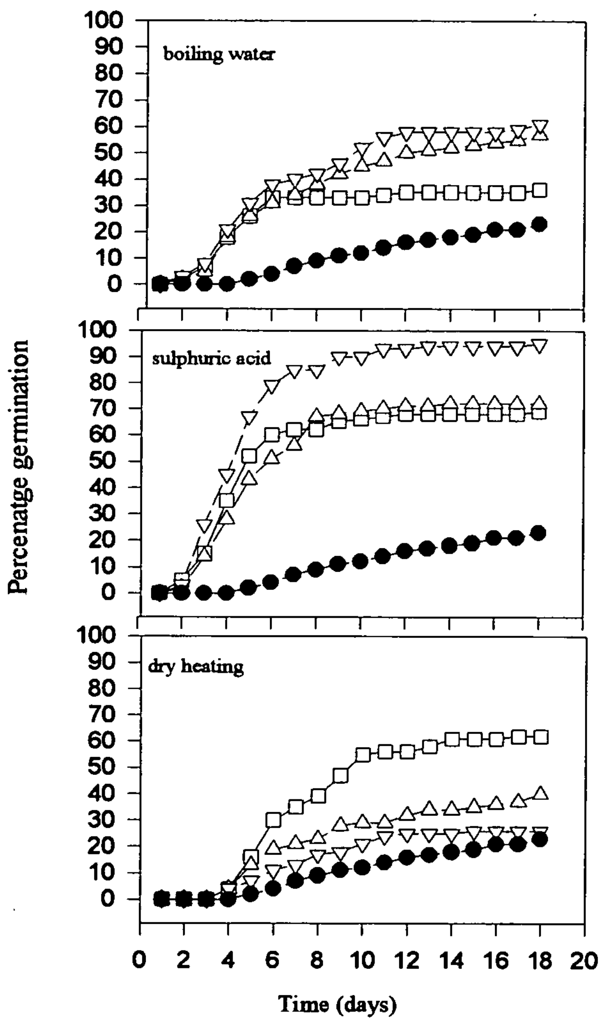


Figure 3.8 Percentage germination of *Acacia tortilis* under the three treatments with control: in boiling water (□) 1 minute, (Δ) 5 minutes, (∇) 10 minutes and control (O). Sulphuric acid (□) 10 minutes, (Δ) 20 minutes, (∇) 40 minutes and control (O). Dry heating (□) 10 minutes, (Δ) 20 minutes, (∇) 30 minutes and control (●).

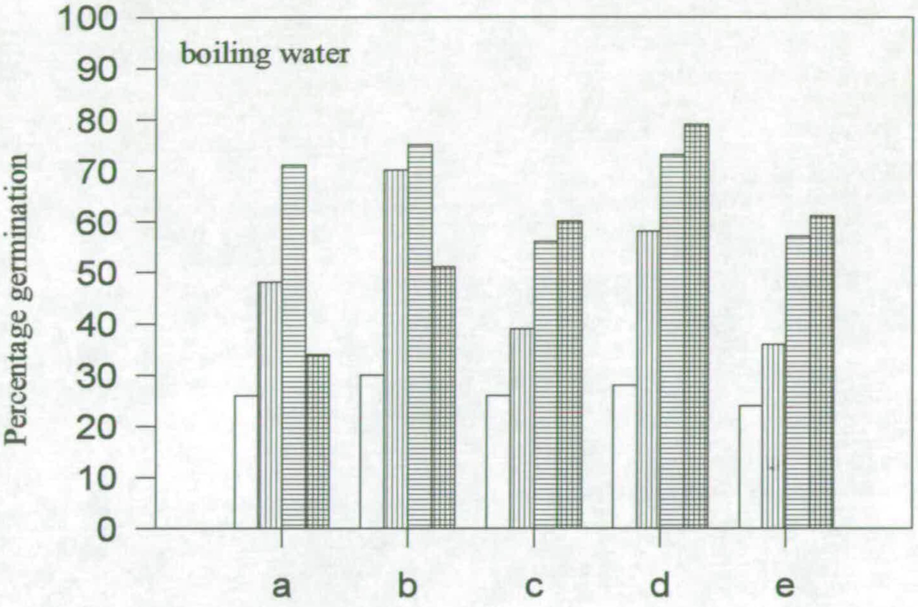


Figure 3.9: The final germination percentage of the seeds of *Acacia negrii* (a), *A. asak* (b), *A. seyal* (c), *A. ehrnbergiana* (d) and *A. tortilis* (e) which were treated by boiling in water for 1 minute ▥, 5 minutes ▤, 10 minutes ⊞ and □ not treated (control)

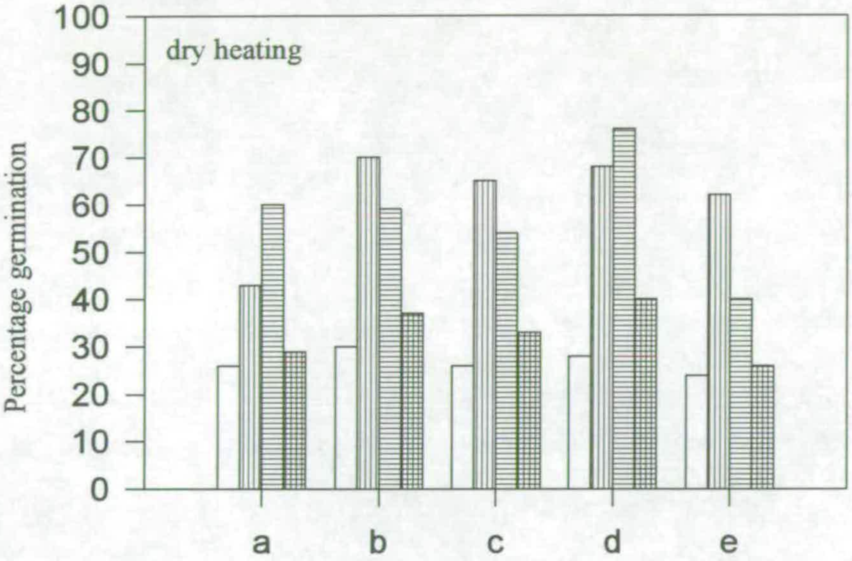


Figure 3.10: The final germination percentage of the seeds of *Acacia negrii* (a), *A. asak* (b), *A. seyal* (c), *A. ehrnbergiana* (d) and *A. tortilis* (e) which were treated by heating dry oven 80 °C for 1 minute ▥, 5 minutes ▤, 10 minutes ▦ and □ not treated (control)

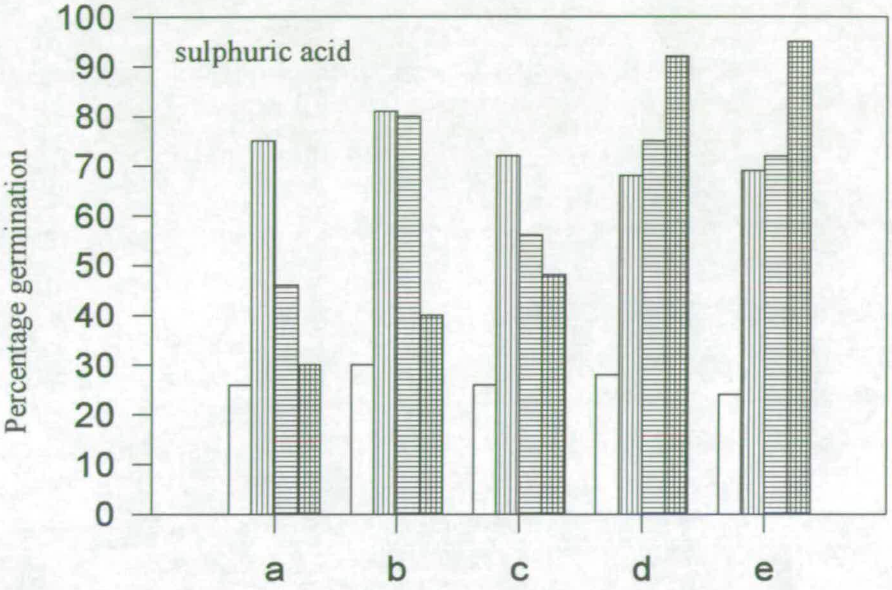


Figure 3.11: The final germination percentage of the seeds of *Acacia negrii* (a), *A. asak* (b), *A. seyal* (c), *A. ehrnbergiana* (d) and *A. tortilis* (e) which were treated by sulphuric acid for 10 minutes ▥, 20 minutes ▤, 40 minutes ▦ and ☐ not treated (control)

3.5 Discussion

Since survival of young seedlings of desert plants such as *Acacia* species is largely controlled by the environment, by temperature extremes and by uncertain rainfall it is important for germination of these plants to be controlled by precise perception of the environment (Koller, 1962; Kramer, 1983). One very common mechanism which regulates germination and contributes to survival of desert plants is the presence of a water-soluble germination inhibitor in the seeds or fruits of these plants. Minimal levels of precipitation are needed to leach them from of the seed and/or seedbed (Beadle, 1952; Koller, 1962). Dormancy and different methods of breaking dormancy have been extensively reviewed by Clement *et al.* (1977), Sadhu and Kaul, (1989); Misra and Singh, (1981). Dormancy could be due under-development of embryo, a hard seed coat or the presence of inhibitors. The results obtained from boiling water, sulphuric acid and dry heating of *Acacia negrii, A. asak, A. seyal, A. ehrnbergiana and A. tortilis* suggests that dormancy here is due to a hard and impermeable seed coat.

The most probable cause of inhibition of germination of these *Acacia* is their seed coat impermeability, which was overcome by pre-treatment by dry heating, hot water and sulphuric acid (Fig 3.4. 3.5, 3.6, 3.7 and 3.8). The untreated seeds which were soaked in distilled water for one hour did not show the swelling which is the sign of imbibition, while the treated seeds were imbibing when they were soaked in distilled water for ten minutes after the treatment. Delayed germination as a result of an impermeable seed coat is common in desert plants (Beadle, 1952; Koller, 1962), and ensures " dispersal in time ". It is the mechanism whereby some of the seeds of a species remain dormant to provide viable propagules for subsequent attempts at seedling establishment (Clemens *et al.*, 1977). One well-established characteristic of desert plants is their long-range distribution of germination through time, which increases their chance of survival under conditions which are extremely variable from year to year (Koller,1969). The hard thick testa of *Acacia* seeds contributes to their great longevity (Clemens *et al.*, 1977).

The scarification of the seeds of the five *Acacia* species by boiling water, sulphuric acid and dry heating are artificial methods of initiating germination. However, in nature, the permeability of the testa is increased by the exposure of the seeds to outdoor environmental factors. Koller, (1962) showed that temperature, relative humidity and modified outdoor environment affected considerably the seed coat permeability of the seeds *Mava aegyptia* and *Trigonella arabica,* two species with a high degree of seed coat impermeability. Work on these seeds suggested that high temperature combined with a high relative humidity in the environment would increase seed coat permeability and give rise to good crops of seedlings in some years (Koller, 1962).

The treatment by sulphuric acid for ten minutes released the *Acacia negrii* and *A. seyal* seeds from dormancy as shown by nearly 75 % germination (Fig 3.9); but prolongation of the treatment time resulted in progressive reduction in the germinability. A treatment time of 20 minutes released the seed coat dormancy of *Acacia asak* to give 80 % germination (Fig 3.9); prolonging the treatment time resulted in an increase in germination. For *Acacia ehrnbergiana* and *A. tortilis,* increased treatment time increased their germinability. The highest germination of 85% and 90% resulted from a treatment time of 40 minutes. These results agree with other studies conducted by Singh *et al.* (1990), who found 88% and 90% germination of *Acacia acuminata* and *A. adshrgens* respectively when treated by sulphuric acid. These results confirmed early findings obtained by Barton (1969) and Bebawi and Mohammed, (1985) who showed that sulphuric acid improved seed coat permeability of *Acacia.* Bebawi and Mohammed, (1985) obtained 84.4, 75.3 and 61.9% germination of *Acacia tortilis, A. ehrnbergiana* and *A. seyal* respectively following treatment in sulphuric acid. In nature, most hard-coated *Acacia* seeds become permeable to water when the seed coat is broken by passage through the digestive tract of animals causing it to crack (e.g Ahmed, 1986). Coughenour and Detling, (1986) reported that seedling populations of *Acacia tortilis* occur where seeds are defecated in goat and camel corrals. The goats and camels feed on the *Acacia* seeds and are responsible for the natural regeneration success in the natural environment, by making the seeds more permeable to water when the seed coat passes through the digestive tract.

The treatment by dry heating at 80 °C for 10 and 20 minutes released the seeds from dormancy in *Acacia negrii* and *A. ehrnbergiana,* as shown by nearly 60% germination (Fig 3.10); prolongation of the treatment time resulted in progressive reduction in the germinability. With treatment at 80 ° C for 10 minutes *Acacia asak, A. seyal* and *A. tortilis* undergo release of seed coat dormancy, as shown by 70% germination (Fig 3.10), Prolonging the treatment time resulted in a progressive increase in the germinability. These results agree with other studies conducted by Washitant (1988) and Shea *et al.*, (1979), who found 90 % and 80 % germination respectively in seeds of species treated dry heat (80 to 90 °C).

In another example the annual fires which occur throughout the dry grass savannah plain of Central Sudan break the testa of these *Acacia* seeds and make them ready for germination. Omar (1975) found the germination of five Acacia species was enhanced by heavy fire. El Amin (1976) noticed that the seeds of *Acacia seyal* germinate successfully only when there is a grassfire in the area; this he noted, breaks the seeds, testa and makes them ready for germination with coming rains. He adds that this fire effect most probably extends to the other *Acacia* in arid zone. Additional support was provided by Sabiiti and Wein, (1987) who found that high fire intensity in natural forest stimulates high seedling emergence of *Acacia siberiana.* At each effective dry heating temperature, the germinable seed fraction increased to the high percentage and then decreased with prolongation of the treatment while imbibed but ungerminated seeds steadily increased as the treatment was continued. There may be an optimal time for successful germination (Laude,1957). These results are very important in the region where the species grow, because the surface temperature of bare ground often rises to 60 to 70 °C during midday hours on clear days in spring or summer (Washitana, 1988). Thus a considerable proportion of seeds of the species should be able to become permeable while retaining their viability at such very high temperature (Warcup, 1980). Quinlivan (1971) found that daily fluctuating temperatures, with maxima between 30-60 °C at the soil surface, caused hard seeds of *Trifolium subterraneum, Lupinus cosentini* and *Medicago truncatula* to soften, provided the treatment was continuous for several weeks.

The treatment by boiling water for 1 and 5 minutes released dormancy of *Acacia negrii* and *A. asak* seeds, as shown by nearly 71 and 75 % germination respectively (Fig 3.11). Longer time in boiling water caused damage of the seeds thereby lowering the per cent germination. Treatment at 5 and 10 minutes, of *Acacia, A. seyal, A. ehrnbergiana* and *A. tortilis* released the seed coat dormancy as shown by 60, 79 and 61 % germination respectively (Fig 3.11). Prolonging the treatment time progressively increased germinability.

This observed relation of seed germination to treatment in boiling water agrees with the result of Sadhu and Kaul (1989) and Shea *et al.* (1979) who found that boiling water softens the stiff seed-coat, thereby increasing its permeability. Cheema and Qadir (1973) found *Acacia senegal* gave 68 % germination after a scalding of 1 minute and 30 % after three minutes. Danthu *et al.*, (1992) found *Acacia senegal* seeds were killed by even a brief scalding in boiling water for more than 5 seconds. The differing results may be explained by the different origin of the seeds and regional variation in seed coat characters.

Judging by the responses of the seed-coat to periods of exposure to the acid, boiling water and dry heating, it seems that, unlike *Acacia negrii*, the impermeability of the seed-coat of *A. ehrnbergiana* is due to the deposition of wax-like material within a comparatively thin testa. Judging by the permeability of the testa (control, Fig 3.9, 3.10, 3.11), it seems reasonable to suggest that in order to make the testa permeable to initiate germination, the time of exposure of the seeds to moist conditions is as follows: *A. ehrnbergiana* > *A. tortilis* > *A. seyal* > *A. asak* > *A. negrii.* It is of interest to note that the ranking in the permeability of the seed-coat is in agreement with the water demand of the five species and with the amount of water likely to be availabl in their habitats. The natural habitats of the species indicate that the order of the species, in relation to their demand for water, is: *Acacia negrii* (above 300 mm rainfall, elevation 2200 m a.s.l); *A. asak and A. seyal* (less than 150 mm rainfall with elevation 500 m a.s.l); *Acacia ehrnbergiana* and *Acacia tortilis* (rainfall between 70-50 mm); *A. negrii, A. asak and A. seyal* are associated with the wettest habitats and are apparently more water demanding and more sensitive to drought than the other two species (*A. ehrnbergiana and A. tortilis*), and seem to possess the most permeable testas. These require a shorter period of wet conditions than the other two species for the seeds to become permeable and to germinate. Thus the impermeability of the testa restricts the seed germination to the time when abundant water is available and may be restricting the distribution of the species to the habitats which normally receive abundant water so that subsequent successful seedling establishment is possible. These findings seem to agree with those of Mohmoud, (1977) for other *Acacia* species. It is worth mentioning that the rapid germination of the seed of these *Acacia,* when the appropriate environmental conditions are available, is of obvious survival value in arid areas where initial rate of root penetration may be critical. Even with successfully germinated seeds, the establishment of the seedlings strongly depends on the duration of the short rainy season which provides favourable conditions for growth.

In the arid region such as Saudi Arabia, the soil surface tends to dry rapidly during the dry spells following the infrequent rains, and the rate of germination and initial growth can be a critical factor in the success or failure of seedlings. In particular, the rate of a seedling's root elongation and its penetration into the deeper layers of the soil, where moisture is retained longer against evaporation, often determines whether the seedling will win or lose its race against the drought, and thus whether it will thrive or die. This point will be discussed in the next chapters.

It is recommended that in experiments like this, a single level of treatment must not be used, as this will give misleading results. Different levels of each treatment should be applied. Thus, different pre-germination treatments should be designed to vary the exposure to boiling water, dry heating and sulphuric acid. Although this has been adopted in most work, I am suggesting a more rigorous approach. Perhaps if more levels had been used in the present experiment different results would have been found.

3.6 Conclusions

Acacia species (*A. negrii, A. asak, A. seyal, A. ehrnbergiana* and *A. tortilis)* from different environments along an elevation gradient in South west of Saudi Arabia showed different patterns of germination.

1. The poor germination found in untreated seeds may be attributed mainly to the impermeability of the seed coats to water and gases. It is recommended that seed coat of *Acacia negrii, A. asak, A. seyal, A. ehrnbergiana* and *A. tortilis* be specially treated before sowing.

2. The germination of *Acacia negrii, A. asak* and *A. seya* is increased by pre-germination treatment with boiling water, dry heat or sulphuric acid, but prolongation of the treatment results in progressive reduction in the germinability.

3. Concentrated sulphuric acid is easily available but requires careful handling. Therefore, for practical purposes the use of hot water and dry heat are recommended,.

4. Seeds of *Acacia* species germinate easily in the laboratory following pre-treatment at temperatures of 80 °C for 10 and 20 minutes.

5. The present study emphasises the need to standardise the pre-germination treatment for each species in order to get high germination value in the species.

CHAPTER 4

The Effect of Water Stress on the Water Relations *Acacia negrii, A. asak* and *A. ehrnbergiana*

4.1 Introduction

In the arid regions the essential requirements for seedling establishment and growth in the physical environment are availability of moisture and nutrients and a suitable soil medium for the growth of the root and mechanical support of the plant (Evenari *et al.*, 1971; Solbrig, 1977). In silviculture, these factors can be modified to some extent by choice of the proper type and time of cultivation, and elimination of competition between seedlings for better conservation and utilisation of available moisture and nutrients. Parker and Pallardy, (1988) reported that the species composition of a plant community is controlled by microclimatic and edaphic factors which characterise a given site, and the genetic potential of local species for growth and survival under prevailing environmental conditions (Abrams, 1988). Species abundance along soil moisture gradients may differ greatly according to the water relations of each species (Whittaker, 1975; Kramer, 1983; Sobrado, 1983). Drought adaptation to tolerate protoplasmic dehydration (Hsiao *et al.*, 1976; Kramer, 1983), has been closely related to species distribution (Hinckley *et al.*, 1983; Kramer, 1983; Kozlowski *et al.*, 1991).

Hsaio, (1973) indicated that under water stress the water relation characteristics of leaves may be modified to enable them to withstand a lower tissue water deficit. High levels of osmotic solutes can accumulate in some species when exposed to water stress (Parker and Pallardy, 1988; Turner, 1986). This mechanism is known as osmotic adjustment and it has been reported to increase the capacity of a particular species to withstand water deficit (Parker, 1968). By the increasing of solutes in the symplast, turgor can be maintained at low tissue water potential (Turner, 1978). This is of great importance, as low water potential enables the plant extract water from dry soil (Turner, 1980). The maintenance of turgor is vital for cell expansion (Jones and Rawson, 1979; Turner, 1986; Khalil and Grace, 1992), and consequently for root growth (Sharp and Davies, 1979). As the solutes accumulate there is often an increase in cell wall thickness and a reduction of cell size (Cutler *et al.*, 1977; Rascia *et al.* (1990). Water deficit reduces leaf production (Khalil and Grace, 1992) and leaf expansion rate and stem elongation (Metcalfe, *et al.*, 1990).

It is widely accepted that the growth and stomatal conductance of plants are affected by water deficit. Stomatal sensitivity to water stress has been proposed to be an important component of drought resistance in trees (Kelliher *et al.*, 1980). As soil dries, the soil and root water potential falls leading to a decline in leaf water potential and, it has been presumed, a consequent closure of stomata (Turner, 1974; Quraishi and Kramer , 1970; Kramer, 1988). In some studies the plant response to soil drying reveals that stomatal closure can occur before any change in shoot water is detected, for example as reported in a field study of cow-pea (Bates and Hall, 1981). Hsiao *et al.*, (1976) reported that stomata in *Brigalow* phyllodes apparently remain partly open even at water potential as low -5 MPa. More recently it has become clear that leaf conductance is more strongly correlated with soil water content than with leaf potential, and this realisation has forced a reappraisal of concepts of stomatal regulation under field condition (Davies and Zhang, 1991). This response of stomata to soil drying is thought to be based on a chemical signal ascending from the root to the leaves and leads to the closure of stomata in direct relation to the level of the soil water stress (Davies and Zhang, 1991; Khalil and Grace, 1992).

The trees of *Acacia* are able, during the period of drought, to gradually shed their leaves and replace them with smaller new leaves (Evenari *et al.*, 1971; Migahid, 1978). A wide range of adaptations exist to counter water deficit. In natural plant communities many of these mechanisms appear to be more important for plant survival than for high productivity (Turner, 1981), but a number do appear to confer advantage for improved production under conditions of drought and therefore may be useful in increasing crop productivity when water shortages prevail (Turner, 1979; 1986).

Because recurrent drought is a feature of arid environments, vegetation must be able to cope with such stress to provide stable communities (Solbrig *et al.*, 1977) *Acacia* species such as *A. ehrnbergiana, A. asak* and *A. negrii* are successful species in the relatively dry area of South western Saudi Arabia. Little is known about how these species survive an annual six-month drought (May-September).

The following experiment compares the effect of water stress on the water relations of *Acacia* seedlings from different ecological zones, sea level, 500m and

2200m. An understanding of the water relation characteristics of *Acacia* species with regard to their geographical distribution is important for the future selection of drought hardy species. It can be hypothesised on the basis of distribution, that the species will show a ranking of drought tolerance as follows: *Acacia ehrnbergiana* most tolerant > *A. asak* > *A. negrii*.

4.2 Material and Methods.

4.2.1 Plant material and design of the experiment

In January 1993 more than 400 *Acacia* seeds (*A. negrii*, *A. asak* and *A. ehrnbergiana*) were germinated in the glasshouse at the Institute of Ecology and Resource Management, The University of Edinburgh. Seedlings at the two leaf stage were transplanted into small pots 6 cm diameter and 10 cm depth, containing a mixture of loam, sand, and peat compost in the ratio 1:2:1 by volume. An additinal supply of nutrents came from ENMAG fertiliser (see appendix 7) (600 g) and 300 g of finely-ground calcium bicarbonate were mixed thoroughly per 100 litres of soil. The pH of the compost was 7.0-7.5. Seedlings were kept on the glasshouse bench, under a natural photoperiod of 11-14 h, with mean temperature 25 °C (it is the minimum during growth season in their native region). While in the glasshouse, seedlings were watered daily to field capacity. Four months later, 100 plants were selected for vigour and transplanted to a glasshouse under natural light.

These plants were transplanted into soil columns containing the compost, to allow relatively unrestricted root growth. Each column contained one seedling. Each column was 60 cm long and 16 cm diameter, and contained in a 70 cm long black polythene tube, perforated at its base and on its walls at 10 cm intervals from the base to the middle of the tube to allow free drainage and aeration of the soil. Tubes were packed with soil to a uniform bulk density. During establishment, irrigation was carried out every other day.

After a few weeks 20 seedlings were selected for each of the three species. They were selected on the basis of similarity in vigour and height, and half were randomly assigned to the water stress (WS) treatment whilst the other half were designated well watered (WW) control. Water was withheld from WS plants until the end of the experimental period (11 weeks).

The WW plants were watered every other day to field capacity. Approximately every week, starting from day one, measurements were made of stomatal conductance, leaf water potential and soil water content. All measurements were made between 11.00 - 16.00 h.

4.2.2 Microclimate

The microclimate was uncontrolled in the glasshouse. To show the variation of conditions during the experimental period, the photosynthetic photon flux density incident inside glassnhouse, temperature, and vapour pressure deficit were measured every 15 s, and five minutes the means were recorded on a data logger (CR 21x, Campbell Scientific Ltd. Leicestershire, UK). The vapour pressure deficit (δe) was calculated as:

$$\delta e = e_s\ (T_a)\text{-}e$$

where e_s (T_a)= saturation vapour pressure (kPa) at T_a, and e =actual vapour pressure (kPa) given by:

$$e = e_s(T_w) - \gamma(T_a - T_w)$$

where e_s (T_w)= saturation vapour pressure (kPa) at T_w, and γ = psychrometric 'constant', taken as 0.08 kPa $°C^{-1}$ for the unaspirated 'wet-bulb'. 'Dry-bulb' temperatures T_a and 'wet-bulb' temperatures T_w were measured.

Hourly averages were obtained as an average of readings recorded at 5 minute intervals. These data were recorded for a period of 66 days from the beginning of the experiment to the end of the drying cycle.

4.2.3 Soil water content

Soil water content was measured as follows. Three of the experimental tubes (60 cm lengths and 16 cm diameter) were prepared for determination of soil water content at field capacity. They were watered until runoff occurred. The tubes were covered by black polythene, to prevent evaporation and left for 24 hours to drain .

Each column was opened and divided into three horizontal layers (20 cm length) and subsampled for determination of soil water content as percentage of oven dry weight (80 °C, 48 h). Further subsamples were taken to measure mean bulk density of each layer. Columns were sectioned into 20 cm layers and weighed after oven drying at 105 °C for 72 h. Subsequently, during each measurement, three random samples from each treatment, for determination of gravimetric water content of each 20 cm soil layer were taken from each treatment by removing 2 cm diameter cores from the midpoint of each layer. The holes were then refilled with compost and sealed. Gravimetric determinations were converted to volumetric water content by multiplying by the bulk density, assuming that the density of water is 1.0 g cm^{-3}.

Table 4.1 : The mean soil water content at field capacity (SWC = volume of water per unit volume of soil), and the mean bulk soil density (BD = weight of soil per unit volume of soil) of the different soil layers measured downwards from the soil surface. Values are means of four replicate ± standard error.

Soil layer (cm)	SWC (cm^3 cm^{-3})	BD (g cm^{-3})
0-20	0.28± 0.04	1.06± 0.03
21-40	0.32± 0.03	1.15± 0.04
41-60	0.40± 0.02	1.19± 0.02

4.2.4 Stomatal conductance

Measurements of surface conductance were made using a steady-state null-balance porometer (LI 1600, Li-cor Inc. Lincoln, Nebraska, USA). The most recent fully expanded leaf was measured. Eight seedlings of each species were measured between 11.00-16.00 h. The porometer was allowed for about 30 minutes to equilibrate to the glasshouse ambient condition.

4.2.5 Leaf water potential

On finishing the measurement of stomatal conductance, four leaves from each treatment were measured for water potential. A newly expanded leaf was detached from the shoot and placed within a humidified pressure chamber (Scholander *et al.*, 1964), with the cut end protruding from the chamber. The pressure was then applied until water appeared at the cut surface. This is termed the balancing pressure and is considered to be equal in magnitude, but opposite in sign, to the shoot water potential (Scholander *et al.* 1964; Tyree and Hammel, 1972).

4.2.6 Pressure volume curve

Water relations characteristics of the leaves were determined using the pressure-volume technique (Tyree and Hammel, 1972,). This technique reveals the relationship of the component of water potential to the gravimetric water content of the leaf or other tissue at eleven weeks. As it has been describe of many times in textbooks (e.g. Jones, 1992) we need not describe it again here. The procedure was followed from Richie and Roden (1985) and Khalil and Grace (1992). In the late evening preceding the day of measurement, the shoots were severed from both droughted and watered plants and recut under water, and left to resaturate overnight in distilled water in a cool and dark room for 12 hrs. Before measurement the twig was weighed and immediately placed in a pressure chamber (SKPM 1400, Sky, UK). The initial balance pressure was determined; it varied between 0.08 and 0.18 MPa. Then, an over pressure of 0.6 MPa was applied and held for 4-10 min to force water out of the shoot. The sap was collected in preweighed plastic tubes filled with dry tissue paper fitted over protruding petiole. After 5-10 min, the tubes were removed and immediately reweighed. Pressure was increased by 0.3 MPa, held for approximately 2 min, and then a new balance pressure was determined.

This procedure was repeated many times until three or four data points were obtained on the linear portion of the pressure-volume curve. Shoots were oven-dried at 80°C for 48 hours and weighed to determine dry weight. The relative water content (R*) at each water potential value was calculated as

$$R^* = \frac{\text{fresh weight - dry weight}}{\text{saturated weight - dry weight}}$$

At the end of the experiment, osmotic potential at zero turgor (π_0), osmotic potential at full turgor (π_{100}), relative water content at zero turgor (R_0) and bulk modulus of elasticity (E) were determined by pressure-volume analysis of four well-watered and four water stressed seedlings.

The data obtained were used in a computer program for analysis of pressure-volume analysis (Todd Dawson, personal communication, modified from the work of Schulte and Hinckley 1985). The program handles the otherwise time-consuming task of plotting the graphs and evaluating the parameters.

4.2.7 Leaf production and increase in stem length

The stem length of a typical shoot, developed from node of the main stem was measured. Measurements of the new number of leaves were made on four plants of control and treatment plants of each species (n= 4). Increase in stem length was calculated by subtracting the initial length from lengths measured subsequently.

4.2.8 Dry matter

Harvests were made on the day before imposing treatments, Day 66. Above-ground and below-ground biomass was separated into leaf, stem, and roots. Leaf area was determined by using the leaf area meter (Model - CI 201, Portable Area Meter, CID, Inc, Moscow, U.S.A). Leaf, stem and root material were then dried at 80 °C for dry weight determination.

4.2.9 Data analysis

Mean and standard errors were calculated and presented in the form of graphs. The growth data were analysed using ANOVA. Procedures on SAS and MINITAB packages enabled calculation of least significant difference (LSD).

4.3 Results

4.3.1 Microclimate

During the 66 days period of the *Acacia* species experiment, the range of mean photosynthetic photon flux density (PPFD) was between 190 μmol $m^{-2}s^{-1}$ and 800 μ mol $m^{-2}s^{-1}$. The temperature range was 17 °C to 25 °C. Vapour pressure deficit (kPa) was 0.5 kPa minimum and 2.5 kPa maximum (Fig 4.1).

4.3.2 Soil water content

Witholding water, and permitting rapid water loss from the soil column by evapotranspiration, soon resulted in reductions of soil water content in the upper 15 cm depth of the unwatered soil column for all three species (Fig 4.2, 4.3 and 4.4). After the second week, the decline of soil water in the second layer (35 cm depth) was statistically significant for *Acacia negrii* and *A. ehrnbergiana* (Fig 4.2 and 4), but it was insignificant in the soil column with *Acacia asak* plants (Fig 4.3).

4.3.3 Stomatal conductance

With progressive drying of the top layer of the soil column there was a gradual decline of stomatal conductance ($P<0.05$) in *Acacia negrii*, *A. ehernbergiana* and *A. asak*, although some of their root system had access to the lower moist soil layer. The stomatal conductance of treated plants was equal to that of the control plants on week three of the drying period for all species (Fig 4.2, 4.3 and 4.4), but thereafter declined and approached zero at 12 weeks when the experiment was terminated. With all three species there was linear relationship between stomatal conductance and soil water content (the average of all three depths) and leaf water potential (Fig 4.6, 4.7 and 4.8). The relationship was stronger with soil water content than with leaf water potential.

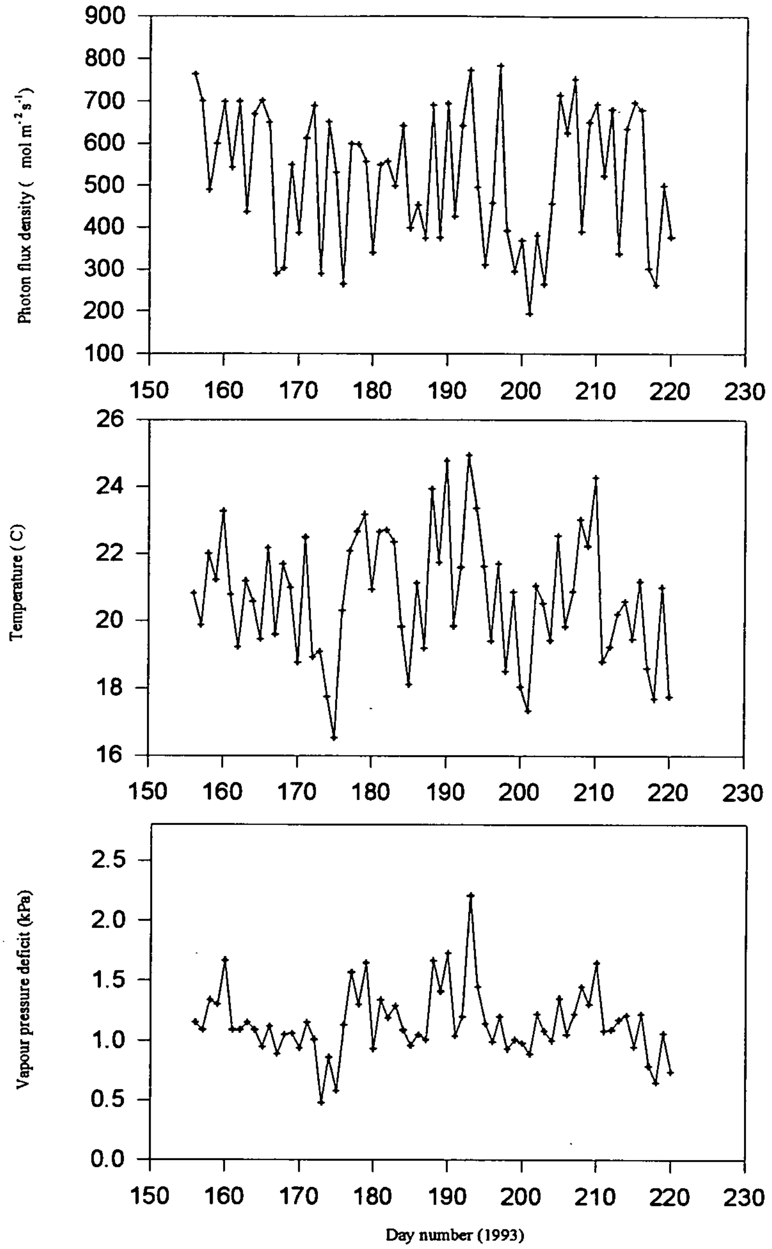


Figure 4.1: Mean photosynthetic photon flux density, temperature, and vapour pressure deficit between 12:00 and 15:00 hrs over a period of 66 days, from the begining of the drying cycle to the end drying cycle.

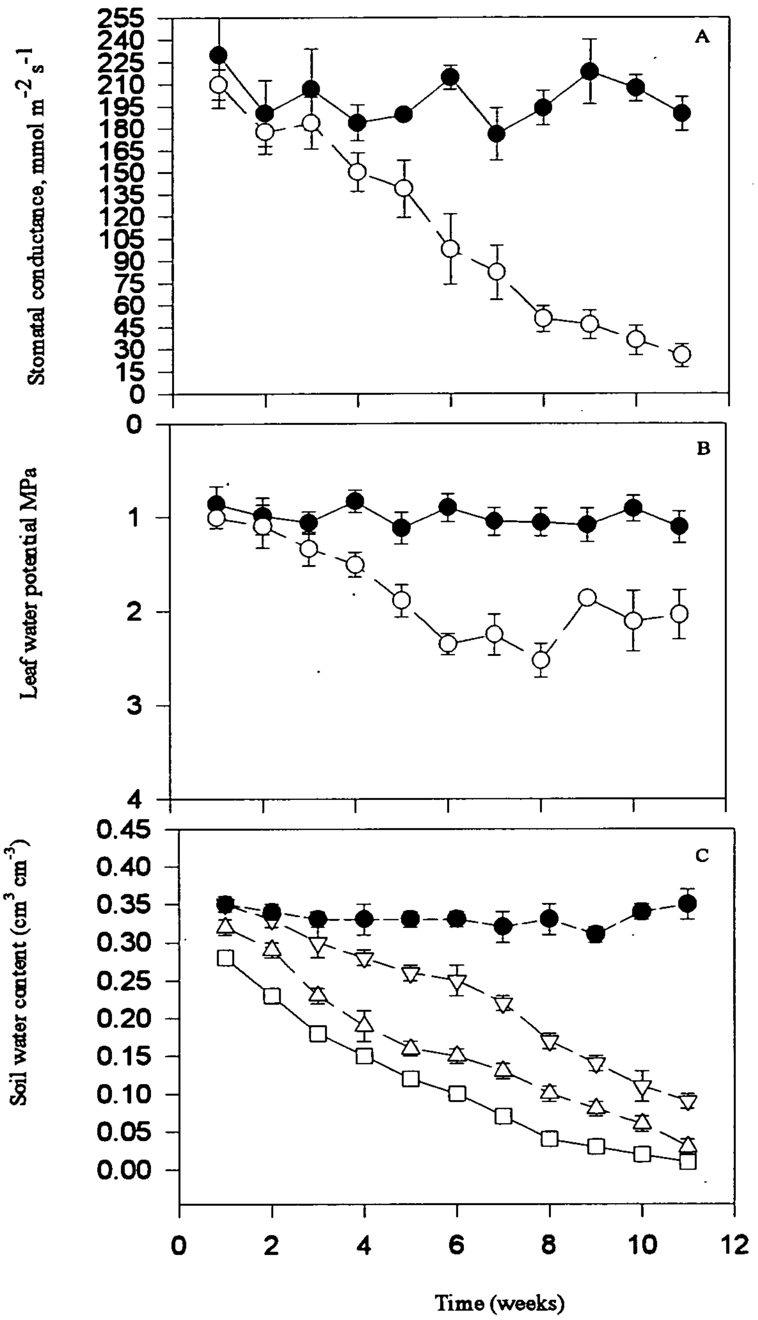


Figure 4.2: Change with time in (A) stomatal conductance and (B) leaf water potential during soil drying for *Acacia negrii* (n=4) of watered (●), and stressed (O) plants. C. Soil water content of three layers (□) depth 15 cm, (Δ) depth 35 cm, (∇) depth 55 cm and control average of all depths (●). Points are means ± standard error.

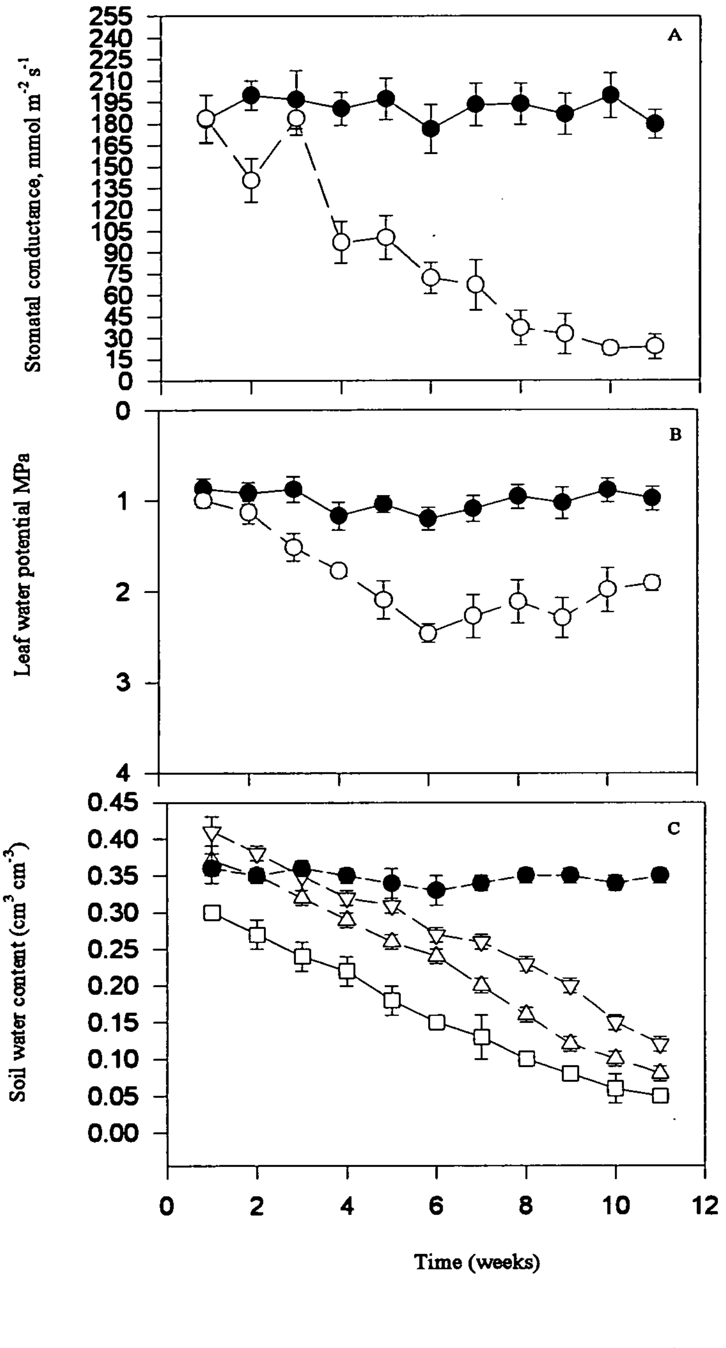


Figure 4.3: Change with time in (A) stomatal conductance and (B) leaf water potential during soil drying for *Acacia asak* (n=4) of watered (●), and stressed (O) plants. C. Soil water content of three layers (□) depth 15 cm, (Δ) depth 35 cm, (∇) depth 55 cm and control average of all depths (●). Points are means ± standard error.

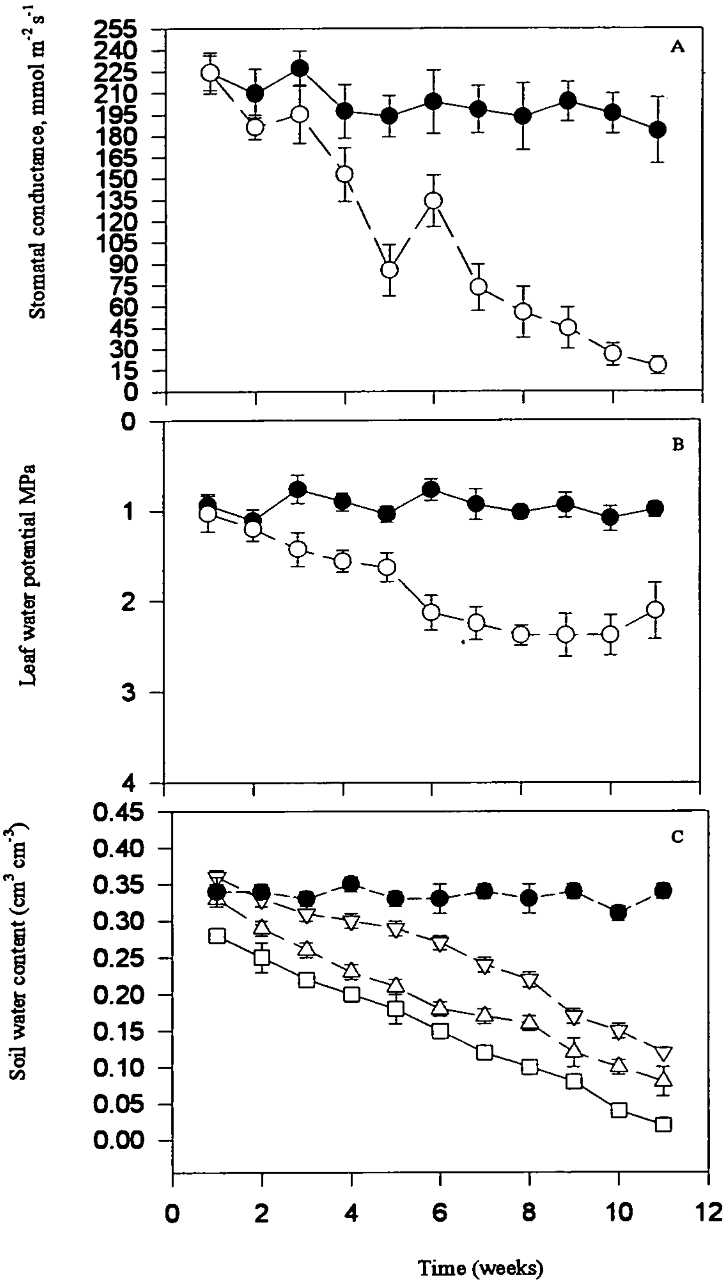


Figure 4.4: Change with time in (A) stomatal conductance and (B) leaf water potential during soil drying for *Acacia ehrnbergiana* (n=4) of watered (●), and stressed (O) plants. C. Soil water content of three layers (□) depth 15 cm, (Δ) depth 35 cm, (∇) depth 55 cm and control average of all depths (●). Points are means ± standard error.

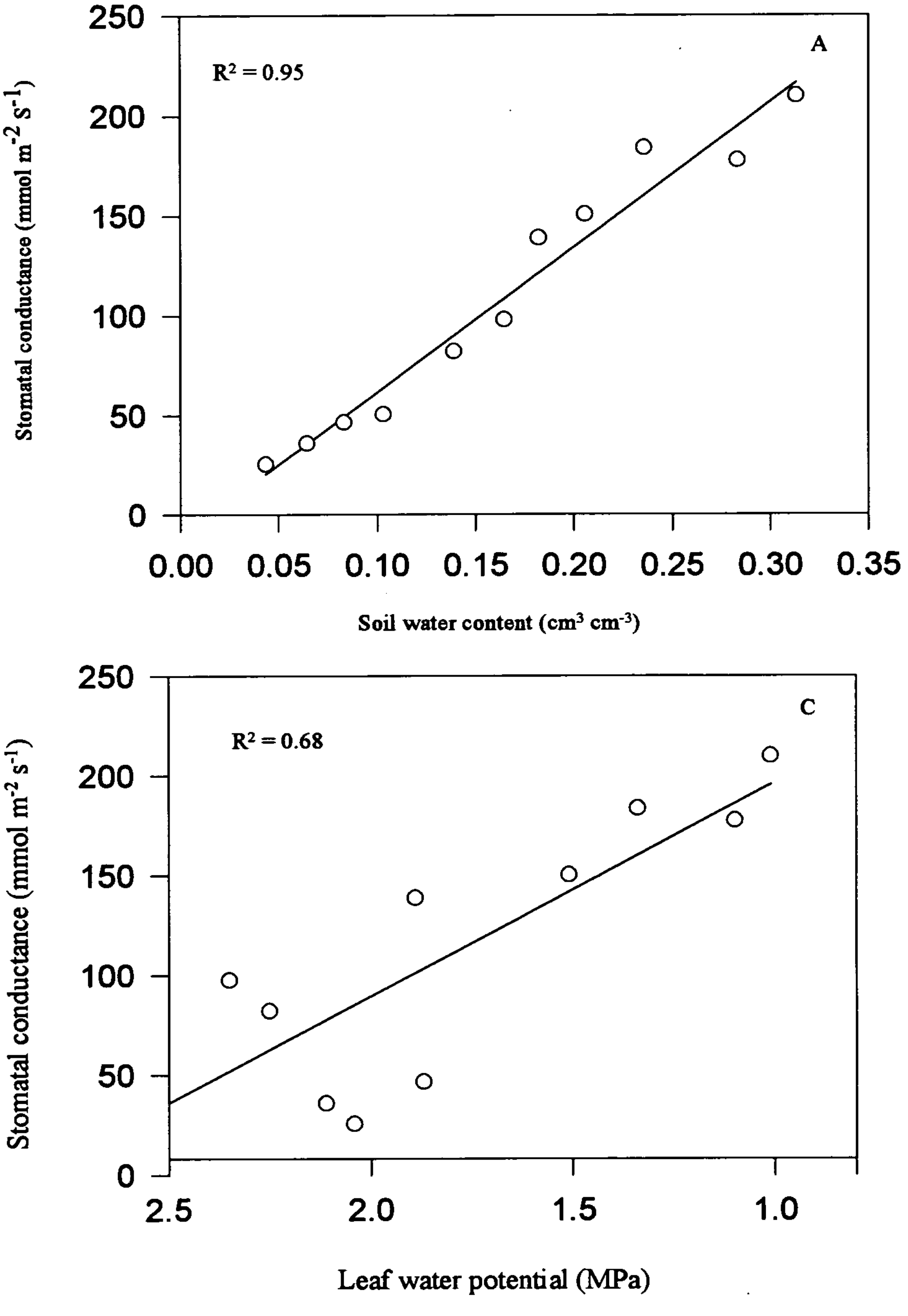
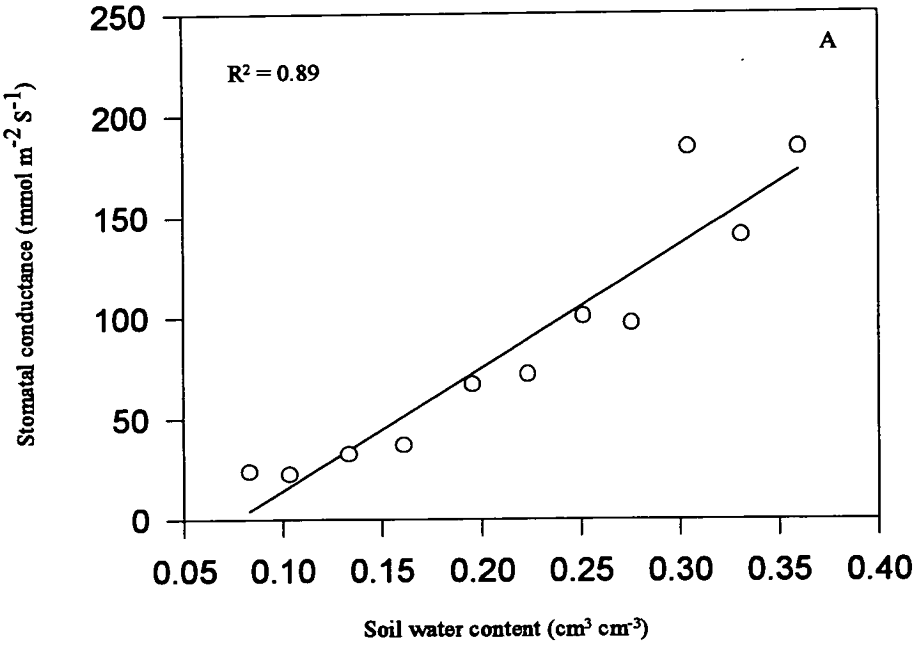


Figure 4.5: A relationship between stomatal conductance and soil water content (A) and leaf water potential (B) of water-stressed seedlings of *Acacia negrii*.



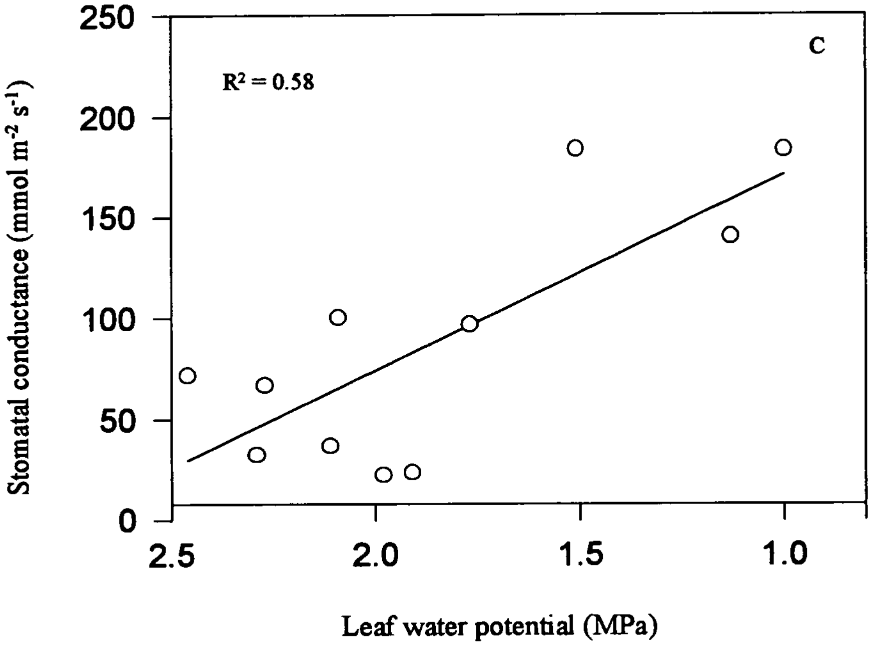


Figure 4.6: A relationship between stomatal conductance and soil water content (A) and leaf water potential (B) of water-stressed seedlings of *Acacia asak*.

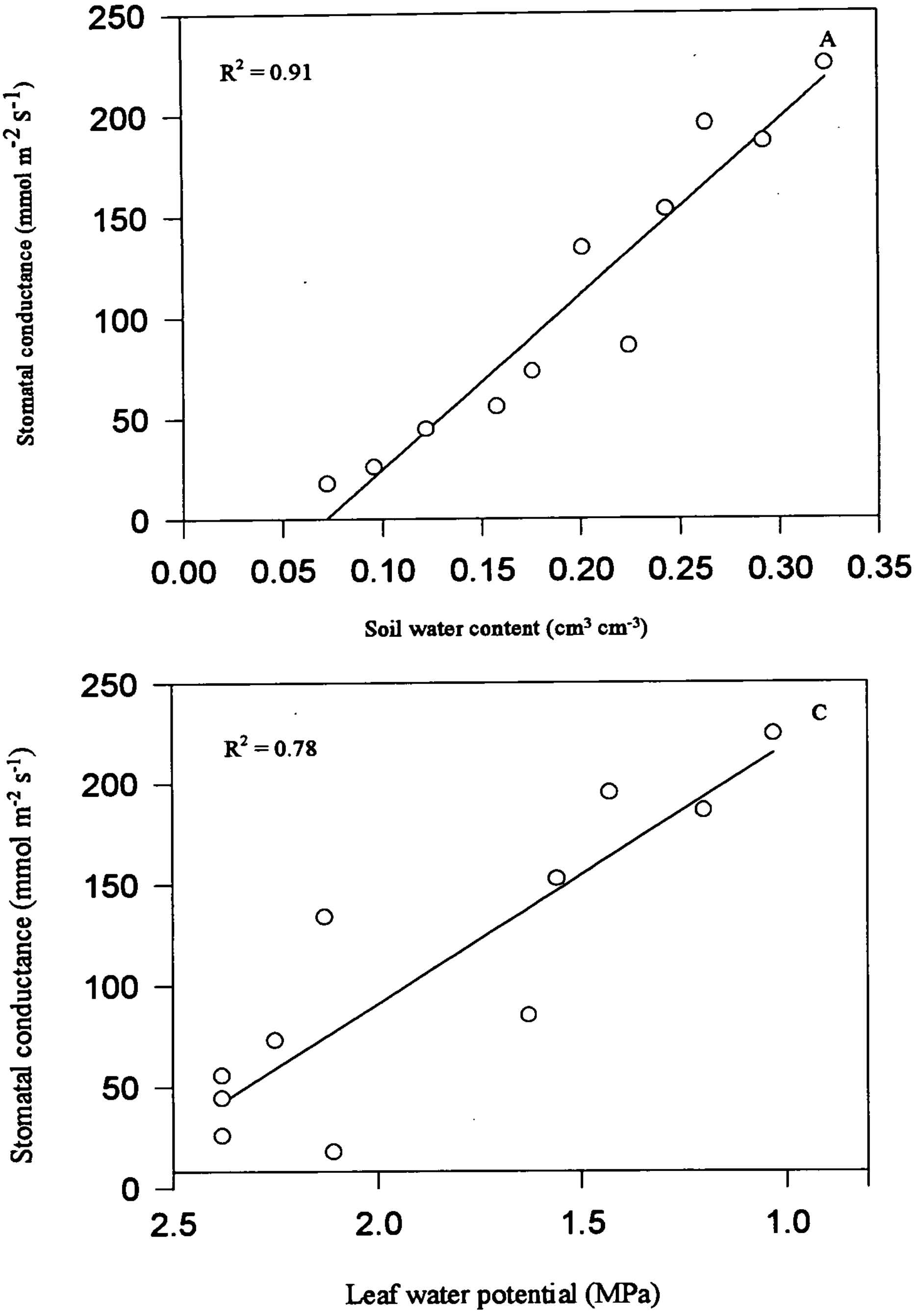


Figure 4.7: A relationship between stomatal conductance and soil water content(A)and leaf water potential (B) of water-stressed seedlings of *Acacia ehrnbergiana*.

4.3.4 Leaf water potential

Both stomatal conductance and leaf water potential declined in all three species during the period following the initial decline of soil water content. With further decline in soil water content (weeks 7-11) stomatal conductance declined further though the leaf water potential increased (less negative) to that of the control plant (see Fig 4.2, 4.3 and 4.4).

The leaf water potential of the stressed seedlings showed no significant response to water stress until week 3 for *Acacia asak* and *A. ehrnbergiana* and week 4 for *A. negrii*. At the end of the experimental period there was highly significant ($P<0.001$) relationship between treatment and species. A linear relationship was found for all three *Acacia* species between stomatal conductance and leaf water potential (Fig 4.5, 4.6 and 4.7)

4.3.5 Pressure-volume analysis of leaf

The water relations characteristics of *Acacia negrii, A. asak* and *A. ehrnbergiana* twigs changed during the period of drought (Table 4.2). Drought significantly reduced osmotic potentials by 0.39 MPa and 0.73 MPa and 0.48MPa and 0.75 MPa for *Acacia asak* and *Acacia ehrnbergian* at full and zero turgor pressure respectively. Similary, reduction were 0.16 MPa and 0.28 MPa for *Acacia negrii* at full and zero turgor pressure respectively.

This reduction indicates significant osmotic adjustment within the plants. Unwatered plants displayed a significant increase ($P< 0.05$) in the bulk modulus of elasticity (E) and a significant increase ($P< 0.05$) in the leaf weight to turigd weight ratio for all species. Elastic modulus of water stressed plants increased substantally in all species (Table 4.2). This increase in bulk modulus of elasticity (E) and dry weight/turgid weight ratio suggested that leaves of water stressed seedlings may have undergone structural acclimation.

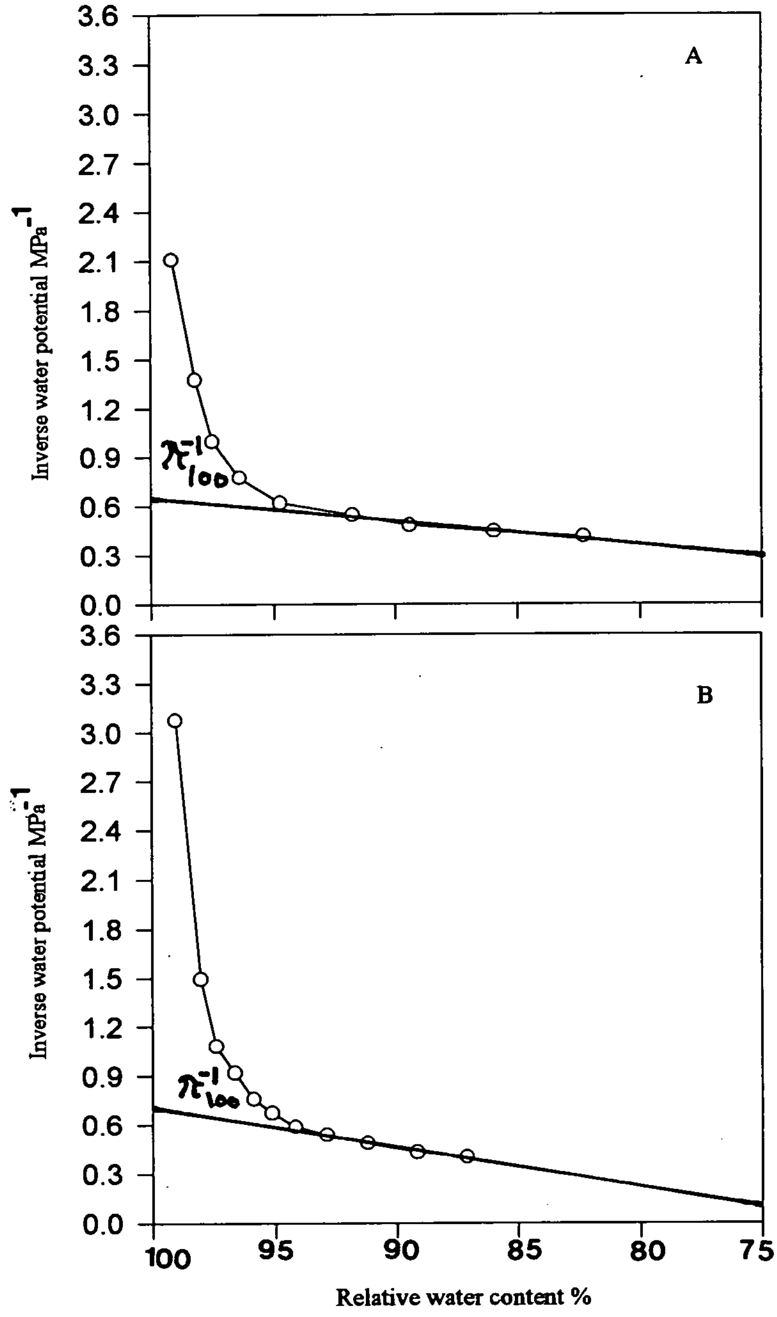


Figure 4.8: Pressure-volume curve for median twigs from *Acacia negrii*, watered (A) and stressed seedling (B). Extrapolation of the linear portion to the ordinate gives an estimate of the inverse osmotic potential at full turgor ($\pi_{100^{-1}}$), and to the abscissa, yields the relative apoplast water content. Turgor loss point is the relative water content where the curve turns linear; and ($\pi_{0^{-1}}$) is the inverse osmotic potential at zero turgor. The elastic modulus *E* is found the curvature as described by (Tyree and Jarvis, 1982).

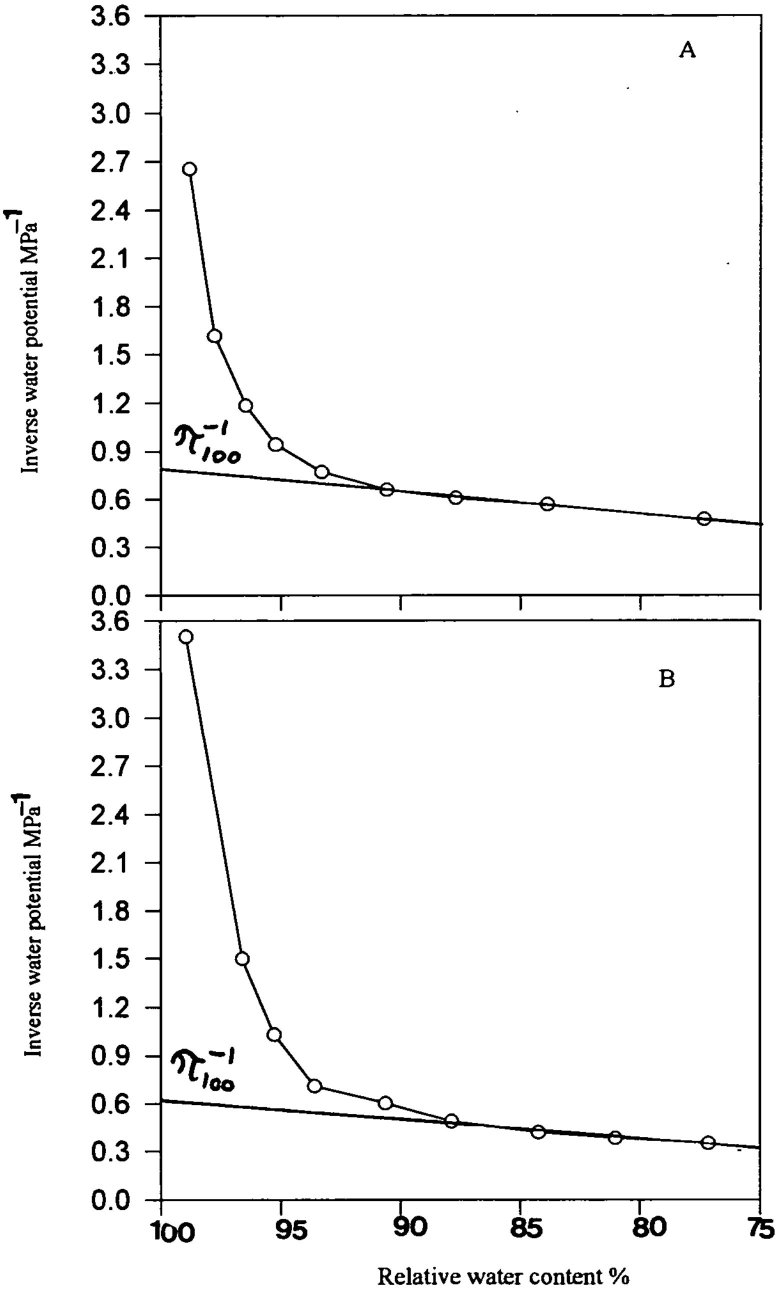


Figure 4.9: Pressure-volume curve for median twigs from *Acacia asak*, watered (A) and stressed seedling (B). Extrapolation of the linear portion to the ordinate gives an estimate of the inverse osmotic potential at full turgor ($\pi_{100^{-1}}$), and to the abscissa, yields the relative apoplast water content. Turgor loss point is the relative water content where the curve turns linear; and ($\pi_{0^{-1}}$) is the inverse osmotic potential at zero turgor. The elastic modulus *E* is found the curvature as described by (Tyree and Jarvis, 1982).

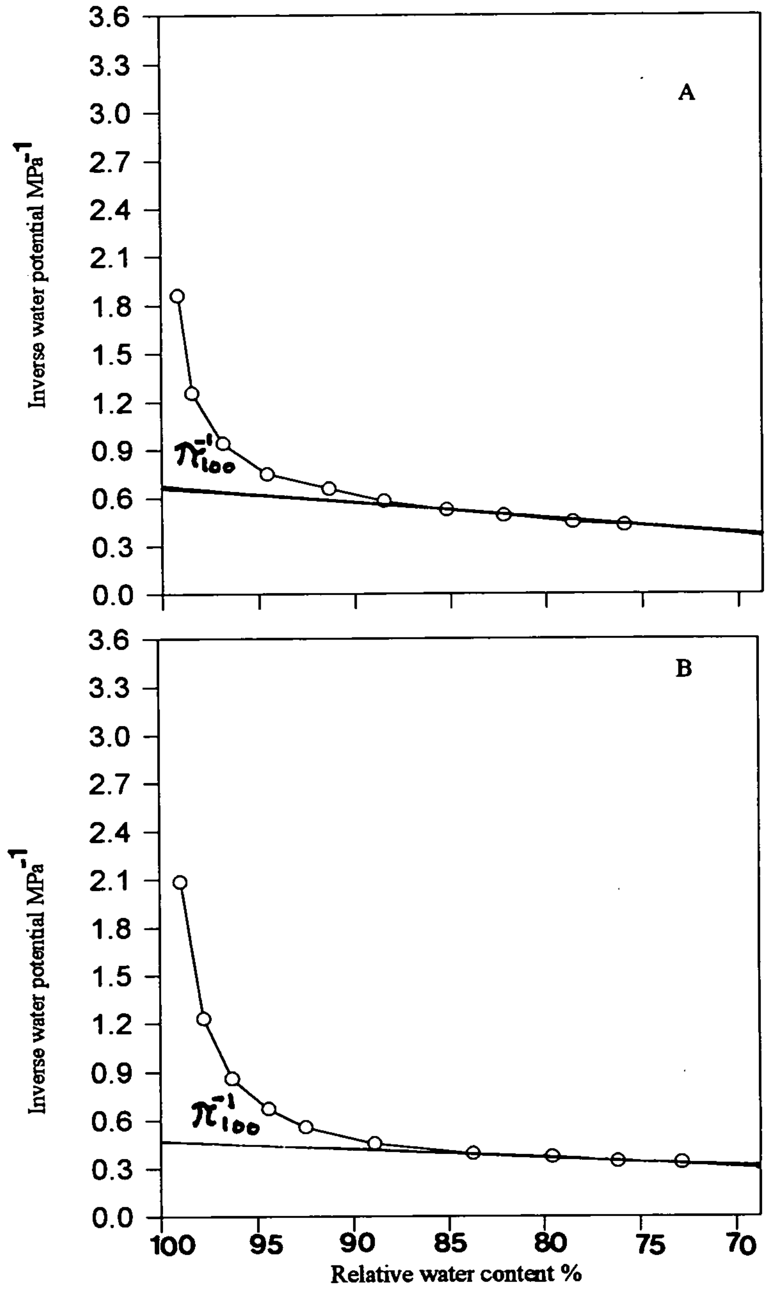


Figure 4.10: Pressure-volume curve for median twigs from *Acacia ehrnbergiana*, watered (A) and stressed seedling (B). Extrapolation of the linear portion to the ordinate gives an estimate of the inverse osmotic potential at full turgor ($\pi_{100^{-1}}$), and to the abscissa, yields the relative apoplast water content. Turgor loss point is the relative water content where the curve turns linear; and ($\pi_{0^{-1}}$) is the inverse osmotic potential at zero turgor. The elastic modulus *E* is found the curvature as described by (Tyree and Jarvis, 1982).

Table 4.2: Effects of water stress on tissue water relation parameters derived from pressure-volume analysis of three *Acacia* species twigs.

Osmotic potential at full turgor (π_{100}), osmotic potential at zero turgor (π_0), relative water content at zero turgor (R_0), bulk modulus of elasticity (E), and dry weight/turgid weight ratio (DW/TW) of leaves, of well watered and water stressed seedling. Value are means of four determinations ± standard error. Comparison of means is by one-tailed t-test with 6 degrees of freedom.

Acacia asak

Variables	**Unwatered**	**Watered**	**t**	*P*
π_{100} (MPa)	-1.81±0.11	-1.42 ±0.06	3.15	0.009
π_0 (MPa)	-2.33 ±0.09	- 1.60 ±0.07	6.25	0.0008
R_0 %	72.25 ±3.01	82.25±5.17	1.66	0.07
E (MPa)	10.12 ±1.5	6.03±0.01	2.49	0.02
DW/TW ratio	0.33 ±.01	0.30 ±0.01	3.07	0.01

Acacia ehrnbergiana

Variables	**Unwatered**	**Watered**	**t**	***P***
π_{100} (MPa)	-1.93±0.24	-1.43 ±0.04	2.02	0.04
π_0 (MPa)	-2.30±0.2	-1.55±0.2	2.9	0.01
R_0 %	80.5±0.96	82.25±3.42	0.49	0.32
E (MPa)	9.27±1.5	6.83±3.42	2.16	0.03
DW/TW ratio	0.32±0.003	0.29±0.006	4.2	0.002

Acacia negrii

Variables	**Unwatered**	**Watered**	**t**	***P***
π_{100} (MPa)	-1.73±0.08	-1.57 ±0.02	1.8	0.05
π_0 (MPa)	-2.13±0.12	-1.85±0.06	2.04	0.04
R_0 %	83.0±1.5	87±1.5	2.37	0.02
E (MPa)	13.04±1.07	9.34±1.54	2.03	0.04
DW/TW ratio	0.33±0.02	0.28±0.01	1.98	0.04

The original pressure-volume curves for the median twigs from watered and stressed seedlings are shown in Figure 4.8, 4.9 and 4.10 and respectively. These curves effectively represented the changes in the water potential components as a consequence of the drying cycles.

4.3.6 Leaf production and increase in stem length

Compared to the control plants, stem elongation of the treated plants decreased significantly with progressive soil drying. The stem elongation rate of these seedling differed significantly ($P<0.05$) from controls (Fig 4.11). This figure shows mean height (cm) for the stems during the course of the experiment. Evidently, the stem of the control seedlings continued increasing in length until the end of the measurement. For the stressed seedlings the stem elongation continued until the sixth week, eighth week and ninth week for *Acacia negrii*, *Acacia asak* and *Acacia ehrnbergian* respectively. The development of new leaves was parallel to stem elongation, so that water stressed seedlings had 20% and 30% fewer leaves than the controls by the end of the experiment.

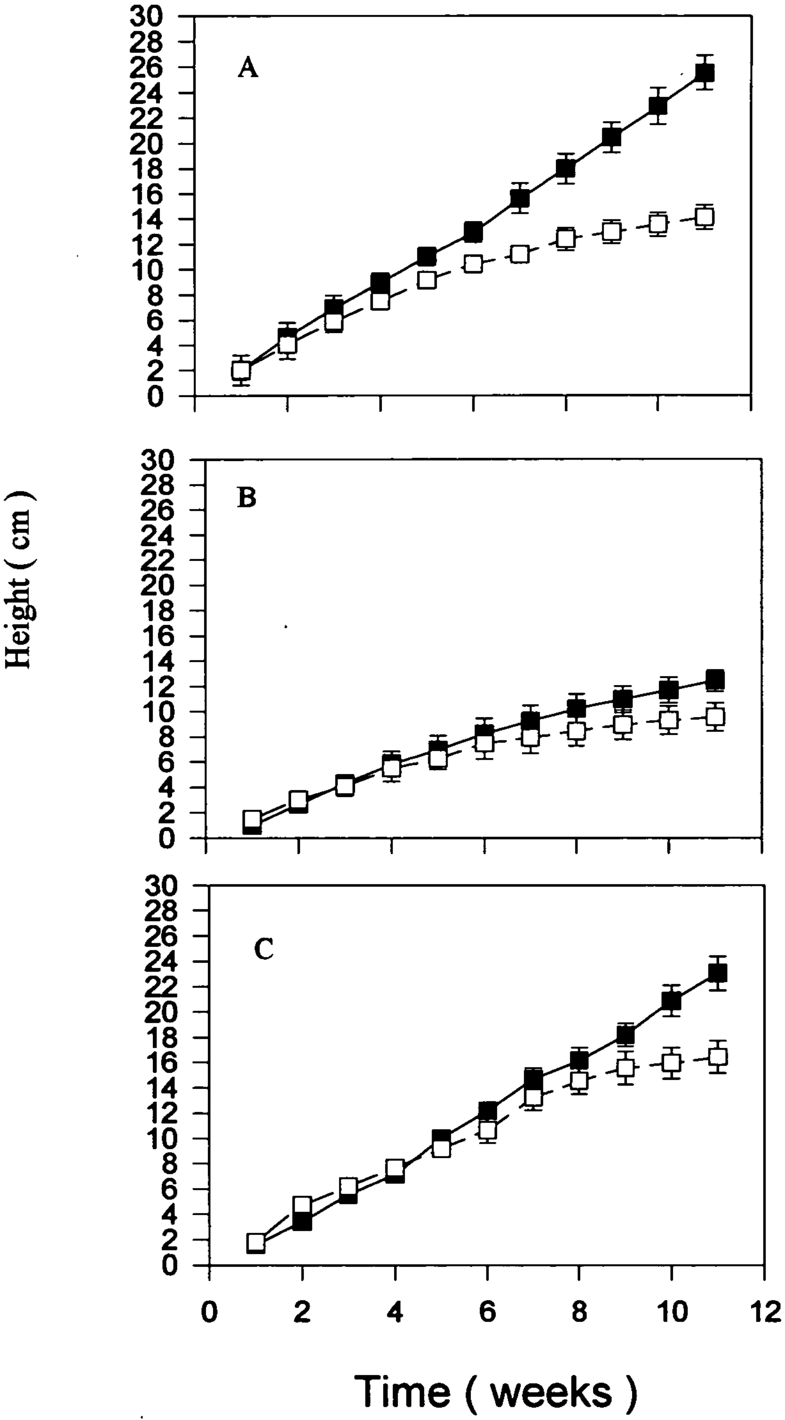


Figure 4.11: Plant height during soil drying for *Acacia negrii* (A), *Acacia asak* (B) and *Acacia ehnrbergiana* (C) of watered (■), and stressed plants (□). Point are means of four observations ± one standard error of the mean.

4.3.7 Dry matter

Total biomass production of each species was analysed at the end of the experiment (Table 4.3). Remarkably, the total biomass was unaffected by soil drying, but differences between species were highly significant ($P < 0.001$) (Table 4.4). The effect of drought was to significantly reduce total leaf area in *Acacia negrii*, but not in *Acacia asak* and *A. ehrnbergiana*. However, leaf dry weight was reduced by drought in *Acacai negrii* and *A. ehrnbergiana* but not in *Acacia asak*. Surprisingly, Soil drying resulted in an absolute increase in root dry weight. Therefore, in water stressed seedlings, there was an increase in root/shoot ratio was due to a substantial shift in dry matter partitioning in favour of below ground development. In general, the shoot fraction of total dry matter decreased in water stressed seedling, while the root fraction increased.

Table 4.3: Analysis of biomass production of *Acacia* seedlings at the end of the experiment (11 weeks period). Values are the means of four determinations ± standard error. Comparison of means is by t-test with 6 degrees of freedom.

Acacia negrii

	Watered	**Unwatered**	t	*P*
Total leaf area (cm^2)	372.5±26.1	263.5±22.34	4.37	0.004
Leaf dry weight (g)	3.70±0.27	2.79±0.18	2.82	0.03
Stem dry weight (g)	3.15±0.38	2.85±0.15	1.9	0.1
Total shoot (g)	7.22±0.65	5.61±0.57	1.8	0.11
Root dry weight (g)	2.49±0.32	4.02±0.65	2.1	0.07
Root shoot ratio	0.35±0.04	0.77±0.2	2.03	0.08
Total biomass (g)	9.70±0.85	9.63±0.67	0.06	0.9

Acacia asak

	Watered	**Unwatered**	*t*	*P*
Total leaf area (cm^2)	63.75±8.07	56.75±7.5	2.11	0.07
Leaf dry weight (g)	1.45±0.31	1.02±0.14	1.37	0.2
Stem dry weight (g)	2.38±0.75	1.37±0.46	2.14	0.07
Total shoot (g)	3.84±0.75	2.39±0.13	1.90	0.1
Root dry weight (g)	1.09±0.12	2.22±0.12	3.6	0.01
Root shoot ratio	0.33±0.1	0.94±0.13	4.1	0.001
Total biomass (g)	4.94±0.79	4.61±0.67	0.36	0.72

Acacia ehrnbergiana

	Watered	Unwatered	t	*P*
Total leaf area (cm^2)	139.22±28.43	128.75±25	1.95	0.09
Leaf dry weight (g)	2.74±0.1	2.06±0.16	3.55	0.01
Stem dry weight (g)	3.44±0.31	2.97±0.6	1.47	0.19
Total shoot (g)	6.19±0.37	5.04±1.7	2.83	0.02
Root dry weight (g)	2.29±0.27	3.0±0.17	7.78	0.03
Root shoot ratio	0.36±0.09	0.66±0.07	2.7	0.009
Total biomass	8.48±0.57	8.35±0.17	3.7	0.84

Table 4.4: The effect of drought on the leaf area (LA), the leaf dry weight (LDW), stem dry weight (SDW), total shoot (TS), root dry weight (RDW), total biomass (TB), root shoot ratio (RSR) and specific leaf area (SLA) of *Acacia negrii*, *A. asak* and *A. ehrnbergiana* for 11 weeks in the glasshouse. Analysis by two way ANOVA (ns = not significant; *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$). See Appendix 4.1

		Level of Significance	
Variable	Species	Treatments	Interaction
LA	***	***	***
LDW	***	***	ns
SDW	***	**	ns
TS	***	**	ns
RDW	***	***	ns
TB	***	ns	ns
RSR	ns	***	ns
SLA	***	ns	ns

4.4 Discussion

The aim of the present study was to compare the effect of water stress on the water relations of *Acacia negrii, A. asak* and *A. ehrnbergiana* seedlings by growing them in tubes to allow a development of water stress, similar to that which occurs in the field (see Table 2.2).

The significant reduction of midday leaf water potential in all three *Acacia* species seedlings towards the end of the experiment is an indication of shoot water stress resulting from a shortage of soil water. The stomatal conductance of all three species was also significantly lower (Fig 4.2, 4.3 and 4.4). Kramer, (1988) claimed that leaf water deficit is a common response to soil drying in the field and that such deficits provide a regulating influence on stomata. However, in the present experiment decrease in stomatal conductance was not accompanied by a particular decline in leaf water potential. Leaf water potential for the stressed plants increased from week 7 and 8 for *Acacia asak* and *A. negrii* respectively. Similarly leaf water potential in *A. ehrnbergiana* increased from week 11.

A significant reduction in stomatal conductance was established over 2 weeks, without any observable change in leaf water potential for *Acacia asak* and *A. ehrnbergiana* seedling under stress (Fig 4.3 and 4.4). *Acacia negrii* stomatal conductance was coupled with water potential during the first 2 weeks, and then the stomatal conductance changed without change leaf water potential (Fig 4.2). The overall non-association of conductance and leaf water potential refutes the classical view that conductance is controlled by water potential. Bates and Hall, (1981) found the stomata of field-grown cowpeas to be more closely coupled to soil water status than to leaf water status. Also Lange *et al.* (1987) reported leaf conductance decreased continuously over time course without change in bulk water potential for *Acacia melanoxylon*. Ullmann (1989) showed a similar pattern of stomatal conductance with a morning peak and a subsequent decrease, which was more pronounced in plants growing under water stress, for more than 40 *Acacia* species in different habitat in central Australia, central Africa and south-western Europe.

The discovery that stomatal conductance is more closely correlated with soil water status than with plant water status (Bates and Hall, 1981; Masle and Possioura, 1987; Turner *et al.*, 1987; Davies and Zhang, 1991; Khalil and Grace, 1993) and the particular evidence from split root experiments (e.g. Khalil and Grace, 1993) has led to a new view of how stomata are controlled by water stress. Most athers suggest that roots are the primary sensors of water deficit and that roots in drying soil produce a chemical signal that serves as a sensitive measure of soil moisture (Masle and Possioura, 1987; Turner *et al.*, 1987) One putative signal, a positive inhibitor (Masle and Possioura, 1987) and likely to be abscissic acid, ABA, is supposed to move through the transpiration stream to the shoot and to cause stomata to close independently of any hydraulic effect.

The accumulation of solutes in the leaf cells during water stress cause a decrease in bulk leaf water potential, together with the partial maintenance of turgor. The result of pressure-volume analysis of *Acacia negrii, A.asak* and *A. ehrnbergiana* leaves (Table 4.2) demonstrated significant changes over 11 weeks in osmotic potential at full turgor, osmotic potential at zero turgor, average bulk elastic modulus, and dry weight to turgid weight ratio of leaves of water stressed seedling. The result was a decline in osmotic potential at full and zero turgor, induced presumably by an increase in solute concentration due to an active accumulation of solute (Premachandra *et al.*, 1989). The degree of osmotic adjustment found in this study is relatively high compared to those reported for other tree species (*Eucalyptus behriana* by Myers and Neales 1984; *Acer pseudoplatanus* L. by Khalil and Grace, 1992). Many studies have suggested that the degree of drought tolerance is associated with an ability to undergo changes in bulk modulus of elasticity (*E*) and osmotic potential at full turgor (π_{100}) (Roberts and Knoerr, 1977; Roberts *et al.*, 1980; Parker *et al.*, 1982; Abrame, 1988). Tan *et al.* (1995) found active solute accumulation and lower osmotic potential as a result of a single drought stress in different families of black spruce. It is likely that these changes are the primary factors enabling *Acacia ehrnbergiana* and *Acacia negrii* to maintain a degree of drought tolerance. Findings of this study, agree with the results of Khalil and Grace, (1992) who found a decline osmotic potential at full and zero turgor in seedling sycamore under water stress. This suggest that *Acacia* species have the ability to increase solute accumulation when they are subjected to water shortage by decreasing osmotic potential in their cells. Generally, the effects are greater in *Acacia*.

Bulk modulus of elasticity of the tissue increased in the stressed leaves of all species. The modulus of elasticity is important to the osmotic and turgor relations of the cell (Cheung *et al.*, 1976). In this study the modulus of elasticity was high for *Acacia asak* seedlings under stressed conditions, which was in agreement with Jones and Turner (1978) who found an increase in elasticity in *Sorghum bicolor* L leaves grown under water stresse. Khalil and Grace, (1992) found that elasticity doubled in sycamore seedlings (*Acer pesudoplatanus* L.), under water deficit. High bulk modulus of elasticity provid a large change in turgor over a given change in water content, (Tyree and Hammel, 1972; Cheung *et al.*, 1975). The increase in elastic modulus coupled with a significant increase in leaf dry weight to turgid weight ratio suggests that water stressed leaves underwent morphological changes, possibly by increasing cell wall thickness and decreasing cell size. Also high dry weight to turgid weight ratio is an adaptive characteristic in leaves developed under water stress (Cutler *et al.*, 1977), and it might be due to accumulation of fibrous components in the leaf e.g hemicellulose (Rascio *et al.*, 1990), which increases water holding capacity. Wilson *et al.* (1980) reported that leaves of species adapted to the arid zone or under water stress leaves should have more cell wall material, thicker walls and more ligification, all contributing to greater tissue rigidity. In this study, all the leaves used in the analysis of pressure-volume curves were developed entirely under stress condition.

The total leaf area of stressed of *Acacia negrii, A. asak* and *A. ehrnbergiana* was reduced because the development of final leaf size was affected by water stress (Table 4.3). Although total leaf area of *A. asak* and *A. ehrnbergiana* showed the same tendency, the effects of water stress were not significant. The growth of *A. negrii* declined after 6 weeks, and the number of new leaves was less in the unwatered plants. However, the growth of *A. asak* and *A. ehrnbergiana* declined after 8 weeks. Metcalfe *et al.* (1990) found that the number of the new leaves and expansion of leaves of the water stressed *Eucalptus globulus* seedlings was lower than that of leaves of controls. However, they eventually attained (after 4 weeks) the same final area. Some authors find that the reduction in leaf area is due to a reduction in the number of leaves or the inhibition of leaf initiation, but others find that the reduction in leaf area is chiefly a result of reduction in leaf size, or both number of leaves and leaf size (Kaul and Kramer, 1965; Metcalfe *et al.*, 1990; Khalil and Grace,1992).

As expected, well-watered controls species had a greater height growth than stressed seedlings (Fig 4.11). Hallgern and Helms, (1992) found that drought reduced height growth in seedling of red fir (*Abies magnifica* A.Murr) and white fir (*Abies concolor* (Gord.& Glend.) Glend) seedlings by preventing summer shoot production. In this study during the early weeks the height of the stressed plant and controls were similar although the stomatal conductance and water potential declined. Kelliher *et al.* (1980) reported that the plants which can tolerate drought stress with the least decrease in stomatal conductance will grow the fastest or grow the longest under drought condition. Metcalfe *et al.* (1990) reported that height growth of *Eucalyptus globulus* seedlings was restricted by drought treatment, but not as severely as leaf growth. The result here suggests that *Acacia* species can tolerate the drought during early growth and can adapt to aridity. *Acacia asak* is more tolerant than *Acacia negrii* and *Acacia ehrnbergiana*.

The root biomass for all three *Acacia* species was not diminished by witholding water. With limited soil water, although total development of plants is reduced substantially, roots often grow deeper (Khalil and Grace, 1992). The distribution of significant amounts of feeding roots of *Acacia asak* and *A. ehrnbergiana* towards the deeper region of the soil is in agreement with this. An absolute increase in root weight occurred by the end of the experiment, which arose from a substantial shift in the biomass being produced (Table 4.3). By week 11 all *Acacia* species were able to develop a system of roots to exploit adequately the water of the soil despite their stressed condition. This may be linked to the genetically-determined deep rooting characteristics of the trees (Osonubi and Davies, 1981). According to Adams (1967), *Acacia mellifera* dominated a grassland in Sudan by extending its roots to depth of 8-15 m.

Acacia asak, *A. ehrnbergiana* and *A. negrii* all show remarkable acclimation to water shortage. This study was done in the glasshouse with seedlings grown in the pots. Consequently their roots have access to only small volumes of soil, and stomatal conductance and leaf water potential develop rapidly during soil drying. In contrast, root of plants growing in the field have access to large volume of soil and stomatal conductance and leaf water potential may be develop slowly. Thus it is suggested that any future program to evaluate a range of *Acacia* species should couple short-term screening experiments with long-term field testing.

CHAPTER 5

Comparative Effects of Drought on the Root Development of Three *Acacia* Species

5.1 Introduction

Studies of establishment and regeneration of the *Acacia* species of Saudi Arabia forest are scarce. However, in the forest zone, it can be expected that seedling establishment will occur during the wet season, when water and nutrients are not seriously limited. Accordingly, seedling growth and relative growth rate are important factors that determine the establishment success of a particular species (Migahid *et al.*, 1972; 1974; Kahlil and Grace, 1992). Root characteristics that enable the seedling to exploit soil resources during the wet season and thereby grow deep in the soil profile before the onset of the dry season, will be a crucial factor in the establishment of the species. Survival of plants in dry habitats is closely related to ability to produce extensive root systems, which penetrate deeply in order to utlilize water most efficiently and postpone possible drought injury (Kozlowski, 1971; Kozlowski and Kramer, 1991). Solbrig *et al.* (1977) identified three sources of soil moisture 1) the water in the upper 20 cm of soil which can easily be extracted by the plant, 2) water at intermediate depth which can be absorbed over a longer during which time these may be a reduction in the evaporative loss and 3) water in depressions and wadis which is abundant and relatively permanent but can be reached only by an extensive system of tap roots.

Most of the desert plants possess a very extensive root system which spreads vertically and horizontally. Vertically, the roots reach great depth, sometimes 10 to 15 meters (Migahid *et al.*, 1974; Batanouy, 1979). This enables plants to absorb water from the deepest layers of the soil. There are also lateral roots close to the surface of the soil, which enable these plants to exploit water from small rainfall events and even dew fall (Evenari *et al.*, 1971). Thus, plants absorb water from the largest possible volume of soil, compensating for water lost in transpiration (Migahid *et al.*, 1974; Batanouy, 1979). Albertson and Weaver, (1945) concluded that survival of trees in the prairie region of United States during the prolonged drought of the 1930_s was largely dependent on rooting depth. Studies carried out by Migahid *et al.*, (1974) pointed out that *Leptadenia pyrotechnica* is widespread in the Kingdom, has a height which can reach 160 cm, and has roots which can be 11.5 m deep. Evenari *et al.* (1971) found that roots of some desert shrubs are adapted to the moisture conditions of the soil in such a way that a shallow root system is developed when the surface water is adequate. These roots do not penetrate more than 0.5 m and restrict their development to the wet upper layer producing an extensive lateral root system (Batanouy, 1979). The extensive root system of desert plants is usually accompanied by stunting of the shoot. Larcher (1980) reported that seedlings of woody plants in dry regions have tap roots 10 times as long as the shoot. The roots of *Alhagi maurorum*, for example, extend to a depth of 10 m, while the height of the shoot of barely reaches 50 cm (Batannouny and Abdel Wahab, 1973). This allocation to root increases the quantity of water available for the plant and the restriction of shoot growth decreases the amount transpired per plant and per area of ground or per leaf area basis, transpiration is sometimes high a characteristic which enables the plant to cool significantly (Althawadi and Grace, 1986). In general, this to root shoot ratio in drought-adapted plants is very high when compared with other types of vegetation cover. For instance, the root to shoot ratio in the deciduous trees in the temperate zone is 1 : 4, while in some desert plants the root to shoot ratio can be 9 : 1 (Larcher, 1980). For evaluation of the water relations of such species as *Acacia*, the parameter of greatest value may be length of root per volume of soil (Doley, 1981). Many researchers have reported the effect of water stress on growth and dry matter partitioning. Changes in partitioning which increase the root fraction of total biomass are well documented (Kramer, 1983)

From the above evidence, it seems that adaptation of the root system to survive drought by an increase in depth and intensity may be an important criterion for the selection of trees suitable for afforestation of a drought affected area.

To study some of the mechanisms where by *Acacia* seedlings capture resource and become established it is helpful to investigate their root morphology as a first step towards a more functional understanding. Very few studies of this kind have been carred out. Comparative quantitative information on seedling root morphology and dry matter partitioning may also help to explain species coexistence, because distribution and abundance of adults in a plant community is affected by events during establishment (Korner, 1964).

In this chapter I investigate the root growth and morphology of three *Acacia* species in relation to soil moisture content.

5.2 Materials and methods

5.2.1 Experimental material

In February 1993 more than 400 seeds of *Acacia negrii, A. ehrnbergiana* and *A. asak* were germinated in the glasshouse at the Institute of Ecology and Resource Management, The University of Edinburgh. Seedlings were transplanted into small pots 6 cm diameter and 10 cm depth, containing a mixture of loam, sand, and peat compost in the ratio 1:2:1 by volume (see 4.3.1). Seedlings were kept on the glasshouse bench, with regular watering every day until to start of the experiment.

For this study it was convenient to use polyvinylchloride (PVC) tubes as pots (1.5 m length and 7.5 cm diameter). Twelve observation windows (5 x 6 cm) were cut in each tube. A special metal-frame was designed to support the tubes in the glasshouse (Fig 5.1). Double thickness polythene sleeve was inserted in the tubes and sealed at the bottom, perforated at the base and on its walls at 10 cm intervals from the base to the middle of tube to allow free drainage and aeration of the soil. Forty five tubes were set up in the glasshouse under natural light (see Fig 4.1). The observation windows were covered with black polythene sheet except when observations were being made. Tubes were packed with soil to a uniform bulk density and supported at an angle of about 90 ° to the vertical. During establishment irrigation was out carried every other day.

Four months later 45 seedlings were selected for vigour and transplanted into long soil columns of the above described compost, to allow relatively unrestricted root growth. Each column contained one seedling. Three different water levels were applied: dry, intermediate and wet (control). Three holes at the top, middle (75 cm from the top) and bottom (130 cm from the top) were drilled to determine the water level and to facilitate watering of the tubes to the point of overflow from these holes.

5.2.2 Measurement of root length using observation window

Measurements of root length were made on four seedlings from each the of control and the two treatments of each species. The development of the root system was followed using the modified line intersect methods (Tennant, 1975) using a grid (5 × 6 cm and 0.5 cm^2 grid unit). The grid was fitted on the observation window and the number of the root intersections with the vertical and horizontal lines were counted so that the total root length in that window could be assessed by applying the equation

$$L = n \times c$$

where L = the root length

n= the number of intersection

c= length conversion factor (c= 0.3928 for a grid with 0.5 cm^2 unit)

5.2.3 Branch production and increase in stem length

Measurements of the new branches were made on four plants in each of the control and the two treatments of each species. Similarly the new leaves were measured. The stem length of a typical shoot, developed from a node of the main stem was measured.

5.2.4 Total length of root

In order to assess the impact of the soil regimes on the root distribution, four randomly selected seedling of each treatment were selected at the end of the experiment. Root tubes were opened and the upper and lower soil sections were divided into 25 cm sections. Soil was gently washed from the tubes to leave the roots. They were divided into three parts: tap root, secondary root and fine root.

Length of the tap root was measured directly while the secondary and fine root length was estimated by using the method proposed by Newman (1966). For all the three species roots growing from the radical of the plant eventually develop to form a tap root. The secondary and fine root length was determined by putting roots in a rectangular dish of suitable size (6.5 × 13.5 cm). A plastic sheet marked with random straight lines was put under that dish. The number of intersections between the root and the lines was counted. The total root length is given by

$$L = \frac{\pi n A}{2H}$$

where L = the total root length

n = the number of intersections between the root and the straight lines

A = the area of the rectangle

H = the total length of straight lines.

Total root length was then converted into root length density (i.e., root length per unit volume of soil).

5.2.5 Leaf area and dry matter

Initial and final harvests (90 days) were done. Above and below ground biomass was separated into leaf, stem and roots. Leaf area at the end of the experiment was determined by using a leaf area meter (Model- CI 201, Portable Area Meter, CID Inc, Moscow, U.S.A). Leaf, stem and root material were then dried for 48 hours at 80 °C for dry weight determination.

5.2.6 Soil water content

Soil water content was measured at the end of the experiment (90 days). Four tubes from each treatment were divided into 25 cm sections. Then four soil samples from each layer were weighed and dried in an oven at 105 °C for 72 hours. The soil water content was calculated follows:

$$\text{Soil water content} = \frac{\text{fresh weight - dry weight}}{\text{dry weight}} \times 100$$

5.2.7 Statistical analysis of data

The variation in each parameter was investigated by analysis of variance (ANOVA) using the statistical package SAS. The level of significance in differences between treatment means was gauged by the Student-Newman-Keuls (SNK) test.

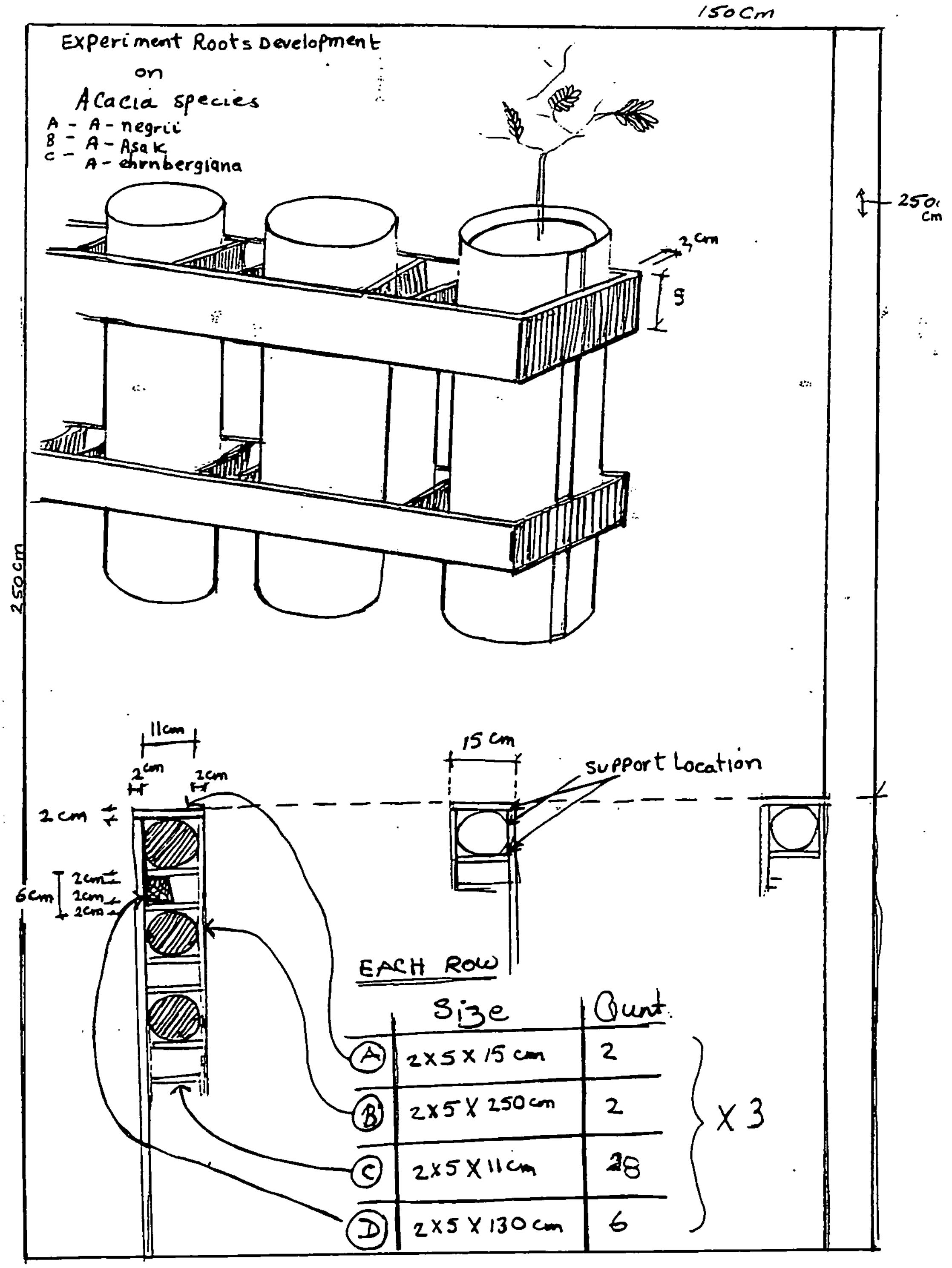
5.3 Results

5.3.1 Soil water content

All tubes showed a vertical profile of water content. There was a greater reduction in water content in dry and intermediate treatments of *Acacia negrii* than *A. asak* and *A. ehrnbergiana* (Fig 5.2, 5.3 and 5.4)

5.3.2 Root length using observation windows

The resulting root development after 90 days is shown in Fig 5.5, 5.6 and 5.7. It was clear that in the intermediate and dry treatment the roots were growing more rapidly than the watered treatment respectively: roots of the dry and intermediate treatments reached a depth of 33, 31 and 30 cm on the second week after the application of the water regime for *Acacia asak*, *A. ehrnbergiana* and *A. negrii* respectively (Fig 5.8). The downward root development became very rapid when the upper soil was drying. By the sixth week all species had reached 75 cm, in the intermediate soil moisture treatment. The *Acacia negrii* reached the bottom layer under the dry treatment before either *Acacia asak* or *A. ehrnbergiana*. By the end of the experiment, roots of all species had reached the bottom layer. Once the tap root reached the moist soil it became branched, forming numerous fibrous roots (Fig 5.9, 5.10 and 5.11). Although the tube system facilitated the observations on rooting depth, it was found at harvesting to have been less useful, indeed misleading, on the question of root quantity. This is because the tap roots are readily visible at the windows, but the development of the other, fibrous, roots cannot be followed. For the watered treatment the root was restricted to the zone above the water level, but new roots were slowly decending. Then, by the end of the experiment *Acacia negrii* had reached the bottom. However *Acacia asak* and *A. ehrnbergiana* had reached 90 and 125 cm respectively in the wet treatment .



	Size	Quant.
Ⓐ	2X5X15 cm	2
Ⓑ	2X5X250 cm	2
Ⓒ	2X5X11cm	28
Ⓓ	2X5X130 cm	6

Figure 5.1: A metal-frame was constructed to support the tubes during the root growth experiment in the glasshouse.

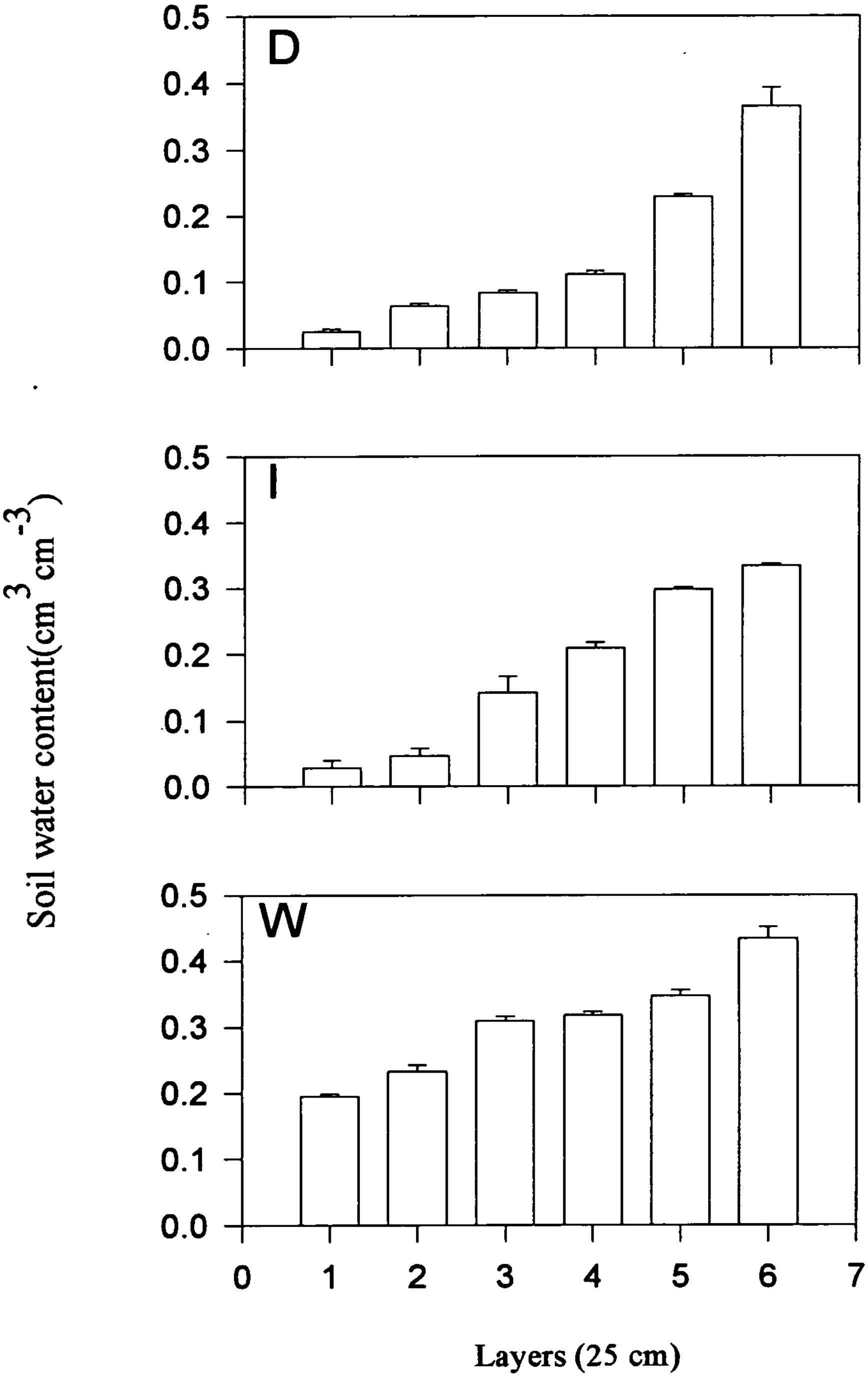


Figure 5.2: The soil water content following three water regimes for *Acacia negrii*, (D) dry treatment, (I) intermediate treatment and (W) wet (control). Columns are means of four observations ± standard error.

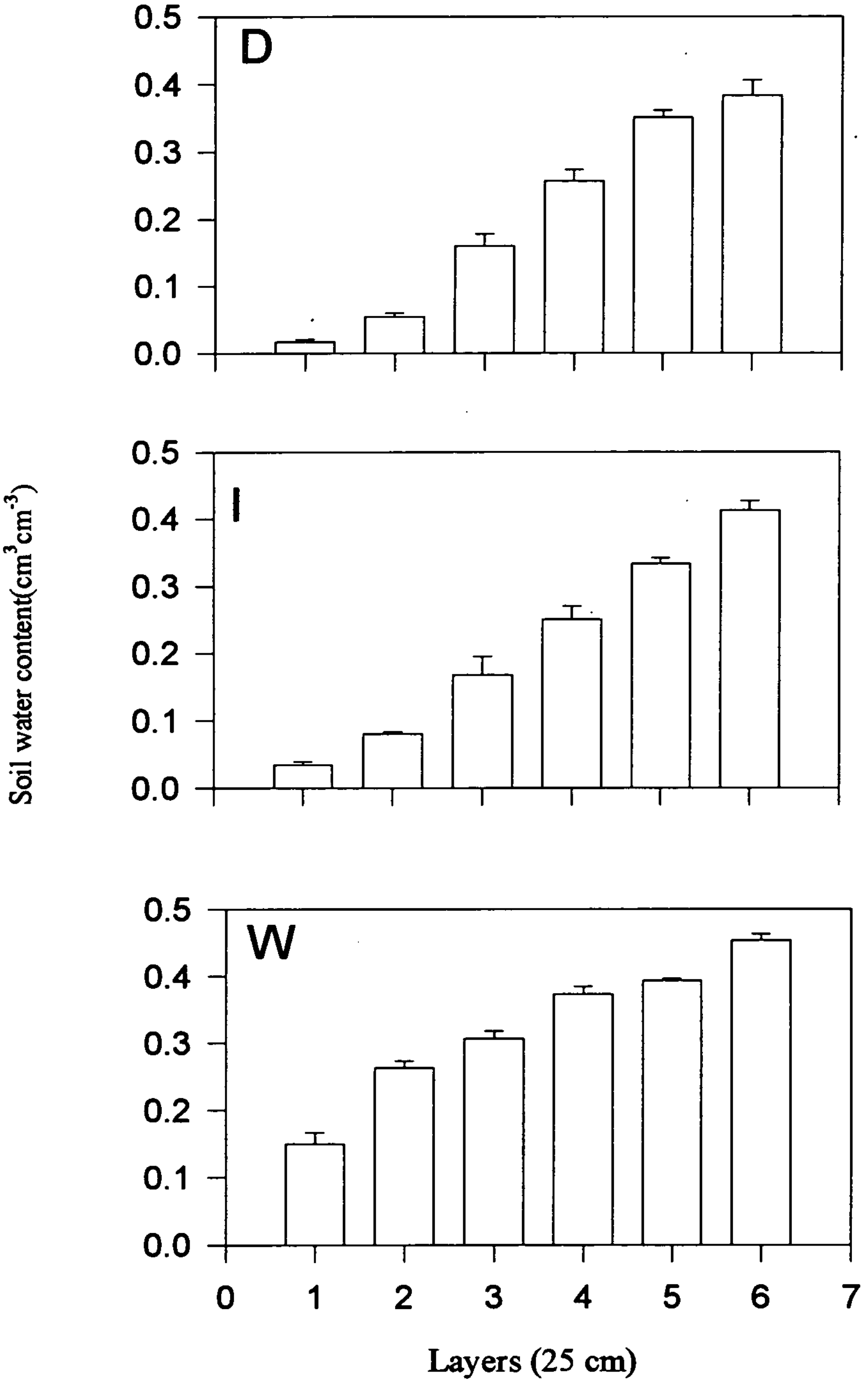


Figure 5.3: The soil water content folowing three water regimes for *Acacia asak*, (D) dry treatment, (I) intermediate treatment and (W) wet (control). Columns are means of four observations ± standard error.

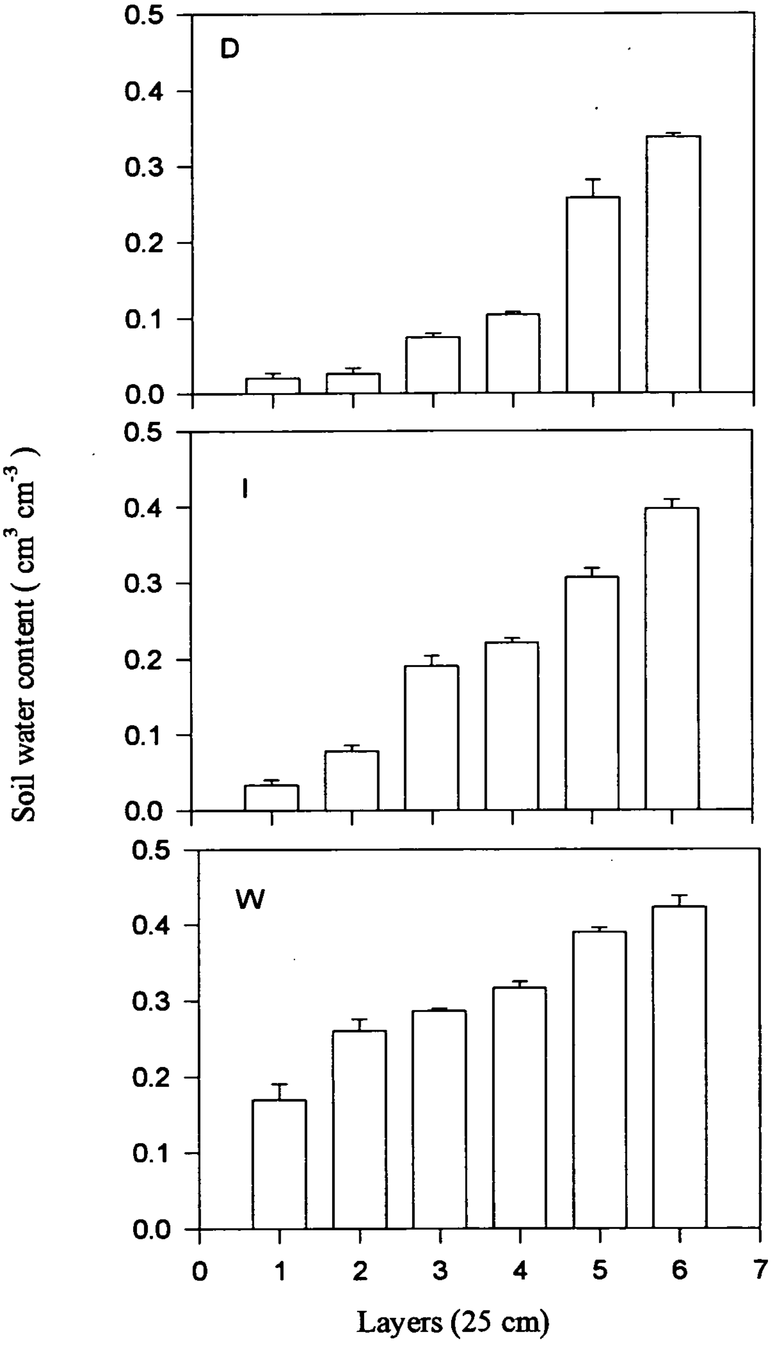


Figure 5.4: The soil water content following three water regimes for *Acacia ehrnbergiana*, (D) dry treatment, (I) intermediate treatment and (W) wet (control). Columns are means of four observations ± standard error.

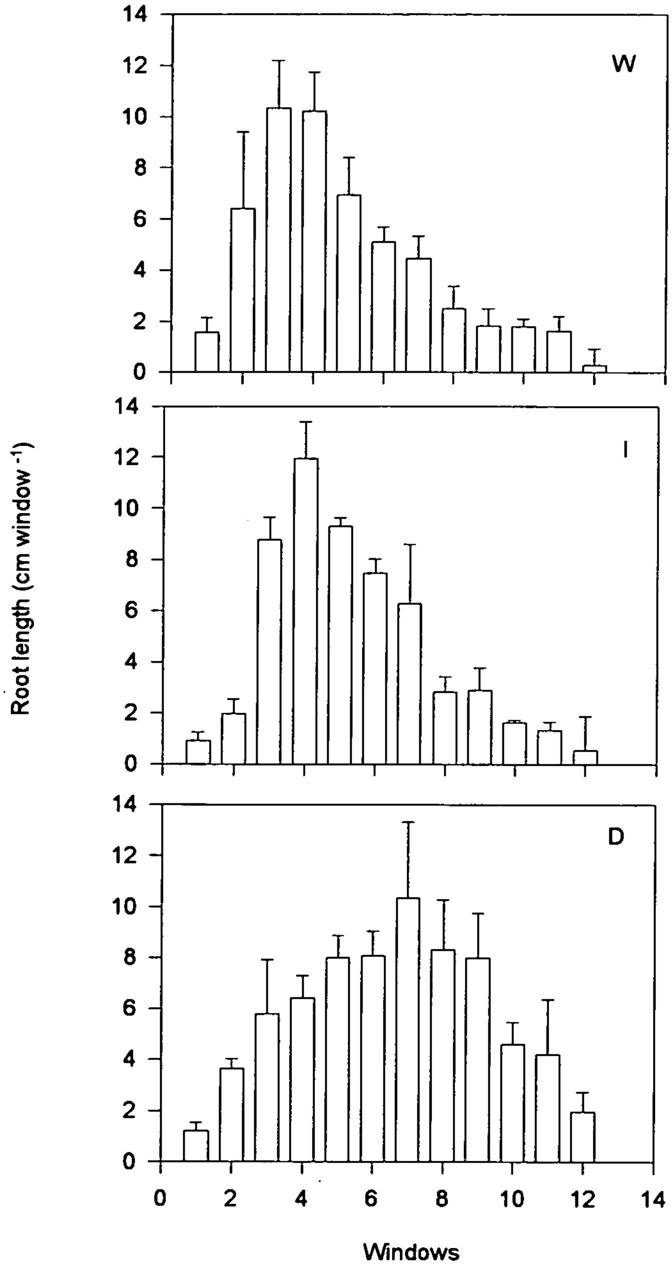


Figure 5.5: Root development after applying the three water level for 90 days is *Acacia negrii,* (W) watered, (I) intermediate and (D) dry treatment . Columns are means of four observation ± one standard error of means. Windows are counted from the top of the tube, and are all 12.5 cm intervals, so that depth = window number (12 × 12.5 cm).

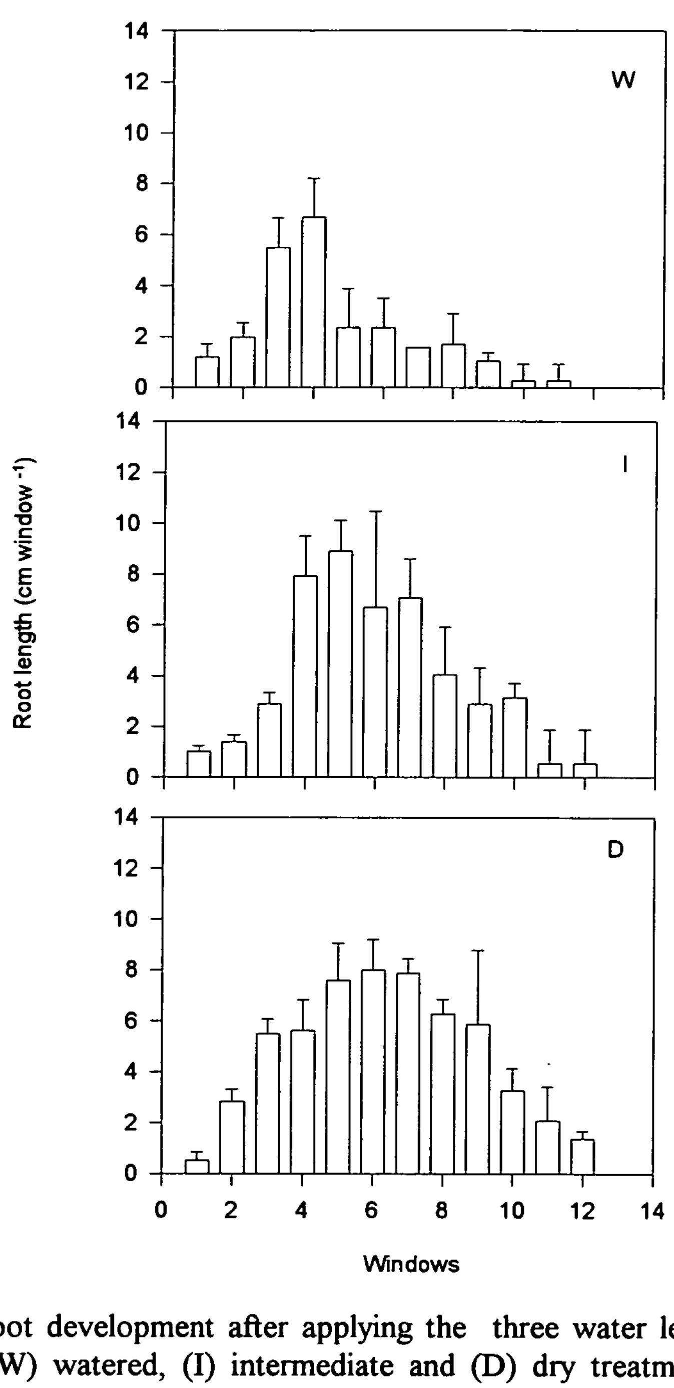


Figure 5.6: Root development after applying the three water level for 90 days is *Acacia asak*, (W) watered, (I) intermediate and (D) dry treatment . Columns are means of four observation ± one standard error of means. Windows are counted from the top of the tube, and are all 12.5 cm intervals, so that depth = window number (12 × 12.5 cm).

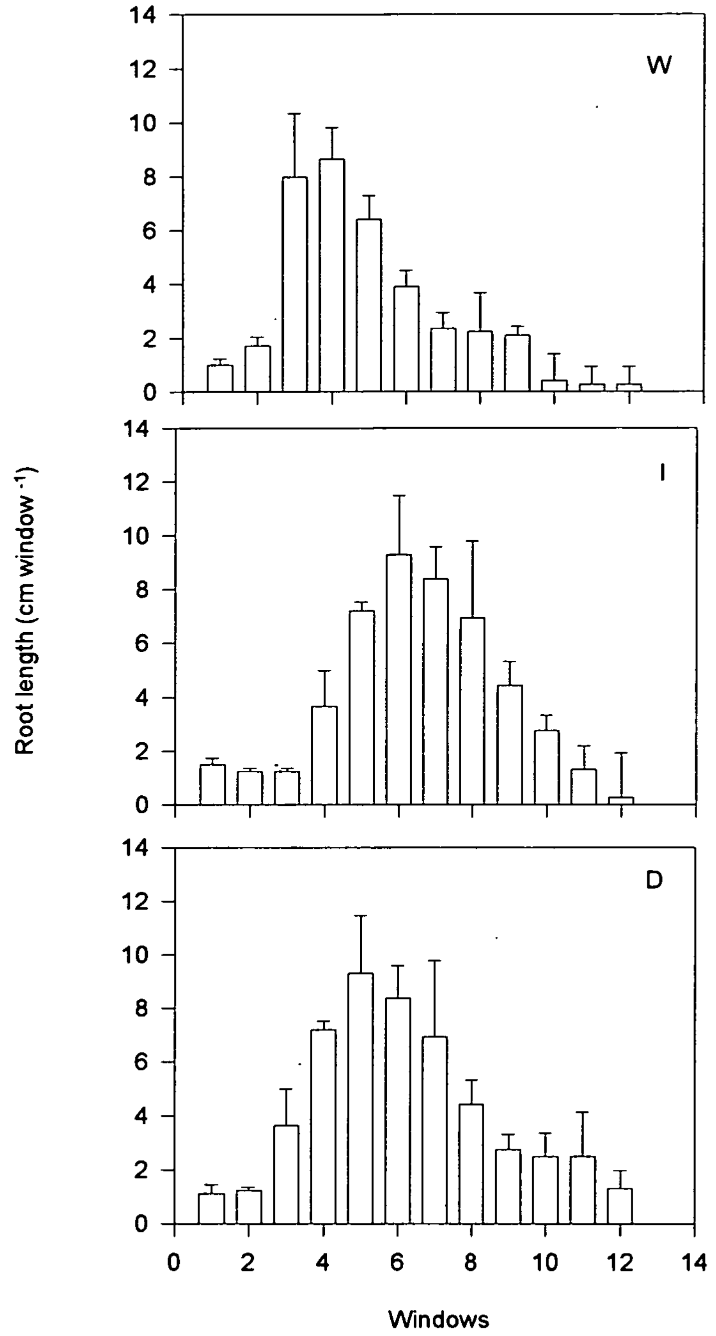


Figure 5.7: Root development after applying the three water level for 90 days is *Acacia ehrnbergiana*, (W) watered, (I) intermediate and (D) dry treatment . Columns are means of four observation ± one standard error of means. Windows are counted from the top of the tube, and are all 12.5 cm intervals, so that depth = window number (12 × 12.5 cm).

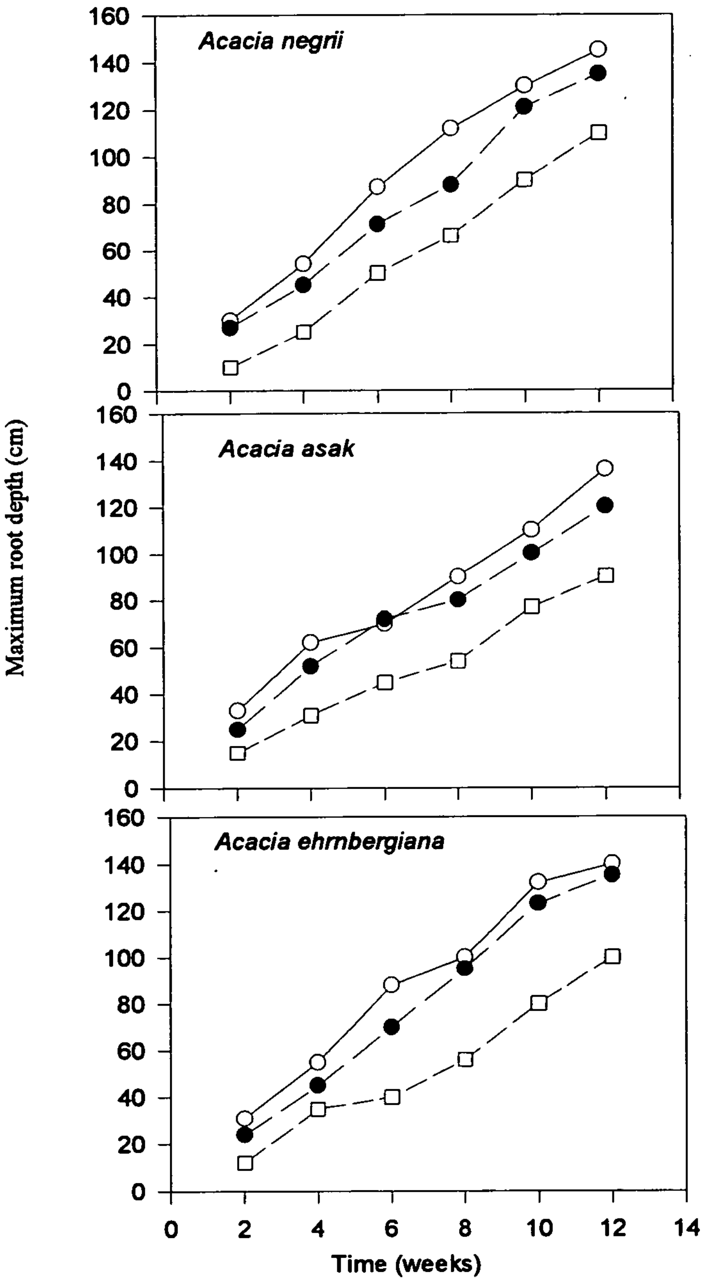


Figure 5.8 : The measurement of the root depth for *Acacia negrii*, *Acacia asak* and *Acacia ehrnbergiana* grown under three level water, (O) dry (●) intermediate and wet (control) (□). Values are means of four observation.

Figure 5.9 : Root system of *Acacia negrii*, grown for 90 days under three water regimes: (A) dry treatment, (B) intermediate treatment and (C) watered.

Figure 5.10 : Root system of *Acacia asak* grown for 90 days under three water regimes: (A) dry treatment, (B) intermediate treatment and (C) watered.

Figure 5.11 : Root system of *Acacia ehrnbergiana,* grown for 90 days under three water regimes: (A) dry treatment, (B) intermediate treatment and (C) watered.

5.3.3 Total length roots

The total root lengths at the end of the experiment for all three species are shown in Fig 5.12. The driest treatment where the water level was very low (130 cm) had the greatest root length for all three species. Total root length was significantly greater in dry and intermediate soil than in watered (controls). There were significant differences between species (Table 5.4)

The tap root length for each layer was significantly different between species. However there was no significant difference between the treatments except layers five and six were significant for *Acacia negrii* more root length in the dry treatment and layer five for *Acacia asak* and *A.ehrnbergiana* also more root length in the dry treatment (Table 5.1).

Comparing the root length of the three species, there were more branches in the watered treatments for *Acacia negrii* than *A. asak* and *A.ehrnbergiana.* Similarly in the dry and intermediate treatment, the tap root became more branched in *Acacia negrii* than *Acacia asak* and *Acacia ehrnbergiana. Acacia negrii* produced more secondary and fine roots than *A. asak* and *A. ehrnbergiana* (Table 5.2 and 5.3).

The rooting density indicates the size of the root and the volume of soil that is explored by the root; these values (Fig 5.13) appear to be small in all the species (<0.5 cm/cm^3).

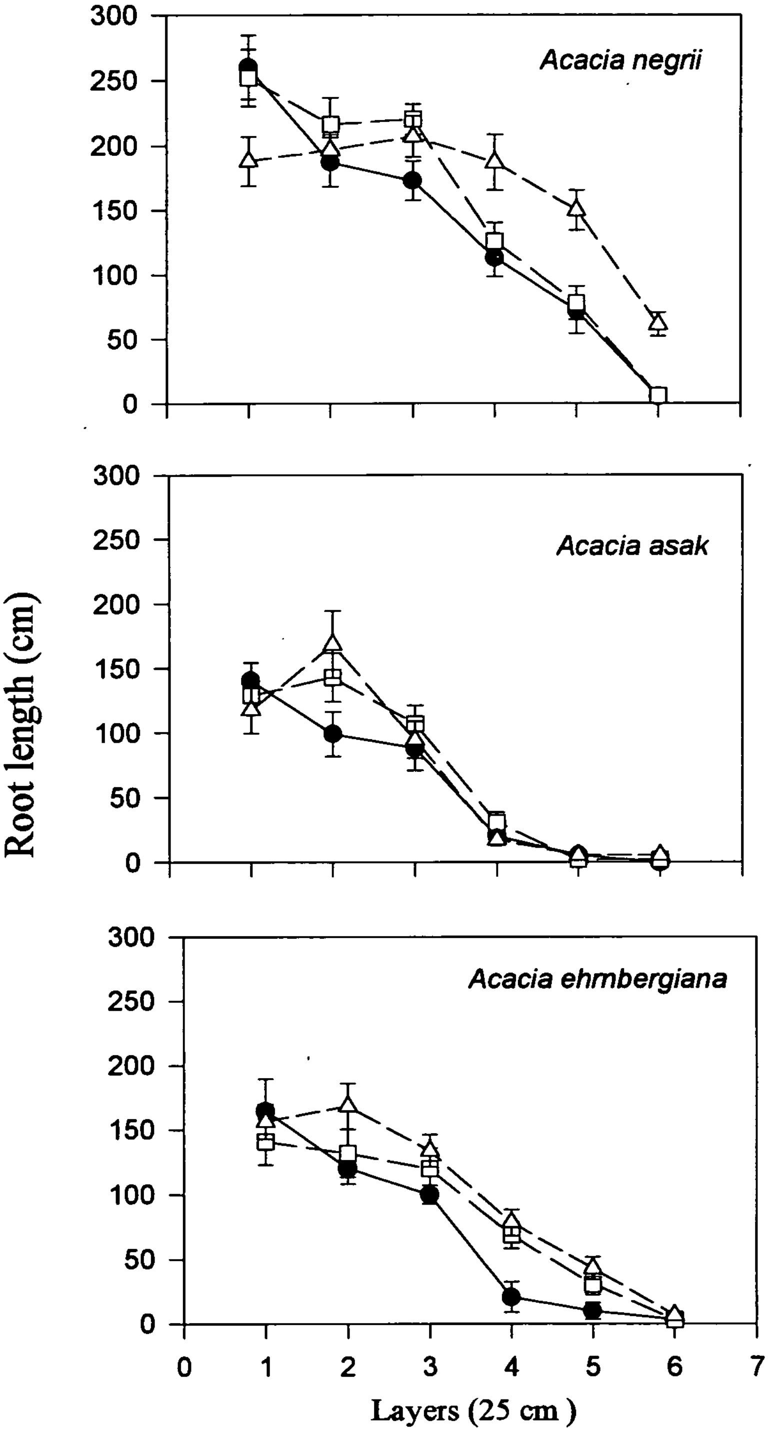


Figure 5.12: Root length of *Acacia negrii*, *Acacia asak* and *Acacia ehrnbergiana* under three water regimes. Watered (●), intermediate (□) and dry treatment (Δ). Means of four observation ± one standard error of means. This was at the end of the experiment.

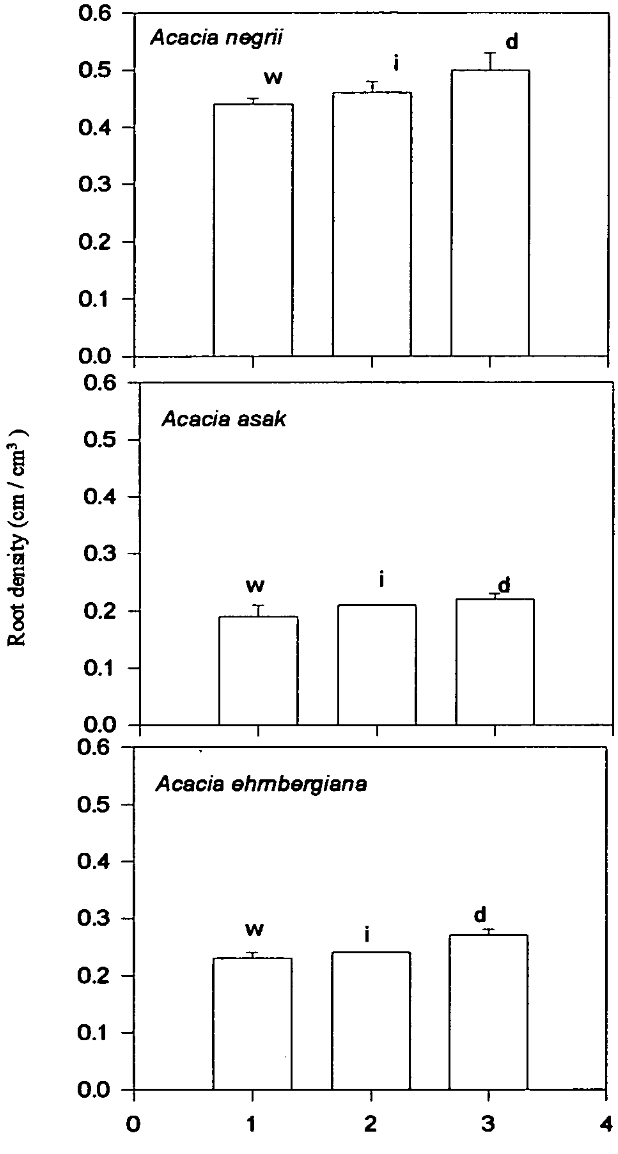


Figure 5.13: Root density (mean total root length per soil volume) of *Acacia negrii*, *Acacia asak* and *Acacia ehrnbergiana*, grown under three water levels intermediate (i), dry (d) and watered (b) over a period of 90 days. Columns are means of four observations ± one standard error of mean.

Tabl 5.1	Effect of soil water regime on the tap root length of ***Acacia negrii***, ***A. asak*** and ***A. hernbergiana***. Mean of four observation ± one standard error of mean. Test Student-Newman-Kuel(**SNK**) ((ns = not significant; *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$). Value followed by the same letter are not significantly different. See Appendix 5.1.

Species (*Acacia negrii*)

Layers	Watered	Intermediate	Dry	SNK
Layer one	a56.8±10.2	a53.4±6.0	a41.0±8.0	ns
Layer two	a40.8±7.4	a45.7±5.3	a43.5±7.4	ns
Layer three	a37.5±6.3	a49.1±8.6	a46.1±8.5	ns
Layer four	a26.0±5.8	a27.5±5.2	a40.0±6.6	ns
Layer five	a17.1±5.3	a17.0±4.0	a31.8±4.9	ns
Layer six	b0.90±0.5	b1.37±0.8	b12.9±2.2	**

Species (*Acacia asak*)

Layers	Watered	Intermediate	Dry	SNK
Layer one	a30.9±5.7	a28.2±5.4	a24.1±1.7	ns
Layer two	a21.9±5.6	a32.2±7.3	a35.3±5.5	ns
Layer three	a19.6±5.3	a24.6±5.6	a19.6±2.4	ns
Layer four	a3.9±6.9	a7.4±2.3	a8.8±2.2	ns
Layer five	b0.98±0.6	b0.51±0.5	a3.8±1.2	**
Layer six	a0.0±0.0	a0.49±0.5	a1.4±0.5	ns

Species (Acacia ehrnbergiana)

Layers	Watered	Intermediate	Dry	SNK
Layer one	a35.2±7.0	a30.7±6.1	a33.9±5.4	ns
Layer two	a25.7±3.6	a27.5±3.2	a37.6±7.7	ns
Layer three	a21.7±3.0	a24.8±1.5	a29.9±5.9	ns
Layer four	a5.1±2.9	b14.8±3.2	b17.8±3.9	*
Layer five	b2.5±1.6	a6.5±1.9	b9.1±2.0	*
Layer six	a0.86±0.5	a0.74±0.4	a1.6±0.61	ns

Table 5.2 Effect of soil water regime on the secondary root length of ***Acacia negrii*, *A.asak*** and ***A. hernbergiana*.** Mean of four observation ± one standard error of mean. Test Student-Newman-Keul (SNK). (ns = not significant; *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$). Value followed by the same letter are not significantly different. See Appendix 5.1.

Species (*Acacia negrii*)

Layers	Watered	Intermediate	Dry	SNK
Layer one	a86.6±8.2	a83.8±7.2	b62.4±12	*
Layer two	a62.3±6.4	a71.7±6.8	a65.5±3.9	ns
Layer three	b57.5±5.1	a73.3±3.9	a68.9±5.2	*
Layer four	b41.7±4.9	a37.6±4.8	a62.2±7.2	*
Layer five	b24.14±6.1	b25.9±6.1	a49.8±5.2	*
Layer six	b1.7±1.0	b1.83±1.0	a20.5±3.1	*

Species (*Acacia asak*)

Layers	Watered	Intermediate	Dry	SNK
Layer one	a33.2±4.7	b47.1±4.9	c36.3±6.0	*
Layer two	b33.0±5.8	a47.7.0±6.3	a56.3±8.6	*
Layer three	a29.4±5.6	a35.7±4.8	a31.6±4.8	*
Layer four	a6.8±2.5	a10.3±2.6	a14.7±4.2	ns
Layer five	b1.8±1.0	b0.68±0.68	b5.8±1.5	*
Layer six	a0.00±0.00	a0.65±0.65	a1.87±0.7	ns

Species (*Acacia ehrnbergiana*)

Layers	Watered	Intermediate	Dry	SNK
Layer one	a54.2±8.1	b46.96±1.4	b52.1±4.4	*
Layer two	a40.1±4.0	a44.0±6.1	b56.0±5.9	*
Layer three	a33.4±2.3	a39.9±5.3	b44.7±40.2	*
Layer four	b6.9±3.9	a22.76±3.8	a26.1±3.4	*
Layer five	b3.3±2.2	a10.2±2.6	a14.1±2.9	*
Layer six	a1.15±0.7	a1.0±0.6	a2.16±0.8	ns

Table 5.3 Effect of soil water regime on the fine root length of ***Acacia negrii*, *A.asak*** and ***A. hernbergiana***. Mean of four observation ± one standard error of mean. Test Student-Newman-Keul (**SNK**). (ns = not significant; *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$). Value followed by the same letter are not significantly different. See Appendix 5.1.

Species (*Acacia negrii*)

Layers	Watered	Intermediate	Dry	SNK
Layer one	a129.9±12.3	a125.8±10.8	b93.6±1.8	*
Layer two	a93.5±9.5	a107.9±10.1	a85.3±24.0	ns
Layer three	b86.3±7.6	a109.9±5.8	a103.1±1.9	*
Layer four	b56.5±7.3	b62.8±7.1	a92.7±3.1	*
Layer five	b36.2±9.2	b38.2±6.3	a72.7±3.5	*
Layer six	b2.55±1.5	b2.75±1.6	a30.7±4.7	*

Species (*Acacia asak*)

Layers	Watered	Intermediate	Dry	SNK
Layer one	c49.9±7.0	b71.9±7.5	a84.4±9.0	*
Layer two	a44.6±8.7	a64.6±9.5	b58.9±12.9	*
Layer three	a50.3±8.5	a53.6±7.2	b37.4±7.2	*
Layer four	b10.3±3.8	a15.5±3.9	a22.0±6.2	ns
Layer five	b2.7±1.5	b1.0±1.0	a8.8±2.3	*
Layer six	a0.00±0.0	a.98±0.98	a2.7±1.0	ns

Species (*Acacia ehrnbergiana*)

Layers	Watered	Intermediate	Dry	NSK
Layer one	a82.2±12.6	b70.4±8.8	b78.1±6.5	*
Layer two	a66.3±6.1	a56.0±9.1	a72.0±8.9	*
Layer three	a50.0±3.5	b46.9±7.9	a56.0±6.2	*
Layer four	b10.3±5.9	a34.2±5.0	a39.2±5.1	*
Layer five	b4.9±3.3	a15.3±3.9	a21.6±4.2	*
Layer six	a1.72±1.0	a1.5±0.9	a3.24±1.2	ns

Table 5.4: The effect of soil water regime on tap root length for six layers of *Acacia negrii*, *A. asak* and *A. ehrnbergiana* for 15 weeks in the glasshouse. Analysis by two way ANOVA (ns = not significant; *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$). See Appendix 5.1.

		Level of Significance	
Variable	**Species**	**Treatments**	**Interaction**
Layer one	***	ns	ns
Layer two	***	ns	ns
Layer three	***	ns	ns
Layer four	***	ns	ns
Layer five	**	**	**
Layer six	***	***	***

Table 5.5: The effect of soil water regime on secondary root length within six layers of soil in *Acacia negrii*, *A. asak* and *A. ehrnbergiana* for 15 weeks in the glasshouse. Analysis by two way ANOVA (ns = not significant; *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$). See Appendix 5.1.

		Level of Significance	
Variable	**Species**	**Treatments**	**Interaction**
Layer one	***	ns	***
Layer two	***	ns	ns
Layer three	***	ns	ns
Layer four	***	ns	***
Layer five	**	***	***
Layer six	***	***	***

Table 5.6: The effect of soil water regime on fine root length within six layers of soil in *Acacia negrii*, *A. asak* and *A. ehrnbergiana* for 15 weeks in the glasshouse. Analysis by two way ANOVA (ns = not significant; *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$). See Appendix 5.1.

		Level of Significance	
Variable	**Species**	**Treatments**	**Interaction**
Layer one	***	ns	***
Layer two	***	ns	ns
Layer three	***	ns	***
Layer four	***	**	***
Layer five	**	***	***
Layer six	***	***	***

5.3.4 Branch of production and increase in stem length

Stem and leaf growth measurements were made to determine how lateral branching, new leaf production and stem growth rates contributed to total biomass and biomass partitioning. As expected, growth of stem length of *Acacia negrii*, *A. asak* and *A. ehrnbergiana* was reduced in the intermediate and dry treatments. Differences between dry and intermediate were generally small for all the species (Fig 5.14). From week 4 to week 9 the growth was reducing compared with the watered treatment for all species. Then when the seedlings roots under intermediate and dry regimes reached the soil moisture at week 8 and 14 respectively, the rate of stem extension unexpectedly increased (Fig 5.14). This suggests that *Acacia* species are capable of reducing shoot growth whilst increasing root growth, when under water stress.

Fig 5.15 illustrates the effect of the watering treatments on the production of new growth. Although the stem height was reduced, there were many branches produced for *Acacia asak* and *Acacia ehrnbergiana* under dry and intermediate treatment. However *Acacia negrii* produced fewer branches than *Acacia asak* and *Acacia ehrnbergiana*, consistent with its normal habit as relatively erect trees. Interestingly, in the dry soil treatment the mean number of branches for *Acacia negrii* was one, but in the same treatment for *Acacia ehrnbergiana* there was a mean of six. *Acacia negrii* produced larger leaves than *Acacia asak* and *A. ehrnbergiana*. However, *A. negrii* had fewer leaves. Approximately 3 weeks after initiation of the watering regime, differences in new leaf production became apparent, resulting in significant differences between treatments at the end of the experiment (Table 5.4).

5.3.5 Dry matter

The root dry weight was significantly different between the treatments for all species (Table 5.6). The total weight of the root for the dry and intermediate treatments was higher than for the wet treatment. The dry weight of the shoot system in the wet treatment was higher than the other two treatments for all shoot varieties. The increased root weight in the intermediate and dry treatment caused a significantly higher ($P<0.01$) root to shoot ratio at the end experiment (Table 5.7).

The leaf dry weight accumulation was significantly affected by water regime and there were clear difference between species (Table 5.8). Surprisingly, the total biomass for all three species was unaffected by the water regime, although the above-ground biomass was affected ($P< 0.01$) and there was a significant reduction ($P< 0.001$) in the total leaf area and new leaf initiation, as well as in stem weight in all case (Table 5.7). In contrast; reduction in soil moisture resulted in an absolute increase in root dry weight. Therefore, in dry and intermediate treatments there was mainly due to a substantial shift in dry matter partitioning in favour of below-ground development. In general, the shoot fraction of total dry matter decreased in the dry treatment and intermediate seedling, while the root fraction increased.

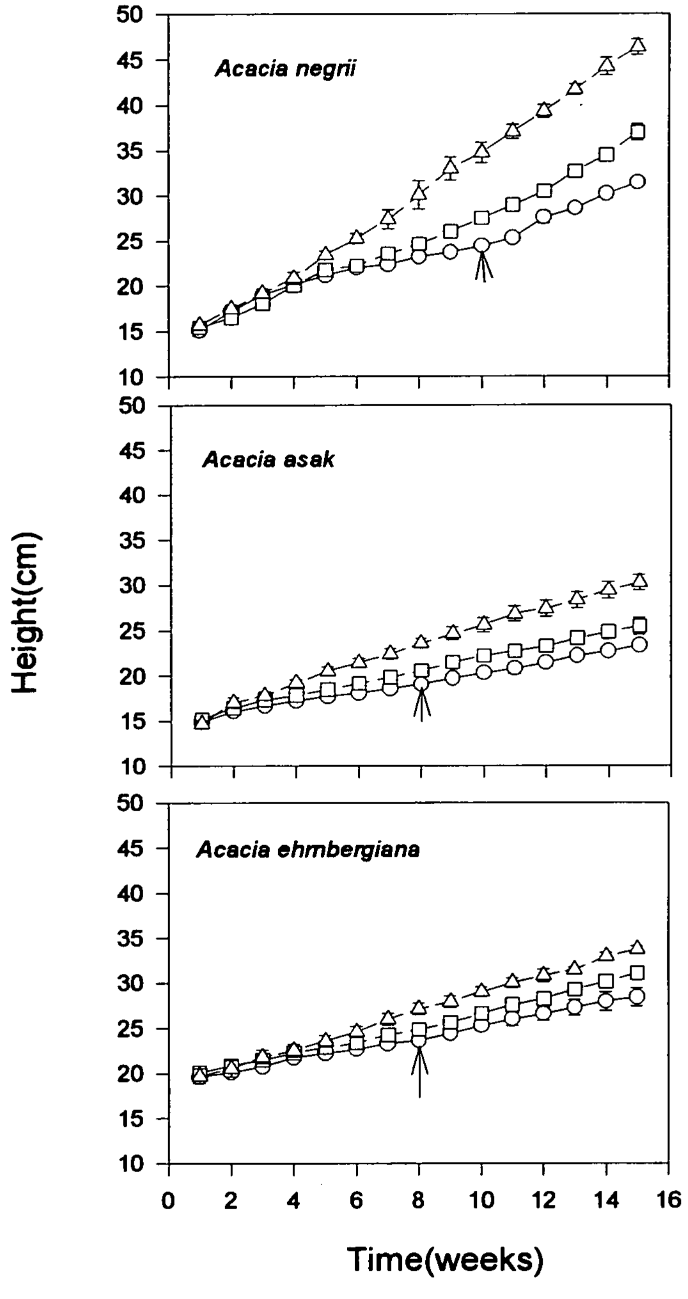


Figure 5.14: Increase in height (cm) of *Acacia negrii*, *Acacia asak* and *Acacia ehrnbergiana* under three water regimes. Dry treatment (O), intermediate (□) and watered (Δ). Means of four observations ± one standard error of means. The rate of height growth increased at the points shown by the arrows. The rates before and after the arrow were as follows: *Acacia negrii*, 0.16 mm day^{-1} to 0.2 mm day^{-1}; *A. asak*, 0.07 mm day^{-1} to 0.10 mm day^{-1} and *A. ehrnbergiana*, 0.08 mm day^{-1} to 0.11 mm day^{-1}.

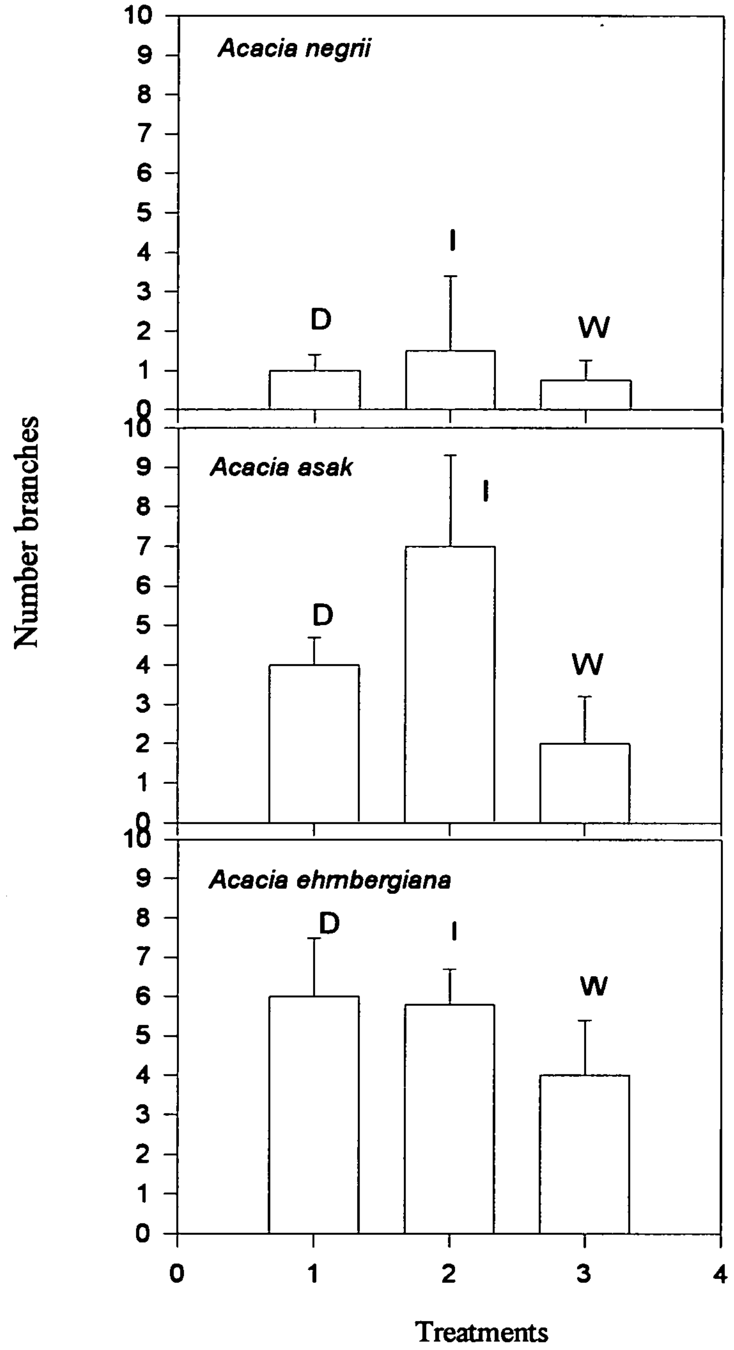


Figure 5.15: Number branches of *Acacia negrii*, *Acacia asak* and *Acacia ehrnbergiana*, grown under three level water intermediate (I), dry (D) and watered (W) over a period of 90 days. Columns are means of four observations ± one standard error of mean.

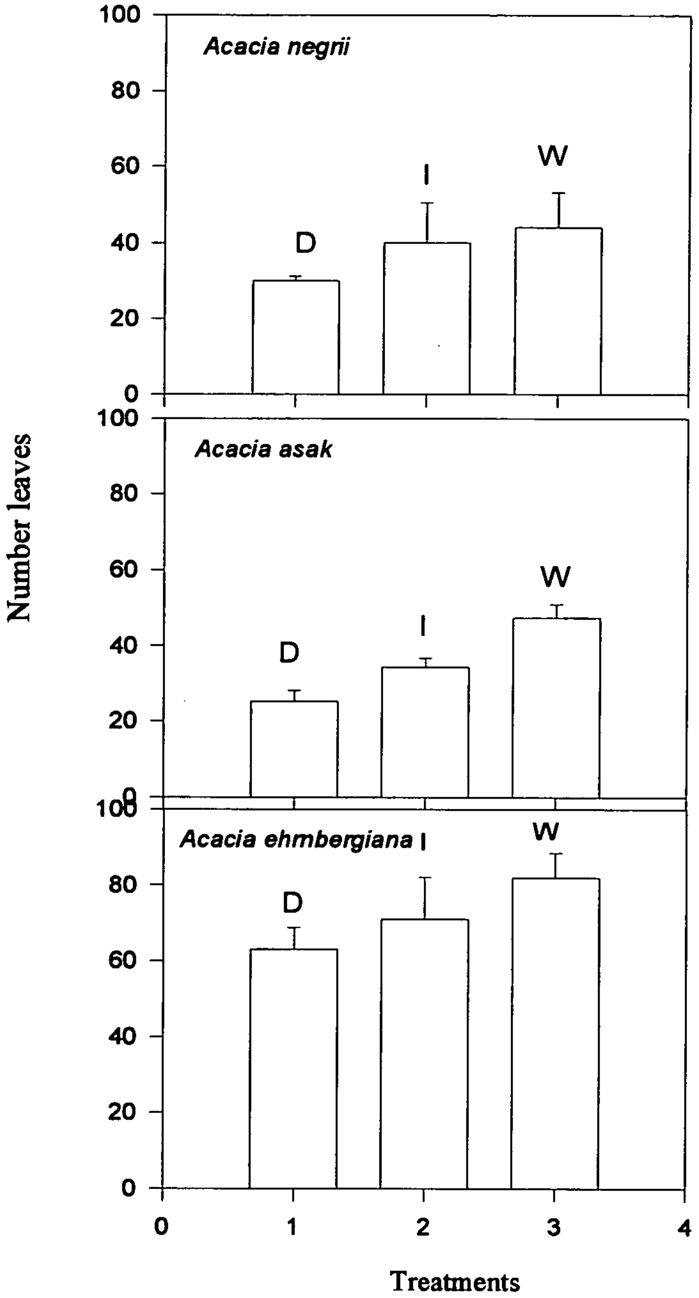


Figure 5.16: Number leaves of *Acacia negrii*, *Acacia asak* and *Acacia ehrnbergiana*, grown under three level water intermediate (I), dry (D) and watered (W) over a period of 90 days. Columns are means of four observations ± one standard error of mean.

Table 5.7

Effect of soil water regime on the growth of ***Acacia negrii*, *A.asak*** and ***A. hernbergiana*.** Mean of four observations ± one standard error of mean. Test Student-Newman-Keul (SNK) (ns = not significant; *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$). Values followed by the same letter are not significantly different. See Appendix 5.1.

Species (***Acacia negrii***)

Variable	**Watered**	**Intermediate**	**Dry**	**SNK**
Leaf area (cm^2)	a392.5±20.1	b345±18.7	c288.4±14	*
Leaf dry weight (g)	a4.27±0.1	a3.80±0.2	b3.1±0.2	*
Stem dry weight (g)	a4.97±0.3	b3.71±0.2	b3.04±0.2	*
Total shoot (g)	a9.24±0.3	b7.51±0.1	c6.14±0.2	*
Root dry weight (g)	b2.04±0.6	b2.99±0.1	a4.30±0.2	*
Root shoot ratio	c0.22±0.07	b0.40±0.01	a0.71±.07	*
Number leaf	a44.0±5.2	a40.0±3.6	a30.0±1.2	ns
Number branches	a0.75±0.5	a1.50±1.9	a1.0±0.4	ns
Specific leaf area cm^2 g^{-1}	a91.8±3.6	a92.3±4.6	a93.2±2.6	ns
Total root length cm	a827.3±17	a877.2±40.9	b956±57.2	*
Total biomass	a11.3±0.8	a10.5±0.3	a10.4±0.1	ns

Species (***Acacia asak***)

Variable	Watered	Intermediate	Dry	SNK
Leaf area (cm^2)	a156.9±14.7	ab136.7±14.7	b120.5±16	*
Leaf dry weight (g)	a2.26±0.2	a1.79±0.2	a1.45±0.2	ns
Stem dry weight (g)	a2.25±0.2	b1.58±0.2	b1.28±0.2	*
Total shoot (g)	a4.52±0.3	b3.37±0.1	b2.74±0.3	*
Root dry weight (g)	c0.86±0.1	b1.37±0.2	a1.86±0.1	*
Root shoot ratio	c0.15±0.03	b0.41±0.07	a0.71±0.1	*
Number leaf	a47.0±3.0	b34.3±2.1	c25±2.6	*
Number branches	a2.0±1.2	a7.0±2.3	a4.0±0.7	ns
Specific leaf area cm^2 g^{-1}	a70.7±10	a80.8±9.2	a82.5±7	ns
Total root length cm	b356.2±35	a407.7±15.3	a425.3±12	*
Total biomass	a5.20±0.3	a4.74±	a4.60±0.2	ns

Species (***Acacia ehrnbergiana***)

Variable	**Watered**	**Intermediate**	**Dry**	**SNK**
Leaf area (cm^2)	a167.0±16.2	b146.5±15.2	b122.5±15	*
Leaf dry weight (g)	a2.18±0.2	b1.54±0.03	b1.38±0.02	*
Stem dry weight (g)	a2.12±0.1	b3.17±0.1	b1.36±0.2	*
Total shoot (g)	a4.31±0.2	a3.17±0.1	b2.73±0.2	*
Root dry weight (g)	b0.94±0.1	b1.21±0.04	a1.54±0.1	*
Root shoot ratio	c0.22±0.02	b0.38±0.2	a0.57±0.07	*
Number leaf	a82±5.8	a71±4.4	a63±6.7	ns
Number branches	a4.0±1.4	a5.8±0.9	a6.0±1.5	ns
Specific leaf area cm^2 g^{-1}	a77.6±4.7	a93.7±2.6	a93.9±2.8	ns
Total root length cm	a435.5±22.2	a450.9±15.6	b512.9±20.3	*
Total biomass	a5.25±0.3	b4.38±0.06	b4.27±0.1	*

Table 5.8: The effect of soil water regime on the leaf area (LA), the leaf dry weight (LDW), stem dry weight (SDW), total shoot (TS), root dry weight (RDW), total biomass (TB), root shoot ratio (RSR) and specific leaf area (SLA), number leaf (NL), number branches (NB), total root length (TRL) of *Acacia negrii*, *A. asak* and *A. ehrnbergiana* for 11 weeks in the glasshouse. Analysis by two way ANOVA (ns = not significant; *** $P\leq0.001$; ** $P\leq0.01$; *$P\leq0.05$). See Appendix 5.1

		Level of Significance	
Variable	**Species**	**Treatments**	**Interaction**
LA	***	***	***
LDW	***	***	ns
SDW	***	***	*
TS	***	***	*
RDW	***	***	*
RSR	ns	***	ns
NL	***	***	ns
NB	***	ns	ns
SLA	***	ns	ns
TRL	***	***	ns
TB	***	ns	ns

5.4 Discussion

The aim of the present study was to compare the root development for three *Acacia* species: *Acacia negrii*, *A. asak* and *A. ehrnbergiana* when grown in soil columns with three different soil water supply regimes: watered (control), intermediate and dry. Morphological adaptation to drought appears to vary substantially among the species studied here. Differences in root growth and root-shoot allocation were especially apparent.

The distribution of the root system through space and time is usually influenced by both genetic characters of the plant and localized soil conditions (Kramer and Kozlowski, 1979; Talor, 1983). Desert plants have the ability to develop a fast growing-root system which appears to seek water (Migahid *et al.*, 1974). Tap roots grow vertically and as soon as each root has reached sufficient soil moisture it starts to produced numerous fibrous roots to facilitate water uptake (Solbrig *et al.*1977; Evenari *et al.* 1971; Migahid *et al.*, 1974). Larcher, (1980) found tap roots 10 times as long as the shoot for seedlings of woody plants. In the present work, root development increased gradually with progressive drying to the bottom soil layer in the all three *Acacia* seedlings, whilst development of the watered roots varied irregularly, suggesting control of the root development independent of soil moisture. The depth of root penetration and their lateral spread, differed among species. The *Acacia* species are adapted to a dry environment, in which they can create a deep and well branched root system. The seedling can extract relatively quickly more water from the soil layer and postpone or delay desiccation effects. Then, it is often recorded that seedlings of woody plants are able produce deep tap roots. Adams, (1967) found roots of *Acacia mellifera* from 8 to 15 m. Osonubi and Davies (1981) reported that the increased root growth of water-stressed *Quercus robur* was due to a change in production from short, thick roots to a profusion of long, thin roots that penetrated deeper into the soil. In contrast Osonubi and Davies, (1981), found root growth of both well watered and unwatered birch (*Betula pendula*)seedlings, a species which is not known for drought tolerance, were restricted to the upper part of the profile.

The root length / leaf area ratio indicates very broadly the structural cost invested in resource-capture surface (Korner, 1987). A bigger ratio reflects a higher expenditure in roots associated with the water cost of sustaining the photosynthetic capacity. There was a tendency in all the species to develop more root length per unit leaf area. In this sense, it seems that *Acacia negrii* is the species more efficient in terms of the expenditure in roots versus leaf area (Fig 5.16).

The extensive root system is believed to increase drought resistance by making more soil water available to a plant (Petrie and Hall, 1992). Increased root density and depth are both important for water uptake (Turner, 1986), but optimal root distribution depends on how water is distributed over depth and time within the soil profile. Dense rooting at the surface may allow roots to quickly absorb light rainfall, before water is lost through evaporation (Talor, 1983). If roots are mainly in the top soil layers, plant water status will decline when the surface soil dries unless any deeper roots can supply the plant with sufficient water (Becker *et al.*, 1987). Great root length density at depth could allow a plant to tap deep reserves of soil water more effectively, if such reserves are present (Petrie *et al.*, 1992). This result indicates that rooting depth is plastic for all three species. The maximum rooting depth of all three species increased significantly in dry and intermediate treatments. Maximum rooting depth is usually established during the seedling stage (Joe, 1991). Coile (1937), found that the density of roots at great depth increases with age, but the horizontal and vertical extent of tree roots is reached at a certain trees age.

Shifting of dry matter allocation to below ground growth in suboptimal environments has been observed elsewhere (e.g., Bawazir, and Idle, 1989; Steingerg, 1990; Khalil and Grace, 1992). Some characteristic differences within and between species occur in root length and root/ shoot ratio. However, root/shoot ratios change with plant age. The result in this study found root /shoot ratio high under dry and intermediate treatments (see Table 5.7). This agrees with the fact that the plant under water stress changes photosynthate partitioning change, at the expense of the shoot system, which leads to an increase in the ratio of the root : shoot (Shulze, 1986; Heth and Kramer, 1975; Heth, 1980). Nour and Weible, (1978) grew sorghum cultivates in sand and found that the drought tolerant varieties had greater volume and weight and higher root / shoot ratios.

Reduced total plant leaf surface has been called one of the most important factors in the survival of some desert plants (Orshan, 1954). The total leaf area of dry and intermediate treatment for all three species were reduced because the development of final leaf size was affected by water supply. This result agrees with Steingerg *et al.* (1990) who found that water stress affected the total leaf area of young peach. The plants in desert conditions usually have a low specific leaf area (SLA) (Larcher, 1980; Fitter and Hay, 1981). The decline of the specific leaf area is generally presumed to provide a water economy, as a thicker leaf contains more photosynthetic machinery and generally has a higher light saturated rate of photosynthesis (e.g. Pitman *et al.*, 1983.; Bjorkman, 1981).

The rate of growth in height of the seedlings was markedly reduced for all the species under dry and intermediate treatments. The different level of moisture supply showed a pronounced effect on both the pattern of height development of the shoot and its final mass for all the plants (Fig 5.14). *Acacia negrii* was the most sensitive to such moisture stress. There was a resumption of the shoot growth, when roots reached the water level and seedlings recovered. This study supports the idea that increased rooting depth facilitates water uptake and sustains shoot growth. This is in agreement with observation reported elsewhere (Kelliher *et al.*, 1980; Turner 1986; Reader *et al.*, 1992), possibly because of reduced cell expansion or shortage of assimilate supply during the stress (Gollan *et al.*, 1985). The number branches were increased in the dry and intermediate treatments for *Acacia ehrnbergiana* and *Acacia asak*, while *Acacia negrii* had fewer branches (Fig 5.15). Characteristics of the desert plants include: short height, leaf shedding and numerous stems (Evenari *et al.* 1971; Migahid *et al.*, 1974). In the present study we observed an increase in the number of branches, shedding leaves and replacement by new smaller leaves. However, the total leaf production was high in the control treatment (Fig 5. 16). Metcalfe *et al.*, (1990) found that leaf production of *Eucalyptus globulus* seedlings was substantially reduced as a result of the drought treatment. The severe development of water stress significantly reduced both leaf initiation and total leaf area of water-stressed *Acer pseudoplatanus* L. seedlings relative to control (Khalil and Grace, 1992). Contrary to that, root elongation into deep layers occurs at higher rates under the conditions of moisture stress. The practical conclusion reached from this study is that newly planted *Acacia* seedlings grown under arid region should be watered at different frequencies according to stage of growth. Earlier responses of shoot and root growth to soil drying could maintain productivity of plants during water shortage before major, damaging effects of water stress develop, and this may be considered as an important mechanism in afforestion situations.

These species are domesticated and are commonly grown together in the same arid zone region, but their responses to similar drought stresses can differ. Most species in the arid zone that can endure drought usually possess mechanisms such as large root systems which help maintain high leaf water potential and postpone desiccation. Regarding morphological traits, probably the best approach would be to develop plants that have characters which postpone desiccation such as reduced leaf area and large root system. Seedlings growing individually in deep soils are able to show their capacity for soil water exploration during soil drying as determined by root dry weight and root penetration. Also it can show and account for the root development without damage the root. The results reported here suggest that the differential root growth responses of *Acacia* seedlings to soil drying could provide basic information on which to base the selection under arid environment, such Saudi Arabia. In this study, *Acacia negrii, A. asak* and *A. ehrnbergiana* were compared. This result indicates **that *Acacia negrii* (2200 m a.s.l) was produced large total length root at these depths than *Acaia asak* (500 m a.s.l) and *A. ehrnbergiana* (sealevel). This suggests that *Acacia negrii* utilised more water at these depths than *A. ehrnbergiana* and *A. asak*.**

The result of these studies indicate guidelines for future species selection after further expanded experiments in a field site. This would help the future afforestation programs in the region.

5.5 Conclusions

1. The major responses to water shortage were: *Acacia negrii* is from upland 2200 m a. s. l., *A. asak* is from 500 m a. s. l. and *A. ehrnbergiana* is from sea level.

2. All the three species under three water regimes increased dry matter to the root at the expense of stem and leaf biomass. This supports the view that root growth of desert living trees may show considerable morphological plasticity enabling them to cope with changes in soil moisture (Bradbury 1990).

CHAPTER 6

The Impact of Soil Drying on the Gas Exchange of *Acacia negrii* and *A. ehrnbergiana*

6.1 Introduction

Water deficits can have a major impact on the establishment success of tree seedlings. Differences in water deficit among various soils and stands have been related to differences in the growth and physiology of seedlings undergoing establishment (Kramer, 1983). The structural and physiological adaptations associated with drought tolerance of plants are numerous and diverse (Turner, 1979; Osonubi and Fasheun, 1987; Pallardy and Rhoads, 1993), although many attributes appear to be more important for plant survival than for high growth rates (Turner, 1986). Decreasing the availability of water is likely to reduce photosynthesis either directly or indirectly. Direct effects on the photosynthetic machinery are manifest as a reduction in the carboxylation rate or as a reduction in the quantum efficiency (Chaves, 1991). Indirect effects may operate through the restriction of CO_2 supply brought about by stomatal closure (Pallardy and Kozlowsky, 1979; Ni And Pallardy, 1991). Control of water vapour loss, by increasing stomatal resistance, allows a tree to tolerate water stress within a certain range (Federer and Gee, 1976; Clement and Jones, 1978). Most desert plants have minimal transpiration as result of an inherently high stomatal resistance, but there do exist the so-called 'water spenders' that have high rates of water loss, deep roots, and fast growth (Levitt, 1972; Ehleringer *et al.*, 1991). Some aridity-resisting plants are able to close their pores remarkably quickly during periods of high temperature, opening them only for short periods in the mornings for photosynthesis to take place (Levitt, 1972). For example the species *Annona coriacea* take 30 minutes to close pores. But *Ziziphus phylacantha* take 5 minutes or less, and opens stomata only for a short period during the mornings when water stress is less severe (Levitt, 1972). Brix (1962) was one of the first to show photosynthesis was reduced in proportion to transpiration when *Pinus taeda* L. seedlings were water stressed, suggesting that the rates were regulated by the stomata but Beadle and Jarvis (1977) calculated that 50 % of the reduction in photosynthetic rate in water stressed *Picea sitchensis* (Bong.) Carr. seedlings was accounted for by decreased mesophyll conductance before stomatal regulation became important.

Chartzoulakis *et al.*, (1993) found that water deficit reduced the rate of photosynthesis by 53 - 64 % in relation to unstressed controls and suggested that the decline was attributable to stomatal closure.

The objective of this study was to determine the effects of water deficits on photosynthesis and the tissue water relations of *Acacia negrii* and *Acacia ehrnbergiana* seedlings during a soil cycle of drying and rewatering. The hypothesis is that the more xeric species exhibit higher photosynthetic rates under water stress, and that water use efficiency of xeric species is greater than that of mesic species regardless of the conditions.

6.2 Material and Methods.

6.2.1 Plant material and design of the experiment

In March 1994 more than 100 seeds of *Acacia negrii* and *A. ehrnbergiana* were germinated in the glasshouse at the Institute of Ecology and Resource Management, University of Edinburgh. Seedlings at the two leaf stage were transplanted into pots 6 cm diameter and 10 cm depth, filled with a soil mixture as described in Section 4.2.1. Seedlings were kept on the greenhouse bench, under a natural photoperiod of 11-14 hours, with mean temperature 25 °C. While in the glasshouse, seedlings were watered daily to field capacity. Four months later 80 plants were selected for vigour and moved to a growth chamber to acclimate for 14 days before gas exchange measurements were begun. At this time shoots were between 35 and 40 cm height. The growth chamber conditions were: 12 hour days with photon flux density of 450 μ mol m^{-2} s^{-1} in the waveband 400-700 nm at ambient temperature 25 °C during the day and 20 °C at night. Relative humidity was between 60 to 70 %.

These plants were transplanted into long soil columns of the above described compost, to allow relatively unrestricted root growth. Each column contained one seedling, and was 30 cm in length and 12 cm in diameter depth. Perforation at the base and on its walls at 10 cm intervals from the base to the middle of the containing tube permitted free drainage and aeration of the soil. Tubes were packed with soil to a uniform bulk density. During establishment, irrigation was carried out every other day.

After four weeks 30 seedlings of similar size and vigour from each species were selected for study and arranged in a randomized design. Half the seedlings were randomly assigned to the water stress (WS) treatment whilst the other half were designated well watered (WW) control. Water was withheld from WS plants until the end of the experimental period.

The WW plants were watered every other day to field capacity. Starting from day one, measurements were made of gas exchange, leaf water potential and soil water content approximately every week. All measurements were made between 11 am and 2 PM. After 24 days, all the water-stressed seedlings were rewatered.

6.2.2 Soil water content

During each measurement, three random samples were taken from each treatment for the determination of gravimetric water content. At the midpoint of each 10 cm soil layer, a 2 cm diameter soil core was taken for each treatment. The holes were then refilled and sealed. The gravimetric determinations were converted to volumetric water content by multiplying by the bulk density.

6.2.3 Gas exchange measurements

Leaf net photosynthesis (A, μmol m^{-2} s^{-1}, leaf area basis) and stomatal conductance (g_s) were measured during a cycle of water stress (24 days). Photosynthesis was also monitored for 17 days after rewatering. Gas exchange rates were measured on nearly fully expanded leaves from the upper third of each seedling. To ensure a good seal, thorns were removed from the stem at the point at which the leaf entered the cuvette (Parkinson conifer leaf chamber, Model 1724, Analytical Develoment LTD, UK). Gas exchange was measured between 11.00 to 14.00 hr, using an Infrared Gas Analyser (LCA-3, ADC Ltd, Hoddesdon, UK). The measurements were made on the bench opposite the growth room in order a) to prevent a build-up of CO_2 inside the growth room (due to breathing in the confined volume) that could have affected the measurements, and b) to ensure saturating light conditions (1500-1600 μmol m^{-2} s^{-1}) by means of an artificial source light (400 watt MBIF). Each plant was brought from the growth room onto the bench immediately before the measurements were made. Inside the leaf chamber, the temperature was 29-30 °C, humidity 15 % and CO_2 concentration was 350 ppm.

Before each session of measurements the IRGA was calibrated using scrubbed air (zero check) and a cylinder of 350 ppm CO_2 , and the humidity sensors were checked with the leaf cuvette closed and empty. The IRGA was swiched on about 30 minutes before starting the measurements to warm up and reach a steady "zero". During the readings the parameters displayed by the analyser (CO_2 differential, reference-analysis

CO_2 concentration , flow rate, air and leaf temperature, relative humidity in and out, and PAR) were monitored. When a steady value of CO_2 differential was apparent a record was made.

The leaf area enclosed in the cuvette was estimated from the leaf length and the leaf width. Photosynthesis and transpiration rates as well as stomatal conductance were calculated according to the von Caemmerer and Farquhar (1981) equations. The drought cycle lasted until plants showed severe symptoms of water stress. The ratio between photosynthesis (*A*) and transpiration (*E*) was used to estimate water use efficiency (Davies and Kozlowski 1977):

$$\mathrm{WUS} = \frac{A}{E}\ (\mu \text{ mol } \mathrm{CO_2}\ \mathrm{m^{-2}s^{-1}} / \text{mmol } \mathrm{H_2O}\ \mathrm{m^{-2}s^{-1}})$$

Transpiration (*E*) rate was calculated using the formula of von Caemmerer and Farquhar 1981:

$$E = ((e_o - e_i)/(p - e_o)) \times w \text{ mol } \mathrm{m^{-2}s^{-1}})$$

Where:

e_o - is the vapour pressure of water, in air in cuvette

e_i - is the vapour pressure of water at inlet

p - is the atmospheric pressure

w - is the mass flow of dry air per unit leaf area (mol $\mathrm{m^{-2}s^{-1}}$)

6.2.4 Leaf water potential and leaf area measurements

After each gas exchange measurement, water potential (Ψ) of four samples per treatment was immediately determined with a pressure chamber (Scholander *et al* 1964). The pressure was then applied until water appeared at the cut surface. The measurements were made during the soil drying treatment to determine the effect of soil water content on the leaf water potential. At the end of the experiment leaf area was determined by portable leaf area-meter (Model CI-201, Moscow, ID, 83843 USA).

6.2.5 Tissue water relations

The tissue water relations of twigs bearing several leaves were determined using the pressure-volume technique (Tyree and Hammel 1972). At the end of the last drying cycle (24 days) and after rewatering (17 days) the procedure was repeated as described in Chapter 4.

4.6.2.6 Dry matter production and partitioning

At the end of the experiment four seedlings were destructively harvested per treatment, to estimate the influence of the drought on dry matter production and allocation among the different parts of the plant and between the species. The plants were divided into leaves, stems and roots. Leaf, stem and root material were then dried at 80 °C for dry weight determination. The leaf area was measured with the portable leaf-area meter.

6.2.7 Data analysis

Plants were randomized over the experimental bench. Unless otherwise indicated, data presented are the mean value ± standard error, calculated from a minimum of four replicates per treatment. Significant differences between treatments, as described in the text, and at each sample interval were determined by the Student's t-test. Where appropriate, the correlation coefficient is used to test the statistical significance of linear relationships.

6.3 Results

6.3.1 Soil water content

Soil water contents in the droughted treatments declined progressively to very low levels at 24 days, whilst the controls remained more or less constant (Fig 6.1).

6.3.2 Leaf water potential

The leaf water potentials of both treatments throughout the experiment are represented in Fig 6.2 and Fig 6.3 for *Acacia negrii* and *Acacia ehrnbergiana* respectively during the period following the initial decline of soil water content. The leaf water potential of the stressed seedlings showed no significant response to water stress until week 2 when a decline was observed in both species. At the end of the experimental period there were highly significant (*P*<0.001) differences between treatments. A good linear relationship was found between leaf water potential and soil water content for both species (Fig 6.4 and 6.5). The relationship between net photosynthesis and leaf water potential was also linear (Fig 6.6 Fig 6.7). Under unwatered conditions, leaf water potential was highest in *Acacia negrii* and lowest in *Acacia ehrnbergiana* The water potential was constant from -0.8 to -1.0 MPa in the control treatment for both species.

Within 24 hours after rewatering leaf water potential rapidly increased from -2.29 to -2.25 MPa for *Acacia ehrnbergiana.* Similarly it increased from -2.55 to -2.26 MPa for *Acacia negrii.* Thereafter, leaf water potential slowly recovered to that of the control seedling for both species.

6.3.3 Stomatal conductance

With progressive drying of the top layer within the soil column there was a gradual decline of stomatal conductance which was significant (*P*<0.05) in both species. After the second week of the drying period stomatal conductance appeared to decrease gradually (Fig 6.2 and 6.3). Thereafter stomata conductance was very sensitive to soil water content for both species.

Stomatal conductance of both species was significantly correlated (*P*<0.05) with the soil water content during the water-stressed period (24 days). There was a linear relationship between stomatal conductance and soil water content and leaf water potential (Fig 6.4 and 6.5 respectively). The relationship between net photosynthesis and stomatal conductance was also linear and highly significant (*P*<0.001) for both *Acacia negrii* and *Acacia ehrnbergiana* seedlings (Fig 6.6 b and Fig 6.7 b respectively)

After rewatering, the stomatal conductance of both species recovered from 0.5 mol $m^{-2}s^{-1}$ to 1.5 mol $m^{-2}s^{-1}$ within 24 hours. Thereafter, the stomatal conductance recovered to that of the control seedlings.

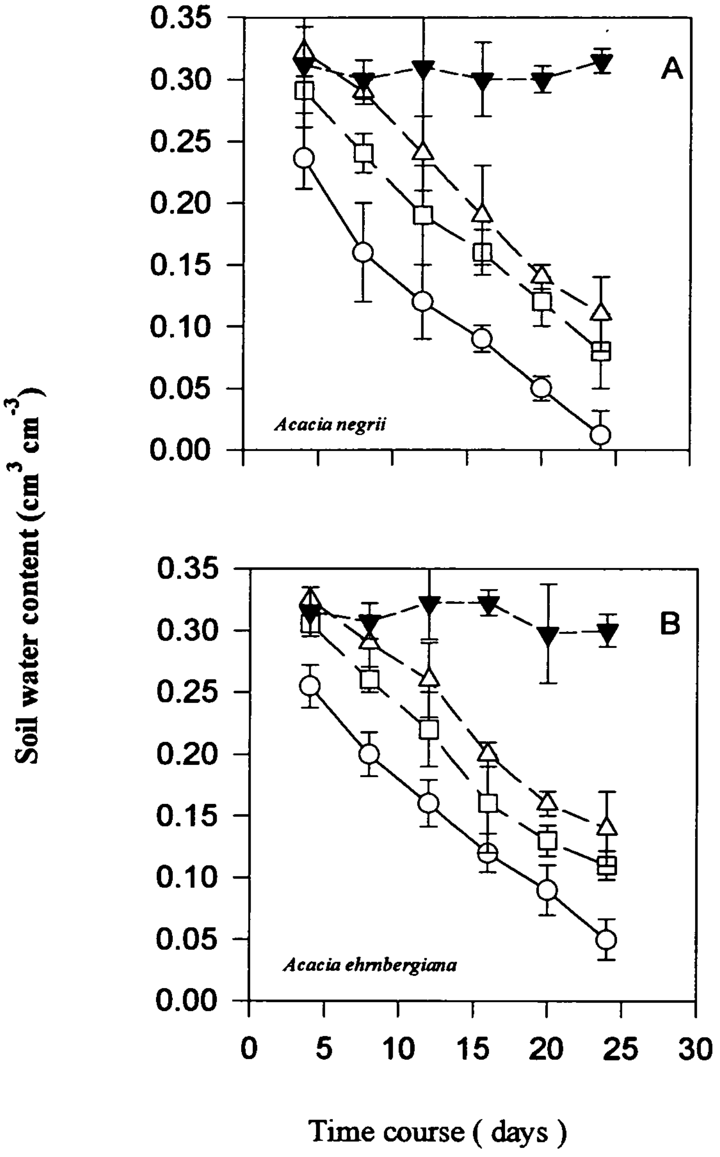


Figure 6.1: Change with time of soil water content for (A) *Acacia negrii* and (B) *Acacia ehrnbergiana* of three layers (O) depth 10 cm, (□) depth 20 cm, (Δ) depth 30 cm and control average of all depths (▼). Points are means of four determinations ± standard error.

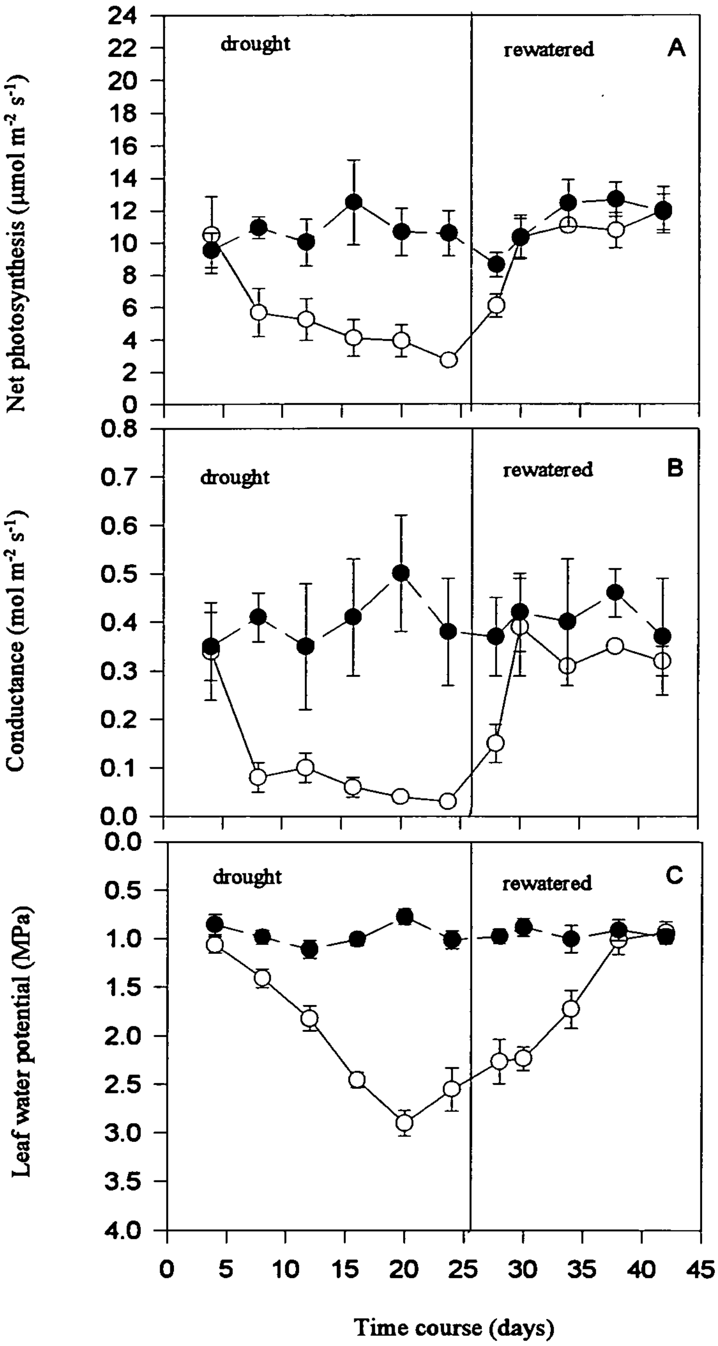


Figure 6.2: Change with time in (A) photosynthesis, (B) stomatal conductance and (C) leaf water potential during soil drying and after rewatered for *Acacia negrii* of watered (●), and stressed (O) plants. Points are means of five determinations ± standard error.

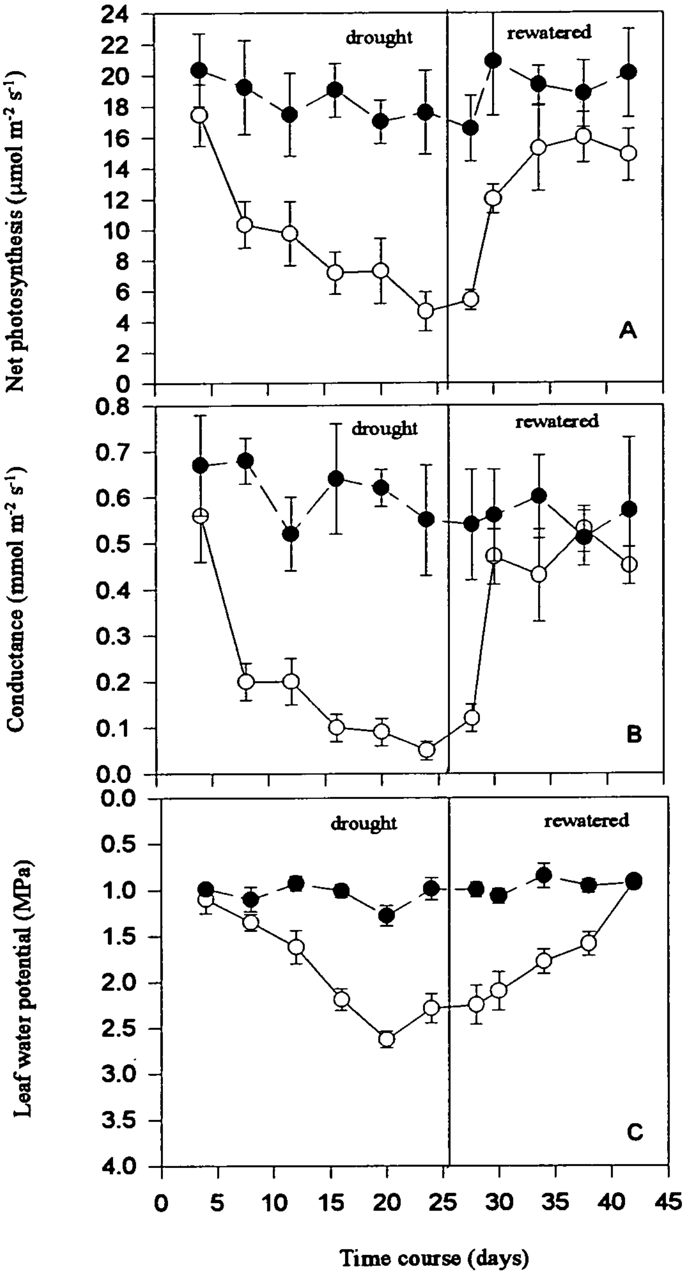


Figure 6.3: Change with time in (A) photosynthesis, (B) stomatal conductance and (C) leaf water potential during soil drying and after rewatered for *Acacia ehrnbergiana* of watered (●), and stressed (O) plants. Points are means of five determinations ± standard error.

6.3.4 Tissue water relations

In both species, the water relations parameters changed in much the same manner as already described in section (4.3.5). The values are tabulated in Table 6.1 and 6.2. On rewatering, the rewatered plants recovered or nearly-recovered to the parameter values of the always-watered controls (Table 6.1 and 6.2)

Table 6.1: Effects of water stress on tissue water relation parameters derived from pressure-volume analysis of *Acacia negrii* twigs.

Osmotic potential at full turgor (π_{100}), osmotic potential at zero turgor (π_0), relative water content at zero turgor (R_0), bulk modulus of elasticity (E), and dry weight/turgid weight ratio (DW/TW) of leaves, of well watered and water stressed seedling. Value are means of four determinations ± standard error. Comparison of means is by t-test with 6 degrees of freedom.

Acacia negrii		**Droughted**		
Variables	**unwatered**	**watered**	**t-test**	***P***
π_{100} (MPa)	-2.19±0.08	-1.88±0.02	3.44	0.006
π_0 (MPa)	-2.39±0.07	-2.11±0.06	2.8	0.01
R_0 %	75.5±2.1	86.25±2.5	3.32	0.007
E (MPa)	19.2±3.1	12.6±4.0	2.0	0.04
DW/TW ratio	0.36±0.02	0.30±0.02	2.5	0.01
Acacia negrii		**Rewatered**		
Variables	**rewatered**	**watered**	**t-test**	***P***
π_{100} (MPa)	-1.65±0.16	-1.23 ±0.15	1.92	0.05
π_0 (MPa)	-1.86±0.17	-1.57±0.12	1.32	0.11
R_0 %	80.7±6.5	83±3.5	0.36	0.36
E (MPa)	17.2±1.4	15.01±3.7	0.83	0.21
DW/TW ratio	0.36±0.03	0.30±0.01	1.96	0.04

Table 6.2: Effects of water stress on tissue water relation parameters derived from pressure-volume analysis of *Acacia ehrnbergiana* twigs.

Osmotic potential at full turgor (π_{100}), osmotic potential at zero turgor (π_0), relative water content at zero turgor (R_0), bulk modulus of elasticity (E), and dry weight/turgid weight ratio (DW/TW) of leaves, of well watered and water stressed seedling. Value are means of four determinations ± standard error. Comparison of means is by t-test with 6 degrees of freedom.

Acacia ehrnbergiana			**Droughted**	
Variables	**unwatered**	**watered**	**t-test**	***P***
π_{100}(MPa)	-2.28±0.2	-1.42 ±0.08	3.96	0.008
π_0 (MPa)	-2.42±0.21	-1.61±0.06	3.55	0.01
R_0 %	67.3±6.6	81.7±3.5	1.22	0.14
E (MPa)	24.0±3.1	15.7±4.2	2.69	0.02
DW/TW ratio	0.36±0.02	0.30±0.01	2.40	0.03

Acacia ehrnbergiana			**Rewatered**	
Variables	**rewatered**	**watered**	**t-test**	***P***
π_{100}(MPa)	-1.68±0.09	-1.66 ±0.13	0.11	0.45
π_0 (MPa)	-2.02±0.17	-1.88±0.16	0.52	0.30
R_0 %	78.5±7.33	78.8±5.2	0.03	0.48
E (MPa)	22.9±3.0	17.8±4.2	1.4	0.10
DW/TW ratio	0.30±0.04	0.30±0.05	0.0	0.5

6.3.5 Net photosynthesis (*A*), water use efficiency (WUE) and internal CO_2 concentration (C_i)

After water was witheld, the rate of net photosynthesis (*A*) decreased immediately (Fig 6.2 and 6.3). Eight days after water was witheld, net photosynthesis in the unwatered treatment was 60 % and 55 % of the control for *Acacia negrii* and *Acacia ehrnbergiana* respectively. The reduction in net photosynthesis was continuous until measurements in the unwatered treatment ceased at 24 days. However, net photosynthesis was significantly different between watered and unwatered plants for *Acacia negrii and A. ehrnbergiana*.

The results in this experiment indicate that water stress conditioning had a significant effect on the response of photosynthesis to decreasing soil water content, for both *Acacia negrii* (Fig 6.2) and *Acacia ehrnbergiana* (Fig 6.3). The relationship between net photosynthetic rate and soil water content was linear and significant ($P < 0.05$) in both *Acacia nergii* (Fig 6.4) and *Acacia ehrnbergiana* seedlings subjected to soil drying (Fig 6.5). In both *Acacia negrii* and *Acacia ehrnbergiana* there were highly significant ($P<0.001$) linear relationships between net photosynthesis and stomatal conductance.

After rewatering, net photosynthesis of the *Acacia negrii* seedlings recovered from 2.9 μmol $m^{-2}s^{-1}$ to 7.0 μmol $m^{-2}s^{-1}$ over 24 hours. Thereafter, net photosynthesis recovered to that of control seedlings. Similarly, the net photosynthesis for *Acacia ehrnbergiana* recovered slowly to a rather lower level than in control seedlings (Fig 6.2, 6.3 and 6.9).

Water use efficiency (WUE) increased from 2.0 μmol $mmol^{-1}$ to 2.7 μmol $mmol^{-1}$ in the second week for water stressed *Acacia negrii* (Fig 6.7), and increased from 1.7 to 1.9 μmol $mmol^{-1}$ for water stressed *Acacia ehrnbergiana* (Fig 6.8). The WUE was higher than in the control plants until the end of droughted period for both species. After rewatering, the WUE for unwatered seedlings of both species recovered to that of the control seedlings (Fig 6. 7 and 6.7).

With the progressive drying of the soil column there was a gradual decline of internal CO_2 concentration (C_i) which was significant in both species (Fig 6.8). At the end of the water stressed period the internal CO_2 decreased from 250 μmol mol^{-1} to 102 μmol mol^{-1} for *Acacia ehrnbergiana*, and decreased from 230 μmol mol^{-1} to 171 μmol mol^{-1} for *Acacia negrii*. After rewatering, the internal CO_2 of droughted seedlings recovered to that of the control plant within 24 hours. Figure 6.10 shows that *Acacia negrii* undergoes reductions photosynthesis that are not caused by reduction in C_i (Fig 6.11).

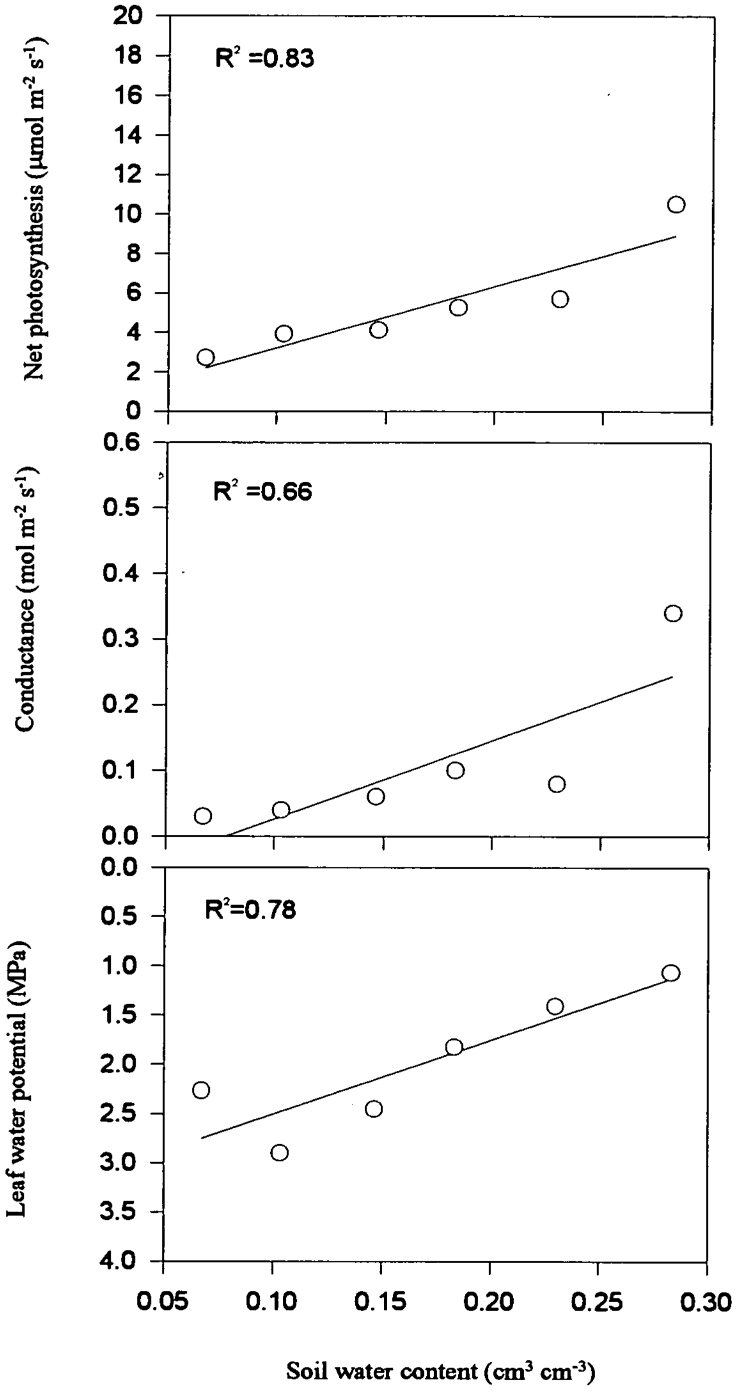


Figure 6.4: Linear relationship between photosynthesis, leaf conductance and leaf water potential versus soil water content of water stressed for *Acacia negrii*. Data points are the means of four samples.

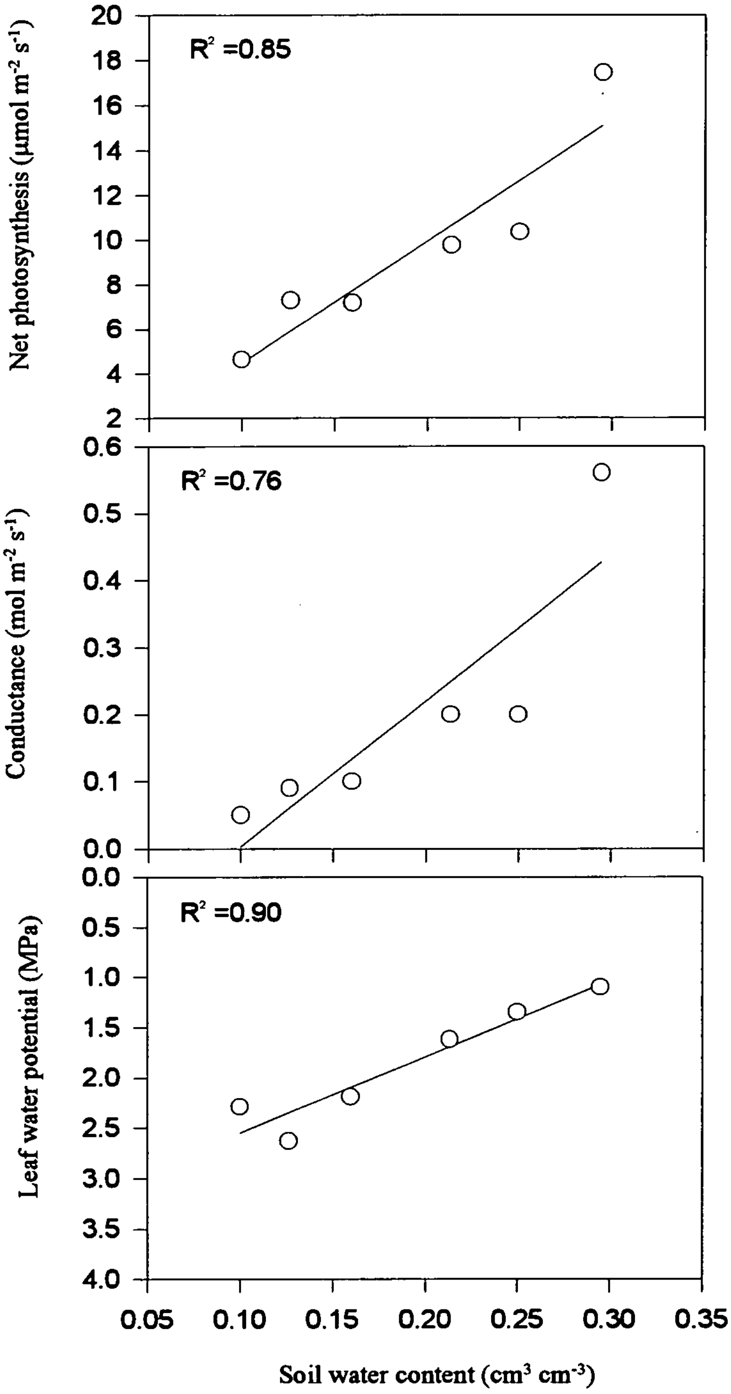


Figure 6.5: Linear relationship between photosynthesis, leaf conductance and leaf water potential versus soil water content of water stressed for *Acacia ehrnbergiana*. Data points are the means of four samples.

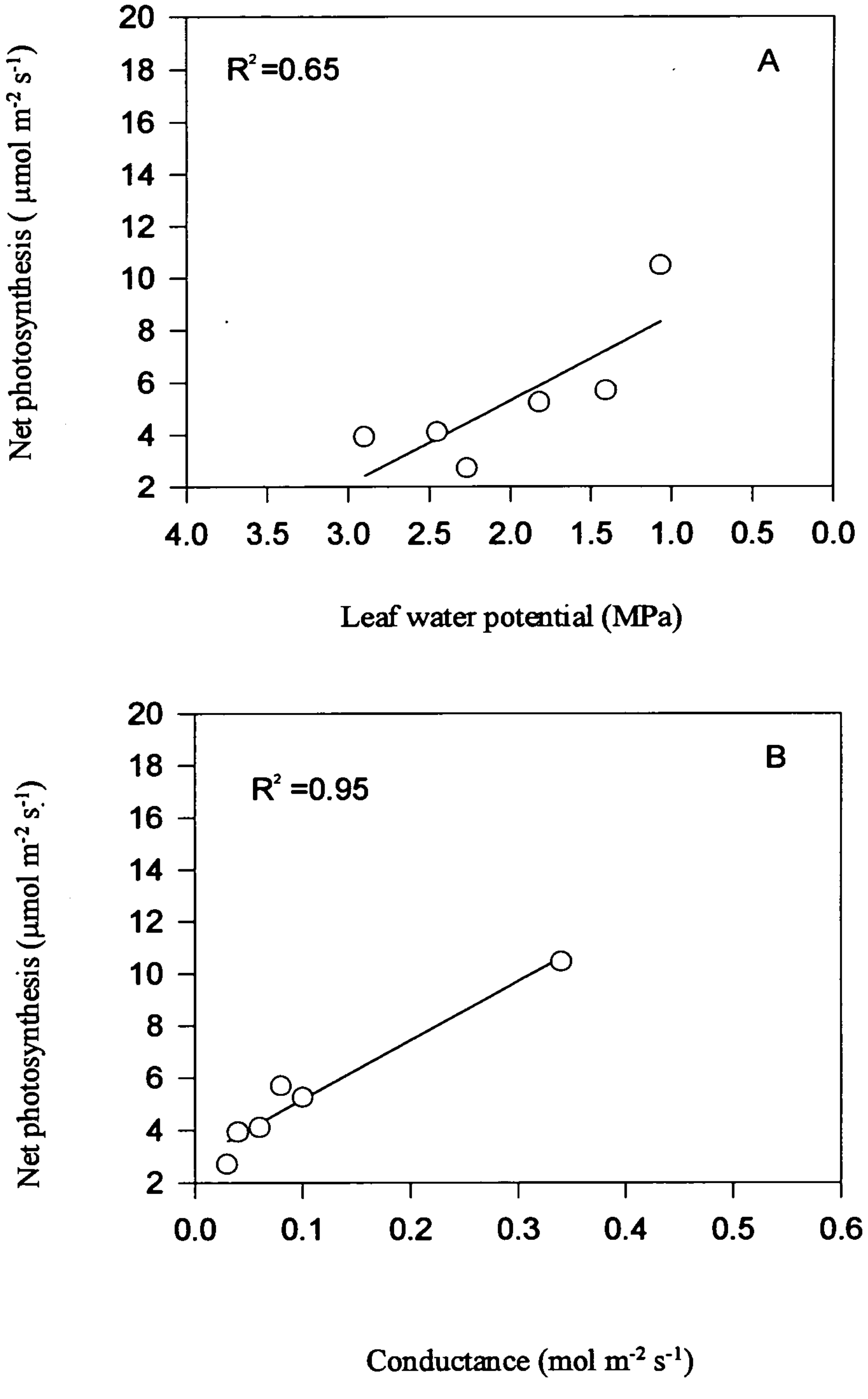


Figure 6.6: Linear relationship between photosynthesis and leaf water potential and photosynthesis and leaf conductance of water stressed for *Acacia negrii.* Data points are the means of five samples.

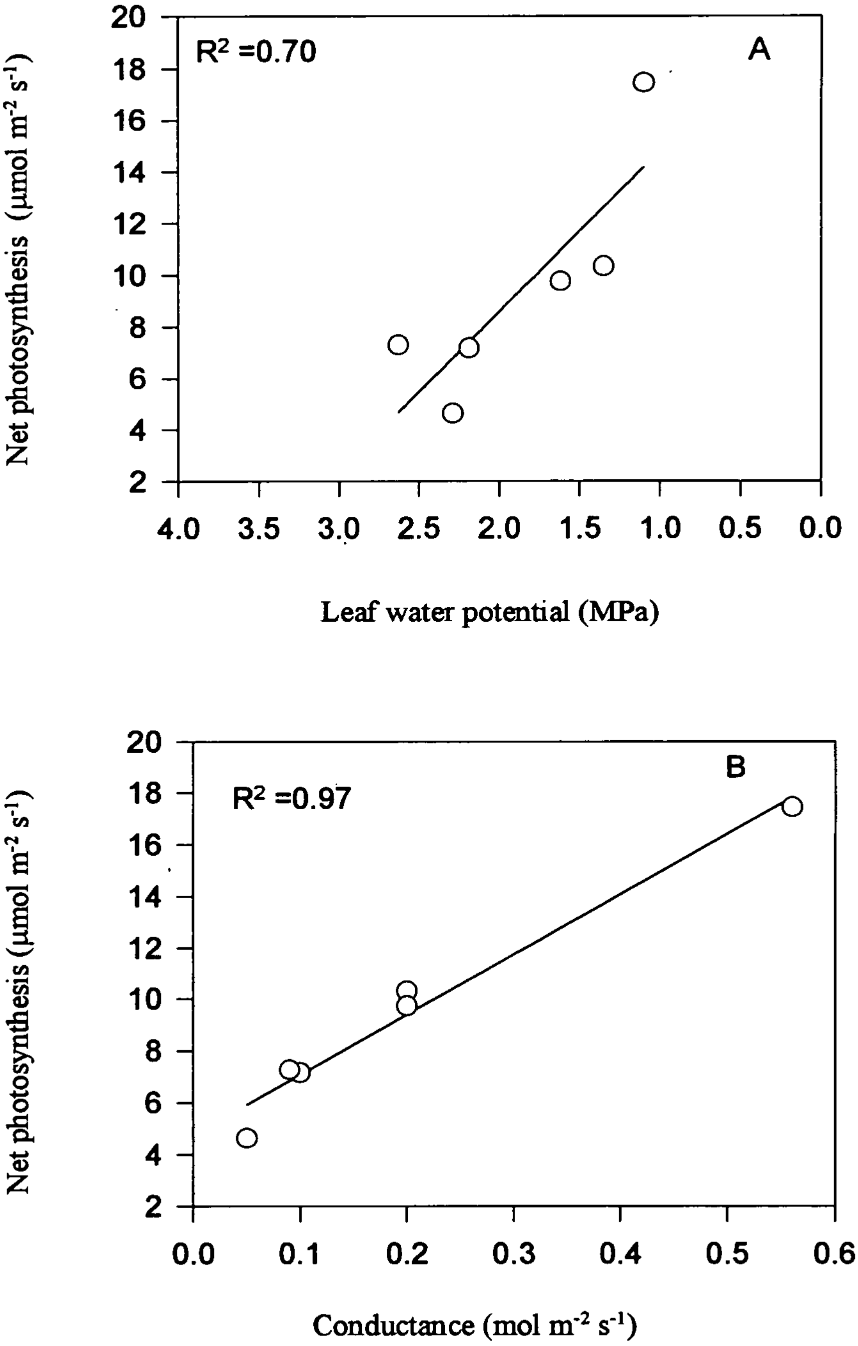


Figure 6.7: Linear relationship between photosynthesis and leaf water potential and photosynthesis and leaf conductance of water stressed for *Acacia ehrnbergiana*. Data points are the means of four samples.

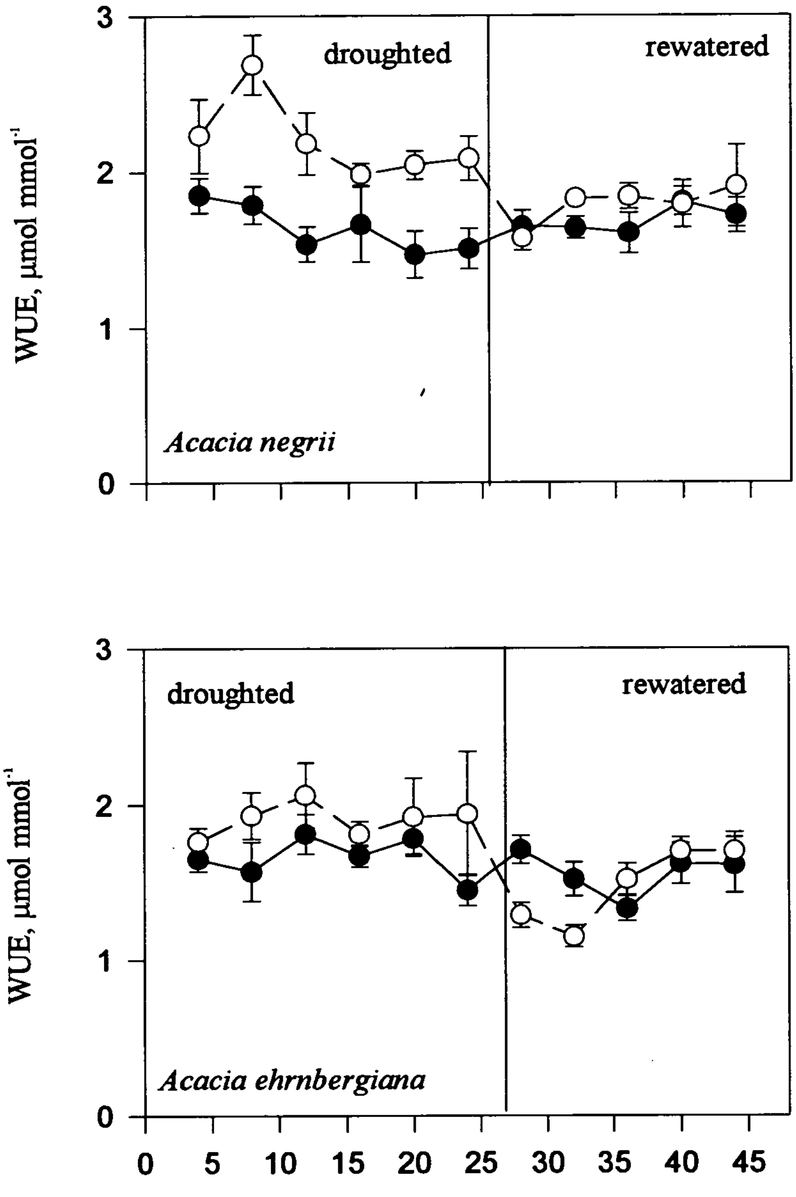


Figure 6.7: Water use efficiency (WUE = photosynthesis/ transpiration) of watered (●) and stressed (O) *Acacia negrii* and *Acacia ehrnbergiana* seedlings, in response to soil drying. Data points are the means of five determinations ±standard error.

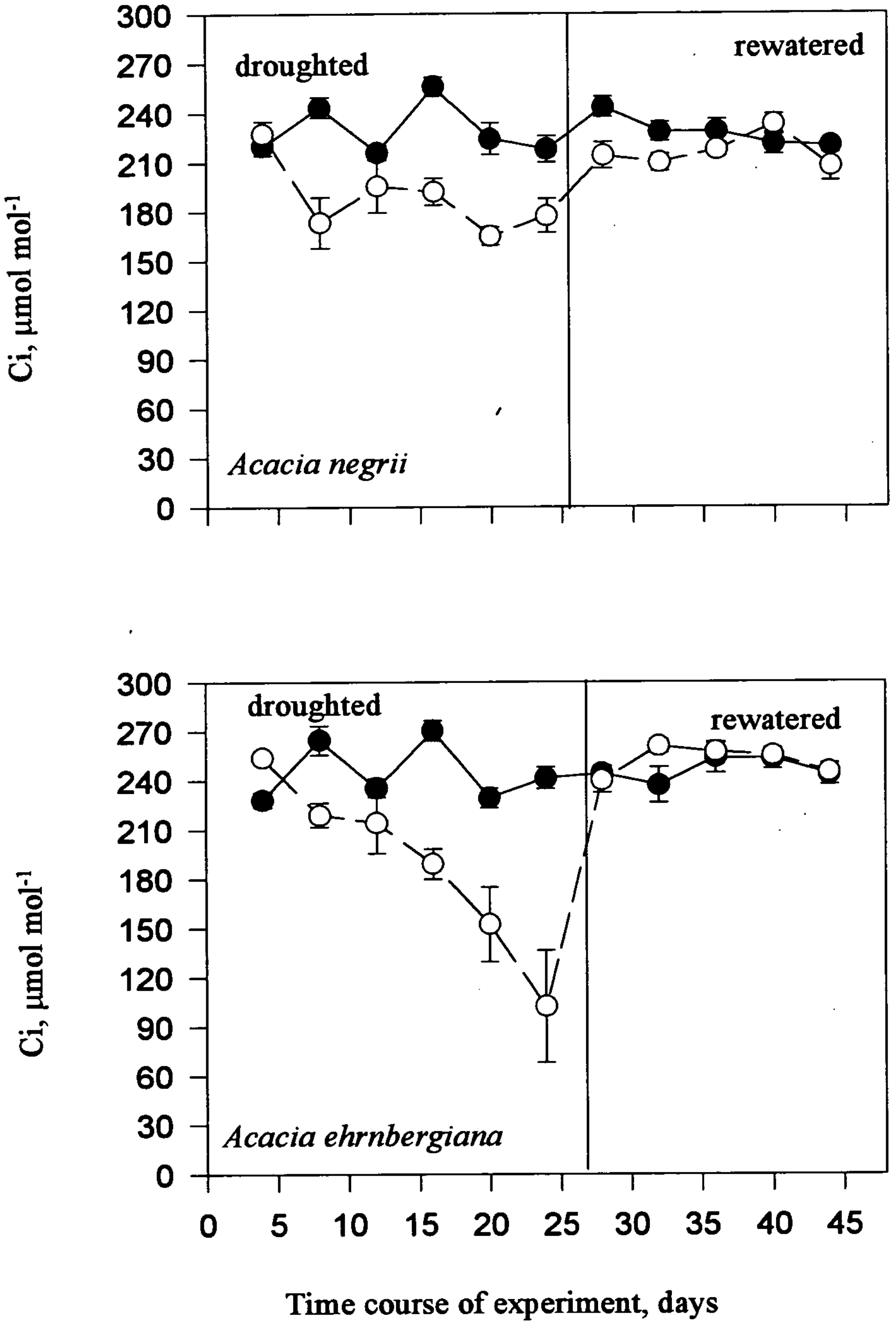


Figure 6.8: Internal CO_2 concentration (C_i) of watered (●) and stressed (O) *Acacia negrii* and *Acacia ehrnbergiana* seedlings, in response to soil drying. Data points are the means of five determinations ± standard error.

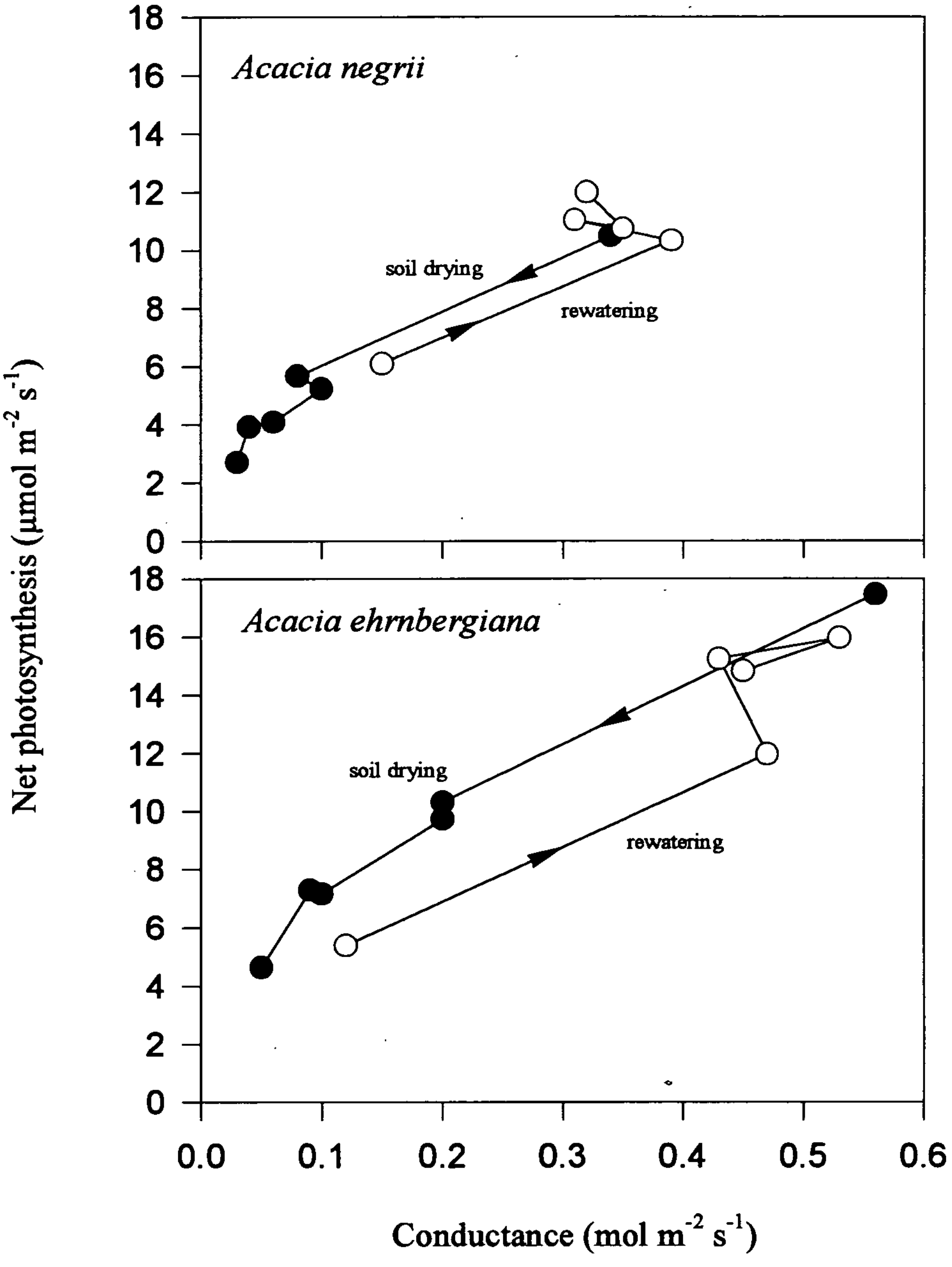


Figure 6. 9: The plot of the net photosynthesis versus stomatal conductance ( ) during soil drying and (O) after rewatering for *Acacia negrii* and *Acacia ehrnbergiana.*

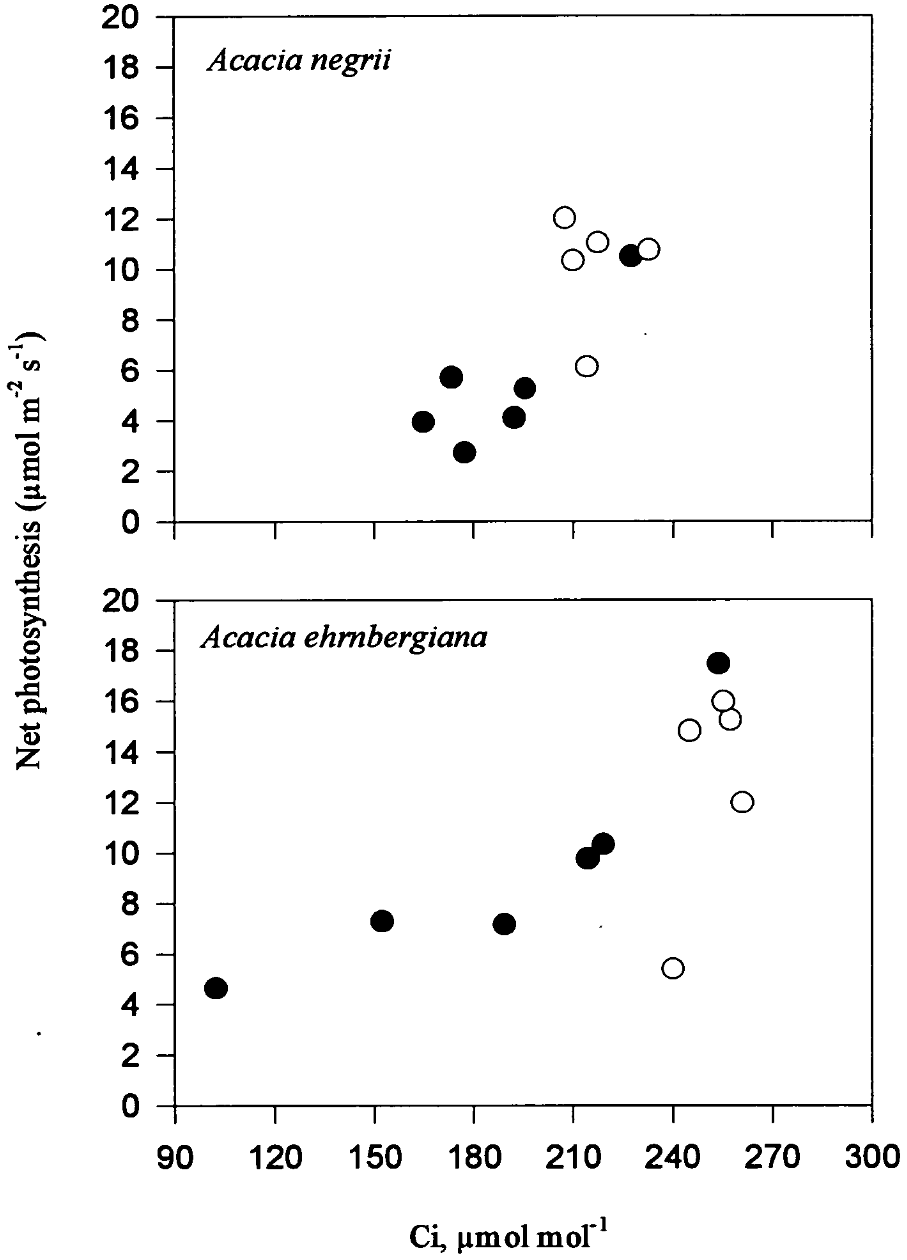


Figure 6.10: The plot of the net photosynthesis versus Internal CO_2 concentration (C_i), (●) during soil drying and (O) after rewatering for *Acacia negrii* and *Acacia ehrnbergiana*.

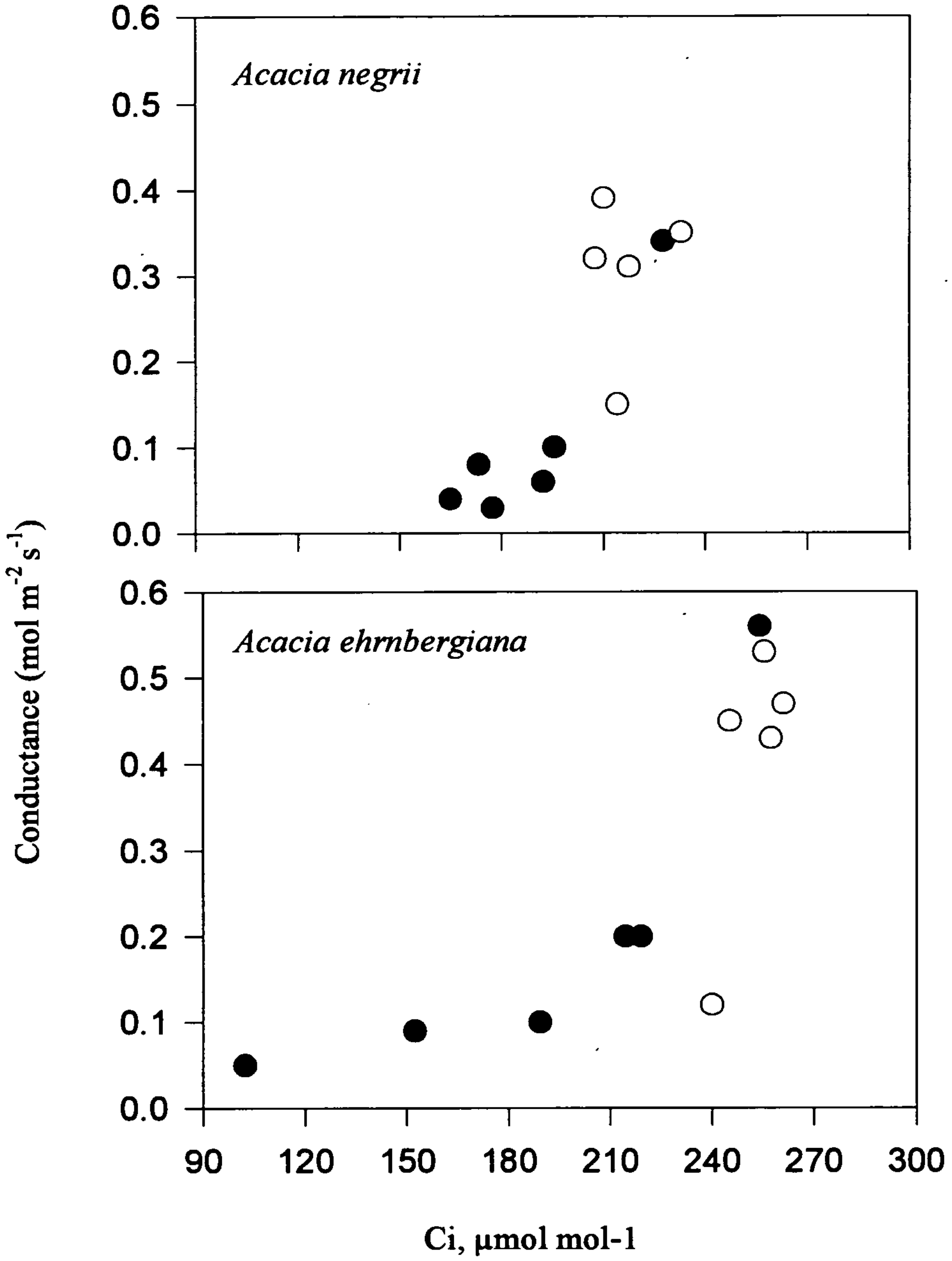


Figure 6.11: The plot of the leaf conductance versus (C_i) Internal CO_2 ( ) during soil drying and (O) after rewatering for *Acacia negrii* and *Acacia ehrnbergiana*.

6.3.6 Biomass production and partitioning

Table 6.3 shows the analysis of the biomass production of the different above and below ground constituents of the watered and unwatered seedlings at the end of the experiment. After 17 days from rewatering, total biomass and leaf area were unaffected by soil drying, but was significantly different between species ($P<0.01$). However, leaf dry weight was significant ($P<0.05$) between treatments for *Acacia. ehrnbergiana.* Soil drying resulted in an increase in absolute root dry weight. Therefore, in water stressed seedlings, the significant ($P<0.05$) increase in root/shoot ratio was due to a substantial shift in dry matter partitioning in favour of below ground development. In general, the shoot fraction of total dry matter decreased in water stressed seedlings, while the root fraction increased.

Table 6.3 : Analysis of biomass production of *Acacia* seedlings at the end of the experiment (44 days). Values are the means of four determinations ± standard error. Comparison of means is by t-test with 6 degrees of freedom.

Acacia negrii

	Watered	**Unwatered**	**t-test**	***P***
Total leaf area (cm^2)	399±33	329±33	1.49	0.18
Leaf dry weight (g)	4.2±0.2	3.4±0.3	2.40	0.05
Stem dry weight (g)	7.8±0.6	6.8±1.1	0.79	0.45
Total shoot weight(g)	12.0±0.5	10.3±1.2	1.37	0.15
Root dry weight (g)	2.7±0.3	3.7±0.6	1.51	0.18
Root shoot ratio	0.22±0.02	0.9±0.1	1.97	0.09
Total biomass (g)	14.8±0.9	14.0±1.2	0.49	0.63

Acacia ehrnbergiana

	Watered	**Unwatered**	**t-test**	***P***
Total leaf area (cm^2)	309±62	223±9.8	1.35	0.22
Leaf dry weight (g)	3.3±0.3	2.1±0.14	3.2	0.01
Stem dry weight (g)	6.7±1.1	5.1±0.6	1.21	0.26
Total shoot weight(g)	10±1.5	7.3±0.4	1.84	0.11
Root dry weight (g)	1.9±0.3	2.5±0.4	1.34	0.22
Root shoot ratio	0.2±0.04	0.3±0.04	2.32	0.05
Total biomass (g)	11.9±1.5	9.7±0.6	1.30	0.23

6.4 Discussion

The aim of the present study was to investigate the impact of soil drying on the gas exchange of two *Acacia* species (*Acacia negrii* and *Acacia ehrnbergiana*). Leaf water potential, stomatal conductance and tissue water relations were measured in order to indicate the mechanisms involved in the growth responses.

The discussion of the leaf gas exchange, as one major component in whole-plant water and carbon flux, shows that stomata are regulated by two 'feedforward' responses namely air humidity and soil water status (Schulze, 1986). He also reported that photosynthesis is inhibited by soil water content, but the magnitude of this effect depends on the pretreatment. The droughted plants showed acclimation in water relations parameters, and in morphology that is much the same as represented in a pervious chapter (Chapter 4). Both species do undergo osmotic adjustment and photosynthetic rate at leaf water potentials as low as -3.0 MPa and -2.8 for *Acacia negrii* and *A. ehrnbergiana* respectively. Maintenance of photosynthesis at lower leaf water potential in cotton plants is associated with active osmotic adjustment (Ackerson, 1981). Osmotic adjustment has also been demonstrated in red spruce seedlings (Seiler and Cazell, 1990), and this response is associated with the maintenance of photosynthesis and turgor at low leaf water potential. These studies gave the primary role of osmotic adjustment to be the maintenance of the stomatal conductance, thereby avoiding stomatal limitations to photosynthesis at lower leaf water potential. Ackerson (1981) found that the stomata of drought adapted leaves remained partially open even at lower soil water content. Thus it is suggested that *Acacia negrii* and *Acacia ehrnbergiana* are able to maintain the stomatal conductance through osmotic adjustment. By this means the plant is able to cope with the adverse environmental conditions by determining the availability of water in the soil and regulating growth rate and gas exchange accordingly.

Both species show a declining stomatal conductance as soil water contents decreased. The linear relationships reported in chapter 4 are maintained, except for the very high conductances in the most hydrated state at the start of the experiment. This pattern of stomatal conductance suggests that soil drying can influence the transmission of non-hydraulic signals involved in root to shoot communication, inducing stomatal closure (Bates and Hall ,1981; Davies and Zhang, 1991). Recently, several investigators have reported that soil water status has an important influence on stomatal conductance independent of leaf water potential, particularly in the initial stages of soil drying (Schulze, 1986; Zhang and Davies, 1989). Although the stomatal conductance in *Acacia* seedlings decreased with decreasing soil water content, this response was significantly modified by a repeated drying cycle (see Chapter 4 and Fig 6.12). *Acacia ehrnbergiana* and *Acacia negrii* originate from the arid zone and are already adapted to drought. This resulted in reduced impact of drought on stomatal conductance such that *Acacia ehrnbergiana* (Fig 6.3) and *A. negrii* seedlings were able to maintain high stomatal conductance at a lower soil water content.

After rewatering, the stomatal conductance of the *Acacia negrii* seedlings recovered slightly more than *Acacia ehrnbergiana* during the 24 hours. These results should be important in any consideration of stomatal responses to water stress. Rapid stomatal closure, accompanied by delayed stomatal opening and subsequent partial closure, in response to change in soil water content, might minimise unnecessary water loss, and account for plant survival under conditions of low water availability (Levitt, 1972; Ehleringer *et al.*, 1991). Following rewatering, it is of some advantage to *Acacia negrii* and *Acacia ehrnbergiana* to limit stomatal opening and thus conserve available water. Maximal stomatal opening was not obtained in *Acacia ehrbergiana* until four days following rewatering. This response suggests that these species might compete successfully on sites where availability of water was very low such as arid zone (Saudi Arabia).

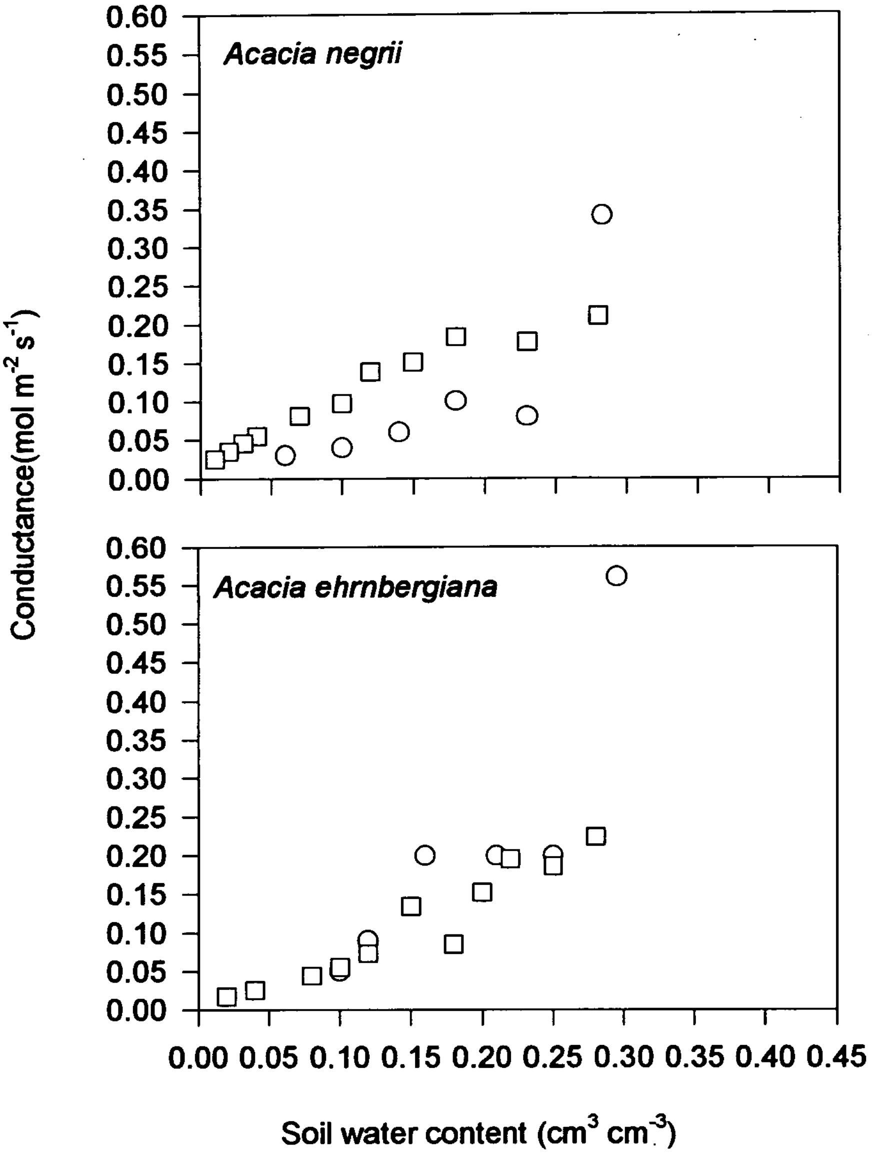


Figure 6.12: A relation between stomatal conductance and soil water content of water-stressed plants. Obtained by replotting the data from Figs (□) 4.6 A, 4.8 A and (O) from Figs 6.4 and 6.5., for *Acacia negrii* and *A. ehrnbergiana*.

As conductance declines, so does photosynthesis. Photosynthesis was reduced 60% and 55% for *Acacia negrii* and *Acacia ehrnbergiana* respectively after 8 days of the drought period (Fig 6.2 and Fig 6.3). There is a near-linear relationship between conductance and photosynthesis (Fig 6.9) with the exception of *Acacia ehrnbergiana* where the photosynthesis rate does not recover completely after rewatering, suggesting that some permanent damage has been done. Apart from this, the data are consistent with the view that drought affects photosynthesis through causing the stomata to shut. The photosynthesis machinery is either unharmed (*Acacia negrii*) or only slightly harmed (*A. ehrnbergiana*). This is the usual trend in photosynthesis as water deficits develop, since both stomatal conductance and chloroplast activity are adversely affected by water stress (Ehleringer *et al.*, 1991). In both species, photosynthesis was less effected water shorage, as there was little change in the photosynthetic rate until surface soil moisture was depleted by 40% during 4 days drought. Furthermore, even when photosynthesis was affected by water stress both species were able to maintain a significant higher photosynthetic rate at any level of soil water content. These results are in agreement with Ehleringer *et al.* (1991) who found that the desert plant *Hetermeles arbutifolia* had active photosynthesis at water potentials as low as -3.3 MPa. Kauhanen, (1986) found the photosynthetic rate was reduced by 25 to 30% at midday of birch (*Betula pubescens*). Positive net photosynthesis, although severely depressed by low stomatal conductance, still persists in such plants under extreme drought (Levitt, 1972; Ehleringer and Mooney, 1983; Ehleringer *et al.*, 1991). *Acacia negrii* and *Acacia ehrnbergiana* might utilize the extra carbon gained to extend their root system to great depths, enhancing water uptake, and consequently might survive longer and accumulate more biomass even over a long period of water stress. Also this result indicates a significant degree of the flexibility in both species, ability to acclimate to water stress with more severe stress resulting in greater acclimation.

The water potential of both species declined during the drought, making the plants more able to take up water. This may have been largely achieved by osmotic adjustment. On rewatering the water potential took 17 days to recover to the level of the controls. This could be because the acclimation to drought endures (Turner *et al.*, 1975), this being a useful feature as it may be that in nature, prolonged drought is followed by only light rains followed by sever drought again. Or, it may be that some cavitation in the xylem occurred, and refilling takes several days. The rapid recovery of photosynthesis after watering in the water stressed seedlings indicates that no long-term damage to the photosynthetic machinery occurred during exposure to water stress (Lee *et al.*, 1989).

The photosynthesis and stomatal conductance under water deficit were near-linearly in *Acacia negrii* and *Acacia ehrnbergiana* seedlings (Fig 6.6 and 6.7 respectively). This is thought to be due to the changes in internal CO_2 concentration (C_i) caused by an alteration in stomatal aperture (Fredrick *et al.*, 1989) (Fig 4.11). The results indicate that photosynthesis, stomatal conductance and the internal CO_2 concentration would change the same direction under water deficit for *Acacia ehrnbergiana* (Fig 4.9). This result is in agreement with Regehr *et al.* (1975) who found a very close correlation between stomatal aperture and photosynthesis in *Populus deltoides*. The stomatal closure causes a proportionately greater decrease in the transpiration than photosynthesis thereby increasing water use efficiency (WUE). The data of the Fig 6.7 shows another important observation in this study which is the substantial increase in water use efficiency in both species as water stress develops. The more mesic *Acacia negrii* had highest WUE whereas the more drought tolerant *Acacia ehrnbergian* a had a lower WUE value. Pereira *et al.* (1987) found a similar trend in *Eucalyptus globulus* where leaf WUE was higher under conditions of moderate drought stress. These results are in agreement with DeLucia and Heckathorn (1989) who found that seedlings of *Artemisia tridentata*, a common shrub of the Great Basin desert, had a lower WUE than did those of the more mesic *Pinus ponderosa*. The primary factor contributing to higher WUE for *Acacia negrii* was the rapid decrease in the stomatal conductance with decreasing water potential. DeLucia and Heckathorn, (1989) reported that the maintenance of high WUE is a conservative physiological strategy that may not be advantageous to native plants in competitive water-limited environments.

Water stress induced a significant shift in biomass allocation patterns in favour of below-ground parts of the plant. This shift was reflected in a significant increase in the root / shoot ratio (Table 6.3). A similar pattern of growth was observed in the present study when *Acacia negrii* and *Acacia ehrnbergiana* seedlings were grown in large soil columns and exposed to a continuous soil drying (Chapters 4 and 5). This response is interesting since root growth has been demonstrated to be important in the drought tolerance of many desert plants (Ehleringer *et al.*, 1991). Droughted *Acacia* species have been found to produce deeper, more extensive root systems, which may provide access to a greater water supply (Adams, 1967). The increased root production coupled with osmotic adjustment would make a significant contribution towards drought tolerance on site with low soil water content and high water stress. Osmotic adjustment alone, without root system changes allowing increase water uptake, would convey little advantage because sustained stomatal opening and CO_2 uptake will expose the plant to greater cellular water stress (Turner, 1986; Parker and Pallardy, 1988). Several differences in morphological and physiological change occurred in *Acacia negrii* and *Acacia ehrnbergiana* in response to drought. These changes include, acclimation of photosynthesis and stomatal conductance to water deficit, lowered transpiration, increased water use efficiency and a shift in biomass allocation pattern in favour of below-ground parts, which result in increased root/shoot ratio. All these modifications result in improvement of drought tolerance in arid environments.

6.5 Conclusion

In this study, there were some differences between seedlings from lowland and upland *Acacia* species in terms of either gas exchange and water relations during period of water stress.

1. Seedlings of the upland *Acacia negrii* had the lower net photosynthesis and stomatal conductance during the 24 days drought, than seedlings of the lowland *Acacia ehrnbergiana*.

2. After rewatering, seedlings of the upland *Acacia negrii* showed rapid recovery of net photosynthesis and stomatal conductance within the first 24 hours, while the lowland *Acacia ehrnbergiana* recovered more slowly. This suggests an importance of the *speed of recovery* in determining drought tolerance, as follows. If a species living in a dry environment restores stomata conductance to its maximum, when rains occur, it may suffer stress subsequently if the rains turn out to be of short duration. Thus, a 'cautious' reopening of stomata may be a more useful mode of behaviour than an immediate reopening.

3. The physiological differences, as far as water relations are concerned, between these two species were not especially large. It should be remembered, that although *Acacia negrii* grows at a higher rainfall than *A. ehrnbergiana*, its environment is neverless a dry one (i.e. both species are adapted to drought) as has been indicated by the data on osmotic adjustment and carbon allocation.

CHAPTER 7

GENERAL DISCUSSION AND CONCLUSION

7.1 Introduction

In general, the results from both the field work and the controlled environmental studies help to explain the patterns and trends of species distributions. One of the main aims of plant ecology is to try to understand the causes for such distributions. Field observations, irrespective of how carefully they are made, can only ever go so far in elucidating the causes. This is because the field environment is complex, varying, and the variables are intercorrelated.

In the greenhouse, experimental conditions permitted comparative studies without the problem of high variability and the confounding effect of environmental factors associated with the field (Kramer, 1983). The controlled environment experiments provided information on the behaviour of seeds to different pre-germination treatments. The morphological and physiological response of *Acacia* seedlings to water stress under modified environmental conditions provides important insights into the way the species acclimates to water shortage. The experimental methods developed for this work may, in addition, provide a promising route for the development of plant material with superior establishment characteristics. However, results obtained under controlled conditions should be used with caution when simulating field conditions or comparing with field data. In the subsequent sections the results are evaluated and their implications for practical silviculture are discussed.

7. 2 Species distribution along an environmental gradient

The Asir mountain range constitutes a distinct ecological unit. It rises to 2600 metres above sea-level near the top of Al Sudah and gradually decreases in height as we go northwards. The abundance and duration of annual rainfall (300 mm to 350 mm per year), the relative of humidity and the low temperatures are linked to altitude. All these environmental factors help to create a dense cover of trees unparalleled in other areas of the Kingdom. On the tops of mountains especially in the areas which have not been altered by man *Juniperus procera* is found in abundance to the extent that it forms dense forests whereas in the areas where man has intervened we find that those forests are less dense and the trees are shorter. As a result of the high humidity, lichens, especially *Usnea articulata,* cover *Juniperus procera* and hang down from its branches. The lichens also cover the rocks. Among the most important plants that co-exist with *Juniperus procera* is *Dodonaea viscosa.* The low areas, especially those which have little rain are covered by drought tolerant plants such as *Acacia* species.

In this unique environment fifteen species are distributed along the environmental gradient. On the eastern slopes three species *Acacia negrii, A. gerradii* and *Juniperus procera* are found in the uplands. These species grow very well because they receive plenty of water. The density of *Juniperus procera* is very high because the local tribes do not use it and it is not used as fuel wood as much as *Acacia* species. *Acacia* woodlands were generally converted into agricultural land and the wood used as fuel (Ministry of Agriculture and Water, 1984). In the lower lying areas species such as *Hyphaen thebaica* and *Tamarix aphylla* are not valuable for browsing and fuel although the wood has traditionally been used for buildings (Ministry of Agriculture and Water, 1984). There has been a lack of management of these species and no attempt to improve or extend their spread. The rest of the species (*Acacia tortilis, A. ehrnbergiana, A. laeta, A. asak,* and *Ziziphus spina-christi*) are both used for grazing and cut for fuel (Ministry of Agriculture and Water, 1984).

The gradient in elevation and soils along our study transect, together with other, associated gradients, interact to generate a complex spatial and temporal gradient of available soil water. The arid environment is characterised by spatial patchiness and temporal variability of resources (Evenari *et al.*, 1971;Solbrig *et al.*, 1977). The rainfall is spatially and temporally variable (Noy-Meir, 1974). This variability of rainfall imposes variability in other factors such as minerals and organic matter. The vegetation composition and biomass in arid regions is controlled by rainfall and by factors affecting the distribution and availability of water, such as topography and soil texture (Whittaker, 1978; Kramer, 1983). The ability of a soil to supply water and nutrients is strongly related to its texture and structure as well as to its depth. Coarse-textured soils, the sands, have a low nutrient content and low water-holding capacity. Fine-textured soils, the clays, may have high nutrient content and have high water-holding capacity. Le Houerou *et al.* (1988) reported that variability of primary production is higher in fine-texture soil compared to coarse textured soils.

The change in the vegetation along the environmental gradient (Fig 2.3, 2.4) reflects a gradient in rainfall and temperature from the high to the low elevations. For example, where the precipitation was more than 350 mm per year *Juniperus procera* was found have its highest density of 60 trees per plot, whilst *Tamarix aphylla* had its lowest density of 6 trees per plot (Table 2.3) where the precipitation was 55 mm per year. This result is in agreement with the argument that the rainfall strongly influences the distribution of species within the arid zone (Evenari *et al.*, 1971). Although the rainfall is very low in the lower elevation, more than twelve species were found. These species have the necessary adaptations to allow them to grow in this arid environment. This adaptation of the vegetation to the variability of rainfall is obtained by several strategies (Noy-Meir, 1974). The most important is the long dormancy of seeds for most of the species (Evenari *et al.*, 1971; Amhed, 1985) and possession of a highly extensive root system which spreads both vertically and horizontally (Evenari *et al.*, 1971; Batanouny and Abdel Wahab, 1973; Migahid *et al.*, 1974). Their roots sometimes reach great depths, of 10 to 15 metres (Evenari *et al.*, 1971). This enables them to absorb any water available in the deepest layers of the soil (Batanouny and Abdel Wahab, 1973 ; Kramer, 1983). These adaptations allow the vegetation to be persistent though not stable (Kramer, 1983).

No new seedlings were found in any of the field observations. The regeneration of the population of desert plants depends upon the suitable conditions for germination and establishment of these plants. (Evenari *et al.*, 1971). There are several factors that affect regeneration

1. The soil moisture during periods of drought.

2. The hard seed-coat for all trees, which need some treatment before sowing.

3. The soil conditions which the seed experiences.

4. The degree of grazing. This is especially important on the western slopes where most livestock are kept.

The first factor is controlled by the amount of rainfall during the season. Often the rainfall is less than the minimum required for germination. New shoots from seedlings are especially palatable to camels and goats and so grazing must be minimizing to allow regeneration of these woodlands. I believe the overgrazing problem has remained intractable because to date no national framework for action has been available. Many areas of woodland are cut for fuel wood and for timber

(Alshodouki, 1990), for example, in the north of the Kingdom, 40 hectares of the rangeland are deforested every year. The removal of a large area of vegetation cover exposes the soil to accelerated erosion and increases runoff, and contributes to desertification (Dregen, 1983). This also makes it difficult for seedlings to establish in this type of soil environment. A future factor is the cutting of fuel wood from live trees which can weaken the tree and if it coincides with drought, can kill it.

Such arguments suggest it is very important to maintain the tree cover in this region. The shading of trees prevents excessive heating and evaporation of precious moisture.

Based on the results obtained the following conclusions can be made:

1. There are seven woody plant families in the study area (Leguminosae Mimosaceae) Tamaricaceae, Palmae, Moraceae, Rhamnaceae, Oleaceae and Cupressaceae).

2. The family Leguminosae (Mimosaceae) is represented here by nine *Acacia* species (*A. negrii*, *A. gerradii*, *A. asak*, *A. seyal A. nubica*, *A. homulosa*, *A. egnbergiana*, *A. laeta* and *A. tortilis*).

3. Within the *Acacia* species the following was found

a. *Acacia ehrnbergiana* and *Acacia tortilis* were distributed from sea level to over 500 m a.s.l. While *Acacia seyal, A. asak* were distributed from 500 m a.s.l to over 1000 m a.s.l.

b. *Acacia homulosa*, *A. nubica* and *A. laeta* were distributed from 1000 m a.s.l. While *Acacia negrii* and *A. gerradii* were distributed from 2100 m a.s.l.

4. *Ziziphus spina-christi* species is the tallest and has the greatest stem diameter, while all the others are characterised by short stems of small diameter.

5. *Juniperus procera* has the highest number of trees in one site.

6. *Tamarix aphylla* has the lowest number of trees per site.

7. Soil degradation was very high and this was associated with very low organic matter and high pH in all sites.

8. New seedlings were absent in all the sites. Contributing to the causes of this absence probably were: hard seed-coats for all species, the intensive grazing and the drought during the growing season.

7.3 Controlled experiments

7.3.1 Germination response to different seed pre-germination

The *Acacia* species, are the dominant perennials in many arid region such as Saudi Arabia, produce substantial quantities of seeds. Germination is the activation of an embryo previously either quiescent or dormant. It usually begins almost immediately when a quiescent seed is placed in conditions suitable for growth, namely at warm temperature with water and air available. However germination may be delayed for long periods and in some species may never occur unless treatments are applied in order to break dormancy. According to Misra and Singh, (1981) seeds are fairly resistant to extreme external conditions, provided they are in a state of desiccation. As a result seeds can retain their ability to germinate, or to remain viable for a considerable period. The length of time for which seeds can remain viable is extremely variable and is determined genetically. The ability of seeds to remain viable under natural conditions varies greatly. The ecological conditions prevailing in a given habitat will affect germination, the determining factor probably being the micro-climatic conditions prevailing in the immediate vicinity of the seed. Seeds in their natural habitat interact with other plants and animals. Interactions with other plants may include the effects of inhibitors, stimulators or modification of the micro habitat. A large proportion of the seeds eaten by animals are returned to the soil without being damaged. Ahmed, (1986) reported that 43% of *Acacia tortilis* seeds eaten by goats are recovered viable. The passage of *Acacia* seeds through animals' digestive tracts has a positive effect on the germination of *Acacia* seeds and on the efficiency of distribution to other habitats. Fire can also affect germination behaviour. Fire stimulates the regeneration of many *Acacia* species by rupture of the testa (Tran *et al.*, 1984). Several factors regulate the germination of seeds in their natural habitat, some of which are internal, whereas others are external environmental factors.

Chapter 3 demonstrates some of the external factors which may play a role in regulating germination. Temperature is important in the breakdown of the hard, waterproof coats present in seeds of *Acacia* species. Heat and fluctuating temperatures are especially important in hard seeds of the arid zone climate. Although *Acacia* seeds may have to endure temperatures of 60 to 70 °C (Bellairs and Bell,

1990) they may be released from dormancy by much higher temperatures caused by fire. For example, Sabiiti and Wein, (1987) found that high fire intensity in natural forest stimulates high seedling emergence of *Acacia siberiana*, (172 seedlings/m^2 after a fire compared to 6 seedlings/m^2 without a fire). Pre-treatments differed in their effect on % germination of *Acacia negrii*, *A. asak*, *A. seyal*, *A. ehrnbergiana* and *A. tortilis*. Heat treatment for ten minutes significantly improved germination for all five species; 20 minutes of heat significantly improved germination *Acacia ehrnbergiana* and *Acacia negrii*; 30 minutes decreased the germination for all the five species. This suggests that prolonged heating at more than 80 °C for more than 20 minutes killed the embryo. Hot water pre-germination treatment resulted in increased germination for all five species. Exposure to this treatment for more than 5 minutes was detrimental to germination for *Acacia asak* and *A. negrii*. Most seeds become permeable to water when the seed coat is passed through the digestive tract of animals (camel and goats). Ahmed, (1986) reported that the germination of *Acacia tortilis* subspecies *spriocarpa* has increased from an average of 19.6% without ingestion to 54.2% after animal ingestion. Sulphuric acid pre-germination treatment caused different behaviour for all species. *Acacia negrii* and *A. seyal* showed improved germination after 10 minutes, but decreased germination for 20 and 40 minutes. *Acacia asak* had improved germination after 10 and 20 minutes, but decreased germination for 40 minutes. *Acacia ehrnbergiana* and *A. tortilis* significantly improved germination for all treatments (10, 20 and 40 minutes). This suggests that the success of the five species depends on the length of exposure to the treatment and the species.

The results therefore, reveal considerable interspecific differences with respect to germination strategy. Seeds of *Acacia negrii*, *A. asak*, *A. tortilis A. seyal* and *A. ehrnbergiana* exhibited seed coat-imposed dormancy. Hard seed coats are known to occur in many plant families (Mimosaceae, Malvaceae, Caesalpiniaceae and Convolvulaceae) and usually cause dormancy by making the seed coat impermeable to water and gases or it may mechanically constrain the embryo. The hard impermeable seed testa of *Acacia* species permits long-distance dispersion of the seeds and enables the *Acacia* to survive in the patchy and unpredictable environment of the arid zone. In nature, most seeds become permeable to water when the seed coat is broken down or punctured by mechanical abrasion, microbial attack, passage through the digestive tract of animals or exposure to alternating high and low temperatures which, by expanding and contracting the seed coat, cause it to crack (Clemens, 1977; Coughenour and Deling, 1986; Tesfaye, 1992).

7.3.2 Biomass allocation and root growth

Shoot and root growth of seedlings is very sensitive to water stress and is much slower if soil is periodically allowed to dry below field capacity than if it is kept near field capacity (Kramer, 1983). Studies with seedlings have shown consistently that dry matter production, and shoot elongation are directly related to soil water availability. One of the damaging effects of water stress is a reduction in leaf area, which reduces the loss of water, but unfortunately also reduces the surface that carries on photosynthesis, thus decreasing the amount of photosynthate available for growth. Reduction in leaf area due to drought can happen through a reduction in leaf initiation or leaf expansion or by leaf shedding. In the present study, the decrease in leaf area was a function of increased rates of leaf shedding and reduced rate of leaf production (Chapter 3 and Chapter 5). The cessation of shoot growth may be due to the functional equilibrium between above and below-ground parts of the plant, with shoot growth depending on the ability of root water uptake to meet shoot water requirements. The trees of *Acacia* are able, during the period of drought, to gradually shed their leaves and replaced them with smaller new leaves (Migahid, 1978). In natural plant communities many of these mechanisms appear to be more important for plant survival than for high productivity (Turner, 1981), but a number do appear to confer advantage for improved production under conditions of drought and therefore may be useful in increasing crop productivity when water shortages prevail (Turner 1979, 1986). Remarkably, the progressive soil drying over a very wide range had no effects on the total biomass production of *Acacia negrii*, *A. asak* and *A. ehrnbergiana* seedlings, a result that is inconsistent with several laboratory experiments (e.g. Seiler and Johnson, 1985; Khalil and Grace, 1992), which document substantial reductions in total biomass of seedlings of woody plants, as a result of water supply being withheld. We presume that *Acacia* has a rather superior suite of acclimatory mechanisms, enabling it to minimise the impact of drought.

Survival of plants in dry habitats is closely related to their ability to produce extensive root systems, which penetrate deeply in order to utilise water most efficiently and postpone possible drought injury (Kozlowski, 1971; Kozlowski and Kramer, 1991). Root growth is decreased or stopped by soil water stress and roots tend to become suberized to their tips, reducing their capacity to absorb water. It seems that *Acacia negrii*, *A. asak* and *A. ehrnbergiana* have the capacity to acclimate to water stress, over a remarkably large range of soil moisture. Competition for soil moisture between vegetation in the arid zone raises the important issue of rooting depth, particularly during the establishment of tree seedlings. Deep penetration of root systems as a result of soil drying (Sharp and Davies, 1985; Khalil and Grace, 1992) occurred for *Acacia* species when grown under three water regimes (watered control, intermediate, and dry treatments), an adaptive mechanism in a drought prone area allowing plants to explore deeper moist soil. However, in the present experiments soil moisture extraction was observed *Acacia negrii*, *A. asak* and *A. ehrnbergiana* from a depth of 130 cm (Chapter 5), suggesting that these three species are able to produced tap roots at an early age to reach the ground-water during the drought period. Rooting depth and root dry matter production were measured in this study. Root length is considered to be a better guide for determining the degree of exploitation of soil. However, increase in root growth is manifested as an increase in both root dry weight and root length (Khalil and Grace, 1992). The main effect of water stress on the biomass of *Acacia negrii*, *A. asak* and *A. ehrnbegriana* seedlings was the substantial shift in allocation in favour of root development (Table 4.3, 5.4 and 6.3), resulting not only in a large increase in root-to-shoot ratio, but also in an absolute increase in root dry weight. The root biomass increased at the expense of stem weight. A combination of specific morphological and physiological adaptations allows xerophytic trees to be particularly well-adapted to regions with an unpredictable summer drought pattern (Tenhunen *et al.*, 1990) by increasing water uptake and decreasing transpiring surfaces relative to total biomass. The significant shift in biomass allocation observed in this study, clearly indicates a high degree of morphological plasticity that might allow *Acacia negrii*, *A. asak* and *A. ehrnbergiana* seedlings to maintain physiological activity in face the of increasing soil water stress. Competition for below-ground moisture is thus thought to be related to the development of the root systems of component species (Reader *et al.*, 1992). During soil drying, root system development varies not only between trees and herbaceous crops but also within both herbaceous and trees species (Osonubi and Davies, 1981). This variation can be attributed to the capacity for solute accumulation and maintenance of turgor in the root tips during soil drying (Sharp and Davies, 1979). The conditions of soil drying may also change the development pattern of a root system even within the same species. For example, rapid soil drying induced a net increase in root growth of maize plants when grown in relatively small soil volumes (Sharp and Davies, 1979) in contrast to the root growth in slower drying, large soil volumes (Sharp and Davies, 1985). These observations indicate that adaptation of the root system to survive drought by an increase in depth and intensity seems to be an important criterion for the selection of trees suitable for afforestation of a drought affected area. This agrees with the fact that under water stress photosynthate partitioning changes at the expense of the shoot system, which leads to an increase in the ratio of root to shoot (Shulze, 1986). Many researchers have shown the effect of water stress on. growth and dry matter partitioning. Changes in partitioning which increase the root fraction of total biomass are well documented (Kramer, 1983). The close coupling of shoot growth and physiology to soil water status would enable these seedlings to 'measure' the availability of soil moisture, with a consequent activation of an efficient, long term utilisation of the limited amount of soil water (Turner *et al.*, 1985).

7.3.3 Soil water deficit and shoot behaviour

Stomata are important because most of the water lost by transpiration escapes through them and most of the carbon dioxide used in photosynthesis enters through them (Kramer, 1983). Plants respond to a reduction in the amount of available water in the soil by reducing their stomatal conductance and growth rate (Kaul and Kramer, 1965; Kramer, 1983; Korner and Cochrane, 1985). Stomatal conductance measurements can best be interpreted by comparing values during soil drying (Khalil and Grace, 1992). Stomatal conductance of *Acacia negrii, A. asak* and *A. ehrnbergiana* seedlings declined during soil drying (Chapter 3 and 6). The result is inconsistent with the historical view of water stress-induced stomatal closure, which suggests an overriding influence of leaf water status on stomatal aperture, particularly in the initial stage of soil drying. In accordance with the conventional view (see Hsiao, 1973), there were instances during the study when stomatal closure was accompanied by lower leaf water potentials in association with the decline in soil water status (Chapter 3 and 6). However, the correlation between stomatal conductance and leaf water potential was weaker than with soil water content (Fig 4.6, 4.7 and 4.7). The decreased stomatal conductance reduced water loss and contributed to the maintenance of leaf water potential, as found by Bates and Hall (1981) and Khalil and Grace, (1992). Increased leaf water potential during water stress might be an indication of drought avoidance by means of deep rooting and effective water uptake (Turner 1986; Khalil and Grace, 1992). Hinckley *et al.* (1983) reported that deep-rooted species avoid stress which would cause prolonged stomatal closure whereas shallow rooted species have to tolerate prolonged periods of closed stomata. The response of stomata to soil drying may be mediated by changes in root water status through chemical signals ascending from roots to the leaves which lead to closure of stomata in concert with the level of soil water stress (Davies and Zhang, 1991). This agrees with the earlier-formulated hypothesis of non-hydraulic influence of roots on shoot functioning during soil drying (Bates and Hall, 1981).

After rewatering, seedlings of the upland *Acacia negrii* showed rapid recovery of stomatal conductance within the first 24 hours, while the lowland *Acacia ehrnbergiana* recovered more slowly. These results should be important in any consideration of stomatal responses to water stress. Rapid stomatal closure, accompanied by delayed stomatal opening and subsequent partial closure in response to change in soil water content, might minimise unnecessary water loss, and account for plant survival under conditions of low water availability (Levitt, 1972). Following rewatering, it is of some advantage to *Acacia negrii* and *Acacia ehrnbergiana* to limit stomatal opening and thus conserve available water. Maximal stomatal opening was not obtained in *Acacia ehrnbergiana* until four days following rewatering. This response suggests that this species might compete successfully on sites where availability of water was low.

7.3.4 Osmotic adjustment and gas exchange

Water relations characteristics of the leaves were determined using the pressure-chamber technique to obtain pressure- volume isotherms (Tyree and Hammel, 1972). The accumulation of solutes in the leaf cells during water stress allows a decrease in bulk leaf water potential at any particular water content, together with the partial maintenance of turgor. Studies of woody plants show that some species can accumulate high levels of osmotic solutes in response to water deficits, resulting in osmotic adjustment adapted towards turgor maintenance at lower levels of water potential (Jones and Turner, 1978; Myers and Neales, 1986). The result of pressure-volume analysis of *Acacia negrii, A. asak* and *A. ehrnbergiana* twigs (Table 4.2) demonstrated that the 11 week period of developing water stress resulted in changes in osmotic potential at full turgor, osmotic potential at zero turgor, average bulk elastic modulus, and dry weight to turgid weight ratio of leaves of water stressed seedlings.

Many studies have suggested that the degree of drought tolerance is associated with an ability to undergo changes in bulk modulus of elasticity (E) and osmotic potential at full turgor (π_{100}) (Jones and Turner, 1979, 1980; Abrams, 1988). A drought induced increase in E would permit the maintenance of a large water potential gradient through the soil-plant-atmosphere continuum with little change in relative water content and therefore increase the ability to extract soil moisture from progressively drier soil (Abrams, 1988). In this study the modulus of elasticity was high for three stressed *Acacia* species. The increase in bulk elastic modulus coupled with high dry weight to turgid weight ratio, is a clear indication of water stress induced morphological changes in the leaf, possibly by increasing the cell wall thickness and decreasing cell size (Turner and Jones, 1980). It is likely that these changes are the primary factors enabling *Acacia ehrnbergiana*, *A. negrii* and *A. asak* to maintain a degree of drought tolerance. The relationship between osmotic potential at full turgor (π_{100}) and dry weight/turgid weight ratio (DW/TW) of leaves indicates that osmotic adjustment was achieved, at least partially, by an accumulation of osmotically active compounds in the tissue. The adaptive significance of the osmotic adjustment observed in this study, is that *Acacia* seedlings can maintain both turgor pressure and a favourable gradient of water potential during water stress, because the net increase in cell solute concentration in the face of decreasing soil water content will lead to a progressive reduction in osmotic potential. The fall in solute potential serves to maintain turgor pressure that is necessary for a continuation of gas exchange. Turner and Jones, (1980) hypothesised that osmotic adjustment arises simply from an accumulation of solutes as a result of the continuation of photosynthesis after the cessation of leaf growth. Therefore, this mechanism would enhance the capacity of plant seedlings to tolerate subsequent water stress with less damage during drought periods than that of well watered controls (Cutler and Rains, 1977).

Desert plants are able close their pores quickly during periods of drought or high temperature (Levitt, 1972). In both *Acacia negrii* and *A. ehrnbergiana* seedlings, photosynthetic rate was little change until the surface soil moisture was depleted by 40% after one week of drought (Chapter 6). Photosynthesis was reduced by 60% and 55% for *Acacia negrii* and *Acacia ehrnbergiana* respectively after two weeks of the drought period. Decreased development of leaf area can also reduce the total photosynthetic productivity of plants experiencing a water deficit. Because of the immediate reduction of leaf expansion caused by water stress (Saab and Sharp, 1989), the photosynthetic area does not increase as in well-watered plants and this may lead to a decrease in total photosynthetic productivity of water-stressed plants. *Acacia negrii* and *Acacia ehrnbergiana* might utilize the extra carbon gained to extend their root system to great depths, enhancing water uptake, and consequently might survive longer and accumulate more biomass even over a long period of water stress. Also this result indicates a significant degree of flexibility in both species, with ability to acclimate to water stress with more severe stress resulting in greater acclimation.

This study indicates that *Acacia negrii* and *Acacia ehrnbergiana* seedlings become more drought tolerant in response to prolonged water stress. Both *Acacia negrii* and *Acacia ehrnbergiana* do undergo osmotic adjustment photosynthetic rate at leaf water potentials as low as -3.0 MPa and -2.8 MPa respectively. Maintenance of photosynthesis at lower leaf water potential in cotton plants is associated with active osmotic adjustment (Ackerson *et al.*, 1980). Osmotic adjustment has also been demonstrated in red spruce seedlings (Seiler and Cazell, 1990), and this response is associated with the maintenance of photosynthesis and turgor at low soil water content. These studies suggest the primary role of osmotic adjustment to be the maintenance of stomatal conductance, thereby reducing stomatal limitations to photosynthesis at lower soil water content. *Acacia negrii* and *A. ehrnbergiana* have the ability to maintain stomata open and therefore to continue assimilation under soil water depletion (see Chapter 6), unlike mesic *Acer pesudopatanus* L. (Sycamore) (Khalil and Grace, 1992) (Fig 7.1). Stomatal closure protects plants against water loss but results in a reduction of carbon dioxide assimilation. Stomatal closure causes a proportionately greater decrease in transpiration than photosynthesis thereby increasing water use efficiency (WUE) (Fig 6.9). This water conservation mechanism may be particularly important in the arid zone habitats of woody plants where the variability of soil water is common.

After 4 days of rehydration the photosynthetic rates of water stressed seedlings were similar to those of well watered seedlings (Fig 6.2 and 6.3). Net photosynthesis in the unwatered treatment was 60% and 50% of the control for *Acacia negrii* and *A. ehrnbergiana* respectively after eight days. The rapid recovery in photosynthesis following rewatering suggests that *Acacia negrii* should be able to take advantage of the summer rainfall by rapidly increasing photosynthesis. However, *A. ehrnbergiana* recovered slowly. These results are similar to those of Lee *et al.* (1989) who found that, after a drought cycle, photosynthesis of red spruce did not recover fully. The rapid recovery of photosynthesis after watering in the water stressed seedlings indicates that no long-term damage to the photosynthetic machinery occurred during exposure to water stress.

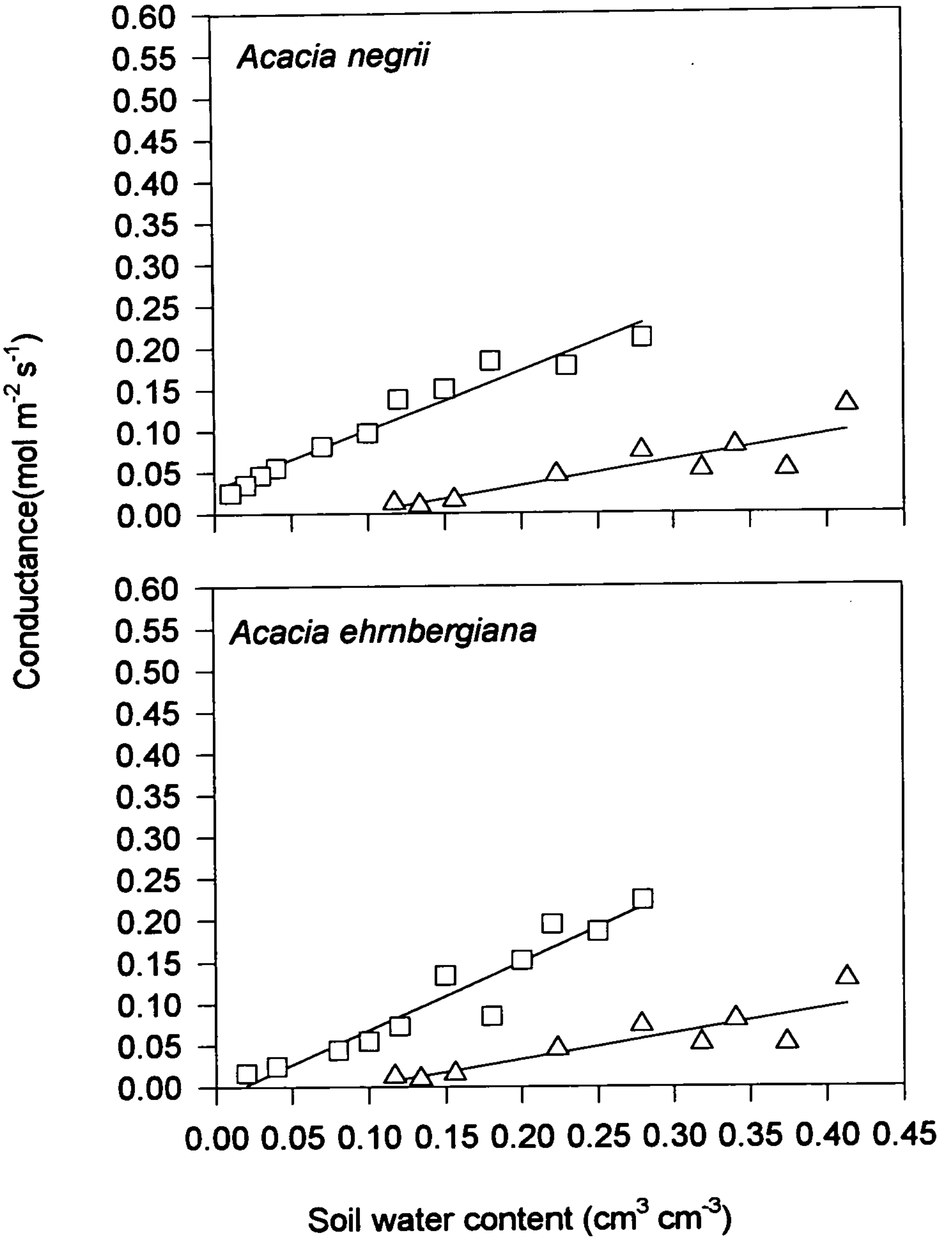


Figure 7.1: A relation between stomatal conductance and soil water content of water-stressed plants, for *Acacia negrii* and *A. ehrnbergiana* (xeric species). Obtained by replotting the data from Figs 4.6 A and 4.8 A (□). And comparison with (Δ) *Acer pesudopatanus* L. (mesic species), data obtained from Khalil and Grace (1992).

7.3.5 Drought resistance and elevational gradient

Plant response to water-stress may help to explain species distribution patterns and performance along environmental gradients.

The results of the experimental study in the glasshouse simulation of drought (Chapters 4, 5 and 6) suggested that drought resistance plays an important role in controlling the elevational positions of *Acacia* species in the Asir mountains.

Jones (1992) emphasized that a number of mechanisms can contribute to drought resistance. The following are several of many plant characteristics that impart drought resistance, and factors that should be considered in aforestation programmes:

1. Large root system or increase in root : shoot ratio
2. Limited leaf area
3. Stomatal closure
4. Turgor maintenance or osmotic adjustment

In the present study, all sites are to some extent dry, but there is a clear gradient of aridity. The coastal regions experience only 55 mm of rainfall and have temperatures up to 53 °C (Table 7.1). We may expect species that inhabit the lower elevations to show the most pronounced adaptations to drought.

The largest root : shoot ratio was observed in *A. asak* and next largest in *A. negrii*, which is not as might be expected. However, the species occupying the desert site, *A. ehrnbergiana* did show a relatively low leaf area, and the leaf area per plant mass (Table 7.1) was 15, 12 and 27 respectively as we look at *A. ehrnbergiana*, *A. asak* and *A. negrii*. This simple parameter may be regarded as an indication of the extent to which the species exposes itself to the atmospheric environment, and we may expect it to be diminished in harsher environments.

It is difficult to comment sensibly on the values of stomatal conductance as they are much the same when stomata are fully open, and the measurement when 'closed' is subject to measurement error.

Perhaps the most important physiological differences are in the pressure volume curves and the associated parameters. The tendency was for the species from the lowland desert zone to have a more negative osmotic potential. This influenced the pressure volume curve, so that this species would have a more negative potential for a given loss of water from the leaves. This can be shown by superimposing the pressure volume curves after acclimation to drought had occurred (Fig 7.2). There are indeed differences between the species but both *A. ehrnbergiana* and *A. negrii* show considerable adaptation to water shortage. Similar variations between three species have been reported by Dawson (1990) for *Salix* although in his case the range of variation was much greater.

The most remarkable aspect of these data is not the variation between the species, but the fact that all species show a high degree of acclimation to drought, so much so that their biomass production was scarcely impaired.

Table 7.1 Summary of the results from field sites and experiments in the glasshouse for three *Acacia* species. The symbol (*) indicates no data available. The physiological data are for 18 week old plants.

Characteristic of the site	*Acacia negrii*		*A. asak*		*A. ehrnbergiana*	
Elevation (m)	2200 to 2400		500 to 1500		sea level	
Aspect	east		west		east	
Temperature (°C)	0-25		*		15-35	
Rainfall (mm)	290		*		55	
Humidity (%)	55		*		66	
Soil type	sand loam		sand		loam sand	
pH	7.4		7.8		7.4	
Organic matter (%)	0.78		0.78		.85	
Mean stem height (m)	3.13		3.8		4.2	
Mean stem diameter (cm)	7.2		8.4		7.9	
Mean number of plants per site	25		30		41	
The result of the glasshouse work **The treatment time giving maximum germination**						
Sulphuric acid 80 % (minutes)	10		20		40	
Dry heating 80 °C (minutes)	20		10		20	
Boiling water (minutes)	1		5		10	
Physiological data	stressed	watered	stressed	watered	stressed	watered
Stomatal conductance (mol m^{-2} s^{-1})	0.015	0.24	0.02	0.21	0.017	0.23
Osmotic potential at full turgor (MPa)	-1.73	-1.57	-1.81	-1.42	-1.93	-1.43
Osmotic potential at zero turgor (MPa)	-2.13	-1.85	-2.33	-1.60	-2.30	-1.55
Bulk modulus of elasticity (MPa)	13.0	9.34	10.12	6.03	9.27	6.86
Dry weight : turgor weight ratio	0.33	0.28	0.33	0.30	0.32	0.29
Total biomass (g)	9.63	9.70	4.61	4.91	8.35	8.48
Total root length (cm)	956	827	425	356	512.9	435
Total leaf area (cm^2)	263.5	372	56.6	63	128	139
Leaf area per unit plant weight (cm^2 g^{-1})	27.4	44.9	12.0	12.4	15.3	16.4
Root : shoot ratio	0.77	0.35	0.94	0.33	0.66	0.36

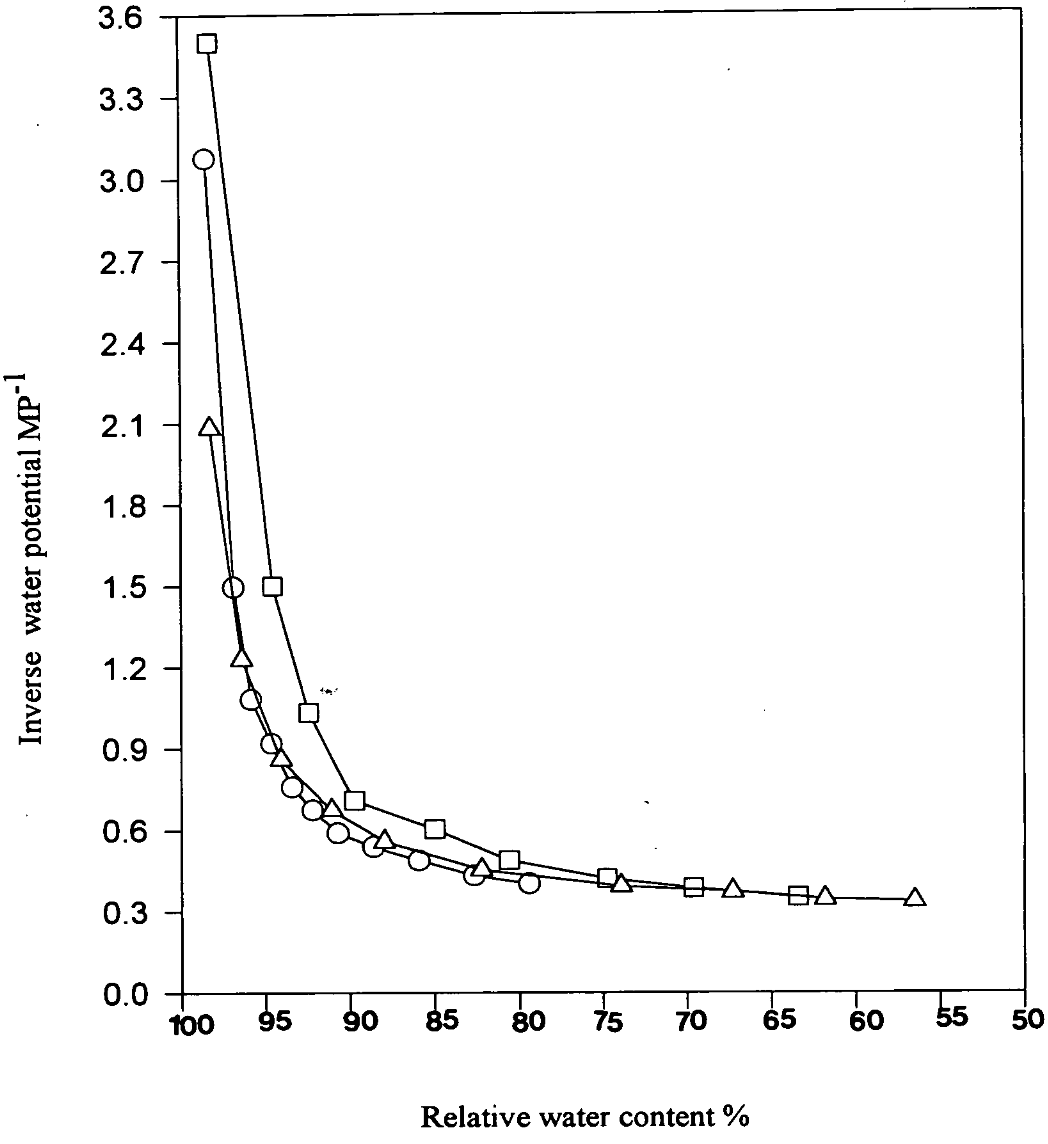


Figure 7.2: Comparison pressure-volume curves for *Acacia ehrnbergiana* (Δ), *A. negrii* (O) and *A. asak* (□).

7.4 Silvicultural implication of study

Few studies have been done in Saudi Arabia to assess the ecology of the natural forest and the response of tree seedlings to the low soil moisture that prevails during the dry season. In particular, there are no studies focused on the ability to acclimate to environmental changes, and on the understanding of several morphological and physiological changes that are induced by the limitation in soil water availability during periods of drought. Prudent forest management requires knowledge of factors that limit productivity such as nutrient availability, temperature and moisture stress. Drought has been implicated as one of the main causes of poor natural regeneration in the arid zone.

The importance of afforestation in Saudi Arabia necessitates the establishment of species trials for the selection of suitable planting stocks. The adaptability of *Acacia* species to different adverse conditions in arid zones has created an interest in evaluating their potential under local environmental conditions (Abo-hassan, 1976). The success of afforestation programmes of the arid zone regions often depends on the effective evaluation and thorough understanding of the physiological basis of responses to water deficits and tolerance of stress (Khalil and Grace, 1992). Assessment of characteristics related to this performance can be made by conducting small scale experiments which enable performance in the field to be predicted. The utilisation of physiological information in the course of the screening work necessitates the establishment of significant association between plant growth and survival under stress and various possible physiological components of drought resistance (Blum, 1989). The growth and physiological responses of plants growing in pots can be reasonably related to their growth and physiological performance in the field, although not all tree seedlings behave similarly. Possibly, soil drying in pots is relatively faster than in the field because of the dense root system that may develop in limited space within the pot.

Thus, using the methods adopted during the present study a successful screening programme can be achieved for the selection of appropriate afforestation in the arid region. The method of growing plants in long soil columns (Chapter 3 and 5) is recommended since it enables observation of root growth behaviour, an important determinant of competition between trees and new seedlings for soil moisture and nutrients, to be easily measured and to be expressed easily without the constriction of small pots. Satisfactory stock specifications must therefore be made to define the physiological and morphological characteristics that adapt stock to the particular biotic and physical conditions of the planting site. Competition from trees may reduce the amount of soil water available to the seedling layer. Increased root density and rooting depth of seedlings are both important for water uptake, but optimal root distribution depends on how water is distributed over depth and time within the soil profile. Dense rooting at the surface may allow roots to quickly absorb light rainfall, before water is lost through evaporation. Moreover, the response of stomatal conductance to partial dehydration of the root system can also be determined since shallow roots are dehydrated during soil drying while deeper roots in moist soil maintain a sufficient shoot water supply (Zhang and Davies, 1989). This fact is important in the choice of species based on growth rates and other physiological attributes. Zhang and Davies, (1989) studied plants in the glasshouse with seedlings grown in small pots. Consequently their roots have access to only small volumes of soil, and low stomatal conductance and leaf water potential develop rapidly during soil drying. In contrast, root of plants growing in the field have access to large volumes of soil and stomatal conductances and leaf water potentials may develop more slowly. Thus it is suggested that a programme to evaluate the more tolerant *Acacia* species should couple short-term screening experiments with long-term field testing.

Results of the seed germination studies can be used for building up stocks of *Acacia* seedlings in the nursery for transplanting into their natural habitats, to maintain populations and avoid the extinction of these important species in this region of Saudi Arabia. Ultimately knowledge of germination characteristics can greatly enhance the efficiency of nursery management. Also from this study it is now possible to suggest that good understanding of the basic morphology and physiology of *Acacia asak*, *A. negrii* and *A. ehrnbergiana* seedlings during soil drying would enable a successful afforestation plantation to be established in the arid region. However, data on growth and physiology of component species are needed from small-scale field trials to validate the work carried out in the greenhouse and pots to show whether it can be demonstrated in large scale afforestation programmes. Such studies of the adaptations of *Acacia negrii*, *A. asak* and *A. ehrnbergiana* to drought will allow the successful deployment of genetic resources in any afforestation programme. The results of this study suggest that drought resistance plays an important role in controlling the elevational positions of *Acacia* species in Asir Mountain. In response to an imposed greenhouse drought, seedlings of lower elevation species continue to groth longer and under lower soil moisture levels than did higher elevation species. Furthermore, seedlings of lower elevation species exhibited less pronounced depression of net photosynthesis and plant water potential during drought. Such observation may facilitate the establishment of *Acacia* plantations under the most favourable conditions in the arid region of Saudi Arabia. The results of this study will lead to improvement in silviculture in Saudi Arabia, which is currently only rudimentary, and consequent management of forest to obtain the greatest benefits.

7.4.1 Implication for *Acacia* in forest sites.

Anything that is done in silviculture should be based on knowledge of the capacities and limitations of the site or habitat in which the trees are to be grown. The establishment of new forests, or the regeneration of old, by planting is one of the most costly steps in silviculture. When selecting any plant for a planting programme it is essential to run treatment trials. As we know, the critical problem in south western Saudi Arabia is the drought during seedling establishment at the site. In the upland 2200 m a. s. l. one such important species is *Acacia negrii*, because it needs more water than other species (see Chapter 5) as is exhibited by it high root production compared to *Acacia asak* and *A. ehrnbergiana*. Also it has large leaf area which requires more water than the others species. This species can germinate in the glasshouse but requires care during the first stage (three to five months) and then transplanted to the field during the rainy season. Direct seeding is an option but may not be feasible.

In the low land from sea level to 500 m a. s. l. the important species are *Acacia asak* and *A. ehrnbergiana* because they are able to grow under stress for long periods and they can produce a tap root to extract deep water from the water table. The results for both species suggest that they should be widely deployed in this area. However seeds must be germinated in the glasshouse and be established during the rainy season. After the seedlings are transplanted their roots will growth deep and follow the soil moisture. Probably the seedlings may survive for three months without water.

7.5 Suggestions for further research

The Asir mountains have unique natural attributes (climate, topography, drainage, plant, animals and people) and very little to recommend them for intensive or extensive agricultural research. The land is more suited for conservation of the natural flora, or for low intensity silviculture. It is therefore important to conduct more research into the ecology, physiology and silvicultural systems of trees in the Aisr mountains. The following are the main priorities;

1. Studies of the survival and protection of rare and endangered species and their habitats in the region;

2. Strict control to prohibit cutting especially for production of charcoal and controls to reduce grazing pressure on the forest area in the region;

3. Studies of seed variability that exists within *Acacia* species, the effect of time of harvest and chronological age and seed size on germination;

4. Establishing a number of forest reserves to protect the largest tree populations or communities found in the region;

5. Teaching people through the media and schools about the ecological importance of native trees and forests to their lives;

6. Ecophysiology research, which should include regional variation in the effects of soil and atmospheric drought on demography, biomass partitioning to root and shoots, root to shoot communication and osmotic and elastic adjustment in relation to gas exchange and growth for *Acacia tortilis*, *A. seyal* and *Juniperus procera*.

7. Field trials, conducted in a similar way to those described in the present study, on a large scale and under different environmental condition. The determination of turgor potential of leaf or shoots by analysis of pressure volume curves is recommended, although it requires enough time for a series of measurements on each sample. However, the measurement of leaf water potential using a pressure chamber enables rapid assessment of the instantaneous total shoot water potential. The pressure chamber, Infrared Gas Analyser (ADC, LCA-3) and transient diffusion porometer (used in the measurement of stomatal conductance and gas exchange) are simple, easy to handle in the field, reasonably cheap and so are acceptable technology for developing countries such as Saudi Arabia.

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Appendix 3.1:

Analysis of variance for the effect of pre-germination treatment on the germination of *Acacia negrii*, *A. asak*, *A. seyal*, *A. ehrnbergiana* and *A. tortilis* in the growth room. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	4	2215.3	553.8	4.68	0.001
Treatment	9	15146.4	1682.9	14.22	0.000
Position	3	345.8	115.3	0.97	0.406
Error	183	21661.7	118.4		
Total	199	39369.2			

Analysis of variance for the effect of pre-germination treatment on the germination of *Acacia negrii* in the growth room.

Source	DF	SS	MS	*F*	*P*
Treatment	9	4553.094	505.8993	12.22	0.0001
Error	30	1242.177	41.40589		
Total	39	5795.271			

Analysis of variance for the effect of pre-germination treatment on the germination of *Acacia asak* in the growth room.

Source	DF	SS	MS	*F*	*P*
Treatment	9	4775.191	530.577	4.04	0.0018
Error	30	3939.799	131.327		
Total	39	8714.989			

Analysis of variance for the effect of pre-germination treatment on the germination of *Acacia seyal* in the growth room.

Source	DF	SS	MS	*F*	*P*
Treatment	9	2749.2585	305.47	5.12	0.0003
Error	30	1759.096	58.636		
Total	39	4508.35			

Appendix 3.1: continued

Analysis of variance for the effect of pre-germination treatment on the germination of *Acacia ehrnbergiana* in the growth room.

Source	DF	SS	MS	*F*	*P*
Treatment	9	6047.3875	671.93	9.77	0.0001
Error	30	2062.239	68.74		
Total	39	8109.626			

Analysis of variance for the effet of of pre-germination treatment on the germination of *Acacia tortilis* in the growth room.

Source	DF	SS	MS	*F*	*P*
Treatment	9	8593.038	954.78	19.99	0.0001
Error	30	1432.62	47.75		
Total	39	10025.66			

Appendix 4.1: Analysis of variance for the effect drought on the growth of *Acacia negrii, A. asak* and *A. ehrnbergiana* seedlings grown under treatment for 12 weeks in the glasshouse. Two-way ANOVA.

Analysis of variance for the effect of drought on leaf area, LA (cm^2) of *Acacia negrii, A. asak and A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	281955.09	140977.54	319.72	0.0001
Treatment	1	10663.53	10663.53	24.18	0.0001
Sp*Treat	2	13415.82	6707.91	15.21	0.0001
Error	18	7936.81	440.93		
Total	23	313971.25			

Analysis of variance for the effect of drought on leaf area, LA (cm^2) of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	23762	23762	19.11	0.0047
Error	6	7462	1243.67		
Total	7	31224			

Analysis of variance for the effect of drought on leaf area, LA (cm^2) of *Acaica asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	98	98	4.47	0.07
Error	6	131	21.91		
Total	7	229			

Analysis of variance for the effect of drought on leaf area, LA (cm^2) of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	219.35	219.35	3.83	0.098
Error	6	343.32	57.22		
Total	7	562.66			

Appendix 4.1: continued

Analysis of variance for the effect of drought on leaf dry weight, LDW (g) of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	16.23	8.11	51.22	0.0001
Treatment	1	2.72	2.72	17.2	0.0006
Sp*Treat	2	0.24	0.12	0.67	0.4824
Error	18	2.85	0.16		
Total	23	22.04			

Analysis of variance for the effect of drought on leaf dry weight, LDW (g) of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	1.6836125	1.6836125	7.99	0.0301
Error	6	1.264575	0.2107625		
Total	7	2.9481875			

Analysis of variance for the effect of drought on leaf dry weight, LDW (g) of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	0.364650	0.364650	1.90	0.2173
Error	6	1.15178750	0.19196458		
Total	7	1.5164455			

Analysis of variance for the effect of drought on leaf dry weight, LDW (g) of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	0.91733512	0.91733512	12.64	0.0120
Error	6	0.43355467	0.07259112		
Total	7	1.35288187			

Analysis of variance for the effect of drought on the stem dry weight (g) of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	8.85637033	4.42818517	13.23	0.0003
Treatment	1	3.46864067	3.46864067	10.36	0.0048
Sp*Treat	2	0.30197033	0.15098517	0.45	0.6439
Error	18	6.02498650	0.33472147		
Total	23	18.6519678			

Analysis of variance for the effect of drought on the stem dry weight (g) of *Acacia negrii,* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	1.2401250	1.24031250	3.61	0.1060
Error	6	2.0593750	0.34322917		
Total	7	3.29968750			

Analysis of variance for the effect of drought on leaf area, the stem dry weight (g) of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	2.08284050	2.08284050	4.58	0.0762
Error	6	2.73096550	0.45516092		
Total	7	4.81380600			

Analysis of variance for the effect of drought on he stem dry weight (g) of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	0.44745800	0.4475800	2.17	0.1908
Error	6	1.23464600	0.20577433		
Total	7	1.68210400			

Appendix 4.1: continued

Analysis of variance for the effect of drought on the total shoot weight, TSW (g) of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse.

Source	DF	SS	MS	*F*	*P*
Species	2	47.2878427	23.6439	23.72	0.0001
Treatment	1	11.7614000	11.7614	11.80	0.0030
Sp*Treat	2	0.2117508	0.10563	0.11	0.9000
Error	18	17.9456847	0.99698		
Total	23	77.2062026			

Analysis of variance for the effect of drought on the total shoot weight, TSW (g) of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	5.13601	5.13601	3.41	0.1142
Error	6	9.02775	1.5046		
Total	7	14.163787			

Analysis of variance for the effect of drought on leaf area, the total shoot weight, TSW (g) of *Acacia asak* in the glasshouse.One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	4.190512	4.190512	3.62	0.1056
Error	6	6.937411	1.15623		
Total	7	11.127923			

Analysis of variance for the effect of drought on leaf area, the total shoot weight, TSW (g) of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	2.64615	2.64615	8.02	0.0299
Error	6	1.980498	0.33008		
Total	7	4.626648			

Appendix 4.1: continued

Analysis of variance for the effect of drought on the root dry weight (g) of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	10.9093854	5.4546927	10.79	0.0008
Treatment	1	9.09142741	9.0914274	17.99	0.0005
Sp*Treat	2	0.28045824	0.14022912	0.28	0.7609
Error	18	9.0959023	0.50533223		
Total	23	29.3772513			

Analysis of variance for the effect of drought on the root dry weight (g) of *Acacia negrii,* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	4.67828166	4.6782166	4.45	0.0795
Error	6	6.31367193	1.0522786		
Total	7	10.9919539			

Analysis of variance for the effect of drought on the root dry weight (g) of *Acacia asak,* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	2.59532544	2.59532544	13.37	0.0106
Error	6	1.16460829	0.19410138		
Total	7	3.75993373			

Analysis of variance for the effect of drought on the root dry weight (g) of *Acacia ehrnbergiana,* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	2.09827885	2.09827885	7.78	0.0316
Error	6	1.61770001	0.2691667		
Total	7	3.71597856			

Appendix 4.1: continued

Analysis of variance for the effect of drought on the total biomass (g) of *Acacia negrii, A. asak and A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	103.583026	51.7915131	34.47	0.0001
Treatment	1	0.1716365	0.1716365	0.11	0.7393
Sp*Treat	2	0.0609423	0.0304711	.02	0.9799
Error	18	27.0475641	1.5026425		
Total	23	130.863169			

Analysis of variance for the effect of drought on the total biomass (g) of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	0.0106799	0.0106799	0.00	0.9485
Error	6	14.1165319	2.3527553		
Total	7	14.1272211			

Analysis of variance for the effect of drought on the total biomass (g) of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	0.19015944	0.19015944	0.13	0.7292
Error	6	8.6689976	1.44483295		
Total	7	8.8591571			

Analysis of variance for the effect of drought on the total biomass (g) of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	0.03173940	0.3173940	0.04	0.8396
Error	6	4.26203451	0.71033908		
Total	7	4.29377391			

Appendix 4.1: continued

Analysis of variance for the effect of drought on the root shoot ratio of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	.05833405	0.02916703	0.57	0.5742
Treatment	1	1.16818290	1.16818290	22.92	0.0001
Sp*Treat	2	0.09995461	0.04997730	0.98	0.3943
Error	18	0.91747061	0.05097059		
Total	23	2.24394217			

Analysis of variance for the effect of drought on the root shoot ratioof *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	0.35155664	0.35155664	4.13	0.0884
Error	6	0.51073631	0.08512272		
Total	7	0.86229295			

Analysis of variance for the effect of drought on the root shoot ratioof *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	0.74216399	0.74216399	13.34	0.0107
Error	6	0.33387208	0.05564535		
Total	7	1.07603608			

Analysis of variance for the effect of drought on the root shoot ratioof *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	0.17441688	0.17441688	14.36	0.0091
Error	6	0.07286222	0.01214370		
Total	7	0.24727910			

Appendix 4.1: Stomatal conductance (mmol m^{-2} s^{-1})

Analysis of variance for the effect of drought on stomatal conductance (mmol m^{-2} s^{-1}) of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	411379	411379	196.49	0.000
Species	2	17975	8988	4.29	0.015
Treat*Sp	2	1898	949	.45	0.636
Error	192	401988	2094		
Total	197	833239			

Analysis of variance for the effect of drought on stomatal conductance (mmol m^{-2} s^{-1}) of *Acacia negrii,* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	757907	757907	441.66	000
Error	130	223083	1716		
Total	131	980990			

Analysis of variance for the effect of drought on stomatal conductance (mmol m^{-2} s^{-1}) of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	596787	596787	292	0.000
Error	130	265022	2039		
Total	131	861808			

i) Analysis of variance for the effect of drought on stomatal conductance (mmol m^{-2} s^{-1}) of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	811317	811317	322.34	0.000
Error	130	327208	2517		
Total	131	1138525			

Appendix 4.1: Water potential

Analysis of variance for the effect of drought on the leaf water potential (MPa) of *Acacia negrii, A. asak and A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	25.0008	25.0008	157.30	0.000
Species	2	0.0181	0.0091	0.06	0.945
Treat*Sp	2	0.2269	0.1335	0.71	0.491
Error	192	30.5164	0.1589		
Total	197	55.7623			

Analysis of variance for the effect of drought on the leaf water potential (MPa) of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	1.013	1.013	3.86	0.052
Error	130	34.139	0.263		
Total	131	35.152			

Analysis of variance for the effect of drought on leaf water potential (MPa) of *Acacia asak* in the glasshouse.One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	0.838	0.838	3.38	0.068
Error	130	32.223	0.248		
Total	131	33.061			

Analysis of variance for the effect of drought on leaf water potential (MPa) of *Acacia ehrnbergiana* in the glasshouse.One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	1	1.096	1.096	3.66	0.058
Error	130	38.883	0.299		
Total	131	39.979			

Appendix 5.1:

Analysis of variance for the effect of water regime on fine root length of layer one (25 cm) for *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	15780.6672	7890.33362	211.40	0.0001
Treatment	2	163.59435	81.79718	2.19	0.
Sp*Treat	4	5632.7777	1408.19430	37.73	
Error	27	1007.77644			
Total	35	22584.8152			

ii) Analysis of variance for the effect of water regime on fine root length of layer one for *Acacia negri* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	3127.21272	1563.606	27.17	0.0002
Error	9	517.919	57.5465		
Total	11	3645.131			

Analysis of variance for the effect of water regime on fine root length of layer one for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	2444.00203	1222.001	29.02	0.0001
Error	9	378.93111	42.103457		
Total	11	2822.9334			

Analysis of variance for the effect of water regime on fine root length of layer one for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	225.1567	112.578398	9.13	0.0068
Error	9	110.926189	12.3251322		
Total	11	336.082986			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on fine root length of layer two for *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	106880.964	5340.48203	18.15	0.0001
Treatment	2	211.7419	105.87099	0.36	0.7011
Sp*Treat	4	2705.6595	676.4148	2.30	0.0847
Error	27	13598.366			
Total	35	21541.7242			

Analysis of variance for the effect of water regime on fine root length of layer two for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1007.8407	503.92036	0.61	0.5665
Error	9	7487.2719	831.9191		
Total	11	8495.1126			

Analysis of variance for the effect of water regime on fine root length of layer two for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	840.086924	420.04346	19.82	0.0005
Error	9	190.69507	21.18834		
Total	11	1030.78199			

Analysis of variance for the effect of water regime on fine root length of layer two for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1069.47388	534.7369	18.13	0.0007
Error	9	265.39160	29.487956		
Total	11	1334.8654			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on fine root length of layer three for *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	20197.1168	10098.558	293.47	0.0001
Treatment	2	303.89707	151.9485	4.42	0.0219
Sp*Treat	4	1680.212	420.05311	12.21	0.0001
Error	27	929.0972	2772.653		
Total	35	23110.3236	34.41101		

Analysis of variance for the effect of water regime on fine root length of layer three for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1201.708	600.854	11.38	0.0034
Error	9	475.170	52.796739		
Total	11	1676.879			

Analysis of variance for the effect of water regime on fine root length of layer three for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	588.4883	294.244	7.48	0.0122
Error	9	354.1576	39.3508		
Total	11	942.6459			

Analysis of variance for the effect of water regime on fine root length of layer three for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	193.912	96.95634	8.75	0.0078
Error	9	99.7689	11.08544		
Total	11	293.6816			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on fine root length of layer four for of *Acacia negrii, A. asak and A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	17919.1907	8959.595	77.91	0.0001
Treatment	2	1753.89	876.9466	7.63	0.0024
Sp*Treat	4	3545.9479	886.48698	7.71	0.0003
Error	27	3104.80505	114.99278		
Total	35	26323			

Analysis of variance for the effect of water regime on fine root length of layer four for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	3011.95672	1505.9783	16.65	0.0009
Error	9	814.27518	90.4750		
Total	11	3826.2319			

Analysis of variance for the effect of water regime on fine root length of layer four for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	734.81488	367.40744	1.83	0.2154
Error	9	1807.134	200.79368		
Total	11	2541.9580			

Analysis of variance for the effect of water regime on fine root length of layer four for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1553.0695	776.5347	14.46	0.0015
Error	9	483.386669	53.70963		
Total	11	2036.45620			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on fine root length of layer five for of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	13523.81	6761.90	95.45	0.0001
Treatment	2	1810.3999	905.199	12.78	0.0001
Sp*Treat	4	2198.6758	549.669	7.76	0.0003
Error	27	1912.79	70.84415		
Total	35	19445.689			

Analysis of variance for the effect of water regime on fine root length of layer five for *Acacia negrii* in glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	3295.07	1647.5387	9.05	0.0070
Error	9	1639.22	182.13589		
Total	11	4934.300			

Analysis of variance for the effect of water regime on fine root length of layer five for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	134.626	67.313	14.03	0.0017
Error	9	43.1824	4.798		
Total	11	177.80			

Analysis of variance for the effect of water regime on fine root length of layer five for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	579.3722	289.686	11.32	0.0035
Error	9	230.3866	25.5985		
Total	11	809.758			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on fine root length of layer six for of *Acacia negrii*, *A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	851.00307	425.501	29.49	0.0001
Treatment	2	908.82393	454.411	31.50	0.0001
Sp*Treat	4	1210.6766	302.669	20.98	0.0001
Error	27	389.54832	14.427716		
Total	35	3360.051			

Analysis of variance for the effect of water regime on fine root length of layer six for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	2096.138	1048.069	29.16	0.0001
Error	9	322.501	35.9446		
Total	11	2419.6399			

Analysis of variance for the effect of water regime on fine root length of layer six for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	16.02706	8.0135	2.87	0.1086
Error	9	25.13028	2.79225		
Total	11	41.15734			

Analysis of variance for the effect of water regime on fine root length of layer six for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	7.3352	3.6676	0.81	0.4761
Error	9	40.9162	4.5462		
Total	11	48.25155			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on secondary root length of layer one for of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	7013.63030	3506.81515	211.40	0.0001
Treatment	2	72.708	36.354277	2.19	0.1312
Sp*Treat	4	2503.4562	625.864054	37.73	0.0001
Error	27	447.9004	16.588907		
Total	35	10037.6955			

Analysis of variance for the effect of water regime on secondary root length of layer one for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1389.872	694.936	27.17	0.0002
Error	9	230.1682	25.5762		
Total	11	1620.058			

Analysis of variance for the effect of water regime on secondary root length of layer one for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1086.223	543.111	29.02	0.0001
Error	9	168.4137	18.7126		
Total	11	1254.6367			

Analysis of variance for the effect of water regime on secondary root length of layer one for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	100.06966	50.03483	9.13	0.0068
Error	9	49.30050	5.47783		
Total	11	149.37016			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on secondray root length of layer two for of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	4747.0946	2373	18.15	0.0001
Treatment	2	94.107506	47.0537	0.36	0.7011
Sp*Treat	4	1202.51	300.62	2.30	0.0847
Error	27	3530.381	130.75		
Total	35	9574.098			

Analysis of variance for the effect of water regime on secondary root length of layer two for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	447.929	223.96	0.61	0.5665
Error	9	3327.67	369.74		
Total	11	3775.605			

Analysis of variance for the effect of water regime on secondary root length of layer one for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	373.37	186.6859	19.82	0.0005
Error	9	84.7533	9.41703		
Total	11	458.125			

Analysis of variance for the effect of water regime on secondary root length of layer one for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	475.321	237.66	18.13	0.0007
Error	9	117.9518	13.1057		
Total	11	593.273			

Appendix 5.1: continued

Analysis of variance for the effet of water regime on secondray root length of layer three for of *Acaica negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	8976.49609	4488.248	293.47	0.0001
Treatment	2	135.065217	67.5326	4.42	0.0219
Sp*Treat	4	746.761105	186.690	12.2	0.0001
Error	27	412.932088			
Total	35	10271.2545			

Analysis of variance for the effect of water regime on secondray root length of layer three for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	534.0925	267.0462	11.38	0.0034
Error	9	211.186	23.4652		
Total	11	745.279			

Analysis of variance for the effect of water regime on secondray root length of layer three for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	261.550	130.775	7.48	0.0122
Error	9	157.4033	17.4892		
Total	11	418.95			

Analysis of variance for the effect of water regimeon secondary root length of layer three for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	86.18344	43.091722	8.75	0.0078
Error	9	44.341787	4.926865		
Total	11	130.52523			

Analysis of variance for the effet of water regime on secondary root length of layer four for of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	7964.08609	3982.0430	77.91	0.0001
Treatment	2	779.5079	389.7539	7.63	0.0024
Sp*Treat	4	1575.9769	393.99	7.71	0.0003
Error	27	1379.9134	51.1079		
Total	35	11699.4844			

Analysis of variance for the effect of water regime on secondary root length of layer four for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1338.647	669.323	16.65	0.0009
Error	9	361.9001	40.2111		
Total	11	1700.547			

Analysis of variance for the effect of water regime on secondary root length of layer four for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	326.5844	163.2922	1.83	0.2154
Error	9	803.1748	89.2416		
Total	11	1129.759			

Analysis of variance for the effect of water regime on secondary root length of layer four for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	690.253	345.126	14.46	0.0015
Error	9	214.838	23.8709		
Total	11	905.0915			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on secondary root length of layer five for of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	6010.58599	3005.29299	95.45	0.0001
Treatment	2	804.6221	402.31106	12.78	0.0001
Sp*Treat	4	977.18919	244.297299	7.76	0.0003
Error	27	850.129711	31.486286		
Total	35	850.129			

Analysis of variance for the effect of water regime on secondary root length of layer five for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1464.4787	732.239	9.05	0.0070
Error	9	728.5434	80.949		
Total	11	2193.022			

Analysis of variance for the effect of water regime on secondray root length of layer five for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	59.8338	29.9169	14.03	0.0017
Error	9	19.1921	2.13246		
Total	11	79.02599			

Analysis of variance for the effect of water regime on secondary root length of layer five for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	257.4987	128.7493	11.32	0.0035
Error	9	102.3940	11.37711		
Total	11	359.89285			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on secondray root length of layer six for of *Acacia negrii, A. asak and A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	378.223647	189.11182	29.49	0.0001
Treatment	2	403.921812	201.960906	31.50	0.0001
Sp*Treat	4	538.07861	134.519652	20.98	0.0001
Error	27	173.132587	6.412318		
Total	35	1493.35665			

Analysis of variance for the effect of water regime on secondray root length of layer six for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	931.617153	465.808576	29.16	0.0001
Error	9	143.778562	15.975395		
Total	11	1075.39571			

Analysis of variance for the effect of water regime on secondray root length of layer six for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	7.1231399	3.5615997	2.87	0.1086
Error	9	11.1690144	1.241001		
Total	11				

Analysis of variance for the effect of water regime on secondray root length of layer six for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	3.26012924	1.6300646	0.81	0.4761
Error	9	18.1850099	2.0205566		
Total	11	21.4451391			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on tap root length of layer one for of *Acacia negrii, A. asak and A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	2949.07284	1474.5360	11.26	0.0003
Treatment	2	19.129509	9.564755	0.07	0.9297
Sp*Treat	4	1072.29400	268.073500	2.05	0.1159
Error	27	3534.85016	130.92037		
Total	35	7375.34575			

Analysis of variance for the effect of water regime on tap root length of layer one for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	556.45352	278.226	1.34	0.3087
Error	9	1864.16365	207.1292		
Total	11	2420.61717			

Analysis of variance for the effect of water regime on tap root length of layer one for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	491.4404	245.720202	2.52	0.1354
Error	9	878.475055	97.608339		
Total	11	1369.915			

Analysis of variance for the effect of water regime on tap root length of layer one for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	43.529585	21.764792	0.25	0.7861
Error	9	792.21145	88.0234947		
Total	11	835.74103			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on tap root length of layer two for of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	2527.52708	1263.76354	7.98	0.0019
Treatment	2	73.598145	36.799073	0.23	0.7942
Sp*Treat	4	389.336684	97.334210	0.61	0.6558
Error	27	4276.38277	158.354547		
Total	35	7266.84484			

Analysis of variance for the effect of water regime on tap root length of layer two for *Acacia egrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	161.052153	80.526076	1.45	0.2850
Error	9	500.52935	55.614373		
Total	11	661.581511			

Analysis of variance for the effect of water regime on two root length of layer two for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2				
Error	9				
Total	11				

Analysis of variance for the effect of water regime on two root length of layer two for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	213.77616	106.88808	1.66	0.2429
Error	9	578.512432	64.279159		
Total	11	792.28859			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on tap root length of layer three for of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	3956.74445	1978.37223	19.25	0.0001
Treatment	2	57.925469	28.962735	0.28	0.1566
Sp*Treat	4	355.638137	88.909534	0.87	0.4973
Error	27	2774.44151	102.757093		
Total	35	7144.74958			

Analysis of variance for the effect of water regime on tap root length of layer three for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	257.996850	128.9984	0.63	0.5548
Error	9	1844.63127	204.95903		
Total	11	2102.62812			

Analysis of variance for the effect of water regime on fine root length of layer three for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	116.93433	58.46716	1.06	0.3845
Error	9	494.121425	54.902380		
Total	11	611.05576			

Analysis of variance for the effect of water regime on fine root length of layer three for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	38.63242	19.3162132	0.40	0.6823
Error	9	435.688815	48.4098684		
Total	11	474.321242			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on tap root length of layer four for of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	3545.72666	1772.86333	25.52	0.0001
Treatment	2	298.55524	149.27762	2.15	0.1361
Sp*Treat	4	648.787008	162.196.196	2.33	0.0810
Error	27	1875.5571	69.465079		
Total	35	6368.62606			

Analysis of variance for the effect of water regime on tap root length of layer four for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	546.04250	272.022625	2.20	0.1664
Error	9	1115.0960	123.89956		
Total	11	1661.14130			

Analysis of variance for the effect of water regime on tap root length of layer four for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	144.688780	72.3443901	1.19	0.3486
Error	9	548.39900	60.9332227		
Total	11	693.087784			

Analysis of variance for the effect of water regime on tap root length of layer four for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	256.60822	128.304111	5.45	0.0282
Error	9	212.060800	23.5624533		
Total	11	648.67030			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on tap root length of layer five for of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	2718.26957	1359.13478	39.92	0.0001
Treatment	2	324.485918	162.242959	4.76	0.0169
Sp*Treat	4	381.758460	95.439615	2.80	0.0456
Error	27	919.367818	34.05660		
Total	35	4343.8818			

Analysis of variance for the effect of water regime on tap root length of layer five for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	571.94066	285.9704	3.16	0.0912
Error	9	814.04495	90.449439		
Total	11	1385.9859			

Analysis of variance for the effect of water regime on tap root length of layer five for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	26.2010848	13.1005424	10.46	0.0045
Error	9	11.274755	1.2527506		
Total	11	37.4758405			

Analysis of variance for the effect of water regime on four root length of layer five for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	108.102327	54.051164	5.17	0.0320
Error	9	94.0810810	10.4497899		
Total	11	202.150436			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on tap root length of layer six for of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	143.49516	71.7475807	21.61	0.0001
Treatment	2	169.26390	84.6319538	25.49	0.0001
Sp*Treat	4	209.266611	52.3166530	15.76	0.0001
Error	27	89.6302299	3.3196407		
Total	35	611.655981			

Analysis of variance for the effect of water regime on tap root length of layer six for *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	372.689993	186.344965	22.94	0.0003
Error	9	73.1186619	8.1242958		
Total	11	445.808592			

Analysis of variance for the effect of water regime on tap root length of layer six for *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	4.006766	2.00338311	2.87	0.1086
Error	9	6.282570	0.69806343		
Total	11	10.2893371			

Analysis of variance for the effect of water regime on tap root length of layer six for *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1.83382281	0.91691140	0.81	0.4761
Error	9	10.2290669	1.3656298		
Total	11	12.0628896			

Appendix 5.1: continued

Analysis of variance for the effect water regime on the growth of *Acacia negrii, A. asak* and *A. ehrnbergiana* seedlings grown under treatment for 15 weeks in the glasshouse. Two-way ANOVA.

Analysis of variance for the effect of water regime on leaf area, LA (cm^2) of *Acacia negrii, A. asak and A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	342512.695	171256.347	534.76	0.0001
Treatment	2	26579.57	13289.785	41.50	0.0001
Sp*Treat	4	9932.456	2483.114	7.75	0.0003
Error	27	8646.7045	320.248		
Total	35	387671.427			

Analysis of variance for the effect of water regime on leaf area, LA (cm^2) of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	30638.0416	15139.0208	29.53	0.0001
Error	9	4668.685	518.743		
Total	11	35306.729			

Analysis of variance for the effect of water regime on leaf area, LA (cm^2) of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	3009.77671	1504.8883	4.59	0.0422
Error	9	2950.0135	327.77928		
Total	11	5959.7902			

Analysis of variance for the effect of water regime on leaf area, LA (cm^2) of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	2864.2088	1432.1044	12.54	0.0025
Error	9	1028.0034	114.2226		
Total	11	3892.2122			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on the leaf dry weight (g) of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	30.654055	15.327022	135.77	0.0001
Treatment	2	5.205905	2.6037952	23.07	0.0001
Sp*Treat	4	0.343112	0.0857780	0.76	0.5605
Error	27	3.047980	0.1128881		
Total	35	39.25272			

Analysis of variance for the effect of water regime on the leaf dry weight (g) of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	2.770880	1.38544033	13.13	0.0020
Error	9	0.93684300	0.10409367		
Total	11	3.7077236			

Analysis of variance for the effect of water regime on the leaf dry weight (g) of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1.3224411	0.6612205	3.47	0.0766
Error	9	1.717219	0.190802		
Total	11	3.039660			

Analysis of variance for the effect of water regime on the leaf dry weight (g) of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1.4573380	0.7286903	16.65	0.0009
Error	9	0.393918	0.0437686		
Total	11	1.8512986			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on stem dry weight (g) of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	39.9506539	19.4753272	138.28	0.0001
Treatment	2	9.285791	4.64289553	32.96	0.0001
Sp*Treat	4	1.599177	0.39979449	2.84	0.0437
Error	27	3.8027884	0.14084386		
Total	35	53.6384407			

Analysis of variance for the effect of water regime on stem dry weight (g) of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	7.70157267	3.8507863	14.64	0.0015
Error	9	2.367162	0.2630180		
Total	11	10.0687347			

Analysis of variance for the effect of water regime on stem dry weight (g) of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1.97765317	0.98882658	9.99	0.0052
Error	9	0.89123250	0.09902583		
Total	11	2.86888567			

Analysis of variance for the effect of water regime on stem dry weight (g) of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1.20574317	0.60287158	9.97	0.0052
Error	9	0.54438975	0.06048775		
Total	11	1.75013292			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on total shoot of *Acacia negrii, A. asak and A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	138.590135	69.2950674	376.94	0.0001
Treatment	2	28.3221671	14.1610835	77.03	0.0001
Sp*Treat	4	2.7912923	0.6978231	3.80	0.0142
Error	27	4.9635075	0.1838336		
Total	35	174.667102			

Analysis of variance for the effect of water regime on total shoot of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	19.3312080	9.665604	41.21	0.0001
Error	9	2.1111050	0.234567		
Total	11	21.442313			

Analysis of variance for the effect of water regime on total shoot of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	6.50605317	3.25302658	14.96	0.0014
Error	9	1.95766775	0.21751864		
Total	11	8.4637209			

Analysis of variance for the effect of water regime on total shoot of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	5.27619817	2.63809908	26.54	0.0002
Error	9	0.89473475	0.09941497		
Total	11	6.17093292			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on the root dry weight (g) of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	27.2932655	13.6466328	61.83	0.0001
Treatment	2	10.8734372	5.43671858	24.63	0.0001
Sp*Treat	4	2.95328683	0.73832171	3.35	0.0239
Error	27	5.95913125	0.22070856		
Total	35	47.0791207			

Analysis of variance for the effect of water regime on the root dry weight (g) of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	10.2956602	5.1478301	9.58	0.0059
Error	9	4.8371247	0.5374583		
Total	11	15.1327849			

Analysis of variance for the effect of water regime on the root dry weight (g) of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	2.82222317	1.4111158	15.62	0.0012
Error	9	0.81317950	0.09035328		
Total	11	3.63540267			

Analysis of variance for the effect of water regime on the root dry weight (g) of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	0.70884067	0.35442033	10.33	
Error	9	0.30884067	0.03431411		
Total	11	1.01766767			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on the root shoot ratio of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	0.01485880	0.00742940	0.57	0.5729
Treatment	2	1.31735822	0.65867911	50.42	0.0001
Sp*Treat	4	0.04470262	0.01117565	0.86	0.5030
Error	27	0.35273444	0.01306424		
Total	35	1.72965408			

Analysis of variance for the effect of water regime on the root shoot ratio of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	0.4916671	0.24563336	22.77	0.0003
Error	9	0.09710171	0.01078908		
Total	11	0.58836843			

Analysis of variance for the effect of water regime on the root shoot ratio of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	0.61579925	0.30789962	14.42	0.0016
Error	9	0.19220612	0.02135624		
Total	11	0.80800537			

Analysis of variance for the effect of water regime on the root shoot ratio of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	0.25499487	0.12749744	18.09	0.0007
Error	9	0.06342660	0.00704740		
Total	11	0.3184148			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on specific leaf area (cm^2g^{-1}) of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	1529.79893	764.899468	5.72	0.0085
Treatment	2	476.000468	238.002344	1.78	0.1880
Sp*Treat	4	609.100316	152.275079	1.14	0.3597
Error	27	3612.13809	133.782892		
Total	35	6227.04237			

Analysis of variance for the effect of water regime on specific leaf area (cm^2g^{-1}) of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	57.1838734	28.5919367	0.74	0.5024
Error	9	345.943820	38.4382022		
Total	11	403.127693			

Analysis of variance for the effect of water regime on specific leaf area (cm^2g^{-1}) of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	325.358458	162.679229	0.52	0.6114
Error	9	2816.19007	312.910007		
Total	11	3141.45830			

Analysis of variance for the effect of water regime on specific leaf area (cm^2g^{-1}) of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	702.56267	351.281336	7.03	0.0145
Error	9	450.00420	50.000467		
Total	11	1152.56687			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on number leaves of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	10240.7222	5120.36111	71.42	0.0001
Treatment	2	1980.22222	990.111111	13.81	0.0001
Sp*Treat	4	108.944444	27.23611	0.38	0.8210
Error	27	1935.75	71.694444		
Total	35	1465.6389			

Analysis of variance for the effect of water regime on number leaves of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	420.16666	210.08333	3.75	0.0655
Error	9	504.75	56.083333		
Total	11	924.91666			

Analysis of variance for the effect of water regime on number leaves of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	999.5000	499.75	18.32	0.0007
Error	9	254.5000	27.777		
Total	11	1245.000			

Analysis of variance for the effect of water regime on number leaves of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	669.50	334.75	2.54	0.1334
Error	9	1185.50	131.7222		
Total	11	1850.00			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on number branches of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	115.05555	57.527778	9.44	0.0008
Treatment	2	37.722222	18.861111	3.10	0.0616
Sp*Treat	4	23.611111	5.9027778	0.97	0.4407
Error	27	164.50000			
Total	35	340.88888			

Analysis of variance for the effect of water regime on number branches of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1.166666	0.5233	0.24	0.7905
Error	9	21.75	2.41667		
Total	11	22.91667			

Analysis of variance for the effect of water regime on number branches of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	50.66667	25.3	2.71	0.1196
Error	9	84.00	9.3		
Total	11	134.6667			

Analysis of variance for the effect of water regime on number branches of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	9.50	4.75	0.75	0.5094
Error	9	58.75	6.5278		
Total	11	68.25			

Appendix 5.1: continued

Analysis of variance for the effect of water regime on the total biomass (g) of *Acacia negrii, A. asak* and *A. ehrnbergiana* in the glasshouse. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	2	288.887267	144.4436	332.81	0.0001
Treatment	2	4.6024841	2.301242	5.30	0.0114
Sp*Treat	4	0.2278351	0.0569588	0.13	0.9696
Error	27	11.7182743			
Total	35	305.435860			

Analysis of variance for the effect of water regime on the total biomass (g) of *Acacia negrii* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	1.756970	0.878485	0.91	0.4348
Error	9	8.6417	0.960196		
Total	11	10.39			

Analysis of variance for the effect of water regime on the total biomass (g) of *Acacia asak* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	0.77865	0.389343	1.74	0.2296
Error	9	2.013349	0.223705		
Total	11	2.792036			

Analysis of variance for the effect of water regime on the total biomass (g) of *Acacia ehrnbergiana* in the glasshouse. One-way ANOVA

Source	DF	SS	MS	*F*	*P*
Treatment	2	2.29466	1.14733	9.71	0.0057
Error	9	1.063159	0.118128		
Total	11	3.3578			

Appendix 6.1:

Analysis of variance for the effect droughted on the growth of *Acacia negrii* and *ehrnbergiana* seedlings grown under treatment for 24 days in the growth room. Two-way ANOVA.

Analysis of variance for the effect of drought on leaf area, LA (cm^2) of *Acacia negrii,* and *A. ehrnbergiana* in the growth room. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	1	38009	38009	6.65	0.023
Treatment	1	24196	24196	4.23	0.060
Error	13	74329	5718		
Total	15	136534			

Analysis of variance for the effect of drought on Leaf dry weight of (g) *Acacia negrii* and *A. ehrnbergiana* in the growth room. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	1	5.1722	5.1722	21.42	0.000
Treatment	1	3.9631	3.9631	16.41	0.001
Error	13	3.1394	0.2415		
Total	15	12.2747			

Analysis of variance for the effect of drought on stem dry weight (g) of *Acacia negrii* and *A. ehrnbergiana* in the the growth room. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	1	7.952	7.982	2.85	0.115
Treatment	1	6.027	6.027	2.16	0.166
Error	13	36.319	2.794		
Total	15	50.298			

Analysis of variance for the effect of drought on the total shoot (g)of *Acacia negrii* and *ehrnbergiana* in the growth room. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	1	24.818	24.818	6.66	0.023
Treatment	1	20.778	20.778	5.58	0.034
Error	13	48.436	3.726		
Total	15	94.032			

Appendix 6.1: continued

Analysis of variance for the effect of drought on the root dry weight (g) of *Accaia negrii* and *ehrnbergiana* in the growth room. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	1	5.748	5.748	3.61	0.080
Treatment	1	1.097	1.097	0.69	0.422
Error	13	20.710	1.593		
Total	15	27.555			

Analysis of variance for the effect of drought on the root shoot ratio of *Acacia negrii* and *ehrnbergiana* in the growth room. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	1	0.01092	0.01092	0.87	0.367
Treatment	1	0.00276	0.00276	0.22	0.646
Error	13	0.16250	0.01250		
Total	15	0.17618			

Analysis of variance for the effect of drought on the total biomass (g) of *Acacia negrii* and *ehrnbergiana* in the growth room. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	1	54.749	54.749	7.81	0.015
Treatment	1	31.201	31.201	4.45	0.055
Error	13	91.088	7.007		
Total	15	177.038			

Analysis of variance for the effect of drought on stomatal conductance (mmol m^{-2} s^{-1})of *Acacia negrii* and *ehrnbergiana* in the growth room. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	1	9.239	9.239	4.48	0.037
Treatment	1	.267	0.267	0.13	0.720
Error	93	191.592	2.060		
Total	95	201.098			

Appendix 6.1: continued

Analysis of variance for the effect of drought on net photosynthesis (µmol m^{-2} s^{-1}) of *Acacia negrii* and *A. ehrnbergiana* in the growth room. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	1	670.20	760.20	28.24	0.000
Treatment	1	1034.90	1034.90	38.44	0.000
Error	93	2503.67	26.92		
Total	95	4298.77			

Analysis of variance for the effect of drought on leaf water potential (MPa)of *Acacia negrii* and *A. ehrnbergiana* in the growth room. Two-way ANOVA

Source	DF	SS	MS	*F*	*P*
Species	1	20.529	20.529	93.08	0.000
Treatment	1	0.004	0.004	0.02	0.896
Error	93	20.511	0.221		
Total	95	41.044			

Appendix 7

Analysis of ENMAG

1. Nitrogen (N) 5%
2. Phosphorus pentoxide soluble in water (SO_4 P_2O_5) 0.5%
3. Phosphorus pentoxide insoluble in water (SO_4 P_2O_5) 23.5%
4. Potassium sulphide (K_2 SO_4) 10%
5. Magnesium (Mg) 10 %