

WATER AND NUTRIENT RELATIONS OF SELECTED TREE SPECIES OF ETHIOPIA

BY

JIREGNA GINDABA

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**PROMOTER DR. ANDREY B. ROZANOV, DEPARTMENT OF FOREST SCIENCE,
STELLENBOSCH UNIVERSITY**

**CO-PROMOTER: PROF. LEGESSE NEGASH, DEPARTMENT OF BIOLOGY,
ADDIS ABABA UNIVERSITY (ETHIOPIA)**

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DECLARATION

I, the undersigned, hereby declare that the work contained in this dissertation is my own original work and has not in its entirety or in part been submitted at any university for a degree.



Signature

Date

ABSTRACT

This study was conducted to evaluate and compare the water and nutrient relations of three indigenous deciduous tree species, viz., *Cordia africana* Lam., *Croton macrostachyus* Del., *Millettia ferruginea* (Hochst.) Baker and two widely planted eucalypts, viz., *Eucalyptus camaldulensis* Dehnh and *Eucalyptus globulus* Labill from Ethiopia. The study was organized as glasshouse and field observations in Ethiopia. Owing to the lack of baseline studies on the water and nutrient relations of the deciduous tree species, the glasshouse experiments involved a wide range of water and nutrient applications. Seedlings were grown with the supply of various levels of water and nutrients during which gas exchange, water potential, relative water content, tissue nutrient content and biomass production were measured. The field observations were limited to the study of surface root distribution and leaf nutrient composition of mature trees and their effects on soil nutrient pool. The observations were made on isolated trees and mixed or pure stands of trees in Badessa area, Eastern Ethiopia. The field site was selected because of the availability of the study species and suitability of the trees for the study.

In the glasshouse, increased water deficit significantly reduced predawn leaf water potential, relative water content, stomatal conductance, photosynthetic rate, whole plant water use efficiency, plant height, diameter, leaf area and biomass production. Both of the eucalypts did not grow faster than the deciduous species under well-watered conditions unlike under water stress conditions. *C. macrostachyus* and *C. africana* had higher transpiration rates and tissue nutrient accumulations than the other species. They also demonstrated higher biomass allocation to roots than all the other species to support the intensive water and nutrient uptake rate. Due to the ability to re-orient its leaves to avoid direct solar irradiance, *M. ferruginea* maintained higher tissue water potential and relative water content than all the other species under water stress regimes.

The impact of imposed drought was quick and more damaging to the eucalypts compared to the deciduous tree species indicating that the eucalypts may not survive extreme drought conditions unlike the deciduous species that drop their leaves and may remain dormant for weeks. The current study gave new experimental proof that *E. globulus* was more vulnerable to drought than *E. camaldulensis*.

Soil N stress resulted in an overall reduction of tissue N concentration, N:P ratio, photosynthetic rate, stomatal conductance and photosynthetic water use efficiency in all the species studied. Plants with high foliar nitrogen concentration had higher photosynthetic capacities indicating that N plays a key role in photosynthesis and growth of all the studied species. The current study showed that for all the tree species, more attention has to be given to soil N than to P as soil P had minor effects on the photosynthetic activities of plants of all species compared to N.

The investigation on tissue nutrient composition confirmed that N:P ratio could be used to detect P-limitation in plants. However, N:P ratio could not distinguish between N-limitation and combined limitations of N and P.

The study of isolated *C. africana* and *C. macrostachyus* trees on soils in Badessa, Eastern Ethiopia indicated improved soil N, P and K under tree canopies whereas no effects were observed on the other soil nutrients studied. Similar to glasshouse conditions, *C. macrostachyus* and *C. africana* produced extensive surface roots, interfering with crops grown in association. Due to their high nutrient cycling potential the net effect on soil was positive. Comparison of *E. camaldulensis* woodlot and a mixed stand composed of deciduous species indicated that the fine root biomass in the surface soil under *E. camaldulensis* was about three times that under the mixed stand. The fine root biomass of *E. camaldulensis* inside the stand and 10 meters away from the stand were comparable in the surface soils showing the presence of root competition with adjacent crops. Therefore, planting of *E. camaldulensis* in association or adjacent to croplands should be avoided. Nutrient and carbon pool of soil inside the mixed stand was generally higher than that of *E. camaldulensis* indicating that trees of the mixed stand recycled more nutrients to the soil.



UITREKSEL

Die doel van hierdie studie was om die verskille tussen water- en voedingstofverhoudings van drie inheemse blaarwisselende boomsoorte te vergelyk, viz., *Cordia africana* Lam., *Croton macrostachyus* Del., *Millettia ferruginea* (Hochst.) Baker en twee bekende eucalyptus spesies, viz., *Eucalyptus camaldulensis* Dehnh en *Eucalyptus globulus* Labil van Etiopië. Die studie het bestaan uit kweekhuis- en veldobservasies in Etiopië. As gevolg van beperkte navorsing ten opsigte van water- en voedingstofverhoudings in bladwisselende boomsoorte, het die kweekhuis-eksperimente bestaan uit 'n wye verkeidenheid water- en voedingstoftoetse. Saailinge is gegroei deur verskillende vlakke van water- en voedingstowwe by te voeg. Gaswisseling, waterpotensiaal, relatiewe hoeveelheid water, hoeveelheid voedingstowwe en produksie van biomassa is gemeet. Die veldobservasies was beperk tot oppervlak-wortelverspreiding en blaarvoedingstof hoeveelhede van volwasse bome, sowel as die effek op grondvoedingstowwe. Observasies was beperk tot geïsoleerde, gemengde en een spesie opstande, in die Badessa area, Oos Etiopië. Die studiearea was gekies op grond van die voorkoms van die gekose boomsoorte, sowel as die toepaslikheid van die bome vir die studie.

In die kweekhuis is gevind dat die verhoogte watertekort die pre-sonop blaarwaterpotensiaal, relatiewe hoeveelheid water, stomatiese geleiding, fotosintetiese tempo, heelplant water-gebruikseffektiwiteit, plant hoogte, diameter, blaararea en biomassa produksie beduidend verminder het. Nie een van die eucalyptus spesies het vinniger as die bladwisselende spesies onder voldoende hidrasie gegroei nie. Dit was egter nie die geval onder die waterbeperkte toestande nie. *C. macrostachyus* en *C. africana* het 'n hoër transpirasie tempo sowel as weefselvoedingstof waardes gehad as die ander spesies. Hierdie boomsoorte se wortelbiomassa was ook meer as die ander spesies, om vir die tempo van water- en voedingstofopname te akkomodeer. As gevolg van die vermoë om blare te kan oriënteer om direkte sonlig te voorkom, het *M. ferruginea* 'n hoër water-weefselpotensiaal en relatiewe waterinname gehad in vergelyking met die ander boomsoorte in beperkte water toestande.

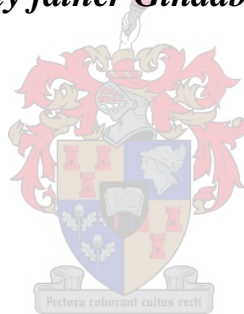
Die impak van geïnisieerde droogte het vinnig voorgekom en het meer skade aan die eucalyptus aangerig in vergelyking met die bladwisselende boomsoorte. Dit dui aan dat die eucalyptus-spesie nie ekstreme droogte kan oorleef nie, waar bladwisselende spesies hul blare laat afval en vir weke aan een dormant kan bly. Hierdie studie gee eksperimentele bewyse dat *E. globulus* minder bestand is teen droogte as *E. camaldulensis*.

Beperkte N in die grond het veroorsaak dat daar 'n algemene vermindering van weefsel N-konsentrasie, N:P ratio, fotosintetiese tempo, stomatiese geleiding en fotosintetiese watergebruiks effektiwiteit in al die bestudeerde spesies was. Plante wat oor hoër blaar-stikstofkonsentrasies

beskik, het hoër fotosintetiese kapasiteite wat aandui dat N 'n belangrike rol in fotosintese en die groei van al die bestudeerde spesies speel. Die oorhoofse bevindings van die studie was, dat daar meer aandag gegee moet word aan grond-N as P omdat grond-P net 'n kleiner rol speel in die fotosintetiese aktiwiteit van plante van al die spesies in vergelyking met N. Die ondersoek na weefselvoedingstof hoeveelhede het bewys dat die N:P ratio gebruik kan word om P-tekorte in plante aan te dui. Die N:P ratio kan egter nie die verskil in N-tekorte en gekombineerde tekorte van N en P aandui nie.

Die studie van die geïsoleerde *C. africana* en *C. macrostachyus* bome op grondtipes in Badessa, Oos Ethiopië het verbeterde grond-N, P en K onder kroondak gebiede getoon, daar was egter geen verskille in die ander grondvoedingstowwe wat bestudeer is nie. In toestand gelykstaande aan die van die kwekhuys, het *C. macrostachyus* en *C. africana* meer oppervlakswortels ontwikkel. Die toename aan oppervlakswortels het ingedring op gewasse wat in assosiasie gegroei is, dit het egter 'n positiewe effek op die grond gehad as gevolg van die hoë voedingstof-siklus-potensiaal. Die *E. camaldulensis* opstand is gevergelyk met 'n gemengde opstand van bladwisselende spesies waar daar gevind is dat die fynwortel biomassa in die oppervlak grond onder die *E. camaldulensis* ongeveer drie keer soveel was as die van onder die gemengde opstand. Kompetisie met aangrensende gewasse is aangeui deurdat die fynwortel biomassa van *E. camaldulensis* binne die opstand en 10 meter weg van die opstand vergelykbaar was in die oppervlakgronde. Dit dui dus aan dat die plant van *E. camaldulensis* in assosiasie of aangrensend aan gewasse vermy moet word. Die teenwoordigheid van voedingstowwe en koolstof in die grond van die gemengde opstand was oor die algemeen hoër as die van die *E. camaldulensis*. Dit is 'n aanduiding dat die bome van die gemengde opstand meer voedingstowwe aan die grond verskaf.

*Dedicated to
my father Gindaba Doti.*

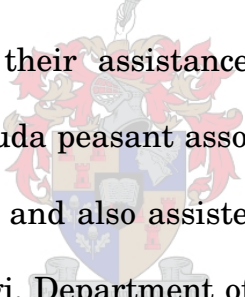


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1. INTRODUCTION

1.1 Plant water and nutrient relations

Water and nutrients are among the major environmental factors that determine the growth and distribution of plants on earth. Worldwide, dehydration caused by excessive transpiration results in a considerable loss of plants (Kramer and Boyer, 1995). Transpiration is the loss of water from plants in the form of vapor and it is the dominant process in plant water relations because of the large volume of water involved and its controlling influence on plant water status. Rapidly transpiring plants could result in depletion of soil moisture, drop of ground water level and reduced stream flow (Florence, 1996).

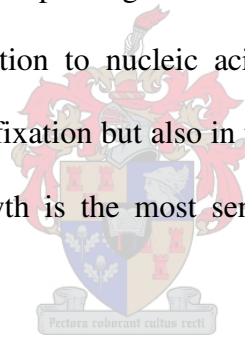
Water and nutrient relations of a plant widely refers to the acquisition, use and release/loss of water and nutrients during the growth process of the plant. Because the supply of and use of water has a direct influence on plant growth, measurement of water status is an important part of understanding plant growth (Beadle *et al.*, 1993). Water potential, relative water content (RWC) and gas exchange have commonly been used to assess the water status and physiological responses of plants under water stress (Pereira *et al.*, 1986; White *et al.*, 2000, Lawlor, 2002). In the majority of plants, water stress results in reduced leaf water potential and RWC, which further induce stomatal closure (Pereira *et al.*, 1986; Kramer and Boyer, 1995; Nilsen and Orcutt, 1996; Lambers *et al.*, 1998; Lawlor, 2002; Lawlor and Cornic, 2002). Stomata play a pivotal role in controlling the balance between water loss and carbon gain, i.e. biomass production.

Leaf RWC, the mass of water held in relation to the mass that can be held at full turgor, has been used to estimate plant water status in terms of cellular hydration under the possible effect of leaf water potential and osmotic adjustments (Kramer and Boyer, 1995). Two plants with the same leaf water potential can have different RWC if they differ in osmotic adjustments (Beadle *et al.*, 1993; Lawlor, 2002). Osmotic adjustment is the net accumulation of solutes when plants are exposed to water deficit. As a consequence of osmotic adjustment and other traits of adaptation to water stress, such as root development and reduced transpiration, water content can be maintained in cells and tissues to allow metabolic activity (Kramer and Boyer, 1995). At the cellular level, RWC affects the physiology of the cell in several ways, including changes in intercellular organelle positions, transport channels, enzyme biochemistry, as well as cell wall shrinkage (Hall, 2001; Lawlor, 2002; Lawlor and Cornic, 2002). Clearly, these changes impact on cellular metabolism, including photosynthesis (Lawlor and Cornic, 2002). Photosynthetic studies have been used as tools to probe the physiological basis of plant growth under environmental limitations including water and nutrient stresses (e.g., Fredeen *et al.*, 1989; Sage *et al.*, 1990; Evans, 1996; Lambers *et al.*, 1998; Rao and Terry, 2000).

Plants differ both in their capacity to acquire nutrients from the soil and in the amount of nutrients they need per unit growth and the nutrient concentration in their tissue (Lambers *et al.*, 1998). Environment strongly affects plant nutrient concentration by changing both allocation among organs and the composition of individual tissues (Aerts and Chapin, 2000). The balance of available nutrients in the environment then alters the proportions of these nutrients in plant tissues (Koerselman and Meuleman, 1996). When nutrient supply declines relative to plant demand, most plants show the following sequence

of events: decrease in vacuolar reserves with little effect on growth, continued reduction in tissue nutrient concentrations, reduced rates of leaf growth and photosynthesis, increased non-structural carbohydrate concentrations, senescence of older leaves, reallocation of reserves to compensate for reduced nutrient status, increased root mass ratio and increased root absorption capacity, greatly reduced photosynthesis and nutrient absorption and dormancy or death of meristems (Chapin, 1991; Reich *et al.*, 1992; Aerts, 1995; Marschner, 1995; Evans, 1996; Lambers *et al.*, 1998; Aerts and Chapin, 2000).

Nitrogen and phosphorus are the main growth limiting nutrients in plants from tropical and subtropical environments (Marschner, 1995). Due to their requirements in the major biochemical processes of plant growth including enzymatic activities, energy transfer and structural contribution to nucleic acids (Marschner, 1995), N and P play pivotal roles not only in carbon fixation but also in the subsequent allocation of carbon and related growth processes. Growth is the most sensitive indicator of nutrient deficiency (Evans, 1996).



Because the bulk of the nutrients required for plant growth usually enter the plant by means of roots, allocation of biomass to roots is an important determinant of nutrient acquisition. Roots of deep rooting trees are capable of pumping nutrients that are otherwise unavailable to shallow rooted plants (Van Noordwijk *et al.*, 1996; Young, 1997). This pumping of nutrients is crucial in tropical environments because many tropical soils are highly leached and depleted of weatherable minerals to great depth (Young 1997). Tree roots selectively absorb these nutrients and accumulate them at the surface by way of litter fall (Van Noordwijk *et al.*, 1996).

Tree species with nutrient rich biomass and faster leaf decomposition rates are regarded as having high litter quality in agroforestry systems (Meyers *et al.*, 1994; Mafongoya *et al.*, 1998). The return of the nutrients to the soil affects the nutrient cycling potential of the system.

1.2 Water and nutrient relations of eucalypts and deciduous trees of Ethiopia

The water and nutrient relations of the eucalypts have been well documented. Several studies (e.g., Ehleringer and Werk, 1986; Pereira *et al.*, 1986; Pereira *et al.*, 1987; Pereira de Almeida and Riekerk, 1990; Gibson *et al.*, 1991; Tesfaye, 1994; James and Bell, 1995; Battaglia *et al.*, 1996; Florence, 1996; James and Bell, 1996; White *et al.*, 1996; Hatton *et al.*, 1998; Osório *et al.*, 1998; James and Bell, 2000; White *et al.*, 2000; Burgess *et al.*, 2001; Pita and Pardos, 2001) conducted on the effects of water stress and related subjects on *Eucalyptus camaldulensis* Dehnh. and *Eucalyptus globulus* Labill showed that both species are tolerant to water stress under various controlled and field conditions. Generally, the former is more tolerant to drought than the latter (Florence, 1996; White *et al.*, 2000).

Although mature *E. globulus* and *E. camaldulensis* have various mechanisms of drought tolerance (Florence, 1996; James and Bell, 1995; White *et al.*, 1996; James and Bell, 2000), seedlings of both species are prone to drought, which causes dieback when planted out in drier areas like in many parts of Ethiopia (Pohjonen, 1989; Tesfaye, 1994; Jagger and Pender, 2003). To compensate for the loss of eucalyptus seedlings from early dieback, farmers and/or plantation agents increase the planting density during the first year, followed by refilling in subsequent years (Pohjonen, 1989; Jagger and Pender, 2003).

Regarding the indigenous trees of Ethiopia, no organized studies and published results have been made available on their growth performances and water and nutrient relations both under controlled and field conditions. However, some recent observations (Legesse, 1995, 2002a; Tadesse *et al.*, 2000) indicate that some indigenous species of Ethiopia including *Cordia africana*, *Erythrina brucei* and *Millettia ferruginea* are fairly fast growing and have an additional advantage of soil fertility improvement (Jiregna, 1997; Tadesse *et al.*, 2000; Abebe *et al.*, 2001; Legesse, 2002a).

1.3 Opportunities and constraints for tree planting in Ethiopia

Although tree planting in Ethiopia has a long history, remarkable initiatives were taken during the 1890s when the then Emperor of the country introduced various exotic species including eucalypts to curb the fuel and construction wood shortage around Addis Ababa (von Breitenbach, 1961). At that time about 40% of Ethiopia was covered by forest (von Breitenbach, 1961, 1962). Currently, FAO (2001) estimated the total forest cover of Ethiopia to be about 4.2% of land area and the annual deforestation during the last ten years (1990 – 2000) to be about 40, 000ha. The main reasons for the destruction of the forest resources were the conversion of forestland to cropland, fire and the cutting of trees for fuel wood and timber (von Breitenbach, 1961, 1962; Pohjonen, 1989; EFAP, 1994; Legesse, 1995, 2002b; FAO, 2001). Forest destruction is still an ongoing activity today (Fig. 1.1).

a)



b)



Figure 1.1 Forestlands in the process of conversion to agricultural land around Badessa, Eastern Ethiopia. a) 5 km west of Badessa, b) 10 km south west of Badessa.

Ethiopia, with over 250,000 ha of eucalypts plantation, mainly of *E. globulus* (Tasmanian blue gum) and *E. camaldulensis* (river red gum) (Davidson, 1989; Turnbull 1999), ranks 9th in world and 3rd in Africa (Eldridge *et al.*, 1994). Friis (1995) identified and described about 55 species of eucalypts in Ethiopia since their first introduction. He also noted that *E. globulus* subsp. *globulus*, *E. camaldulensis*, *E. saligna*, *E. tereticornis*, *E. citriodora*, and *E. regnans* are most widely grown in Ethiopia in areas with over 400 mm rainfall. *E. camaldulensis* and *E. globulus* are among the top performers in tropical and subtropical regions of the world (Eldridge *et al.*, 1994; Florence, 1996).

Though eucalypts were planted extensively all over Ethiopia, fuel wood shortage continued to spread to small towns and even to rural areas, and the requirements grew much faster than the plantations could supply (EFAP, 1994). On the other hand, the eucalypts which were introduced mainly for fuel wood became more valuable for construction wood, pole and post – their use as fuel being limited to litter and small branches (Fig. 1.2). The lack of scientific information regarding indigenous tree species of Ethiopia and the promotion of planting eucalypts by government departments favored the spread of the eucalypts long before the indigenous species of the country were sufficiently studied.

Long after the eucalypts were well accepted by farmers came the issue of their negative impact on plants and the environment at large. Lisanevork and Michelsen (1993) advise not to use *Eucalyptus* spp. in low rainfall areas and where soil conservation is the main purpose of tree planting because of their negative effects including the exhaustion of groundwater, excessive depletion of soil nutrient reserves and allelopathic effects, suppression of understorey and nearby vegetation and decline in the density of mycorrhizal

fungi (Lisanework and Michelsen, 1993; Michelsen *et al.*, 1993, 1996; Jagger and Pender, 2003). Very recently, regional governments in Ethiopia have sought to discourage eucalypts planting through a ban on the planting of eucalypts on farmlands (Hagos *et al.*, 1999). However, a study by Feyera *et al.* (2002) indicates that *E. globulus* can foster the regeneration of native flora in areas where seed sources and dispersal agents are available.

The Ethiopian Forestry Action Program (EFAP, 1994) has proposed a huge tree-planting program to bridge the gap between wood demand and supply in Ethiopia. Given the need to plant trees by farmers for household energy and wood requirements and the limited land holdings by farmers (as a result of increasing population and dependence of the majority of the population on agriculture), the time has come to look for tree species with some desirable qualities for planting in association with crops and/or on degraded lands that are no more profitable for growing crops.

Pohjonen and Pukkala (1988 and 1990); Pohjonen (1989) and Jagger and Pender (2003) argue that the afforestation of bare highland sites with eucalypts is positive compared to the prior barren state of sites. Davidson (1989) presented the arguments for and against eucalypts in the Ethiopian context. Even though the negative impacts of the eucalypts on crops were well recognized even by farmers (e.g. Poschen, 1987), planting of eucalypts continued in Ethiopia (Fig. 1.2). Although no studies have been conducted to compare the performance of the eucalypts with any of the indigenous tree species of Ethiopia, eucalypts are widely believed to grow faster than the deciduous species (Pohjonen, 1989).

a)



b)



c)



Figure 1.2 Woodlots of *E. camaldulensis* established by farmers in Badessa area and its use for construction. a) a two-year old woodlot, b) a seven-year old woodlot being cut for construction, c) a house under construction using *E. camaldulensis*.

Although some studies are underway on the propagation and domestication of selected indigenous species of Ethiopia as reviewed by Legesse (2000b), no attempts have yet been made to evaluate the performance of the deciduous trees regarding growth, water consumption and nutrient relations against the eucalypts that are widely studied. Because of the increasing indications that some of the indigenous tree species of the country are fairly fast growing (Legesse, 1995, 2002a, 2002b; Tadesse *et al*, 2000), the myth that eucalypts grow faster than the indigenous tree species of Ethiopia needs to be evaluated.

Table 1.1 Summary of the distribution, occurrences and uses of three deciduous and two *Eucalyptus* tree species considered for the current study

Species	Family	Distribution in Ethiopia	Distribution else where	Occurrence in Ethiopia	Uses
<i>Cordia africana</i> Lam.	Boraginaceae	1,200-2,200m	Tropical Africa and Arabia	Primary and secondary forests, woodlands, agroforestry, riparian vegetation	Timber, boxes, fodder, shade, firewood, honeybee flora, agroforestry
<i>Millettia ferruginea</i> (Hochst.) Baker	Fabaceae	1000-2500m except in Wollo and Gamo Gofa	Endemic to Ethiopia	Uplands, rainforests, woodlands, ground water forests, agroforestry	Shade, firewood, medicine, timber, boxes, fodder, agroforestry
<i>Croton macrostachyus</i> Del.	Euphorbiaceae	500-3400 m	Tropical Africa and Arabia	Mountain slopes, primary and secondary forests, savannah, waste ground, along rivers, agroforestry	Timber, boxes, shade firewood, Medicinal, agroforestry
<i>Eucalyptus camaldulensis</i> Dehnh.	Myrtaceae	<2000 m	Tropical, sub-tropical and temperate native to Australia.	Plantation, woodlot, roadside	Poles, posts, firewood, charcoal, hardboard, particle board, paper, construction
<i>Eucalyptus globulus</i> Labill.	Myrtaceae	> 1800 m high rainfall areas > 1000 mm annual rainfall.	Tropical, subtropical and temperate, native to Australia.	plantation, woodlot roadside	Poles, posts, pulpwood, firewood mine timber, construction

Sources: Poschen, 1987; Pohjonen, 1989; Thulin, 1989; Booth and Pryor, 1991; EFAP, 1994; Eldridge *et al.*, 1994; Friis, 1995; Gilbert, 1995; Legesse, 1995; WUARC, 1995; Florence, 1996; Tadesse *et al.*, 2000; Abebe *et al.*, 2001.

Therefore, three deciduous species widely used by farmers mainly in agroforestry systems (Fig. 1.3a-c) and two *Eucalyptus* species widely grown all over Ethiopia were considered in the current study. The distribution, occurrence and uses of the species considered for the current study are given in Table 1.1.

The study was composed of glasshouse investigations and field assessments. The glasshouse investigations focused on the effects of water and nutrient (nitrogen and phosphorus) availability on the growth and biomass allocation of the studied species. The field assessment focused on some desirable agroforestry qualities including root distribution and foliar nutrient concentrations of the studied tree species and their effects on selected soil fertility parameters in Badessa, Eastern Ethiopia. Isolated shade trees of the study species in Badessa area are shown in Fig. 1.4.

1.4 Objective

The overall objective of the study was to investigate and compare the use of water and nutrients and the growth performance of two *Eucalyptus* and three deciduous tree species indigenous to Ethiopia under limited and sufficient supplies of water and nutrients and to identify the mechanisms that these species employ to cope with moisture stresses at the seedling stage; and to investigate the effects of isolated trees and stands of these species on some soil fertility parameters under field conditions in Ethiopia.

a)



b)



c)



Figure 1.3 Typical agroforestry system composed of various crops and shade trees in Badessa area, Eastern Ethiopia. The tree components are mainly *C. africana*, *C. macrostachyus* and *F. albida*. a) Kara area and b) Oda Muda area, c) 3 km before Badessa dominated by *C. africana*.

a)



b)



c)



d)



Figure 1.4 Isolated mature trees retained as shade for crops (maize in this case). a) heavily pruned *C. africana* tree, b) *C. macrostachyus*, c) *M. ferruginea*, and d) *F. albida*.

2. EFFECTS OF SOIL MOISTURE DEFICIT ON GAS EXCHANGE, GROWTH AND BIOMASS ALLOCATION OF TWO *EUCALYPTUS* AND THREE DECIDUOUS TREE SPECIES

Abstract

The effects of water deficit on gas exchange, growth and biomass allocation of *C. africana*, *C. macrostachyus*, *M. ferruginea*, *E. camaldulensis* and *E. globulus* seedlings were studied under glasshouse conditions for 104 days. Plants were subjected to four watering regimes, viz. control (well-watered), mild-, moderate- or severe-water-deficit conditions corresponding to 75, 50, or 25% of the control moisture level, respectively. Water deficit resulted in reduced stomatal conductance in all species, with values ranging from 152 mmol m⁻² s⁻¹ for the control, to 16 mmol m⁻² s⁻¹ for the severely water deficient plants. Similarly, photosynthetic rate declined in all the species studied, with values ranging from 13.4 μmol m⁻² s⁻¹ for the control to 0.5 μmol m⁻² s⁻¹ for plants under severe water deficit conditions. Increased water deficit resulted in reduced predawn and midday leaf water potentials in all the species studied. The leaf water potentials of the two *Eucalyptus* spp. showed significant ($P < 0.05$) decline at midday compared to the corresponding predawn measurements on the same species. In contrast to the well-watered plants, severely water deficient plants of *C. africana* and *C. macrostachyus* showed significant ($P < 0.001$) drop in leaf relative water content (RWC). The whole plant water use efficiencies (WUE_{WL}) of the well-watered plants ranged from 3.8 to 6.1 g dry weight (kg H₂O)⁻¹. In contrast, WUE_{WL} in the severely water deficient plants ranged from 1.2 to 2.5 g dry mass (kg H₂O)⁻¹. The photosynthetic water use efficiency ranged from 4.7 mmol CO₂ (mol H₂O)⁻¹ in the severely water deficient plants to 7.5 mmol CO₂ (mol H₂O)⁻¹ in the well-watered plants. *M. ferruginea* used considerably less water for good growth compared to the other species examined. The eucalypts had significantly ($P < 0.05$) higher biomass production under water deficit than the deciduous species. However, all species had comparable biomass production under sufficient water supply. *C. africana* and *C. macrostachyus* invested more biomass

to root, the eucalypts invested more biomass to leaves while *M. ferruginea* invested more biomass to stems. Seedlings under severe water stress shaded their leaves in order to cope with the limited water supply. Increased water supply significantly ($P < 0.01$) increased biomass allocation to leaves in *M. ferruginea* and the two eucalypts whereas it significantly ($P < 0.01$) increased biomass allocation to roots in *C. macrostachyus*. Although species showed significant differences ($P < 0.001$) in specific leaf area (SLA), water deficit did not affect the SLA of all species.

2.1 Introduction

In light of the increasing population and its dependence on woody biomass for fuel and construction, tree planting in Ethiopia has become a question of survival (EFAP, 1994; Legesse, 1994, 2000). The establishment of trees that provide biomass for fuel and environmental services, including watershed management, soil nutrient and water retention, fodder for livestock, and construction material, is a basic requirement for sustained livelihood of farmers.

Although indigenous tree species such as *C. africana*, *C. macrostachyus* and *M. ferruginea* are known to have various environmental, economic and social benefits to farmers in Ethiopia (Demel and Aseffa, 1991; EFAP, 1994; Legesse, 1995; Jiregna, 1997; Tadesse *et al.*, 2000), planting of exotic species, mainly *E. camaldulensis* and *E. globulus* has been promoted for the provision of fuel wood and construction material. The success of *E. camaldulensis* and *E. globulus* as exotic species has been attributed to their superiority to other species in terms of their biomass production, wide adaptation and resistance to various environmental stresses and coppicing abilities (Pohjonen, 1989; Florence, 1996).

Growing *E. globulus* and *E. camaldulensis* under the Ethiopian conditions has been easy (Jagger and Pender, 2003), but the low initial survival of seedlings mainly due to severe moisture deficit during the dry season remains a problem (Pohjonen, 1989; Tesfaye, 1994). Farmers and/or forest technicians compensate for seedling loss during the dry season by increasing the planting density during the first year followed by refilling in the subsequent years (Pohjonen, 1989). Furthermore, no published information has been made available regarding the growth, biomass production and allocation of the indigenous tree species of Ethiopia under a range of moisture conditions. Although the eucalypts are widely believed to grow well and better than deciduous species of Ethiopia (Pohjonen, 1989), no comparative studies have been made in this regard to justify the use of the eucalypts in preference to the deciduous species. Due to the increasing need for tree planting, the Ethiopian Forestry Action Program, (EFAP, 1994), has proposed a huge tree planting program. As a result the search for suitable trees species for the aforesaid objectives has become the heart of forestry research in Ethiopia.

Therefore, the assessment of plant growth performance and biomass allocation under controlled water stress conditions could furnish information on the performance of the plants under field conditions, although plant growth in the field is regulated by several biotic and abiotic interactions (Nilsen and Orcutt, 1996). The extent to which water stress affects the growth performance is of paramount importance to evaluate whether these different species might withstand water stress and grow in drier areas or during the dry season in areas receiving enough rainfall.

The objectives of the study were to investigate and compare the effects of prolonged water deficit on the photosynthetic rate, stomatal conductance, water use

efficiency, growth parameters and biomass allocation of seedlings of three deciduous and two *Eucalyptus* tree species.

2.2 Materials and Methods

2.2.1 Plant establishment and glasshouse conditions

The glasshouse experiment was carried out at the Tree Nursery, University of Stellenbosch (South Africa), from September to December 2002. The Ethiopian National Tree Seed Project, Addis Ababa, kindly supplied seeds of *C. africana*, *C. macrostachyus*, *M. ferruginea*, *E. camaldulensis* and *E. globulus*. Seeds were sown on germination vials filled with vermiculite and maintained in a glasshouse at $26 \pm 2^\circ\text{C}$ day and $20 \pm 2^\circ\text{C}$ night temperatures. The seeds germinated within 5-15 days without pretreatment. The germinants were transplanted to 5-litre plastic bags (diameter, 150 mm; length, 300 mm) containing sand with 3% stone and having a pH (KCl) of 4.7. The growth medium was supplemented with a nutrient powder (COMPEL Chemicult[®]) at a rate of $385 \text{ mg plant}^{-1} \text{ week}^{-1}$ as a top dressing. The nutrient powder consisted of 6% N, 2.7% P, 13% K, 7% Ca, 2.2% Mg, 7.5% S and micronutrients. Potted seedlings were placed on wooden benches and were watered using micro-sprinkler irrigation twice a day during the summer, and once a day during the winter. Metasystox R[®] was sprayed to ward off ants and aphids which were observed on leaves of *C. macrostachyus* and *E. globulus* seedlings. The average minimum and maximum monthly temperatures inside the glasshouse during the growing period were 11.9°C and 31.5°C , respectively (Fig. 2.1). Owing to light attenuation by the glass, the photosynthetic photon flux density (PPFD) inside the glasshouse did not exceed $1200 \mu\text{mol}$

$\text{m}^{-2} \text{s}^{-1}$ while the PPFD outside the glasshouse was about $1700 \mu\text{mol m}^{-2} \text{s}^{-1}$, a value for a typical sunny day.

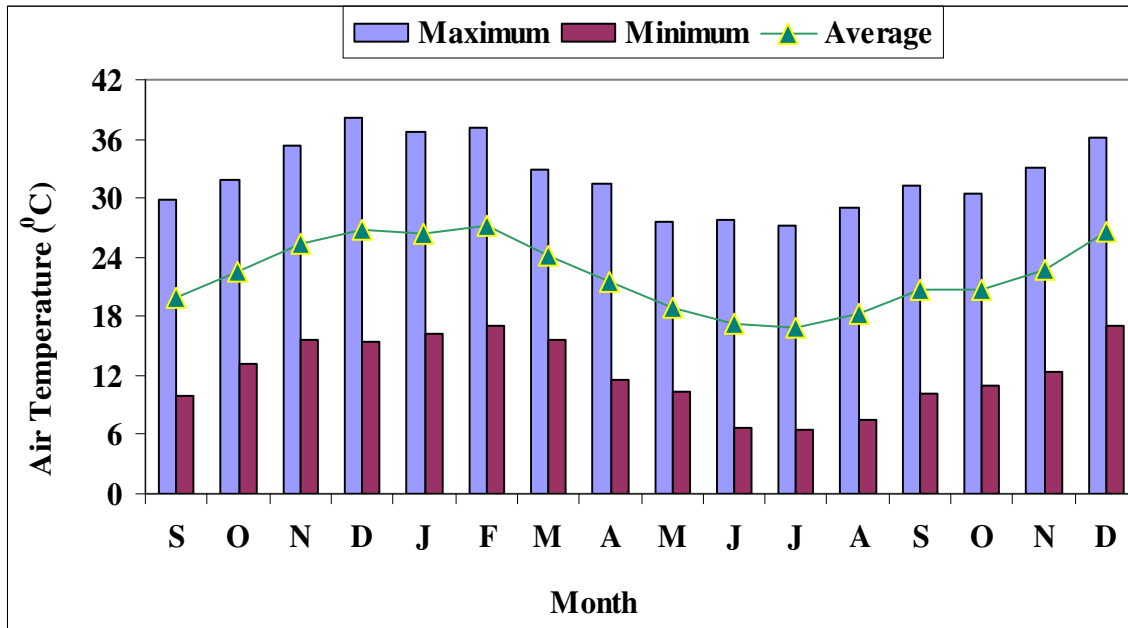


Figure 2.1 Average monthly minimum and maximum air temperature inside glasshouse prior to and during the study.

2.2.2 Treatments

One-year-old seedlings were used for the experiment. Five seedlings from each of the tree species were randomly assigned to four watering regimes as follows:

- 1) Well-watered (to meet the daily transpiration);
- 2) Mild water deficit (75% of the well-watered treatment);
- 3) Moderate water deficit (50% of the well-watered treatment); and,
- 4) Severe water deficit (25% of the well-watered treatment).

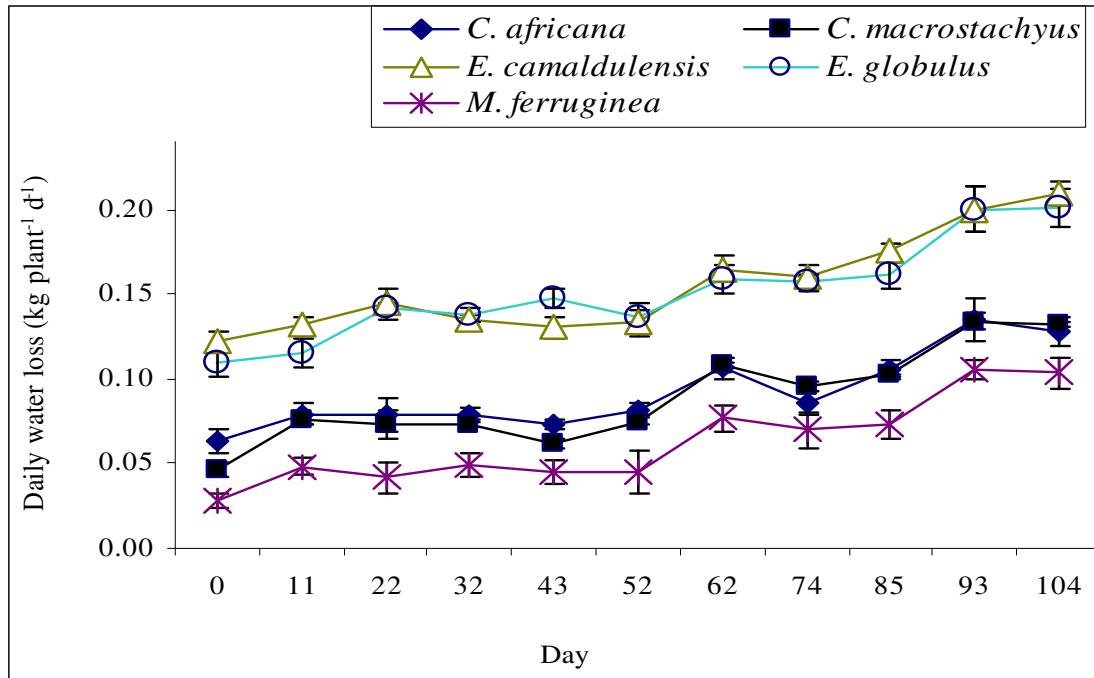


Figure 2.2 Mean daily whole plant water loss of well-watered seedlings of different species during 15 weeks of growth in a glasshouse. Bars indicate \pm SE, $n = 5$.

The bases of the seedling pots were covered by plastic bags to avoid water loss through holes at the bases of the pots and seedlings from different watering regimes were placed on glasshouse benches in a completely randomized design. As water loss from the pots occurs through direct evaporation from the soil and transpiration from plant leaves, these two were considered as the basis for generating the three water deficit levels. Due to differences in initial seedling sizes, species-specific water requirements, and the increase in water demand during active growth, treatment of the different species with the same volume of water was not considered appropriate. The mass of water needed to meet the daily transpiration requirement of control plants was estimated from measurements of pot weight (Fig. 2.2) and this mass of water was supplied to the control plants for the

subsequent 10 -12 days. The volume of water required to meet the 25, 50 and 75% water deficit was then calculated from the values for the well-watered treatment (Table 2.1).

Table 2.1. Total mass of water (kg plant⁻¹) supplied to each species and watering regime during the 104 days of study period

Species	Watering regimes (Treatments)			
	25%	50%	75%	100%
<i>C. africana</i>	3.36	6.71	10.07	13.43
<i>C. macrostachyus</i>	3.23	6.46	9.69	12.91
<i>E. camaldulensis</i>	4.90	9.79	14.68	19.58
<i>E. globulus</i>	4.80	9.59	14.38	19.18
<i>M. ferruginea</i>	2.54	5.08	7.62	10.16

2.2.3 Water potential and relative water content

Predawn and midday leaf water potentials and relative water content (RWC) were measured on days 22, 43 and 104 of the experiment. Water potential was measured using a pressure chamber (ARIMAD-3000, Israel). A well-expanded leaf was selected, cut at the base with a sharp blade, and placed in the chamber with the petiole protruding through the opening of the chamber. In the case of *E. globulus* and *E. camaldulensis*, small branches from the top of the plants were used for measurement, as the leaf of *E. globulus* is sessile and the petiole of *E. camaldulensis* is too short to appear through the opening of the chamber. After tight closure of the chamber, pressure was gradually applied until the very first appearance of water was observed at the cut end of the petiole, and the pressure was recorded in MPa. RWC was measured on leaf discs collected by driving a circular leaf punch of 4.5 cm² internal diameter into randomly selected leaf blades. Part of the blade close to the apex was punched to avoid the large mid-veins close to the base of the leaves.

In the case of *M. ferruginea*, whole leaflets were used. Each leaf disc or leaflet was placed in an airtight vial and immediately taken to the laboratory where it was weighed. The samples were then hydrated to full turgidity by floating the discs on de-ionized water in a closed Petri dish for six hours. The samples were removed from the water, surface moisture blotted off using filter paper, and weighed to get turgid weight. Samples were then oven dried at 85°C for 24 h and dry weights determined. RWC was then calculated using the equation: $RWC (\%) = (W_f - W_d)/(W_t - W_d) \times 100$, where $W(f)$ is the fresh weight, $W(d)$ is the dry weight and $W(t)$ is the turgid weight (Beadle *et al.*, 1993).

2.2.4 Gas exchange measurements

An infrared gas analyzer, (CIRAS-I, PP Systems, Hitchin, UK) was used to measure photosynthetic photon flux density (PPFD, $\lambda = 400\text{--}700$ nm; $\mu\text{mol m}^{-2} \text{s}^{-1}$), net CO_2 assimilation (photosynthetic) rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$) and transpiration rate ($\text{mmol m}^{-2} \text{s}^{-1}$) at a CO_2 concentration of 360 ppm and ambient humidity. All measurements were performed between 8:00 and 10:00 A.M. every three weeks. Measurements were taken on adaxial leaf surfaces of fully expanded leaves in the upper crown, fourth to sixth leaf from the top. Because *M. ferruginea* has pinnately compound leaves and the leaflets are smaller than the cuvette area, adjustments were made by measuring leaflet area placed in the cuvette. Photosynthetic water use efficiency (WUE_{GE}) was calculated as:

$$\text{WUE}_{\text{GE}} = \frac{\text{Photosynthetic rate } (\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1})}{\text{Transpiration rate } (\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1})}$$

The air temperature, PPFD and water vapor pressure difference (WVPD) during the gas exchange measurements are shown in Fig. 2.3. WVPD of the air inside the glasshouse was derived from air temperature and humidity measurements. It was calculated to be equivalent to saturated water vapor pressure (SWVP) minus ambient water vapor pressure of air at the same temperature. The former was calculated according to the formula:

$$\text{SWVP (mbar)} = 6.13753 \times \exp\left[T \times (18.564 - T/254.4)/(T + 255.57)\right]$$

where T is the temperature in °C (Buck, 1981).

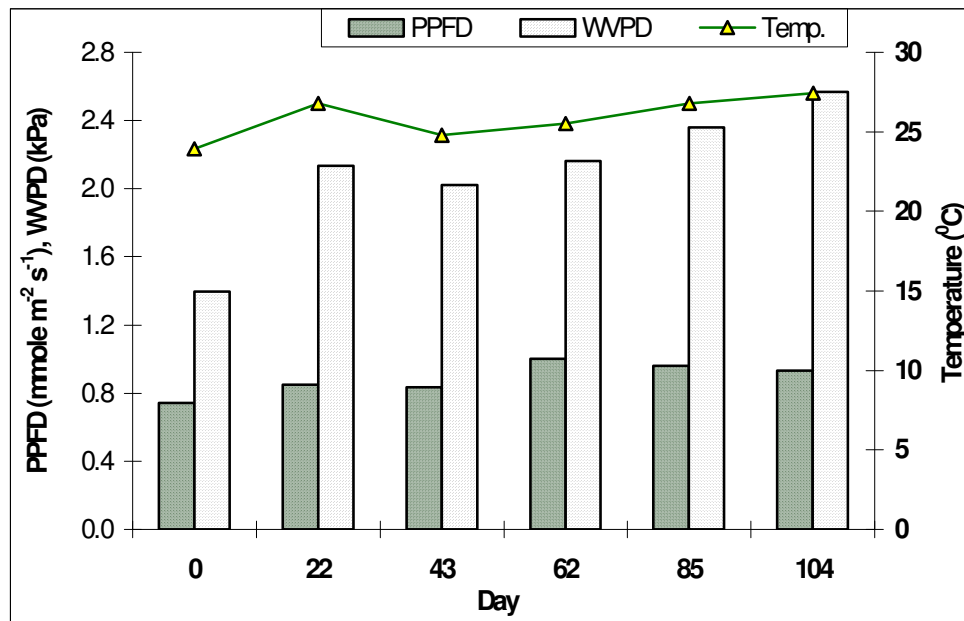


Figure 2.3 The morning (8:00 – 10:00AM) temperature, photosynthetic photon flux density (PPFD) and water vapor pressure difference inside the glasshouse during gas exchange measurements.

2.2.5 Plant water use efficiency

The rate of WL was calculated as the difference in pot weight over a period of 24 h expressed in terms of plant leaf area (kg water m⁻² d⁻¹). Three blank pots, the same as the

experimental pots but without plants, were incorporated for each treatment to correct for direct evaporation from the pots. Differences in water loss from the blank pots were checked and their mean weights were used for correction (Glenn and Brown, 1998; Li, 2000). The plants were harvested on day 104 and total plant dry weights recorded after oven drying at 85°C for 48 h. Plant water use efficiency (WUE_{WL}) was determined as:

$$WUE_{WL} = \frac{DW_{104} (g) - DW_0 (g)}{\sum WL_{(0-104)} (kg H_2O d^{-1})},$$

where DW_{104} is the total dry weight on day 104; DW_0 is the total dry weight on day 0; $\sum WL_{(0-104)}$ is the sum of daily water loss from day 0 to day 104. This sum of daily water loss from each species and treatment was determined from pot measurements carried out every 10 – 12 days.

2.2.6 Biomass measurements

Five seedlings per treatment were harvested at the beginning of the experiment and at the end for biomass assessment. The harvested plants were separated into stem, root and leaf, and dried in an oven at 85°C for 48 hours for dry weight determination. Stem weight ratio (SWR), root weight ratio (RWR) and leaf weight ratio (LWR) were determined at the beginning and end of the study period as the ratios of stem, root and leaf dry matter to the total plant dry matter, respectively. Seedling height and diameter (at the base of the seedlings) were measured at the start and end of the experiment. Percentage biomass, diameter and height increases were determined as [(final measurement-initial measurement)/initial measurement] x 100.

2.2.7 Leaf area estimation

Plant leaf area was estimated at the beginning and end of the experiment. The length and width of leaves of all plants were measured to estimate leaf area using a model established from the relationship between leaf length, leaf width and leaf area as determined from 20 destructively sampled leaves of each species. Total leaf area was determined using the model: $A = \sum(LL* LW*CF)$, where A is the area in mm², LL is leaf length in mm, LW is leaf width in mm, and CF is the correction factor. The correction factors were 0.73, 0.75, 0.69, 0.79 and 0.82 for *C. africana*, *C. macrostachyus*, *E. camaldulensis*, *E. globulus* and *M. ferruginea*, respectively. The correlations between leaf areas measured directly and those predicted using the model were $0.96 < r^2 < 0.99$; $P < 0.001$; $n = 20$).

Leaf area ratio (LAR) was calculated as a ratio of total leaf area to total plant dry matter. Percentage leaf area expansion was determined as [(final leaf area-initial leaf area)/initial leaf area] x 100. Initial and final leaf areas refer to the leaf areas estimated at the beginning and end of the experiment, respectively. Specific leaf area (SLA) was determined at the end of the experiment using leaf discs, each with an area of 4.5 cm², except for the leaflets of *M. ferruginea* in which the leaf disc area was 1 cm². The leaf discs were dried at 85 °C for 24 h, and weighed. SLA was then calculated as leaf disc area per leaf disc dry weight.

2.2.8 Statistical procedures

Two and one-way ANOVA tests were used to determine differences among species and treatments for each of the variables. Tukey's Honestly Significant Difference test was

employed for multiple comparisons when significant differences were found between treatments. Because no significant differences in WL, WUE_{WL} and WUE_{GE} within treatments were observed across the measurement days, pooled data ($n = 25$) were presented for both parameters. All statistical analyses were carried out using SPSS 11.0 for Windows.

2.3 Results

2.3.1 Water potential and relative water content

Increased water deficit resulted in decreased predawn and midday leaf water potentials in all the species studied (Fig. 2.4a, b). The mean leaf water potential differences between the well-watered and the severely water deficient plants at midday were high for *E. globulus* (1.40 MPa) and *E. camaldulensis* (1.14 MPa) compared to ca 0.5 MPa for the three deciduous tree species examined. The leaf water potentials of the two *Eucalyptus* spp. showed significant ($P < 0.05$) decline at midday compared to the corresponding predawn measurements (Fig. 2.4a, b). In contrast to the well-watered plants, severely water deficient plants of *C. africana* and *C. macrostachyus* showed significant ($P < 0.001$) reduction in leaf RWC (Fig. 2.4c, d).

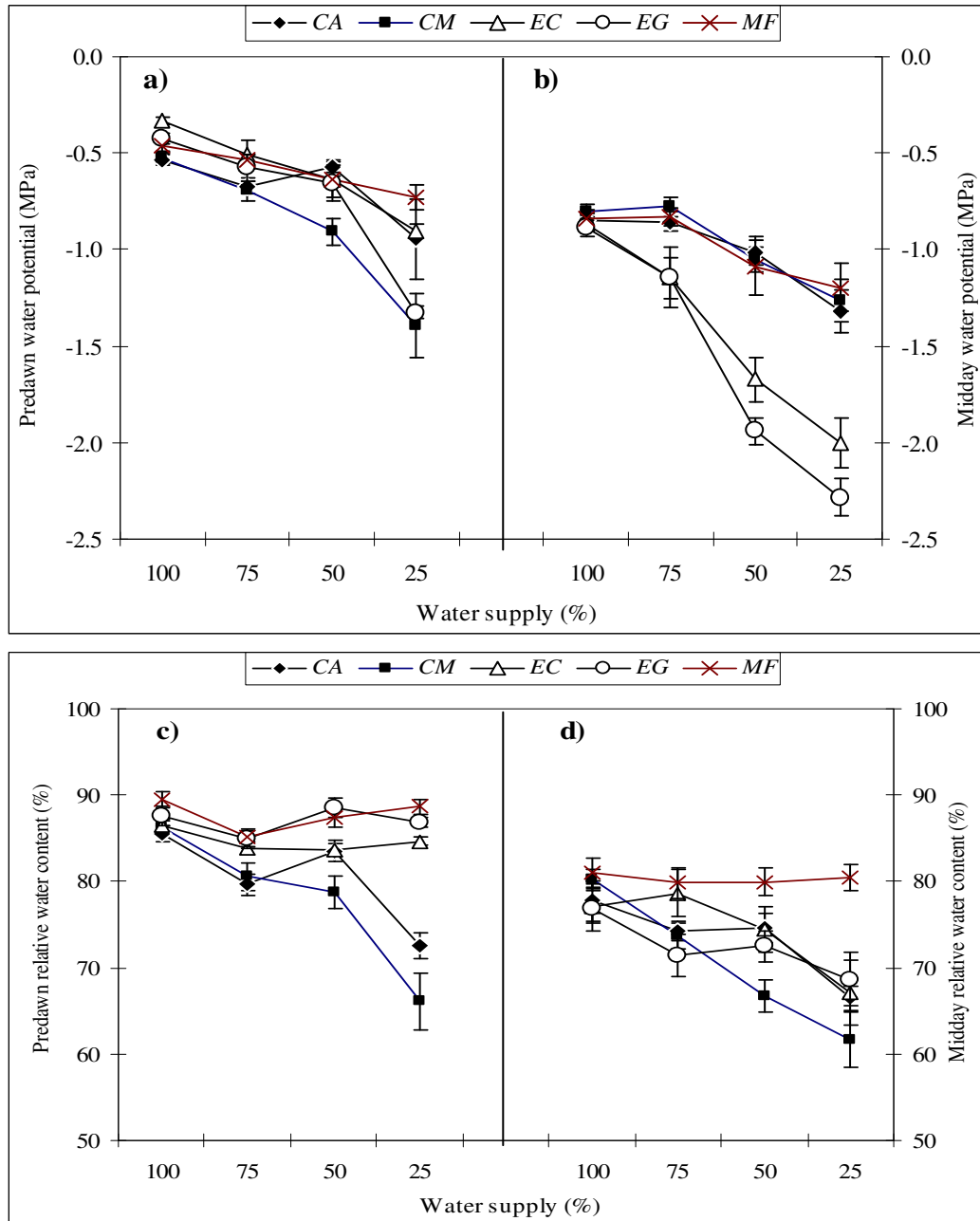


Figure 2.4 Mean water potential (a) predawn, b) midday) and relative water content (c) predawn, d) midday) of seedlings of *C. africana* (CA), *C. macrostachyus* (CM), *E. camaldulensis* (EC), *E. globulus* (EG) and *M. ferruginea* (MF) during growth with four watering regimes (25%, 50%, 75% and 100% of daily transpiration requirements). Bars indicate \pm SE, n = 15.

2.3.2 Stomatal conductance and photosynthetic rate

Increased water deficit resulted in reduced stomatal conductance and photosynthetic rate in all the species studied (Fig. 2.5). However, the reduction in stomatal conductance and photosynthetic rate followed different patterns for the different species investigated. Much of the decline in stomatal conductance and photosynthetic rate occurred during the first 22 days of the experiment, except in *M. ferruginea* where the declines were rather gradual. After 22 days, *C. africana* and *C. macrostachyus* maintained more or less constant physiological functions while the two eucalypts showed declining trends throughout the experimental period. On day 104, stomatal conductances and photosynthetic rates of all the severely water deficient plants were 3–4 and 5–10 times lower than the well-watered plants, respectively.

2.3.3 Water use efficiency

Except for *E. globulus* and *M. ferruginea*, water deficit did not affect the WUE_{GE} of the species investigated (Table 2.2). WUE_{GE} was significantly ($P < 0.01$) reduced due to severe water deficit in these species. Water loss from *C. macrostachyus* and *C. africana* was about 2-3 times those of *E. camaldulensis* and *E. globulus* across all the treatments (Table 2.2). Increased water deficit resulted in reduced WUE_{WL} in all the species studied. The water use efficiencies of the severely water deficient plants were reduced by factors of 3.3, 3.2, 2.7, 1.9 and 3.3 for *C. africana*, *C. macrostachyus*, *E. camaldulensis*, *E. globulus* and *M. ferruginea*, respectively, compared to the well-watered plants (Table 2.2). *C. africana* and *C. macrostachyus* had lower WUE_{WL} across all the four levels of watering regimes. Poor correlations were observed between WUE_{GE} and WUE_{WL} for all species ($r^2 = 0.04 - 0.22$), except for *E. globulus* ($r^2 = 0.42$).

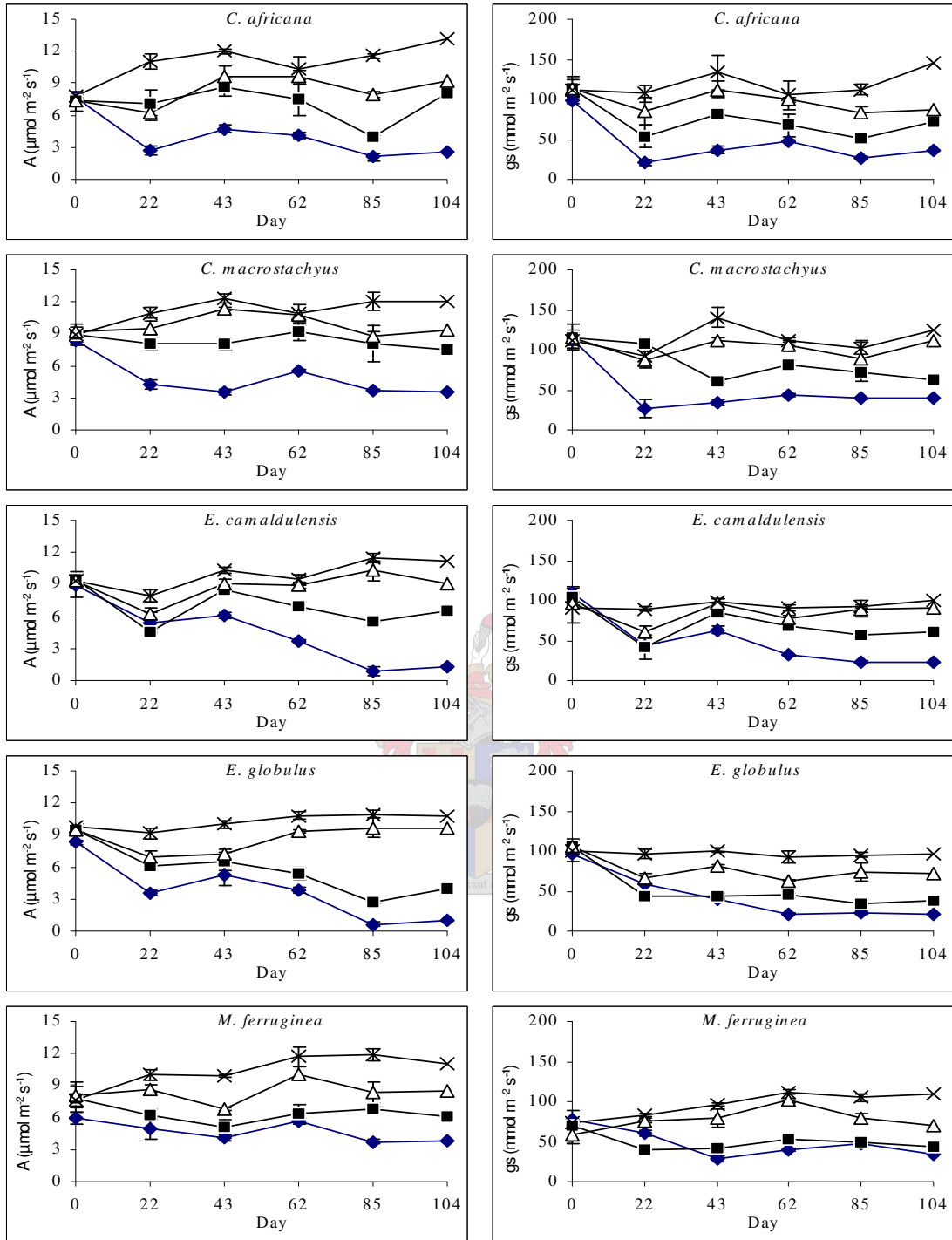


Figure 2.5 Mean photosynthetic rate (A, left) and stomatal conductance (gs, right) of seedlings of five tree species during 104 days of growth with four watering regimes: 25% (◆), 50% (■), 75% (△) and 100% (x) of daily transpiration requirements. Bars indicate \pm SE, n = 5.

Table 2.2 Mean (\pm SE) water loss (WL), plant water use efficiency (WUE_{WL}) and photosynthetic water use efficiency (WUE_{GE}) of seedlings of five tree species grown for 104 days under four watering regimes. Significant P-values of two-way ANOVA are shown for variation among species, treatments and their interactions. Mean values within a row followed by different letters are significantly different ($P < 0.05$) according to Tukey's test; $n = 25$ for WL and WUE_{GE} and 5 for WUE_{WL} .

Species	Water supply (% of control)			
	25	50	75	100
WL ($\text{kg m}^{-2} \text{d}^{-1}$)				
<i>C. africana</i>	0.7 \pm 0.06a	0.7 \pm 0.06a	0.8 \pm 0.07a	0.9 \pm 0.05a
<i>C. macrostachyus</i>	0.9 \pm 0.05a	0.9 \pm 0.07a	1.0 \pm 0.06a	1.1 \pm 0.06a
<i>E. camaldulensis</i>	0.4 \pm 0.05a	0.3 \pm 0.04a	0.5 \pm 0.05a	0.4 \pm 0.02a
<i>E. globulus</i>	0.3 \pm 0.07ab	0.2 \pm 0.02b	0.3 \pm 0.03a	0.4 \pm 0.02a
<i>M. ferruginea</i>	0.4 \pm 0.04a	0.5 \pm 0.06a	0.5 \pm 0.05a	0.4 \pm 0.03a
Species	0.000			
Treatment	0.017			
Species * treatment	0.687			
WUE_{WL} ($\text{g dry mass (kg H}_2\text{O)}^{-1}$)				
<i>C. africana</i>	1.2 \pm 0.26c	2.1 \pm 0.31bc	3.3 \pm 0.37ab	3.8 \pm 0.34a
<i>C. macrostachyus</i>	1.3 \pm 0.14c	2.1 \pm 0.29bc	3.0 \pm 0.44ab	4.2 \pm 0.19a
<i>E. camaldulensis</i>	1.8 \pm 0.20b	4.0 \pm 0.38a	4.5 \pm 0.36a	4.9 \pm 0.42a
<i>E. globulus</i>	2.5 \pm 0.39b	3.6 \pm 0.41ab	4.9 \pm 0.46a	4.9 \pm 0.29a
<i>M. ferruginea</i>	1.8 \pm 0.33c	3.3 \pm 0.83cb	4.1 \pm 0.10ab	6.1 \pm 0.70a
Species	0.000			
Treatment	0.000			
Species * treatment	0.324			
WUE_{GE} ($\text{mmol CO}_2 \text{(mol H}_2\text{O)}^{-1}$)				
<i>C. africana</i>	7.1 \pm 0.36a	6.9 \pm 0.19a	6.9 \pm 0.35a	7.3 \pm 0.34a
<i>C. macrostachyus</i>	6.9 \pm 0.21a	6.9 \pm 0.25a	7.0 \pm 0.31a	6.6 \pm 0.22a
<i>E. camaldulensis</i>	5.7 \pm 0.33a	6.7 \pm 0.37a	6.8 \pm 0.29a	6.3 \pm 0.31a
<i>E. globulus</i>	4.7 \pm 0.38b	7.1 \pm 0.28a	7.0 \pm 0.27a	7.5 \pm 0.32a
<i>M. ferruginea</i>	5.4 \pm 0.29b	7.3 \pm 0.32a	6.5 \pm 0.21ab	6.8 \pm 0.31a
Species	0.003			
Treatment	0.000			
Species * treatment	0.005			

2.3.4 Growth

Seedlings of the study species had already different growth status and biomass allocation patterns before the treatments were made (Table 2.3).

Table 2.3 Mean (\pm SE) growth parameters of seedlings of five study species before treatment of the watering regimes (n = 5).

Growth parameters	<i>C. africana</i>	<i>C. macrostachyus</i>	<i>E. camaldulensis</i>	<i>E. globulus</i>	<i>M. ferruginea</i>
Diameter (mm)	11.12 \pm 0.37	8.38 \pm 0.33	9.07 \pm 0.33	7.55 \pm 0.24	9.05 \pm 0.19
Height (cm)	28.61 \pm 0.86	27.57 \pm 0.71	88.38 \pm 2.28	88.12 \pm 1.76	59.21 \pm 2.34
Leaf area (m ²)	0.06 \pm 0.01	0.03 \pm 0.00	0.17 \pm 0.01	0.26 \pm 0.02	0.07 \pm 0.01
Total biomass (g)	12.74 \pm 0.30	11.02 \pm 0.36	30.69 \pm 0.93	29.61 \pm 0.50	14.58 \pm 0.59
SWR (g g ⁻¹)	0.31 \pm 0.01	0.30 \pm 0.04	0.40 \pm 0.01	0.44 \pm 0.02	0.69 \pm 0.03
LWR (g g ⁻¹)	0.25 \pm 0.02	0.23 \pm 0.02	0.29 \pm 0.02	0.34 \pm 0.01	0.11 \pm 0.01
RWR (g g ⁻¹)	0.44 \pm 0.02	0.46 \pm 0.04	0.31 \pm 0.02	0.23 \pm 0.02	0.20 \pm 0.02
LAR (m ² kg ⁻¹)	4.37 \pm 0.67	2.87 \pm 0.29	5.80 \pm 0.88	7.74 \pm 1.25	4.66 \pm 0.91
SLA (m ² kg ⁻¹)	17.76 \pm 1.09	22.92 \pm 1.39	13.97 \pm 1.56	12.03 \pm 2.13	25.51 \pm 0.79

Soil water deficit resulted in significant ($P < 0.001$) variations in diameter growth between species, treatments and their interactions (Table 2.4). Plants under severe water stress had reduced stem diameter ($P < 0.05$) compared to well-watered plants except for *E. globulus*. The difference in diameter between the well-watered and severely water stressed plants was about seven-fold in *C. africana*.

Table 2.4 Mean (\pm SE) percentage increase in plant diameter, height, leaf area and total dry mass of seedlings of five tree species under four watering regimes: 25%, 50%, 75% and 100% of daily transpiration requirements for 104 days in a glasshouse. The significant P-values of two-way ANOVA are shown for the variation between species, treatments and their interactions. Mean values (row) followed by different letters are significantly different ($P < 0.05$) according to Tukey's test, $n = 5$)

Species	Water supply levels (% of daily transpiration requirements)			
	25	50	75	100
Plant diameter increase (%)				
<i>C. africana</i>	10.0 \pm 2.5c	20.5 \pm 2.6c	35.4 \pm 1.8b	73.9 \pm 4.5a
<i>C. macrostachyus</i>	26.2 \pm 3.3b	34.7 \pm 4.9ab	42.5 \pm 5.0ab	48.2 \pm 7.6a
<i>E. camaldulensis</i>	24.9 \pm 4.7b	41.3 \pm 5.1ab	42.1 \pm 3.8ab	57.3 \pm 8.1a
<i>E. globulus</i>	37.0 \pm 4.6a	36.9 \pm 2.3a	29.7 \pm 2.1a	41.0 \pm 6.2a
<i>M. ferruginea</i>	12.4 \pm 1.8b	24.5 \pm 2.7ab	33.3 \pm 5.2a	32.5 \pm 3.7a
Species	0.000			
Treatment	0.000			
Species * treatment	0.000			
Plant height increase (%)				
<i>C. africana</i>	22.5 \pm 3.2d	48.9 \pm 2.5c	75.3 \pm 1.9b	99.3 \pm 3.6a
<i>C. macrostachyus</i>	12.6 \pm 1.7a	16.8 \pm 4.0b	27.1 \pm 3.0a	34.9 \pm 5.8a
<i>E. camaldulensis</i>	7.1 \pm 1.2b	12.9 \pm 1.4b	37.8 \pm 3.4a	34.2 \pm 3.1a
<i>E. globulus</i>	5.4 \pm 0.6c	27.2 \pm 1.7b	33.1 \pm 1.3b	43.6 \pm 3.2a
<i>M. ferruginea</i>	9.5 \pm 0.9c	12.9 \pm 0.8c	40.2 \pm 5.0b	70.7 \pm 4.8a
Species	0.000			
Treatment	0.000			
Species * treatment	0.000			
Leaf area increase (%)				
<i>C. africana</i>	-11.6 \pm 2.1c	25.2 \pm 1.9c	201.5 \pm 7.7a	121.6 \pm 11.2b
<i>C. macrostachyus</i>	-15.8 \pm 7.9d	80.1 \pm 7.9c	161.6 \pm 9.5b	258.6 \pm 15.4a
<i>E. camaldulensis</i>	-3.9 \pm 7.7a	124.8 \pm 12.5b	188.9 \pm 19.5a	138.6 \pm 16.6b
<i>E. globulus</i>	-7.3 \pm 5.0a	71.9 \pm 5.5b	164.0 \pm 16.0a	102.5 \pm 21.7b
<i>M. ferruginea</i>	-24.2 \pm 2.8b	18.0 \pm 2.2b	141.7 \pm 8.3a	189.9 \pm 13.2a
Species	0.000			
Treatment	0.000			
Species * treatment	0.000			
Total plant mass increase (%)				
<i>C. africana</i>	19.1 \pm 1.5d	68.0 \pm 5.4c	146.0 \pm 8.4b	286.5 \pm 8.6a
<i>C. macrostachyus</i>	23.3 \pm 2.1d	70.2 \pm 8.2c	142.3 \pm 10.6b	334.0 \pm 14.0a
<i>E. camaldulensis</i>	33.6 \pm 3.6d	101.1 \pm 6.8c	157.2 \pm 22.4b	250.5 \pm 11.2a
<i>E. globulus</i>	33.9 \pm 3.3d	83.0 \pm 3.0c	187.9 \pm 13.6b	245.5 \pm 18.7a
<i>M. ferruginea</i>	20.9 \pm 2.5d	70.7 \pm 4.7c	127.6 \pm 7.7b	241.4 \pm 23.7a
Species	0.009			
Treatment	0.000			
Species * treatment	0.000			

Soil water deficit resulted in significant ($P < 0.001$) variations in height growth between species, treatments and their interactions (Table 2.4). The height growths of the severely water stressed plants were reduced by about 3 – 6 fold compared to the well-watered plants in all species, except in *C. macrostachyus* (Table 2.4). In all treatments *C. africana* showed significantly higher ($P < 0.05$) height increment than the other species. Soil water deficit resulted in significant ($P < 0.001$) variations in leaf area expansion between species, treatments and their interactions (Table 2.4). The deciduous tree species showed progressive leaf area increase with increasing water supply (Table 2.4). Well-watered *C. macrostachyus* had the maximum leaf area expansion compared to all the other species ($P < 0.001$). Soil water deficit resulted in significant ($P < 0.001$) variations in biomass production between species, treatments and their interactions (Table 2.4). Severe water deficit reduced the biomass production of *C. africana* and *C. macrostachyus* plants by about 14 fold and those of both eucalypts and *M. ferruginea* only by 7 fold compared to well-watered plants (Table 2.4). Biomass production significantly increased ($P < 0.05$) with increasing water supply in all species. Species did not show variations in biomass production in the mild water deficit and well-watered treatments. Both of the eucalypts produced more biomass under severe water deficit condition than the deciduous species ($P < 0.05$) while *C. africana* and *C. macrostachyus* produced significantly higher ($P < 0.05$) biomass under sufficient water supply compared to all the other species.

2.3.5 Biomass allocation

Significant variations ($P < 0.001$) in SWR were observed both between species and watering regimes (Fig. 2.6a and Table 2.5). In most species a declining SWR was observed with increasing water supply but treatments did not show significant variations for *C. africana*

and *E. camaldulensis*. The SWR of *M. ferruginea* was very significantly higher ($P < 0.001$) than those of all the other species. No significant variations in RWR were observed between treatments (Fig. 2.6b and Table 2.5). However, the variations among species and the interactions of species and treatments were significant ($P < 0.001$). The RWR of *C. macrostachyus* was about twice that for *E. camaldulensis*, and about 2.5 times more than those for *E. globulus* and *M. ferruginea* in all the treatments except under severe water deficit in which differences were comparably smaller. *C. macrostachyus* was the only species that had significant variation in RWR among treatments. Its RWR showed increasing trend with increasing water supply. Significant variations ($P < 0.001$) in biomass allocation to leaves (LWR) were observed between species, watering regimes and their interactions (Fig. 2.6c and Table 2.5). Increased water deficit resulted in significantly reduced ($P < 0.05$) LWR in *E. camaldulensis*, *E. globulus* and *M. ferruginea*. Furthermore, *E. globulus* and *E. camaldulensis* had significantly higher ($P < 0.001$) LWR than the deciduous species in the well watered treatment.

Significant variations ($P < 0.001$) in LAR were observed between species, watering regimes and their interactions. The LAR of *E. globulus* was about twice those of *C. africana* and *C. macrostachyus* at the start of the experiment (Table 2.3) and following all treatments except the severe water deficit treatment (Fig. 2.6d). The LAR of *E. camaldulensis* was also about twice those of *C. macrostachyus* in all treatments.

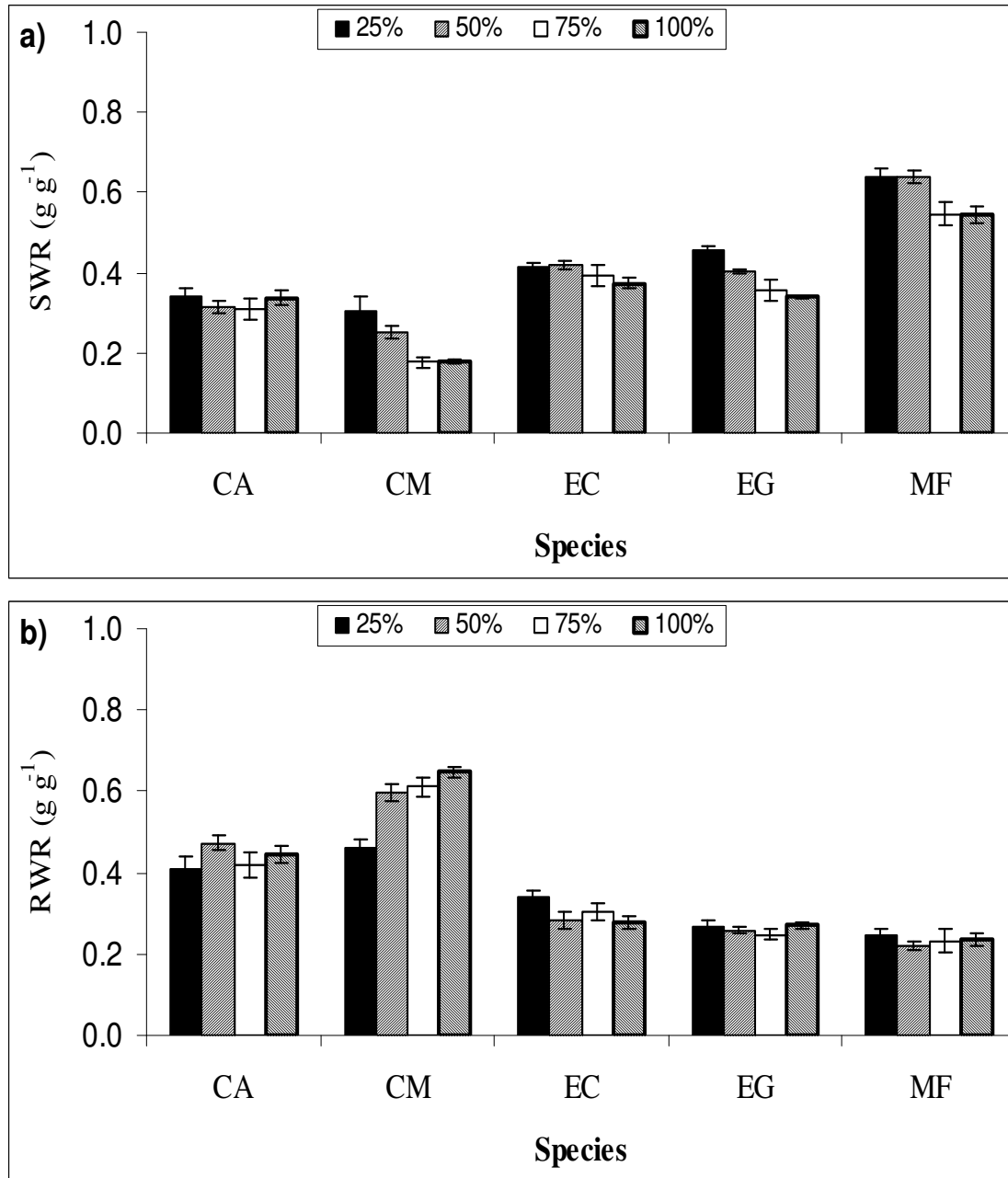


Figure 2.6 (a and b). Mean stem weight ratio (a) and root weight ratio (b) of *C. africana* (CA), *C. macrostachyus* (CM), *E. camaldulensis* (EC), *E. globulus* (EG) and *M. ferruginea* (MF) after 104 days of growth under four water regimes (25%, 50%, 75% and 100% of daily transpiration requirements) in a glasshouse. (Bars indicate \pm SE, n = 5).

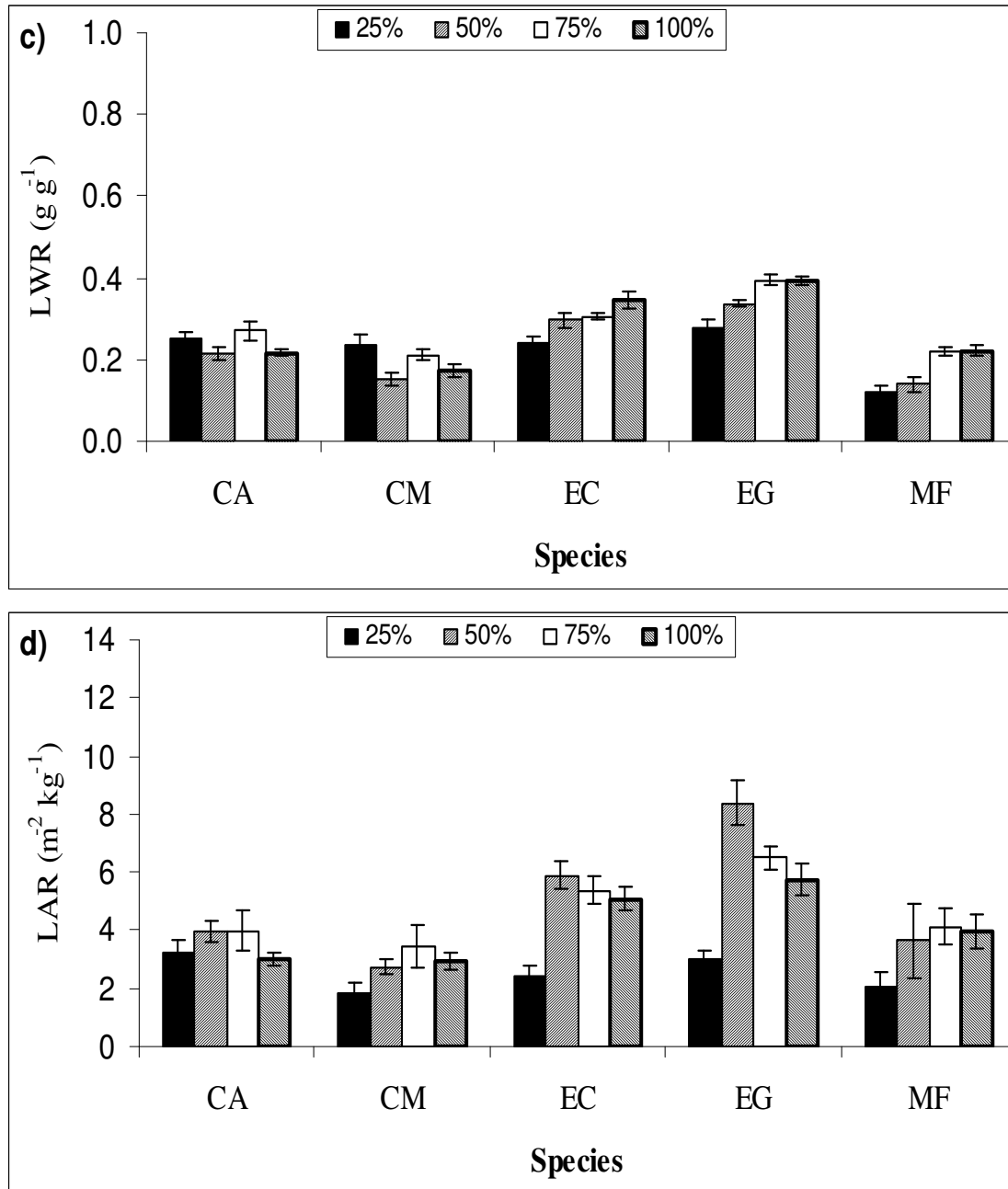


Figure 2.6 (c and d). Mean leaf weight ratio (c) and leaf area ratio (d) of *C. africana* (CA), *C. macrostachyus* (CM), *E. camaldulensis* (EC), *E. globulus* (EG) and *M. ferruginea* (MF) after 104 days of growth under four water regimes (25%, 50%, 75% and 100% of daily transpiration requirements) in a glasshouse. (Bars indicate \pm SE, n = 5).

Variation in SLA was more distinct between species than between treatments (Fig. 2.7 and Table 2.5). Water deficit did not affect the SLA in all species. The SLA of *M. ferruginea* was significantly higher ($P < 0.001$) than all the other species. Both of the eucalypts had comparable and significantly ($P < 0.01$) lower SLA than *C. macrostachyus* and *C. africana*.

The ranking of species based on the observed values of growth parameters is presented in Table 2.6. Different species showed clear distinction regarding SLA and RWR.

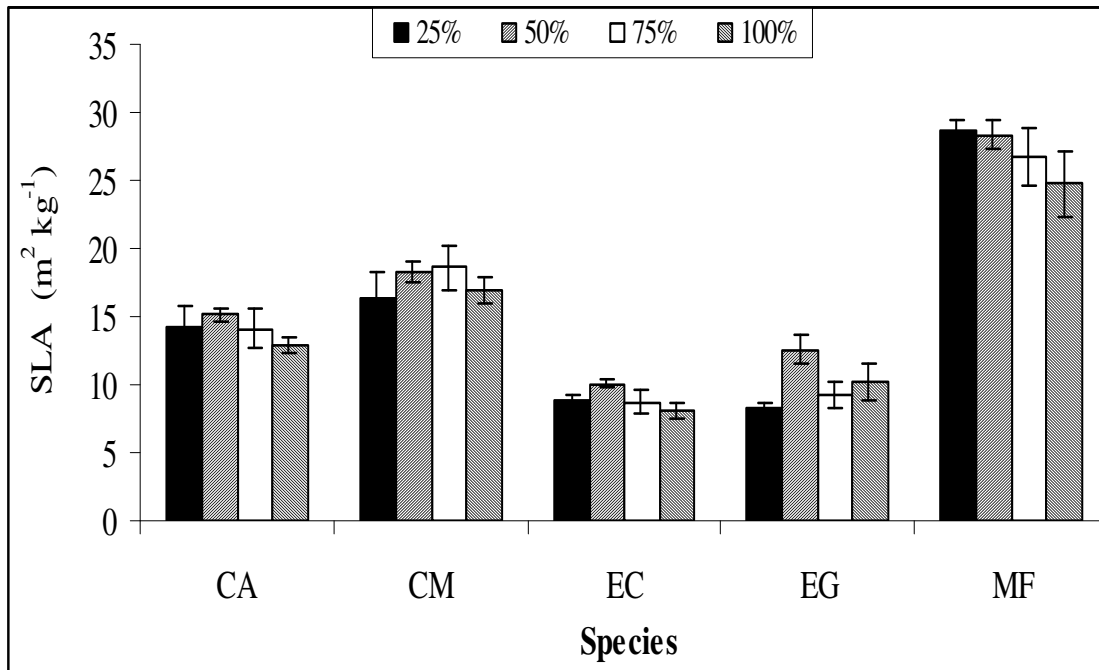


Figure 2.7 The mean specific leaf area of seedlings of *C. africana* (CA), *C. macrostachyus* (CM), *E. camaldulensis* (EC), *E. globulus* (EG) and *M. ferruginea* (MF) after 104 days of growth under four water regimes (25%, 50%, 75% and 100% of daily transpiration requirements) in a glasshouse. (Bars indicate \pm SE, n = 5).

Table 2.5 Summary of a factorial ANOVA carried out to test significant variations in the biomass allocation in seedlings of five tree species (*C. africana*, *C. macrostachyus*, *E. camaldulensis*, *E. globulus* and *M. ferruginea*) grown with four watering regimes under glasshouse conditions for 104 days. Data has been presented in Figs 2.6 and 2.7).

Source	df	F-value	P-value
SWR (g g⁻¹)			
Species	4	196.4	0.000
Treatment	3	19.2	0.000
Species * treatment	12	2.2	0.021
RWR (g g⁻¹)			
Species	4	208.8	0.000
Treatment	3	2.1	0.111
Species * treatment	12	5.0	0.000
LWR (g g⁻¹)			
Species	4	73.0	0.000
Treatment	3	14.0	0.000
Species * treatment	12	5.3	0.000
LAR (m² kg⁻¹)			
Species	4	23.2	0.000
Treatment	3	21.3	0.000
Species * treatment	12	3.6	0.000
SLA (m² kg⁻¹)			
Species	4	147.8	0.000
Treatment	3	3.8	0.013
Species * treatment	12	1.8	0.061

Table 2.6 Summary of the rankings of species based on the observed growth parameters (Figs. 2.6 and 2.7). Rank values were assigned based on comparison of species made across treatments. Rank of 1 is assigned to the highest value.

Observed parameter	<i>C. africana</i>	<i>C. macrostachyus</i>	<i>E. camaldulensis</i>	<i>E. globulus</i>	<i>M. ferruginea</i>
Stem weight ratio	3	4	2	2	1
Root weight ratio	2	1	3	4	5
Leaf weight ratio	3	4	2	1	4
Leaf area ratio	3	4	2	1	3
Specific leaf area	3	2	5	4	1

2.4 Discussion

2.4.1 Water potential and relative water content

The water potentials of *E. globulus* and *E. camaldulensis* were strongly affected by water deficit, especially during middays (Fig. 2.4b). The significantly reduced leaf water content of *C. macrostachyus* (Fig. 2.4c, d) could be the result of pronounced water loss ($0.9 \pm 0.05 \text{ kg m}^{-2} \text{ d}^{-1}$) through transpiration (Table 2.2). At the cellular level, reduced water potential and RWC affect the physiology of the cell in several ways, including changes in intercellular organelle positions, transport channels, enzyme biochemistry; as well as cell wall shrinkage (Nilsen and Orcutt, 1996; Lambers *et al.*, 1998; Hall, 2001; Lawlor and Cornic, 2002). Clearly, these changes impact on cellular metabolism, including photosynthesis (Lawlor and Cornic, 2002).

2.4.2 Stomatal conductance and photosynthetic rate

E. globulus and *E. camaldulensis* showed gradual stomatal and photosynthetic responses compared to *C. africana* and *C. macrostachyus* (Fig. 2.5). In contrast to earlier reports (e.g. Pereira *et al.*, 1986; Pereira *et al.*, 1987; Pereira de Almeida and Riekerk, 1990; White *et al.*, 2000) *E. globulus* and *E. camaldulensis* did not show strong stomatal control when confronted with severe water deficit. During the first six weeks, severely water stressed plants of *E. camaldulensis* maintained open stomata and high photosynthetic rate compared to *C. africana* and *C. macrostachyus*, which showed characteristics of drought tolerant plants (Nilsen and Orcutt, 1996). The eucalypts had been characterized as drought tolerant because they tend to maintain open stomata and tissue function despite a relatively large

depression in water potential (Florence, 1996). However, with the extended severe water deficit, the stomatal conductance of the two eucalypts progressively declined to values of 15-20 mmol m⁻² s⁻¹ (Fig. 2.5). Of the species examined in the current study, *M. ferruginea* had higher tissue water content and photosynthetic rate even under severe water deficit probably due to the ability to re-orient its leaves, thus avoiding direct solar irradiance during midday. It has to be noted that *M. ferruginea* received less than half the volume of water supplied to the control plants of the two *Eucalyptus* spp. (Fig. 2.2). Hence, although the eucalypts had been acclaimed as drought tolerant (e.g., Pohjonen, 1989; Florence, 1996), *M. ferruginea* was found to be more tolerant to severe water deficit as evidenced by its maintenance of high water potential (Fig. 2.4b), high RWC (Fig. 2.4c), and high photosynthetic rate (Fig. 2.5).

C. africana and *C. macrostachyus* responded to severe water deficit through reduced stomatal conductance and photosynthetic rate (Fig. 2.5). These diminished responses appear to be the result of reduced leaf water content with increasing water deficit (Fig 2.4c, d). Lawlor (2002) and Lawlor and Cornic (2002) reported that decreased leaf RWC progressively reduces stomatal conductance. In a study on stomatal responses of five indigenous tree species of Ethiopia to increasing water deficit, Legesse (1992) detected the presence of pronounced midday stomatal closure in *C. africana*.

Stomatal closure is regarded as the initial impact of water limitation on photosynthesis (Nilsen and Orcutt, 1996; Luan, 2002). Although stomata control the flux of CO₂ into the mesophyll cells for photosynthesis, the deleterious effects of dehydration on cellular metabolism suggests the presence of non-stomatal factors that account for reduced photosynthetic rates under severe water deficit (Björkman and Powles, 1984; Ogren and

Öquist, 1985; Kozłowski *et al.*, 1991; Kramer and Boyer, 1995; Nilsen and Orcutt, 1996; Lawlor and Cornic, 2002).

2.4.3 Water use efficiency

Soil water deficit did not affect water use efficiency at the leaf level (WUE_{GE}) except for *E. camaldulensis*, *E. globulus* and *M. ferruginea* plants that were subjected to severe water deficit conditions (Table 2.2). For the severely water deficient plants of *E. camaldulensis* and *E. globulus*, photosynthetic rates were affected more than stomatal conductances resulting in higher transpiration and hence lower WUE_{GE} compared to the well-watered plants.

Whole plant water use efficiency (WUE_{WL}) of the well-watered plants ranged between 3.8 and 6.1 g dry mass (kg H₂O)⁻¹ (Table 2.2). These values are less than the value (6.3 g dry mass (kg H₂O)⁻¹) reported for *Salix viminalis* (Lindroth and Cienciala, 1996). At the whole plant level, increased soil water deficit resulted in reduced water use efficiencies in all the species studied. The low WUE_{WL} observed in plants under severe soil water deficit could be due to limited photosynthetic rate and water loss through transpiration. It has been argued that, although photosynthesis is limited by water deficit, plants should transpire to dissipate excess light energy and regulate leaf temperature (Nilsen and Orcutt, 1996).

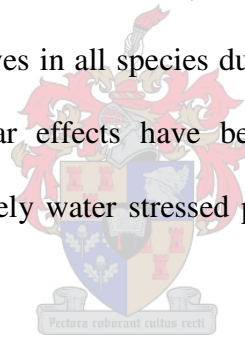
Compared to the two eucalypts, the deciduous species had lower WUE_{WL} under both well-watered and water deficit conditions. This is attributed to their high daily water loss (Table 2.2). However, on the annual basis the WUE_{WL} of the deciduous species may exceed that of the eucalypts because the deciduous species shade their leaves to avoid

water loss during the dry season, while the eucalypts retain their leaves and thrive to grow under high temperature and water vapor deficit that may result in excessive transpiration. However, evergreen woody plants typically have more conservative water use than deciduous woody plants (Hall, 2001). *M. ferruginea* had lower water loss, higher leaf water content and WUE_{WL} than *C. africana* and *C. macrostachyus*, possibly due to its efficient leaf re-orientation to reduce midday solar irradiance and hence transpiration.

The poor relationship observed between WUE_{WL} and WUE_{GE} in all species and treatment levels was mainly because the mass of plant used to determine the former is affected by respiratory losses at night and uptake of nutrients that affect the molecular composition of the dry mass, in addition to CO_2 uptake. Taken for a short time during the day, WUE_{GE} does not detect the diurnal fluctuations unlike WUE_{WL} (Lindroth and Cienciala, 1996). In the current study, WUE_{GE} was measured only during the mornings before the plants experienced high temperature and WVPD at midday that may result in higher transpiration and hence lower water use efficiency. A poor relationship between WUE_{WL} and WUE_{GE} has also been reported by Martin and Thorstenson (1988) and commented on by Kramer and Boyer (1995). WUE_{WL} is considered as the most appropriate method because it shows how dry matter production is affected by water availability (Kramer and Boyer, 1995). However, WUE_{GX} could also provide a valuable insight into the metabolic processes that might control photosynthesis and transpiration under a given set of conditions, especially when measurement of WUE_{WL} is not suitable (Kramer and Boyer, 1995).

2.4.4 Growth

The higher biomass production of both the eucalypts in all the water deficit treatments and their maximum leaf expansion in the mild water deficit treatment compared to the deciduous species (Table 2.4) indicate that the eucalypts were more tolerant to water deficit than the deciduous species. The success of *E. camaldulensis* as an exotic species has been attributed to its high biomass production on poor and dry lands, tolerance to drought and rapid growth when water is available (Pohjonen, 1989; Florence, 1996). Similar to the former report for an irrigated and fertilized *E. globulus* plantation in Portugal (Fabião *et al.*, 1995), water deficit did not affect the biomass allocation to roots in *E. globulus*, *E. camaldulensis* and *M. ferruginea*. However, severe water deficit caused premature senescence and shedding of leaves in all species during the first two to three weeks of the induction of the stress. Similar effects have been reported for various tree species (Kozłowski *et al.*, 1991). Severely water stressed plants also had the smallest height and diameter increment (Table 2.4).



The effect of drought avoidance in the deciduous species, involving high photosynthetic rate and growth under favorable conditions, are offset by the cost of producing new leaves in each new growth period (Lambers *et al.*, 1998; Aerts and Chapin, 2000). The leaf area expansion and biomass production of the deciduous species were comparable or higher to those of the eucalypts under sufficient supply of water. Because deciduous species are more sensitive to moisture stress (Kozłowski *et al.*, 1991) they employ various mechanisms to ensure their water balance. It could be speculated that *C. macrostachyus* and *C. africana* tend to maintain their water balance through: 1) allocation of more biomass to roots to replenish the high water loss through their leaves, 2) maintain

low leaf area to reduce the transpiring surface area, 3) efficient stomatal closure during the midday that would reduce water loss (Chapter 3).

2.4.5 Biomass allocation

The SLA, SWR, LWR of all the study species (Fig. 2.6) were within the ranges reported for tropical tree species (Lambers and Poorter, 1992). The three deciduous species had higher SLA than the evergreen eucalypts (Fig. 2.7 and Table 2.6). Poorter and Remkes, 1990; Lambers and Poorter, 1992) reported that SLA of deciduous species is higher than that of evergreen species. Species with low SLA invest more structural compounds to the leaves and achieve longer leaf life-span compared to high SLA species (Reich *et al*, 1997; Poorter and de Jong, 1999) which invest less on leaf structural material and thus have rapid flush and faster turnover of leaves (Grime, 1994). Higher LAR of the eucalypts compared to the deciduous species could be due to the high leaf lifespan of the former. LAR and the assimilation rate per leaf area are the leading factors that determine plant growth (Lambers and Poorter, 1992). Although both the deciduous and evergreen species had comparable photosynthetic rates, the eucalypts did not show superior growth performance due to their high LAR possibly because their older leaves had low assimilation rate (not measured). Low assimilation rate is often associated with old leaves (Eamus and Prior, 2001). The LAR of the deciduous species was not significantly affected by moisture deficit possibly due to their rapid leaf area adjustment.

The RWR of *C. macrostachyus* was more than three times the upper limit reported for tropical trees (Lambers and Poorter, 1992). Furthermore, increased water supply enhanced biomass investment to root in *C. macrostachyus* (Fig. 6b). Thus, *C.*

macrostachyus could be a species with inherently extensive root systems. Although the high root mass and low leaf area of *C. macrostachyus* and also *C. africana* may indicate their adaptation to resource poor environments, their high biomass production and fairly high photosynthetic rate under sufficient water availability would indicate that they have wide adaptations. Furthermore, the wide distribution of *C. macrostachyus* in all kinds of habitats (500 – 3400 m above sea level) in Ethiopia (Gilbert, 1995) could be due to its extensive root system.

Under field conditions such factors as age of the plant, symbiotic associations with microorganisms, competition with other species, nutrient availability, soil structure and the absence of restriction to root growth could also play a substantial role in determining the degree to which these species may succeed in a water stressed environments. Although these biotic and abiotic interactions may have considerable effects on the growth and biomass allocation of trees under natural conditions, plants with extensive root systems are favored to survive in resource poor environments, because they are more likely to tolerate occasional severe droughts and encounter the nutrients that are distributed irregularly in many soils. Shallow rooted trees with extensive lateral root systems are, however, more competitive and may not be good candidates for instance in agroforestry systems. Based on this glasshouse experiment and from the observations (Chapter 6) that *C. macrostachyus* produces extensive root system under natural conditions, it may be a potential candidate for planting in areas where land stabilization is a priority.

2.5 Conclusion

The current study confirmed that the eucalypts are more tolerant to long-term water stress because they produced higher biomass under water deficit condition. The deciduous species had higher water loss and lower water use efficiencies at the whole plant level compared to *E. camaldulensis* and *E. globulus*. Under well-watered conditions, all the tree species examined had comparable photosynthetic rate, stomatal conductance, water use efficiency and biomass production. However, larger proportions of the biomass produced in *C. macrostachyus* and *C. africana* were invested to roots.

Among the deciduous species, *M. ferruginea* showed high tolerance to water stress as evidenced by its high tissue water potential, RWC and photosynthetic rate under severe water deficit. Provided that its limited root growth and other site conditions are not limiting, the current study shows that *M. ferruginea* could be a potential candidate for planting in drier areas.

Apart from supporting their long survival in water stressed conditions, the extensive root system and smaller leaf area of *C. macrostachyus* and *C. africana* may not be desirable qualities for production purposes in moisture stressed areas. Owing to its extensive root distribution, however, *C. macrostachyus* could be used for land reclamation in areas where stabilization and protection of the soil from erosion is a priority.

3. RESPONSE OF SEEDLINGS OF TWO *EUCALYPTUS* AND THREE DECIDUOUS TREE SPECIES TO DROUGHT STRESS

Abstract

The responses of *C. africana*, *C. macrostachyus*, *M. ferruginea*, *E. camaldulensis* and *E. globulus* seedlings to drought stress were studied in a glasshouse for a period of 12 days. Drought stress was induced by withholding water. The study found that *E. globulus* and *E. camaldulensis* were more vulnerable to drought stress compared to the three deciduous species examined. Drought stress resulted in dehydration and dieback of both *E. camaldulensis* and *E. globulus* seedlings within seven days. In the deciduous tree species studied, drought stress resulted in leaf abscission and significant ($P < 0.05$) leaf area reduction. Only the youngest leaves were retained by the deciduous species throughout the drought stress period. Midday depression in stomatal conductance and photosynthetic rate was highest for *C. africana* followed by *C. macrostachyus*. Of the 5 tree species studied, *M. ferruginea* had the highest water potential and relative water content, as well as the lowest stomatal conductance throughout the water-stress period. In the well-watered group, both *E. globulus* and *E. camaldulensis* had higher stomatal conductance, photosynthetic rate and increased water loss compared to the three deciduous species. Three mechanisms of coping with short term drought stress were identified: 1) stomatal control in all species, but more efficient in *C. africana* and *C. macrostachyus*; 2) reduction of leaf area in the deciduous species; and, 3) change in leaf orientation in *M. ferruginea*.

3.1 Introduction

Plants have different mechanisms for withstanding water stress, including various physiological and morphological changes (Jones, 1993; McKersie and Leshem, 1994; Nilsen and Orcutt, 1996; Lambers *et al.*, 1998). Several studies (e.g. Pook *et al.*, 1966; Pereira *et al.*, 1986,1987; Pereira de Almeida and Riekerk, 1990; Tesfaye, 1994; White *et al.*, 1996; James and Bell 2000; White *et al.*, 2000; Burgess *et al.*, 2001) have been conducted on the effect of drought and related subjects on *E. camaldulensis* and *E. globulus* under various controlled and natural environments.

Although mature *E. globulus* and *E. camaldulensis* have various mechanisms for drought resistance (Florence, 1996; White *et al.*, 1996; James and Bell 2000), their seedlings are prone to drought, thus resulting in considerable dieback (Pohjonen, 1989; Tesfaye, 1994). Although the cultivation of *E. globulus* and *E. camaldulensis* under Ethiopian conditions has been easy, the low initial survival of out planted seedlings remains a problem (Pohjonen, 1989, Tesfaye, 1994). A practice frequented by farmers and/or plantation agents to compensate for seedling losses from early dieback is to increase the planting density during the first year, followed by refilling in subsequent years (Pohjonen, 1989). Concerning indigenous trees of Ethiopia, no published data have so far been made available on their performance under field conditions.

Plant performance in the field is often controlled more by the interaction of multiple factors (e.g. soil, climate, disease, and herbivorous organisms) rather than by a single overriding factor (Nilsen and Orcutt, 1996). Although complex interactions are minimal under a controlled environment, investigations on the effect of drought stress could provide information on how different plant species respond to severe water stress in drought prone

areas. Several studies (e.g. Kramer and Boyer, 1995; Lo Gullo *et al.*, 1998; Ameglio *et al.*, 1999) have indicated that the effect of drought stress on the growth performance of a wide variety of plants can be investigated by withholding water for several days.

Water potential, relative water content (RWC) and gas exchange have commonly been used to assess the water status and physiological responses of plants under water stress (Pereira *et al.*, 1987; White *et al.*, 2000). In the majority of plants, water stress results in reduced predawn leaf water potential, which further induces stomatal closure resulting in reduced gas exchange (Pereira *et al.*, 1986, 1987; Kramer and Boyer, 1995; Nilsen and Orcutt, 1996; Lambers *et al.*, 1998). Stomatal closure is therefore one of the initial responses of plants to the onset of water stress (McKersie and Leshem, 1994; Lambers *et al.*, 1998). In addition to water potential, relative water content (RWC) has been used to estimate plant water status in terms of cellular hydration under the possible effect of leaf water potential and osmotic adjustments (Kramer and Boyer, 1995).

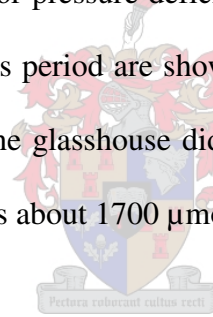
The study on the effects of prolonged water deficit on gas exchange, growth and biomass allocation (Chapter 2) showed that although severe water deficit suppressed most of the physiological and growth processes in all the studied species, *E. camaldulensis* and *E. globulus* showed better performance in terms of biomass under water deficit conditions compared to the deciduous species. However, whether the eucalypts are more tolerant to drought or not should be studied. Study of the response of the seedlings to drought is vital because many places in Ethiopia are prone to drought and seedlings are so vulnerable to drought stress. The objectives of the current study were: 1) to investigate the mechanisms by which two *Eucalyptus* spp. and three deciduous tree species respond to drought stress;

and, 2) to assess the degree to which the indigenous species tolerate drought stress compared to the eucalypts.

3.2 Materials and Methods

3.2.1 Plant establishment and glasshouse conditions

The glasshouse experiment was carried out on seedlings of *C. africana*, *C. macrostachyus*, *M. ferruginea*, *E. camaldulensis* and *E. globulus*, at the tree nursery at the University of Stellenbosch, South Africa. Seedlings were established and grown for one year under glasshouse conditions indicated in Chapter (Section 2.2.1). The average morning and midday temperatures, water vapor pressure deficit, and photosynthetic photon flux density (PPFD) during the drought stress period are shown in Fig. 3.1. Owing to light attenuation by the glass, the PPFD inside the glasshouse did not exceed $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ while the PPFD outside the glasshouse was about $1700 \mu\text{mol m}^{-2} \text{s}^{-1}$, a value for a typical sunny day.



3.2.2 Experimental design

Ten plants having similar size were selected from each of the tree species studied, and were randomly assigned to either the control or drought stress treatment induced by withholding water. The control plants were supplied with the same amount of water lost over the previous 24 h period. The morphological parameters of the plants used for the drought stress regime are shown in Table 3.1. All the plants were watered to field capacity, and pots were placed in plastic bags that were sealed at the base of the seedlings to avoid direct evaporation from the soil.

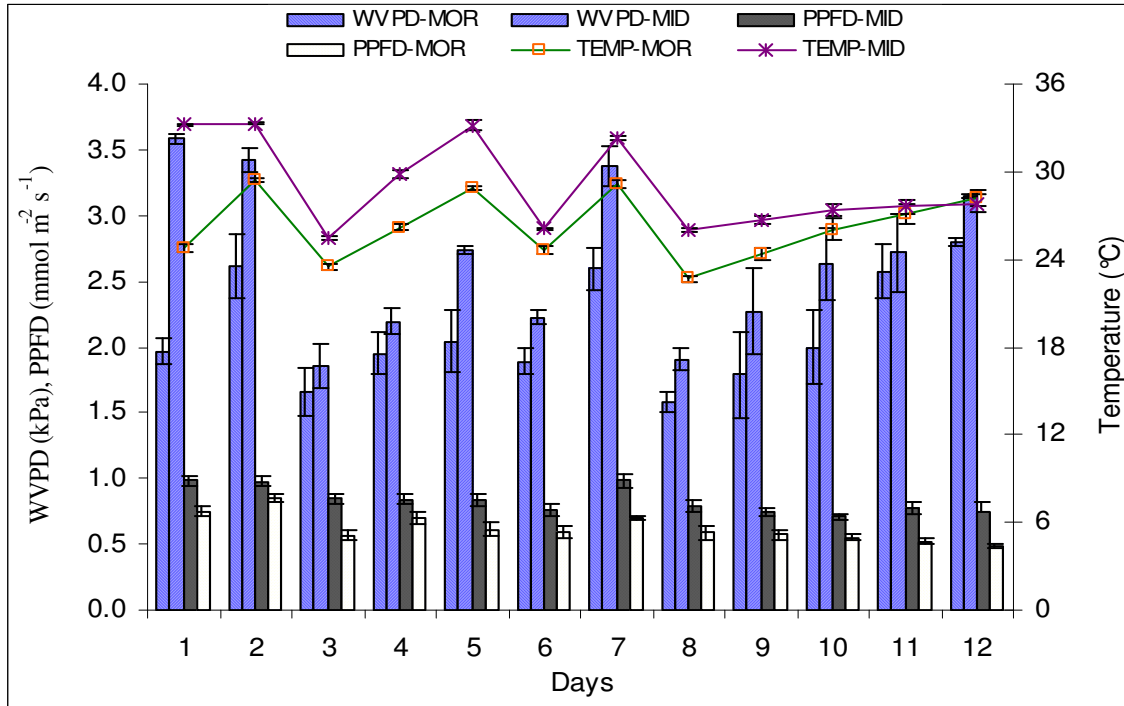


Figure 3.1 Morning and midday photosynthetic photon flux density, temperature and water vapor pressure difference inside the glasshouse during the 12-day water stress period. WVPD-MOR = Water pressure vapor difference in the morning, WVPD-MID = Water vapor pressure difference at midday, PPF-MOR = Photosynthetic photon flux density in the morning, PPF-MID = Photosynthetic photon flux density at midday, TEMP-MOR = Temperature in the morning, TEMP-MID = Temperature at midday. Bars indicate \pm SE, n = 5.

To allow for air exchange between the atmosphere and the root system, pots were randomly pierced with a punch of 2 mm internal diameter. Pots without plants were included to correct for water loss through other means. All the pots were placed on glasshouse benches in a completely randomized design. Every evening, each pot was weighed on an electronic balance to determine the daily water loss. Measurements continued until the plants died or lost most of their leaves. The plant water loss (WL) was calculated in relation to plant biomass and leaf area (Table 3.1), assuming that increment in

biomass and leaf area during the 12-day consecutive measurements was negligible compared to the water loss.

Table 3.1 Mean (\pm SD, n=5) diameter, height, leaf area, total biomass and root/shoot ratio of plants used for the drought experiment.

Species	Root collar Diameter (cm)	Leaf area (m ²)	Plant height (cm)	Plant biomass (g)	Root/shoot ratio
<i>C. africana</i>	1.14 \pm 0.14	0.07 \pm 0.02	28.20 \pm 2.51	12.14 \pm 1.74	1.64 \pm 0.35
<i>C. macrostachyus</i>	0.79 \pm 0.12	0.05 \pm 0.01	29.40 \pm 3.13	11.08 \pm 1.13	2.12 \pm 0.68
<i>E. camaldulensis</i>	0.96 \pm 0.10	0.19 \pm 0.05	87.60 \pm 13.37	25.34 \pm 6.12	0.76 \pm 0.15
<i>E. globulus</i>	0.79 \pm 0.41	0.26 \pm 0.10	98.00 \pm 13.62	24.28 \pm 10.84	0.57 \pm 0.12
<i>M. ferruginea</i>	1.05 \pm 0.14	0.13 \pm 0.05	85.20 \pm 4.66	20.07 \pm 1.54	0.31 \pm 0.04



3.2.3 Water potential and relative water content measurements

Predawn and midday leaf water potentials and RWC were measured daily during the 12-days drought period according to methods described in Chapter 2 (Section 2.2.3) on well-expanded leaves.

3.2.4 Gas exchange measurements

Photosynthetic rate and stomatal conductance were measured twice daily, between 8:00 and 10:00 AM and between 12:30 and 14:00 PM, according to descriptions given in

Chapter 2 (Section 2.2.4). Water vapor pressure deficit (WVPD) of the air inside the glasshouse was derived as described in Chapter 2 (Section 2.2.4).

3.2.5 Statistical procedures

Data were subjected to ANOVA to determine differences among species for each of the physiological variables, at each day and time of day. Tukey's Honestly Significant Difference test was employed for multiple comparisons when significant differences were found between treatments. The effect of drought stress on each species was determined by splitting the data by species and days, and the equality of means of the physiological variables was tested for drought stress and control treatments with a two sample t-test. All statistical analyses were carried out using SPSS 11.0 for Windows.

3.3 Results

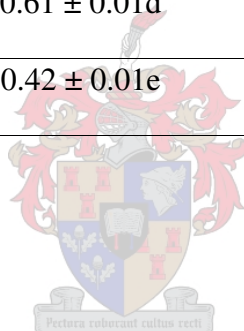
3.3.1 Whole plant water loss



The mean daily water loss (WL) of the control seedlings are presented in terms of the plant biomass and the transpiring surface areas (Table 3.2). In both cases significant differences ($P < 0.001$) were observed between species. Eucalypts with higher leaf area (Table 3.1) had significantly ($P < 0.001$) higher whole plant water loss than the deciduous species. *M. ferruginea* had significantly the lowest ($P < 0.001$) water loss in terms of both leaf area and plant biomass.

Table 3.2 Mean (\pm SE) water loss of control seedlings of five tree species during the 12-day water stress period (n=60). Mean values in each column that are followed by different letters are significantly different ($P < 0.01$) according to Tukey's test.

Species	Water loss in terms of leaf area (kg H ₂ O m ⁻² s ⁻¹)	Water loss in terms of total dry matter (g H ₂ O (g dry matter) ⁻¹ d ⁻¹)
<i>C. africana</i>	0.84 \pm 0.02b	4.70 \pm 0.10c
<i>C. macrostachyus</i>	0.91 \pm 0.02a	4.02 \pm 0.08d
<i>E. camaldulensis</i>	0.73 \pm 0.01c	5.32 \pm 0.11b
<i>E. globulus</i>	0.61 \pm 0.01d	6.30 \pm 0.09a
<i>M. ferruginea</i>	0.42 \pm 0.01e	2.15 \pm 0.06e



3.3.2 Leaf water potential

The declining predawn and midday leaf water potentials of drought stressed and control plants are shown in Fig 3.2a-d. The eucalypts had rapidly declining predawn and midday leaf water potentials, with significantly ($P < 0.05$) lower values compared to the three deciduous tree species studied (Fig. 3.2a,b).

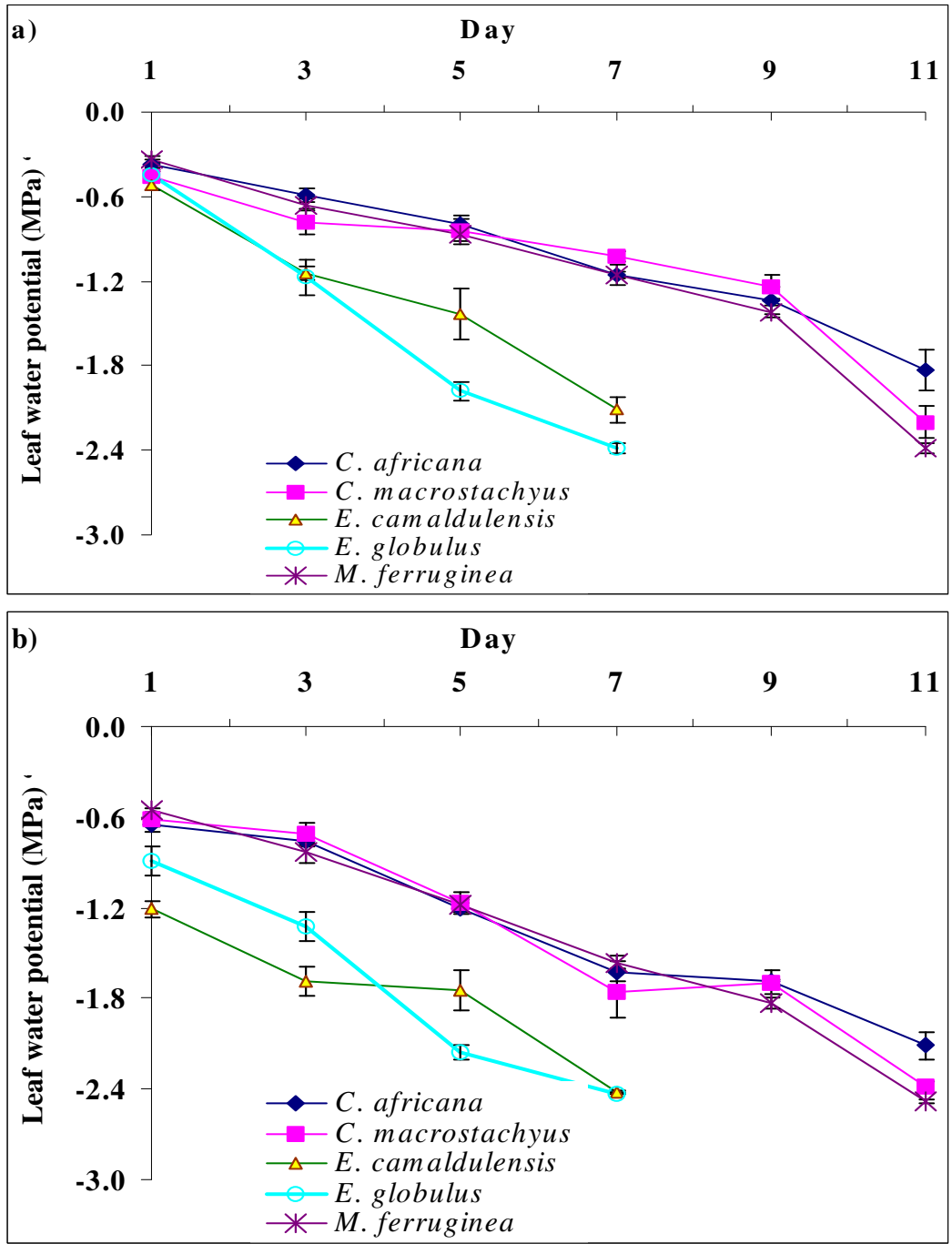


Figure 3.2 (a and b) Mean leaf water potential of stressed seedlings of five tree species during the 12-day drought stress period: a) predawn and b) midday measurements. Bars indicate \pm SE, n = 5.

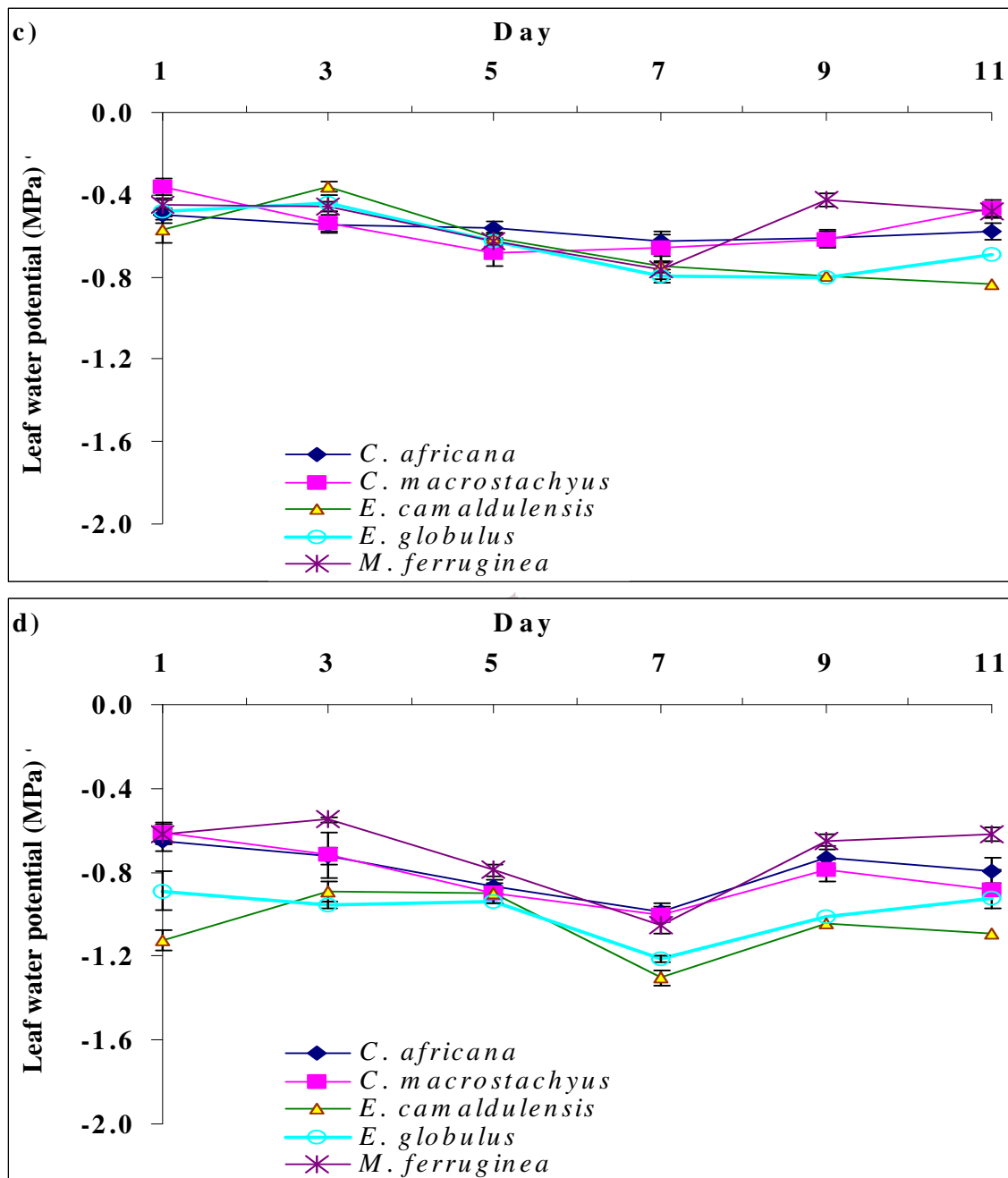


Figure 3.2 (c and d) Mean leaf water potential of control seedlings of five tree species during the 12-day drought stress period: c) predawn; d) midday measurements. Bars indicate \pm SE, n = 5.

Pooled (12 days) mean predawn and midday leaf water potentials of the control plants indicated that *M. ferruginea* had higher predawn (-0.54 MPa) and midday (-0.71 MPa) values which were significantly ($P < 0.05$) higher than the predawn (-0.65 MPa) and midday (-1.06 MPa) values for *E. camaldulensis*, and predawn (-0.64 MPa) and midday (-0.99 MPa) values for *E. globulus*. *C. africana* and *C. macrostachyus* had predawn leaf water potentials of -0.57 and -0.55, and midday leaf water potentials of -0.79 and -0.82 MPa, respectively.

In the two eucalypts, the difference between predawn and midday water potential in the control groups was larger compared to the three deciduous species studied. These differences were 0.43, 0.35, 0.28, 0.22 and 0.19 MPa for *E. globulus*, *E. camaldulensis*, *C. macrostachyus*, *C. africana* and *M. ferruginea*, respectively.

3.3.3 Relative water content

A significant ($P < 0.01$) difference in relative water content (RWC) was observed between the drought stressed and the control plants, beginning from day two of the experiments (Fig. 3.3a-d). The reduction in both the midday and predawn RWC was sharp in *E. globulus* and *E. camaldulensis* compared to the deciduous species (Fig. 3.3a,b). During the first six days of the experiment, the predawn RWC decreased from 91.9% to 20% in *E. globulus* and from 89.9% to 30.6% in *E. camaldulensis* (Fig. 3.3a). The decrease in midday RWC during the same period in these species was from 80.1% to 13.52% and from 78.2% to 20%, respectively (Fig. 3.3b). In contrast, the predawn RWC on the 12th day ranged from 49-56% and the midday RWC on the same day ranged from 36-42% for the three deciduous tree species studied.

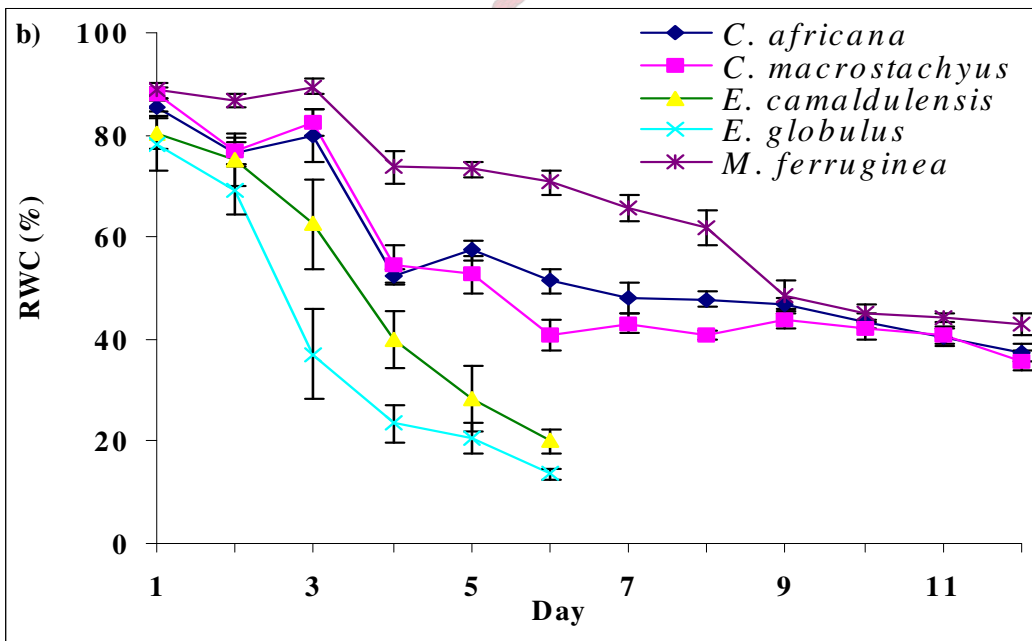
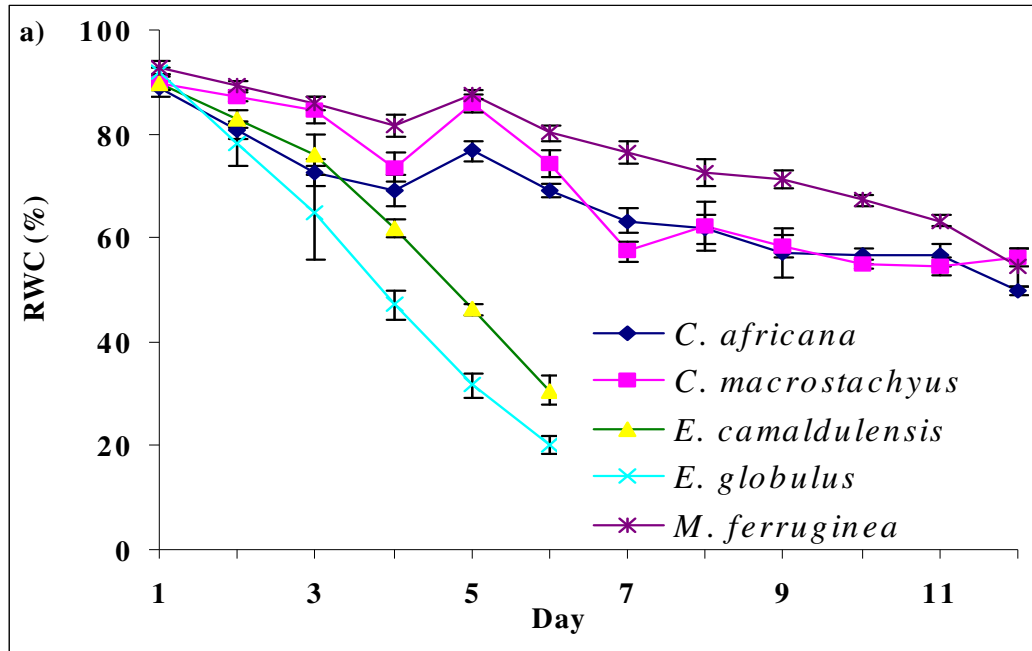


Figure 3.3 (a and b) Mean relative water content of stressed seedlings of five tree species during 12-day drought stress period: a) predawn b) midday measurements. Bars indicate \pm SE, n = 5.

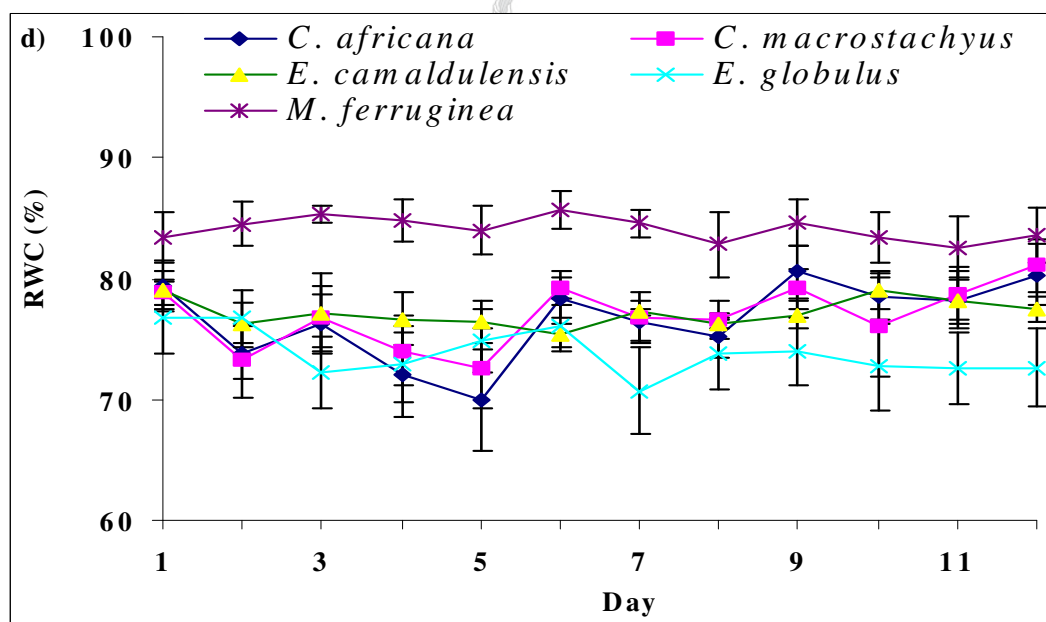
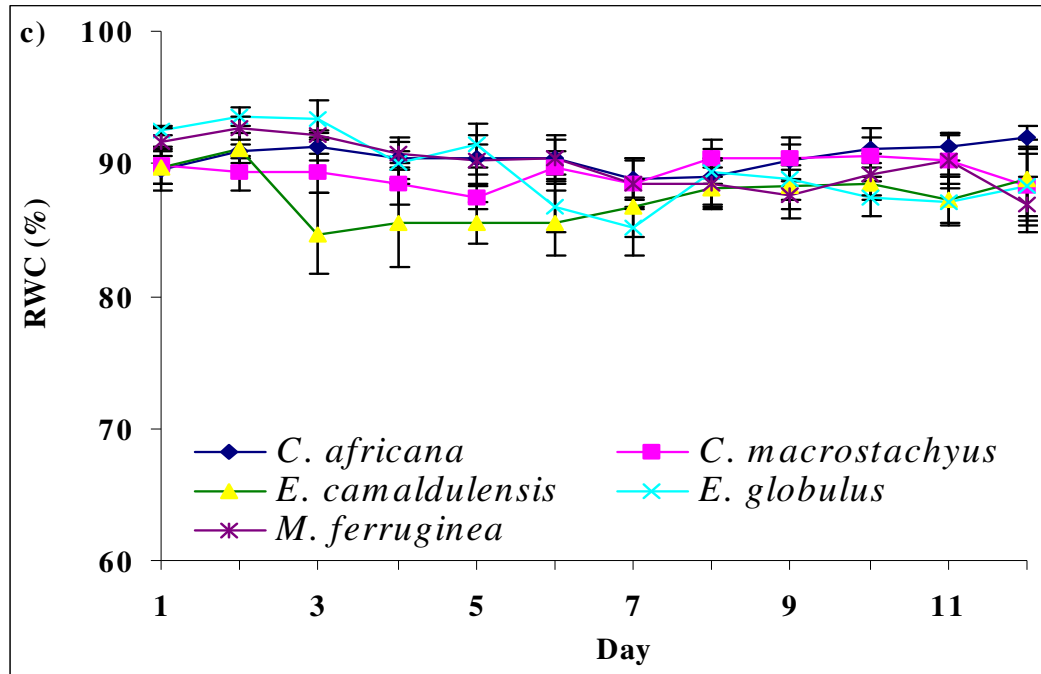


Figure 3.3 (c and d) Mean relative water content of control seedlings of five tree species during 12-day drought stress period: c) predawn and d) midday measurements. Bars indicate \pm SE, $n = 5$.

3.3.4 Photosynthetic rate

The photosynthetic rates of the species studied during the 12-day water stress period are shown in Fig. 3.4a-d. In *E. camaldulensis* and *E. globulus* the photosynthetic rates of the control and drought stressed plants differed significantly ($P < 0.001$) starting from day three, with the photosynthetic rate of drought stressed plants decreasing steadily. Because the drought stressed plants of the two eucalypts wilted on day seven, no further measurements were made thereafter (Fig. 3.4a,b). In *C. africana* and *C. macrostachyus*, the drought stressed plants showed a steady decline in photosynthetic rate from day seven onwards (Fig. 3.4a,b). On the other hand, in the stressed plants of *M. ferruginea* declining photosynthetic rate was observed only from day 9 onwards (Fig. 3.4a,b).

The photosynthetic rates of the control *E. globulus* and *E. camaldulensis* plants were significantly ($P < 0.05$, pooled $n = 60$ (30 for the eucalypts)) higher than those of the deciduous tree species. The midday photosynthetic rates of the drought stressed plants (Fig. 3.4b) were 50, 44, 28, 38 and 25% lower than the corresponding morning measurements (Fig. 4c) for *C. africana*, *C. macrostachyus*, *E. camaldulensis*, *E. globulus* and *M. ferruginea*, respectively (pooled $n = 60$ (30 for the eucalypts)). Similarly, the midday photosynthetic rates of the control plants (Fig. 3.4d) were 53, 50, 32, 34 and 21% less than the corresponding morning measurements (Fig. 3.4c) for *C. africana*, *C. macrostachyus*, *E. camaldulensis*, *E. globulus* and *M. ferruginea*, respectively (pooled $n = 60$ (30 for the eucalypts)).

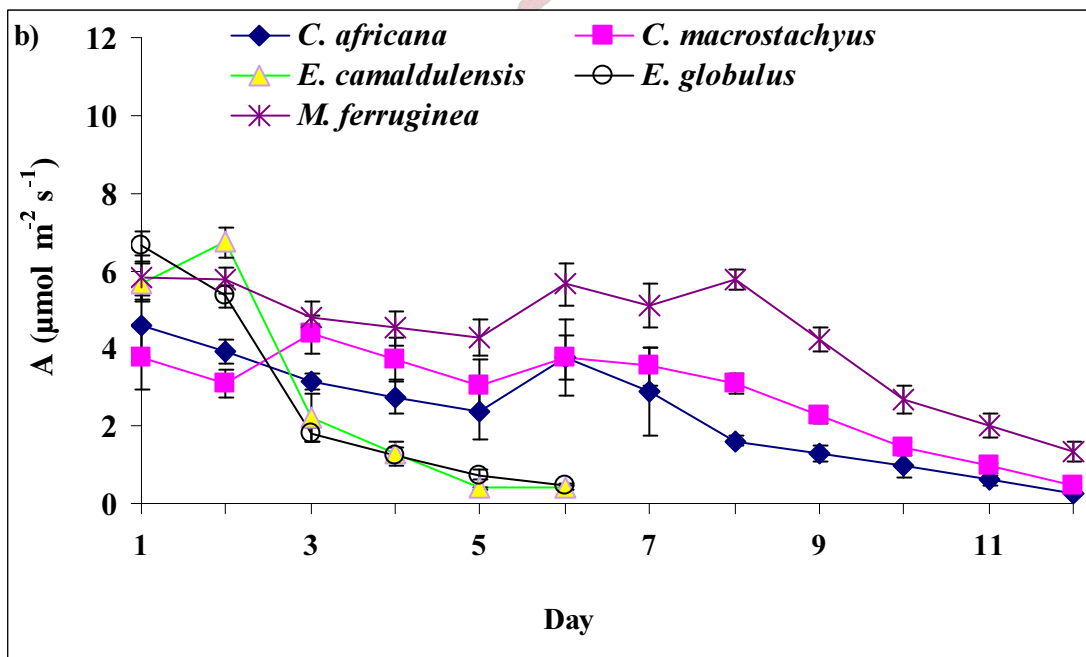
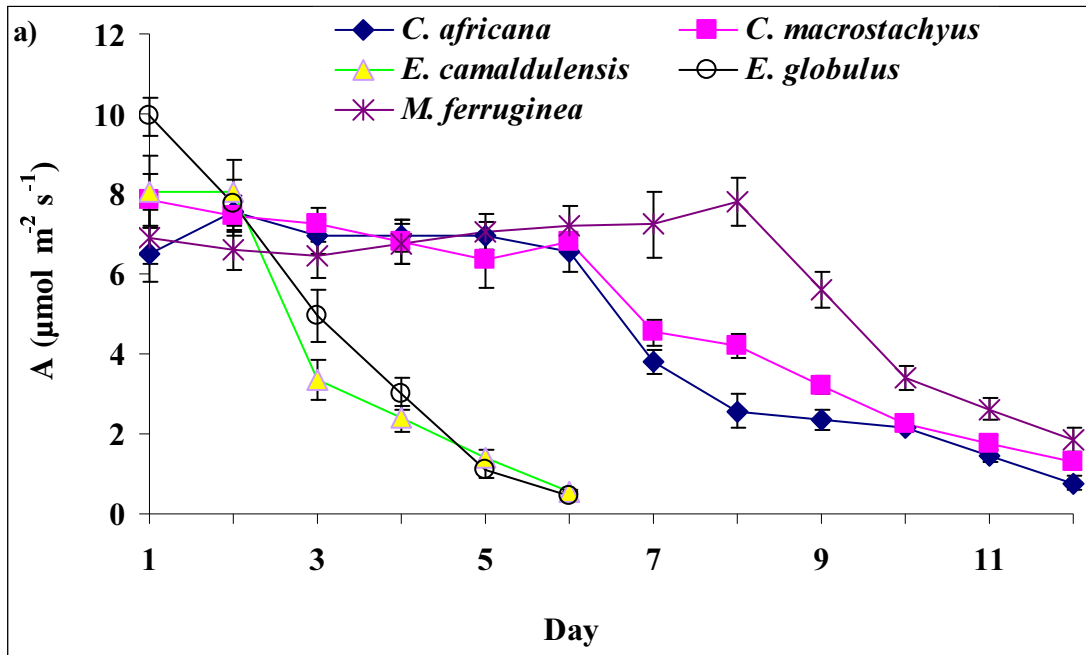


Figure 3.4 (a and b) Mean photosynthetic rate (A) of stressed seedlings of five tree species during 12-day drought stress period: a) morning b) midday measurements. Bars indicate \pm SE, n = 5.

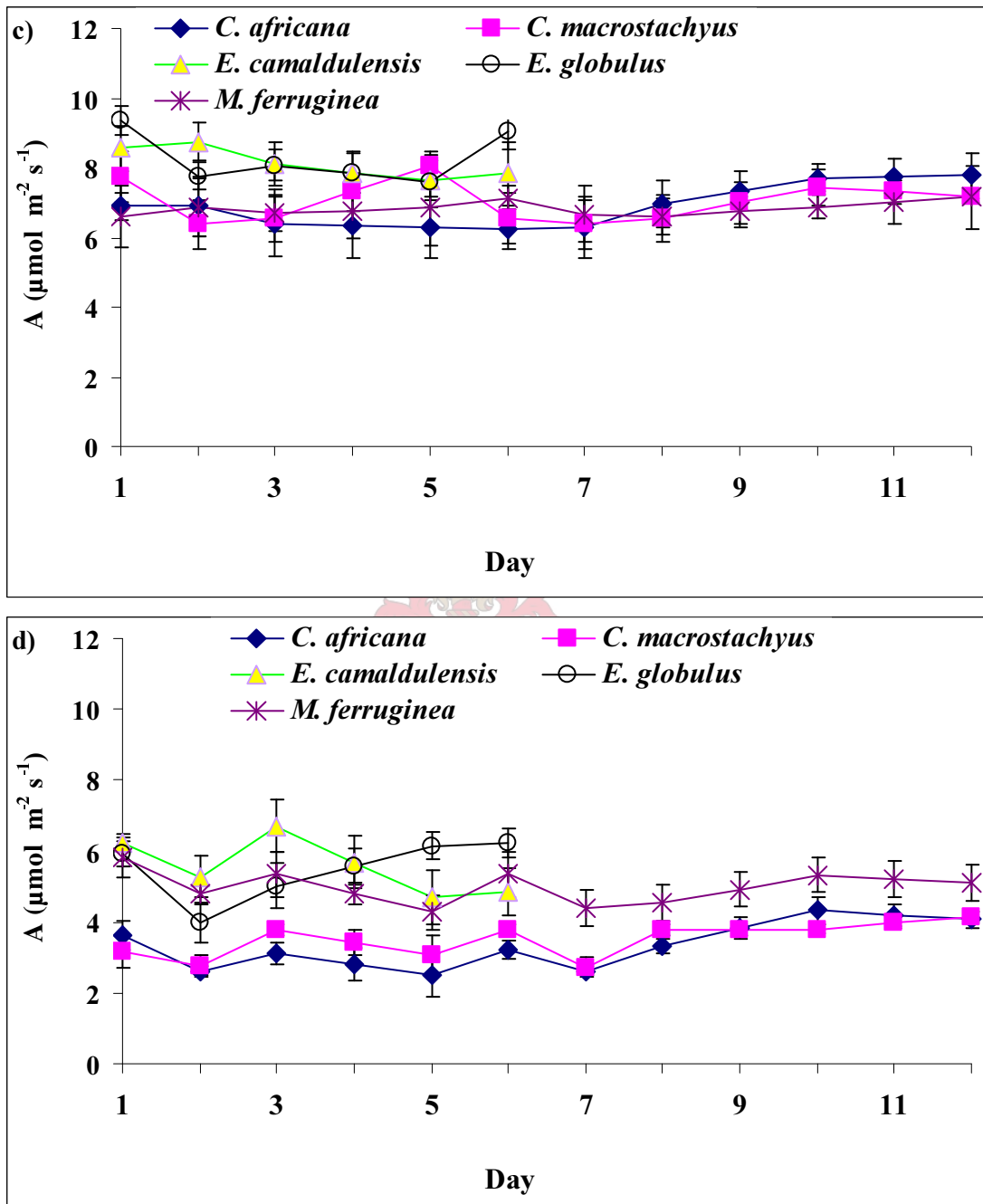
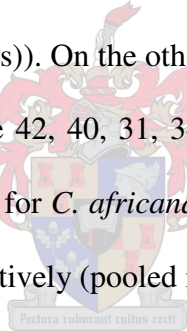


Figure 3.4 (c and d) Mean photosynthetic rate (A) of control seedlings of five tree species during 12-day drought stress period: c) morning and d) midday measurements. Bars indicate \pm SE, n = 5.

3.3.5 Stomatal conductance

There were considerable fluctuations in stomatal conductances within the same treatment and throughout the water stress period in all the species studied (Fig. 3.5a-d). In *E. camaldulensis* and *E. globulus*, midday stomatal conductances of the drought stressed plants declined sharply from over 80 mmol m⁻² s⁻¹ on day 2, to less than 30 mmol m⁻² s⁻¹ on day 3 (Fig. 3.5b).

Midday stomatal conductances of the drought stressed plants (Fig. 3.5b) were 74, 43, 44, 45 and 25% lower than the corresponding morning measurements (Fig. 3.5a) for *C. africana*, *C. macrostachyus*, *E. camaldulensis*, *E. globulus* and *M. ferruginea*, respectively (pooled n = 60 (30 for the eucalypts)). On the other hand, midday stomatal conductances of the control plants (Fig. 3.5d) were 42, 40, 31, 34 and 24% lower than the corresponding morning measurements (Fig. 3.5c) for *C. africana*, *C. macrostachyus*, *E. camaldulensis*, *E. globulus* and *M. ferruginea*, respectively (pooled n = 60 (30 for the eucalypts)).



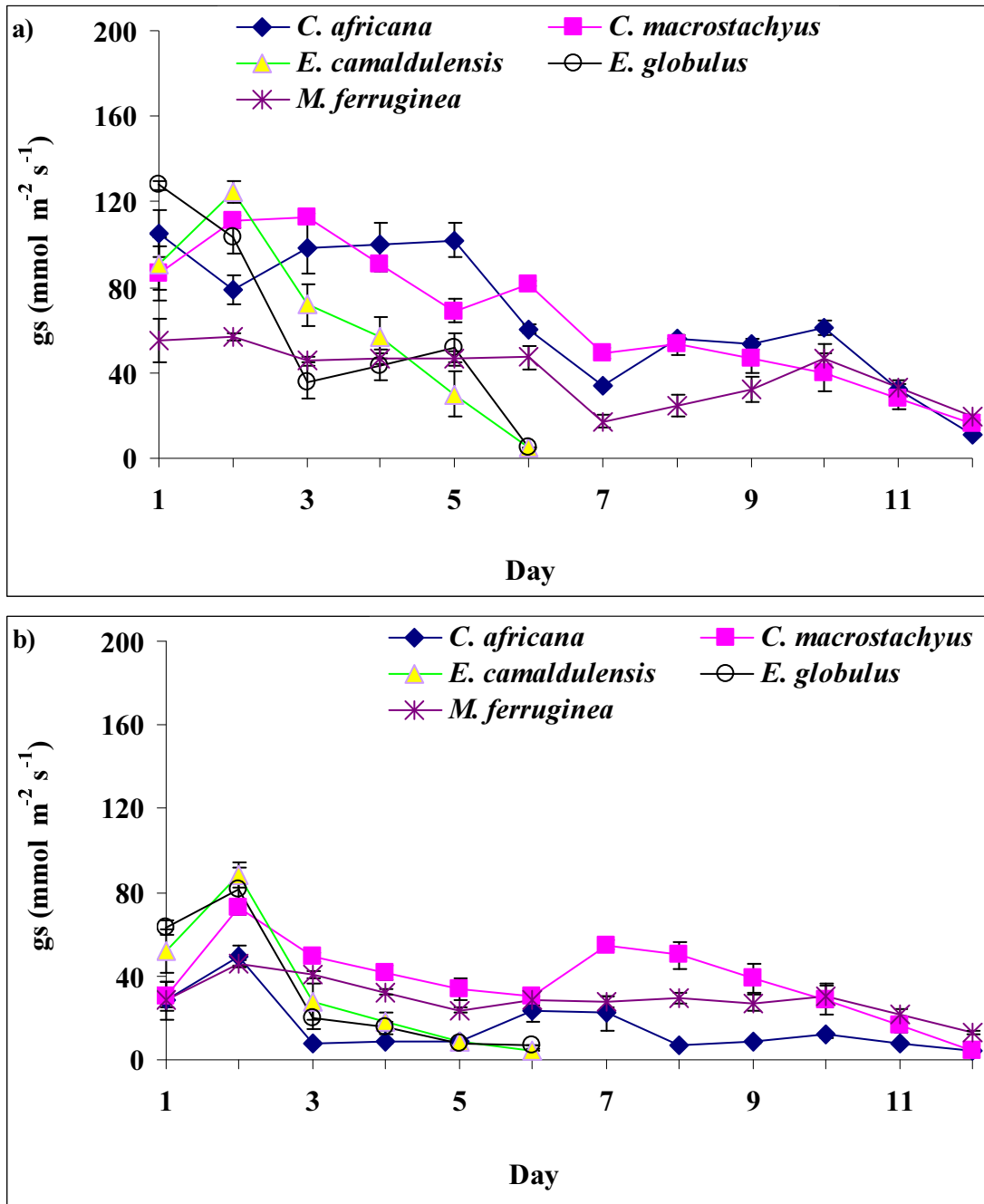


Figure 3.5 (a and b) Mean stomatal conductance (gs) of stressed seedlings of five tree species during 12-day drought stress period: a) morning and b) midday measurements. Bars indicate \pm SE, n = 5.

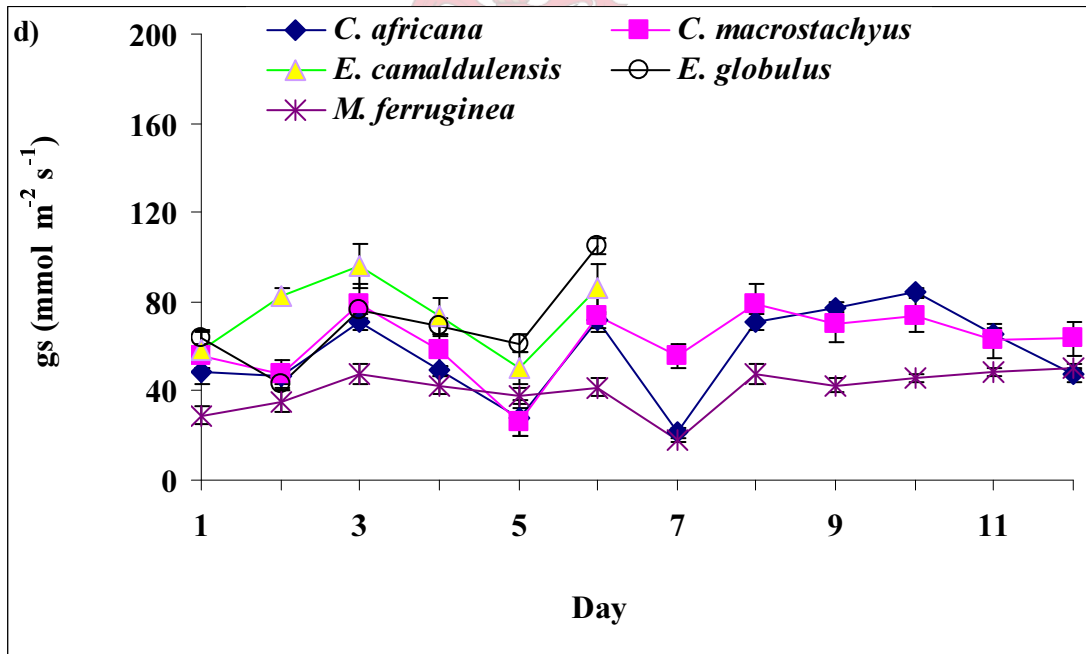
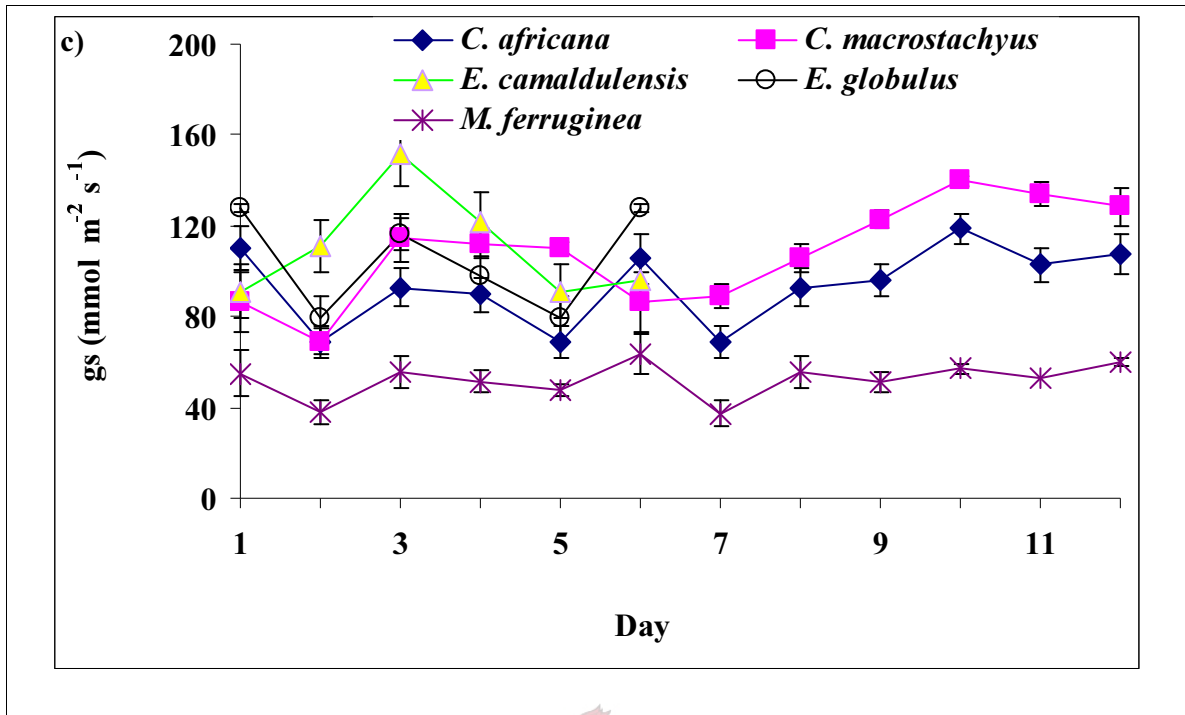


Figure 3.5 (c and d) Mean stomatal conductance (gs) of control seedlings of five tree species during 12-day drought stress period: c) morning and d) midday measurements. Bars indicate \pm SE, n = 5.

3.4 Discussion

Of the five tree species studied, *C. africana* and *C. macrostachyus* showed typical midday depressions under well-watered conditions both in photosynthetic rates (50-52%) and stomatal conductance (40-42%). However, under drought stress conditions, stomatal closure in *C. africana* was about twice, and photosynthetic rate about 10% lower than those in *C. macrostachyus*. Legesse (1992) compared stomatal responses of five indigenous tree species of Ethiopia to increasing water stress and detected the presence of pronounced midday stomatal closure in *C. africana*.

The high photosynthetic rate and high tissue water status (water potential and RWC) of *M. ferruginea* could mainly be due to its ability to re-orient its leaves and leaflets during midday, thus avoiding direct solar irradiance. Leaf movement (heliotropism) has been reported to occur in plants of the family Fabaceae (e.g. Satter and Galston, 1981; Fu and Ehleringer, 1989; McKersie and Leshem, 1994; Lambers *et al.*, 1998). It is a mechanism for avoiding dehydration, and excess light stress and is believed to be triggered by high temperature and blue light (Satter and Galston, 1981; Fu and Ehleringer, 1989).

E. globulus has been characterized to have intermediate stomatal control of transpiration during drought stress compared to other eucalypts and deciduous species (Pook *et al.*, 1966; Pereira *et al.*, 1986; Pereira de Almeida and Riekerk, 1990). *E. camaldulensis* is reported to exhibit strong stomatal resistance under drought conditions compared to *E. globulus* (White *et al.*, 2000). However, this study showed comparable stomatal responses to drought stress conditions (Fig. 3.5a,b). Additionally, this study found that *E. globulus* and *E. camaldulensis* suffered significant water loss (per plant), were more vulnerable to drought stress, and displayed rapid decline in leaf water potential, RWC,

photosynthetic rate and stomatal conductance compared to the three deciduous tree species examined. The high whole plant water losses of the eucalypts compared to *C. macrostachyus* and *C. africana* were due to their higher leaf areas (Table 3.1). This may be why several studies show that eucalypts are water demanding (e.g., Pereira, *et al.*, 1986; Florence, 1996). However, the water losses of *C. macrostachyus* and *C. africana* significantly exceeded that of the eucalypts when viewed in terms of the transpiring surface area. Former reports also indicate that deciduous woody plants have higher transpiration rate than evergreen woody plants (Kozlowski *et al.*, 1991; Hall, 2001).

Rapid stomatal closure in *C. africana* and *C. macrostachyus*, and leaf movement in *M. ferruginea*, helped these tree species survive drought stress, at least during the first 7 days of the water stress period. However, as the soil dried, all three species reduced their total leaf area by shedding the older leaves but retaining younger leaves. As noted by Chaves (1991), tolerance to dehydration by young leaves has the advantage of fast recovery after re-hydration. In contrast, tissue re-hydration at night could not be achieved by the two eucalypts studied due to the depletion of soil moisture, thus resulting in the early deaths of the plants.

Although the containerized eucalypts failed to maintain their water balance beyond the two days of drought stress conditions, their water requirements in the field is fulfilled through water absorption from deep soils and ground water (White *et al.*, 2000; Burgess *et al.*, 2001). Consequently, eucalypts under field conditions retain their leaves even during dry seasons and keep on growing while the deciduous species shed their leaves, thus maintaining reduced growth. Although the traditional practice of Ethiopian farmers involving the increase of eucalypts planting density is frequented to compensate for early

seedling dieback (Pohjonen, 1989), the practice could result in increased competition for water, nutrients and light. As the roots are not well established to acquire water from deeper soil layers, competition for water may even exacerbate the dieback of seedlings, especially during the dry season. For the eucalypt this may pose severe damage because eucalypts have higher LAR and do not shed their leaves to regulate plant water loss under water deficit compared to the deciduous species.

C. africana and *C. macrostachyus* minimized water loss by reducing total leaf area. However, reduction in leaf area diminished total photosynthetic output that in turn resulted in decreased growth rate. Consequently, although short to medium-term survival of these two species in water stressed areas is a possibility, diminished plant productivity remains intractable. Provided that essential nutrients and other conditions are not limiting for its growth, *M. ferruginea* could be a good candidate for drier areas as it has the advantage of higher photosynthetic rate and less water loss under severe moisture stress conditions.

Based on their responses to water stress the five tree species studied could be categorized into three groups: 1) *M. ferruginea* showed changes in leaf orientation to reduce the surface area of leaves exposed to solar irradiance, and maintained high tissue water content and photosynthetic rate; b) *C. africana* and *C. macrostachyus* minimized stomatal conductance, photosynthetic rate and water loss; and, c) *E. camaldulensis* and *E. globulus* maintained open stomata and high photosynthetic rate at low tissue water potential. Additionally, reduction in leaf area was observed in the deciduous species 7 days after the onset of water stress. Pereira and Chaves (1993) viewed stomatal closure as a short term, and leaf area reduction as a long-term acclimation mechanism in response to soil water deficits in the Mediterranean climate. It has been observed that, under mild and

moderate water stress conditions, plants develop adaptive resistance to moisture stress for maintaining vital physiological processes (Chapter 2). However, under drought stress conditions plants may not have enough time for making physiological adjustments that would help them avoid tissue damage (e.g. Pereira and Chaves, 1993; Kramer and Boyer, 1995; Nilsen and Orcutt, 1996). Confinement of the roots to the small pot size in the current study might restrict the hydraulic conductivity of the seedlings. In the field, plants of same species and age may not face such acute moisture shortage because the roots can spread through the soil and have more surface area for moisture absorption.

3.5 Conclusions

The impact of drought stress was quick and more damaging to eucalypts compared to the other indigenous tree species. Owing to its ability for leaf reorientation, *M. ferruginea* avoided direct solar irradiance, showed higher tissue water status and photosynthetic rate, and controlled water loss more efficiently compared to the other tree species. During midday, stomatal closure occurred and photosynthetic rates declined in both *C. africana* and *C. macrostachyus*. The three most important mechanisms of response to mild and drought stress were: a) stomatal closure in all species, with *C. africana* and *C. macrostachyus* closing their stomata more strongly than the other tree species studied; b) reduction in leaf areas and photosynthetic rates in the deciduous species; and, c) changes in leaf orientation in *M. ferruginea*. Further work on the performance of these tree species under field conditions is recommended.

4. EFFECTS OF SOIL NITROGEN AND PHOSPHORUS ON PLANT TISSUE NITROGEN, PHOSPHORUS AND N:P RATIO OF TWO *EUCALYPTUS* AND THREE DECIDUOUS TREE SPECIES

Abstract

The effects of soil nitrogen (N) and phosphorus (P) supply on foliar, stem and leaf N, P and N:P ratio of *C. africana*, *C. macrostachyus*, *M. ferruginea*, *E. camaldulensis* and *E. globulus* seedlings were studied under glasshouse condition. Eight-month-old seedlings were treated with combinations of four N levels viz. 0, 5, 25, and 50 mg N week⁻¹ corresponding to N1, N2, N3 and N4, and two P levels viz. 0 and 150 mg P (applied twice) corresponding to P1 and P2 over a period of six months. The deciduous species i.e., *C. macrostachyus*, *C. africana* and *M. ferruginea*, had significantly ($P < 0.05$) higher stem, root and leaf N and P concentrations than the evergreen eucalypts regardless of soil N and P. However, the combined effects of soil N and P stresses resulted in 40-60, 56-70 and 63-83% reductions in leaf, root, and stem N concentrations, respectively, in all the species studied. Both under P1 and P2, increased soil N significantly ($P < 0.001$) increased plant tissue N concentrations in all species. Among all the studied species *C. macrostachyus* and *C. africana* accumulated more N and P in all plant parts. Increased soil P resulted in increased tissue P concentration for all plant species and all parts of the plants. Increased soil N increased N:P ratio of all plant parts, while increased soil P decreased the N:P ratio of all plant parts for all species. Foliar N:P ratios of 10 to 18 were observed under sufficient N and P supplies depending on the species. Although foliar N:P ratio could not distinguish between N-limitation and N and P limitation, it was proven to serve as a good indicator of P-limitation in the studied species. The high accumulation of N and P by *C. macrostachyus* and *C. africana* indicates their high nutrient recycling abilities.

4.1 Introduction

Although plants tend to maintain a constant tissue N:P ratio of about 8-10 (Ingestad, 1979), they may not maintain their optimum N:P ratio due to the limited availability of either one or both of these nutrients. Soil nutrient composition strongly affects plant nutrient concentration by changing both allocation among organs and the composition of individual tissues (Marschner, 1995). Generally, variations in soil N or P availability result in nutritional imbalances in plant tissues (Koerselman and Meuleman, 1996).

When nutrients are in short supply, plants tend to show a compensatory response to maximize the inflow rate of the scarce nutrient. For instance, plants exhibit a high capacity to absorb phosphate when grown at a very low supply of phosphate and a high potential to absorb nitrate and ammonium ions under conditions when N is in short supply (Chapin, 1991). In addition to enhancing uptake, plants also develop mechanisms for reducing nitrogen losses including increased leaf longevity (Reich *et al.*, 1992) and nutrient resorption from senescing leaves (Aerts, 1990; Wendler *et al.*, 1995; Aerts, 1996). Furthermore, plants cope with limiting nutrients primarily by altering the production of leaves such that new leaves contain minimum of the limiting nutrient (Evans, 1996).

Evergreen plants in nutrient poor environments increase their survival and competitive abilities in the environment by having a high nutrient retention through maintaining low tissue nutrient concentration and low tissue turnover (Aerts, 1995; Aerts and Chapin, 2000). Thus, plants with a long leaf lifespan tend to aggravate the low availability of nutrients in their already nutrient poor environment (Aerts, 1995). The rate of nutrient accumulation in the plant is a measure of the physiological potential of the plant to absorb nutrients under that condition (Pearcy *et al.*, 1989; Lambers *et al.*, 1998).

Grime (1979) stated that rapidly growing plants have a high capacity for acquiring nutrients. Increased nutrient supply increases nutrient accumulation in all plants. Whereas fast growing species utilize the acquired nutrients for growth, slow growing plants have less capacity to achieve this, thus resulting in the accumulation of nutrients (Chapin *et al.*, 1990). Nutrient conserving tree species that do not have rapid turn over of nutrients are not desirable for agroforestry (Golley, 1986; Nair, 1993; Young, 1997). Instead, fast growing species with high nutrient pumping capacity, high foliar nutrient concentrations, and high nutrient turnover rate are desirable for both agroforestry and land rehabilitation purposes (Nair, 1993; Young, 1997). Therefore, in addition to indicating the N and P requirements of the tree species, the study of plant nutrient concentration and its dynamics with soil nutrient status under controlled conditions could show the relative abilities of species to absorb, accumulate and recycle nutrients under poor and ample supplies.

The current study considered two eucalyptus species that are widely grown in Ethiopia and three indigenous deciduous tree species of various uses and wide distribution in Ethiopia. The nutrient relations of these species were studied to generate information for recruiting these species for planting programs including land rehabilitation, large plantations and in combination with crops in Ethiopia. The objective of the study was to investigate the impact of soil N and P availability on N and P concentrations as well as N:P ratios of roots, stems and leaves of five tree species.

4.2 Materials and Methods

4.2.1 Plant establishment and glasshouse conditions

The experiment was carried out in a glasshouse at the tree nursery at the University of Stellenbosch, South Africa, from May to November 2002. Seedlings of *C. africana*, *C. macrostachyus*, *M. ferruginea*, *E. camaldulensis* and *E. globulus*, were established and grown in the glasshouse under conditions indicated in Chapter 2 (Section 2.2.1).

4.2.2 Nutrient application and measurements

The experiment was installed as a factorial with 5 species and 8 treatment combinations (4 levels of N and 2 levels of P). Eight-month-old seedlings were used for the experiment. A total of two hundred seedlings (40 per species) were selected from the supply stock and their soil leached with irrigation water for an hour to minimize pot nutrient reserves. The N and P concentration in the pot were determined using three samples per species (Table 4.1). The amounts of N and P indicated in the table were available for the control groups of each species, i.e., N1P1 treatment.

Table 4.1. The mean (\pm STD) N and P content of the soil medium after leaching with irrigation water. Soil samples were collected from three sample pots for each species at the start of the experiment, i.e., before N and P treatment.

Species	N (mg g^{-1})	P ($\mu\text{g g}^{-1}$)
<i>C. africana</i>	0.33 ± 0.00	1.9 ± 0.82
<i>C. macrostachyus</i>	0.30 ± 0.01	2.2 ± 0.18
<i>E. camaldulensis</i>	0.32 ± 0.01	2.6 ± 1.34
<i>E. globulus</i>	0.29 ± 0.02	1.9 ± 0.91
<i>M. ferruginea</i>	0.32 ± 0.02	2.1 ± 1.28

Limestone ammonium nitrate, containing 28% N, and calcium carbonate and enriched super phosphate, containing 10.5 % water soluble phosphate, 20% calcium and 11% sulfur were used as sources of N and P, respectively. Two applications of phosphorus and a split application of nitrogen was employed. The split application of N involved the top dressing of ammonium nitrate on a weekly basis. Phosphorus was applied at four spots around the seedling pot at the beginning and after 3 months. The different levels of N and P application are shown in Table 4.2. The levels of N and P were selected based on results of soil analysis carried out by Michelsen *et al.*, 1996; Jiregna, 1997; Abebe *et al.*, 2001; Tadesse *et al.*, 2000 under natural conditions in Ethiopia. The investigations consisted of soil samples from parklands, croplands and natural forests, which were found to contain 2.9-9.5 mg g⁻¹ total N and 1.8-56 µg g⁻¹ available P. The values of N and P concentrations in the control pots (low N and P) were comparable with the lower N and P ranges observed in the field.

Table 4.2 Levels of N and P applications as top dressing to seedlings of each species assigned to each treatment.

Treatment Levels	N application rate	P application
N1P1	0	0
N1P2	0	150 mg P*
N2P1	5 mg N week ⁻¹	0
N2P2	5 mg N week ⁻¹	150 mg P*
N3P1	25 mg N week ⁻¹	0
N3P2	25 mg N week ⁻¹	150 mg P*
N4P1	50 mg N week ⁻¹	0
N4P2	50 mg N week ⁻¹	150 mg P*

* applied twice viz at the start and at the middle of the experiment

Along with the N, the plants were supplemented with potassium chloride (100 mg week⁻¹), magnesium sulfate (85 mg week⁻¹) containing 9.7% Mg and 13.1% S, Compel fertilizer G II and iron in the form of chelate (10 mg week⁻¹), LibFer SP fertilizer G II containing 6% Fe. Plants were watered using micro-sprinkler irrigation once a day during the winter and twice a day during the spring.

4.2.3 Soil and plant chemical analysis

After six months of growth, all the experimental plants were harvested, separated into different components, and analyzed for nitrogen and phosphorus. Soil and plant nitrogen were determined with a Nitrogen Analyzer (Leco FP-528, USA). Soil phosphorus was determined in a Bray II extract (Bray and Kurtz, 1945). The phosphorus concentration in the extract was determined with a Varian Vista-MPX ICP-OES (USA). For plant phosphorus determination, one gram dried and milled plant material was ashed in a muffle furnace for eight hours at 480⁰C. The resultant ash was wetted with deionized water and phosphorus concentration in the solution was determined as for soil.

2.2.4 Statistical procedure

Data were subjected to factorial and one-way ANOVA to determine differences in stem, root and foliar N and P concentrations among species and treatments. Tukey's Honestly Significant Difference test was employed for multiple comparisons when significant differences were found between treatments. All statistical analyses were carried out using SPSS 11.0 for Windows.

4.3 Results

4.3.1 Plant nitrogen

Plant tissue N concentrations increased with increased soil N supply in all five species both under low and high soil P contents (Figs. 4.1a, b and c). The response of nutrient content to soil N supply was similar for the different plant parts and different levels of soil P, although the magnitude differed with species.

Significant soil N and P interactions were observed only for stem N concentration ($F = 4.518$, $P = 0.006$) (Table 4.3). The combined effects of soil N and P stress resulted in 40-60% reduction in leaf N (Fig. 4.1a), 63-83% reduction in stem N (Fig. 4.1b) and 56-70% reduction in root N (Fig. 4.1c) concentrations for all species. Although there were slight decreases in plant tissue N concentrations in the high soil P groups, seedling N concentrations were not significantly ($P < 0.05$) affected by soil P level. The effect of soil N on tissue N was significantly higher ($P < 0.001$) for the deciduous species compared to the evergreen eucalypts.

The foliar N concentration for *C. macrostachyus* was more than twice that of both eucalypts regardless of soil N and P levels. *C. africana* ranked second to *C. macrostachyus* regarding stem and root N concentration, while *M. ferruginea* ranked second to *C. macrostachyus* regarding foliar N concentration across the various soil N and P supply levels. Largely there was not significant difference in stem and root N concentrations between the two eucalypts at all levels of N and P supplements.

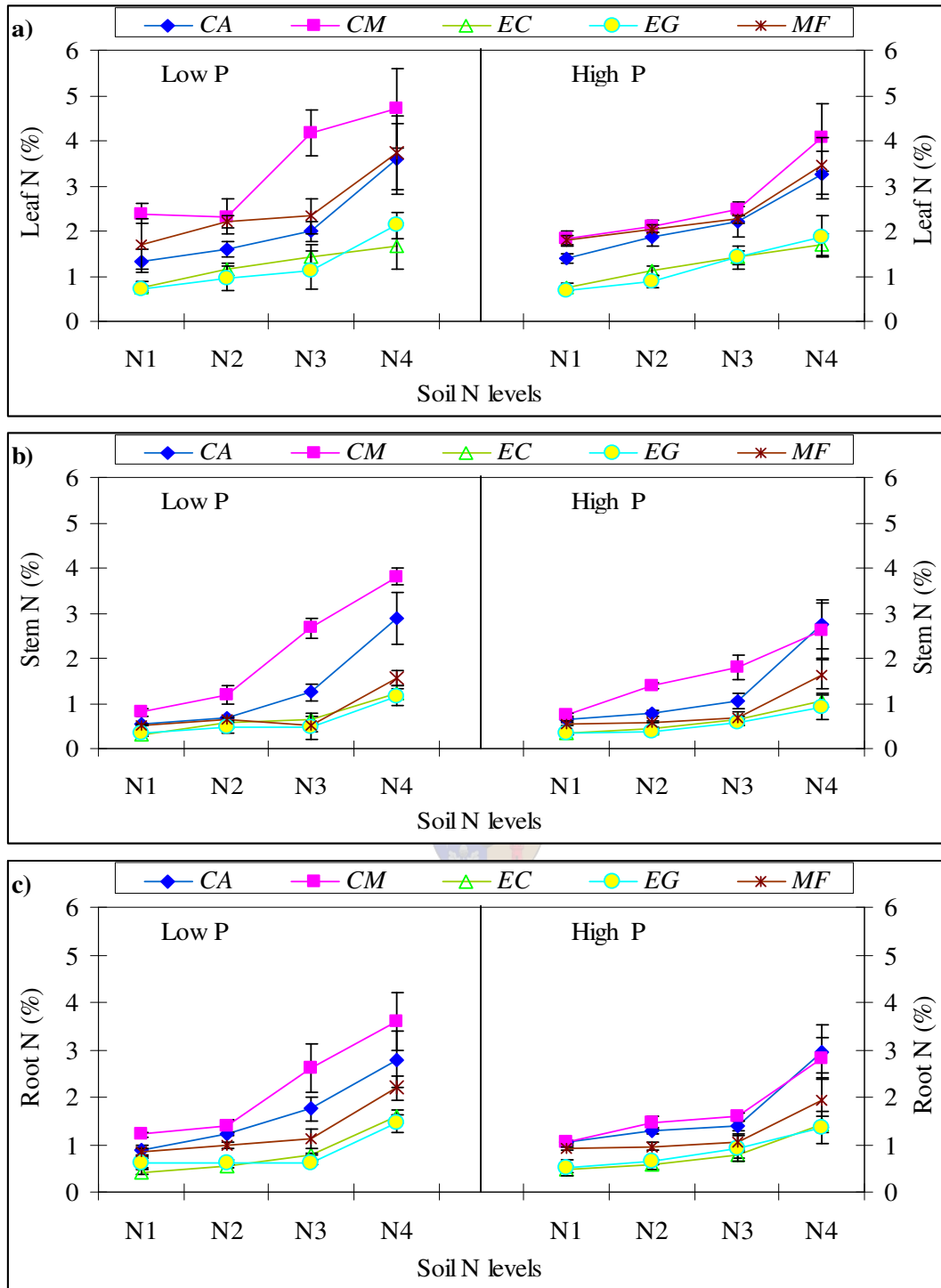


Figure 4.1 The mean ($n = 3$) foliar (a), stem (b) and root (c) N concentration of five tree species: *C. africana* (CA), *C. macrostachyus* (CM), *E. camaldulensis* (EC), *E. globulus* (EG) and *M. ferruginea* (MF) after six months of growth with four soil N (N1, N2, N3 and N4) and two soil P (low P and high P) treatments in a glasshouse. Vertical bar indicates standard error of the mean.

4.3.2 Plant phosphorus

Except for *E. globulus*, the leaf P concentrations were reduced by over 20% due to increased soil N both in the low and high soil P groups (Fig. 4.2a). Root and stem P concentrations were also higher for seedlings grown at low N except for the roots of *E. camaldulensis* and the stems of *M. ferruginea*, which did not decline due to increased soil N (Figs. 4.2b and c).

At all levels of soil N, increased soil P resulted in increased tissue P concentration regardless of plant species and parts of the plant. Significant interactions in soil N and P were observed only for foliar P concentration ($F = 5.415$, $P = 0.002$) (Table 4.3). Generally, increased soil P under N deficiency resulted in 45-65% increase in tissue P concentration in all the studied species. However, increased soil P under high N supply had much less effects on tissue P concentration except for leaves and stems of *C. africana* that showed 50 and 57% increases in P concentrations, respectively.

Except for leaves of *E. globulus*, stems of *C. macrostachyus* and roots of *E. camaldulensis*, N-stressed plants had significantly higher ($P < 0.05$) tissue P concentrations than unstressed plants. Stems of N-stressed *C. africana* and leaves and roots of N-stressed *C. macrostachyus* had higher ($P < 0.05$) P concentrations than those of the other species in the same treatment. Both soil N and P did not affect the foliar P concentration of *E. globulus*. Unlike all the other species, *C. macrostachyus* showed a significantly higher ($P < 0.01$) accumulation of P in all plant parts when soil N was supplied at high rate but P was low.

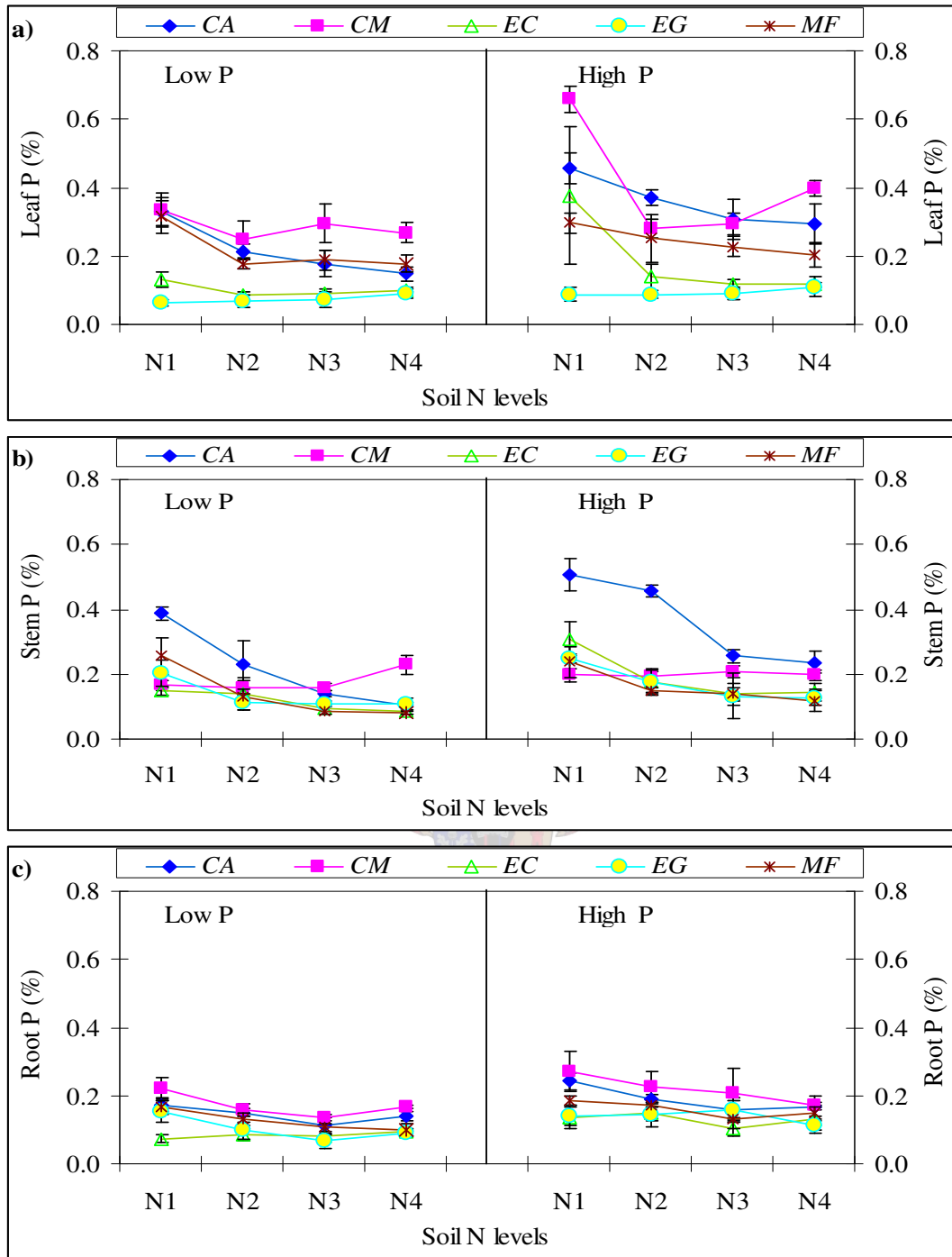


Figure 4.2 The mean (n = 3) foliar (a), stem (b) and root (c) P concentration of five tree species: *C. africana* (CA), *C. macrostachyus* (CM), *E. camaldulensis* (EC), *E. globulus* (EG) and *M. ferruginea* (MF) after six months of growth with four soil N (N1, N2, N3 and N4) and two soil P (low P and high P) treatments in a glasshouse. Vertical bar indicates standard error of the mean.

4.3.3 Plant N:P ratio

The range of foliar N:P ratio in the current study was from 3.2-25.1 for *C. africana*, 2.7-17.5 for *C. macrostachyus*, 2.5-16.8 for *E. camaldulensis*, 8.1-24.3 for *E. globulus* and 6.1-20.9 for *M. ferruginea* (Fig. 4.3a). Similar trends were observed for stem and root N:P ratios (Figs. 4.3b and c). Both under low and high soil P contents, the tissue N:P ratios increased with increasing soil N supply in all the studied species. Significant interactions in soil N and P were observed for foliar ($F = 3.820$, $P = 0.013$), stem ($F = 16.084$, $P = 0.000$), and root ($F = 4.998$, $P = 0.003$) N:P ratios (Table 4.3). The N- stressed seedlings had 52-83% decline in N:P ratio of leaves, 71-95% decline in N:P ratio of stems and 63-77% decline in N:P ratio of roots both in the low and high soil P for all the study species. High soil P availability resulted in a reduced N:P ratio in all species (Figs. 4.2a, b and c). However, *E. globulus* maintained a higher foliar N:P ratios at all levels of soil N and P. *C. africana* had exceptionally high stem N:P ratio in the N4P1 treatment. Except in the N4 treatment, *C. macrostachyus* had significantly higher ($P < 0.05$) stem N:P ratio than all the other study species.

Considering the magnitudes of the differences between treatments, stem N, P and N:P ratios were more sensitive to soil N and P supply than leaves and roots for all species with some exceptions. The exceptions were: a) foliar P was more sensitive to soil N and P than stem and roots for *C. macrostachyus*, b) root N, P and N:P ratio were more sensitive to soil P than those of leaves and stems for *M. ferruginea*.

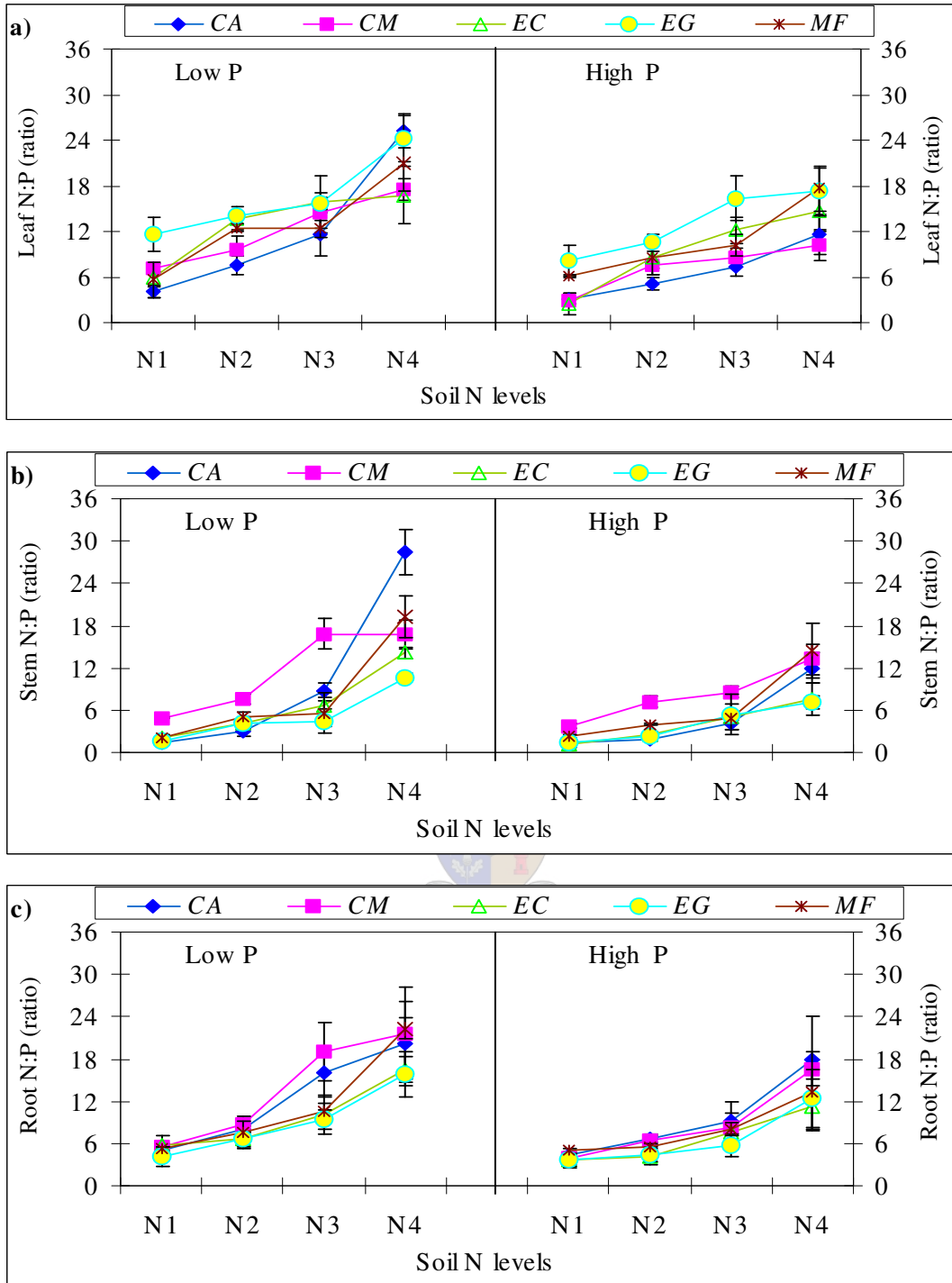


Figure 4.3 The mean ($n = 3$) foliar (a), stem (b) and root (c) N:P ratio of five tree species: *C. africana* (CA), *C. macrostachyus* (CM), *E. camaldulensis* (EC), *E. globulus* (EG) and *M. ferruginea* (MF) after six months of growth with four soil N (N1, N2, N3 and N4) and two soil P (low P and high P) treatments in a glasshouse. Vertical bar indicates standard error of the mean.

Table 4.3 Summary of factorial ANOVA showing the effects of soil N and P on root, stem and leaf N and P concentrations and N: P ratio of seedlings of five tree species after six months of growth in a glasshouse.

Source	Plant part		
	Root	Stem	Leaf
Nitrogen content (%)			
Species	0.000	0.000	0.000
Soil N	0.000	0.000	0.000
Soil P	0.056	0.003	0.015
Species * Soil N	0.000	0.000	0.000
Species * Soil P	0.030	0.000	0.001
Soil N * Soil P	0.181	0.006	0.473
Species * Soil N * Soil P	0.347	0.001	0.261
Phosphorus content (%)			
Species	0.000	0.000	0.000
Soil N	0.000	0.000	0.000
Soil P	0.000	0.000	0.000
Species * Soil N	0.041	0.000	0.000
Species * Soil P	0.809	0.000	0.000
Soil N * Soil P	0.205	0.414	0.002
Species * Soil N * Soil P	0.102	0.046	0.000
N:P ratio			
Species	0.000	0.000	0.000
Soil N	0.000	0.000	0.000
Soil P	0.000	0.000	0.000
Species * Soil N	0.171	0.000	0.015
Species * Soil P	0.503	0.002	0.311
Soil N * Soil P	0.003	0.000	0.013
Species * Soil N * Soil P	0.270	0.000	0.060

4.4 Discussion

Similar to earlier reports based on comparisons of several other deciduous and evergreen species (Reich *et al.*, 1992; Aerts, 1995; Aerts and Chapin, 2000), the deciduous species in the current study had higher tissue nutrient composition than the evergreen eucalypts.

Eucalypts utilize readily available nutrients for rapid new growth, which sometimes leads to the dilution of tissue nutrient concentration (Olsen and Bell, 1990; Bennett *et al.*, 1997).

Evergreen species such as the eucalypts are also reported to have long leaf lifespans compared to deciduous species (Reich *et al.*, 1992). Under poor soil nutrient conditions, longer leaf lifespan in evergreen species may be the major mechanism for nutrient conservation. On the contrary, plants with long leaf lifespan may aggravate the low availability of nutrients in the already nutrient poor environments (Aerts, 1995), especially when combined with other crops or trees. Because of the higher concentration of nutrients and lower concentration of secondary compounds in their leaves, the litter of deciduous trees decomposes and releases nutrients to the soil faster than the litter of evergreen trees (Aerts and Chapin, 2000). This implies that the plant characteristics of deciduous trees not only lead to low nutrient use efficiency (productivity per unit nutrient uptake or loss), but also keep soil fertility high compared to evergreen trees.

The range of foliar N and P concentrations observed for *E. camaldulensis* in the current study is within the range reported for those grown in Australia, Philippines and the Middle East (Judd *et al.*, 1996). According to the ranges for deficient and adequate foliar nutrient concentrations reported for *E. globulus* under Australian conditions (Dell *et al.*, 1995), both the foliar N and P concentrations observed in the current study fall in the deficiency range. However, the former study considered only the youngest leaves while the current study considered all leaves.

Among all species, the eucalypts showed only slight tissue N and P responses to soil N and P supplies although the growth in biomass at higher soil N and P was higher compared to the other species (data not presented). Reports from former studies also

indicated a weak relationship between growth and nutrient status in the eucalypts (Cromer *et al.*, 1975; Olsen and Bell, 1990; Bennett *et al.*, 1997). The leaf P concentration of *E. globulus* was less responsive to both soil N and P unlike the stems and roots. In a study of the response of six-year-old *E. globulus* to N and P fertilizers in Australia, Bennett *et al.*, (1997) observed that N and P additions significantly increased the above ground biomass, without affecting the plant N concentration. However, stem wood showed the greatest relative increase in P concentration due to P additions compared to various plant parts including leaves (Bennett *et al.*, 1997). Olsen and Bell (1990) also found that stems and petioles are better indicators for P than other plant parts.

The mean foliar N concentrations of *M. ferruginea* (3.5%), *C. africana* (3.4%) and *C. macrostachyus* (4.4%) in the high soil N treatment were comparable or higher than that reported for leaves of *Erythrina brucei* Schweinf., a nitrogen fixing species from Ethiopia (Legesse, 2002a). The foliar P concentrations of the three deciduous species in all treatments were higher than that reported for leaves of *E. brucei* (Legesse, 2002a). The eucalypts had largely less foliar N and P concentrations compared to *E. brucei*. Several studies indicate that the tissue N concentration of N-fixing species is higher than that of non-fixing species. However, *C. macrostachyus*, a non N-fixing species, had higher tissue N concentration than *M. ferruginea* and *E. brucei* that are N-fixing species. Similarly, *C. africana* had significantly higher stem and root N concentration than *M. ferruginea*. Although some nodules were observed on roots of the pot grown *M. ferruginea* seedlings, the roots still had lower N concentration compared to the other deciduous species, indicating that the N-fixation in *M. ferruginea* was inefficient at least under the current experimental conditions. A former study under natural conditions in Ethiopia (Jiregna,

1997) also indicates that green leaves of *C. macrostachyus* had significantly higher N and P concentration compared to *M. ferruginea*. The same study indicated that soil under the *C. macrostachyus* canopy had significantly lower P concentration compared to that under *M. ferruginea*.

Owing to its high N and P accumulation and high decomposition rate (Jiregna, 1997), *C. macrostachyus* could be classed among the species with high nutrient recycling potential that are regarded as soil improving in agroforestry systems (Young, 1997). However, due to its extensive surface roots (Chapter 6) it may be very competitive when grown in association with crops or other trees. So far as its nutrient pumping ability is concurred, as indicated by the return of litter with high nutrient concentration, its competitive effects may not result in overall negative consequences for the soil.

The use of N:P ratio to determine N and P limitations in plant growth rather than absolute concentrations has been suggested (Cromer *et al.*, 1981; Olsen and Bell, 1990; Koerselman and Meuleman, 1996) based on the assumption that plant species have optimum N:P ratio and this ratio may increase due to high soil N and low soil P and decrease due to high soil P and low soil N. Cromer *et al.* (1981) proposed a foliar N:P ratio of 15 to be optimal for *E. globulus* after a series of fertilizer experiments in Australia. A fertilizer trial on seedlings of *E. globulus* of Portuguese origin (Ericsson, 1994) indicates that an N:P ratio of 9.5 is optimal for growth of the species. Therefore, there may be some degree of elasticity in N:P ratio for a given species and different species may have different optimal N:P ratios. For instance Olsen and Bell (1990) reported a range between six and ten to be optimum for six other eucalyptus species.

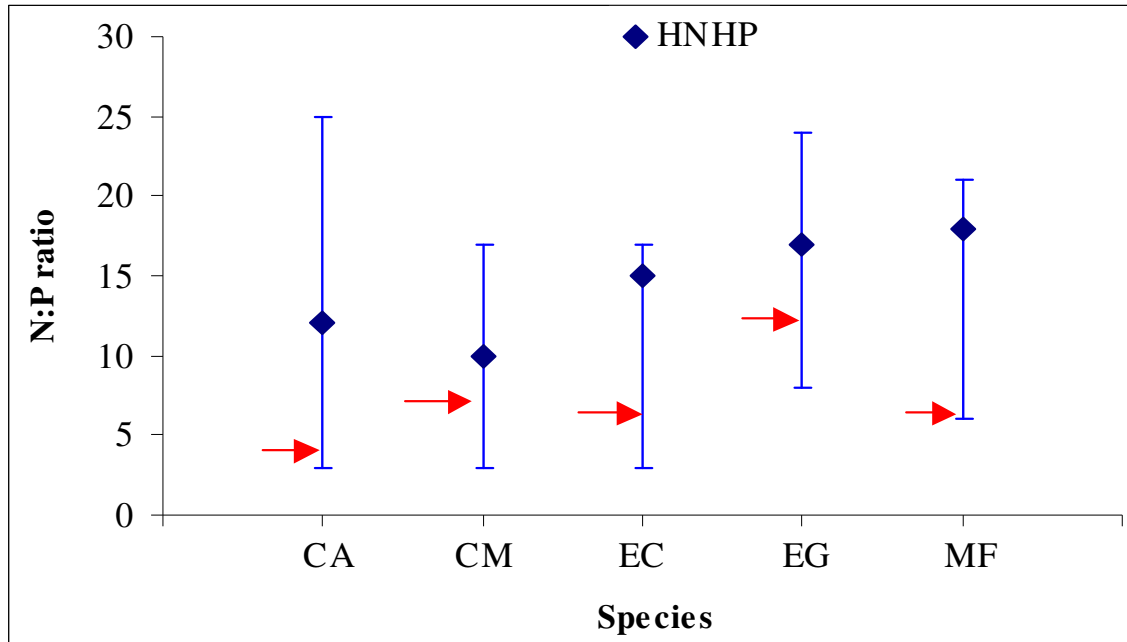


Figure 4.4 The foliar N:P ratio of seedlings of five tree species as observed after six months of growth in a glasshouse under high and low supplies of N and P. HNHP = high N and P supplies, maximum value of the bar = P deficiency, minimum value of the bar = N-deficiency, arrow = values for combined N and P deficiency. Figure 4.3a is redrawn to indicate the range and optimal N:P ratios for each species. CA = *C. africana*, CM = *C. macrostachyus*, EC = *E. camaldulensis*, EG = *E. globulus* and MF = *M. ferruginea*.

The foliar N:P ratios of 10, 12, 15, 17 and 18 observed for *C. macrostachyus*, *C. africana*, *E. camaldulensis*, *E. globulus* and *M. ferruginea*, respectively, under sufficient supplies of N and P (Fig. 4.4) could be considered as ‘optimal’ with the assumption that these plants did not preferentially accumulate either of the nutrients. P-deficiency resulted in higher foliar N:P ratio while N-deficiency resulted in lower foliar N:P ratio. However, in addition to N-deficiency, low N:P ratio was also observed for plants under combined deficiency of N and P. This could be due to the considerable effect of N on growth (Chapter 5) and probably on the absorption of P itself. As a result, unlike the suggestions of

Koerselman and Meuleman (1996) on the use of N:P ratio to detect N or P-limitation in plants, the parameter could not distinguish between N-limitation and the combined limitation of N and P, both of which resulted in reduced N:P ratio (Fig. 4.4). However, N:P ratio could be used to detect P-limitation in the studied species.

4.5 Conclusion

Soil N and P availabilities had considerable effects on the tissue nutrient composition of the studied species. However, the deciduous species accumulated more N and P compared to the eucalypts under all conditions of soil N and P. Regardless of the soil P status the stem, root and foliar N concentrations and N:P ratios increased while foliar P concentrations declined with increasing soil N availability in all the studied species.

Foliar N:P ratios of 10, 12, 15, 17 and 18 were observed for *C. macrostachyus*, *C. africana*, *E. camaldulensis*, *E. globulus* and *M. ferruginea*, respectively, under sufficient supplies of both N and P. The deficiency of P increased these values while the deficiency of N as well as the combined deficiencies of N and P decreased these values.

The high accumulation of nutrients in leaves coupled with a short leaf life span may have a considerably negative impact on the growth rate of the deciduous species, except if these species may have efficient nutrient resorption from leaves before they are shed. However, from a nutrient cycling point of view, these deciduous species have higher nutrient recycling abilities than the eucalypts.

5. EFFECTS OF SOIL NITROGEN AND PHOSPHORUS ON GAS EXCHANGE OF SEEDLINGS OF TWO *EUCALYPTUS* AND THREE DECIDUOUS TREE SPECIES

Abstract

The effects of soil nitrogen (N) and phosphorus (P) on the photosynthetic activities of *C. africana*, *C. macrostachyus*, *M. ferruginea*, *E. camaldulensis* and *E. globulus* seedlings were studied under glasshouse conditions. Twenty eight-month-old seedlings from each species were assigned to combinations of four N and P treatments, viz. low N and P, low N and high P, high N and low P, and high N and P. N stress reduced photosynthetic rate, stomatal conductance and photosynthetic water use efficiency (WUE_{GE}) in all the species examined, except in *C. africana* where stomatal conductance was not affected significantly. Compared to the corresponding high N treatments, N stress resulted in 60-73% and 40-62% reduction in photosynthesis in the low and high P treatments, respectively. As a result of N stress, the WUE_{GE} of seedlings of all the species was reduced by 25-60% and 28-56% in the low and high P treatments, respectively. The apparent quantum efficiency (Φ) and light saturated photosynthetic rates (A_{max}) of all species ranged between 0.0046 – 0.0185 and 2.3 – 12.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. The Φ and A_{max} of all the studied species were more sensitive to N than to P stress. Regardless of soil P status, N content of leaves in each of the examined species was significantly correlated ($r^2 = 0.89$; $P < 0.001$) with the photosynthetic rate of the leaves, suggesting that leaf N content may govern the capacity of leaves to fix CO_2 . However, no direct effect of soil N on photosynthetic nitrogen use efficiency (PNUE) was observed in the current study except in *M. ferruginea* and *C. macrostachyus*. The observed higher PNUE in *M. ferruginea* compared to all the other species may a genetic trait because it was observed under all treatment conditions.

5.1 Introduction

In Ethiopia the re-establishment of trees on the degraded lands has been difficult, especially where nutrient stress is superimposed onto moisture stress (EFAP, 1994; Legesse, 1994, 2000, 2002b). Proper environmental conditions with acceptable soil physical and chemical properties and essential biological associations both at species and community levels have been destroyed following decades of deforestation (EFAP, 1994; EPA, 1998; Legesse 2002b). Furthermore, soil nutrient status has been deteriorating because of poor land management practices. Knowledge on the nutrient requirement of a species is pivotal to understanding its growth potential under limited supply of nutrients, which in turn determines the success of plantation forestry at a larger scale, especially when the rehabilitation of degraded lands is the objective of a plantation program.

Under field conditions, nutrient deficiency ranks probably next to water stress in determining the establishment of tree seedlings. In areas with limited soil nutrients, trees that could tolerate the nutrient stress and grow to an acceptable size are preferred. Although eucalypts are acclaimed to yield higher biomass than most of the indigenous deciduous species in areas of both poor and fertile soil conditions in the Ethiopian highlands (Pohjonen, 1989), they are reported to suffer from dieback in many instances (Pohjonen, 1989; Tesfaye, 1994). Furthermore, eucalypts are known for their negative attributes including excessive depletion of soil water and nutrients (Florence, 1996). Although there could be alternative indigenous species to replace the eucalypts, no published reports have been made available on the effects of soil nutrients on the growth performances of indigenous tree species of Ethiopia.

Growth is the most sensitive indicator of nutrient deficiency (Evans, 1996). Because of the primary role of photosynthesis in plant growth and its response to nutrient availability (Rao and Terry, 2002), a study of the effects of nitrogen and phosphorus nutrition on the photosynthetic performance of different species could provide an insight into the growth performance of the species.

Photosynthetic studies have been used as tools to probe the physiological basis of plant growth under environmental limitations including nutrient stresses (e.g., Evans, 1989; Fredeen *et al.*, 1989; Sage *et al.*, 1990; Fredeen *et al.*, 1991; Evans, 1996, Lambers *et al.*, 1998; Lu and Zhang, 2000; Rao and Terry, 2000; Shangguan *et al.*, 2000). Measurement of CO₂ uptake provides a direct method of measuring carbon exchange with important advantages: it is instantaneous and non-destructive.

The objective of this study was to: 1) investigate the effects of soil nitrogen and phosphorus on the photosynthetic rate, stomatal conductance and photosynthetic water use efficiency of three deciduous indigenous tree species of Ethiopia and two *Eucalyptus* species, 2) to investigate the relationship between foliar N concentration and its photosynthetic rate in these species. Nitrogen and phosphorus were chosen in the study because they are the main growth limiting nutrients for plants in tropical and subtropical environments (Marschner, 1995, Koerselman and Meuleman, 1996). The indigenous species were selected on the basis of their wide use for environmental, economic and social benefits in Ethiopia (Demel and Aseffa, 1991, Fichtl and Admasu, 1994; EFAP, 1994; Legesse, 1995; Jiregna, 1997; Tadesse *et al.*, 2000).

5.2 Materials and Methods

5.2.1 Plant establishment and glasshouse conditions

Seedlings of *C. africana*, *C. macrostachyus*, *E. camaldulensis*, *E. globulus* and *M. ferruginea* were established in a glasshouse at the tree nursery in the University of Stellenbosch, South Africa under conditions described in Chapter 2 (Section 2.2.1). The experiment was carried out from 24 May 2002 to 22 November 2002.

5.2.2 Treatment

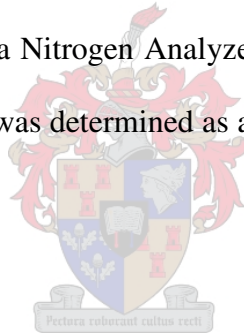
The experiment was carried out on the same plants used for experiment in Chapter 4. Plants that received low N and P, low N and high P, high N and low P, and high N and P treatments were used for the current study.

5.2.3 Gas exchange

Gas exchange measurements were carried out every 10 days during the mornings between 8:00 and 10:00 using an infrared gas analyzer (CIRAS-I, PP Systems, Hitchin, UK) from 22 August 2002 to 22 November 2002. Details of the measurement procedures are given in Chapter 2 (Section 2.2.4). Photosynthetic response curves were obtained by measuring leaf net CO₂ assimilation (photosynthetic) rate at different PPFD. Measurements were made at a CO₂ concentration of 360 μmol mol⁻¹ and a leaf temperature of 24 ± 1 °C. Different degrees of shading were achieved using shade cloths of different densities. Photosyn Assistant Software (Version 1.1, Dundee Scientific) was used to plot and analyze the response curve of photosynthesis (A) to light level (Q). The curve was drawn by fitting the data to a model of nonrectangular hyperbola (Prioul and Chartier, 1977);

$$A = \frac{\Phi \cdot Q + A_{\max} - \sqrt{[(\Phi \cdot Q + A_{\max})^2 - 4\Phi \cdot \Theta \cdot Q \cdot A_{\max}]} }{2\Theta} - R_d$$

where A_{\max} is the light saturated rate of CO₂ assimilation described as the upper asymptote, Φ is the apparent quantum efficiency determined from the initial slope of the curve, R_d is the apparent respiration determined from the axis intercept and Θ is the convexity (bending of the curve). To investigate the relationship between foliar N concentration and photosynthetic rate, samples of the well-expanded leaves used for gas exchange measurements were collected for the determination of leaf N on 22 November 2002. Foliar N content was determined with a Nitrogen Analyzer (Leco FP-528, USA). Photosynthetic nitrogen use efficiency (PNUE) was determined as a ratio of leaf photosynthetic rate to leaf nitrogen concentration.



5.2.4 Statistical procedure

Data were subjected to factorial and one-way ANOVA to determine differences among species and treatments for each of the physiological variables. Tukey's Honestly Significant Different test was used for multiple comparison when significant differences were found between treatments and species. The effect of N and P supply on each species was determined by splitting the data by species and treatment. Apart from the photosynthetic response, which was carried out using Photosyn Assistant Software (Version 1.1, Dundee Scientific), all statistical analyses were carried out using SPSS 11.0 for Windows.

5.3 Results

5.3.1 Stomatal conductance

Phosphorus availability did not affect the stomatal conductance of all three deciduous species both at high and low N availability (Table 5.1). Soil N and P had significantly ($P < 0.01$) interacting effects on the stomatal conductances of *E. camaldulensis* and *E. globulus*. Seedlings of *E. camaldulensis* and *E. globulus* with low P had significantly ($P < 0.05$) higher stomatal conductance than those with high P at both levels of N. The stomatal conductance of *C. africana* was not affected by N availability. Similarly, the stomatal conductance of *C. macrostachyus* was not affected by N availability in the seedlings treated with high P. However, for the two eucalypts and *M. ferruginea*, N stress resulted in 10 - 45% reduction in stomatal conductance. The effect of N stress on stomatal conductance of *C. macrostachyus*, *E. camaldulensis* and *E. globulus* was two-fold for plants with low P.

5.3.2 Photosynthetic rate

Nitrogen stress caused a 60 - 73% decline in photosynthesis in the low P seedlings and a 40 - 62% in the high P seedlings in all the studied species (Table 5.1). The photosynthetic rates of *C. macrostachyus* and *E. camaldulensis* were significantly reduced ($P < 0.001$) by the combined effects of N and P stresses compared to the other species. However, *E. camaldulensis* had a lower photosynthetic rate than all three deciduous species even in the high N and high P treatments. In the low N treatment, reduced P resulted in 26 - 50% loss of photosynthesis in all the studied species except in *E. globulus* where reduced P failed to significantly affect photosynthesis.

Table 5.1 Mean (\pm SE, $n = 50$) stomatal conductance, photosynthetic rate and photosynthetic water use efficiency of seedlings of four tree species grown with high or low soil N and P applications. Significant *P*-values for variations within species are shown in rows (one-way ANOVA) and those for N, P and interactions between N and P (factorial ANOVA) are shown in the right hand columns.

Species	Low N		High N		<i>P</i> -values		
	Low P	High P	Low P	High P	N	P	NxP
	Stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)						
<i>C. africana</i>	104 \pm 5.3	104 \pm 3.4	102 \pm 4.1	106 \pm 6.9	0.961	0.713	0.698
<i>C. macrostachyus</i>	84 \pm 4.5	86 \pm 4.5	107 \pm 5.8	96 \pm 8.2	0.005	0.468	0.282
<i>E. camaldulensis</i>	84 \pm 6.6	76 \pm 3.0	150 \pm 7.2	92 \pm 5.9	0.000	0.000	0.000
<i>E. globulus</i>	89 \pm 4.8	72 \pm 4.1	155 \pm 8.5	97 \pm 6.0	0.000	0.000	0.001
<i>M. ferruginea</i>	85 \pm 4.3	80 \pm 3.4	95 \pm 4.7	97 \pm 5.3	0.003	0.641	0.452
<i>P</i> (one-way)	0.030	0.000	0.000	0.681			
	Photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$)						
<i>C. africana</i>	3.2 \pm 0.1	4.4 \pm 0.2	9.0 \pm 0.2	10.1 \pm 0.2	0.000	0.000	0.812
<i>C. macrostachyus</i>	2.4 \pm 0.1	4.7 \pm 0.2	8.8 \pm 0.4	9.8 \pm 0.3	0.000	0.000	0.017
<i>E. camaldulensis</i>	2.4 \pm 0.1	4.7 \pm 0.2	8.3 \pm 0.3	7.6 \pm 0.2	0.000	0.000	0.000
<i>E. globulus</i>	3.4 \pm 0.2	3.4 \pm 0.1	8.6 \pm 0.2	8.9 \pm 0.4	0.000	0.610	0.475
<i>M. ferruginea</i>	3.0 \pm 0.1	4.1 \pm 0.2	9.0 \pm 0.3	9.4 \pm 0.3	0.000	0.010	0.189
<i>P</i> (one-way)	0.000	0.000	0.431	0.000			
	Water use efficiency ($\text{mmol CO}_2 (\text{mol H}_2\text{O})^{-1}$)						
<i>C. africana</i>	3.1 \pm 0.2	3.5 \pm 0.3	6.7 \pm 0.3	7.5 \pm 0.2	0.000	0.010	0.593
<i>C. macrostachyus</i>	2.4 \pm 0.1	3.9 \pm 0.2	7.0 \pm 0.4	8.0 \pm 0.3	0.000	0.000	0.333
<i>E. camaldulensis</i>	3.4 \pm 0.2	4.5 \pm 0.3	4.7 \pm 0.3	6.2 \pm 0.3	0.000	0.000	0.514
<i>E. globulus</i>	3.7 \pm 0.3	3.3 \pm 0.2	4.9 \pm 0.2	7.4 \pm 0.3	0.000	0.000	0.000
<i>M. ferruginea</i>	2.5 \pm 0.1	3.5 \pm 0.2	6.2 \pm 0.2	6.2 \pm 0.3	0.000	0.031	0.038
<i>P</i> (one-way)	0.000	0.005	0.000	0.000			

However, in the high N treatment, reduced P did not significantly affect ($P > 0.05$) the photosynthetic rate of *E. globulus* and *M. ferruginea*. For the other species photosynthetic rate declined significantly ($P < 0.05$) with reduced P

5.3.3 Photosynthetic water use efficiency

The WUE_{GE} of all the species was reduced by 25- 66% in the low phosphorus treated and 28 - 56% in the high phosphorus treated seedlings due to N stress (Table 5.1). Soil N and P had significantly interacting effect on the WUE_{GE} of *E. globulus* ($P < 0.001$) and *M. ferruginea* ($P < 0.05$). Increased P availability resulted in a significantly ($P < 0.05$) higher WUE_{GE} at both levels of N for all the studied species except in the low and high N treatments of *E. globulus* and *M. ferruginea*, respectively. The eucalypts had a significantly higher ($P < 0.05$) WUE_{GE} than the deciduous species in the low N and P treatment.

5.3.4 Light response

Nitrogen stress reduced the photosynthetic activity of all the study species at light saturation level (Fig. 5.1a – e). Leaves of all species grown with low soil N supply had lower light saturation point, apparent quantum efficiency (Φ) and A_{max} compared to those grown with high soil N supply (Fig. 5.1 and Table 5.2). The Φ and A_{max} of all species ranged between 0.0046 – 0.0096 and 2.3 – 4.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the low N group and 0.0107 - 0.0185 and 5.3 – 12.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the high N group, respectively (Table 5.2). The effect of soil P on Φ and A_{max} was slight compared to that of N.

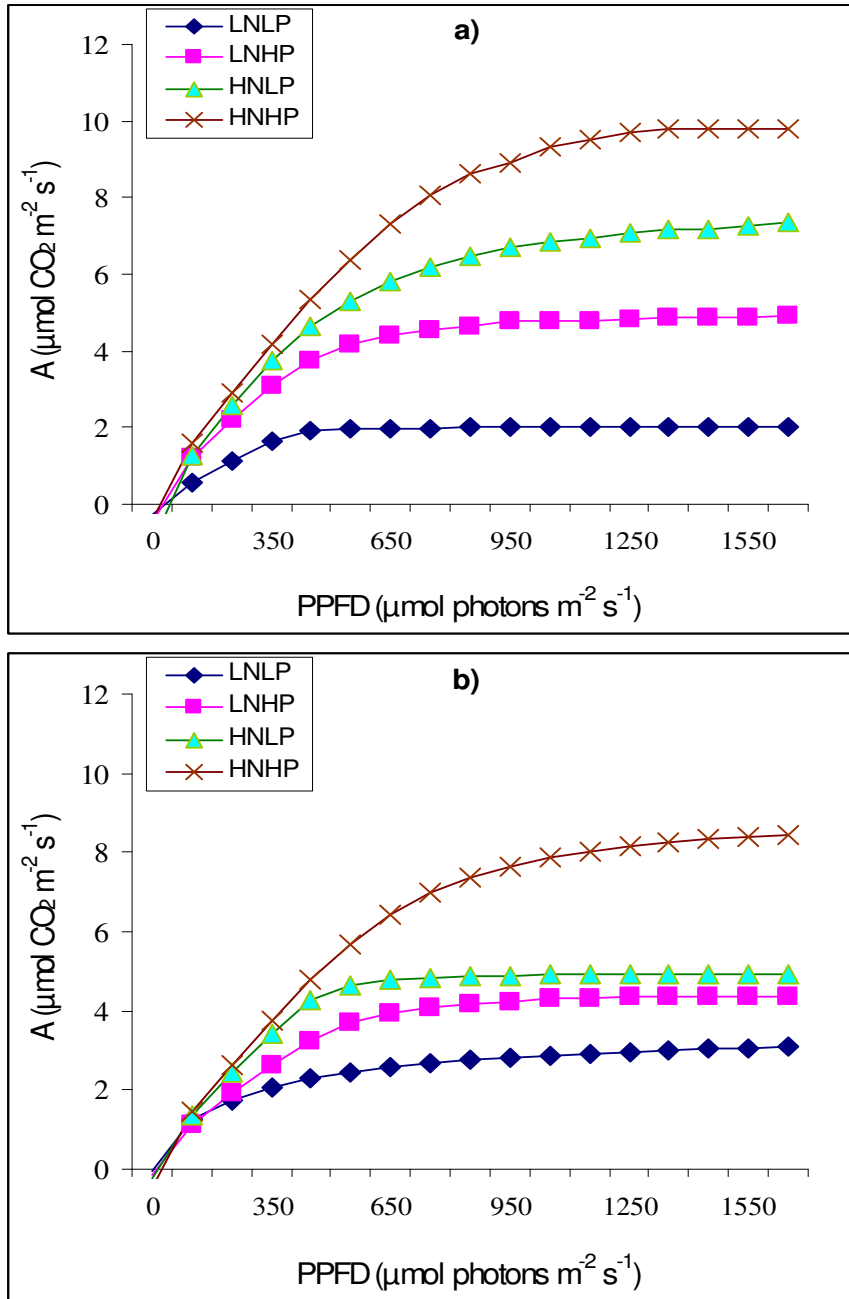


Figure 5.1 (a and b) Photosynthetic light-response curves of *C. africana* (a) and *C. macrostachyus* (b) seedlings treated with four different N and P combinations and maintained under glasshouse conditions: LNLP = low N, low P; LNHP = low N, high P; HNLP = high N, low P; HNHP = high N, high P. Each point is the mean of five replicates.

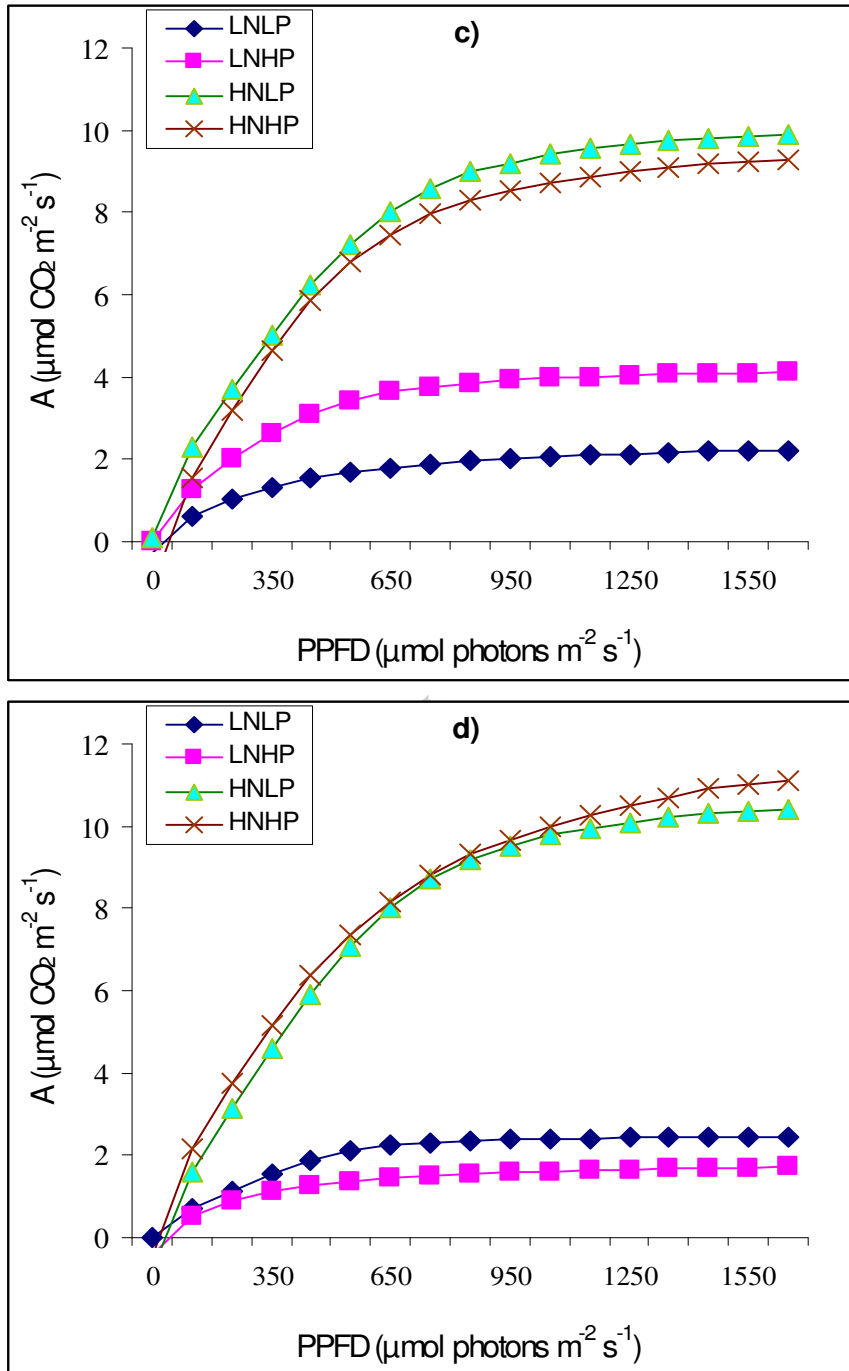


Figure 5.1 (c and d) Photosynthetic light-response curves of *E. camaldulensis* (c) and *E. globulus* (d) seedlings treated with four different N and P combinations and maintained under glasshouse conditions: LNLP = low N, low P; LNHP = low N, high P; HNLP = high N, low P; HNHP = high N, high P. Each point is the mean of five replicates.

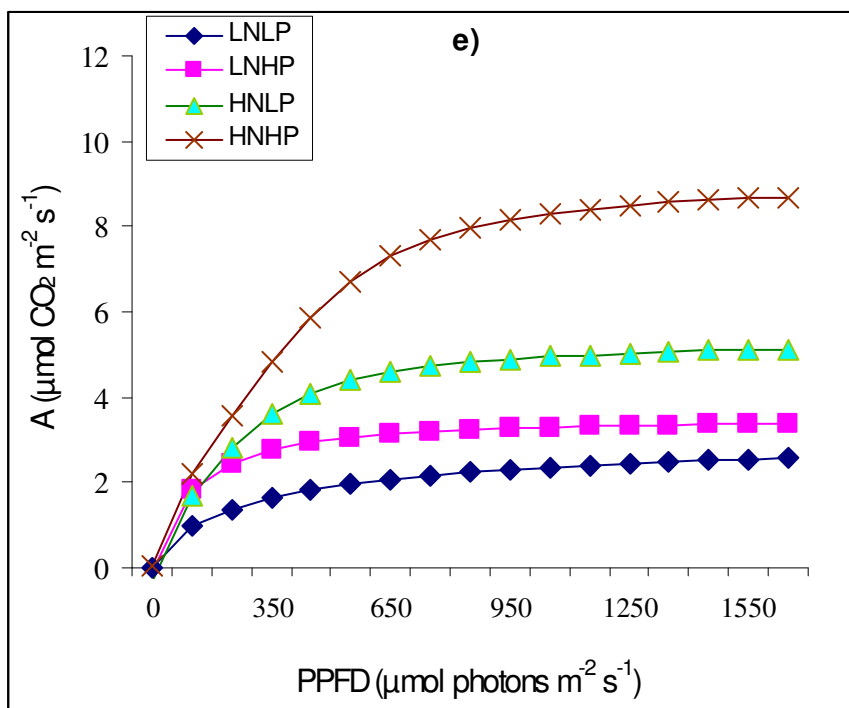


Figure 5.1(e) Photosynthetic light-response curves of *M. ferruginea* seedlings treated with four different N and P combinations and maintained under glasshouse conditions: LNLP = low N, low P; LNHP = low N, high P; HNLP = high N, low P; HNHP = high N, high P. Each point is the mean of five replicates.

5.3.5 Leaf N and photosynthetic rate

Regardless of soil P status N content of leaves from each of the examined species had a significantly strong correlation ($r^2 = 0.89$; $P < 0.001$) with the photosynthetic rate of the leaves (Fig. 5.2). The correlation was stronger for *C. africana* than for the other species. In contrast, there was no significant correlation between leaf P and the photosynthetic rate for all the species studied (data not presented).

Table 5.2 Mean estimated (\pm SE) light saturated photosynthetic rate (A_{max}) and apparent quantum efficiency (Φ) of seedlings of five tree species grown in a glasshouse under four N and P treatments (LNLP = low N, low P; LNHP = low N, high P; HNLP = high N, low P; HNHP = high N, high P). Values were estimated by fitting data to a nonrectangular hyperbola model (Fig. 5.1).

Species	LNLP	LNHP	HNLP	HNHP
Light saturated photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$)				
<i>C. africana</i>	2.3 \pm 0.21	4.5 \pm 0.40	9.1 \pm 0.83	11.0 \pm 1.01
<i>C. macrostachyus</i>	3.6 \pm 0.48	4.6 \pm 0.44	8.2 \pm 0.73	9.4 \pm 0.39
<i>E. camaldulensis</i>	2.8 \pm 0.39	4.1 \pm 0.31	10.2 \pm 0.74	11.0 \pm 0.85
<i>E. globulus</i>	2.5 \pm 0.28	2.3 \pm 0.30	11.7 \pm 1.38	12.9 \pm 1.51
<i>M. ferruginea</i>	3.0 \pm 0.34	3.6 \pm 0.75	8.9 \pm 0.68	9.1 \pm 0.23
Apparent quantum efficiency				
<i>C. africana</i>	0.0056 \pm 0.0010	0.0093 \pm 0.0019	0.0162 \pm 0.0034	0.0136 \pm 0.0022
<i>C. macrostachyus</i>	0.0086 \pm 0.0067	0.0084 \pm 0.0020	0.0107 \pm 0.0032	0.0129 \pm 0.0011
<i>E. camaldulensis</i>	0.0073 \pm 0.0033	0.0081 \pm 0.0013	0.0149 \pm 0.0019	0.0185 \pm 0.0026
<i>E. globulus</i>	0.0047 \pm 0.0009	0.0085 \pm 0.0045	0.0162 \pm 0.0035	0.0185 \pm 0.0040
<i>M. ferruginea</i>	0.0096 \pm 0.0043	0.0091 \pm 0.0176	0.0166 \pm 0.0060	0.0149 \pm 0.0000

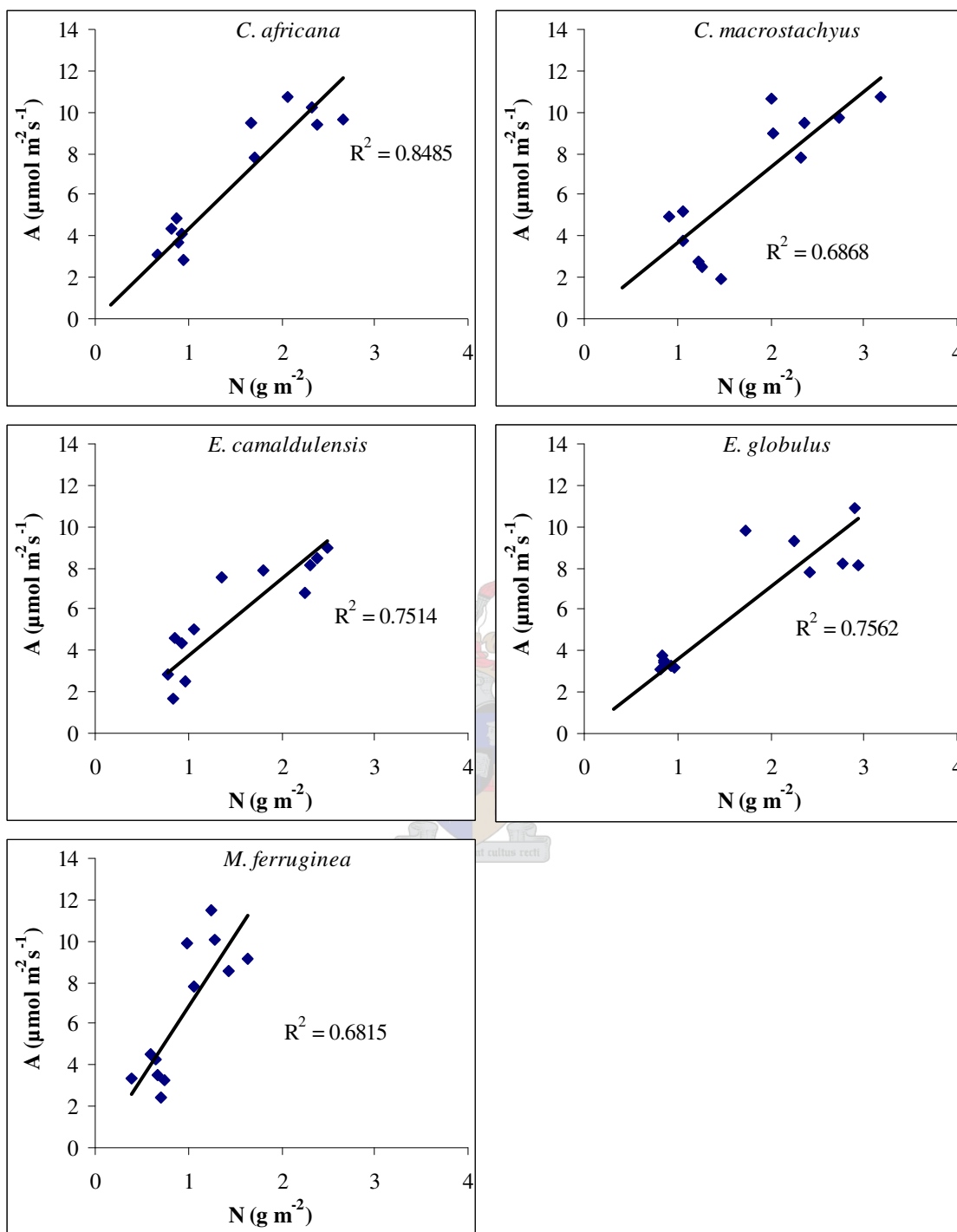


Figure 5.2 Linear relationship between net assimilation rate (A) and leaf N concentration of seedlings of five tree species.

Soil N supply did not significantly affect PNUE in *C. africana* and the eucalypts (Table 5.3). However the PNUE of *M. ferruginea* and *C. macrostachyus* were significantly reduced by soil N and P limitation, except in the high P group in the latter. Generally, increased soil P increased PNUE except that seedlings of *E. camaldulensis* grown with high N and P had significantly lower ($P<0.05$) PNUE than those grown with high N and low P. *M. ferruginea* had significantly higher ($P<0.01$) PNUE compared to all the other species under all treatment conditions. The combined effect of soil N and P significantly reduced ($P<0.01$) the PNUE in *C. macrostachyus* compared to those of all the other species.

Table 5.3 Mean (\pm SE) photosynthetic nitrogen use efficiency ($\mu\text{mol CO}_2$ ($\text{mol [N]} \text{ s}^{-1}$)) of seedlings of four tree species grown with high or low soil N and P applications. Significant *P*-values for variations within species are shown in rows (one-way ANOVA) and those for N, P and interactions between N and P (factorial ANOVA) are shown in the right hand columns. Mean values within a column followed by different letters are significantly different ($P<0.05$) according to Tukey's test

Species	Low N		High N		<i>P</i> -values		
	Low P	High P	Low P	High P	N	P	N*P
<i>C. africana</i>	55.4 \pm 1.43b	71.6 \pm 2.10b	56.7 \pm 1.6bc	71.0 \pm 0.87b	.820	.000	.540
<i>C. macrostachyus</i>	26.0 \pm 1.49d	64.8 \pm 2.45b	50.1 \pm 1.70bc	61.9 \pm 1.19bc	.000	.000	.000
<i>E. camaldulensis</i>	38.4 \pm 1.64c	69.2 \pm 1.13b	59.1 \pm 4.09b	51.0 \pm 0.84c	.589	.001	.000
<i>E. globulus</i>	53.3 \pm 2.58b	55.7 \pm 1.57c	46.1 \pm 2.69c	59.1 \pm 3.39bc	.529	.022	.087
<i>M. ferruginea</i>	77.7 \pm 3.38a	89.9 \pm 0.50a	96.1 \pm 2.10a	117.0 \pm 5.61a	.000	.001	.246
<i>P</i> -value	0.000	0.000	0.000	0.000			

5.4 Discussion

The present study showed that the availability of soil N and P has a direct effect on growth performance of seedlings of the study species. Both N and P deficiencies resulted in lower photosynthetic rate and WUE_{GE} of all the studied species, although P had much less effect than N. Several studies have shown that N and P stresses reduce the photosynthetic capacity of various plant species (Wong *et al.*, 1985; Fredeen *et al.*, 1991, Evans, 1996; Lambers *et al.*, 1998; Lu and Zhang, 2000). The significant effects of N and P on the photosynthetic rate of all the species studied were due to the requirement of these nutrients in the major biochemical processes of plant growth including enzymatic activities, energy transfer and structural contribution to nucleic acids (Marschner, 1995).

The strong limitation of soil N stress on photosynthesis could be due to the role of N in the synthesis of major components of the photosynthetic apparatus. Nitrogen stress is reported to reduce the chlorophyll content in maize (Lu and Zhang, 2000). Both N and P deficiencies result in the simultaneous reduction of maximum photosynthetic rate and Rubisco activities (Fredeen *et al.*, 1989, 1991; Evans, 1996; Lambers *et al.*, 1998).

Under N stress, stomatal conductance declines synchronously with the photosynthetic capacity so that carbon gain per water transpired is relatively stable (Evans, 1996). In this study, however, the N stressed plants could not maintain their WUE_{GE} at a comparable rate with those under sufficient N supply. The main reason may be that stomatal conductance and transpiration rate were not as responsive as photosynthetic rate to N deficiency. For instance, the stomatal conductance of *C. africana* was not significantly affected by N treatment. Therefore, for *C. africana* the effect of N deficiency may be more influential on reducing the carboxylation efficiency than reducing the entry of CO_2 through

stomata. In fact the internal CO₂ concentration in leaves of *C. africana* under N stress was about twice that for unstressed leaves (data not presented). Rao and Terry (2000) indicated that although stomata may remain open under nutrient stress, mesophyll conductance might be reduced because of a reduced carboxylation efficiency resulting in high internal CO₂ concentration. In the current study, stomatal conductance was probably maintained in the low N and P to reduce leaf temperature by dissipating heat through transpiration, although the CO₂ assimilation capacity of the leaf was restricted due to the N and P deficiency. Compared to plants treated with low N, those treated with high N had much higher WUE_{GE}. The result of this study concurs with that of Fredeen *et al.* (1991) who reported a decreasing ratio of carbon gain to water loss with N stress for sunflower under dry summer day condition in the field. The authors indicated that under limited availability of N, stomata might open further, causing high photosynthetic nitrogen use efficiency (PNUE) at the expense of WUE_{GE}. This may be the case for *C. africana* in which the WUE_{GE} of N limited plants was significantly reduced because of open stomata directed to maintain high PNUE. In this species no significant differences in stomatal conductance (Table 5.1) and PNUE (Table 5.3) were observed between N-limited and unlimited plants.

The reason why the stomatal conductances of the two *Eucalyptus* spp. were reduced by the increased supply of P both in the low and high N groups (Table 5.1) was not clear. Perhaps, it may indicate the elasticity of the eucalypts to maintain gas exchange over a wide range of soil P without any significant effect on the photosynthetic rate (Table 5.1) and light saturated photosynthetic rate (A_{max}) (Fig. 5.2d).

A study on the carbon allocation of soybean plants revealed that the effect of low P on the photosynthetic rate was moderate (Fredeen *et al.*, 1989). Unlike N, P plays a

regulatory role in photosynthesis (Lambers *et al.*, 1998). The low photosynthetic rate of plants grown under low P supply may reflect a feedback inhibition due to slow growth and low concentration of inorganic phosphate in the cytosol or low concentration of Rubisco and other photosynthetic enzymes (Rao and Terry, 2000). Consequently, the partitioning of the products of photosynthesis between export to the cytosol versus storage in the chloroplasts is largely determined by the availability of phosphorus in the cytosol (Lambers *et al.*, 1998). Unlike N deficiency that reduces the amount of thylakoid and Rubisco proteins, P deficiency affects specific proteins (Lambers *et al.*, 1998). With P deficiency, low photosynthetic rate is matched by a lower activation state and slightly lower Rubisco content (Brooks, 1986).

Photosynthesis responds to irradiance in a curvilinear manner, with the light saturated rate depending on the photosynthetic capacity of the leaf (Prioul and Chartier, 1977; Sage *et al.*, 1990; Lambers *et al.*, 1998). In the current study (Fig. 5.2), because the entire photosynthetic process had been suppressed by the deficiencies of N and P and the leaves could not utilize the intercepted light. The effect of soil N deficiency was more suppressive to Φ and A_{max} than that of soil P deficiency. According to Evans (1996) the photosynthetic potential of leaves is determined by the amount of protein (organic N) per unit leaf area suggesting that photosynthesis is strongly related to leaf N. However, the magnitude of the effect of soil P was higher in the deciduous species compared to the eucalyptus.

Earlier studies also indicated that nitrogen deficiency strongly reduces the A_{max} of sunflower (Ciompi *et al.*, 1996), winter wheat (Shangguan *et al.*, 2000) and maize (Lu and Zhang, 2000). The reduced Φ and A_{max} of nitrogen deficient seedlings could be due to a

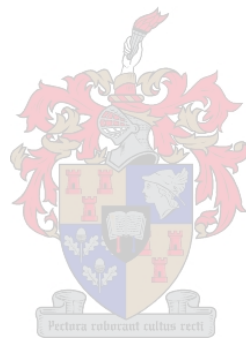
decreased concentration and/or activity of Rubisco. The inhibition of Rubisco results in photosynthetic energy consumption in the Calvin cycle (Evans, 1996; Lambers *et al.*, 1998).

Significantly strong relationships were observed between foliar N concentrations and photosynthetic rates of all the studied species (Fig. 5.3). A strong direct relationship between foliar N content and photosynthetic rate (Evans and Terashima, 1987) and Rubisco activity (Evans, 1983) had also been reported for other species. Although soil N supply had significant effect on foliar N concentration, direct effect of soil N on PNUE was not observed except in *M. ferruginea* and *C. macrostachyus* in the current study (Table 5.2). The presence of a strong linear relationship between PNUE and SLA has been well described by Poorter and Evans (1998) and Eamus and Prior (2001). In the current study as well, *M. ferruginea* with high SLA (Chapter 2) had significantly higher PNUE than all the other species. Although increased soil N and P increased the PNUE in *M. ferruginea*, the higher PNUE of the species observed under all treatment conditions compared to all the other species may be a genetic capacity of the species.

5.5 Conclusion

Soil N stress resulted in an overall reduction of gas exchange capacities including photosynthetic rate, stomatal conductance and WUE_{GE} of all the species studied. Owing to the strong relationship between leaf N concentration and its photosynthetic rate, N deficiency reduced the maximum photosynthetic capacities of all the studied species. Thus, soil N controlled foliar N content, which further governed the capacity of the leaf to fix CO_2 . The effect of soil P on the photosynthetic rate was moderate compared to that of N in

all the species examined. It did not affect the photosynthetic rate of *E. globulus* and the stomatal conductance of the deciduous species. No direct effect of soil N on PNUE was observed in the current study except in *M. ferruginea* and *C. macrostachyus*. The observed higher PNUE in *M. ferruginea* compared to all the other species may be a genetic trait because it was observed under all treatment conditions.



6. ROOT DISTRIBUTION OF ISOLATED TREES AND THEIR EFFECT ON SOIL FERTILITY IN THE AGRICULTURAL SETTING IN BADESSA, EASTERN ETHIOPIA

Abstract

The fine root distribution of isolated *C. africana*, *C. macrostachyus* and *Faidherbia albida* (Del.) A. Chev. trees, their foliar nutrient composition and effects on soil fertility parameters were investigated in Badessa, Eastern Ethiopia. Surface (0-15 cm) and subsurface (30 –45 cm) soil samples were collected from under the canopy, edge of the canopy and three times the radius of the canopy away from the sample trees. Roots were collected from a trench at the edge of canopies at five vertical distances. Trees of the three species improved soil nitrogen (N), available phosphorus (P) and exchangeable potassium (K^+) under their canopies compared to the corresponding soils away from their canopies. Surface soils had significantly higher ($P < 0.05$) N, P and K^+ than the corresponding subsurface soils. The P composition of the surface soils under the canopies of *F. albida* and *C. macrostachyus* was more than double that for *C. africana*. Furthermore, N was highly enriched under *F. albida* than under *C. africana* and *C. macrostachyus*. Species comparison for K^+ showed no significant differences. The isolated trees of all species had no significant influence on the horizontal and vertical abundance or values of soil pH, cation exchange capacity and exchangeable calcium and magnesium. The foliar N of *C. africana* and *C. macrostachyus* was less than half that for *F. albida*, due to the nitrogen fixing ability of the latter. Typically higher fine root biomass was observed in the surface samples than the subsurface samples. Fine root biomass of all species showed a steady decrease with increasing depth at the edge of the canopies. *C. macrostachyus* had significantly higher ($P < 0.05$) fine root biomass than *F. albida* at all vertical and horizontal distances. Although the presence of numerous roots in the crop zone entails the existence of competition between trees and crops, the three tree species improved the under-canopy soil nutrient pool. Owing to its low root biomass in the crop zone, high foliar nutrient composition and outstanding contribution to under-canopy soil N and P, *F. albida* is the most beneficial agroforestry species compared to *C. africana* and *C. macrostachyus*.

6.1 Introduction

In areas like Badessa, Ethiopia, where people depend fully on biomass for household energy and construction, the role of trees on the well-being of the people is immense. In an effort to get the greatest possible return from their piece of land, farmers of Badessa area practice a mixed farming system (Fig. 1.3). Due to the shortage of wood for construction and fuel, some farming households established their own eucalyptus woodlots for short rotation (Poschen, 1987, Fig. 1.2). However, it has been well documented that short rotations of eucalypts are damaging to the site especially when coupled with the removal of surface litter for fuel (e.g., Florence, 1996). In addition, eucalypts are not suitable for mixed farming/agroforestry systems due to their negative impacts on crops (Lisanework and Michensen, 1993). Unlike the eucalypts, several deciduous indigenous tree species have been maintained and managed on croplands in Ethiopia because of their services and products.

Among the major agroforestry tree species grown in Badessa area (Eastern Ethiopia) *C. africana*, *C. macrostachyus* and *Faidherbia albida* (Del.) A. Chev. are the most abundant (Fig. 1.4). Elsewhere in Ethiopia as well, these species were proven to be promising agroforestry species (Poschen, 1986 and 1987; Demel and Aseffa, 1991; Kamara and Haque, 1992; EFAP, 1993; Jiregna, 1997; Yeshanew *et al.*, 1999; Abebe *et al.*, 2001). The distribution of these species in Ethiopia was reported by Thulin (1989); Gilbert (1995) and Legesse (1995). The biology, germination, propagation and uses of *C. africana* and *F. albida* have been discussed by Legesse (1995). In addition, positive effects of *C. macrostachyus* and *C. africana* on soil physical and chemical properties were reported (Jiregna, 1997; Yeshanew *et al.*, 1999; Abebe *et al.*, 2001).

In mixed agroforestry systems where trees and crops grow in combination (e.g. Fig. 1.3), various types of interactions take place between the associates (Nair, 1993; Van Noordwijk *et al.*, 1996; Young, 1997) at the tree-crop interface. Several agroforestry trees have been reported to improve soil fertility parameters mainly because their leaf and root litter contribute to the maintenance and replenishment of soil fertility (Nair, 1993; Mwiinga *et al.*, 1994; Young, 1997). However, tree roots are also agents of the competition between trees and crops. According to Van Noordwijk *et al.* (1996), a tree with a deep root system having limited lateral extension in the surface soil, hence without much interference with the crop root system, is ideal from a nutrient cycling perspective. Root distribution is an important parameter to evaluate the suitability of any tree species for agroforestry, especially when trees and crops grow on the same land management unit. Therefore, the re-examination of the existing farming system, especially the role of trees in terms of root distribution, and some nutrient cycling potentials is imperative as far as intensified mixed agriculture/agroforestry is concerned. Because the contribution of foliar litter to the agriculturally important surface layers of soils is higher compared to that of root litter in trees, emphasis was given to foliar litter.

The objectives of the study were 1) to assess the root distribution of *C. africana*, *C. macrostachyus* and *F. albida* in the soils under the tree canopies and away from canopies, 2) to investigate the effects of *C. africana*, *C. macrostachyus* and *F. albida* on soil fertility parameters, and 3) to investigate the nutrient content of the leaves of these species in the Badessa area.

6.2 Material and Methods

6.2.1 Study area

The study was carried out on farmers' plots in two peasant associations: Oda Muda and Kara, in Kuni District, West Harerghe, Ethiopia. Kuni, commonly called Badessa, is situated at 8° 52' N and 40° 40' E (Fig. 6.1). Badessa is situated at an elevation of 1740 m above sea level. The minimum and maximum temperature of the area range from 9 - 14°C and 25 - 30°C, respectively. The rainfall is bimodal with small intermittent rain in spring and heavy rain in autumn (Fig. 6.2). The average annual rainfall is 1190 mm. In general sedimentary rocks were the parent rocks of Badessa area, though igneous rocks contributed in some areas (Murphy, 1968). Three major soil types, i.e., chromic and vertic luvisols and chromic vertisols occupy the largest proportion of the area (Murphy, 1968; EMA, 1981). The soils are generally clay with 55 - 60% clay, 12 - 15% silt and 25 - 30% sand. Soil color ranges from reddish brown on hillsides to dark brown at the low-lying areas.

The mixed farming system (agroforestry system) composed of annual crops, perennial crops, trees and livestock is the dominant farming system in the district (Fig 1.3). The major agroforestry practices include: shade trees on crop lands (e.g. Fig. 1.4), woodlots mainly of eucalypts (e.g. Fig. 1.2), boundary and road side planting of eucalypts and shrubs suitable for fencing, home gardens composed of various fruit trees, chat (*Catha edulis* L.) and coffee (*Coffea arabica* L.), separately or combined with shade trees, and alley cropping of chat with various crops.



Figure 6.1 Map of Ethiopia showing the field study site in Badessa area.

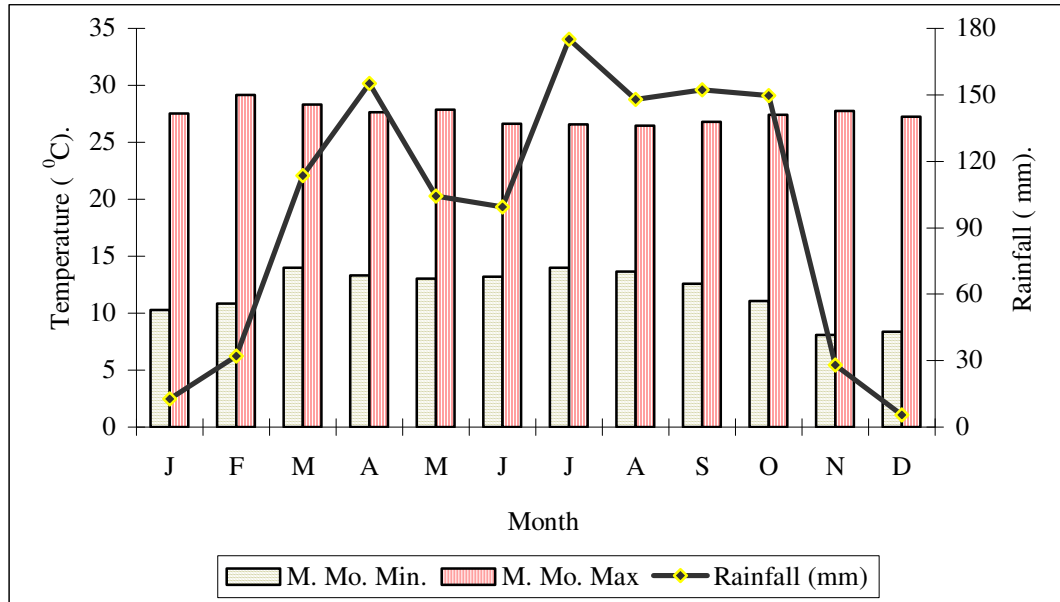


Figure 6.2 Average monthly maximum and minimum air temperatures and rainfall of Badessa area (1990 - 2001).

Individual *C. africana*, *C. macrostachyus* and *F. albida* trees were considered as replicates. Eighteen isolated trees (six for each species) of about 25 –40 years old were selected for the study. All the six *F. albida* trees were from Kara because those in Oda Muda were associated with perennial crops and were not suitable for sampling. For *C. africana* and *C. macrostachyus* three trees each from Kara and Oda Muda were selected. The average diameter at breast height, height and crown diameter were 62.8 cm, 15 m and 10.2 m for *C. africana*; 34.8 cm, 9.7 m and 7.4 m for *C. macrostachyus* and 81.3 cm, 16.9 m and 17.3 m for *F. albida*, respectively. No significant differences in soil nutrients were observed between Kara and Oda Muda except that soils at Kara had higher ($P < 0.05$) exchangeable K^+ and Ca^{2+} than those at Oda Muda. The plots used for the assessment did not have any history of fertilizer amendments. At sampling, the area was covered with four

weeks old maize. Isolated trees with similar maize cover both under the canopy and away from the canopy were selected.

6.2.2 Soil and root sampling

Sampling transects were laid in three directions from the tree base (at an angle of about 120°). Soil sampling plots were laid along the transects at three distances: half of the canopy radius under the tree, canopy edge or radius of the canopy and at three times canopy radius away from the trunk. At each distance soils were sampled from two depths: 0-15 cm (surface) and 30-45 cm (subsurface). The former depth represented the tillage zone and crop roots, while the latter depth represented a zone beyond tillage (or hoeing) and less crop roots. At each distance a pit of 30 cm wide and 50 cm deep was dug for soil sampling.

Three sets of soil samples were collected at each sampling spot, i.e., the first set for bulk density, the second set for root biomass and the third set for chemical analysis. A cylindrical soil corer of 5 cm internal diameter was used for sampling the former two sets. For the set of samples used for bulk density, the soil was taken to the laboratory; oven dried at 105°C for 24 h and dry weight was taken. Bulk density (g cm^{-3}) was calculated as the weight of the corer content divided by the corer volume.

A 300 cm long and 120 cm deep trench was opened on one side of the canopy to investigate the vertical fine root distribution at the edge of the tree canopy. The trench was laid perpendicular to the direction of the main lateral root(s) from tree bases. The trench profile was divided into five layers: 1) 0-15 cm, 2) 15-30 cm 3) 30-45 cm, 4) 55-70 cm and 5) 85-100 cm. Two sets of samples (each with three replications) were collected from each

layer – one set for bulk density and the other for fine root distribution following the same procedure as described above.

6.2.3 Root distribution

The sample collected for root biomass was soaked in 500 ml water in a beaker overnight to separate roots from soil. Soil lumps were broken by stirring the soil-water- mixture after which the roots tended to float while larger soil particles tended to settle. The suspension containing roots was then wet sieved through a 2 mm diameter mesh to remove debris. Roots of herbs, crops and dead roots were sorted and removed using hand forceps. Visual judgment based on their brittleness, color and resilience was employed to distinguish tree roots from others. Dead roots were grayish and break easily when manipulated. Roots of diameter less than 2 mm were considered fine roots. Root diameter was sorted using root caliper. Fine root length was determined using the intersection method described by Anderson and Ingram (1993) and van Noordwijk *et al.* (1996). Following the determination of total fine root length, samples were oven-dried at 105°C for 24 hours to determine fine root dry weight. Both fine root length and weight were expressed in terms of the volume of soil as fine root length density (RLD, cm. cm⁻³) and fine root weight density (RWD, g.cm⁻³).

6.2.4 Soil analysis

Samples from the same distance and depth under each tree were merged to form a composite sample for chemical analysis. All soil samples were analyzed following standard procedures described by Anderson and Ingram (1993) and Rowell (1994). Total soil

organic carbon (OC) was determined by the dichromate oxidation method; total soil nitrogen (N) was determined using the Kjeldahl method. Available phosphorus (P) was determined by following the Olson method. The ammonium acetate extraction procedure was employed to determine exchangeable basic cations (Ca^{2+} , Mg^{2+} , K^+ and Na^+) and cation exchange capacity (CEC) of the soil. Exchangeable potassium (K^+) and sodium (Na^+) were determined using a flame photometer. Exchangeable calcium (Ca^{2+}) and magnesium (Mg^{2+}) were determined using an atomic absorption spectrophotometer. Soil pH was determined using a pH meter.

6.2.5 Leaf sampling and analysis

Small branches of the sample trees were removed from both the upper and lower parts of the tree crown for leaf collection. Fully expanded leaves were removed from the cut branches and evenly mixed to form 2 kg of fresh leaves per sample tree. After sun drying, leaf samples were oven dried at 85°C for 48 h. Samples were then ground and analyzed for nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na) following standard methods described by Anderson and Ingram (1993) and Rowell (1994). N was determined using the standard Kjeldahl method. After digestion with sulfuric acid and hydrogen peroxide, P was determined colorimetrically using a spectrophotometer, K and Na were determined using a flame photometer and Ca and Mg were determined using an atomic absorption spectrophotometer.

6.2.6 Statistical Analysis

All statistical computations were made using SPSS for Windows Version 11.0. Factorial ANOVA was employed to test variations between species, distance and depth for the

measured parameters. When significant differences were observed, Tukey's HSD test was used for mean comparison. Pearson's correlation coefficients were used to determine the degree of association between various parameters.

6.3 Results

6.3.1 Foliar nutrient composition

Foliar nitrogen (N) concentration of the three studied species ranged between 1.03 and 4.82% (Table 6.1). Leaves of *F. albida* had more than twice N concentration but significantly lower ($P < 0.05$) Ca and Na concentrations compared to those of *C. africana* and *C. macrostachyus*. Leaves of all the studied species had comparable P and K while *C. macrostachyus* leaves had about twice as much Mg as *C. africana* and *F. albida*. The foliar N:P ratios of *C. africana* and *C. macrostachyus* were less than half that for *F. albida* (data not presented).

Table 6.1 Mean (\pm SE) foliar nutrient concentrations and of three tree species from Badessa. Significant *P*-values (ANOVA) show variations in foliar nutrient concentrations among species. Mean values in same column followed by different letters are significantly ($P < 0.05$) different ($n = 3$).

Species	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Na (%)
<i>C. africana</i>	1.29 \pm 0.07 b	0.19 \pm 0.01 a	1.15 \pm 0.11 a	0.46 \pm 0.07 a	0.34 \pm 0.03 b	0.24 \pm 0.01 a
<i>C. macrostachyus</i>	1.29 \pm 0.06 b	0.24 \pm 0.02 a	0.87 \pm 0.07 a	0.41 \pm 0.05 a	0.63 \pm 0.04 a	0.25 \pm 0.011 a
<i>F. albida</i>	4.32 \pm 0.22 a	0.23 \pm 0.02 a	0.96 \pm 0.09 a	0.28 \pm 0.04 b	0.28 \pm 0.00 b	0.16 \pm 0.00 b
<i>P-value</i>	0.000	0.059	0.115	0.084	0.000	0.000

6.3.2 Root distribution

6.3.2.1 Horizontal distribution

Trees of all species extend their fine roots to at least three times their crown radius. The RLD in the surface soil was 75% - 200% higher than at the subsurface for all distances except under the *C. africana* canopy (Figs 6.3a, b).

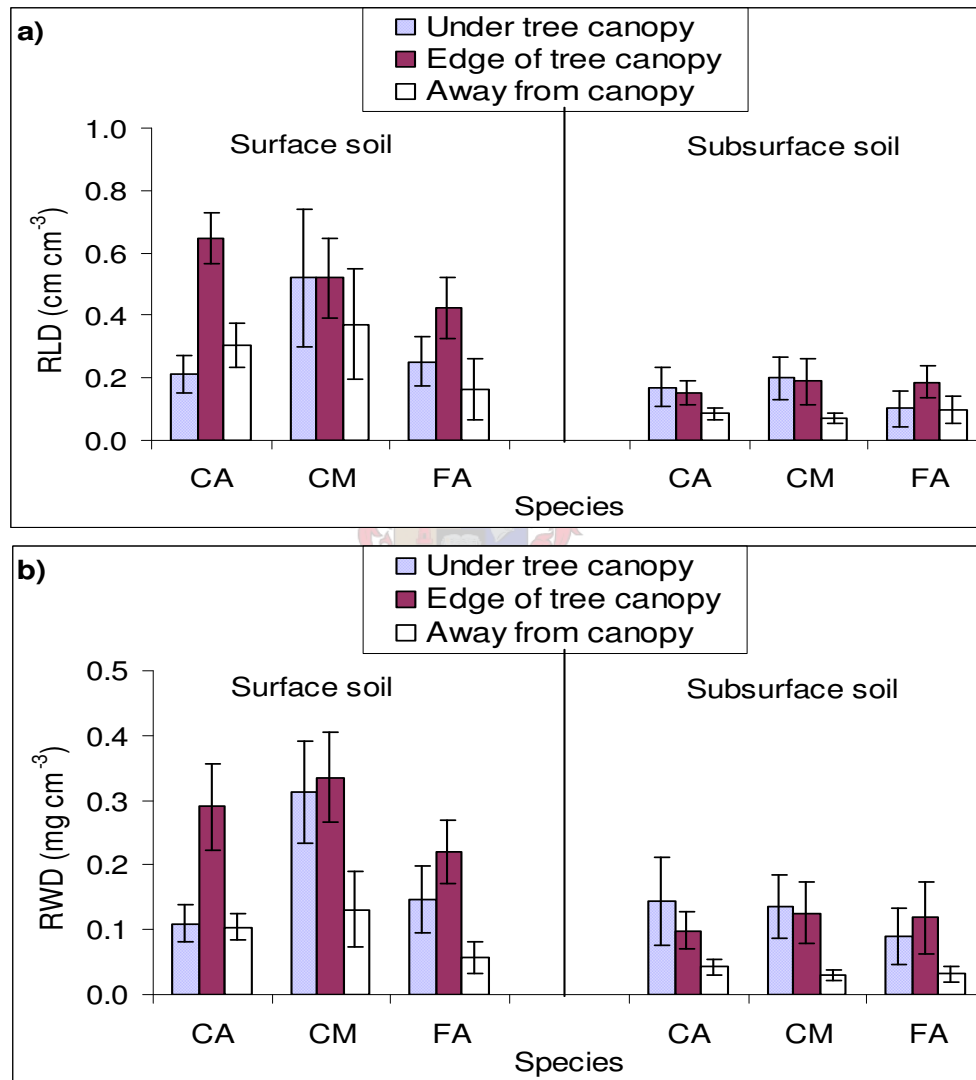


Figure 6.3 Mean a) RLD and b) RWD in the surface (0 – 15 cm) and subsurface (30 – 45 cm) soils from under and away from canopies of isolated *C. africana* (CA), *C. macrostachyus* (CM) and *F. albida* (FA) trees on croplands in Badessa. Vertical bars indicate standard errors of the means (n = 6).

ANOVA (Table 6.2) for mean RWD indicated a significant difference ($P < 0.01$) between the surface and subsurface layers for the three species. Significant ($P < 0.001$) distance and depth interactions were observed for both RLD and RWD only for *C. africana*. RWD of *F. albida* in the surface soil was higher at the canopy edge compared to under the canopy and away from the canopy ($P < 0.05$). Unlike for *C. africana* and *F. albida*, the RLD and RWD of *C. macrostachyus* did not show significant decline ($P > 0.05$) with increasing distance from the tree base to the open area (Table 6.2).

Table 6.2 P-values (ANOVA) showing the variations in RLD and RWD between three distances and two depths for isolated trees of *C. africana*, *C. macrostachyus* and *F. albida* in Badessa.

Source	<i>C. africana</i>		<i>C. macrostachyus</i>		<i>F. albida</i>	
	RLD	RWD	RLD	RWD	RLD	RWD
(1) Distance	0.000	0.001	0.530	0.147	0.000	0.000
(2) Depth	0.000	0.000	0.000	0.000	0.000	0.000
1*2	0.000	0.003	0.895	0.885	0.058	0.156

6.3.2.2 Vertical distribution

The vertical distributions of roots of the study species were observed at the edges of the canopies of the trees to investigate the extent and depth of root extension beyond the influence of the tree canopies (Fig. 6.4a). The RLD of the three species varied significantly ($P < 0.01$) between soil layers. Comparison of mean RWD from the five vertical distances show that the upper profiles, i.e. 0-15 cm and 15-30 cm had significantly ($P < 0.05$) higher RWD than the deeper profiles layers, i.e. 55-70 cm and 85-100 cm (Fig. 6.4b).

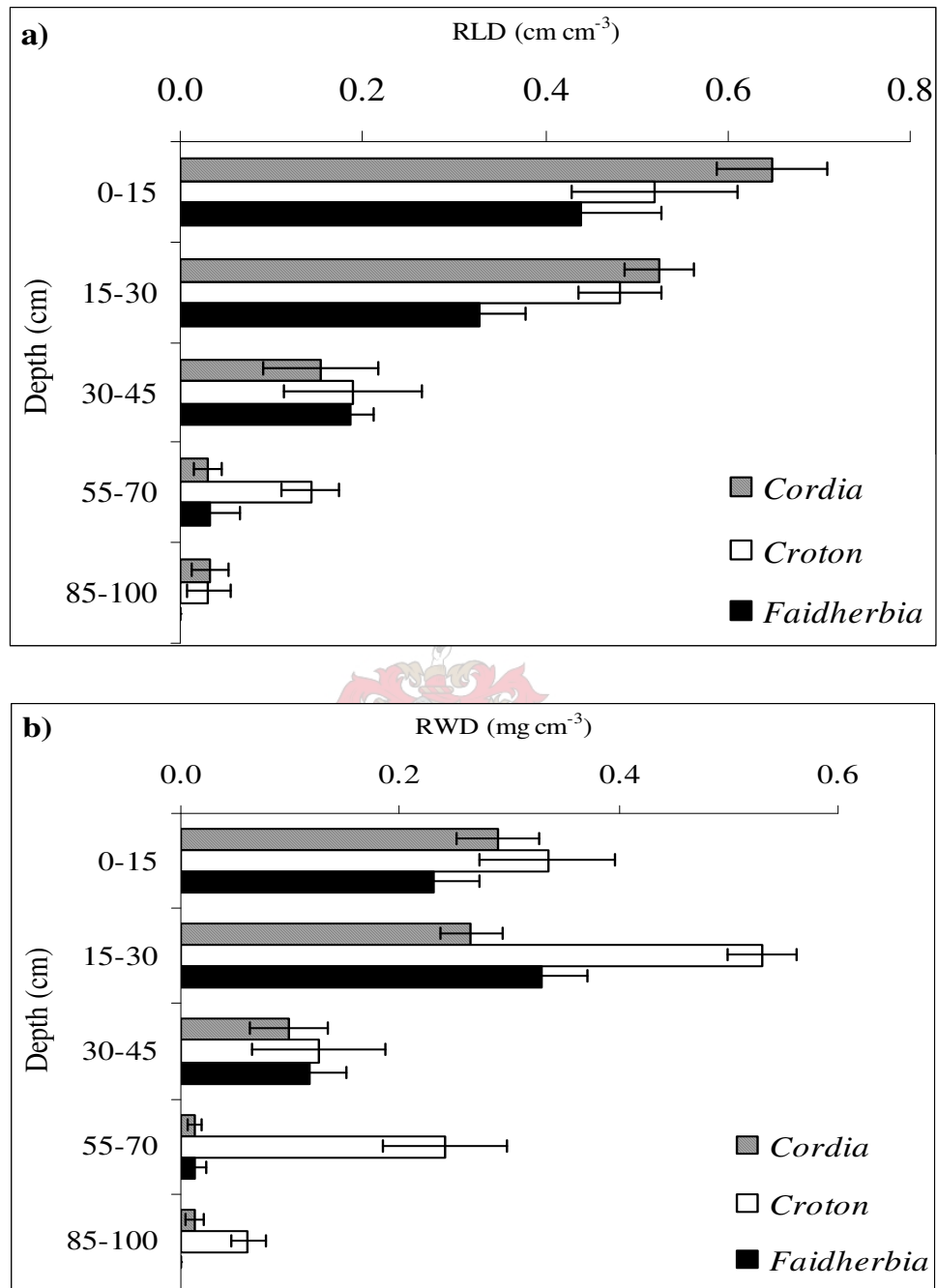


Figure 6.4 (a and b) Mean a) RLD and b) RWD of isolated *C. africana*, *C. macrostachyus* and *F. albida* trees with increasing soil depth at the edge of tree canopies in Badessa. Vertical bars indicate standard errors of the means (n = 18).

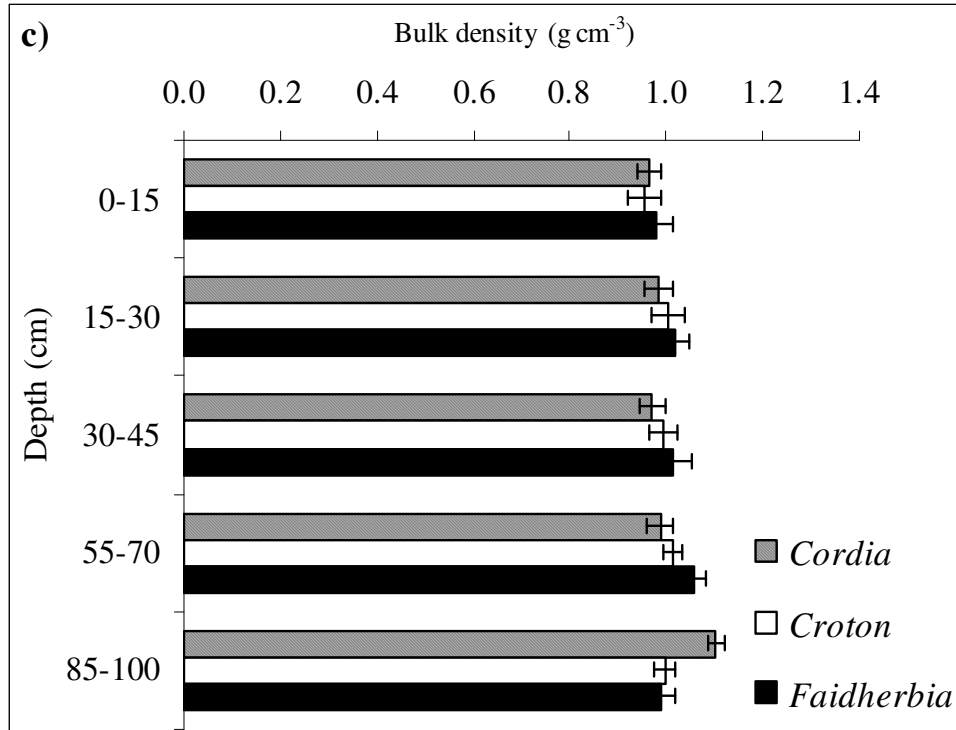


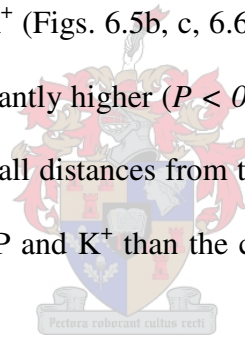
Figure 6.4 (c) Mean bulk densities of soils with increasing depth at the edges of isolated *C. africana*, *C. macrostachyus* and *F. albida* tree canopies in Badessa. Vertical bars indicate standard errors of the means (n = 18).

C. macrostachyus had significantly ($P < 0.05$) higher RWD at all depths compared to *C. africana* and *F. albida*. Furthermore, roots of *C. africana* and *C. macrostachyus* with diameter of up to 30 and 70 mm, respectively, were observed in the 30 and 70 cm depth. A significant correlation ($0.88 < r^2 < 0.93$, $P < 0.001$) was observed between RLD and RWD for each species. There was no significant variation ($P > 0.05$) in bulk densities between the different profile depths (Fig. 6.4c).

6.3.3 Effects of trees on soil

The presence of isolated trees on farms in Badessa area had no significant influence on the horizontal and vertical abundance or values of soil pH, Ca^{+2} , Mg^{+2} and CEC and (Figs 6.5d, 6.6b, 6.6c, 6.7a and Table 6.3). The surface soil OC under the three tree species was significantly higher ($P < 0.05$) than that at the subsurface soils, except for *F. albida* (Fig. 6.5a). However, no significant differences in OC were observed between distances both in the surface and subsurface profiles for all the studied species.

In plots under the canopies of all studied species had significantly higher ($P < 0.05$) N, P and K^+ than plots away from tree canopies both in the surface and subsurface profiles except for *F. albida* regarding K^+ (Figs. 6.5b, c, 6.6a and Table 6.3). The N concentrations in the surface soils were significantly higher ($P < 0.05$) than the immediate subsurface soil for *C. africana* and *F. albida* at all distances from the trees. Furthermore, surface soils had significantly higher ($P < 0.05$) P and K^+ than the corresponding subsurface profiles in all three species.



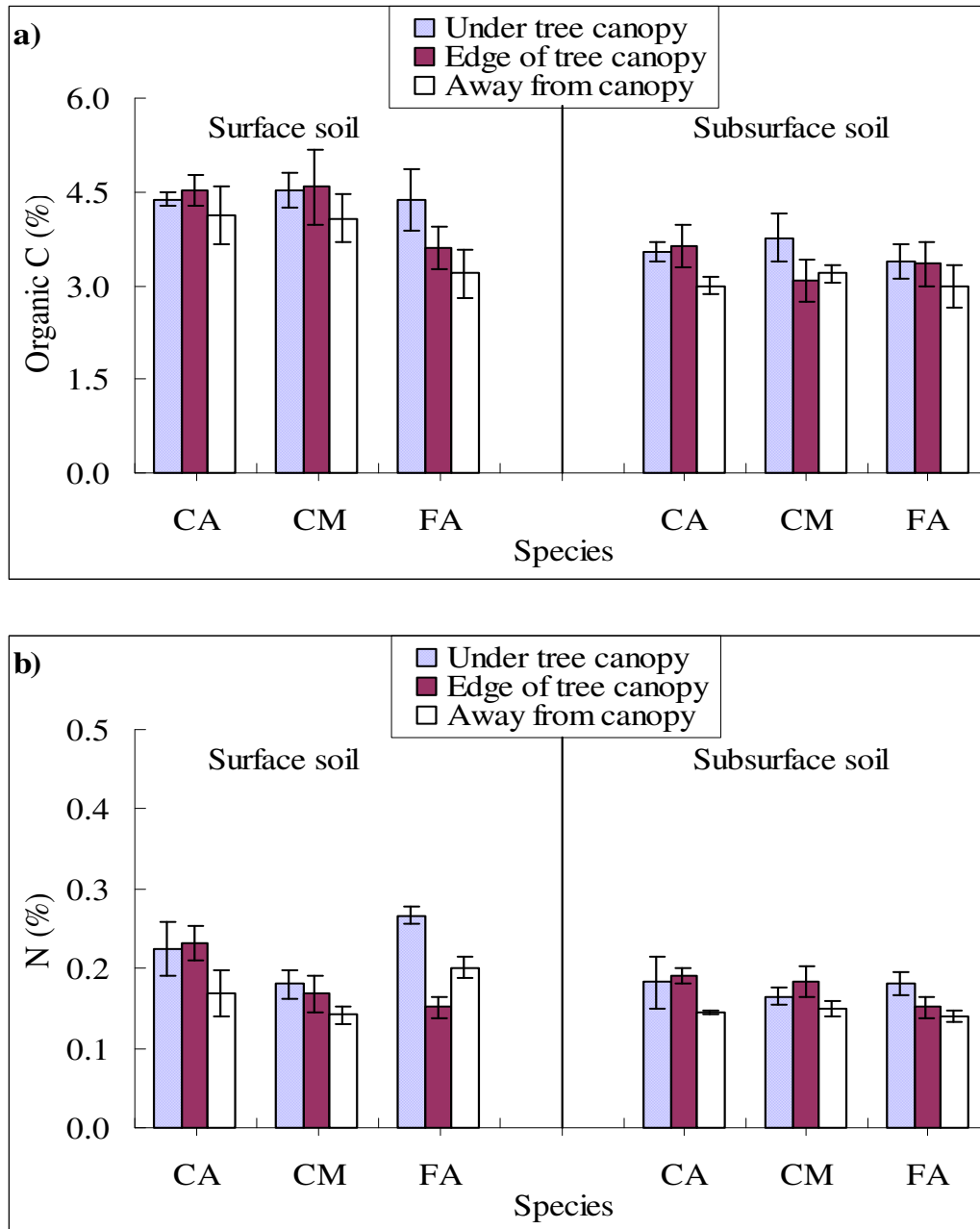


Figure 6.5 (a and b) Mean soil a) organic carbon and b) total nitrogen in the surface (0-15 cm) and subsurface (30-45 cm) soils from under and away from canopies of isolated *C. africana* (CA), *C. macrostachyus* (CM) and *F. albida* (FA) trees on croplands in Badessa. Vertical bars indicate standard errors of the means (n = 6).

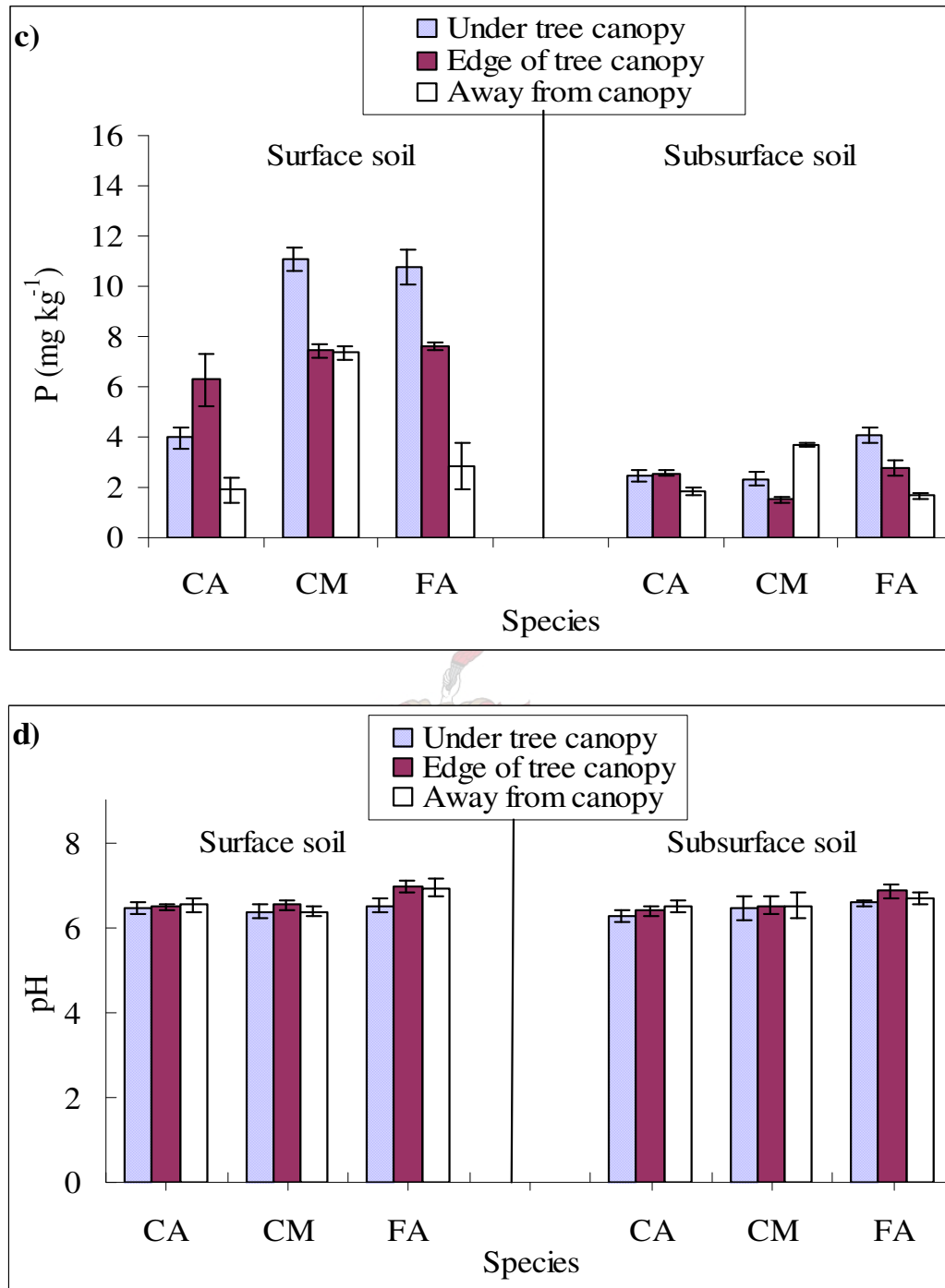


Figure 6.5 (c and d) Mean soil c) available phosphorus and d) pH in the surface (0-15 cm) and subsurface (30-45 cm) soils from under and away from canopies of isolated *C. africana* (CA), *C. macrostachyus* (CM) and *F. albida* (FA) trees on croplands in Badessa. Vertical bars indicate standard errors of the means (n = 6).

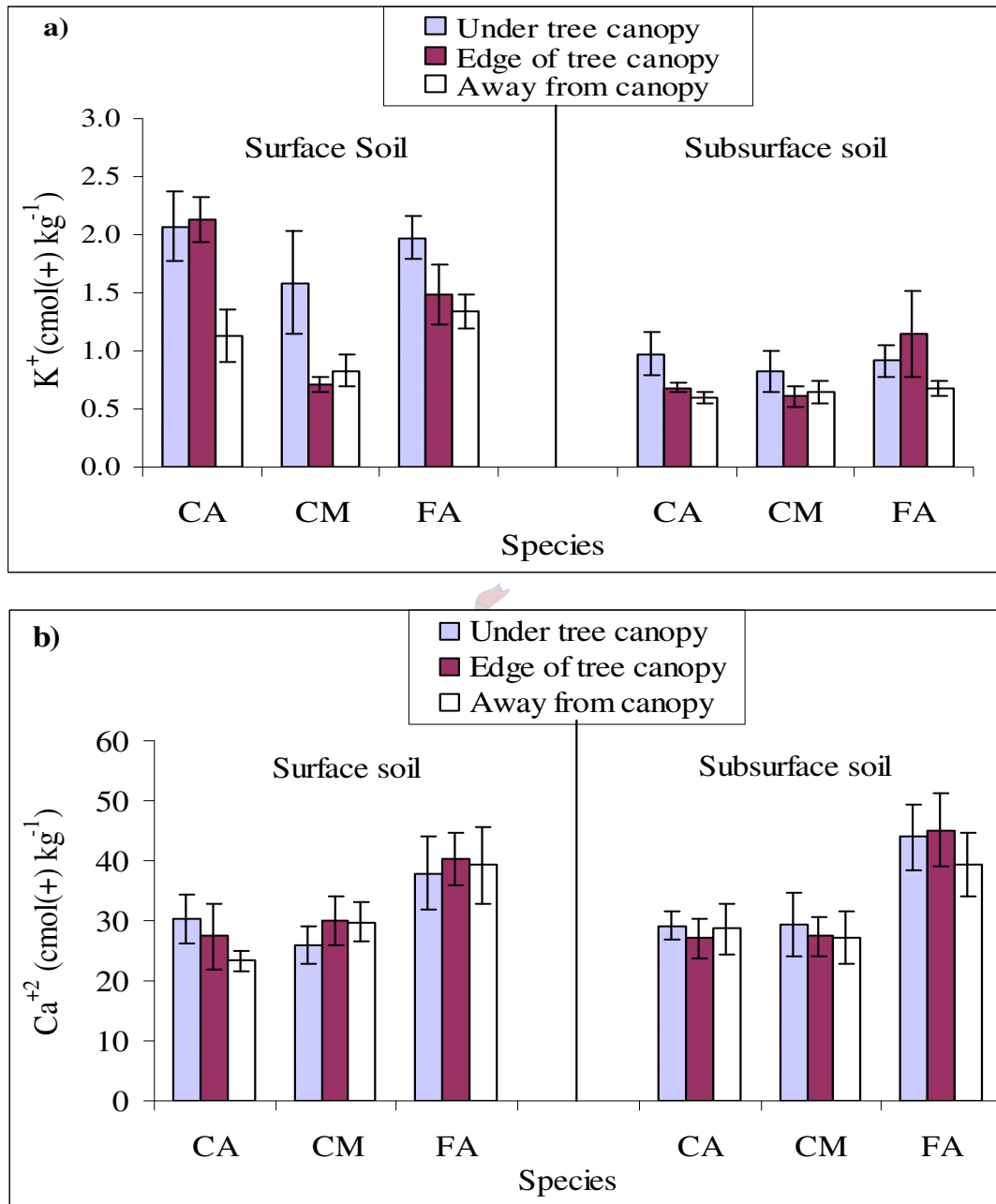


Figure 6.6 (a and b) Mean soil exchangeable a) K⁺ and b) Ca⁺² in the surface (0-15 cm) and sub-surface (30-45 cm) soils from under and away from canopies of isolated *C. africana* (CA), *C. macrostachyus* (CM) and *F. albida* (FA) trees on croplands in Badessa. Vertical bars indicate standard errors of the means (n = 6).

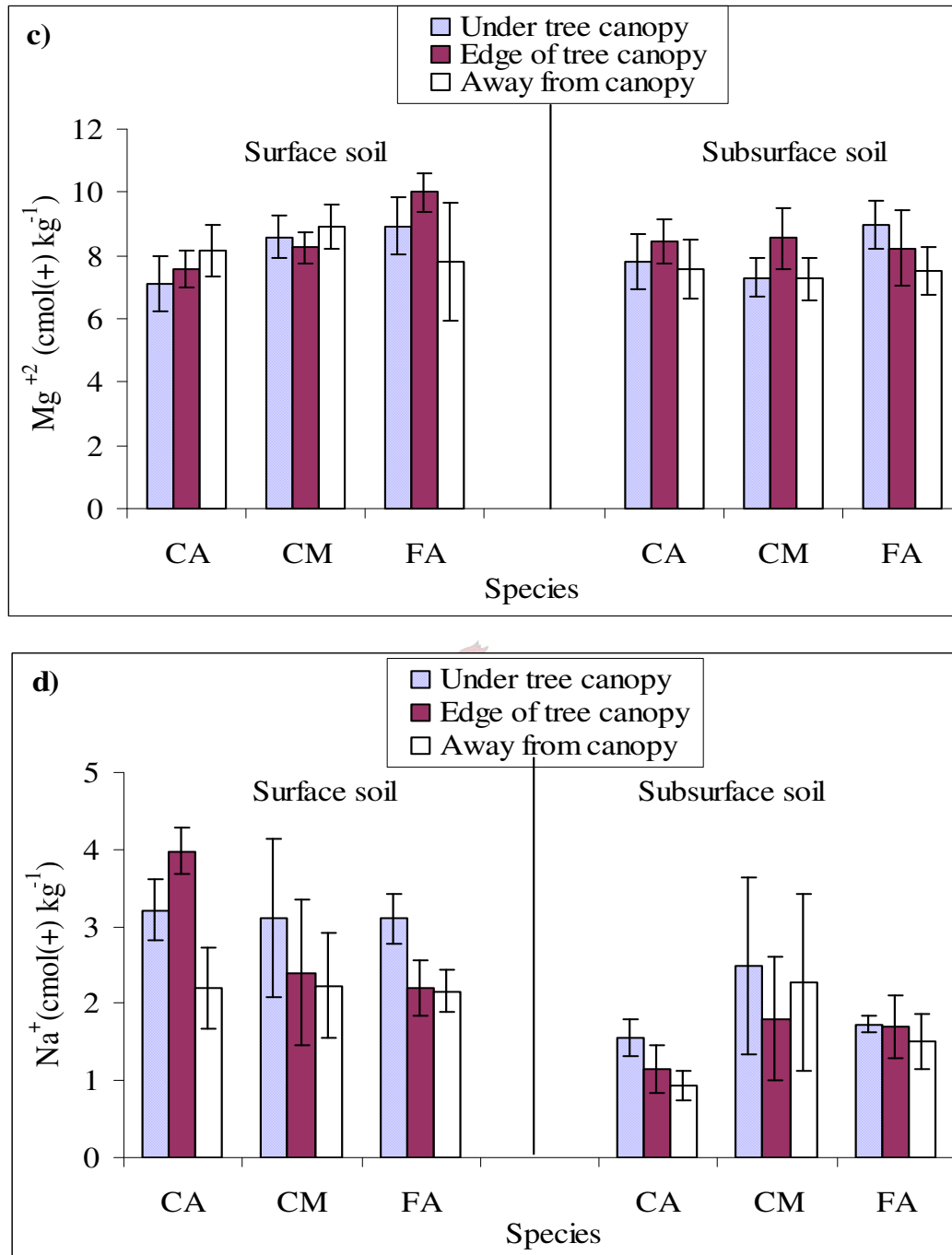


Figure 6.6 (c and d) Mean soil exchangeable c) Mg²⁺ and d) Na⁺ in the surface (0-15 cm) and sub-surface (30-45 cm) soils from under and away from canopies of isolated *C. africana* (CA), *C. macrostachyus* (CM) and *F. albida* (FA) trees on croplands in Badessa. Vertical bars indicate standard errors of the means (n = 6).

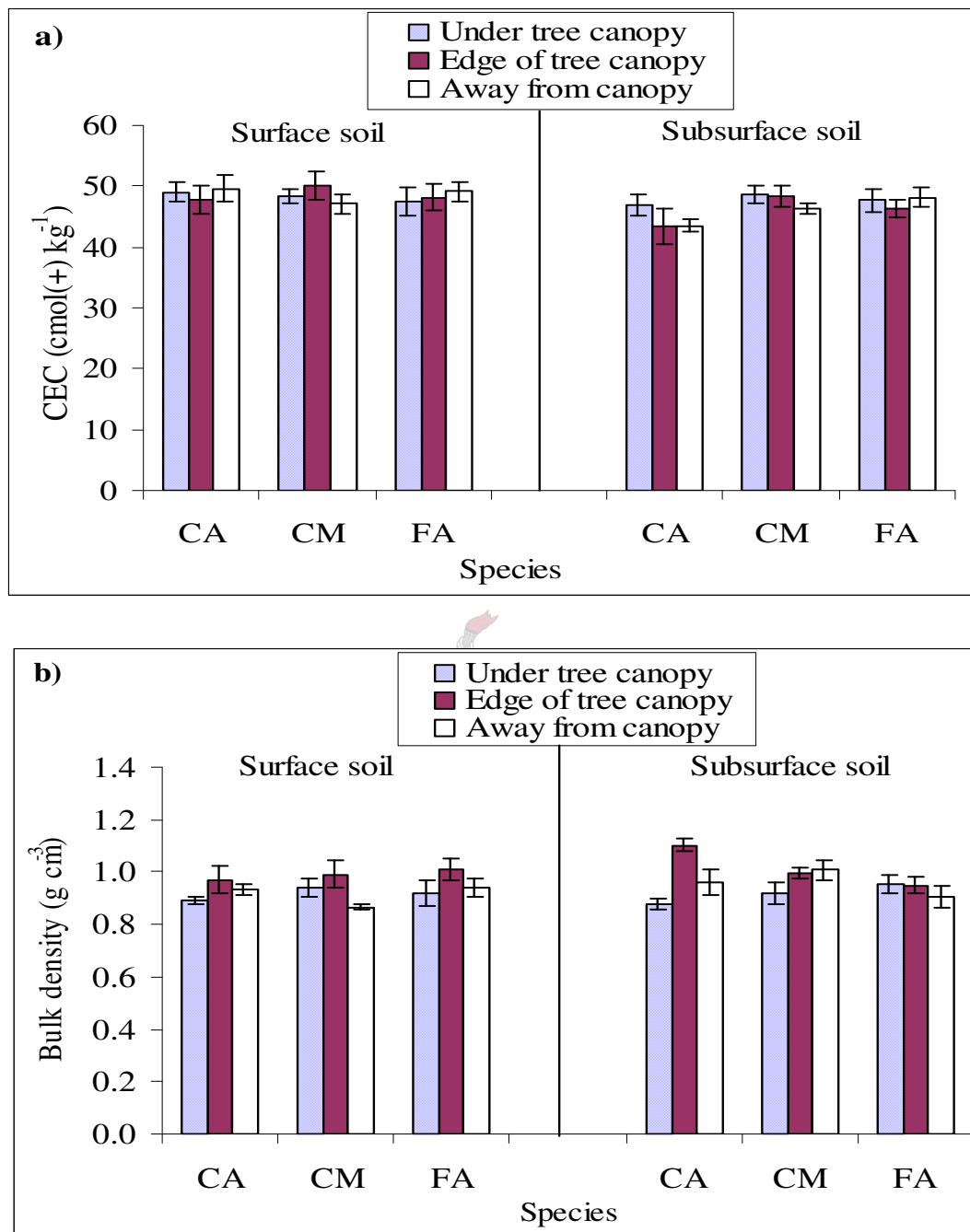


Figure 6.7 Mean soil a) CEC and b) bulk density in the surface (0-15 cm) and sub-surface (30-45 cm) soils from under and away from canopies of isolated *C. africana* (CA), *C. macrostachyus* (CM) and *F. albida* (FA) trees on croplands in Badessa. Vertical bars indicate standard errors of the means (n = 6).

The P composition of the surface soils under the canopies of *F. albida* and *C. macrostachyus* was more than double that for *C. africana*. Furthermore, N was significantly ($P < 0.05$) enriched under *F. albida* than under *C. africana* and *C. macrostachyus*. K^+ in the surface soils under all the species canopies was almost twice the amount in the immediate subsurface. Species comparison for K^+ showed no significant differences.

A significantly higher ($P < 0.05$) Na^+ was found in soils under *C. africana* trees compared to the corresponding plots away from trees both in the surface and subsurface profiles (Fig. 6.6d). Generally surface soils had lower bulk densities than subsurface soils and this was significant ($P < 0.05$) only at the edge of *C. africana* canopy and open area close to *C. macrostachyus* (Fig. 6.7). No difference in bulk density was observed between distances for all the species.



6.4 Discussion

6.4.1 Foliar and nutrient composition

The high N and N:P ratio observed in *F. albida* leaves compared to the other species (Table 6.1) was attributable to its nitrogen fixing ability. The foliar P, Mg and Na concentrations of *C. macrostachyus* found in the present study were higher than those reported by Jiregna (1997) from parkland in Wondo Genet area, Southern Ethiopia. Similarly, soil under *C. macrostachyus* had higher P, Mg and Na than those under *C. macrostachyus* in Wondo Genet indicating that soil nutrient status might govern the foliar nutrient concentration of the species (Chapter 2).

The high N in leaves of *F. albida* suggests that the species supplies quality litter for soil enrichment and animal fodder. Earlier studies support the desirability of *F. albida* in agroforestry systems due to its deep root system and less competitiveness with crops, nitrogen fixing ability, improvement of underneath soil and crop yield, provision of fodder and shade during the dry season and wide ecological adaptation (Poschen, 1986; Vandenbeldt, 1991; Kamara and Haque, 1992; Legesse, 1995; Rhoades, 1995; Young, 1997). The current investigation shows that P enrichment of *F. albida* in the underneath soil was relatively higher compared to N-enrichment (Figs 6.5b, c). The high litter decomposition rate leading to the mineralization of organic nitrogen (due to the high foliar N of the legumes (Palm, 1995)), could cause a loss of N from the system via volatilization, denitrification and leaching (Browaldh, 1995; Marschner, 1995) thus resulting in a reduced N accumulation under *F. albida*.

Foliar litter of *C. macrostachyus* was found to be fast decomposing compared to *Millettia ferruginea*, a leguminous species (Jiregna, 1997). Furthermore, the study reported that green and abscised leaves of *C. macrostachyus* decomposed and released 50% of their C, N, P, K within eight weeks of the onset of decomposition. According to Mwiinga *et al.* (1994), tree species with high nitrogen, phosphorous and potassium concentrations and high decomposition rates have a great potential as green manure for soil improvement.

Table 6.3 Summary of factorial ANOVA for the effects of isolated trees of *C. africana*, *C. macrostachyus* and *F. albida* on soil fertility parameters at three horizontal distances from the base of the trees and two depths at each distance in a traditional agroforestry system in Badessa, Eastern Ethiopia. Asterisks *, **, **** represent significance at $P \leq 0.05$, 0.01 and 0.001; ns = not significant at $P \leq 0.05$.

Species	Effect	OC (%)	Tot. N (%)	Av. P (mg kg ⁻¹)	Exchangeable cations (cmol(+) kg ⁻¹)				CEC (cmol (+) kg ⁻¹)	PH	BD (g cm ⁻³)
					K ⁺	Ca ⁺⁺	Mg ⁺⁺	Na ⁺			
<i>Cordia africana</i>	(1) Distance	ns	****	****	**	ns	ns	*	ns	ns	****
	(2) Depth	****	**	****	****	ns	ns	****	*	ns	*
	1*2	ns	ns	****	ns	ns	ns	ns	ns	ns	*
<i>Croton macrostachyus</i>	(1) Distance	ns	*	****	****	ns	ns	ns	ns	ns	ns
	(2) Depth	****	ns	****	**	ns	ns	ns	ns	ns	ns
	1*2	ns	ns	****	*	ns	ns	ns	ns	ns	ns
<i>Faidherbia albida</i>	(1) Distance	ns	****	****	ns	ns	ns	ns	ns	ns	ns
	(2) Depth	ns	****	****	**	ns	ns	**	ns	ns	ns
	1*2	ns	**	****	ns	ns	ns	ns	ns	ns	ns

6.4.2 Root distribution

Although the presence of tree roots in the crop root zone could contribute to the buildup of soil through decomposition, the presence of numerous roots in the crop zone also implies the presence of competition between trees and crops for moisture and nutrients during the growing season. Soils of Badessa area, like many tropical soils (Szott *et al.*, 1991; Mesfin,

1998), have less nutrient reserve in the subsoil making spatial separation of the rooting zone of crops and trees virtually impossible.

Farmers discourage the extension of tree roots in the surface soil whenever they come across tree roots during tillage and hoeing. But this is restricted to the visible roots and roots with large diameter. Due to root cutting, deep tillage and hoeing, root distribution in the cropping zone has been minimal. In the absence of those practices, much higher fine root mass and length could have been observed. Furthermore, areas nearby tree canopies that do not receive litter-fall but exploited by tree roots may be impoverished.

It is apparent that competition between trees and crops for soil resources is only seasonal and is restricted to the crop root zone. Nevertheless, tree root competitiveness is not a fixed characteristic of a species but could be influenced by tree management practices. The traditional tree management system in Badessa area involving seasonal shoot pruning and pollarding as well as root cutting may influence root development and the contribution of the trees to underneath soil. Schroth and Zech (1995) stated that intensive shoot pruning of a tree during the growing season would reduce root mass and length during crop development. Furthermore, these practices could affect the contributions of trees firstly because the woody branches are used for fencing, minor constructions and ultimately for fuel. Secondly, the foliar biomass of *C. africana* and *F. albida* are good sources of fodder for livestock due to which no sufficient leaf litter may be left for soil enrichment - only the leaves that fall naturally would return to the soil.

According to Van Noordwijk *et al.* (1996) and Young (1997), a tree with a deep root system and a limited lateral extension in the surface soil is ideal from a nutrient cycling perspective because it poses no interference with crop root system. Trees of the

study species produced lateral roots that could extend beyond the canopy zone both in the surface and subsurface profiles. Furthermore, less root mass and length was observed at deeper profiles (55-70 and 85-100 cm) indicating the occurrence of more root distribution in the surface profiles (0-15, 15-30 and 30-45 cm) in all the species (Figs 6.4a, b). Van Noordwijk, *et al.* (1996) summarized that root length densities of most crops, excluding deep-rooted trees, decreased with depth and with increasing distance from the plant in the horizontal direction. Among the three studied species, *C. macrostachyus* had higher root mass and length in the plots away from the trees (Fig. 6.3).

6.4.3 Effects of trees on soils

The buildup of nutrients under trees has been reported for various leguminous as well as a few non-leguminous trees and shrubs (Young, 1997). The result of the present study also supports previous findings that scattered trees of *C. africana* (Nyberg and Hogberg, 1995; Abebe *et al.*, 2001), *C. macrostachyus* (Jiregna, 1997; Yeshanew *et al.*, 1999) and *F. albida* (Kamara and Haque, 1992) improved underneath soil nutrient deposit compared to areas outside the influence of the trees. Because areas away from the sample trees (three times canopy radius) were exploited by tree roots but did not receive foliar litter input from the trees, the contribution of the trees to booting soil nutrients under their canopies compared to away from canopies might be exaggerated in the current study.

Due to the high clay content of the soil and to some extent high organic matter in the soil, the concentrations of both the monovalent and divalent cations were maintained at a relatively higher level. A similar study conducted in the Debrezeit area, central Ethiopia (Kamara and Haque, 1992), demonstrated that *F. albida* does not influence soil pH and

exchangeable Ca^{2+} and Mg^{2+} . However, investigations in other parts of Ethiopia, e.g Bako, central western Ethiopia (Abebe *et al.*, 2001) on *C. africana*, Wondo Genet, southern Ethiopia (Jiregna, 1997) on *C. macrostachyus*, and Bure-Adet, northwestern Ethiopia (Yeshanew *et al.*, 1999) on *C. macrostachyus*, indicated that these trees improved soil exchangeable Ca^{2+} and Mg^{2+} . However, the exchangeable Ca^{2+} and Mg^{2+} in these areas were lower than that found during the present study. The increased K^+ pool under canopies of *F. albida* is in agreement with the findings of Kamara and Haque (1992). However, exchangeable Na^+ was also found to be higher under *F. albida* trees compared to the plots away from canopies. The observed higher exchangeable Ca^{2+} under and away from *F. albida* canopy compared to those of *C. africana* and *C. macrostachyus* were due to the inherently higher Ca^{2+} composition of Karra soils compared to Oda Muda soils (Section 6.2.1). The isolated trees studied did not significantly influence the bulk densities of the soils under their canopies, except for the case at the edge of *C. africana* canopy. Although the bulk densities of the surface soils might be more influenced by the cultivation practices than by tree root and organic matter inputs, no variations were also observed between the surface and subsurface profiles. Lower bulk densities were observed under isolated *C. macrostachyus* (Jiregna, 1997; Yeshanew *et al.*, 1999) and *M. ferruginea* (Tadesse *et al.*, 2000) trees elsewhere in Ethiopia.

The present study confirmed previous findings regarding the contribution of dispersed *C. africana* (Nyberg and Hogberg, 1995; Abebe *et al.*, 2001) and *C. macrostachyus* (Yeshanew *et al.*, 1999) to the improvement of soil nitrogen and phosphorus compared to open areas in the immediate vicinity. Similar to earlier study in Wondo Genet area (Jiregna, 1997), higher N was recorded under dispersed *C.*

macrostachyus. The increased soil nutrient pool under the scattered trees could mainly be due to the foliar and root litter input from the trees. Although root litter production of trees could be high, the magnitude of the contribution of root litter to surface and subsurface soils may be low in deep rooting trees, like *F. albida*.

6.5 Conclusions

Due to its low root biomass in the crop zone, nitrogen-fixing ability, high foliar nutrient composition and outstanding contribution to underneath soil N and P, *F. albida* is the most beneficial agroforestry species compared to the other two species. Although the roots of *C. macrostachyus* and *C. africana* may interfere with crops grown under and close to their canopies, both species have improved the nutrient pool under their canopies.

Because of their role in maintaining soil fertility and their various products and services, the continued use of these species in the agricultural setting of Badessa and possibly other areas in the Ethiopian highlands where these trees grow naturally is recommended. For farmers with low cash income and cannot afford the cost of commercial fertilizer these trees would allow a significant soil nutrient supplement that could sustain the fertility of their land. Furthermore, with the availability of biomass for fuel, construction and fodder from the tree components, farmer could use crop residues and animal dung to replenish their croplands.

7. ROOT DISTRIBUTION AND EFFECTS OF *EUCALYPTUS CAMALDULENSIS* DEHNH. WOODLOT AND MIXED STAND ON SOIL FERTILITY IN BADESSA, EASTERN ETHIOPIA

Abstract

The growth, fine root distribution, and foliar nutrient composition of *Eucalyptus camaldulensis* woodlots and a mixed stand of four tree species and their effects on soil fertility in Badessa area, Eastern Ethiopia was studied. The mixed stand consisted of trees of *C. africana*, *Erythrina burana* Chiov., *M. ferruginea* and *Leucaena leucocephala* (Lam.) De Wit established as shade for coffee. The latter three species are legumes. Leaves of *E. camaldulensis* had lower nutrient concentrations than those of the other species. The legume species had about twice as much foliar N and N:P ratio than *C. africana* and *E. camaldulensis*. Both plantations improved the surface soil nutrient pool inside the plantations compared to the plots away from plantations. However, the pools of phosphorus and calcium inside the mixed plantation were generally higher compared to those of the *E. camaldulensis* plantation. The surface soil fine root weight density (RWD) inside the *E. camaldulensis* plantation was about three times that of the mixed plantation. The fine root distribution of *E. camaldulensis* from inside the stand and the plot (about 10 m away from the stand) was comparable indicating that planting *E. camaldulensis* around agricultural crops may pose competition.

7.1 Introduction

The management of deciduous tree species as shade for crops and growing of *E. camaldulensis* as a woodlot are the major tree growing practices at farmers' level in Badessa area (Poschen, 1987; Demel and Aseffa, 1991). *C. africana*, *E. burana* and *M. ferruginea* have been reported as the major tree species maintained on farms for their use as shade, fodder, soil fertility maintenance, live fencing, fuel wood and pole (Poschen, 1987; Demel and Aseffa, 1991; Legesse, 1995; Nyberg and Hogberg, 1995; Tadesse *et al.*, 2000, Abebe *et al.*, 2001). Furthermore, *M. ferruginea* and *E. burana* have the additional advantage of fixing nitrogen.

With the depletion of these native species, farmers started planting blocks of *Eucalyptus* spp. mainly for pole and fuel wood (Poschen, 1987). Most tree planting programs and subsidies also promote the use of well-known, often exotic species, due to the existence of knowledge on their biology, cultivation and uses. As a result, several eucalypts and other exotic species have been promoted both for large plantations and planting by farmers in Ethiopia (Pohjonen, 1989).

However, the negative effects of eucalypts on major crops in Ethiopia have been well documented (e.g. Lisanework and Michelsen, 1993). Although these authors recommended avoiding *Eucalyptus* spp. in low rainfall areas and where soil conservation is the main purpose of tree planting, farmers and forestry projects have not used alternative species. Farmers in Hararghe, Eastern Ethiopia keep on planting eucalyptus more than any other species, due to its superiority for fuel wood and construction material (Poschen, 1987; Fig. 1.2). Farmers' perceptions on the growth performance of the native tree species

and their impacts on the soil were reported to be both positive and negative (Poschen, 1987).

Consequently, forestry departments and various forestry promoting organizations in Ethiopia have been looking for indigenous tree species that could grow rapidly to meet the short-term wood requirements of farmers and the long-term environmental rehabilitation (e.g. Legesse, 1995, 2002b). Apart from the provision of several services and products, indigenous species are believed to be more suitable than exotics because 1) they are better adapted to local environmental conditions; 2) seeds and other propagules are locally available; 3) farmers are familiar with them and their uses; 4) the use of indigenous tree species in productive systems helps preserve genetic diversity of local flora and fauna (Montagnini *et al.*, 1993; Legesse, 1995, 2002b).

The objectives of the current study were to investigate 1) the foliar nutrient concentration of four tree species in a mixed stand and trees of *E. camaldulensis* woodlots in Badessa area, Eastern Ethiopia; 2) the fine root distribution of both plantations in the surface and subsurface profiles inside and away from the stands; 3) the effects of trees of the mixed stand and *E. camaldulensis* on soil fertility parameters.

7.2 Material and Methods

7.2.1 Study area

The study was carried out in Badessa (8⁰ 52' N and 40⁰ 40' E), Kuni District, eastern Ethiopia (Fig. 6.1). The elevation of Badessa area is 1740 m above sea level. The minimum and maximum temperatures of the area range from 9 - 14 °C and 25 - 30 °C, respectively (Section 6.2.1). Badessa has a bimodal rainfall pattern with low rainfall in spring and heavy

rain in autumn. The average annual rainfall is 1190 mm. In general sedimentary rocks were the parent rocks of Badessa area, though igneous rocks contributed in some areas (Murphy, 1968). Three major soil types, i.e., chromic and vertic luvisols and chromic vertisols occupy the largest proportion of the area (Murphy, 1968; EMA, 1981). The soils are clay with 55 - 60% clay, 12 – 15% silt and 25 – 30% sand. Soil color ranges from reddish brown on hillsides to dark brown at the low-lying areas. Farmers in the district practice a mixed farming system consisting of various combinations of annual crops, perennial crops, trees and livestock.

E. camaldulensis woodlots of about 0.5 - 0.6 ha established in 1987/88 by farmers and a mixed species stand composed of agroforestry species, i.e., *C. africana*, *E. burana*, *M. ferruginea* and *L. leucocephala* planted on one hectare of trial plot as shade for coffee in 1984/85 were used for the study. The latter three species in the mixed stand are legumes and among them *M. ferruginea* and *E. burana* are endemic to the country (Thulin, 1989). Trees of the *E. camaldulensis* woodlots were planted at a spacing of 1.5 m x 1.5 m but few trees were cut by the farmers for construction purpose and the stumps were well coppiced. Coffee was planted at a 2 m x 2 m spacing (2500 plants ha⁻¹) while the shade trees of different species were planted at a 5 m x 5 m spacing (400 trees ha⁻¹). However, due to some illegal cuttings, the number of the shade trees was reduced to 165 trees ha⁻¹, i.e. 58 *M. ferruginea*, 53 *E. burana*, 30 *C. africana* and 24 *L. leucocephala* trees. Grasses and herbs dominated inside the *E. camaldulensis* woodlots, whereas only some herbs (weeds) were present in the mixed plantation. The two *E. camaldulensis* woodlots and the mixed stand were located within a 5 km radius.

7.2.2 Tree measurements

Every third tree of *C. africana* and *L. leucocephala* and every sixth tree of *E. burana* and *M. ferruginea* within a row were used as sample trees. Eight trees per species were sampled. For the *E. camaldulensis* stand eight randomly selected trees of each stand were used for measurements. Tree height was measured using a hypsometer, diameter was measured at breast height using a caliper and crown diameter was estimated by tracing the canopy cover on the ground. Leaf samples were also collected from these same trees (see Section 7.2.5).

7.2.3 Soil and root sampling

Soil samples were collected from the interior and the edge of the stands. For *E. camaldulensis* a plot positioned at three times the canopy radius away from the stand was sampled. The plots away from the stand were positioned in about four weeks old maize farm. This cropland had no history of fertilizer application and farmers practice deep tillage and hoeing during cultivation and weeding. During the tillage practice, they discourage lateral roots from the *E. camaldulensis* stand. No samples were collected away from the mixed stand because other trees and shrubs surrounded it. Consequently, the plot away from the *E. camaldulensis* was also used for comparison with plots inside the mixed stand. At each location soils were sampled from two depths: 0-15 cm (surface) and 30-45 cm (subsurface). Three samples at each distance and depth were taken from the *E. camaldulensis* stand while six samples were taken from the mixed stand at each location and depth. Inside the plantations, samples were collected randomly at one meter away from trees in the stand. A pit of 30 cm wide and 50 cm deep was dug for soil sampling at each

sampling spot. Three sets of soil samples were collected at each spot, i.e., one for bulk density and the second set for root biomass and the third for chemical analysis. A cylindrical soil corer of 5 cm internal diameter was used for sampling the former two sets. For the set of samples used for bulk density, the soil was taken to the laboratory; oven dried at 105⁰C for 24 h and dry weight was taken. Bulk density (g cm⁻³) was calculated as the weight of the corer content divided by the corer volume.

Samples were processed according to the descriptions given in Section 6.2.3. The vertical distribution of fine roots at the edge of the *E. camaldulensis* stand canopy was assessed by opening a 300 cm long and 120 cm deep trench on one side of the canopy. The trench profile was divided into five layers: 1) 0-15 cm, 2) 15-30 cm 3) 30-45 cm, 4) 55-70 cm and 5) 85-100 cm. Three replicate samples were collected from each layer.

7.2.4 Soil analyses

Soil organic carbon (OC), total soil nitrogen (N), available phosphorus (P), pH, exchangeable basic cations (Ca²⁺, Mg²⁺, K⁺ and Na⁺), and cation exchange capacity (CEC) were determined following standard methods as indicated in Section 6.2.4.

7.2.5 Leaf sample collection and analyses

Fully expanded leaves of each of the sampling trees were collected from all positions of the canopy and mixed to obtain a composite sample per tree and analyzed for nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na) using standard methods indicated in Section 6.2.5.

7.2.6 Statistical analyses

All statistical computations were made using SPSS for Windows Version 11.0. Factorial ANOVA was employed to test variations between the various parameters measured from the inside canopy, edge of the canopy and away from the canopy as well as the vertical distribution of *E. camaldulensis* roots at the edge of the canopy. When significant differences were observed, Tukey's HSD test was used for mean comparison. Surface and subsurface soil parameters and comparisons between species were made using a student t-test. Reported correlations are Pearson's correlation coefficients.

7.3 Results

7.3.1 Tree growth

Among the trees in the mixed stand, the height of *M. ferruginea* was significantly higher ($P < 0.05$) than all the other species (Table 7.1). *L. leucocephala* had significantly lower ($P < 0.05$) diameter at breast height (DBH) than all the other species (Table 7.1). The rest of the species had comparable DBH. The crown diameters of *C. africana* and *M. ferruginea* were more spreading and wider than those of *L. leucocephala* and *E. burana* (Table 7.1).

Table 7.1 Mean (\pm SE) height, diameter at breast height DBH and crown diameter of five tree species in a mixed stand or pure plantation in Badessa. Mean values within a column followed by different letters are significantly ($P < 0.05$) different ($n = 8$).

Species	Height (m)	DBH (cm)	Crown Diameter (m)
<i>C. africana</i>	12.0 \pm 0.41c	26.0 \pm 1.65a	8.7 \pm 0.80a
<i>E. burana</i>	10.2 \pm 0.48c	26.2 \pm 0.86a	3.6 \pm 0.24b
<i>E. camaldulensis</i> *	17.0 \pm 0.40a	15.7 \pm 0.35b	3.5 \pm 0.13b
<i>L. leucocephala</i>	10.8 \pm 0.58c	16.4 \pm 1.02b	4.5 \pm 0.47b
<i>M. ferruginea</i>	14.6 \pm 0.50b	27.2 \pm 1.49a	7.8 \pm 0.37a

*trees of *E. camaldulensis* were three years younger than those of the other species

7.3.2 Foliar nutrients

L. leucocephala and *M. ferruginea* had higher foliar N than *E. burana* and more than twice those of *C. africana* and *E. camaldulensis* (Table 7.2). *E. burana* had the highest foliar P but the mean P concentration was not significantly different from the other two legumes but significantly higher ($P < 0.05$) than that of *C. africana* and *E. camaldulensis*. The N:P ratio of *L. leucocephala* and *M. ferruginea* was twice those of *C. africana* and *E. camaldulensis*. The N:P ratio of the latter two species was not significantly different from that of *E. burana*.

Table 7.2 Mean (\pm SE) nutrient concentration in leaves of five tree species in a mixed stand or pure plantation in Badessa. Significant *P*-values (ANOVA) show variations in foliar nutrient concentrations among species. Mean values within a column followed by different letters are significantly ($P < 0.05$) different ($n = 3$).

Species	N (%)	P (%)	N:P (ratio)	K (%)	Ca (%)	Mg (%)	Na (%)
<i>C. africana</i>	1.30 \pm 0.07b	0.18 \pm 0.01b	7.45 \pm 0.55c	1.14 \pm 0.11a	0.46 \pm 0.07a	0.33 \pm 0.03ab	0.22 \pm 0.01b
<i>E. burana</i>	2.58 \pm 0.35ab	0.23 \pm 0.01a	11.24 \pm 1.50bc	0.87 \pm 0.15a	0.46 \pm 0.06a	0.36 \pm 0.02a	0.10 \pm 0.01d
<i>E. camaldulensis</i>	1.40 \pm 0.20b	0.14 \pm 0.01b	9.65 \pm 1.07c	0.40 \pm 0.05b	0.36 \pm 0.04a	0.23 \pm 0.02b	0.29 \pm 0.01a
<i>L. leucocephala</i>	3.47 \pm 0.56a	0.19 \pm 0.01ab	18.74 \pm 3.06a	0.98 \pm 0.01a	0.57 \pm 0.04a	0.44 \pm 0.05a	0.16 \pm 0.01bc
<i>M. ferruginea</i>	3.11 \pm 0.42a	0.18 \pm 0.01ab	17.26 \pm 2.27ab	0.96 \pm 0.05a	0.37 \pm 0.04a	0.34 \pm 0.02ab	0.12 \pm 0.01cd
<i>P</i> -values	0.000	0.002	0.000	0.000	0.091	0.002	0.000

All the species had similar foliar K concentration except that *E. camaldulensis* leaves had less than half the values for the other species. No significant differences were found among all the five species in foliar Ca concentration. The foliar Mg of *L. leucocephala* was about twice that for *E. camaldulensis*. All the deciduous species had

significantly lower ($P < 0.05$) foliar Na than *E. camaldulensis*. Na was significantly ($P < 0.05$) higher in *C. africana* than in the three legume species except for *L. leucocephala*.

7.3.3 Soil nutrients

The surface and subsurface soil OC, N, P, pH, K^+ , Ca^{2+} , Mg^{2+} , Na^+ , CEC and BD from three distances from *E. camaldulensis* and mixed species stands is presented in three figures (Figs 7.2a-d, 7.3a-d and 7.4a-b). For both plantations, significant variations in soil N, P and K^+ were observed between the distances (Table 7.3). Furthermore, significant variations in soil OC, Na^+ and CEC were observed between distances for *E. camaldulensis* unlike for the mixed stand in which no differences were observed (Table 7.3). However, for the mixed stand, Ca^{2+} showed significant variation across distances. Significant differences in all the studied soil parameters were also observed between surface and subsurface soil samples except for N and Ca^{2+} for *E. camaldulensis* and Ca^{2+} and Mg^{2+} for the mixed stand (Table 7.3). Significant depth and distance interactions were observed for soil P and N in the case of the mixed stand (Table 7.3). The phosphorus content of surface soil inside the mixed stand was more than three times that of the immediate subsurface (Fig. 7.2c). Surface soil N, K^+ , Na^+ , CEC and pH were significantly higher ($P < 0.05$) than in the subsurface soil for the plot away from the stand.

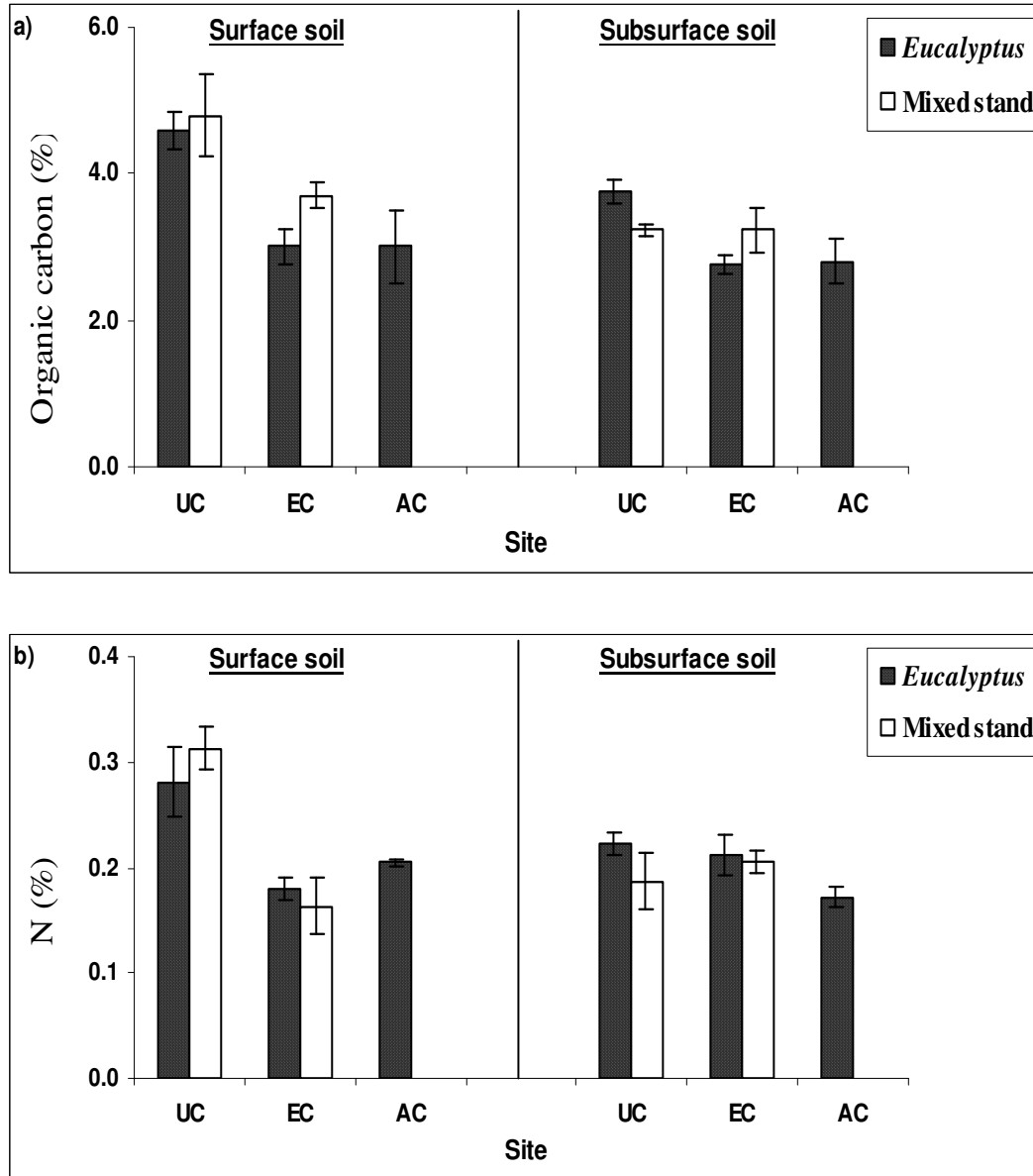


Figure 7.2 Mean surface (0-15 cm) and subsurface (30-45 cm) soil a) organic carbon and b) total nitrogen from under canopy (UC), edge of canopy (EC) and away from canopy (AC) of *E. camaldulensis* woodlot and mixed stand of four tree species in Badessa. Vertical bars indicate standard errors of the means (n = 6).

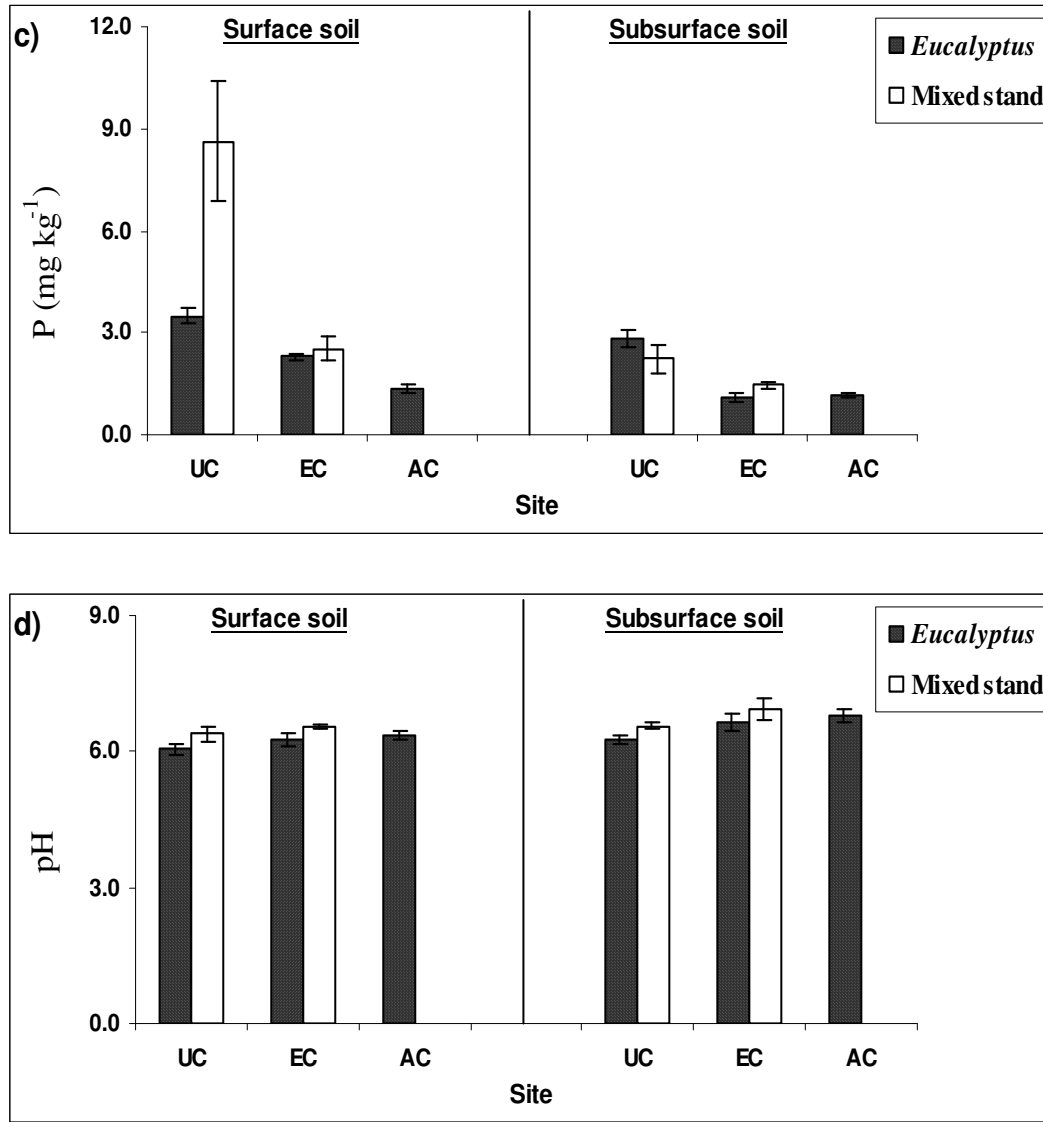


Figure 7.2 (c and d) Mean surface (0-15 cm) and subsurface (30-45 cm) soil c) phosphorus and d) pH from under canopy (UC), edge of canopy (EC) and away from canopy (AC) of *E. camaldulensis* woodlot and mixed stand of four tree species in Badessa. Vertical bars indicate standard errors of the means (n = 6).

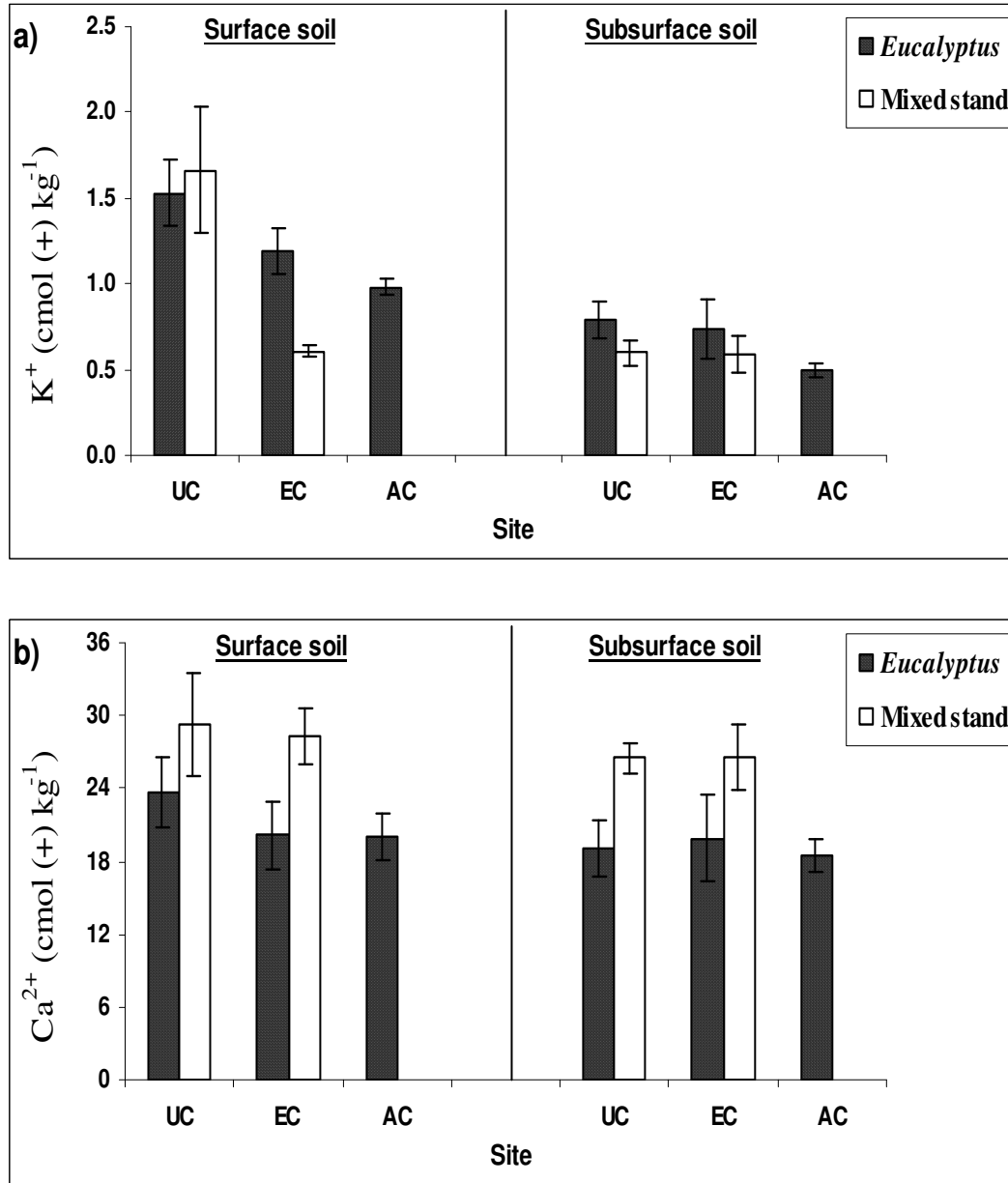


Figure 7.3 (a and b) Mean surface (0-15 cm) and subsurface (30-45 cm) soil exchangeable K⁺ (a) and Ca²⁺ (b) from under canopy (UC), edge of canopy (EC) and away from canopy (AC) of *E. camaldulensis* woodlot and mixed stand of four tree species in Badessa. Vertical bars indicate standard errors of the means (n = 6).

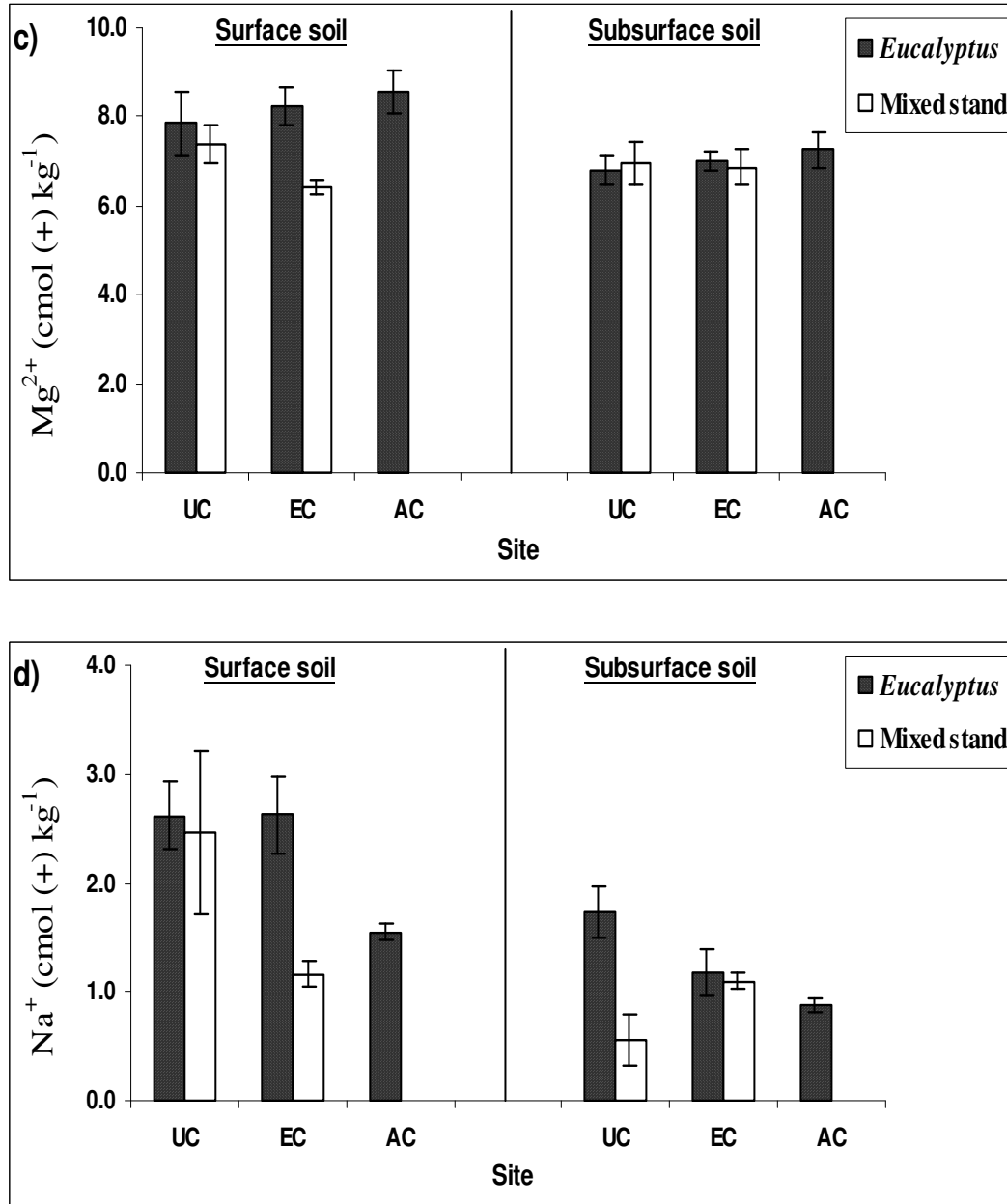


Figure 7.3 (c and d) Mean surface (0-15 cm) and subsurface (30-45 cm) soil exchangeable Mg^{2+} (c) and Na^{+} (d) from under canopy (UC), edge of canopy (EC) and away from canopy (AC) of *E. camaldulensis* woodlot and mixed stand of four tree species in Badessa. Vertical bars indicate standard errors of the means (n = 6).

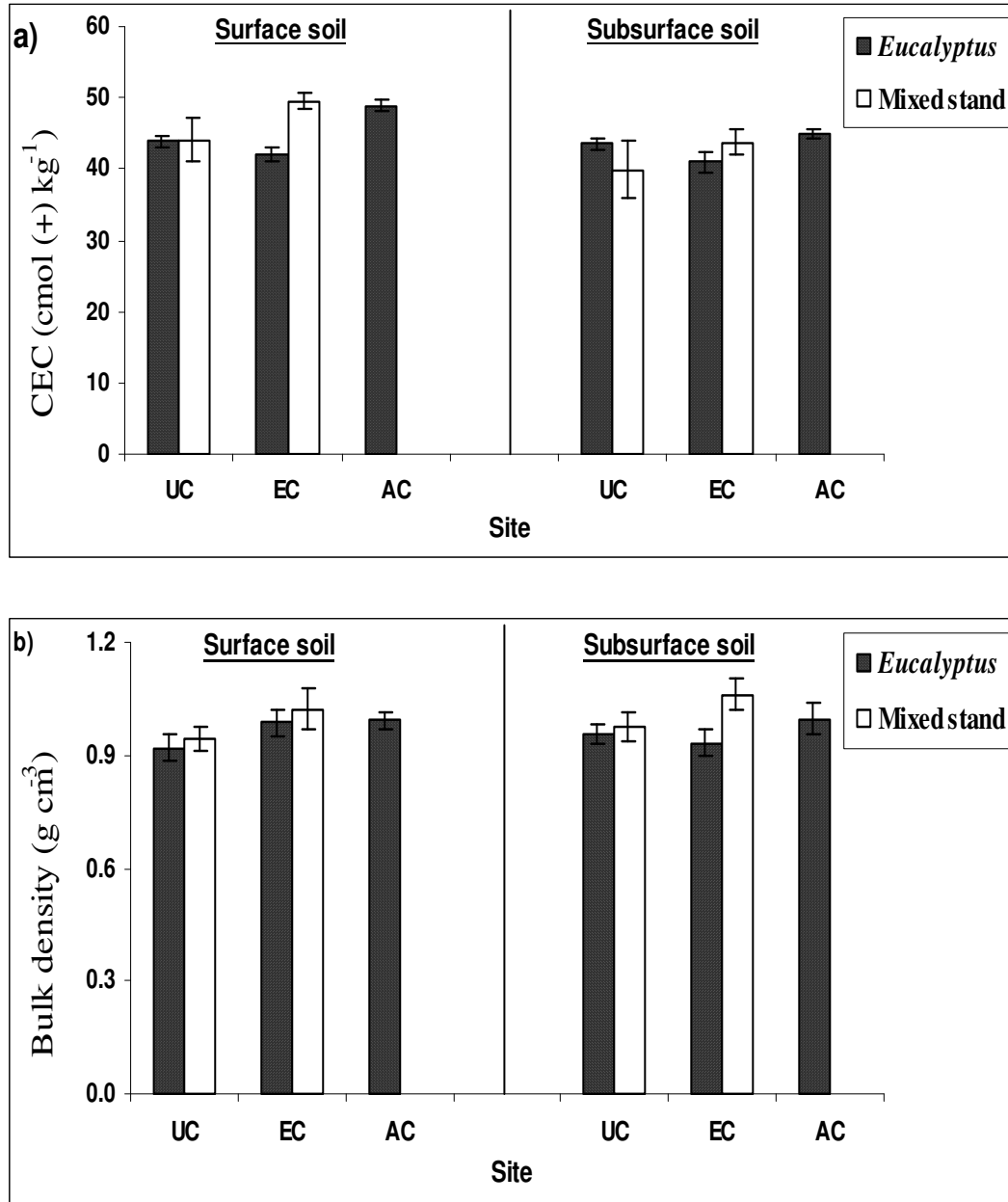


Figure 7.4 Mean surface (0-15 cm) and subsurface (30-45 cm) soil CEC (a) and bulk density (b) from under canopy (UC) edge of canopy (EC) and away from canopy (AC) of *E. camaldulensis* woodlot and mixed stand of four tree species in Badessa. Vertical bars indicate standard errors of the means (n = 6).

Table 7.3 Summary of factorial ANOVA showing the effects of *E. camaldulensis* stand and mixed stand of four tree species on soil fertility parameters at three horizontal distances from the stands and two depths at each distance in Badessa, Eastern Ethiopia. Asterisks *, **, *** represent significance at $P \leq 0.05$, 0.01 and 0.001; ns = not significant at $P \leq 0.05$.

Parameter	<i>E. camaldulensis</i>			Mixed stand		
	Distance	Depth	Distance* Depth	Distance	Depth	Distance* Depth
OC (%)	***	*	ns	ns	**	ns
Tot N (%)	*	ns	ns	**	*	**
P (mg kg ⁻¹)	***	**	ns	***	**	***
K ⁺ (cmol (+) kg ⁻¹)	*	***	ns	*	**	ns
Ca ²⁺ (cmol (+) kg ⁻¹)	ns	ns	ns	**	ns	ns
Mg ²⁺ (cmol (+) kg ⁻¹)	ns	*	ns	ns	ns	ns
Na ⁺ (cmol (+) kg ⁻¹)	**	***	ns	ns	*	ns
CEC (cmol (+) kg ⁻¹)	***	*	ns	ns	*	ns
pH (H ₂ O)	**	**	ns	ns	*	ns
BD (g cm ⁻³)	ns	ns	ns	ns	ns	ns
RLD (cm cm ⁻³)	ns	*	ns	-	-	-
RWD (mg cm ⁻³)	ns	ns	ns	-	-	-

At all distances and depths soil pH and Ca²⁺ were higher under the mixed plantation than the *E. camaldulensis* plantation (Figs 7.2d and 7.3b). Similarly OC and P were also higher in the mixed plantation compared to the *E. camaldulensis* plantation except in the

subsurface soil at the edge of plantation. However, in most cases the differences were not statistically significant ($P > 0.05$).

7.3.4 Root distribution

The RLD and RWD of surface soil inside the *E. camaldulensis* stand were significantly higher than those inside the mixed stand (Table 7.4). However, both RLD and RWD were higher in the surface soils at the edge of the mixed plantation compared to *E. camaldulensis*. The RLD of the former was about twice that of the latter in the surface and subsurface soils at the edge of canopies. The surface soil RWD inside the *E. camaldulensis* plantation was about three times that of the mixed plantation. For the *E. camaldulensis* plantation, both RLD and RWD declined with increasing distance from the stand, however, the differences were not significant.

Observation of fine roots of *E. camaldulensis* crossing the canopy edge to the crop zone indicated the presence of fine roots in all the studied layers to the depth of 100 cm (Fig. 7.5). However, both the length and mass of the fine roots declined steadily with depth of the soil profile with the layers (0 – 30 cm) and (55 – 100 cm) showing significant differences ($P < 0.05$) both in RLD and RWD. Although only fine roots of <2 mm were sampled at the edge of *E. camaldulensis* canopy (about 2 m from the trees at the edge of the stand), numerous lateral roots of 2 – 30 mm were also observed from the trench, especially in the depths from 15 – 45 cm.

Table 7.4 Mean (\pm SE) surface (0 – 15 cm) and subsurface (30 – 45 cm) soil RLD and RWD under canopies (UC), at the edge of canopies (EC) and away from the canopy of *E. camaldulensis* plantation (OC) and mixed stand in Badessa area. (n = 6).

Root Parameter	Depth (cm)	Mixed stand		<i>E. camaldulensis</i>		
		UC	EC	UC	EC	OC
RLD (cm cm ⁻³)	0 - 15	0.51 \pm 0.10	1.69 \pm 0.59	0.94 \pm 0.24	0.66 \pm 0.16	0.70 \pm 0.20
	30 - 45	0.62 \pm 0.19	0.74 \pm 0.28	0.43 \pm 0.07	0.33 \pm 0.05	0.30 \pm 0.19
RWD (mg cm ⁻³)	0 - 15	0.32 \pm 0.06	1.05 \pm 0.32	1.00 \pm 0.26	0.78 \pm 0.27	0.65 \pm 0.22
	30 - 45	0.62 \pm 0.18	0.75 \pm 0.23	0.72 \pm 0.19	0.47 \pm 0.11	0.22 \pm 0.01

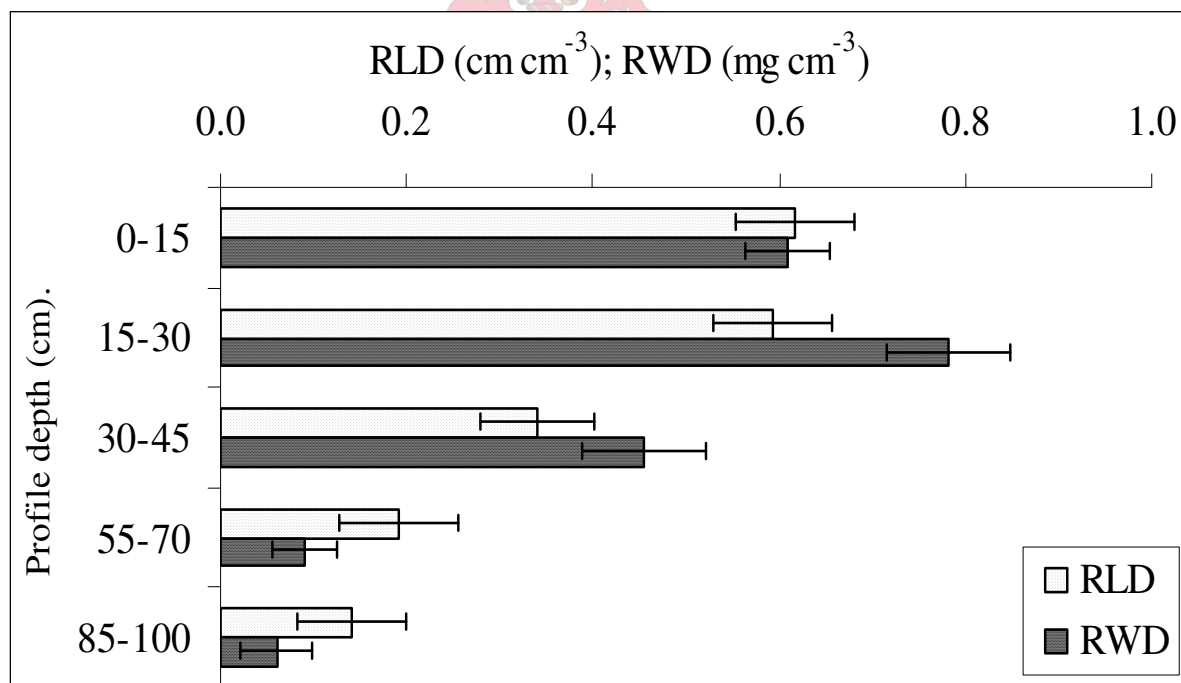


Figure 7.5 Mean RLD and RWD of *E. camaldulensis* woodlot with increasing soil depth at the edge of the stand canopy in Badessa. Vertical bars indicate standard error of the mean (n = 6).

7.4 Discussion

7.4.1 Tree growth

The height, DBH and crown diameter of *M. ferruginea*, *C. africana* were exceedingly higher than that of *L. leucocephala* (Table 7.1). Although *L. leucocephala* has been considered as one of the fast growing agroforestry species all over the tropics (Nair, 1993; Young, 1997), the deciduous species of Ethiopia used for the current agroforestry trial showed better growth performance than *L. leucocephala*. Because of the lack of information on the growth performance of such native tree species, several exotic tree and shrub species including *L. leucocephala*, *Acacia* spp. and *Eucalyptus* spp. had been introduced in the past. However, the current study showed that native species such *M. ferruginea* and *C. africana* compare favorably to both of the exotic species, *E. camaldulensis* and *L. leucocephala*.

7.4.2 Foliar nutrients

All the three leguminous species had significantly higher foliar N concentration than *E. camaldulensis* and *C. africana* (Table 7.2) probably due to their nitrogen fixing capacity. Earlier studies (e. g., Nair, 1993; Young, 1997) indicated that the tissue N concentration of N-fixing species is higher than that of non-fixing species. Within the legumes the variations in foliar N, P, K, Ca and Mg were not significant, although all the nutrients, except P, were slightly higher in leaves of *L. leucocephala*. According to Mwiinga *et al.* (1994), tree species with high nitrogen, phosphorous and potassium concentrations and high decomposition rates have a great potential as green manure for soil improvement.

The foliar N concentrations of *E. burana* (2.58%), *M. ferruginea* (3.11%) and *L. leucocephala* (3.47%) were high, indicating that these species replenish the soil with high

quality litter (Palm, 1995). According to Palm (1995), plant material with more than 2% N would result in net mineralization of N that may be readily available for uptake. In addition to a low N, leaves of *E. camaldulensis* had lower P, K, Ca and Mg, indicating that it supplied lower quality litter to the underneath soil compared to the deciduous species. However, the foliar N and P concentrations observed for *E. camaldulensis* in the current study were within the ranges reported for those grown in Australia, Philippines and the Middle East (Judd *et al.*, 1996). Earlier studies involving comparisons of several other deciduous and evergreen species (Reich *et al.*, 1992; Aerts and Chapin, 2000, Chapter 4) also indicate that leaves of evergreen species have lower nutrient concentrations than deciduous species.

The foliar N concentrations of *M. ferruginea* and *L. leucocephala* were similar but foliar P and K were higher compared to those reported for the nodulated leaves of *Erythrina brucei* (Schweinf.); N = 3.3%, P = 0.14% and K = 1.1%, a nitrogen fixing species from Ethiopia studied by Legesse (2002a). The non-nodulated leaves of *E. brucei*, however, had higher N than all the current species. The foliar N concentration of *E. burana* (2.58%) was much less than those for both nodulated and non-nodulated leaves of *E. brucei* (Legesse, 2002a).

Due to its high overall growth performance and high foliar nutrient concentration (Table 7.2), *M. ferruginea* could be a leading agroforestry species in the future. Farmers in the Gedeo – Sidama areas in southern Ethiopian plant *M. ferruginea* for its soil improving quality, sparse branching that allows light penetration for crops (Fig. 7.6), provision of fuel wood and prolific coppicing ability following pruning (Legesse, 1995; Tadesse *et al.*, 2000).



b)



Figure 7.6 Agroforestry trees planted as shade for coffee a) young *M. ferruginea* with a spreading crown, b) mixed stand shade trees composed of *M. ferruginea*, *C. africana*, *E. burana*, and *L. leucocephala*.

7.4.3 Soil nutrients

The contribution of the mixed stand to the soil nutrients and organic carbon was higher compared to the *E. camaldulensis* stand (Figs 7.2 and 7.3). The increased soil nutrient status within both plantations was due to retrieval of the nutrients from deeper soil layers and deposition at the surface as litter that decomposes and releases the nutrients. The most prominent differences between the two plantations regarding soil nutrient composition were that: a) surface soil P was much higher inside the mixed plantation compared to both the *E. camaldulensis* and the plots away from the stand, b) Ca^{2+} was higher both in the surface and subsurface soils inside and at the edge of the mixed plantation compared to those of *E. camaldulensis* stand and the plots away from the stand. The improved status of soil nutrients inside the plantation could be due to the input of quality litter that contains higher concentration of these nutrients. The increased organic matter also serves as both storage and supply of the nutrients. Due to the higher proportions of the basic cations inside the mixed plantations, the pH of these soils were higher compared to that of *E. camaldulensis*.

Because the proportion of leguminous shade trees in the mixed stand was over 80%, much more accumulation of nitrogen in the stand was expected than what was reported here. However, the accumulation of N under the mixed stand could be hindered due to a) uptake by the understorey coffee and the non-legume component of the stand, b) the expected high decomposition leading to the mineralization of organic nitrogen (due to the high foliar N of the legumes (Palm, 1995)) which may be lost from the system via volatilization, denitrification and leaching (Browaldh, 1995; Marschner, 1995).

The reduced bulk density under both plantations compared to plots at the edge of and away from the plantations and the plots could be due to increased organic matter inside the plantations. Soil with lower bulk density is characterized by good aeration, higher water infiltration, easy root penetration and reduced surface run-off (Killham, 1994).

7.4.4 Root distribution

The higher root biomass in the surface soil inside the *E. camaldulensis* stand (Table 7.3) compared to the mixed plantation showed that *E. camaldulensis* has extensive shallow roots. This high fine root biomass of *E. camaldulensis* in the surface soil may result in an increased competition with plants that may regenerate under its canopy. Apart from the under canopy, the RLD and RWD of *E. camaldulensis* observed in the plots away from the stand (Table 7.3) indicated a possibility of root interference with the nearby crops. Although root densities at the edge of the mixed stand were higher compared to the eucalyptus, it was not possible to distinguish the contribution of each species of the mixed stand to the higher densities. Furthermore, because soil samples were not collected from areas nearby the mixed stand (section 7.2.3), it was not possible to estimate and compare root extension into adjacent plots.

Species with an extensive root system are considered to be more competitive than those with less root extension (Lambers *et al.*, 1998; Marschner, 1995). Although *E. camaldulensis* is reported to be deep rooting (Jonsson *et al.*, 1988; Bacon *et al.*, 1993), some studies (Stone and Kalisz, 1991) have demonstrated that the species has roots that extend several tens of meters from the trunk horizontally. Later studies by Burgess *et al.* (2001) showed that *E. camaldulensis* has a dimorphic root system with a single taproot

penetrating to a significant depth as well as numerous lateral roots. This concurs with the results of the present study in which *E. camaldulensis* was found to have extensive shallow roots.

In a study on the farming systems of the Hararghe highlands (which included the current study area as one sampling site), Poschen (1987) reported that over 70% of farmers in the area were aware of the negative impact of the eucalypts on crops. Lisanework and Michelsen (1993) also pointed out the importance of considering interactions between *E. camaldulensis* and agricultural crops if the two species are to be planted in the same cropping system because of the allelopathic effects of the former on major agricultural crops. However, May and Ash (1990) demonstrated that the magnitude of these effects may be influenced by rainfall because allelochemicals are highly soluble and rainfall is likely to dilute and leach them out. In Badessa area where rainfall is erratic, the allelochemicals may accumulate in the soil and exacerbate the growth of understorey plants and crops nearby the stand. According to Inderjit and del Moral (1997), allelopathy is strongly coupled with other environmental stresses including insects, diseases, herbivory, temperature and radiation extremes and nutrient and moisture stresses. As a result Inderjit and del Moral (1997) explained the difficulty of differentiating allelopathy from competition, especially under field conditions. Although it is difficult to tell the relative importance of the effects of competition and that of allelopathy, the current study showed that *E. camaldulensis* could pose root competition in addition to its potential allelopathic effects.

In an effort to avoid the impact of eucalypts, farmers in Badessa area and elsewhere in the Hararghe highlands, prefer growing eucalypts as a woodlot (e.g. Fig. 1.2) or as boundary

planting without mixing it with crops (Poschen, 1987). Regardless of the farmers' efforts to discourage the spread of roots in the surface soils in the adjacent croplands, the root biomass at a distance of 10 m away from the canopy (in the adjacent cropland) was comparable to that inside the *E. camaldulensis* stand. The effect of the eucalyptus stand on the nearby crop could easily be observed from the difference in the growth of crops close to and away from *E. camaldulensis* (Fig. 7.7).



Figure 7.7 Suppressed maize growth adjacent to *E. camaldulensis* woodlot in Badessa area.

Removal of shallow roots from the surface soil may not significantly reduce fine roots biomass possibility because the fine roots emerge from coarse roots in the subsurface layer. Therefore, necessary precaution must be taken when growing eucalypts in association with or in close proximity to crops. If planting eucalypts is a priority, farmers may practice deep root trenching around the woodlot to discourage root expansion into croplands. However, planting indigenous tree species such as *M. ferruginea* may be more beneficial because the species is fast growing and has the advantage of improving the soil nutrient pool (Tadesse *et al.*, 2000).

7.5 Conclusions

The native agroforestry species of Ethiopia have shown a better growth performance than, and similar foliar nutrient composition to *L. leucocephala*. Both the mixed stand and *E. camaldulensis* stand improved soil nutrient status compared to plots at the edge of the stands and away from the stands. However, the magnitude of the contribution was higher for the mixed species stand regarding phosphorus and calcium.

The presence of a block of *E. camaldulensis* nearby croplands may have negative effects on the soils and crops. The negative effects of a block of *E. camaldulensis* on nearby cultivated lands could be substantial in areas like Badessa where the average land holding of a household is about 0.7 hectares. If planting *E. camaldulensis* around field crops is unavoidable, or inevitable, farmers have to practice cutting trenches next to the eucalypt woodlot, or keep the *E. camaldulensis* woodlot at a good distance from the crops.

8. CONCLUDING REMARKS

1. Soil water and nitrogen stress resulted in overall reduction of gas exchange parameters including photosynthetic rate, stomatal conductance and WUE_{GE} for all the studied species. However, different species reacted to stress in various manners and to different degrees in their physiological performance. These differences may be used as a basis for selecting the tree species for such purposes as agroforestry and land reclamation. The field study in Badessa area has strengthened the general hypothesis on agroforestry, viz, apart from provision of wood for various purposes, growing trees in combination with crops can foster soil fertility.

2. Based on the results presented in this thesis, it can be stated that *M. ferruginea* has the potential to become flagship species of agroforestry in Ethiopia and other tropical and subtropical areas prone to droughts and deficits in soil nutrients. Some of the identified desirable qualities of the species include:

- i. better growth, high PNUE and WUE_{WL} compared to *C. africana* and *C. macrostachyus* both under glasshouse (Chapter 2 and 5) and field conditions (Chapter 7);
- ii. production of lower RWR in pots (Chapter 2);
- iii. possession of a spreading crown that would allow for light penetration (Fig. 7.6a);
and,
- iv. ability to fix nitrogen, improve soil fertility, use in animal fattening (flowers), shade for coffee trees, use as fuel wood, easy propagation and acceptance by farmers (Negash, 1995; Hailu *et al.*, 2000).

3. The glasshouse experiment (Chapter 2) found that the studied deciduous species indigenous to Ethiopia showed growth rates comparable to the *Eucalyptus* spp. provided that moisture is available.

4. The glasshouse experiments (Chapters 2 and 3) showed that leaves of *C. macrostachyus* and *C. africana* had significantly higher transpiration rate and plants had less biomass per water transpired, showing less water use efficiency compared to the studied eucalypts studied. When moisture is limiting, *C. macrostachyus* and *C. africana* lose their leaves rapidly to reduce water loss, which also results the in the reduction of photosynthetic surface area and hence overall growth.

5. After shedding their leaves, the studied deciduous trees can survive long periods of water stress by remaining dormant. The two *Eucalyptus* species were tolerant to water stress but not to severe/sudden drought because they do not have requisite physiological/morphological mechanisms for of avoiding or mitigating drought like the deciduous species, at least at the seedling stage. Of all the studied species, *M. ferruginea* has the most advanced mechanism of avoiding moisture stress and water loss, which enables it to utilize water in a very conservative manner.

6. The studied species ranked in a descending order of *C. macrostachyus*, *C. africana*, *M. ferruginea*, *E. camaldulensis* and *E. globulus* regarding overall tissue N and P accumulation. Although the availability of soil N and P had a considerable influence on the accumulation of these nutrients in tissues, this ranking of species was not affected by soil N or P status. However, only *M. ferruginea* showed a markedly high photosynthetic rate per accumulated nitrogen compared to all the other species. This high PNUE of *M. ferruginea*

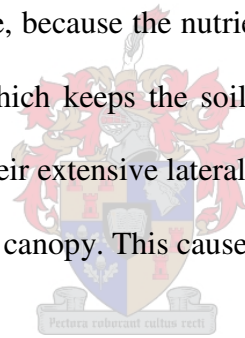
might be a genetic trait because it was maintained regardless of the various N and P treatments. Soil P had minor effects on the photosynthetic performance of plants of all the studied species as opposed to soil N supply, which had a marked effect. Leaves with high nitrogen content showed high capacity for fixing CO₂. Foliar N:P ratios of 10, 12, 15, 17 and 18 were observed for *C. macrostachyus*, *C. africana*, *E. camaldulensis*, *E. globulus* and *M. ferruginea*, respectively, under sufficient supplies of both N and P. These values may serve as benchmarks for interpretation of foliar analysis of the studied species to indicate N and P deficiency.

7. Both under field and glasshouse conditions *C. macrostachyus* and *C. africana* produced intensive roots, indicating the presence of potential competition with crops. The two species tend to produce intensive root to meet their high nutrient and water demands. The extensive root growth and accumulation of high proportion of the nutrients in the root may reduce their potential use in agroforestry, especially that of *C. macrostachyus*. Although the field experiment proves their positive impact on some soil nutrients, some corrective domestication practices are required to achieve good results in terms of fostering soil fertility. Therefore, the use of these species in association with crops should be accompanied by tree management traditionally practiced by Ethiopian farmers:

- i. the amputation of surface roots as practiced by farmers of Badessa area; and,
- ii. management of the tree canopies for light penetration especially in the case of *C. africana*;
- iii. avoiding the removal of litter for other purposes especially in areas of low soil fertility. If leaves of the trees are removed either for fuel or fodder, the site may be severely depleted due to the removal of the leaves that are rich in nutrients.

Both *C. macrostachyus* and *C. africana* do not suppress undergrowth and produce intensive root systems to hold the soils together, which make both species good candidates for planting on hillsides where erosion is a problem. The efficient cycling of nutrients contributes to their potential use in rehabilitation of degraded lands.

8. Although, the glasshouse experiments showed that the studied *Eucalyptus* species can perform better than the deciduous species under water deficit conditions, the field observations have once again proved the substantially negative impact of eucalypts on the site quality and on the adjacent crops. One of the observed ‘disadvantages’ of the eucalypts is that they retain their leaves for several seasons including the dry season. This has negative implications for the site, because the nutrients retained in the leaves do not return to the soil in the short term, which keeps the soil bare and poor in nutrients. The other ‘disadvantage’ of eucalypts is their extensive lateral root expansion, which was observed as far as 10 meters away from their canopy. This causes high levels of competition with crops.



9. The findings in this thesis strongly suggest that the planting of eucalypts in the immediate proximity or together with agricultural crops should be avoided. The planting of eucalypts in Ethiopia is usually preferred by farmers due to the short term wood requirements. Thus, if planting *E. camaldulensis* around field crops is essential, or unavoidable, farmers should be advised to

- i. keep a maximum possible distance between eucalypts and crops,
- ii. practice cutting trenches between the eucalypt woodlot and cropland to reduce the extension of roots to croplands.

9. REFERENCES

- Abebe, Y., Fisseha, I. and Olsson, M. (2001) Contribution of indigenous trees to soil properties: The case of scattered trees of *Cordia africana* Lam. in croplands of western Oromia. *Ethiopian Journal of Natural Resources* 3 (2): 245-270.
- Aerts, R. (1990). Nutrient use efficiency in evergreen and deciduous species from heath lands. *Oecologia* 84: 391–397.
- Aerts, R. (1995). The advantages of being evergreen. *Trends in Ecology and Evolution* 10: 402-407.
- Aerts, R. (1996). Nutrient resorption from senescing leaves of perennials: Are there general patterns? *Journal of Ecology* 84: 597-608.
- Aerts, R. and Chapin III, F.S. (2000) The mineral nutrition of wild plants revised: A re-evaluation of processes and patterns. *Advances in Ecological Research* 30: 1-67.
- Ameglio, T., Archer, P., Cohen, M., Valancogne, C., Daudet, F.A., Dayau, S. and Cruiziat, P. (1999). Significance and limits in the use of predawn leaf water potential for tree irrigation. *Plant and Soil* 207: 155-167.
- Anderson, J.M. and Ingram, J.S.I. (1993). *Tropical Soil Biology and Fertility: A Handbook of Methods*. Second edition. CAB International, UK, 221pp
- Bacon, P.E., Stone, C., Binns, C.L., Leslie, D.J. and Edwards E.W. (1993). Relationships between water availability and *Eucalyptus camaldulensis* growth in a riparian forest. *Journal of Hydrology* 150: 541–561.
- Battaglia, M., Beadle, C. and Loughhead, S. (1996). Photosynthetic temperature

- responses of *Eucalyptus globulus* and *Eucalyptus nitens*. *Tree Physiology* 16: 81-89.
- Beadle, C.L., Ludlow, M.M. and Honeysett, J.L. (1993). Water relations. *In*: Hall, D. O., Scurlock, J. M. O., Bolhàr-Nordenkampf, H. R., Leegood, R. C. and Long, S. P. (eds.) *Photosynthesis and Production in a Changing Environment: A Field and Laboratory Manual*. Chapman and Hall, London, UK.
- Bennett, L.T., Weston, C. J. and Attiwill, P.M. (1997). Biomass nutrient content and growth response of fertilizers of six-year-old *Eucalyptus globulus* plantations at three contrasting sites in Gippsland, Victoria. *Australian Journal of Botany* 45:103-121.
- Björkman, O. and Powles, S.B. (1984). Inhibition of photosynthetic reactions under water stress: interaction with light level. *Planta* 161:490-504.
- Booth, T.H and Pryor, L.D. (1991) Climate requirements of some commercially important eucalyptus species. *Forest Ecology and Management* 43:47-60.
- Bray, R.H. and Kurtz, L.T. (1945). Determination of total, organic and available forms of phosphorus in soils. *Soil Science* 59: 39 – 45.
- Brooks, A. (1986). Effects of phosphorus nutrition on ribulose 1,5-bisphosphate carboxylase activation, photosynthetic quantum yield and amounts of some Calvin-cycle metabolites in spinach leaves. *Australian Journal of Plant Physiology* 13:221– 37.
- Browaldh, M. (1995). The influence of trees on nitrogen dynamics in agricultural system in Sweden. *Agroforestry Systems* 30: 301–313.
- Buck, A. L. (1981). New equations for computing vapor pressure. *Journal of Applied*

Meteorology 20: 1527–1532.

Burgess, S.S.O., Adams, M.A., Turner, N.C., White, D.A. and Ong, C.K., (2001). Tree roots: conduits for deep recharge of soil water. *Oecologia* 126: 158-165.

Chapin, F. S., Schulze, E. D. and Mooney, H. A., (1990). The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* 21: 423-447.

Chapin, F. S. (1991). Effects of multiple stresses on nutrient availability and use.

In: Mooney, H. A., Winner, W. E. and Pell, E. J (eds.) *Response of Plants to Multiple Stresses*. Academic Press, San Diego. pp 67-88.

Chaves, M. M. (1991). Effects of water deficits on carbon assimilation. *Journal of Experimental Botany* 42: 1-16.

Ciampi, S., Gentili, E., Guidi, L. and Soldatini, G.F. (1996). The effect of nitrogen deficiency on leaf gas exchange and chlorophyll fluorescence parameters in sunflower. *Plant Science* 118:177–174.

Cromer, R. N., Raupach, M., Clarke, A. R. P. and Cameron, J. N. (1975). Eucalyptus plantations in Australia-the potential for intensive production and utilization. *Appita* 29, 165-173.

Cromer, R. N., Cameron, D., Cameron, J. N., Flinn, D. W., Neilsen, W. A., Raupach, M., Snowdon, P., and Waring, H. D. (1981). Response of eucalypt species to fertilizer applied soon after planting at several sites. *Australian Forestry* 44: 3-13.

Davidson, J. (1989). *The Eucalyptus Dilemma, Arguments for and Against Eucalyptus Plantation in Ethiopia*. Seminar Note Series No. 1 Forestry Research Center, Addis Ababa, Ethiopia.

Dell, B. Malajczuk, N and Grove, T. S. (1995). *Nutrient Disorders in Plantation*

- Eucalyptus*. ACIAR Monograph 31, Canberra, Australia. 110pp.
- Demel, T. and Aseffa, T. (1991). Shade trees of coffee in Harerghe, eastern Ethiopia. *The International Tree Crop Journal* 7: 17-27.
- Eamus, D. and Prior, L. (2001). Ecophysiology of trees of seasonally dry tropics: comparisons among phenologies. *Advances in Ecological Research* 32: 113-197.
- EFAP. (1994). *Ethiopian Forestry Action Program. Draft Final Report Vol II. The Challenge for Development*. Ministry of Natural Resources and Environmental Protection, Addis Ababa, Ethiopia.
- Ehleringer, J.R. and Werk, K.S. (1986). Modifications of solar-radiation absorption patterns and implications for carbon gain at the leaf level. In: Givnish, T.J. (ed) *On the Economy of Plant Form and Function*. Cambridge University Press, Cambridge. pp 57-82.
- Eldridge, K., Davidson, J. and Harwood, C. and Van Wyk, H. (1994). *Eucalypt Domestication and Breeding*. Oxford, UK.
- EMA (1981). National Atlas of Ethiopia. Ethiopian Mapping Agency. Addis Ababa. 83pp
- EPA. (1998). Background information on drought and desertification in Ethiopia. Environmental Protection Authority (EPA), Addis Ababa, Ethiopia., 99pp.
- Ericsson, T. (1994). Nutrient requirement of *Eucalyptus globulus* seedlings. In: Pereira, J. S. and Pereira, H. (eds.) *Eucalyptus for Biomass Production. The-State-of-the-art*. CEC, ISA: Lisbon, Portugal. pp 224-234.
- Evans, J.R. (1983). Nitrogen and photosynthesis in the flag leaf of wheat (*Triticum aestivum* L.). *Plant Physiology* 72:279-302.

- Evans, J.R. and Terashima, I. (1987). Effects of nitrogen nutrition on electron transport components and photosynthesis in spinach. *Australian Journal of Plant Physiology* 14: 59-68.
- Evans, J.R. (1989). Photosynthesis - nitrogen relationships in leaves of C₃ plants. *Oecologia* 78: 9–19.
- Evans, J.R., Jakobsen, I. and Ögren, E. (1993). Photosynthetic light-response curves. 2. Gradients of light absorption and photosynthetic capacity. *Planta* 189:191–200.
- Evans, J.R. (1996). Developmental constraints on photosynthesis: effects of light and nutrition. In: Baker, N. R. (ed.) *Photosynthesis and the environment*. Kluwer Academic Publishers. pp. 281-304.
- Fabião, A., Madeira, M. Steen, E. Kätterer, T., Ribeiro, C. and Araújo, C. (1995). Development of root biomass in an *Eucalyptus globulus* plantation under different water and nutrient regimes. *Plant and Soil* 168 – 169: 215 – 223.
- FAO. (2001). *Global Forest Resources Assessment 2000*. Main Report FAO Forestry Paper, Rome. 140: 127-131.
- Feyera, S., Demel, T. and Näslund, B. (2002). Native woody species regeneration in exotic tree plantations at Munessa-Shashemene Forest, southern Ethiopia. *New Forests* 24: 131-145.
- Fichtl, R.A. and Admasu, A. (1994). *Honeybee Flora of Ethiopia*. Weikersheim, Verlag, Germany.
- Florence, R. G. (1996). *Ecology and Silviculture of Eucalypt Forests*. CSIRO Publishing. Australia, 413 pp.

- Fredeen, A.L., Rao, I.M. and Terry, N. (1989). Influence of phosphorus nutrition on growth and carbon partitioning in *Glycine max*. *Plant Physiology* 89:225-230.
- Fredeen, A.L., Gamon, J.A. and Field, C.B. (1991). Response of photosynthesis and carbohydrate partitioning to limitations to nitrogen and water availability in field grown sunflower. *Plant, Cell and Environment* 14:963-970.
- Friis, I. (1995). *Myrtaceae*. In: Edwards, S., Mesfin T. and Hedberg, I. (eds), *Flora of Ethiopia and Eritrea, Vol.2 (2)*. Addis Ababa University, Addis Ababa and Uppsala University, Uppsala. pp. 71-106.
- Fu, Q.A. and Ehleringer, J.R. (1989). Heliotropic leaf movements in common beans controlled by air temperature. *Plant Physiology* 91: 1162-1167.
- Gibson, A., Hubick, K.T. and Bachelard, E.P. (1991). Effects of abscisic acid on morphological and physiological responses to water stress in *Eucalyptus camaldulensis* seedlings. *Australian Journal of Plant Physiology* 18:153-163.
- Gilbert, M. G. (1995) *Euphorbiaceae*. In: Edwards, S., Mesfin T. and Hedberg, I. (eds.) *Flora of Ethiopia and Eritrea, Vol. 2 Part 2, Canellaceae to Euphorbiaceae*. Addis Ababa University, Ethiopia and Uppsala University, Sweden.
- Glenn, E. and Brown, J. (1998). Effect of soil salt levels on the growth and water use efficiency of *Atriplex canescens* (Chenopodiaceae) varieties in dry soil. *American Journal of Botany* 85 (1): 10-16.
- Golley, F. B. (1986). Chemical plant-soil relationships in tropical forests. *Journal of Tropical Ecology* 2: 219-229.
- Grime, J. P. (1979). *Plant Strategies and Vegetation Processes*. Wiley, Chichester, UK.
- Grime, J.P. (1994). The role of plasticity in exploiting environmental heterogeneity. In:

- Caldwell, M. Percy, R. (eds.) *Exploitation of Environmental Heterogeneity in Plants*. Academic Press Inc., New York. pp.1-19.
- Hagos, F., Pender, J. and N. Gebreselassie, N. (1999). *Land degradation in the highlands of Tigray and strategies for sustainable land management*. Socioeconomic and Policy Research Working Paper No. 25, Livestock Policy Analysis Project, International Livestock Research Institute, Addis Ababa.
- Hall, A.E. (2001). *Crop Responses to Environments*. CRC Press LLC. USA.
- Hatton, T., Reece, P., Taylor, P. and McEwan, K. (1998). Does leaf water efficiency vary among eucalypts in water-limited environments? *Tree Physiology* 18: 529-536.
- Inderjit and del Moral, R. (1997). Is separating resource competition from allelopathy realistic? *Botanical Reviews* 63 (3): 221-230.
- Ingestad, T. (1979). Nitrogen stress in birch seedlings. II. N, K, P, Ca, and Mg nutrition. *Physiologia Plantarum* 45: 149-157.
- Jagger, P. and Pender, J. (2003). The role of trees for sustainable management of less-favored lands: the case of eucalyptus in Ethiopia. *Forest Policy and Economics* 5: 83-95.
- James, S.A. and Bell, D.T. (1995). Morphology and anatomy of leaves of *Eucalyptus camaldulensis* clones: variation between geographically separated locations. *Australian Journal of Botany* 43:415 - 433.
- James, S.A.; Bell, D.T. (1996). Leaf orientation in juvenile *Eucalyptus camaldulensis*. *Australian Journal of Botany* 44:139-156.
- James, S.A. and Bell, D.T. (2000). Leaf orientation, light interception and stomatal conductance of *Eucalyptus globulus* ssp. *globulus* leaves. *Tree Physiology* 20: 815 - 823.

- Jiregna, G. (1997). *Decomposition and nutrient release from leaves of Croton macrostachyus and Millettia ferruginea for soil improvement in agroforestry systems*. M.Sc. Thesis, Swedish University of Agricultural Sciences, Sweden.
- Jones, H.G. (1993). Drought tolerance and water use efficiency. *In: Smith, J.A.C. and Griffiths, H. (eds) Water Deficits: Plant Responses from Cell to Community*. Bios Scientific Publishing. pp 193-203.
- Jonsson, I., Fidjeland L., Maghembe, J.A. and Hogberg, P. (1988). The vertical distribution of fine roots of five tree species and maize in Morogoro, Tanzania. *Agroforestry Systems* 6: 63-69.
- Judd, T.S., Attiwill, P. M. and Adams, M. A. (1996). Nutrient concentrations in Eucalyptus: a synthesis in relation to differences between taxa, sites and components. *In: Attiwill, P.M. and Adams, M.A. (eds) Nutrition of Eucalypts*. CSIRO Publishing, Australia. pp123 –154.
- Kamara, C. S. and Haque, I. (1992). *Faidherbia albida* and its effects on Ethiopian highland Vertisols. *Agroforestry Systems* 18: 17-29.
- Killham, K. (1994). *Soil Ecology*. Cambridge University Press. First Edition. Cambridge, UK, 242pp
- Koerselman, W. and Meuleman, A. F. M. (1996). The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* 33: 1441-1450.
- Kozlowski, T.T., Kramer, P.J. and Pallardy, S. (1991). *The Physiological Ecology of Woody Plants*. Academic Press, Inc. San Diego, USA, 657 pp.
- Kramer, P.J. and Boyer, J.S. (1995). *Water Relations of Plants and Soils*. Academic Press USA. 495 pp.

- Lambers, H. and Poorter, H. (1992). Inherent variation in growth rate between higher plants: A search for physiological cause and ecological consequences. *Advances in Ecological Research* 23: 187-261.
- Lambers, H., Chapin, F.S. and Pons, T.L. (1998). *Plant Physiological Ecology*. Springer-Verlag, New York Inc, 540pp
- Lawlor, D.W. (2002). Limitation to photosynthesis in water-stressed leaves: stomata vs. metabolism and the role of ATP. *Annals of Botany* 89: 871-885.
- Lawlor, D.W. and Cornic, G. (2002). Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant, Cell and Environment* 25: 275-294.
- Legesse, N. (1992). Stomatal responses of *Cordia africana* Lam. and four other indigenous tree species of Ethiopia to increasing water stress. *SINET: Ethiopian Journal of Science* 15(1): 45-56.
- Legesse, N. (1994). Africa's indigenous forest species: Problems and proposed research approaches with special reference to Ethiopia. *In: Supporting Capacity Building in Forestry Research in Africa*. Proceedings of the First International Symposium held at ICRAF Headquarters, Nairobi, Kenya, 28 June -1 July 1994, pp. 175-184.
- Legesse, N. (1995). *Indigenous Trees of Ethiopia: Biology, Uses and Propagation Techniques*. Printed by the SLU Reprocentralen, Umea, Sweden. 285pp
- Legesse, N. (2000). The tortuous path ahead: Facing the grim reality of contemporary Ethiopia. *Ethiopian Architects Association Journal* 4:28-31.
- Legesse, N. (2002a) *Erythrina brucei*: Propagation attributes, leaf nutrient concentration and impact on barley grain yield. *Agroforestry Systems* 56: 39-46.

- Legesse, N. (2002b). Review of research advances in some selected African trees with special reference to Ethiopia. *Ethiopian Journal of Biological Sciences*. 1:81-126.
- Li, C. (2000). Population difference in water-use efficiency of *Eucalyptus microtheca* seedlings under watering regimes. *Physiologia Plantarum* 108: 134-139.
- Lindroth, A. and Cienciala, E. (1996). Water use efficiency of short-rotation *Salix viminalis* at leaf, tree and stand scales. *Tree Physiology* 16, 257-262.
- Lisanework, N. and Michelsen, A. (1993). Allelopathy in agroforestry systems: the effects of leaf extracts of *Cupressus lusitanica* and three *Eucalyptus* spp. on four Ethiopian crops. *Agroforestry Systems* 21: 63-74.
- Lo Gullo, M.A., Nardini, A., Salleto, S. and Tyree, M.T. (1998). Change in root hydraulic conductance (K_R) of *Olea oleaster* seedlings following drought stress and irrigation. *New Phytologist* 140: 25-31.
- Lu, C-M. and Zhang, J-H. (2000). Photosystem II photochemistry and its sensitivity to heat stress in maize plant as affected by nitrogen deficiency. *Journal of Plant Physiology* 157:124–130.
- Luan, S. (2002). Signaling drought in guard cells. *Plant, Cell and Environment* 25: 229-237.
- Mafongoya, P.L., Giller, K.E. and Palm, C.A. (1998). Decomposition and nitrogen release patterns of tree prunings and litter. *Agroforestry Systems* 38: 77-97.
- Marschner, H. (1995). *Mineral nutrition of higher plants*. Academic Press, London. 889 pp.
- Martin, B and Thorstenson, Y. R. (1988). Stable isotope composition (^{13}C), water use

efficiency and biomass productivity of *Lycopersicon esculentum*, *Lycopersicon prunellii*, and the F₁ hybrid. *Plant Physiology* 88: 213 – 217.

May, F. and J. Ash. (1990). An assessment of the allelopathic potential of *Eucalyptus*.

Australian Journal of Botany 38: 245–254.

McKersie, B.D. and Leshem, Y.Y. (1994). *Stress and Stress Coping in Cultivated Plants*. Kluwer Academic Publishers.

Mesfin, A. (1998). *Nature and Management of Ethiopian Soils*. Alemaya University of Agriculture, Ethiopia, 272pp.

Meyers, R. J. K., Palm, C. A., Cuevas, E., Gunatilleke, I. U. N. and Brodsard, M, (1994).

The synchronization of nutrient mineralization and plant nutrient demand. *In:* Woomer, P. L. and Swift, M. J. (eds.) *The Biological Management of Tropical Soil Fertility*, John Wiley and Sons, West Sussex, UK. pp 81-116.

Michelsen, A., Lisanework, N. and Friis, I. (1993). Impacts of tree plantations in the Ethiopian highlands on soil fertility, shoot and root growth, nutrient utilization and mycorrhizal colonization. *Forest Ecology and Management* 61: 299-324.

Michelsen, A., Lisanework, N., Friis, I. and Holts, N. (1996). Comparison of under storey vegetation and soil fertility in plantation and adjacent natural forests in the Ethiopian highlands. *Journal of Applied Ecology* 33: 627-642.

Montagnini, F., Ramstad, K. and Sancho, F. (1993). Litter fall, litter decomposition and the use of mulch of four indigenous tree species in the Atlantic lowlands of Costa Rica. *Agroforestry Systems* 23: 39-61.

Mwiinga, R.D., Kwesiga F.R. and Kamara C.S. (1994). Decomposition of leaves of six

- multipurpose tree species in Chipata, Zambia. *Forest Ecology and Management* 64: 209-216.
- Murphy, H.F. (1968). A Report on the fertility status and other data on some soils of Ethiopia. College of Agriculture, Haile Selassie I University. *Experimental Station Bulletin* No. 44: 100-255.
- Nair, P.K.R. (1993). An Introduction to Agroforestry. Kluwer Academic Publisher. The Netherlands, 499pp.
- Nilsen, E.T. and Orcutt, D. M. (1996). *The Physiology of Plants Under Deficit. Abiotic Factors*. John Wiley and Sons, Inc. USA, 689pp
- Nyberg, G and Hogberg, P. (1995). Effects of young agroforestry trees on soils in on-farm situations in western Kenya. *Agroforestry Systems* 32: 45-52.
- Ogren, E. and Öquist, G. (1985). Effects of drought on photosynthesis, chlorophyll fluorescence and photoinhibition susceptibility in intact willow leaves. *Planta* 166: 380-388
- Olsen, J. K. and Bell, L. C. (1990). A glasshouse evaluation of 'critical' N and P concentrations and N:P ratios in various plant parts of six eucalypt species. *Australian Journal of Botany* 38: 281-298.
- Osório, J., Osório, M. L., Chaves, M.M. and Pereira, J.S. (1998). Water deficits are more important in delaying growth than in changing patterns of carbon allocation in *Eucalyptus globulus*. *Tree Physiology* 18: 363 - 373.
- Palm, C. A. (1995). Contribution of agroforestry trees to nutrient requirements of intercropped plants. *Agroforestry Systems* 30: 105-124.
- Pearcy, R.W., Schulze, E.D. and Zimmermann R. (1989). Measurement of transpiration

- and leaf conductance. In: Pearcy, *et al.* (eds) *Plant Physiological Ecology: Field Methods and Instrumentation*. Chapman and Hall, London, UK pp. 137 – 160.
- Pereira de Almeida, A. and Riekerk, H., (1990). Water balance of *Eucalyptus globulus* and *Quercus suber* forest stands in southern Portugal. *Forest Ecology and Management* 38: 55-64.
- Pereira, J.S., Tenhunen, J.D., Lange, O.L., Beyschlag, W., Meyer, A. and David, M.M., (1986). Seasonal and diurnal patterns in leaf gas exchange of *Eucalyptus globulus* trees grown in Portugal. *Canadian Journal of Forest Research* 16: 177-184.
- Pereira, J.S., Araaújo, M.C.C., Borralho, N. and Leal, L. (1987). The effect of water supply on primary productivity and biomass in three clones of *Eucalyptus globulus* in the juvenile phase. In: Grassi, G, Delmon, B., Molle, J. and Zibetta, H. (Eds.) *Biomass for Energy and Industry*. Elsevier, London, pp 531-534.
- Pereira, J.S. and Chaves, M.M. (1993). Plant water deficit in Mediterranean ecosystems. In: Smith, J.A.C and Griffiths, H. (eds). *Water Deficits: Plant Responses from Cell to Community*. Bios Scientific Publishing. pp 237-251.
- Pita, P. and Pardos, J.A. (2001). Growth, leaf morphology, water use and tissue water relations of *Eucalyptus globulus* clones in response to water deficit. *Tree Physiology* 21: 599–607.
- Pohjonen, V. (1989). Establishment of fuel wood plantations in Ethiopia. *Silva Carelica* 14: 1-388.
- Pohjonen, V. and Pukkala, T. (1988). Profitability of establishing *Eucalyptus globulus* plantations in the central highlands of Ethiopia. *Silva Fennica* 22: 307-320.
- Pohjonen, V. and Pukkala, T. (1990) *Eucalyptus globulus* in Ethiopian Forestry. *Forest*

Ecology and Management 36: 19-31

- Pook, E.W., Costine, A.B. and Moore, C.W.E. (1966). Water stress in native vegetation during the drought of 1965. *Australian Journal of Botany* 14: 257-266.
- Poorter, H. and Remkes, C. (1990). Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* 83: 553-559.
- Poorter, H and Evans, J. R. (1998). Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. *Oecologia* 116: 26-37.
- Poorter, H. and de Jong, R. (1999). A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist* 143: 163–176.
- Poschen, P. (1986). An evaluation of the *Acacia albida*-based agroforestry practices in the Harerghe highlands of Eastern Ethiopia. *Agroforestry Systems* 4: 129-143.
- Poschen, P. (1987). The Application of Farming Systems Research to Community Forestry: A Case study in the Hararge Highlands, Eastern Ethiopia. In: Knuth, D. (Ed.) *Tropical Agriculture* 1: 1–250.
- Prioul, J.L. and Chartier, P. (1977). Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO₂ fixation: A critical analysis of the methods used. *Annals of Botany* 41: 789-800.
- Rao, I.J. and Terry, N. (2000). Photosynthetic adaptation to nutrient stress. In: Yunus, M., Pathre, U. and Mohanty, P. (eds) *Probing photosynthesis: mechanisms, regulation and adaptation*. Taylor and Francis. pp. 379–397
- Reich, P.B., Walters, M.B. and Ellsworth, D.S. (1992). Leaf lifespan in relation leaf, plant

- and stand characteristics among diverse ecosystems. *Ecological Monographs* 62:365-392.
- Reich, P. B., Walters, M. B. and Ellsworth, D. S. (1997). From tropics to tundra: global convergence in plant functioning. *Proceedings of National Academy of Science USA* 94: 13730 – 13734.
- Rhoades, C. (1995). Seasonal pattern of nitrogen mineralization and soil moisture beneath *Faidherbia albida* (syn *Acacia albida*) in central Malawi. *Agroforestry Systems* 29: 133-145.
- Rowell, D. L. (1994). *Soil Science: Methods and Applications*. Longman, UK, 350pp.
- Sage, R.F., Sharkey, T.D. and Pearcy, R.W. (1990). The effect of leaf nitrogen and temperature on the CO₂ response of photosynthesis in the C₃ dicot *Chenopodium album* L. *Australian Journal of Plant Physiology* 17:35-360.
- Satter, R.L. and Galston, A.W. (1981). Mechanisms of control of leaf movements. *Annual Review of Plant Physiology* 32: 83-110.
- Schroth, G. and Zech, W., 1995. Root length dynamics in agroforestry with *Gliricidia sepium* as compared to sole cropping in the semi deciduous rainforest zone of West Africa. *Plant and Soil* 170: 297-306.
- Shangguan, Z., Shao, M. and Dyckmans, J. (2000). Effects of nitrogen nutrition and water deficit on net photosynthetic rate and chlorophyll fluorescence in winter wheat. *Journal of Plant Physiology* 156:46-51.
- Stone, E.L. and Kalisz, P.J. (1991). On the maximum extent of tree roots. *Forest Ecology and Management* 46: 59-102.
- Szott, L. T., Fernandes, E. C. M. and Sanchez, P. A. (1991). Soil-plant interactions in

- agroforestry system. *Forest Ecology and Management* 45: 127-152.
- Tadesse, H., Legesse, N. and Olsson, M. (2000). *Millettia ferruginea* from southern Ethiopia: impact on soil fertility and growth of maize. *Agroforestry Systems* 48 (1): 9-24.
- Tesfaye, A. (1994). Growth performance of some multipurpose trees and shrubs in the semi-arid areas of southern Ethiopia. *Agroforestry Systems* 26: 237-248.
- Thulin, M. (1989). *Fabaceae*: In: Hedberg, I. and Edwards, S. (Eds.) *Flora of Ethiopia, Vol. 3: Pittosporaceae to Araliaceae* Addis Ababa University, Ethiopia and Uppsala University, Sweden. pp 49-251.
- Turnbull, J. W. (1999). Eucalypts plantations. *New Forests* 17:37-52.
- Vandenbeldt, R. J. (1991). Rooting systems of western and southern African *Faidherbia albida* (Del.) A. Chev. (syn. *Acacia albida* Del.) –A comparative analysis with biogeographical implications. *Agroforestry Systems* 14: 233-244.
- van Noordwijk, M, Lawson G, Soumare A, Groot J. J. R. and Hairiah, K. (1996). Root distribution of trees and crops: competition and/or complementarity. In: Ong, C.K. and Huxley, P.A. (eds.) *Tree-Crop Interactions: A Physiological Approach*. CAB International, Wallingford, UK, pp319-369
- Von Breitenbach, F. (1961). Exotic Trees in Ethiopia. *Ethiopian Forestry Review* 2: 19-38.
- Von Breitenbach, F. (1962). National Forestry Development Planning, A Feasibility and Priority Study on the Example of Ethiopia. *Ethiopian Forestry Review* 3 / 4: 41 – 68.
- Wendler, R., Carvalho, P. O., Pereira, J. S. and Millard, P. (1995). Role of nitrogen

- remobilisation from old leaves for new leaf growth of *Eucalyptus globulus* seedlings. *Tree Physiology* 15: 679-683.
- White, D.A., Beadle, C.L. and Worledge, D. (1996). Leaf water relations of *Eucalyptus globulus* ssp. *globulus* and *E. nitens*: seasonal, drought and species effects. *Tree Physiology* 16: 469-476.
- White, D.A., Turner, N.C. and Galbraith, J.H. (2000). Leaf water relations and stomatal behavior of four allopatric *Eucalyptus* species planted in Mediterranean southwestern Australia. *Tree Physiology* 20: 1157-1165.
- Wong, S.C., Cowan, I.R. and Farquhar, G.D. (1985). Leaf conductance in relation to rate of CO₂ assimilation. I. Influence of nitrogen nutrition, phosphorus nutrition, photon flux density, and ambient partial pressure of CO₂ during ontogeny. *Plant Physiology* 78:821-825.
- WUARC. (1995). *Commercial Timbers of Ethiopia*. Research Report-Technical Bulletin Number 2. Ministry of Natural Resource Development and Environmental Protection. Ethiopia 1-101.
- Yeshanew, A., Tekalign, M. and Olsson, M. (1999). Changes in some soil chemical properties under scattered *Croton macrostachyus* trees in the traditional agroforestry system in northwestern Ethiopia. *Ethiopian Journal of Natural Resources* 1 (2): 215-233.
- Young, A. (1997). *Agroforestry for Soil Management*. Second Edition. CAB International, UK, 320pp.

10. SYMBOLS AND ABBREVIATIONS

A	Photosynthetic rate
A_{max}	Light saturated photosynthetic rate
Ca	Calcium
CA	<i>Cordia africana</i>
CEC	Cation exchange capacity
CM	<i>Croton macrostachyus</i>
DW	Dry weight
EC	<i>Eucalyptus camaldulensis</i>
EG	<i>Eucalyptus globulus</i>
FA	<i>Faidherbia albida</i>
gs	Stomatal conductance
K	Potassium
LAR	Leaf area ratio
LWR	Leaf weight ratio
MF	<i>Millettia ferruginea</i>
Mg	Magnesium
N	Nitrogen
N:P	Nitrogen to phosphorus ratio
Na	Sodium
OC	Organic carbon
P	Phosphorus
PNUE	Photosynthetic nitrogen use efficiency
PPFD	Photosynthetic photon flux density
Q	Incident light (PPFD)
Φ	Apparent quantum efficiency
Θ	Convexity
R_d	Apparent respiration
RLD	Root length density
RWC	Relative water content
RWD	Root weight density
RWR	Root weight ratio
SLA	Specific leaf area
SWR	Stem weight ratio
SWVP	Saturated water vapor pressure
WL	Water loss
WUE_{GE}	Photosynthetic water use efficiency
WUE_{WL}	Whole plant water use efficiency
WVPD	Water vapor pressure deficit