IMPROVEMENT OF TRADITIONAL *ACACIA SENEGAL* AGROFORESTRY: Ecophysiological characteristics as indicators for tree-crop interaction on sandy soil in western Sudan

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Academic dissertation

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ABSTRACT

The aim of the present study was to investigate the suitability of *Acacia senegal* stands for agroforestry with regard to soil moisture depletion and physiological traits. In the first set of experiments, the effect of tree size on soil water depletion and on such tree characteristics as photosynthesis, stomatal conductance, leaf water potential, relative humidity and inter-cellular CO_2 concentration was examined. The physiological behavior of *A. senegal* was assessed to elucidate its drought adaptation mechanisms. In the second set of experiments the effect of the density of a planted *A. senegal* stand on two traditional food and cash crops, sorghum and karkadeh, was evaluated to determine the interaction between trees and field crops, using gum and agricultural crop yields and physiological characteristics as criteria.

The study was conducted during two rainy seasons in the Domokeya reserve forest near El Obeid town in western Sudan.

Soil moisture was measured initially with a theta probe and subsequently with a neutron probe from different soil strata to the depth of 250 cm. A portable photosynthesis system was used for measuring, in trees as well as in field crops, the photosynthesis rate, stomatal conductance, relative humidity and inter-cellular CO_2 concentration. The leaf water potential was measured with a pressure chamber.

The results indicated that as the tree size increases the amount of water depleted from the soil profile also increases. Significant positive correlation was found between the amount of water in the profile and the tree photosynthetic rate. The data indicated that water uptake by trees of different sizes came mostly from the 0-150 cm soil layer, with less uptake from deeper layers. The morning leaf water potential and stomatal conductance in trees were significantly affected by tree size. Gum production and tree physiological traits were found to be highly responsive to changes in soil water. It was concluded that *A. senegal* is capable of physiological adjustment in response to soil moisture as a form of ecological adaptation.

All measured traits in trees were significantly affected by tree density and by the presence of agricultural crops. There was little evidence of complementarity in resource sharing between trees and crops, since both trees and field crops competed for soil water from the same soil depth. This was the most important interaction noticed between trees and crops. Gum yield increased when sorghum was inter-cropped with trees, and the per-tree and per-area gum yields were higher when the density of trees was higher. With intercropping of karkadeh, the gum yield showed an increasing trend at a low tree density and a decreasing one at a high tree density, but these effects were not statistically significant. This, however, supported the finding that gum production depends on the soil water status.

In both field crops, when grown in an agroforestry system, the yield was higher with a lower density of trees but did not reach the yield level obtained in pure-culture. This effect seemed to depend on soil water availability. Overall, *A. senegal*, when planted at 266 trees ha^{-1}, reduced the karkadeh flower yield by about 26% and its biomass by 37%, and the sorghum grain yield by 19% and biomass by 9%. Planting of 433 trees ha^{-1} reduced the karkadeh yield by 55% and biomass by 57%, and the sorghum grain yield by 44% and biomass by 45%, relative to sole crops. This variation seemed to be caused by the influence of intercropping design on soil water. *A. senegal* agroforestry system seemed to have a higher rain use efficiency as compared to pure tree stands or crops. Intercropping design significantly affected the soil water status, photosynthesis, stomatal conductance and leaf water potential both in trees and in crops. Karkadeh appears to be more appropriate for intercropping with *A. senegal* than sorghum and particularly recommendable in combination with a low tree density. Overall, it was concluded that, in *A. senegal* agroforestry, tree density affects the competition for soil water between agroforestry system components. Modification of tree density can be used as management tool to mitigate competitive interaction in the intercropping system.

Key words: *Acacia senegal*, agroforestry, gum arabic, soil water, tree-crop interaction, sorghum, karkadeh, Sudan.

PREFACE

The present study is a part of research project initiated in 1998 under the name "Improvement of traditional *Acacia senegal* agroforestry in the Sudan" by the Viikki Tropical Resources Institute (VITRI), Department of Forest Ecology, University of Helsinki. The project (now "Trees, agroforestry and land use in dryland Africa", TALDA) is funded by the Academy of Finland.

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List of acronyms and abbreviations

A	Photosynthesis rate (μmol CO_2 $m^{-2}s^{-1}$)
ABA	Abscisic acid
ANOVA	Analysis of variance
ARC	Agricultural Research Corporation
C_i	Intercellular carbon dioxide concentration
DBH	Diameter at breast height
FNC	Forests National Corporation
g_s	Stomatal conductance (mol CO_2 $m^{-2}s^{-1}$)
ha	Hectare
H_I	Harvest index
IWUE	Intrinsic water use efficiency
MPa	Megapascal
N	Nitrogen
OC	Organic carbon
PAR	Photosynthetically active radiation
ppm	Parts per million
RH	Relative humidity
VPD	Vapor pressure deficit
μmol	Micro mole
Ψ_{Lm}	Morning leaf water potential (MPa)

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1. Introduction

1.1 Background

Sudan is a vast country with an area of approximately 2.5 million square kilometers. The most prominent feature of the country is the Nile valley. The Nile River is constituted by the Blue Nile and its tributaries which originate in the Ethiopian highlands, and the White Nile and its tributaries which originate from the Equatorial lakes. The soil in about 60% of the country in the northeast, north and northwest is predominantly sand. Heavy cracking clay soils form a triangular central and eastern plain, which makes up to 30% of the country. Red soils of different types are characteristics of the remaining southwestern portion. Most of the country is flat, except for some few mountain massifs such as Imatong Mountains, Jebel Marra and Erkawit, and other rocky hills. The country is characterized by its long latitudinal extension from approximately 3°N to 22°N, and as such it extends from the region of tropical mixed deciduous forests in the south with an annual rainfall exceeding 1500 mm to the northern desert with a negligible amount of rainfall.

Sudan’s total population in 1999 was 29.9 million, of which 75% are rural. The total population growth rate is estimated at 2.9% per year. The economy is mainly agriculture (including livestock production, forestry and fishing), which contributes about 48% to the Gross Domestic Product (GDP). The forestry sector currently contributes 12% of the Sudanese GDP, a ratio expected to decrease with the increase of the oil revenue (Abdel Nour 1999).

1.2 Forest Resources

Forests in the Sudan render direct and indirect benefits. The indirect benefits include the protection of the environment, watershed protection, soil improvement, work opportunities, browsing and grazing for domestic and wild-life animals, biological diversity conservation, recreation, etc. The most important direct benefits are fuelwood and industrial and building timber. The Forest Products Consumption Survey (FNC, 1995) showed that 70% of the energy consumption in the Sudan is in the form of wood fuel and other biomass. This is equivalent to eight million tons of oil annually. In addition, Sudan is the world's largest producer and exporter of gum arabic, contributing 80 to 90%of the world supply of this commodity. In the mid-60s, gum was exported in great volumes, around 50,000 tons per annum, but the export has decreased steadily to 18,800 tons during the 90s (El-Dukheri 1997).

The coverage of the natural forests was estimated by FAO (1990) as being 19% of the total land area (Mohamed and Bulgies 1997). The recent Global Forests Resources Assessment (FRA) undertaken by FAO (FAO 2000) gave a country forest cover estimate of 17% and an area for other wooded land as 10%, giving a total area of 27% of the country under forest or wooded vegetation cover. The annual deforestation rate was estimated as 1.4%. Taking the FRA (2000) figures, the deforestation rate in the Sudan is still higher than world average (0.24%) or the African average (0.78%). The rate of deforestation in the country has been estimated as being almost 29 times higher than the rate of the reforestation (Mohamed 1997).

The survey of forest product consumption (FNC 1995) and the National Forest Inventory (FNC 1998) gave a very grim picture of deforestation in Central Sudan (Mohamed and Bulgies 1997). The demand and supply study results projected to 1998 gave a total annual consumption of wood of 18.2 million m^3, compared to an annual allowable removal estimate of 11.7 million m^3. The same study also estimated that the deforestation rate was about 4.5%, a rate that can be considered very alarming. As a result, national attention has been given to agroforestry and community forest management. The government has realized that it lacks the capacity of managing these vast areas and coping with this situation.

Gum Arabic Belt

The most important forest in the Sudan may be the gum arabic belt, which lies within the low-rain savanna zone. The term gum arabic belt is used to indicate a zone of mainly 520,000 km^2 in area that extends across Central Sudan between latitudes 10˚ and 14° N, accounting for one fifth of the country's total area (IIED and IES 1990). The belt is considered as an important area because it accommodates around one fifth of the population of the Sudan and two thirds of its livestock population. The belt acts as a natural barrier to protect more than 40% of the total area of Sudan from desert encroachment. The belt is also represents a site of intense and diverse human activities where most of the agriculture and animal production are practiced. This includes irrigated agriculture, mechanized rainfed agriculture, traditional rainfed agriculture and forestry (Ballal 2002).

The commercial gum arabic is an ancient ingredient that has been used since 4000 BC or before. It exudes from *Acacia senegal* (L.) Wild. trees in the form of large (5 cm diameter) nodules or “tears”. Mature trees, 4.5-6 m tall and 5-25 years old, are tapped by making incisions in the branches and stripping away the bark to accelerate exudation. *A. senegal*, the tree commonly known as “hashab”, grows naturally in this belt. The tree has an important role in fulfilling household wood energy and fodder demands, besides enriching the soil fertility, possibly also through biological nitrogen fixation (Ballal 1991). Based on a classification by Harrison and Jackson (1958), *A. senegal* occurs in a number of vegetation types ranging from the semi-deserts and grassland zone in the north of the Sudan to the *Terminalia-Sclerocarya-Anogeissus-Prosopis* savanna woodland in the south of the country.

1.3 Land use, shifting cultivation and agroforestry

A typical land use practice that prevailed in Kordofan, western Sudan, in the past was shifting cultivation with or without bush-fallow (Seif El Din 1984). The *A. senegal* agroforestry system is practiced as a means of restoring the soil fertility and promoting gum arabic production (FAO 1978, DANIDA 1989). Gum production is a pillar of family economy and considered as an income-generating source that requires only a low input of work after the rainy season. The bush-fallow system was built in a way that achieves ecological balance using traditional shifting cultivation, where a long fallow period maintains the soil fertility. Until recently, the traditional *A. senegal*-based agroforestry system was recognized and considered one of the most successful forms of natural forest management in the tropical drylands (Fries 1990), and regarded as sustainable in terms of its environmental, social and economic benefits (Ballal 1991).

Traditionally, the *A. senegal* tree is managed in a time succession with agricultural crops such as sorghum (*Sorghum bicolor* (L.) Moench), pearl millet (*Pennisetum typhoideum* Rich.), groundnut (*Arachis hypogaea* L.), sesame *(Sesamum indicum* L.) and karkadeh (*Hibiscus sabdariffa* L.). This agroforestry system allows a period of 10-15 years for restoring the soil fertility after a short period of arable cultivation (Ballal 2002). The cycle thus consists of a relatively short period of cultivation followed by a relatively long period of fallow.

Ballal (2002), in his study on yield trends of gum arabic, described how the bush-fallow cycle starts by clearing an old gum garden (15-20 years old) for the cultivation of field crops such as millet, sesame, groundnut and watermelon. Trees are cut at 10 cm from the ground surface, and stumps are left to initiate a vigorous coppice re-growth. The cleared area is cultivated for a period of 4-6 years, during which time the coppice shoot re-growth is removed to improve the establishment and growth of agricultural crops. However, when the soil fertility declines (judged by low crop yield), crop growing ceases and the area is left as fallow under *A. senegal*. The remaining trees are tapped for gum arabic until the age of 15-20 years, after which they are cleared again for crop cultivation. Therefore, the final tree stand is mainly the result of coppice regeneration, in addition to some regeneration from seeds dispersed naturally or sometimes from deliberate enrichment planting (Ballal 2002).

The bush-fallow system of cultivation proved to be a successful, sustainable farming system, particularly on the marginal lands of Kordofan. It supports well the livelihoods of the local populations, because it is the major source of both cash, and subsistence. Gum arabic, the main product of *A. senegal*, is a worldwide cash crop, and in addition, fuelwood is obtained from this tree for household consumption and for sale (Sharawi 1986).

Disruption of the bush-fallow system

Establishment of a processing factory of vegetable oil in North Kordofan in the 1940s encouraged many farmers to intensify their groundnut and sesame production, in response to the more favorable prices and productivity of oil seeds. This development, however, has taken place at the expense of the gum orchards, and the traditional rotational fallow cultivation cycle has been dramatically shortened or completely abandoned (Awouda 1973). Consequently, the negative impact on the soil and water has been substantial, to the extent that commercial agriculture is also facing problems (Ballal 2002). Signs of imbalance in the system have been noticed decades ago, and, at present, the area experiences a serious fertility decline, soil erosion and desertification.

Moreover, sustainable management of the gum gardens is threatened because of severe droughts and indiscriminate clearing of *A. senegal* stands for firewood and charcoal production for a short-term, albeit unsustainable, source of income (Elfadl et al. 1998). This has resulted in more land being degraded. Accordingly, the removal of *A. senegal* trees and a general deterioration of stands resulted in reduction of gum arabic production by 30-70% between 1973-1984 (Bayomi 1996). Several authors (Bakhiet 1983, Suliman and Darag 1982) suggested that the spread of desert-like conditions was a result of both physical conditions and misuse of resources. Yagoup et al. (1994), in their investigation on the recovery of biomass productivity in North Kordofan, concluded that land degradation and the ecological imbalance associated with drought cycles and mismanagement could be reversed, if rational management practices were applied in accordance with the availability of water from rainfall.

Generally, agricultural productivity in the Sudan is low as compared to international standards particularly in North Kordofan, the state in which the present study was conducted. The low level of crop production can be attributed to the low and highly variable rainfall, pests and diseases and poor genetic quality of cultivated plant stocks (El-Dukheri 1997). Overall, it seems that unpredictable agricultural productivity poses a threat to all development efforts in the region.

Agroforestry

Agroforestry is an approach to land use based on deliberate integration of trees with crop and/or livestock production systems (Young 1989, Kang et al. 1999). It has the potential to provide rural households with a wide range of products for sale and domestic use such as tree, crop and livestock products, while at the same time ensuring the sustained productivity of crops and animals by protecting and improving the natural resource base. Agroforestry is an ancient practice, but it has benefited from systematic research and experimentation only since the 1970s (ICRAF 1997). At research stations as well as on farms throughout Sub-Saharan Africa, researchers and farmers have already developed new agroforestry practices (Franzel et al. 2001).

Agroforestry production systems show a wide range of applications under different conditions, also including the drylands, and they provide a multitude of products and benefits (Huang and Xu 1999). More efficient sharing of site resources between trees and other intercropping components together with nitrogen fixation and micro-climate modification by trees may significantly increase the overall net production of phytomass (Sharrow and Ismail 2004). In studying carbon and nitrogen storage in agroforestry systems, Sharrow and Ismail (2004) stated that agroforestry could lead to efficient carbon and nitrogen sequestration over time. Research over the past 20 years has confirmed that agroforestry can be more biologically productive, more profitable, and more sustainable than other land use systems. Traditional agroforestry systems in drylands are characterized by high diversity of vegetation, and these systems can also maintain high levels of biodiversity (Nair 1993).

When the nutrient supply in the soil is limited, agroforestry and other tree-based systems are more efficient than herbaceous and mono-cropping systems in the utilization of nutrients to sustain the required levels of agricultural production (Nair 1993, Kang et al. 1985). There is also strong evidence that agroforestry can potentially improve the water use efficiency of agroforestry systems by minimizing the unproductive part of the available soil water (Ong et al. 2002). Plant growth is dependent on the availability of light, water and nutrients, which means that manipulation of tree density in agroforestry systems can modify the biomass production of component species by controlling the inter-specific competition for these resources (Eastham and Rose 1990). Benefits in terms of biomass and grain yields from agroforestry are to be expected only when there is complementarity of resource sharing by trees and agricultural crops (Cannell et al. 1996). The tree density has been shown to have a strong effect on the distribution and depth of the stand roots (Boswell et al. 1975).

In addition to their potential role in preventing excessive erosion, agroforestry systems have been recognized as a tool for rehabilitating already degraded lands (Bandolin and Fisher 1991). Trees improve crop productivity by reducing the wind flow and thereby reducing water loss through evapotranspiration (Zinkhan and Mercer 1997). In order to improve the productivity of agroforestry systems much work has already been done in studying tree-crop interaction under varying tree spacing regimes (cf. Gupta et al. 1998). Agroforestry systems can considerably increase the rainfall utilization as compared to annual cropping systems, largely due to the temporal complementarity of system components (Ong et al. 2002).

1.4 The aim of the study

The overall goal of the present study was to provide management tools for natural *A. senegal* forests that are under threat of being cleared for farming purposes and for *A. senegal* plantations, on the sandy soils of the western part of the Central Sudan, so as to maintain a natural or planted tree component in the farming system and to enhance its sustainability.

Specific objectives

The specific objectives were as follows:
1. To quantify the physiological responses of *A. senegal* trees and associated agricultural crops as affected by soil water conditions.
2. To elucidate the adaptation mechanisms of *A. senegal* in relation to drought and specifically to determine how competition for water is associated with physiological responses of crops and trees in such an agroforestry system.
3. To determine the effect of tree size on soil water depletion, as reflected in photosynthesis, stomatal conductance and leaf water potential.
4. To determine the effect of *A. senegal* tree density on the performance and yield of traditional agricultural crops intercropped with trees.
5. To establish the role of an agroforestry system in enhancing the utilization of available water to increase the overall productivity, particularly as related to gum yield.

2.Theoretical framework and setting of hypotheses

2.1 Agroforestry potential

The development of dryland agroforestry systems rests on the idea that trees owing to their deep root systems penetrate deeper into the soil than crop roots and access water and nutrients that are inaccessible to the crop. However, it is well known that in many situations tree roots compete with associated crop roots for soil water and under these circumstances the system must be modified or managed in such a way as to optimize the root functions to stimulate the facilitative effects of tree roots (if any) and reduce the negative competitive effects (Huang 1998, Schroth 1999).

The potential of agroforestry systems to increase agricultural production on dryland can be viewed in the ability of the system components to utilize efficiently the available resources to increase production. Woody species usually compete with their companion annual crops for the limited water and nutrients, hence, the production of crops and forage often decreases in intercropping systems (Kessler and Breman 1991).

To increase the production of agroforestry, one has to consider carefully which woody species and which properties in them could serve the identified objective, where and under what circumstances (Kessler and Breman 1991). Therefore, clear understanding of structure and function of an agroforestry system is considered to be essential for planning and management of the systems. Careful input-output calculation of all components is needed. This includes not only capital and human inputs, but also the space occupied and overlaps of niches between all components especially if environmental stability is the main reason to introduce trees in agriculture (Kessler and Breman 1991).

High production from agroforestry systems needs efficient and judicious management of resources, which in turn will depend on an appropriate combination of tree and crop species and management interventions such as tree pruning and tree density and arrangement regimes (Ong et al. 1992). Management of the interaction of all components in agroforestry systems aims at maximizing the positive and minimizing the negative interaction (Huang 1998).

The most difficult problem in managing agroforestry systems on drylands is how to achieve the positive effects of trees on the soil while reducing the negative effects of below-ground competition for limited resources, so as to provide opportunities for temporal and spatial complementarity (Ong and Leakey 1999). A key issue is the degree of complementarity, either spatial or temporal, in the location of root systems of all components in agroforestry (Odhiambo et al. 2001). Mack and Harper (1997), Fowler (1981) and Davidson et al. (1985) demonstrated that the behavior of the plant in a mixture of two species may be quite different from its behavior in a more diverse mixture.

The most important measure for managing competition in agroforestry systems is to weaken, or re-direct, the competition between trees and associated crops (Huang 1998, Ong and Leakey 1999). The plant density in agroforestry systems may vary widely, depending, for instance, on how a species controls water loss, or increases water uptake, or adapts to soil characteristics (Migahid and Elhaak 2001).

2.2 Tree-crop interactions

2.2.1 Competition and facilitation

In intercropping situations, competition among plants occurs below and above the ground (Casper and Jackson 1997; Huang 1998; Ong and Leakey 1999). On dryland, soil water is a major determinant of the competitive relationships between trees and ground vegetation in forests (Sand and Nambiar 1984, Collet et al. 1996), on savannas (Scholes and Archer 1997) and in agroforestry systems. In agroforestry, trees and crops interact in many ways leading to positive or negative impacts on their growth and performance.

The influence of one species on another one through influencing the environment relates to the theory of ecological niche. A state in which a species lives in an original unchanged niche is called the fundamental niche, while the realized niche is considered as a state in which a species lives in an environment modified by other species (James et al 1984; Hill 1990; Huang 1998). In agroforestry, associated plants may interact in many ways, ranging from severe competition through complementarity to facilitation. Trees are planted on agricultural land for many reasons, and in various types of planting arrangements and tree densities. Agroforestry system productivity is the result of positive or negative interaction between components. Facilitation and competition occur together in nature, co-occurring within the same community and other systems (Callaway et al 1991, Callaway and Walker 1997).

Competition

The most important (and relatively well understood) mechanism that reduces the yield of plants in polyculture as compared to monoculture is the process of competition (Sanchez 1995). Agroforestry components utilize spatially or temporally the same resources, such as water, nutrients and light (Nair 1993). Competition occurs when plants grow in proximity and interact in negative ways causing reduction in each other's performance and production (Sanchez 1995, Huang 1998). Competition can manifested itself as interference competition or exploitation competition (resource competition) (Huang 1998, Nair 1993). However, the term interference has also been used as a term for negative interaction (Vendermeer 1989).

In many situations, when water is adequate and the soil relatively fertile, competition for light may be the main limiting factor, while competition for nutrients can be severe, especially for agricultural crops in an agroforestry system (Nair 1993).

Competition for soil water, which is likely to take place in most agroforestry systems, occurs when the root zones of neighboring plants overlap (Le Roux et al. 1995; De Montard et al. 1999; Ong and Leakey 1999).

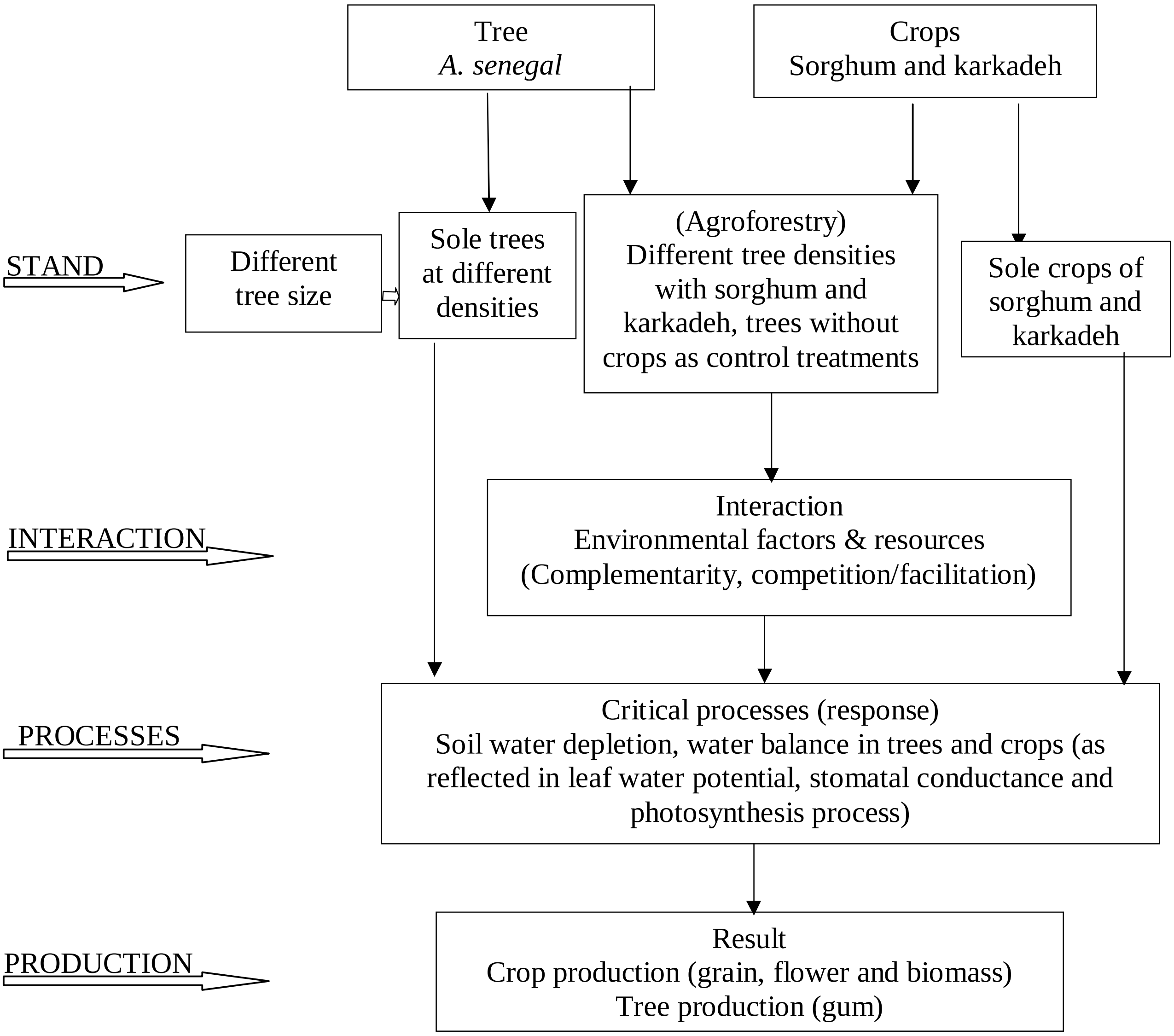

Figure 1. Assessment of the suitability of *A. senegal* as an agroforestry component through analysis of tree-crop interaction in relation to different environmental conditions. Adapted from Tuomela (1997).

Below-ground interaction is the most important factor determining the yield reduction in the arid and semi-arid tropics, where water is the prime factor limiting crop growth (Ong et al. 1991, Ong and Leakey 1999). Generally, since the movement of nitrogen and water in soil is similar, the main soil resources most likely to be subject to below-ground competition between plants are nitrogen and soil water (Bruke et al. 2001). Allelopathy and microclimate modification for pests and disease have been described as interference interaction in many agroforestry systems (Nair 1993).

Facilitation

Facilitation can be defined as the process in which positive interaction between individuals or population exists. In agroforestry, positive effects of plants on the establishment and growth of other plants have longer recognized (Vendermeer 1989). A plant can facilitate another by modifying the shared environment so as to provide more favorable conditions for better growth. It has been pointed out by Holmgren (1997), who presented selected examples from a variety of ecosystems, that facilitation is the process in which net primary productivity can be increased by enhancing the potential of resource capture and improving the environmental conditions, and by efficient use of resources, production of stimulators, reduction of allelopathic effect, preventing of competitors and pathogens and attraction of pollinators. Facilitation is more dominant in drier areas (Holmgren 1997).

Facilitative interaction is influenced by the development stage of the interacting species (Callaway 1995). Facilitation also occurs as indirect interaction, when a third species or population modifies the interaction between the two other species (Miller 1994). Facilitative interaction may strongly depend on plant age and density (Kellman and Kading 1992), hence both of these factors can alter the balance between competition and facilitation.

Competition and facilitation management

Management of resources in agroforestry is highly concerned with maximizing the potential of resource sharing and minimizing the interference between components (Huang 1998). Appropriate management of trees in agroforestry is essential for effective pest and disease suppression and control (Staver et al. 2001). Resource sharing can be spatial or temporal and include above and below-ground resource use. Sustainable agroforestry should minimize the pest problem and achieve protection mainly by creating environmental conditions that deter pests and build up favorable conditions for their natural enemies (Rao et al. 2000). Studying of endemic pests and their natural enemies is essential when designing an agroforestry system. Agroforestry can play an important role in substituting the chemical pest control by affecting such factors as the microclimate and soil nutrients (Staver et al. 2001).

Frieda et al. (2001) concluded that greater light availability under an open tree stand may allow other land uses such as grazing or cultivation of agricultural crops. Trees can contribute to prevention of soil erosion, amelioration of soil fertility and soil organic matter, and to the improvement of the microclimate, particularly as barriers against dry winds and high temperature. Effects on trees by the crop are determined by the particular intercropping design and technology and by the specific environmental conditions (Kho 2000).

It becomes evident that, in intercropping, shallow-rooted crops and deep-rooted trees can be grown together to share the resources in a complementary manner. However, arguments have been raised against the occurrence of complementarity in dryland environments (Rao et al. 1997) and, consequently, competition can be understood as being inevitable. Other researchers have argued for complementarity that even can be enhanced by tree pruning or adjustment of tree spacing and density (Huxley et al. 1994, Schroth 1999).

Another management tool that can alter competitive interaction in intercropping systems is the manipulation of tree density. This factor has been found to modify the water use and the productivity of both the trees and the understorey annual crops (Eastham et al. 1990). This adjustment to water (plants per water unit) is used in many Sahelian crops, instead of adjustment to land (plants per unit of land). Strong proponents of agroforestry (cf. Wallace 1995) argue that combining trees and annuals improves the water use of the system, since the amount of water utilized by trees can by no means be greater than the evaporation loss from bare soil. However, some Sahelian sandy soils form a dry non-capillaric layer on top, protecting the water deeper in the soil profile; hence, evaporation may be less than transpiration. In contrast, to Wallace's (1995) view, Le Roux et al. (1995) concluded that both shrubs and grasses in a West African savanna obtained most of their water from the topsoil layer, causing strong competition for soil water and nutrients.

As pointed out by Huang (1998), coexistence (existing together, at the same time, or in the same place) is crucial to the success of any agroforestry model designed to increase the yield or to achieve other advantages, because it provides opportunities for intercropping components with management adaptation not only to the environment they share, but also to each other. He also emphasized that, in an agroforestry system, resources can be shared horizontally by managing the spatial dispersion and regulating the composition of coexistent systems. Consequently, understanding of the ecophysiological aspects of forests and agroforestry systems practiced in them is vital for setting better management guidelines.

Theoretically, the water conducting system of a plant should, on the one the hand, be built in a way that allows for high water flow rates, a high degree of stomatal opening, and high transpiration and thus also high carbon assimilation rates. On the other hand, it should be built so that xylem embolism is avoided, even when the plant water potential becomes very negative, under harsh drought conditions (Bettina et al. 2000).

Water stress can be a limiting factor in agroforestry systems. Soil moisture depletion mainly occurs in the topsoil layer (Leyton 1983). The greatest depletion of water under an evergreen forest usually occurs at depths between two and three meters, whereas other, shallow-rooted plants take up relatively little or no water from that depth (Eales 1980). Understanding of how crops grow and survive under harsh conditions, when the availability of water is the most limiting factor, is important for successful establishment and production of crops on drylands.

Plants in dry environments depend to a large extent on their ability to adjust to soil moisture fluctuations. For each species, there is a specific adaptation mechanism to offset detrimental effects of both soil and atmospheric water deficits (Elfadl 1997). Many species in tropical forests experience a prolonged dry season with little rainfall and the upper soil layer undergoing acute drying (Mulkey et al.1996). Stable-isotope-based studies have shown that trees of different size classes belonging to the same species tap different sources of soil water (Dawson 1996). Spatial and temporal utilization of soil water in larger trees, due to their higher nutrient demand associated with their wide crown leaf area, may reflect a necessary trade-off (Meinzer et al. 1999). The upper layer of the soil profile is usually characterized by a higher soil nutrient content (Jobbagy et al. 2001) and the lowest water content during the dry season. Although soil water is freely available at greater depths during the dry season, the abundance of the most limiting nutrient for the plant at these depths can be expected to be lower than that of the topsoil (Meinzer et al. 1999, Jobbagy et al. 2001).

2.2.2 Physiological adjustment in response to soil water

Physiological mechanisms associated with drought tolerance have been studied in several tree species (cf. Bongarten and Boltz 1986; Bongarten and Taeskey 1986; Teskey et al. 1987; Bernier et al. 1994; Johnsen et al. 1996; Tuomela 1997; Li 1999). These studies also indicate significant, and potentially exploitable, *intra-specific* variation in a number of morphological and physiological traits related to drought tolerance, including the rates of gas exchange and stomatal behavior (cf. Cregg and Zhang 2001). When water is limiting, regulation of water utilization and water balance is a key component of adaptation to the environmental conditions (Meinzer et al. 2003). Comparative studies of plant water relations frequently rely on leaf-level measurements of variables such as stomatal conductance, transpiration and water potential, which often differ markedly among co-occurring species (Meinzer et al. 2003). Plant species have developed many physiological, morphological and anatomical adaptation mechanisms to cope with water deficit and drought (Arndt et al. 2001).

The movement of water through the soil-plant-atmosphere continuum is controlled by plant function: plants take up, store, and release water in response to different environmental and physiological stimuli, and the plants also affect the soil hydrology (Burgess et al. 2000). A basic principle of plant ecophysiology is the trade-off between the capability of a genotype to grow when resources are rich, and its capacity to tolerate shortage in resources (Chapin 1980; Huston 1994; Bazzaz 1996). On drylands, especially where long dry periods prevail, a conservative water-balance behavior is common, because it allows the plant to use the available water efficiently and leaves soil water also to be used later during the dry period (Jones 1980, Tuomela 1997).

Reduction of the soil water availability as a result of soil drying brings on restriction of water uptake by the plant and consequently a reduction of the tissue water content (Kramer 1988). The stomata have a greater effect on CO_2 exchange than on transpiration due to the additional resistance associated with CO_2 diffusion relative to water in the leaf (Cowan 1982, Nobel 1991). However, at light-saturation, the stomatal conductance can be used as the reference parameter to reflect drought intensity; a common response pattern has been observed that is not much dependent on species or environmental conditions (Medrano et al. 2002).

Light and moisture regimes influence the ability of plants at different stages of development to assimilate carbon and access water. In split-root experiments, it was found that the stomatal behavior changed when only part of the root system was in drying soil (Ali et al. 1999). Jones and Sutherland (1991) have proposed that the prime role of the stomata might be in leading to avoidance of damaging plant water deficits.

Changes in physiological traits during the aging and development of woody plants can provide insight into factors that influence the recruitment and survival of the species (Donovan and Ehleringer 1991, 1992; Franco et al. 1994). Measurements of the stomatal conductance in large tree crowns indicate a considerable degree of responsiveness to environmental and plant physiological variables. This is consistent with many observations reported for other plants (Wullschleger et al. 1998; Jones and Sutherland 1991; Hubbard et al. 2001). In field crops, it is also known that water deficiencies, if severe, can cause serious damage, or alternatively lead to adaptation through physiological and morphological mechanisms to offset the damaging water deficit (Jones 1980; Deng and Shan 1995; Liang and Zhang 1999; Shan et *a*l. 2000; Moriana et al. 2002).

Stomatal function mediates one of the most important physiological trade-offs in vascular plants, preserving a favorable water balance in leaf tissues while providing CO_2 for the photosynthesis process (Cowan et al. 1972, Cowan 1982). Analysis of the effect of stomatal behavior on total gas exchange can provide empirical evidence on the principles that govern the adaptive stomatal role for plants under different environmental conditions; it can also explain the nature and mechanisms of the stomatal response (Meinzer 1982).

Better understanding of the use of rain by plants requires precise information on responses of gas exchange to rainfall (Schulze 1986). On a seasonal basis, stomatal conductance and canopy transpiration have been found to be mainly related to the pre-dawn leaf water potential and thus to soil moisture and rainfall (Marcelo et al. 2000).

The fact that tree mortality from xylem dysfunction is relatively rare (e.g. Kavangh and Zaerr 1997), would indicate that the mechanism regulating stomatal aperture is highly sensitive to the balance between water supply and water loss (Meinzer and Grantz 1991; Jones 1998; Maier-Maercker 1998; Davies and Zhang1991; Atkinson et al. 2000). Photosynthesis depends on many environmental factors such as light, temperature, CO_2 concentration, and nutrient and water supply. Assuming the other factors constant, the variation in the photosynthetic rate can be presented as a function of soil moisture or the plant water status (Beardsell et al. 1973; Lovett and Tobiessen 1993; Reich et al. 1993). Usually there is an initial range of leaf water potential that leads to little or no reduction in stomatal conductance or net assimilation rate. If the water potential continues to decline during drought, a point is reached where stomatal conductance starts to decrease rapidly. The water potential at which this happens is termed the water potential threshold (Sobardo and Turner 1983).

Leaf water potential is a key indicator of the water status of plants and its relationship with atmospheric factors (cf. Correia and Martins 1995, Atkinson et al. 2000). Leaf water potential can also be used as a measure of active root distribution and the use of soil water or rainwater by plants (Flanagan et al. 1992, Donovan and Ehleringer 1994).

2.2.3 Water use efficiency

With increasing worry about the availability of water resources in both irrigated and rainfed agriculture there is a high interest in developing and understanding of how to improve the water use efficiency (WUE) and also how land use systems can be modified to use the available water more efficiently (Jerry et al. 2001). Identification of the factors underlying variation in the WUE is important, since they can either positively or negatively affect the productivity, depending on the main processes than determine the changes in WUE (Udayakumar et al. 1998). WUE in general terms accounts for any measure that reduces the amount of water used per unit of any given activity. WUE measurements are promoted as a way of benchmarking the efficiency of rainfall use, and for identifying factors that limit the efficiency of use of the available soil water.

French and Schultz (1984), when studying a complex situation to estimate WUE from rainfall, calculated the rain use efficiency as kg $ha^{-1}mm^{-1}$ of rainfall. In their study, runoff, drainage, and initial and final soil moisture were neglected. The overall rainfall use efficiency can be improved through adoption of more intensive cropping systems in arid and semiarid environments (Jerry et al. 2001).

Because agroforestry practices alter the microclimate, they also affect the WUE of plants growing in those systems (Kohli and Saini 2003). Tree canopy alters not only the air humidity but also the light and temperature regimes around intercropped agricultural plants (Wallace and Verhoef 2000). Agroforestry systems can improve the WUE through influence on rainfall interception, infiltration and evapotranspiration, while the total water use of the system may increase as well as decrease (Uffe and Kirsten 2001).

Many researchers argue that the field crops and trees in an agroforestry system intercept rain and increase the evaporative area by their leaves, stems and branches. The term WUE is somewhat misguided, as plants loose water to the atmosphere rather than use it as a raw material for the production of biomass (Monteith 1993). However, WUE expressed as harvestable dry matter mass per unit of available water mass (Nair 1993) or per unit of rainfall in mm (French and Schultz 1984) would be a convenient measure for many purposes.

A higher production per unit rainfall is one of the fundamental challenges in dryland management. Improvement of the intrinsic water use efficiency, i.e. the ratio of CO_2 assimilation to transpiration rate at the stomatal level, may be one means of achieving higher production per unit rainfall (Condon et al. 2002). Available data indicate that it is likely that a high intrinsic water use efficiency is associated with conservative water use but also with conservative growth and production, if there is no water stress (Condon et al. 2002). The intrinsic water use efficiency can be calculated as the slope of the linear portion of the regression line for CO_2 assimilation versus stomatal conductance (Osmond et al. 1980; Martin et al. 1994; Pimentel et al. 1999). The WUE may be estimated from measurements of dry weight accumulation over time relative to the amount of water transpired or by measurement of gas exchange (instantaneous water use efficiency). The instantaneous WUE may be calculated as a ratio of CO_2 assimilation rate (A) to stomatal conductance (g_s) or to transpiration rate (T) (A/g_s or A/T), since T is the function of both g_s and water vapor pressure deficit (Cregg and Zhang 2001, Howell 2001).

2.3 Hypotheses

The following hypotheses were constructed based on the above specific aims:
1. The variation in water balance characteristics in *A senegal* follows the variation in the soil moisture regimes.
2. Soil water depletion depends on tree size and density.
3. In addition to shedding of leaves, regulation of stomatal conductance acts as the principal mechanism for adaptation to drought in *A. senegal*.
4. Competition between trees and crops for water depends on tree density and intercropping design.
5. Agricultural crops have no effect on gum production when grown with *A. senegal*.
6. In an *A. senegal* agroforestry system the yield and physiological behavior of agricultural crops are strongly affected by different intercropping designs.

3. Material and methods

3.1 Agricultural crops in Kordofan, Sudan

Kordofan or the region lying between the White Nile region in the east and the Darfur region in the west is known for being a drought-prone zone. Due to recurrent drought periods, especially during the 1970s and 1980s, agricultural production has declined and food shortage has become a prominent feature in the area (KFIS 2003). Farming in North Kordofan State is essentially rainfed, mainly on sandy soils, where farmers grow agricultural crops for subsistence and for cash to generate income (El-Dukheri 1997).

Sorghum bicolor (L.) Moench; or sorghum is one of the most important cereals globally and considered as the principal food crop in Sudan for the rural and urban population. It constitutes two thirds of the cereal production of the country (Bedawi et al 1985). Sorghum can be grown under a wide range of climatic and soil conditions. In Sudan, it has also been considered a strategic crop. This grain and fodder crop is well adapted to the drier climates due to its ability to withstand high temperature. It has a large number of fine roots to extract moisture from the soil (Appendix, Fig. 46. It has an ability to remain dormant during drought, and shoot parts of the plant grow only after the establishment of the root system. Sorghum competes favorably with most weeds and has a higher net photosynthesis rate, using the C_4 system, compared to many other cereals (Bennett et al.1990, Meeske and Basson 1995). In Kordofan, the largest group of sorghum producers are the small-scale poor farmers who have no access to production inputs such as fertilizers or pesticides. Production trends for sorghum and other cereals have been declining and fluctuating in North Kordofan State, where the yield is low compared with productivity in the whole Kordofan region and at the national level (Bedawi et al. 1985). The average sorghum production of farmland in North Kordofan is estimated as 131 kg ha^{-1} for grain and 931 kg ha^{-1} of total above ground biomass (MAF 1990;2000).

Among the main cash crops, *Hibiscus sabdariffa* L., known as karkadeh in Sudan, is an important cash crop in Kordofan due to its steadily increased demand and consistently high prices over many seasons. It grows successfully on the sandy, well-drained soil of the Kordofan region, and it contributes to alleviation of poverty and increase in food security due to its value as cash crop (KFIS 2003). *Hibiscus sabdariffa* is an annual semi-herbaceous shrub of the Malvaceae family. Karkadeh is an ideal cash crop for North Kordofan because it is drought-tolerant, easy to grow, and can be grown as part of an intercropping system, and because it has limited pest problems (Eltohami 1997, KFIS 2003). Data collected on karkadeh production in North Kordofan over a period of 10 years estimate the average farmland production as 36 kg ha^{-1} for flower and 418 kg ha^{-1} for above-ground biomass (MAF 1990-2000). In addition to flowers, it produces fodder and fiber. The main harvested part is the bright-red calyx of the flower. As described by Eltohami (1997): "The petals of *Hibiscus sabdariffa* contain flavonoids and red pigment comprising gossipten and hibiscin together with phytosterolin and organic acids malic, citric, tartaric, ascorbic and hibiscic acids. The seeds also contain a high percentage of mucilage (62 %) and a fixed oil. The ripe calyces are used for hot and cold beverages. Medicinally it is used as antispasmodic, hypotensive, antimicrobial and for relaxation of the uterine muscle" (Eltohami 1997).

3.2 Study area

The study was conducted during the period from July 1999 to November 2000 at Domokeya forest (13°16' N; 30°12'E) in western Sudan. The forest lies 31 km east of El-Obeid town (Fig 2). Rainfall in this area varies greatly in time and space (Appendix Fig. 44). The long-term average annual rainfall at this location is 300 mm; and it occurs from July to September. The first rainy season (1999) during the study was characterized by a markedly high rainfall, 364 mm (typical for a wet year), while the second season (2000) was characterized by low rainfall 226 mm (typical for a dry year). The mean relative humidity is 34%, decreasing to 14% during the drier months and increasing to 60% in the wet season. The mean annual evaporation is 15.5 mm/day and increases to 20 mm/day in the hot summer months (Ballal 2002). The daily mean minimum and maximum temperatures are 20 and 34^{o}C, respectively. Temperatures can be as high as 46°C during the hot summer months. Analysis of soil samples collected from all experimental sites indicated that the soil at the experimental sites consisted of deep, highly uniform sandy soils, classified as sandy, siliceous, isohyperthermic typic Torri psamments which are easy to work but poor in organic matter and essential nutrients. Results show that all nutrient elements in the soil were below the optimum requirement for maximum growth. Such soils are non-saline and non-sodic and slightly acidic with low water holding capacity. The total

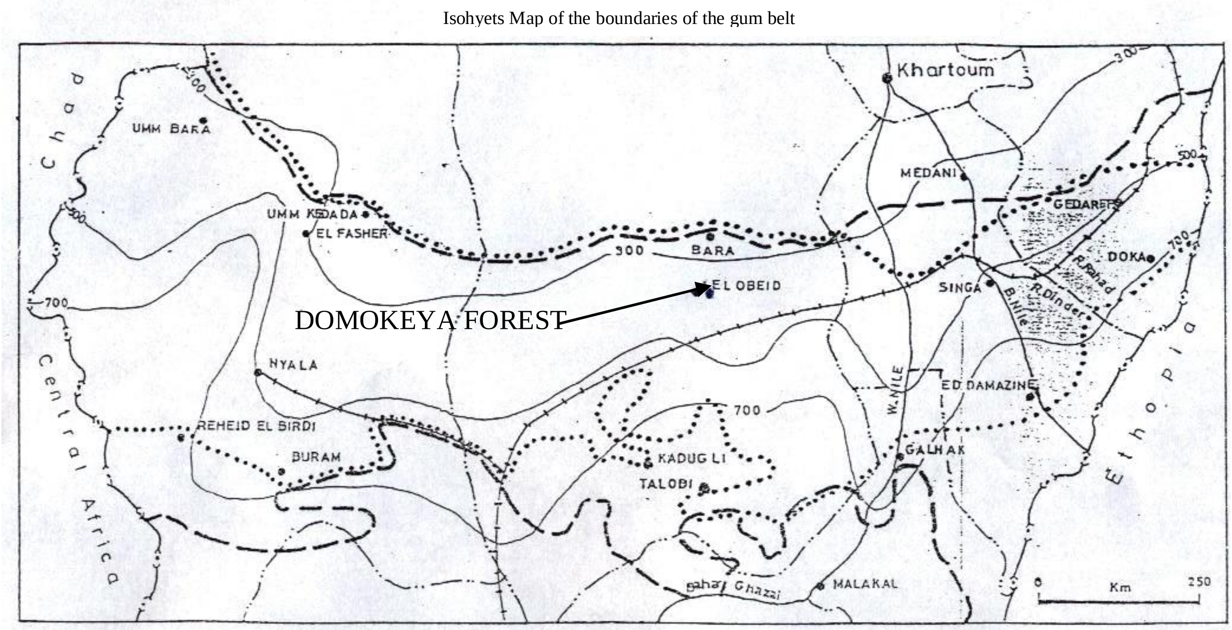
Isohyets Map of the boundaries of the gum belt

Figure 2. Map of the gum arabic belt in the Sudan showing the study area (Domokeya reserve forest), isohyets, and the "gum belt" of Sudan according to different authors. Adapted from Ballal (2002).

available water (water retained between field capacity and permanent wilting point) was measured as about 16%. The infiltration rate as measured with double ring infiltrometer was high (6.0 mm/min), thus surface runoff is not common on these sites (Table 1).

Existing trials with *A. senegal* provenances, methods of stand establishment, tree age groups, and the density of plantations, as well as the occurrence of natural *A. senegal* stands makes this experimental forest an appropriate site for the present research (cf. Ballal 1991). El Obeid is the national center for gum arabic research in Sudan under ARC.

Table 1. Soil properties at the experimental sites. CS: Coarse sand; FS: fine sand.

Soil depth (cm)	Mechanical analysis (%)				Exchangeable bases (Cmol$^+$/kg)		P (ppm)	pH 1:5	Total water (% w/w)	
	CS	FS	Silt	Clay	K	Ca			-0.1 bar	-15 bar
0-25	42	51	4	3	0.11	48.5	6.0	6.5	18	2
25-50	41	51	3	5	0.14	56.0	5.2	6.4	17	3
50-75	42	53	2	3	0.08	28.7	5.0	6.4	18	2
75-100	43	52	2	3	0.09	24.6	5.2	6	18	3
100-125	34	56	5	5	0.09	23.3	6.6	6	19	3
125-150	42	53	3	2	0.09	38.3	6.2	6.2	18	2
150-175	41	53	3	3	0.09	31.4	3.3	6	17	2

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3.3 Field experiments

Natural forest: Interaction of tree size, soil water and physiological traits

The natural forest experiment started with random selection and numbering of fifty natural *A. senegal* trees in the Domokeya forest. The basal diameter, diameter at breast height, height and the canopy diameter were measured and used to differentiate the tree size classes. Basal diameter was chosen to be the criterion. Accordingly, trees were arranged into five size classes: <5cm, 5-10 cm, 10-15 cm, 15-20 cm and 20-25 cm of basal diameter. Two trees from each size class were randomly selected for data collection.

Measurement of rainfall was made by use of a rain gauge installed at the site. The first reading of soil moisture was taken on 16/8/99 by using a theta probe (Delta-T Devices, Cambridge, UK) by inserting the probe into the soil to different depths. Soil moisture was measured at 1-m distance from the tree trunk at soil depths of 25, 50, 75, 100, 150, 200 and 250 cm. For easier work, from the second reading onwards, the measurements were taken every two weeks during the rainy seasons (1999 and 2000) by use of a neutron probe (Troxler, Model 4302). Moreover additional readings were taken monthly during the dry period October 2000- September 2001.
Ten vertical access tubes, each 3 m long, were installed in the soil 1 m away from the tree trunk. Readings were taken from the same depths as previously described for the

theta probe. Total soil water to 75 cm, 150 cm and 250 cm depths (as recommended by ARC soil specialist) was used for comparison and correlations.

Water depletion was calculated as the difference between the previous total soil water added with the rainfall and the measured total soil water (subsequent readings). Both Theta probe and neutron probe were calibrated for the site. Data were collected and recorded.

Soil samples were collected from different depths (0-25, 25-50, 50-75, 75-100, 100-125, 125-150, 150-175 cm) for chemical and physical analysis.

Simultaneously with every measurement of the soil moisture during first and second year, a pressure chamber (SKY, SKPM 1400, UK) was used to measure the morning leaf water potential (ψ_{Lm}) of selected trees. Two readings from each tree were taken and averaged. The mean was calculated for each size class (n=2). At the same time of measuring leaf water potential and soil moisture, a portable closed photosynthesis system (Li-6200, Lincoln, Nebraska, USA) was used to measure the net photosynthesis rate (A), stomatal CO_2 conductance (g_s), relative humidity (RH), and intercellular CO_2 concentration (C_i). Three readings were taken from each tree and averaged. Adult, healthy leaves were selected for measurements. Leaf areas were determined and entered into the data logger. The mean was calculated for each size class (n=2). Measurements were carried out before mid-day (from 8-10 h local time).

Ten selected trees were tapped in the local conventional way by using the traditional “sonki”) tool. Five branches from each tree were tapped (for the tapping intensity study) from mid October onwards (five pickings), and the gum from each tree was collected and weighed. The first gum picking was carried out six weeks after tapping and subsequently, the remaining pickings were done every 15 days from the pervious one.

Field experiment: agroforestry

A field experiment of 1.9 ha was established in a six-year-old *A. senegal* plantation in the Domokeya research forest during the rainy season of 1999. The experiment was arranged in a randomized complete block design (RCBD) with three replications and 24 plots (600 m^2 each). Two densities of *A. senegal* were chosen, and thinning was performed, when appropriate, to adjust the density. These densities were 16 or 26 trees/plot, corresponding to 266 or 433 trees/ha. Two crops, sorghum (*Sorghum bicolor* (L.) Moench ‘Zinari’ and karkadeh (*Hibiscus sabdariffa* L.), local variety, were sown during the two rainy seasons (1999 and 2000) as soon as the rainfall was sufficient to moisten the soil. These crops were established solely and with the two selected tree densities. Sorghum was sown at 75x35 cm spacing and karkadeh with 75x25 cm spacing corresponding to ARC recommendation. The monocropping plots and weed-free stands of trees with the two densities were used as controls. The experimental layout can be summarized as follows:

Main plot factor: *A. senegal* tree density	Sub-plot factor: Intercrop
Level 1: 16 trees/plot (226 trees/ha)	Level 1: sorghum
Level 2: 26 trees/plot (433 trees/ha)	Level 2: karkadeh
Level 3: no trees	Level 3: no crops

Combinations of these factors resulted in the total of 8 treatments. These were arranged to the three complete blocks (24 plots in all). Sole *A. senegal* at two densities, sole sorghum and sole karkadeh served as control treatments.

In this experiment, the measurement of the rainfall was also done by use of a rain gauge installed at the site of the experiment. Soil moisture for the trees and crops was measured in each plot with the neutron probe. Two vertical access tubes, one 3-m long and at 1 m distance from a randomly selected tree in the middle of each plot, and another 1 m long and four meters away from the same tree, were installed in the soil in the intercropped area. In addition, an access tube of 3-m was also installed in each plot (6 plots) of pure *A. senegal*. An access tube 1-m long was also installed in each plot of pure crops (6 plots). As described for the natural forest experiment, readings were taken at depths of 25, 50, 75, 100, 150, 200 and 250 cm from the 3-m access tubes and at 25, 50, and 75 cm from the 1-m access tubes. Since, the bulk of the lateral and fine root was found to be at the topsoil as indicated by ocular inspection of root distribution of trees and crops, the total soil water to 75 cm and 250 cm depths was calculated for comparison between different intercropping designs. Readings were taken every two weeks during crop development (August-December), covering the early stage (establishment), mid stage (flowering), and late stage (maturity).
The morning leaf water potential (ψ_{Lm}) for both trees and crops was measured in replicates simultaneously with the soil moisture measurements in all treatments using a pressure chamber (SKY, SKPM 1400, UK). Two readings were taken and averaged. All measurements were carried out before mid-day from 8-10 h local time.

Using adult healthy leaves of both trees and crops, a portable closed photosynthesis system (Li-6200, Lincoln, Nebraska, USA) was employed to measure the photosynthesis rate (A), stomatal CO_2 conductance (g_s), relative humidity (RH) and intercellular CO_2 concentration (C_i) for both trees and the crops every two weeks simultaneously with soil moisture and leaf water potential measurements. Leaf areas were determined and entered to the Licor instrument. Three readings were taken and averaged.

Crop air-dried yield and above-ground air-dried biomass (total dry matter) were weighed after harvest. Trees in all replicates were tapped (five branches per tree) from mid-October onwards for five gum pickings, and the gum yield in each treatment (intercropping design) was collected and weighed. The harvest index was calculated for both agricultural crops as a fraction of economic yield in relation to their total dry matter production.

The intrinsic water use efficiency (IWUE) for both trees and crops was calculated by dividing net photosynthetic rate by stomatal conductance (μmol CO_2 mol^{-1} CO_2). The rain use efficiency was calculated for trees as gum yield per unit rainfall and for field crops as harvestable yield per unit rainfall (kg ha^{-1} mm^{-1} rainfall). The rain use efficiency was calculated for different cropping designs as economical yield (gum + grain, gum + flower, and sole gum, grain or flower) per unit rainfall (kg $ha^{-1}mm^{-1}$ rainfall).

Soil samples were collected from both experimental sites of experiments for determining the soil moisture characteristic curve (Fig. 43) and the infiltration rate. Soil analysis and the determination of a soil moisture characteristics curve and the infiltration rate was done in the ARC soil laboratory.

Nitrogen and carbon under A. senegal

The existence of nodules in *A. senegal* was tested during 1999 and 2002 before and during the rainy season. The roots of ten trees of different size classes from both experimental sites (five trees each) were excavated for ocular inspection of root distribution and presence of nodules to a depth of 1.5 m (Fig. 46). Soil samples were collected at two occasions both in 1999 and in 2002 from under mature *A. senegal* trees of different size classes from a depth of 0-30 cm, 30-60 cm, 60-90 cm and 90-120 cm and also from the vicinity of two non-nitrogen fixing tree species, namely *Balanites aegyptiaca* Del. (heglig) and *Azadirachta indica* A. Juss. (neem) for control. Samples were air-dried and brought to the ARC laboratory for N and C analysis.

3.4 Statistical analysis

Statistical analyses were performed with the JMP (3.2.2) statistical software by SAS Institute Inc. (JMP 1995). Scatter plot, regression techniques were employed to determine the relationship between soil water status, gum yield, CO_2 exchange and other physiological traits. Linear fit and polynomial fit (degree=2) were used for regression lines. Treatment effects were considered significant if $p< 0.05$. For yield comparison among intercropping designs and grouped means, one-way Anova was used for all replications in a randomized complete block design. When significant difference was detected, a comparison of all mean values was done by Tukey-Kramer HSD and Duncan at Alpha = 0.05. Regression modeling for comparison of the effect of soil water at different depths on water depletion was also used. Microsoft Excel was used for graphical presentation.

4. Results

4.1 Soil water and physiological characteristics of *A. senegal* in the natural forest

4.1.1 Water in the soil profile

The within-profile water content under natural *A. senegal* trees during a 12-month measurement period (October 2000 to September 2001) shows that there was an increase in soil water in February- March and in May (Fig. 3). The findings suggest that hydraulic redistribution of soil water during the dry season may take place under *A. senegal*, particularly during the later gum production period (January to March) and before the onset of the rainy season (early May) when the trees start to have new leaves. This result indicates that an increase in soil water during the dry season in different soil layers may be due to upward movement of water from moister to drier portions of the profile via root systems. This finding also suggests that *A. senegal* with its deep taproot and far-reaching lateral roots could potentially redistribute soil water from deep layers to the sandy soil surface.

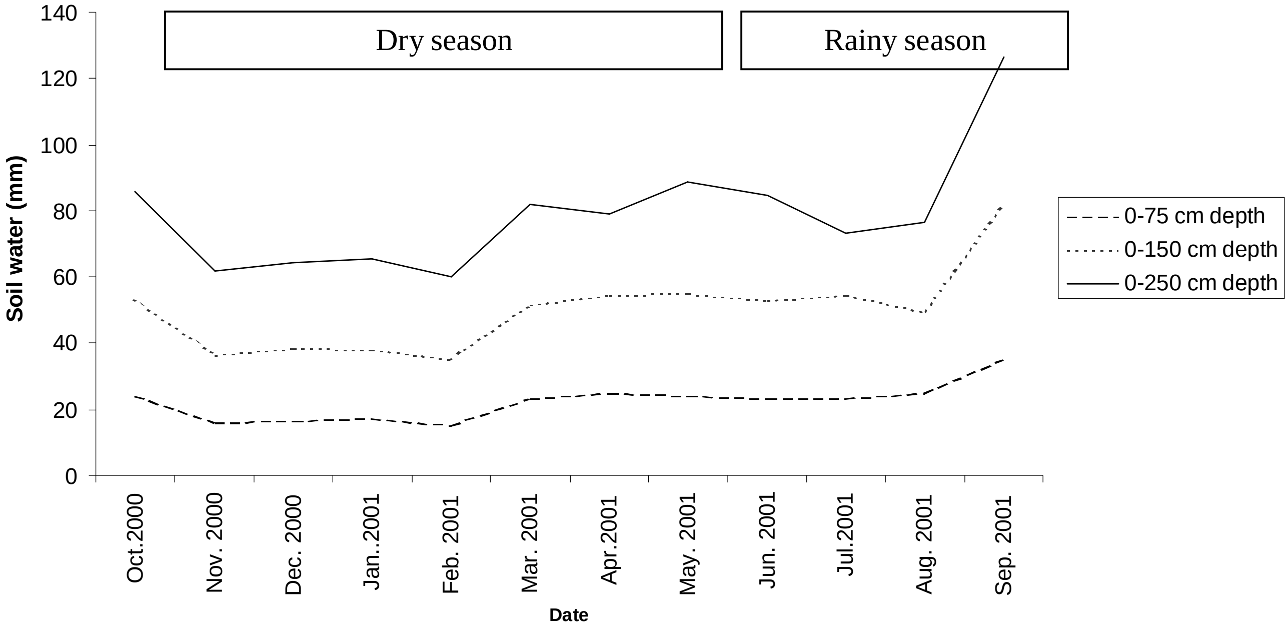

Figure 3. Total soil water in 0-75, 0-150, and 0-250 cm soil layers under *A. senegal* trees during the period October 2000 to September 2001. Data were collected from the two largest tree size classes.

4.1.2 Effect of tree size on soil moisture

The total soil moisture contents in the 0-75 and 0-150 cm soil layers were significantly ($P< 0.0001$) affected by tree size (Table 2). The highest soil moisture was found under the smallest (< 5 cm basal diameter) and the lowest soil moisture under the largest (20-25 cm) trees. Total soil water in the 0-250 cm soil layer was also affected but less significantly (*P*=0.002) by tree size.

Table 2. Effect of tree size on the amount of water (mm) in 0-75, 0-150 and 0-250 cm soil layers during two rainy seasons. Means followed by the same letter are not statistically different at *P* = 0.05. The data were collected from the pure natural stand with different tree size classes of *A. senegal*.

Tree size class	Amount of soil water (mm)		
	0-75 cm	0-150 cm	0-250 cm
>5 cm	23.97 a	53.22 a	82.19 a
5-10 cm	23.14 a	50.01.3 a	74.88 ab
10-15 cm	19.97 ab	44.83 b	69.30 ab
15-20 cm	18.69 b	44.62 b	73.81 ab
20-25 cm	19.81 b	44.42 b	72.08 b
Significance level	*P*=0.0002	*P*<0.0001	*P*<0.002
Std error	0.93	1.51	2.35

The water depletion rate was highest during the rainy seasons (August-September) and decreased gradually towards the dry period (Fig. 4). This indicates that *A. senegal* utilizes water rapidly when water is available.

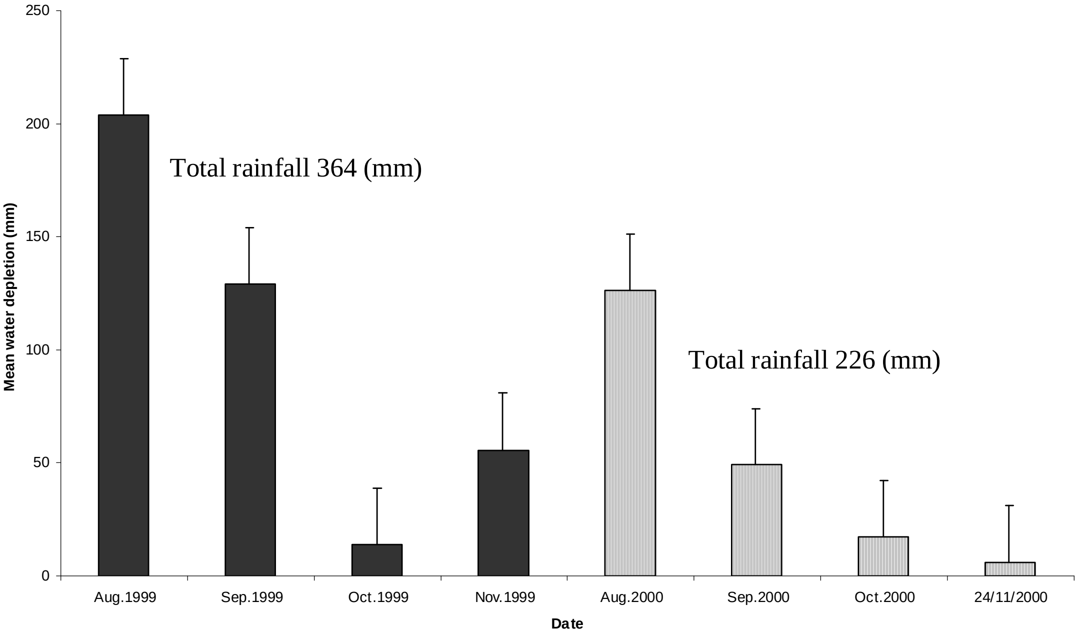

Figure 4. The average soil water depletion under *A. senegal* during two rainy seasons (1999 and 2000). Data were collected from different tree size classes (showing the avearge). Bars indicate standard error.

Regression modeling as shown in Fig. 5 a - c indicates that the soil water depletion under *A. senegal* seemed to be a function of the amount of water retained in the soil profile; this was true for the three different layers studied, namely 0-75, 0-150 and 0-250 cm (because of the calculation procedure, water depletion may accordingly exceed the amount of water stored, cf. Chapter 3.2). Multiple regression modeling to predict water depletion as a function of total soil water in the 0-150cm and 0-250 cm soil depth shows that 66% of water depletion can be explained by total soil water retained in the 0-150 cm and 0-250 cm soil depths. The effect was found mainly by the soil water in the 0-150 cm soil depth (Fig.5 d). This indicates that the water depleted came mostly from the 0-150 cm soil layer.

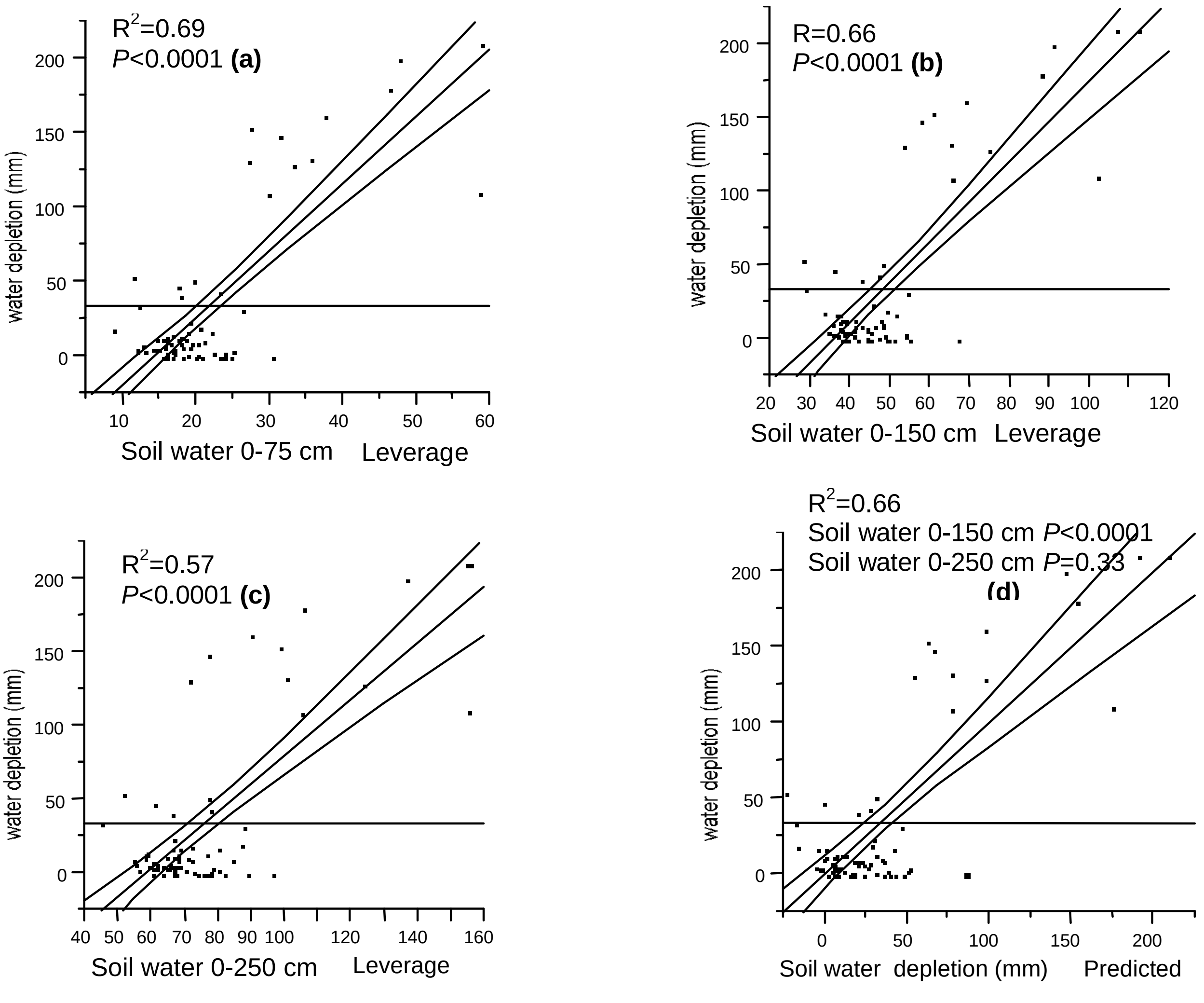

Figure 5. Relationship between soil water depletion under *A. senegal* and total soil water contained in the different soil layers. Data were collected during two rainy seasons from stands representing different tree size classes. The middle line is the mean response and curves are show the confidence curve fit.

4.1.3 Effect of soil water on physiological characteristics

Stomatal conductance

The stomatal CO_2 conductance (g_s) correlated positively (R^2 =0.70) and highly significantly (P <0. 0001) with the total soil water in the 0- 250 cm soil layer and, somewhat less significantly, with soil water in the 0-75 cm and 0-150 cm soil layers (R^2 = 0.64 and 0.65, respectively); (Fig. 6 a-c). This result suggests that the soil water content determined the stomatal aperture, and that the mechanism regulating the stomata was highly sensitive to water supply and loss under the conditions now observed.

A significant difference (P=0.004) in average stomatal conductance (g_s) existed between the wetter year (364 mm rainfall, showing a higher conductance) and the drier year (226 mm rainfall, showing a lower conductance); Fig. 7. This result suggests the role of g_s in the adaptation of *A. senegal* to drought.

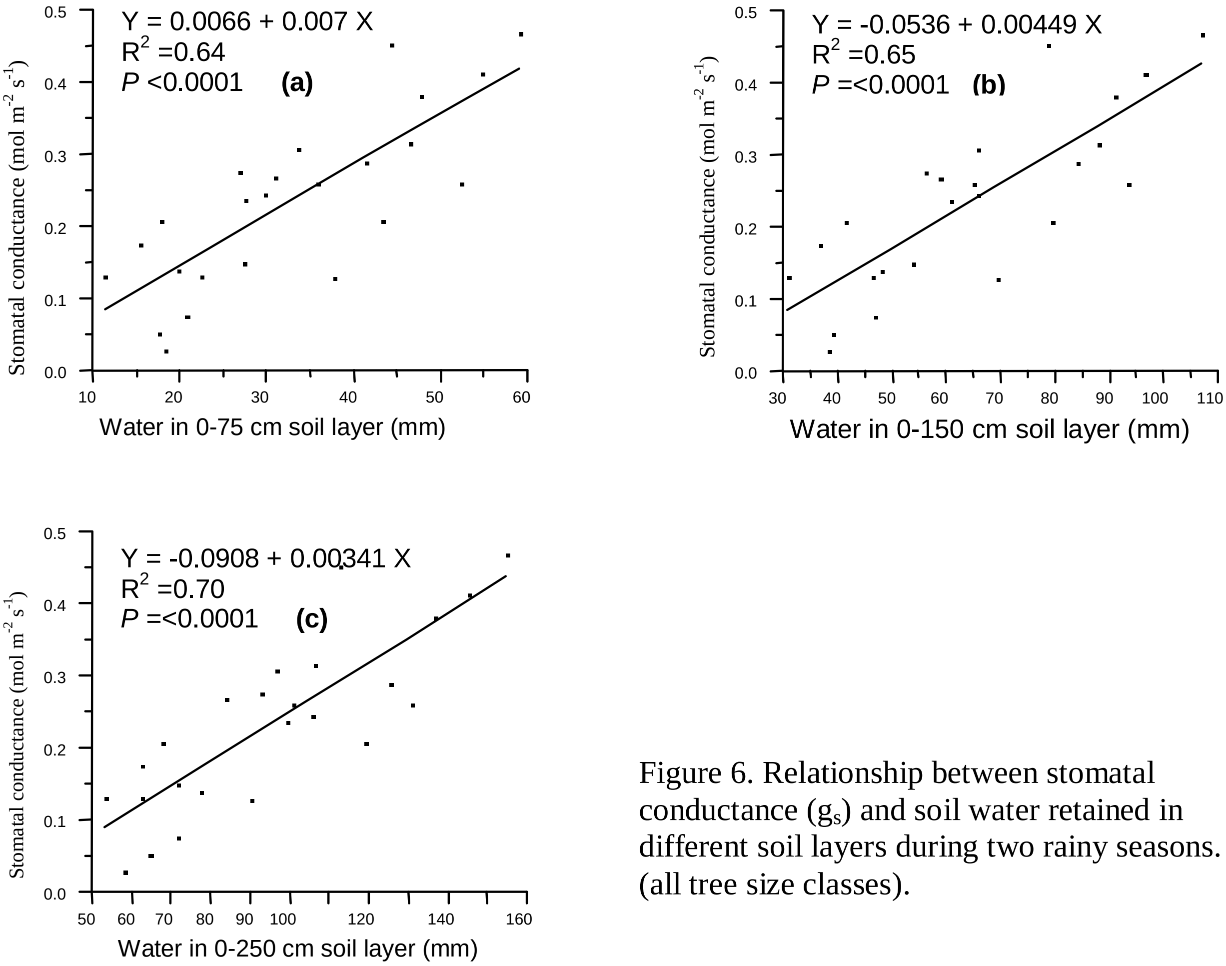

Figure 6. Relationship between stomatal conductance (g_s) and soil water retained in different soil layers during two rainy seasons. (all tree size classes).

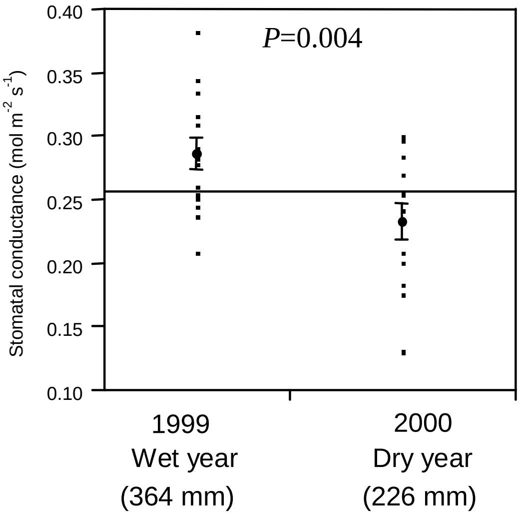

Figure 7. Comparison between stomatal conductance (g_s) in *A. senegal* during a wet and a dry year. Data were collected during and one month after the rainy seasons. Wet year: 364 mm rainfall, dry year: 226 mm rainfall. Line indicates the mean of response and bars indicate standard error.

Photosynthesis

The rate of net photosynthesis (*A*) correlated significantly (R^2=0.66) with the total water content in the 0-250 cm soil layer (*P*=0.0004); (Fig. 9c), while the correlation with soil water in the 0-150 cm or 0-75 cm layer (Fig 9 a b) was lower (R^2 = 0.49 and 0.47, respectively) but still significant (*P* =0.005 and 0.007, respectively). *A. senegal* seemed to respond to short-term water shortage by closing the stomata as a mechanism to reduce water loss and thus reducing the leaf photosynthesis. CO_2 exchange rates were clearly coupled with the water status in the soil profile.

There was no significant difference in photosynthetic rates (A) observed in the wet and the dry year (Fig. 8). In other words, *A. senegal* showed little variation in photosynthesis in relation to the annual rainfall. This could reflect adaptation to drought by maintaining a stable photosynthetic activity even under low leaf water potential.

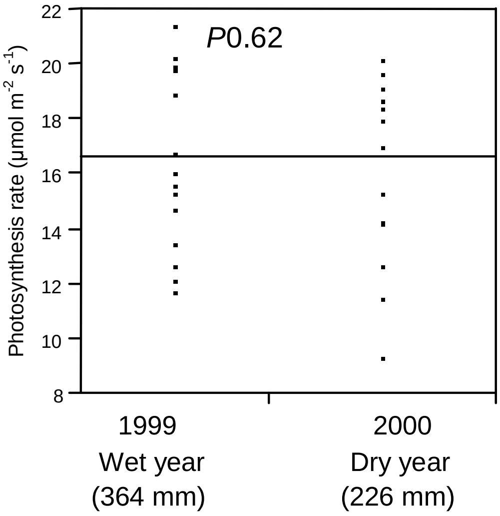

Figure 8. Comparison between morning photosynthetic rate (A) in *A. senegal* during a wet and a dry year. Data were collected during and one-month after the rainy seasons. Standard error = 1.21. Line indicates the mean of response.

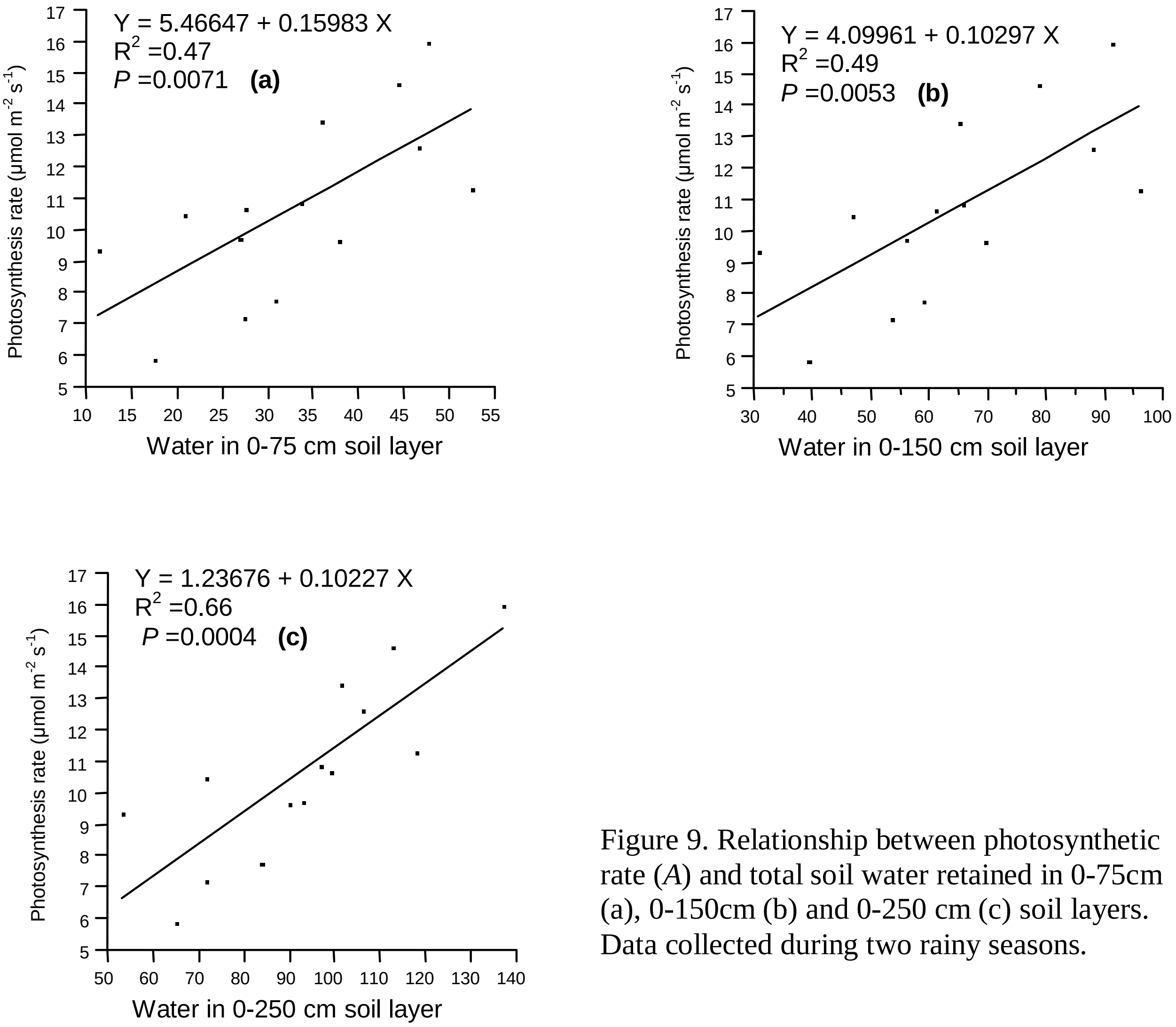

Figure 9. Relationship between photosynthetic rate (*A*) and total soil water retained in 0-75cm (a), 0-150cm (b) and 0-250 cm (c) soil layers. Data collected during two rainy seasons.

Morning leaf water potential

The morning leaf water potential (ψ_{Lm}) in the natural *A. senegal* trees was significantly and positively correlated with soil water retained in all soil layers (Fig. 10 a - c). Thus ψ_{Lm} was an indicator of soil water status effect on *A. senegal* leaves. Consequently, ψ_{Lm} can provide a useful indirect measure of the soil water status and the efficiency of water uptake in this tree species.

In the present study a comparison was made between the morning leaf water potential (Ψ_{Lm}) behavior in the wet year when the rainfall was 364 mm and the dry year when the rainfall was 226 mm (Fig. 11). A significant difference was found in the morning leaf water potential in the dry year (lower than -3.0 MPa one month after the rainy season) as compared with that in the wet year (about -2.0 MPa one month after the rainy season). This result indicates that access to soil water was the primary factor influencing the variation in the leaf water potential in *A. senegal*. This can also be explained as a mechanism for improved water uptake during incipient water decrease.

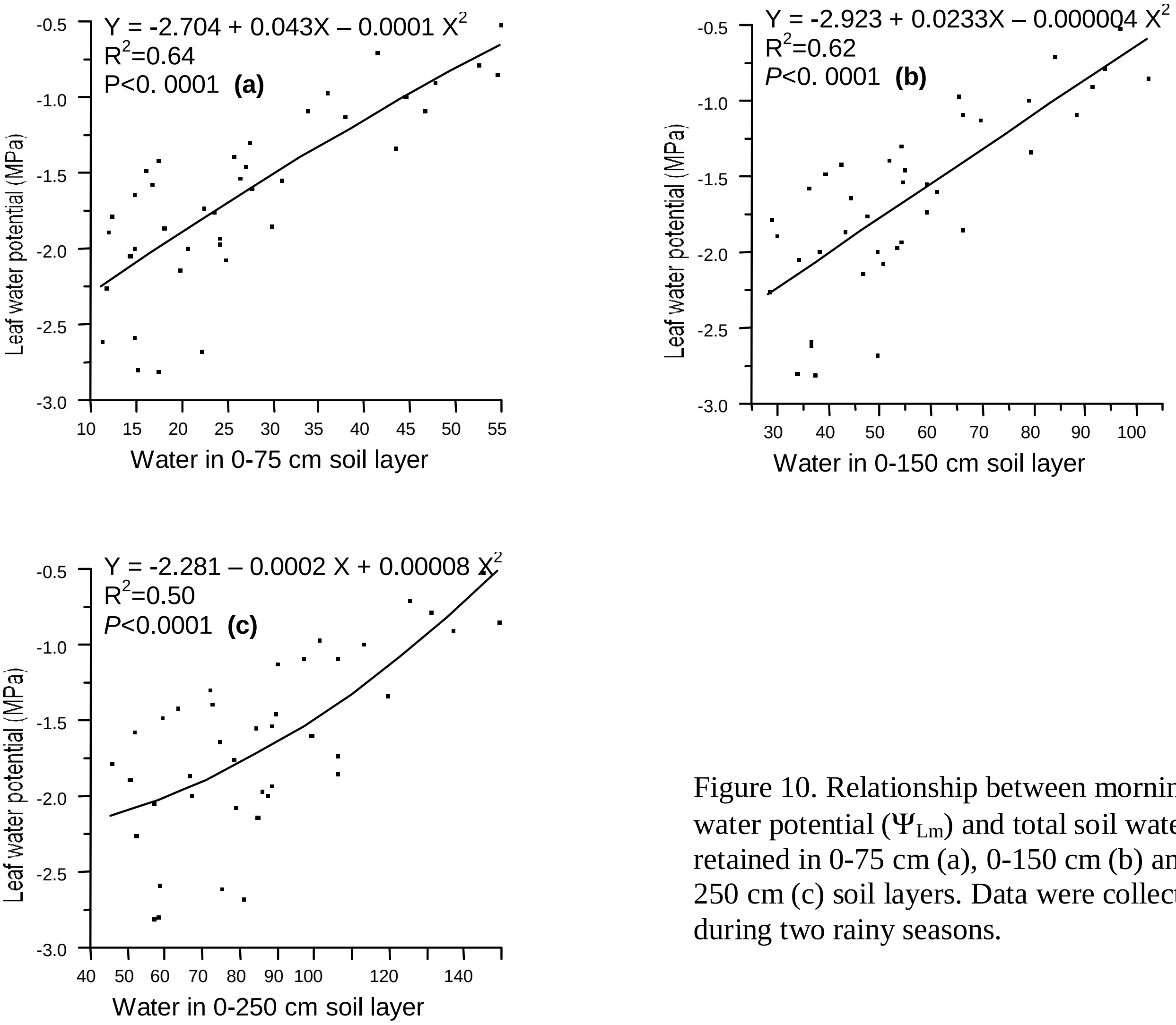

Figure 10. Relationship between morning leaf water potential (Ψ_{Lm}) and total soil water retained in 0-75 cm (a), 0-150 cm (b) and 0-250 cm (c) soil layers. Data were collected during two rainy seasons.

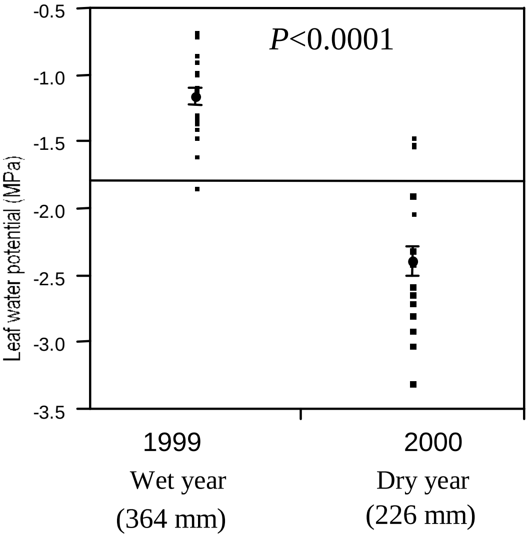

Figure 11. Comparison between morning leaf water potential (Ψ_{Lm}) in *A. senegal* during a wet and a dry year. Data were collected during and after mid-rainy seasons. Diamonds indicate the mean values, The line indicates the mean of response and bars indicate standard error.

4.2 Tree size and physiological characteristics in the natural forest

Statistically significant differences (*P*= 0.005) between morning leaf water potential ψ_{Lm} were detected between the tree size classes (Table 3). Measurements of the morning stomatal CO_2 conductance (g_s) obtained in the crowns of *A. senegal* trees suggested a considerable (*P*<0.0001) degree of responsiveness to tree size. The morning stomatal conductance (g_s) tended to increase with the increase in tree size (Table 3).

Table 3. Effect of tree size on morning leaf water potential (ψ_{Lm}) and stomatal conductance (g_s) in *A. senegal* (data collected during two rainy seasons). Means followed by the same letter are not statistically different at *P* = 0.05.

Tree diameter class	Leaf water potential (MPa)	Stomatal conductance (mol m^{-2} s^{-1})
< 5 cm	-1.56 a	0.2184 b
5-10 cm	-1.49 a	0.2930 b
10-15 cm	-1.32 ab	0.3766 b
15-20 cm	-0.98 b	0.7341 a
20-25 cm	-0.79 b	0.9132 a
Significance level	*P* =0.005	*P* <0.0001
Std Error	0.15	0.031

4.3 Correlations between physiological characteristics in the natural forest

The stomatal CO_2 conductance (g_S) correlated significantly (R^2 =0.74, *P* <0.0001) with the relative air humidity (Fig. 12). This result shows that the relative air humidity is a good predictor of stomatal conductance and hence of net photosynthesis in *A. senegal* (see Fig. 16).

The intercellular carbon dioxide concentration (C_i) in *A. senegal* was positively correlated with the stomatal CO_2 conductance (g_s) in the morning (R^2 =0.63,*P* =0.0001); (Fig. 13).

Fig. 14 illustrates how, in *A. senegal*, the stomatal CO_2 conductance (g_s) correlated positively with the morning leaf water potential (ψ_{Lm}) (R^2 =0.65, *P* <0.0001). The stomatal conductance (g_s) was thus found to be highly sensitive to a wide range of leaf water potential (which closely followed the variation in soil water balance, cf. Fig. 10) during the morning hours in the rainy season.

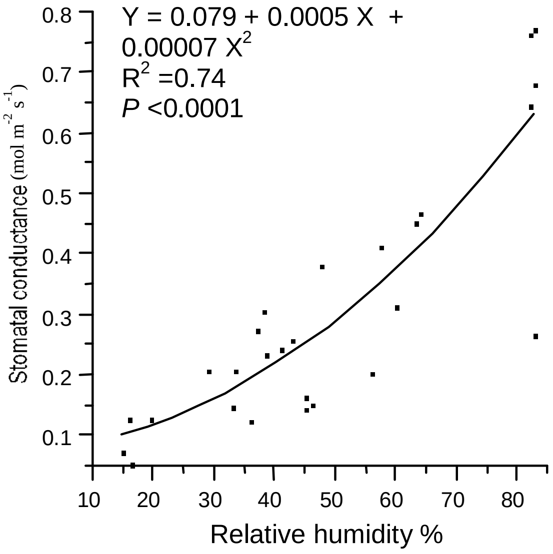

Figure 12. Relationship between stomatal conductance (g_s) in *A. senegal* and relative air humidity. Data were collected from different tree size classes during two rainy seasons.

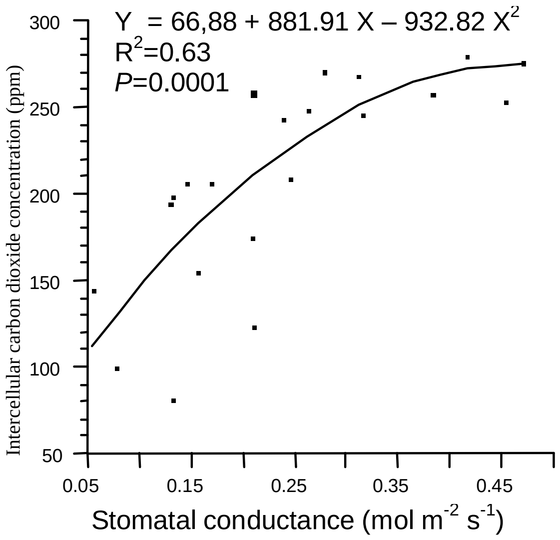

Figure 13. Relationship between stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) in *A. senegal*. Data were collected from different tree size classes during two rainy seasons.

The morning (8-10 h) measurements in *A. senegal* indicated that the photosynthesis rate (*A*) correlated significantly ($P = 0.0018$) with the leaf water potential (ψ_{Lm}) (Fig. 15). This observation corroborated the role of leaf water potential as a key indicator of water balance and CO_2 exchange in this species. In these measurements, the photosynthesis rate (*A*) also correlated significantly ($P = 0.0024$) with the stomatal CO_2 conductance (g_s) (Fig. 16). This particular relationship was more distinctly linear than those described above. The result demonstrated the expected role of the stomata as regulators of the CO_2 flux. Consequently, a low photosynthesis rate, when occurring in *A. senegal* in the morning, can be probably more ascribed to stomatal control of carbon dioxide uptake than to low leaf water potential. This would, however, also imply that *A. senegal* has a stomatal regulation mechanism that can ensure net photosynthesis even at a relatively low water potential.

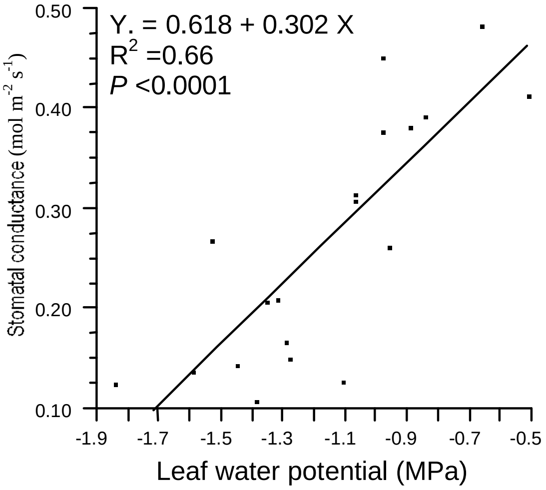

Figure 14. Relationship between leaf water potential (ψ_{Lm}) and stomatal conductance (g_s) during two rainy seasons. Data were collected from different tree size classes.

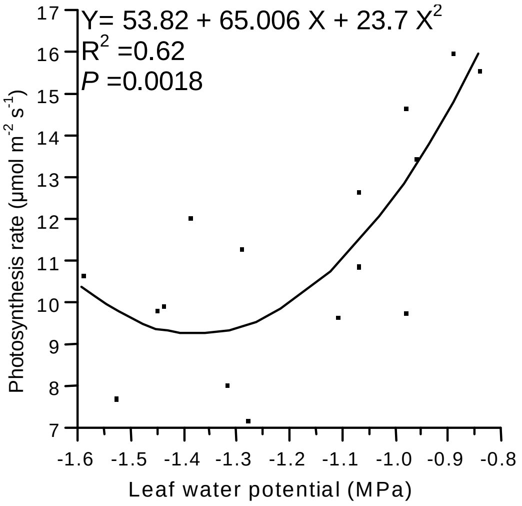

Figure 15. Relationship between leaf water potential (ψ_{Lm}) and photosynthesis (A) during two rainy seasons (August –September). Data were collected from different tree size classes.

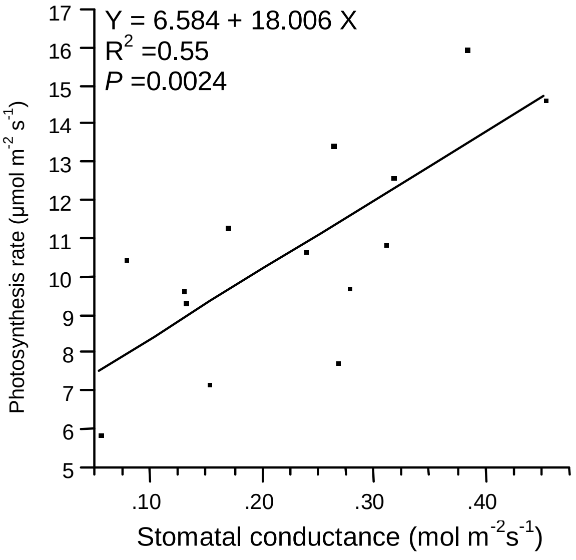

Figure 16. Relationship between stomatal conductance (g_s) and photosynthesis. Data were collected during two rainy seasons (July-September).

4.4 Gum production

Soil water and gum production

The gum yield in the tapping (dry) season was affected by the availability of soil water during the preceding rainy season. The yield correlated significantly with the total soil water in the 0-75 cm and 0-150 cm soil layers ($R^2 = 0.65$, $P<0.0001$and 0.43, $P=0.0001$, respectively); (Fig. 17 a, b), while, in contrast, there was no significant correlation between gum production and the total soil water in the 0-250 cm soil layer (Fig. 17 c). This indicates that gum production was strongly affected by the topsoil water but not by that in the deeper soil layers.

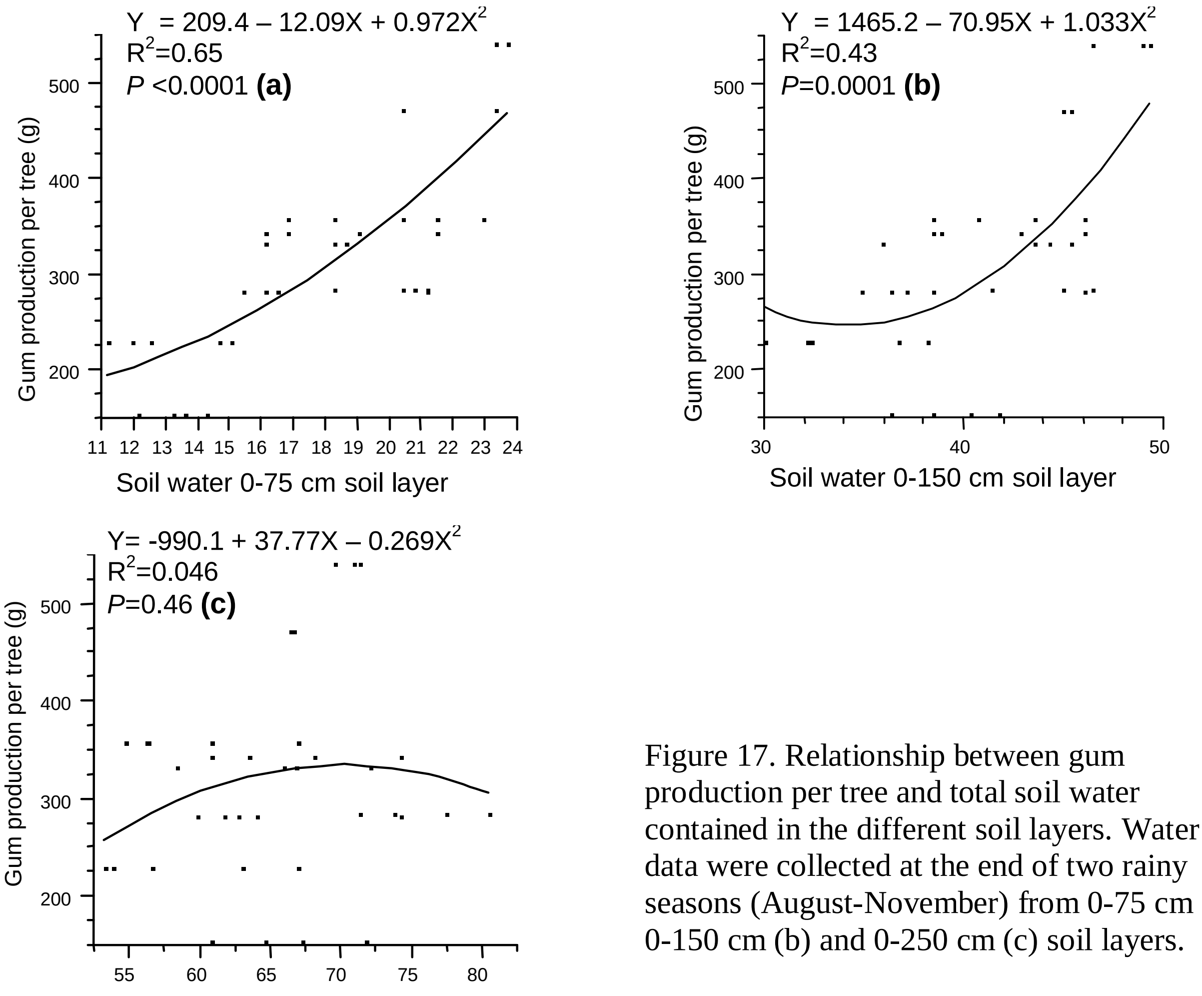

Figure 17. Relationship between gum production per tree and total soil water contained in the different soil layers. Water data were collected at the end of two rainy seasons (August-November) from 0-75 cm (a), 0-150 cm (b) and 0-250 cm (c) soil layers.

Trees obviously extracted most of their water requirement from the 0-150 cm soil layer. The results also show that the soil water availability during the rainy season is a limiting factor in the process of gum production.

Stomatal conductance and gum production

The gum production per tree also exhibited a significant negative correlation (R^2 = 0.81, $P<0.0001$) with the stomatal CO_2 conductance measured prior to the gum tapping season, (Fig.18). This could reflect a gradual effect of stress in trees during the gum production season, when the soil is successively getting drier and the trees adjust themselves physiologically (through g_s and ψ_{Lm}) to overcome the combined effects of water stress and tapping damage.

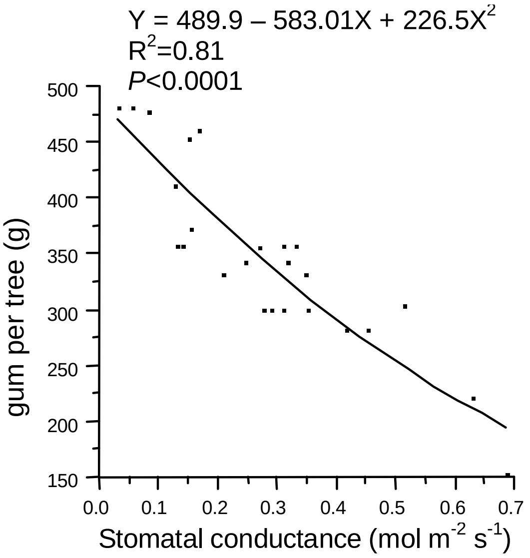

Figure 18. Relationship between tree gum production and stomatal conductance. Data on stomatal conductance were collected from trees representing different size classes during the period September-October.

Tree size and gum production

The analysis of variance showed a statistically significant (P=0.006) effect of tree size on per-tree gum production. A high dependency of gum production per tree on tree size was observed; somewhat surprisingly, the highest production was obtained from the middle size class (10-15 cm), followed by the smallest size class, and the lowest gum production was obtained from trees representing the largest size class (20-25cm basal diameter) (Table 4).

Table 4. Effect of tree size on per-tree gum production. Data were collected during two years. Means followed by the same letter are not different at P= 0.05.

Tree diameter class	Per-tree gum production (g)
< 5 cm	409.5 ab
5-10 cm	366.1 ab
10-15 cm	433.4 a
15-20 cm	335.8 ab
20-25 cm	284.7 b
Significance level	P= 0.006

4.5 Nitrogen and carbon under natural *A. senegal*

In the natural forest, the amount of soil nitrogen in the 0-120 cm soil stratum increased gradually as the *A. senegal* tree size increased (Table 5), but this variation was not statistically significant. The amount of nitrogen in the uppermost soil layer (0-30 cm) was significantly higher than that in the other layers. This also highlights the important role of water in the topsoil.

Soil nitrogen was also studied at the experimental site under two non-nitrogen-fixing tree species. The amount of nitrogen was higher under *A. senegal* at all different soil depths than under *Balanites* or *Azadirachta*; these differences were statistically significant (cf. Table 6 and Fig. 19). These differences were mainly caused by a difference in N in the top 0-30 cm soil layer. This result was in contrast to the finding obtained from root excavation during two rainy seasons. Roots of ten *A. senegal* trees were exposed in order to examine the presence of nodules. Nodules were not observed in these trees, even during the period of most active growth.

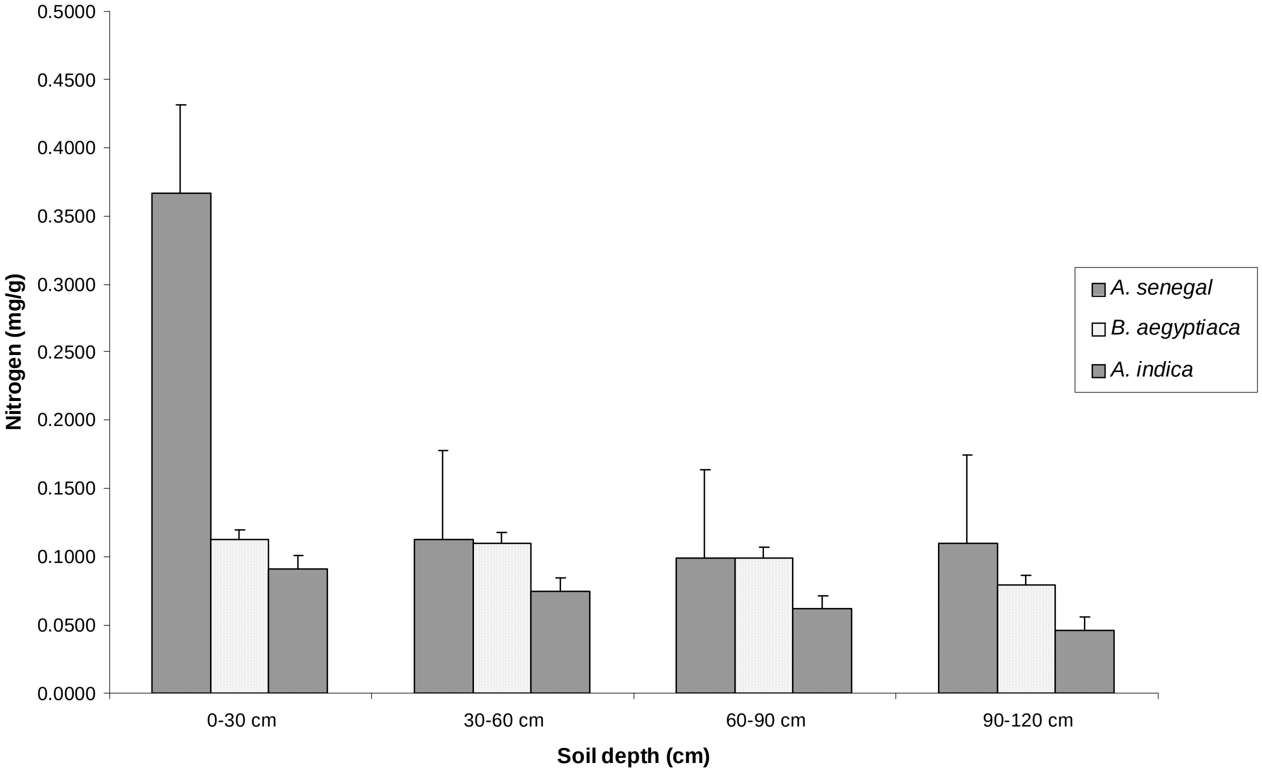

Figure 19. The amount of soil nitrogen at different depths under *Acacia senegal, Balanites aegyptiaca* and *Azadirachta indica* trees. Bars show standard error.

Table 5. Amount of nitrogen at different soil depths (5 a) and under trees of different size classes (5 b). Means followed by the same letter are not significantly different at *P*= 0.05.

Table 5 a

Soil depth (cm)	N (mg/g)
0-30	0.218 a
30-60	0.106 b
60-90	0.101 b
90-120	0.085 b

Table 5 b

Tree diameter class	N (mg/g) in 0-60 cm soil layer
< 5 cm	0.075 a
5-10 cm	0.088 a
10-15 cm	0.138 a
15-20 cm	0.163 a
20-25 cm	0.172 a

Table 6. Paired-sample t-tests on total soil nitrogen content under *Acacia senegal, Balanites aegyptiaca* , and *Azadirachta indica* in the 0-120 cm soil layer.

Pair	Total N (mg/g)	df	t	Significance (2-tailed)
Pair 1				
A. Senegal	0.2792	14	3.654	0.003
Balanites	0.1502			
Pair 2				
A.senegal	0.2792	14	4.112	0.001
Azadirachta	0.1096			

Table 7. The total amount of organic carbon (OC) under *A. senegal* at different soil depths (7 a) and under different tree diameter classes (7 b). Means followed by the same letter are not significantly different at *P*= 0.05.

Table 7 a

Depth (cm)	OC (mg/g)
0-30	0.139 a
30-60	0.075 b
60-90	0.006 bc
90-120	0.005 c

Table 7 b

Tree size class	OC (mg/g) (0-120 cm soil depth)
< 5 cm	0.052 c
5-10 cm	0.006 cb
10-15 cm	0.084 ab
15-20 cm	0.091 b
20-25 cm	0.114 a

The amount of organic carbon was highest under *A. senegal* in the 0-30 cm soil layer and it decreased with soil depth, especially below 60 cm (Table 7 a). This variation was statistically significant. Soil organic carbon also significantly increased with tree size as also indicated in Table 7 b. The distribution of organic carbon in the soil followed the same pattern as found in soil nitrogen.

4.6 Agroforestry (intercropping)

4.6.1 Correlation with soil water content

Effects of intercropping on soil moisture

Stand designs for trees and agricultural crops varied significantly (*P*<0.0001) in terms of their effects on the total soil water in the 0-75 cm soil layer during the growing season (Fig. 20). The highest soil water content was found when field crops were grown alone, and karkadeh decreased the soil water more than did sorghum. Intercropping and sole acacia trees resulted in lower and rather similar soil water contents.

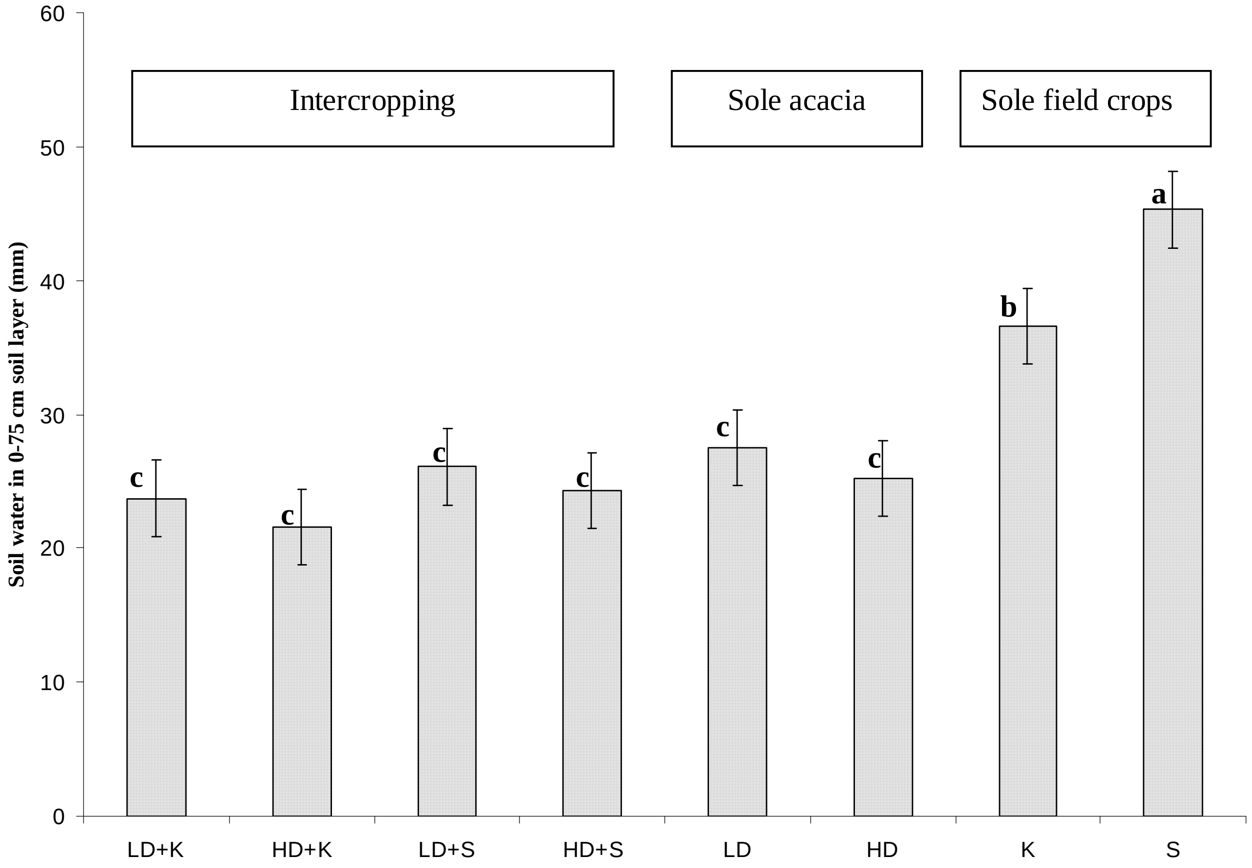

Figure 20. Effects of different intercropping designs on average soil moisture. Data collected during two rainy seasons (July-September). LD = 266trees ha^{-1}with, HD = 433 trees ha^{-}, S= sorghum, K= karkadeh. Bars show standard error. Values marked with the same letter are not significantly differed at the *P*=0.05. Significance level according to Duncan test.

Effects of soil water on tree physiology during intercropping

It was found that when acacia trees were grown in combination with crops the tree photosynthesis rate (*A*) correlated significantly with soil water in both soil layers (0-75 and 0-250 cm)(Fig. 21 a,b), but correlation with the water in the 0-75 cm soil layer was found to be very low. In sole tree stands the photosynthesis rate (A) correlated significantly with the soil water in both layers (0-75 and 0-250 cm) (Fig. 21 c,d).

Tree stomatal CO_2 conductance (g_s) under intercropping was found to better correlate with the soil water in the 0-75 cm-topsoil layer than with that in the 0-250 cm soil layer, as shown in Fig. 22a, b.

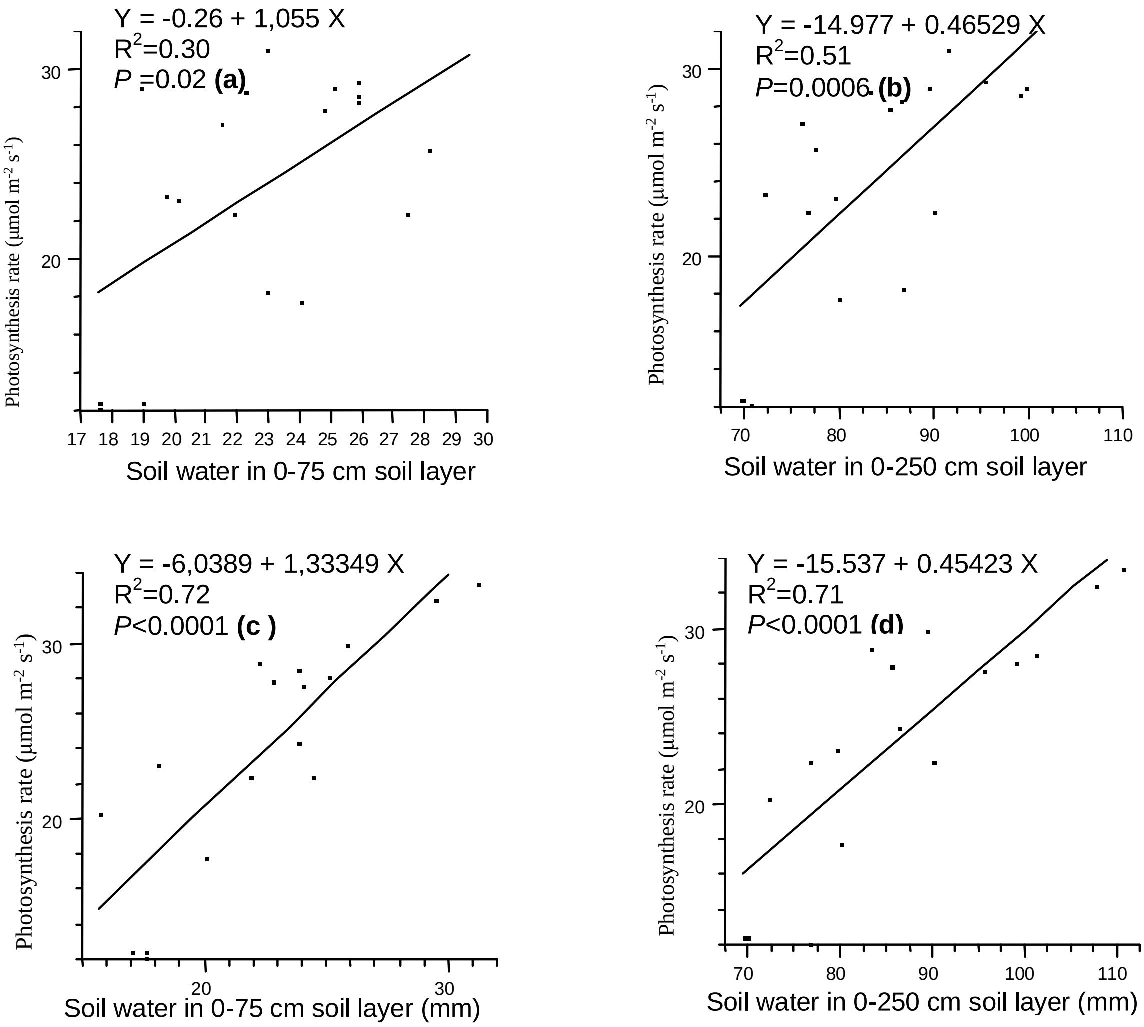

Figure 21. Relationship between tree photosynthesis rate (A) and total soil water in the 0-75 and 0- 250 cm soil layers in intercropping (a, b) and in sole trees (c, d). Data were collected during two rainy seasons (July-September); Data in intercropping include both sorghum and karkadeh and each data point represent the average of all plots.

Effect of intercropping design on tree intrinsic water use efficiency in trees

The highest tree intrinsic water use efficiency (IWUE) in trees was obtained when sorghum was intercropped with trees at high density (433 tree ha^{-1}) and also when karkadeh was grown with trees at high density (Fig. 23), but these differences in IWUE were not statistically significant.

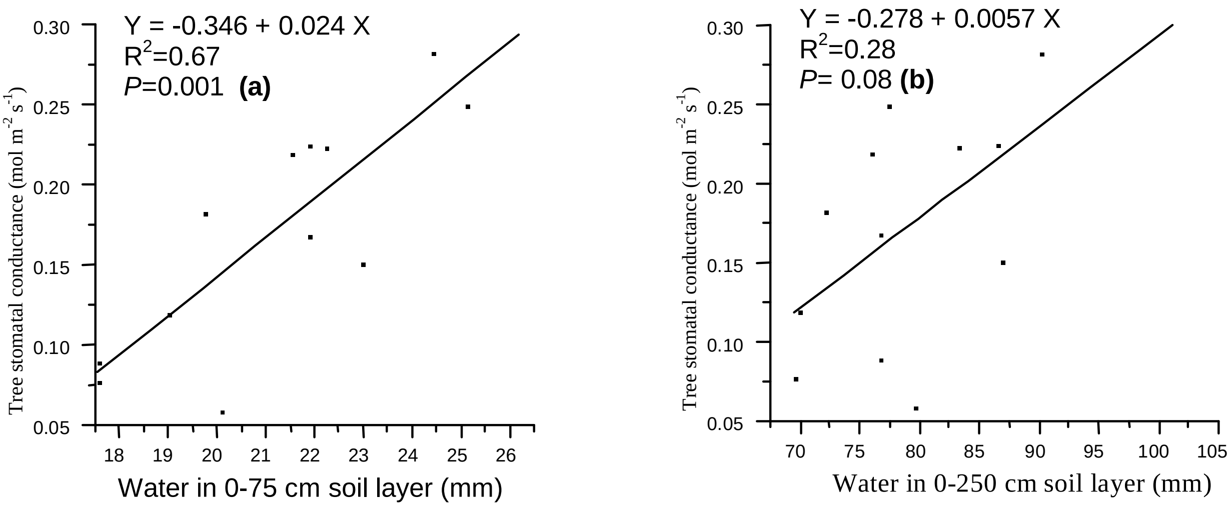

Figure 22. Relationship between tree stomatal conductance (g_s) and soil water in the 0-75 cm (a) and 250 cm (b) soil layer during intercropping. Data collected during two rainy seasons.

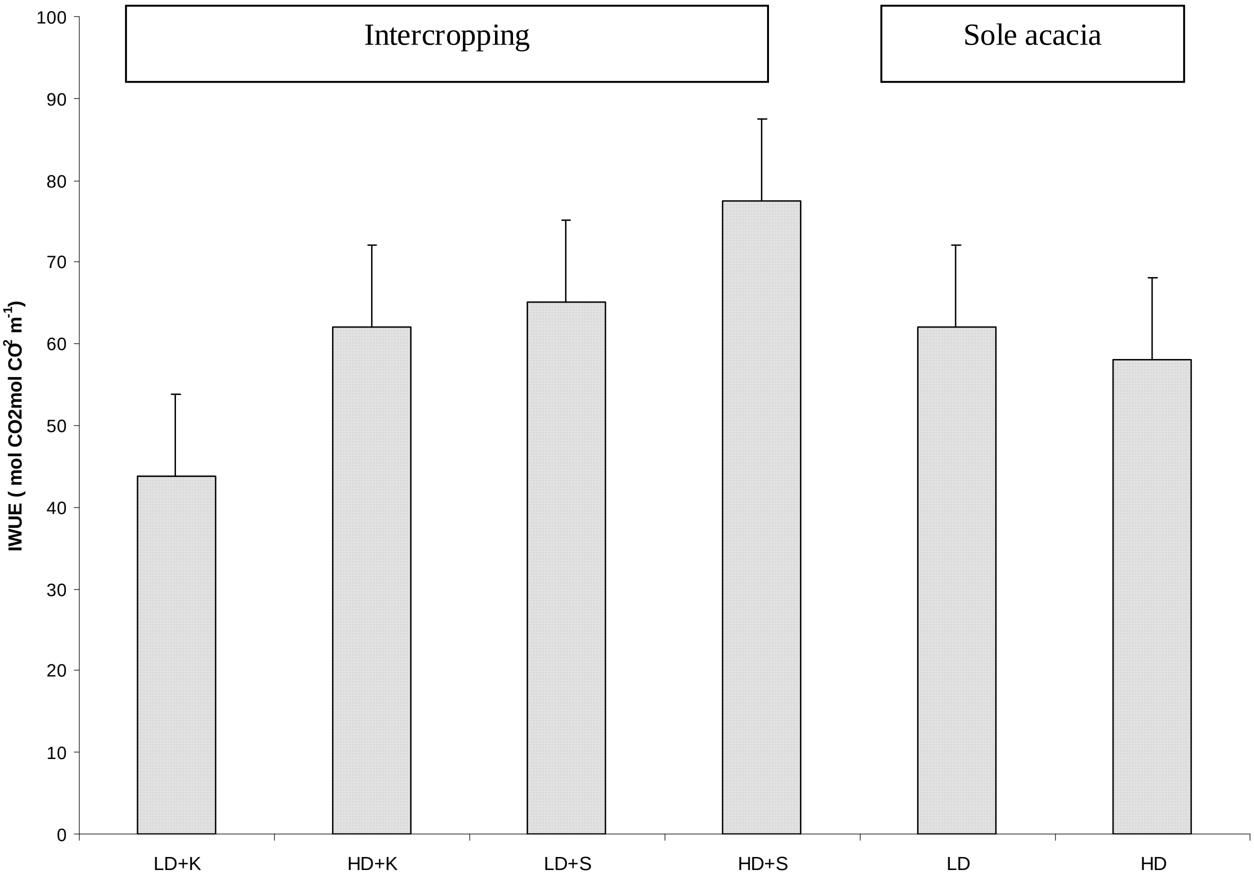

Figure 23. Effect of intercropping design on tree intrinsic water use efficiency (A/g_s). LD= 266 trees ha^{-1}, HD= 433 trees ha^{-1}, S= sorghum, K= karkadeh.

4.6.2 Gum production

Gum yield in agroforestry

Intercropping with the two field crops generally affected the gum production per tree positively (Fig. 24). The highest production per tree was obtained from a combination of sorghum with trees at high density (433 trees ha^{-1}).

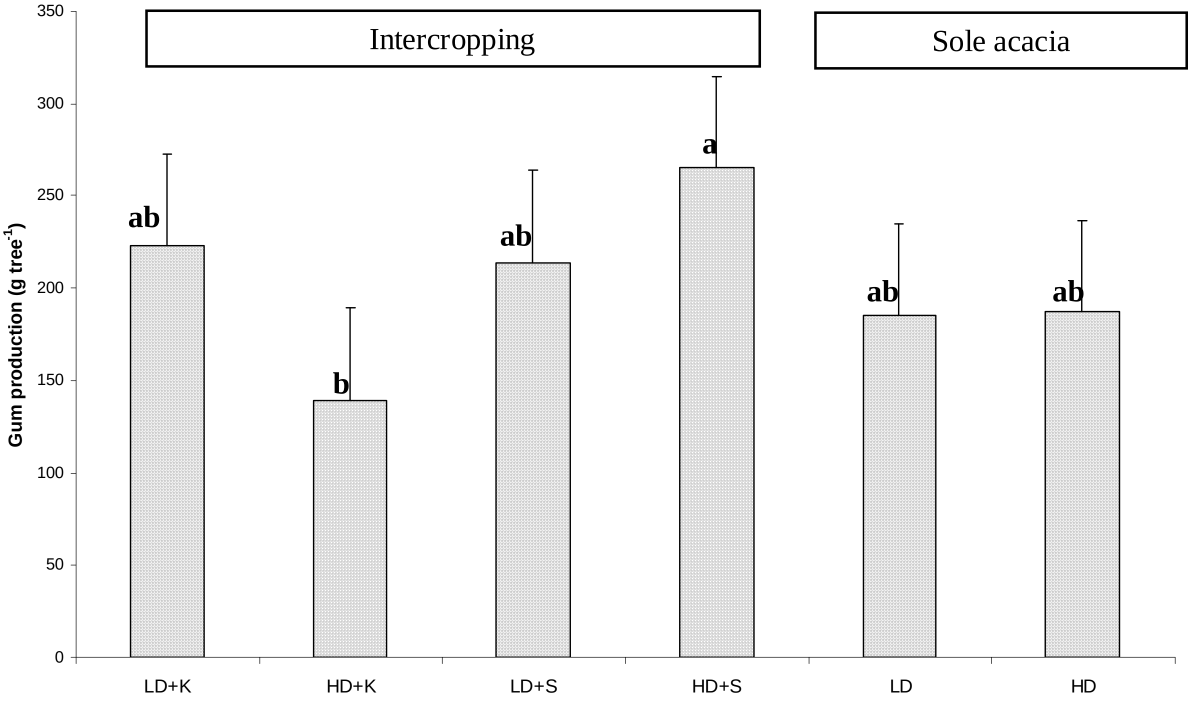

Figure 24. Gum yield per tree as affected by intercropping design. LD= 266 trees ha^{-1}, HD= 433 trees ha^{-1}, S= sorghum, K= karkadeh. Bars show standard error. Mean values marked with the same letter are significantly different at *P*=0.05 according to Duncan test.

Table 8. Effects of different intercropping designs on gum yield per hectare. Means followed by the same letter do not differ statistically significantly at P= 0.05. LD= 266 trees ha-1, HD= 433 trees ha-1, S= sorghum and K= karkadeh.

Treatment	Gum yield ha^{-1} (kg)
LD+K	59.3 b
HD+K	60.2 b
LD+S	57.0 b
HD+S	114.7 a
LD	49.2 b
HD	81.0 b

The highest gum yield per hectare was obtained from trees at high density intercropped with sorghum. It is noteworthy that this gum yield was significantly higher (115 vs. 81 kg ha^{-1}) than that obtained from the same density of *A. senegal* trees without intercropped sorghum. At the lower tree density, intercropping with sorghum seemed to slightly increase the gum yield per hectare, but this effect was not statistically significant.

Of the per-hectare yield differences, only that between the best combination (trees at high density with sorghum) statistically differed from the other combinations Table 8. The obvious positive effect of sorghum intercropping on gum yield both per tree and per hectare was a key finding of the present experiments and has important management implications.

Soil water and gum production

In the present study the gum yield during the dry season was found to increase in relation to the soil moisture as observed at the end of the rainy season (Fig. 25 a,b). Soil water in the 0-250 explained about 66% of the observed variation in gum yield. There was a significant positive correlation between the gum production per tree and soil water in the 0-75 cm soil layer (R^2 =0.29, *P*=0.0056) and in the 0-250 cm soil layer (R^2 =66. *P* <0.0001) (Fig. 25 b), when *A. senegal* was planted with agricultural crops. When trees were grown solely, gum production per tree exhibited a significant and high dependence on soil water in the 0-75 cm soil layer (R^2=0.83, *P*<0.0001), while there was no relation between tree gum production and soil water in the 0-250 cm soil layer (Fig. 26 a,b). This finding probably reflects the competitive effect of field crops on the dependency of tree gum production on soil water at different soil depths.

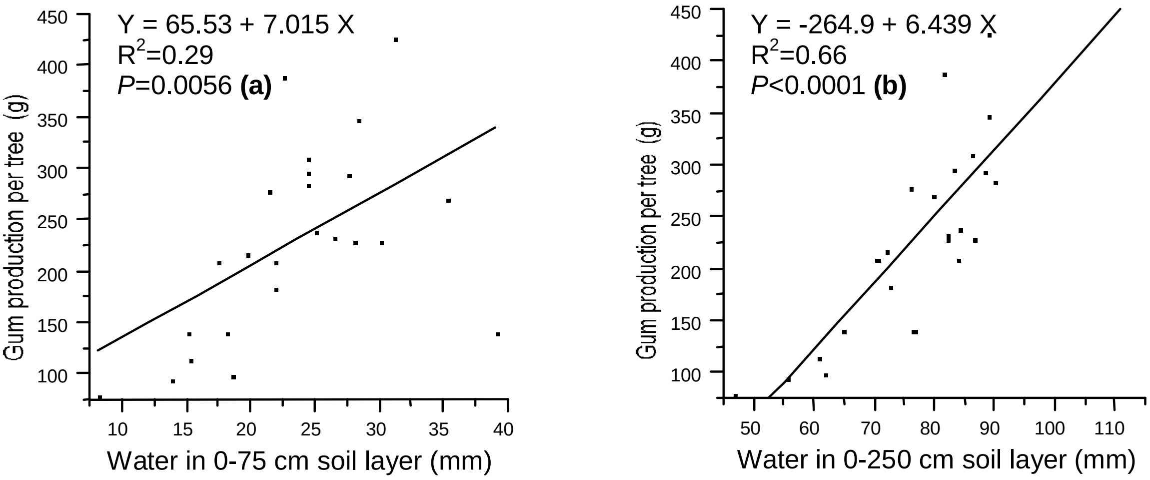

Figure 25. Dependence of per-tree gum production on average soil water in 0-75 cm (a) and 0-250 cm (b) soil layers in intercropping. Data were collected during the preceding rainy season and up to the end of November from intercropped *A. senegal* with crops karkadeh or sorghum.

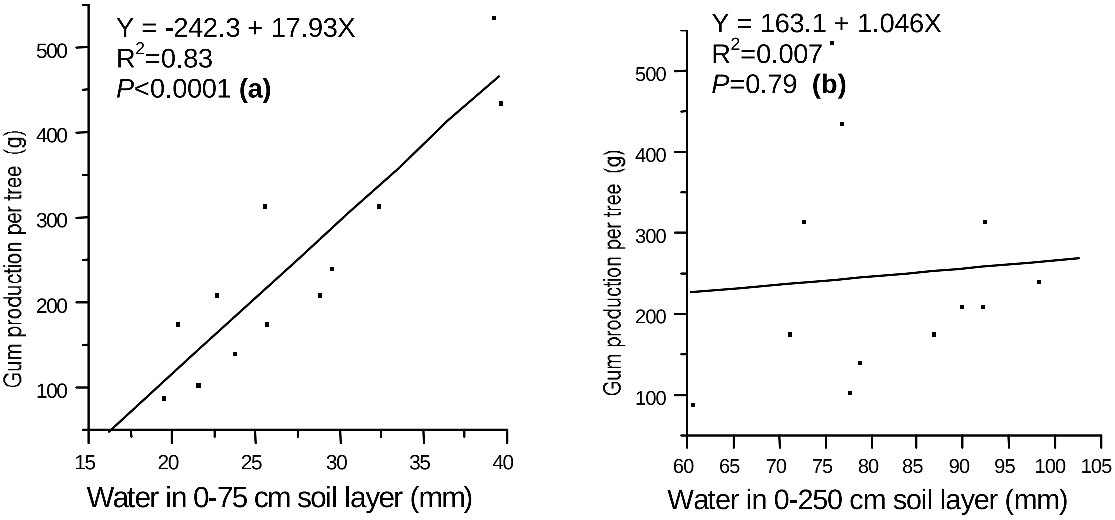

Figure 26. Dependence of per-tree gum production on soil water in 0-75 cm (a) and 0-250 cm (b) soil layers without intercropping. Data were collected during the preceding rainy season and up to the end of November from pure *A. senegal* plots corresponding to those shown in Fig. 25.

Effect of intercropping on rain use efficiency (RUE) of gum production

The rain use efficiency (RUE) was expressed as gum yield per unit rainfall. Since the same rainfall amount was available for all the treatments, RUE values followed those of gum yields (see Table 8). The highest rain use efficiency was received in combination of trees at high density (433 trees ha^{-1}) with sorghum. The result can be interpreted as suggesting that competition with field crops increases the rain use efficiency of acacia.

Table 9. Effect of intercropping on tree rain use efficiency. Means followed by the same letter are not significantly different according to Duncan test at P = 0.05. LD= 266 trees ha^{-1}, HD= 433 trees ha^{-1}, S= sorghum and K= karkadeh.

Intercropping design	RUE (gum kg ha^{-1}mm^{-1})
LD+K	0.2010 b
HD+K	0.2041 b
LD+S	0.1932 b
HD+S	0.3888 a
LD	0.1668 b
HD	0.2746 b

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4.6.3 Soil water and agricultural crop physiology

The morning leaf water potential (ψ_{Lm}) of both crops correlated strongly (P<0.0001) with soil water in the 0- 75 cm soil layer (Fig. 27 and Fig.28). A gradual decline in morning leaf water potential (ψ_{Lm}) was the result of the soil water decreasing in the topsoil during the growing season. The morning leaf water potential (ψ_{Lm}) in sorghum exhibited higher responsiveness to water in the 0-75 cm soil layer (R^2=0.67, $P<0.0001$; Fig.27) than that in karkadeh (R^2=0.40, P=0.001; Fig. 28).

The stomatal conductance (g_s) exhibited a significant correlation with soil water at 0-75 cm soil depth during the mid and final stages of development in both crops (Fig. 29 and Fig. 30).

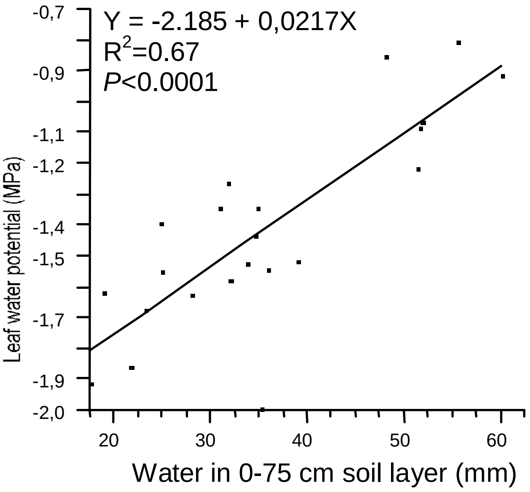

Figure 27. Effect of water in 0-75 cm soil layer on morning leaf water potential (ψ_{Lm}) in sorghum. Data were collected during two rainy seasons (July-September).

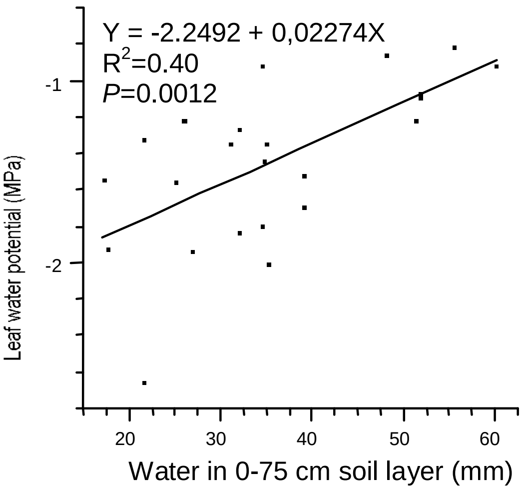

Figure 28. Effect of water in 0-75 cm soil layer on morning leaf water potential (ψ_{Lm}) in karkadeh. Data were collected during two rainy seasons (July-September).

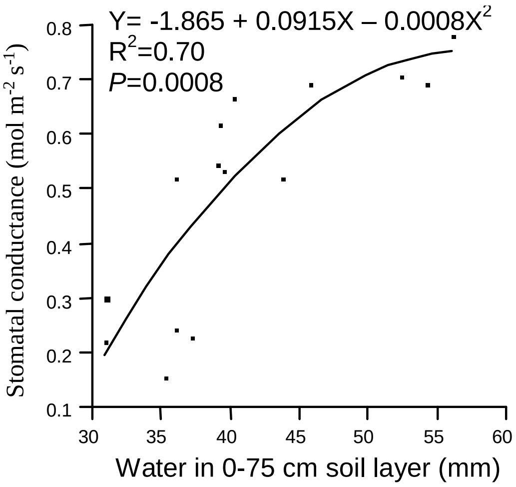

Figure 29. Effect of water in 0-75 cm soil layer on morning stomatal conductance in sorghum. Data were collected during two rainy seasons from intercropping and sole plots (July-September).

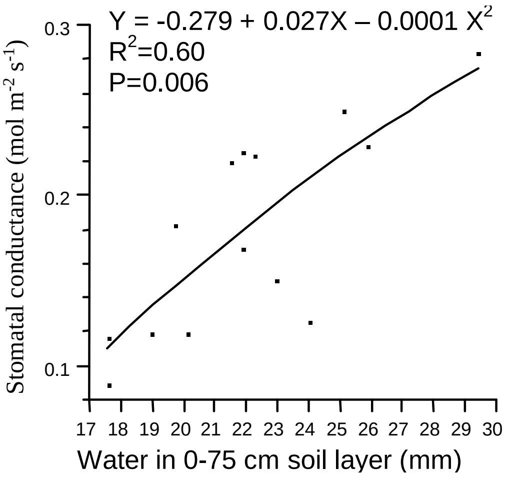

Figure 30. Effect of water in 0-75 cm soil layer on morning stomatal conductance in karkadeh. Data were collected during two rainy seasons from intercropping and sole plots (July-September).

As was found in the leaf water potential above, the morning stomatal conductance in sorghum was more responsive to water in the 0-75 soil layer (R^2=0.70, P=0.0008) than that of karkadeh (R^2=0.60, P=0-006). A decrease in topsoil water caused a decrease in g_s, which affected crop photosynthesis as shown in Fig.31 and Fig. 32. The correlation between morning photosynthesis rate (A) and water in the 0-75 cm soil layer was more distinct in sorghum than in karkadeh.

The stomatal conductance (g_s) correlated positively and highly significantly (P <0.0001) with the morning photosynthesis rate (A) in both crops (Fig. 33 and Fig. 34).

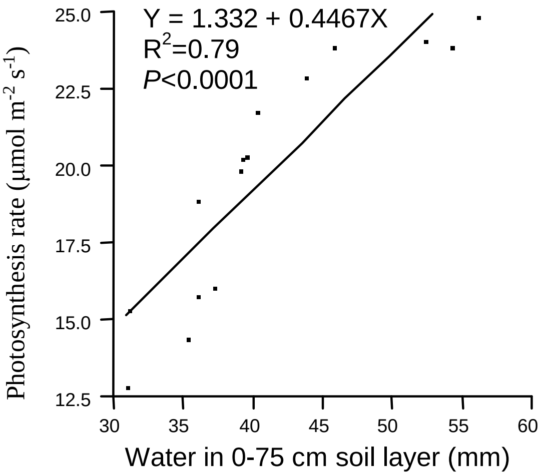

Figure 31. Effect of water in 0-75 cm soil layer on morning photosynthesis (A) in sorghum. Data were collected during two rainy seasons from intercropping and sole plots (July-September).

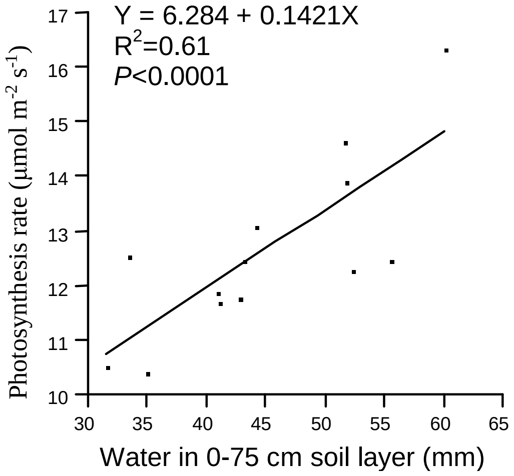

Figure 32. Effect of water in 0-75 cm soil layer on morning photosynthesis (A) in karkadeh. Data were collected during two rainy seasons from intercropping and sole plots (July –September).

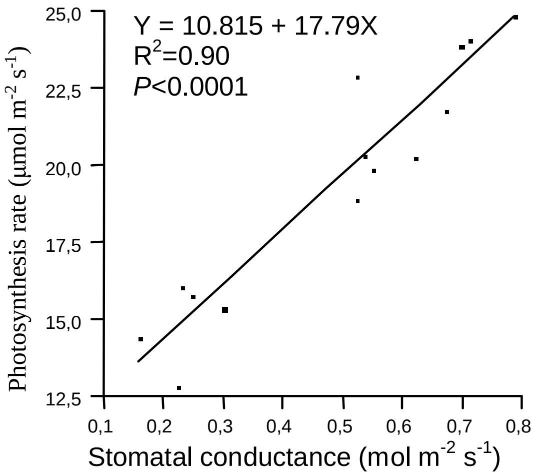

Figure 33. Relationship between stomatal conductance (g_s) and photosynthesis rate (A) in sorghum. Data were collected during two rainy seasons.

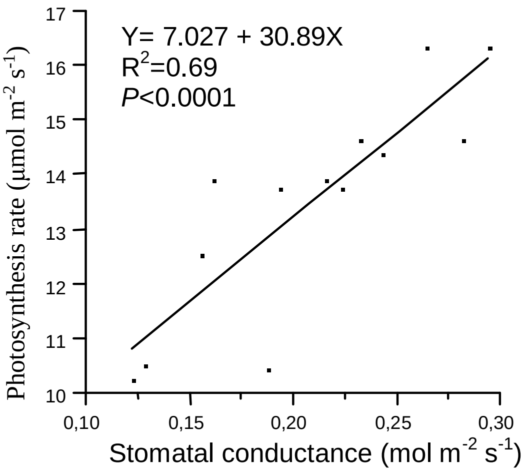

Figure 34. Relationship between stomatal conductance (g_s) and photosynthesis rate (A) in karkadeh. Data were collected during two rainy seasons.

Intrinsic water use efficiency (IWUE) in crops

In this study, the intrinsic water use efficiency (IWUE) was expressed as the ratio of photosynthesis (*A*) to stomatal CO_2 conductance (g_s) in both karkadeh and sorghum. The IWUE for karkadeh increased when it was intercropped with a low density of trees (266 trees ha^{-1}) and decreased in combination with a high density (433 trees ha^{-1}) (Fig. 35). The trend was opposite in sorghum; a higher tree density increased and a lower one decreased the IWUE. The IWUE value was highest for sorghum intercropped with *A. senegal* at high density (433 trees ha^{-1}).

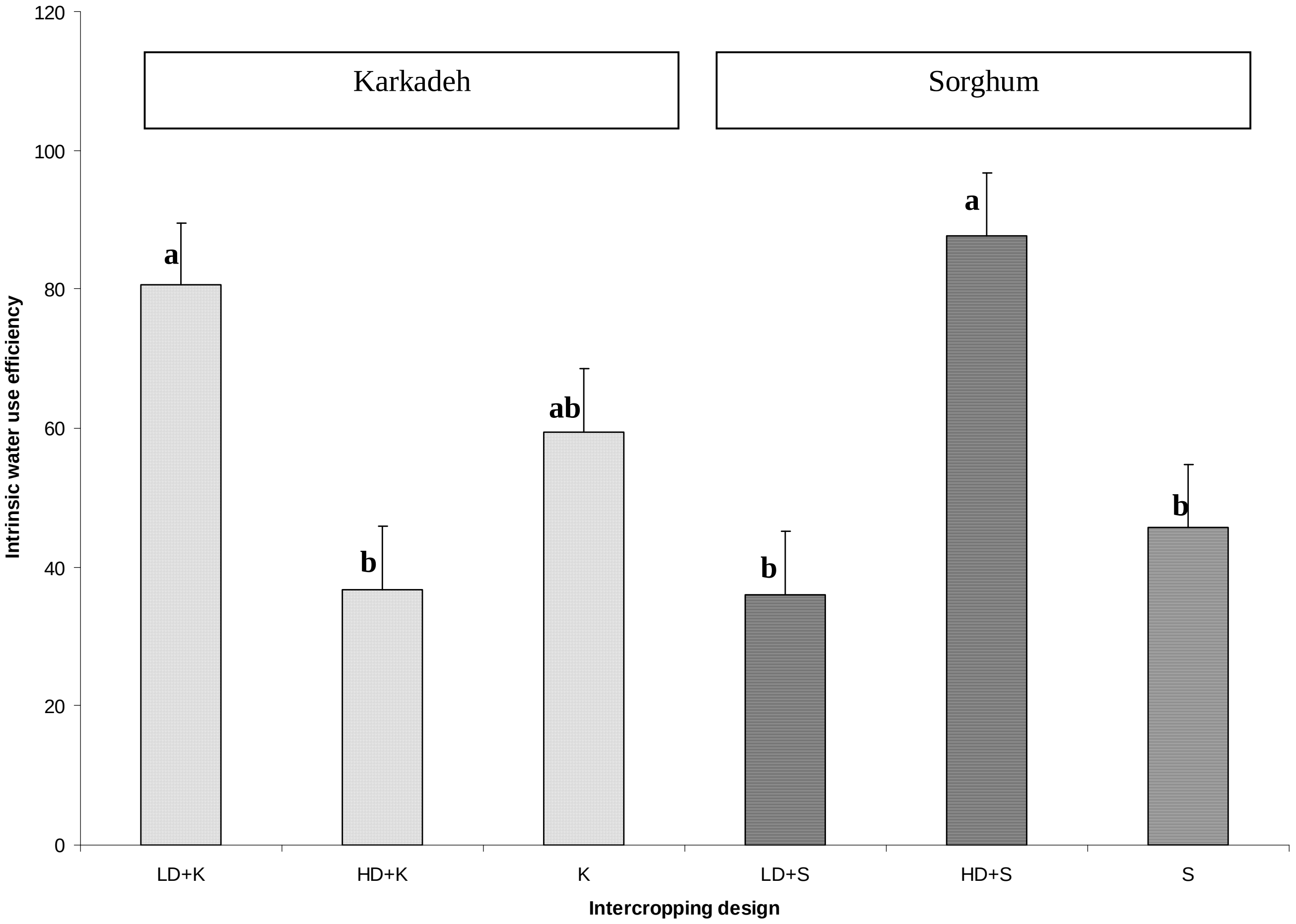

Figure 35. Effect of intercropping design on crop intrinsic water use efficiency (IWUE). LD= 266 trees ha^{-1}, HD= 433 trees ha^{-1}, K= karkadeh, S= sorghum. Bars indicate standard error. Means followed by the same letter are statistically different at *P*=0.05 according to Duncan test.

4.6.4 Agricultural crop production

Intercropping and agricultural crop production

The yields of both karkadeh and sorghum were affected by intercropping design (Fig. 36 and 37). Sole sorghum gave the highest harvest of 166 kg ha^{-1}, while a lower density of trees decreased it to 135 kg ha^{-1} and a higher one to 92 kg ha^{-1}. In karkadeh,

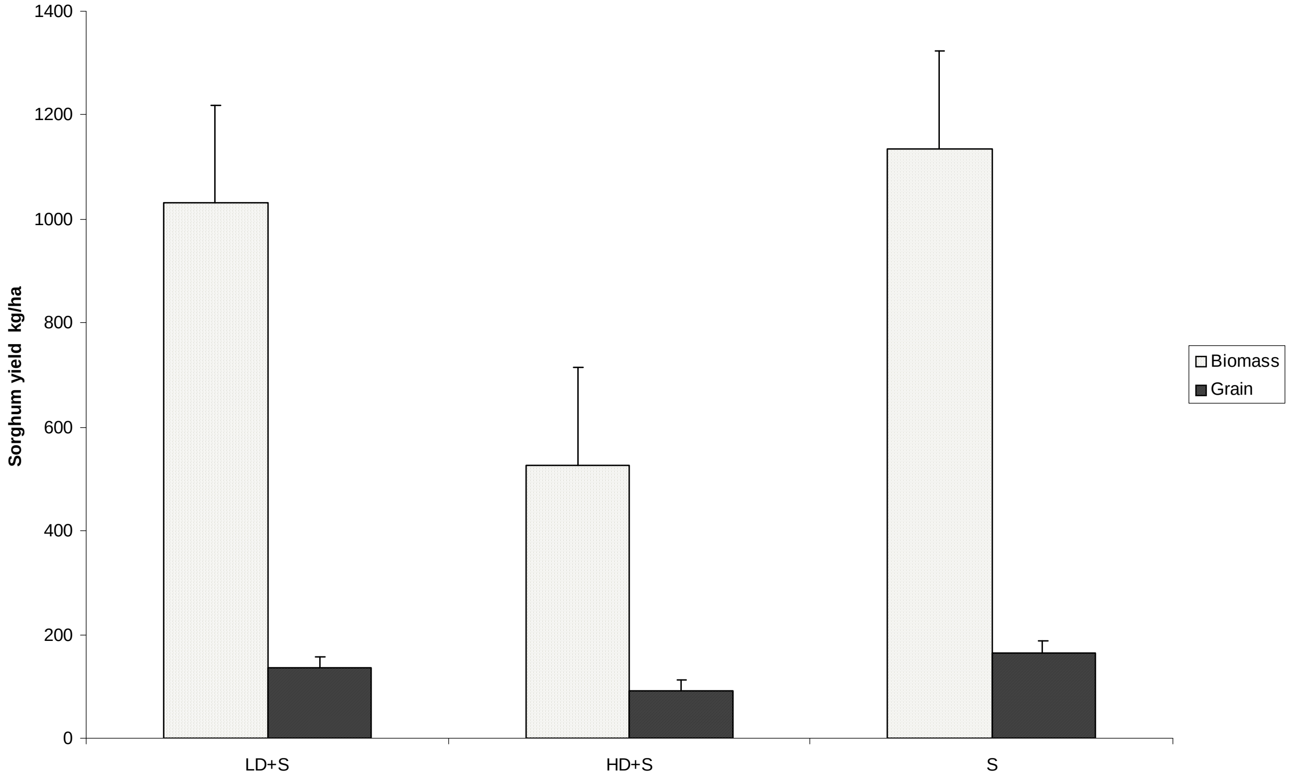

Figure 36. Effect of intercropping design on sorghum yield. LD= 266 trees ha^{-1}, HD = 433 tree ha^{-1}, S= sole sorghum. Bars show standard error.

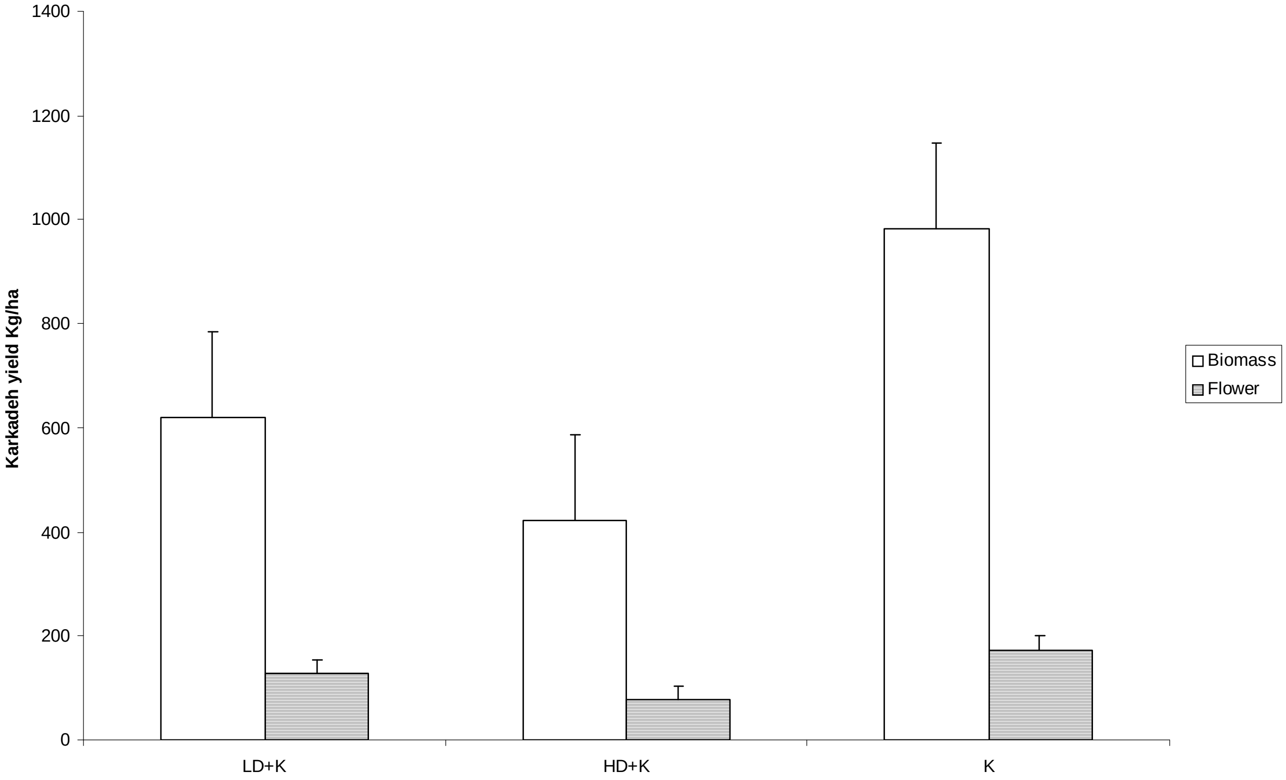

Figure 37. Effect of different intercropping designs on karkadeh yield. LD= 266 trees ha^{-1}, HD= 433 trees ha^{-1} and K= karkadeh. Bars show standard error.

the highest harvest of 172 kg ha^{-1} was obtained from the sole crop, while a lower density of trees decreased it to 127 kg ha^{-1} and a higher one to 77 kg ha^{-1}. Crop yields and biomass were significantly reduced by the presence of trees.

Crop harvest index

A strong linear relationship existed between the harvestable yield and dry matter production for sorghum and karkadeh (Fig. 38).

Statistically significant differences between sorghum harvest indices in different intercropping designs were detected. The harvest index in sorghum seemed to increase as the tree density decreased (Fig. 39 a). The highest value was obtained from sole crops. There was no statistical significant variation in the karkadeh harvest index under different intercropping designs (Fig. 39 b).

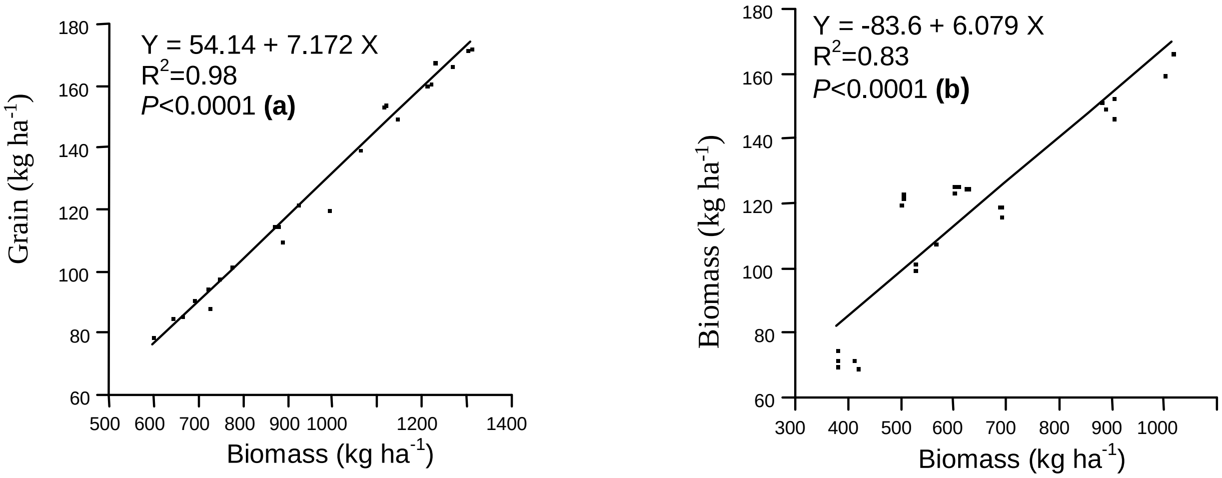

Figure 38. Relationship between economic crop yield and biomass for sorghum (a) and karkadeh (b). Data collected from intercropping and sole plots during two rainy seasons.

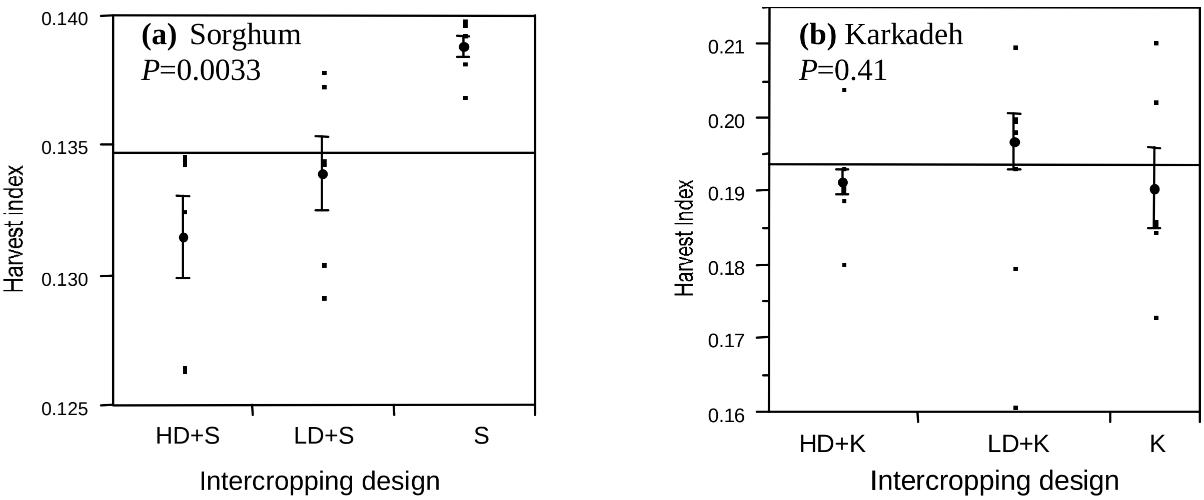

Figure 39. Comparison of harvest indices in sorghum (a) and karkadeh (b) under different intercropping designs. LD= 266 trees ha^{-1}, HD= 433 trees ha^{-1} and K= karkadeh, S= sorghum. Line represents the mean response and bars standard error.

Soil water and crop production

The yield in both crops correlated significantly with the soil water in the 0-75 soil layer (Fig. 40 and Fig. 41). The sorghum yield (in terms of harvestable parts and biomass) was affected more (R^2= 0.70, 0.61, P <0.0001) than the karkadeh yield (R^2= 0.62, 0.55, P< 0.0001) (Fig. 40 and Fig. 41).

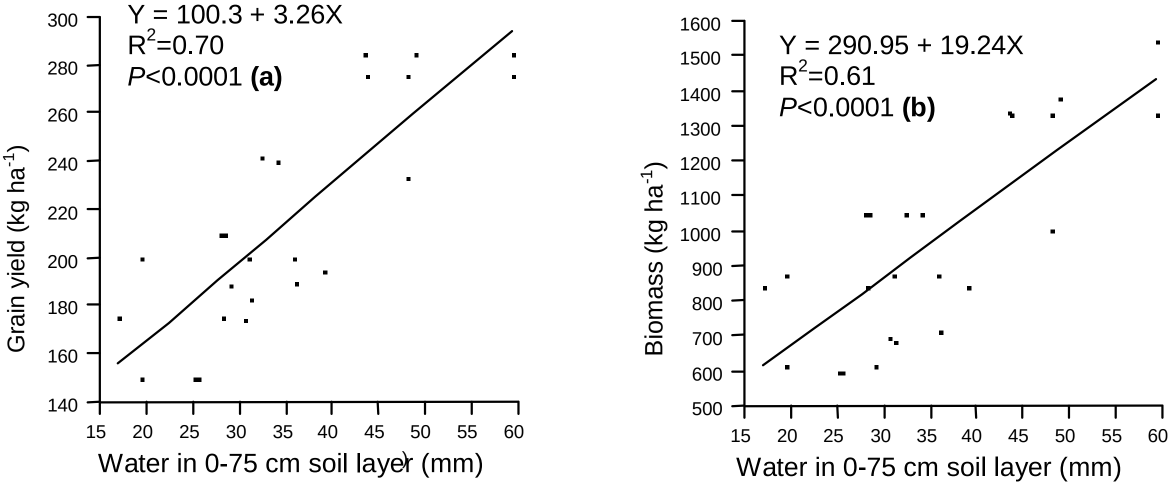

Figure 40. Effect of water in 0-75 cm soil layer on sorghum grain (a) and biomass (b) production. Data were collected during two years from all intercropping and sole plots.

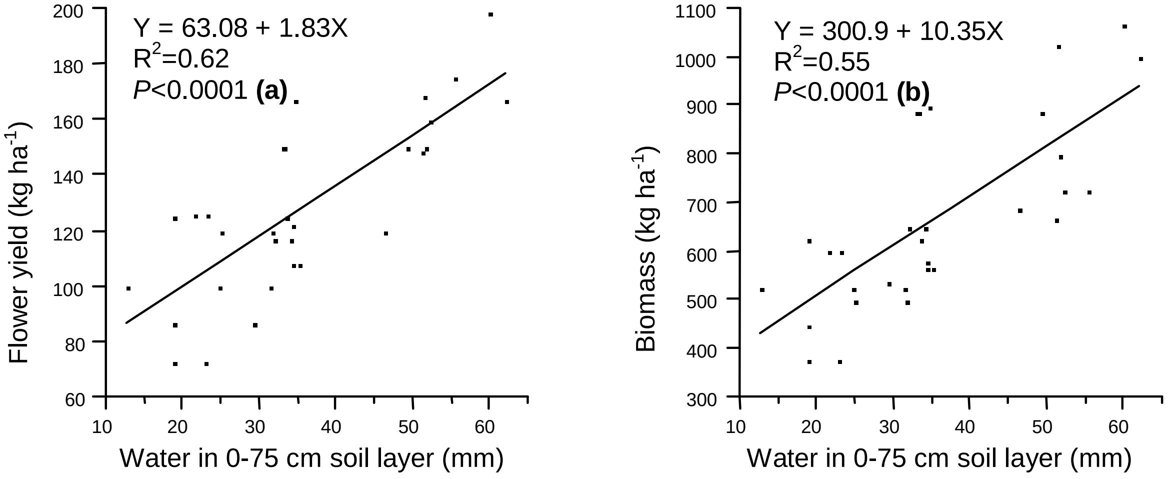

Figure 41. Effect of water in 0-75 cm soil layer on karkadeh flower (a) and biomass (b) production. Data were collected during two years from intercropping and sole plots.

Crop rain use efficiency (RUE)

Rain use efficiency (RUE) was expressed as the yield obtained per unit rainfall. The highest RUE was obtained when both crops were grown solely (Table 10). There was significant variation in crop RUE values between different intercropping designs for both karkadeh and sorghum.

Table 10. Effects of intercropping design on rain use efficiency (RUE). Means followed by the same letter are not significantly different at *P*= 0.05. LD=266 trees ha^{-1}, HD26= 433 trees ha^{-1}.

Intercropping design	RUE (kg $ha^{-1}mm^{-1}$)	
	Karkadeh (flower)	Sorghum (grain)
LD+crop	0.431 ab	0.457 ab
HD+crop	0.261 b	0.312 b
Sole crop	0.583 a	0.563 a

4.6.5 Effect of agroforestry on cropping-system rain use efficiency (RUE)

Table 11. Effect of intercropping design on rain use efficiency. RUE was expressed as the economic production (gum, grain or flower) in each design per unit rainfall. LD = 266 trees ha^{-1}, HD= 433 trees ha^{-1}, S= sorghum, K= karkadeh. Means followed by the same letter are not statistically different at *P*=0.05. Standard error = 0.017.

Intercropping design	RUE (kg $ha^{-1}mm^{-1}$)
LD+K	0.631 ab
HD+K	0.465 b
LD+S	0.650 ab
HD+S	0.701 a
LD	0.166 c
HD	0.275 c
K	0.583 ab
S	0.563ab

Higher RUE was obtained in a combination of trees at high density with sorghum, followed by trees at low density with sorghum. The lowest RUE values were obtained from pure tree stands. With karkadeh, a low tree density seems to increase the RUE of the cropping system.

Soil water: agroforestry vs. bare land

A comparison was also made between the amount of soil water in an agroforestry system and on bare land at the site studied (Fig. 42). There was no significant difference in soil water in the 0-250 cm soil layer between these two situations after the rainy season in November. However, for most of the rainy season there was less soil water in all agroforestry plots compared with bare land.

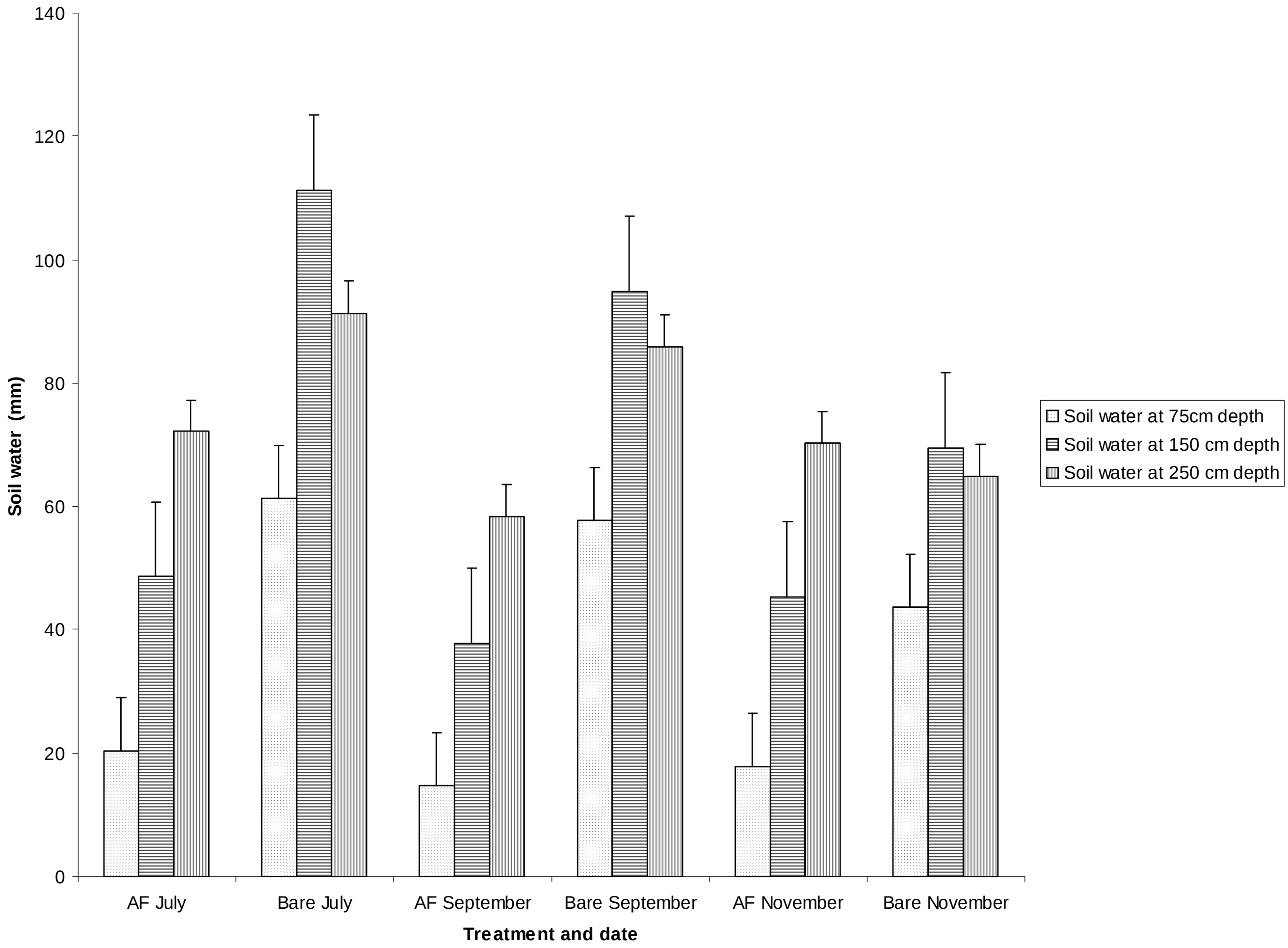

Figure 42. Soil water under agroforestry system and on bare land during and after rainy season. Bars indicate standard error

5. Discussion

5.1 Interaction of tree size, soil water and tree physiological traits

5.1.1 Effect of tree size on soil moisture

The total soil moisture content decreased linearly as the tree size increased. The water uptake by trees mostly came from the 0-150 cm soil layer, with less uptake from deeper layers. This can be explained by differences in root system size and distribution in the soil horizon in different tree size classes. Roots were found to be mostly concentrated in the topsoil layers. De Soyza et al. (1996) also confirmed that differences observed in gas exchange patterns in different tree size classes provide evidence for the same hypothesis that larger-basal diameter trees use more water than the smaller ones (cf. Teskey and Sheriff 1996). In his stable-isotope-based studies Dawson (1999) showed that trees of different size classes belonging to the same species could tap different sources of soil water. Small trees have a smaller total transpirational surface and root mass and, therefore, a lower demand for water (Freckman and Virginia 1989; Matzner et al. 2003).

Water deep in the soil may or may not be used only when the water availability in the upper strata is limited. As observed by Meinzer et al. (1999), a number of factors may lessen the potential negative consequences of soil water utilization by large trees; for instance, the extensive horizontal area that the root systems of large trees occupy may compensate for reduced water content in the upper soil profile.

The capability of trees to tap deeper soil water when upper soil layers dry out has been reported in woody species in different types of habitat (Mensforth et al.1994, Thorburn and Walker 1994, Dawson and Pate 1996, Meinzer et al. 1999). In the present study, the largest decrease in soil water content was observed during the rainy season. Leafing in *A. senegal* occurs with the onset of rains, and most of the trees shed their leaves in November or December after the end of the rains, implying that tree growth continues mainly during the rainy season (Ballal 2002).
In the present study, redistribution of soil water was found during the dry period, with high soil water availability in deep layers. This was obviously due to reduced demand for water caused by a reduced leaf area, when trees shed their leaves. This may be considered as a conservative behavior in *A. senegal* of using the available water efficiently but allowing a reasonable amount of soil water to be used later after rainy season. This result is in line with earlier ones (Jones 1980, Hoffmann et al. 2003).

The increase in soil water under *A. senegal* during the dry season in different soil layers may be due to an upward movement of water from moister to drier portions of the profile via root systems (Dawson 1993, Caldwell et al. 1998). Redistribution of water under *A. senegal* may be mediated by fine roots in drier soil through water uptake by roots from moister greater depths (Meinzer et al. 1999). Redistribution of water by roots within the soil profile, for instance, by a “hydraulic lift”, a process whereby roots extract water from moist soil depth and release it into the upper soil profile can potentially influence the water balance of *A. senegal*. Such redistribution is suggested to be significant during the gum production period (Burgess et al. 1998) and also when tree starts to have new leaves before the onset of the rainy season. Many published data show that capillary rise from a water table or an unsaturated upward water flux from below the root zone can contribute significantly to the water balance of an ecosystem (Maraux and Lafolie 1998). This may be also the case under *A. senegal*. In the present study, lateral movement of water in sandy soil may have been another reason.

5.1.2 Effect of tree size on physiological characteristics

Large trees with their wide emergent crowns are exposed to a high evaporative demand particularly during the dry season. Dependence on only a small pool of available water in the upper soil profile would seem to bring the risk of damage through leaf water deficit; this can lead to marked stomatal limitation of transpiration and photosynthesis (Meinzer et al. 1999). The morning leaf water potential (ψ_{Lm}) was now found to be strongly affected by tree size. An increase in leaf water potential in relation to tree size implies root expansion deep into the soil profile. This relationship may be conveniently used for assessing the soil water status under *A. senegal.*

Tree size was found to be a significant source of intra-specific variation in morning leaf water potential in pines in an earlier investigation by Kolb and Stone (2000). In the present study, stomatal conductance (g_s) also positively correlated with tree size. As in the case of leaf water potential above, this relationship is a sensitive indicator of the soil water status under *A. senegal*. These findings could also be related to the stem volume, as larger trees have greater water storage than smaller ones (Philips et al. 2003). Physiological measurements of different age classes of red oak in their natural environment during a wet and a dry year have shown that plants at different ontogenetic stages are affected differentially by drought (Cavender and Bazzaz 2000). Variations in stomatal conductance in mature *A. senegal* tree appeared to be caused by the tree size. It has also been found that the diurnal pattern of stomatal conductance (g_s) is also related to tree size (Matzner et al. 2003).

De Soyza et al. (1996) provided evidence of variation in physiological responses of different-sized shrubs of *Prosopis glandulosa*. They found that small shrubs are less coupled to variation in soil moisture than large shrubs. Higher stomatal conductance in large trees enables them to have a faster net assimilation rate and transpiration rate than found in small ones. Size-dependent differences in photosynthesis, stomatal conductance and water use have been reported also in different tree species by Brown and Archer (1990) and Donovan and Ehleringer (1991, 1992), who also confirmed that physiological parameters related to carbon and water relations may change with plant age, size and developmental stage.

5.1.3 Effect of soil water on tree physiological behavior

It has been concluded that a consistent picture of plant responses to soil water content can be obtained by expressing physiological performance as a function of the soil water content (cf. Ritchie 1981).

Leaf water potential.

The morning leaf water potential (ψ_{Lm}) was in the present study significantly affected by soil water in the topsoil (0-75 cm) and by soil water up to the 250 cm depth. Comparison of the total soil water content (0–250 cm stratum) with leaf water potential indicated a rather low R^2 but still highly significant relationship. This is obviously explained by the mechanism of water uptake, since lower leaf water potentials are required for faster water uptake; this may in turn cause stronger stomatal limitation of the photosynthetic carbon gain (Yoder et al. 1994; Hubbard et al. 2001; Gries et al. 2003). This also confirms that the morning leaf water potential (ψ_{Lm}) in *A. senegal* can be used as an indicator for the soil water status in the whole 0-250 cm soil layer (cf. Hsiao 1973).

Factors involved in the control of the leaf water potential can be separated into three classes: those affecting the soil water potential, those controlling the transpiration rate and those affecting the internal hydraulic resistance (Jones 1985). Present findings confirmed the capacity of *A. senegal* to adjust the difference in water potential between root and leaf (cf. Eamus and Prior 2001): as the soil water declines, the leaf water potential also decreases, which maintains a favorable gradient of soil water potential for water uptake from soil to leaf.

In the present study a clear difference was found between morning leaf water potentials during a dry year (rainfall 226 mm) and a wet year (364 mm rainfall). *A. senegal* exhibited higher morning leaf water potential (ψ_{Lm}) values in the wet year than in the dry year (averaging -2 and -3.0 MPa, respectively). This could reflect an adaptive mechanism contributing to efficient water uptake at low soil water availability.

Stomatal conductance (g_s)

In the present study the stomatal conductance (g_s) correlated distinctly with the total soil water to 250 cm depth and somewhat less with soil water in the 0-75 cm and 0-150 cm soil strata. A declining soil water content resulted in a decrease in stomatal conductance (g_s). This stomatal response to soil water has been reported for many other tree species (Arndt et al. 2001, Eamus 2001).

Greenhouse and field studies have shown that the stomatal conductance decreases with low soil water availability (Davies and Zhang 1991, Davies et al. 1992). High responsiveness of stomatal conductance to soil water in *A. senegal* suggests that this mechanism might also function through a root-to-leaf signal under different soil water status (cf. Comstock and Ehleringer 1984). In general, plants respond to reduction in water supply either by structural or by physiological adjustment (Martin 2001). However, at light-saturation, which was the case in the present work, the stomatal conductance can be used as reference parameter to reflect the drought intensity (Medrano et al. 2002).

Comparison of stomatal behavior between a wet year (364 mm rainfall) and a dry year (226 mm rainfall) showed that there was a significant difference in stomatal conductance values between these years. This suggests that efficient regulation of stomatal conductance according to soil water availability seems to play an important role in the adaptation *of A. senegal* to drought, since the stomatal movement is also considered to be a protective mechanism against xylem cavitations (Tyree and Sperry 1988). Previous studies also indicate that water stress can also be ameliorated by modification of stomatal functioning (Kramer 1980).

Tree photosynthesis

In the present investigation, the stomatal behavior of trees was reflected in tree photosynthesis. The rate of photosynthesis (A) was strongly dependent on the total water content to 250 cm soil depth, while the correlation with soil water to 150 cm or 75 cm depth was poorer but still significant. This confirms that CO_2 exchange rates in *A. senegal* are coupled with the water status of the soil and tree. Arndt et al. (2001) demonstrated that the relationships between g_{leaf} and ψ_{leaf} or A and g_{leaf} were maintained in *Zizyphus* sp. (a tree considered to be well-adapted to dryland conditions) in drought treatments as the soil dried.

A comparison of average photosynthesis rates between a wet (364 mm rainfall) and a dry year (226 mm rainfall) showed no significant differences. This finding suggests that photosynthesis in *A. senegal* similarly to ψ_{Lm} and g_s, reflects adaptation of *A. senegal* to its native habitats. As a whole, *A. senegal* seems to be adapted to soil water deficit in diverse ways that allow the species to maintain a high photosynthesis rate for the longest possible period when the tree produces leaves rapidly at the onset of the rainy season and when soil moisture becomes available. This conclusion is supported by a previous study by Yordanov et al. (2000) who confirmed that mild drought induces in plants regulation of water loss and uptake, allowing maintenance of their relative water content within a limit where the photosynthetic capacity shows no or little change.

5.1.4 Interaction between physiological characteristics

The stomatal CO_2 conductance (g_s) in trees was in the present study also found to be strongly related with the intercellular carbon dioxide concentration (C_i) in the morning. This can be explained either by sensitivity of intercellular carbon dioxide concentration (C_i) to stomatal conductance or by dependency of g_s on C_i. Results obtained by Huxman and Monson (2003), when studying the stomatal response of *Flaveria* species to light and C_i, demonstrated that there is a high sensitivity of stomatal conductance to C_i.

Findings from the present work suggest that, in *A. senegal*, CO_2 supply-limiting photosynthesis can be a result of the decrease in stomatal conductance that cause C_i to become depleted in the morning (Farquhar and Sharkey1982). This reasoning is supported by Brodribb (1996) who observed a characteristic biphasic response in nine conifer species where an initial stomatal control phase resulted in a reduction in C_i as the stomatal conductance decreased.

Early studies on Norway spruce by Luukkanen (1978) suggested that water deficit-induced increases in photorespiration may lead to increases in C_i which result in lower stomatal conductance and reduced net photosynthesis rate. Many previous studies have confirmed that reduction in the internal carbon dioxide concentration (C_i) enhances the stomatal opening (Mott 1990) and showed that the intercellular carbon dioxide concentration is more dependent on stomatal conductance than on leaf water potential (cf. Escalona et al. 1999). Ogle and Reynold (2002), in particular, emphasize that “the stomatal conductance is typically positively correlated with C_i in the morning and negatively correlated with C_i later in the day”. The same pattern is reported by Schulze et al.(1974), Mott (1988) and Assmann 1999).

In the present study the stomatal conductance correlated with the relative air humidity (RH). It is well known that changes in relative humidity have an effect on transpiration, and the stomatal conductance (g_s) can respond indirectly to relative humidity through transpiration and a subsequent decrease in leaf water potential. Laboratory and field studies have demonstrated that the stomatal conductance decreases with leaf exposure to drier air; however, there is disagreement on how to precisely interpret the dependence of stomatal conductance on relative humidity. Talbott et al. (2003) identified the air relative humidity as a key environmental factor mediating the changes in stomatal sensitivity to CO_2. They stated that humidity regulation of stomatal CO_2 sensitivity could function as a signal for leaves inside dense foliage canopies, promoting stomatal opening under low light and low CO_2 conditions.

A high degree of responsiveness of the stomata in *A. senegal* to air humidity could also be a direct transpiration response (Mott and Pakhrurst 1991). Livingston and Black (1987) found that temperature and relative humidity (e.g. VPD) are good predictors of stomatal conductance to water vapor or CO_2 in white spruce as well as in a wide range of other conifers.

It is known that under natural conditions the transpiration rate is determined by radiation, air water pressure saturation deficit and stomatal conductance (cf. Squire 1979). The stomatal conductance in *A. senegal* now exhibited a high sensitivity to the air relative humidity, as do many other species that grow and survive in arid and semi-arid areas; this could be considered to be an acclimation adjustment (Ludlow 1980). The active response of the stomata that makes them more sensitive to humidity could be considered an adaptive adjustment particularly because it reduces water loss and increases the intrinsic water use efficiency.
In the present study the stomatal conductance (g_s) correlated positively with the leaf water potential (ψ_{Lm}), whereby a decline of the leaf water potential in the morning caused g_s to decrease. Tuzet et al. (2003), when modeling stomatal conductance, photosynthesis and transpiration, explained the hysteresis in stomatal conductance versus leaf water potential by the fact that the leaf water potential is a function of the dynamics in the distribution of soil matric potential around the roots. They showed that when the soil starts to dry, the matric potential near the roots becomes less negative in the morning, so for a given level of atmospheric demand for water loss from the leaves, stomatal conductances are higher earlier in the day.

When plants are subjected to a series of drying and watering cycles, a change in the g_s/ψ response is observed (Jones 1985, Eamus 2001). The obviously high sensitivity of *A. senegal* stomata to leaf water potential, as found in the present study, may also indicate a control effect that osmotic adjustment (which extends the range of water potential over which the plant can function) have on stomata. This was mentioned by Ludlow (1980), who believes that there is a strong correlative and mechanistic evidence showing that osmotic adjustment is the main process responsible for stomatal regulation.

Present findings are in line with many other studies that have confirmed a high correlation between g_s and ψ_{Lm}. Brodribb et al. (2003) reported high sensitivity of g_s to leaf water potential in deciduous species, where stomatal conductance responded to a range of less than 0.5 MPa. Similar results were obtained by Medrano et al. (2002), who also confirmed that the leaf water status interacts with stomatal conductance, especially under water deficit when a good correlation between leaf water potential and stomatal conductance is observed. This finding is in line with those by other researchers (Gries et al. 2003; Giorio et al. 1999; Davies et al. 1994; Dettori 1985; Jones 1974). Similarly: " The regression of leaf water potential on stomatal conductance provides a method of estimating the degree of stomatal control" (Higgs and Jones 1991).

In the present work, the photosynthesis rate (*A*) correlated significantly with the morning leaf water potential (ψ_{Lm}). This can be explained by the role of leaf water potential ψ_{Lm} in water uptake, which is essential for photosynthesis. Photosynthesis and stomatal response are controlled by many factors, such as VPD, the amount of water available to the plant, and the associated leaf water potential. Leaf water potential is a measure of how tightly or strongly a leaf holds its moisture and so it reflects the plant water status. Evidently, under low leaf water potential, high leaf temperature may be a factor that leads to slight stomatal closure and decreased assimilation rate (Pearcy 1987). Osmond et al. (1980), in their investigation on twelve woody species native to habitats ranging from streamside to desert, showed that the non-stomatal component of CO_2 fixation began to decline at the same water potential as stomatal conductance.

In the present study, the photosynthesis rate (*A*) was also related to stomatal conductance (g_s) in the morning. This can be explained as a function of the CO_2 flux when stomatal conductance increases. From different experiments in an extensive literature it can be concluded that the variation in photosynthesis in plants can be ascribed to stomatal control of carbon dioxide uptake (Osmond et al. 1980; Lawlor 1993; Martin et al. 1994; Lovett and Tobiessen 1993; Ovaska et al. 1993; Morrison and Reekie 1995). The high dependence of photosynthesis on stomatal conductance now found in *A. senegal* suggests that stomatal limitations to photosynthesis were dominant (cf. Medrano et al. 2002, Farquhar and Gemmerer 2001).

A. senegal, like other drought-adapted species, shows stomatal regulation that results in a high photosynthetic rate when water is available and in lower rate when water is limiting (Zhang et al. 1997). Medrano et al. (2002) tested the generality of the relationships of different photosynthetic parameters with stomatal conductance. From their results and those of Gulias et al. (2002) on six Mediterranean trees and shrubs, it was concluded that photosynthetic parameters depend on stomatal conductance. Kolb and Stone (2000) also found that the stomatal conductance correlated with photosynthesis in oak and in pine; for old-growth oak and old-growth pine photosynthesis and stomatal conductance also correlated with the daytime leaf water potential.

Responses of stomatal conductance in *A. senegal* to changes in soil water indicate their adaptive significance in arid environments. A decrease in stomatal conductance (g_s), which reduces water loss, is frequently cited as a mechanism by which plants adapt to drying soil (Davies and Zhang 1991). Nobel (1976, 1977) noted that desert succulents responded rapidly to small rainfall events by variation in stomatal conductance and water potential. Such a response of stomata in *A. senegal* to change in soil water may be related to the different mechanisms employed by drought-tolerant species to survive in harsh environment.

Responsive stomata and deep root systems in *A. senegal* both seem to increase the ability of the tree to endure drought for considerable periods of time without becoming severely dehydrated (cf. Kramer 1980). Zhang et al. (1997) confirmed that seedlings of a drought-tolerant ponderosa pine population were more sensitive to water availability than seedlings from other populations. In conclusion, *A. senegal,* in addition to its shedding of leaves, seems to be able to adjust physiologically to a wide range of prevailing environmental conditions. Moreover, changes in physiological traits during the growth cycle of woody plants can provide insight into factors that influence the recruitment and survival of species (Donovan and Ehleringer 1991, 1992). *A. senegal* obviously can tolerate drought because of both morphological and physiological adaptation but also rely on an ability to take up water and control the water loss efficiently when the soil water decreases.

5.1.5 Gum production

The gum production process in *A. senegal* is not yet fully understood. Whether the exudates are results from a normal metabolic activity of the tree, a defense mechanism by the tree to seal wounds created by damage, or a result of bacterial or fungal infection or disease is yet to be determined (Ballal 2002). Furthermore, the intensity of tapping has its bearing on the life span of the tree (Ballal 1991).

The present study shows that the gum production was strongly affected by soil water and expressly correlated with the total soil water to 75 cm or 150 cm soil depths; in contrast, there was no clear correlation with the total soil water in the 0-250 cm-soil layer. As discussed above, the same effect was found in ψ_{Lm}.

Tree gum production during the tapping season also exhibited a significant negative correlation with stomatal conductance as measured during and shortly after the previous rainy season. This can be explained by the effect of the water status on the tree during gum production. While the soil is becoming drier, the tree adjusts physiologically through changes in stomatal conductance and leaf water potential, which contributes to overcoming the adverse conditions. Tapping is usually carried out after the rainy season, when the growth has ceased and the leaves become yellowish. The gum production process thus takes place during the season when the water loss is minimal.

The production of gum strongly depends on soil water. Ballal (2002) found that the gum yield was positively correlated with rainfall in North Kordofan State. There is a general trend of increase in gum yield with an increasing intensity of tapping (Ballal et al. 2005), which, however, may severely damage the tree. In general, the highest gum production in *A. senegal* appears to coincide with the start of dry conditions after the rainy season when the air temperatures rise (Awouda 1973). Awouda (1973) also considered gum formation to be a direct result from adverse environmental conditions.

The relationship between gum yields of the first or the second picking and the total gum production per tree was found to be highly significant (Fig. 45). This result suggests that the first and second picking can be used as indicators for the total gum production per tree. The finding is in line with results obtained by Ballal (2002), who studied the yield trends of gum arabic as related to some environmental and management factors. He also confirmed that the first and second picking could be relied on to predict or estimate the total gum yield of an *A. senegal* tree.

In the present study it was found that the per-tree gum yield was strongly affected by tree size. Mid-sized trees (10-15 cm basal diameter trees) gave the highest gum production, and the lowest gum yield was obtained from the largest (20-25 cm basal diameter). This finding is in line with those by Abdel Rahman (2001) and Ballal (2002), who showed that there is a significant effect of tree age on gum yield. They also confirmed that the maximum gum yield is obtained from trees about 15 year of age.

5.1.6 Soil nitrogen status under **A. senegal**

Next to water availability, nitrogen seems to be the most important factor limiting productivity in arid land ecosystems (Gutierrez and Whitford 1987, Noy-Meir 1973). Several early researchers have studied *A. senegal* as a nitrogen fixing tree (e.g. Habish 1970, Gerakis and Tsangarakis 1970). In the present study, excavation of the root system of ten trees of different sizes during two rainy seasons showed no presence of nodules even during the period of most active growth. Nodulation in *A senegal* has only been reported during the seedling stage (Ndoye et al. 1995). Attempts to find the nodules in the roots of large trees seem to have consistently failed (cf. Masutha et al. 1997).

The amount of soil nitrogen increased as the *A. senegal* tree size increased, but there was no statistically significant difference between amounts of nitrogen under trees of different size classes. The amount of nitrogen in the topmost (0-30 cm) soil layer was higher than that at other depths. This is in line with other studies that have shown that the nitrogen availability is highest in the upper soil layers and declines strongly with depth (Evans and Ehleringer 1994; Stark 1994; Jobbagy and Jackson 2001). This probably also reflects the tree dependence on water in the topsoil, where more nutrients are available (Jobbagy and Jackson 2001), and possibly explains the high concentration of lateral and fine roots of *A. senegal* near the soil surface. Several experimental studies on below-ground competition have suggested that water and nitrogen uptake occur together (e.g. Casper and Jackson 1997).

The amount of nitrogen was higher under *A. senegal* at different depths than that under *Balanites aegyptiaca* or *Azdirachta indica*. The variation in total nitrogen under these species was statistically significant. However, this result was in contrast to the finding obtained from root excavation during two rainy seasons, where nodules were not observed in *A. senegal*, even during the period of most active growth. *A. senegal* was listed as a low-nitrogen fixing species by Wolde-Meskel et al. (2004).Present results strongly suggest that the capability of *A. senegal* to fix nitrogen needs further investigations in mature stands.

The amount of organic carbon was significantly higher in the 0-30 cm soil layer and decreased with soil depth, following the same trend as found in nitrogen. This result is in line with other studies (Jackson et al. 1996; Carter et al. 1997; Jobbagy et al. 2000). Since *A. senegal* is a deciduous tree that sheds its leaves during the dry season and is adapted to harsh environmental conditions, the accumulation of organic carbon and nitrogen in the topsoil may be a result of leaf litter decomposition. Soil organic carbon storage and distribution is controlled by the balance of C inputs from plant production and outputs through decomposition (Schlesinger 1996, Burke et al. 1998).

The present results also show that the amount of soil organic carbon was significantly affected by tree size. The organic carbon under *A. senegal* increased as the tree size increased, and this was probably due to a higher biomass and higher input of carbon into the soil from large trees during many seasons. Jobbagy and Jackson (2001) found significant variation in soil carbon and other nutrient storage profiles among vegetation types that can be explained, in part, by differences in root distribution and biomass cycling rates. Above and below-ground allocation also affects the relative amount of C that eventually falls to the soil surface from the tree canopy.

5.2 Agroforestry

5.2.1 Effect of tree density on soil moisture

Below-ground plant interaction is the most important factor regulating the yield in the semi-arid tropics, where water is the prime environmental factor limiting crop growth (Ong et al. 1991). In the present study the intercropping design (different tree densities with crops; pure trees and pure crops) caused variation in soil moisture and physiological traits of both trees and crops. In particular, the effect was clear in the 0-75 cm topsoil layer. This finding is in line with that by Ansley et al. (1998), who found that resources necessary for growth of individual *Prosopis glandulosa* trees become gradually more limiting under increasing stand density.

In the present study, the low soil water content at the higher tree density was obviously due to a higher water uptake caused by high transpiration demand and hence a higher rate of depletion of soil moisture. The water depletion was much higher when trees were grown at a high density with agricultural crops than found in connection with mono-cropping. The roots of *A. senegal* in the sandy soils of Kordofan were now mostly found within the top-150-cm layer. The root systems of both agricultural crops used in the experiments, sorghum and karkadeh, were confined only to a depth of approximately 1-m. It is impossible that the trees were utilizing ground water, since the water table was at a depth of more than 60 m. In this case trees and crops competed for a limited supply of water from the same soil profile. However, it is possible that trees also partly utilize water from the deeper sub-soil below 150 cm. This could be especially true during the dry season when the topsoil water is depleted. The effects of different tree densities on soil water content was reflected in the yield of both trees and crops and in their physiology.

5.2.2 Effects of intercropping design and soil water on gum production

A significant correlation was found between per-tree gum yield and soil water especially in the 0-75 cm and 0-250 cm soil layers, when crops were grown with *A. senegal* trees, while the gum production was significantly correlated only with soil water in the 0-75 soil layer when *A. senegal* was grown solely. This could reflect the effect of field crops on gum yield through effects on soil water: when the soil is getting drier due to the crop competition, trees adjust to utilize water in deeper soil layer during gum formation.

The gum yield increased in relation to soil moisture at the end of the previous rainy season. This relationship appears to not fully control the gum production, because the highest gum yield was not obtained with the highest amount of soil water. This finding implies that there is a threshold soil moisture at which maximum gum production is achieved. The highest gum yield per tree and per hectare was obtained from a combination of sorghum with trees at high density (433 trees ha^{-1}). In the present study, inter-cropping with either one of the other agricultural crop affected the gum production per hectare positively compared with that (49 kg ha^{-1}) obtained from a pure tree stand at low density (266 trees ha^{-1}). The per-tree gum production increased by 115% and 120% when sorghum and karkadeh were inter-cropped with trees at this low density, respectively. The highest increase (143%) in per-tree gum production, in comparison to the pure stand at low density, was obtained when sorghum was intercropped with trees at high density (433 trees ha^{-1}).

Agroforestry thus caused variation in gum production per hectare. The highest yield, 115 kg ha^{-1}, was obtained when sorghum was grown with trees at high density. There was also a trend of an increasing gum yield per hectare with the addition of either sorghum or karkadeh, when trees were grown at a low density. Intercropped with trees at high density, only sorghum had an increasing effect on gum yield, and karkadeh seemed to decrease the gum yield. The gum production thus increased in both cases when sorghum was intercropped with trees and especially when the tree density was increased from 266 trees to 433 trees ha^{-1}.

The per-tree gum production in the agroforestry system correlated negatively with the morning leaf water potential (ψ_{Lm}) and stomatal conductance of the trees as measured at the end of the rainy season. This may have been through the effect of soil water on gum production, on stomatal conductance and on ψ_{Lm}. Similarly to the observation in natural *A. senegal* trees discussed earlier, it was also found in the agroforestry experiment that there was a strong negative correlation between gum production during the dry season and the tree leaf water potential (ψ_{Lm}) or stomatal conductance at the end of the rainy season. Ballal (1999) reported that the gum yield is strongly affected by rainfall. However, it is believed that, in agroforestry, deep tree roots may utilize water and nutrients from beneath the root zone of the associated annual crop, thus reducing competition effects (Eastham and Rose 1990).

3.2.3 Effects of soil water and intercropping on tree physiology

In the agroforestry experiment, the tree morning photosynthesis (*A*) showed high dependence on soil water to 250 cm soil depth, while a low dependency of photosynthesis on topsoil water (to 75 cm depth) was observed. Morning photosynthesis only in the pure *A. senegal* stand showed a highly significant positive correlation with soil water at the 0-75 and 0-250 cm soil depths. This indicated that trees use the soil water of deeper soil layers later in the season, at the time of gum exudation (October), when field crops are still taking water from the topsoil. At that time the topsoil is probably depleted and trees have to rely on deep-soil water to maintain the level of CO_2 assimilation. Nevertheless, a general observation is that plants may have a high concentration of roots in the topsoil and still have some very deep roots which may increase their drought tolerance (Schroth 1999). Such results have been obtained in several tree species (Buwalda 1993, Sanford and Cuevas 1996).

The tree stomatal conductance (g_s) varied with agroforestry design. This can similarly be explained as a result of the effects of intercropping on soil water. The tree stomatal conductance (g_s) strongly correlated with the soil water in the 0-75 cm soil layer, while no correlation was found with soil water in the 0-250 cm soil layer. In studying the effect of watering and drying on wheat stomatal conductance, Liang et al. (2002) proved that the drying and wetting alternation had a significant effect on the stomata that could reduce the wheat transpiration rate. They concluded that stomatal conductance of wheat steadily decreased with a decrease in days of drying and in leaf water potential. These results are also supported by findings in other studies, which indicate that the soil water content may control stomatal aperture (Fischer et al. 1970; Masle and Passioura 1987; Tardieu et al. 1991).

5.2.4 Effects of intercropping design on tree intrinsic water use and rain use efficiency

The intrinsic water use efficiency was expressed as the ratio of photosynthesis (*A*) to stomatal conductance (g_s). Decrease in stomatal conductance, faster photosynthesis rate, or a combination of both can lead to increase in IWUE (Ehleringer et al. 1993). The intercropping of sorghum and karkadeh with trees at high density (433 tree ha^{-1}) resulted in the highest tree IWUE. In the present study, indices of intrinsic water use efficiency increased with soil dryness. Similarly, the rain use efficiency of trees (RUE), which was expressed as gum yield per unit rainfall, was significantly higher in intercropping of sorghum with trees at high density (433 tree ha^{-1}), as compared to other intercropping designs. This can be considered as a tree response to a water deficit that is due to high competition with crops. It is also reasonable to hypothesize that plants use resources more efficiently when these resources are in scarce supply.

5.2.5 Effects of intercropping design on crop yield and physiology

Dry matter production and harvestable yield

The amount of soil water in the 0-75 cm soil layer was in the present study found to significantly affect the agricultural crop yield in an agroforestry system. Previous data from 37 global studies on sorghum by Unger and Baumhardt (1998) show that the yield increased during the period 1956-1997 by 139%, of which 46% resulted from the use of improved hybrids and the remaining 93% mainly from better availability of soil water. Many other studies (e.g. Doorenbos and Kassam 1979, Stone et al. 2001) show results similar to the present findings.

The yields of both karkadeh and sorghum were in the present study affected by the intercropping design. Crop yield and biomass depended on variation in topsoil water, and, a decreasing effect on crop yield by inter-cropping with trees could be discerned. A reduced tree density obviously minimizes the competition for soil water.

Sorghum, because of its shallow root system, was more dependent on the topsoil (0-75 cm) water than karkadeh, which obviously was capable of extracting water from up to 150 cm soil depth. This reflects the effect of the root system arrangement of both agricultural crops on the soil water and thus on the final crop yield. In their studies, Jonsson et al. (1998) found that different rooting habits in different types of plants modify the soil water uptake of trees and annual crops in regard to spatial and temporal patterns. In the present study, it was found by root excavation that the concentration of lateral and fine roots in both trees and crops were maximal in the topsoil (for sorghum in the 0-75 and for karkadeh in the 0-150 cm layer).

In studying the root distribution in a *Grevillea robusta*- maize agroforestry system in semi-arid Kenya, Smith et al. (1999) found that tree roots were dominant in such an agroforestry systems at all times. Observations in Kenya also include results from controlled agroforestry experiments, where *Melia volkensii* trees were found to be highly competitive with agricultural crops even if crown-pruned (Ong et al. 2002). Overlapping distribution of tree and crop roots within the crop rooting zone were highlighted by traditional methods of root excavation which indicated an apparent lack of significant spatial complementarily for this species. The same finding was obtained even in the tree species that are regarded as highly compatible for simultaneous agroforestry systems (Odhiambo et al. 1999; Schroth 1999; Ong et al. 2002). Like in other tree species, root concentrations in *A. senegal* have been shown to be highest near the soil surface and to decrease with soil depth (cf. Schroth 1999).

In the present study, *A. senegal*, when planted at a low density of 266 trees ha^{-1}, reduced the karkadeh flower yield by about 26% and the above-ground karkadeh biomass production by 37%, as well as the sorghum grain yield by 19% and the sorghum biomass production by 9%. When planted at 433 trees ha^{-1} it reduced the karkadeh flower yield by 55% and the biomass production by 57%, and the sorghum grain yield by 44% and the sorghum biomass production by 45%, relative to pure crops. This effect was obviously caused by the effect of different root densities on soil water. Significant correlation was also found between field crop yield and soil water. These results are in line with many previous studies (Chaves 1991; Bisht et al. 2000; Dhyani and Tripathi 2000). Generally, tree competition reduces the growth of individual crop plants growing near to tree rows, and it often reduces the production of plants nearest to and furthest from competing trees when compared with controls (James et al. 2003).

The arrangement and management of trees in relation to crops within an agroforestry practice have a bearing on microclimatic factors. A combination of *A. senegal* trees with crops affects negatively the total yield harvested from the land. Akbulut et al. (2003), in studying the effect of alley cropping on agricultural crops and arthropods, found that agroforestry caused both negative and positive effects on the yield of crops and mainly a negative effect on tree growth. However, planting *A. senegal* trees at a wider spacing reduced the negative impact of intercropping. Crop yield and biomass were significantly reduced by the presence of trees in studies conducted by Narain et al. (1998). Le Roux et al. (1995) concluded that both shrubs and grasses in an African savanna obtained most of their water from the upper soil layer, potentially implying strong competition for soil water.

Plant growth is dependent on the availability of light, water and nutrients; consequently, manipulation of the tree planting density in an agroforestry system may modify the biomass production of component species by controlling intra-specific competition for resources (Eastham and Rose 1990). Tree density has by Eastham et al. (1990); been found to modify the water use and productivity of tree species and understorey annual crops reduction of tree density freed both trees and crops from inter-specific and intra-specific competition. Jones et al. (1998) found that the grain yield of sorghum at final harvest was significantly higher in a monocropping control than when intercropped with pruned or unpruned *Prosopis juliflora* or *Acacia nilotica* trees.

Karkadeh seemed in the present study to deplete the soil moisture more than sorghum. This may be related to the fact that karkadeh possesses a taproot system capable of extracting soil moisture from greater depths, as compared to sorghum, which is a shallow-rooted crop. This ability helps karkadeh to survive under low rainfall better than sorghum. Overall, karkadeh shows superior performance as compared to sorghum in the rate and depth of root growth. Sorghum showed higher dependence on soil water in the 0-75 soil depth than karkadeh, due to the difference in root systems in these species.

Loyd et al. (2001) stated that when water is stored at greater soil depths, crop selection would assist in optimizing the water use efficiency of the cropping system. Karkadeh shows more intensive root growth into deep soil layers and thus occupies a larger soil volume than sorghum, which is shallow-rooted. From the viewpoint of agricultural crop production, karkadeh, therefore, has better characteristics as an agroforestry crop than sorghum, as it is better adapted to competition with trees, increases the gum yield per unit area and shows a smaller effect on the harvest index. In their studies, Miller et al. (2003) also concluded that differences in soil water use among crops were attributed to rooting depths. Recent reviews of root research indicate that there appears to be limited scope for spatial differentiation in rooting between trees and crops (i.e. spatial complementarity) in water-limited environments, unless ground water is accessible to tree roots (Ong et al 2002).

In the present study, a comparison between stored water at different depths of the soil profile in agroforestry and on bare land showed that the amount of water remaining in the 0-250 cm soil stratum at the end of the growing season (November) was not much different in the two cases. This may have been due to loss of water through high evaporation from bare unprotected sandy soil. Agroforestry systems can thus effectively store soil water and improve its utilization. In other studies (Nyadzi et al. 2003, Gupta et al. 1998) intercropping has been found to increase the competition for water and, despite a higher water use in a tree-pasture association, the amount of soil water in the 0-300 mm soil stratum was found to be higher than or similar to that of the open pasture. Guevara-Escobar et al. (2000) also observed that tree shading decreased evapotranspiration and led to accumulation of water under trees.

Crop physiology

In the present study intercropping designs affected the crop physiological behavior through their effects on soil water. This effect was due to differential soil water depletion under different tree densities. The morning leaf water potential (ψ_{Lm}) of both crops was strongly correlated with soil water in the 0-75 cm soil layer. A progressive decline of the morning leaf water potential of sorghum (-0.7 to -1.95 MPa) was a result of the soil water supply decreasing in the topsoil from 60 mm to near10 mm. A similar decline of morning leaf water potential in karkadeh (<-1 to >-2 MPa) was a result of the soil water decreasing from 60 mm to less than 10 mm. This can be explained by a decline in crop leaf water potential leading to a steeper gradient for water to flow from the soil to the leaves. In a similar study, during soil watering and drying, the leaf water potential of wheat changed rather sharply depending on the soil water content (Liang et al. 2002).

A decline in soil water is well known to reduce the leaf water potential in field crops (cf. Naor et al. 1994). In the present study, differences in the responsiveness of the leaf water potential in sorghum and karkadeh to water in the different soil layers can be explained by the root distribution patterns of these crops and their effect on soil water extraction. Sorghum, with its shallow root system, depended mainly on the water in the top 0-75 cm soil layer, while karkadeh also depended on the whole 0-250 cm soil layer. In general karkadeh also exhibited more negative values of morning leaf water potential than what was the case in sorghum.

An analysis of the role of the stomata in the control of water use and gas exchange is complicated by the existence of several feedback mechanisms in which variation in net assimilation or transpiration rates resulting from variations in stomatal conductance can themselves affect the soil water (Cowan 1972; Jones 1992; Jarvis and Davies 1998).

The crop stomatal conductance (g_s) exhibited a significant correlation with soil water in the 0-75 cm soil layer. Obviously as a result of different root distribution patterns in sorghum and karkadeh, the stomatal conductance in sorghum was more dependent on topsoil (0-75 cm) water than that of karkadeh. A decrease of the stomatal conductance in karkadeh from >0.3 to >0.1 mol m-^{2}s^{-1} was observed when the amount of soil water decreased from 29 mm to 16 mm in the 0-75 soil layer, while in sorghum the stomatal conductance decreased from 0.1 to 0.8 mol m^{-2}s^{-1} when the topsoil water supply decreased from 55 to 30 mm. This indicates that stomatal conductances of both crops are sensitive to change in soil water, thus leading to prevention of plant damage resulting from competition with trees. Such an effect could also be caused by ABA accumulation resulting from water stress when the soil at the root zone starts to dry (Davies and Zhang 1991).

The stomatal conductance also correlated positively with the crop photosynthesis rate. This relationship was stronger in sorghum than in karkadeh. A decrease in the stomatal conductance from 0.8 to 0.1 mol m^{-2} s^{-1} caused a decrease in photosynthesis from 25 to 12.5 μmol m^{-2}s^{-1} in sorghum. A decrease in the stomatal conductance from 0.3 to 0.1 mol m^{-2} s^{-1} caused a decrease in photosynthesis from 16.5 to 10 μmol m^{-2}s^{-1} in karkadeh. There was a response of gas exchange in karkadeh and sorghum grown on sandy soil to changes in soil water in the topsoil caused by associated tree density (cf. Gollan et al. 1986, Rosenthal et al. 1987).

Previous studies by Raschke (1975) and Gourdriaan and van Laar (1987) have proposed that the stomatal control by a crop plant, when water is not limiting, can be characterized as (1) *regulating*, when the internal CO_2 concentration is kept within narrow limits, or (2) *non-regulating*, when the internal CO_2 concentration is not controlled by the plant. Responses of *A. senegal* to a reduction in soil water content while maintaining CO_2 assimilation consist of reduced stomatal conductance, control of water loss, maintenance of the leaf water potential and an increase of the intrinsic water use efficiency (cf. Arndt et al. 2001).

Examples from the literature on sorghum, apple and maize exposed to a wide range of soil moisture content show positive or negative correlations between stomatal conductance and leaf water potential or soil water potential (Jones 1998). In the present study, the crop photosynthesis rate correlated with soil water at the 0-75 cm soil depth. The rate of photosynthesis declined as the soil water decreased. Reduction in photosynthesis and stomatal conductance of both field crops seemed to be caused by below-ground competition.

Turner et al. (2001), when studying the adaptation of chickpea to water-limited environments, found that a decrease in leaf photosynthesis occurred as the leaf water potential decreased with progressive soil water depletion. Among the variables strongly affected were crop yield, photosynthesis rate and transpiration (as a result of g_s control). Kumar et al. (2000), when studying genotypic differences in photosynthesis and its associated parameters in relation to yield among twelve genotypes of barnyard millet (*Echinochloa frumentacea*), concluded that the mean rate of leaf photosynthesis, canopy photosynthesis, stomatal conductance and total dry matter had significant positive association with grain yield.

Harvest index (H_I)

The present study indicated a high degree of self-correlation between the grain yield of sorghum or flower yield of karkadeh on the one hand and the total dry matter production of the crop on the other. This is explained by the harvest index equation that also assumes a high degree of self-correlation: $Y=H_I (p_s + Y)^{-1}$, where H_I is the harvest index, Y is the yield in kg ha^{-1}, and p_s is the above-ground dry matter.

A linear relationship has earlier been found to exist between grain yield and above-ground dry matter yield in many crops (Sinclair 1998). A similar relationship between the economic yield and biomass has been observed in other studies (cf. Snyder and Carlson 1984, and Slabbers et al. 1979). Thus both parameters can be used to predict each other.

There was a strong effect of different intercropping designs on the harvest index in sorghum, while there was stability in the karkadeh harvest index. The sorghum harvest index was significantly affected by the presence of trees and the highest harvest index was obtained, when sorghum was grown solely. The variations found in the harvest index in sorghum could probably be explained by differences in soil water and assimilation during the late, grain filling stage (cf. Hammer and Broad 2003)

Comparison of present crop yield with average harvests for Kordofan (Table 12) (139 kg ha^{-1} for sorghum grain and 36 kg ha^{-1} karkadeh flower) shows that, in the case of sorghum, intercropping with a low density of trees, resulted in a grain yield close to the regional average and higher total biomass than the regional average. Monocropping inside the forest resulted in a grain yield that by 19% exceeded the regional average.

Table 12. Sorghum and karkadeh production in agroforestry system in the present study and average sorghum production on farmland in North Kordofan state. Data on average production collected from Agricultural Research Corporation, El Obeid and Central Ministry of Agriculture reports. LD = 266 trees ha^{-1}, HD = 433 trees ha^{-1}. LD+crop, HD+crop and monoculture represent the different intercropping designs in the present study.

Intercropping design	Sorghum grain (kg ha^{-1})	Sorghum biomass (kg ha^{-1})	Karkadeh flower (kg ha^{-1})	Karkadeh biomass (kg ha^{-1})
LD+crop	135	1030	127	621
HD+crop	92	625	77	421
Monoculture	166	1135	172	982
Average farmland	139	931	36	418

However, it cannot be concluded from the present experiments how trees affect the agricultural crop yields over a longer period of time. For proper, comprehensive analysis, comparable sets of data from permanent agroforestry, temporary agroforestry (e.g. traditional shifting cultivation) and permanent monocropping should analyzed.

In the case of karkadeh, growing of the sole crop now resulted in a nearly five times higher yield and intercropping with trees in 2-3.5 fold increases in yield as compared to the regional average. Again no evidence can be drawn from the experiment on the long-term performance of this crop in agroforestry system.

Intrinsic water use efficiency (IWUE) and rain use efficiency (RUE) in crops

The intrinsic water use efficiency was expressed as the ratio of photosynthesis rate (A) to stomatal conductance (g_s) for both karkadeh and sorghum. In crops in general, a decrease in stomatal conductance, faster photosynthesis rate, or a combination of both can lead to an increase in IWUE (Ehleringer et al. 1993). Present results show that the IWUE in both crops increased when intercropped with high-density trees (433 trees ha^{-1}); (Fig. 40). This could have been due to high competition between trees and crops for topsoil resources. As in the present study, when considerable overlap in functional root systems exist among species, variations in IWUE (A/g) may in part contribute to the coexistence gain of those species (Walker et al. 1981; Scholes and Archer 1997; Huang 1998).

In the present study, a much higher IWUE was observed in karkadeh than in sorghum. This suggests that karkadeh and *A. senegal* at high tree density may compete more vigorously for the available soil water than found in other intercropping designs. More research is obviously needed to explore the extent to which tree roots directly compete with crops for resources and affect the water balance.

Present results also show that the rain use efficiency in agricultural crops was strongly affected by different intercropping designs. In both crops the RUE increased as the tree density decreased. This was obviously due to the different competition situations for soil water in the different intercropping designs. Consistent with this trend, the highest RUE was obtained when crops were grown without association with trees.

Effect of intercropping design on cropping system rain use efficiency

The present results also show that the rain use efficiency of the whole cropping system was significantly affected by intercropping design. Higher RUE was obtained when sorghum was grown with trees at high density followed by karkadeh grown with trees at low density and sorghum with trees at low density. The lowest RUE values were obtained from sole trees and sole crops. It is conceivable that, in addition to it s environmental benefits, tree-crop intercropping can make full use of and optimize the rain use efficiency. In other words, competition in an agroforestry system can maximize the exploitation of rainwater throughout the entire soil profile during the rainy and the dry season.

6. Conclusions

Agroforestry systems based on *Acacia senegal* can, apart from their environmental benefits, also make full use of the available resources and thus lead to a higher combined yield as compared to growing trees or agricultural crops alone. This is a result mainly from improved use of water.

A key result from the present studies from the viewpoint of gum arabic management is that the gum yield can be significantly increased when the trees are interplanted with agricultural crops, such as sorghum or karkadeh. The economic yield of these field crops is lower in combination with *A. senagal* than in pure culture; however, agricultural crop yields in gum gardens compare well with the average farm production level in Kordofan. A decrease in crop yield that results from competition between trees and crops can be tolerated, if the economic gain from gum production can be assumed to compensate for any loss in crop yield.

With farming based on *Acacia senegal* agroforestry, North Kordofan State holds a considerable agricultural potential, despite land vulnerability, adverse climatic factors and poverty. *A. senegal* agroforestry seems to be especially feasible for the area when considering the role of gum gardens in traditional land-use and the national and local economy, and the multipurpose nature of this particular tree species. New research is needed to clarify the roles of different manager or land-owner groups in gum garden production and economy, including the small holder farmes, the landless population, large landowners, enterprises, and the government.

In the present study, little evidence was found of complementarity in resource sharing between trees and agricultural crops that compete for soil water. However, the root distribution of different agroforestry system components was found to have an effect on gum and agricultural crop production. In an agroforestry system based on *A. senegal* it is vital to select an appropriate tree density, so as to minimize the effect of root competition and to reduce the trade-offs between crop and tree productivity.

Below-ground competition is inevitable when the root systems of trees and crops are likely to have rather similar distribution in the topsoil, as found in the present study. However, all sources of available water are not used equally. Changes in soil moisture provide an indicator for predicting the response of agroforestry components in terms of water use, gum production, biomass, and crop harvest.

Karkadeh is superior to sorghum in the rate and depth of root growth. This makes karkadeh a better choice as crop, if the soil water conditions are adequate. Sorghum seems to be superior to karkadeh in an agroforestry system where the amount of soil water is inadequate, or when the production system is directed towards maximizing the gum production.

Measurements of morphological and physiological characteristics in *A. senegal* and associated agricultural crops facilitate the prediction of spatio-temporal resource sharing in such an agroforestry system and contribute to finding an optimal system design. Tree spacing is an effective tool for controlling root competition between trees and associated agricultural crops. The selection of the agricultural crop component should be based on information on the root growth pattern in that particular crop.

For most of the rainy season there seems to be less soil water in an *A. senegal* agroforestry system in comparison to bare land. However, such a difference is minimal at the end of the rainy season. Evidently, even in the dry conditions of Kordofan, some utilizable water remains in the soil after crop harvest (as well as under bare land), which makes a more efficient water use of the cropping system a feasible aim. An agroforestry system can be expected to fulfil this aim and utilize the water well in the entire soil profile during the dry season.

Stomatal conductance, in trees or in agricultural crops, can be used as an integrating parameter for the water balance in the soil and in system components. This characteristic also indicates well the physiological response of trees or crops to water stress during the growing season under these dryland conditions.

A. senegal is adapted to soil water stress through morphological and physiological mechanisms. In addition to shedding of leaves, *A. senegal* is capable of physiological adjustment in response to an increase or decrease in soil moisture. This contributes to avoidance of damaging effects of water deficits and to an increase in the intrinsic water use efficiency. As a whole, this adaptive strategy enables *A. senegal* to survive and develop in an adverse dryland environment and in man-made production systems in such an environment.

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APPENDIX 1. COMPLEMENTARY FIGURES

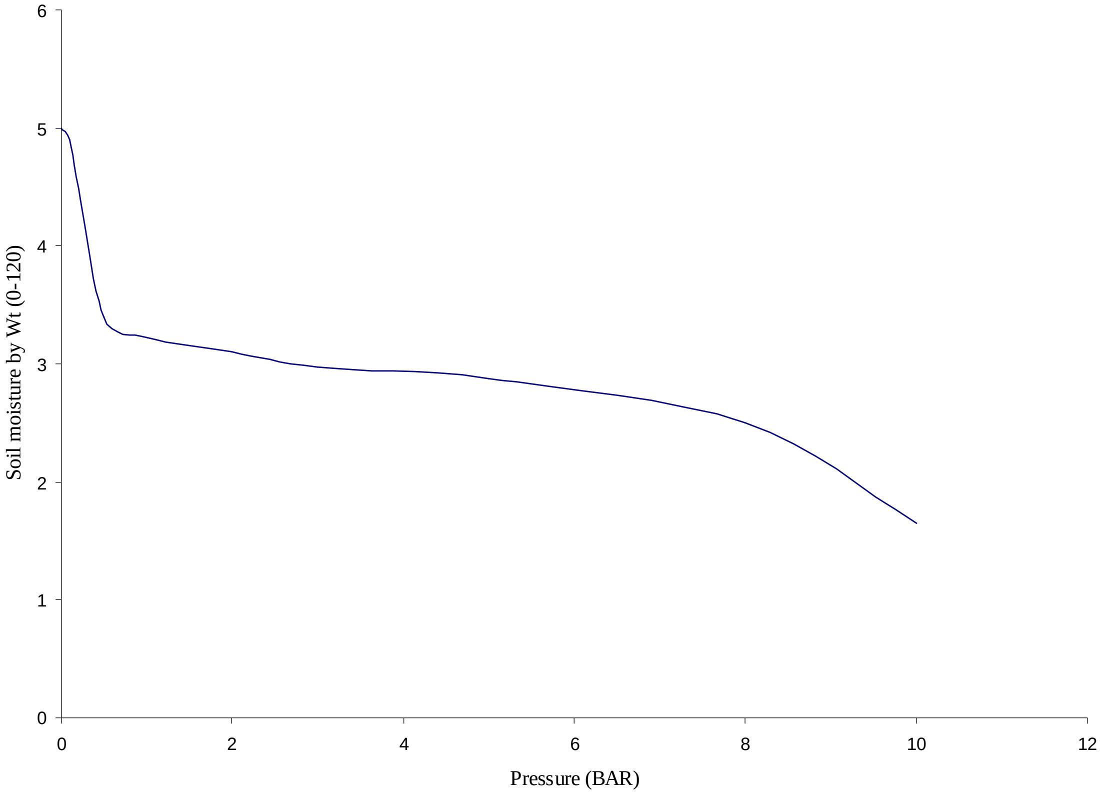

Figure 43. Soil moisture characteristic curve for experimental sites.

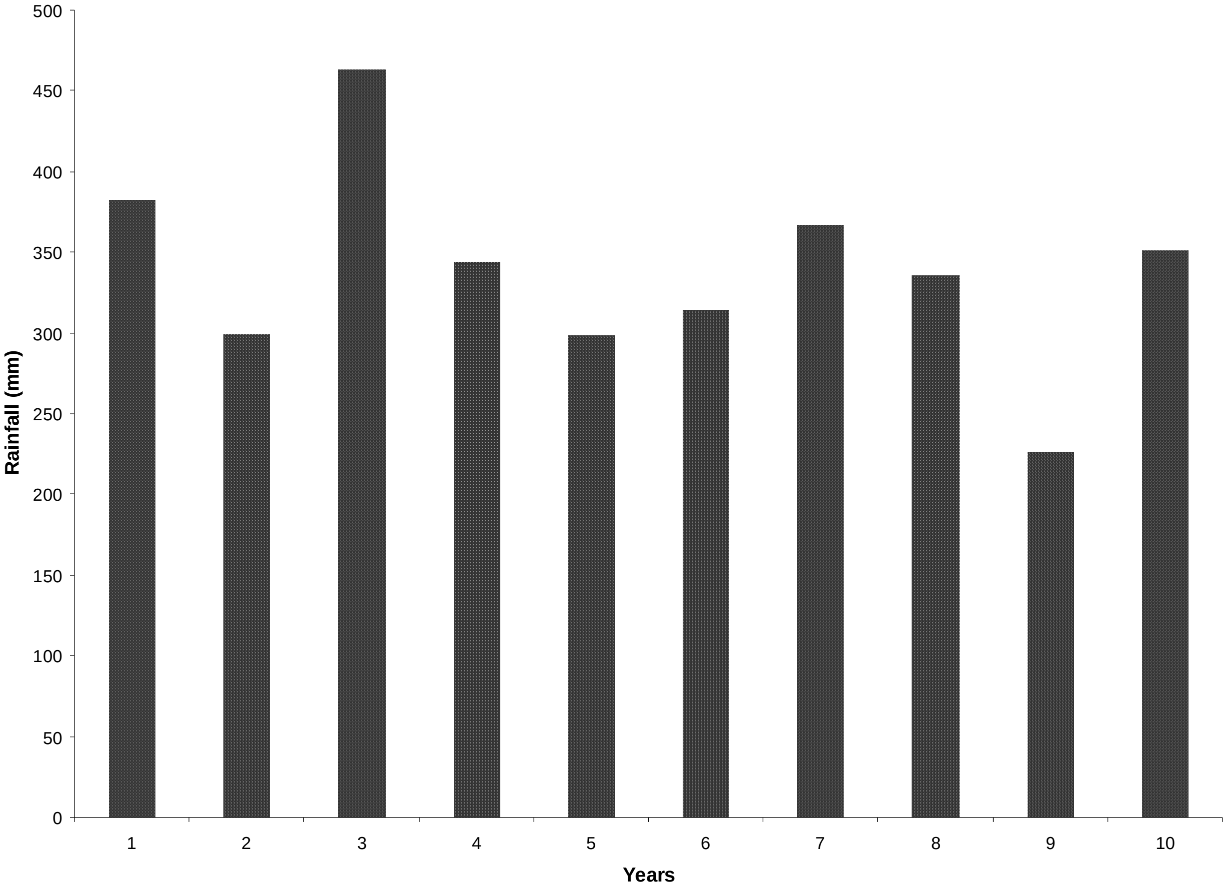

Figure 44. Rainfall (mm) during the period 1992-2001 in North Kordofan.

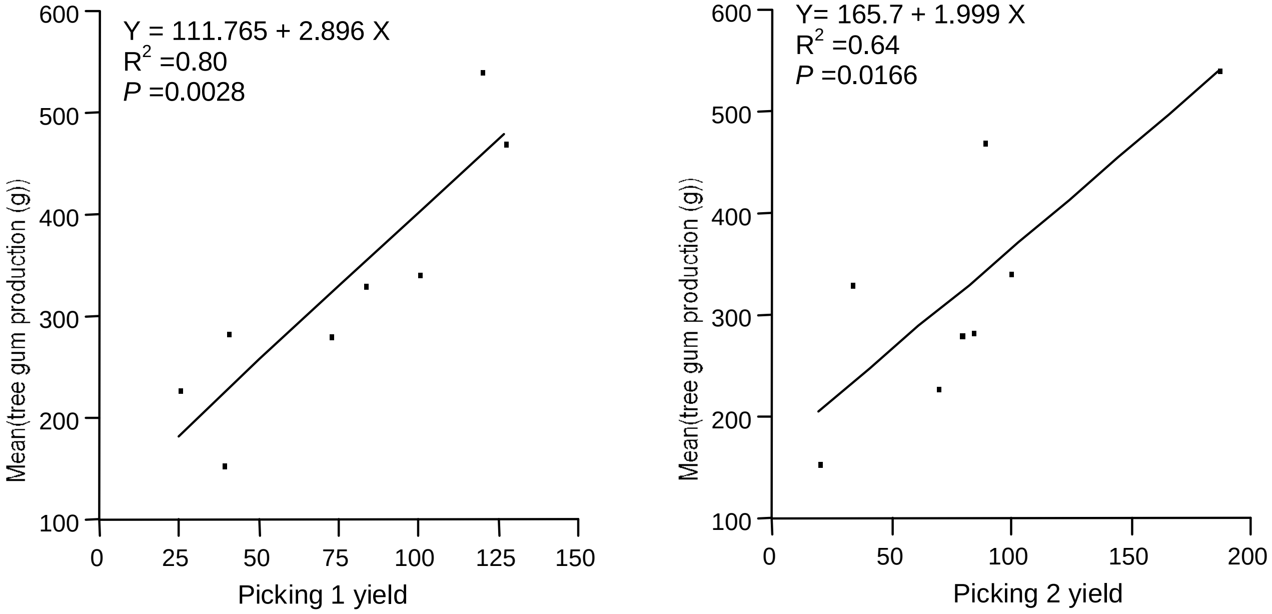

Figure 45. Relationship between total tree gum production and yield in the first two pickings. Each data point is the mean of five readings. Data collected from different tree size classes during two rainy seasons.

Figure 46. Illustration of *A. senegal* and sorghum (mid stage) root distribution at the experimental sites. Sorghum roots shown are from the same site but not from the actual experiment. (Photographs by A. Gaafar).