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Nitrogen Dynamics of the Acacia Senegal Agroforestry System in the Sudan

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NITROGEN DYNAMICS OF THE ACACIA SENEGAL AGROFORESTRY SYSTEM IN THE SUDAN

by

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Abstract

The low-rainfall and high-heat climatic characteristics of the African savanna have resulted in some soil types that are generally deficient in nutrients and permitted the drought tolerant legume, *Acacia*, to dominate the vegetation formation. A number of *Acacia* agroforestry systems are practiced in the savanna. The *Acacia senegal* agroforestry system (acronym ASAS) evolved in the Sudan over a century ago and spread to many sahelian countries to improve soil conditions, ecological and economic stability and food supply. The system is attractive to low income farming communities as it permits the use of hand implements for cultivating sandy soil, provides labor well into the dry season and supplies gum arabic for export, fodder and fuel from trees.

The ASAS has received meager attention from the sahelian and international scientific and planning communities, particularly from an ecosystem's perspective. This work investigated the biotic, climatic and edaphic interactions of the system with a view of obtaining a better understanding of the processes that govern soil N accumulation, inputs and outputs. It specifically aimed to test the effects of the above-mentioned interactions on soil and plant nitrogen, and genetic differences within and among populations. The effects of limited plant growth resources on nodulation, rates of nitrogen fixation and biomass were examined. These growth resources included soil, space, nutrients, and photoperiod. The study also aimed to test the possibility of identifying and isolating microbes from high nitrogen yield combinations of soil and seed, and use these microbes to infect plants raised in sterile soil. Different morphological appearances of nodules warranted closer anatomical monitoring of nodules using electron microscopy.

Natural and artificial stands of *A. senegal* in four localities within the species range in the Sudan were selected and composite soil samples and corresponding tissues and climatological data were collected and analyzed. Genetic variation among populations was investigated by electrophoresis.

Certain combinations of soil type of high clay contents and seed from various study localities resulted in higher nitrogen input than others, judging from the higher numbers of viable nodules formed in these combinations. Bacterial strains extracted from these combinations were used to infect seedlings raised in sterile soil resulting in variable nodule numbers. Nodule formation was affected by soil type and by the phenological condition of the plant as impacted by photoperiod. The peak of red functional nodules was eight weeks. When this period was extended to 90 days most of the nodules degenerated.

The impact of varied competition intensities on nodulation and biomass was quantified. Competition intensity correlated negatively with individual plant biomass and nodule number, while total plant biomass was not affected. Sites had specific production potentials expressed as total plant biomass that seemed to be achieved irrespective of plant number. Tissue chemical analysis revealed that seeds, leaves, and twigs, as deciduous, dynamic and harvestable tissues of the system, contained the highest concentration of nitrogen. Iron and phosphorus were highly variable among tissues.

Acacia trees growing in moist sites retained fresh green leaves longer than those on a dry site. Fresh green leaves contained higher concentrations of nitrogen than old leaves just about to be shed. Nitrogen as a mobile element gets translocated from senescent leaves prior to leaf absission. It was observed that leaf shed was out of phase with microbial activity and soil moisture; soil carbon accumulation was impacted by grass fires and herbivory by livestock and microfauna.

The bush fallow rotation phase increased soil nitrogen, phosphorus and pH; the longer the fallow, the more the accumulations and eventual improvement in soil fertility and stability against wind erosion. Agricultural crops drastically reduced soil nitrogen. Sandy soil in Dubeibat (D) study site was more acidic than Elobeid (E) site. Acidity impacted nodulation. The elevated acidity in site D soil may be due to leaching of basic cations from the exchange complex due to higher rainfall in site D than E. Both sites had low clay contents and subsequently low cation exchange capacity.

The different soil types and climate, in addition to isolation by long distance and two big rivers, seemed to have lead to genetically different populations. The artificial selection for mother trees with high gum production potential in site E has resulted in location and identification of superior gum production mother trees. At the end of their rotation these trees are recommended to be treated as seed stand for dissemination of genetically superior seed. The high gum yield varieties produced less biomass than the low yield trees. Their differences in soil nutrients were insignificant. The low gum producers yielded more biomass than high gum yield trees. Tree density in natural stands of *A. senegal* was less than the recommended density and was far less than that in which trees were raised by machine seeding in which the density of sowing apparently was not controlled.

The overall conclusions of this research were that the drought tolerant *Acacia* trees enhanced the successional processes in the sahelian savanna by increasing soil nitrogen, pH and phosphorus , and served a variety of economic, social and environmental purposes in their environment. Improved soil conditions can be obtained if the bush fallow is maintained for a period of twenty or more years. It is recommended that tree density should not exceed 600 trees per hectare as high density leads to competition and a reduced rate of nodule formation and nitrogen input. The best seed source for tree cultivation is the local seed origin as it is more adapted to the local conditions over a long time period than imported seed. Increased soil carbon stabilized soil against wind erosion which removes the top soil where the plant nutrients are mostly concentrated. Genetic differences occurred within and among populations and affected the gum yield. The high yield gum trees have reached the rotation age. They should be treated as a seed stand. Further selection within each region should be encouraged. Trees that yielded a higher amount of gum were less productive in terms of biomass.

بسم الله الرحمن الرحيم

حركه النايتروجين في دورة الهشاب الزراعيه في السودان

خلاصه البحث:

اتسم طقس السافنا الشجريه القليله الامطار في السودان بالحراره العاليه والامطار الموسميه القليله مما ادى الى انواع من التربه تميزت عموما بانخفاض معدلات عناصر غذاء النبات سواء اكانت التربه الرمليه المنقوله بواسطه الهواء من الصحراء الكبرى او الطينيه المنقوله بواسطه الماء من المرتفعات الحبشيه خلال الحقب الجيولوجيه الحديثه • هذه البيئه سمحت بسياده النباتات الشوكيه من عائله الاكاسيا لما لها من خاصيه زياده نسبه النايتروجين والفحم و درجه التفاعل بالتربه و تحمل الجفاف•

ولقد نشأ في هذه البيئه عدد من انظمه زراعه المحاصيل في دورات مع اشجار الاكاسيا منها انظمه الحراز و الطلح و الهشاب لما لهذه الاشجار من فوائد متعدده مثل توفير العلف الغني بالبروتين و تخصيب التربه ، وقد امتاز نظام الهشاب على ما سواه نسبه لاتساع رقعه هذا النوع في التربه الرمليه و الطينيه وانتاج الصمغ العربي الذي يتصدر السودان قائمه الدول المصدره له ، ولم يحظ نظام الهشاب بلاهتمام العلمي الجدير باهميته البيئيه و الاقتصاديه والاجتماعيه في السودان نسبه لقله الموارد البشريه و الماديه •

اهداف البحث:

اولا : أ- التوصل لفهم تفاعل العناصر الجويه و الحيويه و الترابيه في دوره الهشاب و اثر ذلك التفاعل على الفوارق الوراثيه بين مجموعات اشجار الهشاب في اربعه من مناطق انتشار الهشاب الطبيعي في الاراضي الرمليه و الطينيه

ب- و اثر الفوارق الوراثيه علي ايراد النايتروجين بالتربه و معدلات انتاج الصمغ العربي ،

ثانيا : أ- ايجاد شتلات للهشاب تنتج عقد باكتيريا اكثر من غيرها

ب- وعزل الباكتيريا من تلك العقد و تربيته و اضافته الي تربه معقمه تنمو عليها شتلات الهشاب لمعرفه أثر ذلك في زياده عقد الباكتيريا

ثالثا : دراسه اثر تقليل عناصر نمو النبات عن طريق المنافسه بدرجات متفاوته بين النباتات و تقليل فتره الضوء اليوميه على نمو النبات و عدد العقد و معدلات تثبيت النايتروجين بالتربه •

ألنتائج :

أنخفضت معدلات الامطار السنويه في الاراضي الرملية بنسبه ٢٠ ـ ٢٧ ٪ مما أدى الى تفاقم ظواهر التصحر بالمناطق الرمليه اكثر منه في الاراضي الطينيه حيث كان انخفاض الامطار بين ٣ ـ ٥ ٪ فقط• ينمو الهشاب في معدلات مطريه اعلا في الاراضي الطينيه اكثر منه في الاراضي الرمليه وذلك لصعوبه حصول النبات على الماء من التربه الطينيه لشده تمسكها بها ،ورغما عن ذلك فأن انتشار اشجار الهشاب على الاراضي الرمليه اجود منه على الاراضي الطينيه •

التربه الرمليه في جنوبي حزام الصمغ شديده الحموضه حيث تراوحت بين ٤٪ ـ ٥٪ أمّا في الاراضي الطينيه فتراوحت معدلات تفاعل التربه بين ٨ ـ ٩ ،وفي المناطق الوسطى فقد كانت معتدله ،ويعزى انخفاض الحموضه في مناطق الحزام الجنوبيه الى ارتفاع معدلات الامطار السنويه وغسلها للعناصر القلويه من التربه ، وقد يعزى ايضا لارتفاع نسبه الحديد الناتج عن تقدم التفتت الكيميائي للصخور التي تحتوي على قدر يسير من معدن الجبسايت والهيماتايت•

وتفاوتت محتويات التربه لكل من الكربون والفسفور والبوتاسيوم بين المناطق الطينيه والرمليه حيث كان تركيز العناصر في التربه الطينيه اعلا منه في التربه الرمليه بلا فوارق هامه في النوع الواحد من التربه ، وكانت نسبه تركيز النايتروجين الكلي والنايتروجين (النترات) ذات علاقه ايجابيه عاليه مع كميه الامطار السنويه

الخلافات في التربه والطقس وانعزال حزام الصمغ بموانع جغرافيه مثل النيلين الابيض والازرق ادت هذه العوامل الي احداث فوارق وراثيه بين مجموعات الاشجار في مناطق الدبيبات والابيض على حده و منطقه سنجه ، اما منطقه القضارف فلم تكن تختلف عن مناطق الرمال من حيث الفوارق الوراثيه بين مجموعات الهشاب الشجريه •

كما اتضح وجود فوارق احصائيه هامه بين انتاج الصمغ من الاشجار التي استزرعت من امهات شجريه معروفه بانتاجيتها العاليه للصمغ من مناطق امروابه •

الفوارق في انتاج الصمغ لم تنعكس على انتاج النايتروجين ولا الفحم، وهناك علاقه عكسيه ضئيله الاهميه بين انتاج الصمغ والوزن الجـــاف•

واتضح ايضا الفوارق في عدد عقد الباكتيريا ونسبه تثبيت النايتروجين بالتربه بين

الشتلات التي نمت في تربه رطبه واخرى تحتوي على قدر من الطين كما اتضحت امكانيه عزل الميكروبات من العقد ذات العدد الكبير و النسبه العاليه من النايتروجين و استزراعها ووضعها في تربه تنمو عليها شتلات الهشاب مما ادى الى انتاج المزيد من عقد الباكتيريا ، وتلاحظ ان الشتول من منطقه سنجه قابله للتلقيح و انتاج عقد بأعداد اكبر من شتول من مناطق اخرى، واتضح ان الشتلات اذا تعرضت لفتره ضوئيه منخفضه فأن ذلك يؤدي الى تساقط الاوراق ووقف امداد الغذاء للعقد مما يؤدي الى موت الباكتيريا •

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DEDICATION

To my family for enduring my long absence

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CHAPTER ONE

AN OVERVIEW OF THE BIOTIC AND ABIOTIC ENVIRONMENTS OF THE ACACIA SENEGAL AGROFORESTRY SYSTEM IN THE SUDAN

INTRODUCTION

The *Acacia senegal* agroforestry system (acronym ASAS, Arabic word meaning origin, foundation or basis) is a major type of land use in the low rainfall woodland savanna ecosystems in Africa. The system results in a stabilized and a more fertile soil, more food and cash income and generally more stable social and environmental systems than the regular slash-and-burn traditional practices. The products of the system are many and varied. They are described in more detail in the section dealing with land use practices. The nitrogen dynamics of the *Acacia senegal* agroforestry system have not been studied in a system's perspective. The general theme of this work is to identify the interactive physical and biological processes that affect the nitrogen dynamics of the *Acacia senegal* agroforestry system in the Sudan.

This paper is divided into three chapters. In Chapter One an outline is presented on the general agricultural environment of the Sudan, touching briefly on the land use practices currently adopted in the low woodland savanna zones where *A. senegal* is distributed. The climate, soil and vegetation are briefly described. In particular agroforestry and its potential in the arid land environment of the Sudan are stressed. The *Acacia senegal* agroforestry system, its uses and the challanges facing it are described. In Chapters Two and Three, experimental manipulations and field studies are presented. This work was done in an effort to obtain an understanding of the factors that impact or enhance the system in general and the nitrogen dynamics in particular.

SUDAN: LOCATION, ENVIRONMENT AND SOCIOECONOMICS

Location

Sudan has the largest area in the African continent, approximately 2.5 million square kilometers and it is sparsely populated (22.4 million people). It extends from 3 53 to 21 55 N and 21 54 to 38 30 E. Essentially it is a country of vast plains interrupted by rolling topography and a few widely separated groups of hills and mountains (Andrews 1948)(Fig. 1). It is divided from north to south by the River Nile and its affluents. The population distribution, livestock, vegetation formations and area are given in Tables 1-3.

Human interactions: The land tenure system

Sudan is a country of weak economic infrastructures, increasing birth rate, very low productivity and uncontrollably soaring inflation. Due to repeated droughts, increasing animal population over the range carrying capacity, lack of effective administrative structure, and long civil war, the environment of the country has suffered an increasing rate of tree destruction, desertification and mass human migration to towns, particularly Khartoum, the capital.

The traditional tribal system of land tenure has been communal in nature. The land occupied by gum trees *A. senegal* used to belong to the tribe under the custody of the tribal chief, locally known as *Nazer* , who delegated some of his government-given powers to district heads or (*Omdas*). The district heads in their turn passed some powers to village chiefs or *Shieks*. Land allotment was vested on village chiefs who saw to it that *Hashab* or *A. senegal* were well protected from fires, illicit felling, excessive tapping for gum, or excessive grazing. Under such a system the *Acacia* trees and the overall environment was well protected against fire and excessive tree felling. Inter-village firelines were opened communally and each farmer was responsible for protecting their trees and observing the rotation system. In low rainfall years villagers were instructed not to tap the trees for gum , or tap very lightly, as tapping trees under

Fig. 1. Map of the Sudan showing the major vegetation divisions and physical features. The study sites Elobeid (E), Aldubeibat (D), Algedaref (G) and Singa (S) are indicated (+)

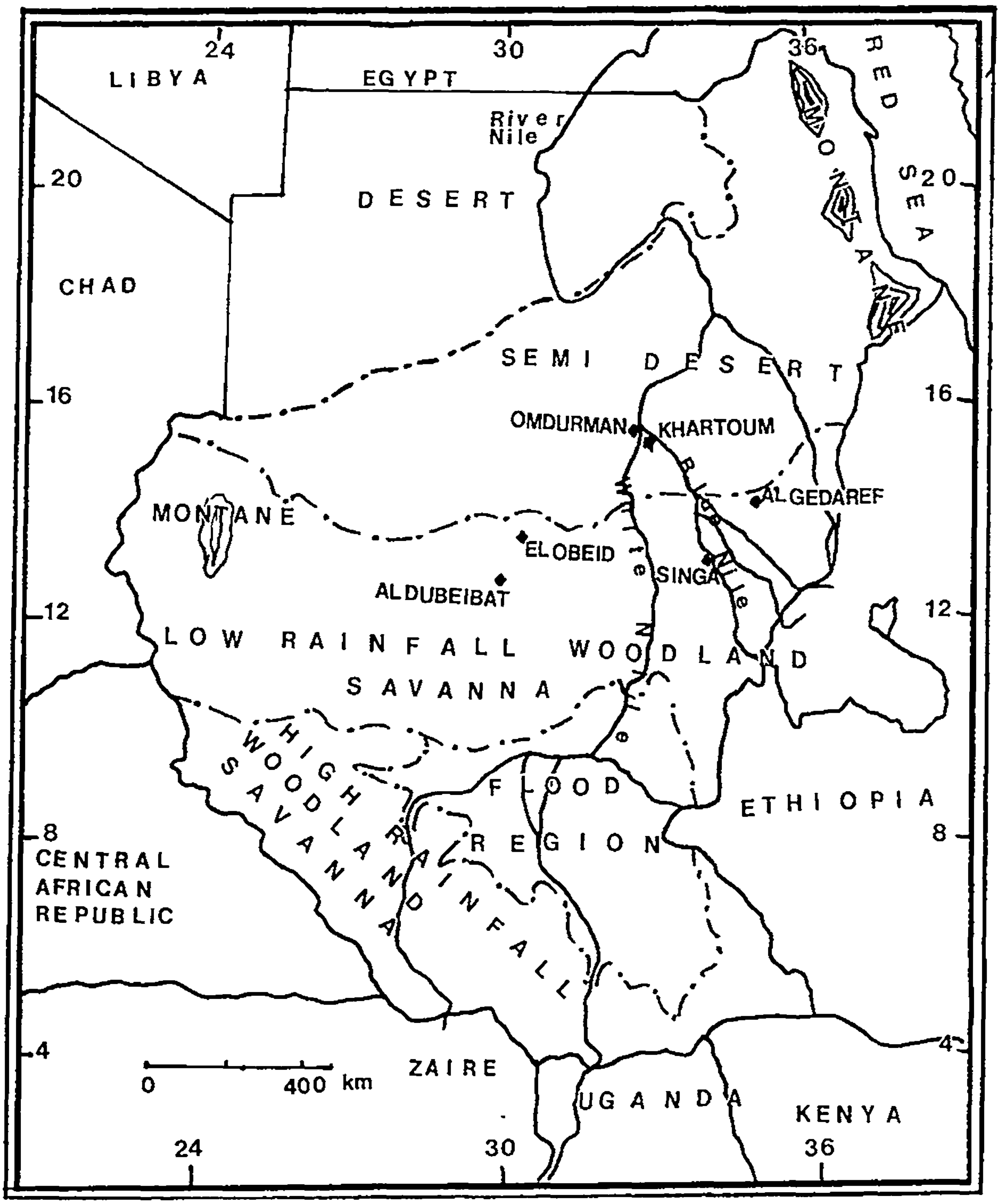


Fig. 1. SUDAN: VEGETATION DIVISIONS AND STUDY SITE LOCATIONS

drought stress predisposed them to insect infestation and/or fungal attack, or outright death. Village chiefs were also responsible for receiving and distributing *Acacia* seeds and ideas from local government extension agents to serious farmers. By so doing they were an effective environmental planning mechanism.

Such a hierarchical tribal system was abolished in 1969, when Sudan came under military rule, and was replaced by a bureaucratic system which was not well accepted by the people. In 1970 the Land Ownership Act was passed which stipulated that all unregistered lands (not within cultivable distance from the river bank) were to be considered government-owned. Although the Forest Ordinance of 1932 was ammended and strengthened in 1974 to provide protection for trees inside and outside forest reserves, the shortage of manpower and means of transport prohibited effective implementation of the forest ordinance. This, in addition to lack of afforestation programs for provision of fuelwood, has resulted in environmental degradation and colossal tree loss and soil erosion.

Shifting cultivators living in low rainfall savanna dominated by *Acacia senegal* have realized that the soil becomes unproductive after 5 or so years of continuous cultivation. The shifting cultivators practiced transhumance before they finally settled. During the rainy season transhumants reside temporarily and practice limited crop cultivation, because they do not have to move since they have water and fodder available. They set vegetation on fire for quick release of nutrients. They avoid the more fertile clay soil of higher rainfall because of the difficulty to cultivate heavy textured soil with simple hand tools.

The environment

The recent sahelian droughts have caused a great deal of mortality among *Acacia* trees as well as severe food shortages. Many local and international donor organizations have embarked upon planning activities to rehabilitate the degraded environment (Noel et al. 1990). Most of these project facilities are centered around the *Acacia* system. Such developments make the need for more research and information about the system imperative. MacLeod (1976) suggested that rectification of these conditions be sought through application of revegetation techniques with the object of realizing maximum biological productivity.

Repeated famines and generally low food production potential is blamed mainly on low rainfall and low levels of soil nitrogen. The long experience in cultivating sandy soils under low rainfall has evolved a system of shifting cultivation that combines annual crop cultivation, tree raising and herding. But excessive human activity caused modification of the land surfaces by deforestation, desertification and overgrazing due to increased human and livestock populations and too ambitious expectations from the limited resource environment. Such activities resulted in increased dust in the air and surface albido which suppressed cloud formation causing droughts and famines (Glantz 1976).

The current drought in the Sahelian zone of Africa has brought about widespread loss of human lives, mass human migration with social disruption and large scale degradation of the fragile sahelian ecosystems. Millions of livestock have succumbed and vast tracts of savanna have been buried under desert sands. Nomads have abandoned seasonal movement and concentrated in much smaller areas with subsequent overstocking on rangelands and excessive deforestation which further aggravated the desertification processes. Livestock are increasing in numbers as a result of intensive veterenary care without improving the feed supply situation; therefore, they are exceeding the carrying capacity of the natural range (Bunderson et al. 1990). Water receiving sites and runnels have richer vegetation and are more diverse in composition and structure. These are also sites of livestock concentration as they avoid the high heat of the day and seek shelter in the shade of big trees. Livestock act as a seed dispersal agent and soil nutrient improvers. Such microhabitats are fairly regular in places but can be few and far between. They occur in both types of soil and carry various sized trees, shrubs and grass layers.

The latter is lost as the dry season progresses. Away from these special sites of microhabitats only two layers of trees and grass occur. The animal types and numbers are shown in Table 2.

THE CLIMATE, SOIL AND VEGETATION

Climate

Lying between the Tropic of Cancer and the Equator, Sudan is subjected to the movement of the intertropical front of air masses that follow the aparent biannual movement of the sun. The climate is characterised by two distinct seasons: a short rainy season and a long dry one. The former starts in April at the southern reaches of the country and advances northwards with time until it reaches its northern most limit (Latit.16 N.) in August when it starts to retreat southwards again. North of latitude 16 nitrogen hardly any rain falls; consequently no soil or vegetation develop, giving rise to the Sahara Desert. The climate is tropical continental with long summers of 38-45 C and cool winters of 5-16 C. The temperature shows considerable diurnal variation. The length of seasons varies with latitude. The rainfall varies from almost zero near the northern boundary to about 1200 mm/year in the southern reaches where it falls in 7-8 months. The effective rainfall in central Sudan is concentrated within a period of 3 months of July-September. During most of the year the humidity drops to about 20 %; the plain is then covered with drought-tolerant shrubs devoid of leaves. Pre-rain dust storms transport dry soil long distances and are thought to have an appreciable effect on the nutrient dynamics and climate. The effects of such a drastic climatic regime on biotic and edaphic development is significant. At the semi-desert northern area the rains are experienced in July and August with an annual mean of 100 mm.

The rainy season is followed by cool dry months of November-February with temperatures varying 5 to 25 C. This is followed by hot dry months of March-June during which the temperature soars to a maximum of 45 C. The specific length and intensity of each season follows a latitudinal pattern. A summary of climatic data is given in Table 5. These data include mean annual rainfall, relative humidity, evaporation, wind speed and direction. They also include sunshine duration as % and in hours of bright sunshine, in addition to the maximum, minimum and mean temperatures. These data were analyzed for statistical significance using ANOVA and multiple comparison tests to determine whether the study sites were exposed to significantly different climatic conditions. The climatological variations between study sites are described in detail in Chapter Two.

Many hypotheses have been advanced about the possible causes of the repeated sahelian droughts. African farmers were blamed for causing the catastrophe by overgrazing, excessive tree felling or using inappropriate machinery with light soil, causing dust to hang in the atmosphere. Others claimed that the phenomenon was an inherent part of the sahelian weather system. Kerr (1985) held that the sub-Saharan drought of the 15 years previous to 1985 was the worst in 150 years. The exceptional persistence, severity and broad expanse suggest that man's role in causing the catastrophe was limited. Lamb (1983) compiled weather data for sub-saharan west Africa and proposed a 5-year drought cycle which peaked in 1972, 1977 and 1983. The last one was even more severe than the others. He also compiled longer records and showed that at no time in this century had the sahel received a lower rainfall than the reported 15 year period. Because of the continent-wide scale of drought it was noted that claims that Africans themselves brought on the drought by stripping the vegetation and altering the reflective properties of the soil was unfounded.

Prior to the present century climatological records were unreliable in Africa. The measure of drought was assessed by the level of lakes and rivers. Lamb (1983) found that the past century was generally wetter than the present, but between 1820 and 1840 the sub-Sahara suffered a drought that was certainly as long and probably more intense than the present one.

Glantz (1987) reported that the drought is part of the region's climate and will occur repeatedly. He also reported that paleoenvironmental research findings show that both extended dry periods and extended wet periods occurred in various parts of sub-Saharan Africa for thousands of years. He suggested that droughts are aperiodic phenomenon, and that variability of rainfall in both time and space within the rainy season can be quite high. Breman and de Wit (1983) described the sahel as a semiarid transitional zone between the desert and the savanna of west and central Africa. The dominant climatic factor of this region is a single short rainy season that extends between two and four months and the rest of the year is dry. Some atmospheric scientists have speculated that the prolonged drought may be the first manifestation of a global warming resulting from an increased loading of the atmosphere by biproducts of fossil fuel burning.

Desertification can increase the amount of dust in the lower atmosphere and lead to relative cooling of the atmosphere, reducing the atmospheric activity that leads to rainfall. The second human activity of concern is the modification of the land surfaces by deforestation, desertification and overgrazing. Such an activity can result in increased surface albido which leads to suppressed cloud formation.

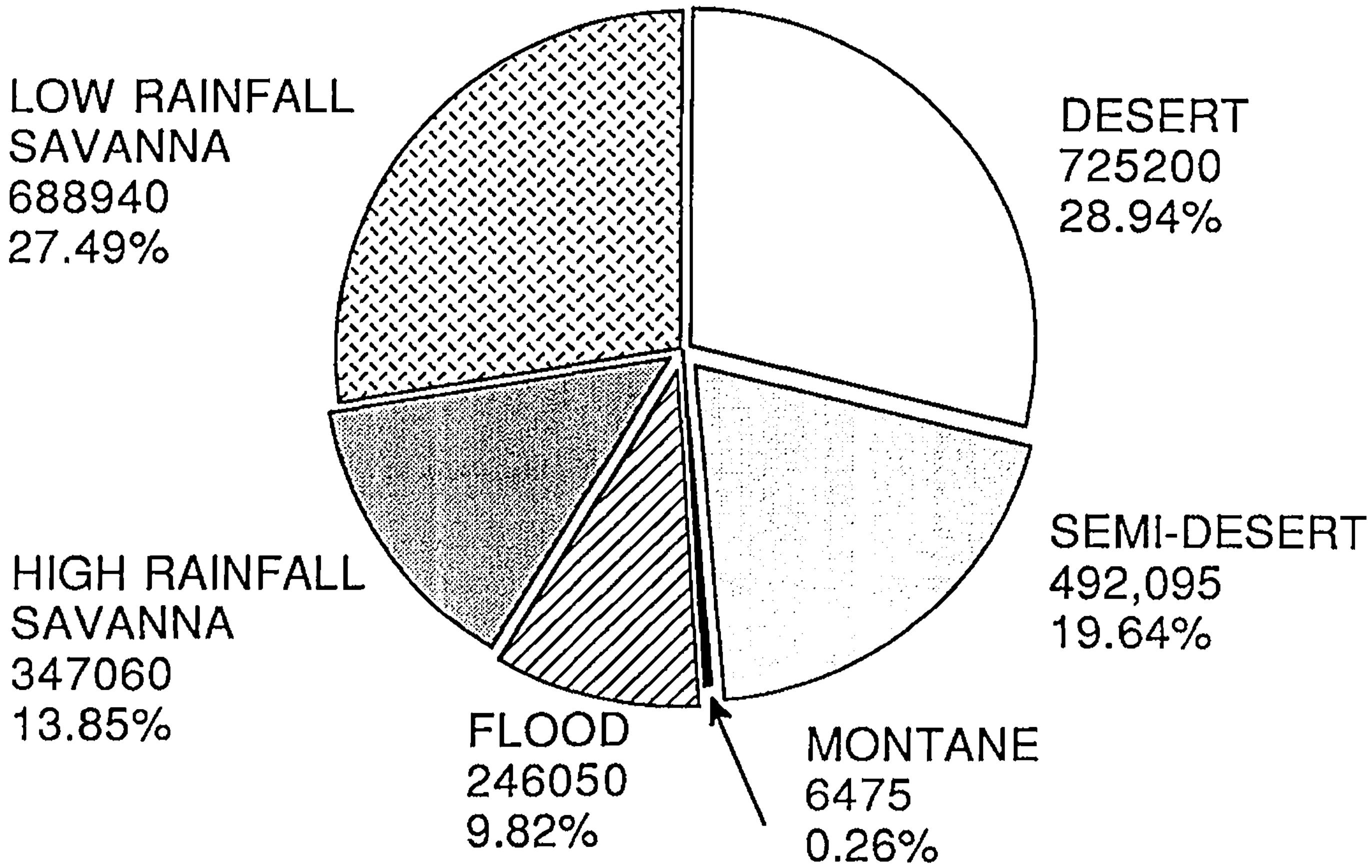
Soil and vegetation

As classified by Harrison and Jackson (1958) the vegetation of the Sudan can be separated into five main divisions based on isohyets and soil type (Table 3 and Fig. 2). The vegetation type that is of particular concern to shifting agriculture in western and eastern Sudan is the Low Rainfall Woodland Savanna - the subdivision termed *Acacia senegal* Savanna on Sand (western Sudan) or Clay in eastern Sudan. This subdivision occurs on isohyets 280-450 mm and is characterised by pure stands of *A. senegal*. Towards its drier range of natural distribution it merges into semi- desert while on the wetter fringes it alternates with *Combretum* domi-

Fig. 2. Area of the major vegetation divisions of the Sudan based on Harrison and Jackson (1958); areas are in square kilometers and percentages

FIG. 2.

VEGETATION DISTRIBUTION IN THE SUDAN
IN SQUARE KILOMETERS



nated plant communities. North of isohyet 100 mm the prevalent soils are various types of loose skeletal desert soils with sand, gravel or parent rock. In the semi-desert area (isohyet 100-300 mm), the soils are immature and in pavements of hard gravel surface (Smith 1949). The isohyets 300-500 mm mark the type of stabilized sand dunes, the eastern limit of which is the White Nile. South of isohyet 500 mm vast expanses of clay plains exist east and west of the White Nile.

The soil is divided into four main types. The following outlines should serve as a general description of the main soil types of the range:

1. Sandy soils (Order Entisol) cover the northern parts of central and western Sudan in the desert and semi desert biomes. The scanty to nonexistent rainfall in these areas results in skeletal soil and lack of vegetation. The sands of Kordofan and Darfur are of geologically recent invasion from the north, the Sahara. They are large-grained red sands which carry a vegetation type that is comparatively heavy for the available rainfall. Gradual increase in vegetation is observable as one proceeds southwards into the woodland sand savanna where scattered *Acacia* shrubs occur over a grass cover during the rainy season (Table 3).

Some authors (Kaiser 1983, Bate 1983) have suggested that most savanna plant species begin to grow at the end of the dry season in response to increased atmospheric vapor pressure occuring before the onset of the actual rain. The change in wind direction, and the increase in relative humidity is clearly sensed by humans, livestock and plants. While livestock and wildlife start their rutting season triggered by elevated atmospheric humidity and their expectation of increased food supply as a result of the oncoming rain, plant leaves begin to show on trees ahead of actual rain. Menaut and Cesar (1982) reported that a rapid regrowth and the first wave of flowering of herbaceous species occur even before the onset of the rains. Grasses, however, do not start to germinate until they have received actual rain drops because of the limited food reserves in their seeds.

Tree seeds follow a trend similar to that of grasses, but the new plants do not show on the soil surface except after a grass cover has been established, as a protection against grazing. Tree seedlings take more time to establish a deeper tap root system than the superficial grass root system. The tap root system at the young seedling stage is an important feature that increases the chance of survival when the upper soil layers progressively dry out. In the dry season (October-May) the grass dries, is grazed or burned and the *Acacia* shrubs shed their leaves as a water conservation measure. Leaf shed marks the begining of low soil moisture, no photosynthate manufacture, and consequently, no diazotrophy which is an energy-demanding group of processes. *Acacia senegal* is present in this soil type mixed with other species. Pure *A. senegal* covers an area of 64,750 km in Kordofan and Darfur regions (Andrews 1948) where the system of *A. senegal* agroforestry has been practiced for decades under low rainfall of 150-300 mm/yr on sand.

Despite its limiting nutrient status, light sandy soil is preferred to more fertile heavy clay soils for cultivation by hand implements for the relative ease of cultivation, freedom from water-borne diseases, less competetion from grass growth and availability of drinking water from shallow wells. The *A. senegal* agroforestry system evolved traditionally in this environment. The River Nile and its main tributaries stopped the sand from moving east of the river, but they did not stop the species migration. They acted as desertification barriers but not biotic ones.

2. Cracking clay soil (Order Vertisol) covers vast expanses of eastern, central and western Sudan. They are alkaline in nature with calcium carbonate concretions, and they become sticky when wet. They occur under 400-700 mm/yr rainfall and support more lush vegetation than sandy soil. *Acacia seyal* , *Balanites aegyptiaca* and *A. mellifera* are dominant species. *Acacia senegal* is also found on clay soil and its agroforestry importance is also recognized here. Clay soil holds much more moisture at a given potential than sand, because it has a much higher sur-

face area due to the small particle size than sand. As much as half or even more of the water held by clay is not available to plants. because it is held so tightly that plants cannot remove it. This explains the *A. senegal* distribution on lower isohyets on sand and higher ones on clay and also explains the low soil nitrogen and carbon.

The poor clay soil water relationship results in gully erosion when the rainfall exceeds the soil absorptive capacity. Rain falls in torrential short-period storms, preceeded by high winds. These winds cause a great deal of soil erosion, removing fine soil from the surface and moving it long distances. On the sandy soil sites wind erosion is much more active, particularly on sites devoid of vegetation. Nitrogen is also washed out of the system with eroded soil, particularly the top soil in which the nitrogen concentration and soil carbon are highest. The trees remain leafless for most of the 8-9 month dry period during which they appear lifeless. They are adapted to xeric conditions. On local depressions where higher soil moisture is available, trees remain green longer and attain larger dimensions than those on flat sites and humps. *Acacia senegal* seems better adapted to the dry sands of the western Sudan than they are to the higher rainfall clay soil; in the former region they cover a wider area in pure stands (Harrison and Jackson 1958, Elamin 1976).

The clay plains are the end products of former hill masses, locally weathered, or carried from distant areas of erosion (Smith 1949). The parent material of these clays is an alkaline basaltic alluvium brought down in the past pluvial periods from the Abyssinian highlands and deposited in swamps or seasonal lakes. The minerals found in the clay resemble those of Abyssinian basalt. The landscape was thought to have developed on Basement complex rocks, Nubian sandstones and dried materials (Bunting and Lea 1962). Ephemeral xeric types of plants are confined to depressions and water channels which originate further south or may have resulted from infrequent rains.

Expanded mechanized crop cultivation on recently cleared clay land is practiced with no fertilizer input. When soil is exhausted by overcultivation, the area reverts to trees. *Acacia seyal* is a fire climax species. It is quick to invade and attain dominance. Its agricultural importance is also recognized in providing fodder, fixing nitrogen as a legume and producing fuel wood and gum inferior in quality to that of *Hashab*. *Acacia senegal* is favored on such lands and is sown on these fields, where fire is prevented to reduce competition from *A. seyal*. *Acacia senegal* artificial cultivation to improve soil quality is adopted as a policy because nitrogen fertilizers are not available locally or are too expensive. Some species are fire climax as they respond to fire with seed germination, following light charing to their seed testa. *Acacia seyal* is one of these species that covers vast areas in pure stands. Its bark is corky and imparts fire resistance. It is dominant on clay soils, pure or mixed with *Balanites aegyptiaca* and *A. senegal*. Its importance in the nitrogen dynamics of the system is well recognized. More is mentioned about this species in the inoculation study section.

3. The high rainfall areas in southern Sudan have more permeable acid non-cracking ironstone soils. The vegetation is a broad-leaf dense forest type. *Acacia senegal* is found only scantily distributed, or nonexistent on high isohyets.

4. Along banks of rivers and seasonal water courses, alluvial soils develop and support large trees, e.g., *A. nilotica* and *A. albida* among other species. *Acacia senegal* is lacking where soil moisture becomes high. This point should be taken into consideration when planning introduction of the *A. senegal* agroforestry system in exotic, high rainfall areas. The system may only partially be successful, though possible failure may take place as in a moist west African locality where the species was introduced, but failed to produce gum.

Soil moisture seems the most limiting factor for plant and soil development. Noy-Meir (1973) held that water, above all else, influences all biological activity in arid land. Where quartzite parent material is coupled with low soil moisture and low vegetation cover, a soil is produced that is low in nutrient level, particularly nitrogen, phosphorus and potassium . and is weak in soil profile development. The low soil nitrogen level inherent in semiarid tropical soils is ameliorated by growing legume bushes. *A. senegal* in rotation with annual crops. These crops are highly demanding on nitrogen and other nutrients. The major source of nitrogen coming into the system results from the symbiotic association in the root nodules of *Acacia senegal* with *Rhizobium* species. Artificial plantings of *A. senegal* have been embarked upon by the government and various donor agencies as a means to combat desertification following recent sahelian droughts, and to rehabilitate agricultural areas abandoned due to low soil fertility. The affected localities include both sand and clay soils in western and eastern Sudan.

A minor quantity of nitrogen input may come from the throughfall and insect activities in the canopy (Boring and Swank 1984). An additional source may be from nomadic livestock passing through the *A. senegal* system. Termite mounds are widespread in these forests and are thought to be an important source of nitrogen in these systems. Heterotrophic nitrogen fixers also contribute to the pool. Abiotic nitrogen input sources include precipitation and lightning, dust and dry ammonia deposition. The estimate of amounts vary tremendously.

Leaf litter decomposition

Leaf litter decomposition is limited to the wet period when bacterial and fungal activities are induced by soil moisture, and general favorable climatic conditions. The high temperature of day and relatively low night temperatures cause mechanical breakdown of litter into small size easily incorporated in the soil to be acted upon by soil fauna and flora when the climatic conditions permit microbial activities. The high heat and humidity during the rainy season are particularly important to microbial decay. Leaf litter falls off trees in the dry season on clay soil when cracks start to form at the same time or shortly before. The leaf litter gets incorporated into the cracks and is later mixed with the soil when the rains fall once again. The process of decomposition will not start unless the soil moisture rises to a level compatable with microbial activity. The process of mixing of leaf litter in sandy soil is affected by mutual movement of sand particles and leaf litter by wind action. The decay process during the dry season is limited to mechanical churning of litter with soil. Limited grazing takes place by insect saprophages. Limited humification also occurs due to the low and decreasing soil moisture.

Fire and livestock seem to affect most of the leaf litter conversion in savanna soil for most of the year. The products of such conversion are not incorporated in the soil until the soil moisture situation improves. The major biotic process of tree litter conversion is consumption by grazing livestock, particularly goats and camels (Table 2). They devour tree foliage and dry, shed leaves later in the season. Leaf fall takes place at the beginning of the dry season, when the ground cover also becomes dry. *Acacia* leaves and pods are avidly sought after for their high protein contents and lack of objectionable compounds like tannins.

ACACIA SENEGAL

Acacia senegal (L.) Willd., syn. *Mimosa senegal* L. or *Acacia verek* Guill. is a member of the Leguminoseae, sub-family Mimosoideae. *Acacia senegal* is a drought tolerant legume distributed over a wide range of soil types and rainfall. The species does not favor high rainfall areas. It is a small sized bush to a medium tree averaging 6 m in height, attaining 12 m in places, with flat to round crown and a grey bark which is cream colored when young. Leaves are pinnately compound with three prickles at each node. Flowers are creamy white in cylindrical spikes (Sahni 1968), usually longer than leaves. Pods are light brown-colored, flat, papery venose and accuminate. The characteristic feature of the species is a group of three prickles at each node, two of which point forward and one recurved (Elamin 1976).

Leaves appear on trees before the onset of the rainy season, the process probably triggered by increases in atmospheric humidity that are felt following rain in more southerly areas: this humid air is known locally as *Da'ash* , which is felt in western Sudan sands in late June before the begining of rains. Flowers appear in August or September, pods in October and seed in November or December. Leaf shed starts in November-December and continues through March. Seed number per kg varies from 6000 to 11,000 depending on locality, climate, tree age and general state of health of the tree. Seed germination starts within five days after sowing and continues over 16 days during which an average germination of 65 percentage can occur, if seeds were pretreated by soaking them in water prior to sowing. This depends upon freshness and freedom from insect infestation.

Trees are tapped for gum in October to early November. Tapping refers to the process of mechanically injuring the tree by means of a knife to separate bark from wood. Gum starts to exude from the wound 4-6 weeks after tapping. Gum nodules can be collected every two weeks from late November through summer until leaf set in May/June. Trees start to exude gum at 4-5 years of age with maximum production at age 15 years. Production per tree per year varies a great deal depending on inherent, ecological, silvicultural and socio-economic factors.

Gum arabic is a viscous exudate that oozes out of trees and solidifies into globularly shaped nodules when it comes in contact with air and dries. Chemically it is a complex polysaccharide which on hydrolysis yields the sugars galactose, arabinose, rhamnose and glucuronic acid (Anderson, 1977). The best grades are used mainly in confectionary, as an adhesive, a thickener, a stabilizer or emulsifier in a wide variety of food stuff. The main market of gum arabic is the USA, West Germany, U.K., France, Italy and Japan.

The natural distribution of A. *senegal* in the Sudan and elsewhere has been described by various authors (c.f. Andrews, 1948; Harrison and Jackson, 1958, Elamin 1976, 1973). Its ecology and silviculture have been covered by Obeid and Seif El Din (1969, 1970). Socioeconomic and silvicultural importance of the species as a major producer of gum arabic in Sudan and Nigeria were studied by Obeid and Seif El Din (1969) and Philip (1975). Anderson (1985, 1978) has published extensively about its chemistry and industrial importance.

The species is widely distributed in Africa from Senegal and Nigeria in the west to the Red Sea coast, and southwards over Uganda. Kenya and Ethiopia to South Africa. It is also distributed on the Arabian Peninsula and the Indian subcontinent (Obeid and Seif El Din, 1969). The gum tree *A. senegal* grows on sand dunes of Kordofan with a 75-300 mm annual rainfall and thrives equally well on dark cracking clays in southern Kassala province under a rainfall of 500 mm (Smith 1949), and in the Blue Nile province. Elamin (1976), however, maintained that the species is more successful on western sands of Kordofan and Darfur than on eastern clay plains. He suggested that annual grass fires help it spread in central Sudan. The species forms pure stands on sand where the rainfall range is 280-450 mm (Jackson and Shawki, 1950; Obeid and Seif El Din, 1969). On the lower rainfall edge of its distribution it merges into *Acacia mellifera* thornland and on the higher rainfall edge it merges into *A. seyal* , *Balanites aegyptiaca* savanna on clay. The National Research Council (1979) reported that different races or subspecies of *A. senegal* occur in different regions, some with flat crowns and others with round ones; some produce gum while others do not. They further reported that little is known about these races and the genetic effect on gum yield and quality.

Gerakis and Tsangerakis (1970), studying the influence of *A. senegal* on the fertility of a sand sheet soil in central Sudan, concluded that the species increases total nitrogen and organic carbon while pH, texture , available phosphorus and available potassium are not affected. Obeid and Sief El Din (1969, 1970) described the importance of *A. senegal* in the bush fallow cultivation system and investigated the species distribution and regeneration as affected by land use, goat-grazing and amount and distribution of rainfall. Arnold (1983) summarized the *A. senegal* system of agroforestry and described it as an important economic and ecological land use system.

Fire is an important ecological factor in the savanna country. Some species are termed fire climax because they need fire for seeds to germinate, following light charing to their seed testa. Farmers have realized that fires release nutrients from vegetation at a high rate. So the slash-and-burn type of shifting cultivation evolved in the savanna as a quick and dirty method of soil nutrient release and in lieu of chemical fertilizers and in the absence of efficient decay processes. *Acacia* foliage from coppice is cut and placed on various parts of the farm to be burned prior to seed sowing as a means to supplement soil nutrients. Late in the dry season when range grasses have dried out and become fouled with excessive grazing, herders set the grass ablaze. Despite lack of rain a new green grass emerges and provides a fresh but scanty post-burn browse.

Brady (1990) maintained that shifting cultivation is primarily a system of nutrient conservation, accumulation and recycling, in which erosion control is achieved through natural vegetation surrounding cultivated plots. He further suggested that burning destroys weed seeds, insects and disease organisms.

LAND USE PRACTICES

Various land use methods evolved in Sudan, depending on the local environmental conditions and the socioeconomic standing of the users. *Acacia albida* are big trees growing gregariously on river banks. Unlike all other savanna vegetation, they shed their leaves during the rainy season and provide shade, shelter and fodder in the dry season. An agroforestry system unique to *A. albida* evolved in this species range and is practiced mostly in west Darfur region of the Sudan. In the *A. seyal* - *Balanites aegyptiaca* association the trees are removed and their clay soils are cultivated by machines for sorghum production without using fertilizers. The land loses fertility fast and is reverted to *hashab* cultivation as in localities of Algedaref, Singa, and Habila in the Nuba Mountains.

Shifting agriculture

The fragile nature of the ecosystem in many parts of the sahelian Sudan dictates shifting cultivation practices to be adopted as the main theme of making a living for many people. The physical and chemical characteristics of sandy semi-desert soil coupled with the prevailing climatic regime of a long dry season and a shorter unpredictable rainy season interact to formulate a type of vegetation which is necessarily limited in quality and quantity. Such an environment cannot support permanent settlement without inflicting degradation and the loss of already meager ground cover and soil. A marginal resource like this can only support a fragile ecosystem and a weak economy.

Shifting cultivation is a practice of constraints -- ecological, economic or sociocultural. The shifting cultivators are thought to be nomads in nature who for various pressures tend to settle. During the rainy season nomads reside temporarily and practice limited crop cultivation, because they do not have to move since they have water and fodder available. They burn the vegetation for quick release of nutrients. They avoid the more fertile clay soil of higher rainfall because of the difficulty of cultivating heavy textured soil with simple hand tools. The appearance of witchweed parasitic plants (locally known as *Buda*) on sorghum is a warning signal to farmers that productivity has declined and they have to shift to a new parcel of land. Brady (1990) suggested that the short cropping period discourages the build up of harmful weeds and diseases.

The effects of the slash and burn practices on nutrient dynamics

Agricultural residue and tree coppice and branches are habitually burned by sahelian farmers to achieve a quick release of nutrients prior to cultivation. Burning substantially reduces organic matter which would otherwise have been incorporated in the soil to enhance microbial activity and serve as soil particle cementing matter to protect the soil against erosion. As a result of burning the soil becomes unprotected and exposed to rain and sunlight. Nitrification and soil humus content decrease following burning. pH. exchangable Ca and phosphate status were improved by burn treatment. It has been maintained (Guillermo 1984) that recurrent fires in the savanna contribute to the impoverishment of soil by causing the loss of volatile elements during the fire and washing away of ashes by wind or surface runoff. An increase in nutrient concentration was noticed on the surface layer only. Most nutrients are taken up by grass roots following a burn due to the superficial fibrous grass root system and their fast rate of growth. Mineral nutrients are transferred from the tree layer to the grass layer, with a long term possibility of retrogression of savanna ecosystem to grasslands.

The grass cover is the fastest to appear and also disappear by drought and by fire. The time of leaf shed coincides with low microbe activity in the soil and low soil moisture. The leaf litter adds to the organic pool of dried grass and is subject to herbivory or fuel savanna fires.

Burning is the major factor determining tree spacing and distribution, giving the savanna the character of grassland punctuated by woody plants except at water channels and depressions. On such moist sites woody crowns dominate to the exclusion of the grass layer or replace it with a shrubby understory. Grass removal from the site can cause further degradation of the created grasslands to deserts, which is happening in many parts of the sahel.

Skylab space mission 1973 noticed a great deal of dust leaving sahelian Africa to the outer atmosphere. Climatologists implicated atmospheric dust as preventing cloud formation, and causing droughts which recurred over the sahel in the last few decades. Smoke has also been implicated to have caused similar problems.

A long series of grass fires results in nitrogen exhaustion. Seasonal fires are started annually by lightning, or deliberately by nomads in search of grazing, and by cultivators practicing (*Harig*) or burn cultivation. Fire climax species, however benefit from burning: they produce ample regeneration e.g. *Acacia seyal* has inferior quality gum and timber, although its nitrogen fixation potential is recognized (Habish 1970). Burning influences the presence or absence of tree species and affects tree form. Meiklejohn (1955) suggested that the post burn increase in nitrogen content in the top 25 cm in savanna soil in Kenya was due to temporary disturbance to soil microflora. Burning effects an abrupt release of nutients stored in dead leaves and straw which would have otherwise gradually become available by the slow decay of plant litter.

Acacia senegal agroforestry system

Agroforestry is defined as a land use strategy whereby trees are utilized to improve farm potential. Many definitions have been proposed; Bunderson et al. (1990) defines agroforestry as implying that trees are combined in space and/or in time with either farm crops or domestic animals or both to achieve a stable production system. King (1979) defined agroforestry as "a sustained land management system which increases the yield of land, combines the production of crops (including tree crops) and forest plants and/or animals, simultaneously or sequentially, on the same unit of land and implies management practices that are compatable with the cultural practices of the local population". The National Research Council (1983) defined agroforestry as a term covering a variety of land use systems in which woody perrenials are directly associated with agricultural crops and/or livestock in order to realise higher productivity, more dependable economic returns and a broader range of social benefits on a sustainable basis.

It is generally agreed that farm forestry (or agroforestry) is the only recourse as forests disappear and farms are abandoned. Agroforestry is a new term for an old practice of growing woody plants with herbaceous crops and/or livestock on the same piece of land. Such a diversified land management system reduces risk due to failure of one crop. In addition it provides the farmer with periodic fertile land. fuel and forage for livestock. King (1979) maintained that the agroforestry system of land management is superior to the traditional forest plantation system in a socio- economic sense. in that it provides intermediate returns from food crops. fodder crops. or animals which are permitted to graze on and among trees. Arnold (1983) suggested that the system provides the farmer with access to fertile land and a low cost alternative to fertilizers and soil conditioners. Trees also provide shade, shelter and protection against wind and run-off.

Benefits of an agroforestry system that contribute eventually to social stability are many and may be summarized as:

1. increased variety and stability of food supply, increased water quality and wildlife habitat.

2. sustained low cost fuelwood, low conservation cost and soil erosion.

3. wood production for local homes and farm implements;

4. protection of site productive potential;

5. safeguard sustainability and improving socioeconomic conditions;

6. development of land use systems that make optimal use of both modern technology and traditional local experience.

The *Acacia senegal* agroforestry is a major type of land use in Sudan and elsewhere in the African sahel (Bunderson et al. 1990). The system's effects on the region are many and varied; they include soil nutrient improvement by nitrogen fixation processes, provision of protein -rich fodder and production of gum arabic of commerce. Gum sale improves the income of the farmers and the foreign exchange of the country. Fuelwood, local building timbers, sand dune stabilization and the possibility of bee honey production are other contributions of the *Acacia* system. Brady (1990) suggested that the decline in the per capita food production in Africa is caused mainly by the reduction in the tree fallow period.

Known locally as the Bush-Fallow Cultivation System, the *Acacia senegal* agroforestry system is an improved system which has evolved traditionally on sandy soils, in the low rainfall woodland savanna of the Sudan, where the natural vegetation is dominated by *A. senegal* (L.) Willd. The salient features of the system are that the trees are allowed to grow on part of a farm for 10-15 years during which time they contribute to soil fertility through the process of nitrogen and carbon fixation. Nitrogen fixation is possible because of a symbiotic relationship with rhizobial nitrogen fixing bacteria (Habish, 1970; Allen and Allen, 1981). Further, the trees provide protein-rich leaves, pods and seeds which are utilized by grazing animals. During the tree phase the soil total nitrogen and organic carbon are increased (Gerakis and Tsangerakis, 1970). Aweto (1981 and 1981a) reported that nutrient and organic matter increases were confined to the top 1-10 cm of soil. The product of nitrogen fixation is reported to be rapidly removed from the rhizosphere to various locations in the tree. The maximum gum yield takes place in year fifteen of tree rotation. It remains to be tested whether an optimum rotation exists and whether it coincides with that of gum yield rotation of 15 years. Habish (1970), working on the nodulation of *A. senegal* on sandy soil, concluded that the higher nitrogen content in the top soil is partly caused by symbiotic fixation. Gum acacia is one of the major products of the *A. senegal* agroforestry system. An average annual production of 35,000 tons is exported every year from Sudan, and it may reach 56,000 tons. Kordofan gum has achieved an international reputation for high quality, and all gums are graded in reference to it (Adamson and Bell 1974).

When the bush-fallow period is terminated, crops are cultivated and that results in a nutrient drain from the system. Sorghum and millet are planted in the first year or two following the bush-fallow since they are demanding on nutrients and the soil nutrient status is at its best.

In the third year a legume is usually planted to improve the nutrient level. followed by millet or sorghum which are the main staple crops.

At harvest time the farmers collect and remove the grain, the straw goes for hut making, and the grass is bailed for dry season animal feed. They deprive the soil of all cover and carbonaceous material. Animal manure is also removed from the soil and used as a binder in brick-making, or as a water and termite resistant layer on grass huts and mud houses, or as a source of energy to the emerging biogas industry. These practices deprive the soil of a cheap source of nitrogen and organic matter that is essential to microbes as a source of carbon and energy. Agriculture is a radical disturbance to climax ecosystems. Postgate (1982) reported that in a disturbed climax ecosystem non-nitrogen nutrients are recycled and the local store of available nitrogen soon becomes limited. The dynamics of the system have had little investigation to enable adequate scientific development and improvement to take place.

The *A. senegal* system has been suggested by the National Research Council, (USA), (1979) as the most effective method of land use in the Sahel of Africa. Non-tangible benefits of the *Acacia* system include grazing of animals, improvement of soil fertility and sand dune stabilization in addition to improved microclimate and protective hedges. The advantages of the system are numerous and were outlined previously. The present study should point out strengths and weaknesses of the system and may produce insights which could benefit millions of small farmers currently adopting the system for their livelihood and improve the sahelian ecosystem at large.

Table 1. Human population: (Population Census 1983)

Sector	Numbers (millions)	%
Rural sedentary	14.5	64.73
Rural nomadic	2.5	11.16
Town dwellers	5.4	24.11
Total	22.4	100.0

Table 2. Livestock: (Animal Census 1973)

Type	millions
Cattle	15.40
Sheep	16.24
Goats	11.30
Camels	2.36
Horses	0.09
Donkeys	0.80
Total	46.19

Table 3. Vegetation types: (Harrison and Jackson 1958)

Type	Rainfall (mm)	Area (sq. km)	%
Desert	00-75	725,193	28.94
Semidesert	75-300	492,095	19.64
Woodland Savanna			
Low rainfall	300-800	688,933	27.49
High rainfall	800-1000	347,056	13.85
Flood Regions	Variable	246,047	9.82
Montane	"	6475	0.26
Total		2,505,800	100.0

CHAPTER TWO

THE EFFECTS OF TREE-SITE INTERACTIONS ON SOIL AND PLANT NUTRIENT CONTENT

INTRODUCTION

Increasing agricultural production in the African savanna is a strategic prerequisite for social stability and is a basic requirement for national development in order to meet the food need of increasing populations in various sahelian countries. Farm yield in the rainfed sector of the sahelian agriculture on sandy and clay soils is low due to a variety of factors, among which is the inherent low soil nutrient status, particularly nitrogen. Low rainfall and year-round high temperatures permit little nitrogen to be fixed and stored in the soil, and allow meager plant cover and soil to develop.

Since chemical fertilizers are not available locally and peasants could not afford them if they were, soil improvement by biological techniques becomes the best option for sahelian agriculture. *A. senegal* agroforestry system, (ASAS), evolved locally to serve that purpose. The salient features of the system were described in Chapter One. During the tree phase the soil total nitrogen and organic carbon are increased, (Gerakis and Tsangerakis 1970; National Research Council 1979; Habish 1970; Habish and Khairi 1970; Brady 1990). Since tree leaves, seed and pod are rich in protein contents, they provide nourishment for livestock, leading to more meat production and consequently more food. The same tissue types are deciduous and a major portion decomposes and increases soil nutrients.

The major source of nitrogen coming into the system results from the symbiotic associations in the roots of legume plants. Minor components come from throughfall and insect activity through the canopy, nomadic livestock passing through the ASAS, and dust transporting nutrients for long distances. Various pathways of nitrogen output exist, mainly removal of vegetal matters through the deciduous tissues e.g. seeds, pods, leaves, and also through gum and wood. Soil erosion further depletes the nitrogen reserves of the system, particularly the top soil in which nitrogen concentration is the highest and which is more likely to be transported by wind or washed down water channels. The major nitrogen loss from the system occurs through agricultural crops.

This research aimed to quantify certain parameters relating to climate, soil and vegetation, and compare them within each study site over time and space by testing them for statistical significance among the study sites. A description of four selected representative study sites follows. Nix (1983) suggested that the major climatic elements of the tropical savanna ecosystem are solar radiation, temperature, evaporation and precipitation. Several key parameters associated with the climate, plant and soil were analyzed. With respect to climate the objective was to characterize climatological parameters and test them for significant variations among the selected study sites to find out whether the climatic aspects of various localities within the species range were different. The nutrient contents, particularly nitrogen, potassium and phosphorus , in the soil and plant tissues were quantitated and tested for statistically significant variation. The effects of cultivation and *A. senegal* trees, young and old, on soil nitrogen, carbon and pH were examined. The fallow period has been shortened from 15 years to 7-10 years because of increasing population, droughts and too high ambitions from such a limited resource environment. The impact of such a reduction in the fallow period on nutrient status was quantified. Due to a difference in soil pH between selected sites on sandy soils, soil iron contents was suspected to have caused the pH drop; its concentration was determined and correlated with soil pH.

STUDY SITES

Four study sites were selected (Fig. 1) where the species *Acacia senegal* naturally regenerates on sand and clay soils, and where the ASAS is traditionally used and extensive artificial plantings of *A. senegal* have been established and planned for the future. The selected study sites represented the prevailing types of soil and rainfall regimes where the ASAS is largely adopted at present and where desertification problems and pressure on land are immense. Localities G (Algedaref or Gedaref) and S (Singa) represent *A. senegal* in cracking clays. Both lie in eastern Sudan, the former is on the northeast of the range and the latter on the southeast. They are centers of afforestation activities where records of plantation and seed sources can be found. Expanded mechanized cultivation of sorghum conducted in these localities for decades relied only on the natural soil fertility. When fields lose fertility the land is reverted to trees, and farmers shift to another locality. It is an organized, government-supervised sort of shifting cultivation of a high magnitude.

Localities E (Elobeid) and D (Dubeibat) are central to the *A. senegal* range (known locally as the gumbelt) on sand. The former is central and the latter is southern to the range. These localities are separated from localities S and G by two big rivers, namely the White Nile and the Blue Nile and a vast expanse of clay plain, the Gezira, which lies between the two rivers. Study site descriptions are listed in Table 2. Localities G and S are accessible from Khartoum by road while E is accessible by plane or train. Locality D is a two hour drive to the south of site E on a rough track. Fig. 1 shows study site locations, vegetation and soil types and the River Nile system.

The four localities are centers of afforestation activities with a main emphasis on *A. senegal* monoculture on government reserved lands and farmers fields. The Central Forest Administration supervises an annual planting program executed by local forest authorities. Local farmers received food incentives, seed and seedlings as an encouragement for planting and protecting trees on their private holdings.

Table 4. Study site descriptions (Sudan Meteorology Department Report 1987)

	Site			
	Eloheid	Dubeibat	Gedaref	Singa
Latitude (N)	13-05	12-45	14-02	12-44
Longitude (E)	30-14	29-30	35-24	34-08
Elevation (m)	570	523	600	445.0
Atmospheric Pressure (mb)	944.4	948.5	941.6	957.3
Mean Daily Temp (C)	27.3	27.0	28.7	28.2
Highest max (C)	44.4	44.1	45.1	45.5
Lowest min (C)	4.4	5.6	6.6	5.7
Radiation (MJ/m2)	NA	NA	NA	21.98
Annual Rainfall (mm):				
1951-80	361	450	593	557
1981-87	263	335	570	521
Mean Relative Humidity	36	40	44	46
Relative Humidity range	14-72	18-74	24-73	22-76
Bright Sunshine (hr)	9.4	8.8	9.3	8.8
Bright Sunshine (per cent)	78	75	77	74
Evaporation (mm)	15.5	12.3	11.9	12.1
Wind Speed (kmph)	11.9	10.9	8.7	10.7

METHODS

Climate

As a background to savanna ecosystem processes and their dynamics, the marked seasonality in rainfall and temperature seems an important driving force that needs to be explored. The climatic differences between the study sites needed to be characterized in order to determine whether the study sites were different. The climatological data collected by the Sudan Meteorological Department, a government agency responsible for field data collection, compilation and dissemination were analyzed for statistical significance in order to determine whether the study sites were climatically different. The climatic data for the study sites were extracted from the records of the Sudan Meteorological Department. The data were separated into two sets: the first covers the 30 year-period 1951-1980 and the second included individual year records for 1981-1987, each year separately. The importance of the second set of data stems from the fact that they represented the drought years that hit the African sahel during the latter part of the 1970s and 1980's. I also examined the rates of evapotranspiration from data reported by Awadalla (1983) to determine whether variations among sites were significant.

Soil chemical analysis

Due to soil erosive forces in the past, parallel ridges of stabilized sand dunes were formed with marked troughs and crests. The troughs are water receiving sites and the crests are more dry and less fertile. They both had *A. senegal* trees and were expected to exhibit some variation in their nutrient dynamics. On the clay sites of Singa (site S) and Algedaref (site G), and on the sand sites of Elobeid (site E) and Dubeibat (site D) where natural stands of *A. senegal* were encountered, soil and tissue samples were collected.

Ten trees were randomly selected from each site. Nine composite soil samples were collected from each tree at three radii from each tree trunk and three soil depths at each radius. The radii were 25, 75 and 175 cm. These distances corresponded with stems, middle and edge of crown respectively. The soil depths at 10, 25 and 40 cm matched leaf litter layer, shallow and deep tree roots respectively.

Soil mechanical analysis was conducted in order to characterize soil according to particle size proportions. The samples were analyzed for N, P, K, organic carbon and pH. Because striking variation was found between soil reaction of sites E and D which were supposedly similar, I tested them for iron contents. Fe hydrolyzes, setting free hydrogen, could have caused the elevated acidity of site D. In addition to soil, I sampled various available tissues including leaves, pods, seeds, wood, bark and twigs in order to determine their N, K and P concentrations.

Sandy soils were analyzed for total nitrogen and iron using a fast neutron generation system. Soil samples in powder form were weighed and placed in glass vials. They were irradiated for ten minutes by fast, 14 Meu neutrons produced by a neutron generator. After a short waiting period the neutrons were counted for ten minutes using a highly purified Germanium detector (HPGe) gamma-ray spectrometer coupled to a 35-Plus Canberra multichannel analyzer. Fe foils were used as neutron flux monitors. The elemental content was computed in comparison to standards of known concentration treated similar to the samples. This technique was applied to the sandy soil samples of sites E and D.

The clay soil samples from sites G and S were analyzed for total nitrogen using the Kjeldahl method because the neutron generation system was out of order. Doty et al. (1969; 1970) demonstrated that a good correlation existed between total nitrogen determined by the Kjeldahl technique and that determined by the automated neutron activation nitrogen technique. Phosphorus, potassium and organic carbon were also determined. In each locality *A. senegal* trees of similar age were located in forest plantations, and in addition, randomly selected trees were marked and sampled in naturally regenerated stands. Since nitrogen fixation differs among sites (Brewbaker 1984), two sites were selected in each plantation. Ten trees were sampled for plant tissue and 15 trees for soil. Soil was expected to be more variable than plant tissues. Soil pH was determined using a portable digital Corning pH meter. The objective was to test soil and tissue nitrogen variations as affected by treatments e.g. the low vs. high gum yielding tree strains, dune top vs. dune bottom site, and cultivation vs. tree fallow, where young trees were tested against old ones and against cultivation. Clay soil analysis was conducted in the Soil Chemistry section of the ARC (Agricultural Research Corporation).

Soil samples were dried at room temperature and crushed by pestle and mortar. For pH determinations, 10 g from each sample were weighed and placed in a 50 ml beaker to which 10 ml of distilled water was added. The soil-water suspension was stirred and the slurry was allowed to stand for a few minutes, with occasional stirring. A Corning digital pH meter was calibrated with 4.0 and 7.0 pH buffers, and used to read the sample pH.

Plant chemical analysis

Plant tissue samples were collected simultaneously with soil samples. Tissue samples concurrently collected from each tree included leaves, twigs, bark, root, seeds and pods. Gum samples were collected and their protein and moisture contents determined using a wet combustion digestion method followed by ammonia titration with a solution of sodium hydroxide. Iron was determined with an atomic absorption spectrophotometer. For the total Kjeldahl nitrogen (TKN) determination specific plant tissues were dried in an oven to a constant weight at 70 C and ground to fine powder using a Wiley mill and a size 40 mesh. The samples were dried in a desiccator and 0.25 g portions were used for acid digestion. To each sample 0.175 g mercuric oxide dissolved in 3.5 ml concentrated sulfuric acid was added in a 75 ml digestion tube. The mixture was heated in a block digestor at 375 C for 70 minutes. The digestates were allowed to cool to room temperature. diluted to 75 ml and filtered. Tissue sample analysis for total Kjeldahl nitrogen (TKN) and total phosphorus (TP) were conducted with an Orion Scientific Instruments autoanalyzer as described by Day (1982). Iron concentration was determined by an atomic absorption spectrophotometer.

Tree dimensions were measured in each of the study sites in order that total biomass and leaf litter be assessed. Height was measured by a Relascop, a Swedish height measuring device, and the diameter by linen tape. I was unable to determine the leaf biomass that an average tree produces each year because of site inaccessiblity at the desired time. The height and circumference of the *A. senegal* trees were measured and their ages were obtained from a forest record book kept for each managed forest. The objective was to estimate biomass and leaf litter in order to assess the amount of nitrogen that recycles through the system. The growth parameters in Table 19 were utilized for growth rate comparisons between sites. The distance between trees was measured to enable determination of the tree density. *Acacia senegal* plantations were raised at 4x4 m spacings, while naturally grown trees were significantly less dense. I chose to select for different ages where the record of plantation age was available.

Variation among the four study sites in seed size was investigated. Ten trees from each site were chosen at random and seeds were collected from each one separately. Five samples were taken from each tree and their weights determined. The number of seed per gram for each site was then calculated. N concentration of seed was determined.

Soil conditions under cultivation and under trees of various ages

A study was conducted to compare the effects of age of *A. senegal* and crop cultivation on soil pH, nitrogen and carbon. Farms were located where cultivation was practiced for five years, and soil samples collected and analyzed for nitrogen, carbon, and pH. In the same general locality *A. senegal* trees of known ages were located and soil samples collected from them and compared to those of the farms. The samples were analyzed for nitrogen, carbon and pH as described before. The option of soil without trees was overlooked.

Statistical analysis

The experimental design for the soil and plant chemistry study was a randomized block, split split-plot design with study sites representing whole plots, distance from tree trunk subplot, and soil depth sub sub-plot. ANOVA with multiple comparisons and MANOVA were used where appropriate to test for significant treatment effects. The data were checked for test assumptions. When the test assumption of normality was violated, data transformation was performed. For the climate studies, analysis of variance (ANOVA) was conducted to test whether the study sites were climatologically different. Significant differences among means were separated by Duncan multiple range test. The variation in nutrient concentrations with site, soil depth and distance from tree trunk was tested using multivariate analysis of variance.

RESULTS

Climate: Temperature

As collected from the Sudan Meteorological Department, the climatological means are shown in Table 5. The mean maximum temperature did not vary significantly with site, nor with years during the 1981-87 period. The mean maximum temperature ranged between 40.8 for site E and 41.2 for D (the two sand sites), and 41.4 for site G and 42.3 for site S. The clay soil sites were not significantly hotter than the sand sites.

The mean minimum temperature was not significantly different among the tested sites, but was significant among years (P<.029). It is interesting to note that year 1984 was lowest in rainfall and highest in maximum and minimum temperatures, whereas 1981 was highest in rainfall and lowest in maximum and minimum temperatures. March - June was the hottest period of the year in all sites. The mean minimum temperature was not significantly different between sites, but was significant between months (ANOVA, P < 0.0001). The lowest temperature occurred during December-February with a range of 4.4-6.0 C.

Radiation

Radiation did not vary significantly with site but it did with months (ANOVA P < 0.0001). Sunshine duration varied significantly with month (ANOVA, P < 0.0001) and site (P < 0.001). Sites E and G had significantly higher sunshine duration than sites D and S. The two former sites are more northerly than the latter sites; they receive less clouds than the other sites and consequently more sunshine. Sites G and D were not significantly different.

Moisture

There was no significant difference between site S and G with respect to 1981-87 rainfall. The difference in rainfall for the period 1981-87 was not significant among years but was significant between sites (p=0.026). Sites G and S were not different from one another, but were significantly higher than site E. The difference between months and between sites was found to be significant (ANOVA, P< 0.0001) with respect to rainfall. With respect to humidity sites S and G were not significantly different. Sites E and D were significantly different from one another (p<0.0001) and from S and G. Site S had highest average humidity (45.75). The two former sites were significantly different from E. Sites G and D were not significantly different from each other. The mean humidity ranged between 35.75 per cent for E and 45.75 for S. It is interesting to note that the lower rainfall semi-desert areas of Elobeid and Dubeibat sites were more severely affected by drought than the wetter sites of Singa and Algedaref. based on the relative drop in mean annual rainfall.

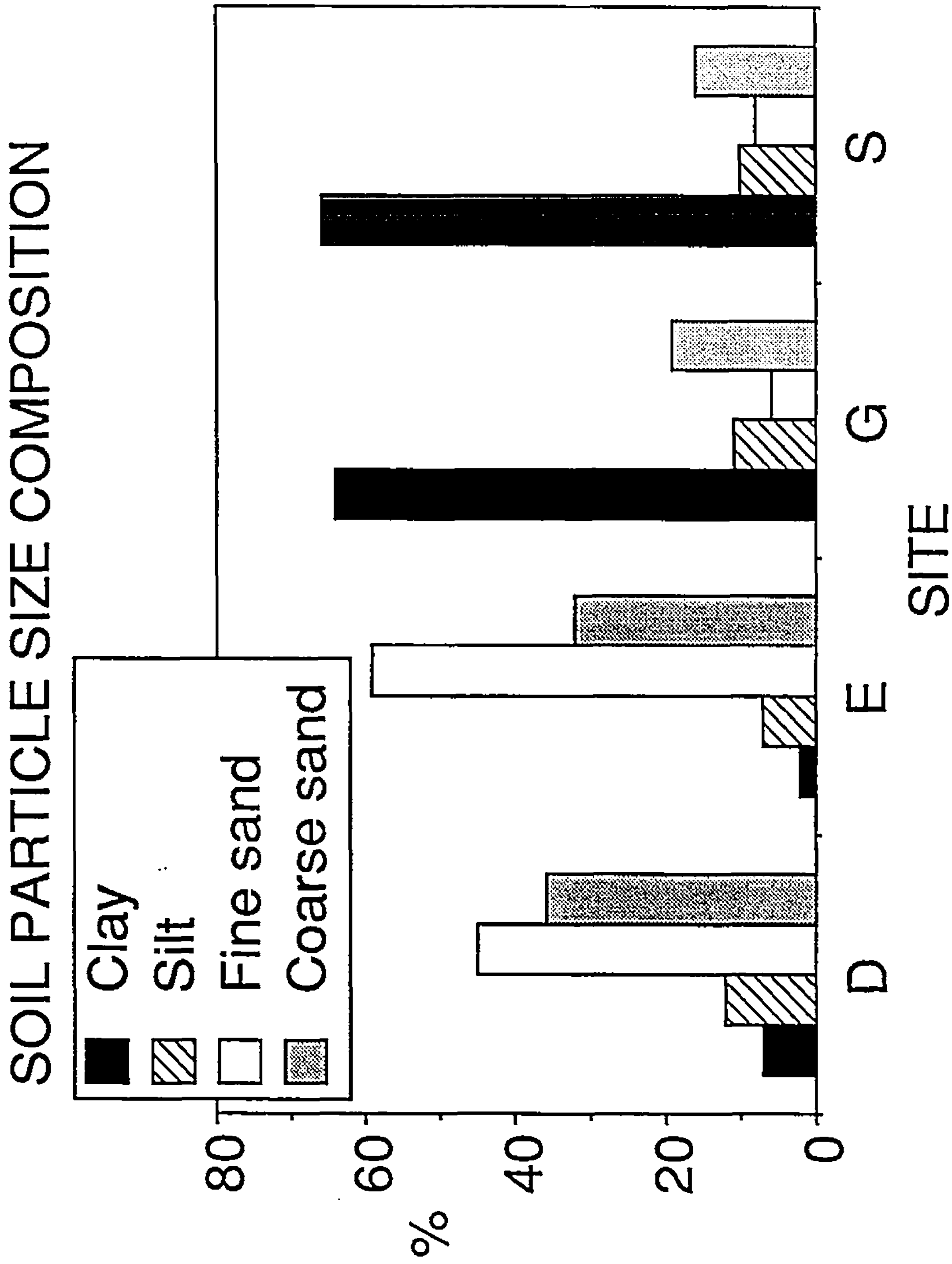
Evaporation was significantly different between sites and months. Site E had the highest mean rate of evaporation (15.45) followed by and significantly different from D (13.34). Both sites were significantly different from sites S and G which are not themselves significantly different. The wind speed was significantly higher on sites E, D, and S than G. It ranged between 5.5 to 7.4 mph. It was significantly different between sites and months. The wind speed and evaporation decreased with site in the order of E, D, S, and G while rain was in the reverse order of G, S, D, and E. The relationship between them was inverse. Sunshine and humidity had an inverse relationship also.

The two sand soil sites were not significantly different. Potential evapotranspiration rates were calculated by Awadalla (1983) for sites S, G and E, using Penman's formula. I analyzed his data for statistical significance using ANOVA. There was significant variation in the evapotranspiration rate between months, but not between sites. Site E had the highest rate followed by site G, while site S had the lowest rate of the three sites. All sites were not significantly different from each other with respect to evapotranspiration. The rate was highest in May and declined starting in June when the rainy season began at all sites (Table 6 (a)). All months were significantly different from one another, except July and February were not significantly different from one another; September and December were also not significantly different from one another, (Table 6 (b)).

Soils: Soil mechanical analysis

Soil composition analysis revealed interesting results (Table 7 (a)). The ANOVA (Table 7 (b)) reflects the statistical comparisons. There was no significant variation between S and G in

Fig. 3. particle size comparison of soils sampled at the four study sites. Percent particle proportions are shown on the Y-axis.


SOIL PARTICLE SIZE COMPOSITION
Clay
Silt
Fine sand
Coarse sand
%
0
20
40
60
80
D
E
G
S
SITE

the clay and silt fraction or in the sand fraction. Sites E and D were significantly different with regards to their sand fraction. D had significantly more sand than E ($P<.05$). These two sites had significant clay-and-silt proportion differences.

ANOVA and multiple comparisons were conducted to test soil mechanical composition for statistical significance. A multiple comparison (Bonferroni) summary (Table 7 (c)) shows the results. The total sand fraction was significantly higher in site E than site D.

It is concluded from this study that soil texture of site S and G were identical. However, their pH was significantly different, (Table 8 (a)). Sites D and E were surprisingly significantly different in each component of their soil texture and also in their pH (Table 8 (b)). By using the U.S. Soil Survey textural classification system, the soil of site E was classified as sand, that of site D as loamy sand, and sites S and G as clay soils.

Soil pH

Soil pH results are listed in Table 8 (a) for each of the four study sites. A comparison was made between old and young trees, sand dune top and low yield to find out if they varied in pH. There was a highly significant difference due to site, treatments, depth, and site and depth interactions (MANOVA $PR>F=.0005$, .0004, .0002 respectively). The drier and more sandy soil site (E) had near neutral soils ranging in pH from 6.3 to 7.3. The wetter site (D) had soils more acidic in reaction and ranged between 4.7 and 5.1.

Sites G and S had dark cracking clay soils. The former had slightly more (570 mm) rainfall than the latter (520 mm). Both sites had alkaline soils; site G's pH range was 7.9-8.2, and S was 9.1-9.3. Within-site variations were not significant although there was a tendency towards less acidity or more alkalinity with distance from tree trunk. The difference between sites with similar soil types was more pronounced in the sandy soil site (4.7-7.2) than in clay sites (7.9-9.3).

The pH difference in similar sandy soil sites could be due to leaching of basic cations by heavier rains in site D. Indeed, a high correlation (R=0.93) existed between soil pH and rainfall. It was even higher (0.98) in clay soil. Iron as a micronutrient implicated in nodulation and nitrogen fixation was analyzed in sandy soils as they showed lesser nodule numbers than clay soils. Soil iron content (Table 9 (a)) was significantly higher in site D than in E (P <0.0001) (Table 9 (b)). There was no significant variation due to depth or distance from tree trunk.

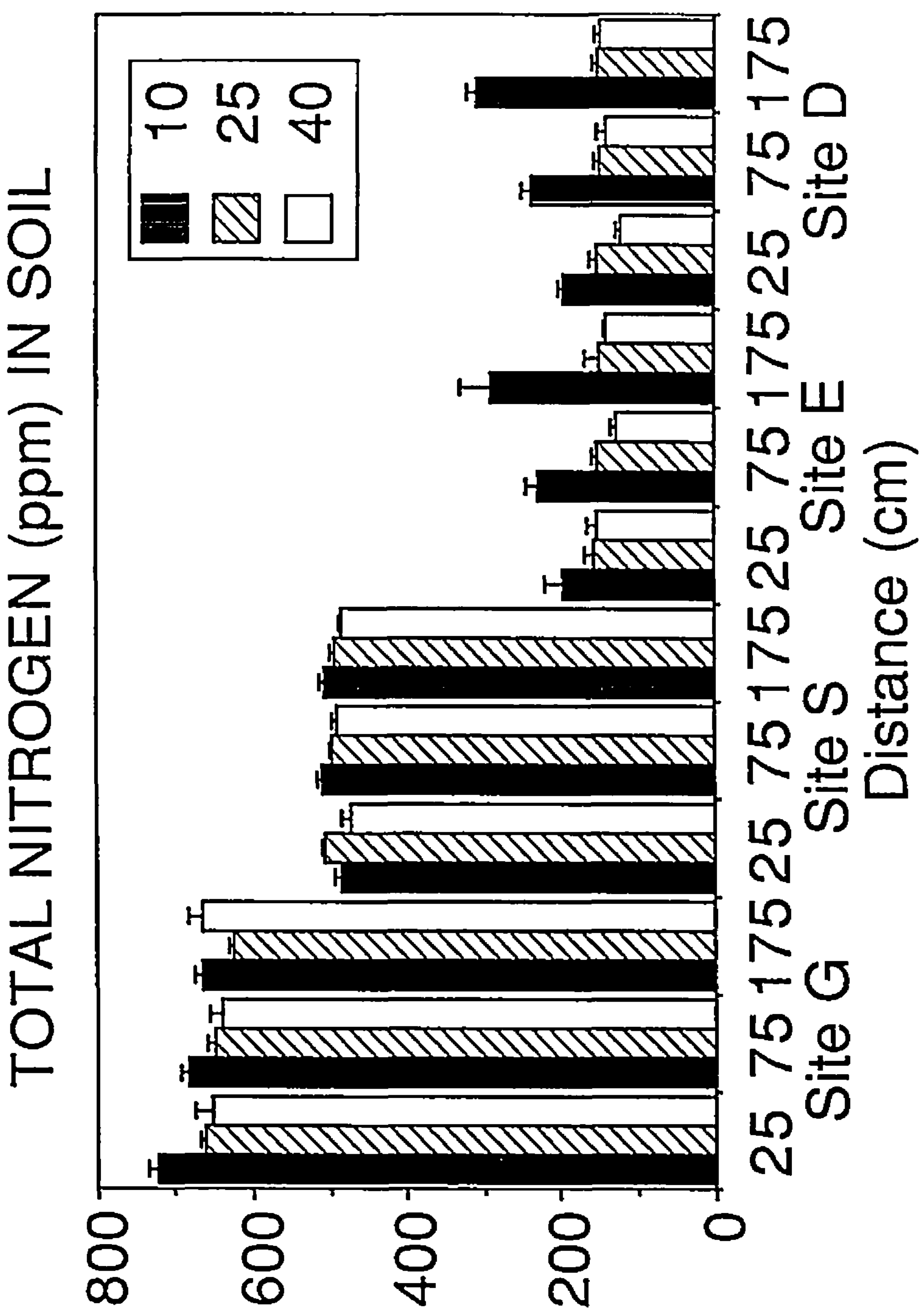
Soil total nitrogen

Total soil nitrogen under *A. senegal* on the clay sites G and S was remarkably higher than sandy soil sites E and D (P<0.0001) (Table 10 and Fig. 4). It is the difference in soil type that caused this rather than tree type. Variation with depth was also highly significant (P<0.0001). There was a tendency towards increased concentration closer to the soil surface and tree trunks for site G. The distance to tree trunk had no significant effect. Site G was significantly higher than site S. The lowest concentration occurred at depth 25 and distance 175 cm.

The site S soil profile exhibited a trend generally similar to that of site G. The concentration in the top soil layer was only slightly higher than that of depth 25 cm. With respect to distance from tree trunk there was no clear trend.

The total nitrogen was not significantly different between the two sandy sites. They exhibited higher concentration in the top 10 cm of soil that increased with distance from tree trunk, but decreased with depth. The mean annual rainfall was correlated against soil total nitrogen concentration in the 25-cm upper soil layer in the study sites. A strong positive correlation (R=0.93) was revealed.

Fig. 4. Soil total nitrogen in ppm for the study sites D, E, G and S. The composite soil samples were collected at distances 25 cm, 75 cm and 175 cm. The sampling depths were 10 cm, 25 cm and 40 cm. The Y-axis shows the total nitrogen concentration.


TOTAL NITROGEN (ppm) IN SOIL
10
25
40
0
200
400
600
800
25 75 175 25 75 175 25 75 175 25 75 175
Site G
Site S
Site E
Site D
Distance (cm)

Soil nitrate nitrogen

There was highly significant variation between sites with respect to NO3-N (Table 11 (a) Fig. 5). Sites S and G were significantly higher than sites D and E. which were not different from one another. There was no significant difference between soil depth or distance from tree trunk in nitrate nitrogen (Table 11 (b)). Sites G and S were not significantly different from one another. The depths and distances examined did not reflect appreciable differences in NO3-N.

The means of the four sites for total nitrogen were correlated with the means for NO3-N. A high correlation of 98.23 per cent was revealed. However, the concentrations of these forms of nitrogen were compared with respect to sampling sites; correlation between total and nitrate nitrogen was very weak, and was in fact negative in sites D and G. Correlation of the mean annual rainfall with nitrate nitrogen revealed a fairly strong ($R=0.85$) positive relationship.

Phosphorus and potassium

Phosphorus analysis revealed significant variation among sites E, S and G, (Fig. 6). The variations did not follow soil textural differences. Site S was the highest with mean concentration of 7.18 ppm. Site G was 3.81 ppm and E was in between the clay sites with a mean of 5.12 ppm (Table 12 (a)). There was no significant variation between soil depths or distances from tree trunks. Soil potassium (Table 13 (a), Fig. 7), as one of the most important essential elements in tropical soils, revealed no significant difference between sites, but showed significant variation due to depth (Table 13 (b)). The top soil layer was significantly higher in potassium ($P< 0.003$) than the other layers. The effect of distance from tree trunk was not significant. The two sandy soil sites had variable potassium concentrations between depth and radii from tree trunk. Site E varied between 7 and 25 ppm, while site D was between 11 and 55 ppm. There was a general decrease in potassium concentration with depth. The decrease was more pronounced in sand than in clay which exhibited remarkable similarity in potassium concentrations. The effects of phosphorus in terrestrial nitrogen cycling have been studied by Cole and Heil (1981). They hypothesized that supply of nitrogen comes into balance with that of phosphorus if allowed sufficient time. They claim that close linkages exist between organic carbon, nitrogen accumulation and phosphorus content of parent material, and also during nutrient depletion (Table 12 (a)).

Organic carbon

Organic carbon distribution in clay sites (S and G) soil profiles is summarized in Table 14 (a) and Fig. 8. A comparison between a young stand , old stand and a cultivated area is shown in Table 21. The young stand was under *Acacia* for 5 years and the old for 20 years. The old site carbon content was significantly higher than young or cultivated sites. Site G was significantly higher than site S in organic carbon content; site E was lowest. There was no significant within-site variation away from the tree trunk (Table 14 (b)). Site E exhibited significant variation down the soil profile with depth 10 cm containing the highest carbon. Site G was significantly higher than site S ($P < .0001$). Distance and depth did not reflect a significant increase in soil carbon.

Fig. 5. Soil nitrate nitrogen in ppm (Y-axis) for the four study sites. The sampling distances were 25 cm, 75 cm and 175 cm; the depths were 10 cm, 25 cm, and 40 cm.

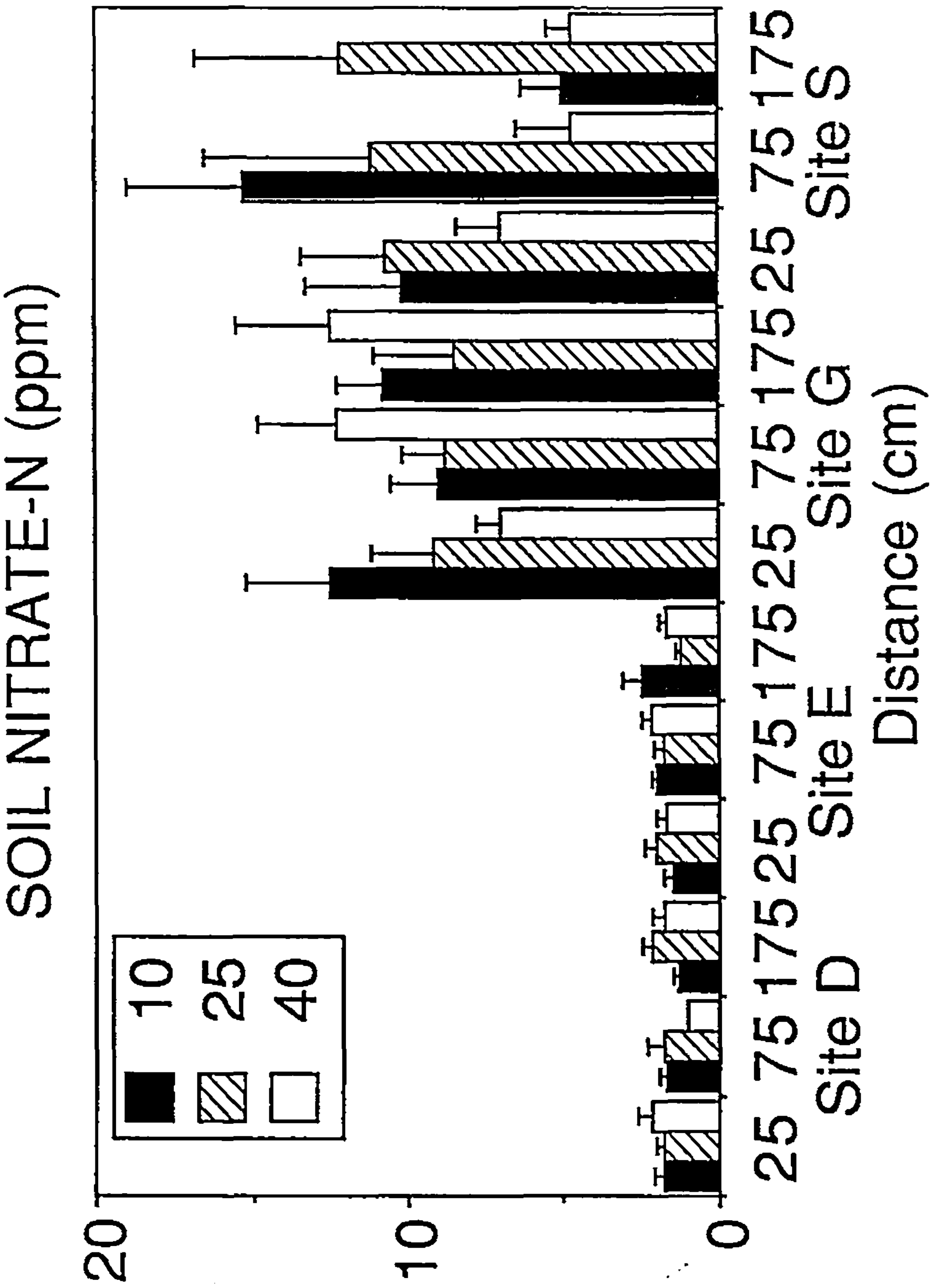

SOIL NITRATE-N (ppm)
20
10
0
10
25
40
25 75 175 25 75 175 25 75 175 25 75 175
Site D
Site E
Site G
Site S
Distance (cm)

Fig. 6. Soil phosphorus in ppm (Y-axis) for the four study sites. The sampling distances were 25 cm, 75 cm and 175 cm; the depths were 10 cm, 25 cm, and 40 cm.

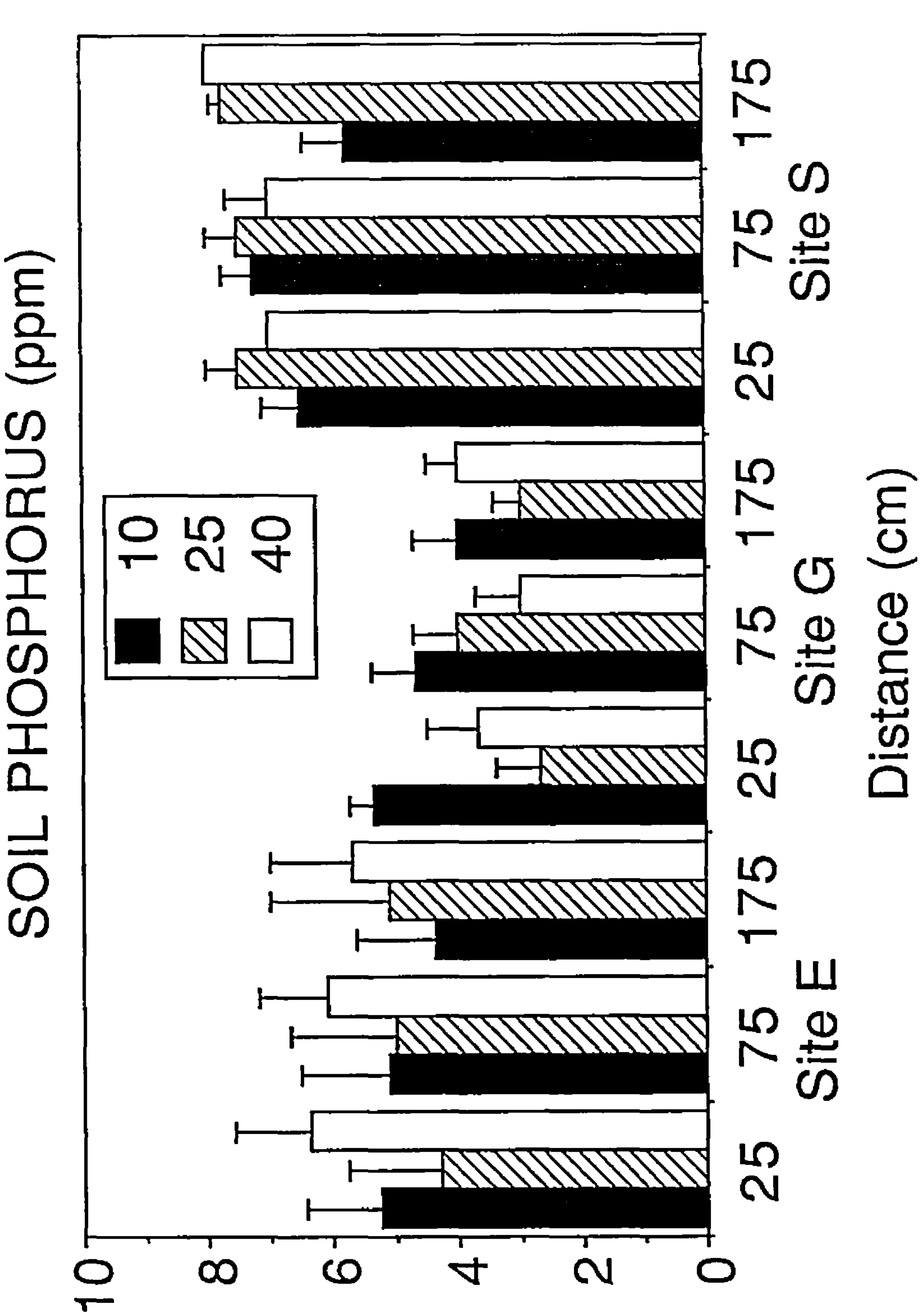

SOIL PHOSPHORUS (ppm)
10
25
40
0
2
4
6
8
10
25
75
175
Site E
Site G
Site S
Distance (cm)

Fig. 7. Soil potassium in ppm (Y-axis) for the four study sites. The sampling distances were 25 cm, 75 cm and 175 cm; the depths were 10 cm, 25 cm, and 40 cm.

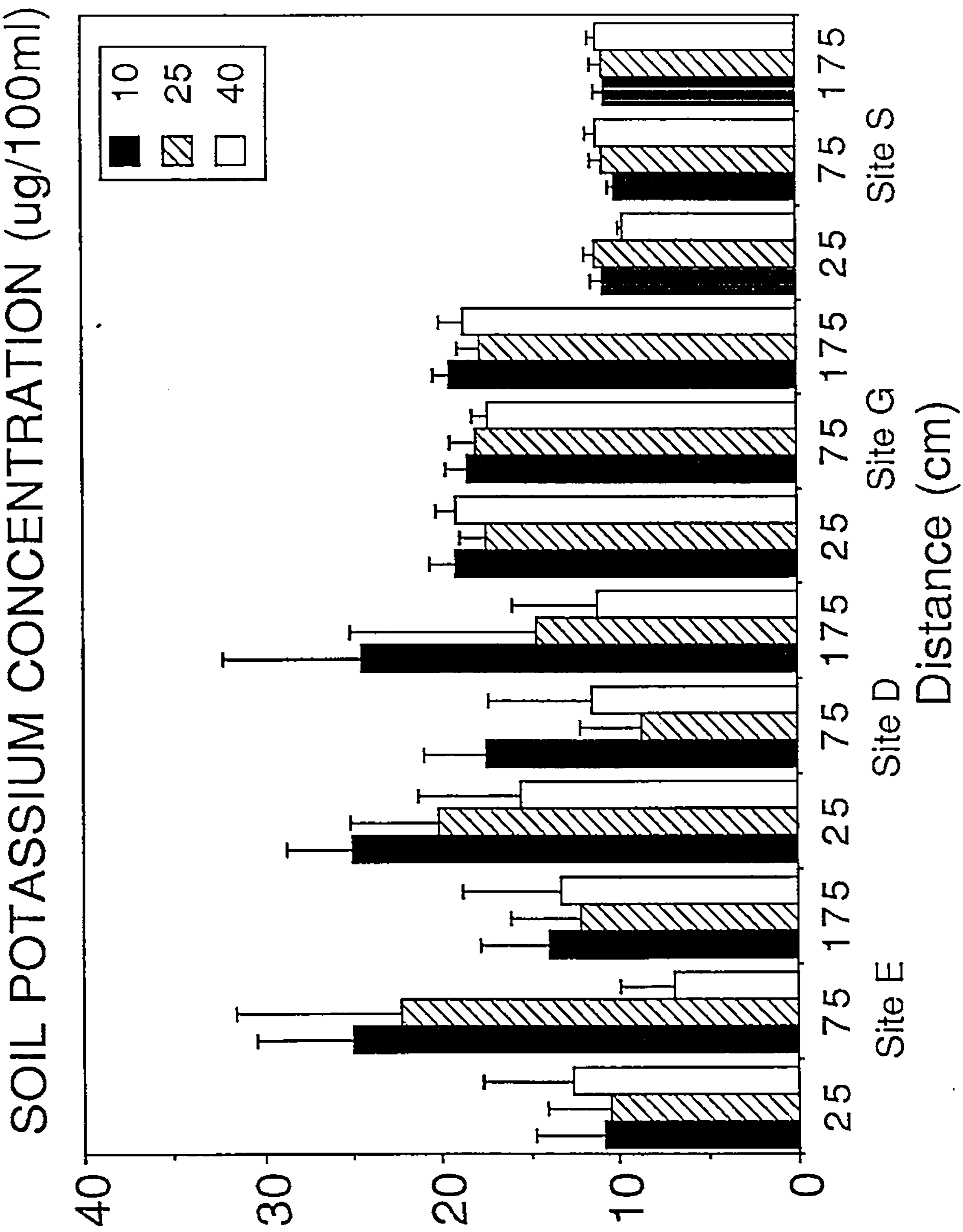

SOIL POTASSIUM CONCENTRATION (ug/100ml)
10
25
40
25 75 175 25 75 175 25 75 175 25 75 175
Site E
Site D
Site G
Site S
Distance (cm)
0
10
20
30
40

Fig. 8. Soil organic carbon (Y-axis) for the four study sites. The sampling distances were 25 cm, 75 cm and 175 cm; the depths were 10 cm, 25 cm, and 40 cm.

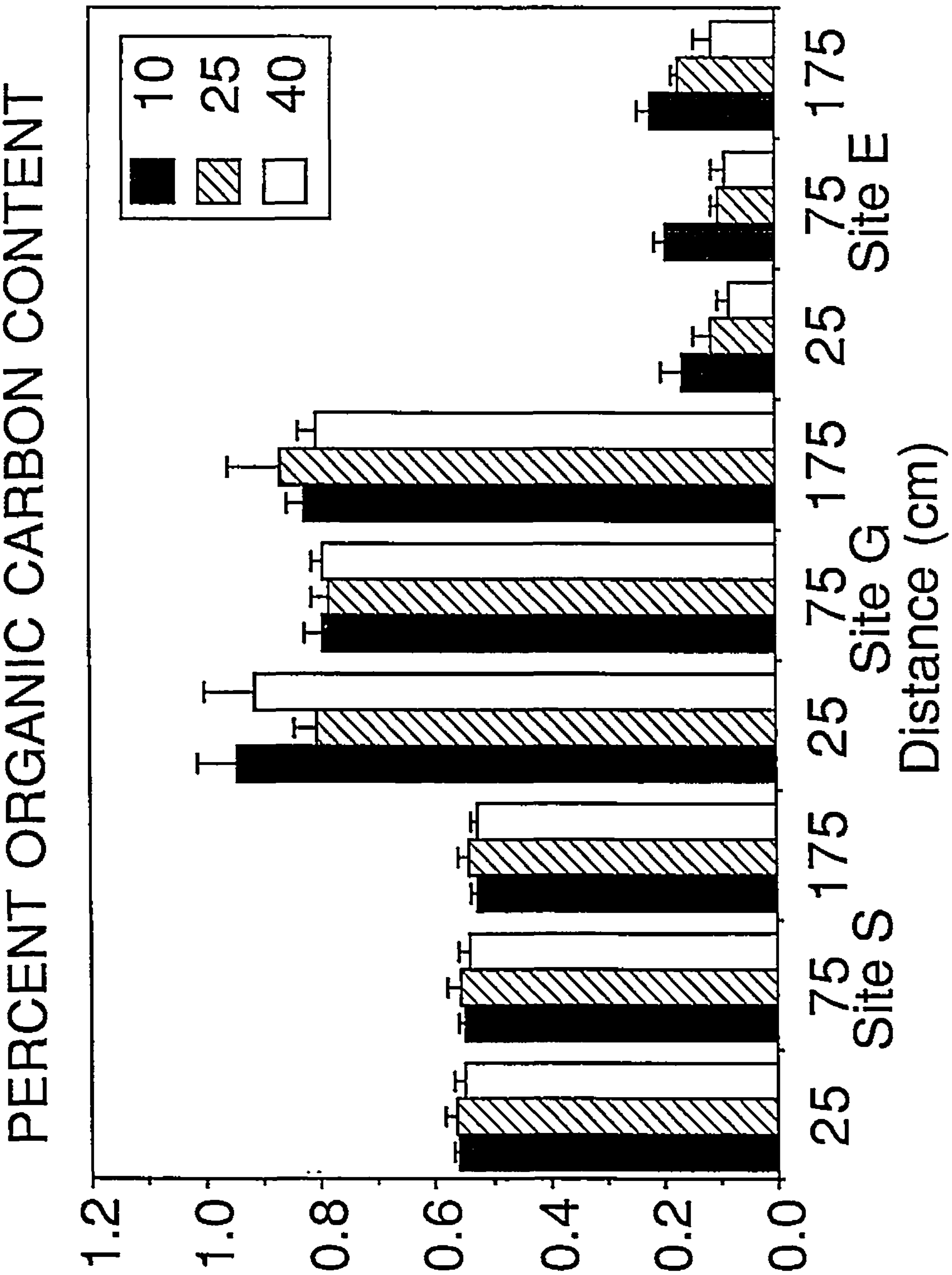

PERCENT ORGANIC CARBON CONTENT
10
25
40
1.2
1.0
0.8
0.6
0.4
0.2
0.0
25
75
175
Site S
25
75
175
Site G
25
75
175
Site E
Distance (cm)

Table 5 . Climatological monthly variables 1951-1980

Site	Mo	Tmx C	Tmn C	Rad. MJ/m2/day	Sun Shine Hr	Hum. %	Rain mm	Evap. mm	Wind kmph
D	Jan	39.5	8.4	21.6	10.2	22.0	0.0	16.8	12.87
D	Feb	41.2	7.7	23.0	10.2	19.5	0.0	17.5	12.87
D	Mar	43.6	12.8	23.8	9.6	17.0	0.0	19.3	11.26
D	Apr	44.8	13.8	24.3	9.8	22.0	2.0	18.5	9.66
D	May	44.3	16.7	23.0	9.2	36.0	13.0	15.6	9.66
D	Jun	42.6	18.3	20.8	7.7	54.0	37.0	12.2	12.87
D	Jul	40.3	19.6	18.8	6.5	69.0	125	6.9	11.26
D	Aug	38.0	17.3	18.4	6.7	77.5	140	5.1	8.05
D	Sep	39.6	16.8	18.6	7.3	71.4	85.0	5.8	6.44
D	Oct	40.8	12.4	20.2	8.8	48.6	23.0	11.6	9.66
D	Nov	40.5	10.6	21.8	10.5	28.4	0.0	15.6	11.26
D	Dec	38.8	7.3	21.1	10.4	26.2	0.0	15.2	14.48
E	Jan	38.2	6.3	21.6	10.4	22.0	0.0	16.3	14.48
E	Feb	40.5	4.4	23.0	10.4	18.0	0.0	19.1	12.87
E	Mar	42.9	9.0	23.8	10.1	14.0	0.0	22.0	12.87
E	Apr	44.4	13.0	24.2	10.2	16.0	3.0	22.0	11.26
E	May	44.3	17.2	23.0	9.7	26.0	10.0	19.8	9.66
E	Jun	43.7	19.0	20.8	8.5	44.0	22.0	15.7	14.48
E	Jul	39.7	17.3	18.8	7.2	64.0	111	9.9	12.87
E	Aug	39.0	17.5	18.4	7.4	72.0	137	6.1	9.66
E	Sep	40.0	17.4	18.6	8.0	63.0	61.0	7.6	8.05
E	Oct	40.6	14.5	20.1	9.5	40.0	17.0	13.8	9.66
E	Nov	39.0	9.2	21.8	10.7	25.0	0.0	17.5	12.87
E	Dec	37.6	5.8	21.1	10.5	25.0	0.0	15.7	14.48
G	Jan	40.2	6.6	20.5	10.1	35.0	0.0	13.0	9.66
G	Feb	42.3	6.6	22.7	10.2	29.0	0.0	15.1	8.05
G	Mar	44.2	9.8	24.0	9.9	26.0	1.0	18.0	9.66
G	Apr	45.0	10.6	24.6	10.1	24.0	5.0	18.1	8.05
G	May	45.1	17.3	24.0	9.7	34.0	21.0	16.1	8.05
G	Jun	43.5	22.0	22.5	8.7	50.0	93.0	10.9	11.26
G	Jul	40.0	20.9	20.9	7.4	66.0	173	6.7	11.26
G	Aug	37.3	18.7	21.2	7.5	73.0	177	4.6	9.66
G	Sep	38.9	18.9	22.1	8.6	66.0	90.0	5.5	8.05
G	Oct	40.3	18.0	20.1	9.4	50.0	29.0	8.7	4.83
G	Nov	40.2	12.0	20.7	10.1	35.0	4.0	13.5	6.44
G	Dec	40.1	7.4	19.5	9.9	37.0	0.0	12.7	9.66
S	Jan	41.7	15.2	20.5	10.4	32.0	0.0	14.2	11.26
S	Feb	44.0	7.5	22.7	10.4	26.0	0.0	16.7	11.26
S	Mar	45.4	10.0	24.0	10.0	22.0	0.0	19.5	11.26
S	Apr	45.3	13.7	24.6	9.9	23.0	3.0	19.3	9.66
S	May	45.3	17.3	24.0	8.3	37.0	28.0	16.2	12.87
S	Jun	44.4	16.7	22.5	7.4	54.0	102.0	11.4	14.48
S	Jul	41.0	18.5	20.9	6.2	69.0	142	6.3	11.26
S	Aug	38.1	18.2	21.2	5.7	76.0	147	3.9	9.66

S	Sep	39.5	17.9	22.1	7.6	73.0	104.0	4.3	8.05
S	Oct	41.4	13.1	21.1	8.9	60.0	27.0	7.2	8.05
S	Nov	40.8	10.0	20.7	10.5	42.0	3.0	12.8	9.66
S	Dec	40.8	8.4	19.5	10.4	35.0	0.0	13.5	11.26

Table 6(a). Potential monthly average evapotranspiration indexes (Awadalla 1983)

Month	G	Site S	E
January	171.2	164.6	178.7
February	174.9	167.9	188.1
March	221.2	212.6	230.1
April	230.4	230.1	227.2
May	237.1	234.5	244.6
June	213.7	193.8	223.9
July	182.4	165.4	192.6
August	164.6	151.4	162.2
september	168.1	159.7	169.0
October	176.7	172.7	199.7
November	169.8	163.9	187.4
December	165.0	152.7	174.8
Mean	189.6	180.8	198.2
S.D.	27.6	29.6	27.0

Table 6 (b). MANOVA table: Evapotranspiration rates

Dependent variable: Evapotranspiration rate

Sources	DF	Type III SS	M.S.	F	PR>F
Site	2	0.157	0.0787	913	0.0001
Month	11	1.98	0.1802	2090	0.0
Month*Site	22	0.062	0.0002	32	0.0001
Error	72	0.0062	0.00008		

Table 7 (a). Soil particle size composition. S.E. in parenthesis.

Fraction	Site			
	D	E	G	S
Clay	7(.08)	2(.01)	64(.4)	66(.4)
Silt	12(.7)	7(.07)	11(.7)	10(.8)
Fine sand	45(.7)	59(.4)	6(.07)	8(.06)
Coarse sand	36(.8)	32(.6)	19(.6)	16(.5)
Texture	loamy sand	sand	clay	clay

Table 7 (b). Site comparisons of soil particle size composition: ANOVA table

Dependent variable	Type III SS	F	PR>F
All sand	19022.4	2326.9	0.0001
Clay+silt	18714.1	2096.8	0.0001
Clay	18071.2	1867.8	0.0001
Silt	83.3	48.3	0.0001
Fine sand	10162.5	1489.0	0.0001
Coarse sand	1551.3	154.4	0.0001

Table 7 (c). Multiple comparison summary table for soil texture

Fraction	Site			
	D	E	G	S
Coarse sand	.a	b	c	c
fine sand	b	a	c	c
All sand	b	a	c	c
Silt	a	c	b	b
Clay	b	c	a	a
Silt and clay	b	c	a	a

Table 8 (a). Soil pH variation with distance and soil depth

Depth (cm)	Distance (cm)			
	25	75	175	Mean
		Site D		
10	5.2	5.3	5.2	5.23(0.058)
25	4.9	5.1	4.9	4.97(0.115)
40	4.8	4.7	4.7	4.73(0.058)
Mean	4.97	4.93	4.98	
S.E.	0.21	0.30	0.25	
		Site E		
10	6.6	6.6	7.2	6.80(0.35)
25	6.9	7.0	7.2	7.03(0.18)
40	6.4	6.3	7.3	6.67(0.55)
Mean	6.63	6.63	7.23	
S.E.	0.25	0.35	0.06	
		Site G		
10	7.9	8.1	8.1	8.03(0.115)
25	8.0	8.1	8.2	8.1(0.10)
40	8.2	8.2	8.2	8.2(0.00)
Mean	8.03	8.13	8.17	8.11
S.E.	0.16	0.06	0.06	0.07
		Site S		
10	9.1	9.1	9.2	9.13(0.06)
25	9.1	9.1	9.2	9.13(0.06)
40	9.2	9.3	9.3	9.27(0.06)
Mean	9.13	9.17	9.23	9.18
S.E.	0.06	0.12	0.06	0.05

Table 8 (b). MANOVA table. Dependent variable: soil pH.

Source	DF	Type III SS	M.S.	F	PR > F
Treatment	2	2.52	1.26	7.71	0.0005
Distance	2	0.09	0.05	0.30	0.74
Depth	2	3.04	1.01	6.19	0.0004
Sit*Distance	2	0.41	0.21	1.25	0.29
Site*Depth	2	2.86	1.43	8.72	0.0002
Site*Distance * Depth	8	0.97	0.12	0.75	0.65

Table 9 (a). Per cent iron contents in sandy soil (S.E. in parenthesis)

Depth (cm)	Distance (cm)		
	25	75	175
		Site D	
10	0.76(.11)	0.70(.15)	0.70(.17)
25	0.77(.07)	1.01(.11)	0.90(.03)
40	0.54(.13)	1.03(.05)	0.65(.2)
		Site E	
10	0.58(.11)	0.48(.11)	0.50(.10)
25	0.43(.13)	0.49(.12)	0.37(.10)
40	0.39(.06)	0.34(.09)	0.44(.10)

Table 9 (b). MANOVA table: Soil iron concentrations

Source	DF	Type III SS	M.S.	F	PR > F
Site	1	3.10	3.1	38.5	0.0001
Distance	2	0.195	0.09	1.21	0.303
Depth	2	0.178	0.09	1.1	0.336
Site*distance	2	0.29	0.14	1.8	1.7
Site*depth	2	0.3	0.15	1.93	0.15
Site*distance*depth	8	0.6	0.07	0.93	0.49
Error	90	7.25	0.08		

Table 10. Soil total nitrogen (ppm). S.E. in parenthesis

Depth (cm)	Distance (cm)		
	25	75	175.
	Site G		
10	723(11.8)	684(6.7)	665(7.9)
25	660(7.6)	648(8.6)	624(6.7)
40	653(21.6)	639(16.8)	665(18.0)
Mean	678(38.5)	657(23.9)	651(23.3)
	Site S		
10	486(6.7)	511(4.0)	507(6.7)
25	507(3.5)	497(4.0)	493(6.7)
40	473(12.8)	491(7.2)	486(3.5)
Mean	489(17.4)	499(10.0)	495(10.7)
	Site E		
10	195(23.9)	230(14.6)	290(40.1)
25	155(11.5)	150(7.3)	148(18.6)
40	150(13.7)	126(5.6)	138(5.4)
Mean	166(24.7)	168(54.2)	192(84.9)
	Site D		
10	196(4.9)	238(10.8)	308(12.8)
25	151(9.1)	148(5.4)	150(8.2)
40	120(5.8)	140(12.4)	148(5.4)

Table 11 (a). Soil nitrate nitrogen (ppm). S.E. in parenthesis

Depth (cm)	Distance (cm)		
	25	75	175
		Site D	
10	1.8(0.3)	1.7(0.2)	1.3(0.2)
25	1.8(0.2)	1.8(.5)	2.2(0.3)
40	2.2(0.4)	1.0(0.00)	1.8(0.4)
		Site E	
10	1.5(0.3)	2.0(.2)	2.5(.6)
25	2.0(0.4)	1.8(0.3)	1.2(0.2)
40	1.7(0.3)	2.2(0.3)	1.7(0.2)
		Site G	
10	12.5(2.7)	9.0(1.6)	10.8(1.5)
25	9.2(2.0)	8.8(1.4)	8.5(2.6)
40	7.0(.8)	12.3(2.5)	12.5(3.0)
		Site S	
10	10.2(3.1)	15.3(3.7)	5.0(1.3)
25	10.7(2.7)	11.2(5.3)	12.2(4.6)
40	7.0(1.4)	4.7(1.8)	4.7(0.8)

Table 11 (b). MANOVA table. Dependent variable : Total and nitrate nitrogen

Source	DF	Type III SS	M.S.	F	PR > F
Dependent variable: Nitrate nitrogen					
Site	3	3035.3	1011.8	74.24	0.0001
Depth	2	56.9	28.45	2.09	0.127
Distance	2	15.5	7.75	0.57	0.567
Site*depth	6	247.1	41.18	3.02	0.008
Site*distance	6	63.26	10.54	0.77	0.59
Site*depth*distance	16	336.15	21.0	1.54	0.09
Dependent variable: Total nitrogen					
Site	3	9247596	3082530	2964	0.0
Depth	2	161714	80857	77.77	0.0001
Distance	2	6782	3391	3.26	0.041
Site*depth	6	57302	9550	9.19	0.0001
Site*distance	6	29608	4934	4.75	0.0002
Site*depth*distance	16	56893	3555	3.42	0.0001

Table 12 (a). Soil phosphorus (ppm). S.E. in parenthesis

Depth (cm)	Distance (cm)		
	25	75	175
		Site E	
10	5.23(1.2)	5.10(1.4)	4.33(1.3)
25	4.27(1.5)	5.0(1.7)	5.10(1.9)
40	6.37(1.2)	6.10(1.1)	5.70(1.3)
		Site G	
10	5.33(0.4)	4.67(0.7)	4.00(0.7)
25	2.67(0.7)	4.0(0.7)	3.00(0.4)
40	3.67(0.8)	3.00(0.7)	4.00(0.5)
		Site S	
10	6.50(0.6)	7.25(0.5)	5.75(0.7)
25	7.50(0.5)	7.50(0.5)	7.75(0.2)
40	7.00(0)	7.00(0.7)	8.00(0)

Table 12 (b). MANOVA table: Soil phosphorus

Source	DF	Type III SS	F	PR > F
Site	2	238.67	113.3	0.0001
Dist	2	0.422	0.10	0.9047
Depth	2	3.089	0.73	0.484
Site*depth	2	25.2	6.95	0.0017
Site*distance	2	0.56	0.15	0.86
Site*distance*depth	8	20.56	1.42	0.20
Error	72	130.6	1.18	

Table 13 (a). Soil potassium concentration (ug/100ml). S.E. in parenthesis

Depth (cm)	Distance (cm)		
	25	75	175
		Site E	
10	10.83(1.3)	25.0(1.8)	14.0(1.3)
25	10.50(1.2)	22.33(3.0)	12.17(1.3)
40	12.67(1.7)	6.83(1.0)	13.33(1.8)
		Site D	
10	55.00(3.8)	17.50(1.2)	24.50(2.2)
25	20.17(1.8)	8.67(1.2)	14.63(3.2)
40	15.50(1.8)	11.50(1.9)	11.17(1.5)
		Site G	
10	20.67(1.4)	19.33(.82)	23.0(1.8)
25	16.33(1.0)	18.7(1.6)	20.0(2.0)
40	16.67(1.1)	16.67(1.2)	20.0(2.6)
		Site S	
10	10.83(.66)	10.13(.35)	10.67(.6)
25	11.27(.58)	10.87(.58)	10.83(.66)
40	9.73(.16)	11.17(.56)	11.2(.43)

Table 13 (b). MANOVA table: soil potassium concentration

Source	DF	TYPE III SS	F	P
Site	2	927.0	3.0	0.053
Distance	2	541.9	1.73	0.177
Depth	2	2266.5	7.3	0.0009
Site*distance	4	2975	4.82	0.0012
Site*depth	4	2311.3	3.74	0.0064
Site*depth*distance	12	3044	1.64	0.87
Error	135	20852	154.5	

Table 14 (a). Percent organic carbon content. S.E. in parenthesis

Depth (cm)	Distance (cm)		
	25	75	175
		Site S	
10	0.558(0.01)	0.548(0.01)	0.526(0.01)
25	0.562(0.02)	0.557(0.02)	0.541(0.02)
40	0.548(0.02)	0.541(0.02)	0.526(0.01)
Mean	0.546	0.555	0.539
		Site G	
10	0.944(0.07)	0.794(0.03)	0.824(0.03)
25	0.804(0.04)	0.784(0.03)	0.867(0.09)
40	0.911(0.09)	0.794(0.02)	0.804(0.03)
Mean	0.886	0.791	0.832
		Site E	
10	0.16(0.04)	0.19(0.02)	0.22(0.02)
25	0.11(0.03)	0.10(0.01)	0.17(0.01)
40	0.08(0.02)	0.09(0.02)	0.11(0.03)
Mean	0.12	0.13	0.17

Table 14 (b). MANOVA table: percent organic carbon contents

Source	DF	Type III SS	F	PR>F
Site	2	1.831	169	0.0001
Distance	2	0.058	2.68	0.074
Depth	2	0.005	0.23	0.794
Site*distance	2	0.03	1.32	0.27
Site*depth	2	0.007	0.35	0.71
Site*dist*depth	8	0.07	0.74	0.66

Plants

Total Kjeldahl nitrogen (TKN)

Nitrogen concentrations in different plant tissues are listed in Table 15 (a) and MANOVA results (15 (b)) are also tabulated. Harvestable or deciduous tissues included leaves, seed. pods and twigs, and unharvested tissues contained bark, wood and roots. There was a highly significant variation among sites and among tissues.

The seed subcompartment was the highest of all tissue types in nitrogen concentration, ranging from 5.7 to 7.6 per cent. There was no clear correlation between seed soil type (sandy or clay) and seed nitrogen contents. Seeds infested with boring insects contained higher concentrations than sound seeds. Mixed seeds (containing sound, infested and seed debris) were least of the seed group and significantly lower than sound seeds. Sound and infested seeds were not significantly different.

The leaf as a subcompartment of the above ground biomass came second to the seed subcompartment in nitrogen content, ranging from 1.9 in high gum yielding tree strains, 2.3 in sand dune bottom and clay soil old leaves, to 4.9 in young leaves on clay. Leaves collected from low gum yielding strains (LYS) had (3.2 per cent) significantly higher nitrogen concentration than (1.9 per cent) those from high gum yielding strains (HYS) ($P < 0.05$). Those from the sand dune bottom site (GBS) were not significantly different from the sand dune top site (GTS), but were similar in their nitrogen concentrations. Sand dune bottom site on sand was moister than dune top site. Their tissue nitrogen contents were similar. Plantations P1 and P2 from site S were 10 years different in age. But site SN, which was a natural plantation in site S, was moister than site SP (artificial plantation in site S) and contained significantly higher N concentration in the leaves. The natural stand N1 grew along a moist site and had new leaf growth which was included in the samples from S site. N2 occupied a dry site and the leaves were at a late stage of growth prior to fall. Seasonal variation in tissue nutrient concentration due to mobile element translocation and leaching losses was well expressed in these observations. N concentration in young leaves was 4.9 per cent and in senescent leaves 2.3 per cent with a 53 per cent difference accounted for by leaching and translocation. The young leaves of the moist site contained significantly higher nitrogen concentration than those of the drier site ($P < .05$).

The wood and bark of branches from clay site S were significantly higher in nitrogen than those from sand site E ($p < 0.05$) (Table 15 (a)). Twigs contained 1.69 ug/g nitrogen and showed no appreciable difference with respect to stand type, i.e. natural or artificial. They were not statistically different from roots or pods, but were significantly different from the rest of the tissue types. Shoot bark and root bark had significantly different concentrations. The root bark was higher in nitrogen than the shoot bark.

Tissue iron concentrations

Plant tissue iron concentration was determined because iron is required in a small amount for the formation and functioning of the nitrogenase enzyme proteins implicated in the process of nitrogen fixation. Its concentration in site D soil was higher than in site E (Table 17 (a)). The plant tissue types analyzed for iron content included leaf, twig, shoot bark, root bark, and bark mixed with wood and root. Iron concentration of leaves was significantly higher than all tissues except root (Table 17 (b)). Root iron also was significantly higher than all tissues except leaves. Bark wood contained significantly more iron than leaf and root, but there was no significant difference between bark and the other tissues. Twigs, shoot bark and root bark were significantly different from leaves and roots, but not from the other tissues.

Mutiple comparisons (Tukey) revealed that there was a significant variation due to tissue and also due to site. Leaves contained significantly greater iron concentration than B+W (bark and wood mixed together), twigs, shoot bark (SB) and root bark. Roots were significantly higher than B+W, twigs, SB and RB. All other comparisons were not significantly different.

Sand dune top and bottom sites were not significantly different, nor were sites D and D2. High yield strains were significantly higher than low yield strains. Singa natural stands of *A. senegal* were significantly higher than plantations of the same species.

Gum samples from the four study sites were analyzed to determine the quantity of nitrogen that escapes through gum harvest. At an average dry weight concentration of 0.29 percent nitrogen (Anderson 1978), gum export from the Sudan removes 101.5 - 162.4 tons of nitrogen each year. The leaf crude protein is a valuable source of fodder for camels and goats in the sahelian agricultural systems. An estimate of leaf crude protein was obtained from each study site (Table 18).

Plant biomass and tree growth

Site E (1) represented the high yield trees of gum acacia (or gum arabic) and E (2) the normal trees (Table 19). E (3) was the bottom of the sand dune site (GBS), and E (4) was the top of the dune site (GTS). The differences in tree height and basal diameter were significantly affected by treatments (MANOVA $P<0.0001$ and 0.0091 for diameter and height measurements respectively). With respect to diameter growth, site E treatments were significantly higher than treatments of sites G, S and D (Tukey's $P< 0.05$). All other treatment comparisons were not significantly different in diameter. Height measurements reflected significant differences for all treatment comparisons except for site S vs. E.

There was an inverse relationship between gum yield and biomass; the varieties low yielding in gum tended to be more productive in biomass than varieties higher yielding in gum.

The low gum yield variety produced higher biomass (i.e. larger girth and height) than the high yield variety. The difference was not statistically significant. The dune bottom site was a trough that received moisture from the top site. The differences in girth and height between the top and bottom sites were not significant. Two areas were chosen in site D based on a difference in understory grass cover density. Girth was higher on site 1 (D) while the height averages were identical.

Tree growth rate was highest at young and middle age, and tapered off at old age, exhibiting the normal sigmoid curve. Tree height growth and age of *Acacia* trees raised on clay soils of site S approximated a straight line. Height and age correlated positively (r=0.976). The highest growth rate on clay was for four year old plants (33.2 cm / yr), which declined to 23.7 cm / yr at age 13 and leveled off at 17 years. Middle- (15 yr) and old-age (21 yr) site G gave higher rates than site S. Site G gave the highest height growth rate of all sites for age 15 and 21 years because of the higher rainfall than site S. The advantage of site G was reflected only in height growth, but not in diameter growth. It is comparable to site S in soil type but had slightly more rainfall. There was a tendency towards an inverse relationship between gum yield and biomass; the varieties low yielding to gum exhibited slightly more height growth than varieties higher yielding in gum. For similar age groups (21 yr) raised on sand (E and D) compared to those on clay, the latter group was significantly faster growing than the former. This was expected because of the higher soil fertility on clay than on sand and the higher rainfall. The higher density of trees on site S, as expected, slowed down tree growth compared to site G. A plantation 15 years old on site S would fall in between 13 and 17 with a growth rate of 21.0 cm / year. The 15-year plantation of G was 24.1 (Table 19). Dubeibat site had a lower growth rate on average than Elobeid site. The sand dune top site was a particularly poor site, deficient in moisture and nutrients and is expected to yield a poor crop.

More measurements were taken from site E than any other site. These included high and low gum yielding strains, and dune top and bottom sites. Low gum yielding trees were taller and had bigger girth than the high yield group. The dune bottom site carried taller trees of larger diameter than the dune top site. The growth rates of the bottom site trees rivaled that of the low gum yield trees. The dune bottom site was a trough that received moisture from the dune top site. The differences in girth and height between top and bottom sites were not significant. Two areas were chosen in site D based on a difference in understory grass cover density. Girth was greater on site 1 (D) while the height averages were identical.

No significant differences among sites were detected using seed size variations. The data were also separated according to soil types (Elobeid and Dubeibat sands against Singa and Algedaref clays). Again the difference with respect to soil type was insignificant. On the same type of soil, however, there seems to be a weak trend towards larger seed number per gram i.e. smaller seed with higher rainfall (Table 24). This might indicate adaptation of the tree species to dry conditions. Indeed its distribution ceases at higher isohyets. Table 19 summarizes the tree growth statistics.

Soil conditions under cultivation and under trees of various ages

Ideally this experiment should have included a treatment in which soil without trees is compared for nitrogen and carbon, but this option was not included as an oversight. It was found (Table 21) that 20 year old *Acacia* stands had an appreciable effect on soil nitrogen and soil pH, while the concentration of carbon was greater under cultivation. The young stand of *Acacia* accumulated a mean of 241 ug/g nitrogen in the whole soil layer compared to 382 under the old stand and 229 under cultivation. The top soil is important as it is the layer occupied by grass and crop roots. In that layer the nitrogen level under the old stand was double that of the young stand and 2.7 times that under cultivation. This significant variation particularly in the top soil layer revealed the importance of tree age in nitrogen accumulation in agroforestry systems. It also revealed the importance of maintaining a tree cover on farms to protect the soil against erosion by wind for sandy soil and surface or sheet erosion by water in clay soil areas.

Carbon concentration in the old stand was about 10 times more than the young stand. In cultivated soil, though, carbon concentration was about that of the old stand. This also showed that the older the stand of trees, the more accumulated nitrogen and carbon it will have in the soil (Table 21).

DISCUSSION

Climate

The analysis of the available data suggested that the four study sites could be divided into two main types: S and G sites had more rainfall and higher mean maximum temperature than sites E and D. Essentially sites S and G were similar in all their responses to the analysis and therefore they form a fairly uniform climatic environment. Site E and D were significantly different from S and G, and can be treated as climatically similar. They were similar in their maximum and minimum temperature and radiation due to close proximity. Site D was significantly more humid than E and had less sunshine because of more cloud cover, but similar exposure to wind. The two sites were about 70 km apart, E more northerly toward the desert and D more southerly and more protected by vegetation from evaporation and wind speed effects. It is close to the southern edge of the sandy soil of the semidesert which grades imperceptably into the savanna. The *Acacia* species range covers both sites and therefore from the tree distribution stand point the two sites are phytogeographically not different. For the purpose of this study these two sites were considered sufficiently similar and warrant similar treatment.

It was observed, however, that reduction in the mean annual rainfall was more on the sandy, low rainfall sites than on the clay sites. The impact of rainfall reduction on biotic and edaphic factors of the sahelian environment was catastrophic.

Soils: Soil pH

Acacia senegal thrives well on both acid and alkaline soils (Smith 1949), but it certainly does better in neutral E site soil than it does in the more alkaline sites S and G or the more acidic site D, despite the higher rainfall in site D. This might indicate that plants receiving an optimum rainfall grow better on neutral soil than on acid or alkaline soil. Indeed the optimum plant growth pH is 6.8 This is supported by the faster growth rate and higher gum yield in site E than other sites, in addition to the fact that E is located latitudinally central to the range of the species which might indicate optimum growth conditions for the species. Soil pH affects the chemical environment of plants and animals in such a way that nutrient availability and plant and animal responses are immediately affected by it (Melsted and Peck 1973). Plants in nature will compete best if the soil has optimum pH for their growth. Some species have a narrow range of tolerance to soil reaction, and may be outcompeted if the pH changes unfavorably. *A. senegal* distribution on near neutral sandy soil was better than on acid sands or alkaline clay soils. Elamin (1976) and Habish (1970) supported this.

FitzPatrick (1980) held that the lowest pH value occurs in the surface horizons in association with acid deposition products of organic matter. Acid forming factors include organic and inorganic acids formed following decomposition. This observation was supported at all sites except D where the top layer was slightly more alkaline than the layers below it, possibly as an effect of leaf litter accumulation and addition of base cations in oxic condition. Annual rainfall at site D (335 mm) was more than that of E (263 mm) which could cause the drop in pH in D by leaching of base-forming cations from sandy soils that predominated in both sites. It was also found that iron concentration in site D was higher than in site E. Upon hydrolysis the ferrous ions enhance acidity, as it reacts with the OH group, and sets hydrogen ions free.

Because of the low organic matter and no clay content of sandy soil (95 percent sand) of site D, soil pH tends to be acidic, with low available nutrient cations, which leach easily from sandy soil. The higher amount of rainfall of site D has caused more leaching of basic cations than in site E. Carbonic acid is the simplest and most widely found acid: it assists in dissolving and leaching of base cations e.g. calcium, magnesium, potassium and sodium by lowering soil solution pH.

Brady (1990) stated that the availability of nitrogen, sulfur and molybdenum is somewhat restricted at low pH, whereas that of phosphorus is best at moderate pH. Molybdenum has been implicated in nodulation of legume plants and its availability enhances nodule formation. Most plants grow best in soil with a pH 6.5-6.8, although some thrive best on acid soil of pH 4.5-5.5. Bacteria and Actinomycetes function best under intermediate and high pH conditions. Tree age was not old enough to affect a significant change in soil pH due to leaf litter accumulation. Organic matter is low because of the low plant cover resulting from limited rainfall and low soil fertility. Soil profile development was hampered by low rainfall and subsequently low vegetation cover in the sandy entisol (psamments) typical of semi-arid zones of Africa.

Soluble salts accumulate in soils of semiarid regions in significant proportions because the annual precipitation is insufficient to leach the soil. In such soils absorbed calcium and magnesium dominate the exchange complex, where 2:1 type silicate clays are prominant (Brady 1990). Sites G and S soils are classified as vertisols which are dark cracking soils with a high content of fine sized clays of montmorillonitic composition (Bunting and Lea 1962).

Clay soils are expected to be alkaline as they contained higher levels of exchangable base-forming cations e.g. potassium, calcium, sodium and magnesium, and had high cation exchange capacity. Weathering processes are more pronounced under higher rainfall on clay minerals resulting in the release of these cations. In arid regions leaching water does not remove most of the base-forming cations as they are weathered from soil minerals (Brady 1990). Lack of extensive leaching leaves the level of the base forming cations fairly high. Consequently the saturation percentage remained high.

Sandy soils had less rainfall and their mineralogical composition does not yield many base-forming cations. Therefore they were expected to be acidic or near-neutral in reaction. Organic and inorganic acids formed following decomposition cause a drop in soil reaction. Much stronger acids are formed as a product of plant decay and exudates of plant roots. Inorganic acids are also formed by organic decay and microbial action which might explain the acidity at site D. The small amount of rain that these soils received could cause leaching because of the ease with which water dissolved salts and moved down the sandy soil profile; whereas in clay soils, water movement was hindered due to expansion following wetting of clay minerals.

There was a slight but consistent increase in pH with distance from tree trunk at all sites particularly at depths 10 cm and 25 cm and distance 175 cm. That was in agreement with a previous observation that leaves on tree crowns were concentrated more on the outer branches than inside the crown. When leaves fell, their effect on soil reaction was concentrated more at distance 175 cm than closer to the trunk. Acidity increased down the profile in sandy soils because the effect of leaf litter was concentrated in the top soil layer. Alkalinity increased with depth in clay soil due to leaching of base forming cations with rain water down the soil profile. Ca, Mg and P become less available in acid soil, whereas Fe, Mn, Zn, and B become less available above pH 7.

This wide range of soil reaction is expected to affect the nitrogen dynamics. Indeed FitzPatrick (1980) reported that low pH is unfavorable to the bacteria involved in the nitrogen cycle. Habish (1970) found that pH 6.5-7.0 was optimum for nodulation and that 8.5-9.0 caused reduction in effective nodulation in a nursery experiment.

Dark soils are usually high in organic matter and hold larger amounts of water. Clay sites are flat and black in color and therefore retain a high amount of heat: whereas, sand soil is pale yellow and undulating, hence retaining a lower quantity of heat than clay. The clay soil profile exhibited little or no soil development. Stratified profiles did not develop because of the seasonal cracking and consequent circulation of materials. Montmorillonite causes shrinkage in the dry season and swelling in the wet season. Cation exchange capacity was demonstrated by Brady (1990) to increase with pH, which tends to relate to rainfall. Sites G (570 mm) and S (521 mm) had more rainfall than sites E and D. Recycling of nutrients from deep soil by means of deep rooted plants brings cations to the soil surface and accounts for the relatively high pH of semiarid soils.

Soil nitrogen

Nitrogen is probably the most deficient vital element in arid regions (Dregne 1968; Charley 1972). It is the element that plants require in greatest quantity. It is assimilated by plants as nitrates or as ammonium, but mostly in the former, which is the main form of available nitrogen (Dahnke and Vasey 1973), and the form that accumulates in the soil. The importance of nitrogen in savanna ecosystem stems from the fact that it is always in short supply and the biological processes that influence it are seasonally restricted. Bate (1981) held that seasonal aridity leads to annual cessation of nitrogen cycling in the savanna ecosystem. Indeed, nitrogen input from rain and that transported by dust or '*haboob*' are active only during and at the begining of the rainy season respectively. Primary production, decomposition and symbiotic nitrogen fixation are processes greatly influenced by and essential to the nitrogen dynamics. During the dry season plants and microorganisms are dormant. Skujins (1981) argued that the climatic pattern is the major factor limiting biological activities and nitrogen availability in deserts and arid regions. It is now well established (Kaiser 1983) that under tropical conditions primary productivity depends mainly on the mineralization of organic nitrogen. N in the soil is present mostly in very complex organic form that was not available to plants. It becomes slowly available through microbial decomposition. Nitrates are very soluble in water and can easily be leached or accumulated depending on the total annual rainfall of the site. Nitrates are generally subject to leaching, denitrification or immobilization by soil microorganisms.

Chemoheterotrophic organisms decompose organic residues producing ammonia which can be oxidised to nitrites and then nitrates. Plant uptake of nitrogen during early growth is highly correlated with NO3-N in the soil.

It was observed that lower soil layers in some instances had a tendency to contain higher nitrogen than upper layers (Table 6). This is in agreement with Baethgen and Alley (1987) that more fixed or nonexchangeable ammonium nitrogen and nitrate nitrogen in savanna according to Kaiser (1983) in the lower horizon in cultivated Virginia soils was a means of nitrogen conservation for later release.

The clay soil's higher nitrogen concentrations were due to the fact that organic matter is produced and accumulates more in clay soils than sandy soils because clay soil is more fertile and more productive. Higher precipitation on sites S and G encourages soil and plant development. Ammonium cations adsorb to the cation exchange sites of clay but leach easily from sand. Site D has more rainfall than E, and G more than S. This may explain the differences between sites in similar soil types. Soil mineral nitrogen concentration in clay was expectedly higher than that in sand because the clay exchange sites hold ammonium ions, whereas sandy soil has few or no exchange sites, depending on how little clay it contains. In addition the biomass on clay is usually higher and results in a higher storage pool in clay. The bulk of nitrogeneous material is organic and hence unavailable for plants. Microbial decomposition of these compounds and conversion to mineral forms slowly makes it available for plant growth. The rate of mineralization is believed to be positively correlated with the total nitrogen content of soil, which supports my finding.

The significance of legume plants in arid region soil nitrogen dynamics has been well established. Rundel et al. (1982) maintained that desert and semidesert plant communities have very low productivity due to low soil moisture, low soil nutrients and high heat, except where the ecosystem is dominated by woody legumes. Nitrogen in these systems is constantly being recycled from soil to plants and back to the soil through litter and decomposition products. The variations with soil depth and distance from tree trunk were expected. The higher concentration in the top soil layer exhibited by all site profiles is due to the leaf litter deposition and various other wet and dry depositions and subsequent nitrification which is concentrated on the top soil layer. This is supported by Rundel et al. (1982) in their investigation of a *Prosopis* woodland in the Sonoran desert, and Gerakis and Tsangerakis (1970) with *A. senegal* in Sudan.

Oxidation of ammonium ions to nitrates occurs at 27-32 C (80-90 F) and is negligible at 10 C. Nitrate ions, being soluble, are present in the soil solution and are easily leached. Leaching however is not a serious ecological problem in the semi arid tropics because of the rainfall limitation. The major loss of nitrogen pool is caused by ammonia volatilization and some denitrification. Ammonium ions adsorb to the clay exchange sites and become gradually oxidised to nitrates and then leached. In savanna ecosystems seasonal aridity leads to cessation of nitrogen cycling. Restoration of the cycle is initiated by increase of atmospheric humidity , increase in soil moisture, and subsequent carbon fixation in plants. A savanna ecosystem is adapted to low nitrogen level. The total nitrogen is related to annual rainfall. Nitrogen from rainfall varies between 2-5 kg N/ha/yr. That from symbiotic fixation reaches 30 kg N/ha/yr. Losses by leaching, fire and animal export are generally small.

Climatic patterns of low rainfall and high heat and insolation are limiting factors for biological activities in the arid and semi arid regions. This is because aridity commonly limits nitrogen availability. Most plants and microorganisms are dormant during the dry season; during the short wet periods all biological activities including nitrogen mineralization and fixation processes exhibit high rates.

Plant litter is less than in most other biomes and many nitrogen transformation processes in the soil may be carbon limited. The major biological nitrogen input may be through legume-rhizobium associations in the rhizosphere or by photoautotrophic fixation. Major pathways of losses are denitrification followed by ammonium volatilization. Physical input by precipitation or by particulate deposition may be important to maintain a delicate nitrogen balance. Leaching may be negligible and erosion of sandy soil redistributes nitrogen within the ecosystem.

Effect of cultivation and trees on soil condition

Bush fallow increased soil nitrogen, carbon and pH, particularly on the top soil layer mostly utilized by crop roots. The longer the fallow period, the higher the soil nutrient levels and more crop production. Cultivation lead to reduction in organic carbon and nitrogen. Such a reduction was more pronounced on the top soil layer where annual crop roots were confined than lower depths. This was supported by Bate (1981) who demonstrated that nutrients in vegetation and soil increased during the fallow period. Garcia-Moya and McKell (1970) found that desert shrubs differed considerably and showed no clear relationship to legume or non legume classification in their study in the Mojave desert. They found that *Cassia* and *Acacia* nitrogen concentrations were similar to those of other non-leguminous shrubs. Yet mounting evidence suggests that the legume tree fallow period allows accumulation of nitrates in the top soil layer as the leaf litter is richer in nitrogen than other species (Allen and Allen 1981; Habish 1970 and this work).

Nitrate concentration was found to be more on the top soil than down the profile, which is the layer that is richer in organic carbon and where dry and wet deposition and microbial action concentrated. It is also the layer that is easily eroded by water and wind, particularly in sandy soil for lack of cohesion in comparison to clay soil. Russell (1966) suggested that nitrates are produced more rapidly at the commencement of the rainy season and are more rapidly formed in soils subjected to alternate drying and wetting. Another reason for the concentration of nitrates on the top soil layer is the upward movement of water in which they dissolve as the water evaporates in the dry and hot season. Nitrates, being very soluble in water, may accumulate in arid land soils for lack of sufficient rain to leach them. Chemoheterotrophs decay organic matter producing ammonia which can be oxidized to nitrites and eventually to nitrates by soil bacteria.

Phosphorus and potassium

Phosphorus is included in this study as it affects general plant and microbial performance. It is essential in the ATP energy transfer processes and for protein synthesis. The importance of phosphorus in ecosystem dynamics is that it enhances biomass production and rates of microbial transformations. Both types of sand and clay soil had low phosphorus concentrations which were higher in site S than G. These concentrations did not seem to be affected by soil type, vegetation or rainfall as there was no clear trend. Cole and Heil (1981) maintained that close linkages exist between phosphorus and nitrogen cycling. Soils generally have low phosphorus concentrations because phosphorus is fixed by Fe, Al and Mn in acid soils, and by Ca and Mg in clay soils. Brady (1990) suggested that clay reduces phosphate availability whereas organic matter increases it.

Potassium is important in regulating stomatal opening, water uptake, and for protein and starch syntheses. It is also important in grain formation and tuber development. Crop removal of potassium is high, equalling that of nitrogen (Brady 1990). Relatively high proportions of it are held in the primary structures of feldspar and mica which are resistant to weathering, and it is, therefore , unavailable to plants.

Amount and distribution of plant accumulated nitrogen (TKN)

An appreciation of the phenology of *A. senegal* and a perception of external signals and seasonal impulses that triggered plant phenology were important in understanding the nutrient dynamics of this agroforestry system. The species' phenology has been described (Obeid and Seif El Din 1970, Sahni 1969. Andrews 1948). A summary of the phenology of *A. senegal* has been outlined in the introductory section of this study. The dynamic or 'harvested' tissues in this system included leaves, seed and twigs, which implied that they were naturally shed at a specific time and under climate induced conditions. Nodules were also included in the dynamic tissues as they degenerated following leaf fall. The nature of the nodule dynamics differed from that of seed and foliage in that nodule nutrient content was largely transported into the plant system prior to degeneration and shed. Leaves followed a similar trend; whereas seeds were shed with their nutrients unaffected by translocation. Young roots were thought to naturally degenerate and their nutrients added to the pool.

The spatial distribution of nitrogen was influenced by the canopy characteristics; horizontally the higher concentration was under the canopy and generally at the edge where the leaves tended to concentrate, while there was a decrease towards the outer edge of the plant. Vertically the distribution is affected by many factors including soil type, climatic conditions and tree health, size and age.

Temporally, leaf shed was a continuous process; the rate of which was slow and unnoticeable throughout the growing season. Only when the rainy season ended did the rate of defoliation become accelerated until the trees were bare of leaves. At that time the soil was drying out and microbes declined in number and activity. Leaf shed and microbiological activities were out of phase in the savanna, and it seemed that microbial decomposition was delayed until leaf litter was acted upon by herbivores and/or excessively dried by high temperature before the commencement of the following rainy season. Resident herbivores lacked green food material during the dry season, and were faced with the option of migration or reliance on dry grass, foliage and seeds.

Of all the tissues examined, seeds, leaves and twigs contained the highest concentration of nitrogen. Seeds were produced in large quantities almost every other year, but they represented a conservative pool in the sense that they remained in the soil seed bank protected from decomposition processes by their cellulosic seed coat and awaited favorable germination conditions. Seed nitrogen content is thought to sustain each plant for its initial growth (Harper and Obeid 1967). Not all seed that reached the soil germinated. A germination study with *A. senegal* revealed that under optimum laboratory conditions only 65 per cent germination was achieved even when the seeds were soaked in water as a pre-sowing treatment. Under natural conditions of low rainfall only low germination could be achieved. Obeid and Seif El Din (1970) have shown that low germination takes place in sandy soil under a simulated normal rainfall regime, and even lower under clay soil. It is also well known that seed stored for a long time lose viability and become incorporated in the soil nutrient pool. It is rare to observe complete germination even in such highly managed ecosystems as arable fields. An important contribution to the soil nitrogen pool comes from seed. Insect infestation renders seed ungerminable. Infested seed and seed that are naturally abortive contribute to the soil pool.

Acacia leaves are a mesomorphic type that shed in response to drought conditions. In moist local sites the trees remained greener longer than on a slope or flat dry site and contained higher nitrogen concentration. Menaut (1983) maintained that savanna leaves are only productive for a short period (June-October), less material is used in their formation and they are therefore more efficient producers. He also suggested that when savanna plants shed leaves they also shed part of the previous year's shoot and that accounts for the general slowness of growth. This is in agreement with my findings; I observed that twigs were third in nitrogen concentration, exceeded only by seeds and leaves. They were a dynamic tissue of this system in the sense that they were shed (also supported by Menaut (1983)).

Young leaves contained higher nitrogen concentration than old ones. Goh and Kee (1978) suggested that plant growth limited by drought and plants damaged by pests or disease may accumulate more nitrogen since protein synthesis is inhibited. Jones and Eck (1973) and Tinker (1978) maintained that nitrogen concentration is at a maximum during early growth. and as the season progresses and dry matter increases, N concentration in the whole plant and in the vegetative parts typically declines. This supports my finding of increased nitrogen concentration in trees grown on moist sites, retaining young leaves longer than on dry sites. Leaf litter provides an easily measured compartment for the input of organic matter and associated nutrients to the soil and was believed to constitute the major route for the return of nutrients to the soil. Monk and Day (1985) held that nutrient concentrations generally ranked leaves highest and wood lowest with bark, roots and twigs intermediate, and that seasonal changes in nutrient levels were more dramatic in leaves. They did not include seed in their study.

Harvested plant parts contain higher amounts of nitrogen than non-harvested parts (Goh and Haynes 1986). Nitrogen as a mobile element gets translocated prior to leaf shed and becomes part of a temporary storage pool until the new growing season. It is interesting to note that leaves of high gum yield trees contained lower nitrogen than low gum yield trees. Some nitrogen is used in the manufacture of gum. Gum nitrogen is lost from the system.

The root bark nitrogen content was higher than that of shoot bark. The latter hardly participates in the systems dynamics as it is fire resistant, difficult to slough off the tree trunk and is water proof. The bark thickness varies between 10.4-32.5 mm and is thicker down the trunk. Savanna trees have well developed root systems; most of the root biomass is confined to the top 30-50 cm (White 1976). Most of the roots are lateral and flattened out in order to provide the best chance to absorb water from the upper soil layer after a light rain (Rutherford 1980). They have developed a thick, hard corky or woody bark to protect them against drought, fire and high temperature and strong insulation. The rate of root decomposition in grass and shrub savanna were 52 and 68 per cent per year (Bate 1983). The rate is certainly not uniform throughout the year. It was reported that 33 per cent of the roots disappear between October and November, 27 per cent December and January, and no roots were decomposed during the summer months. Roots with thick bark allow plants to survive drought and fire. Isolated *Acacia* trees have roots spread to more than 7X their crown diameter, as a response to shortage of water and possibly nutrients, growing disproportionately to the areal part. At the end of the growing season water and nutrient reserves become stored in the root through absorption and translocation from the shoot. With such a relatively large reserve of water and nutrients, the trees can grow as soon as they receive an impulse of increased atmospheric humidity.

Organic matter

Leaf litter is shed in response to drying conditions at the end of the growing season when soil moisture and microbial activity start to decline. Grasses are faster to dry than trees because of the nature of their shallow root systems and the fact that soil dries from the top downwards. Leaf litter is then added to the already dry grass layer and becomes fuel for seasonal savanna fires or gets consumed by herbivores. Minor quantities get buried in the sand or caught in clay cracks before they are closed once again when soil moisture increases. The clay soil carbon therefore did not exhibit marked variation down the profile. The proportion that was consumed by herbivores would partly be returned to the soil as excrement. The assimilated part was likely to be exported outside the system. Near human settlement livestock excrement was largely removed from cycling for local usages e.g. as a binder in brick-making, as a termite and water proofing material on grass houses or as carbon source for the emerging local industry of biogas. Litter decomposition at the soil air interface is probably limited by soil moisture. Bate (1983) implied that soil moisture influences microbial conversion of organic matter to mineral nitrogen. Kaiser (1983) held that the major part of the food resource for soil organisms in the savanna is composed of grass residues, of which 15-25 per cent of it consists of shrub leaves.

The amount of nitrogen available to plants is a function of the rate at which organic nitrogen is mineralized in the soil by microorganisms. Microbial action varies between and within seasons depending on climatic conditions which impose seasonal limitations on productivity. Root decomposition constitutes the second major process whereby organic matter is made available to microbes.

Tree growth and plant biomass

The high and low gum yield varieties experiment was well looked after by way of regular weeding to reduce competition from grass. The higher growth rate the trees exhibited reflected the preferential treatment they received. The high gum trees yielded lower timber than low gum trees. Gum and wood production were inversely correlated. This could be genetic or could also reflect the fact that more energy was expended on gum production, which impacted wood yield.

Trees grown in the sand dune bottom site had larger volume than the dune top site ones because water and nutrients accumulated in the trough. In addition the dune bottom is protected from wind and excessive heat and sunlight. Site D had two plantations identical in height but not in girth. They receive slightly more rainfall than site E, but less attention. Their locality is a place where livestock concentrated in the rainy season. Excessive grazing could be the reason for the lower height than site E.

Sites S and G received more rain than sites E and D. This was clearly reflected in their growth rates; at age 17, site S growth rate rivaled that of site E at 21 years. Leaf litter production, presumably linear with biomass production in both sites, is expected to be more on high rainfall sites than low. The regular stocking of plantations for trees spaced at 4m x 4m is 625 trees per hectare. Site S had much higher stocking because it was regenerated by seeding (direct sowing) using a seed drill pulled by a tractor. The operation was unnecessarily costly in seed expenditure and more importantly in excessive competition among plants, which was clearly reflected in low per-tree biomass production, i.e low growth rate. It is expected that root competition is very high in site S, with consequent reduction in nodule numbers and reduced nitrogen input to the system. Site SN was occupied by a naturally regenerated stand of trees. Natural stocking in site SN (natural, moist) was 277, significantly lower than the artificial regeneration density of 625 trees per hectare. Growth rate was not calculated for this stand as the age was unknown.

Table 15 (a). Total plant tissue nitrogen concentration (TKN). S.E. in parenthesis

Site	Treatment	Tissue	TKN	N
D	Old stand	Leaf	2.67(0.1)	10
D	Young stand	Leaf	2.71(0.1)	10
D	Sound	Pods	2.05(0.1)	5
D	Infested	Seed	7.65(0.1)	8
D	Mixed	Seed	5.79(0.1)	8
D	Sound	Seed	6.79(0.1)	5
E	GBS	Leaf	2.32(0.1)	10
E	GTS	Leaf	2.18(0.1)	10
E	HYS	B+W	0.14(0.01)	10
E	HYS	Leaf	1.94(0.2)	15
E	LYS	Leaf	3.20(0.2)	15
G	Natural stand	B+W	0.92(0.1)	10
S	Sound	Pod	1.43(0.1)	10
S	Infested	Seed	6.34(0.2)	5
S	Mixed	Seed	6.19(0.1)	10
S	Sound	Seed	6.20(0.1)	10
S	Natural	B+W	1.30(0.1)	10
S	Natural	Leaf	4.91(0.1)	10
S	Natural	Root	1.32(0.1)	10
S	Natural	Twigs	1.65(0.1)	12
S	Natural 2	Leaf	2.32(0.1)	10
S	Plantings	B+W	1.12(0.1)	10
S	Plantings	Leaf	2.10(0.1)	10
S	Plantings	Root	1.19(0.19)	20
S	Plantings	Shoot bark	0.03(0.01)	10
S	Plantings	Twig	1.73(0.1)	20
S	Plantings 2	B+W	1.16(0.1)	9
S	Plantings 2	Leaf	2.53(0.1)	10

LYS, HYS, GBS, and GTS were defined in the text. B+W=Mixed Bark and Wood.

Table 15 (b). MANOVA table. Dependent variable: TKN

Source	DF	Type III SS	M.S.	F	P
Site	11	53.58	4.87	32.80	0.0001
Tissue	7	382.81	54.69	368.2	0.0
Site*Tissue	8	38.3	4.79	32.26	0.0001
Error	260	38.6	0.15		

Table 16. Total plant tissue phosphorus concentration (TP). S.E. in parenthesis

Site	Treatment	Tissue	TP	Samples
D	Old stand	Leaf	0.09(0.003)	10
D	Young stand	Leaf	0.08(0.005)	10
D	Sound	Pods	0.008(0.003)	10
D	Infested	Seed	0.11(0.01)	5
D	Mixed	Seed	0.45(0.01)	10
D	Sound	Seed	0.18(0.02)	5
E	GBS	Leaf	0.07(0.004)	10
E	GTS	Leaf	0.06(0.002)	10
E	HYS	Leaf	0.06(0.001)	15
E	LYS	Leaf	0.07(0.003)	10
E	HYS	B+W	0.04(0.002)	15
G	Planting	B+W	0.07(0.003)	10
S	Sound	Pod	0.2(0.01)	10
S	Infested	Seed	0.23(0.02)	5
S	Mixed	Seed	0.29(0.01)	10
S	Sound	Seed	0.07(0.01)	5
S	Natural	B+W	0.07(0.009)	10
S	Natural	Leaf	0.23(0.01)	10
S	Natural	Root	0.04(0.004)	10
S	Natural	Twigs	0.13(0.01)	12
S	Plantings	Leaf	0.1(0.01)	6
S	Plantings	Root	0.04(0.002)	10

LYS, HYS, GBS, and GTS were defined in the text. B+W=Mixed Bark and Wood.

Table 17 (a). Plant tissue iron contents

Treatment	Tissue					
	Leaf	Twig	B+W	Root	Bark Shoot	Root
D	.088(.01)					
D2	.1(.01)					
GBS	.4(.01)					
GTS	.1(.01)					
HYS	.09(.01)					
LYS	.01(.003)					
SN	.10 (0.01)	.04 (0.004)	.02 (0.002)	.11 (0.01)		
SP	.12 (0.01)	.025 (0.001)	.012 (0.001)	.06 (0.01)	.02 (0.001)	.015 (0.0005)
GP			.02(.002)			

Table 17 (b). MANOVA table. Dependent variable: Total iron content in plant tissues

Source	DF	Type 3 SS	M.S.	F	PR>F
Site	8	0.1309	0.016	13.23	0.0001
Tissue	5	0.1692	0.0338	27.35	0.0001
Site*Tissue	4	0.055	0.0139	11.21	0.0001
Error	239	0.2956	0.0012		

Table 18. Gum and leaf protein analysis

Site	Material	Protein %	N %	Moisture %
Elobeid	Gum	0.49	0.08	8.67
	Leaves	22.55		
Dubeibat	Gum	0.51	0.09	8.61
	Leaves	20.71		
Singa	Gum	0.66	0.11	8.67
	Leaves	27.06		
Gedaref	Gum	0.59	0.09	8.44
	Leaves	24.19		

Table 19. Tree growth parameters. S.E. in parenthesis

Site	Variable	Age (yr)	Girth (cm)	Height (cm)	Stocking (#/ha)	Growth (cm/yr)
E	High yield	21	50.3(3.2)	386(19.99)	625	18.4
E	Low yield	21	51.8(4.1)	411(19.45)	625	19.3
E	Dune bottom	21	42.9(2.88)	395(16.60)	625	18.8
E	Dune top	21	39.4(2.49)	314(17.65)	625	14.9
D	Site 1	21	37.7(1.55)	343(16.91)	625	15.4
D	Site 2	21	33.4(2.83)	323(14.34)	625	15.4
G	Plantation	15	35.0(2.19)	375(11.99)	625	24.1
G	Plantation	21	44.3	493(18.29)	625	25.8
S	Plantation	4	11.3	133	2010	33.2
S	Plantation	17	27.6(1.37)	324(9.87)	2190	19.2
S	Plantation	13	29.4(1.37)	316(9.87)	2300	23.7
S	Natural, moist	-	53.4(4.2)	425(19.60)	277	-
S	Natural, dry	-	44.6(2.72)	466.4(20.93)	-	-

Table 20. Soil nutrient concentration under high and low gum trees

Gum yield	Distance cm	Depth cm	N %	Fe %	K %
High	25	10	.82	.63	.29
		25	.77	.35	.15
		40	.67	.36	.13
	75	10	.76	.49	.14
		25	.78	.62	.29
		40	.95	.27	.18
	175	10	.80	.33	.12
		25	.75	.52	.05
		40	.62	.49	.19
Low	25	10	.78	.52	.06
		25	.79	.61	.35
		40	1.03	.65	.15
	75	10	.55	.38	.07
		25	.77	.45	.15
		40	.72	.26	.11
	175	10	.73	.45	.12
		25	.69	.17	.08
		40	.62	.38	.08

Table 21. Effects of trees and cultivation on soil conditions

Site	Soil (cm)	pH	Nitrogen (ug/g)	Carbon (ug/g)
Young stand	0-10	6.7	375	0.038
(5-10 yr)	0-40	6.7	182	0.114
	40-90	6.8	168	0.082
mean		6.7	241	0.078
S.E.		0.06	115	0.038
Old stand	0-10	6.9	770	0.686
(15-20 yr)	10-60	7.3	196	0.043
	60-100	7.4	179	0.400
mean		7.2	381.7	0.38
S.E.		0.26	336.4	0.32
Cultivation	0-10	6.9	280	0.215
(3 yr)	10-30	6.8	210	0.975
	30-100	6.0	196	0.072
mean		6.6	228.7	0.42
S.E.		0.49	45.0	0.48

Summary and conclusions

The climatic elements investigated were grouped into heat [(solar radiation intensity and duration and temperature (max. and min.)], moisture (precipitation and evaporation, evapotranspiration and humidity) and wind (speed and direction). No one group of elements could be singled out as the major climatic factor affecting the systems studied. However, moisture seems to be the most important since it is the limiting element which controls biomass production and soil development and nutrient cycling in unison with heat, which is not limiting in the savanna ecosystems.

Although the general climate of the ASAS is dry tropical continental, local variations among study sites and even microsites within each locality proved sufficiently different, and coupled with variation in soil types have produced a wide range of biomass and nutrient concentrations.

The ASAS is practiced on clay and sand soils. Despite the higher rainfall on clay sites, the better soil moisture relation on sand yielded trees more productive in biomass. Clay in the nursery soil mixture produced more biomass and more nitrogen when the soil moisture difference was nullified by similar watering treatment and more time allowed for clay to absorb it.

The two sandy soil locations had a pH, nutrient and a texture gradient which affected biomass production and the system's dynamics. The pH drop was caused by leaching of basic cations on all soils. The clay soil was higher in pH, carbon, potassium, phosphorus and nitrogen than sand. Nutrient concentration in the top soil layer correlated positively with the mean annual rainfall.

Tissue nitrogen concentrations varied between site and tissue. Deciduous tissues e.g. seed, leaf and twig contained higher concentrations than non harvestable tissues. Due to translocation of nitrogen from senescent leaves the element concentration was lower than in young leaves.

Harvestable young tissues seem to offer a reasonable possibility of use as organic manure with crops. The young age of tissues coincide with the time of high demand of crops for nitrogen.

Trees on moist sites yielded nitrogen rich leaves later in the season when dry site trees shed old leaves. Moist sites could be used for raising *Acacia senegal* plantations managed specifically for foliage production at high spacing to allow for bigger crowns.

Agriculture and possibly soil erosion are the main removers of nitrogen from the system. The longer the trees fallow, the more soil stability and fertility are generated. Alley cropping is an attractive agroforestry system recommended in situations where the fallow is not long enough. Leaf shed and decomposer activity are temporally out of phase.

CHAPTER THREE

THE EFFECTS OF PLANT-SOIL-ENVIRONMENT INTERACTIONS ON NODULATION, BIOMASS AND GUM YIELD

INTRODUCTION

Acacia senegal interactions with soil and environment have received little attention. At the community level the species is spatially distributed over a wide geographic range with contrasting soil types of varied physical and chemical characteristics and over a climatic gradient. The selected afforestation centers are separated by a vast expanse of land of various soil types, large distances and effective geographic barriers. Such combinations of factors should provide a basis for *A. senegal* population evolution which might lead to genetically variable attributes controlling nitrogen input, biomass production and gum yield. It was desirable to know whether *A. senegal* populations have developed genetic variability. The variable soil and climate may also have nurtured different strains of *Rhizobium* or a different phenotype of the same strain.

At the population level a tree plantation study revealed that high plant density impacted biomass production. The effect of competition on nodulation and nitrogen fixation in the ASAS has not been investigated previously, nor has the effect of reduced photoperiod and natural or induced leaf shed on nodule ultrastructure and nitrogen fixation rate. It was expected that leaf shed would result in low or no energy supply to the nodules and would impact the diazotrophic machinery and processes.

Since nitrogen fixation is genetically controlled, some combinations of soil type, seed source and environment were assumed to yield higher rates of nitrogen fixation than others. It was expected that certain combinations were highly efficient in nitrogen fixation while other combinations were essentially non-functional. This hypothesis is supported by Hall et al. (1979) in their study with *Alnus glutinosa* symbioses with *Frankia* spp. inocula which indicated significant host genotype/Actinomycete strain interactions. A primary objective of this study was to identify and locate a naturally occuring host/microbe combination and soil type that produce nitrogen at a higher rate than other combinations within the *A. senegal* range in the Sudan. Such combinations needed to be identified and located. Selected superior strains of microbe extracted from these combinations were used to inoculate seedlings raised on sterile soil with the object of obtaining uniformly high rates of nitrogen fixation.

This chapter describes experimental manipulations conducted to test the species performance as it interacted with the biotic and abiotic environments at various levels with the object of obtaining a better understanding of the system. A specific objective of this research also included a study of the effect of competition on nodule number and biomass among *A. senegal* seedlings. The chapter also includes an attempt to determine the rate of nitrogen fixation using acetylene reduction assay, and also a description of the nodule ultrastructure utilizing electron microscopy. The aim was to study the effect of induced reduction of photoperiod on nitrogen fixation and nodule anatomy. The effects of soil source, seed type and plant density on nodulation and biomass were tested and promising combinations were used with the objective of obtaining high yielding strains of *Rhizobium* to inoculate seedlings.

It was observed in some instances that plants that grew along the pot walls carried more nodules than plants growing in the middle of the pot. The validity of that observation was tested in order to quantify the differences in biomass, plant length and nodule numbers.

Assuming that inoculation with a particular rhizobial strain would yield higher rates of nitrogen fixation, I artificially inoculated seedlings with rhizobial strains that were isolated from various localities to compare their performance. Since the host species thrives on sand and clay soils, under various natural and artificial conditions, the effects of soil type, seed sources and tree density on nodulation and biomass production were investigated.

Another objective of this study was to identify the host plant/microbe symbiont combination that could yield the highest amount of nitrogen. It is of practical importance to compare the performance of rhizobia collected from different localities within the *A. senegal* range to induce nodulation on seedlings from various sources. The testable hypothesis was that seedling and tree competition on a limited environment would have an adverse effect on nitrogen and biomass production.

The tree populations are expected to be genetically variable because of geographic separation by two big rivers and the significant climatic and edaphic differences within the species range and that may affect the nitrogen input into the system. Various localities have their own strains of rhizobial microbes which necessarily vary in performance and interaction with tree hosts. Genetic variability among tree populations at four study sites was examined.

A previous study indicated that *Acacia* plants raised on clay soil produced more nodules per plant than those raised on sandy soil. The ultrastructure of these nodules has not been investigated before, nor has the rate of nitrogen fixation. The objectives of this experiment were to determine the rate of nitrogen fixation adopting the method of Hardy et al. (1968), and to examine the nodule structure under the scanning electron microscope.

The goals of the gum study were to determine the annual average gum yield per tree, the relationship between tree age, mean annual rainfall and gum yield and the tree age for maximum gum yield. It was also intended to investigate if the high yield trait persists on progenies of *A. senegal*, i.e. whether gum yield was genetically controlled. The study also had a long term objective of identifying and locating high yielding progenies, isolate them from inferior pollen sources and treat them as a seed stand with the overall objective of disseminating improved seeds to ensure future high yield to meet the anticipated international demand.

The testable hypothesis was that since gum exudation is a genetically and environmentally controlled parameter in conifers and deciduous trees (Wright 1962), there must exist in nature some genetically superior individuals of *A. senegal* which yield higher amounts of gum than normal.

The relationship between gum yield, biomass and nitrogen yield was tested. The objective was to correlate nitrogen yield with gum yield in what has been established as superior gum producing strains of *A. senegal*. Genetically controlled traits in forest trees include resin and gum production, tree form, timber yield and pest resistance. Nitrogen fixation is controlled genetically in the host plant or macrosymbiont and microbial nitrogen fixing organism. *Acacia senegal* yield of gum arabic has been found to vary with strains. The data collected annually from individual trees revealed significant differences in yield among strains tested. The testable hypothesis was that high yielding strains of *A. senegal* may also be accumulating greater amounts of nitrogen. Hall et al. (1979) indicated that several traits might be of primary importance in selecting and breeding an improved genotype of alder. The potential for screening for photosynthetic capacity as a means of increasing both nitrogen fixation and overall growth rate has been demonstrated.

The objective of this study was to determine whether the selected study sites had genetically similar or different *A. senegal* populations. Sites E and D occupy sandy soil and are subjected to fairly similar climatic conditions. The testable hypothesis was that environmentally similar sites should have genetically similar populations of the same species since no geographic isolation is evident. Since the sites are separated by soil and climatic differences, genetic separation along these lines were anticipated. I expected to find two genetically different populations: one on clay, and the other on sandy soil.

METHODS

The effects of soil, seed source, and plant density on nodulation and biomass

Soil type and seed source were tested at four levels. The soils tested were from each of the selected sites. Soil types from site E and D are sandy soils, while those from sites S and G are cracking clays. From a previous study it was found that an average of 65 per cent of *A. senegal* seeds germinate. To obtain 10 plants per treatment 16 seeds were sown per treatment to achieve that number. Sixteen soil/seed combinations were examined, the number of replicates for each treatment varied. *Acacia* seeds were collected, washed in water and soaked overnight. They were then placed in plastic bags filled with soil from each source and lightly covered. Holes were drilled in the bottom of the bags to allow excess water drainage and root aeration. Water was applied once or twice daily depending on weather conditions.

Eight weeks after sowing the seedlings were removed with the soil intact. The soil was carefully washed off and the nodules were counted. For lack of a gas chromatograph to determine the rate of nitrogen fixation in the field, nodules were counted instead. Due to a shortage of chemicals, plain water was used for seed pretreatment rather than the regular concentrated sulfuric acid treatment. Plant material was dried in an oven at 80 C for 48 hours and weighed.

It was not feasible to take the dry weight of each individual plant separately because the root systems were entangled together and efforts to separate them would cause nodules and rootlets to break off. However, the length of shoot and root of each plant was taken as the nodules were counted. Then similarly treated plants were dried and weighed and a conversion factor for dry weight per unit length of shoot and root was computed.

To determine the effect of seedling density on nodulation and biomass production varying numbers of seedlings were raised in equal amounts of the same soil type (site G). A preliminary trial was conducted to test two competition intensities of one plant against ten plants per pot.

The seeds used were from site E. Three plant densities were examined: (a) 100 plants per pot to represent high competition intensity, (b) 65 plants (moderate intensity), and (c) 6 plants (low intensity).

Equal quantities of soil were placed in each of the three pots, in which the desired number of plants was raised. The treatments were replicated three times. Nodule count and dry weight determination were conducted as outlined above.

Nitrogen fixation rates by the acetylene reduction assay

This experiment was conducted in the Old Dominion University greenhouse and was similar to the previous experiment except for the reduced photoperiod treatment and the fact that nitrogen fixation determination using the acetylene reduction assay was conducted

Clay and sand soils from natural *Acacia* stands and corresponding seeds were collected from each of the four study sites within the range of *A. senegal* in the Sudan. Seeds from each site were raised in soil from each of the other sites in polythene bags, giving 16 combinations. Ten plants were raised for each treatment, two in each bag. The bags were punctured to allow for root aeration and excess water to escape. Watering was done once or twice daily depending on weather conditions. The experiment was initiated in late July and terminated early November.

A week prior to the acetylene reduction assay all plants were observed to have shed their leaves in response to shortening of day length and reduced photoperiod. Some seedlings started to produce new foliage while others retained a little of the old leaves or dormant buds. The plants were then removed from the polythene bags and the soil carefully removed from them.

For the acetylene reduction assay two plant roots with nodules were severed from shoots and placed in a 10 ml glass vial and covered with a rubber septum through which 1.0 ml air was drawn out and replaced with an equal amount of acetylene (Hardy et al. 1968). After incubation periods of 1, 2 and 4 hours the ethylene content of each sample was determined using a VARIAN 3600 gas chromatograph. The nodules were severed and oven dried at 60 C for a constant weight.

A sample of nodules was selected to be examined under the scanning electron microscope to compare their ultrastructures. The nodules were dehydrated by placing them in 70 per cent ethanol for 24 hours, 95 per cent ethanol for 10 minutes and then 100 per cent ethanol for 10 minutes; the last step was repeated. The nodules were then placed in acetone for 15 minutes. Liquid carbon dioxide was used for critical point drying. The nodules were then mounted on aluminum specimen mounts and treated with gold/ paladium coating. They were scanned on a Cambridge Stereoscan 100 at 10 kv.

Seedling inoculation by selected rhizobium strains

Seed collected from each of the four study localities were scarified by soaking in hot water and steeping in it until they germinated as exhibited by radicle emergence. Three to five seedlings were transferred to plastic bags, each containing 400 g of soil.

Mannitol-salt agar was melted in boiling water, cooled at 45 C and aseptically poured into sterile petri plates. Large nodules from *A. senegal* roots from each locality were removed, rinsed to remove adhering soil particles and surface sterilized by dipping in 95 per cent alcohol. The nodules were allowed to dry on a clean slide. They were cut into halves, one of which was rinsed with water and crushed with an inoculation loop until the water became milky. Sterile loops were used to inoculate the mannitol-salt agar plates with some of the nodule contents; the plates were inverted and incubated at 30 C for 5-7 days. Plant debris was removed from the slides and smears of nodule contents were prepared using sterile loops. The slides were air dried, heat fixed and stained using Loeffler's methylene blue for 5 minutes. The slides were rinsed, dried and observed under the microscope (Atlas et al. 1984). The mannitol salt agar plates were observed after 7 days and colonies isolated from them and cultivated in yeast extract/ mannitol broth as described by Bergersen (1980). Five ml suspensions of *Rhizobia* from each locality were used to inoculate seedlings from other localities. Seven weeks later seedlings were examined for nodule formation. Nodule numbers per plant indicated plant nitrogen fixation potential.

The seed / soil combination experiments shed some light on variations among the specific combinations with respect to nodulation, biomass and germination. The main objective of those experiments was to identify one or more combinations that yield higher nodule numbers than others in order to apply them for further bacteriological investigations. For each of the 16 seed / soil combinations, nodule numbers, biomass and germination percentages were determined. A ranking was adopted based on biomass, nodule numbers and germination. Ranks started from 1 for the combination exhibiting best yield of a particulr attribute, e.g. largest nodule number, biomass or germination. The rank increased by 1 for the next best treatment and so forth until rank 16, with the lowest nodule number, biomass or germination. Each attribute was ranked separately.

The plant soil combination selection was based on nodulation numbers. The combinations that resulted in above average nodule numbers were selected. Bacteria were isolated from nodules by crushing nodules on glass plates and transferring bacteria for cultivation in yeast mannitol agar medium. Mannitol broth was used for inoculation of *A. senegal* seedlings raised in sterile clay soil. The broth was used at 3 ml per pot of 5 seedlings, using sterile pipettes. Seed from each of the four study sites was used in only one soil type viz. Nile silt from the river bank near Khartoum. The soil used to raise the seedlings was heat sterilized for one hour in a timer controlled Camplex soil sterilizer.

The selected bacteria strains for inoculation are listed below and were selected from table 19. The selection was based on nodule numbers, germination and biomass.

These were 3 strains from site G and 3 from site S; both have clay soil. Bacterial strains were isolated from each soil separately in a nutrient agar medium and inoculated onto seedlings from site E seeds raised on sterile clay. The basic plan was to measure the rate of nitrogen fixation in the field using a gas chromatograph. Unable to locate one while in the field, nodule numbers were used instead with two assumptions: (1) that small nodules increase in size with time, and (2) that rate of nitrogen fixation is proportional to nodule number and size. *Acacia seyal* and *A. mellifera* were also obtained and used for comparison.

Table 22. List of selected rhizobium strains

Strain	Seed origin	Soil origin
STRAS	Shambat	Nile silt, Shambat
STRAM	Elain	Silt, Elain
STR5	E	G
STR9	E	S
STR7	S	G
STR6	G	G
STR11	S	S
STR4	D	E
Control	-	-

Each treatment was replicated five times. i.e. five pots per treatment. It was unfortunate that as seeds of this experiment were germinated a lot of rain occurred for two consecutive days. Most pots were inundated. and the study site was inaccessible for many days. I suspect that the sterile soil got contaminated with various bacterial strains. Seeds that rotted were removed from pots and replaced with fresh seeds.

Effects of receptacles on plant growth

Transparent polythene bags are the normal containers for raising seedlings in the forestry practice in Sudan. Some roots growing superficially on the bag soil were observed to carry more nodules than average. The bags were cut to 20 cm length and punctured to allow excess moisture to drain and root aeration to take place. Two sets of plants were then tested: one where seedlings were raised in the middle of the bags and another with seedlings grown along the edge to allow roots to grow superficially along the bag wall. Thirteen plants were raised in each set. Six weeks later nodules on each plant, shoot and root lengths and dry weights were recorded.

Gum yield

The study area was the eastern district of Northern Kordofan Province in Sudan, the center of which is Umruaba town which lies on latitude 12:50 nitrogen and longitude 31:10 E. The climatic and edaphic conditions and the resulting vegetation type have previously been described in this study. In 1966 a survey was conducted among the farmers of that area to identify and locate individual trees which were known for their high gum yield in privately owned land of natural vegetation. The area was chosen because it is famous for high quality gum of good yield in natural tree populations. Six high yield mother trees (HYMT) were located, identified by serial numbers and their seeds collected and germinated. When seedlings attained a height of 20 cm they were planted at a regular spacing of 4x4 m. The total number of high yield progenies (HYP) from all six selected trees was 694. An equal number of normal yielding tree progenies (NYP) was raised for comparison: a forest reserve of similar climatic and edaphic attributes and vegetation cover was used for this experiment. No supplementary watering was done; the only cultural treatment given was weeding around the trees for the first two years to reduce competition for water.

During late October-early November, trees shed their leaves indicating readiness for gum exudation. In 1972 when the trees were five years old gum tapping was conducted by removing bark strips 4-8 cm long and about two cm in width from three branches of the previous year's growth. Gum nodules formed on these incisions 4-6 weeks after bark removal. The first gum picking was made in late November-December, followed every 2-3 weeks by another picking from the same incision until the trees ceased to yield gum in May when leaves began to develop. Gum from each tree was weighed and recorded as soon as a picking was completed. The same procedure was repeated every year from age five to 20 years when the trees would be felled in the normal practice.

Soil and tissue samples were collected from the two types of trees in order to test the effect of gum yield varieties on soil nutrient concentrations.

A. senegal population diversity study using gel electrophoresis

The chemical and physical variations among various soil types coupled with non-uniform climatic changes and the degree of isolation among the study sites were expected to have given rise to populations with variable genetic characteristics. Such genetic variations were investigated using gel electrophoresis.

Electrophoresis is a separation technique whereby charged molecules in solution mainly proteins and nucleic acids, migrate when subjected to an electric field. The rate of migration or mobility through the electric field depends on net electric charge, shape and size of the molecules. It also depends on the ionic strength, viscosity and temperature of the medium in which molecules are moving. Since proteins carry a net charge at any pH other than their isoelectric point, they too will migrate and their rate of migration will depend on the charge density (ratio of charge to mass) of the protein of interest. The application of an electric field to a protein mixture in a solution will therefore result in different proteins migrating at different rates. Electrophoretic mobility is used as an indicator of similarity of amino acid composition when orthologous proteins are compared between individual plants.

Fifty trees were selected randomly from each of the four study sites. Seeds from each tree were collected separately and germinated by soaking them in water at room temperature. Those that imbibed water and started to germinate by protruding radicles were placed in petri plates lined with moist filter paper, and placed in an incubator at 30-32 C. Water was added once or twice daily. When plumules came out, the incubator door was left open to allow light to fall on plants, and the temperature was maintained at 32 C to simulate day time conditions of light and temperature. At about 6 pm the incubator door was closed and the temperature reduced to 25 C, simulating night time in a tropical setting where the species normally grows.

Two weeks after germination plants from each locality were extracted in a buffer (Werth 1985; Bharathalakshmi et al. 1990). Each plant was cut to small pieces in a porcelain spot plate placed in an ice tray to which a few drops of extraction buffer were added. The extraction buffer was removed from the freezer and allowed to thaw for ten minutes; 2 drops of mercapto-ethanol were added to it before use. Test tube bottoms were used to crush plants. Small filter paper wicks were placed in the plant extract to absorb it. Wicks from each plant extract were placed in a well in a plastic tray marked on lines and rows, covered tightly and placed in a freezer at -60 C.

A buffer system was used in order to stabilize the charge, control pH and provide electric contact between the electrodes and the supporting medium (Ferguson 1980). Electrophoresis buffer systems were tested in an experiment in which morpholine, tris-citrate pH 8.0 and tris-citrate pH 5.0 were examined. Morpholine was selected as it worked with all enzymes tested. It was prepared by dissolving 8.4 g of citric acid (monohydrate) in DI water to which was added N-3 (3-aminopropyl)-morpholine until the pH reached 7.0.

Starch gel was prepared by the following manner: 60 g potato starch were boiled in 1:19 diluted morpholine buffer in DI water, continuously stirred to prevent lump formation, and then evacuated to remove air bubbles, using a vaccum line. Molten gel was then poured evenly into a gel mold and left to cool. It was then covered with a plastic wrap to prevent evaporation and placed in a refrigirator prior to use.

Loading samples on to gel was made by removing paper wicks from the freezer and allowing them to thaw. They were lined on a paper towel to remove excess moisture. A slice was cut from the gel and wicks lined on the cut surface The cut portion of gel was then slid back into place and pushed tightly against the wicks by means of a soda-straw. A wick soaked in bromophenol blue was placed at one end as a marker to monitor migration.

Electrophoresis was accomplished by passing a 50 mA current through the gel by means of two electrode buffers wicked onto the gel surface by two sponge pieces placed on either side of the gel. The sponges were soaked over night with concentrated morpholine. The gel was rested on electrode boxes with the origin towards the cathode electrode. The edge of the cathodal sponge was placed 2 cm to the left of the slit where the wicks were aligned. The anodal sponge was placed at an equal distance from the right side of the gel. A pan full of ice was placed on the gel and it was separated from it by an acetate sheet. The ice was used to absorb the heat that was generated as a result of gel resistance to electric current. Heat may cause diffusion or loss of sample activity through protein denaturation. When the dye had migrated 10 cm from the origin, the gels were sliced, and individual slices stained following the protocol suggested by Werth (1985) and modified by Bharathalakshmi et al (1990) for one of the five selected enzymes: IDH, LAP, GOT, malate dehydrogenase (MDH) or 6PGDH. After a short incubation period in the dark, the gels were removed and examined for band formations.

Statistical analysis

Multivariate analysis of variance (MANOVA) and canonical correlations were used to test the effects of soil types and seed sources on germination, nodulation and biomass. The T-test was used to compare the effects of plant locations in receptacles. ANOVA and multiple comparisons were conducted to test the effects of inocula on seedling nodulation, and Chi-square to test heterozygosity (calculated vs. observed).

RESULTS

Effects of seed, soil, and planting density on nodulation and biomass

The initial number of seeds was 16, but the number that actually germinated varied and is shown in Table 23 which lists the number of germinated seeds for each treatment and percentages. Seeds from source E gave significantly higher numbers of seedlings in all soil types than sources G and D, and averaged 80.35 per cent germination, only rivalled by source S with an average of 78.7 per cent (ANOVA and Duncan's multiple range test, $P < 0.0045$). Seeds from the other two sources, G and D, were significantly lower in germination percentages (48.23 and 53.57 respectively). There was no significant difference between sources E and S or G and D.

Variability in germination among seed and soil treatments was very low. The range of coefficient of variability was 55-56 per cent for seed treatments. This range increased slightly with soil treatment to 56-60 per cent. The effect of seed source on nodulation resulted in lower variability than that of soil type. Regression analysis was performed to test an assumed regression model which stated that only seed sources and soil types affected germination, biomass and nodule numbers. The effects of seed and soil type on nodule numbers resulted in low R-square (0.2903) indicating a poor fit of the regression model in which only seed source and soil types were included. Data transformation increased the R-square to 0.5223, which indicated an improvement of the fit of the model. Factors other than just seed sources and soil types affected nodulation and biomass production e.g. micronutrients and soil bacteria numbers, but were not included in the model. There was significant improvement in the R-square by including biomass production which was significantly affected by soil type and seed soil interaction. Eighty one per cent of the variability was explained by soil and only 19 was due to the significant interaction between soil and seed. There was no significant difference in seed germination as a result of soil type treatments. The presowing treatment of soaking seeds in water which was adopted to enhance a rapid and even germination seems to have reduced the effect of soil type and its moisture relationship on germination. The sowing depth of 1 cm might not allow the effect of soil moisture treatment to be detected.

There was a significant difference in germination due to seed sources (ANOVA $P=0.014$, and Duncan's multiple range test); source E gave highest germination and was not significantly different from site S. Site G had the least germination and was not significantly different from D. Site E gave the highest germination percentage and highest seed weight.

Soil type had a strong positive effect on biomass. Sandy soil is skeletal with low available nutrients. This was reflected in biomass production in this study. The clay soil sites were not significantly different from each other. Sandy soils resulted in lower nodule number than clay soils: site D was least of all treatments and significantly lower than site E. Seed sources, however, had no effect on nodule numbers or biomass.

Seed size varied significantly with seed sources (Table 24). Site E gave significantly bigger seed weight than site D or S (ANOVA P=0.0009 and Duncan's multiple range test). Site G was second in seed size and was not significantly different from site S which ranked third, or site D with the least seed weight. Clay soils had significantly larger nodule numbers and biomass than sandy soil (ANOVA, P=0.0001 and Duncan multiple comparison). Seed soil interaction was significant, but seed treatment had no significant effect on nodulation.

The difference between sandy soil of sites E and D on nodulation was unexpectedly significant (Duncan's multiple comparison test). Similarly soil effect on biomass production was significant (P=0.0001). Soil/seed sources interaction was also significant (P=0.0027), but seed source treatment was not.

Germination was significantly affected by seed source, with sites E and S giving better germination than sites D and G. Soil types, however, had no effect on germination. They had a strong positive effect on nodulation while seed sources had no effect. Soil from sites G and S gave significantly higher nodule numbers than soils from E or D, the former two sites were not different from each other while the latter sites were. While clay soil was significantly better than sand for biomass production there was no significant difference between sites with similar soil types. Root biomass amounted to 12.38 per cent of total plant biomass; most biomass was allocated to the shoot, amounting to 87.62 per cent of total biomass. Shoot and total biomass were highly positively correlated (R=0.999).

Plants growing singly produced double the average shoot mass per plant (0.286 g), double the average root mass (0.092 g) and more than the average nodule number per plant (7.47) compared to the average biomass and nodule number of crowded plants. The crowded plants produced 0.153 g dry shoot mass. 0.049 g dry root mass. and 5.87 nodules per plant. From this I concluded that competition leads to reduced average plant mass and nodule number.

High competition expressed as high plant density per unit volume of soil resulted in low individual plant biomass and no nodules (Table 28. Fig. 9). Total biomass was not significantly affected. Moderate competition did not affect total biomass, but reduced nodule numbers. Low competition caused a drop in total biomass but gave the largest nodule numbers. Total plant biomass was not significantly affected by competition, but single plant biomass was adversely affected.

The average conversion factors for shoot and root were 0.00172 and 0.000116 g/cm respectively for eight week old plants. This conversion factor was tested to see if it varied significantly with treatments. There was no significant difference between treatments with regard to the conversion factor.

Fig. 9. The effects of high, medium and low competition intensities on seedling shoot weight, root weight, total plant biomass and nodule numbers.The Y-axis shows the plant and nodule numbers.

EFFECTS OF COMPETITION ON NODULATION AND BIOMASS

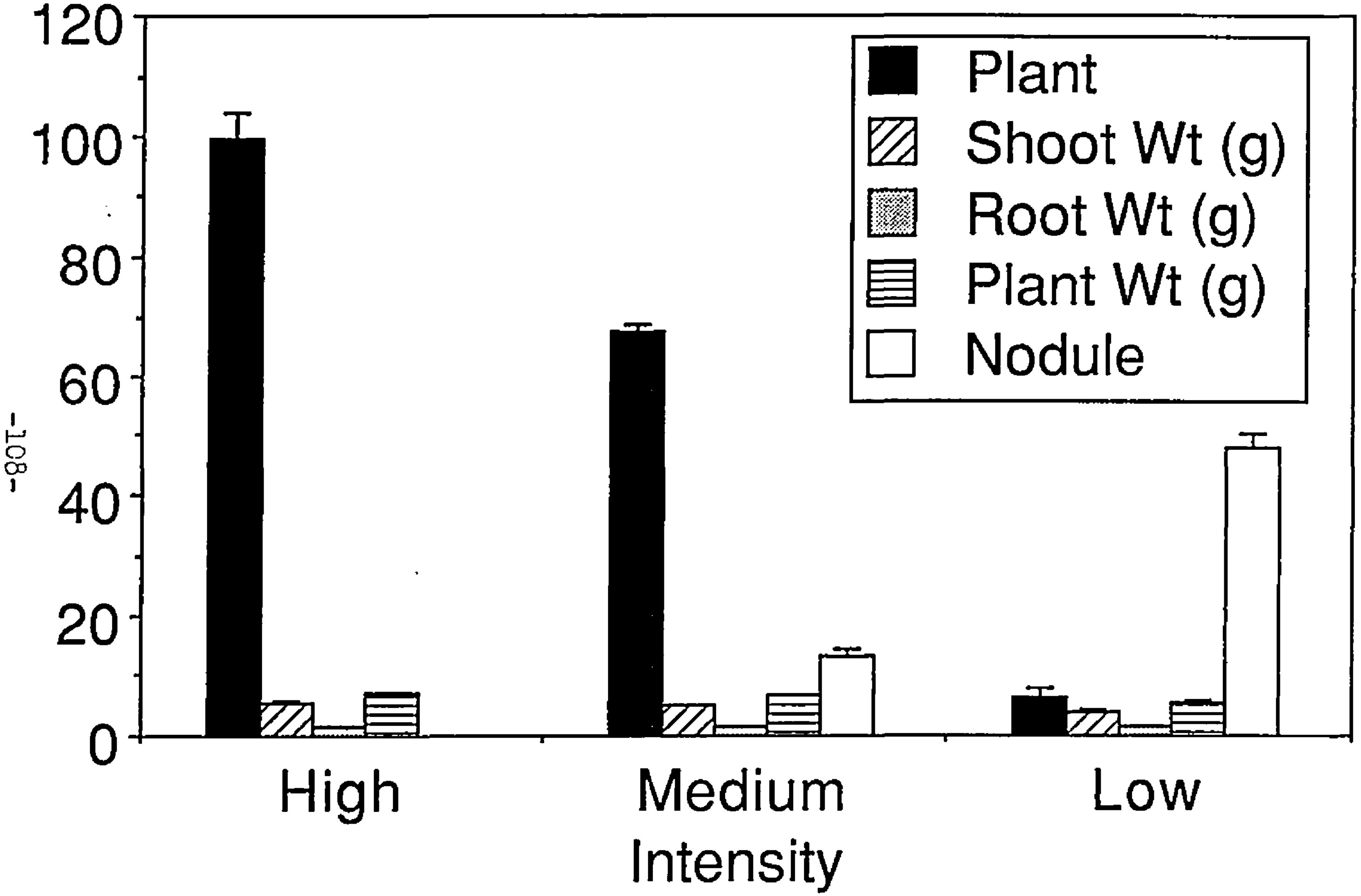


Table 23 The effect of seed source and soil type on germination

Seed sources	Soil types							
	E		D		G		S	
	Seed	%	Seed	%	Seed	%	Seed	%
E	14	100	11	78	10	71	10	71
D	7	50	7	50	10	71	6	42
G	8	57	4	28	8	57	7	50
S	3	92	8	57	13	92	10	71
Mean	10.5	75.0	7.5	53.6	10.2	73.2	8.2	58.9
S.E.	1.8	12.55	1.9	10.3	1.0	7.4	1.0	7.3

Table 24. Seed size variation with site (# seed per g)

	Sites			
Sample	Elobeid	Dubeibat	Gedaref	Singa
1	9.4	8.6	7.7	10.4
2	6.7	10.4	8.1	10.9
3	10.4	7.8	9.6	10.0
4	7.7	10.5	9.9	9.7
5	7.6	10.3	10.2	11.3
6	7.5	9.7	7.6	9.6
7	7.1	11.0	10.4	8.1
8	8.2	11.9	8.8	9.8
9	7.9	10.8	7.9	10.8
10	8.3	9.2	8.6	8.4
MEAN	8.08	10.02	8.88	9.9
S.E.	0.34	0.38	0.33	0.33

Table 25. Effect of soil type and seed source on biomass (dry weight of shoot (s), root (r) and plant (p) in g)

Seed	Soil types											
	E			D			G			S		
	(s)	(r)	(p)	(s)	(r)	(p)	(s)	(r)	(p)	(s)	(r)	(p)
E	.225	.092	.317	.207	.105	.312	.307	.139	.446	.409	.188	.597
D	.194	.109	.303	.110	.050	.160	.323	.129	.452	.430	.188	.618
G	.134	.092	.220	.112	.060	.172	.385	.202	.587	.334	.150	.484
S	.211	.085	.296	.216	.112	.328	.305	.136	.441	.296	.151	.447
Mean	.191	.094	.285	.161	.082	.243	.33	.151	.481	.367	.169	.536
S.E.	.02	.01	.02	.03	.02	.05	.02	.02	.04	.03	.01	.04

Table 26 (a). Effects of soil/seed combination on germination, nodulation and biomass. Rank in parenthesis

Seed Source	% Germination	Nodule Number	Dry Weight (g) Shoot	Root	Plant
		Soil site E			
E	100(1)	6.3(11)	0.225	0.092	0.317(10)
G	57(5)	9.8(8)	0.134	0.092	0.220(14)
S	92(2)	6.1(12)	0.211	0.085	0.296(13)
D	50(6)	10.4(7)	0.194	0.109	0.303(12)
MEAN	75	8.15	0.191	0.094	0.284
S.E.	12	1.13	0.02	0.01	0.02
		Soil site G			
E	71.43(4)	14.0(1)	0.307	0.139	0.446(7)
G	57.14(5)	11.75(4)	0.385	0.202	0.587(3)
S	92.96(2)	13.54(3)	0.305	0.136	0.441(8)
D	71.43(4)	7.10(10)	0.323	0.129	0.452(5)
MEAN	73.25	11.57	0.33	0.151	0.481
S.E.	7.38	1.57	0.02	0.02	0.04
		Soil site S			
E	71.43(4)	13.60(2)	0.409	0.188	0.597(2)
G	50.00(6)	7.43(9)	0.334	0.150	0.484(4)
S	71.43(4)	10.80(5)	0.296	0.151	0.447(6)
D	42.86(7)	10.50(6)	0.430	0.188	0.618(1)
MEAN	58.93	10.575	0.367	0.169	0.536
S.E.	7.36	1.27	0.03	0.01	0.04
		Soil site D			
E	78.57(3)	5.73(13)	0.207	0.105	0.312(11)
G	28.57(8)	3.75(15)	0.112	0.060	0.172(11)
S	57.14(5)	4.25(14)	0.216	0.112	0.328(4)
D	50.00(6)	1.86(16)	0.110	0.050	0.160(16)
MEAN	53.57	3.85	0.160	0.082	0.243
S.E.	10.30	0.80	0.03	0.02	0.05

Table 26 (b). Rank summary table

	First	Second	Third	Fourth
Germination	E	G	S	D
Nodulation	G	S	E	D
Biomass	S	G	E	D
Overall	G	S	E	D

Table 26 (c). Multivariate analysis of variance

Sources	DF	Type III SS	M.S.	F	PR>F
		Dependent variable: Germination %			
Soil	3	52.74	17.58	1.81	0.1489
Seed	3	133.22	44.41	4.57	0.0045
Seed*Soil	9	49.51	5.50	0.57	0.8230
Error	130	1264.0	9.72		
		Dependent variable: Nodules			
Soil	3	1189.14	396.38	9.40	0.0001
Seed	3	86.82	28.94	0.69	0.5620
Seed*Soil	9	806.65	89.63	2.13	0.0317
Error	130	5482.2	42.17		
		Dependent variable: Biomass			
Soil	3	.0046	.0015	36.63	0.0001
Seed	3	.00014	.000047	1.14	0.3374
Seed*Soil	9	.0011	.00012	3.01	0.0027
Error	130	.0054	.00004		

Table 27. Effect of soil and seed source on shoot/root ratio

Seed source	Soil type			
	E	D	G	S
E	2.44	1.97	2.21	2.17
D	1.78	2.20	2.50	2.28
G	1.46	1.87	1.90	2.23
S	2.48	1.96	2.24	1.96
Mean	2.04	2.00	2.2	2.16
S.E.	0.25	0.07	0.12	.07

Table 28. Effects of competition on nodulation and biomass. S.E. in parenthesis

Intensity	Plant #	Shoot Wt (g)	Root Wt (g)	Plant Wt (g)	Nodule #
High	99.67(4.3)	5.47(0.26)	1.43(0.06)	6.91(0.2)	0
Medium	67.33(1.45)	5.14(0.04)	1.52(0.03)	6.66(0.01	13.33(1.2)
Low	6.33(1.45)	3.76(0.37)	1.63(0.1)	5.39(0.45)	47.67(2.40)

Nitrogen fixation rates and nodule ultrastructure:

A high correlation ($R=0.9998$) was obtained between ethylene concentrations and gas chromatograph instrument readings. Nodule dry weight as affected by seed and soil treatments are shown in Tables 29 and 30. The total nodule weight variation with soil treatment was significant (ANOVA $P>0.0042$ and Duncan's test). Soil from site E resulted in significantly higher nodule weight than that from D or S, but not higher than G. G was not significantly different from E, D or S.

The rates of nitrogen fixation were computed for each incubation period in micromoles per gram of dry nodules. Table 31 lists the amount of ethylene in micromoles per gram of dry nodule weight and also the phenological stage of leaf development. Due to an undetected error the amount of ethylene reduction for the 2 hour incubation period was incorrect, and was eliminated from the correlation calculations. High correlation coefficient values were then observed between the incubation period and ethylene reduction readings. These were 0.97, 0.89, 0.96, and 0.99 for soil origins D, E, G and S. The reported data for the rates of nitrogen fixation in this experiment were generated from one replicate and should, therefore, be taken with caution.

Three different stages of nodule development were observed with respect to their outer appearance, color, firmness and inner contents:

a) Firm nodules were light colored, usually pinkish or yellowish when dissected. These physical characteristics conform with general descriptions usually associated with functional nodules (Postgate 1982, Sprent 1973), (Fig. 10 and 11). They were apparently functional and seemed to receive nourishment from plant leaves and exhibited various sizes and shapes.

b) Darkly colored nodules contained yellow fluid which oozed out when they were pressed between the fingers. That fluid was probably exuded or taken up by the plant as the nodule nitrogen contribution of the symbiosis. These nodules were non-functional.

c) Empty sacs which once were functional nodules, lost their source of nourishment or were affected by aging. Their content was either absorbed by the plant or lost into the outside soil through exudation (Fig. 12).

Various microscopic structures were visible at high magnifications (Fig. 13). Rhizobial bacteria were shown with an outer wall that looked shrivelled in some nodules (Fig. 14), probably as a first stage before they lysed and turned into the observed yellow fluid, perhaps rich in bacterial protein and nitrogen. Fig. 15 shows healthy bacteria cells extracted from a nodule supplied with nourishment. The weight of nodules alone did not reflect the capacity of a system to fix nitrogen; the state of nodules whether functional or not gave a better estimate. A comparison of the treatments should not have been delayed until leaf shed in response to reduced photoperiod. The recommended time in the literature for nodule examination is six to eight weeks.

Fig. 10-15. Scanning electron micrographs of cross sectional view of *Acacia senegal root nodules*. Fig. 10. Bacteroids showing two types of cells. A type full of bacterial mass (arrow) . When highly magnified it revealed single, oblong-shaped cells characteristic of the genus *Rhizobium*. Magnified 123x.

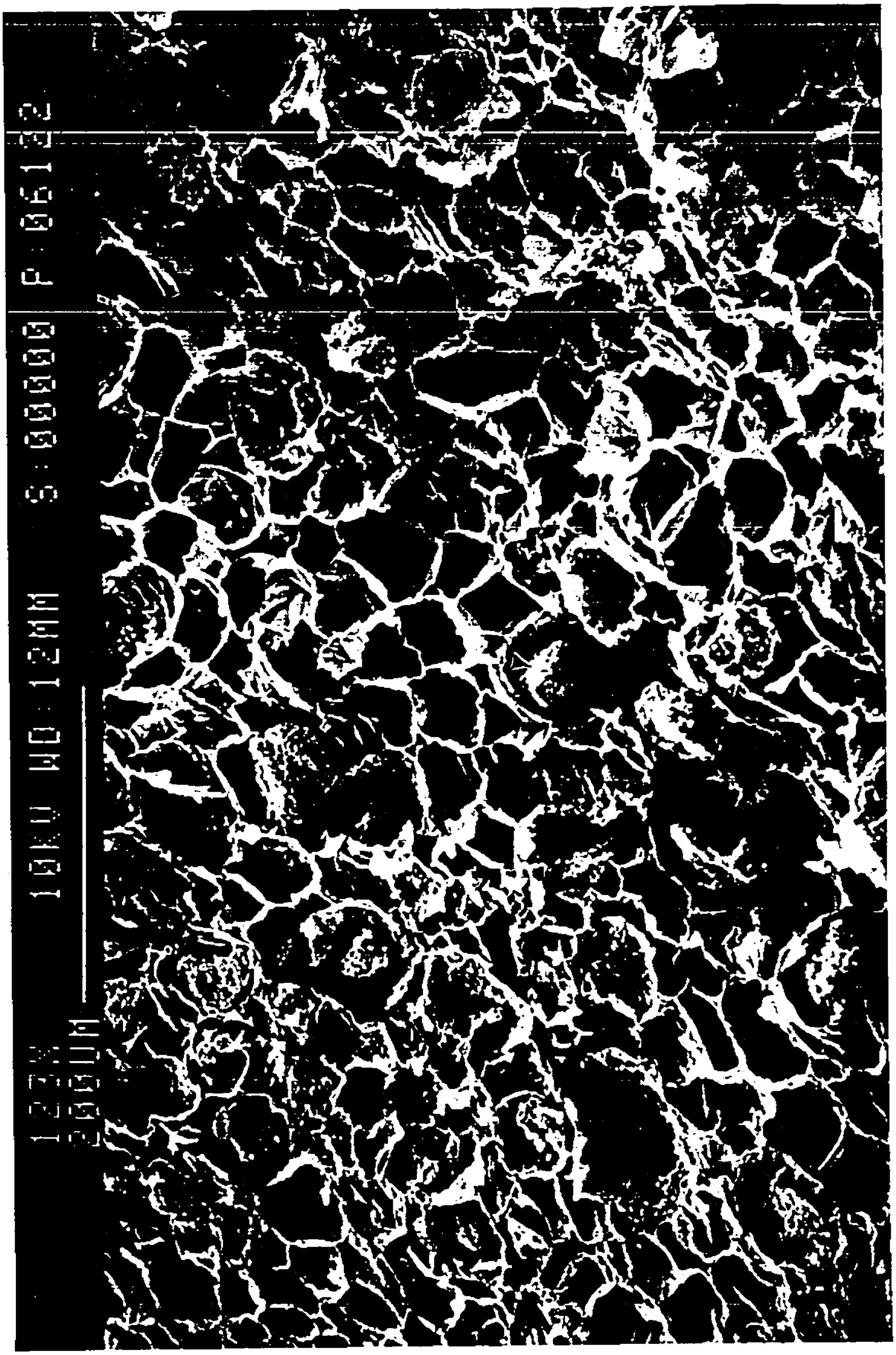

10KV WD:12MM S:00000 P:00132
127X
200UM

Fig. 11. Functional nodules showing bacteroids on the right side of picture, xylem vessel on the center and wide-lumen unthickened cells to the left of center.

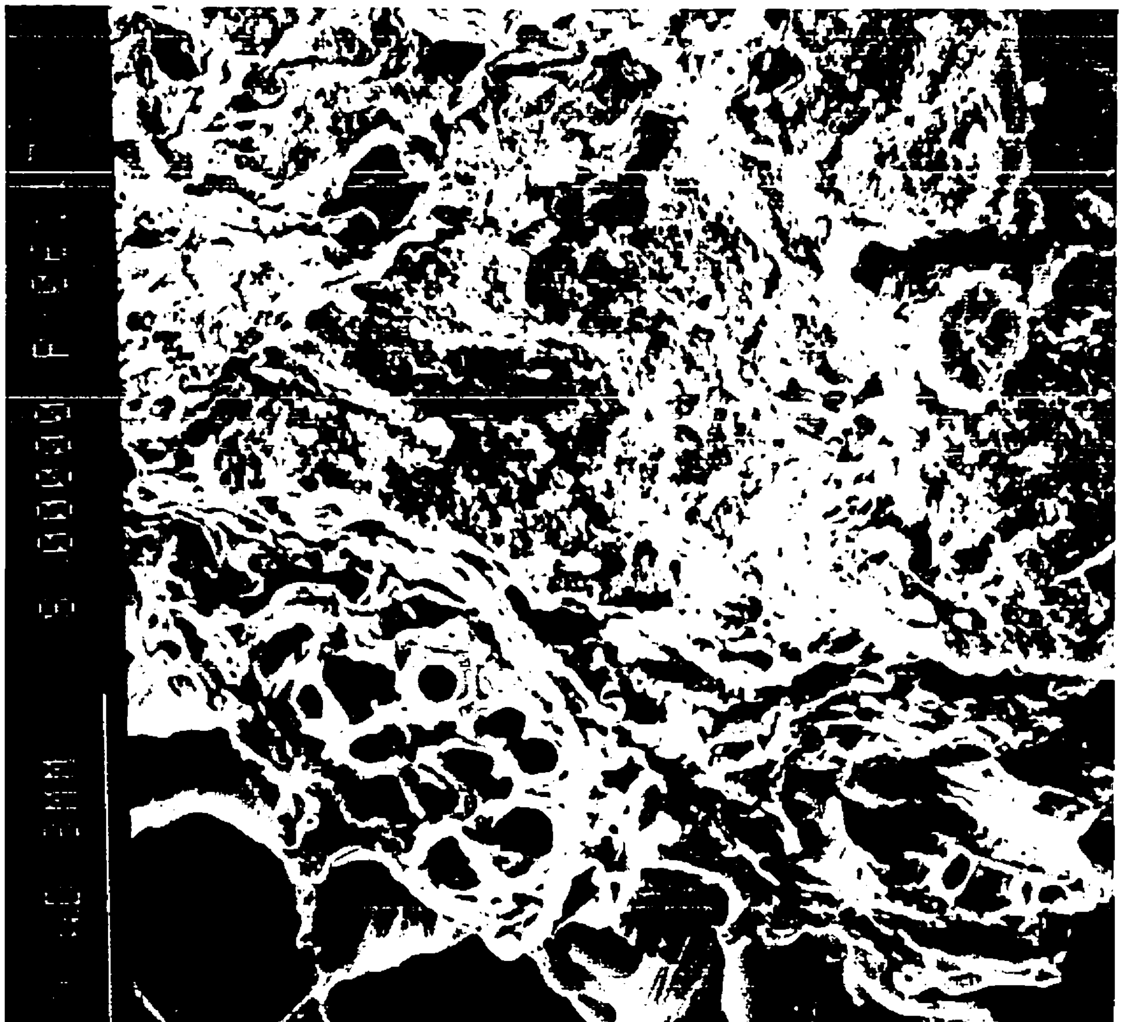


Fig. 12. Non-functional degenerate nodules. Lack of nourishment due to leaf shed caused nodular inner tissues to die forming a yellow viscid fluid that oozed out upon sectioning of nodules.

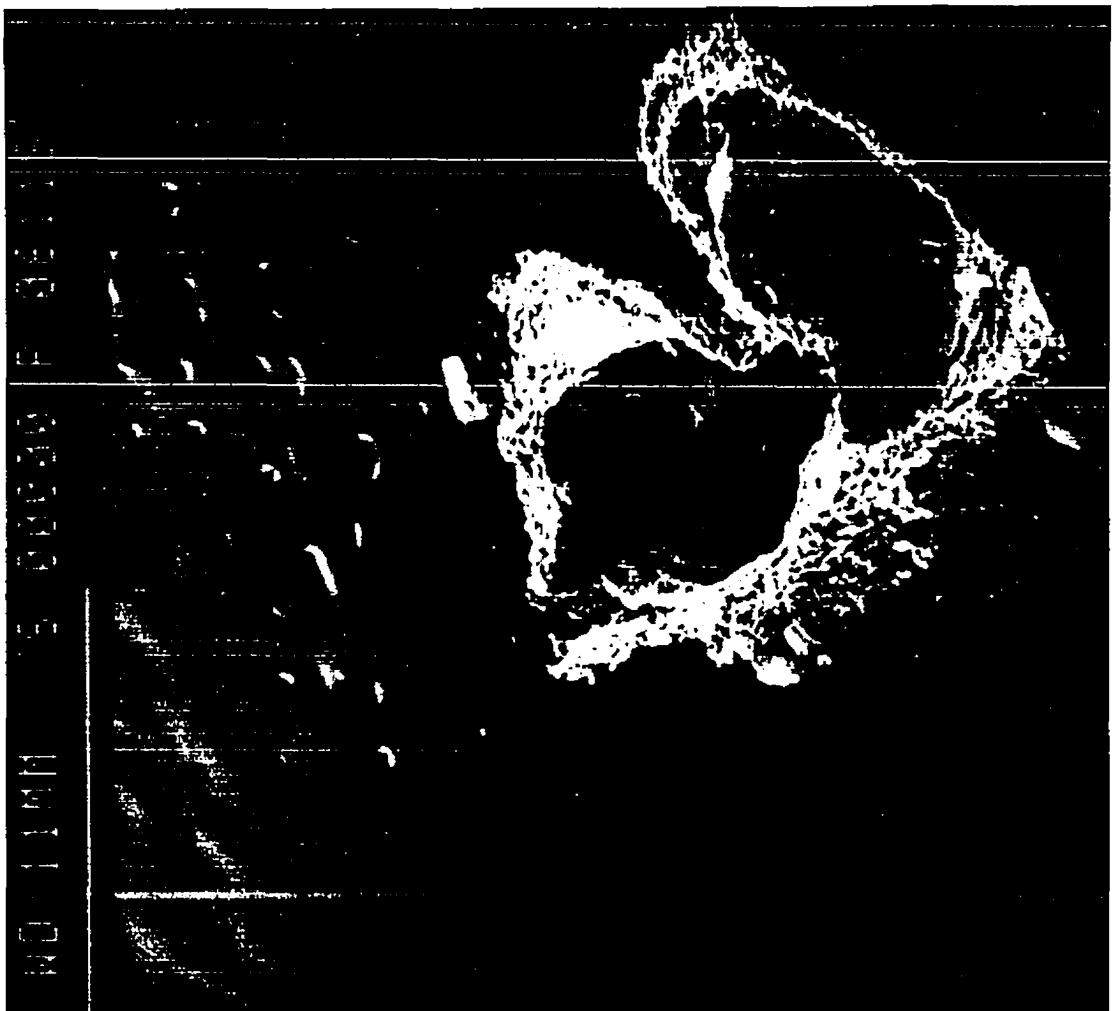


Fig. 13. Wide-lumen cell within a nodule, possibly function as a conduction tissue.

Fig. 14. Rhizobium bacteria cells that looked shrivelled as a result of lack of nourishment following leaf shed. Magnified 9560 x.

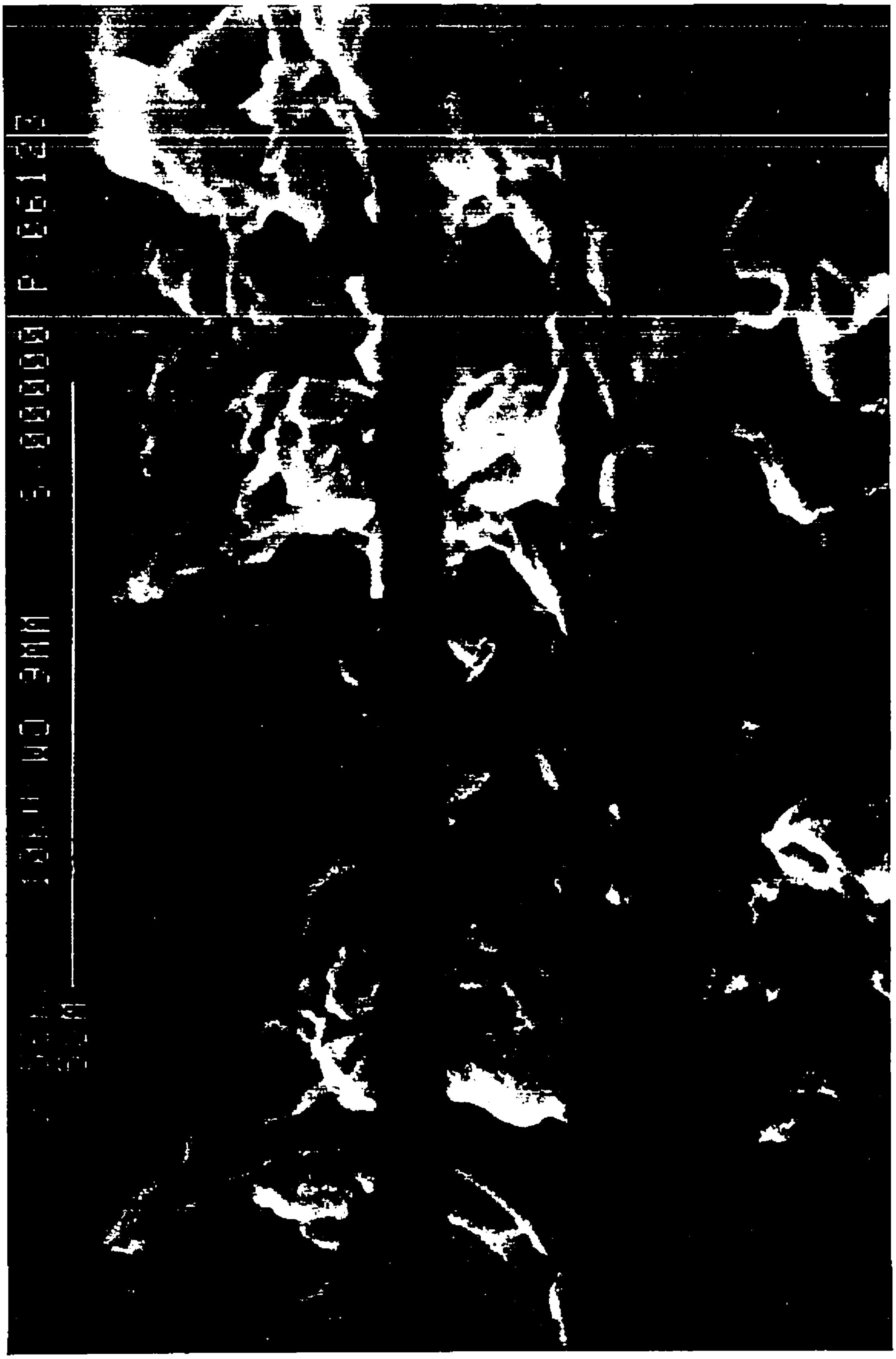
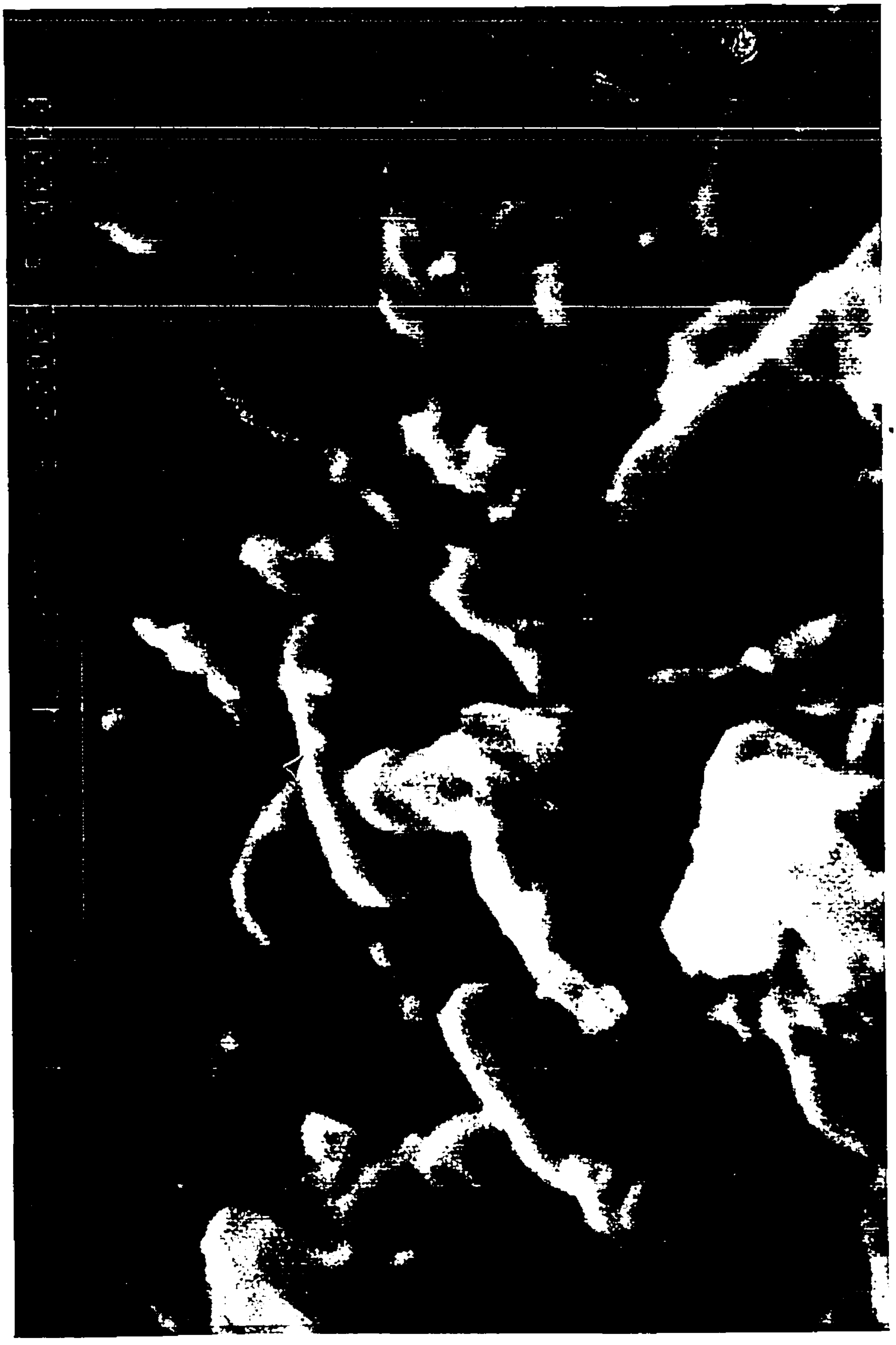


Fig. 15. Normal oblong-shaped rhizobium cell.



Inoculation with selected strains

There were significant differences due to sites (MANOVA $P<0.0028$) and also due to treatments (MANOVA $P<0.005$). Singa seeds produced the highest average nodule number (Table 32) ($p<0.0028$) and was significantly higher than all other sites. All other comparisons were not significant. Significant treatment comparisons were the control and STRAM and also control and STR6. All other treatment comparisons were not significantly different. *Rhizobium* strain extracted from treatment GTGP or strain number STR6 i.e. both seed and soil from site G resulted in the highest nodulation on Singa seedlings. Singa seedlings also gave the second and the third best nodule numbers with ETDP strain (STR4) with *A. mellifera*. STR4 (ETDP) also produced a relatively high number of nodules with G seedlings. *Acacia mellifera* strains resulted in the highest nodulation with E and D site seedlings and gave a high nodule number with seedlings from site S. *A. seyal* strain (STRAS) produced very low nodulation in all seedlings.

There is no clear explanation for *A. mellifera* strain (STRAM) resulting in the highest nodule numbers; whereas STRAS, i.e. strain extracted from *A. seyal*, was least. Algedaref and Singa seedlings were expected to yield high nodule numbers because they both originated from soils that cause nodulation to occur. Singa came true to expectation, but Algedaref failed. Because of the contamination that occurred when all pots were flooded with unexpected high rains, the results from this study are considered only preliminary and need to be confirmed by additional study. Evidence of effective inoculation was obtained by the presence or the absence of nodules. There was significant variation in nodule numbers with respect to strains ($p<.005$) and site ($p<.0028$) from which the treated plant originated. The interaction between strains and sites was also significant ($p<.001$). Site S was superior to and significantly different from sites G, E and D. Sites G, E and D were not significantly different from one another.

There was significant difference between strains with respect to nodulation; strain STRAM was significantly higher than strain STRAS and the control treatment. Strain STR6 was significantly higher than the control treatment

It appeared that strain STRAM which was extracted from *Acacia mellifera* was suitable to inoculate seedlings from all four study sites (Table 33). For site D, the only other strain that resulted in above average nodules was STR11. Seedlings from site E resulted in above average nodulation from strains STRAM, STR11, STR5, and STR9 (Table 27).

The effect of plant position in receptacles on nodulation

Plants raised in the middle of containers grew bigger and produced larger numbers of nodules per plant. They had longer shoots (19.7 cm), longer roots (23.7 cm), greater biomass (0.306 and 0.085 g/ plant for shoot and root) and larger average nodule number (8.3) than plants grown near the edge (Table 29). The plants grown on the pot edge were shorter and lower in shoot mass (13.1 cm and 0.152 g) and root mass (17.3 cm and 0.0659 g) and had fewer nodules (2.6). ANOVA and T-test revealed significant variation in shoot weight (PROB > .0001) and in nodule numbers (PROB > .0006), but not in root weight. Plants grown in the middle had significantly larger shoot weight and nodule number per plant than the edge treatment.

ANOVA and multiple comparison tests revealed significant variation ($P<.0001$) between treatments with respect to nodule numbers and shoot weights. Root weights were not significantly different. The average nodule numbers were 8.3 and 2.6 for middle and edge treatments respectively. Biomass was significantly greater in the middle treatment ($P< 0.0006$) than in the edge. The shoot length was significantly greater in the middle than in the edge treatment ($P<0.0001$); the root length was not. The original observation that more nodules resulted by growing plants on the container edge was not supported. The contrary was found true.

Table 29. Nodule dry weight (mg) as affected by treatments. S.E. in parenthesis

Soil type	Soil origin	Seed origin	Nodule wt (mg) /seed origin	total nodule wt /soil origin	Mean
sand	E	E	0.0		
"	E	D	19.0		
"	E	G	13.6		
"	E	S	53.1		
				87.5	28.6(12.3)
"	D	E	3.6		
"	D	D	16.4		
"	D	G	0.0		
"	D	S	19.7		
				39.7	13.0(4.7)
clay	S	E	6.5		
"	S	D	0.0		
"	S	G	13.2		
"	S	S	7.6		
				27.3	9.1(2.1)
"	G	E	14.7		
"	G	D	4.8		
"	G	G	17.6		
"	G	S	39.1		
				76.2	19.05(8.5)

Table 30. Nodule weight as affected by plant condition

Treatment Soil	Seed	Nodule wt (mg)	Foliage condition
E	E	0	no leaf or nodule
E	D	19.0	old leaves
E	G	13.6	" "
E	S	53.1	bud started to form
D	E	3.6	leaves started "
D	D	16.4	" "
D	G	0	no nodules
D	S	19.7	old leaves
S	E	6.5	" "
S	D	14.0	" "
S	G	13.2	" "
S	S	7.6	" "
G	E	14.7	" "
G	D	4.8	no leaves
G	G	17.6	old leaves
G	S	39.1	" "

Table 31. Rates of fixed nitrogen in micromol/g. S.E. in parenthesis

Incubation period (Hr.)	Soil origin D	E	G	S
1	3.35(1.2)	4.5(1.7)	15.5(8.6)	36.4(20.3)
2	0.1(0.03)	0.7(0.5)	15.5(8.6)	36.4(20.3)
4	7.4(2.5)	6.3(2.7)	34.6(13.8)	418.8(249.4)
R	0.97	0.89	0.96	0.99

Table 32 (a). Effect of inoculation on average nodule number/plant. S.E. in parenthesis

Strains	Seed origin			
	D	E	G	S
Control	3.2(1.3)	3.2(0.7	4.2(1.0)	3.60(0.7)
STRAM	21.0(3.8)	14.2(5.3)	8.2(5.7)	21.8(7.4)
STRAS	4.6(1.9)	6.4(2.0)	6.5(2.5)	4.7(1.4)
STR11	15.8(8.7)	9.6(3.8)	3.0(1.1)	7.0(3.5)
STR4	1.5(0.3)	3.6(1.5)	19.6(4.2)	22.2(5.2)
STR5	3.0(1.8)	10.4(4.9)	12.4(7.2)	8.0(1.8)
STR6	2.7(0.5)	5.0(2.4)	10.0(4.6)	42.4(15.6)
STR7	4.4(0.7)	5.6(1.7)	9.6(5.1)	10.4(4.1)
STR9	4.5(2.8)	10.5(2.5)	3.5(1.3)	11.8(8.1)

Table 32 (b). MANOVA table: Inoculation experiment. Dependent variable: nodule number

Source	DF	Type 3 SS	M.S.	F	P
Site	3	1664	554.7	4.92	.0028
Strains	8	2621	327.7	2.91	.0050
Site*Strains	24	6428	267.9	2.38	.0010
Error	134	15095.2		112.65	

Table 33. Selected inocula and seedling origins

Seedling origin	Suitable strains
D	STRAM, STR11
E	STRAM, STR11, STR5, STR9
G	STRAM, STR4, STR5, STR6, STR7
S	STRAM, STR4, STR5, STR6, STR7, STR8

Table 34. The effect of plant location on biomass and nodule number. S.E. in parenthesis

Parameters	Edge	middle
Shoot weight (g)	0.021(0.001)	0.031(0.001)
Root weight (g)	0.01(0.0007)	0.01(0.0007)
Biomass (g)	0.03(0.002)	0.04(0.001)
Shoot length (cm)	13.1(0.9)	19.7(0.8)
Root length (cm)	17.3(1.2)	20.7(2.1)
Nodule number	2.6(0.9)	8.3(1.1)

Genetic variability using starch gel electrophoresis

Nei and Roychoudhury (1974) maintained that the genetic variability within a population is usually measured by the average heterozygosity per locus, while the genetic differences between populations are determined by the genetic distance. The gene differences between two or more populations may be measured by the genetic distance proposed by Nei (1972) and Nei and Roychoudhury (1974). Variability within a population is usually measured by the average heterozygosity per locus. The band systems observed for each enzyme were classified as fast or slow, and allozyme scoring was done as described by Dedera and Werth (1987). Eight loci (*got, lap, idh, mdh(1 and 2), 6pgdh(1 and 2)* and *skdh),* coding for six enzymes (GOT, LAP, IDH, MDH, 6PGDH and SKDH) were resolved. Two loci *(got and skdh)* were monomorphic across all four populations. Banding was observed for other enzymes, but was poorly resolved and uninterpretable. Four loci exhibited substantial polymorphism, Table 35.

The levels of polymorphism were similar for populations E and D, which were geographically close, not isolated by any physical barrier, and occupied similar soils subjected to similar climatic elements. The percentage polymorphic loci (P) was 41 for populations E and D. The mean number of alleles per locus ranged between 1.8 and 2.2. The mean expected heterozygosity per locus, often considered the most informative index of genetic variability (Bharathalakshmi et al. 1990) ranged between 0.36 for population D and 0.42 for population E.

The genotype frequencies occuring in the four populations and those expected under Hardy-Weinberg equilibrium were statistically compared (Table 38). Wright (1978) fixation index provides a comparison of observed and expected heterozygosity. Its value ranges from 1 to -1. Positive values indicate a deficiency of heterozygous individuals, i.e. high level of inbreeding. Negative values indicate heterozygous excess. A preponderance of negative fixation index values suggested high levels of heterozygosity in all populations.

Allele frequencies for the total samples were calculated for each of the loci used. Allele frequency for gene loci were also calculated (Table 30). From these frequencies I compared the calculated heterozygosity with the observed (Table 30 a). The calculated heterozygosity is H(e)=1-sum of x squared, where xi is the frequency of the ith allele at a locus (Ferguson 1980). The observed heterozygosity is the fraction of heterozygous individuals: if a population is in Hardy-Weinberg equilibrium, then the observed H (o) and calculated heterozygosity H (e) will be very similar.

H (o) and H (e) for sites E, D and G were not significantly different (Table 30). The deviation of H from Hardy-Weinberg expectations was insignificant for E; (H (o) was 0.41 and H (e) was 0.42) and G (Ho 0.37 and H (e) 0.38). For site S there was significant departure from Hardy-Weinberg equilibrium.

I concluded from this observation that sites E, D and G satisfy Hardy-Weinberg expectations. The genetic distance between populations was determined using a cluster analysis which revealed that populations E, D and G were genetically similar. Population S occupied a branch by itself on the dendrogram, indicating genetic difference between site S and the other populations.

TABLE 35. Allele frequencies for four polymorphic loci in *A. senegal* populations. Sample size in parenthesis.

Locus	Allele	Populations E	D	G	S
(idh)	Slow	0.36	0.72	0.41	0.63
	Fast	0.64	0.28	0.59	0.37
		(28)	(18)	(34)	(62)
(lap)	Slow	0.58	0.81	0.89	0.61
	Fast	0.42	0.19	0.11	0.39
		(28)	(16)	(38)	(62)
(mdh(1))	Slow	0.57	0.82	0.77	0.82
	Fast	0.43	0.18	0.23	0.18
		(28)	(44)	(24)	(62)
6pgdh(1)	Slow	0.87	0.69	0.53	0.76
	Fast	0.13	0.31	0.47	0.24
		(8)	(16)	(38)	(46)

Table 36. Intrapopulation variability estimates of the four *A. senegal* populations. S.E. in parenthesis: N is mean sample size: A is mean allele number per locus. and P is percent polymorphic loci.

Population	N	A	P	H(o)	H(e)
E	34.0	2.1(0.21)	41.00(0.1)	0.41(0.1)	0.42(0.06)
D	35.5	2(0.41)	40.75(0.05)	0.41(0.5)	0.36(0.03)
G	45.0	1.8(0.3)	38.25(0.08)	0.37(0.08)	0.38(0.07)
S	56.0	2.2(0.41)	64.00(0.1)	0.54(0.04	0.40(0.03)

Table 37. Calculated and observed heterozygosity

	sites				
Enzyme	E	D	G	S	mean
		Calculated heterozygosity			
IDH	0.46	0.40	0.48	0.47	0.45
LAP	0.49	0.31	0.19	0.47	0.36
MDH(1)	0.49	0.29	0.35	0.50	0.35
6PGDH(1)	0.23	0.43	0.50	0.36	0.36
Hl	0.42	0.36	0.38	0.40	0.39
		Observed heterozygosity			
IDH	0.42	0.33	0.23	0.48	0.36
LAP	0.17	0.37	0.21	0.64	0.35
MDH(1)	0.71	0.36	0.45	0.48	0.50
6PGDH(1)	0.33	0.57	0.58	0.57	0.51
Ho	0.41	0.41	0.47	0.54	0.43

[(Calculated heterozygosity H(e)=1-sum of x i, where xi is the frequency of the ith allele at a locus. Observed heterozygosity H (e) is the fraction of heterozygous individuals)].

Table 38. Comparison of single locus heterozygosity and conformance to Hardy-Weinberg expectations

Population	Locus	Number of heterozygotes Observed	Expected	Fixation index (f)
E	idh	6	6.44	0.068
	lap	3	5.88	0.489
	mdh(1)	10	6.86	-0.46
	6pgdh(1)	1	0.92	-.09
D	idh	3	2.48	0.17
	lap	3	2.48	-0.21
	mdh(1)	8	6.38	-0.25
	6pgdh(1)	4	7.31	0.73
G	idh	4	8.16	0.51
	lap	4	3.61	-0.11
	mdh(1)	9	7	-0.28
	6pgdh(1)	11	9.5	-0.16
S	idh	15	14.57	-0.03
	lap	20	11.16	-0.79
	mdh(1)	29	14.99	-0.93
	6pgdh(1)	11	8.28	-0.33

DISCUSSION

Effects of seed source and soil type on nodulation and biomass

The effect of soil on germination was minimized by the presowing treatment adopted to ensure rapid and even germination. It provided an initial seed hydration that reduced the effect of soil on germination. The seed was sown at a 1-cm depth which would not allow variation due to soil moisture to be detected. The effect of soil on germination was therefore insignificant.

Clay soils contain more nitrogen, phosphorus and potassium than sandy soil. They have higher cation exchange capacity and micronutrients. They also contain more organic matter which is conducive to microbial activities than sands. Clay soils are richer in carbon a than sandy soil. Furthermore, clay soils are more stationary than sandy soils, which are easily transported by wind, causing the top layer with moderate organic matter to be buried or transported. The cracks that result on exposure to drought act like underground storage for organic matter which decomposes at the onset of the rainy (growing) season. For these reasons clay soils were expected to yield higher plant biomass and more nodule formation than sandy soils. Nodule formation was found to depend on soil micronutrients e.g. cobalt and molybdinum which are more available in clay soil than in sandy soil. Other elements like magnesium, iron and sulphur are also more available in clay than in sandy soils, and resulted in higher biomass. Clay soils contain larger amounts of organic matter than sandy soils, and may therefore harbor more active bacteria strains than sands. The plants they produced had more biomass and subsequently more available energy which is an important prerequisite for nitrogen fixation processes.

Effects of plant density on biomass and nodulation

Plants competed for limited nutrients, moisture and space resources. The more intense the competition, the more severe the reduction on individual plant biomass, available energy source and subsequent nodulation. The total plant biomass under the two highest competition intensities was not significantly different from one another, which might indicate that the site potential was fully utilized by 67 plants. An increase in plant number to 99 did not yield a significant increase in biomass. The least competition resulted in highest nodule numbers and highest individual plant biomass. Total biomass, however, was less than in moderate and high competition treatments, which indicates that the site potential was not fully utilized under moderate and low competition intensities. The concept of threshold is important for agronomic and silvicultural practices, particularly at the nursery and early age of forest plantations. Thinning recommendations and schedules in forest science can utilize site production potentials for improving forest yield and timber quality. The threshold range presented is wide and can be considered preliminary, but it could be refined and narrowed down through further study. In their study with soybean in Japan, Kira et al. (1953) took total plant weight as a measure of competition intensity. They found that the log of mean plant weight and the log of density were linear.

Since container volumes remain the same, increase in plant numbers indicates an increase in competition intensities. The highest intensity resulted in 0 nodules, the least intensity gave highest nodule number, while moderate competition intensity resulted in average nodulation. It is speculated that high plant density produces enough allelopathic chemicals to lead to complete eradication of the symbiotic bacteria. An alternative hypothesis is that nutrients, micronutrients and energy were in too short supply to allow the plants to enter into a symbiotic relationship.

There appeared to be a trend towards larger seeds with lower rainfall on a similar soil type. This might indicate an adaptation of the species to lower rainfall regimes. Indeed *A. sene-*

gal distribution ceases at higher isohyets. Seed source variation appeared to have little effect on nodulation or biomass.

Nitrogen fixation rates and nodule ultrastructure

Nitrogen fixation involves a sequence of energy demanding processes. Plants growing vigorously provide the required ATP's to meet the demand. When plants have shed their leaves or are not growing in optimum conditions their ability to support diazotrophy becomes nil or limited. On clay soil, leaves were retained longer by the plant than in sandy soil. The effect of reduced photoperiod was felt faster by plants grown on sand than on clay, i.e. soil fertility seems to have an effect on plant response to photoperiod. The possible role of reduced photoperiod as a mechanism that triggers defoliation has been suggested. It was shown that the onset of dormancy in species is influenced by a slight change in day length. It is evident that the rate of nitrogen fixation was not similar for all treatments. The nodules in the clay were supplied with ATP and were functional. On sand the nodules degenerated for lack of energy and nitrogen fixation processes apparently stopped as the weight of nodules was not reflected in the ethylene produced. When nodules were not present, no ethylene was produced. When they were present in treatments D E (soil from site D and seed from site E) and D D, but not functional because they degenerated with age, ethylene production was not detected either. Seedling raised on soil from site S did not respond to day length limitation and continued to supply the nodules with the needed fuel. Their nodules were functional and their rate of nitrogen fixation was the highest of all treatments.

In the study which examined extension of the duration of nodulated plants from 50 days to 90 days prior to nodule examination, the longer period resulted in mostly degenerate nodules. The shorter period nodules were pink, firm and apparently functional. All nodules start fresh and as time proceeds more nodules degenerate to release their nitrogen to plants or the soil. At a certain time all nodules are expected to degenerate. The reduction of fresh nodule numbers indicates that the nodule formation was not a continuous process. It may be an annual cyclic event that takes place in relation with phenological processes and availability of energy source in order to satisfy the need for nitrogen for processes such as leaf, flower and fruit formation.

The change in photoperiod has induced an unexpected treatment that was not originally planned. Its effect was high enough to mar the difference due to the basic treatments of soil types and their effects on the rate of nitrogen fixation. The data presented does not allow a sound comparison resulting from variation of the soil factor alone. Further investigation along these lines seems necessary.

Seedling inoculation using selected strains

Despite the possibility of contamination that this experiment was subjected to, there appeared to be a trend among the various seedling origins and inocula which suggested that the contamination posibilty was probably insignificant. Seedlings from sites E and D of the sandy soil responded the least to inoculation, whereas the clay site seedlings could be inoculated satisfactorily by five inocula for G and six for S site. Seedlings from site D proved least receptive to inoculation, as they yielded only to STRAM and STR11. Seedlings from S could be inoculated with a wide variety of inocula. There was no clear explanation for these variations; however, there seems to be the possibility that seed micronutrient contents implicated with nodulation was sufficiently variable to warrant these variations. Habish and Khairi (1968) suggested that within the same inoculation group, bacteria are interchangeable. Norris (1972) held that there is a great deal of symbiotic promiscuity among the tropical cowpea group to which the *Acacia* strains belong, in the sense that limited specificity exists among microbes and plants.

The effect of plant location within the receptacle on performance

Although the volume of soil and space allowed for both groups were similar, the edge plants only partially utilized those resources and expectedly were less efficient in shoot biomass and nodule production. Plants growing in the middle of the pot utilized all the available resources and grew at a higher rate than the other treatment. It was expected that root growth becomes impacted by the edge treatment, but that expectation did not materialize as the data did not support it.

It is possible that the treatments adopted did not mimic the situation which resulted in more nodules on edge plants. It might have been due to more than a single factor which combined to exhibit that occurrence.

Gum yield

Defined as a gummy exudate from trees or shrubs of the genus *Acacia*, gum arabic is a complex water soluble polysaccharide which if hydrolysed would yield the sugars galactose, arabinose, rhamnose and glucuronic acid (Anderson 1977, 1985). Gum production is a feature associated with plants adapted to arid climates.

Gum arabic has a variety of important industrial uses such as an ingredient in the confectionary industry, an adhesive, a thickener, a stabilizer and an emulsifier in a wide variety of food stuffs (Anderson 1977). Its preference in the cosmetic industry is favored because it is free from dermatological and allergic toxicity. Recent studies have revealed more uses and applications of gum arabic. McLean-Ross et al. (1981) studied gum arabic metabolism as a fiber in rat colon. Vohra et al. (1979) found that it is a growth depressant for *Trilobium castaneum* larva. Kelly and Tsai (1977) compared the effect of gum arabic with other substances in cholestrol absorption and biosynthesis in rats. It has been used as a pelleting sticker to improve nodulation of *Desmodium ucinatum* in some tropical legumes (Norris 1972). Wagner et al. (1979)

reported its beneficial effect in clover inoculation with *Rhizobium trifolii* when used as a pelleting agent. Small concentrations of gum arabic used to retard evaporation were found beneficial to plant growth in sandy soil (Arya 1984). As the chemical and physical properties of gum arabic are more completely understood, no doubt more uses will be developed to utilize its superior qualities over other gums and synthetic substitutes.

It is expected that the future demand for gum arabic will increase in view of the varied interests among scientists to test its usefulness and applications in various new products and processes as reviewed above. Gum production from Sudan satisfies about 65-80 per cent of the world demand. Increasing areas are brought out of gum production and increasing number of gum tappers and pickers abandon their arduous tasks and move to towns. The planning for future gum arabic production should encourage large scale concentrated plantings in government or company reserved lands where intensive cultural practices utilizing genetically improved cultivars are used and where labor resources can be better and more easily utilized.

This study is a prerequisite to the succeeding one. After the yield variation with tree origin was determined, I examined the nitrogen content in different trees and tried to establish whether or not it was correlated to gum yield.

The paucity of information on tree yield (Philip 1975) is probably due to a complex of interacting factors that affect gum yield singly or in unison. These factors may be genetic, climatic, edaphic and/or bio-socioeconomic. The Sudanese (or Kordofan) gum is generally accepted as being the highest quality gum in the world and standards of other gums are set in reference to it (Anderson 1977; Adamson and Bell 1974). Yet the annual yield per tree and the role the above-mentioned factors play in it are not clearly understood. This provided justification for this study. Gum production represents an export of nitrogen from the system since gum contains nitrogen and other nutrients.

The gum arabic of the *A. senegal* and other *Acacia* species is stored in the layer between the bark and the wood. Since the bark of *A. senegal* is fairly thin, it is not illogical to implicate temperature during tapping season as a factor affecting yield. It has generally been observed (Obeid and Seif El Din 1969) that warm spells during winter were found conducive to gum exudation. Viscosity of gum solution is inversely affected by temperature (Anderson, 1977). It seems possible that the same rule governs gum flow within a tree.

The rhythmic nature in tree phenology has been reported in forestry literature. Wright (1962) described periodicity of seed production in temperate forest trees. A seed year may be followed by one or a number of mast years. This was attributed to gradual build up of carbohydrate reserves within the trees. The rhythmical feature of gum exudation proposed in this paper has not been previously reported for gum from *A. senegal*. Factors that caused gum yield to adopt a cyclic or rhythmic pattern were outside the scope of this work. It seems logical to suggest that high gum yield drains the carbohydrate reserves in trees and it takes a few years for its replenishment. Ecological factors that affect gum yield and deserve intensive study include tree competition and health of stand, intensity of grazing and insect infestation and climatic variables. The intensity of tapping is controlled by the farmer based on the age of trees, ownership and sale price; it should be an integral part of the study.

The conclusions drawn from this experiment were that gum yield from *A. senegal* is genetically controlled, and the trait seems to persist in a generation following open pollination of high yield mother trees. There seems to be a trend of increased gum yield with tree age. Annual gum yield in trees seems to follow a rhythm similar to that exhibited in seed production and caused by build up of carbohydrate reserves in trees.

SUMMARY, CONCLUSION AND SYNTHESIS

The ASAS evolved in the Sudan and spread elsewhere to improve the soil conditions and food supply, and enhance the physical social and economic environments. The climate of the *A. senegal* range in the Sudan was characterised by high heat and low and unpredictable rains. The sahelian drought impacted the lower rainfall sandy soil areas more than the higher rainfall clays.

The soil remained largely undeveloped due to the minimal water effects. The two main types of soil predominant in the species range were sand and clay. The soil texture in the clay type was identical in the two selected sites; the two sandy sites were different in texture and reaction. Nutrient levels correlated positively with rainfall. The total and nitrate nitrogen were higher in clay soils than in sandy soils. The effect of nutrient on biomass and nodulation was higher on clay than sand.

Such limiting climatic and edaphic conditions permitted drought tolerant nitrogen fixing leguminous plants to gain a foothold to increase the soil carbon, nitrogen and stability against desiccating winds. Of the three subfamilies of the *Leguminoseae*, the Mimosaceae were the most successful colonisers many of which were fire resistant. The genus *Acacia* played the most significant role in the sahelian ecosystem. A number of *Acacia* agroforestry systems evolved in the sahel as an improvement over the destructive slash-and-burn method of agriculture. The *Acacia senegal* method was singled out because it covers the largest area, it is more productive and generates hard currency revenues. The system may not be successful on high rainfall areas.

This study aimed to furnish an ecological basis for understanding how the biotic, climatic and edaphic factors interacted to enhance or impact the nitrogen dynamics of the system. *Aca-*

cia senegal populations were compared for genetic variability. Selection for high yield strains of gum was evaluated. The specific study objectives were to identify *A. senegal* seed source and soil type combinations that could yield higher rates of nodulation and biomass production. *Rhizobium* strains were extracted from such combinations and used to inoculate seedlings in a sterile soil to find out whether artificial inoculation is viable, and whether it would lead to an increase in nitrogen. Plant response to competition was also investigated.

The major climatic parameter that varied significantly among the four sites was rainfall (distribution and total annual). The significant drop in annual rainfall in sites E and D had caused a widespread tree and animal mortality, droughts, famines and soil erosion by wind; desertification processes extended the southern limits of the Sahara over lands previously arable. The drop in soil moisture reduced seed germination, biomass and nitrogen input which lead to further degradation in ecological and social systems. Possible loss of genotype and predisposition of plants to infestation by pathogens and harmful insects further impacts the savanna.

The species distribution decreased with increasing rainfall, and ceased completely on ironstone soil with low soil pH in southern Sudan. Leaching caused increased acidity in site D which had more rainfall. Despite its higher annual rainfall, site D had lower growth rate than site E. The current drought conditions should lead to less leaching of sandy soil and encourage the species advance southwards, a hypothesis which theoretically should stand the test of time.

Donor agencies suggest ASAS as a viable alternative for rehabilitating degraded environments. Planners need to keep in mind the rainfall and soil requirements of the species to ensure successful introduction of the species and system into exotic lands. More rigorous site selection should be made for species regeneration. It should take into account the advantages of sand dune bottom sites which should be the starting points in afforestation and reclamation projects as they contain more moisture and nutrients and result in higher biomass production than sand dune top sites.

Plant density in nurseries and forests is a critical issue that needs careful consideration. Excessive plant density in both situations proved deleterious to biomass production and nitrogen input. Management of naturally regenerated and artificial stands gain added dividends by controlling tree density at a young age before the trees reach the age at which their growth rates are highest.

Seed germination averaged 65-70 per cent with presowing treatment in water at room temperature. Soil types had no effect on germination at the regular sowing depth of 1 cm. The management implication of this is that there is no need for use of chemicals if water alone is satisfactory. This suggestion has far reaching ecological and economic implications, particularly in sahelian countries where chemicals and fertilizers are imported for rare foreign currency. The germination percentage quoted applies only for nursery situations. Far less germination takes place in the real field environment because germination requires more moisture than is normally available.

The seed/soil combination experiment shed some light on variations among specific combinations with respect to nodulation, biomass and germination. Clay soils contained higher amounts of nutrients, eg. N, P and K than sandy soils. They contained some of the micronutrients that have been generally associated with nodulation on legume plants, eg. Co and Mo. Furthermore, clay soils are more stationary than sandy soils, which are easily transported by wind, causing the top layer with moderate organic matter to be buried. The cracks that result on exposure to drought act like underground storage for organic matter which decomposes at the onset of the rainy (growing) season. Clay soils are generally higher in carbon than sandy soil. For these reasons clay soils expectedly yielded higher plant biomass and more nodules than sandy soils. The higher amount of organic matter in clay soil than sandy soil was conducive to microorganisms.

The effort to extract, cultivate and transfer microbes to affect higher nodulation in sterile soil was successful. However, there is no clear explanation as to why *A. mellifera* strains resulted in the highest nodule numbers; whereas *A. seyal* was least. Algedaref and Singa seedlings were expected to yield high nodule numbers because they both originate from soil that cause nodulation to occur. Singa came true to expectation, but Algedaref failed.

The range of *A. senegal* extended over a wide climatic gradient and distinctly different soil types separated by vast distances and effective geographic barriers. For these reasons genetic variability occurred within and between populations. Massive seed transfer from El Obeid to Algedaref and to a lesser extent to Singa took place in the 60's to meet the demand of expanded mechanized tree seeding following crop failure. The choise of species was based solely on economic return. The best seed source would be the local origin since the trees are adapted to their environment over a long period of time. The transfer of seed may have marred or completely disrupted the natural selection processes and made population study difficult.

Within locality E, selected strains were tested for gum yield variations. Some strains proved more productive to gum and less to biomass than others. There was no correlation between gum and nitrogen yields.

The variable climatic, edaphic and biotic components of the *A. senegal* system has nurtured a variety of *Rhizobium* strains with varying capacity to fix nitrogen. The search for a soil and seed combination that yielded above average nodulation and biomass culminated in finding more than one strain. These strains were isolated and successfully used to infect plants in sterile soils.

Limited soil and space resources impacted biomass and nodulation. Single plant biomass was severely affected, but total biomass was not. Competition also reduced growth rates in plantations. Reduced photoperiod caused leaf shed that occurred over a period of time. The length of time varied with soil fertility. Leaf shed deprived nodules from photosynthates and they degenerated.

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AUTOBIOGRAPHICAL STATEMENT

Born in Omdurman on the west bank of the River Nile in 1941, the author attended Khartoum University for two years and obtained the B.Sc. (Intermediate). He was sponsored by the Sudan Government for a study course in Forestry at Aberdeen University, Scotland in which he graduated with his basic degree in 1969. He served in the Sudan Government as a silvicultural research officer at Elobeid in Kordofan region until 1971 when he was promoted assistant conservator of forests and transferred to Jebel Marra Forests Circle where he concurrently served as an assistant director for natural resources and silvicultural research officer.

He was transferred to Kadugli in 1974 to serve as Assistant Commissioner for Forests Affairs in South Kordofan Province and as a member of the provincial council. He was appointed member of the executive board of the Mechanized Farming Corporation and a member of the provincial land use committee. During this period he wrote (Saad 1979), a paper presented to a symposium in Khartoum University and published in its proceedings.

In 1979 he was transferred to the National Forest Administration in Khartoum to head the Planning Unit and later the Afforestation Section. He was concurrently assigned to the technical committee sponsored by the Arab Organization for Agricultural Development (AOAD), an agency of the Arab League of Nations. The committee wrote a book on the *"Possibilities for Agricultural Development in Western Sudan"*, of which a chapter on forest resources, (Saad 1982), was writen by him. The book was edited by Hassan M. Beteke and published in Arabic by AOAD in 1982.

He was seconded in 1981 to the Agricultural Research Corporation and transferred to Elobeid as a director of the Agricultural Research Station, and gum research specialist under

WSARP, a project jointly funded by USAID and Sudan Government. During his term in Elobeid he took a temporary part-time consultancy assignment with the Food and Agriculture Organization of the United Nations as a gum arabic research consultant to the Rehabilitation of the Gum Belt Project, which was supported jointly by The Sudan Government, FAO and the Sudano-Sahelian office of the United Nations in New York. During that assignment he wrote four interim reports and a final report, (Saad 1983) concluding his assignment. He also wrote Saad 1983 (a) in which a long term forestry research plan was proposed.

The author came to the USA in 1983 for non-degree training in agroforestry in Idaho University for nine months. He received a Special Doctoral Research Assistantship from Old Dominion University Biological Sciences Department for three years. As a co-principal investigator with his major professor, Dr. F.P. Day Jr. they received a USAID grant for $ 126,000 to conduct his degree research which is presented in this dissertation. During his field research assignment he coauthored chapters 9 and 10, (Noel et al. (1990) and Bunderson et al. (1990)) of *Planning For Agroforestry* which was edited by Budd W.W., I. Duchhart, L.H. Hardsty and F.Steiner, and published by Elsevier in 1990.

He is a member of the American Institute of Biological Sciences. He jointly presented a poster session in the 39th and 40th annual meetings in Davis, California 1987 and Toronto Canada 1988 as a coauther with Dr. F. P. Day Jr. He is also a member of the Association of Southeastern Biologists. He presented a paper at their meeting at Towson State University, Baltimore, Maryland in 1990.