SOME ASPECTS OF THE WATER RELATIONS OF TWO MAHOGANY SPECIES

A thesis submitted by

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I hereby declare that the work presented in this thesis 'Some Aspects of the Water Relations of Two Mahogany Species' was done entirely by me in the Department of Botany, University of Ghana, Legon, from September 1970 to November 1971.

No part or parts of this thesis has been submitted for a degree elsewhere.

(GLADYS DODOO)

ABSTRACT

The general distribution, growth form and economic importance of Khaya senegalensis (Desr) A. Juss. and Khaya ivorensis A. Chev. are described. Some aspects of the water relations of seedlings of these two species, the former a savanna species and the latter a forest species were studied with the view of ascertaining whether moisture plays an important role in determining the pattern of their distribution.

Growth of seedlings under four soil watering regimes namely - -0.3 (A), -0.4 (B), -0.8 (C), and -4.5 (D) bars; and under culture solution and culture solution to which polyethylene glycol was added to give the following osmotic potentials (bars): -0.3 (A), -2.8 (B), -5.3 (C), and -10.3 (D) was studied. The experiment was done in the greenhouse. Growth of K. senegalensis was more sensitive to moderate moisture stress and less sensitive to high moisture stress. K. ivorensis on the other hand showed less sensitivity to moderate stress but high sensitivity to severe stress. However when soil moisture stress was -0.3 bars, growth of K. ivorensis was very poor. This was attributed to a reduction in root permeability due to poor aeration as a result of more permanent near saturation of the soil.

Studies of diurnal patterns of plant water status were carried out by examining leaf relative water content, (R.W.C.) leaf water potential (L.W.P.) and stem diameter variation, in relation to soil moisture stress. R.W.C. was overall higher in seedlings of K. senegalensis than in those of K. ivorensis. L.W.P. on the other hand was lower for K. senegalensis than for K. ivorensis seedlings. Stem shrinkage decreased with decrease of soil moisture content from 100 to about 50%, field capacity. The decrease in K. senegalensis was greater than in K. ivorensis. However at 27% field capacity, shrinkage in K. senegalensis was consistently reduced more than in K. ivorensis. This may indicate better water conservation by the former species.

Transpiration was also studied in relation to the soil moisture treatments, both in the greenhouse and in the research room, the latter being a semi-controlled environment where temperature, relative humidity and light intensity were precisely known. The transpiration of seedlings growing in osmotic solution was also studied in the greenhouse, employing stresses of -0.3 and -10.3 bars. Transpiration generally decreased with moisture stress in the root medium. In the research room transpiration of K. senegalensis was higher than that of K. ivorensis under all soil treatments. In the greenhouse, however, similar higher transpiration rates were recorded for K. senegalensis seedlings than for K. ivorensis seedlings when stress was from -0.3 to -0.8 bars, but at severer stresses (-4.5 and -10.3 bars) transpiration of K. senegalensis was reduced more than that of K. ivorensis.

Infiltration of leaves of *K. senegalensis* and *K. ivorensis* with mixtures of liquid paraffin and commercial Kerosene showed that stomatal conductivity of *K. senegalensis* leaves was greater than that of *K. ivorensis* leaves at low moisture stress. At more severe stress (-4.5 bars) conductivity of leaves of both species was low.

The desorption curve for *K. senegalensis* seedlings was above that for *K. ivorensis* seedlings. Curves of leaves for adult trees of both species were however similar. *K. senegalensis* leaves could tolerate desiccation better than *K. ivorensis* leaves.

Stomata of *K. senegalensis* leaves close at higher relative water content values than those of *K. ivorensis* leaves.

The results are discussed in relation to the distribution of these species and to the general ecological problem of the control of plant distribution between forest and savanna in West Africa.

CONTENTS

INTRODUCTION

General

In general, the natural pattern of distribution of plants in any area is largely controlled by environmental factors. The main physical factors of the environment - temperature, light, moisture, wind and soil, frequently set limits to the occurrence of species, both on a geographical and on an ecological scale (Raunkiaer, 1934; Daubenmire, 1947; Hopkins, 1965). The importance of any of these factors in a given area is determined both by its general mean level and by the range between its minimum and maximum levels.

Temperature is the primary factor responsible for the main vegetational belts of the world. In many geographical regions it is also the overriding factor controlling the pattern of plant distribution on an ecological scale. In West Africa, however, where daily and seasonal variations in temperature are usually small (see Lawson, 1966), this factor is less important in controlling plant distribution. There is rather a general belief that the main division of West African vegetation into forest and savanna is causally related to environmental moisture conditions (see for example Taylor, 1952; Keay, 1959).

Hopkins (1965) and Lawson (1966) in their general accounts of West African ecology point out that in this region rainfall varies greatly between areas, in amount and seasonal distribution. Over 80 ins. (200 cm) of rain falls annually in most parts of the forest areas. This amount decreases progressively inland from the coast until within the savanna areas there is usually less than 45 in. (114 cm) of rain per annum. Rainfall in the forest regions is distributed in such a way that there are not more than two months with less than one inch (2.5 cm) of rain. On the other hand the savanna regions may have up to five or six months with less than 1 inch (2.5 cm) of rain.

The balance between precipitation and potential evaporation is perhaps a more meaningful criterion than amount or distribution of rain for assessing water availability for plant growth. From a simple survey of this balance for Africa, Davies and Robinson (1969) reached the tentative conclusion that the forest-savanna boundary, at least in West Africa, coincides reasonably well with the -200 mm isopleth, where although there is no excess of precipitation over potential evaporation for the year as a whole, there is some amount of water stored in the soil which could support growth of forest species. Thus it is clear that savanna vegetation type is associated with a dry climate, hence the general belief that savanna plants are more drought-adapted than plants of the forest regions. Comparative experimental work to test this belief is however largely lacking so that there is little knowledge of the mechanisms by which plants from these two regions are adapted to environmental moisture conditions.

Mechanisms by which plants adapt themselves to drought have been much studied and reviewed (see for example Parker, 1956, 1968; Stocker, 1956, 1960; Iljin, 1957; Oppenheimer, 1960, 1968; and Kozlowski, 1968). Oppenheimer (1960) points out that these mechanisms generally fall under three main heads: plants may be drought escapers, drought evaders or drought endurers. Drought escapers apparently have no adaptation to withstand drought. They normally complete their life cycle before the unfavourable period. Unlike the escapers, drought evaders survive under drought by preventing the development of internal water stress under a given degree of external stress. This they do by efficient control of transpiration and efficient water absorption. As has been pointed out by several workers (for example Sullivan and Levitt, 1959; Oppenheimer, 1960; and Parker, 1968), numerous adaptive morphological characters are associated with the phenomenon of drought evasion. In contrast to drought escapers or evaders, drought endurers are able to carry on their normal life activities under drought even when there is internal stress. Most studies of plant adaptation to drought have been concerned with identifying which of these mechanisms is paramount in any given situation, and with understanding details of plant attributes which make drought resistance possible. Such studies gain in value when they contribute towards understanding the causal factors of the pattern of plant distribution in any area. To achieve such an understanding is the general objective of the present study.

The Problem

The general paucity of experimental investigations on the water relations of West African plants has already been mentioned. The few studies conducted in this field (for example Lawson and Jenik, 1967; Okali, 1971a), were mostly concerned with mechanisms of adaptation to environmental stress by some species on the Accra Plains of Ghana.

Although vegetation on the Accra Plains is dissimilar to Guinea savanna in many respects (Wills, 1962; Hall and Jenik, 1968), Lawson (1966) nevertheless indicates that the Accra Plains show many interesting ecological factors at work which may throw light on processes in other types of savanna. The vegetation here consists of short grass and tree-thickets which often occur in scattered clumps (Wills, 1962; Aubreville, 1959). Boughey (1957), described the Accra Plains as a kind of steppe. As in true savanna regions, the climate over the plains is relatively dry. Less than 30 in. (76 cm) of rain falls annually, (Lawson, 1966; Lawson and Jenik, 1967). Thus studies of mechanisms of plant adaptation to this habitat may be useful in understanding the general nature of the control of plant life by environmental moisture in West Africa. For example, Lawson and Jenik (1967) in their study of the interrelations of microclimate and vegetation on the Accra Plains, compared transpiration rates (by the rapid weighing technique) and other features of species on the wind-ward and leeward sides of a thicket. In general they found that species on the windward side transpired less and had more xeromorphic features than those on the leeward side, thus demonstrating that microclimate (and here particularly desiccating winds) may exert considerable influence on vegetation.

Okali, (1971a) further studied the water relations of some of the woody species on the plains. Using mainly detached leaves or leaf discs taken from plants growing in the field, he compared transpiration rates and the relationships between leaf water content, leaf water potential, stomatal closure and tissue damage. His results showed that the species studied, exhibited several mechanisms of adaptation to drought.

Neither of the above studies examined the response of whole plants (e.g. growth) to drought, and although they demonstrate the possession of adaptive features by species in a dry area, they do not provide an adequate basis for testing the role of moisture in determining the pattern of plant distribution between forest and savanna, because they examined species adapted to one type of climate alone. A more satisfactory approach for such a test would be to compare the water relations of forest and savanna species.

There is little information in the literature on the water relations of West African forest species. The only suitable data which permit such a comparison to be made were recently given by Hopkins (1970a,b). From a study of species in forest and savanna sites of the Olokemeji Forest Reserve in Nigeria, Hopkins was able to show that for forest species leaf water may be 'severely limiting at the severest part of the dry season'; he could not demonstrate similar limitation for the savanna species although he attributed this to probable effects of leaf age in masking the relation between environmental moisture and leaf water status. Hopkins' study examined only one aspect of the water relations of forest and savanna species and this limits its usefulness as a basis for generalization on the probable role of moisture in controlling plant distribution in this part of the world.

Richards (1952) draws attention to the existence in West Africa of certain tree genera whose component species are restricted to sharply contrasting habitats. He cites the genera *Khaya* and *Lophira* as examples, noting that the former genus is represented by *K. ivorensis* and *K. anthotheca* in the Wet Evergreen forest, by *K. grandifoliola* in the Dry Forest and by *K. senegalensis* in the savanna. *Lophira* is similarly represented by *L. alata* in the forest and *L. lanceolata* in savanna. To these examples may be added such genera as *Afrormosia*, *Daniellia* and *Cussonia* which have both forest and savanna species. If environmental moisture is indeed the overriding factor causing the restriction of these closely related species to contrasting habitats, it should be possible to demonstrate this by comparing the water relations of any two such species of the same genus - the one from forest and the other from savanna.

The object of the study described in this thesis was to examine experimentally the water relations of two such species, Khaya senegalensis (Desr) A. Juss, and K. ivorensis A. Chev, commonly called Dry Zone Mahogany and African Mahogany respectively, to find possible differences between them which might help in understanding the factors responsible for their restriction to contrasting habitats. The two species are not only taxonomically closely related, they are also as is more fully described at a later stage, similar in growth habit, phenology and reproductive biology. Differences between them could therefore be expected to have arisen more as an adaptation to their respective habitats than would be the case if the two species were dissimilar in the above four respects. If environmental moisture plays a large part in determining the restriction of these two species to different habitats, K. senegalensis would be expected to show greater adaptation to drought than K. ivorensis.

Approach to the problem

Several investigators of plant water relations have approached such studies with different objectives. Some investigators have studied single species (for example Weatherley, 1950, 1951, 1965; Gates, 1955a,b; Rutter and Sands, 1958; Aspinall, 1965; Klepper, 1969); others have compared the responses of a group of species to similar environmental conditions (for example Slatyer, 1955, 1957b, 1960; McKell, Perrier and Stebbins, 1960; M.S. Jarvis, 1963; Jarvis and Jarvis, 1963a,b,c and e, 1965; Connor and Tunstall, 1968). The objective when single species have been studied has usually been to understand the processes through which environmental moisture affects plant growth. When several species have been studied together, the implied aim has been to understand the comparative effects of environmental moisture with the view to explaining ecological situations. The latter is the case in the present study.

The value of comparative water relations studies in contributing to an understanding of the causal factors of plant distribution is illustrated by the work of many authors. Thus McKell, Perrier and Stebbins (1960) compared two sub species of *Dactylis glomerata* and concluded that the restriction of the sub species *D.lusitanica* to mesic habitats and *D.judaica* to xeric habitats in Israel might be due to differences in the water demand of the two species. Similarly, investigations by M.S. Jarvis (1963) on factors which limit the distribution of *Saxifraga hypnoides* and Prunus padus to upland areas of North western parts of Great Britain and *Filipendula vulgaris* and *Thelycrania sanguinea* to more low land parts to the

South east showed that this could be attributed to differences in soil moisture in these areas. Sullivan and Levitt (1959) found from their work that a possible explanation for the restriction of Quercus palustris to moist areas and Q. rubra to upland areas in Missouri might be the difference in drought resistance of the two species. Rychnovska and Květ (1963) accounted for the distribution of Festuca domini, Corynephorus canescens and Helichrysum arenarium in Czechoslovakia on the basis of their water relations. Bannister (1964) also related differences in distribution of Calluna vulgaris, Erica cinerea and E. tetralix to the water relations of these species. The distribution of various species of Artemisia in arid and semi arid communities in Kazakhstan has also been related to differences in the internal water balance of these species (Sveshnikova, 1965).

Irrespective of the objective investigators have sought to understand plant water relations by observing growth and transpiration responses of the species to environmental moisture stress (for example Gates, 1955a; Rutter and Sands, 1958; M.S. Jarvis, 1963; Jarvis and Jarvis, 1963a,b,c), by studying the water relations of tissues through, for example, measurements of the relation between water content and water potential of tissue (Slatyer, 1960, 1962c; Connor and Tunstall, 1968), the relation between water content and stomatal closure (Bannister, 1964; Jarvis and Jarvis, 1963d,e), and the relation between tissue water content and tissue damage (desiccation tolerance) (Sullivan and Levitt, 1959; Noy-Meir and Ginzburg, 1969b; Okali, 1971a). Some investigators have followed changes in stem diameter as a measure of variation in plant water status (Kozlowski, 1967; Ogigirigi, Kozlowski and Sasaki, 1970). The present study represents an attempt to combine several of these approaches. Following an analysis of the growth responses of the experimental species to varying moisture status in the root medium, internal water balance over most of the day for plants growing in wet or dry soil was compared. In order to understand the growth responses and diurnal patterns of plant water status more clearly, transpiration and some aspects of tissue water relations of the experimental species were then studied.

These experiments were carried out in the laboratory and mostly with potted plants as has been previously done by several workers such as Slatyer (1957b, 1961), Rutter and Sands (1958), McKell, Perrier and Stebbins (1960), Brix (1962), Jarvis and Jarvis (1963a,b,c,d,e, 1965), and Lawlor (1969). There are clear difficulties in attempting to use laboratory studies in understanding natural distribution of plants, but evidence in the literature, suggests that when these studies are comparative, individual differences revealed could be of ecological significance (cf. McKell, Perrier and Stebbins 1960, M.S. Jarvis, 1963).

CHAPTER I

EXPERIMENTAL SPECIES, MATERIALS AND GENERAL METHODS

1.1. The Experimental Species

The species chosen for this study - Khaya senegalensis (Desr) A. Juss. and Khaya ivorensis A. Chev. are both trees belonging to the family Meliaceae. They are both widely distributed throughout West Africa. Irvine (1961) notes that K. senegalensis extends from Senegambia to Cameroons, Sudan and Uganda while K. ivorensis extends from the Ivory Coast to Gabon. Hutchinson, Dalziel and Keay (1954) however, indicate that K. ivorensis could be found as far south as Cabinda, that is between latitudes 4° and 6° south of the equator and longitudes 10° and 13° east of the Greenwich Meridian.

Throughout their geographical range, the two species occur in distinctly different habitats. Richards' (1952) observation on this has already been mentioned. Hutchinson, Dalziel and Keay (1954) also point out that K. senegalensis is a savanna tree but grows especially by streams. Taylor (1960) describes K. ivorensis as occurring throughout the high forest zone of West Africa. In his book 'Woody Plants of Ghana' Irvine (1961) indicates that K. senegalensis is found in savanna and fringing forest, particularly in low lying places besides streams and K. ivorensis in deciduous and evergreen forests. The contrast in the habitats of the experimental species appears thus to be well documented.

The two species appear to be dissimilar in their soil preferences. K. senegalensis prefers good alluvial soil but not swampy soils, while K. ivorensis is known to favour moist valley soil and apparently can also survive considerable flooding (Kinloch, 1945). Data to be presented later in the present study suggest that tolerance to flooding is limited in K. ivorensis seedlings. Taylor (1960) further points out that K. ivorensis occurs on heavy or rich alluvial soil with good drainage near water courses and damp areas.

The growth form and general morphology of the two species have been adequately described by Lely (1925), Dalziel (1937) and Irvine (1961). K. senegalensis grows up to 30 m in height and three meters in girth. It has no buttresses. The bark is grey and scaly and the slash is red. Unlike K. senegalensis, K. ivorensis grows up to 60 m in height and 4.5 m in girth. It is strongly buttressed and has a tall cylindrical bole up to 27 m above the buttress. The bark is ashy white to brownish black. The slash is crimson.

The crowns of adult trees of both species are dense with branches bearing alternate paripinnate leaves about 25 cm long with 4 - 8 opposite or subopposite, exstipulate, oblong or oblong elliptic leaflets. Examination of K. senegalensis indicates that each leaflet is about 10 cm long and shortly acuminate at the apex. Each leaflet has a petiolule which is about one cm long. Each leaflet of K. ivorensis on the other hand is about 14 cm long and 7 cm wide with well defined drip-tips, (see appendix 1, Plate I), smooth, acuminate and usually rounded at the base with a short petiolule about 1.5 cm long. Observations on seedlings in the greenhouse, on herbarium specimens from trees of different ages as well as on trees in the Botanical Garden, Legon, show that the well defined drip-tips of K. ivorensis leaflets decrease in length as the tree grows older. In general mature leaves of K. senegalensis are comparatively much smaller, with a thick net of veins, than those of K. ivorensis. This is probably a xeromorphic feature (cf. Lawson and Jenik, 1967).

Detailed examination, of the leaves, made on epidermal prints and on microtome sections revealed that stomata occur mostly on the lower surfaces of leaves in both species; those of K. senegalensis being more numerous (Table 1). There are very few stomata (less than $1/mm^2$) on the upper surfaces of the leaves of both species. Metcalfe and Chalk's (1950) statement that stomata occur only on the lower surface in leaves of Khaya species probably therefore does not necessarily apply to seedlings. The stomatal frequencies obtained for the two species are comparable to figures quoted by Yanney-Wilson (1963) for three species on the Accra Plains: Baphia pubescens, Vernonia senegalensis and Fluggea virosa. Yanney-Wilson considers frequencies more than $502/mm^2$ to be an indication of xeromorphy in leaves. On this basis the leaves of both species could be assumed to have some xeromorphic features. Metcalfe and Chalk (1950) note that the palisade mesophyll in Khaya species is more than one layer.

Table 1

Anatomical features of seedling leaves of *Khaya senegalensis* and *K. ivorensis*

Leaf anatomical character	Species	
	K. senegalensis	*K. ivorensis*
Mean thickness of leaf (µ)	822	508
Mean thickness of cuticle (µ)	14	13
Length of stomata (µ)	14-20	11-18
Stomatal frequency (mm^2)	660	580
No. of palisade mesophyll layers	1	1
Mean height of palisade cell (µ)	272	104
Mean width of palisade cell (µ)	46	38
Thickness of spongy mesophyll (µ)	347	324
Mean diameter of spongy mesophyll cell (µ)	56.5	61.0

This has been found to be true of leaves from adult trees of K. senegalensis and K. ivorensis: they have two or three layers of palisade. However mature leaves of seedlings were found to have only a single layer of palisade (Fig. 1) with those of K. senegalensis being much deeper (about 270 microns) than those of K. ivorensis (about 104 microns).

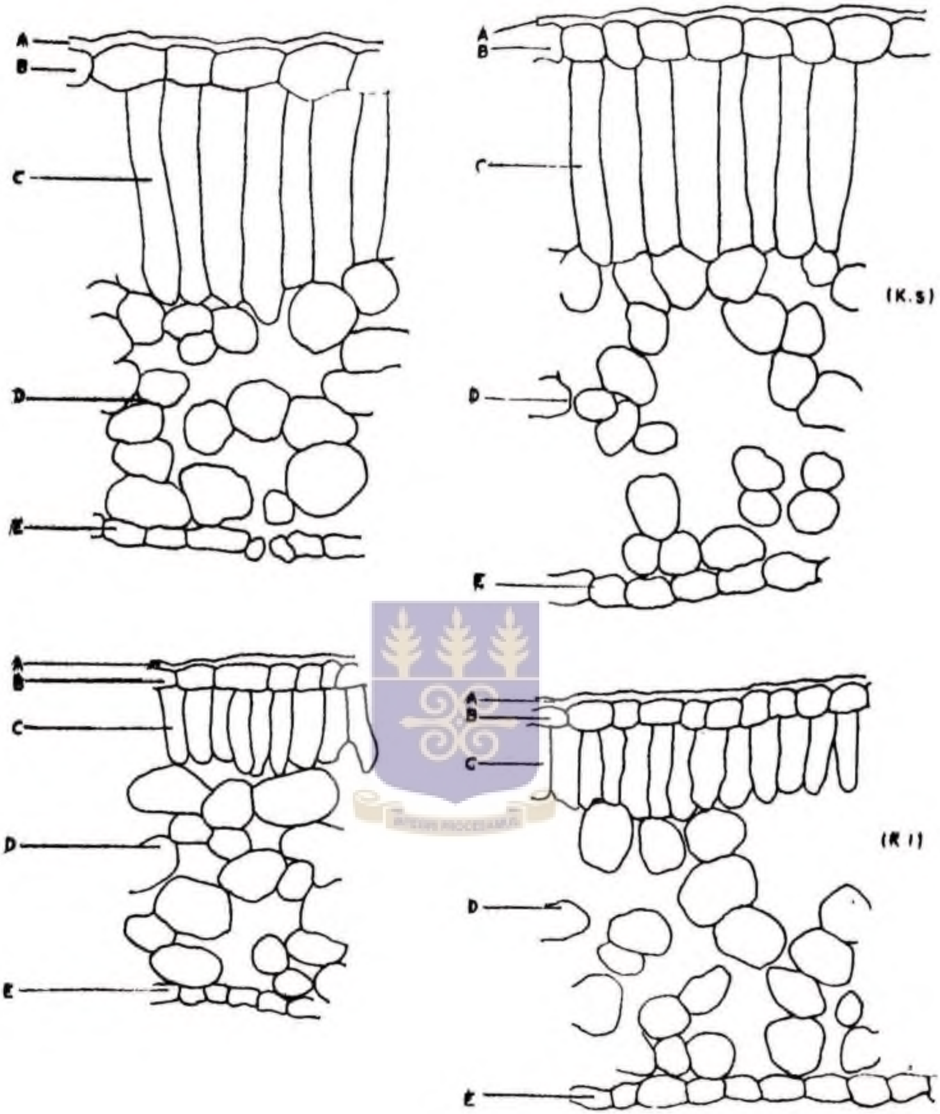
In their natural habitats, K. senegalensis and K. ivorensis are never deciduous (Kinloch, 1945; Taylor, 1960). Kinlock (1945) however indicates that in the drier areas of the high forest zone where K. ivorensis is seldom found, the tree is deciduous for a short period at the beginning of the dry season.

The similarity between the two species extends to their reproductive biology. The flowering season for both species is July to January. Flowers are arranged in axillary panicles. Fruits of both species are capsules. They ripen and open to release their seeds between February to May. The fruit of K. senegalensis is about 6 cm in diameter and generally four-valved, while that for K. ivorensis is about 9 cm in diameter and opens by five valves.

Seeds of the two species are brown and winged. Measurements show that the seeds of K. senegalensis are about 1.8 cm long and 2.4 cm broad and are oblong-elliptic in shape, while that of K. ivorensis are about 2.3 cm long and 3.7 cm broad; they are oblong to triangular in shape. The seed of K. senegalensis is comparatively much thicker with an average dry weight (without testa) of about 16 mg while that of K. ivorensis weighs about 11 mg. Seeds

FIG. 1

CAMERA LUCIDA DRAWINGS OF EXAMPLES OF TRANSVERSE SECTIONS OF LEAVES OF KHAYA SENEGALENSIS (KS) AND K. IVORENSIS (KI) Seedlings. LEFT (THIN LEAVES), RIGHT (THICK LEAVES).



A : CUTICLE
B : UPPER EPIDERMIS
C : PALISADE MESOPHYLL
D : SPONGY MESOPHYLL
E : LOWER EPIDERMIS

FIG.1

of both species are short lived.

Observations in the present study show that germination, in both species, generally starts eleven days after sowing; by the 21st day almost all the viable seeds germinate. Often K. senegalensis seeds start germinating before K. ivorensis, especially when fresh. Germination is hypogeal for both species. The shoot of K. senegalensis is green and that of K. ivorensis is red and slender. The first two leaves of both species are simple and opposite and are borne about 8 - 10 cm above the soil. The areas of these leaves when about two months old are respectively about 14.0 and 11.5 sq. cm for K. senegalensis and K. ivorensis. The next few leaves are also simple but alternate. These are followed by a few unifoliolate leaves. Compound leaves develop later, normally after two months of germination. The first few sets are trifoliolate, later ones are imparipinnate with about 4 - 9 leaflets which are opposite. Leaflets of K. ivorensis are much larger than those of K. senegalensis (see Appendix 1, Plate). One year old seedlings of both species have both paripinnate and imparipinnate leaves.

At emergence seedlings of K. senegalensis are much larger than those of K. ivorensis and by the age of two months, the height of the seedlings is about 13.0 cm with 6 - 9 leaves while that of K. ivorensis is about 10.0 cm with about 4 - 6 leaves. The larger initial size is presumably due to the larger seed size of K. senegalensis (see p. 15). This might be advantageous for quicker establishment.

The two species are not only of ecological interest; they are also economically important species. The first exploitation of Mahogany species for timber for export began in about 1891 (Taylor 1952). It has since remained one of the most important species in the timber economy in this country. Economic reports of the Forestry Department indicate that in 1969 (Anon) the log volume output of K. ivorensis, whose trade name is Dubini, from the forest reserves was about one million cubic feet (28000 cu.m). Over 19 million logs from 34 timber species valued at about 24 million new cedis were exported from January to December, 1969, and out of this about 1.5 million cu. ft. (42000 cu.m) valued at about 2.2 million new cedis was K. ivorensis. Further reports in 1970 indicate that Mahogany yield from forest reserves in the high forest zone, was about 1.3 million cu. ft.(36000 cu.m) out of which one million was K. ivorensis. K. senegalensis being of smaller size is of less importance. The first export of the species as timber was made from the Gambia over a century ago. Although an excellent timber, it is seldom now exported from Ghana because of its small size and weight. Local uses of these two Mahogany species include their conversion to charcoal for fuel. Annual reports of the Forest Products Research Institute here (1968 and 1969) emphasize that because of the general increase in industrial consumption of wood, it is necessary to establish plantations of the more important timber species of which the mahoganies are certainly leading examples. It is clear that successful establishment of such plantations can be enhanced by the availability of adequate information on the ecology of the timber species that are considered as important. Some of the results from the present study might contribute towards providing such information. In particular, the findings from this study might assist in the choice of combination of management practices if it is desired to extend the habitat ranges of these two species with respect to environmental moisture conditions.

1.2. Experimental Plants

Seedlings of K. senegalensis and K. ivorensis were used for this study except in one instance when certain determinations were made on adult trees growing in the Botanical Garden. The main advantage of using seedlings is that they are more convenient to handle in laboratory work. Although the seedling phase represents only a small fraction of the entire life of a plant, distributional patterns of plants in nature are often governed by factors affecting seedlings. (Moore, 1926; Daubenmire, 1943; Jarvis and Jarvis, 1963a).

Seedlings of K. senegalensis for experiments between October 1970 and April 1971 were raised from seed supplied by the Forest Products Research Institute, Kumasi, Ghana. The seeds had been collected from Koforidua in May 1970. Seedlings for later studies were raised from seeds collected in March 1971, from the grounds of the University Campus, Legon where this species lines the main University avenue. Seedlings of K. ivorensis were raised from seed also obtained from the Forest Product Research Institute, Kumasi. The seeds had been collected from Asenanyo Forest reserve, in Ghana, also in May 1970.

For some experiments larger seedlings were used to supply sufficient leaf material for investigations of tissue water relations or to provide stems large enough to enable observations on diameter changes to be made. Some of these seedlings were less than one year old while others were just over one year old. At the time of experiment, these seedlings were between 50 and 80 cm tall in both species.

1.3. Growth media

Plants were grown on soil or in culture solution to which polyethylene glycol was added when it was desired to vary the water potential of the root medium. Both media have advantages and disadvantages for the study of plant water relations. Several investigators (Sands and Rutter, 1959; Jarvis and Jarvis, 1963a,b; Aspinall, 1965), who have used soil as a rooting medium point out that the main disadvantage is that it is not possible to know the exact moisture stress to which roots are subjected, since water potential at the root-soil interface changes continuously with transpiration by the plants and as roots grow into new regions of soil. Exact knowledge of soil moisture stress at the root-soil interface is however important since this factor appears to be the main soil characteristic controlling soil water availability for plant growth (Slatyer, 1967). The use of well stirred solutions containing osmotic substrates such as sodium chloride (Slatyer, 1961; Nieman, 1962), mannitol (Gingrich and Russell, 1956; Slatyer, 1961, Jarvis and Jarvis, 1963c,d) and polyethylene glycols (Largerwerff, Ogata and Eagle, 1961; Jarvis and Jarvis, 1963d, 1965; Kaul, 1966; Kaufmann, 1968; Lawlor, 1969, 1970), attempts to overcome this limitation with soil. But there are also disadvantages in using aqueous solutions of osmotic substrates. The first is that the water potential will comprise only an osmotic component whereas soil water potential is made up of both osmotic and matric components, although there is evidence (Wadleigh and Ayers, 1945) that this difference may have little significance for plant growth response. Another disadvantage is that some osmotic substances tend to be absorbed by the roots, thus decreasing plant water potential. For example, Slatyer (1961) found that sucrose, sodium chloride and potassium nitrate were readily diffusible into the roots of tomato. It has however been found by Lawlor (1970) that undamaged roots have low permeability to polyethylene glycols of molecular weights 1000, 4000 and 20,000. Some of these substances, when absorbed, are also toxic to the plant (Largerwerff et al, 1961; Jarvis and Jarvis, 1963d; Macklon and Weatherley, 1965; Leshem, 1966; Lawlor, 1970).

In spite of these disadvantages, both soil and osmotica have been successfully employed, by most of the authors cited above, to study several aspects of plant response to moisture stress in the root medium, hence their use in the present study.

1.4. Culturing technique

Seeds for soil experiments were sown in wooden boxes (51 x 45 x 10 cm) containing John Innes Potting Compost II which was obtained from the Botanical Garden, Legon. Seeds for culture solution experiments were sown in plastic bowls (about 35 cm in diameter and 14 cm deep) containing vermiculite. The containers were placed on a platform in the greenhouse. Germination normally took place 11 to 21 days after sowing. Germinated seedlings in soil were allowed to grow for one month before they were transplanted. Those in vermiculite were allowed to grow only for three weeks before transplanting. The shorter time here was found necessary as it became more difficult to free the roots from the vermiculite when seedlings were allowed to grow for a longer period. At the time of transplanting into the respective media seedlings were mostly at the three to five leaf stage (*K. senegalensis*) or the two to three leaf stage (*K. ivorensis*). John Innes Potting Compost II was also used for subsequent growth of seedlings in soil experiments. This medium allows good aeration while holding sufficient moisture for plant growth. As prepared by the Botanical Garden the mineral nutrient status of the soil was found to be adequate for growth of the experimental seedlings and there were no harmful organisms since preparation included heat sterilization. A bulk quantity of this soil was obtained at the beginning of the experiments. Soil for each experiment was taken from this bulk to maintain uniformity of growing medium. This also meant that characteristics determined on samples from this bulk were applicable to soil used in each experiment.

For culture solution experiments modified half strength Arnon and Hoagland (1940) (see Hewitt 1952) nutrient solution was used. This culture solution was recommended by Dr N.I.C. Nwachuku of this department who had found it suitable for growth of tree seedlings. Seedlings were grown in polyethylene containers. These containers were preferred to porous clay pots because of their lightness and also because they prevented evaporation from their sides. Containers for the soil experiments were 12 cm in diameter with a capacity of about one litre. Five drainage holes were bored at the base of each bucket and over these was placed a small nylon mesh to prevent loss of soil particles. The containers were filled with soil to about 2.0 cm below the rim so that each held 1.4 - 1.5 kilogram soil at field capacity. There was one seedling in each container. Containers for culture solution experiments were 13.0 cm in diameter with a capacity of about 1.1 litres. They were covered with black paper to prevent light reaching the solution in order to limit algal growth. Each container held about 700 ml of culture solution, and was covered by a lid through which seven holes had been made for insertion of seedlings and an aerator. Larger containers were used for culture solution experiments in which transpiration was measured. These were about 15 cm in diameter and about 2.5 litres capacity.

1.5. Experimental growth room

Most of the experiments described in this study were carried out in a greenhouse in the Botany Department, Legon. Thermohygrographs were installed in the greenhouse to record temperature and relative humidity. Midday temperatures in the greenhouse before the actual experimental work were found to be too high (about 40°C); it was therefore found necessary to shade the house with palm leaves. On certain occasions, Piché evaporimeters were installed in the greenhouse to record evaporation. Throughout the experimental period temperatures in the greenhouse never exceeded 36°C: these normally occurred between 11.00 and 14.00 hours depending on the sunniness of the day. Minimum values were obtained at night and these never fell below 18°C. Minimum relative humidities were around 45 to 50%: these also were obtained between 11.00 and 14.00.

Some transpiration experiments were carried out in the Research room of the Botany Department, Legon, where, through air conditioning, temperature and humidity were controlled slightly more precisely than in the greenhouse. Because of the near constant temperature maintained in this room, determinations requiring more precise temperature control were also carried out here.

CHAPTER II.

GROWTH IN RELATION TO MOISTURE STRESS IN THE ROOT MEDIUM

2.1. Introduction.

Normal plant growth is sensitive to both too much or too little water. Hunt (1951), Walker (1962), Hosner and Leaf (1962), Gaertner (1963) and Mueller - Dombois (1964), observed that excess water is detrimental to most species presumably through poor aeration and the consequent reduction in root permeability (Kramer, 1956; Mees and Weatherley, 1957).

Several workers, however, indicate that water deficiency is even more important than excess water in limiting plant growth (Slavik, 1965; Kozlowski, 1968). Thus Marsden (1950, cited by Kozlowski, 1958) observed that drought in New England had been responsible for great reduction in growth of trees, poor fruit development, early leaf fall, dieback, thin foliage, transplanting failures, sunscorch and premature death of trees. In temperate climates, although duration of the growing season is controlled mainly by photoperiod and temperature, water deficiency during the growing season also has influence on growth of forest trees (Zahner, 1968). In tropical regions, the dry season is usually the least favourable period for plant growth, although the relative importance of moisture as against other environmental factors (for example, photoperiod and low night temperatures, Njoku, 1959; 1964; Longman, 1969) is little understood.

Reduction of growth results because of the effects water deficit existing in the root medium has on internal water balance of plants. Plant growth is related directly to the internal water balance of plant (Kramer, 1963; Slatyer, 1967, 1970). In nature plant water status is controlled by the degree of soil moisture stress and the diurnal lag of absorption behind transpiration (Kramer, 1962; Slatyer, 1970). These are in turn controlled by environmental factors such as temperature, solar radiation, humidity and wind, the effects of which are modified by features of the plant which tend to reduce transpiration (e.g. leaf characters) or enhance absorption, (e.g. efficient root system).

During the day transpiration usually exceeds absorption, internal water deficits develop, leading to a steep gradient in water potential between plant and soil. At night when transpiration is low or negligible this gradient promotes the absorption of water into the plant so that the internal water deficit is reduced or even eliminated (Slatyer 1967). The extent to which deficits are eliminated each night depends greatly on soil moisture status. When this is high deficits in plant are rapidly eliminated; but when the soil is dry the overnight improvement in plant water status is limited. Thus the moisture status of the root-medium effectively sets the upper limit of plant water status at the beginning of each day, and this controls plant growth. It is probably for this reason that the effect on plant growth of water stress in the root medium has been studied by a large number of investigators, such as Gates (1955a), Slatyer (1957b), Sands and Rutter (1959), Jarvis and Jarvis (1963a, 1965), M.S. Jarvis (1963), Aspinall (1965) and Lawlor (1969).

Plant growth is the ultimate expression of the various processes that occur in the plant. It reflects the interaction of environment and plant genotype (cf Luxmoore and Millington, 1971) and is known to be directly affected by water stress (Wardlaw, 1968). If environmental moisture has different effects on the two species in the present study, because of any adaptive features they possess, this should be reflected in their growth response to soil moisture stress.

The experiments described in this chapter were carried out to compare the growth responses of the two species, K. senegalensis and K. ivorensis, to increases in moisture stress in the root medium, both when grown on soil and in culture solution.

2.2. Growth response to moisture stress in soil.

Seedlings which had been transplanted singly onto soil in 12 cm diameter containers (see p. 23 Chapter One) were allowed to grow until they were well established and their roots thoroughly permeated the soil mass. During this establishment period, which lasted about four weeks from transplanting, the soil was kept moist to reduce the development of stress in the plants.

Seedlings of each species were divided into five matched groups (I, II, III, IV and V) of eight seedlings each, matching being based on leaf number and partly on height. This was done to reduce possible errors which might arise from differences in initial size of plants. Four of the matched groups of seedlings (II - V) were assigned, each to one of four soil moisture treatments, designated A, B, C and D.

Soil moisture level was controlled by pot weighing. Several workers (e.g. Sands and Rutter, 1959) have pointed out that in an experiment such as this soil moisture status is best expressed in terms of moisture tension since this indicates the force with which the soil holds water, and hence the ease with which the plant can obtain water from the soil. Therefore, in order to relate pot weights to soil moisture tension the moisture characteristic of the experimental soil was determined. The pressure plate apparatus was used to establish the relation between soil moisture content (as percent dry weight) and soil water potential (bars) for the range 0 to -1.0 bars. A pressure membrane apparatus was used for the range -1.0 to -11.0 bars. It was not possible because of technical failure in the apparatus to extend the determination to -15.0 bars, which is generally accepted as the permanent wilting point for most soils (Black, 1957; Russel, 1961). The extension of the curve (Fig. 2) to this range was done by extrapolation. The pressure apparatus, as used here measures only the matric potential of the soil whereas total water potential of the soil includes an osmotic component (cf. Jarvis and Jarvis, 1963a). No attempt was made here to cerrect for this osmotic component as was done by Jarvis and Jarvis (loc. cit.) since there was no good reason to expect this to be high (cf. Slatyer, 1967). Because the apparatus used was loaned from the Soil Science Department, Faculty of Agriculture, Legon, it was not possible to complete determination of the soil moisture characteristic before the experiment was begun. Therefore soil moisture levels in the various treatments were controlled simply by pot weighing throughout the experiment. Conversion of soil moisture contents to the equivalent potentials was done at the end of the experiment. A heavy duty top-pan Mettler balance (Mettler P3) was used for pot weighing so that weights could be obtained to an accuracy of ± 1.0 gram.

The moisture content of the soil at field capacity, that is after standing in water to become thoroughly saturated and allowing the pots to drain for 24 hours was found to be $23.0 \pm 1.6\%$ of the soil dry weight. The pot weight at this point was taken to be 100 percent moisture status. Treatment A consisted of soil kept at near this point by daily addition of water. In the other treatments, the soil, initially at field capacity, was allowed to dry out respectively to 75, 50 and 25% of the weight at field capacity before rewatering. Soil water potentials (bars) corresponding to these weights were subsequently read from the curve in Fig.2 and were as follows:

FIG. 2

THE RELATIONSHIP BETWEEN SOIL WATER POTENTIAL (BARS) AND SOIL MOISTURE CONTENT (% DRY WEIGHT). FOR THE EXPERIMENTAL SOIL, JOHN INNES POTTING COMPOST II.
(SEE ALSO APPENDIX 2, TABLE, i FOR STATISTICAL TREATMENT OF THE DATA).

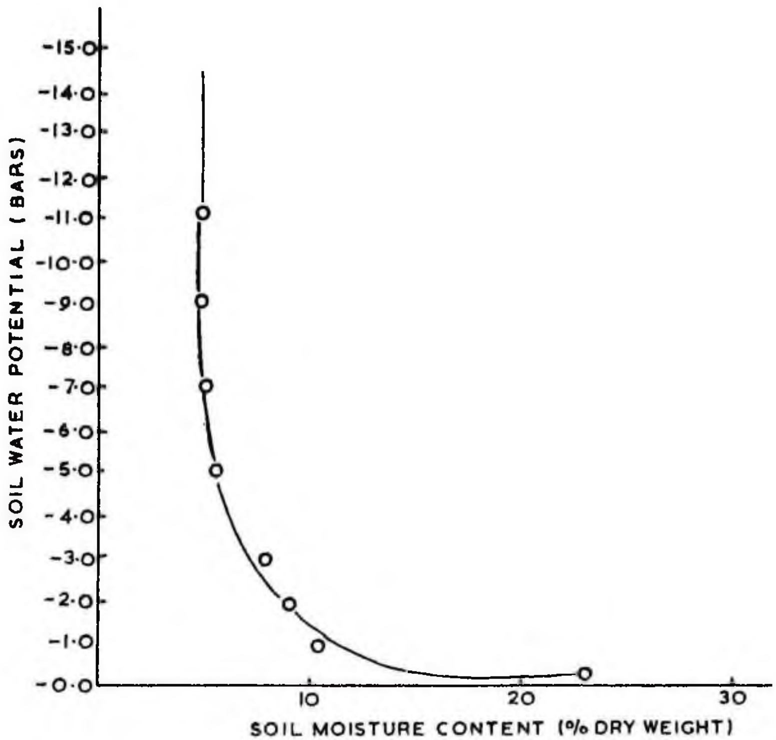

-15·0
-14·0
-13·0
-12·0
-11·0
-10·0
-9·0
-8·0
-7·0
-6·0
-5·0
-4·0
-3·0
-2·0
-1·0
-0·0
SOIL WATER POTENTIAL (BARS)
10
20
30
SOIL MOISTURE CONTENT (% DRY WEIGHT)

FIG. 2

Treatment A (-0.3 bars), Treatment B (-0.4 bars), Treatment C (-0.6 bars) and Treatment D (-4.5 bars). This method of soil moisture control has been successfully used by previous workers (see for example Slatyer, 1957b).

The experiment was carried out in the greenhouse. Over the experimental period (13 November 1970 to 12 January 1971) average temperatures were around 28°C at 09.00 hrs and 33°C at 15.00 hrs; relative humidity was around 60% (09.00 hrs) or 56% (15.00 hrs). The general light intensity within the greenhouse was compared from time to time with light intensity outside. Two matched selenium barrier layer photometers (EEL Lightmaster Model 18) were used for this purpose. Internal lighting was about 40% of that outside. The roof of the greenhouse was fairly heavily shaded to reduce mid-day temperatures (see p. 24 Chapter I).

The experiment was carried out on a centre bench of the greenhouse; a randomized-block design was adopted. Randomization was based on a table of random numbers (Fisher and Yates, 1957). It was found necessary to re-randomize the groups and plant pots weekly because environmental conditions within the greenhouse varied appreciably from one end to the other.

In order to examine as fully as possible how soil moisture stress might operate to control growth in the experimental plants, the growth analysis technique (Gregory, 1917) was used. The remaining group of seedlings, group I, was harvested at the beginning of the experiment. Length and breadth of the leaves of each seedling were measured. The leaves were then blue printed on 'Ozalid' paper and then planimetered to obtain their areas. From the regression of planimetered area on length x breadth (l x b) of these leaves (see Appendix 2, graph I), leaf area of the unharvested plants could subsequently be derived by simple measurements of length and breadth. Dry weights of leaves, stem and roots of the harvested plants were determined separately by oven-drying at 90 - 100°C for 24 hrs.

The unharvested seedlings were allowed to grow on for approximately nine weeks. Periodic measurements of seedling height and leaf area were made over this interval. During this period K. senegalensis and K. ivorensis seedlings in Treatment B received, overall, approximately 26 and 24 watering cycles respectively, while those of Treatments C and D received 12 and 6 cycles respectively for both species. Pots in treatment D did not often reach the predetermined weights when wilting took place, therefore the criterion of watering in this group was the apparent inability of wilted leaves to recover at sunrise.

At the end of the nine weeks the seedlings were harvested; leaf areas and dry weights were determined as for the initial harvest. The initial weights of these seedlings were obtained from their initial leaf areas by using the relation between leaf areas and plant dry weight obtained from plants in the critical harvest (see Appendix 2, graph II).

(b) Analysis of growth

From the total dry weights (W_1 and W_2) and leaf areas (A_1 and A_2) at times t_1 and t_2, relative growth rates (R.G.R.), net assimilation rates (N.A.R.) and mean leaf area ratios (M.L.A.R.) were calculated as follows:

$$\text{R.G.R. (g/g/wk)} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$

$$\text{N.A.R. (g/m}^2\text{/wk)} = \frac{(W_2 - W_1)}{A_2 - A_1)} \times \frac{(\log_e A_2 - \log_e A_1)}{(t_2 - t_1)} \qquad \text{(i)}$$

or

$$= \frac{(W_2 - W_1)}{\frac{1}{2}(A_1 + A_2)} \times \frac{1}{(t_2 - t_1)} \qquad \text{(ii)}$$

$$\text{M.L.A.R. (cm}^2\text{/g)} = \frac{1}{2}\ \frac{A_1}{W_1} + \frac{A_2}{W_2}$$

Fisher (1920) showed that the above equation for R.G.R. is valid irrespective of the relationship between dry weight and time. The equation for N.A.R and M.L.A.R. are however subject to certain limitations. Thus Williams (1946) emphasized that the use of the above equations for N.A.R. and M.L.A.R. is valid only when the total plant weight (W) is linearly related to the total leaf area (A) over the experimental period. In this experiment there were harvests on only two occasions (initial and final harvests) it was not possible, therefore to know the exact relation between W and A over the period. Coombe (1960) has suggested that when the relation between A_2/A_1 is small (less than 2.0) the difference between the two methods of calculating N.A.R. is small. In the above experiment it was found that for most of the treatments A_2/A_1 was less than two; the exceptions are for K. ivorensis in Treatments B and D. N.A.R. was generally calculated by equation (i) except when $A_2 - A_1$ was zero when equation (ii) was used. The above equation for the M.L.A.R. was also used to simplify the arithmetic.

Distribution of dry matter between the main organs - root, stem and leaf - was compared between treatments, at the final harvest by calculating the ratios of dry weights of these organs to total plant dry weight, thus obtaining root-weight ratio (R.W.R.), stem weight ratio (S.W.R.) and leaf weight ratio (L.W.R.). These were expressed as percentages of total dry weight. In addition, root-shoot ratios (R/S) and specific leaf areas (leaf area/leaf dry weight) (S.L.A.), were calculated. To bring out the comparison between the species more clearly all these parameters were further expressed as percentages of the values in Treatment A.

(c) Results

During the experimental period it was observed that some of the leaves of K. ivorensis in Treatment A became chlorotic. Towards the end of the experimental period, one of these seedlings shed most of its leaves. This seedling was not included in any of the final calculations. It was also observed that the length of the watering to drying-out cycles differed from pot to pot within the same treatment; the bigger seedlings with larger leaf areas took a shorter time to get to the predetermined weights. The tensions stated for each treatment are therefore averages of the tensions experienced by all the seedlings in that treatment before rewatering took place.

Changes in height and leaf area of the seedlings over the experimental period are shown in Figs. 3 and 4 respectively. Initial and final heights, dry weights and leaf areas, per plant together with the least significant differences (L.S.D., P = 0.05) between these values are presented in Table 2. A breakdown of the dry weights into leaf, stem and root fractions is given in Appendix 2, Table ii. In Table 3, growth functions and mean leaf area ratios derived from the primary data are similarly presented, together with leaf area ratios and ratios indicating the distribution of dry matter within and between the main organs at final harvest. To aid comparison, the derived data are presented again in Fig.4 and Table 4, as percentages of the values in Treatment A.

K. senegalensis seedlings were by far larger than K. ivorensis seedlings, both at the beginning and at the end of the experimental period. The larger initial size is presumably partly due to the larger seed size of K. senegalensis (see p. 15). This difference is reflected in the initial and final dry weights of the seedlings. The growth

Table 2

[Su]mmary data for the analysis of growth of Khaya senegalensis and [K.] ivorensis seedlings under varying soil moisture treatment: A (-0.3); [B,] (-0.4); C, (-0.8); D, (4.5) bars; t_1 and t_2 indicate initial and [fi]nal harvest occasions respectively.

K. senegalensis

[Pla]nt indices		Treatments A	B	C	D	least sign. diff. (P =0.05)
[Me]an height per plant (cm)	t_1	14.0	13.9	14.0	11.7	3.2
	t_2	16.5	16.7	14.6	14.6	3.7
[Me]an total dry weight per [pla]nt (g)	t_1	0.751	0.829	0.876	0.813	0.097
	t_2	4.100	4.500	3.200	3.000	1.940
[Me]an leaf area per [pla]nt (cm^2)	t_1	114	125	103	114	52
	t_2	225	246	179	174	73

(continued next page)

(Table 2 continued)

K. ivorensis

lant indices		Treatments A	B	C	D	least sign. diff. (P=0.05)
ean height per plant (cm)	t_1	9.7	10.5	10.6	9.6	2.2
	t_2	12.6	13.3	13.1	12.7	2.3
ean total dry weight per lant (g)	t_1	0.460	0.410	0.430	0.370	0.130
	t_2	1.710	2.150	1.980	1.710	0.600
lean leaf area per plant cm^2)	t_1	100	87	93	78	31
	t_2	169	189	182	153	31

rates obtained for the two species are in general comparable to values obtained by Jarvis and Jarvis (1963a) for tree seedlings (aspen, pine and spruce) in a similar experiment using soil moisture tensions ranging from 0 to 4 atmospheres, and to values found by Ampofo (1969) for Afrormosia elata, a West African rain forest tree; but they are lower than most of the values found by Okali (1971b) for some West African forest-tree seedlings in full day light, presumably partly because of the relatively heavy shade (40 per cent of full day light) employed in the present study. These comparisons suggest that, apart from the shade, conditions of growth were relatively good in the present experiment.

(i) Height growth

At the beginning of the experiment mean heights of K. senegalensis seedlings assigned to Treatments A, B and C were similar but significantly different from those of seedlings for Treatment D (Fig. 3). This initial difference was maintained and possibly increased by treatment, over the experimental period. K. ivorensis seedlings assigned to Treatments B and C were similar in height, but significantly taller than seedlings for Treatments A and D, which were themselves similar when the experiment was started. Again, these differences appear to have been maintained, though slightly reduced, over the experimental period. For K. senegalensis, height of seedlings in Treatments A, B and C increased rapidly at the beginning of the experiment but slowed down by the sixteenth day. Seedlings in

FIG. 3

MEAN HEIGHT OF *KHAYA SENEGALENSIS* (KS) AND *K. IVORENSIS* (KI) SEEDLINGS UNDER VARIOUS SOIL MOISTURE TREATMENTS (BARS). TREATMENTS: A (-0.3), B (-0.4), C (-0.8) AND D (-4.5).

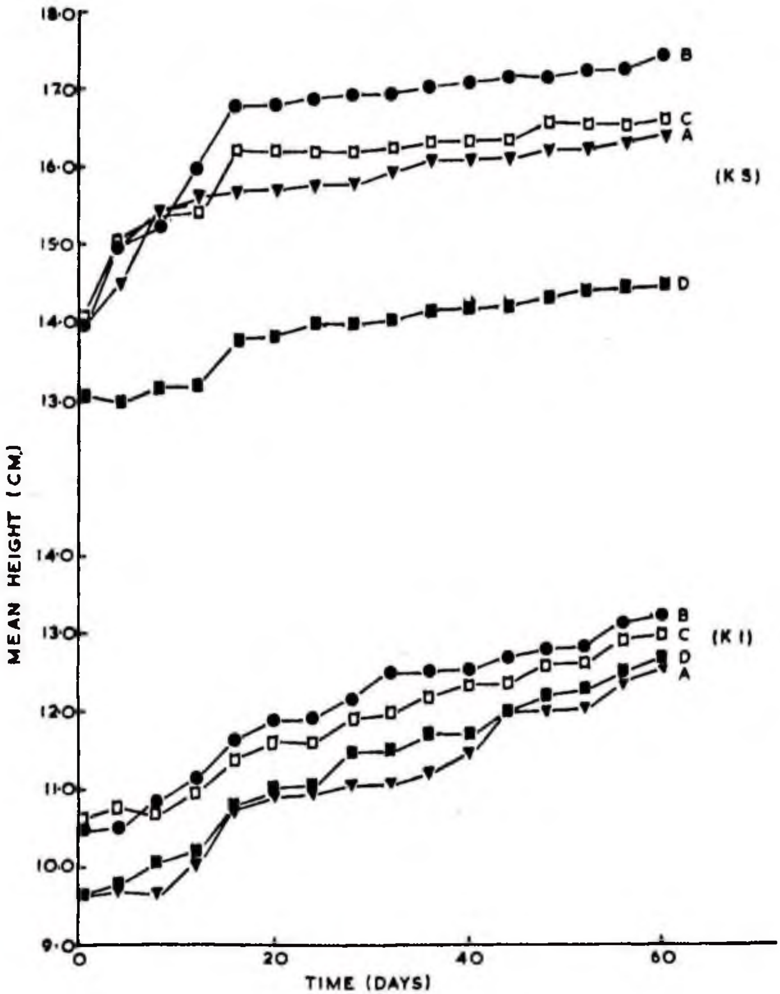

18·0
17·0
16·0
15·0
14·0
13·0
14·0
13·0
12·0
11·0
10·0
9·0
MEAN HEIGHT (CM.)
B
C
A
(K S)
D
B
C
(K I)
D
A
0
20
40
60
TIME (DAYS)

FIG. 3

Treatment D showed a slow rate of height increase throughout the whole period. Unlike seedlings of K. senegalensis those of K. ivorensis showed a more uniform rate of change in height throughout the experimental period. Height growth was more or less linear in this case and there was no striking difference in rate between treatments. However, in both species, there was a tendency for seedlings in Treatment B to be taller than seedlings in all other treatments. This and the slow growth of K. senegalensis in Treatment D were the only observable effects of the treatments applied on height growth.

(ii) Changes in leaf area.

As with height, total leaf area per seedling of K. senegalensis was generally greater than that per seedling of K. ivorensis, both at the beginning and at the end of the experimental period (Fig. 4). For both species initial leaf areas of seedlings assigned to the various treatments were more similar than were heights, and, by the end of the experiment, differences between seedlings in the various treatments were still not significant. This presumably was partly due to the large variability in leaf area of plants within any one treatment. In spite of this, a tendency for more rapid rate of leaf area increase, particularly up to Day 32, is indicated for K. senegalensis seedlings in Treatments A and B. A more uniform rate of leaf area increase is also shown by K. ivorensis seedlings. As with height growth, seedlings in Treatment B, for both species, tended to have higher leaf areas.

FIG. 4

LEAF AREA OF KHAYA SENEGALENSIS (KS) AND K. IVORENSIS (KI) SEEDLINGS UNDER VARIOUS SOIL MOISTURE TREATMENTS (BARS). TREATMENTS: A (-0.3); B (-0.4); C (-0.8), D (-4.5). THE BROKEN LINES INDICATE ACCIDENTAL LOSS OF LEAVES WHEN THE GREENHOUSE WAS SPRAYED TO CONTROL INSECTS.

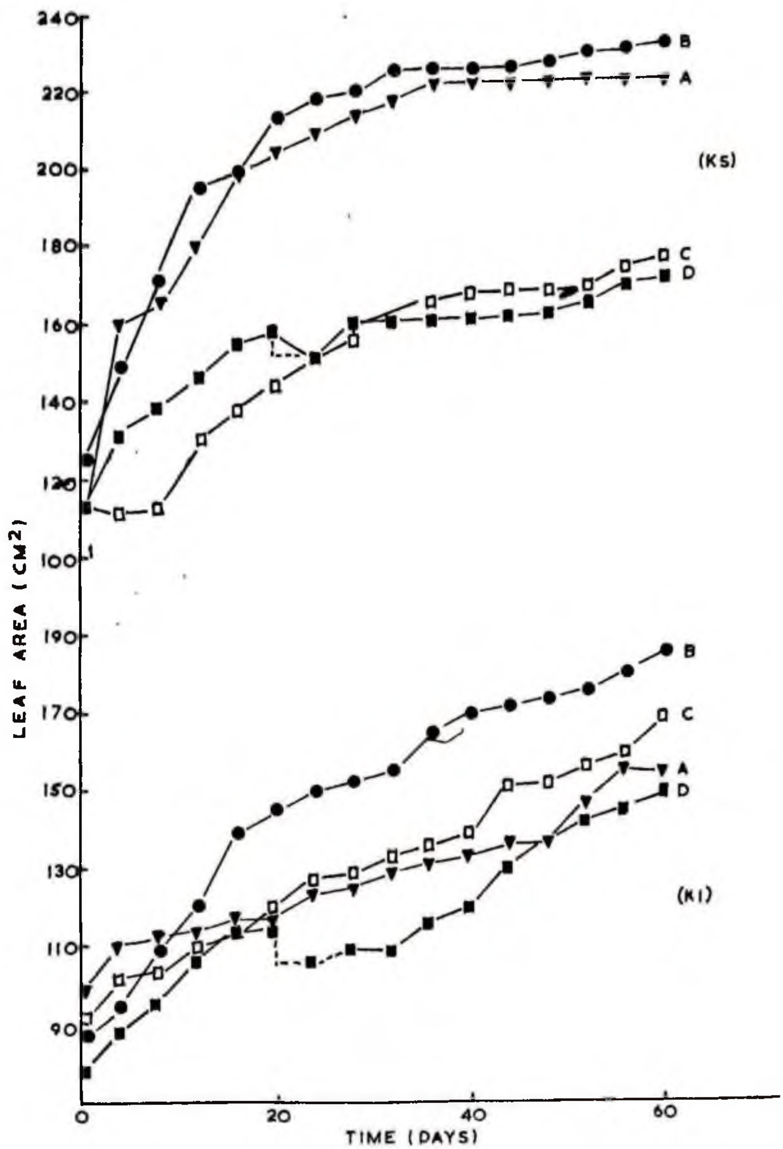

240
220
200
180
160
140
120
100
190
170
150
130
110
90
LEAF AREA (CM2)
B
A
(KS)
C
D
B
C
A
D
(KI)
0
20
40
60
TIME (DAYS)

FIG.4

(iii) Relative growth rate.

In general the relative growth rates of the two species (Table 3) appeared not to be markedly different. They ranged from 0.14 to 0.18 g/g/wk in K. senegalensis and from 0.15 to approximately 0.19 g/g/wk in K. ivorensis. The data presented in Fig.5 suggest that K. senegalensis was more sensitive to the dry treatment than K. ivorensis: its relative growth rate decreased steadily with soil dryness so that in the driest treatment (D) the rate was significantly reduced to 77% of that in treatment A. The differences between seedlings of this species in Treatments A, B and C were however not significant. In terms of growth rates, the response of K. ivorensis seedlings can be considered as that to a wet treatment (Treatment A) and a dry treatment (Treatments C and D) (cf. Jarvis and Jarvis, 1963a). Relative growth rate was highest in Treatment B and tended to be reduced, though not significantly in either wetter or drier soil. The lowest growth rate occurred in Treatment A, and although the rate in Treatment D was slightly higher than in C the difference is not significant.

(iv) Net assimilation rate.

Net assimilation rates obtained for K. senegalensis were much higher than those for K. ivorensis (Table 3). Like the relative growth rates, maximum net assimilation rate for K. senegalensis (22.6 $g/m^2/wk$) occurred in Treatment A and the minimum (15.0 $g/m^2/wk$) in Treatment D. The difference between these two values is significant.

Table 3

Derived growth data and ratios indicating distribution of dry matter between main organs for Khaya senegalensis and K. ivorensis seedlings under varying soil moisture treatments; A (-0.3); B (-0.4); C (-0.8); D (-4.5) bars.

K. senegalensis

Plant indices	Treatments A	B	C	D	least sign. diff. (P = 0.05)
Relative growth rate (g/g/wk)	0.183	0.179	0.170	0.140	0.033
Net assimilation rate ($g/m^2/wk$)	22.6	19.4	21.9	15.0	6.9
Mean leaf area ratio (cm^2/g)	103.6	108.5	106.1	107.6	17.7
Leaf area ratio (cm^2/g)	62.1	64.8	62.5	60.5	23.9
Specific leaf area (cm^2/g)	201.5	219.0	220.2	200.8	59.0
Leaf weight ratio (%)	31.7	29.4	28.6	29.2	2.8
Stem weight ratio (%)	25.0	25.5	24.7	24.2	3.2
Root weight ratio (%)	44.1	45.3	46.3	46.6	6.2
Root shoot ratio (%)	80.0	81.1	87.7	87.5	13.9

(continued next page)

Table 3 (continued)

K. ivorensis

Plant indices	Treatments A	B	C	D	least sign. diff. ($P = 0.05$)
Relative growth rate (g/g/wk)	0.150	0.189	0.165	0.171	0.060
Net assimilation rate ($g/m^2/wk$)	11.3	14.9	13.3	13.5	3.0
Mean leaf area ratio (cm^2/g)	154.2	149.8	151.7	148.4	17.7
Leaf area ratio (cm^2/g)	93.0	88.0	91.3	88.4	17.7
Specific leaf area (cm^2/g)	240.7	217.0	231.6	226.9	34.2
Leaf weight ratio (%)	39.5	40.6	37.7	38.3	5.9
Stem weight ratio (%)	26.7	24.1	24.8	25.1	3.5
Root weight ratio (%)	37.0	35.3	37.2	36.6	9.9
Root shoot ratio (%)	55.2	55.1	59.7	58.6	11.4

FIG. 5

THE RELATION BETWEEN RELATIVE GROWTH RATE (R.G.R.), NET ASSIMILATION RATE (N.A.R.) OR MEAN LEAF AREA RATIO (M.L.A.R.) AND SOIL MOISTURE POTENTIAL (BARS), FOR KHAYA SENEGALENSIS (△) AND K. IVORENSIS (○) SEEDLINGS. THE DATA ARE EXPRESSED AS PERCENTAGES OF THE VALUES IN TREATMENT A.

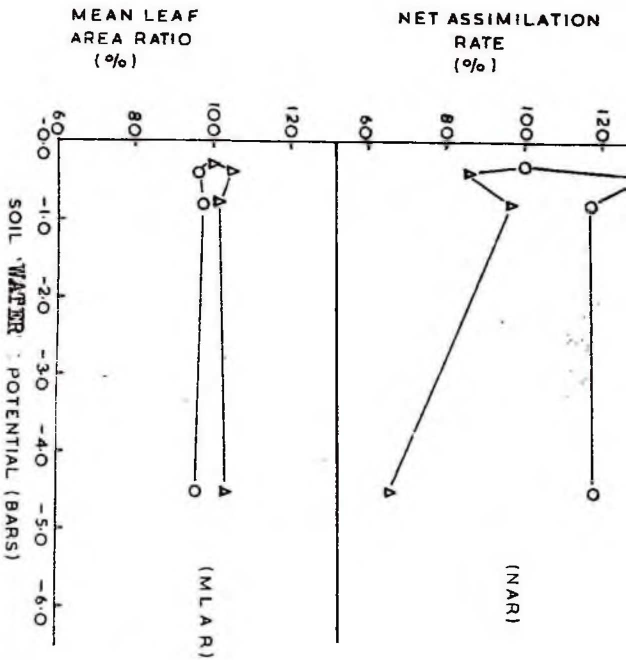
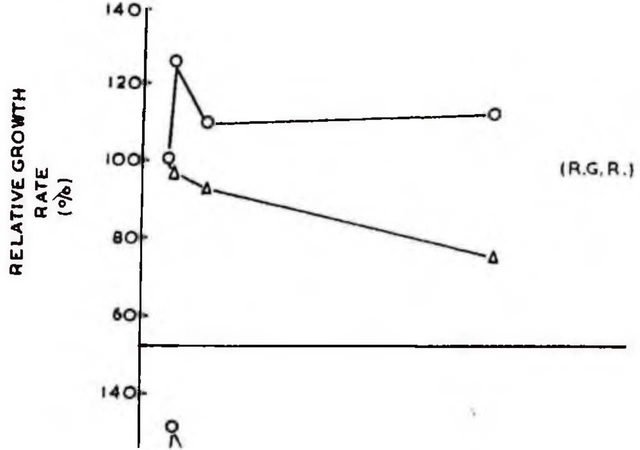

MEAN LEAF AREA RATIO (%)
NET ASSIMILATION RATE (%)
(MLAR)
(NAR)
SOIL WATER POTENTIAL (BARS)

FIG. 5


RELATIVE GROWTH
RATE
(%)
140
120
100
80
60
140
(R.G.R.)

There was, however, no significant difference between either of these values and those obtained for seedlings in Treatments B and C. In *K. ivorensis*, the maximum net assimilation rate (14.9 $g/m^2/wk$) was obtained for seedlings in Treatment B and the minimum (11.3 $g/m^2/wk$) for plants in Treatment A. Unlike the situation with *K. senegalensis* no significant treatment effect was found between *K. ivorensis* seedlings.

(v) Mean leaf area ratio.

In all the treatments, mean leaf area ratios of *K. ivorensis* seedlings were greater than those of *K. senegalensis* seedlings. The differences between treatments within the species were however not significant (Table 3 and Fig. 5).

(vi) Leaf area ratio, specific leaf area and leaf weight ratio at final harvest.

K. ivorensis had higher leaf weight ratio and specific leaf area ratio than *K. senegalensis* so that leaf area ratios at the second harvest were also higher in the former species (Table 3). Within the species, the treatments appeared not to have had any significant effect on any of these parameters.

(vii) Root weight ratio, root-shoot ratio and stem-weight ratio.

For both species the treatments apparently had no significant effect on any of these ratios although root weight ratio tended to increase with soil dryness. *K. senegalensis* had proportionately more dry matter present in the root than had *K. ivorensis*, while the reverse

Table 4

Ratios indicating distribution of dry matter between main organs at final harvest, for Khaya senegalensis and K. ivorensis seedlings grown under various soil moisture treatments - A, (0.3); B (-0.4) C (-0.8); D (-4.5) bars. The data is expressed as percentages of values in Treatment A.

K. senegalensis

Plant indices	Treatments			
	A	B	C	D
Leaf area ratio	100	104	100	97
Specific leaf area	100	109	109	100
Leaf weight ratio	100	93	90	92
Stem weight ratio	100	102	99	97
Root weight ratio	100	103	105	106
Root shoot ratio	100	101	110	109

K. ivorensis

Plant indices	Treatments			
	A	B	C	D
Leaf area ratio	100	95	98	95
Specific leaf area	100	90	96	94
Leaf weight ratio	100	103	95	97
Stem weight ratio	100	90	93	94
Root weight ratio	100	95	101	99
Root shoot ratio	100	100	108	106

is true for the proportion of dry matter in the leaf (Table 3). Similarly higher R/S was obtained for K. senegalensis than for K. ivorensis seedlings. The ratio of stem weight to total dry weight was similar in both species. The greater proportion of root in K. senegalensis may be of adaptive significance, although, in the present experiment its advantage was not apparent.

(d) Discussion

The view of Veihmeyer and Hendrickson (1950) that soil moisture stress is equally available for plant growth within the available range (0 - 15 atmospheres) has been actively contested (Richards and Wadleigh, 1952; Slatyer 1957a; Stanhill, 1957). According to Slatyer (1967), this view was based primarily on field experiments with deep-rooted tree crops. It is now more generally accepted that growth may vary with soil moisture status within the available range. (Richards and Wadleigh, 1952). In the present study, where potted seedlings were used, some reduction in growth of the two experimental species was expected, but the results presented show that any such reduction was small.

Relative growth rate of K. senegalensis generally decreased with increasing soil moisture stress, so that there was a significant reduction for plants in Treatment D (-4.5 bars) as compared with those in Treatment A (-0.3 bars). In K. ivorensis however the rate was apparently not significantly affected by the treatments although there was a tendency for growth to be depressed in the wettest treatment (A).

In general net assimilation rate was lower in K. ivorensis than in K. senegalensis but this was compensated by higher mean leaf area ratios in the former species so that relative growth rates were very similar for both species. Mean leaf area ratios for both species showed very little response to the treatments so that reduction in relative growth rate of K. senegalensis in response to dry soil was due to reduction in net assimilation rate; similarly the tendency for reduced relative growth rate in response to wet soil in K. ivorensis can be accounted for by reduction in net assimilation rate. Jarvis and Jarvis (1963a) obtained a similar relationship between relative growth rate and net assimilation rate in their response to soil moisture status with the species they studied. The apparent low growth rate for K. ivorensis in Treatment A, the wettest treatment, could be attributed to poor aeration. Kramer (1956) and Mees and Weatherley (1957) have pointed out that poor aeration in the rooting medium reduces root permeability sufficiently to cause large reduction in water uptake which may limit growth. Jarvis and Jarvis (1963a) observed a reduction in growth of aspen, birch and spruce in the wettest of the series of water regimes they practised in their study. They also suggested that poor aeration was responsible for low growth rates in response to wet soil. In the present study growth of one of the species, K. senegalensis, was however not reduced by Treatment A. The generally larger size of the seedlings and the amount of root they had may have caused rapid transpiration per plant and hence rapid soil moisture depletion, so that any excess water, which might have caused prolonged water logging after each watering operation, was rapidly removed. Transpiration data to be presented later support this suggestion.

The growth of K. senegalensis was significantly reduced by soil moisture stress of about 4.5 bars while that of K. ivorensis was not significantly reduced over this range. Sands and Rutter (1959) reviewed examples of tensions which have been found to reduce growth significantly in plants and came to the conclusion that for most species considerable restriction of growth was caused by moisture tensions of about 0.5 atmospheres. In their own work with Pinus sylvestris, they found dry weight production by first year seedlings to be sensitive to this tension. Jarvis and Jarvis (1963a) however found that maximum growth of birch, aspen, spruce and pine occurred in soils at this tension but that dry weights of the conifers were reduced by about 33% in soils dried to 1.7 atmospheres and those of the angiosperms by about 10 - 20% in soils at 2 atmospheres. M.S. Jarvis (1963) also observed that measurable growth (as assessed by leaf development) of Saxifraga hypnoides and Filipendula vulgaris ceased at tensions of 0.5 and 2.0 atmospheres respectively. Although she could not reach a definite conclusion it appeared that for the woody species, Prunus padus and Thelycrania sanguinea, growth ceased at soil moisture tension above 2 - 3 atmospheres. In contrast to the above results indicating low soil moisture tensions for the cessation of growth, Wadleigh and Gauch (1948) studying the effect of increasing total soil moisture stress on the daily elongation of cotton leaves, found that elongation ceased at a narrow range of stress values, close to 15 atmospheres. Slatyer (1957b) also observed that for privet and cotton increases in dry matter ceased at dawn values of leaf water status corresponding to the permanent wilting point for these species. It thus appears that a variable range (low or high) of soil moisture stress has been found by different workers to reduce plant growth. Some plants may be sensitive to low moisture tensions while others are sensitive to high tensions.

The growth response described here indicate that K. senegalensis, a savanna species was more sensitive to moderate soil moisture stress than K. ivorensis which is a forest species. This result was not expected. M.S. Jarvis (1963) has however observed that high desiccation resistance and ability to grow well at moderate moisture stresses may be inversely correlated in some species. Thus a plant with high sensitivity to small reduction in water potential may still possess strong drought resistance, because other features which promote drought resistance e.g. rapid stomatal closure at relatively low moisture stress or slow rate of water loss per unit decrease in water potential of tissues, may be disadvantageous for growth. Stomatal closure increases carbon dioxide diffusion resistance and this could limit growth. Data to be presented later show that K. senegalensis possesses some drought resistant features.

Interpretation of differences which arise in plant growth response to soil moisture stress is complicated by the difficulty of knowing the precise moisture stress experienced by plants, particularly at the root-soil interface, throughout an experimental period. In the present case it is possible that the correct stress which existed at the root-soil interface has not been adequately described. Since the same type of soil was used and the two species transpire at different rates (see later), the stress experienced at the root surface may have been different (cf. Jarvis and Jarvis, 1963a), because of different rates of depletion of soil moisture in the root zone. The more rapidly transpiring plant could be expected to have experienced greater stress than the plant with a lower transpiration rate. Evidence to be given later indicate that K. senegalensis generally transpires more rapidly than K. ivorensis. It is possible therefore that the significant reduction in growth shown above for K. senegalensis was in response to more severe water stress than occurred in K. ivorensis or than was detected by weighing of the whole soil mass.

The differences in growth of the two species might also have arisen because of variation in the length of time seedlings took to reach the predetermined weights before watering took place, so that the method of taking the mean soil moisture tensions of the individual seedlings in a treatment to represent the tension experienced by the group (see p. 35) was probably inadequate. M.S. Jarvis (1963), in order to obtain estimates of the amounts of effective soil moisture tensions experienced by the seedlings she worked with, summed up the areas beneath the drying out curves she obtained for seedlings in each treatment and expressed the results in percentage atmosphere-days. In this way the length of the drying out cycle was accounted for in each treatment. Jarvis (1963) also adopted a similar method for estimating effective soil moisture tensions in his experiments. In the present experiment however no attempt was made to account for the length of the drying out cycle; therefore, differences in the growth results which are due to this factor are not known.

In addition to the above complications, Owen and Watson (1956) indicate that experimental comparison of plant growth response to soil moisture stress is further confounded by the effect of re-watering on plants which had been subjected to drought. They observe that re-watering could cause temporarily greater increases in dry matter production in plants which have been subjected to prolonged drought as compared with irrigated plants that had never been subjected to severe water stress.

For the reasons outlined above it became necessary to examine further the growth responses of the two species to moisture stress in the root medium, this time using a root medium in which the water potential could be more precisely controlled; hence the water culture experiment which is described in the section that follows. By using a culture solution technique it was also possible to extend the severity of stress applied; to see whether the pattern of response is similar under both high and low stress conditions. As a further improvement upon the soil experiment it was thought desirable to grow the two species in the same container so that there would be no doubt about the similarity of the water potential experienced by the two species at the root surface. This condition however introduces inter-species competition, but there was no good reason to expect large interference effects.

2.3. Growth response to moisture stress in culture solution.

a. Method

Seedlings for this experiment were raised from seed sown in vermiculite (see p. 22). They were transplanted into half-strength Arnon and Hoagland culture solution (see below) held in two large (38.0 cm diameter) polyethylene containers. The solutions were not sterilized as had been done by previous workers (for example Jarvis and Jarvis, 1963d, 1965). The solutions were however aerated continuously, and the seedlings were allowed to grow in this condition until they were required for experiment. This took about four weeks from transplanting. The seedlings were then divided into matched lots, corresponding to the number of pots to be used in the experiment. Matching was based on leaf number alone; seedling height was not used for this purpose because at this stage seedling stems (particularly in K. ivorensis) were too short. After matching, the seedlings were carefully inserted through holes made in the lids of the experimental pots. They were supported with cotton wool. In order to ensure that the growth medium was the same for the two species in each treatment, each experimental pot carried three seedlings of each species so that there were six seedlings per pot. The experimental pots each held 700 ml half-strength Arnon and Hoagland solution aerated continuously. The seedlings were allowed to grow for a further period of two weeks before the experiment was started. It was necessary after each transplanting operation, to allow the seedlings to grow for some time so that any root damage caused by the transplanting operation could heal. Lawlor (1970) has shown that uptake of polyethylene glycols by plant roots is reduced if roots are undamaged. The total length of time allowed for recovery from any root damage in this experiment was six weeks - four weeks after the initial transfer from vermiculite and two weeks after transfer from large pre-treatment containers to experimental pots.

Preliminary experiments, by growing the seedlings in different strengths of Arnon and Hoagland (1940), (see Hewitt 1952) solution, showed that the half-strength concentration was optimum for growth of the seedlings. The basic culture medium used consisted of:

$Ca(NO_3)_2 4H_2O$	0.354 g
$MgSO_4 H_2O$	0.247 g
KNO_3	0.404 g
KH_2PO_4	0.136 g
$NH_4H_2PO_4$	0.231 g
*Microelements	0.5 ml
Distilled water	1000 ml

*(The composition of the microelements solution was: $MnCl_2.4H_2O$, 1.810 g/L; $CuSO_4.5H_2O$, 0.080 g/L; $ZnSO_4.7H_2O$, 0.220 g/L; H_3BO_3, 2.860 g/L; and $(NH_4)_6MO_7O_{24}.4H_2O$, 0.124 g/L).

The seedlings were subjected to four levels of osmotic potential in the root medium: A (control, -0.3 bars), B (-2.8 bars), C (-5.3 bars) and D (-10.3 bars). Treatment A consisted of plants grown in the culture solution alone; the quoted osmotic potential for this medium is derived from the literature (Hewitt, 1952) for half-strength of solutions of identical composition. The solutions in Treatments B, C and D were made respectively by dissolving 100, 150 and 256 g of polyethylene glycol (molecular weight 4000) in a litre of the half-strength culture solution. These weights were derived from the curve of Lawlor (1970, Fig. 1) relating concentration to osmotic potential for polyethylene glycol of the same molecular weight. The osmotic potentials quoted are therefore only approximate. Because of peculiarities in behaviour of polyethylene glycols (cf. Lagerweft et al, 1961), there was no ready means of measuring osmotic potentials of these solutions directly.

Two containers were assigned to each treatment. The volume of solution in each container was maintained at 700 ml by daily addition of distilled water. The solutions were renewed twice over the experimental period of 21 days. The first renewal took place seven days after the experiment had started and the second was ten days after the first renewal.

This experiment also was carried out in the greenhouse. Over the experimental period (12 July 1971 to 2 August, 1971) average temperatures were around 26°C at 09.00 hrs and 30°C at 15.00 hrs; relative humidity was around 75% (09.00 hrs) or 60% (15.00 hrs). The sky was never overcast during this period; this made it impossible for light intensity measurements to be made as was done for the soil experiment. The light intensity might be lower than that encountered in the soil experiment. In all, growth conditions were comparatively less severe for this experiment than during the soil experiment. As in the previous case the experiment was carried out on the centre bench of the greenhouse and a randomized block-design was adopted.

At the beginning of the growth period, ten seedlings of K. senegalensis and nine of K. ivorensis were harvested. At this time also, marks were made with white paint a few millimeters above the pot lid, on the stems of the plants allowed to grow on. These marks served as the base line from which height measurements were subsequently made. Height and leaf area measurements were made at intervals during the experimental period. Leaf area and dry weights of leaves, stem and roots were determined for the harvested plants as was done in the soil experiment. Similar determinations were made at the final harvest. As in the soil experiment, the results were examined by the growth analysis technique.

b. Results

Wilting was observed frequently in almost all the seedlings of the two species in Treatment D during the experiment. Occasional wilting was also observed in most of K. ivorensis seedlings in Treatment C.

The results of the height and leaf area measurements are expressed in graphs (Figs. 6 and 7 respectively). Table 5 shows the primary growth data together with the least significant differences (L.S.D, P = 0.05), while Table 6 presents the derived growth data and ratios indicating distribution of dry matter between the main organs for both K. senegalensis and K. ivorensis, also with the L.S.D. (P = 0.05).

Table 5

Primary data for the analysis of growth of Khaya senegalensis and K. ivorensis seedlings in culture solutions of different osmotic potentials (bars): A (-0.3); B (-2.8); C (-5.3); D (-10.3); t_1 and t_2 indicate initial and final harvest occasions respectively. Treatment A consisted of culture solution alone, B, C and D consisted of culture solution plus polyethylene glycol.

K. senegalensis

Plant indices		Treatments A	B	C	D	least sign diff. (P = 0.05)
Mean height per plant (cm)	t_1	15.4	16.3	15.8	14.3	2.3
	t_2	16.6	17.3	16.2	14.4	2.2
Mean total dry weight per plant (g)	t_1	0.359	0.406	0.459	0.418	0.117
	t_2	0.921	0.781	0.743	0.547	0.223
Mean leaf area per plant (cm^2)	t_1	42.1	47.8	53.1	48.5	12.9
	t_2	90.2	64.6	62.6	61.4	17.9

K. ivorensis

Plant indices		Treatment A	B	C	D	least sign diff. (P = 0.05)
Mean height per plant (cm)	t_1	10.1	12.4	10.4	9.7	2.3
	t_2	11.3	13.3	11.0	9.9	2.0
Mean total dry weight per plant (g)	t_1	0.205	0.205	0.209	0.201	0.104
	t_2	0.370	0.312	0.202	0.236	0.176
Mean leaf area per plant (cm^2)	t_1	32.1	31.9	32.5	31.1	16.4
	t_2	61.0	45.7	35.1	34.1	25.2

In appendix 2, Table iii, is shown the breakdown of the total dry weights at the initial and final harvests into the weights for the main plant organs. Table 7 and Fig. 8 show the derived growth data and the other ratios presented as percentages of the values in Treatment A.

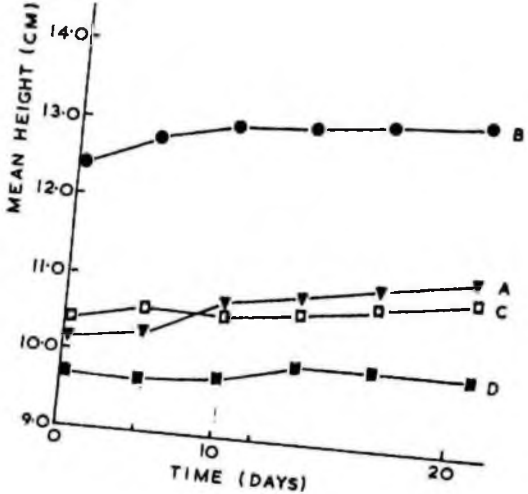
Total dry weights of both species decreased with decreasing solution osmotic potential with those of K. senegalensis decreasing less than those of K. ivorensis. The relative growth rates and net assimilation rates of K. senegalensis in this experiment were comparatively higher (maximum values are 0.31 g/g/week and 29.2 $g/m^2/wk$ respectively) than in the soil experiment. K. ivorensis on the other hand showed lower values here (maximum values being about 0.18 g/g/wk and 11.3 $g/m^2/wk$ respectively) than in the soil experiment. In spite of these lower values for K. ivorensis, the rates on the whole suggest that growth conditions were again relatively good.

(i) Height growth

For both species changes in seedling heights over the experimental period were small (Fig.6). The intial heights of seedlings assigned to the various treatments were variable with those of Treatment D being the lowest (Table 5). Differences between treatments were not significant for K. senegalensis seedlings while for K. ivorensis mean seedling height in Treatment B was observed to be significantly different from that of seedlings in Treatment D. Differences between these and the other treatments were however not significant. Changes in seedling heights over the experimental period both within and between the species appeared

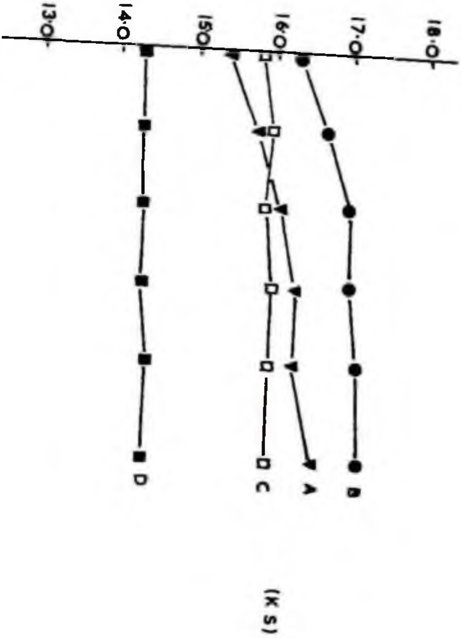
FIG. 6

MEAN HEIGHT OF KHAYA SENEGALENSIS (KS) AND K. IVORENSIS (KI) SEEDLINGS GROWN IN CULTURE SOLUTIONS OF DIFFERENT OSMOTIC POTENTIALS (BARS). TREATMENTS: A (-0.3); B (-2.8); C (-5.3); D (-10.3). TREATMENT A, CONSISTED OF CULTURE SOLUTION ALONE; B, C AND D CONSISTED OF CULTURE SOLUTION PLUS POLYETHYLENE GLYCOD.



(KI)

FIG. 6


13·0
14·0
15·0
16·0
17·0
18·0
B
A
C
D
(K S)

similar. There was however a significant difference between heights of seedlings in Treatments B and D for K. senegalensis at the end of the experiment. The difference observed for K. ivorensis seedlings in Treatments B and D could be attributed to the initial difference between these seedlings. There was no marked difference in rate of height increase between seedlings under these treatments.

(ii) Changes in leaf area

Initial leaf area of seedlings assigned to the various treatments were similar within the species (Table 5). Leaf area of K. senegalensis seedlings were generally larger than those of K. ivorensis. Leaf development in both species was stimulated by Treatment A, so that there was a rapid increase in leaf area throughout the experimental period (Fig.6). This effect was comparatively more pronounced in K. senegalensis than in K. ivorensis. Leaf area increase was however affected when stress was imposed so that at final harvest (see Table 5) leaf area in both species, for plants in Treatment A was greater than that for plants in the other treatments. The difference between Treatments A and B plants of K. ivorensis was however not significant; that between plants in Treatments B, C and D was also not significant for either species.

(iii) Relative growth rate

Relative growth rate decreased significantly with decreasing osmotic potential of the root medium (Table 6). Negative rates of growth were recorded for some seedlings of K. ivorensis in Treatments C

FIG. 7

LEAF AREA OF KHAYA SENEGALENSIS (KS) AND K. IVORENSIS (KI) SEEDLINGS GROWN IN CULTURE SOLUTIONS OF DIFFERENT OSMOTIC POTENTIALS (BARS).
TREATMENTS A (-0.3); B (-2.8); C (-5.3); D (-10.3).
TREATMENT A CONSISTED OF CULTURE SOLUTION ALONE: B, C AND D, CONSISTED OF CULTURE SOLUTION PLUS POLYETHYLENE GLYCOL.

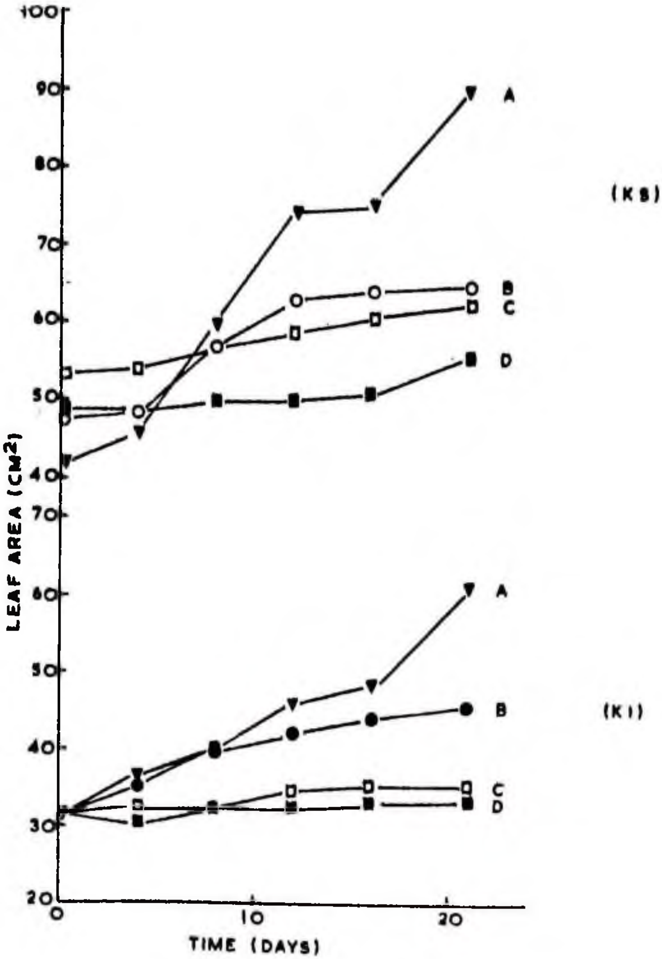

LEAF AREA (CM2)
100
90
80
70
60
50
40
70
60
50
40
30
20
A
B
C
D
(KS)
A
B
C
D
(KI)
0
10
20
TIME (DAYS)

FIG. 7

Table 6

Derived growth data and ratios indicating distribution of dry matter between main organs at final harvest, for Khaya senegalensis and K. ivorensis seedlings grown in culture solutions of different osmotic potentials (bars). A (-0.3); B (-2.8); C (-5.3), D (-10.3). Treatment A consisted of culture solution alone; B, C and D consisted of culture solution plus polyethylene glycol.

K. senegalensis

Plant indices	Treatment A	B	C	D	least sign diff. (P = 0.05)
Relative growth rate (g/g/wk)	0.310	0.212	0.163	0.083	0.009
Net assimilation rate ($g/m^2/wk$)	29.2	23.5	16.8	9.1	6.7
Mean leaf area ratio (cm^2/g)	107.8	100.9	100.9	106.6	14.6
Leaf area ratio (cm^2/g)	98.0	84.0	86.0	97.0	14.6
Specific leaf area (cm^2/g)	225.0	221.0	215.0	210.0	28.2
Leaf weight ratio (%)	44.0	38.0	40.0	46.0	4.5
Stem weight ratio (%)	24.0	28.0	29.0	27.0	4.5
Root weight ratio (%)	32.0	34.0	31.0	28.0	7.3
Root shoot ratio (%)	51.0	53.0	47.0	40.0	11.3

(continued next page)

Table 6 (continued)

K. ivorensis

Plant indices	Treatments A	B	C	D	least sign diff. (P = 0.05)
Relative growth rate (g/g/wk)	0.184	0.134	0.025	0.045	0.08
Net assimilation rate ($g/m^2/wk$)	11.3	9.3	1.8	3.3	5.4
Mean leaf area ratio (cm^2/g)	157.7	151.0	159.9	157.5	39.6
Leaf area ratio (cm^2/g)	171.0	146.0	165.0	160.0	39.6
Specific leaf area (cm^2/g)	311.0	318.0	320.0	317.0	71.1
Leaf weight ratio (%)	55.0	46.0	52.0	50.0	4.9
Stem weight ratio (%)	25.0	31.0	29.0	25.0	5.1
Root weight ratio (%)	20.0	23.0	19.0	25.0	5.8
Root shoot ratio (%)	26.0	30.0	24.0	33.0	6.8

and D. Fig. 8 suggests that K. senegalensis was more sensitive to moderate moisture stress (up to about -2.8 bars) than K. ivorensis, so that around this point relative growth rate of K. senegalensis was significantly reduced to 68% of that in Treatment A, while that of K. ivorensis was still about 73% of the value in Treatment A. However K. ivorensis showed greater sensitivity to moisture stress beyond -2.8 bars so that at 5.3 bars the rate was significantly reduced to 14% of that in Treatment A while the rate for K. senegalensis was reduced only to 53%. For K. ivorensis the percentage was however slightly raised to 24% in Treatment D (-10.3 bars) but this was still slightly lower than the percentage reduction for K. senegalensis which was about 27% at this point. The slight increase for K. ivorensis was accounted for by one large value out of six in the sample. Without this value which was 0.149 g/g/wk, the mean relative growth rate for K. ivorensis at 10.3 bars would be 0.024 g/g/wk which is about 13% of the rate in Treatment A.

(iv) Net assimilation rate

Net assimilation rates (Table 6) were higher for K. senegalensis than for K. ivorensis. The responses of net assimilation rate to decreasing osmotic potential for both species followed the same tread (Fig. 8) as was encountered with relative growth rate. It is remarkable that there was no significant difference between the net assimilation rates of seedlings of K. ivorensis subjected to Treatments A (-0.3 bars), and B (-2.8 bars). This further indicates the tolerance of this species to low moisture stress (cf. p. 51).

FIG. 8

THE RELATION BETWEEN RELATIVE GROWTH RATE (R.G.R.), NET ASSIMILATION RATE (N.A.R.) OR MEAN LEAF AREA RATIO (M.L.A.R.) AND MEAN WATER POTENTIAL OF THE ROOT MEDIUM FOR KHAYA SENEGALENSIS (▲) AND K. IVORENSIS (●) SEEDLINGS. THE DATA ARE EXPRESSED AS PERCENTAGES OF THE VALUE IN TREATMENT A.

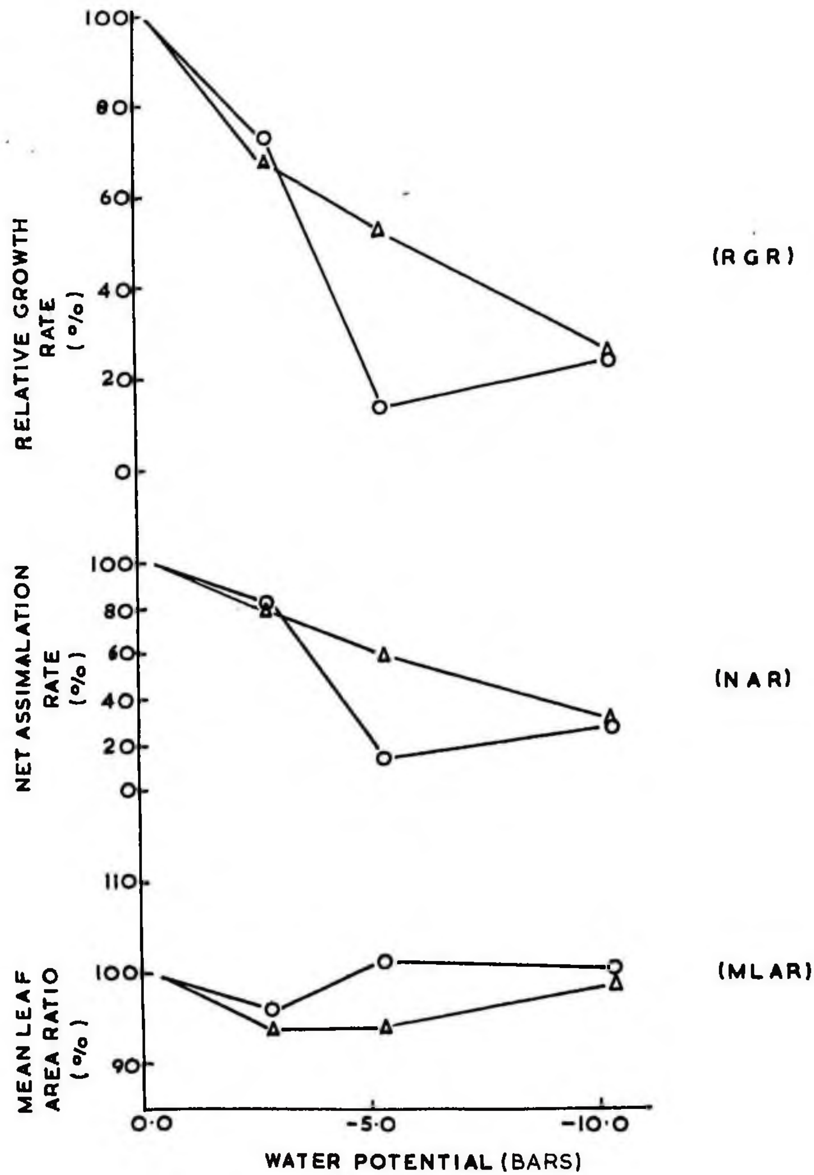

RELATIVE GROWTH RATE (%)
100
80
60
40
20
0
(RGR)
NET ASSIMALATION RATE (%)
100
80
60
40
20
0
(NAR)
MEAN LEAF AREA RATIO (%)
110
100
90
(MLAR)
0·0
-5·0
-10·0
WATER POTENTIAL (BARS)

FIG. 8

(v) Mean leaf area ratio

K. ivorensis had higher mean leaf area ratios than K. senegalensis (Table 6). Within the species, there appear to be no significant treatment effects on this ratio. Thus the reductions in relative growth rates could not, again, be attributed to changes in mean leaf area ratio.

(vi) Leaf area ratio, specific leaf area and leaf weight ratio at final harvest

The results presented in Table 6 shows that leaf area ratio, specific leaf area and leaf weight ratio, at final harvest, for K. ivorensis were greater than those for K. senegalensis. The osmotic potentials imposed apparently had no significant effects on any of these parameters. However specific leaf area for K. senegalensis decreased slightly with decrease in osmotic potential.

(vii) Root weight ratio, root-shoot ratio and stem weight ratio.

For both species the treatment effect did not seem to have followed a particular trend (Table 6). However for K. senegalensis the difference between root/shoot ratios of Treatments A and D was significant. K. ivorensis had the greatest root development in Treatment D and poor development in Treatment C, but there appears to be no marked difference in the root weight ratios of Treatment A and B plants. Stem weight ratio was also not greatly affected by the stresses imposed on the seedlings of both species.

Table 7

Ratios indicating distribution of dry matter between main organs at final harvest, for Khaya senegalensis and K. ivorensis seedlings grown in culture solutions of different osmotic potentials (bars); A (-0.3); B (-2.8); C (-5.3); D (-10.3). The data are expressed as percentages of values in Treatment A. Treatment A consisted of culture solution alone; B, C and D consisted of culture solution plus polyethylene glycol.

K. senegalensis

Plant indices	Treatment			
	A	B	C	D
Leaf area ratio	100	85	88	99
Specific leaf area	100	87	84	82
Leaf weight ratio	100	86	91	105
Stem weight ratio	100	117	120	113
Root weight ratio	100	106	97	88
Root shoot ratio	100	104	92	78

K. ivorensis

Plant indices	Treatment			
	A	B	C	D
Leaf area ratio	100	85	96	94
Specific leaf area	100	102	103	102
Leaf weight ratio	100	84	95	91
Stem weight ratio	100	124	116	100
Root weight ratio	100	115	95	125
Root shoot ratio	100	115	92	127

(c) Discussion

Although Collis-George and Sands (1962) had earlier shown that osmotic and matric potentials may have different effects on germination of some seeds, McWilliam and Phillips (1971) have recently shown that over a range of water potentials, from 0 to -15 bars, both substrate osmotic and matric potentials are equivalent in their effect on germination processes in some seeds. There is more evidence for the view that osmotic and matric potentials have similar effects on plant growth (Wadleigh and Ayers, 1945; Richards and Wadleigh, 1952). Slatyer (1961) gave a summary of this extensive evidence. He however showed by his experiments that osmotic and matric potentials could be equal in their effect only if the root acts as an efficient osmometer so that solute is not able to enter the plant to a significant degree. The seedlings used in the present study had mostly undamaged roots (see p. 55). They could therefore be considered to have acted as reasonably efficient osmometers to the polyethylene glycol used if, as suggested by Lawlor (1970), entry of this substance through roots into plants is rapid only when roots are damaged. The results obtained in this experiment could therefore be directly compared with those in the soil experiment.

Relative growth rate of K. senegalensis was more sensitive to moderate moisture stress than was that of K. ivorensis. This agrees with the growth rate response shown by these species in the soil experiment. However when stress was increased (beyond 2.8 bars) K. senegalensis became less sensitive while K. ivorensis showed more sensitivity. As in the soil experiment, net assimilation rate of K. senegalensis was higher than that of K. ivorensis, but in this case there was no compensation made by a higher mean leaf area ratio of the latter species, so that the relative growth rate of K. senegalensis was higher than that of K. ivorensis. Again, as in the soil experiment, mean leaf area ratio for both species did not change appreciably with varying water potential of the root medium. Blackman and Wilson (1951) point out that reduction in relative growth rate can arise from reduction in leaf area ratio or net assimilation rate. From the results presented here it is clear that leaf area ratio showed little response to the treatments. The sensitivity in growth shown by the two species in relation to moisture stress could therefore be largely explained by the response of net assimilation rate (Fig. 8). This agrees with the results obtained in the soil experiment.

Unlike the soil experiment where dry matter was found to be proportionately greater in roots than in stem or leaves for K. senegalensis, in this experiment, more dry matter was present in the leaves. K. ivorensis still had the greater proportion of its dry matter in leaves. Root development of K. ivorensis was stimulated when osmotic potential of the root medium was reduced to -10.3 bars so that maximum root-weight and root:shoot ratios were obtained in this treatment. Eaton (1942) obtained similar stimulation of root growth of corn, tomato and wheat with increasing concentrations of chloride and sulphate in the culture solution he used. The greater proportion of root in K. ivorensis when subjected to high moisture stress may be of some adaptive significance; it may partly explain the relatively higher (though not significantly) relative growth rate and net assimilation rate obtained in Treatment D (-10.3 bars) when compared with Treatment C (-5.3 bars). However this kind of response was expected more for K. senegalensis, the species from the drier habitat, than for K. ivorensis which is a forest species. Stocker (1960) points out that root growth is favoured more than shoot growth in plants which grow in dry soil. Although root development in K. senegalensis was greater than in K. ivorensis, as was found in the soil experiment, root growth was apparently not stimulated by increasing moisture stress (cf. Jarvis and Jarvis, 1963a).

2.4. General discussion of growth experiments

Jarvis and Jarvis (1965) indicate that response to moisture stress induced in solution is more directly physiological than that induced by soil. Most of the problems encountered in the soil experiment were solved by using osmotic solution. If comparison, between the two species and using data from both the soil and culture solution experiment, is allowed, then it could be said that growth of K. senegalensis was more sensitive to low moisture stress than to high moisture stress, while growth of K. ivorensis showed more sensitivity to high moisture stress than to low moisture stress. As was mentioned in the introduction to this chapter, external moisture stress affects plant growth indirectly by causing internal deficits in the plant. Growth could be affected by these internal deficits directly through effects on the processes of photosynthesis. Internal deficits reduce photosynthesis; photosynthesis on the other hand directly determines the rate of net assimilation. As has been indicated, the reduction of growth in the present experiment was due more to reduction in net assimilation rate than to changes in leaf area ratio. Photosynthesis generally occurs in the leaf so that differences in 'desorption curves' of K. senegalensis and K. ivorensis are of particular interest.

In general the desorption curve that is the curve relating leaf relative water content to leaf water potential may be such that (a) a large volume of water is lost from the leaf for a small decrease in leaf water potential or (b) a small decrease in leaf water content corresponds to a large decrease in leaf water potential. When species are exposed to conditions of low stress, the loss of equal amounts of water will lead to greater stress in terms of decrease in water potential, in species with type (b) than in those with type (a) leaves. This greater stress will result in greater direct reduction in net assimilation rate; thus growth of species with type (b) leaves will be more affected than that of species with type (a) leaves. On the other hand when the external stress is very severe, for a species to continue absorbing water from this external medium, a very steep gradient in water potential must exist between the plant and the medium. A species with (a) leaves would have to lose quite a large amount of water from its leaves in order to reach the low leaf water potential which is required to steepen the potential gradient between plant and soil. This loss however may lead to the critical water status for tissue damage so that the survival of this species would be endangered. A species with type (b) leaves however needs to lose only a small volume of water to reach the low leaf water potential required to maintain a steep gradient for continued water absorption, so that such a species is unlikely to reach the leaf water content that is critical for tissue damage. A species with type (b) leaves thus stands a greater chance of continued survival under high external stress condition. Data to be presented later show that K. senegalensis could be said to have leaves of type (b), while K. ivorensis has leaves of type (a). It is possible that the growth responses observed in these two experiments reflect this difference in tissue water relations of the two species. When moisture stress was low (0 to -4.5 bars) growth of K. senegalensis was depressed more than that of K. ivorensis; but with more severe stress (up to -10.3 bars, in culture solution) the growth of K. ivorensis was more severely limited than that of K. senegalensis.

CHAPTER III

THE DIURNAL PATTERN OF PLANT WATER STATUS

3.1. Introduction

The results of the growth experiments reported in Chapter Two show that growth of *Khaya senegalensis* and *K. ivorensis* seedlings may be differentially limited by moisture stress in the root medium. It is well known that such a reduction in growth results from the effects that water deficits in the root medium have on internal water status of plants (Kramer, 1963; Slatyer, 1967, 1970). When internal water deficits exist, as a result of external stress, many physiological processes leading to plant development are depressed. It is even known that internal water deficits may develop regularly during the middle of the day to cause decreases in photosynthesis, even when the soil is adequately supplied with water (Polster, 1950 as cited by Kozlowski, 1958). Hence it was thought desirable, in the present study, to compare the internal moisture stress experienced by the experimental plants throughout the day, as an aid to understanding the more immediate causes of their growth responses to moisture stress in the root medium.

Kramer (1963) has pointed out that the only way to know whether a plant was being subjected to internal moisture stress was to measure the water status of the plant itself. Among well known indicators of plant water status are leaf water deficits and fluctuations in stem diameter (Hewlett and Kramer, 1963; Ogigirigi, Kozlowski and Sasaki, 1970; Kozlowski, 1967, 1968). These indicators provide a ready means of measuring internal water balance of plants. Leaf water status can be estimated by measuring leaf relative water content, essentially by the method of Weatherley (1950) (see Barrs, 1968). While leaf water content indicates the actual amount of water in the leaf, the force with which water is held in leaf tissue, and hence the degree of internal stress, is more meaningfully measured in terms of leaf water potential which is expressed in energy or pressure terms (Kramer, 1963). Weatherley and Slatyer (1957) indicate that for any given tissue there is a sensitive relationship between relative water content and water potential. Once this relationship is known, water potential can be estimated from measurements of relative water content (cf. Slatyer, 1962c). These methods, more fully described elsewhere in this thesis, together with measurements of stem diameter changes have been used to compare diurnal patterns of water status in the experimental plants in relation to soil moisture stress. This chapter describes these comparisons.

3.2. Methods

(a) Diurnal variations in leaf water status

Leaf water status was measured in terms of relative water content and leaf water potential, using the disc method of Weatherley (1950) as modified by Catsky (1960) (see p. 142). Measurements were made on seedlings that were larger than those used in the growth experiments. These seedlings were about one year old and 50 - 80 cm tall when used for experiment; they were growing singly in correspondingly larger pots (see p. 20). The seedlings were subjected to the same four soil moisture treatments: -0.3 (A), -0.4, (B), -0.8 (C) and -4.5 (D) bars, as were used in the growth experiment with soil. Two seedlings of each species were assigned to each treatment, except that for Treatment A there was only one seedling of K. ivorensis. The experimental seedlings were kept on a centre bench in the green house. Thermohydrographs were installed on this bench, near the seedlings, to record air temperature and relative humidity over the experimental period.

Diurnal patterns of plant water status were compared by measuring leaf relative water content on several days between December 1970 and April 1971. Before each measurement the plant pots were brought to prescribed weights for soil moisture control. On each day discs were taken from the experimental plants at two-hourly intervals starting at 06.00 hrs and ending at 22.00 hrs G.M.T. At each sampling occasion about ten discs (0.95 cm diameter) were punched randomly from mature leaves of the two or one plant in each treatment. Five discs taken randomly from the ten constituted a sample. Duplicate samples were not taken as suggested by Slatyer (1962a) because large errors could arise from delays in weighing many disc (Kreeb and Omal, 1961). Variation between individual discs in each treatment at each sampling occasion was small, so that five discs gave adequate replication.

The discs were quickly weighed singly to obtain fresh weights (F.W.). They were then saturated for three hours in holes in water saturated plastic foam material. Preliminary determinations (see p. 143) had shown that deficits existing in the leaves were completely eliminated by this time. After this period each disc was quickly surface-dried between filter papers, reweighed to get the saturated weight (S.W). All the determinations took place in the research room, under normal room lighting, with temperatures fluctuating between 23 and 25°C. After all these, the discs were dried in an oven at 95°C to obtain dry weight (D.W.). Relative water content (R.W.C.) was then calculated as:

$$R.W.C. = \frac{F.W. - D.W.}{S.W. - D.W.} \times 100$$

The average values for the periodic samples for each species in the different treatments were thus found. The values were then plotted against time of day. The determinations were made for all treatments on 15 December 1970, 6 January, 16 and 30 March and 5 April 1971, except that Treatment B was not represented in the determination on 15 December.

The relative water content data were used to derive the corresponding leaf water potential values, from the curves (see Fig. 20 p. 150) relating these two parameters.

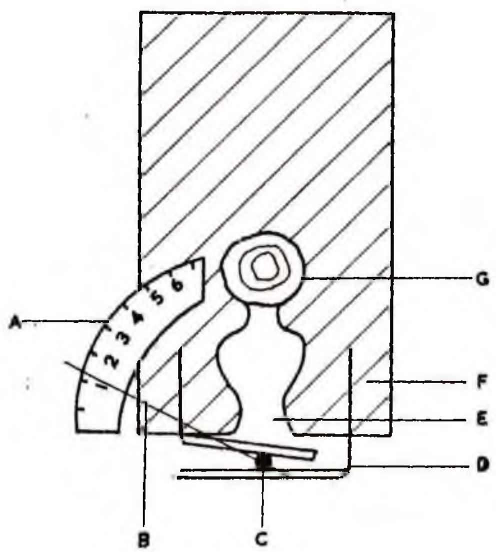
(b) <u>Diurnal variation in stem diameter</u>

Diurnal variation in stem diameter were measured on seedlings similar in age and size to those on which leaf water status was studied. Five seedlings of K. senegalensis and four of K. ivorensis were available for this study. Measurements were based on the use of a simple dendrometer designed by Dr D. Cross of the Cocoa Research Institute, Tafo, Ghana (see Fig. 9 and Appendix 3, plate 1,A,B,C). The main body of the instrument consisted of a flat piece of expanded polystyrene (about 9.5 x 7.0 x 1.5 cm) out of which a wedge, terminating in a semi-circular opening had been cut to fit the stem. Two thin galvanized iron plates were fitted into the polystyrene material at its cut end so as to overlap and hold in a vertical position a sheathed 2.5 cm long nail. A thin metal wire was fixed at one end, with araldite, flat on the head of the nail. The wire was arranged so that its free end served as a pointer on a scale printed on paper and fixed to the body of the polystyrene material. Changes in stem diameter were transmitted through movements in the polystyrene and overlapping metal plates to the vertical nail. The resulting rotation of the nail on its vertical axis caused the pointer to move horizontally along the scale thus indicating the change in stem diameter. The instrument was fixed at about six cm above the soil surface, and each set-up was calibrated individually by comparing dendrometer readings against measurements made directly on the stem, with a micrometer screw guage (see Appendix 3, graph 1).

Changes in stem diameter were recorded at two-hourly intervals starting from 06.00 to 22.00 hours G.M.T. The experiment was carried out again in the greenhouse where temperatures and relative humidity were recorded.

FIG. 9

PLAN DIAGRAM OF THE SIMPLE DENDROMETER USED TO MEASURE STEM SHRINKAGE.
(SEE APPENDIX 3, PLATE 1, A, B AND C FOR PHOTOGRAPHS)



A = SCALE
B = METAL WIRE
C = SHEATHED NAIL
D = GALVANIZED IRON PLATES
E = WEDGE
F = EXPANDED POLYSTYRENE
G = PLANT STEM

FIG. 9

Because there were few seedlings, the method used in applying moisture treatments differed from that employed in the leaf-water status studies. Here the soil was brought to field capacity at the same time for all the seedlings, before being allowed to go through a drying out cycle. Changes in stem diameter were recorded for each seedling on the day when the soil was at field capacity and at intervals during a drying out cycle which lasted about a week. In this experiment also soil moisture was controlled by pot weighing (see p. 28). The moisture content of the soil experienced by the seedlings on any particular day was expressed as a percentage of the value at field capacity.

All the determinations were made in May and first week of June, 1971. The seedlings experienced three drying out cycles during this period.

Taking mean stem diameter at 06.00 hrs G.M.T. on each day to represent 100% stem diameter, variations in diameter throughout the day were calculated as percentages of the initial morning values. This was done in order to eliminate differences in stem diameter changes that were not due to stem water status. The values obtained were plotted against time of day in each case.

3.3. Results

(a) Diurnal variations in leaf water content

The results for the five days are fully presented in Appendix 3, tables i to v. It was found that presentation of all the results in a graphical form complicated the curves for the individual treatments. For this reason only the results for Treatment A, the wettest treatment and Treatment D the driest, have been presented as curves (See Fig. 10).

On all the five days maximum relative humidity was over 80% and this occurred in the early mornings and evenings. Minimum temperatures ranging from 22 to 26°C were recorded also in the early mornings and evenings. Minimum values of relative humidity ranging from 48 to 58% were obtained between 10.00 and 16.00 hours G.M.T. Maximum daily temperature was over 30°C for all the five days with the highest value of 36°C occurring on 5 April. The minimum temperature value was obtained between 10.00 and 16.00 hours G.M.T. Although evaporation was not recorded, it could be assumed that the high temperature and low relative humidity values occurring generally between 10.00 and 16.00 hours were conducive to high evaporation around that time. The early morning and evening low temperature and high relative humidity values conversely reflect low evaporation rates.

As expected from theory (Slatyer, 1967), Fig. 10 shows that under both moist and dry soil and with variable microclimatic conditions, the experimental seedlings started each day with a high water status in their leaves: over 90% relative water content, except on 5 April when K. ivorensis seedlings in Treatment D started with less than this percentage. As evaporation increased, relative water content decreased so that minimum values were attained usually between 10.00 and 16.00 hours.

FIG. 10

DIURNAL VARIATION OF LEAF RELATIVE WATER CONTENT (%) FOR KHAYA SENEGALENSIS (LEFT) AND K. IVORENSIS (RIGHT) SEEDLINGS IN RELATION TO SOIL MOISTURE STRESS (BARS); (TREATMENT A, OPEN SYMBOLS) AND (TREATMENT D, CLOSED SYMBOLS) ON SEVERAL DAYS; I (15/12/70), II (6/1/71), III (16/3/71), IV (30/3/71), V (5/4/71).
(SEE APPENDIX 3, TABLE i TO v FOR FURTHER DETAILS)

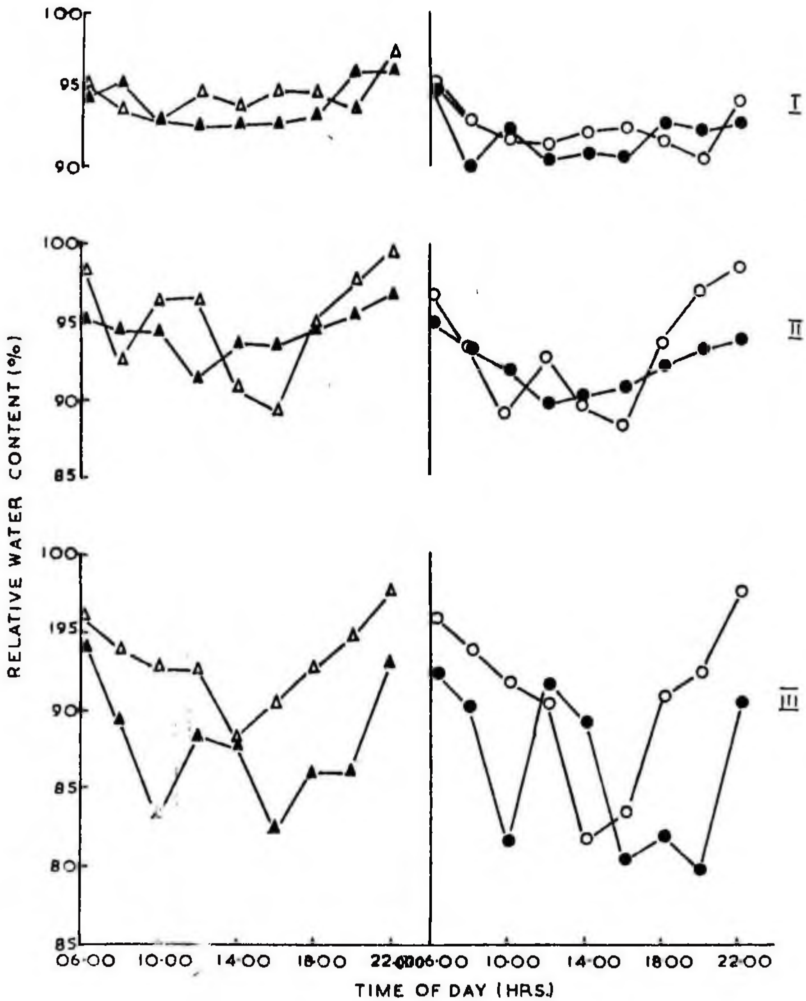
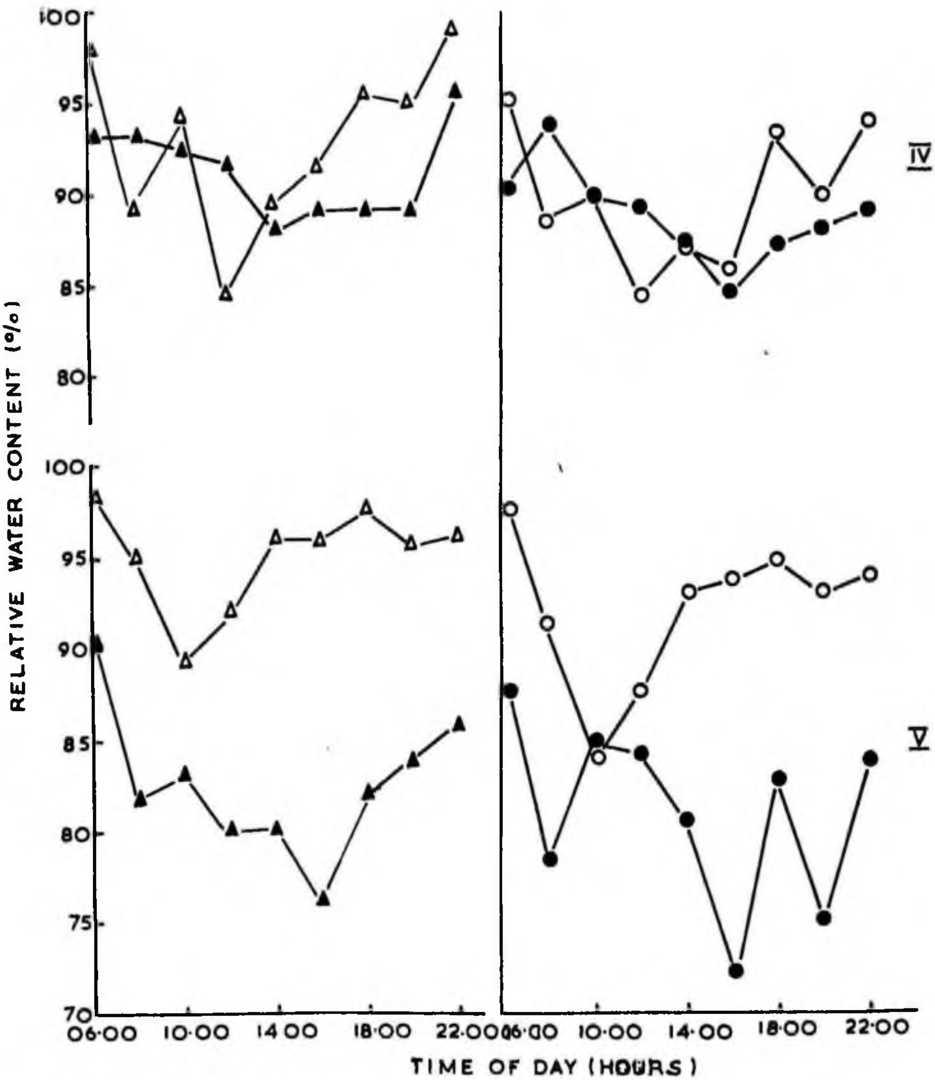


FIG.10

(continued next page)



RELATIVE WATER CONTENT (%)
100
95
90
85
80
75
70
IV
V
06·00
10·00
14·00
18·00
22·00
TIME OF DAY (HOURS)

FIG. 10. (CONT.)

The relative water contents rose again in the evening when microclimatic conditions suggest lowered evaporation. Similar patterns are well documented for other plants (Weatherley, 1951; Rutter and Sands, 1958; and Slatyer, 1962c).

Comparison between the two species under similar soil moisture treatments shows that throughout most of the day seedlings of K. senegalensis maintained overall slightly higher relative water contents in leaves than those of K. ivorensis. Over the experimental period, the maximum values obtained for Treatments A, B, C and D of K. senegalensis were 99.8, 99.4, 97.6 and 96.7% respectively, while the corresponding maxima for K. ivorensis were 99.2, 98.6, 97.7 and 95.0%. Minimum values for these treatments were, in the same order 84.6, 87.8, 85.0 and 76.3% for K. senegalensis and 81.5, 84.2, 81.5 and 72.0% for K. ivorensis. Generally differences between the values for Treatments A, B and C were not great so that comparison between these three treatments appeared to be unprofitable. In contrast, the differences between plants in Treatments A and D were more appreciable. In these latter treatments and for both species, seedlings in Treatment D had lower relative water content values for most parts of the day than did those in Treatment A. Comparison within the species shows that, for K. senegalensis, relative water content curves fluctuated more often in Treatment A than in Treatment D (except in Fig. 10 III and V): that is, seedlings in the latter treatment maintained more constant relative water content values throughout the day than those in the former. Unlike the situation with K. senegalensis, the curves for seedlings of K. ivorensis in Treatment D generally fluctuated as often as those for seedlings in Treatment A (except in Fig. 10, II). Improvement in relative water content in both species generally started when environmental conditions were still severe, between 10.00 and 16.00 hours. As has already been stated, at night, all the seedlings tended to make up for water lost by their tissues during the day.

Recovery of plant water status at night tended to be more complete when soil moisture was readily available. Although measurement was not made throughout any night, the trend towards better recovery in Treatment A, rather than in Treatment D plants was already clear each day by 22.00 hrs when measurement ended. Under this treatment also seedlings of K. senegalensis appeared to recover more fully at night than those of K. ivorensis: the mean relative water contents at 22.00 hrs for the five days of observation were 96 and 94% respectively for K. senegalensis and K. ivorensis. In Treatment D, relative water content values obtained for K. senegalensis seedlings were generally higher than those for K. ivorensis seedlings throughout most of the day and this was so even when K. ivorensis seedlings in Treatment D started the day with slightly higher relative water content values (Fig. 10, curve I) than K. senegalensis seedlings.

Unlike the rest of the curves, curves obtained for the two species on 5 April showed comparatively lower relative water content values for Treatment D. Recovery at night was also very poor, On that day the seedlings in this treatment started the day with much lower values of relative water content, 90.4% and 87.8% respectively for K. senegalensis and K. ivorensis. This might have accounted for the low relative water content values obtained throughout the day.

The dawn values of relative water content, which normally reflect soil moisture regime (Rutter and Sands, 1958), were as follows on the days when observation was made:

Date of observation	Relative water content %							
	K. senegalensis				K. ivorensis			
	A	B	C	D	A	B	C	D
15/12/70	95.3	97.0	94.1	94.6	95.3	-	93.3	95.0
6/1/71	98.6	96.3	96.1	95.1	96.9	95.8	94.5	95.0
16/3/71	96.7	99.4	97.6	94.3	95.8	98.6	97.7	92.5
30/3/71	98.1	99.1	93.5	93.4	95.2	97.2	95.2	90.3
5/4/71	98.4	98.1	95.3	90.4	97.3	98.3	96.9	87.8
Means with standard error	97.3 ±0.7	98.0 ±0.6	95.3 ±0.7	93.6 ±0.8	96.1 ±0.4	97.5 ±0.6	95.5 ±0.8	92.1 ±1.4

- No record

Comparison of mean values for the five days shows that dawn values of relative water content for K. senegalensis seedlings in Treatments A and B were similar but different from those of Treatments C and D, which were themselves dissimilar. For K. ivorensis, values for seedlings in

Treatment B was significantly higher than those in Treatments A, C and D. The values for Treatments A and C seedlings were similar but significantly higher than values in Treatment D. With the exception of Treatment A, where the dawn relative water content values for K. senegalensis were significantly higher than those of K. ivorensis, the values for seedlings of both species experiencing the same treatment were similar.

The minimum relative water content values obtained on the experimental days were as follows:

Date of observation	Relative water content (%)							
	K. senegalensis				K. ivorensis			
	A	B	C	D	A	B	C	D
15/12/70	93.1	91.5	93.9	92.7	91.5	-	92.1	90.0
6/1/71	89.3	92.6	91.3	91.2	88.4	89.5	90.5	89.9
16/3/71	88.8	89.4	85.0	82.5	81.5	86.9	81.5	79.5
30/3/71	84.6	87.8	88.8	89.8	84.1	84.2	89.2	84.7
5/4/71	89.6	89.7	88.2	76.3	84.4	87.4	89.6	72.0
Means with standard errors	89.0 ±1.4	90.1 ±0.8	89.6 ±1.6	86.1 ±3.0	86.0 ±1.8	87.0 ±1.1	88.6 ±1.8	83.2 ±3.4

- No record

Minimum relative water content values for Treatment B of K. senegalensis were significantly higher than those of Treatment D. These values were however not different from those obtained for the other treatments. Similarly for K. ivorensis with the exception of values in Treatment C, which were significantly higher than those of Treatment D, these values were similar to those of the other treatments.

(b) Leaf water potential

The diurnal variations in leaf water potential are shown in Fig.11 and Appendix 3, tables vi to x. As has already been indicated in the method (see p. 77) these data were derived from the measured relative water content values and the curves relating leaf water content to leaf water potential (see Fig. 20, p. 150). Although the relative water content values for K. senegalensis were higher than those for K. ivorensis these corresponded to lower leaf water potentials. Thus the leaf water potential values for K. ivorensis were generally higher than those of K. senegalensis. The dawn values of leaf water potential were as follows:

Date of observation	Leaf water potential (Bars)							
	K. senegalensis				K. ivorensis			
	A	B	C	D	A	B	C	D
15/12/70	-6.5	-4.5	-8.0	-7.5	-4.0	-	-6.5	-4.5
6/1/71	-2.5	-5.5	-5.5	-6.5	-2.5	-3.5	-5.0	-4.5
16/3/71	-5.0	-1.5	-4.0	-7.5	-3.5	-1.5	-2.0	-7.0
30/3/71	-3.5	-2.0	-8.5	-8.5	-4.0	-2.5	-4.5	-9.0
5/4/71	-3.5	-3.5	-6.5	-12.5	-3.0	-2.0	-2.5	-11.5
Mean with standard error	-4.1 ±0.8	-3.4 ±0.9	-6.5 ±0.8	-8.5 ±1.1	-3.4 ±0.3	-2.4 ±0.4	-4.1 ±0.8	-7.3 ±1.3

-No record

FIG. 11

DIURNAL VARIATION OF LEAF WATER POTENTIAL (BARS) FOR _KHAYA SENEGALENSIS_ (LEFT) AND _K. IVORENSIS_ (RIGHT) SEEDLINGS IN RELATION TO SOIL MOISTURE STRESS (BARS): -0.3 (TREATMENT A, OPEN SYMBOLS) AND -4.5 (TREATMENT D, CLOSED SYMBOLS) ON SEVERAL DAYS: (I) 15/12/70, (II) 1/6/71, (III) 16/3/71, (IV) 30/3/71, (V) 5/4/71.
(SEE APPENDIX 3, TABLES vi TO x FOR FURTHER DETAILS)

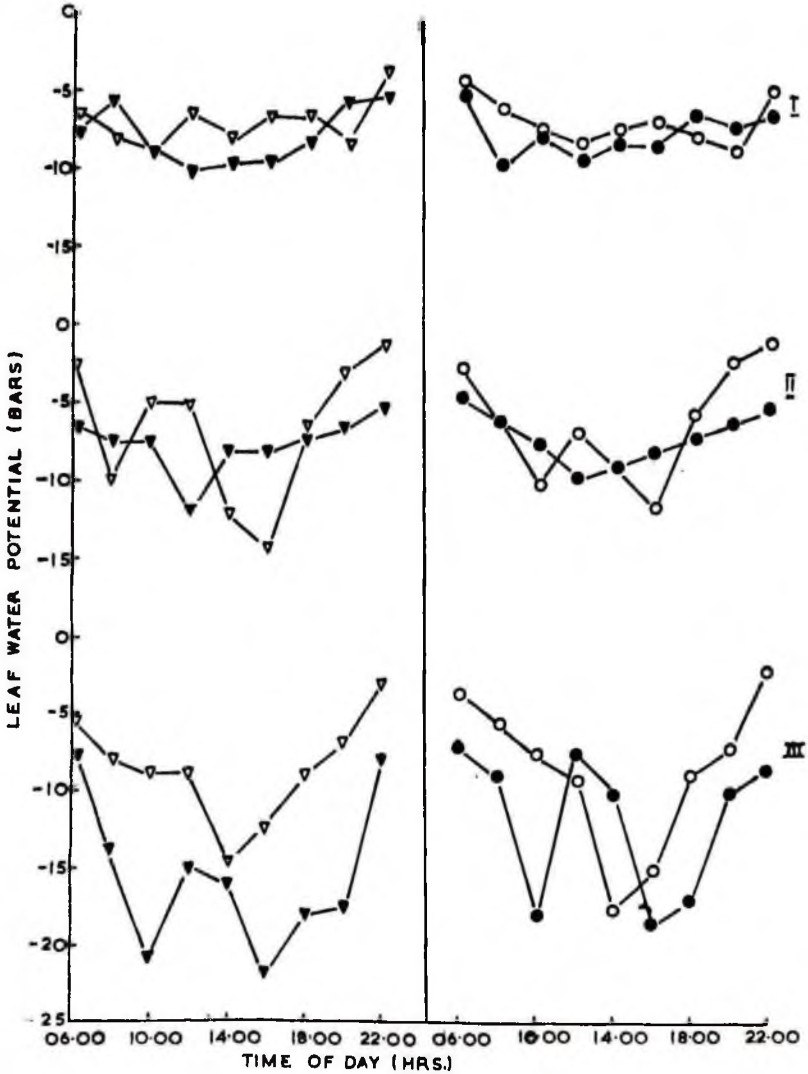


FIG. 11

(continued next page)

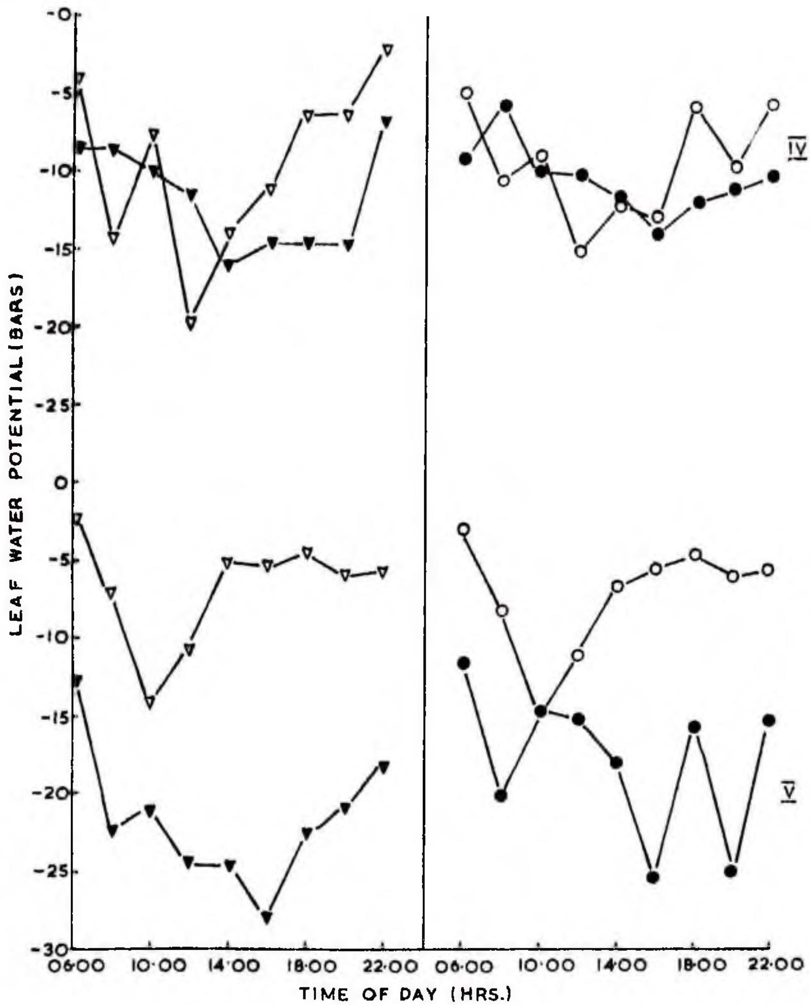

LEAF WATER POTENTIAL (BARS)
-0
-5
-10
-15
-20
-25
0
-5
-10
-15
-20
-25
-30
06·00
10·00
14·00
18·00
22·00
06·00
10·00
14·00
18·00
22·00
IV
V
TIME OF DAY (HRS.)

FIG.11 CONT.

Comparison of the mean using their standard errors shows that for K. senegalensis, seedlings in Treatments A and B had similar dawn leaf water potentials; these were significantly higher than values in Treatments C and D which were themselves significantly different. For K. ivorensis the highest dawn values of leaf water potential were found for seedlings in Treatment B. Values for seedlings in Treatment D were significantly lower than those for seedlings in A and C. The latter were not significantly different from each other.

Minimum values of leaf water potential obtained on each day were as follows:

Date of observation	Leaf water potential (Bars)							
	K. senegalensis				K. ivorensis			
	A	B	C	D	A	B	C	D
15/12/70	-9.0	-11.0	-8.0	-10.0	-8.5	-	-7.5	-9.5
6/1/71	-14.5	-10.0	-12.0	-12.0	-11.5	-9.5	-9.0	-9.5
16/3/71	-14.5	-14.0	-19.0	-22.0	-17.5	-12.0	-17.5	-18.5
30/3/71	-20.0	-16.0	-14.5	-16.0	-15.0	-15.0	-10.5	-14.5
5/4/71	-14.0	-14.0	-15.5	-28.0	-14.5	-12.0	-10.0	-25.5
Means with standard errors	-14.4 ±1.7	-13.0 ±1.0	-13.8 ±1.3	-17.6 ±3.3	-13.4 ±1.6	-12.1 ±1.1	-10.9 ±1.7	-15.4 ±2.0

\- No record

The mean minimum value of leaf water potential obtained for K. senegalensis seedlings in Treatment B was significantly higher than that of Treatment D. Values obtained for these and the other treatments were however similar. For K. ivorensis the effect of soil moisture treatment on minimum leaf water potential values of seedlings in Treatments A, B and C were the same. The effect on Treatment D was however different from those of B and C in such a way that the minimum leaf water potential reached by Treatment D was significantly lower than that reached by Treatments B and C.

(c) Diurnal variation in stem diameter.

The diurnal patterns of variation in stem diameter are shown in Fig. 12: Cycles I, II and III, for 12 to 17 May, 18 to 21 May and 24 to 3 June respectively. The mean stem diameters recorded during the various cycles are shown in Appendix 3, Tables xi to xiii.

The general pattern of shrinkage in stem diameter shown by the two species under the different soil treatments was similar to that obtained in the leaf water status study. The diurnal changes were appreciable. Maximum shrinkage occurred around mid-day and there was, generally, recovery during the evenings (cf. Kozlowski, 1967). Stem shrinkage in K. senegalensis was generally greater than in K. ivorensis.

Comparison between seedlings on soil at different stages of drying out or on soil at the same stages but on different days are perhaps not justified since environmental conditions may have varied (see Table 8). If comparison is allowed, it could be seen that stem shrinkage in K. senegalensis increased gradually with decrease in soil moisture content. Drying out Cycle III was the only case in which seedlings

FIG. 12

DIURNAL VARIATION OF STEM DIAMETER FOR KHAYA SENEGALENSIS (LEFT) AND K. IVORENSIS (RIGHT) SEEDLINGS IN RELATION TO SOIL MOISTURE CONTENT (%) DURING THREE SOIL DRYING-OUT CYCLES (CYCLES I, II AND III). STEM DIAMETER AT EACH TIME OF DAY IS EXPRESSED AS A PERCENTAGE OF THE VALUE AT 06.00 HRS; THE FIGURE ACCOMPANYING EACH CURVE INDICATES MEAN SOIL MOISTURE CONTENT (AS A PERCENTAGE OF THE VALUE AT FIELD CAPACITY) ON DAY OF OBSERVATION.

* THESE RECORDS WERE MADE OUTSIDE CYCLE III, SEE TEXT P. 96

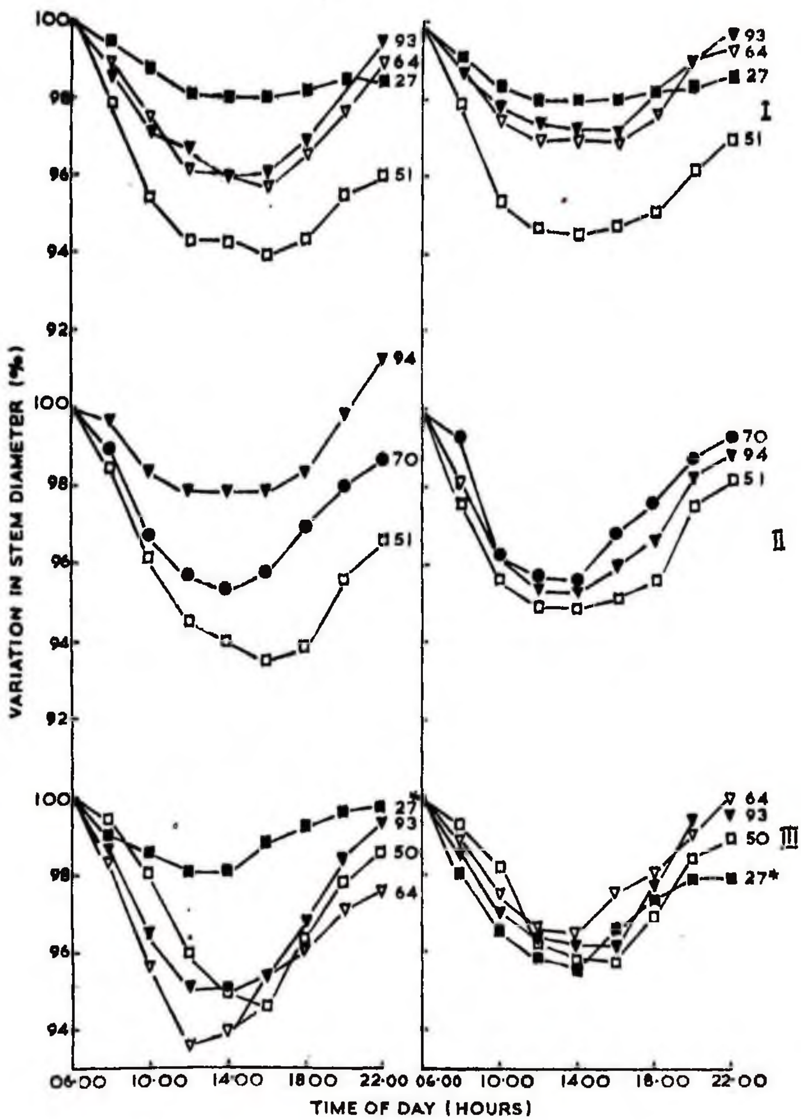

VARIATION IN STEM DIAMETER (%)
100
98
96
94
92
93
64
27
51
I
94
70
51
II
27
93
50
64
III
27*
06·00
10·00
14·00
18 00
22·00
TIME OF DAY (HOURS)

FIG. 12

subjected to soil at about 50% moisture content generally showed less shrinkage than those on soil at 64%. There was a slight shower on the day when the measurements at 50% soil moisture content in Cycle III were made.

Although shrinkage increased with decreasing soil moisture content down to about 50%, when soil moisture content fell to about 27%, stem shrinkage was markedly reduced in K. senegalensis (Cycles I and II).

The pattern of stem diameter change in response to soil moisture treatment in seedlings of K. ivorensis were less variable than for K. senegalensis seedlings, particularly during Cycles II and III. In Cycle I, the shrinkage of seedlings tended to increase gradually with decreasing soil moisture content, from around 100 to 50%, but at 27% soil moisture content very little shrinkage occurred. This response is similar to that observed with K. senegalensis seedlings under this treatment. However K. ivorensis seedlings at about 27% soil moisture content in Cycle III did not show a similar response.

In general it was difficult to repeat observations often enough with seedlings at 27% soil moisture content because stem shrinkage in both species continued to an extent that the pointers of the dendrometer were off the scale and the polystyrene material was no longer fitting firmly to the stem. Towards the end of Cycle I, there was only one seedling for both species, with the pointer still on the scale, so that the results given for 27% in this cycle are based on measurements on one seedling of each species. Although in cycles II and III no seedling of either species

Table 8

Experimental conditions during observations on stem diameter changes in seedlings of Khaya senegalensis and K. ivorensis. Relative humidity and air temperature are taken from thermohygrograph records.

Date of Cycles	Cycles	Soil moisture content (%)	Microclimatic data			
			Relative humidity (%)		Air temperature (°C)	
			Min.	Max.	Min.	Max
12/5/71		93	59.0	88.0	25.0	35.0
to	I	64	54.0	91.0	23.5	36.0
		51	54.0	90.0	24.0	35.0
17/5/71		27	54.0	90.0	24.0	35.0
18/5/71		94	61.0	94.0	22.5	32.0
to	II	70	52.0	90.0	25.0	33.0
21/5/71		51	50.0	90.0	23.0	35.0
24/5/71		94	52.0	94.0	23.0	34.0
to	III	64	50.0	88.0	23.5	34.0
28/5/71		50	68.0	98.0	24.0	34.0
3/6/71		27	60.0	94.0	23.5	33.0

could be measured at 27% for the reason given above, during routine weighing of pots, six days long after Cycle III was completed, a number of pots (two of K. senegalensis and four of K. ivorensis) were found in which the soil had dried to around 27% moisture content. The pointers on the dendrometers on these were also well within the scale hence measurements were made on the seedlings to supplement data already obtained. The curves obtained from these measurements are plotted along with the data for Cycle III (see footnote in Fig. 12). Environmental conditions differed on the two occasions (Cycles I and III) when measurements were made with soil at 27% moisture content, and this may account for the difference in response of K. ivorensis seedlings between these occasions. Environmental conditions were very variable. During Cycle I, maximum temperature for the day was 35°C while relative humidity reached a minimum of 54%. During Cycle III the corresponding values were 33°C and 60% respectively. Thus K. ivorensis seedlings subjected to 27% soil moisture content in Cycle I may have experienced more severe drying conditions than similar seedlings in Cycle III. It is possible that the more severe environmental stress (aerial and soil) was responsible for the reduced shrinkage of K. ivorensis in Cycle I when compared with similar seedlings in Cycle III (cf. data for K. senegalensis). Thus K. ivorensis seedlings can probably regulate their water economy, only when external stress is severe. Since stem shrinkage for K. senegalensis seedlings at 27% soil moisture content was similar on the two occasions, it may be that the regulatory mechanism operates in this species even before environmental stress becomes very severe. Data to be presented later, on the relation between stomatal closure and leaf relative water content, support this suggestion.

3.4. Discussion.

As discussed previously (Chapter II, p. 26) the water status of a plant is controlled by the relative rates of absorption and transpiration (Kramer 1962). Thus plant water status would be expected to change at any one time with variations in the evaporative demand of the air or with the water availability in the soil. (cf. Cowan, 1965). In the experiments reported above, the water status of seedlings of *K. senegalensis* and *K. ivorensis* as measured by leaf water status or stem diameter changes was found to be high at dawn. Thus, relative water content measured at dawn was over 90% for both species on most days and stem diameter was also large around this time. As evaporation increased later in the day plant water status decreased so that minimum values were obtained when evaporation was at its peak which was generally between 10.00 and 16.00 hours, G.M.T. Plant water status subsequently improved in the evenings when there was less evaporation and presumably also because of stomatal closure (see p. 131). Weatherley (1951) working on Gossypium species, Rutter and Sands (1958) on *Pinus sylvestris*, Slatyer (1962c) on *Acacia aneura*, Kozlowski (1967) on *Acer negundo*, *Fraximus americana*, *Picea glauca* and *Pinus resinosa*, and Klepper (1968) on *Pyrus communis* and *Prunus armeniaca*, all obtained similar diurnal patterns in plant water status.

In the present case comparison between the species under study shows that seedlings of K. senegalensis maintained in general a more favourable water balance in terms of relative water content than those of K. ivorensis. This might have arisen as a result of the greater volume of roots of this species than in the former species. The growth results reported in Chapter II showed that K. senegalensis had a higher mean ratio of root: shoot (about 0.8) than did K. ivorensis (about 0.6). This may have contributed to more rapid rate of water uptake in K. senegalensis than in K. ivorensis. Slatyer (1955) observed a similar maintenance of higher water balance by grain sorghum, than by peanut or cotton. He attributed this largely to the more extensive root system of grain sorghum than in the other plants. The comparatively slightly higher relative water content at dawn for K. senegalensis than for K. ivorensis further suggest that a difference exists between the two species in the rate of water uptake.

Both species showed sensitivity to water loss by improving their water status when evaporative conditions were still high. This could be a reflection of the pattern of stomatal opening and closure. Comparison was made between Treatments A, the wettest treatment, and D, the driest treatment. The results showed that there were fewer fluctuations in the relative water content curves of Treatment D than in those of Treatment A for K. senegalensis. Unlike K. senegalensis fluctuations in the curves of Treatments A and D seedlings of K. ivorensis seemed to be the same. Comparison between the species showed that less fluctuations occurred in Treatment D of K. senegalensis than those of K. ivorensis. Slatyer (1962c) observed that diurnal fluctuations in leaf water content of Acacia aneura were more when the soil was moist than when the soil was dry. He attributed this to effective stomatal control when soil moisture was limiting. Thus it is possible that stomatal control of water loss by K. senegalensis seedlings was more effective than that by K. ivorensis.

Kramer (1963) pointed out that knowledge of relative water content as an indicator of leaf water status is meaningless unless it is interpreted in terms of leaf water potential, because plants with similar relative water contents may still be experiencing different internal stresses. Hence, for effective comparison of the water status between the experimental species and their effect on plant processes, the relative water content values were interpreted in terms of leaf water potential. K. senegalensis leaves showed overall lower water potentials than did K. ivorensis seedlings. This may also have contributed to the comparatively more favourable water balance observed at dawn for K. senegalensis rather than for K. ivorensis. Low leaf water potential during the day may have steepened the water potential gradient between seedlings of K. senegalensis and the soil, so that water was brought into the plant at night more rapidly than in K. ivorensis. This added to the more extensive root system in K. senegalensis may have been responsible for the slightly better water balance in this species than in K. ivorensis (cf. Klepper, 1968).

Examination of the effects of the soil treatment on dawn values of leaf water potential in the seedlings of K. senegalensis (Fig. 11) shows that higher leaf water potential; were obtained in Treatments A and B than in Treatment C, and the lowest value was obtained in Treatment D. The highest dawn values of leaf water potential for K. ivorensis were obtained in seedlings in Treatment B. This was followed by the values for seedlings in both Treatments A and C. Here also, Treatment D had the lowest dawn values.

Unlike the study of leaf water status, where discs are punched, saturated and dried before the value at any particular time is known, measurement of stem diameter is made directly on the seedling. There are thus likely to be fewer sources of error in the latter kind of observation; hence the recorded stem diameter changes are probably a reflection of variation in plant water status than are the measured changes in leaf water status.

Diurnal shrinkage in stems of K. senegalensis was observed to be greater than that for K. ivorensis when soil moisture content was about 100 and 50%. This indicates that greater internal moisture stress developed in K. senegalensis than in K. ivorensis. This observation supports the conclusions reached from comparison of leaf water potentials in the two species. The latter were also lower in K. senegalensis than in K. ivorensis. The greater depression in the curves for K. senegalensis then in those for K. ivorensis stem could possibly be attributed to higher transpiration rates in the former species (see p. 129). The apparently greater depression when soil moisture was high than when soil moisture was low for K. senegalensis may be a reflection of lower transpiration rate under low soil moisture content. The present study also shows that shrinkage in stem, when soil moisture was low (around 27% soil moisture content), was less in K. senegalensis than in K. ivorensis. This could be attributed to better stomatal control in the former species than in the latter species. Experiment to be described later (Chapter V) shows that K. senegalensis closed its stomata at higher leaf relative water content than does K. ivorensis when leaves are allowed to dry out from saturation. Hence it was possible that water loss which could have resulted in greater stem shrinkage occurred less often in K. senegalensis than in K. ivorensis as a result of stomatal control.

As has already been stated, growth of plants is expected to be affected by internal water deficits. The results of the present study suggest that this expectation is realised only in a general way. Thus for example the high sensitivity of growth of K. senegalensis seedlings to low moisture stress in the root medium (see Chapter II) could be related to the apparently higher internal deficits experienced by these seedlings when compared with those of K. ivorensis. Similarly the apparently lower growth rate of K. senegalensis seedlings in Treatment D could be attributed to the high deficits which developed in these seedlings. However the higher internal deficits found here for K. ivorensis in Treatment D when compared with other treatments were not reflected in the growth rate observed under this treatment. Other workers have also had difficulty in attempting to explain growth results in detail in terms of internal water deficits. M.S. Jarvis (1963) could not relate the differences she observed in the response of growth rate of Prunus padus and Thelycrania sanguinea to increases in soil moisture tensions in terms of differences in the relation between leaf water deficits and increase in soil moisture tension. Although Lawlor (1969) observed that the growth of ryegrass, cotton and maize in response to decreasing osmotic potential of the root medium were closely related to the leaf water potential which prevailed, he also found that decreased in growth of bean could not be accounted for by the leaf water potential.

The investigations reported in this chapter suggest that differences between K. senegalensis and K. ivorensis, with respect to diurnal patterns of internal water balance, are slight. However, these slight differences reveal a trend which may be important in the water relations of the two species in nature. The lower leaf water potentials and apparently higher tensions in stem for K. senegalensis, when environmental stress is not severe, suggest that under this condition a steeper water potential gradient exists between this plant and the soil, and this may contribute to more rapid water uptake than in K. ivorensis. At the same time, the lower leaf water potentials may mean that growth is more directly limited in K. senegalensis than in K. ivorensis when environmental stress is not severe, hence the lower growth rates already reported (Chapter II, p. 45). On the other hand, when environmental stress is severe (for example, when soil moisture content was reduced to about 27% of its value at field capacity), stem shrinkage in K. senegalensis rather than in K. ivorensis is more consistently reduced from its level at higher soil water contents. This suggests a better mechanism in K. senegalensis than in K. ivorensis for conserving water when stress is severe. Thus, although the differences are small, they provide some support for conclusions tentatively drawn from the growth rate studies.

CHAPTER IV

TRANSPIRATION IN RELATION TO MOISTURE STRESS IN THE ROOT MEDIUM

4.1. Introduction

Attention has already been drawn to the relationships between rate of water loss (transpiration), rate of water absorption and internal water balance of plants (see Chapter II). Plant water status at any one time reflects the rates of transpiration and absorption (Kramer, 1962). When the rate of transpiration exceeds that of absorption water deficits develop within the plant, and when the rates are reversed there is an improvement in plant water status. It is well known (see Kozlowski, 1968) that during the day the rate of transpiration frequently exceeds that of absorption for most plants. A plant which is able to control its rate of transpiration effectively may be able to conserve water, and so have a water balance that is more favourable for growth than would a plant in which control of transpiration is poor.

In this chapter, transpiration rates of the study species are compared, particularly as these are affected by moisture stress in the root medium. Both the experiments on growth (Chapter II) and the observations on diurnal patterns of plant water status (Chapter III) indicate that differences, sometimes only slight, exist between the two species, with respect to their response to moisture stress in the root medium. The primary object of the comparisons described here was to examine the extent to which differences found in the above studies are related to differences in transpiration response.

Since water loss from plants and CO_2 uptake by leaves occur mainly through stomata (Meidner and Mansfield, 1968), when other factors are favourable, transpiration rate should reflect the degree of stomatal conductivity and hence also the ease with which CO_2 may diffuse into the leaves for photosynthesis. In this sense both transpiration and growth may be expected to respond broadly in a similar way to external moisture stress although it is known that additional factors affect the rate of CO_2 supply to chloroplasts. To examine the correlation between transpiration and stomatal opening, especially as these are affected by water stress in the root medium, the diurnal pattern of stomatal opening of the experimental species was compared. This comparison is also described in this chapter.

4.2. Methods

(a) Transpiration

Transpiration was studied mostly with plants growing on soil as the rooting medium. For reasons already discussed (see Chapter II, p. 51) the study was subsequently extended to plants growing in culture solution. The pot-weighing technique was used in all cases.

(i) Transpiration of plants rooted in soil.

The diurnal variation in transpiration of seedlings was measured on several days and under varying soil moisture conditions. The experiments were carried out with seedlings from the same stock as those used for the study of growth in soil. By the time of transpiration measurements the seedlings were about 4 to 5 months old, but were still growing singly in polyethylene containers. Leaf area was determined for each seedling prior to the measurements. Leaf areas of seedlings of both species were comparable at this stage (about 286 and 292 cm^2 for K. senegalensis and K. ivorensis respectively).

Soil moisture treatments were as for the growth experiments, namely: Treatments A (-0.3 bars), B (-0.4 bars), C (-0.8 bars) and D (-4.5 bars).

Two series of experiments were done. The first series was performed in the greenhouse where records of evaporation, temperature and relative humidity were kept throughout each experimental period. Evaporation was measured with Piché evaporimeters with green paper disc (3 cm diameter). Lighting was natural daylight. Measurements were made on at least two seedlings of each species in each treatment. On most days Treatments C and D were not represented because the soil had not dried to the prescribed limits.

The second series of experiments was carried out in the research room where environmental conditions were better controlled. In this environment, temperature ranged between 23 and 24°C and relative humidity fluctuated between 56 and 70%, but was mostly around 60%; light intensity, measured with an 'EEL' lightmaster (Model 18) was between 19.0 and 22.0 Klux at plant level. This intensity was obtained by supplementing normal room lighting (fluorescent tubes) with Osram (150 W) reflector spot lamps. The light from this latter source was filtered through a 3 cm thick layer of running water to reduce the heating effect on the plant. Evaporation was again recorded with Piché evaporimeters. Table fans were used to pass air over the plant at a speed of about 0.3 m/sec.

The same seedlings as in the first series of experiments were also used here. Space did not allow seedlings in all treatments to be measured at the same time. Only four pots could be accommodated at any one time under the lighting and fanning arrangements made. Measurements were therefore staggered such that at each time two pots in Treatment A (one of each species) were always included. The remaining two pots, also one of each species were from any of the other treatments. However, on some days, all the four pots belonged to one species, taking one from each of the four treatments.

On experimental days, each pot was enclosed in a sturdy polyethylene bag, to prevent water loss from the soil surface. The bag was securely sealed with 'sellotape' around the stem. Measurements in the greenhouse were made by weighing the pots at hourly intervals starting at 07.00 and ending at 18.00 hours. In the research room the experiments were run from 06.00 to 18.00 hrs G.M.T. Because of the slow rate of change in weight here, weighing was done at two hourly intervals from 06.00 to 10.00 hrs and from 16.00 to 18.00 hrs.

Weighing was done at hourly intervals for the remaining period, that is, from 11.00 to 14.00 hrs, when rate of weight change was higher.

From measured leaf areas and the recorded weight changes it was possible to calculate rate of transpiration in terms of unit area of leaf ($mg/cm^2/hr$). The calculated rates were then plotted against time.

(ii) Transpiration of plants growing in culture solution.

Transpiration of seedlings growing in culture solution was studied also in the greenhouse. Measurements were made on seedlings that were about five months old. These seedlings had been maintained for about four months in aerated half-strength Arnon and Hoagland solution which was renewed periodically. The containers for these seedlings were 15 cm in diameter with a capacity of about 2.5 litres. These had air-tight lids through which holes had been made to admit the seedlings and an aerator. Each seedling was supported in its hole by two halves of a rubber bung. There were at least two plants in each container, except in one case of *K. ivorensis* which was too large to be studied with another plant. Between experiments the seedlings were aerated continuously through one hole in the lid. On each experimental day and immediately before measurements started the aerator was removed and the hole was blocked with a rubber bung so that the whole container was airtight. There were seven buckets in all, three of *K. senegalensis* and four of *K. ivorensis*.

Measurements were made on 26, 27 and 28 October 1971. Moisture stress in the root medium was varied by replacing the culture solution in some containers with nutrient solution to which polyethylene glycol (Molecular weight 1000) had been added to give an osmotic potential of about -10.3 bars. The concentration (190 g/litre) of polyethylene glycol which gives this potential was again calculated from the data of Lawlor (1970, Fig. 1) (see p. 56). On each of the three days of measurement at least one pot of each species was allowed to remain in culture solution to which no polyethylene glycol had been added. These served as controls against which the effect of adding polyethylene glycol could be observed.

In order to compare transpiration of seedlings in culture solution with that of seedlings growing on soil, and also as a check on earlier measurements, plants growing in soil at field capacity were included in these experiments. There were two such pots for each species, and each pot carried one seedling.

As before, temperature, relative humidity and evaporation were recorded throughout each experimental period. Each experiment lasted four hours and was performed in the morning. Weights were recorded at intervals of 30 min. The short duration of each experiment was designed to reduce any effect of lack of aeration and entry of polyethylene glycol into the seedlings (Slatyer, 1961). At the end of each experiment the polyethylene glycol solution was replaced with culture solution after rinsing the roots and containers with water. Aeration was then re-started in readiness for the next measurement.

Transpiration was again measured as water loss per unit area of leaf ($mg/cm^2/30$ min).

(b) Stomatal conductivity and soil moisture stress.

The method adopted for this study was the infiltration technique. This method has been used successfully by other workers such as Alvim and Havis (1954) and Wormer and Ochs (1959).

Two sets of seedlings were used in this study. The first set were larger seedlings that were just over one year old; the second set of seedlings were about eight-months old. The seedlings were subjected to the usual soil moisture treatments, controlled by allowing pots to dry to prescribed limits: A, -0.3 bars; B, -0.4 bars; C, -0.8 bars and D, -4.5 bars. For each species one pot from each set of seedlings was assigned to one of the treatments.

The observations were again made in the greenhouse, where microclimatic records were kept.

The degree of stomatal opening was estimated by using an infiltration series prepared from commercial kerosene and liquid paraffin (cf. Halevy, 1960a, b; Shillo and Halevy, 1964; Fuehring, Mazaheri, Bybordi and Khan, 1966), in the proportions shown in Table 9. Preliminary trials with several mixtures including Nujol mixed with n-dodecane, Nujol mixed with xylene, had shown kerosene/paraffin to be the most suitable for these experimental leaves. Infiltration was scored on a scale which ranged from 1 to 14. An infiltration score of 10 for example means that mixtures containing up to 45% liquid paraffin penetrated the leaf.

Table 9

Composition of the infiltration series and the infiltration score they represent

Kerosene (ml)	Paraffin (ml)	Infiltration score
10.0	0.0	1
9.5	0.5	2
9.0	1.0	3
8.5	1.5	4
8.0	2.0	5
7.5	2.5	6
7.0	3.0	7
6.5	3.5	8
6.0	4.0	9
5.5	4.5	10
5.0	5.0	11
4.5	5.5	12
4.0	6.0	13
3.5	6.5	14

Measurements were made on mature leaves that were at comparable positions on the plant axis. Observations were made on 3, 14 and 17 June. On all the days seedlings from all four treatments were used. On 3 June smaller seedlings from Treatments A and D were measured in a separate experiment.

Determinations were made by putting a drop of the mixture on the abaxial surface of the leaf, starting from mixtures with low infiltration scores and increasing the scores till there was no penetration. The score of the last mixture which penetrated was recorded. A high infiltration score means the stomata are widely open. For the larger seedlings 2 to 3 leaflets of a leaf were tested, while 1 to 2 leaves of the smaller seedlings were tested at each determination. A day's determinations were made on different parts of a selected leaf. When all parts of the leaf were used up other leaves were selected for the continuation of the day's experiment. At the end of each experiment the mean infiltration scores at each hour were calculated and plotted against time of day.

4.3. Results

(a) Transpiration.

(i) Transpiration of plants rooted in soil.

Transpiration rates of seedlings of *K. senegalensis* and *K. ivorensis* growing in soil in the greenhouse, together with some microclimatic data, are shown in Figure 13, for 4 and 12 February, and in Appendix 4, Tables i to iv, the data for 8, 5, 10 and 11 February are given. Transpiration rates recorded in the research room are similarly summarized in Figs. 14 and 15 and in Table 10.

Microclimatic data collected in the greenhouse over the experimental period show that the rate of evaporation was generally low in the early mornings. Records made up to 08.00 hrs ranged from 0.1 to 0.4 ml/hr. The rate of evaporation increased from 11.00 to 15.00 hrs. Maximum values obtained on the six days ranged from 0.6 to 0.9 ml/hr. The rate of evaporation decreased after 15.00 hrs so that by 18.00 hrs when the experiments ended, the range was from 0.1 to 0.4 ml/hr. The pattern of evaporation adequately reflects changes in humidity and temperature.

Considering first the experiment in the greenhouse, the general pattern observed was a low transpiration rate in the morning when evaporation was low. The rate increased to a maximum from about 11.00 to 15.00 when evaporation was also high; there was generally a reduction in transpiration rate in the evening when rate of evaporation was low.

Comparison between the two species shows that, except on 8 February when rates in Treatment B were observed to be the highest, the transpiration rates on the other days generally decreased with soil dryness. The rates observed for K. senegalensis seedlings were generally higher than those for K. ivorensis seedlings especially when soil moisture was readily available. However the rate when the soil was dry tended to be slightly

FIG. 13

TRANSPIRATION OF SEEDLINGS OF <u>KHAYA SENEGALENSIS</u> (KS) AND <u>K. IVORENSIS</u> (KI) IN RELATION TO SOIL MOISTURE STRESS, BARS: (-0.3), (-0.4), (-0.8), AND (-4.5); TOGETHER WITH MICROCLIMATIC DATA (M) - AIR TEMPERATURE (●—●), RELATIVE HUMIDITY (○---○) AND EVAPORATION (HISTOGRAM). FOR 4/2/71 (LEFT) AND 12/2/71 (RIGHT). GREEN HOUSE

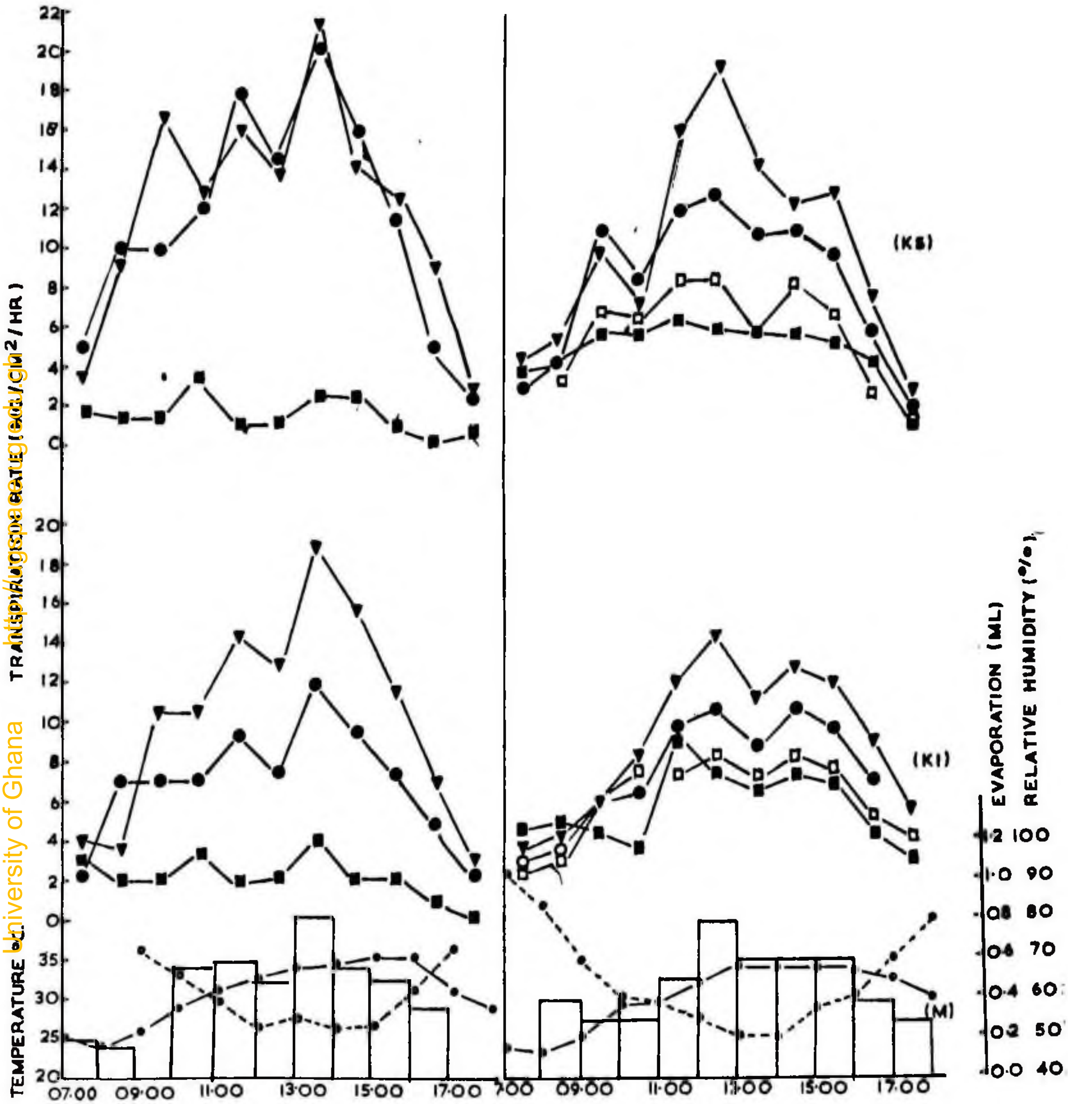

TRANSPIRATION RATE (MG/CM² / HR)
TEMPERATURE °C
EVAPORATION (ML)
RELATIVE HUMIDITY (%)
(KS)
(KI)
(M)
TIME OF DAY (HOURS)
07·00
09·00
11·00
13·00
15·00
17·00

FIG. 13

in lower in K. senegalensis than in K. ivorensis. Thus taking all experimental days together, the maximum rate for K. senegalensis in Treatments A, B, C and D respectively were 21.8, 21.5, 15.6 and 6.7 $mg/cm^2/hr$. Those for K. ivorensis were 18.1, 16.0, 13.3 and 9.5 $mg/cm^2/hr$ for corresponding treatments.

The degree of fluctuation in the curves for the two species tended to decrease with soil dryness. On 12 February no fluctuation was observed in the transpiration rate of Treatment D plants of K. senegalensis. The fluctuations in both species generally occurred between 11.00 and 15.00 hrs when the rate of evaporation was high.

Figure 13, curve I shows the daily mean rates of transpiration recorded for seedlings of K. senegalensis and K. ivorensis throughout the experimental period in the research room. Curves II and III show the daily means for Treatments A and D respectively. The means are made up of the data from five and two experiments respectively for Treatments A and D.

The transpiration rates recorded in the research room for both species were lower than those obtained in the greenhouse. Maximum rates for K. senegalensis seedlings in the research room (see Table 10) for Treatments A, B, C and D respectively were 5.0, 4.7, 4.3 and 3.8 $mg/cm^2/hr$. Corresponding rates for K. ivorensis were 4.8, 4.7, 3.8 and 3.1 $mg/cm^2/hr$. These values are considerably less than those quoted above for corresponding treatments in the greenhouse. Evaporative conditions in these environments cannot account for all this difference.

The recorded maximum rates of evaporation (compare Figs. 13 and 14) are only slightly higher for the greenhouse. The lower temperature in the research room could, conceivably, have had a more direct effect on the plant, perhaps through controlling stomatal opening (see Meidner and Mansfield, 1968) or the rate of water uptake and transport (Slatyer 1967).

The general diurnal pattern obtained with seedlings in the greenhouse was repeated in the research room. Thus lower rates of transpiration were recorded in the mornings and evenings, and the highest rates were recorded between 11.00 and 15.00 hrs. However unlike the greenhouse experiment, this pattern was distinctly less correlated with the evaporation rate in the research room. Thus transpiration rate was low in the evening while evaporation was still high. Further, a distinct drop in rate of transpiration was observed on most days, and for both species, between 10.00 and 12.00 hrs. This drop was more pronounced when soil moisture status was high (Fig. 14, Curve II) than when it was low, and is suggestive of the so-called 'mid-day closure' reported for many plants (see Meidner and Mansfield 1968; Slatyer, 1967). Re-examination of the transpiration curves for plants in the greenhouse (Fig. 13) suggests that this depression also occurred to varying degrees in all the treatments on 8 February. The reasons for its marked occurrence in the research room are not known, but taken together with the low transpiration rates in the evening when evaporation was still high the phenomenon suggests that

FIG. 14

DIURNAL VARIATION IN TRANSPIRATION ($MG/CM^2/HR$) OF SEEDLINGS OF KHAYA SENEGALENSIS (△) AND K. IVORENSIS (○).
I MEAN TRANSPIRATION RATE FOR SEEDLINGS IN ALL TREATMENTS.
II AND III - MEAN TRANSPIRATION RATE FOR SEEDLINGS IN TREATMENTS A AND D RESPECTIVELY. (HISTOGRAM - EVAPORATION (ML))

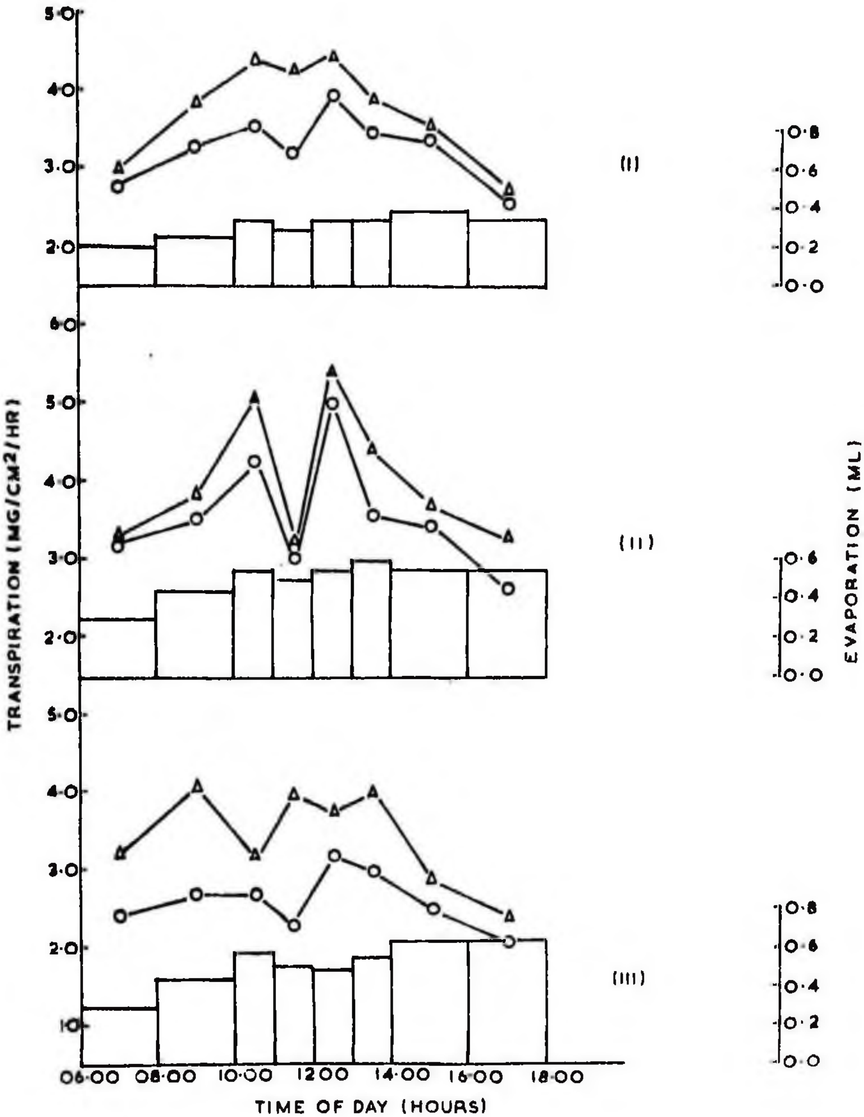

(I)
(II)
(III)
TRANSPIRATION (MG/CM²/HR)
EVAPORATION (ML)
TIME OF DAY (HOURS)

FIG. 14

the patterns of transpiration rate observed in the research room reflect more the characteristics of the plants or their response to soil treatment rather than to the aerial environment.

Curve I (Fig. 14) shows that transpiration in K. senegalensis was generally higher than in K. ivorensis. and that the rates obtained during certain periods of the day were significantly higher in the former species. As in the experiment in the greenhouse, in Treatment A, K. senegalensis seedlings transpired more rapidly than those of K. ivorensis. However the results for Treatment D were in contrast to that obtained in the greenhouse experiment. Here the rate for K. senegalensis remained higher than that for K. ivorensis which is the reverse of what was observed in the greenhouse.

In Table 10 are the mean transpiration rates for seedlings in all four moisture treatments compared at the same time on 19 February and 1 March (for K. senegalensis) and on 21 February and 2 March (for K. ivorensis). These data are presented again in Fig. 15 where each value is expressed as a percentage of the rate in Treatment A at the same time of day. Transpiration of K. senegalensis was generally greater in Treatment B than in Treatment A. Thus most of the points were observed to be more than 100%. Transpiration rate of seedlings of this species in Treatment D was however generally lower than that of those in Treatment A. On both days of measurement transpiration of K. senegalensis in Treatment A was markedly reduced between 13.00 and 14.00 hrs, such that the percentage rate obtained for all the treatments including D was more than 100% of the rate in Treatment A during this time of the day.

Table 10

Diurnal variation in transpiration of seedlings of *Khaya senegalensis* and *K. ivorensis* under varying soil moisture treatments (bars). Treatments A (-0.3), B (-0.4), C (-0.8) and D (-4.5) bars. (The experiment was done under semicontrolled environment).

Time of day (hrs)	Transpiration rate							
	K. senegalensis				K. ivorensis			
	A	B	C	D	A	B	C	D
06.00-08.00	2.2	2.9	2.9	2.0	3.3	3.2	1.9	2.1
08.00-10.00	3.6	4.0	3.9	3.0	4.4	3.8	2.1	2.5
10.00-11.00	3.8	4.6	4.2	2.7	4.4	3.5	2.5	3.1
11.00-12.00	5.0	4.7	4.3	3.8	3.6	3.6	2.9	2.5
12.00-13.00	4.6	3.7	3.6	2.7	4.8	4.7	2.3	2.8
13.00-14.00	2.6	4.1	3.3	2.9	4.7	3.6	2.5	3.1
14.00-16.00	4.0	4.6	3.3	2.7	4.3	3.9	3.8	2.6
16.00-18.00	2.5	3.2	2.1	1.5	3.5	3.0	1.8	1.7

FIG. 15

DIURNAL VARIATION IN TRANSPIRATION OF SEEDLINGS OF *KHAYA SENEGALENSIS* AND *K. IVORENSIS* SUBJECTED TO VARYING SOIL MOISTURE TREATMENTS – B (● , −0.4), C (□ , −0.8) AND D (■ , −4.5) BARS. THE DATA ARE EXPRESSED AS PERCENTAGES OF VALUES IN TREATMENT A (−0.3 BARS).

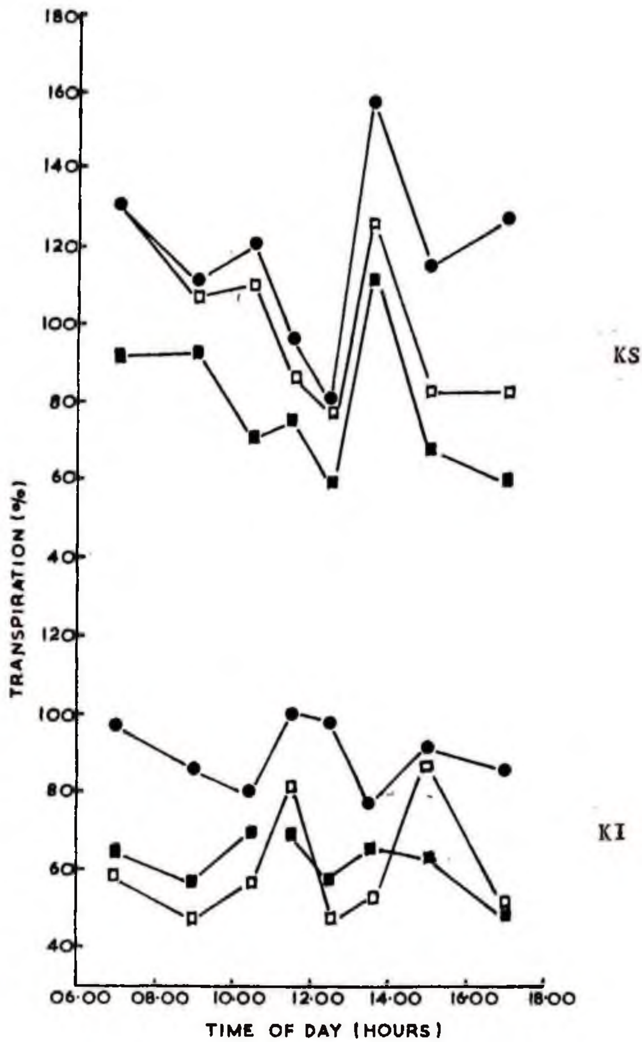

180
160
140
120
100
80
60
40
120
100
80
60
40
TRANSPIRATION (%)
KS
KI
06·00
08·00
10·00
12·00
14·00
16·00
18·00
TIME OF DAY (HOURS)

FIG.15

Fig.15 also shows that unlike transpiration of K. senegalensis, transpiration of K. ivorensis decreased consistently with increasing soil dryness such that Treatment A seedlings transpired more rapidly than those of Treatment B, which in turn transpired faster than seedlings in Treatments C and D. The rates for seedlings in the latter two treatments followed each other closely so that the curves obtained for them overlap at several points (Fig. 15).

Calculation of mean daily transpiration in the greenhouse for Treatments A and D (from data given in Fig.13, left and right) and for both species shows that water loss per cm^2 and day for K. senegalensis in Treatment D was 29.3% of the rate in Treatment A. The corresponding reduction for K. ivorensis was to 47.3%. However, in the research room, the mean daily transpiration in Treatment D as a percentage of Treatment A on days when measurements were made on seedlings from both treatments together were 84.6 and 81.8% respectively for K. senegalensis and K. ivorensis.

It is clear from the results obtained in the research room that transpiration rate of both species was again markedly reduced by the driest treatment (D). K. ivorensis seedlings however appeared to be comparatively more sensitive than those of K. senegalensis under this slightly controlled environmental condition.

(ii) Transpiration of plants growing in culture solution

The results for this experiment, together with the data collected at the same time for seedlings growing in soil, are shown in Fig. 16. The data for evaporation are also given in the figure. Temperature and relative humidity

FIG. 16

TRANSPIRATION RATE OF SEEDLINGS OF KHAYA SENEGALENSIS (LEFT) AND K. IVORENSIS (RIGHT) IN RELATION TO MOISTURE STRESS IN THE ROOT MEDIUM: -0.3 BARS MATRIC POTENTIAL (OPEN SYMBOLS), -0.3 BARS OSMOTIC POTENTIAL (▼) AND -10.3 BARS OSMOTIC POTENTIAL (■) (HISTOGRAM - EVAPORATION (ML)) (I) 25/10/71, (II) 26/10/71, (III) 27/10/71.

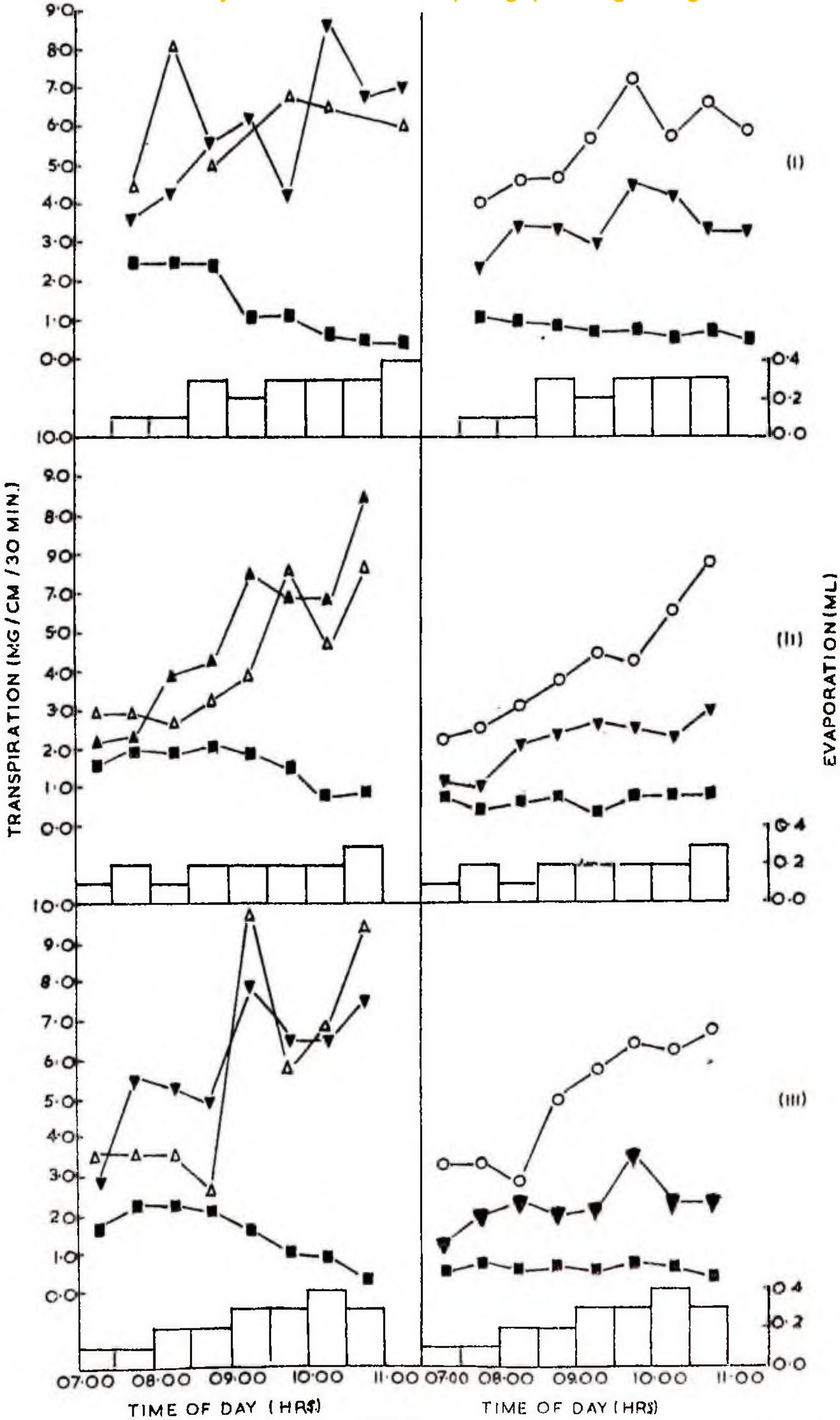

TRANSPIRATION (MG / CM / 30 MIN.)
EVAPORATION (ML)
(I)
(II)
(III)
TIME OF DAY (HRS)
TIME OF DAY (HRS)

FIG. 16

data during the experiments are presented in Appendix 4, Table v.

The transpiration rate recorded, for both species, with seedlings growing in soil here, are comparable to data presented above for seedlings under similar soil moisture treatment (-0.3 bars) (cf. Fig. 13). (Note that transpiration values in Fig. 16 are plotted as rates for 30 min intervals). Comparison of the soil-grown plants here with seedlings in culture solution (-0.3 bars) shows that for K. senegalensis the rates of transpiration of both types of seedlings were closely similar. Thus the effects of both matric and osmotic potentials on transpiration of this species were the same. K. ivorensis seedlings however did not show the same similarity. The curves obtained for seedlings growing in soil were consistently higher than for plants in culture solution. One of the seedlings used in the culture solution experiment had a greater absolute leaf area so that there may have been a considerable degree of mutual shading among its leaves. This may have caused the low transpiration rate recorded for this species under this treatment. However the sensitivity of K. ivorensis to poor aeration has earlier been pointed out (p. 49). It is possible that stopping the aeration (see Methods) during transpiration measurements may have contributed to reduce transpiration of K. ivorensis seedlings in culture solution.

Considering the effect of osmotic potential on transpiration rate of the two species, it was observed that transpiration decreased with decrease in solution osmotic potential. The maximum rate of transpiration for K. senegalensis, taking the three days together, were 8.8 and 2.5

$mg/cm^2/30$ min respectively for Treatments A and D. The transpiration rate of seedlings in the latter treatment remained fairly steady for the first $1\frac{1}{2}$ - 2 hr after exposure to the polyethylene glycol solution; thereafter, it declined steadily while that of seedlings in Treatment A continued to increase. The mean rates obtained for the three days at 11.00 hrs (that is, four hours after the start of the experiment) were about 7.0 and 0.6 $mg/cm^2/30$ min for Treatments A and D respectively.

Maximum transpiration rate of K. ivorensis in Treatment A was 4.6 $mg/cm^2/30$ min, and that for Treatment D was 1.2 $mg/cm^2/30$ min. There was an increase in the initial transpiration rate of seedlings in Treatment A during the experimental period. The initial rates in Treatment D however appeared to have been maintained throughout the experimental period. The mean maximum rates reached on the three days at 11.00 hrs were 3.0 and 0.6 $mg/cm^2/30$ min respectively for Treatments A and D.

Transpiration rate of Treatment A plants of K. senegalensis was greater than that of the corresponding K. ivorensis seedlings. This could be due to the mutual shading which occurred in K. ivorensis leaves, but the results from the other transpiration experiments reported earlier suggest that it could also be a reflection of real species difference.

Under Treatment D, K. ivorensis seedlings seemed to have shown more immediate sensitivity to the moisture stress than did K. senegalensis seedlings. Decrease in transpiration rate from the initial value occurred frequently earlier in the former species. The rate of transpiration of K. senegalensis under this treatment was also initially greater than that of K. ivorensis, but by the end of the experimental period, the rate was similar in both species.

On the whole, these results suggest that reduction in transpiration rate, as a result of decrease in solution osmotic potential to about -10.3 bars, was greater in K. senegalensis than in K. ivorensis. Thus within four hours of applying the treatment, transpiration rate of treated K. senegalensis was reduced to less than 10% of that of untreated plants. The corresponding reduction in K. ivorensis was to about 20%.

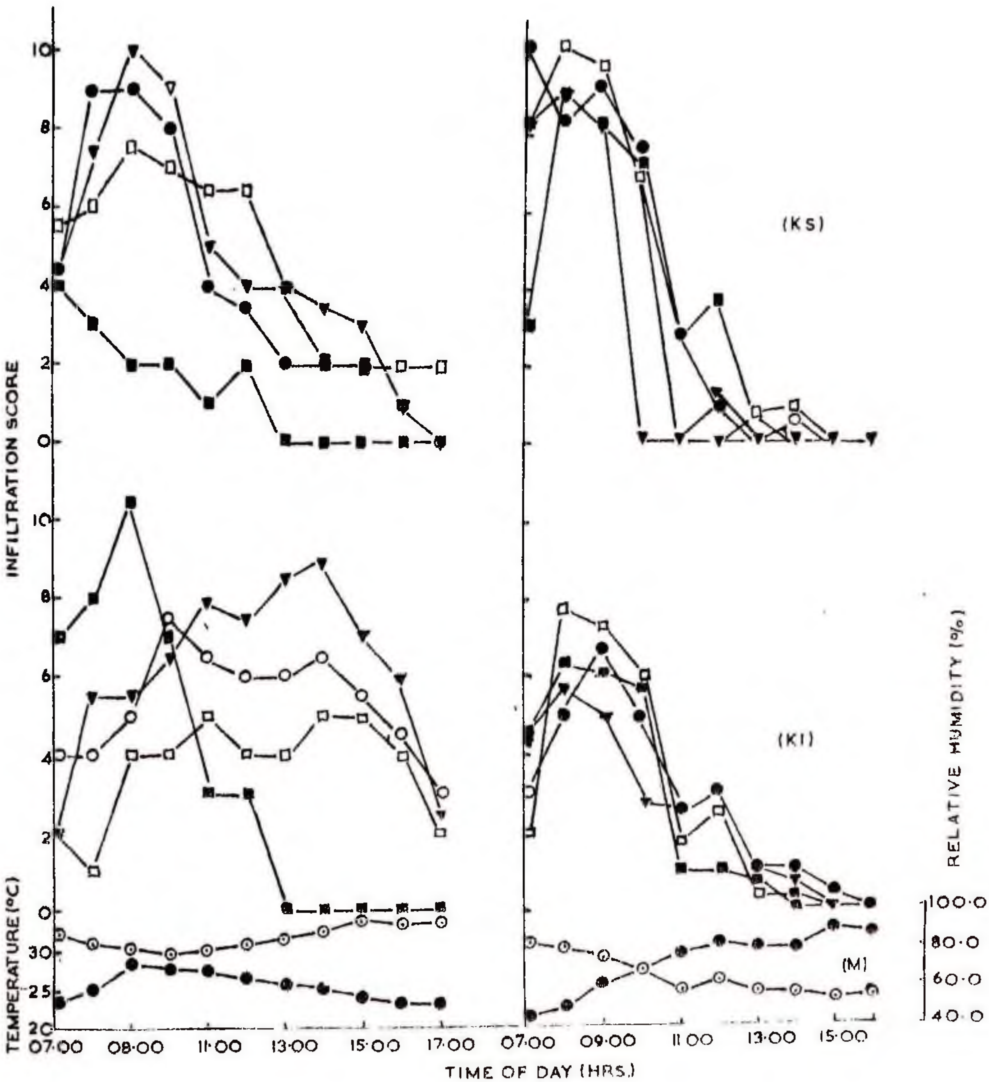
(b) Effect of soil moisture stress on stomatal conductivity.

Patterns of stomatal conductivity are illustrated in Figs. 17 and 18. Fig. 17 shows conductivity on 14 June for smaller, and 17 June for larger seedlings respectively, of all the four treatment for the two species; while Fig. 18 shows conductivity of leaves of Treatments A and D of the two experimental species on 3 June. In Appendix 4, Table vi, are presented data for the smaller seedlings from all treatments recorded also on 3 June. Higher infiltration scores (maximum about 11) were commonly recorded for K. senegalensis than for K. ivorensis (maximum about 9).

The period during which stomata were open and the degree of opening decreased with increasing soil moisture stress, so that stomata were widely open when soil moisture was at -0.3 bars,

FIG. 17

CURVES OF STOMATAL CONDUCTIVITY OF LEAVES OF <u>KHAYA SENEGALENSIS</u> (KS) AND <u>K. IVORENSIS</u> (KI) UNDER VARYING SOIL MOISTURE TREATMENTS (BARS). A (-0.3), ▼), B (-0.4, ●), C (-0.8, ◘) AND D (-4.5,); IN RELATION TO MICROCLIMATE (M)
MICROCLIMATE - AIR TEMPERATURE (●——●), RELATIVE HUMIDITY (⊙--⊙)
SMALLER SEEDLINGS (LEFT) AND LARGER SEEDLINGS (RIGHT).

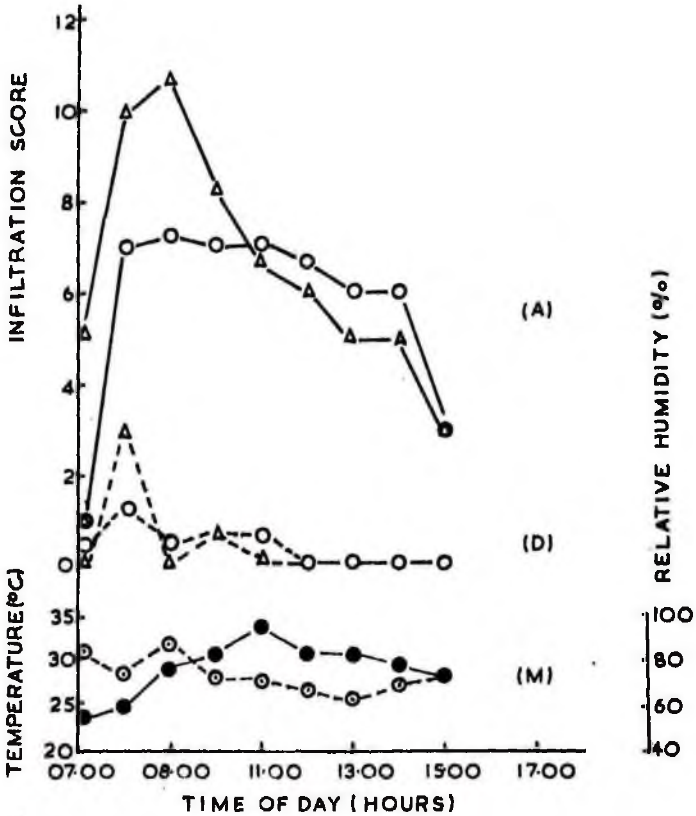


INFILTRATION SCORE
TEMPERATURE (°C)
RELATIVE HUMIDITY (%)
(KS)
(KI)
(M)
10
8
6
4
2
0
30
25
20
100·0
80·0
60·0
40·0
07·00
08·00
11·00
13·00
15·00
17·00
07·00
09·00
11·00
13·00
15·00
TIME OF DAY (HRS.)

FIG. 17

FIG. 18

DIURNAL VARIATION OF STOMATAL CONDUCTIVITY OF LEAVES OF KHAYA SENEGALENSIS (▲) AND K. IVORENSIS (○) UNDER TWO SOIL MOISTURE TREATMENTS (BARS), A (——) -0.3 AND D (- - - -) -4.5 IN RELATION TO MICROCLIMATE (M).
MICROCLIMATE: AIR TEMPERATURE (●—●), RELATIVE HUMIDITY (⊙—⊙).



INFILTRATION SCORE
12
10
8
6
4
2
0
(A)
(D)
(M)
TEMPERATURE (°C)
35
30
25
20
RELATIVE HUMIDITY (%)
100
80
60
40
07·00
08·00
11·00
13·00
15·00
17·00
TIME OF DAY (HOURS)

FIG. 18

(Treatment A), and only partially so when soil moisture stress was about -4.5 bars (Treatment D). This is well illustrated in Fig. 18. The figure also shows evidence of early stomatal closure in leaves of seedlings subjected to Treatment D.

The results, both in Fig. 17 and 18 show that the stomata of K. senegalensis opened widely during the early hours of the day, and generally began to close around 11.00 hrs. In contrast, K. ivorensis kept its stomata widely open longer. In this species closure was observed to start after 14.00 hrs on most days.

The pattern of stomatal opening did not appear to be closely related to environmental conditions (see Figs. 17 and 18). The infiltration score obtained for K. ivorensis smaller seedlings in the early hours of the day (Fig. 17) were surprisingly high and did not agree with the other data for this treatment (see Fig. 18 and Appendix 4, Table iv). Similar early hour high infiltration scores were obtained for leaves of the larger seedlings of both species under this treatment.

The pattern of stomatal opening observed for Treatment A, B, and C on the smaller seedlings (Fig. 17, left) were comparable to the pattern of transpiration shown by similar seedlings under similar treatment in the greenhouse (see for example Fig. 13, right).

4.4. Discussion

Transpiration rates of K. senegalensis and K. ivorensis seedlings were studied, both in the greenhouse and in the research room, in relation to moisture stress in the root medium. In the greenhouse transpiration of both species generally increased from sunrise and attained a peak between 11.00 and 15.00 hrs when evaporation was high. The rate fell in the evening when low evaporation prevailed. In the research room transpiration showed a similar pattern but this was not correlated with changing evaporative conditions.

Both species responded to low moisture stress by high transpiration rate. The transpiration rate of K. senegalensis was however consistently greater than that of K. ivorensis. This is in agreement with the difference in stomatal frequencies of these two species (see Table 1, p. 14) and possibly also with the higher mean ratio of root to shoot in the former species.

For both species the rate of transpiration generally decreased with increasing moisture stress. Several workers have observed similar reductions in transpiration in response to increasing moisture stress. Most of these findings have been summarized by Richards and Wadleigh (1952). In the greenhouse the sensitivity of transpiration of K. senegalensis seedlings subjected to stress of -4.5 bars (in soil) and -10.3 bars (in culture solution) was found to be greater than that of K. ivorensis under similar treatments. The reverse was however observed in the research room where K. ivorensis appeared to be slightly more sensitive than K. senegalensis to soil moisture stress of -4.5 bars. Transpiration of seedlings in culture solution was not investigated in the research room.

Since water loss from plants occurs mainly through the stomata, transpiration rates would be expected to reflect the degree of stomatal conductivity.

A diurnal periodicity was observed in stomatal conductivity of the two species. The stomata were widely open in the morning. For plants subjected to low soil moisture stress (-0.3 to -0.8 bars) the degree of opening generally started to decrease around 11.30 hrs in leaves of K. senegalensis and the larger plants of K. ivorensis (Fig.17). For the smaller plants of K. ivorensis (Fig. 17) stomata remained widely open, up to about 14.00 hrs. For both species the stomata of all plants rooted in soil at -0.3 to -0.8 bars moisture stress generally showed some conductivity after 15.00 hrs. Under conditions of greater stress (-4.5 bars) there was generally no conductivity of stomata of the seedlings after 12.00 hrs. Several workers, for example, Dale (1961) and Wormer (1965) have also observed a diurnal periodicity in the opening of stomata of the species they worked with.

The two species also differ in the degree of stomatal opening - K. senegalensis opening its stomata comparatively wider than K. ivorensis when soil moisture stress was low (-0.3 to -0.8 bars). Under conditions of greater stress (-4.5 bars) stomatal conductivity of both species (Fig. 18) was small.

Earlier stomatal closure and low conductivity of stomata when plants are subjected to severe moisture stress have been observed by other workers such as Loftfield (1921), Magness and Furr (1930), Yemm and Willis (1954) Rutter and Sands (1958) and Wormer (1965). Parker (1968) points out that earlier stomatal closure helps to maintain a more favourable internal water balance.

In the present investigation it is perhaps most meaningful to compare transpiration and stomatal conductivity for the smaller seedlings which were used in both types of investigation in the greenhouse. Although transpiration and stomatal conductivity were measured at different periods, prevailing environmental conditions during these periods were comparable. Thus temperatures and recorded on these occasions ranged from 23.0 to 34°C and 23.5 to 35.5°C on days of the stomatal and transpiration experiments respectively. In the same order relative humidity ranged between 94 to 58% and 96 to 51% respectively.

The general pattern of stomatal conductivity of K. senegalensis under low moisture stress (-0.3 to -0.8 bars) appeared not to be well correlated with the transpiration pattern observed. For instance high stomatal conductivity was observed early in the morning while transpiration rate had just started increasing. The latter attained a peak around 11.00 to 15.00 hrs just at the time when stomata had begun to close. On the other hand there seems to be a better relation between the two patterns for K. ivorensis seedlings when soil moisture stress was around -0.3 to -0.8 bars. This is well illustrated in Figs. 13 (right) and 17 (left), where the patterns obtained for both transpiration and stomatal conductivity appear similar. For both species both transpiration rate and stomatal conductivity were greatly reduced in the evening.

Although the periods of high transpiration rate and of wider stomatal opening, observed in K. senegalensis seedlings when soil moisture was readily available (-0.3 to -0.8 bars) did not coincide, the higher stomatal conductivity of this species may in part account for the higher transpiration rate when compared with K. ivorensis.

Stomata of both species appeared to close by 12.00 hrs when soil moisture stress was about -4.5 bars, while transpiration still continued but under a reduced rate. This is not surprising since several workers, for example Pisek and Winkler (1953) (as cited by Parker, 1968) indicate that stomatal closure may lead to slowing down, but not necessarily complete cessation of transpiration. This probably reflects the fact that there are other passages of water loss such as through the cuticle when the stomata are closed (see Meidner and Mansfield, 1968). In the present case it is also possible that stomata were closed only to a degree which prevented entry of the infiltration mixture used. Thus transpiration could have continued through slightly-open stomata.

The primary objective of the transpiration studies was to see whether differences observed in growth and diurnal pattern of plant water status could be related to differences in transpiration of the experimental species.

Considering first the diurnal pattern of plant water status, it was observed that the overall patterns of this and transpiration were closely similar especially when moisture stress was around -0.3 to -0.8 bars. Thus the plants started each day with a favourable internal water balance. Transpiration sets in and the internal water status is reduced. The greatest reduction occurred around 11.00 and 16.00 hrs. The rate of transpiration was high between 11.00 and 15.00 hrs. In the evening transpiration rate decreased; plant water status was observed to improve around this time, presumably also as a result of increased absorption.

At low soil moisture stress transpiration was observed to be higher in K. senegalensis seedlings than in K. ivorensis seedlings. Higher transpiration means more water loss. The potential gradient which acts as the driving force for water movement into the plant also depends on the amount of water loss, and on the relation between water content and water potential of leaves. Data to be presented later suggest that decrease in leaf water content is accompanied by a greater drop in leaf water potential for K. senegalensis than for K. ivorensis. Thus a steeper potential gradient for water absorption may be expected to exist in K. senegalensis than in K. ivorensis as a result of the differences both in transpiration rate and in the water content: water potential relationship (cf. Klepper, 1968). The steeper gradient would in turn be expected to lead to a more rapid rate of water uptake in K. senegalensis when moisture is freely available in the soil. Such an effect could contribute to a more rapid rate of recovery of plant water status at night following a day of high transpiration. It is probably for this reason that dawn values of leaf relative water content tended to be higher in K. senegalensis than in K. ivorensis, although the differences found were not significant.

Despite its higher transpiration rate, relative water content in leaves of K. senegalensis were generally slightly higher, throughout most of the day, than in leaves of K. ivorensis (see p. 84). However, because of the difference in leaf relative water content: leaf water potential relationship between the two species (see later), the higher relative water contents of K. senegalensis leaves corresponded to lower water potentials. This indicates that severe stress or higher tensions existed and may account for the more marked stem shrinkages in K. senegalensis rather than in K. ivorensis plants, at low soil moisture content.

When seedlings were subjected to a stress of -4.5 bars (Treatment D), the transpiration of K. senegalensis was reduced to about 29.2% of that in Treatment A, while the corresponding reduction was to about 47.3% for K. ivorensis. This may have contributed to the better relative water content observed in leaves of K. senegalensis in comparison with K. ivorensis (see p. 98) and to the greater reduction in shrinkage of stem of K. senegalensis rather than of K. ivorensis under this treatment. Within species, low transpiration and earlier stomatal closure in Treatment D plants probably accounts for their less pronounced stem shrinkage, when compared with plants in the other treatments. However this explanation may not apply to K. ivorensis in all cases. It may be recalled that stem shrinkage under the severest soil moisture condition (27%) (Fig.12) was not consistently reduced in comparison with other treatments for this species.

The other objective of the transpiration studies was to see how far differences in growth response to moisture stress could be explained in terms of differences in transpiration response. Photosynthetic rate on which growth depends is known to be correlated with transpiration rate (Brix, 1962). In the present study, such a correlation was expected. It has earlier been indicated that transpiration rate of seedlings rooted in soil in the research room probably reflect more the species characteristics and response to soil than do those of seedlings in the greenhouse, because the former were less correlated with environmental evaporation conditions. Results from the research room may therefore be used in attempting to interprete the growth of the seedlings in relation to soil moisture stress.

Transpiration rates of K. senegalensis seedlings when soil moisture stress was -0.3 to -0.8 bars (Treatments A to C) were high. Similarly the growth rates of seedlings under this condition were high in comparison with seedlings under severer stress (Treatment D). This higher growth rate could therefore be attributed, at least in part, to wider stomatal opening which favours CO_2 uptake. In the research room also, transpiration of K. senegalensis seedlings in Treatment D (-4.5 bars) was reduced to about 84.6% of that in Treatment A, whereas that of K. ivorensis seedlings under the corresponding treatment was reduced to 81.8%; yet, growth was significantly reduced by Treatment D in K. senegalensis but not in K. ivorensis. It is reasonable therefore to suggest that the significant reduction in growth of K. senegalensis seedlings in Treatment D may not be mainly due to lower rate of CO_2 uptake, but rather to the higher internal water deficits in Treatment D plants. Such a suggestion is supported to some extent by the leaf water potential data. These were lower for K. senegalensis than for K. ivorensis seedlings (see Chapter 3, p. 99).

For K. ivorensis, transpiration also decreased with increasing soil moisture stress; that is, Treatment A seedlings had the highest transpiration rate and seedlings in Treatment D, the lowest. However Treatment A seedlings also showed poor growth, and this was attributed to reduced root permeability as a result of poor aeration due to water logging. The seedlings used in the transpiration experiment were from the same stock as those of the growth experiment, but by the time of the transpiration experiments they were much older. These seedlings had received regular watering during the growth experiment, as for seedlings in Treatment A; but at the end of the growth experiment watering was less regular. Regular watering was started again a week to the transpiration experiment. If water-logging was responsible for the poor growth of K. ivorensis seedlings in Treatment A of the growth in soil experiment, it is possible that with less regular watering during the interval between conclusion of growth experiments and starting of transpiration studies, the seedlings had the opportunity to develop their root systems more fully. Hence, during the transpiration experiments, they were able to absorb any excess water rapidly, after each re-watering, thus reducing the duration of the water-logged condition. This probably accounts for the high transpiration of Treatment A seedlings of K. ivorensis. although their growth under this treatment was poor.

Transpiration was also high in Treatment B, under which the highest growth rate for K. ivorensis seedlings was found. This could be attributed to more rapid CO_2 uptake as a result of wider stomatal opening in seedlings under this treatment. As mentioned earlier transpiration of Treatment D plants of K. ivorensis was reduced to about 81.8% of that of seedlings in Treatment A. Growth of seedlings of K. ivorensis in this treatment appeared however to be unaffected.

Transpiration of both species was greatly reduced when moisture stress was increased to -10.3 bars by addition of polyethylene glycol to the culture solution. This reduction agrees with the growth response shown by the two species under this treatment. The transpiration rate of seedlings in the polyethylene glycol solution, as compared to those in the control (culture solution alone) by the end of the experimental periods, was reduced to about 10% for K. senegalensis and only to 20% for K. ivorensis. Growth was however observed to be reduced more in the latter than in the former species under this treatment. The transpiration data suggest that the greater reduction of growth for K. ivorensis did not arise from a greater reduction in CO_2 uptake. Rather, it is possible that the higher transpiration for K. ivorensis at -10.3 bars resulted in higher internal deficits which affected growth.

The investigations reported in this chapter show that transpiration rate of K. senegalensis and K. ivorensis seedlings is reduced by increasing moisture stress in the root medium. When soil moisture stress was at -4.5 bars, and in the greenhouse, transpiration rate was reduced more for K. senegalensis than for K. ivorensis. However in an environment (research room) where transpiration was less dependent on evaporative conditions, the reverse situation was found. At a moisture stress of -10.3 bars (in solution) transpiration was again reduced more in K. senegalensis than in K. ivorensis. These results are to some extent accounted for by the response of stomata to moisture stress, and themselves provide some explanations for the patterns of plant water status and of growth response described earlier.

CHAPTER V

TISSUE WATER RELATIONS

5.1. Introduction

Plant growth response, transpiration rate and internal water balance in relation to environmental moisture stress are all a reflection of the properties of the tissues of the plant concerned. The results described in the preceding chapters suggest that differences in response to variation in external moisture stress exist between seedlings of *K. senegalensis* and those of *K. ivorensis*. In particular growth of *K. senegalensis* was observed to be more sensitive to low moisture stress than that of *K. ivorensis*, while at high moisture stress the latter species tended to have the greater sensitivity. As previously indicated (p. 51) a plant with a high sensitivity of growth to small reductions in water potential may still possess drought resistance features in its tissues. Therefore examination of some aspects of the water relations of tissues of the study species appeared worth while.

In the present study, changes in growth rate in response to moisture stress in the root medium (Chapter II) were found to be related more to changes in net assimilation rate than to changes in leaf development. Net assimilation rate is determined primarily by net photosynthetic rate, while net photosynthetic rate itself is affected by rate of CO_2 uptake (which depends greatly on stomatal conductivity to CO_2), and by biochemical processes. These processes that control photosynthetic rate are known to be affected by water stress in the plant (Slatyer, 1967,1970; Troughton, 1968) (cited by Slatyer,1970)in a way which may be understood in terms of the water relations of plant tissues. For example, the relationship between water content and water potential of leaf tissue (Weatherley and Slatyer, 1957) indicates the amount of water held by the leaf at different degrees of stress. Conversely, it indicates what tension, in terms of water potential, may be expected to exist in the leaf for the loss of any given amount of water. In two plants in which this relationship differs, different degrees of stress may exist in their leaves for the loss of the same amount of water. To the extent that stress in the leaves limits biochemical processes of photosynthesis (cf. Slatyer, 1970) the rates of growth of these two plants may differ for the loss of similar amounts of water.

Again the extent to which water stress affects photosynthesis through stomatal conductivity depends on the sensitivity of stomata to water stress. If the stomata are very sensitive, CO_2 uptake through them is soon reduced resulting in reduction of photosynthesis, net assimilation rate and hence growth. But high stomatal sensitivity also means that water is readily conserved so that the development of high internal water deficits is checked. On the other hand low stomatal sensitivity, though permitting CO_2 uptake to occur over a wider range of moisture stress, may result in increase in internal water deficit which may directly reduce growth or damage tissues. Thus it is important to know whether a difference exists, between the present study species, in the relationship between leaf water status and stomatal closure.

In the following experiments the relationships between (1) relative water content and water potential of leaves and (2) relative water content and stomatal closure are compared for the two species. The tissue water status at which damage occurs is also briefly compared for the two species. Jarvis and Jarvis (1963e) have already stressed that the tissue water balance for optimum growth of plants depends greatly on these relationships.

5.2. Methods

(a) The relation between relative water content and water potential of leaves.

This relationship was investigated by the gravimetric vapour equilibration technique of Slatyer (1958). The technique basically involves comparing relative water content (R.W.C.) of leaf tissues equilibrated to different water potentials. Relative water content is measured as:

$$R.W.C. = \frac{\text{Fresh weight} - \text{Dry weight}}{\text{Saturated weight} - \text{Dry weight}} \times 100$$

The determination of R.W.C. thus involves saturation of leaf discs by flotation or equilibration in a humid chamber. Saturation is aimed at eliminating, by water uptake, all the deficits existing in the tissue and at providing a standard water content against which the amount of water in the leaf tissue at any time may be compared.

Weatherley (1950) and Barrs and Weatherley (1962) have pointed out that the curve of water uptake during this kind of saturation comprises two distinct phases: an initial phase of rapid but passive uptake (Phase I) followed by a period (Phase II) when there is a slow and steady uptake due to cell growth. Deficits existing in the leaf are normally completely eliminated by the end of Phase I, so that the water content at this point is the ideal basis for estimation of leaf water status. For the present study, it was thus desirable first to determine the duration of the Phase I water uptake period in discs of the experimental species, before determining the relative water content: water potential relationship.

(i) Determination of water uptake curves

Ten discs (diameter 0.95 cm) of each species were punched from mature leaves of about six-month old seedlings and rapidly weighed. They were then placed singly in holes in a humid chamber similar to that used by Okali (1971a) to become saturated. Each disc was reweighed at intervals of one hour until there was negligible increase. Before each re-weighing the discs were quickly dried between four layers of filter paper. The weight of each disc at each re-weighing was expressed as a percentage of the original weight. The mean percentages for each batch of ten discs were then plotted against time to give water uptake curves. The determination was carried out under normal room lighting with temperatures fluctuating between 23 and 25°C. There were six determinations in all.

The results (Fig. 19) show that in both species the first phase of the water uptake curve was virtually complete by 3 hrs, and phase II had probably begun. Many workers (for example Yemm and Willis, 1954; Catsky, 1959), have suggested that over this length of time the contribution made by Phase II uptake to the total water uptake is small. In the studies reported in Chapter III on diurnal patterns of leaf water status, this length of time was strictly adopted as the saturation period. In the present experiment, where the primary object was not just to eliminate existing deficits in leaves, but rather to obtain standard saturation water contents prior to equilibration at different potentials, it was convenient to use a ten-hour saturation period. From the slopes of the curves after 3 hrs (Fig. 19), it is clear that the contribution made by Phase II water uptake to the total saturation weights would still be small after 10 hrs (no more than 1.0 and 1.6% for K. senegalensis and K. ivorensis respectively).

(ii) Determination of leaf relative water content at various water potentials.

Discs 0.95 cm in diameter were punched randomly from mature leaves of seedlings of each species, that were about one-year old. The seedlings were growing in the greenhouse, on well-watered soil. There were about six seedlings of each species. Preliminary comparisons showed that the relative water content: water potential relationship remained constant between lower and upper leaves of the same plant

FIG. 19

WATER UPTAKE CURVE OF LEAF DISCS OF KHAYA SENEGALENSIS (△) AND K. IVORENSIS (⊙). (VERTICAL LINES INDICATE 2X STANDARD ERROR).

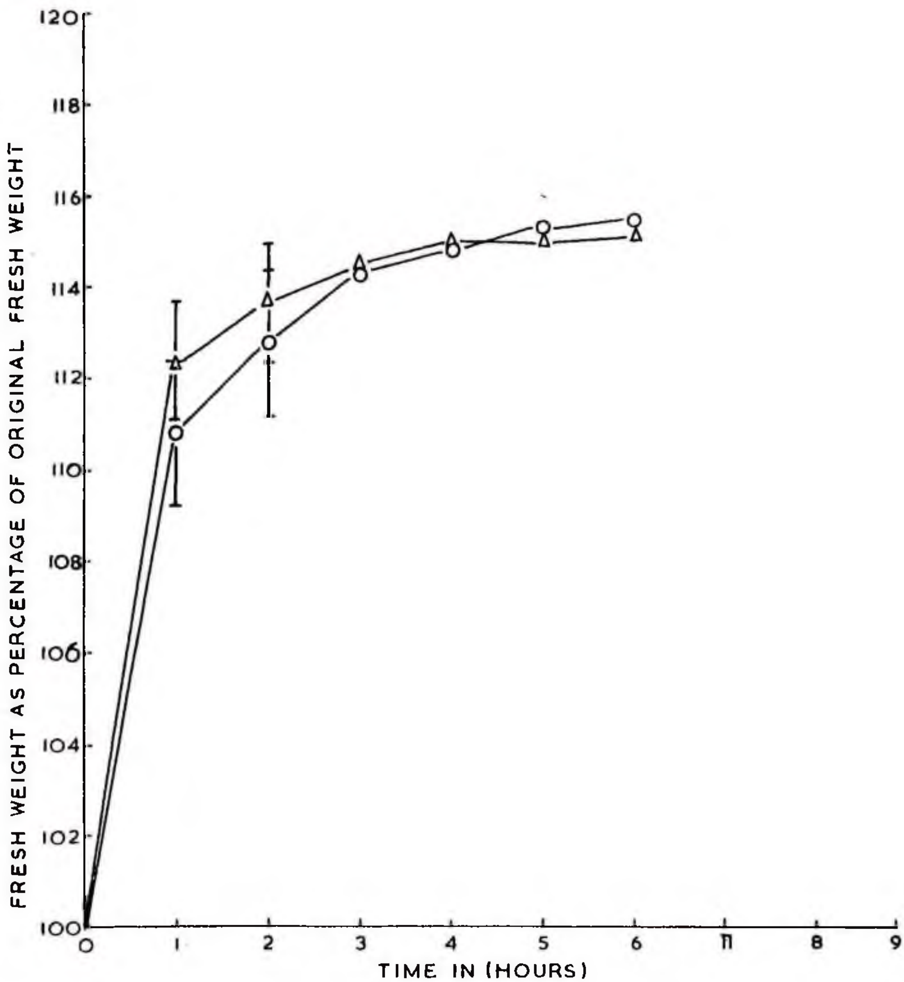

FRESH WEIGHT AS PERCENTAGE OF ORIGINAL FRESH WEIGHT
100
102
104
106
108
110
112
114
116
118
120
0
1
2
3
4
5
6
7
8
9
TIME IN (HOURS)

FIG. 19

or between different plants of the same species, provided the leaves used were mature but not senescent. Therefore 50 discs were taken randomly from six plants of each species. The punched discs for each species were thoroughly mixed before being allowed to become saturated as described in the preceding section. The saturated discs were surface-dried between filter paper and weighed to obtain saturated weights, before they were transferred into ten micro-desiccators. Each microdesiccator consisted of a 130 ml screw-capped jam jar containing plastic foam material soaked in one of the following NaCl (Sodium chloride) solutions; 0.50 M, 1.00 M, 1.50 M, 2.00 M, 2.25 M, 2.50 M, 2.75 M, 3.00 M, 3.50 M and 4.00 M, to give known water potentials (bars). These water potentials were calculated from the data of Owen (1952) relating osmotic potential to molarity of sodium chloride solutions.

A small grid of nylon mesh supported by glass rods, about 0.3 cm above the plastic foam material, carried the discs. Five discs of each species were arranged in a known order in each micro-desiccator, so that there were ten discs in all in a micro-desiccator. The micro-desiccators were tightly closed and were maintained at constant temperature in a double water-bath of which the outer bath was controlled to $25 \pm 0.02^{\circ}C$. Twenty four hours was allowed for equilibration before discs were re-weighed to obtain the equilibration weights (E.W.). From similar determinations carried out previously with these species (Dodoo, 1969) 24 hrs was found to be sufficient for equilibration and also to be more convenient.

The discs were ovendried for 24 hours at 90-95°C to obtain the dry weights (D.W.). The water retained by each disc at each water potential was calculated as, (equilibrated weight-dry weight/saturated weight-dry weight) x 100. The mean percentage for the five discs of each species was then plotted against the corresponding water potential (bars). The determination was repeated three times, giving four mean values of leaf water content for each species and at each sodium chloride concentration.

Since this relationship may vary with age or previous experience of the plant, the determination was further carried out with leaves taken from adult trees. These were about 13 years old and were growing in the Botanical Garden at Legon. There is one tree of K. senegalensis growing about 3 m or 6 m away from two trees of K. ivorensis. The K. senegalensis tree was about 9 m tall while the K. ivorensis trees were 7.6 and 9.0m. The determination with leaves from these trees was done twice and the mean values for the two determinations were plotted, against the corresponding water potentials.

(b) Leaf water status and tissue damage.

Desiccation tolerance of the two species was briefly examined by adopting the methods of both Jarvis and Jarvis (1963e) and Okali (1971a). The former authors assessed tissue damage by the ability of desiccated discs to regain their original saturated weights; while the latter made a visual assessment of tissue damage. In both methods assessment of tissue damage is made on discs which are re-saturated after equilibration over sodium chloride solutions in the usual way.

Discs which had been desiccated over a series of sodium chloride solutions were resaturated over the same period (10 hrs) as for the first saturation. The discs were surface-dried between four layers of filter paper during which visual assessment of damage was made. This was done by observing the potential at which 50% or more of the discs were extensively discoloured and there was heavy discharge of coloured matter. After this, the resaturated weights (R.S.W.) were determined. Dry weights (D.W.) were obtained after drying at 90-95°C for 24 hrs. The percentage recovery of original saturated weight after re-saturation was calculated as:

$$\frac{\text{R.S.W.} - \text{D.W.}}{\text{S.W.} - \text{D.W}} \times 100$$

Percentage recovery was then plotted against equilibration water potential.

As a check on the visual assessment of tissue damage epidermal strips and transverse sections of some of the resaturated discs were stained in equal volumes of 0.015% methylene blue and neutral red solutions by the Ruczicka-Tronchet method (Mclean and Cook, 1952, p. 51). The results obtained from staining were in general agreement with the visual assessment made.

(c) <u>The relation between leaf relative water content and stomatal closure.</u>

The method used was a modification of Hygen's quick weighing method (1951) for the study of transpiration of detached leaves. Leaves were obtained from the same seedlings as described in the previous section but the determinations were made when these were younger (about six

months old). The petioles of the leaves were re-cut under water and the leaves were kept standing in water over night and in sealed polyethylene bags. The bags were kept in the dark overnight.
On the following morning the leaves, still within the bags, were then exposed for 60 min under light from a 150 W Osram reflector spot Lamp, to allow the stomata to open. The light intensity at the level of the leaves, as measured with a photometer ('EEL' Lightmaster Model 18) was about 4,000 lux. After this period, the bags were opened; leaflets were then detached from the leaves. The leaflets were quickly dried between four layers of filter paper and weighed within 10-20 sec on a Mettler H6 balance to obtain their saturated weights (S.W.).
The leaflets were subsequently placed horizontally with their abaxial surfaces upper most on a nylon mesh platform. A fan about 160 cm from the platform passed air at a speed of about 0.3 m/sec over the leaflets. Fresh weights (F.W.) of the leaflets were recorded at intervals of five minutes for 70-90 min. After each weighing the leaflets were returned to the platform.

The experiment was carried out in the research room. A thermohygrograph was installed near the platform to record temperature and relative humidity. Room temperature was about 23°C and relative humidity ranged between 66 and 68%. Temperature read from an ordinary mercury-in-bulb thermometer at the middle of the platform was 24±1.0°C. Evaporation from Piché evaporimeter in the same position was about 0.6 ml/hr.

Dry weights (D.W.) were determined at the end of each experiment. The experiment was repeated six times. Relative water content (R.W.C.) at any point during a drying-out cycle was calculated as:

$$R.W.C. = \frac{F.W. - D.W.}{S.W. - D.W.} \times 100$$

The change in leaf water status with time was then plotted.

A similar determination was made on leaves of the adult trees described earlier. Three determinations were made with these, in all using seven leaves of K. senegalensis and nine of K. ivorensis. The relative water content at point of stomatal closure was also determined for leaves of the two species growing in culture solution (-0.3 bars) and in culture solution with polyethylene glycol added (-10.3 bars). This determination was done only once, using 2 to 3 leaves of each species from each treatment.

5.3. Results

(a) The relation between water content and water potential of leaves.

This relationship is summarized in Fig.20 for seedlings of both species. Each point on the curves is the mean of four determinations. Variation between the four values for each point was not great so that the same relative position was maintained by each species on each determination. The least significant difference between any two points on the curves is 3.2% relative water content (P = 0.05). Hence the curve for K. senegalensis is significantly different from that of K. ivorensis especially at high water potentials (0 to -66 bars).

FIG. 20

RELATIONSHIP BETWEEN RELATIVE WATER CONTENT (%) AND LEAF WATER POTENTIAL (-BARS) OF SEEDLINGS OF KHAYA SENEGALENSIS (▲) AND K. IVORENSIS (●).

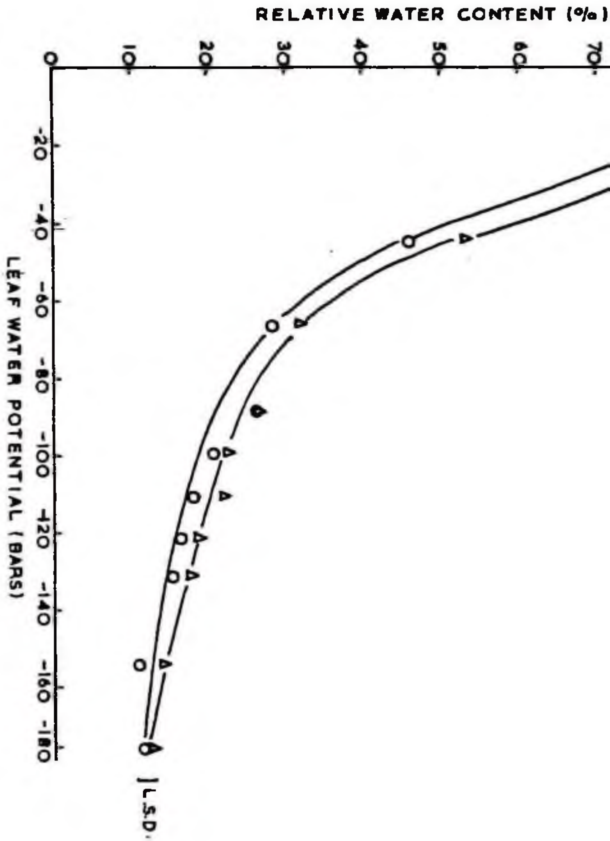
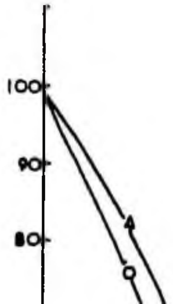

RELATIVE WATER CONTENT (%)
0
10
20
30
40
50
60
70
LEAF WATER POTENTIAL (BARS)
-20
-40
-60
-80
-100
-120
-140
-160
-180
L.S.D.

FIG.20


100
90
80

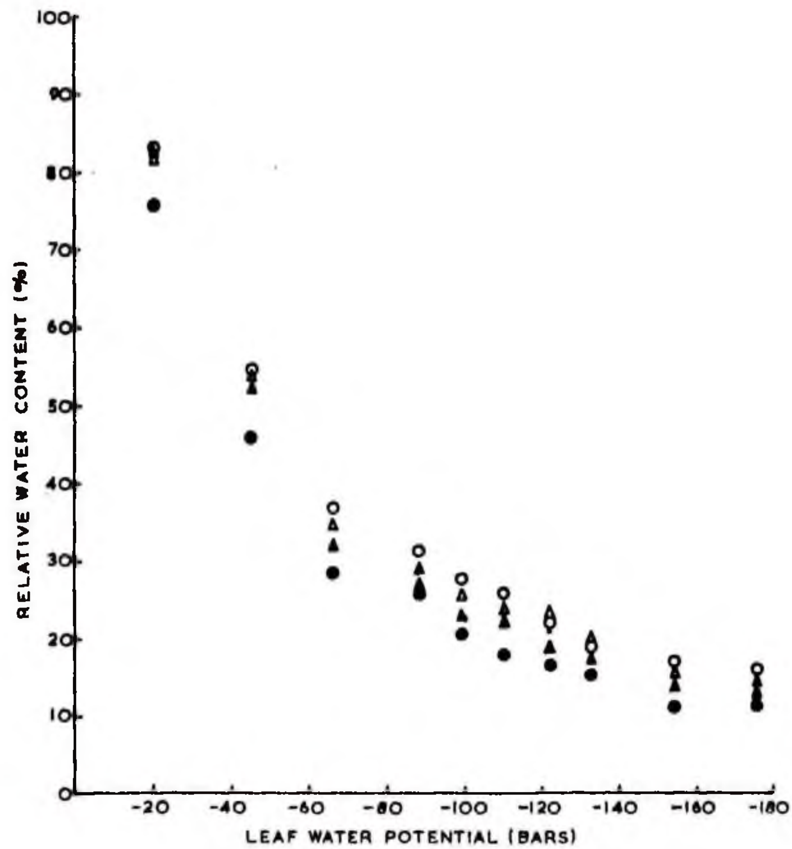
For K. senegalensis the relative water content fell to 88.5% when the water potential was reduced from 0 to -15 bars, and a reduction of water potential to about -46.5 bars was required before the relative water content fell to 50%. In contrast, for K. ivorensis the corresponding values were 84% R.W.C. at -15 bars or a reduction of water potential to -41 bars before water content fell to 50%. Although the values at lower potentials for K. senegalensis remained higher than those for K. ivorensis, they were however not significantly different from those of K. ivorensis (except at -110 and -154 bars). In general, the curves make it clear that a larger decrease in leaf water potential accompanies a unit drop in relative water content in K. senegalensis than in K. ivorensis: the difference though significant in parts is however strikingly small.

The results for the relative water content: water potential relationships for leaves of the adult trees are shown in Fig. 21. On the figure are also plotted the results for the seedlings just described above. The curves for the adult trees of both species were very similar. Thus there seems to be no difference in the relationship, between the two species, when adult trees are compared. Comparing results for adult trees with those for seedlings within each species shows that for K. senegalensis, above -44 bars both adult tree and seedling seem to have similar relationships. However when the potential was lowered there was a tendency for leaves of the adult tree to have higher relative water contents than leaves from seedlings at the same potentials. In contrast, for K. ivorensis the two results

FIG. 21

RELATIONSHIP BETWEEN RELATIVE WATER CONTENT (%) AND WATER POTENTIAL (BARS) OF LEAF TISSUE FOR SEEDLINGS AND ADULT TREES OF KHAYA SENEGALENSIS AND K. IVORENSIS

	ADULT	SEEDLING
K. SENEGALENSIS	△	▲
K. IVORENSIS	○	●



RELATIVE WATER CONTENT (%)
100
90
80
70
60
50
40
30
20
10
0
-20
-40
-60
-80
-100
-120
-140
-160
-180
LEAF WATER POTENTIAL (BARS)

FIG. 21

were quite different. All the points for adult tree leaves were far above those of seedling leaves. Thus there is an upward shift in the curve of the relationship between relative water content and water potential of leaves of K. ivorensis adult trees.

(b) Leaf water status and tissue damage.

The degrees of recovery of desiccated discs, in terms of water content after a period of resaturation expressed as a percentage of original saturated weight (cf. Jarvis and Jarvis, 1963e) are shown in Fig. 22. The curves show that when the equilibration potential was higher than about -44 bars, K. senegalensis tissue showed greater tolerance than K. ivorensis tissue. At this point the recovery percentage was 83 and 81% respectively for K. senegalensis and K. ivorensis. However the response was reversed when the potential was lowered further, (below -44 bars), this time tissues of the latter species appearing more tolerant than those of the former. It was however observed that beyond this low potential desiccated discs which showed extensive discolouration and exuded a great deal of coloured matter gave a higher percentage of weight, than desiccated discs which looked normal. It was thus possible that the high percentages obtained from the former discs were due to extensive infiltration of damaged tissue (cf. Okali, 1971a). The recovery curve of K. ivorensis at low equilibration potentials was above that of K. senegalensis probably because of this infiltration of extensively damaged tissues. The visual assessment of tissue damage was accepted as the more reliable estimate of desiccation tolerance. Results obtained by this method

FIG. 22

CURVES SHOWING THE PERCENTAGE RECOVERY OF RESATURATED DISCS IN RELATION TO EQUILIBRATION WATER POTENTIAL (BARS) <u>KHAYA SENEGALENSIS</u> (▲) AND <u>K. IVORENSIS</u> (○).

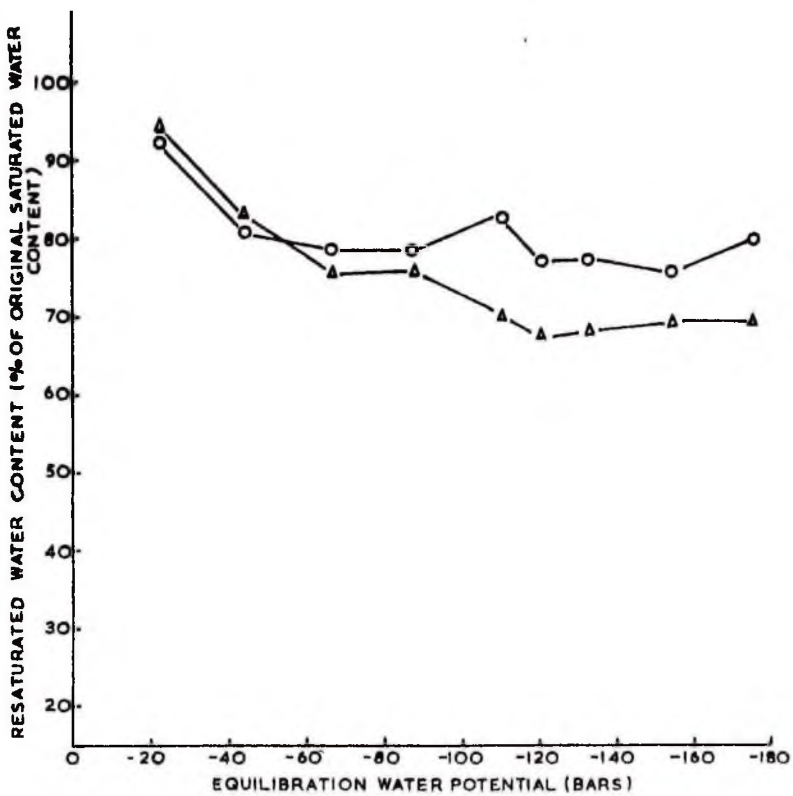

RESATURATED WATER CONTENT (% OF ORIGINAL SATURATED WATER CONTENT)
100
90
80
70
60
50
40
30
20
0
-20
-40
-60
-80
-100
-120
-140
-160
-180
EQUILIBRATION WATER POTENTIAL (BARS)

FIG. 22

agreed well with observations made on vitally stained tissues. The overall results therefore show that the critical levels of relative water content and leaf water potential at which tissue damage occurred were 29.0% and -81 bars for K. senegalensis seedlings and 34.0% and -59 bars for K. ivorensis. These values show that the difference between the critical relative water content for tissue damage of the two species was small (a difference of 5.0%). On the other hand the leaf water potential values differed considerably (a difference of -22 bars). Hence it could be said that K. senegalensis tissues become damaged at a lower potential than those of K. ivorensis.

(c) The relation between leaf relative water content and stomatal closure.

Table 11 summarizes the results obtained for this comparison. In all, seven determinations were made during which 22 leaves of K. senegalensis and 16 of K. ivorensis were observed (see Appendix 5, Table i). Examples of the curves from which relative water content at stomatal closure was estimated are shown in Fig.23. Extrapolation of the straight line portions of such curves (cf. Jarvis and Jarvis 1963d) suggests that the mean relative water content for stomatal closure in seedlings of K. senegalensis was 87.6% and that for K. ivorensis was 81.4%. The standard error of the difference between these means is 3.94%, giving t value of 4.69 ($P < 0.001$). Thus the relative water content at which stomata closed in the two species were significantly different. The stomata of K. senegalensis having the higher relative water content for closure could therefore be said to be more sensitive than those of K. ivorensis.

Table 11

Mean relative water contents (R.W.C.) of leaves of *Khaya senegalensis* and *K. ivorensis* at points of stomatal closure.

Species					
K. senegalensis			K. ivorensis		
Expt.	No. of observations	R.W.C. (%)	Expt.	No. of observations	R.W.C. (%)
1	3	88.0	1	3	81.0
2	3	89.0	2	1	87.0
3	1	93.0	3	2	77.0
4	4	85.0	4	3	82.0
5	5	86.0	5	1	80.0
6	3	81.0	6	3	83.0
7	3	91.0	7	3	80.0
Totals	22	613		16	570
Mean value		87.6			81.4

Standard error of difference = 3.94
$t = 4.69$
$P < 0.001$

FIG. 23

EXAMPLES OF CURVES OF THE RELATION BETWEEN LEAF WATER CONTENT (LOGARITHMIC SCALE) AND STOMATAL CLOSURE, SHOWING EXTRAPOLATIONS OF THE STRAIGHT LINE PARTS INTERSECTING AT CLOSURE. KHAYA SENEGALENSIS (▲) K. IVORENSIS (○)

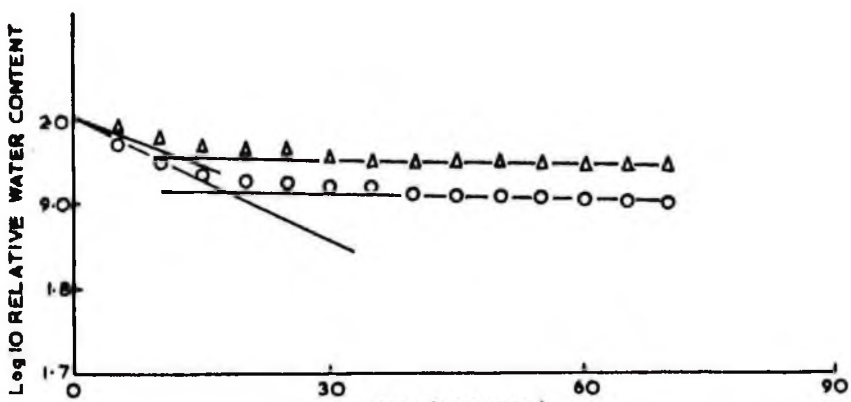

Log 10 RELATIVE WATER CONTENT
2.0
9.0
1.8
1.7
0
30
60
90
TIME (MINUTES)

FIG. 23

The mean relative water content values at stomatal closure recorded for leaves of the adult trees in the Botanical Garden were 90.7±1.5 and 86.2±1.6% for K. senegalensis and K. ivorensis respectively. This also shows that the relative water content at stomatal closure of the two species differs significantly. Similarly seedlings of K. senegalensis and K. ivorensis growing in culture solution were observed to close their stomata at about 93 and 83% relative water content respectively, again showing that K. senegalensis stomata are more sensitive than those of K. ivorensis to water loss. However the trend was reversed when leaves from the -10.3 bars polyethylene glycol solution were compared. This time K. senegalensis had 82% relative water content at stomatal closure and K. ivorensis 86%. These last two experiments (using culture solution and culture solution with polyethylene glycol added) were done only once, so that they may be less reliable than the determinations which were more adequately replicated.

5.4: Discussion.

The curves relating relative water content and water potential of leaves for both species in this study, may be compared with similar curves reported by Okali (1971a) for some woody plants in the Accra Plains of Ghana. Relative water content at -15 bars water potential, or the water potential at 50% relative water content may be used for this comparison (cf. Jarvis and Jarvis, 1963e; Okali, 1971a). The data presented indicate that these values were 88 and 84% or -47 and -41 bars respectively for K. senegalensis and K. ivorensis. Thus K. senegalensis could be placed at the intermediate position in Okali's ranking of drought resistance (see Okali, 1971, Table 5) in terms of this parameter, that is, between Clausena anisata which had 90% relative water content at -15 bars leaf water potential and Dichapetalum guineense with 87% relative water content at the same leaf water potential. K. ivorensis, on the other hand, would be placed nearer the bottom of the scale below the last woody species, Fagara zanthoxyloides, which had 85% relative water content at -15 bars leaf water potential. The evidence from this comparison would then suggest that K. senegalensis like the Accra Plains species is more drought resistant than K. ivorensis in terms of the relative water content: water potential relationship of leaf tissue.

The curves of relative water content and water potential of leaves of adult trees growing in the Botanical Garden, were very similar for both species. At higher potentials (above -44 bars) the curve for K. senegalensis adult trees was similar to that for seedlings. However there was a slight upward shift below this potential. On the other hand K. ivorensis showed a clear upward shift in the whole curve for the adult trees. Slatyer (1960) compared the desorption curves of Acacia aneura of different ages and in different situations, and observed no shift in this relationship which could be attributed to tissue age or to prior treatment. However results have been obtained for other species which suggest that age of plants or their growth localities may lead to a shift in the relation (see for example, Whiteman and Wilson, 1963; Gavande and Taylor, 1967). Jarvis and Jarvis (1963d,e), and Shepherd (1964) also observed that prolonged prior desiccation may result in a shift in the position of the relative water content: leaf water potential curve.

The grounds of the Botanical Garden where the adult trees are growing form part of the Accra Plains, hence environmental conditions here are more or less comparable to those in the natural habitat of K. senegalensis (see p. 4).

The slight upward shift in the curve for K. senegalensis adult tree at lower potential may be attributed to age alone. For K. ivorensis, however, the Accra Plains represent a more severe environment than its natural habitat. It would be expected therefore that K. ivorensis growing on the Accra Plains would show some modifications towards this environment. It is possible that such a modification has led to the change in position in the relative water content:leaf water potential curve in these plants which had grown in the Botanical Garden for 13 years. Of course, the shift could also be an age effect (cf. Whiteman and Wilson, 1963); but it is remarkable that it is more pronounced for this species than for K. senegalensis of the same age.

The upward shift in the curve suggests that a small drop in relative water content would lead to a large reduction in leaf water potential which, as has been pointed out, favours survival under severe moisture conditions, while limiting growth. In this connection, it is interesting to point out that the two trees of K. ivorensis in the

Botanical Garden are much smaller in size (girths about 0.6 and 0.9m) than the K. senegalensis (girth about 1.2 m) growing beside them. They are also smaller (7.6 and 9.1 m tall) than would be expected of trees of similar age growing in forest conditions.

Relative water content:leaf water potential relationships were not determined for seedlings under the various soil moisture treatments. However the stability of the relationship for K. senegalensis along certain parts of the curve, when seedlings and mature trees are compared suggests that the difference between this species and K. ivorensis may be a real interspecific difference. It is possible then to use this difference to attempt an explanation of the growth responses described in Chapter II. There, it was suggested that the high sensitivity of growth of K. senegalensis seedlings to low soil moisture stress and that of K. ivorensis to severe moisture stress could be related to the type of relative water content:leaf water potential curves possessed by the two species. The present data are in agreement with those suggestions (cf. Jarvis and Jarvis, 1963e).

The critical levels of leaf water potential at which tissue damage occurred, was observed to be lower in K. senegalensis (-81 bars) than in K. ivorensis (-59 bars). This suggests that K. senegalensis is more tolerant to desiccation than K. ivorensis.

Comparison of leaf water contents at point of stomatal closure shows that K. senegalensis closed its stomata at a significantly higher relative water content (about 88.0%) than did K. ivorensis (about 81.0%).

The number of stomata per unit leaf area of K. senegalensis is greater than that for K. ivorensis (see p. 14), transpiration was also noticed to be generally higher in the former species than in the latter when subjected to low moisture stress in the root medium. It is therefore remarkable to observe a higher relative water content at stomatal closure in K. senegalensis than in K. ivorensis. Stomatal closure results in reduction in gaseous exchange. In general, a species which possesses a high tolerance to desiccation and a low sensitivity of stomata to desiccation could carry on photosynthesis over a wider range of low water potentials, than can a species which does not possess these features. K. senegalensis showed a high degree of tolerance to desiccation, but its stomatal sensitivity to water stress was equally high. This means that while the leaves of this species may survive severe internal moisture stress, photosynthesis in them may be readily limited by reduced CO_2 uptake as a result of stomatal closure when environmental moisture stress is low. The latter effect may have contributed to the low growth rate of K. senegalensis in response to low moisture stress (Chapter II). This suggestion is supported by the data on transpiration in relation to moisture stress. Transpiration (which depends, partly on stomatal conductivity to water vapour) was found to be lowered when soil moisture stress was at -4.5 bars. Stomatal studies also showed earlier diurnal stomatal closure under this treatment for K. senegalensis.

K. ivorensis on the other hand was comparatively less tolerant to desiccation, but it also showed a lower relative water content for stomatal closure. Its lack of sensitivity to low moisture stress in terms of growth rate, may reflect this lower water content at which stomata close. On the other hand, its poor growth rate when moisture stress was high may be a reflection of its poorer tolerance to desiccation, and of the fact that a larger amount of water is lost for a given decrease in water potential, when compared with K. senegalensis.

It is significant to note that although the absolute values of leaf relative water content at which stomata close differed between the one year-old seedlings growing in soil near field capacity, on which this relationship was mainly investigated, and adult trees or seedlings grown in culture solution, the trend of difference between the two species was always the same. Stomata in K. senegalensis always closed at a leaf relative water content that was 4.5 - 10% higher than that at which they closed in K. ivorensis. However in the single unreplicated experiment in which plants that had grown in polyethylene glycol solution (water potential about -10.3 bars) were used, the trend was reversed. The stomata of K. ivorensis closed at a leaf relative water content of 86% as against 82% for K. senegalensis. Whether this reversal is a real effect is not known; but it may reflect differences in absorption of polyethelene glycol by the two species (cf. Jarvis and Jarvis, 1963d), although all necessary precuasions were taken to reduce this.

Although the aspects of tissue water relations examined in this chapter contribute to understanding growth and transpirational responses of the experimental species, it is much more difficult to apply them to explaining the diurnal patterns of plant water status described earlier. However comparing the relative water content at stomatal closure with the diurnal relative water content values obtained in Chapter III, shows that relative water content low enough to cause stomatal closure, occurred during the day for both species especially when soil moisture stress was high. The frequency of occurrence of such low leaf water content was observed to be comparatively higher in K. senegalensis than in K. ivorensis. This may have contributed to the better water status observed in Treatment D of K. senegalensis than in K. ivorensis seedlings.

The studies described in this chapter perhaps, provide the clearest evidence of a difference in adaptation to drought by the species under comparison. It is clear that the leaves of K. senegalensis possess adaptive features - a slower rate of water loss for a given drop in potential and a greater tolerance to desiccation - which may enable this species to survive severe drought better than K. ivorensis. Its higher stomatal sensitivity to water loss however can only allow it to grow at a slower rate than K. ivorensis when moisture stress is not severe.

CHAPTER VI

GENERAL DISCUSSION

Taylor (1952) suggests that moisture conditions are the most important factors controlling the division of the natural vegetation of West Africa into forest and savanna regions. Forest regions are known to receive, on the whole, higher rainfall and so are moister than savanna regions (Lawson, 1966). Distribution, growth-form and physiological behaviour of plants in this geographical area may therefore be expected to reflect control by environmental moisture. However, very few experimental studies have been carried out to test this expectation. The few studies that have been made were concerned mostly with mechanisms of drought-adaptation, in certain species on the Accra Plains of Ghana, a type of dry environment (cf. Lawson and Jenik, 1967, Okali, 1971a). It was only recently that Hopkins (1970,a,b) attempted to make a direct comparison of leaf water status of forest and savanna species in the Olokemeji Forest Reserve in Nigeria. He observed that for the forest species leaf water may be 'severely limiting at the severest part of the dry season'. He was however unable to demonstrate such a limitation for the savanna species.

The investigations cited above do not provide an adequate basis for testing the role of moisture in determining the patternof plant distribution between forest and savanna, because the studies were either, not comparative between species taken from the two contrasting habitats, or they were concerned with only one aspect of plant water relations.

The present study was therefore undertaken to compare experimentally and more fully the water relations of two species, one from each of these two contrasting habitats. It was hoped that if environmental moisture as against other factors such as fire, exerts the most control, species from these two habitats would show differences in their water relations.

In order to observe differences which result mainly from adaptation to habitat, comparison was made between two species that are taxonomically closely related, the Mahogany trees - *Khaya senegalensis* and *K. ivorensis*. These two species are restricted to contrasting habitats, the former to savanna and the latter to forest (Richards, 1952), but they are similar in their growth habit, phenology and reproductive biology; hence, differences observed from comparing them may be expected to be largely due to adaptation to habitat.

The experiments were essentially carried out in the laboratory. Their relevance to the field situation derives therefore mainly from their comparative nature.

Again although seedlings were mostly used for these investigations, there are indications that seedlings respond sensitively to environmental factors such as moisture, and that differences in seedling response may affect plant establishment and hence the pattern of distribution of adult plants.

Comparison of leaf morphology of the two species suggested *a priori* that the species differ in their structural adaptation to drought. The leaves of *K. senegalensis*, for example, have thicker veins than those of *K. ivorensis*. Mature leaves of the former species are also thicker (about 0.8 mm) than those of the latter (about 0.5 mm), and stomata per unit leaf area are more in K. senegalensis than in K. ivorensis leaves. All these features are generally known (Oppenheimer 1960) to be associated with drought-adapted plants, and have been noted, in particular, for West African plants of dry habitats (Yanney-Wilson, 1963; Lawson and Yenik, 1967).

Since plant growth summarizes all plant processes, it was argued that any difference in adaptation of two species to environmental moisture conditions should be shown in the growth responses of such species to varying environmental moisture.

In the present study, comparison of growth in relation to moisture stress in the root medium (Chapter II) showed that K. senegalensis the savanna species, is perhaps adapted to more severe drought than K. ivorensis, the forest species. The latter species was however less affected by moderate stress in the root medium. Thus the experiment on the effect of varying soil moisture stress (-0.3 to -4.5 bars) on growth showed that the growth rate of K. senegalensis was significantly reduced at -4.5 bars as compared with -0.3 bars. The growth rate at -4.5 bars was about 77% of that at -0.3 bars. The growth rate of K. ivorensis was however not significantly affected by this degree of reduction in soil water potential although it tended to be reduced by the wettest treatment, presumably as a result of sensitivity to poor aeration.

When moisture stress was varied in solution by addition of polyethylene glycol, the higher sensitivity to low moisture stress in K. senegalensis as against K. ivorensis was again observed (Fig.8). But with severer stress (for example below a water potential of -5.3 bars in the root medium) growth rate of K. senegalensis was comparatively less reduced than that of K. ivorensis.

K. ivorensis seedlings did not show poor growth in aerated culture solution (-0.3 bars) as they did under a similar potential in soil.

The growth analyses carried out suggest that reduction in growth of the two species under increased moisture stress was probably caused by changes in net assimilation rate rather than changes in mean leaf area ratio. The analyses also showed that K. senegalensis had proportionately more root than K. ivorensis seedlings. The ways by which water stress may have caused the observed difference in growth response of the two species, through its effect on net assimilation rate are suggested by the results of the investigations on diurnal pattern of plant water status, transpiration and especially tissue water relations.

The comparative studies on diurnal pattern of plant water status showed that a difference existed between the two species in internal water status. In terms of relative water content of leaves K. senegalensis maintained overall a more favourable internal water balance than did K. ivorensis. But in terms of leaf water potential and also in terms of tension in the stem (as indicated by degree of stem shrinkage) stress was greater in K. senegalensis seedling when external moisture stress was moderate.

The greater reduction in growth rate of K. senegalensis when external stress was moderate probably reflects a direct effect of this higher internal tension on photosynthesis and hence on net assimilation rate and growth rate, rather than an indirect effect through limitation of CO_2 uptake. That CO_2 uptake was not the main limiting factor is suggested by the results of the transpiration studies particularly in the research room. Here, transpiration rate, which partly reflects the degree of stomatal conductivity, was reduced less in K. senegalensis than in K. ivorensis when soil water potential was about -4.5 bars, yet the growth rate of K. senegalensis alone was significantly reduced by this soil tension.

When external moisture stress was low (-0.3 to -0.8 bars) transpiration rate was higher for K. senegalensis than for K. ivorensis (Figs.13 to 16). It is possible that this higher transpiration rate, combined with the type of relative water content: water potential relationship exhibited by K. senegalensis leaf tissue, contributed to cause tensions high enough to limit growth in this species when external stress was low. Fig. 20 shows that water loss from leaves is associated with greater reduction in tissue water potential for K. senegalensis than for K. ivorensis.

Growth rate was reduced more for K. ivorensis than for K. senegalensis when external stress was increased by reducing water potential in the root medium (solution) to -10.3 bars. Transpiration rate under this potential was however reduced more (to about 10% of that in the control) for K. senegalensis than for K. ivorensis (20% of control). Thus it is unlikely that the greater reduction in growth rate of K. ivorensis at -10.3 bars derived from a greater limitation to CO_2 uptake. The higher sensitivity of growth of K. ivorensis to severe stress was probably then due to large deficits which existed in its tissues as a result of higher transpiration rate.

The high sensitivity of K. ivorensis to severe stress may also be due to the fact that the tissues of this species are more readily damaged by desiccation than those of K. senegalensis (see Chapter V). Thus tissues of the former species were damaged when exposed to a stress of -59 bars as compared to -81 bars for those of K. senegalensis.

It is worth while drawing attention here to the agreement between the results of the growth studies and theoretical expectation from considering the desorption curves of the study species. Jarvis and Jarvis (1963e) had suggested that a species which loses comparatively little water, for a given decrease in water potential, could withstand more severe moisture stress than a species which loses a greater amount of water for a similar drop in potential. Conversely, the latter type of species is at an advantage from the point of view of growth when moisture stress is moderate. The evidence in this study suggest that K. senegalensis represents the first type of species while K. ivorensis represents the latter.

These considerations taken together with the results from comparison of stomatal sensitivity to water loss (Fig. 23) are perhaps the strongest evidence that K. senegalensis is more drought-adapted than K. ivorensis. Stomata of K. senegalensis consistently closed at higher relative water content (around 88%) than those of K. ivorensis (around 81%). The relevance of this to the maintenance of a favourable internal water balance has already been pointed out. Perhaps the greater reduction in transpiration rate at -10.3 bars or the less pronounced stem shrinkage when soil moisture status was 27% of field capacity, for K. senegalensis rather than for K. ivorensis. reflect this higher sensitivity of stomata in K. senegalensis.

As has already been mentioned moisture is believed to play an important role in the control of the main pattern of plant distribution in West Africa. K. senegalensis. one of the studied species, is restricted to the savanna region, a dry habitat, while K. ivorensis the other species, is restricted to the forest region which is moister. The results of the present experimental study confirm that one possible basis of this difference in distribution of the two species is a difference in drought adaptation. K. senegalensis possesses features which adapt it to severer drought conditions than does K. ivorensis. An ability to reduce transpiration rate more effectively through high stomatal sensitivity to water loss perhaps helps K. senegalensis to conserve water, when environmental moisture is severely limiting. A more gradual rate of water loss from its leaves with increasing environmental dryness, as is suggested by its desorption curve, coupled with a greater tissue tolerance to desiccation assist this species rather than K. ivorensis to survive and thus grow better under severe drought.

It is possible also that the better development of the root system in K. senegalensis combined with the steeper water potential gradient which may develop between its tissues and the soil (see Chapter III) contributes to enhance water uptake from a wider area of soil when moisture is freely available. Enhanced water uptake may support higher transpiration rate in *K. senegalensis* than in *K. ivorensis*. Higher transpiration rate was generally observed in *K. senegalensis* when moisture was freely available (see p. 129). The higher transpiration rate of *K. senegalensis* under such conditions may help to lower the temperature of the leaves and so prevent them from overheating in the more exposed conditions of its natural habitat (cf. Gates 1964).

Though not a drought adaptive feature, the rapid growth rate of seedlings of *K. senegalensis* is another factor which may help this species to compete actively with fast growing annuals which are abundant in the savanna, but not in the forest habitat.

Conversely *K. ivorensis* is less adapted to drought and does not have most of the features mentioned above. Its natural habitat is comparatively always moist so that drought adaptive features are not essential to its survival. However its tolerance to moderate moisture stress as shown by its growth response may be of ecological importance. The forest regions experience one or two months of dry season during the year. This feature may therefore help *K. ivorensis* to withstand this period of reduced water availability.

The results of the present study clearly cannot be extended to apply to all forest and savanna species, but if the findings can be shown to apply to a wider variety of plants, especially to pairs of species from these contrasting habitats, they could provide a more valid basis for the assumption that moisture plays an important role in determining the pattern of plant distribution between forest and savanna regions in West Africa.

In the introduction to this thesis it was pointed out that the species studied, particularly Khaya ivorensis, are of economic importance. Establishment of plantations and nurseries of these species are at the moment being given attention by the forestry department of this country. The results presented here on the water relations of these two species may perhaps be of value in providing information on suitable sites of establishment of such nurseries or plantations. For example, since K. ivorensis is sensitive to water-logging, it may not do well particularly as seedlings in sites which are often water-logged. Similarly, while K. ivorensis clearly cannot be considered for planting in very dry habitats such as extreme savanna regions, the evidence presented suggest that it may do as well as K. senegalensis in moderately dry environments such as the margins of forest areas.

A complete investigation of the role of moisture in the distribution of West African plants should probably be extended to the field situation. This has not been done in the present study. However comparisons such as have been attempted here will always be of value at some stage of such a complete investigation.

SUMMARY

1. The water relations of two Mahogany species *Khaya senegalensis* and *K. ivorensis*, the former a savanna species and the latter a forest species, were studied in an attempt to understand the role moisture plays in determining their distribution.

2. Leaves of *K. senegalensis* were generally thicker (about 822 μ) with thicker veins than those of *K. ivorensis* (about 508 μ thick) and thin veins. Stomata in the former species are denser (about 660 per mm^2) than in the latter species (about 580 per mm^2). These mostly accurred on the lower epidermis in both species. Stomata on the upper epidermis are fewer than 1 per mm^2 in both species.

3. Seedlings of *K. senegalensis* grow faster than those of *K. ivorensis*: at the age of two months the mean height of seedlings of *K. senegalensis* is about 13.0 cm with 6 to 9 leaves while that of *K. ivorensis* is about 10.0 cm with about 4 to 6 leaves.

4. Growth of the two species was examined when both soil and osmotic solution were used as rooting medium. The soil treatments used were - A (-0.3), B (-0.4), C (-0.8) and D (-4.5) bars. The osmotic solutions (bars) were - A (-0.3), B (-2.8), C (-5.3) and D (-10.3).

5. Considering first the growth in relation to soil moisture stress experiment.

Height growth and leaf area of seedlings of both species in Treatment B tended to be greater than in all the other treatments.

6. Relative growth rate of *K. senegalensis* ranged from 0.14 to about

0.18 g/g/wk, while that of K. ivorensis ranged from 0.15 to about 0.19 g/g/wk.

7. Relative growth rate of K. senegalensis decreased with soil dryness, so that value in Treatment D was significantly reduced to 77% of that in Treatment A. However differences between Treatments A, B and C, and B, C and D were not significant. For K. ivorensis relative growth rate was highest in Treatment B (about 0.19 g/g/wk). The rate tended to be reduced though not significantly in both Treatment A, the wettest treatment and Treatment C & D which were comparatively dry soils. Treatment A of K. ivorensis gave the lowest growth rate (0.15 g/g/wk) for this species. Most leaves of this treatment were observed to be chlorotic during the experimental period.

8. Net assimilation rate of K. senegalensis seedlings was higher than that of K. ivorensis seedlings. The rate of the former species ranged from 15.0 to 22.6 $g/m^2/wk$. Here also the rate for Treatment A was significantly higher than that for Treatment D. The net assimilation rate for the latter species ranged from 11.3 to 14.9 $g/m^2/wk$. Treatment B of this species gave the highest net assimilation rate while Treatment A gave the lowest rate.

9. Mean leaf area ratio, leaf area ratio, specific leaf area and leaf weight ratio of K. ivorensis were greater than those of K. senegalensis. For both species the treatments did not have any significant effect on any of these parameters when both soil and culture solution were used as rooting medium.

10. The ratio of root to shoot obtained for K. senegalensis seedlings in all treatments was about 0.8 as against about 0.6 for K. ivorensis seedlings.

11. In the growth in osmotic solution experiment growth was observed to decrease with decreasing osmotic potential.

12. Leaf development in both species was greatest in Treatment A but this was more pronounced in K. senegalensis than in K. ivorensis. When stress was imposed the leaf area was greatly reduced in both species, so that for K. senegalensis there was a significant reduction in Treatments B, C and D as compared with A. For K. ivorensis however differences between Treatments A and B, and C and D were not significant. Leaf development was however reduced in Treatments C and D as compared with Treatment A.

13. Relative growth rates obtained in the culture solution were higher at the same water stress than those in the soil experiment; for example Treatment A of K. senegalensis gave a rate of 0.31 g/g/wk in the former treatment as compared with about 18 g/g/wk in the soil experiment. The corresponding rates were 18/g/g/wk and 15g/g/wk respectively for K. ivorensis seedlings.

14. The lower sensitivity of K. ivorensis to moderate stress in the root medium was observed up to -2.8 bars (Treatment B) osmotic potential. K. ivorensis showed higher sensitivity down to this potential. However the sensitivity at lower potential was reversed - K. senegalensis growing comparatively better than K. ivorensis.

15. Net assimilation rate followed the same trend as relative growth rate. In this case also there was no significant reduction in net assimilation

rate of seedlings of K. ivorensis in Treatments B as compared with A.

16. Root development was greater in K. senegalensis than in K. ivorensis. However the root to shoot ratio of the latter species was more stimulated when osmotic potential was at -10.3 bars (Treatment D).

17. Diurnal pattern of leaf water status was studied by examining the relative water content (R.W.C.) leaf water potential (L.W.P.) and stem shinkage in relation to soil moisture stress. For R.W.C. and L.W.P. the four soil moisture treatments (see 4) were adopted. For stem shinkage studies, the soil moisture contents (S.M.C.) treatments were expressed as percentages water content values at field capacity.

18. Differences in R.W.C. and L.W.P. was observed to be small for seedlings in Treatments A, B and C of both species. Treatment D gave the lowest R.W.C. and L.W.C. values.

19. In general K. senegalensis maintained overall higher R.W.C. and lower L.W.P. values than K. ivorensis.

20. Diurnal stem shrinkage in K. senegalensis was observed to be greater than in K. ivorensis when soil moisture content was high: 100 to about 50%. However around 27% soil moisture content, diurnal shrinkage of stem was greatly reduced in this species.

21. K. ivorensis stem shrinkage did not consistently follow any particular pattern. Thus on most occasions stem shrinkage was observed to be similar under all treatments. However on one occasion when both aerial and soil moisture conditions were severe, less shrinkage was observed in stems subjected to 27% S.M.C.

22. Transpiration was also studied in relation to the four soil moisture treatments (see 4), both in the greenhouse and in the research room. The experiment was repeated with seedling growing in soil at -0.3 bars and in osmotic solution at -0.3 and -10.3 bars. The pot weighing technique was adopted. Transpiration rate for both species decreased with increase in moisture stress.

23. Higher transpiration rate was observed in K. senegalensis than in K. ivorensis seedlings both in the greenhouse and in the research room when the moisture stress was -0.3 to -0.8 bars. At -4.5 bars (Treatment D of soil experiment) transpiration per cm^2 and day in the greenhouse of the former species was reduced to 29.3% of the rate in Treatment A (-0.3 bars). The corresponding reduction was to 47.3% for the latter species.

24. In the research room the mean daily transpiration in Treatment D as percentage of values in Treatment A were 84.6 and 81.8% respectively for K. senegalensis and K. ivorensis.

25. The effects of both matric and osmotic potentials of rooting medium on transpiration of K. senegalensis seedlings were observed to be similar. For K. ivorensis lower rates were recorded when osmotic solution was used as root medium than when soil was used.

26. Transpiration of K. ivorensis seedlings showed an immediate decrease when transferred from culture solution (-0.3 bars) to -10.3 bars osmotic solution, than did K. senegalensis seedlings. But while the rate of the former species remained steady, that of the latter species decreased gradually so that four hrs after the beginning of the experiment the average

rate for the three experimental days recorded for the two species was $0.6/cm^2/30$ min. The reduction for K. senegalensis was to about 10% of that of the control (-0.3 bars), the corresponding reduction was to about 20% of the control for K. ivorensis.

27. Stomatal conductivity studied by the infiltration technique showed that conductivity decreased with soil dryness. K. senegalensis leaves showed greater conductivity when soil moisture stress was -0.3 to -0.8 bars than K. ivorensis leaves.

28. High conductivity was observed in the mornings. Conductivity of leaves of K. senegalensis seedlings in soil at -0.3 to -0.8 bars generally started decreasing around 11.30 hrs while that of K. ivorensis showed decrease about 14.00 hrs. Some conductivity was recorded for both species after 15.00 hrs. When the moisture stress was -4.5 bars no conductivity was recorded for any of the species after 12.00 hrs.

29. The desorption curves for both species showed that the R.W.C. at -15 bars L.W.P. or the L.W.P. at 50% R.W.C. were 88 and 84% or -47 and -41 bars respectively for leaves of K. senegalensis and K. ivorensis seedlings.

30. R.W.C./L.W.P. curves for leaves of adult trees of the two species were very close together. Comparison of curves for adult tree leaves with those of the seedlings showed that for K. senegalensis the position of the curve at higher potentials (-44 bars) remained constant. But there was a slight upward shift at lower potentials for the adult tree leaves. On the other hand, there was a distinct upward shift in the curve for leaves of the adult trees of K. ivorensis as compared with that of the

seedlings.

31. The critical levels of leaf water potential at which tissue damage occurred were -81 and -59 bars respectively for K. senegalensis and K. ivorensis seedlings. The corresponding R.W.C. values were 29 and 34% respectively for the former and latter species.

32. The R.W.C. at which stomatal closure occurred was about 88.0 and 81.0% for K. senegalensis and K. ivorensis seedlings respectively. The corresponding R.W.C. values for adult trees in the Botanical Garden were 90.7±1.5 and 86.2±1.6 for K. senegalensis and K. ivorensis respectively.

Appendix 1, Plate I

Three months old seedlings of Khaya senegalensis and K. ivorensis (Note the drip tips and large size of leaves of the latter species). The seedlings shown were taken from the soil moisture treatment experiments so that, A, B, C and D, denote soil tensions of -0.3, -0.4, -0.8 and -4.5 bars respectively.

K. senegalensis

Appendix 1, Plate I (continued)

K. ivorensis

Appendix 2

Table i

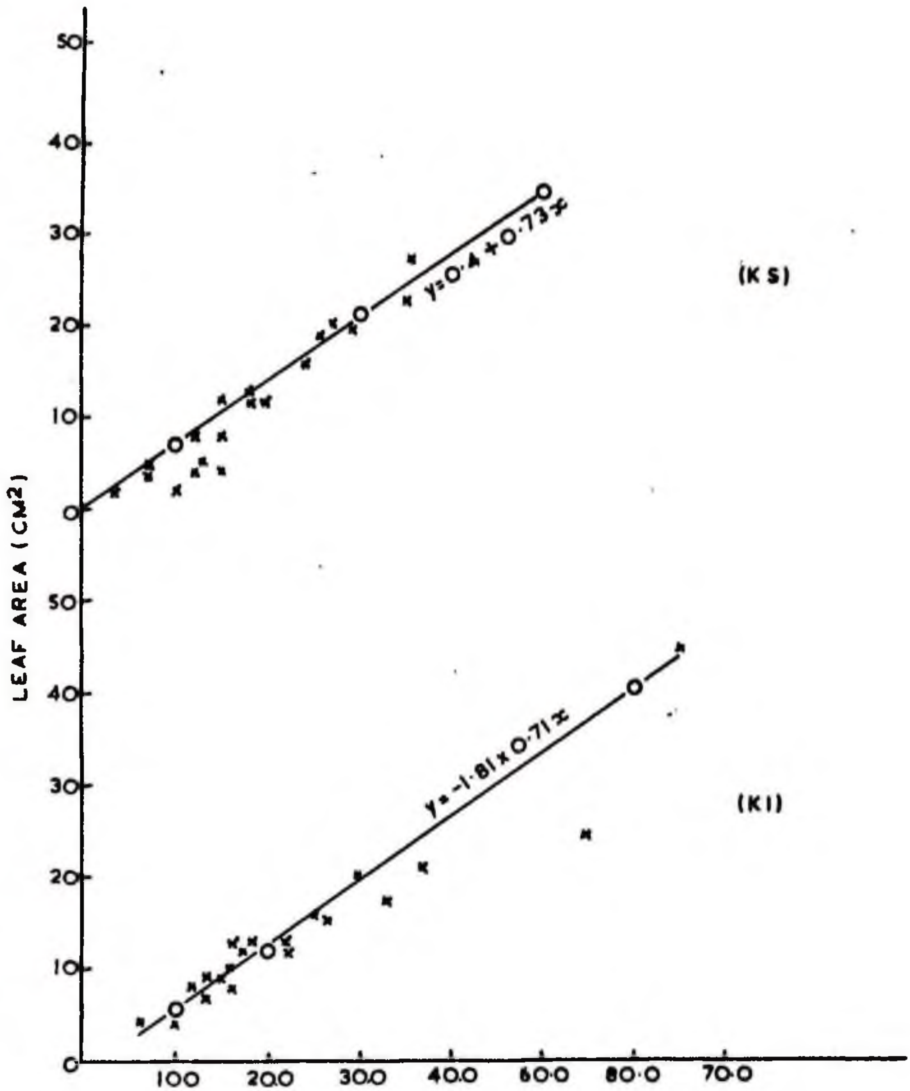
The relationship between soil water potential (- bars) and soil moisture content (% dry weight) of the experimental soil, John Innes Potting Compost II.

Soil water potential (bars)	Soil moisture content (% dry weight)
-0.3	23.1±1.6
-1.0	10.4±0.6
-2.0	8.8±0.5
-3.0	7.9±0.5
-5.1	5.5±0.8
-7.1	5.0±0.8
-9.1	5.0±0.8
-11.2	4.9±0.8

APPENDIX 2, GRAPH 1

THE REGRESSION OF PLANIMETERED AREA ON LENGTH X BREADTH OF LEAVES OF SEEDLINGS OF KHAYA SENEGALENSIS (KS) AND K. IVORENSIS (KI) GROWING ON SOIL AT THE INITIAL HARVEST. THE REGRESSION WAS DETERMINED FOR EACH TREATMENT AT THE FINAL HARVEST. THE REGRESSION EQUATION OBTAINED ARE AS FOLLOWS:

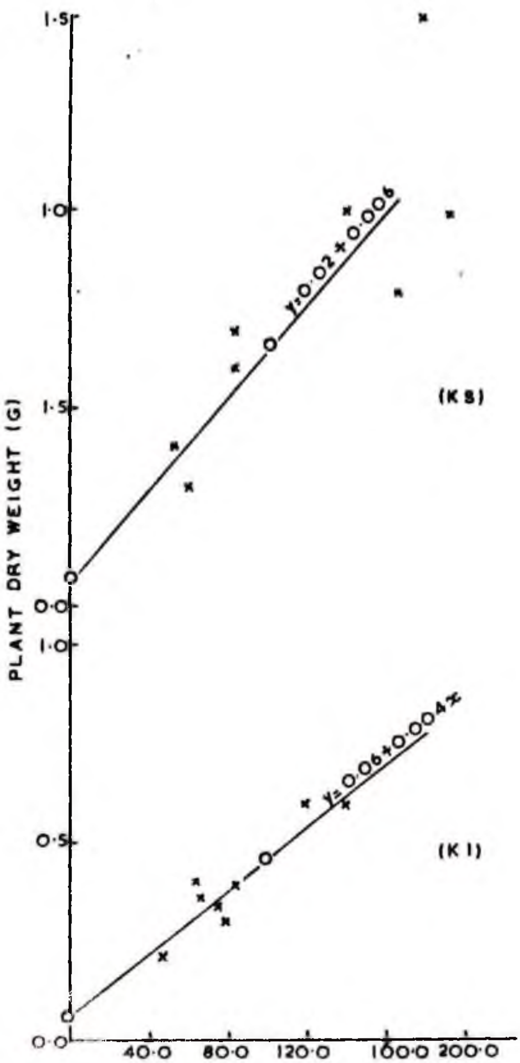
TREATMENT	K. SENEGALENSIS	K. IVORENSIS
A	y = -0.25 + 0.72 x	y = 0.50 + 0.60 x
B	y = 0.79 + 0.66 x	y = -0.37 + 0.64 x
C	y = -1.25 = 0.76 x	y = -0.28 + 0.62 x
D	y = 0.46 + 0.67 x	y = -2.26 + 0.67 x



APPENDIX 2,
GRAPH 1.

APPENDIX 2, GRAPH 2

THE REGRESSION OF DRY WEIGHT ON PLANIMETERED TOTAL LEAF AREA PER SEEDLINGS OF *KHAYA SENEGALENSIS* (KS) AND *K. IVORENSIS* (KI) GROWING IN SOIL.



APPENDIX 2 GRAPH 2 .

Appendix 2

Table ii

A breakdown of the total dry weights (g) at initial and final harvests into the weights for the main plant organs for seedlings of <u>Khaya</u> <u>senegalensis</u> and <u>K. ivorensis</u> under various soil moisture treatments; Treatments A, (-0.3); B, (-0.4); C (-0.8); D (-4.5) bars.

K. senegalensis

Plant organ	Initial harvest	Final harvest Treatments			
		A	B	C	D
Mean leaf weight per seedling (g)	0.383	1.185	1.237	0.864	0.855
Mean stem weight per seedling (g)	0.213	1.065	1.219	0.834	0.736
Mean root weight per seedling	0.181	1.806	2.010	1.496	1.379
Total plant dry weight	0.777	4.056	4.466	3.194	2.970

(continued next page)

Appendix 2

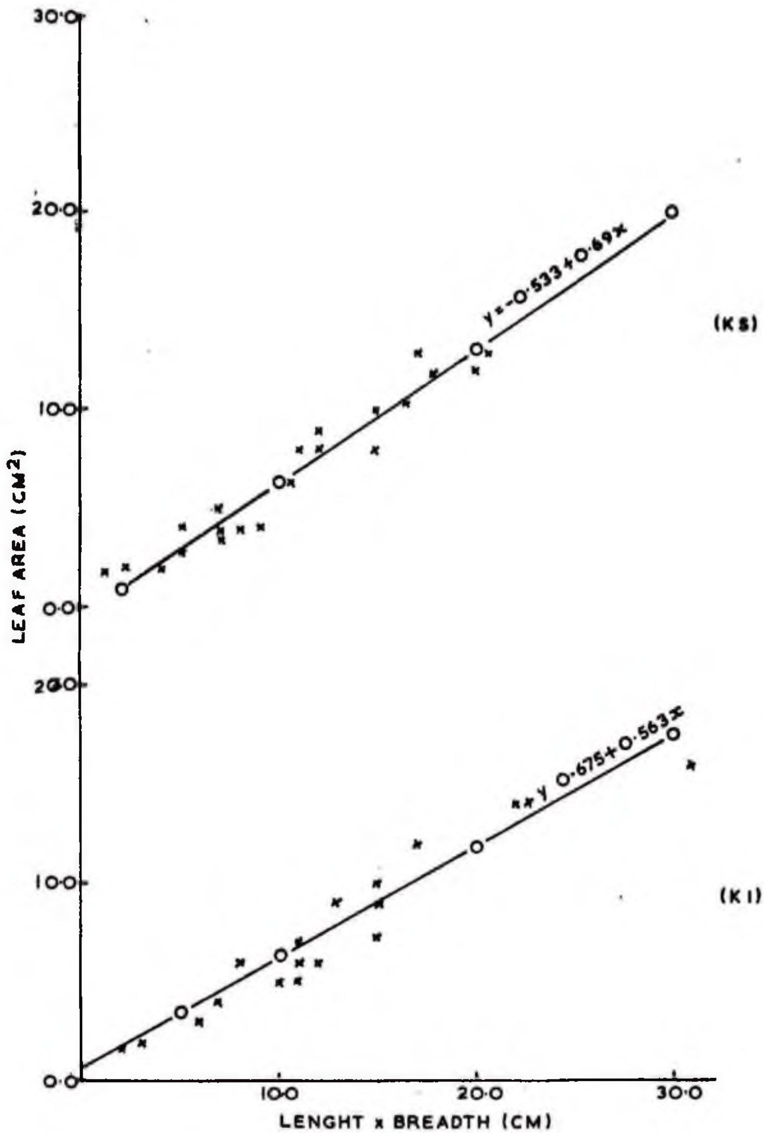
Table ii (continued)

K. ivorensis

Plant organ	Initial harvest	Final harvest A	Final harvest B	Final harvest C	Final harvest D
Mean leaf weight per seedling (g)	0.221	0.712	0.850	0.722	0.656
Mean stem weight per seedling (g)	0.099	0.471	0.526	0.503	0.434
Mean root weight per seedling (g)	0.075	0.676	0.769	0.755	0.644
Total plant dry weight	0.395	1.859	2.145	1.980	1.734

APPENDIX 2, GRAPH 3

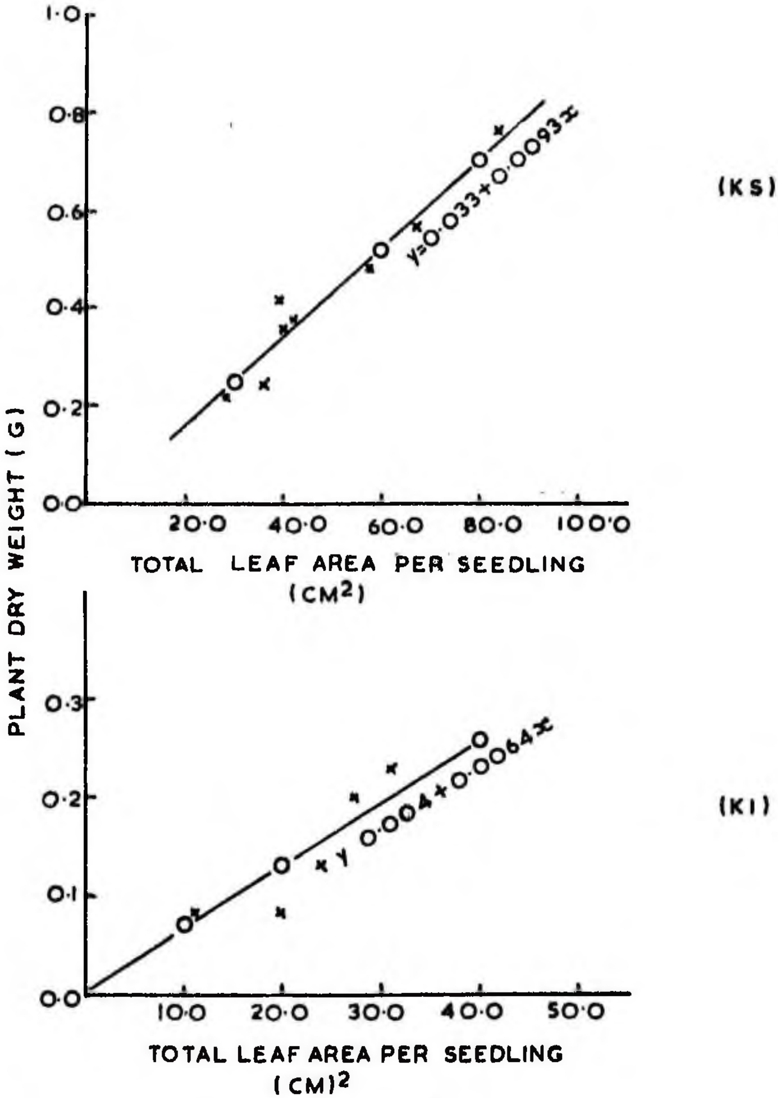
THE REGRESSION OF PLANIMETERED AREA ON LENGTH X BREADTH OF SEEDLINGS OF KHAYA SENEGALENSIS (KS) AND K. IVORENSIS (KI) GROWING IN CULTURE SOLUTION.



APPENDIX 2 GRAPH 3

APPENDIX 2, GRAPH 4

THE REGRESSION OF DRY WEIGHT ON PLANIMETERED TOTAL LEAF AREA PER SEEDLING OF KHAYA SENEGALENSIS (KS) AND K. IVORENSIS (KI) GROWING IN CULTURE SOLUTION.



APPENDIX 2 GRAPH 4

Appendix 2

Table iii

A breakdown of the total dry weights (g) at initial and final harvests into the weights for the main plant organs for seedlings of *Khaya senegalensis* and *K. ivorensis* grown in culture solution of different osmotic potential (bars). Treatments A, (-0.3); B (-2.8); C (-5.3); D, (-10.3) bars. Treatment A, consisted of culture solution alone; B, C and D consisted of culture solution plus polyethylene glycol.

K. senegalensis

Plant organ	Initial harvest	Final harvest Treatment A	B	C	D
Mean leaf weight per seedling (g)	0.208	0.409	0.293	0.293	0.246
Mean stem weight per seedling (g)	0.129	0.216	0.218	0.209	0.144
Mean root weight per seedling (g)	0.102	0.294	0.273	0.241	0.157
Total plant dry weight	0.437	0.919	0.784	0.743	0.547

(continued next page)

Appendix 2

Table iii (continued)

K. ivorensis

Plant organ	Initial harvest	Final harvest			
		A	B	C	D
Mean leaf weight per seedling (g)	0.077	0.208	0.146	0.116	0.117
Mean stem weight per seedling (g)	0.046	0.091	0.097	0.066	0.062
Mean root weight per seedling (g)	0.028	0.072	0.070	0.047	0.057
Total plant dry weight	0.151	0.371	0.313	0.299	0.236

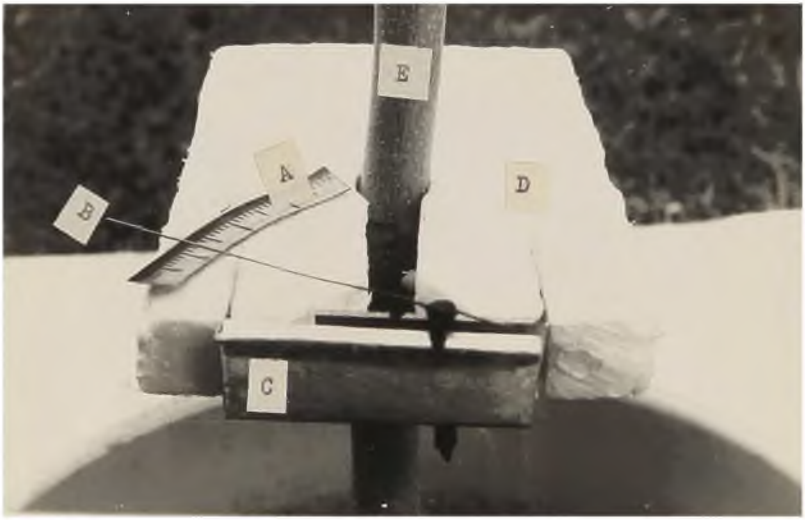
Appendix 3, Plate IA

Photograph of the simple dendrometer used to measure stem shrinkage, in location on seedling.

Appendix 3, Plate IB

Photograph of the simple dendrometer used to measure stem shrinkage, showing details of galvanized metal plates, and pointer arrangement.

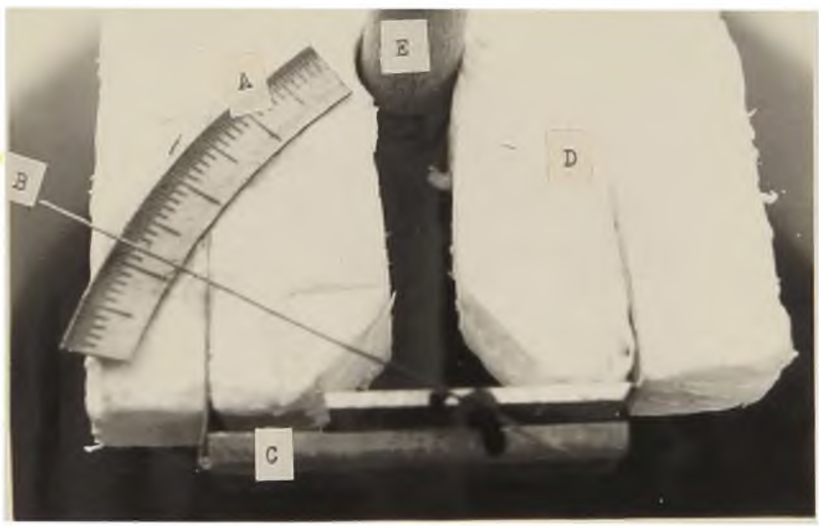
A = Scale
B = Metal wire (pointer)
C = Galvanized iron plates
D = Expanded polystyrene
E. Plant stem



Appendix 3, Plate IC

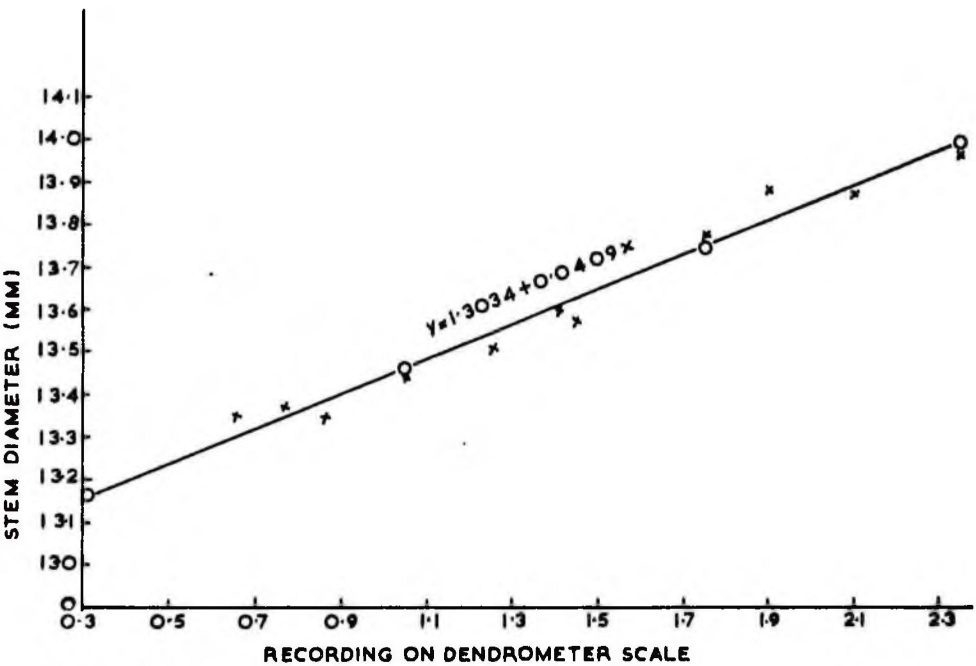
Photograph of the simple dendrometer used to measure stem shrinkage showing details of pointer lying over scale.

A = Scale C = Galvanized iron plates E = Plant stem
B = Metal wire D = Expanded polystyrene



APPENDIX 3, GRAPH I

AN EXAMPLE OF THE REGRESSION OF STEM DIAMETER ON RECORDINGS ON DENDROMETER SCALE.



APPENDIX 3 GRAPH I

Appendix 3

(Tables i - v)

Diurnal variation of leaf relative water content for *Khaya senegalensis* and *K. ivorensis* seedlings in relation to soil moisture stress (bars) on several days, together with microclimatic data. Treatments A (-0.3), B (-0.4), C (-0.8), D (-4.5) bars.

Table i

(15/12/70)

Time of day (hrs)	Relative water content (%)							Microclimatic data	
	K. senegalensis				*K. ivorensis*			Relative humidity (%)	Air temperature °C
	A	B	C	D	A	C	D		
06.00	95.3	97.0	94.1	94.6	95.3	93.3	95.0	87	22
08.00	94.1	93.2	95.3	95.4	93.1	93.7	90.0	76	25
10.00	93.1	93.1	95.4	93.0	91.9	93.4	92.5	51	30
12.00	94.9	91.5	93.8	92.5	91.5	92.1	90.5	60	33
14.00	93.8	93.1	94.4	92.7	92.4	92.6	91.3	48	30
16.00	95.0	94.9	94.9	92.7	92.7	93.7	91.0	56	30
18.00	95.0	95.2	93.9	93.6	93.6	92.1	93.4	69	26
20.00	94.2	92.5	96.7	96.3	90.7	94.8	92.7	76	25
22.00	97.8	95.5	95.6	96.3	94.8	95.0	93.4	80	24

Appendix 3

Table ii
(6/1/71)

Time of day (hrs)	Relative water content (%)								Microclimatic data	
	K. senegalensis				K. ivorensis				Relative humidity (%)	Air temp. °C.
	A	B	C	D	A	B	C	D		
06.00	98.6	96.3	96.1	95.1	96.9	95.8	94.5	95.0	92	23
08.00	92.6	92.6	93.9	94.4	93.6	91.6	93.0	93.3	90	24
10.00	96.6	95.9	94.7	94.4	89.3	94.3	95.0	92.0	72	28
12.00	96.6	93.9	91.8	91.2	93.0	92.3	91.2	89.9	63	30
14.00	90.8	92.8	91.3	93.6	89.8	89.5	91.4	90.1	53	33
16.00	89.3	92.6	92.9	93.5	88.4	91.9	90.5	91.2	60	32
18.00	95.0	94.8	92.1	94.6	94.1	94.8	93.6	92.4	84	28
20.00	98.0	95.7	94.9	95.4	97.6	94.0	97.2	93.6	90	27
22.00	99.8	97.0	93.6	96.6	99.2	95.6	93.3	94.3	97	25

Appendix 3

Table iii

(16/3/71)

Time of day (hrs)	Relative water content (%)								Microclimatic data.	
	K. senegalensis				K. ivorensis				Relative humidity (%)	Air temp. °C
	A	B	C	D	A	B	C	D		
06.00	96.0	99.4	97.6	94.3	95.8	98.6	97.7	92.5	91	25
08.00	94.1	97.9	92.8	89.4	94.0	96.2	94.5	90.3	85	25
10.00	93.0	94.9	88.6	83.4	91.9	90.5	87.7	81.2	68	33
12.00	92.9	93.8	89.2	88.5	90.4	90.8	90.5	91.9	58	35
14.00	88.8	89.1	94.8	88.0	81.5	86.9	94.0	89.2	61	34
16.00	90.7	92.9	85.0	82.5	83.6	90.6	81.5	80.3	66	33
18.00	93.2	95.2	91.8	86.2	91.0	90.6	93.1	81.9	76	30
20.00	94.8	94.1	91.0	86.6	92.4	92.3	89.7	79.5	87	28
22.00	98.2	93.4	94.5	93.5	98.0	90.9	95.6	90.9	90	27

Appendix 3

Table iv
(30/3/71)

Time of day (hrs)	Relative water content (%)								Microclimatic data	
	K. senegalensis				K. ivorensis				Relative humidity (%)	Air temp. °C
	A	B	C	D	A	B	C	D		
06.00	98.1	99.1	93.5	93.4	95.2	97.2	95.2	90.3	99	23
08.00	89.2	93.9	95.2	93.3	88.7	91.9	94.7	93.9	91	24
10.00	94.4	94.8	93.8	92.4	90.1	93.3	92.2	89.8	86	28
12.00	84.6	89.2	92.0	91.7	84.1	84.2	89.2	89.1	50	33
14.00	89.6	92.9	90.8	87.8	87.2	89.5	90.8	87.5	50	35
16.00	91.4	87.8	88.8	88.9	85.8	87.3	89.7	84.7	52	34
18.00	95.6	96.0	91.7	89.1	93.7	94.2	92.2	87.4	75	30
20.00	95.0	96.1	93.6	89.2	90.0	93.2	94.6	88.0	84	28
22.00	99.0	93.3	92.5	95.5	94.2	95.4	91.8	89.3	91	26

Appendix 3

Table v

(5/4/71)

Time of day (hrs)	Relative water content (%)								Microclimatic data	
	K. senegalensis				K. ivorensis				Relative humidity (%)	Air temp. °C.
	A	B	C	D	A	B	C	D		
06.00	98.4	98.1	95.3	90.4	97.3	98.9	96.9	87.8	98	25
08.00	95.1	91.5	93.9	81.8	91.4	87.4	90.2	78.6	87	31
10.00	89.6	91.0	88.2	83.6	84.4	89.1	94.4	84.6	51	36
12.00	92.0	89.7	90.0	80.2	87.9	89.6	89.6	84.3	50	36
14.00	96.4	95.7	92.8	80.0	93.3	91.5	90.6	80.6	53	36
16.00	96.0	93.2	96.7	76.3	93.8	93.8	97.3	72.0	65	36
18.00	97.8	95.8	94.7	82.1	94.7	93.9	94.4	82.8	76	31
20.00	95.7	94.3	95.9	83.8	93.3	95.0	94.5	74.9	86	29
22.00	96.2	97.1	96.5	86.0	94.3	94.5	96.0	83.8	99	26

Appendix 3

(Tables vi-x)

Diurnal variation of leaf water potential for Khaya senegalensis and K. ivorensis seedlings in relation to soil moisture stress (bars), on several days, together with microclimatic data. Treatments: A (-0.3), B (-0.4), C (-0.8), D (-4.5) bars.

Table vi

(15/12/70)

Time of day (hrs)	leaf water potential (bars)							Microclimatic data	
	K. senegalensis				K. ivorensis				
	A	B	C	D	A	C	D	Relative humidity (%)	Air temp. °C
06.00	-6.5	-4.5	-8.0	-7.5	-4.0	-6.5	-4.5	89	22
08.00	-8.0	-9.0	-6.5	-6.0	-6.1	-6.0	-9.5	76	25
10.00	-9.0	-9.0	-6.5	-9.0	-7.4	-6.5	-7.0	51	30
12.00	-6.5	-11.0	-8.0	-10.0	-8.0	-7.5	-9.0	60	33
14.00	-8.0	-9.0	-7.5	-9.5	-7.0	-7.0	-8.0	48	30
16.00	-6.5	-6.5	-7.0	-9.5	-6.6	-6.0	-10.0	56	30
18.00	-6.5	-6.5	-8.0	-8.0	-7.5	-6.0	-6.5	69	26
20.00	-8.0	-10.0	-5.0	-5.5	-8.5	-4.5	-7.0	76	25
22.00	-3.5	-5.0	-6.0	-5.5	-4.5	-4.5	-6.5	80	24

Appendix 3

Table vii

(6/1/71)

Time of day (hrs)	Leaf water potential (bars)								Microclimatic data	
	K. senegalensis				K. ivorensis				Relative humidity (%)	Air temp. °C
	A	B	C	D	A	B	C	D		
06.00	-2.5	-5.5	-5.5	-6.5	-2.5	-3.5	-5.0	-4.5	92	23
08.00	-10.0	-10.0	-8.0	-7.5	-6.0	-8.0	-6.5	-6.5	90	24
10.00	-5.0	-5.0	-7.5	-7.5	-10.0	-5.5	-4.5	-7.5	72	28
12.00	-5.0	-8.0	-11.0	-12.0	-6.5	-7.5	-8.0	-9.5	63	30
14.00	-12.0	-9.0	-12.0	-8.0	-9.5	-9.5	-8.0	-9.0	53	33
16.00	-14.5	-10.0	-10.0	-8.0	-11.5	-7.5	-9.0	-8.0	60	32
18.00	-6.5	-6.5	-11.0	-7.0	-5.5	-4.5	-5.5	-7.0	84	28
20.00	-3.0	-5.0	-7.0	-6.5	-2.0	-5.5	-3.0	-6.0	90	27
22.00	-1.0	-4.5	-8.5	-5.0	-0.8	-4.0	-6.5	-5.0	87	25

Appendix 3

Table viii

(16/3/71)

Time of day (hrs)	Leaf water potential (bars)								Microclimatic data	
	K. senegalensis				K. ivorensis				Relative humidity (%)	Air temp. °C
	A	B	C	D	A	B	C	D		
06.00	-5.5	-1.5	-4.0	-7.5	-3.5	-1.5	-2.0	-7.0	91	25
08.00	-8.0	-3.5	-9.0	-14.0	-5.5	-3.5	-5.0	-9.0	85	25
10.00	-9.0	-6.5	-15.0	-21.0	-7.5	-9.0	-11.5	-18.0	68	33
12.00	-9.0	-8.0	-14.5	-15.0	-9.0	-8.5	-9.0	-7.5	58	35
14.00	-14.5	-14.0	-7.0	-16.0	-17.5	-12.0	-5.5	-10.0	61	34
16.00	-12.0	-9.0	-19.0	-22.0	-15.0	-8.0	-17.5	-19.5	66	33
18.00	-9.0	-6.5	-11.0	-18.0	-8.5	-8.0	-6.5	-17.0	76	30
20.00	-6.5	-8.0	-12.0	-17.5	-7.0	-7.0	-9.5	-19.0	87	28
22.00	-3.0	-8.5	-7.5	-8.5	-2.0	-8.0	-4.0	-8.5	80	27

Appendix 3

Table ix

(30/3/71)

Time of day (hrs)	Leaf water potential (bars)								Microclimatic data	
	K. senegalensis				K. ivorensis				Relative humidity (%)	Air temp. °C.
	A	B	C	D	A	B	C	D		
06.00	-4.0	-2.0	-8.5	-8.5	-4.0	-2.5	-4.5	-9.0	99	23
08.00	-10.5	-8.0	-6.5	-8.5	-10.0	-7.5	-5.0	-5.5	91	24
10.00	-9.0	-6.5	-8.0	-10.0	-9.0	-6.5	-7.5	-9.5	86	28
12.00	-15.0	-14.5	-11.0	-11.5	-15.0	-15.0	-10.3	-10.0	50	33
14.00	-12.0	-9.0	-12.5	-16.0	-12.0	-10.0	-8.5	-11.5	50	35
16.00	-13.0	-16.0	-14.5	-14.5	-13.0	-12.0	-9.5	-14.0	52	34
18.00	-6.0	-5.5	-11.0	-14.5	-6.0	-5.5	-7.5	-11.5	75	30
20.00	-7.5	-5.0	-8.5	-14.5	-9.5	-6.5	-5.0	-11.0	84	28
22.00	-2.0	-9.0	-10.0	-6.0	-5.5	-4.5	-7.5	-10.0	91	26

Appendix 3

Table x

(5/4/71)

Time of day (hrs)	Leaf water potential (bars)								Microclimatic data	
	K. senegalensis				K. ivorensis				Relative humidity (%)	Air temp. °C
	A	B	C	D	A	B	C	D		
06.00	-2.5	-3.5	-6.5	-12.5	-3.0	-2.0	-12.5	-11.5	98	25
08.00	-7.0	-11.5	-28.0	-22.5	-8.0	-12.0	-9.5	-20.0	87	31
10.00	-14.0	-12.0	-15.5	-21.0	-14.5	-10.5	-5.0	-14.5	51	36
12.00	-10.5	-14.0	-13.0	-24.5	-11.0	-10.0	-10.0	-15.0	50	36
14.00	-5.0	-6.0	-9.0	-24.6	-6.5	-8.0	-9.0	-18.0	53	36
16.00	-5.5	-9.0	-4.5	-28.0	-5.5	-5.5	-3.0	-25.5	65	36
18.00	-4.5	-6.0	-7.0	-22.5	-4.5	-5.5	-5.0	-16.0	76	31
20.00	-6.0	-7.5	-5.5	-20.5	-6.0	-4.5	-5.0	-25.0	86	29
22.00	-3.5	-4.5	-4.5	-18.0	-5.5	-5.0	-3.5	-15.0	99	26

Appendix 3

Tables xi to xiii

Diurnal variation of stem diameter (mm) in seedlings of *Khaya senegalensis* and *K. ivorensis* in relation to soil moisture content (expressed as percentage of the value at field capacity), during three soil drying-out cycles (Cycles I to III).

Table xi

Cycle I

(12 to 17 May 1971)

Time of day (hours)	Stem diameter (mm)							
	K. senegalensis				K. ivorensis			
	Soil moisture content (% field capacity)							
	93	64	51	27	93	64	51	27
06.00	13.1	13.2	12.4	13.7	11.8	11.7	11.4	12.2
08.00	13.0	13.0	12.2	13.6	11.6	11.6	11.2	12.1
10.00	12.8	12.8	12.0	13.5	11.5	11.4	10.9	12.1
12.00	12.7	12.7	11.7	13.4	11.5	11.4	10.8	12.0
14.00	12.6	12.6	11.7	13.4	11.5	11.4	10.8	12.0
16.00	12.6	12.7	11.7	13.4	11.5	11.4	10.8	12.0
18.00	12.7	12.7	11.7	13.5	11.6	11.4	10.9	12.0
20.00	-	12.9	11.9	13.5	-	11.6	11.0	12.0
22.00	13.0	13.0	11.7	13.5	11.8	11.7	11.1	12.1

- no record

Appendix 3

Table xii

Cycle II

(18 to 21 May 1971)

Time of day (hours)	Stem diameter (mm)					
	K. senegalensis			K. ivorensis		
	Soil moisture content (% field capacity)					
	94	70	51	94	70	51
06.00	12.6	12.8	13.2	11.5	11.5	11.5
08.00	12.5	12.6	13.0	11.3	11.4	11.2
10.00	12.4	12.3	12.7	11.1	11.1	11.0
12.00	12.3	12.2	12.5	11.0	10.8	10.9
14.00	12.3	12.1	12.4	11.0	10.8	10.9
16.00	12.3	12.2	12.4	11.1	10.8	10.9
18.00	12.4	12.4	12.4	11.2	11.1	11.0
20.00	12.6	12.5	12.7	11.4	11.4	11.2
22.00	12.6	12.6	12.8	11.4	11.4	11.3

Appendix 3

Table xiii

Cycle III

(24 May to 3 June 1971)

Time of day (hours)	Stem diameter (mm)							
	K. senegalensis				K. ivorensis			
	Soil moisture content (% field capacity)							
	93	64	50	27	93	64	50	27
06.00	12.8	12.9	12.7	11.4	11.8	11.9	11.8	11.7
08.00	12.6	12.7	12.7	11.3	11.6	11.6	11.7	11.5
10.00	12.3	12.3	12.5	11.2	11.3	11.5	11.6	11.3
12.00	12.1	12.1	12.2	11.2	11.3	11.4	11.3	11.2
14.00	12.1	12.1	12.1	11.2	11.3	11.4	11.3	11.2
16.00	12.2	12.3	12.0	11.3	11.3	11.5	11.3	11.3
18.00	12.3	12.4	12.2	11.3	11.5	11.6	11.4	11.4
20.00	12.5	12.5	12.4	11.4	11.7	11.7	11.6	11.5
22.00	12.7	12.6	12.6	11.4	11.8	11.8	11.7	11.5

Appendix 4

Tables i-iv

Transpiration rate of seedlings of Khaya senegalensis and K. ivorensis in relation to soil moisture stress (bars); A (-0.3), B (-0.4), C (-0.8), D (-4.5) , together with microclimatic data.

Table i

(8/2/71)

Time of day (hours)	Transpiration rate ($mg/cm^2/hr$)							Microclimatic data		
	K. senegalensis				K. ivorensis			Evapo-ration (ml)	Relative humidity (%)	Air temp. (°C)
	A	B	C	D	A	B	C			
07.00-08.00	4.2	6.6	3.5	2.3	4.2	4.4	4.4	0.2	96.	23.0
08.00-09.00	2.5	3.3	2.5	2.3	4.7	4.9	3.2	0.2	90	24.0
09.00-10.00	6.8	8.3	4.6	2.3	4.4	4.9	4.1	0.3	84	28.0
10.00-11.00	13.3	14.9	6.1	5.3	7.3	13.6	7.4	0.4	77	28.0
11.00-12.00	11.3	14.9	5.2	1.1	5.9	9.9	7.6	0.5	64	28.0
12.00-13.00	19.2	21.5	9.1	4.5	12.7	16.0	8.8	0.6	54	29.0
13.00-14.00	13.3	16.5	5.8	1.1	8.4	11.1	6.2	0.6	56	30.0
14.00-15.00	13.3	14.9	6.1	1.1	9.7	11.1	8.5	0.8	66	35.0
15.00-16.00	7.8	11.6	5.2	1.1	6.8	8.6	5.5	0.3	76	33.0
16.00-17.00	6.3	6.6	3.7	1.1	5.8	3.7	5.9	0.3	80	31.0

Appendix 4

Table ii

(5/2/71)

Time of day (hours)	Transpiration rate (mg/cm^2/hr)						Microclimatic data		
	K. senegalensis			K. ivorensis			Evapo-ration (ml)	Relative humidity (%)	Air temp. (°C)
	A	B	C	A	B	C			
06.00-07.00	2.1	2.4	2.2	2.1	3.4	4.0	0.2	96.	24.0
07.00-08.00	4.1	4.0	2.6	3.5	2.4	4.0	0.2	93	23.5
08.00-09.00	6.8	7.2	6.5	6.4	4.5	5.9	0.2	86	24.0
09.00-10.00	7.9	4.3	6.7	4.7	4.5	5.9	0.2	80	24.5
10.00-11.00	13.7	12.0	7.8	9.6	9.0	7.9	0.6	72	27.0
11.00-12.00	17.6	11.7	15.6	17.7	10.6	13.3	0.6	66	30.5
12.00-13.00	1.3	10.6	11.2	10.1	7.8	9.9	0.5	60	31.5
13.00-14.00	14.1	8.7	10.0	10.5	9.7	9.9	0.5	50	35.0
14.00-15.00	9.3	9.6	8.9	8.2	6.7	7.9	0.4	62	35.0
15.00-16.00	7.9	4.0	7.8	6.4	5.4	7.9	0.3	71	30.5
16.00-17.00	0.7	0.0	0.0	1.3	0.0	1.2	0.1	85	27.0

Appendix 4

Table iii

(10/ 2 / 71)

Time of day (hours)	Transpiration rate (mg/cm^2/hr)					Microclimatic data		
	K. senegalensis			K. ivorensis		Evapo-ration (ml)	Relative humidity (%)	Air temp. (°C)
	A	B	C	A	B			
06.00-07.00	5.4	1.8	4.8	5.5	3.8	0.2	92	24.5
07.00-08.00	8.1	7.3	8.7	6.4	3.8	0.3	83	25.0
08.00-09.00	8.5	8.3	9.6	9.7	7.1	0.3	64	26.5
09.00-10.00	11.9	7.3	9.6	9.0	7.1	0.5	58	31.0
10.00-11.00	21.3	9.9	9.6	13.3	6.2	0.7	54	32.5
11.00-12.00	16.9	9.5	9.6	13.3	8.1	0.8	53	33.5
12.00-13.00	16.2	8.8	9.6	13.3	10.5	0.7	51	34.0
13.00-14.00	21.0	10.9	9.6	12.5	13.3	0.8	55	35.0
14.00-15.00	12.2	7.3	12.1	11.7	9.5	0.5	60	32.0
15.00-16.00	9.7	5.5	9.6	10.6	7.1	0.4	74	31.0
16.00-17.00	3.7	1.8	6.3	5.5	5.7	0.3	78	28.0

Appendix 4

Table iv

(11/2/71)

Time of day (hours)	Transpiration rate ($mg/cm^2/hr$)						Microclimatic data		
	K. senegalensis			K. ivorensis			Evaporation (ml)	Relative humidity (%)	Air temp. (°C)
	A	B	C	A	B	C			
07.00-08.00	5.4	3.6	2.4	3.4	2.1	3.2	0.2	88	24.0
08.00-09.00	8.7	5.5	7.7	6.2	4.5	6.5	0.3	76	24.0
09.00-10.00	10.2	9.1	7.7	7.3	7.2	6.5	0.4	66	27.0
10.00-11.00	13.2	9.1	7.7	9.6	8.2	9.7	0.5	66	30.5
11.00-12.00	11.5	10.9	7.7	10.5	8.2	9.7	0.4	58	31.0
12.00-13.00	19.0	7.3	7.7	15.6	12.2	9.7	0.9	62	32.0
13.00-14.00	13.2	9.1	7.7	11.0	8.8	9.7	0.6	58	35.0
14.00-15.00	14.3	9.1	4.8	14.3	10.0	9.7	0.7	64	34.0
15.00-16.00	10.3	7.3	9.6	8.7	10.1	9.7	0.5	70	31.0
16.00-17.00	5.4	4.4	2.4	9.6	5.5	3.2	0.4	70	29.0
17.00-18.00	3.6	1.8	3.4	5.8	4.0	3.2	0.2	86	28.0

Appendix 4

Table v

Microclimatic data recorded on days when transpiration was measured in relation to osmotic potential in the root medium. Relative humidity (%), Air temperature (°C).

Time of day (hrs)	Microclimatic data					
	25/10/71		26/10/71		27/10/71	
	Relative humidity	Air temp.	Relative humidity	Air temp.	Relative humidity	Air temp.
06.00	84	25	92	24	84	24
07.00	78	25	84	24	78	24
08.00	76	28	70	24	70	24
09.00	70	29	64	25	62	27
10.00	60	30	60	27	56	29
11.00	56	29	54	29	54	30
12.00	58	29	54	31	54	33

Appendix 4

Table vi

Diurnal variation in stomatal conductivity of leaves of Khaya senegalensis and K. ivorensis under varying soil moisture treatments, A (-0.3), B (-0.4), C (-0.8), and D (-4.5) bars, together with some microclimatic data on 3/6/71.

Time of day (hrs)	Infiltration score								Microclimatic data	
	K. senegalensis				K. ivorensis				Relative humidity (%)	Temperature °C.
	A	B	C	D	A	B	C	D		
07.00	10	2	8	0	3	2	5	3	88	23.5
08.00	10	8	13	1	8	7	7	4	77	24.5
09.00	10	7	13	0	10	7	6	2	86	29.0
10.00	10	4	12	0	8	7	7	1	76	30.5
11.00	8	4	9	0	8	7	7	1	70	33.5
12.00	8	4	6	0	8	8	7	0	70	32.0
13.00	7	3	6	0	8	7	6	0	64	30.5
14.00	6	2	4	0	9	5	6	0	78	29.5
15.00	4	1	2	0	6	3	4	0	78	28.0
16.00	6	0	1	0	0	0	0	0	90	26.6

Appendix 5

Table i

Relative water contents of leaves of seedlings of Khaya senegalensis and K. ivorensis at points of stomatal closure.

Experiment	Relative water content (%)	
	K. senegalensis	K. ivorensis
1	82 90 92	78 83 79
2	90 86 90	87
3	79 88 82 89	76 78
4	93	78 79 80
5	89 83 87 86	80
6	85 82 81 81	89 81 80

(continued next page)

Appendix 5 Table i (continued)

Experiment	Relative water content (%)	
	K. senegalensis	K. ivorensis
7	90 91 92	80 79 80
Totals	1908	1287
Mean value	86.7	80.4

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REFERENCES

Alvim, P. de T., and Havis, J. (1954). An improved infiltration series for studying stomatal opening as illustrated with coffee. Pl. Physiol., 29 297 - 98

Ampofo, S.T. (1969). Autecological studies on Afroromosia elata Harms. M.Sc. thesis, University of Ghana, Legon (unpublished).

Annual Report of the Forest Products Research Institute, Kumasi Ghana C.S.I.R. (1968)

Annual Report of the Forest Products Research Institute, Kumasi, Ghana C.S.I.R. (1969)

Anon. (1969). Economic report of the Forestry Department, Ghana

Anon. (1970). Economic reports of the Forestry Department, Ghana.

Arnon, D.I. and Hoagland, D.R. (1940). Crop production in artificial culture solutions and in soils with special reference to factors influencing yields and absorption of inorganic nutrients. Soil Sci., 50. 463 - 485.

Aspinall, D. (1965). The effects of soil moisture stress on the growth of barley. II. Grain growth. Aust. J. agric. Res., 16, 265 - 75.

Aubréville, A. (1959). Les fourrés alignés et les savanes a termitieres buissonnantes Winneba et d' Accra (Ghana). Bois Forets Trop. 67 21 - 4

Bannister, P. (1964). Stomatal responses of heath plants to water deficits. J. Ecol., 52, 151 - 8

Barrs, H.D. (1968). Determination of water deficits in plant tissues. In 'Water deficits and plant growth.' (Ed. by T.T. Kozlowski) Academic Press Inc. New York Vol. I, pp. 235 - 368.

Black, C.A. (1957). Soil-Plant Relationships, Wiley, New York.

Blackman, G.E. and Wilson, G.L. (1951). Physiological and ecological studies in the analysis of plant environment VII. An analysis of the differential effects of light intensity on the net assimilation rate, leaf area ratio, and relative growth.

rate of different species. Ann. Bot. N.S. 15. 375-408

Boughey, A.S. (1957). The physiognomic delimitation of West African vegetation types. Jl. W. Afr. Sci. Ass. 3. 148-65.

Brix, H. (1962). The effects of water stress on the rates of photosynthesis and respiration in tomato plants and loblolly pine seedlings. Pl. Physiol., 15, 10-20

Čatský, J. (1959). The role played by growth in the determination of water deficits in plants. Biol. Plant. Vol. I. P. 277-286

Čatský, J. (1960). Determination of water deficits, in discs out from leaf blades. Biol. Plant., 2. 76-78

Collis-George, N., Sands, J.E. (1962). Comparison of the effects of the physical and chemical components of soil water energy on seed germination. Aust. J. agric. Res., 13, 575-584

Conner, D.J. & Tunstall, B.R. (1968). Tissue water relations for brigalow and mulga. Aust. J. Bot., 16, 487-90

Coombe, D.E. (1960). An analysis of the growth of Trema guineensis. J. Ecol., 48, 219-234

Cowan, J.H. (1965). Transport of water in the soil-plant atmosphere system. J. appl. Ecol., 2. 221-239

Dale, J.E. (1961). Investigations into the stomatal physiology of upland cotton. I. The effects of hour of day, solar radiation, temperature and leaf water content on stomatal behaviour. Ann. Bot., N.S. 25. 39-52

Dalziel, J.M. (1937). The Useful Plants Of West Tropical Africa: an appendix to the Flora of West Tropical Africa by J. Hutchinson and J.M. Dalziel. Crown Agents. London.

Daubenmire, R.F. (1943). Soil temperatures vs. drought as the factor determing lower altitudinal limits of trees in the Rocky Mountains. Bot. Gaz., 105, 1-13.

Daubenmire, R.F. (1947). Plants and Environment: a textbook of plant autecology. Wiley, New York.

Davies, J.A. and Robinson, P.J. (1969). A. simple energy balance approach to the moisture balance climatology of Africa. In 'Environment And Land Use in Africa' (Ed. by M.F. Thomas and G.W. Whittington), pp. 23-56.

Dodoo, G. (1969). The diurnal pattern of leaf water status in two woody species, Khaya senegalensis and K. ivorensis of contrasting habitats. (Dissertation, unpublished)

Eaton, F.M. (1942). Toxicity and accumulation of chloride and sulfate salts in plants. J. agric. Res., 64, 357-399

Fisher, R.A. (1920). Some remarks on the methods formulated in a recent article on 'The quantitative analysis of plant growth'. Ann. appl. Biol., 7. 367-72

Fisher, R.A. & Yates, F. (1957). Statistical tables for biological, agricultural and medical research. 5th (ed. by Oliver and Boyd.) Edinburgh.

Fuehring, H.D., Mazaheri, A. Bybordi, M., and Khan, A.K.S. (1966). Effect of soil moisture depletion on crop yield and stomatal infiltration. Agron. J., 58, 195-198.

Gaertner, E.E. (1963). Water relations of forest trees. In 'The Water Relations of Plant's (ed. by A.J. Rutter and F.H.Whitehead,) pp 366-378. Blackwell Scientific Publication, Oxford.

Gates, C.T. (1955a). The response of the young tomato plant to a brief period of water shortage. I. The whole plant and its principal parts. Aust. J. Biol. Sci., 8. 196-214

Gates, C.T. (1955b). The response of the young tomato plant to a brief period of water shortage. II. The individual leaves. Aust. J. biol. Sci. 8. 215-230

Gates D.M. (1964). Leaf temperature and transpiration. Agron. J., 56, 273-277.

Gavande, S.A., & Taylor, S.A. (1967). Influence of soil water potential and atmospheric evaporative demand on the energy status of water in plants. Agron. J., 59. 4-7

Gregory, F.G. (1919). Physiological conditions in cucumber houses. Exp. and Res. Sta., Cheshunt, Annu. Reps. 3. 19-28

Gingrich, J.R., and Russel, M.B. (1956). Effect of soil moisture tension and oxygen concentration on the growth of corn roots. Agron. J., 48, 517-20

Halevy, A.H. (1960a). Diurnal fluctuations in water balance factors of Gladiolus leaves. Bull. Res. Coun. Israel Sect. D8. 239-246.

Halevy, A.H. (1960b). The influence of progressive increase in soil moisture tension on growth and water balance of gladiolus leaves, and the development of physiological indicators for irrigation. Proc. Am. Soc. hort. Sci., 76. 620-630

Hall, J.B. and Jeník, J. (1968). Contribution towards the classification of savanna in Ghana. Bull, Inst. fr. Afr. noire, ser. A, 30. 84-99

Hewitt, E.J. (1952). Sand and water culture methods used in the study of plant nutrition. Tech. Communs. No.22 of C.A.B. London

Hewlett, J.D. and Kramer, P.J. (1963). The measurement of water deficits in broad-leaf plants. Protoplasma, 57. 382-391

Hopkins, B. (1965). Forest and Savanna. Heinemann, London.

Hopkins, B. (1970a). Vegetation of the Olokemeji Forest Reserve, Nigeria. VI. The plants on the forest site with special reference to their seasonal growth. J.Ecol., 58. 765-93

Hopkins, B. (1970b). Vegetation of the Olokemeji Forest Reserve, Nigeria. VII. The plants on the savanna site with special reference to their seasonal growth. J. Ecol., 58. 795-825.

Hosner, J.F. and Leaf, A.L. (1962). The effect of soil saturation on the dry weight, ash content and nutrient absorption of various bottomland tree species. Proc. Soil Sci. Soc. Am. 26. 401-404

Hunt, F.M. (1951). Effects of flooded soil on growth of pine seedlings. Pl. Physiol., Lancaster 26. 363-368

Hutchinson, J., Dalziel, J.M. (1958). Flora of West Tropical Africa. I. Part 2 Crown Agents, London.

Hygen, G. (1951). Studies in plant transpiration. I. Physiologia Pl. 4. 57

Iljin, W.S. (1957). Drought resistance in plants and physiological processess. Ann. Rev. Pl. Physiol., 8. 257-274

Irvine, F.R.(1961). Woody plants of Ghana. Oxford University Press London.

Jarvis, M.S. (1963). A comparison between the water relations of species with contrasting types of geographical distribution in the British Isles. In 'The water relations of plants' (Ed. by A.J.Rutter and F.H. Whitehead), pp. 289-312. Blackwell Scientific Publication, Oxford.

Jarvis, P.C. (1963). The effect of soil type on the relation between soil water regime and growth of seedlings of Quercus petraea (Matt.) Liebl. In 'The Water Relations of Plant' (Ed. by A.J. Rutter and F.H. Whitehead), pp 313-325. Blackwell Scientific Publication, Oxford.

Jarvis, P.G. & Jarvis, M.S. (1963a). The water relations of tree seedlings. I. Growth and water use in relation to soil water potential. Physiologia Pl. 16. 215-235

Jarvis, P.G. & Jarvis M.S. (1963b). The water relations of tree seedlings. II. Transpiration in relation to soil water potential. Physiologia Pl. 16. 236-253

Jarvis, P.G. & Jarvis, M.S. (1963c). The water relations of tree seedlings. III. Transpiration in relation to osmotic potential of the root medium. Physiologia Pl. 16. 269-275.

Jarvis, P.G. & Jarvis, M.S. (1963d). Effects of several osmotic substrates on the growth of Lupinus albus seedlings. Physiologia pl. 16 485-500.

Jarvis, P.G. & Jarvis, M.S. (1963e). The water relation of tree seedlings. IV. Some aspects of the tissue water relations and drought resistance. Physiologia Pl. 16. 501-516.

Jarvis, P.G. & Jarvis, M.S. (1965). The water relations of tree seedlings. V. Growth and root respiration in relation to the osmotic potential of the root medium. In 'Water Stress in Plants' (Ed. by B. Slavik,). Proc. Symp. Prague, 1963, pp.167-182 Czech. Acad. Sci., Prague.

Kaufmann, M.R. (1968). Water relations of pine seedlings in relation to root and shoot growth. Pl. Physiol., Lancaster, 43. 281-288

Kaul, R. (1966). Relative growth rates of spring wheat, oats and barley under polyethylene glycol-induced water stress. Can. J. Pl. Sci. 46. 611-17

Keay, R.W.J. (1959). An Outline of Nigerian Vegetation. Government Printer, Lagos.

Kinloch, D. (1945). Silvicultural notes on some of the more important Gold Coast trees. Government Printing Dept., Accra.

Klepper, B. (1968). Diurnal pattern of water potential in woody plants. Pl. Physiol., 43. 1931-4.

Koslowski, T.T. (1958). Water relations and growth of trees. J. For. 56. 498-502

Kozlowski, T.T. (1967). Diurnal variations in stem diameters of small trees. Bot. Gaz. 128. 60-68

Kozlowski, T.T. (1968). Introduction. In 'Water Deficits and Plant Growth' Volume I (Ed. by T.T. Kozlowski) Academic Press. pp. 1-21 New York and London.

Kramer, P.J. (1956). Physical and physiological aspects of water absorption. Encyclopedia of Pl. Physiology, 3. 124-159

Kramer, P.J. (1962). The role of water in tree growth. In 'Tree Growth' (Ed. by T.T. Kozlowski) pp. 171-182. Ronald Press, New York.

Kramer, P.J. (1963). Water stress and plant growth. Agron. J., 55. 31-35.

Kreeb, K and Onal. M.(1961). Uber die gravimetrische Methode zur Bestimmurg der Saugspannung und das Problem des negativen Turgors. II. Mitteilung. Die Berucksichtigung von Atmungsverlusten wahrend der Messungen. - Planta 56. 409-415.

Lagerwerff, J.V. Ogata, G. and Eagle, H.E. (1961). Control of osmotic pressure of culture solutions with polyethylene glycol. Science, 133. 1485-1487

Lawlor, D.W. (1969). Plant growth in polyethylene glycol solutions in relation to the osmotic potential of the root medium and the leaf water balance. J. Exp. Bot., 20. 895-912.

Lawlor, D.W. (1970). Absorption of polyethylene glycols by plants and their effects of plant growth. New Phytol. 69. 501-513.

Lawson, G.W. (1966). Plant life in West Africa. Oxford University Press, London.

Lawson, G.W. and Jenik, J. (1967). Observations on microclimate and vegetation interrelationaships on the Accra Plains (Ghana). J. Ecol. 55. 773-85

Lely, H.V. (1925). The useful trees of Northern Nigeria. Crown Agents, London.

Leshem, B. (1966). Toxic effect of carbowaxes (Polyethylene glycols) on Pinus halipensis seedlings. Pl. Soil, XXIV. 322-324

Loftfield, J.V.G. (1921). The behaviour of stomata. Publ. Carnegie Instn., Washington No.314. 1-142

Longman, K.A. (1969). The dormancy and survival of plants in the humid tropics. Symp. Soc. exp. Biol., 23 471-488

Luxmoore, R.J. and Millington, R.J. (1971). Growth of perennial ryegrass (Lolium perenne L.) in relation to water, nitrogen and light intensity. I. Effects on leaf growth and dry weight. Pl. Soil. 34. 269-281

Macklon, A.E.S. and Weatherley, P.E. (1965). Controlled environment studies of the nature and origins of water deficits in plants. New Phytol., 64. 414-427

Magness, J.R. and Furr, J.R. (1930). Stomatal activity in apple leaves. Proc. Am. Soc. hort. Sci. 27. 207

Marsden, D.H. (1950). Dry weather and tree troubles in Massachusetts. Pl. Dis. Reptr. 34. 400-401

McKell, C.M. Perrier, C.G. and Stebbins, G.L. (1960). Response of two species of orchard grass (Dactylia glomerata subsp. lusitanica and judaiea) to increasing soil moisture stress. Ecology, 41. 772-779.

McLean, R.C. and Ivimey-Cook, W.R. (1952). Plant Science Formulae, MacMillan & Co. Ltd. London.

McWilliam, J.R. & Phillips, P.J. (1971). Effect of osmotic and matric potentials on the availability of water for seed germination. Aust. J. Biol. Sci., 24. 423-431.

Mees, G.C. and Weatherley, P.E. (1957). The mechanism of water absorption by roots. II. The role of hydrostatic pressure gradients across the cortex. Proc. Roy. Soc. B. 147. 381-391

Meidner, H. & Mansfield, T.A. (1968). Physiology of stomata. McGraw-Hill, London.

Metcalfe, C.R. and Chalk, L. (1950). Anatomy of the Dicotyledons. Volume I Oxford University Press, London.

Moore, B. (1926). Influence of certain soil and light conditions on the establishment of reproduction in northeastern conifers. Ecol., 7. 191-220

Mueller-Dombois, D. (1964). Effects of depth to water table on height growth of tree seedlings in a greenhouse. Forest Sci., 10. 306

Nieman, R.H. (1962). Some effects of sodium chloride on growth, photosynthesis and respiration of twelve crop plants. Bot. Gaz. 123. 279-85.

Njoku, E. (1959). An analysis of plant growth in some West African species. I. Growth in full daylight. Jl. W. Afr. Sci. Ass., 5. 37

Njoku, E. (1964). Seasonal periodicity in the growth and development of some forest trees in Nigeria. II. Observations on seedlings. J. Ecol., 52. 19

Noy-Neir, I. & Ginzburg, B.Z. (1969b). An analysis of the water potential isotherm in plants tissue. II. Comparative studies on leaves of different types. Aust. J. biol. Sci., 22. 35-53

Ogigirigi, M.A., Kozlowski, T.T. & Sasaki, S. (1970). Effect of soil moisture depletion on stem shrinkage and photosynthesis of tree seedlings. Pl. soil. 32. 33-49

Okali, D.U.U. (1971a). Tissue water relations for some woody species of the Accra Plains, Ghana. J. Ecol., 59. 89-101.

Okali, D.U.U. (1971b). Rates of dry-matter production in some tropical forest-tree seedlings. Ann. Bot., 35. 87-97

Oppenheimer, H.R. (1960). Adaptation to drought: xerophytism. In 'Plant Water Relationships in Arid and Semi-Arid Conditions. Reviews of Research,' p. 105. UNESCO. Paris.

Oppenheimer, H.R. (1968). Drought resistance of Monterey pine needles. Isreal J. Bot., 17. 163-8.

Owen,P.C.J. (1953). The relation of germination of wheat to water potential. J. exp. Bot., 3. 188-203

Owen, P.C. and Watson, D.J. (1956). Effect on crop growth of rain after prolonged drought. Nature, Lond., 177. 847

Parker, J. (1956). Drought resistance in woody plants. Bot. Rev. 29. 123-201

Parker, J. (1968). Drought-Resistance Mechanisms - In 'Water deficits and plant growth' (Ed.by T.T. Kozlowski) Academic Press Inc. New York Vol. 1, pp. 195-229.

Pisek, A., and Winkler, E. (1953). Die Schliess-bewegung der Stomata bei ökologisch verschiedenen Pflanzentypen in Abhiangigkeit vom Wassersätigungszustand der Blätter and vom Licht. Planta, 42. 253-278

Polster, H (1950). Die physiologische Grundlagen der Stofferzeugung im Walde. Untersuchungen uber Assimilation, Respiration und Transpiration unserer Hauptholzarten. Bayerischer Landwirtschaftsverlag. G.n.b.h. Munich.

Raunkiaer, C. (1934). The life forms of plants and statistical plant geography: being the collected papers of C. Raunkiaer. Clarendon Press, Oxford.

Richards, L.A. and Wadleigh, C.H. (1952). Soil water and plant growth. Agronomy 2. 13

Richards, P.W. (1952). The tropical rain forest. Univ. Press, Cambridge.

Russell, E.W. (1961). 'Soil Conditions and Plant Growth,' 9th (Ed. by Longman,) London.

Rutter, A.J., and Sands, K. (1958). The relation of leaf water deficit to soil moisture tension in Pinus sylvestris L. I. The effect of soil moisture on diurnal changes in water balance. New Phytol. 57. 50-65

Rychnovská, M. and Květ, J. (1963). Water relations of some Psammophytes with respect to their distribution. In 'The Water Relations of Plants' (Ed. by A.J. Rutter and F.H. Whitehead), pp. 190-198 Blackwell Scientific Publications, Oxford.

Sands, K., and Rutter, A.J. (1959). Studies in the growth of young plants of Pinus Sylvestris. II. The relation of growth to moisture tension Ann. Bot. (London) (N.S.) 23. 269-284

Shephard, W. (1964). Diffusion pressure deficit and turgidity relationships of detached leaves of Trifolium repens L. Aust. J. agric. Res. 15. 481-98

Shillo, R. and Halevy, A.H. (1964). Experiments in the irrigation of gladioli according to absorption of viscous fluid through stomata. Isreal J. Agric. Res. 14. 89-95

Slatyer, R.O. (1955). Studies of the water relations of crop plants grown under natural rainfall in northern Australia. Aust. J. agric. Res. 6. 365-77

Slatyer, R.O. (1957a). Significance of the permanent wilting percentage in studies of plant and soil water relations. Bot. Rev. 23 585-636.

Slatyer, R.O. (1957b). The influence of progressive increases in total soil moisture stress, on transpiration, growth, and internal water relationships of plants. Aust. J. biol. Sci. 10. 320-336

Slatyer, R.O. (1958). The measurement of diffusion pressure deficit in plants by a method of vapour equilibration. Aust. J. biol. Sci. 11. 349-65.

Slatyer,R.O. (1960). Aspects of the tissue water relationships of an important arid zone species (Acacia aneura F. Muell.) in comparison with two mesophytes. Bull. Res. Coun. Israel. D8. 159-68

Slatyer,R.O. (1961). Effects of several osmotic substrates on the water relations of tomato. Aust. J. biol. Sci. 14. 519-540

Slatyer,R.O. (1962a). Methodology of a water balance study conducted on a desert woodland (Acacia aneura F. Muell.) community in central Australia. U.N.E.S.C.O. Arid Zone Res. 16. 15-26

Slatyer,R.O. (1962c). Internal water balance of Acacia aneura F. Muell in relation to environmental conditions. U.N.E.S.C.O. Arid Zone Res. 16. 137-46

Slatyer,R.O. (1967). Plant-water Relationships. Academic Press, London and New York.

Slatyer,R.O. (1970). The effect of internal water status on plant growth development and yield. Review Paper 3 presented at the UNESCO Symposium on Plant Response to climtic Factors Uppsala, Sweden 1970.

Slavík, B. (1965). The influence of decreasing hydration level on photosynthetic rate in the thalli of the hepatic Conocephallum conicwn. In "Water stress in Plants" (Ed. by B. Slavik,) Proc. Symp. Prague, 1963. p.195. Czech. Acad, Sci., Prague.

Stanhill, G.(1957). The effect of differences in soil moisture status on plant growth: A review and analysis of soil moisture regime experiments. Soil Sci. 84. 205-214

Stocker, O. (1956). Die Durreresistems - In "Handbuch der Pflanzenphysiologie " (ed. by W. Ruhland.) Vol.3, P.696. Springer, Berlin

Stocker, O. (1960). Physiological and morphological changes in plants due to water deficiency. UNESCO Arid Zone Res. 15. 63-104

Sullivan, C.Y. and Levitt, J.(1959). Drought tolerance and avoidance in two species of Oak. Physiologia Pl. 12. 299-305

Sveshnikova,V.M.(1965). Water relations of some species of wormwood in Kazakhstan. In "Water stress in Plants' (Ed. by B. Slavik,) Proc. Symp. Prague, 1963,pp.268-274 Czech. Akad. Sci., Prague.

Taylor, C.J. (1952). The vegetation Zones of the Gold Coast, Bull. Forestry Dept. 4. Accra.

Taylor, C.J. (1960). Synecology and Silviculture in Ghana, Nelson, Edinburgh.

Troughton, J.H. (1969). Plant water status and carbon dioxide exchange of cotton leaves Augt. J. Biol. Sci. 22. 289-302.

Veihmeyer, F.J. and Hendrickson, A.H. (1950). Soil moisture in relations to plant growth. Ann. Rev. Pl. Physiol., 1. 285-304

Wadleigh, C.H. and Ayers, A.D. (1945). Growth and biochemical composition of bean plant as conditioned by soil moisture tension and salt concentration. Pl. Physiol. 20. 106-132

Wadleigh, C.H. and Gauch, H.G. (1948). Rate of leaf elongation as affected by the intensity of the total soil moisture stress. Pl. Physiol., 23. 485-495

Walker, H.O. (1962). Weather and climate. Agriculture and Land Use in Ghana. (ed. by J.B. Wills) pp. 7-50, Oxford University Press. London

Wardlaw, I.F. (1969). The effect of water stress on translocation in relation to photosynthesis and growth. II. Effect during leaf development in Lolium temulentum. L. Aust. J. biol. Sci. 22. 1-16

Weatherley, P.E.(1950). Studies in the water relations of the cotton plant. I. The field measurement of water deficit in leaves. New Phytol., 49. 81-97

Weatherley, P.E. (1951). Studies in the water relations of the cotton plant. II. Diurnal and seasonal variations in relative turgidity and environmental factors. New Phytol. 50. 36-51

Weatherley, P.E. (1965). Some investigations on the water deficits and transpiration under controlled conditions, In "Water Stress in Plants" (ed. by B. Slavik,) Proc. Symp. Prague, 1963, pp. 63-69 Czech. Acad. Sci. Prague.

Weatherley, P.E. and Slatyer, R.O. (1957). The relationship between relative turgidity and diffusion pressure deficit in leaves. Nature, Lond. 179. 1085-6.

Whiteman, P.C. and Wilson, G.L. (1963). Estimation of diffusion pressure deficit by correlation with relative turgidity and beta radiation absorption. Aust. J. biol. Sci. 16. 140-6

Williams, R.F. (1946). The physiology of plant growth with special reference to the concept of net assimilation rate. Ann. Bot. 10. 41-72

Wills, J.B. (1962). The general pattern of land use. In "Agriculture and land use in Ghana" (ed. by J.B. Wills) publ. for the Ghana Ministry of Food and Agriculture, Oxford University Press. London.

Wormer, J.M. (1965). The effect of soil moisture, nitrogen fertilization and some meteorological factors on stomatal aperture of Coffea arabica L. Ann. Bot., N.S. 29. 523-539

Wormer, T.M. and Ochs, R. (1959). Soil moisture, opening of the stomata and transpiration of oil palm and groundnuts. Oleagineux 14. 571-580.

Yanney-Wilson, J. (1963). Leaf anatomy in relation to drought resistance in some shrubs of the Accra Plains, Ghana. J. Sci. 3. 28-34.

Yemm, F.W. and Willis, A.J. (1954). Stomatal movements and changes of carbohydrates in leaves of Chrysanthemum maximum. New Phytol., 53. 373-396

Zahner, R. (1968). Water Deficits and Growth of Trees. In ' Water deficits and plant growth' (Ed. by T.T. Kozlowski) Academic Press Inc. New York. Vol. 2 pp 191-244.