Seedling Growth and Transpiration of Two West African Mahogany Species in Relation to Water Stress in the Root Medium

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SEEDLING GROWTH AND TRANSPIRATION OF TWO WEST AFRICAN MAHOGANY SPECIES IN RELATION TO WATER STRESS IN THE ROOT MEDIUM

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INTRODUCTION

A sizable body of information now exists on the general and descriptive ecology of West African vegetation, but relatively few experimental investigations have been made on the causal relationships between plant distribution and environmental factors. The physiognomic difference between forest and savanna is perhaps the most distinctive feature of this vegetation, yet, although it is known (see, for example, Adejuwon 1971) that environmental moisture is a key factor controlling this difference, comparative studies in the water relations of forest and savanna species of the region are generally lacking. Because savanna, which is drier than forest, is dominated by readily combustible grass and, as a consequence, most savanna is burnt annually (Keay 1959; Hopkins 1965), the majority of relevant studies (see Ramsay & Rose-Innes 1963) emphasize the importance of adaptation against fire as the main differentiating feature between forest and savanna species. The possibility that these species may also show differing responses to water stress is generally played down and only rarely (e.g. Jeník & Hall 1966; Adejuwon 1971) is the selective importance of primary environmental factors stressed.

The object of the work reported here has been to ascertain whether two West African tree species, *Khaya ivorensis* A. Chev., which grows naturally in forest, and *K. senegalensis* (Desv.) A. Juss., a savanna species, differ in their response to drought in a way consistent with their distribution.

K. ivorensis is an evergreen tree, growing up to 60 m in height and 4·5 m in girth; it occurs throughout the high forest zone of West Africa, commonly on rich, well-drained, alluvial soil. By contrast, *K. senegalensis* sheds its leaves early in the dry season, often replacing them long before the early rains begin; it is a small tree frequently less than 30 m tall and 3 m in girth, and is distributed in both the Guinea and Sudan zones of the savanna region. Particularly in the Sudan zone, *K. senegalensis* occurs commonly in low-lying places beside streams, but may also be found in savanna woodland on rocky outcrops (Keay 1959).

The genus *Khaya* provides the African mahoganies of commerce, and is similar to many other West African tree genera in being represented by species that are confined to habitats contrasted primarily by their water relations (see Richards 1952, p. 340; Keay, Onochie & Stanfield 1960, 1964). A study of the water relations of West African mahoganies should therefore be of both economic and ecological interest.

This paper describes growth and transpiration of seedlings in relation to moisture stress in the root medium. The experiments reported were carried out mostly with laboratory-grown material and in this sense represent essentially the first steps towards a

study of the more complex field situation. Because the two species were compared under similar environmental conditions, it was hoped that differences found could still be of value in predicting ecological behaviour (see Jarvis 1963; Grime 1965).

Seedlings used for the experiments were raised from seed supplied by the Forest Products Research Institute, Kumasi, Ghana, supplemented (for *K. senegalensis*) by collections from the grounds of the University at Legon.

METHODS
Growth experiments

Growth response to moisture stress in the root medium was first studied with seedlings grown on soil as the more natural environment. Because of uncertainties about the exact stress experienced at the soil:root interface when soil is the rooting medium (Slatyer 1967), the experiment was later repeated with seedlings grown in aerated culture solution to which an osmotic substrate was added as desired to vary stress experienced at the root surface (cf. Lagerweff, Ogata & Eagle 1961; Jarvis & Jarvis 1965; Lawlor 1970).
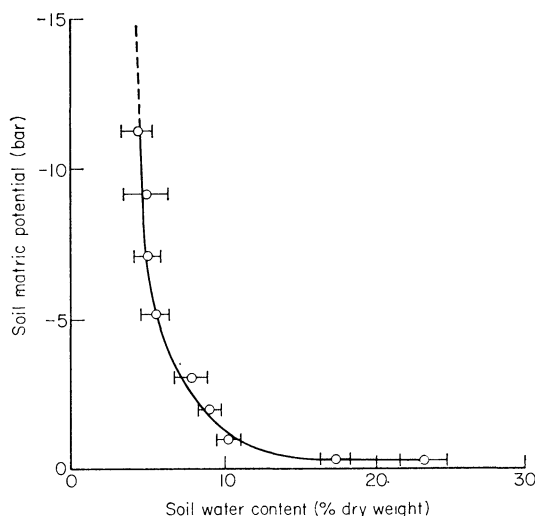

FIG. 1. The moisture characteristic of the soil used experimentally (John Innes potting compost no. 2). Determinations were made by pressure plate apparatus. Because of technical failure in the apparatus determinations were made only to −11·0 bar; extension of the curve beyond this point (pecked line) is by eye. Horizontal bars indicate standard error for mean of fifteen samples.

Growth in relation to soil water potential

Seedlings that were about 1 month old and 9–14 cm tall, with two to five leaves, were transplanted singly on to soil (John Innes potting compost no. 2) of known moisture characteristic (see Fig. 1). The soil was held in 12-cm-diameter plastic containers (capacity *c.* 1 litre) provided with adequate basal drainage holes. Each container was filled with soil to about 2 cm below the rim so that, together with thoroughly wetted soil, it weighed 1·4–1·5 kg after draining for 24 h. The soil in this condition was accepted as being at field capacity. The seedlings were allowed to grow on well-watered soil for 4 weeks during which they became well established and their roots thoroughly permeated the

soil mass. The seedlings of each species were then sorted into five matched groups of eight each, matching being based on height and leaf number. One group of plants of each species was harvested immediately and processed in the usual way (see, for example, Okali 1971) for determination of leaf area and dry weights. The resulting data were used to establish relationships between length × breadth and planimetered area of leaves, and between leaf area and total seedling dry weight. The latter relationship was in turn used to calculate initial dry weights of the unharvested seedlings of known leaf area.

The remaining groups of plants of each species were then assigned randomly, each to one of four soil moisture regimes (A, B, C and D) controlled by pot weighing. In treatment A the pot weight was maintained, by daily addition of water, close to a level corresponding to about −0·3 bar soil matric potential. In treatments B, C and D, the soil initially at field capacity (see above) was allowed to dry out respectively to 75, 50 and 25% of its initial weight before re-wetting to the field capacity weight, to give soil matric potentials of about −0·4, −0·8 and −4·5 bar at the drying limits. In this way, plants in treatment B received overall approximately 24 (*Khaya ivorensis*) or 26 (*K. senegalensis*) drying cycles, while plants in treatments C and D received 12 and 6 cycles respectively over a growth interval of 9 weeks (13 November 1970 to 12 January 1971).

Growth in relation to solution osmotic potential

Three-week-old seedlings raised on vermiculite were transferred to aerated, half-strength, Arnon and Hoagland solution (Hewitt 1966) held in large plastic containers in which they were allowed to grow for 4 weeks to be preconditioned. The seedlings were then matched according to size before transfer to the final experimental pots (13-cm-diameter plastic buckets; capacity *c*. 1·1 litres; blackened to minimize algal growth) such that there were six seedlings, three of each species, per pot. Each experimental pot held 700 ml also of aerated, half-strength, Arnon and Hoagland solution and the seedlings were allowed to grow for a further period of 2 weeks before use, so that any root damage caused by the transplanting operation could heal. Lawlor (1970) has shown that uptake by roots of polyethylene glycol, which was to be used as osmotic substrate (see below), is minimized if roots are undamaged.

At the beginning of the experiment, about ten seedlings of each species were harvested and processed as described above for the soil experiment, to obtain data from which initial dry weights of the unharvested seedlings could be estimated. The remaining plants were grown at four levels of solution osmotic potential (I, II, III and IV). Treatment I (control) consisted of nutrient solution alone (osmotic potential *c*. −0·3 bar as calculated from data in Table 30A of Hewitt (1966)). Treatments II, III and IV consisted respectively of culture solution to which polyethylene glycol 4000 (pure grade, Koch–Light Laboratories) was added at the rate of 100, 150 and 256 g/l of solution, to give osmotic potentials of approximately −2·8, −5·3 and −10·3 bar. These values were derived from the curve given by Lawlor (1970, Fig. 1) relating osmotic potential to concentration of polyethylene glycol 4000, and are corrected for the osmotic potential of culture solution alone. This method is clearly inadequate, but because of peculiarities in behaviour of polyethylene glycols (see Lagerweff *et al*. 1961) osmotic potentials of the solutions could not be derived indirectly from their colligative properties and facilities were not immediately available for direct measurements to be made. The limitation is perhaps not serious for the comparisons made here, especially as the experimental species were grown together in the same containers in each treatment.

There were two containers per treatment. The volume of solution in each was main-

tained at 700 ml by daily addition of distilled water to replace transpiration loss. The solutions were renewed twice, at intervals of 7 and 10 days over an experimental period of 21 days (12 July to 2 August 1971).

Experimental conditions

Both experiments were carried out on a centre bench of a glasshouse where thermo-hygrographs were installed to record temperature and relative humidity. Average air temperature in the glasshouse over the experimental periods was 26–28° C at 09.00 hours and 30–33° C at 15.00 hours GMT; relative humidity fluctuated between night-time maximum values of 90–98% and daytime minima of 50–60%. The higher values of temperature and lower limits of relative humidity apply to the period of the soil experiment which was within the Harmattan season in southern Ghana (Walker 1962). General lighting in the glasshouse, as determined by periodic comparisons with two matched photometers (EEL Lightmaster Model 18), was about 40% of that outside. The roof of the glasshouse had been fairly heavily shaded to reduce mid-day temperatures.

To minimize positional effects the plant pots were frequently re-allocated on the experimental bench during each experiment.

Growth analysis

In both experiments, height and leaf area of the seedlings were recorded at the beginning and at frequent intervals throughout the growth period. At final harvest, the seedlings were separated into root, stem and leaf fractions before determination of dry weights. The relation between length × breadth and planimetered area of leaf was re-determined for each treatment class and used for estimation of final leaf area. The total dry weight (W) and leaf area (A) data were then used to calculate relative growth rate (RGR), net assimilation rate (NAR) and mean leaf-area ratio (MLAR) according to the equations used by Okali (1971). Since the validity of the equations referred to above for deriving NAR and MLAR depends on the relationship between W and A over the growth period (see Coombe 1960), and this relationship could not be known from the two harvests taken, the values for these parameters are only approximate.

Allocation of dry matter between the main organs—root, stem and leaf—at final harvest was assessed by calculating ratios of dry weights of these organs to total plant weight.

Transpiration experiments

Transpiration response was studied with plants grown also on soil and in culture solution for reasons already given (p. 422). The pot-weighing technique was adopted in both cases and the experiments were run in the same glasshouse as for the growth studies. Piché evaporimeters supplied with 3-cm-diameter, green, blotting-paper discs were additionally used to record evaporation during experimental periods. Leaf areas of the plants used in both experiments were measured so that transpiration could be expressed on unit leaf area basis.

Transpiration in relation to soil water potential

In these experiments, the daily march of transpiration was followed on 6 days, between 4 and 12 February 1971. Seedlings growing normally on well-watered soil were subjected to varying soil moisture regimes on days of measurement. Soil moisture conditions were varied and controlled as for the growth study so that there were four

treatments—A, B, C and D—with the letters denoting the same moisture regimes as before. The seedlings used were from the same stock as for the study of growth on soil, but were by the time of transpiration measurements about 5 months old, although they were still growing singly in 12-cm-diameter plastic pots. On 'experimental' days, each pot was enclosed in a sturdy polyethylene bag, which was securely sealed around the stem with self-adhesive tape to prevent water loss from the soil surface, and two to four seedlings of each species were observed per treatment, except that on some days seedlings in treatments C and D were not represented because the soil had not dried to the prescribed limit. The pots were weighed hourly from 07.00 to 18.00 hours GMT on days of measurement.

Transpiration in relation to solution osmotic potential

In the culture solution experiments, 5-month-old seedlings were also used. These had been maintained for about 4 months in aerated, half-strength, Arnon and Hoagland solution which was periodically renewed. The seedlings were grown in 15-cm-diameter, blackened, plastic buckets holding about 2·5 l of solution. Each bucket was tightly fitted with a lid, through which holes admitted seedlings and an aerator, and each seedling was supported firmly in its hole by two halves of a rubber bung. There were two to three seedlings in each container, except in one case where a seedling of *K. ivorensis* was too large to be accommodated with another plant without serious interference. Four containers of *K. ivorensis* and three of *K. senegalensis* were used. Measurements were made on 26, 27 and 28 October 1971. Immediately before commencement of measurement on each day, the aerator was removed and the resulting hole blocked with a rubber bung, so that the whole container was airtight.

Because there were few plants available for the study, the effects of only two treatments were studied. Moisture stress in the root medium was varied by replacing the culture solution in some containers with nutrient solution to which polyethylene glycol 1000 had been added at the appropriate rate (see Lawlor 1970, Fig. 1), to give an osmotic potential of about −10·3 bar. This was done immediately before measurement was started each day. At least one pot of each species contained nutrient solution to which no polyethylene glycol was added, to serve as control. In order to compare transpiration of seedlings in solution with that of seedlings growing in soil, and as a check on earlier measurements, two soil-rooted plants of each species in pots at field capacity were included for measurement at the same time as the solution experiment.

The experiments were of short duration, lasting only about 4 h in the mornings. This was designed to reduce any effects of lack of aeration, and possible entry of polyethylene glycol into the seedlings (Slatyer 1961). Because of the short duration, weights were recorded at intervals of 30 min so that changes in trend of transpiration could be timed more closely. At the end of each experiment, the polyethylene glycol solution was replaced with culture solution after both roots and containers had been rinsed with distilled water. Aeration was then re-started in readiness for the next measurement.

RESULTS

Growth response

Changes in seedling height and leaf area in the soil and solution experiments are depicted in Figs. 2 and 3 respectively. Seedlings of *Khaya senegalensis* were larger than those of *K. ivorensis*, both at the beginning and at the end of each experiment, pre-
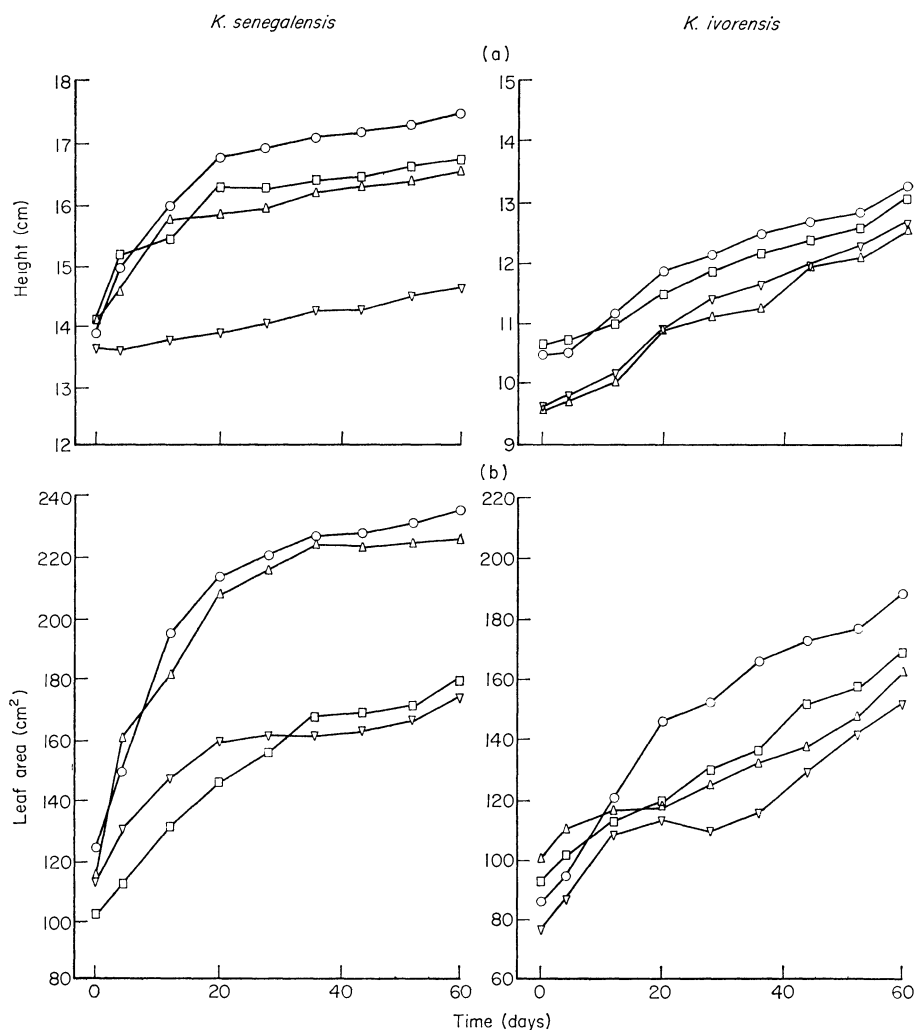
FIG. 2. Changes in height (a) and leaf area (b) of seedlings of *Khaya senegalensis* and *K. ivorensis* grown under varying soil moisture regimes: △, soil maintained near pot capacity (−0·3 bar); ○, □, ▽, soil allowed to dry to −0·4, −0·8 and −4·5 bar respectively before rewetting. Leaf area decrease after day 20 was due to the accidental loss of leaves.

sumably partly as a reflection of the larger seed size of *K. senegalensis*. The mean oven-dry weight of freshly collected seed (without testa) was 157 ± 11 mg for *K. senegalensis* as against 113 ± 10 mg for *K. ivorensis*. Fig. 2 suggests that on soil there were initial rapid increases in height of *K. senegalensis* in all but the driest treatment (D), and in leaf area of both species in some of the wetter treatments. In culture solution (Fig. 3), leaf area expansion alone appeared to be stimulated in both species by the wettest treatment.

The derived growth data for the soil experiment are summarized in Table 1. The growth rates obtained for both species are comparable to values found for other West African forest-tree seedlings (Wadsworth & Lawton 1968; Ampofo 1969); they are, however, lower than some of the values given by Okali (1971) for tree seedlings in full daylight, no doubt partly because of the relatively heavy shade employed in the present study.
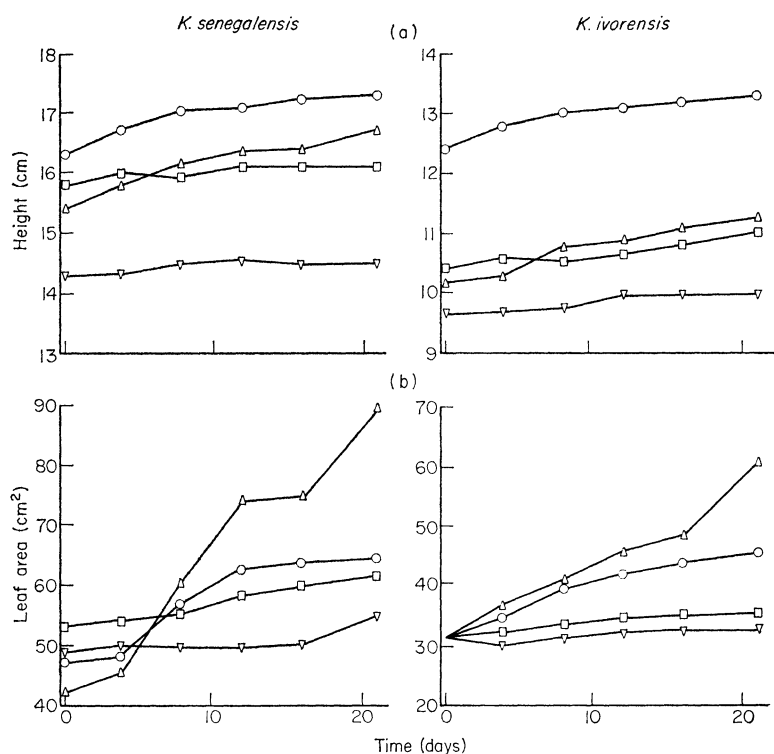
FIG. 3. Changes in height (a) and leaf area (b) of seedlings of *Khaya senegalensis* and *K. ivorensis* grown at various solution osmotic potentials: △, −0·3; ○, −2·8; □, −5·3; ▽, −10·3 bar.

Table 1. *Derived growth data for* Khaya senegalensis (*KS*) *and* K. ivorensis (*KI*) *seedlings, together with standard errors* (*in brackets*), *at various soil moisture regimes*

Growth index	Species	Soil moisture regime			
		A	B	C	D
Relative growth rate (g/g/week)	KS	0·183 (±0·013)	0·179 (±0·012)	0·170 (±0·013)	0·140 (±0·007)
	KI	0·150 (±0·008)	0·189 (±0·008)	0·165 (±0·008)	0·171 (±0·004)
Net assimilation rate (g/m²/week)	KS	22·6 (±2·9)	19·4 (±2·0)	21·9 (±2·7)	15·0 (±1·6)
	KI	11·3 (±0·7)	14·9 (±1·4)	13·3 (±1·1)	13·5 (±0·4)
Mean leaf-area ratio (cm²/g)	KS	103·5 (±1·3)	108·5 (±3·4)	106·1 (±3·0)	107·6 (±2·5)
	KI	154·2 (±2·4)	149·8 (±3·4)	151·7 (±3·6)	148·4 (±2·1)

A, B, C and D denote, respectively, soil maintained at near pot capacity (−0·3 bar), and soil allowed to dry out to matric potentials of −0·4, −0·8, or −4·5 bar before rewetting.

H

These comparisons suggest that, apart from the shade, growing conditions were favourable in this study.

Fig. 4 shows RGR, NAR and MLAR as percentages of the values in treatment A for both species on soil. RGR of *K. senegalensis* decreased with increasing stress, and in treatment D (−4·5 bar) was significantly reduced to 77% of its value in treatment A (−0·3 bar). By contrast, RGR of *K. ivorensis* was not significantly affected by the treatments, although the rate in the wettest treatment tended to be lower than that in any other treatment. The latter response suggests that *K. ivorensis* may be less tolerant of wet soil, with its concomitant poor aeration (cf. Kramer 1956; Mees & Weatherley 1957), than *K. senegalensis*.
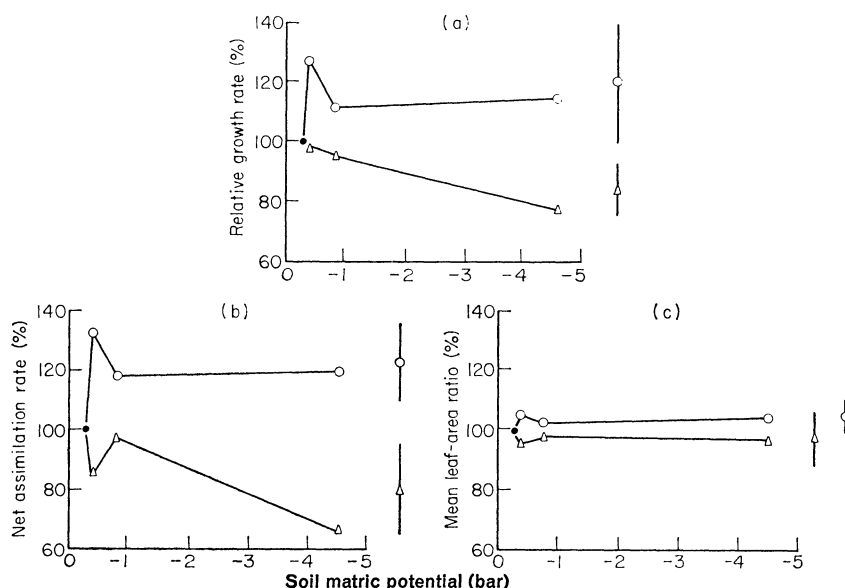

FIG. 4. (a) Relative growth rate, (b) net assimilation rate and (c) mean leaf-area ratio for seedlings of *Khaya senegalensis* (△) and *K. ivorensis* (○) in relation to soil moisture regime, expressed as percentages of the values for the wettest treatment. Vertical lines indicate least significant difference ($P = 0.05$).

Fig. 4 also suggests that the changes in RGR, for both species, were due mainly to the response of NAR, MLAR being little affected by the treatments.

The derived growth data for seedlings grown in culture solution are given in Table 2, and in Fig. 5 RGR, NAR and MLAR are again shown as percentages of the values in the control treatment. For *K. senegalensis*, maximum growth rates were higher in solution than on soil as has been found when comparison is made between soil-grown and solution-grown plants (see Jarvis & Jarvis 1964). The advantage of growing in solution was, however, not observed for *K. ivorensis*, although both species were grown in the same containers to ensure equal aeration. It is possible that the level of aeration practised while adequate for *K. senegalensis* was not for *K. ivorensis* if, as suggested earlier, the latter species is more sensitive to sub-optimal aeration.

Relative growth rate decreased steadily for both species with increasing moisture stress. Negative rates of growth were, in fact, recorded for some seedlings of *K. ivorensis* in treatments III and IV. The most notable result, however, was the apparent reversal of

Table 2. *Derived growth data for* Khaya senegalensis *(KS) and* K. ivorensis *(KI) seedlings, together with standard errors (in brackets), at various solution osmotic potentials*

| Growth index	Species	Solution osmotic potential			
		I −0·3 bar	II −2·8 bar	III −5·3 bar	IV −10·3 bar
Relative growth rate (g/g/week)	KS	0·310 (±0·016)	0·212 (±0·016)	0·163 (±0·014)	0·083 (±0·021)
	KI	0·184 (±0·024)	0·134 (±0·027)	0·025 (±0·022)	0·045 (±0·036)
Net assimilation rate (g/m²/week)	KS	29·2 (±1·7)	23·5 (±3·2)	16·8 (±1·8)	9·1 (±2·3)
	KI	11·3 (±1·9)	9·3 (±2·0)	1·8 (±0·2)	3·3 (±1·6)
Mean leaf-area ratio (cm²/g)	KS	107·8 (±1·4)	100·9 (±2·8)	100·9 (±2·9)	106·6 (±3·3)
	KI	157·7 (±7·7)	151·0 (±3·1)	159·9 (±5·3)	157·5 (±9·9)
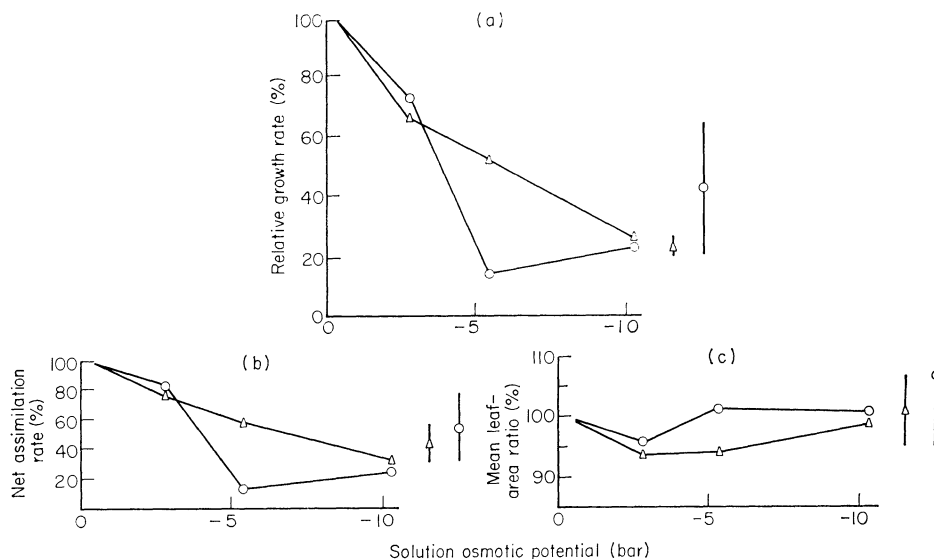
Fig. 5. (a) Relative growth rate, (b) net assimilation rate and (c) mean leaf-area ratio for seedlings of *Khaya senegalensis* (△) and *K. ivorensis* (○) in relation to osmotic potential of the root medium, expressed as percentages of the values for the highest potential (−0·3 bar). Vertical lines indicate least significant difference (*P* = 0·05).

order of sensitivity of the species as stress increased from a low value (Fig. 5). Decrease of water potential to -2.8 bar caused a significant reduction in growth rate of *K. senegalensis* to 68% of its value at -0.3 bar, while growth rate of *K. ivorensis* appeared not to be affected over this range (see Table 2). However, at -5.3 bar, RGR of *K. ivorensis* fell significantly to 14%, while that of *K. senegalensis* was still 53% of the rate in the control treatment. The slight increase in growth rate of *K. ivorensis*, indicated for the severest treatment (-10.3 bar), is more apparent than real and probably results from error. It is accounted for by one large value (0.149 g/g/week) out of six in the sample, without which RGR for *K. ivorensis* under this treatment would be 0.024 g/g/week or 13% of the rate in treatment I, as against 27% for *K. senegalensis*. Fig. 5 also shows that, as in the soil experiment, variation in RGR was in both species due mainly to changes in NAR. In neither experiment was MLAR (Tables 1 and 2) or the pattern of allocation of dry matter between the organs significantly and consistently altered by the treatments. Hence, in Table 3 are given the organ ratios at final harvest of each experiment, averaged over the four treatments, mainly to show that leaf-area ratio (LAR) and leaf-weight ratio (LWR) were consistently higher for *K. ivorensis* than for *K. senegalensis*, while the reverse was true for root-weight ratio (RWR). Stem-weight ratio (SWR) did not vary between the species. The possible significance of these morphogenetic differences is discussed below.

Table 3. *Leaf-area ratio (LAR), and dry-matter allocation to leaf (leaf-weight ratio, LWR), stem (stem-weight ratio SWR) and root (root-weight ratio, RWR) at final harvest, together with standard errors, for* Khaya senegalensis *(KS) and* K. ivorensis *(KI) seedlings grown on soil or in solution*

Organ ratio	Species	Soil expt	Solution expt
LAR	KS	61·7 ± 7·1	91·3 ± 4·9
	KI	90·2 ± 6·2	160·2 ± 13·4
LWR	KS	29·4 ± 1·8	41·8 ± 1·5
	KI	38·2 ± 2·1	50·7 ± 1·7
SWR	KS	24·9 ± 1·0	26·8 ± 1·5
	KI	25·1 ± 1·2	27·6 ± 1·8
RWR	KS	45·6 ± 1·5	31·4 ± 2·5
	KI	36·7 ± 3·4	21·6 ± 2·0

Transpiration response

Transpiration in relation to soil water potential

Examples of the daily march of transpiration of plants rooted in soil are given in Fig. 6, along with records of hourly evaporation for the experimental periods. The diurnal patterns displayed—high transpiration rates more or less coinciding with periods of high evaporation—are typical of results for this kind of study (e.g. Weatherley 1951) and require no special comment. It was not practicable to study plants in all treatments, and of both species, on every day of measurement. Table 4 summarizes data for mean daily transpiration from a variable number of observations for each treatment and species. The highest hourly rates recorded throughout the measurements were as follows.

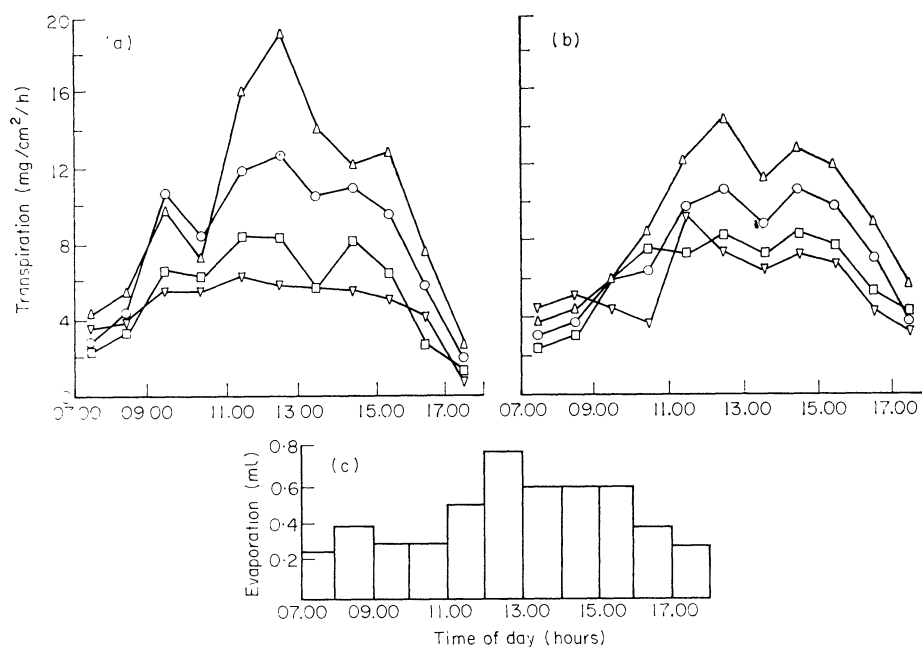|	Transpiration (mg/cm^2/h)			
Treatment:	A	B	C	D
K. senegalensis	21·8	21·5	15·6	6·7
K. ivorensis	18·1	16·0	13·3	9·5

FIG. 6. Transpiration of seedlings of (a) *Khaya senegalensis* and (b) *K. ivorensis* in relation to soil moisture stress: △, −0·3; ○, −0·4; □, −0·8; ▽, −4·5 bar: together with (c) data for hourly evaporation on 12 February 1971.

These data indicate that in both species transpiration decreased with increasing moisture stress. Transpiration was generally higher in *K. senegalensis* than in *K. ivorensis* when soil moisture was readily available (treatments A and B) but in the driest treatment (D), transpiration of *K. ivorensis* exceeded that of *K. senegalensis*. When rates measured on the same days were compared, transpiration in treatment D (−4·5 bar) was found to be reduced, on the average, to 27·5% of that in treatment A (−0·3 bar) for *K. senegalensis*; the corresponding reduction for *K. ivorensis* was to 45·5%, suggesting a more effective control of water loss by *K. senegalensis* when stress was appreciable.

Table 4. *Mean daily transpiration (as % evaporation), with standard errors, for seedlings of* Khaya senegalensis *and* K. ivorensis *in relation to varying soil moisture regimes*

| | Soil moisture regime (matric potential) | | | |
	A −0·3 bar	B −0·4 bar	C −0·8 bar	D −4·5 bar
K. senegalensis				
No. of observations	12	7	7	6
Transpiration (% evaporation)	17·4±1·0	15·7±1·8	10·9±1·0	5·4±1·3
K. ivorensis				
No. of observations	12	8	6	5
Transpiration (% evaporation)	14·3±0·6	11·8±0·5	11·0±1·3	7·7±0·7

To examine how far these transpiration responses could be explained by stomata behaviour, permeability of leaves of seedlings, similar in age and size to the experimental plants, was later briefly compared by an infiltration method. An infiltration series prepared from commercial kerosene and liquid paraffin (cf. Alvim & Havis 1954) was used. Infiltration was scored on a scale ranging from 1 to 14 such that increasing scores indicated penetration by mixtures of increasing viscosity, and hence wider stomatal opening. Plants subjected to the same moisture treatments as in the transpiration (and growth) studies were used, and observations were made on the abaxial surfaces of mature leaflets which were at comparable positions on the plant axis.
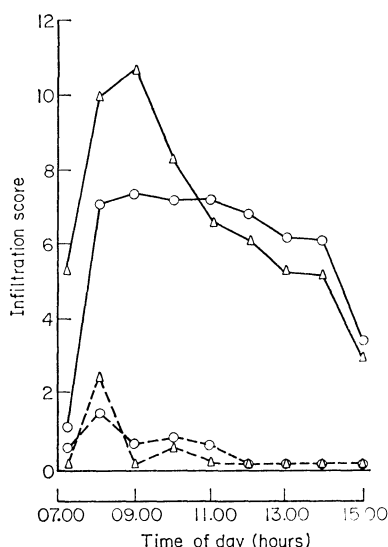

FIG. 7. Diurnal changes in permeability of leaves of seedlings of *Khaya senegalensis* (△) and *K. ivorensis* (○), in relation to soil moisture regime. ———, Treatment A, wet soil, *c.* −0·3 bar matric potential; − − −, treatment D, dry soil, *c.* −4·5 bar. Increasing infiltration scores indicate higher permeability and hence wider stomatal opening. Data for 3 June 1971.

The diurnal variation in leaf permeability was followed on four separate days, when pots in the drier treatments were at their drying limits. Similar results were obtained on each of these days; those for one day (3 June 1971), and for the extreme moisture treatments (A and D) only, are illustrated in Fig. 7. For seedlings in treatment A the results suggest wider stomatal opening, in the early hours of the day, for *K. senegalensis* which may partly explain the higher transpiration rate of this species when compared with *K. ivorensis*, although the difference between the two species later in the day was small. The leaf permeability was markedly reduced in both species by treatment D, suggesting that increased stomatal resistance most likely contributed to cause the low transpiration rate of plants under this treatment (Fig. 6). However, no striking difference in stomatal conductivity was found, to account for the difference in transpiration rates of the two species in treatment D, possibly because the technique employed was not sufficiently sensitive to do so.

Transpiration in relation to solution osmotic potential

Transpiration of plants grown in culture solution is shown in Fig. 8, along with data
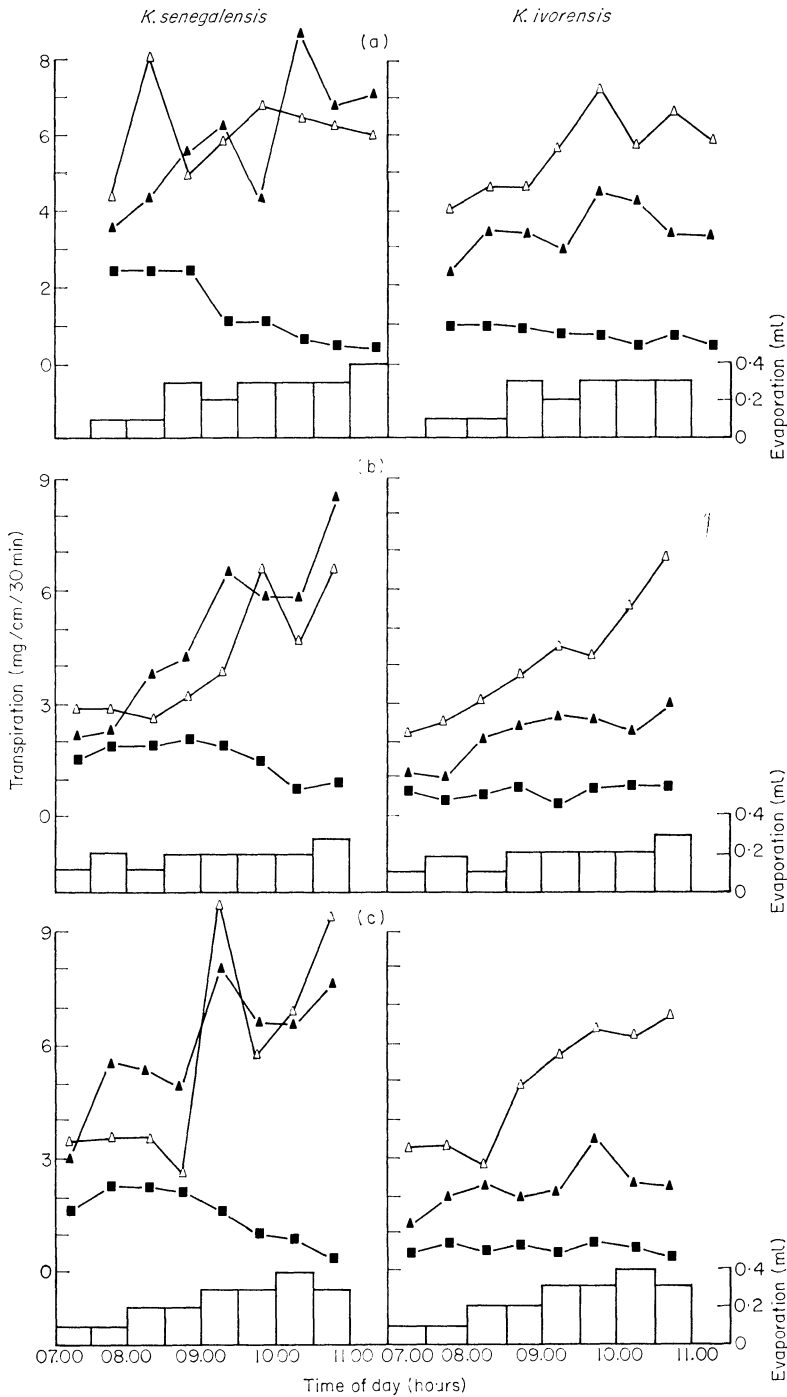
FIG. 8. Transpiration of seedlings of *Khaya senegalensis* (left) and *K. ivorensis* (right) in relation to moisture stress in the root medium, and on three days: (a) 25 October 1971; (b) 26 October 1971; (c) 27 October 1971. △, −0·3 bar soil matric potential; ▲, −0·3 and ■, −10·3 bar solution osmotic potential. Histograms, evaporation in ml.

for soil-grown plants compared at the same time on the three days of observation. Evaporation data for the experimental periods are also given.

For both species, transpiration rates for seedlings growing in soil here are comparable to data presented earlier for seedlings at similar soil moisture status (cf. data for treatment A in Fig. 6). Also, transpiration of seedlings of *K. senegalensis* at −0·3 bar solution osmotic potential closely paralleled that of soil-grown plants, suggesting that for this species the effects on transpiration of growing on soil or in solution were the same. For *K. ivorensis*, however, transpiration of plants in solution was consistently lower than that of soil-grown plants. Sensitivity of *K. ivorensis* to poor aeration has been pointed out earlier. The low transpiration rate found here for plants in solution probably reflects the fact that aeration was discontinued during measurements. Since the same treatment was applied also to *K. senegalensis*, yet transpiration of this species was apparently not impaired, the observation reinforces the suggestion that *K. ivorensis* is less tolerant of poor aeration than *K. senegalensis*.

Transpiration of both species was markedly lowered when osmotic potential of the root medium was reduced by addition of polyethylene glycol. In *K. senegalensis*, while plants in nutrient solution alone attained a maximum rate of water loss amounting to 17·6 mg/cm^2/h, the maximum rate observed on any day of measurement for plants in polyethylene glycol solution corresponds to 5·0 mg/cm^2/h. Transpiration rate of seedlings in the latter treatment remained more or less steady for the first 1–2 h after exposure to polyethylene glycol but declined steadily thereafter, whereas transpiration of plants in nutrient solution alone generally increased over the entire period of measurement. If the three days of measurement are taken together, the mean rates observed at 11.00 hours, that is, 4 h after the start of measurement, amount to 14·0 and 1·2 mg/cm^2/h respectively for plants at −0·3 and −10·3 bar solution osmotic potential.

In *K. ivorensis*, a maximum rate of about 9·2 mg/cm^2/h was attained by plants in nutrient solution alone, as against 2·4 mg/cm^2/h for plants in polyethylene glycol solution. Transpiration rate of seedlings at the higher water potential increased, though less markedly than in *K. senegalensis*, over each experimental period, while the rate for plants at the lower water potential remained more or less steady throughout the measurement period. The mean rates at 11.00 hours were 6·0 and 1·2 mg/cm^2/h respectively for the two treatments.

Because poor aeration may have influenced transpiration of *K. ivorensis* (see above), it is not valid to compare directly transpiration of both species in solution. However, the relative effects of reducing water potential in the root medium may still be compared for the two species. If the mean rates 4 h after the beginning of measurements are taken as the basis for comparison, it can be readily seen that decreasing the water potential of the root medium to −10·3 bar caused the transpiration rate of *K. senegalensis* to be reduced to less than 10% of its value at −0·3 bar. The corresponding reduction for *K. ivorensis* was to about 20%. Since this is the same order of sensitivity as found for plants grown on soil, the observation strengthens the view that, in response to stress, transpiration is more effectively checked by *K. senegalensis* than by *K. ivorensis*.

DISCUSSION

Water stress to which roots in solution are exposed comprises solely an osmotic component, whereas stress experienced by roots growing in non-saline soils, as in the present study, is normally dominated by the matric component of water potential. Evidence

that osmotic and matric potentials may have similar effects on plant physiological processes is given by Wadleigh & Ayers (1945), Richards & Wadleigh (1952), Jarvis & Jarvis (1963c) and by McWilliam & Phillips (1971), but Slatyer (1961, 1967) has stressed that this can be so only where solute entry into the plant is effectively excluded. In the culture solution experiments reported above, this condition was probably satisfied by the use of polyethylene glycol as osmotic substrate, the short duration of some experiments, and by the precautions taken in prolonged experiments to ensure that any roots damaged during transfer operations healed before exposure to polyethylene glycol. In the growth experiments, although wilting frequently occurred in many of the seedlings in treatment IV ($-10\cdot3$ bar) and occasionally in *Khaya ivorensis* seedlings in treatment III ($-5\cdot3$ bar), there was no loss of leaves or other symptoms of absorption or toxicity of polyethylene glycol of the types described for cotton by Lawlor (1970). Hence the results of the soil and solution experiments may be taken together in evaluating the response of the species to a wide range of moisture stress in the root environment.

The results presented indicate a trend of difference, in response to water stress, consistent with the contrast in distribution of the species studied. Growth rate and transpiration of both species were reduced by increasing water stress in the root medium, as is well documented for many other plants (Stocker 1960). The notable result was the observation that relatively moderate stress ($-0\cdot3$ to $-4\cdot5$ bar in soil, or $-0\cdot3$ to $-2\cdot8$ bar in solution) depressed growth rate more in *K. senegalensis*, the savanna species, than in *K. ivorensis*, the forest example; only when stress became more severe (in solution) was the superiority in drought resistance of the savanna plant revealed. The apparent discrepancy between soil and solution in the upper limit of stress at which growth reduction becomes significant for *K. senegalensis* can probably be explained by the inadequacy of the pot-weighing technique for characterizing soil moisture stress. The reversal in sensitivity of the species, coupled with the finding that the growth responses were brought about mainly through changes in net assimilation rate, permits the difference between the species to be understood, at least provisionally, in terms of factors affecting rate of assimilation in leaves. The main effect of applying water stress to the roots was apparently to reduce growth through reduction of assimilation by leaves.

By means of a series of experiments based on the water relations of tree seedlings, Jarvis & Jarvis (1963a–d) made a thorough analysis of the main ways by which growth differences between plants can arise as a result of moisture stress. Briefly, there are differences between species in the extent to which internal deficits may result from exposure to a given degree of external stress; for plants growing in the same environments, these differences are conferred mainly by properties of the root system which control water absorption, and by leaf features which regulate rate of water loss. Further, in response to a given degree of internal deficit, growth rates may differ between plants to the extent that metabolism is directly affected by stress, and to the extent that stomatal closure which limits CO_2 supply for photosynthesis is caused by the given deficit.

It is not possible with the present data to say how far the species investigated differ generally in drought avoidance but, by combining the results of the growth and transpiration studies, it can reasonably be suggested that the greater growth sensitivity of *K. senegalensis* at moderate stress values resulted mainly from the effects of stomatal closure. Evidence shows that, under stress, transpiration was more effectively checked in *K. senegalensis* than in *K. ivorensis*, and that the decline in transpiration rate of both species at low soil water potential partly reflected stomatal closure. In a subsequent report,

more direct evidence will be given to show that, in response to water loss, stomata close at higher relative water contents in leaves of *K. senegalensis* than in those of *K. ivorensis*. Thus it is possible that *K. senegalensis*, through sensitive stomatal response, is more capable of avoiding the development of internal deficits, but in so doing restricts CO_2 entry for photosynthesis; hence there was greater decline of growth rate of this species when moisture stress was only moderate. However, when stress was made more severe, by reducing water potential in solution to -5.3 or -10.3 bar, the advantage of stomata remaining more widely open in *K. ivorensis* was probably outweighed by the disadvantages for growth of the low tissue water potentials resulting from water loss. Such an effect could partly explain the reversal in growth sensitivity as stress was increased from low to high values; a fuller explanation would have to take account of differences between the species in other aspects of leaf tissue water relations, such as in the relationship between water content and water potential of leaves and in desiccation tolerance of leaf tissue (cf. Jarvis & Jarvis 1963d). Current investigations are examining these aspects.

Although distribution of dry matter between the main organs was not in either species consistently altered by the treatments, there were nevertheless consistent differences between the species in the proportions of dry matter in roots and leaves, which could have ecological significance. For example, to the extent that root mass reflects effective root absorbing-surface area, the greater root-weight ratio of *K. senegalensis* may have supported the higher transpiration rate of this species on wet soil, when compared with *K. ivorensis*. A higher transpiration rate in turn suggests a more rapid rate of soil moisture depletion; hence the observation that in the wettest soil treatment growth of *K. ivorensis*, but not that of *K. senegalensis*, tended to be low might be explained by suggesting that *K. senegalensis* was more able to remove rapidly any excess water that could have caused prolonged waterlogging following each re-wetting operation. However, the further observation that, in similarly aerated solutions, growth and transpiration were more impaired in *K. ivorensis* than in *K. senegalensis* suggests that the latter species may be more tolerant of actual waterlogging. To the extent that these differences in root development and in tolerance of waterlogging are shown by field plants, these findings are in agreement with the field report that *K. senegalensis* often grows on flood-prone banks of water courses in savanna (Irvine 1961), while *K. ivorensis* occurs on soil with good drainage even though this may be in damp areas (Taylor 1960).

Also, in both soil and solution, *K. ivorensis* was found to expend a larger proportion of its dry matter in leaf development, both leaf-area ratio and leaf-weight ratio being consistently higher in this species than in *K. senegalensis*. Particularly in solution, specific leaf area (calculated by dividing LAR by LWR) was greater in *K. ivorensis* than in *K. senegalensis*, meaning that leaves were thinner in the former species. The latter difference was further confirmed from measurements made on thin leaf sections of soil-grown seedlings, which showed mean leaf thickness for *K. ivorensis* to be about 130 μm as against 210 μm for *K. senegalensis*. Most of the difference in leaf thickness was due to a greater amount of palisade tissue in *K. senegalensis* as compared with *K. ivorensis*. The leaf features of *K. ivorensis* correspond to those of a plant adapted to shade and doubtless reflect conditions under the forest canopy where seeds of this species might germinate. By contrast, the leaf features of *K. senegalensis* suggest adaptation to more exposed situations, which together with its greater seedling height at emergence after germination, and its higher net assimilation rate, probably enable *K. senegalensis* to compete more successfully in its open savanna environment.

It is clear from the limited comparisons made above that besides more readily

observable differences which may exist, such as in morphological adaptations against fire, forest and savanna plants may differ in other less obvious physiological ways which may equally contribute to their success in their respective environments, or their exclusion from others. Obviously, without examining many more features of forest and savanna plants, and interaction effects on these features of the main environmental factors which vary between forest and savanna (Hopkins 1965), it would be impossible to say which factor is of primary importance in determining species distribution between these two habitats. Certainly, fire may be of decisive importance, but it is conceivable that the susceptibility of a plant to fire is conditioned by the plant's performance with respect to other factors in its environment. In this connection, and for the particular species under comparison, it is noteworthy that both Keay (1959) and Ramsay & Rose-Innes (1963) do not regard *K. senegalensis* as being particularly fire-tolerant; the latter authors indeed describe it as fire-tender. It is possible then that *K. senegalensis* owes its widespread distribution in savanna less to its ability to survive fires *per se* than to its other adaptations to the savanna environment, possibly including drought resistance.

SUMMARY

Seedling growth and transpiration response to increasing moisture stress in the root medium were compared for two West African mahogany species, *Khaya ivorensis* A. Chev. and *K. senegalensis* (Desv.) A Juss., which grow naturally in forest and savanna respectively, to test whether these species differ in adaptation to drought. Growth of *K. senegalensis* was found to be less adversely affected than that of *K. ivorensis* when stress was high (at water potentials below about $-2 \cdot 8$ bar in osmotica), although sensitivity of the species was in the reverse order at more moderate moisture stress. The growth responses were found to be attributable more to changes in net assimilation rate than to variation in pattern of leaf development and, because transpiration was more readily checked by *K. senegalensis* whenever stress was appreciable, the results were tentatively interpreted in terms of a difference between the species in stomatal sensitivity to water loss.

Differences were found between the species in proportions of dry matter allocated to root and leaves.

The data are discussed in light of the frequent emphasis on fire as the most important factor determining species distribution between forest and savanna habitats.

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