Growth features of *Acacia tortilis* and *Acacia xanthophloea* seedlings and their response to cyclic soil drought stress

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Abstract

Seedlings of *Acacia tortilis* (Forsk) Hyne and *Acacia xanthophloea* Benth. were raised under controlled glass-house conditions. Control plants were watered daily while other treatments involved withholding water for 2, 4 and 6 days with 1-day rehydration to container capacity.

Compared to *A. tortilis*, *A. xanthophloea* seedlings showed higher leaf area, relative growth rates and total dry weight production under adequate water supply conditions. However, with increased water stress, *A. xanthophloea* seedlings could not alter their pattern of carbon allocation, retaining their root : shoot (r : s) ratio of about 0.5. By comparison, *A. tortilis* seedlings shifted carbon allocation to the roots, leading to a r : s ratio of 1.5 in water-stressed seedlings, compared to 0.5 in the control plants.

The ability of *A. tortilis* to reallocate carbon to the roots away from the shoots and to actually increase root growth compared to *A. xanthophloea* was a dehydration postponement strategy that may be important in species survival during drought.

Key words: Acacia, carbon partitioning, growth, soil drought

Résumé

On a fait pousser des plants d'*Acacia tortilis* (Forsk) et d'*Acacia xanthophloea* Benth en serre, dans des conditions bien contrôlées. Les plants de contrôle étaient arrosés chaque jour, alors que les autres traitements consistaient à ne pas arroser pendant 2, 4 et 6 jours puis d'arroser un jour à la limite de capacité du container.

Comparés à *A.tortilis*, les plants d'*A.xanthophloea* avaient une surface foliaire supérieure, un meilleur taux de croissance relative et une plus forte production totale de poids sec lorsque les conditions d'apport d'eau étaient correctes. Cependant, lorsque les conditions d'hydratation devenaient plus stressantes, les plants d'*A.xanthophloea* ne pouvaient pas modifier le schéma de leur répartition de carbone, conservant un rapport racines : pousses (r : p) d'environ 0,5. Par comparaison, les pousses d'*A.tortilis* pouvaient déplacer la répartition de carbone en faveur des racines, aboutissant à un rapport r : p de 1,5 chez les plants soumis à un stress hydrique, comparé au 0,5 relevé chez les plants de contrôle.

La capacité qu'a *A.tortilis* de rediriger le carbone vers les racines au lieu des pousses et d'augmenter ainsi la croissance des racines, par comparaison avec ce qui se passe chez *A. xanthophloea*, est une stratégie destinée à retarder la déshydratation qui peut être importante pour la survie des espèces en période de sécheresse.

Introduction

In East Africa, areas that receive erratic and inadequate rainfall are usually associated with sparse tree growth and are classified as arid and semi-arid lands (ASAL). In Kenya, ASAL constitute about 80% of the total land area (IUCN/ODA, 1995). Water is the single most important limiting factor in these arid ecosystems, hindering growth and survival of plants (Kramer, 1980). Water stress influences a wide variety of morphological and physiological processes such as leaf expansion, stomatal opening, membrane functioning and photosynthetic carbon assimilation and partitioning.

In the last 70 years, most trials on selection of trees for arid and semi-arid lands in Kenya have been on exotic fast-growing species (Millimo, 1989; Oballa *et al.*, 1997). Indigenous species have been neglected because of their slow growth. Currently, exotic species are mainly found

as monoculture, and so are threatened by diseases; hence it is imperative that indigenous species are promoted (Oballa *et al.*, 1997). Members of the genus *Acacia* form a significant proportion of the indigenous xeric species in Kenya. They are quite distinct in the woody vegetation and cover large areas, either in pure stands or mixed with other shrubs and trees (Akech, 1987). The multiple use value and relative drought resistance of members of the genus *Acacia* makes it an important resource in these marginal lands. This study was set up to investigate two indigenous *Acacia* species, namely *A. tortilis* (Forsk) Hyne and *A. xanthophloea* Benth.

Commonly known as the 'umbrella thorn', *A. tortilis* is one of the most distinctive and widespread African *Acacias.* It is a slow-growing dryland species, with deep rooting habits and a spreading umbrella-shaped crown, growing to 4–20 m in height. The foliage is feathery and typically *Acacia*-like (Noad & Birnie, 1989).

Acacia xanthophloea is a tree reaching 25 m or more in height, gregarious in high groundwater areas, besides lakes and rivers from 600 to 2000 m above sea level. It often grows on black cotton soil, which has poor water drainage. In the recent past, its density has increased around the highland areas of Nairobi where it is grown as an ornamental. A good population is also grown in the dry parts of the country for wood (Noad & Birnie, 1989).

Acacia xanthophloea is a fast-growing tree that is widely distributed in dry parts of the country. Although some trees have been found to grow in arid regions, it is not clear yet whether their occurrence in such environments is due to an existing high water table or because they have some sort of drought tolerance mechanism. Recent work has also shown that fast-growing species are much more susceptible to drought than slow-growing species (Lediges, 1974). This makes *A. xanthophloea* an interesting indigenous tree species to study, especially with respect to how it responds to drought stress.

In the past, arid and semi-arid lands in Kenya have been regarded as wasteland. However, there is now a considerable interest in such marginal tropical drylands and efforts are being made for their rehabilitation. Although this has started with the planting of trees, climatic and edaphic factors prevailing in such environments have challenged the process. Of all these factors, drought is the single most important factor limiting tree establishment. For this reason, there has been only limited success in dryland tree establishment so far.

Past attempts to select genotypes for arid lands have been based on identifying the most vigorous (for example, fast-growing) genotypes, and discarding the less vigorous genotypes. Field testing of genotypes is expensive, inaccurate and time-consuming. For this reason, procedures are necessary that will accurately predict superior field performance in juvenile tissues. Studies now reveal that species that are capable of withstanding drought do so either through dehydration tolerance or dehydration postponement (Turner, 1986; Osonubi & Fasehun, 1987; Johnson *et al.*, 1996). Those that tolerate drought have tissues that can withstand prolonged periods without water with minimal damage (Martin *et al.*, 1987). Other species are capable of postponing drought through a number of morphological adaptations such as deep and dense rooting systems (high r : s ratio) or by controlling water loss during the hottest part of the day by stomatal closure. Such plants may also drop their leaves in order to reduce transpiration (Turner, 1986) or orientate their leaves to avoid high heat loads (Grace, 1983), hence reducing excessive water loss. A better understanding of these mechanisms may provide us with a basis for designing more convenient and suitable criteria for selecting seedlings for planting out in marginal arid lands.

The objectives of this study were: (i) to identify some morphological characteristics present in the two indigenous *Acacia* species and examine how they are affected by varying intensities of cyclic water regimes; and (ii) to investigate how these morphological characteristics relate to species performance in terms of growth and species survival under drought.

Materials and methods

In October 1996, seeds of *A. tortilis* (Forsk) Hyne and *A. xanthoploea* Benth. which had been collected in August 1996 from dryland areas of the Eastern Province of Kenya were obtained form the National Seed Centre, Kenya Forestry Research Institute (KEFRI), Muguga, Kenya. To initiate germination, seeds were soaked in water heated up to 90 °C and immediately left to cool overnight before germinating them in Petri dishes. The germinating seeds were incubated at 30 °C for 10 days in soaked cotton wool to allow complete germination in the two species.

Eighty germinated seedlings per species were then transplanted into polyethylene pots, 18 cm high by 11 cm in diameter, which had been previously filled with soil from a dryland site at Karai, 20 km south of KEFRI.

This was to try and simulate as far as possible the soil conditions in the dryland areas. The planted pots were then transferred to a greenhouse bench. To facilitate maximum seedling establishment, the seedlings were watered daily to container capacity. Direct heat and light from the sun were reduced by 70% using a muslin cloth pulled over the glasshouse roof, for a period of 1 month prior to subjecting them to the respective drought treatments.

Light intensity, humidity and temperature within the glasshouse were measured. Light intensity was determined by averaging three daily readings taken at 09.00, 12.00 and 16.00 hours for 4 months, using a light meter (LI-COR Model LI-189). During the entire experimental period, light intensity averaged 1200 μmol m^{-2} s^{-1}. The mean daily minimum and maximum temperatures were 15 °C and 35 °C, respectively. Humidity measurements, as an indicator of evaporative demand within the glasshouse, were also carried out using wet and dry bulb thermometers. The average daily humidity was 56.6%. Soil used for potting had a moisture retention capacity of 55% while the bulk density was 0.70 g cm^{-3}.

Beginning 1 month after subjecting the seedlings to the various watering treatments, three seedlings per species per treatment were randomly selected and harvested. This was repeated every 2 weeks for 3 months. After every harvest, leaf area (LA) was measured using an automatic leaf area meter (AAC-400, Hayashi Denkho, Tokyo, Japan). Roots were recovered by washing off soil using running tap water and soil sieves of 2 mm and 4.5 μm pore sizes. The various plant parts (roots, stems and leaves) were then oven dried at 70 °C for 48 h before determining root dry weight (RDW), stem dry weight (SDW) and leaf dry weight (LDW). The above weights were then used to determine the root : shoot (r : s) ratio, LDW/RDW ratio, total dry weight (TDW) and relative growth rate (RGR). All weight measurements were carried out using an electronic balance (Model and FX-200 A & D Co. Ltd, Tokyo, Japan).

The ratio of LA to total root dry weight was determined for the two species. This gave an indication of the balance between transpiration and absorption. Mean relative growth rates were determined by the general growth equation:

$$R = lnW_2 - lnW_1/t_2 - t_1$$

where W_1 = dry wt (g) at time t_1 and W_2 = dry wt (g) at time t_2.

The experiment was a two-way factorial layout (two species × four water regimes with two replications) arranged in four completely randomized blocks. Each block had twenty seedlings per species. In order not to over-stress the seedlings, the treatments were: control (daily watering), 2-, 4- and 6-day drought cycles. During drought, water was withheld, while rewatering was done to container capacity at the end of every drought cycle.

Statistical differences between treatments in LA, LDW, RDW and r : s ratio were tested for each harvest using Tukey's procedure (HSD) at 0.05 significance level (Steel *et al.*, 1997).

Results

Growth rate and total dry weight accumulation

Water stress treatments caused large differences in growth rate, leading to significant differences ($P < 0.05$) in dry matter accumulated after 5 months for both *A. tortilis* and *A. xanthophloea* seedlings (Fig. 1). Mean total dry weight accumulated by individual seedlings of *A. tortilis* after 4 months of growth were 4.20, 3.50, 1.86 and 1.84 g for treatments 1, 2, 3 and 4, respectively (Fig. 1). Under similar conditions, individual seedlings of *A. xanthophloea* accumulated mean total dry weight (TDW) of 5.42, 3.66, 2.27 and 1.84 g for treatments 1, 2, 3 and 4, respectively (Fig. 1). Under sufficient water supply conditions, *A. xanthophloea* had a higher rate of total dry weight accumulation than *A. tortilis* seedlings (Fig. 1). However, seedlings of *A. xanthophloea* experienced greater decline in TDW when subjected to water stress compared to *A. tortilis* seedlings (Fig. 2).

Two-day repetitive water stress did not show any significant effect on the seedlings of *A. tortilis*, but increasing stress to a 4-day cyclic drought had a significant effect on TDW for both species. Six-day repetitive drought did not show any significant difference in TDW accumulation from the 4-day drought.

Mean relative growth rate (R) was reduced from 0.4 mg day^{-1} in the controls to about half (0.19 mg day^{-1}) in stressed seedlings of *A. tortilis*. In *A. xanthophloea*, mean growth rate was reduced by about 33% in the 2-day drought cycle, 58% in the 4-day drought and about 66% in 6-day drought seedlings compared to their controls, which had an R of 0.57 mg day^{-1}.

(a)

A. tortilis

(b)

A. xanthophloea

Control   o— — —o 2 - day stress

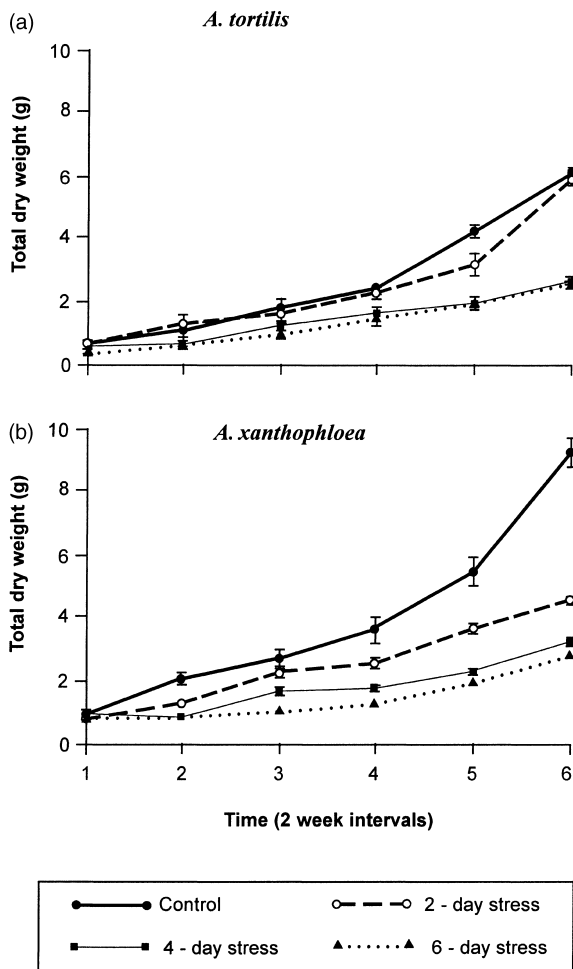■———■ 4 - day stress   ▲·······▲ 6 - day stress

Fig 1 Mean total dry weight (g) accumulation in seedlings of *A. tortilis* (a) and *A. xanthophloea* (b) grown under different levels of water stress, after 3 months of growth. Vertical bars are ±SE of the means

Total leaf area and leaf morphology

The pattern of development of total leaf area (LA) over time was similar to that of the total dry matter (Fig. 3). After 4 months of growth, LA in *A. tortilis* seedlings was 44.3, 33.9, 16.0 and 12.7 cm^2 for treatments 1, 2, 3 and 4, respectively. LA accumulated by *A. xanthophloea* after the same period of growth, under similar drought treatments, was 56.17, 38.13, 28.66 and 23.15 cm^2 for treatments 1, 2, 3 and 4, respectively. Total leaf area was strongly reduced by water stress. Compared with the controls, mild water stress (2-day drought) resulted in a 13% reduction in total leaf area in *A. tortilis* while
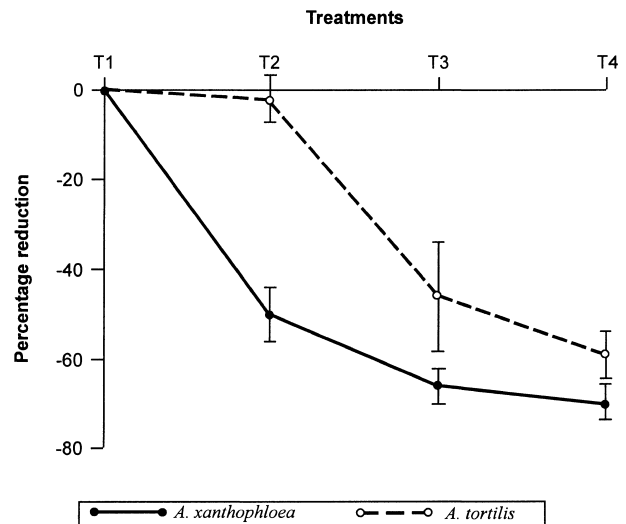
Treatments

A. xanthophloea   o— — —o A. tortilis

Fig 2 Percentage (%) change in dry matter (TDW) production between the controls and the stressed seedlings of *A. tortilis* and *A. xanthophloea* after 3 months of growth. T1 represents the controls, while T2, T3 and T4 represent 2, 4 and 6-day repetitive droughts, respectively. Vertical bars are ±SE of the means

for the same level of water stress, total leaf area was reduced by about 32% in *A. xanthophloea* seedlings.

Four and 6-day repetitive soil drought reduced total leaf area by about 64 and 71%, respectively, in *A. tortilis* and by 33.3 and 60% in *A. xanthophloea*, respectively. There was no significant difference in LA between 4- and 6-day droughted seedlings of *A. tortilis*. However, LA was reduced by about half between 4- and 6-day repetitive stresses in seedlings of *A. xanthophloea*. Individual leaf sizes were also reduced to about half in 6-day stressed seedlings compared to the controls in *A. xanthophloea* while 6-day drought did not show any significant effect on seedlings of *A. tortilis*.

There was no consistency in LA : RDW ratios with regard to treatments in the two species. However, *A. tortilis* had a lower LA : RDW ratio (22.3 cm^2 g^{-1}) than *A. xanthophloea* (42.4 cm^2 g^{-1}) under 4- and 6-day repetitive stress.

Carbon partitioning

Carbon allocation to both root and shoot was also analysed by obtaining a ratio of root dry weight to that of shoot dry weight for all the treatments (Table 1) over the study period. Repetitive 4- and 6-day drought caused a
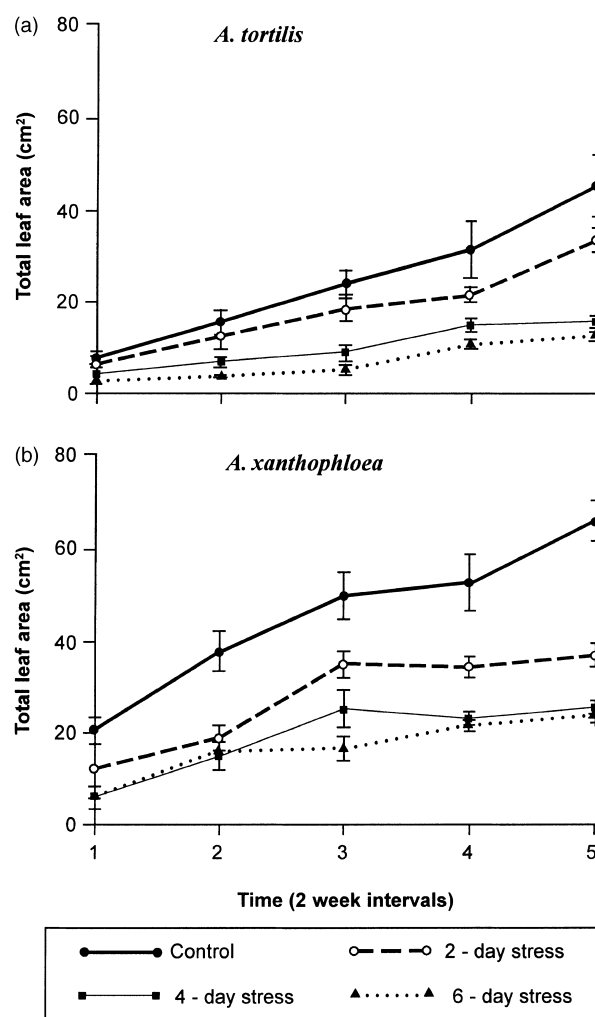
Fig 3 Time course increase in total leaf area (mean LA) of
A. tortilis (a) and *A. xanthophloea* (b) seedlings subjected to
different levels of water stress for 3 months. Vertical bars are
±SE of the means

significant ($P < 0.05$) increase in carbon allocation to the
roots leading to high r : s ratios in stressed compared to
the control seedlings.

After 16 weeks of growth, 6-day drought cycle seed-
lings of *A. tortilis* had an r : s ratio of 1.5 compared to
0.52 observed for the non-water-stressed seedlings. The
high r : s ratio in water-stressed seedlings was largely
due to reduced leaf dry weight. Shoot growth was highly
reduced in *A. tortilis* seedlings that were subjected to
repetitive stress.

Repetitive water stress, however, did not affect carbon
partitioning in *A. xanthophloea* seedlings in which the
r : s ratio was about 0.5 for both repeatedly stressed and
unstressed seedlings, indicating equal partitioning to
both shoot and root. There was a significant increase in
r : s ratio in *A. tortilis* seedlings over time. This was not
observed in *A. xanthophloea*.

Discussion

Repetitive soil drought reduced growth, total dry weight
accumulation and total leaf area in seedlings of both
Acacia species. Under adequate water supply, 5-month-
old seedlings of *A. xanthophloea* showed higher (22%)
total dry weight accumulation and total leaf area than
A. tortilis. In this respect, *A. xanthophloea* appeared to
take better advantage of water availability to increase
biomass accumulation, hence showing greater inherent
abilities to grow faster than *A. tortilis*. Kiplimo (1993)
found that progenies of *A. tortilis* seedlings from humid
environments grew faster under adequate water supply
than those from more xeric habitats but were less tolerant
to water stress. These observations compare favourably
with the response observed for *A. xanthophloea* seedlings,

Table 1 Carbon partitioning to both root and shoot (r : s ratio) in individual seedlings of *A. tortilis* and *A. xanthophloea* grown under four
different cyclic water regimes. Harvests (H*i* = harvest *i*) were made after every 2 weeks. T represents treatment (T*i* = treatment *i*) for every
species. Statistical significance differences ($P = 0.05$) between means as tested by Tukey's multiple range test are indicated by (*)

	Acacia tortilis				*Acacia xanthophloea*			
	T1	T2	T3	T4	T1	T2	T3	T4
H1	0.49	0.40	0.42	0.70	0.29	0.35	0.54	0.40
H2	0.54	0.64	0.79	0.85*	0.45	0.47	0.42	0.48
H3	0.46	0.53	0.56	1.02*	0.62	0.55	0.50	0.62
H4	0.57	0.64	0.79	1.14*	0.57	0.52	0.49	0.48
H5	0.74	0.76	1.04*	1.50*	0.65	0.53	0.60	0.67
H6	0.56	0.62	1.23*	1.50*	0.56	0.52	0.62	0.56

suggesting that the species could be better adapted to grow in mesic environments.

The observed reduction in total leaf area in *A. xanthophloea* as a result of mild water stress, could be attributed to leaf shedding and reduction in leaf size while that of *A. tortilis* was more likely due to reduced leaf emergence and expansion rate. However, further studies are still required to confirm this observation. Reduction in total leaf area as a result of mild water stress, however, did not show any significant effect on total dry weight accumulation in *A. tortilis* seedlings (Fig. 1). This suggests that photosynthetic efficiency of the leaves might not be affected by mild water stress. In this study, leaves of *A. tortilis* appear to be less sensitive to mild water stress compared to *A. xanthophloea*, and therefore, effectively maintained growth rates under mild soil drought than *A. xanthophloea*. The small reduction in LA in *A. tortilis* could be attributed to the species' inherent ability to balance transpirational water loss to available moisture. Although absolute total dry weight accumulation was higher in *A. xanthophloea*, dry matter production per unit leaf area was much higher in *A. tortilis* than *A. xanthophloea*, further suggesting higher photosynthetic capacity and growth potentials in *A. tortilis* under mild water stress.

According to Boyer (1968), leaf growth is one of the first physiological processes to be affected by drought and leaf enlargement is severely inhibited by even small decline in water potential well before photosynthesis and respiration are affected. The reduction in total leaf area observed for the two species could strongly be attributed to soil drought stress. The decline in total leaf area was much higher than in total dry weight accumulation and could mainly be attributed to sensitivity of leaves to water stress than other plant tissues. This resulted in early inhibition of leaf expansion and emergence and also leaf shedding before the stress could be experienced elsewhere, for example, in the roots.

According to Passioura (1976), it is the control of leaf area and leaf morphology that is often the most powerful means a mesophytic plant has for influencing its fate when subjected to long-term water stress in the field. Plants that are adapted to water stress reduce leaf area by accelerating the rate of senescence of physiologically older leaves and leaf shedding (Turner, 1979). With increasing water stress, a large root biomass can provide a large absorptive surface that increases the rate of water uptake (Kozlowski, 1982). Accompanied by reduced leaf area, plant species that shift growth to the roots are better adapted to survive drought (Osonubi & Davies, 1978). This pattern of response was pronounced in *A. tortilis* seedlings in which, as soil drought increased, a large reduction in total leaf area was observed while root biomass increased, leading to reduced LA : RDW (22.4 cm^2 g^{-1}). For *A. xanthophloea*, LA : RDW remained high (42.4 cm^2 g^{-1}) and was apparently not affected by drought stress. The high LA : RDW observed in *A. xanthophloea* is indicative of high transpiration rate and low absorptive capacity, leading to a much lower tissue water potential, limiting physiological processes and growth. *Acacia tortilis*, however, is likely to experience higher tissue water potentials under water stress compared to *A. xanthophloea*, due to low transpiratory leaf surface compared to the large absorptive root biomass. Although *A. xanthophloea* could avoid excessive water loss through leaf shedding, this would mean limited growth under water stress conditions.

In contrast to the slower-growing *A. tortilis*, seedlings of faster-growing *A. xanthophloea* were unable to alter carbon partitioning to both roots and shoots under conditions of limited soil moisture. An increase in r : s ratio as water stress increases is an adaptation for dehydration postponement as it enhances the ability of species to absorb more water from the drying soil (Kozlowski, 1982). Several workers have reported an increase in the ratio of root : shoot in plants subjected to water stress (Lediges, 1974; Osonubi & Davies, 1978; Osonubi & Fasehun, 1987). In some cases, water stress appears to enhance root growth in absolute terms and this could be due to their capacity for osmotic adjustment (Hsiao & Acevedo, 1974). Shoot growth under mild stress may be reduced as a result of decrease in shoot turgor, but stomata may remain open so that photosynthesis continues.

The increased supply of assimilates made available by the reduced strength of the sink in the shoot, then permits osmotic adjustment and extra growth and thus constitutes an adaptive mechanism in that more water will become available to the plant (Osonubi & Davies, 1978). The results obtained in *A. tortilis* compare well with those obtained by Osonubi & Fasehun (1987) on *Parkia biglobosa*. It can be argued that the observed large root dry weight in *A. tortilis* in comparison to the shoot as a result of stress could be due to large sink for assimilates created at the roots as a result of osmotic adjustment. The fact that shoot growth almost ceased at the expense of root growth in 4- and 6-day stressed seedlings of *A. tortilis* supports

the argument above. The large root biomass could lead to increased water absorption, hence, maintaining growth and survival under water stress.

Lediges (1974) observed that *Eucalyptus grandis* seedlings that had higher (0.51) root : shoot ratios were able to survive moderate water stress better than those with lower (0.45) root : shoot ratios. The observed low r : s ratio for *E. grandis* compares favourably with that of *A. xanthophloea* in which r : s ratio remained at 0.5 for both water stressed and unstressed seedlings. Low r : s ratio has been found to correlate with dry matter production in conifers growing in more mesic environments (Tan *et al.*, 1993). A lower root : shoot ratio, as observed for *A. xanthophloea,* would increase photosynthetic capacity under adequate water supply but might increase mortality under drought. This is because the large leaf surface area would increase transpirational water loss under drought. *Acacia xanthophloea* was also unable to alter r : s ratio even when repeatedly stressed, and furthermore there was a large reduction in total dry weight production when subjected to 4- and 6-day repetitive water stress. This may explain why *A. xanthophloea* could be better adapted to grow in mesic environments than *A. tortilis*. The practical significance of this is that *A. xanthophloea* is suitable and is recommended for afforestation of mesic highland areas while *A. tortilis* is suited for dry lowland areas of Kenya.

Acknowledgements

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