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Growth and water relations of Kenaf (*Hibiscus cannabinus 1...*) under water deficit on a sandy soil

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Abstract

The effects of water stress on growth and water relations of Kenaf (Hibiscus cannabinus L.) were investigated. The plants were grown on a loose-textured sandy soil in the greenhouse at CERAAS, Bambey, Senegal. Three watering regimes representing well watered control, moderate stress and severe stress were imposed on the plants. Each watering treatment was replicated four times in a completely randomized design. Soil moisture stress significantly retarded vegetative growth as analysed by plant height, collar diameter growth, leaf development, branching, flowering, and biomass accumulation. Water stress had no effects on biomass allocation, in terms of root—shoot and bark—wood ratios. Kenaf tried to avoid drought by leaf rolling and stomatal closure. The water potential (ψ_n) went as low as -2.53 MPa under severe stress, and -0.50 MPa was bracketed as the most critical ψ_n , below which stomatal conductance and transpiration ceased and leaf—air temperature differential became positive. (* 1998 Elsevier Science B.V. All rights reserved.

Keywords: Growth; Hibiscus cannabinus; Kenaf; Water-deficit; Water relations

1. Introduction

Kenaf (Hibiscus cannabinus, L.) is a herbaceous annual and a source of raw material for pulp and paper production. It is fast-growing,

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and high yielding pulp is easily obtained (Clark et al., 1962). It is also an important source of textile fibres for the manufacture of twines, ropes, burlap bags and carpet backings using traditional retting ponds in Africa, Asia and Latin America (Wilson et al., 1965; Boulanger, 1990). The plant tops, when ground, have high digestibility and can be used as feed for cattle and sheep (Killinger, 1969; Swingle et al., 1978; Hays, 1989).

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Kenaf is being introduced into arid regions (Francois et al., 1992), and is increasingly being grown in other dry, light-textured, marginal soils with the probability of water deficits developing during growth. The adverse effects of water deficit on growth and metabolism arc well known. Water deficits affect many plant species, and drought stress is an important factor limiting crop production even in the rainy season for soils in the humid and sub-humid tropics. The high incidence of drought stress may be attributed to a number of causes, such as erratic rainfall distribution, high evaporation rate, and shallow rooting (Enu-Kwesi et al., 1986).

In general, as water defcit increases in the soil, leaf water potential declines, leading to stomatal closure, decline in CO₂ uptake and limitations in photosynthetic activities, wilting, and tlramatic impairment of many metabolic functions (Kramer, 1983). Prolonged drought leads to retarded growth, reduced yield, and may cause death.

However, kenaf has been shown to respond in a manner that is typical of a moderately salt tolerant non-halophyte (Curtis and Làuchli, 1985, 1986; Francois et al., 1992). There has been some debate as to whether kenaf avoids, tolerates or escapes drought. The present study was undertaken not only to characterize, but also to quantify the whole growth response of kenaf to water deficit on a sandy soil.

2. Materials and methods

2.1. Seed collection

Certified seeds of Kenaf (*Hibiscus cannabinus* L.) were obtained from the Obafemi Awolowo University, Institute of Agricultural Research, Moore Plantation, Ibadan, Nigeria. Cuba 108 cultivar was used on the basis of its high bark—wood core ratio (Webber, 1993), since the harvest index for this experiment was the bast fibre.

2.2. Growth conditions

Sandy soil was used as the potting medium. The chardcteristics of the soil were previously de-

scribed by Annerose (1990). The soil was sun-dried and undccomposed plant materials were removed by sieving. Twenty-eight kilograms of soil was packed in plastic pots (height, 40 cm; diameter, 25 cm) with drainage holes at the bottom, to a bulk density of 1.5852 g cm⁻³. Ten kenaf seeds were planted at 0.5 cm dcpth and the resulting seedlings were later thinned down to one plant per pot at two-leaf stage, to obtain plants with uniform growth vigour. To remove nutrient deficiency as a limiting factor, the plants were fertilized at the beginning of the experiment and 2 months later with compound N.P.K. (15-10-I 5) fertilizer at the rate of 3.0 g/plant, eyuivalent to 200 kg/ha of 70000 stands (White et al., 1970). The pots were placed in a greenhouse at CERAAS. Rambey. Senegal (latitude 14°.42'N and longitude 16°.28′W). At midday, the maximum temperature was 35.5 + 0.95°C; relative humidity was 46.25 +2.27%, while Photosynthetic Photon Flux Density (PPFD) was $690.55 \pm 175.44 \ \mu \text{mol s}^{-1} \text{ m}^{-2}$.

2.3. Soil moisture treatment

Two weeks after germination (at the four-leaf stage), the following treatments were imposed:

- 1. Control (W1) soil water was maintained at field capacity by daily watering. The daily water requirements of the plants were determined as the difference between the weight of a fully irrigated pot and the weight of the pot 24 h later, after the day's evapotranspiration. This determination was done weekly to take care of changing water demands of the plants with age.
- 2. Moderate stress (W2) the plants were watered to field capacity at 3-week intervals.
- 3. Severe stress (W3) the plants were watered to field capacity at 4-week intervals. The choice of these watering regimes was based on the duration of short-term drought usually experienced by this crop in the field.

2.4. Experimental design and statistical analysis

The experimental design was a completely randomized one with three watering treatments replicate d'four times to give a total of 12 experimental units. Each experimental unit was composed of nine pots, as destructive measurements were conducted on some pots during the course of the experiment. The experimental layout was surrounded with a single row of border plants to protect the experimental plants trom external influences. Data collected were subjected to analysis of variance and Duncan's multiple range test was used in partitioning the means, SAS/STAT statistical software was used for data analysis. The age effect was considered as a repeated effect, and repeated measurement analysis was conducted with Proc GLM to test the effects of watering on the whole plant growth cycle.

2.5. Measurements

2.5.1. Physiological measurements

2.5 1. 1. Growth. Height growth was measured weekly with the aid of a meter rule from the base of the stem at the soil level to the terminal bud of the main stem Root-collar diameter was measured at the collar with a calliper gauge (FACOM, 815A) to the nearest 0.001 mm. Dry mai ter production was obtained by carefully uprooting the seedlings from the pot. Each plant was separated into roots, leaves, bark, wood core and the floral parts when available. The bark was separated from the central wood core by peeling. The total weight of the stalk (bark and the wood), the shoot and the total plant matter were also obt fined. The plants were oven-dried at 88°C until constant weights were obtained. The dry weight of each component was determined to the nearest 0.01 g on a top-loading meter balance (Mettler P-120). Leaf area was measured with a leaf area meter (model MK2, AT Area Meter Devices, UK). The leaf area ratio (LAR) was obtained us the ratio of total area of leaf to whole plant dry weight. Root shoot ratio was obtained as the ratio of the dry weight of root to the dry weight of the shoot, while bark wood ratio was obt fined as the ratio of the dry weight of the bark to he dry weight of the wood. These measurements were made every 2 weeks starting from the date of the application of the treatments.

2.5.1.2. Plant water relations. All water relations measurements were made on the fully expanded leaf at the fifth node from the apex Transpiration rate, ambient air temperature, leaf temperatures, and leaf conductance were measured using a steady state porometer (Model LI-1600, LICOR Lincoln, Nebraska). Total water potential (ψ_w) was determined in the greenhouse using Scholander pressure chamber (Model 3000, Plan Water Status Console, Santa Barbara, CA) All measurements were made weekly betucen 11:00.13:00 h

Leaf relative water content (LRWC) was determined gravimetrically on a leaf disc and calculated from the following relationship $[(W_{\rm fresh}-W_{\rm dry})/(W_{\rm turgid}-W_{\rm dry})]\times 100$. Where $W_{\rm fresh}$ is the weight of freshly harvested sample. $W_{\rm turgid}$ is the turgid weight after floating the sample for 4 h in water, and $W_{\rm dry}$ is the oven-dry (85°C for 24 h) weight of the sample (Jensen, 1989). The same leaf was sampled for all the water relations measurements.

2.5.2. Soil moisture measurements

Gravimetric measurements of soil moisture content were taken at weekly intervals after measuring the plant water stress parameters. Soit moisture content was determined at four depth intervals, 0.7, 7.13, 14 - 21, and 21.28 cm. The gravimetric soil water contents were obtained as $[(W_{\text{fresh}} - W_{\text{dry}})/(W_{\text{dry}})]$, where W_{fresh} is the fresh weight of soil sample, and W_{dry} is the oven-dry weight. These were converted to volumetric soil water contents by multiplying with the bulk density. 1.5852 g cm. 3 of the potted soil. The average volumetric moisture content of the four soil levels was then obtained.

3. Results

3.1. Physical growth

The effect of water stress on height collar diameter growth, leaf area, number of bi anches leaves and flowers are shown in Fig. 1. Water deficit reduced the cumulative height growth of kenaf plants when compared with the control

Kenaf plants under continuous irrigation vigorously increased plant height from the beginning of the experiment to its termination at the 10th week. Height increased slowly with the plants under stress, and severe stress had the most detrimental effect on height increases (Fig. 1A). At the end of the growth period, the control had attained a mean height of 2.47 m, moderate stress 1.31 m and severe stress 0.94 m. Moderate stress therefore reduced height by 47% and severe stress by 62% of the control.

Collar diameter growth was significantly retarded by water stress. Moderate stress reduced growth by 32% and the plants attained a radial diameter of 1.3 cm. while severely stressed plants were retarded by 45% having attained a basa1 diameter growth of 1.05 cm when compared with 1.94 cm growth recorded with the control at the end of the experimental period (Fig. 1 B).

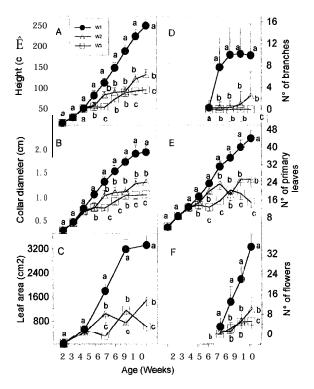


Fig. 1. Mean plant height, root-collar diameter, leaf area, number of primary leaves, branches and flowers of kenaf under water stress. Within age, means followed by the same letter are not significantly different according to Duncan's multiple range test. W2 was watered at the 5th and 8th weeks. and W3 at the 6th week.

Leaf area growth (Fig. 1C) and primary leaf production (Fig. 1 E) were equally affected by water stress. Primary leaf number production slowed down at the 7th week of growth i.e. during flowering, while that of the leuf area growth slowed after the 4th week. Moderate stress reduced primary leaf number by 43%, and leaf area by 55%, whereas severe stress affected primary leaf initiation and leaf area development by a 66% and 82% reduction, respectively.

Branching did not commence until about the 6th week. and these were profuse in the control plants before flowering, after which all the axillary buds were converted to flower buds. Moderate stress drastically reduced branching by 75% while severe stress completely inhibited it (Fig. 1 E). Flowering in all the treatments started at the 7th week of growth, and was adversely affected by moderate and severe stress by 72 and 85% respectively. The flower buds that were formed before the onset of stress withered and dehisced. However, flower production recommenced whenever the plants were relieved of stress (Fig. 1 F).

Fig. 2 shows the effects of the treatments on the number of nodes and the length of internodes at the end of the experimental period. With node numbers of 41 and 27, moderate and severe stress reduced node initiation by 28 and 53% respectively, when compared with 57 nodes produced by the adequately watered control. Internode length decreased with age in all the treatments. The effect of stress on the internode length for W2 and W3 were similar until about the 15th node when moderately stressed plants started branching due to earlier release of stress. The severe stress on the other hand continued a downward decline. The first flower buds were formed on the 29th nodes of the control and the moderately stressed plants. while that of the severely stressed plants were on the 25th node. In the well watered control, long internodes alternated with short internodes more vigorously after the commencement of flowering.

3.2. Biomass accumulation

Biomass accumulation (Fig. 3) was also significantly affected by water stress. Leaf and root dry matter productions were highest after the 4th

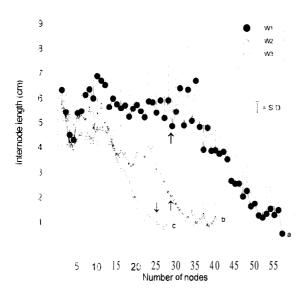


Fig. 2. Nodes and internode lengths of whole kenaf in the greenhouse under three soil moisture treatments. Terminal node numbers followed by the same letter are not significantly different according to Duncan's multiple range test.

week of growth in the control plants. The difference between the moderate stress and the severe stress responses were not significant. The pattern of growth in bark, wood, stalk, shoot and the overall plant production were similar. With respect to the control, there were steep increases in biomass accumulation after the 6th week of growth. At the end of the experimental period, moderate stress reduced dry matter production of the teaf, root, bark, wood, stalk, shoot and total biomass (Fig. 4A) by 74%, and severe stress by 86%.

3.3. Biomass allocation

Root-shoot ratio (Fig. 4B) and bark-wood ratio generally decreased with increase in age, and the steepest decline was at the 4th week of growth. Water stress had no effects on root-shoot ratio and bark-wood ratio (Fig. 4B,D). Lead area ratio (LAR) increased by the 4th week before a downward decline (Fig. 4C). The stressed plants maintained relatively higher LAR throughout the experimental period.

3.4. Plant water relations

3.4.1. Leaf gas exchange

Stomatal conductance declined with age in the control treatment, and all the treatments began a drastic decline after the 4th week of growth. All the levels of stress brought stomatal conductance to zero when watering was withheld. Upon rewatering there were rapid increases in stomatal conductance with a dramatic increase above the control by the severely stressed plants (Fig. 5A).

Simitarty, transpiration rate fairly declined with maturity in the well watered control plants, after an initial increase by the 4th week of growth. Among the stressed plants, there was a steep fall in transpiration rate after the 4th week, that is,

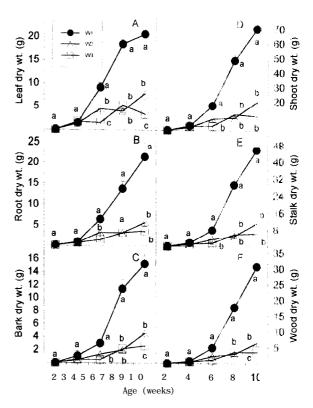


Fig. 3. Effect of water stress on dry matter accumulation of leaf, root, bark, wood core, stalk and shoot of kena? Within age, means followed by the same letter are not significantly different according to Duncan's multiple range test. W? was watered at the 5th and 8th weeks, and W3 at the 6th week.

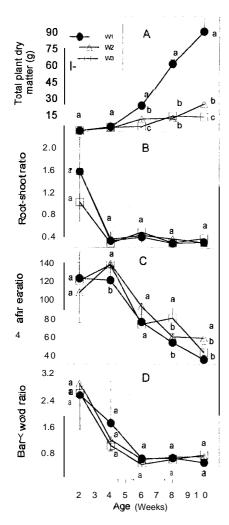


Fig. 4. Total dry matter accumulation, root shoot ratio. leaf area ratio and bark wood ratio of kenaf as influenced by water stress. Within age, means followed by the same letter are not significantly different according to Duncan's multiple range test. WC was watered at the 5th and 8th weeks, and W3 at the 6th week.

after only 2 weeks of stress. It reached 0.59 μ g cm⁻² s⁻¹ for both stressed plants as compared to 14.25 μ g cm⁻² s⁻¹ recorded with the control at the same period. Upon rehydration, transpiration rate rose rapidly, and in severely stressed plants transpiration went above the corresponding control value, only to fall sharply soon afterwards (Fig. 5B).

3.4.2. Water status and microclimate

LRWC' began to drop 2 weeks after the initial withdrawal of watering, and moderate stress LRWC reached a value of 76% wfter 2 weeks of stress, and in severely stressed plants 67% after 3 weeks of stress (Fig. SC). At the end of the experimental period, the LRWC of the moderate and severe stress had dropped to 58.57% and 55. 10%, thereby representing 20.10% and 24.80%

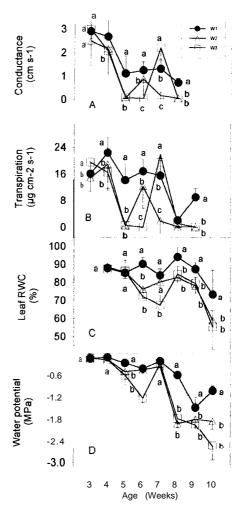


Fig. 5. Stomatal conductance, transpiration rate. LRWC and water potential of kenaf as influenced by water stress. Within age, means followed by the letter are not significantly different according to Duncan's multiple range test. W2 was watered at the 5th and 8th weeks, and W3 at the 6th week.

reductions of the LRWC of the corresponding control, respectively.

The leaf water potentials (ψ_w) during the drying and recovery cycles are show in Fig. 5D. The ψ_w in the control plants fairly decreased as the plants aged, while droughted plants began to show sharp decrease in ψ_w after 2 weeks of stress. Before the first watering session at the 6th week, the severely droughted plants had reached ψ_w of -1.21 MPa. Upon rewatering, the recovery of ψ_w of the leaves was almost as rapid as the rate of drying, in that ψ_w got very close to the control value of -0.4 MPa.

At the second watering session at the 8th week, the ψ_w of moderately droughted plants also dropped sharply to -1.91 MPa after 2 weeks of stress. The severely stressed plants dropped drastically to -1.76 MPa after only 1 week of stress, these are when compared with -0.58 MPa attained by the adequately watered control at the same period. At the end of the experimental period, ψ_w of -1.01, -1.84, and -2.53 MPa had been attained by the adequately watered control, moderately and, severely stressed plants, respectively. There was no significant difference in the values obtained with the stressed plants.

Plant leaf-air temperature differential in the control increased with time up to the 5th week before a gradual decline thereafter. Similar results were obtained with the plants under stress, except after watering sessions when they sharply dropped. As stress increased, the temperature of the stressed plant increased above air temperature and temperature differential became positive, indicating that the leaves were hotter than the air. The leaf-air temperature differential of the well watered control remained negative indicating that the leaves were cooler than the ambient air (Fig. 6A).

Average volumetric water content (cm³ g⁻¹) of the experimental soil obtained at 0-7, 7-14, 14-21 and 21-28 cm soil depths are shown in Fig. 6B. The soil water content was high after the 6th week in the well watered control, corresponding to the period of commencement of flowering. Volumetric soil water content in the stressed pots remained relatively low even after the periodic watering.

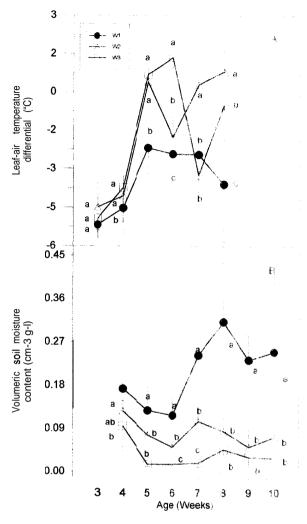


Fig. 6. Leaf air temperature differential and soil volumetric water content as variously affected by water deficit. Within age, means followed by the same letter are not significantly different according to Duncan's multiple range test. W2 was watered at the 5th and 8th weeks, and W3 at the 6th week.

An exponential regression of stomatal conductance (Fig. 7A) indicated that stomata started closing at -0.5 MPa, and finally closed at -1.0 MPa. Similarly, transpiration rate (Fig. 7B) started declining steeply below -0.5 MPa leaf water potential, and eventually ceased below -1.0 MPa. A polynomial regression of teal air temperature differential on water potential showed that leaf temperature would rise above air temperature at about $\psi_{\rm w} > -0.5$ MPa (Fig. 7C).

4. Discussion

4.1. Growth

Stern development and elongation are the critical components of the growth process (Schulze

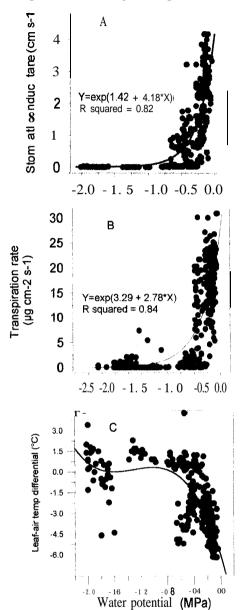


Fig. 7. Regression of water potential on (A.) Stomatal conduc-Lance of kenaf (the curve was fitted with an exponential regression equation); (B) transpiration rate (the curve was fitted with an exponential regression equation) and (C) leaf air temperature differential (the curve was fitted by a threeterm polynomial).

and Matthew, 1993). Physiological efficiency of any particular fibre species is manifested in the increment of plant height and increase in basal diameter. These parameters which result from the respective activities of apical growth and intercalary growth are generally considered dependable yield components of a bast fibre crop.

Water deficit was observed to have significantly reduced height and collar diameter growth of kenaf. That drought reduces plant height and vigour is well known. The alteration of these growth parameters under water deficits are due in part to the role of water in turgidity maintenance necessary for cell enlargement (Kramer. 1983). Cell division also decreases with increased water deficits, because cells apparently must attain a certain size before they can divide (Dolev and Leyton. 1968). As there is no direct method for assessing the fibre yield from a standing crop. plant height and basal diameter are considered as the general guiding criteria for efficient production of fibres in a particular species (Maiti and Chakravarty, 1977). It can therefore be concluded that drought affects the efficient production of fibres in kenaf.

Leaf growth is the most sensitive of plant processes to water deficits and is frequently inhibited in field crops (Hsaio, 1973; Schulze and Matthew. 1993). For a given location and growth duration, the amount of light intercepted is primarily dependent on leaf area development, and these have been shown to be directly linked to leaf turpor (Bunce, 1977: Wenkert et al., 1978). Water deficit adversely affected the number of nodes and leaves produced in kenaf, leaf dry matter and leaf area due to poor leaf expansion and defoliation.

Kenaf usually grows straight and unbranched in dense stands. In this experiment, branching started at the 6th week of growth. However, it stopped when flowering fully commenced at the 8th week, since all the axillary buds had become flower buds. It was highly reduced by moderate stress and completely inhibited by severe moisture stress. High branching is an unwanted luxury under drought because it would be wasteful of soil moisture (Keim and Kronstad. 1981). Inhibition of branching under drought conditions

observed in kenaf could therefore be considered an adaptive mechanism, as it tried to conserve water which could be needed in the more critical stages of development, like flowering.

Flowering of kenaf in the greenhouse started on the 7th week of growth in all the treatments. Water stress, however, reduced flower production by more than 70%. Within a range of germplasms, most of the drought resistance of high yielding crops under drought stress could be attributed to earliness (Chinoy, 1961; Derera et al. 1969). This characteristic would allow a genotype to escape, in relative terms, a gradually increasing drought stress. Kenaf did not employ this escape mechanism in order to resist drought, since flowering started at the same time in all the treatments.

Soil moisture stress reduced biomass accumulation in all components of kenaf that were investigated, namely; the leaf, root, bark, wood core, stalk, shoot and consequently, total dry matter. It is hypothesized that an important result of mild drought stress would be a decrease in the efficiency with which solar radiation is used to accumulate biomass. The loss of accumulation efficiency is associated with a decline in photosynthetic capacity which might have resulted from decreases in leaf gas conductances (Muchow et al., 1986). It has been shown in this study that kenaf closes its stomata almost completely at the onset of drought (Fig. 5A.B). Though this was an efficient drought avoidance mechanism, it was at the expense of carbon accumulation (Nwalozie and Annerose, 1996).

High root shoot ratios are generally a response to water stress in the rooting zone. The root shoot ratio in kenaf decreased with age, and it was not influenced by water deficit. Root growth depends on supply of carbohydrate from the shoot and reduction in leaf area usually reduces root growth (Kramer, 1983); this would have been the case with kenaf. LAR in kenaf decreased with maturity. However, the variations among the stress treatments were not statistically significant at the end of the experimental period, but were significantly reduced with respect to the control. The importance of

leafiness as a component of overall growth is well known. For most plants the LAR decreases with age as the plant size increases (Blackman and Wilson, 1951). A reduction of LAR with age has been observed as a common feature in annuals (Higgs and James, 1969), and this can be related to their shorter life span (Sharma and Ogbonnaya, 1990). The reduced LAR with stress would have been caused, in part, by the high defoliation observed with stressed plants.

Bark wood ratio, like root shoot ratio was not affected by water deficit in kenaf, and this decreased with maturity. Fibre wood ratio is generally considered a dependable yield component and selective index of bast fibre crops (Maiti and Chakravarty, 1977). These two components are direct derivatives of secondary cambium. A higher fibre-wood ratio indicates the plant's efficiency in the production of higher yield of fibres than of wood. This criterion is used as a measuring stick in the production of fibres of different species or varieties. This finding agrees with the report of Francois et al. (1992), that salinity had no significant effect on the proportion of the stem that is bark in kenaf. They reported that bast fibres accounted for approximately 36% of the stem weight at all salinity treatments. This percentage also agrees with bast fibre percentage reported by Muchow (1979) in Australia. Cuba 108 has been shown to have the least percentage wood core material (62%), and greatest bark to wood ratio (0.61). among all the kenaf varieties (Webber, 1993).

4.2. Plant water relations

Drought tolerance levels in plants vary widely among species. Dehydration of sunflower plants to -1.5 MPa, for example, caused injury to about 10% of the cells, while dehydration below -2.0 MPa caused so much injury to organeiles and membranes that recovery was impossible (Fellows and Boyer, 1978). Giles et al. (1976) observed irreversible changes in cell structure of 25% of maize mesophyll cells at -1.8 MPa. Injury has been ascribed to mechanical rupture of protoplasm, degradation of cell membranes.

protein denaturation, and accelerated gene mutations (Kramer, 1983: Roy-Macauley et al., 1992).

Dehydration is usually accompanied by severe damage and disorganization of membranes and organelles. However, desiccation-tolerants retain most of their structure and capacity for physiological activities, and resume normal growth processes soon after rehydration (Kramer, 1983). The results presented in this study showed that kenaf was able to recover alter a deficit of -2.54 MPa. after 4 weeks of drought. In addition, it retained more than 50% of its LRWC. The fact that kenaf was able to recover after a water deficit corresponding to - 2.54 MPa indicates that it is relativety desiccation-toterant. The results of this study are not at variance withr the reports of Maas and Hoffman (1977). Curtis and Làuchli (1985, 1986), François et al. (1992) that placed kenaf as a moderately salt-tolerant non-halophyte, on the basis of its response to salt stress.

A common response to water stress is s'tomatal closure, which reduces both flux of CO₂ and water vapour. Alternatively, stomates may remain open while turgor is maintained through osmotic adjustment. Stomatal conductance and transpiration rate in kenaf progressively declined with age in the adequately watered control. All the levels of stress brought stomatal conductance and transpiration to zero. Kenaf was also observed to roll its leaves during drought. These two mechanisms could be described as drought tolerance by dehydration postponement (Kramer, 1983), equivalent to drought avoidance by Levitt (1980). Upon rewatering, there were rapid increases, with a dramatic increase above the control observed in the severely stressed plants (Fig. 5A). This buttresses the hypothesized desiccation tolerance of kenaf. The exponential regression of stomatal conductance and transpiration rate on leaf water potential bracketed - 0.5 MPa as the most critical water potential, below which, diffusion resistance increased, stomatal conductance transpiration became zero

Cowpea shows a similar response (Hall and Schulze, 1980: Nagarajah and Schulze. 1983). This response enables plants to avoid desiccation by maintaining leaf water potential at relatively high levels. While osmotic adjustment is minimal in

such species (Shackel and Hall. 1983), it cannot be ruled out for kenaf which has been hypothesized to have a high desiccation tolerance capacity. This might be due to membrane resistance and/or osmotic adjustment mechanisms triggered when water deficit surpasse:< the critical point of 0.5 MPa.

Kenaf could therefore be described as opportunistic in relation to water availability, with a high rate of stomatal conductance and transpiration when soit water is available but with markedly reduced leaf conductance and transpiration rate when water is limited. This contrasts with wheat, which utilizes water sparingly when it is available but has only a gradual decrease in photosynthesis as water deficits develop (Henson et al., 1989).

Leaf temperature relationships are used to estimate water stress in plants, because leaf temperature and ambient air temperature differentials are functions of transpiration rates (Halim et al., 1989). The temperature of the stressed plants increased above air temperature and leaf- air temperature differential became positive, indicating when the plants were stressed. At this point, the leaf was hotter than the ambient air. This could be linked to the stomatal closure, poor gas exchange and dccreased transpirational cooling of the plants. A water principal of -0.5 MPa was bracketed as the critical water potential, below which the plant would be stressed and the leaf temperat ure would rise above ambient air temperature.

The stressed plants, therefore, began to face another kind of stress, heat stress, and that is why breeders seldom attempt to separate heat from drought tolerances, probably because drought is usually accompanied by high temperature. High temperature accompanying drought causes release of ammonia from decomposition of protein that injuries; plant tissues (Weiland and Stuttle, 1980).

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References

- Annerose, D.J.M., 1990. Recherches sur les mécanismes physiologiques d'adaptation à la secheresse: Application au cas de l'arachide (Arachis hypegaea L.) cultivée au Sénégal. Doctorat Thèse, Science Naturelles. Université Paris VII.
- Blackman, G.E., Wilson, G.L., 1951. An analysis of the differential effects of light intensity on the net assimilation rate, leaf area ratio and relative growth rate on different species. Ann. Bot. 15, 373.
- Boulanger, J. 1990. Les Hibiscus textile en Arique Tropicale, 2en-e partie, production de la textile du kénaf et de la roscile, IRCT-CIRAD, France.
- Bunce, J.A., 1977. Leaf elongation in relation to leaf water potential in soybean. J. Exp. Bot. 28, 156--161.
- Chinoy J.J., 1961. Physiology of drought resistance in wheat. H. Evaluation of drought resistance in eight varieties of wheat on the basis of growth analysis. Phytonomy 16, 131–139.
- Clark, F.F., Nelson, G.H., Nieschlag, H.J., Wolff, I.A., 1962.
 A search for new fibre crops. V. Pulping studies on kenaf, TAPPI 45, 780–786.
- Curtis, P.S., Lauchli, A., 1985. Response of kenaf to salt stress: Germination and vegetative growth. Crop Sci. 25, 944–949.
- Curtis, P.S., L\u00e4uchli A., 1986. The role of leaf area development and photosynthetic capacity in determining growth of ken if under moderate salt stress, Aust. J. Plant Physiol. 13, 553-565.
- Derera, N.F., Marshal, D.R., Balam, L.N., 1969. Genetic variability in root development in relation to drought tolerance in spring wheat. Exp. Agric. 5, 327–337.
- Doley, D. Leyton, L., 1968. Effects of growth regulating substances and water potential on the development of secondary xylem in *Fraxinus*. New Phytol. 67, 579–594.
- Enu-Kovesi, L., Nwalozie, M.C., Anyanwu, D.L. 1986. Effects of pre-sowing hydration-dehydration on germination, vegetative growth and fruit yield of *Abelmoschus esculentus* grown under two moisture regimes. Trop. Agric, 63, 181 184
- Feilows, R.J., Boyer, J.S.N., 1978. Altered ultrastructure of cells of sunflower leaves having low water potentials. Protopiasma 93, 381–395.
- Francois, L.F., Donovan, T.J., Maas, E.V., 1992. Yield, vegetative growth, and fibre length of kenaf grown on saline soil. Agron. J. 84, 592–598.
- Giles, K.I., Cohen, D., Beardsell, M.F., 1976. Effects of water stress on the ultrastructure of leaf cells of *Sorghum bicolor*. Plant Physiol. 57, 11-14.
- Halim, R.A., Buxton, D.R., Hattendorf, M.J., Carlson, R.E., 1989. Water-deficit effects on alfalfa at various growth stayes. Agron. J. 81, 765-770

- Hall, A.E., Schulze, E.D., 1980. Drought effects on transpiration and leaf water status of cowpea in controlled civir stament. Aust. J. Plant Physiol. 7, 141147.
- Hays, S.M.: 1989. Kenaf tops equal high-quality hay Agric. Res. 37 (6), 18.
- Henson, I.E., Jensen, C.R., Turner, N.C., 1989 Leaf gas exchange and water relation of Lupins and Wheat, I. Shoot responses to soil water deficits. Aust J Plant Physiol. 16, 401–413.
- Higgs, D.E.D., James. D.B., 1969. Comparative studies on the biology of upland grasses. I. Rate of dry matter production and its control grass species. J. licol. 37, 553-363.
- Hsaio, T.C., 1973. Plant responses to water stress Anna Rev Plant Physiol. 24, 519 570.
- Jensen, C.R., 1989. Plant water relations approaches and measurements. In: Persson, R., Wredin, V (Eds Vat trainsbehov och Narings-tillforsel, Foredrag preset ter ade vid NJF-seminarium n. r., 151 Landskrona, 13 Aug ust 1989, pp. 45-63.
- Keim, D.L., Kronstad, W.E., 1981. Drought response of v11 ter wheat cultivars grown under field stress conditions Crop Sci. II. II 14.
- Killinger, C.H., 1969, Kenaf (*Hibiscus cannabinus* 1), a mubi purpose crop. Agron, J., 61, 734-736
- Kramer, P., J., 1983. Water Relations of Plants Acade nic Press. New York.
- Levitt, J., 1 9 8 0. Responses of Plants to Environmental Stresses. Academic Press. New York
- Maas, E.V., Hoffman, G.J., 1977. Crop salt obstance exprent assessment. J. Irrig. Drain. Div Am Soc Civ Ing. 103, 115, 134.
- Maiti, R. K.: Chakravarty, K., 1977. A comparative study of yield components and quality of common Indian bast libres. Econ. Bol. 31, 55-60.
- Muchow, R.C., 1979. Effects of plant population and season on kenaf (*Hibiscus cannabinus* L.) grown under irrigation in tropical Australia, I Influence on the components of yield. Field Crop Res. 2, 55 66.
- Muchow, R.C., Sinctair, T.R., Bennett, J.M., Hammond L.C., 1986, Response of leaf growth, leaf nitrogen, and stomatal conductance to water deficits during vege ta two growth of field-grown soy bean. Crop Sci. 16, 196–1198
- Nagarajah, S., Schulze, E.D., 1983, Responses of Vigua unguiculata (L) Walp, to temperature and soil drought Aast J. Plant Physiol, 10, 385–394.
- Nwalozie, M.C., Annerose, D.J.M 1996 Ston ital bel aviour and water status of C owpea and peanut at low son moisture levels. Acta Agron. Hung. 34 (3), 229-236.
- Roy-Macauley, 1-1.. Zuily-Fodil, Y Kedric, M., Pham hi A.T., Vierra da Silva, J., 1992. Effects of drought stress on the proteolytic activities in *Phaseolus* and *Figna* leaves from sensitive and resistant plants Physiol Phant. 85 yo. 96.
- Schulze, H.R., Matthew, M.A., 1993. Growth, osmotic adjest ment, and cell-wall mechanics of expanding grape lecves during water deficits. Crop s o i 33, 287-294.

- Shackel, K.A., Hall, A.E.. 1983. Comparison of water relations and osmotic adjustment in sorghum and cowpca under field conditions. Aust. J. Plant Physiol. 10, 423-435.
- Sharma, B.M., Ogbonnaya. C.I., 1990. Growth analysis of Setaria barbata (Lam.) K unth in South-west Nigeria. Zizaniology 2, 191-196.
- Swingle, R.S., Urias, A.R., Doyle, J.C., Voigt, R.L., 1978. Chemical composition of kenaf forage and its digestibility by lambs and in vitro. J. Anim. Sci. 46, 1346 1350.
- Webber, C.L., 1993. Yield components of live kenaf cultivars. Agron. J. 85, 533 535.
- Weiland, R.T., Stuttle, C.A. . 1980. Concomitant determination of foliar nitrogen loss, net carbon uptake. and transpi-

- ration. Plant Physiol. 65, 403 406.
- Wenkert, W. Lemon, E.R., Sinclair, T.R., 1978. Leaf elonga-Lion and turgor pressure in field-grown soy bean, Agron. J. 70, 761-764.
- White, G.A., Cummirs, D.G. Whitely, E.L., Fike, W.T.,
 Grieg, J.K., Martin, J.A., Killinger, G.B., Higgins, J.J.,
 Clark, F.T., 1970. Cultural and Harvesting Methods for
 Kenal An Annual Crop Source of Pulp in the Southeast, ARS, U.S. Depart, of Agric, Prod. Res. Report, 113.
- Wilson, F.D., Summers, T.E., Joyner, J.F., Fishler, D.W., Seale, C.C., 1965. Everglade 41 and Everglade 71, Two New Varieties of Kenaf (Hibiseus cannabinus L.) for the Fibre and Seed. Florida Agr. Exp Sta. Cir. S-1 68.