J. Agronomy & Crop Science **185**, 73—82 (2000)

ISSN 0931-2250

Botany Department, Faculty of Science, Mansoura University, Mansoura, Egypt

Effects of Water Stress on Growth, Pigments and $^{14}CO_2$ Assimilation in Three Sorghum Cultivars

M. E. Younis, O. A. El-Shahaby, S. A. Abo-Hamed and A. H. Ibrahim

Authors' address: Drs M. E. Younis, O. A. El-Shahaby, S. A. Abo-Hamed and A. H. Ibrahim (corresponding author), Botany Department, Faculty of Science, Mansoura University, Mansoura, Egypt. E-mail: sinfac@eic.mans.eun.eg

With 4 figures and 3 tables

Received November 26, 1998; accepted September 28, 1999

Abstract

The effects of drought on growth, pigments and $^{14}CO_2$ assimilation were studied in three sorghum cultivars. Water stress applied either at the vegetative or at the reproductive stage was found to reduce relative growth and net assimilation rates. Root growth was less affected by water stress and in certain cases it was increased; consequently, the root/shoot ratio was improved. The sensitivity to drought stress was greater at the reproductive than at the vegetative stage. Dorado was the most drought-tolerant and Giza 15 the least drought-tolerant cultivar, as determined by calculation of the drought susceptibility index for total green leaf area and shoot dry weight. Short-term water stress in the vegetative phase (7 days) improved the chlorophyll content in leaves, and long-term stress in the vegetative and reproductive phases reduced chlorophyll content. Carotenoid content, in general, was not changed by drought stress. $^{14}CO_2$ photoassimilation indicated that soluble, insoluble and consequently total photosynthates were reduced at the end of the stress period at both stages. Drought plus defoliation appeared to increase both chlorophyll content and $^{14}CO_2$ photoassimilation, to a certain extent, as compared with drought alone.

Key words: defoliation — drought — pigments — sorghum — $^{14}CO_2$ assimilation

Introduction

Sorghum is characterized by its ability to tolerate and survive under conditions of continuous or intermittent drought (Hulse et al. 1980). Its drought resistance has been attributed to a dense and prolific root system and the ability to maintain stomatal opening at low levels of leaf water potential, possibly through osmotic adjustment (Wright et al. 1983).

Reduction of plant growth is one of the most conspicuous effects of water restriction on the plant and is mainly caused by inhibition of leaf and stem elongation when water potential decreases below a threshold, which differs among species (Pelleschi et al. 1997). Root growth is less sensitive to a decrease in soil water potential than stem growth (Creelman et al. 1990), and this leads to the increase in the root/shoot ratio that is commonly observed in plants exposed to a water deficit.

A reduction of the pigment content under water deficit conditions has been reported by many investigators (Ashraf et al. 1994, El-Kheir et al. 1994). Among environmental stresses, water insufficiency is one of the main limitations to photosynthesis in mesophytic plants (Kicheva et al. 1994). Drought resistance has been equated with the ability of a plant to maintain a positive carbon balance under desiccating conditions, primary components being the capacities to synthesize and utilize photosynthetic products (Martinez et al. 1995). Defoliation of some plants results in readjustment of plant metabolism for promotion of new leaf area expansion and re-establishment of the photosynthetic capacity (Ryle and Powell 1975), and delays the senescence of the remaining leaves (Klubertanz et al. 1996).

The objectives of this study were (i) to evaluate the growth, pigments, $^{14}CO_2$ assimilation and drought resistance of three sorghum cultivars under water deficit conditions and (ii) to investigate the possible beneficial effects of defoliation on the photosynthetic pigments and on the assimilation of $^{14}CO_2$ by sorghum plants under stress conditions.

Materials and Methods

Plant materials and growth conditions

Three commonly used Egyptian cultivars of sorghum (*Sorghum bicolor* L. Moench) were used in this study. Two of these cultivars are tall (Giza 15 and Hybrid 113) and one is short (Dorado). Pure strains of seeds were obtained from the Egyptian Ministry of Agriculture, which is responsible for the production of growers' seed stocks.

The seeds were surface-sterilized with 0.001 M $HgCl_2$ solution for 3 min and washed thoroughly with distilled water. The seeds were soaked in distilled water for 3 h and then allowed to germinate in Petri dishes for 2 days on filter paper moistened with water. The germinated seeds were planted in plastic pots (20 seeds per pot; 25 cm width × 30 cm height) filled with 6 kg mixture of soil (clay: sand = 2 : 1, v/v). The pots were kept in a greenhouse at the Botany Department of the Faculty of Science, Mansoura University, Egypt and the plants were subjected to natural day/night conditions (minimum/maximum air temperature and relative humidity were: 29.2/33.2 °C and 63/68 %, respectively, at midday during the experimental period). Irrigation to field capacity was carried out when soil water content fell to 60 % of its initial value (the pots were weighed every day to assess the depletion of the stored water). Twenty days after planting, the plants were thinned to five per pot.

Drought stress was applied at two stages of plant development: (i) the vegetative stage, at 45 days from planting for all cultivars, and (ii) the reproductive stage (at anthesis), at 75 days from planting for the Giza 15 and Hybrid 113 cultivars, and 82 days for Dorado. At each stage, the plants of each cultivar were divided into three groups.

1 Control. The plants were irrigated to field capacity when the soil water content was at 60 % of its initial value.
2 Drought. Drought stress was applied by withholding water until yellowing of apical leaf tips was pronounced. This required 12 days for the Giza 15 and Hybrid 113 cultivars and 17 days for Dorado at the vegetative stage, and 10 days for all cultivars at the reproductive stage.
3 Drought with defoliation. The plants were subjected to defoliation in addition to drought stress. Defoliation was achieved by cutting the lamina of the lower plant leaves which corresponded to approximately half of the total leaf area.

Samples for analyses of growth and photosynthetic activity were taken at the end of the stress period, while those for analysis of pigments were taken serially. Soil water content was estimated at each sampling time and the second fully expanded leaves from the shoot apex were used for the different analytical procedures.

Monitoring the water status of the soil

The soil water content (SWC) was estimated as recommended by Ritchie et al. (1990). Measurements were made by obtaining the wet weight of a soil sample from each pot (WW), oven-drying the soil sample for 2 days at 105 °C and weighing the dry soil sample (DW). The SWC was expressed as the mass of soil water per g of dry soil.

Analysis of vegetative growth

1 Leaf area = length H maximum width H 0.75 (Turner 1974).
2 Relative growth rate (RGR):

$$RGR = \frac{\ln W2 - \ln W1}{T2 - T1}$$

(Beadle 1993), where W1 and W2 are the plant dry weights (kg) at times T1 and T2 (days), respectively.
3 Specific leaf area = S/W (Beadle 1993), where S and W are the area and dry weight of plant leaves, respectively.
4 Net assimilation rate (NAR):

$$NAR = \frac{(W2 - W1)(\ln S2 - \ln S1)}{(T2 - T1)(S2 - S1)}$$

(Beadle 1993), where S1 and S2 are the assimilatory areas at times T1 and T2, respectively, and W1 and W2 are plant dry weights at times T1 and T2, respectively.
5 Root plasticity = root length in unwatered soil/root length in watered soil (Reader et al. 1993).
6 Drought susceptibility index (DSI):

$$DSI = (1 - Y_D/Y_P)/D$$

(Fischer and Maurer 1978), where Y_D = yield under drought, Y_P = yield without drought, D = drought intensity = 1 – (mean Y_D of all genotypes)/(mean Y_P of all genotypes). Although this equation was used by Fischer and Maurer (1978) to describe the drought susceptibility index on a grain yield basis, it is also employed here to describe the drought susceptibility index for shoot dry weight and total green leaf area.

Determination of photosynthetic pigments

Photosynthetic pigments (chlorophyll a, chlorophyll b, and carotenoids) were determined using the spectrophotometric method developed by Metzner et al. (1965).

Photosynthetic assimilation of $^{14}CO_2$

As described by Shaddad (1979), a known quantity of fresh leaf discs was introduced into a fixation apparatus designed to allow $^{14}CO_2$ to be photosynthesized by the discs. The experiment was carried out under natural sunlight at 10 a.m. when light intensity was about 3500 Lux. At the end of the fixation period (10 min), the leaf discs were quickly transferred to boiling 85 % (v/v) aqueous methanol for extraction of photosynthates. After cooling, the insoluble fraction was separated from the soluble one by centrifugation at 2000 ***g*** for 10 min. The soluble and insoluble fractions were made up to a volume of 35 cm^3 and then 2 cm^3 of samples were pipetted for radioactivity measurements.

Radioactivity measurements

As described by Soliman (1984), radioactivity measurements of all liquid samples were carried out by liquid scintillation counting using a RackBeta liquid scintillation counter (LKB-Wallac, Model 526). The counts min^{-1} (cpm) obtained were then calculated according to the efficiency of the apparatus used. The radioactivity measured is directly proportional to the amount of CO_2 fixed in the organic compounds, and this was calculated as cpm mg^{-1} fresh weight of leaves which was then related to dry weight.

Statistical analysis

Statistical analyses were carried out using Minitab (ANOVA and GLM) packages for main effects and interactions. A test for significant differences between means at $P = 0.05$ was performed using the LSD test. The correlation coefficients were estimated by using the SPSS programme.

Results

Changes in soil moisture content

Soil moisture content progressively decreased as the duration of the stress period increased (Fig. 1) at both stages of plant growth. Interestingly, the mean value of the soil moisture content of droughted soil at the end of the stress period in the vegetative stage (12 days) was nearly the same as that observed at the end of the stress period in the reproductive stage (10 days).

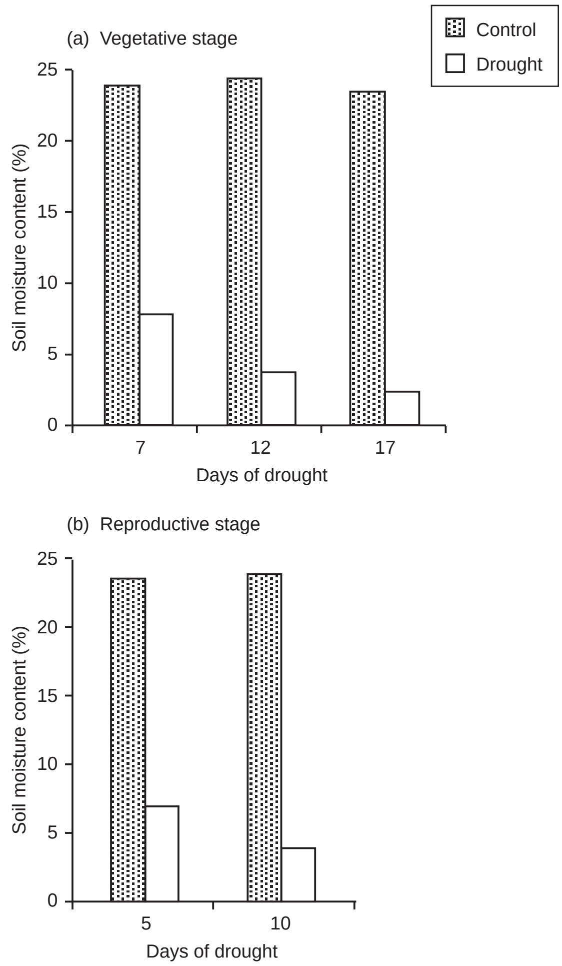

Fig. 1: Changes in soil moisture content (% oven-dried soil dry weight) in (a) the vegetative stage and (b) the reproductive stage

Growth criteria

The results for growth criteria of the cultivars are shown in Tables 1 and 2. The main effect of variety was significant for all growth parameters. Dorado had the smallest shoot and root size and in certain cases Giza 15 was larger in size than Hybrid 113. The main effect of water stress was to reduce all shoot criteria (shoot length, shoot fresh and dry weights, total green leaf area, specific leaf area and new leaf expansion rate) significantly after 12 and 10 days from withholding water in the vegetative and reproductive stages, respectively. The interaction treatment × variety was significant for all these parameters, Giza 15 and Hybrid 113 cultivars suffering greater reductions than Dorado. Increasing the stress period to 17 days in the case of Dorado, in the vegetative stage, generally reduced all shoot criteria to values lower than those at 12 days from withholding water. Expansion of new leaves appeared to be the most sensitive criterion to water deficit.

The main effect of drought stress on root growth was not consistent. Root fresh weight was sig-

Table 1: Effects of drought stress at the vegetative stage on mean values of growth parameters for three sorghum cultivars

Days of drought	Cultivar	Treatment	Shoot length (cm)	Shoot fresh weight (g)	Shoot dry weight (g)	Total green leaf area (cm^2)	Specific leaf area ($m^2\,kg^{-1}$)	New leaf expansion rate ($cm^2\,day^{-1}$)	Root fresh weight (g)	Root dry weight (g)	Root length (cm)	Number of adventitious roots	Root/shoot ratio	Relative growth rate ($mg\,g^{-1}\,day^{-1}$)	Net assimilation rate ($g\,m^{-2}\,day^{-1}$)
12	Giza 15	Control	101.00	8.09	1.01	289.81	63.70	3.77	1.76	0.31	28.83	10.00	0.31	62.48	1.4
		Drought	82.17	3.12	0.75	139.08	40.40	0.76	0.80	0.25	36.00	11.00	0.33	27.60	0.70
	Dorado	Control	61.67	2.98	0.42	135.23	52.03	1.54	0.43	0.07	18.00	8.00	0.17	27.02	0.90
		Drought	54.00	2.15	0.39	83.91	47.90	0.72	0.36	0.09	24.83	8.00	0.23	25.80	0.70
	Hybrid 113	Control	92.29	5.85	0.78	242.10	72.66	3.15	1.73	0.27	31.17	10.00	0.35	54.34	1.30
		Drought	73.33	3.72	0.70	135.50	47.93	0.89	1.06	0.29	33.58	16.00	0.41	33.60	1.00
	LSD (5%)		5.81	0.66	0.09	22.59	4.22	0.24	0.30	0.06	5.58	2.19	0.06	9.26	0.20
17	Dorado	Control	65.30	3.36	0.49	145.50	46.50	1.48	0.48	0.09	21.50	10.00	0.18	30.24	1.13
		Drought	55.63	1.73	0.41	75.77	40.30	0.51	0.26	0.10	25.00	9.00	0.24	12.12	0.64
	LSD (5%)		4.96	0.44	0.05	16.18	3.42	0.16	0.13	0.04	4.73	2.02	0.06	8.60	0.20

Table 2: Effects of drought stress at the reproductive stage on mean values of growth parameters for three sorghum cultivars

Days of drought	Cultivar	Treatment	Shoot length (cm)	Shoot fresh weight (g)	Shoot dry weight (g)	Total green leaf area (cm^2)	Specific leaf area ($m^2\,kg^{-1}$)	New leaf expansion rate ($cm^2\,day^{-1}$)	Root fresh weight (g)	Root dry weight (g)	Root length (cm)	Number of adventitious roots	Root/shoot ratio	Relative growth rate ($mg\,g^{-1}\,day^{-1}$)	Net assimilation rate ($g\,m^{-2}\,day^{-1}$)
10	Giza 15	Control	128.33	19.00	5.41	562.70	38.21	1.33	4.74	1.06	58.13	15.00	0.20	48.25	3.95
		Drought	123.00	7.18	3.80	251.00	22.53	0.17	2.85	1.05	59.13	16.00	0.28	4.25	0.09
	Dorado	Control	93.60	13.77	3.54	497.20	36.68	1.35	2.36	0.68	50.13	16.00	0.19	34.75	1.73
		Drought	83.00	8.94	2.86	274.40	32.50	0.48	1.84	0.71	60.83	16.00	0.25	14.75	0.08
	Hybrid 113	Control	118.83	15.81	4.26	515.00	42.04	1.50	3.90	0.98	57.96	16.00	0.23	42.25	2.95
		Drought	105.83	6.30	3.11	216.30	27.69	0.41	1.90	0.81	55.00	17.00	0.26	8.50	0.09
	LSD (5%)		6.95	1.36	0.40	38.66	3.43	0.10	0.50	0.13	5.11	1.00	0.03	5.20	0.25

Table 3: Mean values of root plasticity and drought susceptibility indices of three sorghum varieties at the vegetative and reproductive stages of plant development

Cultivar	Root plasticity	Drought susceptibility index for: total green leaf area	Drought susceptibility index for: shoot dry weight
Vegetative stage			
Giza 15	1.24	1.13	1.61
Dorado	1.40	0.82	0.42
Hybrid 113	1.08	0.96	0.63
LSD (5 %)	0.14	0.12	0.18
Reproductive stage			
Giza 15	1.02	1.05	1.14
Dorado	1.20	0.85	0.74
Hybrid 113	0.95	1.09	1.04
LSD (5%)	0.19	0.13	0.14

nificantly reduced; root length and number of adventitious roots were increased, while root dry weight was not changed at the end of applied stress during both stages of plant growth. In general, the interaction treatment × variety was significant, and this reflects the improved root growth of Dorado and the restricted root growth of Giza 15 and Hybrid 113, to some extent, in response to water stress.

Drought stress significantly increased the root/shoot ratio and greatly reduced the relative growth rate (RGR) and net assimilation rate (NAR) of sorghum after 12 and 10 days of stress at the vegetative and reproductive stages, respectively. The interaction treatment × variety was significant, and Giza 15 suffered a greater reduction in RGR and NAR than Hybrid 113; in turn, Hybrid 113 suffered a greater reduction than Dorado in response to water deficit.

Dorado appeared to have greater root plasticity than the other cultivars at both stages. The drought susceptibility index (DSI) of Dorado was also lower than those of the other cultivars at both stages of growth. Hybrid 113 had lower susceptibility index values than Giza 15 in the vegetative phase, but the difference was not significant in the reproductive phase (Table 3).

DSI appeared to be positively correlated with shoot size criteria, root dry weight, RGR and NAR ($r = 0.74$–0.95; $P < 0.01$) of sorghum plants in well-watered conditions at both stages. Although a negative correlation was found between the estimated DSI and root plasticity, the effect was significant only in the reproductive phase ($r = -0.77 - 0.89$; $P < 0.01$).

Photosynthetic pigments

The main effects of treatment, variety and time and the interactions treatment × variety, treatment × time and variety × time all were generally significant for chlorophyll a and chlorophyll b contents. Except for the increase of chlorophyll a and chlorophyll b at 7 days post-irrigation in the vegetative phase, chlorophyll contents appeared to decrease in stressed plants at all other sampling times at both stages; the effect being most pronounced in the case of Giza 15 (Fig. 2). Furthermore, chlorophyll content appeared to decrease with time.

Except for the increase maintained in Dorado in the reproductive phase, the carotenoid content did not change in sorghum plants in response to drought stress at either stage of plant growth (Fig. 3). The carotenoid content significantly increased with time at the reproductive stage only. The main effect of treatment was not significant, while the other main effects and the possible two-way interactions were significant for the total chlorophyll/carotenoid ratio at the vegetative stage. Dorado had a higher ratio than the other two cultivars and this ratio decreased significantly with time.

Drought plus defoliation appeared to increase the chlorophyll content to some extent, especially in the reproductive phase, as compared with drought alone.

DSI was not significantly correlated with total pigment content under well-watered conditions.

Photosynthetic assimilation of $^{14}CO_2$

Water deficit significantly reduced the soluble, insoluble and consequently the total photosynthetic metabolites in sorghum after 12 and 10 days of withholding water at the vegetative and reproductive stages, respectively. Generally, Dorado had higher soluble and total photosynthetic metabolites than the other cultivars.

Drought plus defoliation appeared to improve the photosynthetic capability of sorghum leaves and on some occasions the effect was significant as compared with drought alone.

The main effect of treatments on the soluble/insoluble photoassimilate ratio of sorghum generally was not significant, but the interaction was

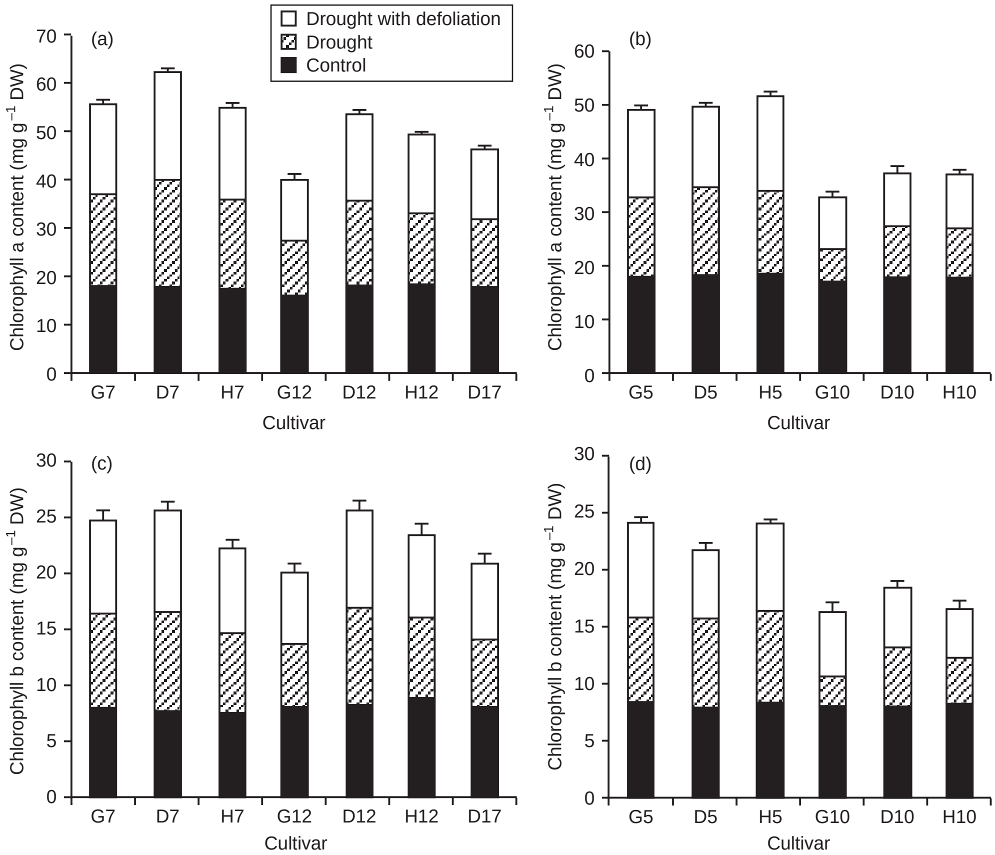

Fig. 2: Effects of drought stress on chlorophyll a and chlorophyll b contents of sorghum plants. (a) Chlorophyll a content at the vegetative stage; (b) chlorophyll a content at the reproductive stage; (c) chlorophyll b content at the vegetative stage; (d) chlorophyll b content at the reproductive stage. Abbreviations: G, Giza 15; D, Dorado; H, Hybrid 113. The numbers 7, 12 and 17 represent days post-irrigation at the vegetative stage, and numbers 5 and 10 represent days post-irrigation at the reproductive stage. The vertical line above each bar represents the LSD value at $P = 0.05$

significant at both stages. Of particular interest, this ratio was markedly increased in the less drought-tolerant cultivar, Giza 15, at the end of water deficit in the reproductive phase. Also, Dorado had a higher ratio in many cases than the other cultivars (Fig. 4).

Discussion

Vegetative growth of all sorghum cultivars was reduced at the end of the water stress periods at the vegetative and reproductive stages, and the effect was most pronounced for Giza 15. Water stress is known to induce loss of turgor which affects the rate of cell expansion and ultimately cell size, and consequently it decreases growth rate, stem elongation, leaf expansion and stomatal aperture (Hale and Orcutt 1987). The reduction of dry matter production under water stress conditions was reported to be mainly due to the reduction of leaf area (Terbea et al. 1995) and net photosynthesis and the increase in the rate of photorespiration (Perry et al. 1983).

The reduction of growth found here was associated with a reduction of all measured shoot characteristics (shoot dry weight, green leaf area, specific leaf area and new leaf expansion rate) and a smaller effect was noted on root growth. In some cases, the root growth was improved as compared with controls and this led to an increase in the root/shoot ratio. This supports the conclusion of Wright et al. (1983) that the reduction in sorghum growth caused by water deficit has proportionally less effect on root growth. Increased root depth will increase total water availability for the plant and this plays an important role in the drought avoidance mechanism (Jordan and Sullivan 1982). Plants exposed to 10 days of water deficit at the reproductive stage suffered a greater reduction in shoot growth, relative growth rate and net assimilation rate than those exposed to 12 days of drought at the vegetative stage. At these times the mean soil moisture content

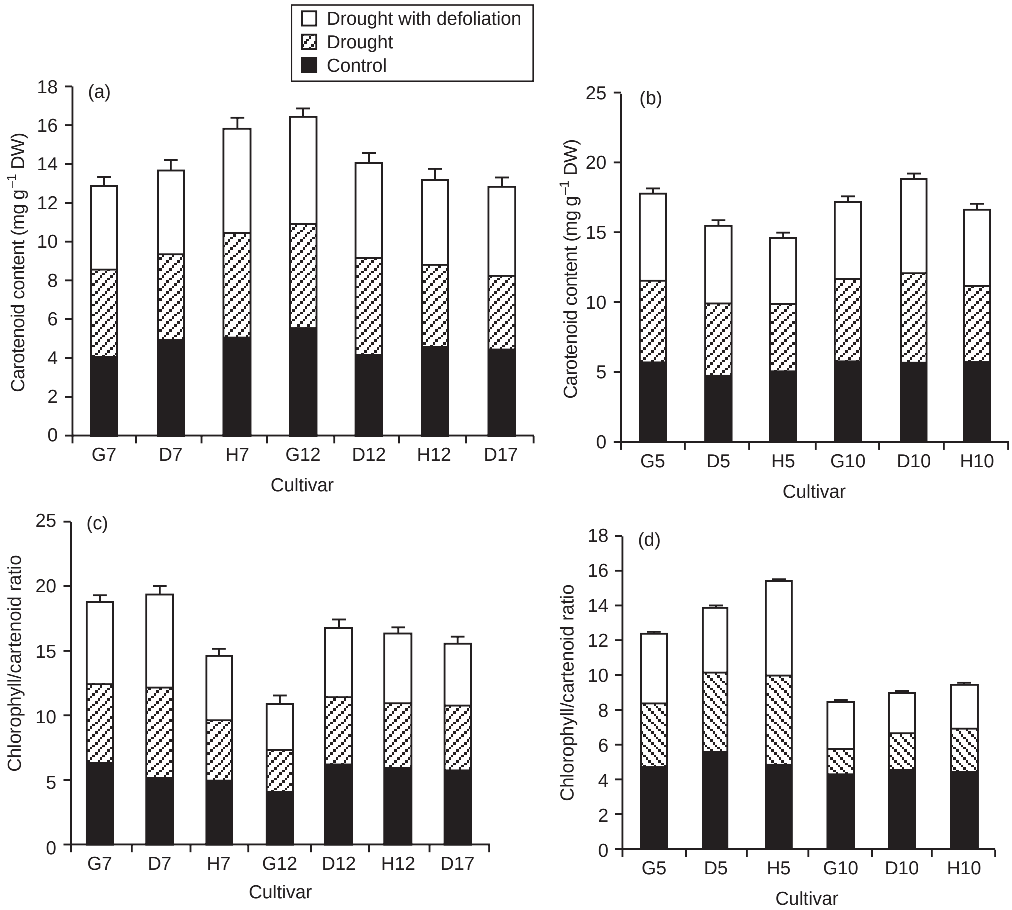

Fig. 3: Effects of drought stress on carotenoids and the chlorophyll/carotenoid ratio of sorghum plants. (a) Carotenoid content at the vegetative stage; (b) carotenoid content at the reproductive stage; (c) chlorophyll/carotenoid ratio at the vegetative stage; (d) chlorophyll/carotenoid ratio at the reproductive stage. For abbreviations, see Fig. 2. The vertical line above each bar represents the LSD value at $P = 0.05$

was 4.18 and 4.13 %, respectively. This supports the general conclusion that the reproductive stage is particularly sensitive to water deficit (Kramer 1983).

Our data indicate that chlorophyll a and chlorophyll b concentrations of all cultivars were elevated in response to short-term water stress (7 days) at the vegetative stage. After 12 days of withholding water at the vegetative stage, the chlorophyll contents of Giza 15 and Hybrid 113 were reduced, while that of Dorado remained unaltered. The chlorophyll content of Dorado was reduced 17 days post-watering. In the reproductive phase, the chlorophyll content was reduced in all cultivars 5 and 10 days post-irrigation. These results are consistent with those of many investigators who reported a reduction in chlorophyll content under drought conditions (El-Haak et al. 1992, El-Kheir et al. 1994), and the reduction appeared more pronounced in drought-susceptible than in drought-resistant genotypes (Ashraf et al. 1994).

In general, the carotenoid content was not changed in sorghum plants in response to water stress at either stage of plant growth. Consequently, there was a general progressive decline of the ratio of total chlorophyll/carotenoid with the progressive increase of the severity of stress conditions at the vegetative or the reproductive phase. This confirms the finding that chlorophylls are more sensitive to drought stress than carotenoids (Barry et al. 1992) and is consistent with the observed leaf yellowing and reduction of green leaf area at the end of the stress periods.

Defoliation appeared to improve, to a certain extent, the chlorophyll content of sorghum plants in the face of drought. An increase in chlorophyll content in the leaves remaining after defoliation has been reported by Suwignyo et al. (1995) under well-watered conditions.

Our data indicate that soluble photosynthates, insoluble photosynthates and consequently total

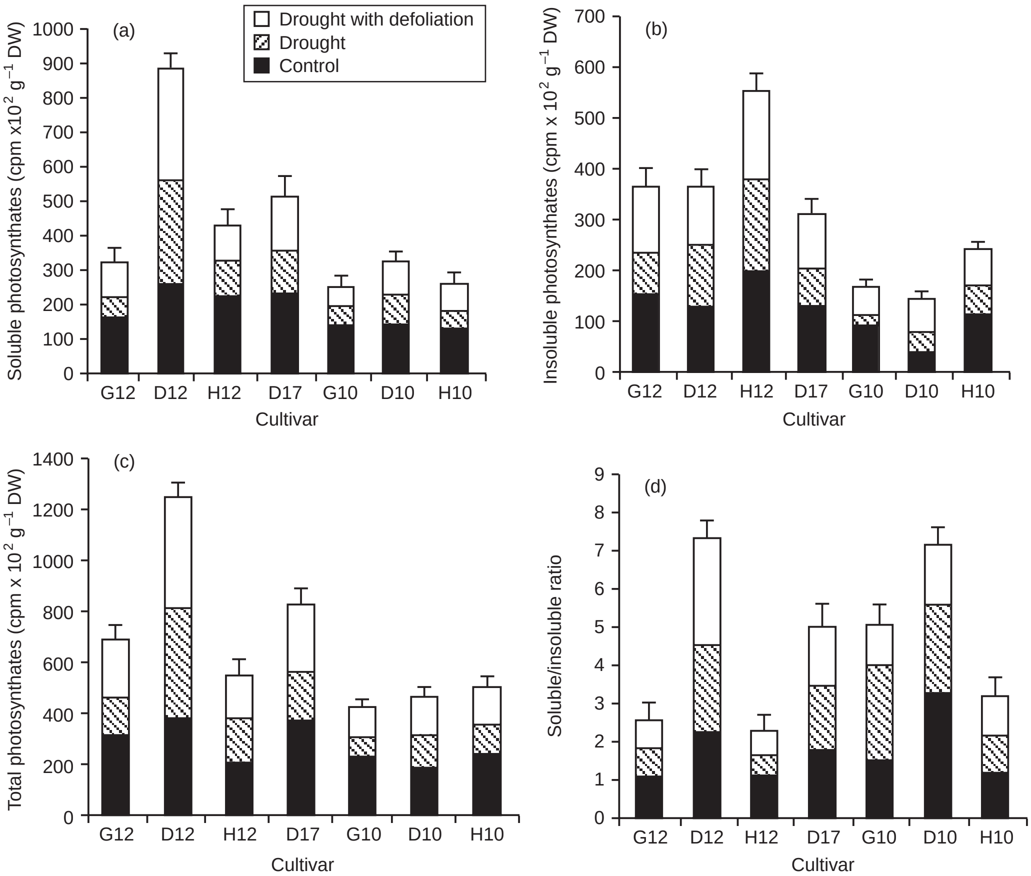

Fig. 4: Effects of drought stress on photosynthetic assimilation of $^{14}CO_2$ in sorghum plants. (a) Soluble photosynthates; (b) insoluble photosynthates; (c) total photosynthates; (d) soluble/insoluble photosynthate ratio. Abbreviations: G, Giza 15; D, Dorado; H, Hybrid 113. The numbers 12 and 17 represent days post-irrigation at the vegetative stage, and 10 represents days post-irrigation at the reproductive stage

photosynthates were reduced in all cultivars at the end of the drought periods in the vegetative and the reproductive phases of plant growth. Dorado had a higher capacity of $^{14}CO_2$ fixation than the other two cultivars and was able to maintain its assimilation rate near that of the control at 12 days post-irrigation at the vegetative stage. In agreement with this result, Younis et al. (1993) demonstrated the effects of soil water deficit on $^{14}CO_2$ fixation in 25-, 45-, 70- and 100-day-old *Vicia faba* plants. They found that soluble, insoluble and total photosynthates were markedly reduced at all stages in response to water stress.

Defoliation partially alleviated the devastating effect of drought stress on $^{14}CO_2$ fixation. Photosynthetic enhancement by defoliation might have been due to the combined enhancement of Rubisco activity and ribulose-1,5-bi-phosphate regeneration rate as found in *Phaseolus vulgaris* (von Caemmerer and Farquhar 1984). The change in phytohormone content, for example the accumulation of ABA, was also proposed to regulate the effects of defoliation on carbon exchange (Suwignyo et al. 1995).

Our results show that the main effect of water stress taken across varieties on soluble/insoluble photosynthate ratios in sorghum was not significant at the end of the stress periods at the vegetative or the reproductive stage. However, the ratios were greatly increased in Giza 15 only in response to water deficit at the reproductive phase. An increase in soluble/insoluble photosynthate ratios under water stress conditions was also demonstrated by Younis et al. (1993). These authors suggested that water deficit inhibits the transformation of soluble photosynthates to insoluble photosynthates. Thus the increased ratio in Giza 15 at the reproductive phase suggests that the inhibition of transformation of soluble to insoluble photosynthates occurs only under severe water deficit conditions. However, the higher soluble/insoluble ratios observed in Dorado than in the other cultivars (control and stressed plants) could not be due to the inhibition of transformation of soluble to insoluble photosynthates, but could be the result of its inherent ability to maintain high contents of soluble metabolites, and this may play an important role in its adaptation to water stress.

In conclusion, the present results showed that Dorado is the most drought-resistant cultivar and Giza 15 is the least tolerant at both stages of growth. The resistance of Dorado could be attributed to its smaller shoot size and growth rate, higher soluble/insoluble photosynthate ratios in control and in stressed plants, higher root plasticity and greater increase in root/shoot ratio than in the other two cultivars under drought conditions. This was also reflected in the ability of Dorado to suffer less reduction in growth and chlorophyll concentration than the other cultivars in response to the stress conditions. This final conclusion is in accord with the results of Matthews et al. (1990), who reported that drought-resistant sorghum lines had slower shoot and root growth rates and slower soil water extraction rates, but higher root/shoot ratios than susceptible lines under control or drought stress conditions.

Zusammenfassung

Einflüsse von Wasserstress auf Wachstum, Pigmente und $^{14}CO_2$ -Assimilation bei drei *Sorghum* Kultivaren

Die Einflüsse von Dürrebehandlungen auf das Wachstum, die Pigmente und $^{14}CO_2$-Assimilation wurden bei drei *Sorghum*-Kultivaren untersucht. Wasserstreß wurde entweder in der vegetativen oder der reproduktiven Phase angewendet und führte zu einer Reduktion der relativen Wachstums-und Netto-Assimilationsraten. Das Wurzelwachstum war geringer beeinträchtigt durch Wasserstreß und in einigen Fällen verstärkt; als Folge war die Wurzel/Spross-Relation erhöht. Die Empfindlichkeit gegenüber Dürrestress war in der reproduktiven Phase stärker als in der vegetativen. Dorado wies die höchste Dürretoleranz auf während Giza 15 über die geringste Toleranz verfügte, wie sich aus der Kalkulation des Dürreempfindlichkeitsindex für Gesamtblattgrünfläche und Sprosstrockengewicht ergab. Kurzer Wasserstress in der vegetativen Phase (7 Tage) erhöhte den Chlorophyllgehalt in den Blättern, langanhaltender Stress in der vegetativen und reproduktiven Phase reduzierte den Chlorophyllgehalt. Der Karotenoidgehalt war grundsätzlich bei Dürrestress nicht beeinträchtigt. Die $^{14}CO_2$ Fotoassimilation weist darauf hin, daß lösliche, unlösliche und als Konsequenz Gesamtfotosynthetate am Ende der Stressperiode in beiden Entwicklungsstadien reduziert waren.

References

Ashraf, M. Y., A. R. Azmi, A. H. Khan, and S. A. Ala, 1994: Effect of water stress on total phenols, peroxidase activity and chlorophyll content in wheat (*Triticum aestivum* L.). Acta Physiol. Plant. **16,** 185—191.

Barry, P., R. P. Evershed, A. Young, M. C. Prescott, and G. Britton, 1992: Characterization of carotenoid acyl esters produced in drought-stressed barley seedlings. Phytochemistry **31,** 3163—3168.

Beadle, C. L., 1993: Growth analysis. In: D. O. Hall, J. M. O. Scurlock, H. R. Bolhàr-Nordenkampf, R. C. Leegood, and S. P. Long (eds), Photosynthesis and Production in a Changing Environment. A Field and Laboratory Manual, pp. 36—46. Chapman & Hall, London.

Creelman, R. A., H. S. Mason, R. J. Bensen, J. S. Boyer, and J. E. Mullet, 1990: Water deficit and abscisic acid cause differential inhibition of shoot versus root growth in soybean seedlings. Analysis of growth, sugar accumulation, and gene expression. Plant Physiol. **92,** 205—214.

El-Haak, M. A., M. M. Migahid, and K. Wegmann, 1992: Response of photosynthetic pigments to drought and salt stress in some desert species. Feddes-Repertorium **103,** 573—577.

El-Kheir, M. S. A., S. A. Kandil, and B. B. Mekki, 1994: Physiological response of two soybean cultivars grown under water stress conditions as affected by CCC treatment. Egyptian J. Physiol. Sci. **18,** 179—200.

Fischer, R. A., and R. Maurer., 1978: Drought resistance in spring wheat cultivars. 1. Grain yield responses. Aust. J. Agric. Res. **29,** 897—912.

Hale, M. G., and D. M. Orcutt, 1987: The Physiology of Plants Under Stress. Wiley-Interscience Publications, New York.

Hulse, J. H., E. M. Laing, and O. E. Pearson, 1980: Sorghum and Millets. Their Composition and Nutritive Value. Academic Press, London.

Jordan, W. R., and C. Y. Sullivan, 1982: Reaction and resistance of grain sorghum to heat and drought. In: L. R. House, L. K. Mughogho, and J. M. L. Peacock (eds), Sorghum in the Eighties, pp. 131—142. ICRISAT.

Kicheva, M. I., T. D. Tsonev, and L. P. Popova, 1994: Stomatal and non stomatal limitations to photosynthesis in two wheat cultivars subjected to water stress. Photosynthetica **30,** 107—116.

Klubertanz, T. H., L. P. Pedigo, and R. E. Carlson, 1996: Soybean physiology, regrowth and senescence in response to defoliation. Agron. J. **88,** 577—582.

Kramer, P. J., 1983: Water Relations of Plants. Academic Press, London.

Martinez, C. A., C. Guerrero, and V. Moreno, 1995: Diurnal fluctuations of carbon exchange rate, proline content and osmotic potential in two water-stressed potato hybrids. Revista Brasil. Fisiol. Vegetal. **7,** 27—33.

Matthews, R. B., D. M. Reddy, A. U. Rani, S. N. Azam-Ali, and J. M. Peacock, 1990: Response of four sorghum lines to mid-season drought. I. Growth, water use and yield. Field Crop Res. **25,** 279—296.

Metzner, H., H. Rau, and H. Senger, 1965: Untersuchungen zur synchronisierbarkeit einzelner pigmentmangel mutanten von *Chlorella*. Planta **65,** 186—194.

Pelleschi, S., J. P. Rocher, and J. L. Prioul, 1997: Effect of water restriction on carbohydrate metabolism and photosynthesis in mature maize leaves. Plant Cell Environ. **20,** 493—503.

Perry, S. W., D. R. Krieg, and R. B. Hutmacher, 1983: Photosynthetic rate control in cotton. Plant Physiol. **73,** 662—665.

Reader, R. J., A. Jalili, J. P. Grime, R. E. Spencer, and N. Matthews, 1993: A comparative study of plasticity in seedling rooting depth in drying soil. J. Plant Ecol. Oxford **81,** 543—550.

Ritchie, S. W., H. T. Nguyen, and A. S. Holaday, 1990: Leaf water content and gas exchange parameters of two wheat genotypes differing in drought resistance. Crop Sci. **30,** 105—111.

Ryle, G. J. A., and C. E. Powell, 1975: Defoliation and regrowth in the graminaceous plant: the role of current assimilate. Ann. Bot. **39,** 297—310.

Shaddad, M. A., 1979: Studies on the effect of salinity on growth, photosynthetic activity and chemical composition of some oil producing plants. PhD Thesis, Assuit University, Egypt.

Soliman, A. I., 1984: Effect of herbicides on photosynthesis and nitrogen metabolism of some green algae. PhD Thesis, Mansoura University, Egypt.

Suwignyo, R. A., A. Nose, Y. Kawamitsu, M. Tsuchiya, and K. Wasano, 1995: Effects of manipulations of source and sink on the carbon exchange rate and some enzymes of sucrose metabolism in leaves of soybean (*Glycine max* L. Merr.). Plant Cell Physiol. **36,** 1439—1446.

Terbea, M., A. V. Vranceanu, E. Petcu, D. S. Craiciu, and G. Micut, 1995: Physiological response of sunflower plants to drought. Romanian Agric. Res. **3,** 61—67.

Turner, N. C., 1974: Stomatal behavior and water status of maize, sorghum and tobacco under field conditions. II. At low soil water potential. Plant Physiol. **53,** 360—365.

von Caemmerer, S., and G. D. Farquhar, 1984: Effects of partial defoliation, changes of irradiance during growth, short term water stress and growth at enhanced, p(CO_2) on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. Planta **160,** 320—329.

Wright, G. C., R. C. G. Smith, and J. R. McWilliam, 1983: Differences between two grain sorghum genotypes in adaptation to drought stress. I. Crop growth and yield responses. Aust. J. Agric. Res. **34,** 615—626.

Younis, M. E., O. A. El-Shahaby, M. N. A. Hasaneen, and A. M. Gaber, 1993: Plant growth, metabolism and adaptation in relation to stress conditions: XVII. Influence of different water treatments on stomatal apparatus, pigments and photosynthetic capacity in *Vicia faba*. J. Arid Environ. **25,** 221—232.