PHOTOSYNTHETICA 35 (1): 129-138, 1998

Effects of water deficit on photosynthetic rate and osmotic adjustment in tetraploid wheats

D. REKIKA*, M.M. NACHIT**, J.L. ARAUS*** and P. MONNEVEUX*,+

UFR de Génétique et d'Amélioration des Plantes, ENSA-INRA,
*2 Place Pierre Viala 34060 Montpellier Cedex 1, France**
International Center for Agricultural Research in the Dry Areas (ICARDA),
*P.O. Box 5466, Aleppo, Syria***
Unidad de Fisiologia vegetal, Departamento de Biologia vegetal, Facultad de Biología,
*Universidad de Barcelona, 08028 Barcelona, España****

Abstract

Osmotic adjustment, accumulation of soluble saccharides, and photosynthetic gas exchange were studied in five durum wheat (*Triticum turgidum* L. var. *durum*) and one wild emmer wheat (*Triticum turgidum* L. var. *dicoccoïdes*) cultivars of contrasting drought tolerance and yield stability. Soil water contents (SWC) were 100, 31, 20, and 12 % of maximum capillary capacity. Under mild water stress (SWC 31 to 20 %), osmotic adjustment capacity and high accumulation of saccharides were found in cv. Chaml, a high yielding and drought tolerant cultivar, and in var. *dicoccoïdes*, while lowest values were noted in the durum wheat landraces Oued-Zenati and Jennah-Khotifa. Under more severe water stress (SWC 12 %), the cv. Chaml maintained higher net photosynthetic rate (P_N) than other genotypes. The observed changes in the ratio intercellular/ambient CO_2 concentration (c_i/c_a) indicated that under mild and severe water stress, the decrease in P_N was mainly due to stomatal and non-stomatal factors, respectively.

Additional key words: drought tolerance; durum wheat; intercellular CO_2 concentration; leaf water status; *Triticum*; water stress; wild emmer wheat.

Introduction

Osmotic adjustment is an important mechanism of drought tolerance in plants under natural conditions (*e.g.*, Begg and Turner 1976, Turner and Jones 1980, Wright *et al.*

Received 24 February 1997, *accepted* 18 June 1997.

+Author for correspondence; fax: (33)-4-67-04-54-15, e-mail: monneveux@ensam.inra.fr

Abreviations: ASS - accumulation of soluble saccharides; c_a - ambient CO_2 concentration; c_i - intercellular CO_2 concentration; P_N - net photosynthetic rate; g_s - stomatal conductance; PPFD - photosynthetic photon flux density; RWC - relative water content; SWC - soil water content; Ψ_w - leaf water potential; Ψ_π - leaf osmotic potential; $\Delta\Psi_\pi$ - osmotic adjustment.

1983). Under field conditions, wheat plants selected for high osmotic adjustment yielded 1.5 and 1.6 times more than plants selected for low osmotic adjustment (Morgan *et al.* 1986). Wheat accumulates saccharides and free amino acids during water deficit (Virgona and Barlow 1991, Kameli and Lösel 1993). Rascio *et al.* (1994) found that the accumulation of reducing saccharides in durum wheat was associated with a decrease in osmotic potential when water stress increased gradually. Kameli and Lösel (1995) reported that the contribution of saccharides to osmotic adjustment was almost 95 %. In other experiments with durum wheat, total concentration of soluble saccharides was positively related with the water stress tolerance of the studied genotypes (Al-Hakimi and Monneveux 1993, Al-Hakimi *et al.* 1995). Accumulated saccharides protect membrane and proteins against dehydration (Crowe *et al.* 1990).

Several works showed that osmotic adjustment maintained stomatal conductance (g_s), and photosynthesis (P_N) in water stressed plants (*e.g.*, Hsiao *et al.* 1976, Turner *et al.* 1978, Turner and Jones 1980, Ackerson and Hebert 1981, Ludlow *et al.* 1985). Nevertheless, contradictory results were also reported (Girma and Krieg 1992, Premachandra *et al.* 1992, Munns 1988).

The aim of the present study was to compare the effect of water stress on osmotic adjustment capacity of five durum wheat and one wild emmer wheat genotypes. Further, the relations between osmotic adjustment and maintenance of gas exchange rate in these plants grown under different soil moistures were determined. The ultimate objective was to examine the possibility of using physiological parameters, namely osmotic adjustment, P_N, and g_s as predictive criteria for drought resistance in wheat.

Materials and methods

Plants: Five durum wheat (*Triticum turgidum* L. var. *durum*) and one wild emmer wheat (*Triticum turgidum* L. var. *dicoccoïdes*) cultivars differing in potential yield were used. Oued-Zenati and Jennah-Khotifa are two durum wheat landraces from Algeria and Tunisia, respectively, with low productivity and yield stability (Meziani *et al.* 1992). Cham1, Korifla, and Kabir are three improved cultivars selected by ICARDA: drought tolerance and yield stability of Cham1 are high (Meziani *et al.* 1992, Pecceti and Annicchiarico 1993), and Korifla is characterized by high yielding and drought tolerance. Kabir was identified as drought susceptible cultivar with low productivity (Ali-Dib *et al.* 1990). The accession of var. *dicoccoïdes* used in our experiment (n° 600808) has been collected in dry areas of Jordan.

Seeds were sterilized in 0.5 % NaOCl for 15 min, then washed 3 times with sterile water, and placed in Petri dishes to germinate. Four-d-old seedlings were transfered to 2 500 cm^3 plastic pots (5 seedlings per pot) of mixed compost and vermiculite (3:1, v:v). Nutrient solution (N, P, K *Hakaphos-BASF*) was added at the two-leaf stage. Plants were grown in a controlled growth chamber with 12 h photoperiod, photosynthetic photon flux density of 450 μmol m^{-2} s^{-1}, and a day/night temperature and relative humidity of 20/18 °C and 60/70 %, respectively.

After 4 weeks of growth (4-leaf stage) with normal water supply, water stress was applied by withholding water for half of the pots, selected at random. The development of water stress was monitored by continuous measurement of soil water content (SWC). Forty randomly selected pots were weighed early in the morning, and the average soil water content was calculated as the per cent of total available water. The soil water content at saturation was determined experimentally by adding a known volume of water to the pots, and calculating the average volume of water that was retained by the substrate of individual pots after drainage. The measurements were done four times during the drought cycle corresponding to 100 (control), 31, 20, 12 % of SWC. In all experiments, five control and four or five stressed plants were sampled from separate pots for each soil moisture and genotype.

Plant water status and osmotic adjustment: Relative water content (RWC) was measured gravimetrically on the youngest fully expanded leaf according to Barrs (1968):

$$\mathrm{RWC}\ [\%] = [(\mathrm{FM} - \mathrm{DM})/(\mathrm{TM} - \mathrm{DM})] \times 100,$$

where FM was the fresh mass, TM the turgid mass, and DM the dry mass. Leaf water potential (Ψ_w) was determined using a Scholander *et al.* (1964) pressure chamber (*Soil moisture 3005*, Santa Barbara, CA, USA), on the penultimate leaf. After Ψ_w measurements, the leaves were wrapped in aluminium foil, immediately frozen in liquid nitrogen, and stored at -20 °C. Osmotic potential (Ψ_π) was measured on these samples using a freezing-point microosmometer (*GS/IJ, Roebling*, Berlin, Germany). The accumulation of total soluble saccharides was measured using an anthrone method according to Shields and Burnett (1960). Osmotic adjustment ($\Delta\Psi_\pi$) was calculated as the difference in osmotic potential at full turgor (estimated according to Wilson *et al.* 1979) between control and stressed plants (Ludlow *et al.* 1983).

Gas exchange rates on intact youngest fully expanded leaves were measured with a portable photosynthesis system *LI-6200* (*LI-COR*, Lincoln, NE, USA) and a 1149 cm^3 leaf chamber at: 570 to 600 $\mu\mathrm{mol\ m^{-2}\ s^{-1}}$ PPFD (provided by mixed incandescent and fluorescent lamps), leaf temperature between 25 and 23 °C, and a leaf-to-air vapour pressure difference of 0.98 KPa. Leaf area was previously determined by multiplying the length by the width of the leaf included within the chamber. Leaf gas exchange rates were automatically calculated from slopes of CO_2 depletion and H_2O increases in the system in 30 s sampling periods. Intercellular CO_2 partial pressure was calculated from g_s, P_N, and external CO_2 partial pressure (Farquhar and Sharkey 1982). Gas exchange measurements were performed at the same levels of soil moisture used in the analysis of osmotic adjustment.

Statistic analysis: Values were subjected to analysis of variance, achieved by the Statistical Analysis System (*SAS Institute*, Cary, USA). Differences of means were based on the Duncan's least significant difference test (LSD).

Results

Leaf water status parameters: Ψ_w, Ψ_π, and RWC of the six tetraploid wheats decreased as water stress increased (Table 1). Significant differences for Ψ_w appeared only under moderate stress (SWC = 31 %). In well watered plants (control), significant differences for Ψ_π were observed among genotypes within each SWC whereas for Ψ_w significant differences were obtained only at 31 and 20 % of SWC.

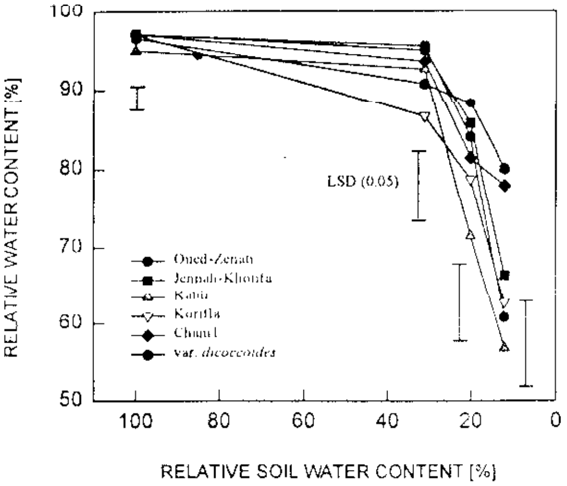

Fig. 1. Relative water content of six tetraploid wheats under increasing water stress conditions. LSD bars for comparison of genotypes at each SWC.

Table 1. Effect of different soil water content (31, 20, and 12 %) on leaf water potential, Ψ_w [MPa] and leaf osmotic potential, Ψ_π [MPa] of six tetraploid wheats. Means within a column not sharing the same letter are significantly different based on the LSD test.

Parameter	Genotype	31%		20%		12%	
		control	stressed	control	stressed	control	stressed
Ψ_w	Cham1	-1.05 b	-1.22 b	-0.81 b	-1.52 a	-0.93 a	-1.74 a
	Jennah-Khotifa	-0.85 c	-1.17 b	-0.76 b	-1.25 b	-0.90 a	-1.69 a
	Oued-Zenati	-0.84 c	-1.14 b	-0.75 b	-1.26 b	-0.89 a	-1.70 a
	Kabir	-1.20 a	-1.26 ab	-1.14 a	-1.29 ab	-1.20 a	-2.10 a
	Korifla	-0.86 c	-1.17 b	-0.73 b	-1.31 ab	-0.79 a	-1.88 a
	var. *dicoccoïdes*	-1.06 b	-1.42 a	-1.10 a	-1.28 ab	-1.01 a	-1.63 a
	LSD (0.05)	0.14	0.16	0.18	0.22	0.49	0.64
Ψ_π	Cham1	-1.22 c	-1.43 a	-1.21 bc	-1.79 ab	-1.20 cb	-2.31 a
	Jennah-Khotifa	-1.29 b	-1.36 a	-1.23 b	-1.50 bc	-1.22 cb	-1.78 bc
	Oued-Zenati	-1.28 b	-1.34 a	-1.18 cd	-1.23 c	-1.20 cb	-1.69 c
	Kabir	-1.40 a	-1.48 a	-1.31 a	-1.94 a	-1.54 a	-2.08 ab
	Korifla	-1.18 d	-1.42 a	-1.16 d	-1.52 bc	-1.15 c	-1.81 bc
	var. *dicoccoïdes*	-1.23 c	-1.43 a	-1.34 a	-1.46 c	-1.29 b	-1.97 abc
	LSD (0.05)	0.04	0.15	0.04	0.29	0.10	0.33

All genotypes with exception of cv. Korifla showed a relatively stable RWC until SWC of 20 % (Fig. 1). Genotypes Chaml and var. *dicoccoïdes* 600808 exhibited a better capacity to maintain RWC at low SWC (RWC of 78.0 and 80.1 % at 12 % SWC, respectively), Jennah-Khotifa and Korifla were intermediate, whereas Kabir and Oued-Zenati exhibited the lowest RWC (56.8 and 60.8 %) at SWC 12 %, respectively.

The differences in osmotic potentials among the genotypes were much less pronounced at 31 % than at either 20 or 12 % of maximum SWC (Table 1). At SWC 12 %, Oued-Zenati and Jennah-Khotifa had the highest osmotic potential (-1.69 and -1.78 MPa, respectively) followed by Korifla, var. *dicoccoides* 600808, Kabir, and Chaml (with values of -1.81, -1.98, -2.09, and -2.31 MPa, respectively).

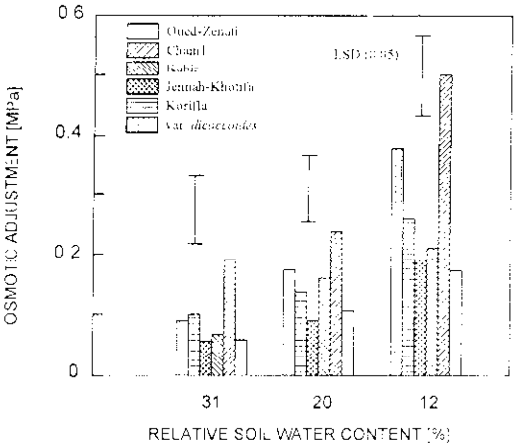

Fig. 2. Osmotic adjustment capacity at different relative soil water content in six tetraploid wheats. LSD bars are indicated at the top for each SWC.

Chaml and the wild emmer wheat showed the highest osmotic adjustment capacity especially at the most severe soil water stress (SWC = 12 %) while Korifla and Kabir exhibited the lowest one (Fig. 2). The two landraces Oued-Zenati and

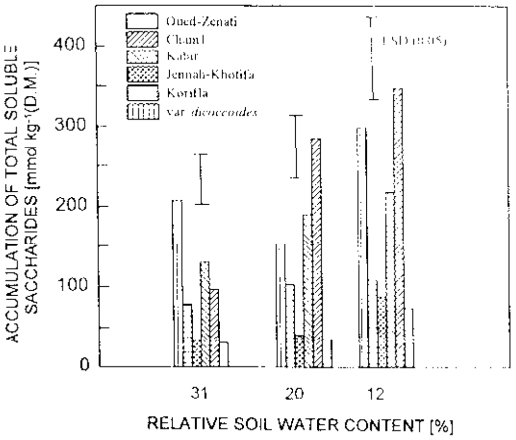

Fig. 3. Accumulation of soluble saccharides of six tetraploid wheats under water stress. LSD bars are indicated at the top for each SWC.

Jennah-Khotifa did not show osmotic adjustment capacity at any level of soil water availability.

Accumulation of soluble saccharides (ASS) regularly increased with increased water stress (Fig. 3) in all genotypes. Under SWC = 12 % this increase was four times greater in Cham1 and var. *dicoccoïdes* 600808 [348 and 300 mmol kg^{-1}(D.M.), respectively] than in Oued-Zenati and Jennah-Khotifa [74 and 89 mmol kg^{-1}(D.M.), respectively] whereas ASS in Korifla and Kabir was intermediate.

Photosynthetic gas exchange: In all genotypes, P_N and g_s declined with increasing water stress (Table 2). As compared with the maximum rate measured at 100 % of SWC, P_N decreased by *ca.* 25 and 55 % at 31 and 20 % of maximum SWC, respectively. At SWC 12 %, mean decrease across genotypes was 75 %; Cham1 had the highest P_N, and Kabir and Oued-Zenati the lowest ones.

The g_s was more affected by water stress than P_N: mean g_s values decreased by 86 % during the change from 100 to 12 % SWC, Cham1 showed the highest g_s (0.07 mol m^{-2} s^{-1}) (Table 2).

Table 2. Effect of water stress on net photosynthetic rate (P_N) [μmol(CO_2) m^{-2} s^{-1}], stomatal conductance (g_s) [mol m^{-2} s^{-1}], and cellular/ambient CO_2 concentration (c_i/c_a) in five durum wheat genotypes. Means within a column not sharing the same letter are significantly different based on the LSD test.

		Relative soil water content [%]			
		100	31	20	12
P_N	Cham1	13.0 ± 0.6 a	11.2 ± 0.7 a	7.2 ± 0.6 a	5.5 ± 0.4 a
	Jennah-Khotifa	12.1 ± 0.5 b	7.9 ± 0.9 c	5.5 ± 0.2 b	2.6 ± 0.3 b
	Oued-Zenati	12.0 ± 0.9 b	8.9 ± 0.6 bc	4.5 ± 0.4 c	2.2 ± 0.6 bc
	Kabir	11.9 ± 0.7 bc	9.2 ± 0.8 b	6.0 ± 0.4 b	1.9 ± 0.9 c
	Korifla	11.1 ± 0.5 c	8.1 ± 1.0 bc	4.0 ± 0.9 c	2.4 ± 0.3 bc
	LSD (0.05)	0.87	1.09	0.62	0.58
g_s	Cham1	0.30 ± 0.02 bc	0.16 ± 0.03 a	0.11 ± 0.04 a	0.07 ± 0.01 a
	Jennah-Khotifa	0.31 ± 0.03 b	0.13 ± 0.03 ab	0.09 ± 0.03 ab	0.04 ± 0.00 b
	Oued-Zenati	0.32 ± 0.03 b	0.12 ± 0.02 ab	0.06 ± 0.02 b	0.03 ± 0.00 c
	Kabir	0.36 ± 0.03 a	0.11 ± 0.04 b	0.05 ± 0.02 b	0.04 ± 0.01 bc
	Korifla	0.27 ± 0.02 c	0.14 ± 0.03 ab	0.06 ± 0.03 b	0.03 ± 0.00 bc
	LSD (0.05)	0.03	0.04	0.03	0.01
c_i/c_a	Cham1	0.74 ± 0.02 a	0.62 ± 0.07 a	0.54 ± 0.07 b	0.63 ± 0.05 c
	Jennah-Khotifa	0.67 ± 0.02 c	0.57 ± 0.05 bc	0.52 ± 0.02 b	0.66 ± 0.03 bc
	Oued-Zenati	0.72 ± 0.03 ab	0.56 ± 0.02 c	0.57 ± 0.12 a	0.71 ± 0.05 ab
	Kabir	0.69 ± 0.02 bc	0.59 ± 0.05 abc	0.52 ± 0.05 b	0.73 ± 0.06 a
	Korifla	0.66 ± 0.02 c	0.61 ± 0.03 ab	0.50 ± 0.04 c	0.67 ± 0.06 abc
	LSD (0.05)	0.03	0.02	0.02	0.06

The g_s was more affected by water stress than P_N: mean g_s values decreased by 86 % during the change from 100 to 12 % SWC, Cham1 showed the highest g_s (0.07 mol m^{-2} s^{-1}) (Table 2).

The c_i/c_a ratio decreased from 0.69 at 100 % SWC to 0.53 at 20 % SWC (Table 2). However, under severe water stress (SWC = 12 %) a strong increase in the c_i/c_a ratio was observed, reaching values of 0.68. For Oued-Zenati this increase was observed already at 20 % SWC.

Discussion

Higher genotypic variation was found for RWC than for leaf water potential under stress; this is in accordance with Schonfeld *et al.* (1988). The better capacity to maintain RWC of Cham1 and var. *dicoccoïdes* 600808 could be associated to their capacity to accumulate higher quantities of soluble saccharides, decreasing thus Ψ_π and increasing osmotic adjustment capacity. These findings are in good agreement with the results presented by Rascio *et al.* (1994) and Kameli and Lösel (1995) for durum wheat plants submitted to water stress. Positive relationships between ASS, RWC, and drought tolerance have also been observed in other tetraploid wheats (Al-Hakimi and Monneveux 1993). The high osmotic adjustment of the improved cv. Cham1 could be associated with its reported high productivity and yield stability under drought (Meziani *et al.* 1992, Pecceti and Annicchiarico 1993), while the drought susceptible cv. Kabir which was more affected by severe water stress showed a low osmotic adjustment capacity. In var. *dicoccoïdes*, the maintenance of RWC could be also associated with its capacity to maintain high Ψ_w under water stress which could be explained by a strategy of stress avoidance (Turner 1986).

Water stress caused a significant reduction in P_N of all genotypes studied. Under mild water stress the decrease in P_N was significantly lower in Cham1 than in the other genotypes. This decrease in P_N could be explained by stomatal closure. Sharkey and Seemann (1989) conclude that reduction in whole leaf P_N caused by mild water stress is primarily the result of stomatal closure, and that there is no indication of damage to chloroplast reactions. At more severe stress, P_N continued to decrease, while the c_i/c_a ratio increased significantly and reached values similar to those obtained in well watered plants. Thus, the decrease in P_N could result from non-stomatal factors which affected photosynthetic capacity (Bradford and Hsiao 1982, Schulze 1986, Martin and Rilling 1995, Biehler *et al.* 1996). In the landrace Oued-Zenati, P_N and g_s were significantly affected by severe water stress. In this landrace a high accumulation of proline (Monneveux and Nemmar 1986) and a limited modification of fluorescence quenching (Havaux *et al.* 1988) have been reported. These physiological traits, in addition to other morphological traits, described by Ali-Dib and Monneveux (1992), could be involved in the capacity of this landrace to tolerate the strong water deficit which characterizes its origin (the Algerian High Plateaux). This tolerance could be, however, associated with a low yield.

The variations in P_N at severe water stress could be mainly explained by genotypic differences in osmotic adjustment capacity observed in isolated chloroplasts by

Berkowitz (1987). Comparable results have been reached by Turner *et al.* (1978) and Conroy *et al.* (1988). The high $\Delta\Psi_\pi$ capacity of var. *dicoccoides* 600808 would be a good trait to introgress into durum wheat germplasm.

In summary, assessment of osmotic adjustment capacity and photosynthesis leads to a better understanding of genotypic behaviour under water stress. The high variability shown for water status parameters and photosynthesis, and the relationship observed between their responses to water stress and drought tolerance suggest the possibility to use these traits as prediction criteria for yield in dry conditions. Assessment of morphophysiological traits and agronomical values is actually conducted on 118 SSD (single seeds descent) lines from the cross Jennah-Khotifa× Cham1 to find QTL's related with these traits.

References

Ackerson, R.C., Hebert, R.R.: Osmoregulation in cotton in response to water stress. I. Alterations in photosynthesis, leaf conductance, translocation, and ultrastructure. - Plant Physiol. **67**: 484-488, 1981.

Al-Hakimi, A., Monneveux, P.: Variation of some morphophysiological traits of drought tolerance in tetraploid wheats. - In: Damania, A.B. (ed.): Biodiversity and Wheat Improvement. Pp. 199-216. John Wiley and Sons, Chichester New York - Brisbane - Toronto - Singapore 1993.

Al-Hakimi, A., Monneveux, P., Galiba, G.: Soluble sugars, proline, and relative water content (RWC) as traits for improving drought tolerance and divergent selection for RWC from *T. polonicum* into *T. durum*. - J. Genet. Breed. **49**: 237-244, 1995.

Ali-Dib, T., Monneveux, P.: Adaptation à la sécheresse et notion d'idéotype chez le blé dur. I. Caractères morphologiques d'enracinement. - Agronomie **12**: 371-379, 1992.

Ali-Dib, T., Monneveux, P., Araus, J.L.: Breeding durum wheat for drought tolerance: Analytical, synthetical approaches, and their connections. - In: Panayotov, I., Pavlova, S. (ed.): Proceedings of International Symposium Wheat Breeding - Prospects and Future Approaches. Pp. 224-240. Agricultural Academy Bulgaria, Albena 1990.

Barrs, H.: Determination of water deficit in plants tissues. - In: Kozlowski, T. (ed.): Water Deficit and Plant Growth. Pp. 235-368. Academy Press, New York 1968.

Begg, J.E., Turner, N.C.: Crop water deficits. - Adv. Agron. **28**: 161-217, 1976.

Berkowitz, G.A.: Chloroplast acclimation to low osmotic potential. - Plant Cell Rep. **6**: 208-211, 1987.

Biehler, K., Migge, A., Fock, H.P.: The role of malate dehydrogenase in dissipating excess energy under water stress in two wheat species. - Photosynthetica **32**: 431-438, 1996.

Bradford, K.J., Hsiao, T.C.: Physiological responses to moderate water stress. - In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (ed.): Physiological Plant Ecology II. Pp. 263-324. Springer-Verlag, Berlin - Heidelberg - New York 1982.

Conroy, J.P., Virgona, J.M., Smillie, R.M., Barlow, E.W.: Influence of drought acclimation and CO_2 enrichment on osmotic adjustment and chlorophyll *a* fluorescence of sunflower during drought. - Plant Physiol. **86**: 1108-1115, 1988.

Crowe, J.H., Carpenter, J.F., Crowe, L.M., Anchrologuy, T.J.: Are freezing and dehydration similar stress vectors? A comparison of modes of interaction of stabilizing solutes with biomolecules. - Cryobiology **27**: 219-231, 1990.

Farquhar, G.D., Sharkey, T.D.: Stomatal conductance and photosynthesis. - Annu. Rev. Plant Physiol. **33**: 317-345, 1982.

Girma, F.S., Krieg, D.R.: Osmotic adjustment in sorghum II. Relationship to gas exchange rates. - Plant Physiol. **99**: 583-588, 1992.

Havaux, M., Ernez, M., Lannoye, R.: Sélection de variétés de blé dur (*Triticum durum* Desf.) et de blé tendre (*Triticum aestivum* L.) adaptées à la sécheresse par la mesure de l'extinction de la fluorescence de la chlorophylle *in vivo*. - Agronomie **8**: 193-199, 1988.

Hsiao, T.C., Acevedo, E., Fereres, E., Henderson, D.W.: Water stress, growth and osmotic adjustment. - Phil. Trans. roy. Soc. London **B 273**: 479-500, 1976.

Kameli, A., Lösel, D.M.: Carbohydrates and water status in wheat plants under water stress. - New Phytol. **125**: 609-614, 1993.

Kameli, A., Lösel, D.M.: Contribution of carbohydrates and other solutes to osmotic adjustment in wheat leaves under water stress. - J. Plant Physiol. **145**: 363-366, 1995.

Ludlow, M.M., Chu, A.C.P., Clements, R.J., Kerslake, R.G.: Adaptation of species of centrosema to water stress. - Aust. J. Plant Physiol. **10**: 119-130, 1983.

Ludlow, M.M., Fisher, M.J., Wilson, J.R.: Stomatal adjustment to water deficits in three tropical grasses and a tropical legume grown in controlled conditions and in the field. - Aust. J. Plant Physiol. **12**: 131-149, 1985.

Martin, B., Rilling, C.: Gas exchange of water-stressed wheat leaves and leaves with simulated patchy photosynthesis. - In: Mathis, P. (ed.): Photosynthesis: from Light to Biosphere. Vol. IV. Pp. 557-560. Kluwer Acad. Publishers, Dordrecht - Boston - London 1995.

Meziani, L., Bamoun, A., Hamou, N., Brinis, L., Monneveux, P.: Essai de définition des caractères d'adaptation du blé dur dans différentes zones agroclimatiques de l'Algérie. - In Monneveux, P., Bensalem, M. (ed.): Tolérance à la Sécheresse des Céréales en Zones Méditerranéennes. Diversité et Amélioration Variétale. Pp. 191-203. INRA, Paris 1992.

Monneveux, P., Nemmar, M.: Contribution à l'étude de la resistance à la sécheresse chez le blé tendre (*Triticum aestivum* L.) et chez le blé dur (*Triticum durum* Desf.): étude de l'accumulation de la proline au cours du cycle de développement. - Agronomie **6**: 583-590, 1986.

Morgan, J.M., Hare, R.A., Fletcher, R.J.: Genetic variation in osmoregulation in bread and durum wheat and its relationship to grain yields in a range of field environments. - Aust. J. agr. Res. **37**: 449-457, 1986.

Munns, R.: Why measure osmotic adjustment? - Aust. J. Plant Physiol. **15**: 717-726, 1988.

Pecceti, L., Annicchiarico, P.: Grain yield and quality of durum wheat landraces in dry mediterranean region of northern Syria. - Plant Breed. **110**: 243-249, 1993.

Premachandra, G.S., Saneoka, H., Fujita, K., Ogata, S.: Osmotic adjustment and stomatal response to water deficits in maize. - J. exp. Bot. **43**: 1451-1456, 1992.

Rascio, A., Platani, C., Scalfati, G., Tonti, A., Fonzo, N.D.: The accumulation of solutes and water binding strength in durum wheat. - Physiol. Plant. **90**: 715-721, 1994.

Scholander, P.F., Hammel, E.A., Hemmingsen, E.D., Bradstreet, E.D.: Sap pressure in vascular plants. - Science **148**: 339-346, 1964.

Schonfeld, M.A., Johnson, R.C., Carver, B.F., Mornhinweg, D.W.: Water relations in winter wheat as drought resistance indicators. - Crop Sci. **28**: 528-531, 1988.

Schulze, E.-D.: Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. - Annu. Rev. Plant Physiol. **37**: 247-274, 1986.

Sharkey, T.D., Seemann, J.R.: Mild water stress effects on carbon-reduction-cycle intermediates, ribulose biphosphate carboxylase activity, and spatial homogeneity of photosynthesis in intact leaves. - Plant Physiol. **89**: 1060-1065, 1989.

Shields, R., Burnett, W.: Determination of protein-bound carbohydrate in serum by a modified anthrone method. - Anal. Chem. **32**: 885-886, 1960.

Turner, N.C.: Adaptation to water deficits: a changing perspective. - Aust. J. Plant Physiol. **13**: 175-190, 1986.

Turner, N.C., Begg, J.E., Tonnet, M.L.: Osmotic adjustment of sorghum and sunflower crops in response to water deficits and its influence on the water potential at which stomata close. - Aust. J. Plant Physiol. **5**: 597-608, 1978.

Turner, N.C, Jones, M.M.: Turgor maintenance by osmotic adjustment: A review and evaluation. - In: Turner, N.C., Kramer, P.J. (ed.): Adaptation of Plants to Water and High Temperature Stress. Pp. 87-103. Wiley and Sons, New York - Chichester - Brisbane - Toronto 1980.

Virgona, J.M., Barlow, E.W.R.: Drought stress induces changes in the non-structural carbohydrate composition of wheat stems. - Aust. J. Plant Physiol. **18**: 239-247, 1991.

Wilson, J.R., Fisher, M.J., Schulze, E.D., Dolby, G.R., Ludlow, M.M.: Comparison between pressure-volume and low point-hygrometry techniques for determining water relation characteristics of grass and legume leaves. - Oecologia **41**: 77-88, 1979.

Wright, G.C., Smith, R.C.G., Morgan, J.M.: Differences between two grain sorghum genotypes in adaptation to water stress. III. Physiological responses. - Aust. J. agr. Res. **34**: 637-651, 1983.