PHOTOSYNTHETICA 34 (1): 67-76, 1997

Photosynthesis of six barley genotypes as affected by water stress

G. ARNAU*, P. MONNEVEUX*, D. THIS* and L. ALEGRE**,***

UFR de Génétique et Amélioration des Plantes, ENSA-INRA,
*2 Place Pierre Viala, 34060 Montpellier Cedex 1, France**
Department of Plant Biology, Plant Physiology Unit, Faculty of Biology,
*University of Barcelona, Avda. Diagonal, 645 08028 Barcelona, Spain***

Abstract

The effect of water stress on plant water status and net photosynthetic gas exchange (P_N) in six barley genotypes (*Hordeum vulgare* L.) differing in productivity and drought tolerance was studied in a controlled growth chamber. Osmotic adjustment (OA), P_N, stomatal conductance (g_s), and the ratio intercellular/ambient CO_2 concentration (C_i/C_a) were evaluated at four different levels of soil water availability, corresponding to 75, 35, 25 and 15 % of total available water. Variability in OA capacity was observed between genotypes: the drought tolerant genotypes Albacete and Alpha showed higher OA than drought susceptible genotypes Express and Mogador. The genotype Albacete exhibited also higher P_N than the others at low water potential (Ψ). The ratios of P_N/g_s and C_i/C_a showed that differences in photosynthetic inhibition betweeen genotypes at low Ψ were probably due to nonstomatal effects. In Tichedrett, a landrace genotype with a very extensive root development, OA was not observed, however, it exhibited a capacity to maintain its photosynthetic activity under water stress.

Additional key words: *Hordeum vulgare*; net photosynthetic rate; osmotic adjustment; osmotic potential; relative water content; stomatal conductance; water potential.

Introduction

The OA in plants (due to the net uptake or production of solutes in cells) often occurs under water stress and it is used for characterization of drought tolerance in plants.

Received 23 November 1995, *accepted* 28 May 1996.

***Author for correspondence. Phone 34 3 4021480; Fax 34 3 4112842.

Abbreviations: C_a - ambient CO_2 concentration; C_i - intercellular CO_2 concentration; g_s - stomatal conductance; OA - osmotic adjustment; P_N - net photosynthetic rate; PPF - photosynthetic photon flux; RWC - relative water content; RWC_{100} - relative water content at full turgor; YI - yield under irrigation conditions; YS - yield under drought; Ψ - water potential; Ψ_π - osmotic potential; $\Psi_{\pi 100}$ - osmotic potential at full turgor.

Acknowledgements: The authors are very grateful to F. Acevedo (CIMMYT Wheat Program, Agronomy and Physiology) for helpful discussion and critical comments.

In field conditions under water deficit, plants with higher OA produce larger grain yields (Morgan *et al.* 1986). The OA maintains g_s and P_N in water-stressed plants (Hsiao *et al* 1976, Turner and Jones 1980, Ackerson and Hebert 1981). The stability of photosynthetic activity at low leaf water potential (Ψ) *via* OA could be also related to greater protoplast volume (Flower and Ludlow 1986, Sen-Gupta and Berkowitz 1987, Meinzer *et al.* 1990). Moreover, there are several reports of inhibition of growth and stomatal opening despite the occurrence of OA (Michelena and Boyer 1982, Munns 1988, Girma and Krieg 1992, Premachandra *et al.* 1992).

The effects of drought on photosynthesis are well documented (*e.g.*, Kramer 1983, Kaiser 1987, Chaves 1991). While much of the reported reduction in CO_2 assimilation is attributed to stomatal closure, part of it has been attributed to the direct effect of water stress on the inhibition of CO_2 fixation (*e.g.*, Sharkey and Seeman 1989). Damage of thylakoid-mediated light reactions in extreme stress has also been indicated (Keck and Boyer 1974, Younis *et al.* 1979, Mayoral *et al.* 1981, Havaux *et al.* 1988). There exist genotype variations in the effect of water stress on g_s and P_N (Johnson *et al.* 1987, Martin *et al.* 1989, Al-Hamdani *et al.* 1991, Gimenez *et al.* 1992, Soldatini and Guidi 1992).

The aim of this study was to determine the capacity for OA in six barley genotypes of contrasting drought tolerance and to assess the relation between OA and the maintenance of gas exchange (g_s and P_N) in plants grown under declining soil water content. The stomatal and nonstomatal effects of water stress on photosynthesis were also studied.

Materials and methods

Plants: Six genotypes of barley (*Hordeum vulgare* L.) were used: Albacete, Express, Plaisant and Tichedrett have six rows on the spike, and Alpha and Mogador have two rows. Albacete is a pure line selected from a landrace of the dry region of Albacete (Spain). Tichedrett is an Algerian landrace. Alpha, Plaisant, Express and Mogador are French improved barleys with high yield. Drought yield field reduction for each genotype was calculated as follows:

$$(YI-YS)/YI \times 100,$$

where YI = mean value of grain yield for a given genotype under irrigation, and YS = mean value of grain yield under drought. Multilocation experiments have identified Albacete as drought tolerant (yield reduction to 76 %), Alpha as moderately tolerant (83 %), and Plaisant, Express and Mogador as drought susceptible (87 and 90 %). Tichedrett is tolerant to severe water stress although it has a low yield potential (Khaldoun *et al.* 1990).

Seeds were sterilized in a 0.5 % NaOCl solution for 15 min, then washed 3 times in sterile water, and germinated in Petri dishes. Three-d-old seedlings were transferred to 15 cm diameter plastic pots (5 seedlings per pot) filled with peat-vermiculite 3:1 (v/v). Plants were grown in a controlled growth chamber at 12 h photoperiod, PPF of 450 µmol m^{-2} s^{-1} (day/night), air temperature 21/18 °C, and relative humidity 60/70 %.

Pots were watered three times per week with deionized water. After 4 weeks of growth, plants were subjected to water stress by withholding water for a period of 10 d. The development of water stress was monitored by continuous measurement of soil water content. Twenty randomly selected pots were weighed early each morning, and the average soil water content was calculated as percentage of total available water. The soil water content at saturation was determined experimentally by adding a known volume of water to the pots, and by calculating the average volume of water that was retained by the substrate of individual pots after drainage. The studies on seedlings were carried out four times during the drought cycle corresponding to 75, 35, 25 and 15 % of total available water. The youngest, fully expanded leaf was used in all experiments to reduce developmental variation, and at least five leaves obtained from plants growing in different pots were used as replicates.

Water relations: Leaf water potential (Ψ) was determined using a Scholander pressure chamber (*Soil moisture 3005*, Santa Barbara, U.S.A.) containing a wet filter paper at the bottom of the chamber. Relative water content (RWC) was ascertained by measuring the fresh, rehydrated (overnight at 4 °C on distilled water) and dry (80 °C for 2 d) masses of a 4 cm^2 section taken from the middle upper-part of the leaf. One leaf section (3 cm^2) was also cut from the middle part of the leaf, sealed in aluminium foil, immediately frozen in liquid nitrogen, and stored at -20 °C. Osmotic potential (Ψ_π) was measured using a freezing-point microosmometer (*GS/IJ, Roebling*, Berlin, Germany). The OA was characterized and RWC values were calculated at Ψ and Ψ_π values of -2.0 MPa (Morgan 1983, 1992).

Gas exchange rates were determined on attached leaves with a Portable Photosynthesis System *LI-6200* (*LI-COR*, Lincoln, U.S.A.). Leaves were placed in a 1 000 cm^3 chamber. The conditions of measurement were: quantum flux 900 µmol m^{-2} s^{-1} (PAR) provided by a mixture of incandescent and fluorescent lamps, leaf temperature 26 ±1 °C, and a leaf-to-air vapour pressure difference 0.96±0.064 kPa. Leaf area was previously determined by multiplying the length (4.5 cm) by the width of the leaf. Gas exchange rates of leaves were automatically calculated from slopes of CO_2 depletion and H_2O increases in the system in 20 s sampling periods. The C_i was calculated from g_s, P_N and C_a (Farqhuar and Sharkey 1982). The measurements were made on the same set of plants used for the analysis of OA.

Statistics: The analysis of variance was achieved by the Statistical Analysis System (*SAS Institute*, Cary, U.S.A.). Differences between means were based on the least significant difference (LSD) Duncan-Test. The regression curves were examined by analysis of covariance using the GLM procedure from SAS.

Results

Osmotic adjustment: Ψ, Ψ_π and RWC decreased with increasing soil water deficits. Throughout the stress cycle, Ψ declined from -0.97 MPa (average value of unstressed plants) to -1.82 MPa (average value of stressed plants), Ψ_π from -1.40 to -2.06 MPa, and RWC from 95 to 65 %.

Fig. 1 (*left*) shows the relationship between RWC and Ψ_π for the six genotypes. Between 86 and 95 % of the variance was explained by this linear regression. The values of RWC at Ψ_π of -2.0 MPa were calculated (Table 1). The results distinguished different groups of genotypes: Albacete and Alpha showed the highest OA while Express and Mogador exhibited the lowest one. Plaisant showed an intermediate behaviour. Tichedrett did not show OA.

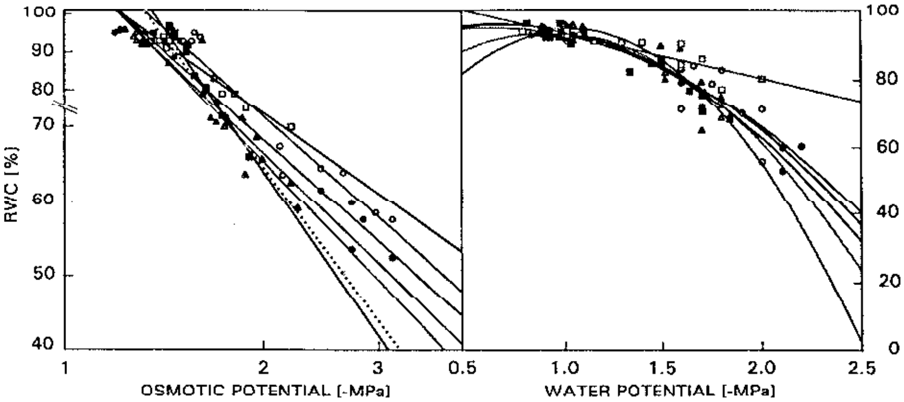

Fig. 1. Relationship between relative water content (RWC) and Ψ_π (*left*) or Ψ (*right*) in Albacete (□), Tichedrett (■), Alpha (○), Plaisant (●), Express (Δ), and Mogador (▲) plants subjected to water stress. *Dotted line* means theoretical decline in Ψ_π due to passive solute concentration effects associated with the decrease in RWC.

In addition, we analyzed the relationship between RWC and Ψ: a 2nd order regression was the best fit for the curve RWC = fΨ (Fig. 1, *right*). RWC values at Ψ of -2.0 MPa distinguished three groups of genotypes (Table 1). Again, Albacete had the highest RWC value (78.3 %), but we were not able to distinguish among the values of OA for Tichedrett, Alpha, Plaisant and Mogador. Express showed the lowest OA with an RWC of 54.7 % at -2 MPa.

Effects of water stress on photosynthesis: In all genotypes studied, the P_N and g_s declined with decreasing soil water content (Tables 2 and 3). Relative to the maximum P_N measured at 75 % soil water content, P_N decreases of 30, 50 and 80 % (on average) were observed for soil water contents of 35, 25 and 15 %, respectively. Nevertheless, the difference in P_N between genotypes was significant only under the most severe stress. Under these conditions, Albacete exhibited the highest P_N, Tichedrett and Alpha were intermediate, and Plaisant, Express and Mogador showed the lowest P_N. There was no significant difference between g_s of genotypes at any soil water content. At 15 % soil water content, g_s was 85 % lower than in well watered plants.

Table 1. RWC [%] at Ψ_π or Ψ = -2 MPa in six barley genotypes. Values of RWC were calculated from equalines: $\ln RWC = a+b \ln\Psi_\pi$ and $RWC = a + b\Psi + c\Psi^2$. Values followed by the same letter within a column are not significantly (p = 0.05) different.

Genotype	RWC [%] at Ψ_π = -2 MPa	at Ψ = -2 MPa
Albacete	76.7±1.02a	78.3±3.34a
Tichedrett	65.8±1.03d	62.5±3.30b
Alpha	76.1±1.06a	64.8±3.10b
Plaisant	71.6±1.05b	65.8±3.10b
Express	65.7±1.07c	54.7±3.15c
Mogador	69.1±1.03c	61.1±3.22b

Table 2. Effect of different levels of soil water availability on net photosynthetic rate, P_N [μmol(CO_2) m^{-2} s^{-1}] in six barley genotypes. Values followed by the same letter within a column are not significantly (p = 0.05) different.

Genotype	Soil water content [%] 75	35	25	15
Albacete	16.2±0.7a	10.7±0.8b	7.5±0.7c	5.9±0.6d
Tichedrett	15.3±0.5a	12.3±0.7b	8.6±0.8c	4.4±0.8df
Alpha	15.5±0.8a	12.3±0.8b	8.9±0.9c	3.8±0.4df
Plaisant	15.5±0.4a	11.6±0.8b	7.1±0.9c	2.9±0.4f
Express	15.7±0.6a	11.8±0.8b	7.1±0.9c	2.6±0.7f
Mogador	16.0±0.7a	11.5±0.5b	7.5±0.6c	2.1±0.6f

Table 3. Effect of different levels of soil water availability on stomatal conductance, g_s [mol m^{-2} s^{-1}] in six barley genotypes. Values followed by the same letter within a column are not significantly (p = 0.05) different.

Genotype	Soil water content [%] 75	35	25	15
Albacete	0.90±0.13a	0.32±0.03b	0.18±0.03c	0.16±0.03d
Tichedrett	1.20±0.17a	0.30±0.02b	0.21±0.04c	0.15±0.02d
Alpha	0.90±0.13a	0.29±0.02b	0.20±0.03c	0.15±0.02d
Plaisant	1.05±0.11a	0.29±0.03b	0.15±0.04c	0.14±0.02d
Express	1.14±0.13a	0.32±0.04b	0.17±0.02c	0.13±0.03d
Mogador	1.15±0.14a	0.27±0.03b	0.22±0.04c	0.13±0.02d

Under water stress, the C_i/C_a ratio decreased from 0.77 at 75 % soil water content to 0.55 at 25 % soil water content (Table 4). At a more severe water stress, 15 %, an increase was observed in the ratio C_i/C_a to values of 0.75, similar to those of well watered plants. As a result of the differential susceptibility of P_N and g_s to water stress, the ratio P_N/g_s was also affected (Fig. 2). An initial increase in this ratio was observed when g_s decreased. However, the ratio decreased when g_s values were below 0.18 mol(CO_2) m^{-2} s^{-1}.

Table 4. Effect of different levels of soil water availability on C_i/C_a [mol m^{-2} s^{-1}] in six barley genotypes. Values followed by the same letter within a column are not significantly (p = 0.05) different.

Genotype	Soil water content [%] 75	 35	 25	 15
Albacete	0.79±0.07a	0.57±0.06b	0.55±0.03b	0.65±0.06a
Tichedrett	0.72±0.06a	0.57±0.04b	0.56±0.02b	0.76±0.07a
Alpha	0.71±0.06a	0.58±0.05b	0.53±0.04b	0.72±0.06a
Plaisant	0.81±0.07a	0.61±0.02b	0.54±0.03b	0.77±0.07a
Express	0.83±0.07a	0.62±0.02b	0.55±0.03b	0.74±0.05a
Mogador	0.75+0.04a	0.57+0.04b	0.57±0.02b	0.77±0.07a

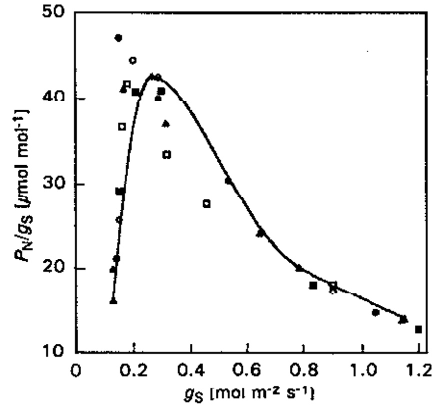

Fig. 2. Relationship between the ratio net photosynthetic rate/stomatal conductance (P_N/g_s) and g_s in Albacete (□), Tichedrett (■), Alpha (○), Plaisant (●), Express (△) and Mogador (▲) plants subjected to water stress.

Discussion

According to Morgan (1983), variations in solute accumulation during a stress cycle can be evaluated by comparing the slope of the responses of RWC/Ψ_π to those expected if OA did not occur (Fig. 1, *left, dotted line*). Substantial differences were observed between the genotypes tested.

The use of the relationship between RWC and Ψ to estimate the OA, as suggested also by Morgan (1983), led to similar results: Albacete and Express were the most contrasted genotypes. However, the rankings given by the two methods were different: the second one did not distinguish between the OA capacities of Plaisant, Alpha, Tichedrett, and Mogador, while the ratio RWC/Ψ_π revealed significant differences between these genotypes. Indeed, this analysis provided only an estimation of OA because the capacity to maintain a higher value of RWC at Ψ of -2 MPa depended only in part on active solute accumulation.

The OA capacity of Albacete could explain its high yield under very dry conditions (Sombrero *et al.* 1993). This genotype was also tested in dry conditions in northern Spain and appeared to be more drought tolerant than Alpha, Plaisant and Mogador. Express was identified by Monneveux *et al.* (1993) as susceptible to drought. Our results showed that Albacete and Alpha had the highest OA, which might explain the low susceptibility index of these cultivars. Express, which showed the lowest OA, was the cultivar with highest index of susceptibility. Thus, again, in genotypes that presented OA as a response to water stress a relation was observed between OA and productivity.

Under severe water stress (15 % soil water content) the P_N was significantly lower in Express, Mogador, and Plaisant than in Albacete. The decrease in P_N in stressed plants could be explained by the stomatal closure, which reduced CO_2 diffusion and thus the C_i/C_a ratio (Table 4). However, no significant difference between genotypes was observed in this ratio. Under severe water stress, P_N continued to decrease, while the C_i/C_a ratio increased significantly to values similar to those observed in well watered plants. Consequently, the effects of severe water stress on photosynthesis could be attributed to nonstomatal effects, as described by Björkman and Powles (1984) or Turner and Wellburn (1985).

The g_s was more affected by water stress than photosynthesis. Consequently, an increase in the ratio P_N/g_s was observed under progressive water stress, down to a soil water content of 25 %, at which P_N/g_s reached a maximum (approximately 40 μmol mol^{-1}) at an average g_s value of 0.18 mol(CO_2) m^{-2} s^{-1}. Afterwards, a decrease in the ratio P_N/g_s was observed for lower values of g_s (Fig. 2), probably due to an inhibition of the efficiency of carboxylation, as postulated in wheat by Martin and Ruiz-Torres (1992). Significant differences in P_N/g_s between genotypes were observed only under severe water stress. In this case, P_N/g_s values were higher in Albacete (36.70 μmol mol^{-1}) than in the other genotypes (22 μmol mol^{-1}), since OA maintained RWC, increased P_N and thus P_N/g_s.

The same pattern was observed in P_N at 15 % of soil water content; P_N in Express was 56 % lower than in Albacete. This suggested that variations in P_N at severe water stress could be mainly explained by genotypic differences in OA capacity, as previously observed in isolated chloroplasts by Berkowitz (1987). The relation observed between P_N and OA could be due mainly to stomatal effects: the ability of stomata to remain open at low water potentials was shown to be linked to OA (Turner *et al.* 1978). Since genotypic variation in g_s was very low in our experiments, other physiological processes could explain the relationship between P_N and OA. Flower and Ludlow (1986), Sen-Gupta and Berkowitz (1987) and Meinzer *et al.*

(1990) pointed out that differences between genotypes in terms of relative sensitivity of photosynthesis at low Ψ could be explained by differences in the extent of protoplast volume reduction. The analysis of RWC/Ψ_π relationship showed that genotypes with higher values of RWC at Ψ_π of -2 MPa were those able to maintain a higher photosynthetic metabolism during the stress cycle. Hence OA could delay the effects of water stress on photosynthesis maintaining higher protoplast volume.

However, OA was not observed in the Algerian genotype Tichedrett that was able to maintain high CO_2 assimilation rates at low Ψ. This behaviour could be explained by its greater dehydration avoidance capacity, probably due to its morphophysiological adaptative traits, such as extensive root developement, or lower residual transpiration. The root characteristics of Tichedrett were compared to those of improved genotypes by Khaldoun *et al.* (1990), who found that Tichedrett had a very extensive deep root system. The analysis of g_s results (Table 3) suggested that stomatal transpiration might not explain the Tichedrett behaviour, since no significant difference was found for this trait between genotypes.

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-Hamdani, S.H., Murphy, J.M., Todd, G.W.: Stomatal conductance and CO_2 assimilation as screening tools for drought resistance in sorghum. - Can. J. Plant Sci. **71**: 689-694, 1991.

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

Björkmann, O., Powles, S.B.: Inhibition of photosynthetic reactions under water stress: interaction with light level. - Planta **161**: 490-504, 1984.

Chaves, M.M.: Effects of water deficits on carbon assimilation. - J. exp. Bot. **42**: 1-16, 1991.

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

Flower, D.J., Ludlow, M.M.: Contribution of osmotic adjustment to the dehydration tolerance of water-stressed pigeon pea (*Cajanus cajan* (L.) Mill sp.) leaves. - Plant Cell Environ. **9**: 33-40, 1986.

Gimenez, C., Mitchell, V.J., Lawlor, D.W.: Regulation of photosynthetic rate of two sunflower hybrids under water stress. - Plant Physiol. **98**: 516-524, 1992.

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

Havaux, M., Ernez, M., Lanoye, 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.

Johnson, R.C., Mornhinweg, D.W., Ferris, D.M., Heitholt, J.J.: Leaf photosynthesis and conductance of selected *Triticum* species at different water potentials. - Plant Physiol. **83**: 1014-1017, 1987.

Kaiser, W.M.: Effects of water deficit on photosynthetic capacity. - Physiol. Plant. **71**: 142-149, 1987.

Keck, R.W., Boyer, J.S.: Chloroplast response to low leaf water potentials. III. Differing inhibition of electron transport and photophosphorylation. - Plant Physiol. **53**: 474-479, 1974.

Khaldoun, A., Chery, J., Monneveux, P.: Etude des caractères d'enracinement, leur rôle dans l'adaptation au deficit hydrique chez l'orge (*Hordeum vulgare* L.). - Agronomie **10**: 369-379, 1990.

Kramer, P.J.: Water deficits and plant growth. - In: Kramer, P.J. (ed.): Water Relations in Plants. Pp. 342-389. Academic Press, New York 1983.

Martin, B., Ruiz-Torres, N.A.: Effects of water-deficit stress on photosynthesis, its components and component limitations, and on water use efficiency in wheat (*Triticum aestivum* L.). - Plant Physiol. **100**: 733 739, 1992.

Martin, M.A., Brown, J.H., Ferguson, H.: Leaf water potential, relative water content, and diffusive resistance as screening techniques for drought resistance in barley.- Agron. J. **81**: 100-105, 1989.

Mayoral, M.L., Atsmon, D.A., Shimshi, D., Gromet-Elhanan, Z.: Effect of water stress on enzyme activities in wheat and related wild species: carboxylase activity, electron transport and photophosphorylation in isolated chloroplasts. - Aust. J. Plant Physiol. **8**: 385-393, 1981.

Meinzer, F.C., Grantz, D.A., Goldstein, G., Saliendra, N.Z.: Leaf water relations and maintenance of gas exchange in coffee cultivars grown in drying soil. - Plant Physiol. **94**: 1781 1787, 1990.

Michelena, V., Boyer, J.S.: Complete turgor maintenance at low water potentials in the elongating region of maize leaves. - Plant Physiol. **69**: 1145-1149, 1982.

Monneveux, P., Chaballier, C., Lewicki, S., Lafarga, A., Sombrero, A., Ontanon, R., Romagosa, I.: Etude du comportement de lignées d'orge dans differentes conditions de sécheresse en Espagne. Estimation du rôle de la capacité d'ajustement osmotique dans l'adaptation à la variabilité environnementale. - In: Monneveux, P., Ben Salem, M. (ed.): Tolérance à la Sécheresse des Céréales en Zone Méditerranéenne. Diversité Génétique et Amélioration Variétale. Pp. 217-237. INRA, Paris 1993.

Morgan, J.M.: Osmoregulation as a selection criterion for drought tolerance in wheat. - Aust. J. agr. Res. **34**: 607-614, 1983.

Morgan, J.M.: Osmotic components and properties associated with genotypic differences in osmoregulation in wheat. - Aust. J. Plant Physiol. **19**: 67-76, 1992.

Morgan, J.M., Hare, R.A., Fletcher, R.J.: Genetic variation in osmoregulation in bread and durum wheats 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.

Premachandra, G.S., Saneoka, H., Fujita, K., Ogata, S.: Osmotic adjustment and stomatal response to water deficits in maize. - J. exp. Bot. **256**: 1451-1456, 1992.

Sen-Gupta, A., Berkowitz, G.A.: Osmotic adjustment, symplast volume, and nonstomatally mediated water stress inhibition of photosynthesis in wheat. - Plant Physiol. **85**: 1040-1047, 1987.

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.

Soldatini, G.F., Guidi, L.: Comparison of photosynthetic responses of sunflower and soybean to mild water stress. - Biochem. Physiol. Pflanzen. **188**: 321-331, 1992.

Sombrero, A., Ontanon, R., Montoya, J.L., Abad, J.L.: La culture de l'orge en Castille et Léon: croissance, développement et production. - In: Monneveux, P., Ben Salem, M. (ed.): Tolérance à la Sécheresse des Céréales en Zone Méditerranéenne. Diversité Génétique et Amélioration Variétale. Pp. 239-252. INRA, Paris 1993.

Turner, L.B., Wellburn, A.R.: Changes in adenylate nucleotide levels in the leaves of *Capsicum annuum* during water stress. - J. Plant Physiol. **120**: 111-122, 1985.

Turner, N.C., Begg, J.R., Tonett, 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. J. Wiley-Interscience, New York - Chichester - Brisbane - Toronto 1980.

Younis, H.M., Boyer, J.S., Govindjee: Conformation and activity of chloroplast coupling factor exposed to low chemical potential of water in cells. - Biochim. biophys. Acta **548**: 328-340, 1979.