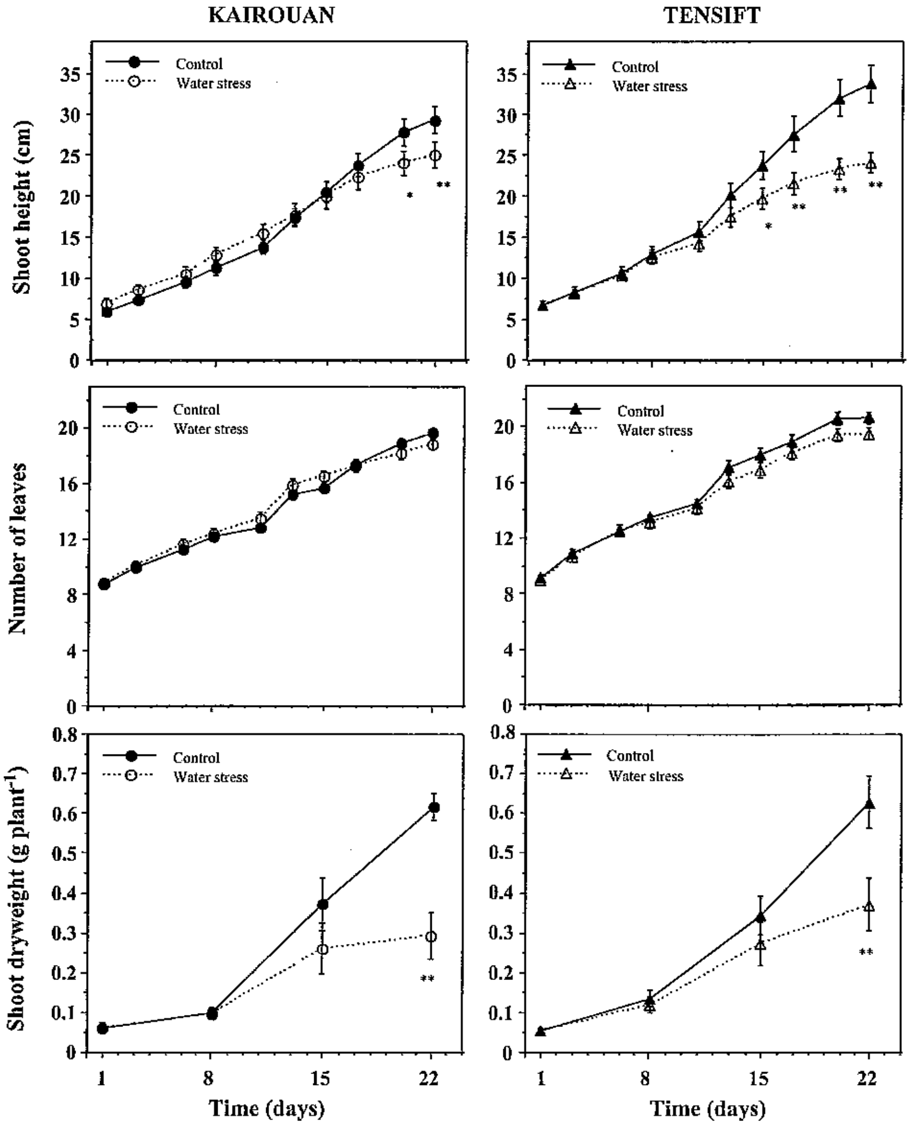

Fig. 1. Shoot height (cm), number of leaves, and shoot DW (g plant^{-1}) of two populations of *Atriplex halimus* (Kairouan and Tensift) under control and water stress conditions. Measurements were done at 1, 8, 15 and 22 days after withholding water for stressed plants. Vertical bars represent SE ($n = 10$). The symbols * and ** indicate that the effect of the treatment was significant at levels $P \leqslant 0.05$ and 0.01, respectively, using Duncan multiple test.

populations after the 8th day ($F = 22.55$ **) (Fig. 3), with a larger increase in Kairouan than in Tensift ($F = 3.91$*) (Fig. 3). The contribution of net solute accumulation (OA^{acc}) was slightly higher in Kairouan than in Tensift. The main difference however concerns contribution of changes in non-osmotic volume which was clearly higher in Kairouan than in Tensift at the end of the stress period.

Osmolytes accumulation

Proline concentration (Table 1) strongly differed between populations but it remained unchanged in response to water stress regardless of the population, with mean values of 13 and 4 μmol g^{-1} FW in Kairouan and Tensift, respectively. The glycinebetaine concentration of unstressed plants increased progressively as a function of time in both populations (Fig. 4). In stressed plants, the increase was larger than in unstressed plants after the 8th day, being significant after 22 days of water withholding ($F = 34.19$ **). At this time, Tensift presented higher glycinebetaine concentrations than Kairouan.

Total soluble sugar concentrations of unstressed plants was slightly higher in Tensift than in Kairouan ($F = 17.56$ **) (Fig. 4) and rose slightly until the

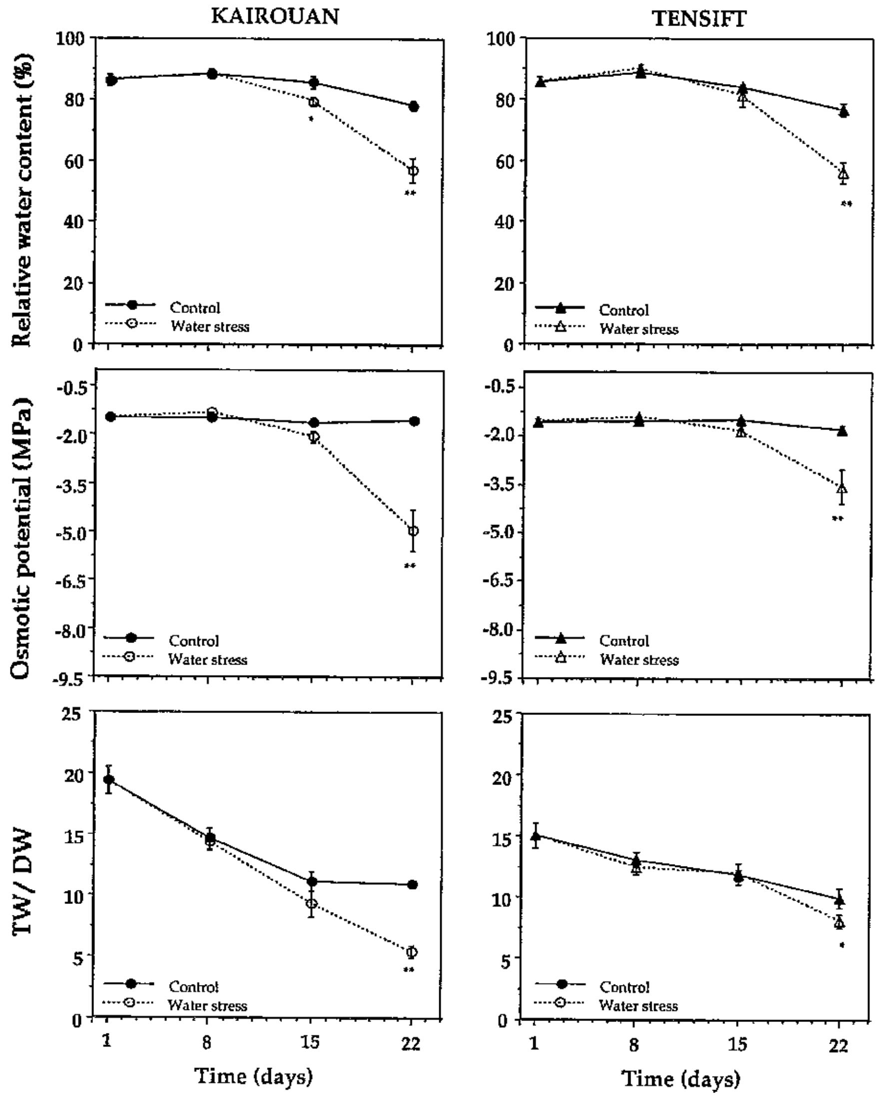

Fig. 2. Leaf RWC (%), osmotic potential (Ψs, MPa), and TW/DW ratio of two populations from *Atriplex halimus* (Kairouan and Tensift) under control and water stress conditions. Measurements were done at 1, 8, 15 and 22 days after withholding water for stressed plants. Vertical bars represent SE ($n = 10$). The symbols * and ** indicate that the effect of the treatment was significant at level $P \leqslant 0.05$ and 0.01, respectively, using Duncan multiple test.

end of the experimental period. In response to the stress, sugar content increased more rapidly after the 8th day in both populations. This increase was highly significant after 22 days of water withholding ($F = 3.7$ **). The ANOVA showed that the interaction between populations and water stress treatment was not significant. Although starch content of young and old leaves was higher in Tensift than in Kairouan under control conditions, the difference between the two populations was not significant. Starch content decreased in stressed plants regardless of population ($F = 8.4$*), but the interaction between treatment and population was not significant.

Discussion

The way the stress was applied in this work allowed a relatively gradual development of water deficit. The dehydration of the plant tissues, caused by this treatment and revealed by the decrease in leaf RWC (Fig. 2), was delayed, however, until after the 8th day of treatment and was similar in both populations. As a result, no one measured parameter was affected by the treatment before that time.

Growth evaluated on a shoot DW basis was reduced in both populations. Tensift presented a tendency to reduce its shoot DW less than Kairouan

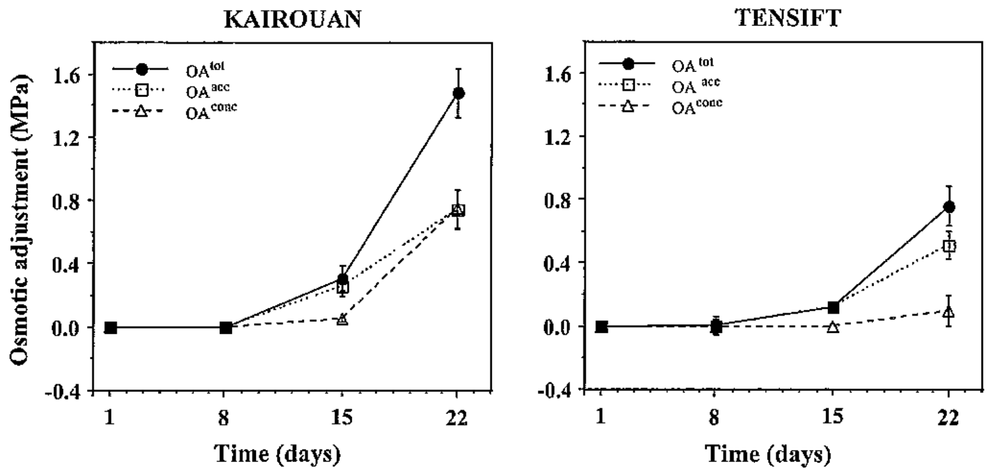

Fig. 3. Total OA (OA^{tot}), OA attributed to net solute accumulation (OA^{acc}) and OA due to changes in nonosmotic volume (OA^{conc}) of two populations of *Atriplex halimus* under water stress conditions. Measurements were done at 1, 8, 15 and 22 days after withholding water. Vertical bars represent SE ($n = 10$).

Table 1. Effect of water stress on proline and starch concentrations ($\mu mol\, g^{-1}$ FW) in young and old leaves of two populations of *Atriplex halimus* (Kairouan and Tensift) under control and water stress treatments

Populations	Leaf age	Treatment	Proline	Starch
Kairouan	Young	Control	12.2±0.7a	65.0±6.5a
		Water stress	14.1±1.1a	43.8±5.0bd
	Old	Control	13.7±1.2a	52.4±5.5bc
		Water stress	11.9±0.5a	36.2±4.5c
Tensift	Young	Control	4.6±0.3a	74.0±5.2a
		Water stress	5.3±0.9a	56.9±7.5b
	Old	Control	3.7±0.4a	64.9±4.7a
		Water stress	3.9±0.5a	45.4±5.7bc

Measurements were done after 22 days of withholding water for stressed plants. The values are adjusted to the leaf RWC of controls of each provenance. Each value represents mean±SE ($n = 10$). Values sharing a common letter in each column are not significantly different at $P \leqslant 0.05$.

and this result thus corroborates previous findings that demonstrated that water stress induces a higher decrease of CO_2 assimilation rates in Kairouan than in Tensift (Martìnez et al., 2003). Shoot height also decreased significantly. The inhibition of growth, as indicated by shoot height and shoot DW (Fig. 1) was recorded when leaf RWC and θ were lower than 75% and 10%, respectively. The inhibitory effect of a water stress upon stem elongation and biomass accumulation is well documented in the literature (Mullet and Whitsitt, 1996; Nonami et al., 1997; Nonami, 1998). Unlike shoot height and shoot DW, leaf number was not affected in response to water stress, regardless of population (Fig. 1). Such a result could indicate that the activity of the meristem was preserved during the stress period and the question thus arises as to whether this is due to a higher tolerance of cell division to dehydration in comparison to cell elongation, as suggested by Kramer and Boyer (1995), or to a better protection against dehydration of the apical bud where higher RWC would be maintained in comparison to older organs and tissues. Another possibility would be that the lag time between primary events occurring in the meristematic tissues and the emergence of the leaves is too long to allow the detection of any effect upon leaf number in a short experimental period.

It has been frequently suggested that the aim of OA is to maintain growth capacity through turgor maintenance at lower external osmotic potentials. The present study demonstrates that there is no obvious correspondence between the OA and the biomass production in *Atriplex halimus* under our water stress conditions. Indeed, leaf Ψs declined

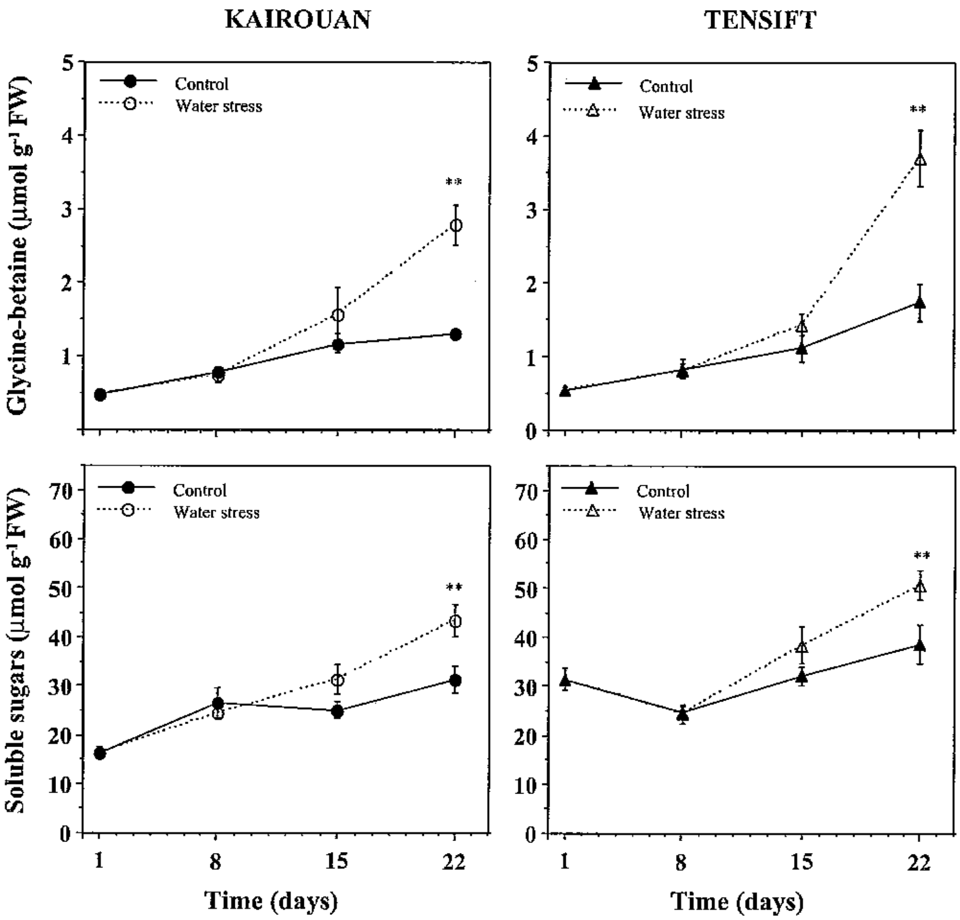

Fig. 4. Glycinebetaine (μmol g^{-1} FW) and soluble sugar (μmol g^{-1} FW) concentrations in leaves of two populations of *Atriplex halimus* (Kairouan and Tensift) under control and water stress conditions. Measurements were done at 1, 8, 15 and 22 days after withholding water for stressed plants. The values are adjusted to the leaf RWC of controls of each population. Vertical bars represent SE ($n = 10$). The symbols * and ** indicate that the effect of the treatment was significant at level $P \leqslant 0.05$ and 0.01, respectively, using Duncan multiple test.

consistently in response to water stress in both populations, but the reduction was larger in Kairouan at the end of the experimental period (Fig. 3). Decreased Ψs are generally considered to be an indicator of OA through the production and/or accumulation of so-called compatible osmolytes, although such decreases could also result from a dehydration of the tissue and/or a reduction of the osmotic volume. A dehydration process was revealed by the reduction of the leaf RWC we recorded, but it is insufficient to account for the Ψs difference existing between both populations at the end of the experimental period (Fig. 3). We found indeed that, after eliminating the effect of tissue dehydration on Ψs and solute accumulation of the sap of leaves submitted to the stress by adjusting leaf Ψs at a defined water status (full turgor) (Blum et al., 1996), OA^{tot} was still higher in Kairouan than in Tensift and was, on average 1.5 and 0.7 MPa for each population, respectively (Fig. 3).

Similarly, after eliminating the effect of solute concentration due to reduced osmotic volume, it still appeared that OA^{acc} was slightly higher in Kairouan than in Tensift under water stress conditions (Fig. 3). Reduced osmotic volume could be the result of an increase in insoluble polymer accumulation, which is reflected in the turgid weight to dry weight ratio (TW/DW) (Girma and Krieg, 1992; Patakas and Noitsakis, 1999). The increase in OA due to change in TW/DW is not considered to be an active OA (OA^{acc}). In *Atriplex halimus* leaves, it was observed that the TW/DW decreased significantly more in Kairouan than in Tensift during the water stress period (Fig. 3). Since starch content was reduced in response to water stress (Table 1), the TW/DW should be due to an accumulation of other polymers such as hemicellulose and cellulose, as