

## A greenhouse investigation of responses to different water stress regimes of *Laurus nobilis* trees from two climatic regions

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### ABSTRACT

Plants from two populations of *Laurus nobilis* (Tunisia issued from a semi-arid inland site and Algeria originating from a coastal sub-humid area) were exposed during three months under similar controlled conditions to two stress intensities of permanent stress (60% (S1) and 20% (S2) of field capacity) or to cyclic water stress, plants being re-watered when the soil moisture dropped to 60% (S11) or 20% (S22) of field capacity. One-year old plants displayed contrasting physiological strategies to cope with water stress. Algeria exhibited a higher decrease in osmotic potential ( $\Psi_s$ ) in relation to stress-induced proline accumulation. Glycinebetaine accumulated in response to drought in response to permanent stress (Algeria) or cyclic stress (Tunisia). The two populations had similar net photosynthesis (A) but Algeria exhibited higher water use efficiency (WUE) than Tunisia. A drought-induced increase in the apoplastic water content (AWC) was noticed in response to mild stress intensities (S1 and S11) in Tunisia and in response to higher stress intensities (S2 and S22) in Algeria in relation to a stress-induced accumulation of pectin and proportion of arabinose within the pectic fraction. Bulk modulus of elasticity ( $\epsilon$ ) increased in Tunisia in response to permanent drought and in Algeria in response to cyclic stress, as a result of a stress-induced increase in cellulose (Algeria) or hemicellulose (Tunisia). It is concluded that water stress tolerance could be achieved by both osmotic and elastic adjustment in the coastal population which did not exhibit a prodigal water use comparatively to the inland population. Differences between populations are strongly influenced by the kinetics of water stress application.

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### 1. Introduction

*Laurus nobilis* (bay laurel) is a large shrub with aromatic evergreen leaves belonging to the family of Lauraceae and native to the southern Mediterranean region (Conforti et al., 2006). This plant species is frequently encountered under semi-arid conditions and thus has to cope with long periods of water shortage, although it is also well adapted to coastal humid environments and requires high amounts of water during the first year of plant establishment (Rhizopoulou and Mitrakos, 1990).

Plant respond to water deficit and adapt to drought through numerous physiological and biochemical changes. Water use efficiency (the amount of dry matter produced per unit amount of water transpired) is a multigene controlled trait which is highly modulated

by the prevailing environmental conditions through various physiological properties (Impa et al., 2005). One of the earliest responses of plants to water shortage is to close stomata in order to prevent excessive loss of water but a negative consequence of stomatal closure is to limit CO<sub>2</sub> diffusion rate and thus photosynthesis (Niinemets et al., 2005). Osmotic adjustment consists in the accumulation of compatible organic solutes in order to decrease the osmotic potential of stressed tissues. It allows turgor maintenance and thus plant growth as well as stomatal opening (Ritte et al., 1999). Accumulation of proline and soluble sugars has been reported in a large set of taxa (Hare et al., 1998). Glycinebetaine was reported to act as an efficient osmocompatible solute in a limited number of stress-resistant taxa (Rhodes and Hanson, 1993) but its presence was never reported in *L. nobilis*. Beside organic compounds, ions (especially K<sup>+</sup>) could also assume key functions in osmotic adjustment (Morgan, 1984).

Regulation of cell wall elasticity and apoplastic water content may also contribute to some extent to water stress resistance strategies, although conflicting data are available in the literature in this respect. Resistance to water stress has been associated with an increase (Patakas and Noitsakis, 1997; Ngugi et al., 2003) or with

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a decrease (Fan et al., 1994) in the bulk modulus of elasticity ( $\epsilon$ ) of mature stressed tissues. Cell wall extensibility of elongating cells was also reported to be quickly affected by drought and both hardening and loosening processes may occur in plants exposed to water stress depending on the considered species (Neumann, 1995 and references therein). Drought-induced modification of water distribution between apoplasm and symplasm has been, at least partly, due to the ability of leaf tissue to increase the apoplastic water content, thus leading to a decrease in osmotic potential without decreasing total leaf water content (Torrecillas et al., 1999; Ngugi et al., 2003). Biochemical composition of the cell wall may directly influence biophysical parameters such as bulk modulus of elasticity and extensibility but also the cell wall water content and the amounts of bound water which is considered to contribute to water stress resistance in numerous plant species (Vertucci and Leopold, 1987; Rascio et al., 1998; Thompson, 2005; Evered et al., 2007). Hemicellulose is an important determinant of cell wall response to water deficit since it constitutes a polymeric gel with important water holding capacities. A decrease in the metabolic turnover of  $\beta$ -glucan through the inhibition of  $\beta$ -glucanase activity may be involved in the alteration of the molecular mass of hemicellulosic polysaccharides (Sakurai et al., 1987). As far as *L. nobilis* is concerned, it has not yet been established whether osmotic and elastic adjustment may occur simultaneously in the same leaf organs and if the relative importance of those strategies differs between populations issued from contrasting environments.

Genotypic variation has been reported for osmotic adjustment within species (Tangpremsri et al., 1991). It was recently demonstrated that populations from a halophyte plant species issued from coastal and inland areas exhibited contrasting behaviours in terms of osmotic adjustment in salt conditions, even when seedlings issued from these populations were tested in a uniform controlled environment (Ben Hassine et al., 2008). It may therefore be postulated that local adaptation of populations from contrasting climatic regions should also occur in response to water stress. Both osmotic adjustment and stress-induced modification in cell wall properties may occur rapidly in response to water stress but are also considered as reversible processes after the stress relief (Chazen and Neumann, 1994). In regions with erratic rainfall, plants are frequently exposed to cyclic events of drought rather than to permanent water stress and there is no exhaustive proof that a given population will react in the same way in response to different kinetics of stress. The tested hypothesis are therefore i) that populations of *L. nobilis* issued from sites differing in annual precipitation display contrasting behaviours for osmotic adjustment and regulation of cell wall properties and ii) that the differences recorded between populations may vary depending on the kinetics and intensity of water stress.

## 2. Materials and methods

### 2.1. Plant materials and experimental design

Seeds of *L. nobilis* L. were collected in October 2003 on plants growing at the location of Bardo (36° 13' N; 10° 23' W), near Tunis and on plants growing in the North-East of Algeria, near the city of Annaba (38° 31' N; 7° 46' W). Tunis is characterized by a semi-arid climate (mean annual precipitation: 340 mm; mean maximal temperature: 35.3 °C) while Annaba encounters a sub-humid climate (mean annual precipitation: 850 mm; mean maximal temperature: 27.9 °C). Distributions of precipitations throughout the year are presented in Fig. 1 for the two considered sites. Plant material issued from Bardo will be hereafter designated as "Tunisia" and plant material from Annaba as "Algeria".

In February 2004 (experiment 1) and February 2005 (experiment 2), fruit pericarp was mechanically removed and seeds were

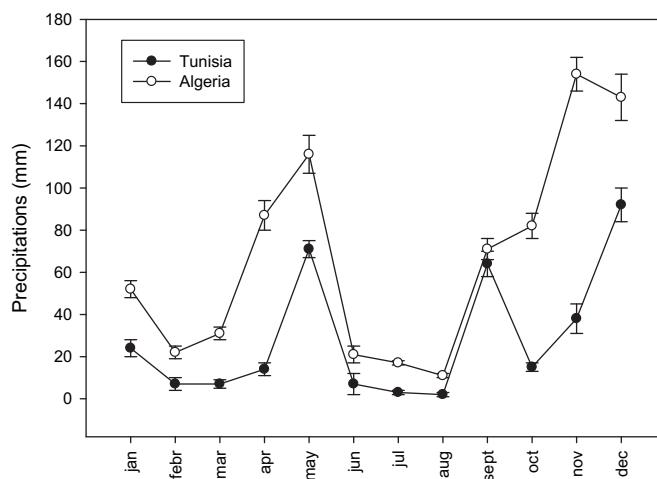


Fig. 1. Distribution of precipitations during the year at the semi-arid site of Tunis (Tunisia) and sub-humid site of Annaba (Algeria). Data presented are means for the years 2000, 2001 and 2003. Vertical bars are standard errors.

surface sterilized with calcium hypochloride 5%. Seeds were then individually placed into pots (0.5 L) filled with a loam–sand mixture (1:2) daily watered at field capacity which was determined according to Jury and Horton (2004). Pots were placed in a greenhouse located in the experimental station of INRGREF at Ariana (36° 50' N; 10° 14' W), Tunisia, under semi-controlled environment with a temperature ranging from 22 to 31 °C during the day and 14–18 °C during the night. A mean PAR of 480  $\mu\text{mol m}^{-2} \text{s}^{-1}$  was maintained at the top of the canopy and relative humidity was fixed to 60 ± 4% during the day and 72 ± 3% during the night. At the 6 leaves stage, all plants were individually transferred to 10 L pots filled with the same substrate and maintained under the same environmental conditions. Water stress was applied after one year for duration of three months; two repetitions were performed (from 15th May to 15th August 2005 and 15th May to 15th August 2006). Five different treatments were considered: control (soil water content maintained at 100% of field capacity by daily irrigation), permanent stresses: S1 (soil water content maintained at 60% of field capacity) and S2 (20% of field capacity) or cyclic stresses: soil was irrigated to field capacity when its water content fell to 60% (S11) or 20% (S12) of the field capacity. Plants were disposed in a complete randomized block design and plants were randomly rearranged weekly in the greenhouse. The amounts of water required for adequate irrigation were estimated according to Van Genuchten (1980) model with slight modifications according to Martínez et al. (2003). The volumetric water content was measured by the method of responding to changes in apparent dielectric constant using the ThetaProbe soil moisture sensor type ML1 (Delta-T Devices Ltd–UK) and converted to gravimetric water content on the basis of calibration obtained for the considered substrate with samples of known gravimetric water contents. All physiological and biochemical parameters were quantified after three months of stress exposure.

### 2.2. Growth measurements

During the stress period, plant height and diameter of the stem base were estimated monthly on all plants. At the end of the stress period, 6 plants per treatment were harvested: leaves, stems and roots were separated. Roots were carefully separated from the surrounding soil and gently washed to remove adhering soil particles (root water status was consequently not analysed in the present study). Fresh weight was estimated immediately after

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