

Understanding physiological mechanism of *Lotus creticus* plasticity under abiotic stress and in arid climate: a review

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Abstract

Lotus creticus (L.) (Leguminosae, Loteae) is a major pastoral and forage legume in the arid climate where salinity and drought are serious production problems. A review note was carried out to understand the physiological behaviour of this species face to salinity and drought. It has been shown through this note that *Lotus creticus* is fairly tolerant to salt at germination and growth phases. For instance, this taxon is able to support a level of salinity around 300 mM in germinative phase. In the growth phase, salinity affects growth of this plant. The fact that the roots were not affected by NaCl, was explained by a relatively greater proline accumulation during the salts stress. However, some research showed that under 70-140 mM NaCl, *L. creticus* grew even better than the control ones during the first month of growth. This aspect can be observed in halophytic and in some glycophytic succulent plants in which growth is stimulated by low to moderate salinity applied for a short time period. For 400 mM, *L. creticus* is able to produce and to allocate dry matter to the different organs. At higher salinity (140 – 400 mM NaCl), the high absorption and accumulation of ions caused important toxic effects and induced leaf tissue dehydration. The osmotic adjustment mechanism in *Lotus creticus* is a beneficial trait when the plants are treated with moderate levels of salinity (70 –100 mM NaCl). Moreover, the presence of hairy leaves allows keeping almost 81% of sprayed water and absorbing the 9% of the water retained, and decreased the epidermal conductance to water vapour diffusion. Research related to water deficiency showed that drought reduces the aerial part and root growth and leaf area. Moreover, water stress may influence the production of *Lotus* trichome increasing water foliar uptake in arid environmental conditions. The responses of *L. creticus* are hardening and osmotic and transpiration adjustments. An avoidance mechanism, which minimizes water losses when stomata are closed, was then considered. It can be deduced that *L. creticus* is a very useful species for revegetation in restored areas under arid and semi-arid Mediterranean conditions.

Keywords: *Lotus creticus*, Stress, Drought, Salinity, Arid Climate, Tunisia

Introduction

Arid climate is characterized by hot, dry summers and cool, cold winters, which limits the use of different species for soil revegetation (Savé *et al.*, 1999). Therefore, the use of native species for revegetation may be an interesting practice especially in those countries with dry climatic conditions, where salinity and drought are often serious problems because of the poor quality of irrigation water during the dry season (Sánchez-Blanco *et al.*, 1998). Salinity has long been known to influence the distribution of plant nutrients in legumes (Greenway and Munns, 1980). NaCl toxicity, the predominant form of salt in most saline soils, enhances the sodium content and consequently affects the absorption of other mineral elements (Greenway and Munns, 1980). Indeed, high levels of Na inhibit Ca and K absorption, which results in a Na/K antagonism (Rubio *et al.*, 1999). Ashraf and McNeilly (2004) suggested that maintenance of high tissue K/Na ratio as criteria for salt-tolerance. On the other hand, the relationship between salt tolerance and the macronutrient accumulation in vegetative organs of legumes was reported earlier (Cordovilla *et al.*, 1994). Plant species adapt to high salt concentrations in soils by lowering tissue osmotic potential with the accumulation of inorganic as well as organic solutes (Gerard *et al.*, 1991; Le Dily *et al.*, 1991; EL Haddad and O'Leary, 1994; Ullah *et al.*, 1994). Cations Na⁺ and K⁺ are known to be the major inorganic components of the osmotic potential (Asch *et al.*, 1999). Water deficiency is a major limiting factor of plant productivity in many arid regions of the Mediterranean basin (Boyer, 1982). Native species called Mediterranean plants are usually considered more tolerant and adapted to dry conditions and to soil salinity (Caballero and Cid, 1993). *Lotus* is a large (150 spp.), cosmopolitan genus that occupies two major centres of diversity, the Mediterranean region (including portions of Europe, Africa, and western Asia) and western North America (Allan *et al.*, 2004). It is one of about 10 genera within the tribe *Loteae* (Polhill, 1981; Sokoloff, 1998) and is the only genus in the tribe with an intercontinental distribution. Species of the genus *Lotus* are increasingly employed in pastures throughout the world because of their high productivity over a wide range of soils (Blumenthal and McGraw, 1999). There is potential for the use of *Lotus* in relation to both salinity and flooding tolerance. In addition, the interest in *Lotus* over the last decade has increased as greater emphasis is being placed on reducing N and P inputs into farming systems and lowering cattle stocking rates to reduce environmental pollution and land degradation (Blumenthal and McGraw, 1999). *Lotus creticus* is considered a good alternative to traditional covering plants because of its rapid growth and its need for little water (Sánchez-Blanco *et al.*, 1998; Cabot and Pages, 1997). It is an important naturalised legume in arid land of Tunisia. Until now, *Lotus creticus* ecophysiology originating from the Mediterranean countries such as Tunisia has been poorly documented (Rejili *et al.*, 2007). In this review, we have first emphasized arid regions and abiotic stress definitions followed by a description of *Lotus creticus* and its habitat relations. Physiological mechanisms of *Lotus creticus* plasticity under abiotic stress and in arid climate have been then reported and discussed.

Arid regions and arid climates

About one-third of the land area of the world comprises arid and semiarid climates (Johnson *et al.*, 1981). Arid desert soils were previously considered economically unimportant; however, during the past three decades, the economic and agricultural utilization of arid lands has emerged as a critical element in maintaining and improving the world's food supply (Skujins, 1984). In Tunisia, arid and semi-arid climate covers more than 3/4 of the total area of the country. Tunisia, located at the north of the 30th parallel, occupies the north part of the African continent, and its total area is a more than 164.000 km². The arid climate of Tunisia is characterized by high temperature, low relative humidity, high evaporation, and scanty rainfall. The desert lands also include saline areas; saline lands represent about 15% of the arid and semiarid lands of the world (Serrano and Gaxiola, 1994; Zahran, 1997). In saline areas, evaporation greatly exceeds precipitation, and soil salination may increase to a sufficient degree to eliminate most plants from these habitats (Batanouny, 1979; Zahran, 1997). Saline lands, like arid lands, have been largely ignored and are usually considered to be abandoned, non productive lands. Desert ecosystems are characterized by a lack of moisture and nitrogen, but drought and salt stresses are probably the most important environmental factors that inhibit the growth of organisms in arid and semiarid regions.

What is stress?

In physical terms, stress is defined as mechanical force per unit area applied to an object (Mahajan and Tuteja, 2005). In response to the applied stress, an object undergoes a change in the dimension, which is also known as strain. As plants are sessile, it is tough to measure the exact force exerted by stresses and therefore in biological terms it is difficult to define stress (Mahajan and Tuteja, 2005). A biological condition, which may be stress for one plant may be optimum for another plant. The most practical definition of a biological stress is an adverse force or a condition, which inhibits the normal functioning and well-being of a biological system such as plants (Jones and Jones, 1989). Drought and salt stresses are among the major stresses, which adversely affect plants growth and productivity.

Relation of *Lotus creticus* growth to different environmental factors

The genus *Lotus* L. contains approximately 100 species (Gunn, 1983; Polhill, 1994), distributed throughout of the World. It includes annual and perennial plants with strong branched taproots (MacDonald, 1946). The genus includes plant species adapted to an ample range of habitats from marine environments to high altitudes, from sandy soils to heavy saline soils (Heyn and Herrstadt, 1967; Heyn, 1970; Montes, 1988; Small, 1989). *Lotus creticus* has a definite capability to adapt to water stress but has specific requirements for water depth and flow rate of the current. These requirements, however, vary with different varieties. The requirement for water quality is not too strict; however, the discharge of phytotoxic chemicals from certain chemical industries is detrimental. Regions that once had an abundance of *L. creticus* plantings have been found to have no

Lotus due to discharges of toxic waste. *L. creticus* can adapt to most soil as long as there is no hardpan. It can grow at pH 5.6 to 7.5 but the optimum is at pH 6.5 (Charlton, 1973; William, 1988). *L. creticus* is a light loving plant and grows best when it is not shaded. During the *Lotus* growing period (April-August), average sunlight is between 4.6-9.0 hours per day. When the sunlight is abundant it also increases the temperature which favours the *Lotus* growth. Optimal temperature of *L. creticus* growth is between 20 and 30°C (William, 1988; Neffati, 1994) with water temperature at 21-25°C. During the early planting time the temperature should be at least above 15°C, otherwise both the seed germination and seedling growth are hindered, resulting in some decaying. The growth of the seedling then increases with the temperature. By June, when the temperature during the day reaches 30°C, the growth is the fastest (Charlton, 1973; William, 1988). Growth is slowed when air temperature is near 40°C. During the seed maturing of *Lotus creticus*, high day temperature and lower night temperatures are optimal (Charlton, 1973; William, 1988). Strong winds can break leaf and flower stalks. Broken leaf stems may allow rain water to enter the underground stem and cause decay. Rain water in the flowers spoils the flower appearance and hinders pollination. Young seedling may be affected by blue mould; buds or small leaves with mold on them may influence growth and photosynthesis. Certain underwater plant feeders may devour some buds. When the plants mature the flower and leaf stalks have some protective sharp protrusions to discourage them (Hovland *et al.*, 1982 *in*, William, 1988).

Response of *Lotus creticus* to drought condition

In general, the plant growth under water stress is reduced, nevertheless, it is known that plants have a suite of morphological and physiological adaptations that allow them to survive water stress and the degree of adaptation to drought may vary considerably between species. Bañón *et al.* (2004) showed that drought promoted significant differences in *L. creticus* stressed plants, reducing the aerial part and root. The reduction in leaf area occurred by effect of irrigation deficit and by high temperature in well-watered soil conditions. It has been considered an avoidance mechanism, which permits minimising water losses when stomata are closed (Blum, 1997). On the other hand, the degree of osmotic adjustment reached by the stressed plants (0.15MPa) was limited and it was insufficient to prevent a turgor pressure decrease and growth reduction. Grammatikopoulos and Manetas (1994) and Morales *et al.* (2000) have suggested that the leaf hairs of Mediterranean species may improve leaf water status by entrapping and retaining surface water, thus, assisting in its final absorption into the mesophyll, or reducing water loss by increasing the resistance of the boundary layer. The response observed in *L. creticus* plants can be considered as an advantageous feature that helps to improve leaf water status (Blum, 1997). Sánchez-Blanco *et al.* (1998), Savé *et al.* (1999), Morales *et al.* (2000), Franco *et al.* (2002) and Vignolio *et al.* (2005) showed that in water stress, the responses of *L. creticus* are hardening and osmotic and transpiration adjustments. Several authors reported the influence of the water deficit on photosynthesis (Flexas *et al.*, 1998; Sánchez-Blanco *et al.*, 2004; Chaves and Oliveira, 2004; Lizana *et al.*, 2006; Tambussi *et al.*, 2007; Yu *et al.*, 2007). Jaballah (2007) showed that the water deficit affects the rate of assimilation A in *L. creticus*. This result is in agreement with several reports on reduction

by water stress of the assimilation A rate (Bloch *et al.*, 2006) resulting from a reduction in the stomatic conductance (Chaves, 1991; Yordanov *et al.*, 2003; Campos *et al.*, 1999; Cornic, 2000) which limit the carbon diffusion by leaves. Moreover, water stress may influence in the production of *Lotus* trichome (Quarrie and Jones, 1977) increasing water foliar uptake in arid environmental conditions. Bañon *et al.* (2004) suggested that *L. creticus* plants exposed to dry soil conditions and low humidity would have more stomata than plants grown in the opposite conditions. In addition, the stomatal density of *L. creticus* plants decreased significantly with temperature on the abaxial surface in deficit irrigation conditions (Bañon *et al.*, 2004), but there was no effect on the adaxial surface. Sharpe (1973) reported that the adaxial and abaxial stomata differ in their responses to light, ambient temperature and water stress in cotton. According to Cihra and Brun (1975), the differences related to stomatal density observed between adaxial and abaxial surfaces can be a function of leaf expansion. This effect could also be related to leaf movements in relation to environmental conditions that show these plants (higher paraheliotropism; Palmer, 1985), which can be associated with greater drought avoidance (Savé *et al.*, 2000). It is clear that frequency and size of stomata vary as a function of leaf position and growth conditions (Jones, 1992). On the other hand, although the processes that regulate root water uptake are complex, it is clear that root anatomy and structure play an important role (Steudle and Peterson, 1998).

One indicator of the plant capacity to absorb and transport water is the density of the xylem vessels and tracheids in a cross-section of the stem or roots. The parameter vessels density provides an estimate of the mean diameter of these components of the xylem, a factor which is strongly related to water conductivity (Jones, 1992). In this sense, the vessels and tracheids developed in the seedlings in nursery conditions improve resistance of *L. creticus* plant to water deficit situations when plants grew in field conditions after transplanting. Franco *et al.* (2002) studied the influence of two irrigation treatments during nursery production on the post-transplant development of *L. creticus*. Their results showed that, during 96 days with irrigating 2 days/week with a total of 2.3 L of water per plant over the whole nursery period, plants had greater rootlength: shoot length ratio and higher percentage of brown roots, an indicator of more resistance to post-transplant stress. Similar results are obtained by Franco *et al.* (2002) in *Lotus* stressed plants after transplanting. In conclusion, *Lotus creticus* showed rather different adaptation responses to water deficit. An avoidance mechanism, which minimises water losses when stomata are closed, was deduced by reducing the transpiration rate resulting from a reduction in the stomatic conductance g_s . This knowledge can be used for improvement of cultivars and cultural practices for *Lotus* species especially in conditions where water deficit are features of the growing season.

Response of *Lotus creticus* to salt stress

Salinity is a serious threat to agriculture in arid and semiarid regions (Rao and Sharma, 1995). Nearly 40% of the world's land surface can be categorized as having potential salinity problems (Clemens *et al.*, 1983); most of these areas are confined to the tropics and Mediterranean regions. Increases in the salinity of soils or water supplies used for

irrigation result in decreased productivity of most crop plants and lead to marked changes in the growth pattern of plants (Clemens *et al.*, 1983). Increasing salt concentrations may have a detrimental effect on soil microbial populations as a result of direct toxicity as well as through osmotic stress (Tate, 1995). Soil infertility in arid zones is often due to the presence of large quantities of salt, and the introduction of plants capable of surviving under these conditions (salt-tolerant plants) is worth investigating (Delgado *et al.*, 1994). There is currently a need to develop highly salt-tolerant crops to recycle agricultural drainage waters, which are literally rivers of contaminated water that are generated in arid-zone irrigation districts (Glenn *et al.*, 1999). Salt tolerance in plants is a complex phenomenon that involves morphological and developmental changes as well as physiological and biochemical processes. Salinity decreases plant growth and yield, depending upon the plant species, salinity levels, and ionic composition of the salts (Delgado *et al.*, 1994). As with most cultivated crops, the salinity response of legumes varies greatly and depends on such factors as climatic conditions, soil properties, and the stage of growth (Cordovilla *et al.*, 1995a; Cordovilla *et al.*, 1995b; Cordovilla *et al.*, 1995c). Variability in salt tolerance among crop legumes has been reported (Zahran, 1991a; Zahran, 1991b).

Lotus creticus is cultivated in many countries; it is widely grown in arid and semi-arid region where soils contain high levels of salts. However, salt affected soils can be utilized by growing salt tolerant crops because such crops would allow expansion of crop production to areas where conventional reclamation procedures are economically or technically limited. In earlier report, we have shown that *L. creticus* is able to support a level of salinity around 300 mM in germinative phase (Rejili *et al.*, 2006). In 2007, Rejili *et al.* showed that salinity affected both biomass production and plant development. Concerning biomass production, Rejili *et al.* (2006) confirmed that dry matter of the aerial organs was significantly affected by NaCl levels exceeding the 100 mM. Le Hou  rou (1986) showed that *L. creticus* was able to support 100 mM of NaCl concentrations. S  nchez-Blanco *et al.* (1998) showed that the young plants treated with 70 and 140 mM NaCl grew even better than the control ones during the first month and the toxic effects of the Cl⁻ and Na⁺ appeared after a longer period of salt stress. This aspect can be observed in halophytic and in some glycophytic succulent plants in which growth is stimulated by low to moderate salinities applied for a short time period (Gorham, 1996).

The effect of salinity on *L. creticus* biomass depends on plant size and its relative average growth (RAG) (Rejili *et al.*, 2007a). The depressive action of salt on growth materializes in a significant reduction of the aerial organ growth activity (Rejili *et al.*, 2007a). For instance, shoots were more affected than stems for two different populations. Compared to the aerial organs, the roots dry matter was not affected by salt stress. The fact that the roots were not affected by NaCl is in accordance with the results obtained in many studies (Kumar and Bharadwaj, 1981; khavari-Nejad and Najafi, 1990; Munns and Termaat, 1986; Niemann *et al.*, 1988). This behaviour has been explained by a relatively greater proline accumulation in roots than in shoots during the salts stress. Proline plays an important role in the cellular osmoregulation and acts as a reserve of nitrogen to sustain root growth (Kalaji and Pietkiewicz, 1993; Misra *et al.*, 1996; Morales *et al.*, 2000).

Several authors suggested that, under saline stress, the osmotic effect is responsible for the aerial organ growth reduction (Munns and Termaat, 1986; Yeo *et al.*, 1991; Rengel, 1992). The response observed in *L. creticus* plants can be considered as an advantageous feature that helps to improve leaf water status under salt stress (Rejili *et al.*, 2007).

Plants exposed to saline stress were prone to an osmotic stress and to specific toxicity effects of Na^+ and Cl^- ions (Bernstein and Hoyward, 1958; Shannon, 1984; Ayer and Westcot, 1985; Hajji *et al.*, 1999). Flowers *et al.* (1977) summarized the depressive effect of salinity on the growth by a nutritional and/or hydrous imbalance. The significant correlation between the aerial biomass production and its Na^+ content suggest that, for *L. creticus*, the growth decrease was due to the ionic toxicity (Rejili *et al.*, 2007).

Generally, the most salt tolerant plants accumulate Na^+ in their shoots whereas sensitive plants do not. In the first type, called "Includers", salt was trapped and accumulated in the aerial organs cells, mainly in its vacuoles (Yeo and Flowers, 1986; Levigneron *et al.*, 1995). In the second type, "Excluders", the salt conveyed to the shoots, fault to be trapped, was re-exported towards the roots by the phloemic tissue (Lessani and Marschner, 1978; Wieneke and Läuchli, 1980; Slama, 1982; Fortmeir and Schubert, 1995). Sánchez-blanco *et al.* (1998) and Rejili *et al.* (2007a) showed that *L. creticus* plants accumulated Na^+ ions in its photosynthetic organs. The higher Na^+ and Cl^- accumulation in leaves of treated plants and the absence of accumulation of amino acids and soluble sugars by saline effects indicated that the osmotic adjustment had been achieved by the elements provided in the saline water as Gibbs *et al.*, (1989) and Alarcón *et al.* (1994) reported. The osmotic adjustment by salt accumulation is less energy and carbon demanding than adjustment by organic solutes (Wyn Jones, 1981). For this reason, the capacity to include salts is considered a salt tolerance trait, when it is accompanied by the ability of plants to compartment NaCl in the vacuole, thus protecting salt-sensitive enzymes in the cytoplasm (Flowers *et al.*, 1977; Alarcón *et al.*, 1994; Wyn Jones and Pollard, 1983). Apparently, *L. creticus* treated with 140 mM NaCl is unable to sequester ions efficiently and the salts were accumulated leading to inhibition of growth (Sánchez-Blanco *et al.*, 1998).

The maintenance of suitable potassic nutrition to support growth of different organs requires a good selectivity, in the aerial organs, of K^+ absorption, accumulation and transport compared to Na^+ . Many studies on halophytes and on some tolerant glycophytes plants showed that a high foliar K^+/Na^+ ratio is a salt tolerance criterion (Gorham *et al.*, 1990; Schachtman *et al.*, 1991; Wolf *et al.*, 1991; Yeo, 1998). Rejili *et al.*, (2007) showed that *L. creticus* is strongly selective for K^+ ions. It is known that the capacity of plants to counteract salinity stress strongly depends on the status of their K^+ nutrition. Increasing the K^+ supply in the root environment may mitigate the reduction of plant biomass due to an increase in salinity (Chow and Tsang, 1990; Delgado and Sánchez-Raya, 1999). Potassium starvation regularly accompanies sodium toxicity (Flowers and Läuchli, 1983), and Peng *et al.*, (2004) have shown that the decline of salt tolerance under low- K^+ conditions might have resulted from increased Na^+ entrance through the high affinity K^+ system.

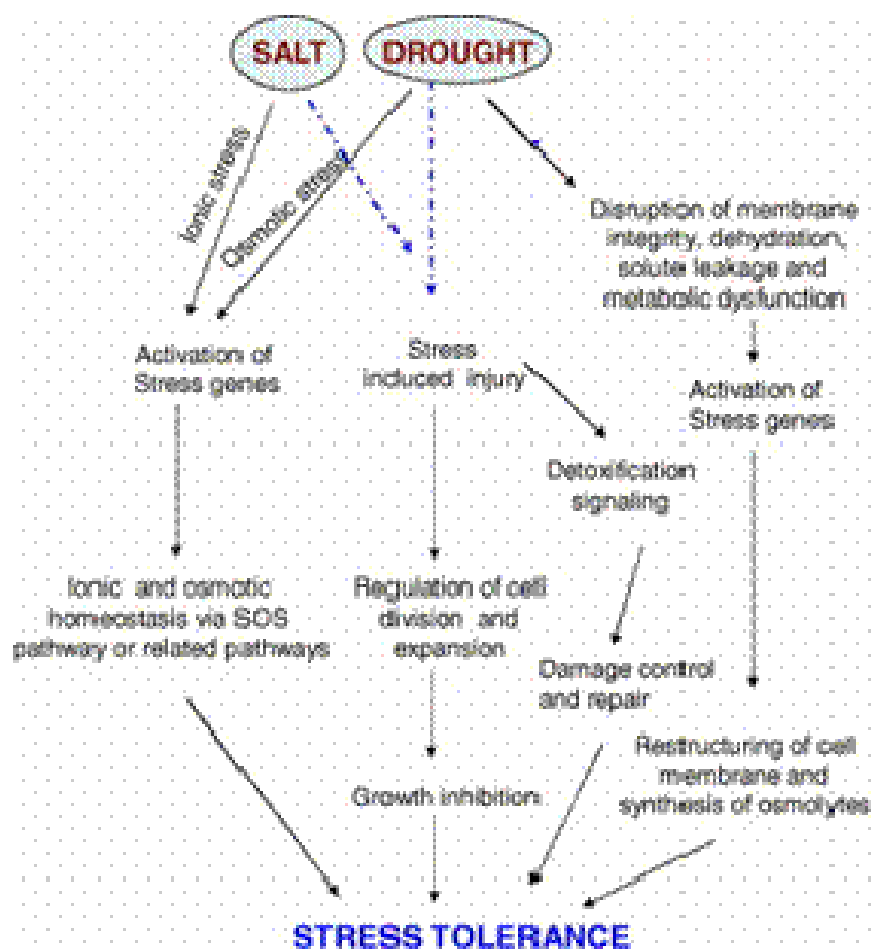


Figure 1. Generic pathway under salt and drought stress (Mahajan and Tuteja, 2005).

In conclusion, the present review has shown that *Lotus creticus* has a great resprouting capability and important growth rates under drought and salinity conditions. It can be deduced that this plant is a very useful species for revegetation in restored areas. Some effort must be conducted in improve its growth patterns under minimum irrigation in arid and semi-arid Mediterranean conditions. It is now well known that the stress signal is first perceived at the membrane level by the receptors and then transduced in the cell to switch on the stress responsive genes for mediating stress tolerance. Understanding the mechanism of stress tolerance along with a plethora of genes involved in stress signaling network is important for crop improvement. Recently, some genes of calcium-signaling and nucleic acid pathways have been reported to be up-regulated in response to both cold and salinity stresses indicating the presence of cross talk between these pathways (Figure 1). Salt and drought disrupt the ionic and osmotic equilibrium of the cell resulting in a stress condition. This triggers the process, which functions to reinstate ionic and osmotic homeostasis leading to stress tolerance. Stress imposes injury on cellular physiology and result in metabolic dysfunction. This injury imposes a negative influence on cell division and growth of a plant. This is an indirect advantage to the plant as reduction of leaf expansion reduces the surface area of leaves exposed for transpiration and thereby

reducing water loss. Stress injury and ROS generated in response to stress also triggers a detoxification signaling by activating genes responsible for damage control and repair mechanism therefore leading to stress tolerance. Moreover, other physiological factors such as rate of photosynthesis, protein assembly and general metabolic processes are severely hampered.

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