



# Growth responses of *Melilotus siculus* accessions to combined salinity and root-zone hypoxia are correlated with differences in tissue ion concentrations and not differences in root aeration



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## ARTICLE INFO

### Article history:

Received 28 April 2014

Received in revised form 17 August 2014

Accepted 18 August 2014

Available online 26 August 2014

### Keywords:

Additive interaction

Antagonistic interaction

Root porosity

Salt stress

Secondary aerenchyma

Waterlogging

## ABSTRACT

Soil salinity and root-zone hypoxia often occur together in saline landscapes. For many plants, this combination of stresses causes greater increases in  $\text{Na}^+$  and  $\text{Cl}^-$  in shoots, and decreases in  $\text{K}^+$ , than from salinity alone. These changes in ion concentrations from combined salinity and hypoxia can have more adverse consequences for growth than from salinity alone. The herbaceous forage legume *Melilotus siculus* naturally occurs in saline soils prone to waterlogging; however, accessions differ in their tolerances, although all form high levels of aerenchyma. We hypothesised that tolerance to combined salinity and hypoxia would be associated with either greater aerenchyma formation in roots or the innate ability of the accessions to regulate tissue ion concentrations. Fifteen accessions of *M. siculus* were grown in nutrient solution with two salinities (0 or 200 mM NaCl) and two aeration treatments (aerated or hypoxic) for 21 days. Dry mass (shoot and root), root porosity and ion concentrations ( $\text{Cl}^-$ ,  $\text{Na}^+$ ,  $\text{K}^+$ ) in shoots and roots were assessed. In the *M. siculus* accessions variation in the shoot dry mass under saline–hypoxic conditions was negatively correlated with shoot  $\text{Cl}^-$  and  $\text{Na}^+$ , and positively correlated with the shoot  $\text{K}^+$ . Shoot ion concentrations under saline–hypoxic conditions were related to concentrations under saline–aerated conditions, but not to the porosity of the main root, which was relatively high (~18 to 25%). Differences in the tolerance of *M. siculus* accessions to combined salinity and root-zone hypoxia were mediated by variation in the plants' ability to regulate ions, and were not related to variation in root porosity, which was relatively high in all accessions. The interaction between salinity and hypoxia was not detrimental to *M. siculus*, a waterlogging tolerant species.

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## 1. Introduction

Soil salinity and waterlogging (hypoxia) are major stress factors that can occur together in saline landscapes (Barrett-Lennard, 2003; Bennett et al., 2009; Barrett-Lennard and Shabala, 2013). For many plants, this combination of stresses causes greater increases in  $\text{Na}^+$  and  $\text{Cl}^-$  concentrations in the shoots than from salinity alone and greater decreases in  $\text{K}^+$  concentrations in the shoots than from

salinity alone (reviewed by Barrett-Lennard, 2003; Colmer and Flowers, 2008; Barrett-Lennard and Shabala, 2013). Furthermore, these changed ion concentrations under combined salinity and hypoxia can have more adverse consequences for growth than salinity alone. For example with wheat, plants exposed for 33 days to salinity under aerated conditions or nonsaline conditions with hypoxia remained alive, but plants exposed to 30 or 60 mM NaCl with hypoxia died (Barrett-Lennard et al., 1999). These deaths with combined salinity and hypoxia were associated with 4–6 fold increases in concentrations of  $\text{Na}^+$  and  $\text{Cl}^-$ , and 40% decreases in the concentration of  $\text{K}^+$ , in the shoots compared with plants grown at the same salinities under aerated conditions (Barrett-Lennard et al., 1999).

At a mechanistic level, salinity and hypoxia can have a variety of effects on plant metabolism. With salinity, there are immediate

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adverse osmotic effects on growth (Munns, 1993). However, in the longer-term there can be increases in Na<sup>+</sup> uptake and decreases in K<sup>+</sup> uptake, which decrease the ratio of K<sup>+</sup>/Na<sup>+</sup> in the cytosol. The physicochemical similarities of these ions mean that Na<sup>+</sup> can compete with K<sup>+</sup> threatening a wide range of key cytoplasmic processes – enzymatic reactions, protein synthesis and ribosome functions (reviewed by Shabala and Cuin, 2007). In addition, salinity can increase the production of reactive oxygen species (ROS), which may cause lipid peroxidation in cellular membranes and also damage to other cellular constituents (reviewed by Bose et al., 2014). Intriguingly, there may be antagonistic feedback between ROS production under saline conditions and K<sup>+</sup> homeostasis. Several types of K<sup>+</sup>-permeable channels are activated by ROS, providing a pathway for K<sup>+</sup> to leak from cells (reviewed by Anschutz et al., 2014). Hypoxia in plant tissues decreases the production of ATP. This has many adverse effects including impacts on the H<sup>+</sup>-ATPases responsible for membrane function; for example membrane depolarisation (e.g. Buwalda et al., 1988; Teakle et al., 2013) can change the control of Na<sup>+</sup> exclusion and K<sup>+</sup> uptake (Barrett-Lennard and Shabala, 2013).

Many marshland species are better adapted to the combination of salinity and waterlogging than dryland species (Colmer and Flowers, 2008; Jenkins et al., 2010; Barrett-Lennard and Shabala, 2013). Species or accessions with tolerance to this combination of stresses appear better able to regulate Na<sup>+</sup> and Cl<sup>-</sup> concentrations and maintain K<sup>+</sup> concentrations in shoots than less tolerant species or accessions (Barrett-Lennard and Shabala, 2013). However, it is not known which mechanisms enable this better ion regulation in tolerant species or accessions. Possibilities include: (i) an innately superior ability to regulate shoot ion concentrations under saline conditions (irrespective of the level of root-aeration), (ii) physiological adaptations that improve internal root aeration (such as high porosity via the development of aerenchyma and perhaps also a barrier to radial oxygen loss—Colmer, 2003), which ensure that the roots can maintain energy production, thereby maintaining ion regulation and growth, or (iii) combinations of both of the above.

Until now, the mechanism(s) enabling better ion relations in shoots of adapted genotypes under saline plus hypoxic conditions have not been resolved. In a study of 17 accessions of *Hordeum marinum*, faster growth in saline-hypoxic solution was associated with lower Na<sup>+</sup> concentrations and higher K<sup>+</sup> concentrations in the expanding leaves (Malik et al., 2009; Barrett-Lennard and Shabala, 2013). However, it was not possible to rule in (or out) the role that better root aeration had in these responses because there was inadequate root material in this study to make replicated measurements of root porosity (Malik et al., 2009).

The present work considers these issues in a study of the tolerance of accessions of the forage annual legume *Melilotus siculus* (Turra) Vitman ex B. D. Jacks (syn. *Melilotus mesanensis*) to the combined stresses of salinity and hypoxia. Amongst pasture legumes, this species is reputed to have exceptional tolerance to these stresses, based on comparisons of *M. siculus* and other pasture legume species to combinations of salinity and hypoxia (Teakle et al., 2012) and to these stresses individually (Rogers et al., 2011). Under nonsaline-hypoxic conditions, a single accession of *M. siculus* at least partly maintained internal root aeration because of the development of a secondary aerenchyma in a highly porous tissue called phellem that grew on the upper portions of the main root axis (tap root) and on lateral roots, as well as the hypocotyl (Teakle et al., 2011; Verboven et al., 2012). In addition, under saline-hypoxic conditions, this species had a superior ability (compared with two others—*Trifolium michelianum* and *Medicago polymorpha*) to regulate ion concentrations (Cl<sup>-</sup>, Na<sup>+</sup> and K<sup>+</sup>) in shoots (Teakle et al., 2012). We build on this understanding here by examining the variation amongst 15 accessions of *M. siculus* in growth, ion relations and root aeration

characteristics to the combined effects of root-zone salinity and hypoxia. Three-week old plants were subjected to combinations of treatments of salinity (0 or 200 mM NaCl) and root-zone aeration (aerated or hypoxic nutrient solution) for 21 days. In addition to the *M. siculus* accessions, a single accession of *T. michelianum* Savi (common name “balansa clover”) was included for comparison; this species is widely grown on slightly saline soils prone to waterlogging (Nichols et al., 2008; Boschma et al., 2008; Rogers et al., 2008). *T. michelianum* is sensitive to salinity (Rogers et al., 2008; Teakle et al., 2012) so it was expected to have a contrasting response to *M. siculus* under conditions of salinity with hypoxia.

One way in which to evaluate the effects of combinations of stresses on plant growth is to compare the impacts of the stresses separately and when combined; this approach has been widely used in studies of heavy metals (see theoretical approach of Berry and Wallace, 1981; Wallace and Berry, 1983). Adapting this approach, stress responses can be assessed by multiplying the effects of each stress individually, and comparing the result to plant growth with the combination of stresses. If the multiplied result is the same as with the combination of stresses the interaction is defined as “additive”; if the multiplied result is greater than with the combination of stresses the interaction is defined as “synergistic”. When the multiplied result is less than with the combination of stresses the interaction is defined as “antagonistic” (Berry and Wallace, 1981; Wallace and Berry, 1983). To illustrate: in the example of wheat referred to earlier (Barrett-Lennard et al., 1999), the individual effects of the salinity and hypoxia were each non-lethal, but the combination of stresses was lethal and therefore clearly antagonistic. The present paper uses this framework to assess the interaction between salinity and hypoxia on the growth and ion relations of 15 *M. siculus* accessions compared with *T. michelianum*.

Not surprisingly, we found that the variation in shoot dry mass (DM) amongst accessions of *M. siculus* was associated with variation in shoot ion concentrations, i.e. accessions with high shoot DM had low Na<sup>+</sup> and Cl<sup>-</sup>, and high K<sup>+</sup>. There seemed to be two possibilities for the underlying mechanism(s). The first possibility (Hypothesis 1) was that differences in the ability of the plants to internally aerate their roots influenced their ion regulation. The second possibility (Hypothesis 2) was that the differences in ion regulation of the accessions were due to variation in the innate ability of the accessions to regulate their shoot ions in aerated saline conditions. Hypothesis 1 would be supported if the concentrations of Na<sup>+</sup>, Cl<sup>-</sup> and K<sup>+</sup> in the shoots under saline-hypoxic conditions were correlated with traits associated with root aeration (e.g. porosity of the main root). Hypothesis 2 would be supported if the concentrations of Na<sup>+</sup>, Cl<sup>-</sup> and K<sup>+</sup> in shoots under saline-hypoxic conditions were proportional to the concentrations of those ions under saline-aerated conditions. Finally, if accessions had a range of levels of root aeration, we might expect the interactions between salinity and hypoxia on shoot ion relations and growth to be additive with high internal root aeration (i.e. high root porosity), but such interactions might become increasingly antagonistic as root porosity decreased.

## 2. Materials and methods

### 2.1. Experimental material and growth conditions

Fifteen accessions of *M. siculus* were selected based on their differential responses to the individual effects of either saline or stagnant deoxygenated nutrient solution, in previous experiments (Rogers et al., 2008, 2011). In addition, one accession of *T. michelianum* (“balansa clover” cv. Paradana), an annual pasture legume, was included for comparison (Boschma et al., 2008; Rogers et al., 2008).

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