Drought and salinity are two frequently combined abiotic stresses that affect plant growth, development, and crop productivity. Sulfate, and molecules derived from this anion such as glutathione, play important roles in the intrinsic responses of plants to such abiotic stresses. Therefore, understanding how plants facing environmental constraints re-equilibrate the flux of sulfate between and within different tissues might uncover perspectives for improving tolerance against abiotic stresses. In this review, we took advantage of genomics and post-genomics resources available in Arabidopsis thaliana and in the model legume species Medicago truncatula to highlight and compare the regulation of sulfate transporter genes under drought and salt stress. We also discuss their possible function in the plant’s response and adaptation to abiotic stresses and present prospects about the potential benefits of mycorrhizal associations, which by facilitating sulfate uptake may assist plants to cope with abiotic stresses. Several transporters are highlighted in this review that appear promising targets for improving sulfate transport capacities of crops under fluctuating environmental conditions.

**Keywords:** sulfate, transporters, abiotic stresses, M. truncatula, Arabidopsis

**INTRODUCTION**

Drought, the incidence of which is expected to increase with climatic changes, is one of the major abiotic constraints on agricultural productivity. Because drought is often associated with salinity, one challenge for sustainable agriculture is to breed crops for enhanced tolerance to both stresses. This requires an understanding of the adaptive mechanisms allowing plants to survive in low-water and high-salt environments. Sulfur is a key component in helping plants to cope with such abiotic stresses (for review, see Chan et al., 2013). For example, sulfur is used for the synthesis of glutathione, which acts in the maintenance of the cellular redox balance and mitigates damage caused by reactive oxygen species. Most of the sulfur taken up by plants is in the form of sulfate, and several studies point to a role of this anion in the plant response to drought and salinity in relation to the phytohormone abscisic acid (ABA), a major regulator of leaf stomatal conductance (Wilkinson and Davies, 2002). It was proposed that sulfate acts as a primary signal to enhance the anti-transpirant effect of ABA reaching the stomata in leaves (Ernst et al., 2010). After a search of the SULTR sequences in M. truncatula and of their closest homologs in Arabidopsis, we discuss and compare their regulation and possible contribution to protection against unfavorable environmental conditions. We also highlight the potential benefit of using arbuscular mycorrhizal (AM) fungi to improve sulfate uptake.

**COMPARATIVE ANALYSIS OF SULTR GENE FAMILIES BETWEEN Arabidopsis AND M. truncatula**

Medicago truncatula is an annual forage species adopted in 2001 as a model for legumes because of its small genome, compared to crop legumes such as pea, and its ability to perform symbiotic interactions with nitrogen-fixing rhizobia and AM fungi, like most legume species (Frugoli and Harris, 2001). The close relationship of the M. truncatula genome with that of pea (Pisum sativum L.) facilitates the transfer of information to the crop, and molecular
markers have been developed for translational genomics between the two species (Bordat et al., 2011). *M. truncatula* is native to the arid and semi-arid environments of the Mediterranean. It is thus adapted to this climate, making it a good model to identify adaptation processes to low-water or high-salt stresses. Genomic resources were developed for this species that we used here to retrieve resources were developed for this species that we used here to acquire data, Burstin J, personal communication) and rice (Kumar et al., 2011).

The recent transcriptome analysis of *M. truncatula* subjected to progressive drought (Zhang et al., 2014a) allowed us to investigate the transcriptional regulation of the MtSULTR gene family in response to this abiotic stress and in comparison with a salt stress response (Li et al., 2009). Data were downloaded from the Gene Expression Atlas (MtGEA)2, and expression fold-change between treated and non-treated samples was calculated (cutoff of 2.0, *Table 1*). Expression of three of the 14 MtSULTR genes (*MtSULTR2;2b, MtSULTR3;3b, and MtSULTR3;4b, Figure 1*) could not be investigated as there was no corresponding probe set in the Affymetrix chip used to build the MtGEA. To compare SULTR gene regulation between *M. truncatula* and *Arabidopsis*, we used transcriptomic data available in *Arabidopsis* for drought and salt stress experiments (Kilian et al., 2007; Huang et al., 2008; Perera et al., 2008; Nishiyama et al., 2012; Geng et al., 2013; Pandey et al., 2013; Wang et al., 2013; Ha et al., 2014). The studies showing the most substantial regulation of SULTR genes are included in *Table 1*. Results are discussed in the light of functional data available, mainly in *Arabidopsis*.

**SULTR of Group 3 Are Strongly Regulated by Abiotic Stresses in Roots**

Of particular interest is the up-regulation of the SULTR3;1 gene in roots of both species subjected to drought and salt stress. Interestingly, the expression of AtSULTR3;1 is enhanced by ABA and required for cysteine synthesis (Cao et al., 2014). Cysteine, whose precursor is sulfate, plays a key role in ABA synthesis as it serves as sulfur donor for the sulfuration of molybdenum, a co-factor needed in its sulfurylated form for the last reaction in the pathway (Xiong et al., 2001). The cysteine formed may also serve for the synthesis of the stress-defense compound glutathione. Cao et al. (2014) proposed that sulfur metabolism and ABA biosynthesis interplay to ensure sufficient cysteine for ABA production under abiotic stresses. From these data and the reported plastid-localization of AtSULTR3;1 (Cao et al., 2013), it is tempting to speculate on a role for this transporter in directing the flux of sulfate toward cysteine biosynthesis in the root plastids that may further be used for ABA production in response to both abiotic stresses. In *M. truncatula*, SULTR3;1 has not been functionally characterized. However, the gene is up-regulated in response to both abiotic stresses (*Table 1*) and co-localizes with quantitative trait loci (QTL) regions for salt tolerance (Friesen et al., 2010; Arraouadi et al., 2012), as also observed for AtSULTR3;1 (El-Soda et al., 2014; Zhang et al., 2014c). This

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1 http://www.jcvi.org/medicago/

2 http://mtgea.noble.org/v3/
Table 1 | Regulation of SULTR gene expression in Medicago truncatula and Arabidopsis subjected to drought and salt stress.

| Group | Gene | Probeset ID | **DROUGHT** | **SALINITY** |
|-------|------|-------------|-------------|-------------|
|       |      |             | **ROOT** | **SHOOT** | **ROOT** | **Late** |
|       |      |             | Mild      | Moderate   | Severe   | Early     | Late     |
|       |      |             |           |           |           |           |          |
| 1     | SULTR1;1 | Mtr.12106.1.S1_at | -3.7 | -13.4 | -15.7 | ns | ns | ns | -2.9 |
| 1     | SULTR1;2 | Mtr.28489.1.S1_at | ns | ns | ns | ns | ns | ns | 3.7 |
| 1     | SULTR1;3 | Mtr.5111.1.S1_at | -3.9 | ns | -1.7 | ns | -2.6 | -3.2 | 1.9 |
| 2     | SULTR2;1 | Mtr.11734.1.S1_at | -2.5 | ns | ns | -5.4 | -4.6 | -6.0 | ns |
| 2     | SULTR2;2a | Mtr.45143.1.S1_at | ns | ns | 1.8 | ns | ns | ns | -1.5 |
| 3     | SULTR3;1 | Mtr.18757.1.S1_at | 4.7 | 14.4 | 27.9 | -1.9 | -3.1 | -2.8 | 2.5 |
| 3     | SULTR3;2 | Mtr.41982.1.S1_at | ns | ns | ns | -2.1 | -4.0 | -4.3 | 7.4 |
| 3     | SULTR3;3a | Mtr.41524.1.S1_at | 2.1 | 1.6 | 2.0 | ns | -2.1 | -2.3 | ns |
| 3     | SULTR3;4a | Mtr.31749.1.S1_at | 3.8 | 5.5 | 5.8 | 2.5 | 2.5 | 1.5 | -1.9 |
| 4     | SULTR3;5 | Mtr.37708.1.S1_at | -2.0 | -2.1 | -3.3 | -1.7 | -1.6 | -1.8 | 25.1 |
| 4     | SULTR4;1 | Mtr.45139.1.S1_at | ns | ns | ns | 1.6 | 1.5 | 1.7 | 2.9 |

The subcellular localization of SULTR3;4 is unknown. Investigating spatial and subcellular localizations in roots for both transporters might help to decipher whether they can have a coordinated function or a functional redundancy in this tissue. It should be noted that in contrast to Arabidopsis, MtSULTR3;1 and MtSULTR3;4a are differentially regulated in response to salt stress (only MtSULTR3;1 is up-regulated) and that a second MtSULTR3;4 gene (MtSULTR3;4b, Figure 1) exists whose response to salt stress is currently unknown.

In *M. truncatula*, the expression of another group 3 SULTR (*MtSULTR3;5*) is strongly up-regulated in roots subjected to salt stress (up to 78-fold; Table 1). Its closest *Arabidopsis* homolog,
AtSULTR3;5, shows opposite trends of expression in roots with a consistent down-regulation in response to salinity. This suggests distinct roles or transcriptional regulation of SULTR3;5 between the two species. In the legume species Lotus japonicus, the SULTR3;5 homolog SST1 (Symbiotic Sulfate Transporter 1) is necessary for nodule formation and essential for the symbiotic supply of sulfur to the bacteria (Krusell et al., 2005). In this connection, Varin et al. (2010) identified sulfur supply as necessary for proper accumulation of nitrogenase and leghaemoglobin, two proteins rich in sulfur amino acids and needed for nitrogen fixation. This highlights the importance of maintaining efficient sulfate transport systems in nodules to exploit the nitrogen-fixing capacity of legume plants in agroecological systems. MitSULTR3;5 is strongly expressed in nodules (Roux et al., 2014) and studies are ongoing to understand the function of MitSULTR3;5 in nodules and to deciphering its contribution to the salt stress response.

RE-EQUILIBRATION OF SULFATE FLUX IN AERIAL PARTS IN RESPONSE TO ABIOTIC STRESSES

In contrast to the functional SST1 (Krusell et al., 2005), AtSULTR3;5 is a non-functional transporter by itself (Kataoka et al., 2004a). This transporter forms a complex with AtSULTR2;1, thus enhancing its sulfate import activity into cells of root vascular tissues for loading into the xylem and transfer to aerial parts, especially when sulfur availability is limited (Takahashi et al., 2000; Kataoka et al., 2004a). The flux of sulfur from roots to shoots is in part controlled by microRNA (Mir)395, which limits expression of SULTR2;1 to xylem parenchyma, thus enhancing sulfate translocation to aerial parts (Kawashima et al., 2011). Interestingly, Mir395 is up-regulated in response to drought stress in rice (Zhou et al., 2010) and under high salinity conditions in maize (Zea mays L.; Ding et al., 2009), suggesting it participates in abiotic stress responses, presumably by maintaining the flux of sulfur toward aerial parts. In roots, the expression of AtSULTR2;1 is not affected by salinity and drought, whereas that of AtSULTR3;5 decreased significantly in response to salt stress (Table 1). Owing to the co-activator function of AtSULTR3;5, this may slow the allocation of sulfate to aerial parts. It is therefore possible that Arabidopsis adjusts the level of sulfate in roots under salt stress by modulating AtSULTR3;5 expression. This could be part of the adaptive mechanisms used by Arabidopsis to load sulfate into xylem vessels while ensuring that sufficient sulfate remains in roots when uptake is limited due to high salt concentrations in soils. In M. truncatula, the SULTR2;1 gene is not significantly regulated in roots in response to salt stress, but down-regulated in this tissue at early stages of water stress. The function of this transporter has not been reported yet, but if we assume a similar role to its Arabidopsis homolog, the down-regulation observed is likely to reflect a need to maintain sulfate in roots at these stages.

A continued loading of sulfate into xylem vessels is of paramount importance for maintaining the synthesis of sulfur molecules in aerial parts. Moreover, sulfate from the xylem acts as a chemical signal for ABA-dependent stomatal closure in leaves during early stages of water stress when ABA biosynthesis is restricted to leaves (Ernst et al., 2010). Several SULTR genes in Table 1 that are regulated in shoots or leaves are good candidates for re-equilibrating the flux of sulfate in aerial parts in response to abiotic stresses. First, SULTR2;1 is significantly down-regulated in leaves of Arabidopsis and M. truncatula subjected to drought. AtSULTR2;1 has been shown to be not only expressed in the xylem parenchyma cells but also in the phloem cells of mature leaves, where it participates in the translocation of sulfate to young leaves (Takahashi et al., 2000). Hence, the down-regulation of SULTR2;1 suggests a decreased flux of sulfate to young leaves, presumably to save sulfate for protection mechanisms, such as those involving ABA. Second, in M. truncatula subjected to drought, one SULTR3 gene, MitSULTR3;4, is significantly up-regulated in aerial parts and more strongly at early stages of water stress (mild and moderate in Table 1). It would be of particular interest to investigate whether this transporter could play a role in leaves in controlling their early response to water stress in strong connection with ABA biosynthesis. In Arabidopsis, AtSULTR3;1 and 3;4 are both significantly up-regulated in leaves subjected to salt stress, reinforcing the hypothesis raised in the previous section that both transporters could act in concert to mitigate the effect of salt stress.

Interestingly, the expression of both vacuolar AtSULTR4 genes is significantly enhanced in leaves by drought and salinity. Moreover, AtSULTR4;1 and AtSULTR4;2 fall in QTL regions for tolerance to both stresses (Juenger et al., 2005; McKay et al., 2008). They are thus good candidates for multiple stress tolerance. The only SULTR4 gene in M. truncatula is also up-regulated in shoots in response to drought with a statistically significant but lower fold-change compared to Arabidopsis. Because in Arabidopsis, the SULTR4 transporters were shown to enable the mobilization of the sulfate stored in the vacuoles, they may play a critical role in ensuring sulfur metabolism in plant cells when sulfate uptake is limited due to environmental constraints. Furthermore, efflux of sulfate from the vacuole may contribute to osmotic adjustments that play a fundamental role in water and salt stress responses. The role of SULTR4 (Kataoka et al., 2004b) has been investigated in roots but their involvement in shoots merits further investigations in relation to abiotic stress tolerance.

REGULATION OF GENES INVOLVED IN SULFATE UPTAKE UNDER ABIOTIC STRESS CONDITIONS

The capacity of roots to take up nutrients generally declines in salt- and water-stressed plants, which may explain the changes in expression of SULTR genes belonging to groups 2, 3, and 4 under these conditions to rebalance sulfate flux between affected tissues. By examining the regulation of the two SULTR1 genes known to control sulfate uptake in Arabidopsis, we observed a contrasted pattern for both genes (Table 1). MsSULTR1;1 appeared down-regulated in roots subjected to both abiotic stresses, whereas MsSULTR1;2 and AtSULTR1;2 were up-regulated in response to salinity and drought, respectively. Barberon et al. (2008) demonstrated that SULTR1;1 and SULTR1;2 display unequal functional redundancy in Arabidopsis and left open the possibility for the SULTR1;1 gene to display an additional function besides its role in sulfate membrane transport. Recent findings also proposed a supplementary role for AtSULTR1;2 in the regulatory or sensing/signaling pathways related to sulfur metabolism (Zhang
et al., 2014b). Further studies are needed to better understand their additional function(s) and contribution to abiotic stress responses.

**AM FUNGI, A PROMISING PERSPECTIVE FOR IMPROVING SULFATE UPTAKE IN FLUCTUATING ENVIRONMENTS?**

The emerging role of sulfate in plant adaptation to abiotic stresses reinforces the need to sustain proper sulfate uptake and use in cultures that face environmental stresses. One specific feature of legumes, compared to *Arabidopsis*, is their ability to perform symbiotic interactions with AM fungi. This mutualistic association is known to increase plant tolerance to drought (Augé, 2001), an abiotic stress limiting the absorption of ions, including sulfate, by roots. Recent studies in *M. truncatula* revealed that AM fungi improve sulfur nutrition in low-sulfate environments (Casieri et al., 2012; Sieh et al., 2013), probably through their capacity to take up and translocate sulfate to the root (Gray and Gerdemann, 1973; Rhodes and Gerdemann, 1978a; Allen and Shachar-Hill, 2009). To date, there is no information available on the regulation of plant sulfate uptake or plant sulfate transporter genes in the presence of AM fungi under drought conditions. However, because drought is associated with reduced sulfate availability, the *SULTR* genes up-regulated at low sulfate concentrations in roots colonized with AM fungi (Casieri et al., 2012; Sieh et al., 2013) might help the plant partner to survive in such environments. This is the case for *MtSULTR1;1* and *MtSULTR1;2*, both up-regulated in roots of AM symbiotic plants, especially at low sulfate concentrations (Casieri et al., 2012). Recently, Giovannetti et al. (2014) demonstrated the induction of the *LjSULTR1;2* gene during the *Lotus japonicus/Rhizophagus irregularis* mutualistic interaction, and the specific expression of this transporter in arbuscule-containing cells, strongly suggesting AM-specific sulfate transport. Investigating the regulation of such genes during AM symbiosis in response to abiotic stresses might help to decipher the roles played by these transporters in fluctuating environments.

**CONCLUSION**

Several *SULTR* genes regulated by drought and/or salinity were highlighted in this review that may contribute to adjust sulfur distribution in plants subjected to abiotic stresses. We discussed their possible roles using information available in *Arabidopsis*, for which considerable advances have been made in the last two decades toward understanding *SULTR* functions, more recently in response to salinity (Cao et al., 2014). *SULTR* genes similarly regulated in *Arabidopsis* and *M. truncatula* are promising targets for improving sulfate transport capacities under fluctuating environmental conditions. Among these are group 3 *SULTR*, also in the list of abiotic stress-responsive genes shared between *Arabidopsis* and *M. truncatula* of Hyung et al. (2014). Group 1 *SULTR* are other potential targets for enhancing sulfate uptake in fluctuating environmental conditions. Members of this group were found to be up-regulated by drought stress and by AM fungi associations that increased significantly the root uptake of sulfate in low-sulfate environments, as it is the case in drought conditions. Broad collections of ecotypes and TILLING mutants are available in *M. truncatula* and in the pea crop (Dalmais et al., 2008; Le Signor et al., 2009; Deulovot et al., 2010) that can be used to study and confirm *SULTR* genes as relevant candidates for discovering favorable alleles for abiotic stress tolerance.

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