Salt tolerance mechanisms in the Lycopersicon clade and their trade-offs

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Abstract
Salt stress impairs growth and yield in tomato, which is mostly cultivated in arid and semi-arid areas of the world. A number of wild tomato relatives (Solanum pimpinellifolium, S. pennellii, S. cheesmaniae and S. peruvianum) are endemic to arid coastal areas and able to withstand higher concentration of soil salt concentrations, making them a good genetic resource for breeding efforts aimed at improving salt tolerance and overall crop improvement. However, the complexity of salt stress response makes it difficult to introgress tolerance traits from wild relatives that could effectively increase tomato productivity under high soil salt concentrations. Under commercial production, biomass accumulation is key for high fruit yields, and salt tolerance management strategies should aim to maintain a favourable plant water and nutrient status. In this review, we first compare the effects of salt stress on the physiology of the domesticated tomato and its wild relatives. We then discuss physiological and energetic trade-offs for the different salt tolerance mechanisms found within the Lycopersicon clade, with a focus on the importance of root traits to sustain crop productivity.

Keywords: Crop improvement; salinity stress; tomato wild relatives.

Introduction
Salinity is one of the most challenging environmental conditions that limit crop growth and yield. It is estimated that more than 20% of cultivated lands are affected by high-salinity conditions (Machado and Serralheiro 2017). Crop yield losses due to salinity amount to $26 billion per year (Singh et al. 2016). Soil salinization can occur via natural processes such as the rising of the water table, accumulation of salts on the soil surface as water evaporates, or by human activities (Shahid et al. 2018). As water availability for agriculture decreases or becomes erratic due to climate change, the use of poor-quality irrigation water, high rates of evapotranspiration and inappropriate use of fertilizers can exacerbate soil salinization, especially in arid and semi-arid regions. Saline areas are expanding at a rate of ~10% per year (Foolad 2004; Liu et al. 2020). A soil is generally considered saline when the electrical conductivity (EC) of the saturation extract in the root zone exceeds 4 dS m⁻¹ at 25 °C (Thorne, 1954). Saline soils can be managed with the use of high-quality water to leach the salts away from the root zone, but this method has become unsustainable and impractical (Boretti and Rosa 2019). Thus, the search for salt-tolerant traits compatible with crop productivity becomes necessary to reduce food insecurity under the increasingly water-limited and saline conditions of the future (IPCC 2019).

Tomato (Solanum lycopersicum) is the most important vegetable crop in the world, with its $119.6 billion production value in 2019 (FAOSTAT 2019), thanks to the versatility of its fruit, which can be consumed fresh, dried and processed, and to its nutritional and organoleptic characteristics. Global annual tomato production equates to roughly 243 million tonnes of fresh fruit produced on 6.1 million hectares in 166...
countries (FAOSTAT 2019). Taxonomically, tomato belongs to the *Lycopersicon* clade, which includes 12 wild relatives (Knapp and Peralta 2016), that are all native to South America (Table 1).

Members of this clade occupy a vast range of contrasting environments, ranging from sea level (e.g. Galapagos Islands) to ~3300 metres above sea level (e.g. Andean highlands), and from xeric to mesic environments (Taylor 1986). Although domesticated tomato is endemic to the same region, the domestication process has narrowed the vast genetic background to less than 5 % of that found in its wild relatives (Miller and Tanksley 1990). The domestication process typically results in larger edible organs (fruit or leaf), more vigorous plants, increased apical dominance, and decreased or loss of photoperiodicity and seed dormancy; however, the trade-off is usually an increased vulnerability to abiotic and biotic stresses (Yang et al. 2019). The process of tomato domestication has targeted numerous traits related to crop management and productivity, including growth habit (e.g. self-pruning gene for mechanical harvest), early flowering and concentrated fruit set, larger fruit size, fruit shape and colour, and crop disease resistance (Stevens and Rick 1986; Bai and Lindhout 2007; Labate et al. 2007; Barrios-Masias and Jackson 2014). Advance in breeding technologies such as markers, quantitative trait loci (QTL) mapping, genome-wide association studies (GWAS) and the use of introgression lines has enabled the widespread use of wild tomato species for breeding purposes (for an extensive review, see Labate et al. 2007 and Chaudhary et al. 2019). The utility of wild species for tomato breeding lies in the immense genetic and phenotypic variation, which has been largely investigated for abiotic and biotic stress tolerance traits (Table 2).

Several tomato wild relatives such as *S. pimpinellifolium*, *S. chilense*, *S. pennelli*, *S. cheesmaniae* and *S. galapagense* are naturally adapted to highly saline soils. Under saline conditions, these species can show less decrease in growth, a greater capacity for achieving ion homeostasis in roots and shoots, a higher ability to accumulate Na⁺ and Cl⁻ in leaves, enhanced hormonal signalling responses and osmotic adjustment, and more antioxidant activity when compared with cultivated tomato under salt stress (Frarry et al. 2010; Albaladejo et al. 2017; Gharbi et al. 2017; Pailles et al. 2020). These characteristics make tomato wild relatives a potential genetic resource for improving salt tolerance in the cultivated tomato. However, the introgression of traits from wild relatives to elite cultivars remains challenging due to the complexity of salt tolerance traits, which can result in the transfer of loci deleterious to plant development and yield, making difficult to recover the genetic background of the elite cultivar in which the traits are being introgressed (Cuartero et al. 2006; Gharsallah et al. 2016; Dariva et al. 2020).

This review aims to compare salinity effects on physiological and biochemical aspects of the domesticated tomato and its wild relatives. We highlight the potential for wild relatives to contribute to improved salt tolerance of the cultivated tomato by discussing root and leaf traits associated with salt tolerance and their associated energetic trade-offs.

### Impact of Salinity Stress on Plant Growth and Physiology

Salt stress impairs not only growth and yield, but also many aspects of tomato plant physiology, such as plant water relations and metabolic processes. The impairment of tomato physiology under saline conditions differs depending on the developmental stage (Foolad 2007).

#### Seed germination

Salt tolerance at the seed germination stage depends on the seed ability to withstand the effects of high concentrations of soluble salts and lower soil water potential (Bradford, 1995). The seed must generate sufficient osmotic potential to improve the water status of the embryo (i.e. imbibition stage), and allow the biochemical processes that enable radicle growth and germination. In tomato, high salinity delays the onset and reduces the rate and final percentage of germination (Singh et al. 2012; Tahir et al. 2018). A number of wild tomato relatives exhibit greater salt tolerance compared to the cultivated tomato at the germination stage (Jones 1986a; Foolad and Jones, 1991; Foolad and Lin 1997; Cuartero and Fernandez-Munoz 1999). For instance, *S. pimpinellifolium* (accession LA722), *S. peruvianum* (accession PI127832) and *S. pennelli* (accession LA716) showed higher germination rates compared with cultivated tomato at 100 mM NaCl (~10 dS m⁻¹) (Tahir et al. 2018). A number of wild tomato relatives exhibit greater salt tolerance compared to the cultivated tomato at the germination stage (Jones 1986a; Foolad and Jones, 1991; Foolad and Lin 1997; Cuartero and Fernandez-Munoz 1999). For instance, *S. pimpinellifolium* (accession LA722), *S. peruvianum* (accession PI127832) and *S. pennelli* (accession LA716) showed higher germination rates compared with cultivated tomato at 100 mM NaCl (~10 dS m⁻¹) (Jones 1986a). The tomato seed embryo is coated by two protective tissues (endosperm and the testa), which must be at least partially degraded for the completion of germination. This degradation is catalysed by hydrolytic enzymes such as β-mannosidase and α-galactosidase, which are known to be inhibited under salt stress (Ali and Elozeiri 2017). A study of the tomato cv. ‘Ciettaicale’ and cv. “San Marzano” revealed that ‘Ciettaicale’ seeds maintained higher endo-β-mannanase, β-mannosidase and α-galactosidase activities under mild salt stress conditions (25 mM NaCl or ~2.5 dS m⁻¹). These elevated glycosyl hydrolase activities were accompanied by higher antioxidant activity as well as greater starch mobilization and higher total soluble sugar accumulation. These changes were especially prominent in ‘Ciettaicale’ at 72 h post salt exposure. Overall, ‘Ciettaicale’ exhibited a higher percentage and rates of germination compared with ‘San Marzano’ (Moles et al. 2019).

#### Vegetative stage

During the vegetative stage, shoot and root growth are impaired under salt stress due to restrictions in cell expansion, which are the result of low soil water potential, nutrient imbalance and ion toxicity. For example, at an early vegetative stage (3–4 leaves stage) *S. lycopersicum* cv. ‘Heinz 1350’ and ‘VF234’ exhibit 60 % reduction in stem elongation rate under saline conditions. By contrast, wild tomato relatives grown under the same conditions exhibited smaller reductions in stem elongation (e.g. *S. pennelli* accession Atico: 55 %, and *S. cheesmaniae* ecotype

| Country          | Tomato wild relatives                                                                 |
|------------------|---------------------------------------------------------------------------------------|
| Chile            | *S. chilense*, *S. peruvianum*                                                         |
| Ecuador          | *S. habrochaites*, *S. neorickii*, *S. pimpinellifolium*                              |
| Ecuador (Galapagos Island) | *S. galapagense*, *S. cheesmaniae*, *S. pimpinellifolium*                          |
| Peru             | *S. arcanum*, *S. chilense*, *chimielewskii*, *S. corneliumulleri*, *S. habrochaites*, *S. huylasense*, *S. neorickii*, *S. pennelli*, *S. peruvianum*, *S. pimpinellifolium* |

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Table 2. Comparison of wild and domesticated tomatoes (Solanum section Lycopersicon) based on habitat and importance for breeding purposes. Data adapted from Peralta et al. (2005); Labate et al. (2007); Bergougoux (2014); Grandillo et al. (2011).

| Species       | Habitat                                                                                                                        | Importance for tomato breeding                                                                                                                       | References                                                                                           |
|---------------|--------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------|
| *S. lycopersicum* | Known only from cultivation or escapes; many escaped plants have smaller fruits (*cerasiforme*); sea level to 4000 m              | Moisture tolerance, resistance to wilt, root-rotting and leaf-spotting fungi                                                                             | Hutton et al. (2010); Wang et al. (2013)                                                             |
| *S. pimpinellifolium* | Dry coastal habitats; 0–500 m, but exceptionally up to 1400 m                                                                   | Colour and fruit quality, resistance to insect, nematode and diseases; drought and salt tolerance                                                       | Salinas et al. (2013); Villalta et al. (2008); Foolad (2007)                                        |
| *S. chilense* | Hyper-arid rocky plains and coastal areas                                                                                       | Drought and salt tolerance; virus resistance                                                                                                         | Kashyap et al. (2020); Tapia et al. (2016); Agrama and Scott (2006)                                 |
| *S. pennellii* | Dry rocky hillside and sandy areas; sea level to 2300 m                                                                          | Drought and salt tolerance; resistance to insects                                                                                                     | Gong et al. (2010); Frary et al. (2010)                                                             |
| *S. habrochaites* | On the western slopes of the Andes; in a variety of forest types, from premontane forest to dry forests; 200–3300 m         | Cold and frost tolerance; resistance to insects due to their glandular hairs                                                                        | Liu et al. (2012); Momotaz et al. (2010)                                                            |
| *S. cheesmaniae* | Arid, rocky slopes, prefers shaded sites; sea level to 1500 m                                                                  | Salt tolerance; Lepidoptera and virus resistance                                                                                                     | Villalta et al. (2008); Ali et al. (2019)                                                           |
| *S. galapagense* | Arid, rocky slopes, sometimes near shoreline within range of sea spray; sea level to 650 m                                         | Salt tolerance; Lepidoptera and virus resistance                                                                                                     | Firdaus et al. (2013); Pailles et al. (2020)                                                        |
| *S. neorickii* | Dry Andean valleys, moist, well-drained rocky slopes; 1950–2600 m                                                               | Resistance to Botrytis cinerea and Oidium lycopersici                                                                                                  | Finkers et al. (2008); Faino et al. (2012)                                                          |
| *S. chmielewskii* | High dry Andean valleys; 1600–3200 m                                                                                           | Fruit quality                                                                                                                                          | Ballester et al. (2016)                                                                             |
| *S. peruvianum* north | *S. aranum* Coastal and inland Andean valleys; lomas formations, dry valleys and dry rocky slopes; 100–2800 m                | Resistance to virus, bacteria, fungi, aphids and nematodes; salt stress tolerance                                                                      | Anbinder et al. (2009); Tapia et al. (2016)                                                          |
|                | *S. huaylasense* Rocky slopes; 1700–3000 m                                                                                      |                                                                                                                                                      |                                                                                                       |
| *S. peruvianum* south | *S. peruvianum* Coastal lomas formations and occasionally in coastal deserts, sometimes near agricultural fields as weed; sea level to 600 m |                                                                                                                                                      |                                                                                                       |
|                | *S. cornelionulleri* Rocky and sandy slopes; 200–3300 m                                                                        |                                                                                                                                                      |                                                                                                       |
no. 1400: 32 %) (Tal and Shannon 1983). One characteristic typical of salt-tolerant tomato wild relatives is that they show less growth under non-saline conditions, but they outperform the domesticated tomato under high levels of salt stress. For instance, at 3–4 leaves stage, the tomato cv. ‘Moneymaker’ showed a greater shoot biomass and growth rate than S. pennellii accession PE-47 during the first 7 days of salt treatment (100 mM NaCl, or ~10 dS m⁻¹). However, after 7 days S. pennellii accession PE-47 outperformed the commercial cultivar (Albaladejo et al. 2017). At the 7–8 leaf stage, a comparison between 28 accessions of S. galapagense, 39 of S. cheesmaniae and two tomato cultivars (Heinz 1706 and Moneymaker) revealed that all wild relative accessions had a lower decrease in total plant biomass under salt stress compared with its control when exposed to saline conditions for a 10-day period in a hydroponic system (200 mM NaCl, or ~20 dS m⁻¹; Païles et al. 2020). In our evaluations of a commercial tomato cultivar (cv. ‘BHN589’), three commercial rootstocks (DRO-141TX, Estamino, Maxifort) and the wild relatives S. chilense (accessions LA2931, LA3115), S. galapagense (accessions LA1400, LA1401) and S. pimpinellifolium (accessions LA1618, LA1629, LA2983) exposed to moderate (6 dS m⁻¹) and severe (12 dS m⁻¹) salinity at the 5–6 leaf stage revealed wide differences in biomass production and carbon allocation after 3 weeks of salinity treatment (Fig. 1). Two accessions each of S. chilense and S. galapagense showed significantly less root and shoot biomass accumulation compared to the cultivated tomato (cv. ‘BHN589’), the three commercial tomato rootstocks and the four accessions of S. pimpinellifolium, under both control and salt stress conditions. Solanum pimpinellifolium is the closest wild relative to the domesticated tomato (Peralta and Spooner 2005), which could explain their more similar behaviour in biomass accumulation under salt stress as compared to S. galapagense and S. chilense. The tomato rootstocks exhibited higher shoot and root biomass than the cv. ‘BHN589’ under salt stress, suggesting that grafting could be an effective technique to increase tolerance to several abiotic stresses (Singh et al., 2020; Bristow et al. 2021). Solanum pimpinellifolium showed higher shoot and root biomass than the cv. ‘BHN589’, but similar to the commercial rootstocks. The relative decrease in root and shoot growth, compared to the control (1.5 dS m⁻¹), was lower in the wild relatives S. chilense and S. galapagense than in tomato rootstocks and S. pimpinellifolium. The root-to-shoot ratio, which is usually related to salt tolerance in the Lycopersicon clade (Taleisnik 1987; Cruz and Cuartero 1990; Maggio et al. 2007), was maintained under salt stress in S. chilense, S. galapagense and the cv. ‘BHN589’, but decreased in the tomato rootstocks and S. pimpinellifolium.

Reproductive stage

Whereas mild salt stress has been demonstrated to improve fruit quality (Meza et al. 2020), high soil salinity is responsible for decreases in tomato crop yields (De Pascale et al. 2003; Massareto et al. 2018). Flower development under salt stress seems to be more impaired by a disequilibrium between source and sink organs, due to the accumulation of carbohydrates in the leaves instead of ion toxicity in reproductive organs (Balbrea et al. 2003; Ghanem et al. 2009). In tomato, fruit size is more affected than fruit number under moderate salt concentrations, but both decrease under severe salt stress (Cuartero and Fernandez-Munoz 1999). A study comparing 94 accession of S. pimpinellifolium and two tomato cultivars (cv. ‘Arka Meghali’ and the inbred line CA4) showed that the S. pimpinellifolium had a larger decrease in fruit number than fruit weight, resulting in a lower per plant yield reduction (~82 %) compared to the two tomato cultivars (~87 % decrease) (Rao et al. 2013). A comparison of S. lycopersicum var. cerasiforme and S. chilense (accession LA4107) revealed that S. chilense had less of a decrease in fruit size than the domesticated tomato (Martinez et al. 2012). Increasing the capacity of the plant to maintain a lower fruit osmotic potential (Ψ) could allow fruit growth under salt stress (Bolarin et al. 2001). A comparison between the tomato cv. ‘Moneymaker’ and S. pimpinellifolium (accession PE-2) showed that the latter was able to use Na⁺ and Cl⁻ to decrease fruit Ψ, and maintain fruit development under salinity conditions, whereas the domesticated tomato used sugars for osmotic adjustment (Bolarin et al. 2001), with higher carbon and energy costs (Tyerman et al. 2019).

Salt Tolerance Mechanisms and Their Trade-offs

Energy demands under salt stress increase due to elevated photorespiration, protein turnover and ion transport activity (Wingler et al. 2000; Miller et al. 2010; Shi and Theg 2013). The ability of a plant to maintain growth and survive under salt stress is considered salinity tolerance, and two main mechanisms for salt tolerance in the Lycopersicon clade have been identified: (i) salt exclusion, which prevents Na⁺ movement to the shoot through active exclusion from or retention in the roots; and (ii) salt inclusion, where tissue tolerance is achieved through compartmentalization in vacuoles to avoid toxicity, and accumulation of compatible osmolytes to balance the osmotic pressure in the cytosol (Shabala 2013; Almeida et al. 2014). Whereas S. lycopersicum generally employs an exclusion mechanism to cope with soil salinity, several wild accessions adapted to saline areas, from wild relatives such as S. pimpinellifolium, S. cheesmaniae, S. galapagense, S. pennellii and S. peruvianum generally utilize an inclusion mechanism (Foolad 2004). However, different reports show discrepancies about this distinction, which can result from the use of different accessions, using plants at different developmental stages and different forms of salinity treatments (Rajasekaran et al. 2000). For this reason, we will consider the distinction between exclusion and inclusion mechanisms as not specific to a tomato cultivar or wild relative species. Different salt tolerance mechanisms have different energetic costs for the plant, which can affect the overall plant growth and yield. The capacity of the plant to efficiently use its energy resources is essential to ensure higher growth and yield under salinity conditions. The maintenance of a favourable plant water status and nutrient uptake rate are also fundamental for maintaining growth and yield. Overall, the concentration of Na⁺ in tomato shoots is not a good indicator of performance under salt stress (Saranga et al. 1991; Almeida et al. 2014), but a suite of biochemical, physiological and anatomical traits can be involved in conferring salt tolerance. Several root and leaf traits that are key for maintaining nutrient balance, plant water status, an efficient use of energy resources and preventing ion toxicity under salt stress are discussed herein and summarized in Table 3.

Effect of soil salinity

In soil, salinity results in particle disaggregation, clay dispersion and increased soil pH, initially leading to an impairment of nutrient availability for plants. Cultivated tomato is moderately sensitive to saline conditions and tolerates soils with an EC of 2.5 dS m⁻¹ (~25 mM NaCl). Above this threshold, crop productivity is reduced at a rate of ~10 % per unit increase of EC (~10 mM NaCl increase) (Saranga et al. 1991). Under salt stress,
Figure 1. Root (A) and shoot (B) dry weight and root-to-shoot ratio (C) from a salt tolerance screening of the tomato wild relatives *S. chilense* (accessions LA2931, LA3115), *S. galapagense* (accessions LA1400, LA1401) and *S. pimpinellifolium* (accessions LA1618, LA1629, LA2983), a commercial tomato cultivar ('BHN589') and three commercial rootstocks (DRO-141TX, Estamino, Maxifort). Three levels of salinity were applied (0, 60 and 120 mM NaCl, corresponding to ~1.5, 6 and 12 dS m$^{-1}$). Data were analysed with two-way ANOVA using anova function in R 3.6.3 (R Core Team 2021). Data were transformed as necessary when ANOVA assumptions were not met. For all models, the alpha for the main effect was set at 0.05 level. When the calculated $P$-value was lower than our chosen alpha, the null hypothesis was rejected and a post hoc multiple-comparison procedure was conducted with the multcomp function (emmeans package) using the Bonferroni method. Mean comparisons are within genotype. Values are mean ± standard error ($n = 3$–$9$).
| Phenotype | Associated genes or proteins | Tomato species | Effect in salt tolerance | References |
|-----------|-----------------------------|----------------|-------------------------|------------|
| Nitrogen uptake and assimilation | AMT1.1, AMT1.2, GSI | S. pennellii | Smaller reduction in biomass | Abouelsaad et al. (2017) |
| Root hydraulic conductivity | TPX1, PPZ1 | | | Lucena et al. (2009); Han et al. (2018) |
| Primary root development | | | | Alaguer-Cordovilla et al. (2018) |
| Lateral root development | | | | Li et al. (2018) |
| Root apoplastic barriers | | | | | |
| Sodium extrusion to the apoplast | | | | | |
| Sodium assimilation | | | | | |
| Sodium xylem retrieval and phloem redistribution | | | | | |
| Sodium transport to the shoot | | | | | |
| Sodium interception and exclusion | | | | | |
| Sodium xylem retrieval and phloem redistribution | | | | | |
| Sodium/calcium ratio | HAK/ATPK, HKT1.2 | S. cheesmaniae | Higher photosynthetic rate and growth | Jaime-Pérez et al. (2017); Zhou et al. (2011) |
| Sodium/potassium ratio | HAK/ATPK, HKT1.2, S. pennellii | | Less Na\(^+\) transport to the shoot | Wang et al. (2010); Romero-Aranda et al. (2009); Gálvez et al. (2012); San Martín-Duque et al. (2017); Albaladejo et al. (2017) |
| Sodium compartmentation | NHX antiporters | S. chilense; S. pimpinellifolium; S. pennellii | Higher efficiency in osmotic adjustment | Gharbi et al. (2017) |
| Intracellular vesicular trafficking | RabGAP, SNARE | S. chilense; S. pimpinellifolium; S. pennellii | Increased endo- and exocytosis, vacuolar Na\(^+\) compartmentalization | Gálvez et al. (2012); Albaladejo et al. (2017) |
| Stomatal conductance | | | Better water status of the leaf | | |
| Stomatal density | | | | | |
| Carbon metabolism | Sucrose synthase, UTP-glucose-1-P | S. chilense | Higher photosynthetic rate and growth | Balibrea et al. (2003); Zhou et al. (2011) |
| Glycolysis | TPI, enolase, NAD-dependent glyceraldehyde-3-P | S. chilense | Reduced glucose level | | |
| Biosynthesis of BCAAs | Ketol-acid reductoisomerase | S. chilense | Energy regeneration, peptide elongation, glutamate recycling, fatty acid synthesis | Gharbi et al. (2017) |
| Organic osmolytes in osmotic adjustment | P5CS | S. lycopersicum | Higher proline accumulation in the leaves | Almeida et al. (2014) |
| Enzymatic antioxidant activity | SOD, CAT, APX, POX | S. pennellii | Higher efficiency in osmotic adjustment | Franey et al. (2010) |
| Non-enzymatic antioxidant activity | Water-soluble antioxidant activity; phenolic flavonoids | S. pennellii | | Franey et al. (2010) |
tomato growth is initially impaired by nutrient imbalance and osmotic effects, and later by the toxicity of high intracellular ion concentrations (especially Na+) (Cuartero and Fernandez-Munoz 1999). Moderately high concentrations of Na+ and Cl− (EC = 3-5 dS m−1) in the soil solution inhibit the uptake of ions such as NH4+, NO3−, K+ and Ca2+ (Munns 2002; Aktas et al. 2006). The inhibition of N uptake might occur by antagonism between NH4+/Na+ and NO3−/Cl− (Shawyer 2014), reduction in plant water uptake capacity, depolarization of cell membranes by high Na+ concentration (Suhayda et al. 1990) and down-regulation of genes responsible for NH4+ assimilation (Wang et al. 2012). A comparison between the domesticated tomato (cv. ‘Manitoba’) and its wild relative S. pennelli (accession LAO716) showed that salt stress inhibited the uptake and assimilation of nitrate in both species; however, S. pennelli presented a smaller reduction in biomass and higher survival rate than cv. ‘Manitoba’, which was attributed to the higher expression of key genes involved in ammonium uptake (AMT1.1 and AMT1.2) and assimilation (GS1) (Abouelsaad et al. 2016). The strong membrane depolarization induced by high Na+ concentration (60–80 mV for 100 mM NaCl) leads to increased efflux and reduced influx of K+ (Shabala and Cuin 2008). As K+ has important structural, signalling and metabolic functions in plant physiology, a high Na+/K+ ratio results in nutritional imbalance (Cramer 2002; Tuna et al. 2007). Potassium is involved in osmotic adjustment, enzyme activation, photosynthesis and respiration, and stomatal regulation (Mauch et al. 2020). As such, maintaining a low Na+/K+ cytosolic ratio in the shoot can result in higher salt tolerance in tomato. The addition of 2 mM K+ to high salt nutrient solutions (100 and 200 mM NaCl; −10 and 20 dS m−1) was shown to decrease Na+ accumulation in the shoot and diminish salt-induced growth inhibition in the domesticated tomato (Al-Karaki 2008). This is likely due to the competition between Na+ and K+ for translocation to the shoot (Shabala and Cuin 2008). Tomato wild relatives, such as S. pennelli, S. chilense, S. galapagense and S. cheesemaniae, have been studied in relation to ion selection and transport and their higher capacity to withstand high Na+/K+ ratios in the leaves (Bolarin et al. 1995; Gharbi et al. 2017; Jaime-Perez et al. 2017; Paillas et al. 2020). The maintenance of a low cytosolic Na+/Ca2+ ratio is also important under salt stress. For instance, the tomato SICLE10 (Calcineurin b-like protein 10, important for balance the Na+/Ca2+ ratio) knock-out mutants showed impaired plant growth and fruit production as well as increased blossom end rot incidence under salt stress (Egea et al. 2018).

Root water uptake

The root system, being the first organ to be exposed to salt stress, has a critical function in sustaining canopy water demands needed for carbon assimilation and plant growth, and plays a key role in crop salt tolerance in horticultural systems (Barrios-Masias et al. 2019). In cultivated tomato, the root apoplastic water flow is 12-fold larger than the cell-to-cell water flow under well-watered conditions (Hernandez-Espinoza and Barrios-Masias 2020). Under salt stress, however, transpiration is limited and the tension that drives water through the apoplastic pathway is reduced. The overall root hydraulic conductivity (Lp) decreases linearly with increasing soil salinity in tomato plants (Rodriguez et al. 1997). Lower Lp, in tomato was related to the overexpression of a basic peroxidase gene (TPX1), whose transcripts are primarily expressed in the epidermal and subepidermal cells of mature roots, and whose expression is also induced by >50 mM NaCl (−5 dS m−1) (Botella et al. 1994). Transgenic tomato overexpressing TPH1 had lower total xylem area, higher ligno-suberization of root exodermis and lower root Lp (Lucena et al. 2003). Aquaporins also play a key role in tomato Lp, and in tomato salt tolerance (Bramley et al., 2009; Gambetta et al., 2017; Jia et al. 2020). Aquaporin genes of the plasma membrane intrinsic protein (PIP) family have been identified in S. lycopersicum and their induction has been shown to improve leaf water status (Li et al. 2016). Under salt stress, the expression of PIP2;1 was significantly lower in the roots of S. pennelli (accession PE-47) compared to the tomato cv. ‘Moneymaker’ after 2 days of salt treatment, but significantly higher in the leaves, allowing for a better regulation of water use at the root level, and better leaf water status under salt stress (Albaladejo et al. 2017). A comparison between S. pimpinellifolium (accession L03708) and the tomato cv. ‘M82’ showed that the former had a higher capacity to maintain Lp under salt stress which was attributed, in part, to S. pimpinellifolium’s capacity to maintain PIP1 transcript abundance (150 mM NaCl, −15 dS m−1) (Han et al. 2021). Root Lp is a complex trait, and variability within the Lycopersicon clade has been found, which warrants further study to provide a more mechanistic understanding of salt tolerance in tomato.

Root system architecture

Soil salts concentrate on the soil surface as a result of soil water evaporation. Root system architecture (RSA) is another important trait that confers plasticity in soil exploration and the regulation of water and nutrient uptake, and can enhance plant salt tolerance (Jung and McCouch 2013). Root system architecture refers to the magnitude and pattern of root branching and growth, internode length, and root angles and diameter (Fitter 1991). Genetic and metabolic pathways involved in RSA modulation have been studied primarily in Arabidopsis and cereals (Jung and McCouch 2013; Rogers and Benfey 2015), but less so in vegetable crops. Many factors are involved in modulating RSA, such as hormones, their receptors and transcription factors that respond to environmental signals (reviewed in Jung and McCouch 2013). For instance, the gene DEEPER ROOTING 1 (DRO1) is associated with the regulation of root deepening and root angles in Oryza sativa (Uga et al. 2011, 2013), and DRO1 orthologs have been identified in Prunus species, Arabidopsis and wheat (Guseman et al. 2017). In domesticated tomato, exposure to salt stress induced a reduction in root length and weight, but led to an increase in the number of fine roots (Lovelli et al. 2012), suggesting that RSA is involved in tomato response to salt stress. Variability in RSA between tomato and its wild relatives during early growth stages has been demonstrated under non-saline conditions (Alaguero-Cordovilla et al. 2018). Two tomato cultivars (cv. ‘Ailsa Craig’, and cv. ‘Moneymaker’) and the wild relatives S. chilense (LA1932), S. huayalense (LA2663), S. galapagense (LA1044) showed higher primary root elongation rate, whereas the tomato cv. ‘Craigella’, the wild relatives S. pimpinellifolium (LA1587), S. corneliiomulleri (LA1274), S. peruvianum (LA1336), S. cheesemaniae (LA1037) and S. arcum (LA2157) exhibited intermediate primary root growth rate, and S. chnielewski (LA2663) had a lower root elongation rate. Interestingly, the domestically tomato cultivars showed a higher lateral root number and growth rate after root-tip excision compared to most of the wild accessions; except for S. pimpinellifolium and S. peruvianum, which had higher and similar lateral root numbers, respectively. The angle of lateral roots was significantly higher in S. arcum and tomato cv. ‘Moneymaker’. This phenotypic response may be related to genetic variability in the DRO1 pathway (Alaguero-Cordovilla et al. 2018). Root system architecture variability within the Lycopersicon clade should be further investigated in relation to salinity tolerance as soil salinity changes across the soil profile.
Passive exclusion of Na⁺ from the root stele

Root apoplastic barriers (e.g. Casparian strip and aliphatic suberin) are thought to be involved in salt homeostasis at the root level by favouring water uptake through the cell-to-cell pathway (Steudle 2000; Blum 2011; Knipfer and Fricke 2011; Barrios-Masias et al. 2015), resulting in higher ion selectivity. In Arabidopsis, several genes involved in Casparian strip development have been identified (Kamiya et al. 2015). Furthermore, knocking out the gene CYP86A1/HORST, which encodes a cytochrome P450-dependent fatty acid ω-hydroxylase, resulted in 60 % decrease in aliphatic suberin, increased salt sensitivity and Na⁺ accumulation in the shoots and the roots compared to the wild-type Arabidopsis under salt stress (15 and 30 mM NaCl after 3, 7 and 14 days) (Wang et al. 2020). Li et al. (2018) studied the regulatory pathways for tomato Casparian strips, and they concluded that there is a functional conservation in the regulatory mechanism of Casparian strips formation between A. thaliana and the cultivated tomato. However, tomato has a more complex root structure (e.g. presence of exodermis), and to understand the role of root apoplastic barriers, as they develop closer to the root tip in response to salinity, more research is required.

Active exclusion of Na⁺ from the shoot

At the root level, Na⁺ extrusion is regulated by a group of Na⁺/H⁺ antiporters encoded by the SOS gene family, which can both extrude Na⁺ to the soil and regulate the Na⁺ partition between different plant organs (Munns and Tester 2008; Olias et al. 2009). The signal transduction pathway of the SOS proteins is based on cytosolic Ca²⁺ concentrations. The increase of Ca²⁺ in the cytosol elicited by salinity is sensed by SOS3, which interacts with SOS2 and activates the plasma membrane Na⁺/H⁺ exchanger encoded by the SOS1 gene, operating to re-establish Na⁺ homeostasis in cells through extrusion of Na⁺ into the apoplast or xylem vessels (Ishitani et al. 2000; Olias et al. 2009). Sodium extrusion is an energetically demanding process. For each mole of Na⁺ effluxed from the cell, the hydrolysis of one mole of ATP is required to power the movement of an H⁺ into the cell by the plasma membrane H⁺-ATPase in order to maintain membrane potential (Malagoli et al. 2008; Munns et al. 2020). Sun et al. (2010) demonstrated that S. pimpinellifolium (accession P1365967) has a more active SOS pathway and lower accumulation of Na⁺ in the shoot relative to Na⁺ in the root, compared to S. lycopersicum cv. ‘Moneymaker’, suggesting that the SOS pathway plays a role in intercepting Na⁺ translocation to the shoot. However, in a study comparing 23 accessions of tomato wild relatives and commercial cultivars, the SOS1 expression in the roots did not correlate with Na⁺ accumulation in leaves, stems or roots (Almeida et al. 2014). In tomato, Na⁺ homeostasis and partitioning is also regulated by HKT1-like transporters (Asins et al. 2013). These xylem parenchyma, plasma membrane-localized transporters function to retrieve Na⁺ from xylem vessels to the xylem parenchyma cells thereby preventing xylem-mediated transport of Na⁺ to the leaves (Sunarpi et al. 2005). Two near-isogenic lines (NIL) homozygous for the S. chilense and S. lycopersicum var. cerasiforme alleles at both HKT1 loci (HKT1;1 or HKT1;2) were used to create transgenic lines silenced in either HKT1;1 or HKT1;2 genes, resulting in salt hypersensitivity (Jaime-Perez et al. 2017). However, the HKT1;2 gene was shown to be more effective in controlling shoot Na⁺/K⁺ homeostasis compared to HKT1;1 (Romero-Aranda et al. 2020). The silencing of the HKT1;2 allele from S. chilense compared to the allele from S. lycopersicum showed a decrease in shoot growth, suggesting a better effectiveness of the former in salt tolerance (Jaime-Perez et al. 2017). The HAK/KUP/KT (high-affinity K⁺/K⁺ uptake/ K⁺ transporter) family transporters are involved in both Na⁺ and K⁺ xylem loading in roots. Recently, a SiHAK20 gene variant, which arose during tomato domestication, was associated with a decrease in Na⁺ versus K⁺ affinity resulting in less root-to-shoot movement of Na⁺ (Wang et al. 2020). Once Na⁺ is retrieved from the xylem sap, it can be compartmentalized into root cell vacuoles, redistributed towards sink organs and tissues through the phloem or extruded to the apoplastic (Jaime-Perez et al. 2017); although the fate of the removed Na⁺ is not clear.

Sodium vacuolar compartmentalization

Sodium vacuolar sequestration happens through the NHX antiporter family, which are (Na⁺, +)H⁺ antiporters that are involved in Na⁺ compartmentalization inside the vacuole, increased K⁺ retention in the cells, and osmotic adjustment by Na⁺ or K⁺ (Rodríguez-Rosales et al. 2008). An evaluation of 23 wild and cultivated tomato accessions for salinity tolerance showed that higher expression of NHX1 and NHX3 genes in roots experiencing salt stress was positively correlated with Na⁺ accumulation in roots and negatively correlated with Na⁺ accumulation in the shoots (Almeida et al. 2014). Concordantly, when compared with S. lycopersicum, S. pennellii (accession PE-47) plants experiencing salt stress had higher NHX3 and NHX4 expression levels in leaves and lower NHX3 and NHX4 transcript accumulation in the roots, and Na⁺ accumulation was lower in roots and higher in leaves (Albaladejo et al. 2017). In a transcriptome analysis of S. chilense (accession LA1972), NHX1 gene was overexpressed in the shoot under severe salt stress (500 mM NaCl, EC 26.8 dS m⁻¹) (Kashyap et al. 2020). Four NHX isoforms were studied in S. pimpinellifolium and the tomato cv. ‘Volgogradskij’ under salt stress (130 mM NaCl; ~13 dS m⁻¹) (Gálvez et al. 2012). The former showed higher expression of the isoform NHX1 in the leaves and the shoot, especially after 1 day of treatment, while cv. ‘Volgogradskij’ increased NHX1 expression only in the leaves after 1 day of salt exposure. The isoforms NHX2 and NHX3 showed a similar pattern of expression and their expression increased more in S. pimpinellifolium (roots, leaves and stem) than in cv. ‘Volgogradskij’, especially after 7 days of salt exposure. The isoform NHX4 was overexpressed especially in stems and fruits in both species, indicating its specific role for reproductive tissue. Solanum pimpinellifolium had higher accumulation of Na⁺ and lower K⁺ in the shoot compared to the tomato cv. ‘Volgogradskij’, and was able to maintain growth after 7 days of salt exposure (Gálvez et al. 2012).

Intracellular vesicular trafficking

Under salt stress, lipids and proteins are mobilized between different organelles (Okazaki and Saito 2014), ion channels and transporters are removed from the plasma membranes (Yang and Guo 2018), reactive oxygen species (ROS) are detoxified (You and Chan 2015) and toxic ions are compartmentalized (Baral et al. 2015). For these functions, an efficient intracellular vesicular trafficking system is necessary, in both leaves and roots. An important family of enzymes involved in vesicular trafficking are the RabGTPases. They switch from the active state (bound to GTP) to inactive state (bound to GDP) (Rehman and Di Sansebastiano 2014). When they are active, they are recognized by effector proteins and facilitate membrane fusion (Vukasínovic and Žáský, 2016). The introgression of the salt-induced gene SchRabGD1, encoding for a protein regulator of the RabGTPase cycle, from S. chilense to A. thaliana conferred salt tolerance, and increased endocytosis and vacuolar Na⁺ accumulation compared to the wild-type A. thaliana.
The differential expression of the RabGAP genes (encoding for GTPase-activating proteins) in roots and shoots of *S. lycopersicum*, *S. pimpinellifolium* and *S. pennelli* under salt stress suggest a possible role for this gene in determinating tomato salt tolerance (Madrid-Espinoza et al. 2019). Although the role of each RabGAP protein under salt stress is not clear, comparisons with the homologues from *A. thaliana* and *O. sativa* revealed that RabGAP21 could be localized in the Trans-Golgi network and the pre-vacuolar compartments, suggesting that it could have an important role in mobilizing transporters and proteins associated with the vacuole (Madrid-Espinoza et al. 2019). Soluble N-ethylmaleimide-sensitive factor attachment protein receptors (SNARE) are involved in membrane fusion and vesicular trafficking in plants. The expression of a number of SNARE genes in roots and leaves in response to salt stress has been analysed by qRT-PCR in *S. lycopersicum*, *S. pimpinellifolium* and *S. chilense*. This analysis revealed that SNARE proteins SchSYP51.2, SchVAMP727 and SchGOS12.2 transcript abundance increased more than 40 times after 12 h of salt exposure in the roots of the salt-tolerant *S. chilense* in contrast to *S. lycopersicum* and *S. pimpinellifolium*, which had only 1- to 8-fold increase (Salinas-Cornejo et al. 2019), suggesting that *S. chilense* may have a more active root vesicular trafficking system.

**Gas exchange regulation**

Due to impaired water uptake capacity, transpiration under salt stress is inhibited, resulting in a lower C assimilation capacity. The maintenance of stomatal conductance during salt stress has been related to salt tolerance (Sanchez-Blanco et al. 1991). A study on 15 tomato cultivars showed that decreases in leaf gas exchange resulted in reduced shoot growth in all cultivars (Amjad et al. 2014). A comparison between the tomato cv. 'M82' and *S. pennelli* (accession PE-47) showed that the latter had higher leaf temperature increase, indicating lower transpiration, together with higher water content of the leaf after 7 and 14 days of salt exposure (100 mM NaCl, ~10 dS m⁻¹) (Albaladejo et al. 2017). Solanum pennelli (accession PE-2) showed a significant decrease in abaxial and adaxial stomatal density under salt stress (Albaladejo et al. 2017), which can lead to lower transpiration rates in tomato (Farber et al. 2016). The trade-off between water saving and carbon assimilation (i.e. water use efficiency) may be counterproductive for biomass accumulation and yield (Khavari-Nejad and Mostofi, 1998), and should be further investigated in tomato and its wild relatives under salt stress. In addition to reductions in stomatal conductance, changes in metabolic processes involved in carbon fixation have been investigated under salt stress within the *Lycopersicon* clade. A proteomics analysis of the wild tomato relative *S. chilense* (accessions LA2747 and LA1958) showed a lower abundance of several Calvin cycle (i.e. sedoheptulose-1,7-bisphosphatase) and photorespiration enzymes (i.e. phosphoglycolate phosphatase, hydroxyypyruvate reductase and glycolate oxidase) in the leaves of salt-treated plants (Zhou et al. 2011). The authors argued that reductions in the abundance of these enzymes could lead to a decrease in both carbon fixation and photorespiration to compensate for the low photosynthetic rate of *S. chilense* under salt stress, resulting in a higher energy use efficiency. Carbon metabolism and partitioning are impaired under saline conditions. A comparison between a salt-tolerant tomato ecotype (cv. 'Pera') and a salt-sensitive tomato (cv. 'Volgogradskij') showed that a higher accumulation of photoassimilates (fructose, glucose and sucrose) in the leaves was correlated with lower photosynthetic activity and growth in the salt-sensitive cultivar (Ballibrea et al. 2000). Under salt stress, higher sink strength and cytoplasmatic sucrolytic activity resulted in higher sucrose metabolism and phloem unloading (i.e. assimilate transport to sink organs) in *S. cheesmaniae* (accession LA530) and *S. chmielewskii* (accession LA1028) compared to the domesticated tomato cv. ‘H-324-1’ (Ballibrea et al. 2003).

**Osmotic adjustment**

Leaf osmotic adjustment is necessary for the maintenance of cell and organ turgor in plants experiencing salt stress. The relative contribution of inorganic ions versus compatible osmolytes to the overall osmotic adjustment will determine the energy costs involved in this tolerance mechanism. Under non-limiting conditions (e.g. no photorespiration), 3 ATP and 2 NADPH are utilized for each molecule of CO₂ assimilated (Wingler et al. 2000). Under salt stress, the energetic requirements for CO₂ assimilation increase to 5.375 ATP and 3.5 NADPH per molecule of CO₂ fixed (Munns et al. 2020). Thus, the use of compatible osmolytes (e.g. organic solutes) to maintain high osmotic potential of the cytosol has considerable carbon and energy costs for the plant. Instead, the accumulation of inorganic ions is less energy demanding (Munns et al. 2020). Sodium contribution to osmotic adjustment in *S. chilense* (accession LA4107) was found to be more than 60 %, while in *S. lycopersicum* cv. ‘Ailsa Craig’ was only 26 % (Gharbi et al. 2017). The concentration of proline in the cv. ‘Ailsa Craig’ was 2.5-fold higher in the leaves than that of the wild relative, but concentrations in the roots were similar (Gharbi et al. 2017). The concentration of proline in the leaves has been negatively correlated with Na⁺ accumulation (Almeida et al. 2014).

**Antioxidant activity**

Increases in salt concentration in plant tissue lead to an increase in the production of ROS (reviewed in Abogadallah 2010), mainly in organelles, plasma membrane and apoplastic (You and Chan 2015). Reactive oxygen species have important functions in sensory and signalling networks during both normal plant developmental and stress responses (Noctor et al. 2014). At high concentrations, ROS become toxic and lead to oxidative stress which can interfere with the proper functioning of organelles such as chloroplasts and mitochondria, and induce damage to nucleic acids, proteins and enzymes, decrease membrane integrity, alter redox homeostasis thereby inducing photoinhibition and induce the activation of programmed cell death (Scandalios 1993). To minimize damage from ROS, plants have developed enzymatic and non-enzymatic antioxidant systems. An effective antioxidant system has been found to be responsible for enhanced salt tolerance in some wild tomato species. For example, increased activities of superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX), as well as increased levels of the reduced form of ascorbate and glutathione, were correlated with decreased lipid peroxidation in the salt-tolerant *S. pennelli* (accession Atico) when compared to tomato cv. ‘M82’ under salt stress (Shalata et al. 2001; Mittova et al. 2004). A separate study of 50 introgression lines (ILs) and their parental lines, *S. pennelli* (accession LA716) and tomato cv. ‘M82’, did not reveal a clear positive relationship between the induction of antioxidant enzymes under salt stress (150 mM NaCl, about 15 dS m⁻¹) and plant growth (Frary et al. 2010). Most ILs had lower plant height, leaf number and leaf dry weight, but increased stem diameter and root growth under salt stress, which was a characteristic response of the salt-tolerant parent (i.e. *S. pennelli*; Frary et al. 2010).

**Conclusion**

Improving salt tolerance in tomato can lead to substantial, positive economic and ecological impacts on horticultural
production. The salt tolerance mechanism of the domesticated tomato (glycophytic-like response) is efficient under mild salt stress, but fails at higher salinity levels or during longer exposures to salt stress (Albaladejo et al. 2017; Meza et al. 2020). Tomato wild relatives, which often exhibit halophytic-like behaviours, show higher growth rates at high salt concentrations (Bolarin et al. 1991; Albaladejo et al. 2017; Pailles et al. 2020); however, they show low capacity for biomass accumulation and yield (Foolad 1996; Tal 1997). Under commercial production, where C assimilation and biomass accumulation is key for high yields, salt tolerance should aim to maintain favourable plant water status by a sustained capacity for uptake of water and nutrients. One approach to sustain C assimilation could be through the improvement of root functional traits per unit root area. For instance, the increase in Ip, and the Na⁺ exclusion mechanisms can allow the influx of low-osmotic-potential water to the roots and maintain a better leaf water status (Ashraf and Shahbaz 2003; Moshelen et al., 2017; Ashraf et al., 2018). Although breeding for salt tolerance in tomato has proven challenging, this review demonstrates that tomato wild relatives possess potentially beneficial mechanisms for coping with salinity, and the identification of leaf and root traits and future integration with breeding efforts and agronomic techniques (e.g. use of rootstocks) could help overcome the transfer of undesirable traits to elite cultivars.

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Contribution by the Authors
MS.B and FBM conceived and wrote the manuscript. D.K.K edited and contributed in sections addressing molecular biology and biochemistry. All authors read and approved the final manuscript.

Conflict of Interest
None declared.

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Data Availability
All data and coding used in this study are available at the following link: https://osf.io/3hcmrz/?view_only=9dabdc47126a4761b8df67e64e5952a9.

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