



# The role of tissue succulence in plant salt tolerance: an overview

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## Abstract

Soil salinity seriously restricts agricultural production. Halophytes adapt to saline environments through several strategies, including leaf or stem succulence. Succulence is associated with the increase in cell size or leaf thickness and high water content per unit of surface area, allowing salts to be diluted within the succulent leaves or stems. The proposed mechanisms of NaCl-induced plant tissue succulence include acidification and subsequent induction of cell wall elasticity, increased water uptake, cell turgor pressure, Na<sup>+</sup> partitioning in vacuoles, abundance of plasma membrane aquaporins, cell wall formation and extensibility, as well as up-regulation of certain genes (e.g., *XTH* and *CEBI*) that control cell expansion and cell wall modification. However, the information on the mechanism of succulence activated by salinity is limited. In this paper, the possible mechanism of salinity-induced succulence, and the role of succulence in plant salt tolerance, are discussed. Understanding the mechanisms that activate succulence in halophytes opens up new opportunities for plant breeding to increase salt tolerance and improve crop productivity in saline soils.

**Keywords** Cell expansion · Salt dilution · Halophyte · Salinity · Tissue tolerance

## Introduction

Soil salinization is a serious problem worldwide due to its adverse effects on agricultural production (Rozema and Flowers 2008; Munns et al. 2020). It has been estimated that only about 1% of the land plant species can survive and

reproduce in saline areas (Rozema and Flowers 2008). The physiological and molecular mechanisms of salinity tolerance in halophytes have been extensively studied (Shabala et al. 2014; Flowers and Colmer 2015; Munns et al. 2020), but it is worth noting that relatively little basic research into salt tolerance has been applied to crop plants (Munns and Gilliam 2015).

Succulent halophytes are plants that can dilute salt by storing large amounts of water within their leaves or stems, which is an important mechanism for their salt tolerance. This trait allows halophytes to achieve high water-use efficiencies and accumulate large amounts of salts, enabling them to extract water from substrates with extremely negative water potentials (Khan et al. 2000; Katschnig et al. 2013; Song and Wang 2015). Halophytes exhibit morpho-physiological adaptations that could be valuable in creating more resilient cash crops under extreme conditions such as high salinity (Rasheed et al. 2022). A particularly notable adaptation is their ability to store water in their living tissues, known as succulence. This enables them to mitigate the effects of drought or salinity stress and allows them to survive in semi-arid and arid regions (Lim et al. 2020).

Several species from the Amaranthaceae family demonstrate increased leaf or stem succulence as a strategy to overcome challenges such as heat and light-induced oxidative

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stress, enabling their survival in drought or saline environments (Griffiths, 2013). The morphological and physiological characteristics of succulence in halophytes have been known and studied for several decades. Halophytes have evolved in a unique environment, leading to a distinct type of succulence integrated into an eco-physiological syndrome that is different from other succulent groups. However, the molecular mechanisms regarding this process and its possible role in breeding salt-tolerant crops have not been well elucidated. Tissue succulence engineering can improve plant salt tolerance, as demonstrated by the overexpression of *Populus euphratica* *PeXTH* (a putative xyloglucan endotransglucosylase/hydrolase gene), which leads to leaf succulence development in transgenic tobacco plants (Han et al. 2013). Recently, Lim et al. (2020) reported that plant tissue succulence engineering improves salt tolerance in *Arabidopsis*. In this paper, the mechanisms of salinity-induced succulence in plants and the potential value of succulence as a target for breeding salt-tolerant plants are discussed.

## The importance of understanding salt tolerance in plants

Excessive concentrations of  $\text{Na}^+$  in cultivated land worldwide seriously affect crop yield and quality (Zhang et al. 2019). Therefore, understanding ion sensing and transport in plants under salinity is beneficial for breeding salt-tolerant crops (Wu 2018).

In root epidermal cells, the primary pathways for  $\text{Na}^+$  uptake involve the glutamate receptor-like (GLRs) channels, cyclic nucleotide-gated (CNGCs) non-selective cation channels, and HKT2 high-affinity  $\text{K}^+$  transporters (Zhao et al. 2020). The salt overly sensitive (SOS) signaling is a key mechanism responsible for excluding  $\text{Na}^+$  from the cytoplasm in root epidermal cells (Halfter et al. 2000; Shi et al. 2000; Wu 2018). This mechanism is considered a milestone in understanding how plants maintain  $\text{Na}^+$  homeostasis (Zhao et al. 2020). Vacuolar compartmentalization of  $\text{Na}^+$  is another important mechanism for maintaining  $\text{Na}^+$  homeostasis in plant salt tolerance. The  $\text{Na}^+/\text{H}^+$  antiporter NHX1 in the tonoplast plays a central role in this process, with its activity controlled by the electrochemical  $\text{H}^+$ -gradient across the tonoplast generated by  $\text{V-H}^+$ -ATPase or  $\text{V-H}^+$ -PPase (Song and Wang 2015; Zhao et al. 2020).  $\text{Na}^+$  compartmentalization in the vacuole prevents the cytoplasm from reaching toxic concentrations, reduces the water potential, and aids water absorption from saline soil (Flowers and Colmer 2015; Cui et al. 2021). Efficient control of tonoplast slow- (SV) and fast- (FV) activating ion channels is crucial for vacuolar  $\text{Na}^+$  sequestration, as these channels could allow  $\text{Na}^+$  to leak back into the cytoplasm (Zhao et al.

2020). The  $\text{Na}^+$  transporter HKT1 plays a role in retrieving  $\text{Na}^+$  from the xylem and may facilitate  $\text{Na}^+$  recirculation from shoots to roots (Zhu 2016), suggesting that the functions of SOS1 and HKT1 transporters may be interrelated in balancing  $\text{Na}^+$  efflux and xylem loading/unloading (Ismail and Horie 2017; Kotula et al. 2020).

Although certain specific key proteins play crucial roles in maintaining  $\text{Na}^+$  homeostasis in plants under salt stress, the application of these fundamental research findings to crop plants has been limited (Munns and Gilliham 2015). Morphological adaptation to salt is important for salt resistance of halophytes. Root apoplastic barriers, such as Casparian bands (CBs) and suberin lamellae (SL), contribute to ion exclusion in some halophytes and crop plants (Cui et al. 2021). It has been estimated that salt avoidance involving ion exclusion by the roots is fundamental since roots exclude up to 95% of salt in soil solution (Munns and Gilliham 2015; Cui et al. 2021). An apoplastic exodermal barrier can decrease energy costs by 18% and 10% in the roots with two- and one-cortical-cell layer, respectively, indicating that energy savings may increase with more cortical layers (Munns et al. 2020). Overall, preventing apoplastic ion leakage from roots to shoots is a key mechanism of salt tolerance (Cui et al. 2021).

Various halophytes have evolved specialized structures to cope with elevated salinity levels. For example, *Chenopodium quinoa* features epidermal bladder cells that accumulate excessive  $\text{Na}^+$  in their vacuoles (Chen et al. 2018; Zhao et al. 2020). Similarly, *Limonium bicolor* possesses salt glands capable of secreting salts from plant tissues to the external environment (Yuan et al. 2016 a, b), which enable such recretohalophytes to adapt to high salinity (Chen et al. 2018; Zhao et al. 2020). Halophytes exhibit organ plasticity in response to salt stress, including leaf or stem specialization and root system adjustment. Leaf or stem succulence is another important morphological characteristic in certain highly salt tolerant halophytes and reflects the ability of plants adaptation to salt stress. Succulence, combined with cuticles and waxes on leaf surfaces, reduces the transpiration area and stomatal number to conserve water (Ma et al. 2019). Succulence is an essential evolutionary strategy for halophytes in saline environments, characterized by larger cells, reduced surface area per tissue volume, reduced stomata, high water content for a given surface area, smaller leaves, and thicker leaf cuticle (Jennings 1968; Gale 1975; Song and Wang 2015). Succulence is a key adaptation trait for dicotyledonous halophytes to regulate their internal ion concentrations. In other words, salt can be diluted within the succulent leaves or stems (Short and Colmer 1999). A study conducted on two succulent halophytes, *Suaeda salsa* and *Salicornia europaea*, concluded that the growth and tissue succulence of these plants were mostly influenced

by variation in cell size (Ma et al. 2019). Plant tissue succulence engineering has been found to improve salt tolerance in tobacco and *Arabidopsis* (Han et al. 2013; Lim et al. 2020), indicating that tissue succulence could be a promising target for breeding salt-tolerant plants. Recent advances in understanding the mechanisms underlying salt stress tolerance in halophytes show promise for the development of salt-tolerant crops (Zhao et al. 2020).

## The role of succulence in plant salt tolerance

Succulence is a typical morphological characteristic in certain highly salt-tolerant halophytes, especially in Amaranthaceae (e.g., Salicornioideae, Chenopodioideae and Suaedoideae) (Flowers et al. 1977; Khan et al. 2001; Rozema and Schat 2013). This adaptation is linked to an enlargement of cell size, a reduction in surface area per tissue volume, elevated water content per unit surface area, and increased leaf thickness (Black 1958; Aslam et al. 1986; Khan et al. 2005; Lim et al. 2020). It was regarded that succulence may be a component trait of the salt tolerance syndrome of certain halophytes (Rozema and Schat 2013). Jennings (1968) hypothesized that Na<sup>+</sup>-induced succulence might be a homeostatic cell mechanism that helps prevent ion toxicity. Salt-induced succulence can also optimize photosynthesis by reducing CO<sub>2</sub> uptake resistance and enabling more gaseous exchange per leaf-unit area (Longstreth and Nobel 1979). *Suaeda monoica* showed both a greater increase in succulence and tolerance to high salinity than *Atriplex spongiosa*, suggesting that the degree of succulence may be related to their salt tolerance (Storey and Jones 1979). In *Salicornia dolichostachya*, its highest succulence (water content per unit leaf area) coincided with its growth optimum at 300 mM NaCl, suggesting that succulence may contribute to its stimulated growth (Katschnig et al. 2013).

In *Carpobrotus rosii*, a succulent halophyte, storage parenchyma cells act as a Na<sup>+</sup> sink, facilitating efficient Na<sup>+</sup> sequestration in leaf tissues. Meanwhile, it was revealed that *Carpobrotus* plants are capable of downregulating the activity of fast vacuolar cation channels (the channel is permeable for monovalent cations only) under salinity. Patch-clamp experiments have shown that this ability is more pronounced in storage parenchyma cells compared to mesophyll cells, providing a foundation for understanding the underlying mechanisms contributing to Na<sup>+</sup> sequestration in the succulent leaf tissues (Zeng et al. 2018). Similarly, in the potential cash crop *Chenopodium quinoa* (Quinoa), which has leaves that display a certain degree of succulence, the negative control of fast- and slow-activating tonoplast channels reduces Na<sup>+</sup> leakage from vacuoles in old leaves. This enables the efficient sequestration of Na<sup>+</sup> to

their vacuoles, allowing for an optimal photosynthetic performance even under saline conditions (Bonales-Alatorre et al. 2013). In the salt tolerant tree species *P. euphratica*, the development of leaf succulence due to an increase in cell number and cell volume leads to Na<sup>+</sup> dilution (Ottow et al. 2005). Even in the salt sensitive crop *Solanum lycopersicum* (tomato), succulence has been regarded to be an important trait for salt tolerance and its introduction through breeding with close relatives such as *S. pennellii*, *S. cheesmanii*, or *S. pimpinellifolium* has been suggested to increase its salt tolerance (Cuartero 1992). Moreover, most modern crops are relatively sensitive to salinity; however, attempts to improve crop salt tolerance have met with limited success (Munns and Gilliham 2015). *Mesembryanthemum crystallinum*, a succulent halophyte, belongs to the C<sub>3</sub> photosynthetic pathway but has the ability to switch to crassulacean acid metabolism (CAM) under saline conditions. *M. crystallinum* plants can store water within leaf tissues and use water-filled epidermal bladder cells, representing modified trichomes, to accumulate Na<sup>+</sup> and other osmotically active substances (Adams et al. 1998; Loconsole et al. 2019). Leaf beet (*Beta vulgaris* var. *cicla*) is an important vegetable resource with a degree of salt tolerance, adapts to salt stress through the development of leaf succulence. The leaf succulence of the species reaches its maximum value at the 0.7% NaCl. Thus, leaf water content and the normal progression of photosynthesis are maintained to a certain extent (He et al. 2022). Some reported NaCl-induced succulence in certain plant species and the possible mechanisms during the process of succulence were summarized in Table 1.

## How does NaCl induce succulence?

Succulent plants typically exhibit two types of anatomic arrangements, namely *Allzellsukkulenz* (or “all-cell succulent”) and *Speichersukkulenz* (or storage succulence). The first one implies a general increase in the size of all photosynthetically active cells. The second type is more common in perennial plants, where photosynthetic cells (chlorenchyma) and water-storage tissue (hydrenchyma) are distinct (Males 2017; Rawat et al. 2022). Succulence enables plants to enlarge their vacuoles, thus enhancing the capacity for vacuolar Na<sup>+</sup> sequestration in halophytes (Shabala 2013). Na<sup>+</sup> can induce an increase in succulence, and it has been proposed that Na<sup>+</sup> may contribute to an increase in ATP synthesis (Jennings 1968). The plasma membrane proton pump (PM H<sup>+</sup>-ATPase) and tonoplast H<sup>+</sup>-ATPase (V-ATPase) are the main drivers for transporters that rely on protons. They are essential for maintaining Na<sup>+</sup> homeostasis during plant salt tolerance (Song and Wang 2015). An electrochemical H<sup>+</sup>-gradient generated by the PM H<sup>+</sup>-ATPase energizes the

**Table 1** Some reported succulent plants and possible mechanism of NaCl-induced succulence

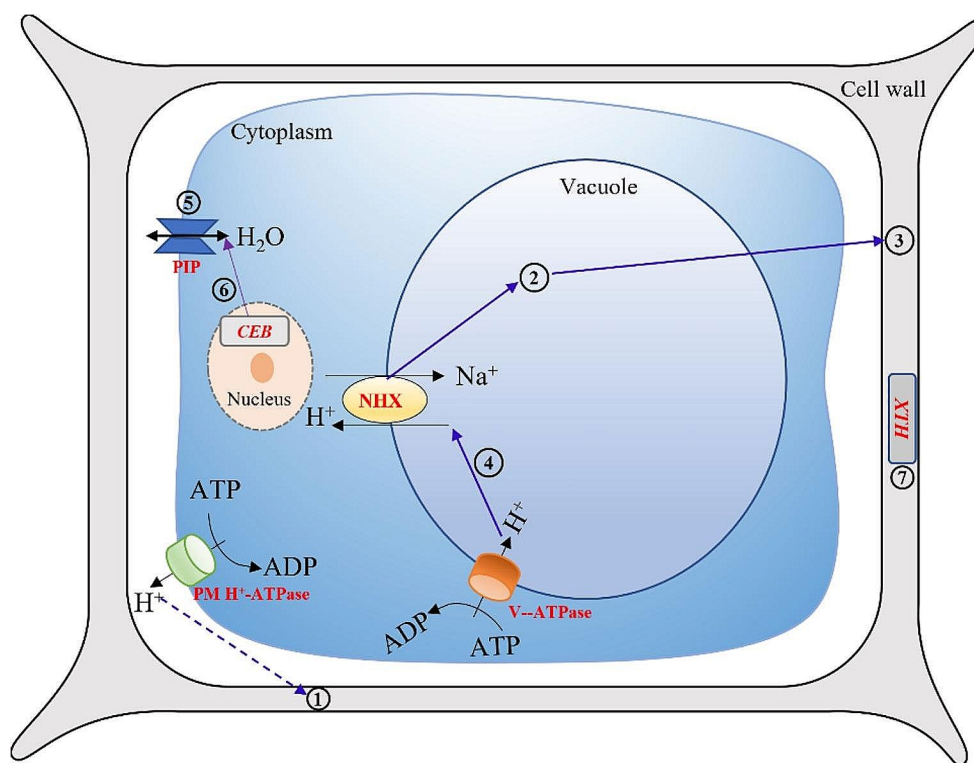
Species	The role of salinity in improving succulence	Reference
<i>Sesuvium portulacastrum</i>	High concentration of Na <sup>+</sup> stimulated demonstrated bigger stem and thicker leaves, as well as significantly expanded epidermal cells	(Wang et al. 2012)
<i>Salicornia europaea</i>	Increased stem succulence due to the increased cell size rather than cell number	(Ma et al. 2019)
<i>Suaeda maritima</i>	Succulent leaves composed of enlarged cells; vacuoles occupy most of the cell volume	(Harvey et al. 1981)
<i>Suaeda salsa</i>	Increased stem succulence due to increased cell size rather than cell number	(Ma et al. 2019)
<i>Populus euphratica</i>	Significant increase in leaf thickness due to the more than 3-fold increase in cell layers in salt-treated leaves	(Ottow et al. 2005)
<i>Cakile maritima</i>	Leaf Na <sup>+</sup> content positively correlated with leaf succulence ratio; enhanced leaf succulence and thickness in salt-treated plants partially explained by high PM H <sup>+</sup> -ATPase activity levels	(Debez et al. 2006)
<i>Laguncularia racemosa</i>	Changes in leaf succulence induced by salinity may result from enlargement of the hypodermis and palisade parenchyma in cell size and layer number	(Sobrado 2005)
<i>Phaseolus vulgaris</i> ; <i>Gossypium hirsutum</i> ; <i>Atriplex patula</i>	Mesophyll thickness increased with salinity due to increased length of palisade cells and increased number of spongy cell layers	(Longstreth and Nobel 1979)
<i>Atriplex hastata</i>	Succulence is due to the increase of leaf thickness	(Black 1958)
<i>Atriplex amnicola</i>	Leaf Na <sup>+</sup> content is positively correlated with leaf succulence, development of succulence at high NaCl associated with increased turgor pressure which may be due to irreversible cell wall growth, or high cell wall elasticity	(Aslam et al. 1986)
<i>Atriplex portulacoides</i>	Salt stress decreased leaf cell elasticity, increasing water reserve of apoplast compartment could be due to thicker cell walls	(Benzarti et al. 2014)
<i>Zygophyllum xanthoxylum</i>	NaCl treatment had a significant impact on promoting leaf succulence, with both palisade and spongy cells enlarged dramatically	(Xi et al. 2018)
<i>Aster tripolium</i>	Increase in leaf thickness due to thicker cell walls, not increased water content	(Shennan et al. 1987)
<i>Mesembryanthemum crystallinum</i>	C <sub>3</sub> species able to switch to CAM metabolism, storage water within leaf tissues, use water-filled epidermal bladder cells to accumulate Na <sup>+</sup> and other osmotically active substances	(Adams et al. 1998; Loconsole et al. 2019)
<i>Carpobrotus rossi</i>	Storage parenchyma cells act as a Na <sup>+</sup> sink, downregulating activity of fast vacuolar cation channels	(Zeng et al. 2018)

Na<sup>+</sup>/H<sup>+</sup> antiporter (SOS1) for Na<sup>+</sup> efflux across the plasma membrane (Shi et al. 2000). Meanwhile, H<sup>+</sup> generated by PM H<sup>+</sup>-ATPase may acidify and subsequently induce the elasticity of cell wall. An electrochemical H<sup>+</sup>-gradient generated by the V-ATPase energizes the tonoplast Na<sup>+</sup>/H<sup>+</sup> antiporter (NHX) for the compartmentalization of Na<sup>+</sup> in the vacuole (Bassil et al. 2012; Bassil and Blumwald 2014). In certain succulent halophytes, e.g., *S. salsa*, an increase in PM H<sup>+</sup>-ATPase activity and abundance was observed under salinity (Chen et al. 2010). Similarly, an up-regulation of the V-ATPase was also observed under salinity (Qiu et al. 2007). Furthermore, NaCl activated the PM H<sup>+</sup>-ATPase in *Atriplex lentiformis* and *C. quinoa* (Bose et al. 2015), and has been observed to activate the V-ATPase in *Mesembryanthemum crystallinum* (Barkla et al. 1995). This suggests that the increased H<sup>+</sup>-ATPase under salinity may be important for salt-induced succulence and salt tolerance in these halophytes.

In two tomato cultivars and three wild relatives, the degree of succulence in different plant parts exhibited a positive correlation with the distribution of Na<sup>+</sup> (Tal and Shannon 1983). In *Atriplex amnicola*, a higher Na<sup>+</sup> concentration in older leaf tissue coincided with a greater degree of leaf succulence in older leaves (Aslam et al. 1986). These results support earlier suggestions that the development of succulence in plants exposed to high external NaCl concentrations is associated with an increase in turgor pressure, probably due to ion accumulation (Jennings 1976). This is supported by a study of the succulent halophyte *Sarcocornia natalensis* which suggested that its high salt tolerance primarily results from substantial inorganic ion accumulation, providing sufficient solutes for osmoregulation, increased water flux, and turgor-induced growth (Naidoo and Rughunanan 1990). Aslam et al. (1986) further suggested that such turgor effects could be attributed either to irreversible cell wall growth or to high elasticity of cell walls. Moreover, when

*S. salsa* plants were treated with 100 mM of different salts, leaf succulence was induced by NaCl, and to some extent NaHCO<sub>3</sub>, but no obvious succulence appeared in leaves of seedlings treated with CaCl<sub>2</sub> or KCl. This suggests that Na<sup>+</sup> plays a key role in leaf succulence of *S. salsa*, indicating that the process of succulence may be Na<sup>+</sup>-specific rather than the osmotic effect of different salts (Qi et al. 2005). Similarly, in the succulent halophyte *Sesuvium portulacastrum*, the diameters of parenchyma and epidermal cells markedly increased after treatment with sodium-based ions. For example, when seedlings were treated with 200 mM NaCl, NaNO<sub>3</sub>, and Na-H, the diameter of epidermal cells was much higher than those in both the control and potassium-based treatments; a similar trend was observed with stem diameter (Wang et al. 2012). Interestingly, sodium-based ions increased shoot water content, while chloride or potassium-based ions significantly reduced it, indicating that Na<sup>+</sup> was more effective than K<sup>+</sup> and Cl<sup>-</sup> in promoting cell expansion, leaf succulence and shoot development in *S. portulacastrum* (Wang et al. 2012). These findings suggest that Na<sup>+</sup> is an important factor for succulence in plants.

Plasma membrane aquaporins (AQPs) facilitate water movement across biomembranes and play a crucial role in controlling trans-cellular water transport. In *S. salsa*, NaCl increases the abundance of transcripts for a plasma-membrane AQP homologous to *AtPIP2;7*. Meanwhile, immunoblot analyses of PIP AQPs in plasma membrane-enriched fractions of *S. salsa* leaves reveal a significant increase under salinity (Qi et al. 2009). This indicates that the increase of AQP activity under salinity may due to both the increased transcript and protein levels, which correlates with the observed increase in leaf succulence of *S. salsa* under salinity (Qi et al. 2009). The mechanisms of NaCl-induced succulence are postulated in Fig. 1. In brief, during this process, NaCl-induced H<sup>+</sup> generated by PM H<sup>+</sup>-ATPase may acidify and subsequently induce the elasticity of cell wall. The up-regulation of V-ATPase by NaCl can generate more H<sup>+</sup> which energizes NHX for Na<sup>+</sup> compartmentalization in vacuoles. Additionally, NaCl can increase the abundance of the transcripts and protein amounts for PIP, which may correlate with the increase in succulence.



**Fig. 1** The postulated mechanisms that may be involved in the process of NaCl-induced plant tissue succulence. During this process, the role of NaCl may be Na<sup>+</sup>-specific. (1) H<sup>+</sup> generated by plasma membrane (PM) H<sup>+</sup>-ATPase may acidize and subsequently induce the elasticity of cell wall; (2) increased Na<sup>+</sup> generated by tonoplast Na<sup>+</sup>/H<sup>+</sup> antiporter (NHX) can decrease osmotic potential and increased water uptake; (3) cell turgor pressure may increase due to water uptake; (4) the up-regulation of tonoplast H<sup>+</sup>-ATPase (V-ATPase) by NaCl can generate more H<sup>+</sup> which energizes NHX for Na<sup>+</sup> compartmentaliza-

tion in vacuolar; (5) NaCl increased the abundance of the transcripts and protein amount for plasma-membrane aquaporins (PIP), which may correlate with the increase of succulence (high water content); (6) NaCl increase the expression of *CEB1*, which controls cell expansion and affects the expression of genes encoding cell wall modification proteins and enzymes, and aquaporins, (7) NaCl upregulates the expression of *XTH*, possibly increased cell wall formation and cell wall extensibility, leading to increased leaf succulence;. The red font indicates the up-regulation or increment

## The evolutionary developmental and genetic control of succulence

Succulent plants were initially described by Johann Bauhin as ‘thick-leaved and juicy herbs’ (Rowley 1997). Eggli and Nyffeler subsequently described succulence as a plant’s capacity to store ‘utilizable’ water, allowing it to sustain physiological activity during short periods of limited water supply (Eggli and Nyffeler 2009). Succulence exists in any vegetative organ, including leaves and stems, roots, bulbs or tubers of geophytes, orchid pseudobulbs, and the parenchymatous rays of pachycaul trees (Eggli and Nyffeler 2009; Nyffeler and Eggli 2010).

Succulence begins at the cellular level with the development of a central vacuole for storing water and other substances, which was an important event in land plant evolution (Becker 2007; Grace 2019). For example, in some plants, the vacuoles may occupy 90% or more of the cell volume (Gibson 1982; Von Willert et al. 1992).

The primary role of succulence is storing water in living cells for later use, facilitating water homeostasis (Griffiths and Males 2017). In some succulence plants, apoplastic mucilage or pectic compounds may also contribute significantly to water storage, as seen in cacti and Asteraceae (Nobel et al. 1992). Succulent plants have a low surface area to volume ratio (SA:V), which maximizes water storage while minimizing transpirational water loss (Griffiths and Males 2017). Adaptations such as thick cuticles, low stomatal density, high stomatal sensitivity to environmental stimuli, low hydraulic conductances and anatomically-reduced vasculature are in line with their conservative water-use strategies (Heyduk 2021).

The genetic regulation of succulent leaf development primarily involves the control of cell size, determination of vascular patterning, and intercellular water transport (Heyduk 2021). Cell size is an essential determinant of succulence and is mainly controlled by cell cycle and cell division timing (Kalve et al. 2014; Griffiths and Males 2017; Conklin et al. 2019). Target of rapamycin (TOR), a master cell cycle regulator in plants (Ahmad et al. 2019), and ribosomal S6 kinases (S6Ks) promote cell expansion through an auxin-TOR signaling cascades (Meyuhas 2008). Retinoblastoma related (RBR) and E2F transcription factors (E2FA and E2FB) form S6Ks-RBR-E2FA/EF2B complexes that regulate entry into the endocycle and rates of cell proliferation via the TOR signaling cascade (Sozzani et al. 2006; Borghi et al. 2010; Henriques et al. 2010; Magyar et al. 2012), indicating that this pathway may contribute to leaf succulence development. Auxin-related genes, such as auxin related gene involved in organ size (ARGOS), aintegumenta (ANT), and organ size related 1 (OSR1), can increase cell sizes and are important in controlling cell proliferation (Hu

et al. 2003, 2006; Feng et al. 2011). In succulent leaves, vascular patterning and intercellular water movement principles ensure hydraulic connectivity (Heyduk 2021). The initiation of 3D leaf venation patterns in thicker leaves may result from auxin’s ability to move through multiple planes.

Auxin biosynthesis and transport play an essential role in vascular patterning (Kleine-Vehn et al. 2009). Pin-formed1 (PIN1) can direct auxin to be formed in procambial cells, aiding in the formation of vascular tissue (Wenzel et al. 2010). Vasculature complexity and connectivity (VCC) control the development of veins in cotyledons (Yanagisawa et al. 2021). VCC and pinoid (PID) regulate PIN1 polarity, which is required for controlling vasculature development (Yanagisawa et al. 2021). All of these factors may affect the formation of tissue succulence and could be potential targets for breeding salt-tolerant plants (Table 2). However, further research is needed to determine whether these factors are involved in the process of tissue succulence and how salinity affects their function.

## Succulence engineering can improve plant salt tolerance

Despite the few advances in the understanding of genetic and ontogenetic mechanisms associated with succulence, little is known about the molecular regulation of salt-induced succulence. Research on succulence has primarily focused on its genetic regulation in leaves through the modulation of cell size, vascular patterning, and water transport between cells, pathways related to succulence as described by Heyduk (2021). Cell wall loosening and rearrangement rely on wall-modifying enzymes, such as expansin, xyloglucan endotransglucosylase, and  $\beta$ -1, 4-glucanase (Cosgrove 2005). Among them, xyloglucan endotransglucosylase/hydrolases (XTHs) play a key role in cell wall extensibility. In *B. vulgaris* ssp. *maritima*, salt treatments influenced the gene expression such as *XTH*, expansin, or glucan endo-1,3-beta-D-glucosidase, potentially leading to increased cell wall formation and extensibility, and therefore, greater leaf succulence (Skorupa et al. 2016). Tobacco plants overexpressing *P. euphratica* *PeXTH* exhibited higher water content per unit area (36%) and a higher ratio of fresh weight to dry weight (39%), characteristics of leaf succulence, compared to wild-type tobacco (Han et al. 2013). The anatomical changes in *PeXTH*-transgenic plants promoted the leaf water-retaining capacity, lowering salt concentration in the succulent tissues and mesophyll cells, due to densely packed palisade parenchyma cells and reduced intercellular air spaces (Han et al. 2013). Moreover, the decrease in intercellular air space also resulting in a 47–78% increase in net photosynthesis (Han et al. 2013). These results indicate

**Table 2** Genes and their putative functions related to succulence under salinity

Gene name	Species	Roles in succulence development	Reference
<i>PeXTH</i>	<i>Populus euphratica</i>	Increased leaf succulence in tobacco via overexpression accompanied by highly packed palisade parenchyma cells rather than greater leaf thickness	(Han et al. 2013)
<i>VvCEB1</i>	<i>Vitis vinifera</i>	Increased degree of succulence due to enlarged cell size and leaf thickness	(Lim et al. 2018, 2020)
<i>SsPIP</i>	<i>Suaeda salsa</i>	Increase AQP activity resulted in higher transcript and protein levels, correlating with increased leaf succulence under salinity	(Qi et al. 2009)
<i>TOR; S6Ks</i>	<i>Arabidopsis</i>	TOR as a master regulator of the cell cycle in plants, ribosomal S6Ks promote cell expansion via an auxin-TOR signalling cascade, forming S6Ks-RBR-E2FA/EF2B complexes that regulate endocycle entry and cell proliferation rates via the TOR signalling cascade	(Sozzani et al. 2006; Borghi et al. 2010; Henriques et al. 2010; Magyar et al. 2012)
<i>ARGOS; ANT; OSRI</i>	<i>Arabidopsis</i>	ARGOS, ANT and OSRI can increase cell sizes, which are important to control cell proliferation	(Hu et al. 2003, 2006; Feng et al. 2011)
<i>PIN1; VCC; PID</i>	<i>Arabidopsis</i>	PIN1 can lead auxin to be formed in procambial cells, which help the formation of vascular tissue, VCC controls the development of veins in cotyledons, VCC and PID regulate PIN1 polarity, which are required to control the vasculature development	(Wenzel et al. 2010; Yanagisawa et al. 2021)

that *PeXTH* overexpression enhanced salt tolerance in tobacco plants by promoting leaf succulence development, i.e., the increased succulence has a positive effect on salt dilution and net photosynthesis in *PeXTH*-transgenic plants (Table 2).

A basic helix-loop-helix (bHLH) transcription factor from *Vitis vinifera* has been shown to promote cell expansion in developing fruit (Nicolas et al. 2013). When the *V. vinifera* cell expansion bHLH (*VvCEB1*) gene was overexpressed in *Arabidopsis*, it resulted in larger cells, leaves, and increased biomass accumulation (Lim et al. 2018). Lim et al. (2020) further reported that tissue succulence

was engineered in *Arabidopsis* by overexpressing a codon-optimized helix-loop-helix transcription factor (*VvCEB1<sub>opt</sub>*) from wine grape, which is responsible for the cell expansion phase of berry development (Lim et al. 2020).

Cell size and the degree of succulence increased, and intercellular air space decreased in *VvCEB1<sub>opt</sub>*-overexpressing *Arabidopsis* lines compared to the wild type (WT), while water-use efficiency (WUE) increased due to reduced stomatal conductance and density, which may contribute to the attenuation of water-deficit stress (Lim et al. 2020). Furthermore, the overexpressed lines demonstrated greater salinity tolerance, attributed to decreased salinity uptake and dilution of internal Na<sup>+</sup> and Cl<sup>-</sup>, compared to WT *Arabidopsis* plants (Lim et al. 2020). This means the overexpressed *Arabidopsis* lines can better adapt to both osmotic stress and ion toxicity due to high salinity, compared to WT *Arabidopsis*. These findings provide valuable information for understanding the role of succulence in plant salt tolerance.

Efficient sequestration of cytotoxic Na<sup>+</sup> in vacuoles is regarded as a critical feature of halophytes, as Na<sup>+</sup> accumulation in vacuoles can help regulate the osmotic balance and alleviate Na<sup>+</sup> toxicity in the cytoplasm (Song and Wang 2015). Halophytic succulence is due to ion accumulation in enlarged vacuoles, sequestering toxic ions away from the cytoplasm (Lim et al. 2020). The larger cells observed in the *VvCEB1<sub>opt</sub>* overexpression lines were considered to offer increased vacuolar storage capacity for sequestering toxic ions under salinity stress (Lim et al. 2020). The higher degree of succulence in transgenic plants provides a high capacity for the dilution of salt compared to WT plants (Han et al. 2013; Lim et al. 2020). Meanwhile, high WUE enable transgenic plants to attenuate osmotic stress resulting from salinity (Lim et al. 2020). Some reported genes and their putative function related to succulence were summarized in Table 2. These studies provide theoretical and practical examples of the viability of engineering increased succulence in plants and support succulence as an important trait in the breeding of salt-tolerant plants.

## Conclusions

Soil salinization has become a serious problem worldwide, limiting the development of agroforestry. Breeding salt-tolerant crops is a promising avenue for sustainable agricultural development in saline lands. Although leaf or stem succulence may help mitigate salt stress, and it has been largely overlooked in agricultural research and crop improvement efforts. This is probably because it is considered a halophytic trait predominantly found in natural environments and is rarely used in agricultural production.

A more detailed understanding of how NaCl-induced succulence works is needed, including the identification of the key genes involved and their mechanisms. Molecular approaches could then be used to engineer crops to produce limited layers of succulent cells, potentially enhancing their ability to tolerate salt. Modern biotechnology offers various tools and techniques for gene screening and function studies. For example, whole genome sequencing, proteomics, transcriptomics, metabolomics, molecular markers, gene-tagging methodologies and bioinformatic analysis have been instrumental in identifying important genes and their functions. Whole genome sequences for crops such as *Chenopodium quinoa* and *Beta vulgaris* are already available (Jarvis et al. 2017; Dohm et al. 2014). However, the genetic transformation techniques for succulent halophytes such as *Suaeda* and *Salicornia* are not well established, hampering gene functional analyses. To overcome this limitation, future research should focus on developing transformation techniques and employing tools such as CRISPR/Cas9, CRISPR/Cpf1, prime and base editing, dCas9 epigenetic changes, and other transgene-free genome editing approaches. These tools can be used to screen for genes involved in succulence beyond the already reported *XTH* and *CEBI* genes. Undertaking such efforts is essential for understanding the roles of these genes in succulence and for breeding salt-tolerant crops.

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## Declarations

**Conflict of interest** Authors declare that they have no conflict of interest.

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