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Review

An appraisal of horticultural plant morpho-physiological and molecular responses to variable salt stress agents

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Abstract: In the coming years, the scientific community, extension specialists and horticulturists will have to deal with growing agronomic and horticultural crops under sub-optimal conditions dictated by a global change scenarios. Salinity which is a water or soil quality concern is one of the most serious threats limiting the productivity of vegetables which are highly susceptible to soil and/or water salinity. In vegetable crops, soil and/or water salinity have been reported to disturb biochemical, morpho-physiological, and molecular processes leading to stunted growth and yield reduction. This article gives an overview of the recent literature on salinity response of vegetable crops (in which sodium chloride, NaCl, is the predominant salt) as well as the physiological and molecular mechanisms of salt tolerance. The physiological mechanisms behind the response of vegetable crops to Na^+ and Cl^- and the functions that directly and/or indirectly affect the produce quality in terms of nutritional and functional quality will be elucidated. In addition, the effects of different salinity sources coming from other ions such as Mg^{2+}, SO_4^{2-}, HCO_3^- and Ca^{2+} are also discussed. Finally, the review paper identifies trendy research areas relevant to salinity as a eustressor for boosting quality of vegetables without compromising yield.

Keywords: Vegetables; eustress; phytochemicals; salinity sources; sustainable horticulture; yield gap.

1. Rationale: population growth, water demand and salinity

Nowadays agriculture plays a strategic role in ensuring food security to meet the increasingly growing population demand and at the same time addressing a host of environmental challenges (Kopittke et al., 2019). In fact, the world population has reached 7.93 billion in March 2022 according to the most recent United Nations estimates elaborated by Worldometer (https://www.worldometers.info/). In addition, AsiaNews, a news agency promoted by the Pontifical Institute for Foreign Missions (PIME), reported in 2017 that more than a billion people around the world have no identities. This means that since they are not registered by their national governments, they are invisible. Many of these "invisible people" live in Africa and Asia, and more than one third are children without any rights (AsiaNews, 2017). According to these data, the world population has probably already crossed the 9 billion mark, and the demand for food has already far exceeded the current production. In these conditions sustainable development looks like an oxymoron; it would be necessary to boost the output of food in the next few years without expanding agricultural land and using less water, fertilizers, pesticides and herbicides per cultivated hectare thus reducing the emissions from production processes and environmental pollution.

The global land area amounts to 13.2 billion ha of which 4.8 billion ha are agricultural (The World Bank, 2019), while 0.9 billion ha are covered with saline (0.34×10^9 ha) or sodic (0.56×10^9 ha) soils. In addition, 25-30% of the 275 million ha of irrigated areas, are affected by a rising groundwater table or secondary salinization (FAO, 2020; Shahid et al., 2018). However, according to a study of Thenkabail et al. (2009) a global irrigated area map (GIAM) created using multiple satellite sensors, Google Earth and ground truth data estimated that the annualised irrigated areas (AIAs) at the end of last century accounted for 467 Mha, increasing also the percentage of salinized irrigated areas. In fact, soil salinization is dramatically exacerbated and accelerated by crop irrigation and fertilization. Irrigation water, whether from canals or underground pumping and including those considered of very good quality, contain some dissolved salts. In addition, salts may originate also from inorganic fertilizers and soil amendments (e.g., gypsum, composts and manures) (Kotuby-Amacher et al., 2000). Therefore, salinized agricultural soils are increasing annually worldwide (Gupta and Huang, 2014), especially in arid and semi-arid regions where precipitation is low, and temperatures and rates of evaporation are high. Estimates reported that 0.25-0.5 Mha of agricultural land is lost annually (Qadir et al., 2014). In these areas the scarcity of water forces the use of alternative water supplies especially for irrigation, in particular irrigation water from agricultural runoff, brackish and reused water from municipal and industrial effluents, which contain high salt concentrations if not treated by mean of expensive desalination processes like reverse osmosis (Bixio et al., 2006; Cirillo et al., 2019; Zalacáin et al., 2019). These salts may originate from several sources such as fertilization, chemical treatments, soaps, detergents, but also chemicals used during the water treatment process (water chlorination) (Elgallal et al., 2016; Qadir et al., 2010). Other problems in addition to the high salinity levels of the water may result in detrimental effects to wastewater irrigated plants, such as excess of nitrates, metals and pathogens (Qadir et al., 2010). However, salinity seems to be the most damaging effect depending on the salt sensitivity of the species and/or cultivars (Colla et al., 2012; Liu et al., 2017), the phenological stage of the plants (Dell'Aversana et al., 2021), or crop management (Colla et al., 2010). Indeed, salinity impairs plant growth, development and yield by exerting pleiotropic effects, among which water stress (Acosta-Motos et al., 2014; Munns and Tester 2008), nutrient deficiency or imbalance (Grattana and Grieveb, 1999; Hu and Schmidhalter 2005; Isayenkov and Maathuis 2019), ion toxicity (Flowers et al., 2015; Ferchichi et al., 2018; Hasegawa et al., 2000), and oxidative damage (AbdElgawad et al., 2016; Annunziata et al., 2017; Gorham et al., 2010). An electrical conductivity (EC) of 4 dS m^{-1} (corresponding to about 40 mM NaCl) represents the threshold limit beyond which most of the glycophytes, among which horticultural crops, start showing a reduced capacity to uptake water from soil (Chinnusamy et al., 2005). This latter determines disorders in stomatal aperture, transpiration and whole plant water relations, affecting tissue expansion, division and growth, thus also reducing the emergence of new leaves and lateral buds and causing wilting (Hasegawa et al., 2000; Läuchli and Grattan 2007; Negrão et al., 2017; Shabala and Munns 2012). If salinity stress persists longer, the salt ions accumulated in the plant cells result in ionic stress, which affects protein synthesis, enzyme activities and photosynthesis (Ferchichi et al., 2018, Hasegawa et al., 2000; Munns and Tester 2008). In particular, the high concentrations of toxic ions in chloroplasts and mitochondria, impair the photosynthetic and mitochondrial electron transport chains, causing photo-oxidation and reactive oxygen species (ROS) formation, as shown in faba bean (Tavakkoli et al., 2010). In addition, photorespiration increases when stomata are totally or even partially closed, decreasing the demand for ATP and NAPH and further affecting the photosynthetic electron transport chain thus causing an additional load of ROS (Voss et al., 2013). In these conditions the first symptoms of necrosis appear at leaf margins and tips (Ayers and Westcot 1985; Geilfus, 2018). If salt stress persists, necrotic lesions spread toward the middle of mature expanded leaves, arresting photosynthesis and export of photosynthates thus causing also the death and loss of younger leaves (Goodrich et al., 2009). However, leaf necrosis is not only evident in tissues that accumulate toxic ions in the cytosol and organelles, but the same agents disturb also leaves that fail to uptake ions from the apoplast to the symplast compartment as found in pea (Speer and Kaiser 1991).

2. Plant responses to salinity

Plants adopt a ubiquitous protective mechanism for increasing salt stress tissue tolerance and defending themselves from stress. This consists in toxic ion compartmentalization in the vacuole, and synthesis of small compatible molecules (e.g., sugars, amino acids, betaines; <500 Da) that are directly or indirectly involved in osmotic balance, ROS scavenging, and stabilization and protection of membranes and macromolecules. The synthesis and accumulation of compatible compounds avoid, at least under short term salinity, the problems related to ion toxicity and oxidative stress (Annunziata et al., 2019; Mansour, 2000; Rhodes et al., 2002; Yancey, 2005). However, if the exclusion of these toxic ions in the vacuole (in particular Na^+) is not osmotically balanced also by beneficial ions (e.g. K^+) in the cytosol, the need to synthesize high levels of compatible compounds (50–70 moles ATP for mole) (Cuin et al., 2009; Raven, 1985) may divert energy and resources away from growth during continuous long term salinity, thus jeopardizing plant survival (Carillo et al., 2011; Ferchichi et al., 2018; Munns and Tester, 2008a). Therefore, most horticultural crops show low tolerance to salt stress when salinity is applied continuously (Machado and Serralheiro, 2017).

In order to cope with salinity-dependent oxidative stress, plants specifically activate enzymatic and/or non-enzymatic antioxidant defense and repair systems to support growth performance under salinity with high energetic costs (Abogadallah, 2010). Salinity was found to upregulate antioxidant enzymes, such as superoxide dismutase and plastid terminal oxidases, while downregulating NADPH oxidase in order to produce less ROS in sugar beet (Hossain et al., 2017). In salt-sensitive pea, long-term acclimation to salinity was successful only when plants were able to increase and fine-tune their antioxidant defense (Hernández et al., 2000).

However, the sensitivity of plants to salts does not depend only on their toxicity and concentration but also on plant growth stage, with seed germination and seedling establishment being the most sensitive phases to salinity. During germination and emergence, tolerance is measured as percent survival, while during later developmental stages it is measured as relative growth (Läuchli and Grattan, 2007) For example, salinity was able to impair cauliflower survival mainly when it was imposed in the first growth stage due to an ion-specific toxicity effect; however, even at inflorescence stage it also restricted water accumulation in the head, thus reducing plant growth and yield (Giuffrida et al., 2017).

3. Sodium and chloride may act as nutrients or promote eustress

Indeed, stress relies on a dose-dependent response, as also stated by Paracelsus in the sentence ‘dose makes the poison’ (Rouphael et al., 2019b). Several plant species, including horticultural crops like tomato, potato and carrot, show beneficial effects from the treatments with salts at low concentrations (Kronzucker et al., 2013; Geilfus, 2018). In fact, 1 mM Na^+ concentration was found beneficial for tomatoes (Woolley, 1957). The application of sodium to soil at $Na^+ : K^+$ ratio of 1 : 8 to 1 : 32 increased fruit yield by about 100% in tomato plants (Kemi Idowu and Adote Aduayi 2007). Adhikari et al. (2019) showed that ~ 5mM NaCl did not affect growth and biomass and did not elicit a defence response in lettuce. *Beta vulgaris* L. (beet) showed enhanced shoot and root fresh and dry weight when treated with NaCl at 1-32 mM (El-Sheikh et al., 1967); area and dry weight (Nunes et al., 1984) and water content and total fresh weight (Lawlor and Milford, 1973) increased in the same species when treated with 2-10 mM NaCl and 16 mM NaCl, respectively. However, the higher salinity tolerance of beet could depend on its descendance from coastal halophytic ancestors (Rozema et al., 2014). A salinity of 10 mM NaCl was able to decrease the content of the antinutrient nitrate in green and red-pigmented perilla (Rouphael et al., 2019a). NaCl at 5 mM increased lutein and β-carotene contents in romaine lettuce without decreasing visual quality or yield (Kim et al., 2008). NaCl at 20 mM enhanced phenolics and radical scavenging capacity (DPPH) in red baby lettuce (Neocleous et al., 2014), phenolics in both green and red-pigmented perilla (Rouphael et al., 2019b), K, Ca, and Mg, ascorbate and lipophilic antioxidants in red lettuce, (but not in green lettuce), slightly affecting fresh yield (Carillo et al., 2020). The increase of lipophilic antioxidants (carotenoids, chlorophylls, and tocopherols) under salinity may serve to protect the structural organization of the lettuce photosynthetic apparatus, but it does positively affect its nutritional quality and shelf life, too (Carillo et al., 2021). NaCl at 30 mM increased phenolic compounds in leaves of artichoke and cardoon (Borgognone et al., 2014), while a NaCl salinity of 6 dS m^{-1} enhanced the content of ascorbate and α-tocopherol in *Cichorium spinosum* (Petropoulos et al.,

2017) thus increasing nutritional quality and post-harvest performance of these products without affecting plant productivity. Even a NaCl- salinity equal to 50 mM was found to increase phenolic concentration and antioxidant activity of red lettuce without affecting the photosynthetic activity and biomass production (Santander et al., 2022). Similarly, Scuderi et al. (2011) found that electrical conductivities of 3.8 and 4.8 mS cm^{-1} in the nutrient solution were able to reduce respiration and browning thus enhancing the post-harvest performance of fresh-cut lettuce. Indeed, Cl^-, as an essential micronutrient, and may have beneficial roles, too. At concentrations lower than 4 mg g^{-1}, it can participate in turgor and pH regulation, and may work as counter anion for stabilizing membrane potential, regulating enzymatic activities and acting as co-factor in the water-splitting complex of photosystem II (Geilfus, 2018; White and Broadley, 2001). Moreover, Cl^- seems to play a role in the repair processes of salt stress-induced DNA damage (Chakraborty et al., 2022). Hence, chloride at low concentrations may exert beneficial effects on horticultural product quality and post-harvest behaviour with a minimal impact on growth and fresh yield. For these reasons, under low Cl^- levels, this ion is actively up taken by a secondary active symport operating a $Cl^-/2H^+$ exchange (Felle, 1994). In contrast, Na^+ influx and/or transport does not happen by mean of its own channels. It enters the root cytosol via the non-selective cation channels (NSCC), the high-affinity potassium transporters (HKTs and HAKs) or aquaporins (Wu, 2018). Whereas SOS1 (SOS Ras/Rac Guanine Nucleotide Exchange Factor 1), a cation-chloride co-transporter (CCC) that is preferentially expressed at the xylem/symplast boundary, has been suggested to play an active role in Na^+ loading into the xylem transpiration stream, enhancing its transport and that of water to the shoot (Foster and Miklavcic, 2019).

4. Sodium and chloride toxicity

Most salinity studies have used NaCl as the main source of salt (Table 1), and stress symptoms have been related, in particular, to sodium toxicity alone (Annunziata et al., 2017; Läuchli et al., 2008; Kong et al., 2011; Rouphael et al., 2017; Tester and Devenport, 2003; Woodrow et al., 2017).

Undoubtedly, NaCl concentrations higher than 30-40 mM can limit plant growth and development by affecting water and ion uptake, thus causing oxidative stress, with a consequent negative impact on photosynthesis, growth/yield and quality in lettuce (Shin et al., 2020). In addition, high concentrations of Na^+ within plant cells can use and also inhibit transporters involved in potassium uptake, such as K^+ influx channels encoded by genes of the *AKT/KAT* subfamily or the *KUP/HAK/KT* family, thus altering K^+ homeostasis (Kronzucker et al., 2013 and references therein). Sodium can also substitute K^+ in key enzymatic reactions, inhibiting enzyme activities and perturbing metabolic processes essential for proper plant cell functioning (Carillo et al., 2008), as also seen in tomato (Rouphael et al., 2018). Moreover, sodium can reduce calcium uptake, decreasing stomatal conductance, CO_2 carboxylation and photosynthetic electron transport, thus causing photo-oxidative stress (Grattan and Grieve, 1999). This decrease in Ca^{2+} uptake seems to depend on a reduced transpiration rate rather than to a competition with Na^+ in tomato plants (Adams and Ho, 1989).

Sodium can also have a negative effect on soil by promoting its physical degradation. At high concentration, in fact, it can replace exchangeable cations, like Ca^{2+} and Mg^{2+}, that mediate the linking of clay particles to humic acids in organic matter, destroying micro-aggregates, damaging soil structure and porosity, and causing soil compactness (Machado and Serralheiro, 2017). The Na^+ dependent deflocculation of soil particles results in the sealing of soil pores, restricting soil water passage (Batakanwa et al., 2015). Sodium together with CO_3^{2-} from HCO_3^- determines soil alkalinization (Machado and Serralheiro, 2017). Moreover, this latter effect, indirectly, reduces also the availability of beneficial mono and bivalent cations for crops, resulting in nutrient deficiencies or imbalances (Machado and Serralheiro, 2017).

However, recent studies have also shown the toxic effects of chloride (Geilfus, 2018; Wang et al., 2020; Wu and Li, 2019), which, in a range of concentration of 4-7 mg g^{-1}, is able to cause more drastic

Table 1. Morphological, physiological and molecular responses of different horticultural species under salinity concentration and sources.

Horticultural species	Salinity treatment	Morpho-physiological, biochemical and molecular responses under salt stress conditions	Reference
Allium cepa L. cv. Rode van Florence, Van der Wal, Hoogeveen	NaCl (100 and 200 mM), Na_2SO_4 (50 and 100 mM) in hydroponics	Cl^- and SO_4^{2-} at equimolar concentrations caused similar reduction of sulphates and growth but had only a slight effect on the plant sulphur metabolism.	Aghajanzadeh et al., 2019
Beta vulgaris subsp. Vulgaris cv. KWS2320	NaCl 300 mM in hydroponics	Increase of Cu-Zn-SOD, Mn-SOD, Fe-SOD3, all AOX isoforms, 2-Cys-PrxB, PrxQ, and PrxIIF. Decrease of Fe-SOD1, 1-Cys-Prx, PrxIIB and PrxIIE, and RBOH transcripts.	Hossain et al., 2017
Brassica juncea L. var. Goldi	Na_2SO_4 (EC 8 and 12 dS m^{-1})	Decrease of sulphate reduction and metabolism, stomatal closure and lower yield parameters.	Khan et al., 2020
Brassica oleracea var. *botrytis* cv. Conero	EC salt solution (4 dS m^{-1})	Stronger effects on the first phase of growth due to ion-specific effects. Salinity applied during inflorescence restricted water accumulation in the head, reducing plant growth and yield.	Giuffrida et al., 2017
Brassica oleracea L. var. Italica	200 mM NaCl	Expression of plant thaumatin-like proteins (TLPs) which regulate ABA, ethylene and auxin-mediated signalling pathways.	He et al., 2021
Brassica rapa cv. Komatsuna	NaCl and KCl 50 and 100 mM, Na_2SO_4 and K_2SO_4 25 and 50 mM	Sulphate salts, in particular Na_2SO_4, reduced growth more than other salts. Ionic compositions of salts regulate gene expression of enzymes involved in glucosinolate biosynthesis, concentration and pattern.	Aghajanzadeh et al., 2018
Brassica rapa cv. Komatsuna	NaCl 100 mM, KCl 100 mM, Na_2SO4 50 mM and K_2SO_4 50 mM	Na_2SO_4 reduced Ca, Mn and P, and the efficiency of PSII, affecting growth more than NaCl; even K_2SO_4 also affected growth more than NaCl. Under sulphate salt stress plants down-regulated root genes for primary sulphate uptake and up-regulated the vacuolar sulphate transporter Sultr4;1.	Reich et al., 2017; 2018
Capsicum annuum L.	NaCl and Na_2SO_4 (EC 2, 3, 4, 6 and 8 dS m^{-1})	High EC strongly decreased fruit yield, size, and quality and thus marketable fruits. Sulphate treatments were less deleterious than chloride treatments at moderate EC.	Navarro et al., 2002
Cucumis sativus L.	$CaCl_2$ 12 mM vs. NaCl 24 mM	Vegetative growth and fruit yield damaged more by NaCl than $CaCl_2$.	Trajkova et al., 2006
Cucumis sativus L. cv. Akito, ungrafted or grafted onto the commercial rootstock *‘PS1313’ (Cucurbita maxima Duch. × Cucurbita moschata Duch.*	27 mM Na_2SO_4, or 40 mM NaCl	NaCl more than Na_2SO_4 decreased yield, shoot and root biomass photosynthesis, pigment synthesis, and membrane integrity. Grafted cucumber under Na_2SO_4 maintained higher assimilation rates, chlorophyll content, better membrane selectivity and nutritional status (higher K, Ca and Mg and lower Na) probably due to the inability of the NaCl treated rootstock to restrict Cl^- uptake and transport to shoot.	Colla et al., 2012

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Cucumis sativus L. cv. Chunqiu353	$Ca(NO_3)_2$ 70 mM	Reduced root length, root surface area, number of root tips, but increased root diameter in seedlings. Increase of ROS and MDA, and decrease of SOD, POD and CAT activity, with damage to mitochondrial membrane structures. Increase of cellular content of NO_3^-, NH4+ and NO, while nitrate reductase (NR), nitrite reductase (NIR), and nitric oxide synthase (NOS) decreased.	Yang et al., 2020
Cucumis sativus L. cv. Ekron	$CaCl_2$ 20 mM vs. NaCl 30 mM	Toxic effects of Cl^- causing higher susceptibility of cucumber marketable yield to $CaCl_2$ compared to NaCl salinity.	Colla et al., 2013
Cynara cardunculus L. subsp. *scolymus* (L.) Hegi *and Cynara* *cardunculus* L. var. altilis DC	NaCl and KCl 30 mM or $CaCl_2$ 20 mM (EC 5.1 dS m^{-1})	NaCl and KCl but not $CaCl_2$ reduced biomass production. KCl treatment enhanced total phenolic and flavonoid contents more rapidly than NaCl. Irrespective of salinity, leaves of cardoon had higher polyphenols, flavonoids and antioxidant activity than those of artichoke.	Borgognone et al., 2014
Lactuca sativa L.	60 mM NaCl	Reduction of N, K and Mg, efficiency of PSII, dry matter and yield, while Na and Na:K ratio increased	Breś et al., 2022
Lactuca sativa L.	NaCl > 30-40 mM	Oxidative stress and consequent negative impact on photosynthesis, growth/yield and quality in lettuce	Shin et al., 2020
Lycopersicon *esculentum* Mill.	$NaCl:Na_2SO_4$ (9:1) 40, 80, 120 and 160 mM; $NaHCO_3:Na_2CO_3$ (9:1) 29, 40, 60 and 80 mM	Alkali decreased stomatal conductance, photosynthesis, and growth more than salt stress. High-pH affected the control of Na^+ increasing its root uptake and transport to shoot, while decreased that of Cl^-, $H_2PO_4^-$ and SO_4^{2-}. Because of a shortage of inorganic ions, ion balance was exerted by organic acids under alkali stress.	Wang et al., 2011
Lycopersicon *esculentum* var. VF 145	NaCl supplied to growth media (EC 5-10 dS m^{-1})	Decreased water and N uptake also at high N values, and impaired growth. Cl^- probably suppressed also P uptake and transport to shoots.	Papadopoulos and Rendig, 1983
Ocimum basilicum L. cv. Fine	Na_2SO_4 25 mM and NaCl 50 mM	Na_2SO_4 was stronger than NaCl salinity on ion leakage, peroxidation and growth. Different (enzymatic and non-enzymatic) antioxidant mechanisms were involved in H_2O_2 detoxification.	Tarchoune et al., 2012
Pisum sativum L.	Cl^--dominated ($Cl^-:SO_4^{2-}$= 7:3) and SO_4^{2-}-dominated (Cl^-: SO_4^{2-}=3:7) saline sandy soil atcomparable EC 4, 6, and 8 dS m^{-1}	PO_4^{3-} decreased with the increase in Cl^- content of soil possibly due to a restriction in the translocation of SO_4^{2-} by Cl^- at the root-shoot interphase. High levels of Cl^- also decreased K, Mg, and Na.	Mor and Manchanda, 1992
Pisum sativum L. cv. Challis (NaCl-sensitive) and Granada (NaCl-tolerant)	NaCl 70 mM in hydroponics	Transcript levels for mitochondrial Mn-SOD, chloroplastic CuZn-SOD and phospholipid hydroperoxide glutathione peroxidase (PHGPX), cytosolic GR and APX strongly induced in the NaCl-tolerant variety but not in the NaCl-sensitive one.	Hernández et al., 2000

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Pisum sativum (salt sensitive) vs. *Spinacia oleracea* (salt tolerant)	100 mM NaCl for pea, 300 mM NaCl for spinach	Pea sensitivity depends on its inability to control salt accumulation in the shoot, maintain steep ion gradients across the leaf cell plasmalemma, and synthesize compatible solutes.	Speer and Kaiser, 1991
Solanum(S. chacoense, S. bulbocastanum, S. gourlayi, S. papita, S. microdontum and S.sparsipilum)	NaCl 40, 80 and 120 mM, Na_2SO_4 20 and 40 mM in hydroponics	Wild potatoes were more sensitive to high levels of Na_2SO_4 than to iso-osmotic concentrations of NaCl. However, the degree of sensitivity varied among different accessions.	Bilski et al., 2008
Solanum esculentum L., cv. L402	NaCl 75 mM	Root NRT1.1, NRT1.2 and GS1.2 decreased thus reducing nitrate uptake and assimilation.	Yao et al., 2011
Solanum lycopersicum L.	NaCl supplied to growth media (EC 6-12 dS m^{-1})	Decrease in Ca^{2+} uptake depending on a reduced transpiration rate	Adams and Ho, 1989
Solanum lycopersicum L. cv. M82, accession LA3475	200 mM NaCl in hydroponics	Decrease of N, K and Ca, efficiency of PSII and photochemical quenching, shoot and root FW and DW, root length and area.	Van Oosten et al., 2017
Solanum lycopersicum L. cv. Seny	75 mM NaCl supplied to growth media (EC 9.2 dS m^{-1})	Sodium decreased uptake of K^+ and Ca^{2+} and substituted K+ in key enzymatic reactions perturbing plant metabolic processes	Rouphael et al., 2018
Vicia faba L. varieties Nura and line 1487/7	Cl^- salts (15 mM $CaCl_2$, 15 mM $MgCl_2$, and 40 mM KCl), mixture of Na^+ salts (15 mM Na_2SO_4, 15 mM Na_2HPO4, and 40 mM $NaNO_3$), NaCl salt (100 mM NaCl)	Both high Na^+ and high Cl^- reduced growth and photosynthesis, but plants were more sensitive to Cl^-. With the increase of soil NaCl level, Cl^- concentration increased more than Na^+. Cl^- at high concentration caused chlorophyll degradation and affected photosynthetic capacity and quantum yield.	Tavakkoli et al., 2010

conditions of ion imbalance than Na^+ in many sensitive plants, like horticultural species or herbaceous perennial plants (Cirillo et al., 2019; Colla et al., 2013; Geilfus, 2018). Indeed, higher concentrations (15–50 mg g^{-1}) of chloride can exert toxic effects also on Cl^--tolerant species (Tavakkoli et al., 2010). This happens because under excess levels of Cl^-, this ion can be passively transported into root cortical cells and xylem using the NO_3^- transporter NPF7.3 (Lin et al., 2008) or other anion channels like the S-type anion heteromeric channel SLAH1/SLAH3 (Qiu et al., 2016). In addition, high leaf Cl^- concentrations are more dangerous than high Na^+ due to both the lower Cl^- exclusion capacity of leaf blades (Colla et al., 2013; Munns and Tester 2008) and the reduced capacity of basipetal phloem transport of Cl^- toward the roots (Munns, 2002; Geilfus, 2018). In fact, Na^+ can be unloaded from the xylem vessels by AtHKT1, decreasing its concentration both in the leaf tissues and xylem sap (Sunarpi et al., 2005). On the contrary, high leaf concentrations of Cl^- do not only decrease the apoplast osmotic potential interfering with cellular water relations (Geilfus, 2018), but also compete with nitrate (NO_3^-) for its uptake symporters thus diffusing into the symplast while reducing the uptake and concentration of this important nutrient (Carillo et al., 2005; Griffiths and York 2020). Papadopoulos and Rendig (1983) described specific anion-anion uptake competitions between Cl^- and PO_4^{3-} in tomato, that was not found in melon (Navarro et al., 2001). Moreover, a competition between Cl^- and sulphate (SO_4^{2-}) with a negative effect on PO_4^{3-} uptake and translocation to shoot has been hypothesised to exist in pea (Mor and Manchanda, 1992). Therefore, both Na^+ and Cl^- can be toxic when their concentrations increase in the cytosol and organelles (Carillo et al., 2019).

5. Toxicity and/or conflicting effects of other salts

In addition to Na^+ and Cl^-, other ions such as Mg^{2+}, SO_4^{2-}, HCO_3^- and Ca^{2+} or their combination can cause salt toxicity, beneficial effects or conflicting effects because of a competition or predominance of specific ions on others (Colla et al., 2012; Colla et al., 2013; Ntatsi et al., 2017; Scagel et al., 2017; Rabhi et al., 2018; Zörb et al., 2019) (Table 1). Indeed, some salts, like $CaCl_2$, Na_2SO_4 and Na_2CO_3 are present in groundwater or soils of arid and semiarid regions of many areas in the world at concentrations exceeding those of NaCl (Ezlit et al., 2010; Nedjimi et al., 2006; Peleg et al., 2011).

Sulfate salts, such as Na_2SO_4 and K_2SO_4, are able to decrease the efficiency of photosystem II (Fv/Fm) and photooxidation in *Brassica rapa* more actively than NaCl and KCl (Reich et al., 2018).

Sodium carbonate may be more dangerous than equimolar amounts of NaCl and Na_2SO_4 for its capacity to generate saline–alkaline soils by increasing soil pH (Zhang et al., 2012). Excess sulfates are present in marine soils, volcanic soils, irrigated agricultural soils or can be caused by the anthropogenic wet residues from industries or release of atmospheric sulfur gases (Reginato et al., 2021). Aghajanzadeh et al. (2019) found that SO_4^{2-} and Cl^- at equimolar concentrations were able to exert the same negative effects on uptake and distribution of sulfate in onion. Also Khan et al. (2020) found that Na_2SO_4 affected sulfate reduction and metabolism in *Brassica juncea* L. var. Goldi. In particular, Aghajanzadeh et al. (2018) determined in *Brassica rapa* high levels of indole and aromatic glucosinolates and overexpression of genes involved in their synthesis and a decrease of growth under Na_2SO_4 salinity. Therefore, Na_2SO_4 alters sulfur metabolism, eliciting a sharp increase in sulphur containing compounds (e.g. cysteine, glucosinolates, etc.) causing a disorder in carbon metabolism and growth (Reginato et al., 2021). Bilski et al. (2008) reported that wild potatoes were more sensitive to high levels of Na_2SO_4 than to iso-osmotic concentrations of NaCl. Tarchoune et al. (2012) also demonstrated in *Ocimum basilicum* L. cultivar Genovese that the effects of Na_2SO_4 on root, stem and leaf dry weight, root length, shoot height and leaf area were more negative than those exerted by NaCl. However, at low electrical conductivity (EC) the impact of Na_2SO_4 on yield and fruit quality of *Capsicum annuum* L. was less strong than that of NaCl (Navarro et al., 2002). More specifically Reich et al. (2017) explained that the higher toxicity of Na_2SO_4 at high concentrations was due to the capacity to elicit a stronger decrease of divalent cations (Ca^{2+}, Mg^{2+} and Mn^{2+}) than NaCl in *Brassica rapa* L. It was demonstrated that the mechanisms of adaptation of roots to NaCl and/or Na_2SO_4 are different in the diverse species (e.g., cotton, tomato, beans, etc.). In particular, NaCl salinity in growth media caused succulence in roots and decreased growth. Succulence may be an essential adaptive strategy that enables compartmentalization of toxic ions (e.g. Na^+) in the vacuole to protect the cytosol while also preserving water (Grigore and Toma 2017). In contrast, if Na_2SO_4 was present in the media, plants started showing haloxeromorphic characteristics such as enhanced aerenchyma in the root cortex and increase of diameter of the stem cortex, in addition to leaf-pubescence (Strogonov, 1964).

The detrimental effects of salinity can be mitigated by Ca^{2+} treatment, which increases Ca^{2+}/Na^+ selectivity, contributing to preserve membrane structure and function, thus reducing the leakage of cytosolic K^+ (Cramer et al., 1985; Grattan and Grieve 1999; Renault and Affifi 2009; Korkmaz et al., 2017). Calcium at micromolar concentrations may interact with the *Arabidopsis* vacuolar Two Pore K^+ channel 1 (TPK1) making it release K^+ and increasing cytosolic K^+/Na^+ ratios under short term salinity; while Ca^{2+} at sub-micromolar concentrations can help modulate K^+ homeostasis in adapted roots under long term NaCl stress (Latz et al., 2013; Wilkins et al., 2016).

Parvin et al. (2019) reported that calcium supplied at 2-5 mM concentrations improved Ca^{2+} and K^+ selectivity, NUE and ROS scavenging, thus decreasing membrane damage in both shoots and roots of plants under 50-200 mM. However, the efficacy of calcium in increasing plant salt tolerance does not depend only on plant genotype but also on the source of its ions ($CaCl_2$ or $CaSO_4$) (Volkmar et al., 1998). In fact, $CaCl_2$ may elicit more negative osmotic and ion specific effects than NaCl in different horticultural species even at milder concentrations (Colla et al., 2013; Borgognone et al., 2014). The ability of calcium chloride to decrease growth and yield has been mainly ascribed to the toxic effects of Cl^- in cucumber, since its allocation to and re-allocation from leaves is difficult to control, as mentioned above, thus compromising metabolism and development of whole plant (Colla et al., 2013).

Even KCl can be dangerous, but its toxicity mostly depends on the high Cl^- concentrations in plants deriving from KCl fertilization (Geilfus, 2018). In fact, Parker et al. (1983) showed that after KCl supply, Cl^- levels in soybean (*Glycine max*) seeds underwent a 9-fold increase.

High concentrations of $NaHCO_3$ and Na_2CO_3 increase pH, resulting in soil and/or cell alkalization (Fang et al., 2021; Khajanchi and Meena 2008; Machado and Serralheiro 2017). These salts, dependent on high pH in the soil, result in precipitation of Ca^{2+}, Mg^{2+} and $H_2PO_4^-$, inhibiting their uptake (Yang et al., 2007). Since the presence of these salts within the cells alters pH status, in addition to causing osmotic stress, ionic stress and ion imbalance, they decrease the capacity of cell to modulate its osmotic adjustment and antioxidant response, reducing cell membrane integrity, root vitality and photosynthetic efficiency (Fang et al., 2021). $NaHCO_3$ and Na_2CO_3 alkali stresses jeopardise tomato plant growth, which is forced to divert large amounts of carbon skeletons and energy for the synthesis of organic acids (e.g. citrate, malate and succinate) to buffer pH and offset the deficiency of inorganic anions (Wang et al., 2011).

$Ca(NO_3)_2$ is another salt that when present in excess in soil is toxic for plants. In fact, it increases cellular levels of Ca^{2+} and NO_3^-, and causes osmotic stress and ion imbalance increasing oxidative damage to plant structures (Fan et al., 2017). In cucumber seedlings the excess of this salt decreased SOD, POD and CAT activity while increasing ROS and MDA, and damaging mitochondrial membrane structures. Also nitrate reductase (NR), nitrite reductase (NIR), and nitric oxide synthase (NOS) activities were reduced with a consequent increase of cellular content of NO_3^-, NH_4^+ and NO, and a decrease of root length, root surface area number of root tips (Yang et al., 2020).

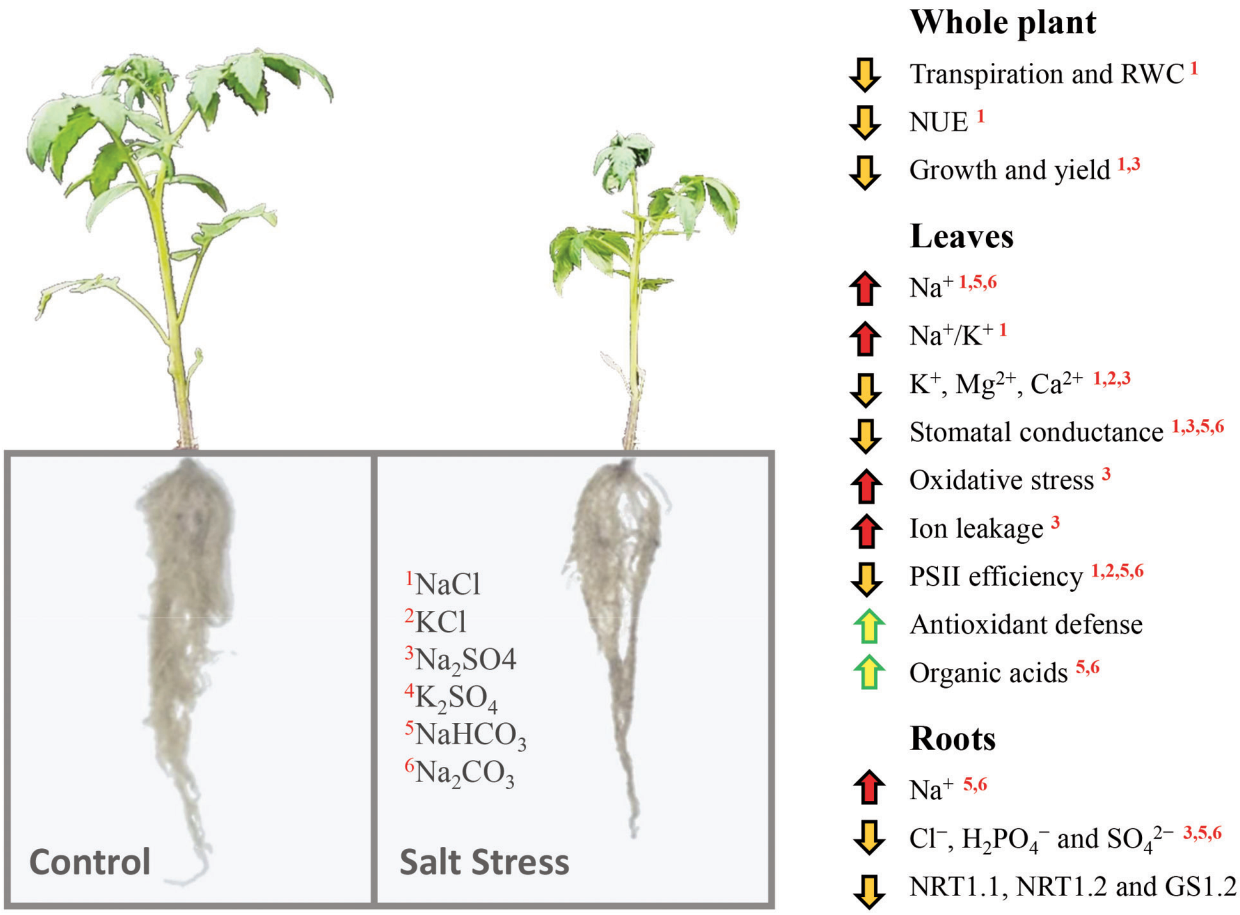

Figure 1. Morpho-physiological changes under different salt stress agents.

6. Conclusions

Salinization is a global environmental phenomenon that affects not only regions with arid or semi-arid conditions but is widespread throughout the world. In these areas, the scarcity of fresh water further aggravates this problem because it forces the farmers to use agricultural runoff water, brackish water and reused municipal and industrial wastewater for irrigation, which contain high concentrations of different salts that, as seen above, can be harmful for crop plants. Rising temperatures globally can accelerate the severity of problems related to salinity, which progresses so rapidly that the natural variability of organisms cannot create plants that can tolerate these adverse conditions. In this scenario, genetic engineering and/or editing techniques have certainly made it possible to create organisms (for most model plants) with a greater tolerance to salt stress. However, their practical translation to the field is hampered by potentially unstable or nonspecific integration of transgenes into the plant genome, legislative issues and, not least, consumer acceptance (Détain et al., 2022). Therefore, the long time needed cannot keep step with changing environmental conditions and abiotic and biotic stress factors. In this scenario, some new agricultural practices, such as the use of biostimulants, or other well-established techniques, like grafting, can respond to the growing demands of the agricultural sector and offer environmentally friendly tools to increase the tolerance of plants to salt stress.

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