

IMPACTS OF SALT STRESS ON THE PHYSIOLOGY OF PLANTS AND OPPORTUNITY TO REWATER THE STRESSED PLANTS WITH DILUTED WATER: A REVIEW

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Abstract. Water scarcity on a global scale declines the availability of fresh water for agricultural usage. This situation demands the urgent need of utilizing saline water as an alternative resource for irrigation. Stressful environments characterized by adverse natural conditions such as drought, salinity and heat impact the normal molecular, biochemical and physiological processes in crops. Plant stress responses to adverse environmental conditions are reviewed with emphasis on growth, physiological and electrophysiological mechanisms of plant tolerance. This review may also help in interdisciplinary studies to evaluate the photosynthetic threshold levels for rewatering of plant with diluted saline water. Furthermore, considering the goal of high plant production, the best rewatering time was found when plants undergo threshold levels. Therefore, this review provides a new method for dilution of saline irrigation based on plant physiology, which has a huge practical and theoretical importance for saline irrigation research.

Keyword: *photosynthetic traits, growth properties, plant tolerance, rewatering time, threshold levels*

Introduction

Salinity is a major abiotic constraint curtailing crop growth and yield all over the world. The soil salinity is a widespread global concern caused as a result of abundant seawater intrusion in coastal areas, occurrence of saline groundwater and inadequate irrigation and/or drainage (Souza Filho et al., 2003; Nadeem et al., 2014; Yepes et al., 2018). Salinity induced stress in crop plants is a severe environmental problem in many parts of the world, particularly arid and semi-arid (i.e., dry) regions (Rady et al., 2018). Increasing soil salinity issues in some parts of the arid and semi arid regions is due to the inadequate drainage facilities which obliges the use of poor-quality water for irrigation, which may cause 30% shrink in cultivable land within the next 25 years (Shahbaz and Ashraf, 2013). In the present scenario, the adverse effects of land salinization become evident for the fact that over 30 m ha of irrigated lands are significantly damaged by the salt build up and about 0.5 m ha are reported to be lost from farming annually (Singh, 2018). Salinity poses adverse effects to almost all growth stages and metabolic processes in plants starting from a reduction in seed germination, a

disruption of node formation, a retardation of plant development and finally ending up with a reduction in final crop yield (Munns and Tester, 2008). This reduction in crop yield will pose a severe threat to the global food security as the world populace is estimated to reach between 9 and 10 billion in 2050 (Lutz et al., 2017). Therefore, in order to feed the burgeoning world populace, sustainable irrigation practices should be adopted that improve the existing salinised agricultural lands (Flowers and Yeo, 1995; Biswas, 2008; Garcia, 2008).

Water scarcity and salinity are two major constraints which affect the agricultural production all over the world and the adoption of different irrigation regimes is the key requisite to improve water use efficiency in agricultural practices (Nangare et al., 2016; Mosaffa and Sepaskhah, 2018). Therefore, knowledge on the understanding of the physiological responses that define the plants' tolerance to surpass salinity stress is essential. By understanding the mechanism of the plants' stress tolerance, it is possible to develop water efficient irrigation regimes for agricultural activities (Zhang et al., 2011). Water saving agriculture is an effective approach to manage the ever increasing demand for food. Practically, this is achieved by amendments in different technological disciplines such as agronomy, biology and engineering. The engineering approaches include efficient utilization of existing water resources, water desalinization, and usage of brackish water or recycled sewage water for agricultural purposes. Meanwhile, agronomic and plant biology approaches include a wide range of innovative methods such as crop rotation, water conservation, water-fertilizer combination, physiological responses of plants, crop management and vegetative growth (Du et al., 2014, 2015).

In case of water scarcity, diluted saline water becomes the inevitable source for irrigation of plants. However, to ensure the safe use of saline water, effective crop management strategies are required to be developed in order to understand the response of crops to salinity (Bustan et al., 2004; Azeem et al., 2017a). The use of diluted saline water as an alternative resource for fresh water to irrigate the moderately salt tolerant crops will reduce irrigation cost, sustain agricultural productivity and save water resources. Thus, this comprehensive review aims to focus on the effect of rewatering or dilution of salted water on the photosynthetic responses in plants *growing* under saline stress (*Fig. 1*). Furthermore, this review emphasized the restoring abilities of plants from salt stress after re-watering or dilution of salted water.

Physiological response of plants to salt stresses

Photosynthetic characteristics

Salinity stress obstructs the physiological processes of plants (Negrão et al., 2017). It imposes a severe impact on the photosynthetic activity of plants (Sayed, 2003; Ashraf and Shahbaz, 2003; Kao et al., 2006; Munira et al., 2015; Habib et al., 2012; Hu et al., 2009). Photosynthesis is the most essential and complex functional process in all plants and a key factor in the development of plants. The stress induced by salinity impacts the overall capacity of photosynthesis (Ashraf and Harris, 2013). During salinity exposure, plants experience changes in photosynthetic characteristics, including transpiration rate (T_R), relative leaf water content (Lee et al., 2005) and photosynthetic pigments (Tort and Turkyilmaz, 2004; Murillo-Amador et al., 2007; Taffouo et al., 2010; Javed et al., 2017). However, the regulation of photosynthesis is being distressed through stomata limitation, thereby reducing T_R and leaf water potential (Ψ_L) (Azevedo Neto et al., 2004; Azeem et al., 2017b).

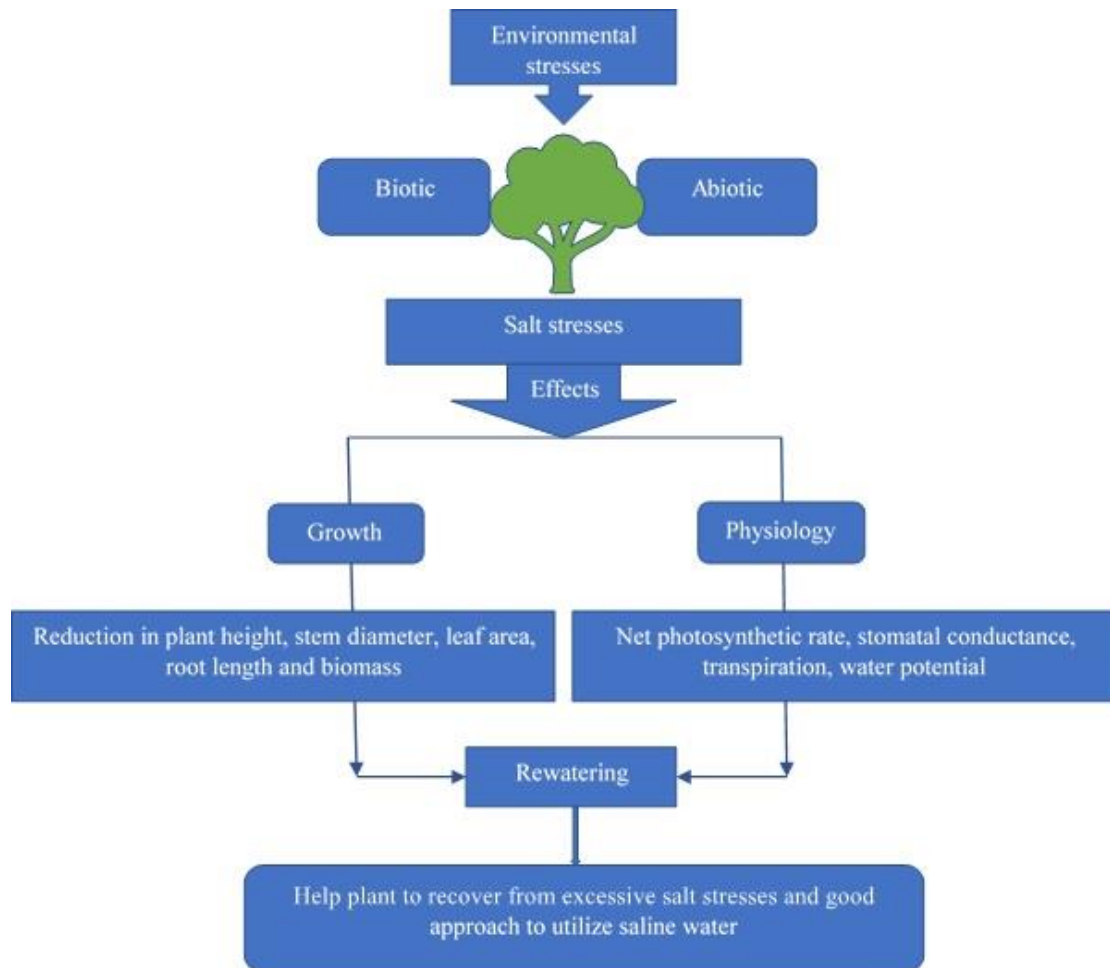


Figure 1. Graphical representation of salt stress on plant and afterwards rewatering effects

Stresses in plants inhibit the net photosynthetic rate (P_N) through stomatal opening-closing restrictions (Saibo et al., 2009; Rahnama et al., 2010), particularly in the case of green plants. Salt-stress in the leaves of tomato plants is increased through increased Na^+ concentration (Ullah et al., 2017). Salt stress of > 80 mM of NaCl strongly inhibited the P_N and stomata conductance (S_g). This indicated that the high salt concentration exhibited toxicity in the leaves of tomatoes, which is the main reason of reduction of S_g and P_N under high-stress (> 80 mM of NaCl) (Wang et al., 2011a). Limitation in S_g has been recorded usually at early stages of drought-stress, which in turn increases the water use efficiency (WUE). Stomatal closure has more inhibitory results on transpiration than diffusion of CO_2 into the leaf tissues (Sikuku et al., 2010). Though in comparison, under severe-stress dehydration takes place in mesophyll cells and initiating marked inhibition of necessary photosynthetic metabolic process as well as reduces WUE of plants (Damayanthi et al., 2011; Anjum et al., 2011). Yousif et al. (2010) examined the salt-tolerance difference mechanisms between water spinach (*Ipomoea aquatica* L.) and New Zealand spinach (*Tetragonia tetragonoides*). The P_N , S_g and T_R of both species are reduced with increasing salt-stress, but P_N , S_g and T_R in New Zealand spinach are maintained at 100 mM NaCl than in water spinach. Chartzoulakis et al. (2002a) observed the salt-stress caused by varying concentrations of NaCl (0, 25, 50, 100 and 200 mM) on the growth and photosynthetic traits of six olive

cultivars (Kalamata, Koroneiki, Mastoidis, Amphissis, Megaritiki and Kothreiki). The P_N and S_g of fully prolonged young leaves of all cultivars were reduced significantly at high concentrations of salinity > 100 mM. In all species, Kalamata showed the higher tolerance to salt stress at 100 mM NaCl, followed by Megaritiki and Kothreiki. Effects of abiotic stresses on plant physiology and their corresponding threshold values are shown in *Table 1*.

Table 1. Effect of stresses on photosynthetic characteristics and their corresponding threshold values

Stress	Plant species	Concentrations	P_N $\mu\text{mol m}^{-2} \text{s}^{-1}$	S_g $\text{mol m}^{-2} \text{s}^{-1}$	T_R $\text{mmol m}^{-2} \text{s}^{-1}$	Threshold levels	Resources
Salt-stress NaCl (mM)	New Zealand spinach (<i>Tetragonia tetragonoides</i>)	0	22.5	1.3	6.6	= 100	Yousif et al., 2010
		50	16.9	0.4	2.6		
		100	15.7	0.2	1.8	= 200	
		200	8.7	0.1	1.1		
Salt-stress NaCl (mM)	Water spinach (<i>Ipomoea aquatica</i> L.)	0	21.0	0.6	3.3	= < 100	Yousif et al., 2010
		50	11.9	0.1	1.4		
		100	10.7	0.08	0.9	= 200	
		200	0	0	0		
Salt-stress NaCl (mM)	Tomato	40	10	0.10	2.0	= < 120	Wang et al., 2011b
		80	7.8	0.07	1.8		
		120	6.0	0.05	1.5	> 120	
		160	5.0	0.04	1.45		
Salt-stress Ec (dsm ⁻¹)	<i>Brassica juncea</i> L. (<i>Varuna</i>)	0	20	0.07	3.2	= 4.2	Wani et al., 2013
		2.8	16	0.04	27		
		4.2	14	0.03	2.5	= 5.6	
		5.6	13	0.03	2.4		
Salt-stress Ec (dsm ⁻¹)	<i>Brassica juncea</i> L. (RH-30)	0	17	0.057	3.0	= < 4.2	Wani et al., 2013
		2.8	11	0.028	2.3		
		4.2	9	0.025	2.0	> 4.2	
		5.6	7	0.02	1.7		
Deficit irrigation ETc (%)	Cabbage (<i>Brassica oleracea</i> L.)	50			10	= 75	Xu and Leskovar, 2014
		75	18.6	0.357	12.1		
		100	21.6	0.472	14.4	= 50	
			23.6	0.673			
Drought stress (FC %)	<i>Medicago laciniata</i> saharian (MI-90)	100	9.2	0.17	3.0	= 75	Yousfi et al., 2016
		75	6.3	0.11	1.8		
		35	4	0.07	1.6	= 35	
Drought stress (days of withheld irrigation)	Astragalus gombiformis Pomel	5	5.41	0.232	4.09	= 15	Boughalleb et al., 2016a
		10	5.61	0.229	4.00		
		15	5.04	0.205	3.58	= 20	
		20	4.95	0.171	3.19		
Irrigation water salinity	Barley cultivar [Morocco]	2	17.0	0.43	6.0	= 10	Mahlooji et al., 2018
		10	15.0	0.25	7.5		
		18	7.0	0.18	4.0		
	Barley cultivar [Nosrat]	2	16.0	0.38	6.9	> 10 < 18	
		10	24.5	0.27	8.5		
		18	14.2	0.25	6.7		
	Barley cultivar [Khatam]	2	22.0	0.35	5.8	= 18	
		10	19.4	0.28	7.4		
		18	19.2	0.26	5.5		

P_N is net photosynthetic rate; S_g is stomatal conductance; T_R is transpiration

Stomatal closure is one of the instant responses to water-stress. Generally the atmospheric vapor pressure and leaf turgor pressure can be disturbed because of reduction in stomatal opening in response to drought and salinity stress (Chaves et al., 2009; Javed et al., 2018). Therefore, reduction in P_N under traumatic conditions like drought, temperature, and salinity, is normally due to suppression in the mesophyll cells and stomatal opening-closing limitation (Flexas et al., 2004; Azeem et al., 2017a).

The research by Boughalleb et al. (2016a) on *Astragalus gombiformis* Pomel, found that P_N , S_g , T_R , and internal CO_2 concentration (C_i) was decreased significantly with water-stress duration as compared to that of well watered conditions. A Cerrado's native plant, *Campomanesia adamantinum* (*C. adamantium*) O. Berg, has a potential to exhibit stress tolerant abilities. It is susceptible to grow in an atmosphere of high temperature, dry land and water deficit region. During the experimental period, the photosynthetic factors are evaluated for *C. adamantium*. Seedlings are more stable for plants under control condition, and vast variations are noted in stress subjected plants. At the thirty-first day of water-deficit, S_g and T_R are reduced and P_N approaches to zero as $0.285 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$. Consequently, WUE also reaches close to zero. Subsequently, the plants are rewatered to recover the photosynthetic metabolic activity (Junglos et al., 2016). Further, the threshold levels of photosynthetic capacity is explained by the extent to which the plants can withstand the stress imposed on the different features of photosynthesis, which can subsequently be used for rewatering of plants to regain the photosynthetic capacity affected by stresses.

Leaf water potential and carbonic anhydrase activity

The leaf water potential (Ψ_L) is termed as the energy status of water in the leaves. The comparative activity of S_g and P_N regulation is directed to water-use efficiency (Vos and Groenwold, 1989) and leaf water potential (Wani et al., 2013). Leaf water potential or leaf water status is a major factor affecting overall behavior and performance of stomata (Ruiz-Sánchez et al., 1988). Salt-stress inhibits photosynthesis process by lowering Ψ_L (Parida and Das, 2005). Gorai et al. (2010) stated that limited supply of water reduced the dry weight of whole-plant, with a reduction in relative water content and Ψ_L . In certain studies, salt-stressed plants exhibit osmotic regulation due to changes in leaf water status (Kaymakanova and Stoeva, 2008; Gama et al., 2009). Among the different physiological parameters recommended to indicate water-status of vine, Ψ_L has been considered more feasible (Baeza et al., 2007) rather than S_g (Cifre et al., 2005) and temperature of leaf canopy (Bernard et al., 2004). However, there still exists some uncertainty as to which time plant shows the best water status, and what time of the day is optimum for measuring the water potential. (Deloire et al., 2004), used predawn Ψ_L as a standard to assess water-status at different stages of plants development in France. In Portugal, (Lopes, 1998), attained a very close relationship between P_N and predawn Ψ_L under water-stress conditions. Sato et al. (2006) checked the validity of predawn Ψ_L as an indicator for irrigation of wheat in northern Syria. Whereas, Intrigliolo et al. (2004) and Salón et al. (2005) measured Ψ_L during daylight and found that Ψ_L at mid-morning or at noon seem to execute the water-status better than predawn Ψ_L .

Williams and Araujo (2002) described that the measurements of plant water status are associated with plant physiology. According to Xiloyannis et al. (1997), olive plants (*Olea europaea*) adopt different strategies to survive under water-stress conditions as: (i) by lowering their Ψ_L and water content (WC) of leaf tissues, and then use soil water

up to -2.5 MPa; (ii) plants stop shoot's growth but not its P_N activity; (iii) adjustment of osmotic pressure, which is found to show a significant part in maintaining leaf cell activities. Generally, good positive relationships are found between S_g , Ψ_L and growth of plants. The growth of New Zealand spinach (*Tetragonia tetragonoides*) showed a notable reduction in Ψ_L and osmotic potential with increasing salinity. Water spinach showed tolerance and survived up to -1.99 Mpa (Yousif et al., 2010). Plant water status and stem water potential are used as indicators for irrigation scheduling, which requires the description of reference values or threshold values, in order to achieve the optimum irrigation levels. Depending on the response of plants in relationship with Ψ_L and WC, the obtained threshold values are -1.04 and -1.46 MPa, respectively for irrigation of apple varieties i.e., *Mutsu* and *CoxOrange* (De Swaef et al., 2009). Increasing salinity reduces the osmotic potential of the bean plants. This variation is considered as one of the defensive mechanism of plants to tolerate stresses. The values noticed indicate an inverse relationship between osmotic potential and salt stress in bean leaves. The statistical analysis revealed that the decline in osmotic potential is significant with increased NaCl concentration > 120 Mm (Qados, 2011).

A decline in water potential was noticed as a result of reducing relative WC (Kalapos, 1994; Bhatt et al., 2008). Therefore, some plants could convert intracellular HCO_3^- into CO_2 and H_2O by carbonic anhydrase activity (CA) to maintain water content. Carbonic anhydrase activity (CA) is very important in biological functions of plants that include reactions of carboxylation and decarboxylation and it is also takes part in the transporting of inorganic CO_2 to active photosynthetic cells (Henry, 1996). CA is a zinc containing enzyme activity, and is found in all living organisms. CA plays a dynamic role in assisting the transport of CO_2 and protons in intracellular spaces and in the layers of the extracellular space, across cell membranes. It is also involved in several other processes like photosynthesis and respiration. CA catalyzes the rapid inter conversion of HCO_3^- into CO_2 and H_2O . Meanwhile, CA activity is pretentious by deficiency of Zn and also takes part in sustaining the inorganic carbon levels (Tavallali et al., 2009). A reduction in CA activity caused by deficiency of Zn may contribute to the decrease in P_N (Hacisalihoglu et al., 2003).

CA activity helps plants to prevent from losses of water under traumatic environmental conditions (Hu et al., 2011). Kicheva and Lazova (1998) elucidated the reduction of CA activity in wheat seedlings in response to slight osmotic-stress. However, it increased rapidly under severe osmotic-stress conditions. It is noted that wheat cultivars differ in their response to drought stress with different CA activities (Guliyev et al., 2008). CA activities varied with plant species, osmotic-stress levels and stress durations. CA activity is higher in *Pharbitis nil* (Linn.) Choisy (*P. Nil*) than *Parthenocissus tricuspidata* (Sieb. et Zucc.) (*P. Tricuspidata*) and *Lonicera japonica* Thunb (*L. Japonica*) under drought-stress. CA activity is undetectable in *P. tricuspidata* but for *L. japonica*, CA activity is lower under medium or high stress, than that of the stress under low level. With an increase in drought stress duration, CA activity sharply decreases (Xing and Wu, 2012).

CA plays an important role in a number of physiological processes, such as maintaining acid-base balance, ion exchange, reactions of carboxylation and decarboxylation, and circulation of inorganic carbon between the cells (Table 2). CA regulates the photosynthetic mechanism in response to low stomata conductance (Wu and Xing, 2012). Xing and Wu (2015) examined the variations in CA activities with fluctuating nutrient levels for 3-climber species. *P. nil* showed higher CA activity when

compared with the other two species. While, *P. tricuspidata* showed the lowest and nearly undetectable CA activity. CA activity of *P. nil* under 1/2 and 1/4 strength nutrient solutions, is slightly higher than those under 1/16 and 1/32 strength nutrient solution. For *L. japonica*, CA activity is lower under control (full-strength nutrient solution) than those which are concealed under 1/4, 1/8, 1/16 and 1/32 strength nutrient solution. In previous studies, it is found that, by the regulation of CA activity P_N increased in *Orychophragmus violaceus* (L.) O. E. Schulz (*Orychophragmus violaceus*) and it is observed as a shade tolerant crop in comparison of other *Brassicaceae* species (Wu et al., 2007; Wu et al., 2005). Therefore, water status in crop can be maintained by the regulation of CA activity. As a result, carbon and water source are provided for the photosynthesis process by the plant (Hu et al., 2011). Hence, CA activity deeds for the survival of plants under stressed environments (Wu et al., 2011).

This section emphasized on two key factors viz., (1) the water status and water potential of stem and leaves to indicate the threshold values for irrigation or rewatering of plants; (2) the role of CA activity for regulation of photosynthesis against stressful environments.

Table 2. The role of CA activity during stress condition

Plant species	Treatment	CA-activity role	Reference
<i>Okra</i>	Salt stress NaCl + CaCl ₂	In moderate and low salt stress levels CA-activity play a main role to maintain plant water status	Azeem et al., 2017a
<i>Orychophragmus violaceus</i> (L.) O. E. Schulz and <i>Brassica napus</i> (L.)	Salt stress (NaCl, Na ₂ SO ₄ , NaCl + Na ₂ SO ₄)	The CA-activity in plants showed good regulatory and was initially activated, when the leaves were under slight stress levels. A substantial increase of CA-activity noted under moderate-stress-levels. Due to regulation of CA-activity, photosynthetic activity was increase and showed development of growth parameters	Javed et al., 2018
<i>Broussonetia papyrifera</i> (L.) Vent. and <i>Morus alba</i> L.	Salt stress NaHCO ₃	The stomatal opening and closing affected through variation in leaf-water potential, initiating an imbalance in gaseous exchange, and disturb the photosynthetic activity. To overcome this situation, CA-activity is become activated in leaves and providing partially carbon-water source to plants suffering from shortage of water	Wu and xing, 2012
<i>Pharbitis nil</i> (Linn.) Choisy, <i>Lonicera japonica</i> Thunb. and <i>Parthenocissus tricuspidata</i> (Sieb. et Zucc.)	Nutrient deficit (1/2,1/4,1/8,1/16,1/32)	CA-activity was increasing with nutrient deficit and activate when plant is going to stress due to nutrient deficit	Xing and Wu, 2015
<i>Brassica napus</i> (L.)	Drought stress (poly-ethylene glycol 6000 (i.e. 0, 20, 40 and 80 g L ⁻¹))	CA-activity is also activated in drought stress when duration of drought was increasing. CA-activity helps plants during drought stress for H ₂ O and CO ₂ regulation and maintain its growth	Xing et al., 2018

CA activity is carbonic anhydrase activity

Electrophysiological properties of plants

Plants are subjected to several diverse abiotic stresses throughout the growing season in the field (Tester and Bacic, 2005). Toxic effects imposed by salt stress decreased the production of new leaves and inhibited leaf expansion (Mansour and Salama, 2004). In plants, salt tolerance is attributed by structural and functional variations, such as plant growth regulation, Ψ_L and osmotic adjustment. Water deficiency and its stability in plants can be described through its electrophysiological properties, in which, Ψ_L of a plant was reflected by WC, capacitance and leaf air temperature.

A miniaturized, nondestructive sensor that employs a microwave micro strip ring resonator is developed for estimation of WC in single grain of wheat (Abraham et al., 2000) detected the amount of applied water/day, soil moisture content and leaf-air temperature based on electrical resistance. Koide (1991) revealed the relationship between Ψ_L with hydraulic resistance and capacitance of a plant. (Turner, 1988) used pressure chamber to calculate Ψ_L . While, Zhang et al. (2015) suggested the rapid measurement of drought resistance in the leaves of *Broussonetia papyrifera* (*B. Papyrifera*) and *Morus alba* (*M. Alba*) based on electrophysiological properties. A significant bonding is detected between physiological capacitance (C_p), WC and Ψ_L . The changes in physiological resistance and C_p , varied the water status in leaves (Table 3). Tensity of plant's leaf cell also can describe the status of water in leaf cells of plants, and that reflects the tolerance of plants to stress (Zhang et al., 2015). The outcomes of this review highlight the electrophysiological characteristics as rapid responses of plants to stress resistance. Furthermore, electrophysiological properties can be used to obtain precise information for irrigation and dilution of saline irrigation on the basis of water status in leaves.

Table 3. Plants responses due to variation in water potential, physiological capacitance and leaf tensity under salt stress and re-watering

Plant species	Salt treatments	Effect	Re-watering effect	Mechanism	Reference
<i>Okra</i> <i>Abelmoschus</i> <i>esculentus</i>	Salt stress (NaCl + CaCl ₂)	Salt stress in every level reduces plant water potential and physiological capacitance	Recovery in the moderate and slow salt levels but could not recover in high salt stress	Plant stop to get water from root zone because of osmotic process	Azeem et al., 2017b
<i>Orychophragmus</i> <i>violaceus</i> (L.) O. <i>E. Schulz</i> and <i>Brassica napus</i> (L.)	Salt stress (NaCl + Na ₂ SO ₄)	Physiological capacitance and leaf tensity of both species decline with increasing concentration of salts under single salts effect and a mixture of salts	Plant show better recovery during re-watering in single and mixture of salts, but single salts recover well	Due to excess amount of salts, plant leaf tissue loss the ability to hold water	Javed et al., 2017
<i>Brassica napus</i> (L.)	Drought stress poly- ethylene glycol 6000 (i.e. 0, 20, 40 and 80 g L ⁻¹)	Leaf water potential and physiological capacitance are decreased with increasing drought stress level	Re-water from 40-0 recover better, but 80-40 could not recover because higher drought damage plant leaf cell badly that could not recover during re-watering	During drought stomatal conductance decreased and effect the water regulation and sustainability	Xing et al., 2018

Plant growth features

Salinity is one of the key limiting factors affecting the physiological processes and its impacts may pose severe consequences on the growth of plants (Vilagrosa et al., 2003). The effect of salinity is different for different plant species and for different genotypes because plants exhibit unique tolerance mechanism (Memon et al., 2010; Gama et al., 2007). Salt stress inflicts biological disturbances in plants, causing adverse effects on plant growth, plant quality, and plant yield (Jouyban, 2012; Siddiqui et al., 2008; Qados, 2011). Mostly, species of brassica are considered to possess inbuilt salt tolerant mechanism because of their ability to cope up with salt-stress (Maggio et al., 2005; Hayat et al., 2007). This mechanism might be particularly significant with concerns for survival of salt tolerant plants. Previous studies point out the effects of salt stress on plant growth characteristics (Riccardi et al., 2014; Boughalleb et al., 2016b; Rameshwaran et al., 2016). Some researchers studied the relationship between the

reduction in plant length by increasing the concentrations of NaCl (Mustard and Renault, 2006; Jamil et al., 2007; Rui et al., 2009). Certain other studies elucidated the toxic effect of NaCl concentrations on leaf characteristics (Netondo et al., 2004; Chen et al., 2007; Yilmaz and Kina, 2008). The harmful effect of salinity on the number of leaves per plant also increases with increasing concentration of salts. Numerous studies have focused on the effect of varying concentration of salts on fresh and dry weight of plants, either positively or negatively, which is dependent on the nature of salt present (Bayuelo-Jimenez et al., 2002b; Niazi et al., 2005; Turan et al., 2007; Taffouo et al., 2009, 2010).

Drought-salt resistance in plants is explained by structural and functional adaptations, such as osmotic adjustment, Ψ_L , S_g limitations and growth regulation (Zollinger et al., 2007). Plants undergo different changes from the very onset period of salinity stress till maturity periods (Munns, 2002). The variations in the plant development differ with differing time scales after salinization. Quick response of salinity to plants result in dehydration of plant's cells and cell shrinkage, but some hours later on there occurs the regaining of cell volume. But this mechanism affects the cell elongation and division and thereby impacting the plant root growth and leaf size (Läuchli and Grattan, 2007). Understanding these times dependent mechanism of plants in response to salinity, lead to the accomplishment of "two-phase" growth responses to salinity (Munns, 2005).

Salinity exceeding 6 dS/m causes constriction in the length of stem and impacts severe consequences on fruit quality (Carter et al., 2005). Among cultivars, there are even dissimilarities with respect to the tolerance mechanism (Ahmad et al., 2005) and these differences are not parallel with seasonal tolerance, as explained by Nerson and Paris (1984) for melon, Heenan et al. (1988) rice, Bayuelo-Jimenez et al. (2002a) bean and Tajbakhsh et al. (2006) barley. The best growth of *Rhizophora mucronata* Lam. is attained at 50‰ seawater, and a further rise in salinity beyond this level scales down the growth (Aziz and Khan, 2001). Experimental results demonstrated that in a salt-stress condition, the mangrove *B. parviflora* shows optimal growth performance at 100 mM NaCl, however a further increase in NaCl concentration retards the growth of plant. A concentration of about 500 mM NaCl was found to be lethal to mangrove plants (Parida et al., 2004). The mangrove *Aegiceras corniculatum* (L.) Blanco shows tolerance up to 250 mM NaCl and is found to be dead beyond this concentration (Mishra and Das, 2003). Increased concentration of NaCl results in a significant reduction of root/shoot ratio and leaf growth biomass (Meloni et al., 2001). There is an overall trend found for the increase in the plant's lengths of the *Vicia faba* L. by using the concentrations of NaCl, 60 mM and 120 mM. More precisely, after treatment of 10 days, the increment is negatively correlated, by increasing NaCl concentration from 60 to 120 mM and consequently, 40% death of the plants occurs at initial stage by using highest concentration of 240 mM NaCl (Qados, 2011). Contrary results are recorded as well, such as Dantas et al. (2005) on cowpea (*Vigna unguiculata* L.), and Memon et al. (2010) on *Brassica campestris* L., specified that the usage of low concentrations of NaCl causes an increase in plant's height, whereas high NaCl concentrations affected the growth of plants. Studies on moth bean (*Vigna aconitifolia* L.) (Mathur et al., 2006), radish plant (*Raphanus sativus* L.) (Jamil et al., 2007) and *Vigna mungo* L. (Kapoor and Srivastava, 2010) indicated that increased NaCl concentrations causes a decline in plant's length.

In the light of the different tolerant mechanisms adopted by plants at their specific developmental stages against salinity, this review encompasses the reference levels or point for re-watering, the plants can endure after being exposed to salinity stress.

Effects of rewatering on the physiology of plants

Recovery of physiological parameters by rewatering

Photosynthetic responses to stresses are very complex and these include the chemistry of restrictions, taking place at diverse spots of leaf cell at different time periods in relation to the growth of plants (Boughalleb et al., 2016b). The stress intensity, duration and progression rate influence the plant responses to salinity and water shortage (Nohong and Nompo, 2015). These factors are associated with acclimation responses under drought stress, thereby affecting the photosynthetic rate indirectly. Under the influence of salinity, acclimation responses also include an adjustment in ion-transport such as uptake and extrusion of ions. These reactions are eventually clue to refurbishment of cellular homeostasis, shows survival of plants under stress (Chaves et al., 2009). Moreover, the carbon balance of plants during a period of water-stress and afterward regaining may depend as much on the recovery of P_N (Flexas et al., 2006). Overall, the plant recovers 40 to 60% of maximum photosynthetic rate only after rewatering, when subjected to extreme water-stress, and recovery is continued through the next days, but maximum P_N is not recovered always (Sofa et al., 2004). The strong influence of severe water-stress on P_N and its recovery has been established by Miyashita et al. (2005), in kidney bean and has been recommended by (Gómez-del-Campo et al., 2015), for *Vitis vinifera L.* plants.

Moreover, the recovery phase after stress release (e.g., irrigation or rewatering), becomes a major part of general plant biological responses to water-stress period. Recovery of the photosynthetic capability of plants from severe water-stress, defines the future growth development and survival of plants. Recently, this area is gaining much attention (Ennahli and Earl, 2005; Gallé et al., 2007; Xing et al., 2018; Javed et al., 2018; Azeem et al., 2017a). There is a need for further studies in order to understand the physiological basis and mechanism of recovery from water-stress. A method to assess the restriction of photosynthetic processes during water-stress time scales and then recovery has been suggested by Grassi and Magnani (2005), who recorded the results by dividing the total limitation into 3-parts: stomatal closure, diffusion of mesophyll and carboxylation activity. These outcomes highlight the importance of mesophyll conductance during stress periods and for further research, it suggests an important involvement in the overall plants adaptation to drought-stress. Additional short-term experiments on water stress revealed a reduction of mesophyll conductance (Galmés et al., 2007), indicating a general trend of stress and afterwards exhibits high resistance during rewatering. However, Badger and Price (1994) and Gillon and Yakir (2000) suggested that CA activity helps for regulation of mesophyll conductance during stress and facilitating diffusion of CO_2 at cellular level, and shows recovery (Flexas et al., 2008). *Campomanesia adamantinum O. Berg*, a salt tolerate plant, subjected to water deficit condition and rewatering which is done on day 31 from the onset of suspension of irrigation. The S_g and T_R began to drop from the 23rd day to 31st -day and photosynthetic rate approached to zero as $0.285 \text{ l mol m}^{-2} \text{ s}^{-1}$. Therefore, WUE and Rubisco carboxylation activity are also reached to zero values. Subsequently, plants are rewatered to regain photosynthetic metabolism (Junglos et al., 2016). According to

Yousfi et al. (2016), there had been a small recovery after rewatering in some species of *Medicago laciniata L.* as a result of severe drought stress. During rewatering phase, the plants recovered their photosynthetic metabolism, with consequent increase rate of S_g , T_R and WUE (Fig. 2).

A small contribution is found in this aspect of study by Galle et al. (2009) in tobacco (*Nicotiana sylvestris*) and Flexas et al. (2009) for hybrid Richter-110 (*Vitis berlandieri* × *Vitis rupestris*), focusing on reduction of P_N under stress followed by rewatering to persuade recovery. In summary, the present literature strongly supports the important of rewatering and recovery of physiological parameters during rewatering as shown in Figures 2 and 3.

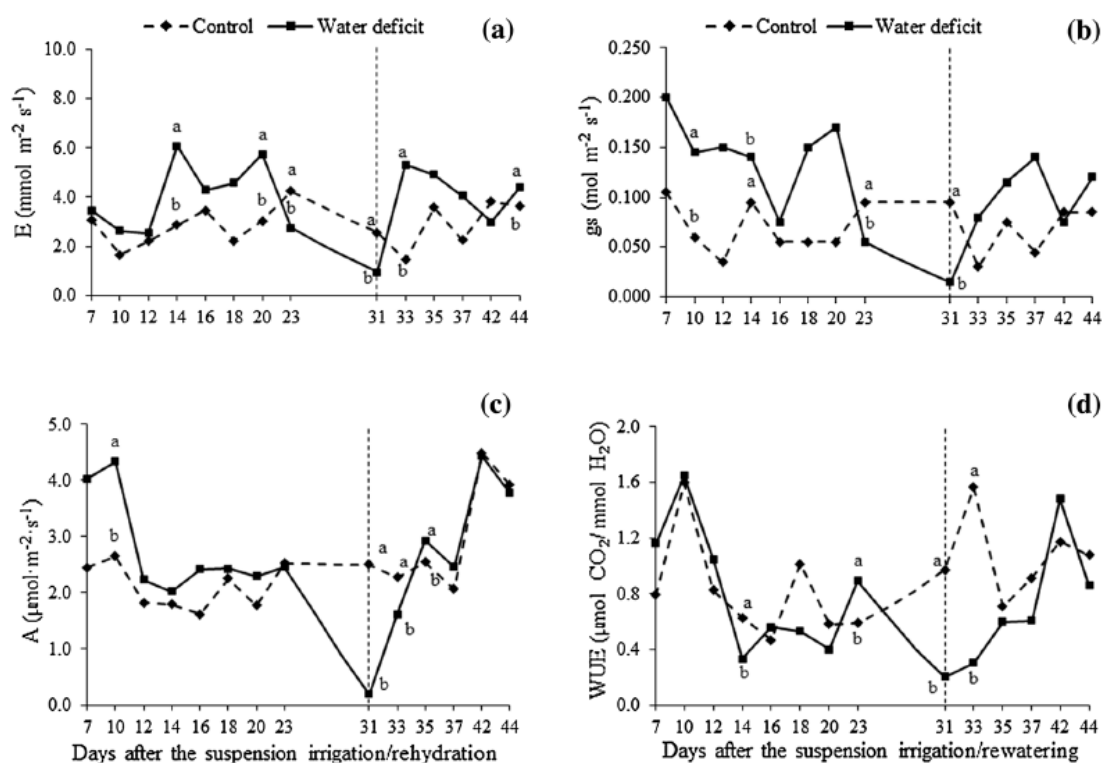


Figure 2. Transpiration ($TR = E$) (a), stomatal conductance ($S_g = gs$) (b), photosynthetic rate ($P_N = A$) (c), and water-use efficiency (WUE) (d) during different intervals when *Campomanesia adamantium* is grown in well-watered and water deficit condition (Junglos et al., 2016)

Dilution of salt water

Generally, plants exhibit different physiological responses when subjected to slight, moderate and high salt stress. Many works have been done by researchers to check the response of different crops by using saline water (Turhan et al., 2014; Al-Harbi et al., 2015; Rameshwaran et al., 2016; Zhang et al., 2016; Martinez et al., 2018; de Cássia Alves et al., 2018; El-Mogy et al., 2018; Rodriguez-Ortega et al., 2017). Rewatering facilitates a positive response for plant water status and plant growth development. Over the last few years, many researchers have addressed the reaction of photosynthesis to rewatering after water-stress, which highlights the influence of salt stress and subsequent rewatering with pure water on plants (Hura et al., 2006; Pérez-Pérez et al.,

2007; Luo et al., 2008; Gomes et al., 2008). But none of these studies reflect the dilution of salted water or rewatering with saline water. However, by doing so it is possible to utilize the saline water resources for agricultural activities.

Moderately, salt-tolerant crop can be irrigated by diluted saline water, when freshwater resources are limited. Diluted saline water becomes the readily available water for irrigation of plants. The order of dilution or re-watering is that the plants are suffering in high concentration of salts irrigated with moderate concentration of salts. In another sense, at threshold levels, the plant can be re-watered with diluted saline water (Javed et al., 2017). The regime is considered very important in plants to adopt the behavior of salt tolerance under drought stress environment, at which P_N is sustained and recovered throughout the phases of water-stress (Chartzoulakis et al., 2002b). Junglos et al. (2016) rewatered *Campomanesia adamantinum* O. Berg plants when photosynthetic rate approached to zero. Therefore, it is essential for plants to be re-watered with diluted saline water prior to their wilting stages instead of applying direct saline-water to crops.

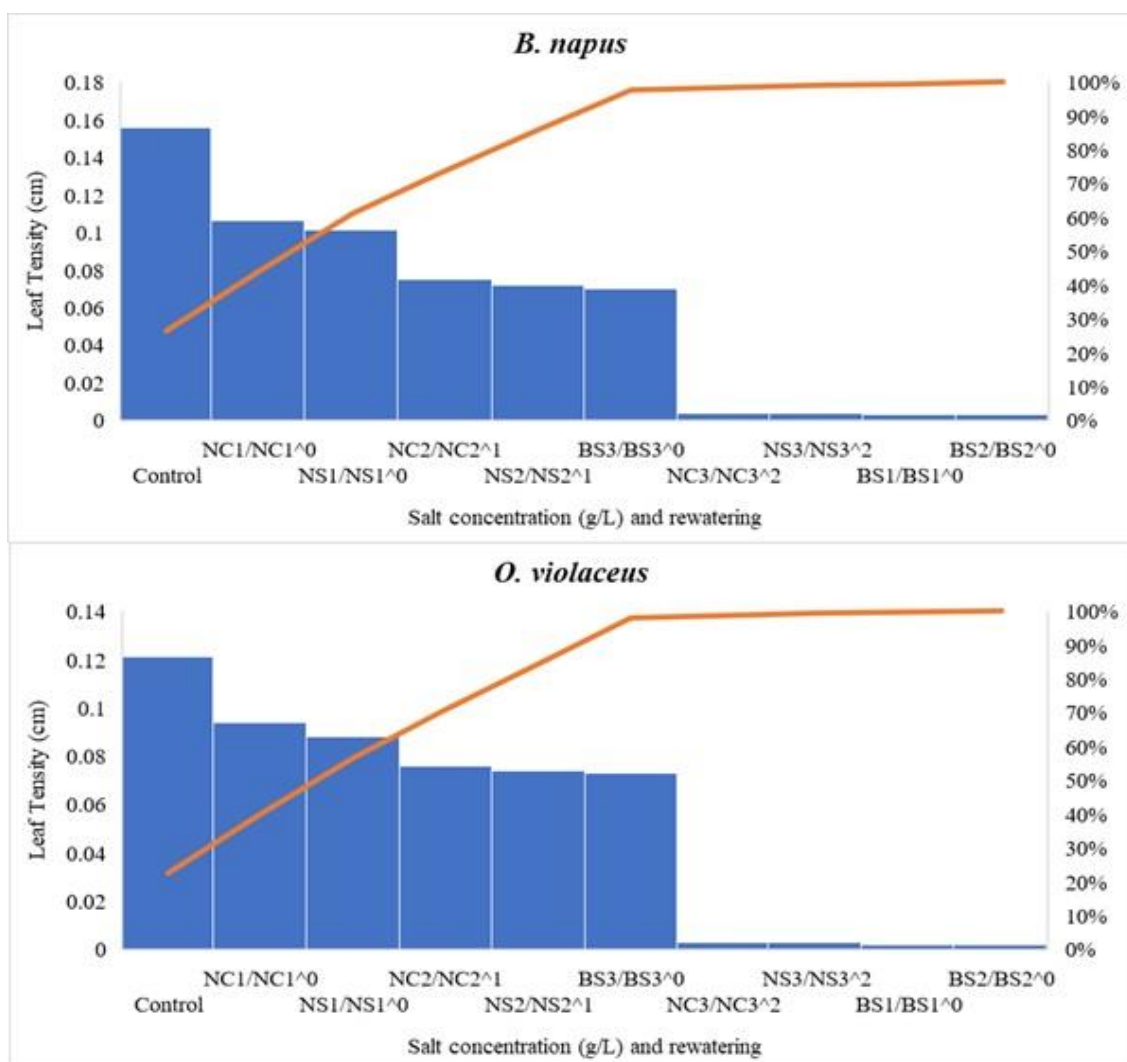


Figure 3. Effect of salt stress on leaf tensity of *Brassica napus* and *Orychophragmus violaceus* under salt stress conditions followed by recovery during re-watering (Javed et al., 2017)

This review thus suggested new insights in the agricultural field to design irrigation scheduling by considering the salt tolerant capability of crops as explained well in *Figure 4*.

Afterwards, irrigation water use efficiency can be ascertained through the application of precise irrigation quantity, based on the rewatering point. It would be an affirmative step, if implemented, to increase crop production in salt affected regions. It will aid in maintaining the stability between the irrigation amount and optimum crop water consumption and effective utilization of salt water, thereby reducing the everlasting demand fresh water resources for irrigation purposes.

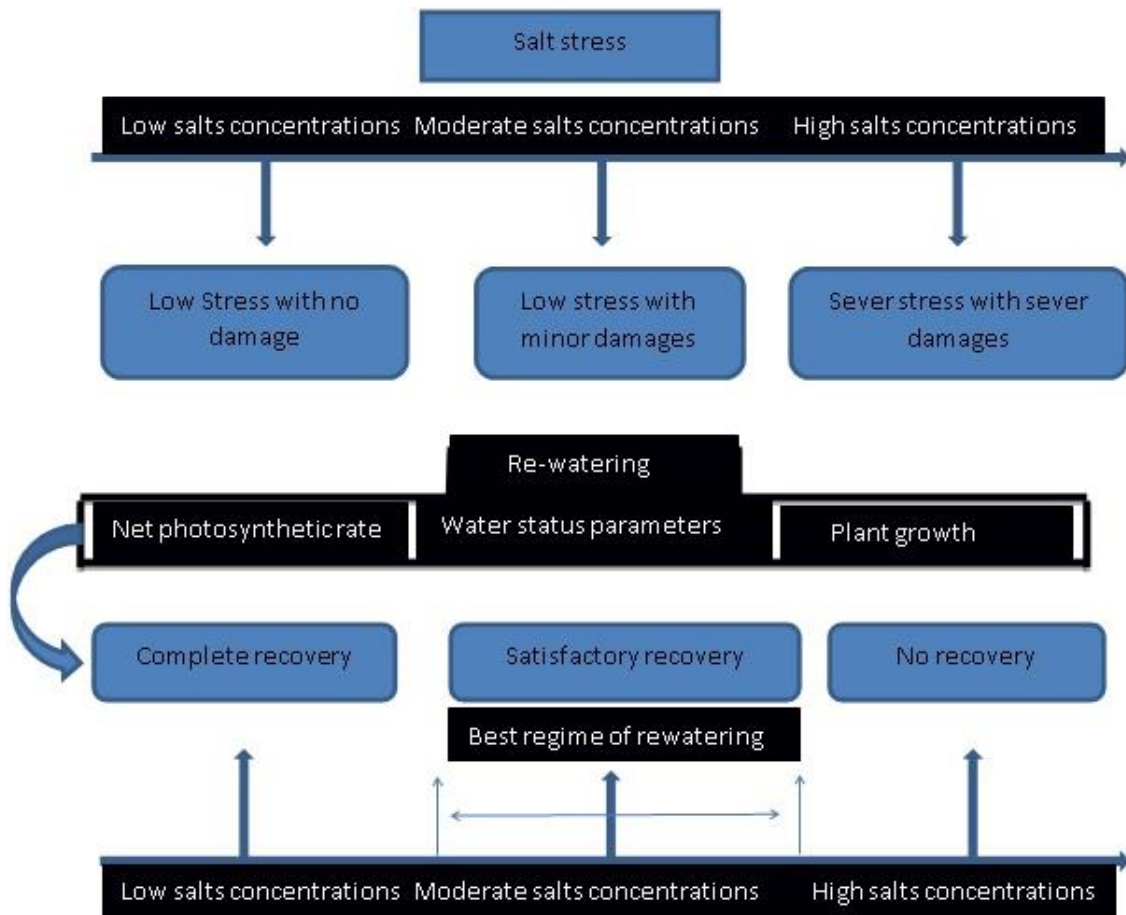


Figure 4. Irrigation scheduling by considering the salt tolerant capability of crops

Conclusion

This review briefly described the stress effects with respect to tolerance and physiological performances of plants. The review provides information for precise theoretical and practical irrigation based on physiological and electrophysiological characteristics. Efforts have been made to link the relative tolerance of several plant species to salt stress and subsequent rewatering with regard to toxicity under stress and their recoveries after rewatering. Present facts offer some strategies to counteract salt stress in crops through rewatering. Hence this review affirms the promising future of increasing crop production even under saline conditions. However, the vast majorities of research have focused on stress responses based on irrigation of plants. Plant

response to stresses and then rewatering with saline water is a good approach in the field of saline irrigation and is a boon for regions where fresh water resources are limited. Therefore, the effect of salinity in plant could be reduced by diluting the saline irrigation (re-watering) response to threshold growth and photosynthetic values. Application of dilution of saline irrigation could be helpful to save water resources, maintain crop productivity even in stressful environments and reduces irrigation cost. It is recommended based on findings of this review; short experiment in controlled environment can be done to determine the dilution point for re-watering of different crops before wilting. Afterwards, this information can be utilized for irrigation of open field crops with diluted water.

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