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Salt-induced regulation of photosynthetic capacity and ion accumulation in some genetically diverse cultivars of radish (*Raphanus sativus* L.)

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Summary

Salt-induced changes in growth, various gas exchange characteristics, and ion accumulation were examined during a greenhouse experiment on six radish (*Raphanus sativus* L.) cultivars i.e., Radish Red Neck, Radish Lal Pari, Radish Mino Japoni, Radish 40 Days, Mannu Early and Desi. Varying levels of salt (0, 80, and 160 mM NaCl) of the growth medium markedly decreased the shoot and root dry weights, relative water contents, osmotic potential, photosynthetic and transpiration rates, stomatal conductance, substomatal CO₂ concentration, C_i/C_a ratio, water use efficiency, leaf and root K⁺ and Ca²⁺, while increasing the leaf and root Na⁺ and Cl⁻ of all six radish cultivars. Of all cultivars, Mannu Early and Desi were higher in shoot and root dry weights than the other cultivars, and thus, they were ranked as relatively salt tolerant. However, none of the earlier mentioned physiological attributes was found to be an effective criterion in discriminating the six radish cultivars. Overall, the response of each cultivar to salt stress appraised using various physiological attributes was specific.

Introduction

It is now well established that high salt concentrations in water or soil adversely affect various biochemical and physiological processes leading to poor plant vigor and yield in most plant species (ASHRAF, 2004; MUNNS and TESTER, 2008). Salt-induced osmotic stress and ion toxicity are the major causes of plant growth reduction (ZHU, 2001; SAIRAM and TYAGI, 2004). A number of mechanisms involved in plant salt tolerance, ion homeostasis, and differential regulation of biochemical and physiological processes have gained a significant importance (ASHRAF, 2004; MUNNS, 2005; GENC et al., 2007).

Previously, it was found that growth suppression may be a non-specific effect of salts, depending more on the total concentration of soluble salts than on specific ions (MAAS and NIEMAN, 1978). It is well documented that the accumulation of Na⁺ and Cl⁻ ions in the leaves is the most important factor which causes considerable injury to ultra-structure of different organelles of plants subjected to salt stress (MARTINEZ-BARROSO and ALVAREZ, 1997). It is suggested that generally crop cultivars which show more tolerance to salt stress, accumulate Cl⁻ in their roots and as a whole prevent the negative effects of salt on plant growth (SAIED et al., 2003). Cellular K⁺/Na⁺ and Ca²⁺/Na⁺ ratios also can affect salt tolerance of plants to a varying extent (YASAR, 2007; YILDIZ et al., 2008).

Salt stress also adversely affects plant photosynthesis (DUBEY, 2005; ARFAN et al., 2007; NOREEN and ASHRAF, 2008). However, it is difficult to assess whether a reduced rate of photosynthesis is the cause of growth reduction, or merely the consequence of growth reduction (MUNNS and TESTER, 2008). For instance, salt-induced reduction in growth of barley (FRICKE et al., 2004) and maize (CRAMER and BOWMAN, 1991) has been due to rapid change in leaf expansion rate resulting into a buildup of unused

photosynthates in growing tissues (MUNNS, 1993; MUNNS et al., 2000). In view of PAUL and FOYER (2001) accumulation of unused photosynthates under saline conditions may generate feedback signals to down-regulate photosynthesis to compensate the reduced demand arising from growth inhibition. However, at high salt stress, excessive accumulation of salts in the cytoplasm or chloroplast of mesophyll cells inhibits photosynthetic enzymes thereby reducing the photosynthetic rate (MUNNS, 1993; DUBEY, 2005). The reduction in photosynthesis under salt stress can also be attributed to a decrease in stomatal closure because higher stomatal conductance is known to increase CO₂ diffusion into leaves thereby favoring higher photosynthetic efficiency (DOWNTON, 1977; SEEMANN and CRITCHLEY, 1985). During a greenhouse experiment on radish plants, salt stress (90 and 240 mM NaCl) considerably decreased the photosynthetic activity resulting in reduced plant growth, leaf area, chlorophyll contents and chlorophyll fluorescence (JAMIL et al., 2007).

Radish (*Raphanus sativus* L.), being a potential vegetable, is utilized in a variety of ways, e.g., fresh, pickled, dried, cooked as well as a fodder. It is an important source of medicinal foods and one of the most recalcitrant crop plants in nature (CURTIS, 2003). Generally, radish is categorized as moderately sensitive to salinity (MAAS and HOFFMAN, 1977), while SONNEVELD (1988) reported a low sensitivity of radish to salt stress. Despite of being a potential vegetable crop world-over, little is known about its mechanism of salt tolerance. Thus, the premier objectives of this study were to observe the effect of varying levels of salt on some key physiological processes such as photosynthetic capacity and mineral nutrient accumulation in six genetically diverse radish cultivars. It was also examined whether photosynthetic capacity and pattern of accumulation of nutrients could be used as effective selection criteria for salt tolerance in radish.

Materials and methods

To examine changes in growth, gas exchange characteristics, some water relation attributes and nutrient accumulation in six cultivars/lines of radish (*Raphanus sativus* L.) i.e., Radish Red Neck, Radish Lal Pari, Radish Mino Japoni, Radish 40 Days, Mannu Early and Desi, a greenhouse experiment was conducted at the Botanical Garden, University of Agriculture, Faisalabad. The seeds of all cultivars were obtained from the Ayub Agricultural Research Institute, Faisalabad, Pakistan. Five seeds of each cultivar were sown per plastic pot (23.5 cm diameter and 29 cm deep) filled with 10 kg dry river sand. The plants were thinned to two plants per pot after 14 d of growth. Three NaCl treatments (0, 80, and 160 mM) in Hoagland's nutrient solution were applied to three week-old plants. The NaCl concentration was increased step-wise in aliquots of 40 mM every day until the appropriate concentration attained. After 20 days of salt treatment, two plants from each pot were uprooted carefully and separated into shoots and roots. The plant samples were oven dried at 65 °C and dry weights recorded. Before harvesting the plants, the data for the following parameters were recorded:

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Leaf osmotic potential

One fully expanded youngest leaf from each plant was excised and frozen in a freezer below -20°C for more than seven days after which time the frozen leaf material was thawed and the sap extracted by pressing the material with a glass rod. The sap was used directly for the determination of osmotic potential in a vapor pressure osmometer (Vapro, 5520).

Relative water content (RWC)

Relative water content was determined following JONES and TURNER (1978) by using a leaf of uniform size from each replicate.

Gas exchange characteristics

To measure different gas exchange parameters such as net CO_2 assimilation rate (A), transpiration (E), stomatal conductance (g_s) and sub-stomatal CO_2 concentration (C_i), an infra-red gas analyzer (Analytical Development Company, Hoddesdon, England) was used. All measurements were made on a fully expanded youngest leaf of each plant from 10.00 to 12.00 h with the following specifications/adjustments of the leaf chamber: atmospheric pressure 99.9 kPa, water vapor pressure into the chamber ranged from 6.0 to 8.9 mbar, temperature of leaf ranged from 28.4 to 32.4°C , ambient temperature ranged from 22.4 to 27.9°C , molar flow of air per unit leaf area $403.3 \text{ mmol m}^{-2} \text{ s}^{-1}$, PAR at leaf surface was maximum up to $918 \mu\text{mol m}^{-2} \text{ s}^{-1}$, and ambient CO_2 concentration was 352 ppm.

Determination of mineral elements in plant tissues

The dried ground plant leaf or root material (0.1 g) was taken in a digestion flask and to this digestion flask, 1 mL of digestion mixture (0.42 g of Se and 14 g of $\text{LiSO}_4 \cdot 2\text{H}_2\text{O}$ to 350 mL of H_2O_2 , mixed

well and 420 mL of conc. H_2SO_4 were added slowly to it keeping it in an ice bath) was added and placed the flask on a hot plate. The temperature was increased gradually from 50°C to 200°C . When the mixture turned black, 0.5 mL of HClO_4 was added to the sample, and heated again until the material became colorless (ALLEN et al., 1986). The flasks were removed from the hot plate and cooled down. The solution was diluted up to 50 mL in a volumetric flask and filtered. The filtrate was used for the determination of K^+ , Ca^{2+} and Na^+ .

Statistical analysis

Analysis of variance of all parameters was computed using the MSTAT computer package (Mstat Development Team, 1989). Standard errors of means were also calculated to observe intra-mean variation.

Results

Salt stress markedly suppressed the shoot and root dry weights of all radish cultivars, though radish cultivars differed significantly in response to varying NaCl concentrations of the growth medium (Fig. 1). From the mean data, it is apparent that lines Mannu Early and Desi had greater shoot and root dry biomass than the other cultivars at all salt regimes.

Leaf osmotic potential in all radish cultivars significantly decreased ($P \leq 0.001$) with increase in NaCl concentration in the growth medium. Cultivar Desi followed by Radish Red Neck was the lowest in leaf osmotic potential of all radish cultivars at the highest salt regime, whereas Desi followed by Radish Mino Japanese was lower than the other cultivars at 80 mM NaCl.

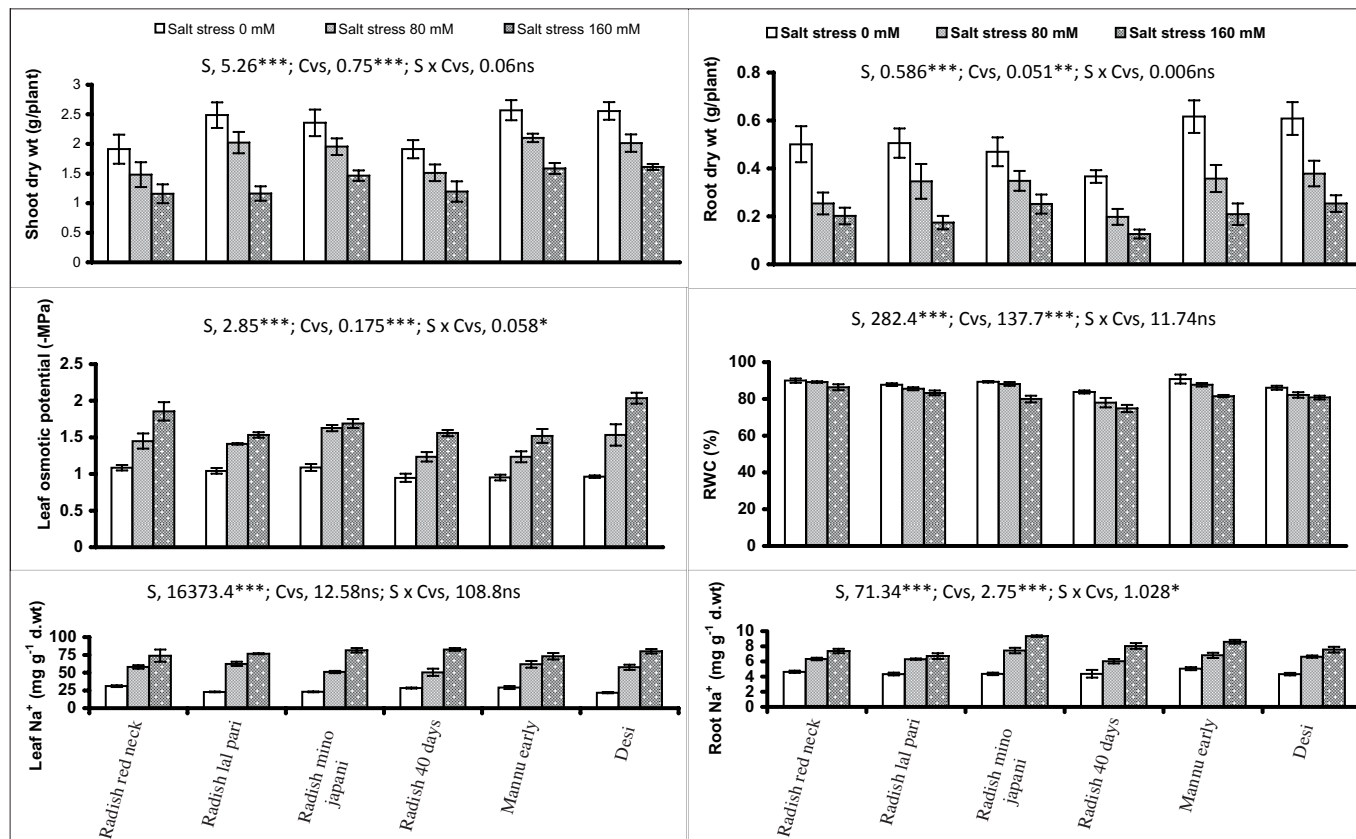


Fig. 1: Shoot and root dry weights, leaf osmotic potential, relative water contents and shoot and root Na^+ concentration of six radish (*Raphanus sativus* L.) cultivars subjected to different concentrations of NaCl (Means \pm S.E; $n = 4$). Values showing mean squares from analysis of variance of data for each variable. *, ** and *** significant at 0.05, 0.01 and 0.001, respectively; ns = non-significant; S = Salt stress; Cvs = cultivars.

Leaf relative water content (RWC) of all radish cultivars significantly decreased with increase in NaCl of the growth medium (Fig. 1). The cultivars also differed significantly in this water relation attribute. Leaf RWC was found to be highest in Radish Red Neck followed by Radish Lal Pari at the highest (160 mM) NaCl level (Fig. 1).

Addition of salt to the rooting medium caused a significant reduction in all gas exchange attributes (net CO₂ assimilation rate, transpiration rate, stomatal conductance, sub-stomatal CO₂, C_i/C_a ratio, water use efficiency) (Fig. 2) and the cultivars did not differ significantly in all these gas exchange attributes except in transpiration rate. However, Radish Lal Pari followed by Radish Red Neck and Radish Mino Japoni had greater transpiration rate than the other cultivars at the highest salt regime.

Na⁺ concentrations in the leaves and roots of the six radish cultivars increased significantly with increase in salt level of the rooting medium (Fig. 1). Cultivar Radish 40 Days had considerably higher leaf Na⁺ concentration than the other cultivars at the highest salt concentration. In contrast, root Na⁺ concentration was the highest in cv. Desi of all cultivars at the highest salt stress. While, at 120 mM NaCl, cvs. Desi and Mannu Early were higher in root Na⁺ as compared with the other cultivars.

Leaf and root Cl⁻ concentrations increased significantly in the six radish cultivars with the addition of NaCl to the growth medium, and the cultivars also differed significantly in these physiological attributes. Cultivars Radish Red Neck, Radish Mino Japoni and Desi had greater leaf Cl⁻ than the other cultivars at the highest salt regime, while root Cl⁻ was higher in Radish Red Neck and Radish 40 Days compared with the other cultivars at 120 mM NaCl (Fig. 3).

A marked reduction in K⁺ accumulation in the leaves and roots of the

six radish cultivars was observed due to imposition of salt stress to the growth medium, particularly at the highest salt regime (Fig. 3). A maximum leaf K⁺ was observed in Radish Lal Pari followed by Radish Mino Japoni and Desi at the highest salinity level, whereas the same was true for root K⁺ in Mannu Early and Desi (Fig. 3).

Leaf and root Ca²⁺ of the six radish cultivars decreased significantly with increase in salt level of the rooting medium (Fig. 3). The cultivars also differed significantly in accumulation of Ca²⁺ in the leaves or roots. Leaf Ca²⁺ was higher in Radish Red Neck and Radish Lal Pari compared with the other cultivars at 120 mM NaCl. However, cultivar Radish Red Neck followed by Radish Mino Japoni had greater accumulation of Ca²⁺ in the roots at the highest salt regime.

Discussion

In the present study, varying levels of salt caused a marked reduction in the shoot and root dry weights in the six radish cultivars. Salt-induced reduction in the radish cultivars is analogous to what has earlier been observed in a number of plant species including rice (ALAM et al., 2004), wheat (ARFAN et al., 2007; SHAHBAZ et al., 2008), spinach, cucumber and pepper (KAYA et al., 2001), sunflower (AKRAM et al., 2009; NOREEN et al., 2009), tomato (SATTI and AL-YAHYAI, 1995), cotton (LEIDI and SAIZ, 1997) etc. The present study also revealed considerable inter-cultivar variation in salt tolerance in the set of six genetically diverse cultivars of radish. Earlier, a great magnitude of inter-cultivar (intra-specific) variation has been observed in many crop plants, e.g., barley and wheat

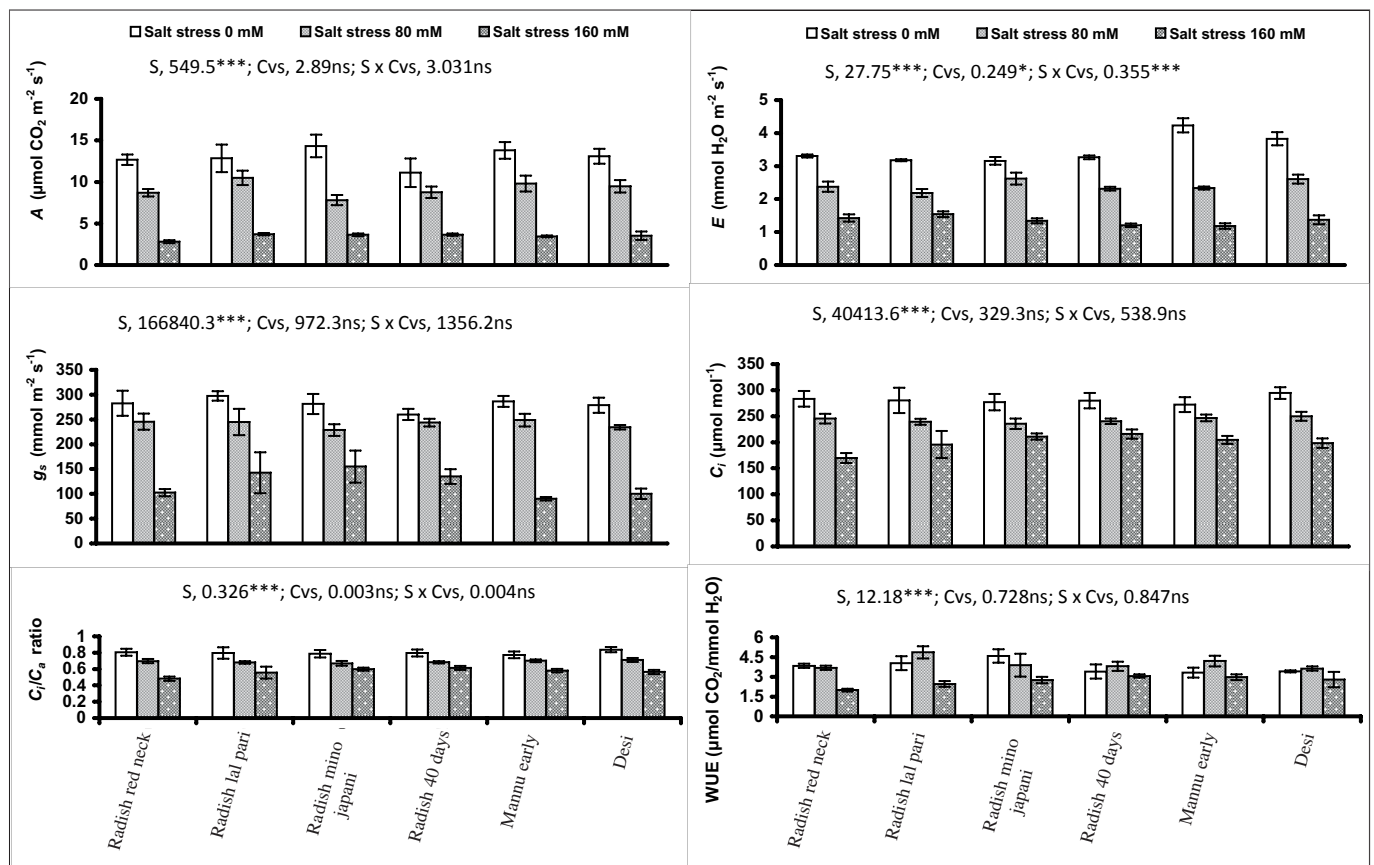


Fig. 2: Different gas exchange characteristics of six radish (*Raphanus sativus* L.) cultivars subjected to different concentrations of NaCl (Mean \pm S.E; n = 4). Values showing mean squares from analysis of variance of data for each variable. * and *** significant at 0.05 and 0.001, respectively; ns = non-significant; S = Salt stress; Cvs = cultivars.

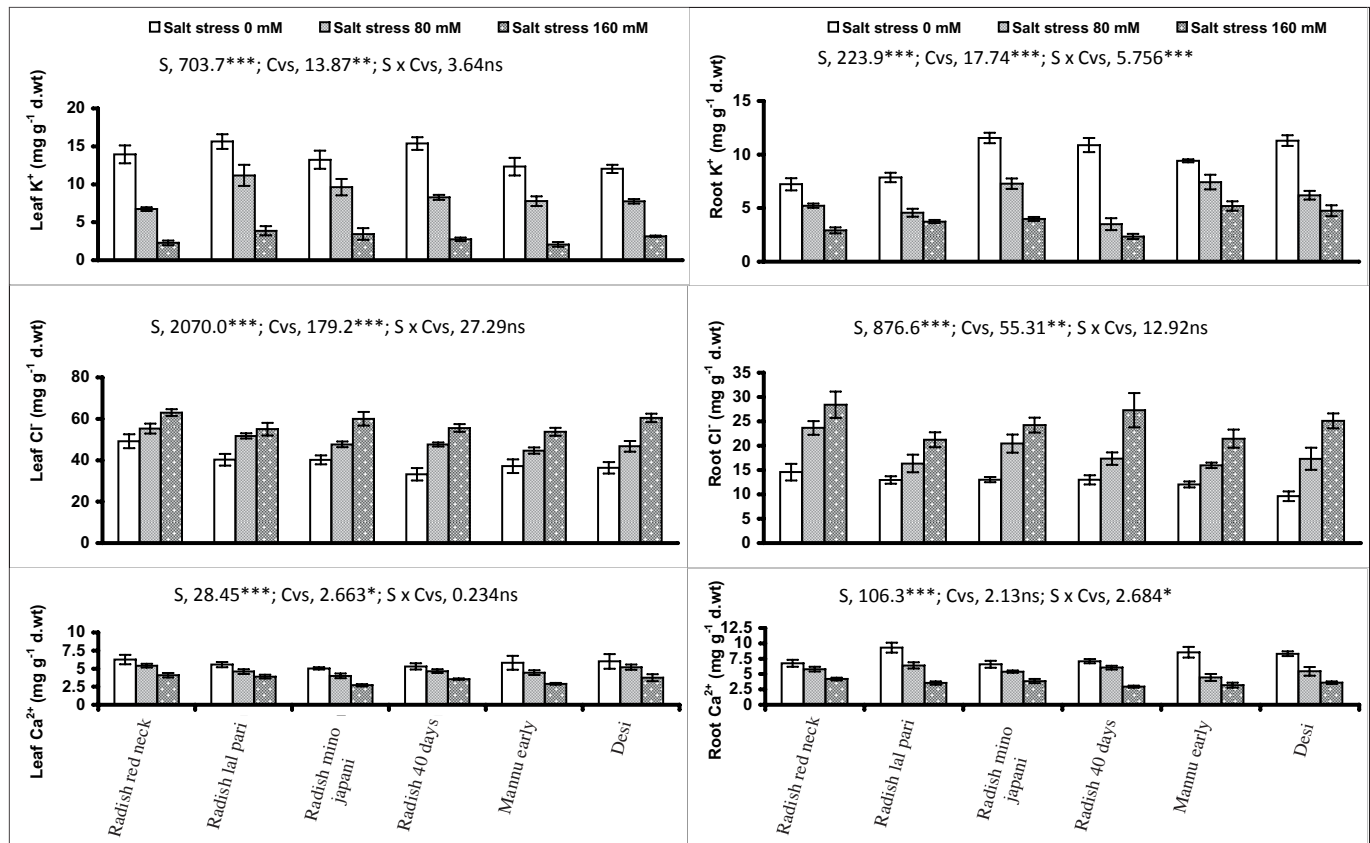


Fig. 3: Shoot and root K^+ , Cl^- and Ca^{2+} concentrations of six radish (*Raphanus sativus* L.) cultivars subjected to different concentrations of NaCl (Mean \pm S.E.; $n=4$). Values showing mean squares from analysis of variance of data for each variable. *, ** and *** significant at 0.05, 0.01 and 0.001, respectively; ns = non-significant; S = Salt stress; Cvs = cultivars.

(RICHARDS et al., 1987), rice (AKBAR and YABUNO, 1974), canola (ULFAT et al., 2007; ATHAR et al., 2009), and tomato (FOOLAD, 1996; PEREZ-ALFOCEA et al., 1996). The growth reduction in the radish cultivars might have been due to a limited supply of metabolites to young growing tissues, and regulation of a number of biochemical or physiological processes including photosynthesis, leaf water relations and nutrient imbalance (MAAS and NIEMAN, 1978; MUNNS and JAMES, 2003; ASHRAF, 2004; JUAN et al., 2005).

In the present study, photosynthetic and transpiration rates, stomatal conductance (g_s), sub-stomatal CO_2 (C_i), and relative intercellular CO_2 (C_i/C_a) of all the radish cultivars were reduced linearly with increase in salt concentration of the growth medium. The reduction in photosynthesis under salinity stress can also be attributed to a decrease in stomatal closure, because higher stomatal conductance is known to increase CO_2 diffusion into leaves thereby favoring higher photosynthetic activity (SEEMANN and CRITCHLEY, 1985; DUBEY, 2005). In the present study, net CO_2 assimilation rate (A) had a positive relationship with all these gas exchange variables (A vs g_s or C_i or C_i/C_a or E , $r = 0.740^{***}$; 0.666^{***} ; 0.665^{***} ; 0.794^{***} ; and g_s vs C_i $r = 0.681^{***}$). These results indicate that salt-induced reduction in growth in all six radish cultivars was due to decline in photosynthesis, and decline in net photosynthesis under salt stress occurred principally due to stomatal closure, which is in agreement with a number of earlier studies (BRUGNOLI and BJORKMAN, 1992; DIONISIO-SESE and TOBITA, 1998; RAZA et al., 2006; ULFAT et al., 2007). However, it was not possible to discriminate among the radish cultivars on the basis of these gas exchange attributes. For instance, salt tolerant cultivars cvs. Mannu Early and Desi were lower in g_s compared to the salt sensitive cultivars (Fig. 1), but they were similar in photosynthetic capacity. These results support the argument that

g_s is not always associated with A . This has earlier been observed in different crops such as sunflower (RAWSON and CONSTABLE, 1980), and *Andropogon glomeratus* (BOWMAN, 1987). These findings suggest that cultivar variation for salt tolerance in radish was not due to differences in stomatal conductance and thus it cannot be used as an effective selection criterion for salt tolerance in radish. In view of some earlier reports it is evident that a positive relationship between photosynthetic rate and crop growth or yield under saline conditions exists in different crops such as *Spinacia oleracea* (ROBINSON et al., 1983), *Asparagus officinalis* (FAVILLE et al., 1999), six *Brassica* diploid and amphiploid species (NAZIR et al., 2001; ASHRAF, 2001), wheat (RAZA et al., 2006), and 34 canola cultivars (ULFAT et al., 2007). All these reports suggest that the rate of photosynthesis can be used as a selection criterion for salt tolerance, particularly where a close relationship between photosynthesis and growth under salt stress is found (QASIM et al., 2003; ASHRAF, 2004).

If we draw relationships between shoot dry biomass and net CO_2 assimilation rate of six radish cultivars differing in salt tolerance, growth in terms of dry biomass of all cultivars was positively associated with net CO_2 assimilation rate (A vs shoot dry weight $r = 0.591^{***}$). However, such a relationship was not found when individual radish cultivars differing in salt tolerance were compared with respect to their rate of photosynthesis. For example, salt tolerant cvs. Mannu Early and Desi higher in growth were similar to the salt sensitive Radish Lal Pari in net CO_2 assimilation rate, at different salt concentrations of the growth medium. These results are in close conformity with some earlier findings in different crops in which a non-significant relationship between growth and photosynthetic rate was observed such as in *Diplachne fusca* (MYERS et al., 1990), *Trifolium repens* (ROGERS and NOBLE, 1992), and spring wheat

(HAWKINS and LEWIS, 1993; ASHRAF and O'LEARY, 1996). Thus, these results show that photosynthetic rate cannot be used as a potential selection criterion for salt tolerance in radish.

In the present study, leaf osmotic potential or RWC was also not associated with the growth of six radish cultivars. These results are supported by the conclusive statement of MUNNS (1993) in a comprehensive review that relationship between leaf turgor and salt tolerance occurs occasionally i.e. maintenance of higher plant water status is not associated with salt tolerance. Thus, the differential growth of radish cultivars under salt stress may have been due to factors other than water relations.

The most prominent effect of salinity on plant growth is the excessive accumulation of Na⁺ and Cl⁻ in the leaves resulting in ionic imbalance, specific ion effects, and nutrient-deficiency symptoms in plants (GRATTAN and GRIEVE, 1999; ZHANG and BLUMWALD, 2001; MUNNS, 2002; ASHRAF, 2004). Thus, it is imperative to assess pattern of ion accumulation of toxic ions in different plant parts of a crop species to understand as to whether the species uses partial exclusion or inclusion mechanism for tolerating toxic ions present in its growth medium. In the present study, the radish cultivars differed significantly in accumulation of Na⁺ K⁺, Ca²⁺ and Cl⁻ in the leaves and roots. For example, the relatively salt tolerant cvs. Mannu Early and Desi accumulated relatively higher concentrations of Na⁺ in their roots thereby checking the uptake of this toxic ion to the shoot. Such kind of mechanism has already been observed in different crops such as *Hordeum vulgare* (CARDEN et al., 2003), tomato (FOOLAD, 1996), wheat (WYN JONES et al., 1984; MUNNS and JAMES, 2003), and *Trifolium alexandrinum* (ASHRAF et al., 1986).

Overall, the decline in the growth of all six radish cultivars examined in the present study was due to reduction in photosynthetic capacity and ion accumulation. However, a positive correlation was observed between shoot dry weight and photosynthetic rate as well as reduction in photosynthesis was found to be closely associated with decreased stomatal conductance. However, none of the physiological attributes determined in the present study was found to be effective in discriminating the radish cultivars for salt tolerance.

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