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European Journal of Agronomy 16 (2002) 197–206

European Journal of Agronomy

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The effects of elevated carbon dioxide on static and dynamic indices for tomato salt tolerance

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Received 18 April 2001; received in revised form 3 August 2001; accepted 23 August 2001

Abstract

Although there is consensus that water use efficiency increases at elevated concentrations of CO_2, there are few studies on the interacting effects of elevated CO_2 on plant salt tolerance. The objectives of this study were, (1) to determine the effect of ambient and twice ambient concentrations of CO_2 on tomato (*Lycopersicon esculentum* Mill.) responses to salinity; (2) to compare the salt tolerance threshold values based on the classic root zone salinity [J. Irrig. Div. ASCE 103, (1977) 115], or ion flux to the shoot, a measure recently defined as Salinity Stress Index (SSI) by Dalton et al. [Plant Soil 192 (1997) 307; Plant Soil 219 (2000) 1; Plant Soil 229 (2001) 189]. For all salinities, the water use of the twice ambient CO_2 treatment was significantly reduced. The effect of twice ambient CO_2 was to increase the root zone salinity threshold value from 32 to 51 mmol dm^{-3} Cl. The threshold SSI value of 1.05 mmol Cl per g shoot DW for the twice ambient CO_2 treatment was almost identical to that of the ambient treatment and to those previously obtained when plant growth was modulated by root temperature ($SSI = 1.19$ and 1.10 at 25 and 18 °C, respectively [Plant Soil 192 (1997) 307]) and photosynthetic photon flux density (PPFD) (($SSI = 0.97$ and 1.10 at 400 and 600 μmol m^{-2} s^{-1} PPFD respectively [Plant Soil 229 (2001) 189]). The twice ambient CO_2 treatment showed a slightly lower root/shoot ratio (0.138 ± 0.001) than the ambient CO_2 treatment (0.156 ± 0.014). Consistent with the predictions of the SSI, leaf chloride per plant and leaf chloride concentration showed significant reduction for the twice ambient CO_2 treatment which follows from the supposition that water and salt uptake are linked. Based on the SSI, it was shown that the intrinsic salt tolerance of tomato is invariant to an increase in atmospheric CO_2 as has been previously shown for root temperature and solar radiation, while at the same time, the root zone salinity threshold value is dependent on environmental factors. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: *Lycopersicon esculentum* Mill.; Salinity; CO_2; Water use efficiency

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Abbreviations: SSI, salinity stress index; WUE, water use efficiency.

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PII: S1161-0301(01)00128-9

1. Introduction

Agriculturally important plants seldom are grown in their optimum environment. The main environmental factors responsible for diminished yields are drought, temperature and salinity stress (Boyer, 1982). Understanding the possible effects of global climate change on agricultural production is an important concern for maintaining the future food supply. In particular, the anticipation of increasing concentrations of atmospheric carbon dioxide has elicited many studies on whole plant response to elevated levels of CO_2. For unstressed conditions, water use is decreased while growth increases in most C3 plants (Munns et al., 1999). There is generally an increase in starch accumulation in leaves, which is manifested by greater leaf area and leaf thickness (Acock and Allen, 1985). All plants increase the biomass of all yield components (Rogers et al., 1992; Idso, 1997) in response to elevated CO_2. In terms of leaf gas exchanges, a variable response has been documented (Kimball et al., 1997; Dahlman et al., 1985). The evaluation of the effects of elevated CO_2 on plant growth under salinity stress is far more limited than under non-stressed conditions, yet it is under stress that CO_2 effects may be most significant. Schwarz and Gale (1984) found that four species of C3 and C4 plants grown at elevated CO_2 and subjected to salinity showed an increase in relative growth compared with non-salinized controls and that the shoot responded more to elevated CO_2 than the roots. CO_2 supplementation appeared to increase plant growth at low levels of salinity. Bowman and Strain (1987) studied the effect of elevated CO_2 on a non-halophyte C4 plant (*Andropogon glomeratus*) at 100 mmol l^{-1} NaCl and found that biomass and leaf area increased in the salt stressed plants but growth decreased in non-salt stressed plants. There was a decrease in stomatal conductance with increasing salinity stress resulting in higher water use efficiency.

Since plant water use is generally reduced at elevated CO_2 concentrations, Ball and Munns (1992) reasoned that if water and salt uptake are coupled, then reduced transpiration should result in reduced rates of salt accumulation in the leaves. They found that maintenance of stable salt concentrations in plant tissues implied a two-way communication between roots and shoots, which controls salt balance to adjust for environmental factors affecting the availability of water and ions to the roots. Consequently, to maintain similar ion concentrations with lower water use at elevated CO_2, the concentration of ions in the xylem fluid must increase, as was experimentally observed for barley and mangroves (Munns, 1985; Ball, 1988).

One such regulatory mechanism that also predicts a nonlinear relation between xylem solution concentration and transpiration rate has been described by Dalton et al. (1975) which is based on the coupling of water and salt uptake by plants. In order to incorporate the effects of growth, a dynamic salinity stress index, SSI, was proposed that integrates environmental factors that simultaneously affect growth and salt load to the shoot (Dalton et al., 1997). The model proposed by Dalton et al. (1997, 2000, 2001) show that the order of magnitude of total salt accumulation depends on more than just the magnitude of root zone salinity. It also depends on environmental parameters that simultaneously affect water use and growth, root extent and temperature dependent bio-physical transport parameters for water and salt (Dalton and Poss, 1989). Independent of any conceptual model for salt accumulation in the shoot, the SSI can also be obtained by simply measuring the total salt accumulation in the shoot relative to biomass production over the growing period.

Based on the functional definition of the SSI, it is predicted that if growth is modulated such that the plant reduces water use and increases shoot biomass, as is the case with elevated CO_2, it will tend to reduce the SSI. Therefore, the plant increases its apparent salt tolerance by being able to withstand a higher root zone salinity. A limited number of reports supports this hypothesis with respect to the effects of elevated CO_2 concentration but the available data are only partially conclusive with respect to its effect on plant salt tolerance.

The historical analytic basis for determining plant salt tolerance is based on plant response functions obtained by correlating yield with root zone salinity (Maas and Hoffman, 1977). This is done by using a piece-wise linear regression (threshold-slope model) of experimental data relating yields to root zone salinity. Accordingly, yields remain constant with increasing root zone salinity until a critical threshold value is reached. Above the threshold value, yields are reduced at a crop specific rate proportional to increases in root zone salinity. The threshold values of root zone salinity are measured in terms of salt concentration, osmotic potential or electrical conductivity of the soil water, and are used to rank salt tolerance among species and cultivars. There are no studies of the interactive effects of salinity and CO_2 on plant response functions based on either root zone salinity or SSI.

The purpose of this investigation was to determine the effect of increasing atmospheric CO_2 on tomato (*Lycopersicon esculentum* Mill.) plant response functions to salinity in terms of root zone salinity and SSI tolerance thresholds, water use efficiency and root–shoot ratio.

2. Materials and methods

2.1. Growth conditions

Plants were grown in an environmental chamber in continuously aerated saline base nutrient solution (BNS). The BNS (in mol m^{-3}) was composed of 2.5 $Ca(NO_3)_2$, 3.0 KNO_3, 1.5 $MgSO_4$, 1.7×10^{-1} K_2PO_4, 5.0×10^{-2} Fe (as sodium ferric diethylenetriamine pentaacetate), 2.3×10^{-2} H_3BO_3, 4.8×10^{-3} $MnSO_4$, 4.0×10^{-4} $ZnSO_4$, 2×10^{-4} $CuSO_4$, 2.0×10^{-4} H_2MoO_4. The temperature in the growth chamber was regulated at 25 °C. The photosynthetic photon flux density (PPFD) at the top of the canopy was 450 μmol m^{-2} s^{-1}. The light cycle was set at 12-h light:12-h dark with a 1-h linear ramp to reach maximum light intensity and darkness photoperiods.

2.2. Treatments

The experiment consisted of measuring the vegetative yields of tomato, at 14 levels of salinity, with two replications. Concentrations of atmospheric CO_2 were either 400 or 900 μmol mol^{-1} (hereafter ambient and twice-ambient, respectively). The experiments were performed serially in the same growth chamber, first at ambient CO_2 and then at elevated CO_2. Tomato seeds (cultivar Heinz 1350) were sown in vermiculite and kept moist until the 8-day-old seedlings were transplanted into temporary BNS pots at ambient temperature in a growth chamber. Sixteen days after germination, 28 plantlets were transferred individually in 10 l plastic containers and arranged on the growth chamber bench in two blocks of 14 plantlets each. The containers were supplied with snap-lids having a central hole through which plants were allowed to grow. This system was designed to minimize water loss by evaporation. Within each block, salinity treatments were randomly imposed. CO_2 was introduced into the growth chamber with over-head manifolds. Mixing occurred within the air circulation system of the growth chamber. The elevated CO_2 concentration was maintained at 900 μmol mol^{-1} by adjusting a flow valve until steady state conditions were achieved as measured by a LI-6200 infra-red gas analyzer (LI-COR, Lincoln, Nebraska, USA). Salinization was accomplished as described previously (Dalton et al., 1997), by adding equal increments of NaCl, $CaCl_2$ (2, 1 molar basis) over a 5-day period to decrease the osmotic potentials (OP) of the BNS to approximately 0, −0.03, −0.07, −0.10, −0.13, −0.17, −0.20, −0.23, −0.27, −0.30, −0.33, −0.37, −0.40, and −0.50 MPa.

2.3. Measurements

The water loss from each 10 l bucket (evapotranspiration) was replenished daily. Transpiration was assessed as the difference between the evapotranspiration and the average water loss from four buckets (without plants) randomly placed on the growth chamber bench. The specific water use was calculated as the ratio between transpiration and plant leaf area. Plants were harvested 25 days after maximum salinization. Fresh and dry weights of shoot and root where measured. The leaf area was measured using a leaf area meter (LI-COR, Lincoln, Nebraska, USA). Since chloride was the dominant salinizing ion, Cl^- was used as a measure of the total salt flux to the shoot. The total chloride load to the shoot was obtained by measuring shoot chloride concentration in the leaves and stem. Chloride determinations were made on dilute acetic acid and nitric acid extracts of leaves and stems by coulometric–amperometric titration (Cotlove, 1963). Total chloride transport to the shoot, in moles, was then calculated as the product of chloride concentration on a dry weight basis and total shoot dry weight.

2.4. Calculation of the SSI

The SSI was calculated as the total shoot chloride [mmol], without regard to partitioning, relative to total shoot biomass [g]. A detailed discussion of the basis of this index and its analytic definition is developed in a previous set of papers (Dalton et al., 1997, 2000). Briefly:

$$\mathrm{SSI} = \frac{\int A_r(t) J_s(t) \mathrm{d}t}{\int G_s(t) \mathrm{d}t} \quad (1)$$

where:

$$\int A_r(t) J_s(t) \mathrm{d}t = \text{moles solute to shoot} \quad (2)$$

$$\int G_s(t) \mathrm{d}t = \text{shoot biomass} \quad (3)$$

For analytic simulations, the integrals are to be evaluated over the growing period, t, where $A_r(t)$, is the root surface area development rate, [$m^2\ s^{-1}$]; $J_s(t)$ is the time dependent solute flux to the root, [$mol\ s^{-1}\ m^{-2}$]; $G_s(t)$ is the time dependent biomass production of the shoot, [$g\ s^{-1}$].

Dalton et al. (1975), Dalton and Gardner (1978) developed an analytic formulation for J_s based on the concept of coupled flow of salt and water across plant root membranes. G_s is a growth rate function measured on a mass basis. Under ideal environmental conditions, the unstressed value of G_s is limited only by genetic constraints and represents the maximum genetic potential for growth of the species or cultivar in any given environment.

3. Data analysis

3.1. Curve fitting

Plant response functions were obtained by using two methods of analysis that relate yield to the independent variables, root zone salinity and dynamic SSI. A locally weighted least squares technique for nonparametric curve fitting routine, ‘lowess’, was used (software provided by Axum TriMetrix, Seattle, WA, 1995). The ‘lowess’ method fits a smooth curve to a scatter plot of the associated data. Compared with the forced parametric regressions, this method is capable of giving a more realistic fit of the data (Cleveland, 1993; Dalton et al., 2001) and is useful for detecting ‘anomalous’ trends that can otherwise be overlooked.

3.2. Statistical analysis

For statistical inference a parametric non-linear least squares method was used. The parametric model was a piece-wise linear function, (Maas and Hoffman, 1977):

$$Y = Y_m - s(x - xT) \qquad \text{for } x > xT$$

$$Y = Y_m \quad \text{for } x < xT$$

where Y, Y_m, s, x, xT are the yield, maximum yield, slope, correlating index (root zone salinity or dynamic index) and threshold value of the correlating indices respectively. The non-linear least squares program, NLIN, from SAS was used for parametric analysis.

4. Results

Both parametric and nonparametric analyses of dry and fresh weight yield data show significant CO_2–salinity interactions. The linear-piecewise parametric analysis is shown only for dry weight yield in order to illustrate the similarity between nonparametric and parametric analyses of the resulting plant response functions (Fig. 1a and b). In this example, the nonparametric analysis of the fresh weight data illustrates the ability of the model to deviate from the strict threshold slope model while indicating the same threshold. The effect of twice ambient concentration of CO_2 was to increase the threshold value of root zone salinity from about 32 to 51 mmol dm^{-3} Cl (arrows) for both fresh and dry weight. Plant dry weight did not significantly change in presence of elevated CO_2, possibly because of a growth-limiting non-saturating light level. However, plant fresh weight for the elevated CO_2 treatment was generally lower at root zone salinities below the threshold value.

For all salinities, the total water use per plant of the twice ambient CO_2 treatment was significantly reduced (Fig. 2a). Even though the shoot biomass was not different for the two CO_2 treatments (Fig. 1), water use decreased by half for the twice ambient treatment (Fig. 2a), indicating a greater water use efficiency. A range of threshold values for water use was observed that approximately correspond to the root zone salinity threshold value for each treatment. The effect of CO_2 on transpiration may be judged more effectively by comparing the water use per unit leaf area (Fig. 2b). The water use per leaf area for the twice ambient CO_2 treatment is significantly smaller than for the ambient CO_2 treatment. Both curves show a rapid decrease in water use with salinity up to about 60 mmol dm^{-3} Cl and then remain relatively constant.

Water use efficiency (WUE, biomass per unit water use) was higher at elevated than at ambient CO_2 (Fig. 3). There was no effect of root zone salinity on WUE at ambient CO_2 treatment but WUE at twice ambient CO_2 showed a gradual

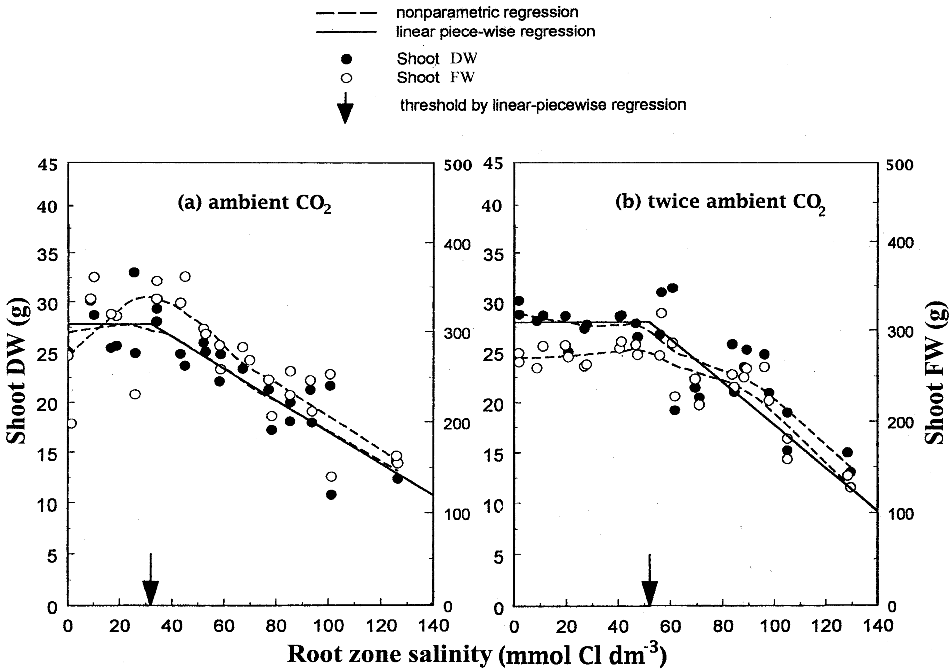

Fig. 1. (a) Tomato dry and fresh weight yield as a function of root zone salinity at ambient CO_2 concentration. (b) Tomato dry and fresh weight yield as a function of root zone salinity at twice ambient CO_2 concentration.

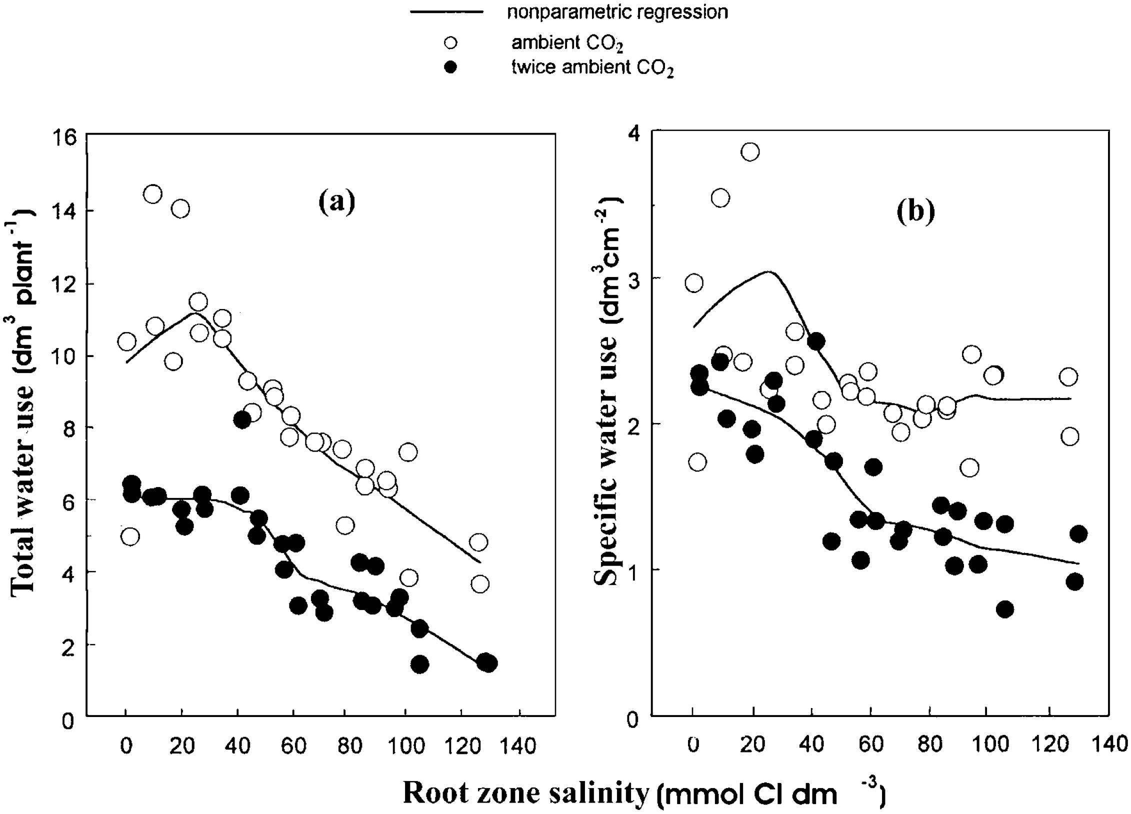

Fig. 2. (a) Total water use in tomato (through harvest for each plant) as a function of root zone salinity for ambient and twice ambient CO_2 concentrations. (b) Tomato specific water use as a function of root zone salinity for ambient and twice ambient CO_2 concentrations.

increase above the root zone salinity threshold value. At low salinity stress, WUE for the twice ambient treatment was more than double that of the ambient treatment. It then gradually increased to more than three times that of the ambient CO_2 treatment at the higher salinity stress values.

The root–shoot ratio for both CO_2 treatments did not seem to be significantly dependent on root zone salinity (Fig. 4). However, the twice ambient CO_2 treatment showed a statistically significant lower root–shoot ratio, 0.138 ± 0.001, than the ambient CO_2 treatment, 0.156 ± 0.014.

The lowess nonparametric analyses of plant response functions based on the dynamic salinity stress index, SSI, are shown in Fig. 5a and b. For the twice ambient treatment (Fig. 5b) there is a sharp discontinuity in the plant response function which delimits an SSI threshold value of 1.05 mmol Cl g^{-1}. The variability of the data set for the ambient CO_2 treatment at low levels of salinity (Fig. 5a) results in a more diffuse threshold region as indicated by cross hatching. Notwithstanding this variability, an SSI threshold value around 1.0 mmol Cl g^{-1} can be recognized which is not unlike the SSI thresholds identified previously (Dalton and Poss 1989; Dalton et al., 1997, 2000, 2001). These results corroborate the stability of the SSI under variable environmental conditions and its use as an index for evaluating the intrinsic plant salt tolerance properties.

Fig. 6a and b show the total leaf chloride accumulation (per plant) and leaf chloride concentration, respectively, for the two CO_2 treatments as a function of root zone salinity. In all cases, leaf chloride and leaf chloride concentration showed significant reduction for the twice

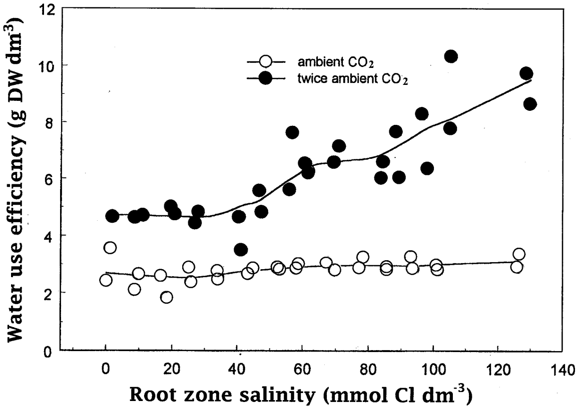

Fig. 3. Water use efficiency in tomato as a function of root zone salinity for ambient and twice ambient CO_2 concentrations.

ambient CO_2 treatment which follows from the supposition that water and salt uptake are coupled.

5. Discussion

5.1. Elevated atmospheric CO_2 and salinity tolerance

A twice ambient concentration of CO_2 caused a 38% increase in the root zone salinity tolerance threshold. The ameliorating effect of elevated CO_2 on plant response in saline environments is in agreement with the general observations of Schwarz and Gale (1984), Bowman and Strain (1987) and it appears to indicate that tomato could expand its range of salt tolerance and grow, at least during the vegetative phase, at elevated root zone salinity (Fig. 1). In contrast, the SSI threshold was very similar at the two CO_2 levels tested (Fig. 5) and it was almost identical to those previously obtained when plant growth was modulated by root temperature (Dalton et al., 1997, 2000) and photon flux density (Dalton et al., 2001). Since the SSI is a measure of the internal salt status of the shoot, then it follows that intrinsic metabolic pathways responsible for the onset of yield decline are likely to be independent of the environment. This is to be contrasted with the observation that plant salt tolerance, as defined by root-zone salinity, are heavily dependent on environment. However, when the SSI exceeds its threshold value, the rate of yield (growth) decline is greater for the twice ambient CO_2 treatment than for the ambient CO_2 treatment (Fig. 5b). In this situation, physiological mechanisms responsible for growth that resides in the shoot become more sensitive to salt at the elevated concentrations of CO_2. This association may provide insights to important salt sensitive metabolic pathways that govern growth and become more sensitive at elevated concentrations of CO_2.

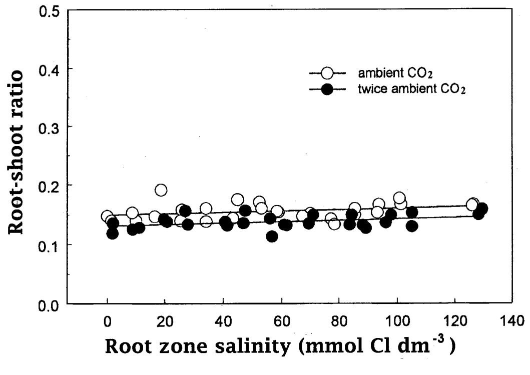

Fig. 4. Tomato root–shoot ratio as a function of root zone salinity for ambient and twice ambient CO_2 concentrations.

5.2. Effects of atmospheric CO_2 on water use and growth

The interaction between transpiration, growth and salinity tolerance at high atmospheric CO_2 has been extensively discussed (Munns et al., 1999). It is recognized that this is a complex and not well-understood relationship because higher CO_2 simultaneously affects both plant growth and salinity tolerance by increasing the carbon supply and by reducing the transpiration rate (Sultana et al., 1999; Jarvis et al., 1999). As shown for tomato, the decreased transpiration reduces/delays the salt load to the shoot and consequently the onset of yield reductions. In addition, we found that water use did not proportionally decrease with increasing root zone salinity (Fig. 2b). This result indicates that, in tomato, at Cl concentrations >60 mmol l^{-1}, the total water use is

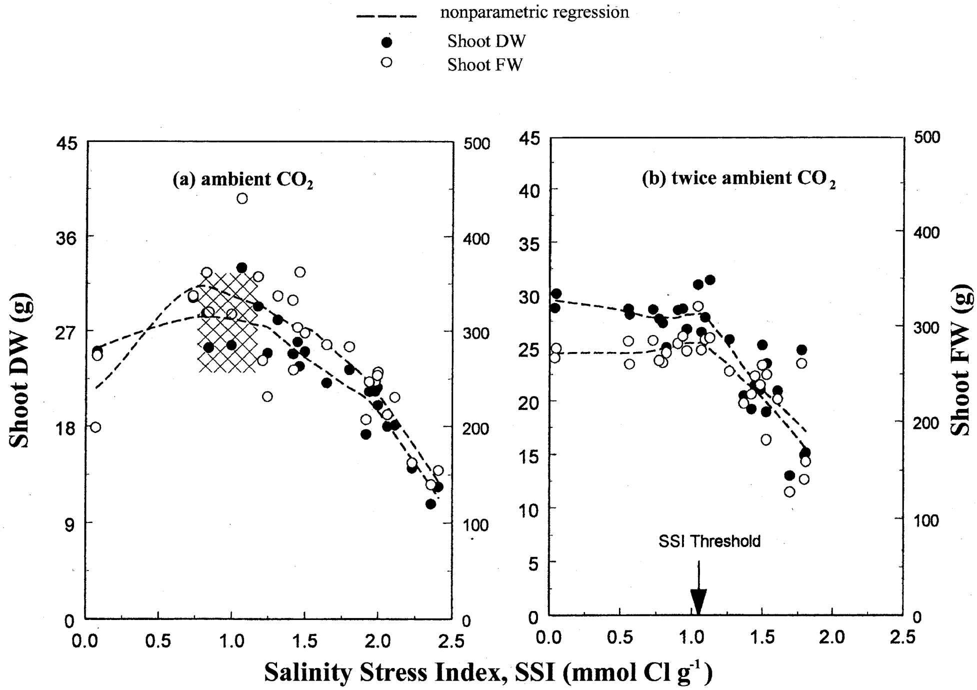

Fig. 5. (a) Tomato dry and fresh weight yield as a function of the dynamic salinity stress index, SSI, at ambient CO_2 concentration (cross hatching indicates SSI threshold region). (b) Dry and fresh weight yield as a function of the dynamic salinity stress index, SSI, at twice ambient CO_2 concentration.

restricted more by the effects of reduced canopy growth than it is by the effects of nutrient solution osmotic potential on water uptake. Interestingly, the water use response functions showed threshold values that are similar to the root-zone salinity thresholds for the plant response function and they may be considered as a good parameter for assessing plant response to salinity. The increased water use efficiency in CO_2-treated plants is in agreement with the results of Morison and Gifford (1984) who studied 18 species of C3 and C4 plants under variable soil water stress and found that all but two species increased their water use efficiencies between 40 and 80% in presence of high atmospheric CO_2.

5.3. Root–shoot ratio

Root–shoot ratios are an important indication of the complex interaction between carbon assimilation and carbon partitioning (Arp, 1991; Hilbert and Reynolds, 1991; Hunt et al., 1998; Luo et al., 1994). The root–shoot ratio was significantly lower in presence of high CO_2. This result was similar to those found for a root temperature–salinity interaction and photon flux density–salinity interaction (Dalton et al., 1997, 2001). In both cases, the plant environment that produced the highest tolerance to root zone salinity also produced the lowest root–shoot ratios, indicating that this ratio is a homoeostatic property of the tomato plant. With respect to the effects of CO_2, these results are similar to those found for soybean (Hunt et al., 1991) and 16 species of C3 and C4 plants (Morison and Gifford, 1984). Significant increases in root development with elevated CO_2 concentrations have been reported by Rogers et al. (1992) and Del Castillo et al. (1989). However, the results of root–shoot measurements appear to be mixed, with multiple examples of the root–shoot ratio showing either no response, or both positive and negative responses (Hunt et al., 1998). The root–shoot ratio can provide valuable information for validating carbon partition models that have been developed using the balanced activity hypothesis (Luo et al., 1994; Hilbert and Reynolds, 1991). Indeed, an optimized allocation of carbon and nitrogen resources, which eventually control plant growth rate and final size may be of critical significance in saline environments.

5.4. Leaf chloride accumulation

Leaf chloride contents were consistent with the assumption that water and salt uptake are coupled. The accumulation of the dominant salinizing anion (chloride) has been previously modeled in terms of transpiration flux, root development rate, and temperature dependent bio-physical transport coefficients of the root for water and salt (Dalton et al., 2000). From this, it is concluded that the salt load to the shoot is a non-linear function of the transpiration rate. Although, some authors query the existence of a linkage between water and salt uptake (Ball and Munns, 1992; Nicolas et al., 1993; Munns et al., 1999) it may be possible that this is a species and/or environment-dependent phenomenon. In addition, to assess the effects of the relationship between water and ion uptake, one needs to know the transpiration flux, root surface area, salt concentration in the root zone and the salt exclusion properties of the root. Theoretical considerations also show small differences in solute flux to the shoot when transpiration rates are low (Dalton et al., 1975). In general, quantitative measures of salt load to the shoot should be reported in moles per plant and not in terms of concentration (mol g^{-1}) because the latter depends on biomass production, which in turn depends on the plant's response to salinity. To account for this interdependence, the SSI was analytically defined as the total chloride transported to the shoot relative to total biomass production without regard to partitioning.

These results confirmed that the SSI is a powerful approach to describe the intrinsic plant salt tolerance properties. Understanding the physiological and molecular bases underlying the variability of the root zone salinity threshold and the stability of the SSI tolerance threshold will open new avenues to explore the complexity of plant response in saline environments.

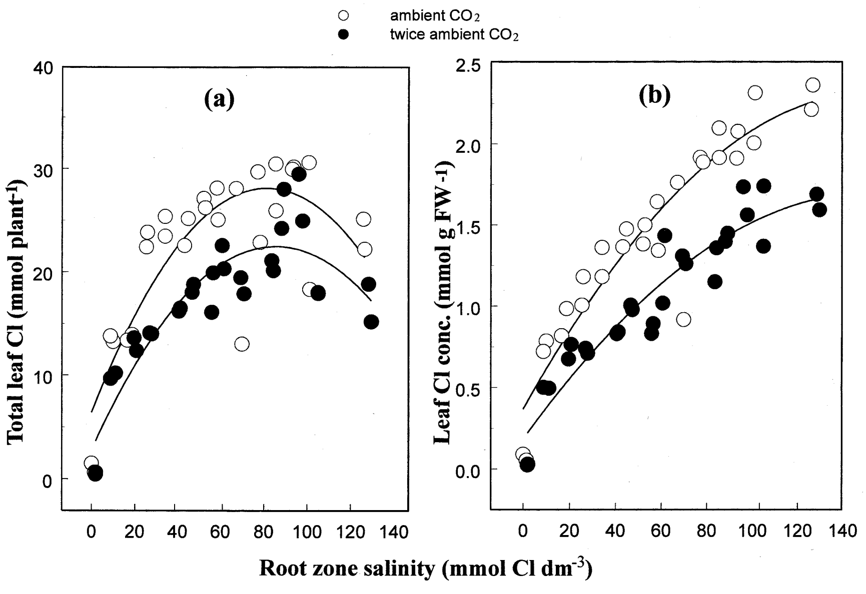

Fig. 6. (a) Total leaf chloride in tomato plants as a function of root zone salinity for ambient and twice ambient CO_2 concentrations. (b) Tomato leaf chloride concentration as a function of root zone salinity for ambient and twice ambient CO_2 concentration.

Acknowledgements

The authors contributed equally to this work. Names and products are mentioned for the benefit of the reader and do not imply endorsement or preferential treatment by the USDA.

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