

Running title: Root aeration, hypoxia and salinity in a heavy clay soil

Root aeration improves yield and water use efficiency of tomato in heavy clay and saline soils

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Abstract

Water-logging and salinity of the soil alter both the physical and biological environment of plant roots. In two experiments, we investigated the effects of imposed aeration on yield and the physiological response of tomato (*Lycopersicon esculentum* L.) cv: Improved Apollo growing under protected conditions over a range of salinities (the salinity experiment), and under constant field capacity (FC) or drier soil conditions (the moisture experiment). Subsurface irrigation with aerated water (12% air in water) stimulated above-ground growth, and enhanced the reproductive performance through earliness for flowering and fruiting compared with the control. Fruit yield of tomato with aeration in the moisture experiment was increased by 21 percent compared with the control (4.2 vs. 3.7 kg per plant), and the effect of aeration on fruit yield was greater in FC than in the drier treatment. . Fruit yield was increased by 38 percent in saline soil due to aeration compared with the non-aerated control. Increasing salinity from 2 dS m⁻¹ to 8.8 and 10 dS m⁻¹ reduced fruit yield by 18 and 62 percent respectively, but 4 dS m⁻¹ did not suppress yield. Aeration in both the experiments increased plant water use and water use efficiency (WUE), expressed as weight per unit of applied water. Biomass WUE was greater by 16 and 32 % in the moisture and saline experiments, respectively. The increased yield with aeration was also accompanied by an increased harvest index (HI) defined as the proportion of dry fruit biomass to total dry biomass, greater mean fruit weight, high fruit DM, and increase in leaf chlorophyll content and shoot: root ratio, and a reduced water stress index (computed from the difference between air and leaf temperature). The benefit gained from aerating irrigation water was not only observed

under conditions where air-filled porosity may be low (e.g., in poorly structure sodic soils, or at field capacity in clay soils), but also in drier soils.

Keywords: Lycopersicon esculentum; Aeration; Salinity; Subsurface drip irrigation; Vertisol

1. Introduction

Tomato (*Lycopersicon esculentum* L.) can be grown in a wide range of soil types (Kinet and Peet, 1997). However, the ideal soil for tomato should be well drained and yet capable of retaining moisture. As drip irrigation develops a wetting front near emitters, the root zone of the crop remains near-saturated for a proportion of the time between irrigation events, especially on heavy cracking clay (Vertisols) making them the least desirable soil types for drip irrigation. Particularly in poorly drained soils, flood irrigation and wet weather cause water to replace air in the soil thus reducing the availability and mobility of oxygen that remains trapped in soil pores (Meek et al., 1983). By decreasing the supply of soil oxygen to plant roots, heavy rainfall or irrigation on such soils can constrain yields to well below their potential (Poysa et al., 1987). The roots of most crop species need a good supply of oxygen in order to satisfy the water and nutrient needs of the shoots (Meek et al., 1983). Paradoxically, one of the first symptoms of excessive soil wetness is drought stress in the leaves. If these conditions are prolonged for more than a few days, then further serious damage can be effected via nutrient deficiency, build-up of metabolic poisons and increased incidence of root diseases (Vartapetian and Jackson, 1997).

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2 The tomato crop is one of the most sensitive of all crop species to excesses of soil
3 moisture and poor soil oxygen supply (Bradford and Yang, 1981). Periods of excessive
4 soil water content tend to result in smaller crop canopies, and greatly reduced yields.
5 Excess of salt in the soil on its own, or in combination with waterlogging, also has severe
6 consequences for crop production, including that of tomato (Zhang and Blumwald, 2001).
7 Salinity in clay soil is often associated with sodicity, which reduces the porosity in the
8 soil, and the supply of soil oxygen to the roots (Munns, 2002).

9

10 Plant roots require adequate oxygen for root respiration as well as for sound metabolic
11 function of the root and the whole plant. Amelioration of an anoxic/hypoxic root zone in
12 order to improve effective soil aeration is, therefore, crucial in order to improve plant
13 performance in Vertisols and in saline conditions. Compacted soils are also known to
14 lack sufficient oxygen to sustain root activities (Rengasamy, 2002). Because of the
15 delicate nature of subsurface drip irrigation (SDI) lines, cultivation does not take place to
16 their depth, therefore predisposing the soil around the lines to compaction. SDI minimises
17 alternate wetting and drying of the soil surface, a phenomenon that might otherwise
18 predispose them to the cracking that could locally alleviate the lack of aeration. By direct
19 injection of air alone, by irrigation of a crop with aerated water, or by injection of
20 hydrogen peroxide in the root zone, aeration of the crop root zone can now become a
21 reality (Bhattarai et al., 2004). Injection of air alone is expensive and the injected air
22 moves away from the root zone due to the chimney effect (Goorahoo et al., 2001). The
23 economics of golf course greens can sustain commercial-scale aeration with air injection

(Walker et al., 2000). Recent studies (Bhattarai et al., 2004) show the promise of using SDI to provide aerated water to improve crop performance in Vertisols. We define oxygation as the delivery of aerated water by way of SDI systems. Aerated through a venturi principle, or with solutions of hydrogen peroxide, SDI provided yield benefits to a range of crops including cotton, zucchini and vegetable soybean. In this study, we examined the effect of aerated subsurface irrigation water on the glasshouse performance of tomato at different soil moisture levels and over a range of salinity levels in a Vertisol. Aeration of the rhizosphere increased most measured parameters of irrigated tomato, including fruit yield, on a Vertisol, whether saline or not.

2. Materials and Methods

2.1. Location, soil and crop details

Two experiments, the moisture experiment and the salinity experiment, were undertaken at Rockhampton, Australia (23° 22', 0.345'' S latitude, 150° 31', 0.53'' E longitude). The tomato variety Improved Apollo was directly sown on 19 April and 29 April 2003 for the salinity and moisture experiments, respectively. A black cracking clay, which is referred to as a *Vertisol* (Australian Soil Classification System as 6AUG-12) was filled in sealed black pots of 28 cm diameter x 45 cm height for the moisture experiment, and 25 cm x 24 cm for the salinity experiment, with 26.00 and 10.79 kg of soil, respectively, to maintain a bulk density of 1.3 g cm⁻³. All pots were fitted with Netafim subsurface drippers placed five centimeters above the base of each pot, and the soil surface was covered with a layer of black low-density polyethylene beads to minimize

1 surface evaporation. The emitters delivered 0.8 L h^{-1} water at a line pressure of 83 kPa.
2 Plants were spaced 75 cm x 60 cm between and within rows maintaining one plant per
3 container by thinning excess plants at the three-leaf stage. Plants were individually
4 staked, and pruned to maintain a branch-less single stem.

6 *2.2. Air injection and soil moisture monitoring*

8 A “Mazzei” venturi air-injector (Model 384-X designed and manufactured by Mazzei
9 Injector Corporation, USA) was installed in-line immediately following the pump (1 HP
10 Davey designed and manufactured by Davey Australia Pvt. Ltd). Pressure gauges either
11 side of the venturi, in association with a valve-regulated bypass line, permitted the
12 control of inlet/outlet pressure and thus the pressure differential within the venturi. This
13 controlled the amount of air ingress into the irrigation line (12% air by volume of water).
14 The air injection using the Mazzei air-injector followed the Bernoulli’s principle. Aerated
15 water was delivered to the soil through the pot drippers, and the excess in the line was
16 returned to the tank. Soil water was measured daily in one pot per plot using a calibrated
17 Micro-Gopher system (Soil Moisture Technology, Australia), the probe of which consists
18 of a capacitance sensor. Irrigation was carried out on a 1 to 3 day interval, between 7:00 h
19 to 12:00 h, based on the readings from the Micro-Gopher; refill was when the soil
20 moisture reached 32 mm (in the FC treatment) and 21 mm (in the dry treatment) and 32
21 mm per 100 mm of soil depth in the salinity experiment, respectively.

2.3. *Experimental design and treatments*

The moisture experiment was laid out as a 2x2 factorial Randomized Complete Block (RCB) design in a screen-house with tomato grown at two soil moisture levels - field capacity (FC - 43 mm H₂O per 100 mm of soil depth) and drier (22-32 mm H₂O per 100 mm) with and without aeration. Soil moisture was measured in the middle of the pot, 5 cm away from emitter and soil water content was periodically verified gravimetrically. Treatments were replicated three times. The salinity experiment was laid out as an RCB split-plot design with two blocks in a temperature-controlled glass-house. Main plots comprised of aeration and control. Sub-plot treatments comprised four-selected NaCl levels equivalent to EC_e 2.0, 4.0, 8.8 and 10.0 dS m⁻¹ created by uniformly pouring 20, 45, 75, and 95 mM NaCl solutions to the designated pots. Pots were maintained between the refill point (32 mm) and field capacity (43 mm). The appropriate NaCl solutions were introduced in three equal applications of 1161.1 mL. The initial one third was introduced to the pots seven days after the majority of seedlings had germinated (day 7), and the second and the final amounts on day 9 and day 13 respectively bringing the soil in the pots to FC so as to make the distribution of the salt as uniform as possible. Radiation receipts were 67% of full sunlight in both experiments and aeration was begun as soon as the first true leaf was visible. The nutrient requirement of the crop in both experiments was supplied through fertigation using a “Peter’s Professional” general-purpose water-soluble fertilizer (20N [28% nitrate, 20% ammonium and 52% urea]:8.7P:16.6K and 0.01%B, 0.004%Cu, 0.05%Fe, 0.03%Mn, 0.001%Mo, 0.003%Zn) at the rate of 0.5 g L⁻¹ continuously. To account for different uptake rates of water between treatments, at times

irrigation was applied without fertigation to ensure that all plots received the same amount of fertilizer. In the salinity experiment foliar liquid fertilizer (“Stop it”- manufactured by Phosyn Plc, UK which contains calcium chloride 16% W/V) as a 1 % solution was applied twice to the foliage (12 ml per plant) whereas in the aeration experiment it was applied 6 times (36 ml per plant) during the season in an attempt to avoid blossom end rot.

2.4. Data recording

Weather data were recorded from an adjacent weather station. Soil temperature was measured in the moisture experiment, one probe in each plot at 10 cm depth and 5 cm from the pot wall.

The oxygen concentration in the soil solution was monitored using PST3 oxygen sensitive fiber optic minisensors (Optodes) with a Fibox-3 oxygen meter (PreSens GmbH, Regensburg Germany). Probes were located at 15 cm depth from the soil surface in all treatment combinations in the moisture experiment, and in the 2 and 8 dS m⁻¹ treatments with and without aeration in the salinity experiment. Due to the small number of sensors, un-replicated, data were collected on 39-46 days after sowing in the moisture experiment, and 53-56 days after sowing in the salinity experiment. Growth and development parameters such as plant height, leaf area, individual leaf size and stem diameter, and reproductive parameters such as days to flowering, fruit set, and the lower most flowering node number were recorded from individual plants at fortnightly intervals and at final

harvest. Data on fruit yield, including number and weight per fruit, were recorded from fruits harvested over different dates as fruits ripened on the plants. The dry matter data for leaf, stem, and roots were derived from final plant harvest. Components were dried for 48 hours at 70 °C.

Leaf gas exchange parameters (photosynthesis, transpiration and stomatal conductance) were measured using an infrared gas analyzer (IRGA) model LCA-4 (ADC, Hoddesdon UK) between 10 am and 12 noon, leaf water potential at predawn was measured with a Scholander pressure bomb by soil moisture Inc. USA following Joly (1985), canopy temperature and the crop water stress index (CWSI - values range from 0 (no stress) to 1 (severe stress where transpiration ceases completely) using an infrared Ag multimeter (Everest Inc., Tucson USA) between 1-2 pm and canopy light interception using a PAR ceptometer (Decagon, Pullman USA) at midday. Leaf chlorophyll concentration was measured with a SPAD-520 chlorophyll meter (Minolta, Osaka Japan) on the youngest fully extended two leaves of each plant. Sample leaves were analysed using the acetone chlorophyll extraction method following EPA (Anonymous, 1994) to calibrate SPAD data. All these parameters were measured on five occasions throughout the season.

Plant water use was determined using the stem sap flow system as described by Baker and Bavel (1987). Stem sap flow in the moisture experiment was monitored on one plant per treatment at the 50% flowering stage over the period of three days (83-85 days after sowing (das)). Plant water use efficiency was expressed as season-long water use efficiency of biomass ($WUE_{Biomass_{SI}}$ as g of biomass per litre of applied water over the

season), season-long water use efficiency of fruit yield ($\text{WUE}_{\text{Fruit}_{\text{sl}}}$ as g of fruit per litre of applied water over the season), instantaneous water use efficiency (WUE_i – μmol of CO_2 fixed per mmol of H_2O transpired derived from IRGA data), and leaf carbon discrimination, (Δ ‰) as described by Farquhar et al. (1991).

The integrity of leaf membranes, expressed as the electrolyte leakage ratio, was measured on day 79 in the salinity experiment on the 3rd topmost fully expanded leaves of all treatment x replicate combinations following the method described by Renault et al. (1998). The specific leaf area (SLA - defined as leaf area per unit mass of leaf) was determined at the same time following Garnier et al. (2001). Washed leaf samples (sample leaves first washed immediately in RO water, followed by rinsing in double distilled water, and then spread on clean paper towel until dry) three per plant, were also analysed for the determination of Na^+ , Cl^- , Ca^{2+} , K^+ , and Mg^{2+} and other major nutrients following routine methods by CSBP, an Australian accredited laboratory. For the salinity experiment plants were harvested once-over on 97 days after sowing whereas for the moisture experiment fruits were harvested as ripening progressed and final harvest took place on day 164.

2.5. Root samples

One core sample per pot in the moisture experiment was collected 145 days after sowing by coring with a 3 cm diameter soil corer to the entire depth of the pot. Core

1 samples were soaked in 1% solution of groundbreaker (active constituent 10 g L^{-1}
2 buffered poly(lignosulfonate) for 2-3 hours and roots were separated from soil using a 45-
3 micrometer sieve following the floatation technique. The living roots were separated
4 manually by discarding the dead based on visual observation of tissue colour as described
5 by Caldwell and Virginia (1991), and the root length and diameter of the former was
6 determined using a Hewlett Packard scanner and Delta-T software. The washed root
7 samples were oven-dried for 48 hours at 70°C for the determination of dry weight.

9 *2.6. Data analysis*

11 The data collected were subjected to an analysis of variance using the general linear
12 model procedure for a factorial randomised complete block design employing SYSTAT
13 version 9. Where interactions were not significant, main effects only are presented. In the
14 salinity experiment the effects due to salinity x aeration in the split plot design were not
15 significant. Therefore, only the main effects due to salinity and aeration are presented
16 herein.

18 **3. Results**

20 **3.1. Soil Moisture Experiment**

22 *3.1.1. Environmental parameters and water applied to the crop*

The mean ambient temperature measured outside the screenhouse averaged 19.5 °C and ranged from 10.4-25.3 °C whereas soil temperature averaged 24.8° C and ranged from 20 to 31 °C. There was a gradual decrease in temperature from April to July and a slight increase from August to October. Relative humidity averaged 26 % and ranged from 17 % to 43 % and solar radiation within the growing environment averaged 10.6 MJ m⁻² d⁻¹, with a minimum of 1.6 to a maximum of 17.7 MJ m⁻²d⁻¹. Following irrigation dissolved O₂ declined by 45% in non-aerated pots while in aerated pots soil O₂ decreased by only 25% (Figure 1). Oxygen measurements in the rhizosphere over a 72 hour period during the flowering stage revealed greater dissolved oxygen concentration with aerated treatments compared with the control at both FC (8.1 ± 0.96 vs 7.1 ± 1.0 mg L⁻¹) and drier (9.2 ± 0.82 vs 8.1 ± 1.39 mg L⁻¹) conditions. In general, dissolved O₂ concentration was higher at night and lower between 2-4 pm (Figure 1).

The cumulative water applied throughout the season was greater for FC compared with the drier treatment but aeration per se had no effect on the amount of water applied. Crop applied water at FC was greater by 10% compared to the drier treatment (Table 1). As illustrated in Figure 2, soil water content was maintained effectively at 24-28 and 40-43 mm H₂O per 100 mm soil depth throughout the season in drier and FC treatments, respectively.

3.1.2. Plant growth characteristics

Plant height at harvest did not differ due to aeration, but plants under FC were somewhat taller than in the drier treatment (Table 2). A marked positive effect of aeration

was observed on leaf area per plant, primarily because of larger individual leaves (262 vs 239 cm², SED (6 df) = 4 cm²), however, these leaf properties were not affected by soil moisture treatment (Table 2). The interaction effect on leaf area was significant, showing a greater positive effect of aeration at FC. Stem diameter did not vary in response to soil moisture or aeration.

3.1.3. Plant reproductive performance

The first flowering node occurred at a significantly lower node number under aeration compared with the control, but soil moisture had no effect (data not presented). Similarly, first flowering was significantly earlier for aeration, and the dry treatment was also earlier compared with FC (Table 2). The fruit set percentage did not vary significantly in response to treatments (data not presented).

3.1.4. Fruit yield and yield components

Fresh fruit yield was significantly greater for aeration compared to the control and almost so for FC compared to the dry treatment (Table 2). Although the effect of aeration and soil moisture was not significant for number of fruits per plant, the individual fresh fruit were significantly heavier due to aeration compared to the control (136 vs. 124 g fruit⁻¹, SED (6 df) = 1 g). The soil moisture effect on weight per fruit was not significant. Fruit dry yield per plant did not differ significantly in response to soil moisture but aeration increased fruit dry yield compared to the control (Table 2).

3.1.5. *Dry matter partitioning*

Dry weight of root and leaf did not vary significantly in response to soil moisture or aeration. However, stem dry weight was significantly greater at FC compared with the dry treatment but did not differ significantly between aerated and control treatments (Table 2). Aboveground dry biomass and harvest index (HI - the proportion of dry fruit biomass to total fresh biomass) were significantly greater and the root:shoot ratio was lower with aeration compared with the control (Table 2). The effect of soil moisture on these traits was not statistically significant. The interaction effect was significant for above ground dry biomass such that aeration showed a greater positive effect in the dry than in the FC treatment (data not presented).

3.1.6. *Water relations and water use efficiencies*

The stem sap flow measured over three days at the flowering of the 6th inflorescence (83-85 das) indicated that plant transpiration increased by 8 % with aeration compared to the control and by 18% with FC compared to the dry treatment (Table 1). Aeration significantly reduced the crop water stress index (CWSI – derived from the difference between air and canopy temperature) compared to the control (Table 1). Likewise, FC significantly reduced CWSI compared with the dry treatment. The LWP was only affected by the soil moisture treatments such that a significantly more negative LWP was recorded for the dry compared to the FC treatment. The WUE_i (i.e. instantaneous water use efficiency) did not differ significantly between treatments, but biomass WUE_{sl} (i.e.

season long water use efficiency) was significantly higher for the dry treatment compared with the FC and for aeration compared with the control (Table 1). Fresh fruit WUE_{sl} was significantly greater in the aeration treatment compared to the control but did not differ significantly between the soil moisture treatments. WUE assessed with carbon discrimination (Δ ‰) technique did not differ significantly due to either soil moisture or aeration treatments (Table 1).

3.1.7. Leaf properties and gas exchange

The leaf chlorophyll concentration was greater with aeration but was not affected by soil moisture (Table 3). Leaf gas exchange properties did not differ significantly between treatments. Similarly the effect of treatment was also not significant for canopy light interception or specific leaf area although aeration tended to produce thicker leaves (Table 3).

3.2. Salinity Experiment

3.2.1. Water input, soil water content and soil oxygen concentration

Water applied to the crop over the season decreased with salinity and increased, although not significantly so, with aeration (Table 4). Soil water content was maintained between 25-37 mm per 100 mm H_2O per 100 mm soil depth throughout the season and

was on average lower with aeration and with lesser salinity, reflecting their greater water use (Table 4). Oxygen concentration in the soil solution was greater for the aeration compared with the control treatment, and was less with increase in salinity (Figure 3).

3.2.2. *Plant growth characteristics*

Plant height decreased with increasing salinity and plants treated with aeration were significantly taller than those in the control (Table 5). Total leaf area per plant was lowest at the highest salinity due to an effect of salinity on both leaf number and leaf size. Differences in total leaf area per plant and its components were too small to be significant between aeration and its control (Table 5). However, the SLA was significantly smaller with aeration (317 vs. 366 cm² g⁻¹, SED (49 df) = 20.6).

3.2.3. *Reproductive performance*

A marked effect of salinity and aeration was observed on reproductive performance of the crop (Table 6). Number of inflorescences counted at 87 das increased significantly with aeration and decreased with increasing salinity levels. Flowering was delayed significantly by higher salinity but the delay by aeration was not significant. No difference in fruit set was observed between treatments (experimental average = 57%) although number of fruits per plant was greater in the aeration compared to its control and lower at higher salinity levels (Table 6).

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2 *3.2.4. Dry matter accumulation and partitioning*

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4 With the exception of the root, all other components and total biomass weight
5 decreased significantly ($P < 0.05$) at higher levels of salinity (Table 7) and consequently
6 the root: shoot ratio was greater at higher salinity. In contrast, the HI was greatest at the
7 lowest salinity. The difference between aeration treatments was significant only for fruit
8 weight and total biomass, although the components were consistently heavier under
9 aeration compared to the non-aerated control (Table 7).

10

11

12 *3.2.5. Leaf gas exchange properties*

13

14 Neither salinity nor aeration significantly affected photosynthesis, transpiration rate or
15 chlorophyll concentration (data not presented) although there were tendencies for
16 photosynthesis and transpiration to decline, and chlorophyll concentration to rise with
17 increasing salinity.

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19 *3.2.6. Plant water use and water use efficiency*

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21 Significant effects of both aeration and salinity were noted for water use efficiency of
22 biomass and fresh fruit. Aerated plants achieved higher water use efficiencies for both
23 fruit and biomass compared with the control, although WUE decreased significantly with
24 increasing soil salinity (Table 8). Unlike the WUE_{sl} of biomass and fruits, WUE_i did not

differ significantly between salinity or aeration treatments (data not presented). WUE assessed by carbon discrimination revealed a significant improvement in WUE with increasing salinity levels but not due to aeration (Table 8).

3.2.7. Leaf salt analysis

Leaf tissue concentrations of Na^+ , Cl^- , Ca^{2+} , and the $\text{K}^+:\text{Na}^+$ ratio were significantly affected by both the aeration and salinity treatments (Table 9). Potassium concentration was not affected. Na^+ concentration in the leaf tissue steadily increased with increase in salinity from 2-10 dS m^{-1} and in non-aerated compared to the aeration treatment. Non-aerated plant Na^+ tissue concentrations were 42 % higher than their aerated equivalent (Table 9). Similarly, leaf Cl^- concentration differed significantly due to salinity with the highest recorded at 10 dS m^{-1} . Higher calcium leaf tissue concentrations were evident with increased salinity. The effect of aeration on Ca^{2+} was also significant; non-aerated plants had leaf tissue concentrations greater than those of aerated plants (Table 9). Although differences in the K^+ concentrations in leaf tissue were not significant, the ratio of $\text{K}^+:\text{Na}^+$ differed significantly due to salinity and aeration. The ratio decreased progressively with increased salinity, and aeration resulted in a significantly greater ratio than that of the control (Table 9).

4. Discussion

Both aeration and soil salinity influenced tomato growth, development and yield. Leaf properties i.e. leaf size and area, were significantly enhanced by aeration in the moisture experiment. This positive effect of aeration on leaf area was mainly evident at FC (aeration - 0.817 m² vs. control - 0.673 m², SED (18 df) = 0.04) and only minimally (+8%) in the dry treatment. A positive effect of aeration on leaf area at the higher moisture level in the Vertisols may be due to an alleviation of O₂ deficiency in the rhizosphere. Root respiration has been shown to be favoured by aeration while irrigating to FC (Bhattarai et al., 2004). Aeration maintained higher dissolved soil O₂ concentrations in both the FC and dry treatments (Figure 1).

Although statistically non-significant in the salinity experiment, leaf area and leaf dry weight were somewhat greater for the aeration treatment compared with the control. They were, however, significantly reduced by the most saline treatment (Tables 5 and 7). Reduction of leaf area and leaf dry weight due to suboptimal soil moisture and increasing salinity were observed by Rudich and Luchinsky (1986) to be due not to a reduction in number of leaves but to a reduction of both leaf area and leaf thickness, i.e. an increase in SLA. Our own data also show that the SLA increased as salinity increased (steadily but non-significantly from 331 to 363 cm² g⁻¹), as it did without aeration. Reduction in leaf growth rate has been related to reduction in cell turgidity or cell wall properties (Li and Stanghellini, 2001), which results in reduced leaf water potential as evidenced by a lower leaf water potential for non aerated and higher salinity treatments (data not presented).

Plants in both experiments were pruned to a single stem and as a consequence the leaf area index for each was low (LAI of 1.43-2.09 for the moisture experiment) compared to values of non-pruned plants. The reductions in leaf area brought about by salinity (Table 5), and shown in previous studies (Li and Stanghellini, 2001), almost certainly contributed to low fruit yield, just as enhanced leaf area (Table 2) and light interception (Table 3) in the moisture experiment contributed to higher yields in the aeration treatment, for leaf capture of solar energy is related to fruit yield in many crops (Olympios et al., 2003).

Aeration and salinity were found to markedly affect the reproductive performance of the tomato crops. Earlier flowering (Table 2 and Table 7) and a lower position of the lowermost flowering nodes (data not presented) were evident in the aerated treatment in the moisture experiment, and more fruits were harvested in less saline treatments. Sharaf and Hobson, (1986) also reported an enhanced earliness due to the shorter time period required from ovule fertilization to fruit ripening in saline compared with non-salinized conditions. Greater fruit yield in our aerated or less saline treatments was more dependent on the size of the fruit rather than the number of flowers and fruit set per se. Pollen fertility of salt-treated tomato plants has been found to be similar to that of the control (Adams and Ho, 1992). The implication from the work of Johnson et al. (1992) is that such reductions in fruit size were related to lowered water potential that constrained the rate of fruit expansion. The reduction in fruit size due to salinity is variety specific. In general, the larger the fruit size, the more important is its reduction in size by salinity

(Cruz et al., 1990). The variety used in these experiments has a large fruit and, therefore, the reduction in fruit size in response to salinity and lack of oxygen was likewise large.

Of interest, the effects of aeration and salinity were not evident in terms of leaf gas exchange properties. The rate of photosynthesis is generally reduced under salt stress (Cuartero and Fernandez-Munoz, 1999). However, no such marked effect was noticed in our experiments. In tomato, growth declines more rapidly, and at lower concentrations of Na^+ in the leaf, than does photosynthesis (Yeo and Flowers, 1989; Alarcon et al., 1994). Similarly, growth in response to salinity has been shown to decline more than photosynthesis in long-term studies (Seemann and Critchley, 1985); and tomato is sink—rather than source limited with respect to carbon assimilation (Hooking and Steer, 1994) which means that the tomato can withstand a certain loss in photosynthetic rate with only little effect on fruit growth. Indeed, mild water stress had no effect on the rate of photosynthesis (Hsiao, 1993). If the reduction in the rate of photosynthesis caused by salinity and reduced aeration were the major limiting factor for a low yield, possibly such loss of photosynthetic rate could be counteracted by minimizing the pruning-induced loss of leaf area.

Salinity and reduced aeration in general showed detrimental effects on the total and component biomass of tomato. This is in contrast to the report by Li and Stanghellini (2001) who showed that dry weight was not responsive to increased salinity over the same salinity range as in our trial. However, superimposed upon a clay soil, the negative effects of salinity on soil structure and aeration in our experiment may have been

1 responsible for such an effect. In spite of the reported negative effects of salt on root
 2 growth of other species (Cordoba et al., 2000), root growth in tomato appears to be less
 3 affected by salt than shoot growth, hence the root:shoot dry weight ratio increased with
 4 respect to salinity (Table 7). The rise in the root:shoot dry weight ratio under salt stress
 5 must be accompanied by changes in the allocation of assimilates between root and shoot.
 6 Previously, Perez-Alfocea et al. (1996) have shown that in salt-treated tomato plants a
 7 greater proportion of assimilate was allocated to the root compared to that in control
 8 plants.

9

10 In line with the expected, whole plant transpiration measured with the stem sap flow
 11 method over the period was greater in the FC compared with the dry treatment, and in the
 12 aerated compared with the control treatment (Table 1), but accumulated water use to
 13 harvest indicated that a difference was only evident between the moisture treatments
 14 (Table 1). Although no significant differences were recorded in term of instantaneous
 15 transpiration rate, stomatal conductance or WUE_i , trends were as expected and tomato
 16 plants grown on more saline soil had a lower water use and consistently moister soil
 17 compared with less saline treatments (Table 4). Strong inverse relationships between
 18 increasing salinity and plant water use in tomato have been reported (Pessarakli and
 19 Tucker, 1985) and in other species a positive relationship has been shown between
 20 improved soil aeration and plant water use (Bhattarai, et al., 2004). Temporal variation in
 21 terms of transpiration (E), stomatal conductance (Sc) and leaf photosynthesis (A) occurs
 22 in tomato. Data recording for E, Sc and A were only made between 9:00-12:00 h in these
 23 experiments and it is possible that long term monitoring of A, E, Sc and monitoring of

night time water consumption (Santamaria et al., 2004) would help to establish a firm relationship between crop water use as influenced by aeration and salinity. Tomato plants with their root system in a medium with heterogeneous salt concentration, such as occurs in the soil (Vaughan et al., 2002), develop more roots and absorb more water in the less saline part of the medium. However, our plants were grown in pots in which the soil was uniformly exposed to salinity, and for which surface evaporation was minimised, so preferential absorption of water from less saline areas would not have been possible. Working with cotton and bean, Pessarakli and Tucker (1985) suggested decreased root permeability and Rodriguez et al. (1997) suggested reduced root hydraulic conductance as responsible for reduction in uptake of water in saline environments. Such alteration in root permeability and root conductance has direct bearing on the crop WUE. Our data suggest that WUE_{sl} decreased with increasing salinity and increased with aeration. Carbon discrimination (an integrated indicator of WUE) did not differ due to aeration but did for salinity such that Δ (‰) was significantly lower in the highest salinity level (Table 8) indicating a greater stomatal control of transpiration. Similar results with increasing levels of salinity have been reported for other crops (e.g., for pistachio – Hockmabadi et al, 2005). However, in neither experiment were carbon discrimination and WUE_{sl} closely related across the aeration treatments. Similar poor correlations between Δ (‰) and WUE_{sl} or WUE_i were previously reported by Bhattarai et al. (2004) for aeration treatments in cotton and soybean.

In general Na^+ has been reported to increase, and Ca^{2+} and K^+ slightly decrease, in the leaf with increasing salinity in most tomato species (Adams, 1986). Tomato leaf tissues

1 in the current experiment accumulated more Na^+ at higher salinity and less Na^+ in
 2 response to aeration. Letey (1961) has earlier reported a decrease in Na^+ uptake with
 3 aeration of the rhizosphere. The accumulation of Na^+ in the leaf of tomato occurs at the
 4 expense of K^+ , Ca^{2+} , and Mg^{2+} . Salinity generally reduces leaf K^+ , Ca^{2+} , and Mg^{2+} .
 5 However, in contrast in the current experiment, high calcium concentration was observed
 6 at higher salinity, possibly due to the impact of the foliar application of a foliar liquid
 7 fertilizer containing Ca^{2+} . The crop at 10 dS m^{-1} had only 61% of the leaf area of the 2 dS
 8 m^{-1} treatment, yet received the same amount of spray. The ratio between the ion content
 9 of tomato leaves under saline conditions and the corresponding values in the control plant
 10 is referred to as the ion regulation index (Cuartero and Fernandez-Munoz, 1999). The ion
 11 regulation indexes in terms of $\text{K}^+ : \text{Na}^+$, $\text{Ca}^{2+} : \text{Na}^+$ and $\text{Mg}^{++} : \text{Na}^+$ were higher for the
 12 aeration treatment (Table 9). Rengel (1992) also used these ratios as an indicator of the
 13 salt stress in tomato and reported that Na^+ concentration of the leaf tissue samples alone
 14 is not an adequate indicator of salt stress. Our data on ion regulation as reflected by the
 15 higher $\text{K}^+ : \text{Na}^+$ ratio of the aerated treatment suggest that aeration improved plant
 16 tolerance, or perhaps more correctly sodium avoidance (because of the lesser uptake), in
 17 the saline medium. Transverse sections taken from roots showed that those without
 18 aeration were with a greater incidence of root necrosis (unpublished data); a condition
 19 that would favour indiscriminate uptake of ions including Na^+ .

20
 21 In summary, aeration in both non-saline and saline soil environments influenced
 22 growth, development and reproductive performance of tomato in a Vertisol. An increase
 23 in the leaf biomass, earliness of flowering, and an increase in fruit size were observed due

1 to aeration, and they all contributed toward an improved tomato yield. Aeration
2 increased fruit yield by 21% in the moisture experiment and by 38% in the salinity
3 experiment, and also increased season long water use efficiency of fruit by 11% and 77%,
4 respectively. Reduced Na^+ content in the leaf samples and increase in the ion regulation
5 index, defined as the proportion of potassium and calcium to sodium, were recorded for
6 the aerated treatments compared with the control. Supplementary aeration was also
7 shown to improve plant tolerance to the hypoxic soil. Irrigation at FC in the heavy clay
8 soil resulted in a lower oxygen concentration in the rhizosphere, which potentially could
9 lead to hypoxia. As aeration improved dissolved oxygen concentration at FC, and
10 improved the performance of tomato plants, it is considered that aeration contributed
11 towards avoidance of hypoxia. This would be particularly so under conditions where air-
12 filled porosity may be low (e.g., in poorly structure sodic soils, or at field capacity in clay
13 soils). Nevertheless, the benefit of aeration was also evident in the dry treatment in the
14 moisture experiment, for most measured parameters, and it can be concluded that the
15 benefit of aeration is not only to offset hypoxic conditions, but also to satisfy an unmet
16 demand, presumably for oxygen, in the root zone.

17
18 The cumulative stem sap flow recorded over a three day period showed greater canopy
19 transpiration by the aeration treatment compared to the control, and by FC compared to
20 the dry treatment. As the instantaneous measurements of stomatal conductance and leaf
21 transpiration rate did not differ significantly, it is possible that the higher stem sap flow
22 rate was related to greater leaf area per plant due to aeration. Further studies are required
23 to determine whether the increase in water flow through the root system is due to changes

in the water potential gradient across the root system, to changes in hydraulic conductance produced by modifications of the root structure, or to both.

Acknowledgements

Financial support for these studies was provided by Central Queensland University. Thanks to A/Prof Kerry Walsh, Dr N. Ashwath, Kele, Barry Hood, Ajay Sharma, and Tracey Howkins for help at various stages of these experiments. We thank two anonymous reviewers for useful suggestions that improved the manuscript.

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Table 1

Effects of soil moisture and aeration on cumulative applied irrigation, sap flow, leaf water potential, crop water stress index and water use efficiency for tomato in a Vertisol. Means for main effects, with LSD for comparison.

Variables	Levels	Water relations				Water use efficiency (WUE) parameters			
		Cumulative applied water (L plant ⁻¹)	Average daily sap flow (g plant ⁻¹ 83-85 das)	¹ LWP (-kPa)	² CWSI	Biomass _{sl} (g L ⁻¹)	Fruit _{sl} (g L ⁻¹)	Instantaneous ³ (A/E)	Δ (%)
Moisture	Field capacity	110.94	652	1100	0.18	4.23	36.40	5.43	20.42
	Dry	99.42	554	1360	0.26	4.59	38.42	5.50	20.28
Aeration	Aeration	104.68	625	1220	0.20	4.73	39.15	5.41	20.33
	Control	105.57	580	1240	0.24	4.09	35.16	5.52	20.37
	LSD (6 df)	1.79	54.2	54.0	0.04	019	2.17	ns	ns

¹LWP= Leaf water potential (measurements of negative leaf water potentials)

²CWSI= Crop water stress index (1 = completely stressed, 0 = no stressed)

³A/E= Instantaneous water use efficiency calculated as, A = net leaf photosynthesis rate (μmol CO₂ m⁻²s⁻¹); E = leaf transpiration rate (mmol H₂O m⁻²s⁻¹)

Table 2

Effects of soil moisture and aeration on plant height, leaf area, flowering, fruit and biomass yield, dry matter partitioning and harvest index (HI) for tomato in a Vertisol. Means for main effects, with LSD for comparison.

Variables	Levels	Plant height (cm)	Leaf area plant ⁻¹ (m ²)	Days to first flowering	Fruit number, weight and yield			Dry weight (g plant ⁻¹)				Above ground biomass (g plant ⁻¹)	HI
					No. per plant	g per fruit	kg per plant	Root	Stem	Leaf	Fruit		
Moisture	Field capacity	192.2	0.745	47.2	31	130	4.03	12.19	55.38	97.83	315.88	467.37	0.66
	Dry	181.7	0.760	45.7	29	130	3.81	11.11	49.53	93.37	312.76	455.67	0.62
Aeration	Aeration	190.0	0.803	45.3	31	136	4.15	10.88	53.26	96.36	343.93	493.56	0.68
	Control	183.8	0.701	47.5	30	124	3.70	12.42	51.64	94.84	284.71	431.19	0.64
	LSD (6 df)	9.01	0.023	1.73	1.3	0.85	0.25	2.71	4.6	ns	10.54	23.1	0.04

Table 3

Effects of soil moisture and aeration on % fruit dry matter (DM), root:shoot ratio, specific leaf area (SLA), chlorophyll concentration, leaf gas exchange properties and light interception for tomato in a Vertisol. Means for main effects, with LSD for comparison.

Variables	Levels	Fruit DM (%)	Root: Shoot ratio	SLA ($\text{cm}^2 \text{g}^{-1}$)	Chlorophyll concentration ($\mu\text{g cm}^{-2}$)	Leaf gas exchange properties and light interception			
						Photosynthesis ($\mu\text{mol CO}_2 \text{m}^{-2}\text{s}^{-1}$)	Stomatal conductance ($\text{mol m}^{-2}\text{s}^{-1}$)	Transpiration ($\text{mmol m}^{-2}\text{s}^{-1}$)	Light interception (%)
Moisture	Field capacity	7.8	0.026	222	58	13.35	0.10	2.57	54.8
	Dry	8.2	0.025	219	58	13.46	0.11	2.62	53.4
Aeration	Aeration	8.3	0.022	209	59	13.38	0.10	2.59	55.3
	Control	7.7	0.029	233	57	13.32	0.11	2.60	52.9
	LSD (6 df)	0.14	0.003	44.6	1.78	ns	ns	ns	ns

Table 4

Comparison of the soil moisture (mm H₂O per 100 mm soil) seasonal means for salinity and aeration treatments and cumulative applied water over the crop period.

Salinity treatment EC _(e) (dS m ⁻¹)	Soil moisture (mm per 100 mm soil depth)		Cumulative applied water per plant (L)	
	Aeration	No aeration	Aeration	No aeration
2.0	22.90	24.17	22.34	21.48
4.0	24.71	26.31	19.83	19.40
8.8	24.01	27.50	19.69	18.23
10.0	27.43	31.18	15.43	16.12
LSD Aeration	2.20 (7 df)		0.96 (37 df)	
LSD Salinity	3.11 (7 df)		1.35 (37 df)	

Table 5

Crop growth and leaf characteristics (per plant) for tomato as affected by aeration and soil salinity treatments.

Factor	Levels	Plant height (cm)	Number of trusses	Number of leaves	Area per leaf (cm ²)	Total leaf area (m ²)	Leaf chlorophyll concentration (µg cm ⁻²)
Salinity treatment EC _(e) (dS m ⁻¹)	2	148	6	21	154.1	0.33	51
	4	132	5	21	145.4	0.30	53
	8.8	131	5	20	163.3	0.34	50
	10	94	4	17	114.6	0.20	49
	LSD 5% (38 df)	20	0.76	2.43	52	0.07	ns
Aeration treatment	Aeration	130	5	20	141.2	0.29	51
	No aeration	123	5	19	148.9	0.30	50
	LSD 5% (38 df)	14	ns	ns	ns	ns	ns

Table 6
Flowering, fruit yield and yield attributes for tomato as affected by aeration and soil salinity treatments

Factor	Level	Inflorescences plant ⁻¹ (87 days)	Days to 50% flowering in the first inflorescence	¹ Fruits per plant at harvest (87 days)
Salinity treatment EC _(e) (dS m ⁻¹)	2	5.0	47	7.7
	4	4.6	56	7.7
	8.8	4.5	60	7.3
	10	3.2	67	3.7
	LSD 5% (38 df)	0.85	6.1	2.7
Aeration treatment	Aeration	4.5	60	7.8
	No aeration	4.1	55	5.5
	LSD 5% (38 df)	0.60	ns	1.9

¹ The crop was harvested once over at 87 days after seeding without leaving the plant for the full season

Table 7

Dry matter and partitioning, root:shoot ratio and harvest index (HI) for tomato at harvest as affected by aeration and soil salinity treatments.

Factor	Levels	Dry weight plant ⁻¹ (g)					Root: shoot ratio	HI
		Root	Stem	Leaf	Fruits	Total biomass		
Salinity treatment EC _(e) (dS m ⁻¹)	2	11.16	18.47	30.31	37.61	97.56	0.13	0.38
	4	14.27	18.86	30.82	25.96	89.91	0.19	0.29
	8.8	13.02	17.37	26.55	20.79	75.46	0.21	0.28
	10	12.02	9.41	13.24	10.31	44.97	0.36	0.23
	LSD 5% (38 df)	ns	4.61	7.36	9.71	19.99	0.20	0.07
Aeration treatment	Aeration	12.77	17.80	28.39	31.25	89.87	0.14	0.35
	No aeration	12.49	14.71	22.95	17.58	67.51	0.18	0.26
	LSD 5% (38 df)	ns	ns	ns	6.86	14.14	ns	0.05

Table 8

Water use efficiency for tomato as affected by aeration and soil salinity treatments.

Factor	Levels	WUE for biomass (g L ⁻¹)	¹ WUE of fruit (g L ⁻¹)	Carbon discrimination (Δ ‰)
Salinity treatment EC _(e) (dS m ⁻¹)	2	4.26	1.64	21.39
	4	4.54	1.32	21.09
	8.8	4.00	1.07	21.12
	10	2.85	0.65	20.13
	LSD 5% (38 df)	0.87	0.45	0.72
Aeration treatment	Aeration	4.65	1.62	21.01
	No aeration	3.56	0.93	20.79
	LSD 5% (38 df)	0.61	0.32	ns

¹ Determination of WUE of fruit based on dry fruit weight.

Table 9

Salt accumulation, leaf membrane integrity (according to Renault et al. 1998), and root properties as affected by soil salinity and aeration on tomato in a Vertisol.

Factor	Level	Na ⁺ (g 100g ⁻¹)	Cl ⁻ (mg kg ⁻¹)	K ⁺ (g 100g ⁻¹)	Ca ²⁺ (g 100g ⁻¹)	K ⁺ :Na ⁺	Leaf membrane leakage (%)	Root length in sample core (mm)	Root weight (g plant ⁻¹)
Salinity treatment EC _e (dS m ⁻¹)	2	0.22	0.99	2.83	1.51	15.4	15	7820	11.38
	4	0.25	1.39	3.04	1.82	13.14	18	5852	14.27
	8.8	0.31	1.83	2.73	1.85	9.28	20	7486	12.97
	10	0.49	2.56	2.56	2.35	4.12	33	5440	10.72
	LSD (7df)	0.14	0.33	ns	0.34	6.4	LSD=17.9 (38 df)	LSD = 64.6 (38 df)	LSD=5.19 (38 df)
Aeration treatment	Aeration	0.26	1.91	2.75	1.62	13.78	20	7169	12.63
	No aeration	0.37	1.47	2.82	2.15	7.19	26	6160	12.03
	LSD (7df)	0.10	0.13	ns	0.24	4.5	ns	LSD = 15.8 (38 df)	LSD=3.67 (38 df)

Figure Captions for Bhattarai et al.

Fig. 1. Concentration of soil oxygen as affected by aeration (open symbols) or no aeration (closed symbols) at two soil water contents on a Vertisol with tomato.

Fig. 2. Soil water content (mm H₂O per 100 mm of soil depth) in field capacity or drier pots containing tomato plants with (open symbols) or without aeration (closed symbols). Irrigation was withheld close to final harvest.

Fig. 3. Concentration of soil oxygen as affected by aeration (open symbols) or no aeration (closed symbols) at two soil salinities in a Vertisol with tomato.

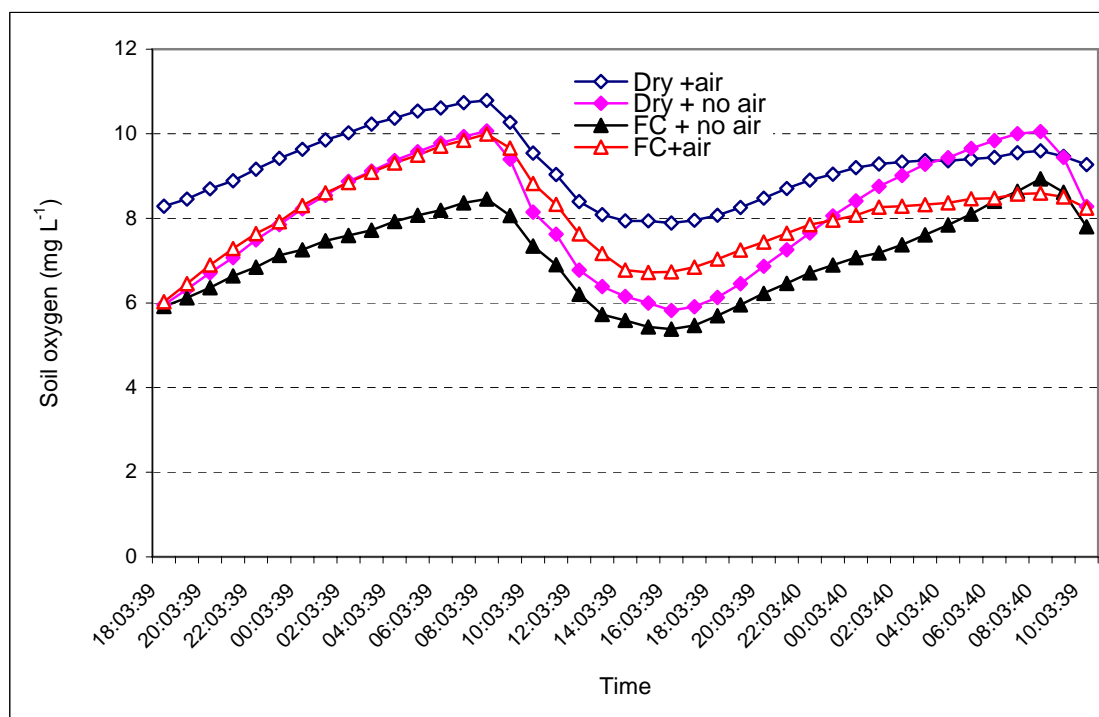


Figure 1

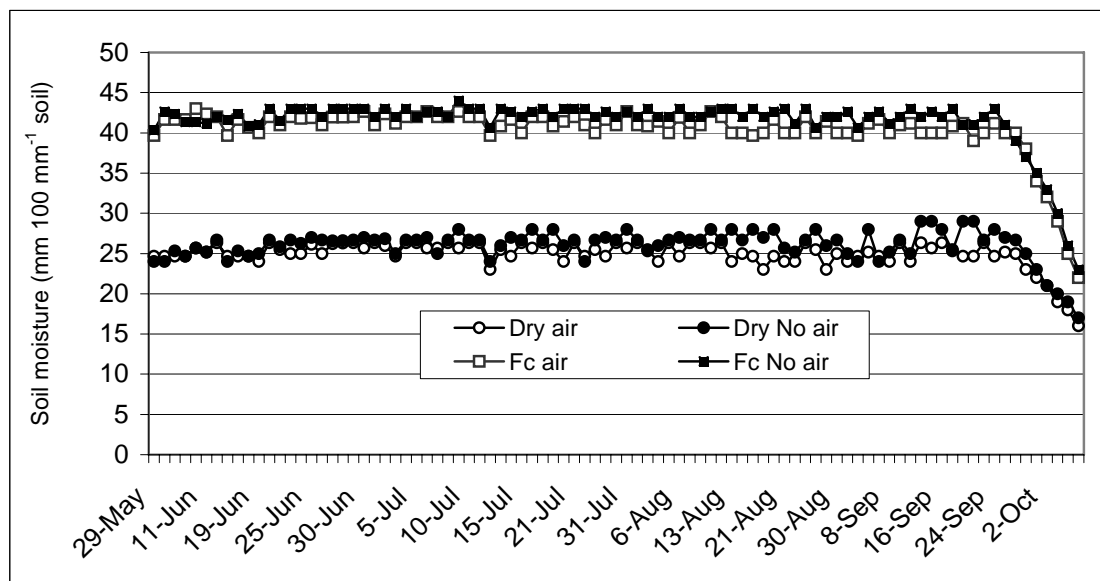


Figure 2

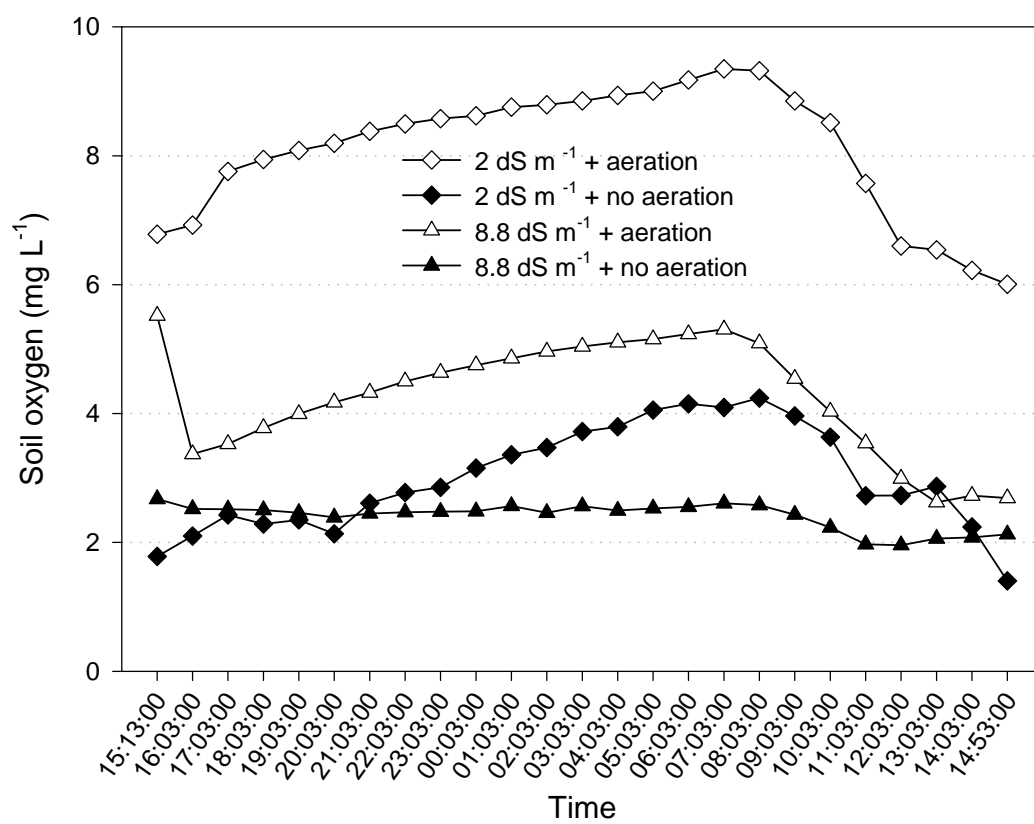


Figure 3