Effects of compost on water availability and gas exchange in tomato during drought and recovery

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ABSTRACT

Compost can increase soil water availability and nutrient uptake by plants, but it is not clear whether it can also improve the ability of plants to recover after drought stress. Tomato plants (*Lycopersicon esculentum* L.) were grown in sandy soil without compost or with compost either incorporated or mulched. There were two water treatments: (i) plants grown under sufficient water supply throughout the experiment and (ii) plants grown with sufficient water supply until day 33 after which water was withheld until stomatal conductance was close to zero. Compost addition increased water content at both field capacity and permanent wilting point, but only incorporated compost increased total available water. Compost addition increased shoot and root growth under well-watered and drought stressed conditions with a greater effect by incorporated compost. At sufficient water supply, the rates of photosynthesis and transpiration were similar in all treatments. Drought stressed plants with incorporated compost wilted earlier than control plants, whereas mulched compost increased water availability to plants and hence the number of days until wilting. Photosynthesis and transpiration recovered faster in plants grown with incorporated compost compared to other treatments. The rapid recovery of plants after drought with incorporated compost could be due to their greater root length.

Keywords: organic amendment; re-watering; stomatal conductance; transpiration; water stress

Water stress is one of the major constraints to plant growth and affects agriculture and horticulture worldwide. Plants that have experienced water stress usually show decreased growth and development, low leaf water and turgor potentials (Tahi et al. 2007) and transpiration rates (Ozenc 2008). Many cellular functions of plants, such as protein synthesis, nitrogen metabolism and cell membrane function can also be impaired under prolonged drought (Saneoka et al. 2004).

Composts are used in agriculture and horticulture to improve soil fertility and quality because they can increase organic matter content, especially in sandy soils which have low water and nutrient holding capacity (Lakhdar et al. 2009). By increasing soil organic matter content, composts improve soil physical properties such as structural stability (Tejada et al. 2009), total porosity and hydraulic conductivity (Aggelides and Londra 2000), aggregate formation (Sodhi et al. 2009), and water holding capacity (Curtis and Claassen 2005). Soil fertility can be further increased by the addition of nutrients from compost. However, the effect of composts on plant available water (PAW) varies, depending on soil type, the type of compost and application rate. Weber et al. (2007) reported that the effect of compost application from municipal solid waste on PAW was transient, lasting only about one month after application, whereas there was no effect after two or three years. Zebarth et al. (1999) showed that poultry and food waste compost increased the water retention capacity of a sandy soil two years after application. Compost produced from organic dairy cattle manure can result in higher soil water content under Kentucky bluegrass (*Poa pratensis* L.) after 8 days without addition of water (Johnson et al. 2009).

With the prediction of prolonged dry periods in some regions in the world as a result of climate change, it is important to better understand how compost affects soil water content, nutrient uptake and plant growth under drought conditions.

The aim of this study was to assess the effect of compost addition on shoot nutrients concentrations, water availability, growth and gas exchange during drought and recovery periods of tomato plants. Tomato was used as a test plant because it is sensitive to water stress (Torrecillas et al. 1995, Rao et al. 2001, Ozenc 2008).

MATERIAL AND METHODS

Plant material. Tomato seeds (*Lycopersicon esculentum* L. cv. Grosse Lisse) were germinated on coco peat in a glasshouse under natural light conditions. After 20 days, one seedling of ~ 5 cm height was planted in a 2.9 L pot lined with a plastic bag to prevent water drainage. The pots were filled with 2.5 L sandy soil which was unamended or amended with compost either incorporated or mulched after which the pots were placed in the glasshouse. The average temperature was 22°C and relative humidity 60%. The experiment was carried out during April–May (corresponding to autumn in the southern hemisphere).

Soil and amendment treatments. The sandy soil was collected from 0–15 cm in Monarto, South Australia (35°6'S, 139°37'E), and was air-dried at room temperature and all the plant debris was removed manually before being sieved to < 2 mm. It had the following physical and chemical characteristics; sand 92.5%, silt 2.5% and clay 5%, $pH_{(H_2O)}$ 8.7, $EC_{1:5}$ 73 µS/cm, total N 387.3 mg/kg and total P 78.0 mg/kg, total organic carbon (TOC) 3.7 g/kg, available N 52.2 mg/kg and P 0.7 mg/kg, water holding capacity (WHC) 77 g/kg, and bulk density 1.2 g/cm^3.

Compost from garden (prunings and lawn clippings) and food waste ($pH_{(H_2O)}$ 8.0, $EC_{1:5}$ 1.6 mS/cm, total N 12.7 g/kg and P 2.04 g/kg, TOC 114 g/kg, available N 25.3 mg/kg and P 236.5 mg/kg) was collected from a local commercial producer. The water content of compost was 32% at the time of application. There were three treatments: without compost (control) and amended with 250 g (~ 0.35 L) compost per pot either incorporated into the soil (incorporation) or as a layer on the soil surface (mulch). This rate corresponds to a compost layer of about 2 cm, which is a common compost rate in horticulture and is equivalent to 3.7 g of total N and 0.6 g of total P per pot. For the incorporation treatment, compost and soil were mixed thoroughly and then placed into the pots. No additional nutrients were added because one aim of the experiment was to assess if compost can increase nutrient uptake compared to soil without compost addition.

Watering and transient drought stress. Twenty plants per amendment treatment were watered

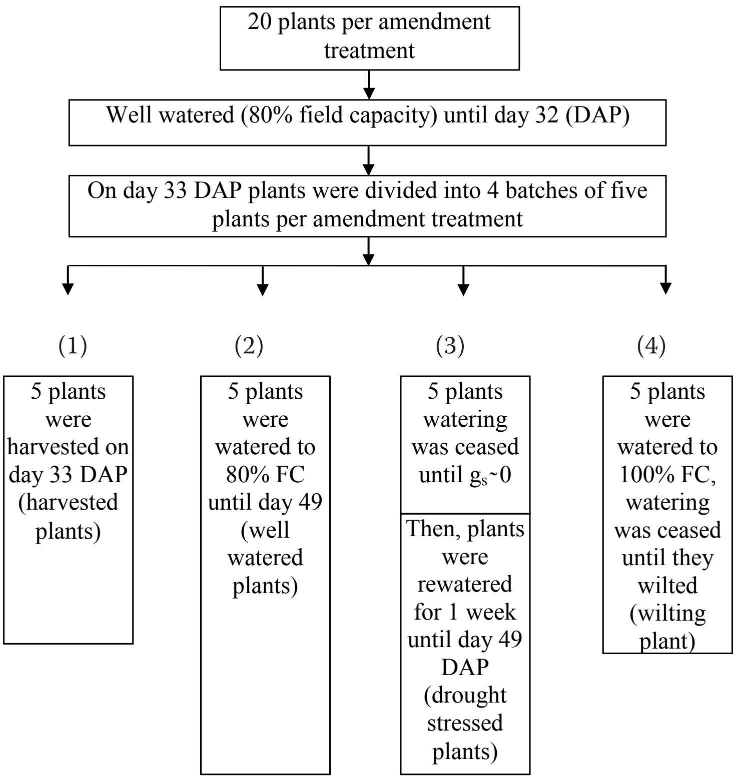

Figure 1. Schematic diagram of the water treatments. All plants were well watered to 80% field capacity (FC) until 32 days after planting (DAP). On day 33 DAP, they were divided into 4 batches of five plants per amendment treatment; 1 – harvested plants; 2 – well watered plants; 3 – drought stressed plants, and 4 – wilting plants

with reverse osmosis water every second day to maintain to 80% field capacity (FC) until day 32 (for experimental design see Figure 1). On day 33, when the plants had the first open flowers, five plants of each amendment treatment were harvested for dry mass and nutrient uptake analysis before drought stress was imposed (i.e. 1 in Figure 1). Another five plants of each treatment were maintained at 80% FC by daily watering until day 49 (i.e. well-watered plants, 2 in Figure 1). For another five plants of each amendment treatment watering was ceased until the stomatal conductance (g_s) was approximately zero at noon which was considered the point of maximum drought stress (i.e. drought stressed plants, 3 in Figure 1). Then, these plants were re-watered at 80% FC until day 49. On day 49, the plants were harvested for dry mass and nutrient uptake analysis. In addition, at day 33, five plants of each treatment (i.e. wilting plants, 4 in Figure 1) were watered to 100% FC (soil water content at FC) and then watering was ceased until all plants in a given treatment were visually wilted (water content at permanent wilting point, PWP).

Analyses. Soil texture was determined as described by Gee and Or (2002). The total organic carbon (TOC) concentration was determined by wet oxidation and titration (Walkley and Black 1934). Bulk density was calculated and the WHC was determined after Wilke (2005). The pH and EC were determined in a 1:5 soil:water extract (Rayment and Higginson 1992).

Available N and P, and total N and P were determined in soil and compost. Available N was extracted by shaking the soil or compost for 1 h with 2 mol/L KCl at a 1:10 dry soil/solution ratio and measured by the Kjeldahl method (Keeney 1982). Available P was extracted by using the anion exchange resin method after Kouno et al. (1995) and the P concentration was determined by the Murphy and Riley method (Murphy and Riley 1962). To determine total N and P in soil, compost and shoots, the material was acid-digested (6 HNO_3:$HClO_4$), and for total K with the plant material was digested with H_2SO_4. Nitrogen was measured by the distillation method (McKenzie and Wallace 1954). Phosphorus in the digest was measured by the phosphovanado-molybdate method according to Hanson (1950). Total K in the plant digests was determined by flame photometry (Herrera et al. 2008).

Data collection. Shoot length (cm) was measured weekly throughout experiment. Dry weight of shoots and roots was determined after drying in an oven at 65°C to constant weight. The roots were thoroughly washed for total root length which was determined by an image analysis system (WinRHIZO, Regent Instruments Inc., Quebec, Canada).

For wilting plants, total available water (TAW, L/pot) was determined in the pots which were watered to 100% FC and then watering was ceased until the plants had visually wilted (i.e. wilting plants). Soil water content was recorded with a time domain reflectometer probe (Hydrosense, Campbell Scientific Inc., North Logan, USA) at FC and when the plants were permanently wilted (PWP). Therefore, the total water available in the soil was calculated as the soil water content at FC minus that at the PWP (TAW = FC – PWP). Pot weights were also recorded at the FC and PWP to obtain relative pot weight loss. Time to wilting (days) was assessed from observations made at noon until all plants in a given treatment were visibly wilted.

In well-watered and drought stressed plants, the soil water content was recorded daily from the beginning until the end of the drought stress period. Water availability to the plants, after onset of the drought stress (33 days after planting, DAP) was calculated as the measured soil water content of a given day minus the soil water content at PWP obtained from the wilting plant treatment.

Photosynthetic rate (A, μmol $CO_2/m^2/s$), transpiration rate (E, mmol $H_2O/m^2/s$) and stomatal conductance (g_s, mmol/m^2/s) were measured on the third mature pentafoliate leaf from the top from the beginning of the drought stress (33 DAP) by a portable photosynthesis system (LCA4, ADC BioScientific Ltd., Hoddesdon, UK). Five plants from each amendment treatment were used to measure these parameters between 11:00 and 14:00.

Statistical analysis. All pots were arranged in a randomized complete block design with 3 amendment treatments (control, incorporation and mulch) × 2 water treatments (well-watered and drought stressed) × 5 replicates per treatment. For plants harvested before the imposed drought stress (after 33 days) and wilting plants, the assessed parameters were analyzed using one-way ANOVA ($n = 5$). For plants harvested at the end of the experiment, water availability to plants and gas exchange were analysed by three-way ANOVA [amendment treatments × water treatments × time (days after planting)]. Shoot and root dry weight and shoot nutrient concentrations were analysed by two-way ANOVA (amendment × water treatments). Differences between means were assessed using a Duncan analysis ($P \leq 0.05$) with GenStat® 11th (GenStat® for Windows® 11th Edition 2005, Hempstead, UK).

Table 1. Dry mass, root length per plant, shoot to root dry weight ratio and shoot to root length ratio, and shoot N concentration of plants grown in the unamended control or in soil with compost incorporated or mulched harvested before drought stress at 33 days after planting ($n = 5$ for dry mass and root length, and $n = 4$ for shoot N concentration)

Treatment	Dry mass (g/plant)		Root length (cm/plant)	Shoot to root ratio (g/g)	Shoot to root length ratio (g/m)	Shoot N concentration (g/kg)
	shoot	root				
Control	1.09^{a}	0.16^{a}	1187^{a}	7.36^{a}	0.10^{a}	10.50^{a}
Incorporation	3.26^{c}	0.33^{b}	1991^{b}	8.60^{ab}	0.15^{b}	14.65^{c}
Mulch	2.91^{b}	0.34^{b}	1951^{b}	10.10^{b}	0.17^{b}	12.89^{b}
$LSD_{0.05}$	0.25	0.08	479	2.1	0.03	1.67

Within columns, means followed by the same letter are not significantly different ($P > 0.05$)

RESULTS

Plant growth and nutrient concentration. There were no significant differences among amendment treatments in tomato shoot growth until two weeks after planting (data not shown). From day 22 after planting, the control plants had significantly lower shoot growth, compared to the plants with incorporated and mulched compost. In all water treatments, compost addition increased shoot and root dry weight, and root length, compared to the unamended soil, especially with the incorporated compost (Tables 1 and 2). Drought stress did not affect total shoot and root dry weight, and total root length (Table 2). Compared to the unamended control, compost addition increased the shoot-to-root dry weight and shoot dry weight to root length ratio in plants harvested before drought stress, with no differences between incorporation and mulch (Table 1, Figure 2).

Compared to the control, both incorporated and mulched compost increased tomato shoot N and K concentrations only in the drought stressed plants, but compost had no effect on shoot nutrient concentrations in the well watered plants (Tables 1 and 2). Drought stress decreased shoot P concentrations compared with well-watered plants (Table 2). Compared to the unamended soil, only incorporated compost increased soil organic C concentrations two fold and increased available P concentrations (data not shown). There were no differences in available N between amendment treatments (data not shown).

Field capacity and permanent wilting point, and total available water. Compared to the una-

Table 2. Dry mass, root length per plant and shoot nutrient concentrations of well watered and drought stressed plants grown in the unamended control or in soil with compost incorporated or mulched at 49 days after planting ($n = 5$ for dry mass and root length, and $n = 4$ for shoot nutrient concentrations)

Treatment	Dry mass (g/plant)		Root length (cm/plant)	Shoot nutrient concentrations (g/kg)		
	shoot	root		N	P	K
Well watered plants						
Control	0.76^{a}	0.14^{a}	1715^{a}	11.66^{ab}	4.75^{c}	41.10^{ab}
Incorporation	3.21^{c}	0.46^{c}	3687^{de}	12.71^{b}	4.33^{bc}	47.86^{b}
Mulch	2.42^{b}	0.39^{b}	3177^{cd}	13.22^{b}	3.58^{ab}	45.81^{b}
Drought stressed plants						
Control	0.80^{a}	0.18^{a}	2248^{ab}	10.20^{a}	3.18^{ab}	34.41^{a}
Incorporation	3.01^{c}	0.51^{c}	4282^{e}	13.18^{b}	3.19^{ab}	43.18^{b}
Mulch	2.47^{b}	0.34^{b}	2870^{bc}	12.77^{b}	2.71^{a}	44.53^{b}
$LSD_{0.05}$[1]	0.44^{ns}	0.06	728^{ns}	2.10^{ns}	1.09^{ns}	7.57^{ns}

[1]Least significant difference (LSD) for the interaction of amendment × water treatments; ^{ns}not significant. Within columns, means followed by the same letter are not significantly different ($P > 0.05$)

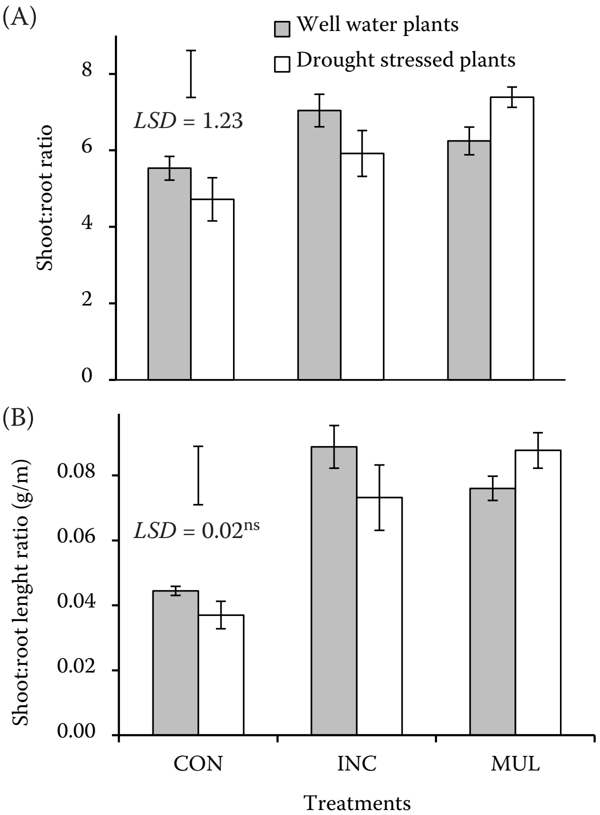

Figure 2. Shoot-to-root dry weight ratio (A) and dry shoot weight to root length ratio (B) of plant grown in control (CON), incorporation (INC) and mulch (MUL) treatments in well watered and drought stressed conditions. *n* = 5 ± standard error. Vertical bars are *LSD* for the interaction of amendment × water treatments. [ns]not significant

mended soil, incorporated and mulched compost significantly increased soil water content at FC and PWP, but only incorporated compost significantly increased TAW (Table 3). Plants without compost wilted when there was 0.08 L of water per pot, while plants with compost wilted when the water content was 0.11 L of water per pot (Table 3). Mulched compost extended the time until the plants were wilted by 2 days compared to the other two treatments. However, pots with incorporated and mulched compost lost more water during the drying period than the pots with unamended soil (Table 3).

Water availability to the plants. In the well-watered treatments, compost addition increased water availability to the plants, compared to the unamended treatment (Figure 3A). During drought stress, the amount of water per pot decreased steadily in the first 6 days (until 39 DAP) in all amendment treatments (Figure 3A). Until 38 DAP there were no significant differences in water availability among the amendment treatments.

Gas exchange. There were no significant differences in the rate of photosynthesis (A) among amendment treatments. In drought stressed plants, the rate of A decreased in plants with compost, particularly with incorporated compost, but was not affected in plants growing in the unamended soil (Figure 3B). The transpiration rate (E) and stomatal conductance (g_s) decreased in both well-watered and drought stressed plants in the first week with no differences among the amendment treatments (Figures 3C–D). After 38 DAP, the E rate was lower in the plants with incorporated compost than those in the unamended soil and mulched compost treatments (Figure 3C). In the drought stressed plants, the rate of E decreased fastest in plants with incorporated compost and slowest in the control plants (Figure 3C). After re-watering, the rate of E and g_s increased most rapidly in the plants with incorporated compost. One day after re-watering (which was 40 DAP for plants with incorporated compost, and 43 DAP for plants without compost or with mulched compost), the photosynthesis and transpiration rates of plants with incorporated compost recovered to

Table 3. Soil water content at field capacity (FC) and permanent wilting point (PWP), and total available water (TAW), days until wilting (all leaves and top tip were visually wilted) and pot weight loss; for unamended soil or soil with incorporated or mulched compost (*n* = 5). Parameters were measured in plants which were first watered to 100% FC and then water was withheld until they were permanently wilted

Treatment	Water content (L/pot)		TAW (L/pot)	Days until wilting	Pot weight loss (g/pot)
	FC	PWP			
Control	0.28^{a}	0.08^{a}	0.20^{a}	13.4^{a}	226.4^{a}
Incorporation	0.38^{b}	0.11^{b}	0.27^{b}	13.0^{a}	287.0^{b}
Mulch	0.36^{b}	0.11^{b}	0.25^{ab}	15.0^{b}	298.0^{c}
$LSD_{0.05}$	0.06	0.01	0.06	0.8	7.74

Within columns, means followed by the same letter are not significantly different (*P* > *0.05*)

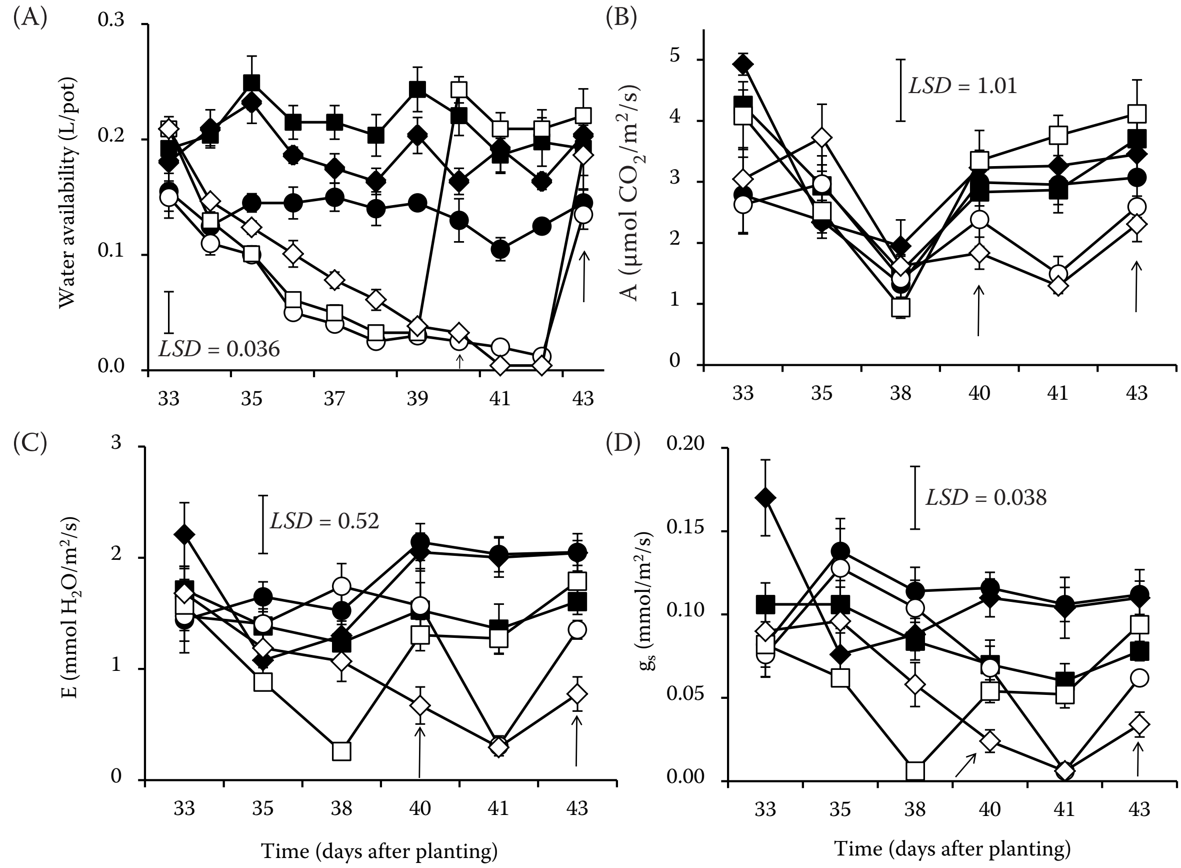

Figure 3. Water availability to plants (A), photosynthetic rate (B), transpiration rate (C) and leaf stomatal conductance (D) in well watered (solid symbols) and drought stressed plants (open symbols) during the drought stress and recovery period in control (●, ○), incorporation (■, □) and mulch (♦, ◊) treatments. Arrows indicate (from the left) 1st day after rewatering for incorporated compost (40 DAP), and mulched compost and unamended control (43 DAP). n = 5 ± standard error. Vertical bars are *LSD* for the interaction of amendment × water treatments, × time (days after planting)

the level of well-watered plants faster than in the control plants and those with mulched compost (Figure 3D).

DISCUSSION

This study showed that compost incorporation into the soil increased water availability to the plants under well-watered conditions and accelerated recovery of plants after drought stress. The rates of A and E of drought stressed plants decreased strongly during drought stress, compared to the well-watered plants. The quicker recovery of the plants with incorporated compost is most likely due the greater root system, whereas the larger shoot biomass led to greater water loss during the drought period. Mulched compost increased shoot N and P concentrations and water availability to plants during drought, but did not affect the speed of recovery after re-watering due to the smaller root system compared to the plants with incorporated compost.

General effects of compost on plant growth. The positive effect of compost on plant growth (Tables 1 and 2) is most likely due to increased nutrient availability (Curtis and Claassen 2005, Johnson et al. 2009), which in the present study resulted in increased shoot N and K concentrations (Tables 1 and 2). The shoot nutrient concentration indicated that all plants were deficient in N, thus compost addition did not provide sufficient N for plants [adequate nitrogen concentration for tomato leaves 27 to 50 g/kg (Jones 2008)]. The shoot P and K concentrations were sufficient. The increased shoot P and K concentrations with composts could be due to nutrient addition by the compost and the greater root system of the plants (Tables 1 and 2). The higher K concentration may have contributed to conservation of water during drought (low rates of A and E) and the more rapid recovery of plants with incorporated compost after re-watering because it is well known that K is important for plant water status, turgor pressure of cells, and stomata regulation (Marschner 2012).

Incorporated and mulched compost enhanced soil water content at FC and PWP but only incorporated compost increased TAW (Table 3) which is in agreement with previous studies (Curtis and Claassen 2005, Johnson et al. 2009). The increased TAW with incorporated compost is likely due to greater organic C content as organic C can increase soil WHC (Courtney and Mullen 2008).

Effect of compost in drought stressed plants. The results in this experiment confirmed several previous studies showing that water deficit stress significantly affects water relations and physiology in tomato (Rao et al. 2001, Tahi et al. 2007). After watering ceased, the water availability to the plants decreased in all amendment treatments. In plants with incorporated compost the rate of A (Figure 3B) and E (Figure 3C) as well as g_s (Figure 3D)decreased faster than in the other two treatments which can be explained by the larger shoots which would have led to greater water loss via E. Despite the strong effect on gas exchange during drought, plants with incorporated compost were able to recover rapidly after re-watering which is most likely due to the greater root system and thus ability to take up the added water (Johnson et al. 2009).

The effect of mulched compost was not as pronounced as that of incorporated compost, possibly because of the smaller root system in the drought-stressed plants with mulched compost and thus greater shoot/root and shoot/root length ratio compared to plants with incorporated compost (Figures 2A–B). The slower recovery of the plants in unamended soil and with mulched compost could be due to the smaller root system as well as the longer drought period. Miyashita et al. (2005) found that the level of the recovery of kidney bean was decreased as the drying period became longer.

This study showed that incorporated compost increased plant growth and accelerated recovery after drought stress although gas exchange was low during the drought period, compared to the unamended soil and mulched compost treatments. This response is most likely due to the larger plant size which would increase water loss via transpiration during drought period, but the larger root system would increase the ability of the plants to take up water after re-watering. Mulching had less effect than incorporation, but may help to maintain a more stable soil water content by reducing evaporation in the longer term.

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