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Metabolite changes in cucumber xylem sap under rhizosphere aeration

Hongbo Chen[1], *Xu Zhao*[2]*

[1]*Zhejiang Shuren University, Hangzhou, P. R. China*
[2]*Institute of Vegetables Shandong Academy of Agricultural Sciences, Ji Nan, P. R. China*

**Corresponding author: zx18753189832@163.com*

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Abstract: The impact of rhizosphere aeration on the composition of xylem sap in cucumber grown in soil was studied to determine its effects on (i) water and nutrient uptake, (ii) xylem transport, and (iii) amino acid synthesis in the roots. Plants grown under three different aeration conditions were subjected to progressive gas stress throughout the whole growth period. The shoot and root growth, xylem nitrate (NO_3^-) concentration, potassium (K^+) concentration, xylem sap flow rate, and amino acid concentrations were higher in the Z1 treatment plants than in the control (CK) plants, and the former also showed a lower CO_2 (0.25–0.84%) and a higher O_2 (18.22–20.02%). However, the Z3 treatment plants exhibited decreased xylem loading of amino acids, NO_3^- concentrations, and K^+ concentrations and a lower flow rate of xylem sap, which restricted shoot and root growth due to poor aeration caused by a higher CO_2 (0.75–3.68%) and a lower O_2 (11.51–18.6%). Furthermore, the xylem pH in these plants was lower by approximately 0.17 units, and the conductivity was decreased by approximately 0.31 mS/cm. Based on the observed results, the CO_2 and O_2 in the soil can potentially regulate root and shoot growth and the xylem sap composition in cucumber. Therefore, rhizosphere aeration is important for the vigorous growth of plants.

Keywords: rhizosphere CO_2; rhizosphere O_2; xylem sap; cucumber growth

Rhizosphere aeration has been recognized for years as an important factor in plant competition and crop production. Most of the research on aeration suggests that plant roots are surprisingly tolerant to low O_2 and high CO_2 partial pressures (Huang et al. 1997; Gibbs et al. 1998). Short-term experiments, however, might fail to show small differences in root growth or absorption rates of ^{18}O, which would accumulate over time (Andrews et al. 1994; Boru et al. 2003; Darwent et al. 2003).

Plants are usually under conditions of high CO_2 and low O_2 due to poor rhizosphere aeration resulting from conventional production practices (Ratcliffe et al. 1997). Poor rhizosphere aeration affects nutrient uptake and root growth and ultimately inhibits shoot growth and development (Kirk 2003). High CO_2 and low O_2 restrict both respiration and energy metabolism and lead to a decrease in the adenylate energy state (Kerbel et al. 1990; Johnson et al. 1994; Greenway et al. 2003). Xylem sap enables translocation of compounds between the roots and shoots; therefore, the flow rate and chemical composition of xylem sap are believed to indicate root activities or root health under field conditions (Kerbel et al. 1990). The composition of nitrogenous compounds in xylem sap can reflect important changes in root N metabolism (Kirk et al. 2003). N transport in the xylem occurs predominantly via amino acids and nitrate (NO_3^-). The amount of N transported as amino acids relative to NO_3^- is believed to reflect the rate of NO_3^- assimilation in the roots. Moreover, the composition of amino acids in xylem sap can change under cer-

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tain stress conditions. Non-nodulated soybean with a root system that is subjected to flooding ultimately experiences hypoxia, which leads to large increases in xylem alanine transport, and these increases are associated with changes in root metabolism (Saglio et al. 1988; Sand et al. 1998). Evidently, the amino acid composition of xylem sap can potentially be used for monitoring the response of primary N metabolism in the root system of plants in response to stress (Thomson et al. 1989; Summers et al. 2000; Lammertyn et al. 2001).

In the present study, using three different methods of rhizosphere aeration, we measured the natural changes in CO_2 and O_2 in the soil during plant development and growth. However, thus far, related studies in cucumber have emphasized changes in substances in the xylem sap because these potentially act as signals in root-shoot communication (Bown 1985; Begg et al. 1994).

MATERIAL AND METHODS

Plant materials and growth conditions. Rhizosphere aeration experiments were conducted, and cucumber (*Cucumis sativus*) was used as an indicator plant species. Cucumber seeds were observed in growth media consisting of a mixture of vermiculite and perlite (1:1, v:v) in pots in a greenhouse. Six leaves per seedling were transferred into an aeration device that was filled with loam soil. The same amounts of fertilizer and water were applied to all the pots to ensure identical environmental conditions in addition to aeration differences. The aeration device (Z) consisted of a stainless steel scaffold (S) (15 cm in width, 10 cm in height, mesh < 0.05 mm in diameter) at the bottom of the pot, and loam soil was placed on top. The function of the stainless steel scaffold is to support the upper soil and allow space for gas exchange with the air.

Treatments. Three treatments were applied via the aeration device (Z):(Z1) pipe aeration, in which a hollow pipe (15 cm in length, 2 cm in diameter) was inserted on top of the stainless steel scaffold to allow gas exchanges through the pipe; (Z2) pore aeration, which involved free diffusion of gas completely dependent on the soil pores; and (Z3) no aeration, in which the pots were sealed with plastic film and aluminum foil to ensure zero gas exchange. The control (CK) treatment lacked a stainless steel scaffold but otherwise involved traditional cultural practices. The treatments were arranged in accordance with a randomized block design and were replicated in different pots.

CO_2 and O_2 determination. The soil atmosphere was sampled through small copper tubes placed in the soil at the beginning of the experiment, and measurements were made with a Haldane gas analyzer.

Xylem sap collection. Xylem sap was collected beginning after 15 days of treatment and was sampled every 15 days – five times across all development stages. The xylem sap was collected according to the methods described by Meclure and Igiael (1979) for 5 hours (morning: 06:00–11:00) after the stems were cut. Each cut was made 2 cm above the base of the stem. The cut was washed with distilled water and blotted dry with filter paper, and the first few microliters of sap was discarded. The sap was collected with a glass capillary and transferred to a tube kept on ice at intervals of less than 2 minutes. The samples were stored and frozen until analysis. Three replicates of each treatment were included, and each replicate was composed of pooled material from the three plants in each pot.

Measurements of the xylem sap pH and conductivity. The xylem pH and conductivity were measured using pH and conductivity meters (pHM95, pH/on meter, Danmark ALS, Denmark, radiometer; CDN210, conductivity meter).

Analysis of amino acids. Individual amino acids were separated and quantified based on their O-phthaldialdehyde derivatives using an HPLC system as described previously (Puiatti, Sodek 1999). The recorded data are the means of three independent analyses.

Determination of element concentrations. The total P and NO_3^- concentrations in xylem sap were analyzed using the Kjeldahl method and the molybdovanadate method (Kai et al. 2007), respectively, using a spectrophotometer (Model UV-2401PC, Shimadzu, Tokyo, Japan). The K, Ca and Mg concentrations were assayed using an atomic absorption spectrophotometer (Model AA-6300, Shimadzu, Tokyo, Japan).

RESULTS

Effect of rhizosphere aeration on soil O_2 and CO_2. As shown in Figure 1, a significant difference in O_2 and CO_2 in the soil was found in response to the different mechanisms of aeration during development,

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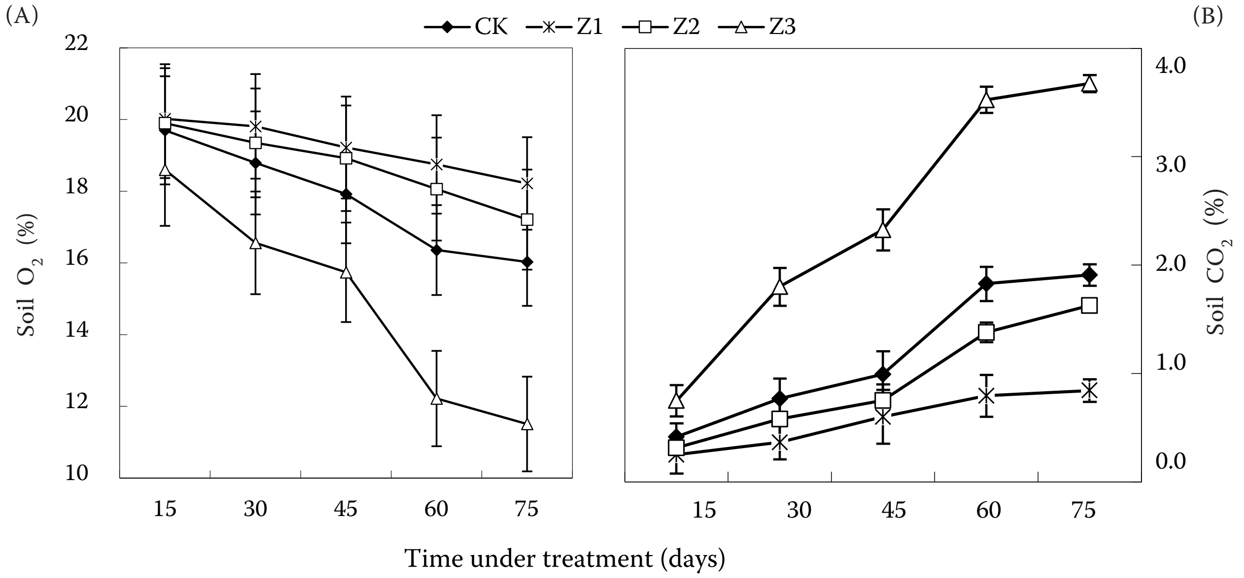

Figure 1. Effect of rhizosphere aeration on the concentration of O_2 (A) and CO_2 (B) in soil

particularly after 45 days. The O_2 showed a gradual decrease, and the CO_2 increase was accompanied by increased root respiration. At harvest, the Z1 and Z2 plants exhibited a higher O_2 (13.66%, 7.30%) and a lower CO_2 (55.85%, 14.66%) compared with the CK plants. In contrast, a lower O_2 decrease (28.19%) and a higher CO_2 (92.38%) were observed in the Z3 plants compared with the CK plants.

Effect of rhizosphere aeration on pH, conductivity and flow rate of xylem sap. As shown in Figure 2, the greatest influence of rhizosphere aeration was found on the xylem sap flow rate, followed by the sap pH and conductivity. The differences among the treatments increased gradually with increasing development. Moreover, the difference between the Z1 and Z2 plants was relatively small compared with that between the Z3 and CK plants. At harvest, the Z1 and Z2 plants showed a higher xylem sap flow rate (35.42%, 8.02%) than the CK plants, whereas the flow rate, pH and conductivity of xylem sap of the Z3 plants were reduced by 9.88%, 5.67% and 5.66%, respectively, compared with those of the CK plants. The difference in xylem sap constituents among treatments partly reflected the potential for water uptake, nutrient uptake and acropetal transport in plants, and low values were found for the Z3 plants due to poor aeration.

Effect of rhizosphere aeration on the amino acid composition of xylem sap. The amino acid concentrations at harvest were determined (Table 1), and significant differences in the total amino acid concentrations in the xylem sap were found among the treatments. Compared with that in the CK plants, the concentrations in the Z1 and Z2 plants were 26.72% and 9.89% higher, respectively, whereas the concentration in the Z3 plants was 72.37% lower. Compared with those in the CK plants, the concentrations of individual amino acids (excluding Gly and Tyr) were higher in the Z1 and Z2 plants, whereas those in the Z3 plants, with the exception of Cys and Phe, were notably lower.

Effect of rhizosphere aeration on the inorganic ion concentration in xylem sap. Throughout the growing season, as shown in Figure 3, rhizosphere aeration had a greater influence on the concentrations of NO_3^- and potassium (K^+) in xylem sap, followed by the phosphate, Ca and Mg concentrations. The ion concentrations were higher in the Z1 and Z2 plants than in the CK plants, whereas the Z3 plants showed the opposite pattern. At harvest, the Z1 and Z2 plants exhibited higher levels of NO_3^- (20.36%, 13.69%), $H_2PO_4^-$ (14.97%, 9.82%), K^+ (15.76%, 12.76%), Ca^{2+} (8.04%, 4.09%) and Mg^{2+} (5.18%, 1.67%) compared with the CK plants, whereas these compounds and elements were decreased by 9.14%, 12.50%, 20.65%, 2.96% and 4.20%, respectively, in the Z3 plants.

Effect of rhizosphere aeration on cucumber growth. Rhizosphere aeration had significant effects on plant growth (Table 2). The highest biomass was found in the Z1 plants, and the total biomass of the plants, roots, stems and leaves of the Z1 plants were 21.73%, 13.67%, 30.37% and 19.96% higher, respectively, compared with those

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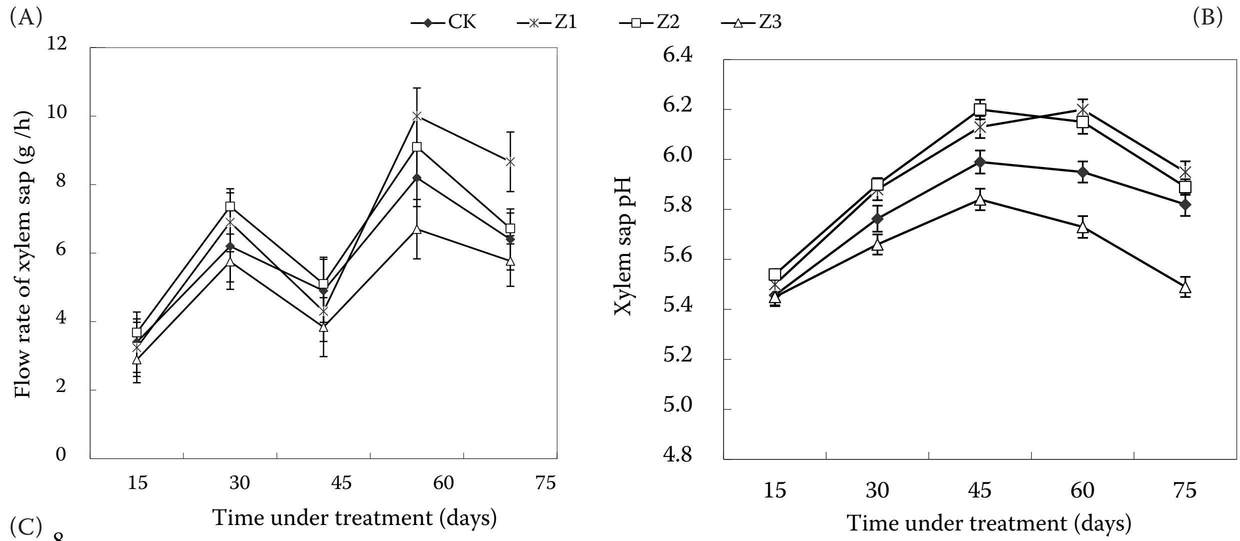

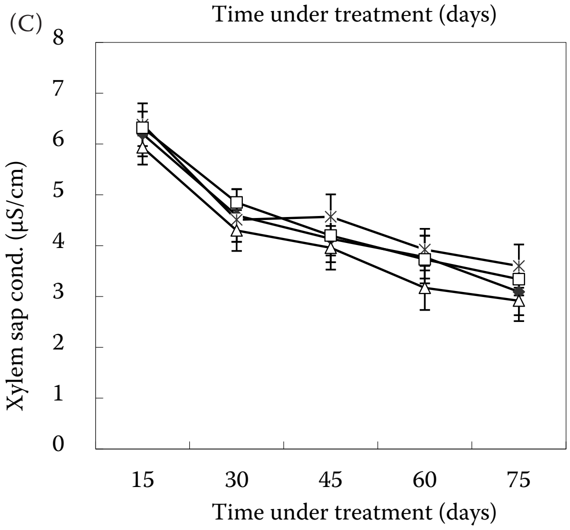

Figure 2. Effects of rhizosphere aeration on the xylem sap flow rate (A), xylem conductivity (B) and xylem pH (C)

of the CK plants. The biomass of the Z2 plants did not significantly differ from that of the CK plants, but the highest shoot-root ratio was found in the Z2 plants. In contrast, significantly suppressed shoot and root growth was detected in the Z3 plants due to poor aeration.

DISCUSSION

In the present study, cucumber roots were subjected to progressive gas stress via three different methods of rhizosphere aeration during the development and growth of the plants. With increasing development, the soil O_2 showed a gradual decrease, and the observed increase in soil CO_2 was accompanied by root respiration and poor aeration. Therefore, a negative correlation appears to exist between the soil O_2 and the soil CO_2 (GHIMIRE Archana 2022).

We found that both plant growth and xylem sap exhibited striking differences among the treatments due to differences in O_2 and CO_2 in the soil. The Z1 treatment exhibited a better aeration effect with a lower CO_2 (0.25–0.84%) and a higher O_2 (18.22–20.02%), and compared with the plants subjected to the other treatments, the Z1 plants presented greater shoot and root dry matter production, faster xylem sap flow rates and denser xylem sap compositions; in contrast, the Z3 plants accumulated less dry matter and presented less dense xylem sap compositions due to a higher CO_2 (0.75–3.18%) and a lower O_2 (11.51–18.6%). As noted by Boru et al. (2003), the adverse effect of a high CO_2 during anaerobiosis of the nutrient solution could be related to its inhibition of ethylene action, as indicated by a pronounced reduction in the number of adventitious roots of soybean plants (Visser et al. 1997; Qu Y et al. 2021). A number of researchers have observed a reduction in plant growth and decreases in metabolic activities

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Table 1. Concentrations of amino acids in xylem sap of cucumber from different aeration treatments

Amino acid	Aeration treatments (mg/L)			
	CK	Z1	Z2	Z3
Thr	269.71 ± 12.2	353.51 ± 18.5	305.47 ± 15.1	50.88 ± 17.6
Glu	41.50 ± 5.5	42.55 ± 6.1	41.20 ± 9.2	14.12 ± 9.8
Ary	18.49 ± 6.7	23.41 ± 9.5	19.44 ± 3.5	4.81 ± 2.2
Val	13.80 ± 7.9	16.42 ± 5.8	14.99 ± 6.4	7.49 ± 4.4
Lys	11.03 ± 8.1	17.19 ± 4.4	12.26 ± 4.6	4.76 ± 2.8
Ile	10.58 ± 4.6	13.48 ± 6.9	14.17 ± 1.8	2.56 ± 1.7
Cys	10.17 ± 5.3	12.42 ± 9.1	13.68 ± 7.1	10.29 ± 6.9
Phe	8.37 ± 4.5	10.18 ± 7.6	14.45 ± 4.3	8.53 ± 2.2
Met	5.83 ± 2.2	7.05 ± 3.8	4.16 ± 1.2	4.17 ± 2.5
Leu	3.33 ± 1.6	3.26 ± 2.4	3.86 ± 0.2	0.78 ± 0.5
His	3.26 ± 2.2	5.35 ± 2.5	5.06 ± 2.5	1.15 ± 0.7
Gly	2.18 ± 2.3	0.57 ± 0.1	0.86 ± 0.1	0.39 ± 0.1
Tyr	1.59 ± 0.9	0.95 ± 0.5	1.22 ± 0.3	–
Ala	0.92 ± 0.3	1.16 ± 0.8	1.02 ± 0.5	0.45 ± 0.2
Ser	–	0.33 ± 0.2	0.56 ± 0.1	0.35 ± 0.1
Total amino acids	400.75 ± 15.1	507.83 ± 10.5	452.35 ± 14.5	110.73 ± 12.5

Amino acid concentration are expressed as milligram per litre of xylem sap and are averages of three replications; standard errors are shown

under O_2-deficient conditions. A number of factors may have been responsible for these changes, and these include decreased uptake of water and nutrients, lower N metabolism in the roots and reduced xylem sap flow, which ultimately decrease the ability of compounds to translocate between the shoots and the roots (Leigh 2001).

It seems likely that ATP contents would be lower in oxygen-deficient roots due to a decrease in the rate of oxidative phosphorylation (Qi et al. 1994). Raven et al. (1994) suggested that a low O_2 may restrict respiration by decreasing the transcript levels of nucleus-encoded respiratory genes. Root respiration is a major metabolic process in the root system and is largely affected by a low O_2. Both the Cyt pathway and the cyanide-resistant alternative respiratory pathway are active in the roots. Cyt pathway respiration (terminating at cox) couples electron transport to the generation of a proton motive force for the synthesis of ATP. It is likely that this decrease was triggered by a decreased O_2 in the roots because the Cyt pathway capacity and Cox are suppressed under low O_2 conditions. When Cox activity becomes limited by O_2, the efficiency of ATP formation and the energy status are sharply reduced, which restricts cellular metabolism and function. In the present study, a decrease in the ion concentrations in the xylem sap was observed in the Z3 plants, whereas the Z1 plants showed significant increases in both anions and cations, with the exception of Mg^{2+}. Overall, the main difference in ion concentrations among the treatments was found in the con-

Table 2. Effect of rhizosphere aeration on plant growth

Treatments	Dry weight (g/plant)				Shoot/Root
	total plant	root	stem	leaf	
CK	50.24 ± 3.02^{b}	3.16 ± 0.19^{b}	10.37 ± 1.22^{ab}	36.71 ± 4.41^{b}	14.90 ± 0.89^{b}
Z1	61.16 ± 4.5^{a}	3.59 ± 0.22^{a}	13.52 ± 2.15^{a}	44.04 ± 3.12^{a}	16.01 ± 1.12^{a}
Z2	56.10 ± 4.12^{ab}	3.11 ± 0.16^{b}	9.98 ± 1.03^{ab}	43.01 ± 3.09^{a}	17.06 ± 0.91^{a}
Z3	35.11 ± 3.51^{c}	2.44 ± 0.31^{c}	7.68 ± 0.78^{c}	24.99 ± 5.13^{c}	13.39 ± 0.35^{c}

$^{a–c}$Shown as the means of four replicates ± S.D. Values followed by same letters in a column are not significantly different according to Tukey tests at 5% level

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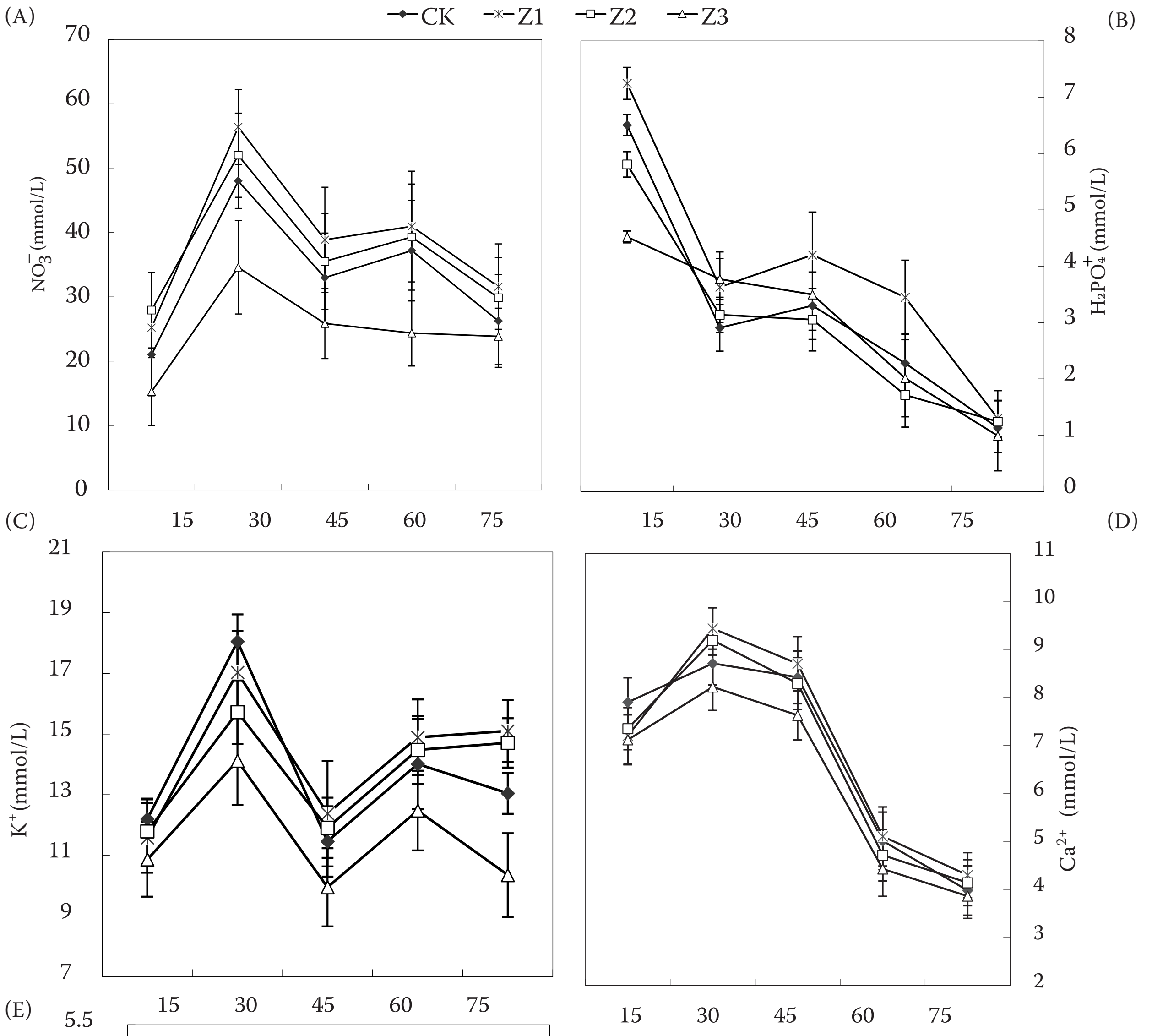

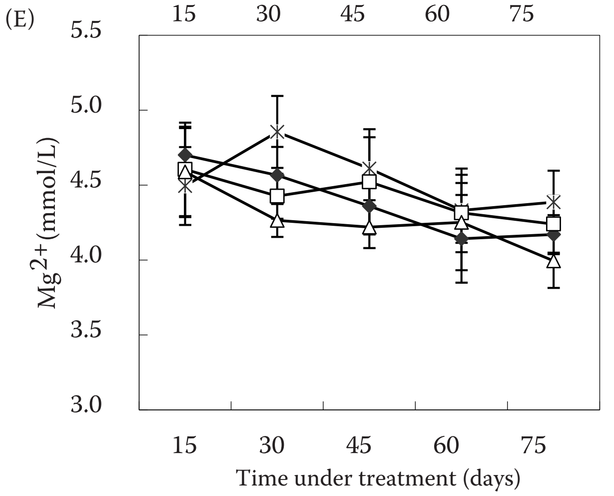

Figure 3. Effects of rhizosphere aeration on the concentrations of NO_3^- (A), $H_2PO_4^-$ (B), K^+ (C), Ca^{2+} (D) and Mg^{2+} (E) in the xylem sap of cucumber. All the data are presented in millimolar concentrations. The data are means ± SEs of three replicates

centrations of NO_3^- and K^+ under poor aeration conditions. The observed decrease was accompanied by other changes in the flow rate of the xylem sap. The decrease in xylem exudation may indicate difficulties in the absorption of water and nutrients into and through the roots due to the viscosity of water and the permeability of the membrane (Armstrong et al. 2000; Colmer, 2003a; Colmer, 2003b).

The xylem sap pH exhibited a small but significant decrease in the Z3 plants throughout the treatment

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cycle, and this decrease was on average 0.2 units lower than that observed in the CK plants. The xylem pH may be influenced by the ionic composition of xylem sap (Darwent et al. 2003). Xia et al. (1996) found that a reduction in the xylem pH was correlated with an increase in the xylem NO_3^- concentration and excess HCO_3^- in the xylem sap caused by a high CO_2. When the rhizosphere has a high level of dissolved inorganic carbon, its uptake into root cells becomes dominated by the high permeability of plant membranes to CO_2 because CO_2 is a weak acid and because plant cells rapidly take up many weak acids in their undissociated form. CO_2 produced by the aerobic catabolism of roots can be removed from the xylem stream by rapid transpiration (Dacey et al. 1982; Jackson et al. 1999), and an increase in dissolved inorganic carbon HCO_3^- in xylem sap can change the pH of the xylem sap with regard to metabolism. The usual pH of the cytoplasm of 7.5 was maintained, and every increase of 10 kPa CO_2 would result in an increase of 75—90 mM HCO_3^- in the cytoplasm. pH maintenance depends on the biochemical and biophysical pH states (i.e., regulatory systems). Furthermore, there are indications that metabolism is adversely affected when the concentration of HCO_3^- in the cytoplasm surpasses 50 mM or even a lower level; succinic dehydrogenase and cytochrome oxidase are inhibited by HCO_3^- at a concentration as low as 10 mM (Xia et al. 1996; Darwent et al. 2003).

We characterized the effect of rhizosphere aeration on the chemical composition of xylem sap in cucumber. The major change is caused by the CO_2 and O_2 in the soil (Beckett et al. 1988; Ma et al. 2001). It would also be interesting to determine whether a high CO_2 concentration is adverse to the zones receiving sufficient O_2 for oxidative phosphorylation (Bouma et al. 1997) and/or to the anaerobic zones. The components, such as amino acids and mineral nutrients, and pH of xylem sap have been shown to potentially act as signals of root-shoot communication under conditions of rhizosphere aeration. The NO_3^- concentration and xylem pH of xylem appear to be fairly sensitive parameters that may allow the plant to finely tune transpirational control under anoxic conditions (Ranathunge et al. 2004). In summary, our data demonstrated that root energy and metabolic activities that eventually suppressed plant growth decreased significantly lower when the O_2 was lower than 11.5% and the CO_2 was higher than 3.68%. Apparently, the aeration conditions are important for the vigorous growth of plants grown in soil.

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