2012

Effects of Root-Zone Temperature and N, P, and K Supplies on Nutrient Uptake of Cucumber (Cucumis sativus L.) Seedlings in Hydroponics

Qiuyan Yan

Zengqiang Duan

Jingdong Mao
Old Dominion University, jmao@odu.edu

Xun Li

Fei Dong

Original Publication Citation

Yan, Q. Y., Duan, Z. Q., Mao, J. D., Li, X., & Dong, F. (2012). Effects of root-zone temperature and N, P, and K supplies on nutrient uptake of cucumber (*Cucumis sativus L.*) seedlings in hydroponics. *Soil Science and Plant Nutrition, 58*(6), 707-717. doi:10.1080/00380768.2012.733925

Soil Science and Plant Nutrition (2012), **58**, 707–717 http://dx.doi.org/10.1080/00380768.2012.733925

ORIGINAL ARTICLE

Effects of root-zone temperature and N, P, and K supplies on nutrient uptake of cucumber (*Cucumis sativus* L.) seedlings in hydroponics

Qiuyan YAN[1], Zengqiang DUAN[1], Jingdong MAO[2], Xun LI[1] and Fei DONG[3]

[1]*State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing 210008, China,* [2]*Department of Chemistry and Biochemistry, Old Dominion University, 4541 Hampton Blvd., Norfolk, VA 23529, United States and* [3]*Agricultural Bureau of Xiangfen County, Shanxi Province, 041500, China*

Abstract

The nutrient uptake and allocation of cucumber (*Cucumis sativus* L.) seedlings at different root-zone temperatures (RZT) and different concentrations of nitrogen (N), phosphorus (P), and potassium (K) nutrients were examined. Plants were grown in a nutrient solution for 30 d at two root-zone temperatures (a diurnally fluctuating ambient 10°C-RZT and a constant 20°C-RZT) with the aerial parts of the plants maintained at ambient temperature (10°C–30°C). Based on a Hoagland nutrient solution, seven N, P, and K nutrient concentrations were supplied to the plants at each RZT. Results showed that total plant and shoot dry weights under each nutrient treatment were significantly lower at low root-zone temperature (10°C-RZT) than at elevated root-zone temperature (20°C-RZT). But higher root dry weights were obtained at 10°C-RZT than those at 20°C-RZT. Total plant dry weights at both 10°C-RZT and 20°C-RZT were increased with increased solution N concentration, but showed different responses under P and K treatments. All estimated nutrient concentrations (N, P, and K) and uptake by the plant were obviously influenced by RZT. Low root temperature (10°C-RZT) caused a remarkable reduction in total N, P, and K uptake of shoots in all nutrient treatments, and more nutrients were accumulated in roots at 10°C-RZT than those at 20°C-RZT. N, P, and K uptakes and distribution ratios in shoots were both improved at elevated root-zone temperature (20°C-RZT). N supplies were favorable to P and K uptake at both 10°C-RZT and 20°C-RZT, with no significantly positive correlation between N and P, or N and K uptake. In conclusion, higher RZT was more beneficial to increase of plant biomass and mineral nutrient absorption than was increase of nutrient concentration. Among the three element nutrients, increasing N nutrient concentration in solution promoted better tolerance to low RZT in cucumber seedlings than increasing P and K. In addition, appropriately decreased P concentration favors plant growth.

Key words: cucumber, root zone temperature, dry weight, nutrient concentration, uptake, transport ratio.

INTRODUCTION

Protected cultivation in greenhouses and plastic tunnels has been widely used for off-season growing. However, in recent years, incorrect fertilizer application in greenhouses has led to severe soil salinization and limited crop productivity (Atallah *et al.* 2002; Yu *et al.* 2004). Generally, fertilizers were usually applied to soils regardless of soil nutrient conditions and plant requirements in an equal nitrogen, phosphorus and potassium (NPK) formulation (Atallah *et al.* 2000); and the excessive nutrients which accumulated in soils were difficult for plants to absorb.

Root-zone temperature (RZT) is an important factor affecting plant growth and uptake of water and nutrient (Mozafar *et al.* 1993; Marschner *et al.* 1996; Bode Stoltzfus *et al.* 1998). Numerous studies on different

Correspondence: Zengqiang DUAN, Institute of Soil Science, Chinese Academy of Sciences, 71# Beijing East Road 210008, Nanjing, People's Republic of China. Tel: +86-25-86881562. Fax: +86-25-86881000. Email: zqduan@issas.ac.cn
Received 13 May 2012.
Accepted for publication 23 September 2012.

species have shown that plant growth is greatly influenced by root temperature (Lyr and Garbe 1995; Lahti *et al.* 2005; Solfjeld and Johnsen 2006; Díaz-Pérez *et al.* 2007; Nxawe *et al.* 2009). Actually, plant growth is controlled by various factors, especially root temperature and nutrient supply. In particular, nutrient uptake is affected by soil temperature (Xu and Huang 2006). Soil temperature may influence the physico-chemical and biological processes which affect nutrient availability in soils, and in turn affect plant nutrient uptake (Hussain and Maqsood 2011). Clarkson *et al.* (1992) reported that specific absorption rates of plant nutrients depended on soil temperature to a large extent; even a small raise in soil temperature could induce large changes in plant growth and nutrient absorption. This indicates that RZT is crucially important in plant nutrient uptake and utilization.

In cold seasons, air temperature in greenhouses can rise suddenly on sunny days from a low night temperature of 12°C to high temperatures of 30°C (Miao *et al.* 2009), while the soil or solution temperature may change slowly and stay around 10°C. So, root physiology is usually limited by low RZT, even as shoots are at a suitable temperature. Lee *et al.* (2004) reported root pressure, hydraulic conductivity and nutrients active transport were seriously reduced when roots were exposed to low temperature. So, nutrient uptake could be inhibited by low RZT (Peng and Dang 2003). In another example, tomato (*Lycopersicon esculentum* Mill.) shoot mineral element uptake was shown to be significantly slowed at RZT cooler than 15°C (Cornillon 1974). On the other hand, elevated root temperature promoted plant nutrient uptake by (1) increasing new root formation (Daskalaki and Burrage 1997; Domisch *et al.* 2002), (2) changing root physiology and improving nutrient uptake (Carey and Berry 1978; Marschner 1990; Kozlowski and Pallardy 1997), and (3) accelerating nutrient mineralization in soil (Domisch *et al.* 2002).

Over a wide range of nutrient concentrations, plant performance has been shown to be affected by different root temperatures (Niedziela, Jr. *et al.* 2008; Ambebe *et al.* 2009). Engels (1993) reported different K and P uptake rates between maize (*Zea mays* L. cv. Bastion) and wheat (*Triticum aestivum* L. cv. Star) at different root zone temperatures. Maize shoot demand for nutrients seemed to control N, and K uptake and translocation, but not P at low solution temperatures (Engels *et al.* 1992). Moreover, P uptake was usually more suppressed by low soil temperatures than the uptake of other nutrients (Bravo-F and Uribe 1981). The effect of temperature on nutrient uptake is difficult to generalize because these effects vary with different physiological processes and plant organs. In many studies, the nutrient solution was varied by increasing or decreasing the whole NPK concentration, while neglecting changes in single element concentrations and their effects at different RZT. We find that plant response to different RZT is affected by varying single N, P or K nutrient concentration. Quantification of the effects of RZT on nutrient uptake should be investigated separately for each nutrient element.

Significant research has focused on the relationship between RZT and plant utilization of nitrogen (N); such as the effect of RZT on selective absorption of nitrate (NO_3^-) and ammonium by soybean (*Glycine max* L. Merr. cv. Wells) (Duke *et al.* 1979), ryegrass (*Lolium multiflorum* and *Lolium perenne*) (Clarkson and Warner 1979), arctic plant species (Atkin and Cummins 1994), *Eucalyptus nitens* (Deane and Maiden) Maiden (Garnett and Smethurst 1999), and rose (*Rosa* × *hybrida* cv. Grand Gala) plants (Calatayud *et al.* 2008). However, little information is available on the interaction between RZT and P or K concentrations.

To some extent, this research models the soil salinization problem. The growth environment was a greenhouse, and only root temperature was controlled, the aboveground plants being exposed to the usual greenhouse conditions. The objectives of this study were: (1) to examine whether differences exist between N, P, and K effects on cucumber (*Cucumis sativus* L.) seedlings, (2) to correlate between the N, P, and K uptake and RZT to determine which element might promote growth at low RZT, (3) to provide a basis for choosing the best variety and quantity of fertilizer for the growth of season cucumber seedlings in the cold season.

MATERIALS AND METHODS

Plant materials and growth conditions

A cold-tolerant cultivar of cucumber (*Cucumis sativus* L.), Jinlv 3, was used in the present study. Seeds were germinated in a light chamber at a temperature of 28°C and a relative humidity of 70% on 14 December 2011. Two days later, the seeds with 1-cm long radicle were transplanted to a peat-vermiculite mixture [2:1, volume/volume (V/V)] in trays. After emergence of one true leaf on 4 January 2011, seedlings were transplanted to plastic pots (1 L), each pot containing 1 L of nutrient solution.

The temperature control equipment consists of a polyvinyl chloride box, plastic pots, sand, and heating wires. The internal dimensions of the polyvinyl chloride box are 240 cm long, 70 cm wide, and 20 cm deep. Each box contained 48 pots. The space between pots in the polyvinyl chloride box was filled with sand, in which heating wires (DV, Ningbo China, 800 W 100 m) were embedded. Through the heating wires, heat was

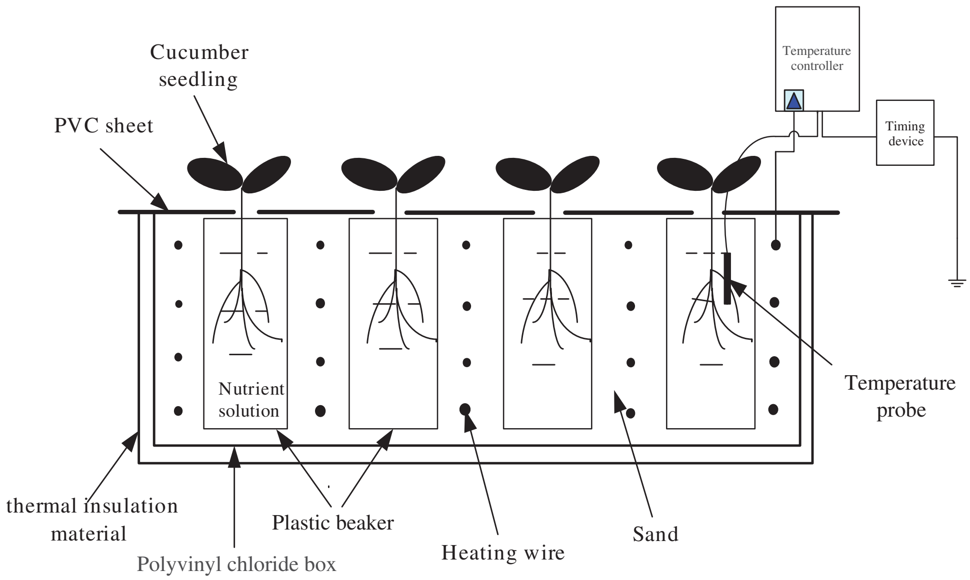

Figure 1 Partial cut-away view of the temperature control system. Cucumber, *Cucumis sativus* L.

Table 1 Nutrient treatments applied to cucumber (*Cucumis sativus* L.)†

Treatments	Nitrogen (N) (mmol L^{-1})	Phosphorus (P) (mmol L^{-1})	Potassium (K) mmol L^{-1})
Complete	7.5	0.5	3
Low-N	1.875	0.5	3
High-N	18.75	0.5	3
Low-P	7.5	0.125	3
High-P	7.5	1.25	3
Low-K	7.5	0.5	0.75
High-K	7.5	0.5	7.5

†Each treatment also contained 0.1 mmol L^{-1} of ethylenediaminetetraacetic acid ferric sodium salt (EDTA-Fe-Na), 20 µmol L^{-1} of boric acid (H_3BO_3), 5 pmol L^{-1} of ammonium molybdate [$(NH_4)_6Mo_7O_{24}$], 1 µmol L^{-1} of manganese sulfate monohydrate ($MnSO_4$), 0.2 µmol L^{-1} of copper sulfate ($CuSO_4$), and 1 µmol L^{-1} of zinc sulfate ($ZnSO_4$).

delivered to the sand, and then to the solutions in the plastic pots. Temperature was regulated by a temperature controller and timing device (Fig. 1). The temperatures were recorded by an intelligent digital recorder (LGR-WD41, Hangzhou Logger Technology. CO. LTD, China). The heating time ranged from 6:00 pm to 8:00 am the next day.

Based on 1/2 strength Hoagland's solution as the complete nutrient treatment which contained 2 mmol L^{-1} of calcium nitrate [$Ca(NO_3)_2$], 3 mmol L^{-1} of potassium nitrate (KNO_3), 0.5 mmol L^{-1} of ammonium dihydrogen phosphate ($NH_4H_2PO_4$), and 1 mmol L^{-1} of magnesium sulfate ($MgSO_4$); with total N of 7.5 mmol L^{-1}, total P of 0.5 mmol L^{-1}, and total K of 3 mmol L^{-1}. Other treatments were set as Table 1. In all treatments, calcium chloride ($CaCl_2$), potassium sulfate (K_2SO_4), sodium dihydrogen phosphate (NaH_2PO_4) and sodium nitrate ($NaNO_3$) were chosen to supplement the Ca, K, P and N deficiency, respectively. The pH of the solutions was adjusted to 6.2–6.4 with 0.1 mol L^{-1} sodium hydroxide (NaOH) or 0.1 mmol L^{-1} hydrochloric acid (HCl). The nutrient solutions were changed weekly in order to ensure a consistent nutrient supply. A completely randomized block design was used with 12 replicates (pots) for each nutrient treatment.

Plants were grown in polycarbonate greenhouse at one of two different nutrient solution temperatures while their aerial parts were subjected to the same air temperature conditions. Plant roots were subjected to each treatment from the day when they were transferred to the root-containers. They were allowed to acclimate to the nutrient concentration for one week and then exposed to different root temperature for three weeks. After four weeks from planting, a sample of eight plants with the same growth vigor was selected from each temperature-nutrient treatment from each box.

Determination of plant dry weight

Plants were separated into shoot and root tissues after the whole plants were removed from the pots. Before weighing, the fresh shoots and roots were dried carefully at 105°C for 30 min, and then further dried at 80°C for 24 h.

Nutrient element measurements

Fresh plants were separated into shoot and root tissues, and then washed with tap water followed by distilled

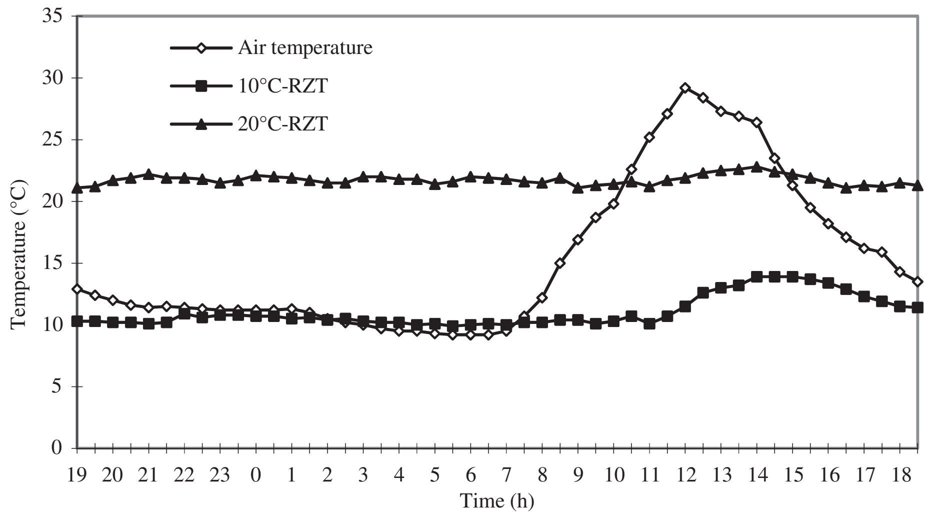

Figure 2 Diurnal variations of air and root-zone temperatures (RZT) in a day from 7:00 pm to 8:00 am the next day (14–15 January 2011).

water. Seedlings were oven-dried at 80°C for 48 h and weighed. The dry samples were ground to pass through a 0.5-mm screen. 0.3 g dry samples of shoots or roots were soaked in 10 mL sulfuric acid (H_2SO_4) for 24 h then digested in digestion systems in a fume hood, heated to 180°C for 3 h, followed by the addition of 5 mL hydrogen peroxide (H_2O_2). The extracted solution was transferred to 100-mL volumetric flasks, then diluted to 100 mL with deionized water for N, P, and K assays. The N concentration was analyzed using the automatic Kjeldahl apparatus method (K9840). P concentration was measured using the molybdate-blue colorimetry method (Murphy and Riley 1962). K concentration was determined with a flame photometer (Model 410, USA).

Statistical analysis

Analysis of variance (ANOVA) and multiple comparisons (least significant difference [LSD]) was performed using SPSS (17.0) software with Duncan's multiple range test (DMRT) at the 5% level.

RESULTS

Diurnal variations of air-and root-zone temperatures

Figure 2 showed the air- and root-zone temperature changes. The unheated nutrient solution temperatures, ranged from 8°C at 6:00 pm to 11.9°C at 8:00 am of the next day, for the treatment of 10°C ± 2 (10°C-RZT), with the heated solution temperature was kept at constant 20°C ± 2 (20°C-RZT) during this period.

Growth of cucumber seedlings

The leaf number was five in all nutrient treatments at 10°C-RZT and six at 20°C-RZT. Leaf areas were ranged from 85.17 to 132.56 cm^2 at 10°C-RZT and 121.47 to 174.43 cm^2 at 20°C-RZT, respectively (data not shown). The dry weight from each treatment was listed in Table 2. Under the same nutrient level treatment, total plant and shoot dry weights at 20°C-RZT were significantly higher than those at 10°C-RZT. At 10°C-RZT, total plant and shoot dry weights were increased with higher N concentration. Significantly higher total plant and shoot dry weights were obtained in High-N and Low-P treatments than in other nutrient treatments. At 20°C-RZT, total plant dry weight in High-N was significantly higher than those of other nutrient treatments, followed by Low-P and High-K. Shoot dry weights in most nutrient treatments had no significant difference. The highest total plant and shoot dry weights were observed under High-N treatment at both 10°C-RZT and 20°C-RZT. Root dry weights in most nutrient treatments had no significant difference between 10°C-RZT and 20°C-RZT, except the highest root dry weight in High-N treatment at 10°C-RZT. Shoot-to-root ratios had no significant difference at 10°C-RZT, but significant difference was observed in Complete and Low-P nutrient treatments at 20°C-RZT.

Nutrient concentration and uptake in different organs of cucumber seedlings

Concentrations and uptake of mineral elements in the shoots and roots were strongly affected by the interacting effects of root-zone temperature (RZT) and nutrient solution concentration (Fig. 3). Nevertheless, not all

Table 2 Effects of root zone temperature (RZT) and nitrogen (N), phosphorus (P), and potassium (K) supplies on dry weight and shoot-to-root ratio values of cucumber (*Cucumis sativus* L.) seedlings†

		Dry weight (g Plant^{-1})			
RZT	Nutrient treatment	Total plant	Shoot	Root	Shoot-to-root ratio
10°C-RZT	Complete	1.37d	1.13d	0.24bc	4.69d
	Low-N	1.24d	1.04d	0.20bcd	5.08d
	High-N	1.96c	1.61bc	0.36a	4.50d
	Low-P	1.88c	1.60bc	0.28ab	5.71d
	High-P	1.65cd	1.39cd	0.26b	5.25d
	Low-K	1.54d	1.29cd	0.25bc	5.17d
	High-K	1.25d	1.05d	0.21bcd	5.10d
20°C-RZT	Complete	2.09c	1.93ab	0.16cd	12.13a
	Low-N	1.90c	1.66bc	0.25bc	6.72d
	High-N	2.41a	2.18a	0.23bc	9.45bc
	Low-P	2.23b	2.01ab	0.22bc	9.08bc
	High-P	1.96c	1.85ab	0.12d	15.91a
	Low-K	1.78cd	1.62bc	0.16cd	10.06b
	High-K	2.29b	2.09a	0.20bcd	10.35b

†Values followed by different letters within a column indicated significant differences at $P < 0.05$.

elements were affected to the same extent. Plants grown at the lower temperature solution (10°C-RZT) showed lower levels of N concentrations in the shoots, but higher N concentrations than those at the elevated temperature solution (20°C-RZT) (Fig. 3a). At 10°C-RZT in all nutrient treatments, the N concentrations in shoots and roots had little difference, while higher N concentrations in shoots were found than those in roots at 20°C-RZT in all nutrient treatments. Moreover, shoot and root N concentrations in high-N and complete were higher than those in low-N treatments at 10°C-RZT, while shoot and root N concentrations increased as the solution N concentration increased at 20°C-RZT. At 20°C-RZT, shoot and root N concentrations in all P and K treatments were higher than those in complete (Fig. 3a). More N was accumulated in shoots than in roots at both temperatures (Fig. 3b). For all nutrient treatments, shoot N uptake at 20°C-RZT was higher than that at 10°C-RZT, but root N uptake at 10°C-RZT was higher than that at 20°C-RZT (Fig. 3b). N uptake increased with increasing N concentration in solution at the two RZT. Low-P treatment promoted N uptake. N uptake in K treatments was different at the two RZT. N uptake at 10°C-RZT decreased as the K concentration increased, but higher N uptake was obtained in High-K than Complete and Low-K treatments at 20°C-RZT (Fig. 3b).

P concentrations in most nutrient treatments of shoots were higher than those of roots at both temperatures except for a slight difference between P concentrations of shoots and roots under Low-N treatment at 10°C-RZT. Greater differences between those of shoots and roots were found at 20°C-RZT (Fig. 3c). Furthermore, shoot P concentrations were obviously promoted at 20°C-RZT compared to those at 10°C-RZT regardless of the solution nutrient concentration (Fig. 3c). Shoot P concentrations under Low-N and High-N at 10°C-RZT were lower than those of the Complete, but at 20°C-RZT they were higher than the Complete. Root P concentrations decreased as the solution N concentration increased (Fig. 3c). Shoot P concentrations under High-P and complete at 10°C-RZT had no difference and lower P concentration was obtained under Low-P treatment. Root P concentrations under Low-P and High-P treatment were lower than those in the Complete (Fig. 3c). There was no difference between P concentrations of Low-K and Complete treatment, but a lower value under High-K treatment at 10°C-RZT was observed. Root P concentration at 10°C-RZT increased as the solution K concentration decreased (Fig. 3c). Both shoot and root P concentrations at 20°C-RZT increased as the solution P concentration increased. Shoot P concentrations under Low-K and High-K were higher than those of the Complete, while root P concentration decreased as solution K concentration increased (Fig. 3c). The lowest level P concentration was observed under Low-P treatment in both shoots and roots at the two RZT (Fig. 3c). On the other hand, shoot P uptake was evidently promoted in all nutrient treatments after increasing the root temperature, but root P uptake at 20°C-RZT was relatively lower than that at 10°C-RZT (Fig. 3d). In most nutrient treatments at 10°C-RZT, shoot P uptake increased as the solution nutrient concentration increased, except for a decrease of P uptake with increased solution K concentration (Fig. 3d). Shoot P uptake at 20°C-RZT increased with the increasing

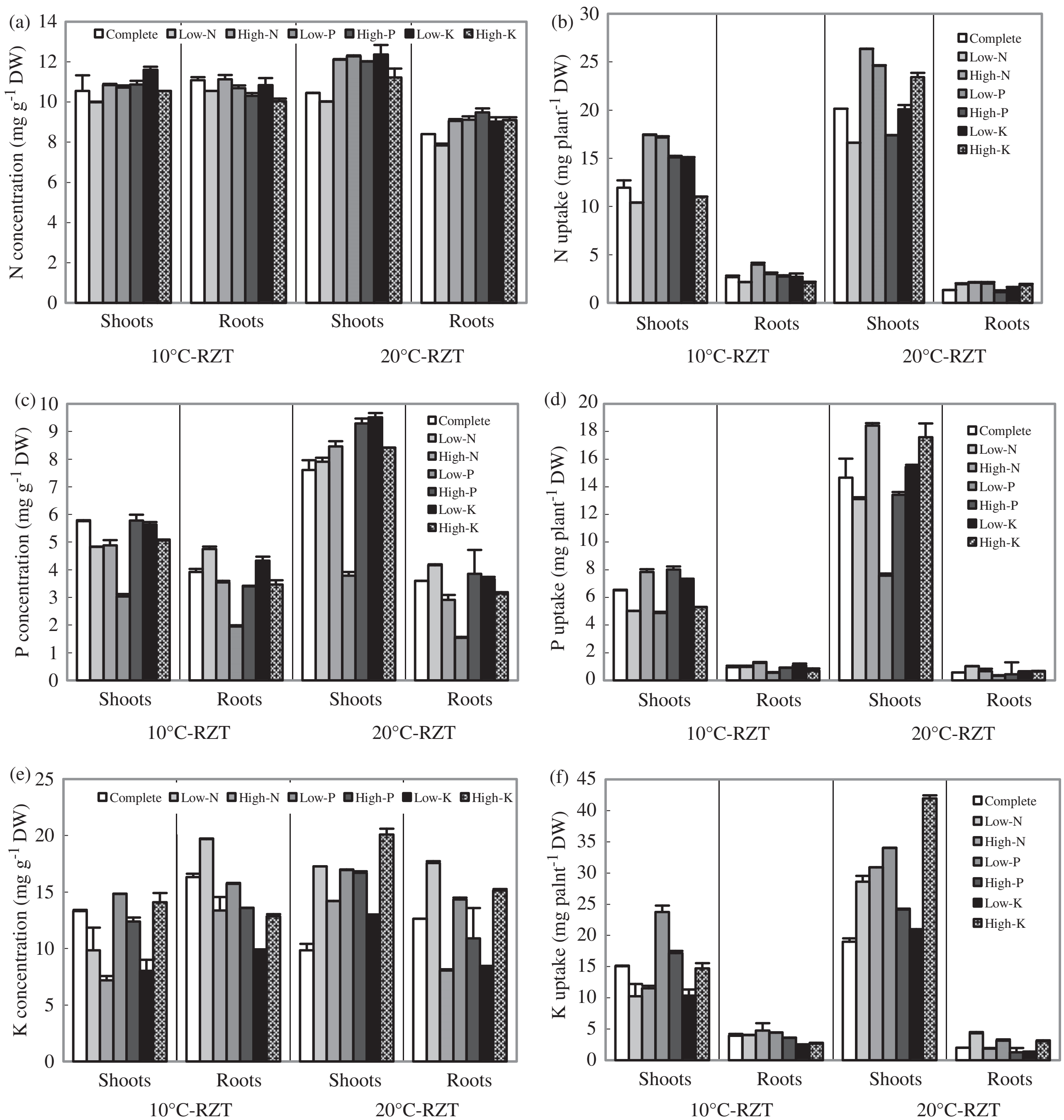

Figure 3 Effects of root-zone temperature (RZT) and nitrogen (N), phosphorus (P), and potassium (K) supplies on nutrient concentrations [mg g^{-1} dry weight (DW)] and uptake (mg Plant^{-1}DW) in different organs of cucumber (*Cucumis sativus* L.) seedlings. Error bars indicate standard errors of the averages of three replicates.

solution N concentration, but was inhibited under Low-P and High-P treatment compared to complete, and promoted under High-K and Low-K treatments (Fig. 3d).

In contrast to P concentration, shoot and root K concentration was more sensitive to changes in solution nutrient concentration than to RZT (Fig. 3e). At 10°C-RZT, shoot K concentrations were inhibited under High-N and Low-N treatments, whereas root K concentration decreased as the solution N concentration increased (Fig. 3e). K concentration in shoots decreased as the solution P concentration increased, while root K concentration was inhibited under Low-P and High-P treatments (Fig. 3e). Shoot K concentration improved as solution K concentration increased, but root K

Table 3 Effects of root zone temperature (RZT) and nitrogen (N), phosphorus (P), and potassium (K) supplies on total nutrient uptake of cucumber (*Cucumis sativus* L.) seedlings

		N uptake (mg Plant^{-1}DW)		P uptake (mg Plant^{-1}DW)		K uptake (mg Plant^{-1}DW)	
RZT	Nutrient treatments	Total N uptake	To complete (%)	Total P uptake	To complete (%)	Total K uptake	To complete (%)
10°C-RZT	Complete	13.48d	100	7.45cd	100	18.98cd	100
	Low-N	12.53d	92.99	5.98d	80.28	14.25d	75.08
	High-N	21.36b	158.46	9.10c	122.14	16.29cd	85.82
	Low-P	20.16b	149.52	5.40d	72.52	28.16bc	148.31
	High-P	17.80c	132.03	8.91c	119.53	20.75c	109.31
	Low-K	17.66c	131.01	8.34c	111.87	12.78d	67.31
	High-K	13.08d	97.07	5.99d	80.45	17.37cd	91.52
20°C-RZT	Complete	21.47b	100	15.23b	100	20.97c	100
	Low-N	18.53bc	86.3	14.14b	92.8	32.94b	157.03
	High-N	28.43a	132.37	19.08a	125.27	32.75b	156.13
	Low-P	26.61a	123.91	7.92cd	51.98	37.15ab	177.09
	High-P	18.47bc	86.02	13.87b	91.06	25.41c	121.14
	Low-K	21.52bc	100.21	16.03ab	105.24	22.20c	105.83
	High-K	25.27a	117.66	18.21a	119.55	44.99a	214.46

†Values followed by different letters within a column indicated significant differences at $P < 0.05$. DW, dry weight.

concentration was inhibited under higher and lower K treatments (Fig. 3e). At 20°C-RZT, shoot K concentration in all treatments was higher than in the complete (Fig. 3e). Root K concentration was suppressed under high N and P concentrations, but increased as the solution K concentration increased (Fig. 3e). The largest K concentration was found in the Low-N treatment in roots (Fig. 3e). Similar to N and P uptake, shoot K uptake was also promoted by increased root-zone temperature, with more K accumulated in roots at 10°C-RZT than 20°C-RZT (Fig. 3f). Shoot K uptake at 10°C-RZT was higher in Low-P and High-P treatments than in the complete, whereas at 20°C-RZT shoot K uptake was improved in all other element treatments compared to the complete treatment (Fig. 3f).

Total nutrient uptake by cucumber seedlings

For each nutrient treatment, total N, P and K uptake at 20°C-RZT was promoted than that at 10°C-RZT (Table 3). At 10°C-RZT, total N uptake under High-N and Low-P was significantly higher than that of other nutrient treatments. Total P uptake and total K uptake in most nutrient treatments had no significant difference (Table 3). Highest total N and P uptake was observed under High-N treatment, whereas more total K uptake was obtained under Low-P treatment at 10°C-RZT (Table 3). At 20°C-RZT, total N uptake under High-N, Low-P and High-K treatments was significantly higher than that of other nutrient treatments. Total P uptake under High-N and High-K was significantly higher than that of other nutrient treatments. Total K uptake was promoted in all nutrient treatments compared with the Complete, and total K uptake under High-K treatment was significantly higher than that of other nutrient treatments (Table 3).

Shoot nutrient uptake were increased at the same nutrient level after elevating RZT compared with 10°C-RZT, ranging from 15.21% (High-P) to 112.52% (High-K) of N, from 55.92% (Low-P) to 232.51% (High-K) of P, and from 40.62% (High-P) to 184.51% (High-K) of K (Table 4). However, root N uptake decreased at 20°C-RZT in all nutrient treatments, ranging from −59.61% to −10.35%. Root P uptake also decreased at 20°C-RZT, except for a 5.85% increase in the Low-N treatment. Root K uptake decreased in most nutrient treatments except for Low-N and High-K treatments (Table 4). High root-zone temperature facilitated the nutrient distribution to shoot more than cold solution temperature. Shoot N, P, and K distribution ratios in all nutrient treatments at 20°C-RZT were higher than those at 10°C-RZT (Table 5). However, more N, P and K were accumulated in roots at 10°C-RZT than those at 20°C-RZT (Table 5). Total N, P, and K uptake showed no significant correlation with each other at both 10°C-RZT and 20°C-RZT (data not shown).

DISCUSSION

Low root-zone temperature (10°C-RZT) suppressed the increase of shoot biomass of cucumber seedlings under each nutrient treatment, but a relative higher root dry

Table 4 Increased percentages of shoot and root nitrogen (N), phosphorus (P), and potassium (K) uptake at 20°C-RZT compared with those at 10°C-RZT at the same nutrient level

	N uptake (%)		P uptake (%)		K uptake (%)	
Treatments	Shoots	Roots	Shoots	Roots	Shoots	Roots
Complete	86.28	−49.99	125.16	−39.43	26.02	−48.93
Low-N	59.89	−10.35	161.34	5.85	179.56	7.56
High-N	51.39	−47.44	134.70	−46.94	167.89	−61.07
Low-P	43.31	−32.92	55.92	−38.00	43.09	−28.36
High-P	15.21	−59.61	67.48	−50.14	40.62	−64.71
Low-K	34.12	−46.18	112.61	−45.20	101.51	−44.17
High-K	112.52	−10.83	232.51	−10.58	184.51	15.90

RZT, root-zone temperature.

Table 5 Effects of root-zone temperature (RZT) and nitrogen (N), phosphorus (P), potassium (K) supplies on the shoot and root nutrient distribution ratios of cucumber (*Cucumis sativus* L.) seedlings†

		N distribution ratio (%)		P distribution ratio (%)		K distribution ratio (%)	
RZT	Nutrient treatments	Shoots	Roots	Shoots	Roots	Shoots	Roots
10°C-RZT	Complete	81.72	18.28	87.34	12.66	79.28	20.72
	Low-N	82.84	17.16	83.83	16.17	71.82	28.18
	High-N	81.46	18.54	86.16	13.84	70.79	29.21
	Low-P	85.16	14.84	89.93	10.07	84.37	15.63
	High-P	84.71	15.29	89.94	10.06	82.74	17.26
	Low-K	84.71	15.29	87.09	12.91	80.93	19.07
	High-K	84.25	15.75	88.14	11.86	84.83	15.17
20°C-RZT	Complete	93.78	6.22	96.25	3.75	90.42	9.58
	Low-N	89.59	10.41	92.75	7.25	86.88	13.12
	High-N	92.68	7.32	96.50	3.50	94.34	5.66
	Low-P	92.46	7.54	95.74	4.26	91.51	8.49
	High-P	94.05	5.95	96.78	3.22	95.03	4.97
	Low-K	93.25	6.75	96.32	3.68	93.87	6.13
	High-K	92.73	7.27	96.51	3.49	93.21	6.79

†Distribution ratio = shoot or root nutrient uptake/total nutrient uptake.

weight at 10°C-RZT than those at 20°C-RZT was observed. Similar responses of shoot growth to different RZT have been observed for seedlings of *Eucalyptus nitens* (Garnett and Smethurst 1999), melon (*Cucumis melo* L.) (Y.P. Zhang *et al*. 2008), wheat (Equiza *et al*. 2001) and trembling aspen (*Populus tremuloides* Michx.) (Wan *et al*. 1999). However, the responses of roots to RZT were different among these species. For example, Wan *et al*. (1999) reported that the root growth of trembling aspen seedlings at 10°C was lower than that at 20°C soil temperature. In contrast, in the present study root biomass of cucumber seedlings at 10°C was higher than those at 20°C. In agreement with our results, Lyr and Garbe (1995) also found a higher root mass in *Pinus sylvestris* L. at 10°C than at 20°C. Low root temperature usually resulted in lower shoot-to-root ratio (Clarkson and Warner 1979). In the present study, significantly lower shoot-to-root ratios were found in most nutrient treatments at 10°C-RZT than at 20°C-RZT.

Furthermore, we found that low nutrition is probably not the major factor leading to lower biomass in cucumber seedlings at low RZT (10°C-RZT). These results are similar to what Zhang and Dang found (Zhang and Dang 2007). Low soil temperatures could slow the nutrient uptake rates (such as N) that they turned out to limit vegetative growth rates (Clarkson and Warner 1979). However, at 20°C-RZT, plant dry weights were significantly affected by nutrient concentrations, which increased with increasing N and K concentrations. This indicates that low RZT inhibited high nutrient concentration effects on plant growth (Setter and Greenway 1988).

In addition, higher shoot N, P, K nutrient concentrations and uptake were obtained at 20°C-RZT than at

10°C-RZT. It can be concluded that higher shoot nutrient concentration has a greater effect on plant growth at elevated RZT. Similarly, Daskalaki and Burrage (1998) reported that all nutrients [N, P, calcium (Ca), and K] uptake of cucumber could be promoted significantly when root temperature was increased from 12°C to 20°C. Hood and Mills (1994) also found RZT near 22°C produced higher growth and nutrient uptake of snapdragon (*Antirrhinum majus* L. 'Peoria') compared to 8 and 15°C. Element concentrations in difference parts of organs in Scots pine seedlings increased as the soil temperature increased (Domisch *et al.* 2002). Nutrient uptake by cucumber seedlings at 10°C-RZT probably was reduced due to low root nutrient transport, and more nutrients were accumulated in roots (Table 4). The higher nutrient distribution ratio in shoots at 20°C-RZT resulted in increased stem growth and thus higher shoots nutrients concentrations (Lahti *et al.* 2005).

Differences in nutrient uptake existed between species affected by RZT. For example, increasing solution temperature at 14°C ± 2 and 20°C ± 2 in cucumbers showed an increased NO_3^- uptake, with no effect on phosphate uptake compared to unheated treatment. For melons (*Cucumis melo* L. cv. Arava), increased phosphate uptake was observed with elevated solution temperature (Urrestarazu *et al.* 2008). While Cumbus and Nye (1981) found shoot N concentrations of rape (*Brassica napus* cv. Emerald) were little affected by root temperature.

N nutrient uptake was stimulated by increased N supply and high soil temperature, which is in agreement with Gavito *et al.* (2001). Reddy and Portier (1987) indicated that ^{15}N fertilizer uptake by *Typha latifolia* L. was 5.3% at 10°C, 37.5% at 20°C of applied N in the soil and N uptake increased with N application under greenhouse conditions. We found that a supply of high concentration of N at low RZT increased P uptake. A shortage of N may decrease P and K uptake at the two root-zone temperatures, but a shortage of P favors K uptake. Shoot N concentrations of *Eucalyptus nitens* at 10°C for pre-treated plants were lower than those at 20°C for pre-treated plants (Garnett and Smethurst 1999). This result is in agreement with our findings with cucumber seedlings. Nevertheless, the same root N concentration was found at both 10°C and 20°C in *Eucalyptus nitens* (Garnett and Smethurst 1999). In contrast, we found higher N concentrations in roots at 10°C than those of 20°C. N element concentration, NO_3^-, and amino acids in leaves of tomato increased at all of the heated regimes: constant, day, and night root heating compared to no heating, while higher N concentration was found in no heated treatment than in heated treatments, as noted by Gent and Ma (2000). The extent of growth reduction showed direct relationships with solution N concentration and was inhibited by low root temperature, possibly due to reduced NO_3^- reductase in the plants (Atkin and Cummins 1994). Therefore, increasing solution N concentrations could improve cucumber seedlings growth and yield, and simultaneously promote plant N, P and K uptake at both 10°C-RZT and 20°C-RZT. Solution NO_3^- uptake was improved when plants were grown in the cold solution to obtain higher amounts of nutrients with less water absorption (Calatayud *et al.* 2008). Romero *et al.* (1999) reported that plant N and P concentrations generally increased with increasing N level in solutions, but not with that of P. We also found that increasing RZT enhanced N utilization and more N was absorbed by plants. For example, at the same Low-N concentration level, plant total N uptake at 20°C-RZT was increased by 47.88% compared to that at 10°C-RZT, almost equal to the total N uptake at High-N level at 10°C-RZT.

Low P level treatment did not significantly inhibit plant biomass, possibly owing to the fact that increased N and K uptake facilitated plant growth. In addition, the transportation of assimilates from aboveground to root was improved under Low-Pcondition and the utilization efficiency of assimilates by roots was also promoted (Rufty, Jr. *et al.* 1993). Moreover, low P concentration positively affected taproot elongation (Sánchez-Calderón *et al.* 2005). Shoots P and K uptake was significantly increased at the higher RZT. Gosselin and Trudel (1983) also demonstrated that raising the root zone temperature to 24°C increased the shoot P and K concentrations of tomato compared to those at 12 or 15°C. High-P concentrations at 10°C-RZT improved total N, P, and K uptake, while N and P uptake was inhibited under High-P treatment at 20°C-RZT, but a higher total K uptake was observed. Also, a negative interaction between P and K uptakes was found at 10°C-RZT (data not shown). On the other hand, the effect of high K concentrations on nutrient uptake depended on the treated root temperature. The N, P, and K uptake did not increase with the solution K concentration increase at 10°C-RZT, but did increase at 20°C-RZT. This indicated K^+ is more sensitive to root temperature. Therefore, it is necessary to take into account RZT when estimating the effect of K on cucumber.

Low nutrient uptake was not the result of weak root nutrient uptake, because root nutrient uptake at 10°C-RZT was higher than that at 20°C-RZT. This might be due to the decrease in nutrient metabolic rates from root to shoot at low temperatures (Adam *et al.* 2003). Gent and Ma (2000) also revealed that low temperatures restrained NO_3^- translocation from roots to leaves more than roots uptake from soils. A better understanding of the relationship between nutrient metabolism and transport from roots to shoots is needed and should be the subject of further study.

Conclusion

In greenhouse conditions, major elements such as N, P, and K fertilizers were required for plant growth, but the effectiveness of N, P, and K nutrient concentrations were affected by root temperatures. Low root-zone temperature (10°C-RZT) suppresses or decreases the biomass and nutrient uptake of cucumber seedlings. Slow growth at a low root temperature of 10°C was not associated with a shortage of nutrient uptake in root. More nutrients are accumulated in roots and less are transported to shoots at 10°C-RZT compared to those at 20°C-RZT. At higher root temperatures, however, plant dry weight and total N, P, and K uptake are all improved under each nutrient treatment, and higher nutrient distribution ratios in shoots induce higher shoot nutrient uptake for better growth. Moreover, higher nutrient concentrations usually favor plant nutrient uptake with the increase of RZT, but low RZT inhibits the effects of high nutrient concentration supply except for N. Moreover, plants grown in low P concentration have higher biomass performance at low temperature. Therefore, nutrient types and appropriate proportions should be taken into account in order to allow plants to absorb nutrients effectively at low RZT. Added fertilizer N is more important and crucial for cucumber growth during the cold growing season than other mineral elements. Suitably decreased P concentration favors plant biomass formation. Besides, properly increasing night-time RZT in winter may increase nutrient uptake and utilization, as well as reduce the overuse of fertilizers.

ACKNOWLEDGMENTS

This work was financially supported by the National Natural Science Foundation of China (No. 41101272).

REFERENCES

Adam ML, Michael Kell J, Graves WR, Dixon PM 2003: Net nitrate uptake by red maple is a function of root-zone temperature. *J. Plant Nutr.*, **26**, 203–222.

Ambebe TF, Dang QL, Li JL 2009: Low soil temperature inhibits the effect of high nutrient supply on photosynthetic response to elevated carbon dioxide concentration in white birch seedlings. *Tree Physiol.*, **30**, 234–243.

Atallah T, Darwish T, El Moujabber M 2002: Modality of fertigation of protected cucumber and nitrogen use efficiency under field conditions. *In* Water Balance: Fertigation for Crop Improvement in West Asia. Results of a Technical Cooperation Project, IAEA-TECDOC-1266, Ed. International Atomic Energy Agency, pp. 41—48. IAEA, Vienna.

Atallah T, Darwish T, Ward R 2000: Modality of fertigation of protected cucumber and nitrogen use efficiency in closed systems. *Leb. Sci. J.*, **1**, 27–32.

Atkin OK, Cummins WR 1994: The effect of root temperature on the induction of nitrate reductase activities and nitrogen uptake rates in arctic plant species. *Plant Soil*, **159**, 187–197.

Bode Stoltzfus RM, Taber HG, Aiello AS 1998: Effect of increasing root-zone temperature on growth and nutrient uptake by 'Gold Star' muskmelon. *J. Plant Nutr.*, **21**, 321–328.

Bravo-F P, Uribe EG 1981: Temperature dependence of the concentration kinetics of absorption of phosphate and potassium in corn roots. *Plant Physiol.*, **67**, 815–819.

CalatayudÁ, Gorbe E, Roca D, Martínez PF 2008: Effect of two nutrient solution temperatures on nitrate uptake, nitrate reductase activity NH_4^+ concentration and chlorophyll a fluorescence in rose plants. *Enviro. Exp. Bot.*, **64**, 65–74.

Carey RW, Berry JA 1978: Effects of low temperature on respiration and uptake of rubidium ions by excised barley and corn roots. *Plant Physiol.*, **61**, 858–860.

Clarkson DT, Jones LHP, Purves JV 1992: Absorption of nitrate and ammonium ions by *Lolium perenne* from flowing solution cultures at low root temperatures. *Plant Cell Environ.*, **15**, 99–106.

Clarkson DT, Warner AJ 1979: Relationships between root temperature and the transport of ammonium and nitrate ions by Italian and perennial ryegrass (*Lolium multiflorum* and *Lolium perenne*). *Plant Physiol.*, **64**, 557–561.

Cornillon P 1974: Behavior of the tomato in terms of substrate temperature. *Ann. Agron.*, **25**, 753–777.

Cumbus IP, Nye PH 1981: Root zone temperature effects on growth and nitrate absorption in rape (*Brassica napus* cv. Emerald). *J. Exp.Bot.*, **33**, 1138–1146.

Daskalaki A, Burrage SW 1997: The effect of root zone temperature on the growth and root anatomy of cucumber (*Cucumis sativus* L.). *Acta. Hortic.*, **449**, 569–574.

Daskalaki A, Burrage SW 1998: Solution temperature and the uptake of water and nutrients by cucumber (*Cucumis sartivas* L.) in hydroponics. *Acta. Hortic.*, **458**, 317–322.

Díaz-Pérez JC, Gitaitis R, Mandal B 2007: Effects of plastic mulches on root zone temperature and on the manifestation of tomato spotted wilt symptoms and yield of tomato. *Sci. Hortic.*, **114**, 90–95.

Domisch T, Finér L, Lehto T, Smolander A 2002: Effects of soil temperature on nutrient allocation and mycorrhizas in Scots pine seedlings. *Plant Soil*, **239**, 173–185.

Duke SH, Schrader LE, Henson CA, Servaittes JC, Vogelzang RD, Pendleton AW 1979: Low root temperature effects on soybean nitrogen metabolism and photosynthesis. *Plant Physiol.*, **63**, 956–962.

Engels C 1993: Differences between maize and wheat in growth-related nutrient demand and uptake of potassium

and phosphorus at suboptimal root zone temperature. *Plant Soil*, **150**, 129–138.
Engels C, Münkle L, Marschner H 1992: Effect of root zone temperature and shoot demand on uptake and xylem transport of macronutrients in maize (*Zea mays* L.). *J. Exp. Bot.*, **43**, 537–547.
Equiza MA, Mirave JP, Tognetti JA 2001: Morphological, anatomical and physiological responses related to differential shoot vs. root growth inhibition at low temperature in spring and winter wheat. *Ann. Bot.*, **87**, 67–76.
Garnett TP, Smethurst PJ 1999: Ammonium and nitrate uptake by *Eucalyptus nitens*: effects of pH and temperature. *Plant Soil*, **214**, 133–140.
Gavito ME, Curtis PS, Mikkelsen TN, Jakobsen I 2001: Interactive effects of soil temperature, atmospheric carbon dioxide and soil N on root development, biomass and nutrient uptake of winter wheat during vegetative growth. *J. Exp. Bot.*, **52**, 1913–1923.
Gent MPN, Ma YZ 2000: Mineral nutrition of tomato under diurnal temperature variation of root and shoot. *Crop Sci.*, **40**, 1629–1636.
Gossenlin A, Trudel MJ 1983: Interactions between air and root temperatures on greenhouse tomato. II: Mineral composition of plants. *J. Am. Soc. Hort. Sci.*, **108**, 905–909.
Hood TM, Mills HA 1994: Root-zone temperature affects nutrient uptake and growth of snapdragon. *J. Plant Nutr.*, **17**, 279–291.
Hussain A, Maqsood MA 2011: Root zone temperature influences nutrient accumulation and use in maize. *Pak. J. Bot.*, **43**, 1551–1556.
Kozlowski TT, Pallardy SG 1997: Mineral nutrition. *In* Physiology of Woody Plants, Eds. TT Kozlowski, SG Pallardy. pp 210–250. Academic Press, San Diego.
Lahti M, Aphalo PJ, Finér L, Ryyppö A, Lehto T, Mannerkoski H 2005: Effects of soil temperature on shoot and root growth and nutrient uptake of 5-year-old Norway spruce seedlings. *Tree Physiol.*, **25**, 115–122.
Lee SH, Singh AP, Chung GC, Ahn SJ, Noh EK, Steudle E 2004: Exposure of roots of cucumber (*Cucumis sativus*) to low temperature severely reduces root pressure, hydraulic conductivity and active transport of nutrients. *Physiol. Plant.*, **120**, 413–420.
Lyr H, Garbe V 1995: Influence of root temperature on growth of *Pinus sylvestris*, *Fagus sylvatica*, *Tilia cordata* and *Quercus robur*. *Trees*, **9**, 220–223.
Marschner H 1990: Nutrient availability in soils. *In* Mineral Nutrition of Higher Plants, Ed. H Marschner. pp 500–503. Academic Press, London.
Marschner H, Kirkby EA, Cakmak I 1996: Effect of mineral nutritional status on shoot-root partitioning of photoassimilates and cycling of mineral nutrients. *J. Exp. Bot.*, **47**, 1255–1263.
Miao M, Zhang Z, Xu X, Wang K, Cheng H, Cao B 2009: Different mechanisms to obtain higher fruit growth rate in two cold-tolerant cucumber (*Cucumis sativus* L.) lines under low night temperature. *Sci. Hortic.*, **119**, 357–361.
Mozafar A, Schreiber P, Oertli JJ 1993: Photoperiod and root-zone temperature: Interacting effects on growth and mineral nutrients of maize. *Plant Soil*, **153**, 71–78.
Murphy J, Riley JP 1962: A modified dingle solution method for determination of phosphate in natural waters. *Anal. Chim. Acta*, **27**, 31–36.
Niedziela CE Jr, Kim SH, Nelson PV, De Hertogh AA 2008: Effects of N-P-K deficiency and temperature regime on the growth and development of *Lilium longiflorum* 'Nellie White' during bulb production under phytotron conditions. *Sci. Hortic.*, **116**, 430–436.
Nxawe S, Laubscher CP, Ndakidemi PA 2009: Effect of regulated irrigation water temperature on hydroponics production of spinach (*Spinacia oleracea* L). *Afr. J. Agr. Res.*, **4**, 1442–1446.
Peng YY, Dang QL 2003: Effects of soil temperature on biomass production and allocation in seedlings of four boreal tree species. *For. Ecol. Manage.*, **180**, 1–9.
Reddy KR, Portier KM 1987: Nitrogen utilization by *Typha latifolia* L. as affected by temperature and rate of nitrogen application. *Aquat. Bot.*, **27**, 127–138.
Romero JA, Brix H, Comín FA 1999: Interactive effects of N and P on growth, nutrient allocation and NH_4 uptake kinetics by *Phragmites australis*. *Aquat. Bot.*, **64**, 369–380.
Rufty TW Jr, Israel DW, Volk RJ, Qin J, Sa T 1993: Phosphate regulation of nitrate assimilation in soybean. *J. Exp. Bot.*, **44**, 879–891.
Sánchez-Calderón L, López-Bucio J, Chacón-López A, Cruz-Ramírez A, Nieto-Jacobo F, Dubrovsky JG, Herrera-Estrella L 2005: Phosphate starvation induces a determinate developmentalprogram in the roots of Arabidopsis thaliana. *Plant Cell Physiol.*, **46**, 174–184.
Setter TL, Greenway H 1988: Growth reductions of rice at low root temperature: Decreases in nutrient uptake and development of chlorosis. *J. Exp. Bot.*, **39**, 811–829.
Solfjeld I, Johnsen Ø 2006: The influence of root-zone temperature on growth of Betula pendula Roth. *Trees*, **20**, 320–328.
Urrestarazu M, Salas MC, Valera D, Góme A, Mazuela PC 2008: Effects of heating nutrient solution on water and mineral uptake and early yield of two cucurbits under soilless culture. *J. Plant Nutr.*, **31**, 527–538.
Wan XC, Landhäusser SM, Zwiazek JJ, Lieffers VJ 1999: Root water flow and growth of aspen (*Populus tremuloides*) at low root temperatures. *Tree Physiol.*, **19**, 879–884.
Xu Q, Huang B 2006: Seasonal changes in root metabolic activity and nitrogen uptake for two cultivars of creeping bentgrass. *Hort Sci.*, **41**, 822–826.
Yu HY, Li TX, Zhou JM 2004: Salt accumulation, translocation and ion composition in greenhouse soil profiles. *Plant Nutr. Ferti. Sci.*, **13**, 642–650 (in Chinese).
Zhang S, Dang QL 2007: Interactive effects of soil temperature and CO_2 on morphological and biomass traits in seedlings of four boreal tree species. *For. Sci.*, **53**, 453–460.
Zhang YP, Qiao YX, Zhang YL, Zhou YH, Yu JQ 2008: Effects of root temperature on leaf gas exchange and xylem sap abscisic acid concentrations in six cucurbitaceae species. *Photosynthetica*, **46**, 356–362.