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Effects of root temperature on leaf gas exchange and xylem sap abscisic acid concentrations in six Cucurbitaceae species

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Abstract

Roots of six Cucurbitaceae species were exposed to low (14 °C), middle (24 °C), and high (34 °C) temperatures while aerial parts of plants were maintained at ambient temperatures between 23 and 33 °C. The highest dry mass (DM), photon-saturated rate of net photosynthesis (P_{Nsat}), and stomatal conductance (g_s) were found at 14 °C in figleaf gourd and turban squash plants, at 24 °C in cucumber and melon plants, while bitter melon and wax gourd plants had lower DM, P_{Nsat}, and g_s at 14 °C than at 24 or 34 °C. Sub- or supra-optimum root temperatures did not induce photoinhibition but induced slight changes in the quantum efficiency of photosystem 2, PS2 (Φ_{PS2}) and photochemical quenching (q_p). Meanwhile, xylem sap abscisic acid (ABA) concentration followed a contrasting change pattern to that of g_s. Thus the change in P_{Nsat} was mainly due to the change in g_s and roots played an important role in the regulation of stomatal behaviour by delivering increased amount of ABA to shoots at sub- or supra-optimum root temperatures.

Additional key words: adaptation; CO_2 assimilation; photosystem 2 photochemistry; photosynthesis; stomatal behaviour.

Introduction

Temperature limits geographic distribution and agronomic productivity of crops. Temperature stress has significant impacts on physiological metabolism both in roots and shoots by influencing processes such as photosynthesis, respiration, ion and water uptake, antioxidant metabolism, and signal transduction (Allen and Ort 2001, Atkin and Tjoelker 2003, Erice *et al.* 2006, Hewezi *et al.* 2006). There exists signal communication between roots and shoots in plants and the relationship between them has been an important research topic especially under sub- and supra-optimal growth conditions (Jackson 1997, Hansen and Dörffling 1999, Sobeih *et al.* 2004, Felle *et al.* 2005, Else *et al.* 2006, Nakagawa and Kawaguchi 2006). For example in cucumber, net photosynthetic rate (P_N) and photochemical efficiency of photosystem 2 (PS2) were considerably decreased when the root temperature was lower than 15 °C even though the aerial temperature was kept optimal (Ahn *et al.* 1999). Meanwhile, high soil temperature caused more severe oxidative damage to leaves than high air temperature by limiting antioxidant enzyme activities and inducing lipid peroxidation in turf (Huang *et al.* 2001). Limitations to photosynthesis in lettuce grown at high ambient temperatures could be alleviated to a great extent by root-zone cooling, leading to a successful production under tropic conditions (He *et al.* 2001). Thus metabolic damage caused by temperature stress could be alleviated to a great extent by keeping the root system at an optimal temperature since injury to the plants may be partly mediated by the disruption of root functions.

Photosynthesis is very sensitive to changes in root environment. Low or high root-zone temperature could limit photosynthesis through stomatal closure or other processes involved in the photosynthesis (Nada *et al.* 2003). Root-borne signals such as ethylene, the ethylene precursor, 1-aminocyclopropane-l-carboxylic acid (ACC), auxin, cytokinin, and especially abscisic acid (ABA) play an important role in the regulation of photosynthesis by regulating stomatal behaviour and plant water status (Jackson 1997, Foo *et al.* 2001, Sauter *et al.* 2001, Sobeih *et al.* 2004, Haisel *et al.* 2006). Roots may use these signals to provide shoots with early warning of

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deteriorating soil conditions to increase their resilience to stress (Jackson 1997). ABA is implicated in the regulation of photosynthesis by modifying stomatal aperture or osmotic potential of guard cells and gene expression (Pospíšilová 2003). Furthermore, ABA increases plant tolerance to stresses such as freezing, chilling, drought, salt, heavy metals, and flooding (Borel *et al.* 2001, Guschina *et al.* 2002, Hsu and Kao 2003). However, there is little information about the relationship between ABA delivery from xylem and adaptation for different plant species after exposure to different root temperature.

Cucurbitaceae crops, as important horticultural crops around the world, are usually defined as thermophilic plants adapted to warm climates. Large differences, however, have been observed in their tolerance to sub- or supra-optimal temperatures (Tindall 1983). Several species have been used as rootstock to improve the tolerance of shoots to suboptimal temperatures (Tachibana 1987). Until now, however, no extensive and systematic studies have been carried out to characterize the adaptation of Cucurbitaceae crops to different root temperatures. To clarify the role of roots in the regulation of leaf gas exchange, six economically important crops with different origins were used to compare their adaptation to low, middle, and high root temperatures. Plant growth, photosynthesis, and xylem sap ABA contents were determined to test the hypothesis that ABA delivery is an important factor in determining plant growth at suboptimal growth temperature.

Materials and methods

Plants and growth measurement: Figleaf gourd (*Cucurbita ficifolia* Bouché, C.f) and turban squash (*Cucurbita maxima* Duch. cv. Lvtianbao, C.ma) are cold tolerant and heat sensitive species (group I). Cucumber (*Cucumis sativus* L. cv. Jinyou No. 40, C.s), and melon (*Cucumis melo* L. cv. Xiangyu, C.me) are cold and heat sensitive species (group II). Bitter melon (*Momordica charantia* L. cv. Cuiyuyoukugua, M.c) and wax gourd (*Benincasa hispida* Cogn. cv. Fenpidonggua, B.h) are cold sensitive and heat tolerant species (group III) (Tindall 1983). Seeds were sown in a greenhouse in trays filled with moist vermiculite. Seven days later, groups of eight seedlings per species were transplanted into a tank (39×27×13 cm) filled with half-strength Enshi nutrient solution (Yu and Matsui 1997). The solution was continuously aerated with the aid of a pump. The mean daily maximum and minimum air temperatures were 33/23 °C (day/night), respectively. After two weeks of pre-culture, plants with 3–5 leaves were used for the temperature treatments. There were three solution temperature treatments: 14±1, 24±1, and 34±1 °C. Solution temperatures were maintained throughout the day by cooling and heating pipe systems which were connected to respective tanks. Seven days later gas exchange and chlorophyll (Chl) fluorescence were measured. Plants were then harvested, oven-dried at 80 °C for 4 d and weighed. Each treatment had 18 plants with three replicates.

Leaf gas exchange and Chl fluorescence: On the 7th day of temperature treatment, simultaneously leaf gas exchange and Chl fluorescence were measured using a steady state gas exchange system (*LI-6400*, *LI-COR*, Lincoln, NE, USA) with an integrated fluorescence chamber head (*LI-6400–40* leaf chamber fluorometer, *LI-COR*). The fourth fully developed leaves were used for these measurements. Leaf photon-saturated rate of CO_2 assimilation (P_{Nsat}), intercellular CO_2 concentration (C_i), and stomatal conductance (g_s) were measured while maintaining air temperature at 30 °C, air relative humidity at 80–90 %, CO_2 concentration at 400 μmol(CO_2) mol^{-1}, and photosynthetic photon flux density (PPFD) at 1 000 μmol(photon) m^{-2} s^{-1}. The stomatal limitation value (L_s) was calculated according to Berry and Downton (1982). Fluorescence parameters were calculated on the basis of the dark-adapted and light-adapted fluorescence measurements. The quantum efficiency of PS2 (Φ_{PS2}) and photochemical quenching (q_p) were calculated as $(F_m' - F_s)/F_m'$ (Genty *et al.* 1989) and $(F_m' - F_s)/(F_m' - F_0')$ (van Kooten and Snel 1990), respectively. The Φ_{CO2} was determined by dividing the rate of CO_2 assimilation by the rate at which quanta were absorbed (Fryer *et al.* 1998).

Xylem sap ABA analyses: The main stem was cut below the cotyledons and xylem sap exuded from root stumps was collected with a pressure chamber using a pressure of 0.5 MPa. The initial 20–30 mm^3 of exudates from each stump were discarded to avoid contamination (Vernieri *et al.* 2001). Sap from 3 or 4 plants was bulked for each sample and stored at −80 °C until used.

Prior to analysis of ABA concentration, the sap samples were thawed, purified, marked with internal standards, dried, and trimethylsilanized with fresh *N,O*-bis(trimethylsilyl)trifluoroacetamide (BSTFA) and pyridine. ABA analysis was performed using gas chromatography, GC (*Shimadzu GC-14B*, Kyoto, Japan). A *DB-1* capillary column (30 m×0.25 mm, *J&W Scientific*) was used for the GC with N_2 as carrier gas. After injection, the oven temperature was maintained at 150 °C for 2 min, and then increased to 255 °C at a rate of 5 °C min^{-1}. Injector and detector temperatures were set to 250 and 300 °C, respectively.

Statistical analyses: The data were analyzed with a one-way analysis of variance and differences between treatment means were distinguished using the least significant difference (L.S.D.) test at the $p<0.01$ level. *SAS 8.0 for Windows* (*SAS Institute*, Cary, NC, USA) was used for statistical analysis. The strength of the correlations between each two measured parameters was assessed by Pearson's linear correlation.

Results

The six Cucurbitaceae species exhibited different responses to the changes in root temperature. Figleaf gourd and turban squash (group I) had the highest dry mass (DM) at 14 °C, which decreased progressively at 24 and 34 °C. Cucumber and melon (group II) showed the highest DM at 24 °C and the lowest DM at 14 °C, respectively. Bitter melon and wax gourd (group III) showed the lowest DM at 14 °C and no significant difference in DM was found between the 24 and 34 °C treatments (Fig. 1).

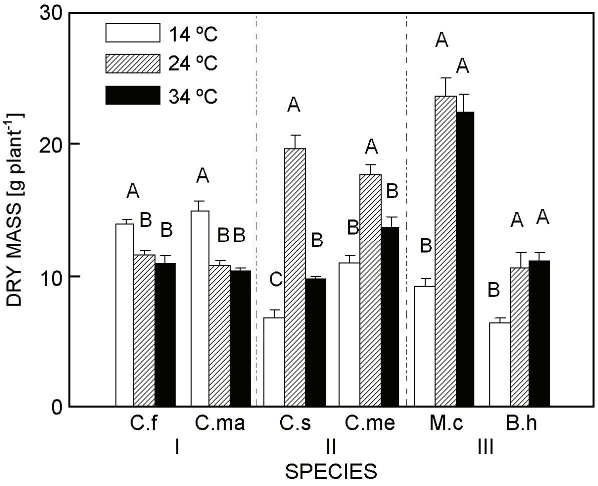

Fig. 1. Changes in plant dry mass (DM) as influenced by root temperature. C.f = figleaf gourd, C.ma = turban squash, C.s = cucumber, C.me = melon, M.c = bitter melon, and B.h = wax gourd, respectively. Means of four or five replicates with standard errors shown by vertical bars. Bars with different letters are significantly different (p<0.01).

There were significant species differences in P_{Nsat} (Fig. 2). Cucumber and melon, for example, always had high P_{Nsat} values while figleaf gourd and turban squash had low P_{Nsat} values. Figleaf gourd and turban squash plants showed their highest P_{Nsat} values at 14 °C while cucumber and melon showed the highest P_{Nsat} values at 24 °C. In comparison, bitter melon and wax gourd exhibited their lowest P_{Nsat} values at 14 °C and no significant difference was found between the 24 and 34 °C treatments. The changes in g_s occurred in a manner similar to those in P_{Nsat} (Fig. 2*B*). Plants with higher P_{Nsat} always showed higher g_s. However, a contrasting trend was observed in L_s (Fig. 2*C*).

Significant differences were found in Φ_{PS2} and q_p among the six species (Fig. 3*A,B*). Species with high P_{Nsat} usually exhibited high Φ_{PS2} and q_p. The change pattern for Φ_{PS2} and q_p was similar to that in $P_{Nsat,}$ the temperature-dependent change in Φ_{PS2} and q_p, however, was not as significant as that in $P_{Nsat,}$ For example, turban squash (group I plant) showed the lowest Φ_{PS2} and q_p at 34 °C while wax gourd (group III plant) showed the lowest Φ_{PS2} and q_p at 14 °C. The changes in Φ_{PS2} and q_p were almost independent of root temperatures in group II plants except that melon plants showed a lowed Φ_{PS2} value at

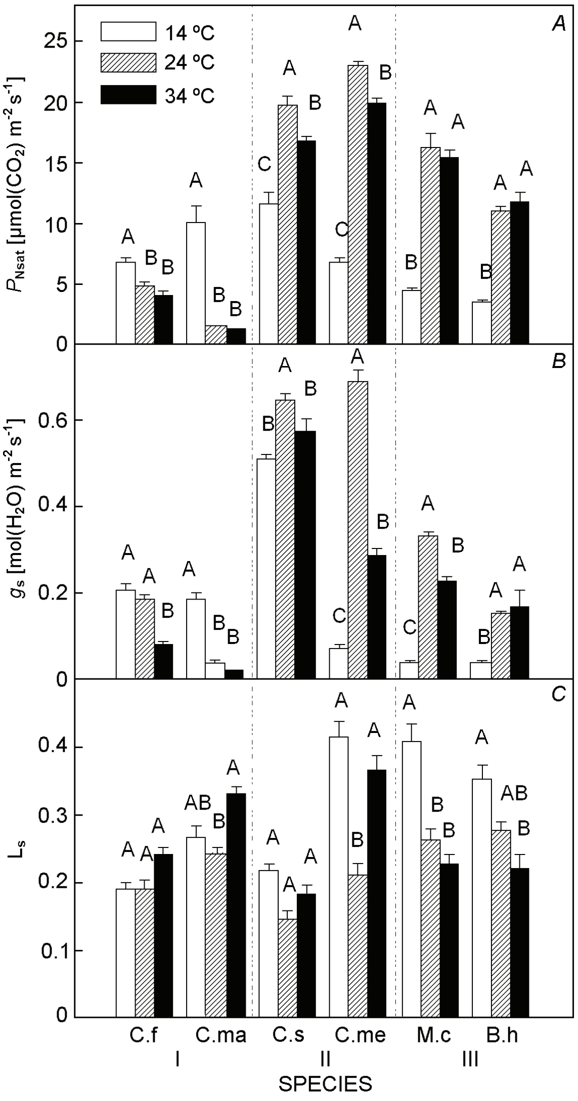

Fig. 2. Changes in photon-saturated rate of CO_2 assimilation (P_{Nsat}, *A*), stomatal conductance (g_s, *B*), and stomatal limitation value (L_s, *C*) as influenced by root temperature. C.f = figleaf gourd, C.ma = turban squash, C.s = cucumber, C.me = melon, M.c = bitter melon, and B.h = wax gourd, respectively. Leaf temperature was maintained at 30 °C at 1 000 μmol(photon) m^{-2} s^{-1}. Means of four to six replicates with standard errors shown by vertical bars. Bars with different letters are significantly different (p<0.01).

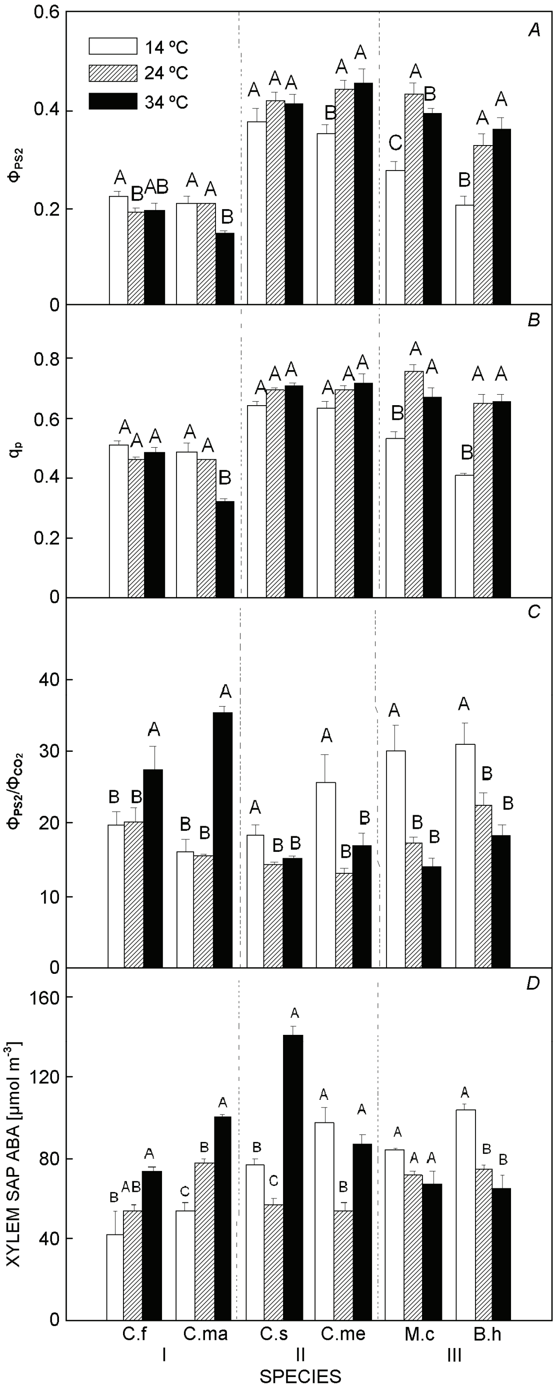

Fig. 3. Changes in the quantum efficiency of PS2 (Φ_{PS2}, *A*), photochemical quenching (q_p, *B*), Φ_{PS2}/Φ_{CO2} (*C*), and amount of xylem sap abscisic acid (ABA) (*D*) as influenced by root temperature. C.f = figleaf gourd, C.ma = turban squash, C.s = cucumber, C.me = melon, M.c = bitter melon, and B.h = wax gourd, respectively. Leaf temperature was maintained at 30 °C with 1 000 μmol(photon) m^{-2} s^{-1} incident PPFD. Means of four replicates with standard errors shown by vertical bars. Bars with different letters are significantly different (p<0.01).

14 °C. Root temperature, however, had little effects on the efficiency of excitation energy capture by open PS2 reaction centres (F_v'/F_m') and the maximal photochemical efficiency of PS2 (F_v/F_m) (data not shown).

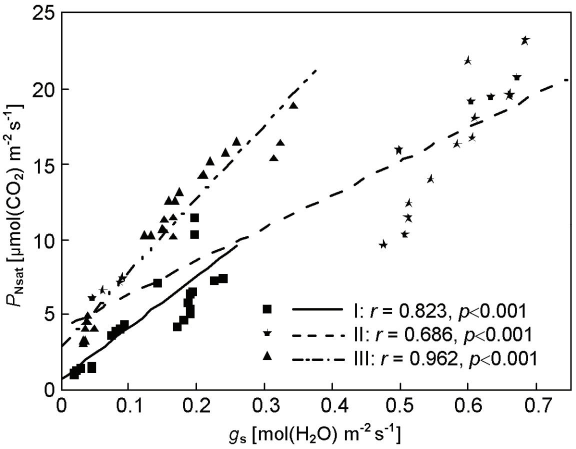

Fig. 4. The relationship between g_s and P_{Nsat} in I, II, and III group leaves of Cucurbitaceae plants as influenced by different root temperature treatment. I = figleaf gourd and turban squash, II = cucumber and melon, and III = bitter melon and wax gourd.

The relationship between Φ_{PS2} and Φ_{CO2} was examined at 21 % O_2 pressure (Fig. 3*C*). There were significant increases in the ratio of Φ_{PS2}/Φ_{CO2} for figleaf gourd and turban squash leaves after their roots were exposed to 34 °C. In comparison, a decrease in the root temperature from 24 to 14 °C significantly increased the ratio of Φ_{PS2}/Φ_{CO2} in group II and group III plants.

Fig. 3*D* shows the changes of xylem sap ABA concentration for different plants after exposure to different root temperatures. Xylem sap ABA concentration increased with the increase in root temperature in figleaf gourd and turban squash plants (group I). However, a contrasting change pattern was observed in bitter melon and wax gourd plants (group III). In comparison, cucumber and melon plants (group II) had the lowest xylem sap ABA concentration at 24 °C.

There was close relationship between g_s and P_{Nsat} in I, II, and III group leaves of Cucurbitaceae plants after exposure to different root temperatures (Fig. 4). Meanwhile, close correlations between xylem sap ABA concentration and g_s, L_s, and P_{Nsat} were also found in plants of I, II, and III groups (Fig. 5).

Discussion

We found that group I plants grew better at 14 °C than at 24 or 34 °C. On the contrary, bitter melon and wax gourd plants grew better at 34 and 24 °C than at 14 °C, while cucumber and melon plants showed the highest growth rate at 24 °C, intermediate growth at 34 °C, and least growth at 14 °C. This is in agreement with early classification based on shoot performance at different temperature (Tindall 1983). Accordingly, root temperature had significant effects on shoot growth and roots played an important role in the adaptation of plants to temperature fluctuation.

Root temperature had an influence on P_{Nsat} similar to that on plant growth (Figs. 1 and 2). Accordingly, change in P_{Nsat} was mainly responsible for the change in plant growth under our experimental conditions. The similarity in the trends for P_{Nsat} and g_s as well as the high correlations between them suggest that stomatal factor was mainly responsible for the changes in P_{Nsat} induced by root temperature and this was also evidenced by the similarity in L_s changes (Figs. 2 and 6). Similar to our results, Wan *et al.* (2004) found that low soil temperature induced a decrease in g_s in aspen. He *et al.* (2001) also reported that the light-saturated g_s and photosynthetic CO_2 assimilation were highly correlated with each other when lettuce root temperature was changed from a fluctuating (23–40 °C) one to a constant (20 °C) one. In comparison, decrease in photosynthetic rate by aerial temperature stress was partly attributed to the decrease in ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) activation in leaves of cucumber and alfalfa plants (Zhou *et al.* 2004, Erice *et al.* 2006). It is, however, unknown whether root temperature stress impaired photosynthesis by altering RuBPCO activation.

Chl fluorescence parameters reflect the PS2 response to environmental conditions. In comparison to the little change in the maximal photochemical efficiency of PS2 (F_v/F_m) (data not shown), Φ_{PS2} changed in a manner similar to P_{Nsat} although the degree was not as significant as that of P_{Nsat} (Figs. 2 and 3). Accordingly, changes in root temperature did not induce photoinhibition and changes in Φ_{PS2} were mainly attributed to a down-stream regulation by the changed demand for ATP and NADPH in Calvin cycle under our experimental conditions. Since root temperature had no significant effects on the efficiency of excitation energy capture of open PS2 reaction centre (F_v'/F_m') (data not shown), root temperature-induced changes in PS2 electron transport (Φ_{PS2}) were mainly attributed to the changes in the number of open PS2 reaction centres (q_p) but not to the efficiency of energy capture by these open centres (F_v'/F_m') (Genty *et al.* 1989).

Here we found that group I and III plants showed their highest Φ_{PS2}/Φ_{CO2} ratio at 34 and 14 °C, while group II showed the lowest Φ_{PS2}/Φ_{CO2} ratio at 24 °C, respectively (Fig. 3*C*). This is in agreement with earlier finding that plants experience an increase in the ratio of Φ_{PS2}/Φ_{CO2} when they are exposed to stressful growth temperature (Fryer *et al.* 1998, Zhou *et al.* 2004). Increase in the ratio of Φ_{PS2}/Φ_{CO2} suggests that electron sinks other than CO_2 assimilation function properly. Photorespiration, cyclic flow of electron within PS2, and the water-water cycle are potential pathway involved (Demmig-Adams and Adams 1992, Asada 1999). Our

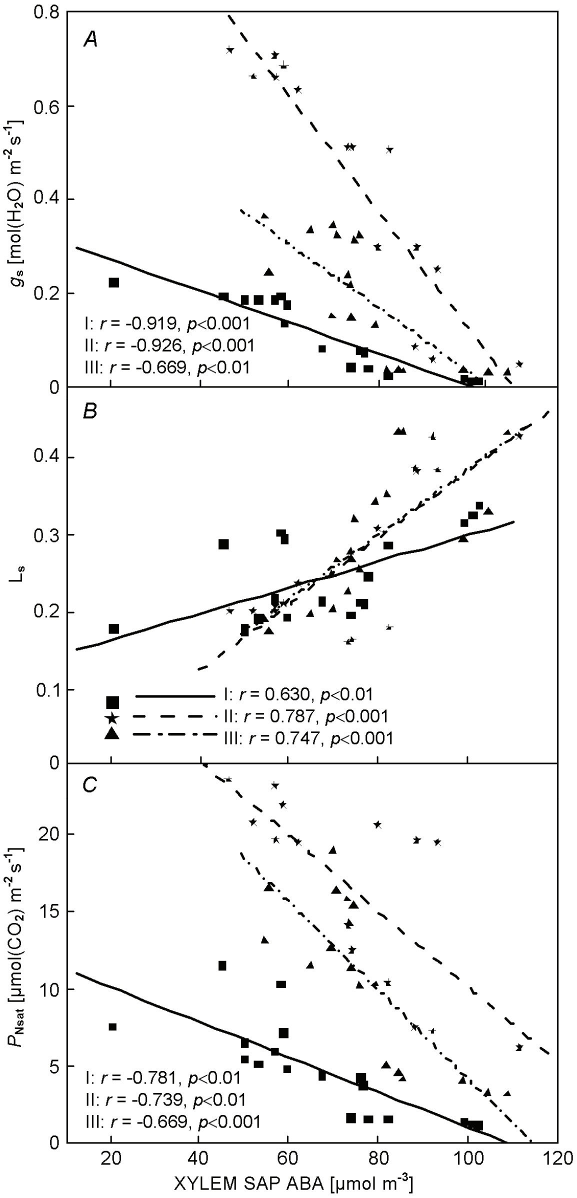

Fig. 5. The relationship between xylem sap abscisic acid (ABA) concentration and stomatal conductance (g_s, *A*), stomatal limitation value (L_s, *B*), and photon-saturated net photosynthetic rate (P_{Nsat}, *C*) in I, II, and III groups of leaves of Cucurbitaceae plants as influenced by different root temperature treatment. I = figleaf gourd and turban squash, II = cucumber and melon, and III = bitter melon and wax gourd.

earlier experiment found that group I and III plants had their highest membrane peroxidation at 34 and 14 $^{\circ}$C, while group II showed lowest peroxidation at 24 $^{\circ}$C, respectively (Zhang *et al.* 2007). Accordingly, increased reactive oxygen species may be generated in leaves when their roots are exposed to stress, as observed in turf (Huang *et al.* 2001).

There is much evidence for the involvement of root-borne signals in the regulation of g_s in stressed leaves (Pei *et al.* 2000, Wang *et al*. 2001). Increased ABA content in xylem sap has been reported in water-stressed leaves (Bahrun *et al*. 2002, Sobeih *et al.* 2004). We also found that most plant species had higher ABA concentrations in xylem sap at suboptimal than optimal root temperatures (Fig. 3*D*). Furthermore, changes in ABA concentration were in agreement with those of L_s and opposite to P_{Nsat} and g_s (Figs. 2, 3*D*, and 5). These results suggest that xylem sap ABA played a role in the regulation of stomatal operation in our experiment. Tardieu *et al.* (1996) testified the role of ABA by feeding synthetic ABA to well-watered plants and found similar relationship between g_s and xylem sap ABA as seen in drying soil. Roots probably synthesized increased amount of ABA to cause a decrease in g_s and further P_{Nsat} *via* the xylem (Gollan *et al.* 1992, Schurr *et al.* 1992, Tardieu *et al.* 1996).

In conclusion, we have characterized root adaptation to different temperatures for six Cucurbitaceae crops and found that changes in photosynthesis induced by root temperatures were mainly attributed to corresponding changes of g_s. Decreases in CO_2 assimilation under sub-optimal root temperatures resulted in a down-regulation of the quantum efficiency of PS2. Meanwhile, roots were important in the regulation of stomatal behaviour by delivering ABA to shoots at sub-optimal or supra-optimal root temperatures. We also found that cooling or heating of the root system could be a useful approach for improving shoot growth at sub-optimal or supra-optimal temperatures.

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