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Influence of potassium and calcium on leaf temperature of Chinese cabbage

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Abstract. In Taiwan, heat stress can be a major factor limiting the growth of greenhouse crops during the summer. Though many attempts had been made to alleviate this, methods that enhance the heat-stress-relieving mechanism of transpiration had yet to be investigated. Since stomatal opening, and therefore transpiration, is affected by potassium and calcium, the influence of these nutrients on the leaf temperature of hydroponically-grown cabbage was studied. The leaf temperature of cabbages grown in solutions of low calcium concentration were significantly lower than of those grown in high-calcium solutions. When transpiration demands were moderate, the leaf temperature of cabbages grown in solutions of high potassium concentration were lower than of those treated with low potassium. These results agree with the known affect of calcium and potassium on stomatal opening. When transpiration demands were high, however, the leaf temperatures of high-potassium treated cabbages were higher than of those treated with low potassium. We speculate that the stomatal opening was suppressed by physiological and/or biochemical reactions resulting from reduced nitrogen uptake due to antagonism with the potassium.

Keywords: Calcium; Heat stress; Leaf temperature; Nutrient uptake; Potassium; Stomatal opening; Transpiration.

Introduction

Transpiration is, among other functions, a heat-stress relieving mechanism of plants. Of the factors which control the rate of transpiration, stomatal aperture plays a major role, affecting leaf resistance and therefore the amount of water transpired. As reviewed by Jarvis and Mansfield (1981) and Willmer (1983), many experiments on epidermis or on detached leaves have shown that potassium and calcium have significant influence on stomatal aperture.

For stomatal opening, potassium is required in guard cells. Fischer (1971) showed that the stomatal opening of *Vicia faba* incubated in KCl solution under illumination increased linearly when the potassium in guard cells increased from 200 to 500 mM. Penny and Bowling (1974) indicated that the stomata of *Commelina communis* opened and closed when the potassium concentrations in guard cells were 448 and 95 mM, respectively. Other evidence implicating potassium in stomatal movement has been discussed in several reviews (Raschke, 1975, 1979; Thomas, 1975; Hsiao, 1976; MacRobbie, 1981; Willmer, 1983).

Depending on the concentration, calcium either reduced or completely suppressed K-stimulated stomatal opening in epidermal strips of many species (Meidner and Willmer, 1975). De Silva et al. (1985) found that stomatal opening of *Commelina communis* decreased dramatically when epidermal strips were incubated in increasingly concentrated solutions of $CaCl_2$ (0.1 to 0.5 mM); stomata were completely closed when incubated in 1 mM $CaCl_2$. Mansfield et al. (1990) suggested that Ca^{2+} reduced the influx of K^+ to guard cells, thereby reducing the turgor pressure of guard cells and thus reducing stomatal opening.

Due to antagonisms, the concentration of potassium and calcium ions in culture solutions can also affect the nutrient uptake of whole plants. It has been shown that uptake of calcium and ammonium ions decreased at elevated potassium levels (Johansen et al., 1968; Lin and Shen, 1985; John, 1989). Bell et al. (1989) found that uptake of both nitrogen and phosphorus increased and that of magnesium decreased when the Ca^{2+} concentration in culture solutions was increased. Tanaka et al. (1991) found that increased calcium concentration in culture solution could lower the contents of potassium and magnesium in tomato leaves.

In Taiwan, heat stress can be a major factor limiting the growth of crops grown in greenhouses during the summer. Though many attempts had been made to alleviate the heat stress, methods that enhance the heat-

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stress-relieving mechanism of transpiration had yet to be investigated. It was our intention, therefore, to examine how leaf temperature may be affected by changing the potassium and calcium concentration in culture solution.

Materials and Methods

Chinese cabbage (*Brassica campestris* L.) plants were grown hydroponically in a greenhouse. The concentration of culture solution followed that of Wu and Wang (1991). The potassium and calcium concentrations were each varied by adjusting the amount of K^+ and Ca^{2+} in the culture solution to 1.5 and to 3 mM using KCl and $CaCl_2$, respectively. Potassium and calcium experiments were replicated three times between June 1991 and January 1992. In fall and winter, when noon-time air temperatures inside the greenhouse were usually lower than 35 °C, the cabbages were covered by a clear polyethelene tent. A ventilated heating system automatically maintained diurnal air temperature variations inside the tent similar to those occurring in summer. For each run of experiments, the culture solutions were not replenished or replaced after transplanting. The influence on leaf temperature of various concentrations of the same composition of solutes was also studied. This experiment was conducted by growing cabbages in two culture solutions having electrical conductivities of 0.9 and 2.4 mS cm^{-1}, respectively.

In each experiment, the leaf temperature was measured with a fine-wire (75 μm) thermocouple inserted in a vein of the sixth leaf of 14-day old cabbage. For each treatment, at least twelve plants were fitted with thermocouples; one per plant. Details of thermocouple insertion and fixation are described in Lin et al. (1992). Air temperature, relative humidity, and radiation intensity above the canopy were also measured by a fine-wire thermocouple, a ventilated psychrometer (WVU, Delta-T Device), and a quantum sensor (LI-190, LICOR). Time-averaged readings were recorded by a data logger (21X Micrologger, Campbell Scientific) at 15-min intervals.

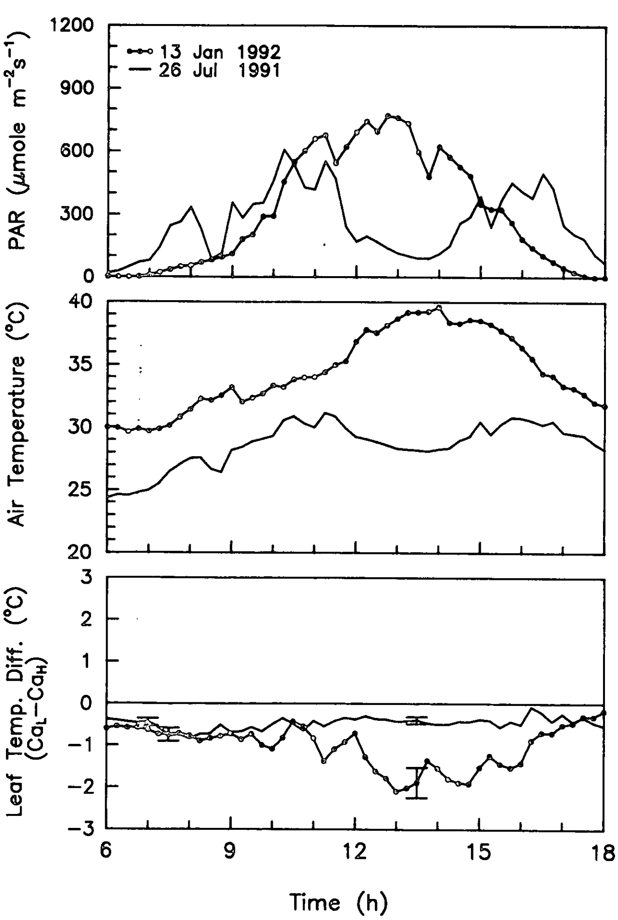

Fig. 1. Influence of concentration of calcium in culture solution on leaf temperature of cabbage under different environmental conditions. PAR = photosynthetically active radiation. Error bars represent standard errors of means.

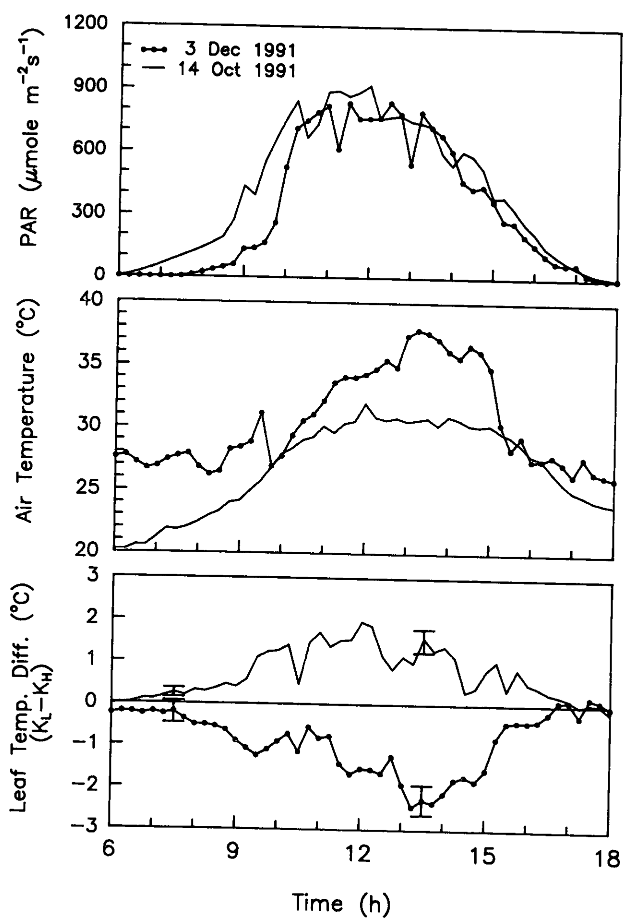

Fig. 2. Influence of concentration of potassium in culture solution on leaf temperature of cabbage under different environmental conditions. PAR = photosynthetically active radiation. Error bars represent standard errors of means.

Table 1. Influence of calcium, potassium, and concentration of culture solution on contents of macronutrients in leaves of Chinese cabbage.

Environments	Concentration of nutrients (mole kg^{-1})					mole ratio
	N	P	K	Ca	Mg	Ca/K
3.0 mM Ca	2.63	0.20	1.31	0.68	0.33	0.52
1.5 mM Ca	2.59	0.20	1.23	0.52	0.38	0.42
(LSD [5%])	0.44	0.07	0.74	0.15	0.06	
3.0 mM K	2.09	0.20	1.49	0.53	0.36	0.36
1.5 mM K	2.40	0.22	0.94	0.55	0.38	0.58
(LSD [5%])	1.04	0.13	0.32	0.29	0.26	
0.9 mS cm^{-1}	3.19	0.25	2.05	0.61	0.27	0.30
2.4 mS cm^{-1}	1.39	0.10	0.86	0.42	0.24	0.49
(LSD [5%])	0.53	0.11	0.80	0.32	0.19	

After each experiment, the cabbages were harvested and dried at 70 °C for 48 h. The total-nitrogen contents were determined by the Kjeldahl method, phosphorus by the molybdenum-yellow method, potassium by flame-emission spectroscopy, and calcium and magnesium by atomic-absorption spectroscopy.

Results and Discussion

The influence of potassium and calcium concentration on the nutrient contents of leaves is shown in Table 1. Though the contents of potassium and calcium in the plants were significantly changed by the treatments, the contents of other cations (except nitrogen) did not differ significantly. Total nitrogen was lower in high-potassium treatments than in the others, a result of antagonism between K^+ and NH_4^+. Molar ratios of Ca/K were lower in low-calcium and in high-potassium treatments, as expected.

As shown in Fig. 1, the leaf temperatures of cabbages grown in low-calcium solutions were significantly lower than in those treated with high calcium. Under environments that created greater transpiration demands, i.e. strong incident solar radiation and high air temperatures, the differences were greater. Generally, differences of 1-2 °C were observed. High calcium content in leaves reduced stomatal opening and decreased transpiration, resulting in higher leaf temperatures.

The influence of potassium treatments on leaf temperature are shown in Fig. 2. When transpiration demands were moderate, the leaf temperatures of

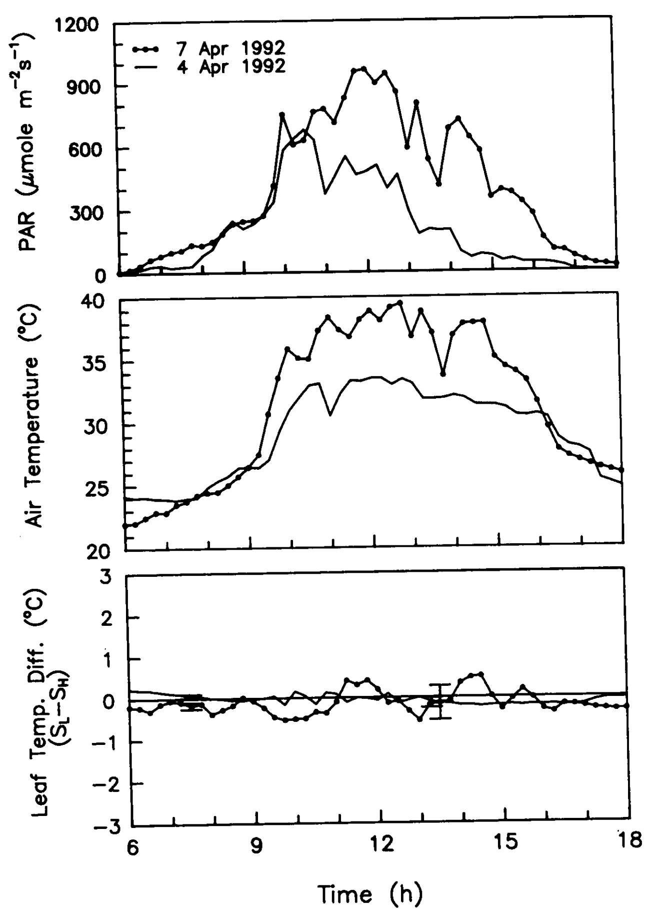

Fig. 3. Influence of concentration of culture solution on leaf temperature of cabbage under different environmental conditions. PAR = photosynthetically active radiation. Error bars represent standard errors of means.

high-potassium treated cabbages were lower than in those treated with low potassium. This agreed with well-known affects of potassium on stomatal openings, i.e. high potassium increases stomatal apertures and the amount of transpiration. When both incident solar radiation and surrounding air temperatures were high, however, leaf temperatures of high-potassium treated cabbages were higher than in those treated with low potassium. Similar results were obtained in a repeat of the experiment (data not shown).

We first speculated that under high transpiration demands, water potentials in the stomatal cavities of cabbages undergoing high-potassium treatment were lower than in those treated with low potassium . The higher leaf temperature might result from decreased transpiration due to reduced vapor pressure gradients across the leaf boundary. To study whether this reasoning was valid, the leaf temperatures of Chinese cabbages cultivated in various concentrations of solutions with the same composition of nutrients were compared. Table 1 shows that the concentration of the major nutrients in leaves differed considerably, but measured leaf temperatures did not differ significantly under various transpiration demands (Fig. 3). Therefore, changes of water potential in stomatal cavities alone should have little affect on the observed leaf temperature. The cause of the adverse influence of high potassium levels on leaf temperature under environments of high transpiration demands, is more complicated.

Considering that nitrogen uptake was inhibited when the concentration of potassium in the culture solution was high (Table 1), we speculated that stomatal opening might be suppressed by physiological and/or biochemical reactions resulting from reduced nitrogen uptake. Although, as reviewed by Nagao (1989), many investigations of the formation of heat-stress protein in leaves have been conducted, to the authors' knowledge, few reports provide evidence for or against the explanations proposed above.

Conclusion

Leaf temperatures can be altered by changing the concentration of potassium and calcium in the culture solution. Responses of leaf temperature to changes in calcium concentration are in agreement with the known influence of calcium on stomatal opening, i.e. solutions high in calcium can cause higher leaf temperatures. Responses of leaf temperature to changes in potassium concentration, however, vary with environmental conditions. When the transpiration demand is low, cabbages grown in high potassium have much lower leaf temperatures than do those treated with low potassium. When the transpiration demand is high, however, leaf temperatures of cabbages grown in high potassium solution are greater than in those grown in low potassium solution. Therefore, if heat stress is to be avoided, it is more appropriate to lower the calcium concentration in the culture solution than to raise the potassium concentration. Further research needs to be conducted to refine our knowledge of the factors involved.

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鉀鈣離子對小白菜葉溫的效應

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由於鉀鈣離子會改變葉片的氣孔開度與蒸散量，本研究乃利用小白菜為材料，探討水耕液中鉀鈣離子濃度對葉溫之影響。試驗結果指出，不論在高溫或適溫環境下，於低鈣環境中栽培的小白菜的葉溫都低於在高鈣環境中栽培者。在適溫環境下，於高鉀環境中栽培的小白菜的葉溫也低於在低鉀環境中栽培者。這與鉀離子有增加氣孔開度與蒸散量的功能，而鈣離子反而有抑制作用的已知結果相符合。但是，在高溫環境下，於高鉀環境中栽培的小白菜的葉溫，反而高於在低鉀環境下栽培者，推測其原因，可能是由於在高鉀環境下栽培的小白菜，由於鉀－氨離子間的擷抗，使得氮的吸收減少，再經由生理或生化的反應，反而使得葉片的氣孔開度變小，蒸散量減少，因而導致葉溫升高。

關鍵詞：熱逆境；葉溫；養分吸收；鉀；鈣。