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https://hdl.handle.net/2324/8149

出版情報：BIOTRONICS. 18, pp.15-21, 1989-12. Biotron Institute, Kyushu University
バージョン：
権利関係：

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BIOTRONICS **18**, 15–21, 1989

EFFECT OF ROOT TEMPERATURE ON GAS EXCHANGE AND WATER UPTAKE IN INTACT ROOTS OF CUCUMBER PLANTS (*CUCUMIS SATIVUS* L.) IN HYDROPONICS

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(Received August 19, 1989; accepted September 5, 1989)

YOSHIDA S. and EGUCHI H. *Effect of root temperature on gas exchange and water uptake in intact roots of cucumber plants* (Cucumis sativus *L.*) *in hydroponics*. BIOTRONICS **18**, 15–21, 1989. Dissolved O_2 and CO_2 concentrations in nutrient solution and water uptake rate in intact cucumber roots were examined at different root temperatures of 8 to 28°C by using the on-line measurements in an air-tightened hydroponic system under the controlled environment. The root temperature effects on gas exchange and water uptake in roots were found in the sigmoidal pattern, and the patterns of the gas exchange and the water uptake on root temperature appeared almost parallel with each other: The responses decreased with root temperatures lower than 12°C and increased with root temperatures higher than 16°C.

Key words: *Cucumis sativus* L.; cucumber plant; root temperature; gas exchange; water uptake rate; hydroponics; O_2 concentration; CO_2 concentration.

INTRODUCTION

The plant growth and the physiological activities are affected by rhizosphere environment through various root functions (*2*, *4–7*, *10*, *17*, *21*, *22*). The basal environmental factors are soil moisture, soil gaseous composition, nutrition and root temperature (*12*). Root temperature is known to be essential for water uptake and gas exchange in roots. Several workers have reported the root temperature effect on water relation in plants and root gas exchange (*3*, *8*, *13–15*, *18–20*). In particular, Andersen *et al.* (*1*) and Everard and Drew (*9*) have reported that water relation in plants are associated with root gas exchange.

The present paper deals with analysis of the root temperature effects on water uptake and gas exchange in intact roots by on-line measurements in an air-tightened hydroponic system, aiming at understanding of interrelations among root gas exchange, root water uptake and root temperature.

MATERIALS AND METHODS

Hydroponic and measurement systems

The air-tightened hydroponic system which has been reported in the previous paper (*23*) was used for root temperature control and for on-line measurements of water uptake rate and gas exchange in intact roots. The hydroponic system was installed in a growth chamber (*16*) where air temperature and relative humidity were controlled in artificial light. The solution temperature in a stainless steel pot (3.7 litre) was controlled by a water bath method. A polarographic dissolved O_2-meter (UD-1, Central Kagaku Co., Ltd.), a potentiometric membrane electrode CO_2-meter (CGP-1, Toa Electronics Ltd.) and a pH-meter (HM-7E, Toa Electronics Ltd.) were employed for the on-line measurements of dissolved O_2 and CO_2 concentrations in the solution. The solution was slowly stirred for the measurements. The sensors were fixed in the pot by using rubber corks with silicone grease. Water uptake rate in roots was measured automatically by a potometer: The surface level of nutrient solution in the potometer was detected by a float which was connected to a potentiometer, where the solution surface of the potometer was sealed with paraffin liquid layer to prevent diffusion of air into the solution. The respective sensor signals were transmitted to CPU through interfaces.

Plant material and experimental condition

Cucumber plants (*Cucumis sativus* L. "Chojitsu-Ochiai") were used in this experiment. The plants were grown in fully aerated hydroponics at an air temperature of 23°C, a relative humidity of 70% and a light intensity of 250 μmol m^{-2} s^{-1} (metal halide lamps; Yoko lamp, DR400, Toshiba Corp.) in photoperiod of 12 h. The 3rd leaf stage plant was transplanted to the air-tightened hydroponic system after keeping the plant under the respective experimental root temperatures for 18 h in order to adapt the plant to the experimental conditions. The water uptake and the gas exchange in roots were measured for 4 days under the condition of an air temperature of 25°C, a relative humidity of 40% and continuous light with a intensity of 200 μmol m^{-2} s^{-1} (flourescent lamps; FLR110-EHW/A, Toshiba Corp.) in the growth chamber. The root temperatures were controlled in a region of 8 to 28$\pm$0.1°C. The pH in the solution distributed from 4.5 to 6.5. After the measurements for 4 days, the dry weight of the detached whole roots was measured.

Analysis of CO_2 concentration

Dissolved CO_2 is hydrated and subsequently ionized, and the components of inorganic carbon, which are CO_2, H_2CO_3, HCO_3^- and CO_3^{2-}, are in equilibrium in the solution, as described by Helder (*11*). The relationships between unionized and ionized components of the inorganic carbon in the solution are represented by Henderson-Hasselbach equations as follows,

$$\left.\begin{aligned} \log \frac{[HCO_3^-]}{[CO_2+H_2CO_3]} &= pH-pK_{a1} \\ \log \frac{[CO_3^{2-}]}{[HCO_3^-]} &= pH-pK_{a2} \end{aligned}\right\} \quad (1)$$

where K_{a1} and K_{a2} are equilibrium constants for the ionization of dissolved CO_2 in the solution, $pK_{a1}=-\log K_{a1}$, and $pK_{a2}=-\log K_{a2}$. The equilibrium constants at a given temperature of T(K) can be calculated by Eqs. (2) and (3):

$$\ln K_{a1} = -14554.21\ T^{-1}+290.9097-45.0575 \ln T \quad (2)$$

$$\ln K_{a2} = -11843.79\ T^{-1}+207.6548-33.6485 \ln T \quad (3)$$

The molarity of total inorganic carbon is obtained from summing respective molarities of the unionized components (CO_2 and H_2CO_3) and the ionized components (HCO_3^- and CO_3^{2-}). The molarity of unionized components can be measuerd by the CO_2 electrode, and the molarities of ionized components were calculated from respective Eqs. (4) and (5) by using measured pH and measured molarities of the unionized components.

$$\log [HCO_3^-] = \log [CO_2 + H_2CO_3] + pH - pK_{a1} \quad (4)$$

$$\log [CO_3^{2-}] = \log [HCO_3^-] + pH - pK_{a2} \quad (5)$$

Thus, CO_2 concentration was evaluated in this experiment by using the molarity of the total inorganic carbon.

RESULTS AND DISCUSSION

Dissolved O_2 and CO_2 concentrations in nutrient solution and water uptake rate in roots were measured at different root temperatures. Figure 1 shows examples of the time course patterns of O_2 and CO_2 concentrations and water uptake rate at respective root temperatures of 12, 20 and 28°C. The O_2 concentration, which was initially 0.25±0.01 mmol l^{-1}, decreased to 0.01 mmol l^{-1} in 38 h at 12°C, in 18 h at 20°C and in 8 h at 28°C (Fig. 1a). The velocity of the O_2 decrease was enhanced with the higher root temperatures. On the other hand, the initial CO_2 concentration was 0.06±0.01 mmol l^{-1}. At the root temperature of 28°C, the CO_2 concentration reached to about 3.1 mmol l^{-1} in 80 h, and thereafter it was kept steady-state. At the root temperatures of 12 and 20°C, the CO_2 concentration continued to increase in the time course of 96 h (Fig. 1b). The velocity of the CO_2 increase was enhanced with higher root temperatures as well as the velocity of the O_2 decrease. Thus, CO_2 concentration continued to increase even after the time when O_2 concentration decreased to 0.01 mmol l^{-1}. In the previous paper, the same results have been obtained, and it has been supposed that gas exchange in intact roots relates to leaf gas exchange through stomatal openings (*23*). From these results, it became clear that the CO_2 release in roots can be caused even in the O_2 deficit solution. So, it was difficult to calculate the root respiratory quotient from the balance of O_2 uptake and CO_2 release in the nutrient solution.

Water uptake rate at the root temperature of 12°C was kept remarkably lower than those at the higher root temperatures: The water uptake rate at the root temperatures of 20 and 28°C became higher during 30 h after the start of the measurements and gradually decreased (Fig. 1c). Thus, it was obvious that both gas exchange and water uptake in roots are inhibited with lower root temperatures and are enhanced with higher root temperatures.

To examine root temperature effect on gas exchange and water uptake in roots, O_2 decrease rate, CO_2 increase rate (per root dry weight) and water uptake rate (per plant) were evaluated by using the mean of the measured values in 4 plants in the root temperature region of 8 to 28°C. Figure 2 shows the distribution of O_2 decrease rates (μmol l^{-1} g^{-1} s^{-1}) on root temperature. The root temperature effect on O_2 decrease rate was found in a sigmoidal pattern: The O_2 decrease rate

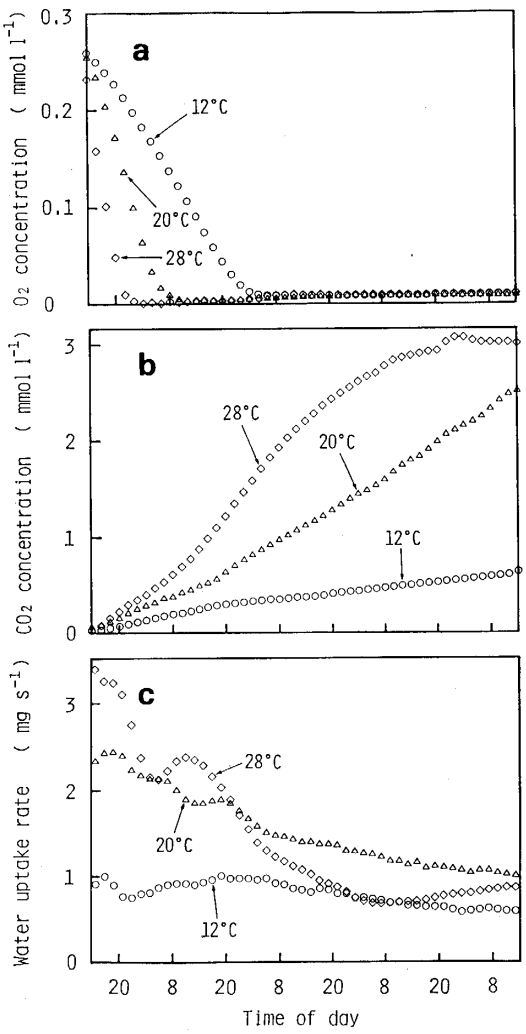

Fig. 1. Time course patterns of dissolved O_2 (a) and CO_2 (b) concentrations in nutrient solution and water uptake rate in intact roots (c) at respective root temperatures of 12, 20 and 28°C in an air-tightened hydroponic system.

appeared lower at the root temperatures lower than 12°C and was saturated at the root temperatures higher than 16°C. Figure 3 shows the distribution of CO_2 increase rates (μmol l^{-1} g^{-1} s^{-1}) on root temperature. The CO_2 increase rate became lower at the root temperatures lower than 16°C and was saturated at the root temperatures higher than 20°C. Thus, almost similar patterns were found in both O_2 decrease rate and CO_2 increase rate. In detail of the patterns, however, there was small difference in root temperature effect between O_2 decrease rate and CO_2 increase rate: The O_2 decrease rate was saturated at 16°C, while the CO_2 increase rate was saturated at 20°C.

Figure 4 shows the distribution of water uptake rates on root temperature. The root temperature effect on water uptake rate was also found in the sigmoidal pattern: Water uptake rate was lower at the root temperatures lower than 12°C and was

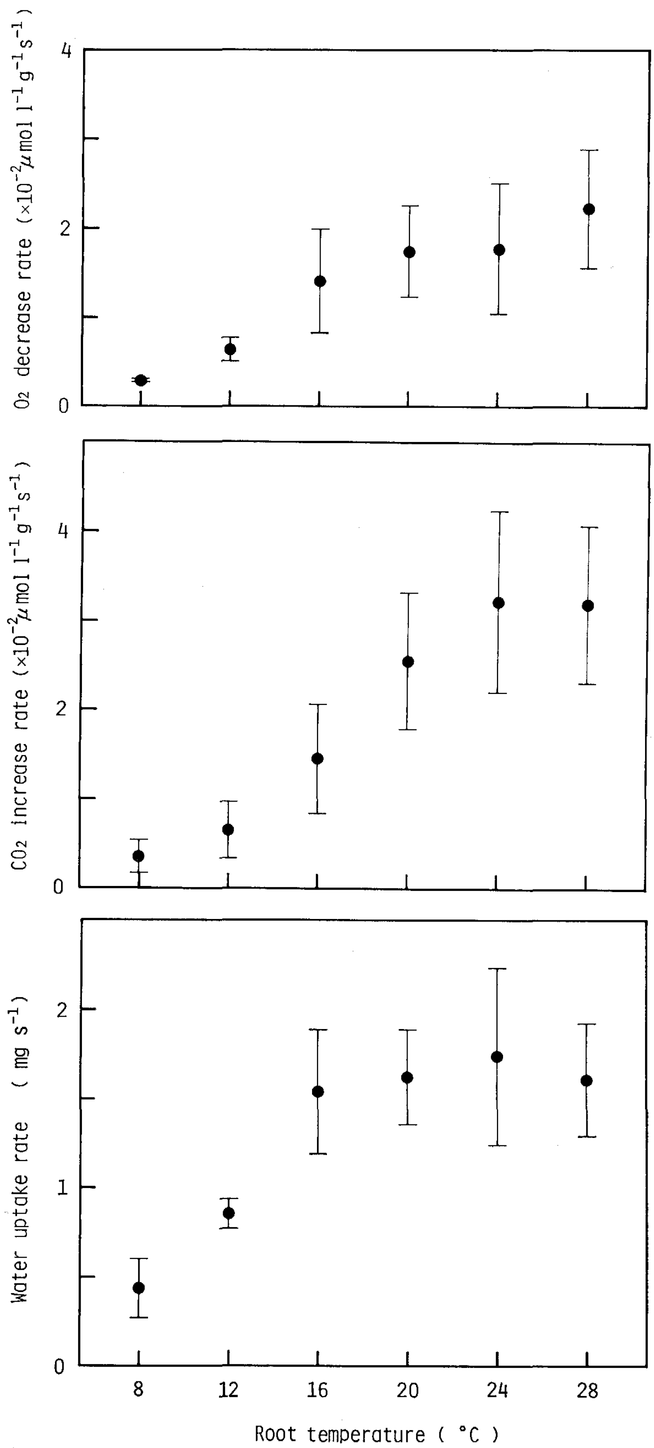

Fig. 2. The distribution of decrease rates of O_2 concentration in nutrient solution on root temperature, where the means of values measured in 4 plants are plotted with 95% confidence intervals.

Fig. 3. The distribution of increase rates of CO_2 concentration in nutrient solution on root temperature, where the means of values measured in 4 plants are plotted with 95% confidence intervals.

Fig. 4. The distribution of water uptake rates in intact roots on root temperature, where the means of values measured in 4 plants are plotted with 95% confidence intervals.

kept higher and almost constant at the root temperatures higher than 16°C.

These sigmoidal patterns of O_2 decrease rates, CO_2 increase rates and water uptake rates on root temperature agreed with the results that Clarkson *et al.* (*3*), Macduff *et al.* (*14*), Markhart *et al.* (*15*) and Running and Reid (*18*) have obtained in uptake rates of water and nutrition in relation to the root temperature. Eguchi and Koutaki (*8*) have reported the similar effect of root temperature on leaf transpiration.

Thus, the gas exchange and the water uptake in roots clearly responded to the root temperature, and their response curves on root temperature appeared almost parallel with each other in the sigmoidal pattern where the response rates decreased at root temperatures lower than 12°C and increased at root temperatures higher than 16°C in cucumber plants. This event may help to understand the dependence of water relation in plants on the root temperature.

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