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Yoshida, Satoshi
Biotron Institute Kyushu University

Eguchi, Hiromi
Biotron Institute Kyushu University

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RELATIONSHIP BETWEEN GAS EXCHANGES IN INTACT ROOTS AND WATER UPTAKE IN RESPONSE TO LEAF TRANSPIRATION IN HYDROPONICS

S. YOSHIDA and H. EGUCHI

Biotron institute, Kyushu University 12, Fukuoka 812, Japan

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YOSHIDA S. and EGUCHI H. *Relationship between gas exchanges in intact roots and water uptake in response to leaf transpiration in hydroponics.* BIOTRONICS **17**, 59–68, 1988. A hydroponic system was developed for intact measurements of water uptake rate, dissolved O_2 and CO_2 concentrations in nutrient solution under controlled environment. The relationship between water uptake rate and gas exchange in intact roots of cucumber plants was analyzed in response to stomatal transpiration in the treatments that leaf transpiration was promoted by lighting and was inhibited by applying ABA and microcrystalline wax to the leaves. The decrease rate of O_2 was not necessarily associated with water uptake rate. On the other hand, increase rate of CO_2 was higher in the lighted plants in which leaf transpiration and water uptake were inhibited. The CO_2 concentration continued to increase even in O_2 deficit solution in the transpiring plants. From the fact that water uptake is caused by leaf transpiration and gas exchange in leaf is promoted in transpiring leaf, gas exchange in leaf was considered to be responsible for gas exchange in roots, and it is possible that O_2 transported from leaves to root system may be used for root respiration.

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

INTRODUCTION

Plant growth is inhibited by O_2 deficiency or toxicity of accumulated CO_2 in flooded soil (*4*, *8*, *16*, *24*, *25*) and in poor aerated root medium (*6*, *14*, *20*, *31–33*). The gas exchange in roots is responsible for water uptake, water movement (*1*, *13*, *23*, *30*), and the plant growth (*3*, *7*, *9–12*, *15*, *17*, *18*, *27–29*, *34*). For better understanding of root system, it is further necessary to examine environmental effects on root function.

The present paper deals with analysis of gas exchange in roots of whole plant in hydroponics.

MATERIAL AND METHODS

Hydroponic system

A hydroponic system was designed and constructed to measure water uptake rate in intact roots, pH, O_2 and CO_2 concentrations in nutrient solution under controlled environment. Figure 1 shows the hydroponic system. Ambient air temperature and relative humidity were controlled at 25°C and 40% in a growth chamber where light intensity was 200 μmol m^{-2} s^{-1} (fluorescent lamps; FLR110-EHW/A, Toshiba Corporation). Temperature of nutrient solution in a stainless steel pot was controlled at 25±0.1°C by a water bath where water (15 l min^{-1}) was circulated from water temperature controller (constant temperature circulator; CL-300, Taiyo Scientific Industrial Co., Ltd.). The water bath was covered with styrofoam for insulating heat.

Measurements

Polarographic dissolved O_2 meter (UD-1, Central Kagaku Co., Ltd.), CO_2 meter (CGP-1, Toa Electronics Ltd.) and pH meter (HM-7E, Toa Electronics Ltd.) were employed for the measurements in nutrient solution. The stainless steel pot was filled with nutrient solution (3.7 litre) saturated with air, and roots of a material plant was submerged in the solution. The plant and sensors were fixed at the pot surface by using rubber corks where silicone grease was applied to airproof the system. The solution was continuously stirred by a magnetic stirrer to homogenize

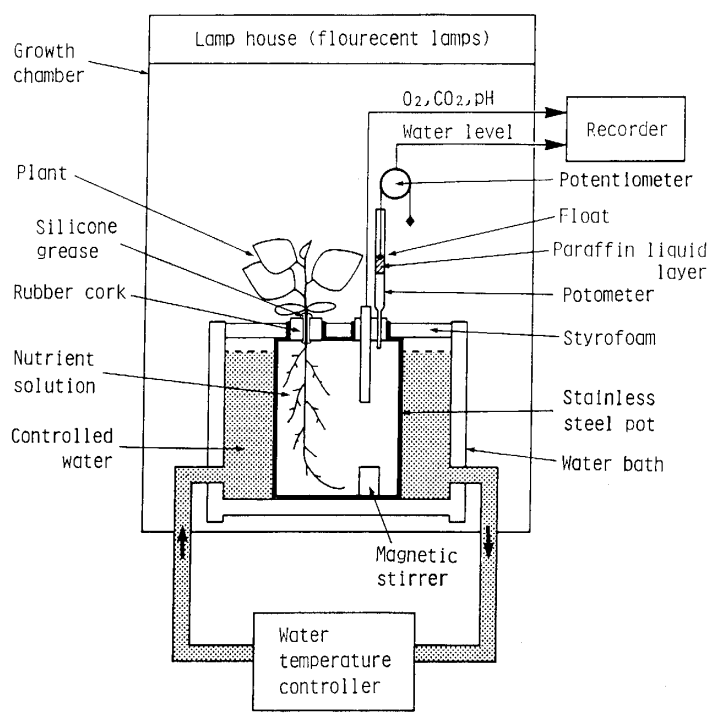

Fig. 1. Schematic diagram of hydroponic system for on-line measurements of pH, water uptake rate, dissolved O_2 and dissolved CO_2 concentrations in controlled temperature of nutrient solution.

the solution. Water uptake rate in roots was measured automatically by a potometer: Decrease of the solution in the potometer was detected by a float which was connected to a potentiometer. Surface of the solution in the potometer is sealed with paraffin liquid layer to prevent diffusion of air into the solution. The sensor signals of the level of the solution in the potometer, pH, O_2 and CO_2 concentrations in the solution were recorded in course of time.

Plant material

Cucumber plants (*Cucumis sativus* L. "Chojitsu-Ochiai") were used in this experiment. Plants were grown at air temperature of 23°C, relative humidity of 70%, and light intensity of 250 μmol m^{-2} s^{-1} (metal halide lamps; Yoko lamp, DR400, Toshiba Corporation) in photoperiod of 12 h. The seeds were sown in Vermiculite moistened with tap water. The seedlings were transplanted at the cotyledonary stage to hydroponic system and were grown in fully aerated nutrient solution at about 0.25 mmol l^{-1} of dissolved O_2. The 3 leaf stage plant was kept under the experimental condition for 18 h in the growth chamber. Thereafter, measurements were started, as soon as the plant was transplanted to the pot of the hydroponic system shown in Fig. 1.

Total leaf area, fresh and dry weight of whole root system in the cucumber plant used were 577±99 cm^2, 6.0±1.3 g and 0.22±0.06 g, respectively.

Analysis of CO_2 concentration

Dissolved CO_2 in water is hydrated to form H_2CO_3 and unhydrated CO_2 is in equilibrium with H_2CO_3 as expressed by

$$CO_2 + H_2O \rightleftharpoons H_2CO_3$$

Then unhydrated and hydrated CO_2 are ionized to form HCO_3^- and CO_3^{2-} as follows;

$$CO_2 + H_2O \rightleftharpoons H^+ + HCO_3^-$$
$$CO_2 + OH^- \rightleftharpoons HCO_3^-$$
$$H_2CO_3 \rightleftharpoons H^+ + HCO_3^-$$
$$HCO_3^- \rightleftharpoons H^+ + CO_3^{2-}$$

For analysis of increase of dissolved CO_2 related to gas exchange in roots in hydroponics, it is necessary to evaluate concentration of total inorganic carbon in nutrient solution.

The equilibrium constants are defined at constant water temperature on respective reactions in dissociation and ionization of inorganic carbon. However, Ka_1 is commonly applied to the first ionization of unhydrated and hydrated CO_2 molecules;

$$Ka_1 = \frac{[H^+]\,[HCO_3^-]}{[CO_2 + H_2CO_3]}$$

The second ionization constant is defined as

$$Ka_2 = \frac{[H^+]\,[CO_3^{2-}]}{[HCO_3^-]}$$

Molarity of respective components of inorganic carbon at constant temperature is related to pH of solution as represented by Henderson-Hasselbach equations;

$$pH = pKa_1 + \log \frac{[HCO_3^-]}{[CO_2 + H_2CO_3]}$$

$$pH = pKa_2 + \log \frac{[CO_3^{2-}]}{[HCO_3^-]}$$

where $pKa_1 = -\log Ka_1$, and $pKa_2 = -\log Ka_2$
From the fact that pH of nutrient solution was 5.0 to 6.0 in this system, it was estimated that the components of inorganic carbon in the solution are CO_2, H_2CO_3 and HCO_3^-, and total inorganic carbon molarity is total molarity of these components of inorganic carbon.

The CO_2 sensor employed can detect both CO_2 and H_2CO_3, and the sum of them was used as CO_2 concentration. So, the molarity of HCO_3^- was calculated from measured values of CO_2 concentration and pH as follows;

$$\log[HCO_3^-] = \log[CO_2 + H_2CO_3] + pH - pKa_1$$

where $Ka_1 = 4.45 \times 10^{-7}$ (mol l^{-1}) at solution temperature of 25°C as given by Helder (*19*). Thus, CO_2 concentration of the solution in the hydroponic system was evaluated by the molarity of total inorganic carbon.

RESULTS AND DISCUSSION

For examination of gas exchange in roots, dissolved O_2 and CO_2 concentrations in nutrient solution of hydroponics were measured. The concentrations of O_2 and CO_2 in fully aerated solution were 0.24 ± 0.01 mmol l^{-1} and 0.05 ± 0.02 mmol l^{-1}, respectively. Figure 2 shows water uptake rate, O_2 and CO_2 concentrations in the hydroponics where plants were cultured in photoperiod of 12 h. The concentration of O_2 decreased to about 0.1 mmol l^{-1} at 30 h after the start of measurements, and thereafter became constant. The concentration of CO_2 continued to increase even after the time when O_2 concentration was the lowest, and it reached steady-state at about 3.7 mmol l^{-1} at 130 h after the start of measurements. Water uptake rate oscillated, synchronizing with the photoperiod: It increased in the light and decreased in the dark. This oscillation gradually damped, and water uptake rate became lower in course of time. Figure 3 shows water uptake rate, O_2 and CO_2 concentrations in the solution in which the plants were cultured in the continuous light. The concentration of O_2 decreased to about 0.1 mmol l^{-1} at 20 h after the start of measurements, and the concentration of CO_2 increased to about 3.5 mmol l^{-1} at 90 h after the start of measurements in the light. Even in the continuous light, periodical change of water uptake rate was observed during 2 days and was considered to be caused by habituation of the photoperiod during seedling culture. Thereafter, water uptake rate gradually decreased. Thus, it was found that CO_2 release in intact roots

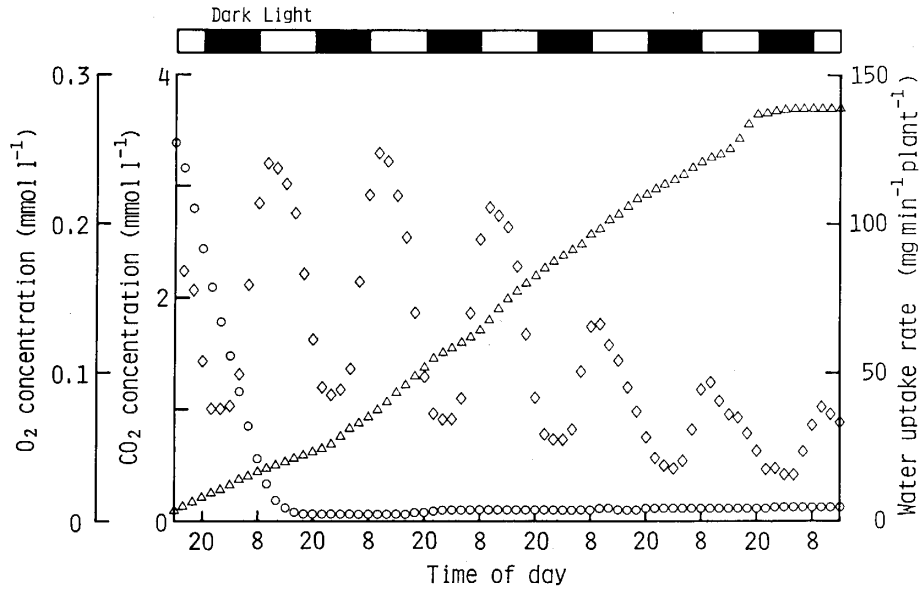

Fig. 2. Time course patterns of water uptake rate (◇), dissolved O_2 (○) and dissolved CO_2 (△) concentrations in hydroponics in photoperiod of 12 h (8: 00–20: 00).

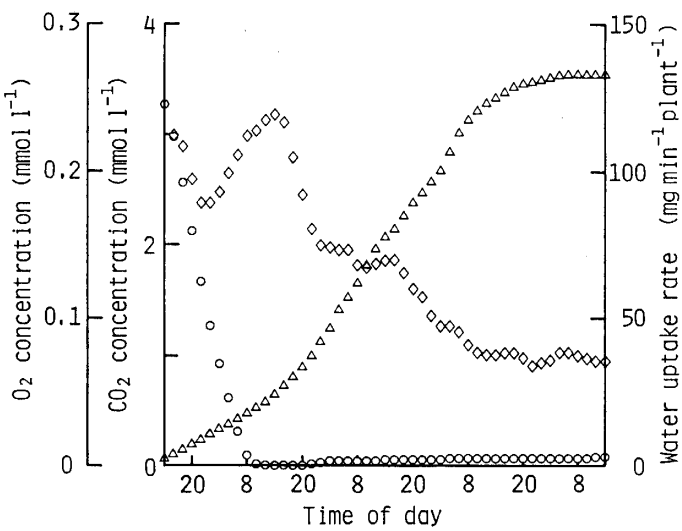

Fig. 3. Time course patterns of water uptake rate (◇), dissolved O_2 (○) and dissolved CO_2 (△) concentrations in hydroponics under continuous light condition.

was caused even in the O_2 deficit solution.

Figure 4 shows water uptake rate (a), O_2 (b) and CO_2 (c) concentrations in the solution of hydroponics where the plants were lighted and were kept in the dark. Water uptake rate in the light was about two times as much as that in the dark. Decrease rate of O_2 and increase rate of CO_2 in the light were higher than those in the dark. The CO_2 concentration in the light was about four times as much as that

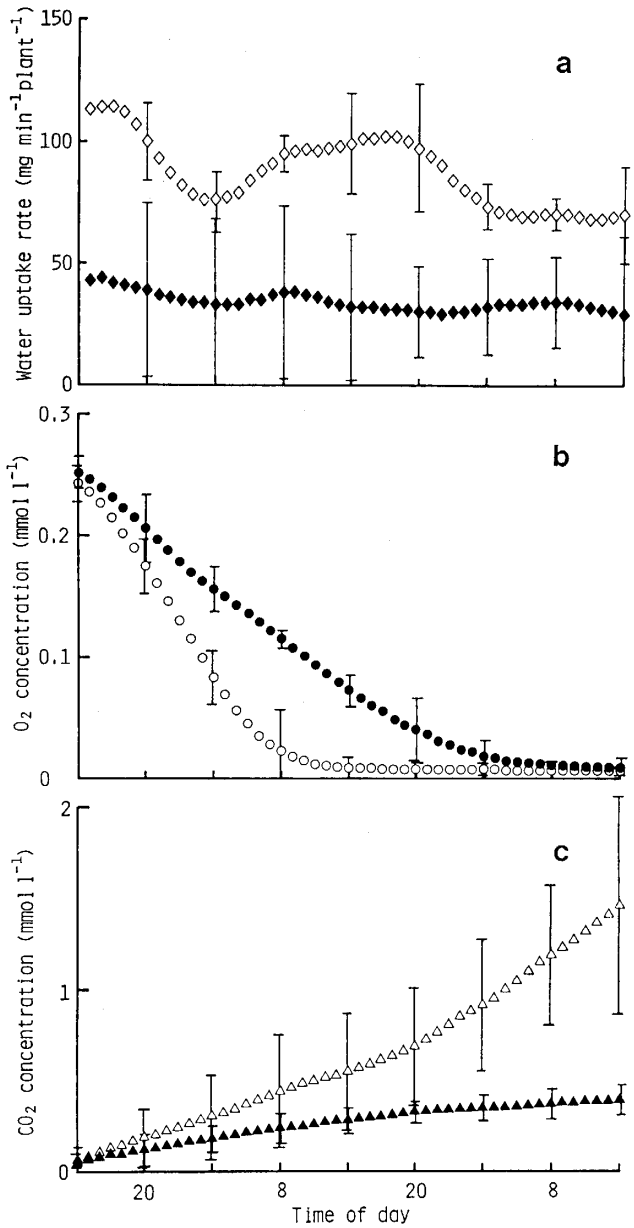

Fig. 4. Time course patterns of water uptake rate (a), dissolved O_2 (b) and dissolved CO_2 (c) concentrations in hydroponics of intact plants under light and dark conditions, where means of measured values in 3 plants are plotted with 95% confidence intervals: Open symbols, continuous light condition; closed symbols, dark condition.

in the dark at 48 h after the start of measurements. The difference in CO_2 concentration between the light and the dark was significant at 5% level. Thus, lighting to leaves appeared to be responsible for gas exchange in roots as well as water uptake rate, and it was suggested that stomatal movement is related to gas exchange in roots.

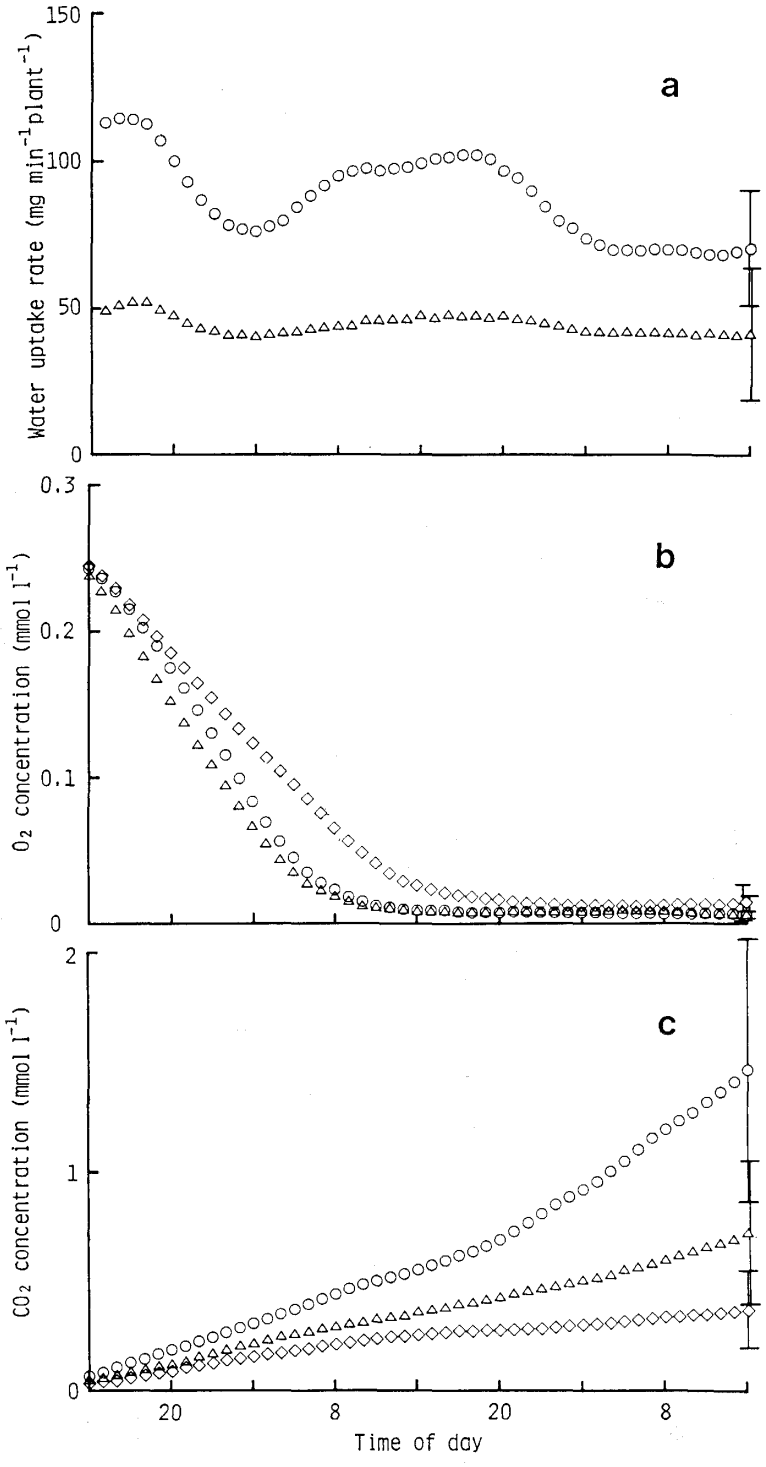

Fig. 5. Time course patterns of water uptake rate (a), dissolved O_2 (b) and dissolved CO_2 (c) concentrations in hydroponics under continuous light condition, where means of measured values in 3 plants are plotted with 95% confidence intervals at 48 h after the start of measurements: ○, untreated plants; △, plants treated with ABA and microcrystalline wax; ◇, detached roots.

For inhibition of transpiration and the gas exchange in leaves, abscisic acid (10^{-3} mol l^{-1}) and microcrystalline wax were applied to leaves. Furthermore, detached root system was used to examine influence of leaves on the gas exchange in roots. Figure 5 shows water uptake rate (a), O_2 (b) and CO_2 (c) concentrations in hydroponics where plants were continuously lighted. Water uptake rate in plants treated with ABA and the wax was half as much as that in untreated plants. Decrease rate of O_2 in detached roots was lower than that in untreated whole plants. The difference in O_2 decrease was very small between treated and untreated plants. On the other hand, increase rate of CO_2 in the treated plants was lower than that in untreated plants. At 48 h after the start of measurements, difference in CO_2 concentration between the treated and untreated plants was significant at 5% level. Thus, increase in CO_2 concentration was inhibited in plants treated with ABA and the wax and in detached roots.

Water uptake rate, decrease rate of O_2, and increase rate of CO_2 are listed in Table 1. In the light, water uptake rate in plants treated with ABA and the wax was lower than that in untreated plants. Although decrease rate of O_2 in the treated plants was similar to that in untreated plants, increase rate of CO_2 was lower in the treated plant as compared with untreated plants. On the other hand, water uptake rate in the dark was lower than that in the light, and decrease rate of O_2 and increase rate of CO_2 in the dark were similar to those in detached roots. Thus, decrease in O_2 concentration was not necessarily associated with water uptake, but increase in CO_2 concentration was related to water uptake.

Water uptake in roots is caused by leaf transpiration, and gas exchange is caused through stomata opening in transpiring leaf (*2*, *22*, *26*). Internal O_2 transport from the leaf to roots has been reported in several plant species (*5*, *21*). In this experiment, increase rate of dissolved CO_2 concentration was higher in the case of higher water uptake rate, and the CO_2 concentration continued to increase even in the O_2 deficit solution. From these facts, it is possible that O_2 transported from leaf to root system may be used for root respiration.

Table 1. Water uptake rate, decrease rate of dissolved O_2 concentration, and increase rate of dissolved CO_2 concentration, where means of measured values in 3 plants with respective 95% confidence limits are listed

Treatments	Light condition	Water uptake rate (mg min^{-1} $plant^{-1}$)	O_2 decrease rate (μmol l^{-1} min^{-1})	CO_2 increase rate (μmol l^{-1} min^{-1})
Applying ABA+micro-crystalline wax to leaves	Light	44.1* (±20.0)	0.24 (±0.10)	0.24* (±0.10)
Detaching roots	—	0.0* (± 0.0)	0.16 (±0.08)	0.12* (±0.05)
Untreated	Dark	34.2* (±26.7)	0.14 (±0.11)	0.12* (±0.01)
Untreated	Light	87.2 (± 6.6)	0.23 (±0.11)	0.49 (±0.22)

*; significant difference at 5% level in comparison with untreated plant in the light.

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