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ANALYSIS OF GROWTH, WATER BALANCE AND RESPIRATION OF TOMATO FRUITS UNDER WATER DEFICIT BY USING A MULTIPLE CHAMBER SYSTEM

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ARAKI T., KITANO M., HAMAKOGA M. and EGUCHI H. *Analysis of growth, water balance and respiration of tomato fruits under water deficit by using a multiple chamber system*. BIOTRONICS 27, 61–68, 1998. A multiple chamber system was developed for on-line measurements of gas (CO₂ and H₂O) fluxes in intact fruits and leaflets of tomato plants, where fruit growth rate and pedicel sap flux can be also measured. By using the system for the simultaneous measurements with six plants, effect of water deficit on fruit growth was analyzed in relation to water balance and respiration in the fruits and to photosynthesis and transpiration in the leaflets. The water deficit caused drastic depression in fruit growth in the daytime, which was considered to be associated with depressions in pedicel sap flux, fruit respiration and leaf photosynthesis. Furthermore, sap backflow and fruit shrinkage corresponding to about 2% of the fruit volume were induced by rise in evaporative demand under the water deficit. These results suggest that the multiple chamber system developed can be applied to quantitative analyses of environmental effects on fruit growth, translocation and sink-source relationship in tomato plants.

Key words: *Lycopersicon esculentum* Mill.; tomato fruit; fruit growth; sap flux; fruit respiration; fruit water balance; water deficit; multiple chamber system

INTRODUCTION

Fruit production in tomato plants is affected by expansive growth and sugar accumulation of the fruits, which depend on dynamics of water balance and carbon balance in the fruits. For environmental studies on the fruit production, it is desired to measure dynamics of expansive growth, sap flux, transpiration and respiration of the intact fruits in addition to leaf photosynthesis and transpiration by using the matured plants older than the fruit bearing age (2, 5, 11–13). Such matured plants usually exhibit undesirable variations in their responses, which may bring sampling errors in the measurements (6). Therefore, it is necessary to develop the system which enables the simultaneous measurements with intact fruits and leaves in group of the matured plants.

By growth analyses with the harvested tomato fruits, root water condition

such as water availability and salinity has been indicated to be one of the important environmental factors affecting expansive growth and sugar accumulation of the fruits (1, 3, 16, 17). In these analyses with the harvested fruits, however, dynamics of water balance and carbon balance in the intact fruits has not been analyzed.

In the present paper, a multiple chamber system was developed for the simultaneous measurements with group of the plants, and effect of water deficit on fruit growth was analyzed in relation to sap flux, transpiration and respiration in the intact fruits and photosynthesis and transpiration in the leaflets.

METHODS AND MATERIALS

Measurements by a multiple chamber system

A multiple chamber system was developed for on-line measurements of gas (CO_2 and H_2O) fluxes in intact fruits and leaflets of tomato plants, where fruit growth rate and pedicel sap flux can be also measured. Figure 1 shows a schematic diagram of the system developed for the measurements with six fruits and six leaflets. The system is composed of six fruit chambers (FC1~FC6; $12 \times 6.0 \times 4.0$ cm), six leaf chambers (LC1~LC6; $26 \times 15 \times 7.5$ cm), a gas analyzing unit and an on-line computer. The respective chambers are made of transparent acrylic plates and are equipped with an air mixing micro fan and a ventilation unit, where the ventilation is manipulated by on-off action of air pumps (P) and motor-driven shutters (S) of the ventilating openings (11). The gas analyzing unit consists of an infrared CO_2 and H_2O gas analyzer (IRGA; LI-6262, LI-COR, Inc., Nebraska, USA), a multiple air-sampling path of Teflon tubing and a pair of 13-way solenoid valves for selecting the chamber for CO_2 and H_2O gas analyzing. The 13-way solenoid valve is made up of 12 micro solenoid valves (030E1, Koganei Corp., Tokyo, Japan) connected in parallel.

An intact fruit or a leaflet was enclosed in each chamber, which was ventilated enough by the air pump through the ventilating openings. The multiple sampling path for 12 chambers was switched in rotation from FC1 to LC6 at intervals of 30 s by the synchronized on-off action of the solenoid valves. In the chamber being selected for the gas analysis for 30 s, the air sampled from chamber was circulated into IRGA, and the signals of CO_2 and H_2O gas concentrations ($[\text{CO}_2]$ and $[\text{H}_2\text{O}]$) in the chamber were transmitted to the computer at interval of 1 s. For only 15 s during this 30 s gas analysis, the chamber was temporarily kept as "the closed system" by shutting down the ventilation, where $[\text{CO}_2]$ and $[\text{H}_2\text{O}]$ varied almost linearly according to the respective gas fluxes from the fruit or the leaflet enclosed. Each gas flux was evaluated on-line by the product of the change rate of the gas concentration ($d[\text{CO}_2]/dt$ or $d[\text{H}_2\text{O}]/dt$) and the air volume (V_{SYS}) within inner spaces of the closed system, where $d[\text{CO}_2]/dt$ and $d[\text{H}_2\text{O}]/dt$ were evaluated on-line, and V_{SYS} for each chamber was predetermined by the methods established in the previous study (11). After this 30 s gas analysis in the selected chamber, the ventilation

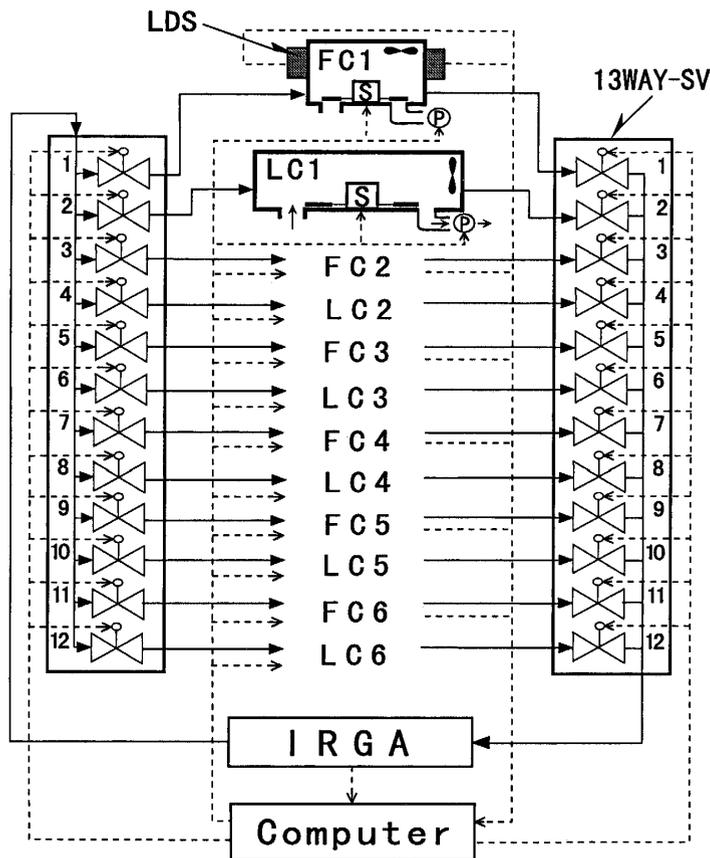


Fig. 1. Schematic diagram of a multiple chamber system for on-line measurements of CO_2 and H_2O gas fluxes in six fruits and six leaflets in tomato plants, where fruit growth rate and pedicel sap flux can be also measured. In the system, 12 chambers for the gas flux measurements in fruits and in leaflets can be connected in parallel with an infrared CO_2 and H_2O gas analyzer through a pair of 13-way solenoid valves: FC1~FC6, fruit chambers; IRGA, infrared gas analyzer for measuring CO_2 and H_2O gas concentrations; LC1~LC6, leaf chambers; LDS, laser displacement sensor for measuring fruit growth rate; P, air pump for ventilating each chamber; S, shutter of the ventilating openings; 13-way SV, 13-way solenoid valves for switching the sampling path; solid line, air sampling path; broken line, signal line.

of the chamber was restarted, and the sampling path was switched to the next chamber. That is, a rotation of the gas analysis with the respective 12 chambers took 6 min, and therefore the gas fluxes in each chamber were evaluated at intervals of 6 min. The switching of the sampling path, the on-off action of the ventilation unit and the data processing were performed on-line by the computer.

Each fruit chamber is also equipped with a pair of laser displacement sensors (LDS; Z4M-W40, OMRON Corp., Kyoto, Japan) for evaluating fruit expansive growth: Diameter of the fruit in the chamber was measured by the LDS system with a resolution of $1.5\ \mu\text{m}$, and the fruit expansive growth on volume base was

evaluated on-line on the basis of the predetermined relationship between diameter and volume in the tomato fruits (9). Furthermore, the pedicel sap flux imported into the fruit through phloems and xylems was evaluated by the sum of the fruit growth rate and the fruit H₂O gas efflux (i.e. volume increment in the berry plus transpiratory water loss from the berry and the calyx). Those variables in the fruit and in the leaflet were represented by the values per unit berry volume and per unit leaf area, respectively.

Plant materials and experimental conditions

Tomato plants (*Lycopersicon esculentum* Mill. cv. Hausu-Momotaro) were potted in 13 L hydroponic pots filled with a complete nutrient solution and were grown hydroponically in a phytotron glass room at a day/night air temperature of 25/15°C and a relative humidity of 70%. The plants were pinched at two leaves above the first truss before anthesis of the second truss, and three fruits were left on the first truss after fruit thinning. A few weeks after anthesis on the first truss, i.e. at the stage of rapid sugar accumulation (7), six plants were transported into a growth cabinet with an artificial light of metal halide lamps (DR400/T(L), Toshiba Corp., Tokyo, Japan) at a *PPFD* of 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in a photoperiod of 12 h (6:00–18:00) under a day/night air temperature of 25/15°C, a relative humidity of 70% and a CO₂ gas concentration of around 370 $\mu\text{mol mol}^{-1}$. After two days acclimation to the growth cabinet condition, the simultaneous measurements were started at midnight with the six plants, where three of the plants (i.e. the water deficit plants) were subjected to the water deficit by dewatering completely those hydroponic pots at the start of the measurements at midnight, and the other three plants (i.e. the control plants) were always supplied with the sufficient nutrient solution.

RESULTS AND DISCUSSION

Effects of the water deficit on the gas fluxes in the fruits and the leaflets and fruit expansive growth and pedicel sap flux were analyzed by comparison between the water deficit plants and the control plants. Figure 2 shows diurnal variations of respiratory CO₂ efflux and transpiratory H₂O efflux of the fruits in the water deficit plants and the control plants under a day/night air temperature of 25/15°C. Fruit respiratory CO₂ efflux in the control plants was rapidly enhanced with temperature rise from 15°C to 25°C just after lighting, as observed in the previous study (12). This enhancement in fruit respiratory CO₂ efflux was remarkably suppressed in the water deficit plants, and consequently the cumulative CO₂ efflux during the daytime in the water deficit plants was depressed to 53% of that in the control plants. Thus, the water deficit remarkably depressed fruit respiration under the light. Fruit transpiratory H₂O efflux was also enhanced just after lighting, but the water deficit decreased the cumulative H₂O efflux during the daytime by 38%. It has been reported that about two-thirds of the transpiratory water loss from the fruit (i.e. berry + calyx) is through transpiration from the calyx having stomata (2). Therefore, it could

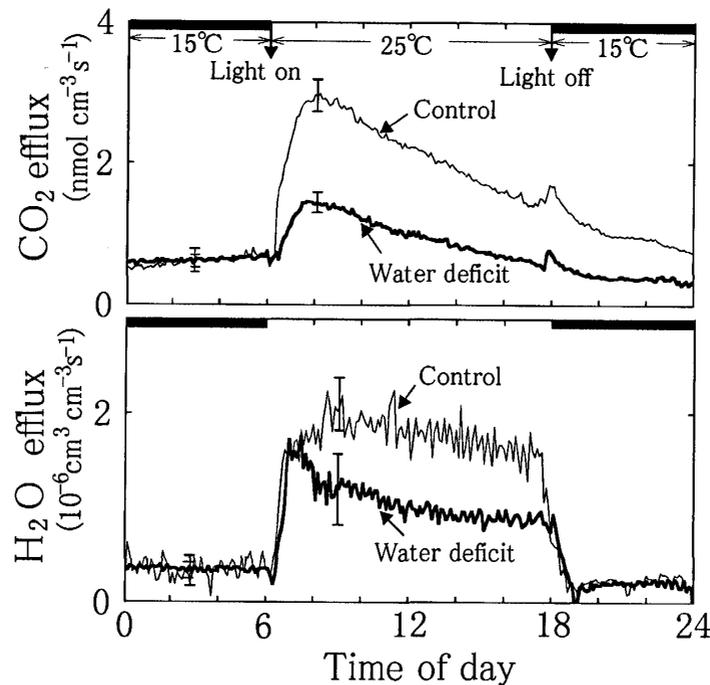


Fig. 2. Diurnal variations of respiratory CO_2 efflux and transpiratory H_2O efflux of the fruits in the water deficit plants and the control plants under a day/night temperature of 25/15°C in the artificial light growth cabinet, where the hydroponic pots of the water deficit plants were dewatered completely at midnight (0:00), and the control plants were supplied with the sufficient nutrient solution. Values were means of three plants, and vertical bars indicate standard deviation.

be estimated that this depression in fruit transpiration by the water deficit was mainly attributed to the depressed transpiration in the calyx. Figure 3 shows diurnal variations of photosynthetic CO_2 influx and transpiratory H_2O efflux of the leaflets in the water deficit plants and the control plants. Photosynthetic CO_2 influx and transpiratory H_2O efflux of the leaflets rose rapidly just after lighting, but those in the water deficit plants, where leaf water potential dropped to -1.08 ± 0.21 MPa at noon, were suppressed to less than 25% of those in the control plants.

Figure 4 shows diurnal variations of fruit growth rate and pedicel sap flux in the water deficit plants and the control plants. In the control plants supplied with the sufficient nutrient solution, fruit growth rate and pedicel sap flux were clearly enhanced after lighting and temperature rise to 25°C. A major portion (i.e. about 75%) of the fruit growth and the imported sap flux were brought during the light period, and fruit volume was increased by 11% during the daytime. In the water deficit plants, on the other hand, fruit shrinkage and sap backflow were found to start three hours after dewatering. These fruit shrinkage and sap backflow were remarkably accelerated by lighting for a few hours. Thereafter, the growth rate and the sap influx recovered but appeared to be inhibited to nearly zero: The cumulative sap flux during the daytime was

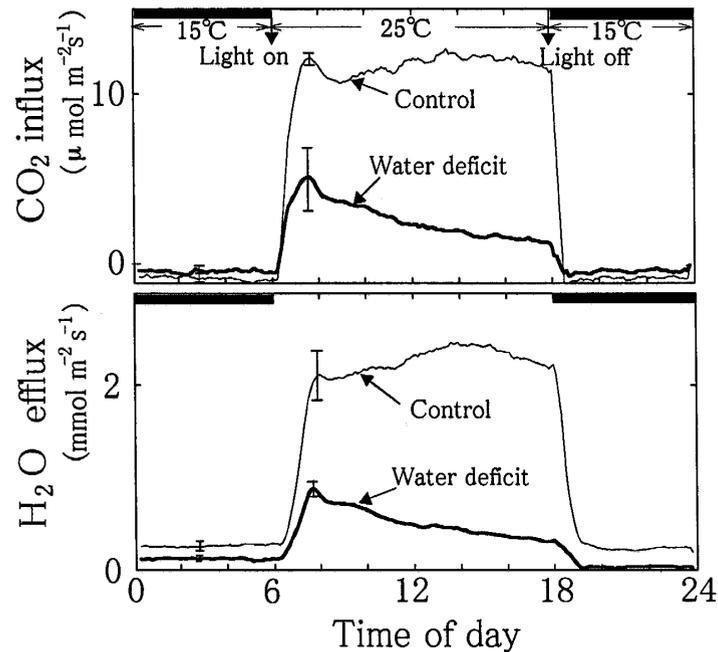


Fig. 3. Diurnal variations of photosynthetic CO_2 influx and transpiratory H_2O efflux of the leaflets in the water deficit plants and the control plants under a day/night temperature of $25/15^\circ\text{C}$ in the artificial light growth cabinet, where the hydroponic pots of the water deficit plants were dewatered completely at midnight (0:00), and the control plants were supplied with the sufficient nutrient solution. Values were means of three plants, and vertical bars indicate standard deviation.

decreased by 90% by the water deficit. Volume of the sap backflow corresponded to 2% of the fruit volume, and consequently the fruit lost 2.5% of its volume in the daytime under the water deficit.

Thus, the water deficit caused drastic depressions in expansive growth, sap influx, transpiration and respiration in the fruit as well as depressions in photosynthesis and transpiration in the leaflet. In tomato plants, a major portion of sap flux into the fruits has been estimated to be via phloems (7). The phloem sap flux transporting photoassimilates and water into fruits is driven by the pressure potential gradient along phloems from leaves to fruits, which can be regulated by the loading of photoassimilates on sieve tubes in source leaves and the osmotic water influx to sieve tubes from xylems (15, 18, 19). Therefore, it can be considered that undesirable drop in xylem water potential under the water deficit retarded the phloem sap flux through depressions in the loading of photoassimilates in source leaves and in the water influx to sieve tubes. The preceding study (13) has suggested that respiration of tomato fruits contributes to expansive growth and sugar accumulation of the fruits through regulation of the energy-dependent postphloem sugar transport in the fruits. This implies that the suppressed fruit respiration in the water deficit plants (Fig. 2) also affected the depressions in fruit growth and sap influx. Furthermore, the accelerated sap backflow found in the water deficit plants just after lighting was

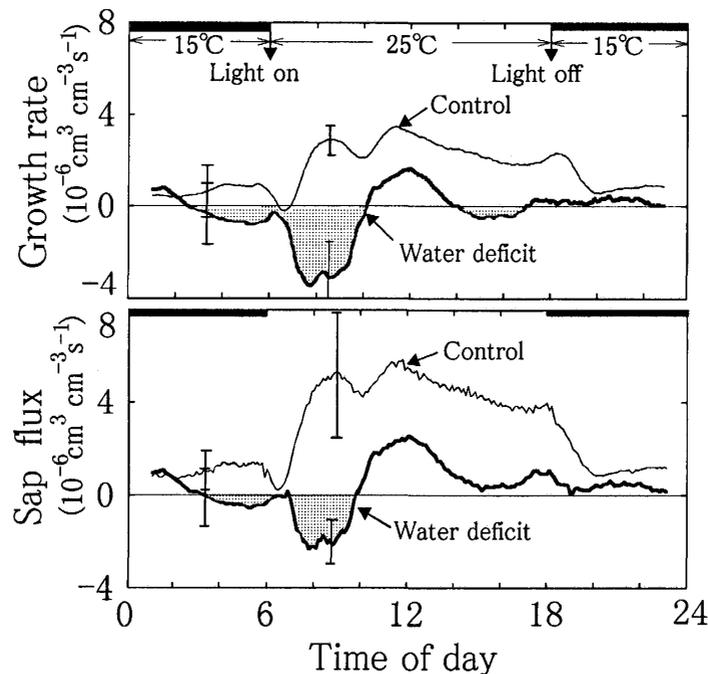


Fig. 4. Diurnal variations of fruit growth rate and pedicel sap flux of the fruits in the water deficit plants and the control plants under a day/night temperature of 25/15°C in the artificial light growth cabinet, where the hydroponic pots of the water deficit plants were dewatered completely at midnight (0:00), and the control plants were supplied with the sufficient nutrient solution. Values were means of three plants, and vertical bars indicate standard deviation. Dotted areas in fruit growth rate and pedicel sap flux indicate fruit shrinkage and sap backflow, respectively.

considered to be caused by the excessive increase in evaporative demand under the inhibited root water uptake, which might reverse the water potential gradient along xylem from the stem to the fruits (4, 8, 10, 14).

These results suggests that the multiple chamber system developed can be applied to quantitative analyses of environmental effects on fruit growth, translocation and sink-source relationship in tomato plants.

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