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Kitano, Masaharu Biotron Institute Kyusyu Univercity

Yokomakura, F. Biotron Institute Kyusyu Univercity

Eguchi, Hiromi Biotron Institute Kyusyu Univercity

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INTERACTIVE DYNAMICS OF FRUIT AND STEM GROWTH IN TOMATO PLANTS AS AFFECTED BY ROOT WATER CONDITION II. RELATION WITH SUCROSE TRANSLOCATION

M. KITANO, F. YOKOMAKURA and H. EGUCHI

Biotron Institute, Kyusyu Univercity 12, Fukuoka 812-81, Japan

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KITANO M., YOKOMAKURA F. and EGUCHI H. Interactive dynamics of fruit and stem growth in tomato plants as affected by root water condition. II. Relation with sucrose translocation. BIOTRONICS 25, 77-84, 1996. Dynamics of sucrose translocation in hydroponic tomato plants (Lycopersion esculentum Mill.) were analyzed with reference to fruit and stem growth as affected by water relations. Sucrose flux through a pedicel was evaluated by bathing the cut end of the pedicel into a chelating agent of ethylenediaminetetraacetic acid (EDTA) solution under on-line measurement of fruit and stem growth. Sucrose flux and fruit and stem growth were affected by change in root water conditions and appeared in different patterns dependent on change in xylem water potential during dewatering. In the case of larger decrease in xylem water potential and significant stem shrinkage during dewatering, fruit growth was kept higher with decrease in sucrose flux, but rewatering induced immediate swelling of stem and sap backflow from the fruit. On the other hand, the smaller decrease in xylem water potential during dewatering resulted in highly enhanced sucrose flux and fruit growth after rewatering. These results suggest that fruit growth and sucrose translocation can be controlled by the root water condition through interactive dynamics with water relations of translocation path responding to change in xylem water potential.

Key words: tomato plants; *Lycopersion esculetum* Mill.; sucrose translocation; fruit growth; stem growth; water relations; EDTA method.

INTRODUCTION

In tomato fruits, accumulation of dry matter as well as water is one of important factors responsible for fruit yield and quality. Dry matter accumulation depends on phloem translocation of photoassimilates, in particular, sucrose in tomato plants (15). Phloem translocation has been analyzed by collecting phloem sap exuded by the aphid menthod (6, 14), the incision method (3, 4) or the EDTA (ethylenediaminetetraacetic acid) method (7). The former two methods are useful for analysis of composition of the sap exuded from a small part of phloem, and the EDTA method is considered to be applicable to evaluation of flux of photoassimilate translocated through the cut end of a

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petiole or a pedicel bathing into a chelating agent of EDTA solution.

The flux of photoassimilates translocated into the fruit varies with volume of phloem sap flux and concentration rate of photoassimilates in the sap (5). The phloem sap flux into tomato fruit has been reported to predominate fruit expansive growth (1, 5) and also reported to be reduced by long term and steady treatment of high salinity or water deficit through changes in plant water relations (1, 2, 5, 13). For optimalizing root water condition in tomato fruit production, it is essential to understand dynamic interaction among phloem translocation, fruit expansive growth and plant water relations under variation of root water conditions.

In the preceding paper (9), interactive dynamics of fruit and stem growth affected by watering and dewatering were analyzed by developing the laser displacement sensor (LDS) system. The present paper deals with dynamic analysis of sucrose translocation, fruit and stem growth and plant water relations by applying the EDTA method and the LDS system.

MATERIALS AND METHODS

Plant materials and experimental conditions

A pair of tomato plants (Lycopersion esculentum Mill cv. Hausu-Momotaro) were potted in a 13 L hydroponic pot filled with complete nutrient solution and grown hydroponically in a phytotron glass room at a day/night tempreture of $23/18^{\circ}$ C and a relative humidity of 70%. The plants were pinched at two leaves above the first truss before anthesis of the second truss. About 3 weeks after pollination of the second fruit on the first truss, the plants potted in a pair were transported into a growth cabinet and grown with the sufficient nutrient solution at an air temperature of 20.5° and a relative humidity of 70% under an artificial light of metal halide lamps (YOKO lamp, DR400, TOSHIBA CORPORA-TION, Tokyo, Japan) through heat absorbing filters (HG, Ohara Optical Glass Mfg. Co. Ltd., Tokyo, Japan) with a PPFD of $300 \,\mu mol/m^2/s$ in a photoperiod of 8:00-20:00. After 4 days acclimation to the growth cabinet condition, the plants were used for the experiment, where root water condition was changed by watering and dewatering: The nutrient solution in the pot was withdrawn from the pot at the start of the experiment, and the plants were dewatered immediately for six hours and rewatered with the nutrient solution after the 6 h One of the plants potted in a pair was used for time course dewatering. evaluations of sucross flux through a pedicel and xylem water potential. The other was used for on-line measurement of fruit and stem growth.

Evaluation of sucrose flux through a pedicel

Phloem sap exuded through the pedicel of a fruit was collected by applying a chelating agent of EDTA (ethylenediaminetetraacetic acid) solution, which has been reported to inhibit callose formation in phloem sieve tubes (7). The second fruit on the fruit truss in one of the plants potted in a pair was excised from the pedicel, and the cut end of the pedicel was bathed into 20 mM EDTA solution in



Fig. 1. Schematic diagram of the EDTA (ethylenediaminetetraacetic acid) method for collecting phloem sap through the cut end of a pedicel.

a 1.4 mL vial as shown in Fig. 1. The solution in the vial was sampled and filtered through a membrane with a pore size of $45\,\mu$ m. Soluble sugars (sucrose, glucose and fructose) were analyzed by using a high performance liquid chromatography (LC-10AD, SHIMADZU CORPORATION, Kyoto, Japan) with a stainless column (Shim-pack SCR-101N, SHIMADZU CORPORATION, Kyoto, Japan) packed with stylene-divinylbenzene copolymer. Concentration rates of the soluble sugars in the solution were detected with a differential refractometer (RID-6A, SHIMADZU CORPORATION, Kyoto, Japan). The major component of the soluble sugars was sucrose which was about 90% of the soluble sugars in the exuded sap. In this experiment, sucrose flux (J_{SUC}) translocated through the pedicel was evaluated by the product of the sucrose concentration rate and the total volume of the solution in the vial. This EDTA method made it possible to collect phloem sap during a whole day.

Other measurements

Fruit diameter (D_F) , fruit volume (V_F) , stem diameter (D_S) and xylem water potential (Ψ_X) were measured by the methods applied in the preceding study $(9): D_F$ and V_F of the second fruit on the first truss and D_s at the internode below the first truss were measured on-line by applying two set of the laser displacement sensor (LDS) systems. Ψ_X was evaluated by water potential measured psychrometrically in matured leaflets covered with an opaque polyethylene bag (9).

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RESULTS AND DISCUSSION

Figure 2 shows diurnal patterns of $D_{\rm F}$, $V_{\rm F}$, $D_{\rm S}$ and $J_{\rm SUC}$ in the case without the treatment of dewatering. There was no remarkable effect of lighting on fruit and stem growth. On the other hand, sucrose flux was clearly enhanced by lighting, while the enhanced $J_{\rm SUC}$ was declined in the late afternoon. That is, sucrose translocation did not necessarily vary in parallel with fruit expansive growth.

Figure 3 shows diurnal patterns of $D_{\rm F}$, $V_{\rm F}$, $D_{\rm S}$, $\Psi_{\rm X}$ and $J_{\rm SUC}$ in the case that larger decrease in $\Psi_{\rm X}$ was induced during the 6 h dewatering. Stem began to shrink drastically 30 min after the start of dewatering with larger decrease in $\Psi_{\rm X}$: During the 6 h dewatering, $D_{\rm F}$ and $\Psi_{\rm X}$ decreased by 370 μ m and 0.7 MPa, respectively. Fruit growth, however, was kept higher at about 0.05 mm³/s even under remarkable stem shrinkage during dewatering, and $V_{\rm F}$ was increased by 1.8 cm³ during the 6 h dewatering. Sucrose flux was enhanced in the morning but gradually depressed to nearly zero under dewatering. Just after rewatering, the contracted stem swelled immediately with rise in $\Psi_{\rm X}$, but in contrast the fruit



TIME OF DAY

Fig. 2. Diurnal patterns of fruit diameter (D_F) , fruit volume (V_F) , stem diameter (D_S) and sucrose flux (J_{SUC}) through a pedicel in the case without the treatment of dewatering.



TIME OF DAY

Fig. 3. Diurnal patterns of fruit diameter (D_F) , fruit volume (V_F) , stem diameter (D_S) , xylem water potential (Ψ_X) and sucrose flux (J_{SUC}) through a pedicel in the case that larger decreases in Ψ_X and D_S were caused by the treatment of rapid dewatering for 6 h.

shrank by about 0.6 cm^3 at extremely high rates of about $-0.20 \text{ mm}^3/\text{s}$ as observed in the preceding paper (9), and this volume loss in the fruit did not recover in about three hours after rewatering. Furthermore, there found no significant recovery of sucrose flux, and zero sucrose flux appeared in about two hours after rewatering.

In the case that decrease in Ψ_X during dewatering was smaller and stem shrinkage appeared insignificant as shown in Fig. 4, fruit growth was cleary depressed by dewatering together with sucrose flux: The respective decreases in Ψ_X and D_S during dewatering were only about 0.3 MPa and 50 μ m, and the negative fruit growth rate was found after dewatering. The rewatering,

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TIME OF DAY

Fig. 4. Diurnal patterns of fruit diameter (D_F) , fruit volume (V_F) , stem diameter (D_S) , xylem water potential (Ψ_X) and sucrose flux (J_{SUC}) through a pedicel in the case that smaller decreases in Ψ_X and D_S were caused by the treatment of rapid dewatering for 6 h.

however, made clear recovery in the fruit growth which was accompanied with highly enhanced sucrose flux. The enhanced J_{SUC} became extremely higher than J_{SUC} before dewatering. Figure 5 shows time course patterns in the case that the decreases in Ψ_X and D_S during dewatering appeared intermediate between those shown in Figs. 3 and 4. The responses of fruit growth and sucrose flux also appeared in the intermediate patterns shown in Figs. 3 and 4.

Both fruit expansive growth and sucrose translocation were affected by transient change in root water condition, and those appeared in different patterns dependent on changes in xylem water potential and stem shrinkage (Figs. 3, 4 and 5). The nonparallel correlation between fruit expansive growth and sucrose flux (Figs. 2 and 3) indicates that the phloem sap flux into fruits and the sucrose concentration rate in the sap can vary independent of each

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TIME OF DAY

Fig. 5. Diurnal patterns of fruit diameter (D_F) , fruit volume (V_F) , stem diameter (D_S) , xylem water potential (Ψ_X) and sucrose flux (J_{SUC}) through a pedicel in the case that decreases in Ψ_X and D_S during the treatment of rapid dewatering appeared intermediate between those shown in Figs. 3 and 4.

other. The larger drop in xylem water potential during dewatering (Fig. 3) is considered to induce the withdrawal of water from the stem tissues into the stem vascular bundle, which resulted in larger shrinkage of the stem. This water supply from the water reservoir of stem tissues during dewatering can be considered to contribute to pressure potential gradient along the translocation path which drives sap flow to fruits (10-12). This implies that herbaceous stem tissues can act as a transient water reservoir not only for leaf transpiration (8), but for maintenance of the sap flow to fruits. In the long term treatment of high salinity or water deficit in tomato plants (1, 2, 5, 13), it has been estimated that the phloem sap flux into fruit is reduced but the dry matter accmulation can be maintained by high concentration of photoassimilates in the sap. However, the decreasing sucrose flux found during dewatering (Figs. 3, 4 and 5)

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indicates that sucrose concentration rate in the translocating sap was not enhanced during transient dewatering. Furthermore, zero sucrose flux accompanied with drastic fruit shrinkage just after rewatering (Fig. 3) demonstrates the sap backflow from the fruit. On the other hand, the sucrose flux was enhanced by rewatering in the case that decrease in xylem water potential during dewatering appeared smaller (Figs. 4 and 5). This highly enhanced sucrose flux suggests that rewatering after transient water deficit can promote sucrose translocation by enhancements of sap flux into the fruit and sucrose concentration in the sap. Thus, the EDTA method with the help of on -line measurement of fruit and stem growth was reliable for dynamic analysis of phloem translocation in a tomato plant as affected by transient change in root water condition. From the results, it is concluded that fruit expansive growth and sucrose flux into fruits are affected by transient change in root water condition through dynamics of water relations in the translocation path.

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