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RESPIRATION, SAP FLUX, WATER BALANCE AND EXPANSIVE GROWTH IN TOMATO FRUIT

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ARAKI, T., KITANO, M. and EGUCHI, H. *Respiration, sap flux, water balance and expansive growth in tomato fruit.* BIOTRONICS **26**, 95–102, 1997. Diurnal changes in respiration, pedicel sap flux, water balance and expansive growth in a fruit of tomato plant (*Lycopersicon esculentum* Mill.) were analyzed in an artificial light growth chamber, where the fruit at the stage of rapid sugar accumulation was used. The higher respiration of the intact berry was clearly found under the light where the sap flux and the growth rate were kept higher, but darkening, removal of the calyx and excision of the pedicel brought the lower berry respiration with significant depression in the sap flux and the growth rate. Transpirational water loss from each of the berry and the calyx was only 10% and 20% of the imported sap flux, and the residual 70% of the imported sap flux contributed to expansive growth of the berry. From these results, it is conceivable that respiration of the tomato fruit at the stage of rapid sugar accumulation closely relates to the phloem sap flux which is responsible for sugar accumulation and expansive growth of the fruit.

Key words: tomato plant; *Lycopersicon esculentum* Mill.; fruit respiration; pedicel sap flux; fruit water balance; fruit growth.

INTRODUCTION

Phloem translocation from leaves to sink organs is driven by the pressure flow of phloem sap which is regulated by the respective processes of loading in leaves, long distance transport through phloem, unloading and postphloem transport in sink organs (*3, 5, 7, 11–15*).

In tomato plants, the postphloem transport in fruits (i.e. sugar transport from phloem to storage pericarp tissues) has been considered to be the determinant process for sugar accumulation into fruits (*17*), and it has been proved that the postphloem transport at the stage of rapid sugar accumulation (i.e. a few weeks after anthesis) is apoplastic transport involving energy-dependent sugar transport across plasma membranes (*16*). Furthermore, phloem sap flux transporting sugar into tomato fruits has been demonstrated to be also the principal source of water for fruit expansive growth (*6*). Therefore, relationships among respiration, sap flux and water balance in the intact tomato fruit should be analyzed in environmental and physiological studies on translocation and fruit growth in tomato plants (*4, 18*).

The present paper deals with quantitative analyses of respiration, pedicel sap flux, water balance and expansive growth in tomato fruit by using the on-line system newly developed in the preceding paper (*10*).

MATERIALS AND METHODS

Plant materials and experimental conditions

Tomato plants (*Lycopersicon esculentum* Mill. cv. Hausu-Momotaro) were potted in 8 *l* pots filled with vermiculite and were grown in a phytotron glass room at day/night temperature of 23/18℃ and relative humidity of 70%, where the vermiculite in the pots was kept moistened enough by dripping complete nutrient solution. The plants were pinched at two leaves above the first truss before anthesis of the second truss. A few weeks after anthesis of the second proximal fruit on the first truss, the plant was transported into a growth chamber with air temperature of 20℃ and relative humidity of 70% under the artificial light of metal halide lamps (YOKO lamp, DR400 TOSHIBA CORPORATION, Tokyo) with *PPFD* of 300 μmol m^{-2} s^{-1} in a photoperiod of 08:00–20:00. After two days acclimation to the growth chamber condition, the plant was used for analyses of respiration, pedicel sap flux, water balance and expansive growth in the second proximal fruit on the first truss a few weeks after anthesis: The immature tomato fruit a few weeks after anthesis has been reported to be at the stage of rapid sugar accumulation (*6, 16*). The analyses were performed under different three cases of the fruit, that is, the attached berry with the calyx ("berry+calyx"), the attached berry without the calyx ("berry") and the detached berry without the calyx ("detached berry"). In the case of "berry", the calyx was removed, and in the case of "detached berry", sap flux into the berry were prohibited by excision of the pedicel.

Measurements in a tomato fruit

For analyses of respiration, water balance and expansive growth in the fruit, CO_2 flux (J_{CF}, respiratory CO_2 efflux minus photosynthetic CO_2 influx), H_2O flux (J_{WF}, transpirational water loss), pedicel sap flux (J_P+J_X, phloem sap flux plus xylem sap flux imported into the fruit through the pedicel) and growth rate (*RGR*, relative growth rate on volume base) were evaluated on-line by using the fruit chamber system developed in the preceding study (*10*): J_{CF} and J_{WF} were evaluated at intervals of 1min on the basis of the respective change rates of CO_2 and H_2O gas concentrations in the fruit chamber which was temporarily kept in the closed state by shutting down the ventilation for only 15s every minute. *RGR* was evaluated by applying the laser displacement sensors system (*8*) equipped in the fruit chamber, and furthermore J_P+J_X was evaluated by $J_{WF}+$ *RGR* on the basis of fruit sap balance. The details of these evaluations are described in the preceding paper (*10*). Means of values per unit berry volume obtained from three replications were compared among the three cases of "berry +calyx", "berry" and "detached berry".

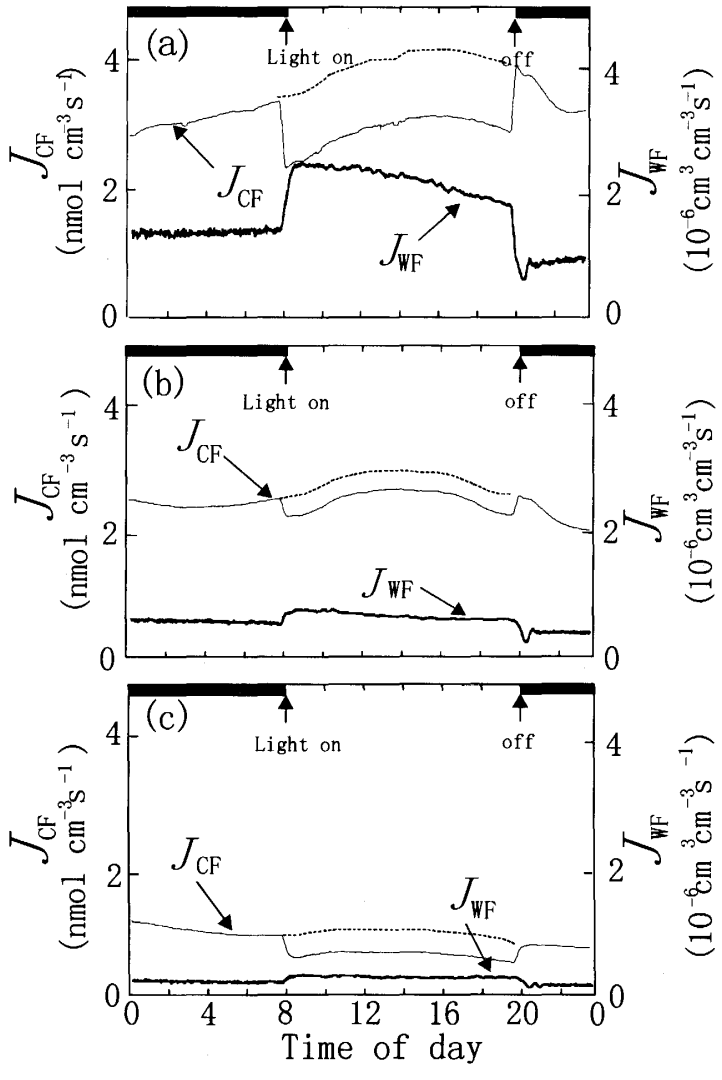

Fig. 1. Diurnal time courses of CO_2 flux (J_{CF}) and H_2O flux (J_{WF}) in the respective cases of the attached berry with the calyx (a, "berry+calyx"), the attached berry without the calyx (b, "berry") and the detached berry without the calyx (c, "detached berry"). Broken line in J_{CF} shows the respiratory CO_2 efflux under the light, which was evaluated by adding the photosynthetic CO_2 influx absorbed by the fruit. Values are means of three plants.

RESULTS AND DISCUSSION

Figure 1 shows diurnal time courses of J_{CF} and J_{WF} in the fruit under the different three cases of "berry+calyx", "berry" and "detached berry". In the case of "berry+calyx", J_{CF} under dark (i.e. the respiratory CO_2 efflux) increased early in the morning, but the lighting induced abrupt drop in J_{CF} by the start of photosynthetic CO_2 absorption in the calyx and the berry, and thereafter J_{CF} in the light gradually increased till the late afternoon: The photosynthetic CO_2 influx in the calyx and the berry under the light was estimated to be about 1.0

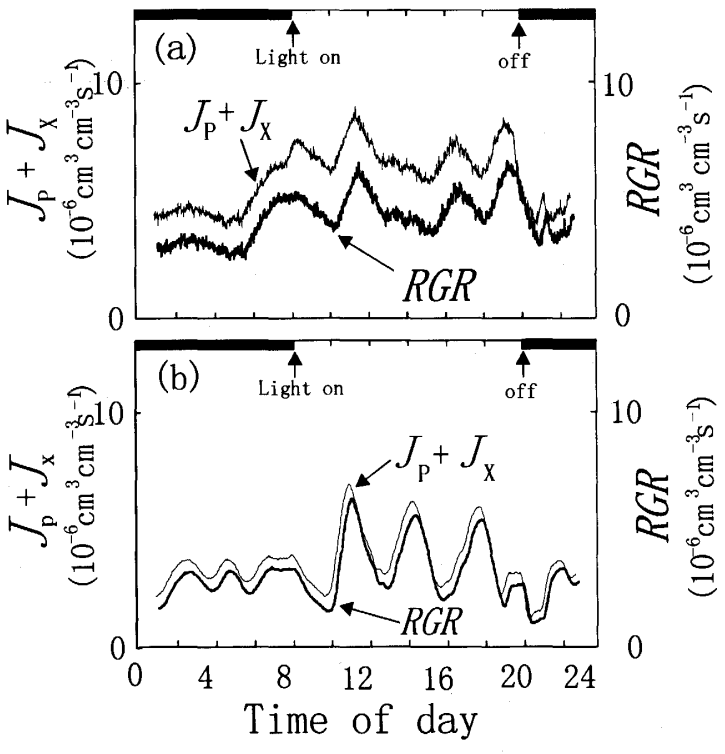

Fig. 2. Diurnal time courses of pedicel sap flux (J_P+J_X) and relative growth rate (*RGR*) of berries in the respective cases of the attached berry with the calyx (a, "berry+calyx") and the attached berry without the calyx (b,"berry"). Values are means of three plants.

nmol cm^{-3} s^{-1}, and the respiratory CO_2 efflux in the light (broken line) was evaluated by J_{CF} plus the photosynthetic CO_2 influx. Darkening at 20:00 stopped the photosynthetic CO_2 absorption, and J_{CF} immediately rose by about 1.0 nmol cm^{-3} s^{-1}, which was followed by a few hours decrease under dark. From this time course of J_{CF}, it was estimated that the respiration in the berry continued to increase from the early morning till the late afternoon under light and decreased for a few hours after darkening. The transpirational water loss (J_{WF}) was largely enhanced under the light by stomatal response in the calyx. In the case of "berry" without the calyx (Fig. 1b), the elevations of J_{CF} and J_{WF} were remarkably lowered by removing the calyx. The gradual increase pattern of J_{CF} in "berry" appeared clearly under the light as found in "berry+calyx", but the light enhancement of the photosynthetic CO_2 influx and the transpirational water loss was largely depressed. This indicates active photosynthesis and transpiration in the calyx of the immature tomato fruit. Furthermore, in the case of "detached berry" (Fig. 1c), where phloem sap flux and xylem sap flux into the berry were inhibited by excision of the pedicel, J_{CF} was extremely depressed, and the increase pattern of the respiratory CO_2 efflux found under light in the attached berry was disappeared. J_{WF} was also depressed significantly in the detached berry as compared with that in the attached berry.

Figure 2 shows diurnal time courses of J_P+J_X and *RGR* in the cases of "berry

Table 1. Cumulative CO_2 flux (ΣJ_{CF}), H_2O flux (ΣJ_{WF}), fruit growth rate (ΣRGR) and pedicel sap flux $\{\Sigma(J_P+J_X)\}$ during the light period (L: 08:00–20:00) and the dark period (D: 00:00–08:00 and 20:00–24:00) in the respective cases of the attached berry with the calyx (berry+calyx), the attached berry without the calyx (berry) and the detached berry without the calyx (detached berry). ΣJ_{CF} values in parentheses represent the cumulative fruit respiration during the light period, which were evaluated by adding CO_2 influx absorbed by fruit photosynthesis. Values are means of three plants, and differences among the three cases were significant at 5% level.

	ΣJ_{CF} (mmol cm^{-3})		ΣJ_{WF} (cm^3 cm^{-3})		ΣRGR (cm^3 cm^{-3})		$\Sigma (J_P+J_X)$ (cm^3 cm^{-3})	
	L	D	L	D	L	D	L	D
berry+calyx	.129 (.173)	.139	.095	.051	.207	.129	.302	.180
berry	.109 (.121)	.100	.028	.021	.149	.101	.177	.122
detached berry	.028 (.044)	.058	.012	.008	−.004	−.003	.008	.005

+calyx" and "berry" attached. In both cases, only small proportion of sap flux through the pedicel was allocated to transpirational water loss, and *RGR* fluctuated synchronizing with J_P+J_X at the lower elevation. In "berry+calyx" (Fig. 2a), J_P+J_X and *RGR* began to increase early in the morning and fluctuated under light at the elevation higher than that under dark. By removing the calyx (Fig. 2b), the elevations of J_P+J_X and *RGR* were lowered as compared with those in "berry+calyx", and the fluctuations appeared more unstable than in "berry+calyx".

Table 1 shows cumulative respiration (ΣJ_{CF}), transpiration (ΣJ_{WF}), fruit growth (ΣRGR) and sap influx $\{\Sigma(J_P+J_X)\}$ during the light period (08:00–20:00) and the dark period (00:00–08:00 and 20:00–24:00) in the respective cases of the attached berry with the calyx ("berry+calyx"), the attached berry without the calyx ("berry") and the detached berry without the calyx ("detached berry"), where the cumulative fruit respiration during the light period (i.e. ΣJ_{CF} in parentheses) was evaluated by adding photosynthetic CO_2 absorption. In the cases of "berry+calyx" and "berry", where sap flux was imported into the berry, berry respiration was higher in the light than in the dark and was significantly lowered by removing the calyx. ΣJ_{CF} (0.129 mmol cm^{-3}) in "berry+calyx" under the light involving the photosynthetic CO_2 absorption by both of the calyx and the berry became higher than ΣJ_{CF} (0.109 mmol cm^{-3}) in "berry" without the photosynthetic CO_2 absorption by the calyx. This result suggests that the removal of the calyx lowered respiration in the berry. Furthermore, the berry respiration was remarkably depressed in the detached berry without import of the sap. Transpirational water loss became larger in the light than in the dark and remarkably decreased by the removal of the calyx. The effect of the calyx appeared more clearly in the light because stomatal transpiration was enhanced in the light: The proportion of transpirational water loss through the calyx to the water loss in the "berry+calyx" was estimated to be 70% in the light, 60% in the dark and 66% in a whole day. Furthermore, in the detached berry, transpirational water loss was remarkably depressed as compared with that in

Table 2. Proportions of transpirational water loss (ΣJ_{WF}) and fruit growth (ΣRGR) to pedicel sap influx $\{\Sigma (J_P+J_X)\}$ in the respective cases of the attached berry with the calyx (berry+calyx) and the attached berry without the calyx (berry) during the light period (L: 08:00–20:00), the dark period (D: 00:00–08:00 and 20:00–24:00) and the whole day (L+D). Values are means of three plants, and differences between "berry+calyx" and "berry" were significant at 5% level.

	$\Sigma J_{WF}/\Sigma(J_P+J_X)$			$\Sigma RGR/\Sigma(J_P+J_X)$		
	L	D	L+D	L	D	L+D
berry+calyx	31.5	28.3	30.3 (%)	68.5	71.7	69.7 (%)
berry	15.8	17.2	16.4	84.1	82.8	83.6

the attached berry, while transpiration from the detached berry has been assumed to be equivalent to that from the attached berry (*2, 6*).

Fruit growth and sap flux in the cases of "berry+calyx" and "berry" became higher in the light than in the dark, and the removal of the calyx brought substantial decrease in the fruit growth and the sap influx. This effect of the calyx appeared more clearly in the light where the calyx photosynthesized and transpired more actively, and therefore it may be suggested that the calyx of the immature tomato fruit contributes to sap import and expansive growth in the berry through its active photosynthesis and transpiration. The detached berry contracted slightly by the transpirational water loss from the berry surface, and the sap influx, which evaluated by $\Sigma J_{WF}+\Sigma RGR$ with minor errors, was nearly zero.

Table 2 shows allocation of the imported sap flux to the transpirational water loss and the fruit expansive growth. In the case of "berry+calyx", about 70% of the sap influx through the pedicel contributed to the expansive growth of the berry, and the residual 30% was transpired through the calyx and the berry. From ΣJ_{WF} in Table 1, transpiration through the calyx was estimated to be responsible for 66% of the transpirational water loss from the fruit (berry+calyx), and therefore the sap influx through the pedicel was estimated to be allocated at the respective proportions of 70% to the berry expansive growth, 20% to the calyx transpiration and only 10% to the berry transpiration. In the berry without calyx, 84% of the imported sap flux was availed to expansive growth of the berry, and transpirational water loss through the berry surface was only about 16%. These lower proportions of the transpirational water loss confirm the lower contribution of the xylem sap flux, as Ho *et al.* (*6*) have been estimated that more than 85% of sap influx to tomato fruits was imported via phloem and only about 15% via xylem.

Phloem translocation into a tomato fruit at the stage of rapid sugar accumulation has been proved to be regulated by the energy-dependent apoplastic sugar transport in the fruits (*16, 17*), and sugar translocation through the tomato pedicel has been reported to be enhanced under the light (*1, 9*). Walker and Ho (*18*) have been observed that respiration of a tomato fruit oscillated diurnally and became the maximum at midday and the minimum

around midnight and that this oscillation was damped by darkening the fruit only. In this study, the higher respiration of the intact berry was clearly found in the light where the sap flux and the growth rate were kept higher, but darkening, removal of the calyx and excision of the pedicel brought lower berry respiration with depression in the sap flux and the growth rate. Furthermore, transpirational water loss from each of the berry and the calyx was only 10% and 20% of the imported sap flux, and the residual 70% of the imported sap flux contributed to expansive growth of the berry. From these results, it is conceivable that respiration of the tomato fruit at the stage of rapid sugar accumulation closely relates to the phloem sap flux which is responsible for sugar accumulation and expansive growth in the fruit.

REFERENCES

1. Araki T., Kitano M. and Eguchi H. (1997) Evaluation of photoassimilate flux through a tomato pedicel. *Biotronics* **26**, 21–29.
2. Ehret D. L. and Ho L. C. (1986) Effects of osmotic potential in nutrient solution on diurnal growth of tomato fruit. *J. Exp. Bot.* **37**, 1294–1302.
3. Fisher D. B. and Oparka K. J. (1996) Post-phloem transport: principle and problems. *J. Exp. Bot.* **37**, 1141–1154.
4. Grange R. I. and Andrews J. (1995) Respiration and growth in a tomato fruit. *Plant, Cell and Environ.* **18**, 925–930.
5. Ho L. C. and Baker D. A. (1982) Regulation of loading and unloading in the long distance transport systems. *Physiol. Plant.* **56**, 225–230.
6. Ho L. C., Grange R. I. and Picken A. J. (1987) An analysis of accumulation of water and dry matter in tomato fruit. *Plant, Cell and Environ.* **10**, 157–162.
7. Johnson R. W., Dixon M. A. and Lee D. R. (1992) Water relation of the tomato during fruit growth. *Plant, Cell and Environ.* **15**, 947–953.
8. Kitano M., Hamakoga M., Yokomakura F. and Eguchi H. (1996) Interactive dynamics of fruit and stem growth in tomato plants as affected by root water condition. I. Expansion and contraction of fruit and stem. *Biotronics* **25**, 67–75.
9. Kitano M., Yokomakura F. and Eguchi H. (1996) Interactive dynamics of fruit and stem growth in tomato plants as affected by root water relation. II. Relation with sucrose translocation. *Biotronics* **25**, 77–84.
10. Kitano M., Araki T., Hamakoga M. and Eguchi H. (1997) On-line measurements of CO_2 and H_2O gas fluxes, pedicel sap flux and expansive growth in an intact tomato fruit. *Biotronics* **26**, 85–94.
11. Komor E., Orlich G., Weig A and Köchenberger W. (1996) Phloem loading-not metaphysical, only complex: towards a unified model of phloem unloading. *J. Exp. Bot.* **47**, 1155–1164.
12. Milburn J. A. (1975) Pressure flow. Pages 328–353 *in* M. H. Zimmermann and J. A. Milburn(eds) *Transport in plants* I. *Phloem transport, Encyclopedia of Plant Physiology, New Series, Vol. 1*, Springer-Verlag, Berlin.
13. Münch E. (1927) Dynamik der Saftströmungen. *Ber. Deut. Bot. Ges.* **44**, 69–71.
14. Patrick J. W. (1990) Sieve element unloading: cellular pathway, mechanism and control. *Physiol. Plant.* **78**, 298–308.
15. Patrick J. W. and Offler C. E. (1996) Post-sieve element transport of photoassimilates in sink regions. *J. Exp. Bot.* **47**, 1165–1177.
16. Ruan Y.-L. and Patrick J. W. (1995) The cellular pathway of postphloem sugar-transport in developmental tomato fruit. *Planta.* **196**, 434–444.
17. Ruan Y.-L., Patrick J. W. and Brady C. (1997) Protoplast hexose carrier is a

determinate of genotypic difference in hexose storage in tomato fruit. *Plant, Cell and Environ.* **20**, 341–349.

18. Walker A. J. and Ho L. C. (1977) Carbon translocation in the tomato: Carbon import and fruit growth. *Ann. Bot.* **41**, 813–823.