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TEMPERATURE DEPENDENCE OF POSTPHLOEM TRANSPORT REGULATED BY RESPIRATION IN TOMATO FRUITS

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KITANO M., ARAKI T. and EGUCHI H. *Temperature dependence of postphloem transport regulated by respiration in tomato fruit.* BIOTRONICS **27**, 33–39, 1998. Temperature effect on postphloem transport in tomato fruits was analyzed by measuring fruit growth rate, pedicel sugar flux and fruit respiratory CO_2 efflux under changes in air temperature around fruits. Dynamic responses of fruit growth rate and pedicel sugar flux to temperature change around fruits were clearly found to be associated with change in fruit respiration. Fruit growth rate and pedicel sugar flux were remarkably enhanced with fruit respiration by temperature rise around fruits, where those Q_{10} values between 20°C and 30°C distributed around 2.3. These enhancements in fruit growth and sugar translocation by the temperature rise were not found in the truss with the respiration-inhibited fruits. From these results, it can be suggested that respiration in tomato fruits contributes to the temperature effects on the expansive growth and the sugar accumulation through regulation of the energy-dependent process of the postphloem sugar transport in the fruits.

Key words: *Lycopersicon esculentum* Mill.; tomato fruit; postphloem transport; fruit respiration; fruit growth; sugar translocation; temperature effect.

INTRODUCTION

Expansive growth and sugar accumulation in fruits depend on sap flux transporting water and photoassimilates into the fruits. In tomato plants, a major portion of sap flux into the fruits has been estimated to be via phloems (*4*). The phloem sap flux is driven by pressure potential gradient along phloems from leaves to fruits, where the postphloem transport in fruits (i.e. sugar transport from phloems to storage pericarp tissues) can regulate the pressure potential gradient through change in sugar concentration around the unloading sites (*2, 3, 9–11*).

Postphloem transport in tomato fruits at the stage of rapid sugar accumulation (i.e. a few weeks after anthesis) has been proved to be switched to the apoplastic route which inevitably involves energy-dependent sugar transport across the plasma membranes of the storage pericarp tissues (*13*). This sugar transport across the plasma membranes depends on hexose/proton symport driven by H^+-ATPase on the membranes (*2, 11, 12*). Ruan *et al.* have demon-

strated by using tomato pericarp tissues *in vitro* that activity of the hexose/ proton symport across the plasma membranes can be a determinant for sugar accumulation into the storage tissues under a sufficient supply of hexose (*14*). Furthermore, Kitano *et al.* have observed that expansive growth and sugar accumulation of tomato fruits were remarkably enhanced with fruit respiration activated by temperature rise around the fruits in the daytime (*8*).

The present paper deals with analysis of temperature effect on the post-phloem transport in intact fruits by measuring fruit growth rate, pedicel sugar flux and fruit respiration rate under different conditions of air temperature around the fruits.

MATERIALS AND METHODS

Plant materials

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 23/18℃ 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 (*4*), the plants were used for the experiments in an artificial light growth cabinet.

Measurements

By using the fruit chamber system developed for measuring gas exchange and growth rate of the intact fruit in the previous study (*7*), respiratory CO_2 efflux and growth rate of the fruit on the first truss were measured on-line: The CO_2 efflux from the fruit (berry and calyx) were evaluated at intervals of 1 min on the basis of increase rate of CO_2 gas concentration in the fruit chamber, which was temporarily kept in the closed state at intervals of 1 min by shutting the ventilating openings for only 15 s. The evaluated CO_2 efflux indicates the net efflux, i.e. respiratory CO_2 efflux minus photosynthetic CO_2 influx in the fruit. The fruit growth rate was evaluated on volume base by applying the laser displacement sensors (Z4M–W40, OMRON Corp., Kyoto, Japan) system equipped in the fruit chamber.

Furthermore, sugar flux exuded through the cut end of a pedicel on the first truss was evaluated at intervals of 30 min by applying the improved EDTA (ethylenediaminetetraacetic acid) method established in the previous study (*1*): The pedicel cut end was immersed into 20 mM EDTA solution bath of 1000 μL, and sampling of the EDTA solution loaded with exudate and replenishment of the solution bath with the fresh EDTA solution were repeated at intervals of 30 min. Then, the pedicel sugar flux was evaluated by analyzing sugar balance in the EDTA solution bath. The details of these evaluations have been described in the previous papers (*1*).

Experimental conditions

The experiments were conducted in the growth cabinet with the artificial light of metal halide lamps (DR400/T(L) Toshiba Corp., Tokyo, Japan) at a *PPFD* of 300 μmol m^{-2} s^{-1} in a photoperiod of 12 h (6:00–18:00) under an air temperature of 20±0.5℃, a relative humidity of 70±15% and a CO_2 gas concentration of 370±30 μmolmol^{-1}. The measurements were started after two days acclimation of the plant to the growth cabinet condition. For examining temperature effect on the postphloem transport, air temperature around fruits on the first truss was changed from 20℃ to 30℃ or to 10℃ by introducing temperature–controlled air from an air conditioner to the ambient of the first truss, where air temperature around leaves and solution temperature in the hydroponic pot were kept constant at 20℃ under air temperature control in the growth cabinet. In the previous study (*8*), fruit growth and sugar translocation in tomato plants under the light have been observed to be remarkably enhanced with fruit respiration activated by temperature rise from 15℃ to 25℃ at the start of lighting. Therefore, for examining contribution of fruit respiration to the temperature effect on the postphloem transport, respiration of fruits on the first truss was inhibited by wrapping the berries in the grease–coated polyvinylidene chloride film under temperature rise from 15℃ to 25℃ at the start of lighting.

RESULTS AND DISCUSSION

Under the condition that air temperature around leaves and solution temperature in the pot were kept constant at 20℃, air temperature around fruits was raised from 20℃ to 30℃ in the light, and after four hours the raised temperature was returned to 20℃. Figure 1 shows time course variations of air temperature around fruits, fruit respiratory CO_2 efflux, fruit growth rate and pedicel sugar flux. Fruit respiratory CO_2 efflux, fruit growth rate and pedicel sugar flux started to increase simultaneously with the temperature rise from 20℃ to 30℃. The respiratory CO_2 efflux reached the maximum three hours after the temperature rise, and fruit growth rate and pedicel sugar flux reached the respective maximums five hours after the temperature rise. Values of the respective maximums at 30℃ were more than twice the values at 20℃. When air temperature around fruits was returned to 20℃, respiratory CO_2 efflux, fruit growth rate and pedicel sugar flux decreased to the respective levels before the temperature rise. In the case that air temperature was dropped from 20℃ to 10℃, simultaneous decreases in respiratory CO_2 efflux, fruit growth rate and pedicel sugar flux were found (data not shown). Thus, dynamic responses of fruit growth and sugar translocation to change in temperature around fruits were found to be associated with change in fruit respiration affected by temperature.

Figure 2 shows respiratory CO_2 efflux, fruit growth rate and pedicel sugar flux in the light at the respective air temperatures around fruits of 10, 20 and 30℃ under the condition where air temperature around leaves and the solution temperature were kept at 20℃. The values were evaluated as the mean values
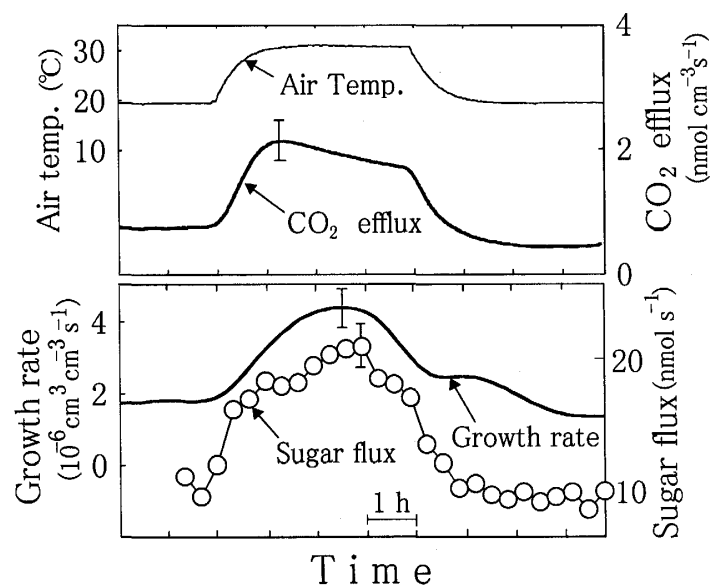
Fig. 1. Time course variations of air temperature around fruits, fruit respiratory CO_2 efflux, fruit growth rate and pedicel sugar flux, where the set value of air temperature around fruits was changed from 20℃ to 30℃ and vice versa under a constant temperature of 20℃ around leaves and in the hydroponic pot. Values were means of three plants, and vertical bars indicate standard deviation.

during four hours under the respective air temperatures. The CO_2 efflux was depressed to nearly zero at 10℃ but remarkably increased with the temperature rise. This indicates that fruit respiratory CO_2 efflux at 10℃ balanced with fruit photosynthetic CO_2 influx and that fruit respiration was more sensitive to temperature rise as compared with fruit photosynthesis. Fruit growth rate and pedicel sugar flux were also enhanced with temperature rise around fruits. The value of Q_{10} between 20℃ and 30℃ was 2.8 in fruit respiratory CO_2 efflux, 2.1 in fruit growth rate and 1.9 in pedicel sugar flux. Furthermore, Kitano *et al.* have reported that fruit growth and sugar translocation in tomato plants under light were remarkably enhanced with fruit respiration highly activated by the temperature rise around fruits from 15℃ to 25℃ at the start of lighting, as compared with those under a constant air temperature of 20℃ (*8*).

From these temperature effects, it is supposed that the fruit growth and sugar translocation enhanced by the temperature rise can be attributed to the highly activated fruit respiration. Therefore, the temperature effects were examined in the first truss in which all the berries were wrapped with the grease –coated polyvinylidene chloride film to inhibit fruit respiration. Figure 3 shows time course variations of fruit respiratory CO_2 efflux, fruit growth rate and pedicel sugar flux in the truss with the wrapped berries (i.e. the respiration-inhibited fruits) and in the truss with the non-wrapped berries, where air temperature was raised from 15℃ to 25℃ at the start of lighting. As observed by Kitano *et al.* (*8*), fruit growth rate and pedicel sugar flux in the truss with the non-wrapped berries were extremely enhanced with fruit respiration highly
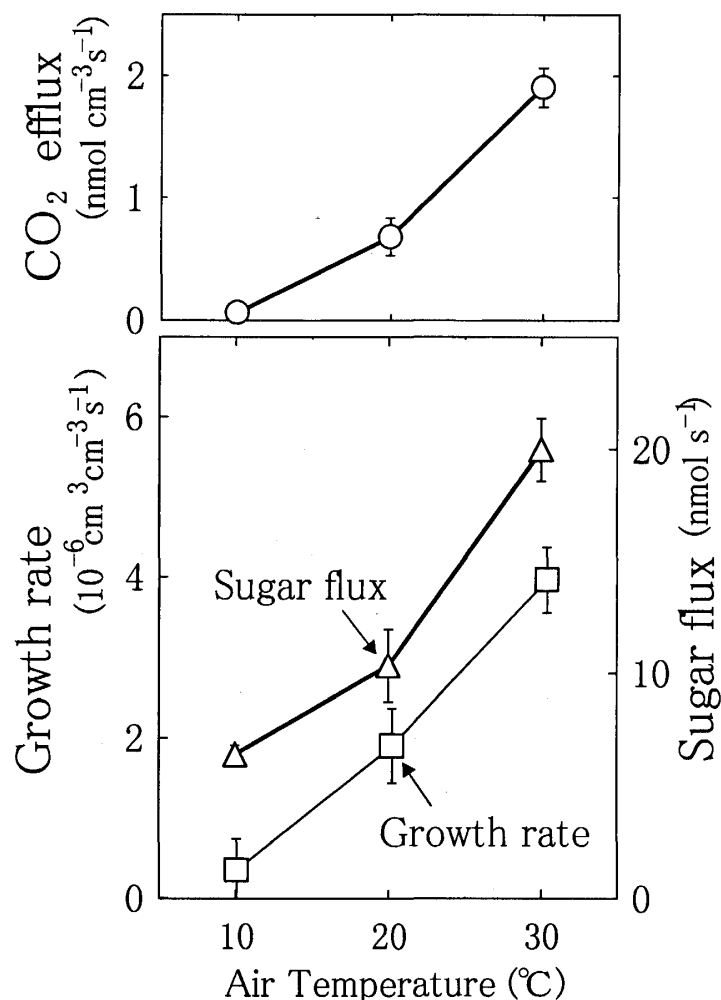
Fig. 2.   Dependencies of fruit respiratory CO_2 efflux, fruit growth rate and pedicel sugar flux on air temperature around fruits under a constant temperature of 20℃ around leaves and in the hydroponic pot. Values were means of three plants, and vertical bars indicate standard deviation.

activated by the temperature rise under the light. On the other hand, in the truss with the wrapped berries, respiratory CO_2 efflux was almost inhibited, and fruit growth rate and pedicel sugar flux after lighting were not enhanced by the temperature rise. That is, in the truss with the respiration-inhibited fruits, remarkable fruit shrinkage was found, which was considered to result from sap backflow through the pedicel (5, 6, 15), and pedicel sugar flux under the light was restrained, although photosynthesis in the source leaves was activated by lighting. Thus, the phloem sap flux, which can be activated by the temperature rise in the light, was retarded by the inhibition of fruit respiration. The pressure potential gradient driving the phloem sap flux into fruits can be affected by change in sugar concentration around unloading sites in the fruits, and this sugar concentration can be considered to be very sensitive to change in activity of the postphloem sugar transport, which involving the hexose/proton symport
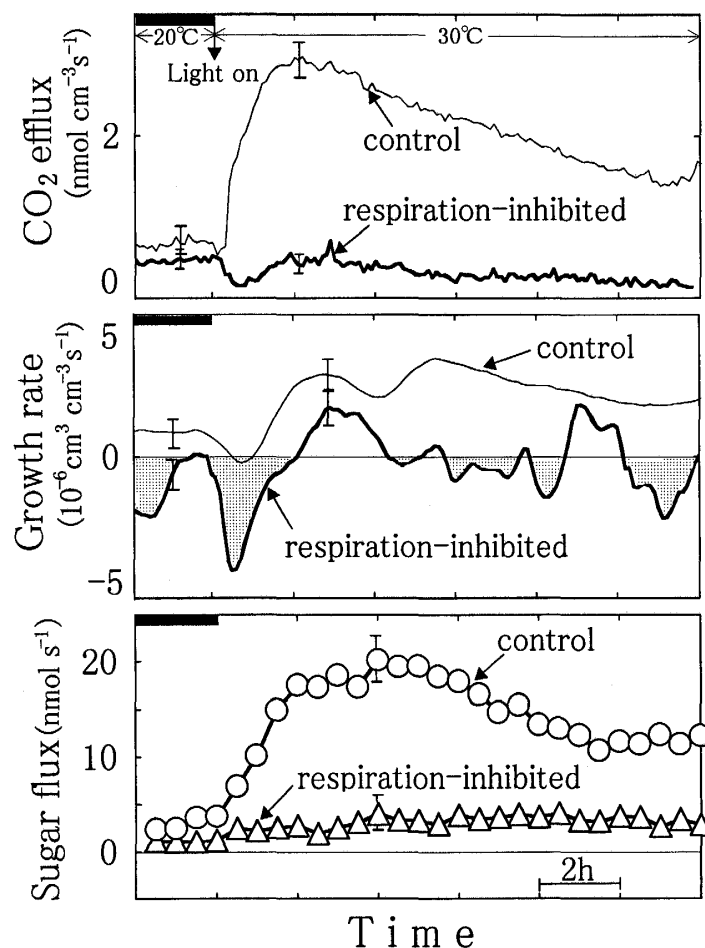
Fig. 3. Time course variations of fruit respiratory CO_2 efflux, fruit growth rate and pedicel sugar flux in the truss with the wrapped berries (i.e. respiration-inhibited) and in the truss with the non-wrapped berries (i.e. control), where air temperature was raised from 15℃ to 25℃ at the start of lighting. Values were means of three plants, and vertical bars indicate standard deviation. Dotted area in growth rate indicates fruit shrinkage.

driven by H^+-ATPase on the plasma membranes of the storage pericarp tissues (*11*). Therefore, it can be suggested that respiration in tomato fruits contributes to temperature effects on expansive growth and sugar accumulation through regulation of the energy-dependent postphloem sugar transport in the fruits.

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