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DAILY VARIATIONS OF XYLEMIC EXUDATION RATE IN TOMATO

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ABSTRACT: Tomato plants (*Lycopersicum esculentum* cv. Prisca) were grown on perlite or rock-wool substrates in a greenhouse or in nutrient culture in a growth chamber. At the beginning of flowering and at the fruiting period, the plants were detopped at the base of the stem (1 plant every hour over the 24 hours), then exuded xylem sap was collected hourly for 24 to 48 hours. Exudation rates could be taken into account for about 2 to 10 hours after cutting the stem depending on the development stage of the plants. Cyclic variations of the rate of exudation were observed which followed a daily rhythm with a maximum at midday in the greenhouse as well as under the constant conditions of the growth chamber. The rhythmicity of these variations was also observed in continuous darkness, thus indicating its endogenous nature. The meaning of such a daily rhythm is discussed.

INTRODUCTION

Water flow in plants depends on external factors such as light, temperature, relative humidity or nutrition and on internal factors such as age or ontogeny of plants or organs. Diurnal variations of water flow occur whatever the development stage since transpiration rate varies with the daily rhythm of stomatal opening (2,9,7). Translocation of minerals in the plant is linked to water movement in xylem sap and the efficiency of mineral nutrition of the whole plant depends on how translocation is adjusted to the needs of each part of the plant.

Among other methods, exudation after detopping has been used to study the mineral composition of xylem sap. Exudation occurs naturally in plants with high

root pressure, whereas in plants with low root pressure, it requires roots to be subjected to additional pressure (15), or stems to vacuum succion (5). With tomato, which has a positive root pressure, the method of natural bleeding after detopping is generally used.

Exudation of excised plants has been observed as early as the 1930s (6), but so far plant exudation has been studied only at early vegetative stages. Many authors have reported diurnal variations of xylemic exudation in numerous species (17,10,13,3,11). A cyclic variation of exudation in the tomato cultivar "Groseille rouge" (*Lycopersicum racemingerum*) has been observed (12) whose periodicity was 12 h with two maxima, at midday and at midnight. Cyclic variations of exudation rate has also been observed for several days after detopping with a gradual decrease of the oscillations. (17,13,11).

This paper reports a study on exudation in tomato at later developmental stages such early flowering and fruiting, in order to obtain some insight into water and nutrient needs of plants under soilless cultivation in relation with the quality of fruit production. In the greenhouse mineral elements are usually provided to tomato plants by watering with the same nutrient solution throughout the light and dark periods; however, nutrient needs may differ between day and night.

In order to test this hypothesis and thus to observe possible daily variations in water and mineral flow, we studied tomato exudation hourly during a 24-hour cycle.

MATERIALS AND METHODS

Plant Material

Experiment I: Plants of tomato (*Lycopersicum esculentum* cv. Prisca) were grown in a glasshouse one plant per pot containing 10 liters of perlite. Nutrient solution supply varied with the rate of potential evapotranspiration, which was calculated hourly as a function of solar radiation (18). On the day of the experiment 24 waterings of 110 mL (for 2 minutes each) were provided per pot, 5 waterings per hour was the maximal rate between 12.00 a. m. and 1.00 p.m. Four waterings were supplied for 2 minutes each during the night (120 mL at 9.00 p.m., 12.00 p.m., 3.00 a.m. and 6.00 a.m.). The mineral composition of the nutrient solution was as follows: 12.4 mM NO₃; 1.5 mM H₂PO₄; 1.9 mM SO₄; 6.2 mM K; 3.7 mM Ca; 1 mM Mg; 2 mM NH₄. Micronutrients were supplied from a commercial solution, "Kanieltra", and pH was adjusted to 5.8 with HNO₃.

The sole source of light used throughout the culture was the sun. The experiment was done in October, *i.e.* four months after sowing. At that time sunrise was at 6.00 a.m. and sunset at 6.00 p.m.; the plants were approximately 2 meters high (8 trusses) and fruiting had almost ceased.

Experiment II: Plants of tomato (*Lycopersicum esculentum* cv. Prisca) were grown in a glasshouse on rock-wool. Nutrient solution supply was as in Experiment I. Three treatments were made, which consisted in supplying a different volume of nutrient solution in order to induce three different leaching rates (5-10 %, 10-30 %, and 30-40 %).

Plants were not watered during the night. The mineral composition of the nutrient solution was as follows: 12 mM NO₃; 1.9 mM H₂PO₄; 1.9 mM SO₄; 7.4 mM K; 2.65 mM Ca; 1.65 mM Mg; 1.7 mM NH₄. Micronutrients were supplied from a commercial solution, "Kanieltra", and pH was adjusted to 5.8 with HNO₃. The experiment was done in May, *i.e.* five months after sowing. At that time sunrise was at 6.00 a.m. and sunset at 9.00 p.m.; the plants were 2 meters high (7 trusses) and were already fruiting.

Experiment III: Plants of tomato (*L. esculentum* c.v. Prisca) were grown in a growth chamber. Experimental growing conditions were controlled and maintained constant (22°C; 12 h light (OSRAM HQI 150-300 µE/m²s); 60% relative humidity). The plants were supplied with nutrient solution (hydroponic culture method) (6 plants in 120 L of nutrient solution), the composition of which was as follows: 11.2 mM NO₃; 1.5 mM H₂PO₄; 1.9 mM SO₄; 7 mM K; 3.85 mM Ca; 1.35 mM Mg. Micronutrients were supplied from a commercial solution, "Kanieltra", and pH was adjusted to 5.8 with HNO₃. On the day of the experiment the plants were 60 days old and 50 cm high, and were beginning to flower.

Experiment IV: The experimental conditions were as in Experiment III, except that continuous darkness was applied to the plants during the period of excision and xylem exudate collection.

Water Absorption

Water absorption was determined only in Experiment II for whole plants of one treatment (30-40 % leaching rate) and estimated by the difference between the watering and leaching volumes.

Xylem Exudate Collection

Experiment I: Plants were detopped by cutting the stem below the cotyledons.

A 5-cm section of polyethylene tubing was fitted to each excised stem which had been treated with lanoline to avoid leakage. In order to follow variation of exudation rate, one plant was detopped every hour. The xylem sap exuded freely and the content of each tube was collected hourly over a period of 48 h. Exudate samples were weighed and frozen at -18°C immediately after collection.

Experiment II: The method of exudate collection was as described in Experiment I. Three plants were detopped at 5.00 a. m. and exudates were collected every hour over a 24-hour period.

Experiments III and IV: The method of exudate collection was as described in Experiment I. Three plants were detopped every 2 hours and exudates were collected every hour over a 24-hour period.

RESULTS

Climatic Parameters in the Glasshouse

During Experiment I, temperature and relative humidity varied daily with external conditions (Fig. 1A). During the first day of the exudation, air temperatures in the glasshouse ranged from 29°C (day) to 12°C (night), and relative humidity from 30% (day) to 86% (night). Substrate temperature varied between 25°C at the end of the day and 18°C at the end of the night. Evapotranspiration rate (ETR) as a function of solar radiation varied daily as shown in Figure 1B with a maximum in the middle of the photoperiod. Evapotranspiration rate is a theoretical prediction of water absorption by the whole plant, and hence the watering frequency was determined directly from it.

Exudation Rate

Exudation started immediately after the plants had been detopped, and continued for several hours (Fig. 2), and in some cases for up to 6 days (data not shown). For all plants, exudation rate depended on collection time and showed a maximum during the photophase. For a plant excised during the dark period exudation rate increased during the first half of the light period, then decreased until the following dark period. Exudation rate at night was quite low and steady. Moreover, exudation rate depended on the excision time, particularly in the middle of the photophase since exudation rate was higher at 12.00 a.m. for a newly excised plant than for a plant excised the previous night. Exudation rate at night seemed to be less dependent on the excision time (Fig. 2).

All these data needed to be sorted to get maximum information on the daily

Figure 1A : Variations of climatic parameters in the glasshouse over the exudation experiment.

Figure 1B : Variations of evapotranspiration rate (ETR) and plant waterings in the glasshouse over the exudation experiment.

Figure 2 : Influence of excision time on the variation of exudation rates.

variation of exudation rate and the best methodology to choose. Therefore exudation rates at given times were plotted against time between collection and excision (Figs. 3A and 3B). In Experiment I (Fig. 3A) in the greenhouse, three stages characterized the volume of the exudates collected during the light period. A maximum value was observed for the first hour between collection and excision, then a steady lower value (20% to 40% less than for the first hour) for the next 12 to 22 hours and finally a still lower value (75% less than for the first hour), which remained stable the next 2-3 days. Such a phenomenon was not observed for the exudates collected during the dark period, whose values were quite steady for at least 2 days. In Experiment III in the growth chamber (Fig. 3B), the exudation rates for the plants excised during the light as well as dark periods decreased almost regularly. However, these plants were younger.

Exudation rates were also plotted against collection times after excision (Fig. 4). A daily cycle was found, that showed an increase of exudation rates from dawn to the middle of the photoperiod, followed by a decrease until dusk. The curve for the first hour of exudation after excision showed the largest amplitude

Figure 3A : Influence of the time elapsed between collection and excision on the exudation rate at given times for plants grown in a greenhouse.

Figure 3B : Influence of the time elapsed between collection and excision on the exudation rate at given times for plants grown in a culture chamber.

Figure 4 : Daily variation of the exudation rate versus collection time at different times after excision.

Figure 5 : Daily variation of the exudation rate versus collection time for averaged values.

(8- fold) between maximum and minimum compared with the *ca.* 4-fold amplitude observed for the other curves.

Mean values for exudation rates are plotted in Figure 5. Each point is the mean of all the data collected, *i.e.* the exudation rate at a given collection time (x) for plants excised for 1 to x hours. The daily variation of exudation rate clearly appeared.

Influence of Watering Volumes on the Exudation Rate

In Experiment II, three leaching rates (5-10%, 10-30%, and 30-40%) were obtained by supplying the plants with the same nutrient solution at the same watering frequency but in three different volumes. Nutrient solution uptake was calculated as the difference between watering volume and leaching volume, as shown in Figure 6.

Figure 6 : Influence of watering rates on the daily variation of exudation rate and the daily variation of water uptake by intact plants grown in a greenhouse.

In the intact plants nutrient solution absorption varied daily with a maximum rate in the middle of the photophase. Uptake over the dark period was not estimated since the plants were not watered. In the excised plants, no real differences in exudation rate in relation with the treatment were found. The same daily variation in exudation rate was observed for the three leaching rates, which was highly correlated with the daily variation of nutrient solution uptake by the intact plants. However, exudation rate in the excised plants was about 7-fold lower than uptake rate in the intact plants.

Exudation under Constant Growing Conditions

In Experiment III, tomato plants were grown in a growth chamber under roughly steady conditions.

Plants were grown under a 12:12 light:dark regime throughout the growing and exudation periods. Under such constant conditions, exudation rate varied daily, with a very low steady value during the dark period and a markedly higher steady value during the light period (Fig. 7A).

In order to remove the last external climatic parameter which could induce the daily cycle of exudation, excision and exudates collection were performed in continuous darkness (Experiment IV). Exudation rate varied with collection time in the same manner as with light and dark alternation (Fig. 7B), but with a smaller amplitude which was mainly due to a lower value of the maximum rate.

DISCUSSION

In the intact plants the flow of water results from evapotranspiration and root pressure. The latter factor is the main cause of exudation after stem excision and is of particular importance for the long-distance transport of minerals when transpiration rates are low, especially at night and in low-transpiring organs such as fruit. In this paper, a study of the day-night variations of exudation rate is reported for tomato plants.

Firstly, exudation rate depended on the time between collection and excision times, and on the plant development. In the plants excised at early flowering, exudation rate in the middle of the photophase decreased as the time between excision and collection increases (*id.* for exudation rate during the night). In the plants which were already fruiting, the decrease of exudation rate related to the time between collection and excision was also observed, but appeared in three successive phases; then, for exudates collected during the night, exudation rates

Figure 7A : Variation of the exudation rate at different times after excision for plants grown in a culture chamber.

Figure 7B : Variation of the exudation rate in continuous darkness at different times after excision for plants grown in a culture chamber.

were quite stable for several hours after excision. Consequently exudation rate could be taken into account for about 10 hours in mature plants but only for 1 or 2 hours in young plants. In other words, exudates were collected for 15-18 hours from a mature plants excised early in the morning and only for 1 or 2 hours in young plants.

Secondly, on account of these restrictions, circadian variations were observed for the exudation rate in detopped plants, with a maximum in the middle of the photophase regardless of the plant development.

The natural environment of plants is characterized by circadian photo- and thermoperiodic conditions to which they have adapted. Therefore, numerous biological and physiological processes show circadian rhythms (8). Some of them are endogenous, *i.e.* they persist when plants are placed under constant conditions of temperature and light. In the experiments carried out in the greenhouse, environmental factors such as temperature, relative humidity and light were not controlled. As the sun arose air temperature began to increase and the relative humidity to decrease, but these climatic parameters could only affect the plant shoot, which has been removed for the experiment.

Therefore, substrate temperature seemed to be the only external parameter, which could influence the roots. Daily variations in substrate temperature have been observed; however, they lagged behind those of exudation rate, which indicates that they are not related.

Besides, the variations of the exudation rate were correlated with the watering frequency in agreement with the estimated need of intact plants as described above. However, exudation rate was unlikely to depend on the volume of nutrient solution supplied to the roots. In Experiment II, exudation rate was indeed the same for the three treatments which all differed in watering volume. Therefore, external parameters did not seem to induce variations in exudation rate.

In order to confirm this hypothesis, two experiments were carried out under controlled conditions. Steady day-night temperature and humidity levels were combined with permanent availability of nutrient solution in the growth chamber. Exudation rate varied as in the greenhouse, but with a smaller amplitude probably due to the earlier stage of development of the plants. Under such conditions only the light-dark alternation could have induced the exudation cycle. However, when the plants were kept in the dark over the 24-hour period of excision and exudate collection, the exudation rate still showed a circadian rhythm. The latter

observation is a valuable indication of endogenous daily variations in exudation rate.

What could be the biological significance of such an endogenous rhythm ? A circadian rhythmicity of root resistance to water transport has been reported to show a maximum during the night and a minimum during the day (2,13,16), but the significance of this circadian behavior is still unknown (14). However, we can observe the coincidence between maximum water uptake and exudation rate in the intact and excised plants respectively. Besides, a minimum root resistance to water around midday could allow water flow to increase in response to the increase of transpiration rate in the intact plants.

In our experiment, the plants exuded freely after their stem had been cut, which indicates that the exudation was only due to the root pressure. Thus, the daily fluctuation in exudation rate observed could be considered as a daily fluctuation in root pressure. Root pressure is interpreted as a regulatory phenomenon of the osmotic status in root (1)

Water absorption and transfer into the xylem is the response to an osmotic gradient between external and internal root media due to the absorption and transfer of minerals. Therefore, circadian variations in root pressure could be interpreted as a circadian phenomenon of mineral uptake by the root. Thus, the exudation cycle observed might be considered as a passive response to a salt uptake cycle. Analysis of the mineral composition of exudates should provide more details about this interpretation and the transfer of minerals in plants (4)

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