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PHLOEM AND XYLEM IMPORT OF WATER AND SOLUTES IN TOMATO FRUITS

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SUMMARY

The contents of K^+ , Mg^{2+} , Na^+ , Ca^{2+} , Rb^+ , Mn^{2+} , Cu^{2+} , Al^{3+} , P, Br^- , and Cl^- were measured in tomato fruits, which were picked from the plant at various stages of development, starting from the day of anthesis. Determinations were also carried out of transpiration rate, increase in fruit water, and dry and combustable fruit materials.

Measurements of the ion contents in the fruit, and the import characteristics of Ca^{2+} indicated that the ratio of CO_2 production and photosynthetic CO_2 fixation rates did not appreciably change during the entire period of fruit growth. The overall efficiency of conversion of imported to fruit dry matter was assumed to be about 100%.

The high initial ion concentrations in the fruit have been attributed to an initially high rate of water and solutes supply by the xylem. The varying fractional contribution of the xylem to ion and water import results in varying import rates of solutes in the fruit. The maximal percentage of phloem delivery during the period of highest growth rate could be estimated as 99, 98, 94, 0, 99, 78, 93, 94, 98, 97 and 97% for K⁺, Mg²⁺, Na⁺, Ca²⁺, Rb⁺, Mn²⁺, Cu²⁺, Al³⁺, P, Br⁻, and Cl⁻ respectively.

The average fractional phloem contribution to the import of dry matter and water could be determined as 98 and 84% respectively. The amounts of Ca^{2+} , imported during the early stages of fruit development, were shown to be important with respect to the avoidance of the occurrence of blossom-end rot during the period of highest growth rate of the fruit.

1. INTRODUCTION

The mineral composition and dry matter content of many fruits can be largely explained by supposing them to be built up from sieve-tube fluid (van DIE & WILLEMSE 1980). Calcium is a notable exception as it is generally present in fruits in considerably higher concentrations than can be explained by a phloem delivery only (ANSIAUX 1959). The phloem fluid seems unsuitable as a means of calcium ion transport (van GOOR & WIERSMA 1974), and the fruit-calcium content may be explained by xylem delivery.

A xylem origin of fruit calcium implies that also other xylem elements may be supplied along that pathway. In the present study the changes with time of water, ionic, and organic matter contents of tomato fruits have been examined, starting from the day of anthesis. To get more detailed information about the flow of water to developing fruits, measurements were carried out of the amounts of water vapour transpired during fruit growth.

From the relations between the mentioned parameters with fruit age, growth rate, and other fruit dimensions, information was obtained about the differential

contributions of xylem – and phloem – delivered materials to fruit material. An important presupposition in this work was that under normal conditions of growth no quantitatively important export occurs of water and nutrients from the growing fruit to the vegetative plant parts (cf. ZIEGLER 1963, WALKER & Ho 1977, VAN DIE & WILLEMSE 1980).

Direct application of fruit mineral concentrations in import studies implies pre-information with respect to the efficiency by which imported organic material is converted to fruit dry matter during fruit growth. Overall efficiency (THORNLEY 1970, PENNING DE VRIES, BRUNSTING & VAN LAAR 1974), depending on maintenance, conversion, and photosynthetic reactions, is reported to range from 40 to 100% for various organs and plant species (VAN DIE & WILLEMSE 1980, LAMBERS 1985). In the present paper, overall efficiency of dry matter conversion in tomato fruits was assumed to be 100%.

2. MATERIALS AND PLANTS

2.1. Plants and plant culture

Tomato plants (an inbred line of the red cherry tomato Lycopersicon esculentum Mill, cv. Tiny Tim) were used throughout. They were raised in soil in 5-L pots in a heated glasshouse (20–25 °C, RH 70%) with a 12 h photoperiod (high pressure Hg lamps, PHILIPS, irradiance 50 W \cdot m⁻²). Flowers and fruits were labelled so that fruit age could be determined.

2.2. Transpiration measurements

Tomato fruits were picked and their fresh weights were determined before and after sealing the pedicel sites with lanoline/vaseline (1/1). The fruits were put into an dessicator with saturated NaNO₃ at 25 °C, giving a RH of about 73%, which was assumed to be a good approximation of average glasshouse conditions. After 24 h the fruit fresh weights were measured again (cf. VAN DIE & WILLEMSE 1980), giving the fruit transpiration rates for various initial fresh weights.

2.3. Ion measurements

Fruit dry weights were determined after drying to constant weight at 75 °C. The content of combustable dry matter was determined by dry ashing at 500 °C. The phosphorus content was measured after wet destruction by using a spectorphotometric phospho-molybdate method (VAN DIE & WILLEMSE 1980). Potassium, sodium, magnesium, and calcium were measured after dry ashing at 500 °C by standard atomic absorption spectrophotometric methods, or were determined in dried fruits by non-destructive neutron activation analysis (DE BRUIN & KORTHOVEN 1972; 1974, KORTHOVEN & DE BRUIN 1977). All other elements were also determined by neutron activation analysis.

2.4. Data fitting prodedures

Many of the data obtained are presented in graphs. The lines were obtained by fitting the data to mathematical descriptions with use of a computer program

IMPORT OF WATER AND SOLUTES IN TOMATO FRUITS

for non-linear least squares regression, giving constants of the functions applied, together with correlation coëfficient r^2 . Where indicated, functions are shortly mentioned together with the relevant constants and r^2 . The functions applied were:

POLY-(k-1)	f(x) =	$\sum_{k=1}^{n} a_{k} \cdot x^{k-1} \text{ for } (k-1) \text{ graded polynomials}$
KWPR	f(x) =	$\frac{a_1x^2 + a_2x + a_3}{a_4x^2 + a_5x + 1}$

ERFF $f(x) = a_1[2-ERFC(a_2(x-a_3))] + a_4$

Linear relations could be fitted with POLY-k functions with $k \ge 2$.

3. RESULTS

3.1. Fruit water, transpiration and dry matter

Fig. 1a gives the fruit dry weight as function of its age. A significant increase of dry weight with time starts only after 10 days from fertilization (cf HOBSON & DAVIES 1970), followed by the well-known S-shaped growth curve. The fruit water content is given in *fig. 1b*, indicating a fruit dry weight percentage of about 8.9%. The function constants indicate a smaller dry weight percentage in the very early stage, which may be explained by an initial conversion efficiency less than 100%, or by a relatively high xylem participation in fruit dry matter influx. A high xylem participation in early stages may be concluded from *fig. 1c* (indicating a higher ash-dry weight ratio in early than in later stages and showing a relatively high initial transpiration rate).

Fig. 3 shows the transpiration rate as percentage of the rate of increase of fruit water, indicating a minimal relative transpiration at about 2 g fruit water. About 92% of the fruit dry weight is combustable dry matter, except for the early development stages, where it is less (fig. 2).

Summation of the ash and combustable dry matter content gives a total of 101.5% of the actual fruit dry matter content, indicating the accuracy of the fitting procedures.

3.2. Main fruit cations

The main cations measured in the fruit were Na⁺, K⁺, Na²⁺, and Ca²⁺. Fig. 4 shows their accumulation in the fruit as function of fruit dry weight. The Ca²⁺ import resembles the H₂O transpiration (*fig. 1c*). The import of the other cations corresponds more or less to the import of fruit water (*fig. 1b*). These data imply that the Ca²⁺ concentration on dry weight basis fluctuates with the fruit transpiration rate, whereas the other cations are present in a relatively constant concentration. Fig. 4 shows deviations from these concentrations during early stages of fruit growth. The high initial concentrations (dry weight basis) are shown in detail in *fig. 5*. The Ca²⁺ concentration rapidly drops to approximately 5% of its first measured value, whereas the K⁺ concentration does not change more

than about 25%. Attribution of the concentration drops entirely to changes in the efficiency of dry matter conversion should lead to similar changes of concentration for all cations. Assuming Ca^{2+} to be imported entirely in the xylem, the Ca^{2+} concentration drop means a xylem import contribution changing to 5% of its initially measured value.

3.3. Cation concentrations in xylem and phloem

The Ca²⁺ concentration versus fruit dry weight (*fig. 5*) can be extrapolated, resulting in an initial Ca²⁺ – concentration of 58.3 mg Ca²⁺ g⁻¹ dry weight. Plotting the Ca²⁺ import versus transpired water results in an initial Ca²⁺ concentration of 0.56 mg Ca²⁺ g⁻¹ H₂O (results not shown), indicating a xylem dry weight percentage of 0.96%.

The Ca²⁺ concentration in later stages of fruit growth can be calculated as 2 mg Ca²⁺ g⁻¹ dry weight (*fig. 5*), although the Ca²⁺ import per g dry weight imported can be derived from *fig. 4* as 0.63 mg Ca²⁺ g⁻¹ dry weight. These data indicate that, during fruit growth, the import of Ca²⁺ drops to about 1% of its initial value, whereas the xylem fluid delivery decreases to approximately 9% of the total fluid import (*fig. 3*). However, the 9% xylem contribution to fluid import results in a fruit dry weight import contribution from the xylem of also only 1%, due to the small xylem dry weight percentage. These results indicate a 100% xylem delivery of Ca²⁺.

The fact that the fruit Ca^{2+} concentration remains higher than explained by the small Ca^{2+} import rate at specific stages of fruit development, indicates the effect of early imported Ca^{2+} .

Plots of Na⁺, K⁺, and Mg²⁺ concentrations versus fruit dry weight and fluid import, taking into account the decrease in xylem contribution, result in values for their concentration in xylem and phloem as given in *table 1*. These calculated data are based on the differences in cation import rates between the initial stage of fruit development and the period of smallest xylem contribution tot total ion import (cf Ca²⁺ calculations). Therefore, the given results should be interpreted as maximal values for the contribution of the phloem to total ion import. During any other period of fruit development phloem contribution will be less.

Fig. 4 shows that the increasing xylem contribution to ion import in later stages of fruit development has no noticeable effect on import rates of K^+ , Mg^{2+} , and Na⁺. This may be ascribed to the relatively large phloem contribution to the total import of these ions. These results are in agreement with results obtained by HOCKING (1980) with Nicotiana glauca Grah., and PATE (1975) with

Fig. 1. a): Relation between fruit dry weight and fruit age. The line drawn was fitted by an ERFFfunction ($r^2 = 0.99$) with constants $a_1 = 223.0$, $a_2 = 0.186$, $a_3 = 17,26$, $a_4 = 0.405$. b): Relation between fruit H₂O and fruit dry weight. The line drawn was fitted by a POLY-1 function ($r^2 = 0.99$) with constants $a_1 = 0.036$ and $a_2 = 0.010$. c): Relation between fruit ash content (left axis, full circles) and fruit dry weight, and between transpired H₂O per fruit (right axis, open circles) and fruit dry weight. Lines drawn were fitted with a POLY-1 function (ash content; $r^2 = 0.98$, $a_1 = 0.45$; $a_2 = 0.092$) and with a KWPR-function (H₂O losses; $r^2 = 0.99$, $a_1 = 0.0068$, $a_2 = 12.04$, $a_3 = -16.27$, $a_4 = -0.00006$, $a_5 = 0.043$).





Fig. 2. Relation between combustable dry matter per fruit and dry weight. The line drawn was fitted with a POLY-1 function ($r^2 = 0.99$; $a_1 = -0.67$, $a_2 = 0.92$).

Lupinus albus and Lupinus angustifolius, who reported similar differences between the phloem and xylem concentrations of K^+ , Na^+ , Mg^{2+} , and Ca^{2+} .

The fractions of fruit cations delivered by the phloem are given in *table 1*. The 100% xylem delivery of Ca^{2+} , was presupposed in all calculations, and indicated by *figs 1c*, 4, and 5. VAN DIE & WILLEMSE (1980) reported of only 7% phloem delivery of Ca^{2+} in *Yucca* fruits, and a very small phloem delivery of Ca^{2+} in the fruit may be considered as negligible with respect to the calculated values of cation concentrations given in *table 1*.



Fig. 3. Relation between transpiration rate (as percentage of rate of increase of fruit H_2O) and amount of H_2O per fruit. The line drawn was calculated from the lines drawn for fruit transpiration (*fig. 1c*) and fruit H_2O content (*fig. 1b*). In the origin only a xylem import was assumed.



Fig. 4. Ion quantities per fruit as a function of fruit dry weight. Amounts of Ca^{2+} , Mg^{2+} , and Na⁺ are shown on left axis, amounts of K⁺ on right axis. Functions fitted were KWPR (Ca^{2+} ; $r^2 = 0.95$, $a_1 = 0.0020$, $a_2 = 1.12$, $a_3 = -0.0098$, $a_4 = -0.00024$, $a_5 = 0.197$) and POLY-1 (Mg^{2+} ; $r^2 = 0.96$, $a_1 = 2.70$, $a_2 = 0.123$; Na⁺; $r^2 = 0.95$, $a_1 = 2.46$, $a_2 = 0.058$; K⁺; $r^2 = 0.98$, $a_1 = 4.91$, $a_2 = 0.904$).

3.4. Other fruit cations and fruit phosphorus

In addition to the cations Na⁺, K⁺, Mg²⁺, and Ca²⁺, also fruit P and several other ions were measured. The amounts of P are given on a Mol. basis, as are its calculated concentrations in xylem and phloem. The xylem and phloem concentrations and import contributions for P, Rb⁺, Mn²⁺, Cu²⁺, Al³⁺, Br⁻, and Cl⁻ are given in *table 2*.

As with the data for the main fruit cations, the results in *table 2* should be interpreted as maximum values for the phloem contribution to total ion import. During any other period of fruit development the fractional delivery of ions in the phloem will be less (see Discussion).

Taking the ratio between phloem and xylem concentration as a criterion, from *tables 1* and 2 four groups of cation mobility in the phloem can be distinguished. The relative phloem mobilities for the various measured ions can be clustered in decreasing order as

 $K^+, Rb^+ > P, Mg^{2+}, Br^-, Cl^- > Cu^{2+}, Na^+ > Mn^{2+}, Al^{3+}, Ca^{2+}.$



Fig. 5. Changes in the ion concentrations in tomato (dry weight basis) as a function of fruit dry weight. Concentrations of Ca^{2+} and K^+ are shown on left axis, concentrations of Mg^{2+} and Na^+ on right axis.

The various cation mobilities in the phloem are in reasonable agreement with phloem mobilities of mineral elements given by ZIEGLER (1975), although Na⁺ is classified as relatively little mobile in the present paper. This may be due to differences in the methods of calculation of phloem mobility. Mobilities given by ZIEGLER (1975) are mainly based on reported export rates from source leaves of foliar-applied radio-tracers (cf BUKOVAC & WITTWER 1957, PITMAN 1975).

4. DISCUSSION

In the present paper the import in tomato fruits of water and solutes was presupposed to occur in both xylem and phloem. This assumption was based on results obtained by e.g. ANSIAUX (1959), WIERSUM (1966, 1966^a), VAN DIE & WILLEMSE (1980).

Theoretically, changes in concentrations of ions in the fruit may be due to improving the efficiency of conversion of imported to fruit organic materials after the initial stage of fruit growth, but the variations in concentration changes of several ions (*fig. 5*) indicate otherwise.

Indications for a unit ratio between respiration rate and rate of photosynthesis have been given by BOLLARD (1970) for citrus fruits. According to HOBSON & DAVIES (1970) and MILLER (1983) the tomato fruit (and also many citrus fruits) has a cuticula without any stomata, pores, or transcuticular canals. In this way, the fruit cuticula forms an almost gas-tight envelope around the fruit. Produced CO_2 will be trapped within the fruit, resulting in possible internal CO_2 concentrations of up to 10 vol % (BURG & BURG 1965) The trapped CO_2 can be reconverted



Fig. 6. Changes in the fractional contribution of the phloem to the ion import in tomato fruit, as a function of fruit age. Arabic numbers indicate ions $K^{+}(1)$, $Rb^{+}(2)$, P(3), $Mg^{2+}(4)$, $Br^{-}(5)$, $Cl^{-}(6)$, $Na^{+}(7)$, $Cu^{2+}(8)$, Mn^{2+} , $Al^{3+}(9)$, and $Ca^{2+}(10)$.

to carbohydrate level in carbon compensation reactions by photosynthesis during daylights hours (Kok 1976).

Table 1. Cation concentrations and fractional transport in xylem and phloem, calculated from their accumulation in the fruit. Xylem dry weight percentage: 0.96%; Phloem dry weight percentage: 8.9%. Calculations of fractional delivery were based on smallest possible xylem contribution to ion import.

Cation	Xylem $(\mu g m l^{-1})$	Phloem (µg ml ⁻¹)	Fractional delivery (total = 100)		
			Xylem	Phloem	
Ca ²⁺	560		100	0	
Mg ²⁺	35	132	2	98	
КŤ	375	3134	1	99	
Na ⁺	86	112	6	94	

Ion	Xylem (µg ml ⁻¹)	Phloem (µg ml ⁻¹)	Fractional delivery (total = 100)		
			Xylem	Phloem	
Rb+	0.55	3.54	1	99	
Mn ²⁺	0.67	0.21	22	78	
Cu ²⁺	0.15	0.19	7	93	
Al ³⁺	0.31	0.11	21	79	
Br ⁻	0.07	0.24	3	97	
CΓ	0.11	0.31	3	97	
Р	2.88*	11.0*	2	98	

Table 2. Ion concentrations in xylem and phloem, and calculated percentual contributions of xylem and phloem to ion import in tomato fruit. Calculations were based on smallest possible xylem contribution to ion import. Concentration in μ mole ml⁻¹*.

Fruit photosynthesis producing carbohydrates faster than can be used in respiration, may result in fixed carbon stored as starch (CLAYTON 1964), but, according to HOBSON & DAVIES (1970) in tomato the starch concentration never exceeds 10% of the fruit dry weight. Therefore, conversion efficiency has been assumed to be 100% during the whole period of fruit growth, and differences and variations of ion concentrations in the fruit were attributed entirely to import phenomena.

The rapid decrease of the concentration of Ca^{2+} in many fruits has been linked to fruit physiological disorders, such as bitter pit in apples (REDMOND 1975), blossom-end rot in tomato (WIERSUM 1966^a), or poor quality of ground nuts (WIERSUM 1951). The striking similarity of Ca^{2+} import and fruit transpiration suggests that the Ca^{2+} content of the tomato fruit depends entirely on the import

Substance	Fractional delivery in the phloem (maximal = 100)	
H ₂ O	84	
Dry matter	98	
К÷́	98	
Rb ⁺	97	
Na ⁺	87	
Mg ²⁺	95	
Mn^{2+}	61	
Ca ²⁺	0	
Cu ²⁺	87	
Al ³⁺	62	
P	95	
Br ⁻	95	
CI⁻	93	

Table 3. Average fractional contribution of the phloem to the imported amounts of water and solutes in a 28 days old tomato fruit with a fresh weight of 5.27 g.

304

IMPORT OF WATER AND SOLUTES IN TOMATO FRUITS

in the fruit (cf WIERSUM 1966, 1966^a). The import rate of Ca^{2+} drops to only 0.63 mg Ca^{2+} imported per g dry weight. According to WIERSUM (1966^a), tomato fruits containing less than 0.8 mg Ca^{2+} g⁻¹ dry weight will always be affected with blossom-end rot. The smallest Ca^{2+} concentration observed in tomato during the present investigations was about 2 mg Ca^{2+} g⁻¹ dry weight, which occurred during the period of 0.63 mg Ca^{2+} imported per g dry weight import. These data indicate the importance of earlier imported Ca^{2+} for the prevention of the occurrence of blossom-end rot.

As the fractional deliveries of fluid by xylem and phloem vary during fruit growth (*fig. 3*), the fractional contributions of xylem and phloem to ion import will also vary during the development stages of fruit growth.

The fractional element deliveries in xylem and phloem, as presented in *tables 1* and 2, are based on the period of fastest increase in fruit dry weight, that is, the period in which xylem fractional import is minimal. The variation in the fractional contribution to ion import of the phloem, due to growth rate and xylem import variations, for a 20 days period of fruit growth is shown in *fig. 6*. The maximum values for the relative participation of the phloem to ion import (*fig. 6*) coincide with the point of inflexion in the growth curve shown in *fig. 1a*.

The highest growth rate could be calculated as about 45 mg drwt d⁻¹, 18.4 days after anthesis. The transpiration rate relative to the increase in fruit H₂O (*fig. 3*) will be minimal during the period of highest rate of increase of fruit H₂O and dry matter. At the end of the 20 days period (*fig. 6*) the tomato fruit had a water content of 4.80 g, and had transpired 0.94 g H₂O. From these data, and the results given in *tables 1* and 2, the average import contribution of the phloem could be calculated, as given in *table 3*.

The results of the present study indicate that also manganese is relatively immobile in the phloem. According to WIERSUM (1966^a), in experiments with broad bean, this phenomenon may be responsible for the occurrence of Marsch-spot (induced by low Mn^{2+} content) in peas.

The data on Ca^{2+} indicate that the high initial ion concentrations (dry weight basis) in tomato results from a water and solutes supply by the xylem. These results are in agreement with results obtained by REDMOND (1975) with apples, and, according to WIERSUM (1966, 1966^a), may have a wide applicability, since in many fruits and storage organs (potatoes, apples, tomatoes, beans) reduction of the growth rate will relatively enhance the xylem supply, delivering cations which are important for the avoidance of physiological fruit disorders.

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