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RESEARCH PAPER

Effect of P-deficiency on photoassimilate partitioning and rhythmic changes in fruit and stem diameter of tomato (*Lycopersicon esculentum*) during fruit growth

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Abstract

Tomato (*Lycopersicon esculentum*) plants were grown in liquid culture inside the greenhouse of Hiroshima University, Japan. At the first fruiting stage, P was withdrawn from the rooting medium for a period of 19 d and its effect was studied on photosynthesis, stomatal conductance, transpiration, partitioning of ^{13}C and ^{15}N, P contents of various organs, and changes in stem and fruit diameter of the plant in order to identify the mechanism of resource management on the part of the plant at low P. Compared to the control, P-deficiency treatment decreased biomass growth of all organs except the roots. The treatment also depressed leaf photosynthesis, stomatal conductance and diameter of fruit and stem after a lag period of about 1 week. The stem diameter of the plant shrank during daytime and expanded during the night; the adverse effect of P-deficiency on stem diameter change was more evident during the night than the day. The circadian rhythm in fluctuations of diameter was less manifested in the fruit compared with the stem. P-deficiency induced daytime shrinkage and reduced night expansion of fruit. However, within the plant, P-deficiency encouraged partitioning of ^{13}C, ^{15}N and P into the fruit at the cost of autotrophic organs such as leaves and the upper parts of the stem. The results were discussed in the light of a plausible effect of P-deficiency on water relations of the plant. It is concluded that, in spite of the preference in partitioning of C and N received within the plant parts, assimilate flow into the fruit is limited at low-P compared with the control, owing to the restriction in fruit expansion.

Key words: Fruit and stem diameter, micro-morphometry, partitioning, phosphorus, tomato.

Introduction

Phosphorus is a major essential element for plants and deficiency of this nutrient primarily reduces CO_2 assimilation in leaf photosynthesis (Fredeen *et al.*, 1989; Jacob and Lawlor, 1992). The reduction in biomass production in the source leaves affects growth of the plant (Khamis *et al.*, 1990; Schachtman *et al.*, 1998; De Groot *et al.*, 2001) and its organs, roots (Mollier and Pellerin, 1999) and shoot (Fredeen *et al.*, 1989; Adu-Gyamfi *et al.*, 1990; Rychter and Randall, 1994). In addition, some other workers believe that the effects of P-deficiency on sinks are direct and not mediated through source activity (Pieters *et al.*, 2001). Sub-optimal supply of phosphorus limits cell division at the meristematic apex of the shoot (Chiera *et al.*, 2002) restricting expansion of newly developed leaves (Radin and Eidenbock, 1984; Chiera *et al.*, 2002).

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For resolving the divergence in opinions, a precise methodology is necessary to measure the effects of P-deficiency on both source and sink organs of the plant. Moreover, the effect of P-deficiency on a meristematic sink such as the shoot apex may be different from that of a storage sink such as fruit. However, methods for monitoring the effects of P-deficiency on plants during fruit growth period are lacking.

It is stated that the decrease in leaf number and size is one of the earliest and most reliable responses of P-deficiency on the plant (Lynch *et al.*, 1991). Leaf expansion occurs due to cell multiplication and elongation of the newly formed cells in plants and turgor pressure is a crucial factor for cell expansion (Hsiao, 1973; Munns *et al.*, 2000). There were instances, where P-deficiency decreased the hydraulic conductivity of water in the roots (Radin and Eidenbock, 1984; Radin, 1990; Clarkson *et al.*, 2000). The attendant reduction in delivery of water to the growing leaf curtailed cell expansion (Radin and Eidenbock, 1984). The decrease in hydraulic conductivity of the root and stomatal conductance of the leaf, resulting in a severe reduction of leaf expansion under P-deficiency, was also found to be similar to the response of nitrogen stress (Radin and Boyer, 1982; Radin and Matthews, 1989; Clarkson *et al.*, 2000). These published reports indicate that P-deficiency primarily restricts the activity of meristematic sinks of the plant and a lack of demand for assimilates in growth may be responsible for the reduction of source activity or photoassimilate partitioning. However, evidence in favour of a direct effect of P-deficiency on a storage sink such as fruit is rare.

It was reported that the diameters of the stem (Garnier and Berger, 1986; Simonneau *et al.*, 1993; Urban *et al.*, 1994; Genard *et al.*, 2001) and fruit (Johnson *et al.*, 1992; Berger and Selles, 1993; Link *et al.*, 1998) of plants fluctuated diurnally to coincide with the changes in the water status of the plant. All of the turgor-deficient growth inhibitions or poor cell expansion under the provision of sub-optimal N (Radin and Boyer, 1982) or P (Radin and Eidenbock, 1984) only occurred during the day, when the plant water potential was low due to active transpiration. Huguet (1985) developed a very simple technique for measuring micromorphometric shrinkage and expansion of stem diameter. This non-destructive technique can be used to measure the changes in water content of the plant resulting from the adverse effect of nutrition stress. In the present study, the objective is to monitor the effect of P-deficiency on stem and fruit diameter of tomato plants during fruit growth, while simultaneously recording the adverse effect of stress on primary production and assimilate partitioning. In the process, it is necessary to know the magnitude of response which the stress imposes on the source and sink activities of the plant during fruit development and to identify the process of resource management on the part of the plant at low P.

Materials and methods

Plant material and culture

Tomato (*Lycopersicon esculentum* L. cv. Momotarou) plants were grown in pots inside the greenhouse of the Graduate School of Biosphere Science, Hiroshima University, Japan. Each pot (70 l) was filled with nutrient solutions, consisting of 30 mg l^{-1} N (NH_4NO_3), 12 mg l^{-1} P (NaH_2PO_4), 60 mg l^{-1} K (K_2SO_4/KCl 9:8), 20 mg l^{-1} Ca ($CaCl_2.2H_2O$), 20 mg l^{-1} Mg ($MgSO_4.7H_2O$), 3 mg l^{-1} Fe (Fe^{3+}EDTA), 1 mg l^{-1} Mn ($MnSO_4.4H_2O$), 0.01 mg l^{-1} Zn ($ZnSO_4.7H_2O$), 0.01 mg l^{-1} Cu ($CuSO_4.5H_2O$), 0.05 mg l^{-1} B (H_3BO_3), and 0.01 mg l^{-1} Mo ($MoO_4.2H_2O$). There were six pots; each pot contained three plants. At the first fruiting stage (65-d-old), P was withdrawn from the nutrient medium in three pots and this treatment was continued for 19 d. The plants in the control condition received full nutrition. The plants were grown under natural light. The maximum irradiance was 700 W m^{-2} h^{-1} and maximum and minimum temperatures were 32 °C and 23 °C, respectively. The relative humidity of the greenhouse varied between 45–65%.

Measurement of biomass production

Plants from both control and P-deficiency treatment were harvested at 1, 9 and 19 d after treatment in three replicates. The plant was separated into roots, leaves, fruits, peduncle, and stem. The plant parts were dried in an open air draught oven at 70 °C for 72 h for the estimation of dry weight. The dry plant parts were ground to powder with a vibrating sample mill (Model T1-100, Heiko Co Ltd., Fukushima, Japan) and aliquots were taken for analysis of phosphorus.

Measurement of minerals

Aliquot of the plant material was digested with nitric sulphate. The P concentration in the digest was estimated by the molybdenum blue method (Murphy and Riley, 1962).

Measurement of photosynthesis, transpiration and stomatal conductance

Photosynthetic rate, transpiration and stomatal conductance of the first and second leaves below the fruiting truss were measured with a portable infrared gas analyser (Model L1 6400, Li-Cor Co. Ltd., Lincoln, Nebraska, USA). The leaf chamber was open type and measurements were taken once at 11.00 h on each day in both control and P-deficiency treatment plants during the 19 d period of treatment. The photosynthetically active radiation during measurement was above 1000 μmol m^{-2} s^{-1} and observations were recorded after the plant reached a steady photosynthesis state. All measurements were recorded three times and differences between the observations were negligible.

Measurement of stem and fruit diameter

Changes in stem and fruit diameter were continuously recorded in both control and P-deficient plants during the period of treatment with a shrinkage type micro-displacement detector (Iwao and Takano, 1988). The sensors were connected to a computerized data acquisition system (NEC, Sanei Kogyo Co. Ltd., Tokyo). The sensors were fastened to the stem or a growing fruit and connected to the power system and data logger. The blank runs were done by putting a glass rod in place of the plant sample and the sensitivity in measurement was within a limit of 2 μm. All measurements were recorded three times and the pattern of response was similar in all.

$^{13}CO_2$ feeding

$^{13}CO_2$ feedings were given to the leaf immediately above the first fruiting node on days 7 and 17 after P-deficiency treatment in both control and treated conditions. The leaf was enclosed in a transparent

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plastic bag and 200 ml of gas mixture comprising 80% nitrogen, 19% oxygen and 350 μl l^{-1} of $^{13}CO_2$ (99 ^{13}C atom% excess) was introduced from a cylinder. The leaf was allowed to assimilate $^{13}CO_2$ for 1 h. During the assimilation process, the PAR was above 1700 μmol m^{-2} s^{-1}. The plants were harvested 48 h after feeding by separating into $^{13}CO_2$-fed leaf, fruits and peduncle on the axil of the fed leaf, other leaves, fruits, stem, and other plant parts. The plant parts were ground to powder for measurement of ^{13}C abundance.

^{15}N feeding

The roots of the tomato plants were dipped into a solution of ^{15}N-NO_3 (10 atom%, 100 ppm) in a 20 l container for 24 h before the initiation of P-deficiency treatment. The plants were harvested 19 d after the imposition of the P-deficiency treatment. The plants were separated into leaves, stem, fruits, and roots. The plant materials were dried in an oven for 72 h for the estimation of dry weight. The materials were ground to powder for the determination of ^{15}N abundance.

^{13}C and ^{15}N analyses

The ^{13}C or ^{15}N abundance in the powdered plant sample was determined with a mass spectrometer (model Delta plus, Finnigan Co., San Jose, CA, USA) (Nobuyasu *et al*., 2003). The ^{13}C atom% excess in the plant sample was calculated as the difference in ^{13}C atom% between the sample and standard pure chemical glycine. The amount of labelled C in the plant sample was calculated using the equation shown below.

$$A = \frac{^{13}\text{C abundance in the sample}}{100} \times \text{amount of C in the sample}$$

The amount of total C was determined by the element analyser facilitated in the mass spectrometer. Similarly, the amount of labelled N in plant sample was calculated. The total N of the plant material was determined by the micro-kjeldahl method (Bremner, 1960).

Statistical analysis

The experimental data were analysed for the effect of P-deficiency treatment according to the expected mean squares given by McIntosh (1983). For mean separation, treatment sum squares was partitioned by method of orthogonal contrasts. The coefficients of variation for all response variables were below 10%.

Results

Dry mass accumulation

Increase in dry mass accumulation was slower in the P-deficient plants compared with the control during the 19 d period of treatment (Fig. 1). P-deficiency affected fruit and leaf growth more than the other organs during the first 9 d of treatment; during the last 10 d of treatment, fruit growth recovered partly, but not leaf growth. The effect of P-deficiency on root growth was not significant.

Stem and fruit diameter

During the period of treatment, the diameter of the stem in the control exhibited daytime shrinkage and night-time expansion and increased temporally up to 19 d after treatment (Fig. 2). There was similar rhythmic shrinkage

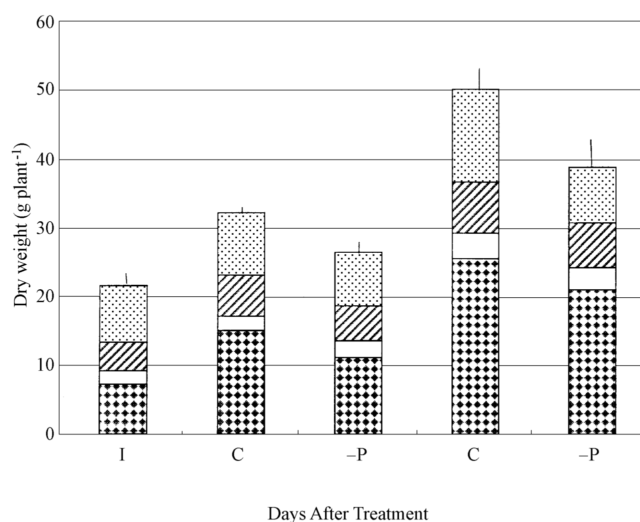

Fig 1. The effect of P deficiency on dry weight of various parts of tomato. I, initiation of treatment; C, control; –P, P deficiency. Vertical bars denote SEM for whole plant weight. Fruit (black and white checks), root (white), stem (diagonal stripe), leaves (spotted).

and expansion in the stem of the plants subjected to P-deficiency. However, during the first half of the treatment period, the diameter of the P-deficient plant was larger than the control, but in the second half, it was lower in the former than the latter. With the exception of the first 5 d, there was no increase in stem diameter of the P-deficient plants. The daytime contraction of the stem diameter was initiated early in the morning and the shrinkage was high throughout the day before complete recovery in the evening (Fig. 3). The diameter of stem expanded during the night period. During the initial period, P-deficiency reduced daytime shrinkage and encouraged night-time expansion of stem diameter compared with the control. This effect was gradually obliterated at the mid-point of the treatment period; the night-time expansion was very low in the treated plant, in contrast to the control by the end of the treatment period (Fig. 3).

The diameter of the fruit increased with the passage of time in both control and P-deficient plants during the period of treatment (Fig. 4). P-deficiency increased expansion during the first half, but this effect gradually declined and expansion was poorer in the treated plant compared with the control in the last part of the treatment period. The circadian rhythm in the contraction and expansion of fruit diameter was not as distinct as that of the stem (Fig. 5). In the early part of treatment period (Fig. 5A), there was no shrinkage in fruit diameter and expansion occurred throughout the 24 h daily period in both control and P-deficient plants. However, daytime expansion was mostly slower compared with the night and fruit of P-deficient plant expanded more than the control. At day 9 after treatment, the fruit diameter did not change during the day and expanded during the night in the control (Fig. 5B). But P-deficient plants exhibited larger daytime

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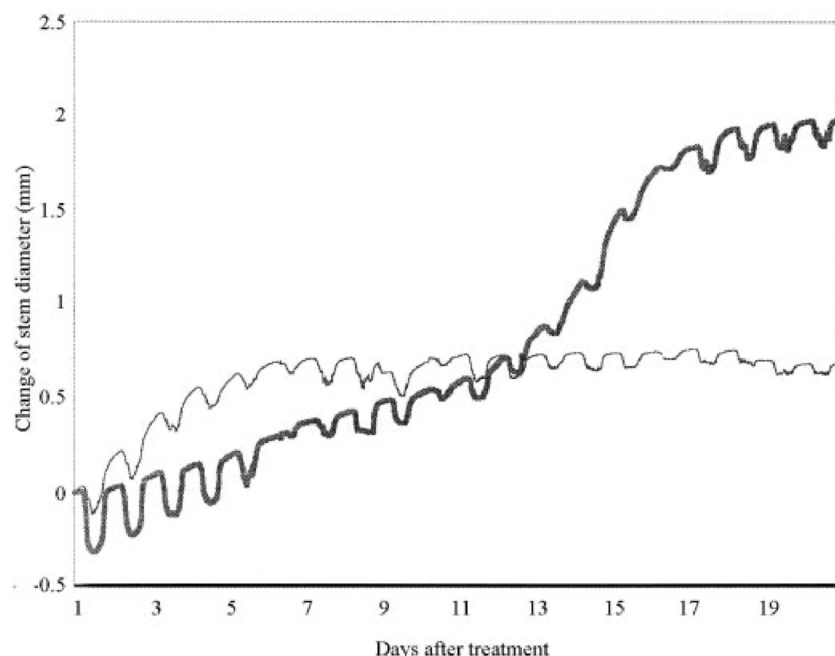

Fig. 2. The effect of P-deficiency on changes of stem diameter in tomato. Changes in stem diameter were monitored by a shrinkage type micro-displacement detector. Data represent the means of three plants. Control (thick line), –P treatment (fine line).

shrinkage and lower night-time expansion of fruit diameter compared with the control. This effect of P-deficiency was also more evident on day 19 (Fig. 5C).

Apparent photosynthetic rate/stomatal conductance

The apparent photosynthetic rate, stomatal conductance, and transpiration rate (Fig. 6) mostly remained similar in both and control and P-deficient plants during the first 10–12 d of treatment. Subsequently, the activities were lower in the P-deficient plant compared with the control.

P uptake and partitioning

Among the plant organs, the fruits possessed the highest concentration or amount of P in both control and P-deficient plants (Table 1). In the control plants, the amount of P increased in roots, leaves and fruits during the 19 d period, but not in the stem. By contrast, the P concentration of all organs except the roots of control plants declined during the same period. Although the P concentration of the leaf was low, the plant parts continued to gain biomass with the passage of time (Fig. 1). P-deficiency significantly reduced the amount of P and the concentration of P in all plant parts compared with the control. P-deficiency altered the partitioning of P among the organs; more preference was given to the fruits at the cost of P contents of roots and leaves.

^{13}C partitioning

Among the plant organs studied, ^{13}C atom% was very high in the fed leaf and it was followed by the fruits (Table 2). The percentage of the isotope was very low in the other leaves, upper stem and roots on day 9. On day 19, the concentration of the isotope receded in the fruits and peduncle and increased in the other leaves and upper parts of stem, but no major fluctuation occurred in the concentration of the fed leaf. P-deficiency improved ^{13}C atom% of the fruits on day 19; in the case of roots, the treatment improved ^{13}C atom% on days 9 and 19. The export rate of ^{13}C into other plant parts from the fed leaf in the control was lower on day 9 after treatment than on day 19 (Fig. 7). P-deficiency decreased the export rate of ^{13}C from the fed leaf into other parts on days 9 and 19 after treatment. Most of the ^{13}C assimilated into the plant was partitioned into the fruits and the other plant parts only received a small part of the isotope (Fig. 8). P-deficiency decreased the partitioning of ^{13}C to fruits on day 9 after treatment, but on day 19, it had the opposite effect. Similar to fruits, P-deficiency increased partitioning to roots and the lower parts of the stem at the cost of partitioning to leaves and the upper part of stem.

^{15}N partitioning

In contrast to ^{13}C, less ^{15}N was partitioned into the fruits (Fig. 9). In the control, partitioning was maximal to the leaves, with the fruits being the next favourite destination. P-deficiency significantly increased partitioning to the fruits, largely at the cost of the leaves. P-deficiency also reduced partitioning to roots and stem.

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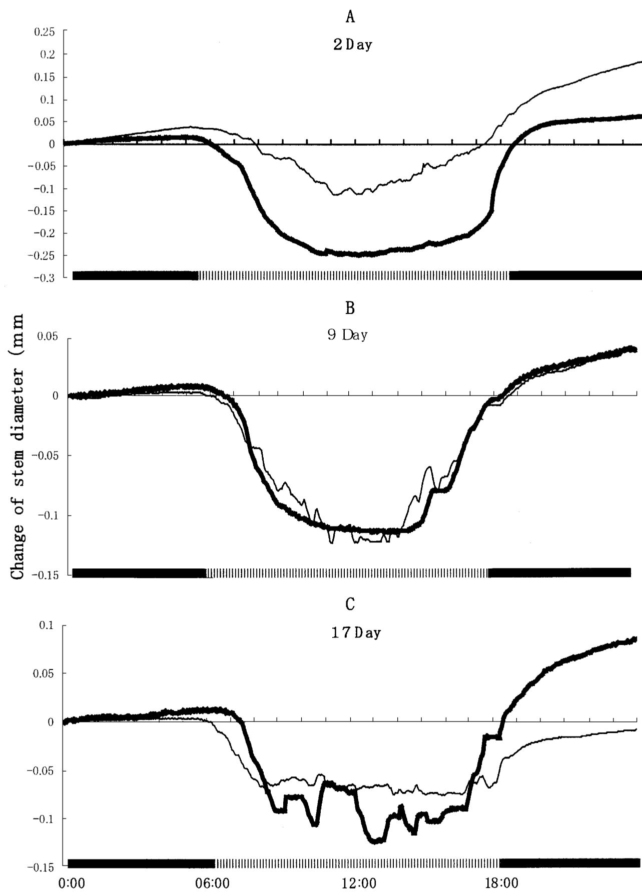

Fig 3. The effect of P deficiency on diurnal changes of stem diameter of tomato plants. On each occasion, the diameter changes in both control and P-deficient plants were recorded with reference to 'Zero change' at midnight (00.00 h). Night-time (black bar), day time (bar with vertical lines), control (thick line), –P treatment (fine line).

Discussion

P-deficiency is reported to affect growth, photosynthesis and dry matter partitioning of young tomato plants (De Groot *et al.*, 2001). In addition to these effects, the present study revealed the adverse effect of P-deficiency stress on fruit growth, the expansion of stem and fruit diameter, and the partitioning of carbon, nitrogen and phosphorus to the fruits. The effects of low P on expansion and contraction of stem and fruit diameter provided new insights into the influence of P-deficiency on the sink from that of the source. In the Münch pressure flow hypothesis, carbon and nitrogen solutes are passively transported with water from the source to the sink in the phloem (Patrick, 1997). Thus, partitioning of solutes to the fruit from the source leaf is dependent on adequate phloem turgor; the low water potential of the phloem reduces the driving force for sap flow into the fruit. Johnson *et al.* (1992) observed a strong correlation between circadian rhythm changes in diameter and the water potential of the stem and fruit of tomato plants and concluded that low stem water potential reduced phloem turgor, thus decreasing the driving force for the entry of sap to the fruit. In the present experiment, although the effect of low P on leaf water potential was not recorded, it may be assumed to reduce stem and fruit expansion by lowering the water potential of the plant. In the process, the partitioning of carbon, nitrogen and phosphorus was affected. It was stated that P-deficiency affected the hydraulic conductance of roots (Radin and Eidenbock, 1984) and reduced the water potential of the plant, possibly by lowering the activity of the water channel proteins, aquaporins (Clarkson *et al.*, 2000; Steudle, 2000).

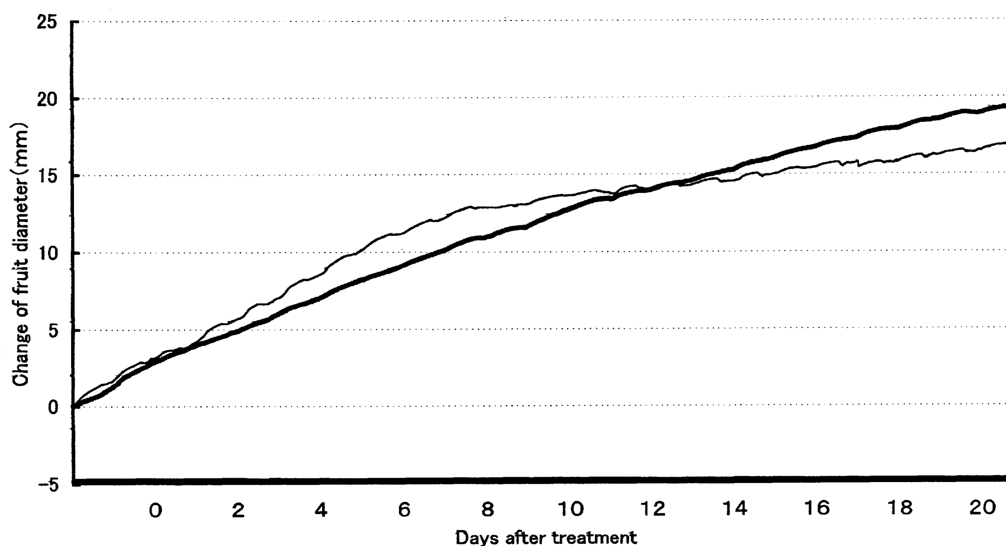

Fig 4. The effect of P deficiency on changes in fruit diameter in tomato. Changes in fruit diameter was monitored as described in Fig. 2. Control (thick line), –P treatment (fine line).

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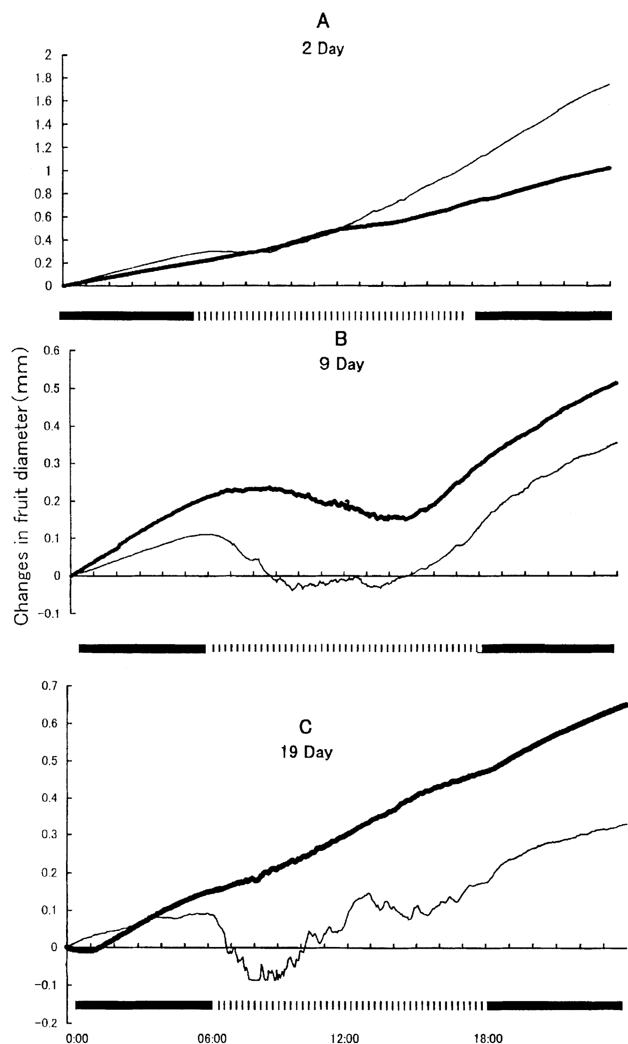

Fig 5. The effect of P deficiency on diurnal changes of fruit diameter of tomato plant. On each occasion, the diameter changes in both control and –P plants were recorded with reference to 'Zero change' at midnight (00.00 h). Night-time (black bar), daytime (bar with vertical lines), control (thick line), –P treatment (fine line).

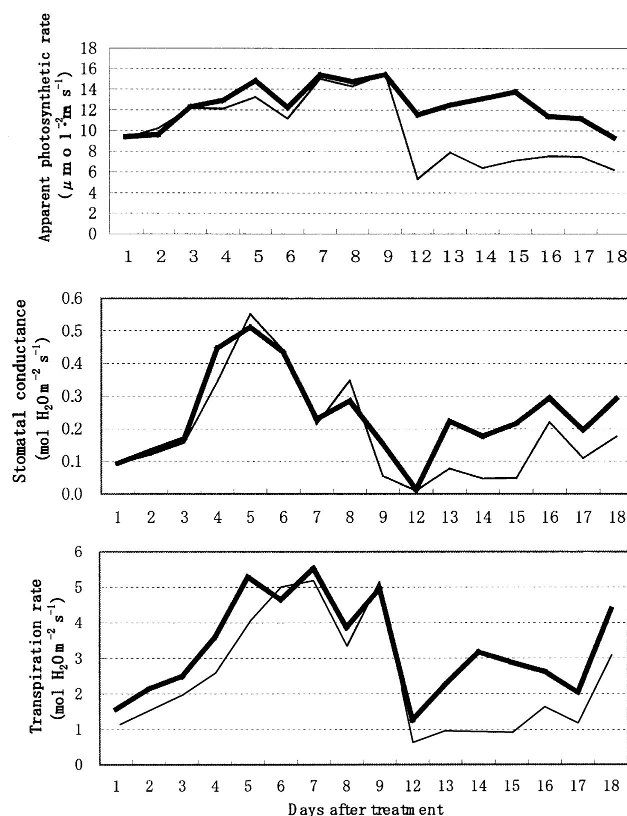

Fig. 6. The effect of P deficiency on apparent photosynthetic rate, stomatal conductance and transpiration rate of the leaf immediately below the first truss of tomato. Control (thick line), –P treatment (fine line).

Although the relationship existing between nutrient stress and water channel activity remains obscure, it is assumed that the incoming nutrients absorbed by root cells activate the aquaporins in their cell membrane and nutrients inside the plant do not have any role in the process (Clarkson *et al.*, 2000). The observations recorded in this study, however, do not entirely agree with this assumption. Withdrawal of P from the culture medium, marginally increased stem and fruit diameter during the first week of treatment, before reducing it subsequently (Figs 2, 4). It may be that P-deficiency has a lag period for action, during which the cytoplasmic-P maintains the hydraulic conductivity of water in the roots. It is also possible that P-deficiency induced the closure of stomata (Radin, 1984, 1990) improving the water potential of these organs temporarily. The effect of sub-optimal P on the temporal fluctuation of water status of the fruit and stem, did not have an identical commensurate influence on the growth of the organs, in the present experiment. The fruit of the P-deficient plants maintained growth at a reduced rate throughout the treatment period, although the diameter was larger and smaller than the control during the first and second halves of the treatment period, respectively. It was reported that, in tomato fruit, the demand for water generated by transpiration and low fruit osmotic potential were met by sap flow in the phloem (Ho *et al.*, 1987; Lee, 1989). These reports proposed a direct correlation between dry matter accumulation of fruit and water flow into it. While it may be prudent to accept this proposition under normal circumstances, it may not be so under perturbed situations, where the effects of stress are not identical on transpiration and carbon partitioning. In this experiment, ^{13}C partitioning into the P-deficient fruit declined during the first half of the treatment period (Fig. 8), when there was no effect of the stress on stomatal conductance and transpiration (Fig. 6). By contrast when stomatal conductance was low in the second half, the partitioning of ^{13}C as well as ^{15}N (Fig. 9) into the fruit was high. Although both apoplasmic water and carbon solutes of the phloem sap move in the same direction in the pedicel of tomato

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Table 1. *The effect of P deficiency on P concentration and amount in various parts of the tomato plant during fruit development*

	P (g kg^{-1})			P (mg $plant^{-1}$)		
	0 DAT	19 DAT		0 DAT	19 DAT	
		Control	P deficiency		Control	P deficiency
Fruit (1st)	8.90±0.27	6.44±0.18	5.14±0.32	60.2±10.6 (38.0)	122.0±14.4 (43.6)	111.1±44.3 (61.8)
Fruits (2nd)	6.57±2.10	5.53±0.44	5.45±0.41	0.2±0 (0.1)	20.8±0.1 (7.4)	12.7±2.7 (7.1)
Leaves	7.53±0.10	6.17±1.21	2.94±0.12	61.7±11.9 (39.0)	87.2±10.7 (31.2)	28.9±3.5 (16.1)
Stem	6.13±0.62	3.13±0.39	2.37±0.21	25.7±0.06 (16.2)	25.1±4.1 (9.0)	13.1±1.9 (7.3)
Root	5.13±0.50	5.89±0.33	3.75±0.55	10.6±1.5 (6.7)	24.7±3.8 (8.8)	13.9±1.7 (7.7)
Whole plant	–	–	–	158.4 (100)	279.8 (100)	179.7 (100)
Average±SEM						

Figures in parentheses indicate the proportion of P amount in individual plant parts relative to the whole plant P amount.
DAT, days after treatment.

Table 2. *The effect of P deficiency on ^{13}C atom% excess in various parts of tomato plants at different times after treatment*

Plant parts	9 DAT		19 DAT	
	Control	P deficiency	Control	P deficiency
Fed leaf	0.557±0.014	0.795±0.044	0.583±0.034	0.564±0.130
Other leaves	0.006±0.001	0.004±0.001	0.038±0.002	0.009±0.0003
Fruits	0.115±0.021	0.096±0.007	0.048±0.005	0.059±0.007
Peduncle	0.051±0.004	0.027±0.009	0.003±0.001	0.015±0.003
Stem, upper	0.006±0.002	0.006±0.001	0.034±0.008	0.014±0.003
Stem, lower	0.016±0.001	0.026±0.008	0.022±0.005	0.028±0
Roots	0.006±0.001	0.016±0.009	0.004±0.001	0.031±0.005
Average±SEM				

fruit (Walker and Ho, 1977), variation in demand for their utilization in the sink can discriminate in the rate of their movement.

In common bean, P-deficiency was reported to induce more dry matter partitioning in favour of heterotrophic tissue, thus reducing growth of photosynthetic tissue (Nielsen *et al.*, 2001). In the present experiment, partitioning of ^{13}C and ^{15}N was more likely to the fruit compared with other organs at suboptimal P (Figs 8, 9). The other heterotrophic organs such as the lower part of the stem (data not shown in the figure) and roots also received an enhanced allocation of ^{13}C under the stress (Fig. 8). It may be that the carbon and nitrogen were diverted for fruit growth at the expense of their partitioning to vegetative plant parts at low-P. Those are both a consequence of low P; a reduction in plant growth is not a goal for the plant, more a consequence of higher investment in fruit. But, by comparison with the control, the export of the ^{13}C into other parts of the plant from the fed leaf decreased in P-deficient plants, when observations were taken on days 9 and 19 after treatment (Fig. 7). A similar effect restricting sucrose export from the source leaf was recorded in tobacco (*Nicotiana tabacum* L. var. Samsun) under P-deficiency (Pieters *et al.*, 2001). Since carbon and nitrogen metabolism are intricately related in plant organs (Lewis *et al.*, 2000; Noctor and Foyer, 2000), a reduction in the export of carbon from the fed leaf to other organs might have affected nitrogen flow as well in the P-deficient condition. Consequently, fruit weight decreased under sub-optimal P. The reduction in carbon mobility from the fed leaf to sink organs including the fruit could be consequential to the decline in source and/or sink activities. Since source activity in P-deficient plants did not decrease on day 9, it could not be considered a factor for fruit growth limitation in this experiment. Under P-deficiency, photosynthetic activity continued until the time when the depression of fruit growth was enough to impose a feedback inhibition. It was stated that carbohydrate accumulation at the source leaf due to source–sink imbalance can result in the expression of photosynthetic genes (Paul and Foyer, 2001). In P-deficient tobacco plants, low sink demand limited the photosynthesis of the source leaf and this effect was evident nearly 3 weeks after the plants were subjected to low-P (Pieters *et al.*, 2001). Such an effect might have reduced photosynthesis of the P-deficient plants in the present experiment (Fig. 6) and an increase in the unused CO_2 might have reduced stomatal conductance (Jarvis *et al.*, 1999; Fujita *et al.*, 2002). Thus, a reduction in photosynthetic rate under sub-optimal P supply may not be entirely consequential on reduced ATP

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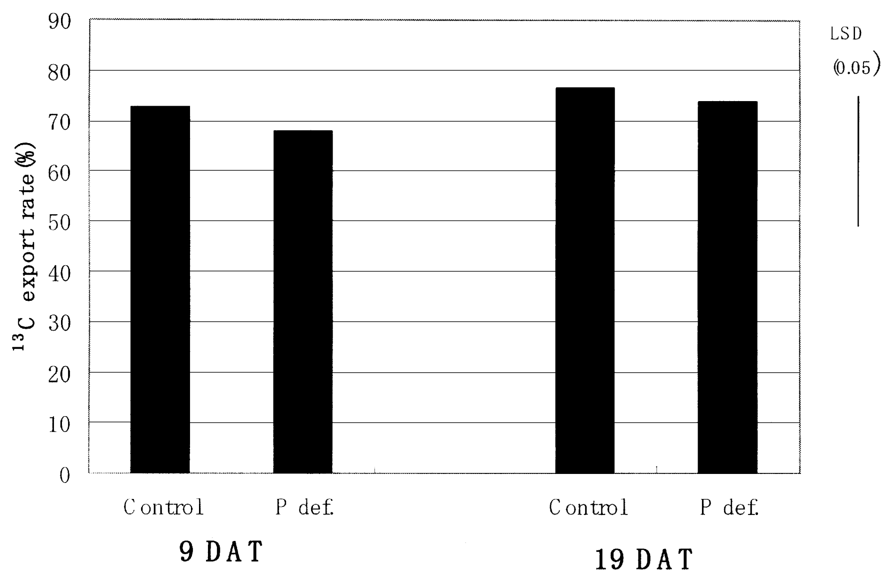

Fig. 7. The effect of P deficiency on ^{13}C export rate from the leaf immediately below the first truss of tomato at 9 d and 19 d after treatment (DAT). P def.: P deficiency.

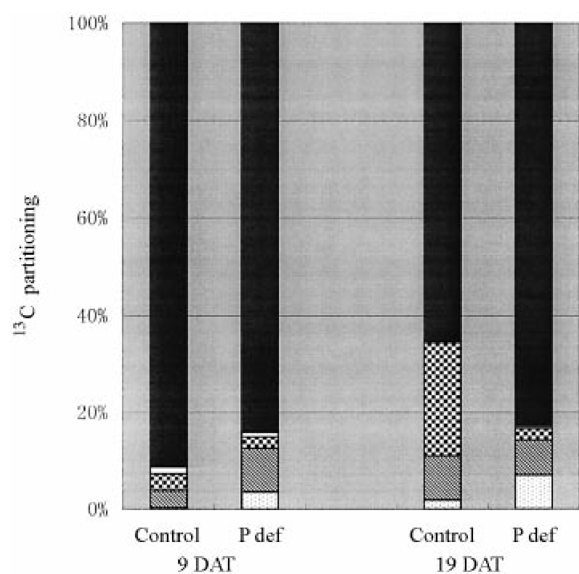

Fig. 8. The effect of P deficiency on ^{13}C partitioning among various parts of tomato plant at 9 d and 19 d after treatment (DAT). P def: P deficiency. Roots (spotted), stem (diagonal lines), leaves (black and white checks), peduncle (white), fruits (black).

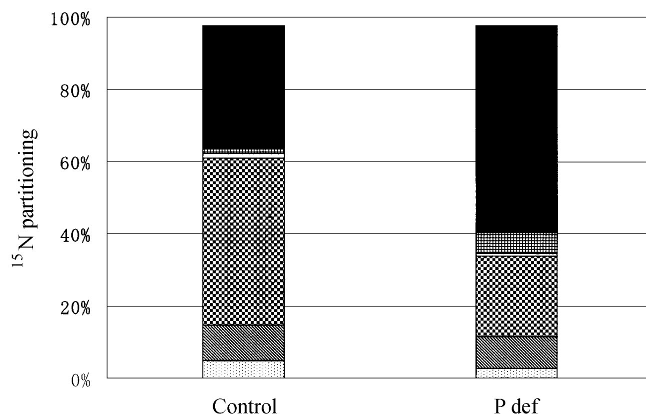

Fig. 9. The effect of P deficiency on ^{15}N partitioning among various parts of tomato plant at 19 d after treatment. P def.: P deficiency. Roots (spotted), stem (diagonal lines), leaves (black and white checks), peduncle (white), others (white checks), fruits (black).

availability for the dark reaction of photosynthesis (Rao and Terry, 1995).

Rapid changes in turgor pressure and the temperature of plant tissues are providing new information about the mechanism of growth (Proseus *et al.*, 2000). The growth rate peaks late at night and remains very low during late afternoon (Schurr *et al.*, 2000). Similarly, the rapid changes in stem diameter that occur throughout the day are closely related to plant water content (Simonneau *et al.*, 1993). In the present experiment, the effect of P-deficiency on the diurnal fluctuation of fruit and stem diameter expansion further clarified the role of the element in plant water relations and growth. The diurnal diameter expansion of fruit and stem was identical (Figs 3, 5) and the distribution of ^{13}C to fruit declined marginally in P-deficient plant compared with the control during the first week of treatment (Fig. 8). These observations indicated no major influence of the stress on water status of the fruit. But in the second half of the treatment period, the expansion of the stem and fruit diameter was seriously restricted by P-deficiency; compared with daytime, night expansion of the stem was affected more. Such an effect on water status of the plant, could have reduced fruit growth,

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leading to a depression of photosynthesis in the second part of the treatment period. Recently, there has been a wealth of information on P-starvation-responsive genes and their action in plants (Baldwin *et al*., 2001; Mukatira *et al*., 2001; Rubio *et al*., 2001; Varadarajan *et al*., 2002). It has been stated that the fluctuation of water status leading to alterations in growth response is not caused by changes in the gene expression of plants (Proseus *et al*., 2000). Hence, the effect of P-deficiency on fruit growth in the present experiment was direct and did not occur due to any change in the metabolic activity of the plant. This inference is similar to that of Pearce *et al*. (1993) who concluded that tomato fruit expansion was more closely related to water status than concurrent photosynthesis. However, in this experiment, there was a lag period of 1 week for the appearance of deficiency symptoms. It might be the time required for the depletion of internal P concentration.

Partitioning of dry matter from the source to economically useful organs is an index for quality of resource management on the part of the plant under limiting conditions. In order to identify the effect of stress on partitioning, the physiological events controlling sink and source activities are generally analysed. Thereby, the role of either source or sink limitation on partitioning is elaborated using the Münch pressure flow hypothesis for the transfer of solutes from the source to the sink in plants. However, recent measurements of the resistance of phloem sap indicated that the source activity can not be viewed in isolation from that of the sink, outdating the concept of source or sink limitation for partitioning (Bancal and Soltani, 2002). Thus, both source and sink organs are parts of a single inseparable system and an effect on one part is bound to have a consequential and concurrent influence on the other. In the present experiment, low-P impaired sink activity directly reducing the size of the fruit and this effect might have been responsible for the depression in leaf photosynthesis and the reduced stomatal conductance. This evidence is indicative of the sink hierarchy in the regulation of source activity. But, it is more apt to accept a holistic approach and opine that P-deficiency disturbed the partitioning of solutes between the source and sink.

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