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Phloem Turgor and the Regulation of Sucrose Loading in *Ricinus communis* L.

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Abstract. The influence of plant water relations on phloem loading was studied in *Ricinus communis* L. Phloem transport was maintained in response to bark incisions even at severe water deficits. Water stress was associated with a net increase in the solute content of the sieve tubes, which resulted in maintenance of a positive phloem turgor pressure (Ψ_p). There was a significant increase in solute flux through the phloem with decreasing xylem water potential (Ψ). In addition, sugar uptake by leaf discs was examined in media adjusted to different water potentials with either sorbitol (a relatively impermeant solute) or ethylene glycol (a relatively permeant solute). The limitations in this experimental system are discussed. The results nevertheless indicated that sucrose uptake can be stimulated by a reduction in cell Ψ_p, but that it is little affected by cell Ψ or solute potential (Ψ_s). On the basis of these data we suggest that sucrose loading is turgor-pressure dependent. This may provide the mechanism by which transport responds to changes in sink demand in the whole plant.

Key words: Feedback regulation – Phloem – *Ricinus* – Sucrose loading – Turgor pressure – Water stress.

Introduction

In the previous papers (Smith and Milburn 1980a, b) we have described some of the osmotic characteristics of phloem-sap exudation from bark incisions in water-cultured *Ricinus* plants. The artificially induced changes in sink demand caused by such incisions give rise to marked changes in solute flux through the phloem (Smith and Milburn 1980b). We argued that these responses must involve associated changes in the rate of solute loading.

The aim of the present work was to examine how changes in the rate of phloem loading are brought about. This may be an important aspect of the way in which phloem transport is controlled in the whole plant. In particular, it has been found that a change in sink demand can bring about a change in the rate of transport (Habeshaw 1973; Moorby et al. 1974; Wardlaw and Moncur 1976). Also, it has been widely supposed that loading is controlled by changes in phloem-sap concentration (e.g. Weatherley et al. 1959; Tammes et al. 1967; Zimmermann 1971; Ziegler 1974; Moorby 1977; Lang 1978). During sap exudation in *Ricinus*, however, large changes in solute flux are associated with only slight changes in sap concentration, and it is possible that loading is sensitive to some other function of phloem water relations (Smith and Milburn 1980b).

In the present paper, we have examined the way in which phloem loading is influenced by plant water relations in excised shoots and in a leaf-disc system. The results indicate that sucrose loading is turgor-pressure dependent.

Materials and Methods

Plant Material and Experimental Techniques

Plants of *Ricinus communis* L. var. *gibsonii* Nichols. were grown on Long Ashton solution under the conditions described previously (Smith and Milburn 1980a). Nine-week-old plants were used for experimentation.

In the description of plant water relations we have used the same nomenclature as given previously (Smith and Milburn 1980a). Phloem sap was collected, sap Ψ_s determined cryoscopically, and xylem Ψ estimated as described earlier (Smith and Milburn 1980a).

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Abbreviations: Ψ = water potential; Ψ_s = solute potential; Ψ_p = pressure potential

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Leaf Ψ was estimated by the same method as xylem Ψ, except that the leaves were taken directly from the plant without previous enclosure in polyethylene bags.

Water deficits were imposed on plants by excision of the root systems. This allowed low values of leaf Ψ to develop quickly, and also ensured that the shoot was the only source of solutes for phloem-sap exudation. Control plants with an unrestricted water supply were ring-girdled by removing the bark at the base of the stem. Measurements were all made within 20 h of excising the root system. Sap flow was maintained by periodically making successive incisions into the stem.

Sugar Uptake by Leaf Discs

Sucrose and glucose uptake by leaf discs were studied using [^{14}C]sucrose and [^{14}C]glucose as tracers, respectively. The analytical methods were based on those of Giaquinta (1977). Uptake was studied with discs incubated on solutions adjusted to different water potentials with either sorbitol (a relatively impermeant solute) or ethylene glycol (a relatively permeant solute).

Areas of the adaxial surface of fully expanded leaves were gently abraded with moist 'Aloxite' 50 Optical Smoothing Powder (The Carborundum Co. Ltd., Manchester, U.K.). This procedure does not disrupt the vascular tissue in *Ricinus* (Smith and Milburn 1980b). Discs of area 40.8 mm^2 were cut from the interveinal tissue with a clean, sharp cork-borer. The discs were rinsed with, and then floated on, 1.0 mol m^{-3} $CaCl_2$, adaxial surface downwards, for 0.75 h at room temperature in a pyrex dish. This was to allow the water deficits incurred in the tissue during preparation to be at least partially alleviated. Subsequently, discs were selected randomly from the total, quickly blotted on absorbent tissue and transferred to the wells of plastic incubation trays containing the osmoticum, on which they were floated adaxial surface downwards for a pre-incubation period of 0.50 h. The discs were then transferred to the incubation media and floated adaxial surface downwards. The composition of the incubation media was as follows: 1.0 mol m^{-3} $CaCl_2$, 20 mol m^{-3} 2-(*N*-morpholino)ethanesulphonic acid buffer, sucrose or glucose at 30 mol m^{-3}, and sorbitol or ethylene glycol at a concentration depending on the required water potential of the medium; the media were adjusted with KOH to pH 6.0, this giving a K^+ concentration of 11 mol m^{-3}. Each well of the trays contained $2.00 \cdot 10^{-6}$ m^3 osmoticum, $50 \cdot 10^{-9}$ m^3 tracer and 6 discs. The tracer concentrations in this $50 \cdot 10^{-9}$ m^3 aliquot were 370 or 364 GBq m^{-3} for [U-^{14}C]sucrose (specific activity 318.2 or 370.0 GBq mol^{-1}, respectively), or 607 GBq m^{-3} for [U-^{14}C]glucose (specific activity 111.0 GBq mol^{-1}). All radiochemicals were supplied by The Radiochemical Centre, Amersham, U.K. The trays were placed on a mechanical shaker in a growth room for the required incubation period; the temperature was 23 °C and the irradiance 16–19 W m^{-2} in the range 400–1000 nm (measured as in Smith and Milburn 1980a).

After incubation the leaf discs were washed three times (10 min each) in 1.0 mol m^{-3} $CaCl_2$ to remove free-space label. Analysis of the wash-out kinetics showed that over 98% of the freely diffusible label was removed by the end of the second wash. The discs were then digested and decolorized in perchloric acid and hydrogen peroxide as described by Giaquinta (1977), and the radioactivity counted by liquid scintillation spectrometry (see Smith and Milburn 1980b). The distribution of radioactivity in leaf discs after uptake of labelled sugars was studied by soluble-compound autoradiography using the method of Weyers and Hillman (1979).

Results

It has been shown previously that phloem-sap exudation will occur from *Ricinus* plants that are severely wilted (Milburn 1975). We therefore examined plants subjected to a range of water deficits to quantify the relationship between phloem transport and the water relations of the shoot.

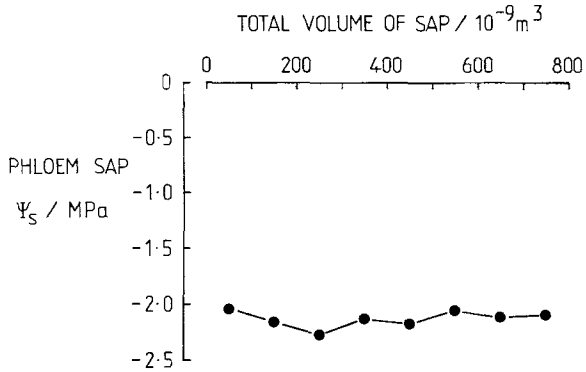

Fig. 1. Phloem-sap Ψ_s determined cryoscopically for successive $100 \cdot 10^{-9}$m^3 volumes of sap exuding from an incision in a stem internode of a water-stressed plant

Figure 1 shows that during exudation from water-stressed plants phloem-sap Ψ_s remained relatively constant, as found for unstressed plants (Smith and Milburn 1980b). The bulk solute concentration of the sap in this example was about 50% higher than in control plants. The constancy of sap Ψ_s suggested that the phloem had attained some form of 'steady-state' with respect to the water relations of the shoot. Further, the volumes of sap exuded were large relative to the estimated total volume of the sieve tubes in the shoot (which was about $400 \cdot 10^{-9}$m^3 for the shoot in Fig. 1, calculated as in Smith and Milburn 1980b). This indicates that, as with unstressed plants, exudation in the water-stressed plants must have been associated with solute loading (see Smith and Milburn 1980b).

The relationship between leaf Ψ and xylem and phloem water relations was investigated in plants stressed for different times after excision of the roots. Exudation was maintained by periodically making successive incisions into the stem: this was to ensure that changes in sap Ψ_s were not caused by solute accumulation in the phloem in the absence of longitudinal transport. The results are presented in Figure 2. Pressure-bomb readings were corrected for a xylem-sap Ψ_s of -0.1 MPa determined separately to give the estimates of leaf Ψ and xylem Ψ.

Figure 2a shows that xylem Ψ decreased linearly with leaf Ψ. Phloem sap Ψ_s also decreased with increasing water stress, and sap exudation occurred in all plants examined. Estimates of phloem Ψ_p were derived from the algebraic difference between xylem Ψ and phloem-sap Ψ_s; the assumptions involved in this procedure were discussed earlier (Smith and Milburn 1980a). These computed values of phloem Ψ_p are plotted in Figure 2b against the corresponding

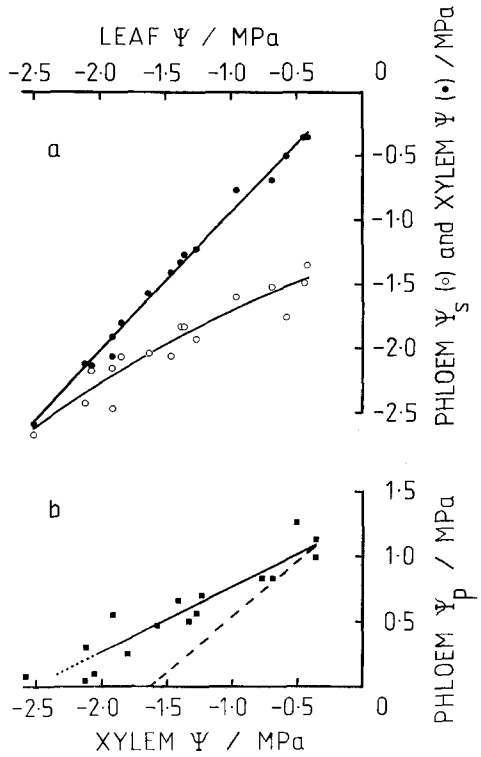

Fig. 2a and b. Changes in osmotic characteristics of phloem sap during water stress. **a** Relationships between leaf Ψ and xylem Ψ (●), and between leaf Ψ and phloem-sap Ψ_s (○), with curves fitted by least-squares analysis to equations $y=0.133+1.074x$ ($r=0.996$, $P<0.001$) and $y=-1.297^{0.279x}$ ($r=0.941$, $P<0.001$), respectively. **b** Relationship between xylem Ψ and estimated phloem Ψ_p (■), with line fitted by least-squares analysis to equation $y=1.270+0.504x$ ($r=0.937$, $P<0.001$); Ψ_p values were computed from difference between xylem Ψ and phloem-sap Ψ_s; dotted portion of line represents region where pressure-bomb estimates of leaf and xylem Ψ are likely to have been less reliable. Broken line shows values of phloem Ψ_p predicted if the net solute content remained constant with changing xylem Ψ; it is extrapolated to the point at which $\Psi_p=0$, and allows for a turgor displacement volume of 12%. The slope of the experimental line is 0.504 ± 0.051, which is significantly different from the predicted slope of 0.852 at $P<0.001$ (Student's *t*-test)

values of xylem Ψ. The dotted portion of the regression line indicates the region in which pressure-bomb estimates of xylem Ψ may have become less reliable because of cavitation in xylem vessels (Milburn 1975). Although phloem Ψ_p decreased with increasing water deficits, it was nevertheless positive in all instances. The broken line in Figure 2b represents the values of phloem Ψ_p predicted if the phloem were to have responded entirely passively to changes in xylem Ψ, i.e. assuming an osmotic efflux of water from the sieve tubes in response to decreasing xylem Ψ without any net change in the amount of solute in the phloem. The slope of the line for the predicted relationship was determined by fixing two co-ordinates thus:

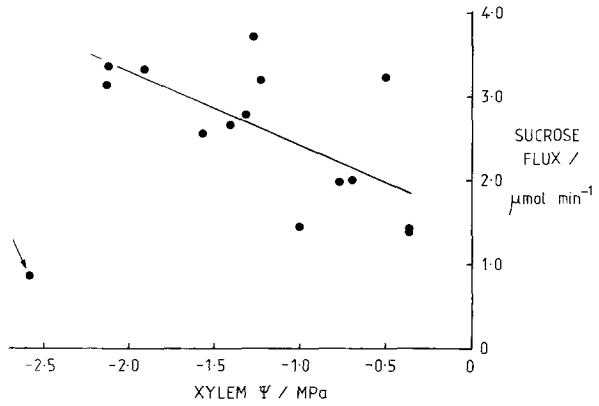

Fig. 3. Relationship between solute flux through the phloem and xylem Ψ for data given in Fig. 2. Solute flux was calculated from sap exudation rate × solute concentration (Ψ_s), and was converted to sucrose flux from the relationship between sap Ψ_s and sucrose concentration determined separately. The regression line was fitted by least-squares analysis to the equation $y=1.54-0.88x$ ($r=0.663$, $P<0.01$). The value at xylem Ψ of -2.58 MPa was not included in the regression analysis

(1) xylem Ψ at which phloem Ψ_p maximum: derived from curves fitted to experimental points in Fig. 2a, i.e. xylem Ψ of -0.36 MPa, phloem-sap Ψ_s of -1.45 MPa, and therefore maximum phloem Ψ_p of $+1.09$ MPa; and

(2) xylem Ψ at which phloem Ψ_p zero: taken as the point at which xylem Ψ = phloem-sap Ψ_s, which would be -1.45 MPa; this must also be corrected for a turgor displacement volume (TDV) of 12% of sieve-element volume at full turgor (Milburn 1972), because as Ψ_p falls the decrease in cell volume will itself reduce Ψ_s; hence, when $\Psi_p=0$, Ψ_s would be -1.64 MPa. The slope of the line derived from the experimental data is significantly different from the slope of this predicted line at $P<0.001$.

The decrease in sap Ψ_s with increasing water stress could not, therefore, be solely attributed to an osmotic efflux of water from the phloem; there must also have been a net increase in the amount of solute in the sieve tubes. If it is assumed that there was mass flow through the phloem (see Smith and Milburn 1980b), there are two ways in which this could have arisen. On the one hand, there could have been an increase in solute flux through the phloem without an equivalent increase in the speed of longitudinal transport. On the other, there could have been a decrease in the speed of longitudinal transfer without an equivalent decrease in solute flux. Indeed, although 'sink demand' was maintained by the incisions, lower exudation rates were found in the water-stressed plants. Consequently, a measure of solute flux is needed to distinguish between these two possibilities.

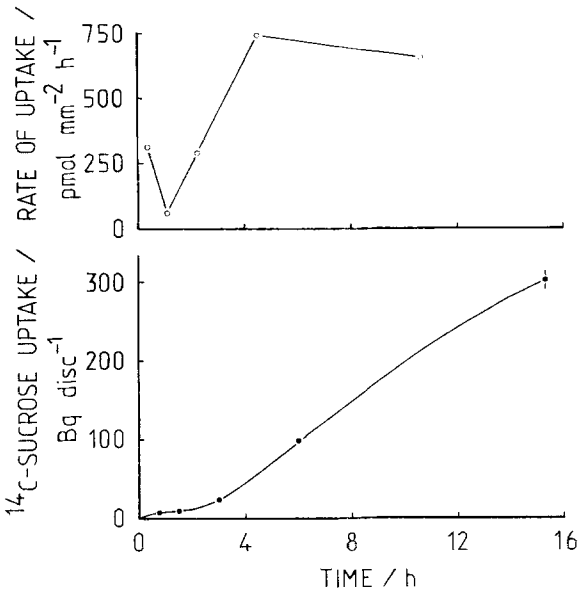

Fig. 4. Time course of tracer uptake by *Ricinus* leaf discs from medium containing [^{14}C]sucrose and 250 mol m^{-3} sorbitol. Values were calculated assuming that sucrose was not metabolized prior to uptake. *Lower graph:* cumulative amount of [^{14}C]sucrose absorbed; points are means for 6 discs, with bar representing ± S.E. where larger than symbol. *Upper graph:* data plotted as rate of sucrose uptake

The data presented in Fig. 3 are estimates of flux derived from the product of exudation rate and solute concentration. They contain an element of random error associated with the difficulty of making incisions across identical cross-sectional areas of conducting tissue in different plants. Further, it is not clear on what basis 'exudation rate' in different plants should be compared: these data are based simply on the time required to collect a standard $100 \cdot 10^{-9}$m^3 aliquot of sap. Nonetheless, Figure 3 shows that the trend was for solute flux to increase significantly with decreasing xylem Ψ. One estimate not included in the regression analysis was that at xylem Ψ of −2.58 MPa. At this level of stress exudation was not sustained, and several incisions were required to collect the standard aliquot of sap.

Solute loading was studied further by determining how sugar uptake by leaf discs is affected by their water relations. To find an appropriate incubation time, we investigated the time course of tracer uptake from a medium containing [^{14}C]sucrose. The rate of uptake (Fig. 4) did not reach a maximum until about 4 h, which could have been related to the time taken for the water balance of the tissues to be restored following preparation of the leaf discs. A standard incubation time of 8.0 h was adopted to ensure that uptake had reached an optimum rate during the experimental period.

Data from an experiment comparing tracer uptake from [^{14}C]sucrose and [^{14}C]glucose in incubation media with either sorbitol or ethylene glycol as the osmoticum are given in Table 1. We assumed that sorbitol behaved as an osmoticum like mannitol, which is only slowly taken up by plant cells (Greenway and Leahy 1970; Jones 1973). In this medium there will be water efflux from the cells, causing a decrease in cell Ψ_p and Ψ (as well as an associated decrease in cell volume and Ψ_s). Ethylene glycol, however, is much more rapidly taken up by plant cells (Greenway and Leahy 1970; Jones 1973). In this instance there will also be water efflux from the cells, but Ψ_p is only transiently reduced: this is because solute entry tends to restore the original Ψ_p and cell volume (see Jones 1973; Lüttge et al. 1977). It is thus possible to determine whether sugar uptake is influenced more by cell Ψ_p or by Ψ and Ψ_s.

The values given in Table 1 are expressed relative to those from the incubation media of higher Ψ_s, in which the cells were assumed to be close to 'full turgor'. In expressing the data as rates of sucrose or glucose uptake, we have assumed that there was no metabolism of these solutes prior to uptake. In *Ricinus* cotyledons, at least, sucrose is taken up very largely without hydrolysis (Kriedemann and Beevers 1967). The results indicate that in the sorbitol medium

Table 1. Effect of decrease in Ψ of incubation medium on sucrose and glucose uptake by *Ricinus* leaf discs. Values are expressed as percentages of those at 'full turgor', and assume that the sugars were not metabolized prior to uptake. The figures are means ± S.E. for 12 discs, with *P* values denoting level of significant differences (Student's *t*-test). The results are from one experiment representative of five

Ψ of incubation medium/MPa	Sorbitol medium			Ethylene glycol medium		
	approximate Ψ_p of tissue	sucrose uptake	glucose uptake	approximate Ψ_p of tissue	sucrose uptake	glucose uptake
−0.15	100	100 ± 4	100 ± 3	100	100 ± 3	100 ± 4
−1.08/−0.88	30	126 ± 6	74 ± 2	~100	108 ± 3	85 ± 3
		($P < 0.01$)	($P < 0.001$)		($P < 0.05$)	($P < 0.01$)

the decrease in Ψ_p in the non-plasmolytic range was associated with an increase in the rate of sucrose uptake but a decrease in the rate of glucose uptake. In the ethylene glycol medium of similar Ψ there was a much smaller increase in sucrose uptake as well as a decrease in glucose uptake. Glucose uptake was over twice that of sucrose uptake. Further, preliminary experiments with soluble-compound autoradiography indicated that, after incubation, label from [^{14}C]sucrose tended to be localized in the veins, whereas that from [^{14}C]glucose was evenly distributed between the veins and bulk leaf tissue. It remains to be established to what extent interpretation of the autoradiographs is complicated by metabolism and redistribution of labelled solutes over these relatively long incubation times.

Discussion

These results confirm in a qualitative way that phloem transport can be maintained in *Ricinus* during water stress. Quantitative considerations show that phloem Ψ_p remained positive to lower values of leaf and xylem Ψ than could be accounted for on the assumption that there was no net change in the solute content of the sieve tubes (Fig. 2). This implies that there was some form of osmotic adaptation in response to decreasing water availability. The possible importance of the matric component of the total water potential in this process should not be neglected (Geiger 1976), but the dry-matter content of the sap (Hall et al. 1971) suggests that its contribution is probably insignificant.

The maintenance of a positive phloem Ψ_p was principally a function of a net increase in the solute content of the sieve tubes. Moreover, there was a significant increase in solute flux with increasing water deficit (Fig. 3). We have discussed previously the reasons for believing that solute flux during sap exudation is related to the rate of solute loading (Smith and Milburn 1980b). These results, therefore, are consistent with a feedback regulation of solute loading by phloem Ψ_p, with decreasing Ψ_p causing an increase in the rate of loading, in a manner analogous to that found in a wide range of osmoregulating algae and higher-plant tissues (see Cram 1976; Zimmermann 1978). At low values of leaf and xylem Ψ there will also have been a reduction in the Ψ_p difference between source and sink tissues, since the pressure at an exuding incision (the sink) must have remained close to atmospheric pressure. On the basis of a pressure-flow mechanism, this is a sufficient explanation for the observed decrease in exudation rate (or speed of longitudinal transport).

There are nevertheless serious limitations involved in comparing flux data from different plants in this way (Fig. 3). Under conditions of unrestricted water availability described previously, the comparison of flux values was based on exudation from successive incisions into the same cross-sectional area of tissue for a single plant (Smith and Milburn 1980b). From the overall trend, however, it is clear that solute flux was not decreasing with increasing water deficit. This is notable because photosynthesis in mesophytic plants is severely inhibited at these levels of water stress (Hsiao 1973; Boyer 1976); this in turn can restrict the availability of sugars for export (e.g. Christy and Swanson 1976; Ho 1978). However, experiments in which solute flux has been related to changes in photosynthesis and growth rate of the sinks have indicated that water stress per se may not have much effect on the transport system (Wardlaw 1969; Munns and Pearson 1974; Moorby et al. 1975).

The present results contrast with those from studies on aphid-stylet exudation from *Salix* stem segments, in which a decrease in phloem-sap Ψ_s was associated with a decrease in solute flux (Weatherley et al. 1959; see also Peel 1975). From this observation it was proposed that the rate of loading was governed by the solute concentration in the phloem sap (Weatherley et al. 1959). However, in the stem segments the solutes must have originated mainly from storage in vascular parenchyma and ray cells. It is possible that this loading system possesses different properties from the specialized sieve element-companion cell complex in source leaves.

The leaf-disc experiments also support the view that a decrease in cell Ψ_p can bring about an increase in the rate of loading. The advantages of leaf-disc tissue for such studies have been discussed by Vickery and Mercer (1964) and Giaquinta (1977). Nevertheless, the lack of long-distance transport following sugar uptake by the discs represents an important difference between this system and loading in the intact plant. Detailed studies are also required to determine how much redistribution of tracer occurs following uptake over such time courses. The fact that glucose uptake exceeded that of sucrose has been noted in other species (Weatherley 1954; Giaquinta 1977), and this may represent uptake mainly into the mesophyll tissue. *Ricinus* phloem sap does not contain reducing sugars (Hall and Baker 1972), which, together with our preliminary results from autoradiography, argues for some specificity of the phloem loading system for sucrose.

The considerably greater increase in sucrose uptake from the sorbitol medium than from the ethylene glycol medium, in comparison with their respective controls, indicates that loading was influenced mainly

by cell Ψ_p rather than total Ψ. The small increase in the ethylene glycol medium suggests either that total Ψ may have a slight effect on loading, or that there was not complete penetration of this solute. Metabolism and transport seem generally to be little affected by total Ψ (see Jones 1973; Lüttge et al. 1977). Also, the fact that sucrose uptake was not inhibited in the ethylene glycol medium shows that cell-sap Ψ_s was relatively unimportant in influencing solute loading. The inhibition of glucose uptake in both media was qualitatively distinct from the responses of sucrose uptake.

Our results indicate that sucrose loading can be modulated by changes in phloem Ψ_p. When the plant is subject to water deficits, this response is essentially osmoregulatory and serves to maintain a positive phloem Ψ_p, as postulated by Plaut and Reinhold (1967). These data do not support the suggestion that loading is controlled by changes in phloem-sap Ψ_s (see references in Introduction). If this were the case, the conditions under which phloem Ψ_p was lowered should have led to a decrease in the rate of loading. We observed instead an increase in the rate of loading under circumstances in which if anything the functioning of the loading process may have been restricted.

Conclusions

The way in which phloem loading is regulated has important implications for the control of long-distance transport. The existence of a turgor-pressure dependent loading mechanism would explain how successive bark incisions in normal water-cultured plants cause large changes in solute flux, even though sap Ψ_s remains virtually constant (Smith and Milburn 1980b). We suggest that this may be the basis on which phloem loading responds to changes in sink demand in the intact plant. Under at least some conditions, the rate of phloem transport appears not to be limited by the transport pathway (Milthorpe and Moorby 1969; Wardlaw 1976). Localized changes in phloem Ψ_p resulting from changes in sink activity would therefore cause some change in Ψ_p at the sites of loading, because of the physical characteristics of the sieve-tube system (Smith and Milburn 1980b). If mass flow is occurring through the sieve tubes, an increase in sink demand may cause a decrease in phloem Ψ_p (as do the direct incisions), and thereby bring about an increase in the rate of solute loading.

This scheme for feedback regulation of sucrose loading is summarized in the form of a block diagram in Fig. 5. The net longitudinal flux through the sieve tubes at any one point will be a function not only of solute loading but also of solute efflux, which in the case of K^+, for example, could be pressure-dependent (Smith and Milburn 1980a). This diagram does not attempt to depict the forms of thermodynamic control operating on the transport processes. Indeed, it is not possible at this stage to distinguish between a direct effect of Ψ_p on sucrose loading and a dependence of loading on cell volume or the volumetric elastic modulus of the cell wall (see Zimmermann and Steudle 1978). Furthermore, the rate of phloem loading will also be affected by assimilate supply in the source leaves (e.g. Christy and Swanson 1976; Troughton et al. 1977; Ho 1978). However, we can find no evidence to support the assumptions made by Huisinga (1979) about the way in which changes in phloem turgor are brought about.

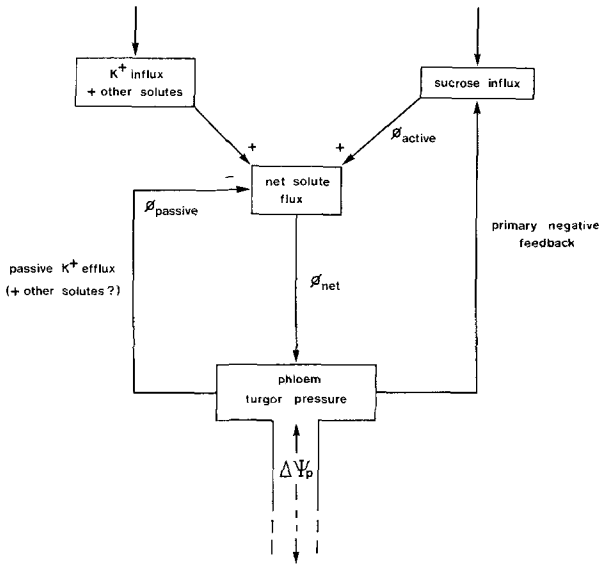

Fig. 5. Block diagram showing way in which net solute flux into the phloem (i.e. phloem loading) may be affected by phloem turgor. The scheme is not intended to specify the forms of thermodynamic control operating on the transport processes

In the same way that maintenance of turgor is essential for expansion growth at the cellular level, it is also presumably a prerequisite for maintenance of transport in the phloem at the supracellular level. It would be the unique property of a pressure-flow mechanism that a pressure-dependent loading process could itself serve to control the driving force for long-distance transport.

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References

Boyer, J.S.: Photosynthesis at low water potentials. Philos. Trans. R. Soc. London, Ser. B: **273**, 501–512 (1976)

Christy, A.L., Swanson, C.A.: Control of translocation by photosynthesis and carbohydrate concentrations of the source leaf.

In: Transport and Transfer Processes in Plants, pp. 329–338, Wardlaw, I.F., Passioura, J.B., eds. New York, San Francisco, London: Academic Press 1976

Cram, W.J.: Negative feedback regulation of transport in cells. The maintenance of turgor, volume and nutrient supply. In: Encyclopedia of Plant Physiology, New Series, vol. 2, Transport in Plants II, Part A, Cells, pp. 284–316, Lüttge, U., Pitman, M.G., eds. Berlin, Heidelberg, New York: Springer 1976

Geiger, D.R.: Phloem loading in source leaves. In: Transport and Transfer Processes in Plants, pp. 167–183, Wardlaw, I.F., Passioura, J.B., eds. New York, San Francisco, London: Academic Press 1976

Giaquinta, R.: Phloem loading of sucrose. pH dependence and selectivity. Plant Physiol. **59**, 750–755 (1977)

Greenway, H., Leahy, M.: Effects of rapidly and slowly permeating osmotica on metabolism. Plant Physiol. **46**, 259–262 (1970)

Habeshaw, D.: Translocation and the control of photosynthesis in sugar beet. Planta **110**, 213–226 (1973)

Hall, S.M., Baker, D.A.: The chemical composition of *Ricinus* phloem exudate. Planta **106**, 131–140 (1972)

Hall, S.M., Baker, D.A., Milburn, J.A.: Phloem transport of ^{14}C-labelled assimilates in *Ricinus*. Planta **100**, 200–207 (1971)

Ho, L.C.: The regulation of carbon transport and the carbon balance of mature tomato leaves. Ann. Bot. **42**, 155–164 (1978)

Hsiao, T.C.: Plant responses to water stress. Annu. Rev. Plant Physiol. **24**, 519–570 (1973)

Huisinga, B.: Control of loading and unloading by turgor regulation in long distance transport. Acta Bot. Neerl. **28**, 67–72 (1979)

Jones, H.G.: Photosynthesis by thin leaf slices in solution. II. Osmotic stress and its effect on photosynthesis. Aust. J. Biol. Sci. **26**, 25–33 (1973)

Kriedemann, P., Beevers, H.: Sugar uptake and translocation in the castor bean seedling. II. Sugar transformations during uptake. Plant Physiol. **42**, 174–180 (1967)

Lang, A.: Interactions between source, path and sink in determining phloem translocation rate. Aust. J. Plant Physiol. **5**, 665–674 (1978)

Lüttge, U., Ball, E., Greenway, H.: Effects of water and turgor potential on malate efflux from leaf slices of *Kalanchoë daigremontiana*. Plant Physiol. **60**, 521–523 (1977)

Milburn, J.A.: Phloem transport in *Ricinus*. Pestic. Sci. **3**, 653–665 (1972)

Milburn, J.A.: Pressure flow. In: Encyclopedia of Plant Physiology, New Series, vol. 1, Transport in Plants I, Phloem Transport, pp. 328–353, Zimmermann, M.H., Milburn, J.A., eds. Berlin, Heidelberg, New York: Springer 1975

Milthorpe, F.L., Moorby, J.: Vascular transport and its significance in plant growth. Annu. Rev. Plant Physiol. **20**, 117–138 (1969)

Moorby, J.: Integration and regulation of translocation within the whole plant. Symp. Soc. Exp. Biol. **31**, 425–454 (1977)

Moorby, J., Munns, R., Walcott, J.: Effect of water deficit on photosynthesis and tuber metabolism in potatoes. Aust. J. Plant Physiol. **2**, 323–333 (1975)

Moorby, J., Troughton, J.H., Currie, B.G.: Investigations of carbon transport in plants. II. The effects of light and darkness and sink activity on translocation. J. Exp. Bot. **25**, 937–944 (1974)

Munns, R., Pearson, C.J.: Effect of water deficit on translocation of carbohydrate in *Solanum tuberosum*. Aust. J. Plant Physiol. **1**, 529–537 (1974)

Peel, A.J.: Investigations with aphid stylets into the physiology of the sieve tube. In: Encyclopedia of Plant Physiology, New Series, vol. 1, Transport in Plants I, Phloem Transport, pp. 171–195, Zimmermann, M.H., Milburn, J.A., eds. Berlin, Heidelberg, New York: Springer 1975

Plaut, Z., Reinhold, L.: The effect of water stress on the movement of [^{14}C]sucrose and of tritiated water within the supply leaf of young bean plants. Aust. J. Biol. Sci. **20**, 297–307 (1967)

Smith, J.A.C., Milburn, J.A.: Osmoregulation and the control of phloem-sap composition in *Ricinus communis* L. Planta **148**, 28–34 (1980a)

Smith, J.A.C., Milburn, J.A.: Phloem transport, solute flux and the kinetics of sap exudation in *Ricinus communis* L. Planta **148**, 35–41 (1980b)

Tammes, P.M.L., Vonk, C.R., van Die, J.: Studies on phloem exudation from *Yucca flaccida* Haw. VI. The formation of exudate-sucrose from supplied hexoses in excised inflorescence parts. Acta Bot. Neerl. **16**, 244–246 (1967)

Troughton, J.H., Currie, B.G., Chang, F.H.: Relations between light level, sucrose concentration, and translocation of carbon 11 in *Zea mays* leaves. Plant Physiol. **59**, 808–820 (1977)

Vickery, R.S., Mercer, F.V.: The uptake of sucrose by bean leaf-tissue. I. The general nature of the uptake. Aust. J. Biol. Sci. **17**, 338–347 (1964)

Wardlaw, I.F.: The effect of water stress on translocation in relation to photosynthesis and growth. II. Effect during leaf development in *Lolium temulentum* L. Aust. J. Biol. Sci. **22**, 1–16 (1969)

Wardlaw, I.F.: Assimilate partitioning: cause and effect. In: Transport and Transfer Processes in Plants, pp. 381–391, Wardlaw, I.F., Passioura, J.B., eds. New York, San Francisco, London: Academic Press 1976

Wardlaw, I.F., Moncur, L.: Source, sink and hormonal control of translocation in wheat. Planta **128**, 93–100 (1976)

Weatherley, P.E.: Preliminary investigations into the uptake of sugars by floating leaf disks. New Phytol. **53**, 204–216 (1954)

Weatherley, P.E., Peel, A.J., Hill, G.P.: The physiology of the sieve tube. Preliminary experiments using aphid mouth parts. J. Exp. Bot. **10**, 1–16 (1959)

Weyers, J.D.B., Hillman, J.R.: Uptake and distribution of abscisic acid in *Commelina* leaf epidermis. Planta **144**, 167–172 (1979)

Ziegler, H.: Biochemical aspects of phloem transport. Symp. Soc. Exp. Biol. **28**, 43–62 (1974)

Zimmermann, M.H.: Transport in the phloem. In: Trees. Structure and Function, pp. 221–279, Zimmermann, M.H., Brown, C.L. New York, Heidelberg, Berlin: Springer 1971

Zimmermann, U.: Physics of turgor- and osmoregulation. Annu. Rev. Plant Physiol. **29**, 121–148 (1978)

Zimmermann, U., Steudle, E.: Physical aspects of water relations of plant cells. Adv. Bot. Res. **6**, 45–117 (1978)

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