Acta Bot. Neerl. 28 (1), February 1979, p. 67–72.

CONTROL OF LOADING AND UNLOADING BY TURGOR REGULATION IN LONG DISTANCE TRANSPORT

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SUMMARY

It is proposed that long distance transport of solutes is controlled by regulation of turgor. Turgor constancy is maintained by import or export of solutes and water from or to the apoplast. This will cause changes in the apoplast pressure which will unbalance waterpotential equilibrium between the apoplast and other cells. Turgor changes are thus caused in these cells which will consequently import or export solutes and water to readjust their turgor.

1. INTRODUCTION

In spite of the fact that in the past much research has been done on the transport of solutes in higher plants, there are distinct gaps in our knowledge of this process. It is still not known for instance, how a sudden increase in growth of a shoot or root tip induces an increase in phloem loading in the leaves (REINHOLD 1974, MOORBY 1977) and why phloem exports solutes preferentially in a sink area. According to Münch's theory a sufficient difference between the high solute concentration of the source end of the phloem (leaves) and the lower concentration of the sink end (the growing points e.g.) will cause a substrate flow to the sink area. In many cases, however, sink areas, e.g. growing points, contain higher solute concentrations than the conveying sieve tubes or source cells. An adequate explanation of the solute extraction from the phloem by the sink cells is still missing. The same holds true for the local extraction of solutes from the phloem of the host plant by parasites like *Cuscuta* (WOLSWINKEL 1978).

In fact a mechanism explaining the regulation of the loading and unloading of cells in source and sink regions is not yet recognized. In the following we propose that this regulation is effected by changes in the turgor pressure. No suggestions are given about how changes in turgor pressure are perceived, nor about the intracellular regulation of the reaction of the cell. Once the phloem is loaded in the source region and unloaded in the sink region Münch's theory or any other theory applies.

2. THEORY

Different tissues of plants kept in a constant environment show differences in osmotic value and turgor. Although transport of solutes occurs, these values generally remain stable. This can only be envisaged if some kind of regulating mechanism is operative.

For a regulating mechanism to work it is necessary that a certain 'quantity' in the cells is perceived (measured) and kept constant within a moderate range of fluctuations. In the mechanism proposed here, this quantity is the value of the turgor i.e. the pressure of the plasmalemma against the cell wall, or the deformation of the plasmalemma caused thereby. If the turgor is regulated and thus kept relatively constant, some other value or values must change when there is a change in the cell environment. Experimental data indicate that such changes occur in the osmotic values of the cells. The osmotic value increases after an increase in the transpiration of plants or after a decrease of water potential of the soil; this can be shown quite clearly in the case of water-stressed plants and plants in saline environments (WAISEL 1972, ROZEMA 1975, HSIAO 1973, HSIAO and ACEVEDO 1974).

At the top of large trees where the hydrostatic pressure is decreased by gravity, the osmotic value in the leaves is higher than in leaves lower down on the tree and the osmotic value is proportional to the height of the tree (SCHOLANDER et al. 1965).

In general the environment of the plant cell is the solution in the apoplast. Changes in the pressure or osmotic value of this solution will, if the turgor is to be kept constant, cause a change in the osmotic value of the cells. These changes can be caused in the cell either by reactions that polymerise or depolymerise material or by import or export of osmotic material from or into the apoplast. The first possibility has been shown to occur by HILLER & GREENWAY 1968, and GILES et al. 1976. THIMANN (1977) proposed the term manostasis for these processes. The second possibility also occurs.

In the past years much research has been done on turgor pressure dependent changes in ion fluxes and membrane properties, which has been reviewed and discussed by ZIMMERMANN (1977). This research has been done predominantly on giant algal cells and bladder cells of *Mesembryanthemum*. Data on fluxes of organic matter, however, are scarce. It is clear, however, that changes in turgor can influence fluxes through the cell membranes in such a way that a certain turgor constancy results. Of the two possibilities mentioned, import-export processes may be the most important, as reactions to the perceived turgor changes, since these processes make it possible to envisage a mechanism that regulated the transport of solutes.

3. THE PROPOSED MECHANISM

The proposed mechanism may be visualized by considering a pair of neighbouring cells with their apoplast and turgor *(fig. 1a)*. These cells will export osmotic material if their turgor exceeds the value that is physiologically intrinsic for them. If their turgor value falls below this value, they will import osmotic material from the apoplast. Let the total volume of this pair of cells, including the apoplast, remain unchanged during the processes that will be described. Now the left cell of the pair polymerises part of its osmotic material, rendering it insoluble. (The osmotic term of ψ is decreased.) The water potential (ψ) of the cell increases.

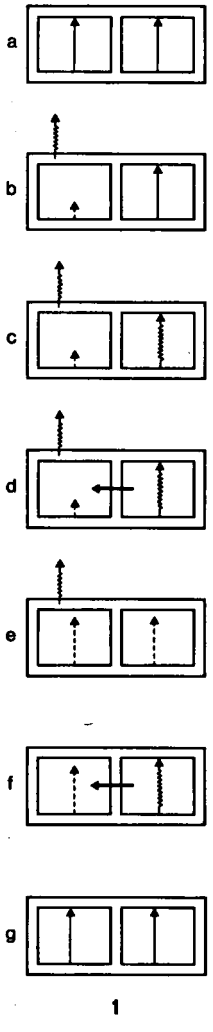

Fig. 1. Pressure changes in two adjoining cells.
The vertical arrows indicate pressure.
——→ means 'normal';
- - - → means 'subnormal';
∿∿→ means 'supranormal' pressure.
The horizontal arrow means solute transport.

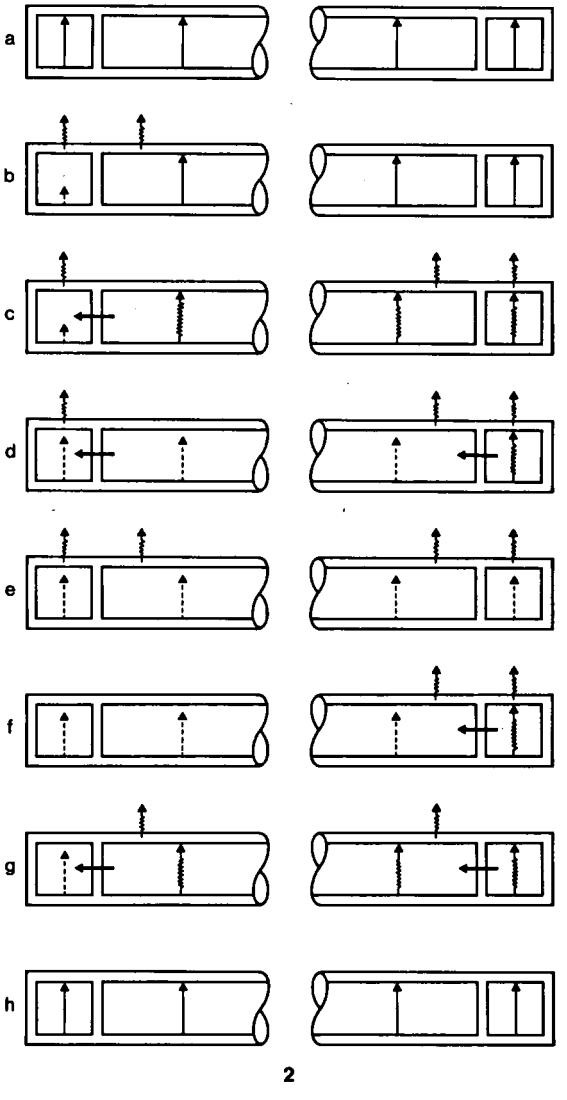

Fig. 2. Three cells, the middle one being very long. The left cell can be regarded as a sink cell, the right one as a source cell. The middle one may be regarded as a sieve tube.

Consequently water will leave the cell causing the pressure in the apoplast to increase (*fig. 1b*). (The ψ of the apoplast is raised by the increase of its hydrostatic pressure term. N.B. this pressure is not to be confused with the cell wall pressure.) The turgor of the cell is thus decreased below its intrinsic value. Now the right cell is not in equilibrium with the solution in the apoplast. As the ψ of the apoplast is higher than that of the right cell, water will enter this cell. So its turgor is raised above its intrinsic value (*fig. 1c*). The cell will export osmotic material. The left cell, its turgor being below the intrinsic value, will import this material (*fig. 1d*). By doing this it lowers its ψ, and water will enter this cell. In the end the turgor of the two cells will be equal (*fig. 1e*). It will be lower than in the initial situation and the pressure in the apoplast remains higher, because osmotic material has been removed from the systems by polymerisation. Now if the right cell produces as much osmotic material as was lost in the left cell between a en b, water will enter this cell raising its turgor and lowering the hydrostatic pressure in the apoplast (*fig. 1f*). Consequently osmotic material is again exported which is taken up by the left cell. The turgor of the two cells will in the end be equal and the same as in the initial situation. The pressure in the apoplast also will be as in the initial situation (*fig. 1g*). In the processes described the right cell has functioned as a source, the left cell as a sink. If no system as the one described above existed the cells would in the final situation remain unequal. Either they would have different turgor values or different volumes or both.

In the mechanism proposed the quantity regulated is the turgor. The signals to which cells react are pressures. The physiologically 'normal' turgor of the two cells can be different as can their osmotic values. In the series given in *fig. 1* the osmotic value of the left cell and its turgor can be higher than that of the right cell. The osmotic material will still be transported from the right cell to the left one.

4. APPLICATION TO PHLOEM TRANSPORT

The expansion of the schemes to three cells in a row will not cause fundamental changes in the processes mentioned above. It will be more interesting if we take a row of three cells, of which the middle one is very long (*fig. 2*). This cell is thus comparable to a sieve tube, the left cell to a cell in a sink area and the right cell to a cell in a source tissue. The scheme is essentially the same as the one shown in *figure 1*.

a. Is the initial stage. All turgors are 'normal'. Then the sink cell polymerises sugars.
b. Shows that the turgor in the left cell has dropped; the apoplast pressure is increased.
c. As a consequence turgor rises in the sieve tube and in the source cell. The sieve tube unloads osmotic material and water, which are taken up only by the sink cell.
d. The turgor in the sieve tube falls and the source exports to the sieve tube.
e. The turgor is lowered equally in all cells. Apoplast pressure remains high (as a consequence of the loss of osmotic material).

f. In the source cell the same amount of sugar is produced as was polymerised in a. The turgor of the source cell increases. Export to the sieve tube follows.
g. Turgor in the sieve tube is raised. The sink cell imports the solutes exported by the sieve tube.

The initial situation, as shown under a, is re-established. This system is essentially a regulation system, based on feedback processes. In this concept in a really steady state no transport will occur.

The system requires the transition of the solute through the apoplasm. Within a continuous symplast such a system could not function, so loading and unloading of the phloem would need an apoplasmatic transition (MOORBY 1977).

The signal from the location where a change takes place to the location where a reaction occurs is a pressure. In a slightly elastic system a small amount of translocated water can cause a large difference in pressure over a long distance.

The system depends on the metabolic activity of the sink. Translocation will stop when sink activity ceases (WALKER & HO 1976, 1977 a and b).

If after an oscillation of the value of the pressure in a long sieve tube the final situation is such that the osmotic value in the source end of the tube remains higher than in the sink end, then equilibrium will be attained by Münch streaming. For in this case the turgor in the sink end is the same as in the source end but the osmotic value is lower. If the turgor value of the sink cells is high, the sieve tube can export water only to the apoplast. This water will flow back through the apoplast and eventually to the xylem.

The sieve tube will exchange solutes over its whole length. In this way reserves in the stem may also be mobilised by an active sink. A sink will take up solutes from all sources available but, due to dissipation of pressure, mostly from the sources with which it is directly connected by a phloem bundle (MOORBY 1977).

If growth occurs in the sink end, the water transported by Münch streaming will remain in the sink area. In the source and everywhere between source and sink tissue it will be replenished from the xylem. Without transpiration a sink area will receive at least the major part of its water from the phloem only. Therefore, substances present in the transpiration stream that are exchanged very fast between apoplast and symplast i.e. between xylem and phloem, will reach the sink areas very quickly. Substances that hardly penetrate the protoplasm will hardly be transported by the phloem e.g. Ca-ions (VAN DIE 1974, 1975, WILLIAMS 1955). Growing organs that cannot transpire sufficiently tend to develop Ca-deficiencies (SKELTON & SHEAR 1971, MOORBY 1977). Differences in water balance may thus cause differences in the composition of plant parts that have developed in dry or in moist environments (BORNKAMM 1975). In the xylem differences in sap concentrations are likely to be caused by turgor regulated processes.

If the pressure in the xylem is raised suddenly, and thereby the pressure in the apoplast around nearby living cells, these cells will export osmotic material in order to maintain an unchanged turgor. Consequently the osmotic value of the xylem sap will rise. Examples of such phenomena can be found in publications by LOPUSHINSKY (1964) and HUBER (1956).

A parasite like *Cuscuta* (WOLSWINKEL 1978) which has a very small evaporating surface may cause a local rise in apoplastic pressure in the place where a haustorium has penetrated its host. This would cause the sieve tubes of the host to export solutes which can be absorbed by the parasite and also by the parenchyma of the host in the vicinity of the haustorium.

REFERENCES

BORNKAMM, R. (1975): Water and the production of organic matter. *Ber. Dtsch. Bot. Ges.* **88**: 197–203.

DIE, J. VAN (1974): The developing fruits of Cocos nucifera and Phoenix dactylifera as physiological sinks importing and assimilating the mobile aqueous phase of the sieve tube system. *Acta Bot. Neerl.* **23**: 521–540.

—(1975): The use of phloem exudates from several representatives of the Agavaceae and Palmae in the study of translocation of assimilates. In: *Phloem Transport.* (S. ARONOFF, J. DAINTY, P. R. GORHAM, L. M. SRIVASTAVA & C. A. SWANSON, eds.), pp. 427–446. Plenum Press, New York and London.

GILES, K. L., D. COHEN & M. F. BREARDSELL (1976): Effects of water stress on the ultrastructure of leaf cells of Sorghum bicolor. *Plant Physiol.* **57**: 11–14.

HILLER, R. G. & H. GREENWAY (1968): Effects of low water potentials on some aspects of carbohydrate metabolism in Chlorella pyrenoidosa. *Planta (Berl.)* **78**:49–59.

HSIAO, T. C. (1973): Plant responses to waterstress. *Ann. Rev. Plant Physiol.* **24**: 519–570.

— & E. ACEVEDO (1974): Plant responses to water deficits, water use efficiency and drought resistance. *Agric Meteorol.* **14**: 59–84.

HUBER, B. (1956): Die Gefässleitung. In: *Handb. Pflanzenphysiol. (W. RUHLAND, ed.).* **3**: 541–582. Springer, Berlin etc.

LOPUSHINSKY, W. (1964): Calcium transport in tomato roots. *Nature* **201**: 518–519.

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

REINHOLD, L. (1974): The effect of externally applied factors on the translocation of sugars in the phloem. In: *Phloem Transport.* (S. ARONOFF, J. DAINTY, P. R. GORHAM, L. M. SRIVASTAVA & C. A. SWANSON, eds.), pp. 367–388. Plenum Press, New York and London.

ROZEMA, J. (1975): An eco-physiological investigation into the salt tolerance of Glaux maritima L. *Acta Bot. Neerl.* **24**: 407–416.

SCHOLANDER, P. F., H. T. HAMMEL, E. D. BRADSTREET & E. A. HEMMINGSEN (1965): Sap pressure in vascular plants. *Science* **148**: 339–346.

SKELTON, R. C. & G. M. SHEAR (1971): Calcium translocation in the peanut. *Agron. J.* **63**: 409–412.

THIMANN, K. V. (1977): *Hormone action in the whole life of plants.* Univ. of Massachusetts Press, Amherst.

WAISEL, Y. (1972): *Biology of halophytes.* Academic Press, New York and London.

WALKER, A. J. & L. C. HO (1976): Young tomato fruits induced to export carbon by cooling. *Nature* **261**: 410–411.

—& —(1977a): Carbon translocation in the tomato: carbon import and fruit growth. *Ann. Bot.* **41**: 813–823.

— & — (1977b): Carbon translocation in the tomato; Effects of fruit temperature on carbon metabolism and the rate of translocation. *Ann, Bot.* **41**: 825–832.

WILLIAMS, R. F. (1955): Redistribution of mineral elements during development. *Ann. Rev. Plant Physiol.* **6**: 25–42.

WOLSWINKEL, P. (1978): Phloem unloading in stem parts parasitized by Cuscuta: The release of ^{14}C and K^+ to the free space at 0°C and 25°C. *Physiol. Plant.* **42**: 167–172.

ZIMMERMAN, U. (1977): Cell turgor pressure regulation and turgor pressure-mediated transport processes. *Symp. Soc. Exp. Biol.* **31**: 117–154.