CENTRUM VOOR AGROBIOLOGISCH ONDERZOEK

Verslagen
nr. 17, 1978

PHLOEM-LOADING VERSUS UNLOADING, WITH REFERENCE TO WHITE LEAVES AND FLOWER LEAVES

by

P.M.L. Tammes

Contents page

Introduction

The physiology of phloem-loading and unloading was treated by Geiger (1975) to whom can be referred for details.

Phloem-loading and unloading are different processes

When a sink stalk of a young Yucca inflorescence is detached, it immediately changes from a sink to a source and produces phloem exudate for a considerable period (Van Die and Tammes 1966). One could suppose that it is a reversible process. When the pressure in the sieve tubes is lowered by detachment, the sink becomes a source.

There is, however, a strong argument that the two are different processes. The reaction on cooling to zero is different. Loading stops at zero Celsius e.g. in Yucca (Tammes et al. 1969). Though longitudinal flow is not inhibited in Yucca.

In short-term experiments on chilling ~~of~~ resistant sugar-beet sink leaves, Geiger (1966, 1975) observed the following at zero cooling: after an adjustion period of 60-90 minutes unloading fell to 40-60% of the control and not to zero as was in loading of Yucca.

In long-term experiments with sinks, however, the sink tissues are not able to grow and cannot take up the unloaded photosynthates. In such experiments, therefore, unloading nearly stops (Wardlaw 1974). In tips of young Yucca stalks which were zero-cooled in an intact state and with a $^{14}CO_2$ label on a leaf of the plant, the cooled tips had roughly 1% of the activity of the controls after 2 and 3 days (Tammes unpublished).

When loading and unloading are both present in the same tissue, the one that prevails will determine whether a source or a sink is present. Along the translocation path the two can be supposed to be in balance, unless some factor is changed. Köcher and Leonard (1971) observed that after detachment of Phaseolus leaves a new sink developed in the petiole; thus along the translocation path, the export of both detached and control leaves was the same.

Recently Giaquinta (1978) observed with sugar-beet leaves that import-export transition took place at 40-50% of leaf expansion. He found that in the export situation the enzyme sucrose-phosphate-synthetase was present. His data indicate two intracellular sucrose pools. One accumulated for export from the mesophyll into the apoplast for phloem-loading, the other the non-transport pool, which however, can enter the transport pool on demand for exported assimilates. Sugars in the non-transport pool are incorporated in proteins and structural carbohydrates.

Stopping of unloading in leaves

Leonard (1939) observed that sugars moved out of darkened mature sugar-beet leaves until the leaves were depleted of sugars (9 days). So no unloading in the empty leaves occurred, or the leaf tissue refused to take up sugar from the phloem.

On some variegated trees, e.g. Acer negundo, short branches of white leaves without chlorophyll occur. Aesculus sometimes bears short branches with pure whiteleaves and some variegated ones.
During their formation, they are phloem-fed, as Weevers (1923) found by bark-ringing experiments. Leaves, developed after bark-ringing, abort. White leaves soon die. Weevers (1923) observed that the white leaves of Aesculus could be plasmolysed in 10% sucrose; normal green leaves could not. After their formation, a second flush especially of Aesculus at the end of June meets the same fate and in August most pure white leaves are either dead or shed. This indicates that by lack of chlorophyll they cannot provide their own nutrition and when, after formation, provision stops, they die from senescence, induced by starvation of photosynthates. It is different from senescence of leaves at the end of the growing season.

It remains to be understood why the white areas on green variegated leaves stay alive during the whole growing season. When, for instance, a half-white half-green Aesculus leaflet ages, the white half dies. A variegated hawthorn with white patches on its leaves showed dead centres of these white patches when they were large. The white areas, especially in Acer are fed by the green ones on the same leaf. With a variegated Pelargonium leaf with a white margin around a green centre, Jones and Eagles (1962) observed that after exposure to $[^{14}CO_2]$ and 5 hours in light, activity had spread from the green centre to the white margin.

That organic substances can spread through leaf tissue, irrespective of veins, is illustrated in an autoradiograph by Mothes published by Sutcliffe (1976, p. 411, Fig. 10.9 a). A circular black spot of $[^{14}C]$ glycine is surrounded by a rather diffuse ring of translocation in the tissue. When white parts can take up food from green parts, the stopping of import is probably due to a stop in phloem-unloading.

There are exceptions where unloading is not stopped in mature leaves. White leaves on a variegated Hedera, in the authors glasshouse lasted a whole season and in a low Euonymus with variegated leaves and white leaves on white twigs, the white leaves also kept well for the whole season. Experimenting with detached sugar-cane leaves with a $^{14}CO_2$ label on the base in light, Hartt (1965) observed that darkened tips became active, thus a source reverted to a sink. In Zebrina, the white strips on the leaves can be fed by bundles coming from the stem (Crafts and Crisp 1971, Fig. 6.2).

The role of hormones in regulating distribution of assimilates within the plant is still far from clear. In an extensive review, Phillips (1975) discussed the significance of the role of hormone-directed transport of metabolites, including hormones themselves. Although Quinlan and Weaver (1969) found that benzyladenine can reverse the assimilation stream from grapevine leaves from export to import, and Sutcliffe (1976) showed that kinetin regulates transport in leaf-tissue (p. 411, Fig. 10.9 c. even from one half to the other), it is more generally accepted that auxins, particularly indoleacetic acid, are primarily involved in regulation of long-distance movement of assimilates. Recently the suggestion was made (Wareing, 1978) that auxins are involved in phloem unloading near the region of a sink.

Flowers

Leaves without chlorophyll in petals or perianth flowers cannot make their own photosynthates and must depend on import, thus unloading, at least during development. Vonk (unpublished) fed detached Iris stems with flowers on $[^{14}C]$ sucrose in successive stages of development. He observed that after a certain stage, the flower tissue showed no label. In autoradiograms the tissue was white, though some fine lines were visible at the sites of vascular bundles. In monocotyledons the vascular bundles have adjacent xylem and phloem. Sugars introduced to the xylem are taken up by the phloem (Tammes et al. 1973 for Yucca). As flowers transpire, xylem transport will continue in all phases. When no label is found in the flower leaves, it must have disappeared from the xylem. Xylem transport can be proved by using a dye that is not readily taken up by the phloem, e.g. a 1% solution of acid fuchsin in water.

There seems to be some parallel between the white leaves on variegated plants and flowers. When unloading stops, as in Vonks experiments, they die of starvation.

Remarkable is that green calyx leaves containing chlorophyll, often persist long on the plant, e.g. strawberries. Dahlia viridiflora with green leaves in its flowerheads can keep from summer to November, till the plants are cut down (Witte 1883). In tulips, it sometimes happens that one of the perianth leaves is green and looks more like a stemleaf and it then stays on the flower for a considerable time.

Nichols and Ho (1975) after feeding $[^{14}C]$ sucrose to petals of carnation, found an export to other flower parts, which was enhanced by ethylene. In a review of research on mineral transport in flowers, Fischer (1967) states that mobile minerals are transported from flower-leaves at a certain stage (through the phloem), as in senescent common leaves. It is, however, quite possible that senescence is induced by starvation and the question must be asked which comes first. Schumacher (1967) speaks of a reversal of transport in flower-leaves for carbohydrates and minerals at a certain stage of development, thus a turning point.

Nichols (1973) determined the sugar content of carnation petals on successive days. For flowers in water, there was indeed a decrease, as expected. But in a sugar solution, an increase in glucose and sucrose was observed. Though the flowers keep much longer on sugar, they ultimately wilt notwithstanding the high sugar concentration in their petals. This indicates that another form of senescence may occur. Here there is possibly a difference from white leaves of variegated plants, though one does not know where sugar is accumulated. Benzyl-adenine (BA) applied after cutting to stems with leaves of carnations, can prolong vase life by 3-5 days, irrespective of whether they were in water or sugar solution (Heide and Ødvin 1969).

It seems that dying or shedding of white leaves on variegated plants is a matter of senescence induced by starvation. They cannot produce their own photosynthates, and, at a stage when unloading stops, they starve. It is thus not a matter of senescence as in leaves at the end of the growing season.

For flowers, it is probable that starvation and possibly another form of senescence both occur. Maybe the formation of ethylene plays a role.

Conclusions

It is argued that phloem loading and unloading are separate processes that can occur together concurrently in a tissue. The one that prevails determines whether a source or sink is present. Along the translocation path, a situation of balance can be supposed. In leaves, the unloading can come to a stop, or import into the tissue fails. In leaves without chlorophyll, this leads to early senescence and death by starvation, due to the absence of photosynthates. It is different from senescence in autumn. A parallel is drawn with petals or perianths, without chlorophyll, in flowers.

Acknowledgements

The author is indebted for suggestions and reading through the script to the following gentlemen: Professor Dr. W. Eschrich, Dr. H.C.M. de Stigter, Dr. H. Veen and Mr. C.R. Vonk.
Mr. J.C. Rigg is thanked for correction of the English.

References

Crafts, A.S. & C.E. Crisp (1971): Phloem transport in plants. Freeman, San Francisco.

Fischer, H. (1967). Der Mineralstofftransport. In Ruhland, W.: Handbuch der Pflanzenphysiologie, Bd. XIII. Springer, Berlin.

Geiger, D.R. (1966): Effect of sink cooling on translocation of photosynthate. Plant Physiol. 41, 1667-1672.

Geiger, D.R. (1975): In Zimmerman, M.H. and J.A. Milburn: Encyclopedia of plant physiology N.S. Vol. 1. Springer Berlin.

Giaquinta, R. (1978): Source and sink metabolism in relation to phloem-translocation, carbon partitioning and enzymology. Plant Physiol. 61, 380-385.

Hartt, C.E. (1965): Light and translocation of ^{14}C in detached blades of sugar-cane. Plant Physiol. 40, 718-724.

Heide, O.M. & J. Ødvin (1969): Effects of 6-Benzylamino-purine on the keeping quality and respiration of glasshouse carnations. Hort. Res. 9, 26-36.

Jones, H. & J.E. Eagles (1962): Translocation of ^{14}carbon within and between leaves. Ann. Bot. N.S. 26, 505-509.

Köcher, H. & A.O. Leonard (1971): Translocation and metabolic conversion of ^{14}C labeled assimilates in detached and attached leaves of Phaseolus vulgaris L. in different phases of leaf expansion. Plant Physiol. 47, 212-216.

Leonard, O.A. (1939): Translocation of carbohydrates in the sugarbeet. Plant Physiol. 14, 55-74.

Nichols, R. (1973): Senescence of the cut carnation flower: respiration and sugar status. J. hort. Sci. 48, 111-121.

Nichols, R. & L.C. Ho (1975): An effect of ethylene on the distribution of ^{14}C-sucrose from the petals to other flower parts in cut inflorescence of Dianthus caryoplullus. Ann. Bot. 39, 433-438.

Phillips, I.D.J. (1975): Apical dominance. Ann. Rev. Plant Physiol. 26, 341-367.

Quinlan, J.D. & R.J. Weaver (1969): Influence of benzyl adenine, leaf darkening and ringing on the movement of ^{14}C labeled assimilates into expanded leaves of Vitis vinifera L. Plant Physiol. 44, 1247-1252.

Schumacher, W. (1967): Die Fernleitung der Stoffe im Pflanzenkorper. In Ruhland, W.: Handbuch der Pflanzenphysiologie Bd XIII, Springer Verlag.

Sutcliffe, J.F. (1976): In Lutge, U. & M.G. Pitman, M.G. Encyclopedia of plant physiology N.S. Vol IIB Springer, Berlin.

Tammes, P.M.L., C.R. Vonk & J. van Die (1969): Studies on phloem exudation from Yucca flaccida Haw. VII. The effect of cooling on exudation. Acta Bot. Neerl. 18, 224-229.

Tammes, P.M.L., C.R. Vonk & J. van Die (1973): Studies on phloem exudation from Yucca flaccida Haw. XL. Xylem feeding of ^{14}C sugars and some other compounds their conversion and recovery from the phloem exudate. Acta Bot. Neerl. 22, 223-237.

Van Die, J. & P.M.L. Tammes (1966): Studies on phloem exudation from Yucca flaccida Haw. III Prolonged bleeding from isolated parts of the young inflorescence. Proc. Kon. Ned. Akad. Wetenschappen C69, 648-654.

Wareing, P.F. (1978): Hormonal regulation of assimilate movement. In: BCPC/BPRGRG Symposium on Opportunities for Chemical plant growth regulation. Univ. of Reading, in press.

Wardlaw, I.F. (1974): Temperature control of translocation. In Bieleski, R.J., A.B. Ferguson & M.M. Cresswell, eds. Bull. 12 Roy. Soc. New Zealand: Mechanisms of regulation of plant growth, 533-538.

Weevers, T. (1923): Ringwondproeven bij bonte takken. Kon. Ned. Akad. Wetenschappen. Versl. Verg. Wis- en Natuurkunde 32, 700-707.

Witte, H. (1883): Floralia. Handleiding voor de kennis en het kweken van lievelingsbloemen, XVII-XVIII, De dahlia. Stelburg, 's-Gravenhage.