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## TRANSLOCATION IN TREES<sup>1</sup>

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In this discussion we shall use the term "translocation" to refer to the movement or transport of water and solutes over distances of considerable magnitude relative to the size of the plant. In the larger trees, this distance may be enormous even in absolute terms, several hundreds of feet, and in the case of certain tropical lianas, closer to a thousand feet.

We are much indebted to forest physiologists for many significant advances in this study. Because of the large size *per se* of trees, they provide excellent material for the investigation of many specific problems in translocation, and it is clearly evident from the literature that some of the most critical data we have on this subject have been obtained from such species.

Translocation may be conveniently considered under three subdivisions: the translocation (1) of water, (2) of mineral solutes, and (3) of organic solutes. The broad scope of this subject and the limitations of time will permit only a very cursory survey of these areas of research.

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## WATER TRANSLOCATION

The problem of the ascent of water in trees is one of the oldest in plant physiology. Interest in this problem reached a climax just prior to the turn of the century with the publication in 1894 of the Dixon-Joly water cohesion-transpirational pull or liquid tension theory. With minor modifications, this theory has been universally accepted for presentation in standard text-books of botany and plant physiology, and the general outlines of this concept are, therefore, well known. This theory provided such a plausible mechanism for the translocation of water that the problem was considered quite satisfactorily solved, and interest in the actual process of water conduction diminished in subsequent years. In rather recent years, however, a number of papers highly critical of the cohesion theory have been published, and it appears now that interest in the problem is gradually being renewed. The present status of the problem has been reviewed recently by Greenidge (1957).

One of the major points of controversy is the tensile strength of water under the actual conditions which obtain during the flow of water through the tracheids and vessels of the xylem. Published values for the cohesive strength of water, arrived at by a variety of techniques and under a variety of conditions, range from only 0.05 atm. to the extremely high values of the order of 15,000 atm. It is commonly accepted that a minimal tensile strength of 20 to 30 atm is required to lift water to the tops of the tallest trees; a critical experiment, therefore, would be to demonstrate conclusively that the tensile strength of water in the conducting elements of the xylem is significantly less than this value.

One technique for determining the limiting negative pressure or tensile strength of water is to measure the force in a centrifugal field required to break a column of water held in a glass capillary. Under rigorously defined conditions, the limiting negative pressure as determined by this method is of the order of 200 atm. at room temperatures, but falls off rapidly at temperatures below 5°C to values of about 20 atm. near 0°C (Briggs, 1950). Thus, it would appear that during the winter season, the tensile strength of the sap is at or near the critical value which permits cavitation, even if the values obtained for water under ideal conditions are adopted. Recently, Scholander *et. al.* (1955) attempted to measure the limiting negative pressure of xylem sap in sections of grape vine stems, using a centrifugation technique. Even though the water columns were under static conditions (non-moving), practically all vessels were found to cavitate under stresses as low as 1 to 1.5 atm. Although the limitations of the centrifugation technique as applied to stem sections must be assessed before these values can be critically accepted, the results of the experiments by Scholander *et. al.* presently indicate disturbingly low values.

Further observations critical of the cohesion mechanism have been provided by the *double saw-cut* technique, a procedure utilized most extensively by Greenidge (1955). Using forest grown trees, Greenidge interrupted all of the vessels in the trunks by making overlapping saw-cuts from opposite sides of the bole slightly more than half way through the tree, the vertical distance separating the cuts being less than the average length of the vessel member or segment of the species under consideration. Presumably, therefore, the liquid columns in all vessels were exposed to atmospheric pressure. Despite these drastic treatments, dye solutions injected into the tree trunks below the lower saw-cut moved rapidly into the terminal branches of the crown. It is difficult, of course, to reconcile these results with the classical concept of the Dixon-Joly mechanism. Although an indeterminate fraction of the water, in Greenidge's experiments, undoubtedly circumvented the incisions by lateral movement through the tracheids, evidence was also obtained, based on staining patterns, that mechanical interruption of the water columns did not lead to wholesale evacuation of the vessel contents, as required by classical theory if the columns were under tension. Rather, the evidence

pointed to only a slight retraction of the menisci at the cut surfaces, a phenomenon which, if correctly inferred, is most difficult to explain. A more plausible interpretation, however, may be that the vessel walls were stained by absorption of dye from the water moving through tracheids contiguous to the vessels.

Various other disturbing observations have been reported, and it is not clear in all cases by what criteria they can be dismissed, unless it be, as has been remarked by others, that equally great or greater difficulties will then be encountered. Although the Dixon-Joly liquid-tension concept continues to be our best explanation, it is evident that one of the more quiescent problems in plant physiology has been considerably reactivated in recent years by continuing work and interest in tree physiology.

#### MINERAL SOLUTE TRANSLOCATION

An extensive literature is available on the subject of mineral solute translocation, based mainly on agronomic crop plants and other herbaceous type plants, but significant contributions to this area of research have also been made using arborescent species. The specific subject of mineral translocation in trees has been recently reviewed by Fraser (1956).

The relative roles of the xylem and phloem in the upward translocation of minerals has been much debated in the literature. The general consensus appears to be that the initial upward transport of the minerals from the roots to the leaves occurs predominantly in the xylem, with subsequent re-translocation in the phloem. This view has been arrived at mostly from studies on herbaceous plants. Recently, however, Fraser (1956), noting the intense localization of  $\text{Ca}^{45}$  in the sieve cells of white pine trees which had been injected with this isotope near the base of the trunk, has suggested that, in trees, the phloem tissue may be more important than the xylem in upward transport of mineral salts. It cannot be ruled out, however, from Fraser's studies that this distribution pattern did not result simply from lateral accumulation of calcium ions from the xylem. As a matter of fact, most studies reveal that calcium compounds are singularly immobile in the phloem (see review by Gauch, 1957). Fraser's view, however, conforms with that of MacDaniels and Curtis (1930). When apple trees were spirally ringed, it was noted that nitrogen from the roots moved principally to the branches above the open end of the spiral, whereas branches on the opposite side of the tree received relatively little nitrogen. Although the tracheary sap of apple trees contains moderate concentrations of nitrogenous compounds throughout the growing season (Bollard, 1953), it seems apparent that the amount of nitrogen compounds transported by way of the phloem from the roots in the experiments of MacDaniels and Curtis was sufficiently greater than that transported in the xylem to control the major distribution pattern of this element in the crown. It is evident that further work must be carried out on this problem before the relative efficiency of the phloem and xylem in upward mineral transport can be quantized with greater accuracy than is now possible. The weight of the evidence from most species studied still strongly favors the classical view of the xylem as the predominant pathway of transport, although a number of apparently contradictory observations remain to be reconciled on this basis.

As previously remarked, calcium is considered one of the phloem-immobile elements. Presumably for this reason, re-translocation of calcium in plants, after its initial movement from the roots to the leaves or other depots, is negligible, inasmuch as the export of minerals in general (perhaps mostly as metal-organic complexes) from the leaves is apparently phloem-limited for the most part. This view has been gained, however, from studies on annuals, and recently Ferrell and Johnson (1956) have reported results which indicate considerable calcium mobility in trees (western white pines). Buds which were produced one and even two years after the time of injection of  $\text{Ca}^{45}$  were found to have appreciable concentrations

of the labeled calcium (corrected for radioisotopic decay). It is possible that this indicated mobility is only apparent, resulting from a leaching of the calcium from the leaves by rain, and subsequent re-entry into the tree from the soil. It is known that calcium and other mineral ions are readily leached from leaves (Tamm, 1951; Long *et al.*, 1956) but the decline each year in the specific activity of the calcium in the buds, in most trees studied, was relatively small, and this fact favors the view that the calcium was redistributed directly from deposition sites in the tissues of the previous year to the new tissues, but whether this re-translocation was effected mainly by way of the phloem or the xylem is not known.

#### ORGANIC SOLUTE TRANSLOCATION

The translocation of organic solutes from one part of a plant to another is a process of considerable magnitude, greater than that of mineral solute translocation, and second, in quantitative terms only to water translocation. An apple orchard, for example, will, under very favorable growing conditions, produce in excess of 60,000 pounds of fruit per acre, containing approximately 4 to 4.5 tons of organic substances. Only a small fraction of this organic increment is the result of photosynthesis in the fruit itself; the much greater fraction is derived from compounds translocated to it from the leaves. Although it may be objected that these large values derive from the acreage basis used in these calculations, the process may be of very sizeable magnitude even at the individual fruit level. In the Zucca melon, for example, a single fruit may attain a dry weight of five pounds. Assuming an average molar weight of 300 grams for the translocatory compounds (on the basis that the translocate is mostly sucrose), and disregarding various second order corrections, approximately  $4.5 \times 10^{24}$  molecules of the organic translocate would have to move into such a fruit to account for the dry weight increase. This number of molecules, if sucrose, placed end to end, would extend a distance of 2.5 trillion miles. It should not be construed, of course, that the molecules are translocated single file; the computation merely serves to emphasize the enormity of the number.

An elegant approach to the problem of organic translocation in trees has been the chromatographic analysis of the sieve tube exudate. A considerable number of such studies have now been made by various investigators (Kennedy and Mittler, 1953; Wanner, 1953; Ziegler, 1956; Zimmermann, 1957a, b, c). The technique is limited, of course, to such species which yield an exudate when the sieve tubes are tapped, but it is possible that utilization of Kennedy and Mittler's aphid technique (1953) may considerably extend the number of species which can be studied. The results of these studies may be briefly summarized as follows. Sucrose was found to be present in the sieve tube exudate of all species thus far studied (about 25), and was the only sugar present in about a third of these species. In the remaining species, raffinose was also found, and in a few species, stachyose and perhaps verbascose, as well. These sugars form a series of oligosaccharides differing from each other in the number of included galactose residues (sucrose none, raffinose one, stachyose two, etc.). During transit within the sieve tubes, these sugars may undergo at least a limited amount of interconversion, for example, stachyose to raffinose to sucrose, although no positive test has yet been obtained for galactose, which would also be produced in these reactions (Zimmermann, 1957a). It is also noteworthy that neither glucose nor fructose has been found in any of the sieve tube exudates thus far tested. These data suggest that hexose sugars do not function in translocation.

A similar conclusion with respect to the translocation of sugars in the Concord grape was reached by Swanson (1957) and Swanson and El Shishiny (1957) based on radiochemical studies using C-14. The carbon label was introduced by supplying  $C^{14}O_2$  to a single leaf on the cane under conditions favorable for photosynthesis. In sugar fractions isolated from the stem (bark) at various distances from

the supply leaf, the highest percentage recovery of C-14 was found to be in sucrose. Appreciable quantities of C-14 labeled glucose and fructose were also found in the bark, but these sugars appeared to be simply hydrolytic products of translocatory sucrose, as inferred from the fact that the ratio of C-14 glucose to C-14 fructose approximated unity. Evidently sucrose molecules which escape from the sieve tubes are readily hydrolyzed to invert sugars in other cells of the phloem and adjacent tissues. The present indications are, therefore, that sucrose is a specific sugar of transport, at least in certain species.

The amino acid content of sieve tube exudates has not been as critically studied as has the carbohydrate content, primarily because of the negligible quantity of this fraction in the exudate. In the sieve tube exudate of white ash, for example, the total amino acid content was usually less than 0.001 M, as contrasted with 0.3 to 0.4 M and higher for the total sugars (Zimmermann, 1957b, c). It thus appears that the types of compounds which are transported over relatively great distances in the phloem in *calorically significant* quantities are quite few in number, being predominantly sugars of the raffinose family, and perhaps in some species, specifically and exclusively sucrose. In this connection it should be noted that fruit culture studies have shown that excised tomato and gherkin ovaries (ovaries) can grow *in vitro* and form fruits which may occasionally even produce viable seeds on a culture medium containing only sucrose, mineral salts, and water (Leopold *et al.*, 1952; Nitsch, 1951). Recently Erickson (1957) reported that grafting immature sour lemon fruits, without scion leaves, on a sweet lemon tree, and vice versa, did not materially change the organic acid composition of the respective fruits when mature. Evidently the organic composition of such fruits, perhaps of fruits in general, is quite independent of the composition of the phloem translocate reaching the fruits from the leaves, or alternatively, the composition of this translocate is essentially the same in many different species (predominately sucrose and related sugars) and biochemical differentiation occurs almost entirely *in situ*, in the same manner as different tissues may be cultured on the same simple substrate. It is not known at present what fraction of the nitrogen and other mineral constituents of the fruit are derived from materials entering via the phloem and what fraction from those entering via the xylem. The organic acid content (mainly amino acids) of the tracheary sap of many species of trees (Bollard, 1956) is considerably higher than that of sieve tubes. It is conceivable, therefore, that nitrogen, and other mineral elements as well, are supplied to the fruit principally through the xylem.

The mechanism of organic translocation has engaged the attention of numerous plant physiologists. We shall not enter here into a discussion of this highly controversial subject, but suffice it to state that the well-known pressure-flow hypothesis, formulated by the forest physiologist Münch (1930) continues to be a highly provocative and productive concept. Recently, Zimmermann (1957c), another forest physiologist, has made an interesting application of this hypothesis to explain gradient reversals in the sieve tubes of white ash. There is no question about the impact of Münch's hypothesis on the thinking of plant physiologists. It is on this note that I wish to conclude this very cursory review of translocation, a note of recognition of our indebtedness to forest physiologists for their many significant contributions to fundamental problems in general plant physiology.

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## DISCUSSION

DENNIS RICHARDSON (*University of Aberdeen, Scotland*): In view of the recent evidence of rapid sugar transformation in plants, do you think that observed temperature coefficients for carbohydrate translocation can be interpreted as illustrating *direct* effects of temperature in sucrose transport?

C. A. SWANSON: So far as I know, the experiments required to give a good answer to this question have not been carried out as yet. The pertinent data which have been published rest on indirect criteria for assessing the effect of temperature on carbohydrate transport and provide little information, therefore, on the specific effects of temperature on sucrose transport *per se*, or even on the effects of sugar interconversions and transformations on translocation rates. I believe it would be of interest to study certain of these effects by varying the temperature of a restricted zone of the stem, and subsequently analyzing the comparative distribution of the C-14 label in compounds from regions of the stem, or preferably the phloem, both proximal and distal to the temperature zone. Mr. Burley of our department has, as a matter of fact, given some consideration to such a problem, but no actual work is as yet underway.

DENNIS RICHARDSON: If Went's experiments indicating a  $Q_{10}$  for translocation of less than unity are explained on the grounds that he was measuring temperature effects on sugar transformation, not translocation, does not this argument apply equally to work which implies a  $Q_{10}$  greater than unity?

C. A. SWANSON: With present information, I believe the only fair answer to this question is "Yes."