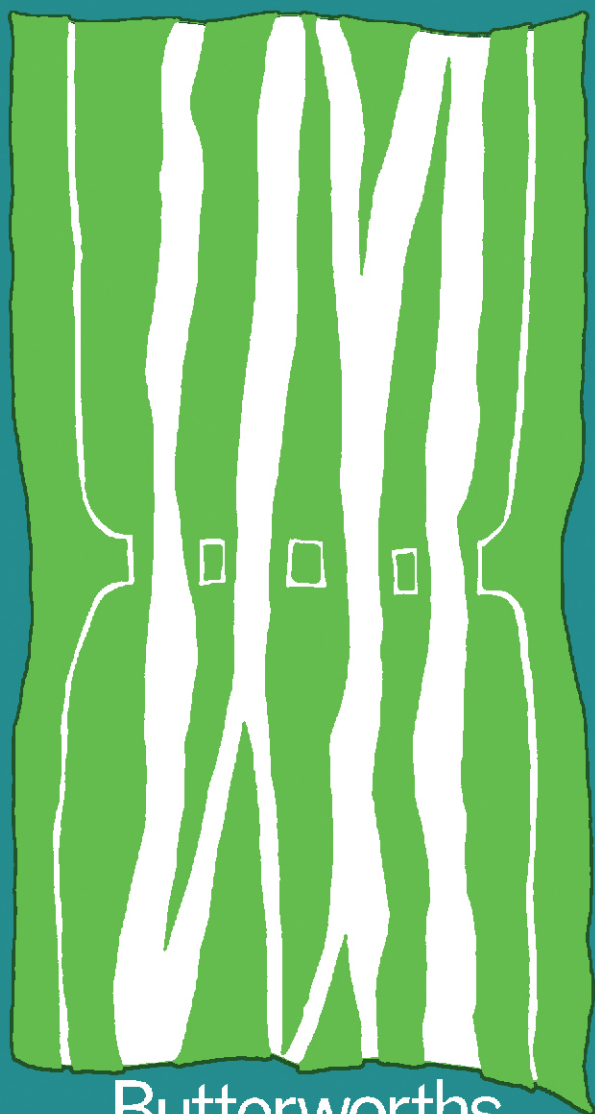


Transport of Nutrients in Plants

A.J. Peel



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Preface

The transport processes of plants present the investigator with some of the most fascinating and complex problems of any area of plant physiology, yet they have not generally received the attention they deserve as indispensable aspects of the life of higher plants. Although studies on nutrient transport can be said to have begun in the eighteenth century with the work of Stephen Hales (incidentally, his book *Vegetable Staticks*, reprinted in 1961, should be read by every serious student of translocation), progress over the past 200 years has been sporadic. Apart from a peak of activity during the late 1920s and early 1930s, produced mainly as a result of the efforts of Mason and Maskell, the only other notable period in the study of translocation has taken place during the last 15 years or so.

Undoubtedly, this latest upsurge of interest has been generated by the discovery of new techniques or the elaboration of old ones to probe the mysteries of the cells, buried deep within other tissues, which conduct solutes throughout the plant. Foremost among these techniques are radioactive tracers, incision or tapping methods for sampling the nutrient streams, and electron microscopy.

Prospective workers on translocation do not need to be physiologists. The field is wide open to those with aspirations in biochemistry (relatively little is known about metabolic processes in phloem and the other vascular tissues) or electron or optical microscopy, and to those who are just interested in plants. If the impetus of the last few years can be maintained, it is possible to visualise the unravelling of some of the major problems within the foreseeable future.

Transport of solutes in plants can take place over both short distances (measured in microns) and long distances (measured in centimetres or metres). Although both are equally important to the growth of all plants consisting of more than a few cells, it is the long distance systems, typified by the xylem and phloem of higher plants, which in many ways are the most fascinating, if only from the point of view of the distances involved.

The magnitude of the long distance transport processes can readily be appreciated in tree species. Here is a growth habit in which the two major sites of nutrient absorption and synthesis—the roots and leaves, respectively—are situated at either end of a long axis. The length of this axis in

the extreme case of the Redwoods can be 100 m. Water and mineral salts must therefore move this distance from the roots to the topmost leaves, while assimilates from the leaves have to be transported, at least a considerable distance, from the lower branches to the roots.

Despite the obvious importance of these transport processes to the growth and development of land plants, we still lack a clear understanding of how nutrient movement is effected and controlled. This may be the reason why only a small amount of space is devoted to translocation in most textbooks on plant physiology. However, despite the deficiencies in our knowledge, there is a considerable body of data which has been accumulated over the past 40 or 50 years (and particularly during the past decade), which has not been adequately presented in book form at an undergraduate or first-year postgraduate level.

The greater part of this book deals with the physiology and cytology of phloem. This should not be taken as implying that the phloem is of greater importance than the xylem in the functioning of the plant. It is merely a reflection of the greater complexity of the phloem, in both structure and function, relative to the xylem. It must also be borne in mind that the xylem and phloem are not isolated from each other; not only are they anatomically close, but the two are also intimately connected in a physiological sense.

The emphasis of this book is upon function. Clearly, it is not possible to separate considerations of function from those of structure, but in view of the number of excellent publications on the gross anatomy of the vascular tissues, it does not seem necessary to duplicate them here. Discussion will therefore be largely confined to the severe problems associated with sieve element ultrastructure.

The first chapter deals with studies on the definition of the cellular pathways of transport; the second, with a consideration of how the mobility of solutes can be measured and the range of chemical species which are moved in xylem and phloem. Then follows a discussion on the concepts of velocity and rate.

The rest of the book is devoted to the characteristics of phloem transport and the ultrastructure of sieve elements, including such topics as the control of movement, solute-loading and -unloading mechanisms, the dependence of transport upon metabolic energy, bidirectional movement and water movement in phloem. Finally an account is given of the movement of endogenous growth regulators and a brief assessment of 'hormone-directed' transport.

Thanks are due to Drs. Behnke, Cronshaw, Gunning and Thaine, who have generously supplied the photographs illustrating aspects of the cytology of phloem; to those members of the Botany Department, University of Hull, who have given freely of their services in the preparation of the figures; to Miss E. Sharpe for typing the manuscript; and, finally, to my wife for her assistance in correcting the manuscripts and proofs.

Introduction

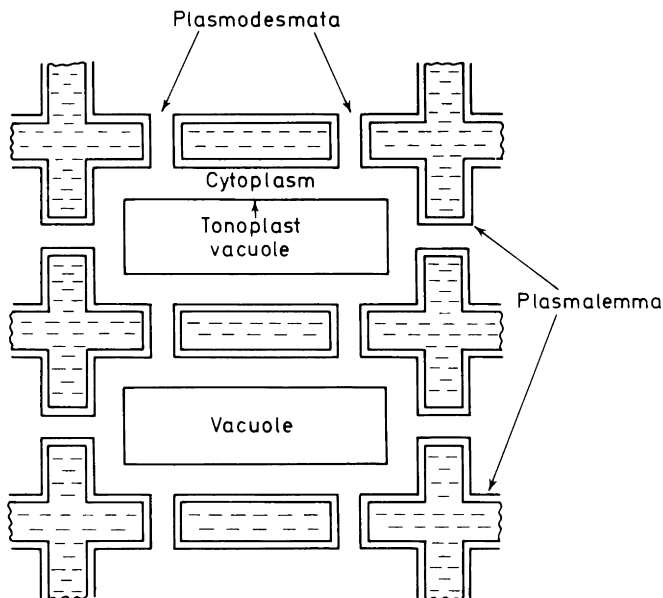
Although the main emphasis of this book will be laid upon xylem and phloem, it is impossible to deal with these two pathways in isolation; water and salts have to traverse the root cortex before they can enter the xylem, and sugars and other solutes elaborated in the cells of the leaf have to be moved into the sieve elements. In addition, as will be shown later, radial transport can readily occur between the phloem and xylem tissues.

In relation to the movement of solutes between the relatively non-specialised (in the sense of transport) parenchyma cells of the leaf, root and main axis, and between these cells and the specialised long distance transport conduits, probably the most important concept which has emerged is that of the symplast–apoplast system (Münch, 1930). This concept envisages the plant body as being capable of division into two distinct, though intimately connected, regions. One of these, the symplast, is composed of the whole mass of living material within the plant. Individual protoplasts of the cells are surrounded by the outer limiting membrane, the plasma-lemma. Vacuoles of the cells are limited by the tonoplast. The plasmalemma extends through the pits in the cell walls as the outer covering of the plasmodesmata, thereby extending as a continuous membrane which encloses the whole of the cytoplasm of the plant. In contrast to the symplast, the apoplast consists of the non-living cell walls of the plant. Like the symplast, the apoplast forms a continuous system throughout the plant which protects and contains the symplast, thereby giving form to the plant. *Figure Int.1* gives a representation of the symplast–apoplast systems.

This division of the plant into living and non-living systems necessarily means that solutes can move by quite different mechan-

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isms in symplast and apoplast. In the latter, movement will be either diffusional or in a bulk flow of solution. Once a solute reaches the plasmalemma at the outer edge of the symplast, it is presented with a permeability barrier which it has to cross, either by the slow process of diffusion or, more generally, by an active transport mechanism.



*Figure Int.1 Diagrammatic representation of the symplast-apoplast system.
Hatched areas show cell walls*

Once across the plasmalemma, intracellular transport of solutes may be aided by cytoplasmic streaming. Intercellular movements in the symplastic system presumably occur mainly through the plasmodesmata. These movements are possibly largely diffusional, although it seems unlikely that movement through plasmodesmata is completely free and non-selective. Electron micrographs of plasmodesmata, e.g. those illustrated between ray parenchyma cells in Figure 5 of the paper by Evert and Murmanis (1965), show dark bands running transversely across the plasmodesmata which could indicate permeability barriers. Thus, active transport may be involved in the movement of certain solutes through plasmodesmata.

The results of some work (Hawker, 1965) on sugar cane have

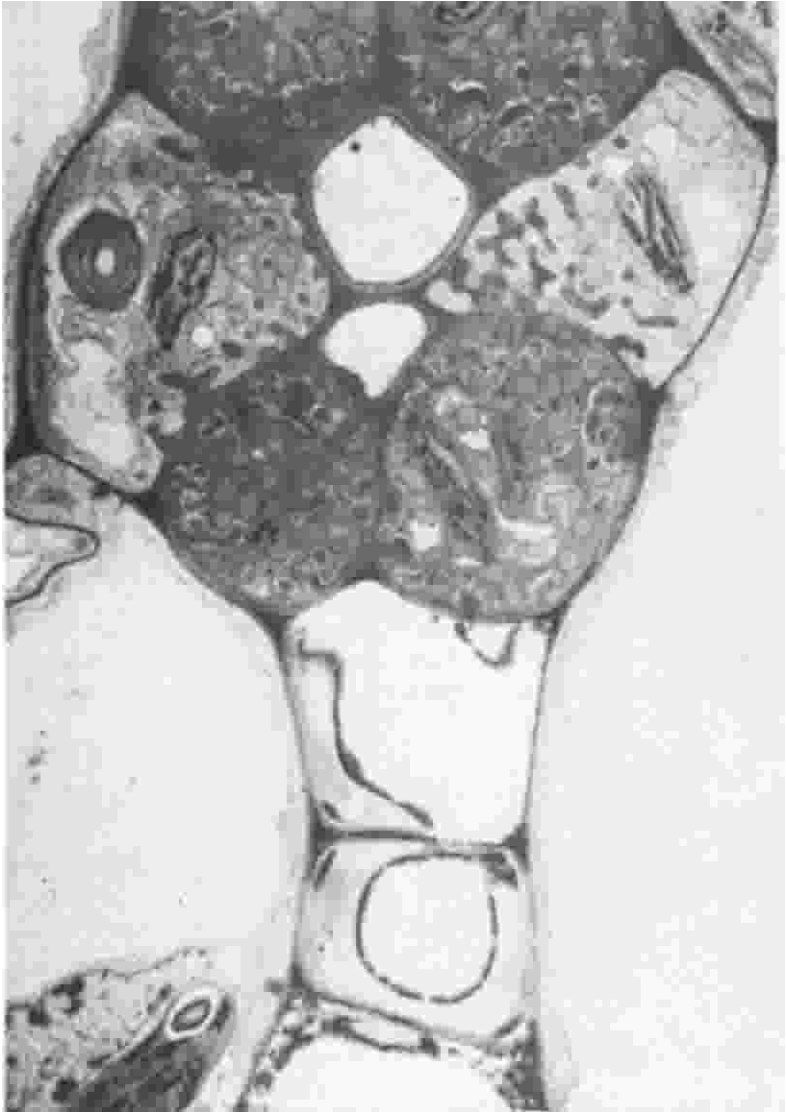


Figure Int.2 Electron micrograph of a leaf vein showing two types of transfer cells. Plasmodesmata occur between one type of transfer cell and the vascular cells of the vein. This type of transfer cell could therefore be involved in solute movement from mesophyll cells to sieve elements and in the interveinal recycling of xylem transported solutes. (From Gunning and Pate, 1974; reproduced by courtesy of the authors and McGraw-Hill)

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indicated that the apoplastic cell walls may be involved in intercellular sugar transport rather than the plasmodesmata. Such a situation does not, however, appear to exist for sugar transport in willow phloem (Peel and Ford, 1968). Possibly, the relative importance of apoplast and plasmodesmata as intercellular transport systems differs according to species.

Before we leave the subject of short-distance intercellular transport, some observations on the occurrence of specialised parenchyma cells should be mentioned. Excellent work by Gunning and Pate (1969) has demonstrated that certain cells possess ingrowths of wall material and that, therefore, these cells have protoplasts with high surface-to-volume ratios. These cells, of which several types have been distinguished by electron microscopy, have been termed 'transfer cells', and are found in a wide variety of anatomical situations in most of the major groups of multicellular plants.

Of particular importance is the occurrence of transfer cells in the vascular tissues of higher plants. They are found associated with both xylem and phloem tissues, and in view of their enhanced surface area, are very possibly involved in the loading and unloading of solutes in xylem and phloem and in the radial transport between these two long-distance transport tissues. *Figure Int. 2* shows an electron micrograph of a transection of a minor vein of a leaf prepared by Gunning and Pate. This demonstrates the intimate association of transfer cells with both the phloem and xylem tissues.

The pathways of long distance transport

The movement of solutes from the roots to the leaves

Transport across the root cortex from the soil solution to the xylem vessels

Studies on the radial movement of solutes from the external milieu to the xylem vessels have been mainly concerned with ions. This is to be expected, since the bulk of solutes which are transported across the root system, at least under natural conditions, are ions on their way to the leaves and other aerial portions of the plant. Movement of ions across the root cortex has been the subject of study by a considerable number of investigators for a period of at least 50 years; even so, problems remain and there is no complete agreement on the pathways and mechanisms involved.

Before commencing a detailed analysis of the work which has been performed on the centripetal ion transport system of roots, it seems desirable to define the problems which have to be solved. Fundamentally, these problems can be stated in the following way: either ion movement across the root cortex is mediated through the symplast system with its attendant active, energy-requiring processes, or transport may be largely passive through the apoplast, ions being swept along in the water stream of transpiring plants. As we shall see, it appears possible that both pathways participate in transport, but the extent to which each contributes to the total ion flux could be dependent upon a large number of factors, two of the most important being the rate of transpiration and the 'salt