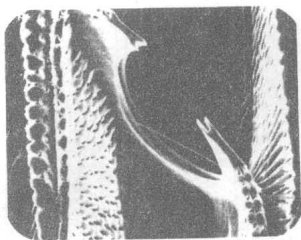


Transport systems in plants

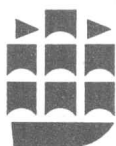
Jeffrey Moorby



Transport systems in plants

Jeffrey Moorby

Agricultural Research Council
London



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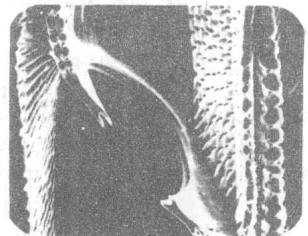
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Preface



transport pathways and mechanisms. However any reasonably complete understanding must include some knowledge of the systems which supply material to the plant and so there will be some mention of transfer processes in the atmosphere and the soil. It will be impossible in the space available to discuss the operation of these in detail, or indeed, to provide a comprehensive coverage of the processes within plants. The aim will be to consider the fundamental problems involved

The first three sections therefore, will, be concerned primarily with section will consider the absorption and transport of ions and water. its transport into and through the 'phloem' of the latter. The third with the movement of carbon into simple and multicellular plants and the later sections of the book. The second section will be concerned for structure is related to the functioning of the tissues will be reserved for developmental anatomy will be provided but discussions of how

these tissues have become more specialized. Some descriptions of transport in the different groups of plants and will try to show how I will be concerned initially with describing the tissues involved in appear to impose any limitations on plant growth.

in very few instances do deficiencies in the internal transport processes modifications. These modifications have been very successful because functioning of the transport processes has resulted in many structural Hence, the evolutionary adaption of plants to permit the efficient within large plants is much more difficult than within a single cell. into, out of and through the plant. Obviously, the transport of materials dependent for survival on the transport of a large variety of substances All plants, from unicellular aquatic algae to large terrestrial trees, are

Preface

and to discuss the various aspects in terms of the simplest and best understood situations. This discussion will then be extended to include other plant types and more unusual conditions.

It must be emphasized that although individual processes will be discussed separately, they operate as a complete system and that a plant functions as an integrated whole. The behaviour of a complex system such as a growing plant is often determined not by the individual parts of the system but by the interrelationships between the parts and how they respond to the constantly changing internal and external environment. The final part of the book will, therefore, extend the discussion beyond mechanistic considerations to the interrelationships between transport and other processes and growth.

J. Moorby
London, 1980

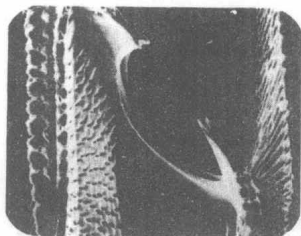
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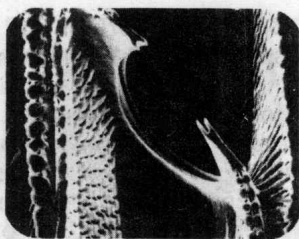
Contents

Preface

Acknowledgements

1	The evolution of transport systems in plants	1
1.1	Introduction	1
1.2	Phloem	2
1.3	Xylem	18
1.4	Symplastic and apoplastic transport	28
2	The movement of carbohydrates	33
2.1	Introduction	33
2.2	Carbon assimilation	33
2.3	Movement of carbohydrates into the phloem	35
2.3.1	Movement in C_3 plants	35
2.3.2	Movement in C_4 plants	39
2.3.3	The kinetics of movement into the phloem	41
2.4	The kinetics of movement through the phloem	47
2.5	The possible, and sometimes impossible, mechanisms of phloem movement	60
2.5.1	The pressure flow theory	63
2.5.2	Active mechanisms	66
2.6	Movement out of phloem	72
2.7	Mathematical models of translocation	73

3	The movement of water and ions	76
3.1	Introduction	76
3.2	The movement of water into cells	76
3.3	The movement of ions into cells	79
3.4	The movement of water and ions into the xylem	82
3.5	The movement of water and ions through the xylem	90
3.6	The movement of water and ions into and through leaves	102
3.7	The movement of ions in the phloem	104
4	Transport systems and plant growth	108
4.1	Introduction	108
4.2	The effect of environmental and other factors on transport systems	109
4.2.1	Water	109
4.2.2	Light	112
4.2.3	Temperature	117
4.2.4	Growth substances	120
4.3	Transport systems and growth	121
4.3.1	Transport and the growth of stem apices and leaves	123
4.3.2	Transport and the growth of stems	139
4.3.3	Transport and the growth of roots	141
4.3.4	Transport and the growth of storage organs and fruit	142
4.3.4.1	Transport and the growth of potato tubers	143
4.3.4.2	Transport and the growth of cereal grains	146
4.3.4.3	Transport and the growth of fruit	150
4.3.5	Transport out of seeds and storage organs	155
4.4	The movement of exotic substances	160
5	Conclusions	163
	Index	165



Chapter 1

The evolution of transport systems in plants

1.1 Introduction

In many plants water, carbohydrates and ions have to move over long distances and hence a variety of tissues and cell types have evolved to cope with this long-distance transport. The selective pressures which have resulted in these changes have been considerable and can be traced primarily to the action of two dominant evolutionary progressions; the development of multicellular forms and the transfer from aquatic to terrestrial habitats.

The tissues concerned with transport in all the plant groups are remarkably similar. I have chosen to emphasize these similarities rather than the differences. The two tissues of primary concern are the phloem and xylem. The general consensus of opinion is that most of the movement of sugars occurs in the phloem whereas ions move in both the phloem and xylem. Other materials such as organic forms of nitrogen and growth substances can also move in either tissue, but their transport is dependent on the species under consideration and is complicated by problems of synthesis and utilization. Water can move in both tissues. This is a gross oversimplification, as will be seen from the discussion which follows, but this is of no immediate concern. It is sufficient to be able to delimit the cells which need to be considered and the evidence which has made this possible has come mainly from two types of experiment. The first involved 'ringing' (removal of a strip of bark and phloem from the stem) or destroying these tissues by heat, coupled with chemical analyses. The second type of experiment involved the direct localization of the mobile materials by histo-

chemical or autoradiographic techniques. Because of work of this type it is now agreed that long distance transport in the phloem takes place through the sieve elements, or their equivalents in lower plants, whereas the tracheids and vessels are the major conduits in the xylem.

Arguably the most primitive cells concerned with the transport of assimilates are to be found in the large brown algae, and these will be described in some detail. The types of sieve elements to be found in other plant groups will be described more briefly except for those of the angiosperms. This group has been used in most of the work on phloem transport and, possibly because of this, there is probably more dispute about the sieve cells in this group than in any other. Hence, the various interpretations of the structure and development of sieve cells in the angiosperms will be considered in more detail than for any other plant group.

For convenience, the development of the xylem will be discussed separately from that of the phloem. There is less dispute about the structure and functioning of xylem than of phloem, but again most of the discussion will be reserved for the xylem of the higher plants.

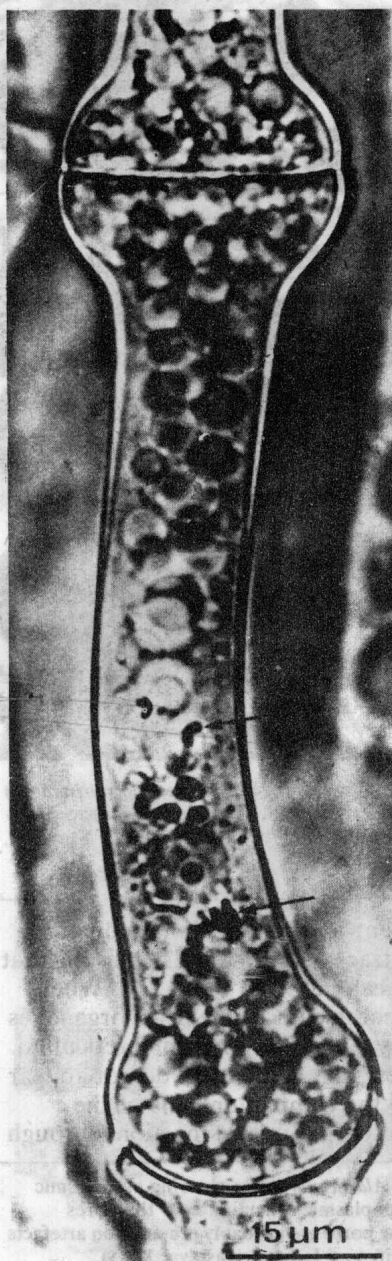
1.2 Phloem

In the algae there is a progression from unicellular to filamentous and colonial forms and eventually the development of large multicellular species such as the brown alga *Laminaria*. The distances over which the transport of assimilates must occur in species such as *Laminaria* are considerable; and autoradiography has shown that this transport takes place through specialised cells, the hyphae and trumpet hyphae (Fig. 1.1).

The trumpet hyphae are elongated cells which, under the light microscope, often appear to be narrower in the middle of the cell than adjacent to the transverse walls. This 'belling' of the ends of the cells is not always seen (cf. Fig. 1.2). It may be an artefact caused by the release of turgor pressure during specimen preparation or it may be caused by the stretching of the cells as the plant grows. The possibility of damage during sample preparation is a problem which bedevils all investigations of the structure of cells concerned with assimilate transport because they all seem to operate under a positive internal pressure.

There are small pores between adjacent hyphae and trumpet hyphae which are lined by the plasmamembrane (Fig. 1.3). These cells

Fig. 1.1 A typical trumpet hyphae in *Laminaria groenlandica* Rosenv. showing vacuoles, nucleus and plastids (arrowed) (after K. Schmitz and L. M. Srivastava, 1974).



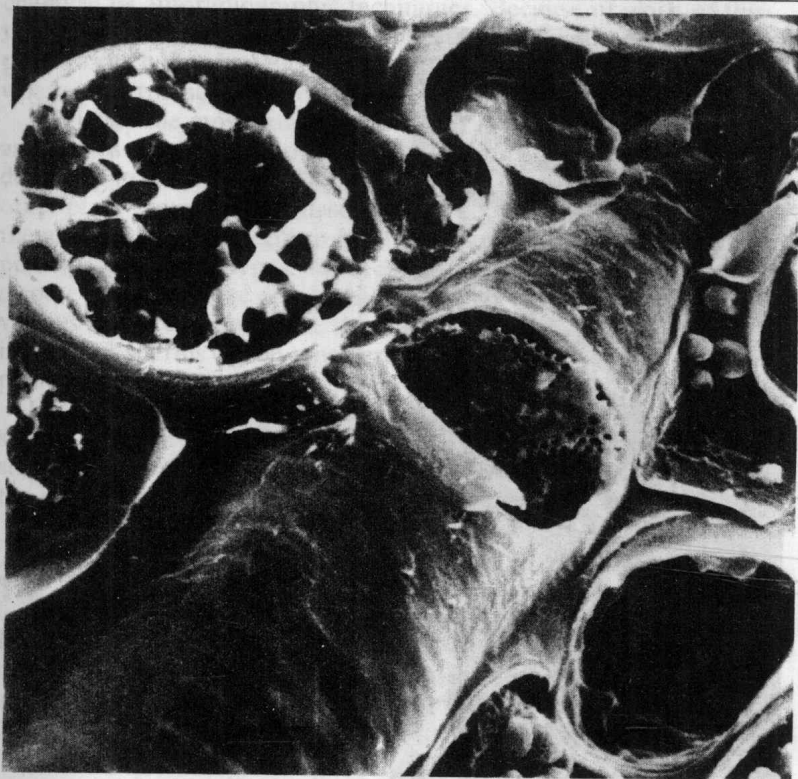


Fig. 1.2 A scanning electronmicrograph of trumpet hyphae in *Macrocystis pyrifera* (L) C. Ag. Part of the cell wall has been broken open to reveal the sieve plate between two cells which show little 'belling' ($\times 5400$) (after J. H. Troughton and F. B. Sampson, 1973).

appear to form a reasonably efficient pathway for longitudinal transport through the plants, some tracer experiments suggesting that the speed of assimilate movement can be up to 0.8 m h^{-1} . When functional the trumpet hyphae appear to contain the usual organelles such as nucleus, mitochondria, plastids and endoplasmic reticulum. They also have many small vacuoles (Fig. 1.4). There do not appear to be associated cells analogous to the companion cells of the angiosperms. In older hyphae the protoplasmic connections through

Fig. 1.4 A cross-section of a sieve plate in *Alaria marginata* showing cytoplasmic connections between adjacent cells and endoplasmic reticulum near the pores (arrowed). NB. The white regions around the pores are probably preparation artefacts and not callose, cf. Fig. 1.5 (after K. Schmitz and L. M. Srivastava, 1975).

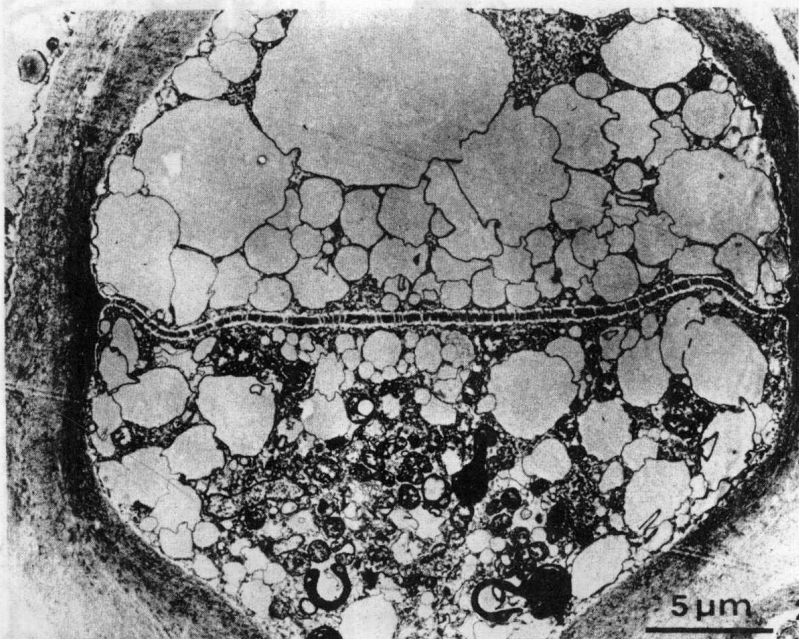
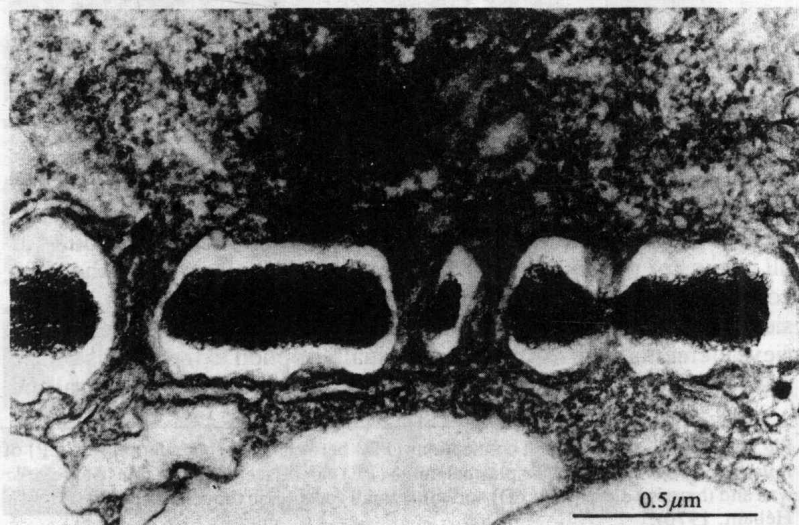


Fig. 1.3 A cross-section across the sieve plate dividing two trumpet hyphae in *Laminaria groenlandica* Rosenv. There are many vacuoles, plastids and mitochondria (after K. Schmitz and L. M. Srivastava, 1974).



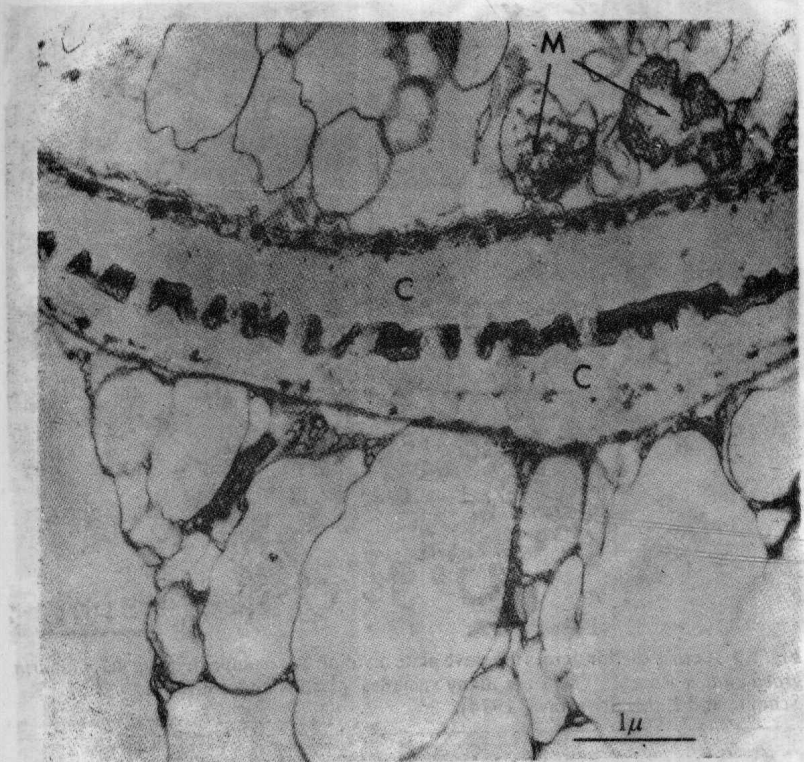
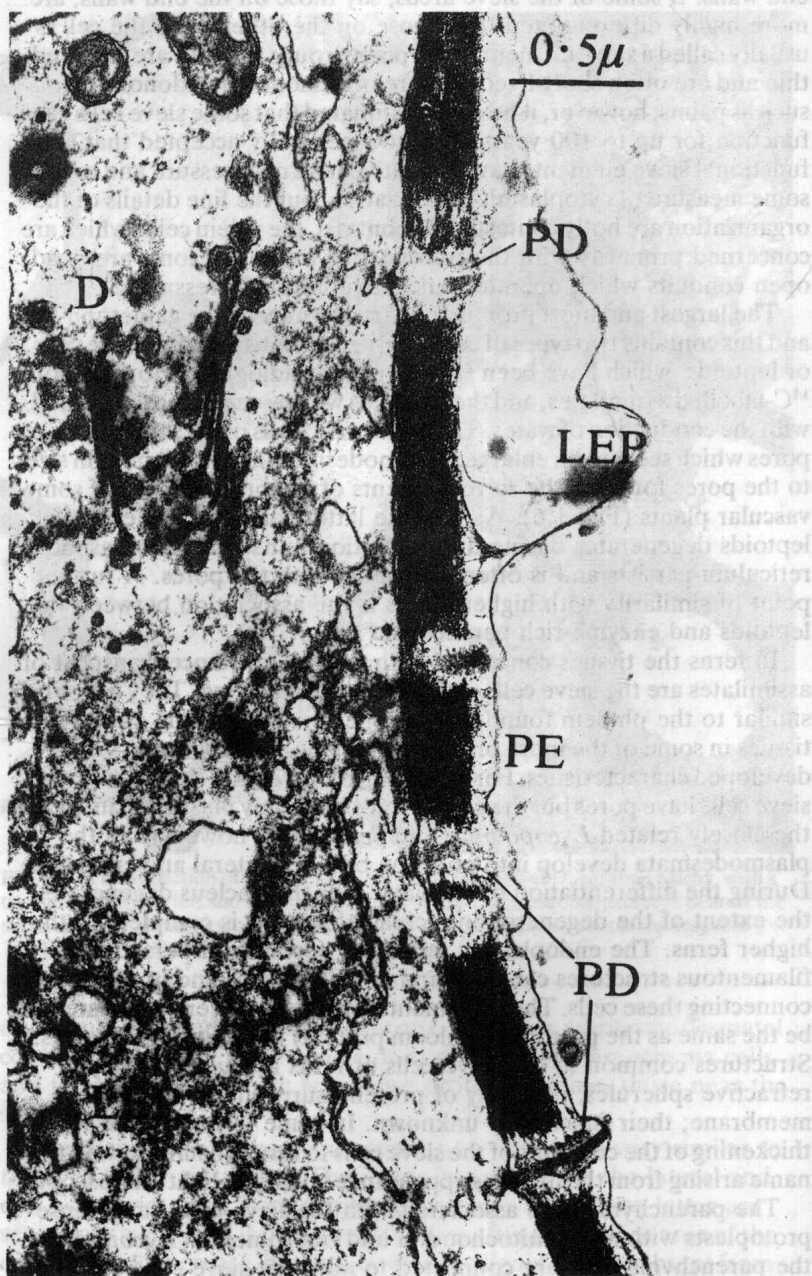


Fig. 1.5 A sieve plate in *Alaria marginata* which has been blocked with callose (C). NB. There are no cytoplasmic connections between the cells and the mitochondria (M) appear to be disintegrating (after K. Schmitz and L. M. Srivastava, 1975).

the pores are lost, the organelles disintegrate and the end walls become lined with callose (Fig. 1.5).

This general pattern of development and senescence can be found in all groups of plants but with variation in detail. Because all the cells concerned with assimilate transport have similar groups of pores, the sieve areas, there is now a tendency to refer to them all as sieve cells or sieve elements. The former term is usually applied to those cells which have sieve areas which are equally well differentiated in the lateral and

Fig. 1.6 The plasmodesmatal connections (PD) between two young leptoids (LEP) of *Polytrichum commune* L. The plasmalemma (PE) can be seen on both sides of the cell wall and there is a dictyosome (D) and some small vacuoles in the cell on the left (after C. Héban, 1970).



The evolution of transport systems in plants

end walls. If some of the sieve areas, say those on the end walls, are more highly differentiated than those on the other walls the cell is usually called a sieve element. In all plant groups the cells are long and thin and are often short-lived. In perennial monocotyledonous plants such as palms, however, it has been estimated that some sieve cells can function for up to 100 years. It is now generally accepted that functional sieve elements have a positive internal pressure and retain some measure of cytoplasmic organization, but the fine details of the organization are hotly contested. In contrast, the xylem cells, which are concerned primarily with the transport of water and ions, are dead, open conduits which operate at negative internal pressures.

The largest and most prominent part of a moss is the gametophyte and this contains two types of cells adapted to transport, the sieve cells, or leptoids, which have been shown by autoradiography to transport ^{14}C -labelled assimilates, and the hydroids which seem to be concerned with the conduction of water. The transverse walls of the leptoids have pores which seem to be enlarged plasmodesmata and are similar in size to the pores found in the sieve elements of the protophloem of some vascular plants (Fig. 1.6). As in these latter cells, the nucleus of leptoids degenerates during differentiation but some endoplasmic reticulum persists and is often associated with the pores. A further point of similarity with higher plants is the association between the leptoids and enzyme-rich parenchyma cells.

In ferns the tissues concerned with the long distance transport of assimilates are the sieve cells and phloem parenchyma. They are very similar to the phloem found in angiosperms whereas the equivalent tissues in some of the more primitive vascular plants show less highly developed characteristics. For example, in *Isoetes*, the end walls of the sieve cells have pores but the lateral walls have only plasmodesmata. In the closely related *Lycopodium* and *Selaginella*, however, all the plasmodesmata develop into pores on both the lateral and end walls. During the differentiation of the sieve cells the nucleus degenerates, the extent of the degeneration increasing until it is complete in the higher ferns. The endoplasmic reticulum becomes dispersed but filamentous structures can be found in mature cells and in the pores connecting these cells. These filaments are not, however, considered to be the same as the p-protein (phloem protein) found in angiosperms. Structures common in the sieve cells of ferns are small, highly refractive spherules, probably of protein, surrounded by a unit membrane; their function is unknown. In some ferns there is some thickening of the cell walls of the sieve cells to form a nacreous wall the name arising from the lustrous appearance under the light microscope.

The parenchyma cells associated with the sieve cells have dense protoplasts with many mitochondria and ribosomes. In *Lycopodium* the parenchyma cells are connected to adjacent sieve cells by

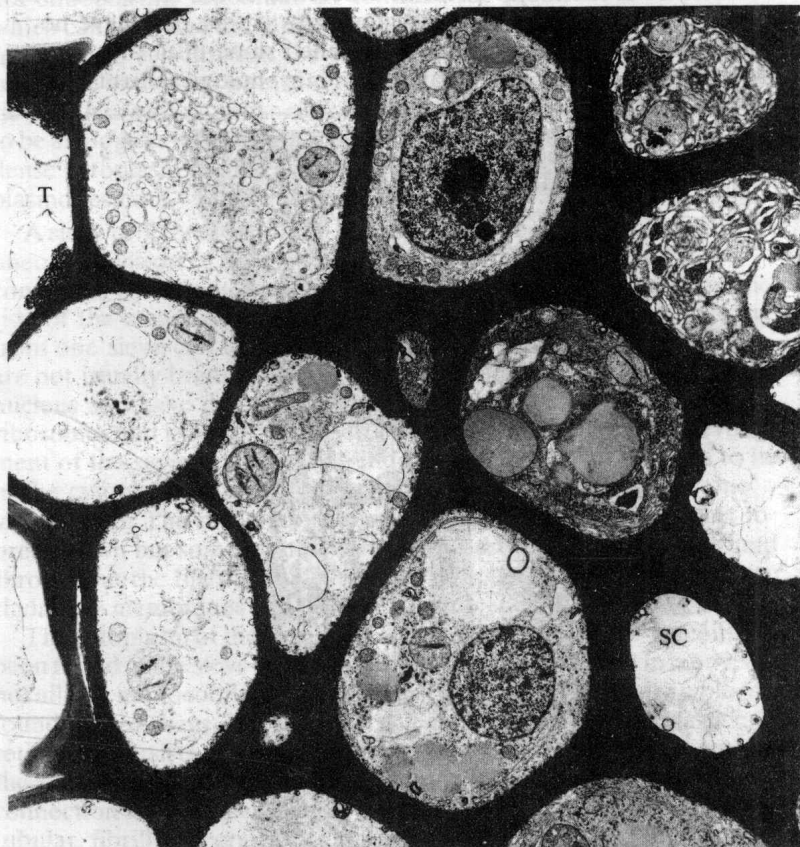


Fig. 1.7 A cross-section of the vascular system of *Lycopodium lucidulum* Michx. with a tracheid (T) on the left and sieve cell (SC) on the right. The parenchyma cells nearest the sieve cell have denser cytoplasm and thicker walls than those nearest the tracheid ($\times 7300$) (after R. D. Warmbrodt and R. F. Evert, 1974).

numerous plasmodesmata. In contrast, there are no plasmodesmatal connections between the tracheids and adjoining parenchyma cells and the latter have much less dense protoplasts than those near the sieve cells (Fig. 1.7).

The sieve cells of the gymnosperms are generally very similar to those of the angiosperms. They have pores in both the lateral and end walls and often form distinct nacreous walls. These latter are secondary walls, that is they are laid-down after the surface area of the cells ceases to increase, but they contain no lignin and are absent from

the sieve areas. The major point of difference of the sieve cells of gymnosperms from those of the angiosperms is that they have no p-protein. Phloem-protein was usually called slime until the mid-1960s. It can occur in several distinct morphological forms but is

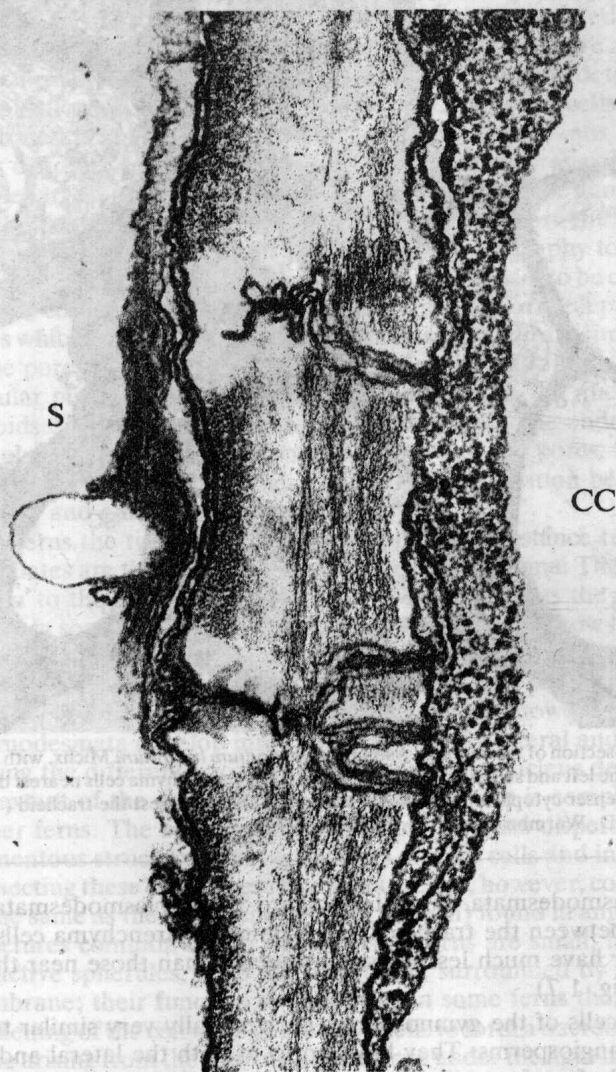


Fig. 1.8 Plasmodesmata between a sieve cell (S) and companion cell (CC) in *Nicotiana tabacum*. In each plasmodesmata there is a single cavity leading to the sieve cell which branches on the side of the companion cell ($\times 60\ 000$) (after K. Esau, 1969).