BIOLOGICAL IMPLICATIONS OF A MODEL DESCRIBING LIQUID FLOW THROUGH CONIFER WOOD

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Summary. A theoretical flow model shortly to be published elsewhere describes the rate of axial flow of liquids through conifer wood in response to known pressure differentials. This is based on certain assumptions as to the structure and ultrastructure of wood. The model predicts very different flow conditions for earlywood and latewood cells. While these predicted conditions are approximately similar to those observed experimentally by tree physiologists, it is not yet clear what advantages the reduced conductivity of latewood cells could convey to the tree.

INTRODUCTION

Experiments involving the measurement of the flow of gases and liquids through wood have often been used as a tool in studies of wood ultrastructure (Bolton & Petty, 1975; Petty, 1974; Petty & Puritch, 1970; Smith & Banks, 1971). Such permeability studies are frequently said to be of relevance both to the timber technologist and to the biologist. Yet surprisingly few attempts have been made to relate the knowledge gained by wood physicists to the findings and problems of the tree physiologist. This is clearly desirable where both are concerned with secondary xylem. In a separate publication an attempt is made to summarise wood physicists' knowledge of variables governing axial flow of liquids through conifer wood in a physical flow model. (Bolton & Petty, in preparation). This model describes the volumetric flow through the tracheid lumen/bordered pit system when a known pressure drop is applied across it. The present paper aims to analyse typical results of such a theoretical approach in the light of some of the findings of tree physiologists.

THE MODEL

Most permeability theory for liquids is ultimately based on the Hagen-Poiseuille equation. This states that conductance, or volumetric flow rate Q in response to a

pressure drop ΔP, through a capillary of radius r and length L is given by

$$\frac{Q}{\Delta P} = \frac{\pi r^4}{8\eta L}$$

where η is the viscosity of the liquid. Resistance to flow is then given by the reciprocal of conductance, or $\Delta P / Q$.

Modifications of this theory have been developed to describe flow through regularly shaped channels other than the perfect cylindrical capillaries considered by Hagen and Poiseuille. When applying such theory to flow through the coniferous tracheid lumen/bordered pit system, two main difficulties arise. Firstly the above theory, and the available modifications of it, are concerned with flow through regular channels—usually with parallel walls. Unfortunately, wood structure does not match this pattern. Hence it is frequently necessary to assume that observed structures conform approximately to regular shapes for which permeability theory is available.

In the present model, the tracheid lumen/bordered pit system is considered to consist of a number of components. Fig. 1 summarises the assumptions made in defining these. Component 6 is the tracheid lumen: the resistance to flow offered by this is assumed to approximate to that offered by a capillary of rectangular cross section. The Kozeny–Carman equation is therefore applied. (Carman, 1956). The resistance to flow generated by the pit margo pores (component 1) and the pit apertures (components 4 and 5) can probably be roughly predicted on the basis of the Hagen–Poiseuille equation above. There remains the truncated conical annulus on each side of the membrane, bounded by the periphery of the torus and the overarching pit border (components 2 and 3). The resitance to flow offered by such a channel can be estimated by applying the theory of Schiller (1921) and Gümbel (1921). Further details of the theory used in the model may be found elsewhere (Bolton & Petty, in preparation).

Wherever the dimensions of a component are difficult to define, the present approach is to estimate the minimum contribution to total resistance to flow made by the component in question. Examples here are the pit apertures: the effective length and radius of these are difficult to assess. The resistance to flow offered by them will probably be *at least as much* as that of the corresponding theoretical components, as defined in Fig. 1. Once defined—however arbitrarily—the measurements of all components can be obtained simply. The calculation of the resistance to flow offered by these individual components is then relatively straightforward.

Inspection of Fig. 1 reveals that parts of the structure are ignored in the model. This is because of the complexity of the shapes concerned, and the uncertain nature of the mode of flow through them. For example, the pattern of flow in the channel between components 1 and 2 is likely to be complicated because one wall of the channel—the pit margo—is permeable.

There remains a second problem in the application of permeability theory to the calculation of total resistance to flow offered by tracheid lumen/bordered pit system—
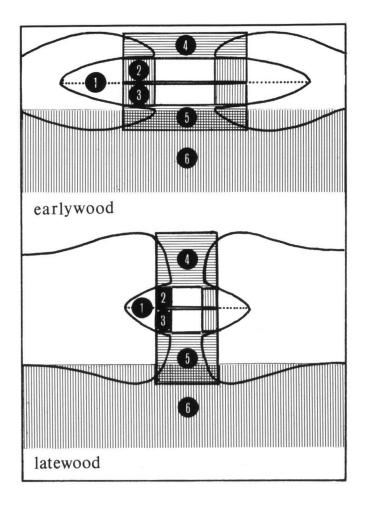
Fig. 1. The definition of the components in the theoretical model.
Component 1: pit margo pores;
Component 2: border/torus annulus on the exit side;
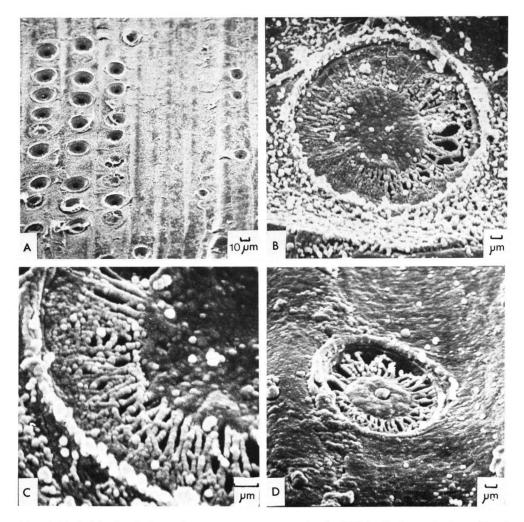Component 3: border/torus annulus on the entry side;
Component 4: pit apertures on the exit side;
Component 5: pit apertures on the entry side;
Component 6: tracheid lumen.

even once the resistance to flow offered by the *individual components* has been calculated by the methods outlined above. This is due to the fact that when a large enough pressure drop is applied across a bordered pit, its internal geometry changes as the membrane displaces, in the direction of the descending pressure gradient, towards one of the pit borders (Gregory & Petty, 1973).

Petty (1972), following the approach of Bailey & Preston (1970), calculated the

Plate 1. Typical bordered pit membrane structure as seen under the SEM for the types of cell considered in *Pinus sylvestris*: A, earlywood/latewood transition × 337; note change in membrane diameter and pit frequency in passing from earlywood to latewood; B, membrane in first formed earlywood × 3,360; C, detail of margo in first formed earlywood cell × 6,750; note encrusted appearance of margo fibrils and the small size of pores; D, membrane from centre of latewood × 3,370; note the narrow diameter of the membrane and the thicker margo fibrils (cf. B).

mechanical force developed during membrane deflection in one of the major radial margo strands supporting the torus. This force is a function of the Young modulus of the strand material, the square of the radius of a margo strand, and the magnitude of a number of other bordered pit dimensions. The total force required to deflect the entire membrane is then given by the product of the mechanical force in an individual strand, and the number of such strands. If these parameters are known, it becomes a straightforward matter to calculate the pressure drop which must be applied across the solid part of the membrane in order to generate the total force needed to bring about a specified membrane deflection.

In the flow model, the only pressure drop present across the bordered pit is that due to resistance to flow of liquid through the system. Hence, the membrane deflection cannot be predicted without first calculating this resistance to flow. Yet this resistance to flow will, itself, be affected by the magnitude of the membrane deflection. This is due to the decrease in the height of the border/torus annulus on the exit (or downstream) side of the bordered pit (component 2 in Fig. 1) as the membrane deflects. In practice, this difficulty can be overcome by a calculation involving successive approximations. A computer programme has been written to execute the above iterative analysis—which is otherwise very laborious to complete.

TYPICAL RESULTS OBTAINED USING THE MODEL

Using the model, it is possible to predict the variation of water flow through the tracheid lumen/bordered pit system with the magnitude of the applied pressure drop. Typical results for single cells in the first formed earlywood and in the centre of latewood of Scots pine (*Pinus sylvestris* L.) are shown in Fig. 2. Both volumetric and linear flow rates are shown—the latter being of some interest to physiologists. (The linear flow rate axes differ for the two types of cell because these present different lumen cross-sectional areas normal to flow).

These results are based on measured dimensions of tracheid lumina and bordered pits observed under the light microscope, or taken from scanning electron micrographs such as those in Plate 1. In taking such measurements the aim was to find realistic average values rather than precise values for a particular tracheid. It should, however, be emphasised that there are considerable uncertainties in some of the dimensional values and physical constants inserted in the model. Some of this stems from natural variability of wood structure. Much more important are uncertainties stemming from our lack of knowledge of margo fibril structure. For example, margo strands observed under the transmission electron microscope are commonly narrower in diameter than those of identical material observed under the scanning electron microscope. The reason for this is not clear; it is possible that some encrustants are removed in the preparation of T.E.M. replicas. Equally, while it is probably correct to regard at least the core of these strands as being cellulosic (Bauch *et al.*, 1968) we have to
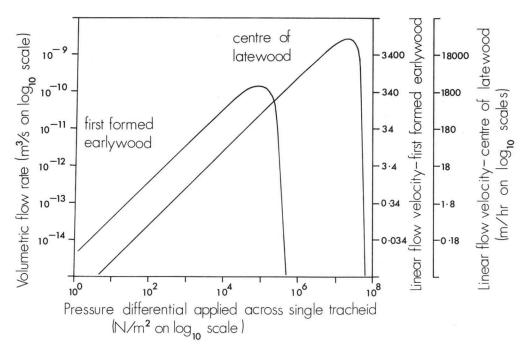
Fig. 2. Variation of water flow through the tracheid lumen/bordered pit system with the magnitude of the applied pressure drop.

assume a value for the Young modulus of them—for lack of fundamental information on the strength properties of wet cellulose.

Errors due to such uncertainties will affect the position, and possibly also the shape, of curves such as those shown in Figure 2. It is, however, very unlikely that such errors are responsible for the striking order of magnitude difference in the calculated conductance of earlywood and latewood cells. This arises chiefly from substantial differences in margo diameter, margo strand radius, and the number of margo strands in the two types of cell. This prediction of a difference in the conductivity of earlywood and latewood cells in Scots pine is borne out by experimental observations of Kozlowski *et al.* (1966).

Another striking feature of the curves shown in Fig. 2 is that departure from linearity is only noticeable at applied pressure differentials about an order of magnitude smaller than those required to aspirate the pit and cause the cessation of flow. According to the model, the membrane starts to deflect at very much lower applied pressure drops (10% of total possible deflection is observed at pressure drops of 1.09×10^2 and 5.59×10^4 Nm^{-2} in earlywood and latewood respectively). In fact, the total resistance to flow is significantly increased only when membrane deflections of 75% (earlywood) and 50% (latewood) of the total possible are observed.

The reason for this becomes apparent when the variation of the distribution of resis-
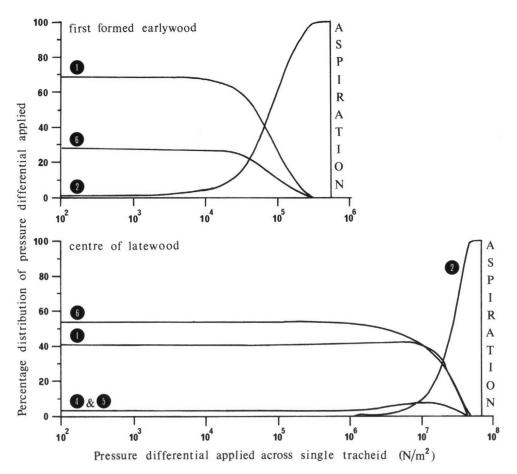
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Fig. 3. Variation of the distribution of total resistance to flow through the tracheid lumen/bordered pit system with the magnitude of the applied pressure drop. The numbering of components is as in Fig. 1.

tance to flow through the tracheid lumen/bordered pit system with applied pressure differential is considered. (Fig. 3). It is only after the percentage of the total resistance to flow offered by the pit border/torus annulus starts to increase dramatically, that the overall conductivity of the system begins to decrease markedly. It is also noteworthy that a significant part of the total resistance to flow at lower applied pressure drops in both earlywood and latewood is generated by the tracheid lumina. This is in agreement with the experimental findings of Bolton & Petty (1975) and Petty & Puritch (1970). The small contribution to total resistance to flow made by the pit apertures in the latewood is in agreement with the experimental observations of Bolton & Petty (1975).

The results of the above theoretical analysis will now be reviewed in the light of some of the findings of tree physiologists.

PHYSIOLOGICAL DATA ON XYLEM SAP PRESSURE GRADIENTS

The question of the mechanism of support of water columns in the xylem of tall trees has long been hotly debated. While many hypotheses have been proposed over the years, only two are currently given much support: the root pressure concept and the so-called cohesion theory. On the present evidence, it seems unlikely that the phenomenon of root pressure is of great significance in sap ascent in conifers—especially at times of rapid transpiration. (Kramer, 1969; White *et al.*, 1958). For this reason, most present physiologists concerned with conifers support the cohesion theory first advanced by Askenasy (1896), Dixon & Joly (1896), and their contemporaries.

In summary, the theory states that where water is lost from a gas liquid interface at the surface of transpiring tissue in the plant, the resulting reduction in water potential in the tissue causes the movement of water towards the interface. The motive force involved is usually traced back to the interfacial forces of minute menisci present in the mouths of small capillaries in the walls of transpiring cells. The water in the xylem may thus be placed in tension. It is argued that since the ultimate tensile strength of water is at least 30 atmospheres—and possibly as high as 300 atmospheres or more (Greenidge, 1957)— it is not unreasonable to regard the columns of water as being suspended from the gas/ liquid interfaces (Dixon, 1914).

The pressure deficit required to maintain a *stationary* column of water 30 m high is *c*. 3 atmospheres. This is equivalent to a negative pressure gradient of 0.1 atm./m (*c*. 1×10^4 Nm^{-2}/m). Since in reality the liquid column is normally not stationary, the negative pressure gradient in the xylem is greater than this minimum value, because the wood structure offers a finite resistance to flow—like any other porous medium. (This is implied in the Hagen-Poiseuille equation). Extra water potentials will also be needed to draw water from the soil into the root xylem, and from the stem xylem into the trans-piring mesophyll cells in the leaf. These extra potentials will be superimposed on the potential required to cause water to flow up the stem. The presence and magnitude of the soil/root and stem xylem/mesophyll parenchyma potentials will thus influence the absolute level of negative pressure in the xylem sap, but *not* the negative pressure *gradient*.

A number of workers have attempted to measure the total negative pressure of the xylem using a variety of experimental techniques. Unfortunately, these studies generally yield little information on the xylem sap pressure gradient. One approach to the estima-tion of maximum sap tension is that of Scholander *et al.* (1965). In this method, a freshly cut twig is placed in a pressure bomb, with its cut end protruding from a seal. Gas pressure in the bomb is then raised until xylem sap is seen to exude from the cut end of the twig. The pressure required to displace the sap may then be regarded as the maxi-mum sap tension at the time of test. Data given by Scholander *et al.* show that in Douglas fir (*Pseudotsuga menziesii*) and Redwood (*Sequoia sempervirens*), the maximum sap tensions were much higher in material taken from the top of the tree than in material taken from near the base of the crown at much the same time. If we assume that the

difference in such recorded pairs of readings represents the potential available for the transport of sap over the distance in question within the crown, we can calculate xylem sap negative pressure gradients for the trees concerned. Rough calculations suggest that this is in every case of the order of 0.1 atm./m. This has the rather surprising implication that, in these species, an almost negligible pressure gradient—over and above that required to maintain stationary columns of sap in the xylem (also 0.1 atm./m—is adequate to supply the transpiring crown with water. Rather higher xylem sap negative pressure gradients are predicted if we assume that the negative pressure at the top of the crown is close to the maximum possible while that at the base of the crown is less than the maximum possible. Although any such considerations are speculative, the pressure bomb technique of Scholander *et al.* has been useful in demonstrating that negative pressures of up to 80 atmospheres or more can be generated by interfacial forces in the leaves of conifers.

Another approach to the measurement of xylem sap pressure gradients is based on measurements of linear sap flow rates in living plants. If the conductivity of subsequently excised xylem is measured, the pressure gradient in the xylem of the living plant can then be estimated. It is apparently by these means that estimates of xylem sap pressure gradients in conifers of the order of 0.6 atm./m have been made (Heine, 1971). Unfortunately, both the measurement of linear sap flow rates (see below), and the measurement of the conductivity of excised xylem to liquids are fraught with experimental difficulties (Kelso *et al.*, 1963).

In summary, there is still a lack of accurate data on xylem sap pressure gradients. It is in this light that Zimmermann & Brown (1971) suggest that the average value for conifers is probably of the order of 0.2 atm./m. Of this, only 0.1 atm./m will arise from resistance to flow.

PHYSIOLOGICAL DATA ON XYLEM SAP FLOW RATES

Both for the reasons mentioned above, and because of their relevance to studies of transpiration, xylem sap flow rates have frequently been measured. Interest has tended to be centred on methods which may be used on intact trees and hence, in particular, on the study of linear flow rates.

The techniques used have involved the study of the rate of movement of dyes (Arndt, 1929; Crafts *et al.*, 1949; Ewart & Reese, 1910; Greenidge, 1958; Groom, 1910; Mac-Dougal, 1926; Marshall, 1958; Preston, 1952), salt solutions—assessed by electrical conductivity measurements or examination of spectra—(Lundegårdh, 1954), radioactive tracers (Baumgartner, 1934; Ferrell & Hubert, 1952; Fraser & Mawson, 1953; Heine, 1970; Klemm & Klemm, 1964; Kuntz & Riker, 1955; Ladefoged, 1960; Moreland, 1950), or heat transport (Baumgartner, 1934; Bloodworth *et al.*, 1955, 1956; Closs, 1958; Daum, 1967; Decker & Skau, 1964; Dixon, 1936; Doley & Grieve, 1966; Gale & Poljakoff-Mayber, 1964; Heine & Farr, 1973; Huber, 1932; Huber & Plankl, 1956;

Huber & Schmidt, 1936, 1937; Kurzmann, 1966; Ladefoged, 1960; Leyton, 1970; Marshall, 1958; Sadler & Pitman, 1970; Schubert, 1940; Skau & Swanson, 1963; Swanson, 1962; Vieweg & Ziegler, 1960).

A large proportion of the techniques used by these authors have the very serious drawback that the xylem must be at least partially cut or bared in the course of the experiments. As mentioned above, the xylem sap is likely to be in tension. Physical damage to the xylem is thus likely to release these tensions and introduce very unnatural conditions in the flow paths. While in some of the more recent heat-pulse techniques the heating of the wood is carried out with only minimal damage to the xylem, all reported xylem sap flow rates must be interpreted with care.

TABLE 1: Summary of maximum linear xylem sap flow rates reported by various authors for coniferous species.

Species	Flow Rate (m/hr)	Method	Author
Abies pectinata	0.60	Dye	Groom (1910)
Larix decidua	2.40	"	" "
Pinus radiata	0.15	"	MacDougal (1926)
Pinus sylvestris	1.20	"	Groom (1910)
Pseudolarix kaempferi	0.78	"	" "
Pinus taeda	1.42	Tracer	Moreland (1950)
Abies alba	0.73	Heat-pulse	Schubert (1940)
Juniperus deppeana	0.25	" "	Decker & Skau (1964)
Juniperus osteosperma	0.25	" "	" "
Larix decidua	1.00	" "	Huber & Schmidt (1936)
Larix decidua	2.80	" "	Schubert (1940)
Picea abies	0.13	" "	Leyton (1970)
Picea abies	1.19	" "	Huber & Plankl (1956)
Picea abies	1.20	" "	Schubert (1940)
Pinus halepensis	0.15	" "	Gale & Poljakoff-Mayber (1964)
Pinus halepensis	0.40	" "	Decker & Skau (1964)
Pinus radiata	3.14	" "	Marshall (1958)
Pinus strobus	1.70	" "	Huber & Schmidt (1937)
Pinus sylvestris	0.93	" "	Schubert (1940)
Pinus sylvestris	1.19	" "	Huber & Plankl (1956)
Tsuga canadensis	2.10	" "	Huber & Schmidt (1936)

Quite a different criticism of the heat-pulse techniques is that due to Marshall (1958). This author showed by a combination of theoretical and empirical means that linear sap velocities obtained by these techniques can be too small by a factor as great as 4. This error arises mainly from the heterogeneous nature of wet xylem with respect to thermal properties. In subsequent experiments, Heine & Farr (1973) found that radio isotope flow velocity through excised xylem was as much as 20 times greater than heat flow velocity. The reason for this lack of agreement with the findings of Marshall is not clear.

An altogether new approach to the measurement of linear sap velocities is the magnetohydrodynamic method of Sheriff (1972, 1974). The technique depends on the measurement of induced voltages in a conducting fluid flowing normal to an applied magnetic field. While the method seems to be very accurate, it does not appear to have been applied to the study of flow rates in coniferous material.

In summary, as seems to be the case with xylem sap pressure gradients, we appear to lack reliable information on xylem sap flow rates. Some existing data for conifers are shown in Table 1.

COMPARISON OF RESULTS OBTAINED FROM THE MODEL WITH THOSE OBTAINED BY PHYSIOLOGISTS

The model used to calculate each of the two curves in Figure 2 is concerned with flow through a single entire tracheid. The pressure differential effective across the entire tracheid will be approximately given by the effective xylem sap pressure gradient multiplied by the assumed tracheid length. In reality, however, liquid flowing axially through wood will, on average, travel rather less than a distance equal to one tracheid length down any one tracheid lumen. This is because tracheid ends overlap. According to Stamm (1946), the mean distance travelled down any one lumen is likely to be 0.75 × tracheid length. Hence the pressure differential effective across an entire tracheid may be taken as the effective xylem sap pressure gradient multiplied by 0.75 and by the assumed tracheid length.

In the absence of evidence to the contrary, we may assume that the effective xylem sap pressure gradient suggested by Zimmermann and Brown (0.1 atm./m) is typical for conifers. This corresponds to a pressure differential of 5.3×10^2 Nm^{-2} applied across the earlywood tracheid lumen/bordered pit system of the model. The value for latewood cells is somewhat smaller, 3.2×10^2 Nm^{-2}, since latewood cells were assumed to be considerably shorter than earlywood cells.

The linear flow rates likely to pertain at these differential pressures may be read from Fig. 2. That for earlywood is c. 6.6 m/hr, and that for latewood is c. 1.4 m/hr. These linear flow rates are in order of magnitude agreement with the values in Table 1 if the heat-pulse technique underestimates true xylem sap flow rates by a factor possibly as great as 4, as suggested by Marshall (1958).

GENERAL DISCUSSION

The model predicts a variation of sap flow with applied pressure differential which conforms reasonably well to the experimental data. Yet the differences between the curves for earlywood and latewood in Figs. 2 and 3 clearly require further consideration: it is by no means certain whether the lower permeability of latewood cells can be regarded as advantageous to the plant in any way.

A clue to the answer to this question may lie in the differing magnitude of pressure differential required to cause full deflection of the membranes in the two types of cell. According to the model, pressure differentials of 5.6×10^5 Nm^{-2} and 6.8×10^7 Nm^{-2} are involved in sap filled earlywood and latewood respectively. However, in the living tree, the presence of rather lower sap potentials will lead to full displacement of the torus. This is because, in the living tree, the xylem sap potential is a function of the rate of water loss due to transpiration. The model predicts that once the maximum possible flow rate for a particular cell type has been reached, any further increase in xylem sap potential brings about an unstable situation: the increased sap potential leads to a higher pressure differential across the pit membrane; this in turn leads to a greater membrane deflection; a greater deflection will increase the sap potential still further. Complete deflection (aspiration) results. The critical pressure differential (that giving maximum possible flow rate) is 7.9×10^4 Nm^{-2} for earlywood, and 2.2×10^7 Nm^{-2} for latewood.

Yet the physiological evidence reviewed above suggests that neither of these critical pressure differentials is likely to be reached. Thus the only circumstances which might lead to aspiration in the living tree are those resulting from cavitation or gas embolism in the xylem. If a gas embolism develops in the transpiration stream—either in response to water stress (Milburn, 1973; Milburn & Johnson, 1966; Milburn & McLaughlin, 1974) or as a result of mechanical injury to the xylem—it will instantly expand very rapidly, since the xylem sap is in tension. The sudden loss of a xylem sap tension of c. 80 atmospheres would provide local pressure gradients quite large enough to aspirate earlywood pits.

In conifers, an embolism will spread from tracheid to tracheid only if two conditions are met: firstly the negative pressure gradient in the xylem must be great enough to force the gas liquid interface through the fine pores of the margo. The magnitude of the pressure gradient required to do this may be termed the bubble point of the margo. Order of magnitude calculations (Gregory & Petty, 1973) based on micrographs such as those in Plate 1 suggest that the bubble point of an earlywood margo might be about 5×10^5 Nm^{-2}. That for latewood could be somewhat lower because of the larger pore size: 2×10^5 Nm^{-2}. Secondly, these margo bubble points must clearly be less than the pressure gradients required to cause aspiration.

Where an embolism is present, but the pressure drop across the membrane is below the membrane bubble point, the membrane will still deflect somewhat. In this situation the pressure drop required to cause unit deflection will be rather smaller than that predicted by the model. The reason for this is as follows: while the *force* required to

cause aspiration is constant, when an interface is present just in front of the membrane, this force is applied over the entire membrane area. When no interface is present—as in the model—the force is applied over a somewhat smaller area due to the porosity of the margo. Since pressure is defined as force per unit area, the pressure gradient required to cause unit deflection will be greater in the absence of an interface than in the presence of one. The pressure drops required to cause aspiration given by Gregory & Petty (1973) were calculated on the assumption that an embolism was present.

However, if the deflection continues until full aspiration, the torus is sealed against the rim of the pit aperture. (In practice, surface roughness of the torus or the border may prevent a perfect seal; this possibility is ignored in the model). It follows that the pressure drop *finally effective* in causing full aspiration is applied only over the cross sectional area of the pit aperture. This conclusion is equally valid whether aspiration is brought about by a pressure gradient in the xylem sap stream or due to the presence of a gas embolism. For the pits considered here, the pressure drop necessary to cause aspiration in the presence of an embolism is thus again of the order of 5.6×10^5 and 6.8×10^7 Nm^{-2} for earlywood and latewood respectively. For the reason given above, these values are about an order of magnitude greater than those predicted by Gregory & Petty (1973) for pits of similar dimensions.

Since the bubble point of the margo and the aspiration pressure are similar in earlywood, it is quite possible that an embolism developing in an earlywood cell would not spread to adjacent cells, because all pits would aspirate. In the traditional view, such behaviour would be advantageous to the plant in limiting the extent of damage to the sap flow path.

At the same time, aspiration will probably not occur in latewood cells, since the margo bubble point is considerably lower than the aspiration pressure. As a result embolisms may spread from tracheid to tracheid. Indeed, Harris (1961) has observed that latewood in *Pseudotsuga menziesii*, *Pinus nigra*, and *Pinus radiata* is not an effective water conducting tissue owing to its low degree of saturation with water. Similar observations have been made by Coutts (1971) in *Abies grandis* and by Vintilla (1939) in *Pinus sylvestris*. Phillips (1933) observed that in a number of coniferous heartwoods most earlywood pits are aspirated, while most latewood pits are not.

The physiological significance of this different behaviour of earlywood and latewood membranes is obscure. Milburn & McLaughlin (1974) have shown that in *Plantago* plants subjected to high water stress, xylem cavitation is a regular—if not diurnal —occurrence. Repair of the transpiration stream during the night due to root pressure prevented this cavitation from being disasterous for the plant. It is conceivable that a similar mechanism for the repair of the transpiration stream could exist in temperate conifers. Such a mechanism might not be efficient in earlywood, even if present: aspiration is only partially reversible (Thomas & Kringstad, 1971). In latewood such a mechanism would be of more use. It is therefore possible that the formation of latewood represents an insurance against blockage of sap flow paths due to gas embolism.

Quite a different view of latewood embolism is taken by Coutts (personal communi-

cation). Coutts has evidence that in *Pinus contorta* the embolised latewood forms an important pathway for the transfer of oxygen to the roots of trees grown on water-logged sites. It is believed that this phenomenon does much to explain the survival of this species where soil moisture contents are apparently intolerably high for some other species.

Coutts further points out that embolised cells with unaspirated pits may provide an important reservoir into which oleoresins may flow in order to form a protective barrier against injury and infection.

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