FLOW OF WATER IN TREES

by

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ABSTRACT

Flow of water through a tree from soil to atmosphere was considered in terms of Darcy's equation, i.e. that flux was proportional to permeability of the xylem, viscosity of the sap, the water potential gradient and the pathway dimensions. Water content was postulated to vary according to water potential, thus introducing a storage component into the system, and permeability was postulated to vary with water content.

A model was set up to simulate the effect of evaporative demand on potential gradients, fluxes, water contents and permeabilities within a tree. Transpiration, the driving force, was defined using the Penman-Monteith equation, and bulk soil water potential was also defined. The dimensions, and relationships between water content, water potential and permeability were defined for each of the four compartments: leaves, branches, trunk and root. The stem was considered as a number of stem disks in hydraulic contact, in each of which flow was defined in terms of storage changes, water potential gradients between disks, and current permeability. The leaf, branch and root compartments were treated as additional elements in the catena.

To validate the model, measurements were made at two heights within intact stems of trees of (a) water potential, using the thermocouple psychrometer method or the pressure chamber method on bagged shoots, (b) water content using attenuation of gamma radiation, and (c) flux, using the heat pulse velocity method, for three *Pinus contorta* trees at the forest of Ae. In addition, laboratory measurements of permeability and water content of stem sections were made after harvesting the trees. Imposing various levels of overall water potential using either hydrostatic or osmotic potentials provided relationships between water content, water potential and permeability. Water potential induced only small changes in water content over the limited range of potentials used, but the same potentials caused large decreases in permeability.

The results of the field measurements were compared with the results of simulations. Although the field results were dominated by high precipitation, soil water potentials close to zero and low evaporative demand, there was evidence that the corresponding simulated values represented field conditions, although overestimating the effect of storage.

Measurement of saturated permeability and sapwood area at breast height in a range of trees were found to be closely related to leaf areas of those trees. There was a strong effect from a fertilizer treatment, and a species or site interaction. Within a single tree, permeability and sapwood area of individual internodes within the crown were also related to the total leaf area above those nodes. The use of dyes indicated that flow paths within particular rings appeared to be discrete, and associated with particular whorls according to ontogenetic development.

DECLARATION

I hereby declare that this thesis has been composed by myself from the results of my own work except where acknowledged to the contrary.

ACKNOWLEDGEMENTS

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INDEX OF CONTENTS

To Catherine

1.0 INTRODUCTION

The simple, lower plants are limited in size and habitat by the requirement for a moist environment for growth. Evolution of higher plants required the development of specialised tissues for the conduction of water, so that those organs exposed to a relatively dry environment could maintain the individual cells in an essentially aqueous medium.

The nature of water transport has long been a matter for conjecture, and the plethora of early postulates - encompassing passive, osmotic, vital, mechanistic and other theories - are well reviewed in texts such as that by Crafts _et_ al (1949).

The cohesion theory for water transport (Dixon, 1914) has gained general acceptance. The forces of cohesion between water molecules and adhesion to cell walls, permit maintenance of liquid continuity under conditions of considerable tension since the theoretical limit for the tensile strength of water is large (Section 4.2.1).

The cohesion mechanism depends on liquid continuity, since if a bubble is formed which fills a conducting element, the element is rendered ineffective. Most objections to the theory have been based on observation of gas in the conducting elements, although many of such observations are invalidated because early workers did not realise that the experimental conditions would have induced column rupture.

The concept that water flowed from the soil through a catena of conducting elements in the roots, stem, branches and leaves to the atmosphere was eventually followed by a unified system of description and measurement of water status in all these compartments. This reinforced the concept that flow occurs along gradients of potential. Electrical analogues have assisted in formalising the concepts of resistances, fluxes and potential differences, and their interrelation.

Non-steady state experiments have suggested the presence of transient storage in plants, since observations of phase lags and large changes in xylem water content can have no other explanation. The difficulty in making any measurement of water status in a tissue - be it flux, water content or water potential - has made it difficult to ascribe either resistance or storage to particular plant organs, since disruption of the columns of water in the xylem is difficult to prevent or even observe.

Recent advances in technology have made both new approaches and new methodology available in the study of plant water relations.

Firstly, the advances in computer science have made it possible to manipulate data on a scale otherwise impossible. In particular, modelling of plants with its requirement for rigorous mathematical statements and limits has formalised the necessity to define experimental conditions and relationships absolutely. Consequently, modelling can provide a framework for research programmes by coordinating experimental objectives and defining those objectives in terms of unified methodology, terminology, experimental treatments and mensuration.

Secondly, methods for measuring water status - water content, water potential, water permeability and flux - have been developed recently to the stage that measurements of some reliability are possible.

In this study, some of these measurement techniques have been used together, to try to establish (a) some of the factors which influence flow in trees, (b) whether changes in water content are related to changes in resistance, and (c) whether changes in stored water on a diurnal time scale has any significance.

To do this, flow was considered in terms of stem dimensions, potential gradient, permeability of wood, storage, and temporal changes in the relationships between water content, water potential and permeability.

Before measurements were made, a model based on Darcy's law was constructed, which contained hypotheses concerning the relationships between water content, water potential and permeability. This was subsequently developed further during the course of the study, enabling the measurements to be put together as a unified whole. Thus the various parameters could be evaluated in terms of the implications for the water relations of the whole tree.

Initially, the study was confined to that part of the trunk beneath the canopy. Subsequent development encompassed the significance of root resistance and the nature of evaporation from the crown, since it was found unrealistic to model flow within a single structure such as a stem.

2.1 MEASUREMENT OF PERMEABILITY

2.1.1 Background Literature and Review of Techniques

The steady-state flow of fluids through wood generally obeys Darcy's law, which states that:

$$K = Q.L.\eta \,/\, (A.\Delta P)$$

where K is the permeability (m^2)

Q is the flux $(m^3 s^{-1})$

L is the length of the sample (m)

A is the cross-sectional area of flow (m^2)

ΔP is the potential difference across the sample $(N\,m^{-2})$

η is the viscosity of the permeating fluid $(N\,s\,m^{-2})$

In this definition permeability is defined solely as a property of the wood matrix, and the viscosity of the permeating fluid is defined as a variable affecting the flow rate, independent of permeability. While this definition is unique, there is a confusion in terms in the literature. Heine (1970) gives the name relative conductivity, also given by Jarvis (1975) as an alternative to the term permeability. Specific conductivity is the term used by Farmer (1918), Cowan and Milthorpe (1968) and Peel (1965), but the use of the adjective 'specific' is now restricted to the meaning 'divided by mass' (Anon.,1969). Leyton (1975) has introduced another alternative, intrinsic permeability.

An alternative definition:

$$k = Q.L / (A \times \Delta P)$$

has caused further confusion. The term k, called conductivity by Ewart (1905,1908), Dixon (1918), Heine (1970) and Jarvis (1975), is the reciprocal of resistance to flow of a particular fluid through a particular matrix and is not a property of the matrix alone. Leyton (1975) calls this hydraulic conductivity.

Jarvis (1975) also uses the term conductance, defined as $Q / \Delta P$ with units of $m\,s^{-1}\,N^{-1}$. Effectively, this is the property measured by those workers who have equated flow with permeability by measuring flow rates at particular potential gradients with a given temperature, fluid and with a matrix of a particular size (e.g. Erickson et al, 1937; Zimmermann, 1978).

Measurement of Permeability

Permeability has been measured by many workers with both liquids and gases for a wide variety of species, sampling sites within the tree, conditions of growth and expermental procedures and objectives. Not surprisingly there are wide disparities in the results.

Measurement of Gas Permeability

Measurement of gas permeability requires that the wood be dried. When the measurements are used to indicate subsequent permeability to preservatives, the normal seasoning or drying treatment is used. However this treatment causes widespread aspiration of pits (Siau 1971), especially under conditions of rapid drying. This can be reduced by solvent exchange and subsequent drying of the new solvent (Erickson and Crawford 1959), but in turn also removes solvent-soluble extractives from the flow paths.

When Darcy's law is applied to gaseous flow, a correction must be applied because the potential gradients at any point are affected by the absolute pressure at that point since gases are compressible. A further correction is necessary to account for the fact that the gas velocity at the surface of a capillary is not zero, as a result of Knutsen or slip flow. Siau (1971) describes both corrections in detail.

Three effects from preparing samples should be considered.

(i) Surface preparation methods will influence the apparent permeability. Sawing to size causes tearing and clogging of the surface tracheids, particularly if the surface is then sanded or similarly smoothed. Unless the tracheid ends are unclogged by microtoming or similarly opening the ends, an additional resistance can grossly affect the measurement especially in short samples (Choong et al, 1975).

(ii) If the sample length is less than that of the tracheids, the effect of cutting both ends of tracheids will cause a large apparent increase in permeability (Siau, 1971).

(iii) Differences in the degree of saturation of the wood with different vapour pressures in the permeating gas causes changes in the permeability of the wood (Isaacs et al, 1971).

Measurement of Liquid Permeability

While the use of liquids to measure permeability eliminates the need to make corrections for the use of gas, several other complications arise. The first is that of decreasing flow with time -

an observation made on conifers by Huber and Merz (1958) and attributed to pit aspiration. However the phenomenon is also seen in hardwoods which do not have pits (Narayanamurti et al, 1951). The effect appears to result from to gas embolism, and can be removed by degassing the permeating liquid, and ultrafiltering to remove the nucleii on which gas bubbles form (Kelso et al, 1963). Degassing the sample before measurement will remove any embolisms already present.

As with gas permeability measurements, spuriously high values are found in samples which are sufficiently short to cut both ends of tracheids. Similarly, surfaces obstructed by dirt or preparation methods will give spuriously low values (Booker, 1977).

The relationship between viscosity and permeability was investigated by Chen and Hossfeld (1964). They flowed a range of glycerine solutions in water through Sitka spruce samples, and obtained a linear regression. The relationship between temperature of water and its viscosity is well established (Hardy and Cottingham, 1949; Swindells, unpubl. data). A change from 15 °C to 25 °C causes a decrease of 22% in viscosity, so that it is desirable to measure permeability in isothermal conditions.

Measurement of the cross-sectional area of flow must take inhomogeneities into consideration. Permeability of sapwood is some two orders of magnitude more than that of heartwood (Siau, 1971). Within sapwood, differences in permeability are associated with ring structure, i.e. the time of production of the tracheid during the year. In earlywood tracheids the lumen diameters, pit numbers and pit dimensions are all considerably larger than in latewood tracheids. Since flow in capillaries is proportional to the fourth power of the radius of a capillary (Poiseille's law), the largest size classes have a very much larger effect than would be suspected on the basis of cross-sectional area alone. Since longitudinal tracheids are by far the largest component of sapwood (93% - Panshin and de Zeeuw, 1970), differences in the proportion of other components - resin canals and parenchyma - have a small effect.

Darcy's law requires that for a particular permeability, flow is proportional to the applied pressure difference. Within the limits of gradients found in intact trees (Zimmermann and Brown, 1971; Hellkvist et al, 1974), this relationship holds (e.g. Sucoff et al, 1965). When the applied potential gradient exceeded 6.9 x 10^{6} N m^{-3} (i.e. more than an order of magnitude larger than *in vivo*) Sucoff et al found the relation between flow and pressure difference became curvilinear. Since this departure was repeatable and not time-dependent, aspiration of the pits and consequent stretching of the margo was not likely to be the cause. The curvilinearity were attributed to turbulence and non-laminar flow.

The values of permeability which have been most widely reported are those of Farmer (1918). They are quoted by Huber (1956) and requoted by many others, including Kramer (1959), Kramer and Kozlowski (1960), Cowan and Milthorpe (1968) and Stiles and Cocking (1969). The values fall in the approximate range of 4 - 6 x 10^{-13} m^2 for evergreens, and up to 4 x 10^{-12} for hardwoods. As with all early workers, Farmer did not deaerate either the permeating liquid or the sample, so that values reported earlier than those by Kelso et al (1963) are likely to be too low. Estimates of softwood permeability involving deaeration techniques have been made by Kelso et al (1963), Comstock (1965) and Markstrom and Hann (1972), and fall in the range of 10^{-12} — 10^{-14} m^2.

2.1.2 Theory of Techniques and Designs Used

The review of literature suggested that a basic measurement of permeability should be made under well-defined experimental conditions which could be related to conditions in vivo.

A basic measurement of the permeability of fully saturated, deaerated wood in the form of complete cross-sections of stem segments was chosen.

Each of the parameters involved in the Darcy equation was considered in turn:

(i) Flow

Measurement of flow involved collecting the outflow for a sufficient time to allow accurate sampling. Assessment was by weighing tared vessels, a method which was rapid and accurate to 0.01 cm^3. The measurement of time could be made within one second over a single measurement.

(ii) Length

Severing tracheids at each end of a sample would cause a large effect if the sample was shorter than the length of a tracheid, i.e. about 3 mm. The samples were always at least two orders of magnitude longer than this.

Of more significance was the nature of the end faces. As indicated in Section 2.1.1, damaged, dirty or otherwise occluded tracheid ends have a significant effect on measurements of permeability. Therefore the samples were prepared by planing the faces in such a way as to remove damaged ends. A check was made under a low-powered microscope. The accumulation of detritus on the inflow face was reduced to negligible levels by the use of clean techniques and the ultrafiltration of the permeating water.

(iii) Viscosity

A good relationship exists between the viscosity of pure water and its temperature (Section 2.1.1), so that temperature was measured rather than directly measuring viscosity. Isothermal conditions were necessary in order to allow a simple conversion, since temperature gradients within the sample would grossly complicate the estimation of viscosity.

Therefore the measurements of permeability were carried out in a room where ambient temperature could be controlled to 22 +/- 1.0 ^{o}C by using a fan heater and thermostat. A check on temperature was made using a thermograph. All samples and water used for permeation were kept in the room for at least 12 hours before use.

(iv) Area

The primary objective in measuring permeability was to obtain a relationship between potential gradients and flow at particular levels in the stem, rather than to measure the permeability of particular tissue types. Since heartwood was confirmed to be essentially non-conducting in the intact tree (see Section 2.1) and could be accurately defined using a dye technique, the measurements were made on the basis of total sapwood area. This basis (rather than the sum of individual lumen areas) was also used for calculations of sap flow based on heat pulse velocity (Section 2.3).

The nodes of stems are larger than the internode region and contain a considerable perturbation of the flow path associated with branching. Therefore unless the nodal area was being specifically investigated, samples were generally cut from the internodes, where the cross-sectional area was similar throughout the sample.

(v) Pressure Gradient

The range of pressure gradients found in vivo is of the order of 0.01 MPa m^{-1} (i.e. gravitation force) to 0.02 MPa m^{-1} (Zimmermann and Brown, 1971) or 0.03 MPa m^{-1} (Leyton, 1975) in rapidly transpiring trees. Therefore the potential gradients which were used for the measurement of permeability were of that order. While differences of potential can be applied using a gravitational head and measured with water manometers, it is necessary to provide for a constant applied pressure head and to be able to read the manometer scale with an accuracy of at least +/- 0.2 mm for the lowest applied pressure differentials.

(vi) Permeating Water

In order to prevent gas embolism or tracheid occlusion through the accumulation of detritus (see Section 2.1), the permeating water must be deaerated and filtered to at least 0.1 μm, i.e. approximately the size of the pores in the pit margo.

2.1.3 Description of the Equipment

Preparation of Water

Freshly distilled water was prefiltered using a 'Whatman' Model Gamma 12-250 in-line filter unit fitted with 'Whatman' Model Gamma 12-03 filters which are specified to remove 98% of particles 0.3 um or larger in diameter. This was followed by filtration through a 'Sartorius' Type SM 11309 cellulose nitrate filter, rated at 0.1um pore size. It was supported on a 145 mm diameter Perspex disc drilled at 5 mm centers with 1.6 mm holes, and set between two further disks 170 mm in diameter. These were separated from the filter element and suporting disk by gaskets made from 5 mm diameter butyl rubber. These just fitted over the rim of the filter element. The whole assembly was clamped together with eight brass bolts, nuts and washers. A head of water of 2.5 m was used overall.

The filtered water was deaerated by causing ultrasonic cavitation in the water while under vacuum. A 2 liter Buchner flask was filled with the filtered water, and a rubber plate fitted across the top through which projected the sonic probe of a MSE Model N114 ultrasonic sound generator. A vacuum was produced using an Edwards water jet pump, and when ultrasonic sound (approx. 25 000 cps) was generated, cavitation and spectacular frothing was produced, which eventually ceased. This procedure reduces the gas content by about 95% (Booker, pers. comm.).

Permeability experiments were conducted with water which had only just been deaerated. Since the rate of diffusion of gases through water is vey slow, reaeration is most likely to occur as a result of convection in the reservoir. Therefore after deaeration, the water was moved as little as possible, the surface area was restricted by the use of conical flasks, and the water was transferred only through tubes.

Pressure Head

Since a steady state measurement of permeability requires a constant applied pressure, a constant-head device was used. This consisted of a Perspex box 100 x 85 x 55 mm, fitted with inflow and outflow ports in the base. A float was constructed of sheet copper to just fit in the top of the box (reducing the surface area of the water in contact with the air), and pivoted towards one end. A brass plug was pivoted from the extreme end, so that it sealed the outlet when the box was full. The whole assembly was placed on a shelf which could be raised and lowered 2 m, by 32 mm increments. The feed reservoir (a 2 liter Buchner flask) was held on another shelf above the constant head device.

The Permeability Apparatus

The basic permeability apparatus consisted of two Perspex plates, 250 x 250 x 12.7 mm, fitted with inflow and outflow ports at the center (Fig 2.1). Eight aligned slots were cut around the edge to allow the plates to be clamped together over the wood sample using OBA threaded brass rod, washers and wingnuts. A gap between each wood face and plate was formed at either end by using 5 mm diameter butyl rubber gasket material, which also served to make the assembly watertight. The gaskets were made to fit over the cambium at each end, by measuring the required lengths and gluing with 'Loctite' IS

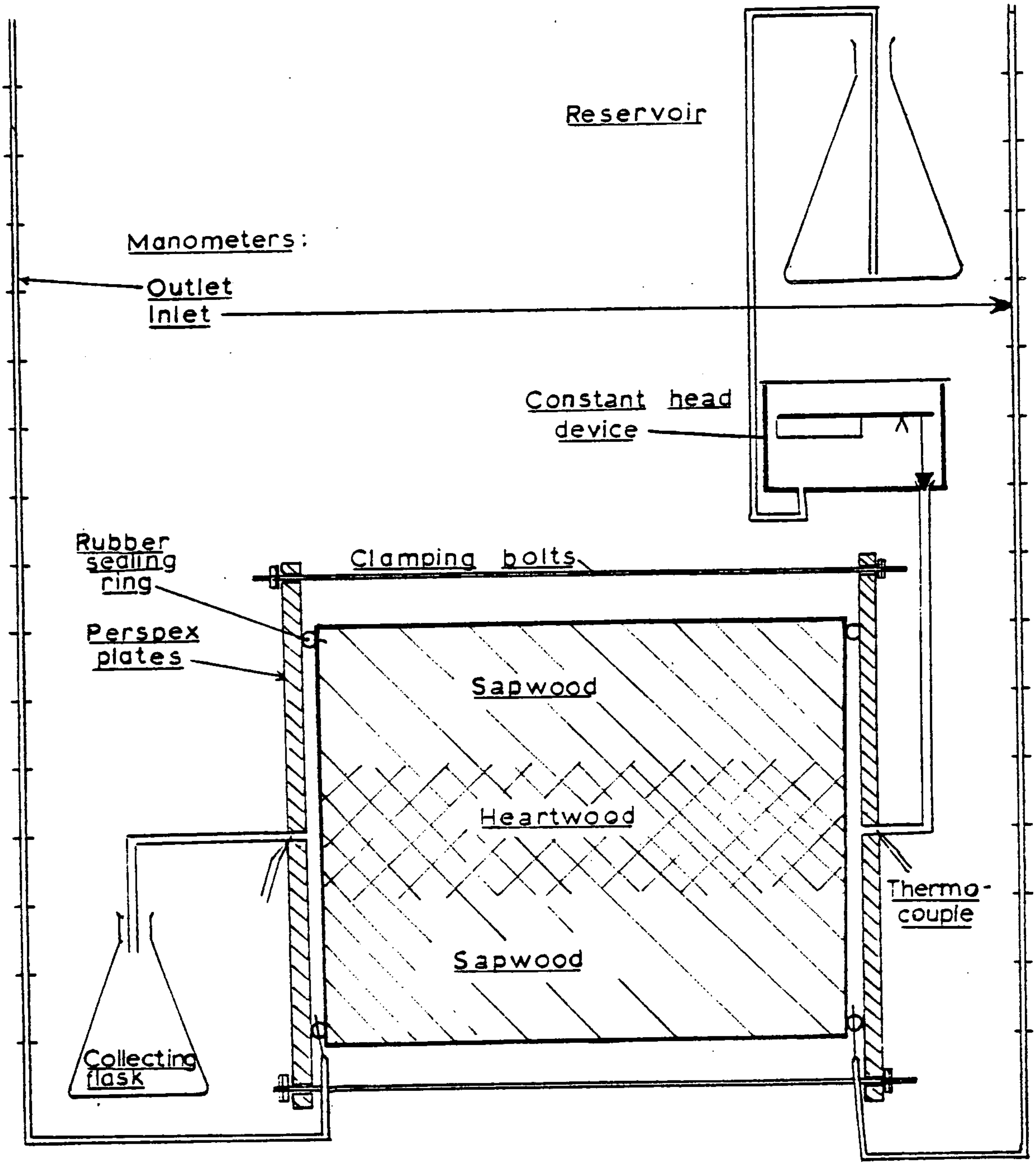

FIG. 2.1 Equipment for measuring saturated permeability.

496 cyanoacrylate adhesive.

The inflow and outflow ports were drilled with a 0.4 mm hole so that a 42 SWG copper/constantan thermocouple could be inserted into the flow path. The holes were resealed with 'Araldite' epoxy adhesive.

The cavities formed by the gaskets were required to be bled of air when setting up the equipment. Initially, a series of holes fitted with short OBA brass screws and sealing washers was used. Subsequently it was found that a hypodermic needle could be inserted through the gasket, simplifying the setting-up procedure considerably.

The standard length of stem section used was 250 mm, but this could be extended to at least 2.5 m if necessary, by using an adjustable steel frame made for the purpose.

Pressure Measurement

The inflow and outflow water manometers comprised two 2 m lengths of narrow bore glass tubing (2 mm ID), clamped on either side of two 1 m rules screwed end to end on a vertical base-board. Reflecting tape underneath the tubes, and a clamping slide cursor above allowed the manometers to be read while viewing horizontally. Use of the same rule to read both manometers facilitated a differential reading.

Initially the manometers were connected to the inflow and outflow tubes using TEE junctions fitted as close as possible to the end plates. Later it was found simpler to clamp the connecting tube to a hypodermic needle, which could be inserted through the rubber gasket directly into the gap between the wood and the Perspex. Although this slowed the response time from 1 - 2 seconds to perhaps 5 - 10 seconds, this was not a problem in steady-state measurements.

The outflow consisted of a tube fitted at the end with a 10 mm length of glass capillary tube, and clamped above a conical flask. The capillary tube prevented air entry into the main outlet tube under low flow rates. The conical flask could be changed for another without spillage, thus allowing for a sequence of continuous readings.

Experimental Procedures

Measurements of permeability were made as soon as practicable after harvesting the stems (usually within two days).

Immediately before measurement, the stem section to be used was prepared by cutting not less than 50 mm from each end with a bow saw to give the required length (not less than 250 mm). The ends were planed with a sharp chisel prepared for the purpose by carefully sharpening to an angle of 10°, and the stem section was soaked under deaerated water and several vacuum cycles for not less than 3 hours. Later it was found that the deaeration process could be carried out more simply by flowing deaerated water through the wood, i.e. as the initial flow during permeability measurement. Flow rates were observed to increase steadily over a period of some 20 - 60 minutes (depending on size), to a level equal to that of initially-deaerated stem sections (Fig. 2.2).

Care was taken that the ends remained wet, and that the stems remained horizontal as far as possible to prevent outflow under gravity.

The stem section was mounted between the permeability plates using previously measured and glued gaskets, which could be accurately placed by observation through the Perspex. Filtered, deaerated water was set up in the reservoir and constant head device, and then flowed

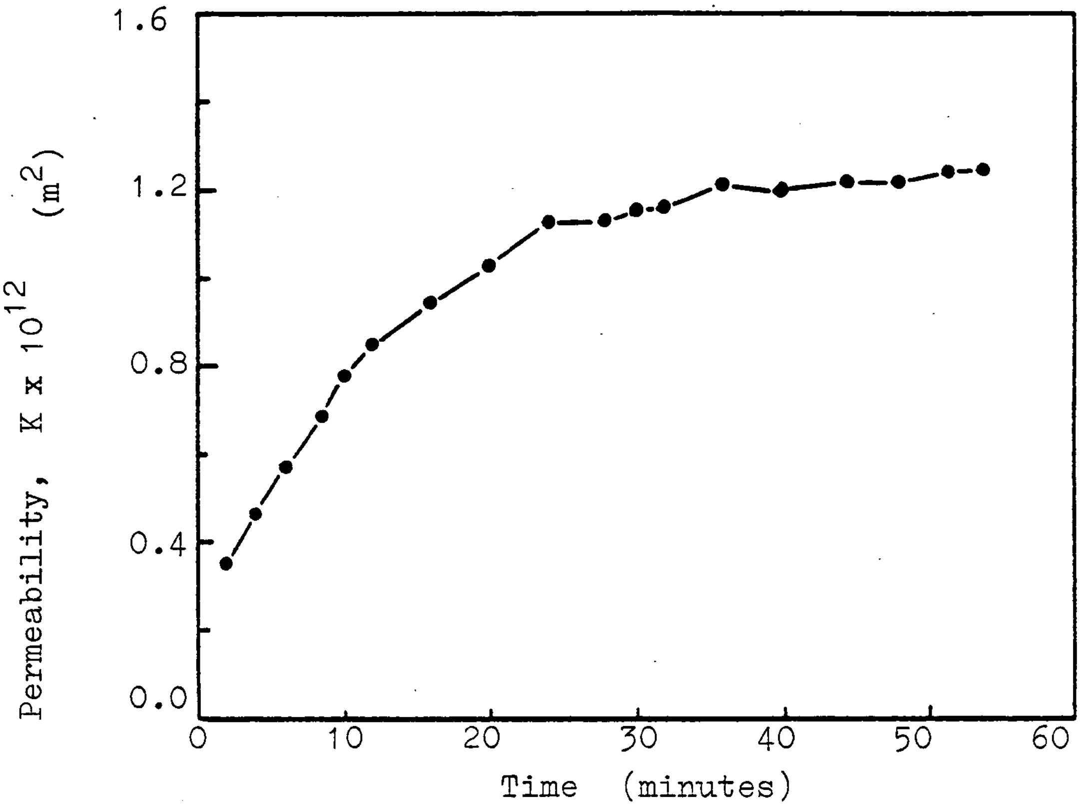

FIG. 2.2 Plot of permeability against time, commencing with an unsoaked stem section. As the log becomes saturated, permeability increases to a steady value.

into the inlet of the permeability apparatus, bleeding the displaced air at the same time by means of a hypodermic needle temporarily pushed through the gasket. The outflow was similarly filled from an auxillary supply, and the outlet capillary tube was then clamped above a tared conical flask. The manometers were attached as above.

Permeability measurements were made by releasing all the tube clamps, and simultaneously starting a stopwatch. The tared flask was replaced at timed intervals (usually three minutes), and the weighed outflow recorded together with the inlet and outlet pressures and temperatures.

On completion of the measurements, 20 ml of a solution of 0.1% Toluidine blue dye was introduced into the inflow. This dye is strongly bound by cellulose (see Section 2.1.3.1), and served to identify the flow paths.

After removal from the permeability apparatus, a thin layer of wood was removed from the inflow face, clearly showing those areas of the wood which were non-conducting, i.e. where the dye had not penetrated. The areas were traced and measured by cutting out and weighing the tracing paper. The definition of the heartwood was confirmed by axially cleaving the stem section, whereupon axial penetration in the conducting sapwood could be seen. If occlusion of the outer sapwood had occurred under the rubber gasket, this was also traced and estimated.

The length of the section was measured in each of four quadrants, and the mean calculated.

2.1.3.1 Use of Dyes to distinguish Flow Patterns

Besides the simple definition of the conducting sapwood area, Toluidine blue dye impregnation was used to estimate radial differences in flow rates.

To do this, sufficient dye solution was introduced to the inflow to penetrate a maximum of about 25 mm into the wood. When the wood was removed and cleaved radially and axially, the degree of penetration gave a striking visual impression of the axial permeability under the experimental conditions. Measurement of the penetration of the dye at any point along the radius was assumed to be proportional to the axial permeability at that point. Similarly, the vertical dyed area of each ring together with the circumferential length of the ring was taken as an indication of its total conducting capacity.

2.1.3.2 Imposition of Stress during Permeability Measurements

The standard conditions for measurement of permeability (Section 2.1.3) were designed for measurement at full saturation, with a water potential of zero at the outflow. However *in vivo*, flow at any point in the stem is the result of a potential gradient which may be at an overall potential considerably below zero. Therefore an attempt was made to impose this condition.

Three techniques were devised:

(i) Imposition of Hydrostatic Potential using Gravity

This simply involved lifting the permeability apparatus above the level of the inflow and outflow. Since these stayed the same relative to one another the potential gradient remained the same, but since the stem segment was higher an overall negative potential was applied to

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the wood. A head of only about 2.5 m of water (-0.025 MPa, the height of the ceiling) could be achieved this way.

(ii) Imposition of a Hydrostatic Potential using a Vacuum Pump

A range of suction pressures was set up using an 'Edwards' water jet pump and a series of water-filled tubes (Rose, 1967) to impose an overall stress on the stem section while still measuring permeability using a hydrostatic gradient. This gave very stable suction pressures, as long as there was only a low outflow of gas through the system.

Each point of the permeability measuring system that was previously exposed to the atmosphere was enclosed or contained, so that an overall suction could be applied to the whole system. This involved

(i) enclosing the entire constant-head device in a sealed desiccating vessel. A rubber bung with three holes in the top gave access to inflow and outflow tubes for the permeating fluid, as well as an evacuation tube.

(ii) A three-way tap system allowed removal of the outflow collecting flask without releasing the overall pressure or interrupting the continuity of flow.

(iii) The tops of the manometer tubes were also subject to the overall pressure, which was measured with a mercury manometer.

With this system, the outflow for particular time periods could be collected, the potential gradient and temperature measured, while maintaining an overall suction between 0 and 0.1 MPa.

(iii) Imposition of Stress using Osmotica

Since hydrostatic methods could not be used above 0.1 MPa without embolisms developing in the tubes of the apparatus, osmotica were used to produce larger stresses. A major difficulty was the requirement to prevent movement of osmotica into the wood, since in the living tree compensation for hydrostatic potentials by osmotic adjustment does not occur in the stem xylem.

This was overcome by casting a membrane on the ends of the stem section, and using a high molecular weight osmoticum (Polyethylene glycol, MW 20000) circulated rapidly using a variable-flow pump ('Charles Austen' Model C15/300) over each face (Fig. 2.3).

Because the membrane was found progressively to clog if cast directly on the wood (probably because of exuded resins), a layer of plaster-of-Paris was first cast directly on the wood. However passing distilled water through the stem dissolved the plaster sufficiently rapidly to cause a considerable change in overall permeability over the course of the experiment, and also loosened the membrane. This was avoided if a saturated solution of calcium sulphate was made up, filtered and then ultrafiltered to 0.45 um pore size, deaerated and used as the permeating fluid. It was subsequently found that the plaster should be laid as thinly as possible, and finally only a thin slurry was used, the surface of the wood being washed clear immediately after spreading. Observation of the surface under a low-powered microscope showed that the plaster had been carried into all the tracheid ends and other cavities. The additional resistance associated with a thicker layer of plaster was thus avoided.

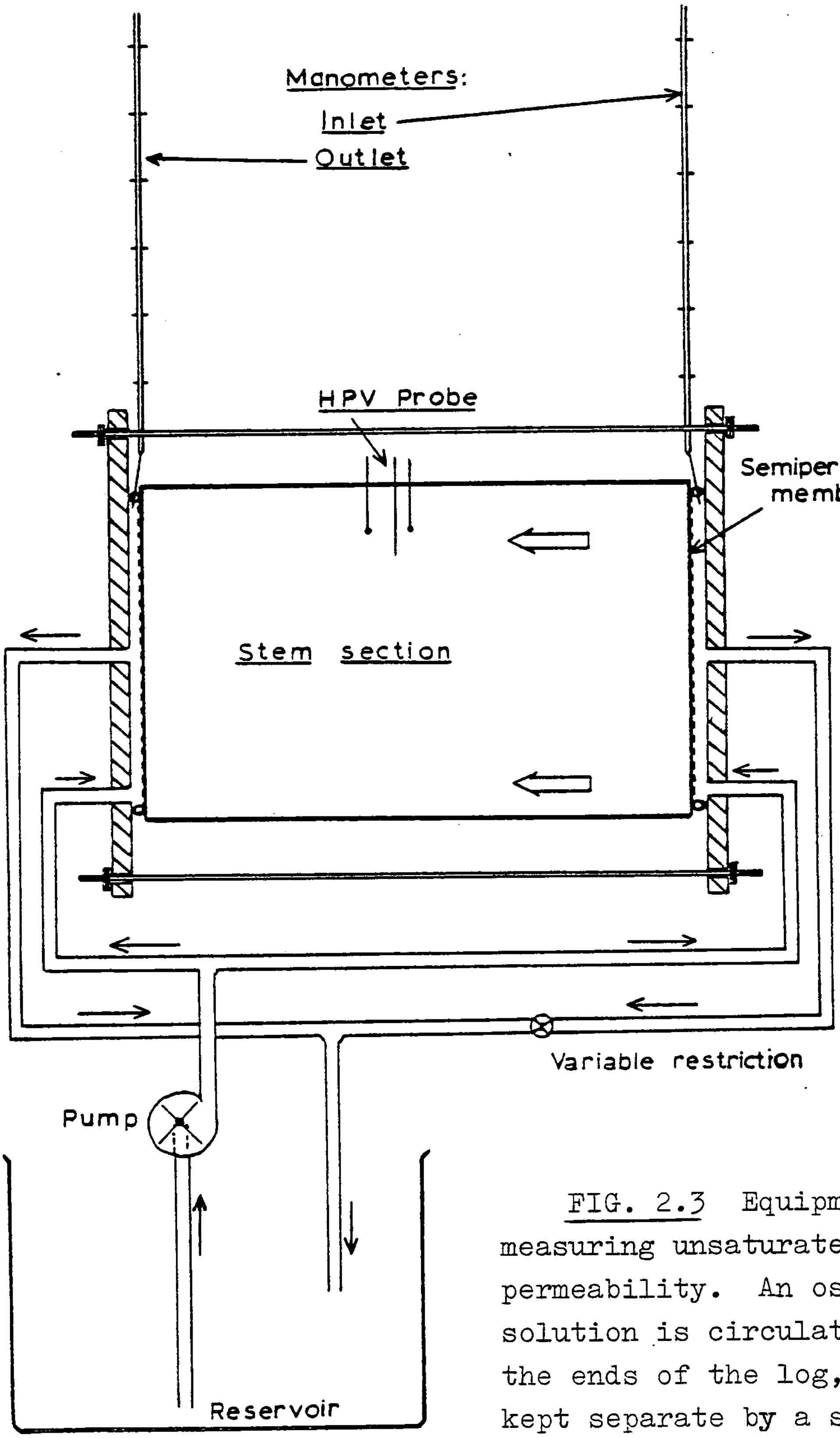


FIG. 2.3 Equipment for measuring unsaturated permeability. An osmotic solution is circulated over the ends of the log, but is kept separate by a semi-permeable membrane cast directly in place.

The membrane was cast using a necol collodion solution containing 14% nitrocellulose (BHD 'Collodion'). It was further diluted by adding two volumes of diethyl ether to one volume, making a solution of approximately 5%. This was applied by brushing as quickly as possible over the surface. Continuity of the membrane so formed was checked by placing drops of water on the surface. If gaps were present, the water disappeared rapidly.

The membrane was made as thin as possible to avoid adding an otherwise considerable resistance.

While osmotica could provide an overall stress, the potential gradient causing flow is more conveniently applied as before, i.e. as a hydrostatic gradient. This was produced by constricting the outflow tube from the proximal face of the stem section, raising the pressure over the face, and thus causing a hydrostatic pressure difference with respect to the other face.

Since the resulting flow could not be measured directly because of the ciculating fluid, a calibrated heat pulse velocity sensor was used (see Section 2.3).

The experimental protocol was as follows:

(i) The stem section was prepared including planing the ends.

(ii) Two heat pulse velocity sensors were implanted, the stem section was mounted in the permeability apparatus and using a filtered deaerated solution of calcium sulphate, the actual flow was calibrated against the heat pulse velocities.

(iii) The stem section was removed, and a plaster of Paris slurry followed by a Collodion membrane was applied to each end.

(iv) The stem was replaced in the permeability apparatus, and connected up so as to circulate a solution from a 5 l reservoir. The manometers were connected.

(v) A deaerated filtered solution of calcium sulphate was placed in the reservoir, all air was bled from the system and circulation was commenced.

(vi) By constricting the outlet from the proximal face, a hydrostatic gradient was produced between the faces. The resulting heat pulse velocities and manometer pressures were measured.

(vii) Deaerated stock solution of polyethylene glycol was substituted in the reservoir so as to produce successively, osmotic potentials of 0.01, 0.03, 10, and 0.3 MPa in the reservoir. At each potential, step (vi) was repeated.

This sequence was intended to produce a relationship between permeability (derived from the heat-pulse measured flow/potential gradient relationship) and the overall osmotically applied stress.

2.1.4 Data Processing

The following data were required each stem section:

(1) Length (mean of four measurements)

(2) Heartwood area (defined by failure to conduct dye)

(3) Sapwood area (limited by the cambium)

(4) Conducting area (i.e. sapwood area less any sapwood occluded by the gasket)

For each measurement, the following were recorded:

(1) Pressures at the inflow and outflow faces

(2) Time of permeation

(3) Temperature of inflow and outflow water, measured using thermojunctions referenced to an electronic ice point

(4) Weight of tare and outflow.

The data were processed by computer. Viscosity was calculated from the water temperatures and permeabilities were calculated in SI units. Intermediate output consisted of sequential observations of time, pressure difference, temperature, flow, permeability and the cumulated time from commencement, and finally the means and standard deviations for all measurements made for a particular pressure were calculated.

When the experiments with osmotica were run, flow was estimated directly from heat pulse velocities based on the initial calibration.

2.1.5 Error Analysis

Accuracy in the results depends on both lack of bias (systematic error), and precision (similarity to the mean).

No independent method of measuring permeability, and hence indicating the likelihood of bias was available. However field measurements of potential gradients and flow or transpiration rates gave some indication that the results were reasonable (see Discussion, Section 7.0).

However, good estimates of precision could be made, both by summing the estimated errors in reading the various measurements as in the following table, and by analysing the variation in a succession of results for the same conditions.

	Range	Precision	Error
Pressure	100-2000 mm	+/-0.1	0.005-0.1%
Temperature	21.5-24.0 °C	+/-0.15	0.6-0.7%
Flow Rate	10-150 mlmin-1	+/-0.01	0.007-0.1%
Length	250-2500 mm	+/-0.2	0.008-0.08%
Area	10-400 mm^2	+/-0.1	0.025-1.0%
		Total	0.6-1.98%

A worst-case of 2% error suggests that most of any error which occurs in the permeability measurement originates because of real changes in the wood. In the experimental conditions, these are likely to result from changes in the volume fractions of air and water, since the wood matrix is dimensionally rather rigid, and from changes in the resistance within the pits.

Typically, a standard deviation for a succession of readings under the same experimental conditions was 0.013×10^{-12} for a mean of 4.585×10^{-12} m^2 (fifteen measurements over 90 minutes), i.e. 0.3%.

2.2 WATER CONTENT MEASUREMENT

2.2.1 Background Literature and Review of Techniques

The various terms used for the expression of water content can be resolved around the basic units of volume fraction. Wood can be considered as comprising three separate volume fractions:

(i) Wood (F_w), composed of

(a) Dry solid cell wall substance having a weight density of 1530 kg m^{-3} in water, a figure that varies little between or within species, given the same experimental conditions (Panshin and de Zeeuw, 1970).

(b) Living cell contents. In mature wood, the contribution of the non-water fraction of living cell contents to the 'wood' fraction is small, and mainly associated with ray parenchyma and resin canals. Typically, wood rays (much of which is composed of tracheids) comprise 6.00% of white pine wood, and longitudinal resin canals comprise 1.00%. The remainder consists of longitudinal tracheids (Panshin and de Zeeuw, 1970). Therefore the material left on oven drying wood is almost entirely the cell wall material of tracheids. Use of the density figure of 1530 kg m^{-3} to relate oven-dry weight to volume of woody material will result in little error.

(ii) Water (F_h), i.e. the water removed by oven-drying, typically at 85 to 103 °C, to constant weight. It includes both intra- and inter-cellular water.

(iii) Gas (F_g). i.e. void space filled by air, water vapour or other gases under unknown pressure or tension. The mass of such included gases can be considered negligible.

These three volume fractions can be combined to give any of the commonly used measures of water content, assuming that the density of water is 1000 kg m^{-3} and that that of the gas fraction is zero:

Water content (fresh weight basis) $= \left(F_h /(F_h + F_w)\right) \times 1530$.

Water content (dry weight basis) $= F_h /(F_w \times 1530)$

Relative water content $= F_h/(F_g + F_h)$

It is clear that none of these various combinations alone give a complete description of the extent of the three phases. Consequently, water content will be referred to primarily in terms of volume fraction, as being a more satisfactory basic unit for describing water content in a wood matrix.

Techniques for measuring water contents of wood can be grouped as either destructive or nondestructive. Destructive techniques are usually direct, relying on separation or removal of water and can produce a generally accurate, repeatable measurement. However, sampling by excision is difficult because any interference with the intact tracheid system tends to result in a redistribution of water as a result of both embolism of tracheids and physically squeezing the tissues. Simultaneous cutting at two points on the stem may avoid the effects of rapid withdrawal of water away from a single cut, and taking a large sample will minimise the relative effect of embolism of tracheids close to the cut. Sampling by increment borer is now recognised as tending to give spuriously low results. Non-destructive methods can be used, often with minimal or negligible interference with the stem of an intact tree, relying on some property of water or indirect consequence to provide the measurement. Calibration is usually required.

(i) Destructive Methods

Gravimetric Methods

The basic gravimetric method consists of weighing the moist sample and then drying to a constant 'oven-dry weight' at a temperature of typically, 85 - 103 degrees C. Errors of as much as 0.5% can result from incomplete drying where the ambient temperature and humidity can cause a significant vapour pressure within the oven. Again, higher temperatures also remove volatile constituents of the wood. Use of a vacuum oven reduces both effects. The variation seen in gravimetric assessment of leaves or fleshy organs as a result of growth or diurnal changes in labile carbohydrates will be negligible in trunks of trees, since F_w forms a comparatively large fraction and there are comparatively few live tissues containing carbohydrates.

Distillation Methods

Where evaporation of volatile components is a significant or unknown factor, water can be extracted within a reflux condenser system with an immiscible solvent to retain these components: i.e. the amount of water removed is measured with a micropipette (Miller, 1942), or by weighing (Miller, 1943), rather than weighing the wood fraction as in the standard gravimetric procedure.

Titration Method

A further way of overcoming the difficulty of loss of volatile constituents is to use direct titration of the water fraction, the method of Karl Fischer (1935) based on the oxidation of sulphur dioxide by iodine in the presence of water, using a standardised 'Fischer Reagent'. Determination of the water content of woody material can be carried out by soaking the tissue in methanol in a sealed tube, and titrating an aliquot (Greene and Marvin, 1958).

(ii) Nondestructive Methods

Changes in Dimensions

Changes in the sizes of various organs can indicate the degree of hydration of tissues which result from changes in water potential. Leaf thickness can be measured directly (Bachmann, 1922, Meidner, 1952) using mechanical devices, but the change in leaf thickness which is correlated with water content was found to be only about 10%, or 10 μm in a total thickness of 100 μm for a thin leaf

(Meidner, op. cit.). Therefore measurements better than 1 um are required even for an accuracy of 10%. A better method is that of beta gauging, reviewed by Nakayama and Ehrler (1964), Barrs (1968) and Slavik (1974). Jarvis and Slatyer (1966) devised a simplified calibration system. Use of beta radiation is only suitable with thin tissue since the rate of attenuation is high, and the range of penetration is limited, in contrast to the true exponential decay of gamma radiation (Wang and Willis, 1965).

Changes in stem diameter have frequently been demonstrated (Barrs, 1968; Hinckley et al, 1978; Woodman, 1979; Lassoie, 1979). Dendrographs provide a more accurate measurement of diameter changes than dendrometers (Braekke and Kozlowski, 1975) and demonstrate continuous changes better (see Kramer and Kozlowski, 1962 for a review of dendrographs, and Borman and Kozlowski, 1962 for a review of dendrometers). Greenidge (1962) showed however that decapitated trees had patterns of diurnal change that were similar to those of entire trees; this is difficult to equate with a relationship between water status and trunk diameter. Further, Richards (1973) showed that most variation in stem diameter occurred exterior to the xylem, presumably in the cambium and phloem tissue. Thus although good correlations exist between stem diameter and either environmental variables or parameters describing the water status of the tree, it appears that such stem deformation may not be simply related to xylem water potential and tissue size. Phloem water potential has components of both hydrostatic potential (which appears to be the main cause of changes in tissue dimensions), and osmotic potential, which is affected not only by cell metabolism but source/detector system to measure trunk density, and the two measurements could distinguish between the wood and water fractions.

Whereas beta rays are suitable for thin tissues, stems require a radiation of higher energy which will penetrate further through woody tissues. Gamma radiation has been used to follow diurnal changes in trunk water content (Klemm 1959). The use of attenuation of gamma radiation to measure density is reviewed more fully in the next section.

The experimental requirements of this project were for (a) a reliable standard method of measuring volume fractions of wood, water and gas phases of excised samples, and (b) a non-destructive method of measuring fluctuations in water content in undisturbed stems of trees in the field. Clearly gravimetric analysis would fulfil the first requirement. Of the nondestructive techniques, either measurement of capacitance or of gamma attenuation offered the best prospect. However, the gamma attenuation technique could be used to investigate radial differences in water content since it depends on a high degree of collimation (see 2.2.4). Therefore, this method was selected for the field measurement of diurnal changes in water content.

2.2.2 Theory of the Technique and the Design Used

Gamma rays are a form of electromagnetic radiation within the energy range 0.63 KeV - 0.63 MeV. This range overlaps that of X-rays which are found from several electron volts upward, but whereas X-rays are produced by extranuclear excitation (either by radionuclides or by bombardment of a metallic target by fast electrons), gamma rays are produced from some transformation of the nucleii of radionuclides.

Gamma radiation can be considered as discrete quanta or photons for the purpose of describing energy interchange. The energy (in electron volts), is linearly related to wavelength, velocity and frequency.

Since photons have neither charge nor significant mass, there is no appreciable force field to interact directly with atoms in their path to produce ionisation. However there are no less than six ways in which gamma rays can interact with matter, three of which are significant to our purpose (Wang and Willis, 1965):

(1) Photoelectric Effect

At low energies (less than 0.5 MeV) a gamma ray will transfer all its energy to eject a target electron. The energy of the ejected electron will equal that of the photon less that of the orbital binding force. The electron can then interact with other atoms in its path to produce ionisation.

(2) Compton Effect

At medium energies of 0.5 - 1.0 MeV, impact of a gamma photon with an orbital electron will cause ejection of the electron with only part of the photon energy, and deflection of the photon in a new direction with reduced energy. Consequently, the energy of the ejected electron can be widely variable.

(3) Pair Production

If the gamma photon has an energy greater than the rest mass of one electron and one positron (1.02 MeV), it can interact directly with the nuclear force field, converting all its energy into a positron and an electron which are ejected. The former is rapidly annihilated with the production of gamma radiation, but the latter can cause ionisation directly.

If the energy of a photon is low, it has a larger probability of capture, so that the mean penetration distance is a function of energy. The rate of removal can be described by the function $(- u_1 . I)$, where u_1 is the linear attenuation coefficient and I is the number of photons in the beam. The attenuation coefficient is affected by both the medium and the energy. If the photons are monoenergetic and in the form of a narrow beam so that reinforcement by scattered radiation does not occur, attenuation through the slice can be considered as the sum of attenuation through many thin slices. Integration of the function

$(-u_l I)$

results in a logarithmic function (Wang and Willis 1965, Appendix I):

$$I=I_o e^{-u_l x} \qquad (2.1)$$

where x is the thickness of the medium

I_o is the incident radiation.

Alternatively, we can use the mass attenuation coefficient, <u>vis</u>:

$u_m = u_l / \sigma$

where σ is the mass per unit area. Since density is effectively included, u_m is more nearly independent of the nature of the medium.

Sensitivity (the change in intensity with density) is found by differentiating equation 2.1 with respect to σ, <u>vis</u>:

$$dI/d\sigma = -uI = -uI_o e^{-u.\sigma}$$

To find where sensitivity is maximised, we may differentiate again with respect to u_l, the linear attenuation coefficient:

$$d/du_l(dI/d\sigma) = -I_o e^{-u.\sigma} (1-u.\sigma)$$

and make this equal to zero.

Thus $u_l = 1/\sigma$

If the density is constant, a similar procedure will give

$$x = 1/u_{l}$$

where $1/u_{l}$ is the mean path length of the gamma photon (Berman and Harris, 1954) i.e. for maximum sensitivity, the length of the specimen should equal the mean path length. In an ideal situation therefore, a narrow, monoenergetic, collimated beam incident upon a thin slab of absorbant medium will reduce the effects of scatter in reinforcing the apparent penetration of the beam. This geometry suggests the attenuation of such a beam will be closely dependent on the mass absorption coefficient of the medium, and hence can be used to measure changes in density of the medium.

Such fixed-geometry, collimated source/detector systems using gamma radiation have been used to measure density changes in soil (Herkelrath and Miller, 1976, Ferguson and Gardner, 1962, van Bavel et al, 1957), in concrete (Harland, 1966), in chipboard (May et al, 1976), in excised wood blocks (Woods et al, 1965), in increment borings for tree ring analysis (Woods 1974) and across stems of living trees (Olszyczka and Crowther, pers. comm.).

A fixed-geometry system appeared to be the most suitable technique to obtain non-destructive measurements of density in tree stems. Further, it offered the possibility of investigating radial differences in density by making sequential measurements across parallel chords.

2.2.3 Design of the Equipment

The source selected was Caesium-137, which produces 84.8% of its radiation intensity over a half-life of 30.2 years at 661.6 KeV (Heath, 1971). This energy level gives good penetration and reduced possibility of scatter compared to less energetic sources such as Americium-243 (Cattrell, *pers. comm.*). Caesium-137 produces ionisations for scintillation counting virtually entirely by the Compton effect, thus closely approximating a monoenergetic source. Other nuclides had other disadvantages such as shorter life, multiple energy peaks or lack of availability.

A source of 13 mCi activity was available, and provided a good compromise between the shielding required (450 mm of lead) and available activity. The source was held at the centre of a lead cylinder 90 x 90 mm, with a 5 mm collimation hole from the centre of one face. A lead plate was fitted with a steel centre-pin which could enter the collimation hole, and a suitable holding mechanism and labelling system was fitted.

The detector system consisted of a sodium iodide crystal scintillation detector and scalar ratemeter. The crystal (25.4 x 50.8 mm) could be shielded within a cylinder of lead 90 mm x 90 mm with a 5 mm collimation hole, and the scintillations were detected by a Model DM1-1 photomultiplier tube linked to a portable scaler spectrometer Model PSR6 (Nuclear Enterprises Ltd, Edinburgh), operated in the differential mode. The equipment permitted counting of the 661 KeV peak while electronically removing the effect of other energy levels, for a range of counting times.

Holders for both source and detector on a rigid steel yoke permitted rapid, repeatable mounting (Fig. 2.4). The distance between the two collimators could accommodate tree diameters up to 250 mm.

A rigid steel table was constructed in two parts, so that it could be fitted around and clamped to tree trunks of various sizes in a stable, repeatable manner. The yoke was placed on the table by sliding two spikes fitted under the two collimators into two slides (of the type used for filing cabinets) which were mounted on either side of the table. A further spike on the rear beam of the yoke could be fitted into holes spaced exactly 10 mm apart on a moveable bar fitted to the table. Adjusting the bar permitted the radiation beam to be passed through various parallel chords starting exactly tangential to the outside of the tree.

A saddle of aluminium was constructed to fit between the two collimators, so that from one to five solid 'Perspex' cylinders, 50 mm x 50 mm could be inserted into the beam for calibration purposes.

2.2.4 Data Processing

The data collected at each measuring time consisted of (i) a count of radiation through air, (ii) counts through one to five 'Perspex' blocks, and counts of attenuation through parallel chords 10 mm apart starting 10 mm in from the tangent at the stem surface.

Data which were constant for each measurement site comprised (i)

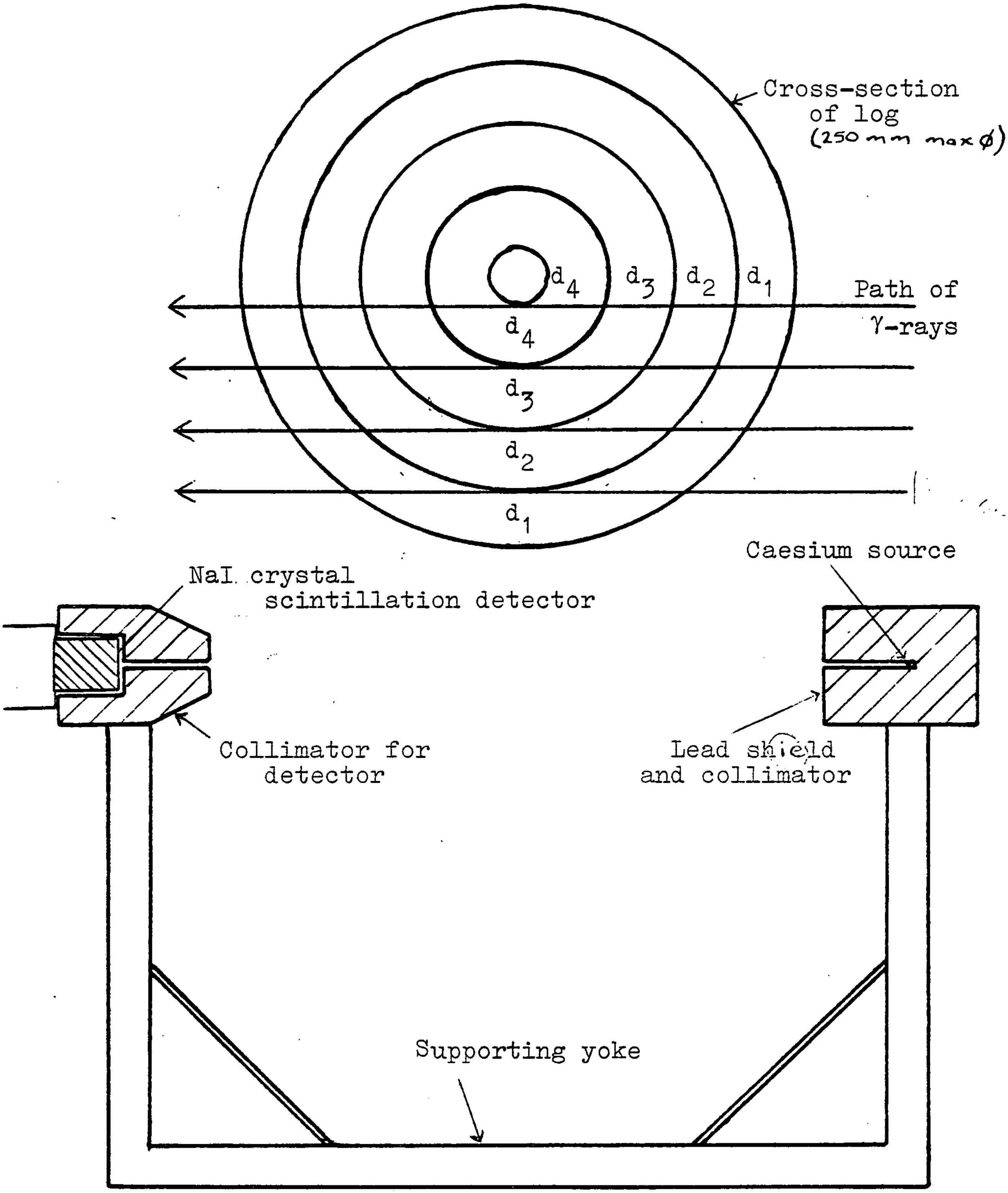


FIG. 2.4 Measurement of water content using γ-ray attenuation. Densities of chords are measured as shown. By assuming homogenous tori, the radial increments of density can be calculated.

chord lengths, (ii) stem diameter at the measurement point, and (iii) oven-dry densities for 10 mm increments starting from (and including) the outer bark.

The expression relating attenuation to path length (equation 2.1) is an expression between incident and emergent path lengths, path length and density, for a given attenuation coefficient. It can be rearranged to give any of these, if the remaining parameters are known.

The measurement site at a particular height up the stem can be considered for analysis purposes as a series of concentric tori, each with a rectangular cross-section and homogenous density (Fig. 2.4). A photon beam passed through the outermost torus will establish its density. The second beam (i.e. the second chord) will intersect the two outermost tori, but since all path lengths can be established mathematically and the density of the first torus is known, the density of the second torus can be established. A process of analogous iterations can sequentially establish the densities of all the tori, to produce a radial sequence.

Clearly this model is intended to fit a perfectly round tree. Since the densities within the sapwood are likely to be rather similar, most deviation will occur if the tree is not round. Some standardisation of the path lengths is desirable to accommodate small deviations from cicularity, and is accomplished as follows:

The mean density of each chord is first established using the measured path lengths (bark to bark) and the incident and emergent radiation levels. Then using the measured cicumference, a standardised model is formulated assuming a round trunk comprising concentric tori 10 mm thick. Chords 10 mm apart intersect with the edges of these tori.

The path length of the beam within each torus, for each chord, can be found. Let R be the radius of the tree, T the torus (numbered from the outside) C the chord (also numbered from the outside) and LTC the path length for one torus and one chord.

Using Pythagorus' Theorum:

$$\begin{aligned} LTC &= 2\sqrt{[(R-C+T)^2 - (R-C)^2]} \\ &\quad - 2\sqrt{[(R-C+T-1)^2 - (R-C)^2]} \\ &= 2\sqrt{(2T(R-C) + T^2)} - 2\sqrt{(2T(R-C-1) + T^2)} \end{aligned}$$

The linear attenuation coefficient (u_m) is found from a linear regession fitted on the relation between logarithmic attenuation and density of the 'Perspex' blocks. The density of each 10 mm increment can then be calculated, as above (see also Appendix II - Programme to calculate water content from radiation attennuation).

The density figure represents the mass of water plus the mass of woody material per unit volume i.e. ($F_h + F_w$ 1530) kg m^{-3}. If the oven-dry density is known from final destructive sampling of part or all of the stem, all three volume fractions (F_h, F_w and F_g) can be derived, and constituted into any of the required expressions of water content. Further, the absolute volume of water within each entire torus, and hence the entire stem cross-section can be calculated.

2.2.5 Testing the Technique and Analysis of Errors

For a set of readings to be accurate (closely similar to the mean), they must be both precise (closely similar within themselves), and unbiassed (not deviating from the mean in a systematic manner). Testing of any technique must incorporate consideration of both aspects.

Counts of gamma radiation by a particular source/detector system form a Poisson distribution. Thus precision of a radiation counting method is ultimately limited by the expression:

$$\text{Fractional standard deviation} = 1/\sqrt{N}$$

where N is a particular count of photons in such a Poisson distribution. Therefore in a given experiment, sufficient counts must be taken to permit this basic precision. A further increase in counts taken will be required to allow for additional random errors. These could arise from

(1) Distal displacement of the source and detector. Intensity of radiation is an inverse-square function of distance (D) from the source:

$$I = k\,D^{-2}$$

Sensitivity to distal movement is therefore

$$I/dI = -2\,dD/D \qquad \text{(Berman and Harris, 1954).}$$

Therefore at an overall spacing of 0.30 m, a 1% change in intensity would result from a change in spacing of 1.5 mm. Clearly a fixed spacing is essential for repeatable readings, and a rigid yoke is necessary.

(2) Angular displacement of the source and detector. The pattern of the beam 300 mm away from the source showed that the penumbra was some 60 mm in diameter. There did not appear to be sufficient difference within this area for small changes in angular displacement to have any effect whatever. However the response of the crystal detector system was sensitive to rotational changes of the unit within the detector collimator.

(3) Temperature effects. Although the temperature stability of the spectrometer was specified to be less than 2 parts per million per degree C, the temperature response of the crystal detector was not known.

Thus when comparing measurements made at different times, both changes in the arrangement and spacing of the source/detector system, and changes in ambient conditions are potential sources of additional random and systematic error. For this reason, all measurements were preceded by a calibration using the Perspex standard blocks.

2.3 MEASUREMENT OF FLOW

2.3.1 Background Literature and Review of Techniques

To measure flow in stems of intact trees without interference with the flow path is difficult. Three general approaches have been made: the use of isotopes or dyes as markers, measurement of perturbations of electrical phenomena caused by flow, and the use of heat as a marker in the sap stream.

Huber (1932) first used a radioisotope, thorium-B, to measure flow rates in various conifers. The technique was developed to estimate sap velocities or transpiration by a succession of other workers: Postlethwait and Rogers (1958), Ferrell et al (1960), Klemm and Klemm (1964), Kline et al (1970, 1976), Owston et al (1972), Heine and Farr (1973), Jordan and Kline (1977) and Waring and Roberts (1979). Typically, P-32 was injected in the base or root of a tree and the rate of ascent related to the total flux using the cross-sectional conducting area (e.g. Waring and Roberts, 1979). Alternatively, deuterium-labelled water can be used and the results of twig analyses assessed by the 'Principle of Occupancy' (described by Orr and Gillespie, 1968), as in the experiments of Kline et al, (1970, 1976). In general all tracer techniques are more suitable for studies of whole trees over several days, since multiple applications of tracers in a short time are not practicable, and measurement precision precludes close examination of diurnal trends.

Dyes have normally been used to delimit areas of conduction (Greenidge, 1952; Vite and Rudinsky, 1959) but they can also be used to give an indication of velocity of sap flow. However the method is destructive, and more suitable for obtaining relative flow rates in different parts of the sapwood.

Steady-state heat transfer methods can be used in the form of a heat balance (Daum, 1967) or by measuring downstream variations in temperature from a continuous heat input (Vieweg and Ziegler, 1960; Cermak _et al_, 1973, 1976a, 1976b). Both require knowledge of specific heat and diffusivity of heat of the wet wood, but are suitable for continuous measurement.

Methods involving electrical perturbations caused by flow are of two types:

(i) The 'magneto-hydrodynamic' system, where a magnetic field is imposed between two diametrically placed electrodes contacting a stem (Sherriff, 1972). The movement of sap induces a voltage, since the sap stream is effectively a conductor moving across a magnetic field. If the stem is considered to comprise a large number of small tubes rather than a single tube the induced voltage is directly proportional to the radius of the stem, as well as the magnetic flux density and the sap velocity (Sherriff, 1974). Sensitivity is proportional to the magnetic flux density, but inversely proportional to the stem radius and the technique is limited to stem diameters less than 15 - 20 mm. Roa and Pickard (1975) showed that electrical conductivity in stems is anisotropic, so that recalibration is frequently required. They consider the method is suitable for short-term relative changes only.

(ii) Tyree and Zimmermann (1971) used the so-called Delta-I system to measure flow of KCl solution in excised stems. An alternating voltage passed between two electrodes placed 1 - 3 m apart axially produced a larger current in the direction of liquid flow than against it due to the larger 'frictional drag'. Such a current difference is proportional to the liquid flow and to the hydraulic conductivity of the pathway. Although potentially useful in living trees, the current differences in excised trees were an order of magnitude lower than those found in intact stems using KCl solution.

(iii) Heat pulse velocity

Huber (1932) first used heat pulses to estimate sap velocity using a single thermocouple downstream from a heater wire, and he encouraged subsequent early work (Baumgartner, 1934; Huber and Schmidt, 1936). The inherent difficulties in deriving sap velocities from such a system were comprehensively analysed by Pickard (1973), who concluded that even using an exponentially increasing heat pulse (his 'simplest system'), the mathematics and assumptions made its usefulness doubtful.

However Huber and Schmidt (1937) realising these difficulties, had conceived the 'compensation method' where the sensors were placed both up-stream and down-stream from a heater wire. The distance to the down-stream sensor was made larger than the distance to the up-stream sensor, and a heat pulse from the heater reached the lower (closer) sensor first, by diffusion. Sap flow carried the pulse upward until the sensors were equidistant from the centre of the pulse. Thus the sensors were initially 'unbalanced' from a state of thermal equilibrium, but were carried back through that equilibrium by the effect of sap movement. A compensating effect was apparent with respect to movement of heat by diffusion, since axial conduction to both sensors was equal even with changing overall water contents. Thus movement of the heat pulse by convection (sap flow) was isolated from movement by diffusion. However Huber incorrectly assumed that the heat pulse velocity thus found was identical to the sap velocity.

Although the compensation method was a considerable advance and simplification, it soon became apparent that heat pulse velocity underestimated sap velocity. The rigorous approach of Marshall's (1958) analysis showed that heat pulse velocity was a function not only of sap velocity, but also the ratios of (i) lumen conducting area to total sapwood area, (ii) density of sap to that of wet wood, and (iii) specific heats of sap to that of wet wood. He considered that the heat pulse moved as if the sap and the woody matrix was a homogenous medium, heat interchanging freely between sap and wood.

A final consideration in the development of the technique arises from the effect of wounding the tree during implantation, invalidating Marshall's (1958) assumption of homogeneity of the woody matrix. This has been analysed by Swanson (pers. comm.) using a computer model for a wide variety of configurations and probe construction materials, and a range of wound dimensions. Using the results of those analyses, sap velocities can be estimated from heat pulse velocities if the wound size, probe characteristics and sapwood water content are known. Swanson also pointed out that the compensation method can be used by measuring the maximum temperatures reached in each of the sensors at two time periods after the initiation of the pulse - a method which is more sensitive for low flows.

Development of Heater Systems

Huber's original (1932) equipment used a resistance wire inserted beneath the bark. Small twigs have been used with heaters consisting of resistance wire wrapped around the stem (Closs, 1958), or held to one side of the stem (Saddler and Pitman, 1970; Heine and Farr, 1972). More recently, Swanson (1974a) used a resistance wire encased in a thin copper tube, making electrical contact at the inner end. This was inserted as a line source into the sapwood.

Indirect heating has been attempted using induction from radiofrequency power (Ladefoged, 1960, 1963; Doley and Greive, 1966; Leyton, 1970), but the practical difficulties in application appear to outweigh considerably any conceptual advantage. Leyton (1970) has used two 'heat exchange units', each comprising one side of a single thermopile and a separate heating element, housed between brass shims. The elements are continuously heated, and the output of the thermopile is dependent on the temperature difference caused by sap flow.

The various forms of measurement techniques for heat pulse velocity have been used on a wide variety of plants, including:

Gossypium hirsutum	Bloodworth *et al* (1955, 1956)
	Skidmore and Stone (1964)
	Stone and Shirazi (1975)
Graminae spp.	Wendt *et al* (1967)
Eucalyptus spp.	Doley (1967)
	Doley and Grieve (1967)
Populus tremula	Hart *et al* (1969)
Populus spp.	Heine and Farr (1973)
Artemisia tridentata	Gifford (1968)

Chamaecyparis obtusa	Morikawa (1974)
Juniperus spp., *Pinus* spp.	Decker and Skau (1964)
Juniperus spp., *Pinus monophylla*	Shaw and Gifford (1975)
Pseudotsuga menziesii	Hinckley (1971)
	Lassoie *et al* (1977)
Pinus radiata	Marshall (1958)
Pinus halepensis	Swanson (1972)
Pinus contorta, *Picea engelmannii*	Swanson (1967)
	Mark and Crews (1973)
Pinus ssp., *Citrus* spp.	Gale and Poljakoff-Meyber (1964)

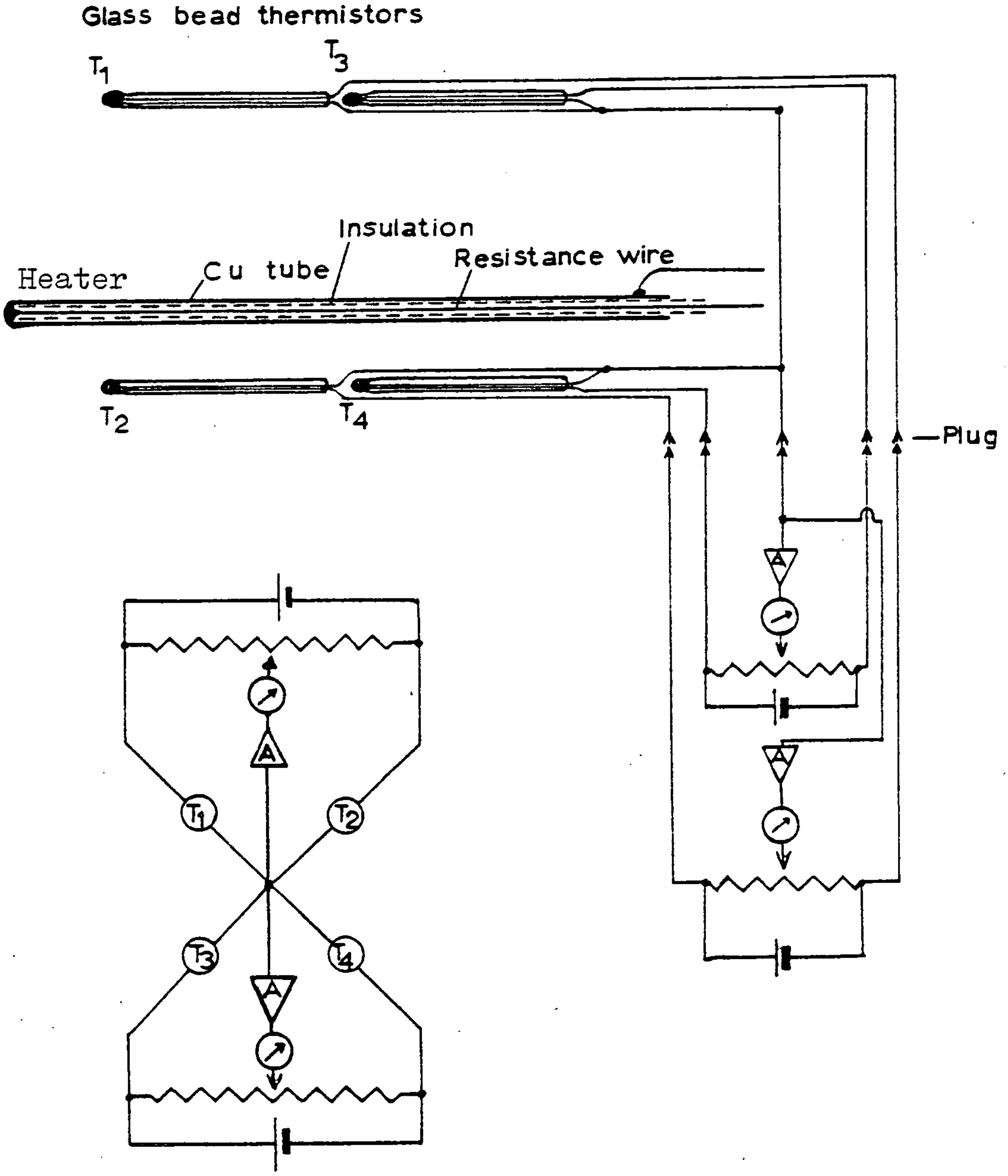
2.3.2 Theory of the Technique and the Design Used

The compensation method of Huber and Schmidt (1937) was used throughout this study, following the technique of Swanson (1974a,b). Heat sensors placed up-stream and down-stream from a line heater permitted separation of the movement of heat by diffusion from that by convection, as described in the previous section (Fig. 2.5). The movement of the pulse from its place of origin to a position situated centrally between the two sensors, can be calculated simply as

$$u = (x - x')/(2t)$$

where u is the heat pulse velocity (m / s)

FIG. 2.5 Measurement of heat pulse velocity. At each of two depths in the xylem, two thermistors are installed at unequal distances from a heater, as shown, and balanced in a Wheatstone bridge. A heat pulse displaces the balance, which is reached again as the pulse is carried through a point equidistant from the thermistors by sap flow.



Schematic diagram

x and x' are respectively, the down- and up-stream distances (m)

t is the time to return through the point of equilibrium (s).

Converting Heat Pulse Velocity to Sap Velocity

Marshall (1958) states '...the stationary wood and moving sap act like a single medium.... Their speed ' (of the apparent homogenous medium) '...is less than that of the sap itself; it is in fact the weighted average of the sap and the stationary wood substance.'

Expressed mathematically, we have:

$$u = v.a.\ \sigma_s\ .c_s/(\ \sigma\ .c) \qquad \text{Equation 2.2}$$

where u is the heat pulse velocity, (m s^{-1})

v is the sap velocity within the lumens, (m. s^{-1})

$a = a_s/A$, the fraction of lumen area in the sapwood,

a_s is the conducting area of the lumens, (m^2)

A is the total sapwood area, (m^2)

σ_s is the sap density, (kg m^{-3})

c_s is the specific heat of sap, (kJ kg^{-1} ^oC-1)

σ is the density of the wood/sap matrix, and (kg m^{-3})

c is the specific heat of the wood/sap matrix (kJ kg^{-1} ^oC-1)

For our purpose, it is more convenient to express sap velocity on the basis of total sapwood area (V'), a device which eliminates the need to consider lumen areas. (Note however that V' is as yet uncorrected for the effect of wounding.) Thus:

$$V' = v.a_s/A$$

and combining with equation 2.3.1

$$V' = u.\sigma.c/(\sigma_s.c_s).$$

The terms for density and specific heat can be simplified by assuming that sap closely approximates pure water (Marshall, 1958; Booker, pers. comm.), that the density of the woody matrix is 1530 kg m^{-3} (Panshin and de Zeeuw, 1970) and that the specific heat of the woody matrix (c_w) is 1.38 kJ kg^{-1} $^oC-1$ (Skaar, 1972 - p. 140 *et seq.*). Thus using volume fraction terms for the woody matrix, water and gas phases in the wood, we have:

$$\sigma_s = 1000 \text{ kg.m}^{-3}$$

$$\sigma = (1530.F_w + 1000.F_h) \text{ kg.m}^{-3}$$

$$c_s = 4.186 \times 10^6 \text{ kJ kg}^{-1} \, ^oC\text{-}1$$

The specific heat of 'fresh' wood, c, can be found as the sum of the contributions of the sap and the woody matrix fractions (Marshall, 1958):

$$c = c_w.1.530F_w/(F_h + 1.530F_w)$$
$$+ c_s.F_h/(F_h + 1.53F_w)$$

$$= (0.33.1.53F_w + F_h)/(F_h + 1.53F_w)$$

$$= (0.505F_w + F_h)/(F_h + 1.53F_w)$$

Substituting these into equation 2.2 we have

$$V' = u.(0.505F_w + F_h)$$

This formula was used to convert from heat pulse velocity to sap velocity throughout the study.

Sap velocities have been based on total sapwood area, in order to avoid measuring the conducting area of the tracheid lumens. Therefore, within an area of sapwood in which sap velocity is uniform, flow can be expressed as the product of velocity and sapwood area.

Correction for Wounding

The computer simulations developed by Swanson (pers. comm.) to correct for wounding include those sensor and heater configurations and construction materials used here. In his model, Swanson used a network of 'nodes' spaced 0.4 mm in a simulated wood block of 80 mm (axial) x 32 mm (tangential) with an assumed radial homogeneity. These dimensions are sufficient to preclude both edge effects and the influence of node spacing. Within this matrix, appropriate nodes were designated to represent sensors or heater, and the flow of heat postulated to originate at the heater was found for each node using nominated heat diffusivities and time intervals.

The heat diffusivities used were:

Glass thermistor	0.058×10^{-5}	m s^{-1}
Brass heater	3.300	"
Wood (axial)	0.024	"
Wood (tangential)	0.012	"

The values for wood were derived from field measurements of *Pinus contorta* and *Picea engelmannii* by Swanson.

An approximation of the real heat input generated by a nichrome wire heater in a one second pulse was made in three stages as follows:

0 - 0.5 s	Linear rise to maximum temperature
0.5 - 1.0 s	Plateau at maximum
More than 1.0 s	Decline from maximum according to the function Tmax/t·10, where t is the time in seconds

The time steps used were less than 0.001 seconds, a necessary constraint when rapid changes in temperature resulted from the presence of copper or brass. Printouts were obtained at one second intervals.

The system was simulated using tri-diagonal matrice equations using the 'Alternating direction implicit' technique described by von Rosenberg (1969).

For the sensor spacings and materials used in this study, the effect of wound size was derived as a set of predictive equations of the form:

$$V = p + q.V' + r.V'^2$$

Wound Size (mm)

	1.6	2.0	2.4	2.8	3.2	3.6	4.0
p	0.144	0.166	0.270	0.332	0.549	0.589	0.491
q	1.358	1.380	1.383	1.364	1.267	1.208	1.232
r	0.026	0.043	0.064	0.096	0.139	0.193	0.243

These coefficients were used throughout the study to correct the derived sap velocities for the effect of wounding.

Spatial Variation in Sap Velocities

Non-homogeneity can exist in both tangential and radial directions.

(i) Tangential Non-homogeneity

The primary source of tangential non-homogeneity is the effect of aspect on radiation (see also Section 3.1): the south-facing side of the tree may be subject to increased transpiration. Several factors will affect this. Firstly, under the prevailing weather conditions at the field site a substantial proportion of transpiration can be attributed to vapour pressure deficit rather than direct radiation -

an effect which is more substantial in forests than in short vegetation because of aerodynamic roughness (Jarvis and Stewart 1979). Secondly, the short tracheid length in gymnosperms contrasts with the long vessel length of angiosperms, to which most reports of the effect of aspect on flow are related. Shorter tracheids will tend to permit higher tangential transfer. Thirdly, the insertion of the probes was carried out randomly within four equally-spaced points around the tree (see Section 2.3.3).

For these reasons flow at one point within the stem at a particular time was considered to be essentially homogenous with respect to tangential direction.

(2) Radial Differences

Permeability of sapwood is known to vary radially (Booker,1977) and flow rates (measured by heat pulse velocity) are known to change radially on a diurnal basis (Swanson, 1974a; Edwards, unpublished data). The magnitude of the differences within a tree, and their variability with time makes a detailed consideration essential.

Within-ring radial differences can be shown using dye techniques (see Chapter 3). Essentially the largest flow is within the first-formed early-wood, steadily declining and falling sharply at the last-formed latewood. When using the heat pulse method, the area sensed approximates 5 mm laterally around the thermistors (Swanson, 1974a). The trees used in this study had an average ring width of about 4 mm within the sapwood, so that within-ring differences in flow rate were largely eliminated. Further, the comparatively large number of measurements taken for each flow measurement (eight) and their random placement with respect to ring structure tended to remove any remaining effect of within-ring differences in flow rate.

Dye studies have suggested that simple curve-fitting procedures of the form

$$Y = aX_1 + bX_2 + c$$

where X_1 is a function of X_2

are a satisfactory way to generalise sap velocities with respect to depth (Edwards and Booker, in prep.). The function using $X_1 = X_2$ squared is particularly valuable, since it has the advantages that a peak flow can be characterised mathematically by the point of inflexion of the parabola, and flexible curve-fitting is permitted within the general parabolic shape (Fig. 2.6). In general a considerable departure from linearity was rare, according to the author's unpublished data from this study and previous work.

Such a function can be fitted to three or more points, and allows statistical derivation of error limits (Snedecor and Cochrane, 1978). No assumptions other than that of a general second order curve (either concave or convex) are involved.

Estimating Volume Flow Rate from Sap Velocities

Flow can be calculated as the product of sap velocity (expressed on a sapwood area basis) and sapwood area. However higher velocities towards the cambium will have a proportionately larger effect on the total flow than those closer to the heartwood, simply because of the larger sapwood area involved. Therefore the sap flux must be calculated as follows:

We have already seen that the sap velocity can be expressed in terms of radial depth, as a parabolic curve (Fig. 2.6). If the curve within the limits of the cambium and the sapwood/heartwood interface is rotated about the axis of a cylindrical log, a torus results. The volume of such a torus represents sap flux (m^3 s^{-1}) since the vertical dimension represents sap velocity.

To find the volume of the torus, the mathematical device of approximating the torus to be a large number of thin, hollow concentric cylinders is used. The volume of each cylinder is equal to its height (which represents sap velocity), and its basal area. The sum of all the cylinders is approximately the volume of the torus, the accuracy of the approximation being proportional to the number of cylinders.

An iterative computer program can readily carry out such calculations.

2.3.3 Description of Equipment

General

The equipment was designed so that two identical sensor circuits could be utilised with each heater unit. Each heat pulse could be sensed at two depths, considerably reducing the time taken for readings.

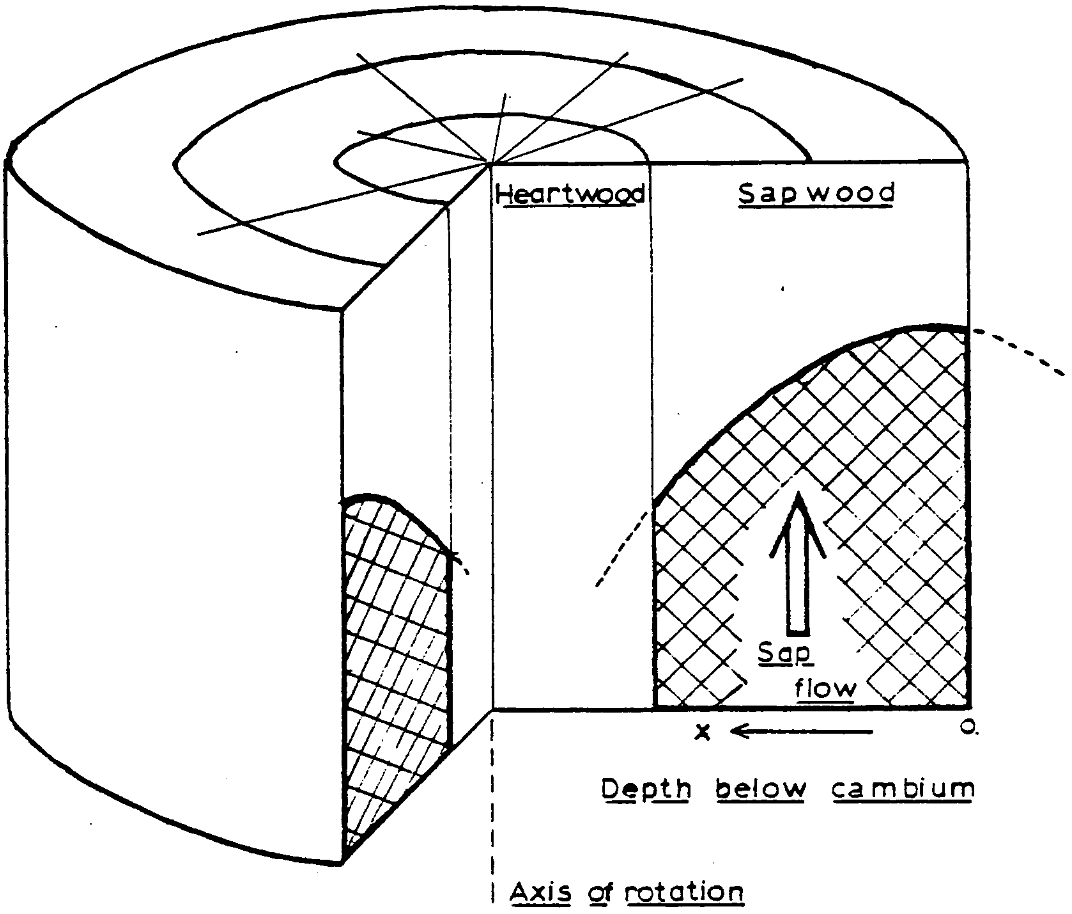


FIG. 2.6 Sap velocities at different depths can be fitted to a parabolic curve. Rotation of the curve about the axial center produces a volume representing sap flux, since the vertical dimension represents sap velocity.

(i) Sensors

The thermistors used to sense temperature changes were glass-encapsulated Fenwal 'Miniprobes', No. GB41M2 (Fenwal Electronics Inc., Framingham, Mass., USA). Their resistance at 25 °C is nominally 10,000 ohms, and is related to temperature by the expression:

$$\frac{R}{R'} = e^{\beta (1/T - 1/T')}$$

where R, R' are resistances at two temperatures

T, T' are temperatures in degrees Kelvin

β is a constant (3574 plus or minus 93 for these probes).

Therefore the resistance at 15 °C can be calculated as 15165 ohm, and the response at that temperature is 670 ohms/°C, or 4.42%/°C.

The thermistors were 1.52 mm in diameter and 12.7mm long. Two sensing probes were used per heater unit, each comprising two thermistors mounted one behind the other so that the beads of sensitive material were always 13.0 mm apart. One wire from each was common. Each pair of thermistors was covered with epoxy adhesive ('Araldite') and slid into a length of 'Heatshrink' plastic tube. Application of heat reduced the size of the assembly, and extruded the surplus adhesive resulting in a tolerably strong, fully waterproof unit. The outer diameter was 1.98 mm over the thermistor beads, and 1.80 mm over the glass support shaft. Suitable lead-in wires were fitted and also made watertight with epoxy adhesive.

(ii) The Heater

The heater consisted of nichrome wire of 26 SWG (0.462 mm diameter), 70 mm long with a total resistance of 0.61 ohm. It was insulated by a Teflon tube and encased within brass tubing of outside diameter 1.74 mm (modellers' 'Pin tubing'). The inside diameter of the tubing was increased by passing through a stream of concentrated nitric acid, to provide a close fit for the Teflon tubing. An electrical contact was made at one end by soldering the resistance wire to the brass tubing. An acid flux was necessary to solder the Nichrome wire. Suitable leads were attached and the heater and probes connected to a pair of 5-pin DIN plugs. Each plug was connected to one of the bridge circuits, and the heater was always attached to the plug used for the pair of thermistors closest to the cambium. Thus wrong lead-in connections to each bridge were prevented in the field.

(iii) Measuring Instrument

Each pair of thermistors at one depth formed two sides of a Wheatstone bridge, the remaining two sides being formed from a tandem 10000 ohm potentiometer and a 10-turn, 1000 ohm potentiometer as a fine control. The bridge was energised by a 1.3 V dry cell, providing either 1.3, 0.7 or 0.13 V options. The lower voltage, although giving a less sensitive response, did not cause any measurable degree of selfheating which was otherwise apparent above 0.4 V. Therefore the lowest voltage was used for the slowest flow measurements where stability was more important with respect to time.

The bridge output was amplified by 1000 times using a '7025' high stability operational amplifier (Radio Spares Ltd. component), driving a 50 - 50 microammeter. Each of the two bridge/amplifier circuits was completely separate, including the power supplies.

The heater/timer circuit was similar to that used by Swanson (1974a), and provided a 1-second pulse to the heater followed by activation of an electromechanical timer.

(iv) Implantation of Probes in a Tree

Axial spacing of the probes relative to the heater is critical to the heat pulse velocity measurement (Swanson, 1974a), and so installation of the probes and heater was carried out using a drilling jig. It comprised a 40 x 40 mm steel plate 10 mm thick, through which three parallel, 1.59 mm diameter holes were accurately drilled in line at spacings of 5.00 and 10.00 mm. The jig was fitted so that it could be firmly strapped to a tree trunk, allowing considerable precision during drilling. A 1.59 mm twist drill, long-shanked to give sufficient drilling depth through the jig, and a battery-powered drill were used in preference to a hand drill, to reduce sideways movement during the operation.

After removal of the jig, three stiff steel rods of the same diameter were run into the holes, a card was held closely to the protruding ends and a tracing made. The same card served to record all relevant information: site, tree, probe, insertion depth, bark depth and stem diameter. Subsequently the distances between the thermistors were estimated by measuring the relevant distances on the tracings under a low powered microscope, making allowance for any departure from parallel.

Implantation was accomplished by increasing the size of the three holes to make a close fit. For the heater, 1.85 to 1.90 mm was sufficient. For the sensors, a 2.00 mm drill was used to the whole depth, but a 2.3 mm hole was bored in theouter wood (the depth depending on the depth of implantation) such that the thicker base of the probes containing the wires could be accomodated. Finally the leads were tied tightly to the trunk with string.

Operation of the equipment consisted of balancing the bridges with the coarse and fine potentiometers successively, and then switching on the heater/timer circuit. The heat pulse, diffusing outwards reaches the lower (closer) thermistor first, unbalancing the bridge. As the pulse is carried up by the sap flow, a point is reached where the pulse is exactly between each thermistor, and the bridge outputs pass through the zero points. The times taken from pulse initiation for the outputs to return through the zero points is recorded manually, for each bridge circuit,ie. each depth.

2.3.4 Data Processing and Error Analysis

The data were processed by computer to provide a relation between sap velocity and radial depth, and hence an estimate of total flow.

The following input data were required:

(i) axial separation of each thermistor from the heater,

(ii) radial depth of each thermistor pair,

(iii) the tangential width of the wound (ie. non-conducting tissue) at that depth,

(iv) the mean trunk diameter at the point of implantation,

(v) the heartwood diameter at the same point, and

(vi) the sapwood water content.

Data were processed according to the following sequence:

(i) Heat pulse velocity was calculated from the time measurements (Equation 2.3 from Section 2.3.3).

(ii) Sap velocity was found according to the volume fractions of water and wood (Section 2.3.3).

(iii) The sap velocity was corrected according to Swansons formula, for the particular probe materials and configuration (Section 2.3.3).

(iv) The corrected sap velocities were fitted to a second-order equation with respect to radial depth.

(v) The positive square root of the equation was found for $V = 0$, i.e. approximately the sapwood/heartwood boundary. This value is constrained not to exceed the known sapwood depth or the length of the radius.

(vi) the point of maximum flow according to the regression equation was found as the second differential of the equation.

(vii) The total flow was be found as the product of the sapwood area and the sap velocity, expressed on a total sapwood area rather than a tracheid lumen area (as indicated above), for a series of thin, hollow, concentric cylinders 1 mm thick (see Section 2.3.2). The flow through each cylinder was calculated as the product of its basal area and the sap velocity at the center of the cylinder wall, calculated on the basis of the regression between sap velocity and radial depth (step (iv) above).

(viii) The mean sap velocity was found as the total flow divided by the total sapwood area (this is not the same as the mean radial velocity, for the same reasons outlined in (vii) above). The standard error of the mean sap velocity was expressed as:

$$(\sqrt{(V^2 - b_1 . SS(V.x) - b^2 . SS(V.x^2))/N})/100$$

(ix) The standard error of the value for total flow, derived from the variation in the residual SS from the regression equation, was expressed as the standard error of the sap velocity divided by the sapwood area.

The sums of squares attributable to the regression was expressed as a percentage of the total sums of squares.

The estimation of errors has two aspects which affect accuracy, viz: bias (systematic error), and precision (indeterminate or random error). The derivation of standard errors by the statistical methods just outlined all relate to the residual error involved in estimating the regression line from sap velocity measurements and are effectively the measure of the contribution of precision to accuracy.

Other errors emanating from the assumptions or measurements concerning the volume fractions of wood and water, wound size, derivation of wound corrections and assumptions of tangential homogeneity are solely concerned with the estimation of bias. Since insufficient data exist on the variability of most of these sources of error, estimation of bias is best carried out by direct comparison with a complementary measurement, known to be accurate.

Harvesting the trees provided such an opportunity. Excision of sections of the stem in which the heat pulse probes were embedded permitted direct measurement of flow at the time that permeability measurements were made (Section 2.1). Simultaneous measurement of heat pulse velocities, followed by sampling to determine volume fractions of water and wood, and wound dimensions allowed direct comparison for bias.

Calibration curves are presented for these data in in Chapter 5.

2.4 MEASUREMENT OF WATER POTENTIAL

2.4.1 Introduction

In the two decades since the classical paper of Spanner (1951) on the development of the thermocouple psychrometer, the concept of the free energy of water has become firmly established as a means of describing water relations within the soil-plant-air continuum. Spanner's theoretical approach based on thermodynamic principles resulted in a technology which allowed unified description within widely differing phases and compartments (Slatyer 1967, Taylor 1968, Milburn 1979).

Flow between such compartments occurs because of differences in water potential. Conversely, changes in potential within a compartment occur because of

(a) fluxes in or out of the compartment,

(b) changes in ion or particle concentration,

(c) changes in physical pressure, or

(d) temperature changes.

We shall consider in this study that zero water potential within a multi-compartment system is equal to that of pure, free water at the same temperature and pressure, although Milburn (1979) discusses alternatives to this. The water potential or chemical activity of water in a compartment relative to such a zero point can be described in thermodynamic terms simply as the vapour pressure of the water relative to that of pure free water at the same temperature:

$$-psi = [R.T.\ln(e/e_o)]/V_w$$

where psi is the water potential, expressed as a negative value,

R is the universal gas constant,

T is the absolute temperature,

e is the actual vapour pressure,

e_o is the vapour pressure of pure free water at the same temperature and pressure, and

V_w is the partial molal volume of water.

The inclusion of V_w permits the expression of the water potential in units of pressure rather than energy.

The major components of water potential are osmotic potential, matric potential and pressure potential. The nature of these component forces is well reviewed by Slatyer (1967), Boyer (1967) and Barrs, 1968).

Methods of Measuring Water Potential

Water potential measurements can be made in both liquid and vapour phases; the techniques are reviewed by Barrs (1968), and Wiebe *et al*, (1971).

Liquid Phase Techniques

Liquid phase techniques fall into three categories:

(i) Establishment of the isopiestic concentration of a surrounding solution. Pieces of tissue are immersed in a range of solutions of different osmotic potential, to find that solution for which liquid exchange does not occur. Cell size or tissue thickness (Ursprung and Blum, 1916), weight (Meyer and Wallace (1941) or volume (Currier, 1943) are suitable dependent variables.

(ii) Establishment of a change in the surrounding solution. The effect on the density of the surrounding solution can be observed (Shardakov 1938, Knipling 1967).

(iii) Measurement of electrical resistance. The resistance between two inserted electrodes is proportional to the water potential of the pathway, and can be calibrated for a direct measurement (Dixon *et al*, 1977).

Vapour Phase methods

Vapour phase methods involve measurement of the vapour pressure of a gas in equilibrium with the liquid phase of a sample under test, or the equilibration of sample and test solution liquid phases through a vapour phase:

(i) Equilibration of standard solutions over a test solution (Ursprung and Blum, 1930).

(ii) Change in sample weight, after suspension over a test solution (Slatyer, 1958).

(iii) Measurement of the vapour pressure directly. The use of thermocouple psychrometers and dew point hygrometers for this purpose is discussed more fully in Section 2.4.4. Briefly, a measurement of the vapour pressure is made by measuring the wet-bulb depression of a thermocouple using the Seebeck effect, or dew point depression.

(iv) The pressure chamber technique. The method involves balancing the water potential of a twig or leaf against an applied gas pressure. The technique is generally attributed to Scholander et al (1964), although Dixon (1914) first attempted it.

The three most reliable methods of measuring leaf water potential are the pressure chamber, the thermocouple psychrometer and the dewpoint hygrometer (Baughn and Tanner, 1976). For measuring water potential in stems of trees, however, the pressure bomb is not suitable. The methods considered for field use included thermocouple psychrometry and dew point hygrometry, and also two other liquid phase methods. The first of these is based on osmotic tensiometry, and the second is a new method involving measurement of injection rates.

2.4.2 Osmotic Tensiometers

2.4.2.1 Theory of the Technique and Design

The concept of using osmotica to extend the range of the soil tensiometer relates the potential of the medium under test to a solution of low osmotic potential, rather than to water (Peck and Rabbidge, 1966, 1969). Whereas the standard soil tensiometer measures pressure changes against a mercury manometer involving a considerable displacement of water, the osmotic tensiometer uses a small volume of osmotica separated from the medium under test by a semi-permeable membrane supported by a ceramic disk, and enclosed within a fixed volume. When placed in contact with a solution of higher potential than the osmotica, a positive pressure within the solution develops rapidly since the volume remains almost constant, and is measured with a pressure transducer in the rear wall of the chamber.

The apparatus is critically dependent on the integrity of the membrane and chamber since high internal pressures can be generated. Response time is dependent on the resistance to flow between the solution under test and the osmoticum, and diffusion rates within the osmoticum.

Although originally developed for the measurement of soil water potential, the units have also been implanted in trees (Richards, 1973).

2.4.2.2 Description of the Equipment

A number of the commercial Peck and Rabbidge units were available, although non-functional. Since the units could not be serviced, an apparently successful attempt was made to replace the semipermeable membranes and refill the chambers with 2.0 MPa polyethylene glycol solution (molecular weight 20,000). However the pressure transducers were subsequently found to have deteriorated, and the units were abandoned.

An alternative design, based on measurement of volume change rather than pressure change was designed and constructed. These consisted of two turned and threaded brass sections which screwed together to hold a semipermeable membrane against a neoprene seal, forming a 0.5 cm^3 chamber. Sections of hypodermic needle (22 gauge) were soldered through the back of the unit. The back plate and front ring were sweat-soldered to the assembly. Volume changes were measured as movement within a fine-bore translucent nylon tube attached to the outlet on the backplate.

Richards (1973) had found that satisfactory contact with the sap stream could be made if his osmotic tensiometers were installed in holes in the tree using a slurry of Plaster of Paris. This also lessened the effect of isolation of the wound (and the tensiometers) by resins.

It was proposed to use the same method of installation, so that no direct ceramic support was included in the design of the new units.

2.4.2.3 Testing the Equipment

The osmotic potentiometers were tested in two ways: (a) by immersion in solutions of different osmotic potential, and (b) by installation in trees. In the latter, the unsupported membranes were cast into a small block of Plaster of Paris, to simulate conditions in the tree. Then the volume changes, although small, were found to be proportional to the osmotic pressure of the test solutions.

However it was found that the time taken to reach equilibrium was excessively long, and there was no prospect of following diurnal changes with a rapid response. Assuming an exponential change in potential following a stepwise change in potential in the surrounding solution, the time constant could be established from a plot of the logarithm of time against volume change. Typically the time constant, the time taken to reach 63 % of the final equilibrium, was of the order of 5 hours for a change of 0.7 MPa in the solution.

2.4.2.4 Conclusions

Clearly, the time response makes an osmotic tensiometer based on volume change impractical for investigating diurnal changes in water potential. The Peck and Rabbidge osmotic tensiometer was made so that the volume change was virtually zero, and equilibrium could be established rapidly. Their instrument does not depend on establishing equality of concentration with the test solution.

Use of osmotic tensiometry was therefore abandoned in favour of other methods.

2.4.3 Pressure Injection Technique

2.4.3.1 Theory of the Technique

If tritium-labelled water is introduced into a hole bored into the sapwood of a tree, it enters the transpiration stream and can be traced moving up the tree (Waring and Roberts, 1976). Since water flows from areas of high water potential to areas of low potential, entry into the tree must occur as a result of the low potential of the transpiration stream since the water in the hole can be considered essentially to be at zero potential. The flow rate into the transpiration stream is a function of (a) the resistance of the pathway, and (b) the potential of the transpiration stream.

While it is not possible to measure the resistance directly, it is possible to measure the flow rate, and also to change the magnitude of the potential gradient by altering the potential of the water in the hole. This is readily accomplished by sealing a tube carrying water into the tree, and varying the pressure at which the water enters the hole by using a reservoir of water pressurised within a pressure bomb.

Let the resistance to flow between the reservoir and the xylem be R. Then if the flow Q_i from the pressurised reservoir to the transpiration stream which is at a potential Ψ_t is measured for two different applied potentials Ψ_1 and Ψ_2, we have:

$$Q_1 = R.(\Psi_1 - \Psi_t)$$

and

$$Q_2 = R.(\Psi_2 - \Psi_t)$$

Therefore

$$\Psi_t = \frac{Q_2 . \Psi_1 - Q_1 . \Psi_2}{Q_2 - Q_1}$$

Alternatively Ψ_t can be found graphically by plotting the applied potential against flow rate and extrapolating to zero. Since the slope of the line is equal to the resistance to flow, multiple changes of pressure will indicate if the resistance is in fact constant.

2.4.3.2 Description and Use of the Equipment

The equipment consists of three parts (Fig.2.7):

(i) A pressure feed system was constructed consisting of a 125 ml plastic bottle filled with distilled, 0.1 micron filtered water, which just fits within the chamber of a standard pressure bomb. A nylon pressure tube could be sealed through the top of the chamber, in the same way that the stem of a twig is sealed in during the normal use of a pressure bomb.

(ii) A flow meter was attached to the nylon tubing, operating on the principle of measuring the velocity of an air bubble moving through a scaled capillary tube. Air bubbles were introduced to the capillary by a hypodermic syringe operating through a valve to a T-junction. At the other end of the capillary, the bubbles were removed using a simple reservoir and bleed valve.

(iii) The sealing head comprised a hypodermic needle tube fitted with a polyethylene sleeve, held between two collars sweat-soldered to the

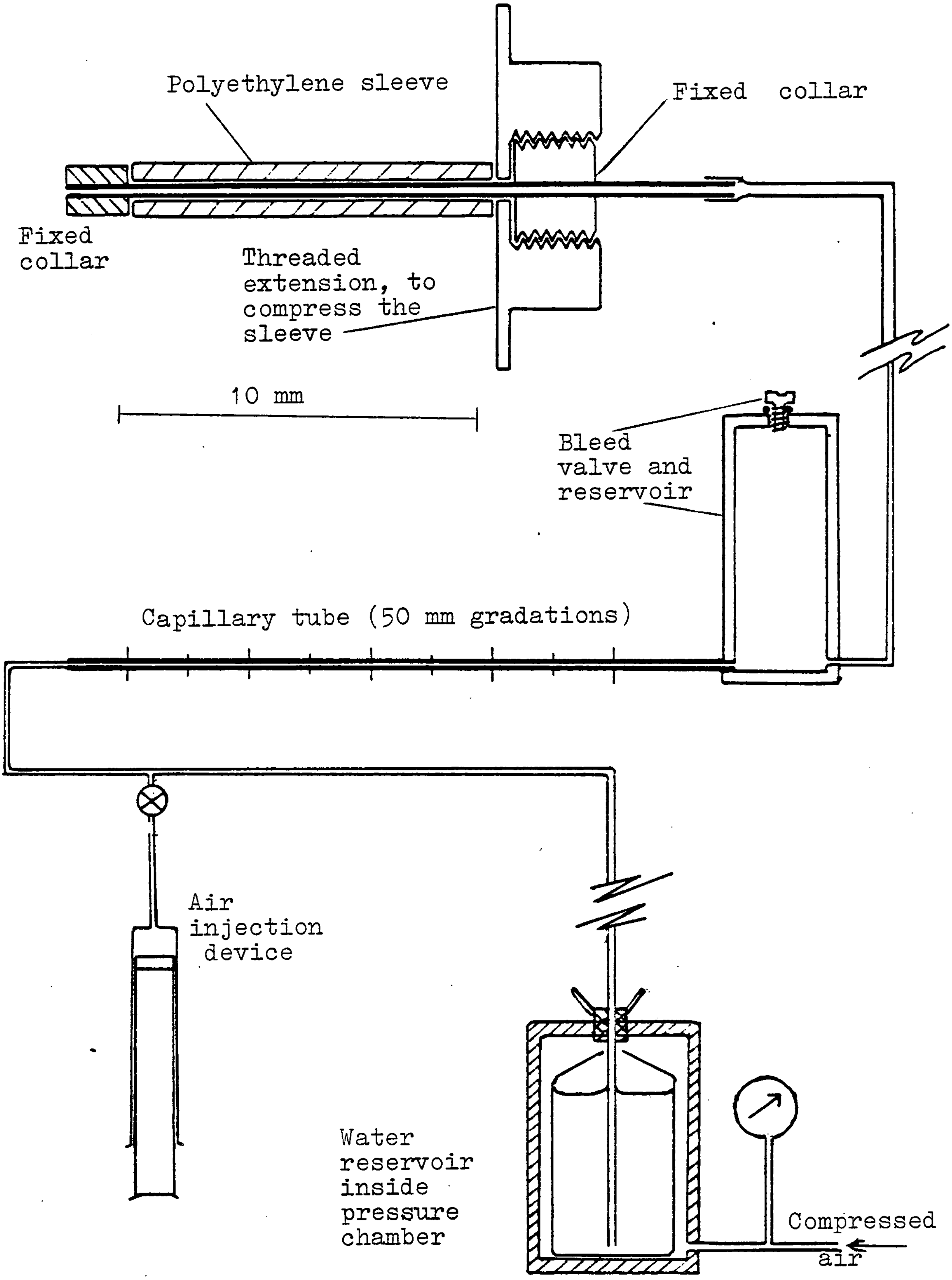


FIG. 2.7 Measurement of water potential by pressure injection. The flow rates induced by injecting water into a tree at several pressures are proportional to the potential gradient between the pressure chamber and the xylem.

needle. A threaded extension to the outer collar permits the sleeve to be squeezed, sealing the needle into the hole. The dimensions were kept as small as possible, to minimise disruption to the flow paths and to minimise local gradients of potential, ie. local flooding.

To use the equipment, a small pressure was applied, the entire system bled free of air and the feed reservoir topped up. A hole was bored through the outer bark (which was smoothed off if rough or very thick), using a drill diameter which would give a loose press fit to the sealing head. The hole was immediately flushed free of air using a hypodermic filled with pure water and a needle which would reach to the bottom of the hole. Then the sealing head, emitting water under about 0.05 MPa pressure, was pushed firmly into the hole and sealed in by screwing the collar so as to compress the plastic sleeve. This process ensued that the hole was air-free, although not necessarily refilling those tracheids with cut ends.

A series of flow measurements was then made over at least two cycles of applied pressure, each comprising a low-high-low sequence. The reciprocal of the time taken for a bubble to move between marks 50 mm apart on the capillary tube was taken as proportional to the flow rate, which in absolute terms was within the range 0 - 90 mm^3 per minute.

2.4.3.3 Field Testing

The technique was tested in the field and the results compared with those of thermocouple psychrometry. Graphed results are presented in Fig.2.8. The initial flow rate did not appear to be representative, and it was not until a higher pressure was applied that entry of water into the sap stream appeared to take place readily. Thereafter, successive changes of applied pressure showed a slowly changing slope, indicating slowly increasing resistance. Extrapolation of the lines joining a particular low-pressure reading to the mean of the two adjacent high-pressure readings cut the y axis at points within the range of +/- 0.05 MPa, thus indicating the precision of a single set of readings.

If an attempt was made to measure the potential in a tree with a static transpiration stream, as in a cut-off tree which was slowly drying, the method gave spurious results which indicated that the potential was always close to zero. Presumably an active transport system is necessary to prevent pooling. Although the quantities of water injected are small - a total of 400 mm^3 or less for a typical run of seven pressure changes - it appears that unless there are potential gradients which are producing flows close by the point of injection this quantity is sufficient to cause local saturation.

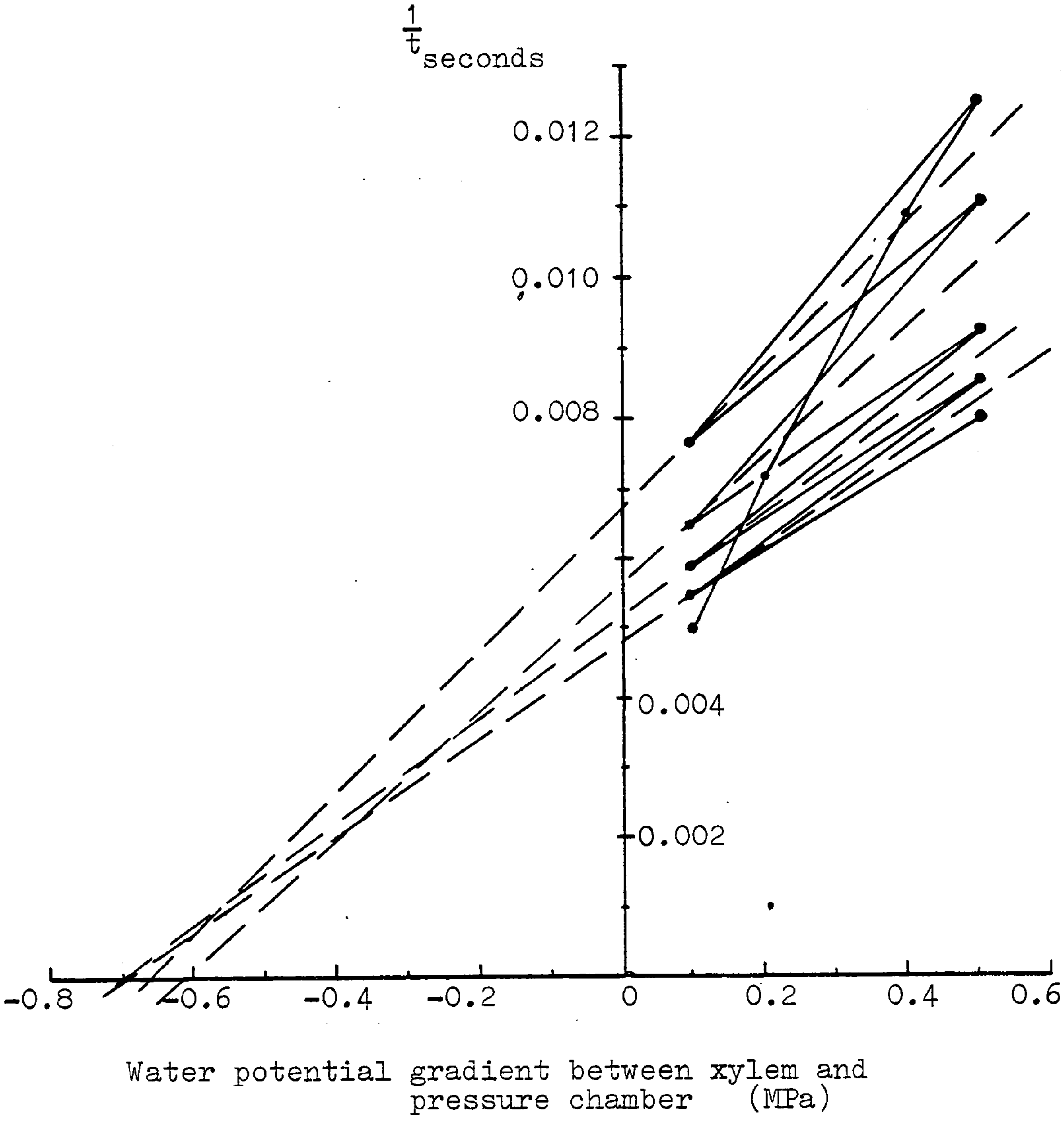


FIG. 2.8 Typical results for the pressure injection method. Varying the pressure between 0.1 and 0.5 MPa in the chamber and extrapolating the resulting lines indicated an approximately constant water potential in the xylem. The change in slope indicates an increasing resistance.

2.4.3.4 Conclusions

The technique offers a new method for an independent measurement of water potential in stems. There appears to be both adequate accuracy and precision. However the method requires injection of small quantities of water, which although not apparently significant in the transpiring tree, appear to cause local perturbations in a static transpiration stream.

Each reading requires up to 10 minutes for an experienced operator, and necessitates a new hole for each reading. The value of the technique is therefore in providing an independent estimate of potential, using a method which is conceptually different from other methods. It is not suitable for the routine measurement of large numbers of points, because of the time required for each measurement and because of cumulative damage.

2.4.4 Thermocouple Psychrometry

2.4.4.1 Introduction

Spanner (1951) showed that measurement of the vapour pressure of a gas phase in equilibrium with a liquid phase was a sensitive means of estimating the water potential of the liquid phase. However the range of interest - 0 to -1.5 MPa for most physiological conditions - corresponds to a changing relative humidity of about 0.01%. Not only must the measurement of vapour pressure be very accurate, but virtually isothermal conditions are necessary to prevent local gradients in vapour pressure, since differences in temperature between sample and chamber cause differences of about 8.0 MPa per degree C. There are two basic methods currently in use:

(i) Thermocouple psychrometry, which measures wet bulb depression. First the junction is cooled by an applied voltage (the Peltier effect) to produce a droplet, the corresponding junctions to the copper lead wires being 'massive' to maintain a vitually constant wall temperature. When a droplet of sufficient size has accumulated, the cooling current is switched off and the temperature of the thermocouple compared to the massive junctions is compared, using the Seebeck effect. The change is attributed to the rate of evaporation, which in turn is related to relative humidity within the chamber, and also the size, shape and wetting characteristics of the junction. Although calibration is required for accurate results, the method allows the zeroing out of bias voltages which can arise from temperature gradients within the chamber and measuring equipment. The technique is little different from Spanners (1951) concept, but the theory and design has been rigorously analysed since then (Rawlins, 1966; Peck, 1968, 1969; Daulton and Rawlins, 1968; Barrs, 1968; Millar, 1971a, 1971b, 1974; Scotter, 1972). Millar(1971a) reviews six sources of large potential error: (i) heat of respiration, (ii) resistance to vapour flux from the sample surface, (iii) adsorbtion error from changes in the chamber wall area during calibration and during measurement, (iv) ambiguous determinations since each instrument reading corresponds to two different water potentials (Monteith and Owen 1958), (v) tissue damage, and (vi) equilibration errors where the sample is not in equilibrium with the atmosphere. Barrs (1968) further reviews errors in calibration and measurement. A variation of the Spanner technique, only suitable for laboratory use, is the Richards and Ogata psychrometer, which uses an applied droplet rather than forming a droplet by using the Peltier effect.

(ii) The second method of measuring vapour pressure in a small chamber is the dew point hygrometer (Neumann and Thurtell 1972, Campbell et al 1973), in which a thermocouple junction is cooled by the Peltier effect to produce a drop of dew, the temperature of which is then maintained by adjusting the cooling current so as to just prevent either condensation or deposition of more water. This temperature is the dew point temperature depression of water vapour in equilibrium with the sample. The instrument of Campbell et al (1973) uses a time sharing procedure alternately to cool and read the dew point temperature, and the degree of cooling is adjusted electronically to establish the equilibrium.

The temperature of the dewpoint hygrometer will always be less than that of the thermocouple psychrometer, since in practise it is not possible for the latter to reach the dew point, because of heat transfer within the psychrometer.

Therefore the dewpoint hygrometer will be less affected by chamber and junction characteristics and will have a higher sensitivity.

However it cannot be zeroed to account for temperature differences between the main junction and the massive junctions, or other sources of bias voltage.

Design Considerations

The requirement for field measurement of water potentials within stems of trees suggests that the most likely sources of error in vapour pressure methods will be temperature fluctuations or gradients, and the tendency for the tree to seal a wound by the production of resins. An investigation into the effect of thermal gradients (G.S. Campbell, pers. comm.) suggested that temperature effects were a significant source of error in many field applications. Further, the overall diurnal variation affecting both the instrument and the thermocouple/chamber unit suggests that a system which would permit zeroing of bias voltages would be desirable.

Therefore it was decided to set up a system using thermocouple psychrometry rather than dew point hygrometry. Use of brass as a construction material rather than ceramics and plastics would reduce the influence of thermal gradients within the tree at any one time. A psychrometer design was chosen which was closely similar to that recently developed by G.S.Campbell.

2.4.4.2 Design of the Equipment

The psychometer consisted of three parts (Fig. 2.9): the thermojunction, the thermojunction mounting, and the main body.

(i) The Thermojunction

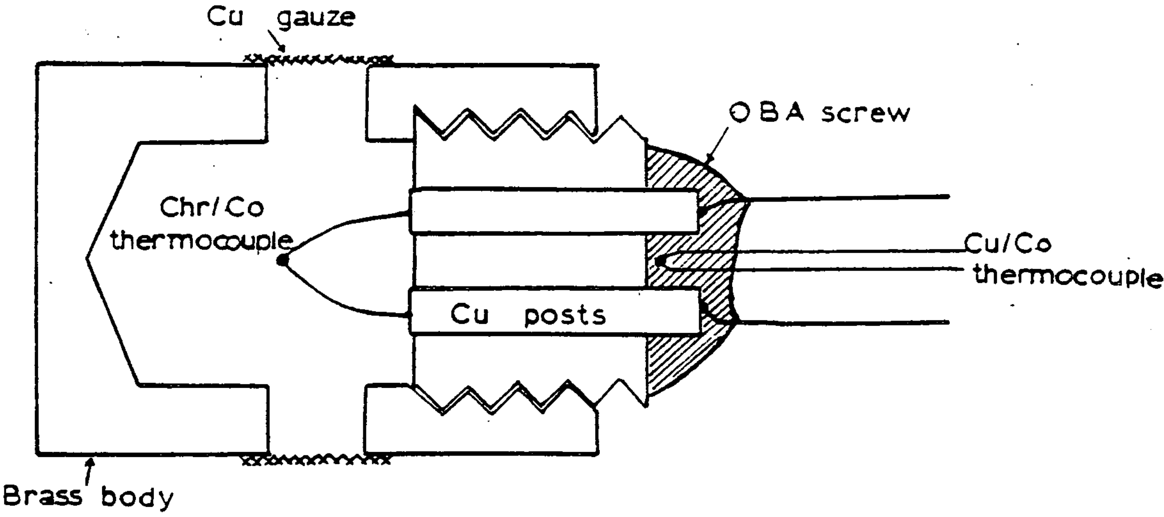
The thermojunction was welded from 0.024 mm diameter (50 SWG) chromel and constantan wires, using a jig to lay out and twist the wires first. The jig consisted of twelve removable bars screwed in pairs to a base plate, each bar being fitted with two screw clamps. Each of the two wires was placed under opposite ends of each bar so that the wires crossed, and the clamps were tightened. The wires were cut between each pair of bars as shown, and the central holding screws removed. Then each pair of bars could be removed carefully from the base, held by one bar and the other twirled twelve full turns. The bars were replaced on the base plate and a scalpel used to cut the wires in the center of the twists.

Each bar then held one length each of the chromel and constantan wires, clamped at one end and twisted together at the other, ready for welding.

The welder power unit consisted of a 250/50 V stepdown transformer operating through rectifiers to provide 50 v D.C. This charged a 50 microfarad electrolytic capacitor through a 250 ohm resistor. The positive lead was attached to a carbon rod (from an ordinary dry cell) held upright with a small oil-filled hollow formed in the top. The negative lead was clipped to a bar holding the thermojunction wires via a 50 ohm resistance and a press-button switch.

To make the weld,the twisted ends of the thermojunction wires were pressed lightly against the carbon block under the oil and the switch

FIG. 2.9 Thermocouple psychrometer, after a design for a soil thermocouple psychrometer by G.S. Campbell. The unit is built from brass to minimise the effects of thermal gradients, and is fitted into the xylem using Plaster of Paris, and sealed to the exterior.



fired. The discharge was sufficient to weld the twists into a single sphere some 5 to 7 times the diameter of the wire.

The thermojunction was then cleaned by immersion in acetone, boiling distilled water and detergent, and finally washed in a stream of distilled water.

(ii) The Thermojunction Mounting

The thermojunction mounting was made from a 5 mm section of OBA threaded rod. In it, two 1.6 mm diameter holes were bored axially centered aproximatel 2.5 mm apart. Using 'Araldite' epoxy resin, two 6 mm long sections of 1.58 mm diameter varnish-insulated copper wire were glued into the holes, just proud of one face. This face was ground flat and a check made for electrical short circuits between the wire posts and the mounting. If present, these could be removed by discharging the output from the welder between the posts and the body. Sufficient power was available to destroy the short circuit, which if present, was always on the ground face.

The mounting was placed in a jig held under a binocular microscope and a cut opened in the ground copper face of each wire post with a scalpel blade. The thermojunction was mounted by placing either the chromel or the constantan wire in the cut, and bending the raised edge of the cut down over the wire. The length of the chromel and constantan wires between the thermojunction and the 'massive' junction at the copper face, was about 3 mm. The surplus was cut off and the process repeated with the second wire. The junction could be pushed gently into a central position.

(iii) The Psychrometer Body

The psychrometer body was turned from 10 mm diameter brass rod 10 mm long, bored in one end to form an inner cavity and threaded sufficiently with an OBA bottom tap to allow the thermojunction mounting to be screwed in flush. Two slots were milled tangentially mid-way in the body, i.e. opposite the thermojunction.

Initially, these slots were fitted with flush-mounted ceramic inserts as used by Campbell in his soil pschrometers. These were later replaced by fine mesh copper gauze (see Discussion, Section 2.4.4.5).

Three 1.6 mm diameter wire spacers, 10 mm long, were glued axially to the body to allow separation from the insertion hole in the tree.

Each unit was rinsed in acetone after construction, boiled in distilled water (initially with detergent), rinsed thoroughly and then dried. Suitable lead wires were soldered to the copper posts, and a copper/constantan thermojunction inset in epoxy resin ('Araldite') between the posts to give a means of measuring ambient temperature. The glue covered all exposed wires and connections. A small quantity of a high quality paraffin wax was run into the OBA thread to seal the rear of the unit (but not to preclude subsequent dissembly), and the correct polarity of the lead wires was established.

The Measuring Unit

The instrument used to produce a cooling current, measure the junction output and also the ambient temperature was based on two '4025' high stability operational amplifiers (RS Components Ltd) in series driving a 0-2 V precision meter. The amplifier which output directly to the meter, doubled as an amplifier for the ambient temperature measurement, when used in that mode. The copper/constantan thermojunction in the body of the psychrometer sensed this temperature and related it to an electronic icepoint (Wescor Inc.). The resulting amplifier output to the meter was adjusted using the amplifier gain and zero pre-set potentiometer controls to provide a direct scale reading of 0 - 30 degrees C.

When used in the 'READ' mode, the psychrometer output was passed through the first amplifier to the second, the gain of the first being adjusted to give a full scale meter reading of 10 microvolts. During use, the zero adjustment of the first amplifier was used to remove bias voltages.

The cooling current was provided by a 4.5 V battery working through a resistance, and could be reversed to provide a heating mode to drive off condensed water from the thermojunction. All batteries used were of the mercury high stability type. All parts of the metal casing were joined by a soldered earth lead to reduce stray voltages. The psychrometer lead terminals were insulated from ambient temperature changes with a suitably shaped expanded polystyrene block.

2.4.5 PRESSURE CHAMBER METHOD

2.4.5.1 Theory of the techniques used

The standard pressure chamber technique has been used in this study to obtain leaf water potentials of transpiring needles or shoots (Dixon, 1914; Scholander et al, 1965; Waring and Cleary, 1967; Hellkvist et al, 1974).

In addition, in one study on Picea sitchensis at Fetteresso Forest, epicormic shoots were bagged according to the method of Richards (1973). The shoots were assumed to equilibrate with the atmosphere in the bag which prevents transpiration, and thus act as 'tensiometers' in contact with the xylem at the point of attachment. No indication of radial variation can be given by this method.

It was necessary to obtain pressure/volume curves for sapwood for use in the computer model (see Sections 4.3 and 6.2.3.1). To obtain the equivalent information for shoots, leaves or needles, the plant material can be set up in a pressure chamber and the outflow from the exposed end collected after each of a series of pressure increases (Tyree and Hammel, 1972; Hellkvist et al, 1974; Cheung et al, 1975; Powell and Blanchard, 1976; Kandiko et al, 1980). Since wood of gymnosperms is composed of tracheids some 3 mm long, a piece of wood can be treated in the same way as a shoot, provided that an adequate area can be exposed for outflow and the length is sufficient to render the end effect small. Pressure on the inlet face of such a billet of wood would approximate pressure applied to the xylem tissue of shoots, since the bordered pits of cut tracheids would prevent air entry.

The data required consisted of changes in relative water content for incremental changes in water potential. Outflow measurements were converted to changes in relative water content by finding (a) each new fresh weight, (b) the volume of the wood block by immersion in water, and (c) the oven-dry weight. The specific gravity of the woody matrix was assumed to be 1530 kg.m^{-3} (Section 2.2).

The relation between relative water content and water potential could then be analysed using multiple regression techniques to give parameters suitable for subsequent modelling.

The data could be further analysed to give the time constant for outflow and the resistance to flow from storage, using a technique described by Landsberg et al (1976), as follows:

The outflow of water following a stepwise change in the applied pressure is assumed to be exponential, viz:

$$W = Wmax\ (1 - e^{-kt})$$

where W is the initial weight,

Wmax is the final weight at the new equilibrium,

t is the cumulated time step for each measuremen of W

k is a constant.

We can further define

(a) the capacitance (C) for each pressure step as the maximum volume of water expelled for a given pressure change, (m^3/(Nm^{-2})), and

(b) the resistance (R) (N s m^{-5}) to flow from storage for that pressure step as the time constant divided by the capacitance. Using the electrical analogue of a capacitor being charged, we can make k_t (the time constant) $\simeq$ 1/(R.C). The function in its linear form is thus:

$$\ln(\mathrm{Wmax} - W) = \ln W_{max} - \cancel{k}\,t/(R.C)$$

Wmax can be found graphically (Landsberg, 1976) or statistically using a least-squares method. A computer program was set up to calculate iteratively the regression for the linear function, starting with a supra-optimal value of Wmax, and reducing it by 0.1% with each iteration. The estimated value of Wmax was accepted as real when the residual mean square was minimised. Then the capacitance, resistance and time constant were calculated, together with fitted estimates of relative water content for the time steps. The time constant (i.e. the product of the resistance and the capacitance) represents the time taken to reach 63% of the final water content change. Twice the time constant represents 95% of the change, and three times, 99% of the change.

2.4.5.2 Description of the Equipment and its Use

A standard Edinburgh pressure bomb was used for all water potential measurements on leaves and shoots.

For pressure/volume extraction curves on billets of wood a special chamber head was machined, having a central hole 25 mm in diameter with a ring groove cut close to the hole on the lower face (Fig. 2.10). This was fitted with a removable 0.5 mm thick rubber gasket.

In the base of the chamber, a circular plate was attached to a compression spring.

The wood sample consisted of a cylindrical billet cut axially from a branch or stem section. The upper face was planed with a sharp chisel to remove damaged tracheid ends, and the length adjusted so

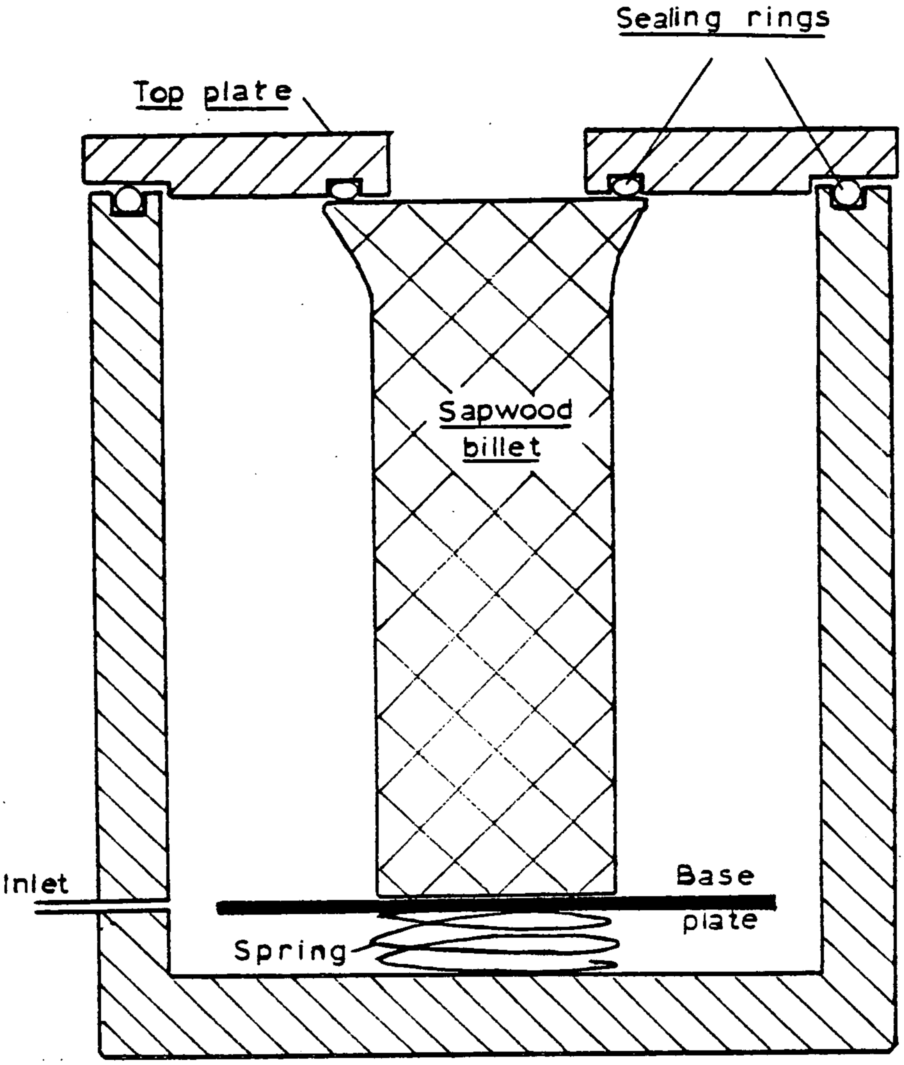


FIG. 2.10 Pressure chamber, modified to produce pressure/volume relationships from xylem sapwood.

that the billet fitted tightly against the sprung lower plate when the chamber was closed. The diameter of the billet was approximately equal to that of the aperture in the top plate, but a shoulder was left to support the sealing ring.

Immediately following cutting and shaping (which was done as quickly as possible), the billet was weighted to +/- 0.001 g, the cylindrical sides were covered with PVC insulating tape to prevent evaporation, and the rubber ring was glued to the top face using 'Loktite' cyanoacrylic glue. The billet was reweighed, mounted in the pressure chamber and pressurised to the first level. The expelled water was collected at set intervals using a tared absorbant towel stored in a plastic vial, removed to wipe the exposed face in a repeatable manner. Except when water was being collected in this way, the chamber aperture was covered with a large rubber plate.

The intervals between collection were 1 minute up to a total of 12 minutes, then three minute intervals until expulsion of water was approximately 0.1% per minute of the running total. Then the billet was removed, reweighed to check the increment of water removed, replaced and the pressure increased to the next level.

The pressures [illegible] used initially were 0.1, 0.3, 0.6, 1.0, 1.5, 2.1 and 2.8 MPa. Subsequently this was adjusted to 0.2, 0.4, 0.6, 0.8, 1.0, 1.5, 2.0, 2.5 and 3.0 MPa because the 0.1 MPa increment took an excessively long time.

On completion of the final pressure sequence the ring and tape were removed, and the 'fresh' weight, 'immersed' weight and 'oven-dry' weight were measured as described in Section 2.2.

These data permitted calculation of the time constant, resistance and capacitance for each pressure increment, as well as relative water contents for each time step at each pressure.

2.5 Leaf Area Measurement

2.5.1 Theory and Description of the Techniques Used

The measurement of leaf area is reviewed in detail by Kvet and Marshall (1971).

The measurement of needle area presents special problems, since the area involved in gas exchange is a function of both the length and the cross-sectional shape and dimension of the needle. Reliable, though tedious determinations of leaf areas of needles and microphyllous species have been made by calculating the surface area of samples from length and circumference, and extrapolating on the basis of weight or numbers (Thompson and Leyton,1971). Many determinations have been made of projected area using photoelectric measurement of light extinction, a method which is considerably faster although relying on calibration. Projected areas can be converted to total surface areas if the geometry of the cross-section of the needles is considered, but the accuracy is dependent on the goodness of fit of the geometry. Conversely, use of the projected area determination without conversion will confound leaf area figures with differences in cross-sectional shape.

Thompson and Leyton (1971) introduced the technique of covering the glued surface of needles with a monolayer of graded fine glass balls ('Ballotini' beads) and finding the weight of adhering beads. Surface area is related to bead weight by calibrating paper or wire of suitable known dimensions. A bed of beads fluidised by an air current facilitates coating the needles (Benecke, 1980; Davies and Benecke, 1980; Rook, pers. comm.). Results from the technique are closely related to results from optical planimetry (Drew and Running, 1975; Leverenz, 1978).

A further method for measuring the leaf area of intact or even attached needles or fascicles relies on the determination of volume by water displacement (Beets, 1977). Surface area is calculated as the square root of the product of volume and length, which is measured concurrently. Results were within 2% of a control method.

In this study, the primary objective was to estimate leaf areas of individual trees, with secondary objectives of estimating leaf areas of individual whorls of single trees, and also whole-stand leaf area indices.

2.5.2 Equipment and Techniques used

Projected leaf areas were measured with a 'Lambda' area meter (Model LI-3100) operated on the high sensitivity option, giving a precision of 0.2% (99% level of confidence) at the rated resolution of 0.1 mm^2. Since projected leaf areas were used as a basis for concurrent determinations of stomatal conductance by other workers, it was also used here without conversion to total area. measurements were made on fresh material stored in plastic bags at 2 ^{o}C to prevent drying and shrinkage.

2.6 Conclusions

Measurement of permeability of saturated stem sections could be carried out on a routine basis, to provide repeatable results.

Several methods were available to observe the effects of an overall potential, in order to make comparisons with similar conditions in intact trees.

Measurement of water cotent could be carried out on the intact tree using attenuation of gamma rays, and the results subsequently compared with gravimetric methods. The accuracy of the attenuation method is heavily dependent on obtaining repeatable gamma beam geometry.

Measurement of flow using heat pulse velocity has been developed to the stage that estimates of total transpiration can be made from theoretical considerations with out recourse to calibration. The method can be checked by comparison with measured outflows measured in the permeability apparatus using different pressures.

Measurement of water potential using the thermocouple psychrometry method was the most satisfactory method used at Ae, although the problems of measuring values close to zero water potential in the field are considerable, andresin is a problem. The pressure injection method gave some validation of the results, but where available, pressure chamber measurement of bagged epicormic shoots was the most satisfactory method, although such shoots were only available at Fetteresso.

A novel use for the pressure chamber was developed, to obtain pressure/volume relationships for wood. From the time course of the outflow flux, resistance to flow from storage could be calculated.

These methods collectively could provide sufficient information to use in a model for flow through a tree, and give at least some field information for verification.

3.0 RELATIONSHIPS BETWEEN SAPWOOD AREA, PERMEABILITY AND LEAF AREA

3.1 INTRODUCTION

The relationship between leaf area and the conducting tissue which upports it has been of considerable interest in predicting foliage iomass, and is well reviewed by Whitehead and Jarvis, (1981). mplied in such relationships is the assumption that evaporation from eaves is proportional to leaf area. Outflow from the leaves can be escribed as proportional to the product of leaf area and leaf onductance, if leaf conductance is assumed to be constant for all eedles. Watts *et al* (1976) showed that differences in stomatal onductance between levels (height) and also between age classes of eedles was of the order of 10 - 20%, and often less in *Picea itchensis*, so the assumption is probably reasonable. However everenz (pers. comm.) has suggested that recent work shows ignificant differences do exist.

Whitehead and Jarvis list a variety of stem measurements which have been used: girth, basal area, diameter, diameter transformed logarithmically, sapwood depth, current stem increment, and trunk volume. In each case the stem measurement differs from sapwood area because of additional factors such as the proportion of heartwood area or bark, differing seasonal or growth conditions, or species variation. Similarly, alternatives to leaf area such as leaf fresh weight, dry weight, dimensions or volume are confounded with factors such as leaf thickness or specific gravity.

Within particular stands, good relationships between sapwood area and leaf area have been obtained (Dixon, 1971; Grier and Waring, 1974; Kline *et al*, 1978; Whitehead, 1978; and various unpublished data listed by Whitehead and Jarvis, 1981).

However Whitehead and Jarvis propose that the relationship between sapwood area and leaf area for a species is also dependent on the conditions under which it is grown. Stem permeability, canopy size and conductance, and the ability of the root system to supply water are all affected by soil water status, evaporative demand, nutritional status and temperature. This results in a relationship between sapwood area and leaf area which is unique. Therefore while close relationships may be obtained for a particular stand, there are good reasons why the relationships should differ between stands in a predictable manner, and such differences have been demonstrated by Whitehead (1978).

Ontogeny and Structure

The primary objective in this study was to model axial flow, but this inevitably leads to a consideration of the 'hydraulic architecture' of the tree, for two reasons. Firstly, derivation of transpiration from heat pulse velocity measurements requires a knowledge of variation in flow rates at different places in the conducting sapwood (Section 2.3). Secondly, the branch structure both in the crown and in the roots may influence the patterns of conduction within the stem.

Structure can best be understood in terms of development. Each annual xylem increment comprises a sheath of new conducting tissue developing from the cambial layer, which covers the previous year's sapwood over the entire structure of the tree as well as producing a new whorl of branches and shoot extension growth at every bud. There is no significant growth in the xylem tissue laid down as conducting tissue in the previous year, and it follows that the last-formed whorl of branches is directly connected to the last-formed xylem sheath. Conversely, each previous whorl of branches is connected to the concurrent annual xylem sheath, plus all the other xylem sheaths exterior to it (Fig. 3.1).

If an annual ring is relatively isolated from its neighbours, this pattern of development may cause close relationships between the size and permeability of the ring, and the leaf area which it supports. Some indication of a low radial permeability between rings is required to support such a hypothesis.

Further, differences in sap velocity across a radius within the stem could also be influenced both by the conducting capacity of the ring (ie. cross-sectional area and permeability) and by the evaporative demand on the foliage it supplies.

This basic description of structure has long been recognised (Huber, 1929; Zimmermann and Brown, 1971; Richter, 1973; Zimmermann, 1978; Milburn, 1979).

'In the living tree only the earlywood conducts water.' (Whitehead and Jarvis, 1981). Evidence in support of this largely relates to aspiration of pits. Aspiration in earlywood occurs at a much smaller potential gradient than that required to move a meniscus of water through the largest pore in the margo of pits (Gregory and Petty, 1973), and so a tracheid rendered non-conducting by aspiration will tend to remain isolated. However in latewood, the pores in the margo are larger and the pit structure such that much larger potential gradients are required to aspirate the pit (Petty, 1972). Consequently, the sealing of embolised tracheids does not necessarily occur and the whole of the latewood may become embolised. Certainly

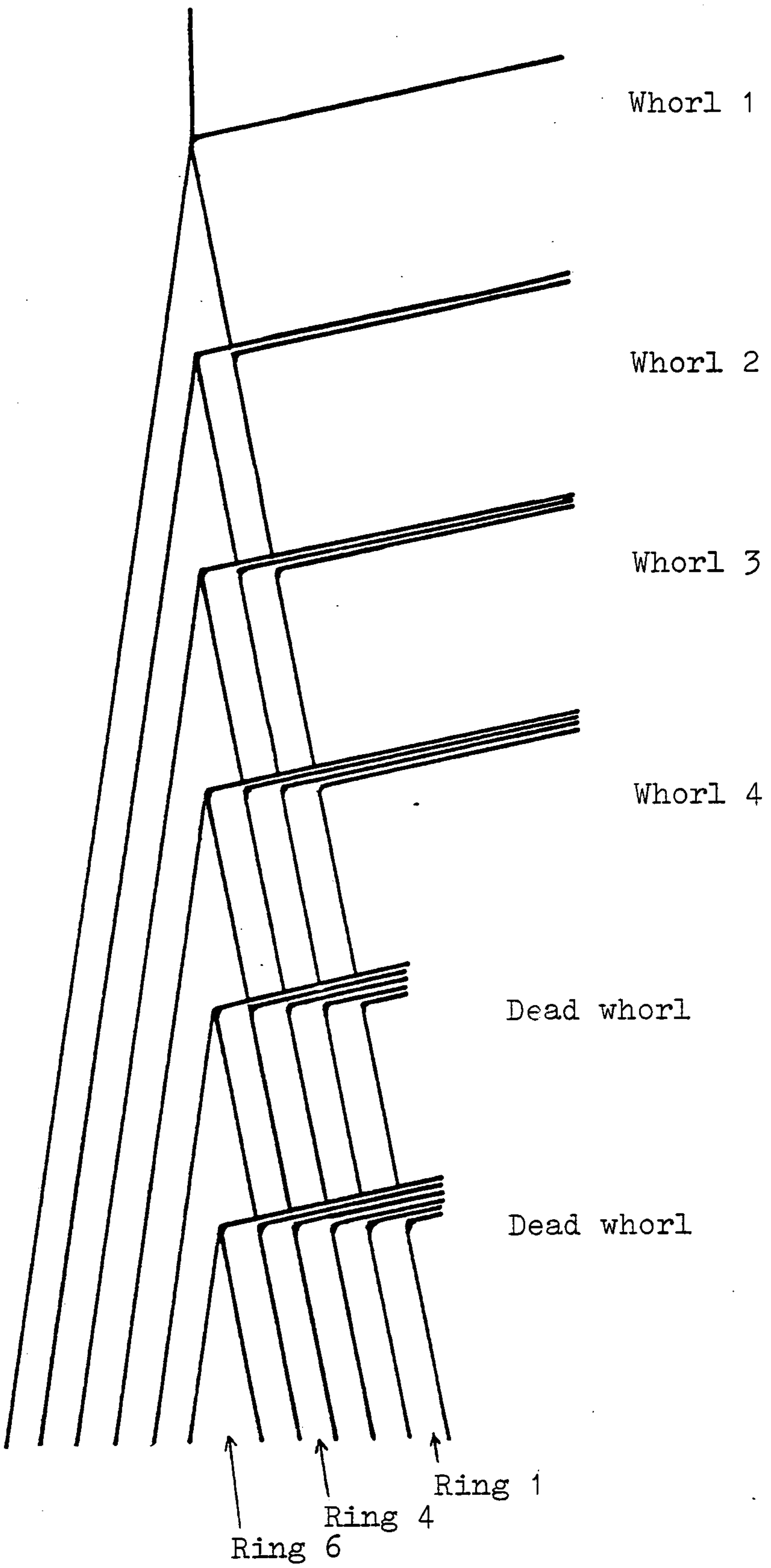


FIG. 3.1 Diagrammatic representation of the development of annual xylem sheaths and whorls of foliage. The inner rings are presumed not to conduct significant amounts of sap, since the lowest whorls are dead.

Harris (1961) associated low water content in the latewood with non-conduction, Booker (1979) demonstrated the low permeability of latewood rings in *Pinus radiata* using a dye technique, and this is confirmed for *P. contorta* and *Picea sitchensis* in the present study (Section 2.1.3.1). Kininmonth (1970, quoted by Booker, 1979) found radial permeability to be only 1/2000 of longitudinal permeability indicating a high radial resistance, and Erickson *et al* (1937) found the axial permeability of earlywood to be 29 - 34 times that of summerwood in a range of species.

These reports collectively suggest that the sap streams within each annual ring tend to remain isolated. However heat pulse velocity measurements amply demonstrate that flow occurs in virtually every ring in the sapwood, which may comprise 10 - 20 rings in a tree within a closed-canopy forest, even though needles are largely lost within three to four years. Therefore paths for transfer from the innermost rings to the outer rings must exist, although their nature is a matter for conjecture. MacDougall *et al* (1929) using dyes, found transfer occurred at the tips of each xylem sheath. On the other hand, the surface area of each xylem sheath is very large, and in spite of the high radial resistance a diffuse general transfer may occur but with flow rates within each ring still largely under the influence of the gradients and resistances associated directly with that ring. However dye studies within the main stem of large trees do not show this inter-ring transfer (e.g. Vite and Rudinsky, 1959; Greenidge, 1955; Werner, 1971).

The same dye studies also suggest that within a ring, flow tends to remain in a rather discrete flow path tangentially, although pronounced spiralling of those pathways can take place. Lateral root pruning leads to the drying of a corresponding strip of xylem (Chalk and Bigg, 1956). Contamination of ditches with sea water in Holland after sea dykes had been breached was associated with death on one side only, of trees planted on the edge of ditches (van Kraayenoord, pers. comm.). Therefore it seems probable that flow paths in stems of trees also tend to be tangentially discrete, although experiments involving disruption of the flow path clearly show that tangential movement can take place in the presence of suitable potential gradients (Hinckley et al, 1978). Further, differences in evaporative demand in different parts of the crown - particularly because of radiation - could lead to tangential differences in flow rate.

In this study, the measurement of permeability and the use of dyes enabled an investigation of the relation between sapwood area, permeability and leaf areas. The study was conducted in two ways: (a) by comparing sapwood area and permeability of internodes within the crown, with the leaf area above those internodes for single trees, and (b) by comparing total sapwood area and permeability at breast height with total leaf area on the tree, for a number of trees.

3.2 Sites, Materials and Methods

3.2.1 Sites

Three plots in two forests were used:

(a) Glentrool Forest

A nutrition experiment was laid down by the Forestry Commission on deep peat, to investigate the application of P and K on pole-stage

Picea sitchensis. The site was at Grid Reference NX360792 at an elevation of 122 m, with moderate exposure, 1750 mm rainfall per annum and not less than a depth of 1 m of peat. The forest was planted in 1948 into sheep-grazed turf on peat. Brashing was completed between April 1970 and July 1971.

The Commission experiment consisted of a 2 x 2 factorial design using the treatments (a) zero fertiliser, (b) phosphate at 50 kgP/ha (as 375 kg/ha of U.P.R. (unreverted phosphate rock)), (c) potassium at 100 kg/ha (as 200 kg/ha of muriate of potash), and (d) both P and K at the same rates. There were four replicates totalling 16 plots, each 30 x 15 m (0.045 ha).

The plots were fertilised in April 1970 at the same time as an overall thinning treatment. Assessment of growth unfortunately was not made until November 1971, so that comparisons were only possible on the basis of total basal area rather than the actual growth since the treatments were applied. Foliage analysis showed that N increased from 1.48% on the control plots to 1.72% of dry weight on the PK plots, P from 0.216 to 0.318%, and K from 0.73 to 1.06%. The basal area measurements were repeated annually from 1972 to 1975, and showed an increase in cumulative basal area of 121, 75, 66 and 57% for the PK plot. The response in a 1972 Commission report is described as 'dramatic', and attributed to 'possibly the combined effect of fertiliser and thinning'. All N, P and K levels were described as satisfactory in all treatments.

A harvesting programme of a representative ten trees from each plot, selected on the basis of diameter class distribution was made in November 1978 by the Research Staff of the Forestry Commission. The opportunity was taken to make concurrent leaf area (Whitehead, pers.

comm.) and stem dimension measurements, and measurements of stem permeability on all ten trees taken from each of the control and PK plots.

Basic measurements of the selected trees were (s.d. in brackets):

	Control	PK Treatment
Height (m)	15.3 (2.0)	16.4 (1.5)
DBH (mm)	172. (28.)	185. (36.)
Sapwood area (m^2)	0.0115 (0.0030)	0.0146 (0.0066)
Leaf area (m^2)	36.7 (16.7)	50.8 (24.8)

(b) Forest of Ae

This was the main experimental field site for the study, and was situated at Grid Reference NY 994956 at an altitude of 260 m with moderate exposure and an annual rainfall of 1450 mm.

The site comprised a 0.655 ha plot planted in Pinus contorta cv. 'Lady Smith', one of a number of similar plots of a wide variety of species planted by the Forestry Commission for evaluation. It was planted in 1959 at a spacing of 1.77 m x 1.46 m into ploughed peat 200 - 400 mm deep.

The mean tree diameter for the whole plot was 106 mm and the leaf area index was 5.54 (Leverenz and Whitehead, pers. comm.).

Ten trees were selected using the DBH size distribution for the plot, to give a representative sample distribution in terms of both mean and standard deviation. The mean dimensions of the sample trees (s.d. in brackets) were:

Height (m)	8.29 (1.09)
Clear bole length (m)	3.73 (0.88)

DBH (mm)	106.8 (40.6)
Sapwood area (m^2)	0.0071 (0.0053)
Leaf area (m^2)	14.5 (15.9)

3.2.2 Methods

The following measurements were made on each tree from all three plots:

(i) Height of each node, and of the terminal bud

(ii) The heartwood and sapwood areas for each internode

(iii) The permeability of an internode taken at DBH

(iv) The leaf area of each whorl for each age class was estimated, using a sub-sampling technique. For each whorl, the total weight of branches was taken. For every second whorl, the leaf area per unit total weight was found by subsampling, removing all needles in each age class and finding the leaf area of a subsample of the needles (Section 2.5). The leaf area of the intermediate whorls was inferred from their total live weight, using graphically-extrapolated values for the leaf areas per unit total weight (J. Cousens, pers. comm.).

(v) For one or two trees from each plot, the sapwood areas of each internode within the crown was found.

(vi) For the same trees, permeability was measured at every second internode within the crown, and the intermediate values inferred graphically.

(vii) For one tree from another phase of this study (Section 5.4.2) five multiple leaders from one tree were compared.

An attempt to relate individual ring areas and permeabilities measured at DBH to leaf areas of particular whorls was abandoned on theoretical grounds. It can be shown that, using the assumptions of flow paths and sinks given in Section 3.1, the flow path of a single ring at BH cannot be uniquely identified with a particular whorl without being confounded with the effect of other whorls. Conversely, a particular whorl cannot be uniquely identified with a particular ring at breast height.

3.3 Results

3.3.1 Between Trees

The relationships between leaf area and (A) sapwood area, (B) permeability of the whole stem cross-section at BH, and (C) the product of sapwood area and permeability (the 'conductance per unit stem length' at breast height), are shown in Fig. 3.2.

The correlation coefficients with leaf area are as follows (the asterisks *, **, *** refer to significance at the 5, 1 and 0.1% levels respectively):

	Ae	G-Control	G-PK
SWA	0.974	0.741 **	0.905***
K	0.663 *	0.013 NS	0.755 **
K x SWA	0975***	0.856***	0.951***

Clearly the relationship between leaf area and sapwood is significant. It is improved by the combination of permeability with sapwood area, although the direct relationship of leaf area with

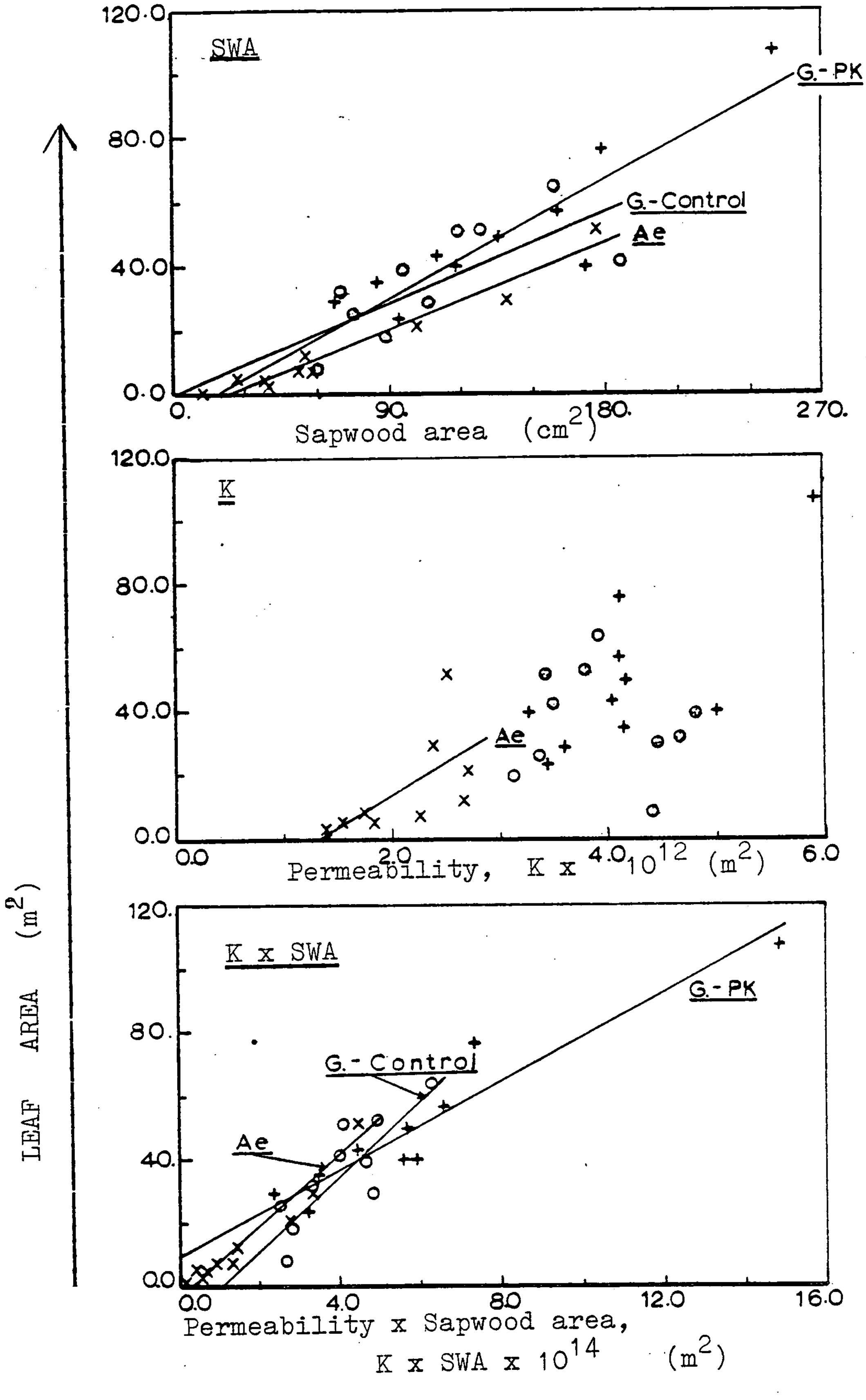


FIG 3.2 Relation between sapwood area, permeability and leaf area, for 10 trees from each of three plots. *P. sitchensis* trees from the fertilised Glentrool plot are marked by (+), those from the Glentool control plot by (o), and *P. contorta* from Ae by (x).

permeability is not particularly good.

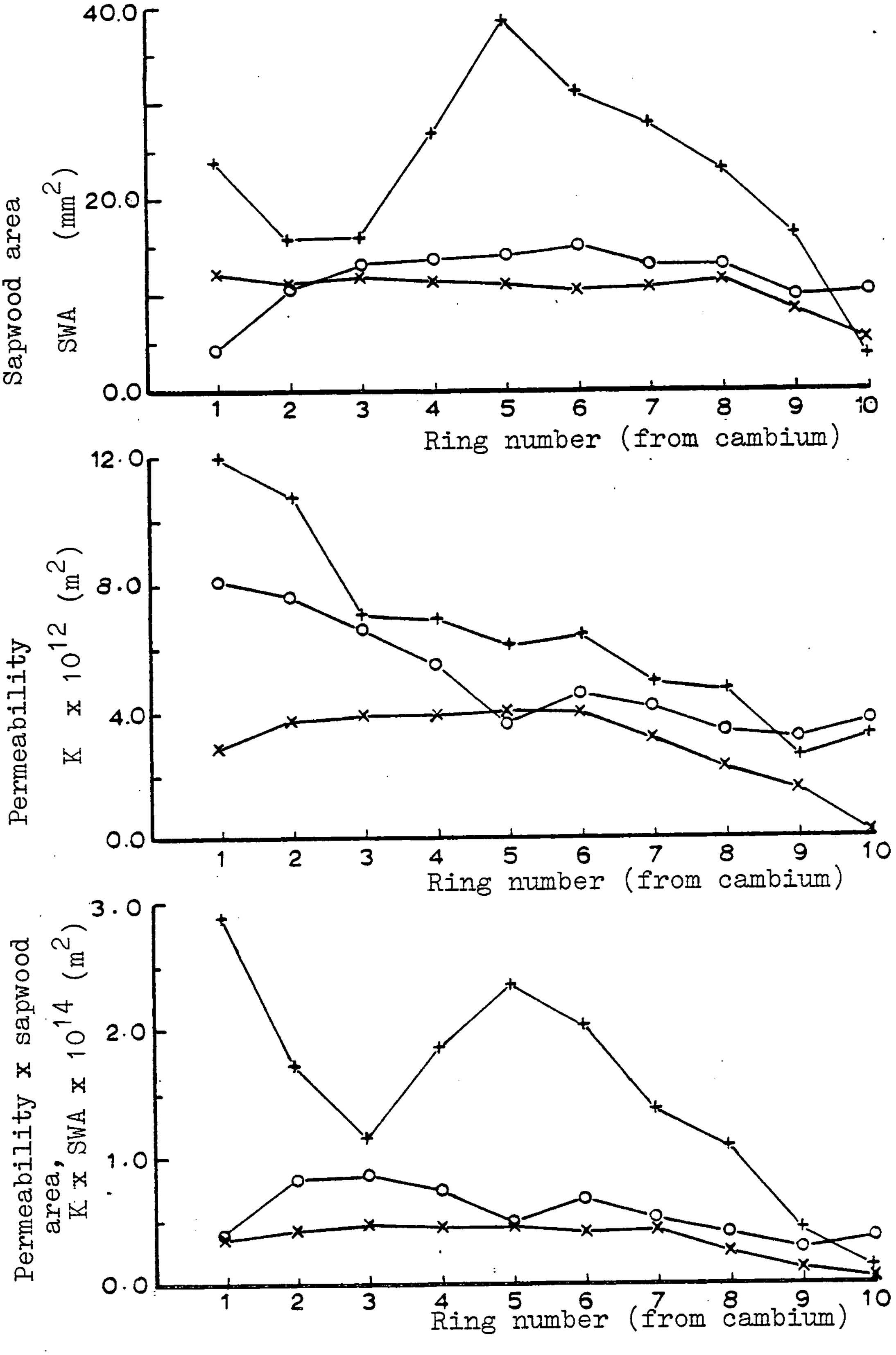
The regression coefficients could not be distinguished statistically between plots except in the case of K x SWA, where the value for Ae (10.84) was significantly larger than that for the fertilized Glentrool plot (6.77) at the 5% level. This may result simply from the fact that the plots at Glentrool were thinned, whereas those at Ae were not.

The positive regression coefficients for the permeability/sapwood area relationships (Fig. 3.2) indicate that larger trees have more permeable stems, probably because more rapid growth results in larger tracheid lumens and larger bordered pits. In general, the regression lines cross the 'X' axis, indicating that at low leaf areas there is an 'excess' of conducting capacity. Probably this reflects the presence of suppressed trees, which are failing to produce a current leaf area commensurate with their previous production of xylem tissue.

Differences between Rings

Fig. 3.3 shows the mean sapwood area, permeability, and sapwood area x permeability product for each annual ring at breast height for the ten trees on each plot. Fertilizer treatments and thinning were carried out in 1970, i.e. corresponding to the ninth ring. Although some trees had a small sapwood area associated with earlier years than those shown, these were omitted for clarity. None were of significant size or high permeability.

A large increase in sapwood area growth is obvious over the five or six years following fertilization in the fertilized Glentrool plot, contrasting with both the control and the unfertilized Ae plot. The downturn in the size of the sapwood increment in the Glentrool control



<u>FIG. 3.3</u> Values of sapwood area, permeability and sapwood area x permeability for 10 trees from the fertilised Glentrool plot (+), Glentrool control plot (o) and the Ae plot (x).

plot has no obvious explanation.

Both the Glentrool plots showed an increase in permeability following thinning, but the increase in the PK plot was much larger, and paralleled the increase in sapwood area.

Because both sapwood area and permeability were increased by fertilizing, the product (K x SWA) is also very much increased. In the other plots, there is a remarkable constancy in the potential ability of each ring to conduct sapflow. Presumably the annual increment of leaf area followed the same pattern, at the time the concurrent growth ring was laid down.

3.3.2 Within trees

The relationships between cumulated leaf area above particular whorls, and (A) sapwood area, (B) permeability and (C) sapwood area times the permeability of the internodes immediately below those whorls, are shown in Fig. 3.4. The corresponding correlation coefficients are:

	Ae	G-Control	G-PK
SwA	0.977***	0.975***	0.980***
K	0.948 *	0.966***	0.935 *
K x SWA	0.963 **	0.968***	0.936 **

In each case in Fig. 3.4, the ringed points represent SWA and K measurements on the Ae data made at different heights within the clear bole of the tree, i.e. supporting the same (total) leaf area. The regression analyses do not include these points, which indicate that within the clear bole, sapwood area decreases with height while

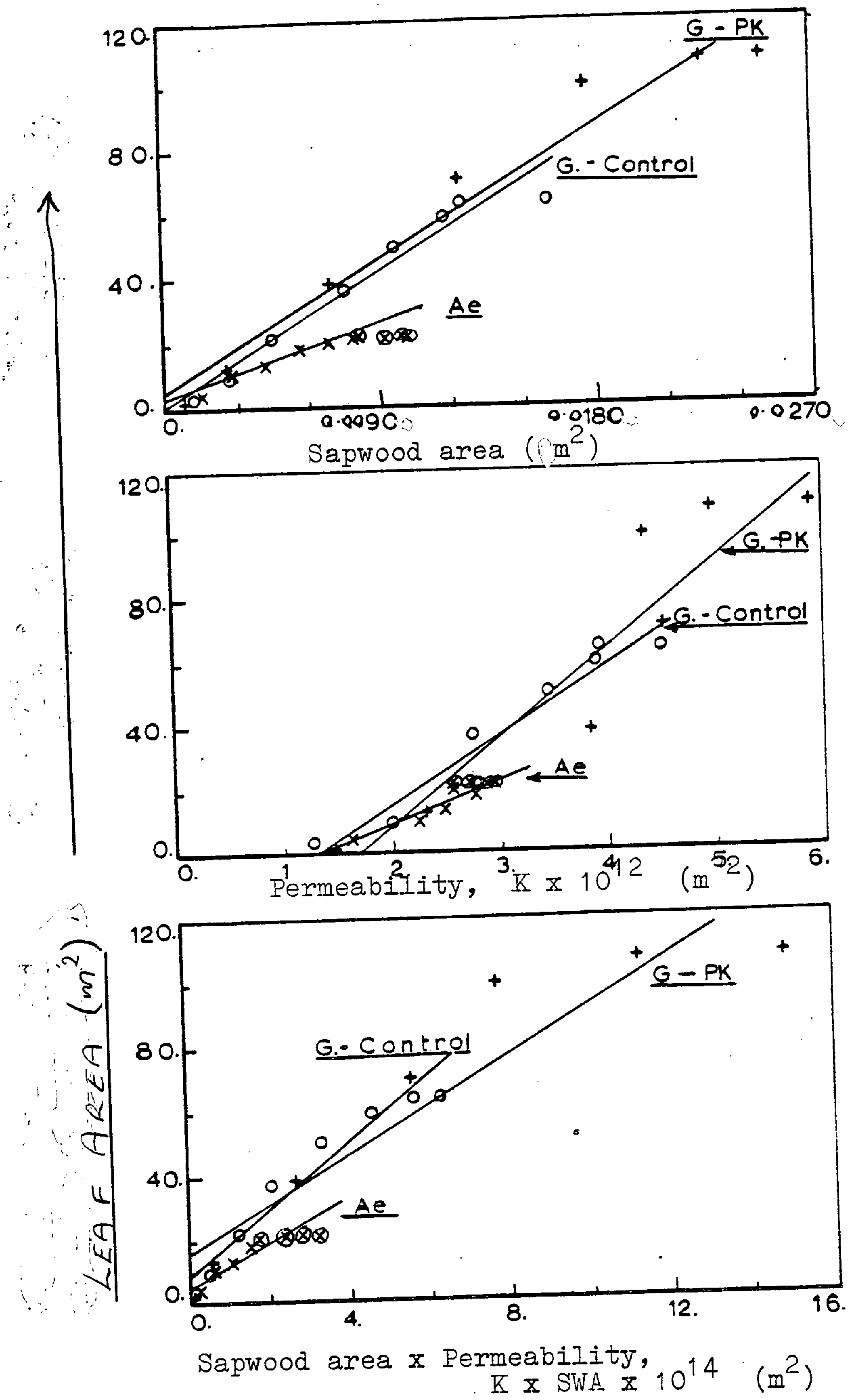


FIG. 3.4 Relation between leaf area, and sapwood area (SWA), permeability (K) and SWA x K, within one *P. sitchensis* tree each from fertilised (+) and unfertilised (o) Glentrool plots, and 1 *P. contorta* tree from the Forest of Ae (x).

permeability increases, apparently coinciding with recently-dead whorls which are associated with xylem tissue which is still capable of conducting, or with larger sapwood areas associated with each ring towards the base of the tree, partly causing the stem taper.

The regressions between leaf area and sapwood area within trees are highly significant. However while the permeability/leaf area regression is also significant, the combination of K x SWA is slightly worse than that of SWA alone. This decrease is in contrast to the result for between-tree regressions. The effect is small, and probably reflects the chronological age of leaf tissue of which tends to become less conductive with age. Therefore towards the top of the tree, a higher proportion of younger foliage is being associated with the sapwood.

For the tree with multiple leaders (Fig. 3.5), the correlation coefficients were higher, indicating an even closer relationship when genetically similar foliage and sapwood from the same height were considered.

The regression coefficients could not be distinguished statistically except in one case. For the sapwood area/leaf area coefficients, that for Ae (0.256) was significantly smaller than that for G-Control (0.462) or G-PK (0.464) at the 5% level, indicating site or species differences.

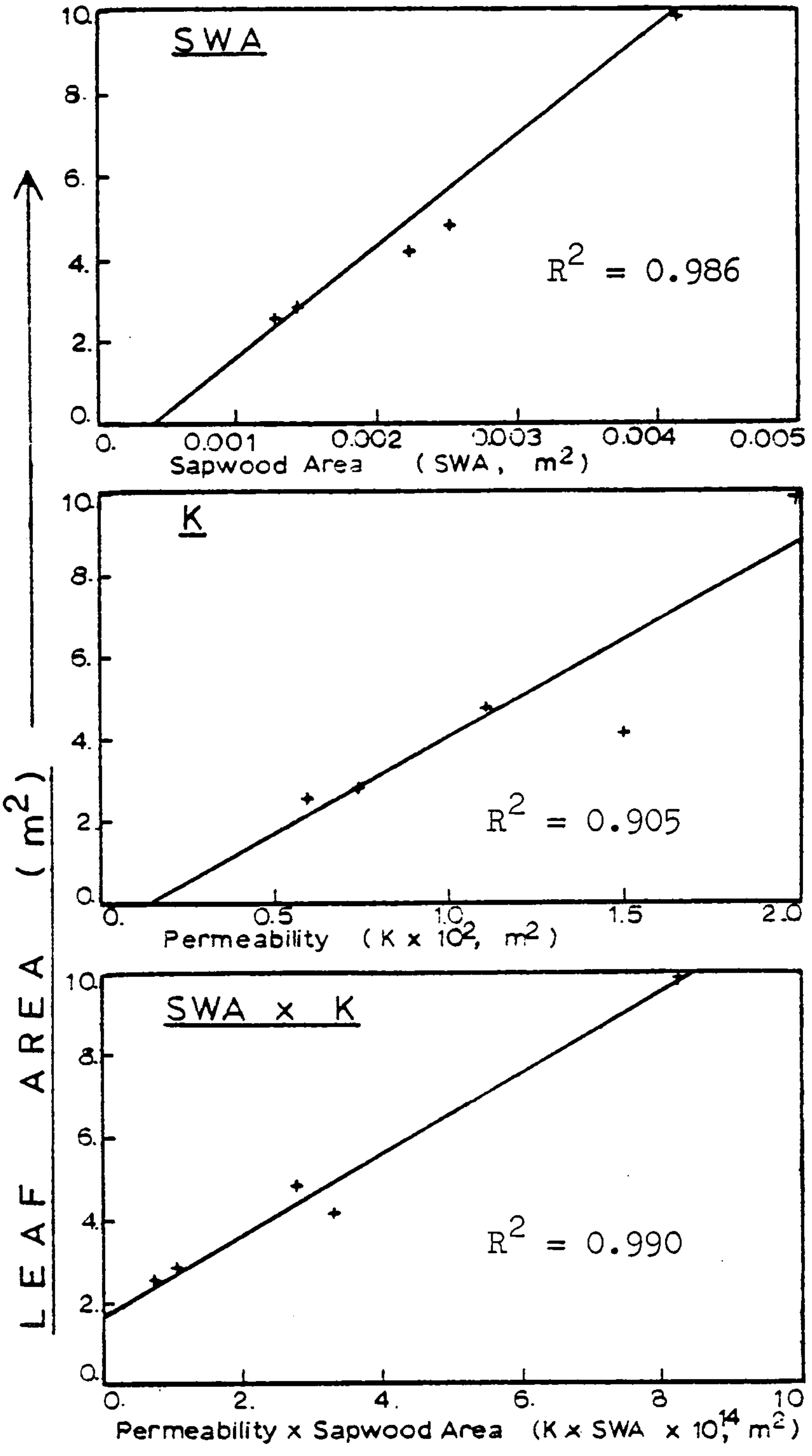


FIG. 3.5 Relationship between leaf area and sapwood area (SWA), permeability (K) and SWA x K for five multiple leaders from a single P.contorta tree from the Forest of Ae.

3.4 Discussion

If flow through a tree trunk from root to leaf (ignoring crown structure) is considered in terms of the Darcy equation, then the potential gradient is proportional to the ratio of the flow rate to conductance, at a given viscosity (i.e. temperature). That is,

$$\frac{\Delta \Psi}{l} = \frac{\eta Q}{K.A}$$

Since flow is proportional to leaf area and stomatal conductance,

$$\frac{\Delta \Psi}{l} \propto \frac{\eta A_l k_l}{K.A}$$

where A_l is leaf area and k_l is stomatal conductance.

It follows that if the ratio $A_l/(K.A)$ is similar (assuming k_l is constant between trees), then given the same evaporative demand the potential gradient is also constant for different trees and needle water potentials will tend to be similar. Conversely, one could suggest that a balance between leaf area and xylem area is maintained presumably by a feedback mechanism, so that an adequate transpiration stream can be maintained without needle water potentials reaching stress levels. Jarvis (1975) suggests that post-thinning stress results from increased evaporative demand on the trees which remain and is caused by an increased proportion of the total incident radiation being intercepted by each individual. The increased flux is subsequently compensated for by increased sapwood area growth. Similarly the application of fertilizer stimulates both needle and sapwood growth, and the ratio is again maintained.

A similar argument can be formulated for within the crown of a single tree. The transpiration rate is again proportional to the product of leaf area above a particular point on the stem, and stomatal conductance. We can suggest that the potential gradient above any internode in the crown and the leaves is proportional to the ratio of leaf area to the sapwood area supporting it.

The presence of genetic variation and/or height differences is implied by the close relationships found in the multiple leader tree, even though only five data points were available.

In the lower part of the crown where needles are not being replaced because of an inadequate light regime, the innermost conducting rings will become redundant and conversion to heartwood presumably follows. It seems reasonable that falling light levels at the base of the canopy would be the trigger mechanism for conversion of sapwood to heartwood, rather than the alternative hypothesis that loss of the lower whorls follows development of heartwood, since those whorls could still be supported by rings exterior to those being converted. Again, the number of conducting rings always equals or slightly exceeds the number of live whorls. Further, the lowest live whorl is usually represented by only one or two branches, and this is represented at a corresponding orientation in the stem cross-section immediately below by an area of conducting tissue in the innermost ring or rings, the remainder of which are otherwise non-conducting. Such branches are always the largest within the whorl, and carry needles highest in the canopy. It seems reasonable therefore, that needle loss is associated with low light levels, not with falling sapwood conductivity, and that conversion of sapwood to heartwood is associated with redundancy of function.

3. Conclusions

There is a good relationship between the sapwood areas of trees at breast height, and the leaf area which each supports, within a homogenous stand. The relationship can be improved slightly by using the product of sapwood area and permeability at breast height (i.e. the conductance per meter). The regression between sapwood area and permeability is significant and positive, indicating that larger trees have more permeable wood.

Within a tree, similar relationships hold when the sapwood area of internodes is compared with the leaf area which each supports. Genetically similar multiple leaders at the same position in the canopy have an even higher correlation between leaf area and sapwood area, indicating a genetic or positional influence.

There is some evidence for the integrity of flow paths within individual rings, and for direct pathways through particular rings to particular whorls.

4.0 RELATIONSHIPS BETWEEN PERMEABILITY, WATER CONTENT AND WATER POTENTIAL

4.1 Implications of the structure of wood

Softwoods conduct water primarily through tracheids, which are interconnected through bordered pit pairs (see detailed descriptions of structure by Panshin and de Zeeuw, 1970; Siau, 1971; Esau, 1977). Wood is composed mainly of longitudinal tracheids in gymnosperms. Typically, Pinus strobus L. has 93% of its volume as longitudinal tracheids, 6% as wood rays and 1% as longitudinal resin canals (Panshin and de Zeeuw, 1970). Earlywood tracheids are large with thin walls, wide lumina and many large bordered pit pairs compared to latewood tracheids. Most pit pairs are found along the tapered radial faces of the longitudinal tracheids, and those on the tangential faces are smaller as well as fewer. Therefore most flow between tracheids takes place in a tangential direction.

The following table gives some dimensions for Sitka spruce (Bolton and Petty, 1975) in μm:

	Earlywood	Latewood
Mean tracheid length	4000.0	2400.0
Tracheid lumen diameter (wide axis)	35.0	25.0
Tracheid lumen diameter (narrow axis)	30.0	8.0
Number of pits per tracheid	100	20
Maximum pit thickness	7.0	12.0
Minimum pit aperture radius	2.7	1.5
Pit membrane diameter	17.0	8.0
Maximum membrane displacement	2.0	2.0

Margo strand length	4.25	2.00
No. of margo strands per pit	100	50
No. of margo pores per pit	200	50
Pit membrane thickness	o.21	0.28
Margo pore radius	0.15	0.20
Torus diameter	8.5	4.0

The property of aspiration of the central torus allows the pit aperture to be sealed when a sufficient potential difference is applied across it, preventing free movement of fluids. Pits can also be occluded with extractives which are soluble in hot water or alcohol, or encrusted with non-extractable lignin-like substances, especially in heartwood (Siau, 1971). Half-bordered pits are found between prosenchyma and parenchyma cells, the half-border facing the prosenchyma cells. Within parenchyma, pitting is simple.

Attempts have been made to determine the sites of resistance to flow in softwoods (see Siau, 1971; Leyton, 1975; Bolton and Petty, 1978 for reviews). If as early workers assumed, virtually all the resistance to flow lies in the pores of the pit margo, then the Adzumi equation (Adzumi, 1937) can be used to find the numbers and mean radius of the pit pores (Petty and Preston, 1969; Siau, 1971). However Petty and Puritch (1970) using the technique of Petty (1970) found deviations from this relationship which they attributed to resistance to flow in the tracheid lumina. In solvent-dried wood (air-dried wood was found to have a high proportion of aspirated pits), 83 % of tracheids were conducting. The pit membrane pores were found to be about 0.1 µm in radius with 27000 pores per tracheid, and caused 61 % of the resistance. The remainder was attributed to resistance in the lumina. Petty (1974) subsequently found that a

Couette correction for flow through short capillaries (i.e. margo pores) was necessary, and he recalculated the values of the membrane pores to be 0.16 µm and the number of pores per tracheid to be 12000. A similar study by Smith and Banks (1971) attributed resistance to both the tracheid lumina and the entire bordered pit system, rather than just the pores of the margo. This was further extended by Bolton and Petty (1975) who defined possible sites of resistance in the pits. These were incorporated by Bolton (1976a, 1976b) in a model which included the pit-margo pores, border-torus annuli, pit apertures and tracheid lumina.

The process of aspiration controls the ability of the bordered pits to conduct fluids, and together with the direct effect of embolism, is responsible for the increase in resistance on drying. However in air-dry wood it is frequently found that earlywood pits are aspirated (e.g. Phillips, 1933) but that sufficient latewood pits remain unaspirated to permit significant conduction. Earlywood aspiration can be largely prevented by replacing the water with fluid of low surface tension before drying, apparently because the low surface tension is insufficient to pull the pit margo into contact with the pit border. Thus measurements of surface tension can be equated with mechanical forces and strength properties of the bordered pits, to establish whether or not aspiration can occur (Petty, 1972; Gregory and Petty, 1973).

4.2 Nature and Implications of Embolism

4.2.1 Cavitation

Liquids have a very small coefficient of compressibility, so that very large changes in pressure are accompanied by very small changes in specific volume. When negative pressures are applied to an 'incompressible' liquid, unless the liquid is specially treated, cavitation occurs. Cavitation is associated with the presence of nuclei which are believed to be small pockets of undissolved gas, usually air (Batchelor, 1967). Since the inward force at the boundary of a small spherical bubble is large, one would expect them to dissolve. However the bubbles are postulated to persist in small hydrophoboc solid particles where the direction of surface tension is outward. The critical negative pressure at which such nuclei can grow is approximately that of the vapour pressure of water.

The application of high pressure appears to destroy gas nuclei (Harvey et al,1947, quoted by Batchelor, 1967). Water compressed to some 70 MPa for several minutes can subsequently stand negative pressures of -2.5 MPa without cavitation, presumably because the gas nuclei are dissolved by high pressure.Similarly water in which gas or gaseous nuclei have been removed remains stable at -30 MPa (Briggs, 1950), and Oertli (1971) suggests that xylem sap columns of an intact plant can stand -10 to -100 MPa. Theoretical estimates for the ultimate tensile strength of water range from 612 MPa (thermal equivalent method) to 1850 MPa (Nobel's energy content method) (Milburn, 1979 - Appendix 5).

Evidence for cavitation in plants comes from two approaches. Firstly, changes in water content have been observed seasonally (e.g.

Gibbs, 1958) and diurnally (e.g. Rothwell, 1976). Such changes are too large to be accounted for by other than tracheid emptying and refilling (reviews by Hinckley et al, 1978; Whitehead and Jarvis, 1981). Secondly, cavitation can be detected acoustically (Milburn and Johnson, 1966) at the rather high water potentials of -0.5 to -0.1 MPa in herbs (Milburn and McLaughlin, 1974). West and Gaff (1976) found cavitation, also observed acoustically, at about -1.2 MPa in apple trees.

Reversibility has not been demonstrated to occur immediately or completely when using acoustic methods (Milburn, 1979 - p. 165), although root pressure could conceivably acheive this in herbaceous plants.

4.2.2 Development of Emboli

The size of a bubble is given by the relationship (Siau, 1971):

$$R = 2.0 \times \sigma/(P_o - P) \qquad \text{Equation 4.1}$$

where P_o is the pressure inside the bubble (Nsm^{-2})

P is the liquid pressure (Nsm^{-2})

σ is the surface tension (Nm-1)

R is the radius of the bubble (m)

Surface tension (or specific surface energy) is 'stored' in the surface of the bubble and can be likened to the energy in a stressed spring. Its magnitude is dependent on the properties of the gas and the liquid, and the pressure of the enclosed gas is proportional to the absolute temperature. Since P_o in a free bubble is always bigger than P, there will be a gradient of diffusion outwards. However if a bubble within a tracheid becomes sufficiently large as a result of negative pressure potential, the adhesion between the liquid and the wall at the liquid/gas interface causes a withdrawal of the liquid, with a resulting bubble pressure given by the following expression (Siau, 1971):

$$P_o - P = \frac{2.\,\rho.\mathrm{Cos}\,\theta_i}{R} \qquad \text{Equation 4.2}$$

where θ_i is the angle of contact
R is the radius of the capillary (μm)

In a small capillary, θ_i tends to zero and the expression becomes that for a small bubble (Equation 4.1).

The radius of the tracheids is not more than about 35 um. Thus if a tracheid is just filled with a stable bubble of the same diameter, the bubble would have a pressure difference across the face of only 0.004 MPa. In contrast, a bubble of say, 3 μm, is stable with a pressure difference of 0.05 MPa across the surface. Clearly a large bubble requires only a small pressure difference to perpetuate its existence , but a small additional pressure will cause a large decrease in size if the enclosed gas can dissolve, i.e. if a concentration gradient exists in the appropriate direction. Epstein and Plesset (1950) have calculated rates of solution for such stationary bubbles in terms of

(i) surface tension,

(ii) the ratio, f, of the concentration of gas in the surrounding liquid to the concentration of a saturated solution of the gas.

They found that if the surrounding liquid was saturated, surface tension would cause a bubble of radius 10 um at 22 °C to dissolve in 6.6 seconds. Alternatively, the bubble would be stable in size at f= 1.2, approximately, i.e. in a supersaturated solution. Again, at f = 0.0, complete solution of a 10 μm bubble would occur in 1.2 seconds; but for the same bubble to double in volume in the same time, a value of f = 1.3 would be required. The authors found that the time taken to dissolve or enlarge was approximately proportional to the square of the initial size of the bubble.

These results emphasise that the size of a bubble is rarely stable. Changes in gas concentration will occur with respiration of living cells in the xylem, and the diurnal variation in the water potential of leaves is reflected in changes in hydrostatic pressure potential in the xylem. Further, temperature changes will affect both surface tension and the pressure inside the bubble.

The role of surface tension is obviously important. Since it is reasonable to expect the transpiration stream in a tree stem to be close to or saturated with gas resulting from respiration, it follows that surface tension will tend to reduce bubble size, eventually causing it to dissolve completely.

Emboli could be initiated either from nuclei already present in the sap, or at much lower hydrostatic potentials, by transmission through the bordered pits. In the latter case, the size of the pit pores indicate the pressure differences required for the passage of an air bubble, using Equation 4.1. Using data from Bolton and Petty (1975), earlywood pit pores of radius 0.15 μm would require a pressure difference of 0.98 MPa, and latewood pits (radius of 0.20 μm) a pressure difference of 0.74 MPa. Pressure differences which will cause aspiration can also be calculated using pit dimensions and physical characteristics of the margo strands (Petty, 1972). Using this method, Gregory and Petty (1973) found that earlywood of Pinus sylvestris required a potential difference of 0.033 MPa to aspirate, but latewood required 7.3 MPa. Thus latewood pits will not aspirate to prevent a latewood emboli from being transmitted through the entire latewood matrix under the potentials normally encountered in an intact tree, but aspiration will ensure that earlywood emboli will remain isolated. They could thus redissolve under the influence of diurnal variations and phase lags in temperature, osmotic potential and total water potential.

Mechanisms for recharge in tall trees remain a fertile field for polemics. There are two current popular theories: firstly, that recharge can occur when dew, fog or rain is absorbed through 'gaps' in the cuticular surfaces of needles, the non-cuticular base of needles or other absorbant sites (Milburn, 1979). Secondly, parenchymatous tissue - especially ray tissue - may permit the transfer of water to embolised tracheids. This could occur if diurnal variation in water potential was accompanied by a phase lag in the osmotic adjustment of the parenchyma. After transpiration ceases at dusk, the osmotic potential of the parenchyma would induce additional entry of water into the cell. Subsequently as the osmotic adjustment was made, this additional water would be expelled, producing a small transitory positive pressure.

It should be noted in this regard, that every longitudinal tracheid is in contact through half-bordered pits, with at least one ray cell (Esau, 1977).

Both these mechanisms would work better soon after the occurrance of cavitation, since initially the gas within the bubble must be mainly water vapour. Presumably this is eventually replaced by air through diffusion. However, if an externally-induced pressure could reduce the size of the emboli sufficiently for surface tension to increase the internal pressure significantly, the bubble may dissolve (Cary *et al*, 1968.

4.3 Effect of Water Potential on Water Content

4.3.1 Introduction

Diurnal and seasonal variations in canopy characteristics and evaporative demand, in soil water supply and root development, and in trunk temperature all suggest that water potential in the trunk also varies, probably within quite wide limits in the upper strata (Richter, 1973; Jarvis, 1975; Milburn, 1979 and many others). From these and also indirect measurements, various authors have suggested that variations in sapwood water content indicate a reservoir for diurnal or seasonal water requirements (Chalk and Bigg, 1956; Clark and Gibbs, 1957; Gibbs, 1958; Doley, 1967; Stewart, 1967; Waggoner and Turner, 1971; Markstrom and Hann, 1972; Kozlowski, 1972; Lassoie 1973, 1975; Richards, 1973; Roberts, 1976, 1977, 1978; Hinckley and Bruckerhoff, 1975). Diurnal phase lags in water potential occur in *Picea sitchensis* (Richards, 1973) and in sap velocity in a range of species (Huber and Schmidt, 1936; Swanson, 1972; Lassoie *et al*, 1977). Such phase lags cannot result from resistance alone and must involve capacitance. The possibility of replacement of water by gas or 'vacuum' is denied by Zimmermann and Brown (1971), who suggest that trunk expansion and shrinkage is the source of capacitance. However most of this change occurrs in the phloem tissues (Section 2.2.1) and the xylem tissue has been found to be virtually unchanging dimensionally (Richards, 1973).

Because of the difficulty in measuring either water content or water potential in intact trees without interfering with the flow paths, few attempts have been made to establish a relationship between these measurements. In one attempt, Waring and Running (1978) suspended uniform 5400 mm^3 sapwood disks above salt solutions of different osmotic potential for 6 weeks (Fig. 4.1). They found that a large drop in water content occurred with a small decrease in potential: 80% of water was removed by only -1.0 MPa. The samples were small and would have exposed many cut tracheid ends, and the time of exposure was very long, increasing the probability of cavitation.

Landsberg *et al* (1976) calculated capacitance from weight and water potential changes in small apple trees removed from water culture, to be approximately 2.0 x 10^{-8} kg kg^{-1} Pa^{-1}.

In the intact tree, the relative water content of sapwood [illegible] rarely reaches 100%. Therefore normally a proportion of the tracheids (almost certainly including earlywood tracheids) are embolised, and in contact with the remaining tracheids *via* bordered pits which may or may not be aspirated. Therefore there is some justification for using excised tissue in equilibration experiments with water potential, since both excised and intact tissue contains embolisms. However if the cut tracheids form a significant proportion of an excised sample, there may be a corresponding increase in the probability of an embolism being transmitted through the matrix.

4.3.2 Measurement Protocol Used

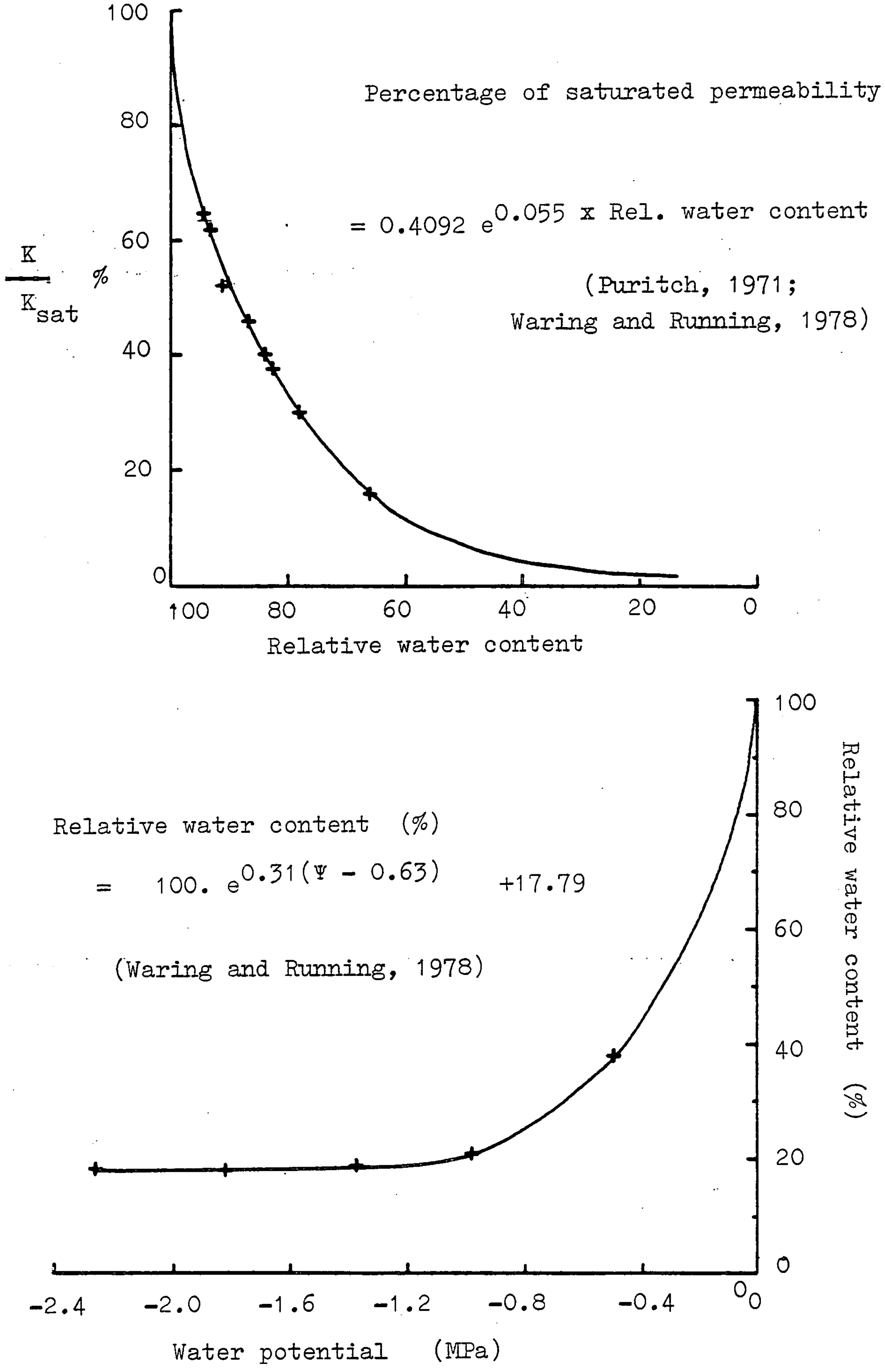


FIG. 4.1 Published relationships between water content, water potential and permeability.

Two laboratory techniques were used to establish a relationship between water content and water potential.

(i) Use of Osmotica. In Section 2.1.3.2 an experiment was described in which osmotica of various potentials were circulated over the cut ends of a stem section, but were kept separated from wood by semi-permeable membranes. Concurrent measurements of water content were made using the gamma radiation attenuation technique (Section 2.2). Thus variation in water content caused by removal of water by the osmoticum should be evident.

(ii) Pressure Chamber Technique. In Section 2.4.5, a pressure chamber adapted to extract water from a billet of wood is described. The statistical theory and method to obtain capacitance, resistance to flow from storage and the time constant for successive pressure increments is also given.

Both these methods give the change in water content for successive changes in an externally-applied water potential.

Experiments using osmotica were run on three separate 450 mm sections of *P. contorta*, one from each of the main experimental trees at the Ae field site. These sections each contained heat pulse velocity probes which had been used *in vivo*. Immediately prior to these experiments, flow through the logs had been compared with heat pulse estimation of flow. Therefore the logs were essentially saturated.

Using the modified pressure chamber technique (Section 2.4.5), pressure/volume determinations were run on both stem and branch wood from *P. contorta*, and from *P. sitchensis* stem sapwood from two

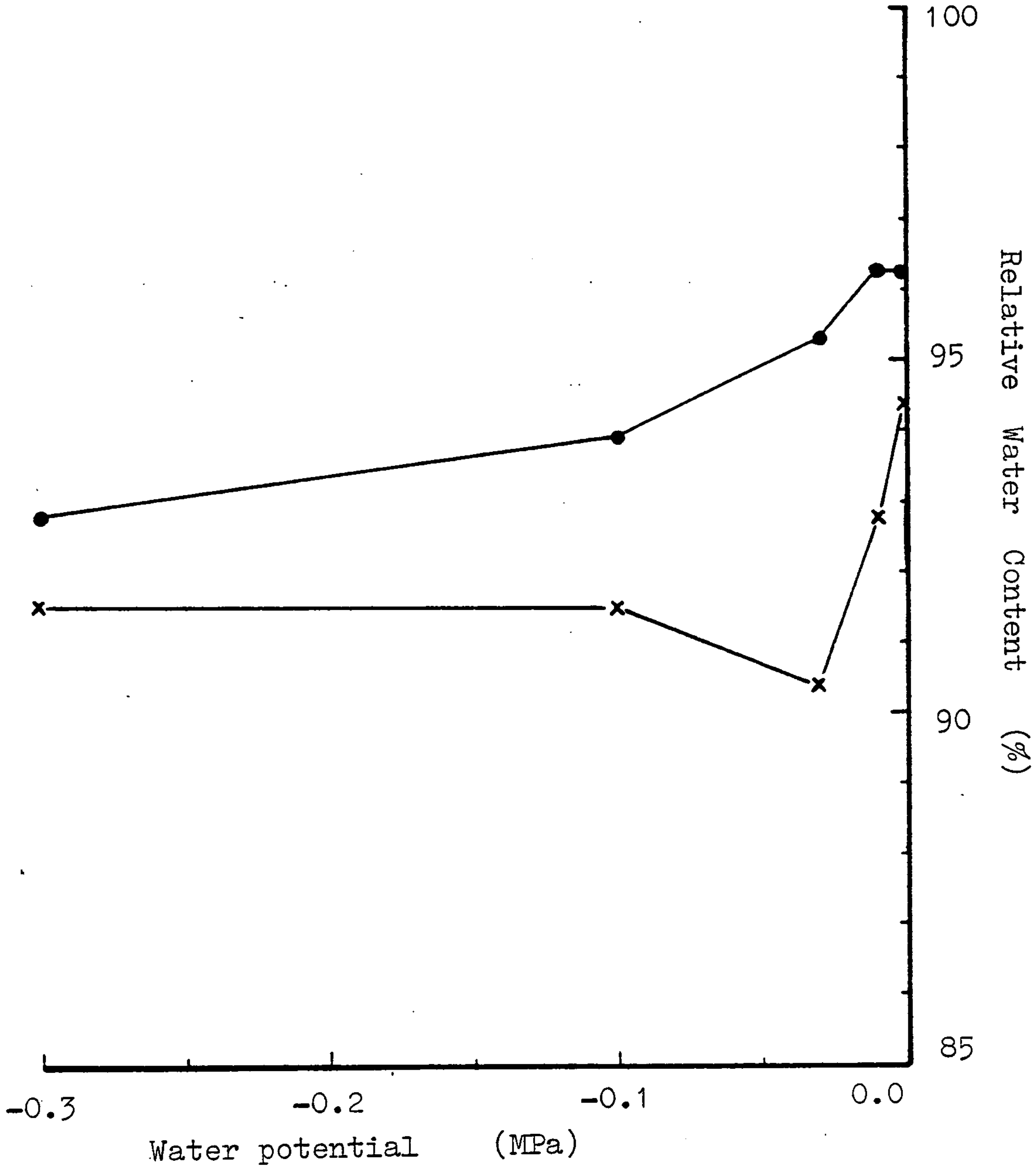


FIG. 4.2

The effect of water potential (imposed by osmotica), on the water content of P.contorta sapwood. (Results of two experiments using the same conditions).

heights. The P. contorta wood was pre-treated by

(i) soaking by immersion,

(ii) soaking the butt end of large branches in water for 48 hours, with the foliage enclosed in polythene, or

(iii) left unsoaked.

4.3.3 Results

The Use of Osmotica. The membranes cast onto the ends of the logs appeared to completely prevent entry of polyethylene glycol (PEG) into the wood, since fluid extracted from the wood did not contain detectable quantities of dry matter when permitted to evaporate at room temperature. The osmoticum circulated rapidly over both faces in a spiral manner as indicated by a small injected dye stream, and a hydrostatic pressure differential indicated by the manometers caused flow, in turn indicated by the heat pulse units (see Section 4.4.3). Therefore the osmoticum was in adequate contact with the exposed faces.

Measurements of water content were made more difficult because of interference by the brass rods with the radiation path - a circumstance which could not always be prevented because of the geometry of the existing equipment.

The osmotica experiments showed a decline in water content with increasing stress, within the experimental limits of 0 to -0.5 MPa (Fig 4.2). Osmotica of higher concentration were more viscous, impairing circulation, and this could not be compensated for by increasing the power of the variable-flow pump.

The Use of the Pressure Chamber

The use of the pressure chamber to obtain pressure/water content curves was considerably simpler technically.

Soaking considerably increased the water content of the wood when immersion was complete, but the additional use of a vacuum was not as successful in removing void space. Soaking the butt end of a branch encased in polythene increased the relative water content by about half that induced by complete soaking (Fig. 4.3).

Increasing increments of pressure up to about 0.4 MPa in P. contorta gave a high initial rate of outflow (Figs. 4.3 and 4.4), which decreased exponentially to about 1.5 to 2.0 MPa. Beyond this level, outflow increased slightly, per unit pressure increase. Outflow from P. sitchensis on the other hand (Fig. 4.5), became very large above 1.5 MPa, and the relative water content at 3.0 MPa was lower than that normally found in vivo.

The results from the pressure chamber experiments showed that the time constants (indicating the time taken to reach 63% of the ultimate change in relative water content) all decreased with each additional pressure increment. The initial values were all large, particularly if a change from 0 to 0.1 MPa was used initially instead of 0 to 0.2 MPa.

The values for resistance to flow from storage refer to each pressure increment, and not from zero to the current applied pressure. Therefore the percentage change in pressure decreased for equal increments of pressure, and is reflected in the apparent fall in resistance with increased pressure.

Resistance to flow from stemwood of both species was initially higher than from branchwood, and higher from the base of P. sitchensis

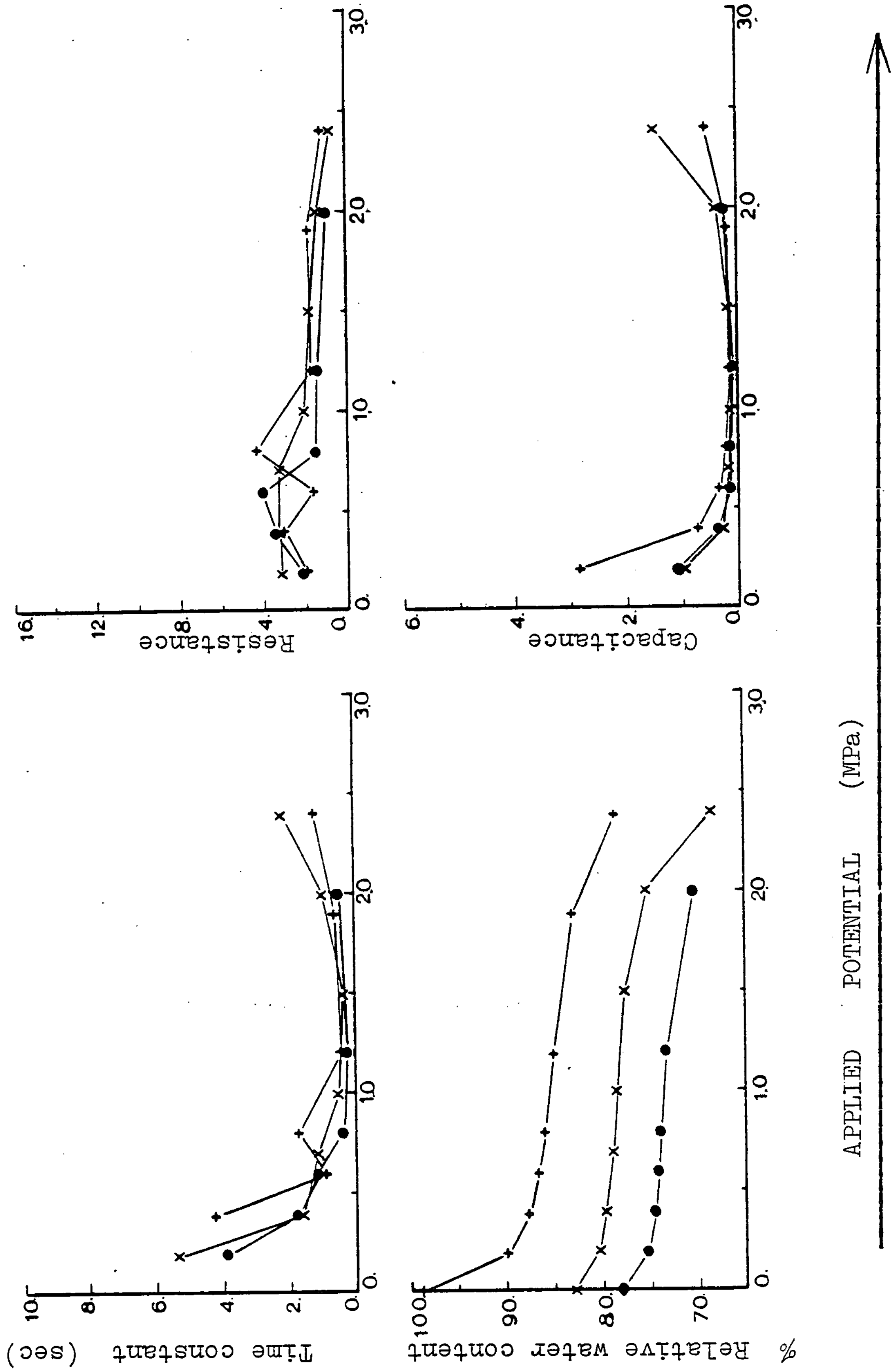


FIG 4.3 The effect of potential gradients applied with a pressure chamber, on the expulsion of water from P.contorta branch sapwood, either as a billet soaked in water (+), from a bagged branch standing in water (x), or untreated (•). The time constant is from an exponentially fitted curve.

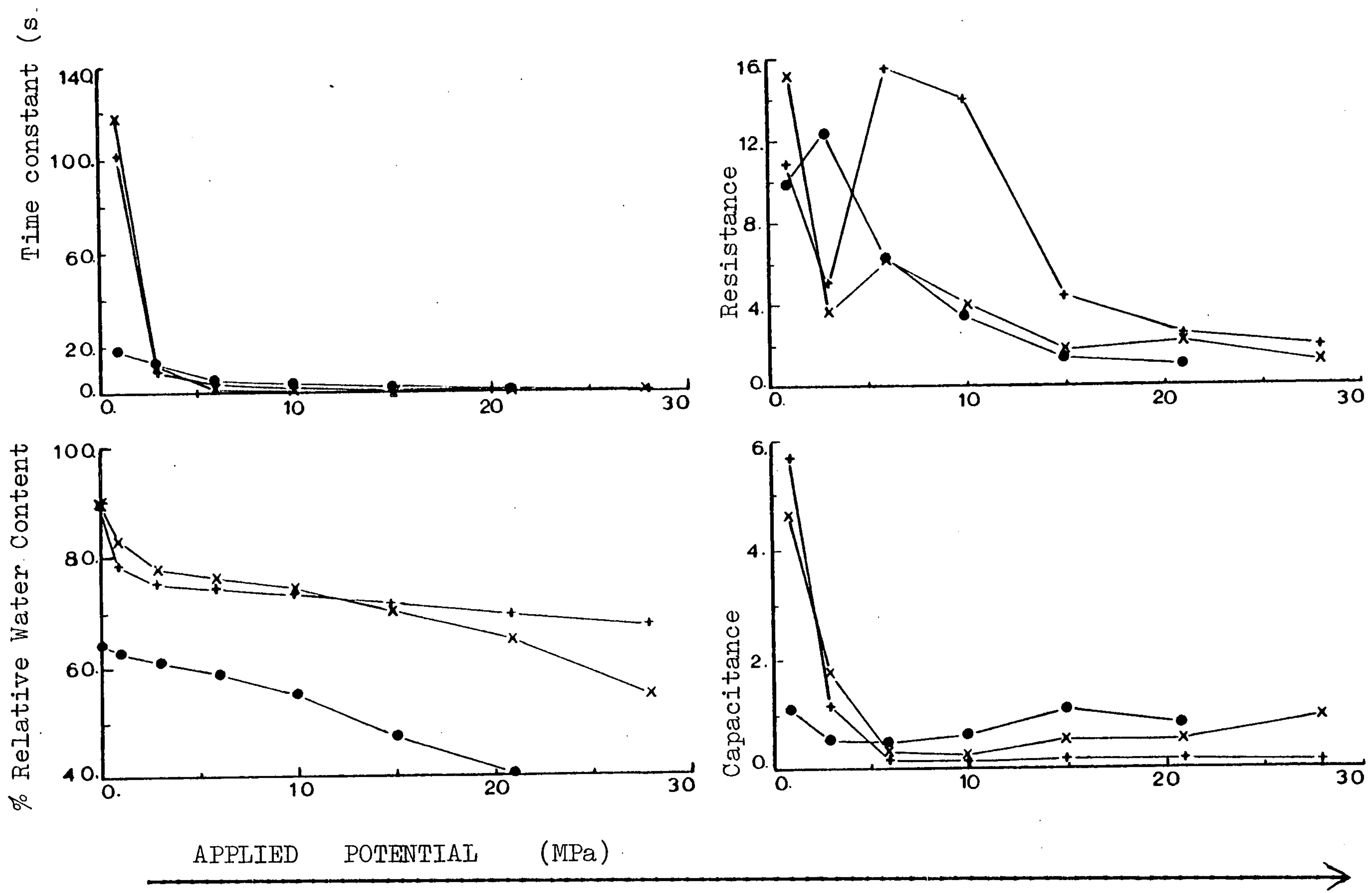


FIG 4.4 As for Fig 4.3, but using P.contorta stemwood, either deaerated under vacuum (+), extracted from wood previously used for measuring saturated permeability (x), or untreated (●).

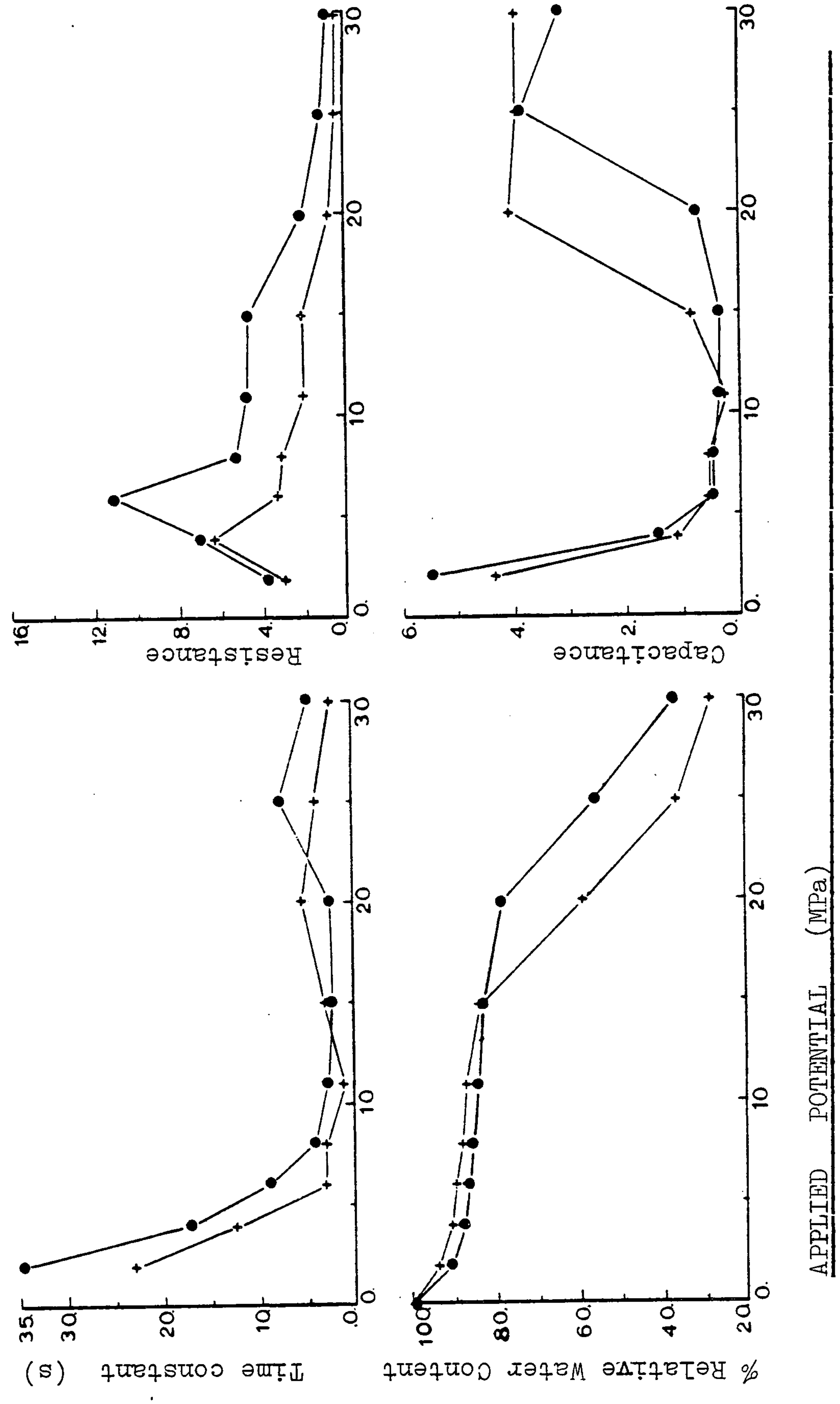


FIG. 4.5

As for Fig. 4.3, but using unsoaked P.sitchensis stem sap wood billets from the base (o), or from just beneath the canopy (+).

stemwood compared to the top. Pretreatment did not appear to influence resistance.

In contrast to the result for resistance, there was a considerable effect of pretreatment on capacitance. In general, water which is absorbed during soaking is easily removed by less than 0.3 to 0.4 MPa applied pressure.

On the basis of graphical interpretation, exponential functions were fitted to pressure/volume curves of saturated stemwood from both species (Fig. 4.6). Data referring to the large outflows above applied pressures of 1.5 or 2.0 MPa was omitted, since an additional process appeared to be involved. The function used was:

$$\text{Relative water content} = c_3 + e^{((\Psi - c_1)/c_2)}$$

The resulting parameters were:

	P. contorta		P. sitchensis
	Top	Base	
c1	9.17	10.78	6.08
c2	5.27	5.84	3.31
c3	0.81	0.84	0.84
Correlation	0.90	0.96	0.98

4.3.4 Discussion

Both techniques gave a similar result, that changes in water potential induced changes in water content. The results from the osmotica experiments confirmed the pressure chamber results, but were

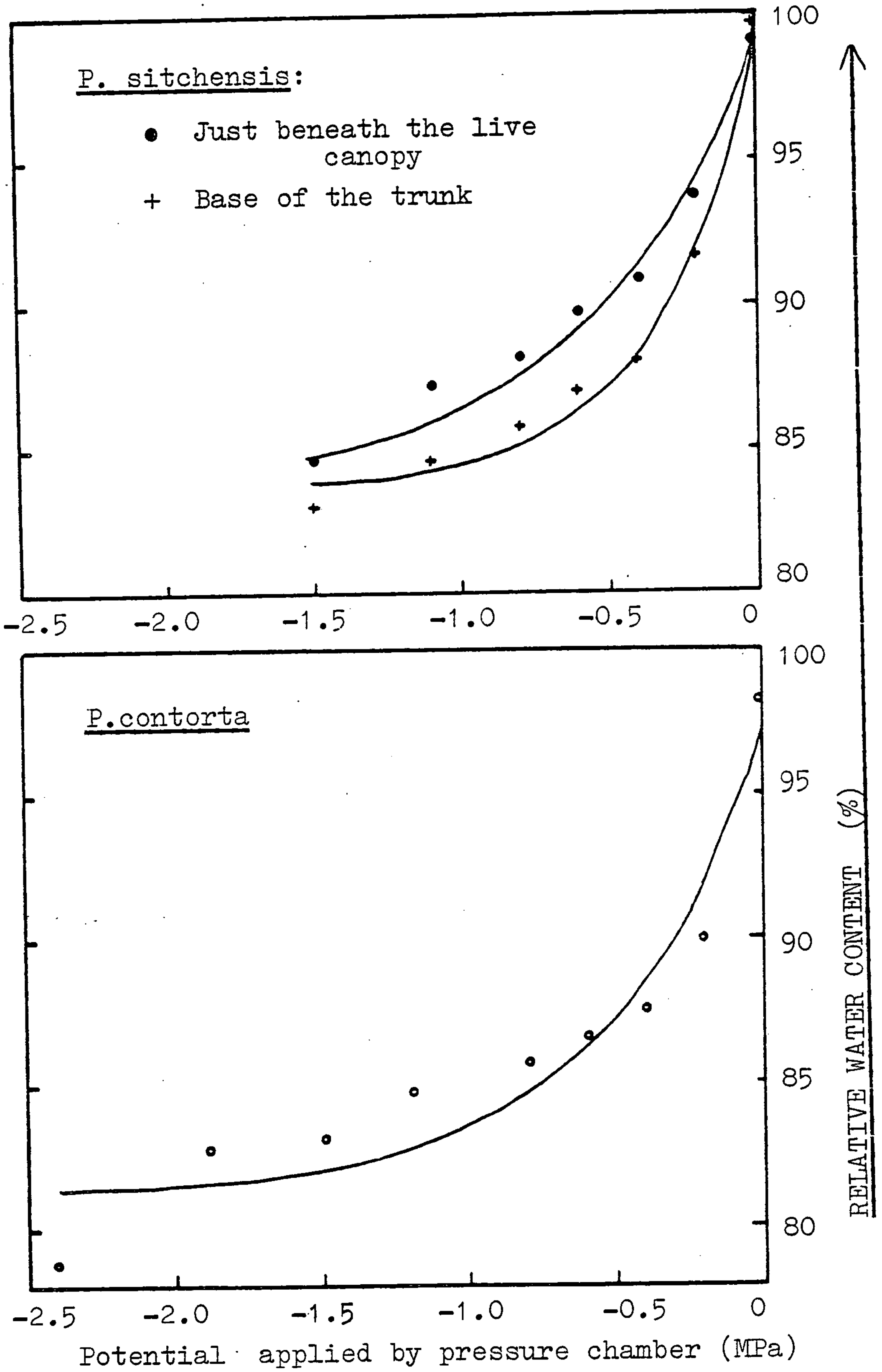


FIG. 4.6 Effect of water potential imposed using a pressure chamber, on water content.

insufficient in range to be fitted as such.

The fall in the value of the time constant with increased pressure is curious, but may be related to the potential gradients causing flow from storage to the top of the wood. While the particular gradient is immediately effective in initiating flow from storage, flow along the pathway to the top of the wood is still proportional to the applied gradient. Initially, this gradient is only 0.1 to 02 MPa, but at 3.0 MPa applied pressure, thereis an order of magnitude difference in the gradient.

Since the resistance to successive increments of pressure can be regarded as in series, summing successively from zero will give the resistances for the total potential change for each increment. This curve will clearly be asymptotic.

Water is removed exponentially from initially saturated wood to an asymptotic value of 81 to 83% relative water content in the range 0 to 1.5 MPa, for both species. Beyond that point, P. sitchensis wood releases a considerable efflux of water at applied gradients which closely approximate those which would be required to pass a bubble through a pit margo pore, i.e. 0.1 to 0.2 μm.

P. contorta results also suggest a similar increased fall in relative water content, but at applied pressures higher than the corresponding values for P. sitchensis Possibly this is because the pores of the pit margo are smaller in P. contorta.

The basic difference between the two methods is that osmotica produce a gradient using negative potentials, but the pressure chamber uses positive pressures. Therefore although the pressure chamber gave consistent and reproducable results, the positive pressures would tend to reduce the size of any bubbles. In the osmotica experiments and in vivo, negative potentials would tend to increase the size of emboli, and a larger fall in relative water content would result for the same change in potential. This is apparent in the results.

4.4 Effect of Water Potential on Permeability

4.4.1 Published Techniques and Relationships

The cohesion-tension theory postulates that water is drawn up in continuous water filled columns from roots to leaves. One consequence of acceptance of the theory has been the difficulty in reconciling any postulate of reversible loss of water from the flow path. Thus Zimmermann (1971, p.184) contends in reference to change in stem water content: "Since it is hardly possible that water is replaced by gas (or 'vacuum') to account for this loss...." , thus denying the possibility of reversal of embolism.

Measurements of permeability have always been conducted using fluids at potentials close to zero (see Section 2.1). While problems associated with cut ends, plugging of pit pores, and emboli induced by gas-saturated water have been resolved, nearly all the measurements of permeability reported in the literature must be regarded as on unstressed tissue.

If in fact reversible embolism does occur, then the effect on permeability is likely to be considerable since flow in capillaries is highly dependent on their radii. The larger capillaries which are easiest to embolise are also those which carry the largest per-tracheid fluxes (Section 2.1). Therefore it is necessary to establish if imposition of an overall stress will affect permeability.

Only one article in the literature refers to such a relationship. Puritch (1971) found that infestation by the balsam woolly aphid in Abies grandis reduced permeability, and this was related to water content. Waring and Running (1978) reworked the data (Fig. 4.1) to produce the relationship:

$$K \times 100 / K_S = 0.4092\, e^{0.055 . R_S}$$

where K is unsaturated permeability (m^2)

K_S is saturated permeability (m^2)

R_S is relative water content (%)

and inferred that the resulting curve reflected the pore size distribution.

This relationship must be interpreted within the context of the original experiment. Puritch's (1971) objective was to compare the permeabilities of sapwood from infected and non-infected trees, and these also happened to have a range of water contents. However the cause for the change in water content is not necessarily the same as that involved in diurnal or seasonal variation in water content in uninfected trees. Puritch was aware of this, and noted other effects of infestation similar to those seen in development of heartwood including incrustation of the pit margo. Possibly the effect of disease modified the permeability /water content relationship by increasing the apparent fall in permeability for small declines in water content.

Byrne et al (1977) found that variations in resistance in plant roots could be related to cavitation in the vessels. The degree of cavitation was 'fixed' by freezing the roots in liquid nitrogen. The gas conductivity of root sections was then measured, while maintaining the temperature below freezing. An asymptotic relationship between gas flow resistance and plant water potential (measured on a transpiring leaf just prior to harvesting the root) was found, with a very large increase in resistance of some two orders of magnitude for a change in potential from -1.0 to -2.0 MPa.

These results may parallel results reported in Section 4.3.3, vis: that there is a large increase in outflow at higher applied pressures, probably related to pit pore size. The method of measuring water potential does not necessarily indicate the potential of the roots at the times of harvesting however, and direct comparison with the results reported here are not possible.

An attempt to find this relationship for sapwood was made by changing the water potential in excised stem sections, and measuring the resulting changes in permeability and water content.

4.4.2 Methods

Three methods of imposing stress were used: by using gravity (0 to -0.02 or -0.1 MPa), by using a suction pump (0 t0 -0.09 MPa) and by using osmotica (0 to -0.5 MPa).

Full details of the experimental techniques are given in Section 2.1.3.2 (permeability) and 2.2 (water content measurement) and the calibrations of flow against single heat pulse units are shown in Fig. 4.7.

The plant material used in each case was a stem section of P. contorta, freshly cut from the stem below the crown and first used for the measurement of permeability (Section 2.1.3). The sapwood was thus fully saturated.

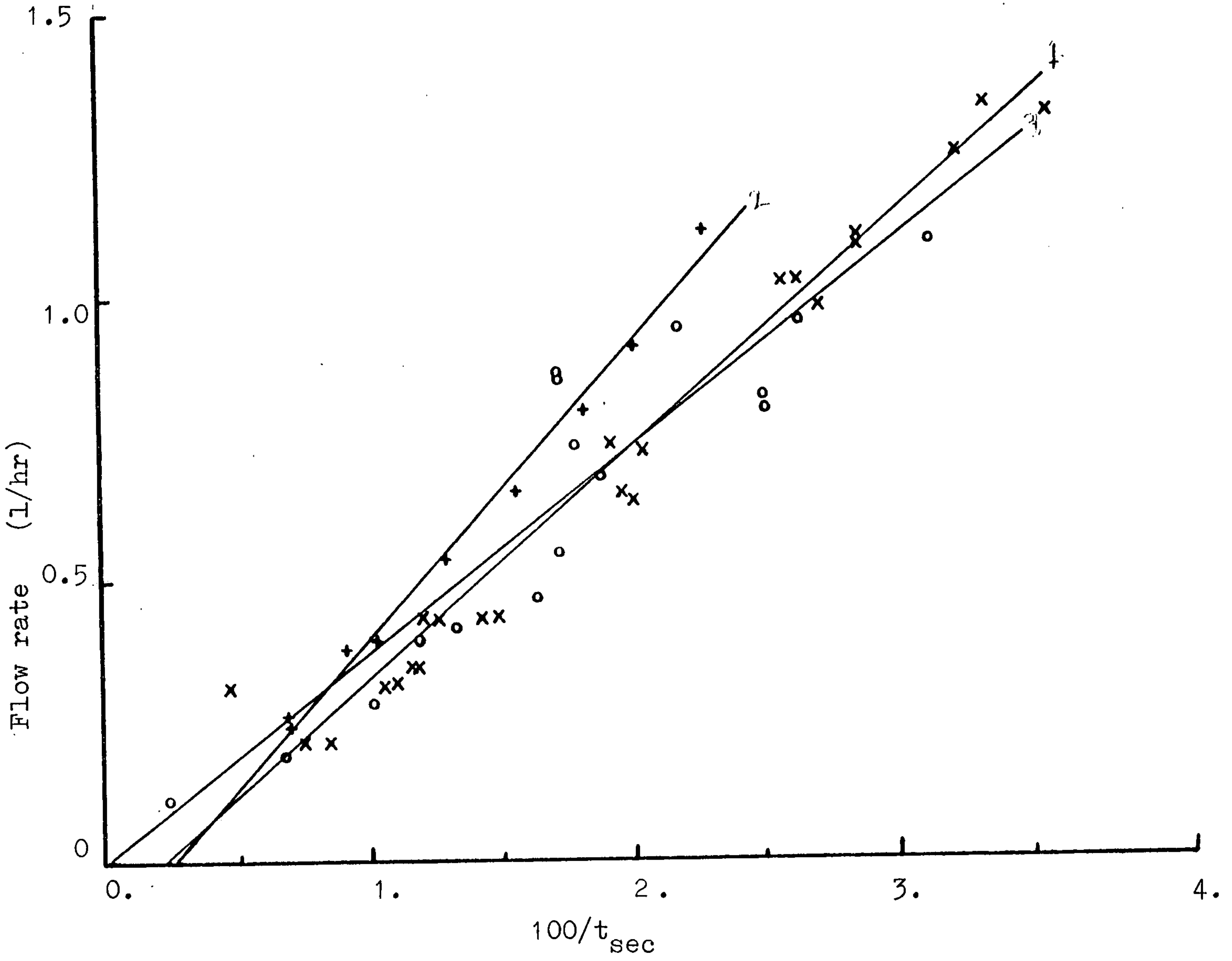


FIG. 4.7 Calibration of flow measured in the permeability apparatus, against a single Heat Pulse Velocity unit, for three P.contorta trees from Ae.

4.4.3 Results

(i) The Use of Gravity

Lifting a 300 mm long stem section to a height of 2 m to impose an overall suction of -0.02 MPa, resulted in a decreasing permeability as follows:

	Permeability $K \times 10^{12}$	% Change
Initial	6.05	0.0
After 5 min	5.57	7.9
After 15 min	5.46	9.7
After 30 min	5.30	12.5
After 60 min	5.12	15.3

Removing the stress resulted in a partial recovery to 89% of the initial permeability value after 10 minutes.

In a second experiment, a stress of approximately 0.1 MPa was applied to another log 300 mm long, by lifting the log (mounted in the permeability apparatus) 10 m above the reservoir for one hour. Then the log was replaced level with the reservoir and permeability was measured in the unstressed state. The effect was:

	Permeability $K \times 10^{12}$	% Change
Pretreatment	6.70	0.0
Immediate Post-treatment	3.47	48.3
After 5 minutes	4.09	39.1

After 15 minutes	4.86	27.4
After 30 minutes	5.23	31.9
After 45 minutes	5.45	18.7

After soaking overnight while unstressed, the permeability of the log increased to 90.3% of the pretreatment value.

(ii) Use of a Suction Pump

A log 2.5 m long was mounted in an extended permeability apparatus, and permeability measured under a range of suctions as described in Section 2.1.3.2.

The following were the permeabilities measured after the times shown at each suction pressure:

Time (min)	Suction (MPa)	Permeability $(K \times 10^{12})$	% Change
Initial	0.0	1.71	0.0
93	-0.030	1.82	106.4
154	-0.049	1.89	110.5
60	-0.071	1.93	112.9
69	-0.085	1.94	113.5
60	0.0	1.40	81.8

These results show an apparent net <u>increase</u> of permeability at higher suctions. The anomaly appears to be caused by changes in capacitance in the large log used, which contained some 0.0277 mm^3 of sapwood. The difference in actual flow rates caused by the suction treatments amounted to a change in relative water content of approximately 8%, and this quantity of water was sufficient to cause the apparent increase in permeability. Two observations support this hypothesis. Firstly, after each increase in suction the outflow increased substantially and then fell, but was still higher than the outflow before the change in suction after more than an hour. Removal from storage is implied. Secondly, on release of suction for the final set of observations with no suction, there was a net inflow from both ends of the log, which continued for several minutes. Thereafter the outflow tube refilled and flow gradually increased until an approximately steady state was reached after 60 minutes. Recharge of storage is implied.

(iii) Use of Osmotica

Three identical experiments were run, each with a *P. contorta* stem section about 450 mm long. Results for the change in permeability (normalised with repect to saturated permeability) with different overall potentials imposed by osmotica are presented in Fig 4.8. Clearly a relatively small increase in stress has resulted in a considerable decrease in permeability.

In considering the relation between permeability and water content for each log, the relative water content estimates for the first experiment were rendered useless because of interference by the brass connecting rods with the gamma beam. For the two remaining experiments, an exponential curve was fitted (Fig.4.6) using a step-wise Gauss-Newton method to test non-linear least squares described by Draper and Smith (1966) (programme by H. Talbot, pers. comm.).

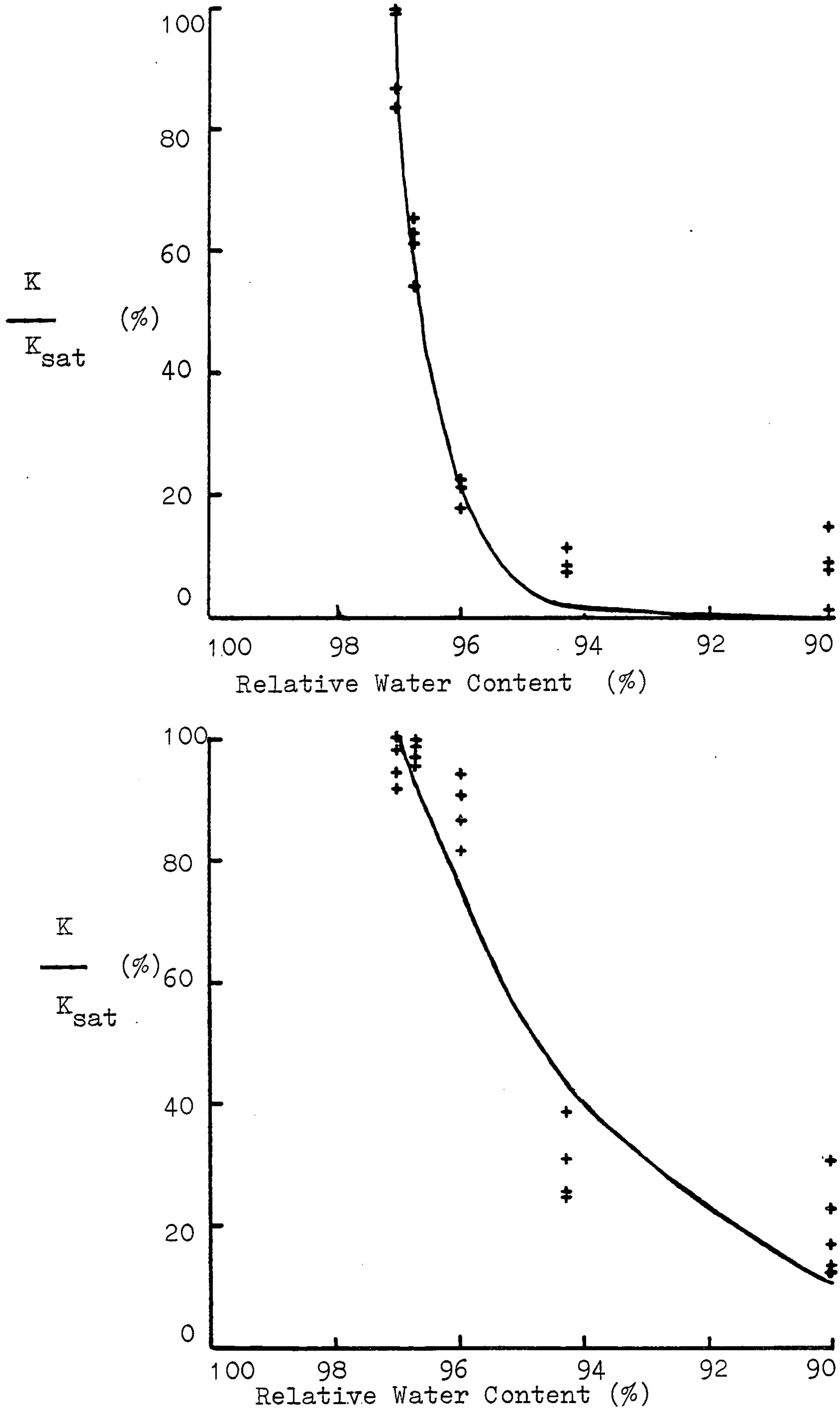


FIG. 4.8 Effect of water potential imposed using osmotica, on permeability of two P.contorta tree stem sections from Ae.

The function used was:

$$\frac{K}{K_{sat}} = P_1 \cdot e^{(P_2 \cdot (R_s - P_3))}$$

where K is measured permeability at a relative water content (R_S) compared with saturated permeability (K_{sat}). P_1, P_2 and P_3 are parameters for the exponent.

The parameter P_1 controls the asymptote, P_2 the shape of the curve, and P_3 permits the curve to be fitted other than through zero.

Values found are as follows:

	Expt 1	Expt 2
P_1	0.991	0.054
P_2	0.318	1.51
P_3	96.8	92.1
Correlation (R^2)	0.910	0.961

Both curves account for a high proportion of the total variability, but exhibit rather different shapes, i.e. values for P_2. In the first experiment there was a consistant drop with decreasing water content, but in the second, permeability did not drop between -0.01 and -0.03 MPa. This resulted in a shallower curve being fitted.

A small change of water content was observed in both experiments for decreasing potentials, using the gamma method:

Applied potential (MPa)	Relative Water Content (%) Expt 1	Relative Water Content (%) Expt 2
0.0	94.3	96.2
-0.01	92.8	96.3
-0.03	90.3	95.3
-0.10	91.5	94.0
-0.30	91.6	92.8

4.4.4. Discussion

The results support the hypothesis that an overall fall in water potential results in a loss of water, and a fall in permeability.

All three methods used demonstrated that the decrease in permeability was large, exceeding that of the only published data (Waring and Running, 1978; derived from Puritch, 1971). Although the experiments were all on excised tissue, the precautions taken go some way towards ensuring continuity of the flow paths at the cut ends. In the osmotica experiment, the membranes excluded polyethylene glycol in spite of a comparatively high flow rate, so that a change in the viscosity of the fluid in the wood would not have occurred. Circulation rates of the osmotica were maintained by increasing the power to the variable speed pump with each increase in concentration of PEG, and appeared to give a reasonable flow rate over each face.

The applied potentials were considerably higher than those expected to cause passage of emboli through the pit pores. The mechanism for decreases in permeability is more likely to be changes in the size of existing emboli. Section 4.4.1 suggests that the size of capillary lumina grossly affected flow rates, and further suggested that water potentials (expressed as pressure potentials in the absence of osmotic potentials or significant matric potentials), would considerably affect the size of bubbles already present. Whether or not a bubble would dissolve or enlarge at a given hydrostatic potential would also be related to the concentration gradient of gas between the gas in the bubble and dissolved in the solution.

The changes in water content measured with decreasing applied osmotic potential were significant, and indicated changes which were similar to those reported in Section 4.3.3.

4.4.5 Conclusions

Permeability of sapwood decreases substantially for relatively small changes in water potential, in a relationship which can be fitted to an exponential curve.

Water content of sapwood also decreases with water potential, in a relationship which also can be fitted to on exponential curve.

5.0 FIELD DATA

5.1 Introduction

The field experiments were designed to

(i) find estimates of evaporation from single trees,

(ii) find real values for flow, water content and water potential along the stem of single trees, in order to compare them with simulated values, and

(iii) find evidence for capacitance, in the form of phase lags.

5.2 Field Site Descriptions

The study was carried out mainly at the Forest of Ae, on the site already described in Section 3.2.

The site was primarily selected because of concurrent work being carried out there, which included maintainance of a weather station and measurements of stomatal conductance (Whitehead and Leverenz, pers. comm.). Access for these measurements was by two 'Hi-Way' towers some 11 m high, with catwalks between.

The automatic weather station was a standard instrument (Strangeways and McCulloch, 1965) provided by the Institute of Hydrology, who also serviced the data manipulation of the tape output.

Data collected were:

(i) net radiation (Funk type instrument)

(ii) solar radiation (Kipp instrument)

(iii) wind direction

(iv) wind velocity

(v) ambient temperature

(vi) wet bulb temperature

(vii) precipitation (twin tipping bucket mechanism)

All measurements were made above the canopy, as events or cumulated values for the five minutes, and the equipment was serviced fortnightly. Computer manipulation gave output for one hour intervals, and daily totals.

In addition to the standard weather data collection, intensive measurements were made periodically of stomatal conductance using the null balance diffusion porometer (Beardsell et al, 1972; Watts, 1977) (Whitehead and Leverenz, pers. comm.). Measurements were made at three levels on three age classes, which represented the spacial and temporal variation inherent in the canopy. The total leaf area in each of the nine sub-classes was estimated for the plot by the methods already described in Chapter 3, and the canopy conductance estimated as the sum of the leaf areas of the individual height/age classes and their respective stomatal conductances.

The frequency of the stomatal conductance measurements was affected by the frequent precipitation, since the method does not permit measurement of wet foliage, and evaporation from damp bark can also seriously affect the measurements. When possible, up to six estimates of stomatal conductance for each height/age class were made per day.

In addition to the site at the Forest of Ae, a short study was conducted in the Fetteresso Forest, at a position 56o 58′ N, 2o 24′ W, (some 27 miles SE of Aberdeen). This study was undertaken because of the generally unsatisfactory weather conditions during the Ae study. It was intended to investigate

(a) diurnal changes in water content, flow and water potential in a trunk under conditions of substantial evaporative demand

(b) the incidence of phase lags between the top and the base of the tree. The site was 280 m above sea level on a 7° slope to the northeast, in a two year-old compartment of _P. sitchensis_ cv. 'Queen Charlotte Island'. The trees were originally planted into degenerate marshy hill pasture with patches of heather, on peat approximately 400 mm deep over shale. The peat was saturated during the time of the experiment.

The forest has been damaged by wind-throw, and open areas exist. The canopy height where complete is some 12 - 13 m, with a leaf area index of 8 to 10 where intact, and a clear bole height of 6 to 7 m.

Where the canopy was not complete, epicormic shoots have developed down the previously-clear bole beneath the former live crown. These were of similar size within one tree, but varied from 50 mm to 0.5 m between trees.

The site was the same one used for the field work reported by Hellkvist et al (1974), but at that time the canopy was not wind-damaged.

5.3 Instrumentation and Measurements of Individual Trees

A total of three trees was selected for intensive study in the Forest of Ae. Access to the stems below the canopy was obtained by planks laid between two 'Hi-Way' tower sections each 2 m high.

On each tree, measurements were made at two heights: firstly, as close to the ground level as practicable such that the trunk dimensions and shape were not affected by the proximity of the root system or by buttressing, and secondly, at the first internode immediately below the live crown.

At each measurement point in each tree, the following measurements were made:

(i) Water content. The gamma attenuation method was used (Section 2.2.). The method requires exact re-establishment of the path geometry for each measurement, if comparisons between readings are to be accurate. The supporting table for the yoke was located using a single spike at the base (usually driven into a knot), some 400 mm below the measurement plane. Laterally, the table was located using grooves cut laterally into the bark to give supporting surfaces, and by using locating marks on the bark.

The bark at the measurement plane was smoothed using a 'Surform' rasp to remove loose material.

(ii) Sap Flow. The heat pulse velocity method was used, as given in Section 2.3.3.

Eight (i.e. four double) probes were inserted at four sites equally spaced around a measurement plane some 250 mm below the water content measurement plane, so that each probe was within the range 5 to 40 mm below the cambium. The thickness of the sapwood was in the range 45 to 50 mm.

Measurements of heat pulse velocity could be used to calculate total flux through the measurement plane, and also estimated the maximum depth where flow occurs, the depth of maximum flow and the average sap velocity.

(iii) Water Potential. At the Forest of Ae, the method used was thermocouple psychrometry, described in Section 2.4.4. In two trees, a single unit was installed at each of two heights, but in the third, four were used at each height.

In addition, two psychrometers were used at a depth of 200 mm in the soil close to a trunk. One was as described in Section 2.4.4.2

but fitted with ceramic insets instead of copper gauze over each slot, and the other was a standard 'Wescor' ceramic soil psychrometer.

Measurements of flow, water content and potential were made intensively on particular days, mainly coinciding with days on which stomatal conductances were also being measured.

On completion of the field experimentation, each tree was harvested and the following measurements taken:

(i) Leaf area of each whorl and each age class was estimated according to the sampling method given in Section 3.3.

(ii) The trunk dimensions were taken, including the division between sapwood and heartwood.

(iii) Two stem sections per tree containing the measurement sites for flow, water content and water potential were cut from each stem, after measuring the stem dimensions.

Iv) In the laboratory, the permeability of the short sections containing the HPV probes were measured.

(v) At the same time, a check was made on the accuracy of the heat pulse velocity estimate of flow, by measuring the actual flow at various pressures and comparing the results with the HPV estimate.

(vi) Also in the laboratory, an estimate of water content using the gamma probe was made as in the field. Then the stem section was cut firstly to measure the actual chord lengths close to the measurement plane, and secondly, to extract a radial band 15 mm wide and 50 mm high. This billet was cut into sections 10 mm thick, so that each represented a 10 mm thick torus from successive depths below the cambium. Weights of each when 'fresh', immersed in water, and oven-dry were taken, in order to estimate the volume fractions of woody matrix, water and air (Section 2.2.2). The values for volume fractions of woody matrix were used within the calculation for relative water content by the gamma technique. Then the volume fractions of gas and water determined gravimetrically as relative water content, could be compared with the same figures determined with the gamma attenuation method.

Finally, a range of overall water potential deficits was applied using hydrostatic or osmotic potentials, and the resulting water content and permeability was measured, for sections of stem 300 to 450 mm long (Chapter 4).

Instrumentation of the Fetteresso tree comprised measurements of flow (heat pulse velocity method), water content (gamma attenuation method) and water potential (pressure chamber measurement of bagged twigs). These measurements were made at two levels as at the Ae site, with access to the top level using scaffolding some 4 m high. No measurements of weather conditions were available, and so leaf area and stomatal conductances were not measured.

5.4 Results

5.4.1 Seasonal and Diurnal Weather Patterns

The summer of 1979 was generally wet at the Ae field site, and there were few occasions when transpiration was substantial. Unless continuously overcast, changes in cloud cover made diurnal paterns of weather irregular.

The main study period at the Forest of Ae during which field measurements were attempted was from July to August, 1979. The equipment was set up for 27 days (periods of known precipitation were avoided), on 15 of which measurements were actually made. The foliage was continuously wet on the remainder. Of the 15 days, rain was recorded (i.e. at least one 0.5 mm increment) by the automatic weather station on five days. There was no day on which the sun shone continuously, and most days were continuously overcast.

During the entire study period the soil was at field capacity or more, with frequent pooling of surface water.

Data for four days at the Forest of Ae are presented, representing the days on which measurements could be made (Figs 5.1 to 5.4). In each case, measured fluxes and sapwood water contents at the top and base of each tree are given, together with weather station measurements of net radiation and vapour pressure deficit, and the derived Penman-Monteith estimate for evaporation from an average tree. Also given are the results for a P. sitchensis tree on one day at Fetteresso Forest, comprising flow, water content and water potential (the latter measured by pressure chamber on bagged leaves) for the top and bottom of the trunk between ground level and the first live whorl (Fig. 5.5). No weather station results for Fetteresso were available.

The measurement day at Fetteresso commenced fine and mild, with no wind. By midday, the conditions had gradually become overcast and then remained steady to about 1600 hours. After this, a light wind developed, the temperature fell somewhat and rain eventually commenced at about 1900 hours.

5.4.2 Measurements After Harvesting

Each experimental tree from Ae was harvested on a separate date:

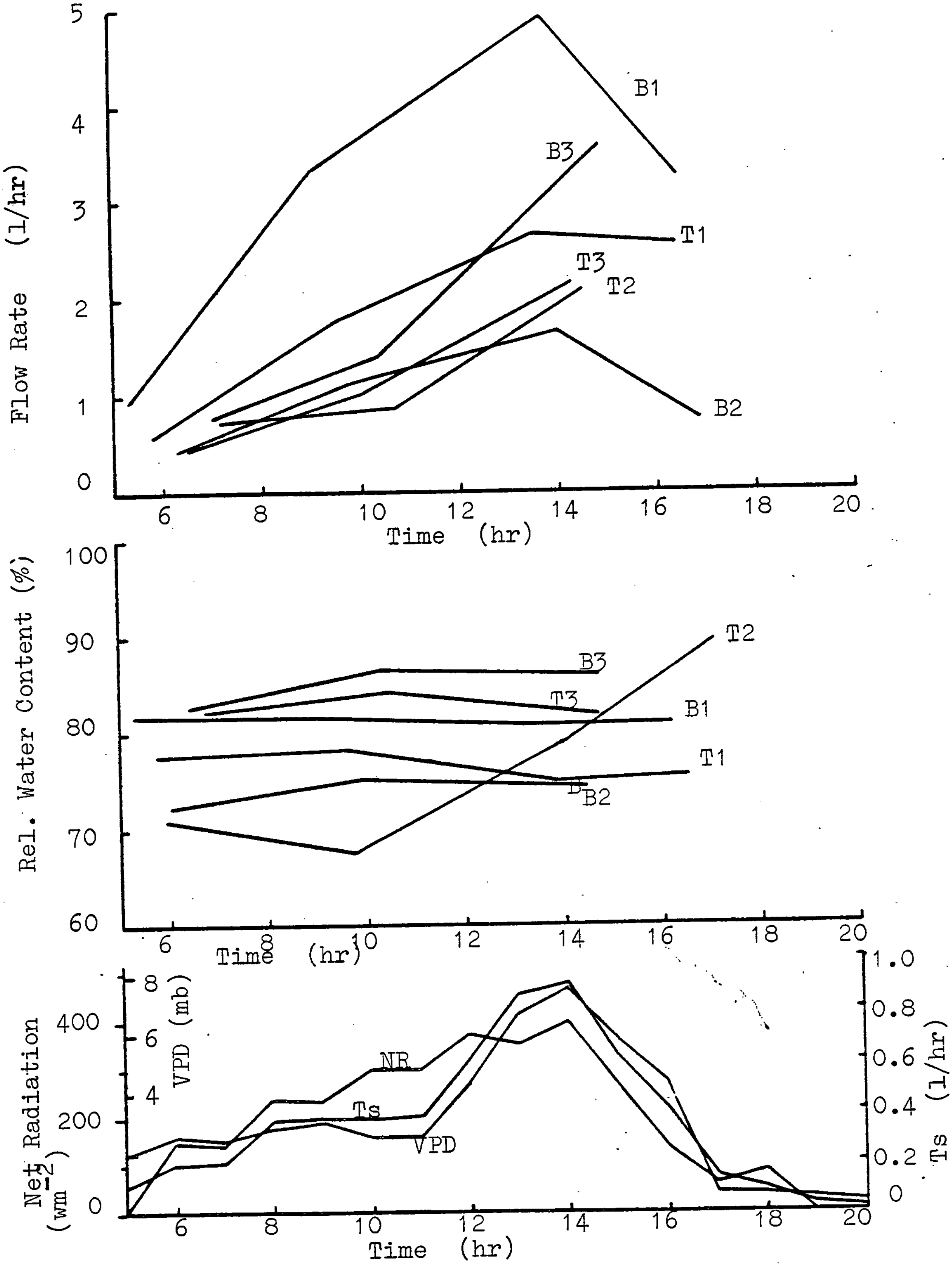


FIG. 5.1 Measurements of flow and water content at the base and top of the trunks of three *P.contorta* trees from Ae for August 8, 1979, together with net radiation, vapour pressure deficit and transpiration measured by the Penman-Monteith equation. (NR, VPD and Ts respectively).

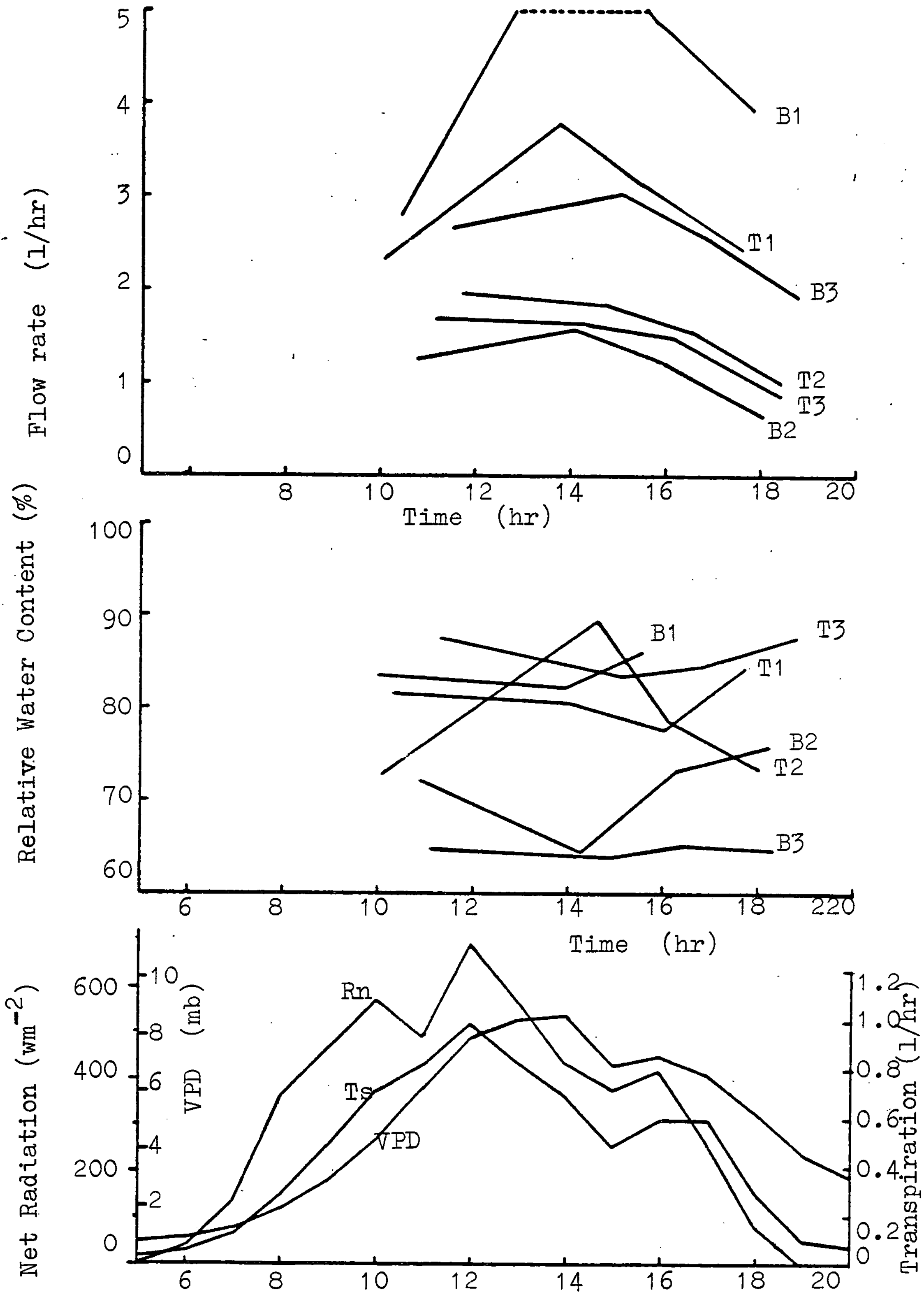


FIG. 5.2 As for Fig. 5.1, but for 9 August, 1979.

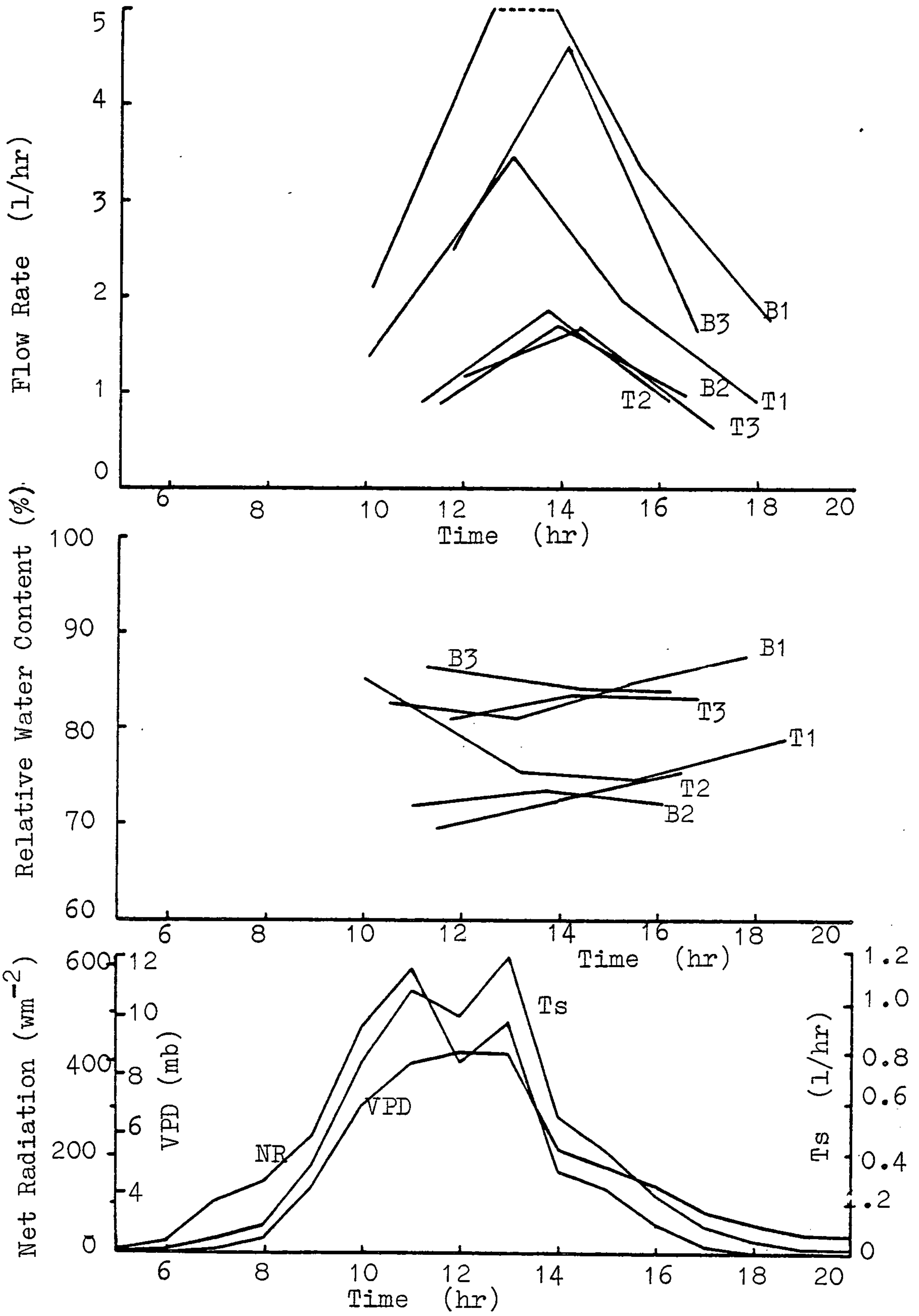


FIG 5.3
As for Fig. 5.1, but for 13 August, 1980.

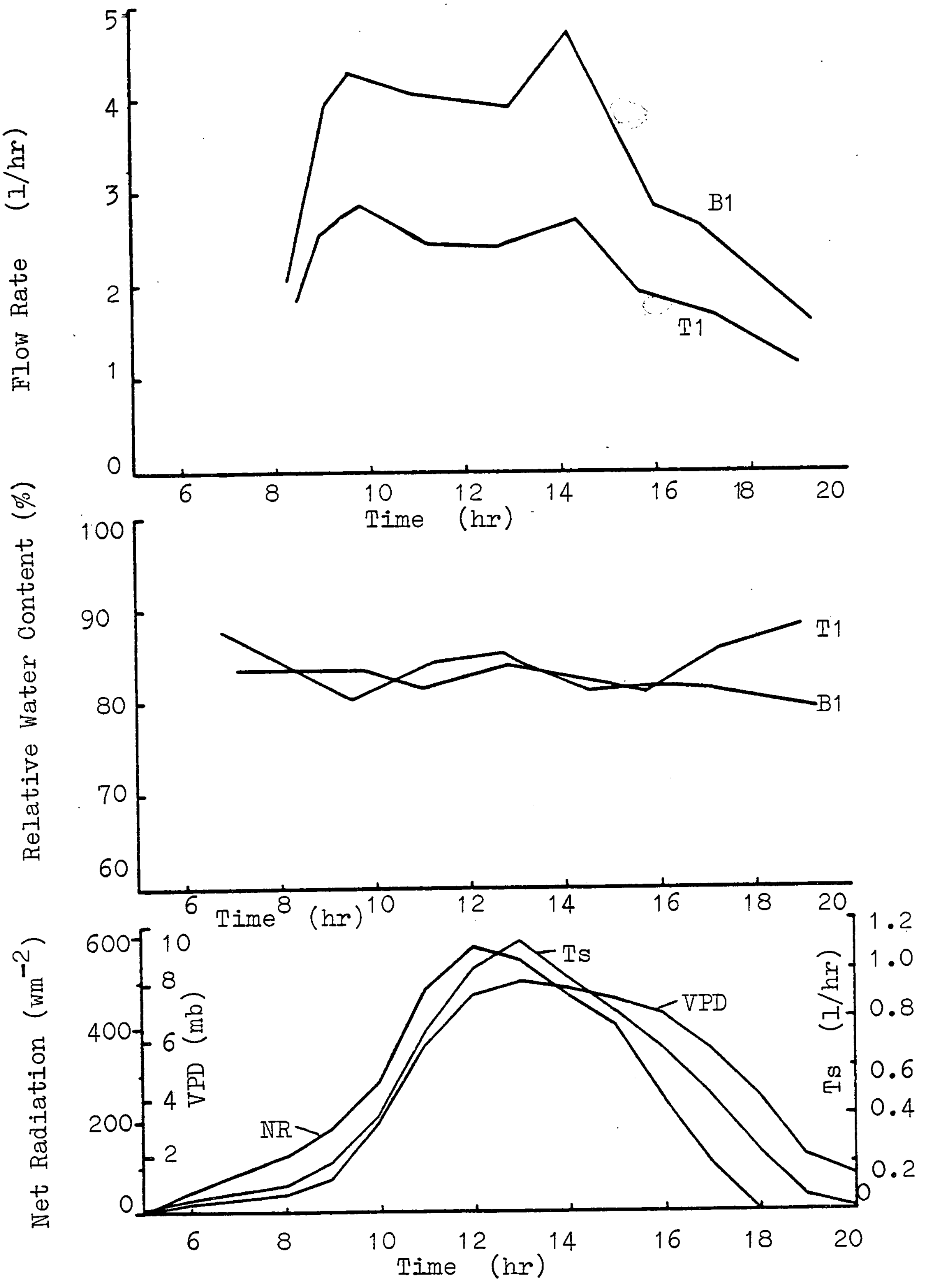


FIG 5.4 As Fig 5.1, but for one tree only, on 28 August, 1979.

6/11/79, 29/4/80 and 15/5/80. Leaf-fall is known to have a considerable effect on the leaf area of a stand, so that the results for leaf area, sapwood area and permeability for the three trees was not included in the relationships 'between trees' given in Chapter 3 for another harvest of ten trees.

Leaf area was measured as the projected area after removal from the fascicles. For the purposes of modelling, needle weights were taken, as well as the weights of the entire remaining crown above and including the lowest living whorl, and the trunk above ground level.

Harvesting at Fetteresso involved only the trunk, since no weather data was available to use in an extended model.

The results were as follows:

	Fetteresso Forest	Forest of Ae		
		Tree 1	Tree 2	Tree 3
Total Leaf Area (m^2)	-	41.6	22.6	23.6
Sapwood Area (DBH) (m^2)	0.0266	0.0162	0.0150	0.0147
Permeability ($K \times 10^{12}\ m^2$)	2.96	1.39	1.79	1.81
Volume Fraction of Sapwood	0.235	0.222	0.227	0.222
Weight of Trunk (kg)	-	108.9	61.3	60.1
Weight of Crown (kg)	-	84.6	56.7	62.9
Weight of Needles (kg)	-	31.3	15.9	18.1

These results were incorporated where appropriate into the computer model.

At the same time that permeability measurements were made, the measured flow was compared with flow estimated with the heat pulse probes. The regression coefficient (b), regression constant (c) and correlation coefficient (r) for the regression of measured flow

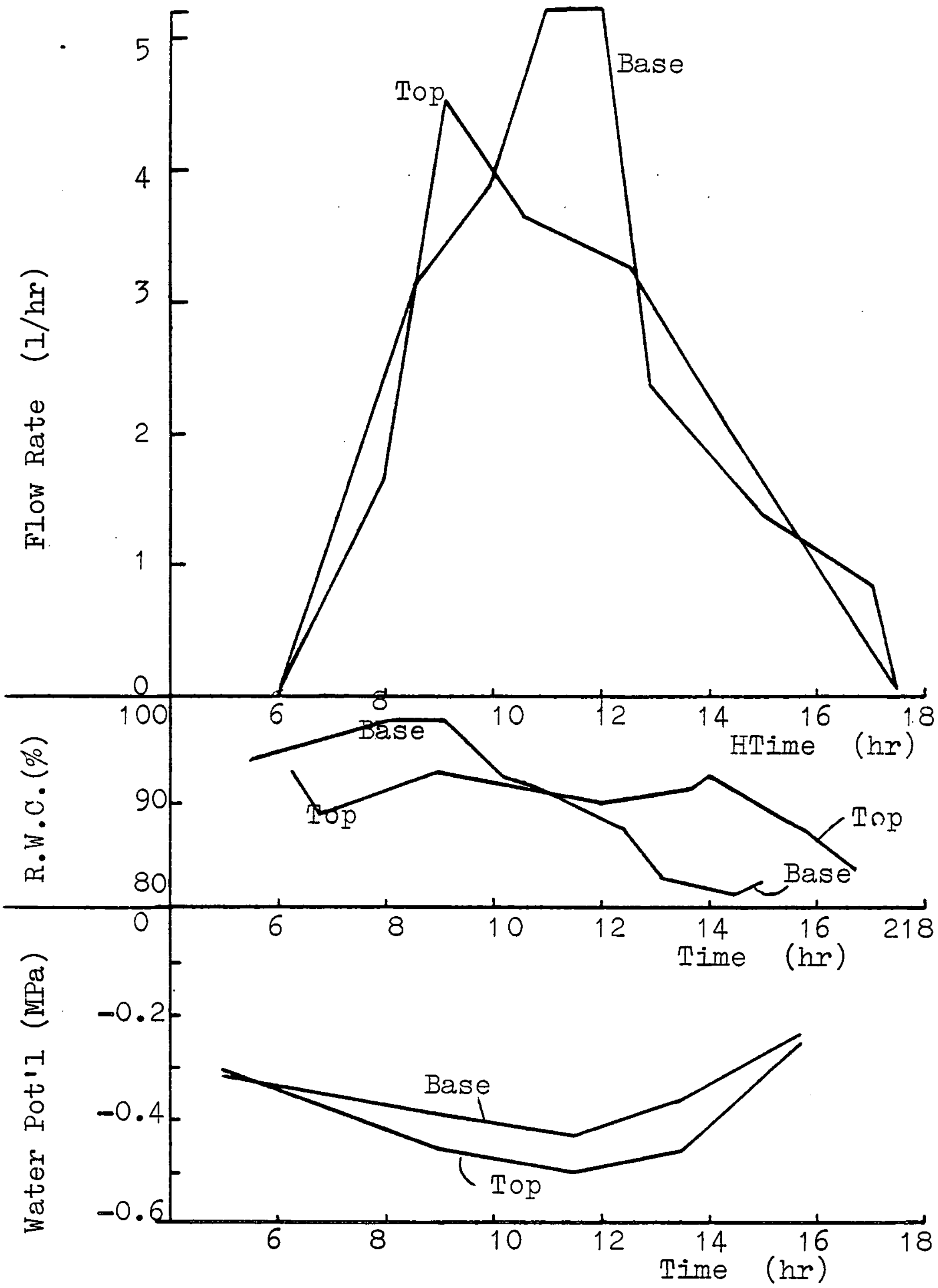


FIG.5.5 Measurement of flow, water content and water potential at two heights in the trunk of a P. sitchensis tree in Fetteresso Forest.

against flow estimated by heat pulse velocity, is as follows:

	b	c	r
Ae 1 Top	1.20	0.277	0.986 ***
Ae 1 Base	0.88	0.783	0.990 ***
Ae 2 Top	0.49	0.512	0.989 ***
Ae 2 Base	0.49	0.512	0.989 ***
Ae 3 Top	1.01	-0.882	0.960 ***
Ae 3 Base	1.29	0.044	0.925 ***
Fett Top	1.05	0.001	0.995 ***
Fett Base	0.96	0.402	0.964 ***

'Ae' denotes a P. contorta tree from the Forest of Ae, and 'Fett', a P. sitchensis tree from Fetteresso Forest. Significance at 0.1% is denoted by ***.

The data and regression lines are presented for the Fetteresso tree (Fig. 5.6) and one representative tree from Ae (Figs 5.7).

At completion of the permeability measurements, water content measurements using the gamma attenuation method were compared with water contents measured gravimetrically on excised samples. The resulting regressions are presented in the same format as for the flow comparisons:

	b	c	r
Ae 1 Top	0.869	13.62	0.971 ***
Ae 1 Base	0.863	2.0	0.750 *

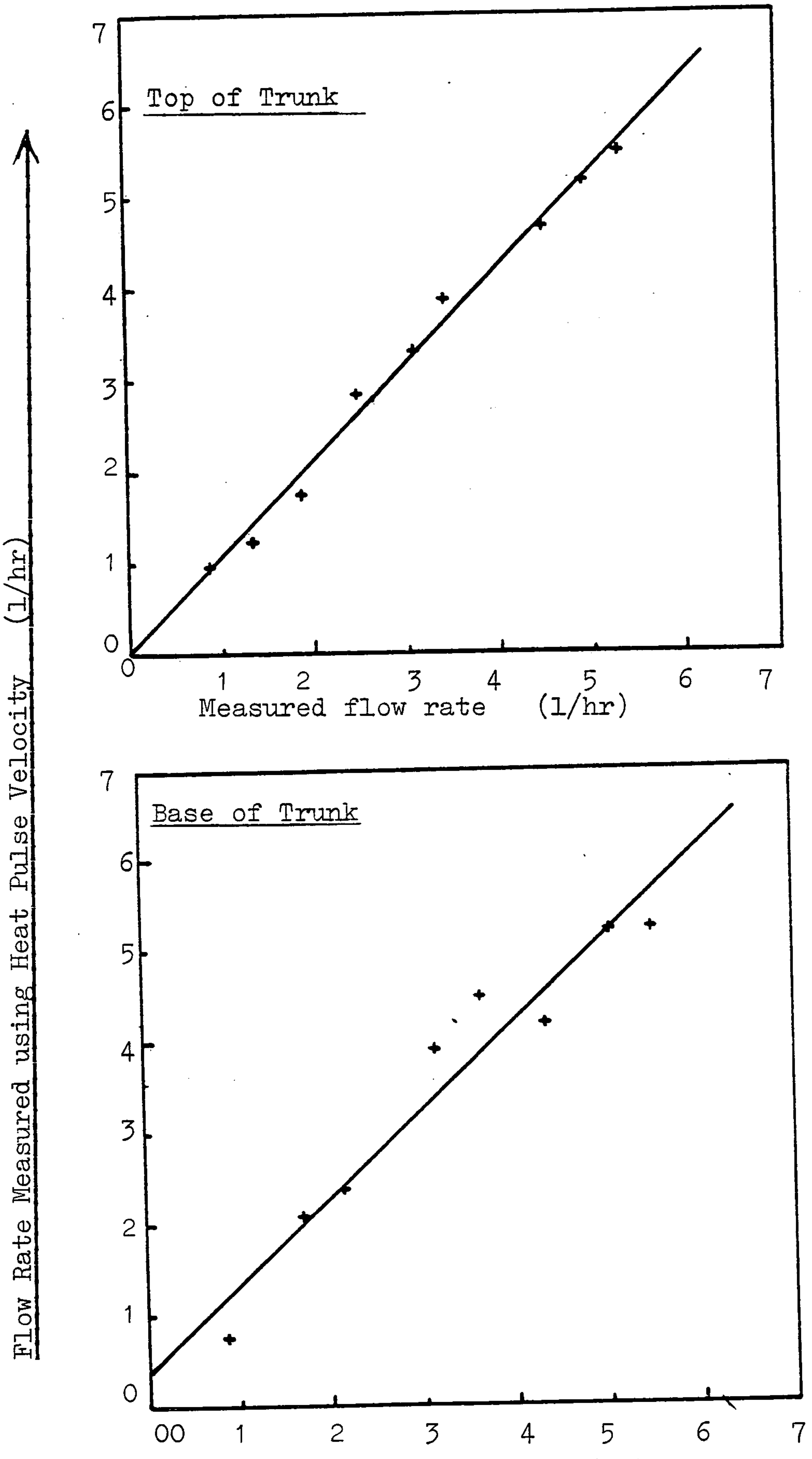


FIG. 5.6 Comparison of flow in excised stem sections from the base and just beneath the canopy of a P.sitchensis tree from Fetteresso, measured either by heat pulse velocity or by measuring the outflow resulting from a range of applied inflow pressures.

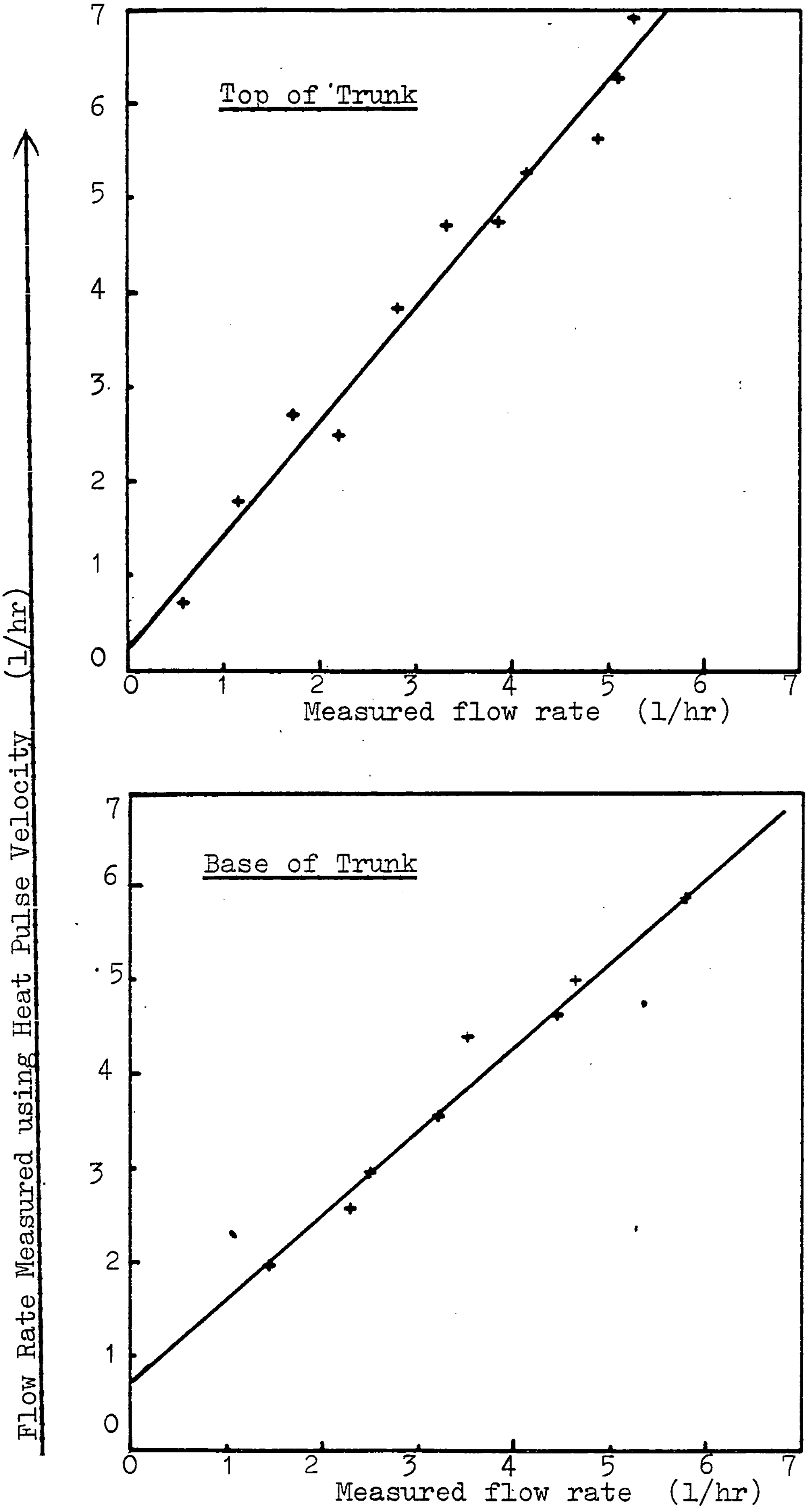


FIG. 5.7 As for Fig 5.6, but for a *P.contorta* tree from Ae.

Ae 2 Top	1.251	-23.98	0.976	***
Ae 2 Base	0.781	21.71	0.928	**
Ae 3 Top	0.910	-4.88	0.938	**
Ae 3 Base	0.418	25.16	0.882	**
Fett Top	0.953	3.74	0.967	***
Fett Base	0.732	31.34	0.861	*

Results from one Ae tree (Fig. 5.8) and the Fetteresso tree are given in Fig. 5.9 .

Finally, using hydrostatic or osmotic potentials, the effect of overall water potentials on permeability and water content of other stem sections was measured. These are reported in Chapter 4.

5.4.3 Measurement of Flow in the Field

Estimates of flow using the heat pulse velocity method indicated a diurnal trend, and the flow at the top tended to slow before the flow at the base (Figs. 5.1 to 5.4). The frequency of measurement was not sufficient to see obvious phase lags at Ae, and even the data for August 28 which was taken more frequently showed that the phase differences in this environment are small. However at Fetteresso a clear indication of a phase lag was seen.

5.4.4 Measurement of Water Content in the Field

Variation in the measurement of water content indicated a midday decline, but the change was small (Fig. 5.1 to 5.4). Consequently random variation tended to obscure the diurnal trends, which were more

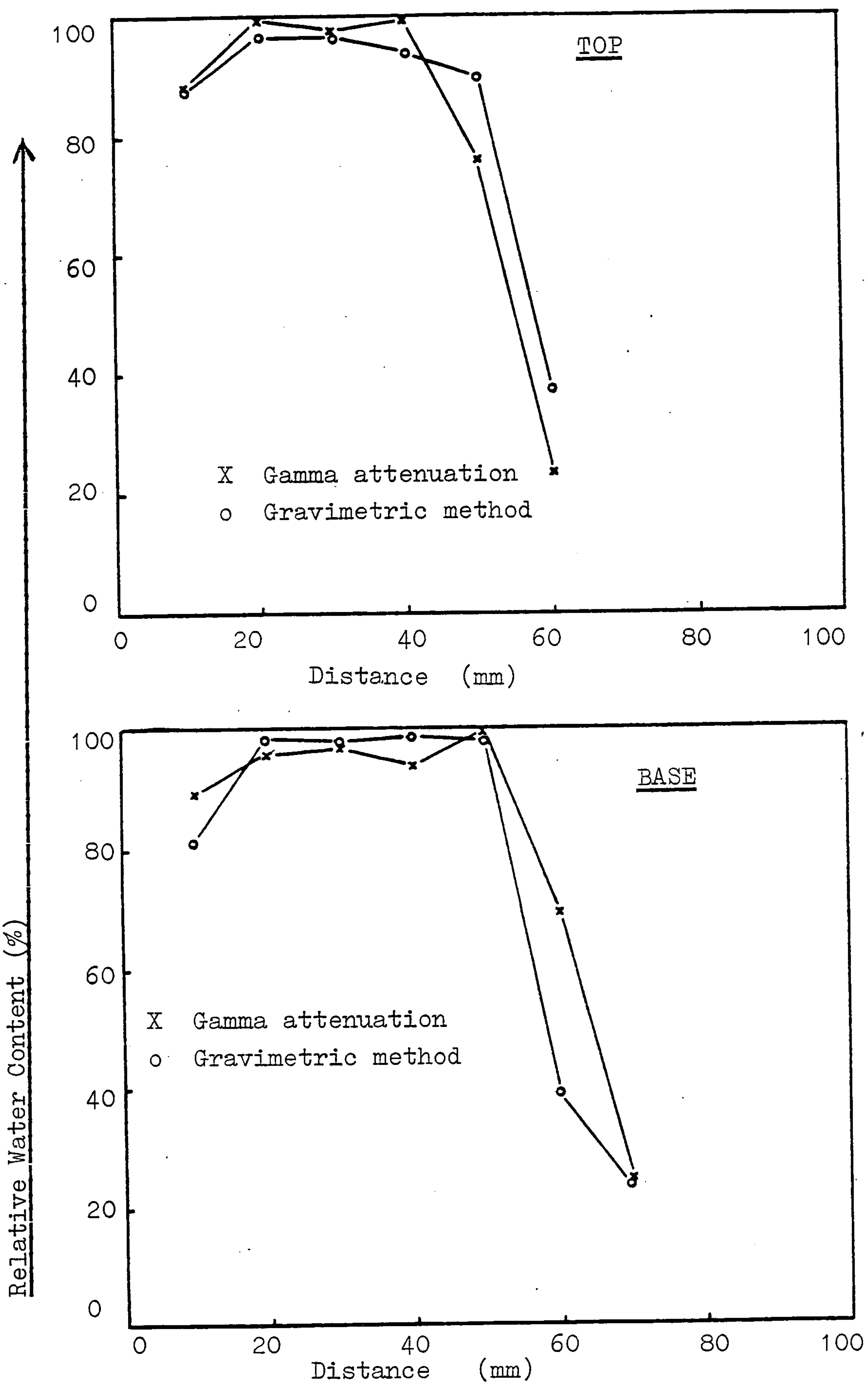


FIG. 5.8
Comparison of water contents at different depths in the xylem, measured by gamma attenuation or by gravimetric methods on excised tissue, for a P.contorta tree from Ae.

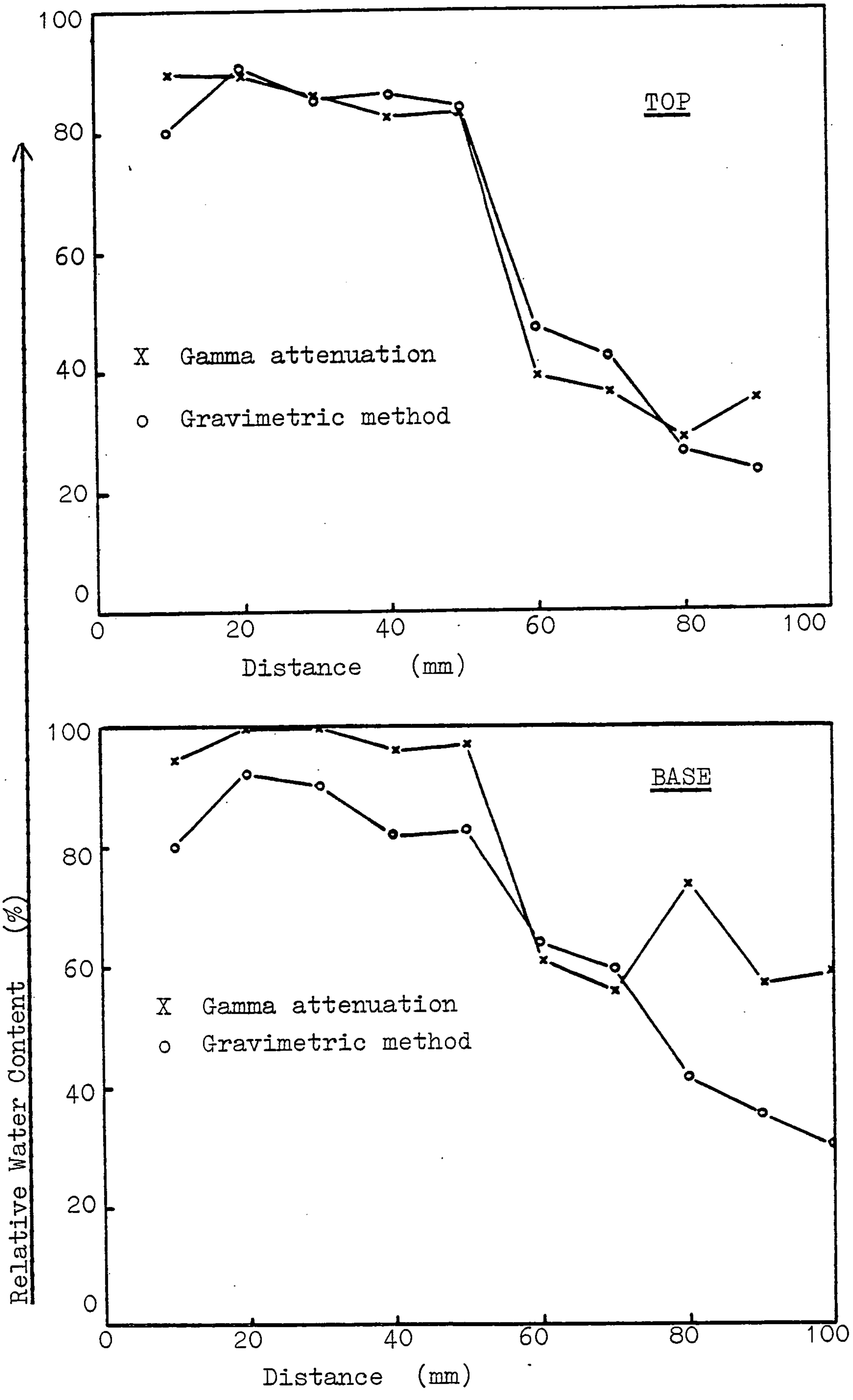


FIG. 5.9 As for Fig 5.8, but for a *P.sitchensis* tree from Fetteresso.

obvious on the days that transpiration was highest.

5.4.5 Measurement of Water Potential in the Field

Since the weather conditions at Ae were generally wet and the evaporation rate low, the trees were never particularly stressed. This is reflected in the water potential measurements using thermocouple psychrometry, which indicated that water potential was usually within 0 to 0.4 MPa, and always within 1.0 MPa. Variation in this range tends to be large for this method, and under field conditions single psychrometers at each height did not show either diurnal variation or phase lags satisfactorily. However they did indicate the general level of water potential.

In one tree at Ae, four thermocouple psychrometers were installed at each measurement height on August 12. The results for the two subsequent days on which measurements could be taken were:

	Top		Base	
	Time (hours)	W.Pot'l (MPa)	Time (hours)	W.Pot'l (MPa)
13 August	11:30	0.73	11:05	0.32
	14:40	0.69	14:25	0.46
	17:10	0.70	19:05	0.49
28 August	10:13	0.41	9:53	0.30
	12:35	0.38	12:25	0.31
	15:50	0.41	15:38	0.36

Measurements of unbagged needles were made at Ae using the pressure chamber on 8, 9 and 13 August, as follows:

	TIME	ψ
August 8	5:40	-0.75 MPa
	7:10	-0.75
	9:25	-0.94
	13:50	-1.06
	16:25	-1.07
August 9	19:15	-0.96
	12:25	-1.15
	15:00	-0.83
	17:35	-1.02
August 13	10:40	-0.90
	13:05	-1.29
	15:10	-0.97
	17:40	-0.72

These are mean values for three levels in the canopy, each of which has a standard error usually less than 0.04 MPa.

Data for water potentials from Fetteresso were based on bagged needles, and showed a clear diurnal trend which was more pronounced at the top measurement point. A phase lag was not obvious.

5.5 Discussion

The calibrations showed that estimates of both flow and water content made in the field were reasonable. The time lapse between implantation of heat pulse probes and recovery of the stem segments to measure the wound reaction and development in th Ae trees resulted in a slight decrease in the accuracy of the heat pulse velocity estimate of flow. The probes from Fetteresso gave a more accurate result because the time between implantation and recovery was only about 10 days.

The gamma attenuation estimates of water content were not affected by wounding, although there was a small growth increment of about 1 mm, which would have given a small systematic error in the final data processing.

Clearly the results were dominated by the weather. While it was unfortunate that conditions precluded observations on trees while under stress from limited soil water or even under particularly high transpiration rates, the weather station data indicated that the conditions were typical for that summer. Consequently the results should be considered to represent conditions for that season and location.

The sensitivity of the Penman-Monteith equation is very dependent on the values of the aerodynamic and canopy resistance parameters, particularly for evaporation from a rough surface such as a forest (Beven, 1979). Therefore evaporation should tend to be related to vapour pressure deficit rather than net radiation, and be affected considerably by the canopy resistance values.

The vapour pressure deficit measurements in the forest lags behind net radiation by several hours, and is affected by precipitation. Thus on August 8 (Fig. 5.1), rain at 10:00 hours prevented the further rise of vapour pressure deficit, but net radiation continued to rise in the normal diurnal pattern, peaking at 14:00 hours. Transpiration was also delayed, because of both intercepted water, and the constant vapour pressure deficit. Heat pulse estimates of flow also peaked at about 14:00 hours, but rain after 16:00 hours prevented further observation.

Measurements on August 9 (Fig. 5.2) indicated an earlier peak of both net radiation and vapour pressure deficit, with flow rates also peaking earlier and higher. There was some indication of a decline in water content at midday.

On August 28 (Fig. 5.4), only one tree was measured intensively. This day was slightly warmer (17.0 °C maximum compared with 14.8, 15.3 and 16.6 °C for the 8th, 9th and 13th August respectively), and was overcast with high thin cloud. The estimate of transpiration followed net radiation and slightly preceded vapour pressure deficit as before, but a midday depression in flow rates was clear. Water content at the top of the tree appeared to decline, and at the base was depressed slightly at midday, possibly indicating an earlier recharge at the base.

The results from Fetteresso indicated a distinct phase lag in the flow rates when comparing the two measurement positions, but the water potential measurements appeared to be in phase (Fig. 5.5). The water content at the base of the tree generally declined during the day, but there was no clear trend at the top measurement site. This experiment was successful in that (a) a definite phase lag was demonstrated with respect to flow, (b) a change in water content occurred, and (c) a diurnal change in water potential was present. Evaporative demand was not high however, and the tree being well saturated due to earlier precipitation was not subject to large fluxes and consequent changes in water content.

5.6 Conclusions

The conditions in the field were such that the trees were never under substantial stress or evaporative demand, and this probably reflects the normal conditions for the site.

During the infrequent periods of significant transpiration that were available, diurnal trends in flow were observed and a phase lag indicating change in storage was observed in the flow measurements at Fetteresso.

Water content changes in the trunk were small, somewhat variable and subject to some random scatter. They generally indicate a fall at about midday, of less than 10%. Water potential in the trunk was always rather close to zero, and hence difficult to measure thermocouple psychrometry. Values were generally lowest around midday, but phase lags were not seen. Using bagged epicormic shoots at Fetteresso, the results were much more precise and indicated a diurnal depression, but still did not indicate a phase lag.

The results showed that flow measurements gave the best indication of dynamic changes in water status for the prevailing weather conditions. While the other measurements indicated diurnal changes, the data did not show obvious phase lags.

6.0 A COMPUTER MODEL FOR FLOW IN STEMS

6.1 Philosophy of the Use of a Model

The functioning of plants can be described at several levels of organisation: molecular, biochemical, cellular, organ, whole-plant, or plant communities. Much of the research presently carried out is 'reductionist', in that it seeks to explain the functioning of plants at one level of organisation. The results of such research are of value in understanding functions or processes at a higher level of organisation only if they can be interrelated or placed in perspective with other processes. In attempting such recombinations, movement over more than two levels of organisation is generally nonproductive since the complexity is enormously increased and the influence of individual inputs, errors and sensitivities make the predictions of doubtful value (Landsberg, 1975).

The concept of modelling is a formalisation of this approach, and is facilitated by the ease and accuracy of computer manipulation of data. The objective in modelling can be the explanation of plant function at one or several levels of organisation, as an 'interconnected field of precise statements which explain in accurate quantitative terms....' (Landsberg, 1975). Therefore empirical information is not particularly useful in producing new knowledge from models since it produces predictions for particular circumstances rather than explains processes. Empirical information can only be justified in a model if no explanatory subsystem is available.

Instead, each subsystem in the model should comprise an explanation of the subsystem output in terms of all the inputs and influences acting upon it. One, or a series of equations should explain the theory, postulate or relationship.

Even within a model spanning one or two levels of organisation, the degree of complexity can obscure the effectiveness of the model if assumptions and simplifications are not made. Only those compartments which are of prime interest can be modelled in detail, and the remainder reduced to elements which directly influence the output.

The objective in modelling in the present case was to put together that knowledge which was available about water status and flow in a tree in a cohesive framework. The implications of making estimates of data, or theorising about relationships could then be explored in a logical manner by observing their effect on a simulated tree.

6.2 Assumptions and Conditions used in the Model

6.2.1 Introduction

Water movement through plants can be described in terms of an Ohms law analogue (van den Honert, 1948) where water flows through a catena of hydraulic resistances. This concept is limited to steady-state conditions if capacitances are also found within the plant (Jarvis, 1975), and in its simplest form it does not account for the complexity of multiple branching (Richter, 1973), or changes in resistance in the various parts of the catena.

The model developed during this study comprised four in-line compartments: roots, trunk, branches and twigs, and leaves. They form a catena between the soil (represented by a bulk soil water supply at a particular water potential), and the atmosphere represented by a particular level of evaporative demand. The trunk was the primary area of interest, so the remaining compartments were simply considered as single homogenous elements, ie. as a 'big leaf', a 'big branch' and a 'big root'; there was no direct involvement of their structure or architecture.

6.2.2 Soil Resistance

When the soil water potential is close to zero, the soil water supply is optimal and the resistance to flow from soil to root is very small. Changes in leaf water potential with changes in transpiration rate will then indicate if changes in the resistance of the water transport system between the soil and the leaf are occuring. Some authors have reported decreases in leaf water potential with increasing transpiration, but others have conflicting evidence (Camancho-B et al, 1974), and the inference of variable resistance with flux remains a source of interest (Boyer,1974; Jarvis, 1975).

The effect of drying soil conditions also remains controversial. Earlier workers considered that on other than very wet soils, resistance to flow in the soil was major, especially close to the roots (Slatyer,1967; Weatherley, 1975), and this was supported by the theoretical models of Philip (1957) and Gardner (1960). However it was disputed by Newman (1969), and evidence has accumulated that the rate of water movement in soil does not normally limit uptake by roots (Landsberg and Fowkes, 1978), although it can remain an important factor.

In the model, it was assumed that the bulk soil water potential could be expressed as a single value, and that this represented an otherwise unlimited source. No attempt was made to introduce a resistance which varied with transpiration rate and soil potential. However this would have been quite feasible given relationships such as those found in Jarvis *et al* (1980).

6.2.3 Root Resistances

There are three ways in which root resistances can be estimated:

(i) by measuring fluxes and potential gradients of excised tissue or in small plants (Newman, 1973; Boyer, 1974; Shoulders and Ralston, 1975; Stone and Stone, 1975),

(ii) by measuring transpiration and potentials in intact trees (Hellkvist *et al*, 1974; Nnyamah *et al*, 1978), and

(iii) by measuring flows and potentials from trees before and after cutting off the roots (Landsberg *et al*, 1976; Roberts, 1976,1977,1978).

The proportion of the total resistance found in the roots has generally been large (Jarvis,1975 - a review). For example, Roberts (1977) found 53% of the total resistance in *Pinus sylvestris* to be in the roots, and Hellkvist *et al* (1974) found the root resistance to be half to one third of that in the stems of *Picea sitchensis* - a similar figure to that found in *Pseudotsuga menziesii* by Nnyamah *et al* (1978). Running (1979) found 67% of the total tree resistance to be in the roots at 7 °C, with a strong negative regression at lower temperatures.

These various studies clearly indicate that root resistance is a significant, if not major component of the total resistance. Although a relationship between water content and root permeability was used in the model, no other relationship such as temperature dependence was incorporated, to avoid complexity. The total root volume was estimated from reported measurements from similar trees (Whitehead and

Jarvis, 1981 - a review).

6.2.4 Stem Resistance

The resistance to flow in the stem was measured directly as its reciprocal, saturated permeability (Section 2.1). Changes in resistance with changes in water content were accounted for in the model using the relationships found in Section 4.4.

The model used the stem resistance as a basis for inferring total plant resistance, by the partitioning of resistance between the four compartments (roots, stems, branches, leaves) according to input data.

The primary assumption made was that within the stem compartment, flow could be described in terms of Darcy's equation. That is, steady-state flow is proportional to a gradient of water potential, viscosity of the sap, and the physical dimensions of the compartment. The validity of this assumption is discussed for excised stem sections in Section 2.3 for both saturated and 'stressed' conditions.

Radial differences in the stem cross-section were not considered in the model. Thus, the permeability, water potential, potential gradient and viscosity of a stem section were found as single values, each representing a range of areas and values found within the stem cross-section.

The cross-sectional area involved in flow was taken as the total sapwood area, assuming that heartwood was essentially non-conducting (Section 2.2). Sapwood area was also the basis for estimating transpiration from heat pulse velocity measurements (Section 2.3.2), and its use eliminated the need to estimate conducting lumen size distibutions.

6.2.5 Branch Resistance

Resistance in the 'branch' compartment is defined as all that pathway resistance between the top of the stem and the base of the needles. It is represented in terms of a total volume, with defined values for the volume fractions of air, water and wood, as for the stem. No allowance is made for branching or other lateral differences in the flow paths.

6.2.6 Leaf Resistance

Richter (1973) suggests that there is little resistance in the flow path through living cells of leaves, since the gradient in potential within transpiring and non-transpiring twigs is virtually the same. Tyree et al (1975) concluded that most resistance in the transpiration flow path was in that part up to the leaf tissue.

The flow path through the stomata is a major variable resistance, with well-established relationships with leaf water potential and environmental variables.

The leaf compartment is represented in the model in a manner similar to that for the branch compartment, except that it is postulated that there is no change in water content, and a linear relationship between water potential and permeability is used.

The Penman-Monteith combination equation is used to find the transpiration rate resulting from evaporative demand; the canopy conductance figure used in the equation was obtained by measurement (see Section 5: Field Data) or from estimates based on the literature.

6.3 Programming the Model

The model is composed of six compartments: root, soil, trunk, branch, leaf and atmosphere, linked in series. Each is represented in the programme by a subroutine, and other subroutines are used for the estimation of viscosity from temperature, output of data, statistical manipulation and programming control and procedure. Various levels of complexity can be used, from simulating flow in the trunk alone from inflow and outflow data, to simulating the whole tree under the influence of diurnal patterns of weather.

The programme is fully controlled by the use of directives, which are also used to define the function parameters, tree dimensions, weather station input or a nominated level of transpiration, entry of field data for statistical comparison, and the ratios of resistances for the compartments at zero flow. They are described fully in Appendix 1.

6.3.1.1 The Stem Compartment

The stem compartment is considered as a number of hollow disks or tube sections one on top of the other and in hydraulic contact, with flow proceding through each on the basis of Darcys law. In addition, three other factors are introduced: a storage factor implied by a change in water content, a relationship between water content and water potential, and a relationship between water content and permeability. Flow is considered to be in discrete time increments.

The following are defined initially:

(i) Parameters controlling the relationships between water content and permeability, and between water content and water potential, both being of exponential form

(ii) Dimensions of the tree including the number of stem increments and the saturated permeability of the wood

(iii) Rates of inflow and outflow from the trunk if these are not to be obtained from other subroutines

(iv) The time increment, defined either as fixed or on the basis of a proportion of water removed from the top section of the trunk by the flow rate

(v) The water content, and consequent water potential and permeability for each trunk section.

The subroutine operates the following sequence for each trunk section, starting at the top:

(i) From the outflow rate and time increment, the change in water content is calculated.

(ii) The consequent changes in permeability and water potential are found.

(iii) Since a potential gradient between the current segment and the segment below now exists, an inflow rate is calculated on the basis of Darcys equation.

(iv) A new water content and potential are found as a result of the inflow for the current time period.

Thus the trunk will develop a gradient of potential and lowered water content, starting at the top and moving down the trunk with successive time increments.

6.3.1.2 The Root Compartment

The root is considered as a single resistance defined as in Section 6.2.3, affecting the flow across the bottom segment of the trunk. The resistance is affected by changes in water content in the bottom segment in the same manner as a trunk segment.

6.3.1.3 The Branch and Leaf Models

Again, these models are effectively considered to be single additional segments. The volume, zero-flow resistance, water content/potential relationship and the water content/permeability relationship are all defined separately, but the model functions as if the branch and stem compartments were additional stem segments. In the case of the leaf model, a linear relationship between water content and water potential is used rather than an exponential curve. The leaf water content is considered to be static.

6.3.1.4 The Transpiration Model

The flow out of the leaves is defined in the transpiration compartment by the Penman-Monteith combination equation (Jarvis, 1975):

$$\lambda . E = \frac{s.H + c_p . \sigma . \Delta e / R_a}{s + \gamma(1 + h_c / R_a)}$$

where λ is the latent heat of vaporisation of water

E is the rate of evaporation per unit stand area

s is the slope of the saturation vapour pressure/temperature curve,

H is the net radiation,

c_p is the specific heat of air,

σ is the density of air,

Δe is the vapour pressure deficit,

R_a is the boundary layer resistance

R_c is the canopy resistance

γ is the psychrometric constant.

The input data required are the net radiation, wet and dry bulb temperature, wind speed and stomatal conductance.

The wind speed above the canopy is found by adjusting the windspeed measured at the top of the canopy using a logarithmic profile, and the boundary layer conductance is found as a function of the adjusted wind speed.

The rate of evaporation from a single tree is found from E the stand evaporation, as a proportion of the leaf area.

6.3.2 Significance of Changes in the Function Parameters

The two functions which relate water content to water potential and to permeability are both exponential, i.e. of the form:

$$y = a.e^{k.x}$$

In the linear form

$$\ln y = \ln a + k.x$$

The intercept is given by ln a, and k is the slope. In the exponential form a controls the asymptote, and k controls the rate of change of slope, i.e. the degree of curvature.

In the model, the function is of the form:

$$\text{Relative water content, } R_s = c + e^{(\Psi-a)/b}$$

where a, b and c are constants. Values of a and c permit the function to be fitted through zero, so that data can be fitted using a least-squares method. Thus parameter a will affect water potential additively, while parameter b controls the curvature (i.e. the sensitivity of water potential to water content).

In the relation between permeability and water content:

$$K/K_{sat} = \gamma . e^{R_s . \alpha}$$

the response of K/Ksat is proportional to γ , and α controls the rate of response, as before.

The effect of the parameters on the output from the model was investigated by setting up a simulated tree trunk to be initially saturated, with zero water potential at the base and a constant outflow from the top. This was run until a steady state was attained. Then each function was increased or decreased by5% in turn, and the process repeated. The resulting water potential, content, flux and permeability were compared.

The following table gives the new values as a percentage of the original values. Each increase or decrease in a parameter is indicated by a + or - sign respectively.

	Water Potential	Water Content	Flow Rate	Perm'y
a +	102.8	99.6	99.7	93.6
a -	98.2	101.0	100.2	10.0
b +	96.0	101.9	100.6	109.0
b -	104.2	98.1	99.4	91.1
c +	97.4	101.3	100.4	106.5
c -	102.6	98.7	99.8	93.8
α +	113.0	98.6	99.6	89.0
α -	87.4	101.5	100.8	137.8
γ +	113.8	98.3	97.6	72.9
γ -	97.6	100.3	100.4	106.

Clearly the largest responses are in water potential and in permeability, and the parameters affecting permeability have the most influence.

The same form of analysis was applied to the physical constants associated with the tree - saturated permeability, volume fraction of the woody matrix, sapwood area and viscosity - but only a decrease in in saturated permeability had effects larger than 5%. These were on water potential which increased to 105.4% and permeability, which decreased to 87.8%.

Generally, the model was remarkably stable to changes in the parameters. The main effect was in permeability, and the potential gradient required to maintain flow through the wood.

6.3.3 Stepwise Changes in Simulated Flow

To investigate the effect of storage changes, a simulation was set up so that a stepwise change in evaporation from the needles was introduced, in a tree based on the dimensions of Tree 1 from the Forest of Ae. In this simulation, all compartments were represented: leaf, branch, trunk and root, and it was intended to see how much water could be removed, and over what time period, before a steady state was attained.

The results are shown in Fig. 6.1. Flow between the branch and leaf compartments responded very quickly to a change in evaporation, and were followed by flow rates in the trunk according to height. After about 36 hours all flows were closely similar. A stepwise cessation of flow eventually led to flows close to zero after about 60 hours.

The water contents changed much more in the leaf and branch compartments, and recharge in all compartments took place earlier than the decrease in flow rates. This occurred because of the comparatively large effect that a small change in water content has on water potential. The overlap in water content occurred because a different function is fitted to the leaf water content/water potential relationship to that used for the branch and trunk.

Water potential changed more in the branch and the leaf compartments than in the trunk, so that the gradient between the top of the trunk and the branch compartment increased considerably. However the proportion of resistance in the four compartments remained rather constant, although the total resistance increased by a factor of 2.30.

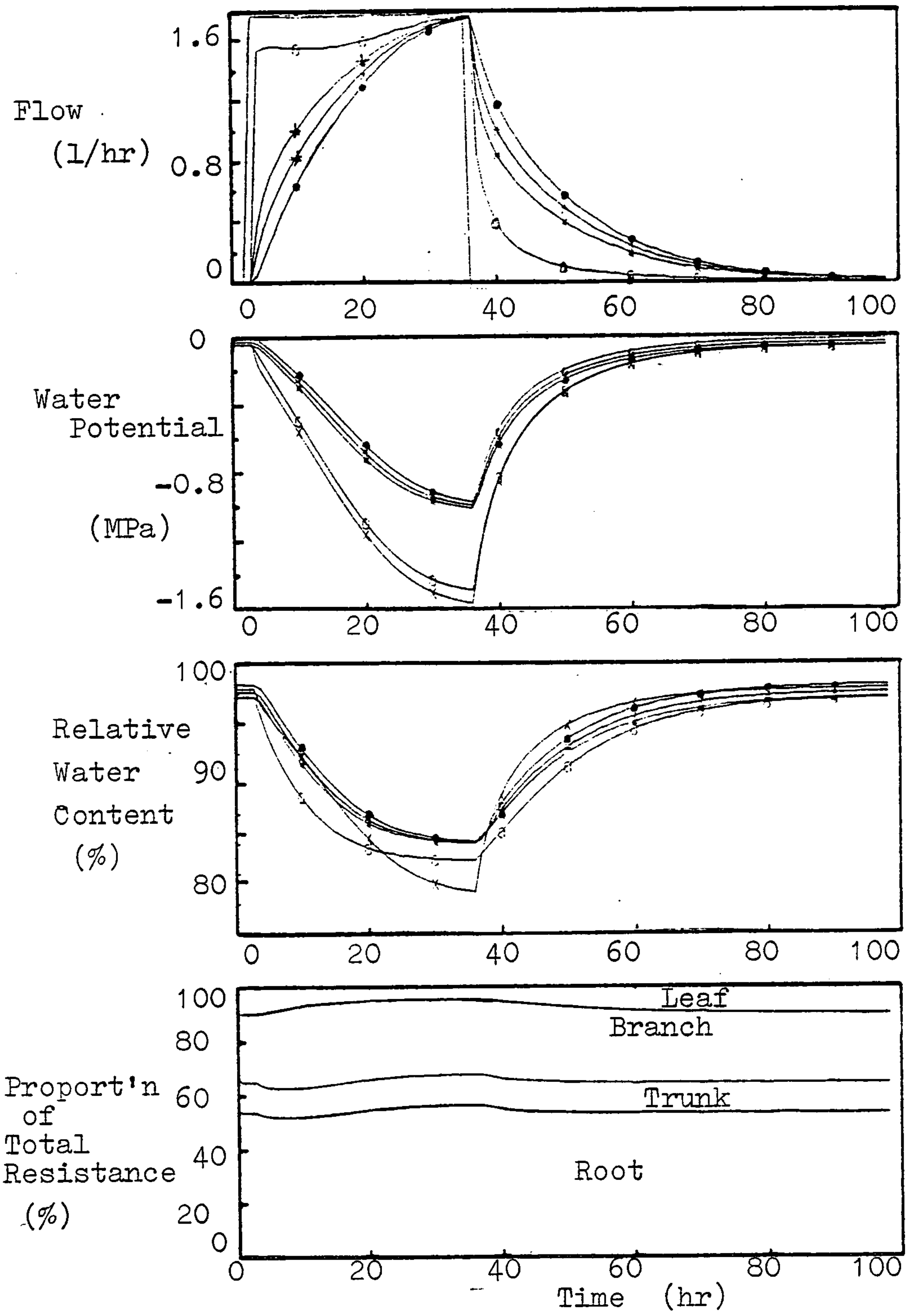


FIG. 6.1 Simulation experiment on a tree trunk modelled on a *P. contorta* tree from Ae, on which a stepwise transpiration rate has been imposed, for 36 hours followed by a zero flow for 60 hours. The tree was initially saturated. Results for flow, water potential, water content, andthe proportion of the total resistance present in each compartment are given. In each graph, the leaf compartment is represented by (x), branch compartment by (o), the top of the trunk by (+),,the middle by (✱) and the base by (●).

6.4 Simulation of Field Data

6.4.1 Data Used

Simulations are presented for each of the three trees, for one day, and for Tree 1 on each of the four days reported in the field data.

The data comprised:

(i) Weather station data. Hourly averages or totals of net radiation, ambient temperature, wet bulb depression and wind speed.

(ii) Stomatal conductance measurements were converted to canopy resistance values at up to six measurement times per day, and hourly values were interpolated.

(iii) Parameters from the water content/water potential and the water content/permeability relationships, fitted to laboratory data.

(iv) Parameters defining tree dimensions.

(v) Soil water potential.

When running the model, the first day's weather data was repeated three times, in order to remove the effects of initial saturation. Thereafter the three remaining days were run sequentially.

Other data required were the number of trees per hectare (3693), the number of segments notionally in each trunk (20), and the time interval for each iteration (10 seconds).

The resistances for each compartment were derived from measurements of trunk permeability, and by partitioning the total resistance between the compartments on the basis of reports from the literature.

Total resistance was inferred from midday fluxes and potential gradients estimated using soil water potentials and pressure chamber measurements taken in connection with stomatal conductivity measurements. Roberts (1977) estimated root resistance to be 54% of the total, and permeability measurements compared with total resistance suggested that trunk resistance was about 12 % of the total. Partitioning of the remaining resistance between needles and branches was done on the basis of data from Hellkvist *et al* (1974). They showed using bagged and unbagged shoots, that shoot resistance was about 10% of the total resistance. The remainder (24%), was attributed to the branch compartment.

6.5 Discussion of Simulations

The model was designed to describe flow at the level of organ and whole-plant. Inevitably, assumptions concerning adjacent levels - cell, and plant community - must be made so that sufficient simplicity is maintained to keep the model practical. The assumptions concerning the plant community (i.e. the stand of trees) were associated with the use of the Penman-Monteith equation. Varying the inputs to the equation while keeping other inputs fixed made it clear that the term for canopy conductance determines the extent to which evaporative demand is translated into fluxes. In turn, canopy resistance is dependent on the adequacy of sampling (a) the leaf area of the various age and height classes, and (b) the accuracy of measuring the stomatal conductivity in each age class. Probably the adequacy of sampling leaf area is the most significant source of error (Leverenz, pers. comm.).

While the remaining data for the Penman-Monteith equation is less likely to produce large errors, a second assumption, that stand evaporation can be partitioned between individual trees on the basis of leaf area may introduce a significant error, since larger trees have a larger proportion of foliage in the upper canopy. Transpiration from dominant trees may be rather more than partitioning on the basis of leaf area alone would indicate.

Consideration of the flow at a cellular level introduces rather more conjecture. Basic to the functioning of the model are the two relationships between water content and (a) water potential, and (b) permeability. Both imply changes at a 'cellular' level, i.e. within the xylem element. In the forms used, the relationships are simple, do not involve hysteresis and are fitted through zero water potential and permeability when the relative water content is 100%. None of these are necessarily correct, although laboratory determinations resulted in reasonable fits. The assumption that both relationships depend on a changing level of embolism implies that the tracheid size distribution would be involved. Further, transmission of emboli between tracheids would depend on the pore size distribution in the pit margos.

The simulations presented here use the laboratory determinations of the relationships. These imply a a relatively large change in water potential for a given change in water content, so that the model is rather sensitive to changes in water content. Consequently while total resistance can change considerably with changes in evaporative demand, the proportion of resistance attributable to each compartment remains rather similar. This is because it is changes in water potential rather than water content which affect the running of the simulated tree.

Running the model with relationships from the literature (Waring and Running, 1978; Puritch, 1971) on the other hand, results in much larger changes in water content for given changes in water potential. Thus the resistance in each compartment changes considerably at the upper extremities of the tree, where water content changes most. Therefore there are large changes in the proportions of total resistance attributable to each compartment.

The simulations of field data (Figs. 6.2 to 6.7) were based on weather station records, measurements of canopy resistance, tree dimensions and the two relationships between water content, potential and permeability. Running the model from an initially saturated tree resulted in a progressive decrease in water content for several days, over and above the diurnal changes. This corresponds to the changes seen in the step-wise simulation, where an eqilibrium ws approximately reached after 36 hours of continuous evaporative demand.

The values found for fluxes in the field are similar to those produced by the simulations, and the changes in water content are also similar. At the base of the tree, however, the simulations indicate that rather more effect from capacitance has been predicted than in fact was measured.

Water potentials in the simulated trunk are all within 0 to 0.5 MPa, i.e. the range measured by the thermocouple psychrometers. Those measurements of water potential made using the pressure chamber on unbagged needles at Ae, are a slightly less negative than the simulated values fot the leaf compartment.

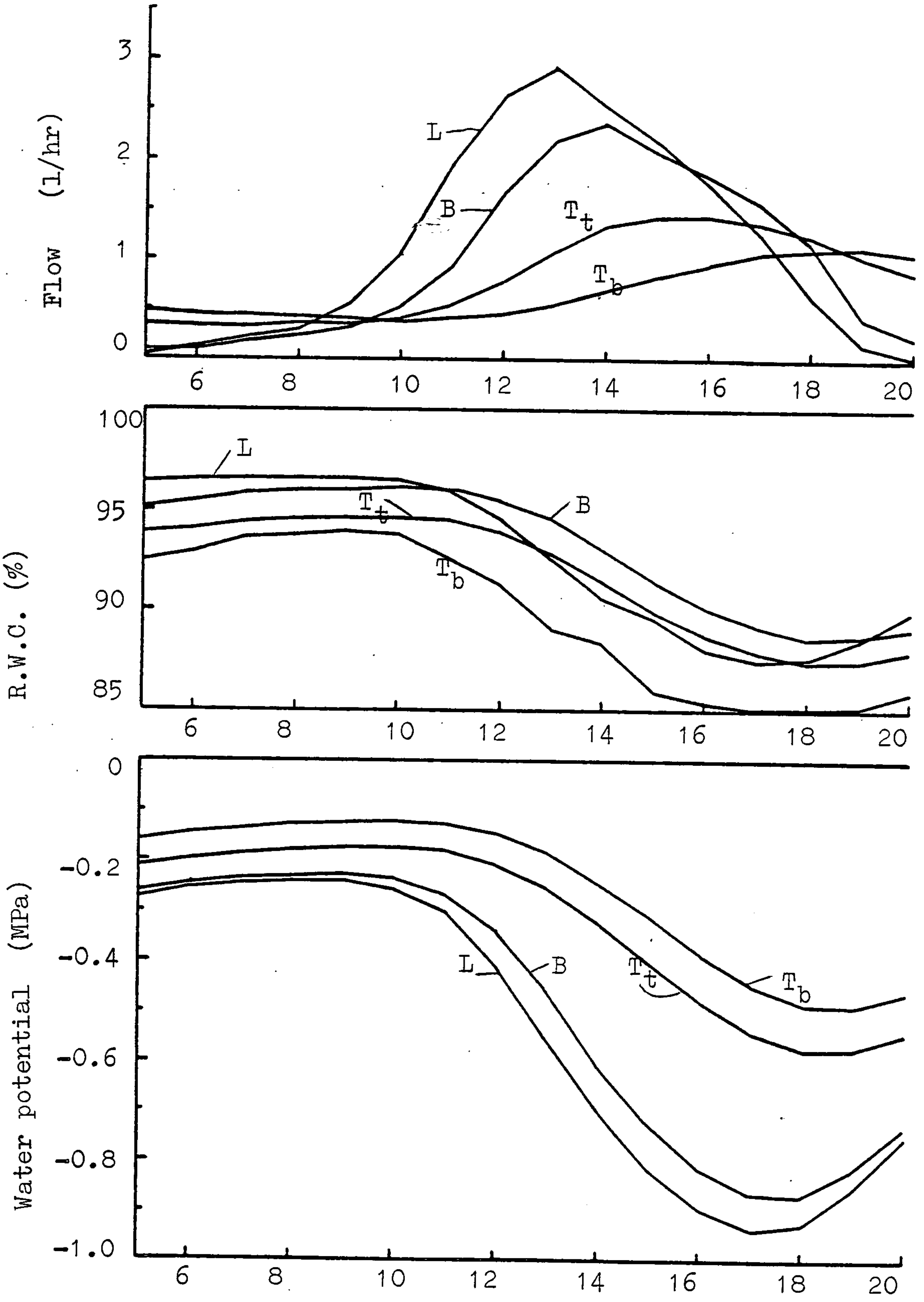


FIG.6.2

Simulated values for Tree 1 at Ae, for 8 August, 1979. In each case, the leaf compartment (outflow from the leaf is repre represented by (L), the branch compartment (or outflow into the leaves) by (B), the top of the trunk by T_t, and the base of the trunk by T_b.

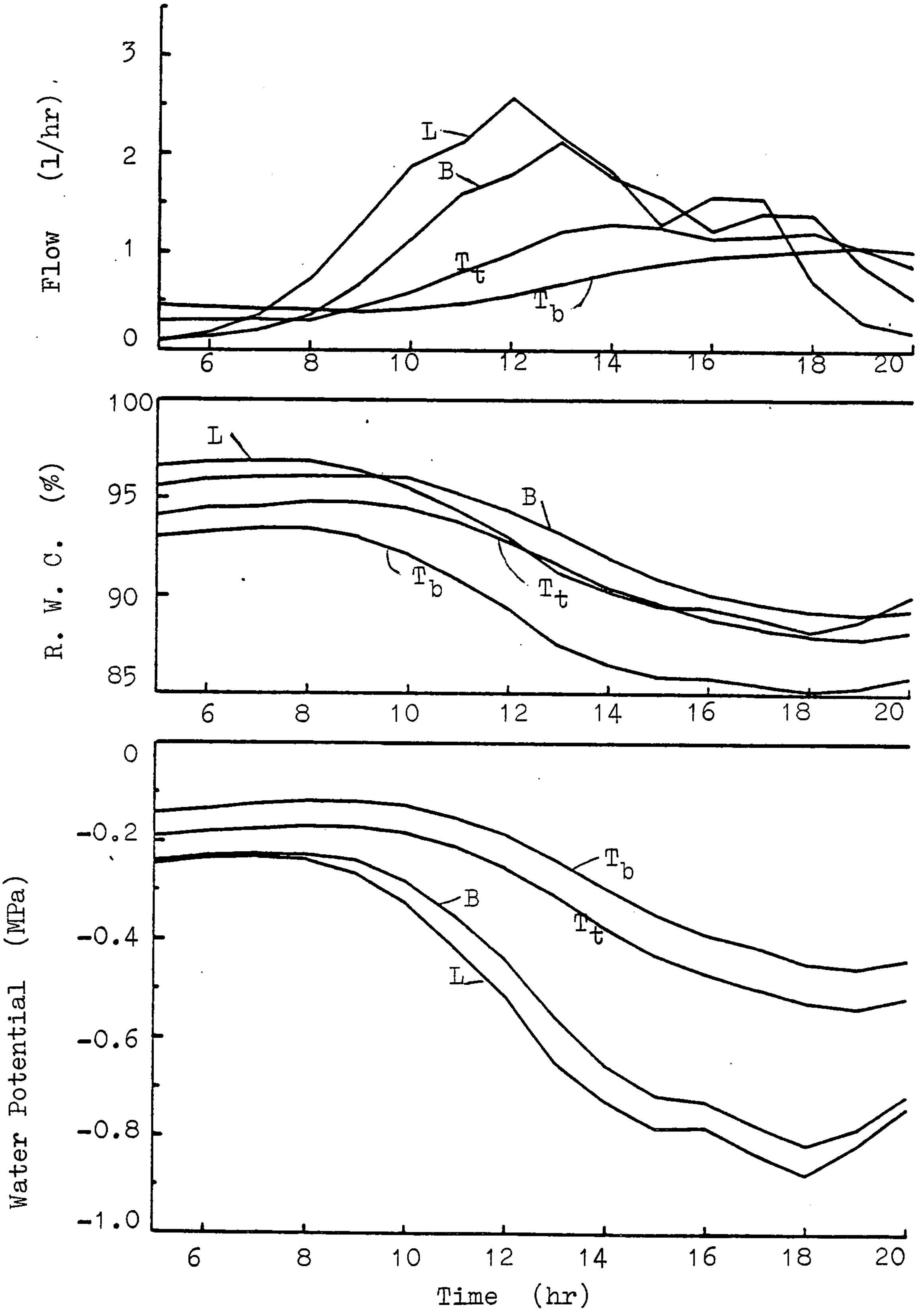


FIG. 6.3 As for Fig 6.2, but simulating 9 August, 1979. (Tree 1)

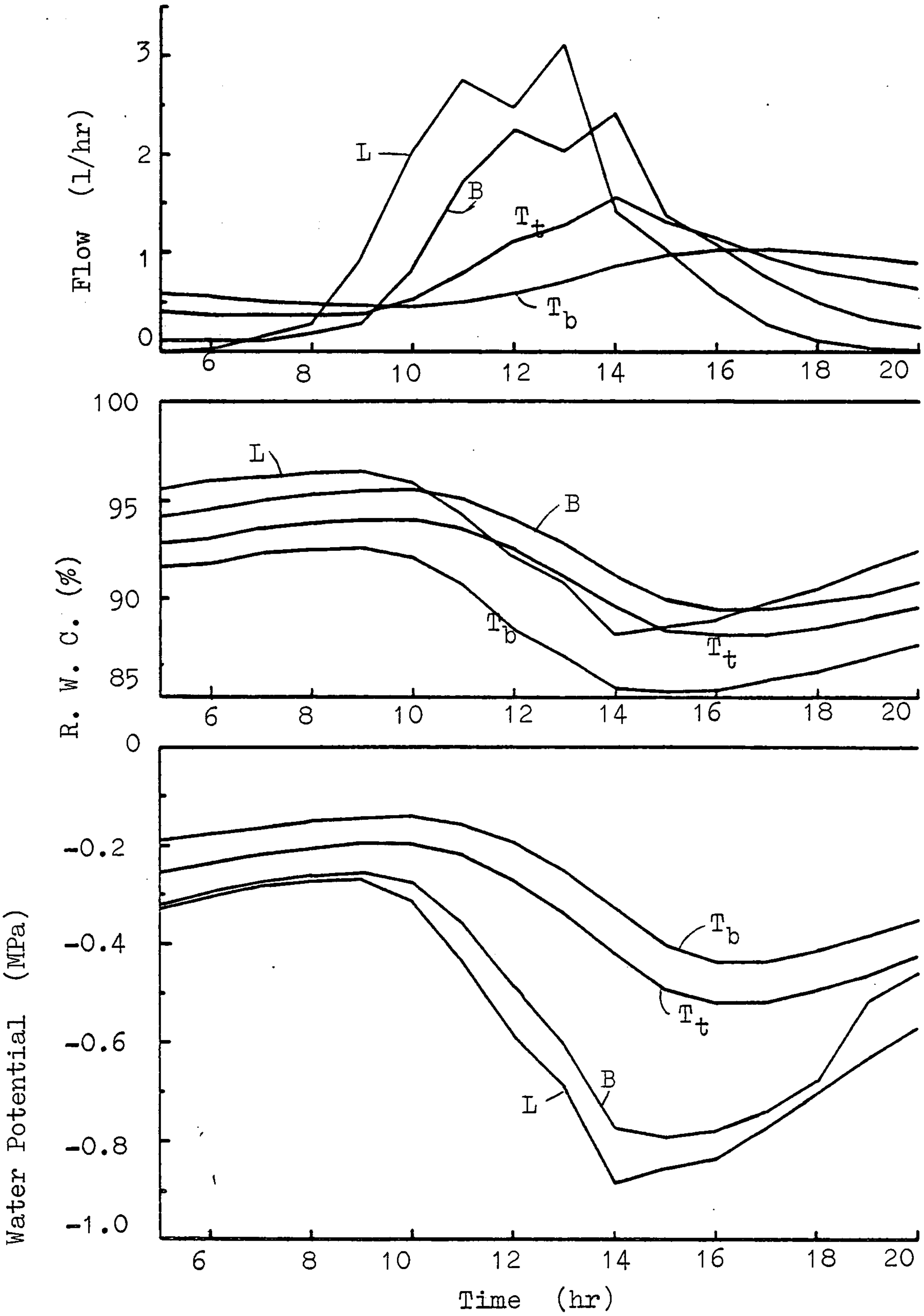


FIG. 6.4 As for Fig 6.2, but simulating 13 August 1979. (Tree 1)

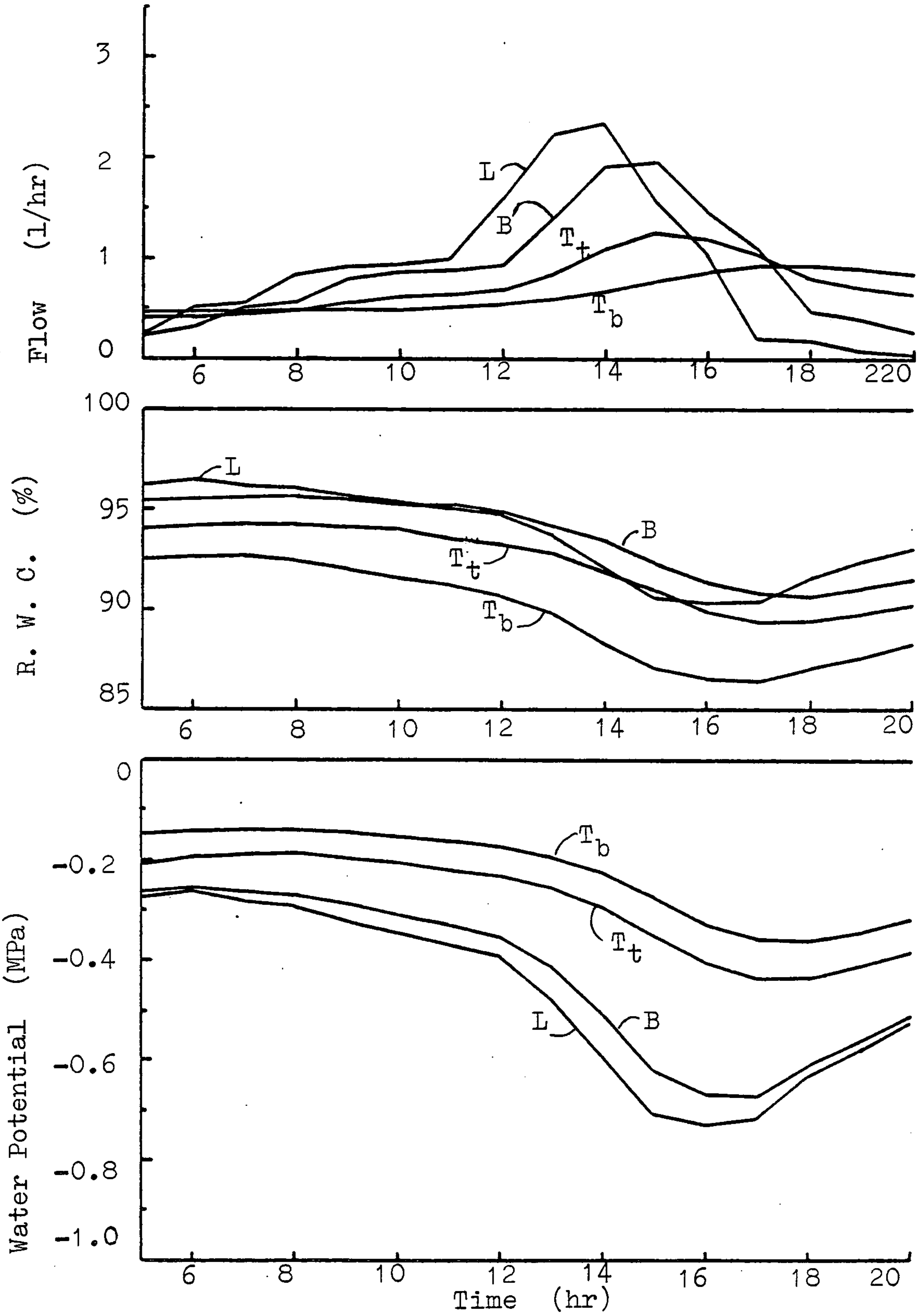


FIG. 6.5 As for Fig 6.2, but for Tree 1 on 28 August 1979.

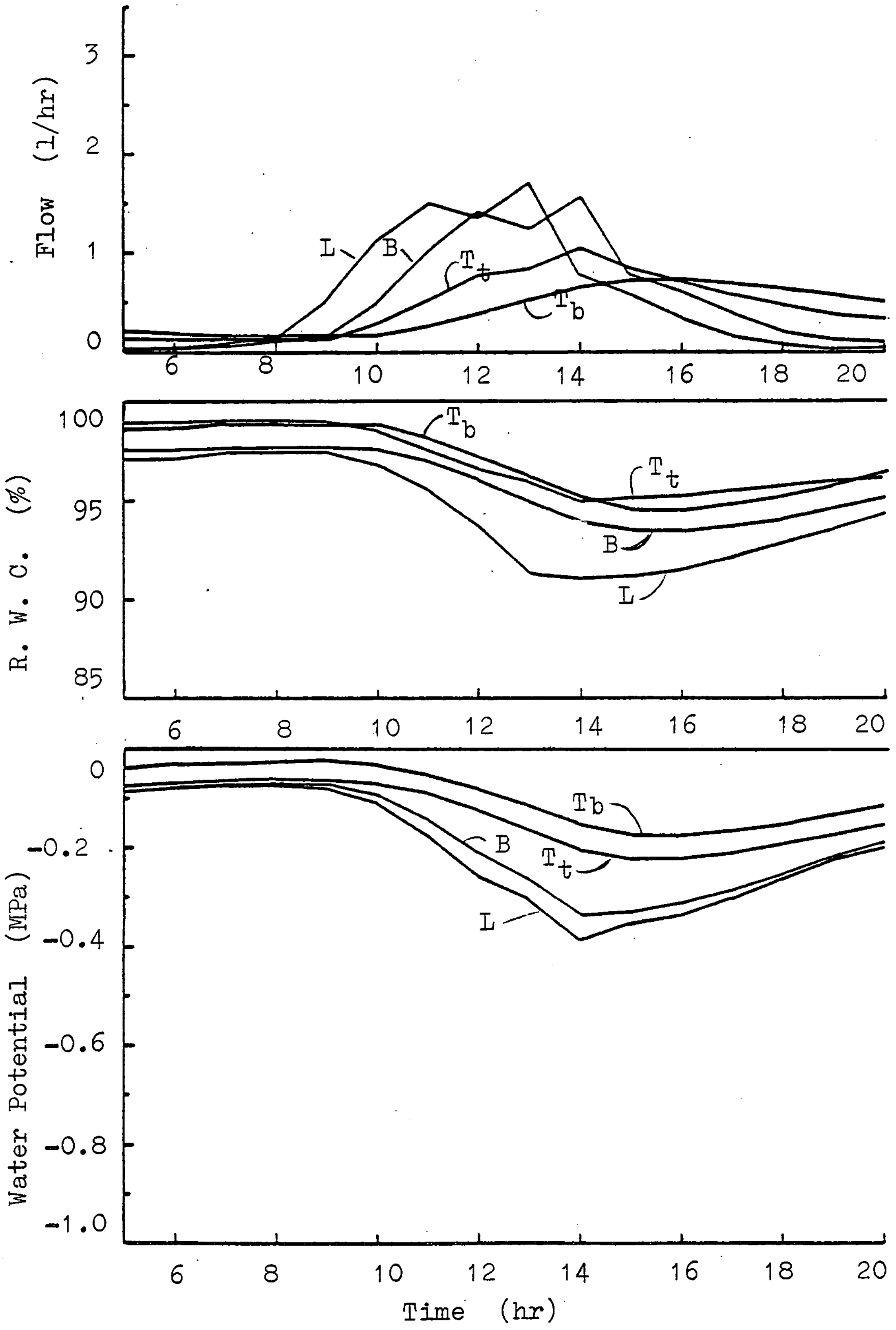


FIG. 6.6 As for Fig 6.2, but for Tree 2 on 13 August, 1979

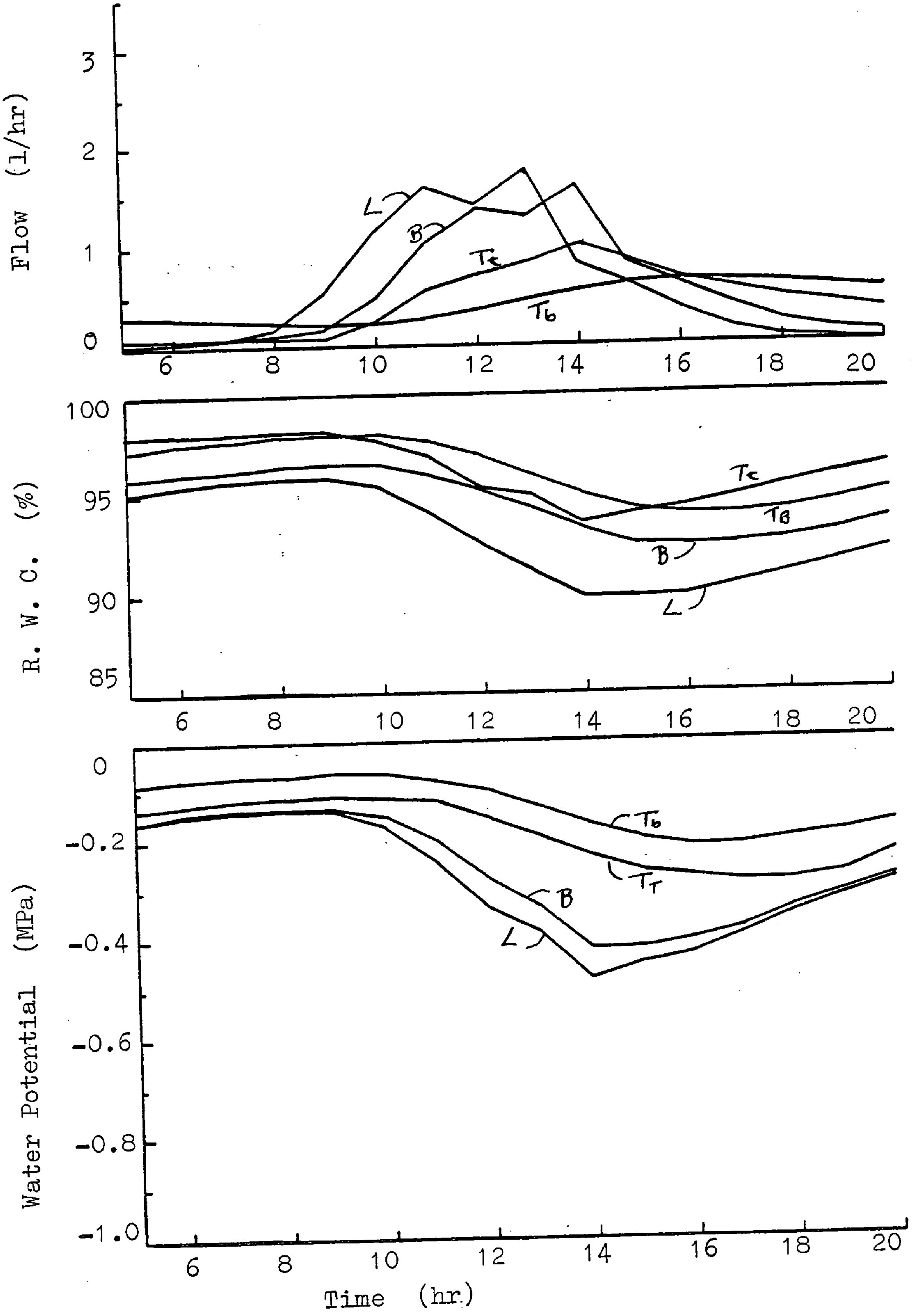


FIG. 6.7

As for Fig 6.2, but for Tree 3 on August 13, 1979.

6.6 Conclusions

The simulations from the model are particularly influenced by (a) canopy resistance, and (b) the relations between water content, water potential and permeability. The total resistance in the simulated trees tend to change considerably with total evaporative demand, but the proportion of resistance in each compartment does not change significantly unless the relationship between water content and permeability permits a relatively large change in water potential.

7.0 DISCUSSION

Dixon's (1914) cohesion-tension theory remains the most widely accepted explanation for the movement of water through plants. In its classical form, the theory requires continuity of water columns in the xylem, and this constitutes a difficulty in understanding the nature of observed changes in water content, both diurnal and seasonal. Such changes imply by their magnitude that xylem elements or tracheids undergo reversible gas embolism. There is limited evidence for this (Chapter 4) although the problems of observation are compounded by the difficulty in observing the xylem without column rupture occurring as a result of the experimental techniques.

The concept of reversible embolism has a number of implications:

(i) Cavitation does not occur in pure water until very high tension are reached, unless gas nuclei are present. These can be retained in crevises of hydrophobic particles, as small stable bubbles under particular conditions, or be transferred through the pit margo pores from adjacent embolised tracheids.

(ii) The nature of the gas within an embolism is significant. In a newly cavitated capillary, the gas is likely to be mainly water vapour under a low hydrostatic pressure. Obviously this is the most likely time for reversal of embolism, but an influx of gas must occur subsequently by diffusion, making reversal less likely.

(iii) A mechanism for reversal must exist. This may partly or entirely consist of physical conditions: the hydrostatic component of water potential, gas concentration in the xylem fluid, size of bubble and capillary, surface tension, and the effect of temperature on surface tension and the size of the bubble. There may be mediation by the living ray parenchyma which is in contact with each longitudinal tracheid. Root pressure may be a factor in some situations.

(iv) Embolism of tracheids must change the permeability. Probably the largest tracheids are the least stable, although according to Poisseuille's law they transport most fluid.

(v) A relation between the size of embolism and water content must exist, and be mediated by water potential through the hydrostatic component.

Adequacy of the Techniques

It seems reasonable to define flow in terms of Darcy's equation, if it is accepted that the parameters in the equation are not necessarily static. In particular, permeability may change with respect to water content, and in turn, to water potential.

The nature of such relationships is not necessarily either simple or mathematical. In fact, if permeability is a function of the number of intact tracheids (ignoring resistance in the bordered pits, or changes in pathways) then the relation between water content and permeability will be a function of the tracheid size distribution. If the effect of bordered pits is included, it will reflect the distribution of different sized tracheids as well. Finally the presence or absence of gas nuclei will affect permeability indirectly because of differing hysteresis effects. Water potential and water content will be affected similarly by embolism.

Therefore fitting a mathematical relationship to these functions is not likely to have any physiological significance.

Given these provisos, Darcy's law is an adequate description of the factors influencing flow. Further, storage can be implied by proposing that decreasing the water potential at a given point will result in a release of water and a decrease in permeability, thus forming the basis for description of flow through the xylem of a tree. The use of a model is a convenient way to represent the hypothesis, and to investigate the effect of changes in the relationships. The information required can be gathered from field measurements of tree dimensions and xylem properties. The simulations can be tested against measured data using suitable techniques.

The development of suitable methods for making field measurements is essential if the model is to be verified.

Sap velocity can be estimated from heat pulse velocity on wholly theoretical grounds, without calibration (Swanson, pers. comm.), and is a useful technique even though there is a small perturbation of the flow path.

Water content measured by gamma attenuation does not interfere with the flow path in any way, and is accurate providing the path geometry can be reproduced accurately and sufficient counts are made to ensure adequate precision.

Water potential is perhaps the most difficult to measure, especially at values close to zero. Thermocouple psychrometry is potentially the most useful technique, if the chamber can be protected from plant resins and if precautions against temperature gradients are taken. The pressure injection technique was of value only in verifying that the psychrometer estimates were of the right order, since it was time consuming and required frequent renewal of holes. It appeared to work only when there was active transport occuring, apparently because local flooding of the tissues occurred in a static sap stream.

Measurement of permeability of saturated wood is relatively simple, accurate method of obtaining a basic measurement, but does not necessarily reflect the permeability of a transpiring tree. Attempts to measure permeability while an overall water potential stress was applied, indicated that permeability decreased substantially with even a small change in potential.

Although none of these methods individually gave results which had a high degree of precision, collectively they provide some evidence for verification of the model.

Sensitivity analysis of the model by changing the inputs clearly indicated the importance of some parameters: in particular, canopy resistance, and the water content/water potential and /permeability relationships which affect potential gradients and capacitance respectively.

In its present form, the model has indicated that rather more capacitance is present than in fact was observed in the field, although the field results were only able to be made in conditions of low stress and low demand. This is likely to be a consequence of the simple exponential curve used. Before a better relation can be used, a better understanding of the processes of cavitation and refilling is required.

The model proved to be a flexible tool with which to bring together the range of measurements made. Its flexibility can accomodate changes in the theories and relationships used here, to test the implications of new advances.

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APPENDIX 1

The construction of the programme is modular so that it is flexible and accessible. Access is by the use of directives, for defining dimensions and properties of the pathway, for defining input data to calculate evaporation, and for controlling the model parameters and output. The time for each iteration is either nominated, or is varied according to the proportion of water removed from the top compartment.

The following are the details for each directive, which is completely identified by two stars followed by two letters.

** ACCURACY Accuracy of the iterative convergence in steady state input is defined as the flow from the top as a proportion of the flow into the base of the trunk.

** AREA The sapwood area at breast height (m^2).

** BOTTOM When the root model is not used, this defines the flow into the base of the trunk.

** ADDTIME To define the starting point in time relative to weather station and field data measurements (hours).

** CONSTANTS To define the constants which relate water content to water potential and permeability (five parameters on one line)

** COMMENT To output an identifying comment into the output file.

** ENTRY To change the input device code.

** FIELDDATA To input field data for comparison with simulated values. Missing values are defined as -99 (default) or by use of the ** MISSING directive. On each line, the measurement time (hours and minutes) is followed by the height of measurement, water content, water potential and flow rate.

** ETA The viscosity ($N \cdot s \cdot m^{-2}$)

** GO Causes the model to be run without the initialisation procedure.

** INITIALISE Causes the model to initialise the trunk values to conditions of zero flow.

** LENGTH The trunk length (m).

** MODEL Defines the compartments to be used with the words LEAF, TWIG, TRUNK, ROOT.

** NUMBER The maximum number of iterations (a protection against excessive iteration).

** NS The number of stems per hectare in the stand, in order to partition the evaporation.

** MISSING See **fielddata

** OUTPUT The output device number.

** PRINT Controls the data output, using either SUMMARY on the next line to indicate that only a printout of the status at completion of the iterations is required, or HISTORYXX, where XX represents the the number of iterations to be completed before listing the status

** RATIO This is the value of the ratio of the leaf area of a particular tree in a stand to the leaf area of an average tree; used for partitioning evaporation from a stand to a particular tree.

** ROOTR Specifies root resistance as a fraction of the total resistance when the plant is not transpiring or under stress from a soil potential.

** RUN Initialises and runs the model.

** SATPERM Defines the saturated permeability of the sapwood (k x 10^{12} m^2).

** SEGMENTS The number of segments the trunk is notionally divided into.

** STOP Stops the programme.

** TEMPERATURE Defines the temperature at which viscosity is to be calculated. It is not required if ** ETA is defined.

** TIME The time interval for each iteration (sec).

** TOPFLOW This is used if the leaf and twig compartments are not used, and defines the outflow from the top (l/h)

** VOLUME The volume fraction of wood.

** VALIDATE To carry out an R squared test of field data at the end of each set of iterations.

** WATERREMOVE Defines the maximum amount of water which can be removed from the trunk at a specified time, as a proportion of the water in the topmost segment.

** WS The weather station data and canopy resistance comprises (each set to a new line) hourly values for (i) time (hours), (ii) Net radiation (watts m^{-2}), (iii) ambient temperature (°C), (iv) wet bulb depression (°C), (v) wind speed (ms^{-1}), and (vi) canopy resistance (sm-1).

** VTWIG The volume of the twig compartment (m^3).

** VZLEAF The volume of the leaf compartment (m^3).

```
C  MAIN PROGRAM TO MODEL THE TRANSPORT OF WATER THROUGH A COMPLETE TREE
C
      DIMENSION INAME(6),CONS(5),ICARD(80),IDIRDA(10),IDIRPR(2,2)
     1,IDIRMO(2,4),H(100),Q(100),PSI(100),THETA(100),AK(100)
     2,IDIR(2,37),WS(6,100),XPCENT(5),FIELD(8,100),CTOP(4)
      DATA ISTAR/'*'/
      DATA IDIRPR/'H','I','S','U'/
      DATA IDIRMO/'T','R','L','E','R','O','T','W'/
C  SET UP DIRECTIVE INDEX
      DATA IDIR/'M','O','S','E','L','E','A','R','T','E','C','O'
     1,1HN,1HU,'S','A','T','I','P','R','S','T','R','U','E','T','T'
     2,'O','B','O','V','O','R','O','I','N','W','S','A','C','E','N'
     3,'N','S','G','O','C','M','W','A','O','U','F','I','V','A','M','I'
     4,'A','D','P','S','R','A','T','W','Z','L','V','L','V','T','C','T'/
C  INITIALISE VARIABLES
      MODLTR=0.
      MODLLE=0.
      MODLRO=0.
      MODLTW=0.
      RATIOL=1.
      TOPFLW=0.
      PSISOIL=0.
      BOTFLW=0.
      XMIS=-99.
      ITEST=0
      JOUT=0
      NFI=0
      NPRINT=11
      JWS=0
      NDIR=37
      INPUT=5
      IOUT=6
      NO=99
      INDETA=0
      INDPR=6
      TEMP=20
      NWS=0
      INDREM=0
      IPCENT=1
      NPCENT=1
      XPCENT(1)=95.
      TIMTOT=0.
      ROOTR=0.
      TWIGR=0.
      ZLEAFR=0.
C  READ A CARD
5     READ(INPUT,1000)ICARD
1000  FORMAT(80A1)
6     IF(ICARD(1).NE.ISTAR.OR.ICARD(2).NE.ISTAR)GO TO 5
      CALL EXTRAC(ICARD,INAME,3,IND,2)
      CALL COMPAR(INAME,IDIR,IND,NDIR,2)
      IF(IND.GT.0)GO TO 10
      WRITE(IOUT,1010)ICARD
1010  FORMAT(' FAULT FOUND IN DIRECTIVE',/,' ',80A1)
      GO TO 5
10    CONTINUE
```

```
      GO TO(15,20,25,30,35,40,45,50,55,60,70,100,75,80,85,90,95,96,2000,
     A97,98,99,103,91,92,2010,2040,2020,2030,2050,2060,2070,2080,
     !2090,2100,2110,2120),IND
C  DIRECTIVE IS MODEL
15    READ(INPUT,1000)ICARD
      J=1
      DO 16 I=1,4
      CALL EXTRAC(ICARD,INAME,J,IPOS,6)
      IF(IPOS.EQ.-1)GO TO 5
      CALL COMPAR(INAME,IDIRMO,IND,4,2)
      IF(IND.EQ.-1)GO TO 17
      GO TO (11,12,13,14),IND
11    MODLTR=1
      GO TO 16
12    MODLLE=1
      GO TO 16
13    MODLRO=1
      GO TO 16
14    MODLTW=1
      IF(IPOS.GE.80)GO TO 5
16    CONTINUE
      GO TO 5
17    WRITE(IOUT,1020)ICARD
1020  FORMAT(' ERROR IN MODEL DIRECTIVE',/,' ',80A1)
      GO TO 5
C  DIRECTIVE IS SEGMENTS
20    READ(INPUT,1000)ICARD
      CALL ZRD(Y,ICARD,0,IND)
      NO=Y
      GO TO 5
C  DIRECTIVE IS LENGTH
25    READ(INPUT,1000)ICARD
      CALL ZRD(Z,ICARD,0,IND)
      GO TO 5
C  DIRECTIVE IS AREA
30    READ(INPUT,1000)ICARD
      CALL ZRD(AREA,ICARD,0,IND)
      GOTO 5
C  DIRECTIVE IS TEMPERATURE
35    READ(INPUT,1000)ICARD
      CALL ZRD(TEMP,ICARD,0,IND)
      GO TO 5
C  DIRECTIVE IS CONSTANTS
40    READ(INPUT,1000)ICARD
      J=0
      DO 42 I=1,5
42    CALL ZRD(CONS(I),ICARD,J,IND)
      GO TO 5
C  DIRECTIVE IS NUMBER OF TIMES
45    READ(INPUT,1000)ICARD
      CALL ZRD(Y,ICARD,0,IND)
      ITIMES=Y
      GO TO 5
C   DIRECTIVE IS SATURATED PERMEABILITY
50    READ(INPUT,1000)ICARD
      CALL ZRD(SATK,ICARD,0,IND)
```

```
      GO TO 5
C  DIRECTIVE IS TIME
55    READ(INPUT,1000)ICARD
      CALL ZRD(TIME,ICARD,0,IND)
      GO TO 5
C  DIRECTIVE IS PRINT
60    J=1
      INDPR=1
      DO 62 I=1,2
      READ(INPUT,1000)ICARD
      IF(ICARD(1).EQ.ISTAR.AND.ICARD(2).EQ.ISTAR)GO TO 6
      CALL EXTRAC(ICARD,INAME,J,IPOS,6)
      IF(IPOS.EQ.-1)GO TO 5
      CALL COMPAR(INAME,IDIRPR,IND,2,2)
      IF(IND.EQ.-1)GO TO 63
      IF(IND.GT.1)GO TO 64
67    CALL ZRD(Y,ICARD,J,IND)
      IF(IND.NE.-1)GO TO 68
      IPOS=IPOS+1
      IF(IPOS.GT.80)GO TO 63
      GO TO 67
68    NPRINT=Y
      GO TO 61
64    NPCENT=0
65    CALL ZRD(Y,ICARD,IPOS,IND)
      IF(IND.EQ.-1)GO TO 66
      NPCENT=NPCENT+1
      XPCENT(NPCENT)=Y
      GO TO 65
66    IF(NPCENT.EQ.0)NPCENT=1
61    INDPR=INDPR*(IND+1)
62    CONTINUE
      GO TO5
63    WRITE(IOUT,1030)ICARD
1030  FORMAT(' ERROR IN PRINT DIRECTIVE',/,' ',80A1)
      GOT O5
C  DIRECTIVE IS STOP
70    STOP
C  DIRECTIVE IS ETA
75    READ(INPUT,1000)ICARD
      CALL ZRD(ETA,ICARD,0,IND)
      INDETA=1
      GO TO 5
C   DIRECTIVE IS TOPFLOW
80    READ(INPUT,1000)ICARD
      CALL ZRD(TOPFLW,ICARD,0,IND)
      GO TO5
C  DIRECTIVE IS BOTTOMFLOW
85    READ(INPUT,1000)ICARD
      CALL ZRD(BOTFLW,ICARD,0,IND)
      GO TO 5
C  DIRECTIVE IS VOLUME FRACTION WATER
90    READ(INPUT,1000)ICARD
      CALL ZRD(VFW,ICARD,0,IND)
      GO TO 5
C  DIRECTIVE IS COMMENT(** CM)
```

```
91    READ(INPUT,1000)ICARD
      WRITE(IOUT,1031)ICARD
1031  FORMAT('1',80A1)
      GO TO 5
C  DIRECTIVE IS WATER REMOVE
92    READ(INPUT,1000)ICARD
      CALL ZRD(REMOVE,ICARD,0,IND)
      INDREM=1
      GO TO 5
C   DIRECTIVE IS ROOT RESISTANCE
95    READ(INPUT,1000)ICARD
      CALL ZRD(ROOTR,ICARD,0,IND)
      GO TO 5
C   DIRECTIVE IS INITIALISE
96    GO TO 100
C   DIRECTIVE IS ACCURACY
97    READ(INPUT,1000)ICARD
      CALL ZRD(ACCUR,ICARD,0,IND)
      GO TO 5
C   DIRECTIVE IS ENTRY
98    READ(INPUT,1000)ICARD
      CALL ZRD(Y,ICARD,0,IND)
      INPUT=Y
      GO TO 5
C  DIRECTIVE IS NSTEMS
99    READ(INPUT,1000)ICARD
      CALL ZRD(Y,ICARD,0,IND)
      ISTEMS=Y
      GO TO 5
C  DIRECTIVE IS WEATHER STATION
2000  READ(INPUT,1000)ICARD
      NWS=1
2001  I=0
      DO 2002 J=1,6
2002  CALL ZRD(WS(J,NWS),ICARD,I,IND)
      READ(INPUT,1000)ICARD
      IF(ICARD(1).EQ.ISTAR.AND.ICARD(2).EQ.ISTAR)GO TO 6
      NWS=NWS+1
      GO TO 2001
C   DIRECTIVE IS OUTPUT TO FILE
2010  READ(INPUT,1000)ICARD
      CALL ZRD(Y,ICARD,0,IND)
      IOUT=Y
      GO TO 5
C  DIRECTIVE IS TEST
2020  ITEST=1
      GO TO 5
C  DIRECTIVE IS MISSING
2030  READ(INPUT,1000)ICARD
      CALL ZRD(Y,ICARD,0,IND)
      XMIS=Y
      GO TO 5
C  DIRECTIVE IS FIELD DATA
2040  READ(INPUT,1000)ICARD
      NFI=1
2041  I=0
```

```
      DO 2042 J=1,5
2042  CALL ZRD(FIELD(J,NFI),ICARD,I,IND)
      READ(INPUT,1000)ICARD
      IF(ICARD(1).EQ.ISTAR.AND.ICARD(2).EQ.ISTAR)GO TO 6
      NFI=NFI+1
      GO TO 2041
C  DIRECTIVE IS ADD TIME
2050  READ(INPUT,1000)ICARD
      CALL ZRD(TIMTOT,ICARD,0,IND)
      GO TO 5
C  DIRECTIVE IS PSISOIL
2060  READ(INPUT,1000)ICARD
      CALL ZRD(PSISOIL,ICARD,0,IND)
      GO TO 5
C   DIRECTIVE IS RATIO LEAF
2070  READ(INPUT,1000)ICARD
      CALL ZRD(RATIOL,ICARD,0,IND)
      GO TO 5
C  DIRECTIVE IS TWIG RESISTANCE
2080  READ(INPUT,1000)ICARD
      CALLZRD(TWIGR,ICARD,0,IND)
      GOTO5
C  DIRECTIVE IS LEAF RESOSTANCE AS A PROPORT'T OF TTL RESIS
2090  READ(INPUT,1000)ICARD
      CALL ZRD(ZLEAFR,ICARD,0,IND)
      GOTO5
C  DIRECTIVE IS VOLUME OF LEAF IN M CUBED
2100  READ(INPUT,1000)ICARD
      CALLZRD(VLEAF,ICARD,0,IND)
      GOTO5
C  DIRECTIVE IS VOLUME OF TWIG IN M CUBED
2110  READ(INPUT,1000)ICARD
      CALL ZRD(VTWIG,ICARD,0,IND)
      GOTO5
C  DIRECTIVE IS CONSTANTS AT TOP
2120  READ(INPUT,1000)ICARD
      J=0
      DO 2125I=1,4
2125  CALL ZRD(CTOP(I),ICARD,J,IND)
      GOTO5
100   CONTINUE
C  SET CONSTANTS FOR TRUNK MODEL
      IPCENT=1
      M=NO+1
      Q(M)=BOTFLW
      SATC=SATK*0.000000000001
      DELTAZ=Z/NO
C  INITIALISE THETA AND PSI TO VALUES IMPOSED BY GRAVITY
      DO 102 I=1,NO
      Q(I)=0.
      H(I)=Z-(I-1)*DELTAZ
      PSI(I)=-9819*H(I)
102   THETA(I)=(1.-VFW)*(EXP((PSI(I)-CONS(3))/CONS(4))+CONS(5))
      TRNKRA=ETA*Z/(AREA*SATC)
      RWC=1.+PSI(1)/CTOP(1)
      PSILF=PSI(1)
```

```
      THETW=THETA(1)
      PSITW=-9819.*H(1)
      THETA(M)=THETA(NO)
      PSI(M)=PSISOIL
      CALL OUTPUT(0,TIME,NO,PSI,SATC,CONS,THETA,VFW,Q,H,IOUT)
C  COMPUTE ETA IF NOT GIVEN
      IF(INDETA.EQ.0)ETA=VISCOS(TEMP)
C   USE APPROPRIATE MODEL:
C  MODLTR=1  FOR TRUNK
C  MODLTW=1  FOR TWIG
C  MODLLE=1 FOR LEAF
C  MODLRO=1 FOR ROOT
      JFI=1
      IJ=0
      I=0
      JPCENT=1
      TRUNKR=1.-ROOTR-TWIGR-ZLEAFR
      XXLFRA=TRNKRA*ZLEAFR/TRUNKR
      XXTWRA=TRNKRA*TWIGR/TRUNKR
      XXRTRA=TRNKRA*ROOTR/TRUNKR
C  INITIALISE ABSOL VALS OF RESISTANCES TO SAT.
      ZEAFRA=XXLFRA
      TWIGRA=XXTWRA
      ROOTRA=XXRTRA
      FLOWTL=0.
      SEGFLW=0.
103   IF(MODLLE.EQ.0)GO TO 114
112   JWS=1
      JPCENT=1
113   CALL PENMON(TOPFLW,WS,JWS,ISTEMS,D,RN)
      I=1
      TOPFLW=TOPFLW*RATIOL
      CALL LEAF(SATC,CONS,THETA,VFW,PSI,TOPFLW,ETA,Z,
     !TWIGR,AREA,TRUNKR,PSILF)
      WPL=PSILF/100000.
      WPTW=PSITW/100000.
      WPRT=PSI(NO)/100000.
      RTOTAL=ROOTRA+TRNKRA+TWIGRA+ZEAFRA
      RRT=ROOTRA/RTOTAL
      RTR=TRNKRA/RTOTAL
      RTW=TWIGRA/RTOTAL
      RLF=ZEAFRA/RTOTAL
      QLF=TOPFLW*3600000.
      QTWLF=FLOWTL*3600000.
      QTRTW=SEGFLW*3600000.
      QRTTR=Q(NO)*3600000.
      QSLRT=Q(NO)*3600000.
      HOURS=(IJ-1.)/60.
      QTR5=Q(5)*3600000.
      WP1=PSI(1)/100000.
      WP5=PSI(5)/100000.
      WP10=PSI(10)/100000.
      THTW=THETW/(1.-VFW)
      T1=THETA(1)/(1.-VFW)
      T5=THETA(5)/(1.-VFW)
      T10=THETA(10)/(1.-VFW)
```

```
      WRITE(7,1078)HOURS,QLF,QTWLF,QTRTW,QTR5,QSLRT,RWC,THTW,T1,T5,T10,
     !WPL,WPTW,WP1,WP5,WP10,RLF,RTW,RTR,RN,D
1078  FORMAT(F5.1,5(1X,F5.2),5(1X,F5.3),5(1X,F6.2),3(1X,F5.3)1X,
     !F6.0,1X,F6.2)
      WRITE(IOUT,1080)WPL,WPTW,WPRT,RWC,THETW,THETA(NO),
     !ZEAFRA,TWIGRA,TRNKRA,ROOTRA,RLF,RTW,RTR,RRT,
     !QLF,QTWLF,QTRTW,QRTTR,QSLRT
1080  FORMAT(1X,/,/,29X,'LEAF',8X,'TWIG',8X,'STEM',8X,'ROOT',
     !/,' WATER POTENTIAL (BAR)',1X,F10.3,2X,F10.3,10X,'- ',2X,F10.3,/,
     !' WATER CONTENT (VF)   ',1X,F10.3,'* ',F10.3,10X,'-',3X,F10.3,/,
     !' RESISTANCE (NSM-5)  ',4(2X,E10.3),/,
     !' RATIO OF RESISTANCES',4(2X,F10.3),/,
     !' FLOW RATE (L/HR)',4X,F7.3,4('<----',F6.3),/,
     !10X,'* AS RWC, NOT VOLUME FRACTION',/,/)
      WRITE(8,1081)HOURS,ZEAFRA,TWIGRA,TRNKRA,ROOTRA,
     !RTOTAL,RLF,RTW,RTR,RRT
1081  FORMAT(F5.1,5(1X,E10.3),4(1X,F8.3))
114   IF(MODLTW.EQ.0)GO TO 108
      CALL TWIG(RWC,PSILF,TOPFLW,
     !CTOP,VLEAF,VTWIG,THETW,Q,SEGFLW,CONS,PSI
     !,TIME,PSITW,FLOWTL,VFW,XXLFRA,XXTWRA,TWIGRA,ZEAFRA)
108   IF(MODLTW.EQ.0)SEGFLW=TOPFLW

      IF(MODLTR.EQ.0)GO TO 111
      IF(INDREM.EQ.0)GO TO 105
      TIME=AREA*DELTAZ*(1.-VFW)*REMOVE/TOPFLW
      IF(AREA*DELTAZ.GT.VLEAF)TIME=VLEAF*0.800*REMOVE/TOPFLW
      IF(AREA*DELTAZ.GT.VTWIG)TIME=VTWIG*(1.-VFW)*REMOVE/TOPFLW
105   CALL TRUNK(NO,M,SATC,VFW,AREA,DELTAZ,ETA,CONS,Q,THETA
     1,TIME,PSI,SEGFLW,H,MODLRO,PSISOIL,TRNKRA)
      IF(MODLRO.EQ.0)GO TO 109
111   CALL ROOT(NO,Q,PSI,DELTAZ,SATC,AREA,ETA,Z,VFW,
     1TIME,THETA,CONS,XXRTRA,ROOTRA)
109   THETA(M)=THETA(NO)
      IJ=IJ+1
      TIMTOT=TIMTOT+TIME/3600.
      IF(INDPR.EQ.3)GO TO 3020
C    TEST FOR HISTORY PRINT
      I=I+1
      IF(I.LE.NPRINT)GO TO 3010
      CALL OUTPUT(IJ,TIME,NO,PSI,SATC,CONS,THETA,VFW,Q,H,IOUT)
      I=0
3010  IF(INDPR.EQ.2)GO TO 3040
C    TEST FOR SUMMARY PRINT
3020  IF(JPCENT.GT.NPCENT)GO TO 3040
      RATIO=Q(NO)*100./Q(1)
      IF(RATIO.LT.XPCENT(JPCENT))GO TO 3040
      WRITE(IOUT,3030)
3030  FORMAT(' ////** * SUMMARY ***')
      CALL OUTPUT(IJ,TIME,NO,PSI,SATC,CONS,THETA,VFW,Q,H,IOUT)
      JPCENT=JPCENT+1
C    TEST FOR FIELD DATA
3040  IF(NFI.EQ.0.OR.JFI.GT.NFI)GO TO 3065
      IF(TIMTOT.LT.FIELD(1,JFI))GO TO 3065
3045  DO 3050 L=1,NO
      IF(H(L).LT.FIELD(2,JFI))GO TO 3060
```

```
3050   CONTINUE
3060   FIELD(6,JFI)=PSI(L)/100000.
       FIELD(7,JFI)=THETA(L)
       FIELD(8,JFI)=Q(L)*3600000.
       JFI=JFI+1
       IF(JFI.GT.NFI)GO TO 3065
C    CHECK IF MORE THAN ONE MEASUREMENT AT SAME TIME
       IF(JFI.EQ.1)GO TO 3065
       JJFI=JFI-1
       IF(FIELD(1,JJFI).NE.FIELD(1,JFI))GO TO 3045
3065   IF(IJ.GE.ITIMES)GO TO 4000
C    TEST FOR W.S.
       IF(NWS.EQ.0)GO TO 103
       IF(TIMTOT.LT.WS(1,JWS))GO TO 114
       JWS=JWS+1
       WRITE(IOUT,3070)
3070   FORMAT(//,' ** * COMPLETED W.S. ITERATION ***')
       CALL OUTPUT(IJ,TIME,NO,PSI,SATC,CONS,THETA,VFW,Q,H,IOUT)
       IF(JWS.GT.NWS)GO TO 4000
       GO TO 113
C   ALL ITERATIONS COMPLETE PERFORM STATS AND PLOT IF REQD
4000   IF(NFI.EQ.0)GO TO 5
       IF(ITEST.EQ.0)GO TO 5
       CALL STATS(FIELD,NFI,RES,SUMSQ,XMIS,IOUT)
       GO TO 5
110    WRITE(IOUT,1070)
1070   FORMAT(' MODEL NOT AVAILABLE')
       GO TO 5
       END



       SUBROUTINE PENMON(TOPFLW,WS,JWS,ISTEMS,D,RN)
       DIMENSION WS(6,100)
       RN=WS(2,JWS)
       TA=WS(3,JWS)
       TD=WS(4,JWS)
       U=WS(5,JWS)
       RC=WS(6,JWS)
       TW=TA-TD
       EA=6.1078*EXP(17.269*TW/(TW+237.3))-TD/3.
       TTA=TA+237.3
       TEXP=EXP(17.269*TA/TTA)
       D=6.1078*TEXP-EA
       SLOPE=25029.4/(TTA*TTA)*TEXP
       RHO=1.292-.00428*TA
       SPHT=1013
       GAMMA=0.646+0.006*TA
       U=U*ALOG(4.)/ALOG((12.-10.*0.76)/(0.06*10.))
       RA=10./U
       XLAT=(2.501-0.002*TA)*1000000.
       ENERGY=(SLOPE*RN+RHO*SPHT*D/RA)/(SLOPE+GAMMA*(1.+RC/RA))
       EFLUX=ENERGY/XLAT
       TOPFLW=EFLUX*10./ISTEMS
       WRITE(6,100)D,TA,RN
100    FORMAT('1',' DEF= ',F10.3,' TEMP= ',F10.3,' RAD= ',F10.3)
```

```
      RETURN
      END
      SUBROUTINE LEAF(SATC,CONS,THETA,VFW,PSI,TOPFLW,ETA,Z,TWIGR,
     !AREA,TRUNKR,PSILF)
      DIMENSION THETA(100),PSI(100),CONS(5)
      GOTO88
      AKK=SATC*CONS(2)*EXP(CONS(1)*THETA(1)/(1.-VFW))
      PSILF=(PSI(1)-TOPFLW*ETA*Z*TWIGR/
     !(AKK*AREA*3600000.*TRUNKR))/100000.
88    CONTINUE
      RETURN
      END




      SUBROUTINE TWIG(RWC,PSILF,TOPFLW,CTOP,
     !VLEAF,VTWIG,THETW,Q,SEGFLW,CONS,PSI
     !,TIME,PSITW,FLOWTL,VFW,XXLFRA,XXTWRA,TWIGRA,ZEAFRA)
      DIMENSION CTOP(4),Q(100),CONS(5),PSI(100)
      ZEAFRA=XXLFRA
      SATK=1./XXTWRA
      SATK=SATK*CONS(2)*EXP(THETW*CONS(1)/(1.-VFW))
      TWIGRA=1./SATK
      RWC=(VLEAF*RWC-TIME*(TOPFLW-FLOWTL))/VLEAF
      PSILF=(RWC-1.)*CTOP(1)
      FLOWTL=(PSITW-PSILF)/ZEAFRA
      WRITE(9,887)PSILF,PSITW,FLOWTL,ZEAFRA
887   FORMAT(E10.3,1X,E10.3,1X,E10.3,1X,E10.3)
      THETW=(VTWIG*THETW-TIME*(FLOWTL-SEGFLW))/VTWIG
      BRAK=THETW/(1.-VFW)-CTOP(4)
      IF(BRAK.LE.0.)BRAK=0.00001
      PSITW=CTOP(3)*ALOG(BRAK)+CTOP(2)
      SEGFLW=(PSI(1)-PSITW)/TWIGRA
C        XPLF=PSILF/100000.
C        XPTW=PSITW/100000.
C        FLTOP=TOPFLW*3600000.
C        FTWLF=FLOWTL*3600000.
C        FSEG=SEGFLW*3600000.
C        XPST=PSI(1)/100000.
C        WRITE(8,888)RWC,THETW,XPLF,XPTW,XPST,FLTOP,FTWLF,FSEG
C  888   FORMAT(8(3X,F8.3))
      RETURN
      END
      SUBROUTINE TRUNK(N,M,SATC,VFW,AREA,DELTAZ,ETA,CONS,Q,THETA,TIME
     1,PSI,SEGFLW,H,MODLRO,PSISOIL,TRNKRA)
      DIMENSION Q(M),THETA(M),CONS(5),PSI(M),H(N)
C
C  THE TRUNK MODRLO
C
C        WRITE(8,7)SEGFLW
C  7     FORMAT(E10.3)
      THTMX=1.-VFW
      CONST=TIME/(AREA*DELTAZ*THTMX)
      CVFW=CONS(5)*THTMX
      THTMX=1.-VFW
```

```
      TRNKRA=0.
      DO 20 J=1,N
      IF(J.NE.1)GO TO 5
      THETA(1)=THETA(1)-SEGFLW*CONST
      GO TO 6
5     THETA(J)=THETA(J)-Q(J-1)*CONST
6     BRAK=THETA(J)/(1.-VFW)-CONS(5)
      IF(BRAK.LE.0)BRAK=0.000001
      PSI(J)=ALOG(BRAK)*CONS(4)+CONS(3)
      IF(MODLRO.EQ.1.AND.J.EQ.N)GO TO 600
      DYDZ=(PSI(J+1)-PSI(J))/DELTAZ-9819.
      Q(J)=DYDZ*AREA*SATC*CONS(2)*EXP(CONS(1)*(THETA(J)+THETA(J+1))/(2.*
     1(1.-VFW)))/ETA
      THETA(J)=THETA(J)+Q(J)*CONST
C  NOW LIMIT THETA TO THETAMAX
      IF(THETA(J).GT.THTMX)THETA(J)=THTMX
C
C  DARCYS LAW
C
      BRAK=THETA(J)/(1.-VFW)-CONS(5)
      IF(BRAK.LE.0)BRAK=0.000001
      PSI(J)=ALOG(BRAK)*CONS(4)+CONS(3)
      TRNKRA=TRNKRA+DYDZ*DELTAZ/Q(J)
20    CONTINUE
600   THETA(M)=THETA(N)
      PSI(M)=PSISOIL
      RETURN
      END
      SUBROUTINE ROOT(NO,Q,PSI,DELTAZ,SATC,AREA,ETA,Z,VFW,
     1TIME,THETA,CONS,XXRTRA,ROOTRA)
C  NOTE THAT ROOT RESIS IS EXPRESSED AS A FUNCTION
C   OF THE WATER CONTENT OF THE BOTTOM SEGMENT.
C   FORTE AS OB9
      DIMENSION Q(100),PSI(100),THETA(100),CONS(5)
      SATK=1./XXRTRA
      SATK=SATK*CONS(2)*EXP(CONS(1)*THETA(NO)/(1.-VFW))
      ROOTRA=1./SATK
      Q(NO)=(PSI(NO+1)-PSI(NO)-9819.*DEL
     ! TAZ)/ROOTRA
      THETA(NO)=THETA(NO)+Q(NO)*TIME/(AREA*DELTAZ*(1.-VFW))
      PSI(NO)=CONS(3)+CONS(4)*(ALOG(THETA(NO)/(1.-VFW)-CONS(5)))
      RETURN
      END
      SUBROUTINE COMPAR(ICHARS,IARAY,IND,NCOMP,NCHARS)
C
C  TO COMPARE CHARS IND IS LOCATION IN ARRAY OF MATCH
C
      DIMENSION ICHARS(NCHARS),IARAY(NCHARS,NCOMP)
      DO 10 I=1,NCOMP
      DO 5 J=1,NCHARS
      IF(ICHARS(J).NE.IARAY(J,I))GO TO 10
5     CONTINUE
      GO TO 15
10    CONTINUE
      IND=-1
      GO TO 20
```

```
15    IND=I
20    CONTINUE
      END
      SUBROUTINE EXTRAC(ICARD,INAME,I,IND,NCHARS)
C
C  TO EXTRACT THE NAME OF A VARIABLE FROM ICARD STARTING
C  AT COLUMN I
C
      DIMENSION ICARD(80),INAME(NCHARS)
      DATA IBLANK/' '/,ICOMMA/','/
C
      N=0
      IND=0
      DO 5 J=1,NCHARS
5     INAME(J)=IBLANK
      K=I
      IF(ICARD(I).EQ.ICOMMA)K=K+1
6     IF(ICARD(I).NE.IBLANK)GO TO 7
      I=I+1
      K=K+1
      IF(I.GT.80)GO TO 16
      GO TO 6
7     L=K+NCHARS-1
      IF(L.GT.80)L=80
      DO 10 J=K,L
      IF(ICARD(J).EQ.IBLANK)GO TO 15
      IF(ICARD(J).EQ.ICOMMA)GO TO15
      N=N+1
      INAME(N)=ICARD(J)
10    CONTINUE
15    I=J
16    IND=1
      IF(N.EQ.0)IND=-1
      I=J
      RETURN
      END
      SUBROUTINE IDIG(I,J)
      DIMENSION IA(10)
      DATA IA(1),IA(2),IA(3),IA(4),IA(5)/1H0,1H1,1H2,1H3,1H4/
      DATA IA(6),IA(7),IA(8),IA(9),IA(10),IDEC/1H5,1H6,1H7,1H8,1H9,1H./
      J=10
      DO 10 K=1,10
      IF(I.NE.IA(K))GO TO 10
      J=K-1
      RETURN
10    CONTINUE
      IF(I.EQ.IDEC)J=-1
      RETURN
      END
      SUBROUTINE IDIG(I,J)
      DIMENSION IA(10)
      DATA IA(1),IA(2),IA(3),IA(4),IA(5)/1H0,1H1,1H2,1H3,1H4/
      DATA IA(6),IA(7),IA(8),IA(9),IA(10),IDEC/1H5,1H6,1H7,1H8,1H9,1H./
      J=10
      DO 10 K=1,10
      IF(I.NE.IA(K))GO TO 10
```

```
      J=K-1
      RETURN
 10   CONTINUE
      IF(I.EQ.IDEC)J=-1
      RETURN
      END
      SUBROUTINE OUTPUT(IJ,TIME,NO,PSI,SATC,CONS,THETA,VFW,Q,H,IOUT)
      DIMENSION  PSI(100),CONS(5),THETA(100),Q(100),H(100),AK(100)
 107  WRITE(IOUT,1040)IJ,TIME
      DO 106 II=1,NO
      PSI1=PSI(II)/100000.
      AK(II)=SATC*CONS(2)*EXP(CONS(1)*(THETA(II)+THETA(II+1))/(2.*(1.-VF
     1W)))*1000000000000.
      QQQ=Q(II)*3600000.
 106  WRITE(IOUT,1050)H(II),PSI1,THETA(II),QQQ,AK(II)
 1040 FORMAT(//' ITERATION NO',I4,' TIME STEP',F10.0,' SECONDS'
     1/' HEIGHT ABOVE',5X,'WATER',10X,'VOLUME',12X,'FLOW',5X,
     1'PERMEABILITY',/,' ABOVE',8X,'POTENTIAL',8X,'FRACTION',12X,'RATE'
     2,8X,'X 10E-2',
     2/,' BASE(M)',10X,'(BAR)',8X,'OF WATER',8X,'(L/HOUR)',9X,'(M**
2)')
 1050 FORMAT(F7.3,6X,2(F10.3,6X),E12.3,4X,F8.4)
      RETURN
      END
      SUBROUTINE STATS(FIELD,NFI,RES,SUMSQ,XMIS,IOUT)
      DIMENSION FIELD(8,100),RES(3,100),SUMSQ(2,3)
      WRITE(IOUT,1001)
 1001 FORMAT('1 HOUR HEIGHT',20X,'PSI',35X,'THETA',34X,'FLOW',
     1/,12X,3(7X,'MEASURED',3X,'PREDICTED',3X,'RESIDUALS'))
      DO 20 I=1,NFI
       DO 10 J=1,3
      K=J+2
      L=J+5
      RES(J,I)=FIELD(K,I)-FIELD(L,I)
      IF(FIELD(K,I).EQ.XMIS)RES(I,J)=XMIS
 10   CONTINUE
      WRITE(IOUT,1000)FIELD(1,I),FIELD(2,I),FIELD(3,I),FIELD(6,I),
     1RES(1,I),FIELD(4,I),FIELD(7,I),RES(2,I),FIELD(5,I),FIELD(8,I)
     2,RES(3,I)
 1000 FORMAT(2F6.2,2(3F12.3,' ! '),3F12.3)
 20   CONTINUE
      RETURN
      END
      FUNCTION VISCOS(TEMP)
      T=TEMP-20
      IF(TEMP.GT.20)GO TO 10
      BRAK=(0.00585*T+8.1855)*T+998.333
      BRAK=1301/BRAK-1.30233
      VISCOS=10.** BRAK
      RETURN
 10   BRAK=(-0.001053*T-1.3272)*T/(TEMP+105.)
      CONS=(0.00585*20.+8.1855)*20.+998.333
      CONS=1301./CONS-1.30233
      CONS=10.** CONS
      VISCOS=CONS*10.** BRAK
      RETURN
```

```
      END
      SUBROUTINE ZRD(Y,IBF,KT,IND)
C   TO READ A REAL NUMBER
      DOUBLE PRECISION X,X1,X2,TEN,A
      DATA XFL,A,KP/-10.E-20,1D75,75/
      DATA IPLUS,IMIN,ISP,TEN/1H+,1H-,1H ,1D1/
      DIMENSION IBF(80)
      IFIN=80
      IND=1
      ISN=0
      N1=1
      IPT=0
      X1=0
      X2=0
1     IF(KT.GT.IFIN)IND=-1
      KT=KT+1
      L=IBF(KT)
      IF(L.EQ.ISP)GO TO 1
      IF(L.EQ.IPLUS)GO TO 2
      IF(L.EQ.TEN)GO TO 3
      IF(L.EQ.IMIN)GO TO 5
      GO TO 3
5     ISN=1
2     KT=KT+1
      IF(KT.GT.IFIN)GO TO 100
3     CALL IDIG(IBF(KT),J)
      IF(J.GT.9)GO TO 100
      IF(J.LT.0)GO TO 20
      X1=J
4     KT=KT+1
      IF(KT.GT.IFIN)GO TO60
      CALL IDIG(IBF(KT),J)
      IF(J.GT.9)GO TO 60
      IF(J.LT.0)GO TO 30
      N1=N1+1
      IF(N1.GT.KP)GO TO 4
      X1=TEN*X1+J
      GO TO 4
20    IPT=IPT+1
      KT=KT+1
      IF(KT.GT.IFIN)GO TO 100
      CALL IDIG(IBF(KT),J)
      IF(J.GT.9)GO TO 100
      IF(J.LT.0)GO TO 20
      GO TO 40
30    IPT=IPT+1
      KT=KT+1
      IF(KT.GT.IFIN)GO TO 60
      CALL IDIG(IBF(KT),J)
      IF(J.GT.9)GO TO 60
      IF(J.LT.0)GO TO 30
40    I1=KT

      IBF(KT)=J
41    KT=KT+1
      IF(KT.GT.IFIN)GO TO 50
```

```
      CALL IDIG(IBF(KT),J)
      IF(J.GT.9)GO TO 50
      IF(J.LT.0)IPT=IPT+1
      IBF(KT)=J
      GO TO 41
50    I=KT-1
      X2=IBF(I)/TEN
51    IF(I.LE.I1)GO TO 60
      I=I-1
      X2=(X2+IBF(I))/TEN
      GO TO 51
60    IF(IPT.GT.1)GO TO 100
      IF(N1.GT.KP)X1=A
      Y=X1+X2
      IF(ISN.NE.0)Y=-Y
      KT=KT-1
      RETURN
100   Y=XFL
      KT=KT-1
      RETURN
      END
FORTE(TREEMAIN,OBJECT)
FORTE(TREECOMPAR,OB11)
FORTE(TREEEXTRAC,OB4)
FORTE(TREEIDIG,OB5)
FORTE(TREEPLOT,OB10)
FORTE(TREEOUTPUT,OB2)
FORTE(TREEPENMON,OB3)
FORTE(TREEROOT,OB9)
FORTE(TREESTATS,OB1)
FORTE(TREETRUNK,OB7)
FORTE(TREEVISCOS,OB6)
FORTE(TREEZRD,OB8)
FORTE(TREELEAF,OB12)
FORTE(TREETWIG,OB13)
```

APPENDIX 2

Programme to Calculate Water Contents from Gamma Attenuation

```
C   DATA INPUT:
C   **** *****
CFIRSTLY, PUT IN A 3-FIGURE NAME.
C  THEN   RAD'N THROUGH AIR,FOLLOWED BY RAD'N
C   THROUGH 1,2,3,4   5.0-CM BLOCKS OF PERSPEX.
CTHEN THE TREE DIAMETER, IN CM.
C   THEN THE LENGTH OF EACH CHORD, 1 CM APART AND
C STARTING FROM THE OUTSIDE, IN CM.
C  THENTHE RAD'N LEVELS THROUGH EACH CHORD, IN THE
C         SAME ORDER.
CIF AVAILABLE, PUT THE VOLUME FRACTIONS WOODY MATERIAL OF
C     SUCCESSIVE 1 CM TORI. IF NOT, PUT 999.
C   THEN, AFTER THE VFWD'S, IF 999 IS ENTERED, WE HAVE
C            TERMINATION.
C  IF 998,PUT IN A NEW SET OF CALIBRATION FIGURES
C  AND THE DIAMETER, BUT NOT THE CHORD LENGTHS
C   OR THE DENSITIES  - JUST THE NEW RAD'N
C      MEASUREMENTS.
C   IF 997 IS ENTERED INSTEAD OF 998,THEN
C    JUST ENTER NEW SETS OF RAD'N FIGURES  - NO
C      CALIBRATION OR DIAMETER.
C   ALL FIGURES ON A NEW LINE EACH.
      DIMENSIONA(50,50)
      DIMENSIONB(50,50)
      DIMENSIONC(50,50)
      DIMENSIOND(50,50)
      DIMENSIONE(50,50)
      DIMENSIONDTA(50,20)
      IAGAIN=0.
10    IF(IAGAIN.NE.0)GOTO15
      DO1I=1,50
      DO1J=1,50
      A(I,J)=0.
      B(I,J)=0.
      C(I,J)=0.
      D(I,J)=0.
      E(I,J)=0.
1     CONTINUE
      K=0
15    READ(5,*)NAME
      READ(5,2)AX,BX,CX,DX,EX,FX,DIAM
      AR=ALOG(AX/AX)
      BB=ALOG(BX/AX)
      CC=ALOG(CX/AX)
      DD=ALOG(DX/AX)
      EE=ALOG(EX/AX)
      FF=ALOG(FX/AX)
```

```
2     FORMAT(7(F10.2,/))
      SUMY=AR+BB+CC+DD+EE+FF
      AMNY=SUMY/6.
      SPROD=(BB*5.9+CC*11.8+DD*17.7+EE*23.6+FF*29.5)-(SUMY*88.5
     ! )/6.
      SLOPE=SPROD/609.17
      AIR=AX
      INC=DIAM/2.
      R=DIAM/2.
      DO30IA=1,INC
      DO30IC=1,INC
      A(IA,IC)=SQRT(2.*IC*(R-IA)+IC**2.)-
     ! SQRT(2.*(IC-1.)*(R-IA)+(IC-1.)**2.)
30    CONTINUE
      BACKSPACE5
      IF(IAGAIN.EQ.1)GOTO49
      DO40IA=1,INC
      READ(5,48)DTA(IA,2)
48    FORMAT(F4.1)
40    CONTINUE
49    CONTINUE
      DO50IA=1,INC
      READ(5,55)DTA(IA,1)
55    FORMAT(F10.4)
50    CONTINUE
      DO60IA=1,INC
      DTA(IA,4)=2.*SQRT(R**2.-(R-IA)**2.)
      DTA(IA,3)=(ALOG(DTA(IA,1)/AIR)/SLOPE)/DTA(IA,2)
      DTA(IA,5)=AIR*EXP(SLOPE*DTA(IA,3)*DTA(IA,4))
60    CONTINUE
      DTA(1,6)=(ALOG(DTA(1,5)/AIR))/((SLOPE)*2.*A(1,1))
      DTA(1,7)=DTA(1,6)*2.*A(1,1)
      DO70IX=2,INC
      IXX=IX-1.
      B(IX,IXX)=AIR*EXP(SLOPE*DTA(1,6)*A(IX,IX))
      C(IX,IXX)=DTA(IX,5)/EXP(SLOPE*DTA(1,6)*A(IX,IX))
      D(IX,IX)=ALOG(B(IX,IXX)/AIR)/(SLOPE)
      E(IX,IX)=ALOG(DTA(IX,5)/C(IX,IXX))/(SLOPE)
      DTA(1,15)=SQRT((1./AIR)+(1./DTA(1,5)))
70    CONTINUE
      DO80IN=2,INC
      DTA(IN,7)=ALOG(C(IN,1)/B(IN,1))/(SLOPE)
      DTA(IN,15)=SQRT((1./C(IN,1))+(1./B(IN,1)))
      DTA(IN,6)=DTA(IN,7)/(2.*A(IN,1))
      N=0.
      NN=1.
      INCC=INC-1
      INCCC=INC-2
      IF(IN.EQ.INC)GOTO80
      DO90IM=IN,INCC
      IMM=IM+1
      N=N+1.
      NN=NN+1.
      D(IMM,NN)=DTA(IN,6)*A(IMM,NN)
      E(IMM,NN)=DTA(IN,6)*A(IMM,NN)
      B(IMM,N)=B(IMM,NN)*EXP(SLOPE*D(IMM,NN))
```

```
      C(IMM,N)=C(IMM,NN)/EXP(SLOPE*E(IMM,NN))
90    CONTINUE
80    CONTINUE
      WRITE(6,120)NAME
120   FORMAT(' ',/,/,/,/,'   READING NUMBER   ',I3,/,
     !'   ********************',/,/,
     !'  INCREMENT        DENSITY OF WET WO',
     ! 'OD    S.D. OF DENSITY')
      DO140I=1,INC
      WRITE(6,130)I,DTA(I,6),DTA(I,15)
130   FORMAT(4X,I2,15X,F10.4,12X,F10.4)
140   CONTINUE
      WRITE(6,145)SLOPE
145   FORMAT(' ','      THE SLOPE OF THE REGRESSION IS',F10.5)
      WRITE(6,147)
147   FORMAT(' ','      ******************************************',)
      IF(K.EQ.1)GOTO160
      IF(IAGAIN.NE.0)GOTO160
      DO160I=1,INC
      READ(5,150)DTA(I,9)
      DTA(I,9)=DTA(I,9)*1.53
150   FORMAT(F10.5)
      IF(DTA(1,9).EQ.999.)GOTO300
160   CONTINUE
      WRITE(6,170)
170   FORMAT(' ','CM FROM   V.F. OF    ',
     ! 'V.F. OF    V.F.OF  W. CONT',
     ! 'ENT   RELATIVE  ML. WATER',/,
     ! ' CAMBIUM        AIR       WATER',
     ! '        WOOD     (FRESH)  W.CONTENT   IN TORUS')
      RAD=DIAM/2.
      WATER=0.
      DO180I=1,INC
      DTA(I,10)=DTA(I,9)/1.53
      DTA(I,11)=DTA(I,6)-DTA(I,9)
      DTA(I,12)=1.-(DTA(I,10)+DTA(I,11))
      DTA(I,13)=(DTA(I,11)*100.)/(DTA(I,11)+DTA(I,9))
      DTA(I,14)=(DTA(I,11)*100.)/(DTA(I,11)+DTA(I,12))
      DTA(I,16)=3.14159*((RAD-I+1.)**2.
     !-(RAD-I)**2.)*DTA(I,11)
      WATER=WATER+DTA(I,16)
      WRITE(6,190)I,DTA(I,12),DTA(I,11),DTA(I,10),DTA(I,1
     !3),DTA(I,14),DTA(I,16)
190   FORMAT(I2,8X,3(F7.4,4X),2(F7.2,4X),F7.2)
180   CONTINUE
      NNN=INC+1
      DO183I=10,16
      DTA(NNN,I)=0.
183   CONTINUE
      DO185I=2,4
      DTA(NNN,12)=DTA(NNN,12)+DTA(I,12)/3.
      DTA(NNN,11)=DTA(NNN,11)+DTA(I,11)/3.
      DTA(NNN,10)=DTA(NNN,10)+DTA(I,10)/3.
      DTA(NNN,13)=DTA(NNN,13)+DTA(I,13)/3.
      DTA(NNN,14)=DTA(NNN,14)+DTA(I,14)/3.
      DTA(NNN,16)=DTA(NNN,16)+DTA(I,16)
```

```
185    CONTINUE
       WRITE(6,187)DTA(NNN,12),DTA(NNN,11),DTA(NNN,10),DTA(
      !NNN,13),DTA(NNN,14),DTA(NNN,16)
187    FORMAT(' ',/,/,' THE MEAN OF THE 2ND 3DR AND 4TH INCREMENTS IS:',
      !/,10X,3(F7.4,4X),2(F7.2,4X),F7.2)
       WCENTR=3.14159*(RAD-INC)**2.*DTA(I,16)
       WATER=WATER+WCENTR
       WRITE(6,195)WATER
195    FORMAT(' ',/,' THE QUANTITY OF WATER IN A TRUNK DIS',
      !'K 1 CM HIGH IS',F10.2,'  ML',/,'  ',/,' ','*',
      !'**************************',
      ! '*************************',
      !'******************',/,' ',' ',/,' ','  ')
       K=1.
       READ(5,200)X
200    FORMAT(F10.4)
       IF(X.EQ.999.)GOTO300
       IF(X.NE.998.)GOTO250
       IAGAIN=1.0
       GOTO10
250    IF(X.NE.997)GOTO270
       IAGAIN=2
       GOTO49
270    CONTINUE
       BACKSPACE5
       GOTO49
300    STOP
       END
```