Water relations of a pine plantation (*Pinus sylvestris* L.) during drought

by

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Abstract

An investigation of the impact of imposed drought on the physiology of 41 year old Scots pine (*Pinus sylvestris* L.) was made in southern Scotland. Measurements were made of the seasonal course of transpiration, canopy stomatal conductance, needle water potential, xylem water content, soil-to-needle hydraulic resistance, and growth. Two new techniques were developed to aid these measurements: (i) the continuous measurement of bole water potential based on relating the elastic deformation of the xylem to the internal water tension and, (ii) the use of time domain reflectometry with short probes to detect changes in xylem embolism. Comparison was made between droughted plots and those receiving average precipitation. Under drought, transpiration rate declined once a threshold soil water fraction of 0.12 over the top 20 cm of soil had been reached, and transpiration was thereafter a near linear function of soil moisture. As the drought became intense, hydraulic resistance between soil and needles increased by a factor of three as pre-dawn needle water potential declined from -0.54 MPa to -0.71 MPa. A small but significant increase in xylem embolism was detected in year-old shoots. Stomatal control of transpiration prevented needle water potential from declining below -1.5 MPa. Basal area, shoot and needle growth was significantly reduced in the droughted treatment. In the year following the drought, canopy stomatal conductance and soil-to-needle hydraulic resistance recovered. Current year needle extension recovered, but a significant reduction in basal area increment was evident. Multiplicative non-linear regression models for relating the canopy stomatal conductance to environmental variables were developed. It was found that a simple model that included the effects of air vapour pressure deficit and soil moisture deficit could explain 56 % of the measured canopy stomatal conductance. Overall results suggest that in response to soil drought mature Scots pine closes its stomata sufficiently to prevent the development of substantial xylem embolism. The reduced basal area growth in the year after the drought is not likely to be a result of residual embolism from the previously droughted period.

Declaration

This thesis has been composed by myself and the work it describes has been carried out by myself except where specific reference is made to other individuals.

James Irvine

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Table of contents

4. STOMATAL CONTROL OF TRANSPIRATION AND HYDRAULIC CONDUCTANCE 40

5. MODELLING CANOPY STOMATAL CONDUCTANCE 64

1. Introduction

1.1 CONTEXT

Forests occupy about one-third of the terrestrial land surface and play an important role in both the global water and carbon cycles (Schlesinger 1997). In order to understand this role under possible scenarios of global warming, which include predictions of both transient and more extended periods of water deficit (Rind *et al.* 1990, Weatherald and Manabe 1995), a greater knowledge of the physiological and climatological controls of forest water use and growth under drought is required. Water deficits develop when the rate of water loss from a plant tissue is greater than the rate of water supply. This leads to a decline in tissue water potential and a reduction in cell turgor, which if sufficiently large, interferes with the normal functioning of the tissue. The first signs of water stress are the cessation of growth and closure of stomata (Hsiao 1973). However many underlying physiological processes may be affected, ranging from the rates of protein synthesis to the initiation of reproductive development; see reviews by Kozlowski (1968; 1972a; 1976; 1981), Hsiao (1973), Paleg and Aspinall (1981), Kramer (1983), Jones (1992).

Whilst it was recognised that tree growth was correlated with water availability as long ago as the eighteenth century (Zahner 1968), we still do not fully understand the complex links between water deficits, stomatal conductance and plant growth. Stomatal conductance controls virtually all the water transpired by plants as well as the carbon dioxide absorbed in photosynthesis. However, stomatal behaviour during drought appears not to be simply regulated by a water potential signal transmitted from a drying soil by changes in xylem sap tension, but also by a signal that is generated in response to changes in the water content of the soil itself. Recent work has suggested that the latter response may involve the transfer of chemical signal from roots to shoots via the transpiration stream (Davies and Zhang 1991, Khalil and Grace 1993, Tardieu and Davies 1993).

The effects and after-effects of water stress on growth (Sands and Rutter 1959, Jarvis and Jarvis 1963, Kaufmann 1968) and stomatal conductance (Lopushinsky 1969, Blake and Ferrell 1977, Beadle *et al.* 1985a, Gollan *et al.* 1985, Jackson *et al.* 1995a) have been described for many tree species. However, most of these studies were concerned with young potted seedlings, and although it is widely recognised that morphological, physiological and phenological traits differ between seedlings and mature trees (Dougherty 1994), few studies have investigated the influence of drought on the growth of mature forests. In particular the phenomenon that drought in one year appears to have consequences for forest growth in subsequent years (Innes 1993, Spiecker *et al.* 1996) requires further investigation. For example, dendrochronological studies have suggested that the climate over a period of as much as six years was a useful predictor of current year growth in silver fir (*Abies alba* Miller) in the NE of France, and this was put forward as an explanation of the apparent periodic crises of decline in silver fir in this region in the 1980's (Becker 1989). Such studies can provide valuable information on how drought has affected tree growth over extended periods and may be combined with carbon isotope discrimination measurements to provide estimates of transpirational responses to drought conditions (Leavitt 1993, Walcroft *et al.* 1997). However these types of studies cannot provide much insight into the physiological mechanisms that could result in a drought in one year having effects on tree growth in subsequent years. Several possible mechanisms for such 'carry-over' effects may be suggested, but physiologists have not usually been able to study the key processes in mature forests over a sufficiently extended period to explain the true nature of the response to drought. One hypothesis, the key theme for this thesis, concerns the apparent vulnerability of the water transport system to cavitation. This process could result in a reduced capacity of the xylem to transport water from the soil to the foliage with possible long term consequences for tree growth (see below for details).

1.2 BACKGROUND

1.2.1 WATER TRANSPORT IN VASCULAR PLANTS

The cohesion theory for the ascent of sap (Böhm 1893, Dixon and Joly 1895) forms the basis of our current understanding of the mechanism of water transport in the xylem of plants. Evaporation from the mesophyll cell surfaces in the leaves results in the development of considerable surface tension in the water at the air-water interface within the leaf cell walls. As a result of the cohesive forces between water molecules, this tension or negative pressure is transmitted to the continuous columns of water in the xylem, and so provides the force necessary for the movement of water between soil and foliage. This theory is implicit in representations of water fluxes from vegetation, as the soil-vegetation-atmosphere-transfer-scheme (SVATS), which provides a convenient conceptual framework for both physiologists and climatologists (Kozlowski and Pallardy 1997a).

The xylem is composed of vessels or tracheids, the cell walls of which constitute conduits and provide a pathway for flow of water from the roots to the transpiring foliage (Milburn 1979, Zimmermann 1983). The flow of water along this pathway is often described using Ohm's law analogy (Richter 1973), because of the similarity between the flow of water between points of high and low water potential (i.e. the soil and foliage respectively), and the flow of current through an electrical circuit. The water that is drawn through the xylem is in a liquid form at pressures below atmospheric, and is vulnerable to rapid transition to vapour, the process of cavitation.

1.2.2 CAVITATION

Cavitation was first detected in the xylem of plant tissues by Milburn in 1963 using acoustic methods (Milburn and Johnson 1966). Since that date it has been found to occur in all species of vascular plants examined (Borghetti 1993), and so appears to be a more common event than first envisaged (Milburn 1993). Cavitation has been shown to occur both during normal and droughted summer conditions (Sperry *et al.*

1994, Jackson *et al* 1995b, Alder *et al.* 1996) and under conditions of freeze-thaw cycles (Sperry *et al.* 1988, Wang *et al.* 1992, Sperry 1993, Magnani and Borghetti 1995). During freeze-thaw cycles cavitation is thought to occur as a result of bubbles coming out of solution as the sap freezes. The bubbles nucleate cavitation after thawing, when tensions in the water are re-established (Hammel 1967, Zimmermann 1983). During summer conditions it is believed that cavitation occurs by the air-seeding mechanism (Zimmermann 1983), whereby air from outside or from neighbouring tracheids or vessels is drawn into functioning conduits through pits in the conduit walls. Cavitation that occurs as a result of air-seeding is thought by some to take place at a critical water tension, which is species specific (Cochard 1992, Pockman *et al.* 1995). The critical water tension is most likely to be generated under conditions of high evaporative demand and low soil water availability, i.e. circumstances of drought stress.

1.2.3 THE VULNERABLE HYDRAULIC SYSTEM AND STOMATAL CONTROL OF CAVITATION

Cavitation inside the xylem conduits and the subsequent diffusion of air into this void produces an embolism or air blockage through which water can no longer flow, so increasing the hydraulic resistance between the roots and the foliage. The xylem can therefore be viewed as a vulnerable hydraulic system and at risk from loosing the ability to efficiently transport water from soil to foliage.

The rate at which water moves through the xylem is proportional to the water potential difference between soil and foliage and inversely proportional to the hydraulic resistance (Ohm's law). If a plant is to maintain the same rate of transpiration after a number of vessels or tracheids have cavitated, a larger water potential gradient across the increased hydraulic resistance will be required. Any further decrease in the foliage water potential to generate such a gradient would predispose the tree to further cavitation, which would then result in a further decrease in hydraulic resistance and a vicious cycle could develop resulting in catastrophic or 'runaway' cavitation with complete dysfunction of xylem water transport (Tyree and Sperry 1988, Jones and Sutherland 1991). The lack of evidence of widespread tree death because of drought stress suggests that this response is unusual. It is more likely that the rate of transpiration may decline after the development of embolism, thus preventing excessive water tensions developing in the xylem, and minimising the risk of further cavitation. The most efficient way of reducing transpiration in the short term is by stomatal closure. Studies on juvenile plants grown in pots indicate that stomatal closure occurs as a result of a negative feed-forward response due to a chemical or hydraulic signal from the roots (Blake and Ferrell 1977, Davies and Zhang 1991, Khalil and Grace 1993, Tardieu and Davies 1993). The nature of this response in mature trees with extensive root systems remains largely unanswered. In such trees there is likely to be a considerable time lag before a chemical signal generated in the roots reaches the foliage, and the roots of such trees can presumably extract water from great depth in times of drought (Canadell *et al.* 1996).

Stomatal closure will inevitably reduce the rates of assimilation. Consequently if there is no recovery of embolised xylem, or if there is inadequate growth of new xylem to replace the lost water transport capacity, the increased hydraulic resistance may be passed on into subsequent years and perhaps explain why drought in one year may have consequences for growth in the future.

1.2.4 REFILLING OF EMBOLISED XYLEM

Some species, notably angiosperms, generate root pressure in spring and therefore are capable of refilling embolised xylem (Sperry *et al.* 1988, Sperry 1993, Sperry *et al.* 1994). There are few reports of root pressures being generated in gymnosperms (O'Leary and Kramer 1965, Lopushinsky 1980), although refilling has been observed under conditions of very low water tensions (Borgetti *et al.* 1991, Sobrado *et al.* 1992, Edwards *et al.* 1994). Such tensions may occur in small saplings under conditions of no transpiration. However in the canopies of mature trees, such small tensions are unlikely to occur, due to the ever-present gravitational component of water potential. Pre-dawn shoot water potentials in tall coniferous trees, measured with the pressure chamber, are usually in the range of -0.3 to -1.3 MPa (Borghetti and Vendramin 1987, Jackson *et al.* 1995b, Sturm *et al.* 1996, Lu *et al.* 1996), considerably more negative than values at which refilling has been shown to occur (Edwards *et al.* 1994). Consequently, it has yet to be demonstrated how embolised tracheids in the canopy of mature coniferous trees can refill following cavitation.

1.2.5 PHYSIOLOGICAL SIGNIFICANCE OF CAVITATION

There is currently little information available concerning the physiological significance of cavitation and the development of embolism is mature forests. Of the studies available the majority have concentrated on monitoring the development of embolism in naturally growing angiosperm species both during freeze-thaw cycles and to a lesser extent during periods of drought (Sperry *et al.* 1994, Tyree *et al.* 1994, Magnani and Borgetti 1995, Alder *et al.* 1996). Angiosperms generally transport water in only the most recently produced xylem and may well depend on growth of new xylem to maintain an efficient hydraulic system in the face of cavitation. In gymnosperms water is often transported in xylem that was laid down several years previously, and so there may be some imperative to refill embolised xylem or prevent cavitation to maintain an effective water transport system. There is little doubt that large seasonal variations in the water content or degree of embolism in the xylem of gymnosperms do occur (Gibbs 1958, Roberts 1976, Waring and Running 1978, Waring *et al.* 1979, Jackson *et al.* 1995b), yet the mechanisms involved in refilling such embolised xylem and the significance of the associated changes in hydraulic resistance to plant gas exchange still remain largely a matter of speculation. For example in one recent experiment on mature Norway spruce no significant embolism developed in the branches of droughted spruce because of tight stomatal control over transpiration (Lu *et al.* 1996). Yet in mature Scots pine, regarded as a drought tolerant species, a large seasonal increase in the degree of embolism in the boles of mature trees was evident during a very dry summer in southern England (Jackson *et al.* 1995b), and this appeared to continue into subsequent years (personal communication). In this study there was no evidence of ‘runaway cavitation’ which would suggest stomatal regulation of transpiration was important. Unfortunately it was not established whether the increased hydraulic resistance in the tree had carry-over consequences for plant gas exchange and future growth.

It is conceivable that the xylem is not a vulnerable hydraulic system and that cavitation is a day-to-day phenomenon, perhaps associated with tissue ageing (Sperry *et al.* 1991), and with no serious consequences for plant function. For example early experiments involving horizontal saw-cuts made across part of the trunk of a tree in order to increase the hydraulic resistance between the soil and foliage would appear to suggest that there was 'spare capacity' in the water transport system. The trees in these studies often remained healthy after such treatments (Greenidge 1955, Kozlowski 1965). However, no account of reductions in transpiration because of stomatal closure were considered in these older studies. More recently, it has been demonstrated that saw cuts made across the stems of *Betula occidentalis* resulted in either 'runaway' cavitation or a significant decline in transpiration (Sperry *et al.* 1993, Saliendra *et al.* 1995).

1.3 THESIS AIMS

This thesis attempts to address some of the major uncertainties concerning the apparent vulnerability of the water transport system in a mature coniferous forest under conditions of drought stress;

(i) Does the hydraulic resistance in the soil-vegetation-atmosphere system increase during drought ? If so, can the increased hydraulic resistance be attributed to development of embolism in the xylem in the woody aerial tissue ? More importantly, does the hydraulic resistance recover when the drought ceases, or are changes in hydraulic resistance carried over into the following growing season ?

(ii) Does stomatal closure occur in response to soil drought in a similar manner as suggested from studies on young trees ? If so, can stomatal closure prevent cavitation by reducing the transpirational flux, so that the critical tension for cavitation is never reached or rarely reached ?

To address these issues a soil-drought was imposed on a stand of mature Scots pine in southern Scotland. This was achieved by isolating plots containing mature trees from the surrounding soil using a system of ditches and plastic barriers. Precipitation was intercepted above these plots by using clear polythene covers which deflected the water outside the previously installed ditches. The drought was imposed for one growing season, and appropriate physiological measurements were made during this and the following non-droughted period.

1.4 THESIS STRUCTURE.

This thesis is divided into 6 chapters. Chapters 2 and 3 are concerned with the development of new techniques which were required for this study and which were subsequently employed during the field experiment. The remaining chapters are concerned with the results from this field experiment. As chapters 2 to 4 have been submitted as manuscripts for publication, all contain sufficient information to be read independently. Only chapter 5 makes reference to experimental protocols that were presented in chapter 4.

Chapter 2: Measurements of water potential are needed at both the base of the tree and in the foliage to partition changes in the hydraulic resistance of the soil-vegetation-atmosphere system into above and below ground components. In Scots pine, resin production prevents the use of stem psychrometers (Dixon and Tyree 1984) to detect changes in the water potential of the xylem at the base of the tree. Consequently, this chapter reports on the development of a new technique to detect changes in the xylem water potential based on measuring the elastic deformation of the wood. It is linked to Appendix 1, which illustrates how data collected using this technique were used in conjunction with sap flux and needle water potential measurements to calculate the changes in the hydraulic resistance in the above- and below-ground components of the soil-vegetation-atmosphere system.

Chapter 3. Changes in embolism in the xylem can be detected as changes in the xylem water content. However the techniques currently available to measure xylem water content were unsuitable for use in the field experiment. This chapter reports on the novel use of time-domain-reflectometry (TDR) to measure changes in the volumetric water content of the xylem at the base of the stem in mature Scots pine.

Chapter 4. This chapter reports the field experiment that was developed to address the issues of whether the xylem is a vulnerable hydraulic system, and the importance of stomatal control of xylem embolism. Comparison was made between droughted plots and those receiving average precipitation. Measurements were made of the seasonal course of transpiration, canopy stomatal conductance, needle water potential, xylem water content, soil-to-needle hydraulic resistance, and growth. The responses of the pine forest to drought stress are presented and discussed.

Chapter 5. Canopy stomatal conductance data, as calculated from information collected during the field experiment, were used to develop an empirical multiplicative non-linear regression model to relate canopy stomatal conductance to environmental variables. This chapter explores the stomatal responses of the pine forest to drought stress through use of such a model in an attempt to resolve the issue of whether stomatal control of transpiration can prevent the development of excessive xylem embolism.

Chapter 6. This chapter provides a brief summary of the thesis together with a commentary on some of the approaches used during the study. The wider significance of the results are discussed together with recommendations for further work.

2. A new technique to measure water tensions*

2.1 PREFACE

To investigate the magnitude of water tensions in the xylem in the trunk of mature *Pinus sylvestris* L. a new technique was developed. This involved relating the elastic deformation of the xylem to water potential. At first it was considered that the traditional technique of using stem psychrometers would suffice, however it became clear that this instrument had major deficiencies, especially when measurements are made on resin-producing species such as *Pinus sylvestris* L. Therefore, from the outset, some effort was spent developing a suitable alternative technique. Initial attempts to re-develop osmotic tensiometers (Peck and Rabbidge 1966) were unsuccessful and therefore abandoned. Consequently the following chapter reports on the development of a technique that relates the diurnal shrinking and swelling of the xylem to water potential.

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* Text is published as a paper : Continuous measurements of water tensions in the xylem of trees based on the elastic properties of wood. Planta (1997) 202: 455-461

2.2 SUMMARY

According to the cohesion theory for the ascent of water in vascular plants, significant tensions should develop in the water columns of transpiring trees. These tensions cause small but detectable changes in the diameter of the xylem as a consequence of adhesive forces between water molecules and the inner xylem walls. The diurnal time course of tension in the water columns in the xylem of the trunk of mature Scots pine (*Pinus sylvestris* L.) was measured during the summer of 1995 by means of a displacement transducer mounted on a rigid steel frame. The apparent elastic modulus of Scots pine wood in the radial direction (E'_r) was determined in the laboratory and then used to estimate tensions from the measured displacement. Laboratory measurements on logs indicated that only the sapwood contributed to dimensional changes of the xylem. Corrections for thermal expansion of the system were included. Water tensions fell by 0.19 MPa over the course of the day, when needle water potentials fell by 0.50 MPa. Such data are consistent with the cohesion theory, and the view that the hydraulic resistance to flow in above and below ground plant parts are of similar magnitude.

2.3 INTRODUCTION

According to the cohesion theory of water transport in vascular plants, water in the xylem of actively transpiring trees is under considerable tension as it is pulled through the body of the plant from soil to sites of evaporation in the leaf, along a complex pathway that includes microcapillaries and living cells which collectively constitute a large hydraulic resistance. The theory, first proposed by Josef Böhm (1893), depends on the well-known high tensile strength of water, brought about by hydrogen bonding between adjacent water molecules, and is consistent with observations of various kinds: leaf water potential made with the pressure chamber (Schölander *et al.* 1965, Hellkvist *et al.* 1974), stem water potential made with stem psychrometer (Dixon and Tyree 1984, Brown and Oosterhuis 1992), calculations based on observed hydraulic resistance of stems (Ewers *et al.* 1989, Yang and Tyree 1994), and recent data from stems spun in a centrifuge to impose tensions (Holbrook *et al.* 1995, Pockman *et al.* 1995). However, some doubt remains following reports that the tensions within the xylem as measured by direct means with the pressure probe are much lower than expected from the cohesion theory (Zimmermann *et al.* 1993, 1994, 1995, Steudle 1995). The pressure probe is invasive and may appreciably influence the local conditions being measured, particularly if there is entrance of air during insertion. This chapter reports a non-invasive method which is direct and capable of continuous operation. This method measures the elastic shrinkage of the xylem detected by sensitive displacement transducers, and infers tensions from laboratory calibration.

Changes in diameter of plant stems results from an irreversible component due to growth and a reversible component due to changes in the water balance of stem tissues, the latter often observed as diurnal changes in stem diameter (Kozlowski 1972b). Information on which tissues within the stem contribute to these reversible changes is scarce. Living tissue (phloem, cambium) can change size as a result of diurnal cycles of hydration whereas mature xylem can contract and expand due to elastic deformation involving little water loss. Early work by Dobbs and Scott (1971) suggested all diameter changes in Douglas fir were in the living tissues external to the xylem, and Molz and Klepper (1973) indicated in cotton that more than 90% of stem contraction occurred in the phloem and associated tissues. Richards (1973) and Brough (1986) provide evidence to support these views with measurements made on Sitka spruce and apple, where at least 75 % of the observed diameter changes could be attributed to the extensible tissues external to the mature xylem. Only Neher (1993) working on Monterey pine has recently suggested that a more significant proportion of this reversible component may be attributed to the xylem. There are no reports in the literature of attempts to quantitatively relate diurnal changes in diameter of the xylem to water potential although Hellkvist *et al.*(1980) making measurements with strain gauge transducers mounted directly on the xylem of Scots pine found a close correlation, with no lag phase, between needle water potential and stem radius. He suggested that such a technique may provide a means of obtaining detailed information about diurnal changes in xylem pressure potential. In this chapter we report the use of such a technique to monitor diurnal changes of the xylem pressure potential in mature Scots pine. Examples of its use together with details of calibration from laboratory experiments are presented.

2.4. MATERIALS AND METHODS

2.4.1 MEASUREMENT OF RADIAL STRAIN.

The apparatus was mounted on logs of Scots pine (*Pinus sylvestris* L.) in the laboratory (Figure 2.1) or the stems of mature trees in the Devilla forest (see below for site details). AC & BD were square steel tubes 19 mm in section, joined by threaded stainless steel rods AB & CD. Nuts on these rods were tightened to trap the tubular steel, leaving a rigid frame slightly larger than the tree under measurement. A small circular plug of bark, phloem and current year's differentiating tracheids were removed at points E & F to allow direct access to the xylem surface. There were only two points of contact with the tree: at E a bolt fixed through AC rested on the surface of the xylem, and at F the measuring tip of a spring-loaded linear variable displacement transducer (LVDT, model DG 2.5, Schlumberger Industries, Bognor Regis, West Sussex, UK) made similar contact with the xylem. The contact points were coated with silicone grease to prevent local water loss. The LVDT passed through a collar in BD which housed a tightening screw to allow minor adjustment and centering of displacement transducer. The frame was supported by 2 mm diameter steel cable attached to stainless steel anchor bolts screwed into the tree at points G & H (Figure 2.1). The cables were tensioned so as to provide a good continuous contact at points E & F. The force acting on bolt E was 10 to 15 N. Any changes in dimension between points E & F was registered by the LVDT. These changes may have been the result of fluctuating tension within the water in the xylem but could also have been a consequence of thermal expansion of the xylem or of the frame elements AB & CD. In order to account for these thermal effects, thermistors (100K6A1, Betatherm, Fleet, Hampshire, UK) were located in the centre of the sapwood and in frame element BD to monitor temperature changes. A 21X datalogger (Campbell Scientific Ltd, Leicestershire, UK) was used to record all signals from the LVDT's and thermistors. All frame elements were encased with 20 mm thick closed cell foam to minimise temperature gradients as a result of heating from direct solar radiation.

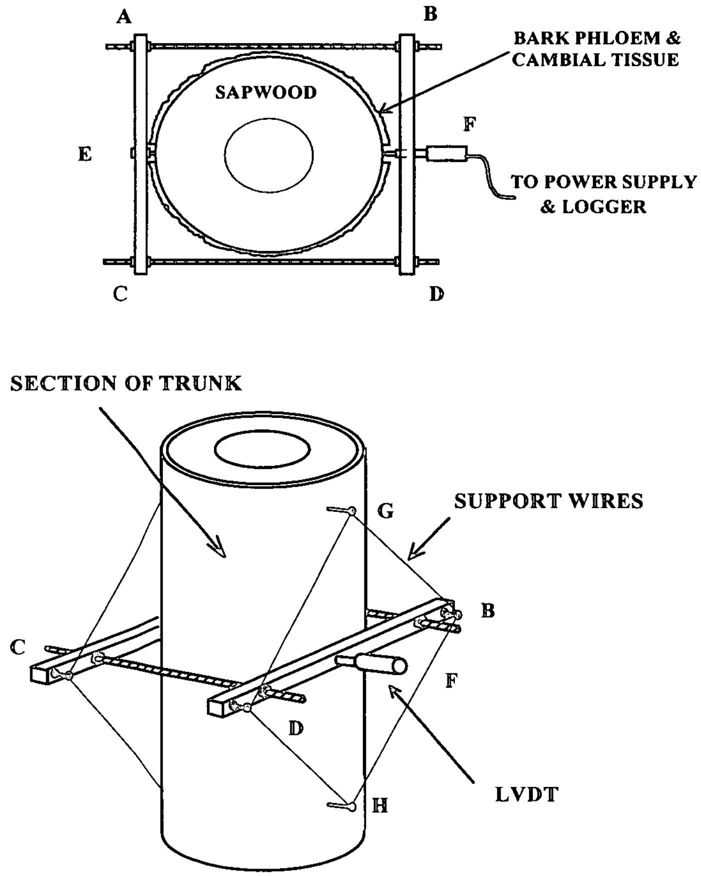

Figure 2.1. Transverse view across bole of tree (upper drawing) illustrating the components of measuring frame. AC & BD were square steel tubes joined by threaded stainless-steel rods AB & CD. The LVDT at F measured dimensional changes within ABCD. Tensioned triangulated steel cables were attached to the tree by anchor bolts at G&H (and at the two opposing hidden points) to provide support and sufficient force for continuous contact at the measuring points E&F (lower drawing).

Corrections to allow for thermal expansion in this apparatus are necessary. An increase in temperature of the measuring frame results in an increase in the length of all frame elements. However, only AB & CD, the projected bolt at E, and the tip of the LVDT at F are in the plane of measurement (Figure 2.1). If the frame diameter increases the output from the LVDT will appear to indicate the diameter of the xylem is decreasing. To correct for this, the expansion of the frame from a set point in time, as calculated by the linear coefficient of expansion for steel (α_{steel}) × length of steel (m) × temp rise (°C), is added to the output from the LVDT. A similar correction can be applied for the thermal expansion of the xylem, but in this case the correction is subtracted from the output of the LVDT.

2.4.2 ESTIMATING E'_r

Xylem is an orthotropic composite cellular solid and although cell walls of individual tracheids will be subject to either tangential tensile or compressive stresses and strains as a result of the pressure or tension in the water columns within their lumens, the behaviour of complete sections of trunk is far harder to predict because of structural heterogeneity. Consequently to link tension in the water in the xylem of living trees with xylem diameter the apparent elastic modulus of wood in the radial direction (E'_r) was defined as follows from the tension or pressure inside the stem P, and the proportional change in radius $\Delta r/r$ that is observed when the tension or pressure is applied experimentally.

$$E'_r = \frac{\text{Stress}}{\text{Strain}} = \frac{P}{\Delta r/r}$$

Where E'_r is the apparent elastic modulus in the radial direction (Pa), r the radius of the xylem (m), and P is the hydrostatic pressure (Pa).

It was important to know whether the whole of the diameter of the xylem including the heartwood contributed to these elastic changes such that a measurement of elasticity per unit length of heartwood or sapwood could be used in the field with trees of different dimensions.

i) Calibration under hydrostatic pressure.

The equipment was set up on freshly felled Scots pine taken from the field site (see below for site details). Logs of length 40 cm and diameters between 15.5 cm and 19.5 cm were used. The measuring point was located at the midpoint between two whorls. To apply water pressure to the log, rubber 'O' rings and heavy ‘Perspex’ plates were fitted over the severed ends of the log to make a closed system [a similar set up to that described by Edwards and Jarvis (1982) to measure hydraulic conductivity]. A pressure bomb (SKPM1400, Skye Instruments Ltd, Llandrindod Wells, Powys, UK) was then used to apply pressurised distilled water through a hole in the centre of one of the perspex plates. A series of cycles of pressurisation/de-pressurisation were then applied. This was repeated on material from three trees on logs of differing diameters. Measurements of E'_r at various depths in the xylem were made by drilling holes radially into a log at the measurement sites to predefined depths and extending the contact points to the base of these holes. Cycles of water pressure were applied at each depth. At the end of all measurements, cores of xylem were taken with a Pressler borer across the diameter of the logs at the measuring point, and these were used to determine the proportions of heartwood and sapwood by inspection under diffused light.

ii) Calibration at below-atmospheric pressures

The equipment was connected to a water-jet vacuum pump which allowed subambient pressures approaching 0.01 MPa to be exerted (ambient = + 0.1 MPa). To apply true tensions, i.e. below 0 MPa, a log with the equipment attached but with its severed ends left exposed was allowed to dehydrate in a controlled environment room for a period of four days. Two stem psychrometers (Plant Water Status Instruments Ltd., Guelph, Ontario, Canada) were left permanently attached to the xylem and a series of measurements made. In this instance, unlike the case when used on living pine trees, there were no problems with resin exudation as all resin pressure had been released on severing the axial resin ducts. Once a water potential of -1.4 MPa had been reached, the tension was released by dipping one end of the log in water, and the rapid recovery of diameter and water potential was monitored.

2.4.3 FIELD MEASUREMENT

Changes in xylem diameter, frame and stem temperature were measured continuously on four 41-year old trees of Scots pine at 1 m above the ground level in Devilla forest (Fife, Scotland, W.3°43' N.56°2') between April and October 1995. Over the same period, on four other trees, sap flux was also measured at the same height using a heat pulse technique (HPV1, Custom Electronics, Hort Research, Palmerston North, NZ). Periodically, dawn until dusk measurements of needle water potential at 10 m above the ground were made using a pressure bomb.

2.5 RESULTS

The cycles of hydrostatic pressure that were applied to a log with xylem diameter ($\varnothing_x$ including sapwood and heartwood) 167 mm, and the resultant changes in diameter are illustrated in Figure 2.2.

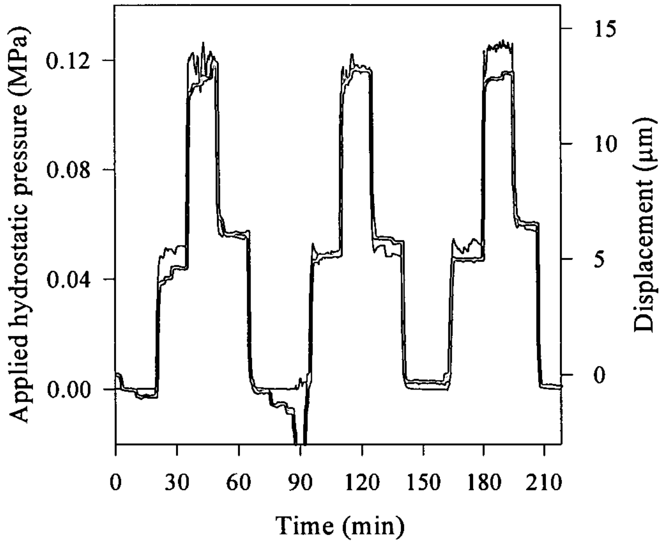

Figure 2.2. Changes in the diameter of the xylem of a field-saturated log of Scots pine in response to applied hydrostatic pressure. The heavy line refers to displacement as measured with the LVDT in response to applied water pressure (fine line).

The cycles were designed to step between 0, 0.05 and 0.12 MPa. However pressure was under manual control giving rise to small fluctuations about each level. It is apparent that there is an instantaneous response of xylem diameter to applied pressure both on pressurisation and de-pressurisation. The change in xylem diameter at 90 min should be ignored as equipment was being adjusted to eliminate a leak. This figure illustrates the elastic nature of the wood with no significant capacitance in the system. The application of tension to a log ($\varnothing_x$ = 158 mm) is presented in Figure 2.3. Here the drying cycle lasted 114 hours whereas on placing the cut end of the log in water recovery took only three hours. Both cycles follow similar linear gradients illustrating the elastic behaviour of the wood. The offset is caused by handling of equipment between the drying and rewetting cycles. It is apparent that E'_r across the sapwood is constant (Figure 2.4). The point at which there is no change in diameter per unit pressure is close to the point of the observed heartwood, suggesting that only the sapwood is responsible for fluctuations in xylem diameter.

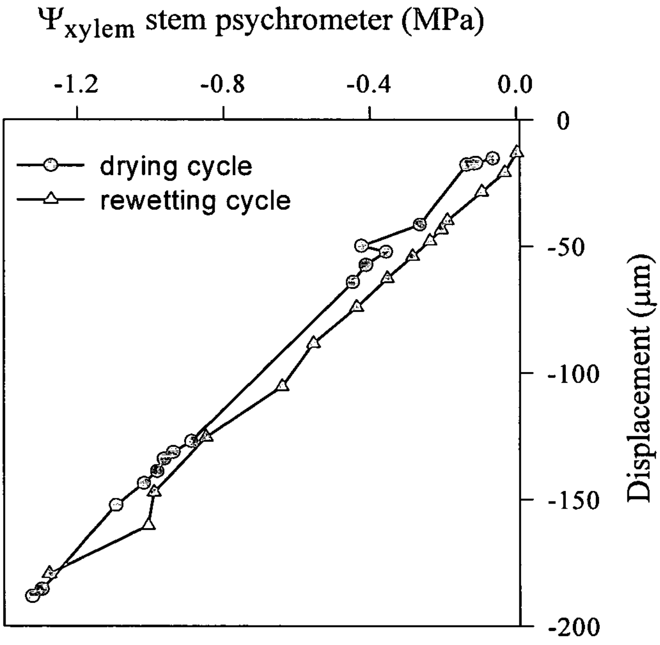

Figure 2.3. Changes in diameter of the xylem of a freshly cut log drying slowly in air (drying cycle) followed by the release of tension by rewetting log ends (rewetting cycle), water potential as measured with stem psychrometers.

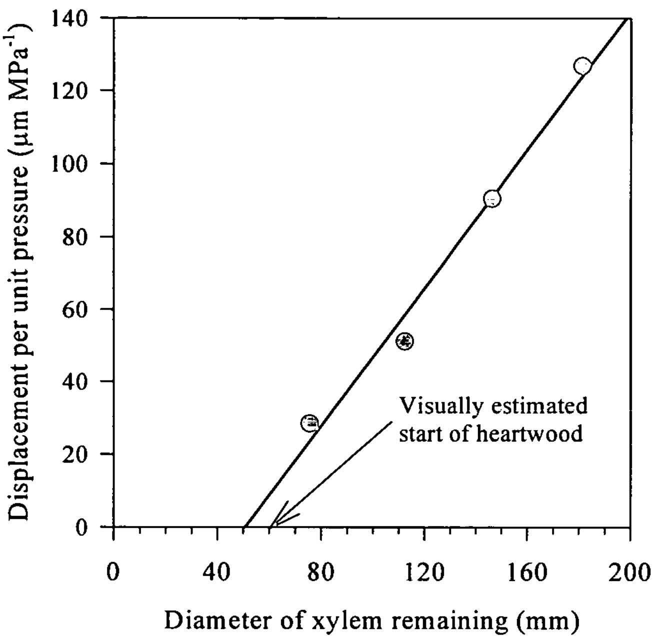

Figure 2.4. Measurements of the response of different sections of the sapwood in Scots pine to applied hydrostatic pressure. Access to different thicknesses of wood were made by drilling holes radially into the xylem. The trend line is a linear regression through the measurements at four depths. Xylem diameter includes both sapwood and heartwood.

Measurements of E'_r by application of hydrostatic pressures or tensions gave similar results: average E'_r *(pressure)*= 0.79 GPa, E'_r *(tension)*= 0.68 GPa. These figures assume heartwood made no contribution to elastic changes, such that the radial dimension used in the definition of E'_r was the radial depth of the sapwood. The mean value for E'_r on all the material used, in both pressure and tension, was 0.75 GPa (SE = 0.04, $n = 5$) .

The relevance of the thermal expansion of the measuring frame is illustrated in Figure 2.5, which represents the typical diurnal pattern of change in the diameter of the xylem for a single tree at the field site (27 June 1995, $\varnothing_x$ = 205 mm). The sapwood shows a fluctuation in temperature about one third of that of the frame with a lag of about four hours. The errors associated with thermal expansion amounted to 40% of the total measurement. The corrections applied are based on figures for the linear coefficient of expansion: $\alpha_{steel} = 20 \times 10^{-6}\ {}^{o}C^{-1}$, $\alpha_{wood} = -4 \times 10^{-6}\ {}^{o}C^{-1}$.

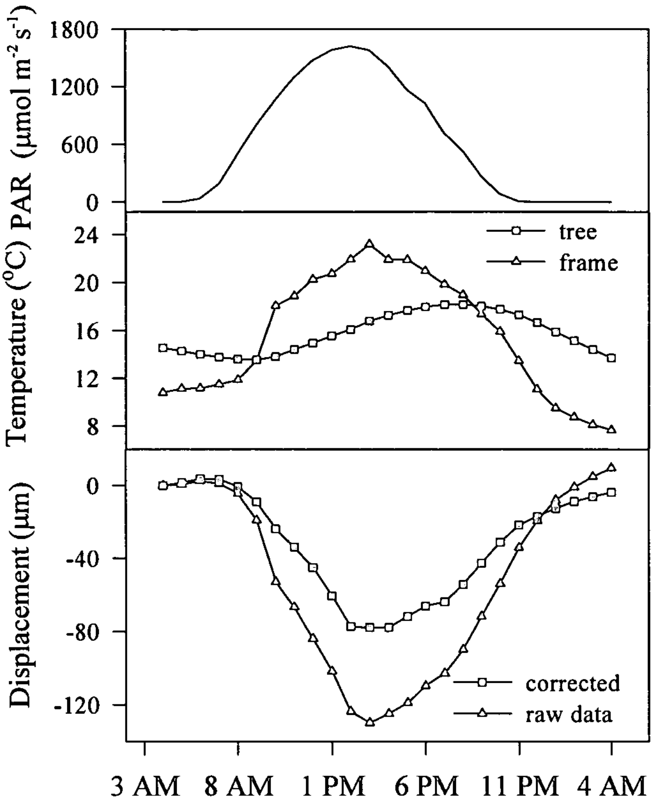

Figure 2.5. Changes in xylem diameter of a single tree at the field site on the 27th June 1995 illustrating the importance of accounting for thermal expansion of both measuring frame and xylem.

Field data over six days, from the base of the stem is three trees is presented in Figure 2.6. For each tree the proportion of sapwood was measured and the laboratory-based figure of E'_r = 0.75 GPa used to convert temperature-corrected diameter changes to water tension. Note the high degree of agreement even though the trees were of different sizes ($\varnothing_x$ = 101, 123, 147 mm). The typical diurnal range of water tension at the base of the trees over these six days was 0.19 MPa compared with a range of 0.50 MPa for needle water potential on the 23rd of May. The sap flux data are based on unit of ground area and are the average from four trees weighted to account for their basal sapwood areas (see Appendix 2). In Figure 2.7 the data of the average value for the water tension at the base of the three trees from the 19th to 24th of May (from Figure 2.6) is plotted against the associated sap flux as measured at the same height. Figure 2.7 shows a linear relationship as expected if sap flow rate is proportional to water tension gradient across the root system.

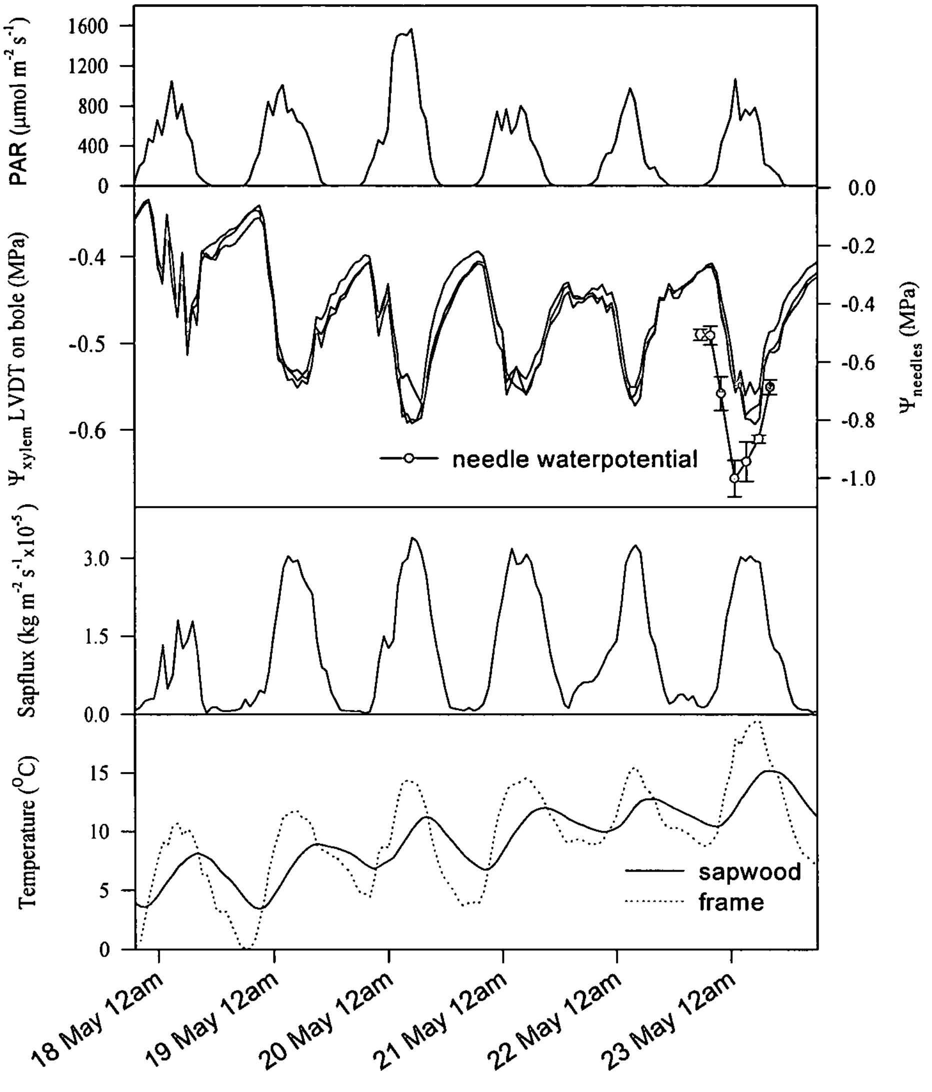

Figure 2.6. Example of diurnal variation in water potential at the base of three trees at field site.

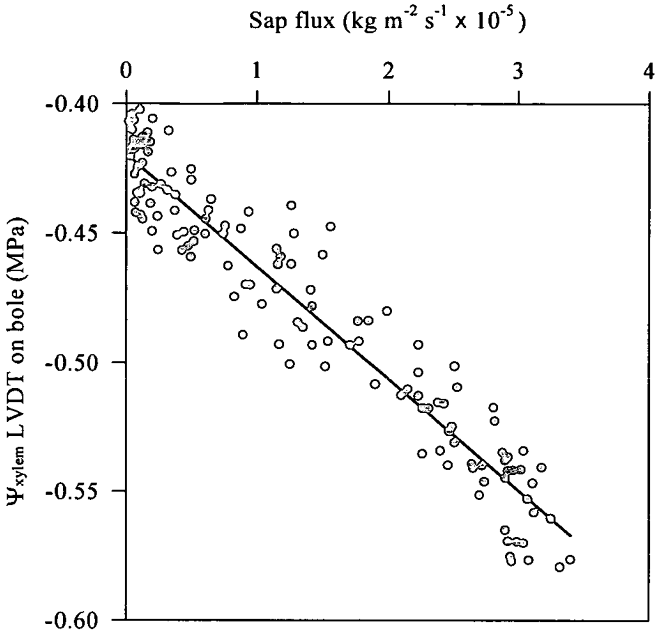

Figure 2.7. Relationship between sap flow and water potential measured at the base of three trees. Data taken from Figure 2.6.

2.6 DISCUSSION

The LVDT technique, has provided data which would have otherwise been unavailable, as traditional methods for estimating water potentials could not be used in this situation. This technique measures changes in water tension or pressure potential [throughout this paper the terms water potential and water tension have been used synonymously, a reasonable approximation considering the osmotic potential of xylem sap is generally small (Hellkvist *et al.* 1974, Borghetti *et al.* 1991), but more importantly is unlikely to change significantly over the course of measurements].

The treatment of wood as an elastic material is a simplification although the results obtained here (Figures 2.2 & 2.3) suggest this is a reasonable approximation given the water tensions and time scales involved. The contribution of living cells (ray parenchyma only in the case of Scots pine) to the total wood volume is small, generally about 7% (Wilson and White 1986) such that any time lags in water potential that are normally associated with the capacitive nature of living tissues can be ignored. The finding that heartwood does not appear to contribute to elastic changes in dimension is supported by similar observations on Monterey pine (Neher 1993). Heartwood is no longer involved with the upward transport of water through the plant and often has a water content approaching the fibre saturation point. Its high degree of embolism, and resin-filled condition of the tracheids, together with pathways of large hydraulic resistance to the sapwood effectively isolate it from changes in tension and minimise any elastic responses it might otherwise exhibit.

The need to use accurate linear coefficients of expansion (α) to correct the raw data for changes in thermal expansion of the measuring frame and the tree is illustrated by Figure 2.5. In general 50 % of the measurement could be attributed to thermal expansion of the measuring frame and only 2% associated with thermal expansion of the xylem. The exact proportions are not fixed but dependent on local meteorological conditions and rates of transpiration. The stainless steel rods used in the frame were an austenitic steel (A2 class 70, 18% chromium 8% nickel) which has tabulated values of α between 14.7 & 16.9 $\times 10^{-6}\ ^{o}C^{-1}$ (Colombier and Hochmann 1967, Kaye and Labey 1986). However, measurements on sample material in our laboratory indicated a figure of $20\times 10^{-6}\ ^{o}C^{-1}$ which was used in the corrections (see Appendix 5). The most commonly reported data for α_{wood} refers to air dried material and is approximately three times that of steel. Data reported by Kubler *et al.*(1973) indicate that field-saturated *Sequoia sempervirens*, beech and Sitka spruce (Yokota and Tarkow 1962) have negative coefficients of thermal expansion. A more detailed study on Norway spruce reports a figure of α radially of -3 $\times 10^{-6}\ ^{o}C^{-1}$ at ambient temperatures (Salmen 1990), whereas we found a figure of $-4\times 10^{-6}\ ^{o}C^{-1}$ for Scots pine, which was used in all corrections (see Appendix 5).

To compute water potentials in the field a zero point or offset value is required from which changes in potential as measured using this technique can be added or subtracted. In the case of Figure 2.6 the offset point was chosen as 0500 hours on the 23rd of May and given a value of -0.42 MPa based on measured predawn needle water potential taking into account gravitational potential. The figure illustrates how the water potentials at the base of three trees changed over a period of six days. The 18th of May was an overcast day with occasional rainfall which is reflected in the low and erratic sap flow. It is clear over the course of this day that sap flow and water potential measured at the same point in the stem are highly correlated. The rapid fluctuations in water potentials that were derived from xylem diameter measurements were too large to be accounted for by effects of temperature and uncertainty in thermal expansion correction factors. Following this day of rainfall, soil moisture and water potential in the rooting zone for the different trees used in measurements would have been reasonably constant and we would expect sap flow and water potential at the base of the tree to be highly correlated and in phase, which is clearly the case (Figure 2.7). These observations provide qualitative evidence that the technique is measuring true changes in water potential at the base of the tree. Figure 2.6 (final panel) provides a record of the temperature of the measuring frames, potentially the largest source of error because of the corrections associated with thermal expansion. There was a gradual increase in temperature over the six days. If an incorrect value for α_{steel} was used we might expect a directional trend in the water potential values at the base of the trees, but there is no evidence for this. Since α_{wood} is approximately a quarter that of steel and the temperature experienced by the sapwood about one third of the frames a small error in the estimation of α_{wood} is unlikely to have a significant effect on the corrected data.

Embolised tracheids are unlikely to contribute to changes in the diameter of the xylem. Measurements taken over time periods when significant changes in embolism may have occurred are likely to need corrections applied to E'_r to take this into account. Reported data for measurements of Young's modulus at different tissue water contents (Cannell and Morgan 1987) have been collected using techniques where tensions are not generated internally. Consequently further investigations in this area would be needed if changes in embolism were considered a significant factor. In this study there were no diurnal changes in embolism and at most a one or two percent change in relative water content over the complete growing season. Accordingly no corrections were applied to these results.

Although there are many published reports containing data of diurnal changes in plant diameter (eg. Lovdahl and Odin 1992, Herzog *et al.* 1995), nearly all measurements have included tissue external to the xylem, thus preventing direct estimation of xylem water potential. It would appear there has been some uncertainty that small changes in diameter exhibited solely by the xylem could be measured successfully in the field. This paper illustrates the feasibility of such measurements on Scots pine with overbark diameters larger than 20 cm. However, as tree size decreases the elastic changes in diameter will be smaller and approach the safe working limits of the resolution of the displacement transducers. In situations where continuous measurements of xylem water potentials are required and sufficient diameter of xylem is available this technique is likely to be valuable. LVDTs are relatively cheap, have low temperature coefficients (< 0.01% full scale $^{\circ}C^{-1}$) and high linearity (< 0.15 %). It is possible to operate them without mains power and use inexpensive datalogging equipment.

The principle utilised by this technique is very different to that employed by both the pressure chamber or psychrometric method. However, the data are consistent with measurements of needle water potential made by the pressure chamber, if the site of measurement on the tree is taken into account. During dry summer weather we detected a diurnal variation in water tension of 0.19 MPa at the base of the trunk in mature Scots pine, at a time when needle water potentials displayed an amplitude of 0.5 MPa. This indicates that approximately 60% of the hydraulic resistance is located in above-ground tissue, a figure in agreement with data collected on coniferous species (Roberts 1977, Running 1980a), suggesting that the technique produces data consistent with the cohesion theory and in accord with our current understanding of plant hydraulic architecture.

3. Using TDR to detect changes in xylem embolism*

3.1 PREFACE

In coniferous species the xylem water content is closely related to the degree of xylem embolism because of the small proportion of living tissue within the bole of the tree. In Scots pine the only living tissues within the xylem are ray parenchyma which typically account for 7 % of the xylem (Wilson and White 1986). To explain a decline of approximately one percent volumetric water content of the xylem in Scots pine, a substantial decline (approximately 20 %) in the volume of the water in the ray parenchyma would be required, assuming no water was lost from elsewhere because of the formation of emboli. Such large declines in the water content of parenchyma cells would be highly unusual as turgor pressure is usually maintained and is rarely zero (Hammel 1967). The only other significant source of water in the xylem which is not within the lumen of tracheids is the bound water fraction within the cell walls. In Scots pine this can account for approximately 14% of the volume of the xylem (Siau 1984) however, this fraction of water will not vary over the range of water potentials experienced by living trees. Consequently, in coniferous species even small changes in sapwood water content can be regarded as changes in the degree of xylem embolism.

This chapter reports the development of a new technique to assess changes in the degree of xylem embolism. This technique involved using time domain reflectometry with very short probes that allowed repeated non-destructive measurements of xylem water content. The development of this technique was essential for this thesis as the traditional method of using increment cores would have resulted in substantial damage to the experimental trees due to repeated sampling.

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* Text is published as a paper : Non-destructive measurement of stem water content by time domain reflectometry using short probes. J.Exp.Bot. (1997) Vol 48, No.308, pp.813-818.

3.2 SUMMARY

Time Domain Reflectometry (TDR) has previously been used to determine the water content of soils. Here, we assess TDR as a method of tracking the seasonal change in water content of the stems of mature trees (*Pinus sylvestris* L.). The longer probes used for soil were replaced by 50 mm probes, inserted radially into the stems at 1 m above the ground. Tests on blocks of wood in the laboratory suggested that the probe is influenced by the water content several centimeters around it, and the sensitivity of the system enables volumetric water fraction (*W*) in the physiological range to be measured to a resolution greater than 0.01. The use of very short probes prevents the development of a universal calibration between measured dielectric constant and *W*. Calibrations for both 50 mm and 20 mm long probes are reported. The effect of temperature on the calibration was negligible. The system was used successfully on mature trees in 1995, and no evidence of wound reaction around the permanently installed probes was apparent in the measurements.

3.3 INTRODUCTION

According to the cohesion theory of water transport, water within the xylem of plant stems comes under considerable tension when transpiration occurs. In certain circumstances the columns of water break, either as a result of air seeding (*sensu* Zimmermann 1983) or by spontaneous cavitation. This results in emboli which reduce the extent of the water transport system within the plant. The resultant increase in hydraulic resistance may influence leaf water status and ultimately affect gas exchange and plant growth (Sperry and Pockman 1993). Seasonal changes in the water content of woody tissues in trees have been detected by many authors (Gibbs, 1958, Roberts 1976b, Waring and Running 1978, Waring *et al.* 1979, Jackson *et al.*, 1995b) some of whom (Sperry *et al.* 1994, Tognetti and Borghetti 1994, Magnani and Borghetti 1995) have provided evidence that these changes can be attributed to cavitation and the subsequent refilling of embolised xylem.

Techniques available to monitor seasonal changes in the water content of woody tissue *in situ* are limited. The traditional technique of taking increment cores (Waring and Running 1978) is time consuming, destructive, and can be prone to error because of movement of water out of the core during sampling. Gamma-ray attenuation (Edwards and Jarvis 1983, Brough *et al.* 1986), nuclear magnetic resonance (Ratkovic and Bacic 1993), and more recently computer axial tomography (Raschi *et al.* 1995) are not readily available, are time consuming to use and can pose a health risk to the operator. Time-domain reflectometry (TDR) is a relatively new technique which has seen widespread use for measuring soil water content and ionic status. To date there are only two published reports of attempts to use TDR to monitor the status of water in tree stems (Constantz and Murphy 1990, Holbrook *et al.* 1992). These authors use TDR probes in excess of 12 cm in length, whereas plant physiologists are most interested in detecting changes in water content of the most recently produced sapwood which is involved in transporting water through the tree. For this purpose it is necessary to use the shortest possible TDR probes (< 10 cm). This chapter reports on the use of TDR probes 2 cm and 5 cm in length to monitor the water content status of woody tissue.

The theory and application of TDR has been covered extensively in the literature of soil science (Topp *et al.*1980, Ledieu *et al.* 1986, Dasberg and Hopmans 1992). Briefly, the propagation velocity of an electromagnetic pulse down a metallic wave guide (probe) depends on the dielectric of the surrounding material. Dielectric or relative permittivity is an intrinsic property of a material that relates to its ability to store and conduct electrical charge. Because the dielectric constant K of water is far higher than that of air or the woody matrix in plant stems ($K_{\text{water}} = 80$, $K_{\text{air}} = 1$, K_{solids} typically < 10) any change in the dielectric of the tissue predominantly reflects a change in its water content. TDR is used to measure the time taken for an electromagnetic signal to travel down a probe embedded in the material. As the water content declines the overall dielectric constant of the material also declines which is detected as a decrease in transit time of the signal. In practice probes are usually steel pins that are inserted into the medium under test. A cable-testing oscilloscope is attached to the protruding pins with coaxial cable, and a series of voltage pulses are sent down the cable and probe. Changes in impedance at points at the start and end of the probe reflect some of the signal thus allowing these points to be identified on the displayed TDR trace and used to measure the transit time for the signal along the probe (Figure 3.1). This chapter reports on the use of this system to track the seasonal changes in water content of *Pinus sylvestris* wood.

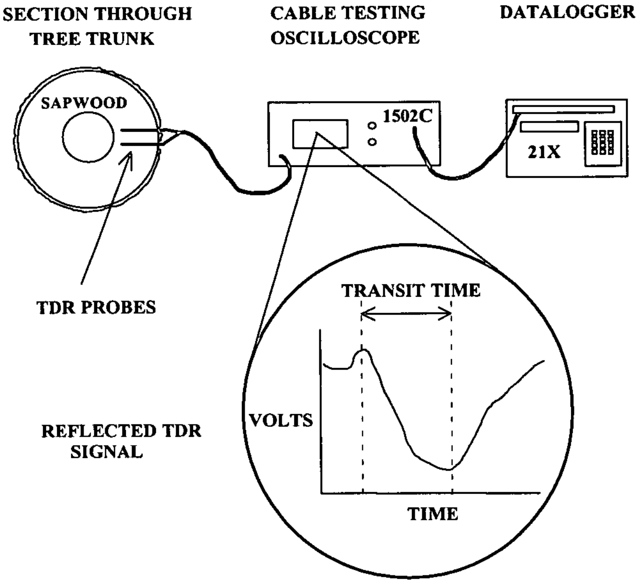

Figure 3.1 Schematic drawing of the equipment used to monitor stem water content. The 21X logger controlled data aquistion and interpretation of the TDR signal from the cable testing oscilloscope.

3.4 MATERIALS AND METHODS

The TDR equipment used was a Tektronix 1502B (Tektronix Corp, Redmond, OR, USA). This was fitted with a SDM1502 interface connected to a 21X datalogger (Campbell Scientific (UK) Ltd., Shepshed). PB30-RG58 cables were used throughout (Campbell Scientific), the ring terminals at the probe end of the cable having been replaced with screw terminals which fitted tightly over the protruding TDR probes to allow rapid changing of cable between different sets of probes. Analysis of the output trace was performed with datalogger software on the specially available PROM. This makes use of the standard procedure of smoothing the trace and finding the end points by calculating where a tangent, drawn on the trace at the point of maximum or minimum first derivative, transects the local maxima or minima of the trace. Control over the time resolution of the processed trace is gained by indicating the real length of the probe in the datalogger program. For the high water contents in living trees compared to soil, it is necessary to use a set probe length longer than the true probe length in order that there are sufficient data points covering the complete TDR signal. A correction to the output must then be applied.

Throughout this chapter it has been assumed that the imaginary part of the dielectric constant (dielectric loss or conductivity) was small enough to be ignored. The term apparent dielectric constant (*sensu* Topp *et al.* 1980) has, therefore, been used in reference to any of the measurements made.

3.4.1 CALIBRATION OF 50 MM AND 20 MM TDR PROBES IN THE SAPWOOD OF SCOTS PINE

In order to calibrate the instrument under controlled conditions, sample material was obtained from 41 year old Scots pine (*Pinus sylvestris* L.) felled in Devilla forest (Fife, Scotland, W 3°43', N 56°2'). Initially a sapwood block was cut approximately 10 cm in length (along the grain), 10 cm in diameter (tangentially) by 6 cm deep (radially across the growth rings) and all the bark, cambium and phloem was removed. Two pilot holes, 2.5 mm in diameter, were drilled at a spacing of 30 mm to a depth of 45 mm such that the point midway between the two holes was in the centre of the tangential face of the block. Stainless steel pins, 3 mm in diameter and 55 mm in length, were hammered into these holes leaving 5 mm protruding from the wood. In order to assess what size of block was necessary to contain the electromagnetic field associated with the TDR signal, measurements of propagation velocity of the signal were made and the block reduced in size in steps until a noticeable decline in apparent water content was observed. This indicated that the volume sensed by the signal had started to include some external air. The dimensions of the block at this point were approximately 5.5 cm by 5.5 cm by 6 cm (radially), and so all blocks used in the subsequent calibrations were larger than this. Calculations by Knight (1992) suggested that more than of 94% of the energy associated with the TDR incident pulse would be confined within the blocks used in the calibrations.

For the calibration of 50 mm long probes, 20 sapwood blocks were cut and probes installed as indicated above. The volume of each block was measured by displacement of water. These blocks were then air dried on a laboratory bench in 10 steps, each step calculated to induce a change in volumetric water fraction (*W*) of 0.04. Once a desired water content had been reached the blocks were left wrapped in plastic film for 24 hours before TDR measurements were made. It had previously been shown that this was sufficient time to allow moisture to reach equilibrium throughout the block. At least 10 TDR measurements were taken on each block before they were weighed and dried to the next desired water content. At the end of the procedure all blocks were oven dried at 80 °C to constant mass.

The calibration for the 20 mm probes followed a procedure similar to that outlined above, and 10 blocks were used. The pins were 2 mm in diameter and 25 mm in length with 5 mm of pin protruding from the blocks.

3.4.2 TEMPERATURE DEPENDENCE OF APPARENT DIELECTRIC CONSTANT.

A series of sapwood blocks with 50 mm TDR probes installed were dried to a range of water contents before being sealed in plastic film and cooled to 3 °C. Each block was then allowed to slowly warm back to room temperature. Over this period block temperature was continuously measured by a thermocouple embedded in the centre of the block and apparent dielectric constant was continuously determined by TDR.

3.4.3 FIELD TESTING OF 50 MM TDR PROBES

As part of a field experiment on a mature Scots pine forest, 50 mm TDR probes were installed in the trunks of 20 trees. To prevent changes in the volume detected by the probes as a result of growth, small rings of bark (15 mm diameter), cambium and phloem were removed from around the site of the probe. TDR measurements were made over the course of a complete year at intervals of two to three weeks. In order to compare the technique of taking increment cores to determine water content with TDR, cores were taken on one occasion to a depth of 50 mm one whorl above the implanted TDR probes using a Pressler borer. They were immediately sealed in Nescofilm ™ to prevent any moisture loss before determining the volumetric water fraction in the laboratory from measurements of fresh weight, fresh volume, and oven dry weight.

3.5 RESULTS

The calibration curves obtained for both 50 mm and 20 mm TDR probes embedded in the sapwood of Scots pine are illustrated in Figure 3.2. Third-order polynomial regression equations of the following form were fitted using Sigma plot™ where W_{50} and W_{20} are the volumetric water fraction measured using 50 and 20 mm probes respectively, and K_{50} and K_{20} refer to the apparent dielectric constant as determined by TDR at that probe length. K is dimensionless.

$$W_{50} = -0.2349 + 0.0541 K_{50} - 1.295\times 10^{-3} K_{50}{}^{2} + 1.1714\times 10^{-5} K_{50}{}^{3}$$

$$W_{20} = 0.2441 - 0.0126\, K_{20} + 5.2782\times 10^{-4} K_{20}{}^{2} - 4.0552\times 10^{-6} K_{20}{}^{3}$$

Polynomial calibration curves such as these are commonly found for water in other porous materials e.g. soil (Topp *et al.*1980). The relationship for the 50 mm probes is curvilinear such that at higher water contents a smaller change in W results in a larger change in apparent dielectric constant. The calibration for the 20 mm probes appears more linear but may only be used for measurements of W up to approximately 0.55.

Figure 3.3 combines calibrations obtained in this work together with others available for woody tissue from the literature, along with that for soil from the calibration of Topp *et al.*(1980).

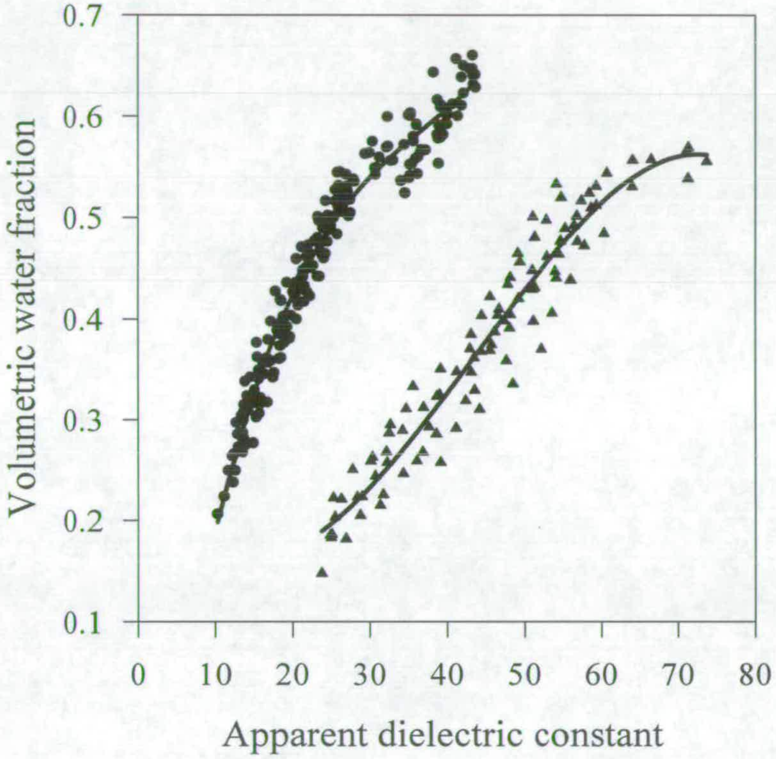

Figure 3.2 Calibration data for Time Domain Reflectometry (TDR) *Pinus sylvestris* L. sapwood water content measurements (● = 50 mm TDR probes, ▲ = 20 mm TDR probes).

Repeated measurements on sets of probes embedded in blocks at a fixed water content indicates that variability between consecutive measurements is small. The standard deviation of five consecutive measurements on 50 mm TDR probes is typically 2 picoseconds (ps) for a transit time of 750 ps. The corresponding data for 20 mm probes is 3.5 ps for a transit time of 440 ps. These transit times are those expected at *W* of about 0.4.

No significant change in apparent dielectric constant was observed with temperature. Some blocks showed very slight decreases whilst others very slight increases, not exceeding 0.024 °K^{-1} and equivalent to a change in transit time of 0.42 ps °K^{-1} These are likely to be associated with time base stability of the instrument over the course of the measurement (10 to 20 h) and not a measurable change in apparent dielectric constant.

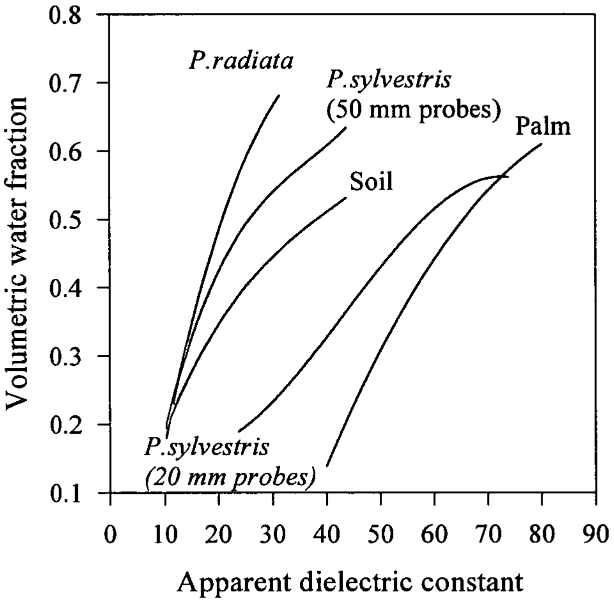

Figure 3.3 Previously published calibrations for TDR measurements on woody tissue; *P.radiata,* Constantz and Murphy (1990); palm, Holbrook *et al.* (1992), together with the calibration of Topp *et al.* (1980) for soil.

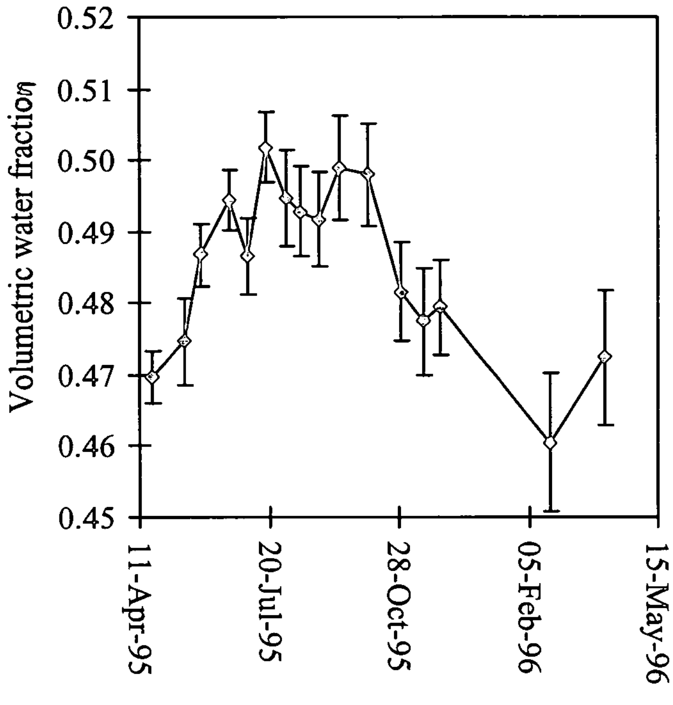

Figure 3.4. Seasonal change in the water content of the sapwood of 41-year-old *Pinus sylvestris* L. in Devilla forest, Fife, Scotland as measured using 50 mm TDR probes installed in the bole of the tree 1 m above the ground. ($n = 20$, ±1 SE)

Measurements on Scots pine in the field using 50 mm probes (Figure 3.4) show a small seasonal range in W of about 0.04. There appears to be some evidence for a decrease in embolism between April and July 1995 followed by an increase in embolism between August 1995 and April in 1996 when water contents appear to have returned to their original value. Comparative measurements between direct sampling using a Pressler borer and TDR suggests that both techniques gave similar results, TDR measured $W = 0.484$, increment cores $W = 0.470$.

3.6 DISCUSSION

The results presented illustrate the successful use of shorter TDR probes than previously reported in the literature. The use of such short probes allows measurements on smaller material than that suggested by Constantz and Murphy (1990) and will minimise those errors associated with crossing zones of changing water content. However, for rigorous and successful use of short TDR probes it is important to be aware of the sources of error and to take whatever steps necessary to minimise their effect.

3.6.1 TDR SIGNAL INTERPRETATION ERRORS.

The time taken for a voltage pulse to be reflected at the end points of a probe, the transition time, limits the accuracy in determining the precise location of these timing markers. As the transition time becomes large with respect to the transit time of the pulse down the probe, as when using short probes, the determination of the exact end points and hence true values of propagation velocity becomes more difficult. This is illustrated by the differences between the calibration curves for probes of different length (Figure 3.2). For the 20 mm probes a much larger value of apparent dielectric constant was evidently measured than with the 50 mm probes at the same water content. This was likely to be a consequence of a systematic error in determining the end points for the 20 mm probes, resulting in an overestimation of the transit time of the signal. This prevented the development of a universal calibration for Scots pine sapwood for use with very short probes. However, within each calibration there was a tight relationship between *W* and apparent dielectric constant, which allowed the use of the length specific calibration in the field.

The almost unchanging *W*, with increasing apparent dielectric constant, at the upper extreme of the calibration for 20 mm probes was thought to be an artefact of the choice of resolution of the TDR trace used for this calibration. At these high water contents (*W* approximately larger than 0.55) insufficient TDR trace was sampled to adequately cover the reflection of the signal at the termination of the probe, this then resulted in an incorrect and non systematic determination of this timing marker.

Kelly *et al.* (1995) attempted to reduce transition time errors by using higher-bandwidth TDR instruments capable of producing incident pulses with sharper step changes in voltage i.e. faster signal-rise times. They suggested that this might lead to improved resolution as a result of more clearly defined end points. Although this may be true in some instances, ultimately the transition time of the signal, which is not solely dependent on the rise time of the incident pulse will limit resolution of the system. Consequently, whether there would be any benefit of using a higher-bandwidth instrument with woody tissue needs further investigation.

3.6.2 INSTRUMENTATION ERRORS

During a TDR measurement the voltage signal is typically travelling at about a quarter of the speed of light; consequently as probe size decreases timing intervals become very small and resolution becomes an increasing problem. Inaccuracies of the timing circuitry within the TDR instrument (time-base errors) will lead to inaccurate timing of the reflected TDR signal. For the Textronix 1502, Hook and Livingston (1995) suggest that these errors are stationary and repeatable for a particular instrument and that by careful selection of cable length the error can be minimised. Care should be taken when applying the calibrations presented here to measurements made with another instrument as time base errors could be different and result in incorrect measurements of W. Concerns about the stability of the timing circuitry over time are unfounded as they are reported to be less than 13 ps (Hook and Livingston 1995). For 50 mm probes the calibration presented suggests a change of 0.01 in W will result in a change in transit time of about 10 ps, so our results suggests measurements can be made with at least this degree of resolution.

3.6.3 TEMPERATURE DEPENDENT MEASUREMENT ERRORS.

The influence of temperature on dielectric constant may be of importance in attempting to measure small changes in water content. Measurements may be taken at different times of day or year at different stem temperatures. The reported variation in dielectric constant for water with temperature is approximately -0.37 K^{-1} (Kaye and Labey 1986). Solids and air are far less sensitive to temperature than this, and consequently any change in dielectric constant with temperature of a tree stem may be expected to most closely follow that of the water. Pepin *et al.* (1995) provide a detailed analysis of temperature dependent measurement errors associated with soil-water measurements, but as yet there is little information on the temperature dependence of dielectric constant in woody tissues. The data we report here suggest that there was no detectable change in dielectric constant with temperature in blocks of pine sapwood. Data collected by Pepin *et al.* (1995) indicate that the change in dielectric constant of free water with temperature is larger than that of water held in a matrix, and the finer the matrix the greater this affect. They suggest that this might possibly be a result of the large active surface areas of the matrix which constrain the rotational freedom of water molecules, i.e. the bound water fraction increases as particle size decreases or organic matter content increases, which would be supported by our measurements.

3.6.4 FURTHER POSSIBLE SOURCES OF ERROR.

Errors may also arise from electrical noise from external sources; multiple reflections of the transmitted signal at impedance discontinuities along the cable/probe system, e.g. at the point of connection to the instrument or probe, or at abrupt changes in water content, e.g. the heartwood/sapwood boundary within the tree; and changes in the location of the starting point of the probe as a result of repeated connection of cables to the probe. Results from consecutive measurements on sets of pins and repeated disconnection and connection of the cable to probes indicate the latter two sources of error are small and through careful placement of the cable and probe, together with repeated measurements all these errors can be minimised.

3.6.5 USE IN THE FIELD

The seasonal variation of *W* measured in the trunk of mature Scots pine with 50 mm probes (Figure 3.4) was small, with no directional trend that could be associated with phenological processes such as the formation of new heartwood in the sensed zone. Limited measurements using 20 mm probes (data not presented) gave values of *W* towards the extreme of the calibration (Figure 3.2), in the region where *W* could not be calculated with adequate precision. These measurements indicated that when *W* across 50 mm of sapwood was 0.48, *W* in the outer 20 mm of sapwood was approximately 0.55 or larger. This decrease in *W* with distance from the cambium to heartwood confirms similar findings in conifers (Chalk and Bigg 1956, Phillips *et al.*

1996), and illustrates the need to use the shortest possible probes to investigate changes in *W* within the physiologically active sapwood

The initial damage from implantation of the probes was small compared with the sensed volume, and no evidence of a wound reaction around the probes was apparent in the measurements after a year. One factor that may have increased the variability within the data was the production of resin which in a few cases completely covered the protruding pins and may have had a small effect on the determination of the starting point of the probe and dielectric constant of the sample. Retrospectively it would have been possible to eliminate this error by allowing a larger length of probe to protrude from the tree leaving the initial resin produced to form an undisturbed seal.

Compared to other techniques TDR is safe, quick, non destructive and simple to use allowing easy replication in the field. The equipment is readily portable and does not require a mains power supply or generator. The use of this rather new technique could open new opportunities for the analysis of seasonal changes in xylem water content and could provide a better understanding of the occurrence and ecological significance of xylem embolism in conifers.

4. Stomatal control of transpiration and hydraulic conductance*

4.1 SUMMARY

An investigation of the impact of drought on the physiology of 41-year-old Scots pine (*Pinus sylvestris* L.) was made in southern Scotland. Measurements were made of the seasonal course of transpiration, canopy stomatal conductance, needle water potential, xylem water content, soil-to-needle hydraulic resistance, and growth. Comparison was made between droughted plots and those receiving average precipitation. Under drought, transpiration rate declined once a threshold volumetric soil water fraction of 0.12 had been reached over the top 20 cm of soil, and transpiration was thereafter a near linear function of soil moisture. As the drought became intense hydraulic resistance between soil and needles increased by a factor of three as pre-dawn needle water potential declined from -0.54 MPa to -0.71 MPa. A small but significant increase in xylem embolism was detected in year old shoots. Stomatal control of transpiration prevented needle water potential from declining below -1.5 MPa. Basal area, shoot and needle growth was significantly reduced in the droughted treatment. In the year following the drought, canopy stomatal conductance and soil-to-needle hydraulic resistance recovered. Current year needle extension recovered, but a significant reduction in basal area increment was evident one year after the drought. The results suggest that in response to soil drought mature Scots pine closes its stomata sufficiently to prevent the development of substantial xylem embolism. The reduced basal area growth in the year after the drought is not likely to be a result of residual embolism from the previously droughted period.

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4.2 INTRODUCTION

It is widely believed that the increasing incidence of summer droughts in northern Europe may be causing a decline in the health of trees, and that drought occurring in one particular summer may cause hydraulic and physiological responses that are carried over into subsequent years (Innes 1993). Yet there have been few experimental studies in which the relevant processes have been demonstrated in droughted versus irrigated plots, and the mechanism involved in such carry-over responses remains a matter of speculation

One hypothesis is that drought induces cavitation of the water columns in the xylem when they reach a critical tension during high transpiration in the summer. Although early experiments involving saw-cuts in the trunks of trees provide evidence for ‘spare capacity’ in the transport system (Greenidge 1955, Kozlowski 1965), it seems likely that the hydraulic resistance of the tree or its branches is certain to increase during drought as a result of cavitation. Some authors have gone so far as to suggest that the increase in hydraulic resistance following cavitation will predispose the tree to further cavitation, resulting in catastrophic or ‘runaway’ cavitation with complete dysfunction of xylem water transport (Tyree and Sperry 1988, Jones and Sutherland 1991). This does, however, overlook the possibility that the stomatal conductance may decline in response to a chemical or hydraulic signal from the roots (Blake and Ferrell 1977, Davies and Zhang 1991, Tardieu and Davies 1993), thus reducing the transport of water in the xylem and hence avoiding the critical tensions that would cause cavitation.

Much of the work that underlies the present state of knowledge on the impact of drought on trees comes from experiments on seedlings and saplings (Gollan *et al.* 1985, Saliendra *et al.* 1995, Jackson *et al.* 1995c). In mature forests, rather fewer experiments on the impact of drought have been possible (Rutter 1967, Black 1979, Running 1979, Borghetti and Vendramin 1987, Schiller and Cohen 1995, Lu *et al.* 1996, Sturm *et al.* 1996). There are good reasons to suspect that mature trees may behave differently from juveniles, as signals from the roots are likely to take a long time to reach the canopy, and the roots may extract water from great depth (Canadell *et al.* 1996). The present study was designed to reduce the major uncertainties in our knowledge of how pine forests respond to drought:

(i) does stomatal closure occur in response to soil dryness, in a similar manner as suggested from studies on young trees ? (Gollan *et al.*1985, Schulze 1987) This knowledge is not only of great theoretical interest, but it also is needed for models of forest growth and yield, and for parameterising the various representations of forest that are currently being used in Global Circulation Models (Sellers *et al.*1997).

(ii) can stomatal closure prevent cavitation by reducing the transpirational flux, so that the critical tension for cavitation is never reached or rarely reached (Jones and Sutherland 1991, Williams *et al.* 1996)?

(iii) does the hydraulic resistance in the soil-vegetation-atmosphere system increase during drought, and can it recover when the drought ceases ? The question of whether or not recovery occurs is important, as refilling of any embolised tracheids is believed to occur only when the tensions in the water columns approach zero (Borghetti *et al.* 1991, Edwards *et al.* 1994).

These issues were addressed by artificially droughting a mature stand of Scots pine in southern Scotland, and carrying out appropriate physiological measurements.

4.3 MATERIALS AND METHODS

4.3.1 STUDY SITE

The site was Compartment 474 of the Forestry Commission's Devilla forest in Fife, Scotland (see Table 1 for details), situated on one of a series of low hills of fine-grained carboniferous sandstone. The soil was a sandy loam, with occasional pockets of heavier less freely-draining soil in the vicinity. The water table was considered to be well below the rooting depth. Ground vegetation was dominated by *Deschampsia flexuosa* (L.) Trin., *Calluna vulgaris* (L.) Hull. and *Vaccinium myrtillus* L. Eight square plots each approximately 100 m^2 containing between eight and fifteen trees were selected.

Table 4.1 The climate data for the area was extracted from the Meteorological Office Climatological Memoranda 108 & 115 and the 20 year average rainfall from a local station (Grangemouth). Diameters at breast height and numbers of trees per hectare were based on measurements of all trees within 0.25 ha. Leaf area index was calculated from 28 hemispherical photographs taken throughout the compartment. Where available one standard deviation is given in brackets.

Site and stand characteristics	
Latitude	56°2'
Longitude	3°43'
Elevation (m)	75
Average January temperature (°C)	2.5
Average July temperature (°C)	14.8
Average annual precipitation (mm)	820
Planting year	1954
Average height (m)	15
Average diameter at breast height (cm)	20.1 (4.9)
Leaf area index (m^2 m^{-2})	1.92 (0.39)
Overbark basal area (m^2 ha^{-1})	28
Sapwood basal area (m^2 ha^{-1}) (excluding heartwood)	21
Trees per hectare	836

Each plot was isolated from the surrounding soil by a 1.5 m deep ditch, the side of which was lined with heavy black polythene sheet before being refilled with soil. This prevented lateral inflow of water and allowed rooting volumes to be droughted (or watered) as desired. Four plots were assigned to a drought treatment whilst the remaining four were maintained at soil moistures close to average conditions by irrigating as required. This treatment will be referred to as the control treatment throughout. Precipitation and stem flow was prevented from reaching the soil in the four droughted plots by construction of clear polythene covers over the plots which deflected intercepted water beyond the previously installed ditches. These covers were inclined, supported at 1.5 m above ground in the centre of the plots and at 0.3 m at the edges, thus enabling access to the soil and boles of the trees, and allowing free movement of air above the plot (see Appendix 3).

To gain access to the forest canopy a 0.6 m wide by 9 m long walkway was suspended between two 15 m high tripole mast towers at a height of about 11.5 m. This walkway spanned a neighbouring droughted and control plot and allowed access to the foliage on 4 or 5 trees per treatment.

The polythene covers and soil moisture barrier were installed in October 1994 and measurements began in April 1995. Soil water, growth, stem and shoot embolism measurements were made at two week intervals. Diurnal time courses of needle water potential were made at approximately three week intervals. At the beginning of November 1995 the covers on the droughted plots were removed and irrigation brought soil moisture back to pre-drought levels.

4.3.2 SOIL MOISTURE

Soil volumetric water fraction (*W*) was determined using time domain reflectometry (TDR), using probes of the two-pin balanced design. Three sets of 20 cm and two sets of 50 cm probes were left permanently installed in each plot. Measurements were made with a Tektronix 1502B cable testing oscilloscope (Tektronix Corp., Redmond, OR, USA) fitted with a SDM1502 interface connected to a 21X datalogger (Campbell Scientific (UK) Ltd., Shepshed). The calibration of Ledieu et al. (1986) was used to calculate *W* from the measured apparent dielectric constant.

4.3.3 MICROCLIMATE

Sensors to measure air temperature and relative humidity (HMP35AC, Campbell Scientific), photosynthetically active radiation (PAR, Skye 215, Skye instruments, Llandrindod Wells, Powys, Wales), wind speed (A100R, Vector Instruments, Rhyl, Clwyd, Wales) and net radiation (Q7, Campbell Scientific) were left permanently installed above the canopy at a height of 17 m. Measurements were made at minute intervals and averaged and stored every hour on a 21X datalogger (Campbell Scientific).

4.3.4 STEM AND SHOOT EMBOLISM

The relative water content (RWC) of the sapwood in the bole of five trees per plot at 0.5 m above the ground was monitored with 0.05 m TDR probes as described by Irvine and Grace (1997). The degree of embolism in the xylem of shoots of current and previous years growth was assessed by destructive sampling. On each measurement occasion four shoots per treatment were collected from the middle to lower canopy with pole pruners, and the needles immediately removed before the sample was wrapped tightly in sealing film to prevent any water loss (Nescofilm™). On returning to the laboratory the shoots were stored at 4 °C for a maximum of 24 h before their xylem RWC was assessed according to the method of Sobrado *et al.* (1992). All measurements of the RWC on shoots were made by Michael Perks.

4.3.5 NEEDLE WATER POTENTIAL AND TURGOR

Needle water potential was assessed at 3 h intervals between pre-dawn and dusk. Shoots were randomly sampled from the middle to lower canopy (no distinction was made between needles exposed to sun or shade) by using pole pruners. They were immediately placed in plastic bags with damp tissue paper to minimise water loss. One shoot per plot was sampled every measurement period and two water potential measurements were made using a pressure chamber (Model 1400, Skye instruments) on single needles that had elongated the previous year. Measurements were made within 20 minutes of the collection of the samples. During the mid-day measurement period, after the needle water potentials had been determined, needles of the same age class were removed from the shoot and placed in a 2 cm^3 plastic syringe, which was then immediately frozen in dry ice. These samples were transferred to a freezer pending measurement of osmotic potential. Once thawed osmotic potential was determined using a vapour pressure osmometer (Model 5100C, Wescor Inc., Logan, UT, USA). Turgor pressure was calculated as the difference between the water potential measured in the field and the osmotic potential determined in the laboratory.

4.3.6 SAP FLOW AND TRANSPIRATION

Sap flux density was measured continuously by the heat pulse (compensation) method on four trees per treatment (one tree per plot) at a height of 1 m using a 'Custom' system (Soil Conservation Centre, Palmerston North, NZ). Heat pulse velocity (HPV) was determined at different depths in the sapwood at four points around the circumference of the tree at 90° to each other. At each point two thermistor probes were inserted into the xylem 10 mm above and 5 mm below a heating probe. Every 20 min a 1 s heat pulse was applied and the HPV recorded. HPV was converted to sap velocity using the theory of Marshall (1958) with corrections as calculated by Swanson and Whitfield (1974) for inhomogeneities caused by sensor implantation wounds. The depth of sapwood, and hence inner boundary at which zero sap velocity was assumed, was determined from cores of wood taken with a Pressler borer at the end of the experiment. By inspecting these cores under strong diffuse light a distinct colour change was discerned, marking the boundary between sapwood and heartwood. The sap velocity profile together with calculations of the area of sapwood that would be experiencing a specific sap velocity was used to calculate sap flux density.

Measurements of sap flux density within any hour period were averaged for the four trees per treatment. This figure together with an estimate of total sapwood area per unit ground area, as estimated from wood core samples and basal area measurements (see Table 4.1), was used to estimate transpiration of the pine canopy on a ground area basis, *E*. Approximately 2500 hourly daylight measurements of transpiration were collected using this technique.

4.3.7 SOIL-TO-NEEDLE HYDRAULIC RESISTANCE

On days during which diurnal measurements of needle water potential were made the hydraulic resistance between soil and needles was calculated from the relationship between needle water potential and sap flux per unit ground area ;

$$R_{\text{soil-needle}} = (\Psi_L - \Psi_{L\ \text{pre-dawn}}) / E \qquad \text{Equation 4.1}$$

Where $R_{\text{soil-needle}}$ is the hydraulic resistance between soil and needles (MPa s m^{-1}), Ψ_L is the needle water potential (MPa), $\Psi_{L\ \text{pre-dawn}}$ is the pre-dawn needle water potential, assumed to equal the soil water potential (MPa), and E the estimate of transpiration of the pine canopy per unit ground area (m^3 m^{-2} s^{-1}), obtained from sap flux data. Linear interpolation between the hourly values of sap flux was used to estimate the value for the same instant water potential was measured.

4.3.8 CANOPY STOMATAL CONDUCTANCE

The canopy stomatal conductance g_c, or its reciprocal canopy stomatal resistance, was computed from sap flux measurements on an hourly basis by inversion of the Penman-Monteith equation ;

$$r_s = \frac{s r_a (A - \lambda E) + \rho_a c_p D}{\lambda E \gamma} - r_a \qquad \text{Equation 4.2}$$

where r_s and r_a are canopy stomatal and aerodynamic resistances respectively (s m^{-1}), s is the rate of change of saturation vapour pressure with temperature (Pa K^{-1}), A is the net radiation available at the level of the pine canopy (W m^{-2}), λ is the latent heat of vaporisation of water (J kg^{-1}), E is the canopy transpiration expressed on a ground area basis (kg m^{-2} s^{-1}), ρ_a the density of dry air (kg m^{-3}), c_p is the specific heat of air (J kg^{-1} K^{-1}), D is the saturated vapour pressure deficit of air (Pa), γ is the psychrometric constant (Pa K^{-1}). The canopy aerodynamic resistance, or its reciprocal canopy aerodynamic conductance, was estimated from the horizontal wind speed above the canopy using the equation for the resistance to momentum transfer (Monteith and Unsworth 1990) ;

$$g_{am} = \frac{k^2 u_z}{\{\ln[(z-d)/z_0]\}^2}$$

where g_{am} is the canopy aerodynamic conductance to momentum transfer (m s^{-1}), which was assumed to approximate to the canopy aerodynamic conductance to water vapour transfer, *k* is von Karman's constant (0.41), u_z is the wind speed (m s^{-1}) as measured at height *z* (17 m) above the ground, *d* is the zero plane displacement height (0.66 ∘ canopy height, m) and z_0 is the roughness length (0.1 ∘ canopy height, m).

4.3.9 LEAF AREA INDEX (LAI)

Leaf area index was estimated from 28 hemispherical photographs by applying an inverted canopy gap fraction model (in-house image analysis software; author Dr.P.R. van Gardingen, analysis provided by Linda Sharp). For coniferous stands it has been recognised that this approach can provide erroneous values (Smolander and Stenberg 1996, Welles and Cohen 1996) because of i) a non-random or 'clumped' distribution of foliage leading to an underestimation of the 'true' LAI and ii) the inclusion of shading elements other than leaves i.e. branches and trunks, leading to a overestimation of 'true' LAI. Whilst these two effects tend to counteract each other, there is currently no universal method to apply a suitable correction to the LAI estimate (Stenberg 1997). Consequently the LAI presented in Table 4.1 may be subject to a degree of error.

4.3.10 GROWTH AND CHANGES IN LAI

Approximately thirty girth bands per treatment installed at 0.2 m above the ground were used to assess the rate of sapwood growth. Current year needle and shoot growth was determined by repeated measurement on three trees per treatment using vernier callipers. Six shoots per tree at mid-canopy level on trees within reach of the aerial walkway were identified and labelled, and needle length measurements were made on a sample of 10 current year needles on each of these shoots on each measurement occasion. Shoot growth was measured on the same shoots. To estimate needle loss over the course of the experiment four shoots per tree on three trees per treatment were sampled. On each shoot between 10 and 20 one and two-year-old needles were marked at their bases with an indelible marker, and at points throughout the experiment a count of those remaining was made. All growth measurements were made by Federico Magnani.

4.3.11 STATISTICAL ANALYSIS

If graphical presentation of measured variables showed a clear interaction between treatment and measurement date for a particular variable, t-tests were performed to test the significance of treatment at each date. If no clear interaction between treatment and date was evident, or if a confused picture was presented by the data, a two-way ANOVA with one repeated measure factor was made. In these instances a correction to the number of degrees of freedom using ε (Greenhouse-Geisser) was made as necessary. All tests were performed using the SAS package (SAS Institute Inc 1988).

4.4 RESULTS

The experimental period was unusually dry for mid-Scotland. Between the beginning of March 1995 and the end of August 1995 the rainfall was 128 mm less than the 20 year average (Fig. 4.1). To prevent the control plots from experiencing drought, irrigation provided 125 mm over the same period.

Soil moisture integrated over the top 20 cm depth was significantly reduced in the droughted plots from the beginning of measurements in April 1995 as a result of winter rainfall being withheld from the droughted treatment (Fig 4.2, upper panel). W in the droughted treatment fell steadily to a minimum of 0.05 by the end of August 1995. The fluctuating nature of soil moisture in the control treatment was due to periodic irrigation over the season, but W never fell below 0.2. Soil moisture integrated over 50 cm depth (not presented) in the control treatment showed similar behaviour to that over the upper 20 cm. In the droughted treatment the values of W over 50 cm depth fell steadily from 0.21 in mid-May 1995 to 0.11 by the end of August 1995.

Pre-dawn needle water potential in the droughted treatment was consistently more negative than in the control treatment throughout the season (Fig. 4.2, panel 2). The largest differences developed from mid-July 1995; all points from this date onwards being significantly different ($P < 0.05$) until the covers were removed from the

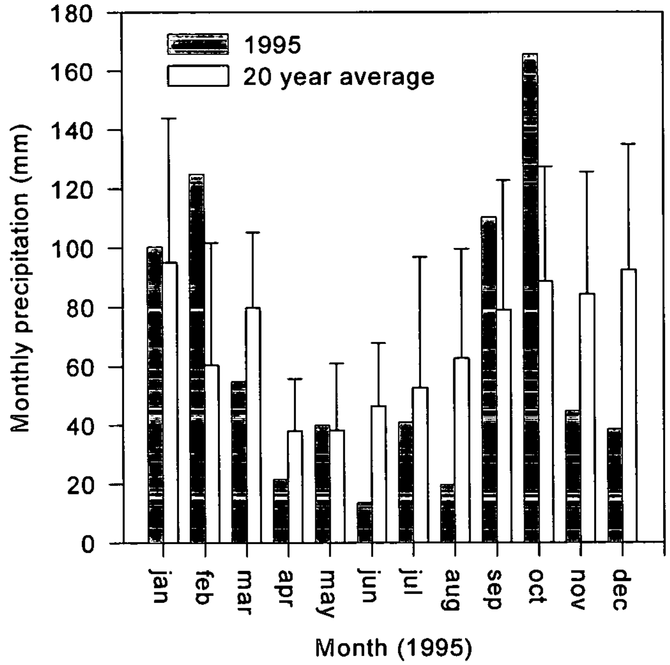


Figure 4.1 The average monthly rainfall distribution (1977-1997) compared to rainfall received during the drought year (1995). The rain gauge was sited 4 km south of the experimental plots. Error bars indicate + 1 SD.

droughted plots at the beginning of November 1995. Values in the control treatment never fell below -0.55 MPa whereas a minimum value of -0.75 MPa was recorded towards the end of August 1995 in the droughted treatment. The abrupt recovery of droughted pre-dawn water potential in mid-September 1995 was regarded as the termination of the drought. At this point a slight inflection in the soil moisture measurements was also seen. This period was associated with several heavy rain events and there may have been lateral movement of water below the installed soil moisture barrier alleviating the drought.

The seasonal pattern of transpiration was evident in the control treatment (Fig. 4.2, panel 3). The higher values of up to 2 mm d^{-1} occured during the summer months. Day-to-day variation was large and consistent with variable weather conditions. To remove daily and seasonal effects the ratio of transpiration rates in control and droughted plots is shown in the lowest panel (Fig.4.2). Transpiration in the droughted treatment was largely unaffected until mid-June 1995 and then showed a steady decline to 30 % of the control value by the end of August 1995, after which some

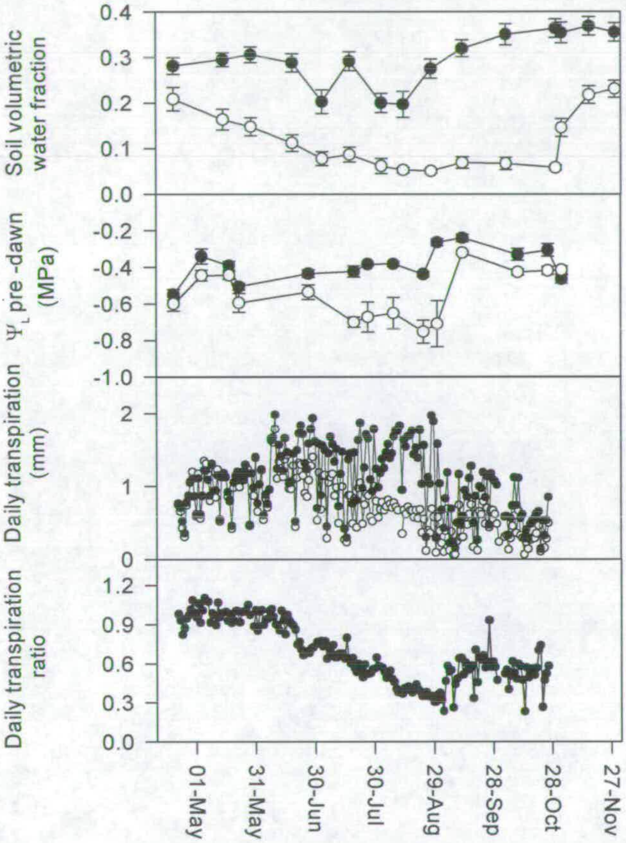


Figure 4.2 Seasonal variation in the volumetric soil water fraction integrated over the top 20 cm soil depth, the pre-dawn needle water potential (Ψ_L pre-dawn), and the daily transpiration for droughted (open symbols) and control treatments (closed symbols) over the course of 1995. The lowest panel is the droughted daily transpiration divided by the control daily transpiration. Error bars indicate ± 1 SE .

recovery occurred. Between mid-May 1995 and the end of August 1995 140 mm of water was transpired in the control treatment, whereas only 93 mm by the droughted treatment. Soil moisture measurements in the droughted treatment over the same time period showed that this corresponded to a change of 50 mm in the top 50 cm of soil.

The minimum daily leaf water potentials were not significantly different ($P > 0.05$) between droughted and control treatments apart from at the height of the drought at the end of August 1995 (Table 4.2). Mid-day bulk needle turgor was consistently larger in the control treatment although not significantly ($P < 0.05$) except at the height of the drought (Table 4.2). There was little evidence for solute concentration in the droughted treatment apart from at the peak of the drought in August 1995 (Table 4.2).

Table 4.2 Plant water relations parameters during the development of the drought in 1995 and one day during the following spring (10th May 1996) after the drought had been terminated. Values for minimum leaf water potential (Ψ_{Lmin}) and mid-day leaf turgor are the mean of 4 values per treatment. Mid-day canopy stomatal conductance (g_c) is calculated from transpiration (sap flux) measurements from four trees per treatment. *P* values refer to t-tests made between the treatments.

	Minimum diurnal Ψ_{Lmin}(MPa)		*P*	Mid-day leaf turgor & {osmotic potential} (MPa)		*P*	Mid day g_c (mm s^{-1})	
	Control	Droughted		Control	Droughted		Control	Droughted
4-May-95	-0.97	-1.12	0.12	1.14{-2.11}	1.07{-2.18}	0.49{0.50}	4.0	4.0
23-May-95	-1.00	-0.95	0.71	1.04{-1.97}	0.93{-1.86}	0.52{0.16}	4.5	4.6
13-Jun-95	-0.98	-0.94	0.66	0.97{-1.95}	0.85{-1.79}	0.27{0.10}	4.9	4.5
27-Jun-95	-1.08	-1.17	0.44	0.76{-1.84}	0.64{-1.80}	0.37(0.66}	4.5	3.3
27-Jul-95	-0.96	-1.17	0.09	1.05{-1.52}	0.88{-1.64}	0.08{0.28}	1.6	0.9
9-Aug-95	-1.19	-1.41	0.11	0.73{-1.71}	0.62{-1.96}	0.09{<0.01}	3.9	1.6
31-Aug-95	-0.68	-1.08	<0.01	0.89{-1.57}	0.64{-1.72}	<0.01{0.07}	8.8	2.5
13-Sep-95	-0.89	-1.11	0.11				3.7	2.4
11-Oct-95	-0.79	-0.91	0.15	1.15{-1.57}	1.05{-1.60}	0.25{0.79}	7.1	3.6
10-May-96	-0.91	-0.98	0.53				8.4	7.2

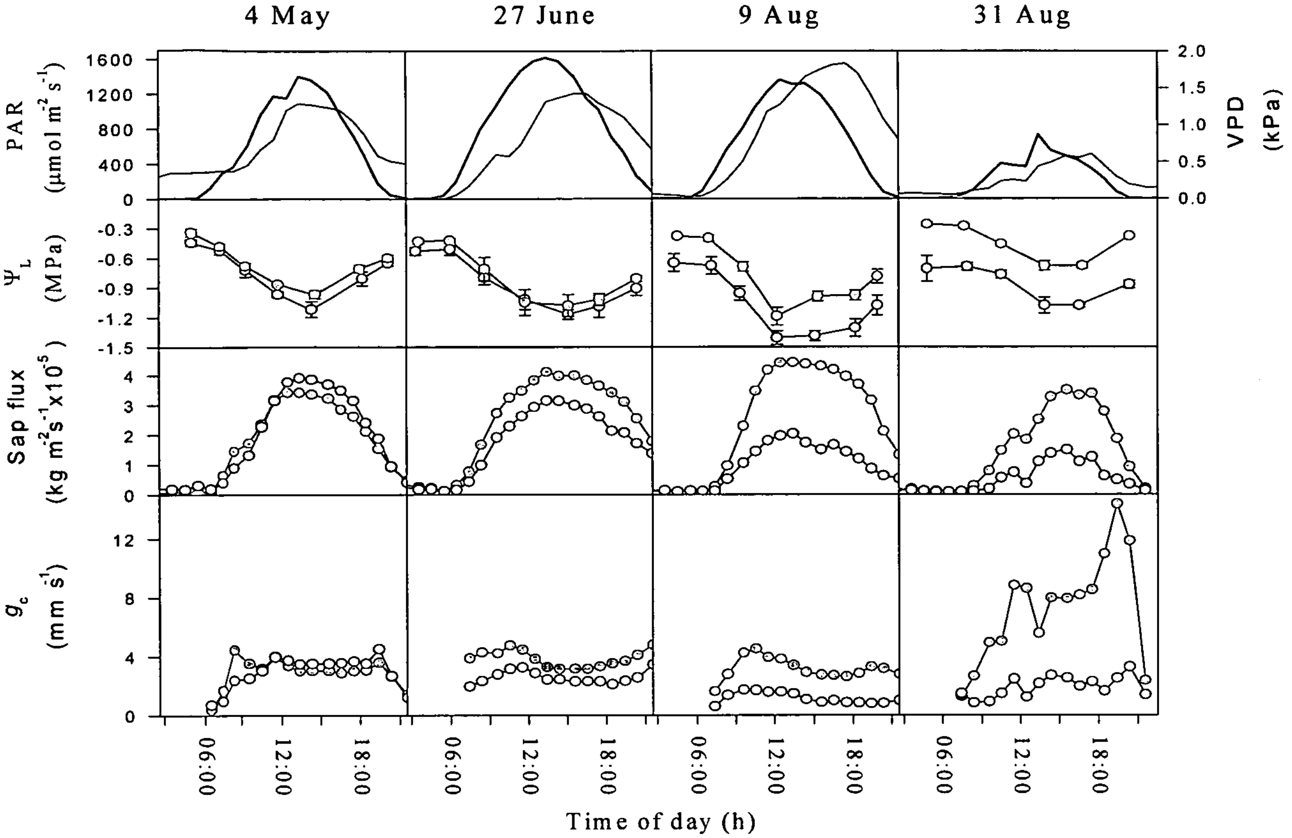


Figure 4.3 Diurnal courses of physiological and meteorological variables during four days as the drought progressed in 1995. Photosynthetically active radiation (PAR, haevy line), air vapour pressure deficit (VPD, fine line), needle water potential (Ψ_L), transpiration rate from the tree canopy estimated from sap flux and expressed on a ground area basis, and canopy stomatal conductance (g_c,). Symbols are open for the droughted and closed for the control treatments respectively. Error bars indicate ± 1 SE

The diurnal behaviour of sap flux, canopy stomatal conductance, leaf water potential and meteorological variables on four days during the drought period are presented in Figure 4.3. On the 4th of May 1995 there is no significant difference between treatments with respect to any of the variables. The saturation vapour pressure deficit (VPD) on this day was relatively high for mid-Scotland. Canopy stomatal conductance shows an initial rise in the morning followed by a mid-day decline and partial recovery in the evening, a pattern which was repeated on other days (Fig. 4.3). On the 27th of June 1995, a day with similar meteorological conditions and patterns in bulk leaf water potentials as on the 4th of May 1995, there is a significant decline in sap flux in the droughted treatment, although no apparent difference between bulk leaf water potential in the two treatments (Fig. 4.3). During the 9th and 31st of August 1995 the continuing decline in sap flux is evident. The 31st of August 1995 was a dull overcast day with low PAR and VPD. There is a high degree of apparent sensitivity of canopy stomatal conductance to VPD on this day.

The relationship between sap flux and leaf water potential on three days throughout the drought and one day in the following spring is illustrated in Figure 4.4. The relationships are more or less linear, with an increasing slope for the droughted treatment over the period. The data points for the droughted treatment on the 9th of August 1995 show a suggestion of hysteresis in the relationship, a tendency that was noted on several other days when the drought was most extreme (data not presented). There is no significant difference between the slopes of this relationship on the 10th of May 1996.

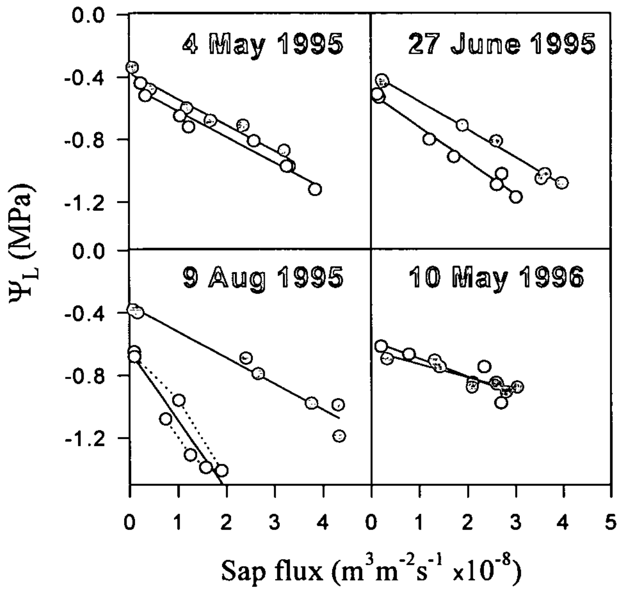


Figure 4.4 Relationship between needle water potential (Ψ_L) and sap flux (on ground area basis) for both droughted (open symbols) and control treatments (closed symbols) for three days during the development of the drought in 1995 and one day the following spring after the drought had been terminated (10th May 1996).

The soil-to-leaf hydraulic resistance, obtained as the gradient of the relationships presented in Figure 4.4, is more or less constant in the control treatment but shows a progressive increase by approximately a factor of three in the droughted treatment (Fig. 4.5). Differences between treatments were significant ($P < 0.05$) between the 27th of June and 31st of August 1995.

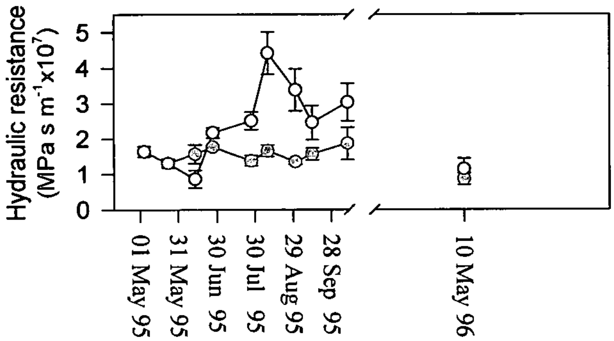


Figure 4.5 Seasonal changes of the soil-to-needle hydraulic resistance for droughted (open symbols) and control (closed symbols) treatments. Error bars indicate ± 1 SE.

Table 4.3 Data reported in the literature for the soil-to-needle hydraulic resistance expressed on a unit basal area sapwood basis , unit ground area basis and unit needle area basis.

Hydraulic resistance			Comments and source
Sapwood	Ground	Needle	
(MPa s m^{-1}x 10^4)	(MPa s m^{-1}x 10^7)		
3.2	1.5	2.8	41-yr-old Scots pine, no drought, Devilla, UK, this paper.
2.5	1.2	2.8	41-yr-old Scots pine (plot 1), UK, Whitehead D. et al. 1984.
-	0.6	2.6	43-yr-old Scots pine, Thetford, UK, Jarvis 1976.
1.9	0.5	1.5	41-yr-old Scots pine (plot 2), UK, Whitehead D. et al. 1984
1.4	-	-	37-yr-old Maritime pine, Landes de Gascogne, FR, Granier A. et al. 1989.
1.0	0.7	1.9	64 -yr-old Maritime pine, Ribatejo, Portugal, Loustau D. et al. 1996
0.8	0.3	0.6	38-yr-old Scots pine, Thetford, UK, Jackson G.E. et al. 1995b.

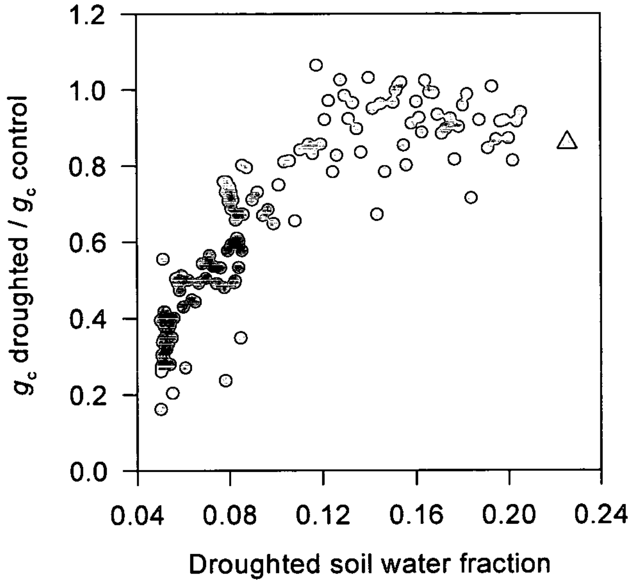


Figure 4.6 Relationship between (mid-day droughted canopy conductance / mid-day control canopy conductance) against droughted treatment volumetric soil water fraction integrated over the top 20 cm soil depth. The triangular symbol refers to a measurement made one day in the spring 1996 after the termination of the drought.

Trends in canopy stomatal conductance are best expressed as a fraction (i.e. g_c mid-day drought / g_c mid-day control). There was no response of the canopy stomatal conductance to soil water fraction as measured to 20 cm depth in the droughted treatment until the water fraction had declined to 0.12 (Fig. 4.6). Between a water fraction 0.12 and 0.05 the decline in canopy stomatal conductance appears to be linear. In the spring (1996) after the termination of the drought the canopy stomatal conductance appears to have almost returned to its pre-drought level (triangular point in Fig. 4.6). The frequency distribution of mid-day canopy stomatal conductance over the droughted period (Fig. 4.7) provides mean values of 5.8 mm s^{-1} and 3.3 mm s^{-1} for the control and droughted treatments, respectively.

Measurements of the RWC of the sapwood in the trunk over the drought period revealed a significant Treatment x Date interaction $F(8,48) = 7.21$ $p < 0.01$ (Fig. 4.8, lower panel), which was due to a significant increase in the RWC of the control treatment $F(8,24) = 26.35$ $p < 0.01$, rather than to a decline in RWC of the drought treatment $F(8,24) = 3.85, p > 0.09$. There was no evidence of a significant treatment effect at any one date.

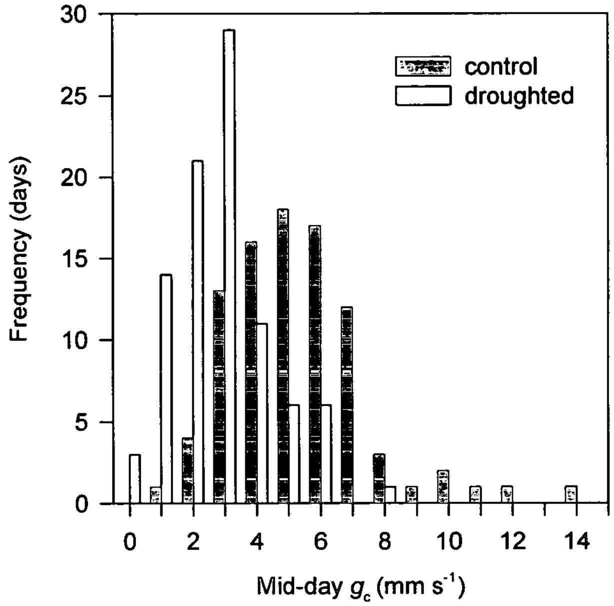


Figure 4.7. The frequency distribution for mid-day canopy stomatal conductance from the beginning of June to the end of August 1995 for droughted and control treatments

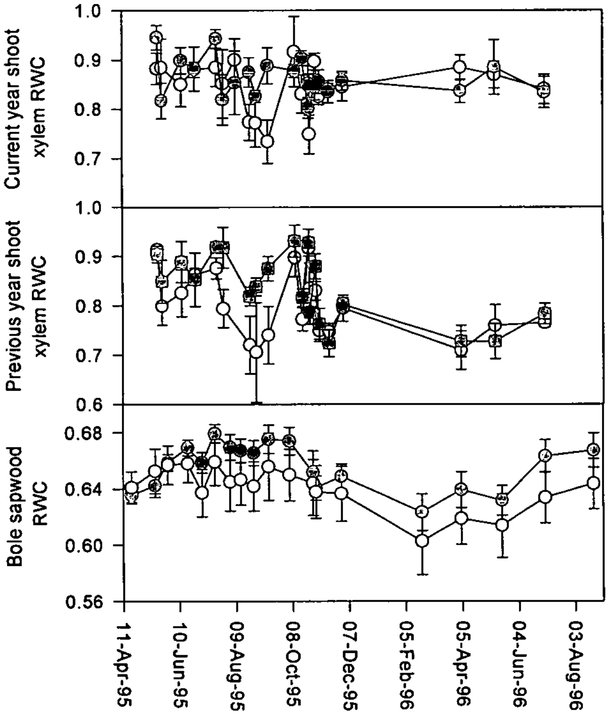


Figure 4.8. The seasonal behaviour of the relative water content (RWC) of the xylem in current year (upper panel) and the previous year shoots (middle panel), together with the RWC of the sapwood (to 5 cm depth) in the bole of the trees over the course of the drought year (1995) and the following year. Open symbols refer to the droughted and closed symbols to the control treatments respectively. Error bars indicate ± 1 SE, n=4.

RWC of the xylem of the shoots was considerably higher than in the bole (Fig. 4.8, upper two panels) with a significant difference between treatments in previous years shoots, when grouped over all dates $F(1,42) = 8.61, p < 0.05$ (Fig 4.8, middle panel). There was no evidence of a significant treatment effect at any one date.

The imposed drought resulted in a 14 %, 34 % and 20 % reduction in basal area, shoot and needle growth respectively in comparison with the control by the end of the 1995 growing season (Fig. 4.9). Needle growth is expressed relative to the final length of needles on the same shoot in 1994 in order to remove any variability that could be attributed to differing light environments. In the case of shoot and needle growth, the differences between treatments were evident from an early stage in the

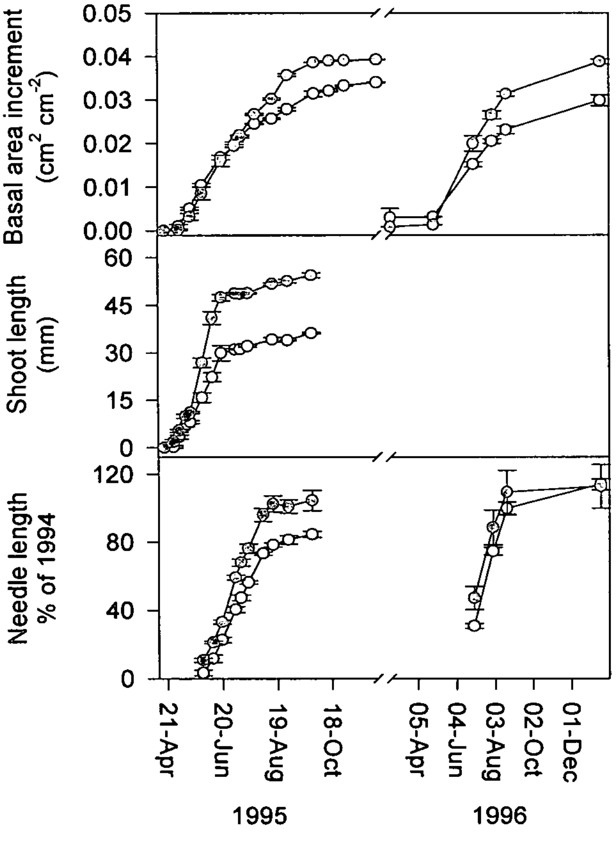


Figure 4.9 Seasonal changes in tree growth for the droughted (open symbols) and control treatments (closed symbols) for 1995 (the drought period) and the following year. Basal area increment (upper panel) is referenced to basal area measured in April 1995. Shoot length data (middle panel) was unavailable for 1996. Needle length is expressed relative to 1994 to remove effects of differing light environments between the sampled needles. Error bars indicate ± 1 SE.

drought (Fig. 4.9, 1995, bottom two panels). However sapwood growth at the base of the tree only showed a reduction in the droughted treatment from mid-August 1995, at a point when drought was becoming most extreme (Fig. 4.9, 1995, upper panel). There was no evidence of greater needle loss during the season in the droughted treatment. Growth measurements in the year following the drought (Fig. 4.9, 1996), when no significant soil moisture deficit developed, indicated no difference in needle growth by the end of the season between the previously droughted and control treatments, but basal area growth had a 23 % reduction in the previously droughted treatment compared with the control.

4.5 DISCUSSION

A significant decline in canopy stomatal conductance was observed once a threshold soil moisture deficit had been reached (Fig. 4.6). Approximately 57% of the extractable soil moisture was removed from the top 50 cm of soil before transpiration became limited. Rutter (1967) reported a figure of 54 % based on water available between 0.01 and 0.1 MPa over a soil depth of 180 cm. Stewart (1988) found no decline in canopy conductance until a soil moisture deficit of 78% was reached over 900 mm depth. Black (1979) working with Douglas fir reported a threshold figure of 40 % extractable soil water content when measured over the rooting depth. More recently Kelliher *et al.* (1997 in press) computed the threshold soil moisture from various studies on pines as a fraction of the soil moisture when soil water potential was 5 kPa and reports an average value of 50%. Gollan *et al.* (1985) and Turner *et al.* (1985) report similar thresholds for both woody and herbaceous species. In our study 54 % of the water transpired by the droughted treatment was extracted from below 50 cm depth and yet a very strong decline in canopy stomatal conductance was evident that appeared to be in response to soil moisture deficit in the upper soil horizons. Since the majority of the roots are contained in these upper horizons (Roberts 1976a) the response of canopy stomatal conductance appears to be linked to the soil moisture deficit experienced by the majority of the roots even if water was being extracted from greater depth.

The range of mid-day values of canopy stomatal conductance (Fig. 4.7) are consistent with other data available for Scots pine (Hellkvist *et al.* 1980, Whitehead *et al.* 1984, Lindroth 1985, Beadle *et al.* 1985a, Stewart 1988, Jackson *et al.* 1995b, Kostner *et al.* 1996). Diurnal behaviour of canopy stomatal conductance was dependent on microclimate and would appear to be highly sensitive to VPD (Fig. 4.3), consistent with other reports (Ng 1978, Beadle *et al.* 1985b). The partial recovery of stomatal conductance later in the day (Fig. 4.3) has rarely been reported in the literature for coniferous species, but is apparent in data presented for *Pinus pinaster* (Fig. 7 in Loustau *et al.* 1996).

The tight stomatal control of transpiration appears not to be mediated by declining leaf water potential since a clear reduction in canopy stomatal conductance was observed between the 4thof May 1995 and the 27thof June 1995 without any apparent differences between treatment bulk leaf water potential (Fig. 4.3). It has been suggested that such a response is indicative of feedforward signalling from root to shoot perhaps involving a chemical signal (abscisic acid, ABA) (Blake and Ferrell 1977, Davies and Zhang 1991, Tardieu and Davies 1993), although this interpretation would be contested by Saliendra *et al.* (1995) who suggest that bulk leaf water potential measurements mask the water potential gradients in the leaf that are likely be important in controlling stomatal behaviour. In herbaceous species chemical signals generated in the roots have been shown to play an important role in controlling stomatal behaviour (Gollan *et al.* 1986, Schurr *et al.* 1992). However, the role of such signals in tall woody plants remains to be thoroughly investigated (see section 6.2.5). In this experiment xylem sap was collected to detect any possible changes in the concentration of chemical messengers, and the results from this analysis will be available shortly (experimental work performed by Michael Perks). The time taken for a root generated chemical messenger to reach the foliage in tall trees (days or weeks) suggest that such signals will be unsuitable for controlling the diurnal pattern of stomatal behaviour. However, the accumulation of such a signal could play a role in the longer term acclimation to drought. Whilst the role of ABA in controlling stomatal behaviour has been widely recognised, ABA also has an inhibitory effect on leaf growth (Van Volkenburgh and Davies 1983), a mechanism by which leaf area and hence transpiration will be reduced in response to drought. There was no support from this experiment for the feedforward hypothesis for stomatal closure in response to air drought as proposed by Farquhar (1978), since there was no evidence of decreasing transpiration rates at high VPDs.

The values for RWC in the bole of the tree are consistent with figures reported by Waring and Running (1978) for Douglas fir, Running (1980a) for lodgepole pine, and Waring *et al.* (1979) for Scots pine, although Roberts (1976b) and Jackson *et al.* (1995b) report lower values for Scots pine during dry summer conditions. Needle water potential never fell below - 1.5 MPa (Table 4.2) and thus prevented the development of substantial xylem embolism (Fig. 4.8) that would have resulted in an increase in the hydraulic resistance of the woody tissue. This view is consistent with the fact that no-one has identified a mechanism by which refilling of embolised xylem can occur under significant tensions (Borghetti *et al.* 1991, Edwards *et al.* 1994). Thus unlike some broad-leaved species which show the ability to refill embolised xylem at the beginning of the season (Sperry *et al.* 1988, Sperry 1993, Sperry *et al.* 1994), the results from this study suggest Scots pine appears to have evolved mechanisms to prevent the development of widespread embolism.

In this study the calculations of transpiration and canopy conductance are expressed on a ground area basis. We could speculate that if these were to be expressed on a foliage area basis, the reduced foliage area in the droughted treatment that was a consequence of reduced current needle growth (Fig. 4.9), could possibly be the mechanism by which transpiration has been dramatically reduced (Fig. 4.2). It can be shown this is not the case. If we conservatively estimate that current years growth accounts for 50% of canopy leaf area, (a figure of 36 % is suggested by Beadle *et al.* 1982), the decrease in needle length can only account for up to 10 % of the 65 % decrease in daily transpiration at the height of the drought (Fig. 4.2, lowest panel). Thus stomatal control appears to be the mechanism by which Scots pine maintains tight control over transpirational water use.

The linear nature of the relationships in Figure 4.4 and the lack of significant hysteresis suggests that the hydraulic capacitance of the trees is unimportant and that the treatment of the soil-to-needle water transport system as a simple resistor is appropriate. The direction of the rather small hysteresis on the 9th of Aug. 1995 (Fig. 4.4) indicates an increase in hydraulic resistance during the day and not a release of stored water from above ground tissue. Since no significant diurnal changes in the RWC of the xylem were observed this increase in resistance must be located either within the roots, as a result of cavitation (Sperry and Ikeda 1997), or in the bulk soil itself.

The values for the hydraulic resistance between soil and needles (Fig. 4.5) are of similar magnitude to data available for pine and other coniferous species (Table 4.3). Granier *et al.* (1989) reported a three fold increase in hydraulic resistance in *Abies bornmulleriana* as pre-dawn water potential declined from -0.18 to -1.14 MPa; Running (1980b) reported a three fold increase in resistance in 40-year-old Douglas fir and figures in Lu *et al.* (1996) suggest a two fold increase in resistance in 30-year-old Norway spruce, both over the same range of pre-dawn water potentials as reported in this thesis. In these studies it was suggested that the increase in resistance was probably located at the soil-root interface or in the soil itself. Since no substantial seasonal development of embolism was observed in above ground tissue, the majority of the increased hydraulic resistance in this study must be located below ground (see Appendix 1). This is consistent with the fact that the hydraulic resistance returned to pre-drought levels once the soil moisture deficit was eliminated (Fig. 4.5, May 1996), and given that no substantial changes in plant xylem RWC were observed over the same period (Fig. 4.8).

Needle, shoot and basal area growth were reduced during the drought period (Fig. 4.9, 1995), although basal area increment was affected only when the drought became most extreme. Shoots are known to be one of the most sensitive tissues to water stress and a threshold soil moisture at which diameter growth declines has been reported for other pines (Dougherty *et al.* 1994). In 1996 when no significant soil moisture deficit developed, needle growth was unaffected by the end of the season, but an even larger decline in basal area increment was observed in the previously droughted treatment compared to 1995 (Fig. 4.9). The bole of the tree is a strong carbon sink and perhaps insufficient resources stored from the previous drought period or assimilated in the current year prevented basal area growth from reaching control treatment levels. Considering that both canopy stomatal conductance and needle water potential had recovered to pre-drought values by this point (Fig. 4.6 & Table 4.2 respectively), reduced assimilation in this post-drought year seems unlikely. Partitioning of resources in favour of root rather than sapwood growth is one alternative explanation. It is likely that higher root mortality occurred in the drought treatment in 1995 and thus resources may have been directed to restore the effectiveness of the root system in 1996 at the expense of basal area growth.

4.6 CONCLUSIONS

In mature Scots pine stomatal closure occurs in response to soil dryness at a threshold soil moisture deficit. This response appears to be linked to the soil moisture experienced by the majority of the roots even if substantial water is being extracted from greater depth. Stomatal closure prevents needle water potentials declining below -1.5 MPa. This response prevents the development of substantial xylem embolism in above ground woody tissue. The large increase in the hydraulic resistance between soil and needles that develops as a consequence of soil drought is likely to be located in the root or soil compartment of the hydraulic system (see Appendix 1). This increased resistance is not carried over into the following growing season when soil moisture has returned to pre-drought levels. Reduced growth in the season following the drought is therefore unlikely to be a consequence of embolism that carries over from one year to the next.

5. Modelling canopy stomatal conductance

5.1 SUMMARY

To investigate the response of canopy stomatal conductance of a mature pine forest to drought stress, a multiplicative non-linear regression model was developed to relate canopy stomatal conductance to key environmental variables. Hourly sap flux data collected over a complete growing season from control and drought stressed trees were used together with an inverted form of the Penman-Monteith equation to determine canopy stomatal conductance. It was found that a model that included the effects of air vapour pressure deficit and soil moisture deficit could explain 56% of the variance of measured canopy stomatal conductance when tested against an independent data set. The model predicted the diurnal behaviour of canopy stomatal conductance satisfactorily although values were underestimated at high measured values of canopy stomatal conductance and were also overestimated for the first two or three points during the day. The reasons for this bias in the fit of the model and the consistency with other published data is discussed.

5.2 INTRODUCTION

In mature forests the rate of transpiration is essentially controlled by stomatal conductance as a result of the high degree of coupling between the water vapour pressure at the leaf surface and that of the bulk air (Jarvis and McNaughton 1986). Moreover, the stomatal conductance also exerts a large influence on the photosynthetic uptake of carbon dioxide. The physiological mechanisms that control stomatal behaviour are not fully understood (Schulze 1997), and attempts to predict stomatal conductance are widely based on empirical representations of stomatal responses to environmental variables (Jarvis 1976, Stewart 1988, Massman and Kaufmann 1991, Dolman *et al.* 1991). In the light of current concerns about the response of forests to climate change, including the possible increased incidence of drought, information is needed on the stomatal response of mature trees to drought stress in order to parameterise models designed to predict the water use and growth of forests. Although Scots pine occupies a considerable area of land in the northern hemisphere, because of its immense natural range extending from Scotland to eastern Siberia between the boreal and temperate zones, there have been few attempts to measure the stomatal response of mature Scots pine to drought stress. In this chapter the stomatal response of the entire canopy of 41-year-old Scots pine to drought is explored by relating the canopy stomatal conductance, calculated from sap flow measurements, to environmental variables under control and droughted conditions.

Approaches available to estimate canopy stomatal conductance can be divided into two groups (Baldocchi *et al.* 1991) (i) the 'bottom-up' integrative approach where measurements made on shoots or needles with porometers are scaled up to the forest canopy, and (ii) the 'top-down' approach based on inverting an exchange model for water vapour and treating the canopy as a single layer or 'big leaf'. The 'bottom-up' approach is complicated by the need for extensive sampling of stomatal conductance throughout the canopy, together with an adequate description of the microclimate and foliage area distribution within the canopy (Leverenz *et al.* 1982, Roberts *et al.* 1993), and thus was considered unsuitable for this study. The 'top down' approach requires an estimation of the water vapour flux from the bulk dry canopy. This information is readily available from micrometeorological techniques such as Bowen-ratio and eddy-correlation (Lindroth 1985, Stewart 1988, Loustau *et al.* 1996). An alternative measurement approach is to use sap flow meters. These are preferable when small sample plots are used, as in field experiments involving treatments such as drought. Sap flow techniques can be automated, are relatively easy to run over long periods such as during the development of a drought, and can provide a continuous data set suitable for modelling purposes. Micrometeorological methods can also be used for automated continuous measurement, but as they are unsuitable for small plots, sap flow was considered as the best technique to employ in this study.

5.3 METHODS

Details of the experimental site, treatments imposed and techniques used can be found in Chapter 4. Canopy stomatal conductance was computed from sap flux estimates on an hourly basis by inversion of the Penman-Monteith equation (Equation 4.2). The seasonal pattern of leaf area index (LAI) was estimated using the model of Beadle (1982) adapted for the phenology at Devilla by using needle growth data (Fig. 4.9) together with a point estimate of total LAI (Table 4.1). Daily estimates of LAI were then used to model canopy stomatal conductance on a projected foliage area basis;

$$g_{\mathrm{cl}} = g_{\mathrm{c}}/L \qquad \text{Equation 5.1}$$

where g_{cl} is the estimate of the mean canopy stomatal conductance expressed per unit projected foliage area (mm s^{-1}), g_{c} is canopy stomatal conductance computed on a ground area basis (Equation 4.2), and L is the leaf area index as computed from the equations in Table 5.1, which varied between approximately 1.6 and 2.2 over the season. The leaf area indices apply to the forest canopy excluding ground vegetation. Meteorological variables were measured using instruments located 2 to 3 m above the canopy (see section 4.3). Readings were taken at minute intervals and averages computed and stored hourly. Soil moisture was measured using time domain reflectometry over 20 cm and 50 cm soil depth at two week intervals (see section 4.3). Linear interpolation between measurement times was used to calculate soil moisture for each day over the experimental period. Soil moisture deficit was calculated from;

Table 5.1. The seasonal pattern of leaf area index during 1995 at Devilla forest.

Day of year (*JD*)	Leaf Area Index	
	Control	Droughted
0 to 139	(-0.043°*JD* +162)/100	(-0.043°*JD* +162)/100
140 to 225	(0.847°*JD* +37.4)/100	(0.647°*JD* +65.41)/100
226 to 316	(-0.744°*JD* +396)/100	(-0.711°*JD* +371.7)/100
317 to 365	(-0.125°*JD* +200.6)/100	(-0.146°*JD* +193.2)/100

$$\delta M = \frac{(M_{\max} - M)}{(M_{\max} - M_{\min})} \qquad \text{Equation 5.2}$$

Where δM is the soil moisture deficit that takes a value from zero to one. M is the measured soil volumetric water fraction with subscripts max and min referring to the maximum and minimum values recorded. For measurements over 20 cm soil depth $M_{\max} = 0.296$ and $M_{\min} = 0.051$, and for measurements over 50 cm soil depth $M_{\max} = 0.282$ and $M_{\min} = 0.109$.

A data set of 51 days out of the 132 days over which the drought developed was selected based on the criterion of no measurable rainfall during daylight hours. Data were discarded when sap flow rates were $< 5 \circ 10^{-6}$ kg m^{-2}(ground) s^{-1} as the heat pulse velocity technique is unreliable at low flow rates (Barrett *et al.* 1995). Data were also discarded when air vapour pressure deficit (D) <0.1 kPa as it was considered that foliage may be wet under these conditions. These two constraints led to rejection of data from periods early in the morning or late in the evening. The remaining data were divided into two sets on an alternating days basis such that each set contained values from both drought and control treatments over the full range of soil moisture deficits. One set of data (Set A) was used for model fitting whilst the other used for model validation (Set B). Each data set contained approximately 650 hourly values of canopy stomatal conductance (g_{cl}), meteorological variables and soil moisture deficit values.

5.3.1 MODELLING CANOPY STOMATAL CONDUCTANCE

The response of canopy stomatal conductance to measured variables can be represented by a multiplicative model (Jarvis 1976) of the general form;

$$g_{cl} = g_{\max} \circ f_1(Q_p) \circ f_2(D) \circ f_3(T) \circ f_4(\delta M)\ldots, \qquad \text{Equation 5.3}$$

where g_{cl} is the canopy stomatal conductance expressed on a projected leaf area basis (mm s^{-1}), $f_1, f_2 \ldots$ are non-linear functions of photosynthetically active radiation (Q_p), air vapour pressure deficit (D), air temperature (T), soil moisture deficit (δM), and other suitable variables. It is assumed that the functions do not interact and that each takes a value from zero to one, g_{max} is a modelled parameter and thus may bear no relation to maximum conductance as measured in the field. Each variable independently reduces g_{cl} as the value of the function falls towards zero.

The forms of the response functions used were obtained from the literature from studies of stomatal responses under controlled conditions and from 'boundary line' analysis of field data, i.e. from the shape of the upper probable limit of g_{cl} with respect to an independent variable (Jarvis 1976). Details of these functions can be found in the Results and Discussion section. Parameter estimation was based on the least squares technique achieved using the Gauss-Newton method with the procedure NLIN in the SAS statistical package (SAS Institute Inc. 1988).

5. 4 RESULTS AND DISCUSSION

Details of the development of the soil drought and the physiological responses of the trees to drought can be found in section 4.4.

5.4.1 FITTING THE MODEL

The response of g_{cl} to each independent variable is shown in Figure 5.1. Figure 5.1A shows a non-linear decline in g_{cl} with D ; Figure 5.1B shows no apparent response of g_{cl} to Q_p ; Figure 5.1C shows a curvilinear peaked response of g_{cl} to T with a restriction of g_{cl} at high and low values of T, and Figure 5.1D shows an insensitivity of the response of g_{cl} to δM until a threshold δM is reached. There was a high degree of correlation between D and T ($r = 0.75$), but the other variables appear to act independently.

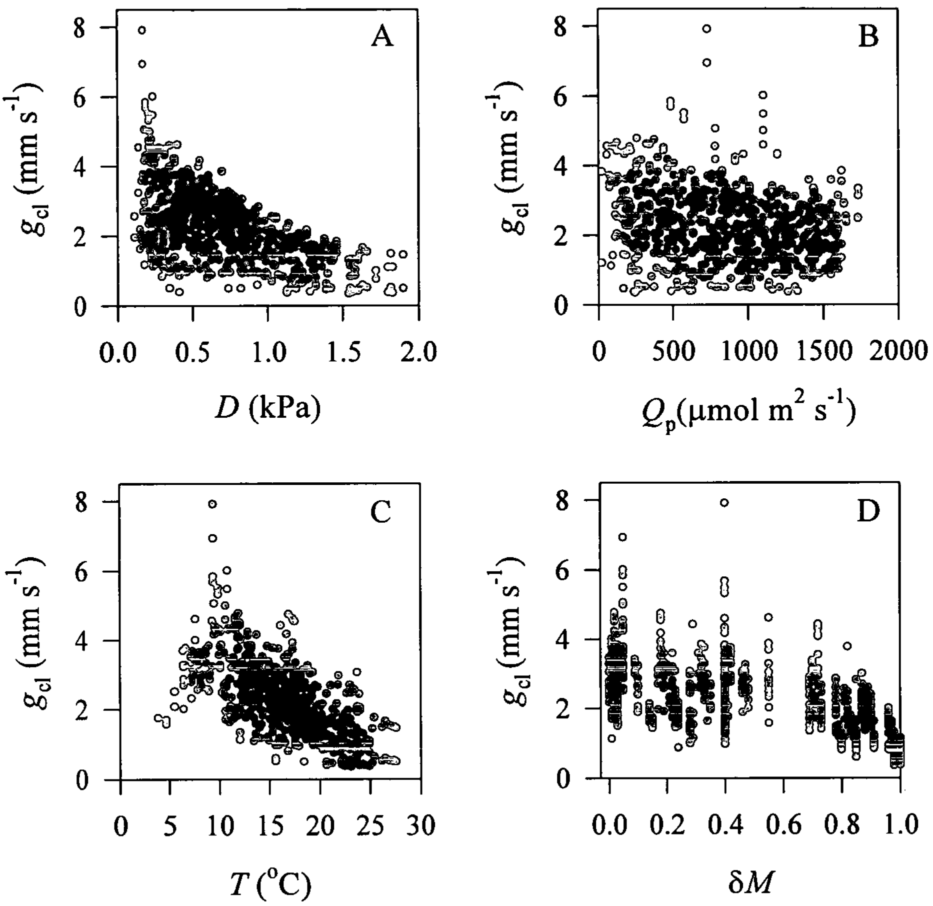


Figure 5.1. The correlation of environmental variables and canopy stomatal conductance expressed on a foliage area basis (g_{cl}) for data set A. The air saturated vapour pressure deficit (D), photosynthetically active radiation (Q_p) and air temperature (T) were measured above the canopy. The soil moisture deficit (δM) was integrated over the top 20 cm soil depth.

Several forms of the function for the response of g_{cl} to air humidity have been proposed; a linear decline of g_{cl} with D (Jarvis 1976) Equation 5.4; hyperbolic relationships of g_{cl} to D (Lohammer *et al.,* 1980 and Farquar 1978) Equations 5.5 & 5.6, respectively; and a linear response of g_{cl} to relative humidity (H) thus combining $f(T)$ and $f(D)$, based on the ideas of Ball *et al.* (1987) Equation 5.7.

$f(D) = 1-(K_{\mathrm{vpd}} \circ D)$ Equation 5.4

$f(D) = 1/(1+D/K_{\mathrm{vpd}})$ Equation 5.5

$f(D) = (1-K_{\mathrm{vpd1}} \circ D)/(1-K_{\mathrm{vpd2}} \circ D)$ Equation 5.6

$f(T)f(D) = H$ Equation 5.7

where K_{vpd} refers to a fitted constant which takes values specific to each response.

Collatz *et al.* (1991) suggest that the linear function (Equation 5.4) may best represent the response of g_{cl} to D in circumstances when changes in D are due to changes in the ambient vapour pressure of water, rather than due to changes in air temperature. The hyperbolic responses (Equations 5.5 & 5.6) may be suitable for circumstances when changes in D are caused by changes in air temperature (such as in a forest canopy), and the linear response to H (Equation 5.7) may be appropriate in both circumstances. In this study, all the responses apart from the Farquhar response (Equation 5.6) were tried in the various forms of the model. This response was not used as there was no evidence of decreasing transpiration at high D, and its use would over-parameterise the model.

The effects of air temperature were represented by a bell shaped function (Jarvis 1976, Massman *et al.* 1991):

$$f(T) = \frac{(T - T_{\mathrm{min}})}{(T_{\mathrm{opt}} - T_{\mathrm{min}})} \circ \frac{(T_{\mathrm{max}} - T)^{a}}{(T_{\mathrm{max}} - T_{\mathrm{opt}})^{a}}$$ Equation 5.8

where T is the current air temperature (°C), T_{min} (set arbitrarily at -5 °C) and T_{max} are the lowest and highest temperatures for stomatal opening respectively (°C), and T_{opt} is the temperature for optimal stomatal opening (°C). The exponent a equal to $(T_{\mathrm{max}}-T_{\mathrm{opt}})/(T_{\mathrm{max}}-T_{\mathrm{min}})$, controls the asymmetry of the response around T_{opt} and was set constant at 0.5. Thus T_{opt} is the only fitted parameter since T_{max} is determined solely by T_{opt}.

The effect of δM was represented by an exponential function (Stewart 1988, Granier and Loustau 1994);

$$f(\delta M)= 1-(K_{\mathrm{soil1}} \circ \exp(K_{\mathrm{soil2}} \circ \delta M)) \qquad \text{Equation 5.9}$$

where K_{soil1} and K_{soil2} are fitted parameters

and the response of g_{cl} to Q_{p} by a hyperbolic function (Massman *et al.* 1991, Granier *et al.* 1994);

$$f(Q_{\mathrm{p}})= (Q_{\mathrm{p}} /(Q_{\mathrm{p}} +K_{\mathrm{par}})) \qquad \text{Equation 5.10}$$

where K_{par} is a fitted parameter.

Attempts to fit this model to data set A including responses to D, Q_{p}, T and δM were unsuccessful because of a noisy response of g_{cl} to Q_{p} (Fig. 5.1C). Consequently Q_{p} was excluded from the model. The three factor model including responses to D, T and δM provided no improvement in terms of goodness of fit as compared with the two factor model that only included responses of g_{cl} to D and δM (Table 5.2). This was found to be due to covariance of T with D. Consequently only the responses of g_{cl} to D and δM were used in the final model. Of the three alternative forms of response to D that were tested, the linear Jarvis model (Equation 5.4) and the Lohammer model (Equation 5.5) provided a better fit than using the linear response to H (Equation 5.7).

The final form of the model used was:

$$g_{\mathrm{cl}} = g_{\mathrm{max}} \circ (1/(1+D/K_{\mathrm{vpd}})) \circ (1-(K_{\mathrm{soil1}} \circ \exp(K_{\mathrm{soil2}} \circ \delta M))) \qquad \text{Equation 5.11}$$

This model can be visualised as a three-dimensional response surface (Figure 5.3). The model was fitted with δM data as measured over 20 cm soil depth; however the fit using δM data as measured over 50 cm soil depth produced almost identical results (data not shown). The distribution of residuals and comparison of modelled to observed g_{cl} (Figure 5.2) suggests there is some bias associated with the model. At high values of observed g_{cl} the model underestimates conductance. This was due to a considerable number of data points with small g_{cl} at low D such that to minimise the residuals associated with fitting the model, the value for the fitted g_{max} parameter is smaller than would perhaps be expected. There is also a small population of points at low to mid observed g_{cl} that are overestimated by the model, these points were generally the first two or three points recorded during the day.

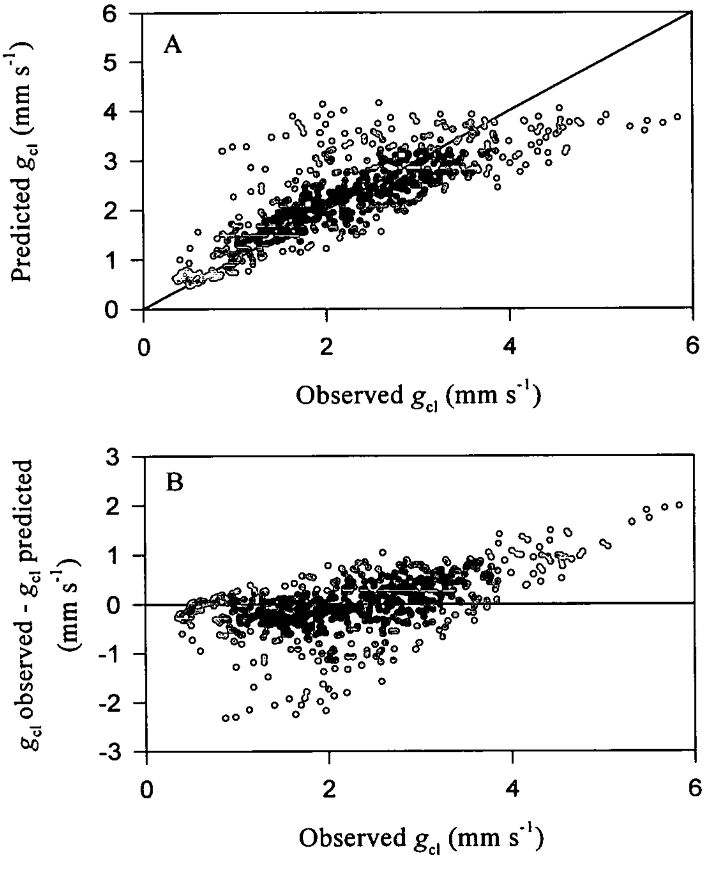


Figure 5.2 Figure A compares predicted and observed g_{cl} (data set A) when using equation 5.11, the line shown is the 1:1 relationship, $r^2 = 0.61$. Figure B is the residual plot.

Table 5.2. The fitted parameters used in the various forms of the model. *f(δM)* took the form of Equation 5.9 and *f(T)* of Equation 5.8. g_{max} is in mm s^{-1}, K_{vpd} is in kPa, and T_{opt} is in °C. r^2 was computed according to Massman and Kaufmann. (1991) as 1-(residual sum of the squares / corrected sum of the squares).

Model	$f(D)$ used:	Parameters fitted					
		g_{max}	K_{vpd}	K_{soil1}	K_{soil2}	T_{opt}	r^2
$g_{cl}=g_{max}\circ f(D)\circ f(\delta M)\circ f(T)$	Equation 5.5	5.171	0.855	0.0075	4.532	16.83	0.57
$g_{cl}=g_{max}\circ f(D)\circ f(\delta M)$	Equation 5.5	4.713	0.899	0.0048	4.965	-	0.61
$g_{cl}=g_{max}\circ f(D)\circ f(\delta M)$	Equation 5.4	4.005	0.430	0.0056	4.821	-	0.61
$g_{cl}=g_{max}\circ f(D)\circ f(\delta M)$	Equation 5.7	4.344	-	0.0040	5.234	-	0.48

5.4.2 MODEL VALIDATION

The parameters for the model obtained using data set A were used to predict the behaviour of g_{cl} with data set B. The model explained 56% of the variance of g_{cl}. The distribution of residuals (not presented) was similar to those associated with fitting of the model to initial data (Set A, Figure 5.2). The diurnal behaviour of the observed and predicted g_{cl} (Figure 5.4) indicates that the model accounts for diurnal variation of g_{cl} reasonably well. The model does however overestimate g_{cl} for the first two or three points in the morning. The model was less able to predict g_{cl} satisfactorily under rapidly changing meteorological conditions as compared to days when cloud cover was absent (as indicated by a smooth diurnal behaviour of Q_p and D). The model responded adequately to soil drought, as the fit remained reasonably tight in the droughted treatment as δM increased from 0.47 (4th May) to 1.0 (17th of August).

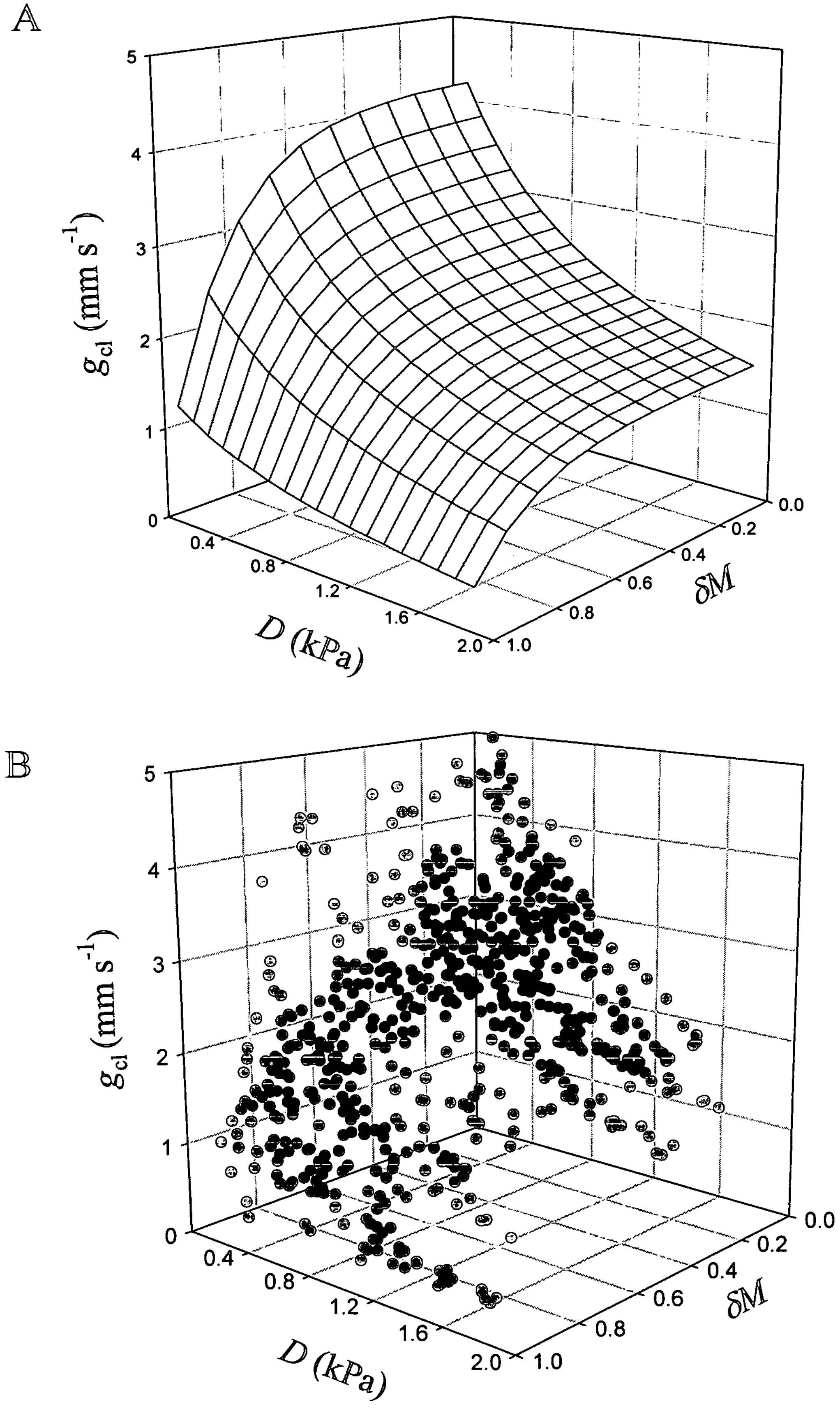


Figure 5.3. Figure A is the multiple regression model (Equation 5.11) fitted to data set A, the data points are shown in figure B.

5.4.3 CANOPY CONDUCTANCE RESPONSE TO ENVIRONMENTAL VARIABLES

The exclusion of $f(Q_p)$ from the final model does not imply g_{cl} is totally unresponsive to irradiance. Experimental studies on single leaves or shoots have demonstrated that $f(Q_p)$ does follow a hyperbolic response as suggested by Equation 5.10 e.g. Ng and Jarvis 1980. Massman *et al.* (1991) were able to account for between 38% and 63% of the stomatal conductance measured on several conifer species growing in non-droughted conditions by only using a light response function. Granier *et al.* (1994) found that although Q_p was the least important variable in a similar model, its inclusion improved the model fit significantly. The lack of apparent response to Q_p has been reported by Whitehead *et al.* (1984) in Scots pine and data presented by Loustau *et al.* (1996, Fig.8) also shows a poor light response in maritime pine. In such studies the response time of stomata in opening (and closing) was likely to be an important factor as the stomatal conductance measurements were made on shoots in a naturally fluctuating light environment. In this study it is likely that the apparent lack of sensitivity to Q_p was a result of the attenuation of radiation by the canopy such that the light environment throughout the crown was heterogeneous. Consequently using Q_p as measured above the canopy inadequately represents the light response. The influence of Q_p is only important at intensities below the asymptote of the response curve. These values are likely to occur during the extremes of the day and this may explain why the model provides a poor fit for the first two or three points in the morning (Figure 5.4). Taking hourly averages of meteorological and sap flux data from the four trees will also tend smooth out any light response that may be present in the raw data, especially if different trees receive their first direct light at different times.

Figure 4.4 illustrated that the hydraulic capacitance of the tree was small. This led to the assumption that sap flux as measured at the base of the tree at any one moment is representative of stomatal conductance at the same instant. However, any capacitance above the sap flow meter will cause an underestimation of canopy conductance at sunrise and an overestimation in the evening. This may explain why the model underestimates canopy conductance at high measured values, since the fitted response surface would be 'pulled down' by 'artificially' low estimates of g_{cl} at low D.

The canopy stomatal conductance model presented here is in general consistent with the current understanding of stomatal response to environmental variables. The modelled g_{cl} shows a large degree of sensitivity to both D and high δM. The rate of decline of g_{cl} with D is consistent with data reported by Whitehead *et al.* (1984, Table 3) for *Pinus* spp. A threshold type response of stomatal conductance to δM is in agreement with other studies (see section 4.5). For soil drought to result in a 10%

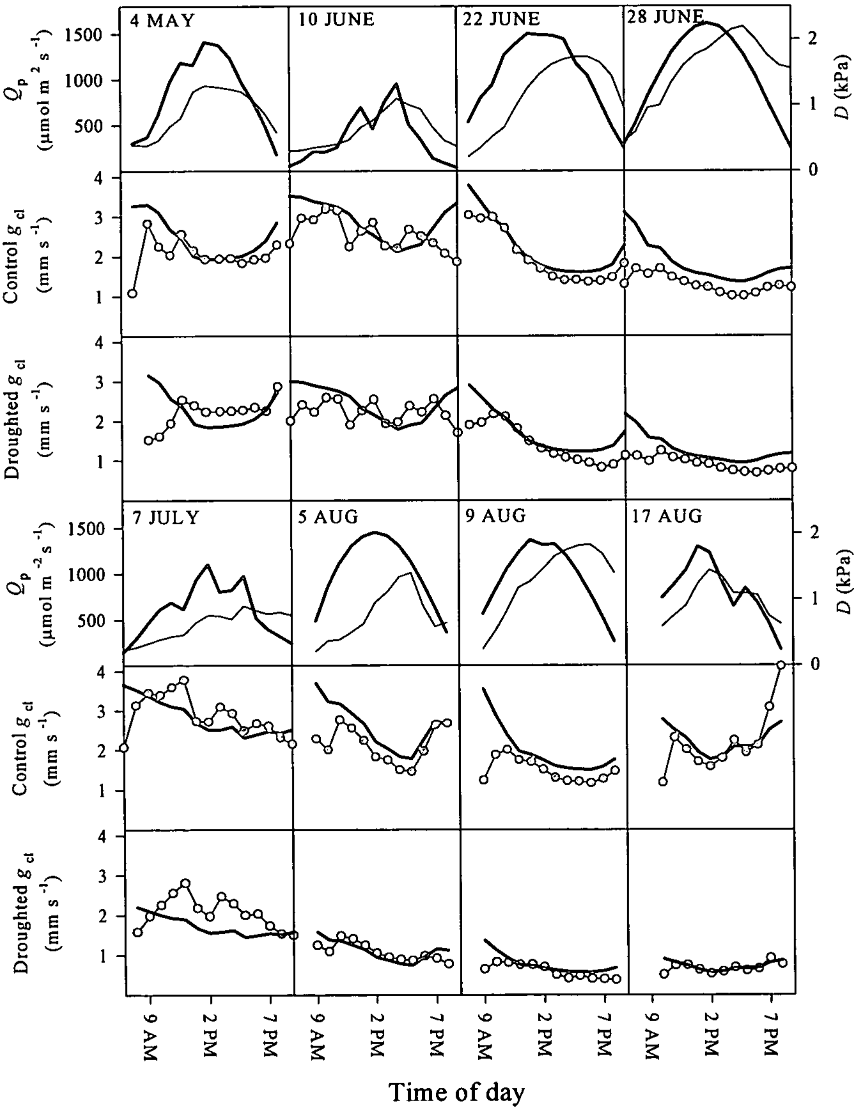


Figure 5.4 The diurnal course of photosynthetic active radiation (Q_p, heavy line), air saturation vapour pressure deficit (D, fine line), observed (circles) and predicted (heavy line) canopy stomatal conductance (g_{cl}) for 8 days in control (closed symbols) and droughted (open symbols) treatments.

reduction in the modelled g_{cl} as computed at no δM, the soil has to dry to a δM of 0.6. This is equivalent to a soil volumetric water fraction threshold of 0.15 over 20 cm soil depth or 0.18 over 50 cm soil depth. Using this 10% reduction criterion, the response presented by Granier *et al.* (1994) provides a value of 0.52 δM for *Pinus pinaster*; for mature Scots pine in Thetford, Fig. 1 in Stewart (1988) suggests a figure of 0.70 δM, and a value of 0.60 δM can be approximated by the data provided in Tajchman *et al.* (1979) for 9-year-old Scots pine. Thus there a reasonable degree of consistency between the data collected in this study and the published reports for the threshold soil moisture that results in a decline in g_{cl} in Scots pine.

6. Discussion

6.1 THESIS SUMMARY

The conceptual framework for the movement of water through the soil-plant-atmosphere-continuum (SPAC) was proposed by Huber in 1924 but only came into general use in the 1960's (Richter 1973). Since then a large body of work has been published covering a wide range of issues concerning the spatial and temporal variations in the water status of trees (Jarvis 1975, Hinckley *et al.* 1978, Whitehead and Jarvis 1981, Kozlowski and Pallardy 1997b). However, there is still little information available concerning changes in the hydraulic resistance of the soil-plant system that develop in response to drought, and the consequences of this for both plant gas exchange and plant growth. This thesis provides information in this area by examining the physiological and climatological controls of water use in a mature Scots pine forest under conditions of soil-drought. In particular two questions were posed:

(i) Does the hydraulic resistance of the SPAC in mature Scots pine increase in response to soil-drought ? If so, is this a consequence of the development of significant embolism in the xylem of woody aerial tissue ? More importantly, does the hydraulic resistance recover when the drought ceases, or can such changes in hydraulic resistance persist into subsequent growing seasons ?

(ii) Does stomatal closure occur in response to soil drought, as suggested by studies on young trees ? If so, can stomatal closure prevent cavitation by reducing the transpirational flux, so that the critical tension for cavitation is never reached or rarely reached ?

The hydraulic resistance between soil and needles in mature Scots pine increased by a factor of three as a soil-drought developed. This increase in hydraulic resistance was located in the soil or roots. There was no evidence of increased embolism in the trunk of the tree. As the drought progressed there was evidence of a small increase in embolism in the xylem of second year shoots which recovered when the drought ceased. The timing of the changes in hydraulic resistance between soil and needles and the recovery of embolism in the shoots was inconsistent with the idea that shoot embolism caused the large increases in hydraulic resistance observed as the drought progressed. By spring of the year following the drought the hydraulic resistance between soil and needles had returned to pre-drought levels and there was no evidence of any carry-over of reduced hydraulic capacity of the water transport system.

Widespread increases in xylem embolism were prevented by tight stomatal control of transpiration once a threshold soil volumetric water fraction of 0.12 over the top 20 cm of soil had been reached. Transpiration in the droughted treatment fell to about 30% of the value of the control treatment when the drought was most extreme, preventing needle water potentials from falling below -1.5 MPa. Reduced needle growth in the droughted treatment could not account for this reduction in transpiration when transpiration was expressed on a foliage area basis. A simple non-linear regression model with functions for air vapour pressure deficit and soil moisture deficit could explain the majority of the variance of the measured canopy stomatal conductance.

The tight control of canopy stomatal conductance had significant consequences for carbon assimilation. Needle, shoot and basal area growth were substantially reduced in the droughted treatment. Although canopy stomatal conductance had returned to pre-drought values in the year following the drought, a reduction in basal area increment in the previously droughted treatment was evident at the end of the year.

6.2 COMMENTARY

6.2.1 THE WIDER SIGNIFICANCE OF CHANGING HYDRAULIC RESISTANCE WITHIN THE SOIL-PLANT-ATMOSPHERE-CONTINUUM

In this study Scots pine showed an isohydric response (Jones 1992, Tardieu and Davies 1993) to drought stress, i.e. it maintained a favourable foliage water status as the hydraulic resistance between soil and foliage increased. The increase in hydraulic resistance may have further consequences beyond the short term stomatal closure that was demonstrated in this study. Several recent publications lend support to the hypothesis that hydraulic resistance governs growth of old trees and perhaps even the natural distribution of tree species (Waring and Schlesinger 1985, Tyree *et al.* 1994, Alder *et al.* 1996, Mencuccini and Grace 1996, Cienciala *et al.* 1997, Ryan and Yoder 1997). Because the hydraulic resistance of the water transport pathway is coupled to stomatal behaviour and photosynthesis, tall trees, or those growing at the extremes of their natural range, may show reduced growth due to stomatal closure as a consequence of a large drop in water potential between the soil and the transpiring foliage. If this hypothesis is correct, and future predictions of transient and more extended periods of water deficit are correct (Rind *et al.* 1990, Weatherald and Manabe 1995), then a greater understanding of the hydraulic pathway within the SPAC in forest ecosystems is essential to predict forest growth and distribution under scenarios of global warming.

To date, there have been only a small number studies that have explored the nature of the hydraulic pathway between soil and foliage in mature trees, and so information on how this may differ with species, tree age and water deficit is limited (Jarvis 1976, Cohen *et al.* 1983, Granier *et al.* 1989, Reich and Hinckley 1989, Mencuccini and Grace 1996). Most studies that address whole tree hydraulic architecture generally overlook the possible significance of seasonal changes in hydraulic resistance (Yang and Tyree 1994, Mencuccini and Grace 1996). On the other hand, those studies that look specifically into the seasonal changes in xylem embolism tend to concentrate measurements on shoots or branches, and do not necessarily relate such measurements to the total hydraulic resistance of the pathway (Sperry *et al.* 1994, Cochard *et al.* 1997). The lack of information in this field can probably be attributed to the technical difficulties of measuring water relation variables such as sap flow and water potentials at various points along the SPAC in mature trees.

6.2.2 TECHNIQUES FOR MEASURING THE SOIL-PLANT HYDRAULIC RESISTANCE

At the present time, there are no simple methods available to make repeated measurements of the distribution of hydraulic resistance within the soil-plant system. Hydraulic resistance is most often calculated from sap flow and water potential measurements using approaches similar to those described in this thesis. Destructive measurements made to assess the degree of embolism and the hydraulic resistance in whole trees are difficult to perform, and although they have been used in occasional circumstances (Tyree 1988, Yang and Tyree 1994), they are logistically difficult to apply repeatedly, as is required for studies monitoring drought effects. Early attempts to partition the soil-plant hydraulic resistance into above-and below-ground fractions involved cutting trees at ground level and suspending the severed end in a reservoir of water (Roberts 1977). This technique can only provide spot estimates of the two components. More recently, the 'root pressure probe' has been developed to provide information on the hydraulic properties of root systems (Magnani *et al.* 1996). However, its suitability for use on mature trees has still to be addressed.

To obtain more spatially detailed information on the hydraulic architecture of trees, the rate of water flow and water potential must be measured at several points in the hydraulic system. Where shoots are found along the full length of the bole, these can be used as 'plugged in tensiometers' to obtain the water potentials at various points in the system (Hellkvist *et al.* 1974). This information can be used together with sap flow measurements to calculate the hydraulic resistance in different organs with in the tree. Unfortunately most mature forest trees lack such shoots, so other techniques must be used to obtain the necessary water potential information. Osmotic tensiometers (Peck and Rabbidge 1969), electrical resistance sensors (Spomer 1968), pressure injection techniques (Edwards 1980, Edwards and Jarvis 1981) and stem psychrometers (Dixon and Tyree 1984) have all been used in the past. Only stem psychrometers now appear to be used widely and problems with thermal gradients, and resin exudation in some species, generally prevent them from being used successfully under field conditions. The novel technique presented in this thesis, based on relating the elastic deformation of the xylem to water tension, may be of value in the future. However, it requires time consuming calibrations and will only be suitable under certain circumstances (see chapter one for details).

There are fewer technical difficulties associated with measuring sap flow. Various commercially available systems are suitable for use on plant material of different sizes (Smith and Allen 1996). However care must be taken when applying widely reported calibrations to specific circumstances, and problems with scaling up measurements from the individual tree to the forest require careful consideration.

6.2.3 TREATMENT OF THE SOIL-PLANT SYSTEM AS A SIMPLE RESISTIVE SYSTEM

Throughout this thesis the soil-plant hydraulic system has been viewed as a simple resistive structure. Although there is evidence to support this view, some recent work emphasizes the significance of hydraulic capacitance in such systems (Tyree 1988, Milne 1989, Loustau *et al.* 1996, Phillips *et al.* 1997). Previous work suggests that the bole of the tree can act as a significant store of water, and in times of water deficit this can be used to allow gas exchange to continue unimpeded for several days (Waring *et al.* 1979, Whitehead and Jarvis 1981, Kozlowski and Pallardy 1997). In this study there was no evidence of substantial diurnal or seasonal changes in sapwood water content. However some of the results reported in Chapter 5 could possibly be explained by a degree of hydraulic capacitance, most probably located in living tissues.

6.2.4 STOMATAL RESISTANCE RESPONSE TO MOISTURE DEFICIT

Whilst little is known about the relative magnitude of the hydraulic resistance of roots, trunks and branches within the SPAC, it is well recognised that the largest resistance to water flow is between the mesophyll air spaces and the boundary layer outside the leaves. The resistance of this pathway is actively controlled by the size of the stomatal pore. Stomatal conductance measurements are widely made in plant water relations studies and there is considerable empirical knowledge about how stomata respond to environmental variables. However, most of this information has been collected from studies on juvenile material and fewer studies have monitored the stomatal response of mature tree canopies. This study has provided a large data set on the response of canopy stomatal conductance of a mature Scots pine forest to soil moisture deficit and climatological variables. Such data is of considerable value to those attempting to develop models of forest growth or much larger models of energy, water and carbon fluxes such as global climate models (GCMs).

6.2.5 MODELLING STOMATAL RESPONSES

An empirical approach to modelling canopy stomatal conductance was used in this study, as the current state of knowledge about the processes that control stomatal behaviour is insufficiently advanced to allow a mechanistic interpretation. Whilst it is recognised that changes in guard cell turgor ultimately control stomatal aperture, the mechanism by which cell turgor is regulated by soil or air drought (high VPDs) remains a matter of debate. In herbaceous species, chemical signals generated in the roots appear to play a vital role in controlling stomatal behaviour (Gollan *et al.* 1986, Schurr *et al.* 1992). However there are few studies of the possible role of chemical signals in controlling stomatal behaviour in mature trees. Such signals are likely to take several weeks to travel from the roots to the foliage, and so are unlikely to provide a rapid response to drought stress. One recent study on oak provided strong evidence against any effect of the chemical signal abscisic acid (ABA) on stomatal behaviour (Triboulot *et al.* 1996). Root pressurisation experiments suggest that in *Betula occidentalis* leaf water status, rather than root water status, has a major influence on stomatal aperture (Saliendra *et al.* 1995). In the field experiment presented in this thesis it is clear that leaf water status may remain constant whilst stomatal conductance declines, which would suggest that leaf water potential is not a suitable parameter to use to predict stomatal conductance in Scots pine.

Many diurnal patterns of stomatal conductance reported in the literature show a maximum conductance in the morning and a general decline in conductance throughout the day (Beadle *et al.* 1985, Dolman *et al.* 1991, Loustau *et al.* 1996). In simple models of stomatal conductance, time of day is sometimes used as an independent variable (Gash *et al.* 1989, Dolman *et al.* 1991). However, such patterns of stomatal behaviour most likely reflect the stomatal response to an increase in air VPD as a result of an increase in air temperature as the day progresses. In maritime situations such as in Scotland, climatic conditions can be highly variable and change rapidly, so the use of the concept of a nominal diurnal pattern of stomatal conductance would be highly misleading. Inclusion of the stomatal response to air VPD would appear to be a more rigorous approach to modelling stomatal behaviour.

Models such as those developed in this thesis assume a uniform response to a particular variable throughout the day. This ignores the possibility of the influence of endogenous circardian rhythms (Kaiser and Kappen 1997). Models developed from field data that ignore such influences may overestimate stomatal conductance in the afternoon (Ogink-Hendriks 1995), although there was no evidence of this in the current study.

6.2.6 THE SIGNIFICANCE OF CANOPY STOMATAL CONDUCTANCE IN GCMS

The importance of considering canopy surface conductance in GCMs was demonstrated when results from early 'bucket' type GCMs were compared with results from more refined models that included vegetation surface conduction properties that could be varied with soil water availability. Simulations from these 'biophysical' models were consistently in closer agreement with available observations than results predicted by the earlier models (Sellers *et al.* 1997). Whilst it is now recognised that the inclusion of canopy conductance is required to develop realistic and consistent GCMs, limited data is available about how canopy stomatal conductance responds to soil moisture in mature trees. Current GCMs usually include a threshold type response of surface conductance to soil moisture (Sellers *et al.*

1997). The nature of this response is an area that requires futher investigation. Soil moisture deficit is not calculated consistently in the reported studies (see section 4.5). This inconsistency is most likely to be a consequence of the lack of information about the rooting distribution of mature forest trees and consequently a lack of understanding of the significance of moisture in different areas of the soil profile. Further complications arise when the realities of natural forest ecosystems have to be taken into account. These ecosystems may show a diverse range of species with an uneven age structure growing on a wide range of soil types. Each of these factors is likely to influence how the surface conductance of the forest is influenced by soil or atmospheric drought.

6.3 RECOMMENDATIONS FOR FURTHER WORK

Whilst this study has demonstrated the significance of stomatal control of transpiration, and the consequent reduction in growth, in response to soil moisture deficit, it can provide little insight into the mechanisms which cause such stomatal behaviour. Such mechanistic insight would be highly valuable for predicting the response of forest growth to changes in environmental conditions. It is dangerous to extrapolate empirical relationships, such as those generated in this study, beyond the conditions of the experiment; and so while such relationships are valuable, they may be of little use to predict stomatal responses to new climatological conditions occurring in the future.

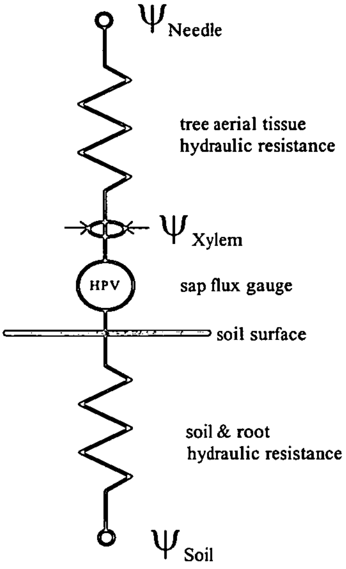
Also requiring further investigation is the observation, made in this study, that stomatal behaviour is linked to changes in the soil moisture content of the upper soil layers. For example does stomatal closure occur in mature Scots pine if only the top few centimeters of the soil are allowed to dry out while the deeper roots are adequately supplied with water ? Could such stomatal closure be triggered by chemical signals generated in the roots ? Studies of this type would provide further insight into the mechanistic behaviour of stomatal responses to soil moisture deficits.

This study indicated that no embolism developed in the bole of mature drought stressed Scots pine. This result is at odds with reports that substantial embolism has been developing in similarly aged trees exposed to several years of soil moisture deficits in Thetford (G. Jackson, personal communication). This contradiction begs the question of whether generalisations can be made from a relatively short-term study such as presented in this thesis. A longer term study of the same nature would provide a much greater understanding of the processes involved in the physiological response of Scots pine to drought. Such a study could also address the issue of whether and how, Scots pine can acclimate to drought. Possible processes involved in acclimation could include the long term behaviour of the stomatal response to water deficit, and the process of maintenance of a functional balance between the area of transpirational tissue and the hydraulic resistance of the xylem.

APPENDIX 1

THE USE OF WATER POTENTIAL AND SAP FLUX MEASUREMENTS TO PARTITION THE SOIL-PLANT HYDRAULIC RESISTANCE

Changes in the hydraulic resistance of the soil-plant system can be partitioned into above- and below-ground components if the water potential is measured both at the base of the trunk and in the foliage, and the rate of water flux through the system is known (FigureA.1). The four frames designed to detect changes in xylem water potential and the four sap flux guages that were installed in each treatment as outlined in sections 2.4.1 and 4.3 respectively, provided the necessary data.



$$R_{\mathrm{aerialtissue}} = \frac{\Psi_{\mathrm{Needle}} - \Psi_{\mathrm{Xylem}}}{E}$$

$$R_{\mathrm{soil\&root}} = \frac{\Psi_{\mathrm{Xylem}} - \Psi_{\mathrm{Soil}}}{E}$$

Figure A.1. Schematic diagram showing how the soil-plant hydraulic resistance was partitioned. Ψ_{Needle} was determined with the pressure chamber (MPa), Ψ_{Soil} was assumed to equal pre-dawn Ψ_{needle} (MPa), Ψ_{xylem} was determined using the technique presented in Chapter 2 (MPa), HPV refers to the heat pulse velocity sap flux gauges that were used to estimate transpiration (E, m^3 (water) m^{-2} (ground) s^{-1}), R refers to the hydraulic resistance (MPa s m^{-1})

This technique assumes that the hydraulic capacitance of the system is minimal and can be ignored. It also assumes that the reference water potential in the soil does not change throughout the day on which the measurements are made. Both the below- and above-ground hydraulic resistance components as calculated by this technique are presented in Figure A.2. It is clear that the resistance in the soil or roots increases in the droughted treatment as the drought becomes most extreme in July-August 1995, and then recovers gradually after the pre-dawn needle water potentials in the droughted treatment recover in mid-September 1995, marking the end of the drought.

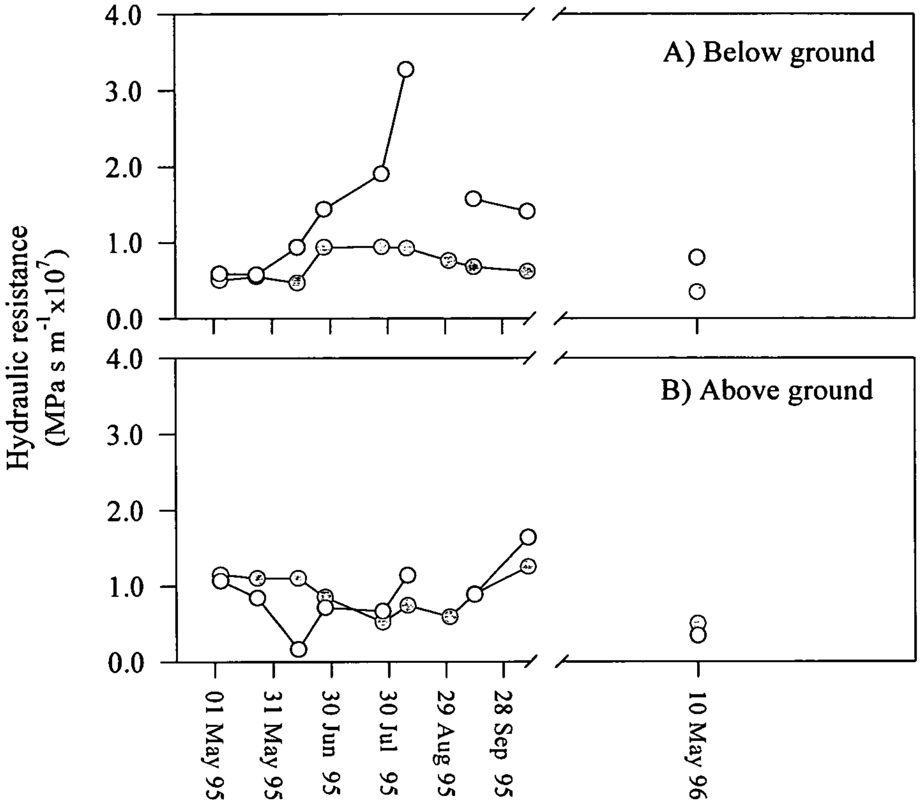


Figure A.2. Seasonal changes in the below-ground (upper panel) and above-ground (lower panel) hydraulic resistance in both droughted (open symbols) and control treatments (closed symbols).

(Figure 4.2). These results confirm the findings reported in Chapter 4, in that the large increase in hydraulic resistance from soil to needles (Figure 4.5) is largely because of increases in resistance below ground.

The results presented in Figure A.2 should be treated with a little caution as the technique developed to detect changes in xylem water potential requires further refinement and testing. One problem that became apparent during the season was that the cambium originally removed from the measurement points (see section 2.4.1) grew back slowly, and that in some cases affected the measurement. When this occurred data had to be discarded and the new cambial tissue had to be removed to allow further measurements. The missing value at the beginning of August 1995 in the droughted treatment (Figure A.2) was a consequence of data from only one replicate being available and thus the data point was discarded. Also of concern is that the data presented in Figure 2.6 suggests that water potential at the base of the tree appears to be recovering throughout the night on some occasions. If the hydraulic capacitance of the system was zero, the water potential at the base of the tree would not vary once the sapflux was zero. This suggests that some capacitance is present in the system, or that the technique to measure water potentials at the base of the tree is subject to some error, e.g. the temperature correction factors may need adjusting.

APPENDIX 2: CALCULATION OF FOREST TRANSPIRATION USING SAP FLOW MEASUREMENTS

Using the heat pulse (compensation) technique to estimate transpiration from a forest stand involves five steps:

1) Measurement of the heat pulse velocity at several depths in the sapwood on a sample of experimental trees.
2) Conversion of the heat-pulse velocity to sap velocity.
3) Correcting the sap velocity for inhomogeneities caused by sensor implantation.
4) Calculating the sap flow rate per tree based on the sap velocity profile across the conducting sapwood.
5) Scaling measurements from the individual tree to the forest.

Steps 2 and 3 are universally calculated using the theory of Marshall (1958) and the corrections of Swanson and Whitfield (1981). The details of these calculations can be found in the sap flow instrumentation handbook (Custom HPV, Soil Conservation Centre, Palmerston North, NZ). Steps 4 and 5 are not calculated in a universal fashion and the details of the approach used in this thesis are presented below.

Step 4 : Calculating the sap flow rate per tree

Four heat pulse velocity sensors were installed per tree in four trees per treatment (refer to section 4.3.6). In each tree sensors were located at 5, 12, 25 and 35 mm distance below the cambium. This arrangement attempts to provide the maximum information on sap velocity in the outer xylem, the region predicted to transport the majority of the transpiration stream. It is virtually impossible to place sensors deeper than 35 mm from the cambium due to the small diameter of the drills used for creating the access hole for the sensor. Since estimates of sap velocity are only available at each of these four depths, a method to calculate sap velocity at any depth in the sapwood is required. Figure A3 illustrates two hypothetical profiles of sap

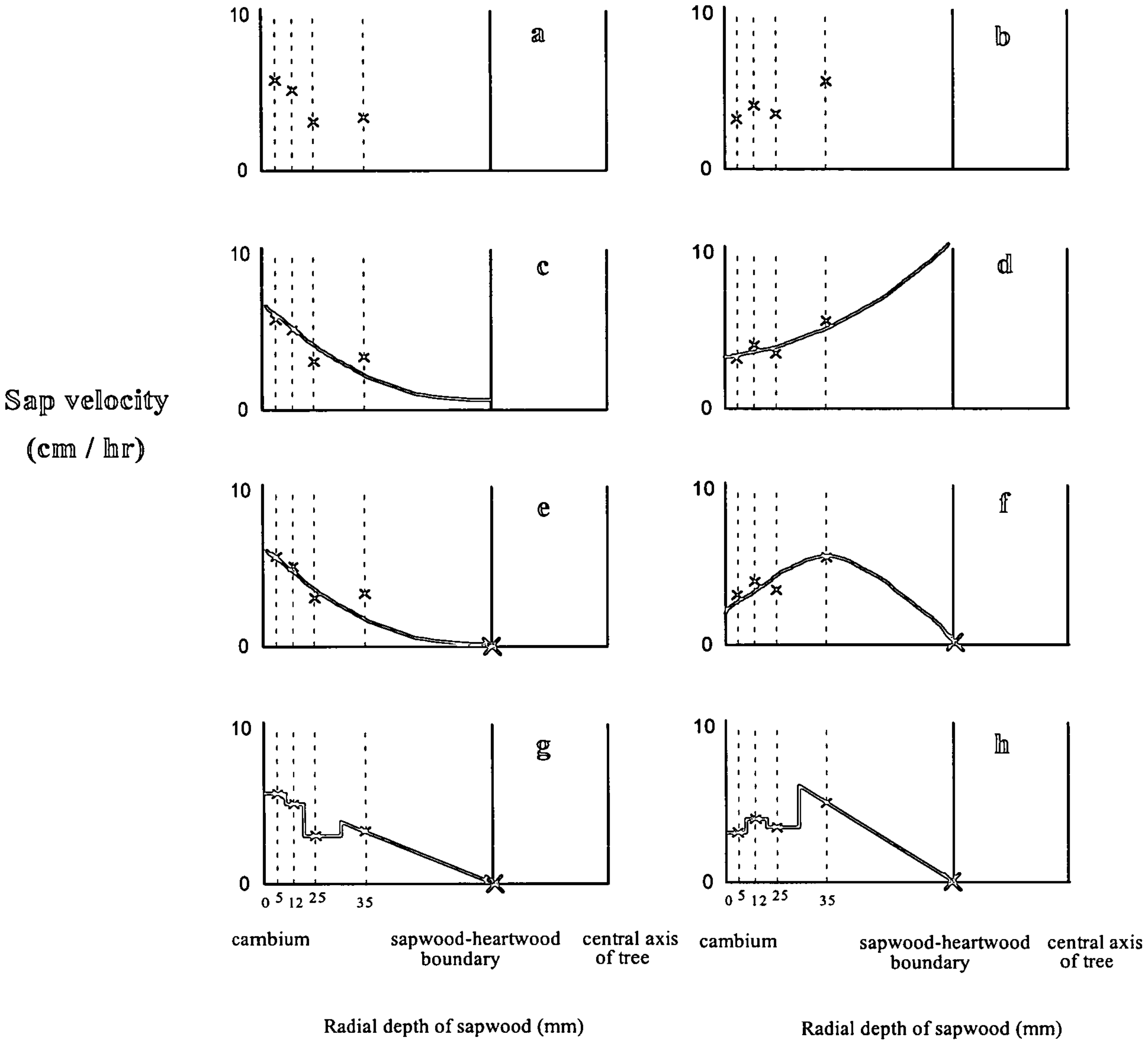


Figure A3 Two hypothetical sap velocity profiles (a) and (b) that illustrate the problem of applying a suitable method to determine sap velocity at locations out with the measurement points. The small crosses indicate measured values of sap velocity, the large cross an artificially generated value of zero velocity at the heartwood boundary. The heavy solid lines are values of sap velocity generated by one of three techniques (see text for methods) (c) and (d) relate to method 1, (e) and (f) to method 2 and (g) and (h) to method 3.

velocity across a tree at any one point in time. In the first profile (a) sap velocity decreases with distance from the cambium, where as in the second profile (b) sap velocity increases with distance from the cambium. In reality a wide variety of radial profiles were observed in the field data. Panels (c) and (d) illustrate one method (method 1) of calculating sap velocity at any depth in the sapwood. In this case a second order equation was fitted through the data:

$$v = (a \cdot depth^2) + (b \cdot depth) + c$$

where v is the sap velocity (cm hr $^{-1}$), *depth* is depth of sap velocity measurement below the cambium (mm) and *a*, *b* and *c* are regression parameters. It is clear that in the case where the sap velocity increases with distance from the cambium (d), sap velocity is most probably overestimated close to the heartwood. The expectation is that the sap velocity is likely to be zero at the sapwood-heartwood boundary and not greater than in the first few rings of xylem closest to the cambium. In panels (e) and (f) an approach of inventing an imaginary zero velocity measurement (heavy cross) at the sapwood-heartwood boundary is used (method 2), which forces the curve fitting procedure to provide a more realistic profile of sap velocity close to the heartwood (f). This procedure has little effect on the profile in which sap velocity naturally declines with distance from the cambium (compare (c) with (e)).

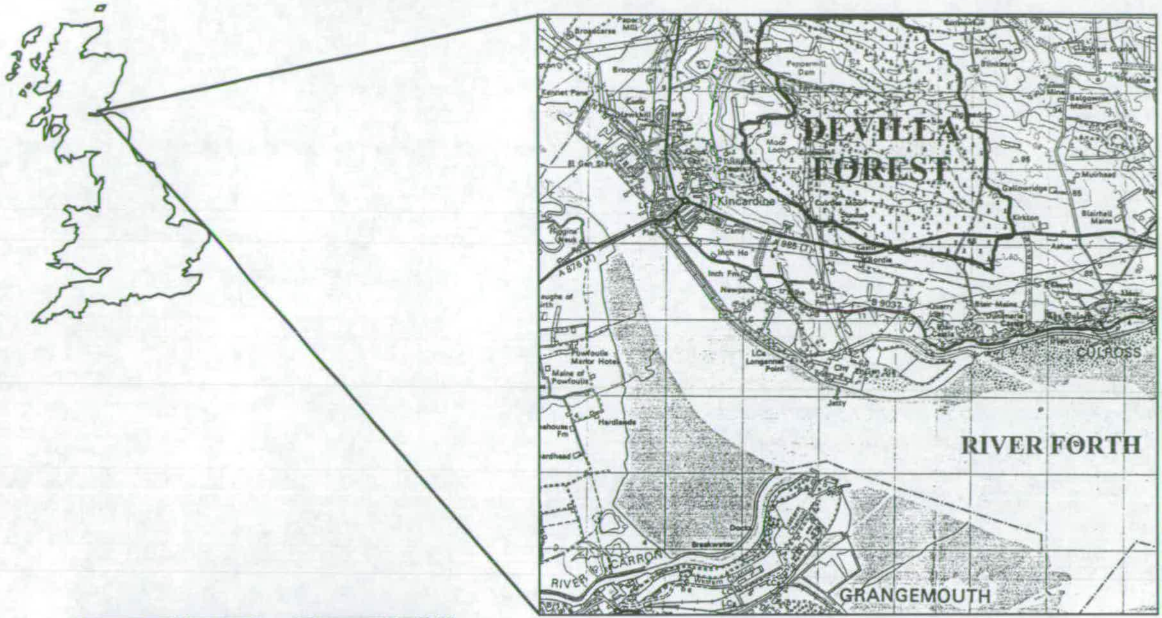
Panels (g) and (h) provide one other alternative method for describing the sap velocity at any depth in the sapwood (method 3). This approach assumes the sap velocity is the same value in the region close to the measured depths and also uses the idea of an imaginary zero velocity measurement at the sapwood-heartwood boundary.

All three of these methods for calculating the sap velocity at any depth in the sapwood were tested on a sample of experimental data. Sap flow rates per tree were calculated by 'rotating' the sap velocity profiles around the stem axis to integrate the sap flow over the entire sapwood area. It was concluded that method 2 produced values of sap flow in close agreement with method 3, with fewer erroneous values compared with method 1, consequently method 2 was employed with all the data collected during this study.

Step 5: Scaling measurements from the individual tree to the forest.

To scale up sap flow measurements from an individual tree to the forest level requires information on how well that individual represents the transpiration of the average tree in the forest. In an uneven age stand this would require adequate sampling of sap flow on trees in all diameter classes. In this study the forest was of even age and so the average sap flow per unit sapwood basal area of the eight trees measured was used to scale to forest level. The sapwood area per unit ground area was calculated by measuring overbark diameter at breast height (DBH) for all trees within a 0.25 ha area (see Table 4.1). Sapwood area was determined by deducting the basal area occupied by bark, cambium, phloem and heartwood. The thickness of the bark, cambium and phloem was measured on a random sample of trees and found to be on average 9 mm. The proportion of heartwood basal area per tree was determined from increment corer samples from the 8 sap flow trees. For trees of DBH>15 cm the heartwood occupied on average 11% of the basal woody area, for trees of DBH<15 cm the heartwood occupied approximately 5 % of the basal woody area. These figures were used together with the measured DBH distribution for the forest to calculate transpiration on a ground area basis.

APPENDIX 3: LOCATION AND PHOTOGRAPHS OF THE FIELD EXPERIMENT



Map 1. (Above) Devilla forest is located on the north side of the River Forth , 2 km NE of Kincardine (Lat. 56^{O} 2' Long. 3^{O} 43' , grid squares = 1 km)

Plate 1. (Left) The experimental plots were isolated from the surrounding soil by a 1.5 m deep ditch, the sides of which were lined in a heavy polythene sheet before being refilled with soil. This prevented lateral inflow of water and allowed the plots to be droughted.

Plate 2. (Right) Clear polythene covers suspended above the droughted plots deflected intercepted water beyond the previously installed ditches.

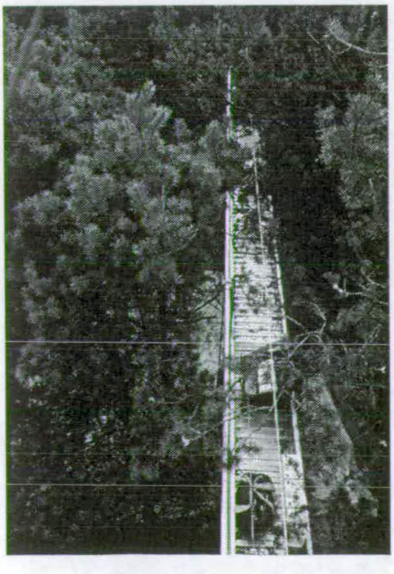


Plate 3. (Left) Access to the canopy was gained by an aerial walkway suspended 11.5 m above the ground between two Tripole masts

Plate 4. Experimental apparatus employed to measure water tensions in the boles of Scots pine at the experimental site. The rigid frame placed around the tree allows measurement of the contraction of the xylem when tensions within the water in the xylem increase. The sensitive displacement transducer (LVDT) can be seen protruding from the frame member towards the right edge of the photograph (see Chapter 2 for details)

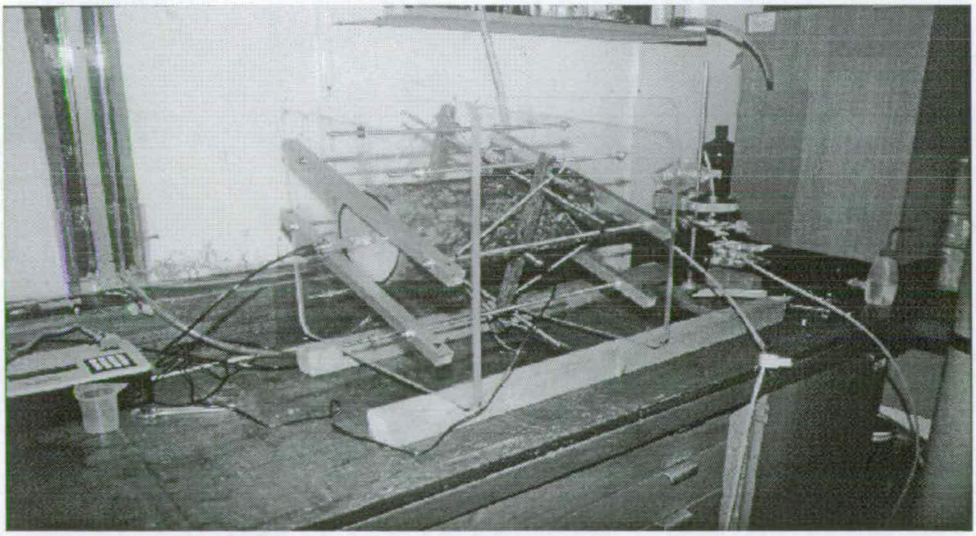


Plate 5. Experimental rig used to impose hydrostatic pressure within the xylem of Scots pine logs in order to provide calibrations for changes in xylem diameter per unit of applied pressure. The frame (see Plate 4) can be seen clamped to the log between the two perspex plates which seal the log to allow water pressures to be imposed.

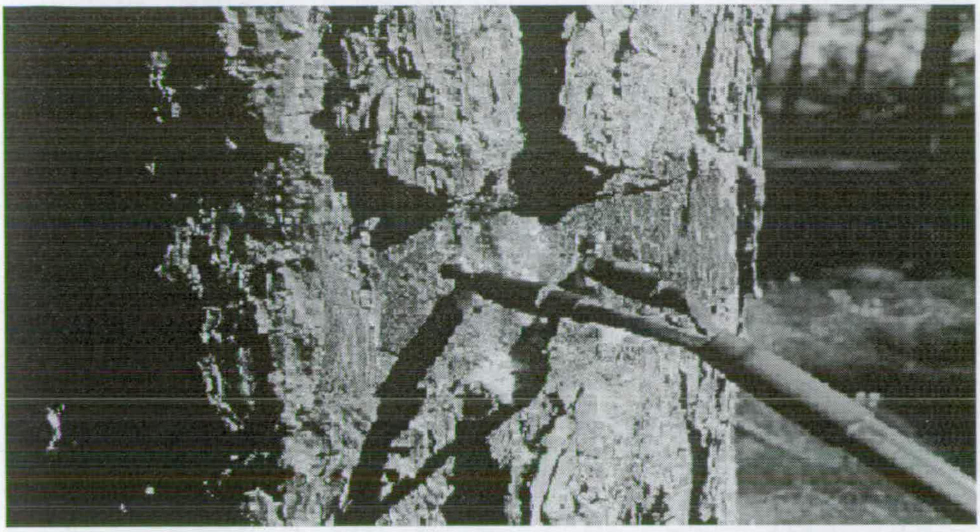


Plate 6. The system used to measure changes in the water content of the xylem. Two 50 mm steel pins hammered radially into the xylem are attached to a cable testing oscilloscope with the brown cabling seen entering the photograph at the bottom right corner (see Chapter 3 for details).

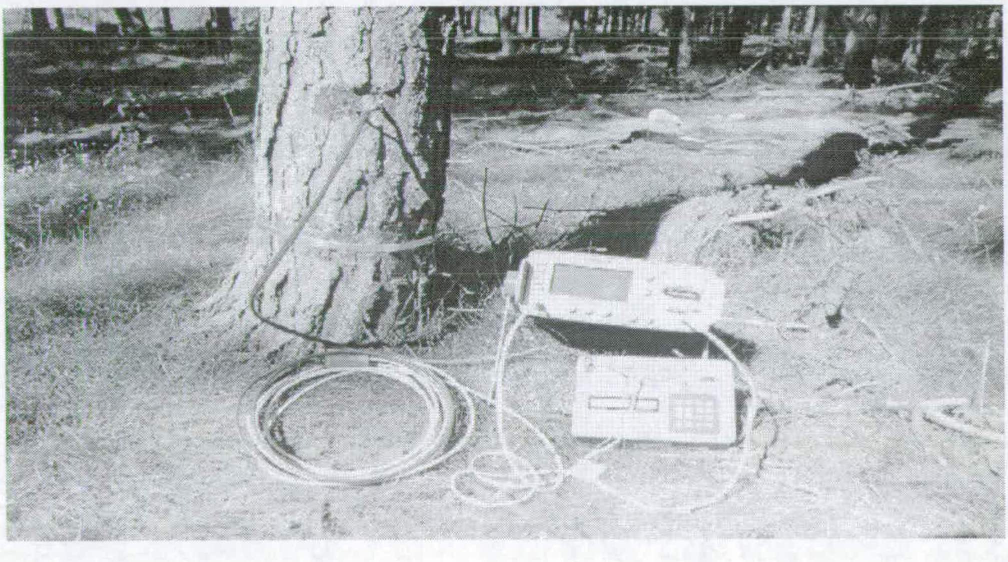


Plate 7. The complete time domain reflectrometry system in use to detect changes in xylem water contents. The brown cabling connecting the probes as illustrated in Plate 6 can be seen coming from the pins in the bole of the tree and connecting to the cable testing oscilloscope. The Campbell 21X datalogger seen below the oscilloscope controls the data acquisition.

APPENDIX 5 : DETERMINATION OF THE LINEAR COEFFICIENT OF EXPANSION (α) FOR STEEL AND WOOD

In chapter two a novel technique was presented that was developed to detect changes in the water tensions within the xylem. Because of the nature of this technique corrections were necessary to account for the thermal expansion of both the steel frame used in the measurement device and the wood in the bole of the tree itself. This appendix provides information on how the linear coefficient of expansion (α) for steel and wood were determined in the laboratory.

The coefficient of linear thermal expansion (expansivity) of a solid can be defined as follows:

$$\alpha = \frac{1}{L} \circ \frac{\mathrm{d}L}{\mathrm{d}t} \qquad \text{(Kaye and Labey 1986)}$$

where α is the expansivity of the material, *L* is the length of the material (m), *dL* is the change in length of the material (m) that occurs in response to a change in temperature *dt* (°C) of the material. Thus in order to determine α, a sample of material must be heated (or cooled) and the resultant change in length measured.

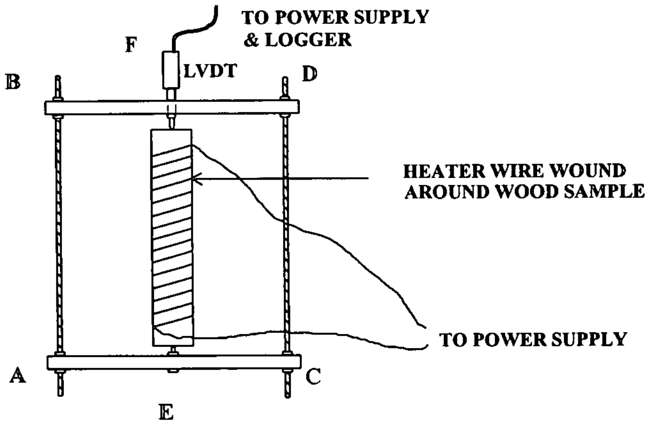


Figure A.4. The experimental equipment used to determine α, in this case for a sample of wood cut from across the diameter of the tree bole (see text for the protocol). The components of the measurement device (A to F) are described in Chapter 2. The thermal insulation wrapped around the sample and the thermocouples to determine the sample temperature have been omitted from the figure to aid clarity.

This was achieved in the laboratory by placing a sample of the steel rod of the type used to build the measuring frame, or a sample of freshly felled wood, inside the measuring device (described in chapter two) in place of where a section of trunk would be (see Figure 2.1 and Figure A.4). In the case of wood samples, these were cut in a radial direction through the bole of a freshly felled tree and had dimensions of approximately 50 mm by 50 mm (tangential face of xylem) by 150 mm (diameter of xylem). An insulated heating wire (constantan) was tightly wrapped around the sample, the sample having previously been covered with aluminium foil to spread the heat more evenly. In the case of wood samples two additional steps were taken i) plastic film was wrapped around the sample to prevent water loss during the measurements and ii) thermal insulation was provided external to the heating wire by covering the sample with 'bubble-wrap'. The temperature of the samples were measured using thermocouples. In the case of the wood samples these thermocouples were placed at several depths inside the sample to determine whether the sample had reached a stable temperature throughout. Heat was applied (DC power supply) and the resultant change in the length of the sample recorded by logging the output from the LVDT, sample temperature was logged simultaneously. The sample temperature was typically raised 20-30 °C above ambient temperature using this technique. If during the course of a series of such measurements the temperature of the measuring frame itself changed, due to fluctuations in ambient temperature, this was recorded and taken into account in the calculation of α. The figures for α_{wood} and α_{steel} obtained using this method are reported in Chapter 2.

APPENDIX 6: HOURLY ENVIRONMENTAL AND PHYSIOLOGICAL VARIABLES

This appendix contains hourly values of variables collected from the field experiment at Devilla. It excludes data collected during periods when net radiation < 0 W/m2, air vapour pressure deficit< 0.1kPa and days during which the foliage was considered wet due to rainfall. The calculations used for the derived variables are described at the relevant points in the main text of the thesis. This data is presented in columns A to Q which contain the following variables:

A	Date and time (hour averages e.g. 0800 hrs averaged from 0700 to 0800 hrs, all times BST)
B	Air temperature (degrees celsius)
C	Air vapour pressure deficit (kPa)
D	Net radiation measured above the canopy (W/m2)
E	Photosynthetically active radiation measured above the canopy (micromoles/m2/s)
F	Control treatment transpiration calculated on a ground area basis (kg/m2/s)
G	Droughted treatment transpiration calculated on a ground area basis (kg/m2/s)
H	Control soil volumetric water fraction integrated over the upper 20 cm depth of the soil profile
I	Droughted soil volumetric water fraction integrated over the upper 20 cm depth of the soil profile
J	Control soil volumetric water fraction integrated over the upper 50 cm depth of the soil profile
K	Droughted soil volumetric water fraction integrated over the upper 50 cm depth of the soil profile
L	Control canopy stomatal conductance (mm/s)
M	Droughted canopy stomatal conductance (mm/s)
N	Leaf area index control treatment
O	Leaf area index droughted treatment
P	Control stomatal conductance (column L/ column N, mm/s)
Q	Droughted stomatal conductance (column M / column O, mm/s)

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
25/04/95 08:00	8.8	0.11	59	266	2.32E-06	1.29E-06	0.28	0.20	N/A	N/A	2.2	1.2	1.57	1.57	1.4	0.7
25/04/95 09:00	8.9	0.11	169	510	5.30E-06	4.39E-06	0.28	0.20	N/A	N/A	4.1	3.3	1.57	1.57	2.6	2.1
25/04/95 10:00	9.3	0.14	298	781	1.21E-05	8.95E-06	0.28	0.20	N/A	N/A	7.2	5.1	1.57	1.57	4.6	3.2
25/04/95 11:00	10.0	0.19	396	969	1.47E-05	1.24E-05	0.28	0.20	N/A	N/A	6.8	5.6	1.57	1.57	4.3	3.6
25/04/95 12:00	10.6	0.22	450	1101	1.99E-05	1.85E-05	0.28	0.20	N/A	N/A	7.8	7.2	1.57	1.57	5.0	4.6
25/04/95 13:00	10.9	0.25	505	1196	1.94E-05	1.93E-05	0.28	0.20	N/A	N/A	6.8	6.8	1.57	1.57	4.3	4.3
25/04/95 14:00	10.8	0.24	455	1102	2.32E-05	2.14E-05	0.28	0.20	N/A	N/A	9.4	8.6	1.57	1.57	6.0	5.5
25/04/95 15:00	9.4	0.17	301	731	1.77E-05	1.98E-05	0.28	0.20	N/A	N/A	10.9	12.4	1.57	1.57	6.9	7.9
25/04/95 16:00	9.5	0.18	324	782	1.42E-05	1.19E-05	0.28	0.20	N/A	N/A	7.9	6.5	1.57	1.57	5.1	4.2
25/04/95 17:00	9.9	0.21	239	578	1.63E-05	1.58E-05	0.28	0.20	N/A	N/A	8.7	8.4	1.57	1.57	5.5	5.3
25/04/95 18:00	9.4	0.19	191	487	1.52E-05	1.49E-05	0.28	0.20	N/A	N/A	9.2	8.9	1.57	1.57	5.8	5.7
25/04/95 19:00	10.1	0.26	131	399	1.40E-05	1.28E-05	0.28	0.20	N/A	N/A	6.7	6.0	1.57	1.57	4.2	3.8
25/04/95 20:00	9.6	0.32	4	176	1.54E-05	1.51E-05	0.28	0.20	N/A	N/A	6.9	6.8	1.57	1.57	4.4	4.3
26/04/95 08:00	3.3	0.12	62	301	1.97E-06	1.90E-06	0.28	0.20	N/A	N/A	1.9	1.8	1.57	1.57	1.2	1.2
26/04/95 09:00	5.1	0.21	195	600	5.24E-06	4.98E-06	0.28	0.20	N/A	N/A	2.6	2.4	1.57	1.57	1.6	1.5
26/04/95 10:00	6.0	0.28	303	788	1.43E-05	1.13E-05	0.28	0.20	N/A	N/A	5.6	4.3	1.57	1.57	3.6	2.8
26/04/95 11:00	6.9	0.33	382	888	1.88E-05	1.60E-05	0.28	0.20	N/A	N/A	6.2	5.2	1.57	1.57	3.9	3.3
26/04/95 12:00	7.3	0.35	360	872	2.05E-05	1.89E-05	0.28	0.20	N/A	N/A	6.7	6.1	1.57	1.57	4.2	3.9
26/04/95 13:00	8.1	0.42	410	956	2.16E-05	1.99E-05	0.28	0.20	N/A	N/A	5.8	5.3	1.57	1.57	3.7	3.3
26/04/95 14:00	8.3	0.43	273	645	2.56E-05	2.52E-05	0.28	0.20	N/A	N/A	7.3	7.2	1.57	1.57	4.7	4.6
26/04/95 15:00	8.0	0.38	306	736	2.47E-05	2.21E-05	0.28	0.20	N/A	N/A	7.7	6.8	1.57	1.57	4.9	4.3
26/04/95 16:00	8.3	0.38	413	970	2.19E-05	2.17E-05	0.28	0.20	N/A	N/A	6.3	6.2	1.57	1.57	4.0	4.0
26/04/95 17:00	7.9	0.37	199	484	2.40E-05	2.21E-05	0.28	0.20	N/A	N/A	8.3	7.6	1.57	1.57	5.3	4.9
26/04/95 18:00	7.4	0.33	101	263	1.96E-05	1.99E-05	0.28	0.20	N/A	N/A	8.1	8.3	1.57	1.57	5.2	5.3
26/04/95 19:00	6.3	0.23	48	140	1.26E-05	1.51E-05	0.28	0.20	N/A	N/A	7.7	9.6	1.57	1.57	4.9	6.1
26/04/95 20:00	6.1	0.26	6	48	8.70E-06	7.82E-06	0.28	0.20	N/A	N/A	4.8	4.2	1.57	1.57	3.0	2.7
27/04/95 07:00	2.8	0.19	5	46	2.46E-06	2.30E-06	0.29	0.20	N/A	N/A	1.7	1.6	1.57	1.57	1.1	1.0
27/04/95 08:00	3.9	0.25	73	214	4.88E-06	5.52E-06	0.29	0.20	N/A	N/A	2.4	2.8	1.57	1.57	1.5	1.8
27/04/95 09:00	5.5	0.37	196	543	1.21E-05	1.01E-05	0.29	0.19	N/A	N/A	3.9	3.3	1.57	1.57	2.5	2.1
27/04/95 10:00	6.4	0.46	330	844	1.97E-05	1.77E-05	0.29	0.19	N/A	N/A	5.1	4.5	1.57	1.57	3.2	2.9
27/04/95 11:00	6.3	0.46	304	733	2.21E-05	1.99E-05	0.29	0.19	N/A	N/A	5.8	5.2	1.57	1.57	3.7	3.3
27/04/95 12:00	6.6	0.49	234	568	2.32E-05	2.05E-05	0.29	0.19	N/A	N/A	5.9	5.2	1.57	1.57	3.8	3.3
27/04/95 13:00	7.3	0.54	295	697	2.31E-05	2.17E-05	0.29	0.19	N/A	N/A	5.0	4.6	1.57	1.57	3.2	3.0
27/04/95 14:00	8.1	0.59	418	966	2.49E-05	2.37E-05	0.29	0.19	N/A	N/A	4.6	4.3	1.57	1.57	2.9	2.8
27/04/95 15:00	8.0	0.56	346	814	2.59E-05	2.71E-05	0.29	0.19	N/A	N/A	5.5	5.7	1.57	1.57	3.5	3.7
27/04/95 16:00	8.3	0.59	346	815	2.84E-05	2.75E-05	0.29	0.19	N/A	N/A	5.7	5.5	1.57	1.57	3.6	3.5
27/04/95 17:00	8.7	0.61	328	759	2.86E-05	2.96E-05	0.29	0.19	N/A	N/A	5.7	5.9	1.57	1.57	3.6	3.8
27/04/95 18:00	8.7	0.57	274	652	2.26E-05	2.49E-05	0.29	0.19	N/A	N/A	4.7	5.3	1.57	1.57	3.0	3.4
27/04/95 19:00	7.9	0.50	61	186	1.81E-05	1.96E-05	0.29	0.19	N/A	N/A	5.2	5.7	1.57	1.57	3.3	3.6
27/04/95 20:00	7.1	0.41	21	115	1.26E-05	1.51E-05	0.29	0.19	N/A	N/A	4.5	5.5	1.57	1.57	2.9	3.5
28/04/95 08:00	5.9	0.24	83	339	3.15E-06	2.81E-06	0.29	0.19	N/A	N/A	1.3	1.2	1.57	1.57	0.8	0.7
28/04/95 09:00	7.2	0.37	215	634	1.16E-05	8.92E-06	0.29	0.19	N/A	N/A	3.2	2.4	1.57	1.57	2.1	1.5
28/04/95 10:00	7.2	0.39	323	872	1.96E-05	1.80E-05	0.29	0.19	N/A	N/A	5.3	4.8	1.57	1.57	3.4	3.1
28/04/95 11:00	8.0	0.53	460	1154	2.46E-05	2.12E-05	0.29	0.19	N/A	N/A	4.7	4.0	1.57	1.57	3.0	2.6
28/04/95 12:00	8.9	0.64	546	1322	2.58E-05	2.60E-05	0.29	0.19	N/A	N/A	4.1	4.1	1.57	1.57	2.6	2.6
28/04/95 13:00	9.7	0.69	570	1323	2.59E-05	2.74E-05	0.29	0.19	N/A	N/A	3.7	3.9	1.57	1.57	2.3	2.5
28/04/95 14:00	9.8	0.69	605	1396	2.82E-05	3.14E-05	0.29	0.19	N/A	N/A	4.2	4.8	1.57	1.57	2.7	3.1
28/04/95 15:00	10.5	0.76	611	1438	2.86E-05	3.00E-05	0.29	0.19	N/A	N/A	3.9	4.2	1.57	1.57	2.5	2.6
28/04/95 16:00	10.3	0.73	502	1227	2.79E-05	3.00E-05	0.29	0.19	N/A	N/A	4.3	4.7	1.57	1.57	2.7	3.0
28/04/95 17:00	10.2	0.69	400	1010	2.57E-05	3.00E-05	0.29	0.19	N/A	N/A	4.3	5.1	1.57	1.57	2.8	3.3

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
28/04/95 18:00	10.1	0.71	278	742	2.38E-05	2.79E-05	0.29	0.19	N/A	N/A	4.1	4.9	1.57	1.57	2.6	3.1
28/04/95 19:00	9.5	0.65	155	468	2.17E-05	2.31E-05	0.29	0.19	N/A	N/A	4.4	4.7	1.57	1.57	2.8	3.0
03/05/95 09:00	12.9	0.15	124	301	5.89E-06	2.84E-06	0.29	0.18	N/A	N/A	3.5	1.5	1.57	1.57	2.2	1.0
03/05/95 10:00	13.7	0.21	114	287	1.23E-05	8.80E-06	0.29	0.18	N/A	N/A	6.5	4.3	1.57	1.57	4.2	2.7
03/05/95 11:00	14.3	0.24	133	321	1.30E-05	1.02E-05	0.29	0.18	N/A	N/A	5.5	4.0	1.57	1.57	3.5	2.6
03/05/95 12:00	14.9	0.27	192	456	1.43E-05	1.08E-05	0.29	0.18	N/A	N/A	5.3	3.8	1.57	1.57	3.4	2.4
03/05/95 13:00	16.4	0.42	492	1183	1.76E-05	1.65E-05	0.29	0.18	N/A	N/A	3.2	3.0	1.57	1.57	2.0	1.9
03/05/95 14:00	17.4	0.58	369	883	2.71E-05	2.85E-05	0.29	0.18	N/A	N/A	4.6	4.8	1.57	1.57	2.9	3.1
03/05/95 15:00	18.1	0.69	258	619	2.86E-05	2.78E-05	0.29	0.18	N/A	N/A	4.8	4.7	1.57	1.57	3.1	3.0
03/05/95 16:00	18.5	0.72	264	645	2.67E-05	2.75E-05	0.29	0.18	N/A	N/A	4.2	4.4	1.57	1.57	2.7	2.8
03/05/95 17:00	19.2	0.84	252	622	2.58E-05	2.76E-05	0.29	0.18	N/A	N/A	3.7	4.0	1.57	1.57	2.4	2.6
03/05/95 18:00	19.2	0.81	151	423	2.49E-05	2.55E-05	0.29	0.18	N/A	N/A	4.0	4.1	1.57	1.57	2.5	2.6
03/05/95 19:00	19.1	0.78	72	258	1.54E-05	1.95E-05	0.29	0.18	N/A	N/A	2.8	4.0	1.57	1.57	1.8	2.5
03/05/95 20:00	17.0	0.52	11	124	1.13E-05	1.36E-05	0.29	0.18	N/A	N/A	3.2	4.0	1.57	1.57	2.1	2.5
04/05/95 08:00	14.2	0.39	81	300	6.33E-06	3.86E-06	0.29	0.18	N/A	N/A	1.7	1.0	1.57	1.57	1.1	0.6
04/05/95 09:00	14.4	0.38	118	372	1.44E-05	8.86E-06	0.29	0.18	N/A	N/A	4.4	2.4	1.57	1.57	2.8	1.5
04/05/95 10:00	15.5	0.46	223	615	1.71E-05	1.30E-05	0.29	0.18	N/A	N/A	3.5	2.5	1.57	1.57	2.2	1.6
04/05/95 11:00	17.7	0.67	390	968	2.35E-05	2.26E-05	0.29	0.18	N/A	N/A	3.2	3.0	1.57	1.57	2.0	1.9
04/05/95 12:00	19.1	0.80	503	1183	3.17E-05	3.13E-05	0.29	0.18	N/A	N/A	4.0	4.0	1.57	1.57	2.6	2.5
04/05/95 13:00	20.9	1.20	476	1155	3.40E-05	3.76E-05	0.29	0.18	N/A	N/A	3.4	3.7	1.57	1.57	2.1	2.4
04/05/95 14:00	21.6	1.29	595	1407	3.41E-05	3.91E-05	0.29	0.18	N/A	N/A	3.0	3.5	1.57	1.57	1.9	2.2
04/05/95 15:00	21.7	1.27	579	1371	3.35E-05	3.85E-05	0.29	0.18	N/A	N/A	3.0	3.5	1.57	1.57	1.9	2.2
04/05/95 16:00	21.3	1.24	508	1227	3.22E-05	3.69E-05	0.29	0.18	N/A	N/A	3.0	3.5	1.57	1.57	1.9	2.2
04/05/95 17:00	20.7	1.20	392	967	2.84E-05	3.48E-05	0.29	0.18	N/A	N/A	2.9	3.6	1.57	1.57	1.8	2.3
04/05/95 18:00	20.4	1.06	293	749	2.61E-05	3.14E-05	0.29	0.18	N/A	N/A	3.0	3.7	1.57	1.57	1.9	2.3
04/05/95 19:00	19.5	0.86	175	485	2.11E-05	2.40E-05	0.29	0.18	N/A	N/A	3.1	3.5	1.57	1.57	2.0	2.3
04/05/95 20:00	17.4	0.58	44	174	1.52E-05	1.86E-05	0.29	0.18	N/A	N/A	3.6	4.5	1.57	1.57	2.3	2.9
05/05/95 07:00	6.8	0.23	1	90	2.40E-06	2.11E-06	0.29	0.18	N/A	N/A	1.4	1.2	1.57	1.57	0.9	0.8
05/05/95 08:00	7.8	0.23	72	211	7.27E-06	4.54E-06	0.29	0.18	N/A	N/A	4.0	2.4	1.57	1.57	2.6	1.5
05/05/95 09:00	9.0	0.22	134	347	1.15E-05	7.92E-06	0.29	0.18	N/A	N/A	6.0	3.9	1.57	1.57	3.8	2.5
05/05/95 10:00	10.5	0.29	221	565	1.50E-05	1.04E-05	0.29	0.18	N/A	N/A	5.7	3.8	1.57	1.57	3.6	2.4
05/05/95 11:00	12.3	0.43	425	1015	2.14E-05	1.85E-05	0.29	0.18	N/A	N/A	4.8	4.1	1.57	1.57	3.1	2.6
05/05/95 12:00	13.4	0.52	419	1012	2.68E-05	2.58E-05	0.29	0.18	N/A	N/A	5.3	5.1	1.57	1.57	3.4	3.3
05/05/95 13:00	14.7	0.73	568	1350	3.10E-05	3.03E-05	0.29	0.18	N/A	N/A	4.5	4.4	1.57	1.57	2.9	2.8
05/05/95 14:00	15.7	0.82	622	1468	3.25E-05	3.57E-05	0.29	0.18	N/A	N/A	4.3	4.8	1.57	1.57	2.8	3.1
05/05/95 15:00	16.5	0.94	573	1370	3.23E-05	3.73E-05	0.29	0.18	N/A	N/A	3.8	4.4	1.57	1.57	2.4	2.8
05/05/95 16:00	17.0	1.03	534	1302	3.18E-05	3.63E-05	0.29	0.18	N/A	N/A	3.5	4.0	1.57	1.57	2.2	2.6
05/05/95 17:00	17.2	1.05	436	1098	2.90E-05	3.45E-05	0.29	0.18	N/A	N/A	3.3	3.9	1.57	1.57	2.1	2.5
05/05/95 18:00	17.0	1.13	322	855	2.69E-05	3.18E-05	0.29	0.18	N/A	N/A	2.9	3.5	1.57	1.57	1.9	2.2
05/05/95 19:00	16.6	1.04	191	567	2.39E-05	2.57E-05	0.29	0.18	N/A	N/A	2.9	3.2	1.57	1.57	1.9	2.0
13/05/95 07:00	2.0	0.14	5	178	6.17E-07	4.84E-07	0.29	0.17	N/A	N/A	0.6	0.4	1.56	1.56	0.4	0.3
13/05/95 08:00	3.1	0.14	123	399	1.83E-06	1.04E-06	0.29	0.17	N/A	N/A	1.2	0.7	1.56	1.56	0.8	0.4
13/05/95 09:00	4.6	0.24	260	683	5.96E-06	4.59E-06	0.29	0.17	N/A	N/A	2.1	1.6	1.56	1.56	1.3	1.0
13/05/95 10:00	5.7	0.37	409	979	1.35E-05	1.10E-05	0.29	0.17	N/A	N/A	3.3	2.7	1.56	1.56	2.1	1.7
13/05/95 11:00	6.2	0.40	397	937	2.06E-05	1.81E-05	0.29	0.17	N/A	N/A	5.1	4.4	1.56	1.56	3.2	2.8
13/05/95 12:00	6.7	0.43	312	745	2.03E-05	2.02E-05	0.29	0.17	N/A	N/A	5.0	5.0	1.56	1.56	3.2	3.2
13/05/95 13:00	7.2	0.47	277	672	2.27E-05	2.12E-05	0.29	0.17	N/A	N/A	5.7	5.2	1.56	1.56	3.6	3.4
13/05/95 14:00	7.6	0.51	476	1119	2.47E-05	2.34E-05	0.29	0.17	N/A	N/A	5.4	5.1	1.56	1.56	3.5	3.3
13/05/95 15:00	8.3	0.54	569	1352	2.48E-05	2.57E-05	0.29	0.17	N/A	N/A	4.7	4.9	1.56	1.56	3.0	3.1
13/05/95 16:00	9.4	0.69	492	1179	3.12E-05	3.10E-05	0.29	0.17	N/A	N/A	5.2	5.2	1.56	1.56	3.3	3.3
13/05/95 17:00	9.7	0.71	368	893	3.13E-05	3.19E-05	0.29	0.17	N/A	N/A	5.4	5.5	1.56	1.56	3.4	3.5
13/05/95 18:00	10.0	0.70	278	684	2.87E-05	2.91E-05	0.29	0.17	N/A	N/A	5.1	5.2	1.56	1.56	3.3	3.3
13/05/95 19:00	9.6	0.63	138	411	2.69E-05	2.70E-05	0.29	0.17	N/A	N/A	5.7	5.7	1.56	1.56	3.6	3.6
13/05/95 20:00	9.0	0.54	68	370	2.38E-05	2.33E-05	0.29	0.17	N/A	N/A	6.0	5.9	1.56	1.56	3.8	3.7
15/05/95 09:00	4.7	0.22	278	758	7.12E-06	6.65E-06	0.30	0.16	0.28	0.21	2.6	2.5	1.56	1.56	1.7	1.6
15/05/95 10:00	6.4	0.40	385	999	1.64E-05	1.27E-05	0.30	0.16	0.28	0.21	4.2	3.2	1.56	1.56	2.7	2.0
15/05/95 11:00	7.2	0.52	512	1246	2.25E-05	1.90E-05	0.30	0.16	0.28	0.21	4.4	3.6	1.56	1.56	2.8	2.3
15/05/95 12:00	7.5	0.53	374	922	2.49E-05	2.24E-05	0.30	0.16	0.28	0.21	5.4	4.7	1.56	1.56	3.4	3.0
15/05/95 13:00	8.3	0.60	366	878	2.56E-05	2.29E-05	0.30	0.16	0.28	0.21	4.7	4.1	1.56	1.56	3.0	2.6
15/05/95 14:00	9.1	0.69	406	970	2.91E-05	2.76E-05	0.30	0.16	0.28	0.21	4.8	4.5	1.56	1.56	3.0	2.9
15/05/95 15:00	10.3	0.81	757	1732	3.09E-05	3.06E-05	0.30	0.16	0.28	0.21	3.9	3.9	1.56	1.56	2.5	2.5
15/05/95 16:00	10.1	0.74	607	1441	3.40E-05	3.49E-05	0.30	0.16	0.28	0.21	5.0	5.1	1.56	1.56	3.2	3.3
15/05/95 17:00	10.7	0.83	573	1344	3.30E-05	3.37E-05	0.30	0.16	0.28	0.21	4.2	4.3	1.56	1.56	2.7	2.8
15/05/95 18:00	10.2	0.70	259	623	3.29E-05	3.30E-05	0.30	0.16	0.28	0.21	6.0	6.0	1.56	1.56	3.9	3.9
15/05/95 19:00	7.6	0.35	122	345	1.66E-05	1.88E-05	0.30	0.16	0.28	0.21	6.2	7.2	1.56	1.56	4.0	4.6
15/05/95 20:00	7.3	0.34	9	129	1.26E-05	1.29E-05	0.30	0.16	0.28	0.21	5.6	5.8	1.56	1.56	3.6	3.7
08/06/95 07:00	9.1	0.37	38	203	1.35E-05	1.07E-05	0.30	0.13	0.27	0.18	5.0	3.9	1.72	1.68	2.9	2.3
08/06/95 08:00	9.4	0.38	97	271	1.76E-05	1.60E-05	0.30	0.13	0.27	0.18	6.3	5.7	1.72	1.68	3.7	3.4
08/06/95 09:00	10.5	0.44	208	509	2.17E-05	1.87E-05	0.30	0.13	0.27	0.18	6.2	5.3	1.72	1.68	3.6	3.1
08/06/95 10:00	11.7	0.54	397	947	2.67E-05	2.47E-05	0.30	0.13	0.27	0.18	5.9	5.4	1.72	1.68	3.4	3.2
08/06/95 11:00	12.5	0.61	411	1000	3.30E-05	2.88E-05	0.30	0.13	0.27	0.18	6.5	5.7	1.72	1.68	3.8	3.4
08/06/95 12:00	12.5	0.61	291	696	3.32E-05	3.27E-05	0.30	0.13	0.27	0.18	6.9	6.8	1.72	1.68	4.0	4.0
08/06/95 13:00	12.5	0.60	241	583	3.20E-05	3.21E-05	0.30	0.13	0.27	0.18	6.9	6.9	1.72	1.68	4.0	4.1
08/06/95 14:00	12.8	0.61	386	910	3.15E-05	3.14E-05	0.30	0.13	0.27	0.18	6.2	6.2	1.72	1.68	3.6	3.7
08/06/95 15:00	12.7	0.59	313	731	3.25E-05	3.27E-05	0.30	0.13	0.27	0.17	6.9	7.0	1.72	1.68	4.0	4.1
08/06/95 16:00	12.4	0.53	315	728	3.01E-05	3.09E-05	0.30	0.13	0.27	0.17	7.0	7.2	1.72	1.68	4.1	4.3
08/06/95 17:00	12.0	0.48	153	373	2.80E-05	2.89E-05	0.30	0.13	0.27	0.17	7.8	8.0	1.72	1.68	4.5	4.8
08/06/95 18:00	12.1	0.48	125	307	2.39E-05	2.45E-05	0.30	0.13	0.27	0.17	6.7	6.9	1.72	1.68	3.9	4.1
08/06/95 19:00	11.9	0.46	173	437	2.28E-05	2.19E-05	0.30	0.13	0.27	0.17	6.3	6.1	1.72	1.68	3.7	3.6
08/06/95 20:00	11.1	0.40	67	202	2.14E-05	2.08E-05	0.30	0.13	0.27	0.17	7.4	7.2	1.72	1.68	4.3	4.3
08/06/95 21:00	10.9	0.44	6	116	1.81E-05	1.84E-05	0.30	0.13	0.27	0.17	5.9	6.0	1.72	1.69	3.4	3.5
09/06/95 07:00	10.7	0.52	52	213	1.70E-05	1.51E-05	0.30	0.13	0.27	0.17	4.6	4.0	1.73	1.69	2.6	2.4
09/06/95 08:00	11.0	0.50	105	342	2.19E-05	1.82E-05	0.30	0.13	0.27	0.17	6.0	4.9	1.73	1.69	3.5	2.9
09/06/95 09:00	12.3	0.56	178	478	2.49E-05	2.14E-05	0.30	0.13	0.27	0.17	5.7	4.8	1.73	1.69	3.3	2.9
09/06/95 10:00	13.3	0.66	339	860	2.89E-05	2.52E-05	0.30	0.13	0.27	0.17	5.3	4.6	1.73	1.69	3.1	2.7
09/06/95 11:00	14.7	0.83	565	1343	3.45E-05	3.22E-05	0.30	0.13	0.27	0.17	4.8	4.5	1.73	1.69	2.8	2.6

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
09/06/95 12:00	15.6	0.92	644	1487	3.68E-05	3.77E-05	0.30	0.13	0.27	0.17	4.6	4.7	1.73	1.69	2.7	2.8
09/06/95 13:00	16.7	1.06	707	1651	3.97E-05	3.96E-05	0.30	0.13	0.27	0.17	4.3	4.3	1.73	1.69	2.5	2.6
09/06/95 14:00	17.2	1.14	707	1656	4.00E-05	3.90E-05	0.30	0.13	0.27	0.17	4.1	4.0	1.73	1.69	2.4	2.4
09/06/95 15:00	17.9	1.26	664	1570	4.03E-05	3.79E-05	0.30	0.13	0.27	0.17	3.8	3.5	1.73	1.69	2.2	2.1
09/06/95 16:00	18.7	1.38	606	1451	3.84E-05	3.69E-05	0.30	0.13	0.27	0.17	3.3	3.2	1.73	1.69	1.9	1.9
09/06/95 17:00	18.9	1.46	513	1263	3.82E-05	3.44E-05	0.30	0.13	0.27	0.17	3.2	2.9	1.73	1.69	1.9	1.7
09/06/95 18:00	18.7	1.46	398	1018	3.58E-05	3.03E-05	0.30	0.13	0.27	0.17	3.1	2.6	1.73	1.69	1.8	1.5
09/06/95 19:00	18.5	1.44	264	734	3.35E-05	2.59E-05	0.30	0.13	0.27	0.17	3.0	2.3	1.73	1.69	1.7	1.3
09/06/95 20:00	14.9	0.73	96	344	2.61E-05	2.19E-05	0.30	0.13	0.27	0.17	4.9	4.0	1.73	1.69	2.8	2.4
10/06/95 07:00	12.2	0.30	14	50	8.18E-06	7.04E-06	0.30	0.13	0.27	0.17	4.0	3.4	1.74	1.69	2.3	2.0
10/06/95 08:00	12.5	0.31	38	106	1.07E-05	8.91E-06	0.30	0.13	0.27	0.17	5.1	4.1	1.74	1.69	3.0	2.4
10/06/95 09:00	13.2	0.35	80	207	1.32E-05	1.04E-05	0.30	0.13	0.27	0.17	5.1	3.8	1.74	1.69	2.9	2.2
10/06/95 10:00	13.7	0.37	79	206	1.49E-05	1.24E-05	0.30	0.13	0.27	0.17	5.5	4.4	1.74	1.70	3.2	2.6
10/06/95 11:00	14.5	0.40	100	255	1.66E-05	1.38E-05	0.30	0.13	0.27	0.17	5.5	4.3	1.74	1.70	3.1	2.5
10/06/95 12:00	15.5	0.47	208	508	1.72E-05	1.47E-05	0.30	0.13	0.27	0.17	3.9	3.2	1.74	1.70	2.2	1.9
10/06/95 13:00	16.7	0.66	292	691	2.61E-05	2.24E-05	0.30	0.13	0.27	0.17	4.6	3.8	1.74	1.70	2.6	2.3
10/06/95 14:00	16.8	0.76	187	459	2.92E-05	2.58E-05	0.30	0.13	0.27	0.17	5.0	4.3	1.74	1.70	2.8	2.5
10/06/95 15:00	17.5	0.92	310	756	2.98E-05	2.52E-05	0.29	0.13	0.27	0.17	3.9	3.3	1.74	1.70	2.3	1.9
10/06/95 16:00	17.7	1.10	393	953	3.48E-05	3.07E-05	0.29	0.13	0.27	0.17	3.8	3.3	1.74	1.70	2.2	2.0
10/06/95 17:00	17.3	1.00	199	508	3.54E-05	3.13E-05	0.29	0.13	0.27	0.17	4.7	4.0	1.74	1.70	2.7	2.4
10/06/95 18:00	17.0	0.94	131	340	3.03E-05	2.65E-05	0.29	0.13	0.27	0.17	4.4	3.8	1.74	1.70	2.5	2.2
10/06/95 19:00	16.0	0.66	43	137	1.92E-05	2.03E-05	0.29	0.13	0.27	0.17	4.1	4.3	1.74	1.70	2.3	2.6
10/06/95 20:00	15.1	0.46	21	81	1.19E-05	1.20E-05	0.29	0.13	0.27	0.17	3.6	3.6	1.74	1.70	2.1	2.1
10/06/95 21:00	14.6	0.37	1	34	8.23E-06	7.43E-06	0.29	0.13	0.27	0.17	3.2	2.9	1.74	1.70	1.9	1.7
11/06/95 06:00	12.0	0.39	2	85	5.64E-06	3.10E-06	0.29	0.12	0.27	0.17	2.0	1.1	1.74	1.70	1.1	0.6
11/06/95 07:00	11.8	0.38	31	186	1.34E-05	8.89E-06	0.29	0.12	0.27	0.17	4.8	3.1	1.74	1.70	2.7	1.8
11/06/95 08:00	12.1	0.41	105	321	1.73E-05	1.29E-05	0.29	0.12	0.27	0.17	5.6	4.1	1.74	1.70	3.2	2.4
11/06/95 09:00	11.9	0.41	92	269	2.00E-05	1.65E-05	0.29	0.12	0.27	0.17	6.6	5.3	1.75	1.70	3.8	3.1
11/06/95 10:00	12.2	0.46	114	294	2.04E-05	1.73E-05	0.29	0.12	0.27	0.17	5.9	4.9	1.75	1.70	3.4	2.9
11/06/95 11:00	12.3	0.55	198	484	2.23E-05	1.84E-05	0.29	0.12	0.27	0.17	5.2	4.2	1.75	1.70	3.0	2.5
11/06/95 12:00	12.7	0.63	460	1088	2.74E-05	2.18E-05	0.29	0.12	0.27	0.17	5.1	4.0	1.75	1.70	2.9	2.3
11/06/95 13:00	13.9	0.83	674	1545	3.50E-05	2.78E-05	0.29	0.12	0.27	0.17	4.7	3.7	1.75	1.70	2.7	2.2
11/06/95 14:00	13.2	0.78	392	920	3.48E-05	3.17E-05	0.29	0.12	0.27	0.17	5.5	4.9	1.75	1.70	3.1	2.9
11/06/95 15:00	13.7	0.79	451	1038	3.55E-05	3.17E-05	0.29	0.12	0.27	0.17	5.3	4.6	1.75	1.70	3.0	2.7
11/06/95 16:00	13.7	0.75	270	661	3.36E-05	3.02E-05	0.29	0.12	0.27	0.17	5.7	5.0	1.75	1.70	3.2	3.0
11/06/95 17:00	13.5	0.65	363	857	3.20E-05	2.85E-05	0.29	0.12	0.27	0.17	5.9	5.2	1.75	1.70	3.4	3.0
11/06/95 18:00	13.2	0.63	282	708	2.92E-05	2.67E-05	0.29	0.12	0.27	0.17	5.8	5.2	1.75	1.70	3.3	3.1
11/06/95 19:00	12.6	0.60	235	648	2.94E-05	2.36E-05	0.29	0.12	0.27	0.17	6.2	4.9	1.75	1.70	3.6	2.9
11/06/95 20:00	12.1	0.54	94	258	2.70E-05	2.23E-05	0.29	0.12	0.27	0.17	7.0	5.6	1.75	1.70	4.0	3.3
11/06/95 21:00	11.4	0.44	15	75	1.83E-05	1.73E-05	0.29	0.12	0.27	0.17	6.1	5.8	1.75	1.70	3.5	3.4
12/06/95 07:00	7.1	0.24	51	300	3.72E-06	4.80E-06	0.29	0.12	0.27	0.17	1.9	2.5	1.75	1.71	1.1	1.5
12/06/95 08:00	8.4	0.34	173	568	1.44E-05	1.16E-05	0.29	0.12	0.27	0.17	5.1	4.0	1.75	1.71	2.9	2.4
12/06/95 09:00	9.3	0.45	308	846	2.22E-05	1.81E-05	0.29	0.12	0.27	0.17	5.7	4.6	1.75	1.71	3.3	2.7
12/06/95 10:00	10.2	0.54	445	1120	2.74E-05	2.32E-05	0.29	0.12	0.27	0.17	5.4	4.5	1.75	1.71	3.1	2.6
12/06/95 11:00	11.5	0.63	569	1365	2.87E-05	2.59E-05	0.29	0.12	0.27	0.17	4.4	3.9	1.75	1.71	2.5	2.3
12/06/95 12:00	12.9	0.79	648	1524	3.19E-05	3.10E-05	0.29	0.12	0.27	0.17	4.1	4.0	1.75	1.71	2.3	2.3
12/06/95 13:00	13.8	0.84	700	1630	3.35E-05	3.26E-05	0.29	0.12	0.27	0.17	3.9	3.7	1.75	1.71	2.2	2.2
12/06/95 14:00	15.0	0.95	700	1642	3.31E-05	3.41E-05	0.29	0.12	0.27	0.17	3.3	3.4	1.76	1.71	1.9	2.0
12/06/95 15:00	15.4	0.97	673	1579	3.04E-05	3.34E-05	0.29	0.12	0.27	0.17	3.1	3.4	1.76	1.71	1.8	2.0
12/06/95 16:00	15.1	0.91	595	1418	2.87E-05	3.24E-05	0.29	0.12	0.27	0.17	3.3	3.8	1.76	1.71	1.9	2.2
12/06/95 17:00	14.5	0.77	514	1245	2.88E-05	3.05E-05	0.29	0.12	0.27	0.17	4.2	4.4	1.76	1.71	2.4	2.6
12/06/95 18:00	13.7	0.66	409	1025	2.67E-05	2.77E-05	0.29	0.12	0.27	0.17	4.6	4.8	1.76	1.71	2.6	2.8
12/06/95 19:00	12.8	0.47	296	752	2.25E-05	2.14E-05	0.29	0.12	0.27	0.17	5.5	5.2	1.76	1.71	3.1	3.0
12/06/95 20:00	12.0	0.36	143	429	1.98E-05	1.88E-05	0.29	0.12	0.27	0.17	7.0	6.6	1.76	1.71	4.0	3.9
12/06/95 21:00	10.9	0.28	23	191	1.43E-05	1.43E-05	0.29	0.12	0.27	0.17	8.1	8.1	1.76	1.71	4.6	4.7
13/06/95 06:00	8.8	0.25	2	124	2.98E-06	3.63E-06	0.29	0.12	0.27	0.17	1.6	2.0	1.76	1.71	0.9	1.2
13/06/95 07:00	10.6	0.37	68	318	9.70E-06	8.49E-06	0.29	0.12	0.27	0.17	3.4	2.9	1.76	1.71	1.9	1.7
13/06/95 08:00	11.1	0.39	174	550	1.69E-05	1.27E-05	0.29	0.12	0.27	0.17	5.1	3.6	1.76	1.71	2.9	2.1
13/06/95 09:00	12.3	0.46	306	833	2.24E-05	1.83E-05	0.29	0.12	0.27	0.17	4.9	3.8	1.76	1.71	2.8	2.2
13/06/95 10:00	12.3	0.42	451	1129	2.58E-05	2.21E-05	0.29	0.12	0.27	0.17	5.7	4.7	1.76	1.71	3.2	2.8
13/06/95 11:00	13.5	0.51	563	1353	2.76E-05	2.28E-05	0.29	0.12	0.27	0.17	5.0	4.0	1.76	1.71	2.8	2.3
13/06/95 12:00	14.0	0.54	640	1510	2.89E-05	2.68E-05	0.29	0.12	0.27	0.17	4.9	4.5	1.76	1.72	2.8	2.6
13/06/95 13:00	13.6	0.45	699	1639	2.65E-05	2.61E-05	0.29	0.12	0.26	0.17	5.1	5.0	1.76	1.72	2.9	2.9
13/06/95 14:00	13.3	0.45	742	1733	2.88E-05	2.65E-05	0.29	0.12	0.26	0.17	5.9	5.4	1.76	1.72	3.3	3.1
13/06/95 15:00	13.2	0.43	694	1622	3.03E-05	2.75E-05	0.29	0.12	0.26	0.17	6.8	6.1	1.76	1.72	3.9	3.6
13/06/95 16:00	12.8	0.38	396	915	2.68E-05	2.55E-05	0.29	0.12	0.26	0.17	7.5	7.1	1.76	1.72	4.2	4.1
13/06/95 17:00	12.0	0.30	183	437	1.97E-05	1.90E-05	0.29	0.12	0.26	0.17	8.0	7.6	1.76	1.72	4.5	4.4
13/06/95 18:00	11.8	0.25	211	508	1.59E-05	1.67E-05	0.29	0.12	0.26	0.17	6.6	7.0	1.77	1.72	3.7	4.1
13/06/95 19:00	11.9	0.23	100	260	1.48E-05	1.28E-05	0.29	0.12	0.26	0.17	8.4	7.0	1.77	1.72	4.8	4.1
13/06/95 20:00	11.6	0.22	43	126	1.23E-05	1.15E-05	0.29	0.12	0.26	0.17	8.2	7.6	1.77	1.72	4.7	4.4
13/06/95 21:00	11.6	0.21	11	56	9.87E-06	9.27E-06	0.29	0.12	0.26	0.17	8.1	7.4	1.77	1.72	4.6	4.3
14/06/95 06:00	11.9	0.42	2	42	9.17E-06	6.72E-06	0.29	0.12	0.26	0.17	3.1	2.2	1.77	1.72	1.7	1.3
14/06/95 07:00	12.2	0.43	38	117	1.29E-05	9.29E-06	0.29	0.12	0.26	0.17	4.2	2.9	1.77	1.72	2.4	1.7
14/06/95 08:00	12.8	0.44	64	176	1.63E-05	1.23E-05	0.29	0.12	0.26	0.17	5.3	3.8	1.77	1.72	3.0	2.2
14/06/95 09:00	13.3	0.47	98	255	1.76E-05	1.34E-05	0.29	0.12	0.26	0.17	5.0	3.6	1.77	1.72	2.8	2.1
14/06/95 10:00	14.3	0.57	214	526	2.09E-05	1.55E-05	0.29	0.12	0.26	0.17	4.5	3.3	1.77	1.72	2.5	1.9
14/06/95 11:00	15.8	0.76	278	679	2.83E-05	2.19E-05	0.29	0.12	0.26	0.17	4.6	3.5	1.77	1.72	2.6	2.0
14/06/95 12:00	16.6	0.89	358	883	3.13E-05	2.71E-05	0.29	0.12	0.26	0.17	4.3	3.7	1.77	1.72	2.4	2.1
14/06/95 13:00	16.7	0.90	308	734	3.26E-05	2.78E-05	0.29	0.12	0.26	0.17	4.4	3.7	1.77	1.72	2.5	2.2
14/06/95 14:00	16.8	0.92	170	436	3.26E-05	2.85E-05	0.29	0.12	0.26	0.17	4.7	4.0	1.77	1.72	2.7	2.3
14/06/95 15:00	18.2	1.07	500	1175	3.25E-05	2.69E-05	0.29	0.12	0.26	0.17	3.3	2.7	1.77	1.72	1.9	1.6
14/06/95 16:00	18.3	1.07	384	943	3.36E-05	2.95E-05	0.29	0.12	0.26	0.17	3.5	3.0	1.77	1.72	2.0	1.7
14/06/95 17:00	19.2	1.15	401	928	3.42E-05	2.90E-05	0.29	0.12	0.26	0.17	3.3	2.8	1.77	1.72	1.9	1.6
14/06/95 18:00	19.7	1.21	429	1066	3.44E-05	2.82E-05	0.29	0.12	0.26	0.17	3.0	2.4	1.77	1.72	1.7	1.4
14/06/95 19:00	18.7	1.04	338	833	3.45E-05	2.59E-05	0.29	0.12	0.26	0.17	3.9	2.9	1.77	1.72	2.2	1.7
14/06/95 20:00	17.4	0.85	152	473	2.83E-05	2.21E-05	0.29	0.12	0.26	0.17	4.4	3.3	1.77	1.72	2.5	1.9
14/06/95 21:00	15.9	0.66	33	224	1.97E-05	1.77E-05	0.29	0.12	0.26	0.17	4.3	3.8	1.77	1.72	2.4	2.2

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
15/06/95 07:00	11.4	0.25	65	245	6.43E-06	7.27E-06	0.29	0.12	0.26	0.17	3.1	3.6	1.78	1.73	1.7	2.1
15/06/95 08:00	13.4	0.51	111	409	1.71E-05	1.26E-05	0.29	0.12	0.26	0.17	4.4	3.1	1.78	1.73	2.4	1.8
15/06/95 09:00	14.3	0.60	295	813	2.37E-05	1.89E-05	0.29	0.12	0.26	0.17	4.1	3.1	1.78	1.73	2.3	1.8
15/06/95 10:00	15.2	0.70	409	1043	2.86E-05	2.51E-05	0.29	0.12	0.26	0.17	4.3	3.7	1.78	1.73	2.4	2.1
15/06/95 11:00	16.9	0.89	509	1246	3.09E-05	2.84E-05	0.29	0.12	0.26	0.17	3.6	3.3	1.78	1.73	2.0	1.9
15/06/95 12:00	17.7	1.01	447	1112	2.89E-05	3.06E-05	0.29	0.12	0.26	0.17	3.1	3.3	1.78	1.73	1.7	1.9
15/06/95 13:00	18.8	1.16	515	1233	3.18E-05	3.07E-05	0.29	0.12	0.26	0.17	3.1	3.0	1.78	1.73	1.7	1.7
15/06/95 14:00	19.3	1.24	590	1409	3.14E-05	3.24E-05	0.29	0.12	0.26	0.17	2.9	3.0	1.78	1.73	1.6	1.7
15/06/95 15:00	19.8	1.29	635	1496	3.28E-05	3.21E-05	0.29	0.12	0.26	0.17	2.8	2.8	1.78	1.73	1.6	1.6
15/06/95 16:00	19.7	1.27	492	1202	3.07E-05	3.22E-05	0.29	0.12	0.26	0.17	2.8	3.0	1.78	1.73	1.6	1.7
15/06/95 17:00	20.0	1.33	545	1333	3.11E-05	3.11E-05	0.29	0.12	0.26	0.17	2.7	2.7	1.78	1.73	1.5	1.6
15/06/95 18:00	19.9	1.31	384	979	2.89E-05	2.65E-05	0.29	0.12	0.26	0.17	2.7	2.4	1.78	1.73	1.5	1.4
15/06/95 19:00	18.3	1.00	292	779	2.57E-05	2.35E-05	0.29	0.12	0.26	0.17	3.2	2.9	1.78	1.73	1.8	1.7
15/06/95 20:00	14.2	0.45	156	474	1.68E-05	1.68E-05	0.29	0.12	0.26	0.17	4.6	4.6	1.78	1.73	2.6	2.7
15/06/95 21:00	12.8	0.34	5	165	1.31E-05	9.96E-06	0.29	0.12	0.26	0.17	5.8	4.3	1.78	1.73	3.3	2.5
20/06/95 11:00	14.4	0.19	304	623	9.63E-06	5.65E-06	0.28	0.11	0.25	0.16	4.0	2.3	1.82	1.76	2.2	1.3
20/06/95 12:00	15.8	0.55	550	1201	2.29E-05	1.55E-05	0.28	0.11	0.25	0.16	3.9	2.6	1.82	1.76	2.1	1.5
20/06/95 13:00	16.5	0.75	642	1444	3.64E-05	2.94E-05	0.28	0.11	0.25	0.16	5.0	4.0	1.82	1.76	2.7	2.2
20/06/95 14:00	16.7	0.89	685	1593	3.93E-05	3.14E-05	0.28	0.11	0.25	0.16	4.8	3.8	1.82	1.76	2.7	2.2
20/06/95 15:00	17.1	1.06	657	1546	4.09E-05	3.51E-05	0.28	0.11	0.25	0.16	4.3	3.7	1.82	1.76	2.4	2.1
20/06/95 16:00	17.3	1.07	605	1432	4.00E-05	3.41E-05	0.28	0.11	0.25	0.16	4.3	3.6	1.82	1.76	2.4	2.1
20/06/95 17:00	17.1	1.03	410	1002	3.93E-05	3.17E-05	0.28	0.11	0.25	0.16	4.6	3.7	1.82	1.76	2.5	2.1
20/06/95 18:00	16.8	0.99	395	978	3.70E-05	2.96E-05	0.28	0.11	0.25	0.16	4.5	3.6	1.82	1.76	2.5	2.0
20/06/95 19:00	16.5	0.95	282	740	3.46E-05	2.58E-05	0.28	0.11	0.25	0.16	4.6	3.3	1.82	1.76	2.5	1.9
20/06/95 20:00	15.6	0.86	134	423	3.06E-05	2.26E-05	0.28	0.11	0.25	0.16	4.8	3.5	1.83	1.76	2.6	2.0
20/06/95 21:00	14.4	0.72	26	209	2.38E-05	1.83E-05	0.28	0.11	0.25	0.16	4.7	3.5	1.83	1.76	2.6	2.0
21/06/95 07:00	9.7	0.13	53	289	4.34E-06	2.49E-06	0.27	0.11	0.25	0.16	3.9	2.1	1.83	1.77	2.1	1.2
21/06/95 08:00	11.5	0.22	162	512	1.22E-05	7.43E-06	0.27	0.11	0.25	0.16	6.0	3.4	1.83	1.77	3.3	1.9
21/06/95 09:00	13.1	0.43	283	770	2.10E-05	1.37E-05	0.27	0.11	0.25	0.16	5.5	3.4	1.83	1.77	3.0	2.0
21/06/95 10:00	13.9	0.54	418	1010	2.96E-05	2.28E-05	0.27	0.11	0.25	0.16	6.1	4.6	1.83	1.77	3.4	2.6
21/06/95 11:00	14.5	0.63	484	1161	3.44E-05	2.78E-05	0.27	0.11	0.25	0.16	6.3	5.0	1.83	1.77	3.4	2.8
21/06/95 12:00	15.2	0.73	489	1152	3.58E-05	2.96E-05	0.27	0.11	0.25	0.16	5.6	4.6	1.83	1.77	3.1	2.6
21/06/95 13:00	15.2	0.70	501	1188	3.60E-05	3.08E-05	0.27	0.11	0.25	0.16	5.9	5.0	1.83	1.77	3.2	2.8
21/06/95 14:00	15.7	0.76	394	890	3.75E-05	3.27E-05	0.27	0.11	0.25	0.16	5.9	5.1	1.83	1.77	3.2	2.9
21/06/95 15:00	15.9	0.78	307	719	3.34E-05	2.77E-05	0.27	0.11	0.25	0.16	5.2	4.2	1.83	1.77	2.9	2.4
21/06/95 16:00	16.5	0.86	296	747	3.42E-05	2.80E-05	0.27	0.11	0.25	0.16	4.9	3.9	1.83	1.77	2.7	2.2
21/06/95 17:00	17.0	0.90	266	636	3.42E-05	2.64E-05	0.27	0.11	0.25	0.16	4.8	3.6	1.83	1.77	2.6	2.0
21/06/95 18:00	17.3	0.92	204	503	3.14E-05	2.34E-05	0.27	0.11	0.25	0.16	4.4	3.2	1.83	1.77	2.4	1.8
21/06/95 19:00	18.4	1.15	313	801	3.25E-05	2.20E-05	0.27	0.11	0.25	0.16	3.5	2.3	1.83	1.77	1.9	1.3
21/06/95 20:00	17.9	1.09	126	412	3.07E-05	2.16E-05	0.27	0.11	0.25	0.16	3.8	2.6	1.83	1.77	2.1	1.5
21/06/95 21:00	17.1	0.95	19	188	2.27E-05	1.68E-05	0.27	0.11	0.25	0.16	3.5	2.5	1.83	1.77	1.9	1.4
22/06/95 07:00	10.8	0.13	57	283	2.88E-06	1.59E-06	0.27	0.10	0.24	0.16	2.3	1.2	1.84	1.77	1.3	0.7
22/06/95 08:00	12.0	0.21	170	530	1.13E-05	7.18E-06	0.27	0.10	0.24	0.16	5.6	3.4	1.84	1.77	3.0	1.9
22/06/95 09:00	13.7	0.35	295	792	1.96E-05	1.34E-05	0.27	0.10	0.24	0.16	5.4	3.5	1.84	1.77	2.9	2.0
22/06/95 10:00	15.2	0.52	368	937	2.84E-05	2.10E-05	0.27	0.10	0.24	0.16	5.5	3.8	1.84	1.77	3.0	2.2
22/06/95 11:00	16.8	0.66	528	1265	3.36E-05	2.61E-05	0.27	0.10	0.24	0.16	5.0	3.7	1.84	1.77	2.7	2.1
22/06/95 12:00	18.4	0.98	588	1389	3.76E-05	3.11E-05	0.27	0.10	0.24	0.16	4.0	3.2	1.84	1.77	2.2	1.8
22/06/95 13:00	19.7	1.26	637	1500	4.15E-05	3.21E-05	0.27	0.10	0.24	0.16	3.5	2.6	1.84	1.77	1.9	1.5
22/06/95 14:00	21.0	1.47	630	1486	4.25E-05	3.23E-05	0.27	0.10	0.24	0.16	3.1	2.3	1.84	1.77	1.7	1.3
22/06/95 15:00	22.0	1.62	625	1478	4.06E-05	3.11E-05	0.27	0.10	0.24	0.16	2.7	2.1	1.84	1.77	1.5	1.2
22/06/95 16:00	22.7	1.69	607	1438	3.91E-05	2.92E-05	0.27	0.10	0.24	0.16	2.6	1.9	1.84	1.77	1.4	1.1
22/06/95 17:00	23.1	1.73	479	1177	3.82E-05	2.68E-05	0.27	0.10	0.24	0.16	2.6	1.8	1.84	1.77	1.4	1.0
22/06/95 18:00	23.1	1.73	411	1036	3.58E-05	2.44E-05	0.27	0.10	0.24	0.16	2.5	1.7	1.84	1.78	1.4	0.9
22/06/95 19:00	22.9	1.64	277	747	3.34E-05	1.95E-05	0.27	0.10	0.24	0.16	2.5	1.4	1.84	1.78	1.4	0.8
22/06/95 20:00	22.2	1.44	151	476	2.97E-05	1.79E-05	0.27	0.10	0.24	0.16	2.7	1.6	1.84	1.78	1.5	0.9
22/06/95 21:00	18.6	0.95	45	243	2.28E-05	1.39E-05	0.27	0.10	0.24	0.16	3.3	2.0	1.84	1.78	1.8	1.1
23/06/95 07:00	10.4	0.12	49	257	3.66E-06	2.03E-06	0.26	0.10	0.24	0.16	3.1	1.6	1.85	1.78	1.7	0.9
23/06/95 08:00	12.0	0.23	161	514	9.69E-06	6.74E-06	0.26	0.10	0.24	0.16	3.7	2.4	1.85	1.78	2.0	1.3
23/06/95 09:00	14.1	0.44	293	792	1.88E-05	1.17E-05	0.26	0.10	0.24	0.16	3.7	2.1	1.85	1.78	2.0	1.2
23/06/95 10:00	16.0	0.62	421	1056	2.77E-05	2.01E-05	0.26	0.10	0.24	0.16	4.0	2.7	1.85	1.78	2.1	1.5
23/06/95 11:00	18.1	0.87	530	1280	3.43E-05	2.50E-05	0.26	0.10	0.24	0.16	3.5	2.4	1.85	1.78	1.9	1.4
23/06/95 12:00	19.9	1.10	611	1446	3.75E-05	2.91E-05	0.26	0.10	0.24	0.16	3.1	2.3	1.85	1.78	1.7	1.3
23/06/95 13:00	20.6	1.28	667	1566	3.92E-05	2.84E-05	0.26	0.10	0.24	0.16	3.1	2.2	1.85	1.78	1.7	1.2
23/06/95 14:00	21.1	1.29	678	1596	3.92E-05	2.75E-05	0.26	0.10	0.24	0.15	3.2	2.2	1.85	1.78	1.7	1.2
23/06/95 15:00	21.1	1.31	654	1546	3.72E-05	2.76E-05	0.26	0.10	0.24	0.15	3.0	2.1	1.85	1.78	1.6	1.2
23/06/95 16:00	21.6	1.36	599	1425	3.64E-05	2.70E-05	0.26	0.10	0.24	0.15	2.8	2.0	1.85	1.78	1.5	1.1
23/06/95 17:00	22.3	1.40	508	1235	3.56E-05	2.29E-05	0.26	0.10	0.24	0.15	2.7	1.6	1.85	1.78	1.4	0.9
23/06/95 18:00	21.8	1.31	398	999	3.37E-05	2.22E-05	0.26	0.10	0.24	0.15	2.9	1.8	1.85	1.78	1.6	1.0
23/06/95 19:00	21.7	1.32	280	742	3.12E-05	1.66E-05	0.26	0.10	0.24	0.15	2.9	1.4	1.85	1.78	1.5	0.8
23/06/95 20:00	21.1	1.18	154	467	2.81E-05	1.49E-05	0.26	0.10	0.24	0.15	3.1	1.6	1.85	1.78	1.7	0.9
23/06/95 21:00	19.3	0.93	39	219	2.16E-05	1.21E-05	0.26	0.10	0.24	0.15	3.2	1.7	1.85	1.78	1.7	1.0
24/06/95 08:00	13.9	0.18	161	439	8.60E-06	6.09E-06	0.26	0.10	0.23	0.15	3.6	2.4	1.85	1.79	1.9	1.3
24/06/95 09:00	14.9	0.23	156	381	1.47E-05	9.92E-06	0.26	0.10	0.23	0.15	6.0	3.6	1.86	1.79	3.2	2.0
24/06/95 10:00	15.9	0.28	240	550	1.69E-05	1.12E-05	0.26	0.10	0.23	0.15	4.8	2.9	1.86	1.79	2.6	1.6
24/06/95 11:00	17.3	0.39	369	855	2.19E-05	1.46E-05	0.26	0.10	0.23	0.15	4.3	2.6	1.86	1.79	2.3	1.5
24/06/95 12:00	17.1	0.41	603	1398	2.71E-05	1.83E-05	0.26	0.10	0.23	0.15	5.5	3.6	1.86	1.79	3.0	2.0
24/06/95 13:00	17.7	0.49	673	1562	3.00E-05	2.05E-05	0.26	0.10	0.23	0.15	4.9	3.2	1.86	1.79	2.7	1.8
24/06/95 14:00	18.7	0.59	687	1594	3.31E-05	2.38E-05	0.26	0.10	0.23	0.15	4.5	3.1	1.86	1.79	2.4	1.7
24/06/95 15:00	19.8	0.70	664	1550	3.41E-05	2.47E-05	0.26	0.10	0.23	0.15	4.3	3.0	1.86	1.79	2.3	1.7
24/06/95 16:00	19.8	0.72	606	1429	3.47E-05	2.42E-05	0.26	0.10	0.23	0.15	4.6	3.1	1.86	1.79	2.5	1.7
24/06/95 17:00	18.7	0.57	513	1235	3.15E-05	2.24E-05	0.26	0.10	0.23	0.15	5.5	3.8	1.86	1.79	3.0	2.1
24/06/95 18:00	17.3	0.37	405	996	2.66E-05	1.89E-05	0.26	0.10	0.23	0.15	7.0	4.7	1.86	1.79	3.8	2.6
24/06/95 19:00	16.5	0.33	286	736	2.15E-05	1.34E-05	0.25	0.10	0.23	0.15	6.7	3.9	1.86	1.79	3.6	2.2
24/06/95 20:00	16.0	0.29	157	451	1.88E-05	1.23E-05	0.25	0.10	0.23	0.15	7.7	4.6	1.86	1.79	4.1	2.6
24/06/95 21:00	15.0	0.19	44	211	1.33E-05	8.30E-06	0.25	0.10	0.23	0.15	11.1	6.0	1.86	1.79	6.0	3.4
25/06/95 10:00	16.0	0.18	388	973	1.43E-05	9.07E-06	0.25	0.10	0.23	0.15	3.6	2.1	1.86	1.79	1.9	1.2
25/06/95 11:00	17.3	0.29	527	1260	2.39E-05	1.59E-05	0.25	0.10	0.23	0.15	4.8	3.0	1.86	1.79	2.6	1.7

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
25/06/95 12:00	16.8	0.25	599	1407	2.67E-05	1.92E-05	0.25	0.10	0.23	0.15	6.7	4.6	1.86	1.79	3.6	2.6
25/06/95 13:00	16.9	0.30	666	1554	2.86E-05	1.91E-05	0.25	0.10	0.23	0.15	6.7	4.2	1.87	1.79	3.6	2.4
25/06/95 14:00	17.3	0.39	684	1599	2.84E-05	1.97E-05	0.25	0.10	0.23	0.15	5.9	3.9	1.87	1.79	3.1	2.2
25/06/95 15:00	18.0	0.45	662	1556	3.04E-05	2.32E-05	0.25	0.10	0.23	0.15	5.4	4.0	1.87	1.79	2.9	2.2
25/06/95 16:00	17.6	0.41	607	1438	2.94E-05	2.16E-05	0.25	0.10	0.23	0.15	6.2	4.4	1.87	1.79	3.3	2.5
25/06/95 17:00	18.3	0.46	522	1258	2.97E-05	2.09E-05	0.25	0.10	0.23	0.15	5.9	3.9	1.87	1.79	3.1	2.2
25/06/95 18:00	19.0	0.52	412	1021	3.01E-05	1.99E-05	0.25	0.10	0.23	0.15	5.7	3.5	1.87	1.79	3.0	2.0
25/06/95 19:00	19.5	0.67	291	760	2.95E-05	1.68E-05	0.25	0.10	0.23	0.15	5.0	2.7	1.87	1.79	2.7	1.5
25/06/95 20:00	18.8	0.63	163	484	2.90E-05	1.69E-05	0.25	0.10	0.23	0.15	6.1	3.3	1.87	1.79	3.3	1.8
25/06/95 21:00	15.3	0.17	49	230	1.74E-05	8.79E-06	0.25	0.10	0.23	0.15	17.6	6.8	1.87	1.80	9.4	3.8
26/06/95 10:00	14.5	0.21	425	1051	1.66E-05	1.08E-05	0.25	0.09	0.22	0.15	4.9	3.0	1.87	1.80	2.6	1.7
26/06/95 11:00	15.6	0.30	536	1275	2.29E-05	1.51E-05	0.25	0.09	0.22	0.15	5.5	3.4	1.87	1.80	2.9	1.9
26/06/95 12:00	16.6	0.46	622	1456	2.99E-05	2.08E-05	0.25	0.09	0.22	0.15	5.8	3.9	1.87	1.80	3.1	2.2
26/06/95 13:00	18.1	0.65	674	1560	3.51E-05	2.33E-05	0.24	0.09	0.22	0.15	5.1	3.2	1.87	1.80	2.7	1.8
26/06/95 14:00	19.7	0.89	690	1606	3.88E-05	2.72E-05	0.24	0.09	0.22	0.15	4.2	2.8	1.87	1.80	2.2	1.6
26/06/95 15:00	20.5	1.04	668	1564	3.91E-05	2.93E-05	0.24	0.09	0.22	0.15	3.7	2.7	1.87	1.80	2.0	1.5
26/06/95 16:00	21.3	1.30	614	1454	3.99E-05	2.78E-05	0.24	0.09	0.22	0.15	3.3	2.2	1.87	1.80	1.8	1.2
26/06/95 17:00	21.7	1.52	526	1272	4.03E-05	2.81E-05	0.24	0.09	0.22	0.15	3.1	2.1	1.87	1.80	1.7	1.2
26/06/95 18:00	21.4	1.61	415	1040	3.85E-05	2.65E-05	0.24	0.09	0.22	0.15	2.9	1.9	1.88	1.80	1.5	1.1
26/06/95 19:00	21.0	1.55	289	774	3.58E-05	2.21E-05	0.24	0.09	0.22	0.15	2.9	1.7	1.88	1.80	1.6	1.0
26/06/95 20:00	19.8	1.36	159	494	3.20E-05	1.73E-05	0.24	0.09	0.22	0.15	3.1	1.6	1.88	1.80	1.7	0.9
26/06/95 21:00	17.9	1.10	35	234	2.49E-05	1.48E-05	0.24	0.09	0.22	0.15	3.2	1.8	1.88	1.80	1.7	1.0
27/06/95 08:00	11.9	0.16	152	500	7.57E-06	4.18E-06	0.24	0.09	0.22	0.15	3.9	2.0	1.88	1.80	2.1	1.1
27/06/95 09:00	13.6	0.35	298	802	1.66E-05	9.78E-06	0.24	0.09	0.22	0.15	4.3	2.3	1.88	1.80	2.3	1.3
27/06/95 10:00	15.9	0.60	428	1064	2.72E-05	1.90E-05	0.24	0.09	0.22	0.15	4.2	2.8	1.88	1.81	2.2	1.5
27/06/95 11:00	16.9	0.57	542	1293	3.24E-05	2.28E-05	0.24	0.09	0.22	0.15	4.8	3.2	1.88	1.81	2.5	1.7
27/06/95 12:00	17.1	0.74	628	1472	3.47E-05	2.62E-05	0.24	0.09	0.22	0.15	4.5	3.3	1.88	1.81	2.4	1.8
27/06/95 13:00	18.2	1.02	679	1583	3.82E-05	2.92E-05	0.24	0.09	0.22	0.15	3.8	2.9	1.88	1.81	2.0	1.6
27/06/95 14:00	19.5	1.31	695	1621	4.11E-05	3.14E-05	0.24	0.09	0.22	0.15	3.3	2.4	1.88	1.81	1.7	1.3
27/06/95 15:00	19.8	1.36	671	1580	3.97E-05	3.13E-05	0.24	0.09	0.22	0.15	3.2	2.4	1.88	1.81	1.7	1.4
27/06/95 16:00	19.9	1.42	590	1405	3.99E-05	2.98E-05	0.24	0.09	0.22	0.15	3.2	2.3	1.88	1.81	1.7	1.3
27/06/95 17:00	19.5	1.43	477	1161	3.83E-05	2.87E-05	0.24	0.09	0.22	0.15	3.2	2.3	1.88	1.81	1.7	1.3
27/06/95 18:00	19.3	1.29	414	1025	3.64E-05	2.61E-05	0.24	0.09	0.22	0.15	3.3	2.3	1.88	1.81	1.8	1.3
27/06/95 19:00	19.3	1.21	267	715	3.41E-05	2.12E-05	0.24	0.09	0.22	0.15	3.5	2.1	1.88	1.81	1.9	1.2
27/06/95 20:00	18.8	1.10	182	531	3.10E-05	2.06E-05	0.24	0.09	0.22	0.15	3.7	2.3	1.88	1.81	2.0	1.3
27/06/95 21:00	17.3	0.91	59	268	2.54E-05	1.70E-05	0.24	0.09	0.22	0.15	4.1	2.6	1.88	1.81	2.2	1.4
28/06/95 07:00	13.7	0.44	57	294	8.38E-06	7.16E-06	0.23	0.09	0.21	0.15	2.5	2.0	1.89	1.81	1.3	1.1
28/06/95 08:00	15.6	0.59	158	520	1.75E-05	1.24E-05	0.23	0.09	0.21	0.15	3.2	2.0	1.89	1.81	1.7	1.1
28/06/95 09:00	17.7	0.95	295	811	2.77E-05	1.84E-05	0.23	0.09	0.21	0.15	2.9	1.8	1.89	1.81	1.6	1.0
28/06/95 10:00	19.2	0.99	426	1064	3.38E-05	2.51E-05	0.23	0.09	0.21	0.15	3.2	2.2	1.89	1.81	1.7	1.2
28/06/95 11:00	20.4	1.34	540	1293	3.81E-05	2.77E-05	0.23	0.09	0.21	0.15	2.8	1.9	1.89	1.81	1.5	1.1
28/06/95 12:00	21.5	1.60	617	1451	4.00E-05	2.93E-05	0.23	0.09	0.21	0.15	2.6	1.8	1.89	1.81	1.4	1.0
28/06/95 13:00	22.1	1.76	674	1572	4.01E-05	2.94E-05	0.23	0.09	0.21	0.15	2.4	1.7	1.89	1.81	1.3	0.9
28/06/95 14:00	22.9	1.84	689	1610	4.02E-05	2.89E-05	0.23	0.09	0.21	0.15	2.3	1.6	1.89	1.81	1.2	0.9
28/06/95 15:00	24.0	2.00	669	1575	3.82E-05	2.80E-05	0.23	0.09	0.21	0.15	2.0	1.5	1.89	1.81	1.1	0.8
28/06/95 16:00	24.8	2.14	608	1450	3.75E-05	2.74E-05	0.23	0.09	0.21	0.15	1.9	1.3	1.89	1.81	1.0	0.7
28/06/95 17:00	25.1	2.19	522	1272	3.72E-05	2.55E-05	0.23	0.09	0.21	0.15	1.9	1.3	1.89	1.81	1.0	0.7
28/06/95 18:00	24.8	2.00	411	1039	3.54E-05	2.24E-05	0.23	0.09	0.21	0.15	2.0	1.2	1.89	1.81	1.1	0.7
28/06/95 19:00	23.2	1.76	286	767	3.27E-05	1.98E-05	0.23	0.09	0.21	0.15	2.3	1.3	1.89	1.81	1.2	0.7
28/06/95 20:00	23.0	1.60	164	503	2.94E-05	1.83E-05	0.23	0.09	0.21	0.15	2.4	1.4	1.89	1.81	1.3	0.8
28/06/95 21:00	22.0	1.55	39	244	2.55E-05	1.65E-05	0.23	0.09	0.21	0.15	2.3	1.4	1.89	1.81	1.2	0.8
29/06/95 07:00	15.6	0.93	45	267	1.23E-05	7.74E-06	0.23	0.09	0.21	0.14	1.9	1.1	1.90	1.82	1.0	0.6
29/06/95 08:00	15.9	0.75	159	520	1.92E-05	1.23E-05	0.23	0.09	0.21	0.14	3.0	1.8	1.90	1.82	1.6	1.0
29/06/95 09:00	17.5	0.99	285	780	2.55E-05	1.72E-05	0.23	0.09	0.21	0.14	2.8	1.8	1.90	1.82	1.5	1.0
29/06/95 10:00	18.8	1.04	420	1051	3.03E-05	2.38E-05	0.23	0.09	0.21	0.14	2.9	2.2	1.90	1.82	1.5	1.2
29/06/95 11:00	19.2	0.86	536	1283	3.18E-05	2.43E-05	0.23	0.09	0.21	0.14	3.4	2.5	1.90	1.82	1.8	1.4
29/06/95 12:00	19.4	0.77	622	1461	3.12E-05	2.54E-05	0.23	0.09	0.21	0.14	3.6	2.9	1.90	1.82	1.9	1.6
29/06/95 13:00	20.7	0.99	673	1569	3.29E-05	2.62E-05	0.23	0.09	0.21	0.14	3.0	2.3	1.90	1.82	1.6	1.3
29/06/95 14:00	22.5	1.30	684	1600	3.52E-05	2.71E-05	0.23	0.09	0.21	0.14	2.5	1.9	1.90	1.82	1.3	1.0
29/06/95 15:00	24.0	1.58	660	1551	3.35E-05	2.74E-05	0.23	0.09	0.21	0.14	2.0	1.6	1.90	1.82	1.0	0.9
29/06/95 16:00	24.9	1.72	600	1428	3.36E-05	2.54E-05	0.23	0.09	0.21	0.14	1.9	1.4	1.90	1.82	1.0	0.8
29/06/95 17:00	24.6	1.55	513	1239	3.28E-05	2.37E-05	0.23	0.09	0.21	0.14	2.2	1.5	1.90	1.82	1.1	0.8
29/06/95 18:00	22.3	1.04	407	1003	2.87E-05	2.14E-05	0.23	0.09	0.21	0.14	2.9	2.1	1.90	1.82	1.5	1.2
29/06/95 19:00	20.2	0.78	288	737	2.44E-05	1.76E-05	0.23	0.09	0.21	0.14	3.5	2.5	1.90	1.82	1.9	1.4
29/06/95 20:00	18.2	0.53	165	466	2.10E-05	1.36E-05	0.23	0.09	0.21	0.14	4.9	3.0	1.90	1.82	2.6	1.7
29/06/95 21:00	16.1	0.26	50	220	1.51E-05	1.00E-05	0.23	0.09	0.21	0.14	8.4	5.1	1.90	1.82	4.4	2.8
30/06/95 12:00	12.8	0.13	143	334	1.05E-05	7.53E-06	0.22	0.09	0.20	0.14	8.0	5.4	1.91	1.83	4.2	2.9
30/06/95 13:00	13.2	0.13	156	366	1.17E-05	9.66E-06	0.22	0.09	0.20	0.14	8.9	7.0	1.91	1.83	4.6	3.8
30/06/95 14:00	13.5	0.15	201	459	1.21E-05	8.29E-06	0.22	0.09	0.20	0.14	7.2	4.7	1.91	1.83	3.8	2.6
30/06/95 15:00	14.6	0.25	306	674	1.52E-05	1.11E-05	0.22	0.09	0.20	0.14	5.2	3.7	1.91	1.83	2.7	2.0
30/06/95 16:00	15.4	0.33	381	844	2.08E-05	1.32E-05	0.22	0.08	0.20	0.14	5.8	3.5	1.91	1.83	3.0	1.9
30/06/95 17:00	15.9	0.38	469	1066	2.60E-05	1.82E-05	0.22	0.08	0.20	0.14	6.4	4.3	1.91	1.83	3.4	2.4
30/06/95 18:00	15.1	0.28	221	519	2.36E-05	1.70E-05	0.22	0.08	0.20	0.14	9.6	6.5	1.91	1.83	5.0	3.5
30/06/95 19:00	14.1	0.21	91	217	1.56E-05	8.32E-06	0.22	0.08	0.20	0.14	10.1	4.8	1.91	1.83	5.3	2.6
30/06/95 20:00	13.6	0.19	33	88	1.08E-05	6.75E-06	0.22	0.08	0.20	0.14	8.2	4.8	1.91	1.83	4.3	2.6
30/06/95 21:00	13.0	0.22	17	56	8.44E-06	4.88E-06	0.22	0.08	0.20	0.14	5.2	2.9	1.91	1.83	2.7	1.6
01/07/95 06:00	10.1	0.14	12	51	2.28E-06	1.75E-06	0.22	0.08	0.20	0.14	2.1	1.6	1.91	1.83	1.1	0.9
01/07/95 07:00	10.5	0.17	85	196	7.48E-06	3.72E-06	0.22	0.08	0.20	0.14	5.2	2.4	1.91	1.83	2.7	1.3
01/07/95 08:00	11.2	0.21	186	424	1.18E-05	8.57E-06	0.22	0.08	0.20	0.14	6.1	4.3	1.91	1.83	3.2	2.3
01/07/95 09:00	12.6	0.31	417	936	1.76E-05	1.21E-05	0.22	0.08	0.20	0.14	5.0	3.3	1.91	1.83	2.6	1.8
01/07/95 10:00	12.8	0.32	372	829	2.40E-05	1.87E-05	0.22	0.08	0.20	0.14	7.4	5.5	1.91	1.83	3.9	3.0
01/07/95 11:00	13.0	0.34	369	826	2.47E-05	1.79E-05	0.22	0.08	0.20	0.14	7.2	4.9	1.92	1.83	3.8	2.7
01/07/95 12:00	13.2	0.38	359	810	2.63E-05	1.71E-05	0.22	0.08	0.20	0.14	7.2	4.4	1.92	1.83	3.8	2.4
01/07/95 13:00	14.0	0.45	548	1224	3.02E-05	2.25E-05	0.22	0.08	0.20	0.14	6.3	4.5	1.92	1.83	3.3	2.5
01/07/95 14:00	15.0	0.68	720	1589	3.56E-05	2.73E-05	0.22	0.08	0.20	0.14	4.9	3.6	1.92	1.83	2.6	2.0
01/07/95 15:00	15.5	0.73	715	1595	3.69E-05	3.07E-05	0.22	0.08	0.20	0.14	4.7	3.8	1.92	1.83	2.5	2.1
01/07/95 16:00	16.0	0.76	681	1517	3.79E-05	3.04E-05	0.22	0.08	0.20	0.14	4.8	3.8	1.92	1.83	2.5	2.1

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
01/07/95 17:00	16.6	0.85	546	1251	3.73E-05	2.90E-05	0.22	0.08	0.20	0.14	4.3	3.2	1.92	1.83	2.2	1.7
01/07/95 18:00	17.2	0.91	396	974	3.55E-05	2.62E-05	0.22	0.08	0.20	0.14	4.3	3.1	1.92	1.83	2.3	1.7
01/07/95 19:00	16.6	0.72	264	690	3.20E-05	2.16E-05	0.21	0.08	0.20	0.14	5.4	3.4	1.92	1.83	2.8	1.9
01/07/95 20:00	16.1	0.64	136	411	2.66E-05	2.03E-05	0.21	0.08	0.20	0.14	5.7	4.1	1.92	1.83	3.0	2.2
01/07/95 21:00	15.6	0.57	33	208	2.05E-05	1.59E-05	0.21	0.08	0.20	0.14	5.7	4.2	1.92	1.83	3.0	2.3
03/07/95 06:00	9.3	0.23	2	39	3.58E-06	1.69E-06	0.21	0.08	0.19	0.14	2.1	1.0	1.93	1.84	1.1	0.5
03/07/95 07:00	9.4	0.31	56	159	9.61E-06	4.37E-06	0.21	0.08	0.19	0.14	4.2	1.8	1.93	1.84	2.2	1.0
03/07/95 08:00	9.6	0.34	94	236	1.44E-05	9.82E-06	0.21	0.08	0.19	0.14	5.5	3.6	1.93	1.84	2.9	2.0
03/07/95 09:00	10.2	0.38	163	388	1.79E-05	1.25E-05	0.21	0.08	0.19	0.14	5.8	3.8	1.93	1.84	3.0	2.1
03/07/95 10:00	11.4	0.45	271	629	2.07E-05	1.54E-05	0.21	0.08	0.19	0.14	4.6	3.2	1.93	1.84	2.4	1.7
03/07/95 11:00	11.6	0.43	220	512	2.44E-05	1.82E-05	0.21	0.08	0.19	0.14	6.8	4.7	1.93	1.84	3.5	2.6
03/07/95 12:00	12.2	0.49	369	840	2.71E-05	2.06E-05	0.21	0.08	0.19	0.14	6.0	4.4	1.93	1.84	3.1	2.4
03/07/95 13:00	12.9	0.51	383	883	2.92E-05	2.23E-05	0.20	0.08	0.19	0.14	6.1	4.5	1.93	1.84	3.2	2.4
03/07/95 14:00	13.6	0.54	348	816	3.03E-05	2.31E-05	0.20	0.08	0.19	0.14	6.2	4.5	1.93	1.85	3.2	2.4
03/07/95 15:00	14.7	0.62	415	988	3.19E-05	2.53E-05	0.20	0.08	0.19	0.14	5.3	4.0	1.93	1.85	2.7	2.2
03/07/95 16:00	15.5	0.77	334	785	3.34E-05	2.60E-05	0.20	0.08	0.19	0.14	5.1	3.8	1.93	1.85	2.6	2.1
03/07/95 17:00	16.1	0.85	333	796	3.45E-05	2.68E-05	0.20	0.08	0.19	0.14	4.9	3.7	1.93	1.85	2.5	2.0
03/07/95 18:00	16.1	0.85	282	747	3.39E-05	2.46E-05	0.20	0.08	0.19	0.14	5.0	3.5	1.93	1.85	2.6	1.9
03/07/95 19:00	16.3	0.87	259	707	3.23E-05	2.09E-05	0.20	0.08	0.19	0.14	4.7	2.9	1.93	1.85	2.4	1.6
03/07/95 20:00	15.5	0.78	153	472	2.94E-05	2.00E-05	0.20	0.08	0.19	0.14	5.0	3.3	1.94	1.85	2.6	1.8
03/07/95 21:00	14.3	0.66	35	222	2.30E-05	1.60E-05	0.20	0.08	0.19	0.14	4.9	3.3	1.94	1.85	2.5	1.8
06/07/95 10:00	16.7	0.31	190	521	1.75E-05	9.84E-06	0.22	0.08	0.20	0.13	6.7	3.6	1.96	1.86	3.4	1.9
06/07/95 11:00	17.5	0.48	393	906	2.55E-05	1.79E-05	0.22	0.08	0.20	0.13	5.9	4.1	1.96	1.86	3.0	2.2
06/07/95 12:00	17.9	0.68	536	1198	3.41E-05	2.63E-05	0.22	0.08	0.20	0.13	5.7	4.3	1.96	1.86	2.9	2.3
06/07/95 13:00	17.4	0.73	423	964	3.56E-05	2.65E-05	0.22	0.08	0.20	0.13	5.8	4.2	1.96	1.86	3.0	2.3
06/07/95 14:00	17.2	0.74	368	863	3.75E-05	2.97E-05	0.22	0.08	0.20	0.13	6.2	4.9	1.96	1.86	3.2	2.6
06/07/95 15:00	17.4	0.76	356	835	3.56E-05	2.81E-05	0.22	0.08	0.20	0.13	5.8	4.5	1.96	1.86	3.0	2.4
06/07/95 16:00	17.7	0.82	423	1013	3.74E-05	2.97E-05	0.22	0.08	0.20	0.13	5.5	4.3	1.96	1.87	2.8	2.3
06/07/95 17:00	18.4	0.90	514	1198	3.88E-05	3.11E-05	0.22	0.08	0.20	0.13	5.1	4.0	1.96	1.87	2.6	2.1
06/07/95 18:00	17.7	0.76	313	770	3.43E-05	2.56E-05	0.22	0.08	0.20	0.13	5.6	4.1	1.96	1.87	2.9	2.2
06/07/95 19:00	16.9	0.61	84	229	3.07E-05	2.08E-05	0.22	0.08	0.20	0.13	7.0	4.5	1.96	1.87	3.6	2.4
06/07/95 20:00	15.7	0.43	63	184	1.81E-05	1.35E-05	0.22	0.08	0.20	0.13	5.9	4.3	1.96	1.87	3.0	2.3
06/07/95 21:00	15.3	0.39	12	114	1.38E-05	1.02E-05	0.22	0.08	0.20	0.13	5.1	3.7	1.96	1.87	2.6	2.0
07/07/95 06:00	12.5	0.16	5	31	3.58E-06	8.06E-07	0.22	0.08	0.20	0.13	2.9	0.6	1.96	1.87	1.5	0.3
07/07/95 07:00	12.8	0.23	46	139	7.22E-06	2.76E-06	0.22	0.08	0.20	0.13	4.1	1.5	1.96	1.87	2.1	0.8
07/07/95 08:00	13.3	0.27	91	282	1.30E-05	6.59E-06	0.22	0.08	0.20	0.13	6.1	3.0	1.96	1.87	3.1	1.6
07/07/95 09:00	14.1	0.33	162	460	1.80E-05	1.03E-05	0.22	0.08	0.20	0.13	6.8	3.7	1.97	1.87	3.5	2.0
07/07/95 10:00	14.8	0.39	234	609	2.19E-05	1.44E-05	0.22	0.08	0.20	0.13	6.7	4.2	1.97	1.87	3.4	2.3
07/07/95 11:00	15.4	0.44	294	687	2.64E-05	1.85E-05	0.22	0.08	0.20	0.13	7.1	4.8	1.97	1.87	3.6	2.6
07/07/95 12:00	15.6	0.46	257	613	2.83E-05	2.08E-05	0.22	0.08	0.20	0.13	7.4	5.2	1.97	1.87	3.8	2.8
07/07/95 13:00	16.4	0.65	394	925	3.01E-05	2.33E-05	0.22	0.08	0.20	0.13	5.4	4.1	1.97	1.87	2.7	2.2
07/07/95 14:00	16.9	0.76	481	1105	3.51E-05	2.49E-05	0.22	0.08	0.20	0.13	5.3	3.7	1.97	1.87	2.7	2.0
07/07/95 15:00	16.9	0.75	334	803	3.70E-05	2.89E-05	0.22	0.08	0.20	0.13	6.1	4.6	1.97	1.87	3.1	2.5
07/07/95 16:00	15.9	0.70	336	821	3.30E-05	2.50E-05	0.23	0.08	0.20	0.13	5.8	4.3	1.97	1.87	2.9	2.3
07/07/95 17:00	16.9	0.90	403	976	3.64E-05	2.84E-05	0.23	0.08	0.20	0.13	4.9	3.7	1.97	1.87	2.5	2.0
07/07/95 18:00	16.4	0.83	200	514	3.36E-05	2.48E-05	0.23	0.08	0.20	0.13	5.3	3.8	1.97	1.87	2.7	2.0
07/07/95 19:00	16.1	0.78	149	392	3.01E-05	1.96E-05	0.23	0.08	0.20	0.13	5.1	3.2	1.97	1.87	2.6	1.7
07/07/95 20:00	16.0	0.81	100	316	2.75E-05	1.78E-05	0.23	0.08	0.21	0.13	4.6	2.9	1.97	1.87	2.3	1.5
07/07/95 21:00	15.4	0.76	39	238	2.32E-05	1.58E-05	0.23	0.08	0.21	0.13	4.2	2.8	1.97	1.87	2.2	1.5
10/07/95 07:00	11.9	0.10	49	239	3.80E-06	1.28E-06	0.24	0.08	0.22	0.13	4.5	1.4	1.99	1.89	2.3	0.8
10/07/95 08:00	12.7	0.16	123	383	1.02E-05	5.45E-06	0.24	0.08	0.22	0.13	7.1	3.6	1.99	1.89	3.6	1.9
10/07/95 09:00	13.6	0.31	233	650	1.61E-05	8.29E-06	0.24	0.08	0.22	0.13	6.1	3.0	1.99	1.89	3.1	1.6
10/07/95 10:00	14.3	0.41	366	932	2.22E-05	1.39E-05	0.24	0.08	0.22	0.13	6.1	3.7	1.99	1.89	3.1	2.0
10/07/95 11:00	14.9	0.49	495	1196	2.81E-05	1.88E-05	0.24	0.08	0.22	0.13	6.4	4.1	1.99	1.89	3.2	2.2
10/07/95 12:00	15.8	0.61	597	1401	3.08E-05	2.23E-05	0.24	0.08	0.22	0.13	5.6	4.0	1.99	1.89	2.8	2.1
10/07/95 13:00	16.7	0.79	608	1411	3.63E-05	2.38E-05	0.24	0.08	0.22	0.13	5.2	3.4	1.99	1.89	2.6	1.8
10/07/95 14:00	17.8	0.99	625	1449	3.74E-05	2.56E-05	0.24	0.08	0.22	0.13	4.3	2.9	1.99	1.89	2.2	1.5
10/07/95 15:00	18.4	1.04	629	1468	3.75E-05	2.62E-05	0.24	0.08	0.22	0.13	4.1	2.8	1.99	1.89	2.0	1.5
10/07/95 16:00	18.1	0.86	572	1345	3.54E-05	2.41E-05	0.24	0.08	0.22	0.13	4.6	3.1	1.99	1.89	2.3	1.6
10/07/95 17:00	18.5	0.92	493	1172	3.39E-05	2.32E-05	0.24	0.08	0.22	0.13	4.3	2.8	1.99	1.89	2.1	1.5
10/07/95 18:00	18.0	0.84	381	929	3.21E-05	2.10E-05	0.24	0.08	0.22	0.13	4.6	2.9	1.99	1.89	2.3	1.6
10/07/95 19:00	17.5	0.79	217	572	2.90E-05	1.67E-05	0.25	0.08	0.22	0.13	4.7	2.6	1.99	1.89	2.3	1.4
10/07/95 20:00	16.8	0.61	136	392	2.44E-05	1.50E-05	0.25	0.08	0.22	0.13	5.3	3.1	1.99	1.89	2.6	1.7
10/07/95 21:00	15.6	0.37	31	161	1.60E-05	1.03E-05	0.25	0.08	0.22	0.13	6.1	3.8	1.99	1.89	3.0	2.0
12/07/95 12:00	18.7	0.27	432	937	1.40E-05	9.63E-06	0.26	0.08	0.23	0.13	2.2	1.5	2.01	1.90	1.1	0.8
12/07/95 13:00	19.8	0.44	299	683	2.30E-05	1.54E-05	0.26	0.08	0.23	0.13	4.0	2.4	2.01	1.90	2.0	1.3
12/07/95 14:00	19.9	0.42	193	464	2.27E-05	1.31E-05	0.26	0.08	0.23	0.13	5.7	2.8	2.01	1.90	2.9	1.5
12/07/95 15:00	20.1	0.41	282	678	2.35E-05	1.50E-05	0.26	0.08	0.23	0.13	5.2	3.0	2.01	1.90	2.6	1.6
12/07/95 16:00	20.2	0.42	283	660	2.56E-05	1.57E-05	0.26	0.08	0.23	0.13	6.1	3.4	2.01	1.90	3.0	1.8
12/07/95 17:00	21.4	0.62	455	1062	3.13E-05	2.10E-05	0.26	0.08	0.23	0.13	4.6	2.9	2.01	1.90	2.3	1.5
12/07/95 18:00	21.7	0.76	397	961	3.52E-05	2.25E-05	0.26	0.08	0.23	0.13	4.7	2.8	2.01	1.90	2.3	1.5
12/07/95 19:00	21.2	0.82	179	487	3.63E-05	2.24E-05	0.26	0.08	0.23	0.13	6.0	3.3	2.01	1.90	3.0	1.7
12/07/95 20:00	20.3	0.67	76	245	2.88E-05	1.82E-05	0.26	0.08	0.23	0.13	6.8	3.8	2.01	1.90	3.4	2.0
12/07/95 21:00	19.1	0.61	8	107	1.86E-05	1.20E-05	0.26	0.08	0.23	0.13	4.6	2.8	2.01	1.91	2.3	1.5
24/07/95 08:00	11.3	0.11	87	277	5.63E-06	4.34E-06	0.25	0.08	0.23	0.12	4.2	3.0	2.11	1.98	2.0	1.5
24/07/95 09:00	12.6	0.18	220	587	1.30E-05	7.94E-06	0.25	0.08	0.23	0.12	6.2	3.5	2.11	1.98	3.0	1.8
24/07/95 10:00	14.0	0.30	248	637	2.14E-05	1.16E-05	0.25	0.08	0.23	0.12	6.6	3.1	2.11	1.98	3.1	1.5
24/07/95 11:00	15.3	0.51	461	1137	3.08E-05	1.76E-05	0.25	0.08	0.23	0.12	5.7	3.0	2.11	1.98	2.7	1.5
24/07/95 12:00	16.3	0.62	408	973	3.81E-05	2.23E-05	0.25	0.08	0.23	0.12	6.6	3.5	2.11	1.98	3.1	1.8
24/07/95 13:00	16.5	0.61	359	842	3.95E-05	2.45E-05	0.25	0.08	0.23	0.12	7.4	4.2	2.11	1.98	3.5	2.1
24/07/95 14:00	16.7	0.55	189	463	3.51E-05	2.11E-05	0.25	0.08	0.23	0.12	8.8	4.4	2.11	1.98	4.2	2.2
24/07/95 15:00	16.8	0.48	281	663	3.13E-05	1.81E-05	0.25	0.08	0.23	0.12	6.8	3.3	2.11	1.98	3.2	1.7
24/07/95 16:00	17.3	0.47	190	465	3.06E-05	1.69E-05	0.25	0.08	0.23	0.12	8.3	3.7	2.11	1.98	3.9	1.9
24/07/95 17:00	17.3	0.40	129	324	2.75E-05	1.36E-05	0.25	0.08	0.23	0.12	9.8	4.0	2.11	1.98	4.6	2.0
24/07/95 18:00	16.9	0.21	150	374	1.88E-05	9.45E-06	0.25	0.08	0.23	0.12	10.0	4.1	2.11	1.98	4.7	2.1
24/07/95 19:00	17.5	0.28	86	212	1.77E-05	1.12E-05	0.25	0.08	0.23	0.12	9.6	4.7	2.11	1.98	4.5	2.4
24/07/95 20:00	17.4	0.23	34	97	1.18E-05	5.18E-06	0.25	0.08	0.23	0.12	9.6	2.8	2.11	1.98	4.6	1.4

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
24/07/95 21:00	17.3	0.20	20	76	8.80E-06	4.21E-06	0.25	0.08	0.23	0.12	7.9	2.8	2.11	1.98	3.7	1.4
25/07/95 08:00	15.7	0.11	92	311	3.29E-06	3.70E-06	0.25	0.07	0.23	0.12	1.9	2.2	2.12	1.99	0.9	1.1
25/07/95 09:00	18.0	0.31	205	550	1.38E-05	8.56E-06	0.25	0.07	0.22	0.12	3.6	2.0	2.12	1.99	1.7	1.0
25/07/95 10:00	19.7	0.49	320	805	2.48E-05	1.48E-05	0.25	0.07	0.22	0.12	4.1	2.1	2.12	1.99	1.9	1.1
25/07/95 11:00	20.6	0.57	446	1070	3.36E-05	1.88E-05	0.25	0.07	0.22	0.12	4.5	2.2	2.12	1.99	2.1	1.1
25/07/95 12:00	22.0	0.78	531	1248	3.98E-05	2.17E-05	0.25	0.07	0.22	0.12	4.4	2.2	2.12	1.99	2.1	1.1
25/07/95 13:00	23.2	1.00	516	1211	4.30E-05	2.27E-05	0.25	0.07	0.22	0.12	4.3	2.1	2.12	1.99	2.0	1.1
25/07/95 14:00	24.1	1.21	470	1146	4.21E-05	2.32E-05	0.25	0.07	0.22	0.12	3.9	2.1	2.12	1.99	1.9	1.0
25/07/95 15:00	25.4	1.60	528	1267	4.09E-05	2.31E-05	0.25	0.07	0.22	0.12	2.9	1.6	2.12	1.99	1.4	0.8
25/07/95 16:00	26.1	1.75	493	1210	4.25E-05	2.26E-05	0.25	0.07	0.22	0.12	2.8	1.5	2.12	1.99	1.3	0.7
25/07/95 17:00	26.5	1.84	433	1067	3.98E-05	1.87E-05	0.25	0.07	0.22	0.12	2.5	1.1	2.12	1.99	1.2	0.6
25/07/95 18:00	26.5	1.78	330	845	3.70E-05	1.81E-05	0.25	0.07	0.22	0.12	2.4	1.1	2.12	1.99	1.1	0.6
25/07/95 19:00	26.4	1.75	207	581	3.38E-05	1.25E-05	0.25	0.07	0.22	0.12	2.4	0.8	2.12	1.99	1.2	0.4
25/07/95 20:00	25.7	1.63	93	337	2.95E-05	1.06E-05	0.25	0.07	0.22	0.12	2.6	0.8	2.12	1.99	1.2	0.4
26/07/95 07:00	14.3	0.19	16	148	3.03E-06	2.90E-06	0.24	0.07	0.22	0.12	2.1	2.0	2.13	1.99	1.0	1.0
26/07/95 08:00	15.6	0.28	75	295	1.05E-05	7.72E-06	0.24	0.07	0.22	0.12	4.7	3.3	2.13	1.99	2.2	1.6
26/07/95 09:00	16.5	0.37	195	582	1.57E-05	7.54E-06	0.24	0.07	0.22	0.12	4.7	2.1	2.13	1.99	2.2	1.1
26/07/95 10:00	18.6	0.73	376	958	2.71E-05	1.52E-05	0.24	0.07	0.22	0.12	4.2	2.3	2.13	1.99	2.0	1.1
26/07/95 11:00	19.9	0.82	454	1110	3.44E-05	1.98E-05	0.24	0.07	0.22	0.12	4.5	2.5	2.13	1.99	2.1	1.2
26/07/95 12:00	21.3	1.05	528	1263	4.03E-05	2.27E-05	0.24	0.07	0.22	0.12	4.3	2.3	2.13	1.99	2.0	1.1
26/07/95 13:00	22.3	1.23	645	1518	4.18E-05	2.28E-05	0.24	0.07	0.22	0.12	3.7	2.0	2.13	1.99	1.8	1.0
26/07/95 14:00	22.8	1.18	641	1516	4.07E-05	2.31E-05	0.24	0.07	0.22	0.12	3.8	2.1	2.13	1.99	1.8	1.0
26/07/95 15:00	22.7	1.07	620	1475	3.67E-05	1.85E-05	0.24	0.07	0.22	0.12	3.7	1.8	2.13	1.99	1.7	0.9
26/07/95 16:00	23.0	1.10	568	1366	3.64E-05	1.73E-05	0.24	0.07	0.22	0.12	3.7	1.7	2.13	1.99	1.7	0.8
26/07/95 17:00	22.5	1.00	483	1184	3.51E-05	1.65E-05	0.24	0.07	0.22	0.12	4.0	1.8	2.13	1.99	1.9	0.9
26/07/95 18:00	21.7	0.84	374	949	3.25E-05	1.51E-05	0.24	0.07	0.22	0.12	4.6	2.0	2.13	2.00	2.2	1.0
26/07/95 19:00	20.7	0.70	254	688	2.93E-05	1.10E-05	0.24	0.07	0.22	0.12	5.2	1.9	2.13	2.00	2.4	0.9
26/07/95 20:00	19.3	0.49	119	391	2.40E-05	8.56E-06	0.24	0.07	0.22	0.12	6.6	2.1	2.13	2.00	3.1	1.1
27/07/95 14:00	18.5	0.28	402	925	1.51E-05	8.50E-06	0.24	0.07	0.22	0.12	3.1	1.7	2.14	2.00	1.5	0.8
27/07/95 15:00	20.6	0.52	577	1332	3.00E-05	1.75E-05	0.24	0.07	0.22	0.12	4.0	2.2	2.14	2.00	1.9	1.1
27/07/95 16:00	22.1	0.73	529	1250	3.83E-05	2.24E-05	0.24	0.07	0.22	0.12	4.6	2.5	2.14	2.00	2.2	1.2
27/07/95 17:00	23.9	0.89	441	1064	3.94E-05	2.13E-05	0.24	0.07	0.21	0.12	4.3	2.1	2.14	2.00	2.0	1.1
27/07/95 18:00	24.7	1.05	339	848	3.81E-05	2.01E-05	0.24	0.07	0.21	0.12	4.0	1.9	2.14	2.00	1.9	0.9
27/07/95 19:00	24.9	1.34	224	603	3.97E-05	1.83E-05	0.24	0.07	0.21	0.12	3.8	1.6	2.14	2.00	1.8	0.8
27/07/95 20:00	24.1	1.20	93	308	3.63E-05	1.16E-05	0.23	0.07	0.21	0.12	3.4	1.2	2.14	2.00	1.6	0.6
27/07/95 21:00	22.9	0.95	19	103	2.12E-05	6.65E-06	0.23	0.07	0.21	0.12	3.6	0.9	2.14	2.00	1.7	0.5
04/08/95 08:00	12.7	0.15	32	85	4.73E-06	9.35E-07	0.20	0.06	0.19	0.12	4.1	0.7	2.20	2.05	1.9	0.4
04/08/95 09:00	13.0	0.18	63	154	9.27E-06	3.20E-06	0.20	0.06	0.19	0.12	6.6	2.0	2.20	2.05	3.0	1.0
04/08/95 10:00	13.3	0.22	117	275	1.34E-05	4.92E-06	0.20	0.06	0.19	0.12	7.3	2.3	2.20	2.05	3.3	1.1
04/08/95 11:00	14.0	0.29	199	455	1.79E-05	9.30E-06	0.20	0.06	0.19	0.12	6.6	3.0	2.20	2.05	3.0	1.5
04/08/95 12:00	14.2	0.32	285	651	2.25E-05	1.06E-05	0.20	0.06	0.19	0.12	7.5	3.2	2.20	2.05	3.4	1.6
04/08/95 13:00	15.0	0.40	508	1155	2.88E-05	1.60E-05	0.20	0.06	0.19	0.12	6.8	3.5	2.20	2.05	3.1	1.7
04/08/95 14:00	15.7	0.48	624	1456	3.46E-05	2.06E-05	0.20	0.06	0.19	0.12	6.7	3.8	2.20	2.05	3.1	1.8
04/08/95 15:00	16.3	0.54	607	1426	3.74E-05	2.25E-05	0.20	0.06	0.19	0.12	6.5	3.7	2.20	2.05	3.0	1.8
04/08/95 16:00	16.5	0.56	552	1312	3.72E-05	2.35E-05	0.20	0.06	0.19	0.12	6.9	4.1	2.20	2.05	3.1	2.0
04/08/95 17:00	17.5	0.65	465	1129	3.79E-05	2.25E-05	0.20	0.06	0.19	0.12	6.3	3.5	2.21	2.05	2.9	1.7
04/08/95 18:00	18.0	0.74	357	898	3.76E-05	1.79E-05	0.20	0.06	0.19	0.12	6.0	2.6	2.21	2.05	2.7	1.3
04/08/95 19:00	17.9	0.70	234	634	3.55E-05	1.23E-05	0.20	0.06	0.19	0.12	6.4	2.0	2.21	2.05	2.9	1.0
04/08/95 20:00	16.8	0.60	70	356	2.89E-05	7.82E-06	0.20	0.06	0.19	0.12	7.1	1.7	2.21	2.05	3.2	0.8
05/08/95 09:00	13.4	0.21	180	483	1.24E-05	7.15E-06	0.20	0.06	0.19	0.12	5.0	2.6	2.21	2.06	2.3	1.2
05/08/95 10:00	15.1	0.37	329	851	2.06E-05	1.16E-05	0.20	0.06	0.19	0.12	4.4	2.2	2.21	2.06	2.0	1.1
05/08/95 11:00	15.4	0.39	457	1113	2.95E-05	1.63E-05	0.20	0.06	0.19	0.12	6.1	3.0	2.21	2.06	2.8	1.5
05/08/95 12:00	16.5	0.50	549	1296	3.32E-05	1.85E-05	0.20	0.06	0.19	0.12	5.7	2.9	2.21	2.06	2.6	1.4
05/08/95 13:00	17.9	0.63	601	1408	3.62E-05	2.04E-05	0.20	0.06	0.19	0.12	4.9	2.6	2.21	2.06	2.2	1.2
05/08/95 14:00	19.5	0.95	620	1452	4.08E-05	2.34E-05	0.20	0.06	0.19	0.12	4.0	2.2	2.21	2.06	1.8	1.0
05/08/95 15:00	20.2	1.11	598	1417	4.13E-05	2.21E-05	0.20	0.06	0.19	0.12	3.9	2.0	2.21	2.06	1.8	1.0
05/08/95 16:00	21.0	1.34	545	1307	4.01E-05	2.31E-05	0.20	0.06	0.19	0.12	3.3	1.8	2.21	2.06	1.5	0.9
05/08/95 17:00	21.0	1.40	461	1131	3.88E-05	2.25E-05	0.20	0.06	0.19	0.12	3.2	1.8	2.21	2.06	1.5	0.9
05/08/95 18:00	19.8	0.91	353	897	3.41E-05	1.69E-05	0.20	0.06	0.19	0.12	4.4	2.0	2.21	2.06	2.0	1.0
05/08/95 19:00	18.3	0.59	233	632	2.87E-05	1.04E-05	0.20	0.06	0.19	0.12	5.8	1.9	2.21	2.06	2.6	0.9
05/08/95 20:00	18.1	0.65	63	357	2.58E-05	8.11E-06	0.20	0.06	0.19	0.12	5.9	1.6	2.21	2.06	2.7	0.8
06/08/95 10:00	15.3	0.25	346	867	1.39E-05	9.37E-06	0.20	0.06	0.19	0.12	4.3	2.8	2.22	2.06	1.9	1.3
06/08/95 11:00	16.5	0.38	459	1117	2.68E-05	1.35E-05	0.20	0.06	0.19	0.12	6.3	2.9	2.22	2.06	2.8	1.4
06/08/95 12:00	17.5	0.53	543	1284	3.19E-05	1.62E-05	0.20	0.06	0.19	0.12	5.6	2.7	2.22	2.06	2.5	1.3
06/08/95 13:00	17.3	0.51	601	1410	3.34E-05	1.92E-05	0.20	0.06	0.19	0.12	6.2	3.4	2.22	2.06	2.8	1.6
06/08/95 14:00	17.7	0.57	609	1432	3.45E-05	1.97E-05	0.20	0.06	0.19	0.12	5.8	3.2	2.22	2.07	2.6	1.5
06/08/95 15:00	18.5	0.68	598	1410	3.60E-05	1.98E-05	0.20	0.06	0.19	0.12	5.3	2.7	2.22	2.07	2.4	1.3
06/08/95 16:00	18.9	0.75	543	1297	3.54E-05	2.02E-05	0.20	0.06	0.19	0.12	4.9	2.7	2.22	2.07	2.2	1.3
06/08/95 17:00	19.6	0.84	455	1106	3.60E-05	1.85E-05	0.20	0.06	0.19	0.12	4.6	2.2	2.22	2.07	2.1	1.1
06/08/95 18:00	19.0	0.82	337	840	3.45E-05	1.81E-05	0.20	0.06	0.19	0.12	5.0	2.5	2.22	2.07	2.3	1.2
06/08/95 19:00	17.5	0.55	210	540	2.98E-05	1.04E-05	0.20	0.06	0.19	0.12	6.9	2.2	2.22	2.07	3.1	1.1
06/08/95 20:00	15.9	0.41	75	223	2.40E-05	7.31E-06	0.20	0.06	0.19	0.12	8.3	2.3	2.22	2.07	3.7	1.1
06/08/95 21:00	14.8	0.28	1	24	1.54E-05	5.08E-06	0.20	0.06	0.19	0.12	8.5	2.5	2.22	2.07	3.8	1.2
07/08/95 08:00	13.4	0.13	60	170	5.75E-06	3.00E-06	0.20	0.06	0.19	0.12	4.7	2.2	2.23	2.07	2.1	1.0
07/08/95 09:00	14.4	0.26	115	282	1.29E-05	7.18E-06	0.20	0.06	0.19	0.12	5.8	2.8	2.23	2.07	2.6	1.4
07/08/95 10:00	14.7	0.30	151	355	1.72E-05	8.20E-06	0.20	0.06	0.19	0.12	6.7	2.8	2.23	2.07	3.0	1.3
07/08/95 11:00	14.9	0.33	167	397	1.92E-05	8.13E-06	0.20	0.06	0.19	0.12	7.0	2.6	2.23	2.07	3.1	1.3
07/08/95 12:00	15.5	0.40	311	712	2.34E-05	1.24E-05	0.20	0.06	0.19	0.12	6.1	3.0	2.23	2.07	2.7	1.5
07/08/95 13:00	15.4	0.41	213	508	2.72E-05	1.29E-05	0.20	0.06	0.19	0.12	8.2	3.5	2.23	2.07	3.7	1.7
07/08/95 14:00	16.0	0.55	360	834	2.81E-05	1.33E-05	0.20	0.06	0.19	0.12	5.5	2.4	2.23	2.07	2.5	1.2
07/08/95 15:00	17.5	0.78	562	1298	3.60E-05	2.14E-05	0.20	0.06	0.19	0.12	4.6	2.6	2.23	2.07	2.1	1.3
07/08/95 16:00	17.4	0.76	452	1057	3.76E-05	2.39E-05	0.20	0.06	0.19	0.12	5.4	3.3	2.23	2.07	2.4	1.6
07/08/95 17:00	17.2	0.71	381	943	3.60E-05	2.01E-05	0.20	0.06	0.19	0.12	5.9	3.1	2.23	2.07	2.6	1.5
07/08/95 18:00	17.0	0.66	243	641	3.68E-05	1.89E-05	0.20	0.06	0.19	0.12	7.2	3.4	2.23	2.07	3.2	1.6
07/08/95 19:00	16.7	0.63	139	417	3.13E-05	1.19E-05	0.20	0.06	0.19	0.12	6.9	2.3	2.23	2.07	3.1	1.1
07/08/95 20:00	15.9	0.56	40	201	2.85E-05	1.32E-05	0.20	0.06	0.19	0.12	7.9	3.3	2.23	2.07	3.6	1.6

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
08/08/95 08:00	11.0	0.15	68	303	5.20E-06	2.02E-06	0.20	0.06	0.19	0.11	3.7	1.3	2.24	2.08	1.6	0.6
08/08/95 09:00	13.4	0.31	185	545	1.55E-05	8.74E-06	0.20	0.06	0.19	0.11	4.6	2.3	2.24	2.08	2.1	1.1
08/08/95 10:00	14.9	0.44	314	819	2.57E-05	1.38E-05	0.20	0.06	0.19	0.11	5.0	2.3	2.24	2.08	2.2	1.1
08/08/95 11:00	16.3	0.59	434	1062	3.31E-05	1.82E-05	0.20	0.06	0.19	0.11	5.0	2.4	2.24	2.08	2.2	1.2
08/08/95 12:00	17.3	0.63	521	1239	3.79E-05	2.11E-05	0.20	0.06	0.19	0.11	5.5	2.8	2.24	2.08	2.4	1.3
08/08/95 13:00	19.3	0.82	586	1369	3.92E-05	2.12E-05	0.20	0.06	0.19	0.11	4.3	2.1	2.24	2.08	1.9	1.0
08/08/95 14:00	20.1	0.89	468	1070	4.07E-05	2.36E-05	0.20	0.06	0.19	0.11	4.7	2.5	2.24	2.08	2.1	1.2
08/08/95 15:00	20.3	0.94	302	753	3.82E-05	1.74E-05	0.20	0.06	0.19	0.11	4.8	2.0	2.24	2.08	2.2	0.9
08/08/95 16:00	21.4	1.15	427	999	3.75E-05	1.74E-05	0.20	0.06	0.19	0.11	3.6	1.6	2.24	2.08	1.6	0.8
08/08/95 17:00	22.3	1.32	398	973	3.83E-05	1.61E-05	0.20	0.06	0.19	0.11	3.3	1.3	2.24	2.08	1.5	0.6
08/08/95 18:00	22.0	1.27	268	707	3.73E-05	1.79E-05	0.20	0.06	0.19	0.11	3.6	1.6	2.24	2.08	1.6	0.8
08/08/95 19:00	22.2	1.28	243	627	3.37E-05	9.51E-06	0.20	0.06	0.19	0.11	3.3	0.9	2.24	2.08	1.5	0.4
08/08/95 20:00	21.2	1.13	38	270	3.05E-05	8.20E-06	0.20	0.06	0.19	0.11	3.9	0.9	2.24	2.08	1.8	0.5
09/08/95 08:00	12.8	0.11	86	303	2.49E-06	9.76E-07	0.20	0.06	0.19	0.11	1.6	0.6	2.24	2.08	0.7	0.3
09/08/95 09:00	14.9	0.25	191	565	9.49E-06	5.08E-06	0.20	0.06	0.19	0.11	2.8	1.4	2.24	2.08	1.2	0.7
09/08/95 10:00	17.1	0.51	309	813	2.28E-05	1.04E-05	0.20	0.06	0.19	0.11	4.2	1.7	2.25	2.08	1.9	0.8
09/08/95 11:00	19.0	0.82	424	1049	3.46E-05	1.43E-05	0.20	0.06	0.19	0.11	4.5	1.7	2.25	2.08	2.0	0.8
09/08/95 12:00	20.7	1.18	514	1227	4.17E-05	1.79E-05	0.20	0.06	0.19	0.11	3.9	1.6	2.25	2.08	1.7	0.8
09/08/95 13:00	21.4	1.27	583	1367	4.41E-05	1.95E-05	0.20	0.06	0.19	0.11	3.8	1.6	2.25	2.08	1.7	0.8
09/08/95 14:00	22.5	1.45	557	1314	4.42E-05	2.02E-05	0.20	0.06	0.19	0.11	3.4	1.5	2.25	2.08	1.5	0.7
09/08/95 15:00	23.5	1.65	559	1320	4.37E-05	1.72E-05	0.20	0.06	0.19	0.11	2.9	1.1	2.25	2.08	1.3	0.5
09/08/95 16:00	24.2	1.75	502	1194	4.30E-05	1.49E-05	0.20	0.06	0.19	0.11	2.7	0.9	2.25	2.09	1.2	0.4
09/08/95 17:00	24.5	1.81	413	1010	4.18E-05	1.65E-05	0.20	0.06	0.19	0.11	2.7	1.0	2.25	2.09	1.2	0.5
09/08/95 18:00	24.7	1.83	305	781	3.95E-05	1.41E-05	0.20	0.06	0.19	0.11	2.6	0.9	2.25	2.09	1.2	0.4
09/08/95 19:00	24.2	1.69	188	531	3.68E-05	1.18E-05	0.20	0.06	0.19	0.11	2.9	0.8	2.25	2.09	1.3	0.4
09/08/95 20:00	23.1	1.40	39	261	3.15E-05	8.45E-06	0.20	0.06	0.19	0.11	3.3	0.8	2.25	2.09	1.5	0.4
10/08/95 08:00	13.3	0.15	67	287	2.65E-06	2.37E-06	0.20	0.06	0.19	0.11	1.2	1.1	2.25	2.09	0.5	0.5
10/08/95 09:00	15.6	0.35	174	536	1.03E-05	5.53E-06	0.20	0.06	0.19	0.11	2.2	1.1	2.25	2.09	1.0	0.5
10/08/95 10:00	18.4	0.74	300	788	2.47E-05	1.04E-05	0.20	0.06	0.19	0.11	2.9	1.0	2.25	2.09	1.3	0.5
10/08/95 11:00	20.7	1.19	415	1018	3.62E-05	1.48E-05	0.20	0.06	0.19	0.11	2.9	1.0	2.25	2.09	1.3	0.5
10/08/95 12:00	22.1	1.42	510	1209	4.12E-05	1.59E-05	0.20	0.06	0.19	0.11	3.0	1.0	2.25	2.09	1.3	0.5
10/08/95 13:00	23.2	1.55	562	1314	4.31E-05	1.75E-05	0.20	0.06	0.19	0.11	2.9	1.1	2.25	2.09	1.3	0.5
10/08/95 14:00	24.5	1.80	569	1330	4.33E-05	1.54E-05	0.20	0.05	0.19	0.11	2.5	0.8	2.26	2.09	1.1	0.4
10/08/95 15:00	24.9	1.83	538	1265	4.28E-05	1.44E-05	0.20	0.05	0.19	0.11	2.5	0.8	2.26	2.09	1.1	0.4
10/08/95 16:00	24.3	1.60	489	1160	4.20E-05	1.39E-05	0.20	0.05	0.19	0.11	3.0	0.9	2.26	2.09	1.3	0.4
10/08/95 17:00	23.6	1.42	410	991	4.04E-05	1.44E-05	0.20	0.05	0.19	0.11	3.3	1.1	2.26	2.09	1.5	0.5
10/08/95 18:00	23.1	1.32	299	752	3.82E-05	1.34E-05	0.20	0.05	0.19	0.11	3.6	1.1	2.26	2.09	1.6	0.5
10/08/95 19:00	23.9	1.56	175	488	3.58E-05	1.08E-05	0.20	0.05	0.19	0.11	3.0	0.8	2.26	2.09	1.3	0.4
10/08/95 20:00	23.1	1.54	34	247	3.21E-05	8.56E-06	0.20	0.05	0.19	0.11	3.0	0.7	2.26	2.09	1.3	0.3
15/08/95 09:00	17.2	0.20	192	544	1.31E-05	5.88E-06	0.20	0.05	0.20	0.11	6.7	2.8	2.27	2.10	3.0	1.3
15/08/95 10:00	18.3	0.35	275	699	2.43E-05	1.03E-05	0.20	0.05	0.20	0.11	7.7	3.0	2.27	2.10	3.4	1.4
15/08/95 11:00	19.4	0.49	407	978	3.33E-05	1.31E-05	0.20	0.05	0.20	0.11	7.3	2.6	2.27	2.10	3.2	1.2
15/08/95 12:00	19.9	0.59	334	821	4.05E-05	1.69E-05	0.20	0.05	0.20	0.11	8.2	3.1	2.27	2.10	3.6	1.5
15/08/95 13:00	20.1	0.65	326	803	4.21E-05	1.79E-05	0.21	0.05	0.20	0.11	8.0	3.1	2.27	2.10	3.5	1.5
15/08/95 14:00	21.1	0.78	365	889	4.47E-05	2.03E-05	0.21	0.05	0.20	0.11	7.0	2.9	2.27	2.10	3.1	1.4
15/08/95 15:00	21.2	0.80	306	756	4.49E-05	1.93E-05	0.21	0.05	0.20	0.11	7.1	2.8	2.27	2.10	3.1	1.3
15/08/95 16:00	21.8	0.87	322	796	4.42E-05	1.84E-05	0.21	0.05	0.20	0.11	6.3	2.4	2.27	2.10	2.8	1.2
15/08/95 17:00	21.9	0.89	330	803	4.42E-05	1.77E-05	0.21	0.05	0.20	0.11	6.1	2.3	2.27	2.10	2.7	1.1
15/08/95 18:00	21.7	0.86	210	547	4.24E-05	1.67E-05	0.21	0.05	0.20	0.11	6.6	2.4	2.27	2.10	2.9	1.1
15/08/95 19:00	21.0	0.68	94	295	3.57E-05	1.13E-05	0.21	0.05	0.20	0.11	7.5	2.1	2.27	2.10	3.3	1.0
15/08/95 20:00	20.2	0.53	14	139	2.41E-05	6.26E-06	0.21	0.05	0.20	0.11	6.9	1.6	2.27	2.10	3.0	0.8
16/08/95 10:00	17.5	0.24	267	693	1.66E-05	8.33E-06	0.21	0.05	0.20	0.11	5.3	2.4	2.26	2.10	2.4	1.1
16/08/95 11:00	19.8	0.46	383	934	3.05E-05	1.20E-05	0.21	0.05	0.20	0.11	6.0	2.0	2.26	2.10	2.6	1.0
16/08/95 12:00	21.1	0.61	438	1050	3.83E-05	1.49E-05	0.21	0.05	0.20	0.11	6.1	2.1	2.26	2.10	2.7	1.0
16/08/95 13:00	21.8	0.71	413	961	4.14E-05	1.57E-05	0.21	0.05	0.20	0.11	6.1	2.0	2.26	2.10	2.7	1.0
16/08/95 14:00	24.0	1.17	591	1378	4.85E-05	2.06E-05	0.21	0.05	0.20	0.11	4.5	1.8	2.26	2.10	2.0	0.8
16/08/95 15:00	24.0	1.23	447	1078	4.90E-05	1.91E-05	0.21	0.05	0.20	0.11	4.6	1.7	2.26	2.10	2.0	0.8
16/08/95 16:00	24.0	1.26	370	886	4.72E-05	1.79E-05	0.21	0.05	0.20	0.11	4.6	1.6	2.26	2.09	2.0	0.8
16/08/95 17:00	23.7	1.21	258	636	4.44E-05	1.44E-05	0.21	0.05	0.20	0.11	4.7	1.4	2.26	2.09	2.1	0.7
16/08/95 18:00	23.6	1.23	197	528	4.12E-05	1.41E-05	0.21	0.05	0.20	0.11	4.5	1.4	2.26	2.09	2.0	0.7
16/08/95 19:00	22.8	1.15	86	311	3.59E-05	1.01E-05	0.21	0.05	0.20	0.11	4.5	1.1	2.26	2.09	2.0	0.5
16/08/95 20:00	22.5	1.13	33	237	2.91E-05	6.82E-06	0.21	0.05	0.20	0.11	3.7	0.8	2.26	2.09	1.6	0.4
17/08/95 09:00	15.9	0.13	136	413	4.08E-06	2.99E-06	0.22	0.05	0.21	0.11	1.2	0.8	2.26	2.09	0.5	0.4
17/08/95 10:00	19.8	0.59	281	735	1.97E-05	9.08E-06	0.22	0.05	0.21	0.11	2.7	1.1	2.26	2.09	1.2	0.5
17/08/95 11:00	21.0	0.75	347	878	3.75E-05	1.33E-05	0.22	0.05	0.21	0.11	5.2	1.5	2.26	2.09	2.3	0.7
17/08/95 12:00	22.1	0.90	434	1033	4.21E-05	1.71E-05	0.22	0.05	0.21	0.11	4.5	1.6	2.26	2.09	2.0	0.7
17/08/95 13:00	23.7	1.23	551	1293	4.80E-05	1.88E-05	0.22	0.05	0.21	0.11	3.8	1.3	2.26	2.09	1.7	0.6
17/08/95 14:00	24.9	1.44	523	1226	4.91E-05	1.72E-05	0.22	0.05	0.21	0.11	3.6	1.1	2.26	2.09	1.6	0.5
17/08/95 15:00	24.7	1.35	376	914	4.68E-05	1.61E-05	0.22	0.05	0.21	0.11	4.0	1.2	2.26	2.09	1.8	0.6
17/08/95 16:00	23.4	1.09	259	644	4.33E-05	1.45E-05	0.22	0.05	0.21	0.11	5.0	1.4	2.25	2.09	2.2	0.7
17/08/95 17:00	23.3	1.09	351	841	4.09E-05	1.35E-05	0.22	0.05	0.21	0.11	4.4	1.3	2.25	2.09	1.9	0.6
17/08/95 18:00	23.3	1.06	279	683	4.11E-05	1.37E-05	0.22	0.05	0.21	0.11	4.8	1.4	2.25	2.09	2.1	0.7
17/08/95 19:00	21.8	0.75	177	460	3.80E-05	1.26E-05	0.22	0.05	0.21	0.11	6.9	1.9	2.25	2.09	3.1	0.9
17/08/95 20:00	21.1	0.63	34	168	3.04E-05	7.63E-06	0.22	0.05	0.21	0.11	9.3	1.6	2.25	2.09	4.1	0.8
19/08/95 12:00	20.3	0.30	433	1014	2.43E-05	8.08E-06	0.23	0.05	0.22	0.11	3.2	1.8	2.24	2.07	1.4	0.8
19/08/95 13:00	21.6	0.63	516	1183	4.49E-05	1.74E-05	0.23	0.05	0.22	0.11	4.3	1.9	2.24	2.07	1.9	0.9
19/08/95 14:00	22.7	0.83	433	1039	4.92E-05	1.97E-05	0.23	0.05	0.22	0.11	5.5	1.9	2.24	2.07	2.5	0.9
19/08/95 15:00	23.1	0.87	542	1271	5.01E-05	1.88E-05	0.23	0.05	0.22	0.11	5.6	2.0	2.24	2.07	2.5	1.0
19/08/95 16:00	23.4	0.90	521	1240	4.69E-05	1.65E-05	0.23	0.05	0.22	0.11	5.8	2.1	2.24	2.07	2.6	1.0
19/08/95 17:00	23.7	0.83	345	822	4.30E-05	1.49E-05	0.23	0.05	0.22	0.11	6.9	2.4	2.24	2.07	3.1	1.2
19/08/95 18:00	23.9	0.98	273	677	3.76E-05	9.60E-06	0.23	0.05	0.22	0.11	5.5	1.8	2.24	2.07	2.4	0.9
19/08/95 19:00	23.0	0.91	159	435	2.39E-05	5.40E-06	0.23	0.05	0.22	0.11	6.0	2.0	2.24	2.07	2.7	1.0
19/08/95 20:00	21.9	0.76	32	181	1.76E-05	4.92E-06	0.23	0.05	0.22	0.11	6.7	2.3	2.24	2.07	3.0	1.1
20/08/95 11:00	17.7	0.13	128	294	1.02E-05	2.73E-06	0.23	0.05	0.22	0.11	6.1	1.3	2.23	2.07	2.7	0.6
20/08/95 12:00	18.8	0.23	238	539	1.45E-05	4.80E-06	0.23	0.05	0.22	0.11	4.1	1.1	2.23	2.07	1.8	0.6

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
20/08/95 13:00	20.7	0.42	457	1034	2.55E-05	8.43E-06	0.23	0.05	0.22	0.11	3.6	1.0	2.23	2.07	1.6	0.5
20/08/95 14:00	21.9	0.58	520	1212	3.74E-05	1.52E-05	0.23	0.05	0.22	0.11	4.7	1.6	2.23	2.07	2.1	0.8
20/08/95 15:00	23.4	0.79	505	1190	4.29E-05	1.60E-05	0.23	0.05	0.22	0.11	4.7	1.5	2.23	2.07	2.1	0.7
20/08/95 16:00	24.3	0.95	447	1074	4.64E-05	1.74E-05	0.23	0.05	0.22	0.11	4.9	1.6	2.23	2.07	2.2	0.8
20/08/95 17:00	25.8	1.32	367	907	4.78E-05	1.74E-05	0.23	0.05	0.22	0.11	4.2	1.3	2.23	2.07	1.9	0.6
20/08/95 18:00	26.6	1.54	246	640	4.71E-05	1.64E-05	0.23	0.05	0.22	0.11	4.0	1.1	2.23	2.07	1.8	0.6
20/08/95 19:00	25.4	1.13	134	393	4.11E-05	1.44E-05	0.23	0.05	0.22	0.11	5.6	1.5	2.23	2.07	2.5	0.7
20/08/95 20:00	22.7	0.60	24	168	2.90E-05	1.03E-05	0.23	0.05	0.22	0.11	13.0	2.5	2.23	2.07	5.8	1.2
21/08/95 10:00	20.7	0.41	238	614	1.16E-05	5.37E-06	0.24	0.05	0.22	0.11	1.9	0.8	2.23	2.06	0.9	0.4
21/08/95 11:00	22.5	0.82	347	845	3.15E-05	1.03E-05	0.24	0.05	0.22	0.11	3.7	1.0	2.23	2.06	1.7	0.5
21/08/95 12:00	23.7	1.03	427	1011	4.32E-05	1.68E-05	0.24	0.05	0.22	0.11	4.3	1.4	2.23	2.06	1.9	0.7
21/08/95 13:00	25.4	1.39	486	1140	4.95E-05	1.86E-05	0.24	0.05	0.23	0.11	3.9	1.3	2.23	2.06	1.8	0.6
21/08/95 14:00	26.5	1.63	486	1138	5.17E-05	1.86E-05	0.24	0.05	0.23	0.11	3.7	1.2	2.23	2.06	1.7	0.6
21/08/95 15:00	27.4	1.82	480	1135	5.16E-05	1.83E-05	0.24	0.05	0.23	0.11	3.3	1.1	2.23	2.06	1.5	0.5
21/08/95 16:00	27.6	1.90	388	943	5.03E-05	1.70E-05	0.24	0.05	0.23	0.11	3.3	1.0	2.23	2.06	1.5	0.5
21/08/95 17:00	27.3	1.82	327	802	4.81E-05	1.63E-05	0.24	0.05	0.23	0.11	3.3	1.1	2.22	2.06	1.5	0.5
21/08/95 18:00	26.9	1.66	229	590	4.39E-05	1.49E-05	0.24	0.05	0.23	0.11	3.4	1.1	2.22	2.06	1.6	0.5
21/08/95 19:00	26.2	1.61	124	372	3.91E-05	1.35E-05	0.24	0.05	0.23	0.11	3.3	1.1	2.22	2.06	1.5	0.5
21/08/95 20:00	25.2	1.39	16	169	3.07E-05	1.01E-05	0.24	0.05	0.23	0.11	3.2	1.0	2.22	2.06	1.5	0.5

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