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WATER TRANSPORT AND LEAF WATER RELATIONS IN WINTER WHEAT CROPS

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For the wonderful and secret operations of Nature are so involved and intricate, so far out of the reach of our senses, as they present themselves to us in their natural order, that it is impossible for the most sagacious and penetrating genius to pry into them, unless he will be at the pains of analysing Nature, by a numerous and regular series of experiments; which are the only solid foundation whence we may reasonably expect to make any advance, in the real knowledge of the nature of things.

Stephen Hales (1727).

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ABSTRACT

Leaf water potential (ψ_L) in winter wheat (*Triticum aestivum* L cv Huntsman) was related to crop evaporation rate and soil water potential. During the day ψ_L responded primarily to changes in evaporation, whereas seasonal changes in ψ_L resulted from changes in soil water potential.

Hysteresis in the relation between ψ_L and the flow of water through the plants was attributed to changes in water storage in the soil-plant system. Modelling this gave estimates of the hydraulic resistance (R) and capacitance (C) of the soil-plant system which agreed with independent estimates.

Components of R and C were also estimated. When the soil water potential (ψ_S) was high, the largest hydraulic resistance could be atrributed to the soil-root system, the stem resistance was half of this. Resistance to water flow in the soil-root system increased when ψ_S was low, and there was evidence of large water potential gradients in the soil around the roots.

There was a systematic decrease in leaf osmotic potential (ψ_π) and increase in leaf turgor potential (ψ_P) from the bottom to the top of the stem. When ψ_L in the youngest leaves decreased so did ψ_π, apparently by a combination of dehydration and solute accumulation in the leaves. Osmotic adaptation therefore tended to maintain ψ_P during water stress. Maintenance of ψ_P was important since stomatal conductance was reduced at low leaf turgor potentials, irrespective of irradiance.

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I would like to thank Dr J M Roberts for his constructive criticism of the penultimate draft of this thesis.

To all these people I am very grateful, but without the love and encouragement of my wife throughout difficult times this thesis would not have been possible. To her I dedicate this work.

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LIST OF SYMBOLS

Roman alphabet		Unit
a_i	stem xylem vessel radius	m
$\bar{a}$	mean hydraulic radius of the stem xylem vessels	m
A	total cross-sectional area of the stem xylem vessels	m^2
b_i	semi-major axis of ellipitcal stem xylem vessels	m
B	bound water fraction in plant leaves	
c_i	semi-minor axis of ellipitcal stem xylem vessels	m
C	hydraulic capacitance of the soil-plant system	$m^3 MPa^{-1}$
d	stem xylem vessel diameter	m
e, e_o	partial pressure of the vapour in equilibrium with water (in solution, leaf etc.), pure free water	Pa
E	crop evaporation rate	Wm^{-2}
I	integration constant	
k	constant	
k_s	stomatal conductance	$cm\ s^{-1}$
K	constant	
ℓ	length of stem xylem vessels	m
m	rate of change of Q with time	$m^3 s^{-2}$
n	stem density (i.e. the number of stems per unit area of ground)	m^{-2}
N	total number of xylem vessels in the stem	
N_B	number of vascular bundles in the stem	
N_x	number of xylem vessels per vascular bundle	
p,P	hydrostatic pressure	MPa
Q	transpiration flow of water per plant stem	$m^3\ s^{-1}$
Q_s	rate of change of water stored in the soil-plant system	$m^3\ s^{-1}$

Roman alphabet		Unit
r, r_1	hydraulic resistivity of the soil-plant system, stem	MPa s m^{-2}
R, R_1, R_2	hydraulic resistance of the soil-plant system, stem, soil-root system	MPa s m^{-3}
RC, R_1C_1, R_2C_2	time constant of the soil-plant system, stem, soil-root system	min
R_e	Reynolds number	
R	universal gas constant	$JK^{-1} mol^{-1}$
S_t	total solar irradiance	Wm^{-2}
t	time	s,min,h
T	temperature	°C, K
u	linear velocity of sap flow in the stem	m s^{-1}
U	soil water extraction rate	m^3 s^{-1}
v	volume of water vapour	m^3
$\bar{v}$	partial molal volume of water	$m^3 mol^{-1}$
V	electric potential difference	µV
W, W_1, W_2	water storage in the soil-plant system, plant tops, soil-root system	m^3
x,y,z	cartesian co-ordinates	

Greek alphabet

α	thermocouple sensitivity	µV K^{-1}
$\delta\psi_\pi$	instrumental error in an estimate of leaf osmotic potential	MPa
Δt	time interval	h
ΔT	dewpoint depression	°C, K
Δv	change in volume per mole of water on vapourization	m^3
$\Delta W, \Delta W_1, \Delta W_2$	change in water storage in the soil-plant system, plant tops, soil-root system	m^3

Greek alphabet		Unit
$\Delta\psi, \Delta\psi_1, \Delta\psi_2, \Delta\psi_S$	gradients in water potential across the soil-plant system, stem, soil-root system, soil around the roots	MPa
$\Delta\psi_L$	change in ψ_L during the day	MPa
η	viscosity of xylem sap	$N\ s\ m^{-2}$
θ_L	relative water content of the leaves	
λ	latent heat of vapourization of water	$J\ kg^{-1}$
μ, μ_o	chemical potential of water (in solution, leaf, etc.), pure free water	$J\ mol^{-1}$
π_v	thermocouple cooling coefficient	μV
ρ	density of xylem sap	$kg\ m^{-3}$
Σ	summation symbol	
ψ	water potential	MPa
ψ_B	effective water potential of the soil	MPa
ψ_G	gravitational potential	MPa
ψ_L	leaf water potential	MPa
ψ_{LO}	leaf water potential at zero flow	MPa
ψ_M	leaf matric potential	MPa
ψ_p	leaf turgor potential	MPa
ψ_{RS}	root surface water potential	MPa
ψ_S	soil water potential	MPa
ψ_W	effective potential of a free water source	MPa
ψ_X	xylem water potential	MPa
ψ_π	leaf osmotic potential	MPa
ψ_π^o	leaf osmotic potential at full turgor (ie when $\psi_L = 0$)	MPa
$\psi_{\pi x}$	osmotic potential of xylem sap	MPa

1. INTRODUCTION

1.1 Historical aspects

The importance of water to plants has long been a matter of common observation. For example, as early as 5,500 B.C. major advances in the agriculture of Southwestern Asia came with the development of irrigation. More recently, there has been an active scientific interest in plant-water relations for several centuries. Early investigations were often descriptive and it was not until the beginning of the eighteenth century that Hales (1727) (see also Cohen 1976) conducted one of the first quantitative studies of water transport in plants. He deduced that water was "imbibed" by the roots and "perspired by way of the leaves", even though he was not aware of the existence of stomata. He also measured the transpiration rate in several plant species. In his attempts to measure the force that caused water to flow through plants he used 'aqueo-mercurial' gauges attached to the roots and branches of fruit trees. The results of these experiments proved, contrary to the opinion of the seventeenth century botanists Malpighi and Grew, that capillary action in the plant stems alone could not account for "the force with which the sap was imbibed". Hales approach to the study of plant water transport, i.e. that of measuring the water flow and the driving force involved, has been used to the present day.

Huber (1924) first proposed that water flow through the soil-plant system could be related using an analogue of Ohm's law, although most modern publications cite van den Honert (1948). It was Gradmann (1928) and then van den Honert (1948) who extended

Huber's original idea to include water movement into the atmosphere. Under steady state conditions the transpiration flow (Q) through all parts of the system is the same and given by an equation of the form

$$Q = \Delta\psi_i/R_i , \tag{1.1}$$

where R_i is the hydraulic resistance of the part (i) of the system in question and $\Delta\psi_i$ is the potential difference across it. Using this approach van den Honert (1948) showed that the largest resistance in the soil-plant-atmosphere system was in the gaseous phase, i.e. where water moves from the sub-stomatal cavity into the air around the leaf. He then concluded that water transport in plants was regulated by the stomata. Although this has subsequently been shown to be correct, the use of a water potential gradient to describe the vapour phase driving force is conceptually incorrect (Ray 1960; Slatyer 1960; Rawlins 1963).

Although water flow through plants could be readily measured, water potential (ψ) in plants could not be reliably estimated until after the introduction of the pressure chamber by Dixon (1914) and the thermocouple psychrometer by Spanner (1951). Subsequent development of the pressure chamber technique (Scholander *et al* 1965; Waring and Cleary 1967; Boyer 1967a) and the psychrometric technique (Monteith and Owen 1958; Boyer and Knipling 1965; Rawlins 1964, 1966; Peck 1968, 1969) led to their common use in studies of plant-water relations and considerable advances were made in this field. Huber's (1924) principles were applied to liquid phase water transport in plants, allowing their hydraulic resistances to be inferred (Tinklin and Weatherley 1966; Weatherley 1970; Janes 1970; Hansen 1974). Plant ψ was widely adopted as an indicator of water stress and its effect on plant physiological processes studied, see, for example, Slavik 1965; Slatyer 1967; Kozlowski 1968a,b; Hsiao 1973, Hsiao *et al* 1976).

ψ is now defined as the partial molal Gibbs free energy of water in a system relative to that of pure free water (Slatyer 1967). It is normally expressed as energy per unit volume of water, with units dimensionally equivalent to pressures. The traditional c.g.s. unit was the bar, but this has now been superseded by the SI unit of pressure, the pascal (Pa). Throughout this thesis the megapascal (MPa) is adopted as a convenient unit for expressing soil (ψ_S) and leaf (ψ_L) water potential (1 MPa = 10 bar $\simeq$ 1,000 J kg^{-1}).

This thesis is concerned with water transport and leaf water relations in two winter wheat crops. Chapters 2 and 3 describe the instrumentation, materials and methods used in this study. Chapters 5 and 6 deal with environmental effects on the gradients of water potential and flow of water in the soil-plant system. The components of leaf water potential (section 1.3) are considered in chapter 7 and their effects on stomatal conductance examined. The remainder of this chapter contains an introduction to water transport in plants and leaf water relations; some relevant literature is reviewed.

1.2 Water transport in the soil-plant system

To predict responses of leaf water potential to the environment a model of water movement in the soil-plant system is required. The simplest models, based on Huber's (1924) approach, relate the total potential drop across the soil-plant system

($\Delta\psi = \sum_i \Delta\psi_i$) and its hydraulic resistance ($R = \sum_i R_i$) as

$$\Delta\psi = QR \qquad (1.2)$$

$\Delta\psi$ is usually taken as the difference in water potential between the soil and leaf, i.e. $\psi_S - \psi_L$ (e.g. see Biscoe, Cohen and Wallace 1976). The assumption that $\psi_S - \psi_L$ is the driving force for water movement appears to be reasonable, at least to a first approximation (Slatyer and Gardner 1965). However, R may not be constant (Rawlins 1963; Macklon and Weatherley 1965) and therefore the validity of equation (1.2) should be tested. This can be done by making concurrent measurements of ψ_L and Q and examining the relation obtained.

1.2.1 Leaf water potential/flow relations

There are a number of reports in the literature of relations between ψ_L and Q in plants, many of which offer conflicting views on the validity of equation (1.2). These have been reviewed recently by Hailey *et al* (1973), Jarvis (1975) and Kaufmann (1976). Where the environment can be controlled the steady state requirements for the application of equation (1.2) can usually be met. In these circumstances two distinct types of relation between ψ_L and Q have been observed. One, where ψ_L increased linearly with Q (curve A, figure 1.1). The second, where ψ_L was constant over a wide range of flow rates (curve B, figure 1.1). A type A response has two interpretations depending on the value of ψ_L at zero flow (i.e. ψ_{LO}). Where $\psi_{LO} = \psi_S$, R was considered constant, e.g. in sunflower and maize (Neumann, Thurtell and Stevenson 1974; Dubé *et al* 1975). Where $\psi_{LO} < \psi_S$, it

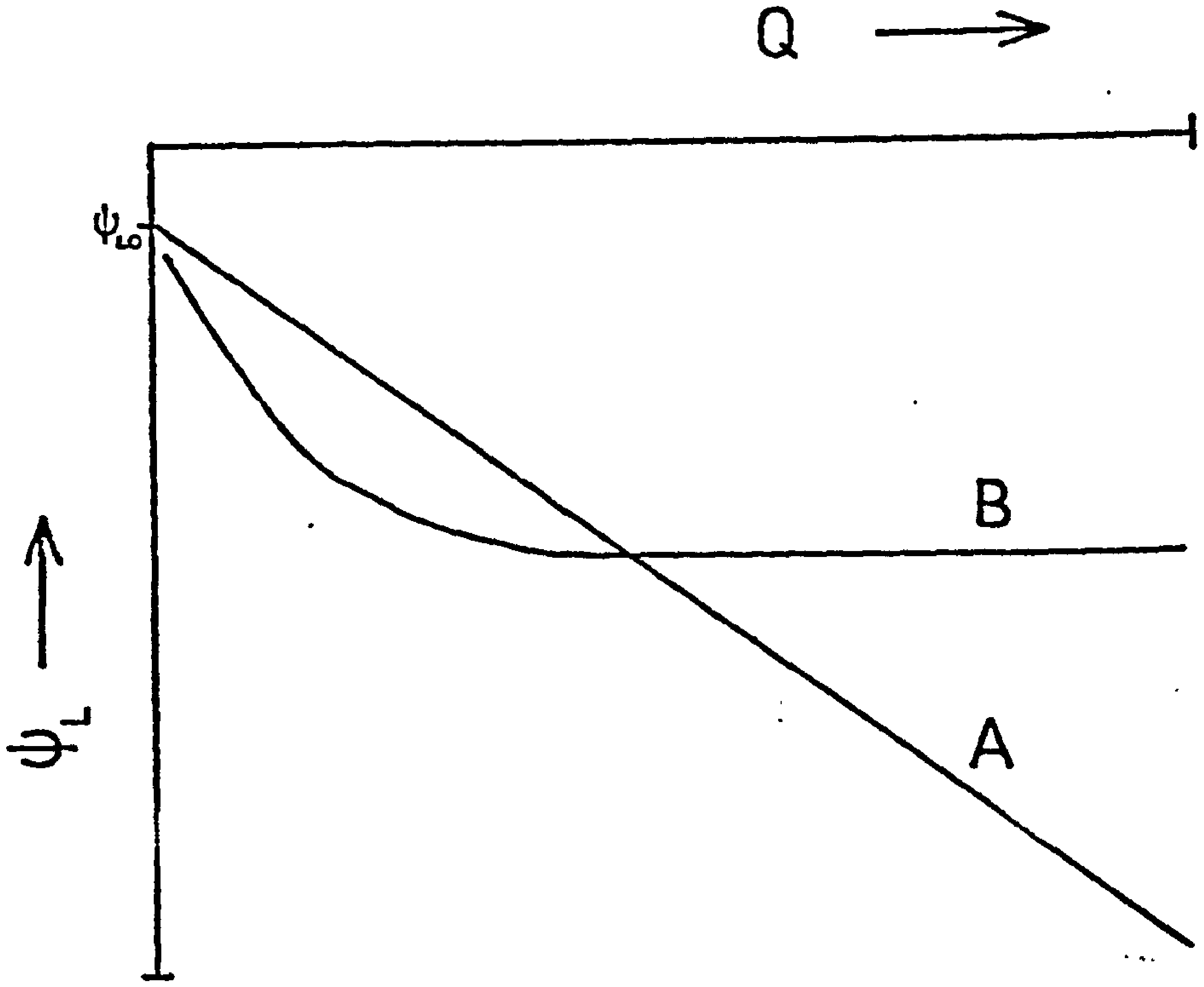


Figure 1.1 Diagrammatic representation of typical relations between leaf water potential (ψ_L) and flow of water (Q) in plants.

was suggested that R decreased as Q increased, e.g. in tomato and pepper (Barrs 1973; Janes 1970). These two different types of linear relation between ψ_L and Q have not been differentiated in recent reviews by Hailey *et al* (1973) and Kaufmann (1976) where R was incorrectly quoted as constant in both cases.

The type of relation between ψ_L and Q is not characteristic of any given species since type B relations (figure 1.1) have also been reported for the above species, i.e. in sunflower (Stoker and Weatherley 1971; Black 1974 - quoted in Weatherley 1976), maize and tomato (Barrs 1973) and pepper (Camacho-B, Hall and Kaufmann 1974). These relations also led to the conclusion that R decreased with increasing flow. The different responses of similar species are difficult to explain. Furthermore, different relations between ψ_L and Q have even been observed in the same variety of tomato (Barrs 1973), pepper (Janes 1970) and sunflower (Cox 1966) grown under different conditions. In maize, soybean and sunflower, Neumann *et al* (1974) found that the variability of R between different plants of a single cultivar of one species was as large as it was between the different species. They were unable to explain these differences in terms of the physiological condition of the plants. The high 'correlation' between the number of different studies of the ψ_L/Q relation and the number of different relations obtained may imply that the responses of plants in controlled environments are peculiar to the imposed conditions which are very unlike those in the field.

There have been few systematic studies of the relation between ψ_L and Q in field grown plants, presumably because of the difficulty in estimating Q under these conditions. Of those available most report estimates of R deduced from measurements of ψ_L at a few flow rates only, e.g. in tobacco (Begg and Turner 1970), spruce (Hellkvist, Richards and Jarvis 1974) and wheat (Denmead and Millar 1976a). Therefore, it was not possible to examine any variations in R with Q. Where sufficient measurements were made different relations between ψ_L and Q were observed. In apple trees Landsberg *et al* (1975) found a type A response (figure 1.1) and deduced a constant value of R for this species. Biscoe, Cohen and Wallace (1976) found a relation between ψ_L and Q in barley which was intermediate between type A and B responses (figure 1.1). They concluded that R decreased in barley as Q increased. Several authors report relations showing hysteresis in the relation between ψ_L and Q (Berger 1969; Jarvis 1976; Sterne, Kaufmann and Zentmyer 1977). The implications of hysteresis in the ψ_L/Q relation are discussed in section 1.2.3 and chapter 6. Clearly though, even these few field studies have observed different ψ_L/Q relations. The relation between ψ_L and Q in field grown wheat is not known. Therefore, to allow a model of water flow through this species to be constructed the relation between ψ_L and Q was examined.

1.2.2 Components of the total hydraulic resistance

Some understanding of the variation in R with Q can be achieved from a knowledge of the relative sizes of the hydraulic resistance of the soil, roots, stems and leaves. Removal of the roots in small herbaceous plants (Tinklin and Weatherley 1966; Jensen, Taylor and Wiebe 1961) and large pine trees (Roberts 1976) resulted in a substantial rise in ψ_L or an increase in Q, or both.

When the stem was also removed by Tinklin and Weatherley (1966) there was little or no additional effect. They concluded that the largest resistance was associated with the root system and the stem resistance was comparatively small. This was confirmed by Boyer (1971), who measured the rate of increase in ψ_L when transpiration was prevented in intact plants and after excision of their roots and stems. He found that the ratio of the resistances in the roots, stems and leaves ranged from 2:1:1 in sunflower to 10:1:2.5 in soybean. Alternatively Duniway (1975) found a ratio of 2.5:1:10 in safflower, indicating that the largest resistance was in the foliage of this species. In Sitka spruce Jarvis (1975) found that the potential gradient in the stem was three quarters of the total gradient in the plants at times of high evaporation. The implication is that the stem resistance was about three times that in the roots. However, Jarvis (1975) also pointed out that such a conclusion based on the potential gradients alone was uncertain. This was because of possible differences in the flow in the roots and stems due to transfer of water from storage in the stem into the transpiration stream. In non-transpiring yew twigs ψ_L was the same as that in transpiring twigs throughout a day (Richter 1973). This implies a negligible leaf hydraulic resistance in this species.

Because roots generally have the largest hydraulic resistance (Kramer 1938; Jensen, Taylor and Wiebe 1961; Boyer 1971) it has been suggested that a type B response of ψ_L to Q (figure 1.1) indicates a decrease in root resistance as Q increases (Weatherley 1970, 1976; Biscoe *et al* 1976). This is supported by Stoker and Weatherley (1971) who demonstrated what when the root system of cotton was killed by immersion in hot water a type B response was converted to type A (figure 1.1).

There is still controversy about whether or not there is an appreciable resistance in the soil around the roots, i.e. a rhizosphere resistance. Several studies, both theoretical (Gardner 1960; Cowan 1965) and experimental (Gardner and Ehlig 1962 a,b; Macklon and Weatherley 1965; Tinklin and Weatherley 1968; Stoker and Weatherley 1971), have claimed significant rhizosphere resistances even when ψ_s was greater than 0.1 MPa. Since roots have been observed to shrink on dehydration, e.g. in cotton (Huck, Klepper and Taylor 1970) and wheat (Cole and Alston 1974), the resultant air gap between the soil and root may cause a high rhizosphere resistance. However, Newman (1969 a,b) critically examined much of the available evidence and concluded that there was no definite experimental evidence to prove the existence of a rhizosphere resistance until ψ_s was near or beyond the permanent wilting point ($\psi_s \approx - 1.5$ MPa). Evidence from experiments on wheat (Andrews and Newman 1969) confirmed this conclusion, since when ψ_s was - 1.5 MPa the rhizosphere resistance was less than 2% of the plant resistance. Hansen's (1974) experiments on young wheat plants also showed a negligible rhizosphere resistance until ψ_s was less than - 1.2 MPa.

Most of the studies of the component hydraulic resistances in the soil-plant system cited here were made with plants in controlled environments. Again their results may be peculiar to the imposed conditions. In the field there is still a need for further experiments designed to determine which components of the soil-plant system have the greatest influence on the response of ψ_L to the environment.

1.2.3 Changes in leaf water potential and plant water storage

The water content of plant tissues changes diurnally (Weatherley 1951; Ackley 1954; Slatyer 1967; Kozlowski 1968 a, b) and the consequent movement of water into or out of these tissues may make a significant contribution to the transpiration flow. The effect of these changes in water storage on the relation between ψ_L and Q can be demonstrated using a simple model of the soil-plant system, figure 1.2. Water storage in the system is represented by the hydraulic capacitance C and ψ_B is the effective potential of the soil. The plant extracts water from the soil at a rate U and transpires at a different rate Q. The difference (Q - U) is equal to the rate of change of stored water (Q_s). ψ_L is determined by the flow of water (U) through R, i.e.

$$\psi_L = \psi_B - UR \qquad (1.3)$$

The type of ψ_L/Q relation obtained using this model is shown in figure 1.3. When leaf water potential is decreasing, water moves out of storage (Q_{s1}) and adds to that extracted from the soil (U_1) to give the transpiration flow Q. The leaf water potential is then ψ_{L1} (figure 1.3). When leaf water potential is increasing water moves back into storage (Q_{s2}) and, therefore, at the same transpiration flow Q, the soil water extraction rate is U_2 ($> U_1$) and the leaf water potential is ψ_{L2} ($< \psi_{L1}$). Relations between ψ_L and evaporation rate similar to that shown in figure 1.3 were observed in Scots pine (Jarvis 1976) and avocado (Sterne, Kaufmann and Zentmyer 1977) trees, which may be expected to have a significant storage capacity (Jarvis 1975). Jarvis (1976) suggested that the small storage capacity of herbaceous

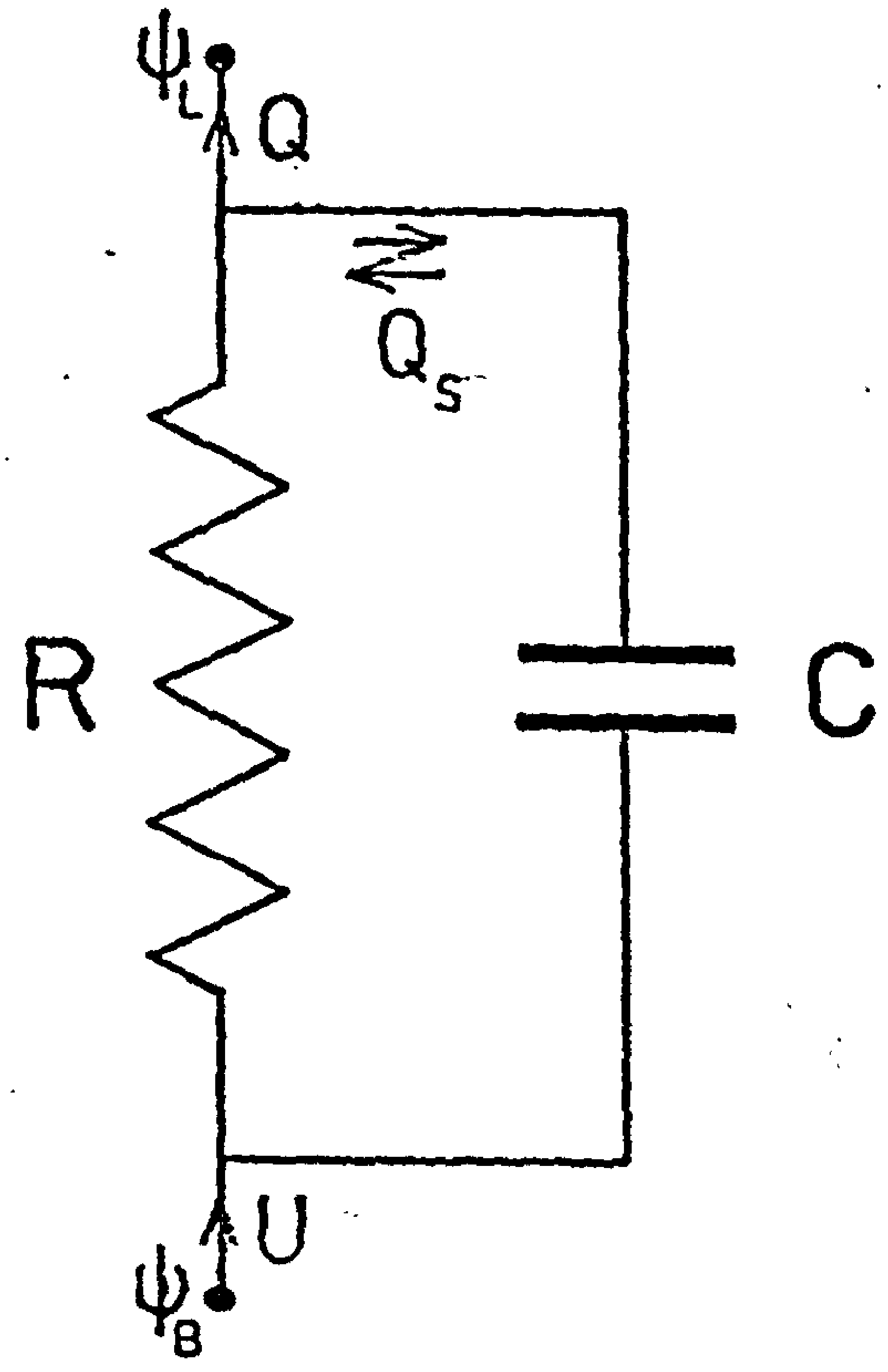


Figure 1.2 Model of flow in the soil-plant system. The symbols are explained in the text.

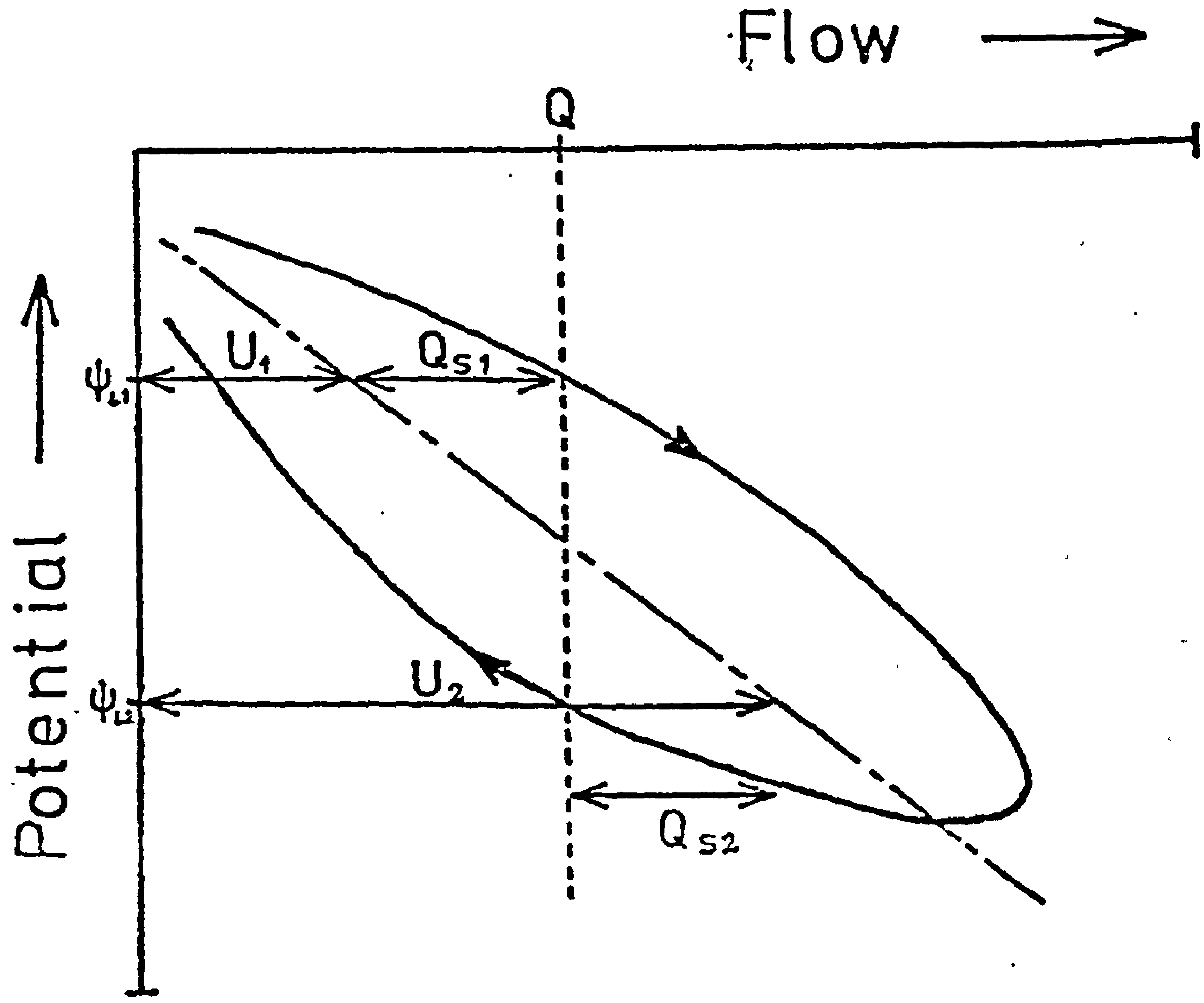


Figure 1.3 Diagrammatic representation of the relation between leaf water potential (ψ_L) and flow predicted by the soil-plant model shown in figure 1.2. The symbols are explained in the text.

plants may have a negligible effect on their ψ_L/Q relation. However, Berger (1969) observed hysteresis in the relation between ψ_L and Q in sunflower and Boyer's (1969; 1971) measurements of the rise in ψ_L when transpiration was prevented in soybean, bean and sunflower imply significant hydraulic capacitances in these herbaceous species. In wheat the existence of any significant hydraulic capacitance has still to be established.

1.3 Leaf water relations and water stress

Water stress in plants influences virtually all physiological processes (see, for example, Slavik 1965; Slatyer 1967; Kozlowski 1968 a,b; Hsiao 1973; Hsiao *et al* 1976). The many phenomena affected include, in order of their sensitivity to water stress, cell growth, stomatal opening and leaf sugar levels. Though ψ_L has been commonly used to quantify water stress, Hsiao *et al* (1976) have pointed out that it is not necessarily the best indicator to use. A greater insight may be achieved by considering the components of ψ_L (Wiebe 1972). Under isothermal conditions these are the osmotic potential (ψ_π), turgor potential (ψ_P), matric potential (ψ_M) and gravitational potential (ψ_G). The total leaf water potential (ψ_L) is the algebraic sum of these four components (Taylor and Slatyer 1961; Warren Wilson 1967a) and we write

$$\psi_L = \psi_\pi + \psi_P + \psi_M + \psi_G. \qquad (1.4)$$

Equation (1.4) can be simplified since ψ_G and ψ_M are usually small compared with ψ_L. ψ_G arises from differences in elevation and has a value of 0.01 MPa m^{-1}. In a wheat crop, which has an overall vertical dimension of about 2.5 m, this can be considered negligible. Normally the matric component (ψ_M) is also considered negligible, since data from a range of plants with different tissue types from Gardner and Ehlig (1965), Wiebe (1966) and Boyer (1967b) show that ψ_M is only a few per cent of ψ_L until severe water stress is reached. However, recent evidence from experiments with wheat by Shepherd (1975) show a mean ψ_M of - 0.3 MPa when ψ_L was - 1.7 MPa. The consequences of ignoring ψ_M in equation (1.4) are discussed in section 2.2.5.4.

Assuming ψ_L can be approximated by $\psi_\pi + \psi_p$ the relation between the three potentials in an 'ideal' leaf can be represented by a diagram similar to figure 1.4 (after Höfler 1920; see also, Warren Wilson 1967 c; Barrs 1968). When ψ_L is zero ψ_p has its maximum value ($= - \psi_\pi$), this is often referred to as full turgor. As ψ_L decreases so does the leaf water content and therefore ψ_π also decreases due to solute concentration. The more rapid decline in ψ_L compared with ψ_π reduces ψ_p, until it becomes zero when $\psi_L = \psi_\pi$. Gardner and Ehlig (1965) and Weatherley (1965) confirmed experimentally that ψ_L, ψ_π and ψ_P were related according to Höfler's predictions.

ψ_P may be a better indicator of water stress than ψ_L, especially for turgor dependent processes such as growth and stomatal function (Meidner and Mansfield 1968; Hsiao *et al* 1976). For example, in a review of stomatal responses in field crops Turner (1974b) showed that stomatal conductance in several species was reduced during water stress. The 'critical' value of ψ_L below which stomatal conductance was reduced varied between species, from - 0.8 MPa in bean to - 2.7 MPa in cotton. However, the corresponding critical values of ψ_P were in a much smaller range, zero to 0.2 MPa. Furthermore, Millar and Denmead (1976) found that the critical

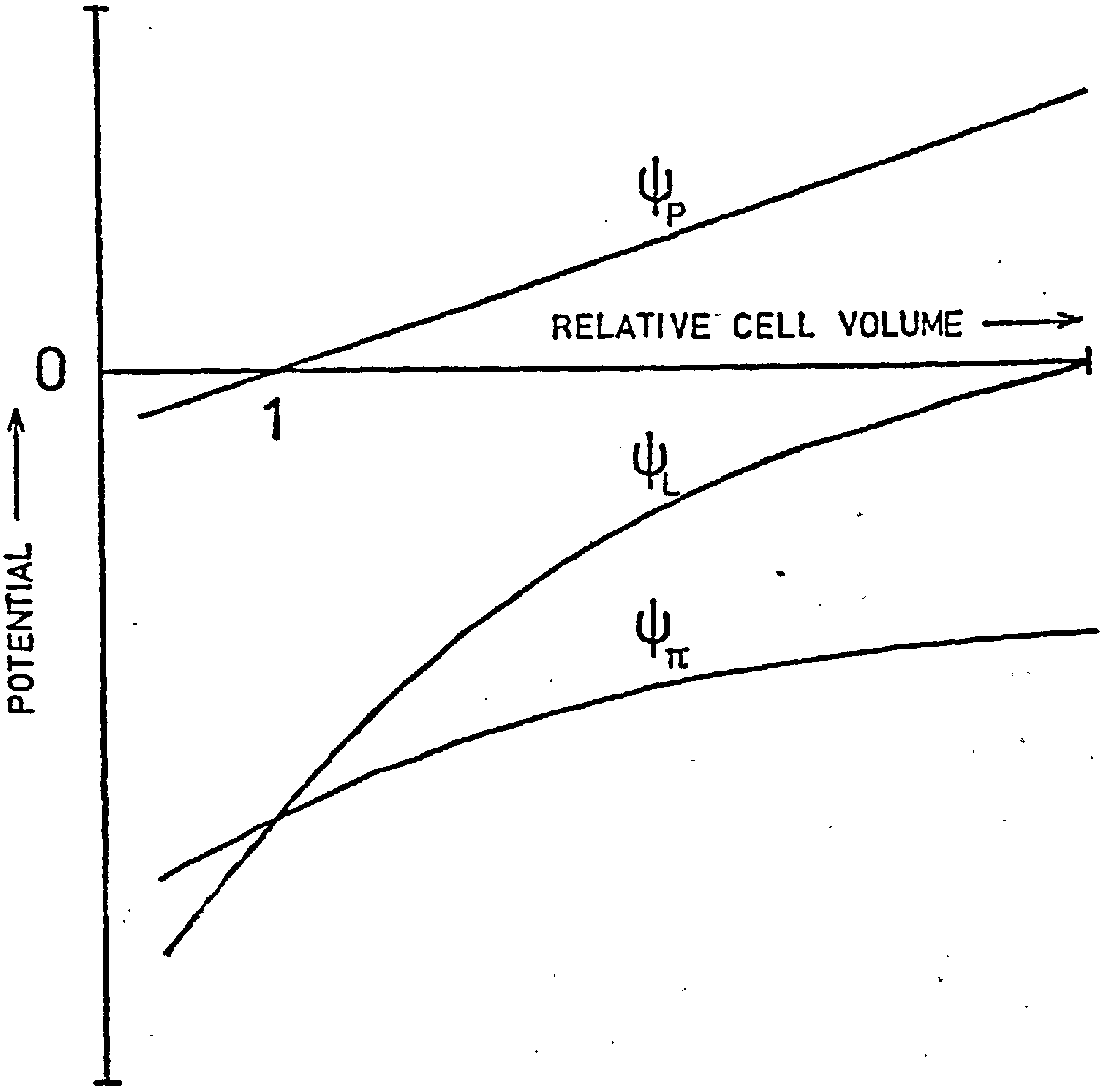


Figure 1.4 The relation between water potential (ψ_L), osmotic potential (ψ_π) and turgor potential (ψ_p) in an ideal leaf (after Höfler 1920).

value of ψ_P in wheat leaves was the same at all positions on the stem (0.8 MPa), whereas ψ_L ranged from - 0.7 to - 1.9 MPa.

During periods of water stress ψ_P may be kept above the critical value by lowering ψ_π, which can occur in two ways. One, by leaf dehydration, i.e. concentration of existing solutes due to the reduction in leaf water content associated with a decrease in ψ_L (figure 1.4). Two, by osmotic adjustment, i.e. an increase in the solute content of the leaf. In practice both mechanisms appear to operate. For example, in a controlled environment study of the leaf water relations of cotton, sunflower, trefoil and pepper Gardner and Ehlig (1965) found that as ψ_L decreased so did ψ_π. The reduction in ψ_π was attributed to leaf dehydration. Conversely, the diurnal and seasonal changes in ψ_π in maize and sorghum crops (Hsiao *et al* 1976) could not be fully accounted for in this way. Osmotic adjustment was said to have occurred in these species.

To further understand plant responses to water stress,more information is needed about the levels of ψ_P below which stomatal conductance is reduced,and how the plants adjust to maintain these during water stress; particularly in plants growing in their natural environment.

1.4 Aims of this study

The present study of a wheat crop was formulated with the following objectives in two main areas:-

(1) Water transport

a. To investigate the factors which affect ψ_L.

b. To evaluate the hydraulic properties (R and C) of the soil-plant system.

c. To locate the major components of R and C.

(2) Leaf water relations

a. To investigate the factors which affect the balance between ψ_L, ψ_π and ψ_P.

b. To examine the influence of ψ_P on stomatal conductance.

1974 and 1975, in which measurements were made, provided a particularly fortunate contrast between seasons of normal and exceptionally low rainfall. This gave an opportunity of measurements under a very wide range of soil moisture conditions.

2. INSTRUMENTATION

2.1 The pressure chamber

2.1.1 Introduction

The pressure chamber technique has been widely used for the estimation of plant water potential, for example by Scholander *et al* (1965); Boyer (1967a); Waring and Cleary (1967); Kaufmann (1968 a, b); Klepper (1968); De Roo (1969a, 1970); Klepper and Ceccato (1969); Barrs *et al* (1970); Begg and Turner (1970); Duniway (1971); Turner, De Roo and Wright (1971); Tormann (1972); Frank and Harris (1973); Campbell and Campbell (1974); Meiri, Plaut and Shimshi (1975); Gandar and Tanner (1975); Baughn and Tanner (1976a); Roberts (1977); Stern, Kaufmann and Zentmyer (1977); Jones and Turner (1978). Although Dixon (1914) was first to describe a pressure chamber for subjecting plant organs to high pressures, it was the innovation of Scholander *et al* (1965) to apply the technique to estimating plant water potential. They showed that when a leaf is cut from a plant and quickly sealed into a pressure chamber, with the cut end open to the atmosphere, the xylem sap returns to the cut end when the pressure applied to the leaf (P) is equal to the negative hydrostatic pressure in the vessels connected with the leaf cells. The xylem water potential (ψ_X) is related to P by

$$\psi_X = -P + \psi_{\pi X}, \qquad (2.1)$$

where $\psi_{\pi X}$ is the osmotic potential of the xylem sap (see, for example, Ritchie and Hinckley1975). Assuming that ψ_X is a measure of the leaf water potential (ψ_L) at the point at which the leaf is is cut, then for accurate determinations of ψ_L the osmotic potential of the xylem sap must be known (equation (2.1)). However, $\psi_{\pi x}$ was found to be greater than - 0.1 MPa in a range of plant species (Scholander *et al* 1964; Klepper and Kaufmann 1966; Boyer 1967a; De Roo 1969a, b; Duniway 1971; Baughn and Tanner 1976a), so that measurements of P alone suffice as estimates of ψ_L in many circumstances. Comparison of pressure chamber estimates of ψ_L with those of other methods are discussed in section 2.1.4.

2.1.2 Design

A pressure chamber was designed and constructed specifically for rapid measurements of the water potential of wheat leaves in the field. Similar to the designs of Powell (pers. comm.) and Jarvis (pers. comm.) the chamber had four clamps securing the top, facilitating rapid sample loading and unloading. The design is shown in figure 2.1. The top had a tapered recess into which a split rubber bung containing an excised leaf could be inserted. The gas inlet and outlet at the base of the chamber were positioned so that the dry gas entering the system could be bubbled through water. This humidified the gas, minimizing transpiration from the leaf whilst it was inside the chamber. A small baffle in the bottom of the chamber prevented the leaf from being splashed with drops of water as the gas was bubbled in. To withstand the high pressures involved in measuring ψ_L the chamber was constructed from stainless steel and tested to a pressure of 6 MPa.

A diagram and photograph of the pressure chamber and fittings are shown in figure 2.2 and plate2.1 respectively. The pressurizing

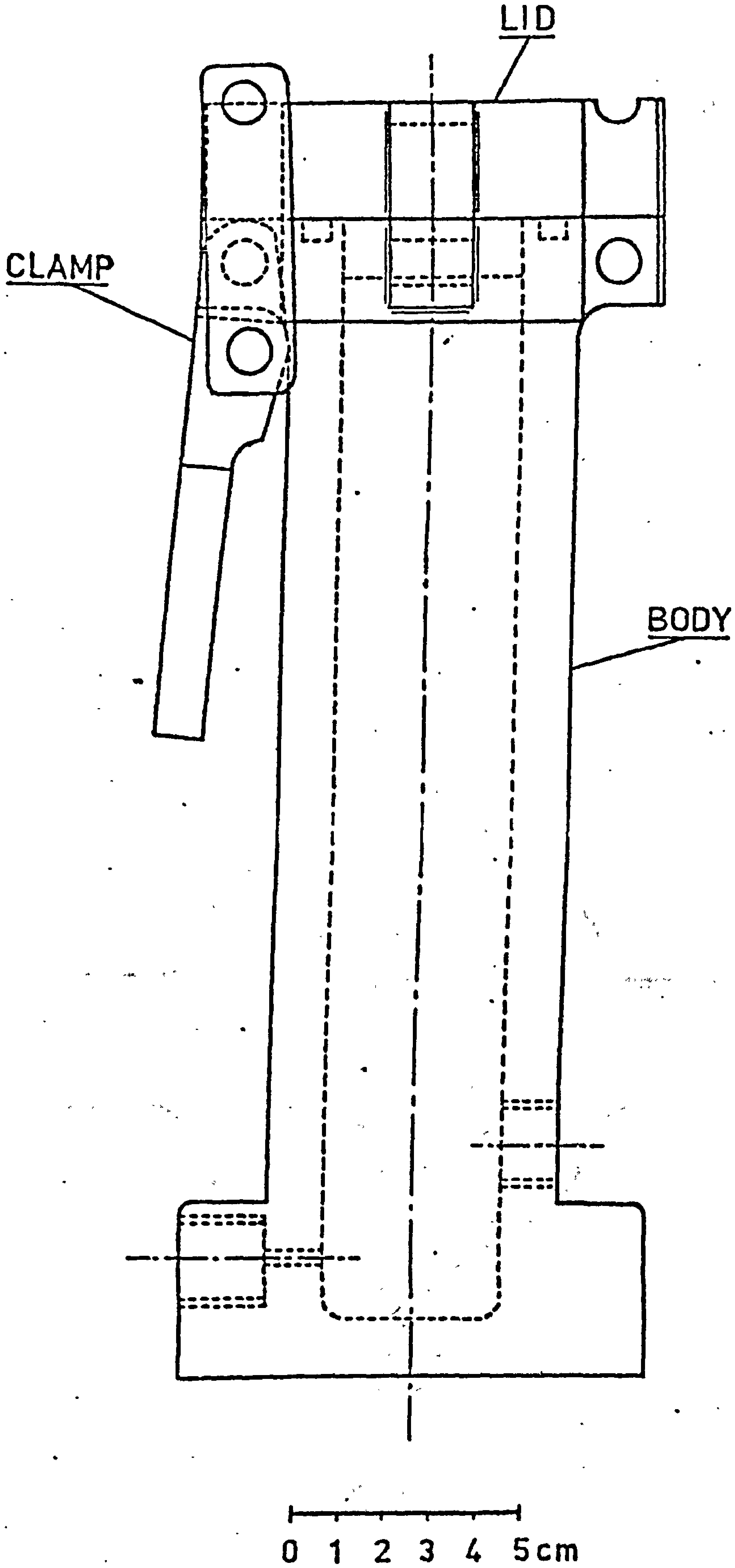
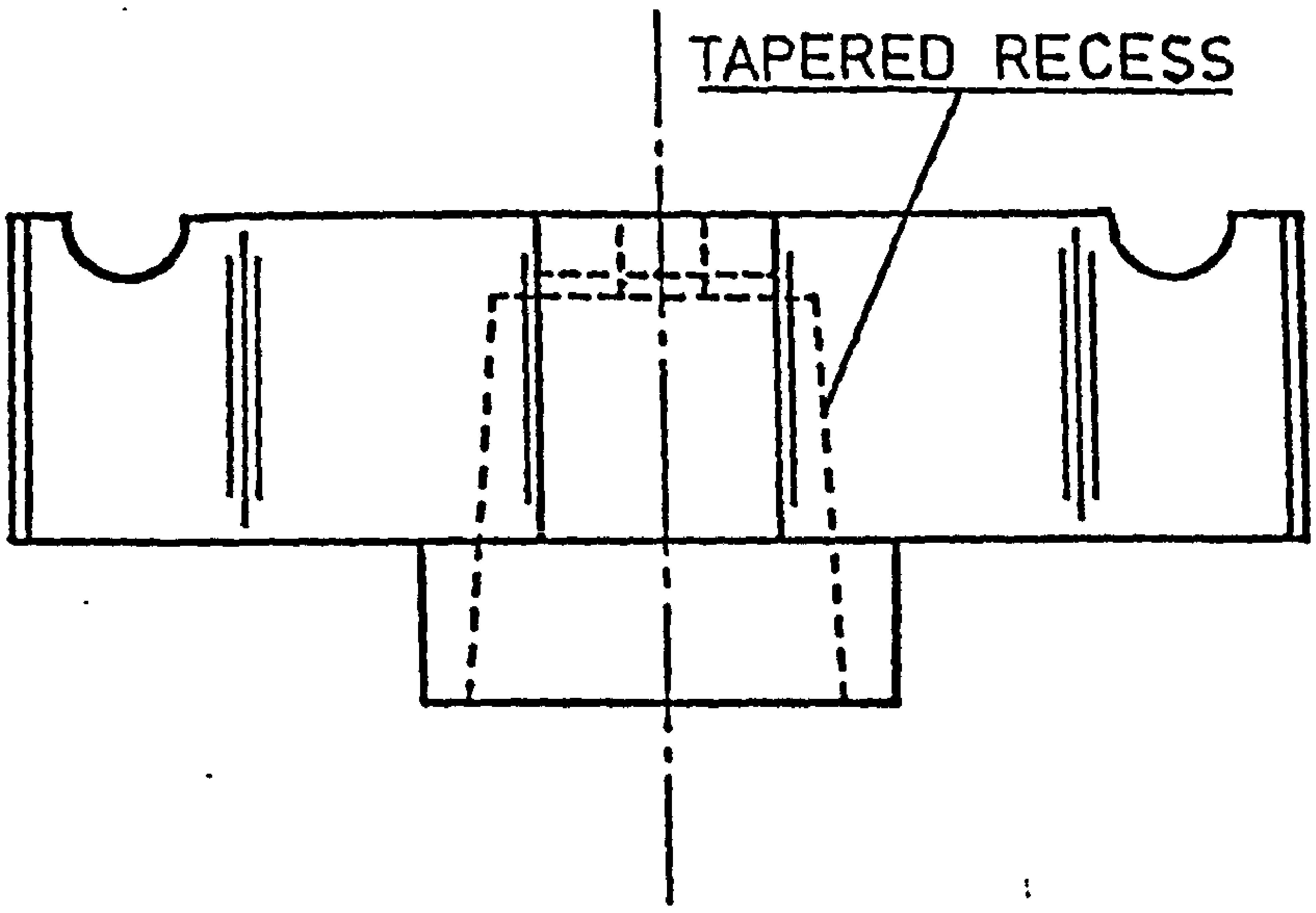
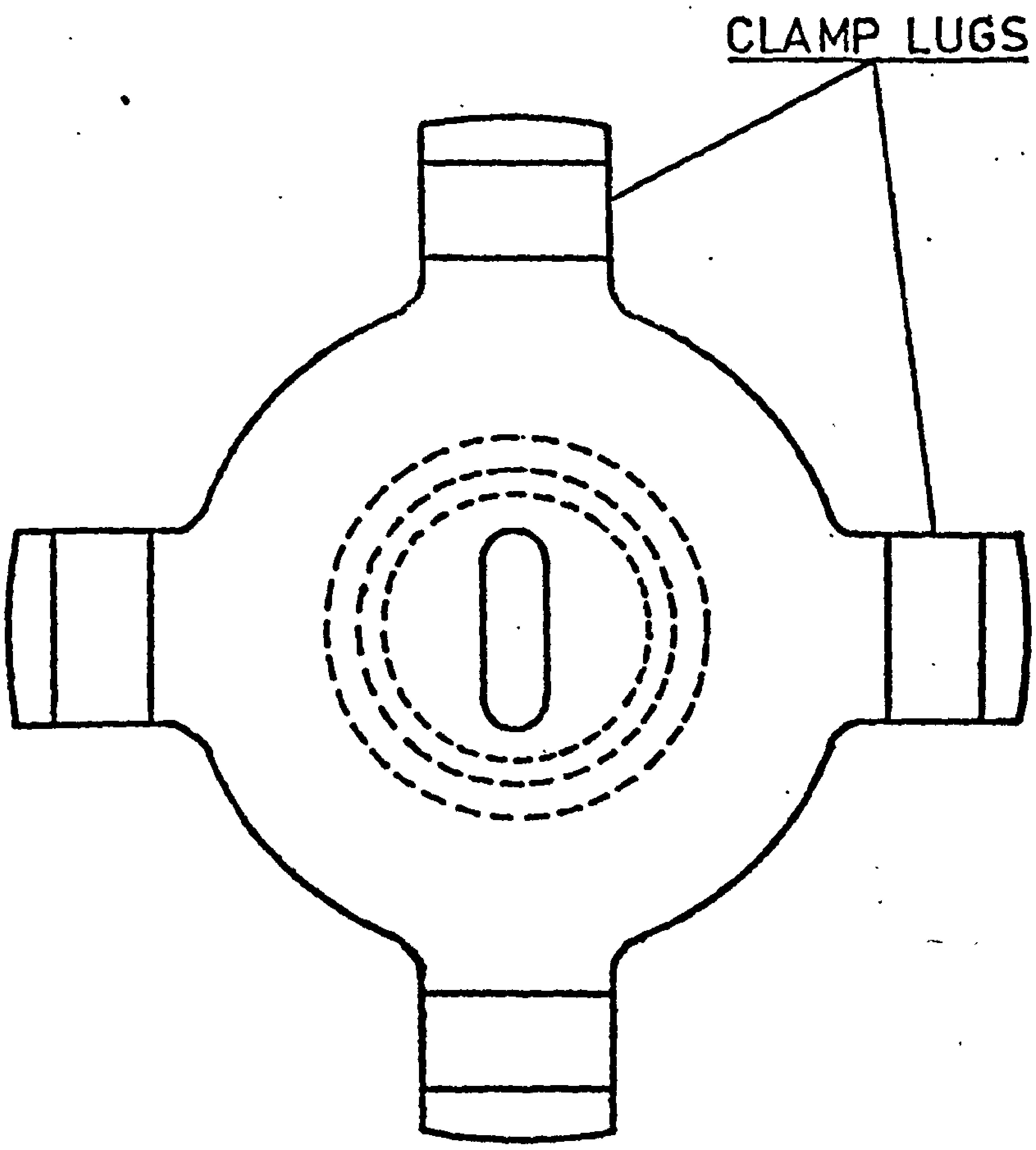


Figure 2.1(a) Scale drawing of the pressure chamber. For clarity only one clamp is shown securing the lid.



ELEVATION



PLAN

Figure 2.1(b) Full size drawing of the pressure chamber lid showing the tapered recess for the rubber bung and the four lugs for the clamps.

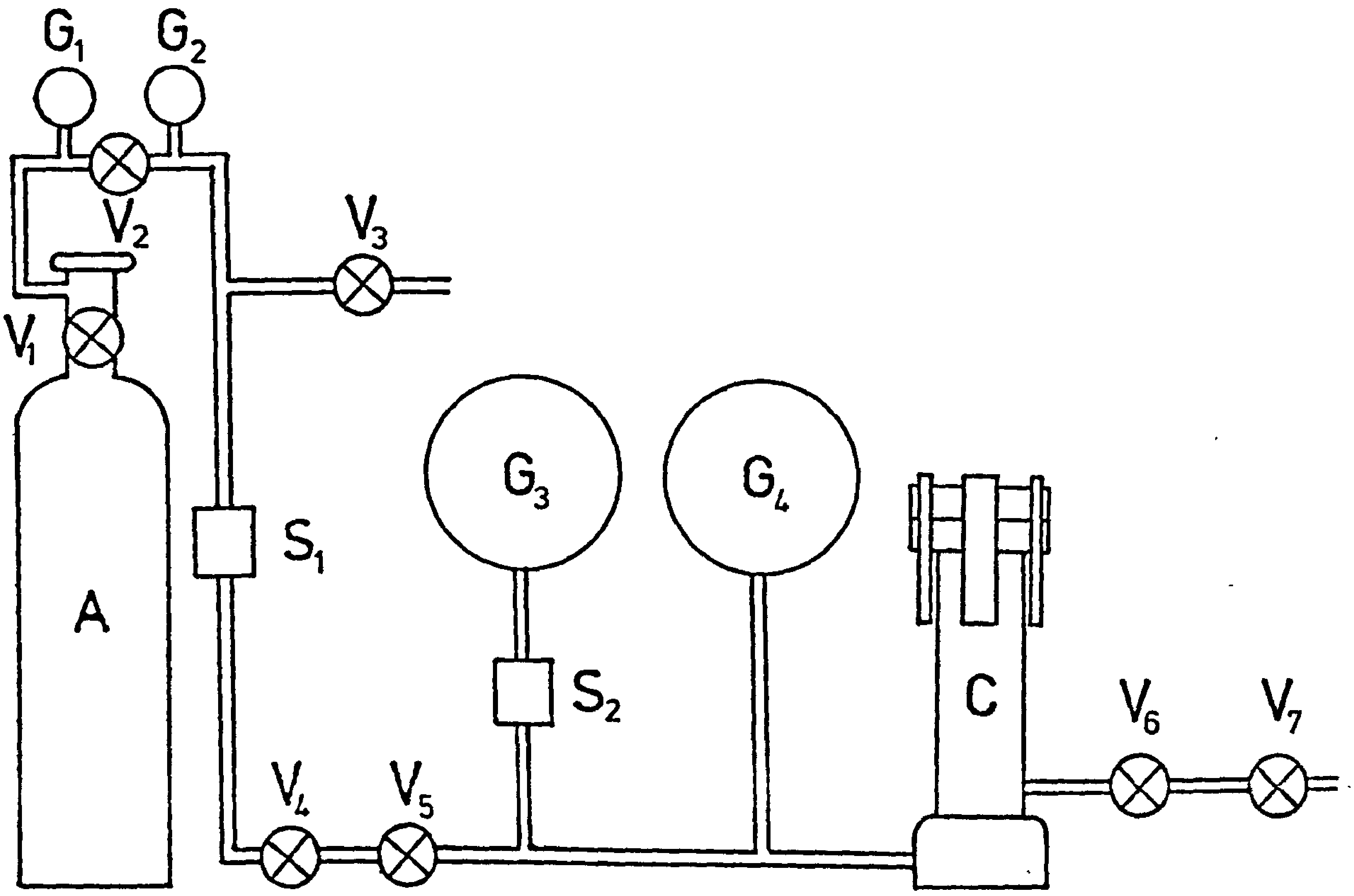


Figure 2.2 Diagram of the pressure chamber (C) and fittings. Nitrogen cylinder (A); cylinder valve (V_1); cylinder pressure gauge (G_1); pressure reducing valve (V_2); reduced pressure gauge (G_2); override outlet valve (V_3); inlet safety valve (S_1); inlet regulating valve (V_4); 'on/off' valve (V_5); gauge protection valve (S_2); zero to 2.5 MPa gauge (G_3); zero to 6 MPa gauge (G_4) outlet regulating valve (V_6); outlet 'on/off' valve (V_7).

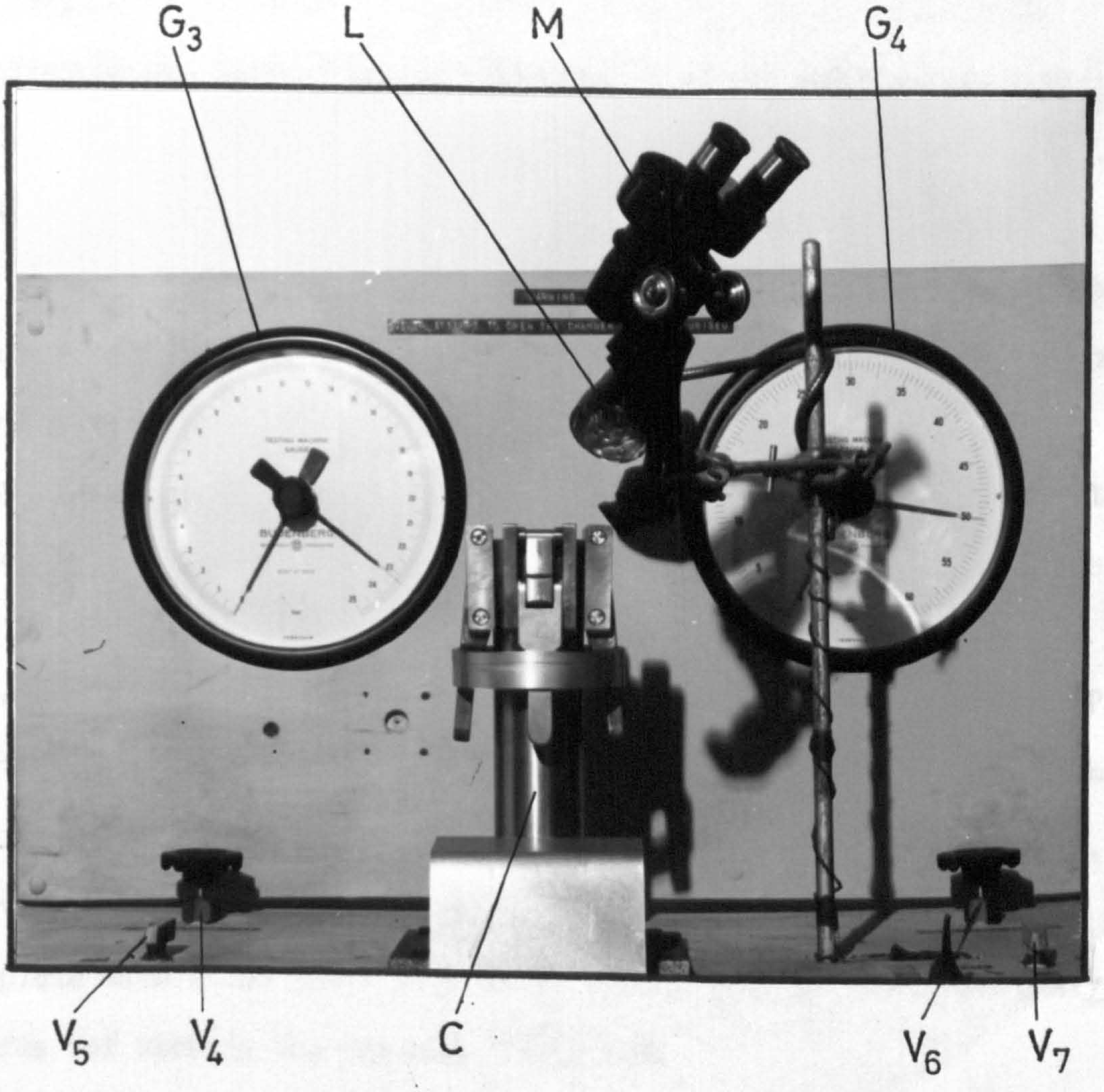


Plate 2.1 The pressure chamber (C) and fittings. Pressure gauges G_3 and G_4; inlet valves V_4 and V_5; outlet valves V_6 and V_7; microscope M and lamp L. The valve and gauge numbers correspond to those in figure 2.2.

gas used in the system was nitrogen, supplied from a cylinder, (A, figure 2.2). With the cylinder valve (V_1) open the pressure applied to the rest of the system, monitored on gauge G_2, was set by the pressure reducing value V_2. The gauge G_1 indicated the pressure inside the nitrogen cylinder. Gas entered the pressure chamber (C) at a controlled rate via the inlet regulating valve (V_4) and the 'on/off' valve V_5. The pressure inside the chamber was displayed on two gauges G_3 and G_4 with ranges of 0 to 2.5 MPa and 0 to 6 MPa respectively. The system could also be depressurized at a controlled rate, via outlet valves V_6 and V_7. For safety the maximum pressure in the system was limited to 4 MPa by the safety valve S_1 on the inlet. The gauge G_3 was protected from pressures greater than 2 MPa by the safety valve S_2. The chamber and fittings were tested to the maximum pressure obtainable in the system, i.e. 4 MPa. The chamber, valves and gauges were all mounted securely on a table (plate 2.1) complete with a low power microscope (magnification x 40) and a light source for viewing the cut end of the leaf.

2.1.3 Method of operation

The excised leaf was placed in a split rubber bung with about 10 mm of leaf protruding at the cut end. The bung was greased with 'vaseline' and pushed into the tapered recess in the chamber lid, which was then clamped onto the body of the chamber. The four securing clamps were closed and a safety ring slid over them to prevent opening of the chamber whilst pressurized. The pressure inside the chamber was increased steadily at a rate of about 0.02 MPa s^{-1}. Higher rates, up to 0.1 MPa s^{-1}, were used to within 0.5 MPa of the balancing pressure in leaves with low ψ_L. Similar pressurizing rates were used by Waring and Cleary (1967), Kaufmann (1968a, b), Jordan (1970), West and Gaff (1971), Haas and Dodd (1972), and Campbell and Pase (1972) without incurring any systematic error in the estimate of ψ_L. As the pressure inside the chamber increased the cut end of the leaf was carefully observed through the microscope and when the xylem sap appeared at the cut surface the pressure in the chamber was noted. The system was then depressurized and the leaf removed from the chamber ready for the next measurement.

2.1.4 Evaluation of the technique

2.1.4.1 Calibration

To assess the reliability of the pressure chamber technique many studies have compared leaf water potential estimates obtained using a pressure chamber with those obtained using a thermocouple psychrometer (see Ritchie and Hinckley 1975). Turner *et al* (1971) discussed the comparisons obtained from six tree species and five herbaceous species and concluded that "if the psychrometer is accepted as the standard, the estimates of leaf water potential obtained with the pressure chamber are clearly accurate enough for many purposes, but sufficient variability has been uncovered to warrant calibration of the instrument before absolute measurements of leaf water potential are undertaken on a new species."

In the present study attempts were made to calibrate the pressure chamber against a dew point hygrometer (see section 2.2) by using the two instruments to estimate the water potential of the same wheat leaves. There was very poor agreement between the leaf water potential estimates by the two techniques. This was due mainly to difficulties in making measurements of ψ_L with the dewpoint hygrometer, discussed in section 2.2.5. However, Kriuijshoop (pers. comm.) has recently compared the pressure chamber estimates of ψ_L made in the field on wheat with those of an *in situ* leaf hygrometer (the Wescor L51-A). His results are shown in figure 2.3. On average the pressure chamber estimate of ψ_L was 0.3 MPa higher than that of the leaf hygrometer. West and Gaff (1971) also found that the pressure chamber overestimated ψ_L in apple, by an amount similar to that found here. They suggested that the osmotic potential of the xylem sap accounted for much of the displacement of the data from the equipotential relation (the 1:1 line in figure 2.3). This is in agreement with Boyer's (1967a) expression relating ψ_L, P and $\psi_{\pi X}$ (equation (2.1)), but contrary to most other calibrations reported in the literature (see Turner *et al* 1971; Ritchie and Hinckley 1975), which found that the pressure chamber underestimated ψ_L. In wheat, Frank and Harris (1973) obtained different linear relations between pressure chamber and psychrometer estimates of ψ_L at two growth stages (late tillering and heading). However, Miller (1974) has shown that the equilibration time used by Frank and Harris in their psychrometric determination of ψ_L (6h) was too short (see also section 2.2.5). Their results therefore need to be viewed with caution. Similarly the poor agreement between psychrometric and pressure chamber estimates of ψ_L in the present study may have been due to systematic errors in the psychrometric estimate of ψ_L. Hence the proviso that the psychrometer be accepted as the standard (Turner *et al* 1971) may not have been acceptable in the present study and that of Frank and Harris (1973). Where reliable psychrometric technique has been used, for example by Campbell and Campbell (1974), the calibrations obtained imply that the pressure chamber can be used to estimate wheat leaf water potential

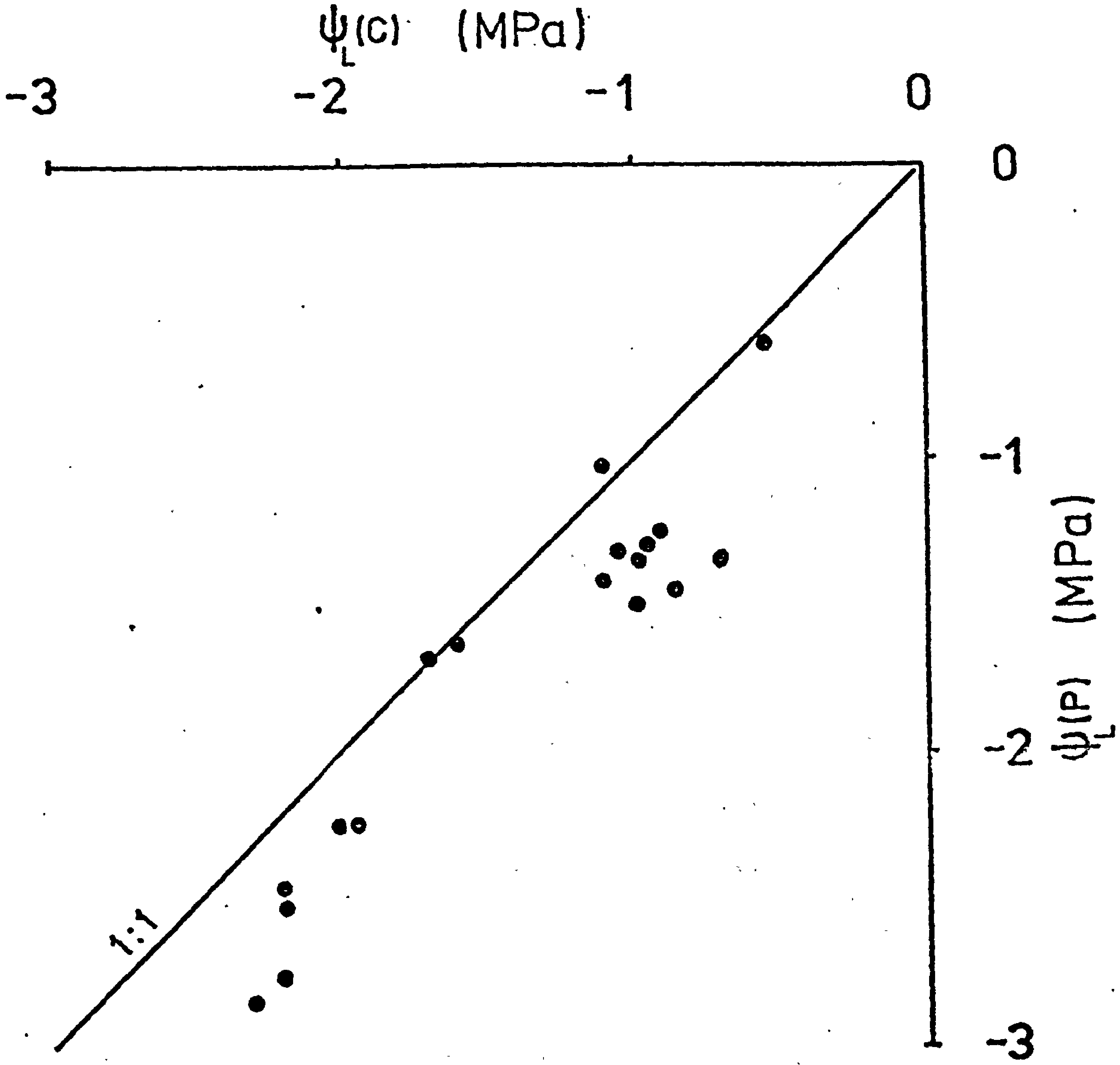


Figure 2.3 Concurrent estimates of leaf water potential with a pressure chamber, ψ_L(C), and psychrometer, ψ_L(P). The 1:1 line is shown for comparison. Data provided by Kriuijshoop (pers. comm.).

water potential to an accuracy of about 0.1 MPa.

2.1.4.2 Errors in the estimates of leaf water potential

There are a number of possible sources of systematic error in estimating ψ_L with a pressure chamber (see Ritchie and Hinckley 1975). These include loss of water from the leaf during the time between excision and measurement of ψ_L and the amount of leaf outside the chamber. The post-excision evaporation effect should be greatest when ψ_L is close to zero. To test this a number of leaves were covered to prevent them transpiring (see section 3.3.3.1) and then cut close to the stem under water. Following Boyer (1969) they were left to equilibrate for one hour with their cut ends immersed in water. ψ_L was then measured at a number of times after insertion into the pressure chamber. ψ_L decreased as the length of time inside the chamber increased, giving a change in ψ_L of 0.1 MPa in 20 minutes. Although this is insignificant in view of the normal measurement time (i.e. less than 2 minutes), a much faster drop in ψ_L occurred when leaves were exposed to the enivronment outside the pressure chamber. For example, under conditions of high evaporative demand ψ_L decreased at an initial rate of 0.1 MPa min^{-1}, similar to that in cotton leaves (Jordan 1970), indicating that leaves should be covered and transferred rapidly to the pressure chamber for accurate estimates of ψ_L.

The length of leaf outside the pressure chamber may also cause errors in the estimation of ψ_L (Waring and Cleary 1967; Boyer 1967b; Kaufmann 1968b). In wheat leaves, with 10 mm excluded from the chamber, Millar and Hansen (1975) found that when ψ_L was - 1.0 MPa the pressure chamber estimate was - 1.1 MPa. Conversely, in a comprehensive study of the water relations of field grown wheat Campbell (pers. comm.) did not find any such effect.

In the field, there is also a degree of uncertainty associated with the hourly mean value of ψ_L which is calculated from a number of measurements made within an hour. This is because ψ_L usually changes continuously with time and also varies spatially within the sampling area. A typical example is shown in figure 2.4, where the hourly mean values of ψ_L and their standard errors were calculated from three measurements made during each hour throughout a day. Generally the standard error increased as ψ_L decreased, ranging from 0.02 MPa when ψ_L was - 0.1 MPa to 0.16 MPa when ψ_L was - 1.4 MPa. The measurement of ψ_L three times per hour was therefore sufficient to give a good indication of the hourly changes in ψ_L during the day.

2.2 The dew point hygrometer

2.2.1 Introduction

The dew point technique was introduced recently by Neumann and Thurtell (1972) for the measurement of water potential. The principle is to measure the dew point depression of the air in equilibrium with the sample, from which its water potential can be inferred (equation(2.12)). An improved dew point hygrometer (Campbell, Campbell and Barlow 1973) was based on maintaining a thermocouple at the dew point temperature. This was done by balancing the sensible heat gain of a wet thermocouple using electrically adjusted Peltier cooling, thereby allowing it to converge on the dew point.

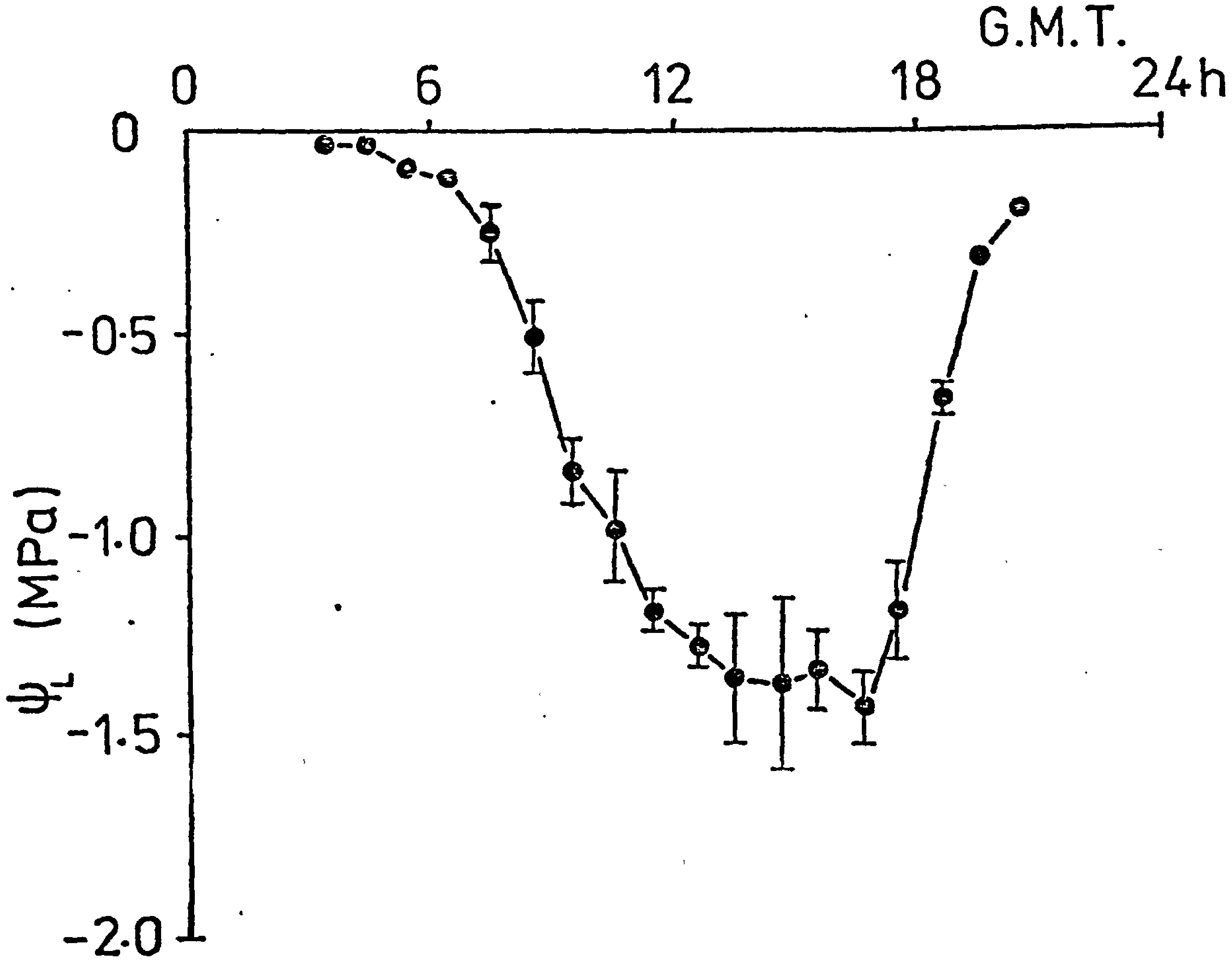


Figure 2.4 Typical changes in the hourly mean leaf water potential (ψ_L) and its standard error, 20 June 1974.

2.2.2 Theory

Theoretical aspects of the design and operation of the dew point hygrometer have already been considered (Campbell *et al* 1973; Wescor 1973). However, there is still a need for a complete description of the thermodynamics involved in the derivation of the relation between the water potential of a sample and the dew point depression of the air in equilibrium with it.

When the chemical potential (μ) of water is lowered (e.g. by the addition of a solute) then the partial pressure (e) of the vapour in equilibrium with it is also lowered. The difference from the chemical potential of pure free water (μ_o) at the same temperature (T) can be expressed in the form

$$(\mu - \mu_o) = RT \ln(e/e_o), \qquad (2.2)$$

after Slatyer (1967), where e_o is the partial pressure of the vapour in equilibrium with pure free water at a temperature T and R is the universal gas constant. The water potential (ψ) of a system whose chemical potential is μ is defined as

$$\psi = (\mu - \mu_o)/\bar{v}, \qquad (2.3)$$

where $\bar{v}$ is the partial molal volume of water. Combining equations (2.2) and (2.3) are rearranging gives

$$\ln (e/e_o) = \bar{v}\,\psi/RT \qquad (2.4)$$

Taking exponentials and rearranging equation (2.4) gives the difference in the partial pressures e_o and e as

$$(e_o - e) = e_o\{1 - \exp(\bar{v}\,\psi/RT)\} \tag{2.5}$$

Over small intervals the slope of the curve relating the saturated vapour pressure and temperature of an aqueous system (see figure 2.5) is

$$de_o/dT \simeq (e_o - e)/\Delta T, \tag{2.6}$$

where ΔT is the dew point depression of the vapour in equilibrium with the system. The Clausius-Clapeyron equation gives another expression for de_o/dT, viz:-

$$de_o/dT = \lambda T\Delta v, \tag{2.7}$$

where λ is the latent heat of vapourization of water and Δv is the change in volume per mole of water on vapourization. Since the volume of water in the gaseous phase (v) is very much greater than that in the liquid phase, then

$$\Delta v \approx v. \tag{2.8}$$

Using the ideal gas law, for one mole of water vapour

$$v = RT/e_o \tag{2.9}$$

Substituting equations (2.8) and (2.9) into equation (2.7) gives

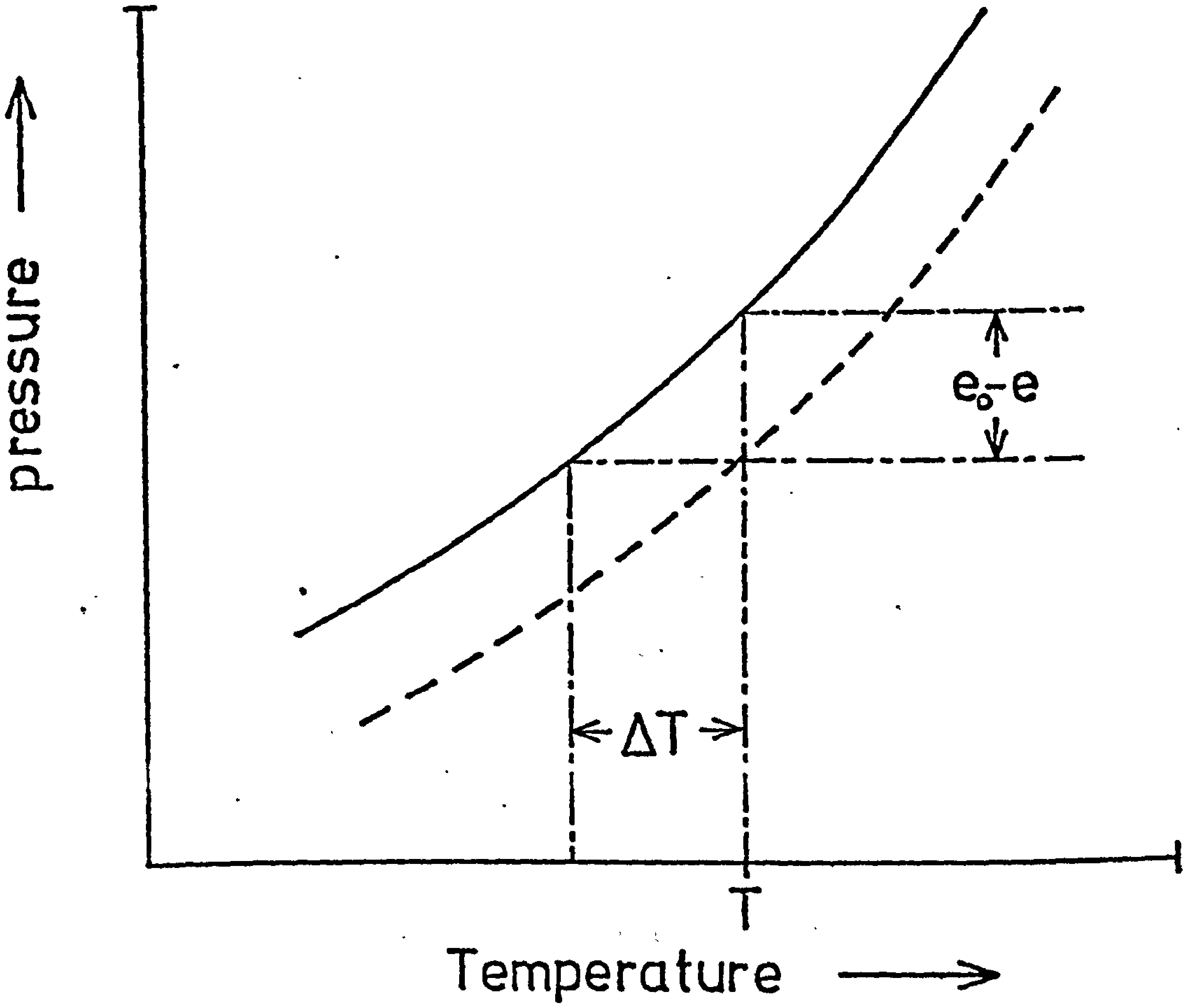


Figure 2.5 Diagrammatic representation of vapourization curves for pure water (——) and a dilute aqueous solution (- - -).

$$de_o/dT = \lambda e_o/RT^2. \qquad (2.10)$$

Comparing equations (2.10) and (2.6) ΔT can be written as

$$\Delta T = (e_o - e)\, RT^2/e_o\lambda. \qquad (2.11)$$

Then substituting for $(e_o - e)$ from equation (2.5) gives

$$\Delta T = (RT^2/\lambda)\,\{1 - \exp(\bar{v}\psi/RT)\} \qquad (2.12)$$

Equation (2.12) relates the water potential of an aqueous system to the dew point depression of the vapour in equilibrium with it. ΔT is measured using a thermocouple and given that its sensitivity is α, then the output voltage (V) is given by

$$V = (\alpha RT^2/\lambda)\,\{1 - \exp(\bar{v}\psi/RT)\} \qquad (2.13)$$

Equation (2.13) is the desired relation between V and ψ. At high values of water potential the exponential term in equation (2.13) can be approximated by the first two terms of a series expansion, so that V can be written as a linear function of ψ, viz:-

$$V = -(\alpha\bar{v}T/\lambda)\psi \qquad (2.14)$$

For the constantan-chromel thermocouple used in the Wescor dew point hygrometers α is 63 $\mu V\ K^{-1}$, and $\lambda/\bar{v}$ is 2,450 MPa, so that when $T = 293$ K

$$V = -7.5\ \psi, \qquad (2.15)$$

where V is in μV and ψ has units of MPa. The form of equations (2.13) and (2.15) are shown in figure 2.6 for a range of water potentials from zero to - 5 MPa at a temperature of 20°C. For most of this range the two curves are sufficiently close to allow the simpler linear function (equation (2.15)) to be used for calculating values of water potential from the hygrometer output. The theoretical linear relation (equation (2.15)) is also very similar to the measured calibration curve (equation (2.16) in section 2.2.5.3).

2.2.3 Description of equipment

A Wescor HR-33 microvoltmeter and three C.51 sample chambers were purchased and used mainly to determine the osmotic potential of sap extracted from wheat leaves taken from the field. The C-51 sample chambers (plate 2.2; figure 2.7) each contained a constantan-chromel thermocouple for use as a dew point hygrometer and a copper-constantan thermocouple, located in the upper heat sink, to monitor the temperature of the sample chamber. Metal sample holders with cylindrical recesses fitted into a slide on the chamber, for insertion into position directly below the hygrometer thermocouple (figure 2.7). The sample holders used had two recess sizes, 'shallow' (1 mm deep x 7 mm diameter) and 'medium' (3 mm deep x 7 mm diameter) suitable for solutions on filter paper and leaf disks respectively.

The HR-33 microvoltmeter (plate 2.2) was used to monitor the voltage output (0 to 35 μV) from the hygrometer thermocouples in the sample chambers. It also contained the electronic circuitry required to balance the sensible heat fluxes to these thermocouples during a measurement of dew point depression. The microvoltmeter function switch allowed the hygrometer thermocouples to be cooled

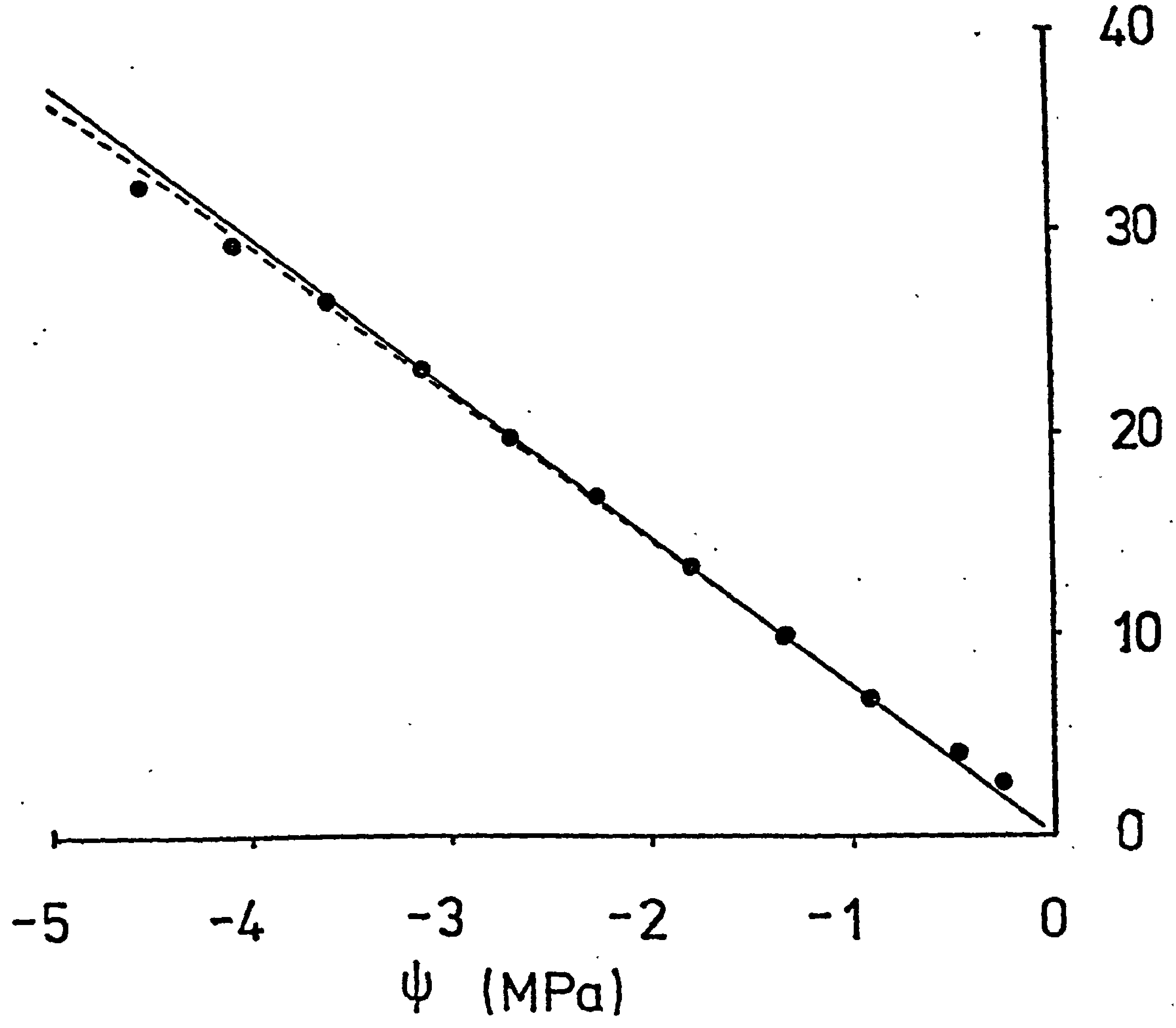


Figure 2.6 The relation between dew point hygrometer output (V) and water potential (ψ) of sodium chloride solutions (●). The theoretical relations, straight line ——— , equation (2.15) and exponential ----, equation (2.13), are also shown.

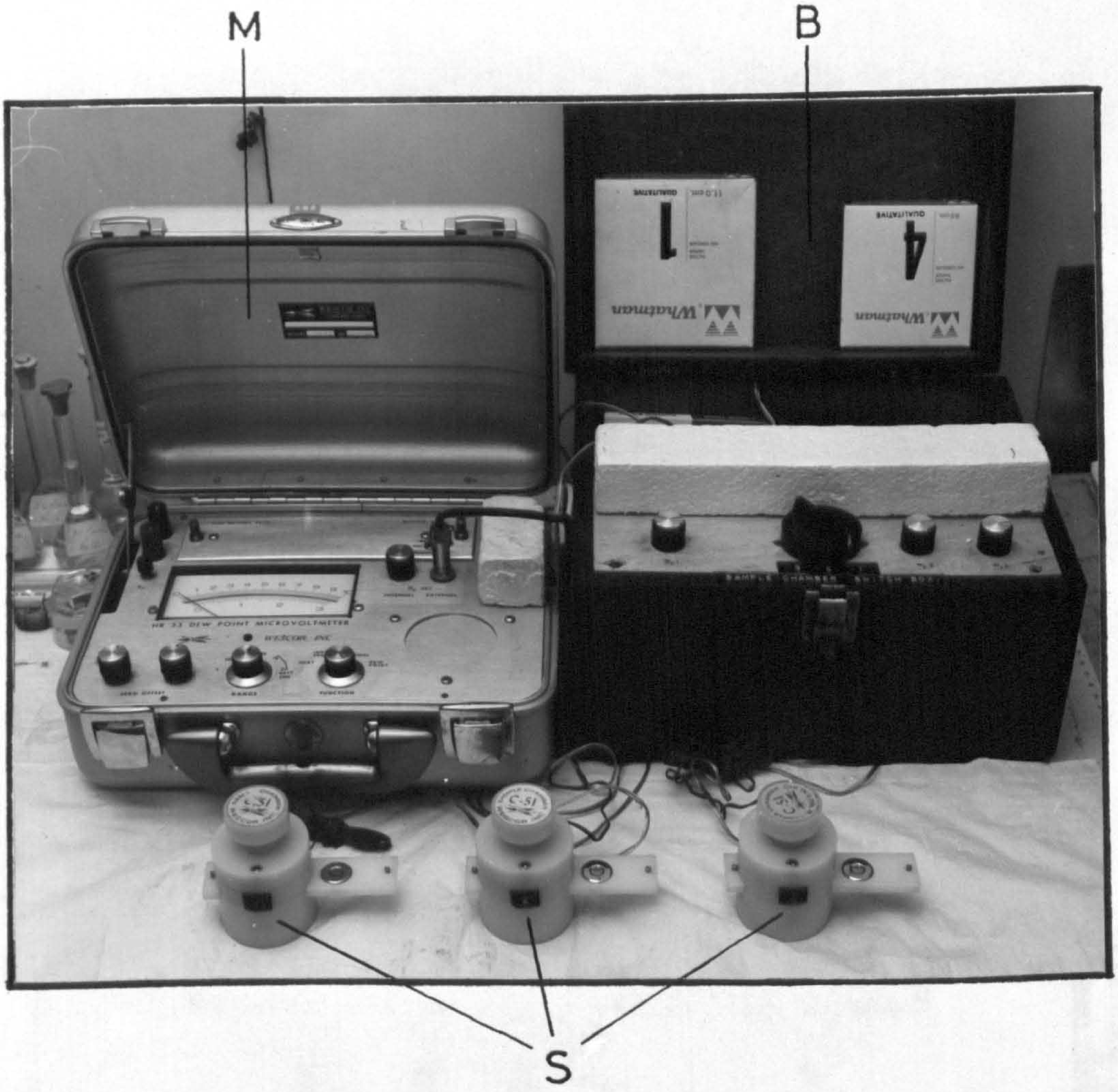


Plate 2.2 Dew point microvoltmeter (M), sample chambers (S) and sample chamber switch-box (B).

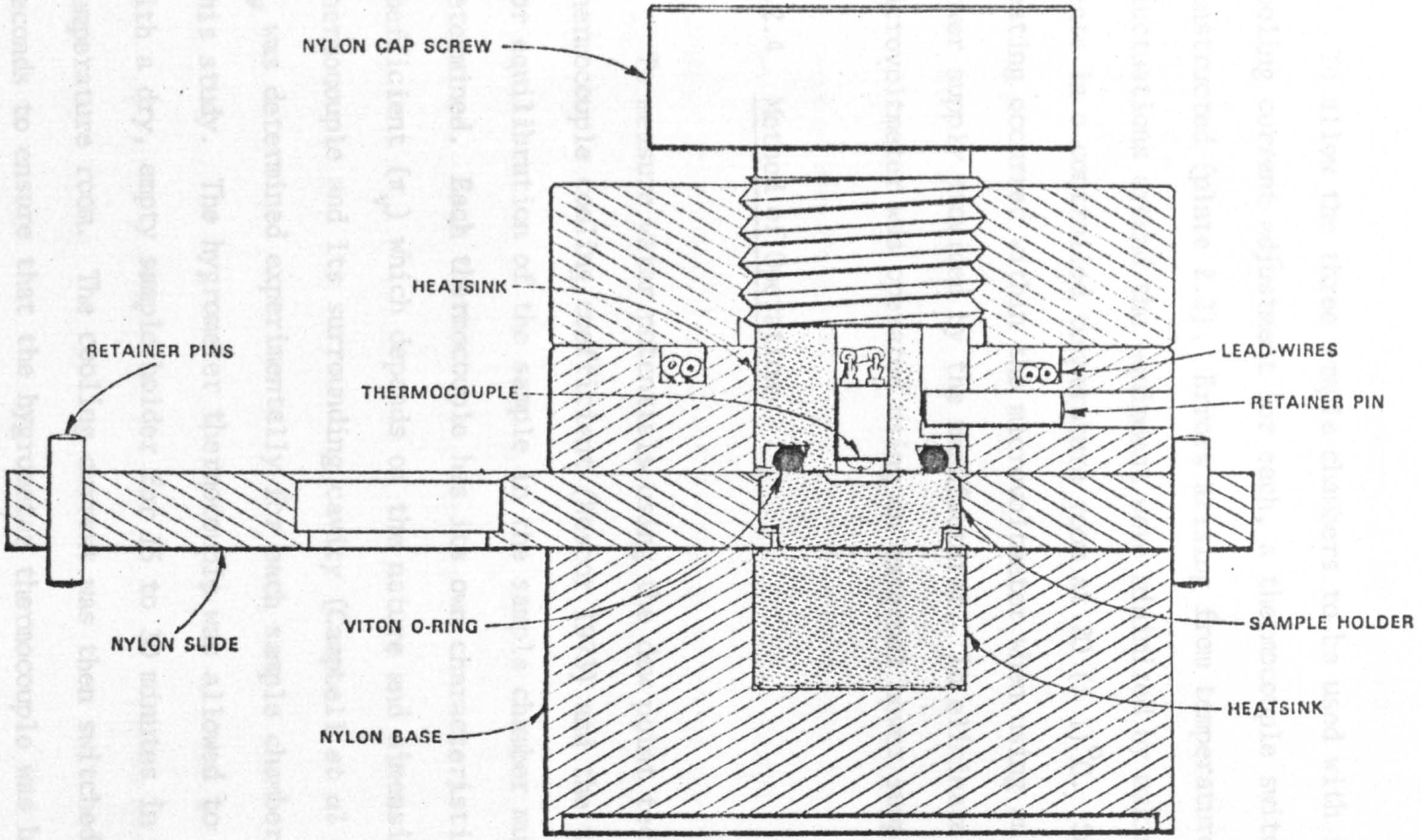


Figure 2.7 Cross-section of the hygrometer sample chamber. (Reproduced from the Wescor C-51 instruction manual).

(or heated) and their temperature depression below ambient temperature measured.

To allow the three sample chambers to be used with independent cooling current adjustment for each, a thermocouple switchbox was constructed (plate 2.2). Errors arising from temperature fluctuations around the equipment were minimized by making measurements in a controlled temperature room at 20 (± 1)°C. Substantial heating occurred within the microvoltmeter when using an internal power supply provided by the manufacturer. To eliminate this the microvoltmeter was operated using an external power supply.

2.2.4 Method of Operation

To measure water potentials using the dew point technique the thermocouple cooling coefficient (Wescor 1973) and the time required for equilibration of the sample in the sample chamber must be determined. Each thermocouple has its own characteristic cooling coefficient (π_v) which depends on the nature and dimensions of the thermocouple and its surrounding cavity (Campbell *et al* 1973). π_v was determined experimentally for each sample chamber used in this study. The hygrometer thermocouple was allowed to equilibrate with a dry, empty sample holder for 15 to 30 minutes in a controlled temperature room. The cooling current was then switched on for a few seconds to ensure that the hygrometer thermocouple was below ambient temperature, the microvoltmeter 'dew point' mode was then selected. After cooling, the thermocouple temperature was about 0.5°C below ambient temperature and, since the dew point depression of the air around it was much greater than this (e.g. 8°C), no water condensed on it. In the dew point mode the temperature of the thermocouple junction was kept constant by adjusting the π_V control on the thermocouple switch box. Once this was set correctly the rate of cooling exactly balanced the sensible heat gains of the thermocouple junction, thereby maintaining its temperature at a constant value below ambient temperature.

With π_V set correctly for each sample chamber the equipment was used to determine the equilibration time of aqueous samples as follows. The sample, a 6 mm diameter disk of leaf or of filter paper saturated with solution, was put into a holder, slid inside the sample chamber and sealed in position below the hygrometer thermocouple. The chamber was then left for a few minutes before the microvoltmeter was zeroed and the hygrometer thermocouple then cooled for 5-10 seconds. This cooling produced a droplet of water on the thermocouple junction by condensation. The microvoltmeter dew point mode was then selected. In this mode the correct amount of cooling was supplied to the wet thermocouple to balance its sensible heat gains, allowing it to converge on the dew point temperature of the surrounding air. The microvoltmeter reading was noted and the cooling current turned off. The sample and chamber were then left for a further 5-10 minutes and then the above sequence, i.e. zero meter, cool, dew point, repeated to obtain another reading. This procedure was repeated until the readings became constant. The sample and chamber were then assumed to have equilibrated.

When the water potentials of samples were determined the full equilibration time was allowed before the dew point depression was measured. The microvoltmeter readings (V) obtained were then converted into the water potentials (ψ) of the samples using the theoretical relationship shown in equation (2.15).

2.2.5 Evaluation of the technique

2.2.5.1 Thermocouple cooling coefficient

Since accurate measurements of water potential can only be made when π_v is set correctly, its sensitivity to variations in ambient temperature was examined. This was done by determining π_v in a field laboratory in which the ambient temperature varied from 13°C to 21°C during the day. These data were combined with π_v determinations made at temperatures up to 25°C in a controlled temperature room and is shown in figure 2.8. For all three sample chambers π_v increased linearly with temperature at approximately the same rate, 0.78 $\mu V\ {}^{o}C^{-1}$. This value is higher than that reported by Campbell *et al* (1973) for their hygrometer, 0.62 $\mu V\ {}^{o}C^{-1}$, which also had a higher π_v, 64 μV at 25°C.

The temperature sensitivity of π_v was large enough, therefore, to require adjustment of π_v when ambient temperature varied substantially, e.g. in the field. However in the controlled temperature room, where the temperature could be held constant to within ± 1°C, there was no need to alter π_v once it was set for the mean air temperature.

2.2.5.2 Equilibration time

When the environment outside the sample chamber was steady, the equilibration time depended on thermal equilibration of the sample within the chamber and equilibration of the water vapour in the chamber with the sample. Thermal equilibrium depended on the initial temperature difference between the sample,

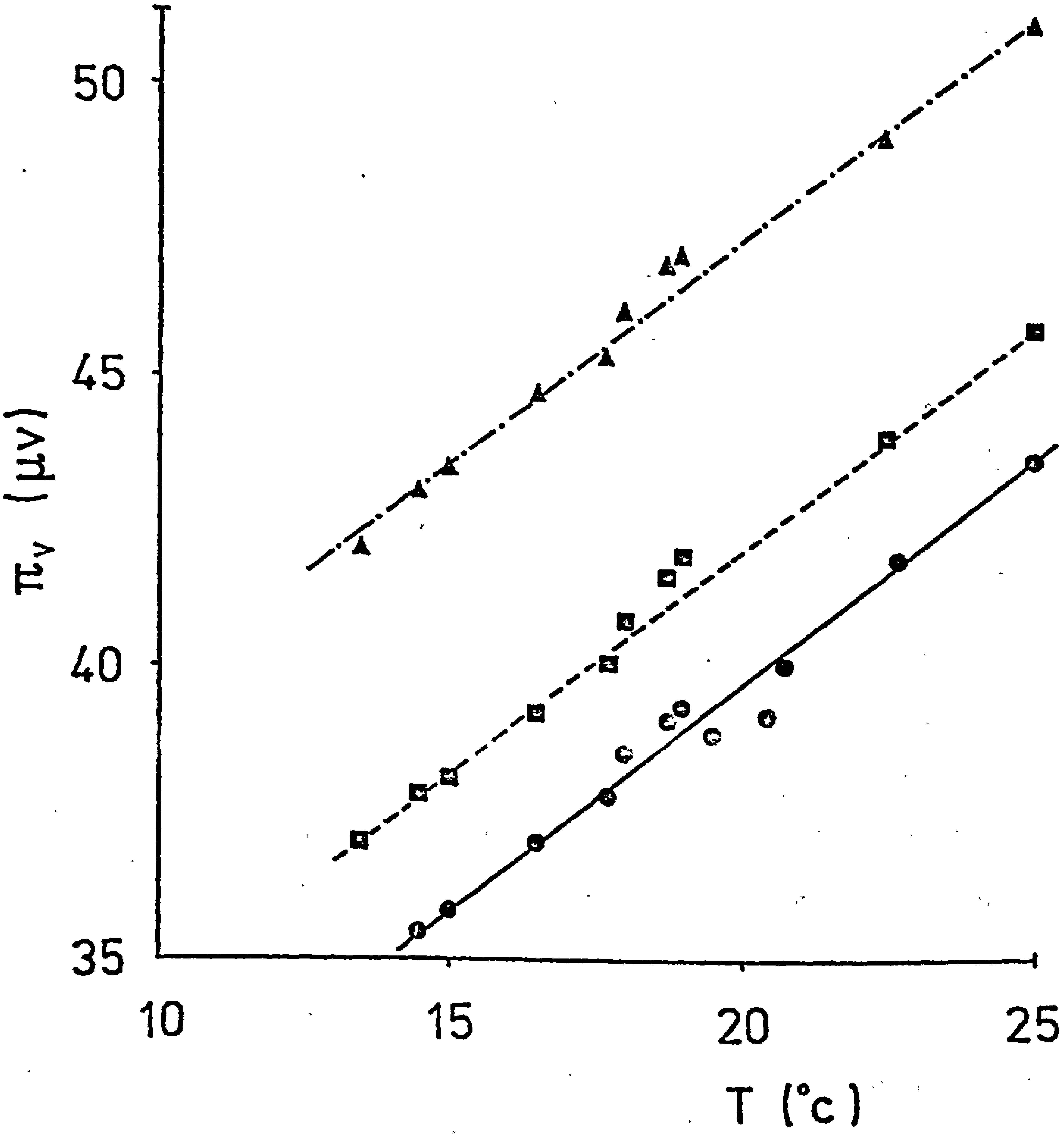


Figure 2.8 The relation between themocouple cooling coefficient (π_V) and ambient temperature (T). Sample chamber 1(▲), 2(■) and 3(●).

sample holder and chamber. The greater these differences the longer the thermal equilibration time. The fastest thermal equilibration was obtained when the sample and sample holders were at a temperature close to that of the chamber. These conditions were best satisfied in the controlled temperature room. The sample holders were also handled with tweezers to avoid heating them by contact with the hand.

Vapour equilibration depended on the volume of the recess in the sample holder and the initial humidity of the air around the hygrometer thermocouple. This is illustrated in figure 2.9, where 0.5 and 0.6 molal sodium chloride solutions equilibrated within 5 minutes on 'shallow' holders, whereas 0.8 molal salt solutions in 'medium' depth sample holders took 30 minutes to equilibrate. The effect of the initial humidity of the air around hygrometer thermocouple can be seen from the equilibration curves for the 0.8 and 1.0 molal salts solutions (figure 2.9). When the initial humidity was less than the equilibrium value, as when the 0.8 molal salt solutions were inserted into dry, empty sample holders, 30 minutes were required to increase the humidity to the equilibrium value. When 1.0 molal salt solutions were inserted after samples of pure water, the humidity decrease to the equilibrium value took 1 hour.

The nature of the sample had the greatest effect on the equilibration time. While the equilibration of salt solutions on filter paper disks was relatively fast (figure 2.9), when leaf disks were used the equilibration was much slower (figure 2.10). The equilibration time for leaf disks was greater than 7 hours. Nelsen, Safir and Hanson (1978) found similar equilibration times for wheat and barley disks in a Wescor dew point hygrometer (6-8h), whereas Millar (1974) found that wheat

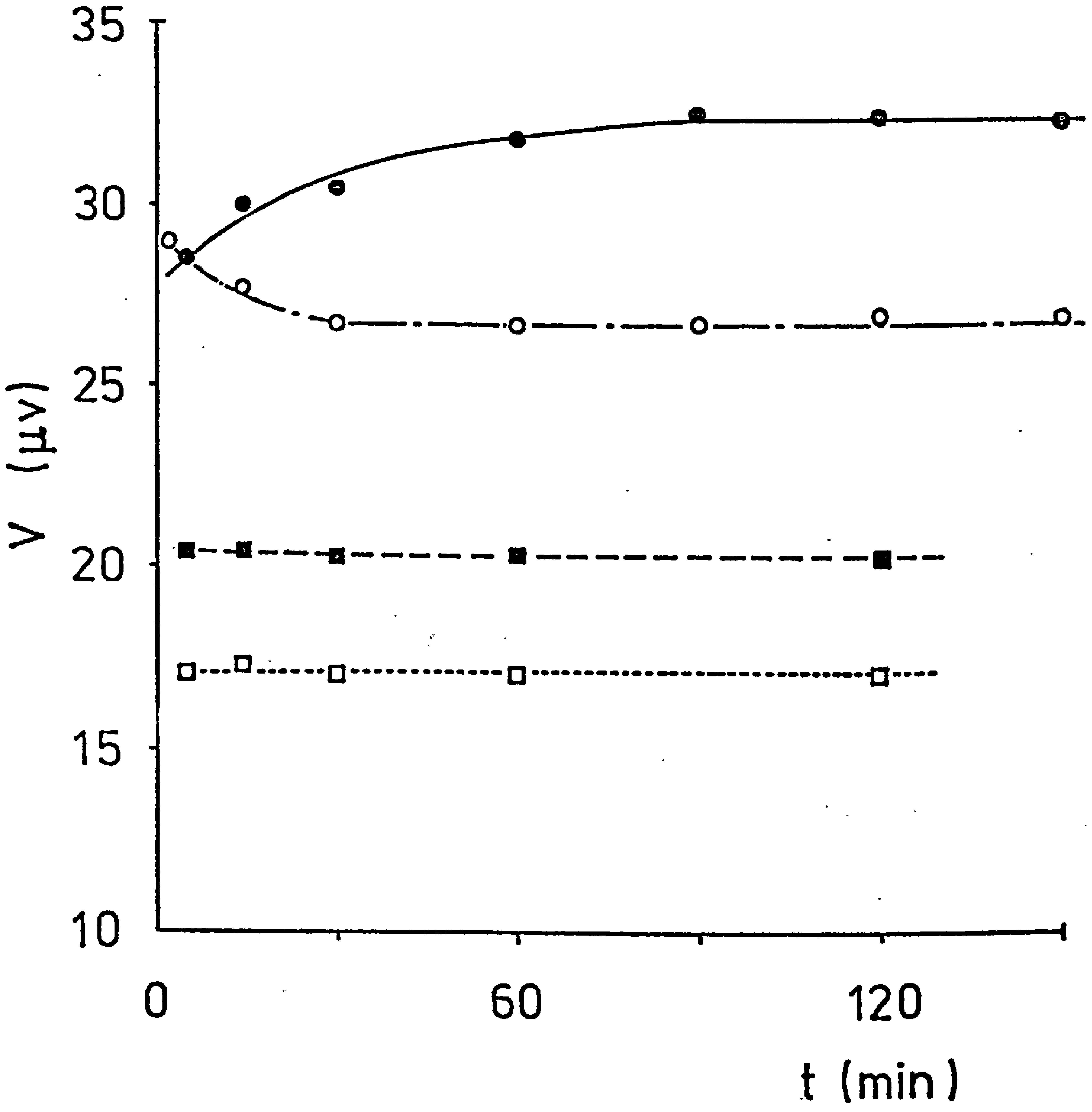


Figure 2.9 The relation between dew point hygrometer output (V) and equilibration time(t) of the sample. 1.0 molal (●) and 0.8 molal (o) sodium chloride in medium depth holders. 0.6 molal (■) and 0.5 molal (□) in shallow holders.

figure 2·9

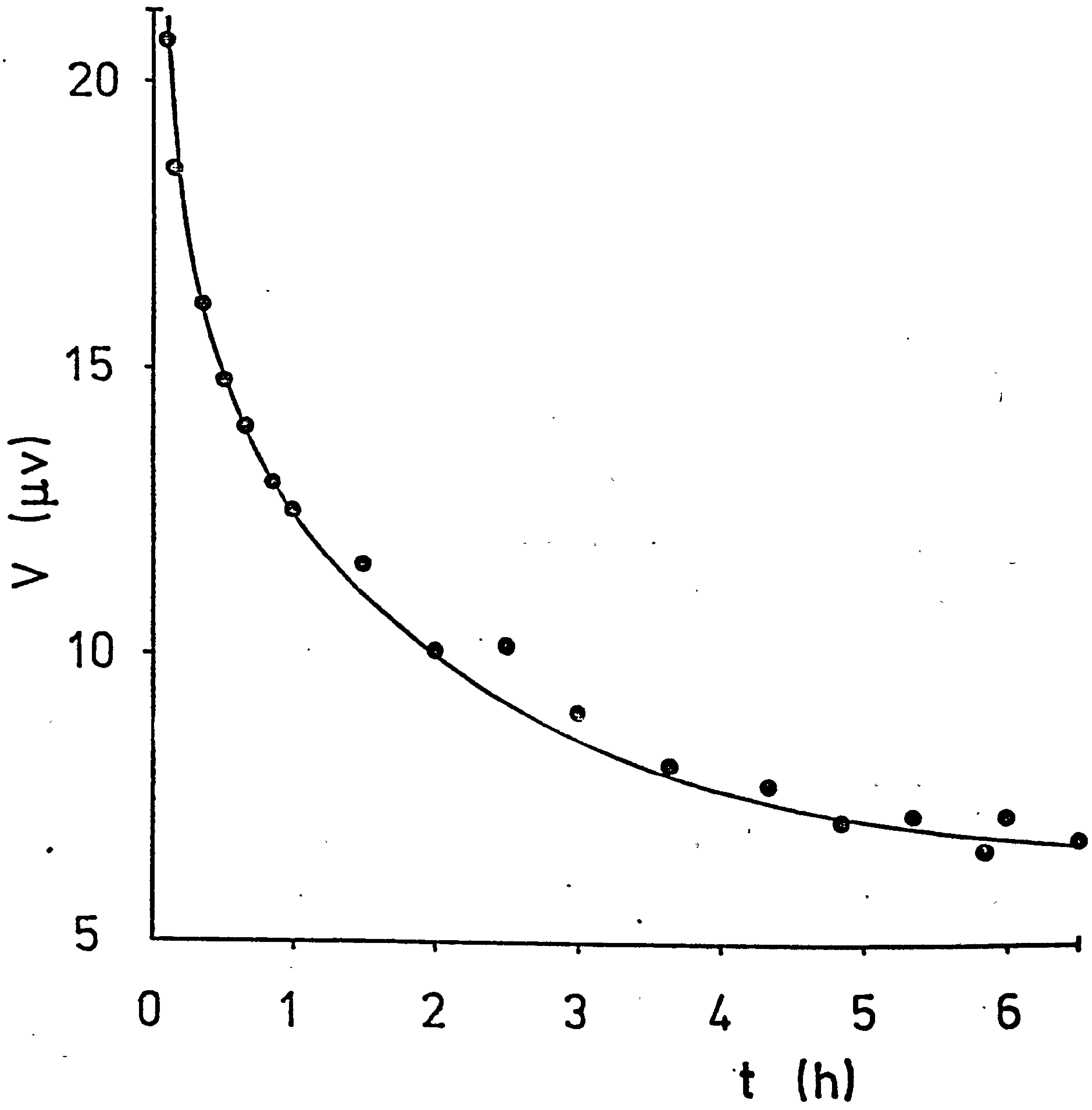


Figure 2.10 Typical relation between dew point hygrometer output (V) and equilibration time (t) for a leaf sample.

leaves took up to 30 hours to equilibrate in his psychrometers. The slow equilibration of leaf tissue may have been due to a number of effects associated with excised leaf tissue psychrometry (Barrs 1968; Barrs and Kramer 1969; Manohar 1971; Millar 1974; Baughn and Tanner 1976b). For example, the relative impermeability of the leaf cuticle to the diffusion of water vapour compared with that of salt solutions on filter paper (Rawlins 1964; Boyer and Knipling 1965; Barrs 1965a; Manohar 1966; Zanastra and Hagenzieker 1977). Also vapour exchange between water sources and sinks in the excised leaf tissue and chamber may have delayed equilibrium (Rawlins 1964, 1966; Barrs 1968; Millar 1974). The delicate thermal balance in the hygrometer chamber may also have been affected by heat of respiration (Barrs 1964, 1965a, 1965b; Boyer 1966; ap Rees 1966).

Because of the long equilibration time required for leaf samples and the errors due to leaf excision the dew point technique was not used to determine leaf water potential. However, the rapid equilibration of solutions enabled its use to measure the osmotic potential of leaf sap.

2.2.5.3 Calibration

The instrument was calibrated at 20°C using eleven solutions of sodium chloride ranging from 0.05 molal to 1.0 molal, corresponding to water potential values of - 0.23 MPa to - 4.55 MPa. The solutions, on 6 mm diameter disks of filter paper in 'medium' depth sample holders, were inserted into the sample chamber and a 30 minute equilibration time allowed before the dew point depression was measured. The correlation between the observed microvoltmeter output (V) and the theoretical output, equation (2.13) and equation (2.15), are shown in figure 2.6. The agreement over the wide range of water potentials, - 4 MPa to - 0.7 MPa, was very good. But when ψ was greater than - 0.7 MPa observed values were slightly higher than the theoretical values. Conversely, at low water potentials ($\psi < -4$ MPa) the observed values were lower than the theoretical values. In both cases this may have been due to instrumental error (Wescor 1973). Campbell *et al* (1973) also obtained good agreement between theoretical and actual dew point hygrometer output, also noting that observed ψ_L was slightly lower than theoretical ψ_L at low water potentials.

A linear regression of the data shown in figure 2.6 gave the fitted straight line as

$$V = -(7.5 \pm 0.1)\,\psi + (0.2 \pm 0.4), \qquad (2.16)$$

which is not significantly different from the theoretical relation (equation (2.15)).

2.2.5.4 Errors in the estimates of leaf osmotic and turgor potentials

The instrumental error in an estimate of osmotic potential ($\delta\psi_\pi$) calculated from the standard error of the slope and intercept of the fitted straight line (equation (2.16)) is

$$\delta\psi_\pi = \pm\,(0.081 + 0.013\,\psi). \qquad (2.17)$$

The error in an estimate of ψ_π throughout the range investigated is, therefore, about ± 0.1 MPa. Contamination of the sample chambers caused additional large errors in subsequent estimates of ψ_π and, therefore, throughout the calibration and measurement procedures frequent contamination checks were made. The checking and cleaning procedures described by Wescor (1973) were followed with care in detecting and removing contamination.

In the field, where ψ_π and ψ_p change temporally and spatially, there are consequent uncertainties in their hourly mean values estimated from a number of samples taken during each hour. A typical example is shown in Figure 2.11, where the hourly mean values of ψ_π and ψ_p ($= \psi_L - \psi_\pi$) and their standard errors were calculated from three samples taken during each hour throughout a day. The standard error in ψ_π did not change significantly with ψ_π and its mean value for the day was 0.1 MPa. The standard error in ψ_p was generally larger for lower values ψ_p, with a mean value for the day of 0.13 MPa. In the subsequent programme for sampling leaves from the field (section 3.3), therefore, three leaves per hour was chosen as the minimum number required to give an adequate indication of the hourly changes in ψ_π and ψ_p during the day.

Another source of error in the estimates of ψ_π and ψ_p arises from ignoring the proportion of water in the leaves which is 'bound' to the tissue by matric forces (see Warren Wilson a, b & c). The bound water fraction was not measured in the present study, however, Campbell (pers. comm.) found it to be about 30% in the leaves of another wheat crop, suggesting that they had a significant matric potential, ψ_M. The effect of ignoring bound water is to overestimate ψ_π and underestimate ψ_p by the amount of ψ_M (see equation 1.4). In wheat leaves Shepherd (1975) found ψ_M decreased linearly from zero to - 0.5 MPa as leaf water potential (ψ_L) decreased from zero to - 3 MPa. If similar values of ψ_M existed in the present wheat crop, the values of ψ_π and ψ_p presented in chapter 7 may be in error by the amounts given by Shepherd. However, since changes in ψ_M are small compared with those in ψ_π and ψ_p, the shape of the diurnal and seasonal trends in ψ_π and ψ_p should not be greatly affected.

Figure 2.11

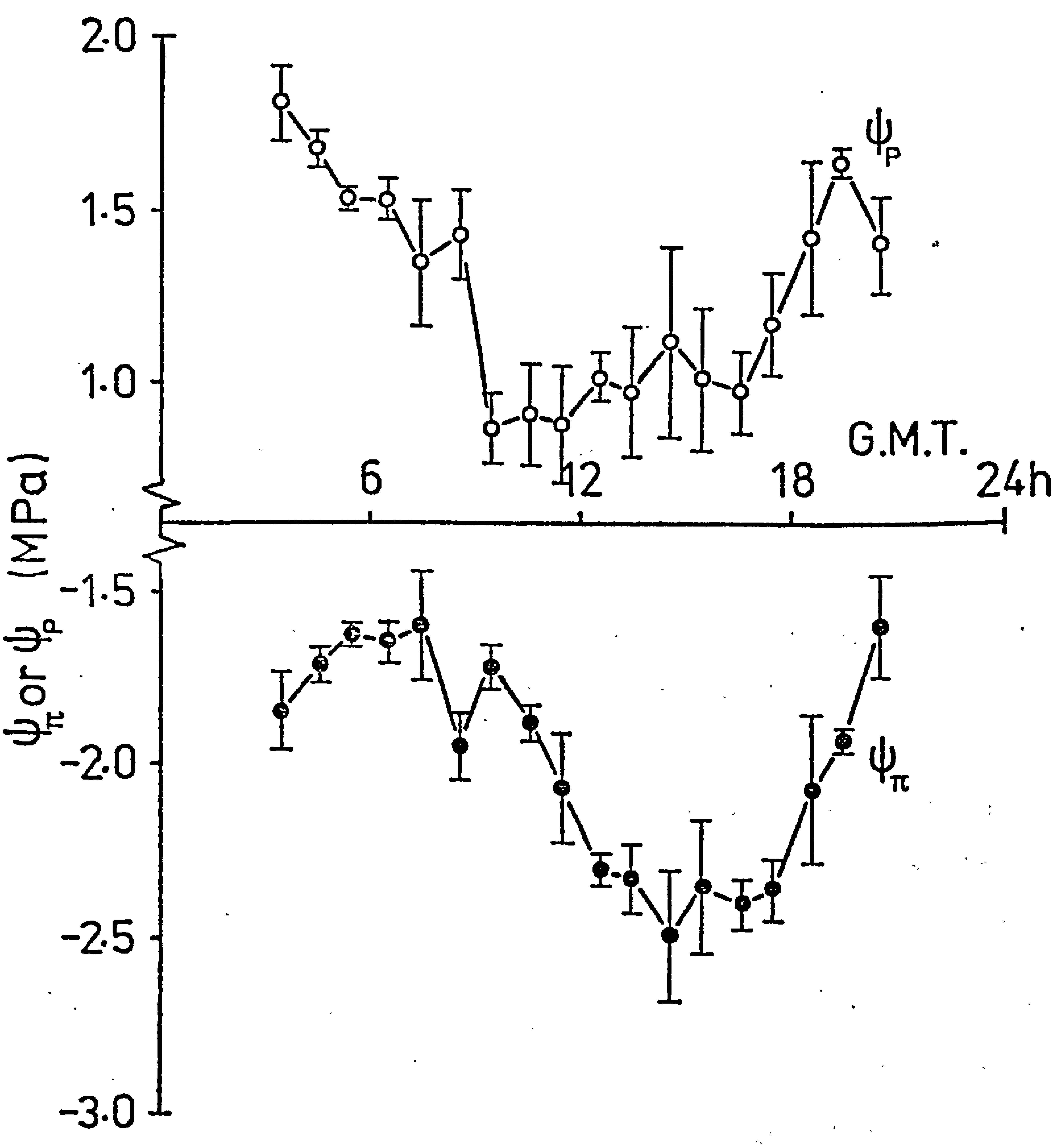


Figure 2.11 Typical changes in the hourly mean leaf osmotic potential (ψ_π) and turgor potential (ψ_p) and their standard errors, 20 June 1974.

3. MATERIALS AND METHODS

3.1 Crop, site and seasons

The winter wheat crops studied (*Triticum aestivum* L cv Hunstman) were sown on 23 November 1973 and 30 October 1974 at a rate of 14 g m^{-2}. The seed bed preparations, sowing, herbicide spraying, fertilizer applications and harvesting of both crops were undertaken as part of the normal agricultural practice of the University farm. Expressed in terms of dry mass of grain, the yields were 5.0 and 5.1 tonnes ha^{-1} in 1974 and 1975 respectively. Further details of the yields and yield components are given by Gallagher and Biscoe (1978).

Figure 3.1 shows a plan of the site at Sutton Bonington, England. In 1973 10 ha of wheat was sown in the east field, a similar area was sown in the west field in 1974. The micrometeorological instruments were positioned near the centre of the fields for optimum fetch, which ranged from approximately 100 to 400 m depending on the wind direction. For compatibility the soil and leaf water status sampling areas were sited close together. However, in the west field some measurements of leaf water status were also made in an area comparatively remote from the soil water sampling area (L_2' in figure 3.1).

Measurements were made during May, June and July in 1974 and 1975, usually on warm days with bright sunshine and no rainfall. The weather conditions during these three months in 1974 were comparable to the average conditions for the site, apart from above average rainfall (table 3.1). In contrast, the corresponding months in 1975 had below average rainfall, with only 19 mm falling between 18 May and 7 July. Also during this period the potential evaporation, calculated using the Penman (1948) formula, was about 15% higher than that in 1974. Further details about

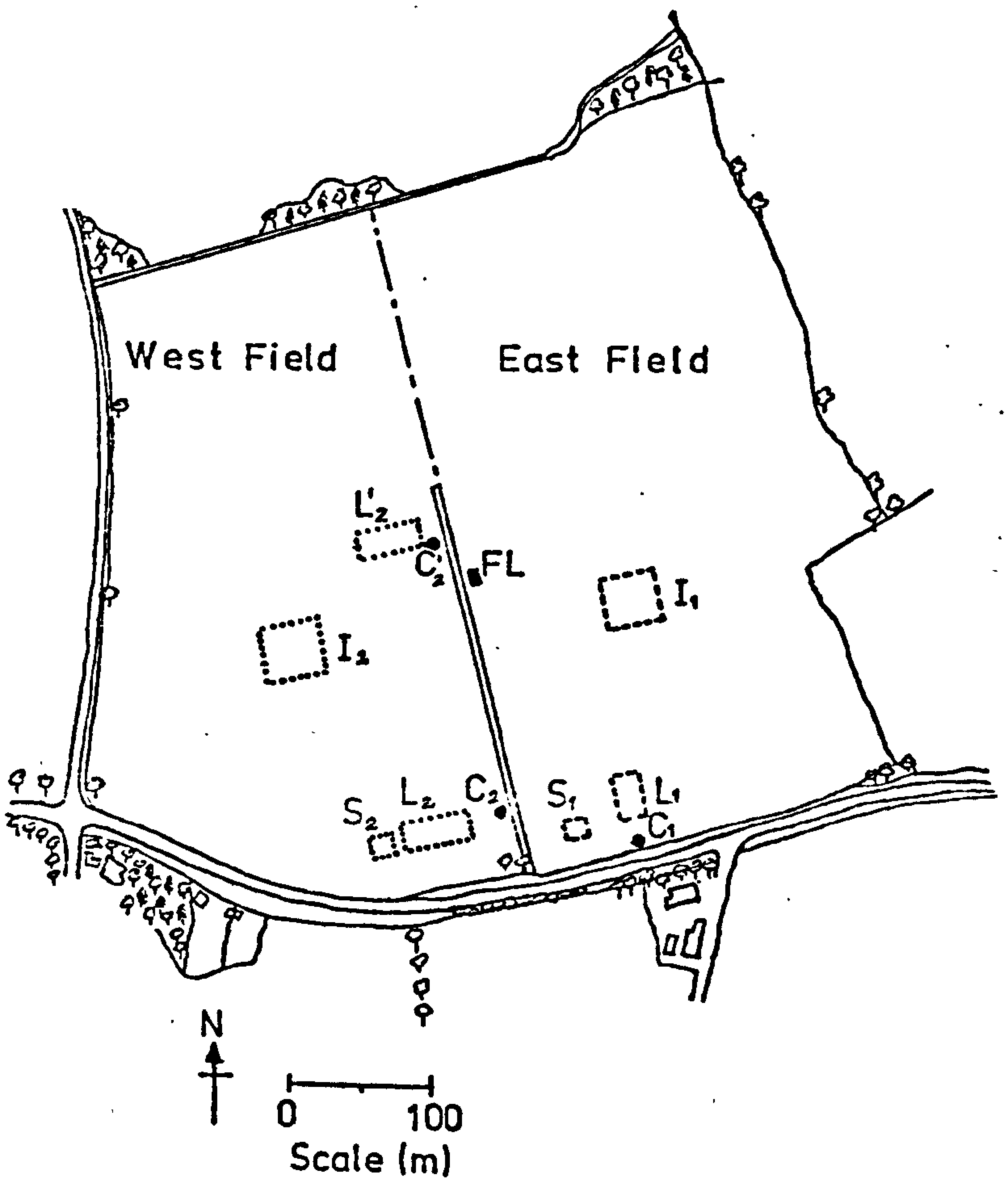


Figure 3.1

Figure 3.1 Site plan, indicating the approximate positions of the field laboratory (FL), micrometeorological instrumentation (I), leaf (L) and soil (S) sampling areas and the pressure chamber (C). The subscripts 1 and 2 refer to 1974 and 1975 respectively.

	Average 1946-1972*			1974			1975		
	May	June	July	May	June	July	May	June	July
Rainfall (mm)	47	47	52	27	70	68	30	19	49
Number of rain days	15	13	12	12	4	4	9	6	14
Sunshine (h)	176	187	175	193	169	167	176	188	175
Mean daily solar radiation (MJ m^{-2})	14.4	16.7	15.0	16.3	15.9	13.7	15.3	19.8	18.0
Mean daily run of wind (km)	233	202	178	245	224	245	276	202	217
Temperature (^{o}C)									
(1) Mean screen maximum	15.8	19.1	20.4	15.7	17.7	19.3	13.6	21.5	22.3
(2) Mean screen minimum	6.4	8.7	10.8	6.3	9.0	10.9	5.3	8.1	12.1
(3) Average of (1) and (2)	13.2	15.5	15.6	11.0	13.4	15.1	9.5	14.8	17.2
Potential evaporation (mm)	85	91	90	86	89	92	80	105	102

* Radiation 1958-1972; mean screen temperature 1955-1972; potential evaporation 1950-1975, excluding 1965-1968. Mean daily run of wind 1962-1973.

Table 3.1 Summary of the average weather conditions at Sutton Bonington and the weather in 1974 and 1975.

the crop, site and weather have been published by Biscoe *et al* (1975) and Gallagher (1979).

3.2 Micrometeorology

During 1974 measurements of temperature, humidity and wind speed were made above the crop by Johnson (pers. comm.). These enabled the hourly rates of evaporation (E) to be calculated using the aerodynamic method. More intensive micrometeorological measurements were made during 1975 by Biscoe (pers. comm.) and E calculated using the Bowen ratio method. The micrometeorological instrumentation and theory used have already been described in detail by Biscoe *et al* (1975) and Biscoe and Saffell (1976).

Following Jarvis (1975), hourly rates of water flow per stem (Q) were calculated using the estimates of E in the relation

$$Q = E/n, \tag{3.1}$$

where n is the stem density (i.e. the number of stems per unit area). n was measured at weekly intervals throughout the two seasons by Hunter (pers. comm).

3.3 Plant water status

3.3.1 Measurement of leaf water potential

Leaves were selected at random from the sampling area and prepared for measurements as follows. During 1974 a complete stem was cut immediately above the soil surface and taken intact to the pressure chamber. The selected leaf was then cut just above the ligule, close to the base of the leaf blade and immediately placed in the pressure chamber to determine ψ_L. During 1975 the selected leaf was covered in the field with a narrow aluminium foil envelope lined with polythene and immediately cut from the plant. The leaf was then taken to the pressure chamber where the envelope was removed and ψ_L measured as before. The purpose of the envelope was to minimize transpiration from the leaf in transit from the sampling areas to the pressure chamber (see section 2.1.4.2).

During the months when measurements were being made there were up to four green leaves on each stem. These were labelled according to their order of emergence, for example, the flag leaf was the eleventh leaf to emerge in 1974, the twelth in 1975. Measurements were made on three samples of each of the green leaves on the stems at hourly intervals between dawn (03h00) and dusk (21h00). This was repeated at approximately weekly intervals during the two seasons.

3.3.2 Measurement of leaf osmotic potential

The same leaves sampled to measure ψ_L were also used to determine ψ_π. Immediately after ψ_L was measured the leaf was removed from the pressure chamber and sealed in a small glass vial. The vial was then immersed in liquid nitrogen to freeze the tissue rapidly and destroy the cell structure (Brown 1972). The samples collected on each day were then transferred to cold storage at -15°C for subsequent determination of ψ_π. After storage the samples were allowed to equilibrate in a controlled temperature room at 20°C. Leaves were then removed from the vials and squeezed to express their sap, which was collected on filter paper disks. The osmotic potential of the sap was then determined using the dew point hydrometer described in section 2.2.

3.3.3 Equilibration with the water source

When transpiration stopped the equilbration of plants with their water source was measured by recording the changes in ψ_L during the night and when transpiration was prevented during the day. This provided information about the hydraulic properties (R and C) of the soil-plant system and the effective potential of the water source (ψ_B). During the night ψ_L was measured at intervals of 1-2h depending on its rate of change. In the day transpiration was stopped and subsequent changes in ψ_L measured as follows.

3.3.3.1 Equilibration with the soil

On a number of days ψ_L was measured just after mid-day. Groups of six stems were then selected at random and transpiration was prevented by covering the youngest leaf on each stem with a self sealing 'cling film' and a polythene lined aluminium foil envelope. Each group of stems was then covered with a plastic tube (1.3 m long x 0.07 m diameter) coated on the outside with aluminium foil. The tubes were pushed several centimetres into the soil so that they remained upright. The water potentials of covered leaves were subsequently determined at intervals up to 4h after covering, depending on the rate of recovery of ψ_L.

Changes in ψ_B in the soil were monitored during a number of days in 1975 by using the plants as 'tensiometers'. At hourly intervals throughout these days transpiration was prevented from selected plants as described previously. The water potentials of the covered leaves were then measured 1h after covering.

3.3.3.2 Equilibration with water

In selected plants transpiration was prevented, as before, but then the stems were cut under water at their base. This was done by surrounding them with an open tube (0.3 m long x 0.2 m diameter) which was pushed into the soil. The tube was filled with water and the stems cut before the water drained into the soil. The cut ends were kept immersed in a beaker of water while the leaf water potentials were measured at intervals up to 2 h after covering. At no time during this procedure were the cut ends of the stems exposed to the air.

3.4 Soil water status

The soil in the field has been classified in the Astley Hall series and has a loamy plough layer overlying a gravelly loam subsoil, which in turn gives way at about 1 m depth to a clay subsoil. The soil and soil profiles are somewhat variable though the drainage is generally good.

The water status of the soil was monitored at weekly intervals during both seasons by McGowan (pers. comm.). Soil water content was measured using a neutron probe. Measurements were made in four access tubes within the sampling areas (S_1 and S_2 in figure 3.1) at 0.1 m intervals down to a depth of 1.6 m. Soil water potentials higher than -0.08 MPa were measured using four sets of tensiometers at the same depths as above. Soil water potentials lower than -0.08 MPa were determined by two different methods. One, during 1974, when they were estimated from water release curves determined in the laboratory on soil samples taken from the field site. Two, during 1975, when they were measured *in situ* using Wescor soil psychrometers (PT-51) located in the soil at depths down to 0.8m. The above measurements gave a comprehensive description of the soil water potential profiles in the rooting zone throughout the seasons studied.

3.5 Stem xylem anatomy

Estimates of the number and size of the xylem vessels in the wheat stem were made using sample plants collected from the field. On two days, 10 June and 2 July 1975 when leaf water potential measurements were being made, six stems were cut at ground level, and then completely immersed in ethanol to kill and fix them. The samples were stored in ethanol and at a later date pieces of node and internode were prepared for sectioning with a freezing microtome. The pieces of stem were first rehydrated by immersing them successively for hourly periods in aqueous solutions of 85%, 70%, 50%, 30%, 15% ethanol and finally, distilled water. The rehydrated samples were then left overnight in a 10% solution of 'gum arabic'. Pieces of stem about 10 mm long were cut from these samples and mounted in gum arabic on the stage of a freezing microtome. Transverse sections about 50 μm thick were cut, between 50 μm and 200 μm apart, and mounted on microscope slides. The sections were examined at known magnifications and photographed. Using these photographs the number and size of the xylem vessels in the wheat stem were measured.

The length of the internodes, leaf sheaths and leaves were also determined from the remaining intact stems stored in ethanol, which represented two different stages of plant growth.

3.6 Stomatal conductance

The stomatal conductance of wheat leaves was measured using an automatic diffusion porometer (Delta-T Devices, Burwell, Cambridge) during 1974 by Cohen (pers. comm.) and in 1975 by Clark and Hotchkiss (pers. comm.). The principle of the instrument is to measure the time taken for a given, fixed increase in the humidity inside a small cup attached to the leaf. This can be converted into a value of stomatal conductance by calibrating the porometer with perforated metal plates of known conductance (Stigter and Lammers 1974). To enable the instrument to be used on wheat leaves a mask with a rectangular aperture 15 mm x 5 mm was fitted into the porometer cup.

The stomatal conductances of three random samples of each of the green leaves in the crop were generally measured at hourly intervals throughout the days when leaf water status was examined. As the calibration of the porometer is temperature dependent, the temperature of the leaf and porometer cup were measured using thermistor beads during each measurement of stomatal conductance. When the porometer cup was clipped onto a leaf, temperature equilibration usually occurred within 30 s, i.e. during the first two to three readings of transit time. However a further three readings were taken to ensure a constant value from which the stomatal conductance could be calculated. In total each estimate of stomatal conductance took about 1-2 min, allowing rapid replicate readings to be made.

4. TEMPORAL CHANGES IN LEAF WATER POTENTIAL

This chapter describes the measured changes in the water potential of the youngest leaves (ψ_L) and the concurrent changes in water flow per stem (Q) and soil water potential (ψ_S). Each hourly value of ψ_L is the mean of three measurements. The standard errors of ψ_L are not shown, but are similar to those in figure 2.4 (section 2.1.4), i.e. about 10% of ψ_L. To distinguish between different leaves on the stem a numeric subscript is added to ψ_L. For example, ψ_{L11} refers to the water potential of the 11th leaf to emerge on the stem. (A diagram of a mature wheat stem, showing the different leaves is shown in figure 5.1).

4.1 Diurnal

4.1.1 1974

During the period when measurements were made, 29 May to 9 July, the youngest leaf on the stem was the flag leaf, leaf 11 in this year. Figure 4.1 shows the changes in flag leaf water potential (ψ_{L11}) and Q measured during four days of high evaporation. In the early morning of 29 May (figure 4.1a), when Q was negligible, ψ_{L11} was high, -0.1 MPa. As Q increased during the morning ψ_{L11} decreased, to a minimum of -1.2 MPa around 13h00, when Q was greatest. When Q decreased again in the afternoon ψ_{L11} increased, to -0.4 MPa at 20h00. On 13 June ψ_{L11} was again -0.1 MPa in the morning (figure 4.1b) but decreased more rapidly than on the 29 May, and reached a lower value, -1.6 MPa, by 10h00. ψ_{L11} then changed little until after 15h00 when it increased rapidly, as Q decreased, reaching -0.4 MPa at 21h00. One week later, on 20 June, the depression of ψ_{L11} was less severe (figure 4.1c). On

Figure 4.1

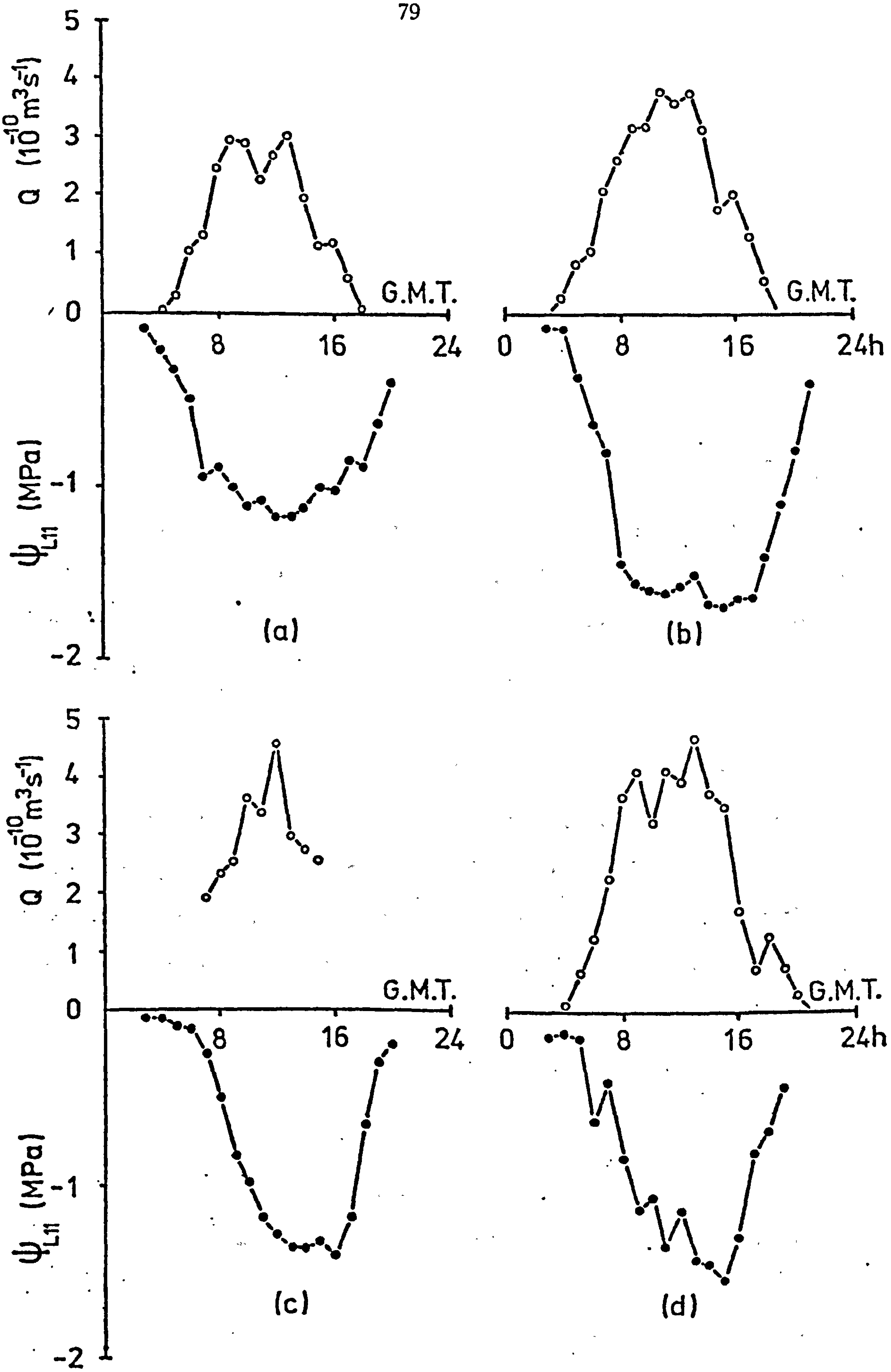


Figure 4.1 Changes in flag leaf water potential (ψ_{L11}) and flow of water per stem (Q) during four days of high evaporative demand in 1974. (a) 29 May, (b) 13 June, (c) 20 June and (d) 9 July.

this day ψ_{L11} decreased more slowly than on 13 June, from -0.05 MPa in the morning to only -1.4 MPa at 14h00, even though the mid-day flow rates were similar on the two days. The changes in ψ_{L11} on 9 July showed greater variation than on previous days (figure 4.1d). However, the diurnal trend was similar to that on 20 June, ψ_{L11} reaching a minimum of -1.5 MPa in the early afternoon.

Figure 4.2 shows the changes in ψ_{L11} and Q on two days of low evaporative demand. During the morning of 19 June (figure 4.2a) Q increased and ψ_{L11} decreased in a similar manner to that on days of high evaporative demand, ψ_{L11} being -1.0 MPa at 10h00. However, the sky then became overcast and in the next few hours both the flow and potential returned rapidly towards zero, until at 13h00 ψ_{L11} was -0.3 MPa. This time is close to that of minimum leaf water potential on bright days (figure 4.1). At 14h00 there was a light shower of rain and readings were discontinued. On 26 June (figure 4.2b) Q was less than half of that at corresponding times on days of high evaporative demand. Consequently, ψ_{L11} was higher throughout this day, and tended to zero over four hours earlier, than on days of high demand.

4.1.2 1975

Figure 4.3 shows the changes in the water potential of the youngest leaves and Q during six days of high evaporative demand. On 16 and 20 May, leaf 11 was the youngest leaf. On (and after) 13 June the youngest leaf was the flag leaf, leaf 12 in this year. The changes in ψ_{L11} on 16 and 20 May (figure 4.3a and b) were similar to those on 29 May 1974. ψ_{L11} decreased from near zero in the morning

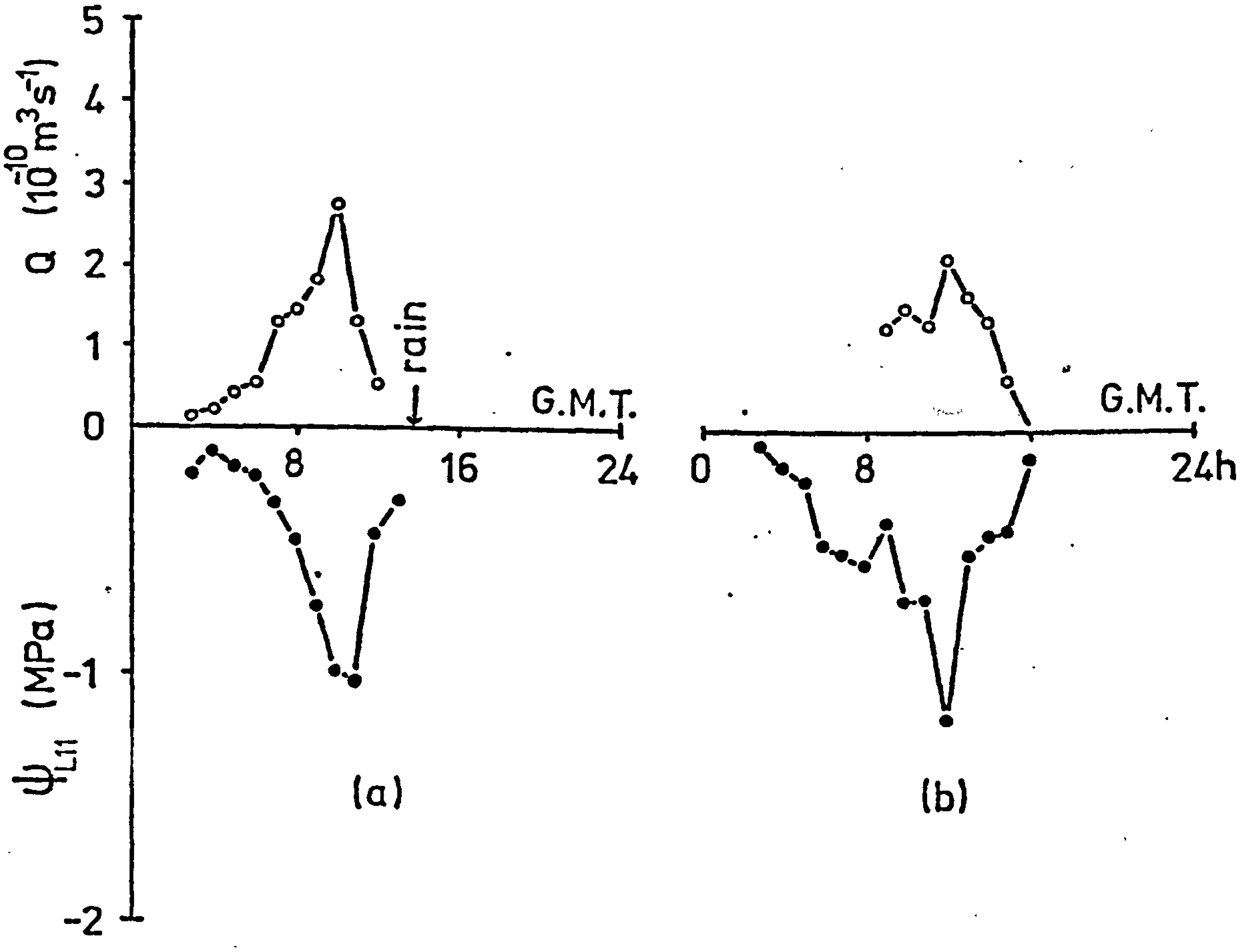


Figure 4.2 Changes in flag leaf water potential (ψ_{L11}) and flow of water per stem (Q) during two days of low evaporative demand in 1974. (a) 19 June and (b) 26 June.

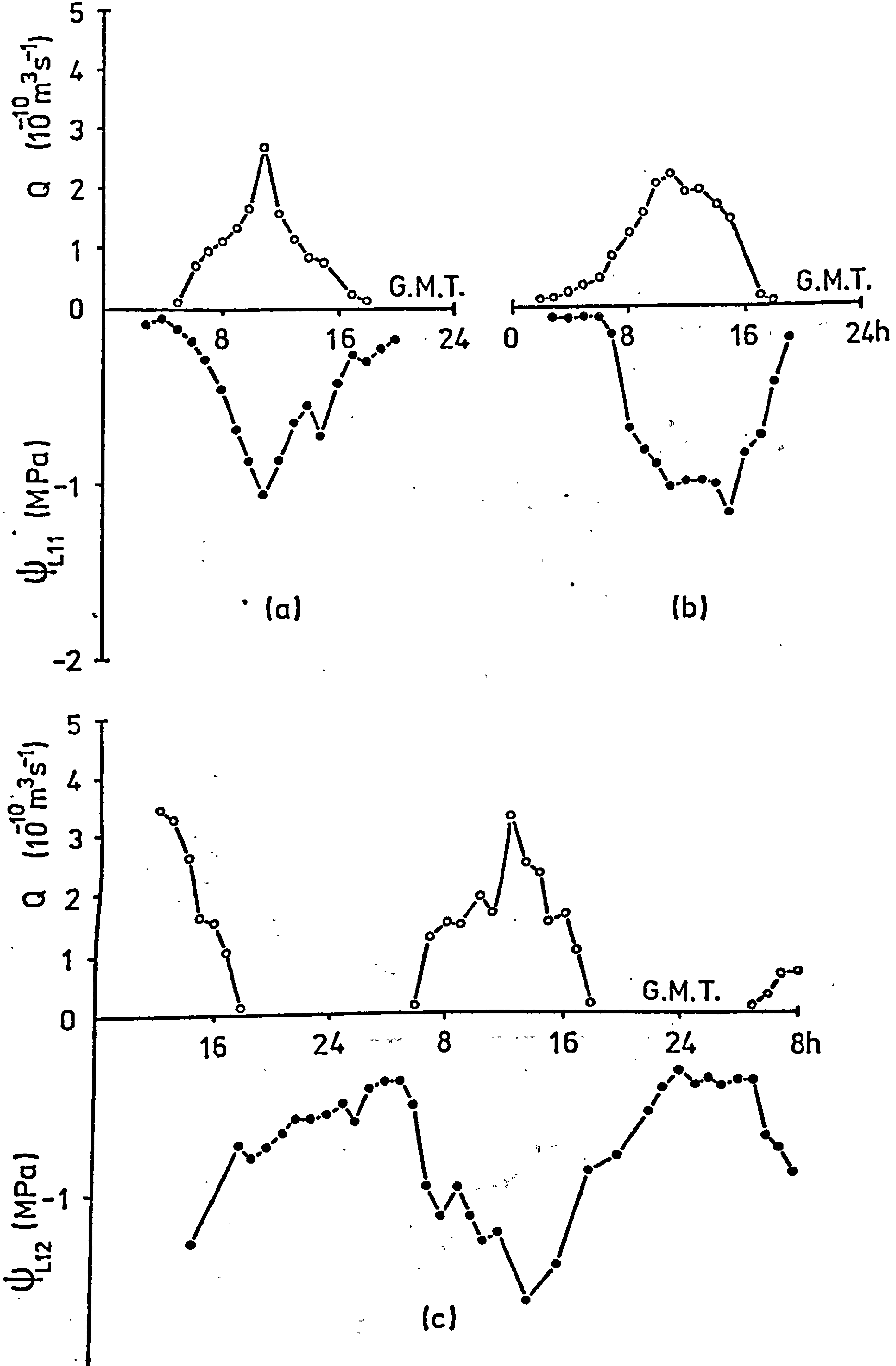


Figure 4.3 Changes in the water potential of the youngest leaf (ψ_{L11} or ψ_{L12}) and flow of water per stem (Q) during six days of high evaporative demand in 1975. (a) 16 May, (c) 14 June, (d) 19 June, (e) 24 June and (f) 2 July.

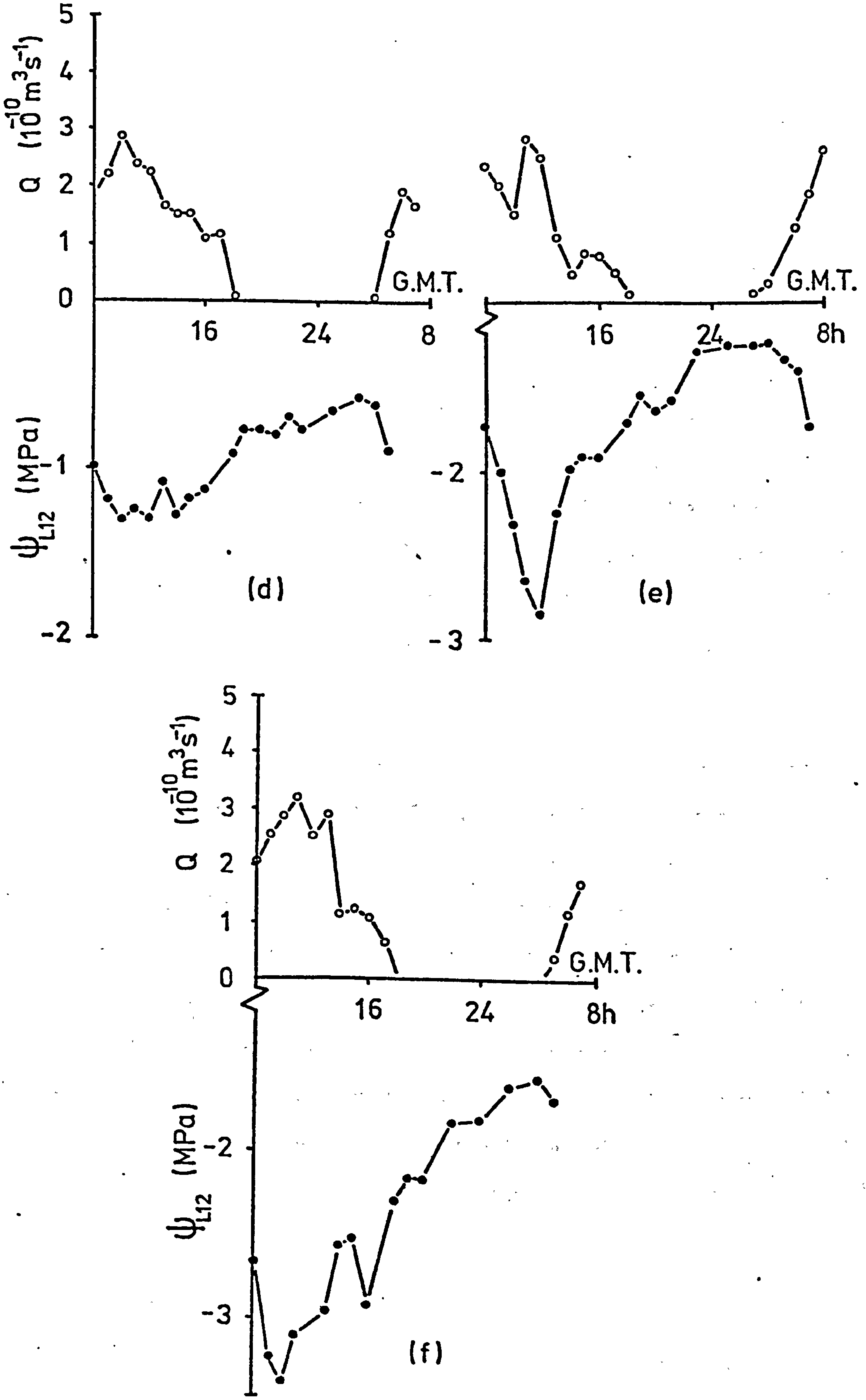


Figure 4.3 continued.

to about -1.1 MPa around midday. One notable aspect of the response of ψ_{L11} on 20 May was that it did not decrease until after 06h00, about two hours later than on previous days. This was associated with the evaporation of a heavy dew. In contrast, the flag leaf water potential (ψ_{L12}) only recovered to -0.4 MPa after 13 June (figure 4.3c). ψ_{L12} decreased to -1.6 MPa during 14 June and again only increased to -0.4 MPa that night. Five days later, on 19 June, (figure 4.3d) ψ_{L12} had a midday minimum of -1.3 MPa, however it increased slowly that evening and only reached -0.6 MPa the following morning. As the drought continued leaf water potentials were further reduced. For example, on 24 June (figure 4.3e) ψ_{L12} reached a minimum of -2.9 MPa and only recovered to -1.2 MPa overnight. By 2 July (figure 4.3f) ψ_{L12} was as low as -3.4 MPa around midday and only increased to -1.6 MPa in the morning, which is lower than the midday minimum leaf water potential on days earlier in the season.

Leaf water potentials were also measured in plants which were irrigated during the drought in 1975. Figure 4.4 shows the changes in flag leaf water potential in these plants, on three days of high evaporation. The changes in ψ_{L12} in the normal, unirrigated crop on the same days are reproduced for comparison. The shape of the dirunal trends in ψ_{L12} were similar in the irrigated and unirrigated crops, but the displacement between them increased, from a mean of 0.4 MPa on 19 June to 1.5 MPa on 2 July, as the soil in the unirrigated crop dried. The daily minimum values of ψ_{L12} in the irrigated plants, -0.9 to -1.6 MPa, were similar to those observed in the unirrigated crop in 1974 and before the drought in 1975.

4.2 Seasonal

It can be seen from figures 4.1 and 4.3 that leaf water potential changed seasonally as well as diurnally, particularly in 1975. Figure 4.5 summarizes the seasonal changes in leaf water potential by showing

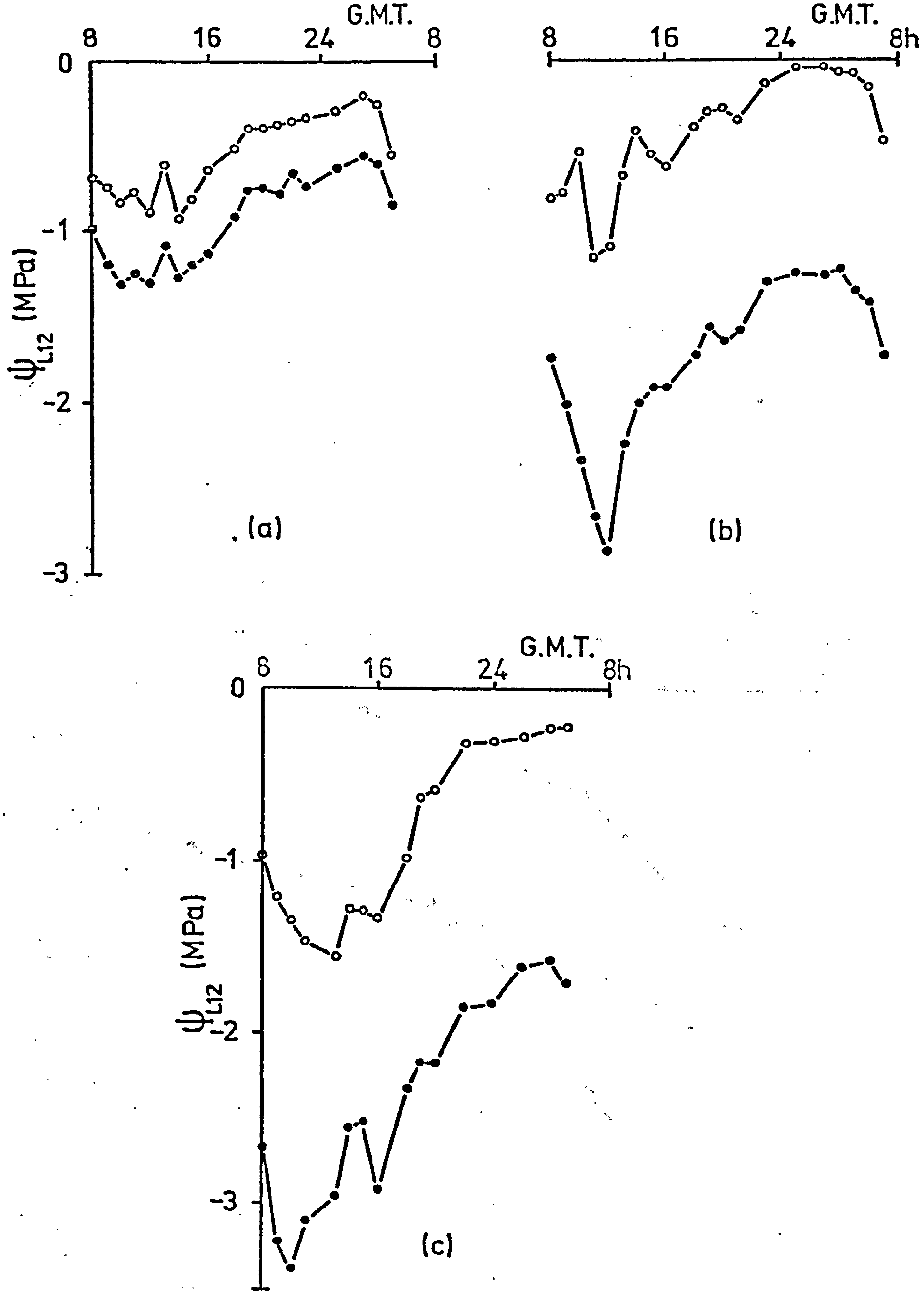


Figure 4.4 Changes in flag leaf water potential (ψ_{L12}) in normal (●) and irrigated (o) plants during three days in 1975. (a) 19 June, (b) 24 June and (c) 2 July.

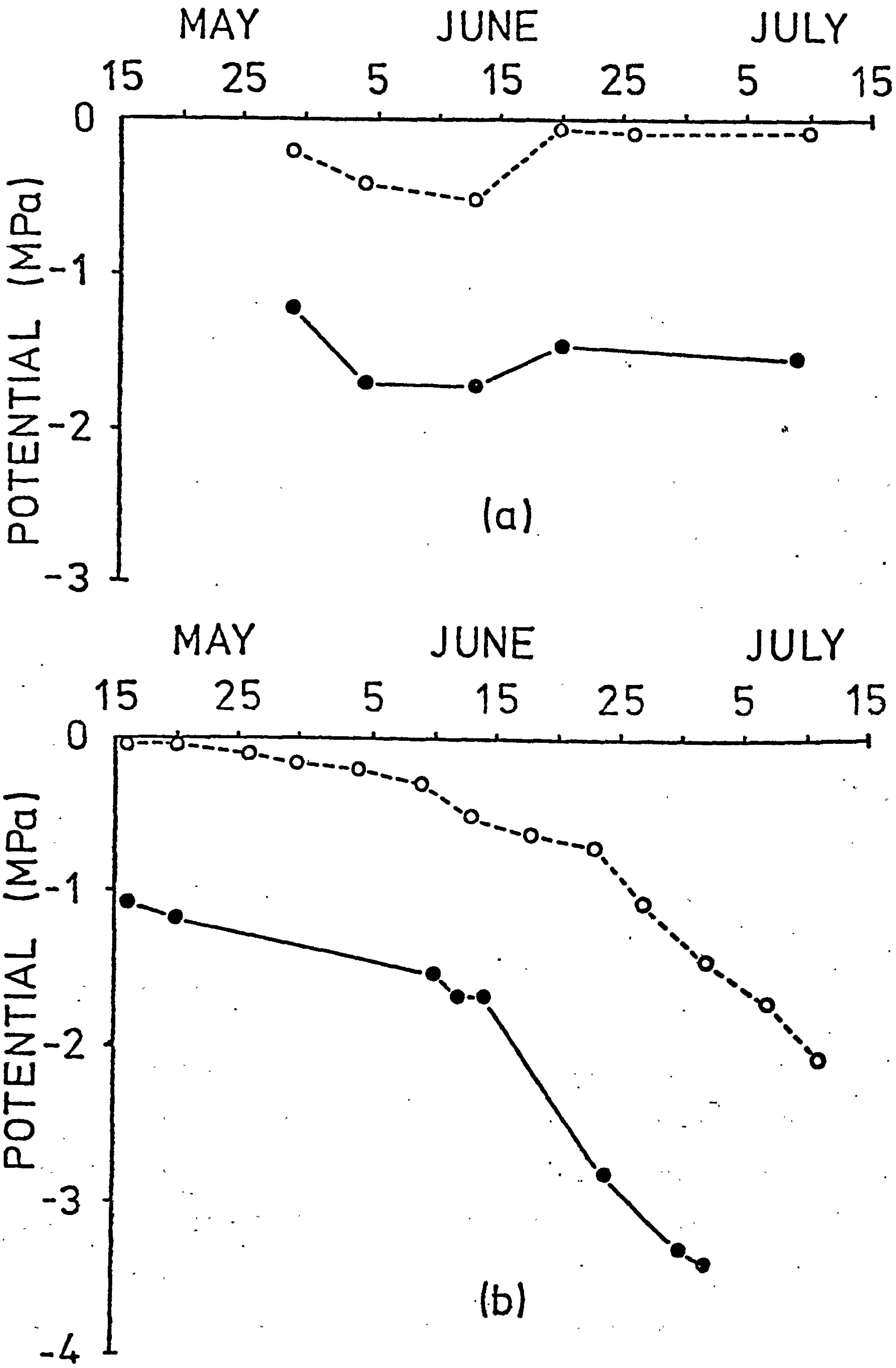


Figure 4.5 Changes in the minimum water potentials of the leaves (●) and soil (o) during (a) 1974 and (b) 1975.

the minimum values of leaf water potential, ψ_L(min), on days of high evaporative demand. The corresponding changes in minimum soil water potential, ψ_S(min), are also shown. During 1974 ψ_L(min) varied between -1.2 and -1.7 MPa, figure 4.5a. The decrease to -1.7 MPa on 13 June coincided with a parallel decrease in ψ_S(min) of similar magnitude. Sufficient rain fell after 13 June to increase ψ_S(min) to about -0.1 MPa on 20 June, and ψ_L(min) also increased, to -1.4 MPa on the same day. The difference ψ_S(min) - ψ_L(min) ranged from 1.0 to 1.5 MPa during this season.

In 1975 the changes in soil and leaf water potentials (figure 4.5b) were very different from those observed in 1974. During 1975 ψ_L(min) decreased monotonically from -1.1 MPa on 16 May to -3.4 MPa on 2 July. During the same period ψ_S(min) also decreased, from -0.02 MPa to -1.4 MPa, and further to -2.0 MPa on 10 July. The difference ψ_S(min) - ψ_L(min) was, however, less variable. It remained almost constant at 1.2 MPa up to the middle of June, a value similar to that observed in 1974. After this time ψ_L(min) decreased more rapidly than ψ_S(min), the difference between them increasing to 2.0 MPa in late June.

4.3 Discussion

There are a number of reports in the literature of diurnal and seasonal changes in leaf water potential in both irrigated and unirrigated wheat (Campbell and Campbell 1974; Connor 1975; Denmead and Millar 1976a,b; Jones 1977; Martin and Dougherty 1975; Miller and Denmead 1976; Whitehead 1975; Yang and de Jong 1971). However, detailed comparison of the present study with those cited above is very difficult, since much of the leaf water potential data is reported without concurrent environmental data, e.g. soil water potentials and transpiration rates. The situation is further confounded by the different techniques involved in estimating ψ_L, some of which gave dubious results (for example, see Millar's (1974) comments on the technique used by Yang and de Jong 1971). There are, however, several aspects of the temporal changes in ψ_L in the present study which have been observed in other studies of wheat. For example, when the soil water potential was high, ψ_L was about -0.1 MPa in the morning, decreased by about 1.2 MPa on days of high evaporation and recovered to around 0.4 MPa in the evening (figure 4.1a, c and d). In comparable environments Whitehead (1975) found similar diurnal changes in ψ_L, but Millar and Denmead (1976) and Martin and Dougherty (1975) reported larger decreases in ψ_L during the day, 1.7 and 2.0 MPa respectively.

The presence of dew on the leaves on the morning of 20 May maintained a high ψ_L for several hours after evaporation had commenced (figure 4.3b). This effect has also been observed in wheat leaves by Martin and Dougherty (1975) and in wheat ears by Dougherty (1973a). Kerr and Beardsell (1975) found a similar effect of dew on ψ_L in paspalum pasture. High ψ_L can result from the absorption of dew by leaves, which usually involves only very small amounts of water (Vaadia and Waisel 1963; Slatyer 1967), or from dew providing a source of water for evaporation, thereby reducing transpiration.

Another notable aspect of the diurnal changes in ψ_L found in the present study is that ψ_L usually reached a minimum in the early afternoon, after Q (and hence E, see equation (3.1)) had reached its maximum value (figures 4.1 and 4.3). Also, the recovery of ψ_L in the afternoon was slower than its decline in the morning. ψ_L has also been observed to reach a minimum in the afternoon, and to recover slowly thereafter, in wheat, by Yang and de Jong (1971), Campbell and Campbell (1974) and Millar and Denmead (1976), and in other plants by Klepper (1968), Berger (1969), Jordan (1970), Millar *et al* (1970), Jordan and Ritchie (1971), Goode and Higgs (1973), Smart and Barrs (1973), Powell (1974), Reicosky, Campbell and Doty (1975), Jarvis (1976), Pereira and Kozlowski (1976), Powell and Thorpe (1977), Roberts (1977) and Reicosky and Lambert (1978). This type of response of ψ_L may indicate significant water storage in the plants, which contributes to the transpiration flow (see section 1.2.3). This aspect of plant water relations is considered in detail in chapter 6.

In the present study, and in general those cited above, the observed changes in ψ_L are consistent with two main factors which affect it, Q (which was generated by the crop evaporation rate) and ψ_S. Although the effects of Q and ψ_S will be considered separately here for clarity, there are obvious interactions between them and it is not implied that they are independent.

4.3.1 Flow

Since Q was calculated by dividing the crop evaporation rate (E) by the stem density (n) (see equation (3.1)), this assumes that evaporation from the soil was negligible. Penman and Long (1960) estimated evaporation from the soil to be 50% of the total evaporation from a wheat crop when the soil surface was wet, and negligible when the soil surface was dry. The total evaporation from the soil during a week in June was 10% of the total crop evaporation. Begg *et al* (1964) obtained a similar value in a field of bulrush millet during a single day's observations. Conversely, Denmead and Millar (1976a) calculated, from in canopy latent heat fluxes, that evaporation from the soil in dry land and irrigated wheat was respectively about 50% and 20% of the total crop evaporation. However, the wheat crops examined by Penman and Long (1960) and Denmead and Millar (1976a) had more open canopies than that in the present study. For example, the total leaf area index was 2 to 3 in the crops examined by Penman and Long (1960) and Denmead and Millar (1976a), compared with values between 2.5 and 5.5 during the experimental period of the present study. Neglecting soil evaporation, therefore, is unlikely to cause any large errors in the estimates of Q in the more dense canopy studied here.

The diurnal changes in ψ_L measured in the present study generally reflect concurrent changes in Q, which is a function of stem density (n) (equation 3.1). Figure 4.6 shows that n decreased by about 30% between mid-May and mid-June, after which it remained constant until harvest (Hunter pers. comm.). At the same evaporation rate, therefore, Q was about 50% greater after mid-June than it was in Mid-May. This greater flow caused a larger potential drop across the soil-plant system, and hence a lower ψ_L. This can be illustrated by considering two days of similar evaporation, but with different stem density. For example, the 29 May and 2 July 1974, when the respective maximum evaporation rates, E(max), were 1.4×10^{-7} and 1.5×10^{-7} m^3 m^{-2} ground s^{-1} and the corresponding stem densities were 480 and 330 m^{-2} ground. Around midday, when ψ_L was changing slowly, the maximum potential drop across the soil-plant system, $\Delta\psi(max)$, may be described using equation (1.2). Then we can write

$$\Delta\psi(max) = E(max)\ R/n. \qquad (4.1)$$

Assuming that the hydraulic resistance of the soil-plant system (R) was similar on the two days (see section 6.3.1), $\Delta\psi(max)$ on the 9 July (denoted by subscript 2) is given by

$$\Delta\psi_2(max) = n_1 E_2(max)\ \Delta\psi_1(max)/n_2 E_1(max), \qquad (4.2)$$

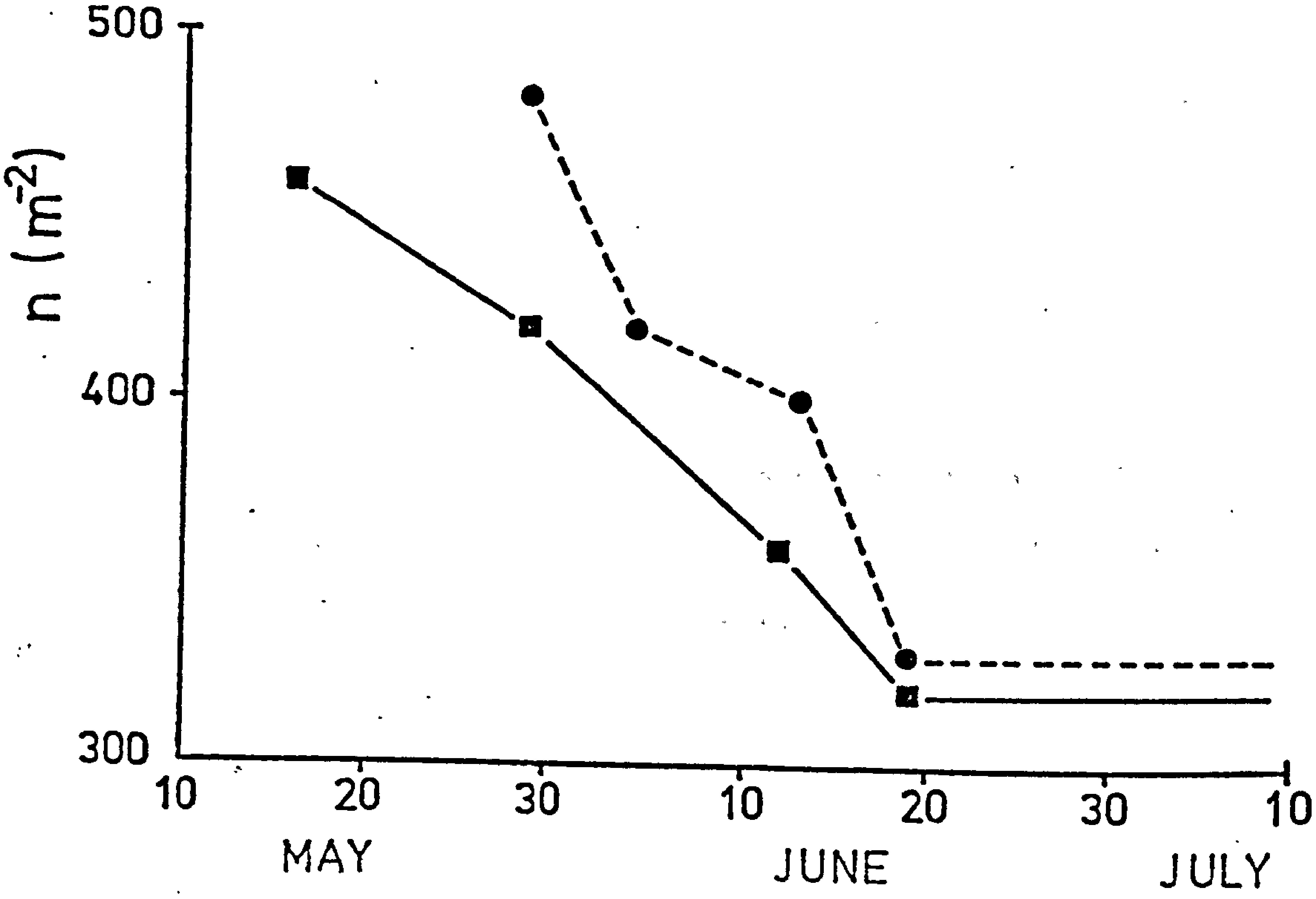


Figure 4.6 Changes in stem density (n) during 1974 (●) and 1975 (■).

Where variables with subscript 1 are those measured on 29 May. $\Delta\psi_1$(max) was 1.0 MPa (figure 4.5a) and substituting this into equation (4.2) along with n_1, n_2, E_1(max) and E_2(max) gives $\Delta\psi_2$ (max) as 1.5 MPa. This is in fact the measured value on this day (figure 4.5a). Decreasing the stem density in wheat, therefore, has the effect of reducing ψ_L, providing evaporation from the ground remains negligible. Jarvis (1975) reported that one effect of thinning a stand of trees was to reduce ψ_L, which can cause post-thinning water stress. In summary, diurnal changes in leaf water potential are a function of the changing flow of water through the soil-plant system, which is determined by the crop evaporation rate and stem density.

4.3.2 Soil water potential

During the growing season changes in ψ_s caused parallel changes in ψ_L when ψ_s was higher than about -0.6 MPa, figure 4.5. For example, in 1974 ψ_s(min) decreased from -0.2 MPa on 29 May to -0.5 MPa on 13 June. Concurrently ψ_L(min) decreased from -1.2 MPa to -1.7 MPa, 0.2 MPa more than the decrease in ψ_s(min). However, the extra decrease in ψ_L(min) can be accounted for by the different stem densities on the two days (480 and 400 m^{-2} respectively), E(max) being similar. When ψ_s(min) was lower than -0.6 MPa, i.e. after mid-June 1975, ψ_L was lower than could be accounted for by ψ_s and Q. This suggests that there was an increase in the hydraulic resistance of the soil-plant system. This is considered in more detail in chapter 6.

Low leaf water potentials, similar to those found in the present study, have also been observed in unirrigated wheat by Campbell and Campbell (1974), Martin and Dougherty (1975), Millar and Denmead (1976) and Whitehead (1975). Doughtery (1973b) has reported very low early morning values of ψ_L in wheat growing in dry soil. For example, ψ_L

was -1.8 MPa at 09h00 when ψ_s was about -1.5 MPa. In the present study similar values of ψ_L were measured on the morning of the 2 July, i.e. -1.6 MPa (figure 4.3f), when ψ_s was -1.4 MPa. Exceptionally low midday leaf water potentials of around -3 MPa, found here in unirrigated wheat on 24 June and 2 July 1975 (figure 4.3e and f), have also been observed by Campbell and Campbell (1974), Connor (1975) and Millar and Denmead (1976) in wheat growing in dry soil on days of high evaporation.

The degree to which soil water potential can affect ψ_L is emphasized by the different diurnal responses of ψ_L in irrigated and unirrigated soil (figure 4.4). ψ_L was up to 1.5 MPa lower in dry soil than wet soil with the same evaporative demand. This difference alone is similar to the maximum depression in ψ_L which occurred during 1974 and the first half of the 1975 season. ψ_s can, therefore, have a substantial effect on ψ_L. In the field this can occur in the long term (weeks to months) if the soil water is not adequately replenished by precipitation. Short term (minutes to hours) changes in ψ_L are caused by fluctuations, in evaporative demand, which determines the flow of water through the soil-plant system.

5. WATER FLOW IN THE STEM

5.1 Introduction

Water transpired by wheat plants has to traverse different paths in the stem to reach different leaves. The supply to the uppermost leaves must travel almost the entire length of stem, whereas the lowest leaves are reached in about one seventh of this distance (figure 5.1). Details of the stem xylem pathways in wheat, given by Percival (1921), Esau (1965) and Patrick (1972), show that there are two parallel vascular systems in the internode. One set of vessels, A in figure 5.2, supply water to the leaf attached to the node at the top of the internode. Another set, B in figure 5.2, conduct water through the node to the internode above. Similar flow pathways in wheat stems have been described by Denmead and Millar (1976a). Group B consists of about half of the large vascular bundles in the internode, the other half plus the smaller vascular bundles in the hypoderm form group A (Percival 1921).

Since water flows to the leaves via the stem xylem, which presents a viscous flow resistance, gradients of water potential between different leaves on the stem may be caused by the different path lengths of stem which the water traverses. The resistance to water flow in the stem (R_1) is characteristic of the flow pathway and, in this study, was estimated in two independent ways, which allowed comparisons to be made. First, by estimating the flow of water and potential gradient along the stem and using a form of the van den Honert (1948) model (equation (5.4)). Second, by measuring the size and number of xylem vessels in the stem, from which R_1 can be calculated (equation (5.5)). The latter method also gave estimates of the components of R_1, i.e. in the internode, node and leaf sheath.

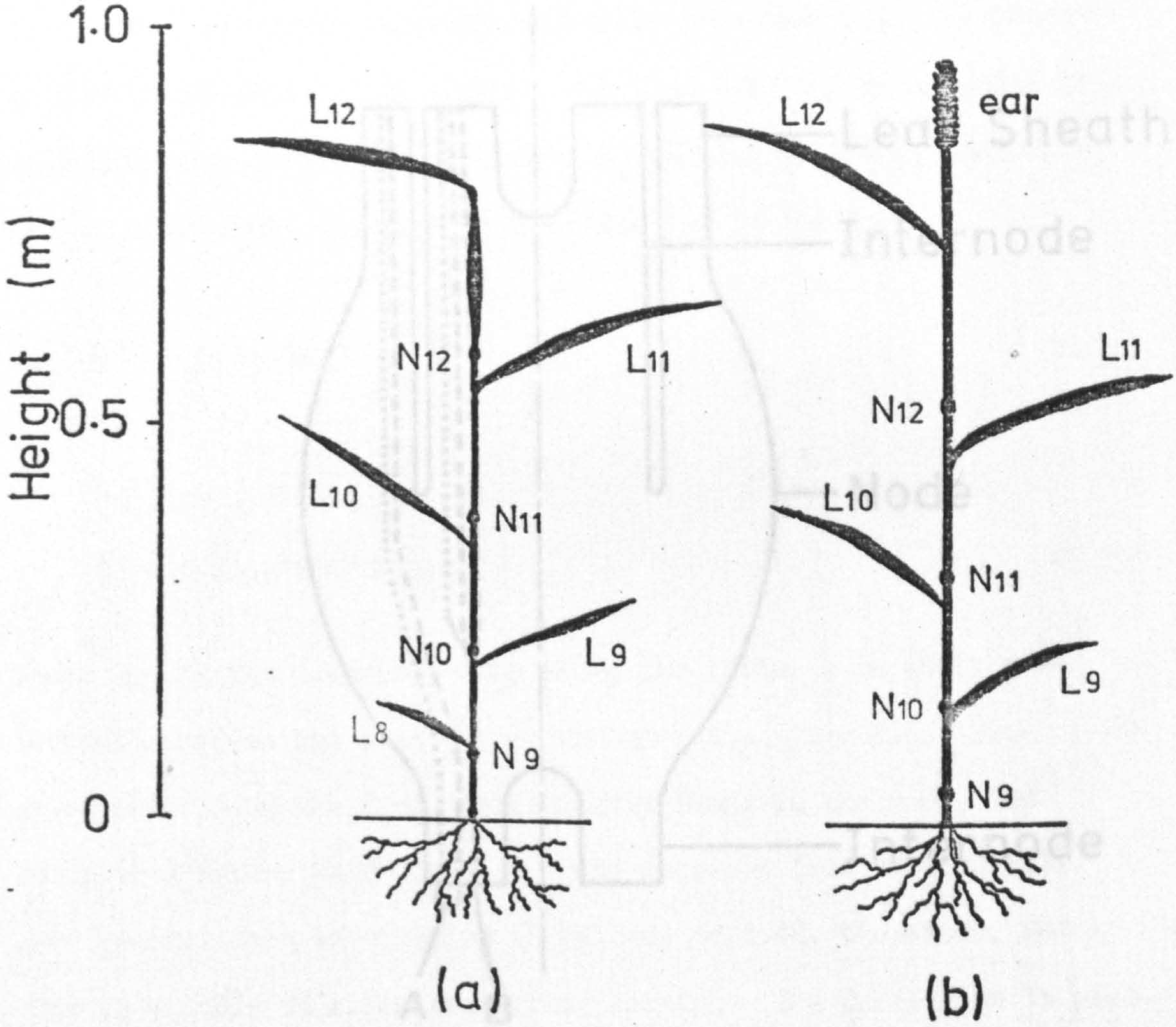


Figure 5.1 Scale drawing of a wheat stem on (a) 10 June 1975 and (b) 2 July 1975 showing the leaf (L) and node (N) numbers 9 to 12.

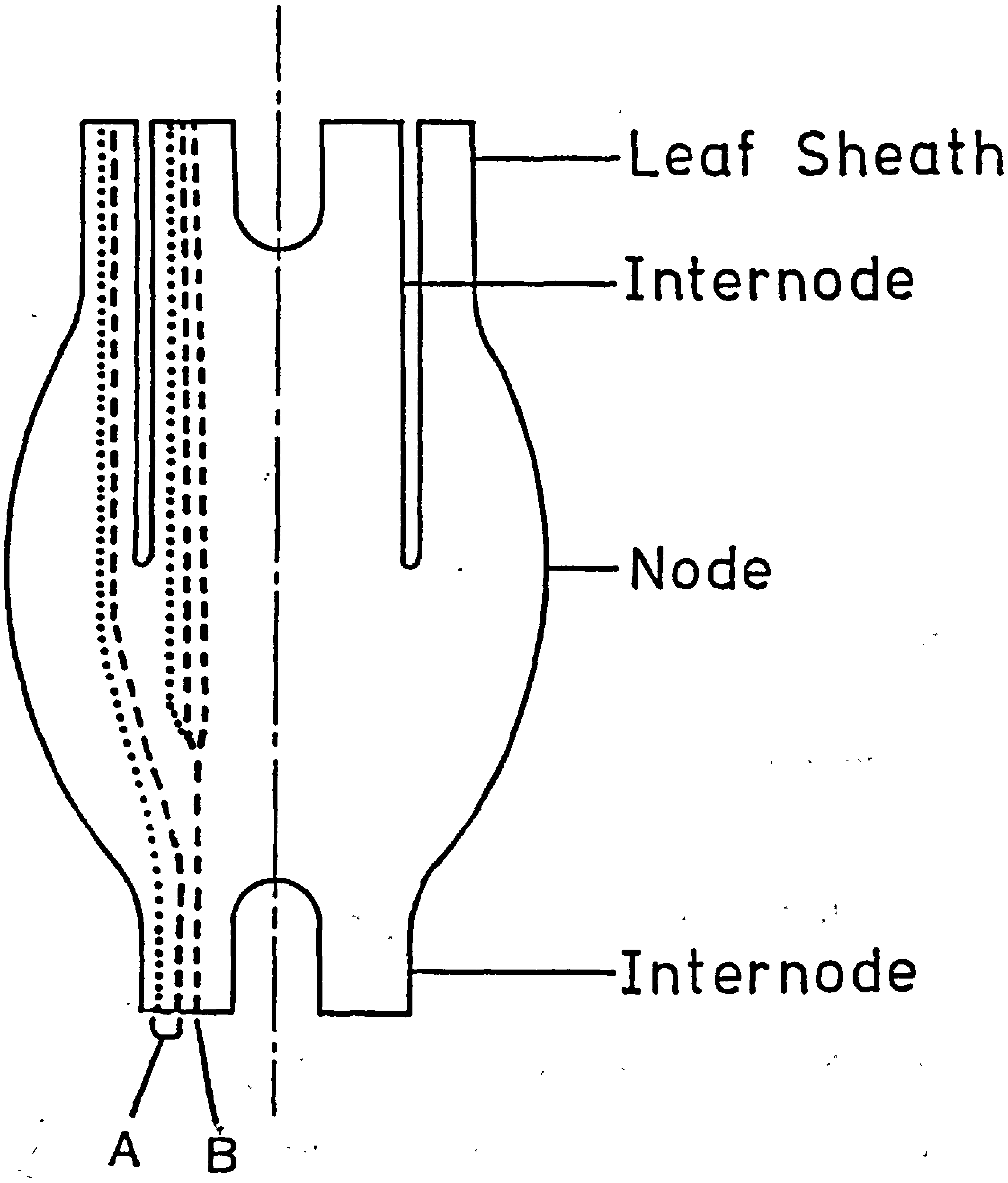


Figure 5.2 Schematic diagram of the path of large (----) and small (····) vascular bundles through a wheat node. Group A connects internode to leaf sheath, group B connects internodes.

5.2 Theory

It has been shown in appendix A.1 that water flow in the stem xylem is laminar, since the Reynolds number is less than 1 in the range of flow rates observed in wheat. The flow rate (Q) in a bundle of N cylindrical xylem vessels of radius a_i and length ℓ may, therefore, be described using the Hagen-Poiseuille law in the form

$$Q = (\pi\Delta\psi_1/8\eta\ell) \sum_{i=1}^{N} a_i^4 \qquad (5.1a)$$

or

$$Q = (\pi\Delta\psi_1/8\eta\ell)\, N(\bar{a})^4, \qquad (5.1b)$$

where $\Delta\psi_1$ is the potential drop along the xylem, $\bar{a}$ is their mean hydraulic radius and η is the viscosity of the xylem sap. Some of the xylem vessels in the stem, particularly those in the node, had elliptical rather than circular cross-sections (see section 5.3). A more general form of equation (5.1a) was derived, therefore, for laminar flow in vessels of elliptical cross-section. The derivation is given in full in appendix A.2 and in this case Q is given by the expression

$$Q = (\pi\Delta\psi_1/4\eta\ell) \sum_{i=1}^{N} b_i\, c_i/(b_i^{-2} + c_i^{-2}), \qquad (5.2)$$

where b_i and c_i are the semi-major and semi-minor axes of an ellipse. Comparison of equations (5.1b) and (5.2) gives an expression for the equivalent mean hydraulic 'radius', $\bar{a}$, of elliptical vessels as

$$\bar{a} = \left\{ (1/N) \sum_{i=1}^{N} 2b_i\, c_i/(b_i^{-2} + c_i^{-2}) \right\}^{\frac{1}{4}} \qquad (5.3)$$

Measurements of b_i and c_i were used in equation (5.3) to calculate the mean hydraulic radius of the stem xylem.

The hydraulic resistance of the stem (R_1), approximated using equation (1.1) is

$$R_1 = \Delta\psi_1/Q \qquad (5.4)$$

Combining equations (5.4) and (5.1) and rearranging gives an expression for R_1 as

$$R_1 = 8\eta\ell/\pi N(\bar{a})^4 \qquad (5.5)$$

R_1 was calculated by (i) substituting measured values of $\bar{a}$ and ℓ into equation (5.5) and (ii) from the slope of the linear relation between $\Delta\psi_1$ and Q (equation 5.4).

5.3 Anatomy of the stem xylem

The first part of this section contains a description of the number and pathway of xylem vessels in the upper stem of wheat. The hydraulic radii of these vessels are presented in the latter part of this section.

Table 5.1 summarizes the number of xylem vessels in the internode connecting nodes 10 and 11, in the plants sampled from the field on 10 June 1975 (see figure 5.1a). There were 33 large vascular bundles in the parenchyma, arranged regularly in a ring (plate 5.1). Each bundle contained four xylem vessels arranged in the form of a 'Y' pointing towards the centre of the stem (plate 5.2). Between 21 and 26 smaller vascular bundles were located in the hypoderm, each containing three xylem vessels (plate 5.3). A similar arrangement of vascular bundles and xylem vessels was found just below node 12 (plate 5.4), in the plants sampled from the field on 2 July 1975. However, at the base

LOCATION	N_B	N_x	N	$\bar{a}$ (μm)
Parenchyma	33	4	132	18
Hypoderm	21-26	3	63-78	11

Table 5.1 The number of vascular bundles (N_B), xylem vessels per bundle (N_x), total number of xylem vessels (N) and their mean hydraulic radius ($\bar{a}$) in the internode between node 10 and node 11. Plants sampled on 10 June 1975.

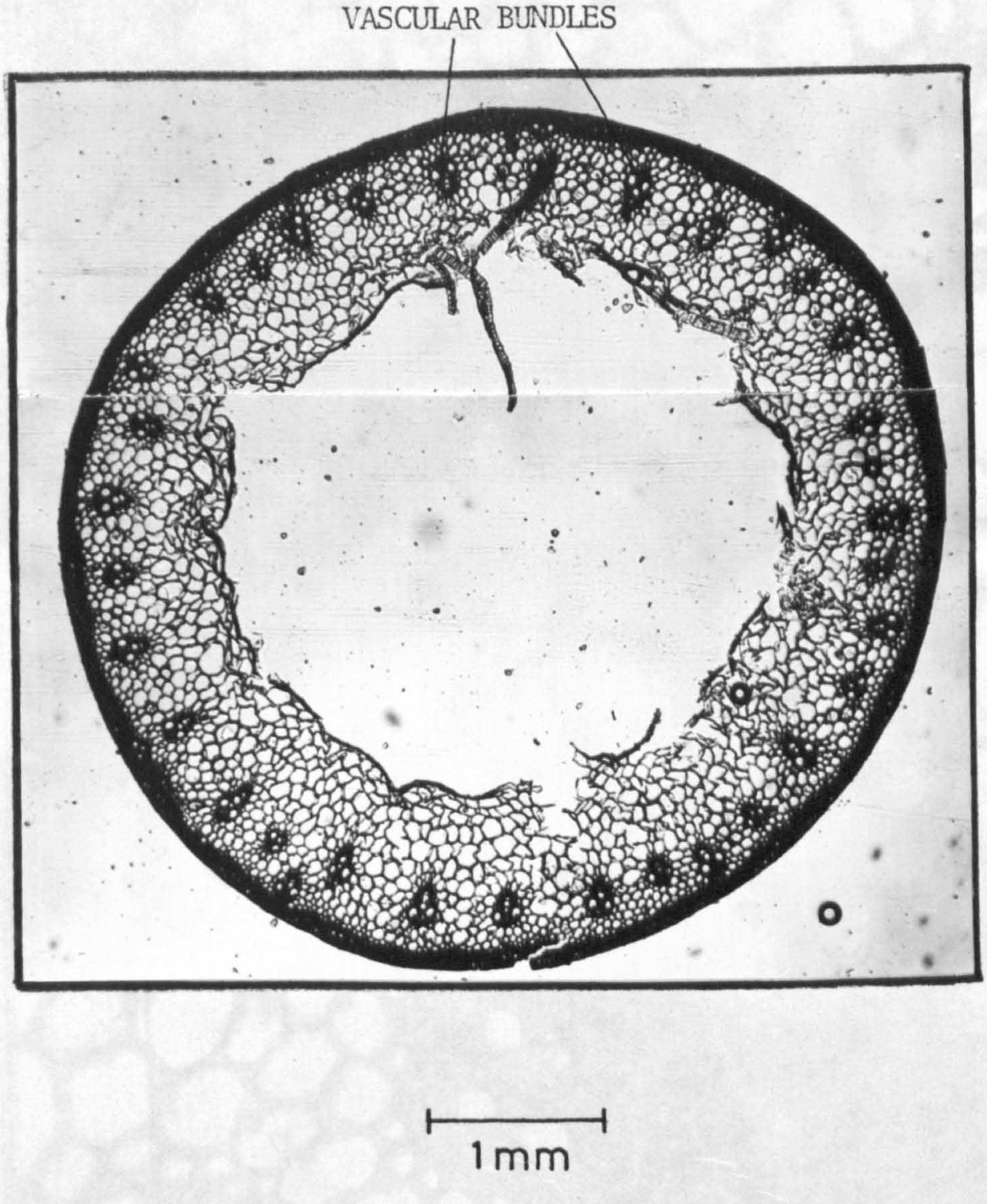
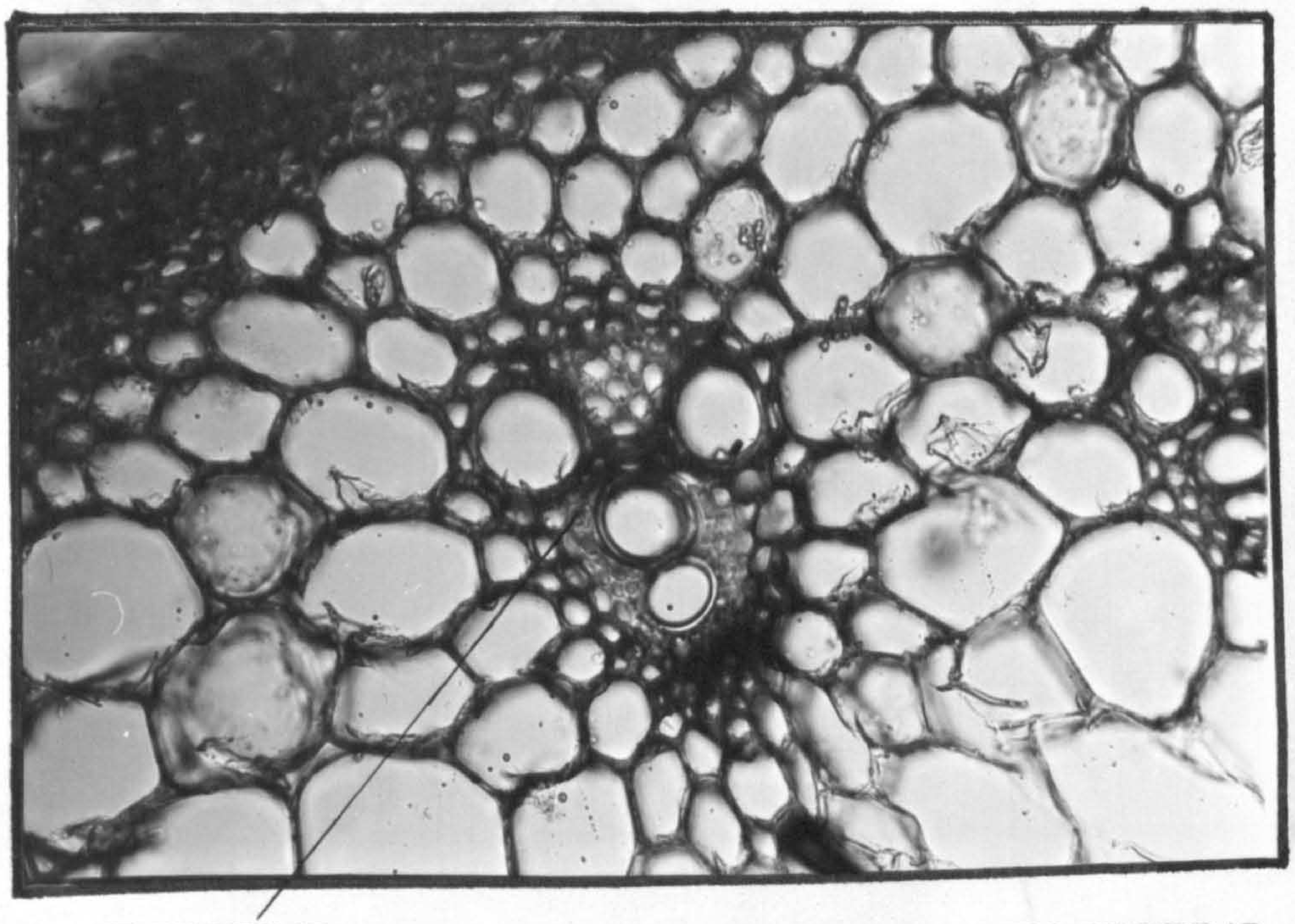


Plate 5.1 Transverse section of a wheat internode showing the large vascular bundles in the central parenchyma.



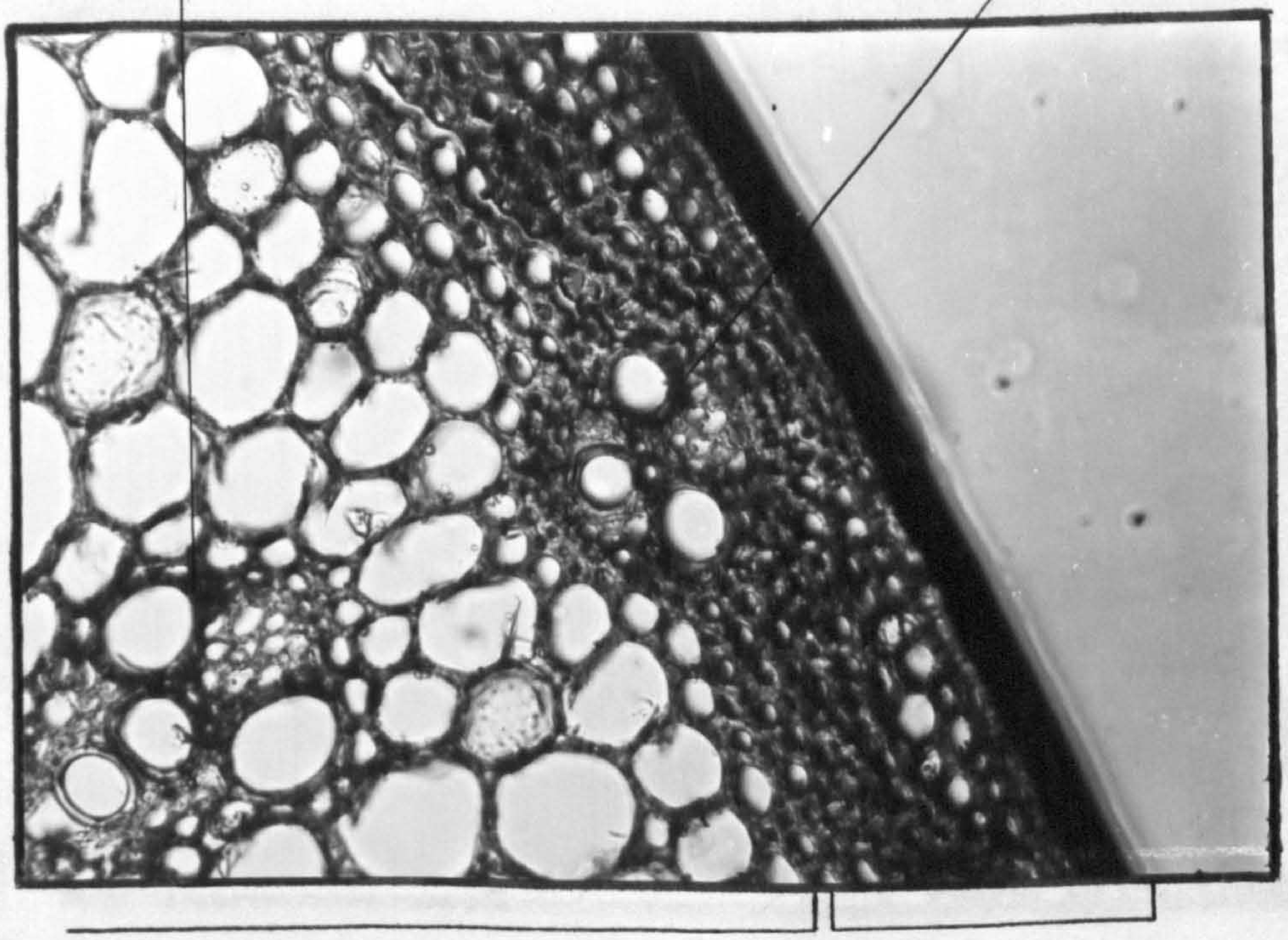
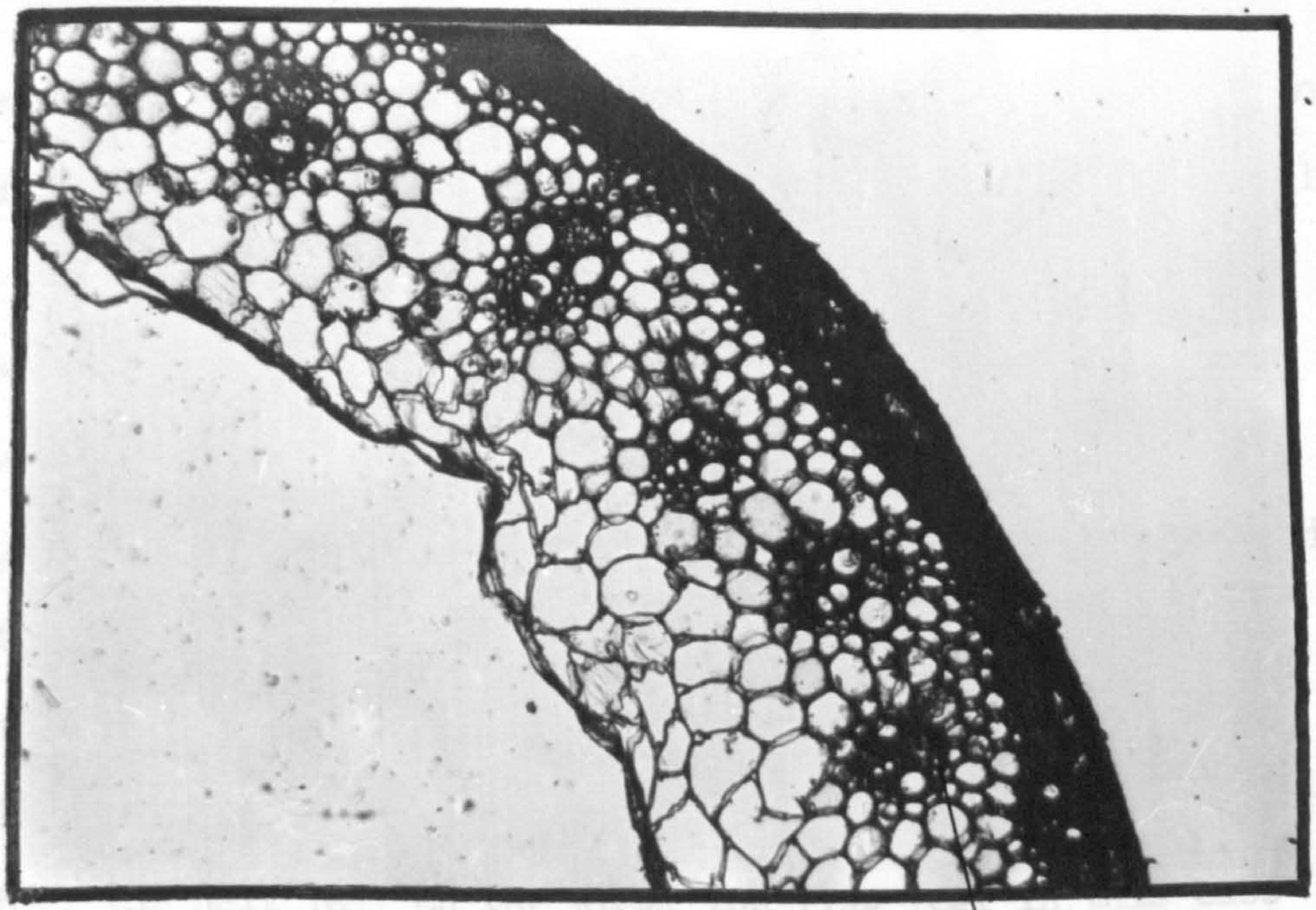


Plate 5.2 (Top) Transverse section of a wheat internode showing a large vascular bundle in the central parenchyma.

Plate 5.3 (Bottom) Transverse section of a wheat internode showing the xylem vessels in a small vascular bundle in the hypoderm.



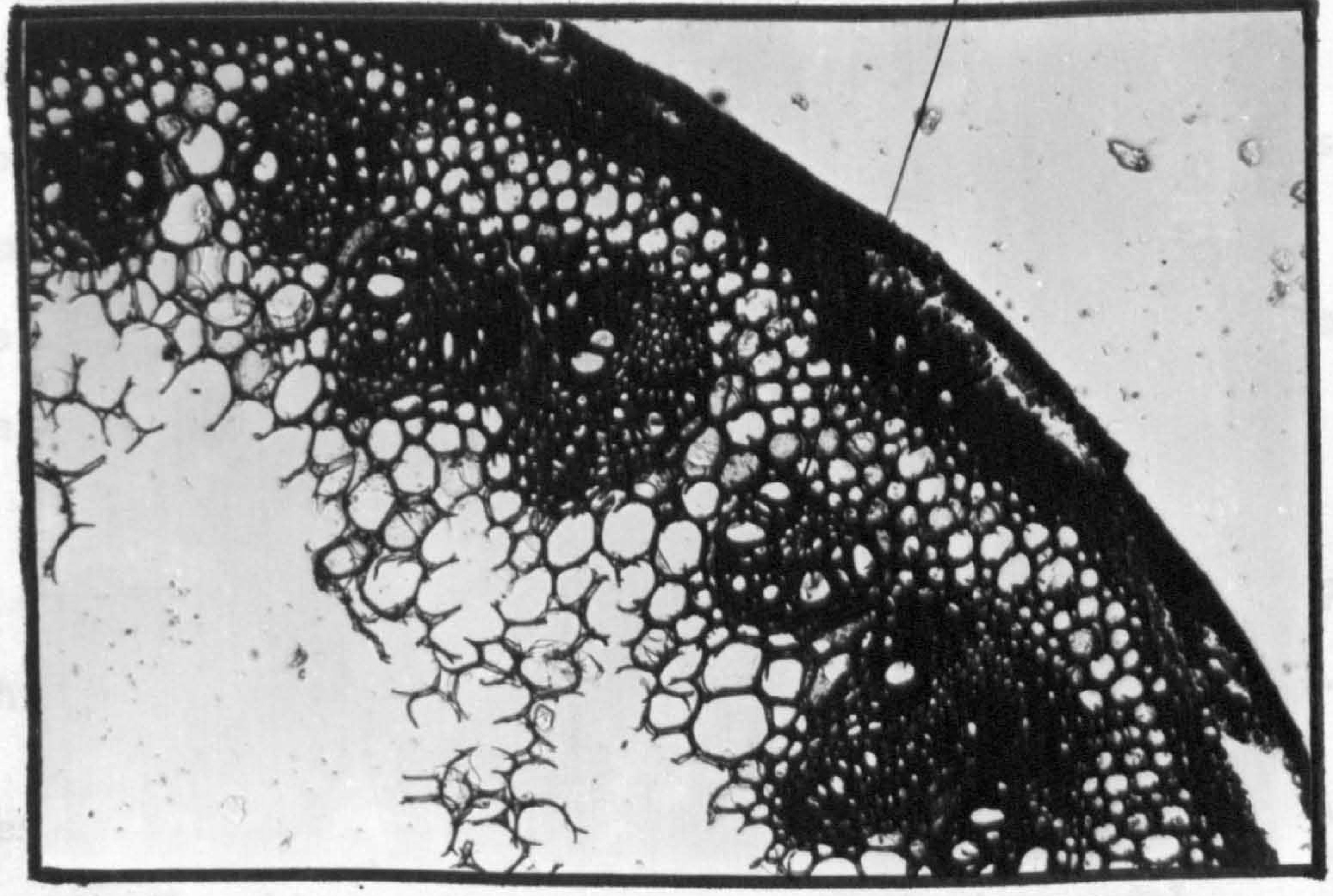


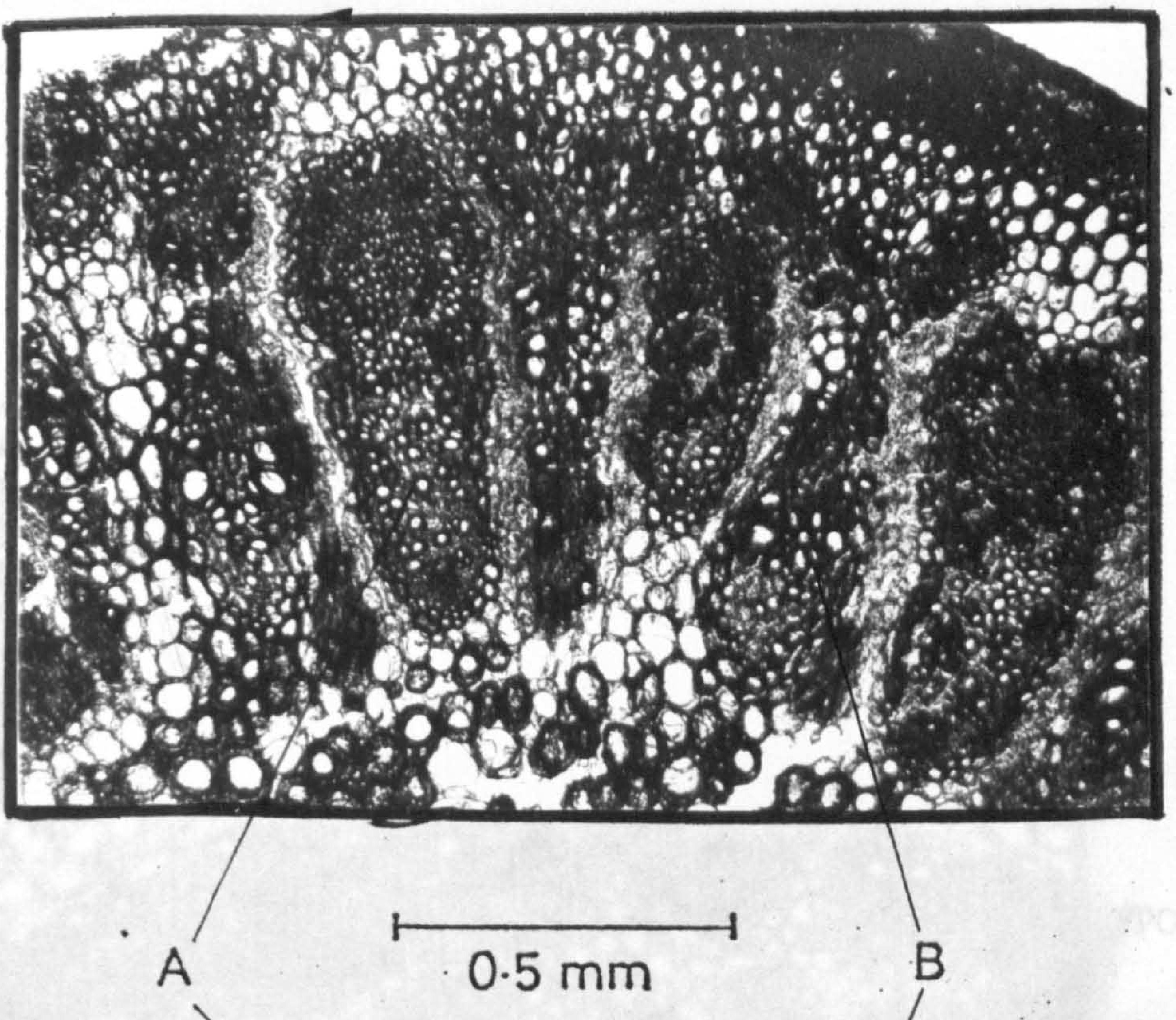
Plate 5.4 (Top) Transverse section of a wheat internode showing the xylem vessel and vascular bundle arrangement just below the flag leaf node.

Plate 5.5 (Bottom) Transverse section of a wheat node showing the xylem vessel and vascular bundle arrangement in the base of the flag leaf node (1.5 mm above plate 5.4).

of the node the vascular bundles and their surrounding stereome tissue became enlarged (plate 5.5), and the number of xylem vessels per bundle increased. Further into the node the vascular bundles and stereome formed an almost continuous ring, with the xylem elements grouped irregularly within them (plate 5.6). Within the node the vascular bundles separated into two distinct groups (A and B in plate 5.7), and by the centre of the node were clearly arranged into two concentric rings separated by the hypodermal ring of the next internode (plates 5.8 and 5.9). The outer ring of vascular bundles (group A) went to the leaf sheath of the next leaf on the stem, the flag leaf in this case (see figure 5.1b). The inner ring of vascular bundles (group B) went through the node to the internode above.

The number and pathway of xylem vessels which traversed node 12 are summarized in table 5.2. Below the node there were 34 large vascular bundles in the parenchyma, each containing four xylem vessels. Similar numbers were found in the internode between nodes 10 and 11 (see table 5.1). On entering node 12 half of the xylem vessels in the parenchyma (group B) each split up into three (on average), forming 204 xylem vessels in the internode above the node. The other half of the xylem vessels in the parenchyma, plus those in the hypoderm (group A) went through the node to the leaf sheath attached to the flag leaf.

Tables 5.1 and 5.2 also show the mean hydraulic radii of the above xylem vessels. The widest xylem vessels were in the internodal parenchyma, their mean hydraulic radii ranging from 13 µm above node 12, to 18 µm below node 11. Those in the hypoderm were narrower. Within the node all xylem vessels were constricted, to between a half and a third of their radius in the internodes. The smallest mean hydraulic radius, 5 µm, occurred in the xylem vessels in the base of



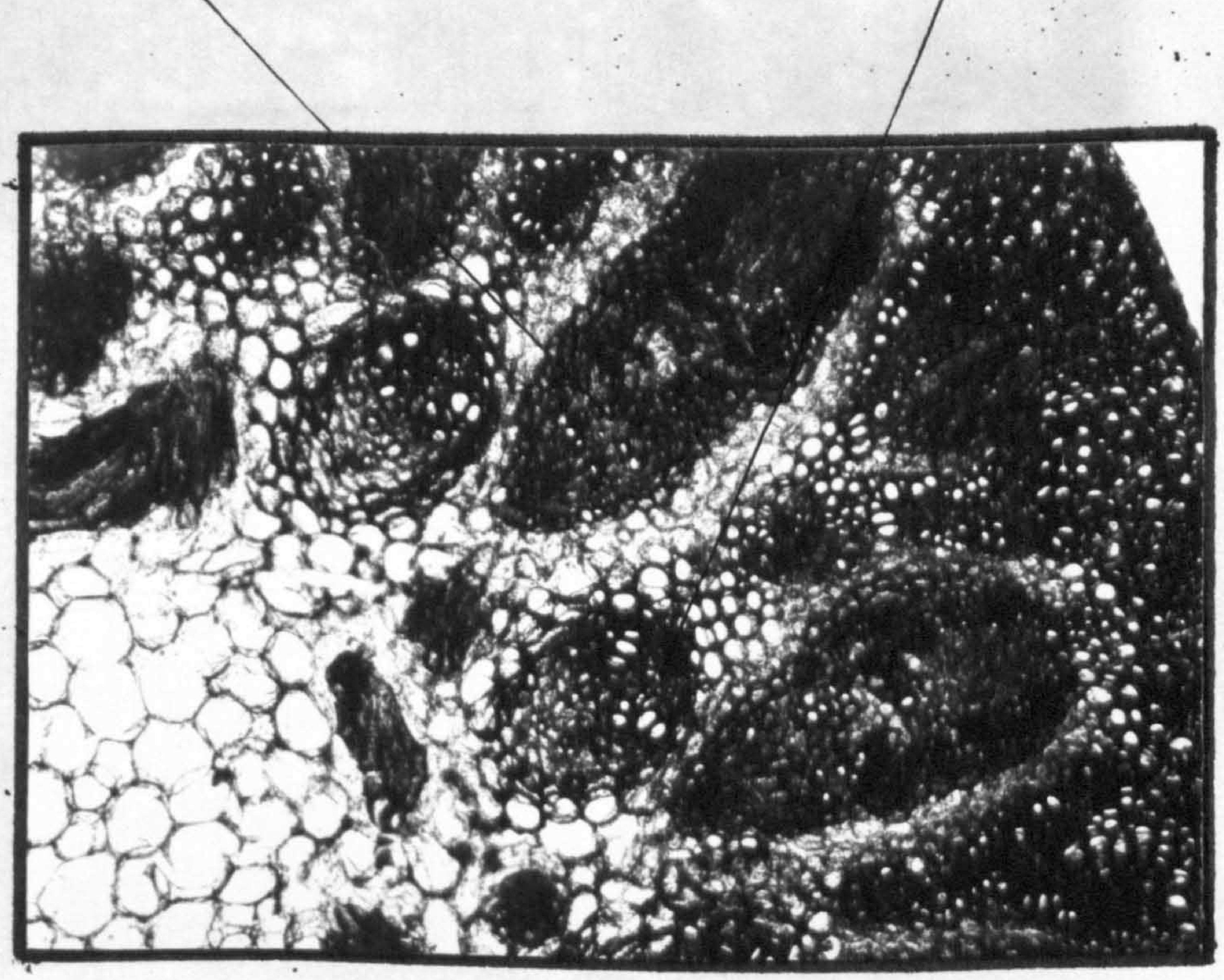


Plate 5.6 (Top) Transverse section of a wheat node showing the xylem vessels which go to the leaf sheath (A) and internode (B) above (1 mm above plate 5.5).

Plate 5.7 (Bottom) Transverse section of a wheat node showing the initial separation of the vascular bundles which go to the leaf sheath (A) and internode (B) above (1.3 mm above plate 5.6).

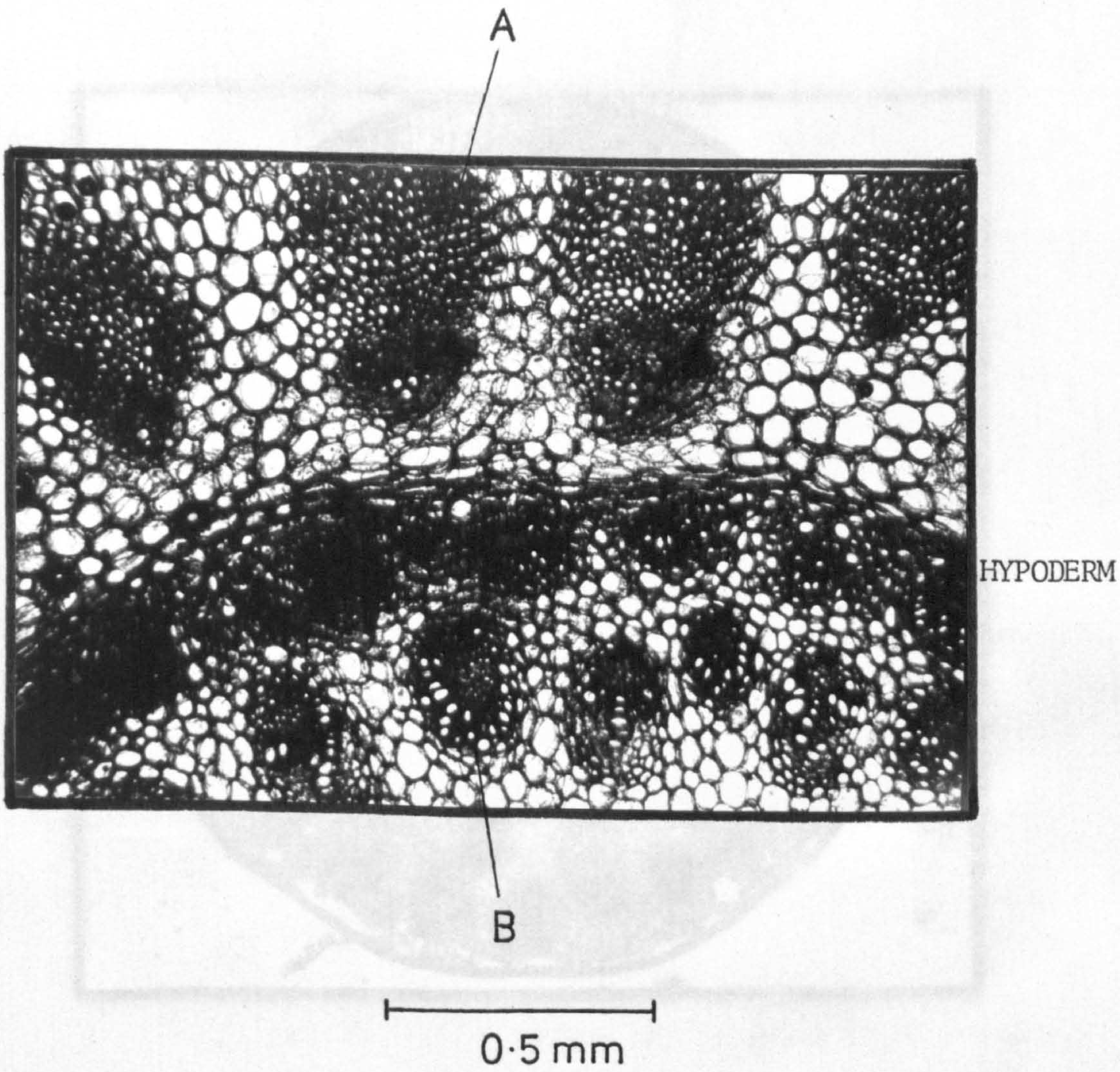


Plate 5.8 Transverse section through the centre of a wheat node showing the separate groups of vascular bundles which go to the leaf sheath (A) and the internode (B) above (1.6 mm above plate 5.7).

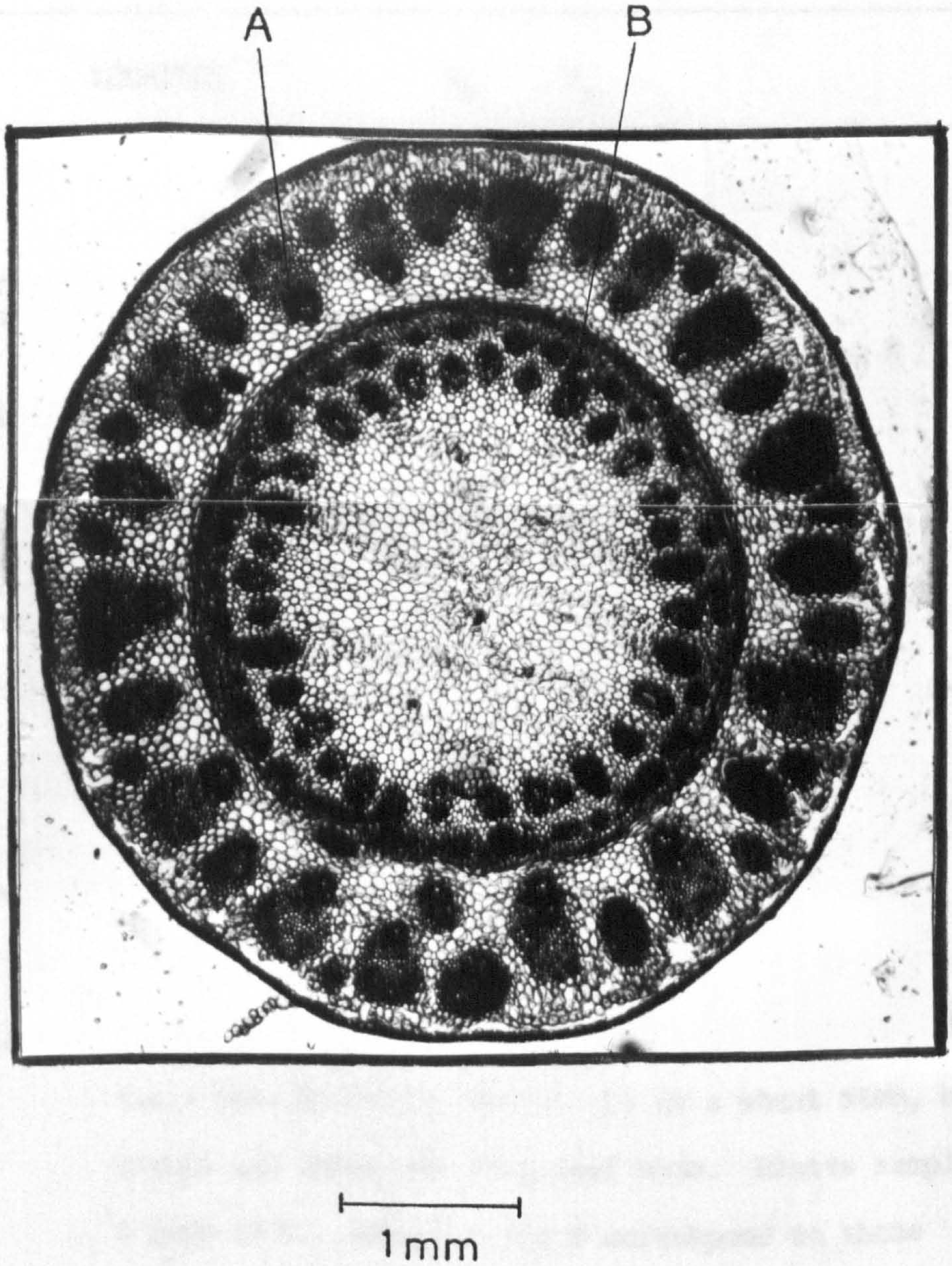
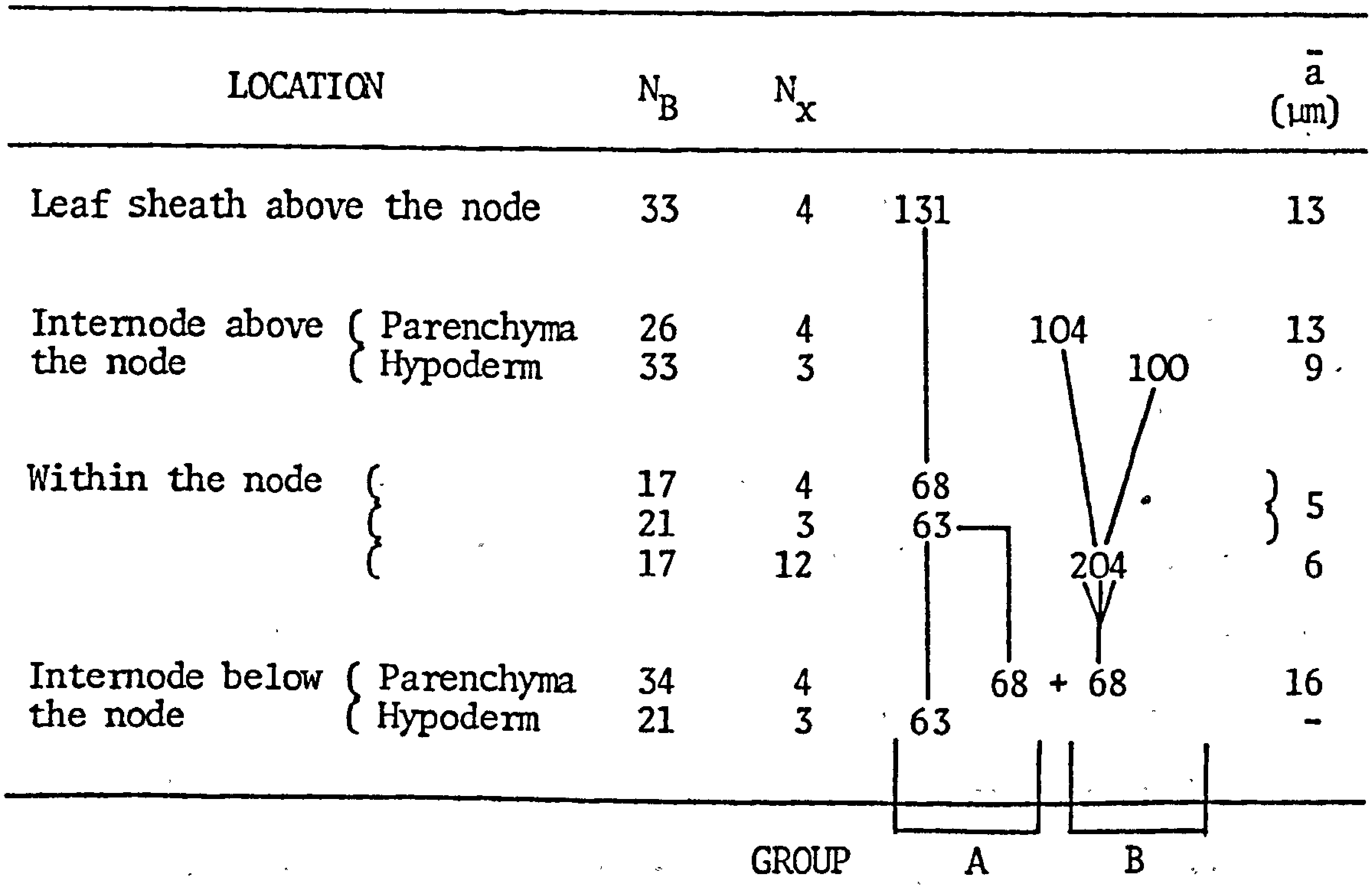


Plate 5.9 Transverse section through the centre of a wheat node showing the vascular bundle arrangement. The outer ring of bundles (group A) go to the leaf sheath above, the inner ring of bundles (group B) go to the internode above.



LOCATION		N_B	N_x		$\bar{a}$ (μm)
Leaf sheath above the node		33	4	131	13
Internode above the node	Parenchyma	26	4	104	13
	Hypoderm	33	3	100	9
Within the node		17	4	68	5
		21	3	63	
		17	12	204	6
Internode below the node	Parenchyma	34	4	68 + 68	16
	Hypoderm	21	3	63	-

GROUP A B

Table 5.2 The number of vascular bundles (N_B), xylem vessels per bundle (N_x), total number of xylem vessels (N) and their mean hydraulic radius (ā) in a wheat stem, below, within and above the flag leaf node. Plants samples on 2 July 1975. Groups A and B correspond to those illustrated in figure 5.2.

the node. The influence of nodal constriction on stem hydraulic resistance and water potential gradients along the stem is discussed in section 5.6.2.

5.4 Gradients in leaf water potential along the stem

As water was transpired by the wheat crops, gradients in leaf water potential developed along the stem. For example, figure 5.3 shows the changes in water potential of the youngest (leaf 11) and oldest (leaf 8) green leaves on 20 May 1975. In the morning and evening ψ_{L11} and ψ_{L8} were not significantly different. But, throughout most of the day ψ_{L11} was lower than ψ_{L8}, for example, by 0.3 MPa at 12h00. However, the youngest leaves did not always have the lowest water potentials around midday Figure 5.4 illustrates this, showing the changes in water potential of leaf 11 and leaf 10 during two days in 1974. The response on 29 May (figure 5.4a) is typical of that early in the season, when the younger leaf 11 was immature and the stem not fully extended. In this case the water potential of the older leaf, ψ_{L10}, was lower than that of the younger leaf, ψ_{L11}, during most of the morning and part of the afternoon. Conversely, ψ_{L11} was the lowest throughout the day later in the season, for example on 20 June (figure 5.4b), when leaf 11 was fully expanded and highest in the canopy.

Figures 5.3 and 5.4 both show that the gradient in leaf water potential along the stem varied diurnally, generally increasing with the flow of water along the stem, Q (see figures 4.1c and 4.3b). To further illustrate this, figure 5.5 shows a plot of Q against the difference in water potential between the oldest and youngest mature green leaves on the stem on three days in 1975. On the 16 and 20 May the oldest green leaf was leaf 8 and the youngest mature leaf was leaf 10. By the 10 June leaf 9 was the oldest green leaf and the flag leaf

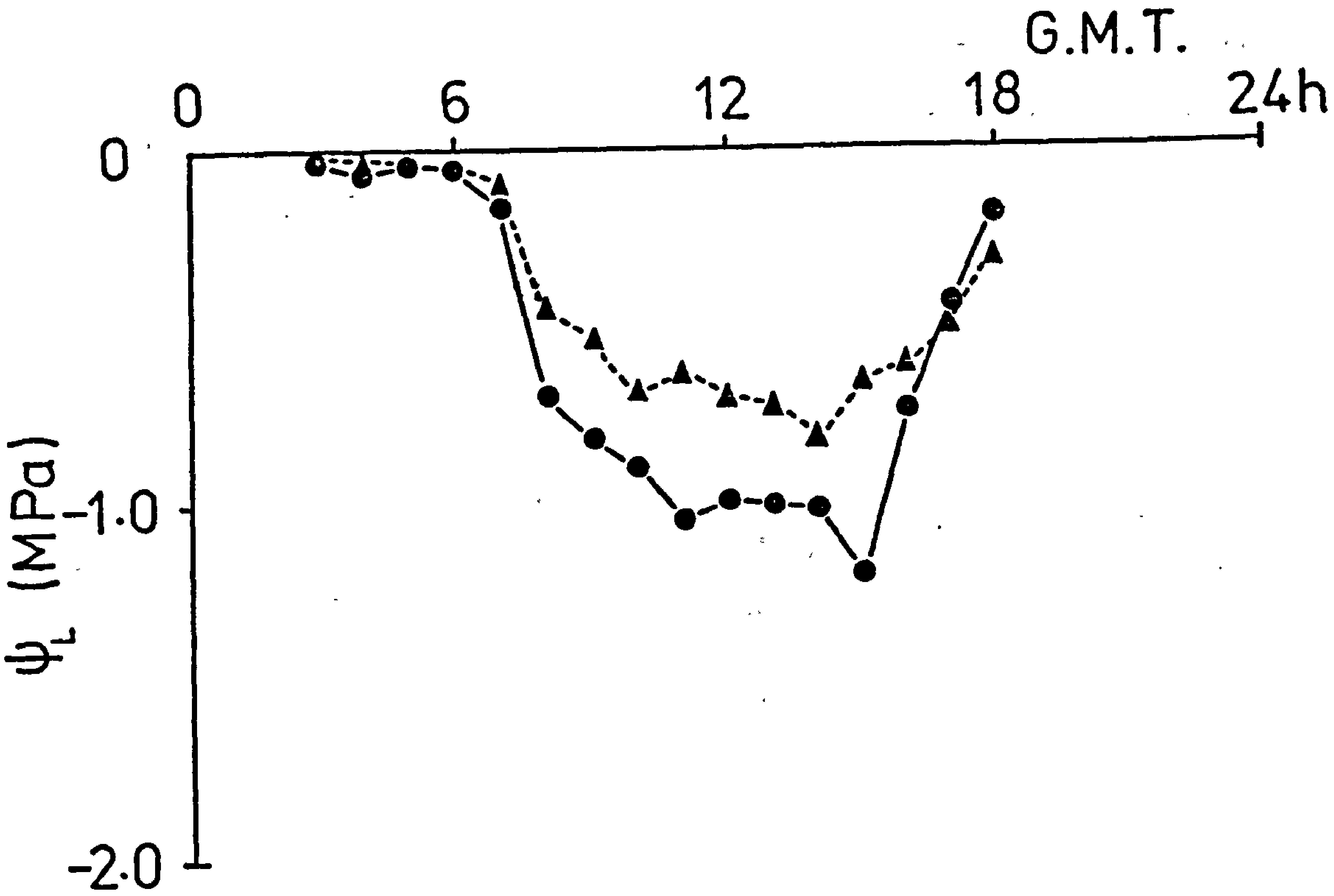


Figure 5.3 Changes in the water potential (ψ_L) of leaf 11 (●) and leaf 8 (▲), 20 May 1975.

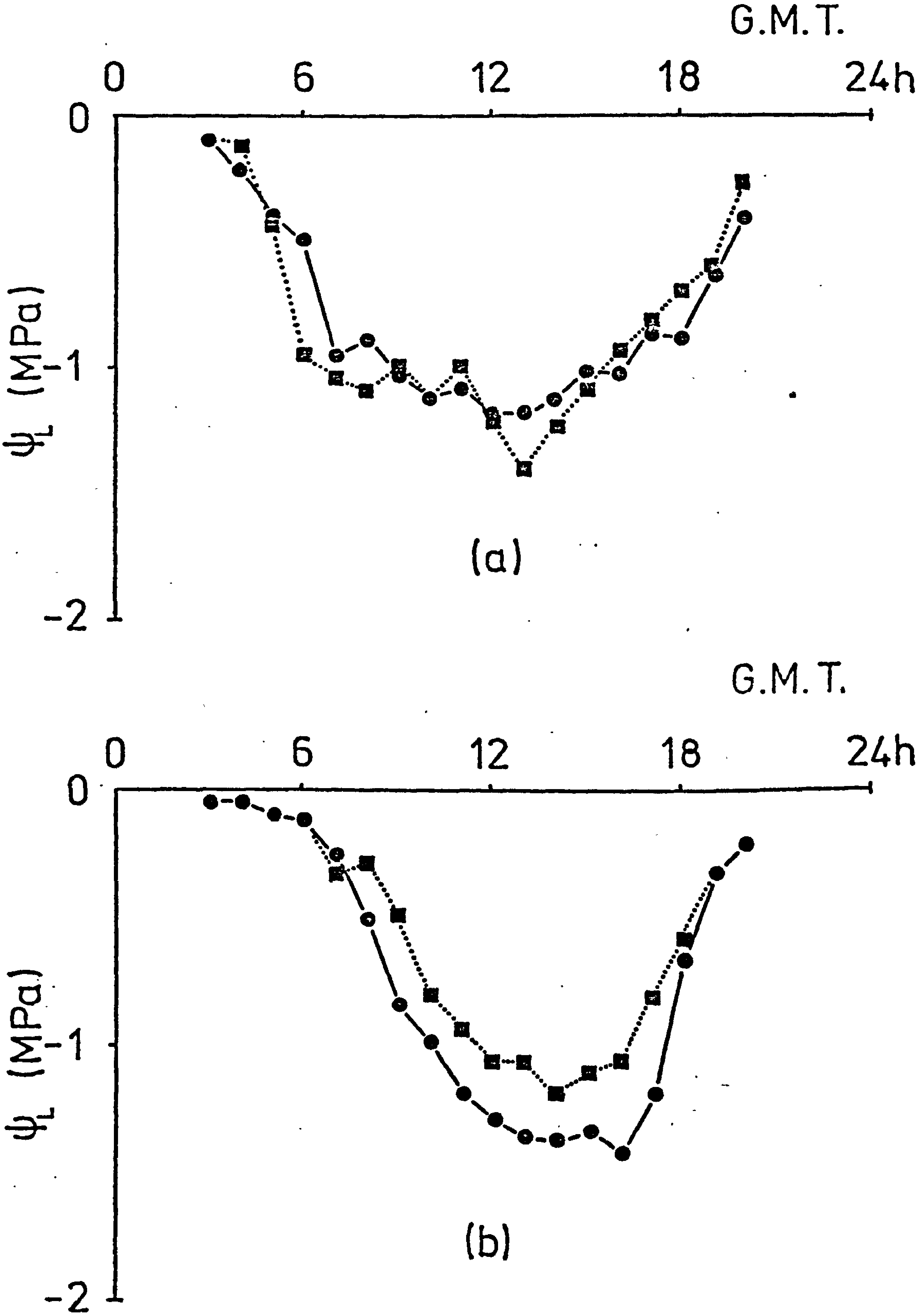


Figure 5.4 Changes in the water potential (ψ_L) of leaf 11 (●) and leaf 10 (■) on (a) 29 May 1974 and (b) 20 June 1974.

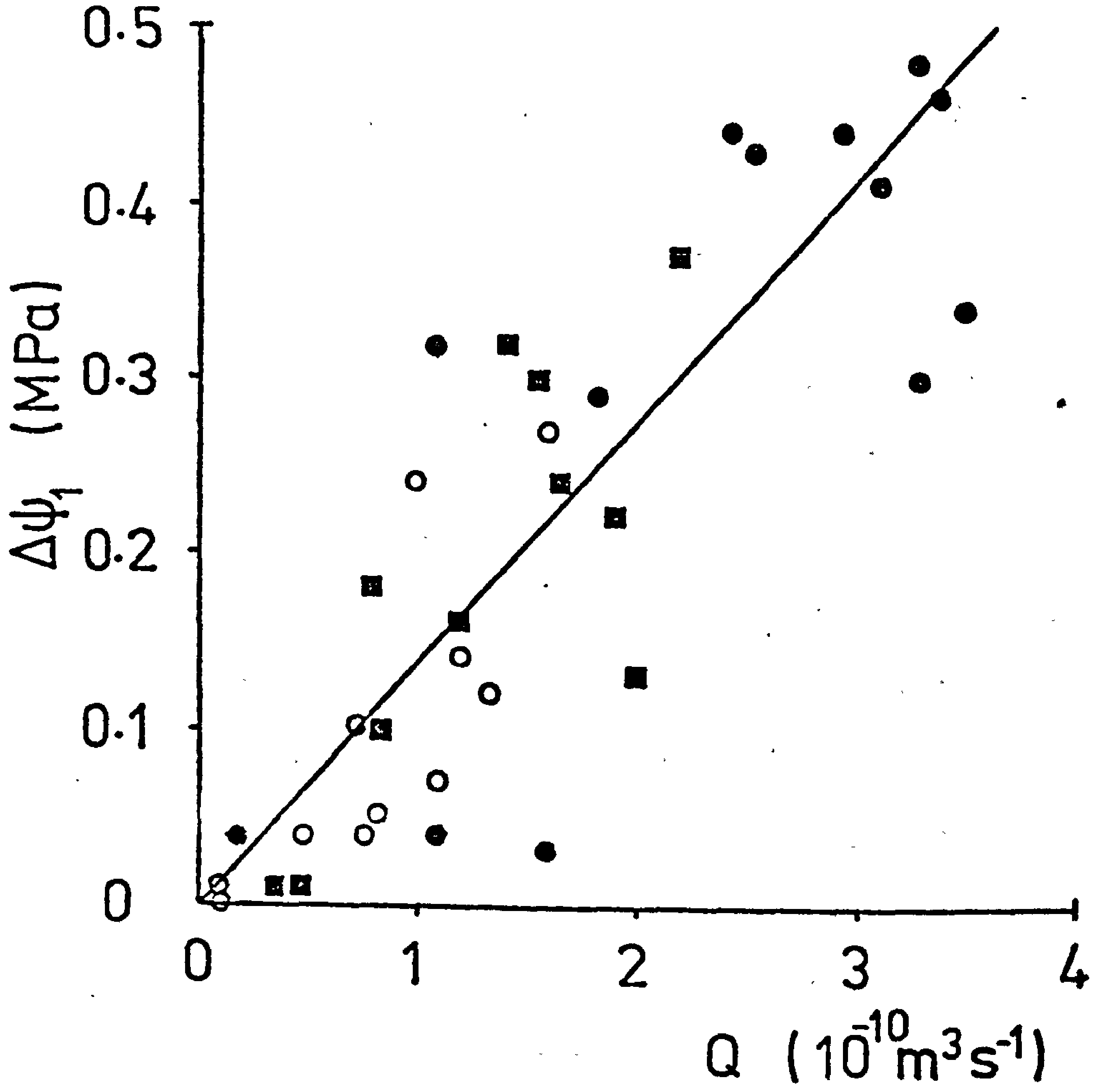


Figure 5.5 The relation between the gradient in water potential ($\Delta\psi_1$) and flow (Q) along the stem on 16 May 1975 (○), 20 May 1975 (■) and 10 June 1975 (●).

(leaf 12) was the youngest. As Q increased, the gradient in leaf water potential along the stem also increased, to a maximum of 0.5 MPa at the highest flow rate observed. The straight line was fitted to the data to give an estimate of the stem hydraulic resistance, which is presented in the following section.

5.5 Estimates of stem hydraulic resistance

The first estimate of stem hydraulic resistance (R_1) was obtained from the relation between the flow of water (Q) and the potential gradient ($\Delta\psi_1$) along the stem. $\Delta\psi_1$ was assumed to be equal to the difference in water potential between the oldest and youngest mature green leaves on the stem. Also, assuming that transpiration was from the uppermost leaves, then from equation (5.4) $\Delta\psi_1$, should be linearly related to Q. A linear regression was, therefore, fitted to the data shown in figure 5.5, and the slope of this line gave R_1 as 14 x 10^8 MPa s m^{-3}. The scatter of the data about the fitted line is due to uncertainties in the estimates of $\Delta\psi_1$ and Q and because not all of the water may have been transpired by the uppermost leaves (see section 5.6.2). Despite these uncertainties the standard error in R_1 was only ± 10% of R_1.

A second estimate of R_1 was calculated from the stem xylem measurements shown in table 5.2, using equation (5.5). The assumptions in this method are (i) flow in stem xylem vessels obeyed the Hagen-Poiseuille law, (ii) all the xylem vessels conducted water and (iii) the radialresistance between the xylem vessels was sufficiently low to allow the vessels at any point along the stem to be at the same potential. Table 5.3 shows the estimates of the components of R_1 in the upper stem. The hydraulic resistance of the internode immediately

LOCATION		R_1 (10^8 MPa s m^{-3})	ℓ (m)	R_1/ℓ (10^8 MPa s m^{-4})
Leaf sheath above the node		1.3	0.20	6.3
Internode above the node		2.3	0.33	7.1
Within the node	To leaf sheath	1.5	0.01	150
	To internode	0.15	0.01	15
Internode below the node		1.4	0.22	6.3

Table 5.3 The length (ℓ), hydraulic resistance (R_1) and resistance per unit length (R_1/ℓ) of the xylem vessels in a wheat stem; below, within and above the flag leaf node. R_1 was calculated using equation (5.5).

below node 12 was 1.4 x 10^8 MPa s m^{-3}, twice that for all the xylem vessels in this internode, since only half of them supplied water to flag leaf (see table 5.2). Similar resistances were calculated for the pathway through node 12 to the leaf sheath, and for the leaf sheath itself. Conversely, the resistance of the nodal pathway to the internode above was about one tenth of these values. To calculate the hydraulic resistance of the entire stem, up to leaf 12, it was necessary to assume that all the nodes and internodes below node 12 had similar resistances to those already described. This gave an estimate of R_1 of 6.6 x 10^8 MPa s m^{-3}, which is about half of that deduced from the stem potential gradient/flow relation.

To emphasize the degree to which nodal constriction of the xylem vessels impeded water flow in the stem, the resistance per unit length of the stem components shown in table 5.3 were also calculated. Expressed in this way, the nodal pathway to the flag leaf presented more than twenty times the resistance to water flow that the internodes and leaf sheath did. This is a reflection of the small radii of the xylem vessels in the node (table 5.2).

5.6 Discussion

5.6.1 Stem xylem anatomy

The number of xylem vessels and their paths through the stem found in the present study are consistent with previous anatomical descriptions of wheat stems (Percival 1921; Esau 1965; Patrick 1972). For example, in a mature stem of another wheat variety (*Triticum vulgare* cv Squarehead), also grown as an ordinary field crop, Percival (1921) found 30 to 41 large vascular bundles and 19 to 32 small hypodermal vascular bundles in the different internodes. Even more variation occurred between different stems, but, in general, one of the two uppermost internodes had the greatest number of vascular bundles. The number of vascular bundles (N_B) found in the uppermost internodes in the present study (see tables 5.1 and 5.2) are, therefore, within the range found by Percival (1921). In the lower internodes of the stem N_B could not be determined in the time available in the present study. A more comprehensive study of xylem anatomy should, therefore, attempt to determine the full range of the variability in N_B, (i) between different internodes on a single stem and (ii) between different stems of wheat varieties other than that examined by Percival (1921).

Although N_B varied considerably in the stem, the total number of xylem vessels (N) in the vascular bundles was less variable, i.e. between 195 and 210. A similar value of N, 198, was found by Denmead and Millar (1976a) in wheat (*Triticum aestivum* cv Heron) grown in Australia. They also gave a range of xylem vessel radii, from 3 to 16 μm, and using this data in equation (5.3) the mean hydraulic radius, $\bar{a}$, of all the xylem vessels was calculated as 11 μm. In comparison, corresponding values of $\bar{a}$ were larger in the present study, for example, 17 μm between nodes 10 and 11 and 15 μm below node 12. In species other than wheat, a range of stem xylem radii have been found. For example, substitution of Dimond's (1966) measurements of stem xylem radii in tomato into equation (5.3) gave $\bar{a}$ as 36 μm. Even larger xylem vessels, with radii up to 430 μm, were found in *Sechium edule* by Giordano *et al* (1978). From measurements of the permeability of the wood of Sitka Spruce and Grand Fir trees, Petty (1970) and Puritch and Petty (1971) deduced tracheid radii of 10 to 14 μm, similar to the stem xylem radii in wheat stems.

Constriction of the xylem vessels in the node (table 5.2) has also been observed in Cottonwood (*Populus deltoides* Bartr.) by Isebrands and Larson (1977). More recently, Larson and Isebrands (1978) reported that the xylem vessels had a median radius of 6 µm in a node of this species, similar to that in the wheat node examined in the present study. The nodal constricted zone has been shown to have a high resistance to water flow (section 5.5). Other investigators have also reported regions of restricted water flow at the nodal junction between stem and petiole (Begg and Turner 1970; Ritchie and Hinckley 1975). The following section contains a fuller discussion of the resistance to water flow in the stem.

5.6.2 Stem hydraulic resistance

The estimate of the total hydraulic resistance of the stem (R_1) from stem xylem measurements was about half of that derived from the stem potential gradient/flow relation (section 5.5). Similar discrepancies between estimates of R_1 by these two methods have also been found in wheat stems (Denmead and Millar 1976a), Red Maple stems (Tyree and Zimmermann 1971) and various herbs and shrubs (Zimmermann and Brown 1974). More recently, Giordano *et al* (1978) measured flow in individual xylem vessels of *Sechium edule* stems, and found R_1, estimated using the Hagen-Poiseuille law, was up to two orders of magnitude lower than that calculated for the measured flow and potential gradient. Conversely, other investigators reported good agreement between estimates of R_1 from xylem dimensions and flow/potential gradient measurements (Dimond 1966; Zimmerman and Brown 1974). One possible reason for the underestimation of R_1 from xylem dimensions is that some of the vessels may have been totally or partially blocked. For example, by cross walls, tyloses or loss of liquid continuity in the xylem. This would affect the number of effective xylem vessles (N) and/or their mean hydraulic radius, $\bar{a}$. Since R_1 is proportional to $1/(\bar{a})^4$, a 16% decrease in the effective value of $\bar{a}$ would double R_1. Dubé *et al* (1975) found a clear relation between the decrease in the number of functional xylem, as indicated by staining tests, and the increased hydraulic resistance in the upper stem of *Zea mays*. Peel (1965) found a similar effect in three tree species. Estimation of R_1 from stem xylem dimensions will, therefore, give uncertain results, since the effective values of N and $\bar{a}$ are very difficult to determine. Furthermore, Giordano *et al* (1978) suggest that the Hagen-Poiseuille law does not apply to flow in xylem vessels, which are not smooth walled, continuous or of constant radius.

Gradients in ψ_L and concurrent water flow along the stem provide a more direct estimate of R_1. Similar to wheat, midday gradients in ψ_L along the stem of about 0.5 MPa have been found in other herbaceous species (Begg and Turner 1970; Jordan 1970; Turner 1975) and in trees (Waggoner and Turner 1971; Hellkvist, Richards and Jarvis 1974). However, larger gradients in ψ_L have been found in wheat stems by Denmead and Millar (1976a) and in barley stems by Millar, Duysen and Wilkinson (1968). The large difference in water flow in the above species implies that their stem hydraulic resistances would also be very different (see Biscoe *et al* 1976). Comparison of the ease with which stems of different species conduct water can be made by calculating their hydraulic resistivity, r_1, defined as

$$r_1 = R_1 A/\ell, \qquad (5.6)$$

(after Jarvis 1975), where A and ℓ are the cross-sectional area and length of the stem xylem respectively. Table 5.4 contains the calculated value of r_1 for wheat and, for comparison, some published values of stem resistivity in other herbaceous and tree species (see also Heine 1971). r_1 in wheat was much greater than that in tomato and sunflower, but similar to that in some tree species. However different techniques were used to determine r_1. For example, the estimates of r_1 in trees were obtained by applying pressure gradients to excised pieces of wood, whereas r_1 in the present study was calculated using estimates of potential gradients and flow along the stem which occurred *in situ*.

The large difference in the two estimates of r_1 in wheat, shown in table 5.4, arises partly from the larger gradients in ψ_L along the stem found by Denmead and Millar (1976a), i.e. about twice those found in the present study at similar flow rates. However, most of the discrepancy in these two estimates of r_1 arises from the different patterns of water flow in the stem. Using in canopy water flux estimates Denmead and Millar (1976a) calculated that large quantities of water were transpired by the lower leaves on the stem. For example, typically 50% of the total transpiration in an irrigated wheat crop was from leaves below the flag leaf. This is in disagreement with transpiration measurements in the present study, where more than 80% of transpiration from the mature crop was from the flag leaf and ear (Marshall pers. comm.). The different stem flow patterns found in these two studies may have resulted from the different leaf areas in the two crops. For example, in the mature crop studied here the total leaf area index was 5.5, compared with 3.2 in the crop examined by Denmead and Millar (1976a). Hence greater radiation interception by the leaves in the present crop may have caused greater transpiration from the upper canopy.

SPECIES	r_1 (MPa s m^{-2})	Source	
Wheat	205	This study	
Wheat	1270	Denmead and Millar (1976a)	
Tomato	25	Jenson *et al* (1961)	
Tomato	4*	Dimond (1966)	
Sunflower	14	Jenson *et al* (1961)	
Yew	2,220	Ewart (1905)	quoted by Heine (1971)
Elm	1,000	Ewart (1905)	
Pear	357	Ewart (1905)	
Elder	250	Ewart (1905)	
Apple	135	Ewart (1905)	
Poplar	105	Heine (1970)	
Poplar	29	Münch (1942)	

* *Calculated using the Hagen-Poiseuille law.*

Table 5.4 The resistivity (r_1) of the stems of various herbaceous and tree species.

The effect of leaf area on stem flow can also be illustrated using the ψ_L data shown in figure 5.4. On 29 May 1974 the flag leaf (leaf 11) area index was only 0.08, compared with 0.54 for leaf 10. Leaf 10 was, therefore, probably transpiring more than the flag leaf, which accounts for its lower water potential (figure 5.4a). On 20 June 1974 the flag leaf and ear had an area index of 1.07, now greater than that of leaf 10 which was 0.86. The flag leaf and ear would then have been the major transpiring organs in the crop, consequently having the lowest water potentials (figure 5.4b).

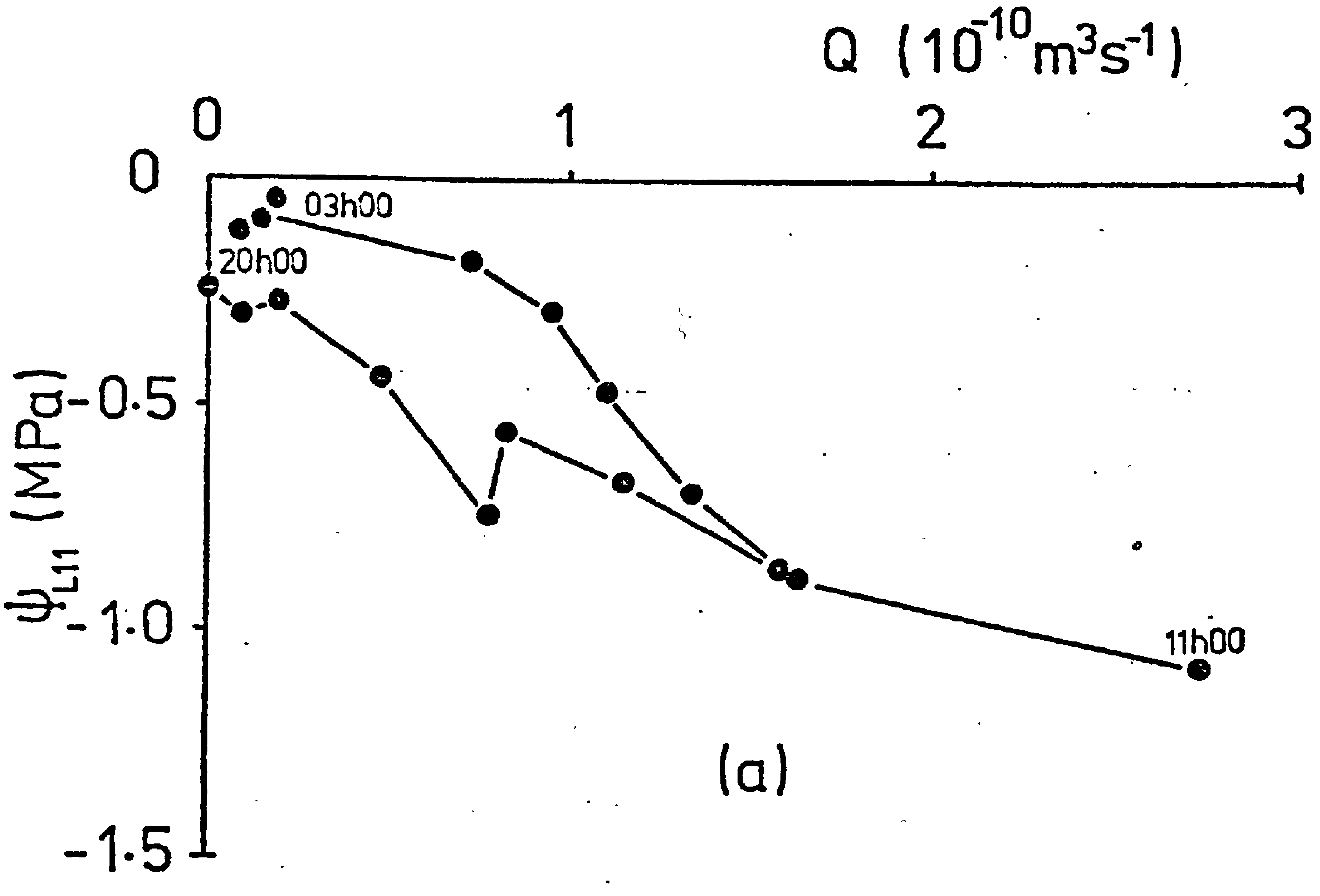
Clearly R_1 estimates, made from ψ_L gradients measured along the stem, depend on the pattern of water flow through the stem. Making allowance for the flow to different leaves, as Denmead and Millar (1976a) did, should provide the correct value of R_1. However, from the viewpoint of predicting ψ_L their model requires knowledge of individual leaf water fluxes. Until a reliable method of determining these is developed the much simpler van den Honert (1948) model, used in this study, provides a useful method of estimating the potential gradients along wheat stems.

Stem hydraulic resistance is only part of the total hydraulic resistance of the soil-plant system (R). The following section contains a description of a model of flow in the soil-plant system, which allowed R to be calculated.

6. A MODEL OF FLOW IN THE SOIL-PLANT SYSTEM

6.1 Introduction

The diurnal changes in leaf water potential (ψ_L), described in chapter 4, were said to reflect concurrent changes in water flow (Q) through the plants. This chapter describes the relation between ψ_L and Q, and the model of flow in the soil-plant system used to simulate it. Figure 6.1 shows two typical relations between ψ_L and Q measured in this study. On both days shown the soil water potential (ψ_s) was high, about -0.02 MPa. There was no simple linear relation between ψ_L and Q, since at the same flow rate ψ_L was lower in the morning than in the afternoon. Hence a model of the soil-plant system was required which could account for the hysteresis between ψ_L and Q. Of the models in the literature which can do this, most introduce a storage term within the soil, but not within the plants (e.g. see Cowan 1965). These models also require several unproven assumptions, and can only be used with certainty when the soil hydraulic properties are known. Furthermore, the soil in the field is highly variable and the soil hydraulic conductivity and its dependence on soil water content are almost impossible to determine accurately with present techniques. Consequently, a much simpler model is presented here, which has the advantage that it does not require any detailed knowledge of the soil hydraulic properties or the exact location of the hydraulic capacitance/s within the system. Using this model the hydraulic resistance (R) and capacitance (C) of the soil-plant system were estimated from the diurnal changes in ψ_L and Q. In addition, some deductions about the location of the major components of R and C were made possible by the results of experiments on the recovery of ψ_L to the source water potential when transpiration was stopped.



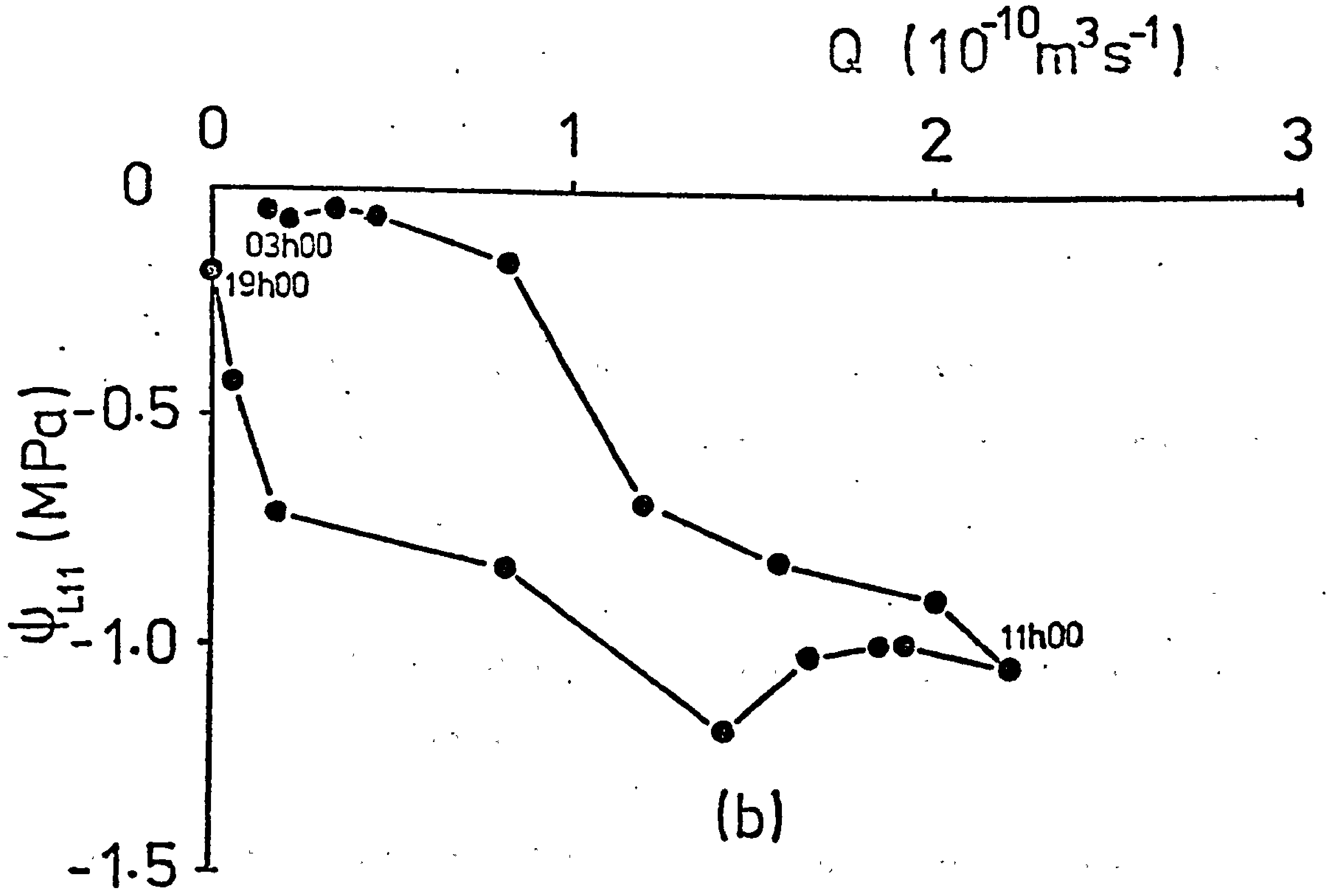


Figure 6.1 Relation between water potential of leaf 11 (ψ_{L11}) and water flow per stem (Q) on (a) 16 May 1975 and (b) 20 May 1975. The times shown are G.M.T.

6.2 Theory

The model representing the soil-plant system is shown diagrammatically in figure 1.2, where ψ_B is the effective potential of the soil and the other terms are as previously defined in section 1.2.3. How this model can explain hysteresis between ψ_L and Q has already been discussed (section 1.2.3). Throughout this section, and the rest of chapter 6, ψ_L refers to the water potential of the youngest, uppermost leaf on the plant. This was leaf 11 before 10 June 1975 and leaf 12 (the flag leaf) after this date in the period used for analysis.

At any time (t) the flow of water out of the model is given by the sum of the flow through R and that to or from C, i.e.

$$Q(t) = \{\psi_B - \psi_L(t)\}/R - C\, d\psi_L/dt. \qquad (6.1)$$

The second term on the right hand side of equation (6.1) is negative since when $d\psi_L/dt$ is negative water flows out of storage, adding to Q(t). The basic equation (6.1) can be used to evaluate R and C (section 6.2.1) or, if they are already known, to calculate changes in ψ_L with Q (section 6.2.2).

6.2.1 Estimation of the hydraulic resistance and capacitance of the soil-plant system

R and C can be evaluated from the measured diurnal changes in Q and ψ_L using equation (6.1) if ψ_B is assumed constant on any day and equal to the maximum value of ψ_L on that day. Also, $d\psi_L/dt$ has to be estimated for each hour during the day. The procedure used for doing this is now described. Figure 6.2 represents the mean values of Q

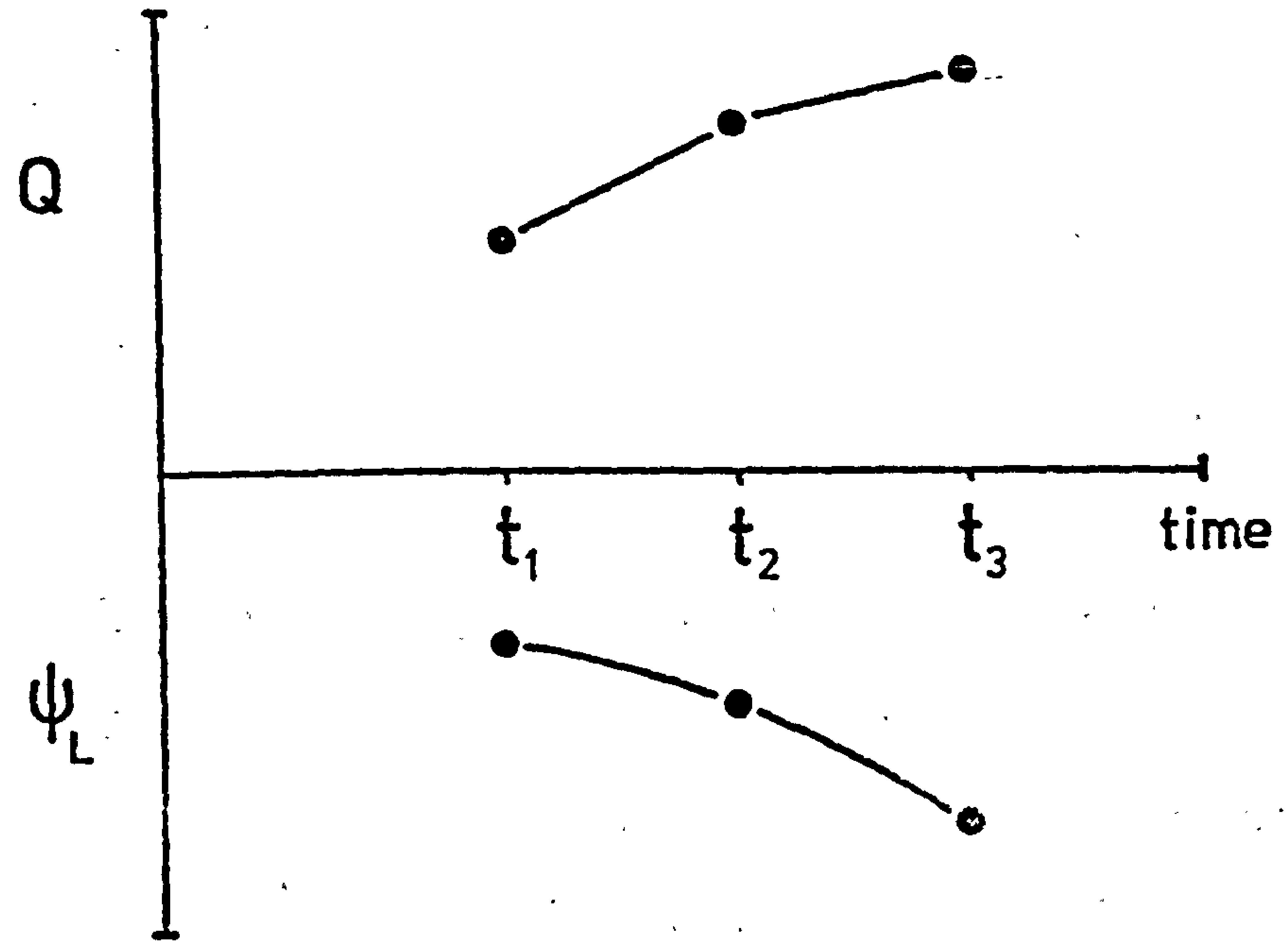


Figure 6.2. Representative changes in leaf water potential (ψ_L) and flow per stem (Q) with time.

and ψ_L on three consecutive hours, t_1, t_2 and t_3. Assuming that over the time interval t_1 to t_3 the relation between Q and t is simply parabolic then, as long as the two time intervals (t_2-t_1) and (t_3-t_2) are equal, say Δt, the slope of the curve at time t_2 is given by

$$d\psi_L/dt \quad = \quad \{\psi_L(t_3) - \psi_L(t_1)\}/2\Delta t \tag{6.2}$$

Substituting equation (6.2) into equation (6.1) gives

$$Q(t_2) \quad = \quad \{(\psi_B - \psi_L(t_2))/R\} + C\ \{\psi_L(t_1) - \psi_L(t_3)\}/2\Delta t \tag{6.3}$$

For each hour of the day substitution of known values of ψ_L and Q into equation (6.3) gives an equation containing two unknowns, R and C. Assuming they remain constant during the day, these equations form a set of simultaneous equations from which R and C can be evaluated by multiple regression.

6.2.2 Predicted changes in leaf water potential

The model shown in figure 1.2 can also be used to calculate ψ_L when R, C and ψ_B are known. To simplify the mathematics let us consider the water potential drop across the model, $\Delta\psi$, where

$$\Delta\psi \quad = \quad \psi_B - \psi_L \tag{6.4}$$

Using equation (6.1) the flow through the system can now be written as

$$Q(t) \quad = \quad \{\Delta\psi(t)/R\} + C\ d(\Delta\psi)/dt \tag{6.5}$$

To solve equation (6.5) the relation between Q and t must be known. In the field Q is not normally a simple function of time. However, assuming that it changed linearly between hourly mean values (e.g. see figure 6.2), in the time interval t_1 to t_2, Q(t) is given by

$$Q(t) = Q(t_1) + mt, \tag{6.6}$$

where m is the rate of change of flow with time and is given by

$$m = \{Q(t_2) - Q(t_1)\}/\Delta t. \tag{6.7}$$

Substituting equation (6.6) into equation (6.5) gives

$$Q(t_1) + mt = \{\Delta\psi(t)/R\} + Cd(\Delta\psi)/dt. \tag{6.8}$$

Equation (6.8) is a linear, first order differential equation in $\Delta\psi$, the solution of which, given in full in appendix A.3, is

$$\Delta\psi(t) = RQ(t_1) + mRt - mR^2C + (k/C)\exp(-t/RC), \tag{6.9}$$

where k is a constant of integration, determined by the initial conditions at time t_1. If we, arbitrarily, take the beginning of the time period as zero, then the initial conditions are,

$$\left.\begin{aligned} t &= t_1 = 0, \\ Q &= Q(0), \\ \Delta\psi &= \Delta\psi\ (0). \end{aligned}\right] \tag{6.10}$$

Substituting equation (6.10) into equation (6.9) gives k as

$$k = C\Delta\psi(0) + mR^2C^2 - RC\,Q(0). \tag{6.11}$$

$\Delta\psi$ at time t_2 can now be calculated using equations (6.7), (6.9) and (6.11). $\Delta\psi(t_2)$ is then taken as one of a new set of 'initial' conditions for the next time interval t_2 to t_3 and $\Delta\psi(t_3)$ calculated in a similar way using $Q(t_2)$ and $Q(t_3)$. The diurnal variation in $\Delta\psi$ can, therefore, be calculated throughout the day by repeating the above procedure, as long as $Q(t)$ is known. Corresponding values of ψ_L are then calculated using equation (6.4).

The change in ψ_L when transpiration stops can also be predicted using the model. In this case the initial conditions are, $\Delta\psi = \Delta\psi(0)$ and $Q = 0$. The value of $\Delta\psi$ at a time t after Q is zero, from equations (6.7), (6.9) and (6.11), is then

$$\Delta\psi(t) = \Delta\psi(0)\exp(-t/RC). \tag{6.12}$$

If the leaf water potential just before transpiration stops is $\psi_L(0)$ then any time thereafter

$$\psi_L(t) = \{\psi_L(0) - \psi_B\} \exp(-t/RC) + \psi_B \tag{6.13}$$

Equation (6.13) was used to estimate the time constant (RC) and ψ_B of (i) plants equilibrating with the soil and (ii) stems equilibrating with a free water source.

6.3 Results

The first part of this section (i.e. 6.3.1) presents the values of R, C and RC calculated using the diurnal changes in ψ_L and Q, measured in 1975, in the model described above in section 6.2. For comparison, independent estimates of RC, calculated from the recovery of ψ_L when transpiration stopped, are given in section 6.3.2. This section also presents diurnal and seasonal changes in ψ_B estimated using equation (6.13).

6.3.1 Hydraulic resistance and capacitance of the soil-plant system

Table 6.1 shows the calculated mean values of R, C and RC on eight days in 1975. The effective water potential of the soil (ψ_B) on each day, used in deriving R and C, is also shown. Between the 16 May and 14 June, R was constant, within the limits of experimental error, since the standard error of R was about ± 0.4 x 10^9 MPa s m^{-3} on each day. The mean value of R during this period was 5.1 (± 0.4) x 10^9 MPa s m^{-3}. R increased later in the season, to 7.2 (± 0.9) x 10^9 MPa s m^{-3} on 2 July. The exception being on 19 June where R, 3.5 (± 0.3) x 10^9 MPa s m^{-3}, was lower than on all the other days shown in table 6.1. The figures in brackets are the standard errors of the mean values. The estimates of C were more variable than those of R, ranging from 3 x 10^{-7} m^3 MPa^{-1} on 2 July to 15 x 10^{-7} m^3 MPa^{-1} on 12 June. The standard error of C was typically ± 50% of C and no simple seasonal trend was evident. The mean value of C for the eight days shown in table 6.1 was 8 (± 4) x $10^{-7} m^3$ MPa^{-1}.

Using the above estimates of R and C in the model, described in section 6.2, allowed the diurnal changes in ψ_L to be calculated. Figure 6.3 shows the measured (dots) and calculated (continuous curve) changes in ψ_L on four of the days shown in table 6.1. This is not an independent test of the model, since the curves shown are derived from the measured Q and ψ_L data. However, figure 6.3 does show the scatter of the ψ_L data about the curves predicted from the daily mean values of R and C. The general agreement between the measured and predicted ψ_L was good, except in the evening and night where the measured increase in

DATE	R (10^9 MPa s m^{-3})	C (10^{-7}m^3 MPa^{-1})	RC (min)	ψ_B (MPa)
16 May	5.0	4	35	-0.05
20 May	5.6	11	100	-0.05
10 June	4.9	10	80	-0.1
12 June	4.5	15	110	-0.4
14 June	5.5	5	50	-0.4
19 June	3.5	10	60	-0.6
24 June	6.6	6	70	-1.2
2 July	7.2	3	30	-1.6

Table 6.1 The hydraulic resistance (R), hydraulic capacitance (C) and the time constant (RC) of the soil-plant system on eight days in 1975. Also shown is the effective water potential of the soil (ψ_B).

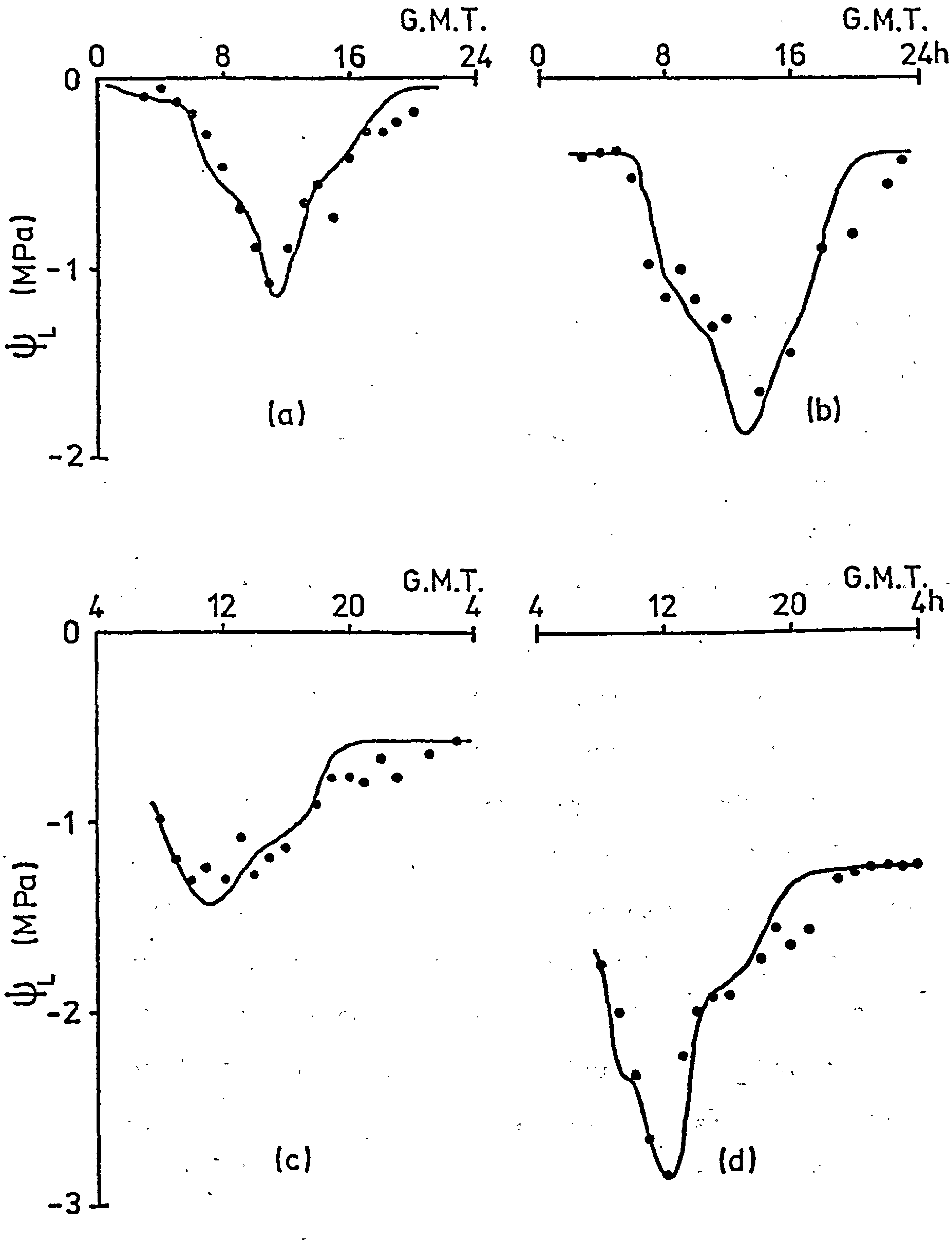


Figure 6.3. Predicted (——) and measured (●) changes in leaf water potential (ψ_L) on four days during 1975. (a) 16 May, (b) 14 June, (c) 19 June and (d) 24 June.

ψ_L was slower than predicted. The recovery of ψ_L during the night is presented in more detail in the following section.

6.3.2 Recovery of leaf water potential after transpiration stops

6.3.2.1 Overnight

During the night the water potential of the leaves (ψ_L) approached that of the soil (ψ_S) and reached a maximum in the early morning of the following day. For example, figure 6.4 shows the changes in ψ_L during four nights in 1975 when ψ_S was different. The minimum ψ_S in the root zone (ψ_S (min)) is shown for each night, the corresponding maximum ψ_S was greater than - 0.05 MPa on each occasion. The rate of recovery of ψ_L during the night became slower as the soil dried. This can be illustrated by calculating the time constant (RC) for the recovery of ψ_L, using the soil plant model (section 6.2). Assuming there was no transpiration at night (Penman and Long 1960) then the recovery of ψ_L is given by equation (6.13). Fitting this equation to the measured values of ψ_L during the night, taking ψ_B as the maximum ψ_L on each night (see below), gave estimates of RC. On 14-15 June, when ψ_S (min) was - 0.5 MPa, the time constant for the recovery of ψ_L was 3h. RC increased to 6h on 2-3 July when the soil was much drier, ie ψ_S(min) = - 1.4 MPa. Both of the estimates of RC during the night are greater than those estimated from measurements of ψ_L and Q throughout the day (see table 6.1).

When the soil was dry, the slow recovery of ψ_L overnight meant that ψ_L could not attain a value within the measured range of soil water potentials before transpiration began the following day (see figure 6.4). The effective water potential of the soil (ψ_B), used in the model, was therefore taken as the maximum leaf water potential achieved overnight. Figure 6.5 shows the values of ψ_B and ψ_S (min) measured on a number of

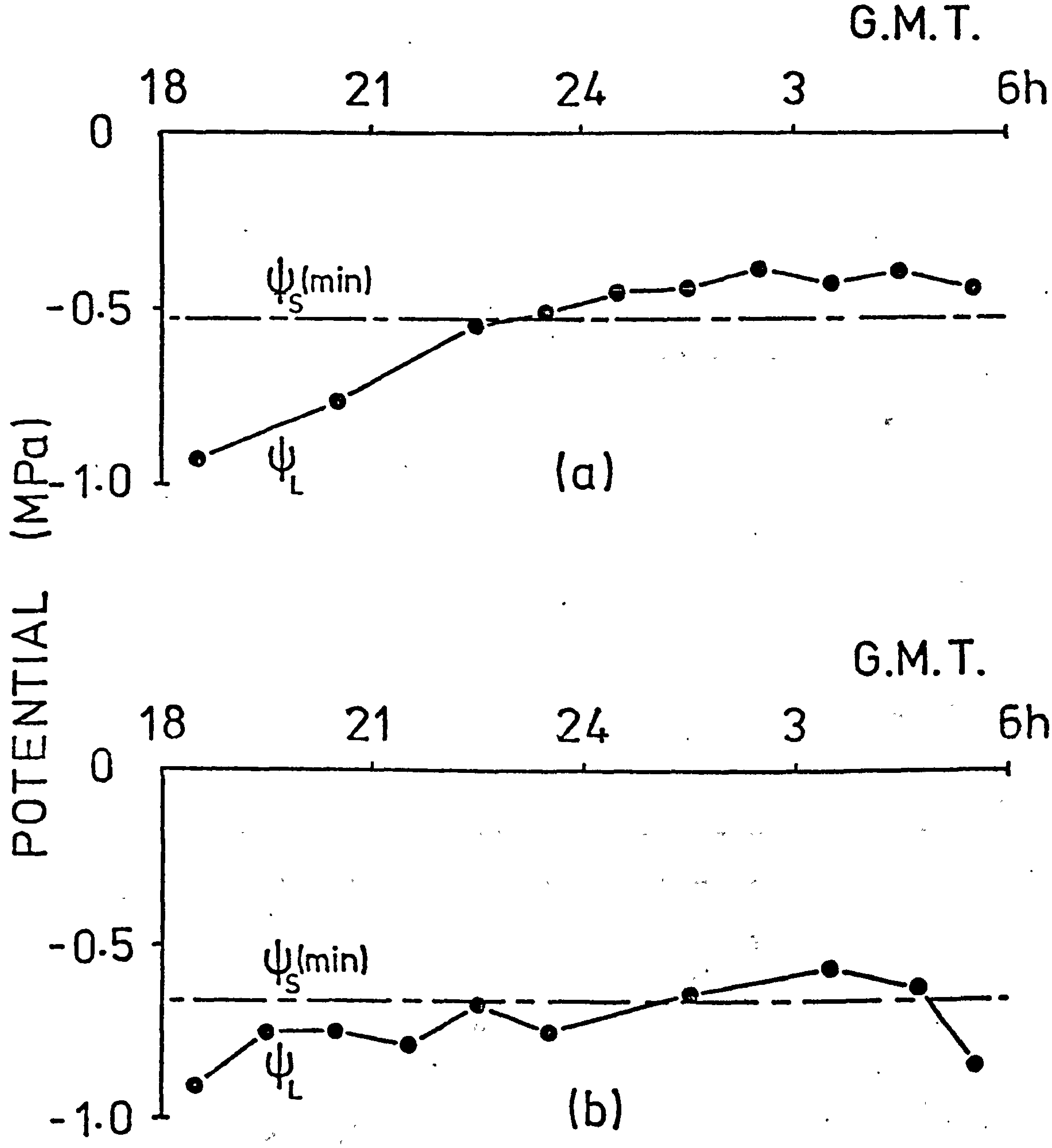


Figure 6.4. Changes in leaf water potential (ψ_L) during four nights in 1975. (a) 14-15 June, (b) 19-20 June, (c) 24-25 June and (d) 2-3 July. The minimum soil water potential, ψ_S (min), on each night is also shown.

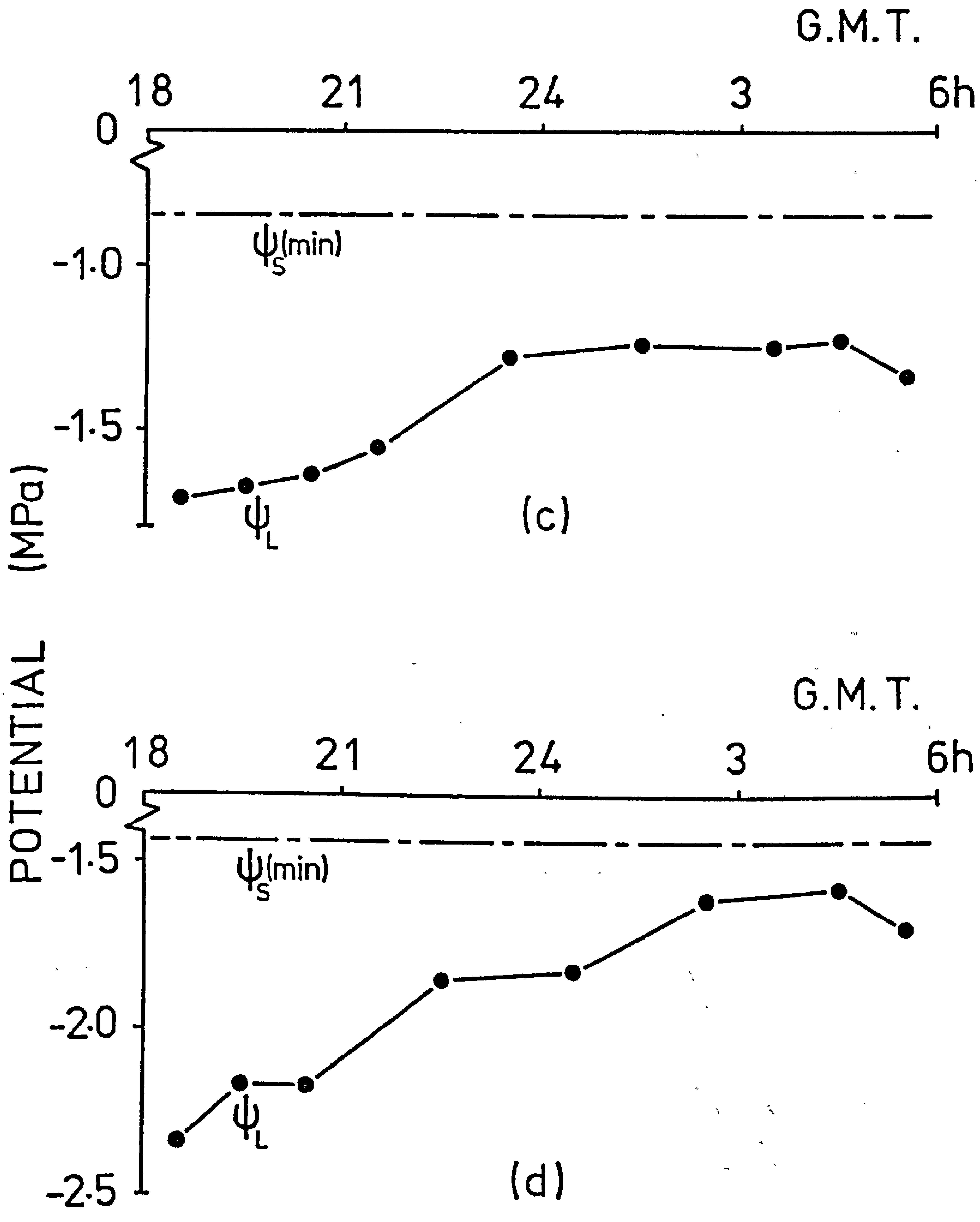


Figure 6.4 continued...

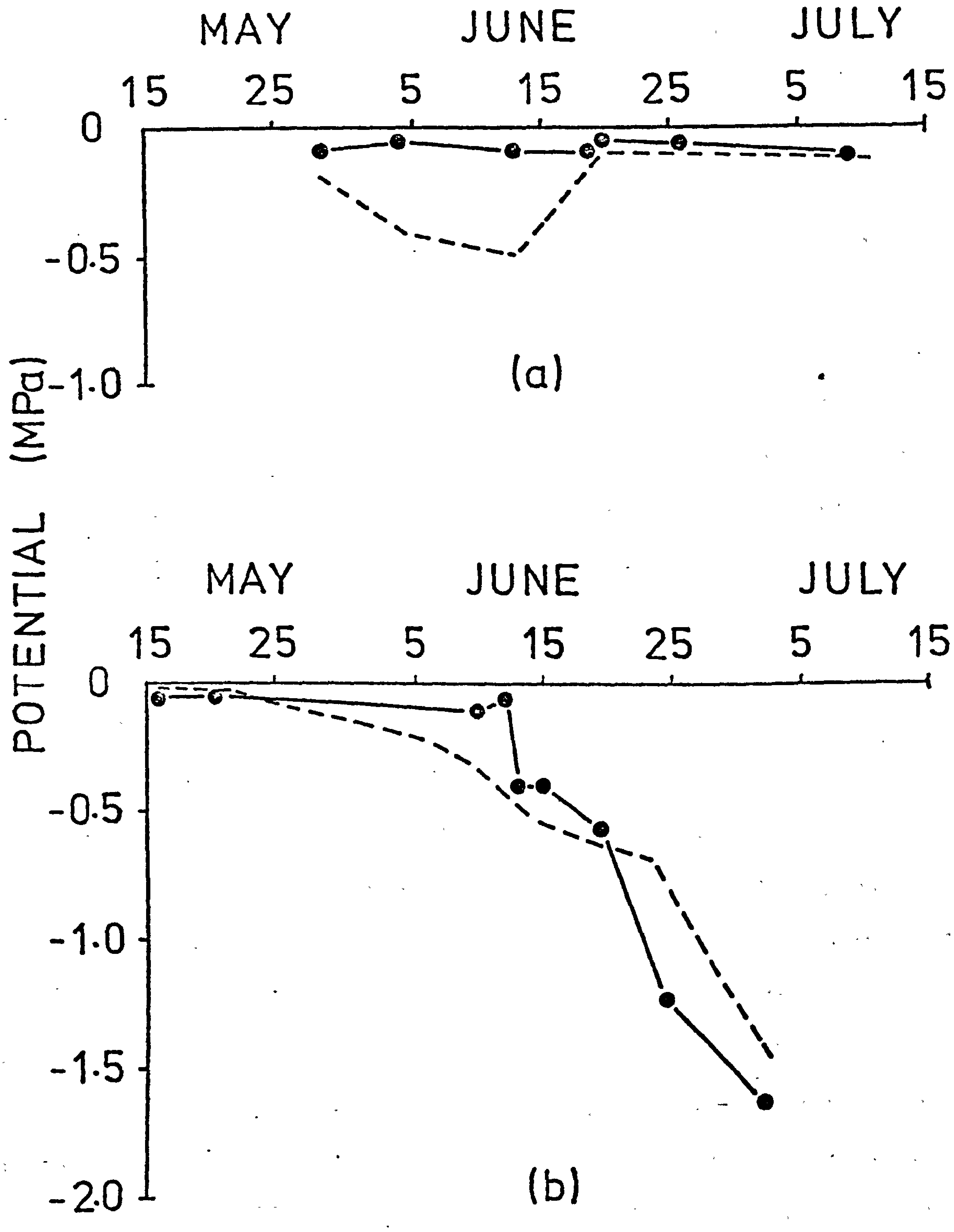


Figure 6.5. Changes in daily maximum leaf water potential (●) and minimum soil water potential (- - -) during (a) 1974 and (b) 1975.

days during the two seasons studied. Again on all of the days shown the maximum soil water potential measured in the root zone was greater than - 0.05 MPa. ψ_B was constant during 1974, within the limits of experimental error, at about - 0.1 MPa and always within the measured range of soil water potentials (figure 6.5a). There was also little change in ψ_B up to the beginning of June in 1975, again it was close to - 0.1 MPa (figure 6.5b). As the drought continued however, ψ_B decreased sharply during June, reaching - 1.6 MPa by the beginning of July. ψ_S (min) also decreased monotonically from - 0.02 MPa on 16 May to - 1.4 MPa on 2 July. However, up to 20 June ψ_B was within the measured range of soil water potentials, whereas after this date ψ_B was lower than ψ_S (min). The effective water potential of the soil also appeared to change during the day. This is described in the next section.

6.3.2.2 During the day

When transpiration was stopped during the day (see section 3.3.3) the potential of the leaves, ψ_L, tended to that of the soil. For example, figure 6.6 shows typical recoveries of ψ_L in the afternoon, measured on three days with different soil water potentials in 1975. On 22 May, when the soil was wet (ψ_S (min) > - 0.05 MPa), ψ_L increased rapidly from - 1.0 MPa, just before transpiration was stopped, to - 0.2 MPa twenty minutes later. In drier soil on 13 June (ψ_S (min) = - 0.5 MPa) ψ_L increased more slowly, taking about 1 h to recover from - 1.3 to - 0.5 MPa. Continuing drought further reduced ψ_S(min) to - 1.0 MPa and it took 3 h for ψ_L to increase from - 2.6 to - 1.4 MPa on the 26 June.

Again the soil plant model can be used to describe the above responses of ψ_L. The curves drawn in figure 6.6 are fitted exponentials of the form of equation (6.13), which gave estimates of the time constant, RC, and

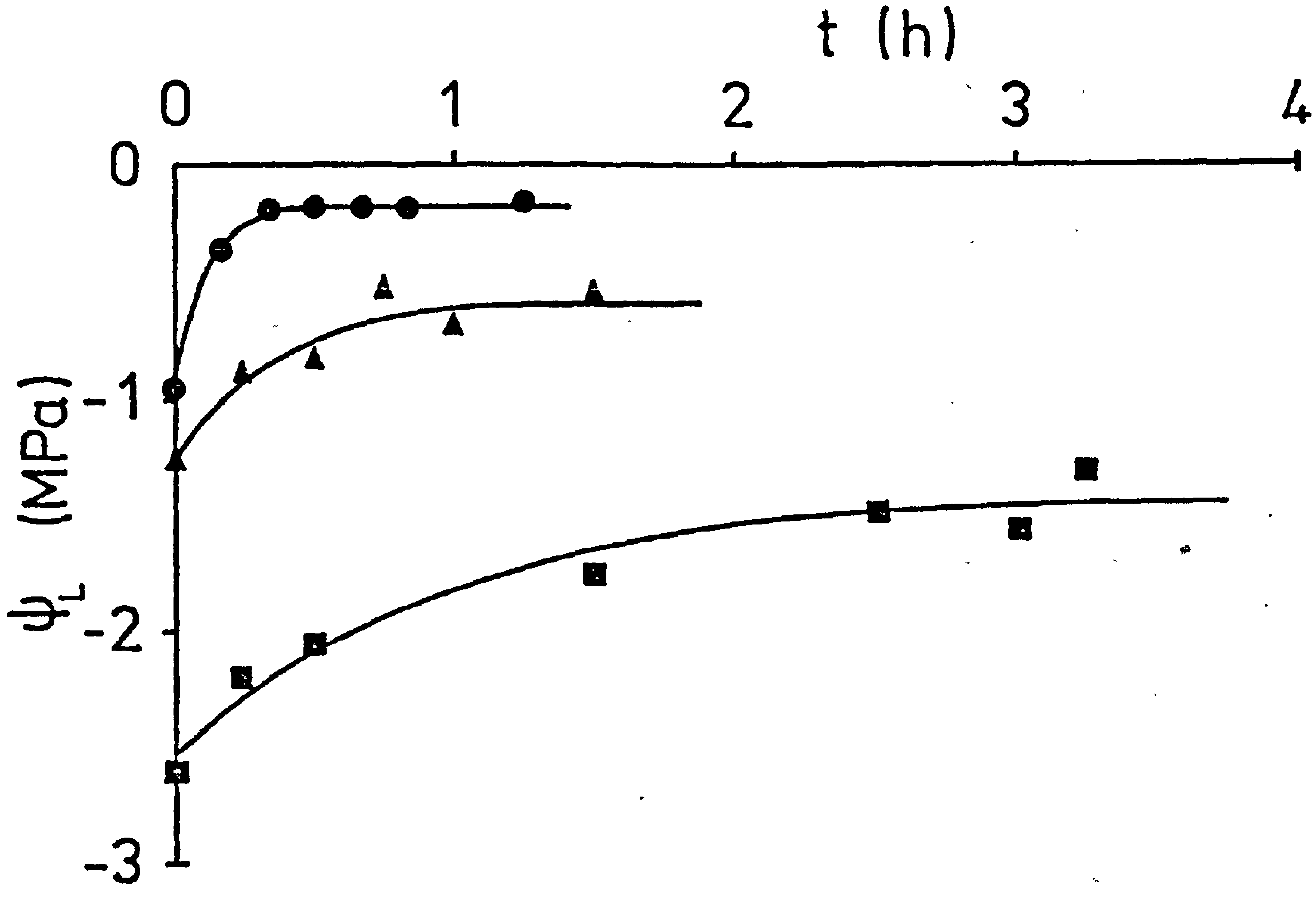


Figure 6.6. Recovery of leaf water potential (ψ_L) in non-transpiring plants on three days in 1975, 22 May (●), 13 June (▲) and 26 June (■) when the soil water potential was different.

the effective soil water potential, ψ_B, shown in table 6.2. The curves shown are a good fit to the data, implying that the model can be used with confidence when describing the recovery of ψ_L with the soil when transpiration stops. Although the standard errors in RC were large, it is apparent that RC increased as the soil dried. Estimates of ψ_B decreased from - 0.17 MPa on 22 May to - 1.4 MPa on 26 June. ψ_B was, therefore, comparable with the daily maximum values of leaf water potential on 13 and 26 June (see figure 6.5), but on 22 May was lower than both the maximum leaf water potential (- 0.05 MPa) and the minimum soil water potential (- 0.03 MPa) at that time.

Figure 6.7 shows that the effective water potential of the soil, ψ_B, also varied during the day with ψ_L. Both days shown were near the 13 June 1975, when ψ_L reached a steady value 1 h after transpiration stopped (figure 6.6). ψ_B was, therefore, taken as the water potential of the leaves on plants from which transpiration had been prevented for 1 h. ψ_B decreased during the day with ψ_L, to a minimum of - 0.8 MPa in the afternoon, when ψ_L also had its minimum value. In the afternoon ψ_B increased as ψ_L increased, reaching a value similar to ψ_L in the evening.

The plant tops (stem and leaves) equilibrated with free water much faster than the intact plants did with the soil. This is shown in figure 6.8. In the two examples shown, from 26 May and 26 June 1975, the initial leaf water potentials were very different, - 0.9 and - 2.0 MPa respectively. However, ψ_L reached the same steady value (about - 0.2 MPa) within 15 min on both occasions. Although the source of water had a potential of zero, the leaves did not reach this potential even after 2 h. Using the soil-plant model the curves drawn in figure 6.8 were fitted (ie exponentials of the form of equation (6.13)), from which the time constant of the plant tops (R_1C_1) and the effective potential of the

DATE	RC (min)	± S.E.	ψ_B (MPa)	± S.E.
22 May	7	± 1	-0.17	± 0.01
13 June	22	± 11	-0.6	± 0.05
26 June	63	± 27	-1.4	± 0.10

Table 6.2 The soil-plant system time constant (RC) and the effective water potential of the soil (ψ_B) on three days in 1975. The standard errors (S.E.) of RC and ψ_B are also shown.

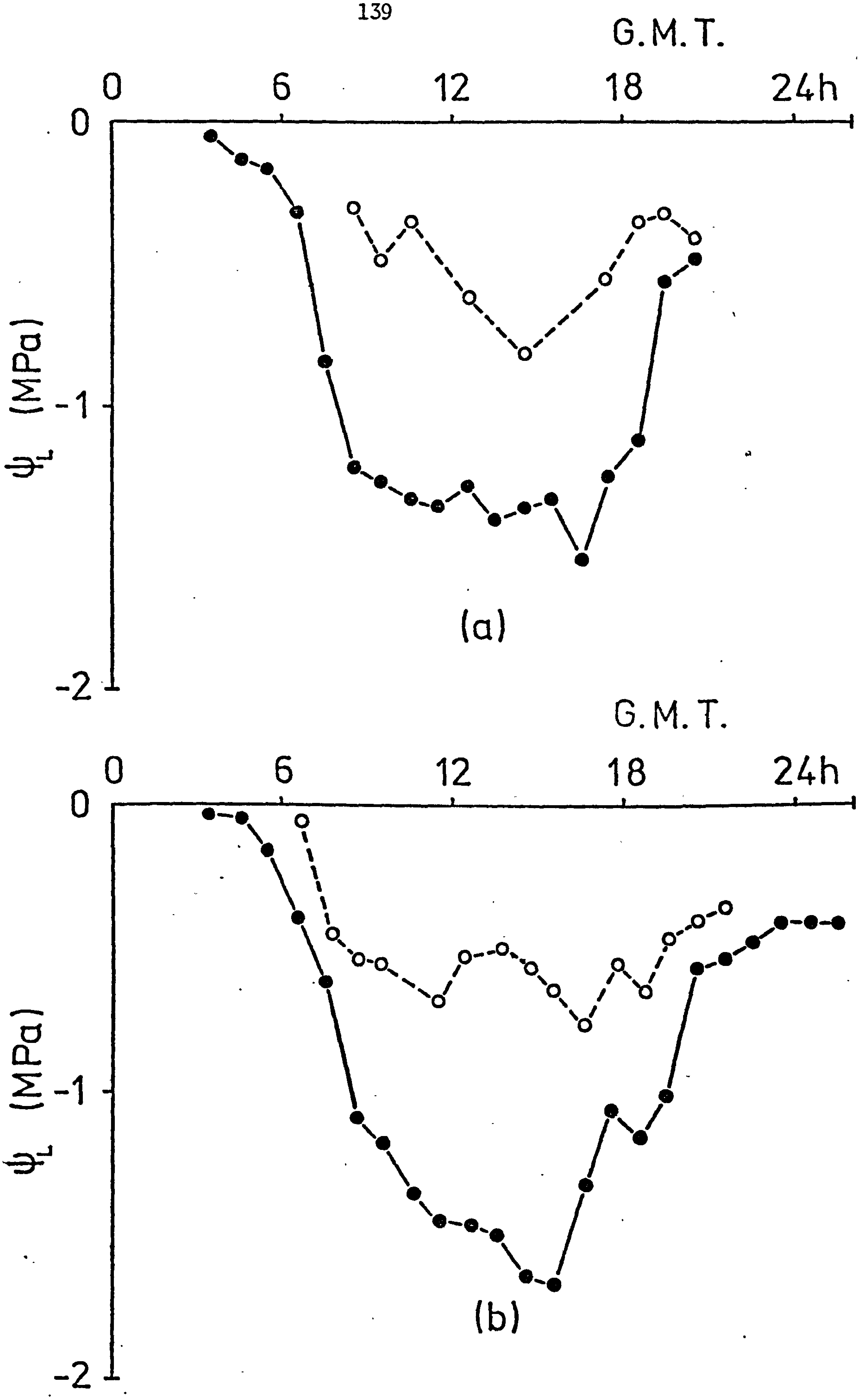


Figure 6.7. Changes in leaf water potential (ψ_L) in transpiring plants (●) and plants from which transpiration was stopped for 1 hour (○) on 10 and 12 June 1975.

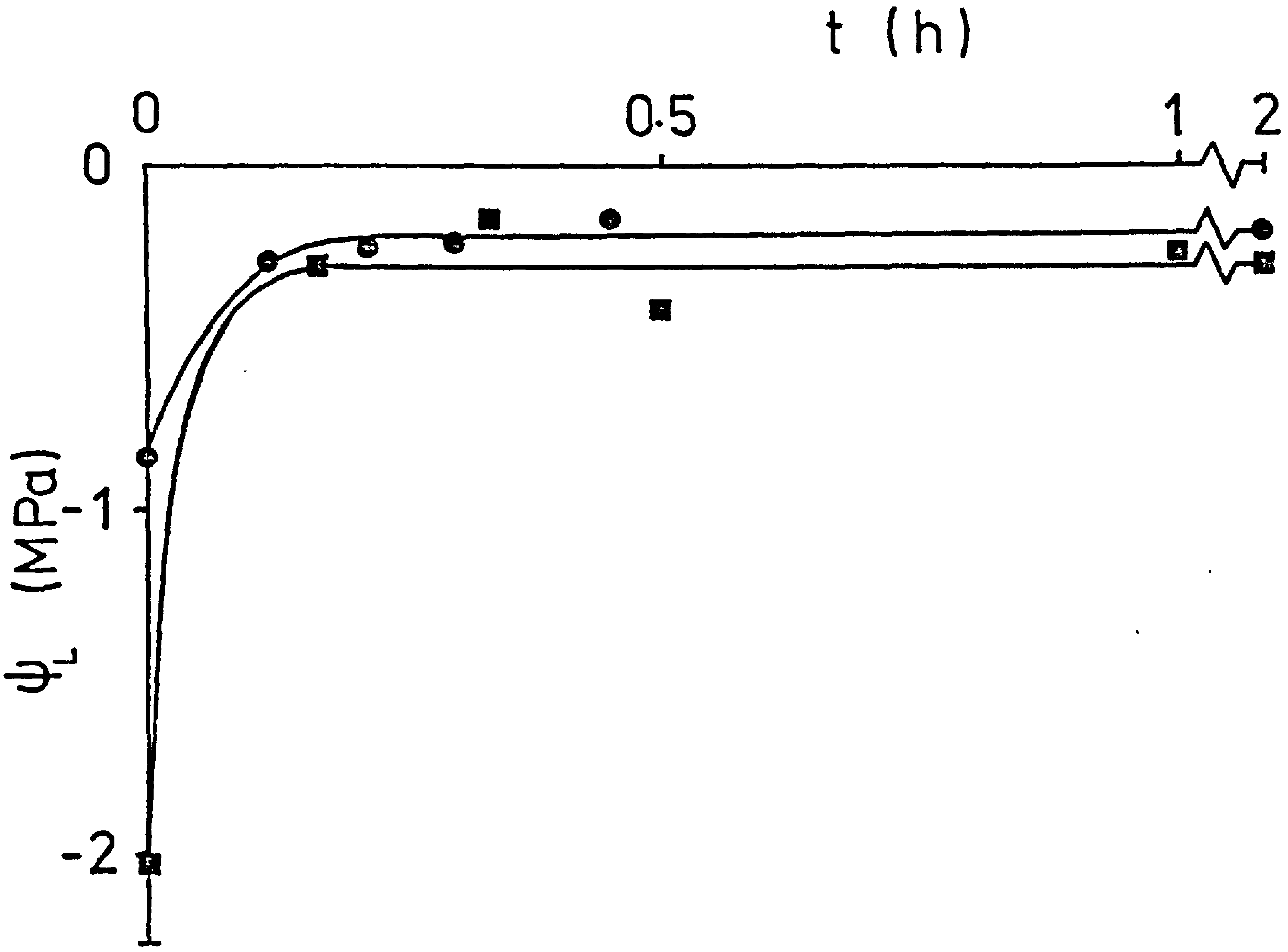


Figure 6.8. Recovery of leaf water potential (ψ_L) in non-transpiring plants, cut at the stem base under water on 26 May 1975 (●) and 26 June (■).

water source (ψ_W) were estimated. The respective values of R_1C_1 and ψ_W were not significantly different on the two days shown in figure 6.8, being 3.7 (± 0.7) min and - 0.19 (± 0.01) MPa on 26 May and 2 (± 4) min and - 0.28 (± 0.06) MPa on 26 June. The time constant of the plant tops was, therefore, about half of that for the entire plants equilibrating with wet soil on 22 May 1975 (see table 6.2). Also, the equilibrium water potential was not significantly different in these two cases.

The values of soil-plant system hydraulic resistance and capacitance and those of the plant tops, derived using the model, are discussed in the following section.

6.4 Discussion

The soil-plant model presented in this chapter evolved from a need to explain hysteresis in the relation between ψ_L and Q, which has also been observed in species other than wheat, for example, in sunflower (Berger 1969), potato (Whitehead 1975), Scots pine (Jarvis 1976) and Avocado pear trees (Sterne, Kaufmann and Zentmyer 1977). Soil-plant models which can account for hysteresis in the ψ_L/Q relation require detailed knowledge of the soil hydraulic properties (eg, see Cowan 1965; Penning de Vries 1972; Hansen 1975) or use a more complex network of hydraulic resistance and capacitance components than was used here (see Powell and Thorpe 1977). The model used in the present study is simple, easy to use and gave estimates of R which are consistent with previously reported values. These are discussed in detail in the next section (ie 6.4.1). Estimates of C are rarely reported in the literature, the few values available are considered in section 6.4.2. Also discussed are the location of the major components of R and C (in section 6.4.3), evidence for large gradients in water potential in the soil around the roots (in section 6.4.4) and diurnal changes in water storage in the soil-plant system (in section 6.4.5).

6.4.1 Hydraulic resistance

As indicated in section 1.2 there have been numerous reports in the literature of estimates of R in plants grown in controlled environments. Generally, the values obtained and their dependence on flow are not comparable with the estimates of R for field grown plants. For example, in a controlled environment study of water transport in young wheat plants, Hansen (1974) found that R increased from 10 x 10^9 to 140 x 10^9 MPa s m^{-3} as the soil dried and the transpiration rate decreased from 0.6 x 10^{-10} to 0.1 x 10^{-10} $m^3 s^{-1}$ plant^{-1}. These values of R are much larger than those found in the present study (table 6.1), though the transpiration rates are much lower than those recorded in the field. Differences in plant morphology, environment and experimental technique may account for these large differences in R. However, it is clear that wheat plants grown in controlled conditions responded very differently to those in their natural environment.

Further comparisons with other field grown plants are summarized in table 6.3. Denmead and Millar's (1976a) model of water flow in wheat plants (discussed in section 5.5.2) did not allow the total hydraulic resistanc in the soil-plant system, R, to be calculated simply. However, to allow comparison with the present study R was calculated from their data by dividing the potential gradient between the soil and the uppermost leaf by the flow of water per stem. The values of R thus obtained are similar to those found in the present study, at both high and low soil water potentials. Biscoe *et al* (1976) reported that R decreased with flow rate in spring barley, from 10 x 10^{10} to 2.5 x 10^{10} MPa s m^{-3} at the maximum flow rate observed (ie 0.8 x 10^{-10} $m^3 s^{-1}$ stem^{-1}). However, even the lowest value of R is

SPECIES	R (10^7 MPa s m^{-3})	SOURCE
Barley	2,500 - 10,000	Biscoe *et al* (1976)
Wheat	720 (low ψ_S)	This study
Wheat	510 (high ψ_S)	This study
Wheat	730 (low ψ_S)	Derived from data in Denmead and Millar (1976a)
Wheat	470 (high ψ_S)	
Tobacco	3.3	Begg and Turner (1970)
Sunflower	3.1	Berger (1969)
Maize	2.9	Shinn and Lemon (1968)
Potato	2.0	Whitehead (1975)
Spruce	1.0	Helkvist *et al* (1974)

Table 6.3 The total hydraulic resistance (R) of various field grown species.

still about five times that in wheat. In the other species shown in table 6.3, R was smaller than in wheat and barley, ranging from 3.3×10^7 MPa s m^{-3} in tobacco (Begg and Turner 1970) to 1×10^7 MPa s m^{-3} in spruce (Hellkvist *et al* 1974). However, the resistances shown were not all calculated in the same way, for example, Shinn and Lemon (1968) used the total daily evaporation to estimate the mean value of R for the whole day.

In similar conditions most of the above species have similar potential gradients between the soil and the leaves, therefore, the wide range of R values mainly reflects the different flow per stem, Q. For example, at the same high evaporation rate of 1.2×10^{-7} $m^3 s^{-1}$ m^{-2} ground (equivalent to a latent heat flux of 300 W m^{-2}) Q in spruce, with a density of 4000 trees ha^{-1} (Hellkvist *et al* 1974), would be 3000×10^{-10} $m^3 s^{-1}$ $stem^{-1}$ compared with 3.7×10^{-10} $m^3 s^{-1}$ $stem^{-1}$ in wheat. As discussed previously in section 5.6.2, the ease with which different species conduct water can be compared by calculating their hydraulic resistivity. The total hydraulic resistivity (r) of the soil-plant system, calculated using the mean value of R (5.1×10^9 MPa s m^{-3}) in equation 5.6, was 750 MPa s m^{-2}. For comparison, in spruce trees Hellkvist *et al* (1974) obtained a value of r of 1,000 MPa s m^{-2}. Therefore, despite the vast differences in the morphology of wheat plants and spruce trees the resistance these two plant communities present to water flowing from the soil to their leaves is similar.

6.4.2 Hydraulic capacitance

There are very few reports of plant hydraulic capacitance in the literature, despite mounting evidence for its significance in transient water flow relations. For example, hysteresis in the relation between leaf water potential and flow (Berger 1969; Whitehead 1975; Jarvis 1976; Sterne, Kaufmann and Zentmyer 1977) and Boyer's (1968; 1969; 1971) experiments on the recovery of leaf water potential after transpiration stops. From estimates of the rate of change of tissue water content with water potential, Powell and Thorpe (1977) calculated the hydraulic capacitance of a small apple tree as 2.2×10^{-4} $m^3 MPa^{-1}$, in a similar way Whitehead (1975) calculated a hydraulic capacitance of 1.3×10^{-4} $m^3 MPa^{-1}$ in potato. Both of these values are two orders of magnitude greater than those obtained for wheat in the present study (table 6.1). The large difference may be expected in view of the relative sizes of these species.

Since there is insufficient data in the literature for comparison, the estimates of hydraulic capacitance obtained in the present study were checked in another way. This is described in full in section 6.4.5, and essentially consists of a comparison of the estimates of the diurnal change in plant water storage calculated (i) using C and (ii) from the relation between the water content and water potential of the plants.

6.4.3 Components of hydraulic resistance and capacitance

Though the soil-plant model (figure 1.2) employs a 'lumped' hydraulic resistance and capacitance, it is possible to draw some conclusions about their component values from the results of the experiments on the recovery of leaf water potential after transpiration stopped (see section 6.3.2) Firstly, consider the plant tops (stem and leaves). These had a short time constant, R_1C_1, of about 4 min and dividing this by R_1, calculated as 14×10^8 MPa s m^{-3} (section 5.4), gave the hydraulic capacitance of the stem and leaves (C_1) as 1.6×10^{-7} m^3 MPa^{-1}. C_1 was apparently unaffected by changes in the water status of the plants and soil, since between mid-May and mid-June 1975 R_1C_1 and R_1 did not change significantly. There are no directly comparable reports in the literature of hydraulic capacitance in other plant stems and leaves. However, from measurements of the increase in leaf water potential in plants recovering from water deficits, Boyer (1968) calculated the time constant of the stem and leaves of sunflower as 12 min, and that of the leaves as 4 min. The different time constants of the stem and leaves of sunflower and wheat might be expected from the different sizes of these plants.

When wheat plants were equilibrating with the soil (see figure 6.6), because of the short time constant of the plant tops, ψ_L may be assumed to have been equal to that at the stem base by 15 min after transpiration was stopped. Subsequent changes in ψ_L can be considered to represent the equilibration of the roots with the soil. The time constant of the soil-root system (R_2C_2) can then be calculated using equation (6.13). For example, table 6.4 contains the values of R_2C_2 calculated using the data from 22 May, 13 and 26 June 1975 shown in figure 6.6, but ignoring the values of ψ_L in the first 15 min after transpiration was stopped. R_2C_2 increased by an order of magnitude between 22 May and 26 June and in an attempt to explain this, further calculations were made to separate R_2 and C_2. Consider the flow and potential gradients in the soil-plant system just before transpiration was stopped. At that time, ie early afternoon, ψ_L was changing slowly and, therefore, the flow of water into or out of storage, $Cd\psi_L/dt$ (equation (6.1)), may be assumed to have been negligible. The hydraulic resistance of the soil-root system, R_2, is then given by the expression

$$R_2 = R_1 \, \Delta\psi_2(0)/\Delta\psi_1(0), \tag{6.15}$$

where $\Delta\psi_1(0)$ and $\Delta\psi_2(0)$ are the respective potential gradients across the stem and the soil-root system just before transpiration stopped. The hydraulic resistance of the stem R_1, is known from section 5.4 and $\Delta\psi_1(0)$ and $\Delta\psi_2(0)$

DATE	R_1	R_2	C_1	C_2	R_1C_1	R_2C_2
	(10^9 MPa s m^{-3})		($10^{-7} m^3$ MPa^{-1})		(min)	
22 May	1.4	2.7	1.6	2.2	4	10
13 June	1.4	3.2	1.6	11	4	60
26 June	1.4	5.0	1.6	12	4	100

Table 6.4 The hydraulic resistance (R), capacitance (C) and time constant (RC) of the plant tops (subscript 1) and the soil-root system (subscript 2) on three days in 1975.

were estimated using the curves that were fitted to determine the time constant R_2C_2. Table 6.4 shows the values of R_2, calculated using equation (6.15), on 22 May, 13 and 26 June 1975. Also shown are the corresponding estimates of the soil-root system hydraulic capacitance (C_2), calculated by dividing the time constant R_2C_2 by R_2. It is encouraging to see that the sum of R_1 and R_2 on 13 and 26 June, ie 4.6×10^9 and 6.6×10^9 MPa s m^{-3} respectively, agrees closely with the total soil-plant hydraulic resistance (R), derived independently from the diurnal changes in ψ_L and Q, at similar times of the season (see table 6.1). However, $R_1 + R_2$ was lower than R in mid-May, but this can be partly explained by the different effective soil water potentials (ψ_B) used in the two methods, - 0.17 MPa on 22 May compared with - 0.05 MPa on 16 and 20 May (see tables 6.1 and 6.2). The increase in R during 1975 was, therefore, caused by an increase in the hydraulic resistance of the soil-root system (R_2). The values of R_2 in the present study are comparable with the hydraulic resistance of wheat root systems in culture solution, estimated by Cox (1966) as 1.2×10^9 to 5×10^9 MPa s m^{-3}. However, Denmead and Millar (1976a) calculated a lower root resistance, 1×10^9 MPa s m^{-3}, in their mature wheat crop. In the present study the largest hydraulic resistance was in the soil-root system (table 6.4). This agrees with most previous studies of hydraulic resistance in plants (for example, by Kramer 1938, 1969; Jensen *et al* 1961; Tinklin and Weatherley 1966; Boyer 1968, 1969, 1971: Stoker and Weatherley 1971; Biscoe *et al* 1976; Roberts 1977), where the roots or the roots + soil also had the highest resistance to water flow.

The increase in soil-root hydraulic resistance, found in the present study (table 6.4), could have been caused by an increase in the hydraulic resistance of the roots and/or the soil around the roots. Root hydraulic resistance could have increased because a greater root length was involved in extracting water from the soil later in the season. This is illustrated in figure 6.9. All the water transpired by the crop prior to 20 May was extracted from the top 0.3 m of soil. As the top soil dried, water was extracted from progressively lower depths, until eventually more water was being taken up from below 1 m than from the top soil. Therefore, water had to traverse a greater length of root to reach the leaves when the soil was dry. This greater root length may have had a larger hydraulic resistance and a greater hydraulic capacitance than that earlier in the season. The effect of the length of roots on their hydraulic resistance has also been considered by Cowan and Milthorpe (1968). Their theoretical analysis suggests that the axial resistance to water flow in roots becomes significant when the roots are longer than 0.1 m (see also Nye and Tinker 1977). This was supported by Passioura (1972), who calculated large potential gradients along cereal roots assuming Hagen-Poiseuille flow in the xylem vessels. There is, therefore, a high axial resistance to water uptake by the lower parts of the root system.

An increase in the hydraulic resistance of the soil around the roots, ie the rhizosphere resistance (Newman 1969a), could also account for the increase in R_2 during 1975. Indirect evidence supporting this comes from the development of significant potential gradients between the bulk soil and the root surface, which occurred in 1975. This is discussed in the following section.

6.4.4 Potential gradients in the soil around the roots

There are several aspects of the responses of leaf water potential described in section 6.3.2 which suggest that there were significant potential gradients in the soil around the roots (the rhizosphere), in both dry and wet soil conditions. For example, assuming that the effective water potential of the soil (ψ_B) was that at the root surface (ψ_{RS}), the estimates of ψ_B shown in figure 6.7 suggest that ψ_{RS} varied during the day. At that

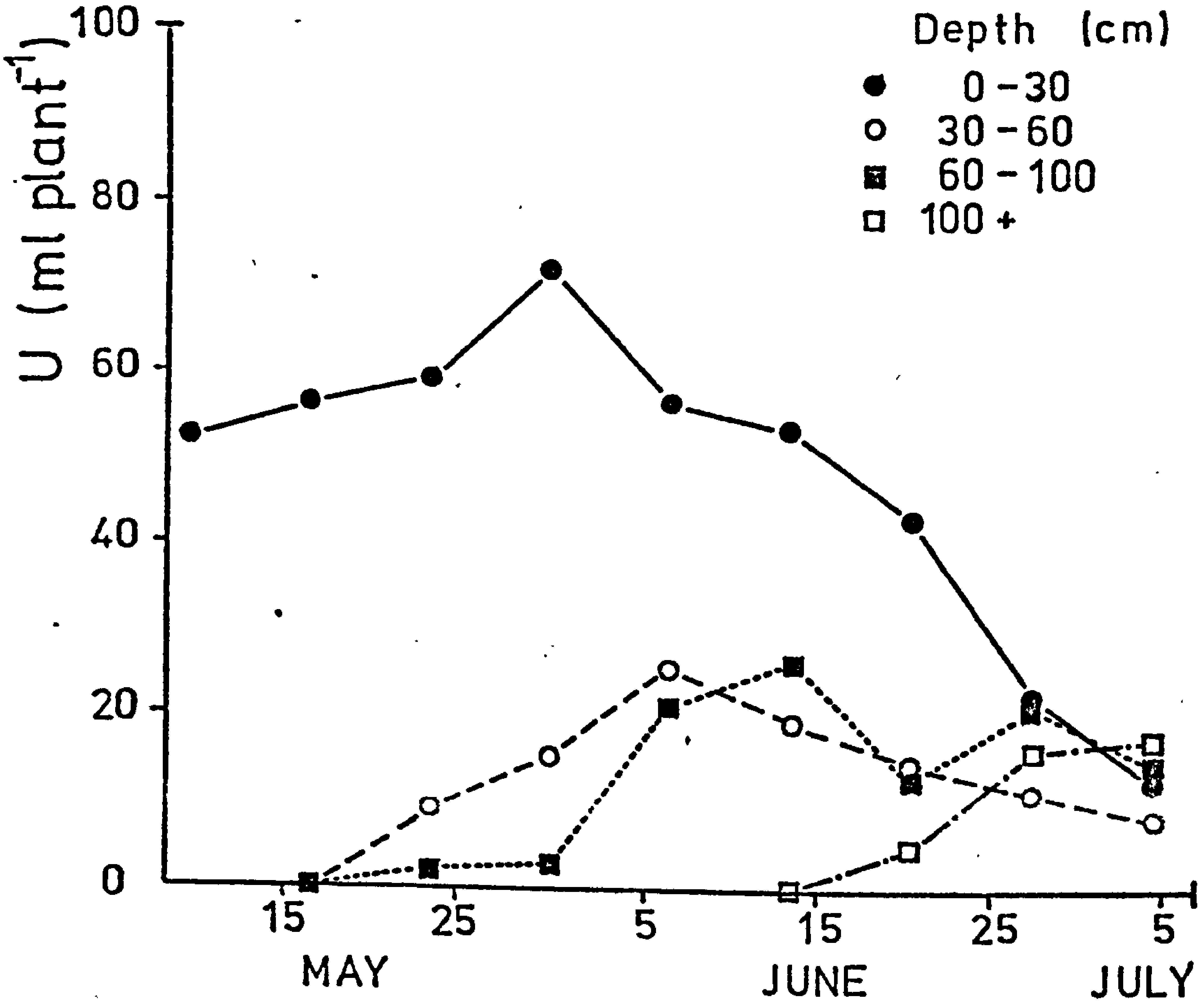


Figure 6.9. Weekly water extraction by plant roots (U) from four soil regions during 1975.

time, the bulk soil water potential (ψ_S) in the active root zone ranged from - 0.4 MPa in the top soil to - 0.02 MPa at a depth of 1 m (McGowan pers. comm.). Therefore, the potential gradient across the rhizosphere, $\Delta\psi_S$ (= $\psi_S - \psi_{RS}$), was between zero and 0.8 MPa, depending on the time of day and the depth in the soil. Large values of $\Delta\psi_S$, up to 0.7 MPa, can also be inferred from Whitehead's (1975) measurements of the leaf water potential in wheat stems 5 h after transpiration was stopped just before midday. More recently, Faiz and Weatherley (1978) measured a potential drop of 0.8 MPa in the soil around sunflower roots using *in situ* soil and root psychrometers, previously described by Fiscus (1972). Furthermore, the diurnal variation in root surface water potential, ψ_{RS}, found in the present study is consistent with that predicted by Cowan (1965), using a model of flow in the soil-plant system.

Further evidence of significant water potential gradients across the rhizosphere comes from the slow recovery of leaf water potential overnight (figure 6.6), a phenomenon which has also been observed in wheat by Campbell and Campbell (1974) and in other plants by Klepper (1968), Jordan 1970, Millar *et al* (1970) and Jordan and Ritchie (1971). The long time constant of the soil-plant system at night found in the present study, 3 to 6 h, was probably caused mainly by slow equilibration of the potential at the root surface, ψ_{RS}, with that in the bulk soil, ψ_S. In fact after 20 June 1975 ψ_{RS} remained lower than ψ_S throughout the night, figure 6.5b, presumably because under these exceptionally dry soil conditions there was a high resistance to water flow across the rhizosphere.

It has already been mentioned that the potential gradient across the rhizosphere, $\Delta\psi_S$, may have varied with depth in the soil. Further consideration of this leads to the suggestion that in certain circumstances $\Delta\psi_S$ may have been negative and that soil water may have been redistributed by the roots. For example, several hours after transpiration stopped on the evening of 14 June 1975, leaf water potential, ψ_L, was higher than ψ_S in the top 0.2 m of soil (see figure 6.4a). Since the water potential at the root surface, ψ_{RS}, must have been higher than (or a least equal to) ψ_L then ψ_{RS} must also have been higher than ψ_S, therefore $\Delta\psi_S$ was negative. Under these conditions the roots could only have extracted water from the soil below 0.2 m, where ψ_S was higher than ψ_L and $\Delta\psi_S$ was positive. Inverted water potential gradients between roots and soil (ie $\Delta\psi_S$ negative) have also been reported by Fiscus (1972) and Taerum (1973). In the present study if the roots were permeable to outward water movement, as demonstrated by Jensen *et al* (1961) in tomato and sunflower plants, water may have entered the roots in the lower soil regions, travelled up the root system and moved out of the roots in the top soil. This would have partially rewetted the soil around these roots, thereby raising its water potential. Conversely, since ψ_L remained lower than ψ_S after 20 June 1975, no redistribution of soil water by the roots could have occurred at this time.

The preceding discussion has implied potential gradients across the rhizosphere, $\Delta\psi_S$, which were always significant and sometimes very large. However, after comprehensive reviews of the theoretical and experimental evidence for rhizosphere resistances Newman (1969a,b) concluded that $\Delta\psi_S$ would only become appreciable when the soil was near or beyond the permanent wilting point. This was later confirmed by Andrews and Newman (1969) and Hansen (1974) from experiments with wheat. For example, Hansen found that $\Delta\psi_S$ became significant when the soil water potential, ψ_S, was lower than - 1.2 MPa. In the present study the appreciable values of $\Delta\psi_S$ inferred at low ψ_S are, therefore, consistent with these previous studies. However, large values of $\Delta\psi_S$ also occurred in wet soil, where ψ_S was greater than - 0.1 MPa, but these do not necessarily conflict with Newman's (1969a,b) conclusions. This is because in the soil regions where these occurred, ie below 1 m, the root density was extremely low. For example, expressed as the length of root (cm) per unit area of ground (cm^2), to allow comparison with the data of Newman (1969a), the root 'density' was 6 cm/cm^2 below 1 m compared with 220 cm/cm^2 above 1 m. Now according to table 1 in Newman (1969a) with 6 cm of $root/cm^2$ the rhizosphere resistance becomes significant when ψ_S is about - 0.1 MPa, a similar potential to that at which large values of $\Delta\psi_S$ were inferred in the present study. The above comparison must be viewed with caution, however, since Newman's calculations were based on the hydraulic conductivity of Pachappa sandy loam, according to Gardner (1960). Furthermore, water uptake by the roots was calculated assuming they were in full contact with homogeneous soil of similar composition to that in bulk. There are however doubts about this, since roots often inhabit cracks or other voids in the soil (see Nye and Tinker 1977), in which contact with soil will be at best partial. On drying beyond - 0.5 MPa, Cole and Alston (1974) found that wheat roots shrank markedly, losing 60% of their original diameter by - 1.0 MPa. Gaps between root and soil could therefore be a serious barrier to water flow to the roots. Tinker (1976) considered that contact around part of the periphery was more probable than a complete gap, and used an electrical analogue to show that such partial contact was unlikely to alter $\Delta\psi_S$ greatly unless the water uptake rate was very large. In conclusion, therefore, calculation of the magnitude of potential gradients in the rhizosphere will remain uncertain until the local values of water uptake by roots and soil hydraulic conductivity can be evaluated.

6.4.5 Diurnal changes in water storage in the soil-plant system

Water storage in the soil-plant system (W) changes diurnally, according to the difference between water uptake by the roots and transpiration (see Section 1.2.3). In the model used in the present study W was represented by the hydraulic capacitance C which, following Powell and Thorpe (1977), is given by

$$C = dW/d\psi_L. \tag{6.16}$$

Changes in W can therefore be calculated using C if the concurrent changes in ψ_L are known. For example, the maximum diurnal change in W is given

$$\Delta W(\max) = C\,\Delta\psi_L(\max), \tag{6.17}$$

where $\Delta\psi_L(\max)$ is the corresponding change in leaf water potential (ie $\psi_L(\max) - \psi_L(\min)$). Substitution of the mean value of C and $\Delta\psi_L(\max)$ measured in 1975, ie 8×10^{-7} m^{3}MPa^{-1} and 1.4 MPa respectively, into equation (6.17) gave $\Delta W(\max)$ as 1.1×10^{-6} m^3 stem^{-1}. This includes the contributions from water storage in the leaves, stem, roots and the soil around the roots. Comparison with the daily total transpiration can be made as follows. On a day of high evaporation, say 4 mm, the total flow per stem from a stand with 320 stems m^{-2} would be 12.5×10^{-6}m^3. Assuming, for simplicity, an equal division of transpiration before and after midday, then about 18% of the transpiration in the morning comes from storage. The water removed from storage is recovered from the bulk soil in the afternoon and evening. A similar calculation to that above, using data reported by Powell and Thorpe (1977), gave the contribution of water storage in an apple tree to its transpiration in the morning as 11%. Bearing in mind the simplifications and assumptions of the present model and that used by Powell and Thorpe, the relative contribution of stored water to transpiration is similar in wheat stems and apple trees, despite the large difference in their hydraulic capacitances (see section 6.4.2). Contrary to the opinion of Jarvis (1976), therefore, the small storage capacity of herbaceous species *per se* does not justify the assumption that the relation between leaf water potential and transpiration in these species will be unaffected by their hydraulic capacitance.

To examine which plant components had most 'available' water the maximum diurnal change in water storage in the plant tops, ΔW_1(max), and in the soil-root system, ΔW_2(max), were calculated. This was done using the hydraulic capacitances C_1 and C_2 (section 6.4.3) in equation (6.17), with $\Delta\psi_L$(max) replaced by the corresponding maximum gradient in water potential across the stem and across the soil-root system respectively. Table 6.5 shows the results for two days in 1975. On both days the soil-root system showed the greatest change in stored water, which is in agreement with independent calculations by Jarvis (1975) for both herbaceous and tree species. The maximum diurnal change in water storage in the entire soil-plant system (ie. ΔW(max)), calculated as ΔW_1(max) + ΔW_2(max), increased by a factor of about five between 22 May and 13 June, mainly because of an increase in water available from storage in the soil-root system. ΔW(max) on the 13 June was close to the mean value of ΔW(max) for the 1975 season, calculated using the total hydraulic capacitance of the soil-plant system (see above).

The values of ΔW(max) calculated using plant hydraulic capacitances were checked by comparing them with independent estimates of the diurnal changes in plant water content, made as follows. The water content of the plant tops (W_1) was calculated, from measurements of their fresh and dry weight made by Hunter (pers. comm.), as 2.8×10^{-6} and $6.8 \times 10^{-6} m^3$ stem^{-1} on 22 May and 13 June respectively. According to the relation between relative water content and water potential in wheat leaves, determined by Campbell (pers. comm.), W_1 would have decreased by a maximum of 5% on 22 May and 7% on 13 June, when leaf water potential was at its lowest on each day. This gave the values of ΔW_1(max) shown in table 6.5 (column (b)), which are both larger than the corresponding values calculated using the hydraulic capacitance of the plant tops. The water content of

DATE	Soil-plant component		$\Delta W(\max)$ $(10^{-6} m^3\ \text{stem}^{-1})$ (a)	(b)
22 May	(i)	Leaves + stem	0.06	0.14
	(ii)	Roots + soil	0.12	0.06*
		Total	0.18	0.20
13 June	(i)	Leaves + stem	0.08	0.48
	(ii)	Roots + soil	0.73	0.13*
		Total	0.81	0.61

Table 6.5 The maximum diurnal change in water storage, $\Delta W(\max)$, in the leaves + stem and the roots + soil calculated from (a) soil-plant capacitances and (b) plant fresh and dry weights, on two days in 1975. **Roots only.*

the roots (W_2) was estimated from the root dry weight, measured by Gregory (1976), by assuming that they contained 90% water (by weight) when fully turgid. However, since a water release curve for wheat roots was not available that used above for wheat leaves was also used to determine ΔW_2(max). The values obtained (table 6.5) were much smaller than those derived using the hydraulic capacitance of the soil-root system, C_2. One possible explanation is that the major portion of C_2 was in the soil around the roots. However, despite the disagreement about the relative contributions of the plant tops and the soil-root system, the two methods gave similar estimates of the total water available from storage in the soil-plant system (table 6.5). Compared to wheat, some other herbaceous crops have much greater amounts of water available from storage, eg Jarvis (1975) calculated that cotton had 15.6×10^{-6} m^3 stem and Whitehead (1975) estimated 132×10^{-6} m^3 $plant^{-1}$ in potato. These larger values may be expected in view of the size of cotton and potato plants compared with wheat.

From the preceding discussion it is evident that the total hydraulic capacitance in wheat, derived using the soil-plant model, gave realistic changes in plant water content, therefore lending confidence to the use of a bulk parameter model. The component hydraulic capacitances, however, predicted changes in water content which disagreed with independent estimates. These latter estimates were based on information which was not originally designed for calculating changes in plant water content. There is, therefore, considerable scope for further studies of changes in the water content and potential of various plant components, with the specific aim of evaluating their hydraulic capacitances. When these are better known, more physically realistic models of water flow in the soil-plant system, like that used by Powell and Thorpe (1977), can be used to predict responses of plant water potential to atmospheric evaporative demand.

7. COMPONENTS OF LEAF WATER POTENTIAL AND STOMATAL CONDUCTANCE

Although leaf water potential is commonly used as an indicator of plant water stress (see section 1.3), understanding how this affects plant physiological functions is limited unless the components of leaf water potential are known. This chapter contains a description of the diurnal and seasonal changes in leaf osmotic potential (ψ_π) and turgor potential (ψ_p) measured in the present study. The relation between ψ_p and stomatal conductance (k_s) is examined and the value of turgor potential below which stomatal closure was induced is identified. Changes in ψ_π during the day and season are discussed in relation to the maintenance of ψ_p above the levels which reduced k_s. Unless otherwise stated, each value of ψ_π and ψ_p is the mean of three estimates (see section 2.2.5.4). The standard errors in ψ_π and ψ_p are not shown here for clarity, but are similar to those shown in figure 2.11. As in chapter 4, different leaves on the stem are distinguished by numeric subscripts. For example, $\psi_{\pi 11}$ and ψ_{p11} refer respectively to the osmotic potential and turgor potential of the 11th leaf to emerge on the stem.

7.1 Results

7.1.1 Diurnal changes in leaf osmotic and turgor potentials

Figure 7.1 (a-d) shows typical changes in the osmotic and turgor potentials of the oldest and youngest green leaves during four days of high evaporative demand in 1974. Flag leaf osmotic potential ($\psi_{\pi 11}$) decreased continuously during 29 May (figure 7.1a), from - 1.8 MPa in the early morning to - 2.5 MPa in the evening. In contrast, the osmotic potential of leaf 8 ($\psi_{\pi 8}$), the oldest green leaf on this day, was

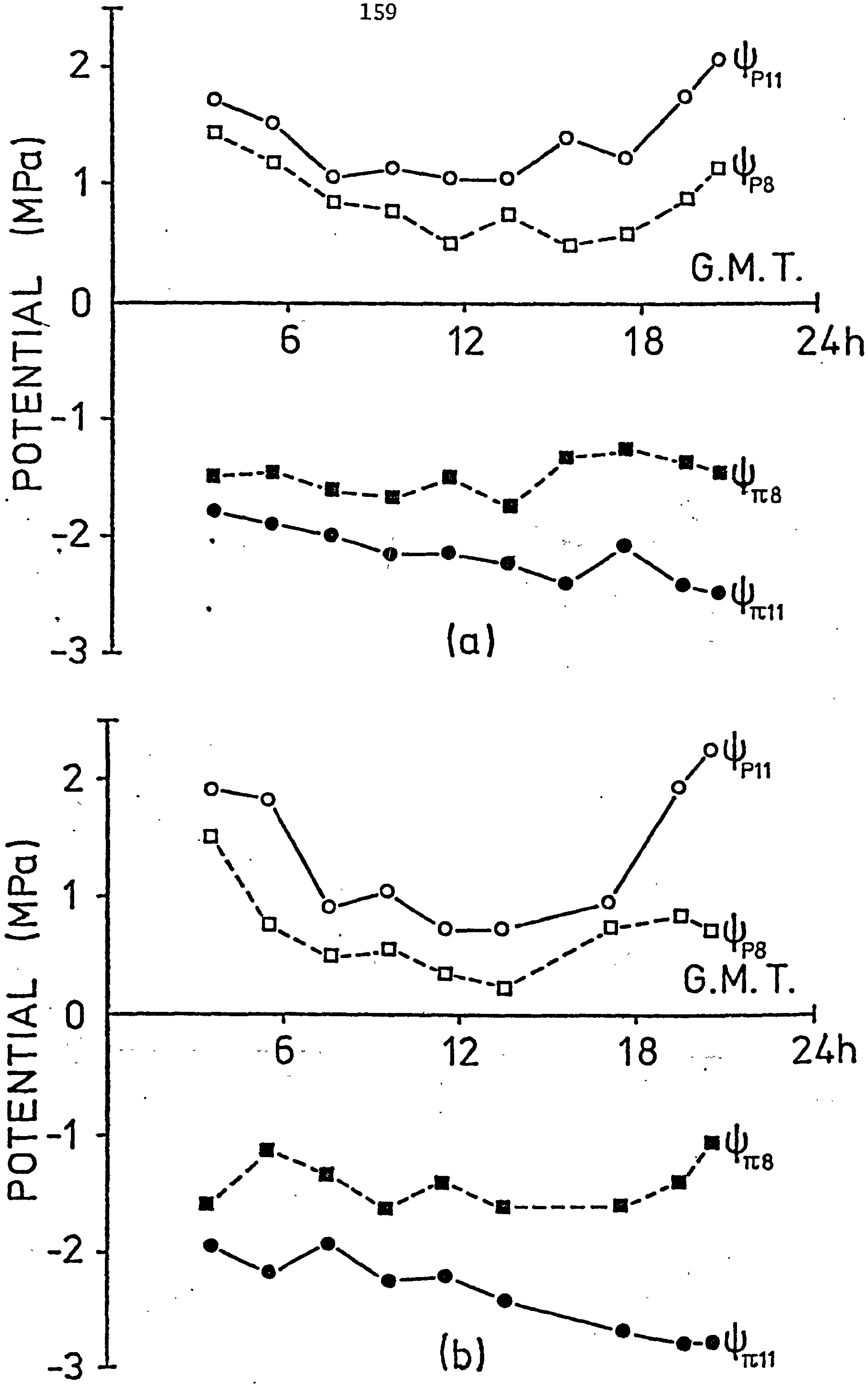
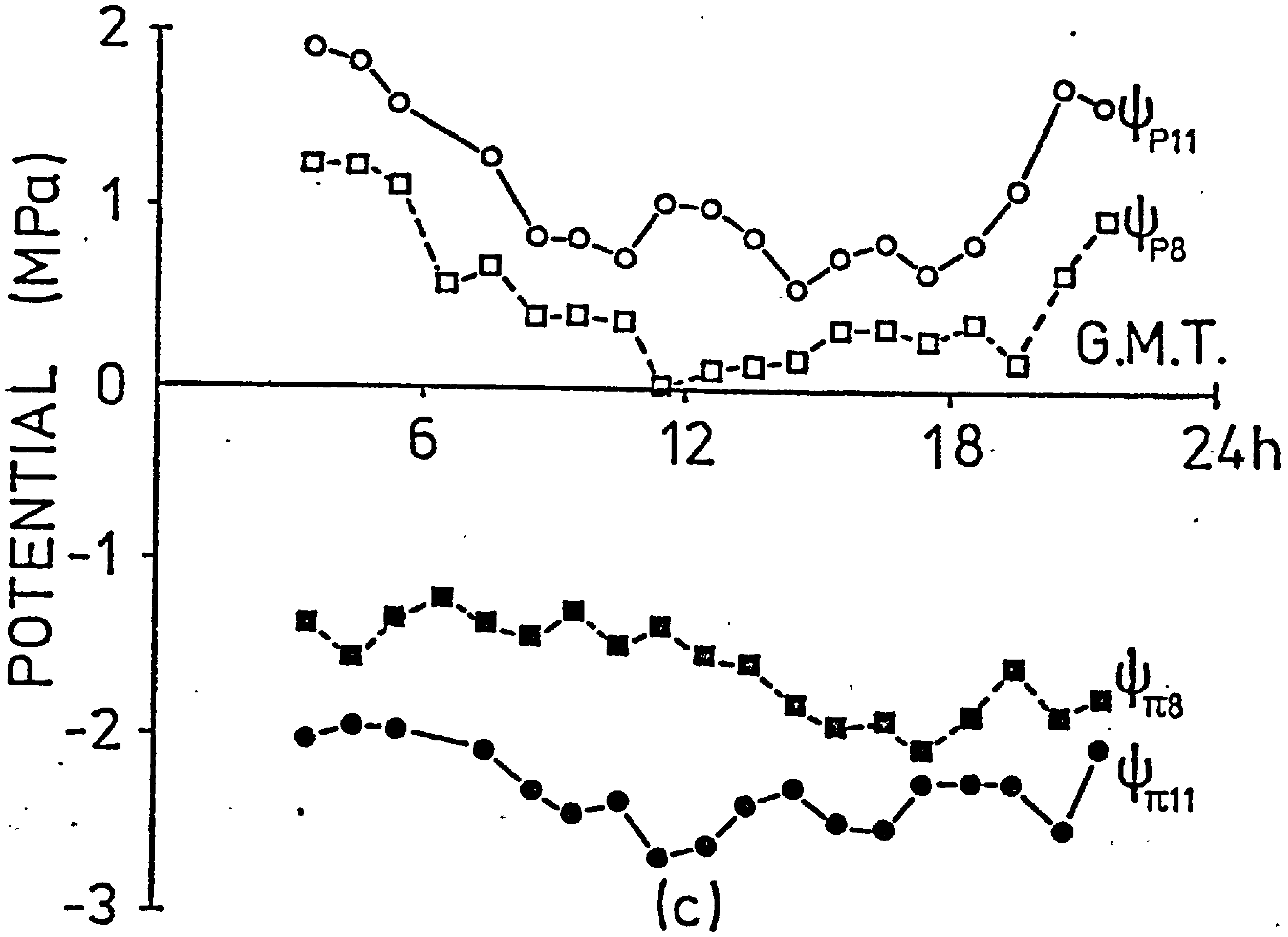
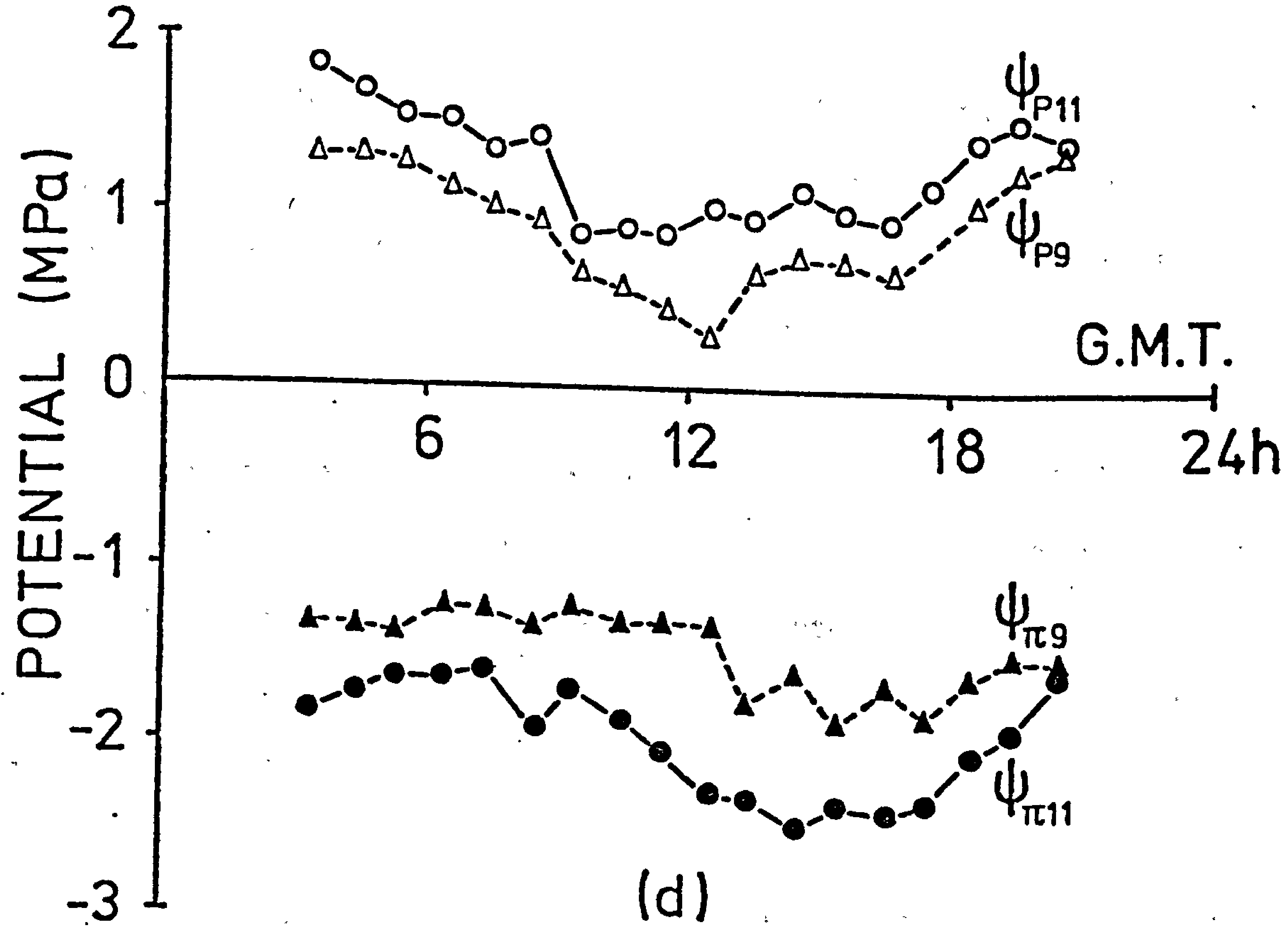


Figure 7.1. Changes in the osmotic (ψ_π) and turgor (ψ_P) potentials of the youngest and oldest green leaves during days of high evaporation in 1974. (a) 29 May, (b) 4 June, (c) 13 June and (d) 20 June.


2
1
0
-1
-2
-3
POTENTIAL (MPa)
6
12
18
24h
G.M.T.
ψ_{P11}
ψ_{P8}
$\psi_{\pi8}$
$\psi_{\pi11}$
(c)


2
1
0
-1
-2
-3
POTENTIAL (MPa)
6
12
18
24h
G.M.T.
ψ_{P11}
ψ_{P9}
$\psi_{\pi9}$
$\psi_{\pi11}$
(d)

higher than $\psi_{\pi 11}$ and did not change significantly throughout the day. The mean value of $\psi_{\pi 8}$ for this day was - 1.5 MPa. Flag leaf turgor potential (ψ_{p11}) was high in the morning, 1.7 MPa, but decreased to 1.0 MPa around midday. After noon it increased again, as leaf water potential increased (see figure 4.1a), to 2.1 MPa in the evening. The turgor potential of leaf 8 (ψ_{p8}) changed during the day in a similar manner to that of the flag leaf, but was lower throughout the day with a minimum of 0.5 MPa around midday. Similar changes in leaf osmotic and turgor potentials were measured on 4 June (figure 7.1b), although flag leaf osmotic potential was 0.2 to 0.3 MPa lower throughout this day. The midday minimum values of leaf turgor potential on the 4 June were also 0.3 MPa lower than the corresponding values on 29 May.

Some differences were observed in the responses of leaf osmotic potential on 13 and 20 June (figure 7.1 c and d). Although $\psi_{\pi 11}$ decreased during the morning as before, it increased again in the afternoon and reached a value in the evening close to that of the early morning. On the 13 June $\psi_{\pi 8}$ was approximately constant up to midday, but then it decreased from - 1.4 MPa to - 2.0 MPa in the afternoon. By 20 June senescence of leaf 8 was so advanced that no further measurements could be made on it, and the oldest leaf studied was leaf 9. Its osmotic potential, $\psi_{\pi 9}$, responded similarly to that of leaf 8 on 13 June, remaining constant at - 1.3 MPa up to midday and then decreasing to - 1.8 MPa in the afternoon. Leaf turgor potentials were lower around midday on 13 June than on 29 May, 4 and 20 June, ψ_{p8} being close to zero just before midday.

For contrast, figure 7.2 shows the changes in the osmotic and turgor potentials of leaves 11 and 9 on a day of low evaporative demand, 26 June 1974. Here $\psi_{\pi 11}$ did not change significantly during the day, its mean value for the day being - 2.1 MPa. $\psi_{\pi 9}$ also remained approximately

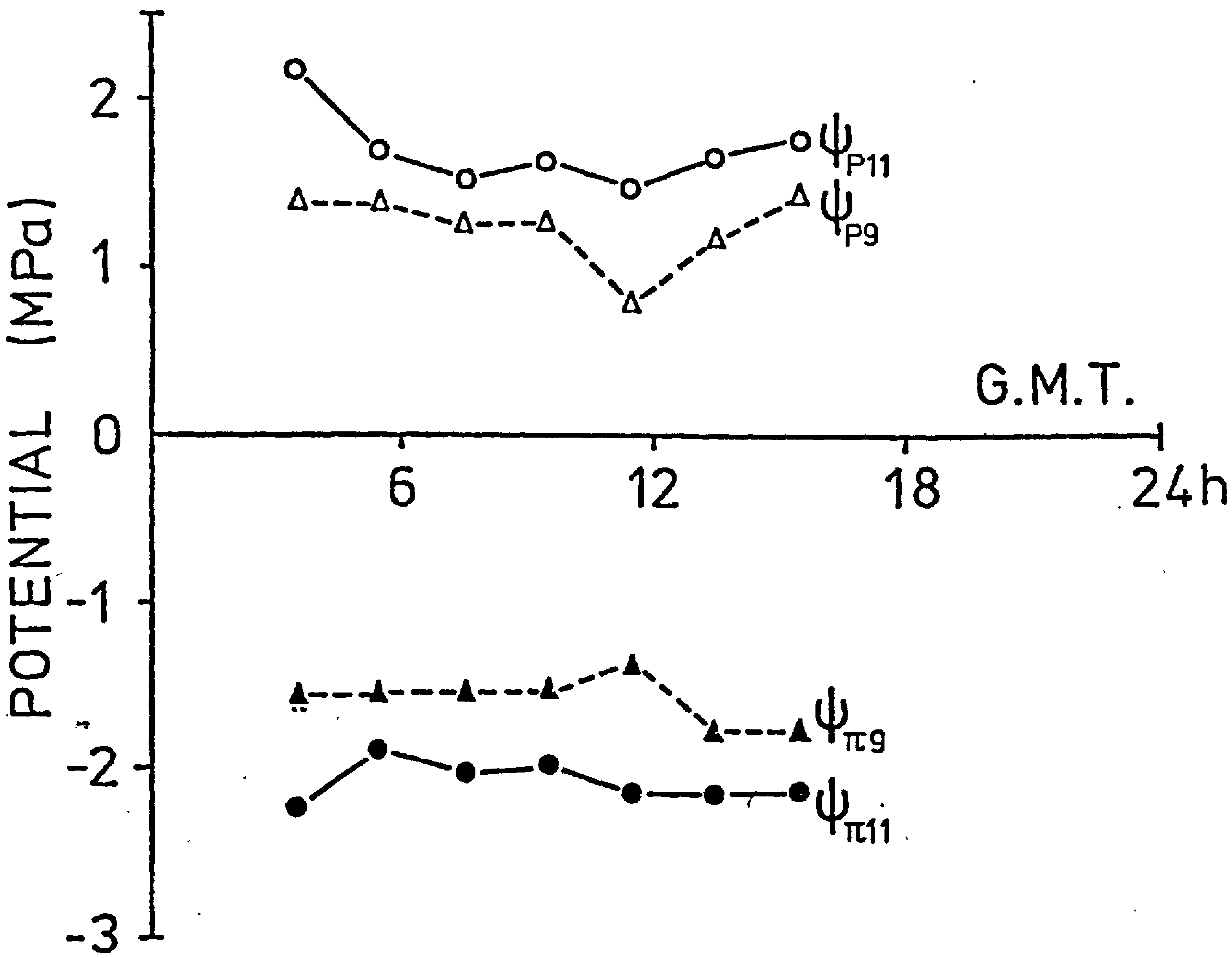


Figure 7.2. Changes in the osmotic (ψ_π) and turgor (ψ_P) potentials of the youngest and oldest green leaves during a day of low evaporation, 26 June 1974.

constant for most of the day, only decreasing by about 0.2 MPa after noon. Leaf turgor potentials were higher throughout 26 June than on days of high evaporative demand. For example, the midday minimum values of ψ_{p11} and ψ_{p8} were 1.5 and 0.8 MPa respectively.

So far only the osmotic and turgor potentials of the oldest and youngest green leaves have been described. Leaves of intermediate age and position on the stem generally had intermediate values of ψ_π and ψ_p. These are presented in the following section, where the seasonal changes in ψ_π and ψ_p observed in 1974 and 1975 are also described.

7.1.2 Seasonal changes in leaf osmotic and turgor potentials

To compare the osmotic and turgor potentials of all the green leaves on the stem their mean values in the period 09h00 to 15h00, signified by $\bar{\psi}_\pi$ and $\bar{\psi}_p$ respectively, were calculated. This period was chosen because it was the time of day when leaf turgor potentials were lowest, and therefore most likely to affect stomatal conductance (see section 7.1.3). Figure 7.3 shows the values of $\bar{\psi}_\pi$ and $\bar{\psi}_p$, for each green leaf on the stem, on six days during 1974. The flag leaf (leaf 11) had the lowest osmotic potential and the highest turgor potential, apart from on 29 May. Generally, the older the leaf and the lower its position on the stem, the higher its osmotic potential and the lower its turgor potential. The gradient in osmotic potential along the stem, calculated as $\bar{\psi}_{\pi 9} - \bar{\psi}_{\pi 11}$, ranged from 0.5 MPa on 29 May to 0.9 MPa on 9 July, with a mean value for the season of 0.7 MPa. The corresponding gradient in leaf turgor potential, $\bar{\psi}_{p11} - \bar{\psi}_{p9}$, ranged from 0.3 to 0.6 MPa on the same dates as above, the mean value for the season being 0.5 MPa.

Seasonal changes in leaf osmotic and turgor potentials can also be seen in figure 7.3. Generally, leaf osmotic potentials changed little

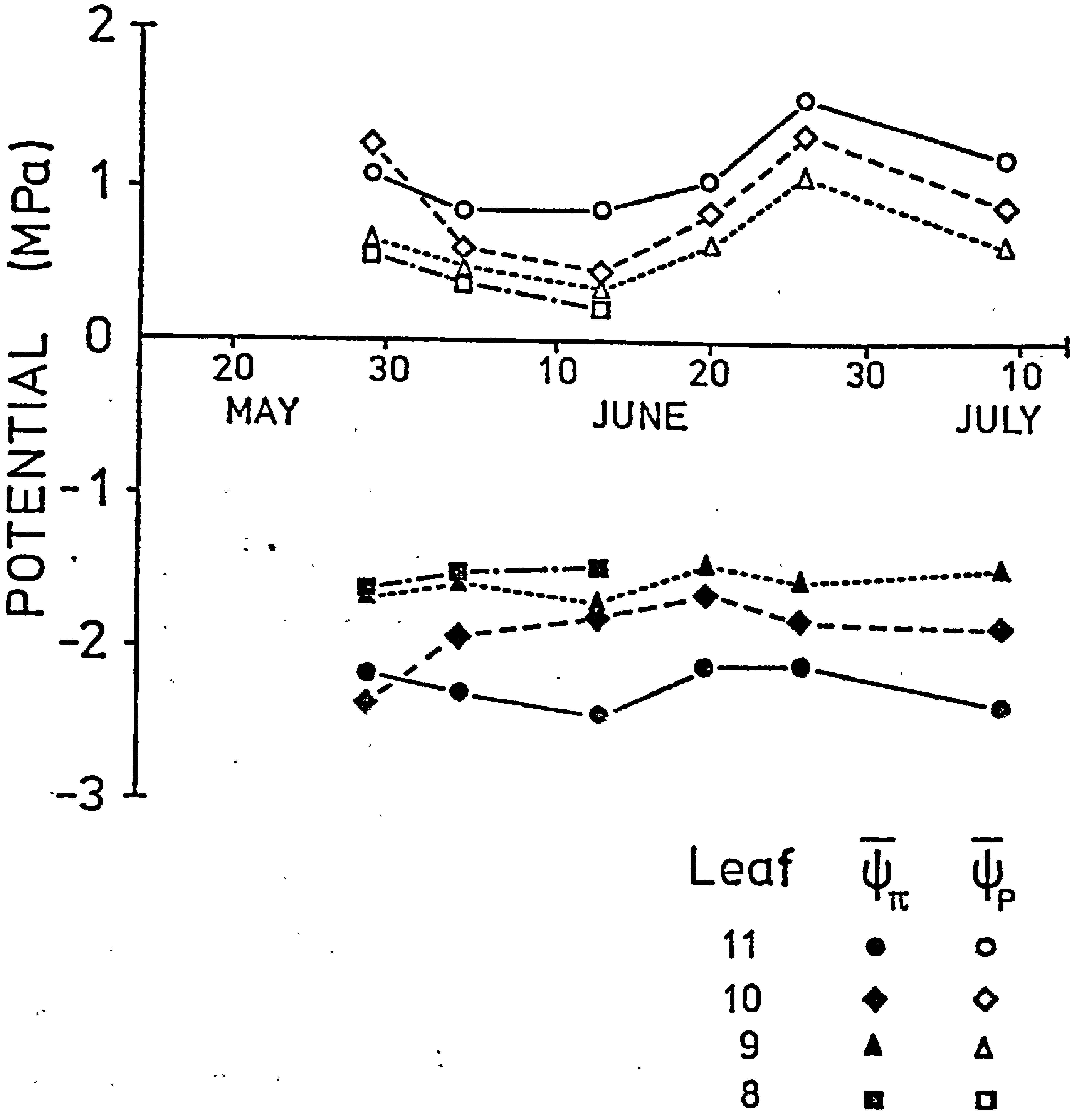


Figure 7.3. Changes in mean leaf osmotic potential ($\bar{\psi}_\pi$) and turgor potential ($\bar{\psi}_P$) in the period 09h00 to 15h00 during 1974.

during the 1974 season. The exception being $\overline{\psi}_{\pi 10}$, which increased by 0.6 MPa between 29 May and 13 June, however, it remained approximately constant for the rest of the season. In contrast, leaf turgor potentials showed a marked decrease in mid-June and recovery thereafter. These changes in leaf turgor potential reflect concurrent changes in leaf water potential. This is illustrated in figure 7.4, which summarizes the changes in leaf water potential, osmotic potential and turgor potential measured in 1974 and 1975. Again mean values in the period 09h00 to 15h00 are shown, i.e. $\overline{\psi}_L$, $\overline{\psi}_\pi$ and $\overline{\psi}_p$, but for clarity only data for the youngest leaves is presented. Between days of high evaporative demand in 1974, ie all the days for which data are shown in figure 7.4a except 26 June, changes in flag leaf osmotic potential, $\overline{\psi}_{\pi 11}$, were coincident with similar changes in leaf water potential, $\overline{\psi}_{L11}$. Flag leaf turgor potential, $\overline{\psi}_{p11}$, therefore remained high, between 0.8 and 1.2 MPa, during the part of the season studied. Leaf turgor potentials were particularly high on 26 June (see also figure 7.2) because the low evaporative demand on this day only depressed leaf water potential by about half of that on previous days of high demand (see section 4.1.1). Clearly there was some degree of osmotic adaptation in the flag leaves during 1974, which maintained high turgor potentials. In contrast, leaves below the flag leaf did not alter their osmotic potential to compensate for changes in leaf water potential (see figure 7.3). Consequently, their turgor potentials were more affected by changes in leaf water potential than flag leaf turgor potential was.

Figure 7.4b shows that osmotic adaptation was much more pronounced in 1975. Up to the middle of June leaf osmotic and turgor potentials were similar to those of corresponding leaves in 1974. However, continuing drought during June 1975 led to a large decrease in flag leaf water potential. During the same period the flag leaves also reduced their osmotic potential, which remained lower than their water potential,

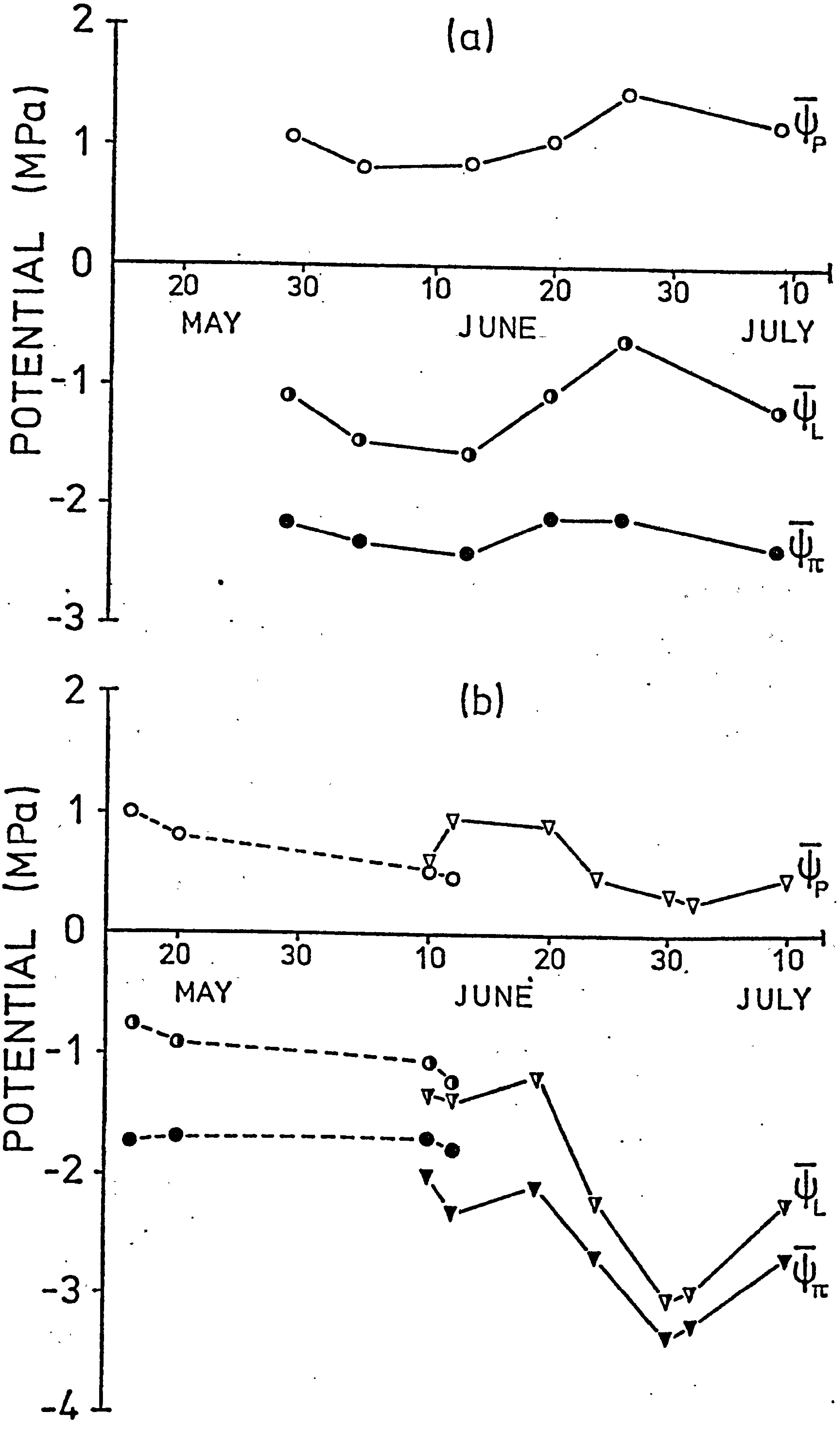


Figure 7.4. Changes in mean leaf water potential ($\bar{\psi}_L$), osmotic potential ($\bar{\psi}_\pi$) and turgor potential ($\bar{\psi}_P$) in the period 09h00 to 15h00 during (a) 1974 and (b) 1975. Circles denote leaf 11, triangles denote leaf 12.

thereby maintaining a positive turgor potential in these leaves. In general, however, leaf turgor potentials were much lower during late June and early July 1975 than they were in the corresponding period in 1974. The importance of maintaining high leaf turgor potential can be seen from the relation between leaf turgor potential and stomatal conductance, which is described below.

7.1.3 Diurnal changes in stomatal conductance

Stomatal behaviour in the field is mainly influenced by two factors, light and leaf water status (Slatyer 1967). Measurements of stomatal conductance, made in the present study by Cohen, Clark and Hotchkiss (pers. comm.), were therefore considered in relation to concurrent estimates of irradiance and leaf turgor potential. For example, figure 7.5 shows the changes in stomatal conductance (k_s) of the adaxial and abaxial epidermis of leaf 10 on two days in 1974. On 20 June the diurnal change in the conductance of the adaxial epidermis was large, with a maximum around midday and zero values about dawn and dusk. The changes in stomatal conductance during 13 June, however, were very different. On this day the conductance of the adaxial epidermis increased rapidly to a maximum in the early morning and then decreased to a minimum about midday. This is the time when maximum stomatal conductances were observed on 20 June. In the afternoon of 13 June there was a slight increase in the conductance of the adaxial epidermis, but the conductance of the abaxial epidermis was zero throughout the afternoon. On both days abaxial conductances were much lower than concurrent adaxial conductances. Since solar irradiance was similar on 13 and 20 June (see figure 7.6), therefore some factor other than light must have caused the reduction in stomatal conductance on 13 June.

Figure 7.7 shows the conductance of the adaxial epidermis of leaf 10

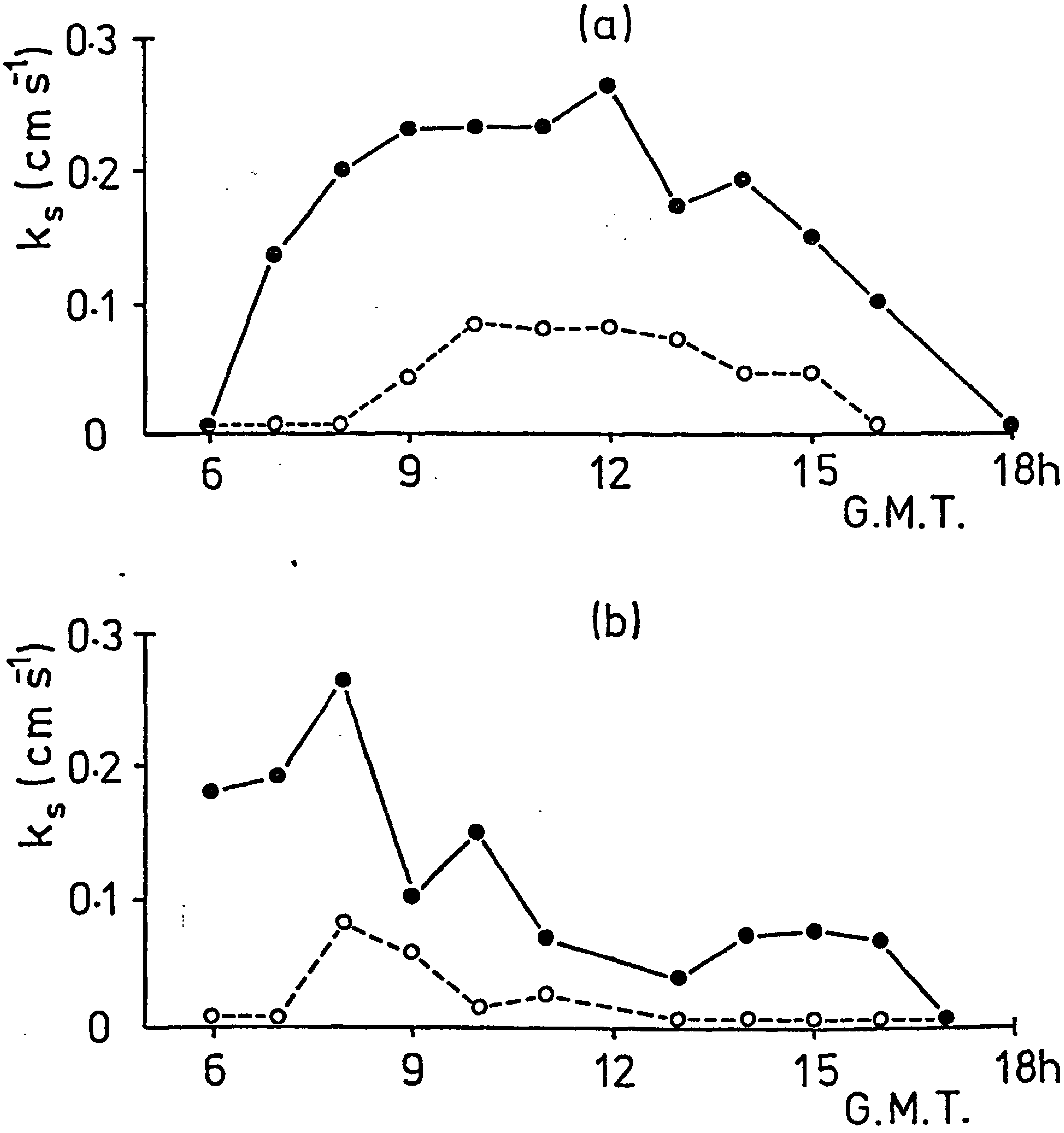


Figure 7.5 Changes in stomatal conductance (k_s) of the adaxial (●) and abaxial (○) epidermis of leaf 10 on (a) 20 June 1974 and (b) 13 June 1974.

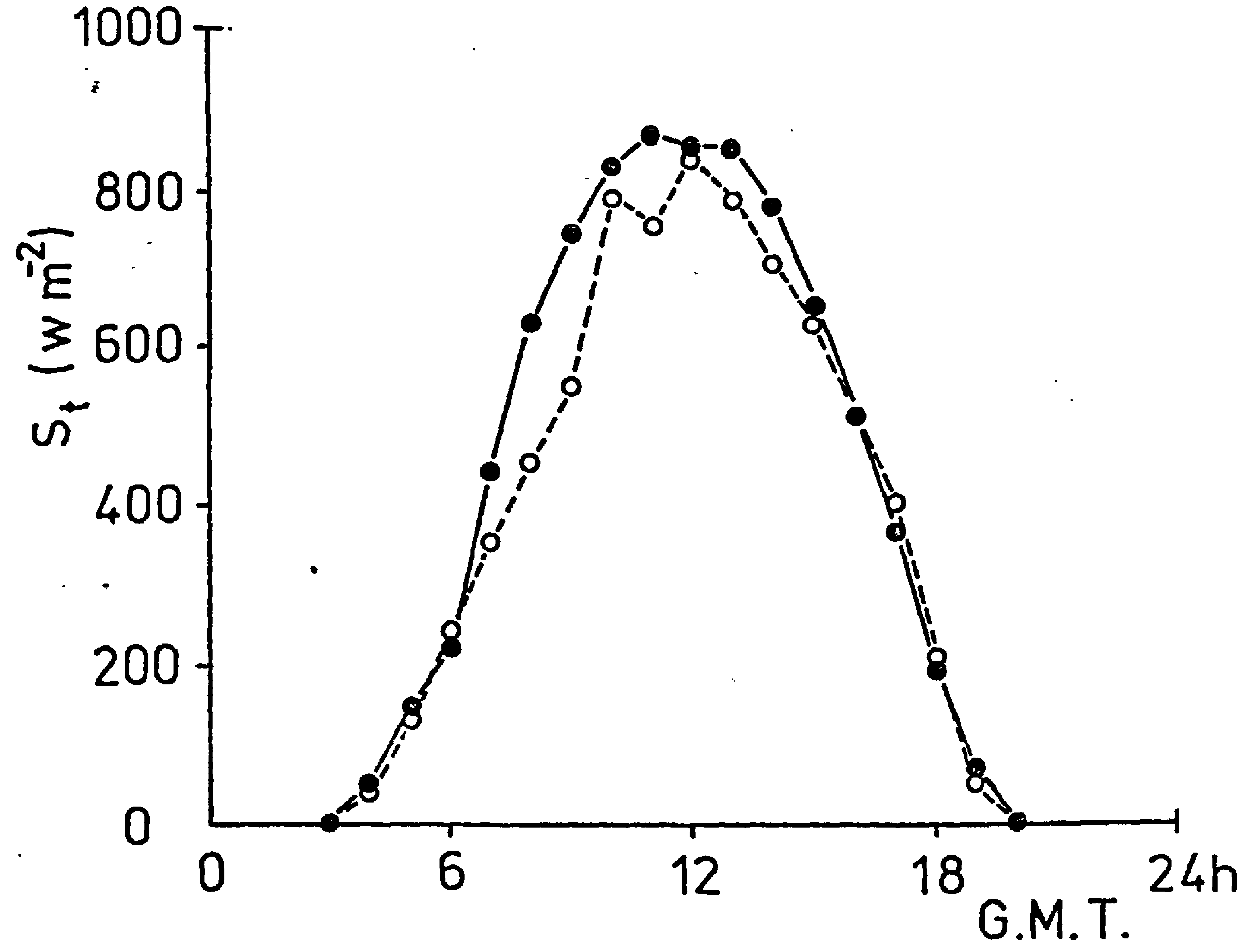


Figure 7.6. Changes in solar irradiance (S_t) above the wheat crop on 13 June 1974 (●) and 20 June 1974 (○).

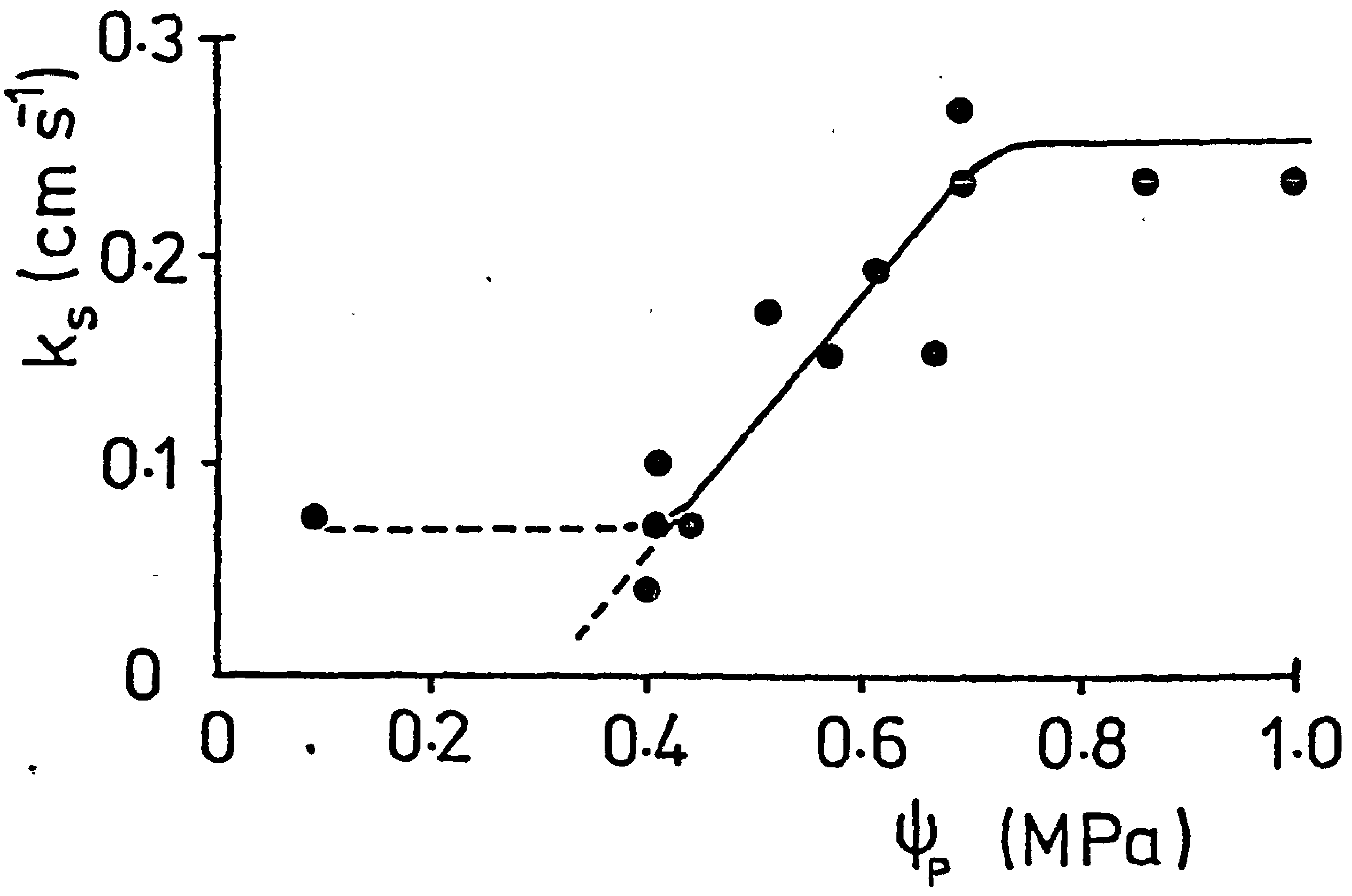


Figure 7.7. The relation between the adaxial stomatal conductance (k_s) and turgor potential (ψ_P) of leaf 10 at high irradiance.

plotted against concurrent estimates of leaf turgor potential on 13 and 20 June 1974. Measurements in weak light in the early morning and evening have been omitted. This is because in the absence of water stress, stomatal conductance varied with irradiances below 300 W m^{-2} and was constant at higher irradiances (see Biscoe *et al* 1976). The changes in stomatal conductance shown in figure 7.7 can therefore be associated with changes in leaf turgor potential. Stomatal conductance decreased from its maximum value when turgor potential fell below 0.7 MPa and reached a minimum when turgor potential was below 0.4 MPa. The scarcity of data at low values of turgor potential makes it uncertain whether stomatal conductance tended to zero or a small value (about 0.7 cm s^{-1}) when turgor potential was less than 0.4 MPa.

7.2 Discussion

7.2.1 Comparison of leaf osmotic and turgor potentials with those in other studies

There are several reports in the literature of leaf osmotic and turgor potentials with which the data presented here can be compared. For example, diurnal variations in ψ_π, similar to those measured in the youngest leaves in the present study, have also been observed in wheat by Millar and Denmead (1976) and in other species by Goode and Higgs (1973); Turner and Begg (1973); Turner 1974, 1975; Whitehead (1975); Hsiao *et al.* (1976). In similar environments, however, the magnitude of ψ_π differed in the above species. For example, on days of high evaporation from plants growing in wet soils, midday ψ_π was highest in potato, - 0.9 MPa (Whitehead 1975), and lowest in sorghum and wheat, - 2.2 MPa (Turner and Begg 1973; This study). In similar conditions Millar and Denmead (1976) measured even lower midday potentials, - 3 MPa, in the leaves of their wheat crop. These differences in ψ_π may reflect the different degrees of drought tolerance of the above species. This is because at a given leaf water potential plants with lower osmotic potentials have higher turgor potentials (see also section 7.2.3). In the present study and those cited above leaf turgor potentials were lowest around midday. Their values at this time, as suggested above, were lowest in potato, 0.1 MPa (Whitehead 1975) and highest in sorghum and wheat, 0.8 MPa (Turner and Begg 1973; This study). These values of ψ_p occurred on days of high evaporation, however, ψ_p was higher under less demanding evaporative conditions, consequently ψ_π changed little during these periods (Millar and Denmead 1976; This study).

At any one time in the present study there was a systematic decrease in ψ_π and increase in ψ_p from the bottom to the top of the stem. This was also the case in the wheat studied by Millar and Denmead (1976) and the maize, sorghum and tobacco studied by Turner and Begg (1973) and Turner (1974, 1975). Furthermore, gradients in ψ_π and ψ_p along wheat stems studied here and by Millar and Denmead (1976) were identical. Unlike the youngest, uppermost leaves, the lower leaves on the stem generally had osmotic potentials which changed little during the day. This can be seen in Turner's (1975) study of maize and also in the present study. However, even the diurnal changes in ψ_π in the youngest leaves were small compared with concurrent changes in leaf water potential, ψ_L. Conversely, during periods of prolonged drought, large decreases in ψ_π accompanied decreasing ψ_L (see figure 7.4b). Similar seasonal changes in ψ_π have also been observed in other field crops. For example, in apple (Goode and Higgs 1973), Sorghum (Hsiao *et al* 1976) and soybean (Sionit and Kramer 1976). Many more controlled environment studies, of a variety of herbaceous species growing in drying soils, found that ψ_π decreased with ψ_L, generally by amounts which were sufficient to keep leaf turgor potential positive (Weatherley 1965; Warren Wilson 1966a; Gavande and Taylor 1967; Millar, Duysen and Norum 1970; Sanchez-Daiz and Kramer 1973; Shepherd 1975; Simmelsgaard

1976; Jones and Turner 1978). Detailed comparison of the varying degrees to which ψ_π changed in the above species is difficult because of the widely different conditions in which the plants were studied. However, Gardner and Ehlig (1965) studied four species and found that, in drying soils, the decrease in ψ_π in trefoil was twice that in sunflower. In the field, Turner and Begg (1973) found that the seasonal change in ψ_π in maize was greater than that in sorghum and tobacco. In consequence, turgor potential remained positive in maize, whereas it was zero in tobacco and negative in sorghum. The different degrees of osmotic adaptation in the above species may reflect differing ability to cope with water stress.

7.2.2 The mechanisms of osmotic adaptation during water stress

It has already been mentioned in section 1.3 that ψ_π can be lowered by dehydration or solute accumulation in the leaves. In practice both mechanisms appear to operate and the relative contribution of each will now be discussed. The effect of dehydration on leaf osmotic potential, ψ_π, can be described using the relation

$$\psi_\pi = \psi_\pi^o/\theta_L, \tag{7.1}$$

following Gardner and Ehlig (1965), where θ_L is the leaf relative water content and ψ_π^o its osmotic potential at full turgor, i.e. when $\theta_L = 1$. In the present study θ_L was not measured, however, to allow calculation of the change in ψ_π due to dehydration, θ_L was estimated from leaf water potential, ψ_L, using the relation between θ_L and ψ_L determined in another wheat crop by Campbell (pers. comm.). Table 7.1 shows the calculated changes in flag leaf osmotic potential, due to dehydration between early morning (03h00) and midday (12h00) on four days in 1974. ψ_π^o was taken as the measured value of ψ_π at 03h00, i.e. when $\psi_L \simeq 0.1$ MPa

	03h00			100			
	ψ_L(MPa)	θ_L	ψ_π(MPa)	ψ_L(MPa)	θ_L	ψ_π(MPa) Calculated	Measured
29 May	-0.1	1	-1.8	-1.2	0.94	-1.9	-2.2
4 June	-0.05	1	-2.0	-1.7	0.91	-2.2	-2.3
13 June	-0.1	1	-2.0	-1.6	0.92	-2.2	-2.6
20 June	-0.1	1	-1.9	-1.3	0.93	-2.0	-2.3

Table 7.1 Changes in leaf water potential (ψ_L), osmotic potential (ψ_π) and relative water content (θ_L) between 03h00 and 12h00 G.M.T. on four days in 1974.

and $\theta_L \simeq 1$, and ψ_π at 12h00 calculated using equation (7.1). The measured values of ψ_π at 12h00 are also shown in table 7.1 for comparison. Since the measured osmotic potentials at midday were consistently lower than the calculated values, dehydration of the leaves can only partially account for the observed reduction in ψ_π. Furthermore, the large decrease in ψ_π during the drought in 1975 (see figure 7.4b) is also only partly ascribable to leaf dehydration. Other investigators have also found that ψ_π decreased during water stress by amounts which were greater than predicted by equation (7.1). For example, Weatherley (1965), Millar *et al* (1970), Shepherd (1975), Hsiao *et al* (1976) and Simmelsgaard (1976). The implication is that there was an increase in osmotically active solutes in the leaves of the species in the above and present studies.

The above conclusion, however, based on calculations made using equation (7.1), is uncertain. This is because such calculations assume negligible bound water in the leaves. Allowing for the bound water fraction, B, Warren Wilson (1966a) derived an expression for ψ_π as

$$\psi_\pi = \psi_\pi^o \{(1-B)/(\theta_L-B)\}. \tag{7.2}$$

Comparison of equations (7.1) and (7.2) shows that for a given decrease in relative water content, θ_L, the calculated decrease in ψ_π is larger when B is greater than zero. B was not measured in the present study, however, assuming it was similar to that measured in another wheat crop by Campbell (pers. comm.), i.e. 0.3, the diurnal changes in ψ_π were recalculated using the data shown in table 7.1 in equation (7.2). The values of ψ_π at midday thus obtained were only 0.1 MPa lower than those already calculated using equation (7.1), i.e. with $B = 0$. Measured changes in ψ_π therefore remain lower than can be accounted for by dehydration, even when bound water is taken into consideration.

Further evidence for solute accumulation in the youngest leaves in the present study comes from the continued decrease in their osmotic potentials during the afternoon (see figure 7.1a, b), when ψ_L and hence θ_L were increasing. In contrast, since the osmotic potentials of the older, lower leaves on the stem were constant when their water potentials (and hence θ_L) were decreasing (see figure 7.1), these leaves may have reduced their solute content around midday. Other studies also claim evidence for solute accumulation in leaves during water stress. For example, Biscoe (1972) found that measured changes in ψ_π in pot grown sugar-beet plants which were deprived of water agreed well with those calculated from changes in leaf dry weight. In sorghum, Jones and Turner (1978) found that stress preconditioning of plants lowered ψ_π at all water contents. They claimed this was unequivocal evidence for osmotic adjustment, which they presumed to occur as a result of cell solute increase. Most species therefore adapt their leaf osmotic potential to maintain turgor potential during water stress and, as in wheat, they do this by a combination of dehydration and solute accumulation in the leaves.

Investigations of the mechanisms of osmotic adjustment require the solutes involved to be identified. In recent reviews of the available evidence, Hsiao (1973), Hellebust (1976) and Hsiao *et al* (1976) reported that many plants grown in saline media adapt their internal osmotic potentials by the uptake and accumulation of the inorganic solutes in the growing medium. For example, chlorine and potassium ions can have a predominant role in osmotic adjustment. In contrast, organic solutes, such as sugars, have been found to accumulate in the leaves of plants under water stress. However, Hsiao *et al* (1976) concluded that the different amounts of soluble sugars in the leaves at different heights in a maize crop were insufficient to account for the measured gradients in osmotic potential. It appears that more information is still required about the nature and regulation of the solutes involved in osmotic adjustment to further our understanding of this phenomena.

Whichever mechanisms were responsible for osmotic adjustment the effect was to increase leaf turgor potential, ψ_p, and this helped to keep ψ_p above the levels which reduced stomatal conductance.

7.2.3 Factors affecting leaf stomatal conductance

Light and water stress appear to have been the main factors which determined stomatal conductance, k_s, in the present study. In the absence of water stress k_s was primarily determined by irradiance (data published previously by Biscoe *et al* 1976). This agrees with previous studies of stomatal behaviour in wheat (Jones 1974; Denmead and Millar 1976b), and in other species (Turner and Begg 1973; Turner 1974b). When plants were under water stress in the present study, k_s was controlled by leaf turgor potential rather than irradiance. The value of ψ_p below which k_s was reduced, 0.7 MPa, is similar to that determined previously in wheat by Millar and Denmead (1976), i.e. 0.8 MPa. Begg and Turner (1973) and Turner (1974), however, found that k_s was not appreciably reduced until ψ_p was close to zero in maize, sorghum and tobacco.

Stomatal conductance has also been found to be correlated with other plant and environmental factors. Many previous studies have related k_s to leaf water potential, ψ_L (e.g. Jordan and Ritchie 1971; Biscoe 1972; Frank, Power and Willis 1973; Turner 1974b; Whitehead 1975). The relations obtained, however, showed widely different 'critical' water potentials, below which k_s was reduced. For example, Miller, Gardner and Goltz (1971) found that k_s decreased in onion when ψ_L was below - 0.3 MPa, whereas k_s was unaffected by ψ_L in cotton until ψ_L fell below - 2.7 MPa (Turner 1974b). However, Turner's review shows that leaf turgor potentials were similar when k_s decreased, between zero and 0.2 MPa. Furthermore, Millar and Denmead (1976) found that the critical value of ψ_p was the same for all the leaves on the stem, whereas ψ_L varied between - 0.7 MPa and - 1.9 MPa. Differences in leaf osmotic potential account for Millar and Denmead's results. Plotting k_s against ψ_L therefore ignores any differences in osmotic potential between the different leaves on the plants and any osmotic adjustment which might occur during water stress.

Stomata have also been shown to respond to factors other than light and water stress. For example, stomatal aperture has been shown to change with atmospheric humidity (Raschke 1970; Lange *et al* 1971; Schulze *et al* 1972). Stomatal conductance, k_s, has been related to vapour pressure deficit (Johnson and Caldwell 1976; Roberts 1978), and Jarvis (1976) has modelled the response of k_s in Sitka spruce with functions which depend on ambient temperature and carbon dioxide concentration. These factors almost certainly only indirectly control k_s, probably via their effect on the turgor potential balance between the guard cells and their surrounding epidermal cells (Beadle 1977). In fact, the relation between bulk leaf turgor potential and k_s obtained in the present study, may have resulted from one of many different types of relation between bulk tissue properties and those in the stomatal complex. Further research should be directed at studying water relations of guard cells and how these are affected by the water status of the bulk tissues. Then, perhaps, we may understand why bulk leaf turgor potential is related to k_s in certain species, whereas in others it is not.

In the present study the severity of water stress on any day may be quantified as the length of time that the turgor potential of the youngest leaves was below the levels which reduced stomatal conductance. Table 7.2 shows that ψ_p fell below 0.7 MPa on only two days during 1974 and never dropped below 0.4 MPa during the entire season. Though ψ_p remained above 0.7 MPa throughout the day in May 1975, by mid-June it was below this value for several hours around midday. As the drought continued, ψ_p fell below 0.7 MPa for most of the day and below 0.4 MPa for a substantial time around midday. These values of turgor potential are for the youngest leaves, however older leaves, lower on the stem, had lower turgor potentials. Since Millar and Denmead (1976) found that k_s was reduced at the same levels of ψ_p in all the leaves on wheat stems, therefore, leaves lower on the stem probably suffered stress induced stomatal closure for longer periods than the youngest leaves did. In summary, during the season of average weather conditions, 1974, there were few occasions when the plants experienced water stress. In contrast, during the drought in 1975 water stress increased until ultimately the plants spent most of the day with their leaf stomatal conductance reduced by low leaf turgor potential, despite osmotic adjustment.

Date:	(a) $\psi_p < 0.7$ MPa	(b) $\psi_p < 0.4$ MPa
29 May 1974	0	0
4 June 1974	0	0
13 June 1974	2	0
20 June 1974	0	0
26 June 1974	0	0
9 July 1974	1	0
TOTAL (1974)	3	0
16 May 1975	0	0
20 May 1975	0	0
10 June 1975	3	1
12 June 1975	1	0
19 June 1975	0	0
24 June 1975	8	4
30 June 1975	12	6
2 July 1975	12	8
TOTAL (1975)	36	19

Table 7.2 The number of hours per day when flag leaf turgor potential (ψ_p) was lower than (a) 0.7 MPa and (b) 0.4 MPa.

8 SUMMARY AND CONCLUSIONS

The results of this study have provided the following information about water transport and leaf water relations in wheat plants.Assuming water flowed through the plants in response to the evaporative demand of the atmosphere, which created a water potential gradient between the leaves and the soil. The magnitude of this water potential gradient ($\Delta\psi$) was determined primarily by the flow of water (Q) and the hydraulic resistance (R) in the plants. Leaf water potential (ψ_L) was given by a combination of $\Delta\psi$ and the effective water potential in the soil (ψ_B). During the day ψ_L responded primarily to changes in evaporation, whereas seasonal changes in ψ_L resulted from changes in soil water potential.

Hysteresis in the relation between ψ_L and Q was attributed to changes in water storage in the soil-plant system. To allow for this, the model used to represent water flow in the soil-plant system incorporated a hydraulic capacitance, C. Estimates of R and C were obtained from measurements of ψ_L and Q using this model, by assuming that R, C and ψ_B were all constant during the day. The values of R obtained were in good agreement with those (a) estimated from the recovery of ψ_L in non-transpiring plants, and (b) from an independent study of wheat (Denmead and Millar 1976a). The estimates of C, although more variable than those of R, were also reasonable since they predicted realistic diurnal changes in soil-plant water storage.

Components of R and C were also estimated. When the soil water potential (ψ_s) was high, the largest hydraulic resistance could be attributed to the soil-root system, the stem resistance was half of this. Resistance to water flow in the soil-root system increased when ψ_s was low, and there was evidence of large water potential gradients in the soil around the roots. Further experimentation and perhaps a more realistic model of flow in the soil-plant system are needed, however, to obtain more accurate estimates of the components of R and C, in particular to separate those of the roots and surrounding soil. Ultimately, however, it may be necessary to make concurrent measurement of flow and potential *in situ*, throughout the soil-plant system.

When ψ_L decreased so did leaf osmotic potential (ψ_π), apparently by a combination of dehydration and solute accumulation in the leaves. Osmotic adaptation therefore tended to maintain leaf turgor potential (ψ_P) during water stress. Maintenance of ψ_P was important because stomatal conductance (k_s) was reduced when ψ_P fell below 0.7 MPa. Leaf turgor potential was considered to be a better indicator of stomatal behaviour during water stress than ψ_L. This was because ψ_P allowed for differences in osmotic potential between different leaves and any osmotic adaptation which occurred during water stress. It is also easier to envisage the stomatal mechanism operating via actual, positive pressures in the leaf cells. However, the present method of estimating ψ_P, as the difference between ψ_L and ψ_π, leaves much to be desired. Estimates of ψ_P by this method remain uncertain because of the errors in estimating ψ_L and ψ_π and since the effects of bound water and matric potential are not fully understood. Furthermore, the components of ψ_L may not be strictly additive quantities, since they may not be independent of each other (see, for example, Brown 1972; Miller 1972). It would therefore be a considerable advantage if leaf turgor potential could be measured directly, and perhaps more research should adopt this goal.

The fact that stomatal closure was initiated at a high turgor potential could have been advantageous to the plants for a number of reasons. For example, the reduction in k_s presumably reduced transpiration, thereby maintaining ψ_P (and ψ_L) and conserving soil water. Maintenance of ψ_P (and ψ_L) may have avoided degradation of physiological processes, such as cell growth, protein synthesis, hormonal activity and translocation of photosynthate (Hsiao 1973). Conservation of soil water may be useful if a drought is impending.

The wheat species studied appears to have been fairly well adapted to drought. This is reflected in the grain yields of the 1974 and 1975 crops which were similar, 5.0 and 5.1 tonnes ha^{-1} respectively, despite the drought in 1975. However, following another drought in 1976, which began earlier in the year, wheat yield on the same site decreased to 3.4 tonnes ha^{-1} (Gallagher and Biscoe 1978). It appears that the timing of water stress in the life cycle of the plants is important, as well as its duration and severity. Further research should be directed at finding out when plants are most sensitive to water stress, and why? Such information would be extremely useful in optimizing yields where water supplies are limited.

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Appendix A.1 CALCULATION OF THE REYNOLDS NUMBER FOR WATER FLOW IN WHEAT STEM XYLEM VESSELS

In fluid dynamics the Reynolds number (R_e) gives an indication of whether flow is laminar or turbulent. For sap flow in xylem vessels, assuming that they can be approximated by smooth walled cylindrical tubes of diameter d, R_e is given by

$$R_e = \frac{\rho \, du}{\eta}, \tag{A.1}$$

where ρ and η are respectively the density and viscosity of the xylem sap (which are approximately equal to those for water, Diamond 1966) and u is the flow velocity. The maximum value of R_e occurs at the fastest flow rate, Q(MAX). Using a figure of 500 W m^{-2} for the maximum evaporation rate from the wheat crop with a density of 320 stems m^{-2}, Q(MAX) is $6 \times 10^{-10}\ m^3\ s^{-1}$. In the wheat stem there are about 200 xylem vessels with a minimum equivalent hydraulic radius of 5 μm. This gives the minimum cross sectional area of the conducting elements as $1.6 \times 10^{-8}\ m^2$. Dividing Q(MAX) by this area gives the maximum value of u as $3.8 \times 10^{-2}\ m\ s^{-1}$ and using equation (A.1) the corresponding value of R_e as 0.38.

Although the xylem vessels do not have smooth walls and are not usually cylindrical this value of R_e is very much lower than that at which the flow in tubes becomes turbulent. Sap flow in the stem xylem vessels is, therefore, likely to be laminar.

Appendix A.2 FLOW IN VESSELS OF ELLIPTICAL CROSS-SECTION

The volume flow rate (Q) in vessels of elliptical cross-section was derived as follows. Using the principles of conservation of mass and momentum the general equation for laminar flow (in the x-direction) can be derived in the form

$$\frac{dp}{dx} = \eta\left(\frac{\partial^2 u}{\partial y^2} + \frac{\partial^2 u}{\partial z^2}\right), \tag{A.2}$$

where p is the pressure and η the viscosity of the fluid, u is its velocity and x,y and z are the cartesian co-ordinates (see, for example, Batchelor 1967). When applied to flow in a tube of elliptical cross-section of length ℓ, the velocity, u(y,z), is given by

$$u(y,z) = \Delta\psi(1 - y^2/b^2 - z^2/c^2)/2\eta\ell(b^{-2} + c^{-2}), \tag{A.3}$$

where the pressure gradient (dp/dx) is given by $\Delta\psi/\ell$ and b and c are the semi-major and semi-minor axes of the ellipse. Equation (A.3) can also be written in the form

$$u(y,z) = K(1 - y^2/b^2 - z^2/c^2), \tag{A.4}$$

where

$$K = \Delta\psi/2\eta\ell\,(b^{-2} + c^{-2}) \tag{A.5}$$

For any element of area, dA, in the elliptical cross-section at a point (y,z) the volume flowing through the element is udA and the total flow through the entire cross-section is given by

$$Q = \int u\,dA = \iint K(1 - y^2/b^2 - z^2/c^2)\,dy\,dz \tag{A.6}$$

Inserting the integral limits we obtain

$$Q = K \int_{-c}^{c} dz \int_{-d}^{d} (1 - y^2/b^2 - z^2/c^2)\,dy, \tag{A.7}$$

where $d = b(1 - z^2/c^2)^{\frac{1}{2}}$. Integrating equation (A.7) with respect to y gives

$$Q = K \int_{-c}^{c} \{(1 - z^2/c^2)y - y^3/3b^2\}_{-d}^{d}\ dz,$$

and substituting for d yields

$$Q = \frac{4bK}{3c^3} \int_{-c}^{c} (c^2 - z^2)^{3/2}\ dz. \tag{A.8}$$

and substituting for d yields

$$Q = \frac{4bK}{3c^3} \{\tfrac{3}{8}\, c^4 \operatorname{Sin}^{-1} z/c\}_{-c}^{c}\ , \tag{A.9}$$

and therefore

$$Q = \frac{\pi K\, bc}{2} \tag{A.10}$$

Substituting K from equation (A.5) into equation (A.10) gives

$$Q = \frac{\pi\ \Delta\psi}{4\ \eta\ell}\ \frac{bc}{(b^{-2} + c^{-2})} \tag{A.11}$$

Equation (A.11) expresses flow in vessels of elliptical cross-section in terms of the potential gradient and vessel size.

Appendix A.3 THE SOLUTION OF EQUATION (6.8)

In section 6.2.2 equation (6.8) was derived in the form

$$Q(t_1) + mt = \frac{\Delta\psi(t)}{R} + C\frac{d(\Delta\psi)}{dt}$$

Dividing by C gives

$$\frac{1}{C}\{Q(t_1) + mt\} = \frac{\Delta\psi(t)}{RC} + \frac{d(\Delta\psi)}{dt} \qquad (A.12)$$

Equation (A.12) is a linear first order differential equation in $\Delta\psi$ which can be solved as follows. Using the integrating factor I, which is

$$I = e^{\int \frac{1}{RC} dt} = e^{t/RC}, \qquad (A.13)$$

multiplication of equation (A.12) by I gives

$$\frac{e^{t/RC}}{C}\{Q(t_1) + mt\} = \frac{e^{t/RC}}{RC}\Delta\psi(t) + e^{t/RC}\frac{d(\Delta\psi)}{dt} \qquad (A.14)$$

This can also be written as

$$\frac{d}{dt}(e^{t/RC}\Delta\psi) = \frac{e^{t/RC}}{C}\{Q(t_1) + mt\} \qquad (A.15)$$

Integrating equation (A.15) with respect to t gives

$$e^{t/RC}\Delta\psi = \frac{1}{C}\{Q(t_1)\int e^{t/RC} dt + m\int te^{t/RC} dt\}$$

or,

$$e^{t/RC}\Delta\psi = \frac{1}{C}\{Q(t_1)RC\,e^{t/RC} + m\,[e^{t/RC}(RCt - R^2C^2)] + k\}, \qquad (A.16)$$

where k is the constant of integration. Equation (A.16) can also be rearranged in the form

$$\Delta\psi(t) = R.Q(t_1) + mRt - mR^2C + \frac{k}{C}\,e^{-t/RC} \qquad (A.17)$$

Equation (A.17) is the required solution of the differential equation (6.8).

Appendix A.4 Paper presented in support of application

Phil. Trans. R. Soc. Lond. B. 273, 565–580 (1976) [565]
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COMMUNITY WATER RELATIONS

Daily and seasonal changes of water potential in cereals

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The paper reports measurements of the water relations of a barley crop (cv. Proctor) and a winter wheat crop (cv. Maris Huntsman), grown on the same site at Sutton Bonington. Throughout the two growing seasons, days were chosen when hourly measurements could be made of leaf water potential, by means of a pressure chamber, and of stomatal resistance, by means of a diffusion porometer. Environmental factors, e.g. radiation, temperature, humidity, were recorded concurrently. Relationships between leaf water potential, stomatal resistance and environmental factors are explored and compared for the two cereals. In particular, as frequent measurements were made over two months, the influence of leaf age on responses to environmental factors can be examined. On selected days with bright sunshine and dry soil the response of both cereals to water stress is analysed with particular reference to the control of evaporation by stomatal closure.

Introduction

The pathway for water movement from the soil through a plant and into the atmosphere has many complex components – soil pores, root cells, xylem vessels, mesophyll cells and intercellular spaces. Electrical analogues have been used to compare the resistances or conductances of these components (e.g. by Cowan 1965), but little is known about how these resistances are related to anatomical features, to age, or to the plant environment. Most published work on the relation between environment and resistances to water flow is based on growth room or laboratory experiments and relatively few systematic studies have been made in the field over the whole life cycle of the plant or crop.

This paper describes how measurements on two cereals grown on the same field site were analysed in terms of conductances to flow. First, the hydraulic conductance of water from the soil to the leaves was examined in relation to hour-by-hour changes in leaf water potential and in the rate of crop evaporation. Second, a relationship between the stomatal conductance of the adaxial and abaxial epidermis and irradiance was determined when the soil water potential was high. Changes in this relationship in dry soil were examined in relation to concurrent measurements of leaf water potential and of osmotic potential. Third, the validity of the concept of crop conductance (Monteith 1965) was examined in relation to measured changes in leaf stomatal conductance on days of different soil water potentials.

MATERIALS AND METHODS

Crops

All the measurements were made on two cereals grown on the same site at Sutton Bonington, England in two different years. A 4 hectare (ha) plot of barley (*Hordeum distichon* L) cv. Proctor was sown in 1972, while in 1974 the crop was a 10 ha plot of winter wheat (*Triticum aestivum* L) cv. Maris Huntsman which had been sown in the autumn of 1973. The seed bed preparations, sowing, herbicide spraying and harvesting of both crops were undertaken as part of the normal agricultural practice of the University farm. Expressed in terms of dry mass of grain, the yields were 5.0 and 7.5 tonnes/ha for the barley and wheat respectively. The green leaf area and total dry mass of the barley crop were measured at weekly intervals from emergence to maturity, while for wheat these measurements were made every three weeks until April and then every second week until maturity. A detailed description of the site and the average weather conditions were given by Biscoe *et al.* (1975).

Stomatal conductance

The stomatal conductance of barley leaves was measured using a diffusion porometer based on the design described by Stiles (1970) and calibrated using the variable path-length method described by Monteith & Bull (1970). Similar measurements were made later on the wheat leaves using an automatic diffusion porometer which allowed rapid replicate readings. This porometer was calibrated more accurately using perforated metal plates as described by Stigter & Lammers (1974). To enable both of these instruments to be used with cereal leaves, a mask with a rectangular aperture 15 mm × 5 mm was fitted into the porometer cups. The stomatal conductances of three random samples of each of the three or four youngest leaves in the crop were measured at hourly intervals. By using separate leaves, the stomatal conductance of the adaxial and abaxial epidermis of each leaf was measured. As the calibration of the diffusion porometer is temperature-dependent, each reading was immediately followed by a temperature reading by using a thermistor bead incorporated into the porometer cup. Temperature equilibration between the leaf and the porometer cup usually occurred during the first two to three readings but a further three readings were taken to ensure a consistent value from which the stomatal conductance could be calculated.

Leaf water and osmotic potentials

A pressure chamber based on designs described by Turner, DeRoo & Wright (1971) and by Odongo (1973) was used for the measurement of leaf water potential. At hourly intervals, three leaves from each of the three or four youngest leaves in the crop were selected at random and used for the determination of leaf water potential. The complete tiller bearing the selected leaf was cut immediately above the soil surface and taken to the pressure chamber where the leaf was inserted into the rubber bung, then cut from the plant and immediately used in the pressure chamber for the determination of leaf water potential. When the leaf water potential of a wheat leaf had been determined, a section was cut from the middle of the leaf and immediately sealed in a small glass vial. These vials were immersed in liquid nitrogen to freeze the tissue rapidly and destroy the cell structure. After storage at −15 °C, the osmotic potential of these samples was determined using a dew point hygrometer described by Campbell, Campbell & Barlow (1973). These measurements were made in a controlled temperature room and the instrument was calibrated using standard sodium chloride solutions absorbed by blotting paper disks.

Micrometeorology

In 1972 temperature, humidity, carbon dioxide concentration, radiation and windspeed were measured above and within the barley crop. The micro-meteorological instrumentation and theory and some of the results have already been described in detail (Biscoe *et al.* 1975). Hourly averages of the relevant quantities were used to calculate the hourly rates of evaporation from the barley crop on days when stomatal conductance and leaf water potential were also

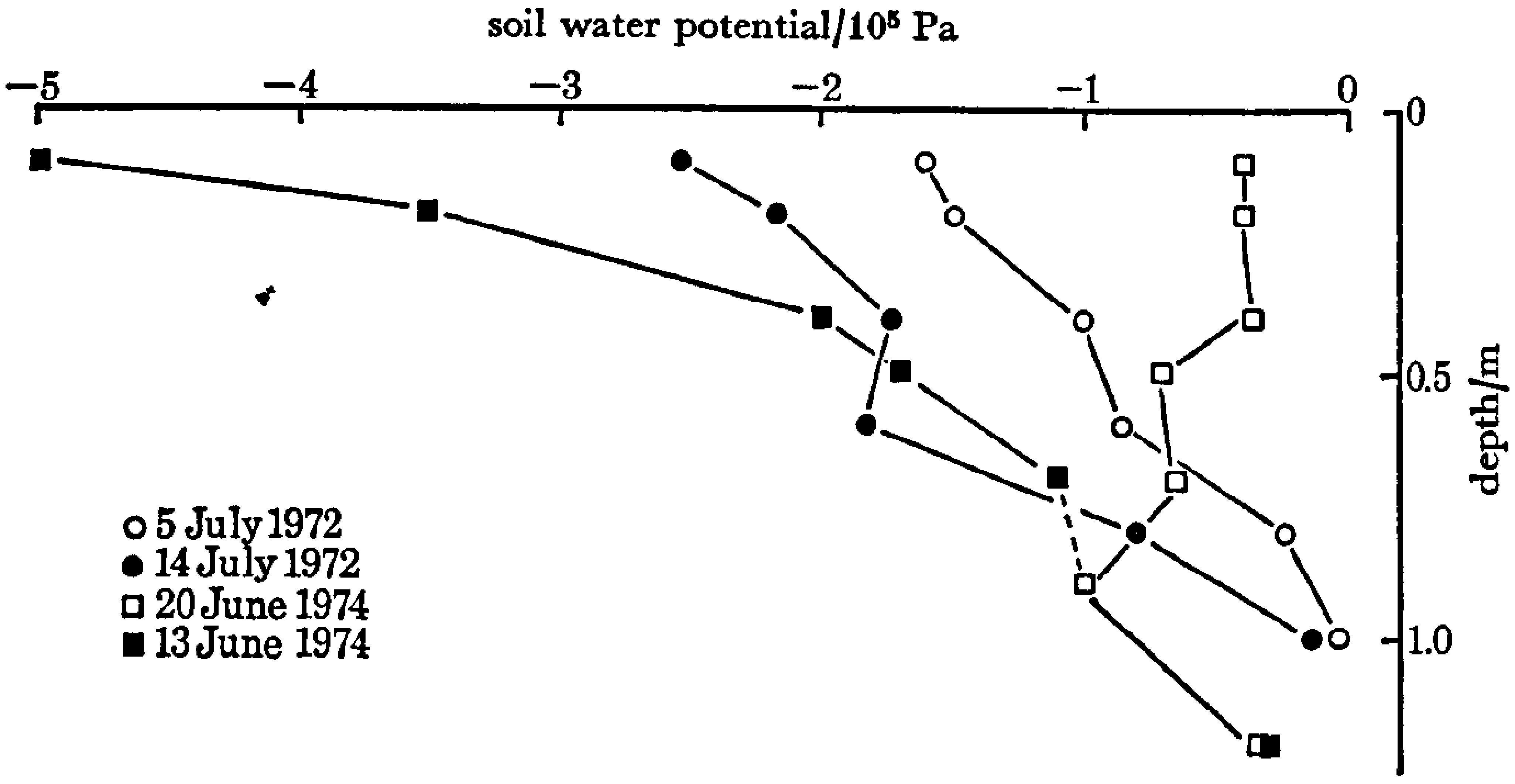

FIGURE 1. Profiles of soil water potential on days when stomatal conductance was measured on barley (○, ●) and wheat (□, ■).

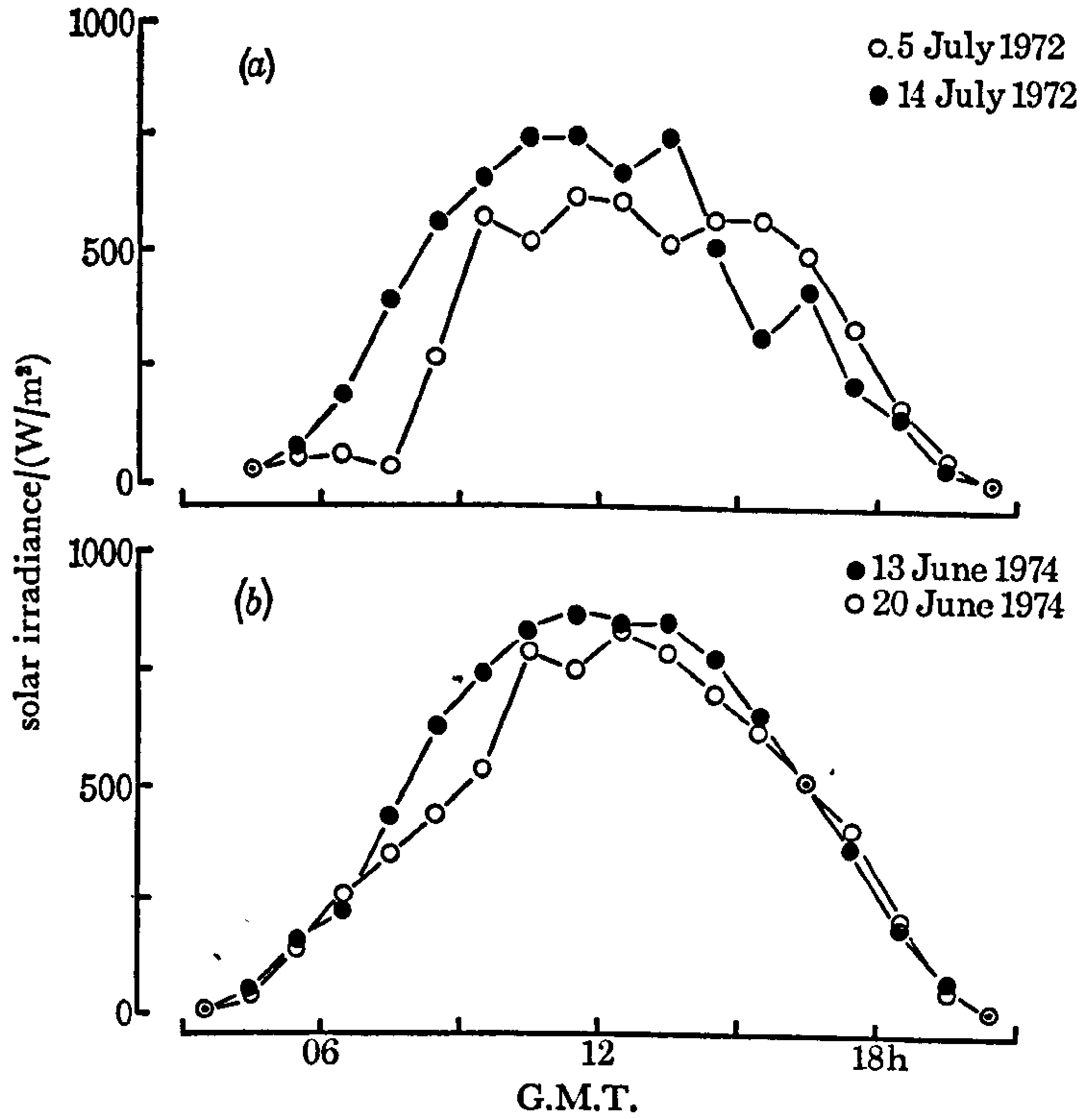

FIGURE 2. Diurnal changes of solar irradiance measured above the crop of (*a*) barley and (*b*) wheat on days when stomatal conductance was measured.

being measured. A continuous record of total solar radiation above the crop was available from a Kipp solarimeter connected to a chart recorder.

Soil water potential

In both crops the soil water content was measured every five to six days to a depth of 1.8 m by using a neutron probe. The water release curves which had been determined on soil samples from the site were then used to calculate the relation between soil water content and soil water potential. For the purposes of this paper two days from each season were selected when the differences in soil water potential were greatest for that season but the diurnal variation in irradiance was similar. The days selected for the barley were 5 and 14 July and for the wheat 13 and 20 of June. Differences in soil water potential and the diurnal variation in irradiance for these days are shown in figures 1 and 2.

HYDRAULIC CONDUCTANCE

In an actively transpiring plant, water is taken up at the root surface and flows in the liquid phase to the sites of evaporation in the leaves. Van den Honert (1948) described this process by an equation with the form

$$q = K\delta\Psi, \tag{1}$$

whrre q is the flow of water through the plant ($m^3\,s^{-1}$), ($\delta\Psi$) is the difference in water potential between the root surface and the leaf (MPa) and K is the total hydraulic conductance of the plant ($m^3\,s^{-1}\,MPa^{-1}$) assumed constant. Equation (1) assumes the existence of a steady state in which the driving force for water movement in the plant is the water potential gradient. This relation has been widely used to describe water movement in plants, e.g. by Tinklin & Weatherley (1966) Janes (1970) Begg & Turner (1970) Barrs (1973) and Hellkvist, Richards & Jarvis (1974). Measurements made on the barley enabled the hourly mean water potential of a fully expanded leaf and the corresponding evaporation rate from the whole canopy E to be calculated. The leaf below the flag leaf, leaf 8, was chosen because it was the largest organ actively transpiring in the crop when the measurements were made and its water potential was assumed to be a good approximation to the mean water potential for the whole canopy. The water potential difference ($\delta\Psi$) defined in equation (1) was then specified as the difference between the average water potential in the soil and leaf 8, ($\Psi_s - \Psi_l$). The hourly values of q ($m^3\,s^{-1}$) were calculated by dividing the crop evaporation rate, E, by the plant density, which was 900 stems m^{-2} for barley. These values of q were then plotted against the corresponding values of $\Psi_s - \Psi_l$ (figure 3). Figure 3 shows that q is not linearly related to ($\Psi_s - \Psi_l$) and so equation (1) cannot be directly applied to the plant as a whole. This restriction can be seen more clearly in figure 4, where the value of K calculated from equation (1) is not constant but increases with increasing water flow through the plant.

The limited amount of data at low flow rates, i.e. q less than $0.25 \times 10^{-10}\,m^3\,s^{-1}$, suggests that the relation between ($\Psi_s - \Psi_l$) and q is nonlinear and that the rate of increase of ($\Psi_s - \Psi_l$) decreases as q increases reaching a minimum value when q is approximately $0.25 \times 10^{-10}\,m^3\,s^{-1}$. Measurements made on the wheat crop showed that during the night the water potential of the leaves tended to equilibrate with the soil water potential. The line representing the variation in ($\Psi_s - \Psi_l$) with q, at low flow rates, has been drawn by eye and tends towards the origin (figure 3).

Restricting further analysis to the data obtained at values of q greater than 0.25×10^{-10} m^3 s^{-1}, the records for both days define a linear relation which can be described by an equation of the form

$$q = K_1 [(\Psi_s - \Psi_l) - \Psi_0] \tag{2}$$

where Ψ_0 is the intercept on the water potential axis obtained by extrapolating the linear portion of the curve to zero flow rate (figure 3). One interpretation of this relation is that a region exists within the plant-root system where the water potential has a constant value $\Psi_p = \Psi_s - \Psi_0$. The total water potential difference across the plant $(\Psi_s - \Psi_l)$ can therefore be represented by the sum of two component potential differences $(\Psi_s - \Psi_p)$ which is constant and $(\Psi_p - \Psi_l)$ whose variation with q is shown in figure 3. Associated with the two potential differences, $(\Psi_s - \Psi_p)$ and $(\Psi_p - \Psi_l)$, are the conductances K_2 and K_1 respectively. Since $(\Psi_s - \Psi_p)$ is constant (figure 3) then from equation (1) K_2 must increase linearly with q (figure 4). On the other hand, the potential difference $(\Psi_p - \Psi_l)$ varies linearly with q (figure 3) therefore K_1 is constant (equation (1)) and has a value of 8.7×10^{-11} m^3 s^{-1} MPa^{-1} (figure 4).

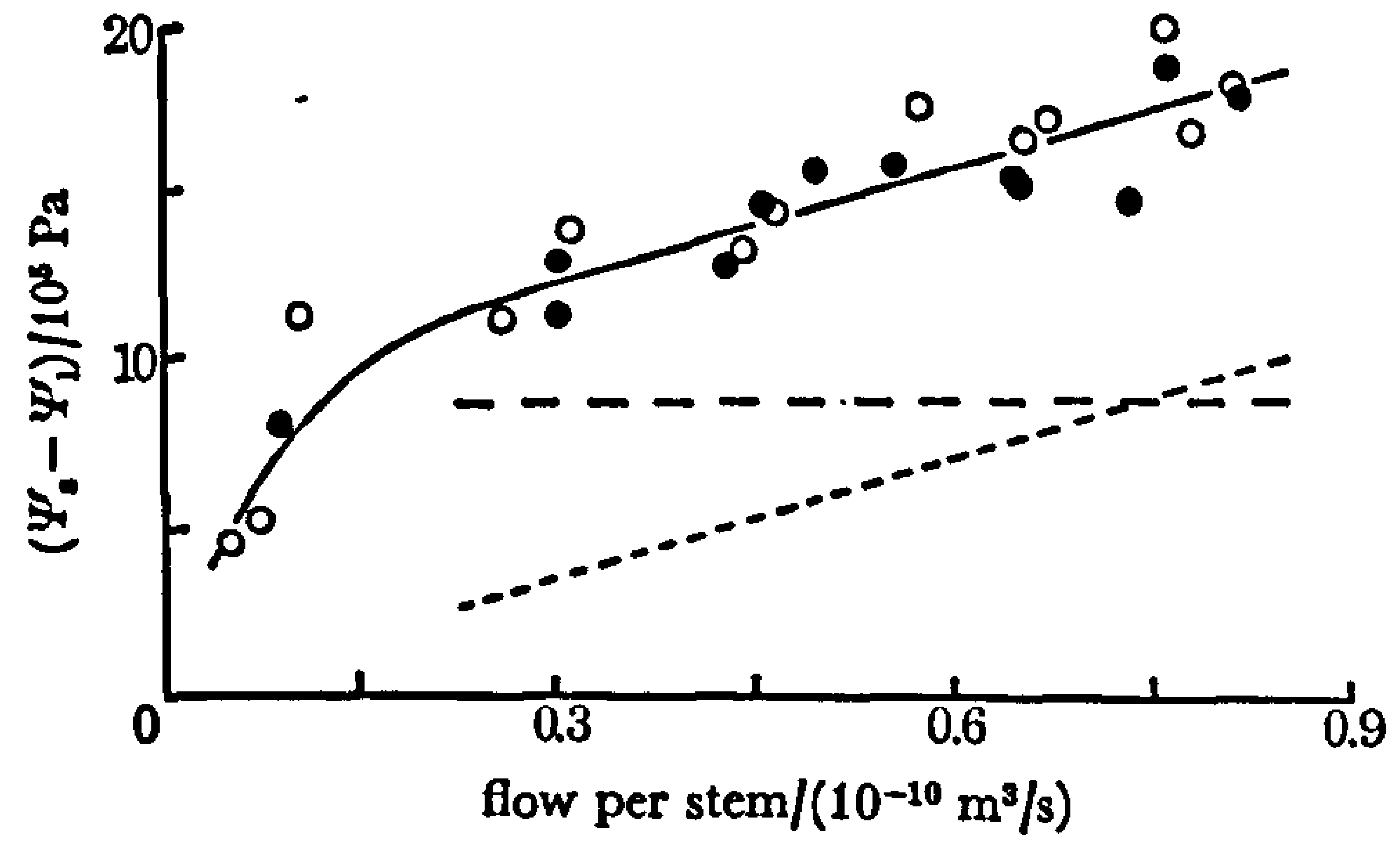

FIGURE 3. The relation between the water flow per stem of barley and $\Psi_s - \Psi_l$, measured on 5 July (○) and 14 July (●), $\Psi_s - \Psi_p$ (– –) and $\Psi_p - \Psi_l$ (—).

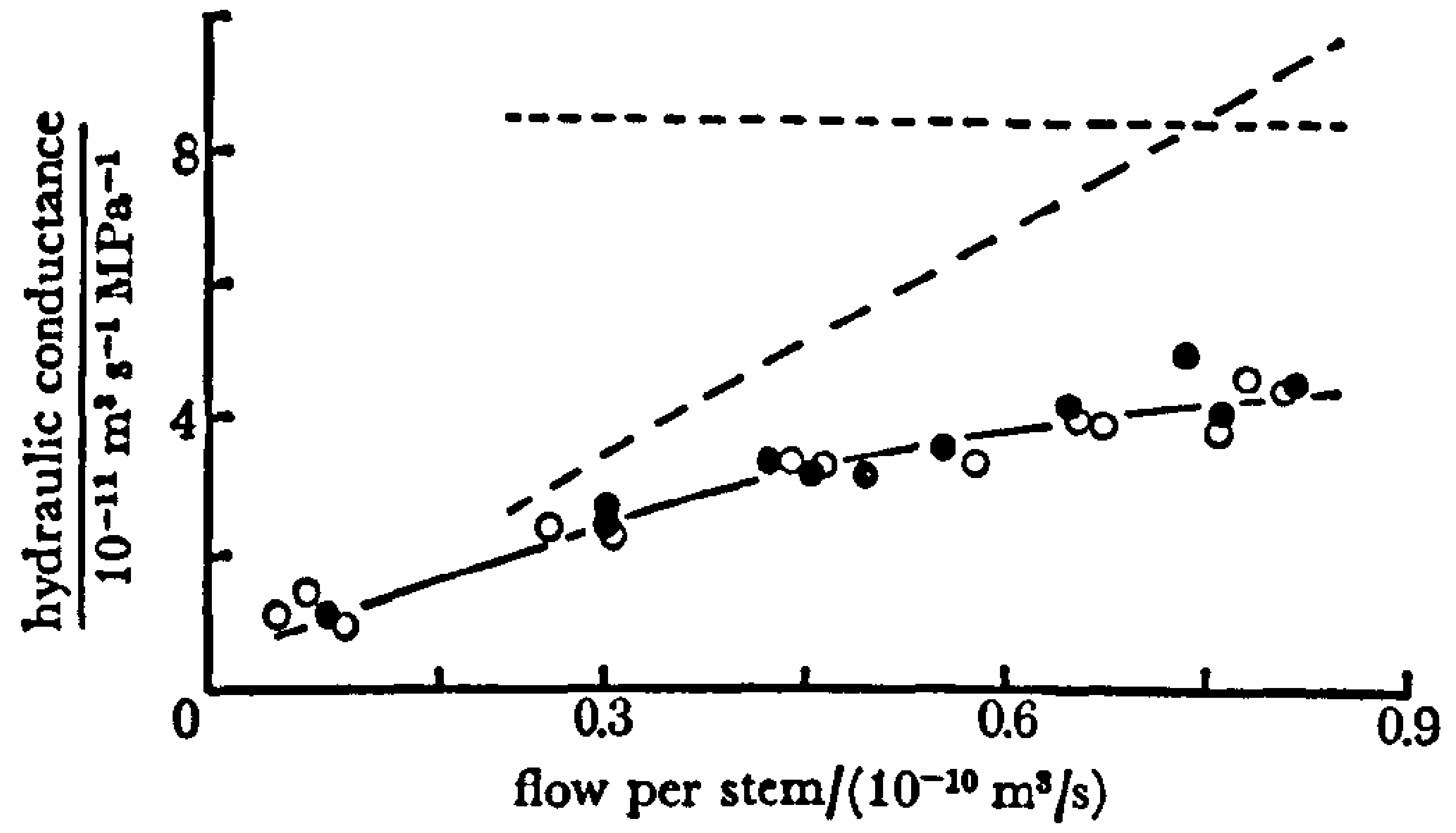

FIGURE 4. The relation between the water flow per stem of barley and the total hydraulic conductance (K) on 5 July (○) and 14 July (●) and the component conductance K_1 (—) and K_2 (– –).

The total hydraulic conductance K is then given by

$$K = K_1 K_2/(K_1 + K_2). \tag{3}$$

The full line in figure 4 shows the variation in K derived from equation (3) and as expected the values of K calculated by using equation (1) are a good fit to this line.

Responses similar to that shown in figure 3 have been frequently observed with other species grown in controlled environments, for example, pepper (Janes 1970), sunflower and maize (Neumann 1973, quoted in Jarvis 1975). However, experiments in which $(\Psi_s - \Psi_l)$ is apparently independent of q at fast flow rates, have also been reported for these species by Camacho-B, Hall & Kaufmann (1974), Stoker & Weatherley (1971) and Barrs (1973) respectively. The latter type of response has been attributed to an increase in root conductance (Stoker & Weatherley 1971) which is generally accepted as being the smallest component of the total hydraulic conductance (Kramer 1938; Jensen, Taylor & Wiebe 1961; Boyer 1971). If this interpretation is valid for barley, then the two components K_2 and K_1 of the total hydraulic conductance may be associated with the roots and the remainder of the plant respectively.

The type of response obtained will be dependent on relative values of the conductances K_1 and K_2. The gradient of the linear portion of the curve in figure 3, is determined by the value of K_1, while the intercept Ψ_0 is determined by the ratio q/K_2. Contrasting responses obtained for pepper, sunflower and maize could be explained by different relative values of K_1 and K_2. For example, if K_2 were very much smaller than K_1, the potential difference across the roots would be much greater than that across the remainder of the plant, so that within the limits of the errors of measurement the water potential difference $(\Psi_s - \Psi_l)$ would appear to be independent of q at fast flow rates. The values of K_1 and K_2 can be affected by the conditions in which the plants are grown, Barrs (1973) showed that the response of the water potential of tomato leaves to increasing flow was different when the same species was grown under normal greenhouse conditions and under continuous high humidity. Cox (1966) also found that the response of the leaf water potential of sunflower to increasing flow was different for plants rooted in water culture and in drying soil.

Flux/gradient relations for barley grown in the field are therefore very difficult to compare directly with measurements reported for other species. Restricting the comparison to other measurements obtained in the field, a large range of values of K was found. Expressed in the same units ($m^3\,s^{-1}\,MPa^{-1}$) these values range from 5.3×10^{-11} for wheat (Denmead 1975), 3.9×10^{-8} for tobacco (Begg & Turner 1970), 3.2×10^{-8} for sunflower (Berger 1973), 3.4×10^{-8} for maize (Shinn & Lemon 1968), to a maximum of 1×10^{-7} for spruce (Hellkvist *et al.* 1974). However, different quantities were used in the calculation of these values, for example Shinn & Lemon (1968) used the total daily evaporation to estimate the mean value of K for the whole day. They were unable to examine the variation of K with q. Although there are large differences in K between species the values of evaporation rate and of water potential difference $(\Psi_s - \Psi_l)$ used in the calculations were of comparable magnitude. For example, when $(\Psi_s - \Psi_l)$ in a stand of spruce was 1.5 MPa (15 bar) the evaporation rate was estimated at $290\,g\,m^{-2}\,h^{-1}$ (Hellkvist *et al.* 1974). The corresponding values for barley were 15 bar (1.5 MPa) and $170\,g\,m^{-2}\,h^{-1}$ respectively. By using plant densities of 0.4 stem m^{-2} for spruce (Hellkvist *et al.* 1974) and 900 stems m^{-2} for barley gave values of q of $2 \times 10^{-7}\,m^3\,s^{-1}$ per stem and $0.5 \times 10^{-10}\,m^3\,s^{-1}$ per stem respectively. This comparison shows that the main difference in the values of K for spruce and barley calculated from equation (1) is a result of the different plant densities. A more appropriate comparison between species may be provided by the hydraulic conductivity σ, defined as

$$\sigma = ql/(\Psi_s - \Psi_l)A, \tag{4}$$

where l and A are the length (m) and the cross-sectional area (m^2) of the conducting elements respectively. The total water conducting area per stem for spruce was found to be $1 \times 10^{-2}\,m^2$

(Hellkvist *et al.* 1974) compared to a value of 3×10^{-7} m^2 per stem for barley. Plant height was taken as 10 m for spruce and 1 m for barley. Substituting these values into equation (4) gave similar values of σ: 1.3×10^{-4} m^2 s^{-1} MPa^{-1} for spruce and 1.1×10^{-4} m^2 s^{-1} MPa^{-1} for barley. However, if the flow of water through a plant obeys the Poiseuille law for laminar flow, then in a bundle of N capillaries of radius r the flow rate q will be proportional to Nr^4. The conductivity defined in equation (4) should therefore vary with r^2. The values of σ for different species calculated from equation (4) will therefore be comparable only if the size of the conducting vessels is similar. Furthermore, since the conducting vessels will not be uniform in size and may also be partially or totally blocked the conductivity of a given species will also depend on the detailed anatomical structure of the pathway for water movement.

STOMATAL CONDUCTANCE

Irradiance

The two major factors influencing stomatal behaviour in the field are light and water stress (Slatyer 1967). The relations between stomatal conductance and irradiance, for both the adaxial and abaxial epidermis, are shown in figures 5 and 6 for barley and wheat respectively. To minimize effects of water stress, all these measurements were made when the soil had recently been wetted by rain. Figure 1 shows the profile of soil water potential on 20 June 1974, the day when the measurements were made on wheat, and the measurements were made on barley on 14 June 1972 when the soil water potential was similar.

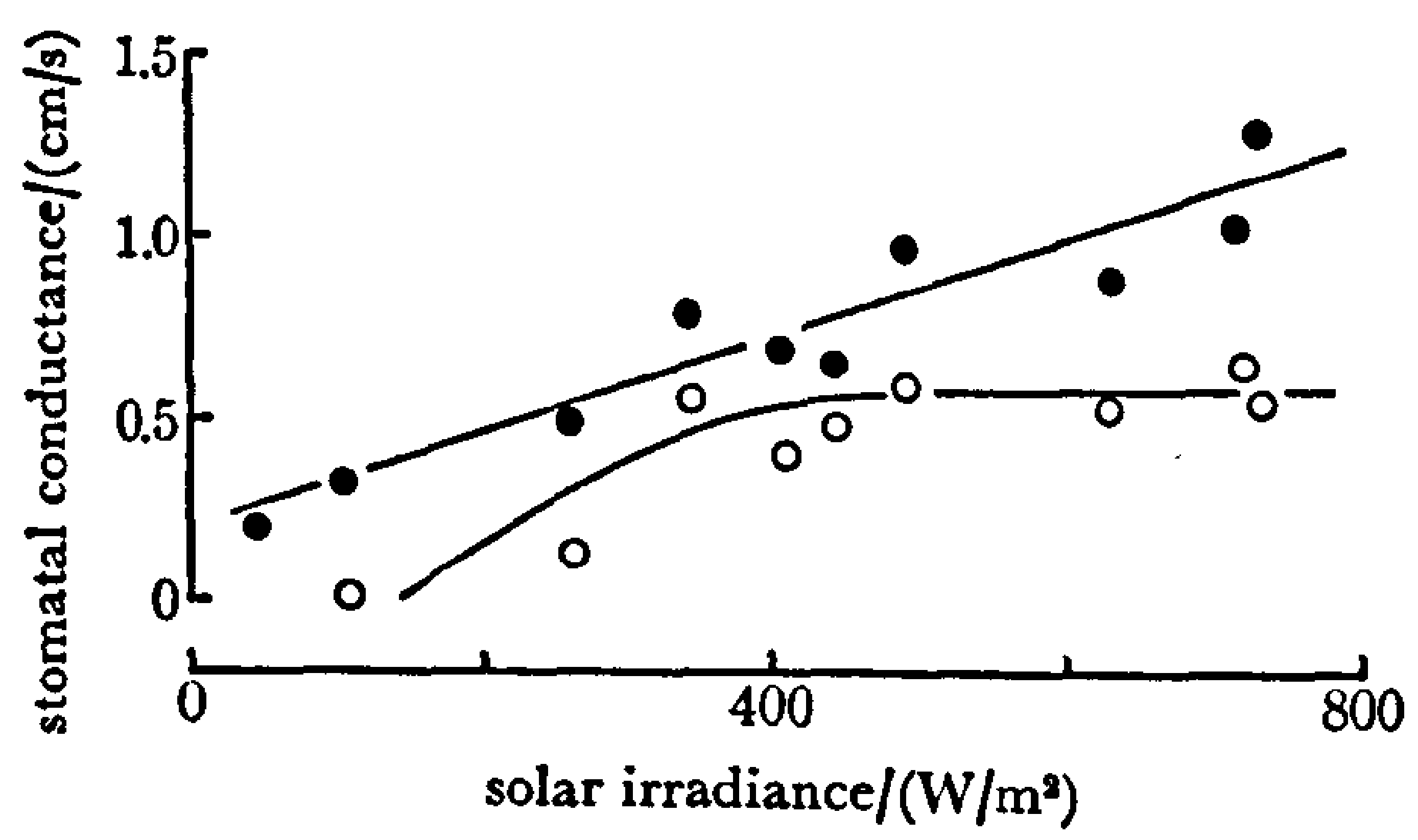

FIGURE 5. The relation between stomatal conductance of the adaxial (●) and abaxial (○) epidermis of leaf 8 and solar irradiance measured above the crop. Each point represents an hourly mean of measurements made on barley, 14 June 1972.

In both crops, the stomata on the adaxial surface were more responsive to light than those on the abaxial surface. First, the difference in irradiance at which stomata on the two epidermides opened was approximately 150 W m^{-2} for both species. As the radiation was measured on a horizontal surface above the crop the irradiance of abaxial stomata by photosynthetically active radiation would often be an order of magnitude less than for the adaxial stomata because of absorption of light by the mesophyll. These results differ from some previous investigations, e.g. the stomata on the abaxial epidermis of snap bean, tobacco and sorghum opened in weaker light than the adaxial stomata (Kanemasu & Tanner 1969; Turner 1970).

Secondly, for both species, maximum stomatal conductances were measured on the adaxial epidermis (figure 5 and 6). Comparisons of the magnitude of these stomatal conductances must involve both the degree of opening of the stomata and stomatal densities. As both wheat and barley have approximately equal numbers of stomata on each epidermis (Meidner & Mansfield 1968; Teare, Peterson & Law 1971) measurements indicate that the stomata on the adaxial surface open wider.

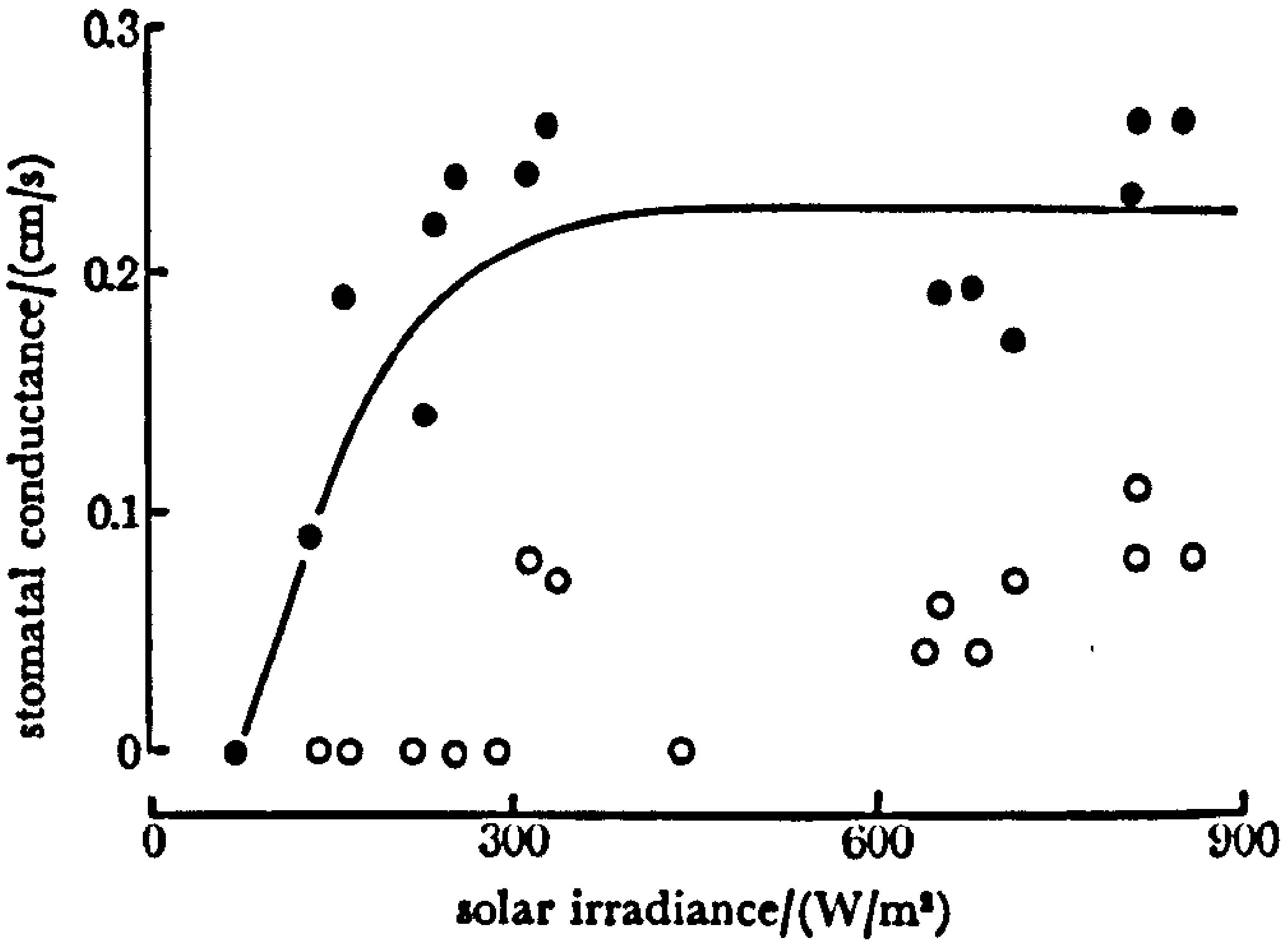

FIGURE 6. The relation between stomatal conductance of the adaxial (●) and abaxial (○) epidermis of leaf 10 and solar irradiance measured above the crop. Each point represents an hourly mean of measurements made on wheat, 20 June 1974.

While the stomata on the adaxial epidermis in both barley and wheat are more responsive to changes of illumination, the shape of this relation was very different. In barley there was a linear relation between stomatal conductance and irradiance over the range of irradiances measured, whereas for wheat there was no increase in stomatal conductance above an irradiance of about 300 W m^{-2}. A recent review of stomatal behaviour suggested that a non-linear response, similar to that obtained for wheat, is the usual relation between stomatal conductance and irradiance (Turner 1974). The degree of nonlinearity was found to vary with species: maize and sorghum had response curves similar to those for wheat (figure 6) while tobacco and sunflower did not reach a constant maximum stomatal conductance at irradiances above 800 W m^{-2} (Turner 1974). However, recent measurements on a wheat crop in Australia clearly show a linear relation between stomatal conductance and irradiance very similar to that for barley (figure 5) (Denmead 1975). The results for barley and wheat (figures 5 and 6) therefore appear to represent just two of the many different relations between stomatal conductance and irradiance obtained in the field (Berger 1973; Biscoe, Littleton & Scott 1973; Turner & Begg 1973; Denmead 1975). The difference between these relations probably depends on species, growth conditions and leaf age.

Leaf water potential

The relation between water stress and stomatal conductance will now be examined by using the measurements made on wheat. As the irradiance on the two days was similar (figure 2*b*) but there were large differences in soil water potential (figure 1) the variations of stomatal conductance have been plotted against time for both days (figure 7 and 8). On 20 June, when the soil water potential was high, the diurnal variation of conductance was large with maximum values occurring at midday and zero values about dawn and dusk (figure 7). The diurnal variation on 13 June was different (figure 8). Stomatal conductance increased rapidly to a maximum value early in the morning and then decreased to a minimum about midday. In the afternoon there was a slight increase in the conductance of the adaxial epidermis, but the conductance of the abaxial epidermis was zero throughout the afternoon. The difference in soil water potential appears to have influenced the diurnal variation in conductance substantially, but even at low soil water potentials the adaxial epidermis has the larger stomatal conductance. The diurnal variation in stomatal conductance shown in figure 8 is characteristic of plants growing in dry soil (Berger 1973; Sharpe 1973; Turner 1974), but measurements on cotton are the only ones which show a partial increase in conductance during the afternoon (Sharpe 1973). Afternoon opening probably depends on the value of the soil water potential, which was approximately −0.2 MPa (−2 bar) for cotton (Sharpe 1973). A minimum value of −0.5 MPa (−5 bar) was measured in this study, whereas Turner (1974) quoted values of −0.7 MPa (−7 bar) during his measurements of stomatal conductance on tobacco.

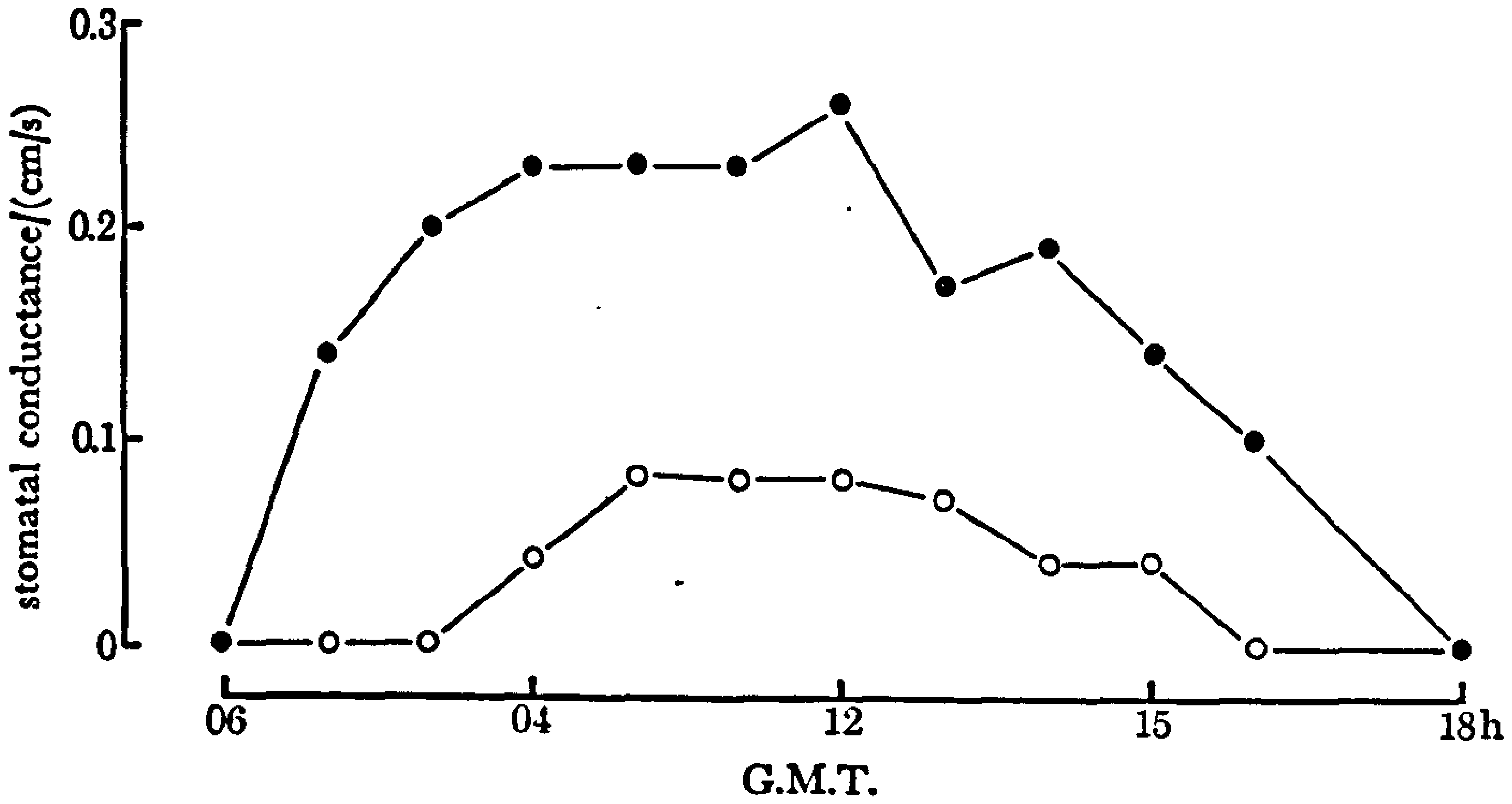

FIGURE 7. The diurnal variation of the stomatal conductance of the adaxial (●) and abaxial (○) epidermis of leaf 10 on wheat, 20 June 1974.

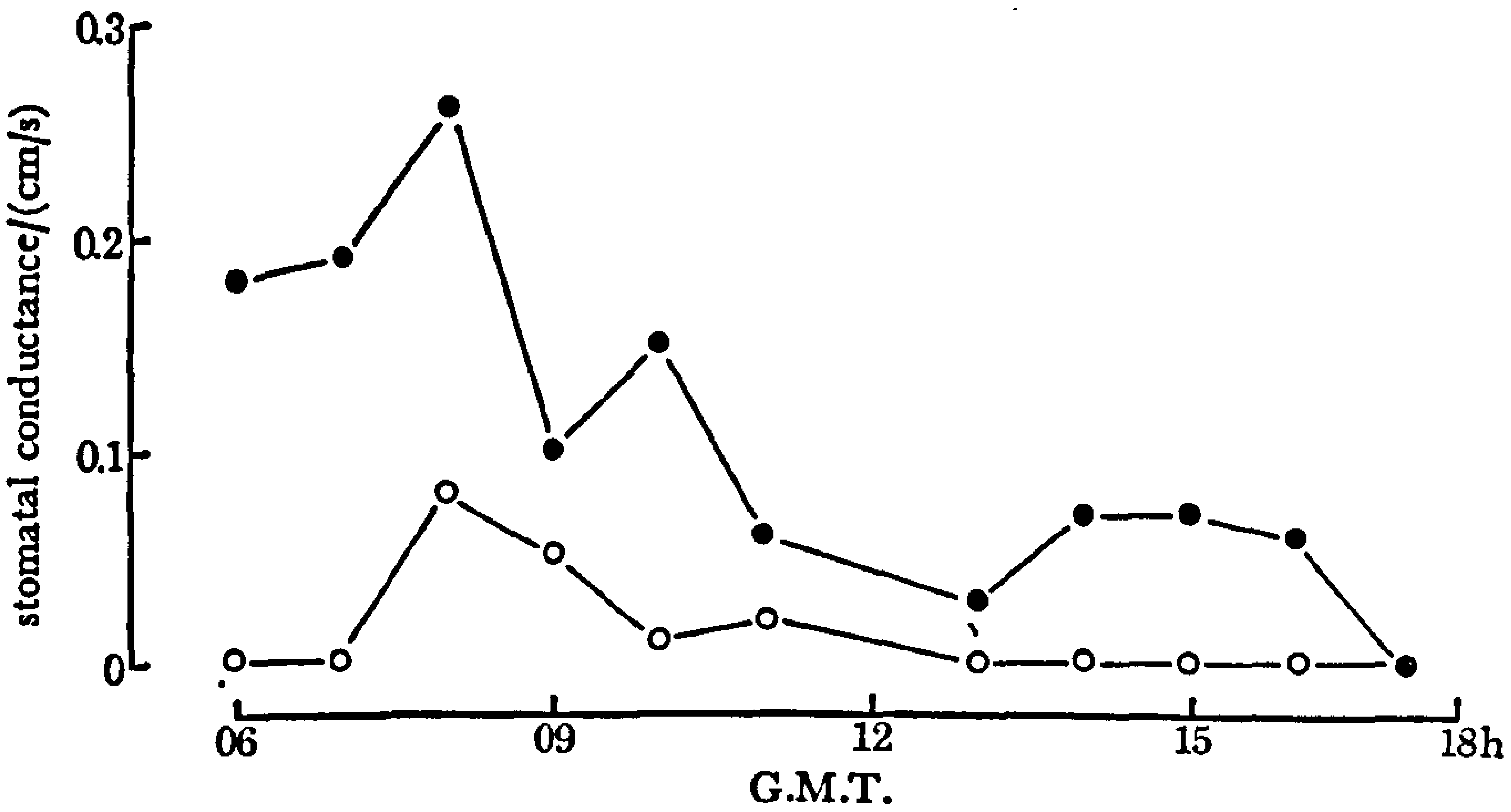

FIGURE 8. The diurnal variation of the stomatal conductance of the adaxial (●) and abaxial (○) epidermis of leaf 10 on wheat, 13 June 1974.

To examine possible reasons for the differences in stomatal conductance on the two days, the measurements of leaf water potential and osmotic potential for both days, are plotted against time in figures 9 and 10. The leaf turgor pressure is estimated as the difference between leaf water potential and osmotic potential. On 20 June, when soil water potential was high, leaf water potential decreased throughout the morning, reached a minimum value of −12 bar (−1.2 MPa) at 14h00 and then increased during the evening. The diurnal variation in leaf osmotic potential was similar but it changed by 0.6 MPa (6 bar) only throughout the day, so that a minimum leaf turgor pressure of 0.7 MPa (7 bar) occurred at midday. On 13 June, leaf water potential decreased very rapidly to −1.5 MPa (−15 bar) at 10h00 and remained approximately constant until late evening. Leaf osmotic potential changed very little during 13 June and hence leaf turgor pressure was about 0.3 MPa (3 bar) for most of the day, less than

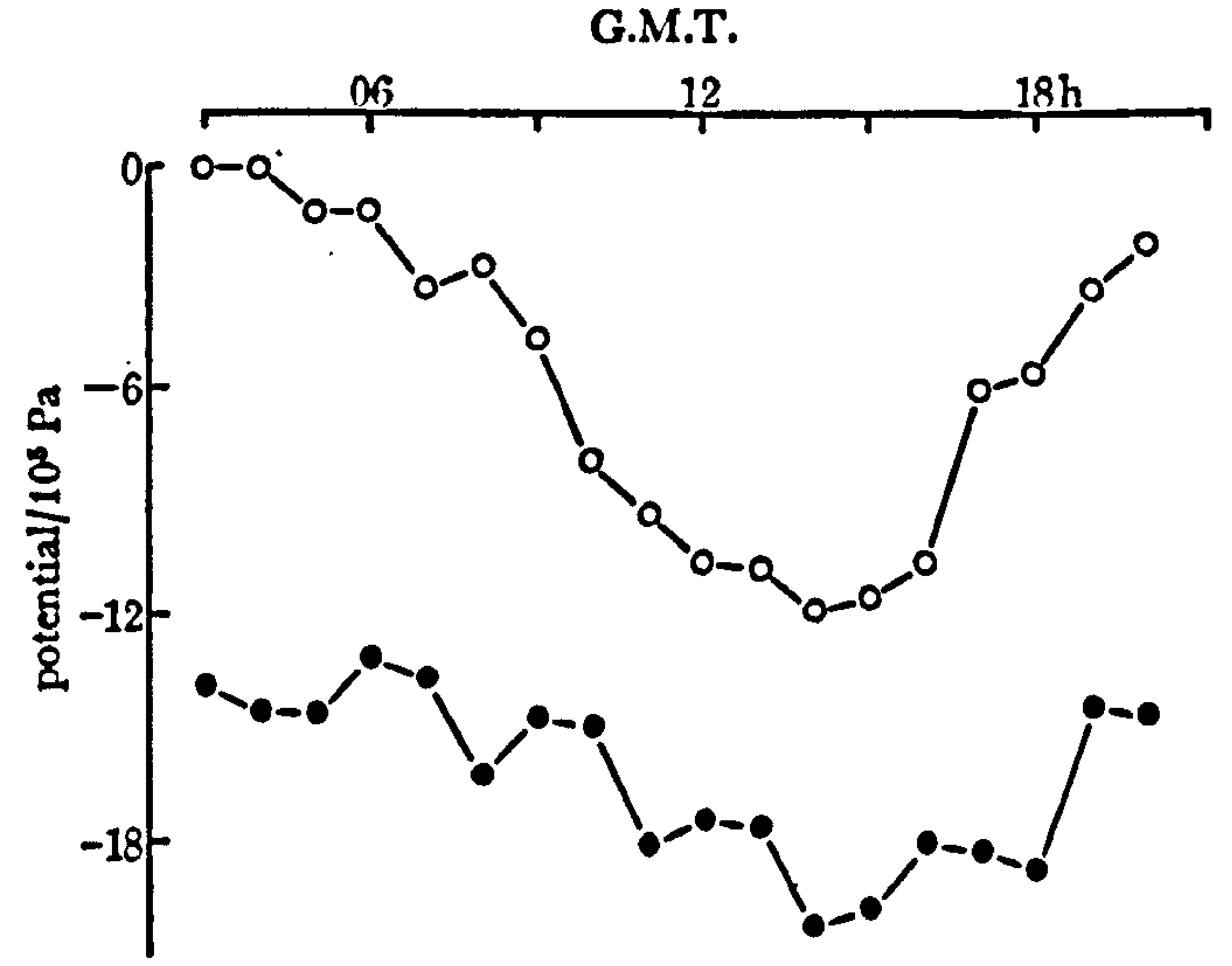

FIGURE 9. The diurnal variation of the water potential (○) and osmotic potential (●) of leaf 10 on wheat, 20 June 1974.

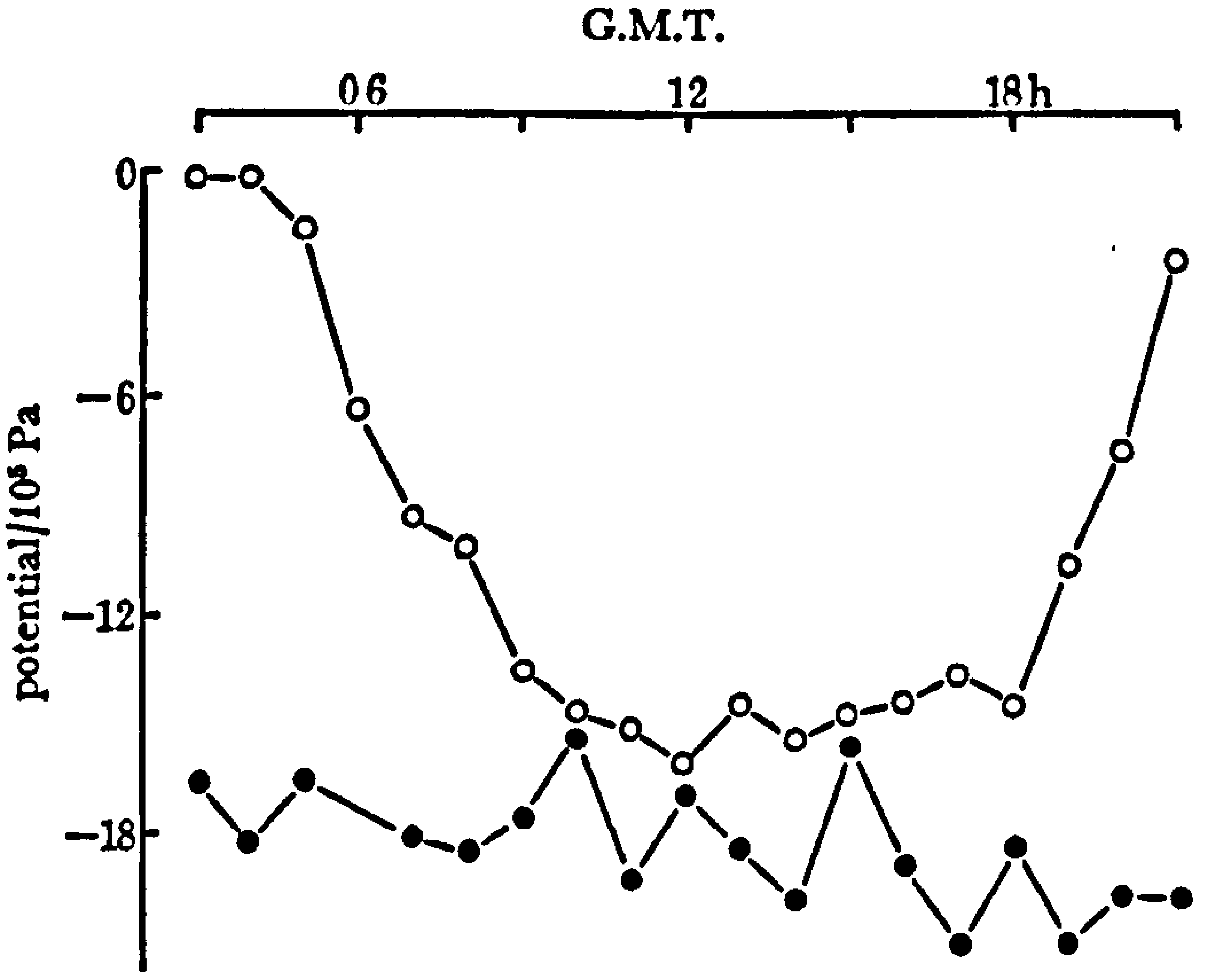

FIGURE 10. The diurnal variation of the water potential (○) and osmotic potential (●) of leaf 10 on wheat 13 June 1974.

half the minimum value measured on 20 June. Comparisons in this type of experiment are always difficult because of differences in variety, cultural conditions and environment, but the results from a recent experiment on wheat in Australia provide an interesting parallel. The Australian measurements were made on a field crop where large differences in soil water potential were created by irrigation and where consistent measurements of leaf water potential, leaf osmotic potential and stomatal conductance were made (Denmead & Millar 1975). With dry soil, the minimum value of leaf water potential measured on the leaf below the flag leaf was -1.3 MPa (-13 bar) compared to -1.5 MPa (-15 bar) measured in this experiment. The results also showed that when leaf turgor pressure decreased between 0.7 and about 0.2 MPa (7 and 2 bar) stomatal conductance decreased irrespective of the irradiance.

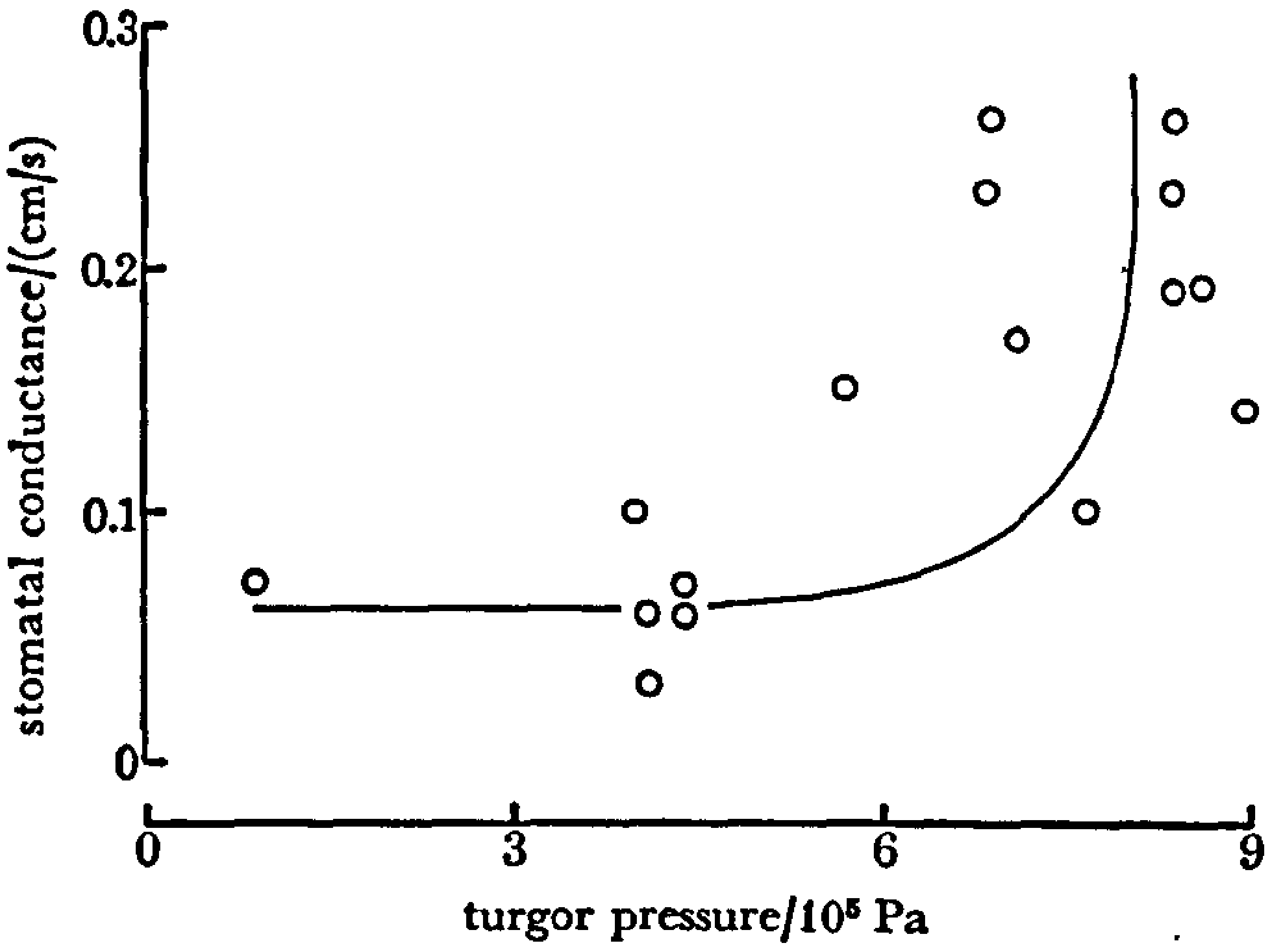

FIGURE 11. Measurements of adaxial stomatal conductance made on leaf 10 of wheat during 13 and 20 June 1974 plotted against the corresponding values of leaf turgor pressure, calculated as the difference between leaf water potential and osmotic potential.

Since the early experiments of Heath (1938) it has been recognized that the mechanism for stomatal movement is the difference in turgor pressure between the guard cells and surrounding subsidiary cells. Relations between stomatal conductance and leaf turgor pressure have been reported for several species growing in the field and controlled environment conditions (Biscoe 1972; Turner 1974; Denmead & Millar 1975 Millar, Drysen & Norum 1970). Figure 11 shows stomatal conductances plotted against corresponding leaf turgor pressures for this experiment, but measurements made under very weak light in the early morning and late evening have been omitted. At high leaf turgor pressures, the variations in stomatal conductance can be explained by changes in radiation. When leaf turgor pressure falls below about 0.5 MPa (5 bar) the stomatal conductance appears to be constant at a minimum value, irrespective of the observed changes in leaf turgor pressure. This response is similar to that described by Denmead & Millar (1975) but it differs from those previously presented by Biscoe (1972), Turner (1974) and Millar *et al.* (1970), who found that stomatal conductance appeared to be independent of changes in leaf turgor pressure until it approached zero when stomatal conductance rapidly decreased.

In general terms, leaf water potential has often been used as an index of water stress and in figure 12 stomatal conductance has been plotted against the corresponding measurements of leaf water potential, again excluding measurements made in the early morning and late evening. The linear relation suggests that the stomata responded to changes in leaf water potential over the range of measurements, unlike the relation between stomatal conductance and turgor pressure (figure 11). Recent measurements on sorghum grown under a range of environmental conditions also define a linear relation between stomatal conductance and leaf water potential (McCree 1974). These results do not support the idea that there is a 'critical' value of leaf water potential at which stomatal conductance suddenly decreases to approximately zero (Berger 1973; Turner 1974). By definition the concept of a 'critical' leaf water potential means that stomata can control the loss of water only by completely opening or completely closing. The present ideas on water movement through leaf cells (Slatyer 1967; Weatherley 1970) and through epidermal cells (H. Meidner, personal communication) suggests that the main pathways for water movement are either the cell walls or the symplast. If most of the water moves along either of these pathways then the water potential in the guard cells and the leaf generally must be similar. Large differences of osmotic potential and hence of turgor are known to exist between guard cells and other leaf cells (Squire & Mansfield 1972; Fischer 1973). Hence if guard cells are sensitive to changes in the water relations of a leaf it seems more appropriate to expect a relation between stomatal conductance and leaf water potential rather than leaf turgor potential. Figure 12 shows this.

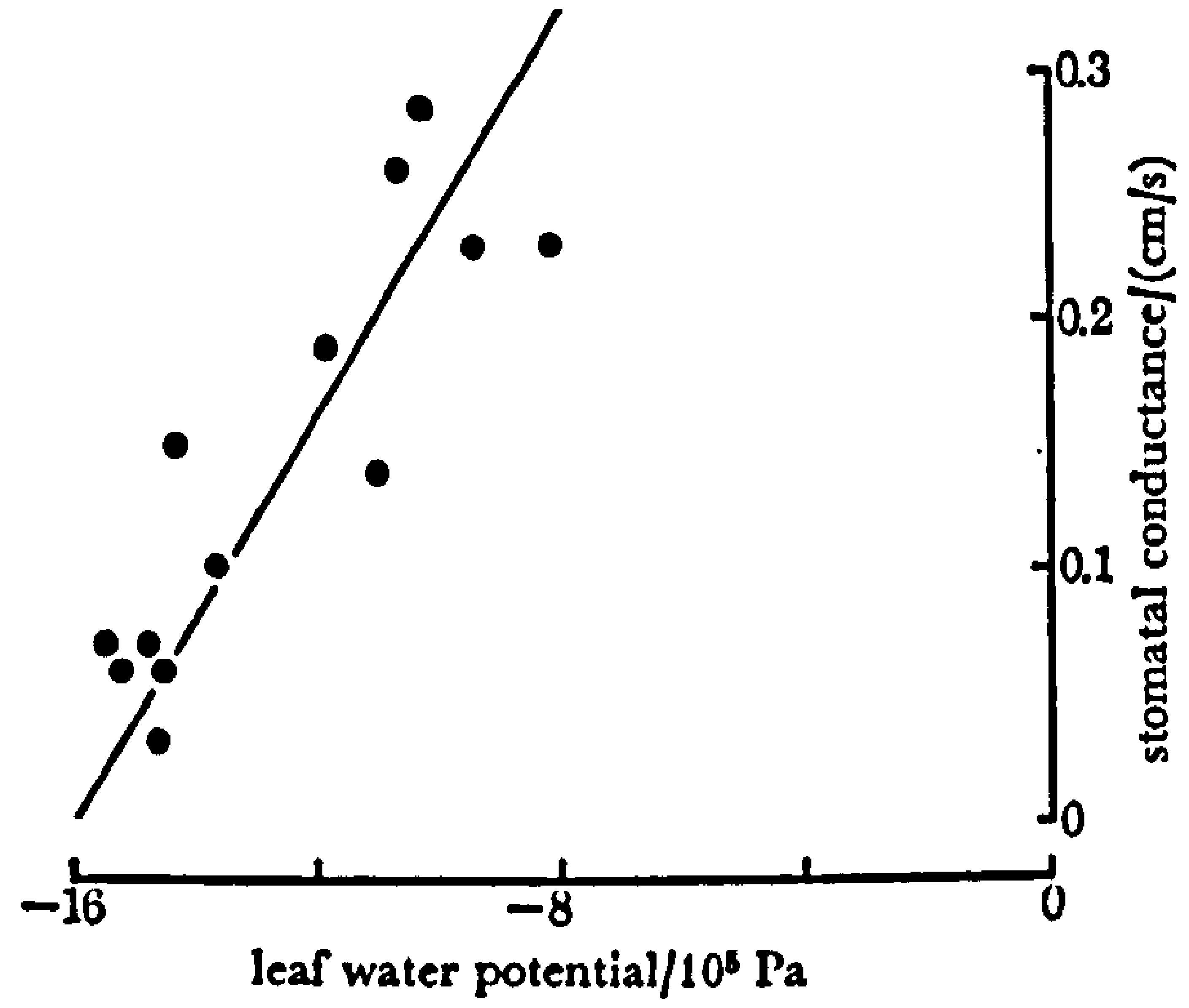

FIGURE 12. Measurements of adaxial stomatal conductance made on leaf 10 of wheat during 13 and 20 June 1974 plotted against the corresponding values of leaf water potential.

CROP CONDUCTANCE

The response of stomata on individual leaves to changes in irradiance and leaf water stress were examined in the previous section. The next question to be considered is the extent to which these changes in stomatal conductance influence the response of the crop as a whole. The idea of a crop conductance, analogous to the stomatal conductance of a leaf, was proposed by Monteith (1965) as part of a combination formula for evaporation from crops, which may be expressed as

$$\lambda E = \frac{\Delta(R_n - G) + \rho c_p(e_s(T) - e)k_a}{\Delta + \gamma(1 + k_a/k_c)}, \tag{5}$$

where λ is the latent heat of vaporization (J g^{-1}), Δ the slope of the saturation vapour pressure curve with temperature (Pa K^{-1}), R_n is the net radiation and G soil heat flux (W m^{-2}),

ρ is air density (g m^{-3}), c_p is specific heat of air (J g^{-1} K^{-1}), $e_s(T)$ is saturation vapour pressure at air temperature (T) and e air vapour pressure (Pa), γ is the psychrometric constant (Pa K^{-1}), k_a is the aerodynamic conductance and k_c crop conductance (m s^{-1}). Experimental evidence presented by Monteith, Szeicz & Waggoner (1965) and others suggests that crop conductance may be uniquely related to the stomatal conductance of the leaves by an equation of the form

$$k_c = \sum_1^n L_1 k_1 + L_2 k_2 \ldots L_n k_n, \tag{6}$$

where n is the number of actively transpiring organs in the crop canopy, k is the mean stomatal conductance of an organ and L is the corresponding area index of that organ. Although the concept of a crop conductance provides a useful method for examining crop responses to the environment, few attempts have been made to confirm the relation expressed in equations (5) and (6) (Szeicz, van Bavel & Takami 1973). All variables necessary to calculate the hourly crop conductance from equation (5) were available from the micro-meteorological instruments operating in the barley crop and hourly rates of evaporation which were calculated by using an energy balance method (Biscoe *et al.* 1975). Concurrent measurements of the stomatal conductance of leaf 8 were also available.

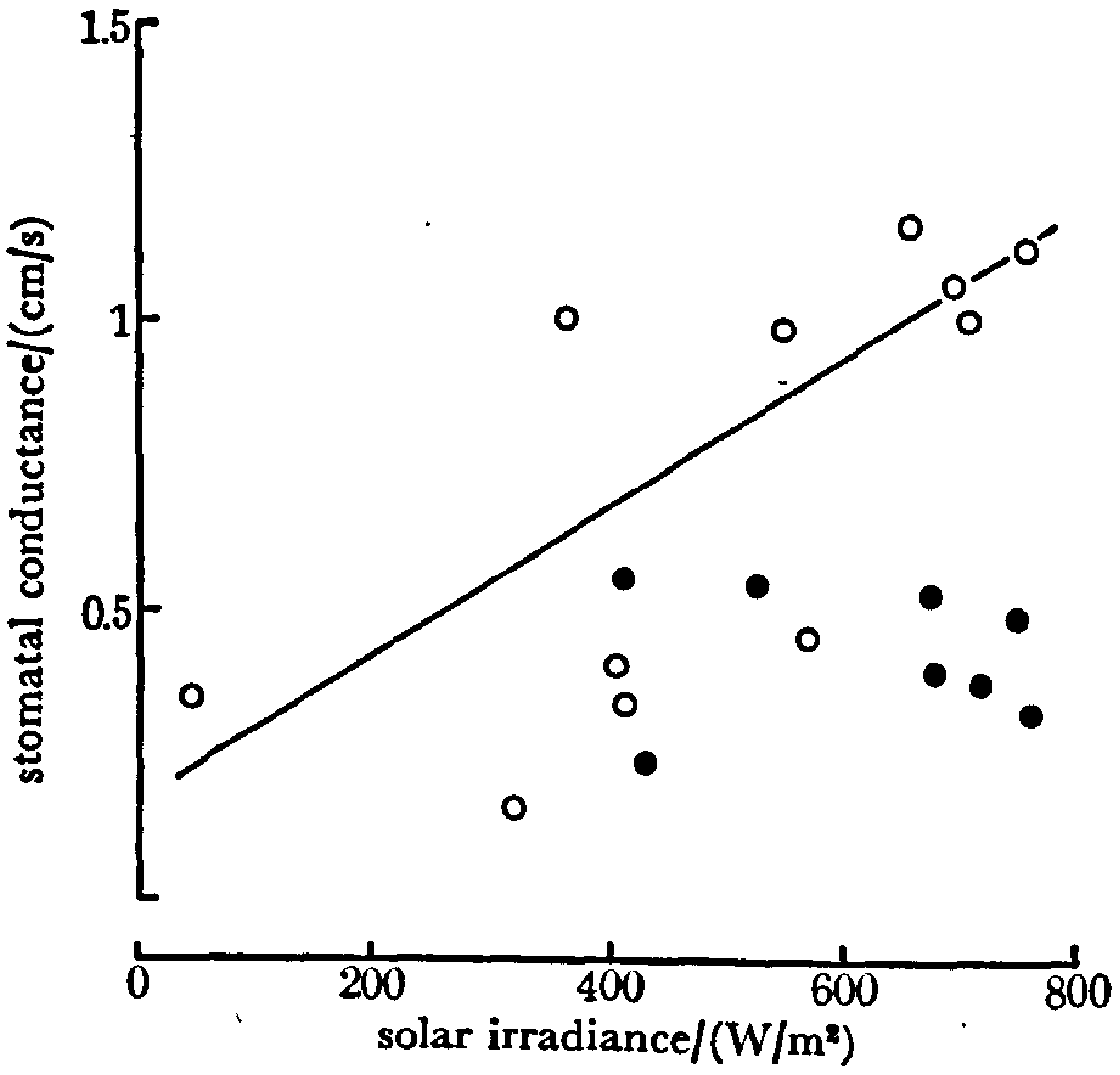

FIGURE 13. The relation between the stomatal conductances of leaf 8 on barley and solar irradiance on 5 July (○) and 14 July (●) 1972. The line drawn through the points was calculated from measurements made on 14 June (figure 5).

The relation between the stomatal conductance of leaf 8 and irradiance for the two days of measurements is shown in figure 13, and the line drawn through the points was calculated from measurements made on 14 June. The measurements made on 5 July are scattered about this line but those made on 14 July all fall below the line. The corresponding relation between crop conductance and irradiance is shown in figure 14 and is linear for all measurements made on 5 July when the soil water potential was high. The same linear relation is also apparent for measurements made in dull light on 14 July, but in strong light this relation does not hold In both cases maximum conductances are approximately half of those obtained on 5 July at similar irradiances. The lack of information on the stomatal conductances of other actively transpiring organs in the barley crop make it impossible to calculate a crop conductance by using equation (6). However, if it is assumed that the variations in stomatal conductance of these other organs are similar to those measured for leaf 8 then the stomatal and crop conductance can be compared in relative rather than absolute terms, e.g. by taking the maximum measured value of stomatal conductance and expressing all the other measurements relative to this value. The same transformation was done with the measurements of crop conductance. Figure 15 shows a comparison of the measurements of stomatal and crop conductance expressed in relative terms from zero to 1, On both days most of the points fall close to the line of unit slope. It is also evident that the maximum values of both conductances were measured on 5 July and these are approximately twice those measured on 14 July, confirming the previous conclusion derived from a comparison of figure 13 and 14. While the measurements do not represent a strict validation of the equality between crop conductances, calculated from equation (5), and

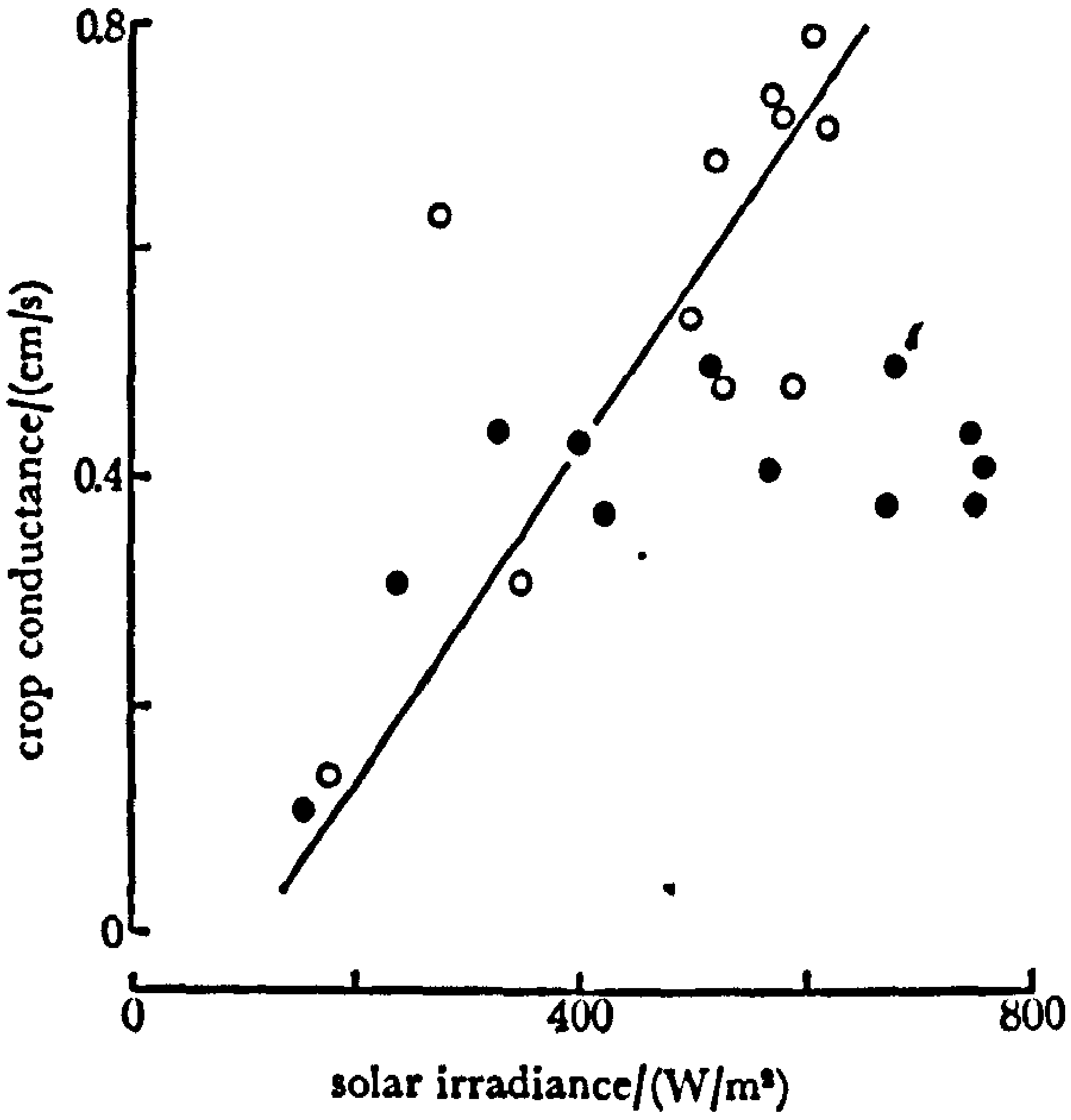

FIGURE 14. The relation between the crop conductance of barley and solar irradiance on 5 July (○) and 14 July (●) 1972. The line of best fit, calculated from the measurements made on 5 July has been drawn through the points.

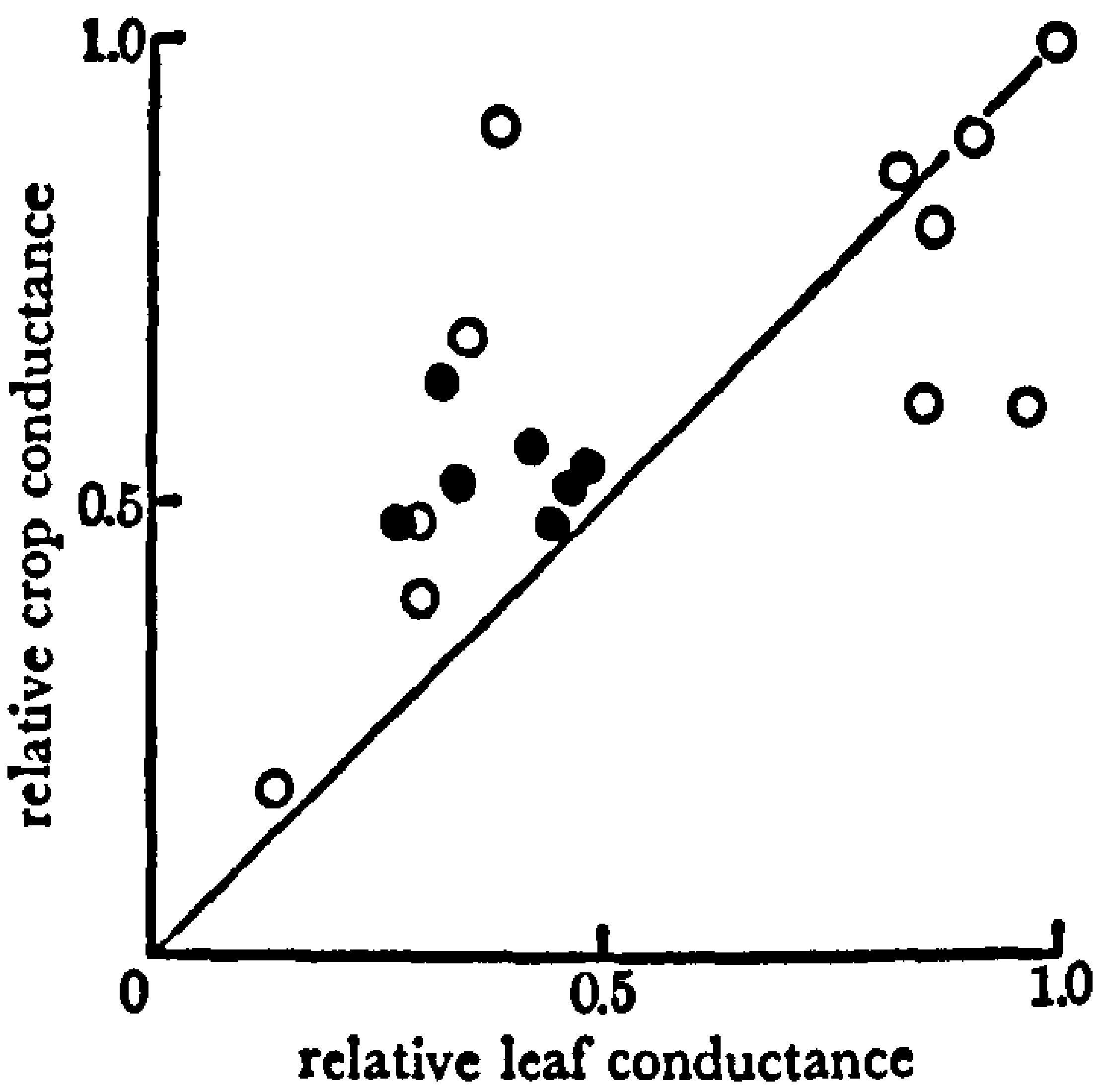

FIGURE 15. Relative crop conductances plotted against the corresponding relative leaf conductances for measurements made on barley during 5 July (○) and 14 July (●) 1972. The line has unit slope.

equation (6) it clearly shows that both conductances responded similarly during the two days when there was a difference in the soil water potential (figure 1).

CONCLUSIONS

The measurements discussed in this paper demonstrate how recent developments in both instrumentation and methodology can be used to study the water relations of plants in the field, as opposed to the growth room where much information has previously been obtained. The porometer, pressure chamber, and dew-point hygrometer enabled many replicate measurements to be made hourly throughout the day and with the porometer it is now possible to distinguish the responses of the stomata on the adaxial and abaxial epidermis. Micrometeorological instrumentation and theory was used to estimate hourly rates of evaporation from a barley crop, providing a degree of discrimintaion rarely achieved even by lysimetry.

The results obtained from the techniques in the field generally confirmed those obtained from growth room studies, with two exceptions. First, the results implied that a component of the hydraulic conductance remained constant with changes in evaporation rate, unlike some previous measurements in controlled environments. It may be significant that the plants were rooted in soil and not sand or water culture as in most growth room experiments. Second, a linear relation between leaf stomatal conductance and irradiance was obtained for barley, a result previously reported for a wheat crop in Australia. When considered together, the measurements clearly showed the response of plants to low soil water potentials and the importance of the stomata in controlling the loss of water from both leaves and crops during these periods. The measurements also were used to explore the dependence of stomatal aperture on plant water status.

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