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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

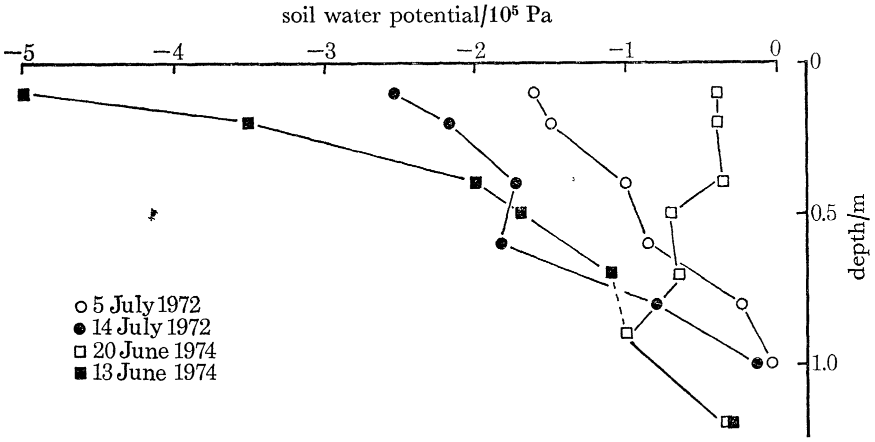

FIGURE 1. Profiles of soil water potential on days when stomatal conductance was measured on barley (○, ●) and wheat (□, ■).

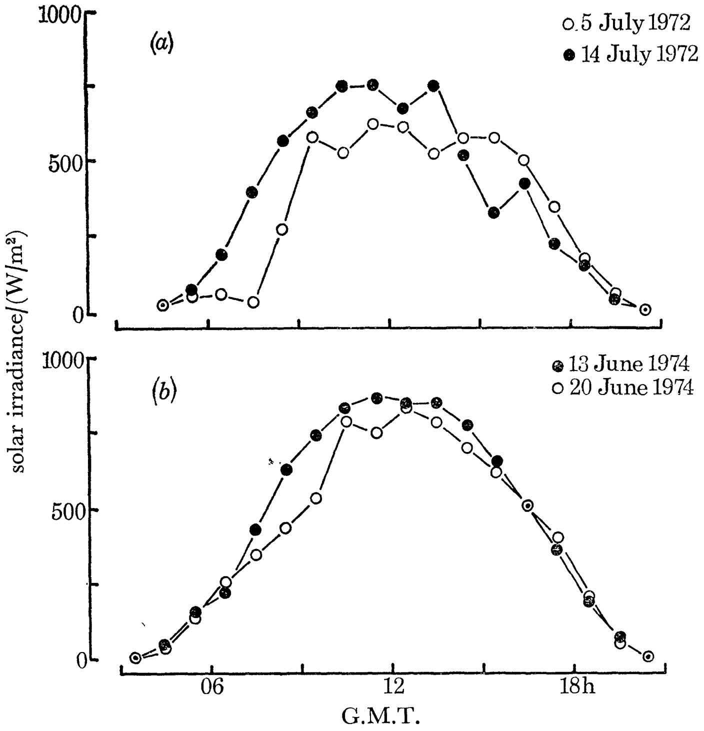

FIGURE 2. Diurnal changes of solar irradiance measured above the crop of (*a*) barley and (*b*) wheat on days when stomatal conductance was measured.

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 ($\mathrm{m^3\,s^{-1}}$), ($\delta\Psi$) is the difference in water potential between the root surface and the leaf (MPa) and K is the total hydraulic conductance of the plant ($\mathrm{m^3\,s^{-1}\,MPa^{-1}}$) 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 ($\mathrm{m^3\,s^{-1}}$) were calculated by dividing the crop evaporation rate, E, by the plant density, which was 900 stems $\mathrm{m^{-2}}$ 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 $0.25 \times 10^{-10}\ \mathrm{m^3\,s^{-1}}$, 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 $0.25 \times 10^{-10}\ \mathrm{m^3\,s^{-1}}$. 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

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

where Ψ_o 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 $\Psi_p = \Psi_s - \Psi_o$. 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).

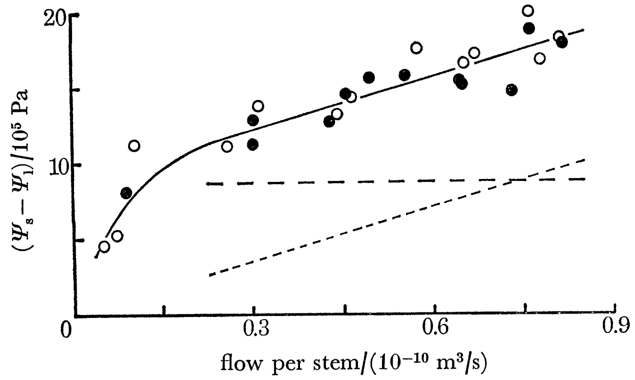

FIGURE 3. The relation between the water flow per stem of barley and $\Psi_s - \Psi_l$, measured on 5 July (○) and 14 July (●), $\Psi_s - \Psi_p$ (— —) and $\Psi_p - \Psi_l$ (----).

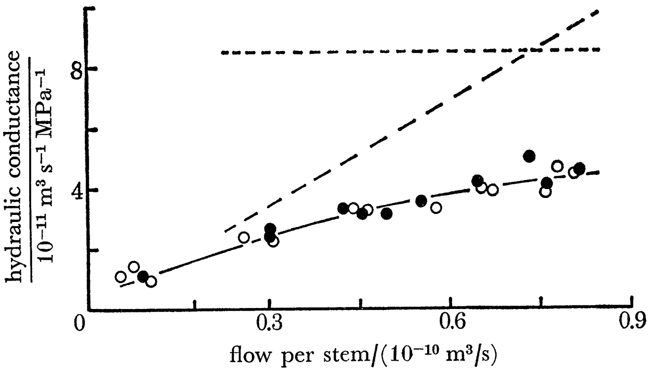

FIGURE 4. The relation between the water flow per stem of barley and the total hydraulic conductance (K) on 5 July (○) and 14 July (●) and the component conductance K_1 (----) and K_2 (— —).

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.

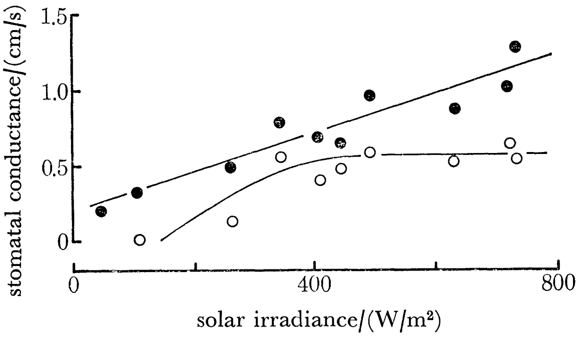

FIGURE 5. The relation between stomatal conductance of the adaxial (●) and abaxial (○) epidermis of leaf 8 and solar irradiance measured above the crop. Each point represents an hourly mean of measurements made on barley, 14 June 1972.

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.

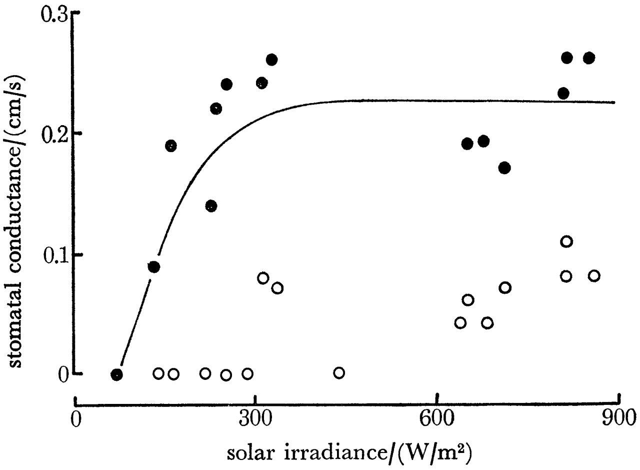

FIGURE 6. The relation between stomatal conductance of the adaxial (●) and abaxial (○) epidermis of leaf 10 and solar irradiance measured above the crop. Each point represents an hourly mean of measurements made on wheat, 20 June 1974.

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 nonlinear 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.

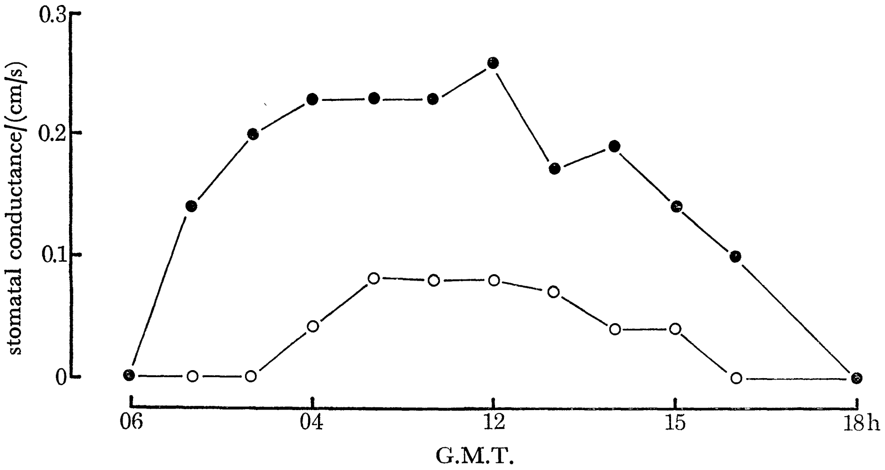

FIGURE 7. The diurnal variation of the stomatal conductance of the adaxial (●) and abaxial (○) epidermis of leaf 10 on wheat, 20 June 1974.

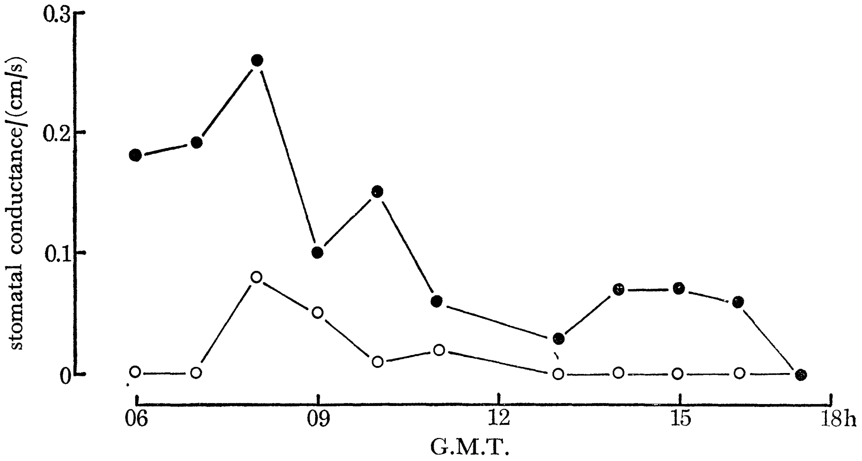

FIGURE 8. The diurnal variation of the stomatal conductance of the adaxial (●) and abaxial (○) epidermis of leaf 10 on wheat, 13 June 1974.

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

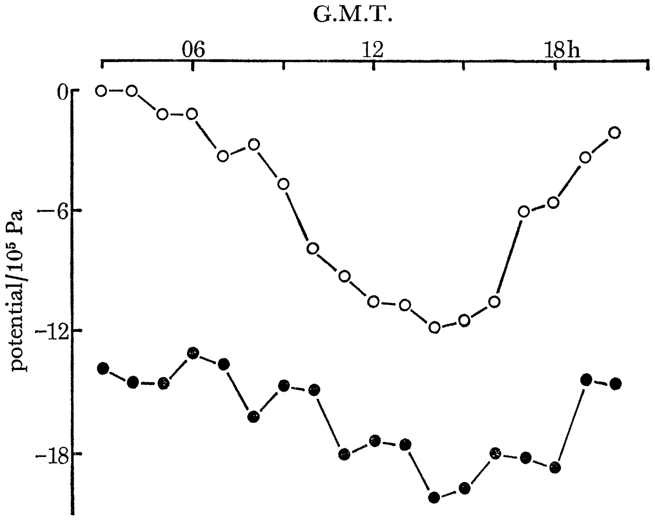

Figure 9. The diurnal variation of the water potential (○) and osmotic potential (●) of leaf 10 on wheat, 20 June 1974.

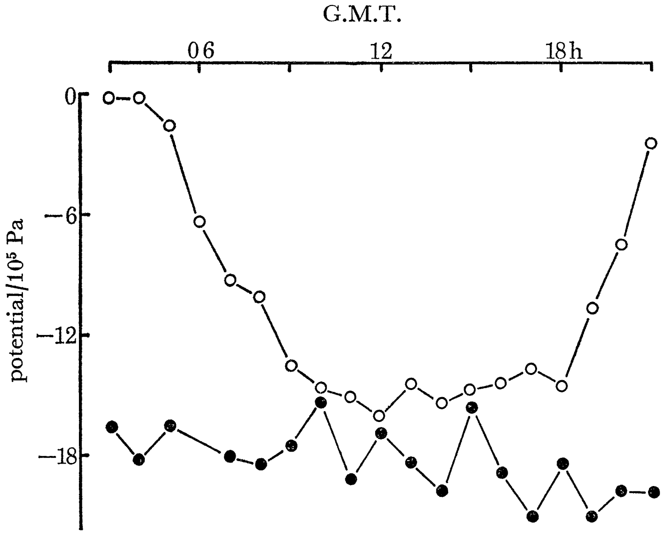

Figure 10. The diurnal variation of the water potential (○) and osmotic potential (●) of leaf 10 on wheat 13 June 1974.

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.

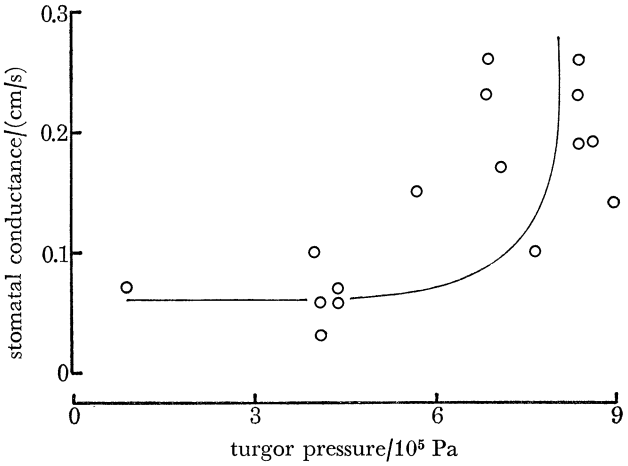

FIGURE 11. Measurements of adaxial stomatal conductance made on leaf 10 of wheat during 13 and 20 June 1974 plotted against the corresponding values of leaf turgor pressure, calculated as the difference between leaf water potential and osmotic potential.

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).

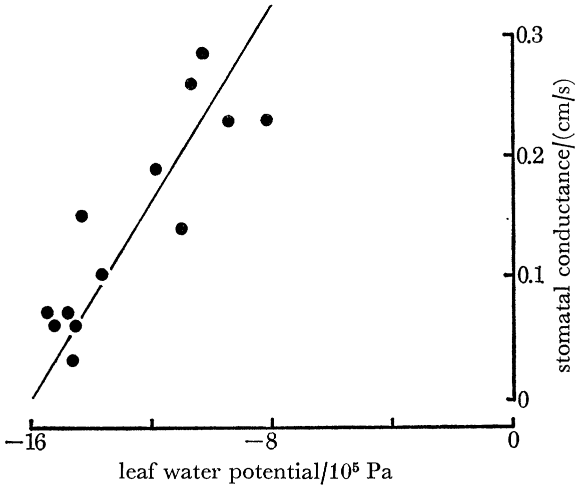

FIGURE 12. Measurements of adaxial stomatal conductance made on leaf 10 of wheat during 13 and 20 June 1974 plotted against the corresponding values of leaf water potential.

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.

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

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

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.

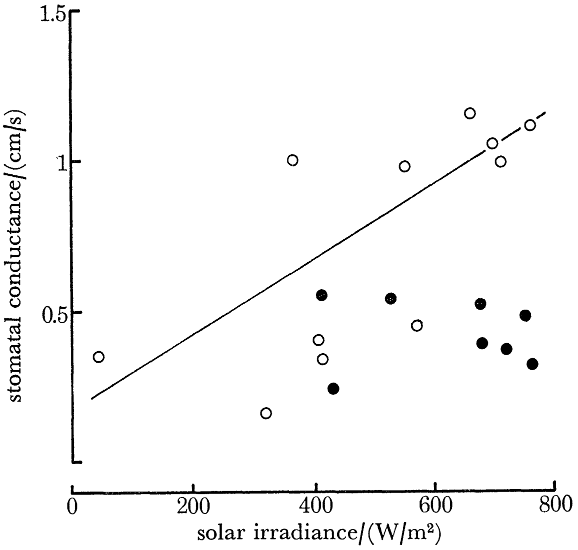

FIGURE 13. The relation between the stomatal conductances of leaf 8 on barley and solar irradiance on 5 July (○) and 14 July (●) 1972. The line drawn through the points was calculated from measurements made on 14 June (figure 5).

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

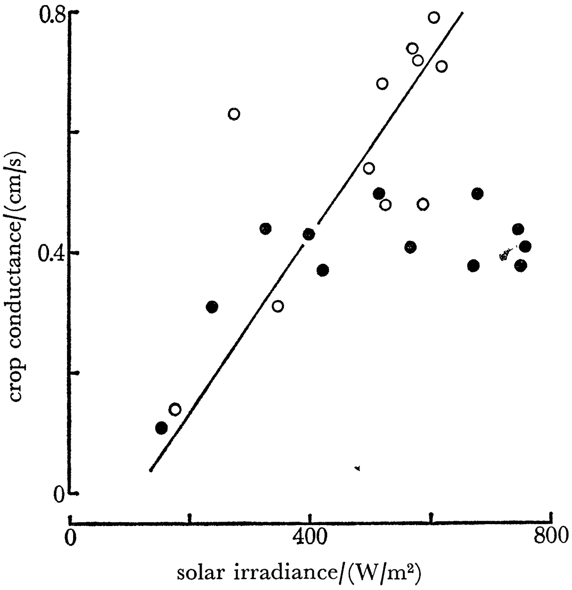

FIGURE 14. The relation between the crop conductance of barley and solar irradiance on 5 July (○) and 14 July (●) 1972. The line of best fit, calculated from the measurements made on 5 July has been drawn through the points.

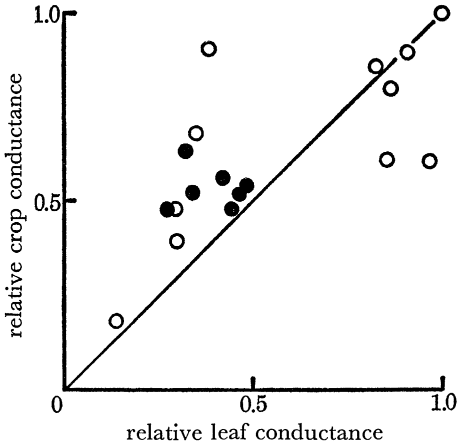

FIGURE 15. Relative crop conductances plotted against the corresponding relative leaf conductances for measurements made on barley during 5 July (○) and 14 July (●) 1972. The line has unit slope.

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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