The Water Relations of the Field Bean Crop

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The water relations of the field bean crop

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The water relations of crops of field beans, *Vicia faba*, are analysed. Three parameters (the solute potential at zero turgor, the relative water content at zero turgor and the slope of the line relating pressure potential to relative water content) are used. All three decrease with water stress.

Measurements of leaf area show that water stress decreases the absolute growth rate but does not affect the duration of growth very much.

1. Introduction

Water stress is of great agricultural importance. In seasonally arid and Mediterranean climates the water balance defines the length of the growing season and may limit yield. Even in temperate climates there is often an increase in biological yield from irrigation. Plant physiologists have shown effects of water stress on photosynthesis and on leaf growth in the laboratory and growth room. There have been, inevitably, fewer studies of the physiological effects of water stress in the field. We have used the field bean (*Vicia faba* L.), a mesophytic plant with paired leaflets, in three field experiments to find:

(1) the pattern of water potential within a plant and how this changes with time,
(2) the scale of the components of water potential and how they change with time, and
(3) any relation between leaf growth and water potential or its components.

Classically, the water relations of a cell, a tissue or an organ have been treated as if the structure were an osmometer with a piston. Such a system, at its simplest, will have two forces acting on the water within the osmometer. One force, due to the presence of a solution in the osmometer, will tend to attract water inwards. This is the solute potential. The other force, due to the pressure with which the piston is held, is the pressure potential. The gradient along which water moves is then defined by the algebraic sum of these two potentials.

Many experimenters now use a convention based on reversible thermodynamics. The water potential of a tissue (Ψ) has three components: solute (ψ_s), matric and pressure (ψ_p) (e.g. Warren Wilson 1967, Weatherley 1970). The matric potential is produced by the adsorption of water onto surfaces of the tissue. None of these components can be measured easily and unambiguously. The system is not reversible and it is seldom isothermal (Dainty 1963). Also, in the field, a tissue is usually not at equilibrium. It may be that parts of the convention are entirely mistaken (Spanner 1973).

However, empirical relations have been found between water potential and a number of physiological processes. Such relations are more difficult to determine in a crop because as the plants grow and age the water relations of the tissues alter and also because the plant-to-plant variation is likely to be larger than under more controlled conditions. It is important that the measurement of water potential is designed so that statistical tests of significance are possible. This requirement means that the methods used must be simple and quick so that all observations may be replicated.

We have therefore used a length-change method, developed by Wadsworth and Warren Wilson (Kassam 1972), for estimating the water potential and the solute potential of leaves at zero turgor (ψ_{so}). The length (L) of strips of bean leaves can be easily measured. The measured solute potential includes the cell matric potential. At the same time we have determined the relative water content (R) of whole leaflets, the ratio of the actual amount of water in the leaf at sampling to the amount in the leaf after 24 h in a saturated atmosphere with its petiole in water. From these measurements we were able to calculate ψ_{s} and ψ_{p} using the following equations:

$$\psi_{\mathrm{s}} = \psi_{\mathrm{so}}\, R_0/R, \tag{1}$$

$$\psi_{\mathrm{p}} = \Psi - \psi_{\mathrm{s}}, \tag{2}$$

$$R_0 = 1 + \frac{(L_{\mathrm{m}} - L_0)\,(1-R)}{L - L_{\mathrm{m}}}. \tag{3}$$

In equation (1) R_0 is the relative water content at zero turgor. We assume that R is a good approximation to cell vacuole volume and that the solutes in the cell behave as in an ideal solution. In equation (2) no additional assumption is needed. In equation (3) L is the length of the strip used in determination of Ψ and the subscripts are as before, with the addition that m refers to the condition at $\Psi = 0$. The formula assumes that L is linearly related to R over the range R_{m} to R_0. This appears to be a reasonable approximation (Kassam 1972),

Experimentally ψ_{p} is linearly related to R (table 1), so that

$$\psi_{\mathrm{p}} = \frac{\Delta\psi_{\mathrm{p}}}{\Delta R}\,(R - R_0). \tag{4}$$

The symbol Δ is used, since experimentally $\Delta\psi_{\mathrm{p}}/\Delta R$ is calculated from $\psi_{\mathrm{p}}/(R-R_0)$. Equation (2) may be combined with equations (1) and (4) to give

$$\Psi = \left\{\frac{\Delta\psi_{\mathrm{p}}}{\Delta R}\,(R - R_0)\right\} + \psi_{\mathrm{so}}\, R_0/R. \tag{5}$$

Ψ then depends upon three parameters, $\Delta\psi_{\mathrm{p}}/\Delta R$, ψ_{so} and R_0 and one variable, R.

Some understanding of the water relations of plants under water stress comes from the relation between changes in pressure potential and changes in cell volume, $\Delta\psi_{\mathrm{p}}/\Delta R$. Where there is a linear relation between ψ_{p} and R then this can easily be calculated for the range R_{m} to R_0. At $R = R_{\mathrm{m}} = 1$, $\psi = 0$ and $\psi_{\mathrm{p}} = -\psi_{\mathrm{s}}$, while at $R = R_0$, $\psi_{\mathrm{p}} = 0$. Therefore we may write:

$$\frac{\Delta\psi_{\mathrm{p}}}{\Delta R} = \frac{\psi_{\mathrm{pm}} - 0}{R_{\mathrm{m}} - R_0} = -\frac{\psi_{\mathrm{so}}\, R_0}{1 - R_0}. \tag{6}$$

The change in ψ_{p} with R rather than the change in Ψ with R is used because of the close relation to the coefficient of enlargement of the cell wall (Broyer 1952). This formula for the slope probably gives an underestimate because in practice a curve of ψ_{p} against R is unlikely to go through the point $R_{\mathrm{m}} = 1$, $\psi_{\mathrm{p}} = -\psi_{\mathrm{s}}$. In our measurements on bean leaves, the curve of R against Ψ does not go through the point $R_{\mathrm{m}} = 1$, $\Psi = 0$ as it should in theory (see Kassam 1971). Whether this disagreement with theory is caused by error in R or in Ψ or in the theory is not clear.

In addition to the classical osmotic relations of cells given in equations (2) and (5) some idea of the way the leaf volume changes with water potential ($\Delta R/\Delta\Psi$) may be useful. Such an expression gives an idea of the way the leaf responds to changes in the balance between water uptake and transpiration. For a small change in water potential a large change in leaf volume (represented by R) may be advantageous to a plant in dry soil by allowing it to keep its stomata open longer than a similar plant with a small ratio. We can call this ratio the 'buffering capacity', B. The average buffering capacity can be calculated easily:

$$B = \frac{\Delta R}{\Delta \Psi} = \frac{R_{\mathrm{m}} - R_0}{\Psi_{\mathrm{m}} - \Psi_0} = -\frac{1 - R_0}{-\psi_{\mathrm{so}}}. \tag{7}$$

Because this number will be small it seems sensible to express the results as % change per bar. In practice, the formula gives an inaccurate result because when $R_{\mathrm{m}} = 1$ Ψ is not zero. We have used $1.1 - R_0$ instead of $1 - R_0$ to give some compensation.

TABLE 1. THE LINEAR REGRESSIONS OF RELATIVE WATER CONTENT (R) ON PRESSURE POTENTIAL (ψ_{p}) FOR FIELD BEANS GROWN AT THREE IRRIGATION TREATMENTS AT SONNING FARM, 1974

treatment	minimum soil water potential MPa		R_0	r
dry	−0.90	$\psi_{\mathrm{p}} = -8.1 + 14.7\,R$	0.55	0.913
medium	−0.45	$-9.1 + 15.7\,R$	0.58	0.756
wet	−0.25	$-16.0 + 23.8\,R$	0.67	0.829

2. MATERIALS AND METHODS

Three field experiments have been made using crops of field beans *Vicia faba*, cv. *Maris Bead*. In 1968 the crop was sown at Hillside Farm, Shinfield, Reading, on 11 March. The soil was a sandy clay loam with flints. In 1969 the crop was sown at University Farm, Sonning, Reading on 27 March. The soil was a sandy clay loam with gravel. In 1974 the crop was sown on 29 March, also at University Farm, Sonning. In 1968 and 1969 measurements were made on sample plants from a single more-or-less uniform plot within the crop. In 1974 the crop was grown under polythene covers to exclude rain and three irrigation treatments were used, to give three levels of soil water potential. Each level was replicated three times.

The wet treatment was irrigated when the leaf water potential soon after dawn fell to −0.25 MPa (−2.5 bar), and there were 9 irrigations during the experimental period. The medium treatment was irrigated when the leaf water potential was −0.45 MPa and received 2 irrigations. In the dry treatment the water potential of the leaves fell to −0.61 MPa at dawn. The dry plots were not irrigated.

In 1968 and 1969 measurements were made at a number of nodes on each plant to give profiles of the water potential and water characteristics of the plant (Kassam 1971). There is a distinct and fairly regular structure to the results, as would be expected. All the measurements given are the average of the values obtained for all leaves sampled at one time (Kassam & Elston 1974).

In 1974 measurements were only made of the fourth unfolded leaf from the top of the plant. This leaf had been shown by Kassam (1971) to be a good indicator of the water status of the whole plant. At the same time measurements were made every two or three days of the leaf area at each node of a number of selected plants, in each of the irrigation treatments.

3. Results for 1968 and 1969

1968 was an average summer with relatively even rainfall while 1969 was dry. In both years Ψ became more negative with time, changing from about -0.3 to about -0.9 MPa, but the trend with time was not smooth (figure 1*a*). Similarly R decreased with time from about 0.94 to about 0.84 (figure 1*b*). Neither Ψ nor R averaged from measurements at a number of nodes was consistently smaller in the drier years. There were no systematic differences in ψ_s between the two years; in both it decreased with time from about -0.9 to about -1.3 MPa (figure 1*c*) and ψ_p fell from about 0.6 to 0.3 MPa (figure 1*d*). During July, ψ_{so} was rather more negative in 1969 (figure 2), and R_0 rather smaller (figure 3). However, $\Delta\psi_p/\Delta R$ was usually lower in 1969, the drier season, though the range, from 7 to 2 MPa was the same for both seasons (figure 4). B fell erratically with time, from about 26%/MPa (2.6%/bar) to about 16%/MPa (1.6%/bar) (figure 5).

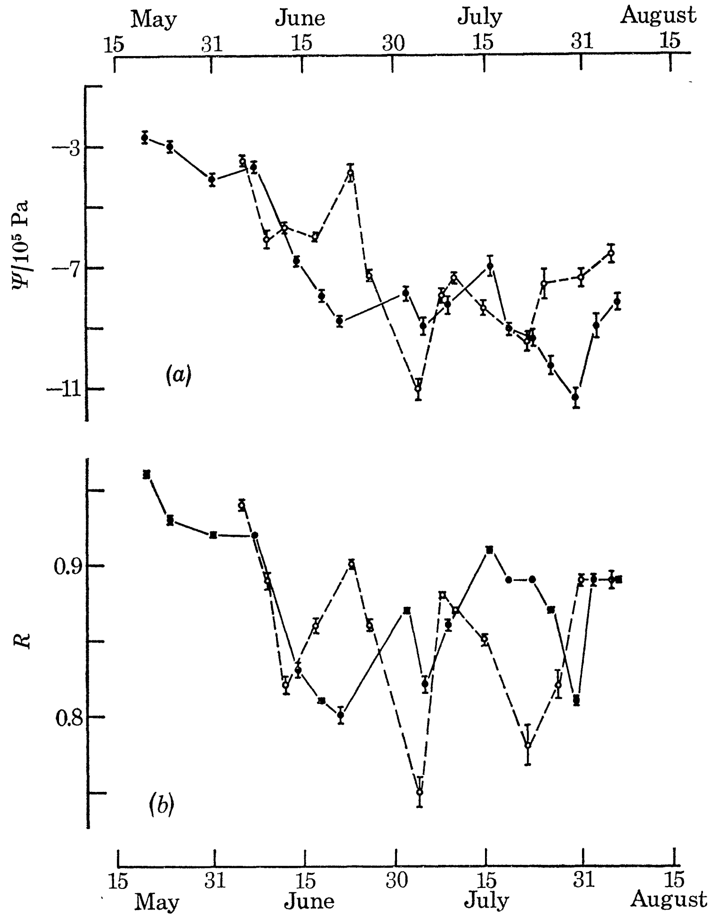

Figure 1 (*a*) The bulk water potential for 1968 (—) and 1969 (-----). (Measurements plotted in all figures are average values for all leaves sampled.) (*b*) The bulk relative water content 1968 (—) and 1969 (-----).

There is no clear and consistent difference in the bulk characteristics of the water relations of the two crops in the two seasons. In both seasons there are similar trends in ψ_{so}, R_0 and $\Delta\psi_p/\Delta R$. In 1969, ψ_{so} decreased rather earlier in the season and R_0 hardly increased at the end of the season. $\Delta\psi_p/\Delta R$ represents the change in pressure as the tissue increases in water content.

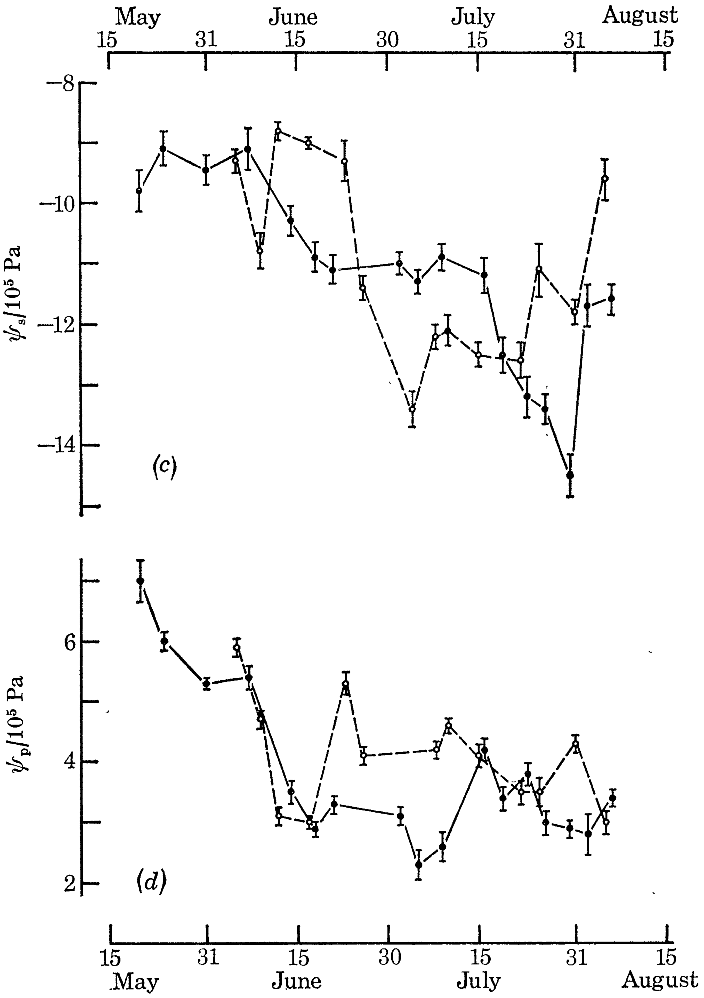

FIGURE 1 (*c*) The bulk solute potential for 1968 (—) and 1969 (-----).
(*d*) The bulk pressure potential for 1968 (—) and 1969 (-----).

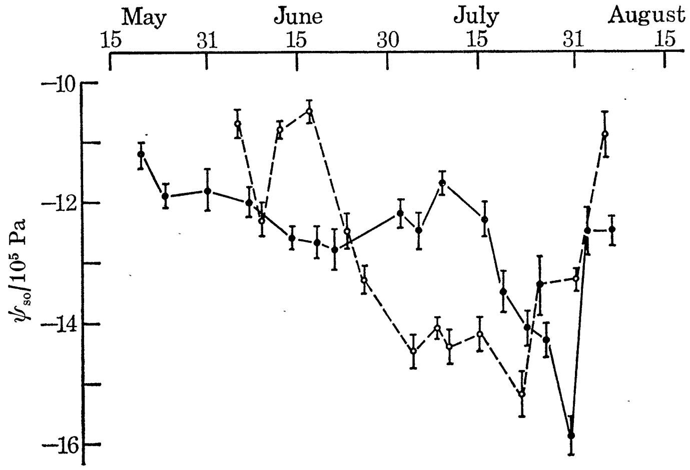

FIGURE 2. The bulk solute potential at zero turgor for 1968 (—) and 1969 (-----).

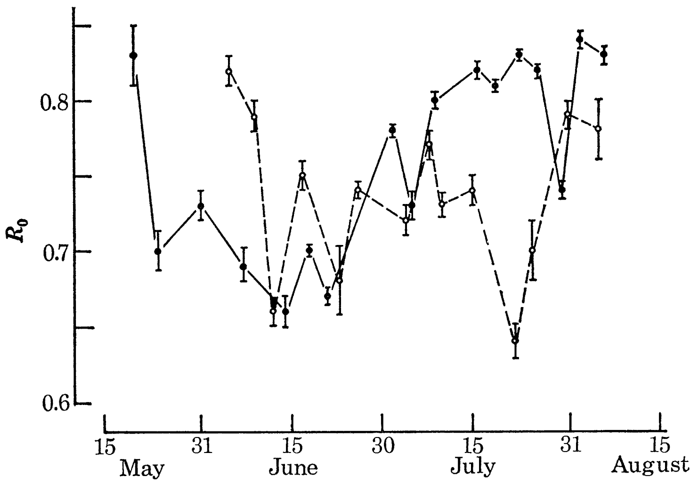

Figure 3. The bulk relative water content at zero turgor for 1968 (—) and 1969 (-----).

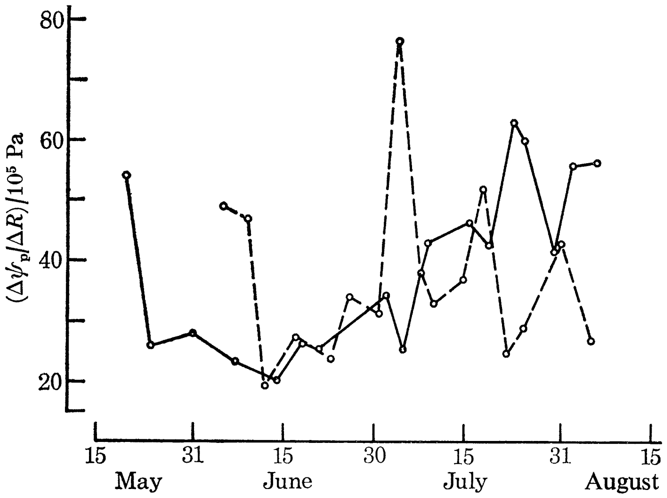

Figure 4. The slope of the pressure potential/relative water content curve for 1968 (—) and 1969 (-----).

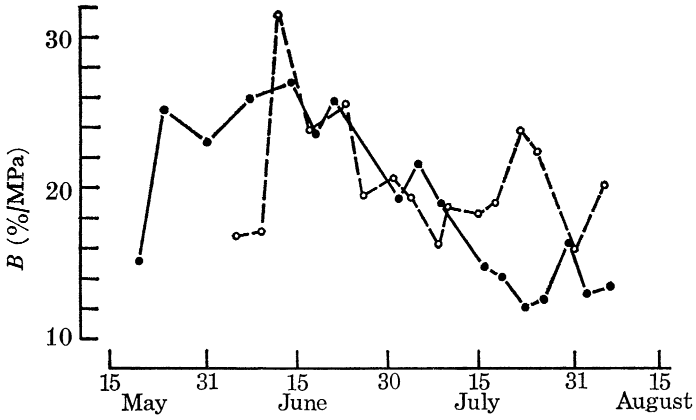

Figure 5. The buffering capacity for 1968 (—) and 1969 (-----).

If $\Delta\psi_p/\Delta R$ is small then any change in the water balance of the leaves will produce a relatively small change in ψ_p and a relatively small change in Ψ for a given change in volume. In other words, the effect of changes in R on the gradient of water potential from soil to leaf will be small when $\Delta\psi_p/\Delta R$ is relatively small.

4. RESULTS FOR 1974

In 1974 there were three irrigation treatments. There were consistent differences in water potential between treatments (figure 6). The mean water potential of the wet treatment from measurements throughout the day was relatively constant at about −0.4 MPa, while that of the dry treatment fell progressively to about −0.8 MPa. There was a similar difference in R (figure 7), which was relatively constant at about 0.92 in the wet treatment but decreased to about 0.75 in the dry. The medium treatment was intermediate, usually rather like the wet treatment.

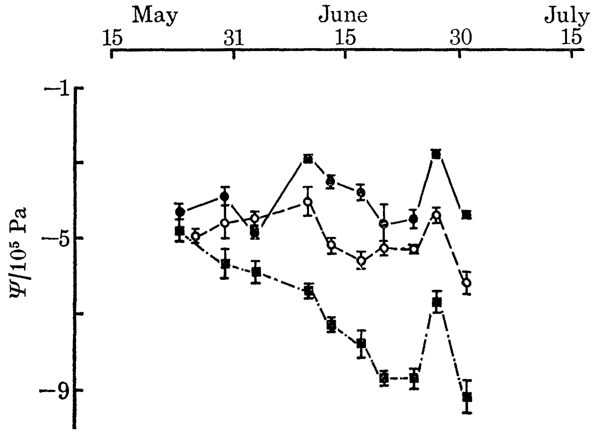

FIGURE 6. The water potentials of the fourth leaf from the top of the plant for 1974, wet (●), medium (○) and dry (■).

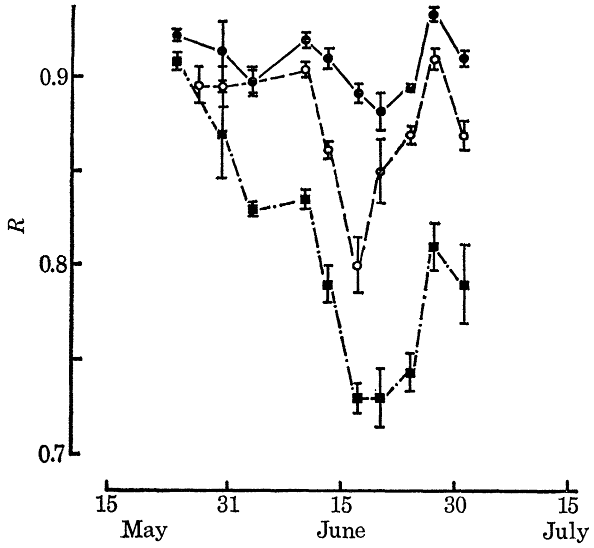

FIGURE 7. The relative water content of the fourth leaf from the top of the plant for 1974, wet (●), medium (○) and dry (■).

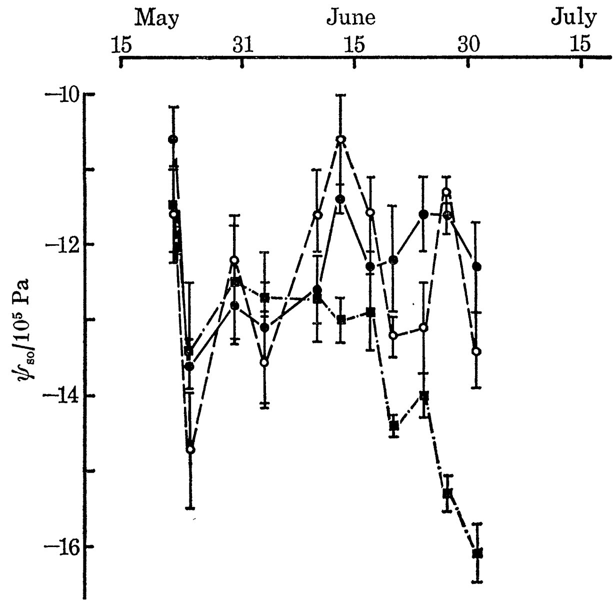

FIGURE 8. The solute potential at zero turgor for the fourth leaf from the top of the plant for 1974, wet (●), medium (○) and dry (■).

The value of ψ_{so} was about -1.2 MPa through the season for the wet treatment but fell to about -1.6 MPa for the dry (figure 8). R_0 varied more (figure 9), but was substantially lower in the dry treatment, falling to 0.61 by 84 days from sowing. The medium treatment showed a big change from 0.62 to 0.71 in 3 days after irrigation on day 83. $\Delta\psi_p/\Delta R$ fell to about 2 MPa and was lower in the dry treatment than in the wet, where it always exceeded 3 MPa (figure 10).

In the dry treatment B was consistently greater than in the wet (figure 11). B decreased towards the end of the period of measurement.

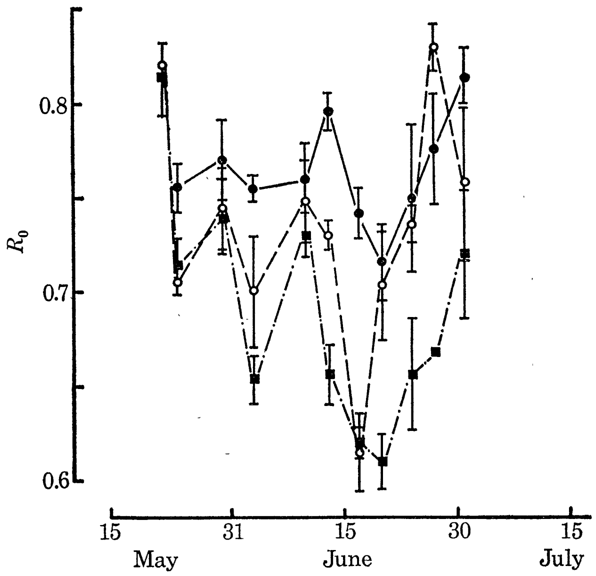

FIGURE 9. The relative water content at zero turgor for the fourth leaf from the top of the plant for 1974, wet (●), medium (○) and dry (■).

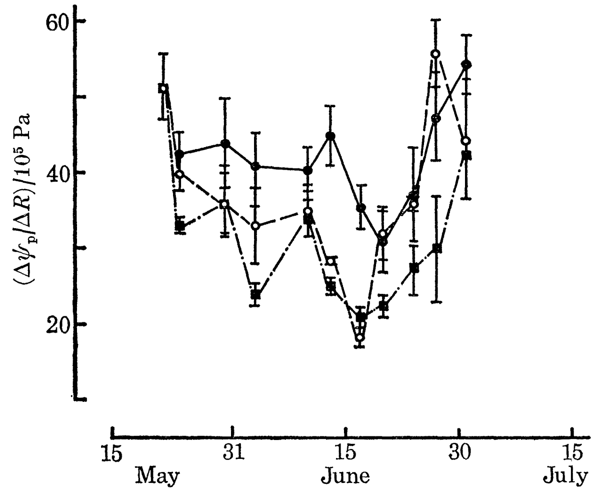

FIGURE 10. The slope of the pressure potential/relative water content curve for the fourth leaf from the top of the plant for 1974, wet (●), medium (○) and dry (■).

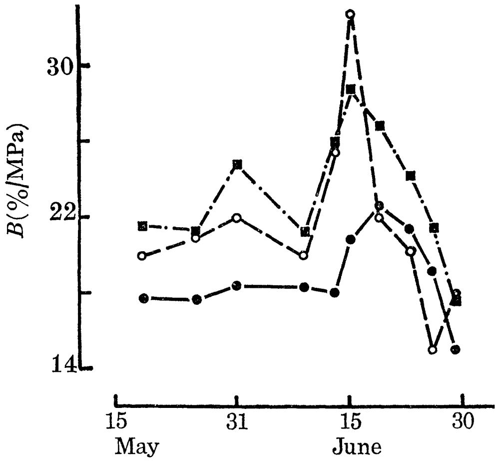

FIGURE 11. The buffering capacity of the fourth leaf from the top of the plant for 1974, wet (●), medium (○) and dry (■).

The sizes of Ψ and R, and their trends, were similar to those for 1968 and 1969. There were consistent differences between the irrigation treatments. These differences occurred in all three parameters, ψ_{s0}, R_0 and $\Delta\psi_p/\Delta R$. The changes in ψ_{s0} and R tend to balance each other, since while ψ_{s0} became even more negative, R_0 became smaller and ψ_s changed little.

The value of $\Delta\psi_p/\Delta R$ was less in the dry treatment, so that Ψ was more negative. A smaller $\Delta\psi_p/\Delta R$ means that larger changes can occur in R with only a small effect on ψ_p. If the cell loses water then ψ_p will decrease less, and will only reach zero at very low water contents.

R_0 represents the relative water content at which incipient plasmolysis would occur. Presumably, the lower R_0 is, then the more the water that can be lost from a tissue before tension damages the cells of the tissue. Perhaps a small value of $\Delta\psi_p/\Delta R$ and a low R_0 represents adaptive responses within the cultivar *Maris Bead* to water stress, maintaining a water potential gradient and avoiding tension.

5. Leaf growth in 1974

Leaf growth is affected by water stress. The rate of growth of leaf area can be measured fairly easily on standard plants. The results of measurements on *Maris Bead* can be organized and generalized using logistic curves (Dennett 1975). Measurements on growing leaves of the length and breadth of the leaflets were made every two or three days. They will be reported in detail elsewhere. However, the measurements can be characterized by the duration of growth, from unfolding to full area (figure 12) and the final area achieved (figure 13). Flowering started at node 10, while the 13th leaf was growing.

For nodes 6 to 11 the growing time was about two days longer in the wet treatment, but from node 12 the growing time was a little shorter. In general, the growing time of leaves at a particular node did not vary very much. There was a substantial difference in the area to which

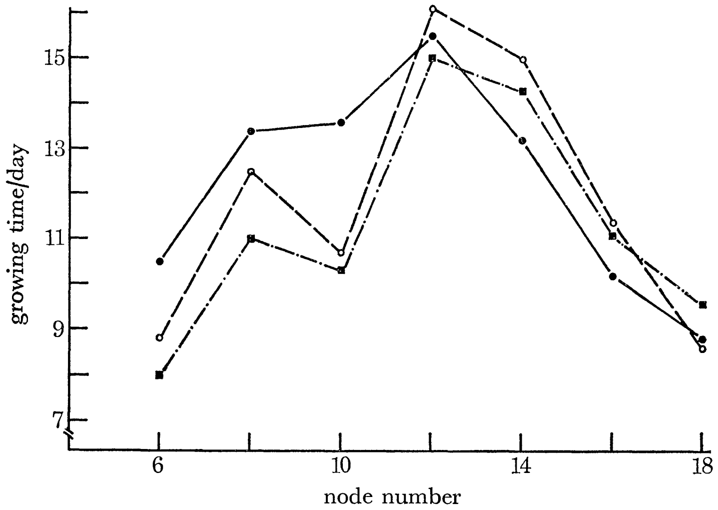

Figure 12. The growing time plotted against node number for the wet (●), medium (○) and dry (■) treatments of 1974.

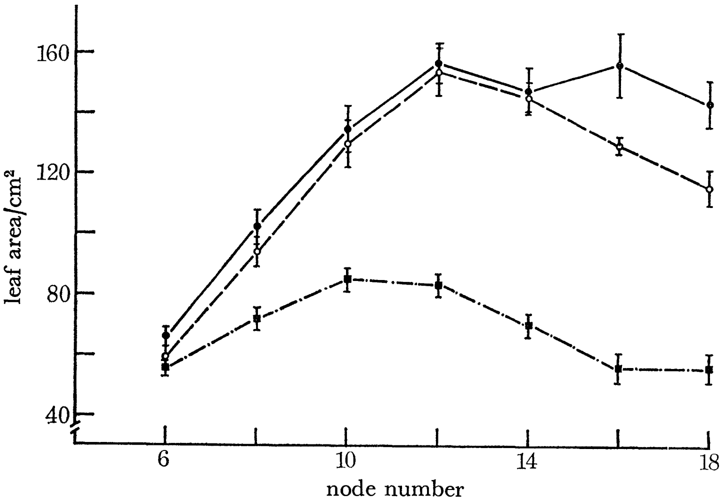

Figure 13. The final area of leaf at each node for the wet (●), medium (○), and dry (■) treatments of 1974.

leaves grew. The leaves of the dry treatment were about half the area of those of the wet treatment from node 10 onwards, about 70 cm^2 instead of 150 cm^2. The absolute growth rate of these leaves was greatly reduced by water stress.

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REFERENCES (Elston *et al.*)

Broyer, T. C. 1952 On volume enlargement and work expenditure by an osmotic system in plants. *Physiologia Pl.* **5**, 459–469.
Dainty, J. 1963 Water relations of plant cells. *Adv. Bot. Res.* **1**, 279–326.
Dennett, M. D. 1975 The effect of temperature on the growth of leaves of *Vicia faba* in the field. Ph.D. thesis, University of Reading.
Kassam, A. H. 1971 Some physical aspects of the water relations of *Vicia faba*, L. Ph.D. thesis, University of Reading.
Kassam, A. H. 1972 Determination of water potential and tissue characteristics of leaves of *Vicia faba* L. *J. Hort. Res.* **12**, 13–23.
Kassam, A. H. & Elston, J. 1974 Seasonal changes in the status of water and tissue characteristics of leaves of *Vicia faba* L. *Ann. Bot.* **38**, 419–429.
Spanner, D. C. 1973 The components of the water potential in plants and soils. *J. exp. Bot.* **24**, 816–819.
Warren Wilson, J. 1967 The components of leaf water potential. *Aust. J. biol. Sci.* **20**, 329–367.
Weatherley, P. E. 1970 Some aspects of water relations. *Adv. Bot. Res.* **3**, 171–206.