

ΓΕΩΠΟΝΙΑ.— **Understanding the origin of the responses of plants to water stress by means of an equilibrium model,**
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A B S T R A C T

The knowledge of the responses of some chemical and physical characteristics of the tissues to water stress may contribute to the understanding of plant water relations. The model proposed by Elston *et al.* (1976) which relates plant water potential (Ψ) to relative water content (R) by means of some parameters of the tissue characteristics is analyzed. The parameters used are the solute potential at zero turgor (ψ_{so}), the relative water content at zero turgor (R_0), and the slope of a linear regression between the pressure potential (ψ_p) and R (ϵ'). The latter is related to Broyer's coefficient of enlargement. The mathematical form of the model is:

$$\Psi = \frac{\psi_{so} R_0}{R} + \epsilon'(R - R_0).$$

The model is applicable to tissues consisting of mature parenchyma cells (e.g. mature leaves) which are considered to behave as ideal osmometers surrounded by an elastic cell wall.

The model was applied to interpret the water relations of two field bean crops during 1974 and 1975. To induce different degrees of water shortage three irrigation regimes were established in each year, wet (W), medium (M), and dry (D). Samplings for the determination of Ψ , R , and ψ_{so} were taken twice a week in the afternoon. Ψ and ψ_{so} were measured with the length change technique, which also allowed an estimate of R_0 . The component potentials ψ_s and ψ_p as well as the parameter ϵ' were derived from calculations.

As expected, Ψ was more negative in the drier treatments in both years. This fall of Ψ was more pronounced in the drier period (1975). From the parameters of the model, ψ_{so} was also significantly reduced in the drier treatments during the second half of both experimental periods. Furthermore, it was relatively unaffected by the daily evaporative demands and showed a lagged response to irrigation in the M-treatments. This behaviour of ψ_{so} was associated with an increase in solute content inside the cells, an osmoregulatory mechanism which required some time to develop and was not easily reversible after rehydration.

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In contrast with ψ_{so} , ϵ' , the parameter associated with cell turgor, showed a slight decrease with increasing soil water stress in the wet (1974) year. On the other hand, ϵ' responded readily to both daily evaporative demands and irrigation. R_o , an index of the dehydration a tissue can tolerate before its turgor drops to zero, showed a behaviour similar to that of ϵ' but it was more distinctly reduced by water stress.

It appears that, in this mesophytic species, adaptation is achieved mainly by means of osmoregulation and not via the cell walls as in many xerophytes. Under severe water shortage, the fall in Ψ , which is necessary to maintain the potential gradient between plant and soil, is attained by a depression in ψ_s while ψ_p does not participate effectively. On the other hand, ψ_p shows great day-to-day variations as a response to the evaporative demand when soil water is adequate.

I N T R O D U C T I O N

Water shortage is an ecological factor which determines to a great extent agricultural production. This is true especially in seasonally arid and Mediterranean climates where drought defines the length of the growing season. But even in more temperate climates, water shortage during some critical stages of plant development can reduce biological and economic yields. It is therefore important for the plant breeders to understand and detect the physiological mechanisms which enable plants to withstand drought.

According to Levitt et al. (1960), drought resistance mechanisms can be divided into two categories: (a) drought avoidance and (b) drought tolerance. In the former there are included mechanisms enabling plants to escape drought (e.g. closure of stomata, development of deep roots). The latter, also known as «drought hardiness», refers to the resistance to desiccation brought about by means of alterations in the physicochemical characteristics of plant tissue. Drought avoidance by means of stomatal closure is not the best solution for a plant in view of the concurrent cessation of CO_2 —uptake, which leads to a suppression of carbon assimilation rates. Therefore, to maintain crop production at high levels under dry conditions, it is important to know the origin of the mechanisms which impair drought tolerance in plant tissues. An

understanding of tissue water relations must be the first step in such a project.

The water status of a plant tissue is expressed thermodynamically as water potential (Ψ) (Slatyer & Taylor 1960) :

$$\Psi = \frac{\mu_w - \mu_w^o}{\bar{V}_w} \quad (1)$$

where μ_w and μ_w^o are the chemical potentials of water in a specific system and in pure free status respectively. Ψ is regarded as consisting of three component potentials, a pressure potential (ψ_p), a solute or osmotic potential (ψ_s) and a matric potential (ψ_m). A full theoretical analysis of this thermodynamic terminology has been given by Slatyer (1967), Taylor (1968) and Noy-Meir & Ginzburg (1967). Since there is an interaction between ψ_s and ψ_m inside a cell (Bolt & Frissel 1960 ; Weatherley 1970), eq. (1) can be expressed as follows :

$$\Psi = \psi_p + f(\psi_s, \psi_m) \quad (2)$$

When matric forces are negligible, eq. (2) becomes :

$$\Psi = \psi_p + \psi_s \quad (3)$$

Apart from this thermodynamic approach, plant water status can also be described in terms of water content. The most usual of such descriptions is the «relative water content» (R) (Barrs & Weatherley 1962). R is the water content of a tissue expressed as a fraction of the water content of the same tissue at full turgor :

$$R = \frac{FW - DW}{TW - DW} \quad (4)$$

where FW, TW, and DW are the tissue weights at sampling, after saturation with water and after drying respectively. Obviously, R equals unity when the tissue is at full turgor.

The relationship between Ψ and R, called the water potential isotherm of a tissue, is used to characterize the internal water relations of plant tissues, just as the moisture characteristic of a soil is used to

describe its water-holding properties (Weatherley & Slatyer 1957 ; Slatyer 1958 ; Jarvis & Jarvis 1963). Given that the general form of the curve relating Ψ to R is determined by the chemical and physical characteristics of the tissue, some models were developed in which this relationship was studied by means of some physicochemical parameters (see, for example, Philip 1958 ; Gardner & Ehlig 1965 ; Warren Wilson 1967 a, b, c ; Kassam & Elston 1974). In this paper, the model proposed by Elston *et al.* (1976) is dealt with. A theoretical description of the model will be given in the first part of the paper. Then, the model will be applied to interpret the water relations of two field bean crops.

T H E O R Y

Nearly all models proposed for the description of cell or tissue water relations presuppose that plant cells behave as ideal osmometers. The concept of the ideal osmotic cell regards cells as consisting of an elastic cell wall of negligible dimensions, a single differentially permeable membrane (comprising the cytoplasm, the plasmalemma and the tonoplast) and a vacuole containing an aqueous solution which conforms to the ideal gas equations. The ideal osmotic cell is not far from reality when dealing with mature parenchyma cells, as, for example, with the cells of the mesophyll (Slatyer 1967). In such cells, the vacuole occupies nearly the whole volume of the cell while the cytoplasm is restricted to a small volume between the cell wall and the vacuole.

If we regard plant cells as ideal osmometers, then gain or loss of water from the cells can be expressed by the law of van't Hoff :

$$\psi_{s,1} \cdot V_1 = \psi_{s,2} \cdot V_2 \quad (5)$$

where V represents cell volume and the subscripts 1 and 2 refer to two different levels of hydration. Eq. (5) is applicable when solute content does not vary with fluctuations in V . The use of V in eq. (5) may produce errors up to 10 per cent, since V contains also the volume occupied by solutes (Warren Wilson 1967 a). The use of the relative

water content is more appropriate as representing the volume occupied by water. Thus, eq. (5) becomes :

$$\psi_{s,1} \cdot R_1 = \psi_{s,2} \cdot R_2 \quad (6)$$

For practical purposes it is more useful to equate the product $\psi_s \cdot R$ at a given state with products at definite reference states, as, for example, at the states of full or zero turgor (incipient plasmolysis). Then, eq. (6) becomes :

$$\psi_s \cdot R = \psi_{sm} \cdot R_m = \psi_{so} \cdot R_o \quad (7)$$

where the subscripts m and o refer to the states of full and zero turgor respectively. Eq. (7) can be used for the calculation of ψ_s when the other terms are known (Slatyer 1960 ; Gardner & Ehlig 1965 ; Kassam & Elston 1974) :

$$\psi_s = \frac{\psi_{sm}}{R} \quad (\text{since } R_m = 1) \quad (8)$$

$$\text{or } \psi_s = \frac{\psi_{so} \cdot R_o}{R} \quad (9)$$

Apart from the osmotic relations of the cell sap, the behaviour of the cell walls is very important as determining cell turgor. Here it is assumed that the change in water volume is linearly related to the change in ψ_p . If so, it can be shown that :

$$\psi_p = \varepsilon' (R - R_o) \quad (10)$$

where ε' is the slope of the linear relation between ψ_p and R. This assumption implies that the cell wall has elastic properties and obeys Hooke's law. ε' is related to the elastic modulus or «coefficient of enlargement» (ε) (Broyer 1952) :

$$\varepsilon' = \frac{\varepsilon}{R_o} \quad (11)$$

Contradictory results have been reported on the form of the relation between ψ_p and R. Some investigators (e.g. Broyer 1952 ; Philip 1958 ; Warren Wilson 1967 b ; Noy-Meir & Ginzburg 1969 ; Elston et al. 1976)

found that a linear relationship was a good approximation. Others (Crafts, Currier & Stocking 1949; Haines 1950; Bennet-Clark 1959; Gardner & Ehlig 1965) found that the relationship was curvilinear. Departures from linearity in the relation between ψ_p and R may be caused by the complex structure of the cell wall. Interacting forces between adjacent cells are also likely to complicate the relationship between ψ_p and R when dealing with whole tissues.

Finally, it was assumed that the matric potential, ψ_m , was negligible inside the protoplast. ψ_m originates from forces of capillarity, adsorption and hydration. Water held by matric forces roughly corresponds to «bound water» (Dainty 1963). ψ_m is important in the cell wall where water is mainly held by surface tension. It may also be significant in the cytoplasm because of the presence of large protein molecules. On the other hand, ψ_m is very small or negligible in the vacuolar sap where macromolecules are usually scarce. Since the cell wall water remains virtually constant over a range of fluctuations in Ψ in the protoplast (Acock 1975; Tyree 1976), the ψ_m of the cell wall does not participate effectively in the water exchanges inside the protoplast. It remains the ψ_m in the cytoplasm, the contribution of which must be small or negligible in view of the small volume occupied by the cytoplasm in a fully vacuolated cell. It seems therefore reasonable to neglect ψ_m and use eq. (3) for fully vacuolated parenchyma cells (Tyree & Hammel 1972). Nevertheless, there have been reported cases (e.g. Slavik 1963) where eq. (6) did not hold, and the deviations were attributed to the presence of ψ_m .

By combining eqs (3), (9), and (10) we reach the following expression for Ψ :

$$\Psi = \frac{\psi_{so} \cdot R_o}{R} + \epsilon'(R - R_o) \quad (12)$$

where the first term on the right-hand side expresses ψ_s and the second one ψ_p . Eq. (12) relates Ψ to R by means of three parameters, ψ_{so} , R_o , and ϵ' , which represent the chemical and physical characteristics of the tissue. The solute potential at zero turgor, ψ_{so} , is the lower limit in the range of ψ_s in which cell turgor is positive. It also determines the

ultimate possibility of plant tissues to extract water from soil without loss of turgor. The relative water content at zero turgor, R_0 , is an indicator of the dehydration a cell can tolerate before its turgor falls to zero. Finally, ε' , the slope of the relation between ψ_p and R , is a measure of the elasticity of the cell walls. The greater the slope, the smaller the elasticity, i. e. the larger the decrease in ψ_p for a given fall in R . Conversely, a smaller slope indicates a greater elasticity of the walls, namely a more gradual decline in ψ_p with decreasing R . The parameter R_0 is not independent of the other two. From eqs (7) and (10) it can be shown that :

$$R_0 = \frac{\varepsilon'}{\varepsilon' + \psi_{so}} \quad (13)$$

Thus, the model could be transformed into one containing only the parameters ψ_{so} and ε' . By combining eqs (12) and (13) we reach :

$$\Psi = \frac{\varepsilon' \cdot \psi_{so}}{R \cdot (\varepsilon' + \psi_{so})} + \varepsilon' \cdot \left(R - \frac{\varepsilon'}{\varepsilon' + \psi_{so}} \right) \quad (14)$$

Nevertheless, the presence of R_0 makes eq. (12) easier to interpret.

In the following part of the paper, the water relations of two field bean crops will be studied by means of the variables and parameters of plant water status of the proposed model.

METHODS AND EXPERIMENTS

Experiments were made in the field during 1974 (29 March to 1 July) and 1975 (6 May to 21 July). Field beans (*Vicia faba* L. cv. Maris Bead) were sown on 29 March in 1974 and 6 May in 1975 at the Reading University Farm (Sonning, Berkshire). The soil was a sandy loam overlying gravel at a depth of 1 m. The average plant density was 20 plants/m² in 1974 and 25 plants/m² in 1975. Fertilizer (0-20-20) was applied before sowing in both years and the crops were sprayed to control weeds and pests. The experimental period in 1975 was drier and warmer than that in 1974 (fig. 1 and Table 1).

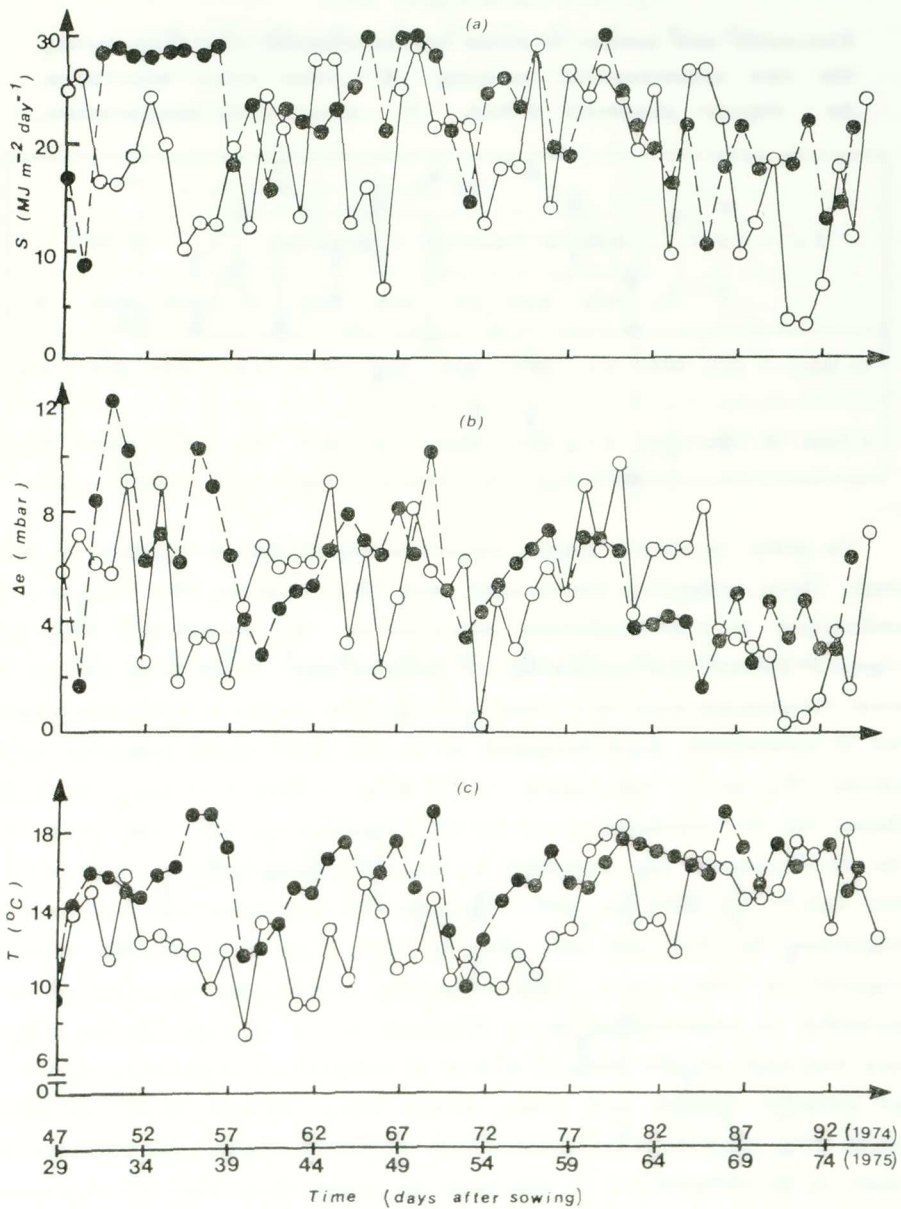


Fig. 1. The time course of some environmental variables during the experimental periods in 1974 (open circles) and 1975 (closed circles). a) Total daily solar irradiance (S). b) Mean daily vapour pressure deficit (Δe). c) Mean daily air temperature (T).

T A B L E 1

Extremes and means of some meteorological variables during the two experimental periods. S : totar solar irradiance, Δe : vapour pressure deficit, T : mean daily temperature.

P e r i o d s	V a r i a b l e s								
	S(MJ m ⁻² day ⁻¹)			Δe (mbar)			T (°C)		
	min	max	\bar{x}	min	max	\bar{x}	min	max	\bar{x}
14 May - 1 July 1974	3.1	29.7	18.9	0.1	9.7	4.9	8.2	19.2	14.0
4 June - 21 July 1975	8.7	30.1	22.3	1.5	13.8	5.7	10.1	20.2	16.7

In order to obtain plants experiencing different degrees of water stress, three irrigation treatments, wet (W), medium (M), and dry (D), randomized in four replicates, were set up. All treatments were fully irrigated before the beginning of observations. From then on, the different treatments were subjected to irrigation cycles of different lengths. The W-treatments were irrigated so as the plant water potential before sunrise (Ψ_d) never fell below -0.3 MPa (1 MPa = 10 bar). With this scheme the W-treatment received 10 irrigations in 1974 and 12 in 1975. The M-treatment has irrigated as soon Ψ_d fell below -0.45 MPa in 1974 and -0.5 MPa in 1975. Thus, the M-treatment received two full irrigations in 1974 and only one in 1975. The D-treatments were not irrigated in either year. This irrigation scheduling was proved to be successful in establishing three different levels of water stress (fig. 2). Rain was kept off the plots by means of rainshelters consisting of wooden and metallic frames and clear, heavy duty (500 μ m thick) polythene sheets. The photosynthetically active radiation under the shelters was found to be reduced by 17 per cent in comparison with the open area. The rainshelters were fixed at 1.0-1.2 m above ground. In each replicate, plots were separated from each other by 1 m wide guardrows.

Plant water status was measured between 55 and 95 days after sowing in 1974 and 34 to 76 days in 1975. Plant water potential was measured twice a week before sunrise (ca. 0500 h) (Ψ_d) and in the after-

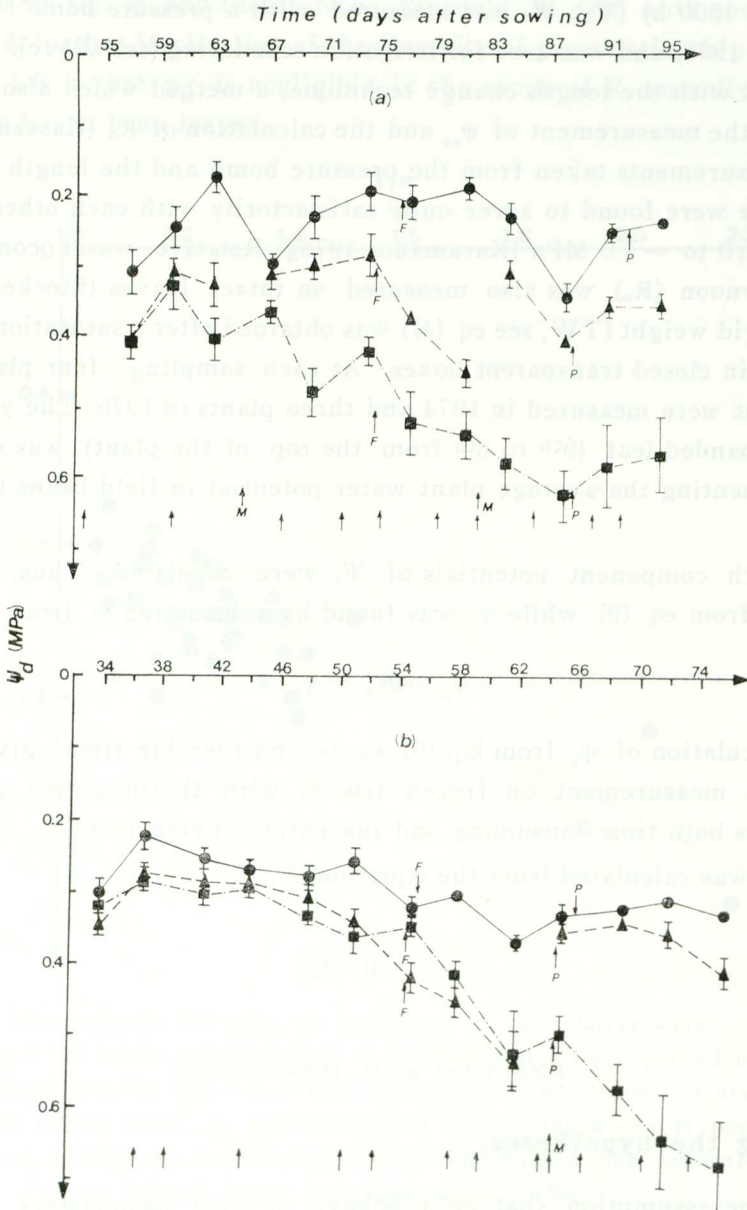


Fig. 2. The time course of the plant water potential at dawn (Ψ_d) during the two experimental periods. Ψ_d is regarded as a good indication of soil water status (Slatyer 1967). ●—●: W, ▲---▲: M, ■-.-■: D treatment. Arrows indicate the irrigation timing in the W- and M-treatments (M). The beginnings of flowering (F) and podding (P) are also indicated with arrows. The vertical bars represent the standard errors of the means.

a) 1974, b) 1975.

noon (ca. 1500 h) (Ψ_a). Ψ_d was measured with a pressure bomb (Waring & Cleary 1967) and was used for irrigation scheduling (see above). Ψ_a was measured with the length change technique, a method which also makes possible the measurement of ψ_{so} and the calculation of R_o (Kassam 1972). The measurements taken from the pressure bomb and the length change technique were found to agree quite satisfactorily with each other in the range of 0 to -1.0 MPa (Karamanos 1976). Relative water content in the afternoon (R_a) was also measured on intact leaves (Stocker 1929). The turgid weight (TW, see eq. (4)) was obtained after a saturation period of 24 h in closed transparent boxes. At each sampling, four plants per treatment were measured in 1974 and three plants in 1975. The youngest fully expanded leaf (5th to 6th from the top of the plant) was sampled as representing the average plant water potential in field beans (Kassam 1971).

Both component potentials of Ψ_a were calculated. Thus, ψ_s was derived from eq. (9), while ψ_p was found by subtracting ψ_s from Ψ_a :

$$\psi_p = \Psi_a - \psi_s \quad (15)$$

The calculation of ψ_s from eq. (9) saves considerable time, given that a direct measurement on frozen tissues with thermocouple psychrometers is both time-consuming and inaccurate (Tyree 1976).

ε' was calculated from the equation :

$$\varepsilon' = \frac{\psi_p}{R - R_o} \quad (16)$$

RESULTS AND DISCUSSION

Testing the hypotheses.

The assumption that cells behave as ideal osmometers and that the vacuolar solution obeys the law of van't Hoff was tested in field beans. A preliminary experiment was set up in which the form of the relation between $1/R$ and ψ_s was examined. In this experiment, ψ_s was determined directly on previously frozen and thawed leaf samples in a thermocouple psychrometer. The relationship was reasonably linear

($r = -0.80$, fig. 3) and therefore eq. (9) could be used with some confidence. A further implication of the linearity of the relationship between ψ_s and $1/R$ is that ψ_m is negligible in the range of R normally encountered in living bean leaves.

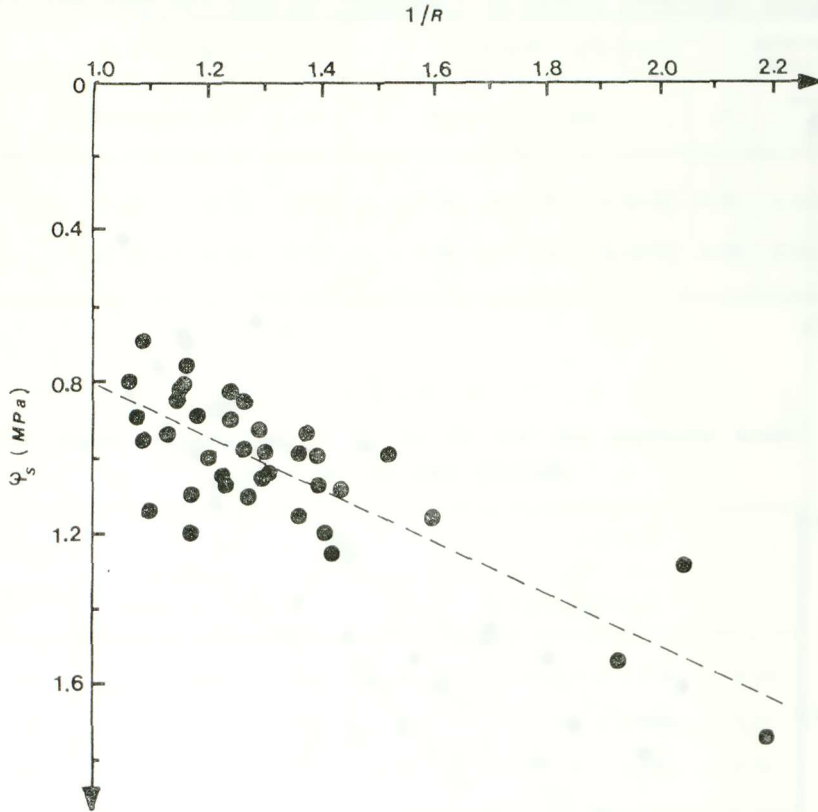


Fig. 3. The relation between the reciprocal of the relative water content ($1/R$) and the solute potential (ψ_s) of the youngest fully expanded leaf in field beans. Results were taken from well watered and stressed plants over a single drying cycle. ψ_s was determined with a thermocouple psychrometer on frozen and thawed leaf tissue. The dashed line indicates the fitted linear regression ($r = -0.80$).

The assumption of a linear relationship between ψ_p and R was tested from the field data. When results from all three treatments were used, a curvilinear (quadratic) regression fitted to the points better than

a straight line in both years (see fig. 4 and Table 2). However, the use of a curvilinear regression reduced significantly the unexplained variation only in 1974. Nevertheless, a linear regression expressed adequately the relation between ψ_p and R_a when data from each treatment were considered separately (Table 3). Therefore, eq. (10) was used only within treatments.

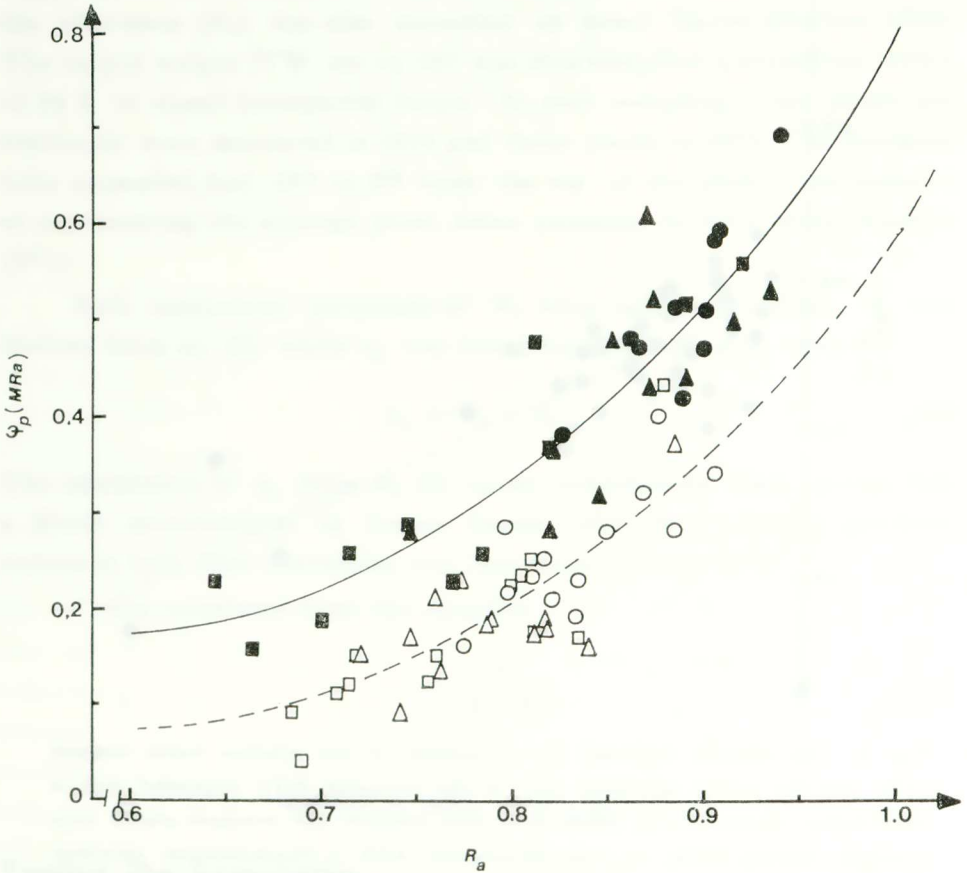


Fig. 4. The relation between the pressure potential (ψ_p) and the relative water content in the afternoon (R_a) during the two experimental periods. ψ_p was derived from eq. (15). Results from all three irrigation treatments throughout the periods. Circles: W, triangles: M, and squares: D-treatments. Closed symbols: 1974, open symbols: 1975. The fitted quadratic regressions for each year are also shown (see also Table 2).

TABLE 2

An analysis of the fitted linear and quadratic regressions on the relations of ψ_p against R_a pooled from all three irrigation treatments in each period. The improvement from the use of quadratic regressions is also shown by means of the F-ratio. *: $p < 0.05$, ns: non-significant.

Year	Linear		Quadratic		Improvement
	Regression	r^2	Regression	r^2	
1974	$\psi_p = -0.85 + 1.52 \hat{R}_a$	0.79	$\psi_p = 1.38 - 4.11 \hat{R}_a + 3.51 \hat{R}_a^2$	0.81	4.42 (*)
1975	$\psi_p = -0.79 + 1.24 \hat{R}_a$	0.70	$\psi_p = 1.20 - 3.77 \hat{R}_a + 3.16 \hat{R}_a^2$	0.72	2.24 (ns)

TABLE 3

The linear regressions of ψ_p on R_a for the separate treatments in the two periods.

Treatments	1974		1975	
	Regression	r	Regression	r
W	$\psi_p = -1.6 + 2.4 \hat{R}_a$	0.85	$\psi_p = -0.8 + 1.3 \hat{R}_a$	0.76
M	$-1.0 + 1.7 \hat{R}_a$	0.75	$-0.6 + 1.0 \hat{R}_a$	0.67
D	$-0.8 + 1.4 \hat{R}_a$	0.90	$-0.8 + 1.3 \hat{R}_a$	0.87

The course of Ψ_a and R_a .

Given that plant water deficits are maximum about midday (see for example Begg *et al.* 1964; Klepper 1968), Ψ_a and R_a represent to a close approximation the most negative daily values of Ψ and R . The time courses of Ψ_a and R_a in both years are shown in figs 5 and 6. The two extreme treatments can be easily distinguished in terms of Ψ_a and R_a in both years. The course in the M-treatments was determined by the adopted irrigation scheduling: in 1974 the two irrigations shifted the courses closer to those in the W-treatment, while in 1975, with only one

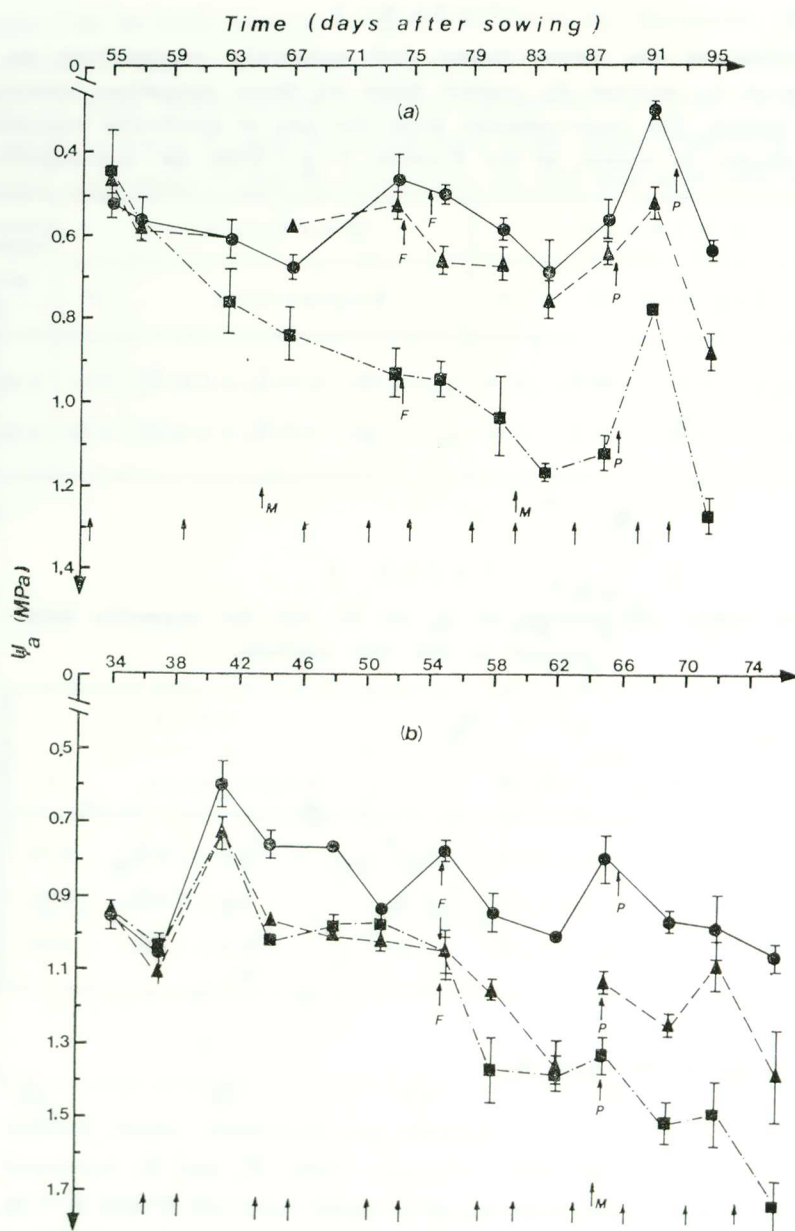


Fig 5. The time course of the plant water potential in the afternoon (Ψ_a) during the two periods. Each point is the mean of 12 determinations in 1974 and 16 in 1975. a) 1974, b) 1975. The symbols are the same as in fig. 2.

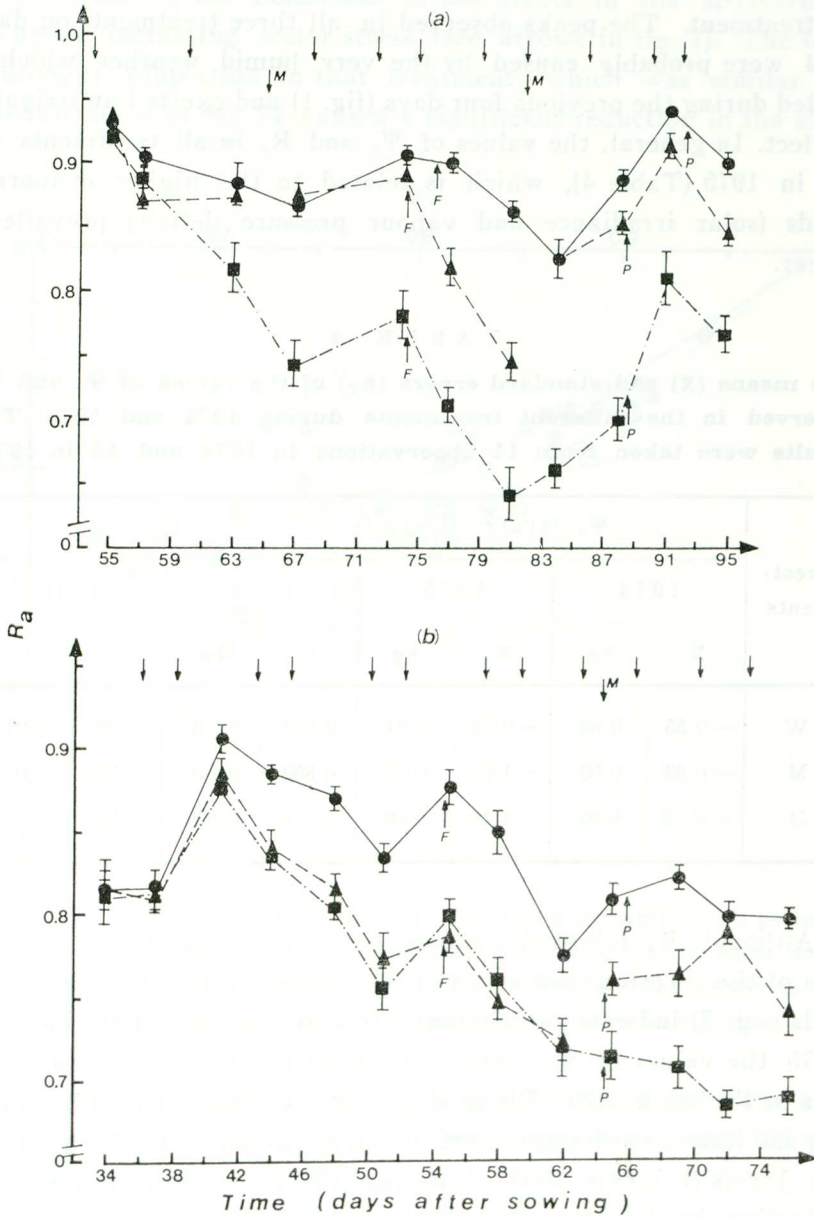


Fig. 6. The time course of the relative water content in the afternoon (R_a) during the two periods. Each point is the mean of 12 determinations in 1974 and 16 in 1975. a) 1974, b) 1975. The symbols are the same as in fig. 2.

irrigation, the courses of Ψ_a and R_a were closer to those observed in the D-treatment. The peaks observed in all three treatments on day 91 in 1974 were probably caused by the very humid weather which had prevailed during the previous four days (fig. 1) and exerted an irrigation-like effect. In general, the values of Ψ_a and R_a in all treatments were lower in 1975 (Table 4), which is related to the higher evaporative demands (solar irradiance and vapour pressure deficit) prevailed in this year.

TABLE 4

The means (\bar{x}) and standard errors ($s_{\bar{x}}$) of the values of Ψ_a and R_a observed in the different treatments during 1974 and 1975. The results were taken from 11 observations in 1974 and 13 in 1975.

Treat- ments	Ψ_a (MPa)				R_a			
	1974		1975		1974		1975	
	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$
W	-0.55	0.03	-0.89	0.04	0.892	0.010	0.836	0.011
M	-0.63	0.03	-1.09	0.05	0.859	0.016	0.789	0.012
D	-0.89	0.08	-1.19	0.08	0.770	0.027	0.768	0.017

Although R_a followed a course parallel to that of Ψ_a , an examination of the sorption isotherms of the tissues in the two experimental periods (fig. 7) indicates a different drought response of the two crops. In 1975 the values of Ψ_a were more negative than those in 1974 for values of R_a below 0.90. There is adequate evidence that plants grown in dry habitats are characterized by steep sorption isotherms (Slatyer 1960; Jarvis & Jarvis 1963; Knipling 1967). A lower Ψ for a given dehydration implies that the plant tissue can withstand drought by maintaining a potential gradient between plant and soil, which is necessary for water absorption. The steeper isotherm found in the drier year may have been induced by long-term adaptive responses of the tissue, a combined effect of atmospheric and soil water stress. This suggestion is

also supported by the behaviour of the plants in the M-treatment in 1974 under increasing water stress (see arrows in fig. 7). The lack of any drought adaptation in that treatment, which was similar to the W-treatment up to day 74, caused a significant reduction in the slope of

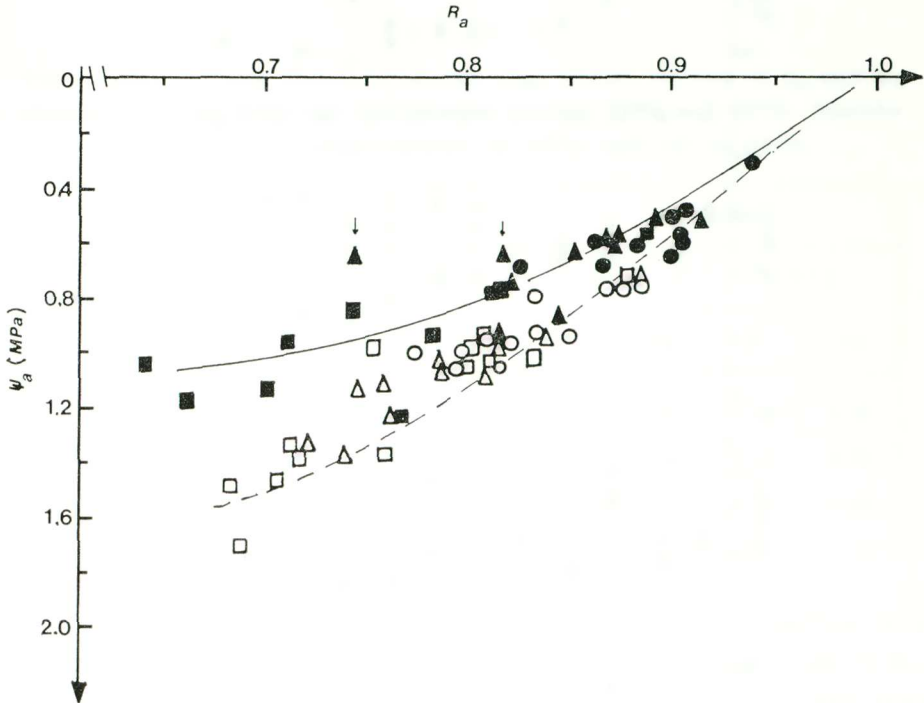


Fig 7. The sorption isotherms of field bean leaves during the two periods. Results from all three irrigation treatments. Symbols are the same as in fig. 4. The curves were fitted by eye. The arrows show the values in the M-treatment in 1974 immediately prior to the second irrigation.

the relationship between Ψ_a and R_a . More information about the nature of the course of Ψ_a can be obtained by examining the courses of its two component potentials.

The solute potential

The time course of ψ_s in both years is shown in fig. 8. The solute potential became progressively more negative with time in the drier treatments. Furthermore, the values of ψ_s were more negative in the

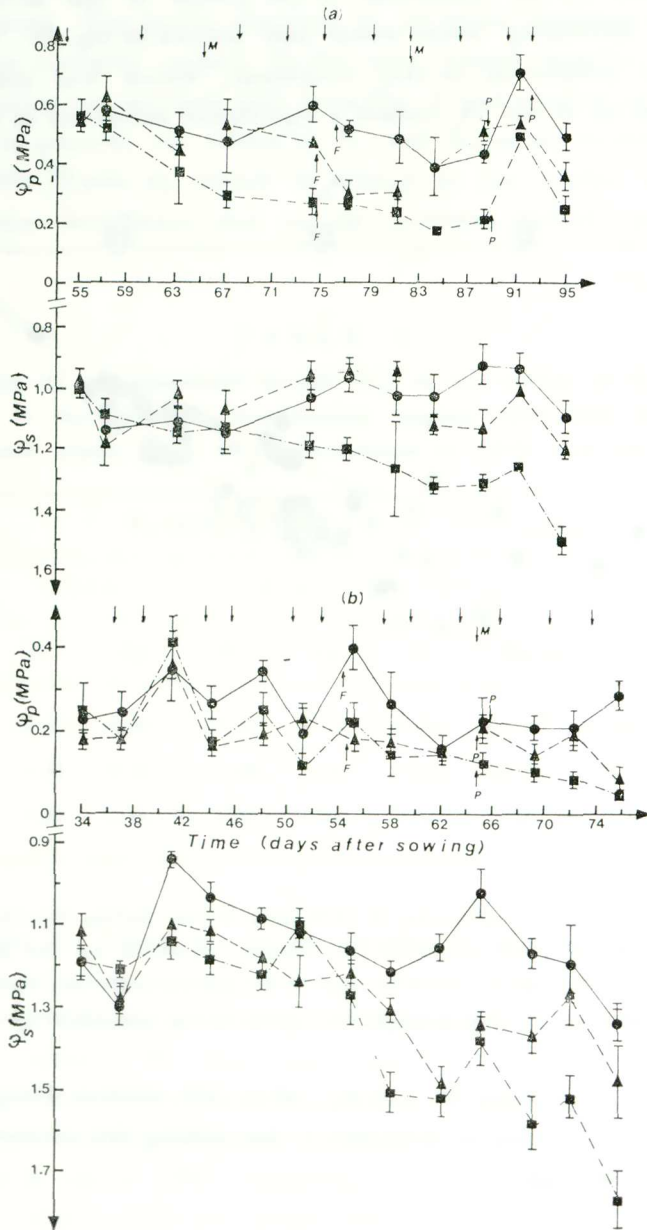


Fig. 8. The time course of pressure (ψ_p) and solute (ψ_s) potentials during the two periods. Each point is the mean of 12 determinations in 1974 and 16 in 1975. a) 1974, b) 1975. Symbols are the same as in fig. 2.

drier year for corresponding treatments (Table 5). It is worth noting that there was a lag in the response of ψ_s after irrigation in the M-treatments: ψ_s did not reach the values in the W-treatments immediately, but with a lag of two or three samplings after irrigation.

TABLE 5

The means (\bar{x}) and standard errors ($s_{\bar{x}}$) of the values of ψ_s and ψ_p observed in the different treatments during 1974 and 1975. Results taken from 11 observations in 1974 and 13 in 1975.

Treatments	ψ_s (MPa)				ψ_p (MPa)			
	1974		1975		1974		1975	
	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$
W	-1.07	0.02	-1.15	0.03	0.51	0.03	0.26	0.02
M	-1.06	0.03	-1.27	0.04	0.43	0.02	0.19	0.02
D	-1.22	0.04	-1.35	0.06	0.32	0.04	0.17	0.03

According to eq. (9), for a given water content, a reduction in ψ_s is possible by means of either a decline in ψ_{s_0} or/and in increase in R_0 . The time courses of ψ_{s_0} and R_0 in the different treatments and years are shown in figs 9 and 10. In both years, ψ_{s_0} differed significantly between the W- and D-treatments in the second half of the experiments. This difference was caused by a decrease in ψ_{s_0} with increasing dryness in the D-treatment. The rehydration of plants in the M-treatments shifted ψ_{s_0} towards less negative values. However, ψ_{s_0} did not respond immediately to irrigation. This is not surprising, given that the first and second samples after irrigations consisted of leaves grown under dry conditions. These leaves are expected to have developed some adaptive mechanisms. The decrease in ψ_{s_0} with increasing dryness can be further demonstrated when comparing the mean values of ψ_{s_0} of the corresponding treatments in the two periods: the values in the drier year were consistently lower (Table 6). A decrease in ψ_{s_0} under dry conditions has also been reported elsewhere (Warren Wilson 1967c; Kassam

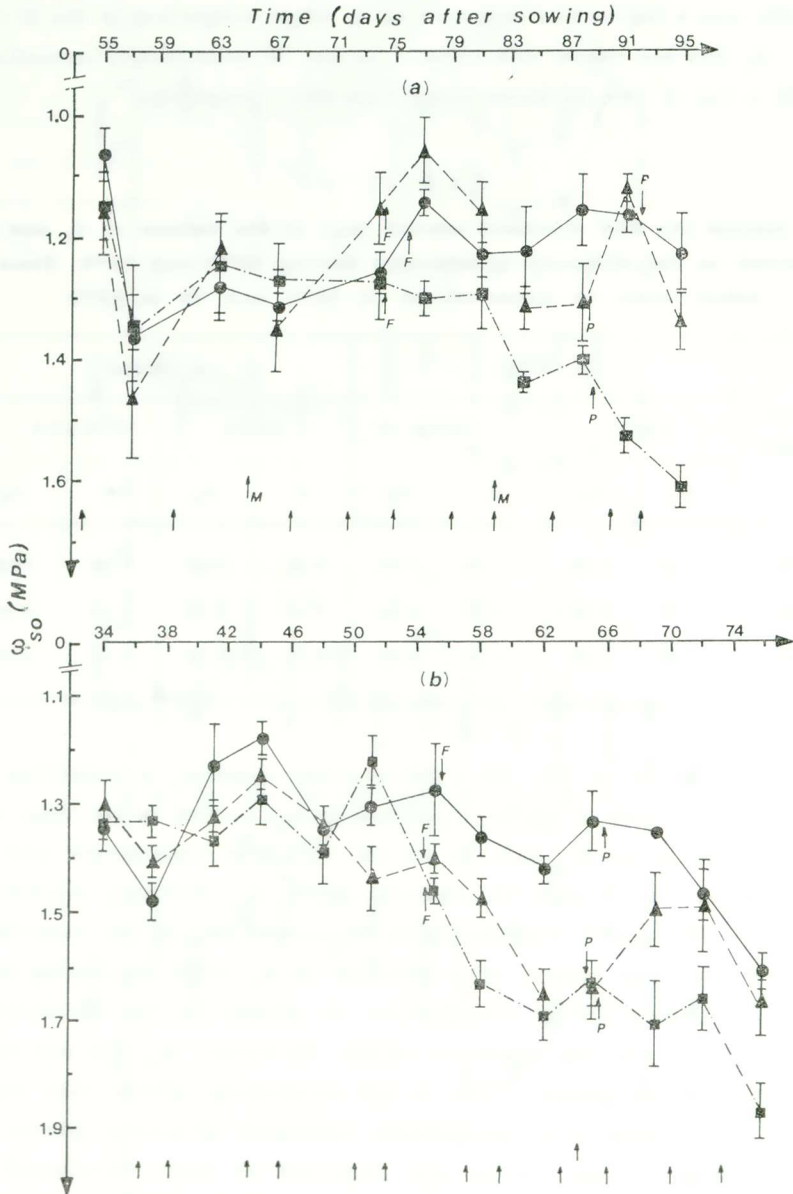


Fig. 9. The time course of the solute potential at zero turgor (ψ_{so}) during the two periods. Each point is the mean of 12 determinations in 1974 and 16 in 1975. a) 1974, b) 1975. Symbols are the same as in fig. 2.

& Elston 1974; Elston *et al.* 1976; Simmelsgaard 1976; Cutler & Rains 1977). This decrease in ψ_{so} was correlated with an increase in solute content inside the cells (Kassam & Elston 1976).

T A B L E 6

The means (\bar{x}) and standard errors ($s_{\bar{x}}$) of the values of ψ_{so} , R_o , and ϵ' observed in the different treatments during 1974 and 1975. Results taken from 11 observations in 1974 and 13 in 1975.

Treatments	ψ_{so} (MPa)				R_o				ϵ' (MPa)			
	1974		1975		1974		1975		1974		1975	
	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$
W	-1.22	0.03	-1.35	0.03	0.764	0.009	0.707	0.013	4.19	0.20	2.32	0.21
M	-1.24	0.04	-1.44	0.04	0.736	0.018	0.696	0.010	3.76	0.28	2.14	0.12
D	-1.35	0.04	-1.49	0.06	0.689	0.018	0.695	0.012	4.14	0.30	2.47	0.19

The pattern of R_o with time was quite distinct between the extreme treatments in 1974, the values for the D-treatment being significantly lower than those of the W during most of the season (fig. 10a). This did not happen in 1975, where the time courses of R_o in the different treatments were overlapping (fig. 10b, see also Table 6). In contrast with ψ_{so} , R_o was easily reversible. This can be seen in its immediate response to irrigation (see M-treatments in fig. 10) as well as in its independence from the increasing plant water stress (cf. D-treatments in fig. 5). The latter conflicts with the existing evidence that a lower R_o is associated with dry conditions (Noy-Meir & Ginzburg 1969). The course of R_o may be interpreted, if we consider the behaviour of its two components, i. e. ψ_{so} and ϵ' (see eq. (13)). A decrease in R_o can be achieved by means of either an increase in the solute content (more negative ψ_{so}) or an increase in cell wall elasticity (decrease in ϵ' , eq. (13)). When $1/R_o$ was correlated with ψ_{so} and ϵ' , it was found that cell wall elasticity mainly determined its behaviour in the wet year, while ψ_{so} was more efficient in the drier year (Table 7). Moreover, in a given period the correlation coefficients between $1/R_o$ and ϵ' decreased from the W- to

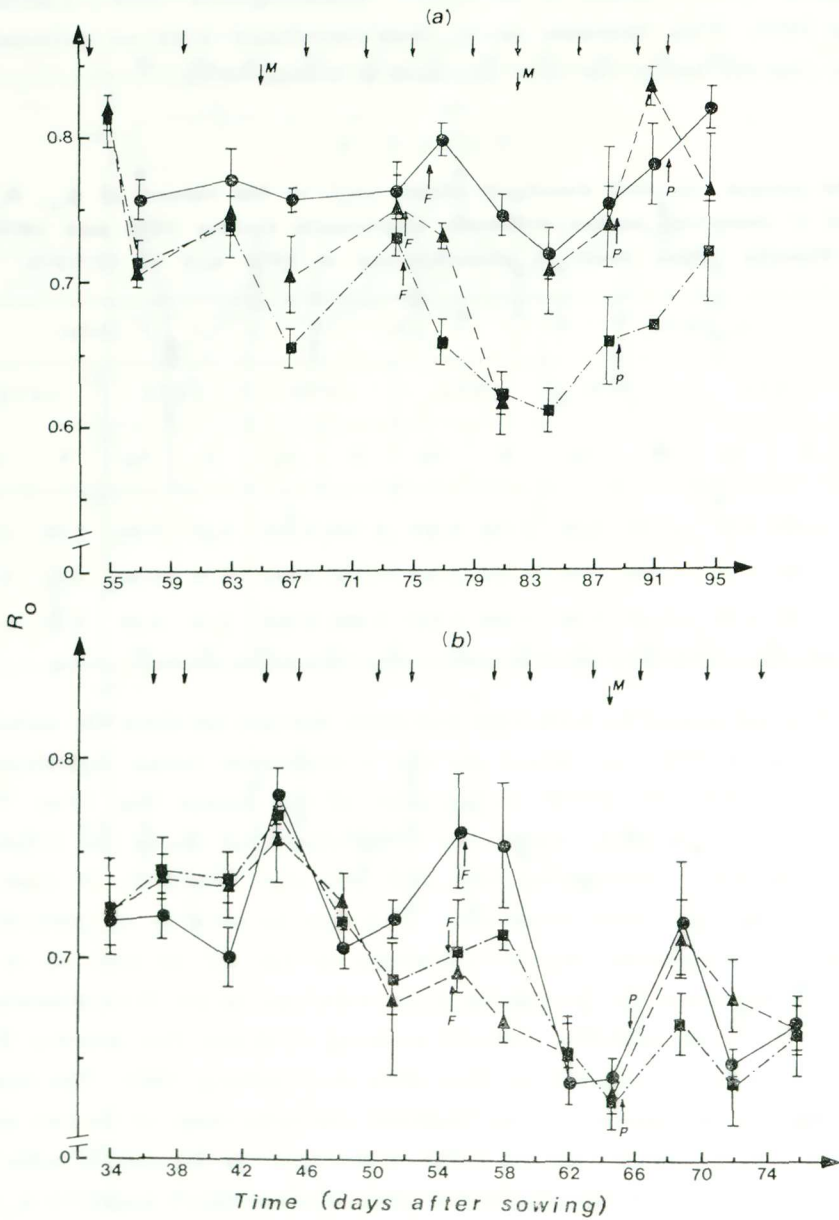


Fig. 10. The time course of the relative water content at zero turgor (R_0) during the two periods. Each point is the mean of 12 determinations in 1974 and 16 in 1975. a) 1974, b) 1975. Symbols are the same as in fig. 2.

the D-treatment, while the opposite was true for the coefficients between $1/R_o$ and ψ_{so} . It appears therefore that the magnitude of R_o is determined by ϵ' when water is abundant and by ψ_{so} under water stress conditions. Thus, ϵ' is responsible for the differences in the behaviour of R_o to water stress as well as for its partial dependence on short-term environmental fluctuations (see below).

T A B L E 7

The linear correlation coefficients between $1/R_o$ against ψ_{so} and $1/R_o$ against ϵ' in the different treatments and years. The level of significance of each coefficient is also shown. * : $p < 0.05$, ** : $p < 0.01$, *** : $p < 0.001$, ns : nonsignificant.

Treatments	1 9 7 4		1 9 7 5	
	$1/R_o$ v. ψ_{so}	$1/R_o$ v. ϵ'	$1/R_o$ v. ψ_{so}	$1/R_o$ v. ϵ'
W	-0.22 (ns)	-0.95 (***)	-0.54 (*)	-0.81 (***)
M	-0.20 (ns)	-0.86 (***)	-0.85 (***)	-0.42 (ns)
D	-0.33 (ns)	-0.61 (*)	-0.73 (**)	-0.56 (*)
All treatments	-0.13 (ns)	-0.54 (**)	-0.68 (**)	-0.63 (**)

In conclusion, it is evident that the drop in ψ_s with increasing dryness did not result from a simple dehydration of the cells. The plants developed mechanisms which increased the osmotic value of the cell sap, thus extending the possibilities of the tissue to absorb water. This reduction in ψ_s was brought about mainly by an accumulation of solutes inside the cells, as the continuous decline of ψ_{so} suggests. Another possible mechanism of decreasing ψ_s , namely by an increase in R_o , was found not to work here. The dependence of ψ_s mainly on ψ_{so} can be further visualized in a multiple linear regression of ψ_s on both ψ_{so} and R_o : the partial correlation coefficients (Snedecor 1956) were 0.86 (1974) and 0.96 (1975) for ψ_s against ψ_{so} and only 0.13 (1974) and -0.66 (1975) for ψ_s against R_o . The accumulation of solutes was clearly an adaptive mechanism, since it required some time to develop and was not easily reversible.

The pressure potential.

The time course of ψ_p in the two years is shown in fig. 8. The values of ψ_p were lower in the D-treatment in 1974 for the greatest part of the season. It was more difficult to distinguish the values of ψ_p in the two extreme treatments on many sampling occasions in 1975 (see also Table 5). It appears that the high evaporative demands in 1975 exceeded the ability of plants for water absorption from soil, even in the W-treatment, and therefore suppressed cell turgor to very low levels. In contrast with ψ_s , ψ_p responded readily to irrigation in both years.

ψ_p depends on both ϵ' and R_o (eq. (10)). The time course of ϵ' in the two years is shown in fig. 11. In 1974 the course of ϵ' resembled to that of R_o : ϵ' was smaller in the D-treatment for most of the period, sensitive to short-term environmental fluctuations, and readily reversible on the release of stress. On the other hand, the time course of ϵ' in 1975 was confusing: in no case did the values of ϵ' differ significantly between treatments. This suggests that soil water stress had little or no effect on ϵ' in the drier year and therefore ϵ' responded only to factors of the aerial environment (Karamanos 1976).

We conclude that when plant tissues are not seriously water-stressed (as for example in 1974), they tend to decrease ϵ' with increasing drought. In this way, cells tend to maintain turgor as much as possible above zero for a given water loss. At the same time, this decrease in ϵ' entails a decrease in R_o which depends strongly on ϵ' . This behaviour of the cell walls is easily reversible on the removal of stress. Conversely, such a differentiation in elasticity was not observed among treatments in the drier year. Nevertheless, the fact that ϵ' was significantly lower in the corresponding treatments in 1975 (Table 6) suggests that the lowest limit of ϵ' was reached in that year even in the W-treatment. The cause of these fluctuations of cell wall elasticity is a matter of speculation. A possible explanation may lie in the dependence of the modulus of elasticity, and hence of ϵ' , on cell volume (Zimmermann, Steudle & Lelkes 1976). However, the great day-to-day variation of ϵ' does not correspond to the pattern of R_a (figs 6 and 11).

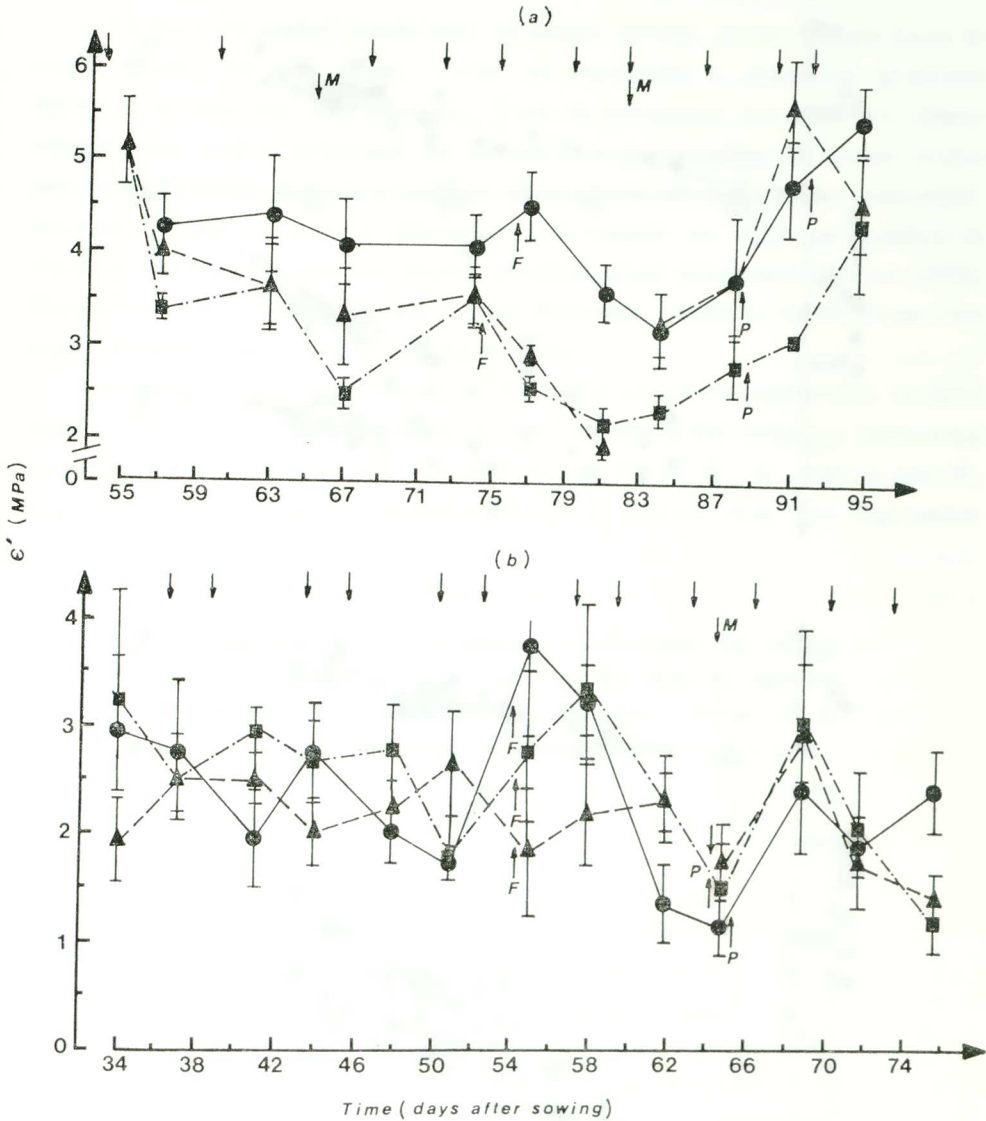


Fig. 11. The time course of the slope of the linear relation between ψ_p and $R_a(\epsilon')$. Each point is the mean of 12 determinations in 1974 and 16 in 1975. a) 1974, b) 1975. Symbols are the same as in fig. 2.

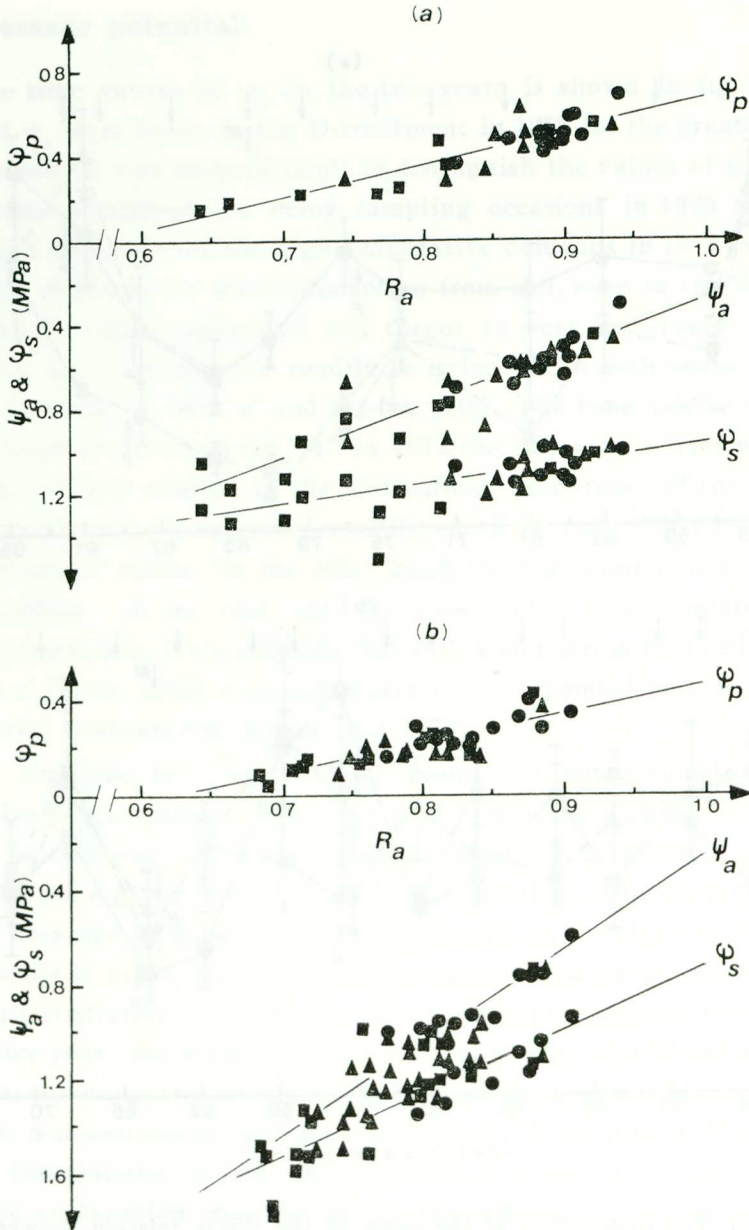


Fig. 12. The relations between R_a and ψ_a , ψ_p , and ψ_s in the two periods. Symbols are the same as in fig. 4. The lines represent the fitted linear regressions to the results (see also Table 8). a) 1974, b) 1975.

CONCLUSIONS

To survive under conditions of water stress, plant tissues have to react mainly in two ways. First, to maintain a potential gradient between themselves and the soil. This is necessary to conserve tissue rehydration and is achieved by means of a suppression of tissue water potential to more negative values than those of soil water potential. Secondly, tissues have to maintain cell turgor as high as possible in view of its significance for many physiological processes (Hsiao 1973). Plants from different habitats invent different ways to fulfil these two contradicting conditions at the same time.

Osmoregulation appears to be the main adaptive mechanism in field beans. This can be first realized, if one compares the sorption isotherms from the two years and fits linear regressions of Ψ_a , ψ_s , and ψ_p on R_a (fig. 12). The regression analysis (Table 8) shows that the regression

TABLE 8

Comparison of the regression coefficients (β) of the linear regressions of ψ_p against R_a and ψ_s against R_a in the two seasons. $s_{\bar{x}}$: standard error of β , n : number of observations.

	ψ_p v. R_a			ψ_s v. R_a		
	β	$s_{\bar{x}}$	n	β	$s_{\bar{x}}$	n
1974	15.24	1.45	32	9.51	2.27	32
1975	12.45	1.34	39	26.33	2.66	39
t-test	1.0 (ns)			3.41 ($p < 0.001$)		

coefficient of ψ_s against R_a was significantly higher in the drier year, which implies that ψ_s decreased more sharply for a given water loss in 1975. At the same time, the decrease in ψ_p was virtually the same in both years. As a result, the decrease in Ψ_a , which was indispensable to conserve water flow under the increased evaporative demand in 1975,

was attained exclusively by means of the reduction in ψ_s . On the other hand, ψ_p showed great day-to-day variations as a response to the evaporative demand when soil water was abundant.

The use of the proposed model conveyed more information about the origin of these responses of ψ_s and ψ_p by interpreting the behaviour of some physical and chemical tissue characteristics under water stress. Thus, the existing evidence of an osmoregulatory mechanism was reinforced by the systematic depression of ψ_{so} in the D-treatments in both years. Such a depression required some time to develop and was neither easily reversible nor strongly dependent on environmental fluctuations. On the other hand, ϵ' , another important parameter associated with cell turgor, was more sensitive to the daily evaporative demand. ϵ' was unaffected by increasing soil dryness in the drier year. In the wet year, ϵ' showed a non-consistent decrease with increasing water stress which was cancelled after rewatering. The absence of adaptive responses in the thin cell walls of field beans is in contrast with the behaviour of some species growing in dry habitats. There, the walls become thicker and more rigid (less elastic) with increasing dryness (Carr & Gaff 1962; Warren Wilson 1967 c; Noy-Meir & Ginzburg 1969). This is indicative of the variety of the drought tolerance mechanisms which can be developed by different plant species.

Π Ε Ρ Ι Λ Η Ψ Η

Ἡ ἀνεπάρκεια νεροῦ εἶναι ἕνας παράγοντας περιοριστικὸς τῆς γεωργικῆς παραγωγῆς τόσο σὲ μεσογειακὰ καὶ ξηροθερμικὰ ὅσο καὶ σὲ περισσότερο εὐκρατα κλίματα. Ἀπὸ τοὺς διαφόρους μηχανισμοὺς προσαρμογῆς ποὺ ἀναπτύσσουν τὰ φυτὰ ὑπὸ συνθῆκες ὑδατικῆς καταπονήσεως, ἰδιαίτερο ἐνδιαφέρον παρουσιάζουν οἱ λεγόμενοι «μηχανισμοὶ ἀντοχῆς στὴν ἀφυδάτωση». Οἱ μηχανισμοὶ αὐτοὶ ἀναφέρονται στὶς προσαρμογές τῶν φυσικῶν καὶ χημικῶν ἰδιοτήτων καὶ λειτουργιῶν τοῦ φυτικοῦ κυττάρου σὲ συνθῆκες ἀνεπαρκείας νεροῦ· ἐπὶ πλέον εἶναι πῶς χρήσιμοι ἀπὸ τὴν ἐλάττωσι τοῦ ἀνοίγματος τῶν στομάτων, ἐνὸς κοινοῦ σὲ ὅλα τὰ φυτὰ μηχανισμοῦ ἀποφυγῆς τῆς ἀφυδατώσεως, ὃ ὁποῖος ὅμως ταυτόχρονα διακόπτει καὶ τὴ φωτοσύνθεση.

Γιὰ τὴν πληρέστερη κατανόηση τῶν μηχανισμῶν ἀντοχῆς προτείνεται ἡ χρησιμοποίηση ἐνὸς μαθηματικοῦ προτύπου (model), τὸ ὁποῖο περιλαμβάνει παρα-

μέτρους τῶν φυσικοχημικῶν ιδιοτήτων τῶν κυττάρων. Ἀρχικὰ γίνεται μιὰ θεωρητικὴ ἀνάλυση τοῦ προτύπου τὸ ὁποῖο εἶναι ἀνάλογο μὲ ἐκεῖνο τῶν Elston *et al.* (1976). Στὸ πρότυπο ὑπάρχουν δύο μεταβλητὲς τῆς ὑδατικῆς καταστάσεως τοῦ ἴστοῦ, τὸ ὑδατικὸ δυναμικὸ (Ψ) καὶ ἡ σχετικὴ ὑδατοπεριεκτικότητα (R). Τὸ Ψ εἶναι ἡ θερμοδυναμικὴ ἔκφραση τῆς ὑδατικῆς καταστάσεως καὶ θεωρεῖται ὅτι ἀποτελεῖται κυρίως ἀπὸ δύο συστατικὰ δυναμικά, τὸ ὠσμωτικὸ (ψ_s) καὶ τὸ δυναμικὸ πίεσεως (ψ_p) τὸ ὁποῖο εἶναι ἀνάλογο μὲ τὴν πίεση σπαργῆς. Τὸ R εἶναι ἡ ἑκατοστιαία περιεκτικότητα τοῦ ἴστοῦ σὲ νερὸ μὲ ἐπίπεδο ἀναφορᾶς τὴν ὑδατοπεριεκτικότητα σὲ πλήρη σπαργή. Τὸ πρότυπο συσχετίζει τὰ Ψ καὶ R μὲ τὴν ἀκόλουθη ἑξίσωση :

$$\Psi = \frac{\psi_{so} \cdot R_o}{R} + \varepsilon' \cdot (R - R_o) \quad (1)$$

ὅπου ψ_{so} εἶναι τὸ ὠσμωτικὸ δυναμικὸ τοῦ ἴστοῦ, ὅταν ἡ σπαργὴ του μηδενίζεται (ἀρχομένη πλασμόλυση), R_o ἡ σχετικὴ ὑδατοπεριεκτικότητα σὲ ἀρχομένη πλασμόλυση καὶ ε' ἡ κλίση τῆς γραμμῆς παλινδρομήσεως μεταξὺ τῶν ψ_p καὶ R . Ὁ πρῶτος ὅρος τοῦ δευτέρου μέλους ἐκφράζει τὸ ψ_s , ἐνῶ ὁ δεύτερος τὸ ψ_p . Τὸ πρότυπο αὐτὸ ἰσχύει γιὰ ἴστους πὺν ἀποτελοῦνται ἀπὸ ὄριμα παρεγχυματικὰ κύτταρα (ὅπως π. χ. τὰ κύτταρα τοῦ μεσοφύλλου), ἢ συμπεριφορὰ τῶν ὁποίων εἶναι παραπλήσια μὲ ἐκεῖνη ἑνὸς ὠσμωμέτρου. Ἡ διαμόρφωση τῆς ἑξ. (1) βασίσθηκε σὲ δύο κυρίως προϋποθέσεις: (1) ὅτι ὁ κυτταρικὸς χυμὸς ἀκολουθεῖ τοὺς νόμους τῶν τελείων ἀερίων καὶ ἐπομένως καὶ τὸν νόμο τοῦ van't Hoff, καὶ (2) ὅτι τὸ κυτταρικὸ τοίχωμα ἔχει ἔλαστικὲς ιδιότητες καὶ ἐπομένως ἡ σχέση μεταξὺ ψ_p καὶ R εἶναι γραμμική.

Μὲ βάση τὸ πρότυπο αὐτὸ ἔγινε μιὰ ἀνάλυση τῶν ὑδατικῶν σχέσεων μιᾶς καλλιιεργείας κυάμων. Τὰ δεδομένα προέρχονται ἀπὸ πειράματα πὺν πραγματοποιήθηκαν στὸν πειραματικὸ ἀγρὸ τοῦ Πανεπιστημίου τοῦ Reading κατὰ τὸ 1974 καὶ 1975. Ὑπῆρχαν τρία διαφορετικὰ ἐπίπεδα ἑδαφικῆς ὑγρασίας, τὰ ὁποῖα δημιουργήθηκαν μὲ διαφορετικὲς συχνότητες ἀρδεύσεων. Στὴν ὑγρὴ (W) μεταχείριση τὰ πειραματικὰ τεμάχια ἀρδεύθηκαν συνολικὰ 10 φορὲς τὸ 1974 καὶ 12 φορὲς τὸ 1975 σὲ ἓνα διάστημα 40 ἡμερῶν. Στὸ ἴδιο χρονικὸ διάστημα ἡ ἐνδιάμεση μεταχείριση (M) ἀρδεύθηκε δύο φορὲς τὸ 1974 καὶ μόνο μιὰ φορὰ τὸ 1975. Ἡ ξηρὴ μεταχείριση (D) ἔμεινε ἀπότιστη καὶ στὶς δύο περιόδους. Ἡ κάλυψη τῶν τεμαχίων μὲ ὑπόστεγα ἀπὸ διαφανὲς πλαστικὸ παρεμπόδιζε τὴν εἴσοδο τῆς βροχῆς καὶ ἐξασφάλισε τὸν ἔλεγχο τῆς ἑδαφικῆς ὑγρασίας. Τὰ Ψ , R καὶ ψ_{so} προσδιορίστηκαν σὲ δείγματα ὠρίμων φύλλων πὺν λαμβάνονταν δύο φορὲς τὴν ΠΑΑ 1978

έβδομάδα κατά τις πρώτες απογευματινές ώρες. Τα R_0 , ψ_s , και ψ_p προσδιορίστηκαν με υπολογισμούς.

Και στα δύο χρόνια παρατηρήθηκε μία αναμενόμενη πτώση του Ψ στις μεταχειρίσεις D συγκριτικά με τις τιμές στις W. Η πτώση αυτή ήταν περισσότερο έντονη στη ξηρότερη περίοδο (1975). Έξετάζοντας την πορεία των παραμέτρων της ξξ, (1) βρέθηκε ότι το ψ_{s0} παρουσίαζε πιδ αρνητικές τιμές στις μεταχειρίσεις D. Η πτώση αυτή του ψ_{s0} με αυξανόμενη ύδατική καταπόνηση ήταν βαθμιαία και παρουσιαζόταν πιδ έντονη πρὸς τὸ τέλος τῶν δύο περιόδων. Ἐπιπλέον, τὸ ψ_{s0} δὲν ἐπανερχόταν στὰ ἐπίπεδα τοῦ W ἀμέσως μετὰ ἀπὸ ἄρδευση. Ἡ συμπεριφορὰ τοῦ ψ_{s0} ὑποδηλώνει τὴν ὕπαρξη ἑνὸς προσαρμοστικοῦ μηχανισμοῦ, ὁ ὁποῖος σχετίζεται ἄμεσα με ὠσμωρρυθμιστικὲς διεργασίες μέσα στὸ κύτταρο. Ἡ δυνατότητα τοῦ φυτικοῦ αὐτοῦ εἴδους νὰ προσαρμόζη τὴν ὠσμωτικὴ τιμὴ τοῦ κυτταρικοῦ του χυμοῦ σὲ διαφόρους βαθμοὺς ὕδατικῆς καταπονήσεως φαίνεται καὶ με τὴ σύγκριση τῶν συστατικῶν δυναμικῶν κατὰ τὶς δύο περιόδους: σὲ μία δεδομένη ὕδατοπεριεκτικότητα τὸ ψ_s , ὅπως καὶ τὸ ψ_{s0} , ἦταν συστηματικὰ πιδ ἀρνητικὸ κατὰ τὴν ξηρότερη περίοδο στις ἀντίστοιχες μεταχειρίσεις.

Ἡ παράμετρος ϵ' ἢ ὁποία σχετίζεται με τὴν ἐλαστικότητα τοῦ κυτταρικοῦ τοιχώματος δὲν ἀκολουθοῦσε πορεία ἀνάλογη με ἐκείνη τοῦ ψ_{s0} . Τὸ ϵ' ἦταν πιδ εὐαίσθητο στις ἡμερήσιες μεταβλητὲς τοῦ περιβάλλοντος καὶ λιγώτερο στὴν ἔλλειψη ἑδαφικῆς ὕγρασίας. Μία ἐλάττωση τοῦ ϵ' (αὔξηση τῆς ἐλαστικότητας) πὸν παρατηρήθηκε στὴ μεταχείριση M κατὰ τὴν ὕγρη περίοδο ἦταν εὐκόλα ἀντιστρεπτὴ μετὰ ἀπὸ ἄρδευση.

Τέλος, ἡ παράμετρος R_0 , ἢ ὁποία ἐκφράζει τὸ βαθμὸ ἀφυδατώσεως πὸν ἀπαιτεῖται γιὰ νὰ μηδενισθῇ ἡ σπαργή, εἶναι συνάρτηση τῆς ἀλληλεπιδράσεως τῶν δύο ἄλλων παραμέτρων. Γενικὰ τὸ R_0 ἐπηρεάζεται περισσότερο ἀπὸ τὸ ϵ' καὶ ἔτσι εἶναι περισσότερο εὐαίσθητο στις μεταβολὲς τοῦ ἑναερίου περιβάλλοντος καὶ λιγώτερο στὴν ἔλλειψη ἑδαφικῆς ὕγρασίας.

Συμπερασματικά, φαίνεται ὅτι στὸ μεσοφυτικὸ αὐτὸ εἶδος οἱ μεταβολὲς τοῦ ὕδατικοῦ δυναμικοῦ τῶν φύλλων μποροῦν νὰ διακριθοῦν σὲ δύο κατηγορίες: 1) σὲ παθητικὲς μεταβολὲς οἱ ὁποῖες εἶναι ἀποτέλεσμα τῆς ἐπιδράσεως μεταβλητῶν τοῦ ἑναερίου περιβάλλοντος, ὅπως τῆς ἡλιακῆς ἀκτινοβολίας καὶ τοῦ ἔλλειμματος κορεσμοῦ, καὶ 2) σὲ ἐνεργητικὲς μεταβολὲς οἱ ὁποῖες εἶναι συνάρτηση τῆς ἑδαφικῆς ὕγρασίας. Οἱ παθητικὲς εἶναι ἐντονώτερες σὲ συνθῆκες ἐπαρκειᾶς ἑδαφικοῦ νεροῦ καὶ πραγματοποιοῦνται βασικὰ με μεταβολὲς τῆς κυτταρικῆς σπαργῆς, δηλ. με μεταβολὲς τοῦ ϵ' , οἱ ὁποῖες εἶναι ἀντιστρεπτές. Οἱ ἐνεργητικὲς

πτώση αυτή έχει μεγάλη σημασία μία πτώση του Ψ κυρίως ως ανάγκη για τη διατήρηση της διαφορᾶς δυναμικοῦ τοῦ φυτοῦ μετὰ τὸ ἔδαφος. Αὐτὴ ἡ ταπείνωση τοῦ Ψ πραγματοποιεῖται μετὰ τὴν ὁσμωρῦθμιση, μία διεργασία προσαρμολογῆς δύσκολα ἀντιστρεπτή, ποὺ ἐπιτυγχάνει τὴν ταπείνωση τοῦ ὁσμωτικοῦ δυναμικοῦ. Στὶς ἐνεργητικὰς μεταβολὰς τὸ ψ_p συμμετέχει ἐλάχιστα καὶ ἔτσι διατηρεῖται σὲ ἐπίπεδα ποὺ ἐπιτρέπουν τὴ συνέχιση τῶν φυσιολογικῶν διεργασιῶν τοῦ κυττάρου. Καὶ τὰ δύο εἶδη τῶν μεταβολῶν ἐπιφέρουν μία μικρὴ πτώση τοῦ R_o , ἡ ὁποία ἀξιάνει τὴν δυνατότητα τοῦ ἴστοῦ νὰ ἐπιζήση καὶ σὲ συνθηκὰς ἐντονότερης ἀφυδατώσεως.

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