Will Increases in Our Understanding of Soil-Root Relations and Root Signalling Substantially Alter Water Flux Models?

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Will increases in our understanding of soil–root relations and root signalling substantially alter water flux models?

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SUMMARY

Three models combining water transport and stomatal control are compared with experimental data to test whether, and how, water flux models that take into account root signalling or more accurate calculations of root water status would differ from current models. Models under study involve stomatal control by either the leaf water status alone, or a root message alone, or an interaction between both mechanisms. They are combined with a model allowing accurate calculation of the root water status in the case when roots are not regularly disposed. The model involving leaf water status alone provides relatively realistic predictions of water relations, but only on a day-to-day timescale and for relatively constant environmental conditions. The model based on root messages alone also needs adjustments, as it does not allow control of leaf water status during a drying period. The model involving interaction provides simulations which are reasonably consistent with experimental data, and applies to a range of environmental conditions without the necessity of adjusting its parameters for each condition. Effects of rooting characteristics, such as those caused by soil compaction, on stomatal conductance and root messages can only be predicted if a direct calculation of root water potential is carried out, therefore avoiding the hypotheses which are implicit in Gardner's classical calculation.

1. INTRODUCTION

Water flux through the plant can be controlled reversibly by stomatal conductance on short timescales, and irreversibly by growth and senescence of leaves and roots on longer timescales. Several models have been designed to simulate these controlling processes in response to water deficits. 'Microscopic' models describe accurately a physiological process or water transport in part of the soil–plant–atmosphere continuum, but are often too complex and have too many parameters to be integrated into whole-plant models. On the other hand, 'macroscopic' models (e.g. Nimah & Hanks 1973; Hillel *et al.* 1976) simulate the plant behaviour by using semi-empirical functions which predict water extraction in each soil layer (e.g. Moltz 1981), water flux and evaporative demand, but there is an increasing gap between these semi-empirical functions and current knowledge on plant behaviour during water deficits. This gap is particularly remarkable in two topics:

1. Current models generally use the leaf water potential (ψl) as a controlling variable for predicting stomatal conductance and leaf growth. However, it has been known for many years (Berger-Landefelt 1936; Stocker 1956) that several 'isohydric' species reduce stomatal conductance as soil dries, in such a way that the leaf water status is unaffected by drought. 'Isohydric' behaviour has since been described in more detail for several species (Bates & Hall 1981; Tardieu *et al.* 1992*b*). In the last decade, a theory has been developed to explain such behaviour, where stomatal conductance and leaf growth are controlled by a chemical message originating in dehydrating roots, and conveyed by the water flux (Gowing *et al.*, this volume). A key question is how far this theory will invalidate current macroscopic models of water flux.
2. In macroscopic models, soil water status is characterized by the soil water reserve or the average soil water potentials of soil layers, while the plant senses the local water potential at the soil–root interface. If root messages have a role in the control of stomatal conductance and tissue expansion, accurate calculations of the root water potential could be crucial for modelling the soil–plant–atmosphere water transfer.

The objectives of this article are: (i) to test whether, and how, current models differ from models that take into account root signalling or more accurate calculations of root water status; (ii) to investigate whether models involving stomatal control by a root message also predict realistic control of leaf water potential or of the message itself; and (iii) to predict which could

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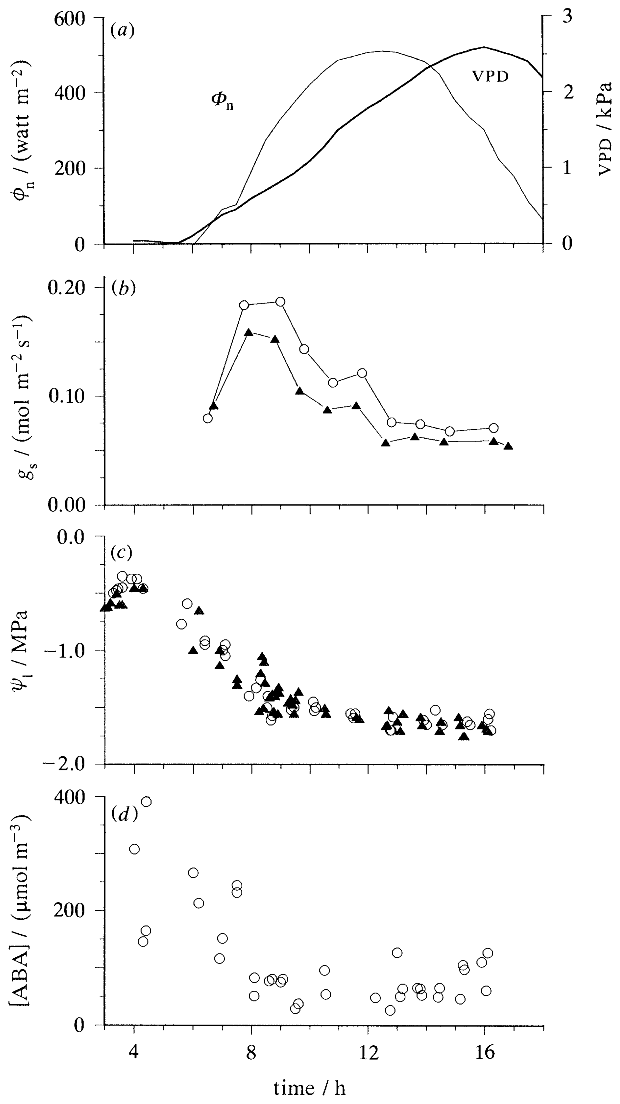

Figure 1. Changes with time of the day in (*a*) net radiation (ϕ_n) and air vapour pressure difference (VPD), (*b*) stomatal conductance (g_s), (*c*) leaf water potential (ψ_l) and (*d*) xylem [ABA] in a maize field with moderately dry soil. Open circles, non-compacted soil; filled triangles, compacted soil. Redrawn from Tardieu & Davies (1992).

be the effects of changing the geometric characteristics of the root system or the ability of roots to synthesize the message.

2. WOULD STOMATAL CONTROL BY ROOT MESSAGES DIFFER SUBSTANTIALLY FROM CONTROL BY LEAF WATER STATUS?

Controversy about the importance of root messages in stomatal control (e.g. Kramer 1988; Passioura 1988) has been resolved, to some extent, since a series of experimental studies now clearly suggest an important role for root messages (Gollan *et al.* 1986; Munns & King 1988; Davies & Zhang 1991). This message is probably abscisic acid (ABA) as under many circumstances there is no necessity to invoke another message (Gowing *et al.*, this volume). Two substantial investigations also suggest strong stomatal control by root-sourced ABA under field conditions (Wartinger *et al.* 1992*a*,*b*).

Nevertheless, we have considered unlikely a stomatal control based on chemical signalling alone (Tardieu & Davies 1993). The determination of xylem [ABA] and the stomatal response to xylem [ABA] must involve the water flux through the plant for the following reasons: (a) if the production of a chemical message depends on the root water status (ψ_r), it will not depend solely on the soil water potential (ψ_s) but also on the water flux through the soil–plant–atmosphere continuum, to which is linked the difference between ψ_r and ψ_s (equation 2); (b) the water flux conveys the message from the roots to the leaves, but also dilutes it in such a way that the concentration of the message should be related to the reciprocal of the water flux; and (c) stomatal sensitivity to the message is increased as leaf water potential falls (Tardieu & Davies 1992; Tardieu *et al.* 1993).

We have, therefore, compared three models of stomatal control involving: (i) a control of stomatal conductance by leaf water status alone ('purely physical' system); (ii) a control by a root message alone ('purely chemical' system); and (iii) a control involving an interaction between both variables ('interaction' system), which was the most likely from our experimental data. Outputs of these models have been compared with experimental data obtained with field-grown maize (Tardieu *et al.* 1992*a*,*b*) either on compacted or on non-compacted soil. Experimental data are presented for a sunny summer day (figure 1), with a relatively dry soil (predawn $\psi_l = -0.49$ MPa), and for a drying period of 20 days (figure 2). One feature of these data is the tight control of leaf water potential (ψ_l) which was almost constant throughout the period. Partial stomatal closure occurred every afternoon, earlier in the day in the compacted treatment despite higher soil moisture. At a given time of the day, stomatal conductance was in good relationship with xylem [ABA]. Change with time of the relationship between g_s and xylem [ABA] could be accounted for by changes in ψ_l ('interaction'). Xylem [ABA] was stable during the day after a decline in the early morning and its daytime values increased with declining soil water reserves for the drying period, with higher values in the compacted treatment.

(*a*) *Control of stomatal conductance by ψ_l alone: 'purely physical' system*

In this system, stomatal conductance (g_s) is a function of light intensity (figure 3*a*) and leaf water potential (figure 3*b*), with a steep decrease in g_s at a threshold leaf water potential (Hsiao 1973), called ψ_l^t hereafter. Evaporative demand is calculated by using the Penman–Monteith equation applied to a one-layer canopy:

$$J_w = \frac{s\,(\phi_n + G) + \rho_a\, c_p\, s(T_a - T_d)\, g_a}{\lambda\,[s + (\gamma\, g_a/g_s)]}, \qquad (1)$$

with J_w (Kg m^{-2} s^{-1}), water flux; T_a and T_d, air and dew point temperatures (°K); g_a and g_s, boundary layer and stomatal conductances (m s^{-1}); ϕ_n, net

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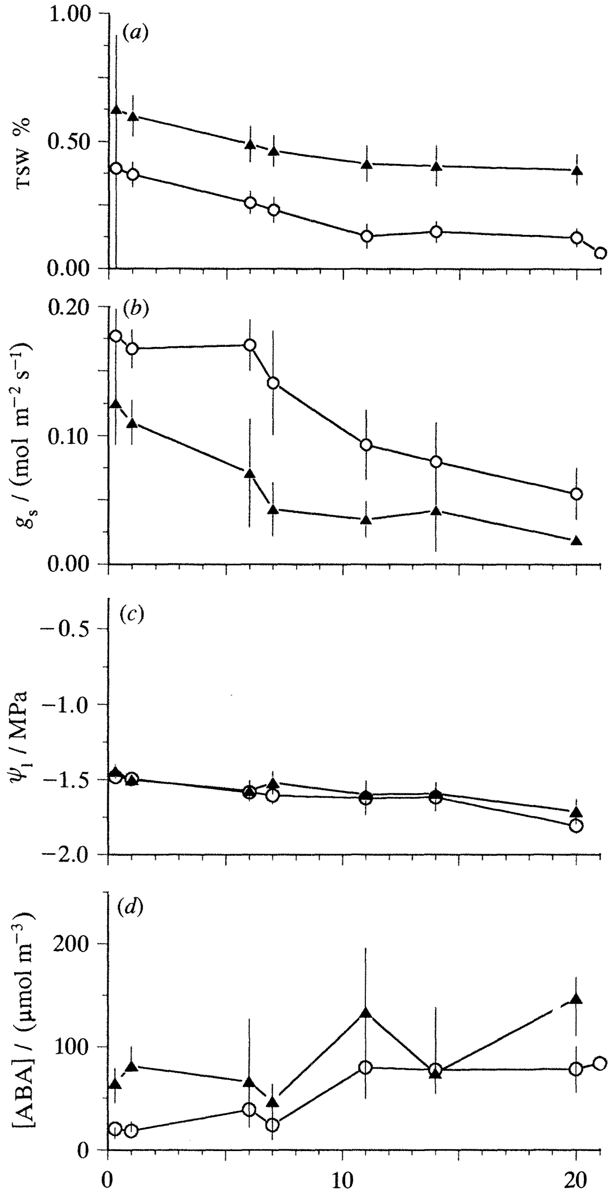

Figure 2. Changes with time of (*a*) transpirable soil water (TSW, % of total soil reserve), (*b*) stomatal conductance (g_s), (*c*) leaf water potential (ψ_l) and (*d*) xylem [ABA] in a maize field during a drying period. Symbols as in figure 1. Redrawn from Tardieu *et al.* (1992*a*,*b*).

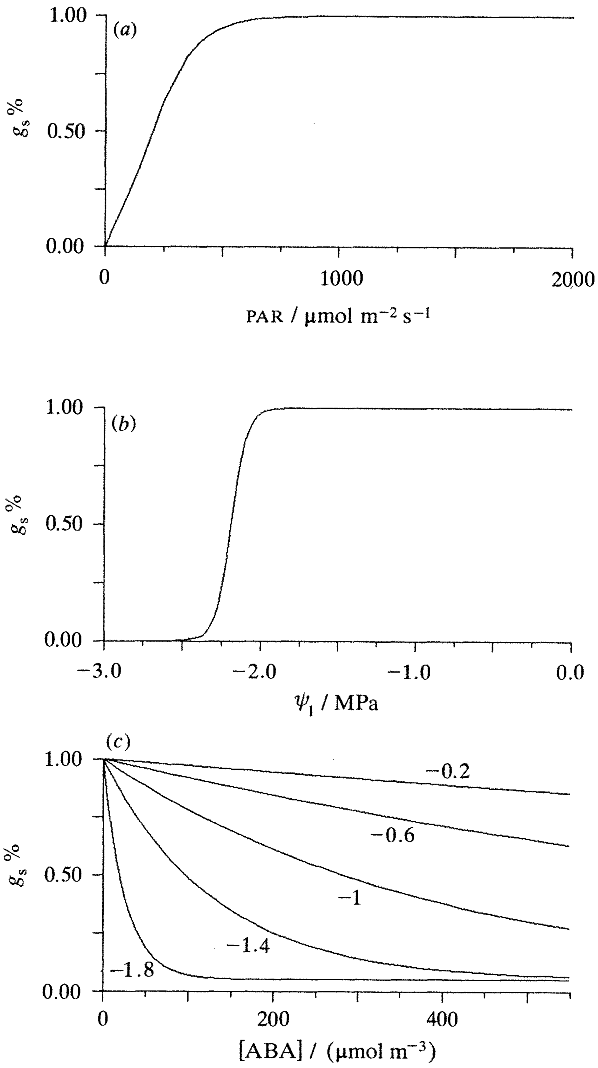

Figure 3. Models of stomatal control in simulations. (*a*) Response to light (PAR); (*b*) response of stomatal conductance (g_s) to leaf water potential (ψ_l) in the 'purely physical' model; (*c*) response of g_s to xylem [ABA] and ψ_l in the 'interaction' model.

radiation; *s*, slope of the curve relating saturation vapour pressure to temperature; G, soil heat storage; γ, psychrometric constant; λ , latent heat of vaporization; ρ_a, density of dry air; c_p, specific heat capacity of air.

Water flux and water stati in root and leaves are calculated from the Van den Honert (1948) equations.

$$-J_w = (\psi_r - \psi_s)/R_{sp}, \tag{2}$$

$$-J_w = (\psi_l - \psi_r)/R_p, \tag{3}$$

where R_p (Pa m^2 s Kg^{-1}) is the resistance to water flow in the plant, considered as independent from the water flux (Passioura 1984; Simonneau 1992). R_{sp} is the resistance in the soil, calculated using Newman's (1969) classical approach:

$$R_{sp} = \frac{1}{4\,\pi\,K(\theta)\,L_a}\ln(d^2/r^2), \tag{4}$$

where *d* (m) is half the mean distance between neighbouring roots, *r* (m) the mean radius of roots, $K(\theta)$ the soil hydraulic conductivity (Kg m^{-1} s^{-1} Pa^{-1}) at the mean soil water content and L_a (m^{-1}) is the root length per unit area.

Input variables of this first system are the soil water potential and the evaporative demand. Parameters are soil hydraulic properties and root properties, classical parameters of the Penman–Monteith equation and ψ_l^t. In order to allow comparison with the other two models, it has been supposed that the root system synthesizes a message (equation 5), which has no controlling effect on stomata.

(*b*) *Models involving a root message: 'purely chemical' and 'interaction' systems*

Equations of water transfer (1–4) apply in these models, but stomatal control is triggered by a root signal synthesized by roots, instead of a threshold leaf water potential. The message is considered as being the concentration of ABA in the xylem sap (and not the ABA flux, see discussion in Gowing *et al.*, this volume). Hypotheses (a) and (b) presented in §2 lead to a simple expression of the message:

$$[\mathrm{ABA}] = J_{\mathrm{ABA}}/(J_{\mathrm{w}} + b) = a\psi_{\mathrm{r}}/(J_{\mathrm{w}} + b), \quad (5)$$

where [ABA] is the concentration of ABA in the xylem sap ($\mathrm{mol\ m^{-3}}$), J_{ABA} is the flux of ABA ($\mathrm{mol\ m^{-2}\ s^{-1}}$), considered to be linearly related to ψ_{r} and diluted by the water flux.

Control of stomatal conductance by root signals alone ('purely chemical')

For saturating PPFD, stomatal conductance is considered to depend on xylem [ABA] only:

$$g_{\mathrm{s}} = g_{\mathrm{s\ min}} + \alpha \exp\{\beta[\mathrm{ABA}]\}, \quad (6a)$$

where $g_{\mathrm{s\ min}}$ and $(\alpha + g_{\mathrm{s\ min}})$ are the minimum and maximum g_{s}, respectively, and β is a fitted parameter, referred to subsequently as stomatal sensitivity to xylem [ABA]. For non-saturating PPFD, a maximum value of g_{s} is given by the relationship in figure 3*a*.

Control of stomatal conductance by xylem [ABA] and ψ_{l} ('interaction')

Stomatal conductance is considered to depend on a combination of xylem [ABA] and ψ_{l} (figure 3*c*), with a maximum value for non-saturating PPFD (figure 3*a*).

$$g_{\mathrm{s}} = g_{\mathrm{s\,min}} + \alpha \exp\{[\mathrm{ABA}]\ \beta \exp(\delta\ \psi_{\mathrm{l}})\}, \quad (6b)$$

where $g_{\mathrm{s\ min}}$ and $(\alpha + g_{\mathrm{s\ min}})$ are as in equation (6*a*), β and δ are fitted parameters. Redistribution of ABA from other parts of the leaf and ABA synthesis in the leaf are not explicitly taken into account in the model, but both mechanisms might participate to the higher sensitivity of g_{s} to ABA at low ψ_{l}.

These two systems, therefore, consist of five equations with five unknowns: g_{s}, J_{w}, xylem [ABA], ψ_{l} and ψ_{r}. Input variables are soil water potential and evaporative demand. Parameters of water transfer are as in the 'purely physical' model; parameters of stomatal control (equations 5, 6) are the response of ABA synthesis to ψ_{r} (*a*) and the stomatal sensitivity to ABA (β in the 'purely chemical' system, β and δ in the 'interaction' system).

(*c*) *Comparison of the three models of stomatal control with experimental data*

Simulations have been run either for a day with constant environmental conditions as in figure 1 ($\psi_{\mathrm{s}} = -0.4$ MPa in simulations), or for a drying period of 20 days beginning with a soil at 'field capacity' (ψ_{s} of *Ca.* -0.01 MPa) with a constant daily evaporative demand ($4.2\ \mathrm{mm\ d^{-1}}$). Soil hydraulic properties, root characteristics and parameters of the Penman–Monteith equation are those experimentally measured in Grignon (Tardieu *et al.* 1992*c*, 1993). Parameters of stomatal control have been determined from a series of experiments on maize in controlled and field conditions (Tardieu *et al.* 1993).

On a short timescale (figure 4), outputs of 'purely physical' and 'interaction' systems are similar to experimental data (figure 1, non-compacted treatment), with a decrease in g_{s} and a relatively constant ψ_{l} during the afternoon. However, the 'physical' system predicts a complete reopening of stomata in the late afternoon, which is usually not observed under natural conditions (figure 1). Simulations are markedly different in the case of a purely chemical control. For a sensitivity similar to that for maize plants grown in a growth chamber (Zhang & Davies 1990), or in the late morning in the field (Tardieu *et al.* 1993), no stomatal control is predicted and ψ_{l} decreases toward unacceptably low values. For a

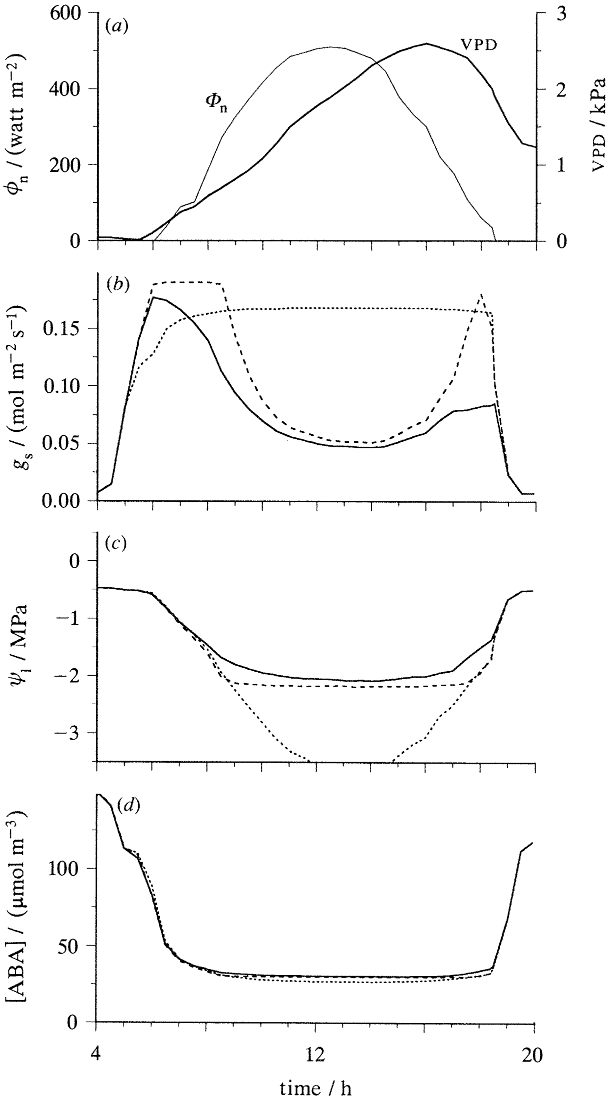

Figure 4. Simulated changes with time of the day in (*a*) net radiation (Φ_{n}) and air vapour pressure difference (VPD), (*b*) stomatal conductance (g_{s}), (*c*) leaf water potential (ψ_{l}) and (*d*) xylem [ABA] for the three models under study. Dashed lined, 'purely physical model'; dotted line, 'purely chemical' model; solid line, 'interaction model'.

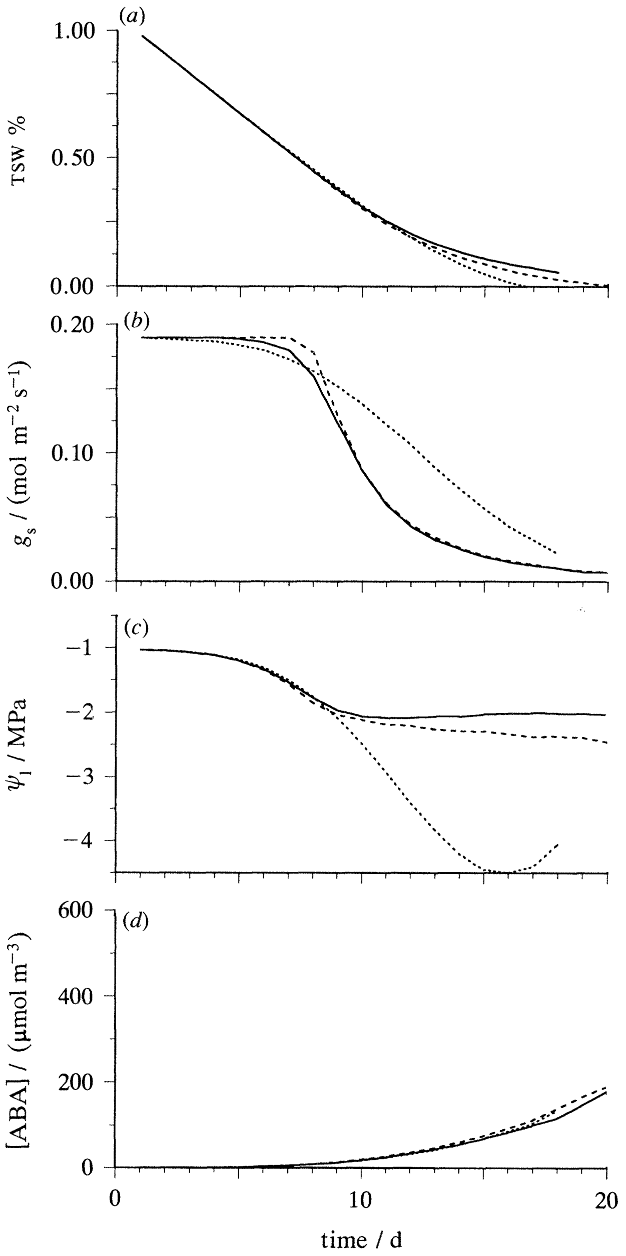

Figure 5. Simulated changes with time of (*a*) transpirable soil water (TSW, % of total soil reserve), (*b*) stomatal conductance (g_s), (*c*) leaf water potential (ψ_l) and (*d*) xylem [ABA] during a drying period, with the three models under study. Symbols as in figure 4.

twofold higher sensitivity, such as that observed in field-grown maize sampled in the afternoon, outputs become more similar to those predicted by the 'purely physical' model, but with a much slower stomatal opening during the morning (data not shown).

Longer-term changes in g_s, ψ_l and xylem [ABA] are presented in figure 5. The 'interaction' and 'purely physical' control both result in a stomatal control from the sixth to the eighth day onwards, respectively (40 and 50% of the soil water reserve). Both systems provide relatively similar outputs, with tighter control of ψ_l in the 'interaction' system. Again, simulations are quite different in the case of a 'purely chemical' control. For a sensitivity corresponding to field-grown maize sampled in the afternoon, commencement of stomatal closure occurs earlier than with the other two systems (fourth day, 75% of the soil water reserve), but g_s and J_w are maintained at higher values throughout the drying period, so ψ_l decreases to very low values. The 'purely chemical' system, therefore, does not allow adequate control of ψ_l. Simulations have been carried out for sensitivities ranging from tenfold lower to tenfold higher, without affecting this conclusion.

As predicted by Jones (1980) and Ludlow *et al.* (1989), stomatal control based on root messages alone would result in an earlier stomatal closure than the systems involving ψ_l, and would therefore save more water in dry environments. However, control of ψ_l is not achieved in the system described by equations (5) and (6*a*). If the root message depends on root water status (Cornish and Zeevaart 1985), it will be linked to the water flux through the soil-plant-atmosphere continuum in addition to the soil water status (see equation 5). Additional regulatory processes, such as changing stomatal sensitivity with leaf water status are therefore necessary to overcome this effect of water flux. These processes apparently exist in maize (Tardieu *et al.* 1992*a*, 1993). It would be interesting to know whether plants which do not control tightly their leaf water potential (such as sunflower or sugar beet) lack of this mechanism.

Although 'purely physical' and 'interaction' models differ in their theoretical bases, they both provide relatively similar predictions of variations in g_s, ψ_l and xylem [ABA] on a day-to-day basis, provided that their parameters are fitted to the same experimental data. This was not the case for the purely chemical model of stomatal control. This similarity has two important consequences.

1. The existence of tight relationships between xylem [ABA] and stomatal conductance, such as those published by Wartinger *et al.* (1990) or Tardieu *et al.* (1992*b*), is not a conclusive argument in favour of a stomatal control by root signals. This relationship can be obtained from figure 5, even in absence of any controlling effect of ABA on stomata, as a result of the greater dilution of the ABA flux with higher g_s.
2. Control of ψ_l can be achieved in the 'interaction' system which does not involve a threshold leaf water potential.

'Purely physical' and 'interaction' models can, therefore, mimic each other's most important feature, namely a relationship between g_s and xylem [ABA] in the 'purely physical' model, and an apparent threshold ψ_l in the 'interaction' model. This does not imply that both models have the same theoretical value. Applying artificial ABA causes stomatal closure with the same relationship between xylem [ABA] and g_s as that obtained in droughted plants (Zhang & Davies 1990, 1991) provided that leaves have similar water potentials (Tardieu *et al.* 1993). In contrast, leaf water potential has frequently been shown to have no direct controlling effect on stomatal conductance (Gollan *et al.* 1986; Turner *et al.* 1985). Without ABA there may be only a very restricted stomatal response to shoot dehydration, as in the wilty, low-ABA mutants (Tal &

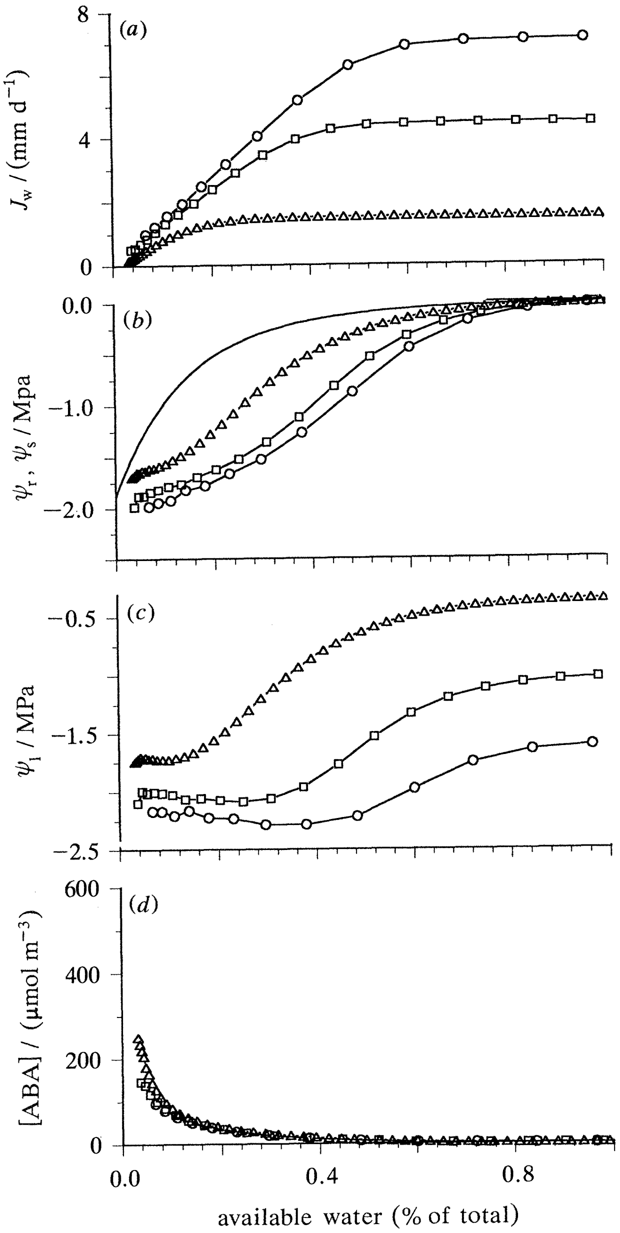

Figure 6. Simulated changes with time of (*a*) water flux (J_w), (*b*) soil and root water potentials (ψ_s and ψ_l), (*c*) leaf water potential (ψ_l) and (*d*) xylem [ABA], plotted against available soil water, during a drying period with three contrasting evaporative demands. The interval between two symbols represents 24 h. Solid line, soil water potential. Symbols: triangles, 1.6 mm d^{-1} evaporative demand; squares, 4.2 mm d^{-1} evaporative demand; circles, 7 mm d^{-1} evaporative demand.

Imber 1966). A purely physical control cannot, therefore, be considered as a general model. A paradox, however, is that several models involving such hypothesis (e.g. Nimah & Hanks 1973; Hillel *et al.* 1976) provide reasonably realistic outputs of water flux and plant water status. The simulations presented here suggest that this could be due to a good correspondence, observed under many circumstances, between the assumed model and a stomatal control involving root messages.

3. CONTROLS OF LEAF WATER POTENTIAL AND XYLEM [ABA]

It is worth discussing here the nature of the apparent threshold leaf water potential (ψ_l^t) triggering stomatal control, which can successfully help in modelling the stomatal control in spite of having no clear physiological basis. ψ_l^t cannot be considered as constant for a given genotype. Studies carried out in growth chambers usually conclude that stomata of maize or sunflower will close at ψ_l ranging from −0.5 to −1 MPa (e.g Hsiao 1973). However, high stomatal conductances have frequently been found for the same species at ψ_l lower than −1.8 MPa in field conditions (e.g. figures 1 and 2), and the apparent ψ_l^t usually increases with evaporative demand. It is important to determine, therefore, whether a model involving root messages can predict this change in apparent ψ_l^t with evaporative demand, and if apparent ψ_l^t would be altered if the root system was able to synthesize more ABA at a given ψ_r. This also involves investigating how xylem [ABA] would change with evaporative demand.

(*a*) *Control of leaf water potential with varying evaporative demand*

Figure 6 presents simulations carried out using the 'interaction' model, with three constant evaporative demands (1.6, 4.2 and 7 mm d^{-1}). Simulations have been run over periods of 47, 20 and 14 days, respectively, corresponding to depletion of the available soil water, and are presented as a function of the soil water reserve. Throughout the drying period, leaf water potential remains higher for lower evaporative demands. As a consequence, ψ_l at stomatal closure (apparent ψ_l^t) decreases with evaporative demand (−1.6, −2 and −2.2 MPa for low, intermediate and high evaporative demands), as it does in the above-mentioned experimental data. Beginning of stomatal closure (reduction in J_w, figure 6) occurs for different levels of soil available water (70, 50 and 30% of the total available water), consistently with the classical reduction in g_s with leaf-to-air vapour pressure difference (linked to ϕ_n, T_a and T_d, equation 1). These simulations therefore suggest that two classical responses of g_s to evaporative demand, earlier stomatal closure and lower apparent ψ_l^t for higher VDP, do not necessarily correspond to a special mechanism, and could be accounted for by a model of stomatal control taking into account root messages and water flux.

(*b*) *Control of xylem [ABA] with varying evaporative demand*

The sap can take up to several hours (days for some trees) to reach stomata from the roots, so the message which it conveys should be relatively independent of the rapid changes in evaporative demand if it is not to reflect an obsolete root status. Such an independence is observed for maize during the day (figure 1) for leaf-to-air vapour pressure difference ranging from 0.8 (morning) to 3.5 kPa (afternoon). It is simulated by the 'interaction' model, both for diurnal variations (figure 4) and long term evolutions with contrasting evaporative demands (figure 6). Simulated xylem [ABA] does not vary, for a given soil water status, when evaporative demand ranges from 1.6 to 7 mm d^{-1}. Increasing evaporative demand results in lower root water potential, but also in higher water flux, so the message predicted by equation (5) is unaltered by changes in evaporative demand. In the view expressed by equation (5), the message would, therefore, be buffered in such a way that it only reflects the conditions of water extraction (soil water status, but also resistance to water flux, see § 4), and not evaporative demand.

(*c*) ***Predicted effects of manipulating the ability of the root system to synthesize ABA***

Since several genetic programmes aim to select plants with high ABA, it is worth simulating what could be the consequences of increasing the capacity of the root system to synthesize ABA (coefficient *a* in equation (5)). The effects on stomatal behaviour of increasing (or decreasing) the capacity of roots to synthesize ABA may be less dramatic than expected (figure 7). Increasing the capacity to synthesize ABA results in an earlier stomatal closure but also in an increase in leaf water potential which reduces the stomatal sensitivity to ABA. As a consequence, changes with time of g_s and soil water reserve would be relatively unaffected. This result would be consistent with experimental data of Quarrie (1991).

Conversely, simulations suggest that the control of leaf water potential would be more affected than that of g_s. In this view, the plateau of ψ_l (apparent $\psi_\mathrm{l}^\mathrm{t}$) would be controlled by a balance between ABA synthesis (coefficient *a* in equation (5)) and stomatal sensitivity to ABA. Higher synthesis or sensitivity would result in higher ψ_l during soil drying, the actual value of ψ_l depending on evaporative demand. Maintenance of high ψ_l throughout the cycle could have many important physiological and developmental consequences, and may justify per se the study of genetic variability of ABA synthesis

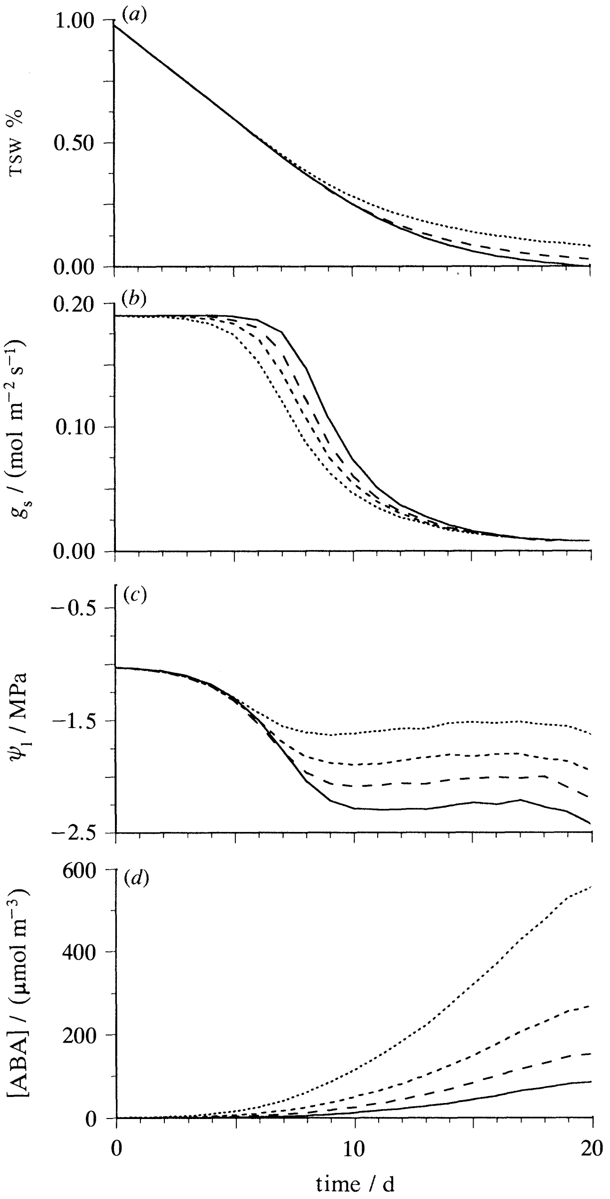

Figure 7. Simulated changes with time of (*a*) transpirable soil water (TSW, % of total soil reserve), (*b*) stomatal conductance (g_s), (*c*) leaf water potential (ψ_l) and (*d*) xylem [ABA] during a drying period, with four root systems showing contrasting capacity to synthesize ABA.

4. THE CASE OF SOIL COMPACTION: CONSEQUENCES OF AN ACCURATE CALCULATION OF ROOT WATER POTENTIAL IN MODELS INVOLVING ROOT MESSAGES

Classical hydraulic models cannot account for reductions in stomatal conductance and leaf growth of plants subjected to soil compaction which are observed when soil moisture availability is high (figures 1 and 2). A possible explanation could be that roots synthesize a signal when they experience high mechanical impedance (Masle & Passioura 1987). However, we suggest here that we can account for this stomatal behaviour without such messages, if the changes in resistance to water flux linked to soil compaction are taken into account.

In classical calculations of ψ_r and R_sp (Gardner 1960, equation 4), it is implicitly assumed that roots are vertical and regularly arranged, since each root is supposed to have access to one soil cylinder whose diameter is the mean distance between neighbouring roots. Despite its simplicity, this system provides reasonably realistic information under many circumstances. However, it does not hold for plants grown in compacted soil, where structural obstacles induce a high degree of root clumping (de Willigen & Van Noordwijk 1987; Tardieu 1988). This is of particular importance in models of stomatal conductance involving root messages because of the important role of ψ_r in such models. We have tested whether the stomatal closure observed in plants grown in compact and relatively wet soil (Tardieu *et al.* 1992*b*; Masle &

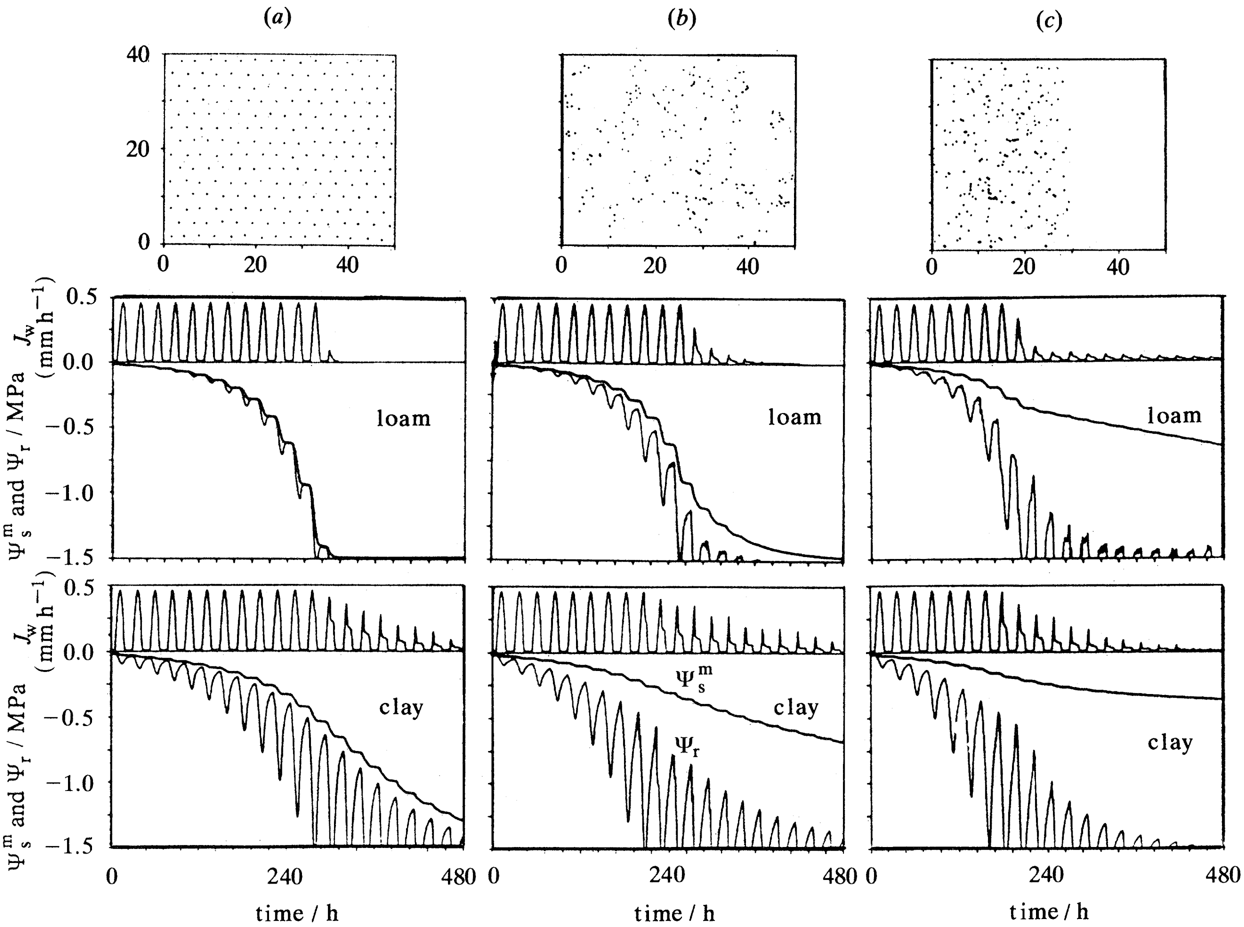

Figure 8. Change with time of the calculated transpiration (J_w), mean soil water potential (ψ_s) and root water potential (ψ_r), for three root spatial arrangements, represented by maps of root contacts on horizontal planes. (*a*) Regular arrangement; (*b*) clustered arrangement around randomly distributed points, simulating light compaction or short branches arising from main roots; (*c*) simulation of the effect of a structural obstacle. Redrawn from Tardieu *et al.* (1992*c*).

Passioura 1987) could be due to appreciable increases in R_{sp}.

Such a test involves an alternative calculation of ψ_r (Lafolie *et al.* 1991), avoiding the hypothesis of a regular root spatial arrangement. Characteristics of the root system are given to the model using a two-dimensional root map, similar to those obtained *in situ* in the field (Tardieu 1988). Water flux to individual roots and ψ_r are simulated by using the finite element method in nodes whose position is determined by tessellation of the root map. Simulations have been run with this model to compare three root spatial arrangements with the same root density (figure 8), representing either the regular pattern generally assumed in models or two degrees of root clumping linked to increasingly compacted situations. They show (figure 7) that the rate of water flux to the roots and the values of R_{sp} are ψ_r are highly affected by the root spatial arrangement. This effect is greater with low hydraulic conductivity (clay) and with high evaporative demand (data not shown). In the regular case, calculated R_{sp} is similar to that calculated by using equation (6), and ψ_r remains close to the soil water potential. Conversely, R_{sp} is considerably increased in the moderately clumped and highly clumped root systems, so ψ_r can differ by up to 1 MPa from soil water potential. For a given soil water status, root clumping following soil compaction affects the resistance to water flux in the soil, therefore decreasing the root water potential and the water flux to the root system. It is noteworthy that a classical calculation of resistance to water flux in the soil (equation 4) would have provided the same value of R_{sp} in the three cases, which do not differ in root density, so reductions in water flux and root water potential would not be accounted for.

The effects of soil compaction on water flux and root water potential could affect the stomatal control by changing the synthesis and the dilution of the message (equation 5). This effect has been simulated (figure 9) by running the 'interaction' model with R_{sp} either as in equation (6), or 5 or 20 times higher. There is a very large effect of such manipulation on simulated values of gs, ψ_l and xylem [ABA]. Reductions in gs and ψ_l occur earlier in the soil drying period with higher R_{sp}, but the plateau of ψ_l, observed after 10 days of soil drying, is unaffected. High levels of xylem [ABA] were observed from the fifth day onwards with high R_{sp}, versus only the twelfth day with a low R_{sp}. These tendencies are consistent with experimental data (figures 1 and 2), where soil compaction caused early stomatal closure and

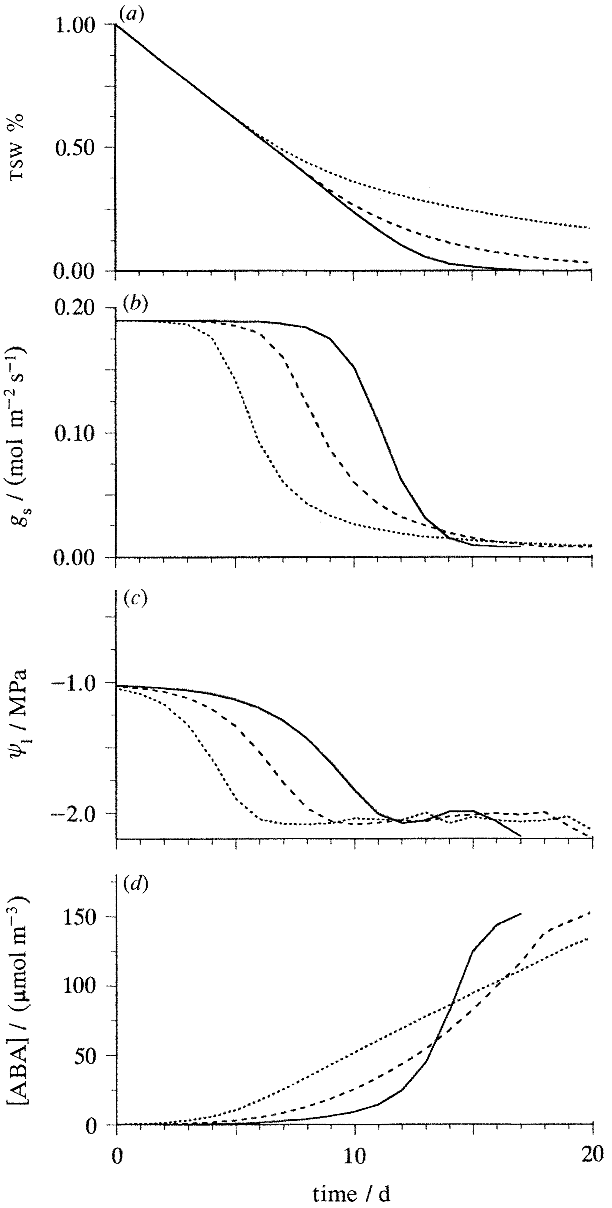

Figure 9. Simulated changes with time of (*a*) transpirable soil water (TSW, % of total soil reserve), (*b*) stomatal conductance (g_s), (*c*) leaf water potential (ψ_l) and (*d*) xylem [ABA] during a drying period, with three contrasting resistances to water flux in the soil. Solid line, R_{sp} as in equation (4); dashed line, R_{sp} multiplied by 5; dotted line, R_{sp} multiplied by 20, simulating water transfer in a compacted soil.

increased xylem [ABA] levels for a given soil water status, but had no appreciable effect on daytime ψ_l.

Stomatal behaviour of plants grown in compacted soil can therefore be simulated by a model of stomatal control involving root messages, if the effect of root clumping on the resistance to water transfer is taken into account. In this case, it is not necessary to take account of a direct message of soil mechanical impedance (Masle & Passioura 1987) to predict stomatal behaviour. Both experimental data (figure 2) and simulations (figure 9) also suggest that xylem [ABA] depends on R_{sp} in addition to soil water status.

5. DISCUSSION AND CONCLUSION

In spite of a physiological basis that is probably unrealistic, a model of stomatal control involving the leaf water status alone could provide relatively realistic predictions of water flux, soil water and plant water potentials. However, this conclusion does not apply for timescales less than 24 h, and for varying environmental conditions. In particular, such a model would not account, without considerable fine tuning, for the plant behaviour under contrasting evaporative demands or in compacted soil. A model based on root messages only also needs adjustment, since it does not allow control of leaf water status during a drying period. One of these possible adjustments is the involvement of both leaf water status and root messages in stomatal control, a mechanism which is apparent from our experimental data.

This 'interaction' model provides simulations which are reasonably consistent with experimental data, and applies to a range of environmental conditions without necessity of adjusting its parameters for each condition. In particular, it applies for changing soil water status in a large range of evaporative demands, and in compacted as well as in non-compacted soils, if an accurate calculation of root water status is included in the model. However, this favourable behaviour of the model does not necessarily imply that the interaction between root message and leaf water status is the main mechanism involved in stomatal control. In this complex controlling system involving several variables, relationships between two or three variables could be accounted for by several models which greatly differ in their bases. In the presented simulations, models could realistically mimic mechanisms which were not involved in their equations (e.g. the effect of evaporative demand on stomatal closure, or the relationship between xylem [ABA] and stomatal conductance in the model involving no stomatal control by xylem [ABA]), so alternative models involving other mechanisms might be able to account for experimental data.

Simulations also suggest possible plant responses, not yet confirmed experimentally.

1. The root message could be buffered in such a way that it would not be affected by changes in evaporative demand. It would be relatively consistent on a day-to-day basis while the stomatal response to this message would depend on the evaporative demand. This stability would avoid crucial problems such as the inadequacy of a slow-moving message for stomatal control in a rapidly changing evaporative demand, or the stomatal response to abrupt changes in xylem [ABA]. The message could also be constant enough to be used as a long-term developmental signal by the plant.

2. If this message is affected by the resistance to water flux in the soil, it would not be linked with a unique relationship with the soil water status. In this view, anything which increases this resistance, such as soil compaction, low root density or unfavourable soil hydraulic characteristics, would increase the message. This message would, therefore, represent the condi-

tions of water uptake rather than the soil water status alone.

3. Manipulating the capacity of the root system to synthesize ABA could have a relatively small effect on the stomatal control, even without a reduction in stomatal sensitivity to ABA which would be likely to result from an increased ABA signal. However, such a manipulation could have an effect on the water flux via other mechanisms, such as reduction in leaf growth or delay in senescence, linked to a better control of leaf water status.

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