

Field Crops Research 47 (1996) 253-266



Soil-water thresholds for the responses of leaf expansion and gas exchange: A review

V.O. Sadras^{*}, S.P. Milroy

Cotton Research Unit, C.S.I.R.O. Division Plant Industry, P.O. Box 59, Narrabri 2390, NSW, Australia Received 23 September 1995; revised 13 December 1995; accepted 15 December 1995

Abstract

Typical responses of leaf expansion and gas exchange rate to plant available soil water (PAW) can be described with two straight lines that intersect at PAW, i.e., the PAW threshold for which the rate of the process in stressed plants starts to diverge from a reference value. PAWt is a parameter widely used in modelling plant responses to water deficits. It also reflects some apparent physiological mechanism because plants appear to be able to sense soil water status or related variable(s). In this paper comparisons are made between PAW, for various species (monocots and dicots) and plant processes (leaf expansion and gas exchange) in order to: (i) point out methodological sources of variation in published values of PAW; and (ii) analyse variations in PAW, in relation to plant and environmental factors. Reported values of PAW, vary over almost the whole possible range of PAW (i.e., 0 to 1). Average thresholds reflect the greater responsiveness to water deficits of tissue expansion (average PAW, = 0.56) relative to gas exchange (0.40). Average PAW, for leaf water potential (0.61) and stomatal conductance (0.37) are very close to the average thresholds for expansion and gas exchange, respectively. Soil water thresholds for leaf expansion are also shown to discriminate between plant types (0.50 for monocots vs. 0.66 for dicots) and soils (0.72 for coarse- vs. 0.43 for fine-textured soils). The simplicity of characterising plant responses to water stress in terms of PAW, is attractive. In agreement with known physiological relationships, however, our analysis highlights how, for given processes and species, the measured value of PAW, can be affected by evaporative demand, root distribution, soil texture and soil bulk density, among other factors, thus making explicit some of the assumptions underlying the use of fixed soil-water thresholds in simulation models.

Keywords: Leaf water potential; Modelling; Stomatal conductance; Leaf expansion; Plant available soil water; Transpiration; Photosynthesis

1. Introduction

Water deficit is a major constraint to crop production worldwide and, even in the humid tropics, crops and natural vegetation are usually exposed to drought periods of varying duration and intensity (Boyer, 1982; McWilliam, 1986). Cell expansion, cell-wall synthesis and protein synthesis in fast growing tissues are among the processes most sensitive to water deficits (Hsiao et al., 1976, Hsiao et al., 1985; Lawlor and Leach, 1985). The result is that, at the plant level, leaf expansion is one of the most sensitive processes to water stress (Boyer, 1970; Hsiao et al., 1985). In fact, reduced leaf area is probably the more obvious mechanism by which plants and crops

^{*} Corresponding author. Tel. (61-67) 931-105; Fax: (61-67) 931-186; e-mail: victors@mv.pi.csiro.au

^{0378-4290/96/\$15.00 © 1996} Elsevier Science B.V. *PII* S0378-4290(96)00014-7

restrict water loss in response to drought (Connor and Jones, 1985; Legg et al., 1979; Schulze et al., 1987; Sadras et al., 1991, Sadras et al., 1993a). Stomatal conductance is less responsive to water deficits than tissue expansion (e.g. Hsiao et al., 1976; Passioura, 1988a; Sadras et al., 1993a). Reduction in gas exchange by reduction in stomatal conductance depends on the extent to which vegetation is coupled to its surrounding atmosphere (Jarvis and Mc-Naughton, 1986). In addition to stomatal limitations, photosynthesis can be reduced by non-stomatal effects of water stress (Chaves, 1991).

Modelling plant responses to water stress requires not only an understanding of, but also quantitative relationships for, the effects of water deficits on leaf expansion and gas exchange rates. This requires in turn, the proper definition of variables to describe plant and crop water status. One frequently used variable is PAW, the amount of soil water that is currently available for the plant expressed as a proportion of the maximum amount of plant available water the soil can hold (Ritchie, 1981):

$$PAW = \frac{\theta_a - \theta_{ll}}{\theta_{ul} - \theta_{ll}}$$
(1)

where θ is volumetric soil water content and subscripts a, ul and ll denote actual, lower limit and upper limit of plant available water, respectively (methods to quantify θ_{ul} and θ_{ll} are discussed in Section 3.1). The concept of PAW has been widely used in modelling (e.g., Jones and Kiniry, 1986; Hammer and Muchow, 1990; Hearn, 1994). The approach is popular for a number of reasons. First, responses of leaf expansion and gas exchange rates to PAW are considered to be robust and can be described by simple models. Second, the parameters of these models can be obtained with data from simple, inexpensive experiments. Third, estimates of PAW that can be generated by current crop models are reliable enough for use as independent variables to scale the rates of relevant plant processes.

Interestingly, plant physiologists have long disregarded PAW as a variable to describe the responses of plant processes to water deficits because of its underlying empiricism. Traditionally, leaf water potential has been the preferred variable to describe plant responses to water deficits on the grounds that it provides a more mechanistic approach. More recently, however, the notion that roots are able to sense soil water status (or a related variable) and produce signals that trigger shoot responses (e.g., changes in leaf expansion rate and stomatal conductance) has challenged our view of plant water relations (Davies and Zhang, 1991; Jones and Corlett, 1992; Passioura, 1988b; Passioura and Stirzaker, 1993; Tardieu and Davies, 1993; Turner, 1986). Thus, the use of soil water content to quantify plant responses to water deficits has a two-fold quality: it is simple and reflects some apparent physiological mechanism.

Typical responses of leaf expansion and gas exchange rate to PAW can be described with two straight lines that intersect at PAW, (Ritchie, 1981), where PAW_t is the threshold for which the rate of the process in stressed plants starts to diverge from a reference value. While the parameter PAW, is useful in describing the outcome of experimentation, its use in simulation modelling normally assumes that PAW, is stable for a species. Estimates of PAW, however, vary widely. For example, reported PAW, for soybean evapotranspiration ranges from 0.20 (Meyer and Green, 1980; Meyer and Green, 1981) to 0.64 (Mason et al., 1980) and for tissue expansion in maize from 0.27 (Muchow and Sinclair, 1991) to 0.85 (NeSmith and Ritchie, 1992). This variation is not altogether surprising considering the range of experimental techniques used and differences in the growth environment. It has been shown, for instance, that PAW, for maize transpiration can vary enormously (0.07 to 0.85) due to variation in evaporative demand (Denmead and Shaw, 1962). The effect of evaporative demand on PAW, has also been demonstrated for leaf expansion (Sadras et al., 1993b). Recent studies have analysed some effects of soil type on PAW, for relative leaf water content in peanuts (Erickson et al., 1991) and transpiration in sorghum (Robertson and Fukai, 1994).

In this paper, a comparison is made of PAW_t for various species (monocots and dicots) and plant processes (leaf expansion and gas exchange) in order to: (i) point out methodological sources of variation in published values of PAW_t ; and (ii) analyse variations in PAW_t in relation to plant factors, evaporative demand, soil type and the plant variable response.

2. Methods

Table 1

Values of PAW_t were collated from the literature. The observations covered a range of species including cereals, legumes, sunflower and cotton. Growing conditions and experimental methods varied widely.

Typical responses of leaf expansion and gas exchange rate to PAW have been described with models of the form (e.g., Al-Khafaf et al., 1978; Milroy and Goyne, 1995; Muchow and Sinclair, 1991):

$$R = \frac{1}{1 + a \exp(b \times \text{PAW})}$$
(2)

where R is the rate of the process measured in stressed plants relative to that in unstressed controls or to some other reference value (e.g., potential

PAW _t for tissue expansion					
Variable	Model ^a	Species	Growing condition	PAW	Source
Leaf + stem expansion	2, SP	Maize	Field	0.85	NeSmith and Ritchie, 1992
	2, SP	Wheat	Field, lysimeter	0.33	Meyer and Green, 1981
		Soybean		0.25	
Leaf + stem expansion	2, SP	Wheat	Field, lysimeter		Meyer and Green, 1980
			Irrigation at sowing	0.43	
			No irrigation ('acclimated')	0.48	
Leaf + stem expansion	2, SP	Pearl millet	Field		McIntyre et al., 1993
			Reference evapotranspiration:		
			6 mm/d	< 0.30 ^{c,d}	
			9 mm/d	0.80 ^c	
Leaf expansion	2, SP	Sorghum	Glasshouse, pot	0.44	Rosenthal et al., 1987
		Sorghum	Field, lysimeter	0.50	
		Cotton	Glasshouse, pot	0.25	
Leaf expansion	1, SP	Cotton	Glasshouse, pot	0.82	Constable, 1982
Leaf expansion	1, SP	Sorghum	Field, pot	0.25	Hammer and Muchow, 1990
Leaf expansion	2, SP	Sunflower	Field, variable evaporative demand:		Sadras et al., 1993b
			5.5 mm/day	0.51	
			8.8 mm/day	0.83	
Leaf expansion	2 ^b	Potato	Field		Jefferies, 1993
			Highly sensitive varietym	1.0	
			(e.g., Pentland Squire)		
			Less sensitive variety	0.73	
			(e.g., Russet Burbank)		
Leaf expansion	1, SP	Maize	Field, pot	0.27	Muchow and Sinclair, 1991
Leaf expansion	1, SP	Barley	Glasshouse, pot	0.66	Milroy and Goyne, 1995
Leaf expansion	1, S	Snapbean	Growth chamber	1.0 °	Rawitz, 1969

^a Model 1: non-linear (Eq. (2) or similar); Model 2: Eq. (3) or similar. When non-linear models are fitted to the data, thresholds are calculated as the PAW for which the control-to-reference ratio is 0.95. SP indicates that upper and lower limits of PAW have been determined taking into account both soil and plant factors while S indicates that these parameters were obtained as a function of soil properties only.

^b Jefferies (1993) fitted linear and quadratic models to his data. Only linear models are considered in this table.

^c Thresholds obtained from graphics in the original papers.

^d No response in expansion was found at the end of the experiments when PAW was 0.30.

Table	2						
PAW.	for	gas	exchange	and	stomatal	conductance	

Crop photosynthesis Sorghum Field 0.35 Sumayo et al., 1977 Crop photosynthesis 2, SP Potato Field 0.60 Jefferies and MacKerron, 1989 Leaf photosynthesis 1, SP Sunflower Growth chamber, variable vapour pressure deficit: 10 Pa/kPa 0.23 c 0.31 c Oollan et al., 1985 Leaf photosynthesis 1, SP Nerium oleander Gollan et al., 1985 Gollan et al., 1985 Leaf photosynthesis 1, SP Nerium oleander Gollan et al., 1985 Gollan et al., 1985 Leaf photosynthesis 1, SP Cotton Glasshouse, pot 0.67 Constable, 1982 Leaf photosynthesis 1, S Soybean Field 0.40 Mason et al., 1980 Evapotranspiration 2, SP Soybean Field 0.40 Mason et al., 1980 Evapotranspiration 1, S Alfalfa Field, variable evaporative demand: 6.3 mm/d 0.30 Socod drying cycle, seminal roots only 0.30 Socord	Variable	Model ^a	Species	Growing condition	PAW	Source
Crop photosynthesis 2, SP Potato Field 0.600 Jefferies and MacKerron, 1989 Leaf photosynthesis 1, SP Sunflower Growth chamber, variable vapour pressure deficit: 10 Pa/kPa 0.23 c 25 c 25 Pa/kPa Golan et al., 1985 Leaf photosynthesis 1, SP Nerium oleander Giashouse, pot, variable vapour pressure deficit: 10 Pa/kPa 0.60 c 25 c 25 Pa/kPa Golan et al., 1985 Leaf photosynthesis 1, SP Cotton Giashouse, pot, variable vapour pressure deficit: 10 Pa/kPa 0.60 c 20 constable, 1982 Leaf photosynthesis 1, SP Cotton Giashouse, pot, variable vapour pressure deficit: 10 Pa/kPa 0.60 c 20 constable, 1982 Leaf photosynthesis 1, SP Soybean Field 0.60 c 20 constable, 1982 Evapotranspiration 2, SP Soybean Field, variable exaporative demand: 6.3 mn/ d 0.64 c 20 constable, 1983 Adul-Jabbar et al., 1980 Evapotranspiration 1, SP Soybean Field, visimeter 0.20 constable, 1981 Evapotranspiration 2, SP Soybean Field, lysimeter 0.20 constable, 1981 Evapotranspiration 2, SP Sunflower Field, lysimeter 0.20 constable, 1972 Evapotranspiration	Crop photosynthesis		Sorghum	Field	0.35	Sumayo et al., 1977
Leaf photosynthesis 1, SP Sunflower Growth chamber, variable vapour ID Pa/KPa Color Gollan et al., 1985 Leaf photosynthesis 1, SP Nerium oleander Gilashouse, pot, variable vapour pressure deficit: D Pa/KPa 0.60 + 0.61 + 25 Pa/KPa Gollan et al., 1985 Leaf photosynthesis 1, SP Coton Gilashouse, pot, variable vapour pressure deficit: D Pa/KPa 0.60 + 0.61 + 0.62 + 25 Pa/KPa Constable, 1982 Leaf photosynthesis 1, SP Coton Gilashouse, pot 0.61 + 0.61 + 0.62 + 0.61 + 0.61 + 0.61 + 0.61 + 0.61 + 0.61 + 0.61 + 0.61 + 0.61 + 0.62 + 0.61 + 0.61 + 0.61 + 0.61 + 0.61 + 0.62 + 0.61 + 0.61 + 0.62 + 0	Crop photosynthesis	2, SP	Potato	Field	0.60	Jefferies and MacKerron, 1989
Leaf photosynthesis1, SPNerium oleander oleanderGlasshouse, pot; variable vapour pressure deficit: 10 Pa/kPa 0.60° 0.60 $^{\circ}$ 0.60 $^{\circ}$ Constable, 1982 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ Constable, 1982 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ Constable, 1980 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ Constable, 1980 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ Evapotranspiration 2. SP0.50 Soybean SoybeanField, variable evaporative demand: 0.30 $^{\circ}$ 7.5 mm/d0.20 $^{\circ}$ 0.20 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ Mason et al., 1980 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ Neger and Green, 1981 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.60 $^{\circ}$ 0.70 $^{\circ}$ 0	Leaf photosynthesis	1, SP	Sunflower	Growth chamber, variable vapour pressure deficit:		Turner et al., 1985
Leaf photosynthesis I, SP Nerium oleander Glasshouse, pot; variable vapour pressure deficit: $10 Pa/kPa = 0.66^{\circ}$ $10 Pa/kPa = 0.66^{\circ}$ Leaf photosynthesis I, SP Cotton Glasshouse, pot 0.67 Constable, 1982 Leaf photosynthesis I, SP Soybean Field 0.40 Hearn and Constable, 1984 1.0 SP Soybean Field 0.40 Mason et al., 1980 1. SP Soybean Field, variable evaporative demand: $5.3 mm/d$ 0.39 7.5 mm/d 0.39 7.5 mm/d 0.30 Keyapotranspiration 2, SP Soybean Field, lysimeter 0.20 Meyer and Green, 1981 Evapotranspiration 2, SP Soybean Field, lysimeter 0.20 Meyer and Green, 1980 Evapotranspiration 2, SP Cotton, sorghum Field, lysimeter 0.20 Meyer and Green, 1980 Evapotranspiration 2, SP Cotton, sorghum Field, lysimeter 0.20 Meyer and Green, 1980 Evapotranspiration 2, SP Cotton, sorghum Field, lysimeter 0.20 Ritchie et al., 1972 Evapotranspiration 2, SP Cotton Sorghum Field, lysimeter 0.20 Ritchie et al., 1982 Crop transpiration 2, SP Maize Field, lysimeter 0.20 Ritchie et al., 1982 Evapotranspiration 2, SP Cotton Field, lysimeter 0.20 Ritchie, 1973 Crop transpiration 2, SP Cotton Field, lysimeter 0.31 Al-Khafaf et al., 1978 Crop transpiration 2, SP Cotton Field, lysimeter 0.31 Al-Khafaf et al., 1978 Crop transpiration 2, SP Cotton Field, lysimeter 0.31 Al-Khafaf et al., 1978 Crop transpiration 2, SP Cotton Field, lysimeter 0.31 Al-Khafaf et al., 1978 Crop transpiration 2, SP Cotton Field, lysimeter 0.31 Al-Khafaf et al., 1973 Crop transpiration 2, SP Cotton Glasshouse, pot 0.33 Wright and Smith, 1983 Crop transpiration 2, SP Covpea Field 0.44 Shouse et al., 1982 Plant transpiration 1, SP Sorghum Glasshouse, pot 0.33 Plant transpiration 1, SP Sorghum Field, pot, variable evaporative dermat: 1.4 mm/d 0.07 6.0 mm/d 0.63 Plant transpiration 1, SP Sorghum Pielot 0.52 Hammer and Muchow, 1990				10 Pa/kPa	0.23 °	
Leaf photosynthesis1, SPNerium oleander pressure deficit: 10 Pa/kPaGollan et al., 1985Leaf photosynthesis1, SPCottonGlasshouse, pot0.67Constable, 1982Leaf photosynthesis1, SSoybean CottonField0.40 1.0Hearn and Constable, 1984Evapotranspiration2, SP 1, SPSoybeanField0.40 0.64Mason et al., 1980Evapotranspiration1, SAlfalfaField, variable evaporative demand: 6.3 mm/dAbdul-Jabbar et al., 1983Evapotranspiration2, SPSoybeanField, lysimeter0.20Meyer and Green, 1981Evapotranspiration2, SPSoybeanField, lysimeter0.20Meyer and Green, 1981Evapotranspiration2, SPWheatField, lysimeter0.20Meyer and Green, 1980Evapotranspiration2, SPCotton, sorghumField, lysimeter0.25Ritchie et al., 1972Evapotranspiration2, SPSunflowerField, lysimeter0.20Meyer and Green, 1980Evapotranspiration2, SPSunflowerField, lysimeter0.20Ritchie, 1973Evapotranspiration2, SPSunflowerField, lysimeter0.20Glashouse, of hydrauic and chemical (ABA)Evapotranspiration2, SPSunflowerField, lysimeter0.31Al-Khafaf et al., 1978Crop transpiration2, SPSorghumField, lysimeter0.31Al-Khafaf et al., 1973Crop transpiration2, SPSorghumField, lysimeter0.31 <td></td> <td></td> <td></td> <td>25 Pa/kPa</td> <td>0.31 °</td> <td></td>				25 Pa/kPa	0.31 °	
Leaf photosynthesis1, SPCottonGlasshouse, pot0.45 $^\circ$ Leaf photosynthesis1, SPCottonGlasshouse, pot0.67Constable, 1982Leaf photosynthesis1, SSoybean CottonField0.40Hearn and Constable, 1984Evapotranspiration2, SP SoybeanSoybeanField0.40Mason et al., 1980Evapotranspiration1, SPAlfalfaField, variable evaporative demand: 6.3 mm/dAbdul-Jabbar et al., 1983Evapotranspiration2, SPSoybeanField, lysimeter0.20Meyer and Green, 1981Evapotranspiration2, SPSoybeanField, lysimeter0.20Meyer and Green, 1980Evapotranspiration2, SPSoybeanField, lysimeter0.20Neger and Green, 1980Evapotranspiration2, SPSouffowerField, lysimeter0.20Neger and Green, 1980Evapotranspiration2, SPSunflowerField, lysimeter0.20Neger and Green, 1980Evapotranspiration2, SPSunflowerField, lysimeter0.20Neger and Green, 1980Evapotranspiration2, SPSunflowerField, lysimeter0.20Nichie et al., 1972Evapotranspiration2, SPSunflowerField, lysimeter0.20Nichie, 1973Crop transpiration2, SPSorghumField, lysimeter0.30Al-Khafaf et al., 1978Crop transpiration2, SPSorghumField, lysimeter0.30Al-Khafaf et al., 1978Crop transpiration <td< td=""><td>Leaf photosynthesis</td><td>1, SP</td><td>Nerium oleander</td><td>Glasshouse, pot; variable vapour pressure deficit:</td><td>0.40.6</td><td>Gollan et al., 1985</td></td<>	Leaf photosynthesis	1, SP	Nerium oleander	Glasshouse, pot; variable vapour pressure deficit:	0.40.6	Gollan et al., 1985
Leaf photosynthesis1, SPCottonGlasshouse, pot0.67Constable, 1982Leaf photosynthesis1, SSoybean CottonField0.40 1.0Hearn and Constable, 1984Evapotranspiration2, SP 1, SPSoybeanField, variable evaporative demant: $6.3 mm/d$ Abdul-Jabbar et al., 1980Evapotranspiration1, SAlfalfaField, variable evaporative demant: 0.40 Abdul-Jabbar et al., 1983Evapotranspiration2, SPSoybeanField, lysimeter0.20Meyer and Green, 1981Evapotranspiration2, SPWheatField, lysimeter0.20 rootsMeyer and Green, 1980Evapotranspiration2, SPWheatField, lysimeter0.25Ritchie et al., 1972Evapotranspiration2, SPCotton, sorghumField, lysimeter0.20 rootsDubbelde et al., 1982Evapotranspiration2, SPMaizeField, lysimeter0.20 rootsDubbelde et al., 1972Evapotranspiration2, SPMaizeField, lysimeter0.20 rootsDubbelde et al., 1973Evapotranspiration2, SPMaizeField, lysimeter0.20 rootsRitchie, 1973Crop transpiration2, SPSorghumField, lysimeter0.20 rootSimulation based on the combination of hydraulic and chemical (ABA) ractors in the control of stomatal conductance0.53Tardieu and Davies, 1993Crop transpiration2, SPSorghumField0.23 field, lysimeter0.28 radieu and Davies, 1993Crop tr				10 Pa/kPa 25 Pa/kPa	0.60 ° 0.45 °	
Leaf photosynthesis1, SSoybean CottonField0.40 1.0Hearn and Constable, 1984Evapotranspiration2, SPSoybeanField, variable evaporative demant: 6.3 mm/d0.40 0.40Mason et al., 1980Evapotranspiration1, SAlfalfaField, variable evaporative demant: 6.3 mm/d0.39 0.46Abdul-Jabbar et al., 1983Evapotranspiration2, SPSoybeanField, lysimeter0.20Meyer and Green, 1981Evapotranspiration2, SPWheatField, lysimeter0.20 rootsMeyer and Green, 1980Evapotranspiration2, SPCotton, sorghumField, lysimeter0.20 rootsRitchie et al., 1972Evapotranspiration2, SPSunflowerField, lysimeter0.20 rootsRitchie et al., 1972Evapotranspiration2, SPMaizeField, lysimeter0.20 rootsRitchie et al., 1972Evapotranspiration2, SPMaizeField, lysimeter0.20 rootsRitchie 1973Crop transpiration2, SPMaizeField, lysimeter0.20 root soRitchie, 1973Crop transpiration2, SPSorghumField, lysimeter0.30 scords clores in the control of stomatal conductance0.53 radice and Davies, 1993Crop transpiration2, SPSorghumField, lysimeter0.30 sorghum0.53 radices in the control of stomatal conductance0.53 radice and Davies, 1993Crop transpiration2, SPSorghumField, lysimeter0.33 radices clores in the control	Leaf photosynthesis	1, SP	Cotton	Glasshouse, pot	0.67	Constable, 1982
Evapotranspiration 2, SP 1, SP Soybean Field, variable evaporative demand: 6.3 mm/d, 0.40 0.40 Adsout et al., 1980 Evapotranspiration 1, S Alfalfa Field, variable evaporative demand: 6.3 mm/d, 0.40 Abdul-Jabbar et al., 1983 Evapotranspiration 2, SP Soybean Field, lysimeter 0.20 Meyer and Green, 1981 Evapotranspiration 2, SP Wheat Field, lysimeter First drying cycle, seminal roots only Second drying cycle, seminal + nodal 0.20 Ritchie et al., 1972 Evapotranspiration 2, SP Cotton, sorghum Field, lysimeter 0.20 Ritchie et al., 1972 Evapotranspiration 2, SP Maize Field, lysimeter 0.20 Ritchie, 1973 Evapotranspiration 2, SP Maize Field, lysimeter 0.20 Ritchie, 1973 Evapotranspiration 2, SP Maize Field, lysimeter 0.30 Ardieu and Davies, 1993 Crop transpiration 2, SP Sorghum Field, lysimeter 0.31 Al-Khafaf et al., 1978 Crop transpiration 2, SP Sorghum Field, lysimeter 0.53 Radieu and Davies, 1993 Crop transpiration 2,	Leaf photosynthesis	1, S	Soybean Cotton	Field	0.40 1.0	Hearn and Constable, 1984
Evapotranspiration1, SAlfalfaField, variable evaporative demant: 6.3 mm/dAbdul-Jabbar et al., 1983Evapotranspiration2, SPSoybeanField, lysimeter0.30 7.5 mm/dMeyer and Green, 1981Evapotranspiration2, SPWheatField, lysimeter First drying cycle, seminal roots only Second drying cycle, seminal roots only roots0.30 0.30 Second drying cycle, seminal roots only orots0.30 0.30 Second drying cycle, seminal roots only 0.30 Second drying cycle, seminal roots only roots0.30 0.30Evapotranspiration2, SPCotton, sorghumField, lysimeter0.25Ritchie et al., 1972Evapotranspiration2, SPSunflowerField, lysimeter0.20 cottivarsRitchie, 1973Evapotranspiration2, SPMaizeField, lysimeter0.31Al-Khafaf et al., 1978Crop transpiration2, SCottonField, lysimeter0.53Tardieu and Davies, 1993 of hydraulic and chemical (ABA) ractors in the control of stomatal conductance0.53Wright and Smith, 1983Crop transpiration2, SPSorghumField0.44Shouse et al., 1982Plant transpiration2, SPSorghum SorghumGlasshouse, pot field, lysimeter0.28 0.37Rosenthal et al., 1987Plant transpiration1, SMaizeField, pot, variable evaporative demattic 0.37Denmead and Shaw, 1962Plant transpiration1, SSorghum SorghumGlasshouse, pot field, lysimeter 0.37Datemat and Muchow, 1990Plant trans	Evapotranspiration	2, SP 1, SP	Soybean	Field	0.40 0.64	Mason et al., 1980
Evapotranspiration2, SPSoybeanField, lysimeter First drying cycle, seminal roots only octs0.20Meyer and Green, 1981Evapotranspiration2, SPWheatField, lysimeter First drying cycle, seminal + nodal octs0.30 Second drying cycle, seminal + nodal 0.20Meyer and Green, 1980Evapotranspiration2, SPCotton, sorghumField, lysimeter0.25Ritchie et al., 1972Evapotranspiration2, SPSunflowerField, early, mid and late maturity cultivars0.20Dubbelde et al., 1982Evapotranspiration2, SPMaizeField, lysimeter0.20Ritchie, 1973Crop transpiration2, SCottonField, lysimeter0.20Al-Khafaf et al., 1978Crop transpiration2, SPSorghumSimulation based on the combinatio ractors in the control of stomal conductance0.31Al-Khafaf et al., 1978Crop transpiration2, SPSorghumFieldSimulation based on the combinatio ractors in the control of stomal conductance0.33Wright and Smith, 1983Crop transpiration2, SPSorghumFieldNeide0.44Shouse et al., 1987Plant transpiration1, SSorghumGlasshouse, pot rield, lysimeter0.37 0.25Planteal, 1987Plant transpiration1, SPSorghumField, plysimeter root0.37 0.25Planteal, 1987Plant transpiration1, SPSorghumField, plysimeter root0.37 0.25Planteal and Shaw, 1962Plant transpiration <t< td=""><td>Evapotranspiration</td><td>1, S</td><td>Alfalfa</td><td>Field, variable evaporative demand: 6.3 mm/d 7.5 mm/d</td><td>0.39 0.46</td><td>Abdul-Jabbar et al., 1983</td></t<>	Evapotranspiration	1, S	Alfalfa	Field, variable evaporative demand: 6.3 mm/d 7.5 mm/d	0.39 0.46	Abdul-Jabbar et al., 1983
Evapotranspiration2, SPWheatField, lysimeter First drying cycle, seminal roots only ocotsMeyer and Green, 1980Evapotranspiration2, SPCotton, sorghumField, lysimeter0.20Ritchie et al., 1972Evapotranspiration2, SPSunflowerField, learly, mid and late maturity cultivars0.70Dubbelde et al., 1982Evapotranspiration2, SPMaizeField, lysimeter0.20 °Ritchie, 1973Crop transpiration2, SPMaizeField, lysimeter0.20 °Ritchie, 1973Crop transpiration2, SCottonField, lysimeter0.31Al-Khafaf et al., 1978Crop transpiration2, SPSorghumSimulation based on the combination of hydraulic and chemical (ABA) factors in the control of stomatal conductance0.53Tardieu and Davies, 1993Crop transpiration2, SPSorghumField0.44Shouse et al., 1982Plant transpiration2, SPSorghumGlasshouse, pot reid, lysimeter0.28 o.33 actionRosenthal et al., 1987Plant transpiration1, SPSorghumGlasshouse, pot reid, lysimeter0.37 o.37 actionDenmead and Shaw, 1962Plant transpiration1, SPSorghumField, pot; variable evaporative demain l.4 mm/d 6.0 m/d0.72 0.85Denmead and Shaw, 1962	Evapotranspiration	2, SP	Soybean	Field, lysimeter	0.20	Meyer and Green, 1981
Evapotranspiration2, SPCotton, sorghumField, lysimeter0.25Ritchie et al., 1972Evapotranspiration2, SPSunflowerField, early, mid and late maturity cultivars0.70Dubbelde et al., 1982Evapotranspiration2, SPMaizeField, lysimeter0.20 cRitchie, 1973Crop transpiration2, SCottonField, lysimeter0.31Al-Khafaf et al., 1978Crop transpiration2, SCottonSimulation based on the combination of hydraulic and chemical (ABA) factors in the control of stomatal conductance0.53Tardieu and Davies, 1993Crop transpiration2, SPSorghumField0.53Wright and Smith, 1983Crop transpiration2, SPCowpeaField0.44Shouse et al., 1982Plant transpiration2, SPSorghum Sorghum CottonGlasshouse, pot Glasshouse, pot (dasshouse, pot (0.250.28 (0.25Rosenthal et al., 1987Plant transpiration1, SPMaizeField, pot; variable evaporative dematurity (do mm/d)0.07 (0.85Denmead and Shaw, 1962	Evapotranspiration	2, SP	Wheat	Field, lysimeter First drying cycle, seminal roots only Second drying cycle, seminal + nodal roots	0.30 0.20	Meyer and Green, 1980
Evapotranspiration2, SPSunflowerField; early, mid and late maturity cultivars0.70Dubbelde et al., 1982Evapotranspiration2, SPMaizeField, lysimeter0.20 °Ritchie, 1973Crop transpiration2, SCottonField, lysimeter0.31Al-Khafaf et al., 1978Crop transpiration2-Simulation based on the combination of hydraulic and chemical (ABA) factors in the control of stomatal conductance0.53Tardieu and Davies, 1993Crop transpiration2, SPSorghumField0.53Wright and Smith, 1983Crop transpiration2, SPSorghumField0.44Shouse et al., 1982Plant transpiration2, SPSorghum Sorghum CottonGlasshouse, pot Field, lysimeter Glasshouse, pot toton0.28 0.37Rosenthal et al., 1987Plant transpiration1, SPMaizeField, pot; variable evaporative demati- 1.4 mm/d 6.0 mm/d0.07 0.85Denmead and Shaw, 1962Plant transpiration1, SPSorghumPots0.22Hammer and Muchow, 1990	Evapotranspiration	2, SP	Cotton, sorghum	Field, lysimeter	0.25	Ritchie et al., 1972
Evapotranspiration2, SPMaizeField, lysimeter0.20 °Ritchie, 1973Crop transpiration2, SCottonField, lysimeter0.31Al-Khafaf et al., 1978Crop transpiration2-Simulation based on the combination of hydraulic and chemical (ABA) factors in the control of stomatal conductance0.53Tardieu and Davies, 1993Crop transpiration2, SPSorghumField0.53Wright and Smith, 1983Crop transpiration2, SPCowpeaField0.44Shouse et al., 1982Plant transpiration2, SPSorghum CottonGlasshouse, pot Glasshouse, pot Cotton0.37 0.25Rosenthal et al., 1987Plant transpiration1, SMaizeField, pot; variable evaporative demati- 1.4 mm/d 0.07 0.85Denmead and Shaw, 1962Plant transpiration1, SPSorghumField, pots0.22Hammer and Muchow, 1990	Evapotranspiration	2, SP	Sunflower	Field; early, mid and late maturity cultivars	0.70	Dubbelde et al., 1982
Crop transpiration2, SCottonField, lysimeter0.31Al-Khafaf et al., 1978Crop transpiration2-Simulation based on the combination of hydraulic and chemical (ABA) factors in the control of stomatal conductance0.53Tardieu and Davies, 1993Crop transpiration2, SPSorghumField0.53Wright and Smith, 1983Crop transpiration2, SPCowpeaField0.44Shouse et al., 1982Plant transpiration2, SPSorghum Sorghum CottonGlasshouse, pot Glasshouse, pot0.28 0.25Rosenthal et al., 1987Plant transpiration1, SMaizeField, pot; variable evaporative demattic 0.07 6.0 mm/d0.07 0.85Denmead and Shaw, 1962Plant transpiration1, SPSorghumField, pots0.22Hammer and Muchow, 1990	Evapotranspiration	2, SP	Maize	Field, lysimeter	0.20 ^c	Ritchie, 1973
Crop transpiration2-Simulation based on the combination of hydraulic and chemical (ABA) factors in the control of stomatal conductance0.53Tardieu and Davies, 1993Crop transpiration2, SPSorghumField0.53Wright and Smith, 1983Crop transpiration2, SPCowpeaField0.44Shouse et al., 1982Plant transpiration2, SPSorghum Sorghum CottonGlasshouse, pot Glasshouse, pot Glasshouse, pot Otton0.28 0.25Rosenthal et al., 1987Plant transpiration1, SMaizeField, pot; variable evaporative demant: 1.4 mm/d 0.85Denmead and Shaw, 1962Plant transpiration1, SPSorghumPots0.22Hammer and Muchow, 1990	Crop transpiration	2, S	Cotton	Field, lysimeter	0.31	Al-Khafaf et al., 1978
Crop transpiration2, SPSorghumField 0.53 Wright and Smith, 1983Crop transpiration2, SPCowpeaField 0.44 Shouse et al., 1982Plant transpiration2, SPSorghum Sorghum CottonGlasshouse, pot Field, lysimeter 0.28 $0.25Rosenthal et al., 1987Plant transpiration1, SMaizeField, pot; variable evaporative demative1.4 \text{ mm/d}0.070.85Denmead and Shaw, 1962Plant transpiration1, SPSorghumPots0.22Hammer and Muchow, 1990$	Crop transpiration	2	-	Simulation based on the combination of hydraulic and chemical (ABA) factors in the control of stomatal conductance	0.53	Tardieu and Davies, 1993
Crop transpiration2, SPCowpeaField0.44Shouse et al., 1982Plant transpiration2, SPSorghum Sorghum CottonGlasshouse, pot Field, lysimeter Glasshouse, pot0.28 0.37 0.25Rosentbal et al., 1987Plant transpiration1, SMaizeField, pot; variable evaporative demand: 1.4 mm/d 0.85Denmead and Shaw, 1962Plant transpiration1, SPSorghumPots0.22Hammer and Muchow, 1990	Crop transpiration	2, SP	Sorghum	Field	0.53	Wright and Smith, 1983
Plant transpiration 2, SP Sorghum Sorghum Cotton Glasshouse, pot Field, lysimeter 0.28 0.37 0.25 Rosenthal et al., 1987 Plant transpiration 1, S Maize Field, pot; variable evaporative demand: 1.4 mm/d Denmead and Shaw, 1962 Plant transpiration 1, SP Sorghum Pots 0.22 Hammer and Muchow, 1990	Crop transpiration	2, SP	Cowpea	Field	0.44	Shouse et al., 1982
Plant transpiration 1, S Maize Field, pot; variable evaporative demand: Denmead and Shaw, 1962 1.4 mm/d 0.07 0.07 0.085 Plant transpiration 1, SP Sorghum Pots 0.22 Hammer and Muchow, 1990	Plant transpiration	2, SP	Sorghum Sorghum Cotton	Glasshouse, pot Field, lysimeter Glasshouse, pot	0.28 0.37 0.25	Rosenthal et al., 1987
Plant transpiration 1, SP Sorghum Pots 0.22 Hammer and Muchow, 1990	Plant transpiration	1, S	Maize	Field, pot; variable evaporative deman 1.4 mm/d 6.0 mm/d	d: 0.07 0.85	Denmead and Shaw, 1962
	Plant transpiration	1, SP	Sorghum	Pots	0.22	Hammer and Muchow, 1990

Table 2 (continued)						
Variable	Model ^a	Species	Growing condition	PAW _t	Source	
Plant transpiration	1, SP	Maize	Field, pot	0.33	Muchow and Sinclair, 1991	
Plant transpiration	1, SP	Black gram Pigeonpea Soybean Cowpea	Glasshouse, pot	0.42 0.36 0.33 0.26	Sinclair and Ludlow, 1986	
Plant transpiration	2, SP	Maize	Glasshouse, pot; source of variation:	0.17 to	Grant et al., 1989	
			timing of stress	0.39		
Plant transpiration	1, SP	Barley	Glasshouse, pot	0.53	Milroy and Goyne, 1995	
Stomatal conductance	1, SP	Sunflower	Growth chamber; variable vapour pressure deficit:	0.25 (Turner et al., 1985	
			10 Pa/kPa	0.35 °		
			25 F a/ KF a	0.35		
Stomatal conductance	1, SP	Nerium oleander	Glasshouse, pot; variable vapour pressure deficit:		Gollan et al., 1985	
			10 Pa/kPa	0.60 ^c		
			25 Pa/kPa	0.50 °		
Stomatal conductance	1, SP	Soybean	Field, lysimeter	0.28 ^c	Meyer and Green, 1980, Meyer and Green, 1981	
		Wheat		0.20 °	,,,,,,	
Stomatal conductance	1	Cotton	Field	0.40	Shimshi and Marani, 1971	
Stomatal conductance	1, SP	Sunflower	Glasshouse, pot	0.62	Sadras (unpublished)	
Stomatal conductance	1		Simulated (as above) Normal plant Plant with clumped roots that restrict water uptake	0.40 0.75	Tardieu and Davies, 1993	
Stomatal conductance	2, SP	Sunflower	Field, variable evaporative demand: 5.5 mm/day 8.8 mm/day	< 0.08 ^b < 0.32 ^b	Sadras et al., 1993b	

T 11 **A** (

^a Model 1: non-linear (eq. (2) or similar); Model 2: Eq. (3) or similar. When non-linear models are fitted to the data, thresholds are calculated as the PAW for which the control-to-reference ratio is 0.95. SP indicates that upper and lower limits of PAW have been determined taking into account both soil and plant factors while S indicates that these parameters were obtained as a function of soil properties only.

No response in stomatal conductance was found at the end of the experiments when PAW were 0.08 (spring) and 0.32 (summer).

^c Thresholds obtained from graphs in the original papers.

transpiration), PAW is measured in the soil of stressed plants, and a and b are fitted parameters. Alternatively, this relation has been described with two straight lines (e.g., Ritchie et al., 1972; Mason et al., 1980; Sadras et al., 1993b):

$$R = 1 \text{ if } PAW_t \le PAW \le 1 \tag{3a}$$

$$R = 1 + b(PAW - PAW_t)$$
 if $PAW < PAW_t$ (3b)

where PAW_t is the PAW threshold at which the rate

in stressed plants starts to diverge from the reference value, and b is the slope of the line (Eq. (3b)) that increases with increasing sensitivity to water deficits. In some cases this model has been further simplified (e.g., Rosenthal et al., 1987): the declining response (for PAW < PAW) is characterised by a straight line between the co-ordinates $(PAW_t, 1)$, (0,0). The model is then reduced to a one-parameter one with b = PAW_{t}^{-1} . Limitations to this approach are discussed below.

The objective definition of thresholds requires that data be fitted to models such as that described by Eq. (3), of which PAW_t is a parameter. To derive thresholds from non-linear models, an arbitrary reduction in *R* needs to be considered. In this paper, thresholds from studies reporting non-linear models were calculated as PAW for which the control-to-reference difference in the response variable is 5%. Some values had to be read from graphs but the level of error introduced by this method is likely to be small for our purposes. For instance, we read thresholds of 0.31 and 0.24 from Muchow and Sinclair (1991) (their Figs. 1 and 2) which compare with calculated thresholds of 0.33 and 0.27 (from their Eqs. (1) and (2)).

Plant variable responses were grouped in three categories: those related to tissue expansion (Table 1), gas exchange (Table 2) and plant water status (Table 3). Average thresholds for each response

variable were calculated and compared. Average thresholds were also compared to simulated thresholds for leaf water potential and stomatal conductance estimated by Tardieu and Davies (1993) with a model that accounts for the effects of hydraulic and chemical factors on stomatal conductance.

To evaluate the effect of soil type on PAW_t for leaf expansion, where possible the soil used in each experiment was classified as 'coarse' (viz. sandy and sandy-loam) or 'fine' (finer than sandy-loam).

3. Sources of variation in PAW_t

3.1. Methodological sources of variation in PAW,

Methodological variation in estimation of PAW_t can be introduced either through the estimation of PAW or through the way in which we measure the

Table 3

PAW	for	plant	water	status	variables

Variable	Model ^a	Species	Growing condition	PAWt	Source
Leaf turgor	2, S	Peanut	Field	0.45	Erickson et al., 1991
Leaf water potential	2, SP	Sunflower	Field, variable evaporative demand		Sadras et al., 1993a
			5.5 mm/d	0.66	
			8.8 mm/d	0.76	
Leaf water potential	2, SP		Field, lysimeter		Meyer and Green, 1980,
					Meyer and Green, 1981
		Wheat	Covered leaf	0.20 ^b	
		Soybean	Covered leaf	0.20 ^b	
		Soybean	Exposed leaf	0.45 ^b	
Leaf water potential	1, SP	Cotton	Glasshouse, pot	0.67	Constable, 1982
Leaf water potential	1, S	Soybean	Field	0.30 ^b	Hearn and Constable, 1984
		Cotton		1.0 5	
Leaf water potential	1		Simulated (cf. Table 2)		Tardieu and Davies, 1993
-			Normal plant	0.60 ^b	
			Plant with clumped roots	0.82 ^b	
Leaf water potential	1, SP	Nerium oleander	Glasshouse, pot; variable vapour		Gollan et al., 1985
			pressure deficit		
			10 Pa/kPa	1.0 ^b	
			25 Pa/kPa	1.0 ^b	

^a Model 1: non-linear (Eq. (2) or similar); Model 2: Eq. (3) or similar. When non-linear models are fitted to the data, thresholds are calculated as the PAW for which the control-to-reference ratio is 1.05 (for leaf water potential). SP indicates that upper and lower limits of PAW have been determined taking into account both soil and plant factors while S indicates that these parameters were obtained as a function of soil properties only.

^b Thresholds obtained from graphs in the original papers.

response of the plant or crop to soil water availability.

3.1.1. PAW determination

The definition of PAW requires an upper and lower limit of soil water content between which water is available to plants (Eq. (1)). These limits have often been considered a soil property, i.e., the water retained by soil between -0.01 and -1.5MPa of matric suction. These limits depend, however, not only on soil but also on plant characteristics and methods have been proposed to account for this by Ritchie (1974). However, as crop water uptake can be affected by nutrition, previous soil water history, compaction and other factors which can vary between seasons, the lower limit defined by Ritchie's approach may likewise vary between seasons for a given species and soil type. On heavy clays with low infiltration and drainage rates there is also difficulty in defining the upper limit of PAW.

Although most recent studies use soil/plant defined PAW, there is still variation in the definitions used to determine the lower limit of soil available water in particular (second columns in Tables 1–3). In pot experiments, for instance, the lower limit has been taken as the soil water content when transpiration rates of stressed plants were $\leq 10\%$ of the rate in well-watered controls (Sinclair and Ludlow, 1986) or the soil water content for which pot weight did not change and leaves remained wilted over a 4-day period (Rosenthal et al., 1987).

By examining the graphs of leaf expansion and transpiration vs PAW in the pot experiment of Rosenthal et al. (1987) it would appear that the definition of lower limit was accurate for sorghum but possibly not quite accurate for cotton as some transpiration still appeared to be occurring at the nominated PAW = 0. The study by Muchow and Sinclair (1991) used the approach of Sinclair and Ludlow (1986) to define PAW and shows that both transpiration and leaf expansion continued for PAW < 0. Errors in PAW, associated with PAW definition in these studies, however, would appear to be in the order of 10%. Larger errors in PAW, associated with errors in the definition of PAW have been suggested by Wright and Smith (1983). They found that sorghum crops (cv. E-57) continued water use at a rate approaching potential evaporation despite very low levels of PAW (ca. 0.1). This was attributed to an underestimation of PAW for this variety (Wright and Smith, 1983).

The calculation of PAW also requires a definition of the soil volume from which roots take up water. Definition of root depth is not a problem in pot experiments because roots usually explore most of the available soil. Pot experiments have, however, the limitation that plant responses cannot, in many cases, be directly extrapolated to field situations (e.g., Jordan and Ritchie, 1971; Dale, 1988; Wise et al., 1990; Radin, 1992; Sadras et al., 1993a, Sadras et al., 1993b).

The usual approach in field studies is to estimate an average depth that defines the soil zone from where most of the uptake occurs (e.g., Jefferies, 1993). This approach has the potential to result in very large variation in the estimated PAW and hence the PAW, derived. Rooting depth for a given species can vary widely between soil types and even show high spatial variability within a soil type. For instance, variations between 0.3 and 1.0 m within a distance of 100 m in duplex soils in Western Australia have been reported by Dracup et al. (1992) who also found species-dependent responses to soil depth. If root depth was taken as 1.0 m and penetration only occurred to 0.3 m, then when the crop had reduced the PAW in the rooted zone to 0.35, the calculated value over the nominal root zone would be ca. 0.8 (assuming initial moisture distribution is uniform).

Clearly this problem not only relates to maximum depth but also to change in rooting depth with ontogeny. Some authors have included variable soil depth in PAW calculations to account for root growth during the season (e.g., Rosenthal et al., 1987; Hammer and Muchow, 1990; Sadras et al., 1993b). Robertson and Fukai (1994) have estimated sorghum transpiration using a two-line model (cf., Eq. (3)) with a $PAW_t = 0.3$. They compared estimates based on PAW calculated for the current root zone or for the total profile, i.e., the maximum root depth. In five out of seven cases, the two methods gave similar predictions because transpiration did not decline until after the root front reached its maximum depth (i.e., after anthesis). These results were obtained under low to moderate evaporative demand (1.8 to 4.9 mm d^{-1}). The combination of high demand and soils with low PAW would lead to changes in transpiration at early crop stages when root depth differs substantially from its maximum. Under these conditions, larger differences could be expected between methods using fixed or variable root depth. Thus, in a comparison of water balance models for wheat, Francis and Pidgeon (1982) found that a model that allowed for a variable root depth performed better than others using a fixed maximum value for PAW under conditions of high evaporative demand early in the season.

Morgan and Condon (1986) demonstrated that the lower limit of extractable soil water can be strongly influenced by a genotype's ability for osmotic adjustment and turgor maintenance. Thus, intraspecific variability for osmotic adjustment, which has been reported for many crop species (Chimenti and Hall, 1993 and literature cited therein) should be considered in the definition of the lower limit of PAW.

3.1.2. Measurement of plant response variables

To characterise responses of tissue expansion to water deficits, non-destructive measurement of leaf dimensions have often been used, but a combination of leaf and stem measurements have been used by some authors (Table 1: NeSmith and Ritchie, 1992; McIntyre et al., 1993). Responses for both photosynthesis and evaporation have been established at the leaf, plant and canopy levels (Table 2). Differences in the successive resistances involved in scaling up from leaf to canopy (Jarvis and McNaughton, 1986) may be a source of variation in the responses at the various levels of organisation (see next section).

Many field studies calculate PAW, including both the soil and plant components of crop evaporation in contrast to pot studies and some field studies (e.g., Shouse et al., 1982) that only considered plant transpiration. In addition, actual evaporation rates from canopies have been estimated with different methods including soil water and energy balances. Likewise, reference evaporation has been determined with a range of methods including water balance of wellirrigated crops or plants (e.g., Denmead and Shaw, 1962), Class A Pan evaporation (e.g., Mason et al., 1980; Dubbelde et al., 1982) or estimates with Penman's or other equations (e.g., Al-Khafaf et al., 1978; Abdul-Jabbar et al., 1983). Ontogenetic changes in responses can also be considerable for both gas exchange and expansion rates.

3.2. Variation in PAW, with physiological process: tissue expansion vs. gas exchange

Soil water content seems appropriate to describe the effects of water deficits on a number of plant processes and characteristics including refraction index of sap (Shimshi and Marani, 1971), ethylene reduction by legumes (Sinclair, 1986), carbon isotope fractionation (Dupouey et al., 1993), xylem sap pH (Lösch and Schulze, 1994), leaf senescence (Mc-Cree and Fernandez, 1989), and crop water stress index based on canopy temperature (Jalali-Farahani et al., 1993). Limited data, however, precludes any systematic analysis except for the more widely investigated responses of leaf expansion and gas exchange.



.

Fig. 1. (A) Average PAW_t (\pm s.e.) for tissue expansion, leaf water potential, gas exchange and stomatal conductance. (B) Simulated PAW_t for leaf water potential and stomatal conductance (Tardieu and Davies, 1993).

Expansion of plant tissues is considered to be more sensitive to water deficits than gas exchange (see Introduction). This difference is frequently reflected by thresholds from studies in which both exchange and expansion processes have been measured under similar conditions (Rosenthal et al., 1987; Milroy and Goyne, 1995; Muchow and Sinclair, 1991; Sadras et al., 1993b). This has been presented by Ritchie (1981) and McCree and Fernandez (1989) as generalised models of the response of these processes to soil water. Our averages across species, growing conditions and methods confirm the generality of the pattern: average PAW_t was 0.61 (SE = 0.09) for expansion and 0.40 (SE = 0.03) for gas exchange (Fig. 1).

Fig. 1 shows that the average threshold for gas exchange coincided with both the average threshold for stomatal conductance (0.37 ± 0.05) and a simulated threshold for stomatal conductance calculated by Tardieu and Davies (1993). The coincidence of thresholds is only a superficial analogy of the responses of stomatal conductance and gas exchange to soil water. In fact, theory suggests that thresholds should be greater for stomatal conductance than for plant and canopy gas exchange because at these scales the responses of transpiration to a small change in stomatal conductance depend on the value of the decoupling coefficient of the transpiring unit (Jarvis and McNaughton, 1986). For the crop species analysed in this paper this coefficient ranges from 0.4 to 0.7 (cf., Jarvis and McNaughton, 1986, their Table 2) and, therefore, we could expect considerable changes in stomatal conductance are needed before crop gas exchange is affected.

The average PAW_t for leaf water potential (0.61 \pm 0.09) also coincided with both a threshold for leaf water potential calculated by Tardieu and Davies (1993) and with the average threshold for expansion (Fig. 1). Relationships between expansion and tissue water potential are discussed below.

3.3. Variation in PAW_t with plant factors

In this section we discuss variation in PAW_t between and within species and the effects of acclimatisation on PAW_t. Conditions of the root system are considered in the next section in the context of soil properties and soil/plant interactions.



In dicotyledonous plants, cell expansion occurs in leaf blades that are exposed to the air in contrast to monocots in which the extension zone is enclosed in the subtending sheaths of older leaves (Dale, 1988). Thus, the expanding tissue in monocot leaves should be exposed to a lower evaporative demand, and because of the effects of atmospheric humidity on leaf expansion (e.g., Squire et al., 1983; Waldron and Terry, 1987), we speculate that soil water thresholds for reduction in leaf expansion should be lower for monocots than for dicots. Although the range of thresholds for both plant types were similarly large (Table 1), average thresholds were consistent with this expectation (Fig. 2).

More detailed comparisons illustrate inter- and intra-specific variability in plant responses to water deficits that can be quantified with PAW, In a comparison between four grain legumes, Sinclair and Ludlow (1986) reported PAW, for plant transpiration in a range from 0.26 (cowpea) to 0.42 (black gram) (Table 2). In a comparison of 19 potato genotypes (Jefferies, 1993), intra-specific variability in leaf expansion was reflected in a range of PAW, from 1 to 0.73 (Table 1). This study also illustrates the limitation of using PAW, as a single measure of sensitivity, because some genotypes with high PAW, showed a slow decline in leaf expansion rate for PAW < PAW, (parameter b in eq. (3)). Similarly, the data of Hearn and Constable (1984) indicate that, under their experimental conditions, photosynthesis in cotton was initially more sensitive than in soybean (i.e., cotton had a greater PAW, but that soybean photosynthesis



declined faster after reaching its threshold. The description of the decline in the process rate (R) with a line through the origin after the threshold has been reached (Eq. (3b), see Experimental) should, therefore, be avoided and independent estimates of both parameters in Eq. (3) should be obtained for comparisons across the whole range of soil water content.

Plants in natural habitats and in most agronomic situations often undergo repeated drying cycles which lead to acclimatisation, i.e., less sensitivity to tissue water deficits (e.g., Brown et al., 1976; Cutler and Rains, 1977; Matthews et al., 1984, Wise et al., 1990). Acclimatised plants, therefore, could be expected to show lower PAW, than plants exposed to a single drying cycle. Exposure to a single drying cycle has, however, been more common in experiments in which PAW, has been determined. In the experiments by Meyer and Green (1980, 1981), wheat plants that where irrigated at sowing had a greater threshold for leaf expansion than plants that received no water (Table 1). Although small, the difference was in the expected direction for differences induced by acclimatisation. These authors also found a higher threshold for the response of evapotranspiration in crops exposed to a single drying cycle ($PAW_t = 0.3$) in comparison with crops exposed to a second drying cycle (PAW, = 0.2) (Table 2). They attributed these differences to differential root development (seminal roots only in the first drying cycle vs. seminal + nodal roots in the second). Acclimatisation mechanisms, however, cannot be discarded as an additional factor contributing to the lower threshold observed after two drying cycles.

Large differences in leaf water potentials necessary to trigger stomatal response were found between glasshouse (≈ -1.6 MPa) and field grown plants (< -2.8 MPa) (Jordan and Ritchie, 1971). If, as proposed by the authors, part of this difference is due to acclimatisation of field-grown plants, then significant variation could be expected between thresholds obtained with plants subjected to single or multiple episodes of water stress. Importantly, dry-wet cycles may lead to variations in the patterns of root and soil water distribution that may further influence PAW₁.

3.4. Variation in PAW_t with soil factors

There is disagreement in the literature as to whether soil type affects PAW_t . Hammer and Mu-

chow (1990) and Muchow and Sinclair (1991) found no effect of soil type on PAW_t for leaf expansion and gas exchange. On the other hand, Erickson et al. (1991) reported significant effects of soil type on PAW_t for leaf turgor. Robertson and Fukai (1994) also showed soil effects on PAW, for gas exchange.

From our calculations, thresholds for leaf expansion where generally greater in coarser soils: averaged across species and growing conditions PAW_t was 0.72 (SE = 0.09) for coarse soils compared with $PAW_t = 0.43$ (SE = 0.05) for fine soils (Fig. 2). Dynamics of water uptake (i.e., rapid removal of water from the larger pores followed by slow removal from the smaller pores) could explain the greater thresholds in sandy soils (NeSmith and Ritchie, 1992). Irrespective of the causes, the data in Fig. 2 and simulation results by Robertson and Fukai (1994) (their Table 4) suggest that PAW_t should only be extrapolated between soil types with caution.

In addition to soil texture and related hydraulic properties, other soil properties may affect PAW_t. Ludlow et al. (1989) reported a two-fold difference in PAW, for leaf expansion in a comparison between sorghum plants grown in containers of repacked soil $(PAW_t \approx 0.5)$ and plants grown in intact soil cores (PAW_t \approx 1). Non-hydraulic effects of high soil mechanical resistance on stomatal conductance and leaf expansion have been reported that could affect the response threshold for these variables (Masle and Passioura, 1987; Passioura and Gardner, 1990; Andrade et al., 1993). Passioura and Gardner (1990), for instance, found that the decline in growth of wheat seedlings occurred at higher soil water content with increasing soil density. Extremely large pores, such as worm holes, may also induce reductions in leaf expansion even with no change in the hydraulic resistance of the soil and plant in relation to soil without such biopores (Passioura and Stirzaker, 1993).

Root system properties including root hydraulic conductance, root density and distribution, and hydrotropic responses (Takahashi and Scott, 1993), may also be responsible for variations in plant responses to soil water deficits. Differences in thresholds for leaf expansion between monocots and dicots (Fig. 2) have been attributed to differential exposure of the growing regions of the leaf (see above) but differences in root hydraulic conductance and root density (Hamblin and Tennant, 1987; Connor and Sadras, 1992) may also be involved. Using a simulation model, Tardieu and Davies (1993) predicted substantially higher thresholds for stomatal conductance and leaf water potential in plants with clumped roots that reduce their ability to absorb water in comparison with 'normal-rooted' plants (Tables 2 and 3). In contrast, transpiration rates of soybean grown in large pots were influenced by soil water content but not by root density (Eavis and Taylor, 1979; cf., also Passioura, 1985).

The dependence of root hydraulic conductivity on the rooting medium (Brar et al., 1990) could lead to soil/root interactions with effects on PAW_t. Hydraulic lift and soil water flux from non-rooted layers (Blum and Johnson, 1992; Richards and Caldwell, 1987; Tardieu and Katerji, 1991; Xu and Bland, 1993) are also potential sources of variation in PAW_t especially in soils with very heterogeneous water distribution.

3.5. Variations in PAW_t with evaporative demand

With few exceptions (Gollan et al., 1985; Turner et al., 1985; cf., Table 2), PAW, increased with increasing evaporative demand. This applies to tissue expansion (Table 1: McIntyre et al., 1993; Sadras et al., 1993a); gas exchange (Table 2: Denmead and Shaw, 1962; Abdul-Jabbar et al., 1983); stomatal conductance (Table 2: Sadras et al., 1993b); and leaf water potential (Table 3: Sadras et al., 1993a). The effects of evaporative demand on PAW, could involve mechanisms by which plants may sense soil (Davies and Zhang, 1991) and atmospheric (Aphalo and Jarvis, 1991) water status independently of each other. Alternatively, water potential may integrate soil and atmospheric water status so that leaf responses may be associated with changes in it. Parallel changes in thresholds for leaf expansion and leaf water potential with evaporative demand have been reported (Sadras et al., 1993a) that are consistent with this hypothesis. Using a simple model of leaf expansion and crop water balance, Villalobos and Sadras (unpublished, 1991) found that simulated plant longevity (i.e., time to PAW ≈ 0) in an environment with terminal drought was greater in plants whose leaf growth was affected by an integrated soil/atmospheric index of dryness than in plants that only responded to soil water.

On the other hand, it has been argued that hormonal root signals are relevant in the control of shoot responses to soil drying (Davies and Zhang, 1991). The often observed lack of correlation between growth and turgor, however, is not sufficient to disprove the role of turgor in growth (Feng et al., 1994; cf., also Pardossi et al., 1994). While it is generally accepted that hormones are important in transducing environmental conditions into growth responses, "there is surprisingly little definitive evidence for the role of any hormone in regulating either shoot or root growth in soils of low water potential" (Munns and Sharp, 1993). Importantly, a solution for the apparent conflict on whether hydraulic or metabolic factors control leaf processes in water-stressed plants (Kramer, 1988; Passioura, 1988b) has been attempted in a number of recent studies that integrate both types of factors (e.g., Matyssek et al., 1991; Tardieu and Davies, 1993; Feng et al., 1994; Passioura, 1994; Correia and Pereira, 1995).

4. Conclusions

The simplicity of characterising plant responses to water stress in terms of PAW_t is attractive. Despite the sources of variability that generate PAW_t values over almost the whole possible range of PAW, thresholds seem to be sufficiently sensitive to account for the greater responsiveness to water deficits of tissue expansion relative to gas exchange. Also, soil water thresholds for leaf expansion seem to be sufficiently sensitive to differentiate between plant and soil types.

It should be recognised, however, that PAW_t is not static for a given process. Evaporative demand has a significant effect on PAW_t for both leaf expansion and gas exchange. Soil texture is a likely source of variation in thresholds for evaporation and care should be taken in extrapolations between extreme soil textures. The influence of soil type on the responses of leaf expansion to soil water deficits deserves further research. This is important not only for modelling but also for the understanding of shoot responses induced by root signals. More work is also needed to assess the effects of acclimatisation and root distribution on soil water thresholds for both gas exchange and expansion. Overall, our analysis showed that variation in measured PAW_t is consistent with known physiological responses to soil, atmospheric and plant factors. The decision to include factors affecting PAW_t in simulation models will depend on: (a) the impact of PAW_t variations on the relevant model outputs, and (b) the accuracy required for specific modelling purposes. The convenience of using a fixed or variable PAW_t can be evaluated by sensitivity analysis, as shown by Robertson and Fukai (1994). Even though the use of constant PAW_t values may be appropriate for many modelling exercises, the identification of plant, soil and atmospheric factors affecting PAW_t in this paper makes explicit the assumptions underlying the use of fixed soil water thresholds.

Acknowledgements

We thank O. Denmead, M. Robertson, J. Passioura, M. Stapper for their comments on the manuscript, and the Cotton Research and Development Corporation of Australia for financial support (Projects CSP39C, CSP28C).

References

- Abdul-Jabbar, A.S., Sammis T.W., Lugg, D.G., Kallsen, C.E. and Smeal D., 1983. Water use by alfalfa, maize, and barley as influenced by available soil water. Agric. Water. Manag., 6: 351–363.
- Al-Khafaf, S., Wirenga, P.J. and Williams, B.C., 1978. Evaporative flux from irrigated cotton as related to leaf area index, soil water, and evaporative demand. Agron. J., 70: 912–917.
- Andrade, A., Wolfe, D.W. and Fereres, E., 1993. Leaf expansion, photosynthesis, and water relations of sunflower plants grown on compacted soil. Plant Soil, 149: 175–184.
- Aphalo, P.J. and Jarvis, P.G., 1991. Do stomata respond to relative humidity? Plant Cell Environment, 14: 127-132.
- Blum, A. and Johnson, J.W., 1992. Transfer of water from roots into dry soil and the effect of wheat water relations and growth. Plant Soil, 145: 141–149.
- Boyer, J.S., 1970. Leaf enlargement and metabolic rates in corn, soybean and sunflower at various leaf water potentials. Plant Physiol., 43: 1056-1062.
- Boyer, J.S., 1982. Plant productivity and environment. Science, 218: 543-548.
- Brar, G.S., McMichael, B.L. and Taylor, H.M., 1990. Hydraulic conductivity of cotton roots as influenced by plant age and rooting medium. Agron. J., 83: 264–266.

- Brown, K.W., Jordan, W.R. and Thomas, J.C., 1976. Water stress induced alterations of the stomatal response to decrease in leaf water potential. Physiol. Plant, 37: 1–5.
- Chaves, M.M., 1991. Effects of water deficits on carbon assimilation. J. Exp. Bot., 42: 1–16.
- Chimenti, C.A. and Hall, A.J., 1993. Genetic variation and changes with ontogeny of osmotic adjustment in sunflower (*Helianthus* annuus L.). Euphytica, 71: 201–210.
- Connor, D.J. and Jones, T.R., 1985. Response of sunflower to strategies of irrigation. II. Morphological and physiological responses to water stress. Field Crops Res., 12: 91–103.
- Connor, D.J. and Sadras, V.O., 1992. Physiology of yield expression in sunflower. Field Crops Res., 30: 333–389.
- Constable, G.A., 1982. Carbon fixation and distribution in cotton: implications of single leaf measurements to plant performance. PhD Thesis, Australian National University.
- Correia, M.J. and Pereira, J.S., 1995. The control of leaf conductance of white lupin by xylem ABA concentration decreases with the severity of water deficits. J. Exp. Bot., 46: 101–110.
- Cutler, J.M. and Rains, D.W., 1977. Effects of irrigation history on responses of cotton to subsequent water stress. Crop Sci., 17: 329–335.
- Dale, J.E., 1988. The control of leaf expansion. Annu. Rev. Plant Physiol. Plant Mol. Biol., 39: 267–295.
- Davies, W.J. and Zhang, J., 1991. Root signals and the regulation of growth and development of plants in drying soil. Annu. Rev. Plant Physiol. Plant Mol. Biol., 42: 55–76.
- Denmead, O.T. and Shaw, R.H., 1962. Availability of soil water to plants as affected by soil moisture content and meteorological conditions. Agron. J., 45: 385–390.
- Dubbelde, E.A., Harris, H.C. and McWilliam, J.R., 1982. Water requirement of sunflower in a semi-arid environment. In: Proc. 10th Int. Sunflower Conf., 14-18 March 1982, Surfers Paradis², Aust. Int. Sunflower Assoc., Toowoomba, Australia, pp. 62-65.
- Dupouey, J.L., Leavitt, S., Choisnel, E. and Jourdain, S., 1993. Modelling carbon isotope fractionation in tree rings based on effective evapotranspiration and soil water status. Plant Cell Environ., 16: 939–947.
- Dracup, M., Belford, R.K. and Gregory, P.J., 1992. Constraints to root growth of wheat and lupin crops in duplex soils. Aust. J. Exp. Agric., 32: 947–961.
- Eavis, B.W. and Taylor, H.M., 1979. Transpiration of soybeans as related to leaf area, root length, and soil water content. Agron. J., 71: 441-445.
- Erickson, P.I., Ketring, D.L. and Stone, J.F., 1991. Response of internal tissue water balance of peanut to soil water. Agron. J., 83: 248-253.
- Feng, Y., Li, X. and Boersma, L., 1994. Roles of osmotic adjustment and turgor potential in leaf area expansion. Physiol. Plant., 90: 1–8.
- Francis, P.E. and Pidgeon, J.D., 1982. A model for estimating soil mositure deficits under cereal crops in Britain. 2. Performance. J. Agr. Sci. Camb., 98: 663–678.
- Gollan, T., Turner, N.C. and Schulze, E-.D., 1985. The responses of stomata and leaf gas exchange to vapour pressure deficits

and soil water content. III. In the sclerophyllous woody species *Nerium oleander*. Oecologia, 65: 356–362.

- Grant, R.F., Jackson, B.S., Kiniry, J.R. and Arkin, G.F., 1989. Water deficit timing effects on yield components in maize. Agron. J., 81: 61–65.
- Hamblin, A. and Tennant, D., 1987. Root length density and water uptake in cereals and grain legumes: how well are they correlated? Aust. J. Agric. Res., 38: 513–527.
- Hammer, G.L. and Muchow, R.C., 1990. Quantifying climatic risk to sorghum in Australia's semiarid tropics and subtropics: model development and simulation. In: R.C. Muchow and J.A. Bellamy (Editors), Climatic Risk in Crop Production: Models and Management for the Semi-arid Tropics and Subtropics. C.A.B. International, pp. 205–232.
- Hearn, A.B., 1994. OZCOT: A simulation model for cotton crop management. Agric. Syst., 44: 257–299.
- Hearn, A.B. and Constable, G.A., 1984. Irrigation for crops in a sub-humid environment. VII Evaluation of irrigation strategies for cotton. Irr. Sci., 5: 75–94.
- Hsiao, T.C., Acevedo, E., Fereres, E. and Henderson, D.W., 1976. Water stress, growth and osmotic adjustment. Phil. Trans. R. Soc. Lond. B., 273: 479–500.
- Hsiao, T.C., Silk, W.K. and Jing, J., 1985. Leaf growth and water deficits: biophysical effects. In: N.R., Baker, W.J. Davies and C.K. Ong (Editors), Control of Leaf Growth. Society for Exp. Biol. Seminar Series 27, Cambridge University Press, Cambridge, pp 239–266.
- Jalali-Farahani, H.R., Slack, D.C., Kopec, D.M. and Matthias, A.D., 1993. Crop water stress index models for bermudagrass turf: a comparison. Agron. J., 85: 1210–1217.
- Jarvis, P.G., McNaughton, K.G., 1986. Stomatal control of transpiration: scaling up from leaf to region. Adv. Ecol. Res., 15: 1–49.
- Jefferies, R.A., 1993. Responses of potato to drought. I. Expansion of individual leaves and osmotic adjustment. Ann. Appl. Biol., 122: 93–104.
- Jefferies, R.A. and Mackerron, D.K.L., 1989. Radiation interception and growth of irrigated and droughted potato (*Solanum tuberosum*). Field Crops Res., 22: 101–112.
- Jones, C.A. and Kiniry, J.R., 1986. CERES-Maize: A simulation model of maize growth and development. Texas A and M University Press.
- Jones, H.G. and Corlett, J.E., 1992. Current topics in drought physiology. J. Agric. Sci., 119: 291–296.
- Jordan, W.R. and Ritchie, J.T., 1971. Influence of soil water stress on evaporation, root absorption, and internal water status of cotton. Plant Physiol., 48: 783–788.
- Kramer, P.J., 1988. Changing concepts regarding plant water relations. Plant Cell Environ., 11: 565–568.
- Lawlor, D.W. and Leach, J.E., 1985. Leaf growth and water deficits: biochemistry in relation to biophysics. In: N.R. Baker, W.J. Davies and C.K. Ong (Editors), Control of leaf growth. Society for Exp. Biol. Seminar Series 27, Cambridge University Press, Cambridge, pp. 267–294.

Legg, P.J., Day, W., Lawlor, D.W. and Parkinson, K.J., 1979. The

effects of drought on barley growth: models and measurements showing the relative importance of leaf area and photosynthetic rate. J. Agric. Sci., 92: 703–716.

- Lösch, R. and Schulze, E.D., 1994. Internal coordination of plant responses to drought and evaporation demand. In: E.D. Schulze and M.M. Caldwell (Editors), Ecophysiology of Photosynthesis, Ecological studies 100, Springer Verlag, pp. 185–204.
- Ludlow, M.M., Sommer, K.J., Flower, D.J., Ferraris, R. and So, H.B., 1989. Influence of root signals resulting from soil dehydration and high soil strength on the growth of crop plants. Current Topics Plant Biochem. Physiol., 8: 81–99.
- Masle, J. and Passioura, J.B., 1987. The effect of soil strength on the growth of young wheat plants. Aust. J. Plant Physiol., 14: 643–656.
- Mason, W.K, Constable, G.A. and Smith, R.C.G., 1980. Irrigation for crops in a sub-humid environment. II. The water requirements of soybeans. Irr. Sci., 2:13–22.
- Matthews, M.A., Van Volkenburgh, E. and Boyer, J.S., 1984. Acclimation of leaf growth to low water potentials in sunflower. Plant Cell Environ., 7: 199–206.
- Matyssek, R., Maruyama, S. and Boyer, J.S., 1991. Growth induced water potentials may mobilize internal water for growth. Plant Cell Environ., 14: 917–923.
- McCree, K.J. and Fernandez, C.J., 1989. Simulation model for studying physiological water stress responses of whole plants. Crop Sci., 29: 353–360.
- McIntyre, B.N.D., Flower, D.J. and Riha, S.J., 1993. Temperature and soil water status effects on radiation use and growth of pearl millet in a semi-arid environment. Agric. Forest Meteorol., 66: 211–227.
- McWilliam, J.R., 1986. The national and international importance of drought and salinity effects on agricultural production. Aust. J. Plant Physiol., 13: 1–13.
- Meyer, W.S. and Green, G.C., 1980. Water use by wheat and plant indicators of available soil water. Agron. J., 72: 253–257.
- Meyer, W.S. and Green, G.C., 1981. Plant indicators of wheat and soybean crop water stress. Irrig. Sci., 2: 167–176.
- Milroy, S.P. and Goyne, P.J., 1995. Leaf area development in barley — Model construction and response to soil moisture status. Aust. J. Agric. Res., 46: 845–860.
- Morgan, J.M. and Condon, A.G., 1986. Water use, grain yield, and osmoregulation in wheat. Aust. J. Plant Physiol., 13: 523–532.
- Muchow, R.C. and Sinclair, T.R., 1991. Water deficit effects on maize yields modelled under current and "greenhouse" climates. Agron. J., 83: 1052–1059.
- Munns, R. and Sharp, R.E., 1993. Involvement of abscisic acid in controlling plant growth in soils of low water potential. Aust. J. Plant Physiol., 20: 425–437.
- NeSmith, D.S. and Ritchie, J.T., 1992. Short- and long-term responses of corn to pre-anthesis soil water deficit. Agron. J., 84: 107–113.
- Pardossi, A., Prichard, J. and Tomos, A.D., 1994. Leaf illumination and root cooling inhibit bean leaf expansion by decreasing turgor pressure. J. Exp. Bot., 45: 415–422.

- Passioura, J.B., 1985. Roots and water economy of wheat. In: W. Day and R.C. Atkin (Editors), Wheat growth and Modelling. Plenum Publishing Corporation, New York, pp. 185–197.
- Passioura, J.B., 1988a. Root signals control leaf expansion in wheat seedlings growing in drying soil. Aust. J. Plant Physiol., 15: 687-693.
- Passioura, J.B., 1988b. Response to Dr P.J. Kramer's article, "Changing concepts regarding plant water relations". Plant Cell Environ., 11: 569–571.
- Passioura, J.B., 1994. The physical chemistry of the primary cell wall: implications for the control of expansion rate. J. Exp. Bot., 45: 1675–1682.
- Passioura, J.B. and Gardner, P.A., 1990. Control of leaf expansion in wheat seedlings growing in drying soil. Aust. J. Plant Physiol., 17: 149–157.
- Passioura, J.B. and Stirzaker, R.J., 1993. Feedforward responses of plants to physically inhospitable soils. In: International Crop Science I, Crop Science Society of America, pp. 715– 719.
- Radin, J.W., 1992. Reconciling water-use efficiencies of cotton in field and laboratory studies. Crop Sci., 32: 13-18.
- Rawitz, E., 1969. The dependence of growth rate and transpiration rate on plant and soil physical parameters under controlled conditions. Soil Sci., 110: 172–182.
- Richards, J.H. and Caldwell, M.M., 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisa tridentata* roots. Oecologia, 73: 486–489.
- Ritchie, J.T., 1973. Influence of soil water status and meteorological conditions on evaporation from a corn canopy. Agron. J., 65: 893–897.
- Ritchie, J.T., 1974. Evaluating irrigation needs for south eastern U.S.A.. In: Contribution of Irrigation and Drainage to World Food Supply. Proc. Irrig and Drainage Division of the American Soc of Civil Engineers (ASAE). Special conference, Biloxi, MS, 14–16 August, Am. Soc. Civil Eng., N.Y., pp. 262–279.
- Ritchie, J.T., 1981. Water dynamics in the soil-plant-atmosphere system. Plant Soil, 58: 81–96.
- Ritchie, J.T., Burnett, E. and Henderson, R.C., 1972. Dryland evaporative flux in a subhumid climate: III Soil water influence. Agron. J., 64: 168–173.
- Robertson, M.J. and Fukai, S., 1994. Comparison between models for grain sorghum under continuous soil drying. Field Crops Res., 36: 145–160.
- Rosenthal, W.D., Arkin, F.G., Shouse, P.J. and Jordan, W.R., 1987. Water deficit effects on transpiration and leaf growth. Agron. J., 79: 1019–1026.
- Sadras, V.O., Whitfield, D.M. and Connor, D.J., 1991. Regulation of evapotranspiration and its partitioning between transpiration and soil evaporation by sunflower crops. A comparison between hybrids of different stature. Field Crops Res., 28: 17–37.
- Sadras, V.O., Villalobos, F.J., Fereres, E. and Wolfe, D.W., 1993a. Leaf responses to soil water deficits: comparative sensitivity of leaf expansion rate and leaf conductance in field-grown sunflower (*Helianthus annuus* L.). Plant Soil, 153: 189–194.

- Sadras, V.O., Villalobos, F.J. and Fereres, E. 1993b. Leaf expansion in field-grown sunflower in response to soil and leaf water status. Agron. J., 85: 564–570.
- Schulze, E.D., Robichauz, R.H., Grace, J., Rundel, P.W and Ehleringer, J.R., 1987. Plant water balance. BioSci., 37: 30–37.
- Shimshi, D. and Marani, A., 1971. Effects of soil moisture stress on two varieties of upland cotton in Israel. II. The Northern Negev region. Expl. Agric., 7: 225–239.
- Shouse, P., Jury, W.A., Stoltzy, L.H. and Dasberg, S., 1982. Field measurement and modelling of cowpea water use and yield under stressed and well-watered growth conditions. Hilgardia, 50: 1–25.
- Sinclair, T.R., 1986. Water and nitrogen limitations in soybean grain production. I. Model development. Field Crops Res., 15: 125-141.
- Sinclair, T.R. and Ludlow, M.M., 1986. Influence of soil water supply on the plant water balance of four tropical grain legumes. Aust. J. Plant Physiol., 13: 329-341.
- Squire, G.R., Black, C.R. and Ong, C.K., 1983. Responses to saturation deficit of leaf extension in a stand of pearl millet (*Pennisetum typhoides* S. and H.). II. Dependence on leaf water status and irradiance. J. Exp. Bot. 34: 856–865.
- Sumayo, C.R., Kanemasu, E.T. and Hodges, T., 1977. Soil mositure effects on transpiration and net carbon dioxide exchange of sorghum. Agric. Meteorol., 18: 401–408.
- Takahashi, H. and Scott, T.K., 1993. Intensity of hydrostimulation for the induction of root hydrotropism and its sensing by the root cap. Plant Cell Environ., 16: 99–103.
- Tardieu, F. and Davies, W.J., 1993. Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants. Plant Cell Environ., 16: 341–349.
- Tardieu, F. and Katerji, N., 1991. Plant responses to the soil water reserve: consequences of the root system environment. Irrig. Sci., 12: 145–152.
- Turner, N.C., 1986. Crop water deficits: a decade of progress. Adv. Agron., 39: 1–51.
- Turner, N.C., Schulze, E.D. and Gollan, T., 1985. The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. II. In the mesophytic species *Helianthus annuus*. Oecologia, 65: 348–355.
- Waldron, L.J. and Terry, N. 1987. The influence of atmospheric humidity on leaf expansion in *Beta vulgaris* L. Planta, 170: 336–342.
- Wise, R.R., Frederick, J.R., Alm, D.M., Kramer, D.M, Hesketh, J.D., Crofts, A.R. and Ort, D.R., 1990. Investigation of the limitations to photosynthesis induced by leaf water deficit in field grown sunflower (*Helianthus annuus* L.). Plant Cell Environ., 13: 923–931.
- Wright, G.C. and Smith, R.C.G., 1983. Differences between two grain sorghum genotypes in adaptation to stress. II. Root water uptake and water use. Aust. J. Agric. Res., 34: 627–636.
- Xu, X. and Bland, W.L., 1993. Reverse water flow in sorghum roots. Agron. J., 85: 384–388.