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Modelling the effects of soil water limitations on transpiration and stomatal regulation of cauliflower

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Abstract

Quantitative knowledge of the drought adaptation processes of crops is an important prerequisite for efficient irrigation management. To study the adaptation of stomatal resistance and transpiration of cauliflower to three different drought situations an experiment using containers with 220 l of soil volume was conducted with three different water supply regimes to obtain a wide variation of plant reactions in time and intensity. One model of transpiration and three models of stomatal conductance based on either soil water potential, leaf water potential, or root signals were developed and parameterised with the experimental data. Specific transpiration, i.e. transpiration per unit leaf area, could be well described with a model based on soil water potential, but the threshold water potential below which specific transpiration declined was dependent on the atmospheric evaporative demand, characterised by potential transpiration. Stomatal resistance of unstressed plants was dependent on the radiation environment, and the threshold soil water potential also increased with increasing atmospheric transpiration requirement. Models using leaf water potential or simulated stomatal closure based on xylem ABA concentration gave also satisfactory descriptions of the experimental data but had other shortcomings like high correlations between model parameters and difficult input requirements that limit their usefulness for the prediction of effects of water limitations.

1. Introduction

The precise determination of irrigation water requirement is an important prerequisite for high irrigation water use efficiency. Irrigation water requirement is a function of the fluxes in the soil–plant–atmosphere system of which transpiration usually is the most important in closed crop canopies. Since the physical measurement of transpiration is very laborious, it is often calculated using soil–crop models. These models frequently quantify actual transpiration, T_{act}, on the basis of reference transpiration, T_{ref}, which is often described using the Penman–Monteith equation (Monteith, 1965) or functions derived from it (Jones and Tardieu, 1998). Reference transpiration, however, does not account for water supply limitations.

Actual transpiration under limited water supply then is calculated by multiplication of T_{ref} with a reduction factor depending either on the proportion of plant available water (Hammer and Muchow, 1994; Manschadi et al., 1998), relative soil water content (Teitinen et al., 1994), or soil water potential in the rooting zone (Belmans et al., 1983; Swan et al., 1990) or on xylem water potential (Stockle et al., 1994).

More mechanistic models calculate T_{act} also using the Penman–Monteith equation, but adapt canopy resistance through stomatal resistance, rs, to actual water supply. In these models, stomatal resistance is expressed using leaf water potential and vapour pressure saturation deficit of the air (Reid, 1990), turgor pressure of guard cells and plant hormonal activity (Johnson et al., 1991), shoot relative water content and CO_2 partial pressure (Thornley, 1996), photosynthetically active radiation (PAR) and leaf water potential (Braud et al., 1995), leaf water potential and global radiation (Lynn and Carlson, 1990), or leaf water potential, air vapour pressure deficit, and PAR (Olioso et al., 1996). In crop water models combined with photosynthesis models (Friend, 1995; Leuning, 1995), rs is not only considered dependent on environmental parameters like saturation deficit,

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E-mail address: stuetzel@gem.uni-hannover.de (H. Stützel).
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temperature and CO_2-concentration, but also on plant assimilation rate or xylem abscisic acid concentration (Tardieu et al., 1993).

The large number of model concepts mentioned above as well as other research, e.g. by Bunce (1997), Jarvis and Davies (1998), Jones (1998), Jones and Tardieu (1998), Monteith (1995) or Turner (1991) indicate that the mechanisms of stomatal regulation are either not fully understood.

The objective of the work, therefore, was to quantify the response of cauliflower to soil water limitations. In this paper, relationships between water supply, transpiration and stomatal regulation are sought using one model for direct calculation of specific transpiration and three models for stomatal regulation, which were developed based on different hypotheses and which differ in their complexity and in number of input variables and parameters.

2. Materials and methods

2.1. Experiment

One cauliflower plant was planted on 2 May 1997 in each of 16 containers with $0.250 \, m^3$ volume (0.58 m diameter, 0.95 m height) filled with loess soil (1% organic C, $1.35 \, Mg \, m^{-3}$ soil bulk density) to a depth of 0.87 m. Containers were placed in an unheated, glass roofed rainout shelter with mesh wire walls in Hannover, Germany (latitude 52.2°N, 54 m a.s.l.), and allocated to four irrigation treatments (Table 1) with four replications. Containers were spaced ca. 1 m (center to center) to avoid competition between neighboring plants. At the start of the experiment mineral nutrient solution containing 15% N, 7% P_2O_5, 22% K_2O and 6% MgO was added to reach 9.4 g N per container in the upper 30 cm. To prevent evaporation the soil surface was covered with a 5 cm layer of quartz gravel. Before planting, the water content in containers of irrigation treatments W1, W2 and W4 was adjusted to 90% water holding capacity (WHC), corresponding to a mean soil water potential of −10 kPa and 60 l of total water of which 38 l were available. Containers of treatment W3 were adjusted to only 75% WHC initially to ensure drought stress during the second irrigation phase. During the first irrigation phase, 0–20 days after planting (DAP), all plants were irrigated optimally (as W1, see below) to provide good conditions for plant establishment. Thereafter, water supply was varied at four levels: the optimal treatment (W1) was watered when soil water potential dropped below −20 kPa in 0–30 cm depth. The containers of the moderate stress treatment

Table 1
Amounts of water applied to the four irrigation treatments (DAP: days after planting)

Irrigation treatments	Water applied (l plant^{-1})		
	0–20 DAP	21–42 DAP	43–68 DAP
Optimal (W1)	7.5	24	92
Moderate stress (W2)	7.5	12	46
Intermittent stress (W3)	7.5	–	92
Severe stress (W4)	7.5	–	–

Table 2
Plant and soil measurements (DAP: days after planting)

Parameter	Measurement time/interval
Weather parameters	Hourly
Transpiration	1–3 days intervals
Soil water potential	1–3 days intervals
Plant dry mass	68 DAP
Leaf area	
Destructively	68 DAP
Non-destructively	Twice per week
Root growth	
Minirhizotrone method	Weekly
Soil cores	68 DAP
Leaf water potential	27, 33, 42, 45, 49, 52, 55, 61 DAP
Stomatal resistance	21, 24, 26, 27, 28, 32, 34, 40, 42, 45, 47, 49, 52, 55, 59, 61 DAP
Leaf gas exchange	35, 39, 42, 45, 47, 49, 52, 55, 61 DAP

(W2) received only half the amount of irrigation water of W1. Plants of W3 were not watered in the phase 21–42 DAP, and optimally irrigated in the phase 43–68 DAP. Plants of the severe stress treatment (W4) were not watered after day 20 after planting. The amounts of water given to each treatment depended on the transpiration of the plants in W1 and are given in Table 1.

2.2. Measurements

Plant measurements taken and their temporal resolution are shown in Table 2. Global radiation, relative humidity, and air temperature were measured hourly using an automatic weather station next to the experiment.

Actual transpiration, T_{act}, was determined by weighing the containers between 5:30 and 8:00 h. Specific actual transpiration rate, T_{actL}, was calculated as the ratio between T_{act} and turgescent leaf area (see below). As a measure of specific potential transpiration rate, T_{potL}, daily values of T_{actL} of optimally supplied plants (W1) were taken. T_{actL} was used instead of T_{act} because leaf areas differed increasingly between treatments as the experiment progressed. Relative transpiration rates, T_{rel}, characterising the effects of stress treatments in relation to optimally watered control were therefore calculated as the ratios between T_{actL} of W2–W4, and T_{potL}.

Soil water potential was measured using tensiometers placed at 30, 55, and 75 cm depth. In addition, TDR sensors (Trase, Soilmoisture Equipment Corp., Santa Barbara, USA) were placed horizontally in 15, 30, 55 and 75 cm depth for measurement of volumetric soil moisture content. When tensiometer readings fell below −60 kPa, soil water potentials were calculated from volumetric soil water contents using the soil water retention curve. Mean soil water potential in the rooted soil, Ψ_S, was calculated as average over the three depths. Since root distribution was relatively homogeneous in the rooted zone within the containers, soil moisture did not vary greatly so that averaging over depths seemed to be justified. In the intermittent stress treatment after rewatering the upper two depths were used only since measurements had shown that more than 95% of the water was taken up from these layers. For determination of plant dry matter cauliflower plants were harvested at the end of the experiment

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and separated into senescent leaves, turgescent leaves, stem and curd. The area of each of these leaves, LA_i, was determined using an optical leaf area meter (Li-3100; Licor Inc., Lincoln, NE, USA). For each leaf i, length, LL_i, and width, LW_i, were measured twice per week for non-destructive leaf area determination. The area of each leaf, LA_i, was calculated using the calibration function:

$$LA_i = 0.000062(LL_i LW_i)^2 + 0.711(LL_i LW_i),$$

$$r^2 = 0.98, \quad n = 1072 \tag{1}$$

Root growth was observed during the growth of the plants using the minirhizotrone method. Three Perspex tubes were placed in the soil at depths of 10–40, 30–65 and 55–80 cm. An endoscope (Technoskop; Wolf, Knittlingen, Germany) equipped with a light projector (Type 4024; Wolf, Knittlingen, Germany) was used to determine rooting depth.

Stomatal resistances were measured using a porometer (Li-1600, Licor Inc., Lincoln, NE, USA) ± 1 h around solar noon on several leaves of different age. For each plant, mean stomatal resistance, rs, was calculated as the average over all leaves measured. To characterise plant water status, leaf water potential, Ψ_L, was determined in the youngest fully expanded leaves, parallel to porometer measurements. Leaf discs of 8 mm diameter were punched using a cork borer and placed in a psychrometer (C52; Wescor Inc., Logan, USA) connected to a data logger (CR7; Campbell Scientific Ltd., Leicestershire, UK) operating in psychrometer mode. After 240 min Ψ_L was measured. Cooling time was 3–12 s.

Daily courses of transpiration were obtained by measuring one container per treatment at 40, 46, 48 and 54 DAP between 7:00 and 19:00 h. In each of these containers also soil water potentials, volumetric soil water contents and stomatal resistances were measured. In addition, leaf water potentials of the youngest fully developed leaf of each plant were determined at 7:00, 11:00, 13:00, 15:00 and 19:00 h. T_{actL}, T_{potL}, and T_{rel}, were calculated as described above.

Daily mean temperatures were calculated as the mean of continuously measured air temperatures. Photosynthetically active radiation, PAR, was calculated as 50% of the continuously measured global radiation, R_G (Szeicz, 1974) and taking the transmissivity of the glass roof into account:

$$PAR = R_G 0.5 \times 0.67 \tag{2}$$

Hourly values of vapour saturation deficit of the air, SD, calculated according to Smith (1992) were averaged to obtain daily mean saturation deficit, SD_{ave}.

2.3. Models

The transpiration model directly predicts transpiration as a function of soil water potential. The actual transpiration per unit of leaf area, T_{actL}, is assumed to equal T_{potL} until a soil water potential threshold in the rooting zone, Ψ_{St}, is reached. Between Ψ_{St} and the soil water potential at permanent wilting point, Ψ_{PWP}, transpiration is assumed to decrease linearly with the (decadic) logarithm of soil water potential. T_{rel} therefore

equals 1 until Ψ_{St} is reached, and declines to 0 at Ψ_{PWP}:

$$T_{actL} = \begin{cases} T_{potL} & \Psi_S \geq \Psi_{St} \\ m_{Tact} \log(|\Psi_S|) + f1_{Tact} & \Psi_S > \Psi_{St} > \Psi_{PWP} \\ 0 & \Psi_S \leq \Psi_{PWP} \end{cases} \tag{3}$$

with $m_{Tact} = T_{pot}/(\log(|\Psi_{St}|) - \log(|\Psi_{PWP}|))$, $f1_{Tact} = -m_{Tact}\log(|\Psi_{PWP}|)$ and $\Psi_{PWP} = -1585$ kPa. For parameterisation all 369 data sets containing measurements of soil water potentials and daily transpiration throughout the growing cycle were used.

To quantify the influence of water supply on mean stomatal resistance, rs, three models for stomatal regulation are constructed. In stomata model 1, rs is primarily dependent on Ψ_S. A linear-and-plateau function similar to Eq. (3) is used:

$$rs = \begin{cases} rs_{min} & \Psi_S \geq \Psi_{Srs} \\ rs_{min} + m_{Srs} \log(|\Psi_S|) & \Psi_{Srs} > \Psi_S > \Psi_{PWP} \\ rs_{max} & \Psi_S \leq \Psi_{PWP} \end{cases} \tag{4}$$

with rs_{min} and rs_{max} denoting minimum and maximum stomatal resistances, Ψ_{Srs} denoting the soil water potential threshold at which stomata begin to close, and $m_{Srs} = rs_{max}/\log(|\Psi_{PWP}|)$.

Since transpiration requirement influences rs (Monteith, 1995; Mott and Parkhurst, 1991), Ψ_{Srs} was assumed to depend on transpiration requirement. Hourly values of saturation deficit which is usually closely related to potential transpiration (Jones, 1992), were used as a measure of transpiration requirement:

$$\log(|\Psi_{Srs}|) = f1_{\Psi Srs} + \frac{f2_{\Psi Srs}}{SD} \tag{5}$$

with $f1_{\Psi Srs}$ and $f2_{\Psi Srs}$ being parameters. For parameterisation all 274 data sets containing leaf water potentials and stomatal resistances were used. These comprised the data from the four daily courses with 2-hourly measurements as well as values from daily measurements (Table 3).

In stomata model 2, the dependence of rs on Ψ_L, was postulated. Until a leaf water potential threshold, Ψ_{Lrs}, is reached, stomata are assumed to have maximal aperture, and rs to increase below Ψ_{Lrs} linearly:

$$rs = \begin{cases} rs_{min} & \Psi_L \geq \Psi_{Lrs} \\ rs_{min} + m_{\Psi Lrs}(\Psi_L - \Psi_{Lrs}) & \Psi_L < \Psi_{Lrs} \end{cases} \tag{6}$$

with $m_{\Psi Lrs}$ being a parameter. For parameterisation all 165 data sets which contained measurements of leaf water potentials and stomatal resistances, i.e. daily measurements plus four daily courses with 2-hourly data acquisition were used.

For comparison with these simple approaches a model proposed by Tardieu et al. (1993) and Jones and Tardieu (1998) was tested which is based on the root signal concept (stomata model 3). Stomatal resistance, rs, is thought to be dependent on xylem abscisic acid concentration, [ABA], and the sensitivity of the stomata to [ABA]:

$$\frac{1}{rs} = rs_{max} + \alpha\, e^{\beta[ABA]+\delta \Psi_L} \tag{7}$$

with rs_{max} denoting maximum stomatal resistance and [ABA] xylem abscisic acid concentration; $\alpha = rs_{min} - rs_{max}$, β, δ are

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Table 3
Mean soil water potential in the rooting zone, Ψ_S, turgescent leaf area, LA, actual transpiration rate, T_{act}, and specific actual transpiration rate, T_{actL}, at day 41 and 54 after planting

Parameter	Day 41 after planting				Day 54 after planting			
	W1	W2	W3	W4	W1	W2	W3	W4
Ψ_S 7:00 h (kPa)	11	36	568	114	14	416	28	1288
Ψ_S 19:00 h (kPa)	13	41	590	148	19	518	38	1288
LA (cm² plant⁻¹)	8306	8294	5702	8242	19,294	20,231	14,197	10,952
T_{act} (l plant⁻¹ day⁻¹)	2.90	3.04	0.78	2.68	3.40	3.10	2.76	0.32
T_{actL} (ml cm⁻² day⁻¹)	0.349	0.366	0.131	0.325	0.176	0.153	0.194	0.029

parameters. Note that stomatal resistances are expressed here in units of m² s mol⁻¹, not in s m⁻¹ as in the models before. [ABA] is assumed to increase in proportion to root water potential, Ψ_R, and to decrease with increasing transpiration rate, T_{act}:

$$[ABA] = \frac{a_{ABA}\Psi_R}{T_{act} + b_{ABA}} \qquad (8)$$

with a_{ABA} and b_{ABA} denoting parameters. Stomata model 3 was parameterised using 81 data sets from the four daily courses containing values for Ψ_S, Ψ_L and rs. Since root water potentials were not measured, values of Ψ_S were taken instead assuming that Ψ_R and Ψ_S are closely related. Values for $a_{ABA} = 4$ μmol m⁻² s⁻¹ kPa⁻¹ and $b_{ABA} = 6.5$ ml m⁻² s⁻¹ as obtained from a field experiment with cauliflower (Kochler and Hartung, unpublished) were used, β, δ, and rs$_{max}$ were estimated.

As criterion for model evaluation model efficiency (Smith et al., 1997) was used.

3. Results

The different irrigation treatments resulted in clear differences of water availability over time (Fig. 1). Noon leaf water potentials showed a similar course as soil water potentials. They remained at around ca. −0.5 MPa in unstressed plants throughout the experiment but dropped in the stress treatments, particularly in the later phases. Mean stomatal resistances of optimally irrigated plants ranged between 100 and 150 s m⁻¹ throughout, while water limitations resulted in increases of rs, largely in parallel to the reductions of soil and leaf water potentials. Stomatal closure strongly influenced actual transpiration rates which in the severely stressed plants (W4) were reduced to <10% of the fully irrigated (W1) from day 52 on. Due to the reduced leaf area of stressed plants relative transpiration rates did not drop as fast as T_{act}. Total volumes of transpired water amounted to 124 l per plant, which was significantly higher than 98 and 97 l of the moderately and intermittently stressed plants, respectively. Severe stress (W4) reduced transpiration to 47 l per plant.

Differential water supply also influenced the courses of Ψ_L, rs and T_{act} on individual days (Fig. 2). Whilst leaf water potentials of the moderately and not stressed treatments remained almost constant at around −0.5 MPa throughout the days, they decreased in the W3 treatment on day 41 and reached around −2 MPa in the evening. Severe stress (W4) resulted in reduced leaf water potentials throughout day 54 after planting. The same

differentiation between treatments was observed with respect to daily courses of rs and T_{act}.

Although the total amounts of transpired water differed between well-watered control and mildly stressed plants (W2 and W4 on day 41, W2 and W3 on day 54), specific transpiration rates were similar (Table 3). Only severe stress as experienced by W3 on 41 DAP and W4 on 52 DAP reduced specific transpiration rates.

To quantify the influence of atmospheric transpiration requirement on the relationship between specific transpiration rate and soil water potential the transpiration data were grouped into seven classes according to potential transpiration. For each class Ψ_{St} was calculated. Linear response and plateau functions described the relationships between T_{actL} and Ψ_S particularly in the lower transpiration classes well (Fig. 3, Table 4). A clear trend towards lower thresholds with increasing transpiration requirements can be observed (Fig. 3). Using the hyperbolic relationship from Fig. 4 to estimate Ψ_{St} in the transpiration model (Eq. (3)) resulted in a good description of transpiration of stressed plants (Fig. 5).

When establishing the models on stomatal regulation it became evident that the influence of radiation on maximal stomatal aperture had to be taken into account since rs$_{min}$ decreased hyperbolically with increasing PAR (Fig. 6). For parameterisation of stomata model 1 the data were categorized according to saturation deficit, SD, as a measure of transpiration requirement. Similar to transpiration, the relationship between rs and Ψ_S could well be described by linear–plateau models (data not shown). The soil water potential threshold for stomatal regulation decreased with increasing SD (Fig. 7). The parameter rs$_{max}$, was held constant at 7000 s m⁻¹ throughout. Using the relationships between PAR and rs$_{min}$, as well as between SD and Ψ_{Srs}, a

Table 4
Soil water potential thresholds for transpiration, Ψ_S, estimated as log($|\Psi_{St}|$) (±S.E.) using Eq. (3) for seven classes of potential transpiration

T_{potL} (ml cm⁻² day⁻¹)	log ($|\Psi_{St}|$)	Ψ_{St} (kPa)	r^2	n
$0.05 \leq T_{potL} < 0.10$ (0.087)	2.526 (±0.049)	−336	0.80	36
$0.10 \leq T_{potL} < 0.15$ (0.126)	2.574 (±0.031)	−375	0.87	51
$0.15 \leq T_{potL} < 0.20$ (0.184)	2.395 (±0.053)	−248	0.76	102
$0.20 \leq T_{potL} < 0.25$ (0.222)	2.242 (±0.081)	−174	0.75	57
$0.25 \leq T_{potL} < 0.30$ (0.275)	2.187 (±0.045)	−154	0.85	54
$0.30 \leq T_{potL} < 0.40$ (0.338)	2.135 (±0.085)	−136	0.60	39
$0.40 \leq T_{potL} < 0.50$ (0.447)	2.111 (±0.102)	−129	0.52	30

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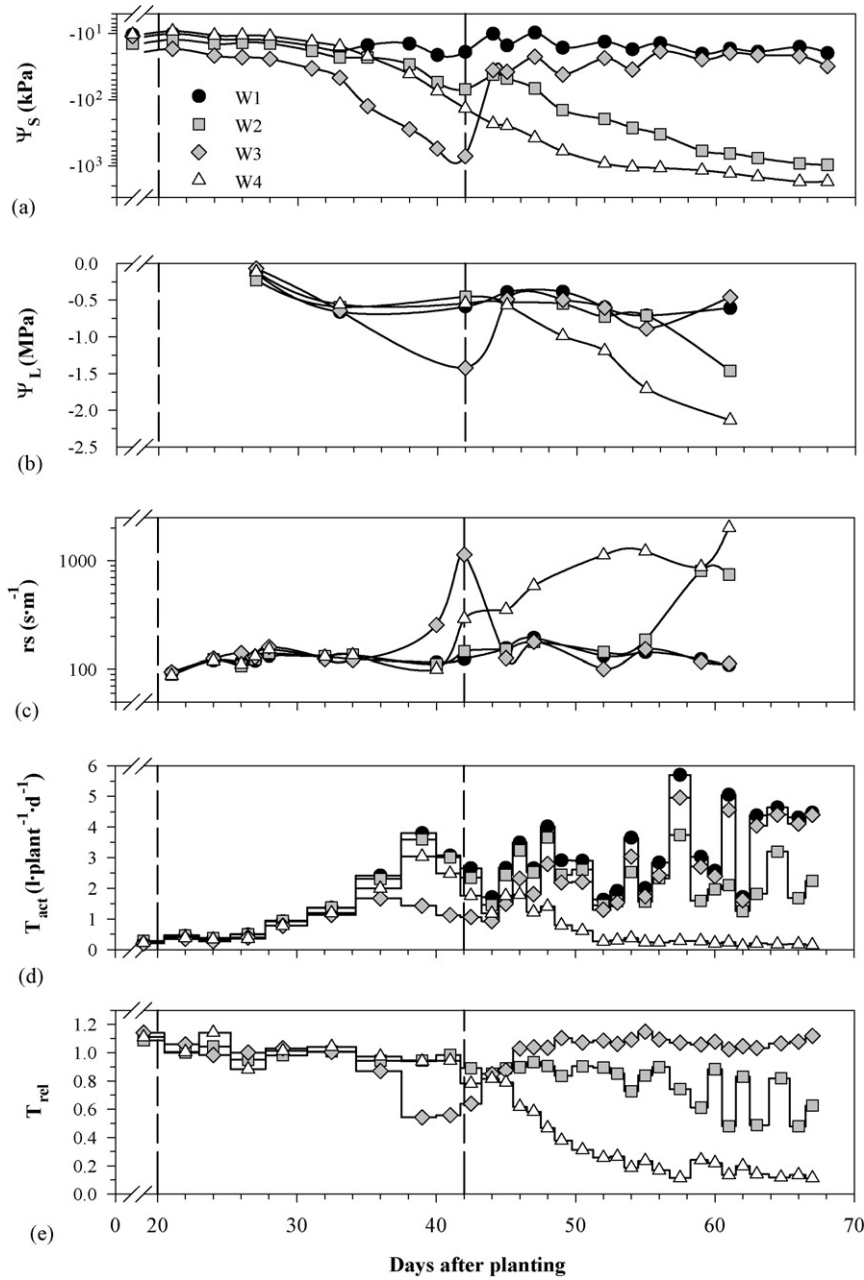Fig. 1. Mean soil water potentials in the rooting zone, Ψ_S, leaf water potentials of the youngest fully expanded leaves, Ψ_L, stomatal resistances, rs, mean actual transpiration rates, T_{act}, and relative transpiration rates, T_{rel}, of plants exposed to four water supply treatments, W1–W4. Dashed lines indicate irrigation phases (see text).

good correspondence between modelled and measured stomatal resistances was found (Table 5).

In stomata model 2 rs is assumed to be a function of leaf water potential, Ψ_L. As before, data were grouped according

to SD. However, since neither the leaf water potential threshold for stomatal closure, Ψ_{Lrs}, nor the coefficient describing the intensity of reaction, $m_{\Psi L}$, seemed to be related to SD, data were combined for regression analysis to estimate $\Psi_{Lrs} = -0.72$

Table 5
Input parameters, estimated parameters, coefficient of determination, r^2, number of observations, n, slope, Y_1, and intercept, Y_0, of the regression measured vs. modelled, and model efficiency, EF, of three models for stomatal regulation; standard errors in parentheses

Model	Input parameters	Estimated parameters	r^2	n	Y_1	Y_0	EF
1	rs_{min}, Ψ_S, T_{pot}, rs_{max}	$f1_{\Psi Srs}$, $f2_{\Psi Srs}$	0.77	274	1.01 ($\pm$0.03)	10.7 ($\pm$19.2)	0.76
2	rs_{min}, Ψ_L	Ψ_{Lrs}, $m_{\Psi Lrs}$	0.74	165	1.00 ($\pm$0.05)	15.2 ($\pm$31.2)	0.73
3	rs_{min}, Ψ_S, T_{act}, Ψ_L, a_{ABA}, b_{ABA}	rs_{max}, α, β, δ	0.73	81	1.07 ($\pm$0.07)	-133.9 ($\pm$61.6)	0.71

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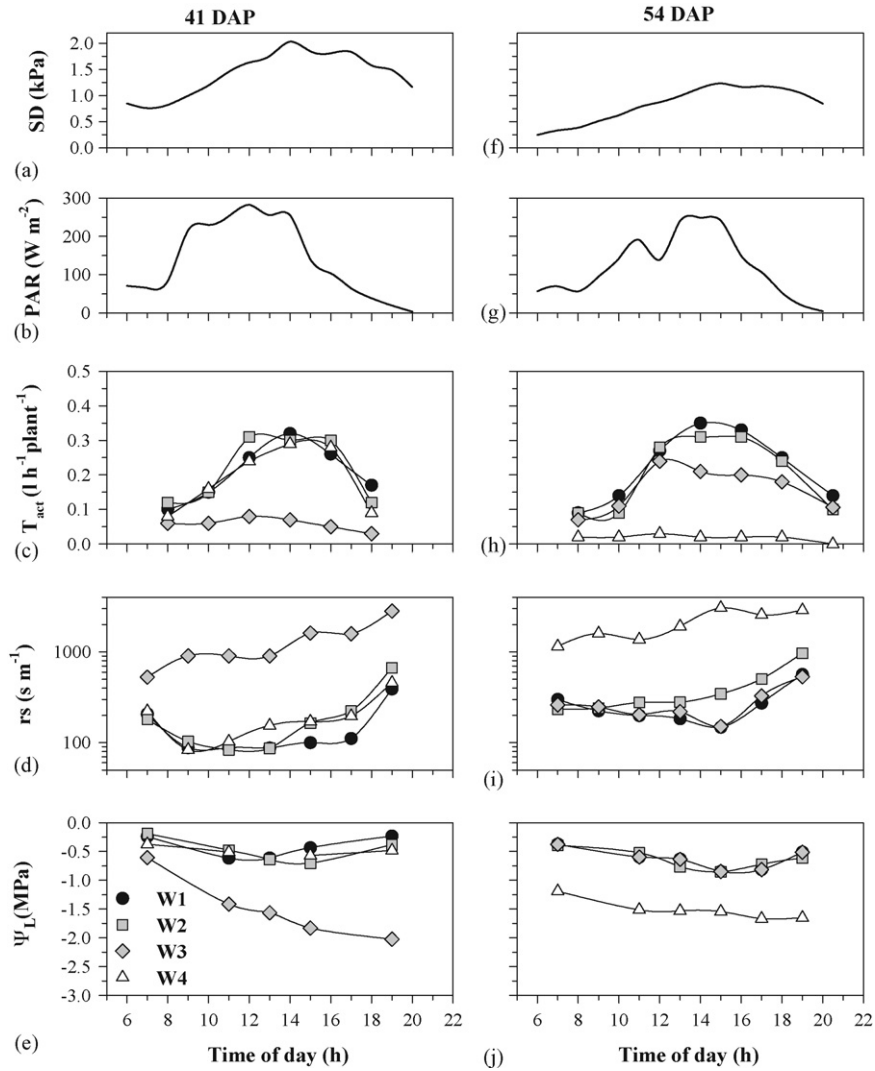Fig. 2. Day courses of water vapour saturation deficit, SD, photosynthetically active radiation, PAR, actual transpiration, T_{act}, stomatal resistance, rs, and leaf water potential, Ψ_L, of plants exposed to four water supply treatments, W1–W4, during days 41 and 54 after planting (DAP).
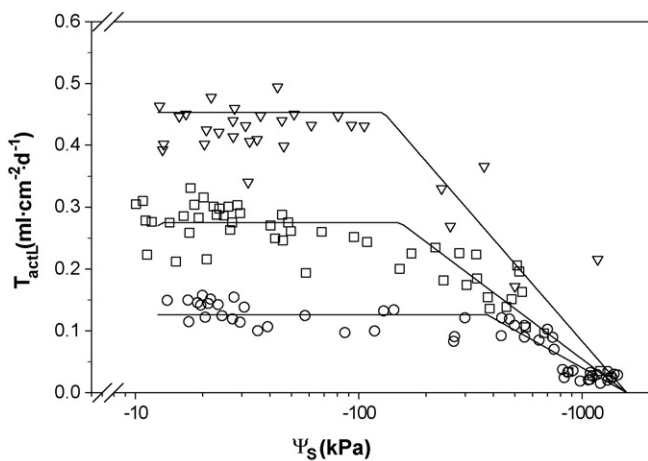

Fig. 3. Actual specific transpiration rate, T_{actL}, as dependent on mean soil water potential, Ψ_S, for three classes of specific potential transpiration: T_{potL}. $0.10 \leq T_{potL} < 0.15$ ml cm^{-2} day^{-1} (○); $0.25 \leq T_{potL} < 0.3$ ml cm^{-2} day^{-1} (□); $0.40 \leq T_{potL} < 0.50$ ml cm^{-2} day^{-1} (▽). For statistics and other transpiration classes see Table 4.
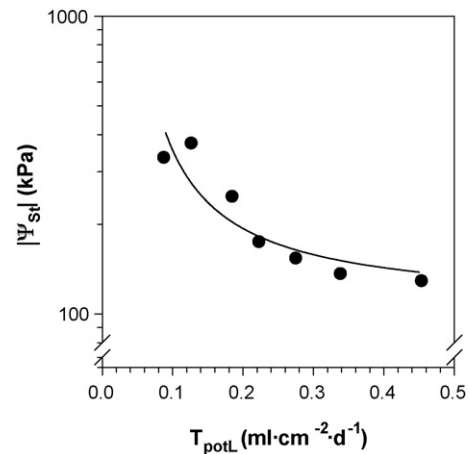

Fig. 4. Relationship between specific potential transpiration rate, T_{potL}, and soil water potential threshold for transpiration, Ψ_{St}; data from Table 4; regression equation: $\log|\Psi_{St}| = 2.02\ (\pm 0.07) + 0.05\ (\pm 0.01)/T_{pot}$, $r^2 = 0.82$, $n = 7$.

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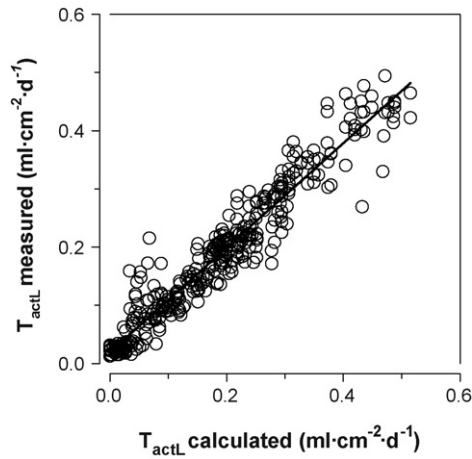*M. Kochler et al. / Europ. J. Agronomy xxx (2007) xxx–xxx*

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Fig. 5. Relationship between measured and specific calculated actual transpiration rates, T_{actL}, of stress treatments W2–W4; regression equation: $y = 0.898$ (± 0.0131) $x + 0.019$ (± 0.0029), $r^2 = 0.93$, $n = 369$.

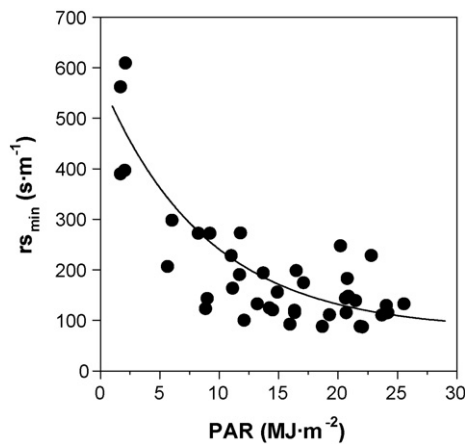

Fig. 6. Relationship between minimum stomatal resistance, rs_{min}, of the optimally irrigated treatment, W1, and photosynthetically active radiation, PAR; regression equation: $rs_{min} = 133$ (± 16.1) ($1 + 4.07$ (± 0.610) $e^{(-0.2296(\pm 0.054695) \, PAR)}$), $r^2 = 0.76$, $n = 40$.
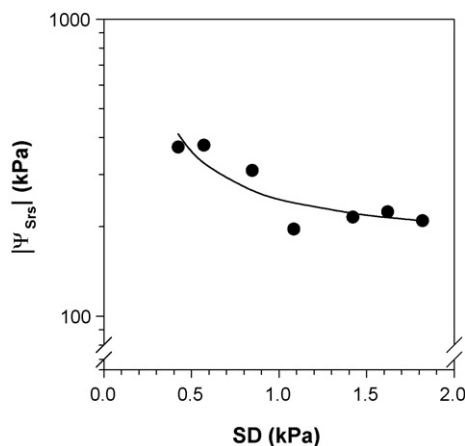

Fig. 7. Relationship between transpiration requirement as characterised by the water vapour saturation deficit of the air, SD, and soil water potential threshold for stomatal regulation, Ψ_{Srs}; regression equation: $\log(\Psi_{Srs}) = 2.23$ (± 0.048) $+ 0.162$ (± 0.0369)/SD, $r^2 = 0.79$, $n = 7$.

(± 0.04) and one for $m_{\Psi BL} = -1458$ (± 90). Using these parameters to model rs yielded good correspondence with measured data (Table 5).

For parameterisation of model 4 representing the root signal approach fewer data sets were available than for the other models. Nevertheless good descriptions of stomatal resistances were achieved with $rs_m = 2425$ (± 236) s m^{-1}, $\beta = -0.0122$ (± 0.003) m^3 μmol^{-1} and $\delta = 1.25$ (± 0.17) MPa^{-1} (Table 5).

4. Discussion

The objective of this study was to quantify transpiration and stomatal resistance based on plant and environmental parameters in order to model reaction of cauliflower to limited water supply.

Water supply was varied in quantity and time. The use of containers with high soil volumes allowed at one hand precise measurements of water balance like in conventional pot experiments, but also provided the plants with enough water reserves to allow gradual adaptation to drought without the need of frequent water addition which would have disturbed the adaptation process. Also, the soil volume of 220 l per plant was comparable to the field situation, allowing growth rates similar to those under practical production conditions. Consequently, leaf water potentials and stomatal resistances were comparable to those measured in various *Brassicas* under field conditions (Clarke and McCaig, 1982; Jensen et al., 1996, 1998a; Kumar et al., 1984, 1994). The high soil volume also ensured that the day course of the soil and plant water parameters was comparable to those measured in field-grown crops, (e.g. Kumar et al., 1994 for *Brassica juncea* L.; Singh et al., 1987 for *Cicer arietinum*). As intended, plants increasingly developed stress symptoms with progressing soil drying.

In contrast to other publications (Hammer and Muchow, 1994; Ray and Sinclair, 1997; Sinclair and Ludlow, 1986; for review see Sadras and Milroy, 1996), soil water potential rather than the fraction of transpirable soil water (FTSW) was used as a measure for plant available soil water. That way the problems connected with determination of FTSW (Savage et al., 1996; Sinclair et al., 1998) could be avoided and transferability to other soil types is expected to be easier. Also, experimental results on the adaptation of lupins (*Lupinus angustifolius*) to drought in different soils (Jensen et al., 1998b) indicate that gas exchange depends rather on mean soil water potential or the fraction of roots in moist soil.

On the whole-plant level with daily resolution the relationship between water availability and specific transpiration, i.e. transpiration per unit of leaf area could be described with a simple linear model. The soil water thresholds at which transpiration began to decrease, Ψ_{St}, ranged between -336 and -129 kPa, corresponding to approximately 20 and 37% of plant available water. This is a similar range as the one reported by Sadras and Milroy (1996) for a variety of other crops. The necessity to take this dependence into account becomes clear from the course of transpiration of the moderately stressed treatment (W2) in Fig. 1: on days with high transpiration requirement, e.g. 61 and 63 DAP, specific transpiration of W2 plants was less than half the transpiration of optimally supplied plants, while on days with

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low transpiration requirement, e.g. 60 or 62 DAP, transpiration in W2 was close to that in W1. The dependence of the soil water potential threshold on transpiration requirement was reported earlier by Denmead and Shaw (1962) and Sadras et al. (1993). The high r^2 value and the coefficients of the regression equation relating modelled and measured values show clearly that daily specific transpiration of cauliflower can be quantified well with this approach. It does, however, not provide for processes taking place at higher temporal resolution and does not lead to a prediction of ground area based transpiration of a crop stand.

As a basis for transpiration models with higher temporal resolution the influence of water supply on stomatal resistance, rs, was investigated. Stomata models 1 and 2 describe rs dependent on soil and leaf water potential using a combination of linear equations. Model 3 is based on the concept that xylem abscisic acid concentration determines stomatal resistance. Due to the different input parameter requirements, the three models were parameterised with different sets of data. This allows no stringent comparison of model quality, but an analysis of advantages and disadvantages regarding model structure, data requirement and data sensitivity may be informative.

Stomata models 1–3 require minimum stomatal resistance, rs_{min}, as input variable. An exponential increase of minimum stomatal resistance with decreasing photosynthetically active radiation has been observed in many crop species (Tardieu and Simonneau, 1998; Turner, 1991) and could be due to reduced leaf photosynthesis (Jarvis and Davies, 1998). An influence of transpiration requirement on rs_{min} would have lead to a depression around noon, but this could not be observed. This corresponds with results from Tardieu and Simonneau (1998) who did also not observe a midday depression in well-watered field-grown sunflowers (*Helianthus annuus*), maize (*Zea mays*) and poplar (*Populus euramericana*).

In the stomata model the hypothesis is tested that stomatal resistance reaches its maximum, rs_{max}, at permanent wilting point. This is supported by data from the extreme stress treatment. From an average soil water potential in the rooting zone, $\Psi_S = -1500$ kPa on, specific transpiration rate is reduced to only ca. 10% of the transpiration in the optimal treatment, i.e. essentially to cuticular transpiration (Kramer, 1983). The dependence of Ψ_{Srs}, and therefore indirectly also rs, on transpiration requirement or saturation deficit is in agreement with other observations (Johnson and Ferrell, 1983; Monteith, 1995; Saliendra et al., 1995; Turner, 1991). No relationship could be found between stomatal resistance and transpiration requirement in stomata model 2. Presumably, effects of saturation deficit were accounted for by Ψ_L in this model.

Despite the higher number of input parameters in the "biochemical" stomata model 3 compared to the "hydraulic" models 1 and 2, model performance was not better. This may be due to the fact that parameters a_{ABA} and b_{ABA} were determined in a different experiment. In an attempt to solve this problem [ABA] in Eq. (7) was substituted by the right hand side of Eq. (8) so that a_{ABA} and b_{ABA} could be estimated by non-linear regression. This, however, revealed another problem: parameters a_{ABA} and b_{ABA} and β were highly correlated indicating that the model was over-parameterised.

The assumption that xylem ABA concentration is reduced by increased transpiration rates, is questionable. This contradicts the fact that relative transpiration of stressed plants is lower at high than at low saturation deficit, i.e. stomata close more at high transpiration requirement. The substitution of root water potential by soil water potential in the model may also be questionable. Whilst a close relationship between root and soil water potential was shown for soil water potentials up to about ca. 0.5 MPa (Ruggiero et al., 1999), drier soils might lead to increasing differences between soil and root water potentials (Schmidhalter, 1997).

A different problem with stomata model 3 might arise when incorporating it into a complete water balance model: Actual transpiration is an output parameter of the water balance model as well as an input parameter for the calculation of stomatal resistance and leaf water potential which in turn are required for the calculation of transpiration. Using leaf water potential as an input parameter may also be problematic since its measurement is very laborious (Hsiao, 1990). It is therefore usually not monitored continuously and has to be calculated from soil water potential, transpiration and plant resistances. These are difficult to determine (Markhart and Smit, 1990; Passioura, 1984; Passioura and Munns, 1984; Reid and Huck, 1990). In addition the above-mentioned problem with transpiration being an input and an output parameter has to be considered. This holds also true for stomata model 2. Stomata model 1, in contrast, is not only based on two parameters, mean soil water potential and potential transpiration, which are easy to calculate, it also had the highest model efficiency. Therefore, it appears to be best suitable for temporally highly resolved modelling of transpiration in cauliflower.

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