Plant and Soil **140**: 205–224, 1992.
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Diurnal courses and factorial dependencies of leaf conductance and transpiration of differently potassium fertilized and watered field grown barley plants

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Received 18 December 1989. Revised November 1991

Key words: barley, drought, microclimate, porometry, potassium, stomatal resistance, transpiration.

Abstract

During the grain filling period we followed diurnal courses in leaf water potential (ψ_l), leaf osmotic potential (ψ_π), transpiration (E), leaf conductance to water vapour transfer (g) and microclimatic parameters in field-grown spring barley (*Hordeum distichum* L. cv. Gunnar). The barley crop was grown on a coarse textured sandy soil at low ($50\,kg\,ha^{-1}$) or high ($200\,kg\,ha^{-1}$) levels of potassium applied as KCl. The investigation was undertaken at full irrigation or under drought. Drought was imposed at the beginning of the grain filling period.

Leaf conductance and rate of transpiration were higher in the flag leaf than in the leaves of lower insertion. The rate of transpiration of the awns on a dry weight basis was of similar magnitude to that of the flag leaves. On clear days the rate of transpiration of fully watered barley plants was at a high level during most part of the day. The transpiration only decreased at low light intensities. The rate of transpiration was high despite leaf water potentials falling to rather low values due to high evaporative demands. In water stressed plants transpiration decreased and midday depression of transpiration occurred. Normally, daily accumulated transpirational water loss was lower in high K leaves than in low K leaves and generally the bulk water relations of the leaves were more favourable in high K plants than in low K plants.

The factorial dependency of the flag leaf conductances on leaf water potential, light intensity, leaf temperature, and leaf-to-air water vapour concentration difference (ΔW) was analysed from a set of field data. From these data, similar sets of microclimatic conditions were classified, and dependencies of leaf conductance on the various environmental parameters were ascertained. The resulting mathematical functions were combined in an empirical simulation model. The results of the model were tested against other sets of measured data. Deviations between measured and predicted leaf conductance occurred at low light intensities. In the flag leaf, water potentials below -1.6 MPa reduced the stomatal apertures and determined the upper limit of leaf conductance. In leaves of lower insertion level conductances were reduced already at higher leaf water potentials. Leaf conductance was increased hyperbolically as photosynthetic active radiation (PAR) increased from darkness to full light. Leaf conductance as a function of leaf temperature followed an optimum curve which in the model was replaced by two linear regression lines intersecting at the optimum temperature of 23.4°C. Increasing leaf-to-air water vapour concentration difference caused a linear decrease in leaf conductance. Leaf conductances became slightly more reduced by lowered water potentials in the low K plants. Stomatal closure in response to a temperature change away from the optimum was more sensitive in high K plants, and also the decrease in leaf conductance under the influence of lowered ambient humidity proceeded with a higher sensitivity in high K plants. Thus, under conditions which favoured high conductances increase of evaporative demand caused an about 10% larger decrease in leaf conductance in the high K plants than in the low K plants.

Stomatal sizes and density in the flag leaves differed between low and high K plants. In plants with partially open stomata, leaf conductance, calculated from stomatal pore dimensions, was up to 10% lower in the high K plants than in the low K plants. A similar reduction in leaf conductance in high K plants was measured porometrically. It was concluded that the beneficial effect of K supply on water use efficiency reported in former studies primarily resulted from altered stomatal sizes and densities.

Abbreviations: E, rate of transpiration; g, leaf conductance to water vapour transfer; r_s, leaf resistance to water vapour transfer; PAR, photosynthetic active radiation; ΔW, leaf-to-air water vapour concentration difference; ψ_l, leaf water potential, ψ_π, leaf osmotic potential; MEST, middle European summer time.

Introduction

Supplemental irrigation and K salt fertilization are common practice in barley cultivation on rough textured sandy soils, which are widespread in the Jutland peninsula of Denmark. In the present investigation additional potassium supply significantly increased the rate of growth of the vegetative parts of the crop and by this way increased the total dry matter yield; however, the final grain yield was not increased by high K application (Anderson et al., 1992a). Nevertheless, potassium fertilization may bring economic gain because an essential part of the barley grown in this area is harvested during the growth stages from anthesis to milk ripe for use as cattle fodder (Andersen et al., 1992a). The increased production of vegetative part under supplemental potassium application was associated with a higher leaf area index (LAI) and an increased tissue water content. The water use efficiency (WUE) was improved up to 12% at high K fertilization compared with low K fertilized experimental plots. This increased WUE resulted from increased vegetative growth under better K supply combined with similar water expenditure despite an enlarged LAI (Andersen et al., 1992b). The higher WUE may result from a better control of transpirational water loss in barley supplied with higher amounts of potassium.

A reduction of transpiration rates of cereal crops due to a higher K supply was found by Brag (1972) in *Triticum aestivum*, and by Jensen (1982) in *Hordeum distichum*, both based on gravimetric determinations of the water loss from potted seedlings. Jensen (1982) also found reduced leaf conductance using a transient diffusion porometer in high K barley seedlings as compared with low K seedlings. Similarly, Lindhauer (1985) using a steady state porometer reported reduced leaf conductances when potted *Helianthus annuus* plants growing in a climatized chamber were supplied with higher levels of K fertilizer, and comparable reports from studies with conifers can be found in the literature (e.g. Bradbury and Malcolm, 1977).

Whereas all these findings correlate a better K salt supply of the plant with reduced transpiration rates and leaf conductances, it is well known that, contrarily, stomatal apparatuses rich in K ions show open pores while reduced K levels in the guard cells are correlated with closed stomata (Lösch, 1978; Outlaw, 1983; Raschke, 1979). Bulk K ion levels in well potassium fertilized barley leaves were substantially increased and they surmounted those in low fertilized ones by 35% (Andersen et al., 1992b). Transpiration rate, however, was reduced by high K supply (Andersen et al., 1992a).

For explanation of this inconsistency, one can think about an unequal distribution of the additional K supply, so that it is concentrated in the mesophyll, the epidermis remaining unaffected. It might be that K ion concentrations in guard cells are sufficiently high already in low K plants for an efficient functioning of stomata, so that an overall increase of leaf K ion content cannot bring about a further widening of pores. On the contrary, the turgor balance between the guard cells and their surroundings could even be shifted resulting in a hydropassive narrowing of the pores. It is conceivable, finally, that morphogenetic changes due to a higher K supply of the leaves affecting stomatal size and density could be the reason for altered leaf conductances.

In order to get more insights into the effects of potassium and water supply on the stomatal control of leaf water losses, we therefore by means of steady state porometry followed diurnal courses of canopy microclimate, transpiration rate and leaf conductance or resistance in differentially irrigated and K fertilized barley plants in the field between heading and harvest. From these data, similar sets of microclimatic conditions were classified and dependencies of leaf conductance on the various environmental parameters were ascertained and used in an empirical simulation model for calculation of leaf conductance. Sizes and density of stomata from plants under the different fertilization treatments were measured too, and leaf conductances based on these morphological parameters were calculated according to Parlange and Waggoner (1970).

Material and methods

Treatments

The investigations were undertaken in 1986 and 1987. Spring barley (*Hordeum distichum* L. cv. Gunnar) was grown in a field trial located in south Jutland at the Governmental Research Station, Jyndevad. The soil is a coarse textured melt water sand low in natural K content and water holding capacity. The textural and chemical properties of the soil have been described previously (Andersen et al., 1992a).

N was applied at a rate of 110–120 kg ha^{-1} as calcium ammonium nitrate, P at a rate of 30 kg ha^{-1} as calcium superphosphate, and Mg at a rate of 30 kg ha^{-1} as kieserite. The plots (each 15.6 m^2) were arranged in a randomized block design of the 2 factor treatments, namely potassium application at rates of 50, 125 and 200 kg ha^{-1} as KCl and irrigation which was performed at a deficit of approx. 30 mm of soil water (fully irrigated treatment, denoted WI) and at a deficit of 50 mm (drought treatment, denoted WD) as detailed by Andersen et al. (1992a). Below we only describe results from plots to which either 50 or 200 kg K ha^{-1} have been applied, denoted KL and KH, respectively.

The drought treatment was obtained with or without use of rain-off shelters (Andersen et al., 1992a). However, in 1986, during which year most of our measurements were undertaken, a long lasting fair-weather period enabled us to use only uncovered plots for the measurements. More details of the meso-climatic conditions are reported by Andersen et al. (1992a).

Measurements

Microclimate, conductance to water vapour (g) and rate of transpiration (E) of leaves were measured with a LI 1600 steady state porometer (LiCor Inc., Lincoln, Nebr., USA). g and E of ab- and adaxial leaf surfaces were measured separately, and the data of these measurements were summed to give the whole-leaf conductance and transpiration values. The leaf resistance to water vapour transfer (r_s) was calculated as the inverse of g; i.e. $r_s = 1/g$. One set of data represented the mean of 4–6 single observations obtained within 15 minutes. One of the leaves was sampled repeatedly during a diurnal course. Other leaves were enclosed in a polyethylene bag after the porometric measurements, and then rapidly cut and transferred to a pressure chamber (Turner, 1988) for measurement of leaf water potential (ψ_l). Immediately upon the ψ_l determination the leaves were frozen in liquid nitrogen, later thawed for about 15 minutes, and the sap expressed with a plastic syringe for determination of the sap osmotic potential (ψ_π). ψ_π was measured by thermocouple hygrometry using a WESCOR C52 sample chamber connected to a Wescor HR33T microvoltmeter

(WesCor Inc., Logan, Utah, USA). The turgor potential (ψ_p) was estimated as the difference between ψ_l and ψ_π, i.e. $\psi_p = \psi_l - \psi_\pi$ (Jensen et al., 1992).

Between heading and harvest every week at least two diurnal courses were measured separately for flag leaves (leaf No 8, counting up from the first developed leaf) and for leaf No 7 and – in July 1986 – for leaf No 6. In 1987 some diurnal courses of the transpiration of the awns were assessed also. This was done with the quick-weighing method (Stocker, 1929; 1956). Awns were cut from an ear and weighed immediately on a sensitive balance (torsion balance SAUTER, sensitivity 0.1 mg) and reweighed after two minutes. Weight loss during this time span was assumed to result from transpirational water loss. Flag leaves, the transpiration of which had been measured porometrically just before, were cut and treated likewise. By this way, a comparison of data of transpiration, determined by weighings and porometrical measurements, was possible.

A fortnight after the end of heading, stomatal length, width, and density were measured in the flag leaves and in leaf No 7 on fully expanded leaves. Stomata in 15 randomly selected plants were measured in the different treatments. Imprints were taken both from the abaxial and adaxial leaf surfaces using suitable diluted nitrocellulose. On the imprints six randomly chosen microscopic fields of 0.30 mm^2 were counted for stomatal distribution (magnification 197×). Exterior length and width of eight pairs of guard cells were measured in six fields per imprint at 315× magnification. These morphological data were used in order to calculate leaf stomatal resistance (r_s) values from stomatal dimensions using the formula proposed by Parlange and Waggoner (1970):

$$r_s = \frac{\dfrac{d}{\pi \cdot a \cdot b} + \dfrac{\ln(4a/b)}{\pi \cdot a}}{D \cdot n}$$

where

a = half the long axis of the pore (cm)
b = half the short axis of the pore (cm)
d = length of pathway for diffusive gas exchange (cm)
n = area density of stomata (number/cm^2)
r_s = leaf stomatal resistance (s/cm)
D = water vapour diffusive coefficient (cm^2/s)

The long axis of the pore was taken to be half the length of the whole stoma; d, being the depth of the pore, was estimated to be half the width of the pair of guard cells. It was assumed in the calculations that both values did not change essentially when the pore between the dumb-bell-shaped guard cells of a gramineous stoma became enlarged or narrowed. Therefore the short axis of the pore remained as the changing variable. This width was taken as a fraction of the total breadth of the pair of guard cells. Using this fraction instead of the absolute size dimensions it was possible to relate the results of the calculations to a common parameter for stomata of different sizes. Values for D are provided by Nobel (1983). For the calculations the value 0.242 $\mathrm{cm}^2\,\mathrm{s}^{-1}$ was used for the diffusion coefficient of water vapour at 20°C.

Results

Diurnal water relations

Figures 1 and 2 illustrate for each week between heading and ripening in 1986 one diurnal course of microclimate, flag leaf resistance (r_s), transpiration (E), leaf water (ψ_l), and osmotic potential (ψ_π) for the different treatments. As detailed by Andersen et al. (1992a), this period was characterized by little precipitation and high actual evapotranspiration. The sky was mostly free of clouds and irradiation increased around noon well above a photosynthetic active radiation (PAR) of 1600 μmol photons $\mathrm{m}^{-2}\,\mathrm{s}^{-1}$. This resulted in maximum leaf and air temperatures of slightly above 30°C, and maximum leaf-to-air water vapour concentration differences (ΔW) of about 20 g m^{-3}.

As long as sufficient water was available in the rooting zone r_s was generally low under the various atmospheric conditions experienced in the field. Due to low r_s-values in leaves of irrigated barley (Figs. 1 and 2, left hand side) water loss by transpiration rose to nearly 10 μg H_2O $\mathrm{cm}^{-2}\,\mathrm{s}^{-1}$. In these plants the ψ_l-values fell

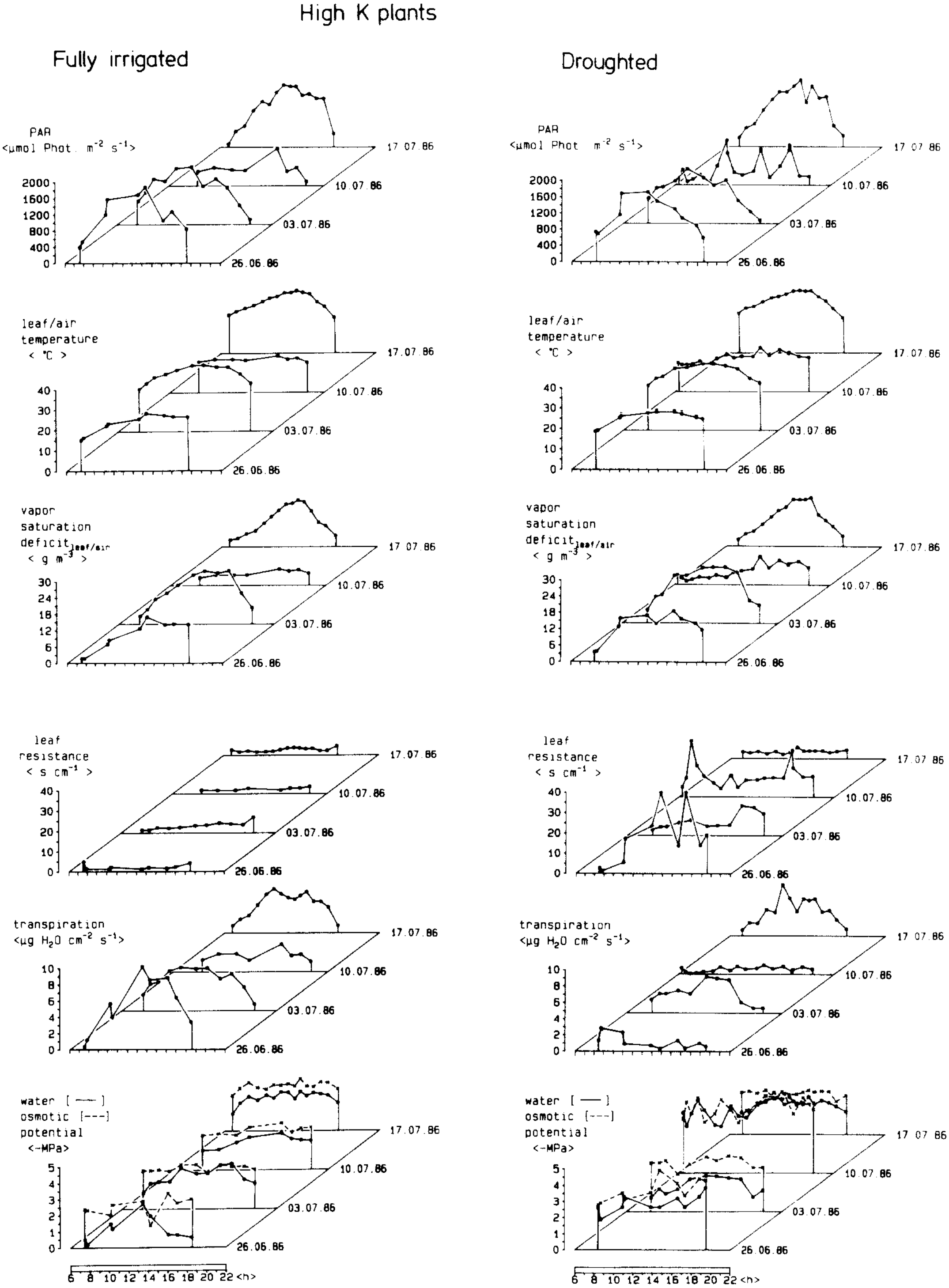

Fig. 1. Diurnal courses of photosynthetically active radiation (PAR), leaf = air temperatures, vapour saturation deficit between leaf and air (ΔW), leaf resistance (r_s), transpiration (E), water (ψ_l) and osmotic potentials (ψ_π) of flag leaves of fully irrigated (WI) and droughted (WD) high K (KH) barley plants in 1986. In fully irrigated plots the soil water deficit was <30 mm, and in droughted plots it was about 45 mm.

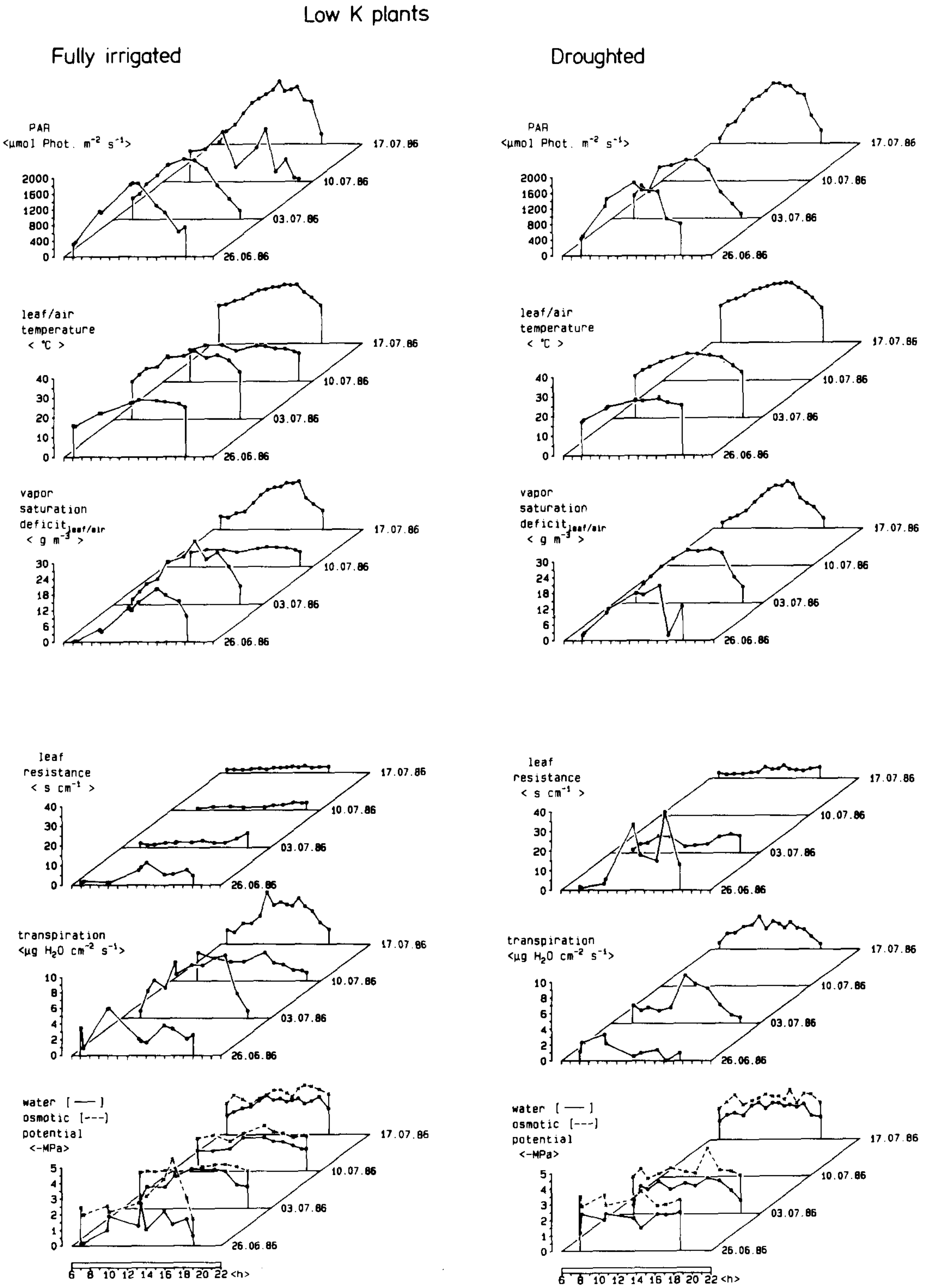

Fig. 2. Same as Fig. 1 but for low K (KL) plants.

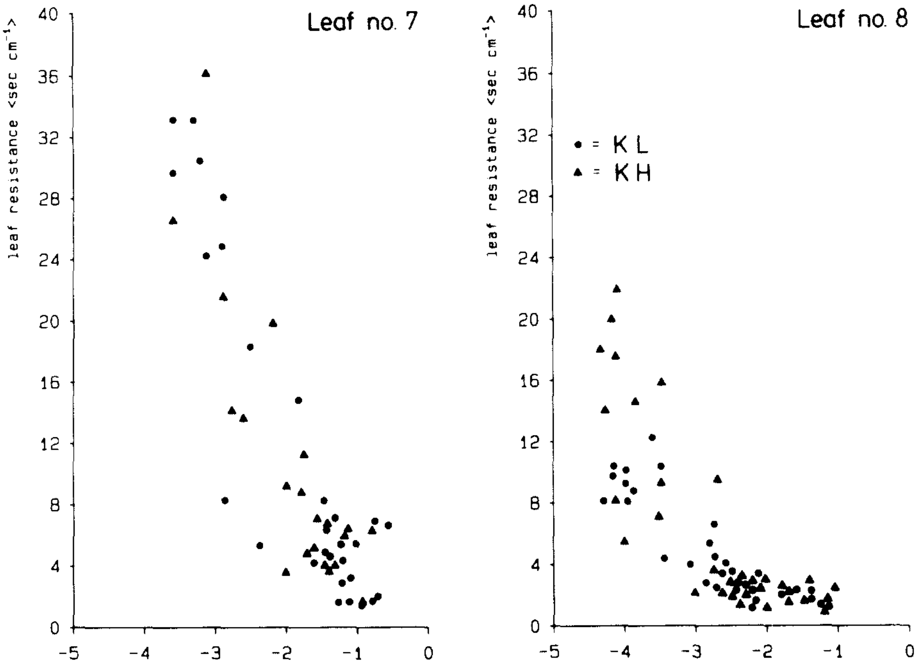

Fig. 3. Leaf resistance (r_s) of leaf Nos 7 and 8 (the flag leaf) as a function of bulk leaf water potential (ψ_l) at low (dots) and high (triangles) K application (data from irrigated and droughted plots).

well below −2 MPa. In spite of this, the leaves remained turgid in most cases due to yet more negative osmotic potentials (for details see Jensen et al., 1992). In Fig. 3 leaf resistances are related to ψ_l measured between 9.00 a.m. and 5.00 p.m. (i.e. omitting the hours of low light intensity). These data were obtained from four diurnal courses in July 1986 in leaf No 8 (the flag leaf) and from two diurnal courses in leaf No 7. Substantial increases in resistance only occurred below ψ_l values of −2.5 MPa in the flag leaf, and below ψ_l values of −1.5 MPa in leaf No 7. However, unirrigated plants (Figs. 1 and 2, right hand side) displayed higher resistance values and lower transpiration rates. Water shortage caused substantial increases in r_s when soil water deficits were greater than 35 mm (Fig. 4). As an average, daily transpirational water loss of the unirrigated low K plants only reached 50–60% of that of irrigated plants. In high K plants water loss under drought was yet more reduced. In one extreme case of a diurnal course (26.6.86) the transpiration of high K plants under drought only reached 20% of that measured in irrigated

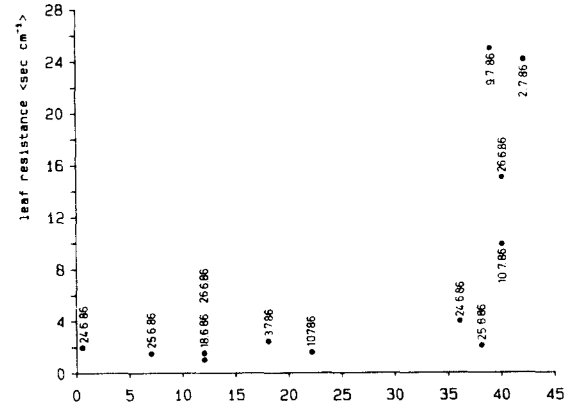

Fig. 4. Midday flag leaf resistance (r_s) as a function of soil moisture deficit from 18.6.86 to 10.7.86.

plants under similar atmospheric conditions. Due to the humid weather in 1987 no diurnal courses were measured with obviously reduced transpiration. Even plants droughted under cover used water unrestrictedly, according to the prevailing evaporative demands.

During the grain filling period at best leaf No 6 to 8 (the flag leaf) were green. Transpiration

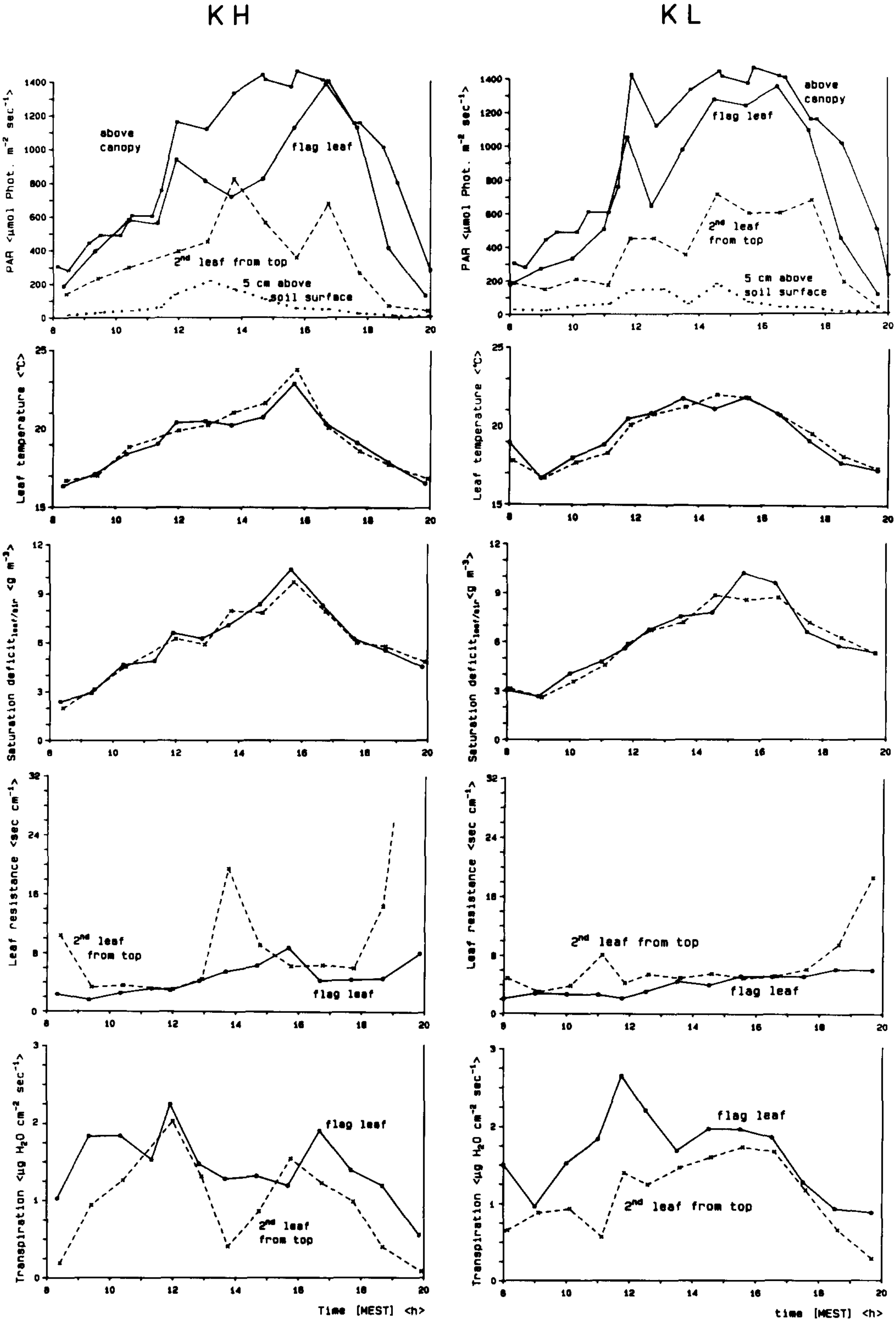

Fig. 5. Diurnal courses of micrometeorological parameters, leaf resistance (r_s) and transpiration (E) of leaf No 7 (the 2nd leaf from top) and the flag leaf; July 8th, 1987 for irrigated treatments WIKL and WIKH.

from leaves at lower insertion was less than that of the flag leaf (Fig. 5). This reduced transpirational water loss was not primarily an effect of more humid conditions within the lower layers of the canopy as temperatures and leaf-to-air water vapour concentration difference (ΔW) of the leaves were not very much altered in comparison with the situation at the level of the flag leaves. Thus, evaporational conditions did not differ much between the insertion level of the flag leaf and that of leaf No. 7. The reduced transpiration of the latter leaf was seemingly a consequence of lower leaf conductance (g) (Fig. 6). The smaller stomatal apertures of the lower leaves may partly be due to the reduced light intensities in the shadow of the canopy, and partly they may be due to leaf senescence. Leaf senescence probably caused the r_s-values of leaf No 7 to increase at ψ_l values half as low as those which caused increase of r_s in the flag leaves (Fig. 3). Leaf senescence also becomes clear from the increase of r_s by age in one and the same leaf during the weeks of heading.

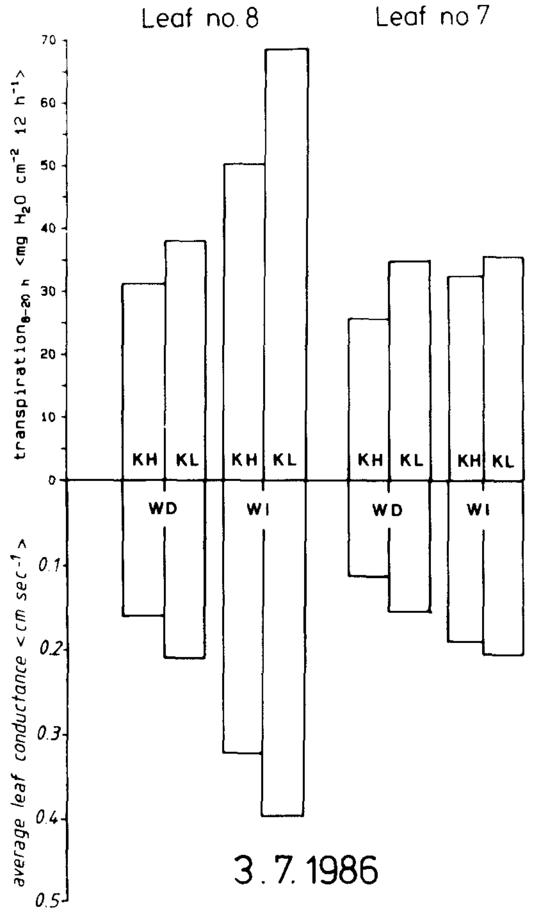

Fig. 6. Integrals of daytime transpiration (E) and average leaf conductances (g) of the flag leaf and the 2nd leaf from the top (leaf No 7) in well watered and drought-stressed high (KH) and low K (KL) plants; July 3rd 1986.

If not suffering from water stress and being the youngest one on a stalk the leaves displayed r_s-values below 2 s cm^{-1} during most hours of the day. After the next leaves had developed, the resistances of those older leaves gradually increased.

In July, on average, the transpirational water loss per unit of leaf area of leaf No 7 amounted to 68% of the transpiration of the flag leaf; and that from leaf No 6, if yet green and turgid at all, made up 34% of the transpiration of the flag leaf.

An essential contribution to the overall transpiration from a barley crop originates from the awns. There existed 1:1 proportionality between the data obtained porometrically and by the quick-weighing method (coeff. of correlation = 0.87; n = 33). Awn transpiration on a dry-weight basis equalled that of the flag leaf (Fig. 7). Significant differences between awns and flag leaves in stomatal responses to environmental factors could not be detected.

Transpiration and conductances of leaves from low K plants surmounted those of high K plants. Diurnal integrals of water loss per leaf area (Fig. 6) clearly indicated that the latter transpired less water than the low K plants under similar conditions. Also the comparison of instantaneous values of r_s showed that on average high K plants exhibited higher r_s-values. When for irrigated and droughted treatments values of r_s of high K plants from the 1986 season were plotted against those of low K plants, 70% of the observations were situated above the 1:1 line (r_s of KH plants = $-0.19 + 1.6 \cdot r_s$ of KL plants).

An empirical model for calculation of leaf conductances (g)

Variable g-values result essentially from integrated stomatal responses to the joint influence of plant internal factors (such as leaf water potential) and micrometeorological parameters. The latter do not usually vary independently on each

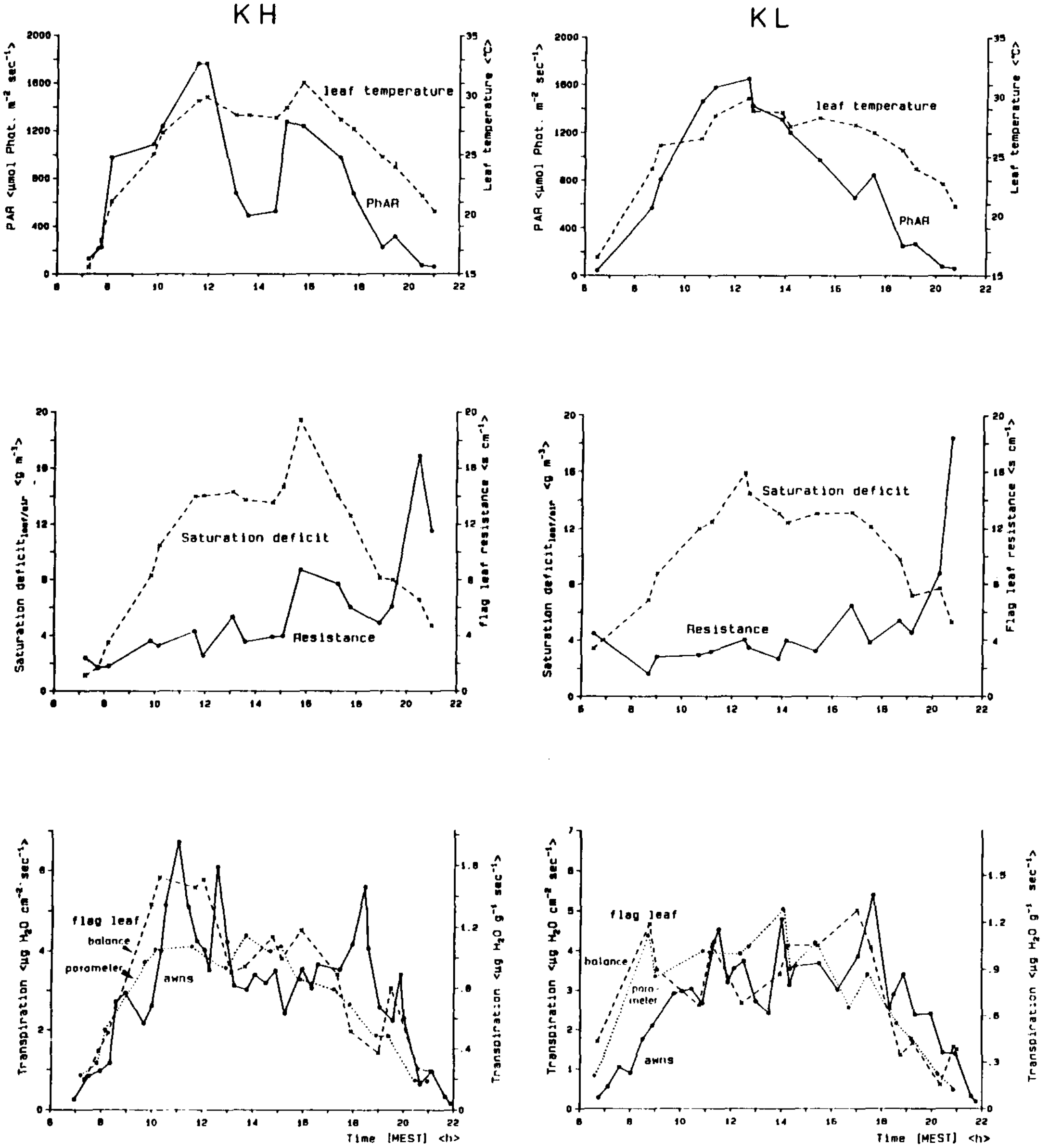

Fig. 7. Diurnal courses of awn (——) and flag leaf transpiration (E) (measured porometrically, ····· -area-related: left ordinate-, and with the quick weighing balance method, ------dry weight-related: right ordinate-, respectively), flag leaf resistances (r_s), and micrometeorological parameters; July 7th 1987; treatments WIKL and WIKH.

other during the course of a day. Nevertheless, from the measurements of micro-climate and g of the flag leaves during more than a dozen diurnal courses of both KH and KL treatments of irrigated and droughted plants, from the about five weeks of barley ripening in 1986, it was possible to single out several sets of combinations of various water potentials, irradiation conditions, temperature and humidity situations. By this means, responses of g in flag leaves to a change of one particular factor could be identified, while the other parameters were more or less constant. The shapes of the resulting response curves were in agreement with those usually found by such analyses (Lösch and Tenhunen, 1981; Jones, 1983); viz. a saturation-type increase of g with irradiation and a linear decrease with increasing leaf-to-air water vapour concentration difference (ΔW). If ψ_l decreased, then in the first instance, g did not decrease significantly. However, with further lowering of ψ_l g gradually approached a zero value at very low water potentials. Conductance values at water potentials above approx. −2 MPa were somewhat higher in low K plants (Fig. 3), but they decreased more sharply with decreasing water potential, so that on average g of leaves from both K treatments did not differ significantly as far as dependency on bulk leaf water potential was concerned. Leaf conductances less that 0.1 cm s^{-1} were generally reached at ψ_l values below −3 MPa. Over most of the measured temperature range g decreased with increased leaf temperature, but below 23°C there was an increase in g with increasing temperatures. Approximately 23°C turned out to be the optimum for temperature-dependent stomatal opening. For sake of simplicity, the optimum curve, which describes the g dependency on temperature, may be described, without very much loss of precision, by two straight lines meeting each other at the optimum temperature (Lösch and Tenhunen, 1981). Half values of stomatal opening in response to increasing values of photosynthetic active radiation (PAR) were reached between 100 and 200 μmol photons m^{-2} s^{-1}. The PAR response was similar in low K and high K plants.

Table 1 summarizes the equations and coefficients which describe quantitatively these dependencies for flag leaves, based on the data from 1986. In the model it was assumed, that in the course of the season the maximal g-values were determined by the water status of the leaves, and during a diurnal course by the light regime. The

Table 1. Empirical simulation model for calculation of leaf conductance in flag leaves of low (KL) and high K (KH) barley plants. The model was based on observed relationships between leaf conductance (g) and leaf water potential (ψ_l), irradiation (PAR), leaf temperature (t), and leaf-to-air water vapour concentration difference (ΔW) when only one of the parameters varied. The relationships were obtained by selecting data from the observations shown in Figures 1 and 2

Relationship	Algorithm for	
	KL plants	KH plants
Leaf conductance versus ψ_l below −1.6 MPa (If $\psi_l > -1.6$ MPa then by definition $\psi_l = -1.6$ MPa)	$g_{\psi} = a + b \cdot \psi_l$ $a = 1.3$ $b = 0.28$	$a = 1.3$ $b = 0.25$
Leaf conductance versus ψ_l and PAR	$g_{\psi,PAR} = g_{\psi}/(1 + c \cdot g_{\psi}/PAR)$ $c = 232.85$	$c = 232.85$
Maximal leaf conductance under otherwise non-limiting conditions versus temperature (t)	$g_{temp.max} = d + e \cdot t_{opt} = f - h \cdot t_{opt}$ $t_{opt} = 23.4°C$	
Reduction of maximal leaf conductance (R) (as calculated for the optimum temperature; t_{opt}) by low PAR and ψ_l	$R = g_{temp.max} - g_{\psi,PAR}$	
Leaf conductance versus ψ_l, PAR, and t below the optimum temperature (t_{opt})	$g^1_{\psi,PAR,t} = d + e \cdot t_{leaf} - R$ $d = 0.63$ $e = 0.016$	$d = 0.56$ $e = 0.019$
Leaf conductance versus ψ_l, PAR and t above the optimum temperature (t_{opt})	$g^2_{\psi,PAR,t} = f - h \cdot t_{leaf} - R$ $f = 1.5$ $h = 0.0213$	$f = 1.6$ $h = 0.0255$
Leaf conductance versus ψ_l, PAR, t and ΔW	$g_{\psi,PAR,t,\Delta W} = g_{\Psi,PAR,t} - i \cdot \Delta W$ $i = 0.023$	$i = 0.024$

g = leaf conductance to water vapour transfer (cm s^{-1}); ψ_l = bulk leaf water potential (MPa); PAR = photosynthetic active radiation (μmol photons m^{-2} s^{-1}, 400–700 nm); t = leaf temperature (°C); ΔW = leaf-to-air water vapour concentration difference (g m^{-3}).

reduction in g due to lowered ψ_l was described by a linear equation. ψ_l-values higher than -1.6 MPa were taken to bring about no reductions of stomatal apertures. The dependency of g on PAR was described by a saturation-type equation (Landsberg, 1977). The maximal leaf conductance (g) to be used in this equation was defined as the conductance under light saturation conditions at optimal temperature and high air humidity, reduced by the influence of ψ_l on g. Both leaf temperatures above and below the optimum temperature, and increases of ΔW reduced the maximal g-value. These dependencies were obtained by linear regression between g and the respective parameter, when neither insufficient irradiation nor ψ_l caused decrease of g. If light regime and ψ_l did not 'permit' maximal g-values, the linear relationship describing g as a function of temperature was displaced to a lower level. In this case the difference between the maximal g-value and the lowered one due to low values of irradiation and ψ_l were calculated and subtracted from the coefficients for the y-axis intercepts in the equations which describe the dependence of g on temperature. The effects of interactions of the influencing parameters on g (Lösch and Tenhunen, 1981) were not sufficiently substantiated by the data sets and were not taken into account in the present model.

The quantitative relationships between leaf conductance and individual parameters were estimated by linear regression calculations. In the case of the rectangular hyperbola describing the relationship between PAR and g linearization was achieved by an inverted notation of the formula (Landsberg, 1977). These calculations were done stepwise with a total of 22 data sets. Thus, e.g. the dependency of g upon temperatures above 23°C was calculated for data sets with $\mathrm{PAR} > 1400$, $1400 > \mathrm{PAR} > 1000$, $1000 > \mathrm{PAR} > 600$, and $600 > \mathrm{PAR} > 200$ μmol phot. $\mathrm{m}^{-2}\,\mathrm{s}^{-1}$, while water potential values ranged between -1 and -2 MPa and those of ΔW between 10 and 20 g m^{-3}. In the same way the dependency of g was calculated, with temperatures <23°C, ΔW, PAR or water potential as the independent variable. In nearly 2/3rd of all calculations the correlation coefficients showed a dependency of g upon the respective parameter at the 5%, and in many cases at the 1% level of probability. The overall statistical significance was checked finally for the relationship between measured and model-calculated g-values. For 191 data pairs of the KH plants the correlation coefficient was 0.71 ($p < 0.01$); for 162 data pairs of the KL plants it was 0.68 ($p < 0.01$).

Similar calculations were attempted also for leaves at lower insertion levels. Measurements on leaf No 7 provided enough data in order to adapt the model algorithms also to these leaves. Here, on average, conductances were reduced by 1/3rd in comparison with those of the flag leaf values. No clear threshold existed for the stomatal response to decreasing water potentials (Fig. 3), and the decrease of conductance with decrease of ψ_l was greater than in the flag leaves. Thus, coefficient b of the model (Table 1) was 0.38 for leaf No 7 for both high and low K plants. The response of leaf conductance to PAR was more sensitive than that of the flag leaf such that the saturation-type increase in conductance of leaf No 7 with increasing PAR was steeper than in the flag leaf. This was expressed in the model by a smaller coefficient c, which was only 186 in leaf No 7 and 172 in leaf No 6, both estimated, but not corroborated statistically. This indicates an adaptation to shade. At lower positions in the canopy stomatal responses became adapted to the reduced radiation resulting from light interception by ears and flag leaves (Fig. 5). The analysis did not indicate any shift in temperature sensitivity of stomata for lower leaves of either K treatment. The model fit became improved if no allowance was given for a humidity response of leaf No 7. This contrasts to the situation of the flag leaf. Apparently, barley stomata became insensitive to changing ΔW with the progress of leaf senescence. Leaf conductances were calculated for diurnal courses of the micro-climatic and water-stress situation and compared with the measured data of leaf No. 7. The correlation coefficients ($g_{\mathrm{measured}}/g_{\mathrm{calculated}}$) were highly significant (KL: $r = 0.67$, $n = 73$; KH: $r = 0.72$, $n = 72$). From the shapes of the diurnal courses there was some indication (Fig. 5) that the conductance of the lower leaves did not adapt to quick changes in light intensity such as those caused by the shadow effect from the ears and flag leaves swaying in the wind. With the model the conductance was calculated using

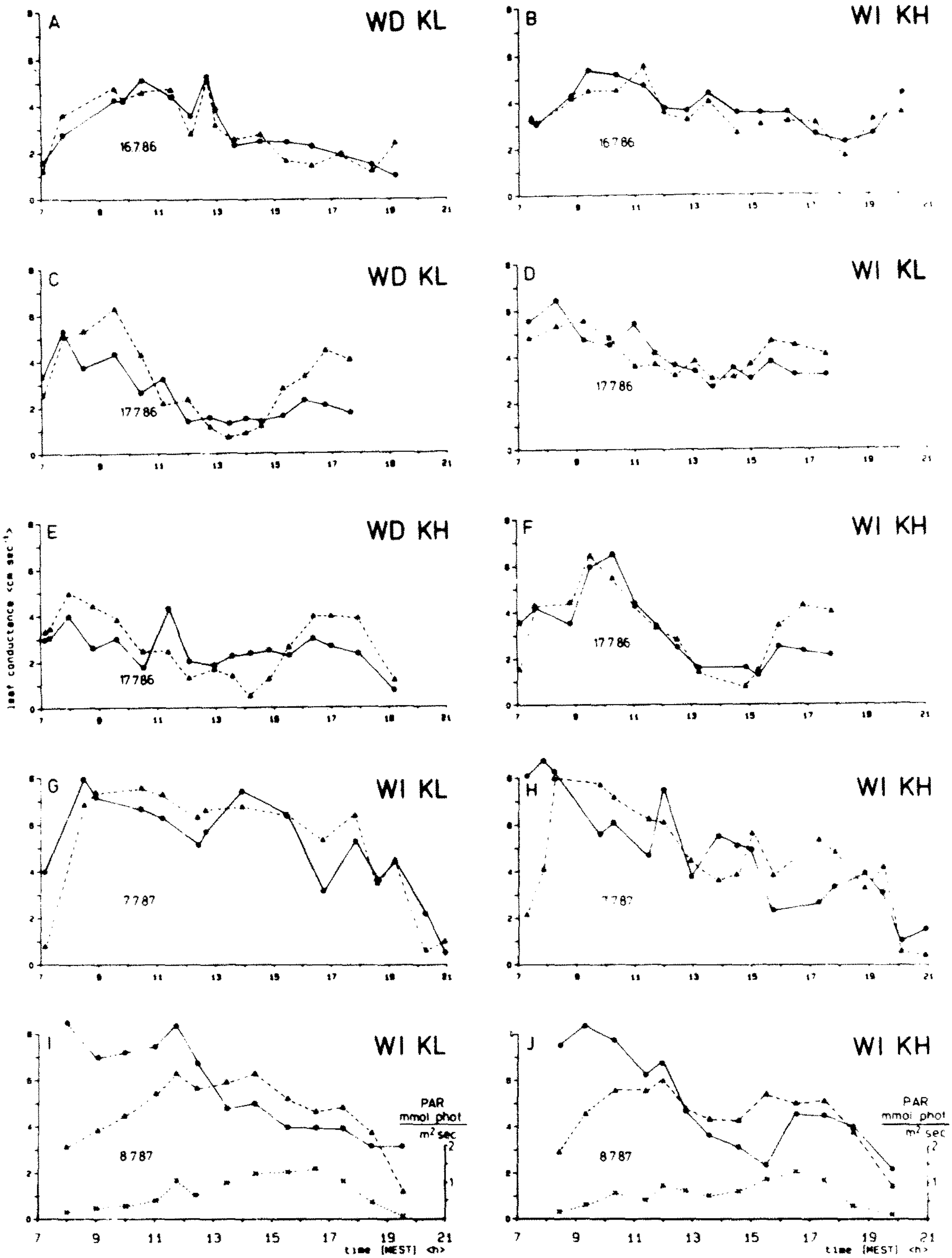

Fig. 8. Examples of measured (points, fully drawn lines) and modelled (triangles, dashed lines) diurnal courses of flag leaf conductances (g) under various treatments and meteorological conditions in July 1986 and 1987. Meteorological data of the diurnal courses A–H, see Figures 1, 2 and 7.

momentary micrometeorological data. Therefore, the real situation will be mirrored only imperfectly, when non-steady-state conditions prevail. This may have been the case also, when model predictions deviated for short-time low saturation deficits of the air at higher temperatures. Then measured g was considerably lower than the predicted ones. This might be interpreted as a retarded adaptation of stomatal apertures to air of higher humidity brought by wind gusts.

In Figure 8 measured and predicted values of flag leaf conductance (g) are shown both for the 1986 and the 1987 seasons. The examples from days in 1986 show that the model, compiled from stepwise regression calculations for the single parameters which influence g, worked as a whole and was able to predict various types of diurnal courses. The data of 1987 served as an independent test of the model predictions. The model predicted the measured diurnal courses of g quite well for both seasons on clear days, and midday stomatal closures were simulated (Fig. 8C–F). However, at low light intensities particularly on cloudy days during the morning hours (Fig. 8I, J), and during the middle of the afternoon (Fig. 8D, H–J) the predicted values were lower and higher, respectively, than the measured values. These discrepancies are discussed below in relation to hysteresis in the diurnal courses. They may be explained also by non-steady-state leaf conductances and by partial decoupling of stomatal apertures from the parameters used in the model.

The differences between high and low K plants were quantified by the slopes of the lines which described the decrease of g with increased ΔW, and with temperatures below and above the optimum temperature for maximal g. These slopes were significantly ($p \leq 0.05$) steeper in high K than in low K plants. This emphasizes that the response of g to a certain step in humidity (or temperature) is more drastic in KH than in KL plants.

Based on the model regressions, flag leaf stomata of the low K plants responded with 16% less sensitivity to changes in temperature, and with 4% less sensitivity to changes in ΔW. The steepness of the line describing the dependence of g on ψ_l in low K plants exceeded that in high K plants by 12%. No clear differences between the K treatments were found for the dependence of g on PAR. The smaller responsiveness of the stomata in low K plants to a given increase in the atmospheric evaporative demand could be due to altered physiological parameters such as membrane semipermeability, but could also originate from a different stomatal geometry in the differently K fertilized plants. This is because g depends directly upon pore sizes which will be different between differently cultivated plants under the same actual environmental conditions if different guard cell sizes and densities were developed during the ontogeny of the leaves.

Leaf stomatal density and size

Stomatal distribution and size in low and high K plants are shown in Table 2. On both leaf sides stomatal density was significantly decreased in flag leaves of high K plants. While the mean length of guard cells from these leaves was somewhat shorter, their width exceeded that of stomata from leaves of low K plants. As a rule, in the second leaf from the top (leaf No 7) no significant morphological differences could be found between high and low K plants.

Table 2. Stomatal density, length and width of the adaxial (ad) and the abaxial (ab) surfaces of the flag leaf (leaf No 8) and of leaf No 7 of low (KL) and high K (KH) barley plants (irrigated plots)

	Stomatal density (stomata mm^{-2})				Length (μm)				Width (μm)			
					of a pair of guard cells							
	KL	KH	LSD	sign.(5%)	KL	KH	LSD	sign.(5%)	KL	KH	LSD	sign.(5%)
Leaf No 8 ad	75.5	68.2	2.41	*	43.2	42.2	0.5	*	11.3	11.9	0.23	*
ab	70.3	66.6		*	45.1	44.8		n.s.	12.4	13.0		*
Leaf No 7 ad	78.9	79.5	3.05	n.s.	41.8	41.2	0.64	n.s.	11.8	11.6	0.31	n.s.
ab	79.6	81.3		n.s.	42.0	43.2		*	13.1	13.7		*

Calculation of leaf conductance (g) from stomata density and dimensions

A calculation of r_s or g according to the formula of Parlange and Waggoner (1970) showed that the g-values of the flag leaves of high K plants were up to 10% smaller than those of low K plants (Table 3). Differences between the calculated g-values of low and high K plants became most pronounced at low conductance. No significant decrease of g in high K plants could be calculated from the leaf morphological data of leaf No 7. Contrary, when stomata were wide open the conductances of the high K plants were insignificantly higher than those of the low K plants.

The up to 10% lower g-values of the high K flag leaves, as calculated from stomatal sizes and densities, may explain the difference in g found in low and high K plants by the porometrical measurements under similar environmental conditions. The more sensitive temperature and

Table 3. Leaf conductances (g) or resistances (r_s) of the adaxial (ad) and abaxial (ab) surfaces of the leaves of low (KL) and high K (KH) barley plants as calculated from stomatal sizes and densities given by Table 2 according to Parlange and Waggoner (1970)

a	b	c	d	e	f	g
Treatment and side of the leaf	Width of the stomatal pore as a fraction of the width of the whole stoma	Width of the stomatal pore (μm)	Calculated ad- or ab-axial conductance (cm s^{-1})	Reduction of KH conductance relative to KL (%)	Calculated leaf resistance (s cm^{-1})	Range of porometrically measured KH resistances when simultaneously measured KL resistances are equal to calculated KL resistances (column f) (s cm^{-1})
Leaf No 8						
KH ad	1/4	2.98	0.74	8.2	1.32	*1.4–3.5*
ab		3.25	0.77			
KL ad		2.83	0.83		1.21	1.2
ab		3.10	0.81			
KH ad	1/10	1.19	0.38	8.5	2.56	*1.6–4.8*
ab		1.30	0.40			
KL ad		1.13	0.43		2.34	2.3
ab		1.24	0.42			
KH ad	1/40	0.30	0.12	9.0	8.2	*5–11*
ab		0.33	0.12			
KL ad		0.28	0.14		7.5	7.5
ab		0.31	0.13			
KH ad	1/100	0.12	0.051	10.4	19.2	*17–26*
ab		0.13	0.053			
KL ad		0.11	0.058		17.2	17
ab		0.12	0.057			
Leaf No 7						
KH ad	1/10	1.16	0.44	−2.2	2.22	*1.9–3.7*
ab		1.37	0.47			
KL ad		1.18	0.44		2.27	2.3
ab		1.31	0.45			
KH ad	1/40	0.29	0.136	−2.1	7.0	*8.0–10.6*
ab		0.34	0.147			
KL ad		0.30	0.137		7.2	7.2
ab		0.33	0.140			
KH ad	1/100	0.12	0.058	0	16.7	*19.8–21.1*
ab		0.14	0.063			
KL ad		0.12	0.059		16.7	16.7
ab		0.13	0.060			

humidity responses of the stomata in high K plants might result in the measured 12% bigger decrease in g in these plants, if evaporation was increased and stomatal pores became narrowed, whereas with fully open stomata the differences in water loss between the two K treatments were small. In No 7 differences in porometrically determined conductances and transpirational water loss between the two K treatments were less (Fig. 6) corresponding to the fact that no significant differences in the stomatal morphology and density were found between the two treatments.

Discussion

Barley transpiration is controlled by varying leaf conductances (g) during the course of the day and during the whole vegetation period. The greatest amounts of the water loss originate from the flag leaves and the awns (e.g. Buttrose and May, 1959; Thorne, 1965). Biscoe et al. (1973) determined by means of gas exchange measurements and diffusion porometry stomatal resistances of barley awns to be in the range 3 to 6 s cm^{-1} which resulted in maximal transpiration rates of about 160 mg H_2O ear^{-1} h^{-1}. 73% of the total transpiration of ears originated from the awns, the rest from the lemmas. Similar relations were determined previously by weighing approaches by Schmid (1898). He calculated the abaxial surface of the hypostomatous awns of one ear to be 42 cm^2. Taking this value as representative, maximal awn transpiration determined by Biscoe et al. (1973) would amount to 2.8 mg H_2O cm^{-2} h^{-1}, which is of similar magnitude as our measurements. Awn stomata respond to solar radiation (Biscoe et al., 1973) and are probably affected also by other micrometeorological factors and by the ear water status, as can be deduced from the diurnal courses depicted in Figure 7. Patterns of increase and decrease of awn resistances to water vapour transfer were similar to those of the flag leaves and did not simply passively follow the evaporative demands.

Being the most external parts of the canopy, the awns and also the flag leaves are not completely enclosed into the gross boundary layer of the field (Jarvis, 1985), and are affected by the diurnal changes of their specific micro-environment. Under drought, as quantified by bulk ψ_l (Fig. 3) or by soil moisture deficit (Fig. 4), the leaf resistance increased considerably after a critical level of water shortage was passed. This threshold ψ_l-value was lower in the flag leaf than in the older leaves. In wheat also, there is an increase in the critical ψ_l-value for stomatal closure with age/position of leaf. While upper leaves of wheat had a critical threshold ψ_l of −1.9 MPa, leaves of intermediate insertion closed their stomata at approximately −1.4 MPa, and the lowest ones closed at −0.7 MPa (Millar and Denmead, 1976). Biscoe et al. (1976) cast doubt about there being a true critical threshold for the water potential sensitivity of stomata. Their data from wheat, however, showed a decrease of leaf conductances (g) which commenced at −0.8 and ended with closed stomata at −1.6 MPa. Also in our measurements with barley, g of the flag leaves remained high over quite a broad range of ψ_l and decreased only when ψ_l fell below −2 to −3 MPa. At least a value of −1.6 MPa, above which water stress does not yet influence g, must be taken into account in a model which aims to quantify the factorial dependencies of the conductances of the uppermost leaf.

Irradiation-dependent increase in g was described in the model by a saturation-type equation. It adequately predicted changes in g during the diurnal courses which resulted from transiently reduced PAR values due to clouds. Often early in the morning divergences could be found between measured and calculated conductances. This divergences probably resulted from a very strong stomatal trend to open at dawn, and a similar trend has lately been demonstrated under natural light conditions in wheat and lupin (Henson et al., 1990). Zeiger et al. (1981) have hypothesized that this is caused by a sensitive response of the blue-light receptor of the stomata (Skaar and Johnsson, 1978; Zeiger and Field, 1982) to the twilight conditions at dawn. In the afternoon-hours, on the other hand, the model often overestimated g. This phenomenon, termed an 'afternoon fatigue' of stomatal opening, can be observed in many species (Tenhunen et al., 1987), but it is not yet explained in terms of its causal dependencies.

Most diurnal variation in flag leaf g results from the joint effect of temperature and ΔW on stomatal apertures. Thus, there exists proportionality between decreases in ambient humidity and g. The reduction of g per unit of ΔW (0.023 and 0.024; Table 1) was 2/3rd of that found by Rawson et al. (1977) for *Hordeum vulgare* cv. Abyssinian (0.035). The latter was cultivated under glasshouse conditions and always adequately watered. Probably, under such conditions the stomatal response is more sensitive to environmental changes. Such different sensitivities of leaf conductance to ΔW depending on growth conditions in a greenhouse or in the field were also reported by Grantz et al. (1987) for sugar cane.

For the temperature response of stomata at similar ΔW, an increase in g with raising temperatures has mostly been found up to an optimum temperature, above which the g-value decreases with increasing temperatures (Lösch and Tenhunen, 1981). In many species this optimum is so high that normally an increase in ambient temperature brings about an increase of leaf conductance or at least no substantial decrease. This, certainly was the case also with *Hordeum distichum*, cv. Gunnar, during many days of the cool and wet year 1987, but not during the ripening period of 1986. With the lowest leaf temperatures around 16°C and the highest ones up to 32°C the leaf temperatures were very often supraoptimal for stomatal opening and contributed substantially to the sometimes very pronounced midday-closure of stomata (Fig. 8C, D). With a broad temperature optimum for stomatal opening between 22° and 24°C the cultivar proves to be best adapted to cool-temperate regions. Optimum temperatures for maximal leaf conductance well below 25°C are also reported for other temperate crops (Hofstra and Hesketh, 1969) and fruit trees (e.g. apple: 23°C; West and Gaff, 1976).

The model in Table 1 described the joint action of the influencing parameters on the flag leaf conductance of barley. If the model was applied to all data sets of the measuring period 1986, the residuals between measured and calculated g in most cases did not deviate from the measured values by more than at most 20%. Apart from the already discussed differences between modelled and measured g-values at dawn and in the late afternoon higher g-values were calculated than measured if ψ_l-values decreased below −2 MPa. This indicates that the model does not yet take sufficiently into account lack of response to short-term changes of ψ_l (Turner et al., 1985). In some cases incorrect values of g may originate from instrumental errors which according to the manufacturer's manual (LiCor 1980) may deviate by up to 10%.

Apart from these special situations during the course of a day, the model simulated the magnitude and pattern of changes in g comparably to other modelling approaches (e.g. Grantz et al., 1987; Jarvis, 1976; Meinzer, 1982; Myers et al., 1984; Pallardy and Kozlowski, 1979). As in our model, it is common for most of these models to describe the multifactorial dependence of stomatal apertures on the environment as being additive. This has the advantage that the empirical quantification of the single dependencies can be easily extended to a yet more causal quantitative description, if knowledge about the functional dependency of the stomatal response to a particular factor is increased. With the additive approach it is also easier in comparisons to single out those responses which are equal in plants differing in their genetics or their ontogeny and those responses which are different (Grantz et al., 1987; Pallardy and Kozlowski, 1979). This type of model stands halfway between purely correlative simulations (like approximations by polynomials of higher order) and true deterministic approaches. While the former will bring better agreement between measured and predicted data (Grantz et al., 1987) deterministic approaches will better link the observed patterns to metabolic events (Lösch, 1985). For strict deterministic functional models knowledge about stomatal ecophysiology is, however, not yet sufficient.

Changes in guard cell physiology during leaf senescence may lie behind the observed decrease of g and the changes in stomatal sensitivities with time. A decrease of g with age has been observed in many plants (e.g. tobacco: Václavík, 1974; broad-leaved trees: Turner and Heichel, 1977; bean: Minter, 1980; Pospisílova and Solárová, 1984). The causal interpretation of this effect follows two lines. Firstly, it may involve changes with age in the sensitivity of guard cells to abscisic acid (e.g. Atkinson et al., 1989; Jordan et al., 1975). Secondly, changes in the content and osmotic effect of potassium in the guard cells may change the sensitivity (Ozuna et al., 1985; Turner and Begg, 1973). Ontogenetic changes in the structure of guard cell walls and membranes may also change the requirements for osmotica needed to bring about a certain degree of change in the turgor differences between the cells in intact epidermal tissue. While guard cell potassium contents of older leaves may suffice to generate turgor for pore opening in isolated pairs of guard cells (Ozuna et al., 1985), substantial amounts of this potassium may be needed *in vivo* simply to keep constant the general turgescence of the stomata in such leaves. In *Veronica* stomata the potassium available for the shuttle between guard cells and their neighbourhood decreases with plant senescence while the total potassium content of the guard cells remains more or less the same (Lösch and Krug, 1979). Diurnal variations of the stomatal apertures consequently will become smaller.

Apparently, maximal amounts or concentrations of potassium in guard cells are relatively similar in differently aged leaves and do not differ substantially in different plant species (Outlaw, 1983). It may be under situations of K shortage, that the guard cells get a potassium allocation by priority, so that their function is unimpaired. A different potassium distribution at the subcellular level, so that metabolic functions of the cytoplasm can continue at the expense of vacuolar potassium contents, has been documented for barley roots (Memon et al., 1985). It is conceivable that a similar unequal distribution of a limited K supply occurs also between leaf mesophyll and epidermis. Leigh et al. (1986) give X-ray microanalysis spectra for both the mesophyll cytoplasm and vacuole, and for the epidermal vacuole of K-deficient and sufficiently K-supplied barley leaves. While for the mesophyll cell vacuoles of K-deficient leaves the K-peak is lacking, only a limited reduction can be seen in the height of K-peaks of the mesophyll cytoplasm and of the epidermal vacuoles. These findings may indicate that guard cells get enough potassium ions also under K deficiency, so that their function will not be affected negatively.

If a higher potassium supply is available, the overall plant turgor will improve (Jensen, 1982; Jensen et al., 1992; Lindhauer, 1985) due to the function of the K ions as a main osmoticum in the vacuoles. This again will result in turgor-induced growth. Altered cell sizes and stomatal densities in the epidermis will result from these differences in growth conditions of high and low K plants.

Morphogenesis of the epidermal structure depends on many factors so that e.g. leaves of the sun and shade crown of a tree differ considerably in stomatal density and size. McConathy (1983) calculated from these anatomical differences diffusion resistances of leaves in the different parts of the crown of a tulip-poplar tree and found good correlations with the different measured diffusion resistances. Also in cereal leaves the anatomical structure of the epidermis is affected by the ontogenetic history. When water stress reduced leaf growth in sorghum the number of epidermal and stomatal cells was reduced (McCree and Davis, 1974). While in this case stomatal density was not altered significantly, guard cell sizes became smaller under the stress treatment. Jones (1977) studied barley lines selected for high and low stomata densities and tested them for differences in transpiration. No differences in leaf conductances were found in these comparisons, because stomatal sizes compensated for different stomatal densities of the cultivars. Low density lines, however, lost more water per plant due to larger individual leaves and a larger amount of biomass per plant. In our barley cultivar 'Gunnar' different potassium fertilization resulted in significantly different densities and sizes of the flag leaf stomata. From their anatomy up to 10% higher conductances could be calculated for the low K plants. Most of the measured higher leaf resistances of the high K plants – and as a result the lower transpiration and better water use efficiency of these plants (Andersen et al., 1992a) – may therefore sufficiently be explained by the anatomical characteristics of the epidermis. If these findings can be extended also to other varieties and species, the beneficial effect of potassium fertilization on water use efficiency generally might be traced back to the morphogenetic response of the crop. Thus, hypotheses about an altered response of the guard cell metabolism will not be needed as an explanation.

Acknowledgements

We are grateful to the Danish Veterinary and Agricultural Research Council (Project Nos 13-3514, 13-3689, and 13-3870) for grants supporting this work. We are grateful to the Danish Research Service for Plant and Soil Science for technical support and field facilities. We thank Dr. I E Henson for helpful comments on the manuscript. The technical help of Mrs H Timm and the typewriting of Mrs E Brush are gratefully acknowledged.

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