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Water deficit and impaired pegging effects on peanut seed yield: links with water and photosynthetically active radiation use efficiencies

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Abstract. Peanut (*Arachis hypogaea* L.) production is frequently affected by unpredictable events of water deficit during pod set, which modulate water use, water use efficiency for biomass production (WUE_B), and biomass partitioning to seeds. We studied the effects of drought-induced impaired pegging on WUE_B and the link between WUE_B and photosynthetically active radiation use efficiency (PAR-UE). Field experiments were conducted that combined: two cultivars of contrasting pegging capacity (ASEM > Florman), two water regimes (irrigated and water stress) and different sowing dates. WUE_B ranged between 6.1 and 6.7 g kPa/mm for irrigated plots, and between 2.9 and 7.1 g kPa/mm for water-stressed plots. WUE for pod production showed similar trends, but was larger for ASEM than for Florman because of higher biomass allocation to pods and pegging capacity of the former. The relationship between standardised values of WUE_B and PAR-UE varied linearly for the post-R6 period, but fitted models differed between water regimes. This difference was attributed to the relative importance of stomata control on gas exchange (direct effects of water deficit) respect to feedback effects on photosynthesis caused by reproductive sink size (indirect effects of water deficit). Variation in post-R6 PAR-UE could be linked exclusively to the latter, but variation registered in WUE_B acknowledged both controls.

Additional keywords: *Arachis hypogaea* L., peanut, pegging capacity, reproductive sink strength, seed yield, soil strength, water deficit.

Introduction

Two thirds of global peanut production comes from environments where water is supplied by seasonal rainfall, and where drought is a frequent limitation to seed yield (Wright and Nageswara Rao 1994). This condition also applies to the main peanut production region of Argentina located in Córdoba province (32–35°S, 62–64°W), where unpredictable water deficit during the period of pod set reduces seed yield markedly (Collino *et al*. 1998). An important objective of breeding programs targeted to this type of environments has been to increase seed yield per unit of available water (Bindu Madhava *et al*. 2003). Several physiological traits related to improved water use efficiency (WUE) have been evaluated in these programs; e.g. root system size and its capacity for water absorption (Klepper 1987), leaf temperature and its correlation with transpiration (Keener and Kircher 1983; Wanjura *et al.* 1990), crop water absorption capacity (Wright and Smith 1983), osmotic adjustment (Chimenti *et al*. 2002) and chlorophyll content as a surrogate for the estimation of biomass production per unit of transpired water (Bindu Madhava *et al.* 2003).

Assuming water as the principal limiting resource for crop growth, seed yield can be defined as the product between water transpired by the crop, WUE for biomass production (WUE_B), and harvest index (HI = proportion of shoot biomass assigned to seed production). In this framework, proposed by Passioura (1996), improved WUE_B is critical for drought tolerance (Hebbar *et al*. 1994; Craufurd *et al*. 1999). As a result of a higher HI caused by a greater partitioning to reproductive structures, increments in WUE for pod biomass production (WUE_P) might be expected. In peanut, several authors have confirmed the existence of genotypic variability in WUE_B at the plant (Hubick *et al*. 1986; Craufurd *et al*. 1999) and crop levels (Chapman *et al*. 1993; Nageswara Rao *et al*. 1993; Hebbar *et al*. 1994; Wright *et al*. 1994; Collino *et al*. 2000), but none of these studies addressed the effects of drought-induced impaired pegging on WUE_B. This restriction, distinctive to peanut crops and determined by increased soil strength due to soil desiccation above a threshold value (Collino *et al*. 2000; Haro *et al*. 2008), is an additional factor controlling seed set in this species. Collino *et al*. (2000) reported differences between cultivars in pegging capacity

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under variable surface soil strength, revealing genotypic differences in WUE_P.

Artificial reduction of pod set by hand-removal of successive cohorts of pegs decreased sink strength, and consequently reduced biomass production due to feedback control of photosynthesis (Haro *et al*. 2007). This response explained part of the associated decline in radiation use efficiency of late-sown peanut crops, which had been customarily attributed to low air temperature (Bell *et al*. 1992) despite lack of evidence for this effect in the temperate environment of Argentina. Similar results were obtained by drought-induced impaired pegging, which helped quantify direct (i.e. drought *per se*) and indirect effects (i.e. those caused by reproductive sink size and its effects on source activity) of water deficit on radiation use efficiency (Haro *et al*. 2008). In these studies, however, possible links between WUE_B, pegging and radiation use efficiency were not explored. To elucidate these links we conducted field experiments in which peanut crops were subjected to variable surface and deep soil desiccation, caused by the combination of (*i*) variable irrigation regimes, and (*ii*) contrasting evaporative demands related to different growing seasons and sowing dates. These conditions were aimed to promote a range in pegging accomplishment of two widely used peanut cultivars of contrasting peg production, Florman INTA (low) and ASEM 485 INTA (high) (Haro *et al*. 2008). Our objective was to quantify the relative contribution of each factor (water regime, variable pegging promoted by surface soil strength, and cultivar) to the variation in WUE_B and WUE_P. Besides, we explored associations between photosynthetically active radiation (PAR) use efficiency (PAR-UE) and WUE_B during the seed-filling period, when sink activity modulates biomass production and could affect WUE_B and its concomitant association with PAR-UE. We hypothesised that (*i*) differences between cultivars in biomass partitioning to pods and pegging capacity under water stress determine genotypic variations in WUE_B and WUE_P, and (*ii*) sink activity during the seed-filling period modulates biomass production, and this affects WUE_B and its relation with PAR-UE.

Materials and methods

Crop husbandry, experimental design and growing conditions

Field experiments (Exp_n) were conducted during (*i*) 2002–03 and (*ii*) 2005–06, as described in Haro *et al*. (2007, 2008). Briefly, cultivars ASEM 485 INTA and Florman INTA (hereafter ASEM and Florman) were sown on 17 October (17-Oct.) and 29 November (29-Nov.) 2002 in Exp_1, and on 14 November (14-Nov.) 2005 in Exp_2, at 14 plants/m^2. Soils were silty loam Typic Haplustoll (USDA Soil Taxonomy, Soil Survey Staff 1998), with 150 mm of plant available water (PAW) for each meter depth (Dardanelli *et al*. 2003). Two water regimes were evaluated: (*i*) irrigated (IRR), where plots were watered to maintain PAW at rooting depth above 60%, and (*ii*) water stressed (WS), where rainfall water was excluded by means of automatic mobile shelters. In Exp_1 WS plots received full irrigation [i.e. equivalent to match maximum crop water use (WU)] until R_1 (beginning bloom; Boote 1982) and no additional water from irrigation or rainfall from this stage onwards. In Exp_2 full irrigation was applied until R_1; partial irrigation (~44% of the amount used in IRR plots) was applied between R_1 and R_5 (beginning seed filling), followed by the addition of small amounts of water (~5 mm/day three times per week) between R_5 and final harvest (FH) to minimise the negative effects of soil strength on pegging and early pod growth. A split split-plot design was used in Exp_1, with water availability in the main plots, sowing dates in the subplots and cultivars in the sub-subplots. In Exp_2, water availability was in the main plots and cultivars in the subplots. There were always four replicates.

Air temperature, relative humidity (RH) and incident solar radiation were measured at hourly intervals in meteorological stations placed within 10 m of the experimental plots. Daytime vapour pressure deficit values (VPD, in kPa) were derived from maximum and minimum daily temperature records. VPD values were estimated daily (Eqn 1) as the difference between saturated vapour pressure (e_a) and actual vapour pressure (e_d). Daily maximum and minimum air temperatures (T_{max}, T_{min}) and daily maximum and minimum relative humidity values (RH_{max}, RH_{min}) were computed according to the procedures of Allen *et al*. (1998) to calculate e_a and e_d at T_{max} and T_{min} (Eqns 2 and 3).

$$\mathrm{VPD} = e_a - e_d \tag{1}$$

$$e_d = \left(\frac{e_a(T_{max})RH_{min}}{100} + \frac{e_a(T_{min})RH_{max}}{100}\right)/2 \tag{2}$$

$$e_a = (0.611\exp^{\left(\frac{17.27\,T_{max}}{T_{max}+237.3}\right)})\,0.72 + (0.611\exp^{\left(\frac{17.27\,T_{max}}{T_{max}+237.3}\right)})\,0.28 \tag{3}$$

Because evapotranspiration occurs during daytime hours, daytime VPD is likely to be a better estimator than daily mean VPD (Howell 1990). Then, we estimated daytime e_a using weighing parameters of 0.72 at T_{max} (which corresponds to daytime) and 0.28 at T_{min}, obtained by Abbate *et al*. (2004) for the same location under study. Experimental years and sowing dates exposed the crops to variable growing conditions (Table 1), which affected crop cycle duration (for details see Haro *et al*. 2008). Delayed sowing caused a decline in mean air temperature and irradiance. VPD dynamics did not match trends in temperature and irradiance regimes, and differed between experiments ($Exp_2 > Exp_1$) and sowing dates within Exp_1 (17-Oct. > 29-Nov.).

Measurements and statistical analyses

Soil water content was measured on each plot at 20-cm intervals from 30 to 290 cm depth using a neutron probe (Troxler Electronic Laboratories, Research Triangle Park, NC, USA). Water content of the uppermost 0–15- and 15–30-cm soil layers was measured gravimetrically. Measurements started at sowing and continued every 15–20 days until FH. Water use (in mm) was calculated from the water balance between successive neutron probe measurements, effective rainfall and irrigation (for more details see Haro *et al*. 2008). PAW was defined according to Ritchie (1981) as the ratio between actual crop available soil water and maximum available soil water (Eqn 4).

$$\mathrm{PAW} = \frac{\theta_a - \theta_{ll}}{\theta_{dul} - \theta_{ll}} \tag{4}$$

where θ_a is the volumetric water content at any time, θ_{dul} is the drained upper limit, and θ_{ll} represents the lower limit obtained from laboratory determinations at –1.5 MPa water potential.

Growth stages (Boote 1982) were monitored using three plants per plot tagged at R_1 (first flower visible in at least 50% of the plants). Thermal time (in degree-days or °Cd) to reach different stages was computed using a base temperature of 11°C. Biomass sampling and light interception measurements started at R_1 in both experiments and continued fortnightly up to FH. In all experiments, sampled plants were separated in leaves plus stems (vegetative biomass), pegs and pods (reproductive biomass), and dried at 70°C until constant weight. At FH, pods with seeds and total seed number were counted manually. Individual seed weight was calculated as the quotient between seed yield and seed number. Corrected total biomass (in g/m^2) was calculated as vegetative biomass plus reproductive biomass multiplied by a 1.65 energy correction factor (Duncan *et al.* 1978). PAR interception (IPAR) was determined in each plot from 10 PAR measurements above the canopy ($\mathrm{IPAR_a}$) and 10 PAR measurements immediately below the green leaves ($\mathrm{IPAR_b}$). Measurements were taken between 11:00 and 14:00 hours on clear days with a line-quantum sensor (AccuPAR – PAR/LAI Ceptometer; Decagon Devices, Inc., Pullman, WA, USA). For $\mathrm{IPAR_b}$ measurements, the sensor was fitted diagonally between the centres of two consecutive inter-row spaces. Fraction of IPAR (fIPAR) was computed as in Eqn 5.

$$\mathrm{fIPAR} = 1 - (\mathrm{IPAR_b}/\mathrm{IPAR_a}) \tag{5}$$

Values of fIPAR obtained with spot measurements performed at solar noon were adjusted for the diurnal variation in fIPAR using the relationship derived by Muchow (1985), which has been applied in previously published research on peanut (Bell *et al.* 1992). This correction was made for avoiding the underestimation of IPAR computations at early stages of crop growth (Kemanian *et al.* 2004). Daily values of solar radiation were converted into PAR by multiplying by 0.50 (Monteith 1972). For cumulated IPAR calculations, we estimated daily values by linear interpolation of IPAR measurements. PAR-UE (in g/MJ of IPAR) was computed from the relationship between cumulated corrected biomass and cumulated IPAR. Post-R_6 PAR-UE and a partitioning ratio (PR, quotient between pod and crop growth rates for the period between R_3 and $R_{6.5}$) were also computed. $\mathrm{WUE_B}$ and $\mathrm{WUE_P}$ were estimated from cumulated corrected biomass and cumulated non-corrected pod biomass, respectively, against WU corrected for VPD ($\mathrm{WU_{VPD}}$). Besides, post-R_6 $\mathrm{WUE_B}$ was computed. We calculated the relationship between standardised post-R_6 $\mathrm{WUE_B}$ and post-R_6 PAR-UE values, by considering the whole set of experimental data. Standardised values resulted from the quotient between each observed value and the maximum one obtained for each combination of experiment and sowing date, either for post-R_6 $\mathrm{WUE_B}$ and post-R_6 PAR-UE.

Treatment effects on the response variables were evaluated by ANOVA, and significance of differences between means were estimated using the *t*-test (InfoStat 2002). Regression

Table 1. Duration (in days from sowing) and cumulative thermal time (TT, in °Cd above 11°C) of different growth phases (S: sowing, R_1: beginning bloom stage, FH: final harvest) of two peanut cultivars (Florman and ASEM) cropped in two experiments ($\mathrm{Exp_n}$) and different sowing dates. Weather conditions are indicated for each treatment combination

Experiment	Sowing date	Cultivars	Growth phase S-R_1 Days	TT	Weather conditions Mean daily air temp. (°C)	Mean solar radiation (MJ/m^2.day)	Vapour pressure deficit (kPa)
$\mathrm{Exp_1}$	17-Oct.	Florman	50	482	20.6	20.5	1.66
		ASEM	50	482	20.6	20.5	1.66
	29-Nov.	Florman	40	480	22.3	21.0	1.48
		ASEM	40	480	22.3	21.0	1.48
$\mathrm{Exp_2}$	14-Nov.	Florman	45	475	22.0	21.8	1.90
		ASEM	45	475	22.0	21.8	1.90
			R_1-FH				
$\mathrm{Exp_1}$	17-Oct.	Florman	137	1475	21.8	19.6	1.42
		ASEM	113	1337	22.8	20.7	1.53
	29-Nov.	Florman	133	1196	20.3	16.9	1.21
		ASEM	125	1175	20.6	17.6	1.39
$\mathrm{Exp_2}$	14-Nov.	Florman	110	1052	20.6	18.9	1.55
		ASEM	106	1049	20.9	19.0	1.56
			S-FH				
$\mathrm{Exp_1}$	17-Oct.	Florman	187	1957	21.5	19.9	1.49
		ASEM	163	1819	22.2	20.7	1.58
	29-Nov.	Florman	173	1676	20.7	17.7	1.26
		ASEM	165	1655	21.0	18.2	1.31
$\mathrm{Exp_2}$	14-Nov.	Florman	155	1527	21.0	19.7	1.64
		ASEM	151	1524	21.2	19.8	1.65

analysis was applied to the relationship between variables. The coefficient of determination (r^2) and the distribution of residuals were used as criteria for selection of the best fitting models. Differences between parameters of these models were evaluated by the F-test (Statistix 2000).

Results

Plant available water and water use

For all plots in both experiments, PAW in the uppermost 200-cm soil depth at the beginning of the drought-imposed period was ~80% of water content at field capacity (Fig. 1). Thereafter, water content varied markedly across water regimes. Mean WU of WS plots during reproductive stages was larger in Exp$_2$ (341 mm, averaged across cultivars) than in Exp$_1$ (229 mm, averaged across sowing dates and cultivars), because the former received additional irrigations for reducing soil strength of the 15-cm topsoil layer. The reduction in WU of WS plots with respect to IRR plots was greater in Exp$_1$ (229 mm *v.* 565 mm) than in Exp$_2$ (341 mm *v.* 572 mm).

Seed yield and seed yield components

Seed yield varied markedly across treatments and experiments (Table 2), and water deficit was the main determinant of this variation. Seed yield reduction in WS plots of Exp$_1$ ($P < 0.0001$) averaged 91% for the 17-Oct. sowing and 75% for the 29-Nov. sowing. Water deficit effects on seed yield were less remarkable for Exp$_2$ ($P = 0.022$), and caused a 51% reduction in this variable compared with IRR plots. In all experiments and growing conditions, seed yield was larger for cultivar ASEM (range between 55 and 520 g/m^2) than for cultivar Florman (range between 35 and 476 g/m^2).

Seed number was severely affected by water deficit in all growing conditions (Table 2), and most part of the variation observed in this trait was attributable to variations registered in the number of pods ($r^2 = 0.98$) and not in pods per seed. Water deficit had a significant ($P = 0.0014$) but moderate effect on seed weight of Exp$_2$ (Table 2) and no effect on this trait during Exp$_2$. As a consequence of the differential effect of water regime on seed yield components, variations in seed yield were well explained by the observed variations in seed number/m^2 ($r^2 = 0.98$, $P < 0.001$), and to a less extent by variations in weight per seed ($r^2 = 0.67$, $P < 0.001$).

Biomass production, PAR-UE and WUE

Water stress reduced biomass production in all tested conditions, with the concomitant negative effect on final biomass (Table 2, Fig. 2) of both experiments. Effects of WS, cultivar and sowing date on the PR to reproductive structures were also found. The PR always declined with WS, being more affected in Florman than in ASEM. This ratio was reduced also by delayed sowing date (i.e. 29-Nov. Exp$_1$ < 17-Oct. Exp$_1$).

Details about the effects of treatments on PAR-UE can be found in Haro *et al.* (2008). Briefly, reduced water availability always caused a marked reduction in PAR-UE. This reduction was larger for Exp$_1$ (high WS) than for Exp$_2$ (moderate WS), and for the early (17-Oct.) than for the late (29-Nov.) sowing in Exp$_1$. Cultivars did not differ in the response pattern, except for IRR plots in the late sowing of Exp$_1$ (PAR-UE ASEM > PAR-UE Florman).

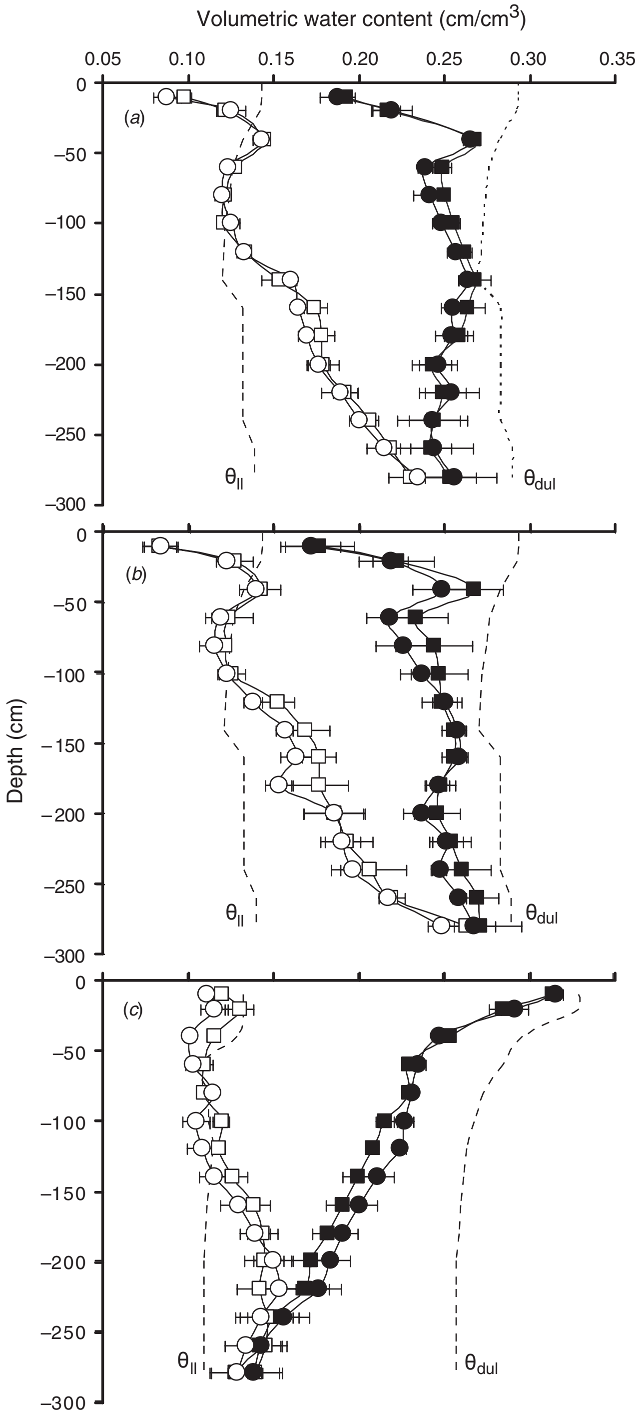

Fig. 1. Soil volumetric water content for cultivars Florman (circles) and ASEM (squares) sown on (*a*) 17-Oct. Exp$_1$, (*b*) 29-Nov. Exp$_1$, and (*c*) Exp$_2$. Black and open symbols represent the start of water stress (WS) and final harvest in WS plots, respectively. Dashed lines represent field-measured drained upper limit (θ_{dul}) and laboratory-determined lower limit at –1.5 MPa water potential (θ_{ll}). Horizontal bars represent s.e.m. ($n = 4$).

Table 2. Mean values for seed yield, seed yield components, corrected total biomass at final harvest (TB$_c$ FH) and partitioning ratio (PR) of peanut cultivars cropped in two experiments (Exp$_n$) and different water regimes (IRR: irrigated; WS: water stress)

Water regime (WR)	Sowing date (SD)	Cultivar (C)	Seed yield (g/m^2)	Seed no./m^2	Pod no./m^2	Weight per seed (g)	TB$_c$ FH (g/m^2)	PR
				Exp$_1$				
IRR	17-Oct.	Florman	476b$^{\text{A}}$	906	521	0.52bc	1723a	0.63
IRR	17-Oct.	ASEM	520a	1023	593	0.51bc	1787a	0.76
IRR	29-Nov.	Florman	313c	634	362	0.49c	1314b	0.58
IRR	29-Nov.	ASEM	455b	835	456	0.54a	1772a	0.68
WS	17-Oct.	Florman	35f	111	74	0.30f	550d	0.43
WS	17-Oct.	ASEM	55f	149	94	0.37d	550d	0.5
WS	29-Nov.	Florman	82e	250	192	0.34e	706c	0.3
WS	29-Nov.	ASEM	108d	269	167	0.40d	748c	0.4
		WR	<0.0001$^{\text{B}}$	<0.0001	0.0005	0.0014	<0.0001	0.0006
		SD	0.0158	0.0543	0.0374	0.0014	n.s.	0.0469
		C	0.0028	0.0105	0.0048	0.0001	0.0039	0.037
		WR × SD	0.001	0.0016	<0.0001	0.001	0.0015	n.s.
		WR × C	0.0114	0.028	0.0034	0.0002	0.0061	n.s.
		SD × C	0.0267	n.s.	n.s.	0.001	0.0081	n.s.
		WR × SD × C	0.0366	n.s.	n.s.	0.0008	0.0148	n.s.
				Exp$_2$				
IRR	14-Nov.	Florman	446	930	486	0.47	1654	0.63
IRR	14-Nov.	ASEM	504	1063	551	0.47	1954	0.64
WS	14-Nov.	Florman	199	473	251	0.41	1080	0.54
WS	14-Nov.	ASEM	262	580	307	0.45	1107	0.59
		C	n.s.	n.s.	n.s.	n.s.	n.s.	0.0401
		WR	0.022	0.0106	0.0122	n.s.	0.0124	n.s.
		WR × C	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

[A] In Exp$_1$, values followed by different letters within a column indicate differences among means due to significant ($P < 0.05$) WR × SD × C interaction effects.

[B] P-values; n.s., not significant.

For all growing conditions, WU$_{VPD}$ during early growth phases (from crop emergence to R$_1$) was not matched by large biomass production (Fig. 2). This situation was probably promoted by low fIPAR values of crops at the R$_1$ stage (0.20, 0.32 and 0.53 for 29-Nov., 14-Nov. and 17-Oct. sowings, respectively), which allowed large amounts of direct solar radiation on the soil surface with the associated increase in the proportion of soil water evaporation respect to plant transpiration. Maximum light interception (i.e. fIPAR $\geq$0.95) was never reached in WS plots of Exp$_1$ (for details see Haro *et al*. 2008), but this incomplete ground cover was not matched by increased soil evaporation because water inputs were excluded by mobile rainout shelters. Therefore, we assume WUE calculations were not biased by soil evaporation in this experiment. Additionally, functions fitted to the relationships between total energy-corrected biomass and WU$_{VPD}$ always excluded values representative of early developmental stages (Fig. 2), and were applied only to data obtained between R$_2$ and R$_3$ and R$_7$ (i.e. with high ground cover). This restriction granted full ground cover in IRR plots for minimising the soil evaporation component of total crop evapotranspiration. Linear functions fitted most datasets adequately (Fig. 2), and the slopes (i.e. WUE$_B$) ranged between 6.1 and 6.7 g kPa/mm for IRR treatments, and between 2.9 and 7.1 g kPa/mm for WS treatments. The only exception to this trend was for IRR plots of cv. Florman in Exp$_1$, for which a curvilinear response of cumulated biomass to WU$_{VPD}$ indicated a decline in WUE$_B$ as the season progressed.

The response of pod biomass production to WU$_{VPD}$ (Figs 3 and 4) was well described by linear models of the type fitted to total biomass. The slopes (i.e. WUE$_P$) were usually larger for IRR (range between 2.08 and 2.61 g kPa/mm) than for WS plots (range between 0.73 and 2.84 g kPa/mm), except in Exp$_2$ (2.68 g kPa/mm for WS and 2.10 g kPa/mm for IRR, averaged across cultivars). WUE$_P$ was always larger for cultivar ASEM than for cultivar Florman, and this difference was captured by an uneven distribution of residuals when a single model was fitted to the whole dataset of each combination of water regime and experiment. Again, a quadratic model gave a better fit than a linear one to IRR data of cultivar Florman in the 29-Nov. sowing of Exp$_1$ (Fig. 3*b*).

Relationship between PAR-UE and WUE during pod growth and seed filling

The post-R$_6$ period represented 34% (14-Nov. Exp$_2$) to 46% (29-Nov. Exp$_1$) of the whole cycle (i.e. between crop emergence and FH), and included the final part of the critical period for pod set (for details see Haro *et al*. 2007). The relationship between standardised post-R$_6$ WUE$_B$ and PAR-UE was well described ($r^2 \geq 0.72$) by simple linear regressions (Fig. 5). For IRR plots this relationship did not differ from the 1 : 1 ratio, evidence of a similar relative response of both efficiencies across the considered biomass range. Contrarily, the slope of the relationship between these efficiencies was above the 1 : 1 ratio under WS conditions, depicting larger effects of water

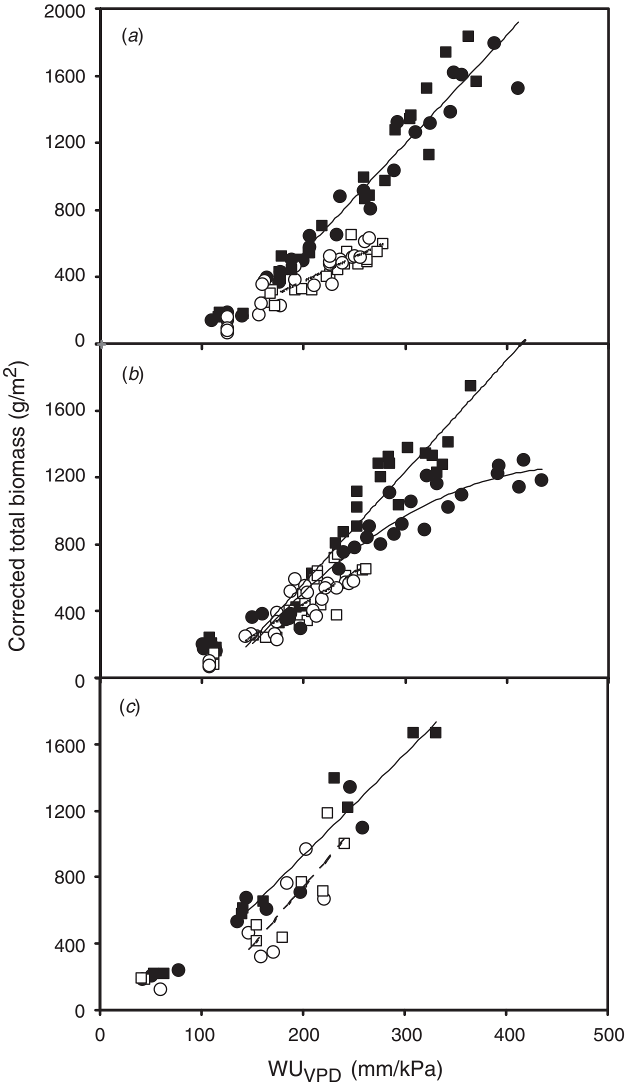

Fig. 2. Relationship between cumulative water use corrected by vapour pressure deficit (WU$_{VPD}$) and cumulative total biomass corrected by energy costs for oil synthesis of cultivars Florman (circles) and ASEM (squares) sown on (*a*) 17-Oct. Exp$_1$, (*b*) 29-Nov. Exp$_1$, and (*c*) Exp$_2$. Black symbols and solid lines represent irrigated plots (IRR). Open symbols and dashed lines represent water-stressed plots (WS). Fitted models were of the type: (i) $Y = a + (b \times X)$, and (ii) $Y = a + (b \times X) - (c \times X^2)$. Each point represents a replicate. Computed models were: (*a*) $Y = -743.73 + 6.47X$; $r^2 = 0.89$; $P < 0.001$ (IRR, both cultivars). $Y = -196.42 + 2.86X$; $r^2 = 0.64$; $P < 0.001$ (WS, both cultivars). (*b*) $Y = -766.27 + 6.67X$; $r^2 = 0.88$; $P < 0.001$ (ASEM, IRR). $Y = -1026.8 + 9.81X - 0.0105X^2$; $r^2 = 0.91$; $P < 0.001$ (Florman, IRR). $Y = -320.91 + 3.81X$; $r^2 = 0.62$; $P < 0.001$ (WS, both cultivars). (*c*) $Y = -289.73 + 6.1X$; $r^2 = 0.91$; $P < 0.001$ (IRR, both cultivars). $Y = -679.56 + 7.07X$; $r^2 = 0.65$; $P < 0.001$ (WS, both cultivars).

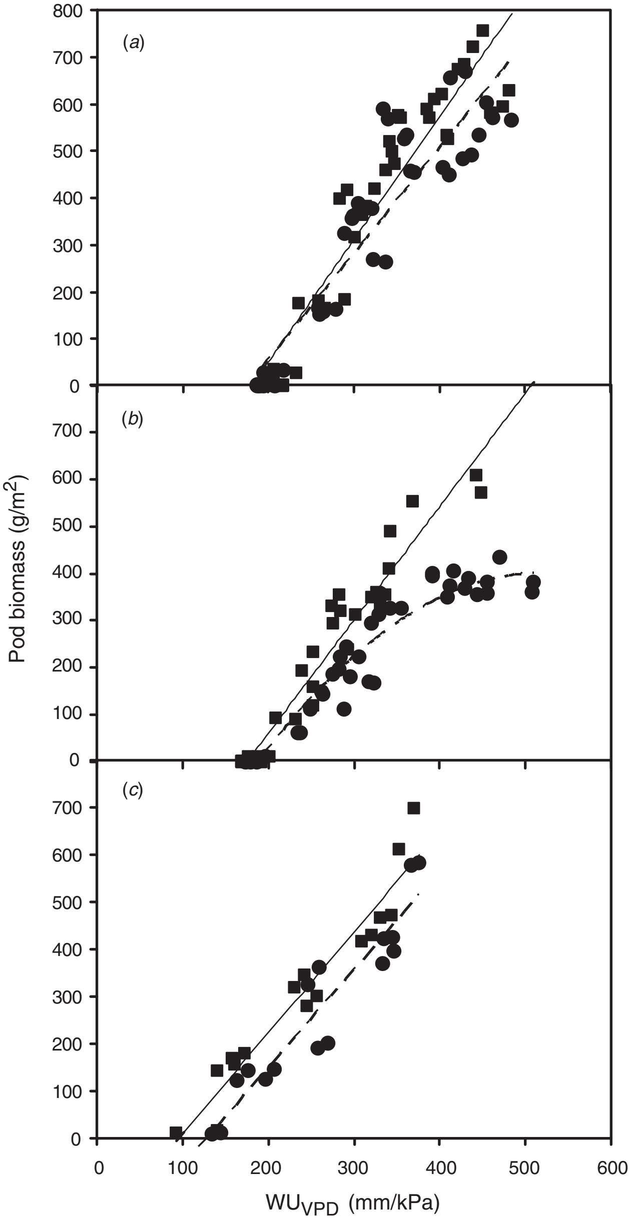

Fig. 3. Relationship between cumulative water use corrected by vapour pressure deficit (WU$_{VPD}$) and cumulative pod biomass of irrigated plots of cultivars Florman (circles and solid lines) and ASEM (squares and dashed lines) sown on (*a*) 17-Oct. Exp$_1$, (*b*) 29-Nov. Exp$_1$, and (*c*) Exp$_2$. Fitted models were of the type: (*i*) $Y = a + (b \times X)$, and (*ii*) $Y = a + (b \times X) - (c \times X^2)$. Each point represents a replicate. Computed models were: (*a*) $Y = -395.34 + 2.25X$; $r^2 = 0.84$; $P < 0.001$ (Florman). $Y = -471.32 + 2.61X$; $r^2 = 0.90$; $P < 0.001$ (ASEM). (*b*) $Y = -580.96 + 3.76X - 0.004X^2$; $r^2 = 0.93$; $P < 0.001$ (Florman). $Y = -420.91 + 2.41X$; $r^2 = 0.93$; $P < 0.001$ (ASEM). (*c*) $Y = -267.11 + 2.08X$; $r^2 = 0.89$; $P < 0.001$ (Florman). $Y = -203.9 + 2.13$; $r^2 = 0.93$; $P < 0.001$ (ASEM).

deficit on the relative variation in WUE$_B$ than in PAR-UE for the period under analysis. The response pattern, however, indicated that part of the decline in PAR-UE under WS (between 50 and 100% of maximum PAR-UE) determined almost no change in WUE$_B$. This condition corresponded to WS plots in Exp$_2$ (triangles in Fig. 5). Contrarily, extremely reduced PAR-UE (less than 20% of maximum) was accompanied by a large decline in WUE$_B$, a condition met by WS plots from the early sowing of Exp$_1$ (squares in Fig. 5).

During the post-R$_6$ period, PAR-UE and WUE$_B$ were strongly ($r^2 \geq 0.85$) related to variations registered in final seed numbers. A single function fitted all PAR-UE data

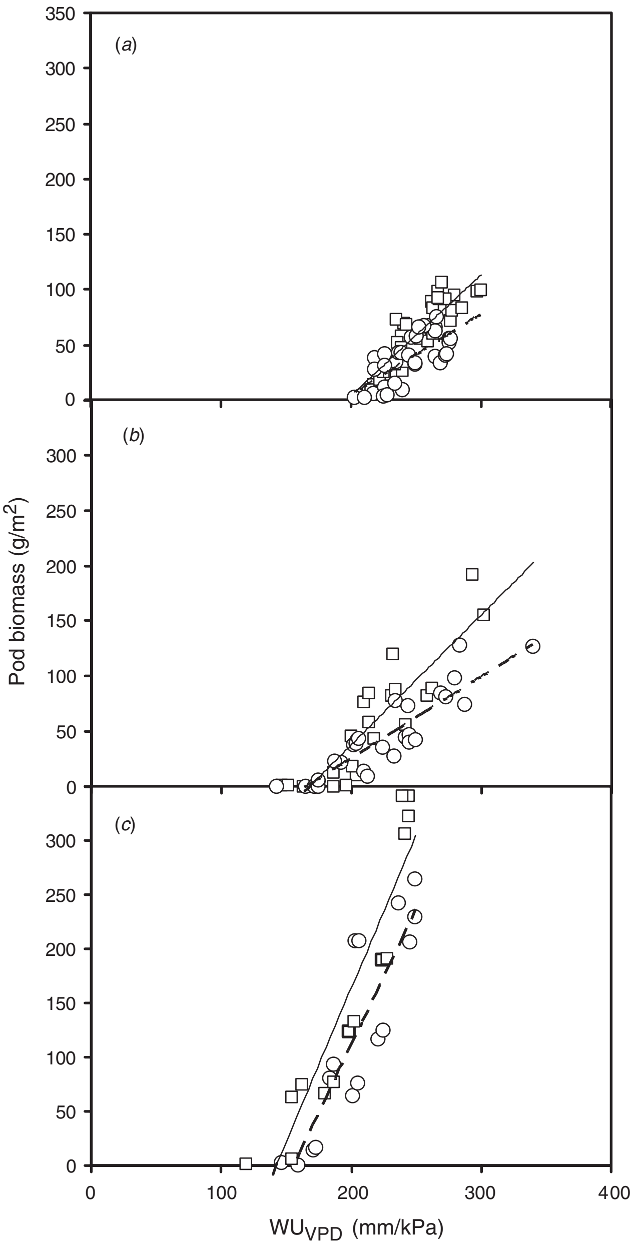

Fig. 4. Relationship between cumulative water use corrected by vapour pressure deficit (WU$_{VPD}$) and cumulative pod biomass of water-stressed plots of cultivars Florman (circles and solid lines) and ASEM (squares and dashed lines) sown on (*a*) 17-Oct. Exp$_1$, (*b*) 29-Nov. Exp$_1$, and (*c*) Exp$_2$. Fitted models were of the type $Y = a + (b \times X)$. Each point represents a replicate. Computed models were: (*a*) $Y = -141.34 + 0.73X$; $r^2 = 0.52$; $P < 0.001$ (Florman). $Y = -213.91 + 1.09X$; $r^2 = 0.74$; $P < 0.001$ (ASEM). (*b*) $Y = -121.5 + 0.74X$; $r^2 = 0.82$; $P < 0.001$ (Florman). $Y = -196.87 + 1.18X$; $r^2 = 0.81$; $P < 0.001$ (ASEM). (*c*) $Y = -391.44 + 2.51X$; $r^2 = 0.77$; $P < 0.001$ (Florman). $Y = -404.25 + 2.84X$; $r^2 = 0.87$; $P < 0.001$ (ASEM).

(Fig. 6*a*), with no particular trend caused by treatments or experiments. Contrarily, two models were necessary for an adequate fit of post-R$_6$ WUE$_B$ data obtained under each water regime (Fig. 6*b*). No difference was detected in the slope of these models.

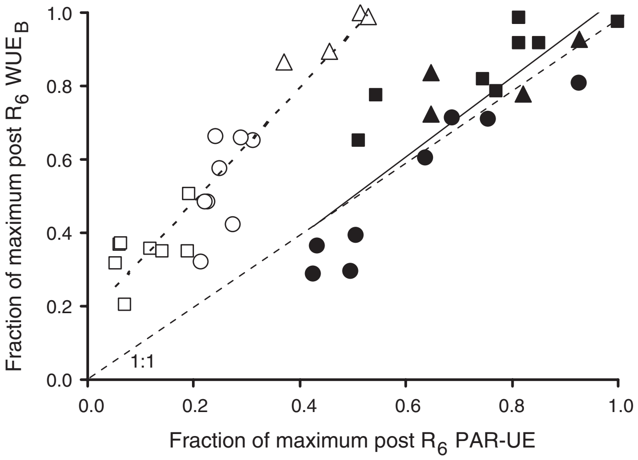

Fig. 5. Relationship between standardised post-R$_6$ radiation use efficiency (post-R$_6$ PAR-UE) and standardised (i.e. relative to the maximum value) post-R$_6$ water use efficiency for biomass production (post-R$_6$ WUE$_B$) of two cultivars (Florman and ASEM) grown under two water regimes in three environments. Black symbols are for irrigation and open symbols are for water stress. Squares are for 17-Oct. sowing in Exp$_1$, circles for 29-Nov. sowing in Exp$_1$, and triangles for Exp$_2$. Each point represents a replicate. Computed models of the type $Y = a + (b \times X)$ were: $Y = -0.0465 + 1.0876X$; $r^2 = 0.72$; $P < 0.001$ (IRR). $Y = 0.1698 + 1.5527X$; $r^2 = 0.87$; $P < 0.001$ (WS).

Discussion

The range in WUE$_B$ obtained for most IRR conditions in our research (6.1–6.7 g kPa/mm) was very high and deserved the following considerations for comparisons with previous findings: (*i*) data correction by energy costs for oil synthesis when data include pod growth (Duncan *et al.* 1978), and (*ii*) correction of crop WU by VPD (Abbate *et al.* 2004; Kemanian *et al.* 2005). Lack of these corrections would have represented mean WUE$_B$ values of 2.8 g/kg for IRR plots of our research, which compared well with those obtained in other environments [1.8–2.9 g/kg for Hebbar *et al.* (1994) and 2.46–3.71 g/kg for Wright and Nageswara Rao (1994)]. However, only the first correction (energy costs for oil synthesis) had to be excluded from our data (4.56–4.95 g kPa/mm) for comparison with previous surveys in the same region (2.25 and 3.9 g kPa/mm) by Collino *et al.* (2000). Differences with these authors may be attributed to the inclusion of early growth stages at low fIPAR in their estimation of WUE$_B$, with its concomitant decrease due to the enhanced contribution of water evaporated from the soil surface rather than from plants (Cooper *et al.* 1983).

WUE$_B$ during the whole reproductive period was more variable under WS than under IRR. Evidence from different crops indicated that WUE$_B$ increases under water deficit (Hebbar *et al.* 1994; Fardad and Pessarakli 1995; Zhang *et al.* 1998; Craufurd *et al.* 1999; Abbate *et al.* 2004). This response is primarily attributed to the differential effect of stomata closure on gas exchange between the plant and the atmosphere, which reduces water loss more than CO$_2$ capture (Sinclair *et al.* 1984; Jones 1992; Martin and Ruiz-Torres 1992). In peanut, Hebbar *et al.* (1994) and Craufurd *et al.* (1999) registered an average increase of 28 and 25% in WUE$_B$ under WS,

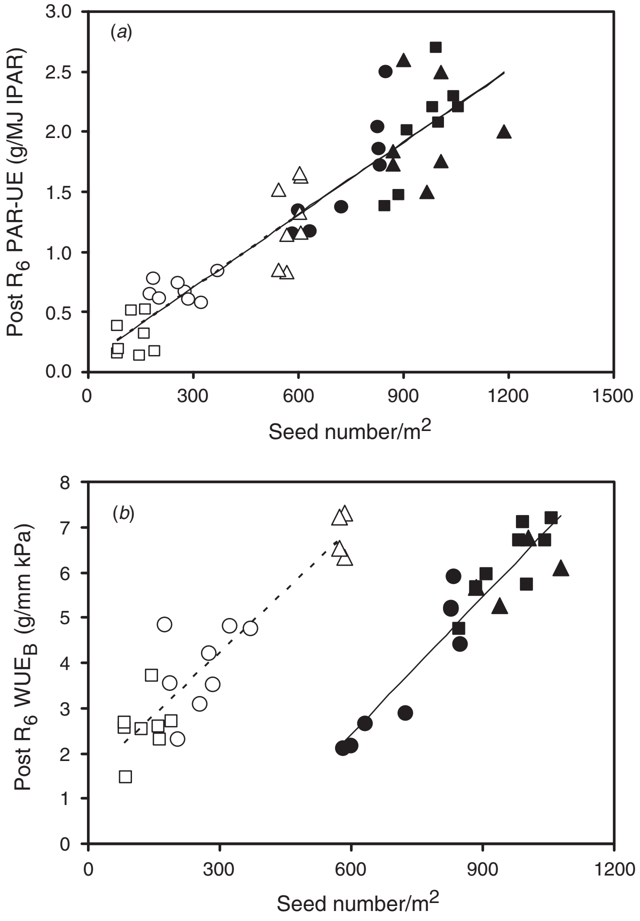

Fig. 6. Response to seed numbers per m^2 of (*a*) post-R_6 photosynthetically active radiation use efficiency (post-R_6 PAR-UE), and (*b*) post-R_6 water use efficiency for biomass production (post-R_6 WUE_B). Data correspond to cultivars Florman and ASEM grown under two water regimes in three environments. Symbols as in Fig. 5. Each point represents a replicate. Computed models of the type $Y = a + (b \times X)$ were: (*a*) $Y = 0.0987 + 0.002X$; $r^2 = 0.85$; $P < 0.001$ (all data). (*b*) $Y = -3.64 + 0.010X$; $r^2 = 0.87$; $P < 0.001$ (IRR). $Y = 1.45 + 0.009X$; $r^2 = 0.85$; $P < 0.001$ (WS).

respectively. In our study, the largest estimate of WUE_B corresponded to WS plots in Exp_2 (slightly higher than its IRR counterpart) and the smallest to WS plots of Exp_1 (markedly lower than its IRR counterpart). The main contrast between these conditions was surface soil strength ($Exp_1 > Exp_2$), which reduced pegging (Haro *et al.* 2008) and final pod number dramatically. These reductions in reproductive sink size caused a reduction in PAR-UE (Haro *et al.* 2008) due to a decline in source activity, attributed to feedback effects on C assimilation (Haro *et al.* 2007). The reduction in PAR-UE was consistent with the remarkable decrease observed in WUE_B under water deficit in two out of three environments included in this study. Therefore, we infer that mentioned feedback effects on C assimilation may have overcompensated the expected benefits of differential stomata control on gas exchange (i.e. larger for water than for CO_2). Although both effects are confounded in our research, it could be deduced that strong impaired pegging previously reported for WS plots in Exp_1 (Haro *et al.* 2008) was responsible for the smaller WUE_B values registered in this condition (2.9 and 3.8 g kPa/mm for the 17-Oct. and 29-Nov. sowings, respectively), with respect to those calculated for Exp_2 (7.1 g kPa/mm).

Variation in WUE_B under WS was not consistent enough to show the influence of the third component in the model proposed by Passioura (1996) for the estimation of grain yield in water limited environments (i.e. biomass partitioning to reproductive structures). This trait was well represented by the PR (Table 2), which included the variation registered in the determinants of reproductive sink strength across treatments and experiments (i.e. seed numbers and pod growth). Genotypic differences have been determined for this ratio (ASEM > Florman), which may be linked to possible differences in flowering dynamics (not addressed in our research) and a demonstrated difference in pegging capacity (Haro *et al.* 2008). This was reflected in the greater WUE_P of ASEM compared with Florman, either under IRR or WS conditions. In fact, ASEM always presented higher values than Florman for this variable, and differences between cultivars increased when impaired pegging was present because of ASEM improved pegging capacity and PR (Haro *et al.* 2008).

The negative effects on pegging of enhanced soil strength caused by severe water deficit (Haro *et al.* 2008) may be responsible of the drastic reductions observed in WUE_P of WS treatments in Exp_1. This behaviour agrees with findings reported in a previous paper carried out in the same region under study and using two contrasting cultivars (Collino *et al.* 2000). Authors found that WUE_P of their WS plots was significantly reduced respect to the irrigated controls, and that cultivars differed for this trait under water deficit. However, no reduction was established in WUE_P of our WS plots in Exp_2, where water management did not allow soil strength to increase high enough for causing a severe restriction to pegging (Haro *et al.* 2008).

The contrasting grouping of WS and IRR data for the relationship between relative efficiencies from R_6 onwards (Fig. 5) deserves some especial considerations. In spite of the severe decline in relative PAR-UE caused by WS in Exp_2 (almost 50% as compared to maximum), a slight increase was detected in relative WUE_B between water regimes (WS > IRR), which supports the idea of enhanced control of stomata closure on water loss respect to CO_2 gain. Contrarily, extremely reduced PAR-UE of WS plots in Exp_1 (less than 20% of maximum) was accompanied by a proportionally larger decline in WUE_B. Previously mentioned differential effects of stomata closure on gas exchange cannot be disregarded in Exp_1, but seemed to be overcompensated by other factors. We acknowledge that part of the response observed under water deficit may be biased by an underestimation of PAR-UE linked to inaccurate measurement of light interception at the end of the cycle (Sinclair and Muchow 1999). Nevertheless, this bias can take place under both water regimes and should not be a larger source of error in fIPAR determination than enhanced leaf folding under WS, which should promote an underestimation of fIPAR and consequently an overestimation of PAR-UE (Sinclair and Muchow 1999). Therefore, the marked decline in relative post-R_6 WUE caused by water deficit in Exp_1 supports the idea of strong stomata closure accompanied by severe photosynthetic decline in this condition. This decline could not be attributed exclusively to direct effects of WS on growth, and acknowledged additional indirect effects related to sink strength (Haro *et al*. 2008).

In agreement with our findings on the relationship between relative efficiencies, the different grouping of IRR and WS data indicated that sink size represented by seed numbers had a strong effect on both efficiencies. Nevertheless, one model sufficed for synthesising the response of post-R_6 PAR-UE to reproductive sink size, while two models were necessary for an adequate fit of the response of post-R_6 WUE_B. We infer that this difference between efficiencies can be attributed almost exclusively to the contrasting effect of above-mentioned differential stomata control on water and CO_2 exchange, which can be captured in the computation of WUE_B but not in the computation of PAR-UE. For the former, sink size effects did not differ across water regimes (same slope for both conditions), but stomata control produced a large variation in WUE_B for the same sink size; e.g. 7 g kPa/mm for WS plots of 14-Nov. sowing in Exp_2 compared with 3 g kPa/mm for IRR plots of 29-Nov. sowing in Exp_1, both with ~600 seeds/m^2.

In summary, variation in WUE_B allowed us to assess the effect of different pegging patterns caused by water management, and variation in WUE_P contributed to the understanding of partitioning differences between cultivars. Analysis along the late-reproductive stages (i.e. post-R_6 period) permitted to establish a new framework for the interpretation of the relationship between PAR-UE and WUE_B across contrasting growing conditions, especially for the distinction of the relative importance of direct (i.e. stomata control) and indirect (i.e. sink strength) effects.

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