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The limit to wheat water-use efficiency in eastern Australia. I.* Gradients in the radiation environment and atmospheric demand

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Abstract. In the wheatbelt of eastern Australia, rainfall shifts from winter dominated in the south (South Australia, Victoria) to summer dominated in the north (northern New South Wales, southern Queensland). The seasonality of rainfall, together with frost risk, drives the choice of cultivar and sowing date, resulting in a flowering time between October in the south and August in the north. In eastern Australia, crops are therefore exposed to contrasting climatic conditions during the critical period around flowering, which may affect yield potential, and the efficiency in the use of water (WUE) and radiation (RUE). In this work we analysed empirical and simulated data, to identify key climatic drivers of potential water- and radiation-use efficiency, derive a simple climatic index of environmental potentiality, and provide an example of how a simple climatic index could be used to quantify the spatial and temporal variability in resource-use efficiency and potential yield in eastern Australia.

Around anthesis, from Horsham to Emerald, median vapour pressure deficit (VPD) increased from 0.92 to 1.28 kPa, average temperature increased from 12.9 to 15.2°C, and the fraction of diffuse radiation (FDR) decreased from 0.61 to 0.41. These spatial gradients in climatic drivers accounted for significant gradients in modelled efficiencies: median transpiration WUE ($WUE_{B/T}$) increased southwards at a rate of 2.6% per degree latitude and median RUE increased southwards at a rate of 1.1% per degree latitude. Modelled and empirical data confirmed previously established relationships between $WUE_{B/T}$ and VPD, and between RUE and photosynthetically active radiation (PAR) and FDR. Our analysis also revealed a non-causal inverse relationship between VPD and radiation-use efficiency, and a previously unnoticed causal positive relationship between FDR and water-use efficiency.

Grain yield (range 1–7 t/ha) measured in field experiments across South Australia, New South Wales, and Queensland ($n = 55$) was unrelated to the photothermal quotient (Pq = PAR/T) around anthesis, but was significantly associated ($r^2 = 0.41$, $P < 0.0001$) with newly developed climatic index: a normalised photothermal quotient (NPq = Pq . FDR/VPD). This highlights the importance of diffuse radiation and vapour pressure deficit as sources of variation in yield in eastern Australia. Specific experiments designed to uncouple VPD and FDR and more mechanistic crop models might be required to further disentangle the relationships between efficiencies and climate drivers.

Additional keywords: photo-thermal quotient, radiation use efficiency, fraction of diffuse radiation, vapour pressure deficit, air temperature.

Introduction

Crop production is a function of the ability of crops to capture resources, chiefly radiation and water, and the efficiency in the use of resources to produce dry matter and grain (Monteith *et al*. 1994). Both water availability and the efficiency in the use of water restrict grain production in the Australian wheatbelt. Water availability is limited by low and highly variable rainfall (Nicholls 1986; Stephens and Lyons 1998; Potgieter *et al*. 2002), often in combination with soils where plant-available water is restricted by physical and chemical constraints to root growth and function (Rengasamy 2002; Nuttall *et al*. 2003; Sadras *et al*. 2003, 2005; Rodriguez *et al*. 2006). Nutrient deficiencies and soil-borne diseases are widespread and further restrict water availability for crops (Angus and van Herwaarden 2001).

Sixty-two percent of Australia's wheat is produced in eastern Australia (ABARE 2006). In south-eastern Australia, maximum water-use efficiency ($WUE_{Y/ET}$ = grain yield per unit evapotranspiration) is around 22 kg grain/ha.mm, whereas the average is around 10 kg grain/ha.mm (Sadras and Angus 2006). There are fewer systematic attempts to characterise water-use

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efficiency in the northern wheat-growing region of Australia, and fragmented evidence indicates lower or similar efficiencies than in southern regions. Average $WUE_{Y/ET}$ reported by Thomas *et al*. (1995) was 8.8 kg grain/ha.mm, and maximum efficiencies of 15–18 kg grain/ha.mm have been reported for south-western Queensland (Radford *et al*. 1992; Thomas *et al*. 1995). Low $WUE_{Y/ET}$ in the subtropical regions of Queensland compared with more temperate regions of Australia has been related to higher temperatures, sometimes higher vapour pressure deficit (VPD), or lower daily totals of incoming radiation (Fischer 1984). For northern Queensland, Angus *et al*. (1980) derived $WUE_{Y/ET}$ and $WUE_{Y/T}$ (after accounting for soil evaporation) similar to those observed in the temperate regions of north-western Victoria.

Empirically derived estimates of maximum efficiencies might seem contradictory when analysed in isolation from the prevailing seasonal conditions, and there is recognition for the need of benchmarks for yield gap analysis. Unfortunately, current estimates of potential yield across Australia have failed to account for the effect of fundamental climate drivers, leading to biased recommendations for future funding in research and development in the area of water-use efficiency (WUE) (Beeston *et al*. 2005). In a context of current water scarcity and projected deterioration associated with hotter and dryer climates, a more comprehensive temporal and spatial characterisation of the environmental potential and limitations to WUE for wheat production in Australia seems highly relevant.

Crop-transpiration efficiency and radiation-use efficiency (RUE) have been individually studied in scaling-up exercises from leaf to canopy, and several climatic influences have been identified (Tanner and Sinclair 1983; Hammer and Wright 1994; Sinclair and Muchow 1999). The inverse relationship between transpiration efficiency and the dryness of the atmosphere, the direct relationship between RUE and fraction of diffuse radiation (FDR), and the inverse relationship between RUE and incident radiation, are all well established. The inverse relationship between RUE and VPD remains controversial (Stöckle and Kiniry 1990; Kiniry *et al*. 1998; Sinclair and Muchow 1999; Kemanian *et al*. 2004; Albrizio and Steduto 2005). No attempts have been made to explore the influence of diffuse radiation on WUE.

Several indices have been developed that relate yield potential to some of these climatic factors (Nix 1976; Fischer 1985*a*). Fischer (1984, 1985*a*) defined a photothermal quotient (Pq) as the ratio between radiation and mean temperature around anthesis. This index involves 3 physiological principles: crop growth rate is related to radiation, the duration of a given growth phase is an inverse function of temperature, and kernel set is defined in a time-window centred on anthesis. Although originally conceived for irrigated wheat crops, Pq was successfully applied to a range of crop species to explain variations in grain yield components in space and time (Fischer 1984; Magrin *et al*. 1993; Veron *et al*. 2004; Poggio *et al*. 2005). Climate indices easily calculated from readily available climate records could also be used to characterise the spatial and temporal variations in WUE and RUE. In this work we aim to identify key climatic drivers of potential WUE and RUE, derive a simple climatic index of environmental potentiality, and provide an example of how a simple climatic index could be used to quantify the spatial and temporal variability in resource-use efficiency and potential yield in eastern Australia.

Framework and hypotheses

Drivers of water- and radiation-use efficiency

Crop shoot biomass (B) can be defined as a function of RUE and water use efficiency ($WUE_{B/ET}$):

$$B = RUE \times IR \tag{1a}$$

$$B = WUE_{B/ET} \times ET \tag{1b}$$

where ET is crop evapotranspiration and IR is intercepted radiation. Here we propose that a top-down view relating WUE and RUE could contribute further insight into their environmental drivers. From Eqn 1*a* and *b*, it follows that:

$$WUE_{B/ET} = RUE\ (ET/IR)^{-1} \tag{2}$$

In well developed canopies where soil evaporation is low in relation to transpiration (T), $WUE_{B/ET} \approx WUE_{B/T}$, and $ET/IR \approx T/IR$. In Eqn 2, transpiration per unit of IR has been interpreted as a measure of canopy conductance (Matthews *et al*. 1988; Sadras *et al*. 1991; Caviglia and Sadras 2001).

For semi-arid environments, de Wit (1958) found that, provided growth was only limited by availability of water, $WUE_{B/T}$ depended mainly on plant species and pan evaporation. Bierhuizen and Slatyer (1965) used VPD of the air instead of pan evaporation to normalise crop-specific canopy-level transpiration water efficiency (*k*, kPa). This coefficient has been traditionally considered to be conservative (Tanner 1981; Tanner and Sinclair 1983), but recent studies suggested that *k* might also depend on day-time VPD (Kemanian *et al*. 2005).

Sinclair and Muchow (1999) summarised key factors affecting RUE. Besides the influences of crop carbon metabolism, water and nutrient availability, RUE decreases with increasing radiation and increases with the FDR (Sinclair and Shiraiwa 1993; Hammer and Wright 1994; Bange *et al*. 1997). The relationship between RUE and VPD is more controversial. It has been proposed that changes in leaf conductance mediate the effect of VPD on RUE. Empirical evidence from field trials shows inverse relationships between RUE and VPD in maize, sorghum, sunflower, wheat, and barley (Stöckle and Kiniry 1990; Kiniry *et al*. 1998; Kemanian *et al*. 2004). Others failed to find such effects and argue about the lack of mechanisms supporting the putative relationship (Sinclair and Muchow 1999; Albrizio and Steduto 2005). Most likely, the presence of correlations among environmental variables, e.g. air temperature, VPD, and radiation environment, confounds the relationship between correlation and causality when a simple statistical approach is used. One of the main objectives of building mechanistic models of crop growth is to avoid the difficulties of assessing the effects of environmental variables that are often correlated with each other (Sheehy *et al*. 2006). In this work we used several empirical and mechanistic techniques to research these issues by testing the following hypotheses.

As WUE and RUE are related by definition (Eqn 2), it might be that:

- (hypothesis 1) empirical correlations between RUE and VPD could be simply explained by the presence of correlations between climate variables, e.g. air temperature, radiation environment, and VPD.

A combined approach to the study of efficiencies, rather than the more common method of dealing with them individually, may shed some light on this issue. Interestingly, there is little if any information on the effect of diffuse radiation on WUE. Again, the link between efficiencies suggests that:

- (hypothesis 2) WUE may increase with larger proportion of diffuse radiation via known effects of diffuse radiation on RUE and biomass production.

Simple climate indices have been developed, e.g. photothermal quotient (Fischer 1985*a*), and widely used to characterise the yield potential in several species and environments (Magrin *et al.* 1993; Cantagallo *et al.* 1997; Andrade *et al.* 2005; Kantolic and Slafer 2005; Rodriguez *et al.* 2005). In most cases, these indices account for the direct relationship between growth and radiation interception and the inverse relationship between the rate and duration of crop growth around a critical time for yield definition. As a corollary of the effects of temperature, VPD, and the radiation environment on WUE and RUE we proposed that:

- (hypothesis 3) the predictive capabilities of simple climate indices based on temperature and IR could be improved if the effects of VPD and the ratio between diffuse and direct radiation are taken into account.

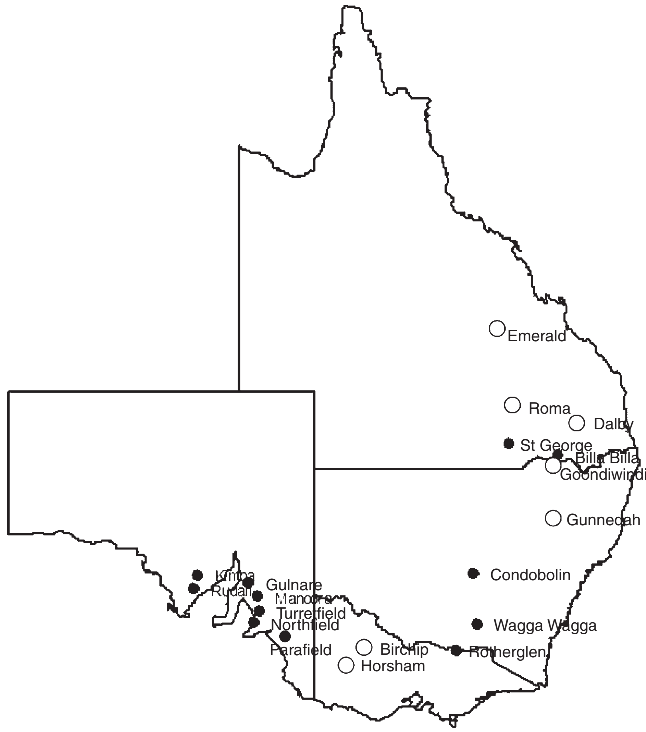

Fig. 1. Map of eastern Australia indicating the locations used in the simulation of water- and radiation-use efficiency, and climatic indices of yield potential (open circles), and the locations corresponding to empirical datasets (closed circles).

Methods

Target locations

We selected 7 locations in a S–N transect in eastern Australia (open symbols in Fig. 1), which span a range of rainfall regimes, from winter-dominated in the south to summer-dominated in the north (Table 1).

Modelled water- and radiation-use efficiency

We used a similar approach to Tanner and Sinclair (1983) to model potential WUE and RUE of wheat crops around anthesis. The model, written in a Macro in Excel, was run for every year between 1957 and 2003, using climate records from the Australian Bureau of Meteorology SILO patch-point dataset (www.bom.gov.au/silo/). For each location and simulated year, typical anthesis dates were derived from Whopper Cropper (www.apsru.gov.au/apsru/), assuming optimal sowing times. Daily canopy photosynthesis and crop growth were calculated for the period from 20 days before to 14 days after anthesis (Fischer 1985*a*, 1985*b*). For this interval, no water limitations and a constant leaf area index of 4 were assumed. Canopy photosynthesis was derived from the amount of direct and diffuse fluxes of incoming photosynthetically active radiation (PAR), their distribution within the canopy, and the photosynthetic light response of single leaves (Spitters 1986).

Table 1. Rainfall (mm), median date of last frost, and simulated potential water-use efficiency ($WUE_{B/T}$, g/m^2.mm), radiation-use efficiency (RUE, g/MJ), and decile 9 grain yield (t/ha) for 7 locations in a S-N transect of eastern Australia

Site	Rainfall Annual	April–Nov.	Seasonality index[A]	Frost Day of last frost[B]	Potential $WUE_{B/T}$[C]	RUE[C]	Yield[D]
Horsham	443	315	0.71	246	9.5	2.9	10.0
Birchip	374	253	0.67	220	8.7	3.0	9.1
Gunnedah	615	289	0.47	229	8.2	2.8	7.7
Goondiwindi	605	269	0.44	222	7.9	2.6	6.5
Dalby	639	263	0.41	230	7.2	2.8	6.6
Roma	602	248	0.41	229	8.4	2.9	5.8
Emerald	590	201	0.34	198	5.9	2.7	5.0

[A]Ratio between April–November rainfall and annual rainfall.
[B]Median last day of the year with minimum temperature equal to or lower than 0°C.
[C]Simulated maximum values.
[D]Derived from results in Fig. 8*b* and decile 9 of NPq (MJ/m^2.day°C.kPa) at each location.

The proportion of direct and diffuse radiation fluxes was calculated from the latitude, day of the year, time of the day, and atmospheric transmission (Spitters 1986). An important difference with our approach was that Tanner and Sinclair (1983) assumed that photosynthesis of shaded leaves was equivalent to the respiration of the whole canopy and therefore those processes were ignored. In our model we explicitly accounted for both assimilation by sunlit and shaded leaves and whole-canopy respiration. This was necessary to quantify the effect of diffuse radiation on crop photosynthesis and growth. The response of leaf photosynthesis to radiation was characterised by its slope at low light intensity, i.e. 0.45 kg CO_2/ha.h.(J/m^2.s), and its maximum rate at light saturation, i.e. 40 kg CO_2/ha.h. The light-saturated rate of photosynthesis was affected by day-time temperature outside the normal range of 10–25°C (Goudriaan and Van Laar 1994). Assimilation for shaded and sunlit leaves was calculated separately for 3 layers in the canopy and 3 time intervals of the day (Goudriaan and Van Laar 1994; Hammer and Wright 1994). The assimilation of single leaves was integrated into daily crop canopy photosynthesis using a 3-point Gaussian integration method, i.e. with respect to canopy depth and time of the day (Goudriaan 1986). Daily above-ground crop biomass production was derived from daily crop canopy photosynthesis after accounting for maintenance and growth respiration, and partitioning of biomass between root and shoot (Penning de Vries and van Laar 1982). Part of the assimilated carbohydrate was lost through maintenance respiration, which was increased by a factor of 2 for every 10°C of increase in temperature over a reference temperature of 25°C (Penning de Vries and van Laar 1982). On any day, crop RUE was calculated as the ratio of crop biomass accumulated on that day and intercepted PAR. Daily potential evapotranspiration was calculated using the Penman-Monteith combination equation (Monteith and Unsworth 1995), assuming a constant wind speed of 1 m/s. Potential evapotranspiration was calculated as the sum of 2 terms accounting for radiation and the drying power of the atmosphere (Goudriaan and Van Laar 1994). Potential canopy transpiration was estimated assuming an unlimited supply of water, and was multiplied by the fraction of radiation intercepted by the canopy. We assumed exponential extinction of radiation with an extinction coefficient of 0.5 on average for visible and near-infrared radiation together. The drying power was assumed to be effective up to a cumulative leaf area index of 2, i.e. lower leaves in the canopy do not contribute much to transpiration because of dim illumination, higher stomatal resistance, and relative humidity in the deeper layers of the canopy. Rainfall interception was discounted from the value of potential crop transpiration, following the observations by Singh and Sceicz (1979). Daily transpiration water-use efficiency ($WUE_{B/T}$, g/m^2.mm) was then calculated as the ratio between the crop shoot biomass accumulated on that day and the potential canopy transpiration.

Climatic indices of grain yield potential

Two climatic indices of yield potential the photo-thermal quotient (Pq) and the normalised photo-thermal quotient (NPq) (Eqns 3 and 4) were calculated using daily climatic records (1957–2003) for the 7 locations indicated in Fig. 1 (open symbols). For consistency with the estimates of WUE and RUE (above), both indices were calculated and are presented as the average for a time-window from 20 days before to 14 days after anthesis.

$$\mathrm{Pq} = \mathrm{PAR}/\mathrm{T} \tag{3}$$

$$\mathrm{NPq} = \mathrm{Pq} \cdot \mathrm{FDR}/\mathrm{VPD} \tag{4}$$

where PAR (MJ/m^2. day) is incoming photosynthetically active radiation, T (°C) is day-time average temperature, FDR is the fraction of diffuse radiation, and VPD (kPa) is day-time vapour pressure deficit.

Validation of resource-use efficiencies and indices of yield potential

We used the empirical data summarised in Table 2 to assess the simulated results and derived relationships between $WUE_{B/T}$ and VPD, RUE and VPD, and grain yield and phototermal quotients Pq and NPq. The relationship between measured grain yield and the normalised photothermal quotient NPq was analysed using the method of Casanova *et al*. (2002), where maximum grain yield $Yield_{Max}$) is calculated after categorising NPq in 10 groups, then determining the 95 percentile of the grain yield corresponding to each of those groups of NPq. An upper boundary function is then defined as the linear regression between $Yield_{Max}$ and average NPq for each group interval. The

Table 2. Description, i.e. determinations, crop, studied variables, location, and authorship, of the datasets used in this work

Determinations	Crop	Variables	Location	Author
Yield, transpiration	Wheat	Season	Argentina	Caviglia *et al*. (2004)
Yield, transpiration	Wheat	Nitrogen supply, season	Argentina	Caviglia and Sadras (2001)
Yield, transpiration	Wheat	Soil type, tillage	Australia	Sadras *et al*. (2005)
Biomass, transpiration	Wheat	Location, season	Argentina	Abbate *et al*. (2004)
Biomass, yield, transpiration	Wheat & barley	Season	USA	Kemanian *et al*. (2004)
Biomass, light interception	Barley	Season	USA	Kemanian *et al*. (2005)
Yield	Wheat	Season	Billa-Billa, Australia	Radford *et al*. (1992)
Yield	Wheat	Sowing time	Horsham, Australia	O'Leary *et al*. (1985)
Yield	Wheat	Season, previous crop	Several in Australia	Evans *et al*. (1991)
Yield	Wheat	Season, sowing time	Rutherglen, Australia	Coventry *et al*. (1993)
Yield	Wheat	Season, sowing time	Several in Australia	Gomez-Macpherson and Richards (1995)
Yield	Wheat	Season, sowing time	Billa-Billa, Australia	Thomas *et al*. (1995)
Yield	Wheat	Season	Nindigully, Australia	Thomas *et al*. (2006)

$\text{Yield}_{\text{Max}}$ line was interpreted as the upper boundary for grain yield for any particular location and season characterised by a value of NPq around anthesis.

Spatial and temporal variation in resource-use efficiencies, indices of yield potential, climate drivers, and their relationships

Regression analysis was used to explore latitudinal and temporal variation of (*a*) climatic variables including day-time VPD (VPD), temperature (T), PAR, and FDR; (*b*) simulated WUE and RUE; and (*c*) climatic indices of yield potential Pq and NPq. All variables were restricted to a time-window between 20 days before and 14 days after anthesis (Fischer 1985*a*, 1985*b*). Medians were used as a central trend measure, and deciles 1 and 9 were used to characterise seasonal variability.

Correlations are expected between key climatic variables, e.g. VPD *v*. temperature, radiation *v*. temperature. The effects of PAR, FDR, T, and VPD (independent variables) on WUE and RUE (dependent variables) may be therefore confounded. To help unravel these confounded effects, we used partial least-squares regression (PLS-R). This regression approach involves a bilinear modelling method for relating the variations in one or several dependent variables to the variations in several independent variables (Esbensen 2002). The PLS-R modelling was performed on centred data. Outliers were removed according to detection at the PLS 2-dimensional plot; full cross-validation was used as validation method. The optimal number of principal components was determined based on the lowest root mean square error of the prediction (RMSEP). Calculations were made using Unscrambler *v.*7.5 (CAMO, ASA, Norway), a software package for multivariate data analysis.

Results

Spatial and temporal variation in climatic factors, $WUE_{B/T}$, and RUE around anthesis

The proportion of annual rainfall corresponding to the wheat-growing season ranges from 71% in the south to 34% in the north. Significant latitudinal gradients were found for VPD and FDR, but not for temperature or PAR (Fig. 2). The median day-time VPD around anthesis decreased southwards from 1.28 kPa at Emerald to 0.92 kPa at Horsham, i.e. 28% or –0.024 kPa/degree latitude (Fig. 2*a*). Both deciles 1 and 9 of day-time VPD decreased southwards (Fig. 2*a*). Median day-time temperature around anthesis declined slightly from Emerald to Horsham, but the gradient was not statistically significant. The median FDR increased from 0.41 at Emerald to 0.61 at Horsham, i.e. increased by 52% or 1.6%/degree latitude (Fig. 2*c*). Decile 1 and 9 of FDR also increased with latitude. Daily PAR around anthesis was ~1 MJ/m^2.day higher in Horsham than in Emerald (Fig. 2*d*) due to differences in daylength.

As expected, VPD was positively associated with both PAR and temperature (Table 3). The association between VPD and T, however, weakened towards the north to the point that the variables were unrelated at Emerald and Roma (Table 3). Even though temperature and radiation are positively related on a seasonal time scale, at the time scale of 5 weeks around flowering

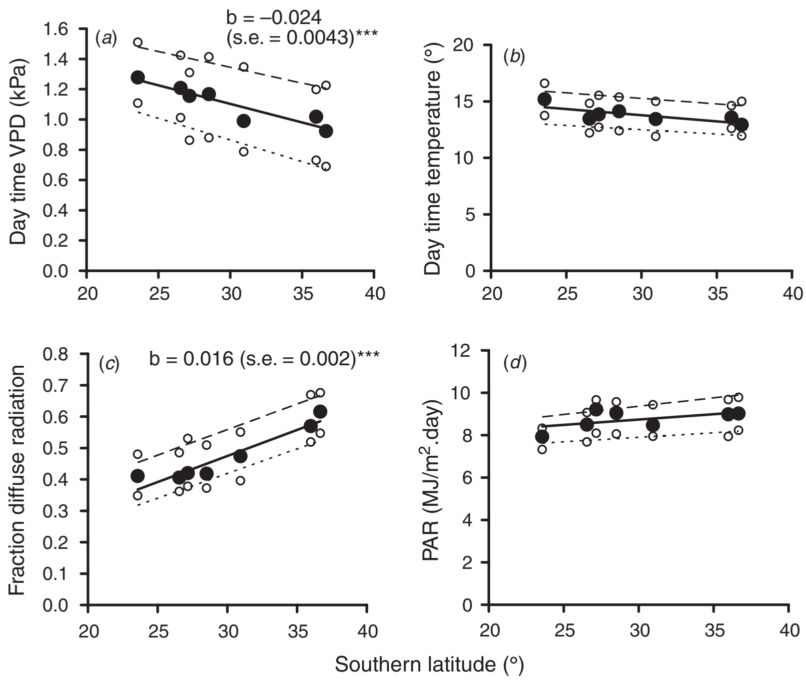

Fig. 2. Latitudinal trends of (*a*) day-time vapour pressure deficit (VPD, kPa), (*b*) temperature (°C), (*c*) fraction of diffuse radiation, and (*d*) photosynthetic active radiation (PAR, MJ/m^2.day). Data are for the period between 20 days before and 14 days after anthesis. Dotted and dashed lines and small open circles show deciles 1 and 9 respectively, solid line and closed large circles show median values. Slopes and their standard errors are shown for median data. Asterisks (***) indicate level of significance for the slope being different from zero at 1% level of probability.

Table 3. Correlation coefficients between photosynthetically active radiation (PAR), fraction of diffuse radiation (FDR), day-time temperature (T), and day-time vapour pressure deficit (VPD) for 7 locations in a S-N transect of eastern Australia

All 4 variables span a window from 20 days before to 14 days after anthesis

	VPD	PAR	FDR
		T	
Horsham	0.78***	0.63***	−0.61***
Birchip	0.78***	0.66***	−0.59***
Gunnedah	0.73***	0.45**	−0.15
Gondiwindi	0.47***	0.13	0.025
Dalby	0.38**	0.19	−0.034
Roma	0.21	−0.14	0.31*
Emerald	0.13	−0.31*	0.37**
		VPD	
Horsham		0.69***	−0.69***
Birchip		0.78***	−0.75***
Gunnedah		0.74***	−0.60***
Gondiwindi		0.69***	−0.64***
Dalby		0.78***	−0.74***
Roma		0.61***	−0.61***
Emerald		0.63***	−0.64***
		PAR	
Horsham			−0.93***
Birchip			−0.75***
Gunnedah			−0.75***
Gondiwindi			−0.83***
Dalby			−0.92***
Roma			−0.81***
Emerald			−0.95***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

of this study, T and PAR were positively related in the south and negatively related in Emerald. Similarly, T was negatively related with FDR in the south, and positively related in the north. The fraction of diffuse radiation was inversely associated with VPD and PAR (Table 3).

Modelled efficiencies increased systematically towards southern locations. The median $WUE_{B/T}$ increased southwards at a significant ($P < 0.01$) rate of 2.6% per degree latitude (Fig. 3*a*). Seasonal variation in $WUE_{B/T}$ also tended to increase with latitude. The median RUE increased southwards at a significant ($P < 0.01$) rate of 1.1% per degree latitude (Fig. 3*b*). Similarly, seasonal variation in RUE tended to increase with latitude.

Variation in WUE and RUE with day-time VPD and FDR

Simulated and empirically derived relationships between $WUE_{B/T}$ and day-time VPD agreed with our present understanding on the functional dependence of $WUE_{B/T}$ on environmental conditions. An inverse non-linear function of day-time VPD fitted both simulated and experimental data (solid line, Fig. 4*a*). Simulated and empirically derived RUEs were also fitted by a non-linear, inverse function of day-time VPD (Fig. 4*b*), and both $WUE_{B/T}$ and RUE increased linearly with the FDR (Fig. 4*c*, *d*).

For the locations included in this paper, day-time VPD and FDR were inversely related (Table 3). Owing to this correlation, the effects of VPD and FDR are confounded in their relationships with WUE and RUE (Fig. 4). Partial least-squares regression (PLS-R) was used to further explore the relationships between PAR, FDR, T, and VPD (independent variables), and the simulated $WUE_{B/T}$ and RUE (dependent variables). The inverse of VPD was used to account for the non-linear relationships with the dependent variables (Fig. 4*a*, *b*). The PLS-R indicated that the selected climate variables were highly related to $WUE_{B/T}$ and RUE, i.e. the R^2 coefficient for their prediction varied from 0.81 to 0.98 (Table 4). The root mean square errors of the prediction were low, particularly for RUE, indicative of the goodness-of-fit of the regression models. The optimal number of principal components was small, ranging from 2 to 4. Table 4 presents the loading weighs for the first two principal components (PC1 and PC2), which express how the information in each independent variable relates to the variation in the dependent variable. Independent variables with large loading weights (positive or negative) account for an important part of the variation of the dependent variable; the sign of the loading weight indicates the direction of the effect. Variables having similar values for PC1 and PC2 are redundant: exclusion of one such variable from the model would hardly affect its predictive capacity.

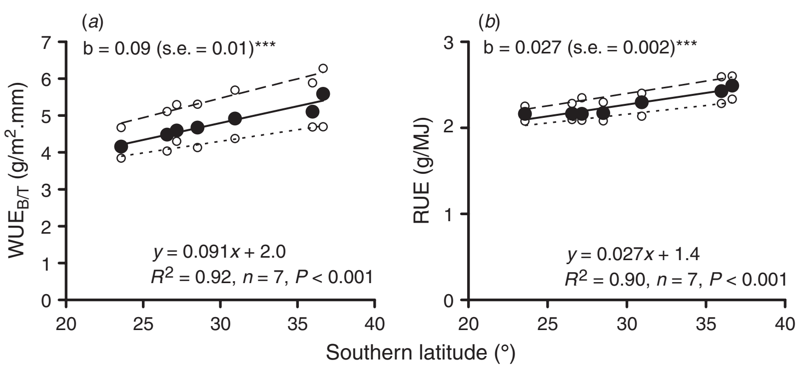

Fig. 3. Latitudinal trends of simulated (*a*) transpiration water-use efficiency ($WUE_{B/T}$, g/m^2.mm); and (*b*) radiation-use efficiency (RUE, MJ/m^2.day) between 20 days before and 14 days after anthesis. Dotted and dashed lines and small open circles show deciles 1 and 9, respectively, solid line and full large circles show median values. Asterisks (***) indicate level of significance for the slope being different from zero at 1% level of probability.

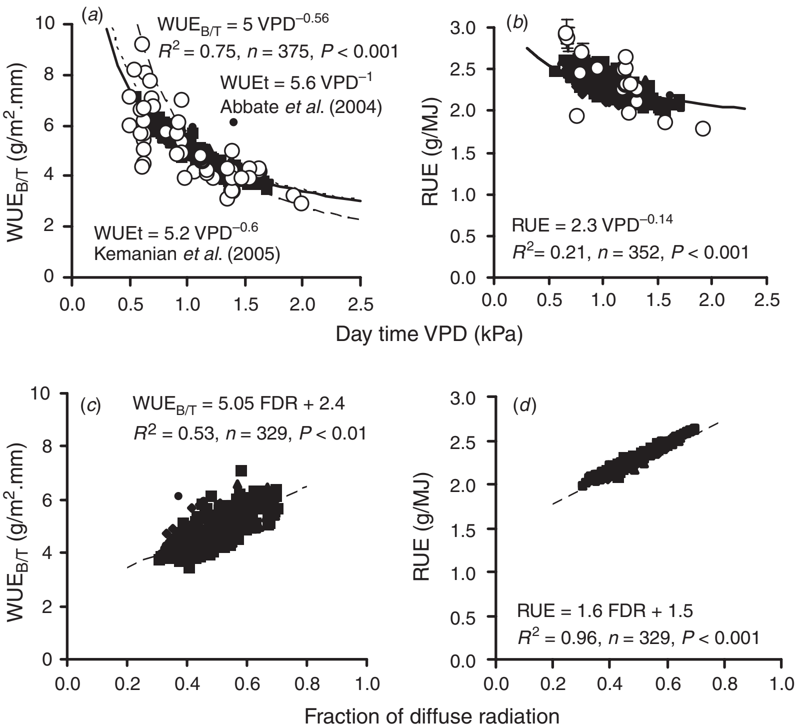

Fig. 4. Relationships between (*a*, *c*) water- (WUE) and (*b*, *d*) radiation-use efficiency (RUE) and (*a*, *b*) day-time vapour pressure deficit (VPD), and (*c*, *d*) fraction of diffuse radiation. All variables were calculated for the period between 20 days before and 14 days after anthesis. Small closed symbols are simulated results (different symbols were used for each location), and large open circles are measured values, see Table 1 for details.

In general the first 2 loading weights explained most of the variation in the dependent variable (not shown). Analysis of PC1 and PC2 for $WUE_{B/T}$ indicated that across the studied transect, no variable could be considered redundant, although different variables had different importance in explaining variations in $WUE_{B/T}$. Important drivers of $WUE_{B/T}$ were VPD, T, and FDR (in that order); at all locations the influence of PAR on $WUE_{B/T}$ was small. As expected, VPD, T, and PAR were negatively related to $WUE_{B/T}$, whereas FDR had a positive effect. The influence of temperature on $WUE_{B/T}$ increased from north to south, in parallel with the increasing strength of the link between T and VPD (Table 3). Both VPD and FDR were equally important drivers of $WUE_{B/T}$ at all latitudes (Table 4). Residual analysis showed that the effect of FDR on simulated $WUE_{B/T}$ was still significant after the effect of VPD was removed (Fig. 5*a*). For values of FDR higher than 0.4, high values of $WUE_{B/T}$ could not only be explained simply by low VPD values. Interestingly, when the flux of diffuse radiation was removed from a modified version of the model in the calculation of canopy assimilation, the effect of FDR on $WUE_{B/T}$ disappeared (Fig. 5*b*), confirming an effect of FDR on $WUE_{B/T}$ via net carbon assimilation processes.

No redundant variables were identified from the PLS-R on RUE. Important drivers of RUE were FDR, PAR, and VPD. Interestingly, the influence of temperature on RUE was close to zero in the north and negative and almost as important as VPD in the south. This was probably related to the closer link between temperature and VPD in the south (Table 3). As expected the effect of FDR on RUE was positive, and the effects of PAR and VPD were negative. Residual analysis showed that the effect of VPD on simulated RUE was still significant after the effect of FDR was removed (Fig. 5*c*), although when the effect of temperature on crop net assimilation, i.e. photosynthesis and dark respiration, was removed in a modified version of the model (Fig. 5*d*), the effect of VPD on RUE disappeared. Therefore, even when the model reproduced a negative relationship between VPD and RUE, there was no causality and the relationship could be simply explained by the high correlation between VPD and temperature.

Relationship between $WUE_{B/T}$ and RUE

The relationship between simulated $WUE_{B/T}$ and RUE was in close agreement with the relationship obtained from experimental sources (Fig. 6*a*). Equation 2 and Fig. 6*a* indicate a linear relationship between WUE and RUE. The robustness of this relationship is particularly relevant for hypotheses 1 and 2, which relate to the indirect effects of environmental factors on efficiencies, i.e. the effect of temperature or related variables (VPD) on RUE, and the effect of FDR on WUE. The relationship in Fig. 6*a* is also consistent with the theoretical, energy-limited upper limit dictated by the latent heat of water. Vapour pressure deficit accounted for much of the scattering in the 2.1*RUE: $WUE_{B/T}$ relationship (Fig. 6*b*). Seasons and/or environments with VPD higher (lower) than 1.16 kPa, had lower (greater)

Table 4. PLS-R between photosynthetically active radiation (PAR), fraction of diffuse radiation (FDR), day-time temperature (T), and day-time vapour pressure deficit (VPD) (independent variables) and water-use efficiency ($WUE_{B/T}$) and radiation-use efficiency (RUE) (dependent variables)
The numbers in parentheses are number of years in the analysis; PC1 and PC2 are the loading weights for the principal components 1 and 2; ONPC is the optimal number of principal components; RMSEP is the root mean square error of the prediction

Location	*Y* variable	*X* variable	PC1	PC2	ONPC	RMSEP	R^2
Horsham	$WUE_{B/T}$ (47)	PAR	−0.09	0.77	2	0.365	0.88
		FDR	0.32	−0.56			
		T	−0.60	−0.11			
		VPD^{-1}	0.71	0.25			
	RUE (47)	PAR	−0.5	−0.16	3	0.063	0.94
		FDR	0.63	0.59			
		T	−0.33	0.40			
		VPD^{-1}	0.48	−0.67			
Birchip	$WUE_{B/T}$ (41)	PAR	−0.2	0.77	3	0.289	0.81
		FDR	0.37	−0.5			
		T	−0.51	−0.12			
		VPD^{-1}	0.74	0.37			
	RUE (47)	PAR	−0.52	0.12	3	0.049	0.96
		FDR	0.62	0.72			
		T	−0.3	0.45			
		VPD^{-1}	0.49	−0.5			
Gunnedah	$WUE_{B/T}$ (47)	PAR	−0.39	0.63	3	0.225	0.92
		FDR	0.37	−0.54			
		T	−0.48	−0.41			
		VPD^{-1}	0.68	0.36			
	RUE (47)	PAR	−0.59	−0.008	3	0.043	0.96
		FDR	0.62	0.57			
		T	−0.15	0.60			
		VPD^{-1}	0.48	−0.55			
Goondiwindi	$WUE_{B/T}$ (44)	PAR	−0.24	0.64	3	0.132	0.94
		FDR	0.4	−0.60			
		T	−0.51	−0.37			
		VPD^{-1}	0.71	0.29			
	RUE (43)	PAR	−0.51	0.52	3	0.022	0.98
		FDR	0.67	0.71			
		T	−0.15	−0.09			
		VPD^{-1}	0.5	−0.45			
Dalby	$WUE_{B/T}$ (47)	PAR	−0.26	0.71	3	0.24	0.88
		FDR	0.41	−0.48			
		T	−0.48	−0.45			
		VPD^{-1}	0.72	0.24			
	RUE (40)	PAR	−0.52	0.59	3	0.027	0.98
		FDR	0.64	0.53			
		T	−0.15	−0.55			
		VPD^{-1}	0.53	−0.23			
Roma	$WUE_{B/T}$ (40)	PAR	0.01	0.77	3	0.154	0.92
		FDR	0.34	−0.48			
		T	−0.24	0.31			
		VPD^{-1}	0.9	0.25			
	RUE (42)	PAR	−0.56	0.12	3	0.0199	0.98
		FDR	0.68	0.45			
		T	0.10	−0.80			
		VPD^{-1}	0.44	−0.35			
Emerald	$WUE_{B/T}$ (42)	PAR	−0.29	0.67	3	0.102	0.92
		FDR	0.44	−0.44			
		T	−0.17	−0.43			
		VPD^{-1}	0.82	0.39			
	RUE (47)	PAR	−0.57	0.0008	4	0.032	0.96
		FDR	0.63	0.45			
		T	0.16	−0.83			
		VPD^{-1}	0.48	−0.3			

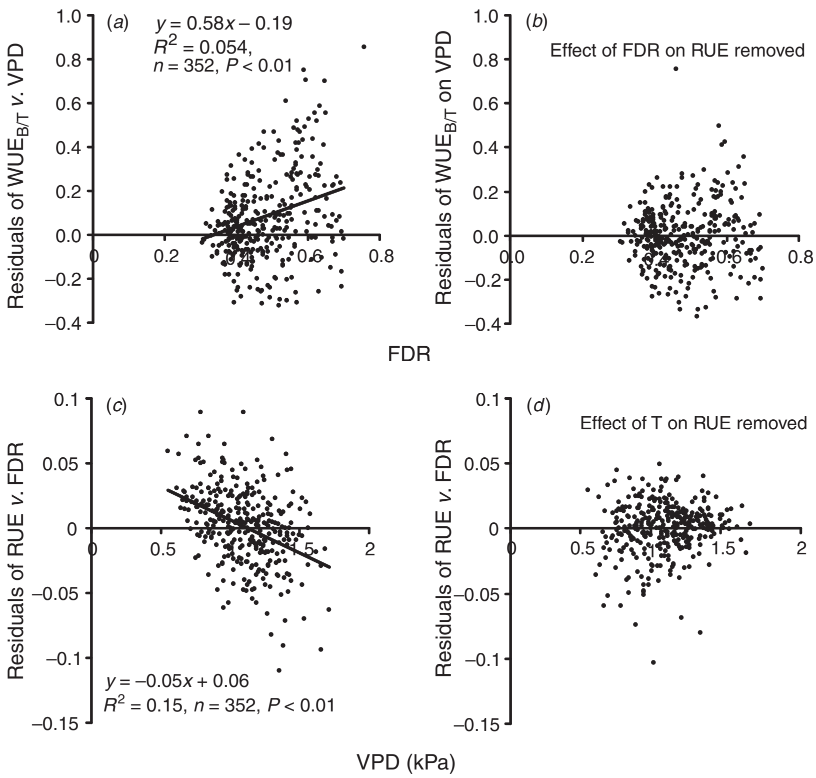

Fig. 5. Residuals of the fitted regression between simulated water-use efficiency (WUE) and vapour pressure deficit (VPD) *v.* fraction of diffuse radiation (FDR) (*a*, *b*), and simulated radiation-use efficiency (RUE) and FDR *v.* VPD (*c*, *d*). The simulation model was run 'unmodified', i.e. assuming direct and diffuse fluxes of radiation and temperature effects on net assimilation (*a* and *c*), and ignoring the diffuse flux of radiation (*b*), or ignoring the effects of temperature on net assimilation, i.e. photosynthesis and dark respiration (*d*).

$WUE_{B/T}$ than that expected from the relationship in Fig. 6*a*. Open symbols in Fig. 6*b* are from those measurements in Fig. 6*a* where VPD was available.

Indices of environmental potential: temporal and latitudinal variation and relationships with yield

The photo-thermal quotient (Pq, Eqn 3) varied from as low as 0.44 MJ/m^2.day°C (decile 1) in Emerald to 0.74 MJ/m^2.day°C in Horsham (decile 9) (Fig. 7*a*). The rates of change with latitude in the median and decile 1 of Pq were not different from zero (Fig. 7*a*).

As air temperature, VPD, and FDR (*i*) varied substantially across the studied locations, and (*ii*) had significant effects on WUE and RUE (Table 4, Figs 4 and 5), we postulated that the value of Pq as an index of environmental potentiality could be improved if VPD and FDR were included in its calculation. A new index of environmental potentiality was then created by normalising Pq by the ratio FDR/VPD; we called this index normalised photo-thermal quotient (NPq, MJ/m^2.day°C.kPa). The median and decile 1 and 9 of NPq increased southwards at a significant ($P < 0.01$) rate of 0.02 MJ/m^2.day°C.kPa (14%) per degree of latitude (Fig. 7*b*). Seasonal variation in NPq also increased with latitude. In Horsham, the gap between deciles 1 and 9 was 2.2-fold, whereas in Emerald it was 1.6-fold (Fig. 7*b*).

Grain yield from field experiments across South Australia, New South Wales, and Queensland ($n = 51$) (Table 2, Fig. 1) was plotted against Pq (Fig. 8*a*) and NPq (Fig. 8*b*). Grain yield was unrelated to the photo-thermal quotient (slope not different from zero) (Fig. 8*a*), whereas a significant positive relationship (slope different from zero, $P < 0.01$) was observed with NPq (Fig. 8*b*). $Yield_{Max}$ was also linearly related to NPq ($R^2 = 0.70$, $n = 10$, $P < 0.01$). High-yielding crops across the whole range of NPq included sites in Rutherglen and Horsham in Victoria, Turretfield and Kimba in South Australia, and Billa Billa and Nindigully in Queensland.

Flowering date, yield potential, and ENSO

Figure 9 shows the influence of the date of flowering on the variation of NPq around anthesis. For a given date of anthesis, NPq was always higher in southern locations. In Horsham, NPq decreased more than 2.5-fold when flowering was delayed from the end of July to mid November. Based on Fig. 8, this translates into a reduction in yield potential of up to 3 t/ha. In the north, delayed flowering had much smaller effects on both NPq and loss of yield potential, i.e. up to 2.2 t/ha at Gunnedah, Goondiwindi, Dalby, and Roma, and up to 0.4 t/ha at Emerald. As shown in Fig. 7*b*, for a given flowering date, seasonal variability in NPq was also higher in the south than in the north. In the south, i.e. Horsham and Birchip, the highest NPq coincided with the

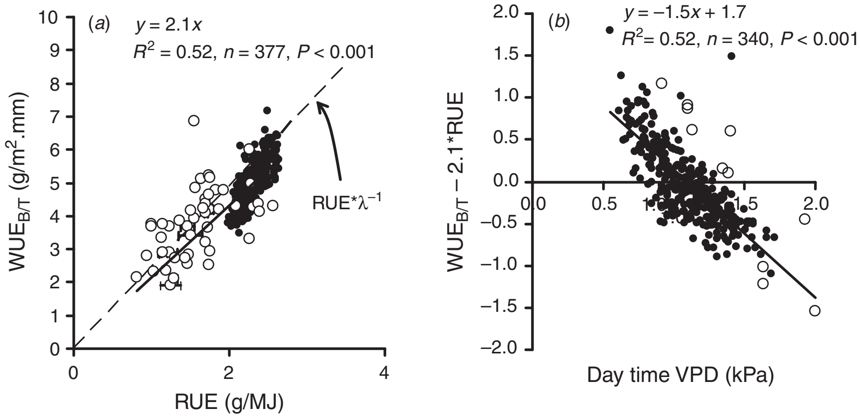

Fig. 6. (*a*) Relationship between water- (WUE) and radiation-use efficiency (RUE). Small closed symbols are simulated results, and large open circles are measured values; see Table 1 for details. The solid line is the fitted regression; the dashed line is a theoretical reference corresponding to a slope equal to the inverse of the latent heat flux of water ($\lambda = 2.45$ kg H_2O/MJ) (as in Matthews *et al*. 1988). (*b*) Residuals of the fitted regression in (*a*) as a function of day-time vapour pressure deficit (VPD). The different number of data points in (*a*) and (*b*) is because not all the datasets had paired values of WUE, RUE, and VPD.

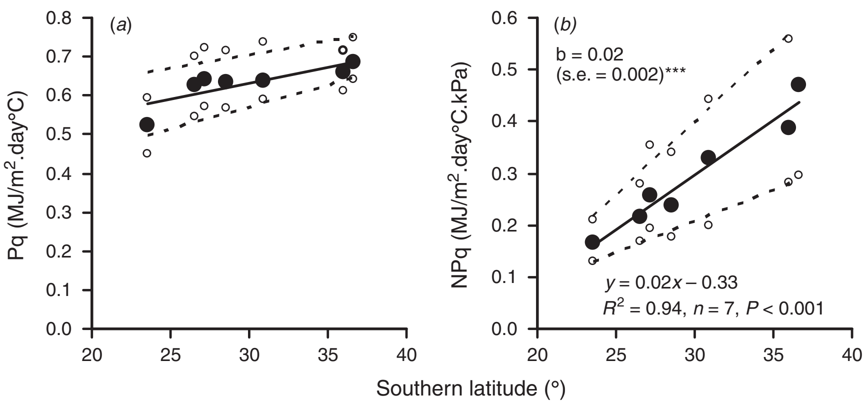

Fig. 7. Latitudinal trends of (*a*) photo-thermal quotient (Pq, MJ/m^2.day°C) (Eqn 3), and (*b*) the normalised photo-thermal quotient (NPq, MJ/m^2.day°C.kPa) (Eqn 4) calculated for the period between 20 days before and 14 days after anthesis. Dotted and dashed lines and small open circles show deciles 1 and 9, respectively; solid line and closed circles show median values. Asterisks (***) indicate level of significance for the slope being different from zero at 1% level of probability.

median date of last frost; north of Gunnedah, the highest NPq was observed before the median date of last frost (Fig. 9).

The higher variation in NPq in the south brings opportunities and opens questions with regards to the possibility of predicting higher and lower than average yielding seasons. In Horsham, seasonal variability in NPq was partially related to the occurrence of El Niño events, i.e. lower NPq during El Niño years in relation to the other years. During El Niño years in the south, FDR tends to be lower, and VPD and T higher than during the other years. In northern locations, there was very small variation in NPq and no relationship was observed with the condition of ENSO (Fig. 10). Based on the results from Figs 8 and 10, and irrespective of ENSO effects on rainfall, median potential grain yield during El Niño events in Horsham can be expected to be up to 1.3t/ha lower than during the other years.

Discussion

Crop growth analysis and calculation of biomass production in simulation models both are based on the concept of capture and efficiency in the use of resources (de Wit 1965; Monteith *et al*. 1994). DSSAT and EPIC are examples of radiation-driven crop models (Hoogenboom *et al*. 1999), whereas CROPSYST and APSIM combine water- and radiation-driven estimates of biomass (Stöckle *et al*. 1994; McCown *et al*. 1996). Water-use efficiency, in its various forms and definitions, is a central concept for both production and environmental aspects of irrigated and dryland agriculture (French and Schultz 1984; Dunin *et al*. 1999; Angus and van Herwaarden 2001; Condon *et al*. 2002). From diverse perspectives, we have accumulated a sound understanding of the major soil, crop, management, and climatic drivers of WUE and RUE. There is consensus, based on theoretical and empirical evidence, that WUE is an inverse

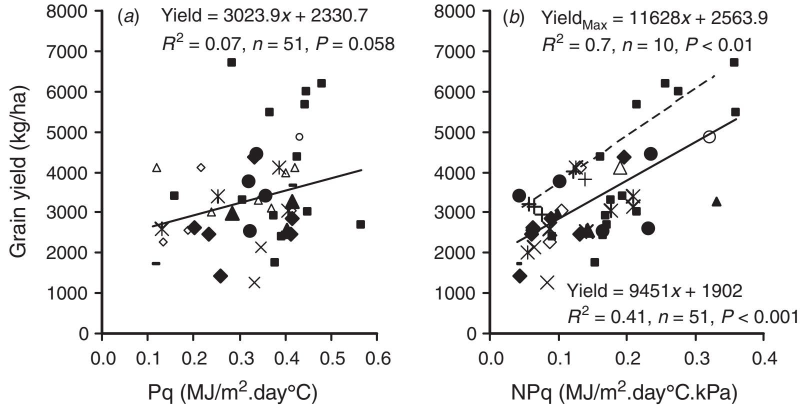

Fig. 8. Relationship between observed grain yields (see Table 1 for details) and (*a*) the photo-thermal quotient (Pq, MJ/m^2.day°C), and (*b*) a photo-thermal quotient normalised by the ratio between the fraction of diffuse radiation and day-time vapour pressure deficit (NPq, MJ/m^2.day°C.kPa), calculated between 20 days before and 14 days after the anthesis. In (*a*) the solid line is a regression line, and in (*b*) the dashed line represents the maximum yield ($\text{Yield}_{\text{Max}}$) that is achievable at any particular level of NPq, and the solid line is a regression line. In (*a*) and (*b*), the different symbols represent different datasets.

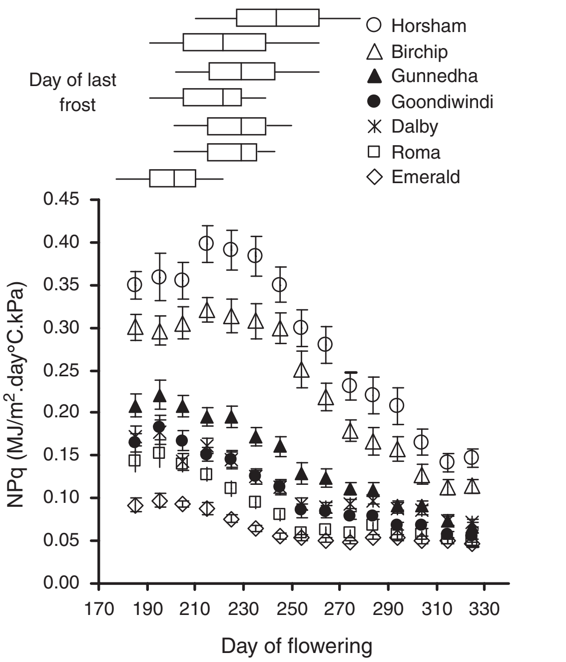

Fig. 9. Relationship between the normalised photo-thermal quotient (NPq) calculated between 20 days before and 14 days after anthesis, and the day of flowering in wheat, for 7 locations in a N–S transect in eastern Australia. Bars are ± 1 standard error. Day of the year of last frost (screen's air temperature <0°C) for each location is represented by whisker box diagrams showing the 0.1, 0.25, 0.5, 0.75, and 0.9 probability levels.

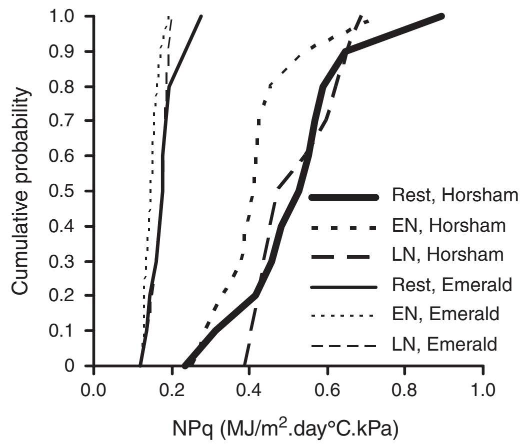

Fig. 10. Cumulative probability distribution functions of the normalised photo-thermal quotient (NPq, MJ/m^2.day°C.kPa) for the El Niño years, La Niña years, and the rest of the years based on the classification proposed by Potgieter *et al.* (2005), for Horsham (Victoria) and Emerald (Queensland).

function of variables related to atmospheric water demand, and that RUE is a direct function of the proportion of diffuse radiation. Much research on these efficiencies has benefited from up-scaling gas-exchange principles from leaf to canopy (Tanner and Sinclair 1983; Sinclair and Horie 1989; Hammer and Wright 1994). Here we used a bottom-up model to address hypotheses derived from a top-down approach (Eqn 2) to: (*i*) further explore the controversial relationship between RUE and VPD (hypothesis 1); (*ii*) develop the previously unexplored relationship between WUE and proportion of diffuse radiation (hypothesis 2); and (*iii*) derive a new and more powerful climate index of environmental potentiality (hypothesis 3). The concepts and relationships derived in this work can be interpreted from direct and indirect effects on the relationship between the efficiencies in Eqn 2.

Effect of environmental conditions on WUE

Based on the close agreement between empirically derived and simulated relationships between $\text{WUE}_{\text{B/T}}$ and RUE and VPD and FDR (Fig. 4), we conclude that our simulations captured the essential processes and drivers of $\text{WUE}_{\text{B/T}}$ and RUE. In our work, modelled and empirically determined $WUE_{B/T}$ were inversely related to day-time VPD. The overall relationship was closer to that reported by Kemanian *et al*. (2005) (dotted line in Fig. 4*a*) than to that reported by Abbate *et al*. (2004) (dashed line in Fig. 4*a*). Empirical approaches to deriving canopy-level *k* values from curve-fitting exercises, primarily assume that canopy $WUE_{B/T}$ is proportional to the ratio between single-leaf photosynthesis and transpiration (Bierhuizen and Slatyer 1965). Again, important assumptions have been made in more 'mechanistic' attempts to up-scale canopy $WUE_{B/T}$ from the photosynthesis and transpiration of individual leaves. Tanner and Sinclair (1983) assumed that the photosynthesis of shaded leaves equals the amount of assimilates consumed in maintenance respiration. This assumption is particularly critical when comparing environments of contrasting climate characteristics, i.e. FDR, PAR, and T. A more mechanistic up-scaling analysis of the transpiration and photosynthesis of individual leaves was therefore necessary to clarify some of the issues above in view of recent experimental evidence (Abbate *et al*. 2004; Kemanian *et al*. 2005).

To the best of our knowledge, this is the first report postulating a positive association between WUE and proportion of diffuse radiation. This correlation can be interpreted as a consequence of improved canopy photosynthetic efficiency under a high proportion of diffuse radiation (Fig. 4*d*), and the association between $WUE_{B/T}$ and RUE (Fig. 6*a*). Alternatively, the relationship between $WUE_{B/T}$ and FDR could be an artefact reflecting the inverse relationship between VPD and FDR (Table 3). Steduto and Albrizio (2005) concluded that FAO-Penman-Montheith reference evapotranspiration was more effective than VPD for normalising $WUE_{B/T}$. There are many methods of calculating day-time VPD (Kemanian *et al*. 2004), which may be a source of noise in normalising WUE. Interestingly, it may also be that reference evapotranspiration accounts for some of the radiation-related effects on WUE. For a given VPD, higher daily total radiation results in greater reference evapotranspiration, which may indirectly capture the negative association between PAR and FDR (Table 3), and a hypothetical residual effect of diffuse radiation on WUE not mediated by its correlation with VPD. However, after modifying our simple simulation model to ignore the flux of diffuse radiation, and its effects on gross assimilation and RUE, no residual effect of FDR on $WUE_{B/T}$ was detected (Fig. 5*b*). This indicates that in high-FDR environments/seasons, high $WUE_{B/T}$ can be expected from the known effects of FDR on canopy assimilation. The higher the FDR the higher the gross assimilation irrespective of the amount of water consumed in transpiration, although this hypothesis might still require empirical confirmation. Other effects we did not take into account include cloud forcing (Barry and Chorley 1998). Cloudiness-driven changes in FDR can have a net atmospheric warming or cooling effect, depending on cloud type and cloud altitude. Here we assumed that these effects were minor in the temporal scale of our study, i.e. a small window of 20 days around the date of anthesis of a wheat crop.

Effect of environmental conditions on RUE

Radiation-use efficiency is affected by incident radiation (Hammer and Wright 1994; Bange *et al*. 1997) and the unevenness of the distribution of the PAR over the leaves, i.e. the extinction of diffuse and direct flux within the canopy (de Wit 1965; Allen and Scott 1980; Sinclair and Shiraiwa 1993). The partitioning of the incoming radiation into its diffuse and direct fluxes causes spatial bimodality in illumination of the leaves: shaded leaves receive diffuse light only, whereas sunlit leaves receive both diffuse and direct fluxes (Spitters 1986). Increasing FDR FDR increases RUE as a consequence of a greater contribution to canopy biomass accumulation from shaded, highly efficient leaves in the lower layers of the canopy. Therefore, high RUE can be expected in environments of low radiation intensity and high diffuse fraction compared with high radiation intensity, low diffuse conditions. We found that these are the main characteristics describing the radiation environment of the studied transect in this work. The period around anthesis in the predominantly winter-rainfall regions of south-eastern Australia is characterised by relatively high FDR and low radiation intensity, although longer days lead to higher daily PAR integrals. This contrasts with the predominantly summer-rainfall regions of north-eastern Australia characterised by less diffuse radiation, shorter days, and higher radiation intensity. Linking the known effects of PAR and FDR on RUE with the climatic patterns in eastern Australia helps in understanding the reduction in potentiality from southern to northern locations.

Controversy exists on the effect of day-time VPD on RUE. Inverse associations between RUE and day-time VPD have been reported in several species and environments (Stöckle and Kiniry 1990; Goyne *et al*. 1993; Kiniry *et al*. 1998; Kemanian *et al*. 2004). Other authors expressed doubts on these relationships, both on theoretical and empirical grounds (Hammer and Wright 1994; Sinclair and Muchow 1999; Albrizio and Steduto 2005). Here we pooled a large set of modelled and empirical data indicating a non-linear, inverse relationship between RUE and VPD (Fig. 4*b*). According to our working hypothesis, this relationship could be explained by the presence of correlations between climate variables, e.g. air temperature, radiation environment, and VPD. Using PLS-R, we showed that with varied north to south importance; FDR and PAR were the primary drivers of RUE (Table 4). In the experiments where Goyne *et al*. (1993) found a negative association between RUE and VPD, their low VPD corresponded with a season of low incoming radiation for which we estimated relatively small values of FDR. Albrizio and Steduto (2005) were not able to reduce the variability in RUE after normalising the cumulative intercepted solar radiation by day-time VPD when comparing C_3 and C_4 species grown under a wide range of VPDs, for which other authors reported significant correlations with RUE (Stöckle and Kiniry 1990; Kemanian *et al*. 2004). Albrizio and Steduto (2005) indicated that contrasting FDR values during the winter, rather than VPD, most likely were behind the variation of RUE in wheat. We came to a similar conclusion after revisiting the data in Kiniry *et al*. (1998), and deriving FDR from sowing to flowering for some of those experiments (sorghum and maize) for which the climate records were available. Available climate records included the trials in Cabelguenne, Toulouse, during 1986 and 1987, and Western Australia (Abetunge 1983) and the Northern Territory (Muchow and Coates 1986). Using these datasets we calculated that FDR explained 60% of the variation in RUE ($y = 5.63x + 0.312$, $n = 6$, $P < 0.06$) for maize and sorghum. In addition, we performed a simulation exercise where we eliminated the effect of temperature in the calculation of the leaf photosynthesis parameters, i.e. the light conversion factor, the CO_2 assimilation rate at light saturation, and maintenance respiration. This test showed that the effect of VPD on RUE disappeared, suggesting that any effect of VPD on RUE could also be explained by the association between VPD and temperature (Fig. 5*c*, *d*). Consequently, even when the original model reproduced a residual effect between VPD and RUE, there was no causality in the relationship.

Climatic indices of grain yield potential

Yield of wheat is primarily related to grain number (Fischer 1985*a*, 1985*b*; Slafer and Andrade 1989; Ortiz-Monasterio *et al*. 1994; Slafer 1994). Grain number and yield increase with increasing radiation during the period of rapid ear growth (Fischer 1985*a*; Evans *et al*. 1991; Rodriguez *et al*. 2005), and decrease with increasing mean temperature in the range 14–22°C, which shortens the period of rapid ear growth (Fischer 1985*a*, 1985*b*). These principles explain the relationship between photothermal quotients around flowering and grain set and yield reported for wheat (Fischer 1985*a*; Magrin *et al*. 1993; Ortiz-Monasterio *et al*. 1994) and other species including field pea (Poggio *et al*. 2005), sunflower (Cantagallo *et al*. 1997), and rice (Islam and Morison 1992). However, in this paper: (*i*) Pq showed little variation (Fig. 7*a*), and (*ii*) it was unrelated to grain yield (Fig. 8*a*). The large latitudinal variation in VPD and FDR and their influence on WUE and RUE indicate that these are important factors. The normalised coefficient NPq showed a much steeper latitudinal response, captured the high temporal variability characteristic of the southern wheat growing environments (Fig. 7*b*), and was significantly associated with measured grain yield (Fig. 8*b*). In common with more sophisticated crop simulation models, this index does not account for extreme temperatures around anthesis, i.e. below 9 or above 31°C (Slafer and Savin 1991; Wheeler *et al*. 1996), which cause sterility and reduce kernel set, or limit potential grain weights (Calderini *et al*. 2001).

The normalised coefficient NPq seemed able to account for the general patterns of yield response to sowing date. In the south, NPq was high and stable for flowering up to late August (240 days), and declined sharply for later flowering. Qualitatively, this pattern is in agreement with the stability in grain yield measured for early-flowering crops (Gomez-Macpherson and Richards 1995) and its rapid decline with later sowing dates (O'Leary *et al*. 1985; Coventry *et al*. 1993). Quantitatively, the estimated rate of decline in potential yield compares with the reported rate for actual yield loss of 17 kg/ha.day delay in sowing (Sadras *et al*. 2002). The smaller changes in NPq with flowering time in the north-eastern wheatbelt also agree with empirical observations in northern New South Wales and southern Queensland (Dalal *et al*. 1998; Thomas *et al*. 2006).

Implications for modelling

This work indicates that irrespective of the approach taken to simulate growth, crop simulation models should take into account the known effects of VPD on $WUE_{B/T}$ and FDR on RUE. This might be particularly important when comparing simulation results from regions with contrasting VPD and FDR. This would also be the case of long-term simulations aiming to quantify the effect of seasonal climate variability. As shown for south-eastern Australia, analyses of effect of climate variability solely based on time series of temperatures or annual or seasonal rainfall would only provide a partial description of the potential incidence of climate variability and ENSO on crop growth and yield. Most appropriately, simulation studies using crop models that integrate the effect of VPD on $WUE_{B/T}$, and FDR on RUE, should be used. This is in line with the observation that the economic value of existing seasonal climate forecasting systems (Stone and Auliciems 1992) is enhanced when key climate variables are integrated in crop modelling exercises (Hammer *et al*. 1996; M. R. Anwar, D. Rodriguez, D. L. Liu, S. Power, unpublished) compared with analyses of shifts in median rainfall.

Conclusions

Modelled and empirical data indicated a confounded relationship between VPD and RUE, and a causal relationship between FDR and WUE. The former is accounted for by the correlation between VPD and temperature, and the latter by the effects of FDR on canopy assimilation. Experiments designed to decouple VPD and FDR are required for definite conclusions, whereas recognition of the link between efficiencies and the benefits of dealing with them in conjunction should contribute to better interpreting experimental evidence. The newly developed climatic index NPq showed an improved capacity to explain observed variability in grain yield across environments characterised by contrasting day-time VPD, total and FDR, and temperature.

Acknowledgments

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