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The limit to wheat water-use efficiency in eastern Australia. II. Influence of rainfall patterns

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Abstract. We investigated the influence of rainfall patterns on the water-use efficiency of wheat in a transect between Horsham (36°S) and Emerald (23°S) in eastern Australia. Water-use efficiency was defined in terms of biomass and transpiration, $\mathrm{WUE}_{B/T}$, and grain yield and evapotranspiration, $\mathrm{WUE}_{Y/ET}$. Our working hypothesis is that latitudinal trends in $\mathrm{WUE}_{Y/ET}$ of water-limited crops are the complex result of southward increasing $\mathrm{WUE}_{B/T}$ and soil evaporation, and season-dependent trends in harvest index. Our approach included: (*a*) analysis of long-term records to establish latitudinal gradients of amount, seasonality, and size-structure of rainfall; and (*b*) modelling wheat development, growth, yield, water budget components, and derived variables including $\mathrm{WUE}_{B/T}$ and $\mathrm{WUE}_{Y/ET}$. Annual median rainfall declined from around 600 mm in northern locations to 380 mm in the south. Median seasonal rain (from sowing to harvest) doubled between Emerald and Horsham, whereas median off-season rainfall (harvest to sowing) ranged from 460 mm at Emerald to 156 mm at Horsham. The contribution of small events (≤ 5 mm) to seasonal rainfall was negligible at Emerald (median 15 mm) and substantial at Horsham (105 mm). Power law coefficients (τ), i.e. the slopes of the regression between size and number of events in a log-log scale, captured the latitudinal gradient characterised by an increasing dominance of small events from north to south during the growing season. Median modelled $\mathrm{WUE}_{B/T}$ increased from 46 kg/ha.mm at Emerald to 73 kg/ha.mm at Horsham, in response to decreasing atmospheric demand. Median modelled soil evaporation during the growing season increased from 70 mm at Emerald to 172 mm at Horsham. This was explained by the size-structure of rainfall characterised with parameter τ, rather than by the total amount of rainfall. Median modelled harvest index ranged from 0.25 to 0.34 across locations, and had a season-dependent latitudinal pattern, i.e. it was greater in northern locations in dry seasons in association with wetter soil profiles at sowing. There was a season-dependent latitudinal pattern in modelled $\mathrm{WUE}_{Y/ET}$. In drier seasons, high soil evaporation driven by a very strong dominance of small events, and lower harvest index override the putative advantage of low atmospheric demand and associated higher $\mathrm{WUE}_{B/T}$ in southern locations, hence the significant southwards decrease in $\mathrm{WUE}_{Y/ET}$. In wetter seasons, when large events contribute a significant proportion of seasonal rain, higher $\mathrm{WUE}_{B/T}$ in southern locations may translate into high $\mathrm{WUE}_{Y/ET}$. Linear boundary functions (French-Schultz type models) accounting for latitudinal gradients in its parameters, slope, and *x*-intercept, were fitted to scatter-plots of modelled yield *v*. evapotranspiration. The *x*-intercept of the model is re-interpreted in terms of rainfall size structure, and the slope or efficiency multiplier is described in terms of the radiation, temperature, and air humidity properties of the environment. Implications for crop management and breeding are discussed.

Additional keywords: *Triticum aestivum*, climate, harvest index, biomass, power law, seasonality, nitrogen, breeding, modelling, root, evaporation, transpiration, water, resource pulse.

Introduction

Climate, particularly rainfall and temperature, gives rise to predictable types of ecosystems: the amount of annual rainfall in a region largely makes the difference between a desert and a rainforest (Specht and Specht 1999; Chapin *et al*. 2002). For a given amount of annual rainfall, seasonality could have a substantial influence on vegetation type, land use, and crop yield. In southern Australia, 400–500 mm/year of winter-dominant rainfall determines a 'high-rainfall' zone favourable for the production of small grain crops. With the same amount of annual rainfall, conditions for agriculture are marginal in the Pampas of Argentina due to the summer bias in distribution (Hall *et al*. 1992). Quantification of rainfall seasonality relies on a series of imperfect, complementary indices including those of Markham (1970) and Walsh and Lawler (1981), and *ad hoc* indices of agronomic relevance such as winter/summer or seasonal/annual ratios (Keating *et al*. 2003; Rodriguez and Sadras 2007).

For a given amount and seasonality, the distribution of rainfall within a season can have considerable effects on the grain yield of annual crops and their water-use efficiency.

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This is a consequence of well defined, relatively narrow time windows when grain set is particularly sensitive to stresses (Fischer 1985; Magrin *et al.* 1993; Cantagallo *et al.* 1997; Rodriguez and Sadras 2007). Models of grain yield based on evapotranspiration use appropriate weighting factors to account for this phenological window of stress susceptibility (Doorenbos and Kassam 1979; Hanks 1983).

For a given amount, seasonality, and intra-seasonal distribution of rainfall, the size structure of rainfall could influence many biologically relevant processes such as depth and turnover of roots, nitrogen mineralisation, species diversity, and fate of water in the ecosystem (Noy-Meir 1973; Sala and Lauenroth 1982; Golluscio *et al.* 1998; Sadras 2003; Sadras and Baldock 2003; Chesson *et al.* 2004; Williamson *et al.* 2005; Monzon *et al.* 2006). Size of events has been characterised with arbitrary size limits (Sala and Lauenroth 1982; Golluscio *et al.* 1998; Loik *et al.* 2004), e.g. 5 mm. More recently, power-laws have been shown to effectively capture the size-structure of rainfall patterns (Peters and Christensen 2002; Sadras 2003).

In the first paper of this series, we characterised potential water-use efficiency in a transect between Horsham (36°S) and Emerald (23°S) in eastern Australia (Rodriguez and Sadras 2007). Driven by temperature, vapour pressure deficit, radiation, and fraction of diffuse radiation, and assuming full canopy cover and no water restrictions, modelled biomass per unit transpiration ($\mathrm{WUE_{B/T}}$) around flowering declined from 95 at Horsham to 59 hg/ha.mm at Emerald. Here we investigated the influence of rainfall patterns in the Horsham-to-Emerald transect on wheat water-use efficiency defined in terms of biomass and transpiration, $\mathrm{WUE_{B/T}}$, and grain yield and evapotranspiration, $\mathrm{WUE_{Y/ET}}$.

The scaling from $\mathrm{WUE_{B/T}}$ to $\mathrm{WUE_{Y/ET}}$ requires consideration of both the soil evaporation component of evapotranspiration, and of harvest index to transform biomass into yield. We expect soil evaporation to decrease northwards in parallel with both a reduction of in-season rainfall and greater frequency of large events (Williamson 2007). Implicit in this hypothesis is the assumption that rainfall pattern is the primary driver of soil evaporation, with secondary effects of atmospheric demand and soil type (Monzon *et al.* 2006). Latitudinal trends in harvest index are harder to foresee. Harvest index is a direct, non-linear function of water availability after flowering (Sadras and Connor 1991). In both northern and southern locations, availability of water after flowering is typically low and conducive to low harvest index. Although terminal drought is common to northern and southern locations, there are important differences that may have relevant agronomic implications. Soil type and temperature regime during grain filling in the north–south transect might affect the behaviour of crops in response to a drying soil profile. In the northern region, the soil profile tends to dry from the top during the growing season, while dry subsoil and subsoil chemical constraints increase crop reliance on seasonal rainfall in the southern region (Sadras *et al.* 2002, 2003; Rodriguez *et al.* 2006). Seasonal variation in temperature, vapour pressure deficit, total radiation, and fraction of diffuse radiation during grain set and filling increase southwards (Rodriguez and Sadras 2007). This, in combination with the greater reliance on seasonal rainfall, might lead to higher variability in harvest index in southern locations. Latitudinal trends in yield per unit evapotranspiration in water-limited crops, if any, would be the complex result of southward increasing $\mathrm{WUE_{B/T}}$ and soil evaporation, and season-dependent trends in harvest index.

Method

Rainfall patterns

Using climate records (1913–2003) from the Australian Bureau of Meteorology, we derived descriptive statistics and frequency distribution of selected rainfall features including total amount, seasonality, and size of events. Seasons comprised the time between sowing and modelled date of harvest for each location and year (see below). Three seasonality indices were considered: (*i*) the ratio between seasonal and annual rain, (*ii*) the index of Walsh and Lawler (1981), and (*iii*) the vector of Markham (1970). The index of Walsh and Lawler (1981) is:

$$\mathrm{WL} = \Sigma|x_\mathrm{m} - \mathrm{R}/12|/\mathrm{R} \qquad (1)$$

where x_m is monthly average rainfall (mm) and R is annual rain (mm); theoretically, this index ranges from zero, if all months have equivalent rainfall, to 1.83, if all rainfall occurs in a single month. This index indicates the strength but not the timing of rainfall concentration. The vector of Markham (1970) quantifies both the intensity of rainfall concentration and the direction of seasonality, i.e. the time of year in which most rainfall occurs. The mean monthly rainfall determines the magnitude of that month's vector, and its direction is given in arc units, e.g. 15° for January. An annual vector is obtained as the result of monthly vectors, and the magnitude of the result is normalised by annual rainfall for comparisons. To account for intra-seasonal variation in rainfall, we analysed rainfall patterns between stages 50 and 70 in the Zadok's scale, comprising the critical period between emergence of inflorescence and beginning of rapid grain filling. Power-law coefficients were used to characterise frequency distributions of size of rainfall events, using the approach of Sadras (2003) with 3-mm intervals.

Modelling yield, water budget, and water-use efficiency

We used APSIM (version 5.1) to model wheat growth, development, yield, and water budget components (www.apsru.gov.au/apsru). Sowing dates for each location were derived from Whopper Cropper (www.apsru.gov.au/apsru/), and ranged from 16 April at Emerald to 16 May at Horsham. Simulations involved sowing of cv. Hartog with default cropping pattern parameters (30 mm sowing depth, 100 plants/m^2, 250 mm between rows), and unlimited nitrogen supply. The soil was held constant along the transect (146 mm maximum plant-available water, half filled in the initial year of simulations) to allow for the identification of rainfall patterns, the focus of this study. The approach of using fixed soil features to unveil climate-related patterns is well established, and is indeed one of the most powerful features of modelling studies (Keating *et al.* 2002; Sadras and Baldock 2003). A limited sensitivity analysis was preformed to glimpse the interaction between rainfall pattern and soil, with selected simulations using soils with plant-available water of 111, 146, and 182 mm. Unless otherwise specified, water budgets were carried over from harvest to sowing of the next crop to account for rainfall and storage of water in the fallow period between successive crops. The analysis focussed on biomass and grain yield, components of the water budget, primarily evapotranspiration and its components soil evaporation and crop transpiration, and derived variables including biomass per unit transpiration and grain yield per unit evapotranspiration. In the previous paper, given our focus on climatic drivers of resource-use efficiency and the lack of reliable temperature and radiation data previous to 1957, our simulations spanned the period between 1957 and 2003 (Rodriguez and Sadras 2007). In the present analysis, simulations used climatic data from 1913 to 2003, for consistency with the analysis of rainfall patterns. We have therefore prioritised reliability and resolution in our analysis of rainfall, the focus of this paper, at the expense of radiation and temperature.

Results

Rainfall patterns

Annual, seasonal (sowing to harvest), and off-season (harvest to sowing) rainfall showed statistically strong latitudinal gradients (Fig. 1). Annual median rainfall ranged from around 600 mm in northern locations to 380–440 mm at Birchip and Horsham (Fig. 1*a*). Median seasonal rain doubled between Emerald and Horsham (Fig. 1*b*). Median rainfall between harvest and sowing ranged from 460 mm at Emerald to 156 mm at Horsham (Fig. 1*c*). The ratio between seasonal and annual rainfall (inset Fig. 1*b*) captured the latitudinal gradient in rainfall seasonality graphically depicted by Markham's vector (1970) (Fig. 2). The seasonality index of Walsh and Lawler (1981) and the module of Markham's vector (Fig. 2) were closely correlated ($n = 7$, $r^2 = 0.99$, $P < 0.0001$) as shown by Williamson (2007) in a larger analysis in Australia ($n = 1137$, $r^2 = 0.98$, $P < 0.0001$). Variability of annual and off-season rain both decreased southwards, whereas no clear latitudinal pattern was evident for the variability of seasonal rain (Fig. 1). Consistent with the shift from summer- to winter-dominant rainfall (Fig. 2), the amount of rain between Zadok's stages 50 and 70 trebled between Emerald and Horsham (Fig. 3). The coefficient of variation for rainfall in this period declined from 177% at Emerald to 67% at Horsham (Fig. 3).

Figure 4*a* compares the contribution of small and large events to total seasonal rainfall at Emerald and Horsham. The approach uses an arbitrary threshold of 5 mm to separate small and large events (Golluscio *et al.* 1998; Monzon *et al.* 2006). The contribution of small events to seasonal rainfall was negligible at Emerald (median 15 mm) and substantial at Horsham (105 mm), as emphasised with the horizontal lines in Fig. 4*a*. Power-law coefficients (τ), i.e. the slopes of the regression between size and number of events in a log-log scale, reflected the contrasting size structure of rainfall in these locations (Fig. 5*a*). Despite significant non-linearity in 6 out of the 7 locations ($P < 0.01$), power laws had $R^2 > 0.94$ ($P < 0.0001$), and captured the latitudinal gradient characterised by an increasing dominance of small events from north to south during the growing season (Fig. 5*b*, closed symbols). Rainfall during the harvest-to-sowing period has a similar size structure along the transect (Fig. 5*b*, open symbols).

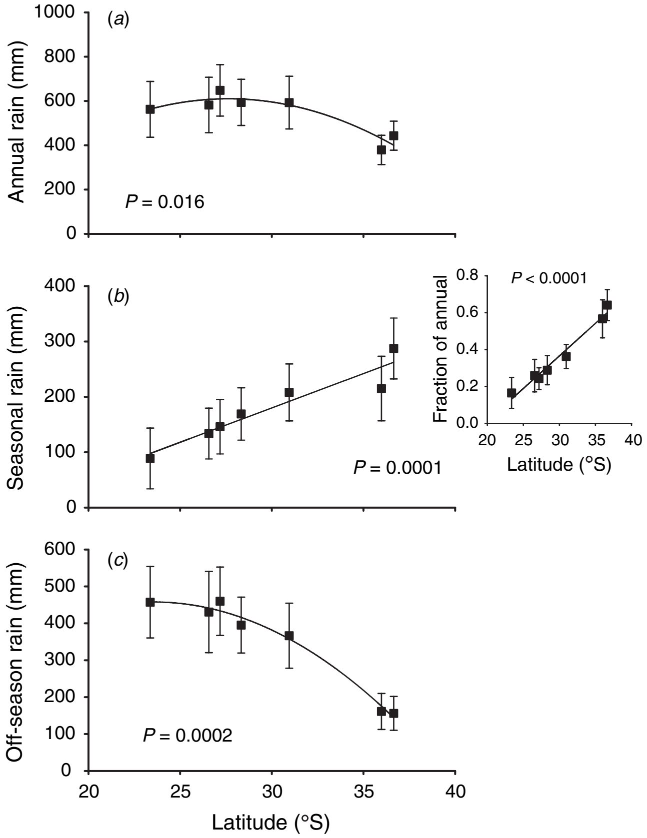

Fig. 1. Latitudinal patterns in median (*a*) annual, (*b*) seasonal, and (*c*) off-season rain in eastern Australia. Inset shows seasonal rain as a fraction of annual rain. Error bars are inter-quartile ranges and *P* indicates statistical significance of latitudinal gradient as assessed by regression.

Modelled soil plant-available water at sowing and flowering

At sowing, the frequency distribution of modelled plant-available water for Horsham was the mirror image of that for Emerald (Fig. 6*a*, *b*). Median plant-available water decreased from 124 to 27 mm, and its variability increased consistently from north to south (Fig. 6*c*, *d*). Sensitivity analysis indicated a change in median plant-available water at sowing of 0.85 mm per mm change in maximum soil plant-available water at Emerald, and 0.13 mm per mm at Horsham (inset Fig. 6*c*).

At flowering, latitudinal gradients were minor for both plant-available water, which was low in average, and its variability, which was large (Fig. 6*c*, *d*). Plant-available water in the soil at sowing accounted for only 5–7% of the variation in plant-available water at flowering in soils with a maximum plant-available water of 112 mm, and this proportion increased to 13% (Horsham) and 24% (Emerald) for soils with maximum plant-available water of 182 mm.

Modelled water-use efficiency

We analysed yield per unit evapotranspiration, $WUE_{Y/ET}$, in terms of biomass per unit transpiration, $WUE_{B/T}$, soil evaporation, and harvest index.

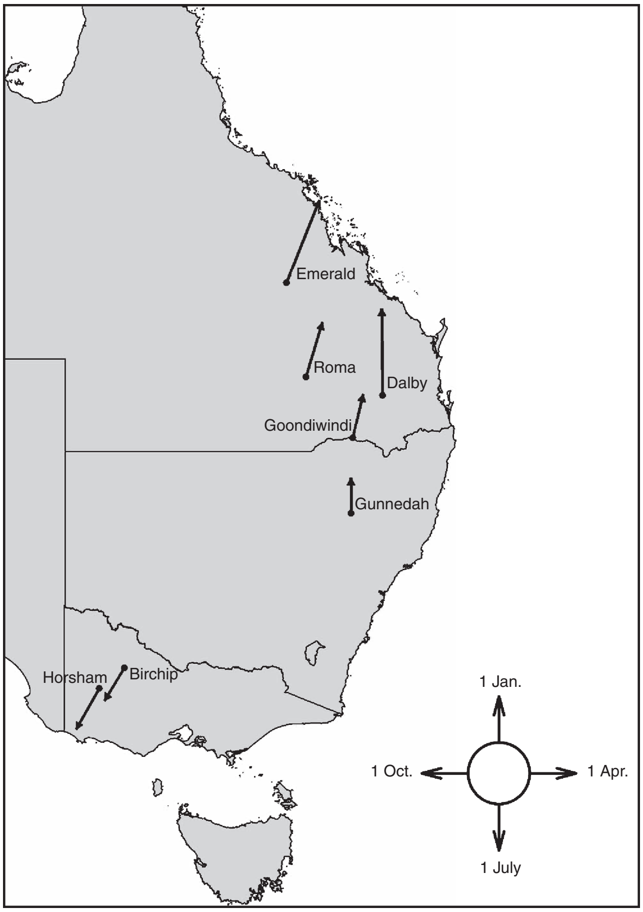

Fig. 2. Markham (1970) seasonality indices in 7 locations in eastern Australia. The direction of the vector indicates seasonal rain concentration in units of arc and the magnitude ranges between 0 (precipitation evenly distributed throughout the year) and 100 (all the precipitation concentrated in a single month). Adapted from Williamson (2007).

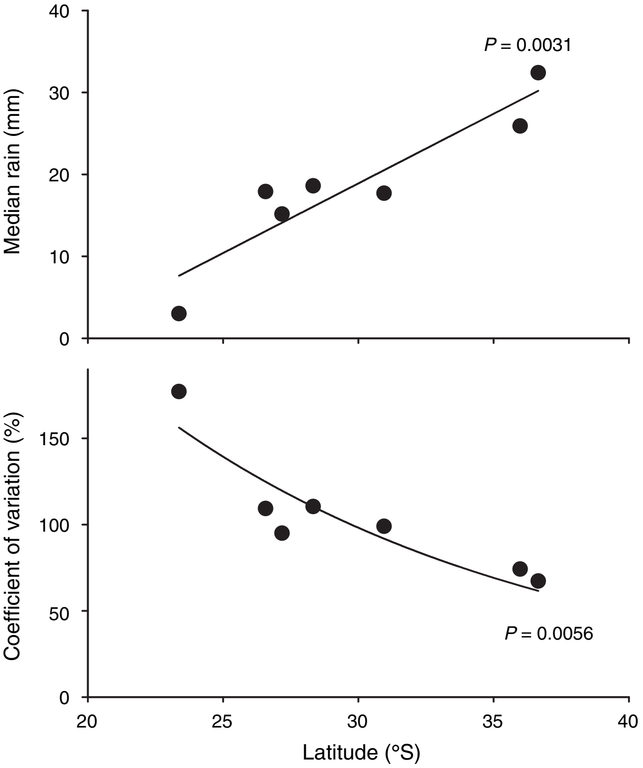

Fig. 3. Latitudinal pattern in median and coefficient of variation of rainfall during the period between Zadok's stages 50 and 70. *P* indicates statistical significance of latitudinal gradient as assessed by regression.

Modelled biomass per unit transpiration increased linearly from 46 kg/ha.mm at Emerald to 73 kg/ha.mm at Horsham (Table 1). This latitudinal gradient was fully accounted for by differences in atmospheric demand, i.e. the differences in modelled $WUE_{B/T}$ disappeared in 'hybrid' climates Emerald–Gunnedah (median $WUE_{B/T} = 64$ kg/ha.mm) and Horsham–Gunnedah (median $WUE_{B/T} = 61$ kg/ha.mm) composed of rainfall from Emerald or Horsham, and evaporative demand from Gunnedah, an intermediate location with median $WUE_{B/T} = 61$ kg/ha.mm. This test allowed us to discard rainfall influences on $WUE_{B/T}$, which could arise from modelling artefacts or correlations between rainfall and vapour pressure deficit in environments with strong rainfall seasonality (Monteith 1993).

Modelled soil evaporation declined linearly from 172 mm at Horsham to 70 mm at Emerald (Table 1, Fig. 7*a*). It was closely related to the size structure of rainfall (Fig. 7*b*) and independent of the amount of rain (Fig. 7*c*).

Modelled harvest index showed no latitudinal pattern for the pooled data (Table 1). There was, however, a season-dependent pattern, i.e. harvest index declined southwards in dry seasons (Fig. 8*a*, *b*). This was explained by the greater frequency of wet profiles at sowing in northern locations (Fig. 6). Furthermore, this pattern was reversed, i.e. higher harvest index at Horsham than at Emerald, when assuming a fixed amount of water at sowing representing both the low plant-available water typical of Horsham, i.e. 18% of maximum, or the high plant-available water typical of Emerald, i.e. 85% of maximum (Fig. 8*b*, *c*).

In contrast to the strong latitudinal trend in biomass per unit transpiration, pooled data of grain yield per unit evapotranspiration showed no latitudinal pattern (Table 1). There was, however, a season-dependent pattern illustrated by the crossing over of the frequency distributions of $WUE_{Y/ET}$ at Emerald and Horsham, i.e. greater efficiency in Emerald in drier seasons, and lower in wetter seasons (Fig. 9*a*). This season-dependent pattern can be explained in terms of the consistent gradients in soil evaporation and biomass per unit transpiration, and the season-dependent gradient in harvest index. The higher yield per unit evapotranspiration in dry seasons in northern locations (Fig. 9*a*, *b*) resulted from lower soil evaporation and higher harvest index, which overrode the intrinsically lower $WUE_{B/T}$ of these environments. In wetter seasons, similar harvest index along the transect and greater biomass per unit transpiration could translate into larger $WUE_{Y/ET}$ in southern locations. This interpretation is reinforced by the crossing over in $WUE_{Y/ET}$ between Emerald and Horsham, which disappeared for the hybrid climates Emerald–Gunnedah and Horsham–Gunnedah (inset Fig. 9).

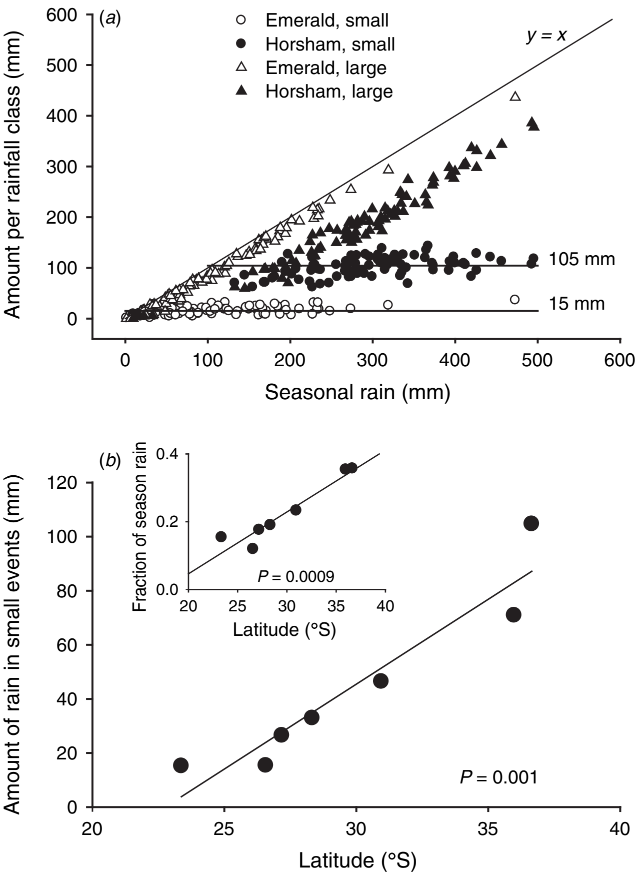

Fig. 4. (*a*) Amount of rainfall received in small (≤ 5 mm) and large (>5 mm) events as a function of seasonal rainfall at Emerald and Horsham, the extremes of the latitudinal transect. Horizontal lines emphasise the median 'background' contribution of small events. (*b*) Latitudinal gradient of median amount of rain in small events. Inset shows the latitudinal gradient of small event contribution to seasonal rainfall. *P* indicates statistical significance of the latitudinal gradient as assessed by regression.

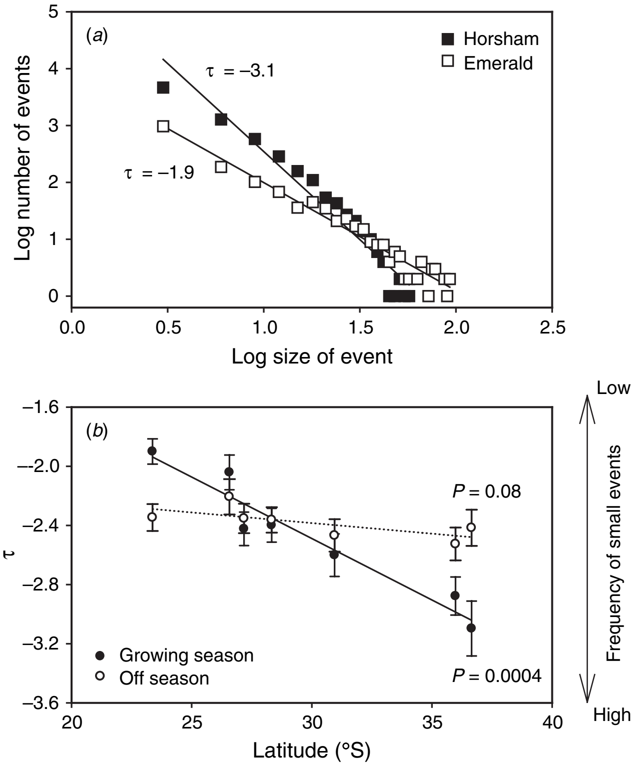

Fig. 5. (*a*) Relationship between log-size (mm) and log-number of rainfall events during the crop-growing season at Emerald and Horsham. (*b*) Latitudinal gradient of τ (dimensionless) during the crop-growing season (sowing to harvest) and during the off-season period (harvest to sowing). Parameter τ is the slope of the linear regression between log-size and log-number of rainfall events; error bars are standard errors and *P* indicates statistical significance of the latitudinal gradient as assessed by regression.

Boundary functions: re-interpreting the x*-intercept in the French-Schultz model*

Quantitatively, the parameters of linear boundary functions fitted in Fig. 10 summarise the interplay between yield per unit transpiration (slope) and soil evaporation (x-intercept) in the latitudinal gradient under study. We assumed: (*a*) a slope of 22 kg/ha.mm for Horsham (Sadras and Angus 2006) and a gradient of 0.2 kg/ha.mm per degree latitude to scale the slope northwards, and (*b*) an x-intercept ranging from 110 mm at Horsham to 27 mm at Emerald (Angus *et al.* 1980; French and Schultz 1984), and a linear latitudinal gradient of 6.3 mm per degree latitude to scale the x-intercept between the extreme locations. The latitudinal gradient assumed for the slope was derived from the modelled data, therefore slopes and data points in Fig. 10 are not independent. The assumptions to calculate the x-intercept were derived from experimental estimates, and this parameter is therefore independent of the modelled data. The x-intercept of the boundary function was a function of the fraction of seasonal rainfall accounting for small events ($P = 0.001$), and parameter τ provided the best quantitative measure of this relationship ($r^2 = 0.93$, $P < 0.0004$; Fig. 11*a*). In contrast, the x-intercept was independent of the amount of seasonal rainfall (Fig. 11*b*).

This is an important finding, which allows for progress in the biophysical interpretation of the x-intercept of the French and Schultz boundary function (French and Schultz 1984). We can write an algorithm for the x-intercept in terms of rainfall segregated in small (≤ 5 mm) and large events:

$$x\text{-intercept} = f_s\text{S} + f_l\text{L} \tag{2}$$

where S and L are the amount of rain in small or large events (mm) and f_s and f_l are the fractions of these rainfall pools lost through soil evaporation. Assuming that most of the rainfall in small events is lost through soil evaporation, i.e. $f_s = 1$, using long-term medians of S and L, and x-intercepts derived as explained above, solving Eqn 2 resulted in f_l from 0.03 at Horsham to 0.26 at Roma. These values are biophysically meaningful: with small events accounting for a 'background' rain of 105 mm at Horsham (Fig. 4*a*), most of the total seasonal rainfall will be lost through soil evaporation in dry seasons, which largely accounts for the x-intercept around 100 mm most widely established for south-eastern Australia. In northern

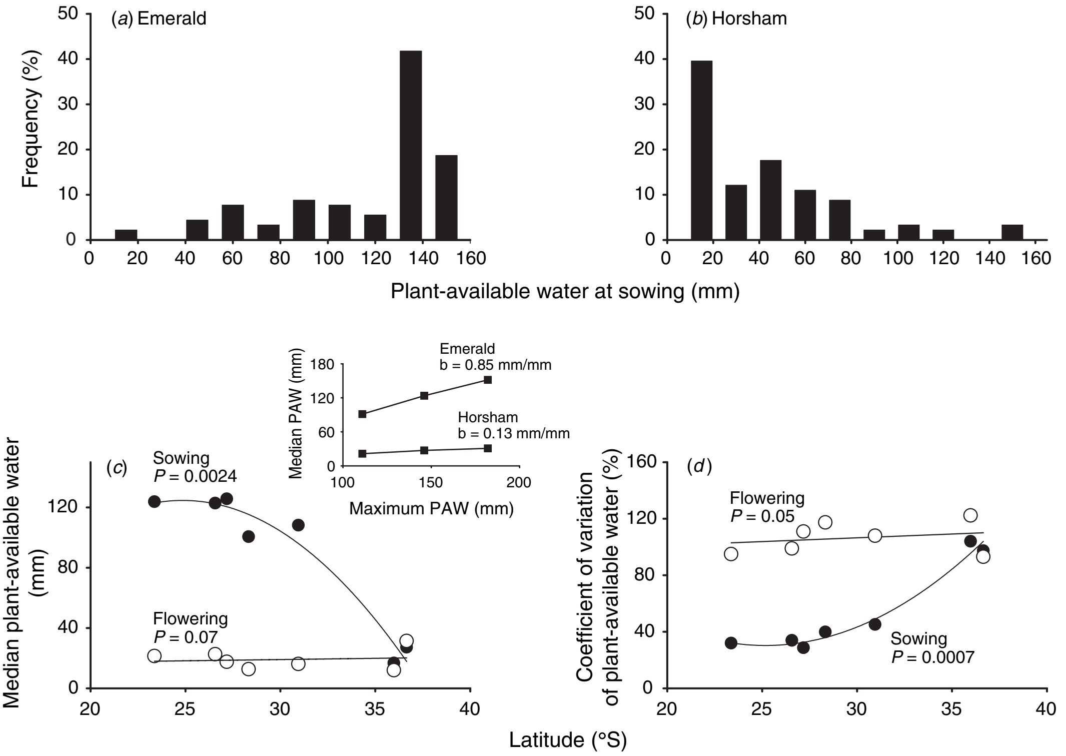

Fig. 6. Frequency distribution of modelled soil plant-available water at sowing for (*a*) Emerald and (*b*) Horsham. Latitudinal pattern in (*c*) median and (*d*) coefficient of variation of modelled soil plant-available water at sowing (closed symbols) and flowering (open symbols). *P* indicates statistical significance of latitudinal gradient as assessed by regression. Simulations in *a–d* assumed a maximum soil plant-available water = 146 mm. Inset shows the variation in median plant-available water at sowing as a function of maximum soil plant-available water for Emerald and Horsham.

Table 1. Latitudinal patterns of biomass per unit transpiration (WUE $_{B/T}$), yield per unit evapotranspiration (WUE $_{Y/ET}$), harvest index, and soil evaporation

P indicates statistical significance of latitudinal gradient as assessed by regression. Results from simulations between 1913 and 2003

Location	Lat. (°S)	WUE $_{B/T}$		WUE $_{Y/ET}$		Harvest index		Soil evaporation	
		Median (kg/ha.mm)	CV (%)	Median (kg/ha.mm)	CV (%)	Median	CV (%)	Median (mm)	CV (%)
Emerald	23.4	46	8	8.8	32	0.332	24	70	33
Roma	26.6	53	8	9.7	35	0.298	25	90	26
Dalby	27.2	56	7	8.7	39	0.263	26	108	21
Goondiwindi	28.3	58	7	8.0	39	0.247	27	110	23
Gunnedah	31.0	61	7	8.7	41	0.268	27	128	23
Birchip	36.0	76	10	7.8	84	0.283	31	158	41
Horsham	36.7	73	8	11.1	52	0.344	26	172	22
P		<0.0001	>0.05	>0.05	>0.05	>0.05	>0.05	0.0001	>0.05

locations, larger events contribute significantly, up to 25%, to the *x*-intercept of the boundary function.

The association between the slope of the boundary functions and climate was explored using the medians of individual variables, i.e. daily average temperature (T), day-time vapour pressure deficit (VPD), photosynthetically active radiation (PAR), and fraction of diffuse radiation (FDR), and 2 derived indices, a photothermal quotient (Pq = PAR/T) and a normalised photothermal quotient (NPq = Pq·FDR/VPD). All variables were calculated for the period 20 days before to 14 days after anthesis, as explained by Rodriguez and Sadras (2007). The slope of the boundary functions in the latitudinal gradient was positively associated with the fraction of diffuse radiation ($r^2 = 0.89$, $P = 0.001$), negatively associated with vapour pressure deficit ($r^2 = 0.88$, $P = 0.003$) and temperature ($r^2 = 0.57$, $P = 0.05$), and unrelated to PAR ($P = 0.19$). The association with Pq was significant ($r^2 = 0.65$, $P = 0.03$) and NPq was the variable that best accounted for the latitudinal gradient in the slope of the boundary function ($r^2 = 0.94$, $P = 0.0003$; Fig. 11*b*).

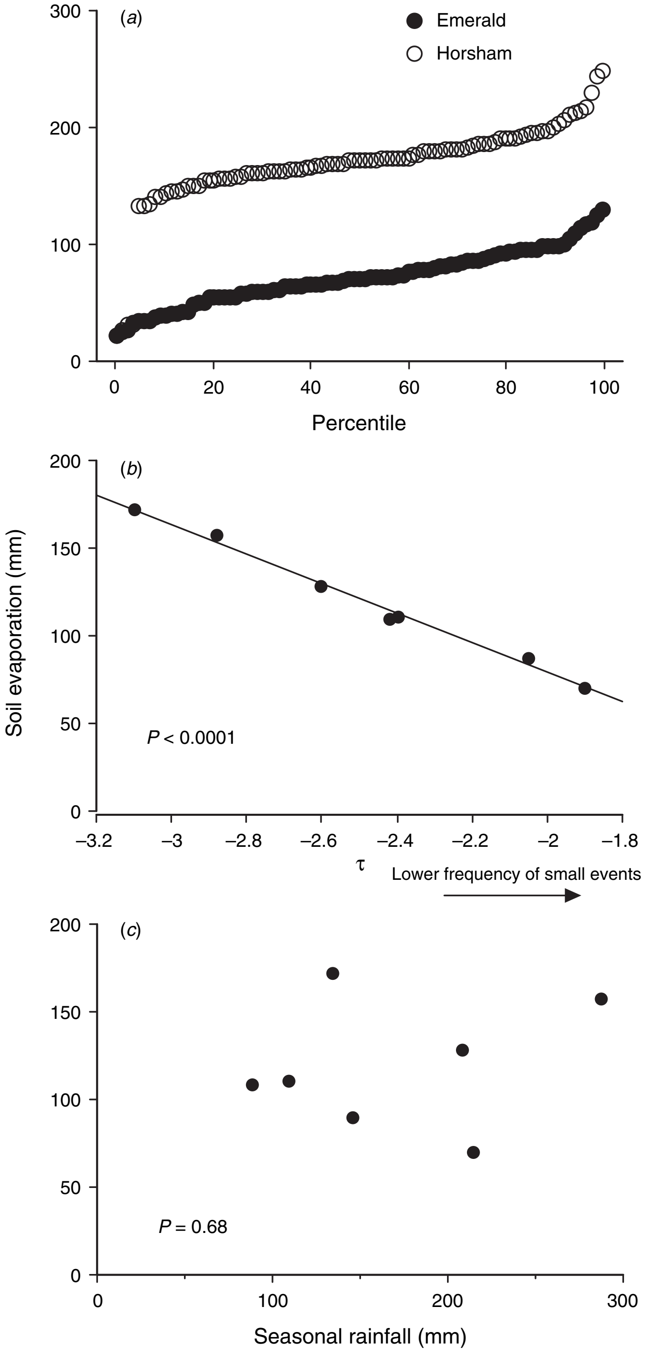

Fig. 7. (*a*) Frequency distribution of modelled soil evaporation at Emerald and Horsham, and relationships between median soil evaporation and (*b*) size-structure of seasonal rainfall characterised with parameter τ (dimensionless), and (*c*) median seasonal rainfall in the transect between Horsham and Emerald.

Discussion

Limitations to the study: modelling and climatic artefacts

In this paper we have characterised rainfall patterns in the transect between Horsham and Emerald, modelled the components of crop water-use efficiency, and explored the links between modelled water-use efficiency and climate factors with emphasis on rainfall properties. Except for a limited sensitivity analysis, we ignored the interactions between soils and rainfall (Kemper 1993; Reynolds *et al*. 2004; Lithourgidis *et al*. 2006); accounting for the distinctive soil features in the environments under study is therefore the next step towards more realistic estimates of water-use efficiency.

Rainfall patterns are straightforward, and we showed several indices of seasonality and size structure that allowed for the quantitative characterisation of latitudinal gradients. The relationships between modelled water-use efficiency and its components and climate variables could involve artefacts from 2 sources. First, model outputs are a function of climatic variables by definition, e.g. transpiration efficiency is calculated as a function of vapour pressure deficit. Second, correlations between climatic variables could lead to misleading explanations, as illustrated in the early and revised interpretations of climatic influences on rice yield (Peng *et al*. 2004; Sheehy *et al*. 2006*a*, 2006*b*). The risk of artefacts in our paper is particularly high because we focussed on a transect where all major climatic variables have strong latitudinal gradients. The consequences of the correlations between climatic variables, and attempts to disentangle them, have been the subject of our previous paper (Rodriguez and Sadras 2007). For instance, the statistically strong correlation between the slope of the boundary function, i.e. maximum $\text{WUE}_{\text{Y/T}}$, and the fraction of diffuse radiation found in this paper is a likely artefact of the correlation between diffuse radiation and vapour pressure deficit (Rodriguez and Sadras 2007), and correlations such as that between the slope of boundary functions and the normalised photothermal coefficient (Fig. 11*b*) should be regarded as descriptive rather than explanatory. All these limitations impinge on the following discussion. It should be emphasised, however, that the questions we asked about the influence of rainfall on water-use efficiency are very unlikely to be answered conclusively with experimental research alone. Our modelling results could be used to: (*a*) improve current benchmarks for yield gap analysis (Beeston *et al*. 2005), (*b*) formulate specific hypotheses and better designed field experiments on the effects of rainfall patterns on water-use efficiency, (*c*) interpret experiments across regions and seasons. Importantly, in the interpretation of the relationships in this study, we have privileged biophysical principles over statistical correlations.

Latitudinal patterns in water-limited water-use efficiency

Potential yield is the 'maximum yield that can be reached by a crop in given environments, as determined, for example, by simulation models with plausible physiological and agronomic assumptions' (Evans and Fischer 1999). By extension, potential water-use efficiency is the relationship between potential yield (grain or biomass) and water use. In a previous study, we investigated the environmental drivers of potential water-use efficiency in a transect from Emerald to Horsham (Rodriguez and Sadras 2007). We found that median $\text{WUE}_{\text{B/T}}$ for the period from 20 days before to 14 days after anthesis, modelled under the assumptions of no water limitations and a constant leaf area index of 4, increased linearly between Emerald and Horsham (Rodriguez and Sadras 2007).

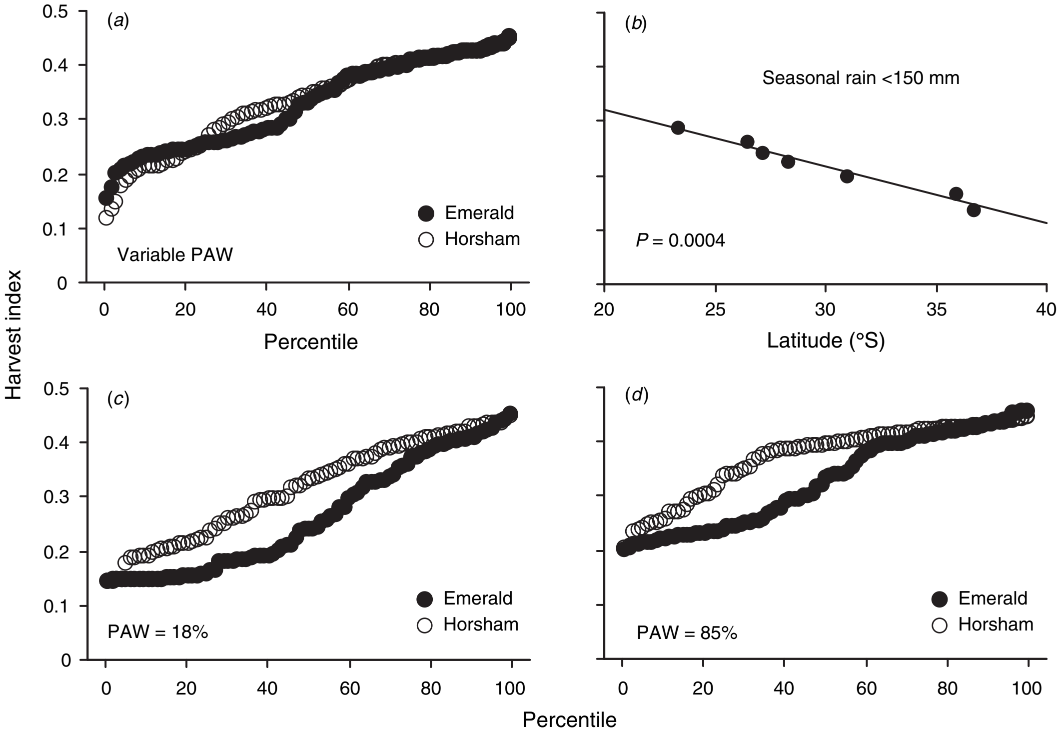

Fig. 8. (*a*) Frequency distribution of modelled harvest index at Emerald and Horsham; plant-available water at sowing is variable, resulting from the water budget from harvest to sowing of the next crop. (*b*) Latitudinal gradient of mean harvest index for seasons with rain below 150 mm (*v*. 10th percentile at Horsham = 175 mm). *P* indicates statistical significance of latitudinal gradient as assessed by regression. Frequency distribution of modelled harvest index at Emerald and Horsham, with plant-available water at sowing fixed at (*c*) 18 or (*d*) 85% of maximum.

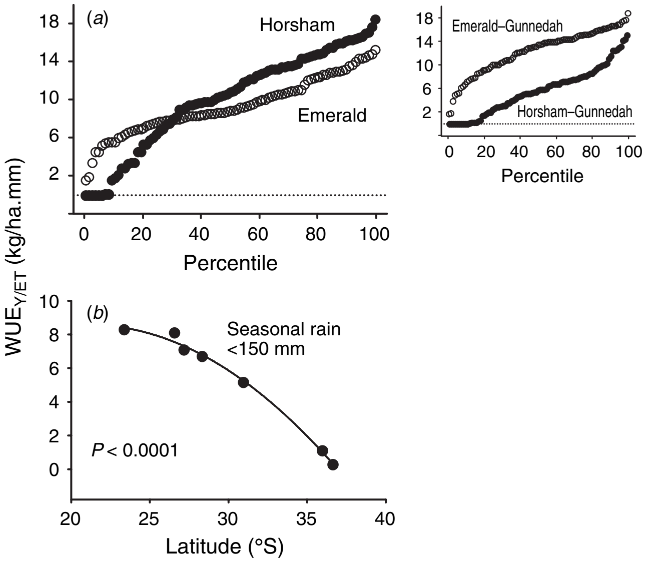

Fig. 9. Season-dependent latitudinal pattern of grain yield per unit evapotranspiration ($\mathrm{WUE}_{Y/ET}$). (*a*) Frequency distribution of modelled $\mathrm{WUE}_{Y/ET}$ at Emerald and Horsham. Inset is the frequency distribution of grain yield per unit evapotranspiration modelled for hybrid climates Emerald–Gunnedah and Horsham–Gunnedah, with rainfall from Emerald and Horsham, and atmospheric demand from Gunnedah. (*b*) Latitudinal gradient of mean yield per unit evapotranspiration for seasons with rain below 150 mm. *P* indicates statistical significance of latitudinal gradient as assessed by regression.

In this paper, our working hypothesis is that latitudinal gradients in yield per unit evapotranspiration of water-limited crops in eastern Australia are the complex result of southward increasing $\mathrm{WUE}_{B/T}$ and soil evaporation, and season-dependent trends in harvest index. Here we found a linear latitudinal gradient in modelled $\mathrm{WUE}_{B/T}$ (Table 1), and a significant correlation between this latitudinal gradient and that reported by Rodriguez and Sadras (2007) ($r^2 = 0.67$; $P = 0.02$). This is remarkable given the use of largely independent models with contrasting approaches to simulate gas exchange (APSIM *v*. modified Tanner & Sinclair), the difference in time windows (whole season *v*. 20 days before to 14 days after anthesis), climate records (1913–2003 *v*. 1957–2003), and major assumptions (actual rain *v*. non-limiting water). Based on known physiological principles, the gradient in $\mathrm{WUE}_{B/T}$ was interpreted in terms of latitudinal gradients in temperature, vapour pressure deficit, radiation and fraction of diffuse radiation affecting water, and CO_2 exchange in crop canopies (Rodriguez and Sadras 2007). Furthermore, simulations with hybrid climates reinforced the importance of atmospheric demand as a driver of both $\mathrm{WUE}_{B/T}$ and $\mathrm{WUE}_{Y/ET}$.

Modelled soil evaporation was consistent with the proposal of a rainfall-dominated process. In previous modelling studies where sources of variation included seasons and locations in south-eastern Australia and Argentina, soil evaporation was primarily associated with amount of rainfall, whereas the structure of size events played a statistically significant but comparatively secondary role (Sadras 2003; Monzon *et al.*

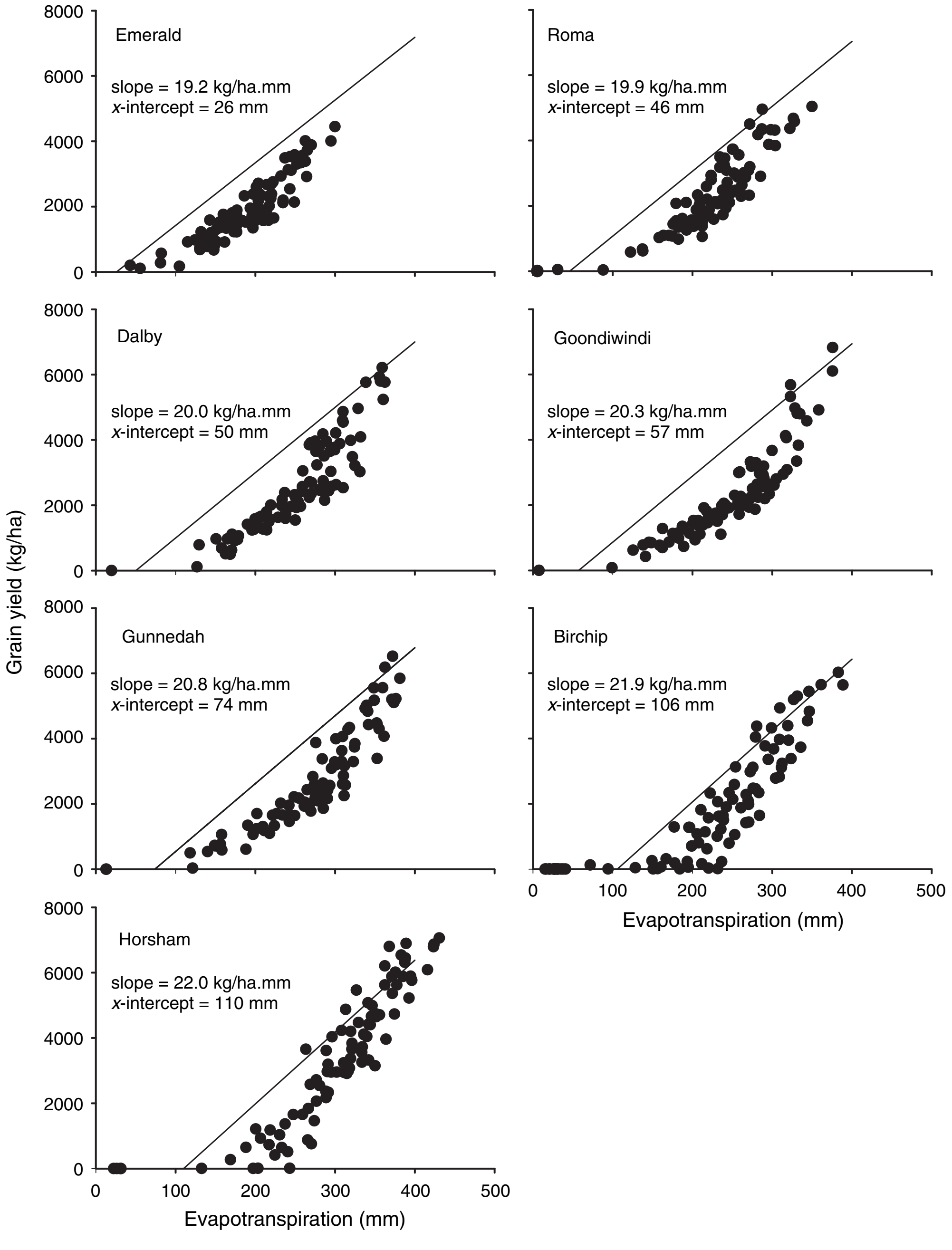

Fig. 10. Scattergram and boundary functions for the modelled relationship between grain yield and evapotranspiration for 7 locations in a north–south transect in eastern Australia.

2006). In contrast, in the latitudinal transect of this study, soil evaporation was largely independent of amount, but tightly related to the size structure of rainfall.

Modelled harvest index ranged from 0.25 to 0.34 across locations, which is realistic in comparison with typical values for cereals under terminal drought in Australia (French and Schultz 1984; Gomez-Macpherson and Richards 1995; Mitchell 1996; Regan *et al.* 1997; O'Connell *et al.* 2002). It had a season-dependent latitudinal pattern that can be interpreted in terms of latitudinal gradients in stored soil water at sowing and in-season rainfall.

On the basis of the modelled patterns in biomass per unit transpiration, soil evaporation, and harvest index, we suggest that yield per unit transpiration conforms to a season-dependent latitudinal pattern. At the drier end of seasonal conditions, high soil evaporation driven by a very strong dominance of small events, and low harvest index, may override the putative advantage of low atmospheric demand and associated higher $\mathrm{WUE_{B/T}}$; hence the lower $\mathrm{WUE_{Y/ET}}$ in southern locations. In wetter seasons, when large events contribute a significant proportion of seasonal rain, higher $\mathrm{WUE_{B/T}}$ in southern locations may translate into high $\mathrm{WUE_{Y/ET}}$.

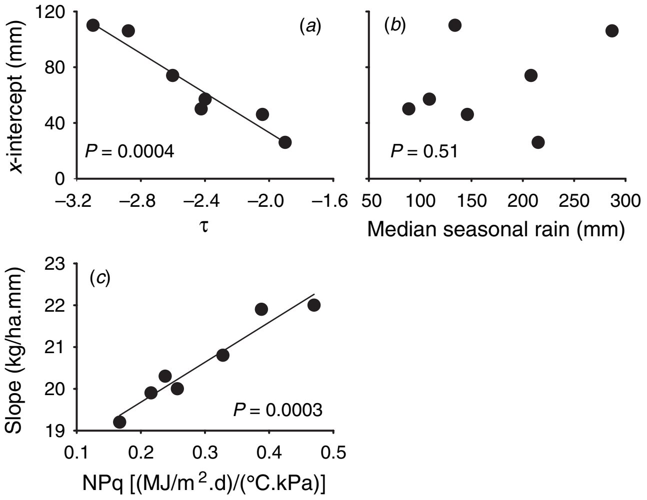

Fig. 11. Climate drivers of the parameters of the French-Schultz boundary function. The *x*-intercept is related to (*a*) rainfall size structure parameter rather than (*b*) amount of rain. τ is the slope of the linear regression between log-size and log-number of rainfall events during the season. (*c*) The slope of the boundary function is a function of a normalised photothermal quotient, NPq = (FDR × PAR)/(T × VPD), where T is daily mean temperature, VPD is day-time vapour pressure deficit, PAR is photosynthetically active radiation, and FDR is the fraction of diffuse radiation. The coefficient was calculated for the period 20 days before to 14 days after anthesis.

Benchmarking water-use efficiency with boundary functions

Linear boundary functions to benchmark water-use efficiency are commonly applied in south-eastern Australia, but their use is less common in northern regions where dynamic simulation models have been used more widely.

In the linear boundary function of French and Schultz (1984), the slope represents the maximum yield per unit transpiration and recent work has shown that this parameter is robust and accounts for the long-term improvement in yield potential through breeding (Sadras and Angus 2006). The influence of atmospheric demand on yield per unit transpiration is also well established (Sadras and Angus 2006; Rodriguez and Sadras 2007), and has been captured in the slopes of the boundary functions in our latitudinal gradient, and in its correlation with a normalised photothermal coefficient. In eastern Australia, the range for the *x*-intercept is 27–170 mm, and has been primarily interpreted in terms of seasonal rainfall (French and Schultz 1984). In this study we propose that size-structure of rainfall, rather than amount, drives this parameter. This hypothesis has been formalised in Eqn 2. In southern environments, small events contribute most of the seasonal rainfall in dry seasons, hence the match between the 'background' rainfall in small events and *x*-intercepts, i.e. $f_s \approx 1$, $L \approx 0$, and *x*-intercept ≈S in Eqn 2. The *x*-intercept of 110 mm derived by French and Schultz (1984) compares with rainfall from small events averaging 86 mm (s.d. = 20.4) at Gulnare, and 104 mm (s.d. = 17.4) at Turretfield. Likewise, the *x*-intercept of 60 mm determined for the Murray Mallee (Sadras and Roget 2004) compares with small events contributing an average 65 mm (s.d. = 15.7) at Walpeup and 57 mm (s.d. = 14.1) at Mildura. In northern locations, it is also reasonable to assume that most of the rain in small events could be lost through soil evaporation ($f_s \approx 1$) or through evaporation from canopy interception, but large events are relatively common, and also contribute to soil evaporation ($L > 0, f_l > 0$). The notion of a 'background' amount of rainfall in small events is consistent with the finding of Golluscio *et al.* (1998) in Patagonia, which demonstrated the high variability in the number of extreme events largely accounting for variation in annual rainfall, against an almost constant contribution of small events to total rain. This pattern is a trademark of arid and semi-arid environments worldwide (Schwinning and Sala 2004). In this paper, we have demonstrated this pattern for agricultural environments of eastern Australia (Figs 4, 5) and highlighted its relevance in terms of water-use efficiency, primarily through the implications for soil evaporation (Figs 7, 10, 11).

The assumption of $f_s \approx 1$ all along the transect is in agreement with the early ideas of Noy-Meir (1973) on the irrelevance of small events for plant growth in dry environments. More broadly, the correlation between the magnitude of pulse event, the magnitude and extent of the biological process it triggers, and the time scale over which these responses unfold suggests a nested hierarchy of responses to resource pulses in low-rainfall ecosystems (Schwinning and Sala 2004). For instance, a brief, shallow pulse could affect top-soil microorganisms with fast response times, whereas the physiology, growth, and reproduction of larger, slower growing organisms such as higher plants would require longer pulses and more water (Schwinning and Sala 2004). Indirect effects of small events, e.g. through nitrogen mineralisation or germination pulses of weeds, could be relevant in dryland farming systems.

Implications for management, breeding, and further research

This section suggests directions for further research and hypotheses derived from our modelling exercise, rather than conclusions drawn from it.

Indirect effects of rainfall size-structure, as mediated by nitrogen mineralisation (Cui and Caldwell 1997; Sadras and Baldock 2003), need further research. Modelling studies in south-eastern Australia revealed 2 seasonal peaks of nitrogen mineralisation, in autumn and spring, which accounted for the seasonal patterns of rainfall and temperature (Sadras and Baldock 2003). After accounting for total amount of rainfall, high frequency of small events seemed to be important for the maintenance of topsoil moisture and mineralisation. In the northern locations in this study, rainfall is concentrated in summer and dominated by large events, thus contrasting patterns of nitrogen mineralisation and leaching can be expected. Modelling and experimental studies on the dynamics of soil and crop nitrogen along the transect in this study are likely to yield valuable information for nitrogen management.

Research along this transect could also shed light on the relative value of tillage and stubble management practices in terms of water storage during fallow (Monzon *et al.* 2006), and the fate of water in the ecosystem, including the role of deep-rooted perennials to reduce deep drainage and recharge of watertables. Keating *et al.* (2002) modelled the fate of water in dryland farming systems in a north–south transect in eastern Australia. They demonstrated a primary effect of annual rainfall, and a secondary effect of intra-seasonal rainfall distribution, but did not consider size of events, which we showed to play a significant role in driving water through the alternative pathways of the water budget. Because the frequency of small events increases southwards, in parallel with the fraction of winter rainfall, correlations between response variables (e.g. water excess) and percent winter rainfall (Keating *et al*. 2002) may be partially reflecting the effect of the size-structure of rain.

Wheat crops in the environments investigated, particularly those at both ends of the transect, are likely to grow under 'terminal drought' but the contrasting rainfall features outlined in this paper need consideration in assessing the putative value of adaptive traits. For crops with healthy roots relying primarily on stored soil water in eastern Australia, yield could be improved by reducing the rate of crop water use early in the season to save water for critical reproductive stages (Richards and Passioura 1981*a*, 1981*b*, 1989). Cooper *et al*. (1987) in West Asia and Northern Africa promoted management practices favouring rapid canopy growth to reduce soil evaporation and increase transpiration. Currently, the view of breeders in Australia has converged with that of Cooper, favouring plant traits associated with rapid water use to prevent soil evaporation in environments with dominant winter rainfall (Richards *et al*. 1993; Rebetzke and Richards 1999; Botwright *et al*. 2002; Richards and Lukacs 2002). This is associated with the realisation that, in the prevalent climate of south-eastern Australia, saving water through reduced water uptake and slow canopy growth produces little or no benefit, as most of the water would be lost trough soil evaporation. Our quantitative analysis reinforces this notion, highlighting the importance of rainfall size structure as a key driver of soil evaporation and suggesting that the value of plant characteristics contributing to early vigour and reduction in soil evaporation would decrease northwards. Furthermore, the early notion that saving water for late growing stages may have some merit in northern locations, where seasonal rainfall is infrequent, and the fraction of soil evaporation relative to total water use is small compared with southern locations (Mitchell *et al*. 2006). We suggest that traits favouring slow canopy cover in northern locations and traits contributing to fast canopy cover in southern locations could be adopted as a primary approach to account for the strong constraints imposed by rainfall patterns, whereas nitrogen management could be used to fine-tune the actual rate of development and final size of crop canopies to account for season-to-season variation and specific growing conditions (e.g. soil types).

A limited sensitivity analysis indicated that soils with greater plant-available water may be more relevant in northern locations, where the likelihood of storing substantial amounts of water between crops is much larger than in southern locations. It could also be speculated that restrictions to root depth, e.g. hardpans, may be more relevant, and the benefits from alleviation much greater, in northern than in southern locations, again in response to the likelihood of replenishing the soil profile. Likewise, genetically determined deep root systems can be of higher value in northern locations. In contrast, other root traits, i.e. rapid generation of superficial roots in response to small events, could be of greater importance in southern locations. Schwinning and Ehleringer (2001) addressed this issue in greater detail. They used a genetic algorithm to identify character suits that maximise carbon fixation for plants grown under 2 water regimes. Under a regime of pulse-dominated water supply from a superficial soil layer, similar to that in the southern locations of our study, favoured traits included small root: shoot ratio, predominantly shallow root system, and high stomatal sensitivity to plant water status. The opposite traits were favoured under continuos but insufficient supply of water from deep soil layers, a regime similar to that in the northern locations in this paper. The adaptive value of osmotic adjustment (Morgan and Condon 1986; Morgan 1995, 2000) may also be different along the transect in relation to the development of water stress in crops growing primarily with stored soil water, in contrast to crops receiving small water pulses through the season.

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