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Weather indices during reproductive phase explain wheat yield variability

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Abstract

When water and nutrients are not limiting, and pests and disease are effectively controlled, crop growth and yield is determined by weather conditions such as temperature and solar radiation. To determine the relationship between weather indices and crop yield, multiple wheat varieties were sown at two sowing times, for five sowing seasons and at two locations. The following weather indices around the 50% anthesis stage were recorded and analysed: mean temperature (T_{mean}), maximum temperature (T_{max}), number of days with temperature >30°C (T30), vapour pressure deficit (VPD), photosynthetically active radiation, photothermal quotient (PQ) and photothermal quotient corrected for vapour pressure deficit (PQ_{vpd}). Overall, for every 1°C rise in temperature, crop yield decreased by 370 kg/ha. For every 1°C rise in temperature, normal sowing window yield decreased by 360 kg/ha while late-sown wheat yield decreased by 640 kg/ha. Correlation analysis was conducted between the weather indices and grain number, grain yield and grain protein. There was a significant positive correlation between PQ and PQ_{vpd} and grain number and grain yield. There was a significant negative correlation between T_{mean}, T_{max}, T30 and VPD and grain number and grain yield. Grain protein content showed a positive correlation with maximum air temperature and a negative correlation with the weather indices PQ and PQ_{vpd}. PQ and PQ_{vpd} can be used to predict grain number and grain yield potential. This study showed that grain number and grain yield predicted using PQ and PQ_{vpd} are more reliable than using temperature and radiation individually.

Introduction

Globally, wheat (*Triticum aestivum* L.) is the third most widely grown crop, behind only maize and rice (Shiferaw *et al.*, 2013). Australia is the fifth largest wheat exporting country (Qureshi *et al.*, 2013). In Australia, wheat is grown mainly in what is commonly called the 'wheat belt', a large area of land spanning from South Australia to Central Queensland on the eastern side of the continent plus large areas in the southern and eastern parts of Western Australia. Where nitrogen fertilizer and water are not limiting, and weeds, pests and diseases are controlled, crop yield is limited mainly by incoming solar radiation and the mean air temperature (Kumar *et al.*, 2016). As a result, agronomic management options are often tailored to maximize adaptation of the crop to the limitations posed by temperature and solar radiation (Sadras *et al.*, 2015). With the rise in global temperatures due to climate change, heat stress is becoming an important limiting factor to crop productivity and food security (Asseng *et al.*, 2011). Although significant research has been done on the impact of drought on crop growth and yield, the impact of heat stress due to rising temperatures has received attention only recently (Cohen *et al.*, 2020).

Global warming has increased the urgency to quantify and manage crop responses to elevated temperatures (Zhao *et al.*, 2017). Average atmospheric temperature is expected to increase by 1.8–5.8°C by the end of this century (Pachauri *et al.*, 2014; IPCC 2022). In Australia, air temperature has increased by about 1.4°C since the turn of the last century (Ababaei and Chenu, 2020; State of Climate 2020, 2023). Depending on the greenhouse gas emission scenario considered, in Australia, the mean air temperature is predicted to increase by 0.6–1.5°C by 2030 and 2.2–2.5°C by 2070 (Anwar *et al.*, 2015). With the increase in temperature due to climate change, the occurrence of crop heat stress is expected to become more frequent (Cohen *et al.*, 2020). Global temperature rise has significantly affected wheat yield already (Poudel and Poudel, 2020). In general, heat stress in wheat occurs between the temperature range of 32–37°C while temperature above 32°C during the reproductive phase can have a significant negative effect on wheat production (Wahid *et al.*, 2007; Narayanan *et al.*, 2015). Average temperatures higher than 35°C have been found to shorten the grain filling period and decrease wheat yield by 6–51% (Bergkamp *et al.*, 2018). Lobell and Field (2007)

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reported 0.6–8.9% reduction in wheat yield per 1°C rise in air temperature. Globally, wheat production is expected to decrease by up to 6% for each 1°C rise in temperature above the optimum growing season temperature range of 20–25°C (Asseng *et al.*, 2015; Ahlawat *et al.*, 2021).

High temperature affects photosynthetic efficiency, crop phenology, pollen viability and crop water use through vapour pressure deficit (VPD) (Wahid *et al.*, 2007). The sensitivity of different phenological stages to heat stress differs with heat stress during the reproductive phase (anthesis and grain filling) being the most harmful (Wollenweber *et al.*, 2003). In most wheat-growing regions, including the 'wheat-belt' of Australia, temperature ordinarily increases during the growing period as the season progresses. In Australia, such elevated temperatures coincide with the reproductive phase of wheat in September and October (Spring in the southern hemisphere) (Telfer *et al.*, 2013). As a result, any heat stress that occurs during the sensitive reproductive stage can lead to significant yield loss (Asseng *et al.*, 2011).

Solar radiation is another important environmental factor that alters leaf architecture, light partitioning, photosynthesis and biomass formation (Sandana and Pinochet, 2011). As a result, crop growth and yield are dependent on solar radiation – the higher the availability of solar radiation, the higher the crop yield and biomass. The combined effect of radiation and temperature can be integrated into a photothermal quotient (PQ) index which improves yield and grain weight prediction (Nalley *et al.*, 2009).

To determine suitable planting windows that minimize the impact of environmental stress, it is important to quantify the relationship between weather indices and crop yield components. Although the effect of environmental conditions on wheat yield has been studied extensively under controlled environment conditions (Prasad *et al.*, 2008; Zhao *et al.*, 2022), a practical way to expose the crop to variable climatic parameters is by sowing different varieties of a crop at different sowing times and at different locations in the field (Martre *et al.*, 2018). The objective of this study was to determine the relationship between weather indices during the critical reproductive stage and grain number, grain yield and protein content of wheat. In addition, the performance of calculated weather indices (PQ and photothermal quotient corrected for vapour pressure deficit [PQ_{vpd}]) for the prediction of grain yield and quality was assessed.

Materials and methods

Study sites and weather data

Crop data for assessing the relationship between weather indices and crop yield were obtained from field trials conducted at two irrigated sites at Leeton Field Station and Wagga Wagga Agricultural Institute (Table 1). The soil at Leeton was a clay Vertosol, while at Wagga Wagga, the soil was sandy clay loam Red Kandosol. Daily weather data of global radiation, minimum and maximum temperature and vapour pressure were sourced from the nearest Bureau of Meteorology weather stations at Yanco Agricultural Institute (−34.62° south, 146.43° east) and Wagga Wagga Agricultural Institute (−35.16° south, 147.46° east) (http://www.bom.gov.au/).

Agronomic practices and crop yield data

The experiments were conducted on a large number of commercial wheat varieties and breeding lines. The details of the field experimental setup (plot size, fertilizer application, irrigation, weed and pest control) were given in Sissons *et al.* (2017). In summary, the data were derived from 515 wheat germplasm materials used to characterize heat tolerance in field experiments (Collins *et al.*, 2017). These were made up of bread wheat and durum lines and consisted of 33 advanced breeding lines obtained from the International Maize and Wheat Improvement Center (CIMMYT), Mexico, 110 released cultivars, 131 landrace materials sourced from heat-prone regions, 61 near-isogenic lines differing at a major gene for heat tolerance (Erena *et al.*, 2021) and 180 recombinant inbred lines used for quantitative trait locus mapping. Altogether, there were 331 bread wheat and 184 durum lines in the germplasm. The objective was to analyse the impact of heat stress on wheat sown at different times as an indicator of the impact of climate change on wheat production. Individual genotypes were not analysed separately.

Crops were sown at two sowing dates each year (a 'normal' sowing date in June and a 'late' sowing date in August). In Leeton, the crop was sown in 2011 (normal sowing on 1 June and late sowing on 1 August) and in 2015 (normal sowing on 2 June and late sowing on 3 August). In Wagga Wagga, wheat was sown in 2012 (normal sowing on 8 June and late sowing on 8 August), 2018 (normal sowing on 1 June and late sowing on 2 August) and 2019 (normal sowing on 1 June and late sowing on 6 August). The late-sown crop in each case is expected to experience more heat stress during the reproductive (anthesis and grain filling) stage. In each trial, the dates of sowing, flowering and maturity were recorded, along with grain yield, and 1000 grain weight.

Weather indices

Temperature and photosynthetically active radiation

Daily maximum and minimum temperatures (°C) and global radiation ($MJ/m^2/d$) for each site were obtained from the closest Australian Bureau of Meteorology weather stations (http://www.bom.gov.au/). Maximum temperature data were used to calculate

Table 1. Characterization of the soils and long-term (1950–2022) average climate of the two sites

			Soil profile		Top soil layer						
Site	Latitude Longitude	Soil type	Soil depth (m)	PAWC (mm)	BD (g/cm^3)	pH	OC (%)	Rain (mm)	GS rain (mm)	GS solar (MJ/m^2)	GS temp (°C)
Leeton	34.73 S 146.55 E	Wunnamu-rra Clay	1.80	293	1.30	7.2	1.8	478	293	13.2	12.4
Wagga Wagga	35.05 S 147.35 E	Kandosol	1.25	128	1.45	6.4	1.7	560	339	12.8	11.6

PAWC, plant available water capacity; BD, bulk density; OC, soil organic carbon; GS, growing season (April to October); Temp, mean temperature.

the number of hot days ($T_{\max} > 30°C$). Photosynthetically active radiation (PAR) was obtained by multiplying global solar radiation by 0.47 (Pinker and Laszlo, 1992).

Vapour pressure deficit

The VPD (kPa) was calculated as the difference between the actual air vapour pressure, VPact and the saturated vapour pressure, VPsat (Equation (1)). VPsat was estimated for a temperature T_i, either maximum ($T_{\max}$) or minimum ($T_{\min}$) (Dreccer *et al.*, 2018). Finally, VPsat was calculated as the weighted average of vapour pressure at $T_{\max}$ and $T_{\min}$ (Jeffrey *et al.*, 2001) (Equation (2)).

$$\mathrm{VPD} = 0.75\left[0.6107 \times e^{\left(\frac{17.4 \times T_{\max}}{239 + T_{\max}}\right)} - 0.6107 \times e^{\left(\frac{17.4 \times T_{\min}}{239 + T_{\min}}\right)}\right] \qquad (1)$$

PQ and PQ_{vpd}

Heat stress during the reproductive stage (anthesis and grain filling) has a significant effect on grain yield and quality. Some previous studies have used either 30 or 45 days before to 0 days after 50% anthesis, or 20 days before to 10 days after anthesis as a critical period for heat stress analysis. In northwest Mexico, Fischer (1985) reported that there is a strong relationship between the PQ value calculated from 30 days before to 0 days after 50% anthesis. However, further studies showed that the critical period spans only about 20 days before to 10 days after anthesis (Ortiz-Monasterio *et al.*, 1994; Abbate *et al.*, 1995). In this work, both indices were calculated as the average for the period 20 days before to 10 days after anthesis.

PQ was calculated as the ratio between PAR and mean temperature for the critical period with a base temperature assumed as 0°C (Fischer, 1985; Soltani and Sinclair, 2011).

$$\mathrm{PQ} = \frac{\sum_{\mathrm{start}}^{\mathrm{end}} \mathrm{PAR}}{\bar{T}_{\mathrm{start-end}}} \qquad (2)$$

where PQ is the cumulative PQ over a given period, the critical period around anthesis ($\mathrm{MJ/m^2/°C}$), PAR is the daily photosynthetically active radiation ($\mathrm{MJ/m^2/d}$) and $\bar{T}_{\mathrm{start-end}}$ is the mean temperature over the given period (°C).

Mean daily PQ is then calculated by dividing the above cumulative PQ by the number of days (30 days, in this case).

A $\mathrm{PQ}_{\mathrm{vpd}}$ ($\mathrm{MJ/m^2/°C/kPa}$) was calculated as the ratio between PQ and mean VPD during the critical period (Rodriguez and Sadras, 2007).

$$\mathrm{PQ}_{\mathrm{vpd}} = \frac{\sum_{\mathrm{start}}^{\mathrm{end}} \mathrm{PAR}}{\bar{T}_{\mathrm{start-end}} \times \overline{\mathrm{VPD}}_{\mathrm{start-end}}} \qquad (3)$$

where $\overline{\mathrm{VPD}}_{\mathrm{start-end}}$ is the mean vapour pressure deficit over the critical period around anthesis (kPa). Mean daily $\mathrm{PQ}_{\mathrm{vpd}}$ is then calculated by dividing the above cumulative $\mathrm{PQ}_{\mathrm{vpd}}$ by the number of days (30 days, in this case).

Data analysis

The weather and crop data were analysed using R (R Core Team, 2022). Linear regression analysis was performed, and Pearson's correlation coefficient was used to quantify the effect of temperature, PAR, VPD, PQ and $\mathrm{PQ}_{\mathrm{vpd}}$ on yield and yield components. The statistical significance of the correlations was determined using *P*-levels. For this purpose, daily indices during the critical stage were averaged for all the cultivars and years of experimentation. Data manipulation and presentation utilized various 'tidyverse' R packages (Wickham *et al.*, 2019).

Results

Summary of weather indices and crop yield and quality

Overall mean of weather indices and crop yield components is given in Table 2. The number of hot days (>30°C) was greater during the second sowing (as expected). Temperature and VPD were higher for the late-sown crop. However, PQ and $\mathrm{PQ}_{\mathrm{vpd}}$ decreased during the second sowing. Compared to wheat sown during the normal sowing period, late-sown wheat had 44 and 40% lower yields, respectively, for Leeton and Wagga Wagga. Grain size was also smaller for the late-sown wheat while grain protein increased during the second sowing. Maximum values of grain numbers were six times greater than the minimum values, whereas maximum grain weights were only twice as large as the minimum values. This indicates that grain number contributed the most to overall grain yield variation.

Effect of temperature, solar radiation and VPD on grain number and grain yield

Tables 3–5 show the correlation between weather parameters and wheat yield components. Both grain number and grain yield are negatively correlated with mean maximum temperature $T_{\max}$, temperature above 30°C (T30), PAR and VPD. The only exception is PAR at Wagga Wagga which is positively correlated with grain number and grain yield. Grain protein is, however, positively correlated with each of these weather parameters. The association between yield and yield components and weather parameters is higher for late-sown wheat compared to the crop sown in the normal sowing window, presumably due to the higher incidence of abiotic stress.

Figure 1 shows the linear relationship between the mean maximum temperature during the critical stage and grain yield. Late sowing exposed the crop to more hot days. Late-sown crops grew under higher maximum temperatures compared to crops sown during the normal sowing window. As the temperature increased, the crop yield decreased. The overall mean result (Fig. 1(g)) shows that for every 1°C rise in temperature, crop yield decreases by 370 kg/ha. In Leeton, for every 1°C rise in temperature, grain yield of wheat sown in the normal sowing window decreased by 360 kg/ha while the late-sown crop yield reduced by 640 kg/ha. The overall impact is higher in Leeton (470 kg/ha) than in Wagga Wagga (310 kg/ha). As the mean temperature during the critical period increases, both grain yield and grain number decrease (Tables 3–5). Temperature explained 51 and 43% of the yield and grain number variation, respectively.

Figure 2 shows the impact of the number of days with temperature above 30°C (T30) during the 30 days around anthesis (20 days before to 10 days after anthesis) on grain yield. Wheat yield decreases as the number of days with temperature above the threshold increases. When all the data are considered, for each day above the threshold temperature, crop yield decreases by 231 kg/ha for every day with $T > 30°C$ (Fig. 2(g)). The decrease is higher for sowing time 2 (ST2, August) compared to sowing

Table 2. Mean weather indices and yield components for wheat sown in Leeton and Wagga Wagga at two sowing times: normal sowing time in June (ST1) and late sowing time in August (ST2). The range of the values is shown in parentheses

	Leeton ST1	Leeton ST2	Wagga Wagga ST1	Wagga Wagga ST2
Yield (t/ha)	5.2 (2.6–9.0)	2.9 (0.2–5.8)	3.5 (2.0–7.8)	2.1 (0.5–4.7)
TGW (g)	41.0 (29.6–58.0)	32.3 (23.0–48.4)	36.8 (25.5–51.5)	36.3 (21.4–47.8)
NG (/m)	12 856 (5476–23 592)	9154 (688–16 759)	9540 (5231–24 454)	6173 (1837–20 082)
Prot (%)	12.9 (10.3–16.4)	13.6 (7.6–17.5)	14.9 (12.0–17.4)	16.2 (12.4–18.8)
T30 (days)	3 (0–12)	9 (5–16)	3 (0–7)	11 (2–17)
T_{mean} (°C)	15.0 (13.6–18.8)	19.2 (16.7–22.2)	14.0 (11.5–18.0)	18.2 (14.3–21.4)
PAR (MJ/m^2/d)	9.0 (8.4–11.3)	10.9 (9.5–11.6)	9.2 (7.4–11.3)	10.4 (9.0–11.8)
VPD (kPa)	1.3 (1.2–1.9)	1.7 (1.4–2.0)	1.6 (1.1–2.1)	2.1 (1.4–2.8)
PQ (MJ/m^2/°C/d)	0.6 (0.6–0.7)	0.6 (0.5–0.6)	0.7 (0.5–0.8)	0.6 (0.5–0.8)
PQ_{vpd} (MJ/m^2/°C/d/kPa)	0.6 (0.4–0.7)	0.4 (0.3–0.5)	0.6 (0.3–0.8)	0.4 (0.2 –0.7)
T_{max} (°C)	22.2 (20. 6–27.1)	27.1 (23.7–30.1)	23.5 (20.0–27.2)	28.0 (22.8–30.5)

TGW, 1000 grains weight; NG, number of grains per m^2; Prot, grain protein; T30, number of days with temperature >30°C; T_{mean}, mean temperature; PAR, photosynthetically active radiation; VPD, vapour pressure deficit; PQ, photothermal quotient; PQ_{vpd}, photothermal quotient corrected for vapour pressure deficit; T_{max}, maximum temperature.

time 1 (ST1, June). For Leeton, for example, the decrease is 300 and 128 kg/ha for ST1 and ST2, respectively.

Figure 3 presents the effect of VPD on wheat productivity. About 57% of the yield variation is explained by VPD. As expected, as VPD increases, crop yield decreases. This is especially pronounced for the second sowing date. Overall results show that for every 1 kPa increase in VPD, crop yield decreases by 2.6 t/ha. The yield loss is higher in the late-sown wheat; with 2.57 t/ha for the late-sown crop compared to 2.11 t/ha for the crop sown in the normal crop sowing window. The impact is higher for the crop sown at Leeton compared to the crop sown at Wagga Wagga (4.66 t/ha *v.* 2.11 t/ha). Compared to temperature and VPD, PAR has only little impact on grain number and yield (data not shown here). This is probably due to the ample radiation during the reproductive (anthesis and grain filling) stage of wheat and radiation not being a limiting factor. Generally, compared to grain number (hence grain yield), grain size was only slightly affected by temperature, VPD and PAR.

Figure 4 shows the effect of maximum temperature on the grain number for wheat sown at Leeton and Wagga Wagga during normal sowing window and sown late, respectively. Similar to the trend observed for grain yield, grain number decreases with the increase in mean maximum temperature. Overall results show that for every 1°C rise in maximum air temperature, the number of grains drop by 935 grains/m^2. The drop in grain numbers is higher for late-sown wheat compared to the crop sown during the normal sowing window (1320/m^2 *v.* 450/m^2). Although the result for grain weight is somehow mixed, generally there is a decreasing trend of grain weight.

Table 3. Correlation coefficients of weather indices and wheat yield components for combined Leeton and Wagga Wagga data

Leeton and Wagga Wagga											
	Yield	TGW	NG	Prot	T30	T_{mean}	PAR	VPD	PQ	PQ_{vpd}	T_{max}
Yield	1.00	0.12	0.94	−0.71	−0.68	−0.51	−0.16	−0.76	0.50	0.74	−0.76
TGW		1.00	−0.20	***0.04***	0.10	−0.20	−0.32	0.12	***−0.01***	0.09	***−0.06***
NG			1.00	−0.69	−0.67	−0.43	***−0.05***	−0.75	0.49	0.68	−0.70
Prot				1.00	0.53	0.16	***0.03***	0.68	−0.22	−0.54	0.55
T30					1.00	0.79	0.28	0.91	−0.70	−0.82	0.95
T_{mean}						1.00	0.63	0.57	−0.66	−0.72	0.84
PAR							1.00	***0.00***	0.16	***−0.04***	0.30
VPD								1.00	−0.71	−0.89	0.92
PQ									1.00	0.89	−0.77
PQ_{vpd}										1.00	−0.93
T_{max}											1.00

Non-significant correlations (at $P = 1\%$) are indicated by ***bold italics***.

TGW, 1000 grains weight; NG, number of grains per m^2; Prot, grain protein; T30, number of days with temperature >30°C; T_{mean}, mean temperature; PAR, photosynthetically active radiation; VPD, vapour pressure deficit; PQ, photothermal quotient; PQ_{vpd}, photothermal quotient corrected for vapour pressure deficit; T_{max}, maximum temperature.

Table 4. Correlation coefficients of weather indices and wheat yield components for first sowing and second sowing (ST1 and ST2) combined, first sowing (ST1) and second sowing (ST2), respectively, at Leeton

Leeton ST1 and ST2

	Yield	TGW	NG	Prot	T30	T_{mean}	PAR	VPD	PQ	PQ$_{vpd}$	T_{max}
Yield	1.00	0.47	0.92	−0.46	−0.69	−0.80	−0.76	−0.73	0.72	0.78	−0.77
TGW		1.00	***0.12***	***−0.11***	−0.43	−0.55	−0.58	−0.50	0.40	0.53	−0.53
NG			1.00	−0.46	−0.63	−0.69	−0.62	−0.63	0.68	0.66	−0.66
Prot				1.00	0.48	0.45	0.43	0.43	−0.39	−0.46	0.44
T30					1.00	0.94	0.86	0.96	−0.79	−0.91	0.95
T_{mean}						1.00	0.96	0.98	−0.84	−0.99	1.00
PAR							1.00	0.96	−0.67	−0.96	0.97
VPD								1.00	−0.75	−0.97	0.99
PQ									1.00	0.82	−0.80
PQ$_{vpd}$										1.00	−0.99
T_{max}											1.00

Leeton ST1

	Yield	**TGW**	**NG**	**Prot**	**T30**	T_{mean}	**PAR**	**VPD**	**PQ**	**PQ**$_{vpd}$	T_{max}
Yield	1.00	***−0.02***	0.92	−0.66	−0.23	−0.51	−0.53	−0.33	0.52	0.53	−0.44
TGW		1.00	−0.38	***0.16***	0.28	0.24	***0.23***	0.29	***−0.12***	−0.25	0.26
NG			1.00	−0.66	−0.33	−0.56	−0.58	−0.42	0.52	0.58	−0.51
Prot				1.00	0.31	0.54	0.54	0.40	−0.54	−0.56	0.49
T30					1.00	0.89	0.78	0.98	−0.58	−0.85	0.93
T_{mean}						1.00	0.95	0.94	−0.79	−0.99	0.99
PAR							1.00	0.88	−0.63	−0.93	0.94
VPD								1.00	−0.62	−0.92	0.98
PQ									1.00	0.83	−0.72
PQ$_{vpd}$										1.00	−0.97
T_{max}											1.00

Leeton ST2

	Yield	**TGW**	**NG**	**Prot**	**T30**	T_{mean}	**PAR**	**VPD**	**PQ**	**PQ**$_{vpd}$	T_{max}
Yield	1.00	***0.18***	0.96	***−0.17***	−0.72	−0.80	−0.64	−0.76	0.66	0.79	−0.79
TGW		1.00	***−0.09***	***0.11***	***−0.16***	***−0.19***	***−0.16***	***−0.18***	***0.16***	***0.18***	***−0.19***
NG			1.00	***−0.20***	−0.70	−0.77	−0.58	−0.71	0.65	0.75	−0.75
Prot				1.00	0.48	0.28	0.28	0.32	***−0.16***	−0.29	0.31
T30					1.00	0.94	0.76	0.93	−0.75	−0.94	0.95
T_{mean}						1.00	0.79	0.96	−0.83	−0.99	0.99
PAR							1.00	0.92	−0.32	−0.81	0.87
VPD								1.00	−0.64	−0.97	0.99
PQ									1.00	0.81	−0.74
PQ$_{vpd}$										1.00	−0.99
T_{max}											1.00

Non-significant correlations (at $P = 1\%$) are indicated by ***bold italics***.

TGW, 1000 grains weight; NG, number of grains per m^2; Prot, grain protein; T30, number of days with temperature >30°C; T_{mean}, mean temperature; PAR, photosynthetically active radiation; VPD, vapour pressure deficit; PQ, photothermal quotient; PQ$_{vpd}$, photothermal quotient corrected for vapour pressure deficit; T_{max}, maximum temperature.

Table 5. Correlation coefficients of weather indices and wheat yield components for first sowing and second sowing (ST1 and ST2) combined, first sowing (ST1) and second sowing (ST2), respectively, at Wagga Wagga

Wagga Wagga ST1 and ST2											
	Yield	TGW	NG	Prot	T30	T_{mean}	PAR	VPD	PQ	PQ_{vpd}	T_{max}
Yield	1.00	−0.13	0.93	−0.81	−0.74	−0.54	***0.11***	−0.79	0.72	0.79	−0.77
TGW		1.00	−0.44	0.18	0.31	***−0.04***	−0.21	0.35	***−0.08***	***−0.07***	0.18
NG			1.00	−0.78	−0.72	−0.45	0.17	−0.78	0.65	0.71	−0.72
Prot				1.00	0.71	0.42	***−0.13***	0.76	−0.77	−0.76	0.73
T30					1.00	0.79	0.13	0.93	−0.75	−0.80	0.95
T_{mean}						1.00	0.5	0.61	−0.68	−0.69	0.85
PAR							1.00	−0.20	0.29	0.22	***0.07***
VPD								1.00	−0.85	−0.89	0.93
PQ									1.00	0.97	−0.88
PQ_{vpd}										1.00	−0.92
T_{max}											1.00
Wagga Wagga ST1											
	Yield	**TGW**	**NG**	**Prot**	**T30**	T_{mean}	**PAR**	**VPD**	**PQ**	PQ_{vpd}	T_{max}
Yield	1.00	0.31	0.91	−0.72	−0.30	***0.04***	0.62	−0.63	0.60	0.67	−0.47
TGW		1.00	***−0.10***	−0.19	−0.22	−0.24	0.39	−0.46	0.56	0.53	−0.46
NG			1.00	−0.68	−0.21	***0.14***	0.49	−0.47	0.39	0.48	−0.30
Prot				1.00	0.37	−0.22	−0.57	0.63	−0.65	−0.63	0.47
T30					1.00	0.69	***−0.06***	0.76	−0.64	−0.65	0.84
T_{mean}						1.00	0.37	0.4	−0.48	−0.43	0.73
PAR							1.00	−0.58	0.63	0.62	−0.28
VPD								1.00	−0.91	−0.96	0.92
PQ									1.00	0.97	−0.90
PQ_{vpd}										1.00	−0.91
T_{max}											1.00
Wagga Wagga ST2											
	Yield	**TGW**	**NG**	**Prot**	**T30**	T_{mean}	**PAR**	**VPD**	**PQ**	PQ_{vpd}	T_{max}
Yield	1.00	−0.61	0.96	−0.80	−0.80	−0.44	0.57	−0.80	0.65	0.75	−0.81
TGW		1.00	−0.77	0.63	0.80	0.32	−0.76	0.82	−0.70	−0.76	0.79
NG			1.00	−0.79	−0.82	−0.48	0.64	−0.83	0.71	0.80	−0.84
Prot				1.00	0.77	0.43	−0.59	0.77	−0.76	−0.79	0.80
T30					1.00	0.40	−0.80	0.99	−0.78	−0.88	0.96
T_{mean}						1.00	−0.43	0.38	−0.77	−0.72	0.61
PAR							1.00	−0.84	0.9	0.86	−0.84
VPD								1.00	−0.80	−0.90	0.97
PQ									1.00	0.96	−0.90
PQ_{vpd}										1.00	−0.98
T_{max}											1.00

Non-significant correlations (at $P = 1\%$) are indicated by ***bold italics.***

TGW, 1000 grains weight; NG, number of grains per m^2; Prot, grain protein; T30, number of days with temperature >30°C; T_{mean}, mean temperature; PAR, photosynthetically active radiation; VPD, vapour pressure deficit; PQ, photothermal quotient; PQ_{vpd}, photothermal quotient corrected for vapour pressure deficit; T_{max}, maximum temperature.

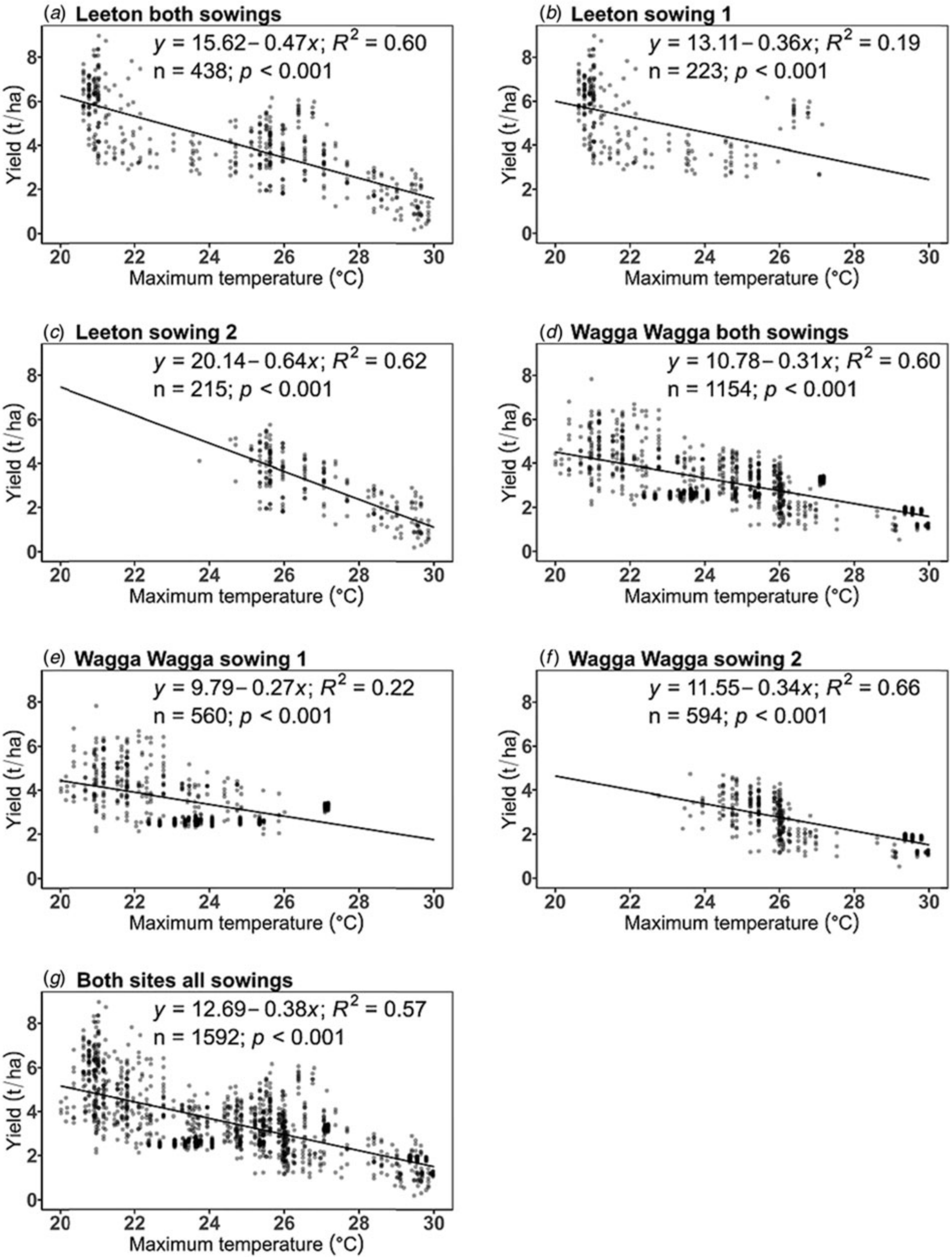

Figure 1. Regression analysis of mean maximum temperature during the critical development stage of wheat and grain yield. Wheat was sown at two sowing dates: normal sowing window (Sowing 1) and late (Sowing 2) in Leeton and Wagga Wagga.

PQ and PQ_{vpd} as predictors of grain yield

Figures 5 and 6 show the linear regression of grain yields *v.* PQ and PQ_{vpd}, respectively. Both grain number and grain yield increase with increasing PQ and PQ_{vpd}. PQ integrates PAR and mean temperature during the critical crop development stage to explain the effect of non-stressful thermal effects on crop

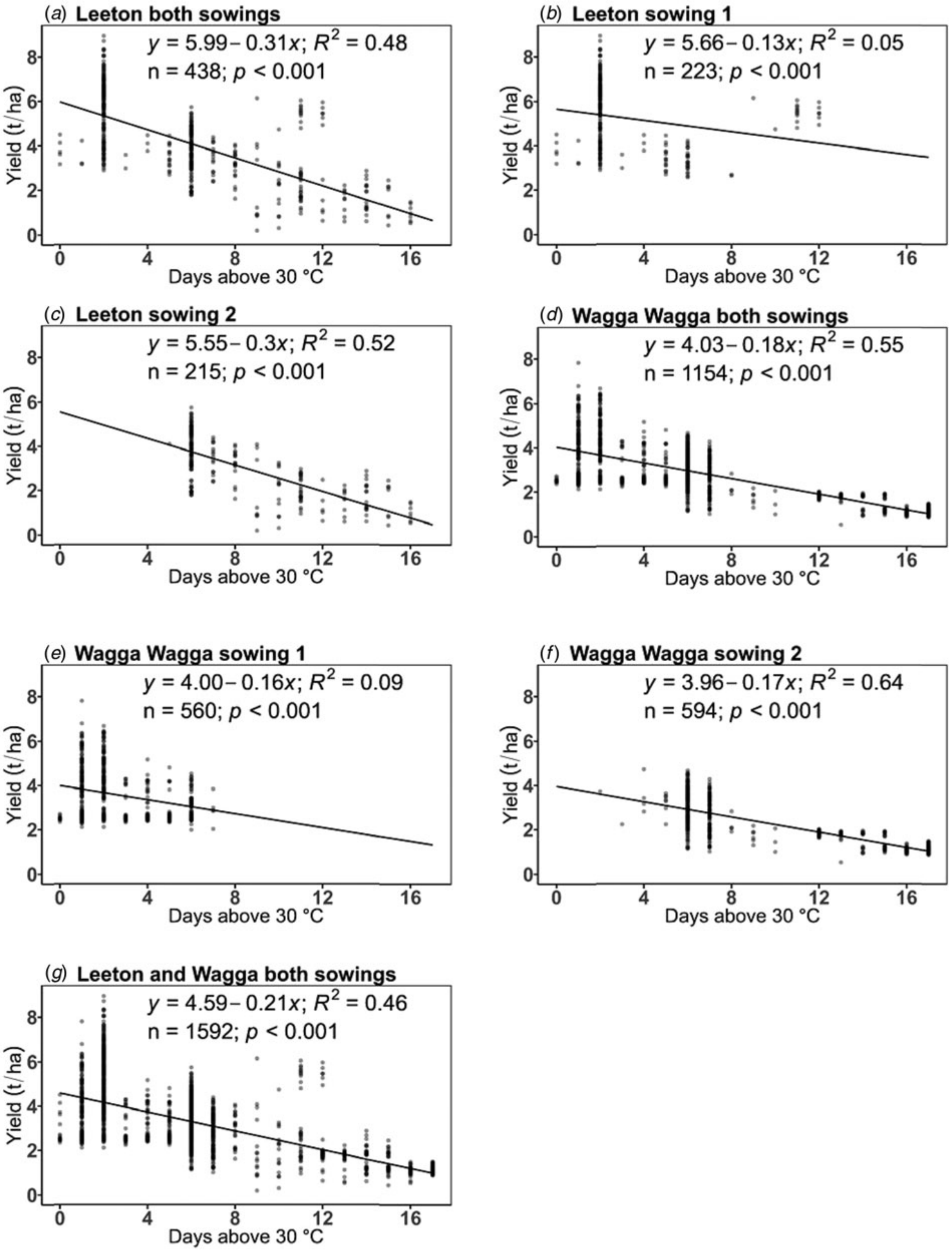

Figure 2. Regression analysis of the number of days with temperature above 30°C during the critical development stage of wheat and grain yield. Wheat was sown at two sowing dates: normal sowing window (Sowing 1) and late (Sowing 2) in Leeton and Wagga Wagga.

development, canopy size and seed set. PQ ranged from 0.50 to 0.80 MJ/m^2/°C/d. Considering the whole data set for Leeton and Wagga Wagga, 52% of grain yield variation can be explained by PQ variation (Fig. 5). The photothermal quotient normalized by VPD (PQ$_{vpd}$) accounted for 60% of the variation in grain yield (Fig. 6).

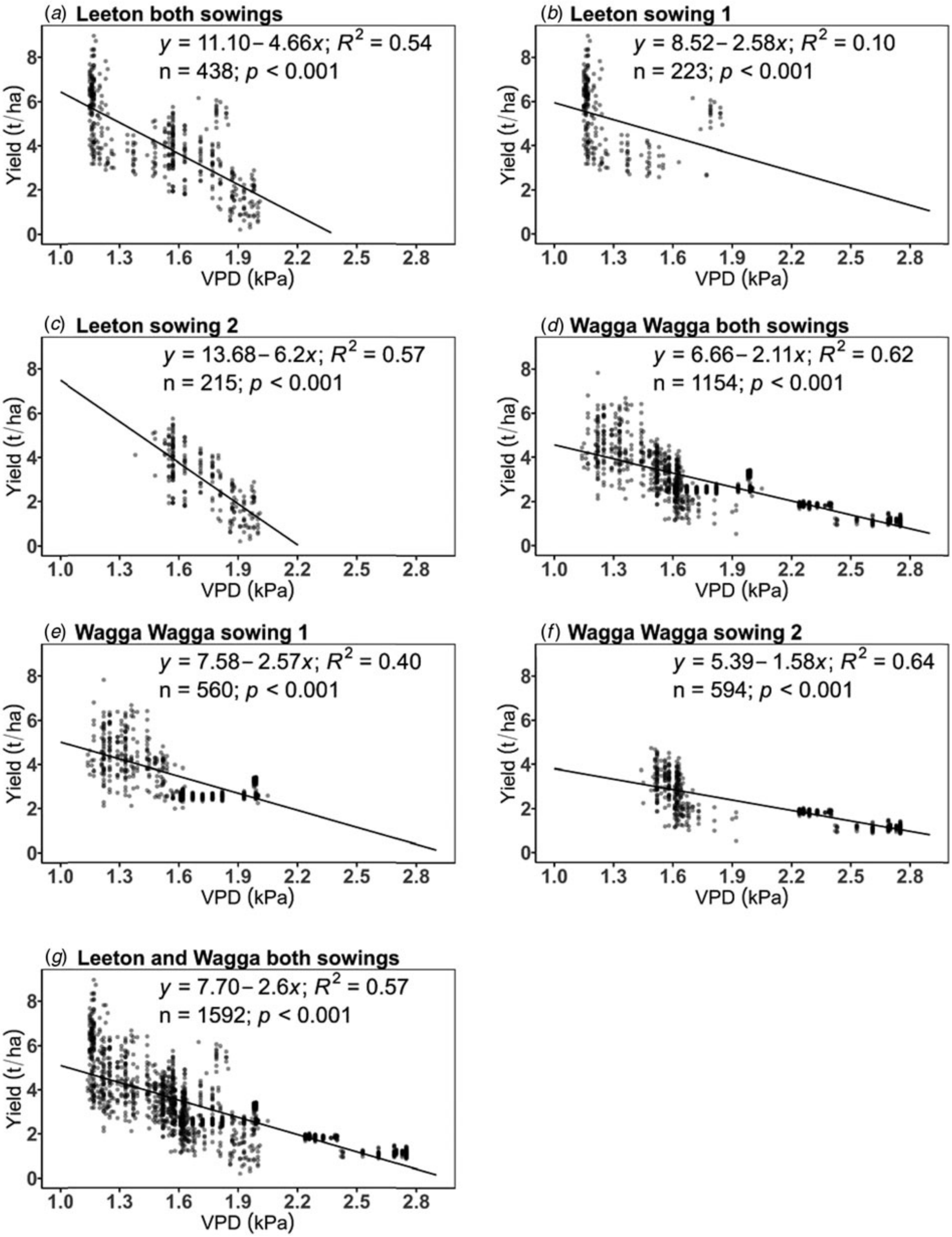

Figure 3. Regression analysis of the vapour pressure deficits (VPD) during the critical development stage of wheat and grain yield. Wheat was sown at two sowing dates: normal sowing window (Sowing 1) and late (Sowing 2) in Leeton and Wagga Wagga.

Impact of weather indices on grain protein

Tables 3–5 show that as maximum temperature, temperature above 30°C threshold and VPD increase, grain protein content increases. Figure 7 shows that mean maximum temperature explains about 30% of grain protein content variation.

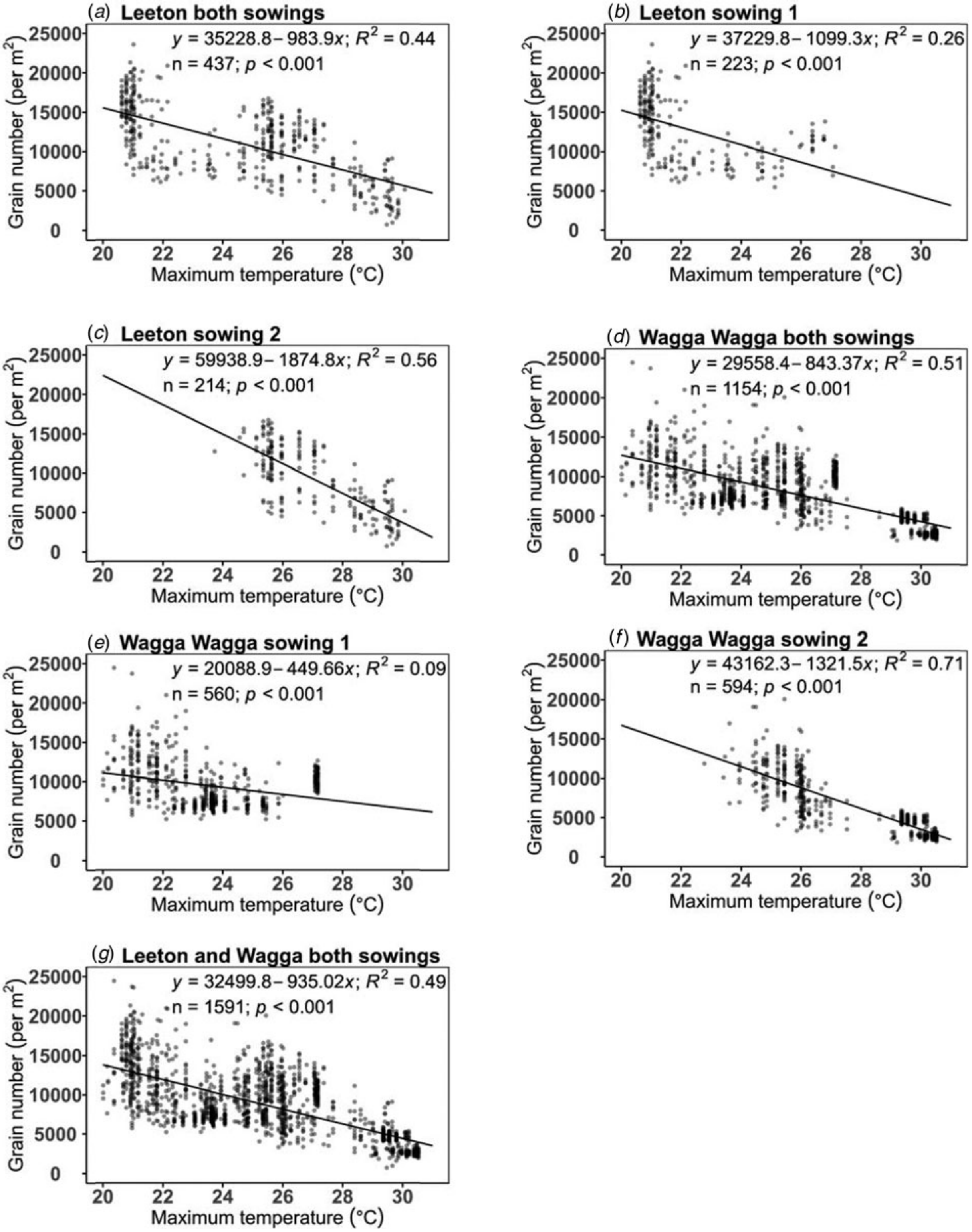

Figure 4. Regression analysis of mean maximum temperature and grain number per square metre during the critical development stage. Wheat was sown at two sowing dates: (normal sowing window (Sowing 1) and late (Sowing 2) in Leeton and Wagga Wagga.

Discussion

Wheat grain yield potential is determined by grain number and grain weight. When water and nutrients are not limiting, these two yield components are largely determined by solar radiation and air temperature. Wheat performs best when grown within the mean temperature range of 12–22°C during the growing season (Farooq *et al.*, 2011). However, in the Australian 'wheat belt', the daily maximum temperatures during the crop reproductive

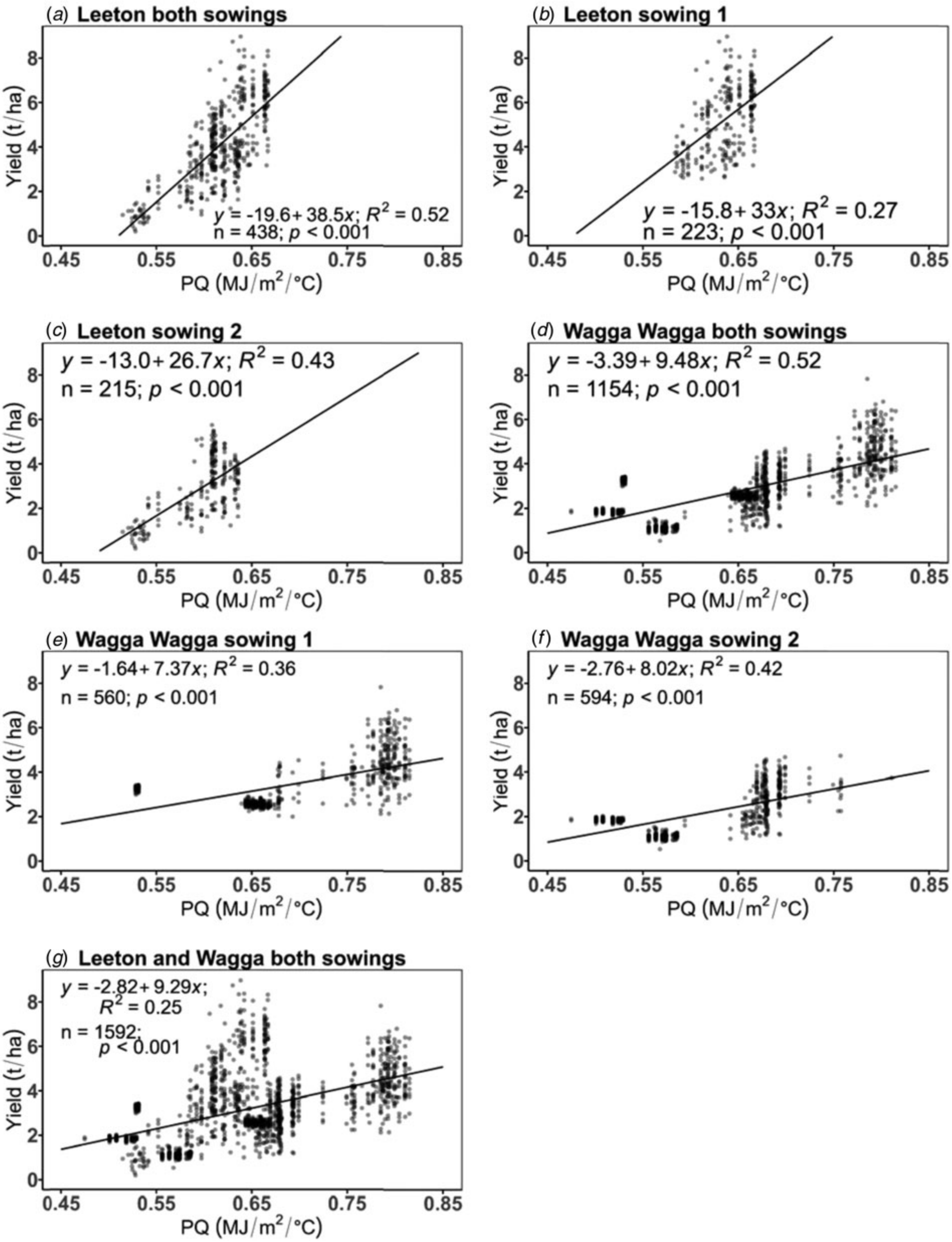

Figure 5. Regression analysis of the photothermal quotient (PQ) during the critical development stage of wheat and grain yield. Wheat was sown at two sowing dates: (normal sowing window (Sowing 1) and late (Sowing 2) in Leeton and Wagga Wagga.

stage are frequently in a higher range which can accelerate the development process and reduces the duration of grain filling and grain weight (Kumar *et al*., 2016). As a result, breeding for heat tolerance would be desirable for wheat grown in the Australian ‘wheat belt’, where mean air temperatures during the reproductive stage are above the optimum.

Crop productivity is becoming limited due to heat stresses resulting from rising atmospheric temperatures (Vollenweider

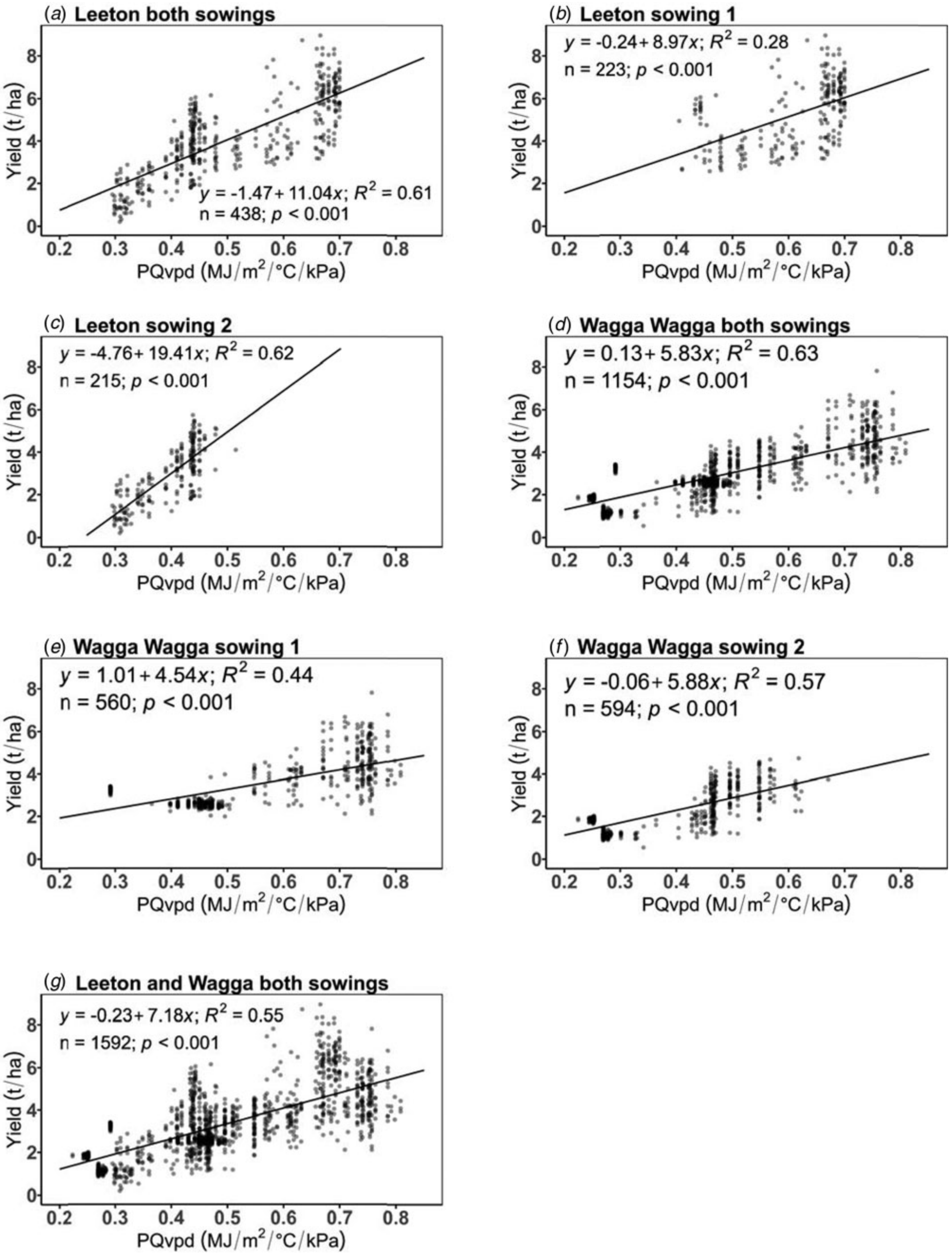

Figure 6. Regression analysis of the photothermal quotient corrected by vapour pressure deficit (PQ_{vpd}) during the critical development stage of wheat and grain yield. Wheat was sown at two sowing dates: (normal sowing window (Sowing 1) and late (Sowing 2) in Leeton and Wagga Wagga.

and Gunthardt-Georg, 2005). In the Australian 'wheat belt', heat shocks due to high temperatures (>30°C) are common during the crop reproductive stages. Impaired photosynthesis and reproductive damage at high temperature have been demonstrated in controlled environments (Wang *et al.*, 2018). Short periods, as short as one day, of high temperatures (>30°C)

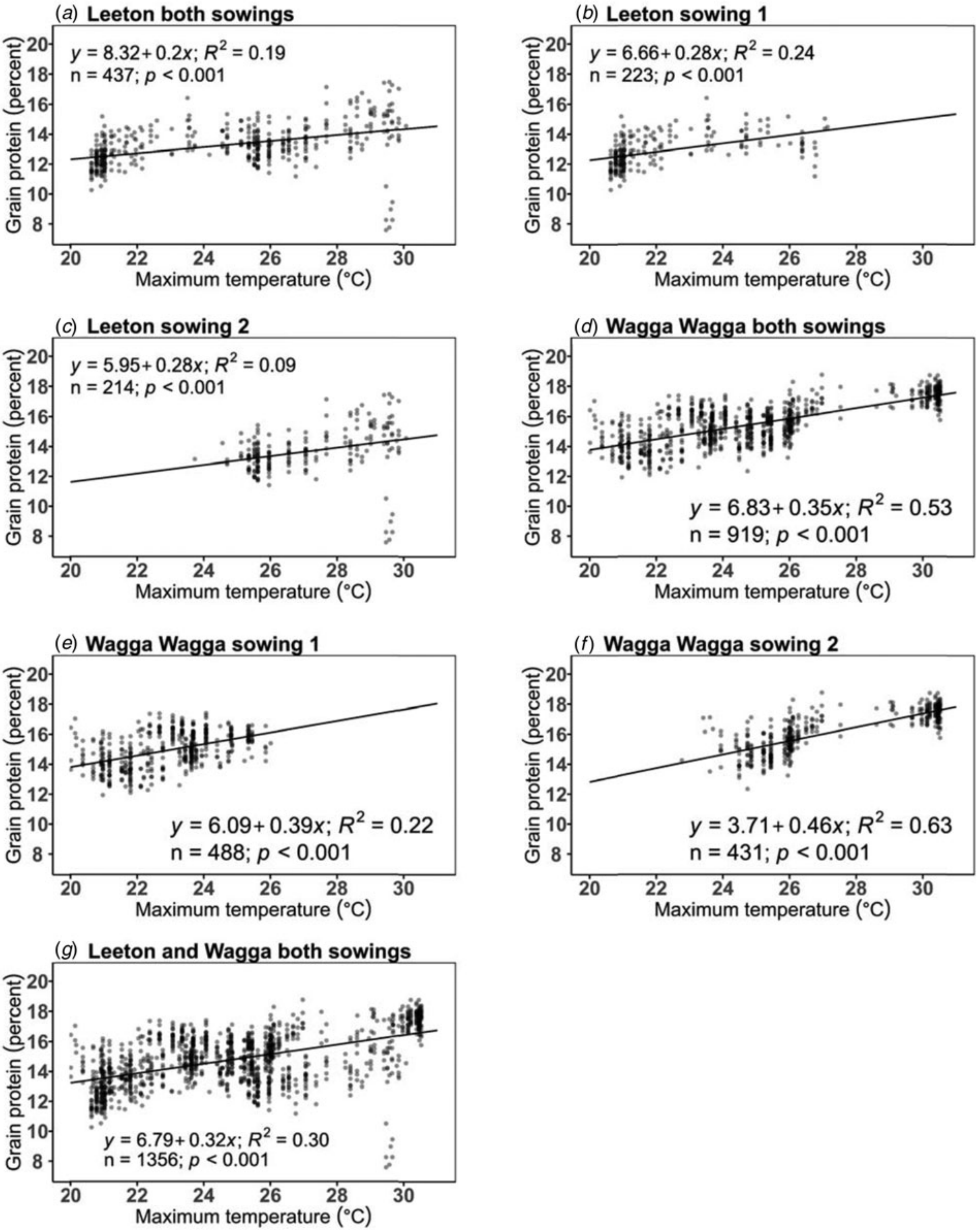

Figure 7. Regression analysis of the maximum temperature during the critical development stage of wheat and grain protein. Wheat was sown at two sowing dates: (normal sowing window (Sowing 1) and late (Sowing 2) in Leeton and Wagga Wagga.

directly affect the crop by reducing photosynthesis and/or causing sterility or reproductive failure, resulting in reduced grain number (Talukder *et al*., 2014; Mirosavljevic *et al*., 2021). The number of stressful temperature days above 30°C increases in frequency later in the season, negatively affecting grain filling, grain weight and grain yield (Savin and Slafer, 1991). Hawker and Jenner (1993) reported that the grain weight of wheat exposed to maximum temperatures of 35°C for four days was reduced by 14–20%. Yield loss per °C at Leeton is 50% higher than that of Wagga Wagga in indicating that the impact of climate change is higher in drier environments (Sreeparvathy and Srinivas, 2022).

Stressful and non-stressful atmospheric temperatures, PQ and PQ_{vpd} were identified to be reliable weather indices for wheat yield prediction. PQ normalized by VPD (PQ_{vpd}) was found to be a better predictor of wheat yield potential than PQ as it integrates more weather data that affects crop growth. Since radiation use efficiency decreases as VPD and maximum temperature increase, there is a better correlation between PQ_{vpd} and grain number and yield in comparison to PQ (Lazaro and Abbate, 2012). PQ_{vpd} captures the detrimental effect of high VPD and high temperature on photosynthesis and reproduction (Sadras *et al.*, 2015). Solar radiation and temperature affect plant growth and development differently (Nix, 1976). A higher PQ indicates high yield potential as radiation increases growth, while lower temperature increases the length of the crop phenological stages. High solar radiation during the crop reproductive stage increases photosynthesis and yield. On the other hand, high temperature around the same period shortens the duration of the reproductive stage and reduces yield. Mean PQ around anthesis (20 days before to 10 days after anthesis) was found to be a good indicator of grain number and grain yield. Ortiz-Monasterio *et al.* (1994) reported that the PQ value 20 days before to 10 days after anthesis predicted grain yield reasonably accurately.

Grain yield is determined by grain number and grain weight. Grain number accounts for much of the variation in yield between crops and environments. Given the strong correlation between grain number and yield, the association between yield and PQ and PQ_{vpd} was also strong, while grain weight is relatively stable for a given crop variety (Fischer, 1985). Since grain number is determined in the period immediately before anthesis, there is a strong association between grain number and the PQ and PQ_{vpd} around anthesis (20 days before and 10 days after).

Global temperature rise is increasing the atmospheric saturation vapour pressure as saturation vapour pressure is a function of air temperature (Lawrence, 2005). As a result, since actual vapour pressure has not been increasing at the same rate, VPD is rising (Grossiord *et al.*, 2020). In most global wheat-growing regions, including the Australian ‘wheat belt’, VPD increases during the reproductive (anthesis and grain filling) stage of the crop. The high VPD causes plants to close their stomata, reduce transpiration rate and reduce photosynthesis (Franks *et al.*, 1997).

In annual crops, grain yield is determined mainly by grain number which depends on the conditions that occur before anthesis, while grain size is determined by the environmental conditions that occur after anthesis (Ortiz-Monasterio *et al.*, 1994). Grain number, rather than grain size, is more sensitive and responsive to high temperatures at anthesis (Fernie *et al.*, 2022). Narayanan *et al.* (2015) reported that grain number was reduced by 17% for wheat exposed to 7-day heat stress at anthesis.

Late-sown wheat has a lower yield but higher protein content. Grain protein content was positively affected by air temperature during the grain filling period. Zhao *et al.* (2022) found that as the maximum temperature during the grain filling period increases, grain protein content increases and grain size decreases as grain protein content is inversely related to grain weight. Heat stress during grain development had adverse effects on starch biosynthesis (reduces grain weight) and increases protein content (Wang *et al.*, 2018). From tests conducted on several genotypes, Barutcular *et al.* (2016) found that protein content increases by an average of 39.6% at a temperature of 26.3°C. In winter wheat cultivars, Liu *et al.* (2016) found that grain protein content increased by 0.80% for every 1°C above 30°C after anthesis. Although heat stress can affect any wheat growth stage, it’s impact is most significant if it occurs during the reproductive stage. On average, as the sowing time is delayed, the crop is exposed to higher daily maximum temperatures and more hot days. Agronomic management such as early sowing can be used to minimize the coincidence of reproductive crop development stage and periods of climatic stresses such as heat and drought. Since grain yield is strongly correlated with grain number and grain number is mainly determined before and during anthesis, the critical period that determines yield is anthesis.

Conclusions

Linear regression analysis showed that weather indices account for much of the variability in grain number and yield. Grain number is the most important component of yield and is strongly correlated with PQ for wheat grown with no water and nutrient limitation. PQ and PQ_{vpd} are better predictors of wheat grain yield and quality than their components (temperature, radiation and VPD) alone. Overall, PQ_{vpd} was the better indicator of yield potential. Therefore, PQ and PQ_{vpd} can be used to predict or explain grain productivity and identify sowing times and growing regions that maximize grain yield potential. Varieties released several years apart can have marked differences in the number of grains and grain yield due to genetic improvement. However, in this study, genetic variability in heat tolerance for both grain yield and quality were not specifically considered as we were more interested in the overall responses for all the cultivars. The variety-by-environment aspects of this work will be investigated further.

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