

Response of lentil to high temperature under variable water supply and carbon dioxide enrichment

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Abstract. Lentil (*Lens culinaris* Medik.) production in arable, Mediterranean-type climates is limited by heat waves and unreliable rainfall. Under climate change scenarios, increased atmospheric carbon dioxide (CO₂) concentration will increase plant growth; however, the net effect of increasing occurrence and intensity of heat waves and drought is unclear. This study tested the response of combined acute high temperature (>32°C) at the early pod-filling stage and (i) crop-available soil water, and (ii) elevated CO₂ on three lentil genotypes in two experiments. The three lentil genotypes selected were commercial cultivar PBA Bolt and two landraces sourced from the Australian Grains Genebank, AGG 71457 and AGG 73838. High soil-water availability (0.42 Mg m⁻³) throughout the growing season increased yield by 28% compared with low soil-water availability (0.35 Mg m⁻³). Across contrasting water treatments, there was no difference in patterns of crop response to high temperature during the early pod-filling phase (5 days at 42°C daytime, 25°C night), where yields were reduced by 45%. A significant interaction between high temperature response and genotype was observed, where reduction in grain number was higher for AGG 73838 (0.20% per degree-hour >32°C) than for AGG 71457 (0.07% per degree-hour >32°C) or PBA Bolt (0.10% per degree-hour >32°C). For heat and CO₂ effects, there was no significant interaction between high temperature (3 days at 38°C daytime, ambient night temperature) and CO₂ treatment on yield components. There was, however, an overall trend of increased biomass, grain number and yield due to elevated CO₂. Although non-limiting soil water did not reduce the impact of high temperature in this study, the range in response across genotypes to high temperature supports opportunity for increased adaptation of lentil toward increasing yield stability under effects of climate change.

Additional keywords: drought stress, heat stress, pulse, reproductive growth.

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Introduction

For cool-season pulses such as lentil (*Lens culinaris* Medik.), water-stress and high temperature are significant abiotic stresses that limit production worldwide (Siddique 1999; Gaur *et al.* 2015; Sehgal *et al.* 2017). This is particularly the case in Mediterranean-type climates such as southern Australia, where rainfall is characteristically low and unreliable (200–600 mm year⁻¹) and heat waves (short-term high temperature) during the reproductive phase are frequent and impact yield stability (Erskine *et al.* 2011). Although crop water availability over the growing season is variable and tends towards terminal drought (water stress), high temperature affects crops through either: (i) above-optimum temperatures for an extended period, which increases supply of assimilates but reduces grain filling period and yield; or (ii) heat wave response, which is a short period of high temperature (>32°C) (Stone and Nicolas 1994; Wardlaw and Wrigley 1994; Shrestha *et al.* 2006; Prasad *et al.* 2008; Mahrookashani *et al.* 2017) that causes a non-recoverable

reduction in grainset and yield potential (Guilioni *et al.* 2003; Vadez *et al.* 2012). Together these abiotic stresses are estimated to cause up to 50% yield loss per annum in pulse crops globally (Gaur *et al.* 2014). Despite, sensitivity to abiotic stresses, lentil has rapidly become a high-value crop within Australia, now cultivated over 355 000 ha, producing 419 000 t grain per annum (ABARES 2017), averaging a gross margin of AU\$783 ha⁻¹ (Rural Solutions SA 2017).

Under climate-change scenarios, both the frequency of heat waves and decreasing rainfall during the growing season are expected to increase (IPCC 2012, 2014), with likely adverse effects on crop production (Vadez *et al.* 2012). For example, in southern Australia, the frequency of heat waves under climate change is expected to increase from a 1-in-10- to a 1-in-3-year occurrence by the mid-21st Century (IPCC 2012, 2014). The global phenomenon of elevated atmospheric carbon dioxide (CO₂) is expected to increase crop growth, whereas the combined effect of short-term high temperature and CO₂ on

lentil growth is unclear. The trend towards expanding lentil into more marginal cropping regions to obtain financial and break-crop benefits such as reducing grass-weed burden, limiting disease carryover and building soil nitrogen potentially increases the likelihood of these abiotic stresses (Kumar *et al.* 2015). For lentil production, variation in genotypic response to high temperature has been observed (Delahunty *et al.* 2015; Gaur *et al.* 2015; Kumar *et al.* 2016), providing opportunity to select genotypes with improved adaptation.

Timing and intensity of exposure to high temperature are critical where response varies across pulse crops (McDonald and Paulsen 1997; Egli *et al.* 2005). Lentil is particularly sensitive to high temperature (>30°C) during the reproductive phase, causing pod and flower abortion and significant reduction in grain yield and quality (Erskine *et al.* 1994; Siddique 1999; Gaur *et al.* 2015; Kumar *et al.* 2016; Sehgal *et al.* 2017; Sita *et al.* 2017). Several days of high temperature limits many physiological processes including photosynthesis, metabolic pathways, electron flow and respiration rates (Redden *et al.* 2014). Yield was reduced by 87% for lentils grown in pots under field conditions with high temperature during the reproductive phase (>38°C daytime, 23°C night) (Bhandari *et al.* 2016), and grainset was observed to be the most sensitive yield component (Gaur *et al.* 2015; Bhandari *et al.* 2016).

In areas where lentil is primarily cultivated, such as the Indian subcontinent, West Asia and Australia, crops often encounter water-limited conditions, with unreliable rainfall and variable soil water, combined with increasing frequency of heat. Soil water therefore becomes an important factor for maintaining yield potential. Gross and Kigel (1994) observed that non-limiting water increased yield by 74% for lentil in Mediterranean-type climates, where grain filling is typically limited by increasing temperature and water deficit. Under drought conditions, plant response to high-temperature events is limited because water stress restricts stomata from opening, thus inhibiting plant cooling through transpiration (Mahrookashani *et al.* 2017). These combined stresses can reduce grain yield (Zhang *et al.* 2010) and are considered synergistic (combination of stresses being more severe than either stress alone, or added), antagonistic (combination of stresses being less severe than either stress alone or added), or hypo-additive (effect of combined stress being higher than individual effects but lower than their sum) effects on grain filling, growth and yield traits (Mahrookashani *et al.* 2017). For pulse crops such as lentil, the indeterminate growth habit may offer a recovery mechanism to maintain grainset by continuing to flower and set pods following short-term high-temperature events, although this will be influenced by timing (Wang *et al.* 2006; Vadez *et al.* 2012) and/or water supply (Hall 1992).

For C₃ plants, the response to elevated atmospheric CO₂ is to increase crop growth universally, with biomass and grain yield increasing by 27% and 24%, respectively, through increased photosynthesis and decreased stomatal conductance, resulting in increased crop water-use efficiency (Leakey *et al.* 2009; Kimball 2016). Yield response to elevated CO₂ was a 19% increase for wheat (*Triticum aestivum*) and a 16% increase for pulse crops (soybean, *Glycine max*; pea, *Pisum sativum*; peanut, *Arachis hypogaea*; common bean, *Phaseolus vulgaris*) (Kimball 2016). Increasing atmospheric CO₂ induces stomatal closure

(Prasad *et al.* 2002) and may limit transpiration and cooling, reducing the capacity to mitigate high-temperature effects (Prasad *et al.* 2002; Prasad *et al.* 2006). The combined effect of high temperature and CO₂ on growth and yield appears to be variable, ranging from no effect (Ahmed *et al.* 1993; Prasad *et al.* 2006; Bourgault *et al.* 2018) to reducing (Ferris *et al.* 1999; Fitzgerald *et al.* 2016) or exacerbating (Heinemann *et al.* 2006) the impact of high temperature.

The objective of this study was to define the response of lentil to acute high temperature with respect to changes in water supply or CO₂ concentration. The results of two controlled-environment experiments are presented. Collectively, this work tested whether impacts of short-term high temperature (~38°C) during the early pod-filling phase are reduced by non-limiting water supply (Expt 1), and if elevated CO₂ increases the impact of high temperature (Expt 2). These questions were addressed across three lentil genotypes from different geographical origins varying in climate.

Method

The experiments were conducted in naturally lit, controlled environments at Horsham, Victoria, Australia (36°43'18.82"S, 142°10'26.56"E; 128 m a.m.s.l.). Two temperature treatments were applied to lentils during the pod-filling phase, where the interactive effects with water and CO₂ enrichment were investigated in two experiments: (i) high temperature and water supply, and (ii) high temperature and CO₂. For the experiments reported, high temperature refers to short periods (3–5 days) of very high maximum temperatures (>32°C daytime) to reflect acute high temperature (heat wave) conditions. The high-temperature treatment was applied by using a growth cabinet for Expt 1 (5-day treatment; 42°C daytime, 25°C night) and purpose-built heat chambers for Expt 2 (3-day treatment; ~38°C daytime, ambient night temperature).

Expt 1: high temperature and water availability

The response of three lentil genotypes to water availability and high temperature was tested within a randomised complete block design replicated four times. The genotypes from different global agro-ecological zones were selected for their potential tolerance to high-temperature stress (Delahunty *et al.* 2015). These genotypes included a commercial cultivar developed by Pulse Breeding Australia (PBA), PBA Bolt (a medium red variety), and two landraces sourced from the Australian Grains Genebank (AGG): AGG 71457 *Lens culinaris* (a small green–brown landrace (origin Jordan), and AGG 73838 *Lens culinaris* (a medium–large green–brown advanced cultivar (origin Albania).

Ninety-six square pots were prepared with a topsoil (5–15 cm) of a grey Vertosol soil, with preparation according to Nuttall *et al.* (2018). Briefly, soil was air-dried (40°C for 4 days) and packed in large sealed square pots (160 mm wide by 160 mm deep by 240 mm high) at 5500 g soil pot⁻¹, which equated to a bulk density of 1.15 Mg m⁻³. The large pot size was used to limit artefact effects of pot volume on treatment response (Bourgault *et al.* 2017a). The field capacity (–30 kPa) and wilting point (–1500 kPa) of the soil were 0.53 and 0.28 Mg m⁻³, respectively. Pots were pre-watered to weight to the equivalent of 0.42 Mg m⁻³.

Seed was inoculated with a peat-based slurry (Group E & F) and 6 seeds pot^{-1} sown (30 May 2015) with basal nutrients of Mallee Mix 1 fertiliser (nitrogen 5.8%, phosphorus 12%, sulfur 1.0%, zinc 1.2%; Incitec Pivot Fertilisers, Southbank, Vic., Australia). The experiment was grown in a naturally lit polyhouse. At the third-node stage, seedlings were thinned to 4 plants pot^{-1} and polyethylene granules applied to the surface to reduce water loss due to evaporation. The water treatments tested four factorial combinations of low and high water availability during the pre- and post-flowering phases (Fig. 1) ranging from low pre- and post-flowering, to high pre- and post-flowering. These treatments were applied from emergence, when the high and low water treatments were to a water content of 0.42 Mg m^{-3} (58% relative available water) and 0.35 Mg m^{-3} (28% relative water content), respectively. The water treatments were maintained by watering to weight using reverse osmosis (RO) water to limit the risk of hypoxia.

For each genotype, the high-temperature treatment was applied at the early pod-filling stage (pod on nodes 10–13 of the basal primary branch visible). The high-temperature treatment constituted 5 days of 42°C for 8 h (daytime) and 25°C for 16 h (night), where response was compared with the equivalent pots grown under ambient temperature. For the high-temperature treatments, plants were periodically transferred from the polyhouse to a controlled growth cabinet (Thermoline Scientific, Wetherill Park, NSW) for the 5-day period. The growth cabinet regulated temperature as above and relative humidity (RH, daytime 20%, night 80%).

Experiment 2: high temperature and CO_2

The response of lentil to elevated CO_2 and high temperature across three genotypes was tested within a randomised complete block design replicated three times with two pots per treatment within each replicate. The three genotypes included were

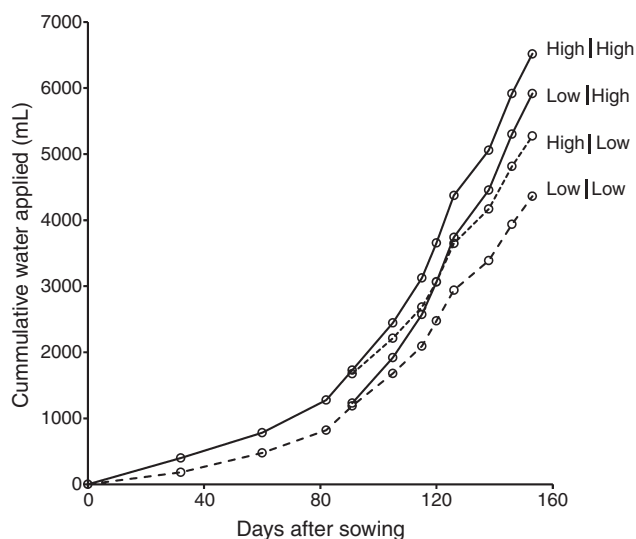


Fig. 1. Cumulative water applied to lentil throughout the growing period under four factorial water treatments in Expt 1. Treatments were high pre-, high post-flowering (High | High); high pre-, low post-flowering (High | Low); low pre-, high post-flowering (Low | High); and low pre-, low post-flowering (Low | Low).

consistent with Expt 1: PBA Bolt, and landrace genotypes AGG 71457 and AGG 73838.

Seventy-six pots were prepared and sown (12 June 2015) consistent with the methodology used in Expt 1. The experiment was grown in a naturally lit glasshouse with refrigerant cooling to maintain temperature. Throughout the experiment, each pot was maintained at a water content of 0.42 Mg m^{-3} (58% relative available water) by watering to weight weekly with RO water.

For the CO_2 treatment, the ambient air CO_2 concentration of 500 ppm within the glasshouse was compared with an elevated CO_2 concentration of 700 ppm, where we induced a differential of 200 ppm, which is sufficient to test plant response to elevated CO_2 (Kimball 2016). Three of six glasshouse rooms were sealed, and CO_2 enrichment was monitored and maintained by using an infrared gas analyser (Guardian SP CO_2 monitor; Edinburgh Instruments, Livingston, UK) attached to a regulation valve controlling the flow of CO_2 from cylinders. The CO_2 gas was injected into each room in proximity to the air-conditioner outflow to ensure even distribution within the rooms. The treatment was imposed from pre-emergence to crop maturity.

High-temperature treatments were applied at early pod-filling stage (pod on nodes 10–13 of the basal primary branch visible), using purpose-built heat chambers (Nuttall *et al.* 2012) that were installed within the six glasshouse rooms. The heat treatment constituted 3 days of 38°C for 8 h (daytime) and ambient temperature for 16 h (night), where the application was staggered to accommodate variation in the development rate across lentil genotypes. The heat chambers consisted of right-angle hollow-section frame boxes (1200 mm wide by 800 mm deep by 500 mm high) clad with Suntuf Greca Laserlight (Mulford Plastics, Dandenong South, Vic., Australia), a transparent UV-stable material. Electric fan heaters (1200 W) were mounted at the top of the chambers, with the temperature controlled by a thermocouple at canopy height. RH was measured but not controlled during the high-temperature treatments, where the design of the chambers allowed for mixing of ambient air.

Heat loads

To account for different high-temperature scenarios (temperature and duration) across the two experiments, we used a calculation of heat load that combines the duration and temperature data together to determine the heat stress or load applied to the plant. For Expts 1 and 2, heat load was calculated as a sum of degrees Celsius ($^\circ\text{C}$) above the threshold value (32°C) for the logged temperature data (5-min intervals), expressed as degree-hours ($^\circ\text{C.h}$), to which the plant was exposed over the duration of the high-temperature treatment (as per Nuttall *et al.* 2018). The cumulative heat load calculated included any occasion when the temperature within the polyhouse (Expt 1) or glasshouse (Expt 2) exceeded 32°C during the growing period. For lentil, growth is reduced between 30°C and 35°C (Siddique 1999; Gaur *et al.* 2015); therefore, within this study, heat load was calculated using a temperature threshold of 32°C .

Data collection

Temperatures for both experiments were recorded for ambient and elevated conditions every 5 min by using TinyTag Ultra 2 TGU-4500 sensors for temperature, RH and dew point (Gemini

Data Loggers, Chichester, UK). Crop development notes were collected throughout the growing period. At maturity, plants were cut at the base and dried at 40°C, and yield components were measured (plant biomass, grain yield, grain number, grain size and harvest index). Grain nitrogen was determined by the Dumas combustion method (AACC 2000), using TruMac equipment (LECO, St. Joseph, MI, USA) based on Approved Method 4630.01.01 (AACC 2000).

Data analysis

Analysis of variance (ANOVA) was used to test for the main effects and interaction of the independent variables high temperature and pre- and post-flowering water supply (Expt 1), and high temperature and atmospheric CO₂ concentration (Expt 2). Linear models were also fitted to the temperature-response data (expressed as heat load). All statistical analysis were done using GENSTAT version 18 (VSN International, Hemel Hempstead, UK). Results are expressed on a per-pot basis, where each pot contained four plants. Individual means for all treatments were compared using least significant difference, where all *P*-values <0.05 were considered significant.

Results

Experiment 1: high temperature and water supply

Heat load

The high-temperature treatments across the 5 days (8 h per day) was maintained at 42°C, which resulted in an average heat load of 347°C.h (>32°C). For the duration of the experiment, the ambient temperature within the polyhouse exceeded 32°C to the extent that 62°C.h accumulated during the late pod-filling stage.

Lentil response

Rate of maturity varied across the three genotypes, where AGG 73838 was earlier to reach 50% flowering and maturity than PBA Bolt and AGG 71457. For PBA Bolt and AGG 71457, 50% flowering was 116 and 119 days after sowing (DAS),

respectively, compared with 112 DAS for AGG 73838. Maturity occurred marginally later for PBA Bolt and AGG 71457, occurring 173 and 174 DAS, respectively, compared with AGG 73838 (169 DAS). The high-temperature and water-availability treatments both had no significant effect on the rate of development across the three genotypes.

The impact of high temperature on lentil growth was not reduced by high water availability during either the pre- or post-flowering phase. Grain yield was reduced by low water availability (pre- and post-flowering treatments), high temperature (at the early pod-filling), and combined low water and high temperature. Water stress during the post-flowering phase caused a reduction in yield of 28%, whereas the high-temperature treatment caused reductions of 47% and 43% for the low and high water-availability treatments (post-flowering), respectively. There was no significant interaction of pre-flowering water supply and high temperature on yield components; however, high water availability during this period significantly increased grain yield by 16%, compared with low water availability. For grain number, individual grain weight, plant biomass and harvest index, there was no interaction of the high-temperature and water-availability treatments in the pre- or post-flowering phase.

Across the three genotypes, high temperature caused grain number of PBA Bolt and AGG 73838 to be significantly reduced, by 38% and 53%, respectively; however, for AGG 71457, grain number was equivalent to that at ambient temperature (Table 1). Under ambient temperature, absolute grain number of PBA Bolt was significantly higher than of AGG 71457 and 73838, whereas under high temperature, grainset of AGG 71457 was equivalent to that of PBA Bolt. High temperature caused a reduction of 16% for individual grain weight, and there was a trend (*P*=0.07) for an interaction between genotype and temperature treatment, where AGG 71457 (20% reduction) had poor stability compared with PBA Bolt and AGG 73838, which were reduced by 11% and 16%, respectively (Table 1). For yield, there was a near-significant interaction (*P*=0.06) of genotype and temperature treatment

Table 1. Effect of high temperature applied at early pod-filling for 5 days (42°C daytime, 25°C night) on yield components of three lentil genotypes in Expt 1
Means are pooled for water-treatment combinations

Yield component	Temperature (T)	Genotype (G)		
		AGG 71457	AGG 73838	PBA Bolt
Biomass (g pot ⁻¹)	Ambient	15.89	8.59	18.58
	High	14.19	6.84	16.27
			G = 1.71, T = 1.39	
Grain number per pot	Ambient	116	79	180
	High	96	37	112
			G × T = 22.62	
Individual grain weight (mg)	Ambient	58.2	55.6	44.34
	High	46.44	49.64	37.39
			G = 2.60, T = 2.30	
Grain yield (g pot ⁻¹)	Ambient	6.66	4.32	7.97
	High	4.48	1.76	4.1
			G = 0.74, T = 0.60	
Harvest index	Ambient	0.43	0.49	0.43
	High	0.33	0.28	0.26
			G × T = 0.06	

(Table 1), whereby the reduction due to heat was lower for AGG 71457 (33%) than PBA Bolt (49%) and AGG 73838 (59%). There were no differences in the response across genotypes for biomass, and high temperature caused an average 13% reduction compared with the ambient treatment. PBA Bolt produced the highest biomass, averaging 14% and 56% higher than AGG 71457 and 73838, respectively (Table 1). Harvest index was reduced by 23%, 40% and 43% for AGG 71457, PBA Bolt and AGG 73838, respectively, as a result of high temperature. Comparing genotypes, AGG 73838 had the highest harvest index in the ambient treatment but was reduced to less than AGG 71457 and PBA Bolt in the high-temperature treatment (Table 1).

There was a significant ($P < 0.05$) interaction between water availability during the post-flowering phase and genotype for biomass, grain number and grain yield (Fig. 2). For plant biomass, under high and low post-flowering water, there was no difference in biomass for AGG 73838, whereas low water availability reduced the biomass of PBA Bolt by 20% and 71457 by 45% (Fig. 2a). A similar trend in response was observed for grain number and yield, where there was no significant difference between high and low water availability for AGG 73838; conversely, the grain number and yield of PBA Bolt and AGG 71457 were reduced by low water availability (both parameters 20% for PBA Bolt and 39% for AGG 71457) (Fig. 2b, c). There was no effect (interactive or main) of soil-water availability or genotype on individual grain weight or harvest index.

Grain nitrogen

There was a significant effect of high temperature on the grain nitrogen concentration (GNC), where high temperature caused an increase of 9% over lentil grain at ambient temperature from 4.23 to 4.64%, respectively. There was no effect of soil-water availability or genotype on GNC.

Expt 2: elevated CO_2 and high temperature

Heat loads

The average temperature for the high-temperature treatment across the 3 days (8 h per day) was 38°C, which equated to an average heat load of 118°C.h (>32°C). Variation in performance across the six heat chambers meant that the heat load applied ranged from 60°C.h to 163°C.h (>32°C). By comparison, the average daytime air temperature and heat load for the ambient control were 19°C and 0°C.h (>32°C), respectively, for the same period (Fig. 3a). RH within the heat chambers was 24%, compared with 60% for the ambient air during the same (daytime) period. For night time, RH levels of 74% and 82% were recorded within the heat chambers and for ambient air, respectively. Over the 3-day period there was a progressive decrease in ambient daytime air RH from 68% to 49%, whereas RH levels were relatively stable within the heat chambers (average 24%) (Fig. 3b). For the CO_2 -enriched treatment, the heat chamber did not influence the concentration of CO_2 (Nuttall *et al.* 2012).

Lentil response

There was no significant interaction between temperature, CO_2 and genotypes on any of the lentil yield components

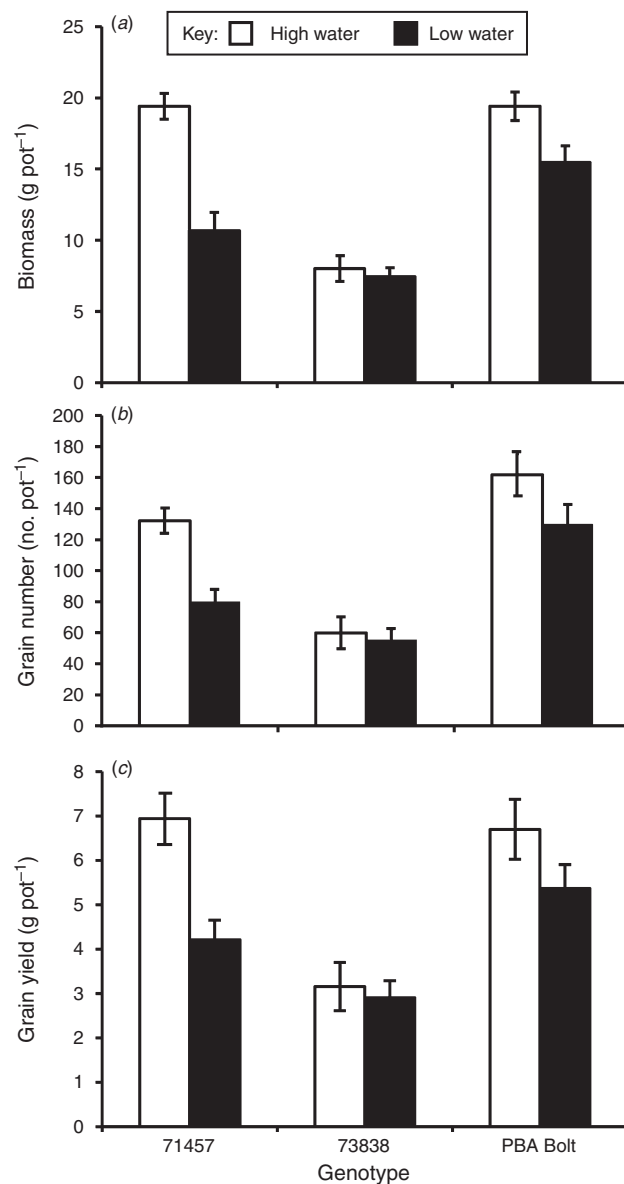


Fig. 2. Lentil response to high and low water availability during the post-flowering phase on (a) biomass, (b) grain number, and (c) grain yield on three lentil genotypes in Expt 1. Lentil genotypes were cv. PBA Bolt and landraces AGG 71457 and 73838. Means are pooled for temperature treatments. Capped lines are ± 1 standard error of water treatment and genotype ($n = 3$).

measured, although there were significant main effects of temperature and genotype. High temperature caused a reduction of 16% for grainset compared with the ambient control, whereas individual grain weight increased by 5% under high temperature (Table 2). High temperature also caused a decrease in harvest index of 10%. For lentil exposed to high temperature, there was no significant effect on biomass accumulation (Table 2).

Although there was no significant effect of CO_2 on lentil yield components, CO_2 enrichment corresponded to an increase in biomass accumulation, grain number and yield of 16%, 11% and 4%, respectively (data not shown). However, there was

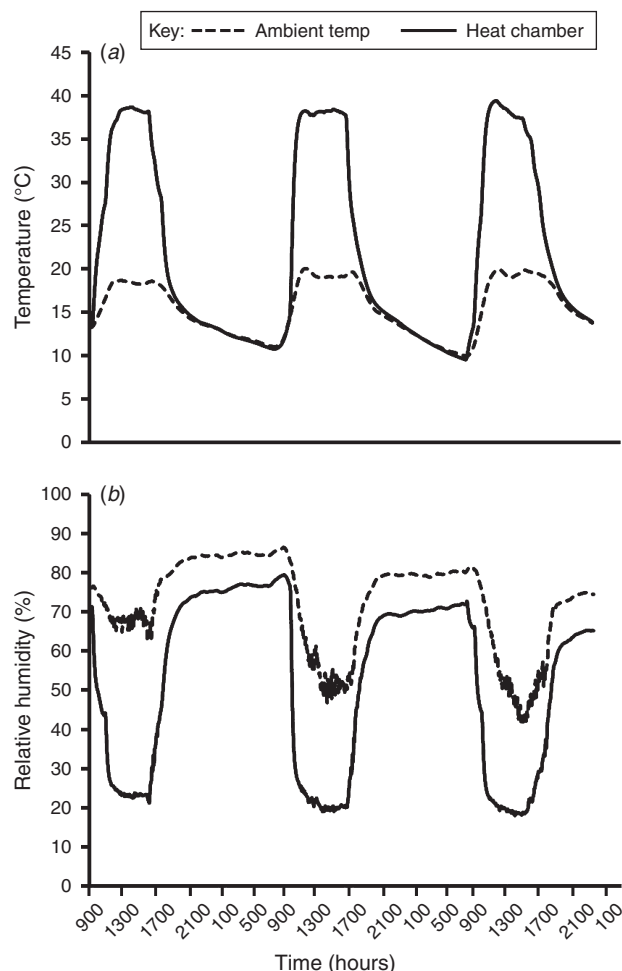


Fig. 3. Temperature and relative humidity during high-temperature treatment in Expt 2. Trace averages of crop canopy (a) temperature and (b) relative humidity for ambient air and heat chambers during the application of high temperature on lentil plants. Time is hours across three consecutive days. High temperature (target temperature 38°C) was applied during early pod-filling stage.

Table 2. Effect of high temperature applied at early pod-filling for 3 days (38°C daytime, ambient night) on yield components of three lentil genotypes in Expt 2

Means were pooled for CO₂ concentration (500 and 700 ppm) and genotype (AGG 71457, AGG 73838 and PBA Bolt). n.s., Not significant ($P > 0.05$)

	High temperature		l.s.d. ($P = 0.05$)
	Control	Heat	
Biomass (g pot ⁻¹)	8.5	8.4	n.s.
Grain number per pot	99.8	83.6	12.2
Individual grain weight (mg)	50.7	53.6	1.3
Grain yield (g pot ⁻¹)	4.9	4.4	0.5
Harvest index	0.59	0.53	0.03

a decline of harvest index and individual grain weight under elevated CO₂ of 11% and 4%, respectively.

Comparing genotypes, there was no significant difference for plant biomass. However, PBA Bolt, produced significantly

Table 3. Effect of genotype on yield components of three lentil genotypes in Expt 2

Means are pooled for CO₂ concentration (500 and 700 ppm) and temperature treatment (3 days at 38°C daytime, ambient night). n.s., Not significant ($P > 0.05$)

	Genotype			l.s.d. ($P = 0.05$)
	AGG 71457	AGG 73838	PBA Bolt	
Biomass (g pot ⁻¹)	8.2	8.9	8.2	n.s.
Grain number per pot	80.8	88.9	105.4	15.0
Individual grain weight (mg)	54.4	55.9	46.2	1.6
Grain yield (g pot ⁻¹)	4.3	4.9	4.8	n.s.
Harvest index	0.54	0.55	0.60	0.04

higher grain number (24%) and harvest index (10%) than both AGG 71457 and 73838, which were equivalent (Table 3). By contrast, individual grain weight was significantly greater for AGG 71457 and 73838 than for PBA Bolt, resulting in equivalent yield across genotypes.

Grain nitrogen

There was no effect of high temperature or CO₂ concentration on GNC. There were, however, significant ($P = 0.01$) differences among genotypes; higher GNC was observed for AGG 73838 than for PBA Bolt and AGG 71457 (5% and 4%, respectively).

Cumulative heat comparison for yield components

The overall response of lentil to high temperature across the two experiments was compared (Fig. 4). The response of lentil to high temperature was a 0.11% reduction in grain number per degree-hour (>32°C) (Fig. 4a). For individual grain weight, there was also a trend across genotypes, where individual grain weight increased up to cumulative heat load of less than 150°C; beyond this, individual grain weight was reduced (Fig. 4b). Overall this translated to a 0.13% reduction in grain yield per degree-hour (Fig. 4c).

There was variation across genotypes in the rate of reduction relative to cumulative heat load for grain number, size and yield (Fig. 4). Response across genotypes followed a similar trend for grain number and yield, where AGG 71457 was the most stable to high temperature at the early pod-filling stage, with a reduction of 0.07% in grain number and 0.10% in yield per degree-hour (>32°C). This compares with PBA Bolt and AGG 73838, with reductions of 0.10% and 0.15%, respectively, in grain number and 0.12% and 0.16% in grain yield per degree-hour. Differential response across genotypes for individual grain weight indicates that for this yield component, AGG 71457 was the most sensitive to high temperature, whereas AGG 73838 was the most stable.

Discussion

In the present study, the impact of high temperature occurring during the early pod-filling phase of lentil was not affected by water supply during either the pre- or post-flowering phase. Overall, the combination of water stress and high temperature caused a 45% reduction in grain yield, which was equivalent to the response observed for lentils exposed to high temperature when water was non-limiting. Evidently, the indeterminate

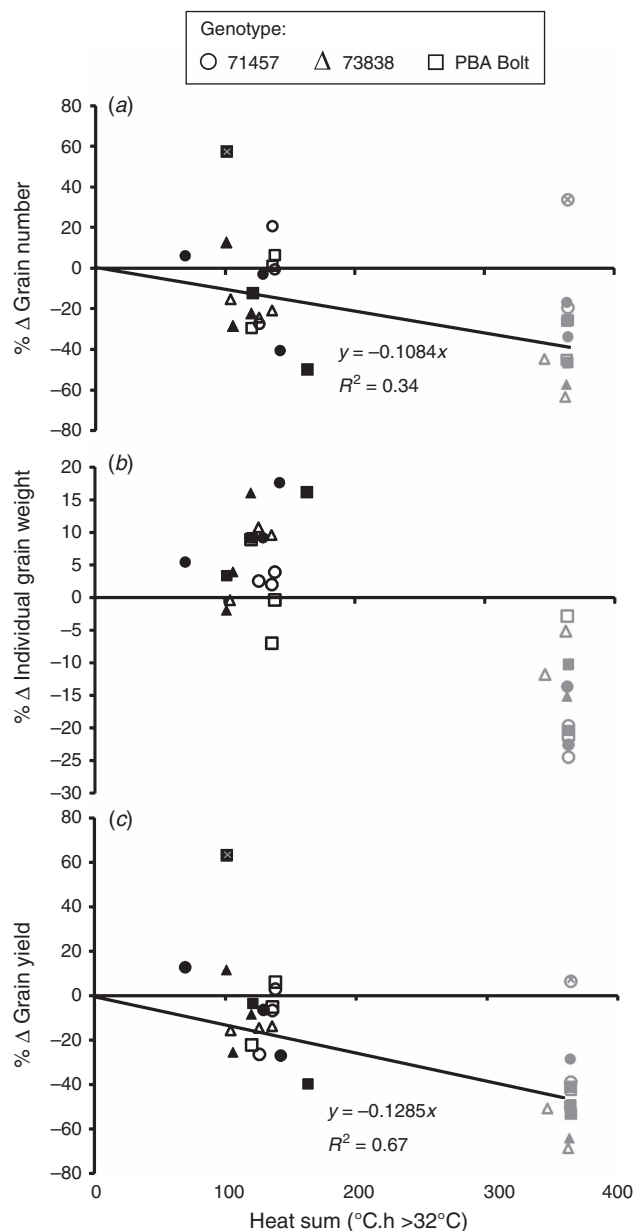


Fig. 4. Overall percentage change of lentil yield components (a) grain number, (b) individual grain weight, and (c) grain yield, due to high temperature at the early pod-filling stage. Interactive effect of two experiments on cumulative heat load (degree-hours, °C.h >32°C) and (i) water availability and (ii) CO₂ concentration are presented. The CO₂ and high temperature experiment had two CO₂ levels: ambient, 500 ppm (black unfilled symbols) and elevated, 700 ppm (black filled symbols). For the water-availability and high-temperature experiment, there were two post-flowering treatments: low water (grey unfilled symbols) and high water (grey filled symbols). For both experiments, three genotypes were assessed AGG 71457, AGG 73838 and PBA Bolt. A trend line was fitted for grain number and yield for AGG 71457 (grain number $R^2 = 0.2$, $y = -0.07x$; yield $R^2 = 0.6$, $y = -0.10x$), AGG 73838 (grain number $R^2 = 0.7$, $y = -0.15x$; yield $R^2 = 0.8$, $y = -0.16x$), where PBA Bolt (grain number $R^2 = 0.3$, $y = -0.10x$; yield $R^2 = 0.7$, $y = -0.12x$) was similar to the overall trend line (grain number $R^2 = 0.4$, $y = -0.11x$; yield $R^2 = 0.7$, $y = -0.13x$). Outliers (x) were excluded from regression analysis.

nature of lentil combined with non-limiting water did not offer a mechanism for recovery from high temperature, where the lack of recovery observed is likely due to insufficient time for further flower development ahead of maturity (Sehgal *et al.* 2017). A similar response has been recorded in other indeterminate crops including soybean, chickpea (*Cicer arietinum*) and sorghum (*Sorghum bicolor*) (Egli and Wardlaw 1980; Wang *et al.* 2006; Prasad *et al.* 2008). For chickpea, Wang *et al.* (2006) observed that high temperature imposed for 10 days at pod development caused plants to add fewer pods during post-stress recovery than equivalent stress imposed at early flowering. In contrast, non-limiting water has also been shown to reduce the impact of high temperature in lentil (Erskine and Goodrich 1991; Zakeri *et al.* 2012). Moreover, Ferris *et al.* (1999) observed that for soybean grown under ambient air temperature (winter growing period) within a glasshouse, high temperature (15°C above ambient) applied at early pod-filling combined with water stress had a synergistic effect, where the combination of stresses significantly reduced grain yield compared with the individual impact.

For our study, high temperature applied at pod-filling in lentil had a greater impact on yield components than low water, indicating the sensitivity of lentil to high temperature. This response is consistent with Sehgal *et al.* (2017), who reported that for lentil, although combined high temperature and water stress had a hypo-additive effect, individually high temperature was more damaging than water stress, causing significant reductions in biomass, grain number and yield. Overall, it is likely that the timing of high temperature relative to the crop growth stage, and time for recovery based on available water supply, are likely to drive the variable outcomes observed across a range of studies. For most lentil-growing regions globally, crops mature into terminal drought, thus limiting the opportunity for recovery by these crops from high temperatures and indicating that the indeterminacy may be of limited value in yield recovery under field conditions.

Under predicted climate-change conditions, the combined effects of a global increase in CO₂ and severity and frequency of high-temperature stress will challenge crop production; thus, understanding the collective effect is important. In studies on the combined effect of CO₂ and temperature, reported response is variable, where there is either no interactive effect, such as for cowpea and kidney bean (Ahmed *et al.* 1993; Prasad *et al.* 2002), or interactive effect (Heinemann *et al.* 2006; Prasad *et al.* 2006; Fitzgerald *et al.* 2016). In the present study, we did not observe any interaction between CO₂ and temperature treatment on grain yield or its components. This concurs with Bourgault *et al.* (2018), who found that high temperature applied to lentil at the flat-pod stage reduced yield by 33% under both ambient and elevated CO₂. Moreover, for soybean, Ferris *et al.* (1999) observed a slight but significant positive interaction between temperature and CO₂ concentration, where high temperature increased grain yield under elevated CO₂ but reduced it under ambient CO₂. These findings indicate that the response to elevated CO₂ in pulses may be affected by temperature, where at supra-optimum temperatures the impact of high temperature is worsened under increased atmospheric CO₂, potentially through increased tissue temperature, caused by partial stomatal closure (Prasad *et al.* 2008). For wheat,

combining elevated CO₂ and high temperature at grain-filling decreased screenings compared with high temperature under ambient CO₂ (Fitzgerald *et al.* 2016). Among grain legumes, (soybean, pea, peanut, common bean), CO₂ fertilisation increases average yield by 16%, compared with 19% for cereals (Kimball 2016). For the present study, there was a trend towards increased biomass and grain number (11% and 16%, respectively) for plants grown under elevated CO₂. The lack of statistically significant response to CO₂ enrichment may be due to both the variable growth habit of lentil causing large variance within treatments, and the forced pseudo-replication due to glasshouse constraints.

In this study, the overall response to high temperature, was a 0.11% and 0.13% reduction in grainset and yield, respectively for every degree-hour exceeding 32°C. This compares with a field study by Bourgault *et al.* (2018), who observed that 3 consecutive days of high temperature (120°C.h) at the pod-filling stage in lentil caused a significant decline in grain number (37%) and yield (33%), whereas individual grain weight was unaffected. The response of individual grain weight to high temperature tends to be variable: decreasing (Prasad *et al.* 2006), increasing (Ferris *et al.* 1999; Heinemann *et al.* 2006), or more commonly remaining the same (Wang *et al.* 2006; Bourgault *et al.* 2018). This range in response probably reflects differences in the timing and severity of the high-temperature scenarios and/or other environmental factors occurring during the grain-filling phase (McDonald and Paulsen 1997), where yield losses associated with a decrease in individual grain weight tend to be soon after flowering (Prasad *et al.* 2008). Furthermore, the initial plant response to high temperature is to reduce grain number, where existing assimilate is used to maintain the size of developing grains (Egli 1998; Shrestha *et al.* 2006). In the present study, the individual grain weight response varied for the two experiments, which differed in temperature treatment, suggesting that reduction in individual grain weight due to high temperature is related to the severity and duration of the high-temperature treatment. Reduction in individual grain weight occurred for Expt 1, where heat load was much higher (347°C.h) than in Expt 2 (118°C.h), where individual grain weight was less affected. A similar response was observed in kidney bean, where individual grain weight declined linearly (0.07 g per degree) only when the temperature scenario exceeded a critical threshold (32°C/22°C) (Prasad *et al.* 2006). In our study, GNC was variable across the two experiments; for Expt 1, acute high temperature caused an increase in GNC of 8%, whereas there was no effect for Expt 2 where heat load was less, indicating a variable response. For lentil, Bourgault *et al.* (2018) reported no change in GNC from 3 days of high temperature during the flat-pod stage or for plants grown under elevated CO₂. Bourgault *et al.* (2017b), however, reported that for field pea, elevated CO₂ significantly reduced GNC by 2%, thus implying that response varies across pulse crops.

The present study demonstrates a significant interaction between high-temperature response and genotype, whereby the grain number of AGG 73838 was significantly more sensitive to high temperature (reduction of 0.15% per degree-hour) than AGG 71457 (reduction of 0.07% per degree-hour). This response is consistent with previous studies in lentil

and chickpea (Gaur *et al.* 2014, 2015; Sita *et al.* 2017) and highlights the opportunity for limiting the impact of high temperature, in that maintaining grainset appears to be more important than the compensatory offset through grain size. Genotypic variation was also observed by Gaur *et al.* (2015), who identified several heat-tolerant (>35°C) lentil genotypes. Temperature tolerance was linked with stability of grainset and limiting pollen sterility at the reproductive phase. Screening for temperature tolerance in chickpea also indicated that variability in pollen viability was linked to tolerance, with tolerant genotypes remaining fertile at high temperatures, thus maintaining grainset (Devasirvatham *et al.* 2010; Sita *et al.* 2017). We demonstrate a significant interaction between water availability and genotype for grain yield, in which response varied across the three genotypes. AGG 73838 was unaffected by limited water supply, indicating a level of drought tolerance, but absolute yield was low. PBA Bolt, however, was moderately stable under low water availability and high temperature as well as having high absolute yield. The response of PBA Bolt indicates the recent success of Australian breeding in the adaptation of lentil to dryland production zones within Australia (Materne and Siddique 2009).

Next steps will include field validation to determine whether the magnitude of the response is equivalent under field conditions and whether the response observed here holds in a canopy context. Controlled-environment studies cannot account for processes occurring within a crop canopy, such as cooling linked with transpiration and/or other artefact effects associated with root temperatures (Passioura 2006; Bourgault *et al.* 2017a). Despite these limitations, controlled environments provide a valuable method for understanding response to targeted treatments where other confounding factors, which may exist in the field, can be controlled.

Conclusion

For lentils exposed to acute high temperature, adequate water supply in either the pre- or post-flowering phase did not buffer the impact of high temperature occurring at the early pod-filling stage. For plants with unlimited soil-water availability, yield was reduced to the equivalent of that observed under low water-availability treatments, and indeterminacy of growth habit did not provide an advantage. Under controlled conditions, there was no interaction between high temperature and contrasting CO₂ concentrations. The overall response of lentil to high temperature occurring at the early pod-filling stage was a reduction in grainset and yield of 0.11% and 0.13% per degree-hour (>32°C), respectively. Although, grainset was universally decreased by high temperature at the pod-filling stage, the variable response across genotypes tested indicates the opportunity to improve adaptation to high temperature by finding genetic solutions through existing lentil germplasm. This study builds our fundamental understanding of lentil response to heat wave conditions, where acute high temperature under limited water had a hypo-additive effect.

Conflicts of interest

The authors declare no conflicts of interest.

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