

Lentil yield and crop growth rate are coupled under stress but uncoupled under favourable conditions

Lachlan Lake^{a,b,*}, Victor O. Sadras^{a,b}

^a South Australian Research and Development Institute, Waite Campus, Australia

^b The University of Adelaide, School of Agriculture, Food and Wine, Australia



ARTICLE INFO

Keywords:

Biomass
Canopy
Crop growth rate
Drought
Harvest index
NDVI
Phenotyping
Stress
Temperature

ABSTRACT

Growth and yield can be decoupled in lentil whereby excessive vegetative growth leads to self-shading, reduced pod and seed set, low harvest index and higher risk of disease and lodging. We evaluated the degree of coupling between growth and yield in 20 lentil lines grown in eight environments varying in water and photothermal conditions returning a 10-fold yield range, from 21 to 221 g m⁻². Calibration curves between shoot biomass and canopy cover measured with NDVI and green canopy cover measured with Canopeo app were improved with canopy height as a multiplication factor returning a 3-D trait. Calibration curves were used to phenotype shoot biomass and calculate crop growth rate.

For the pooled data, yield correlated non-linearly with crop growth rate, with an x-intercept of 0.09 g m⁻² [°Cd]⁻¹, suggesting a minimum plant size for reproduction, and an inflection point at 0.43 g m⁻² [°Cd]⁻¹. Yield correlated with biomass and crop growth rate in the more stressful conditions (yield ≤ 107 g m⁻²) and was decoupled in higher yielding conditions (yield ≥ 170 g m⁻²). Yield associated with harvest index at all yield levels, but more strongly in high-yielding conditions. Biomass and harvest index correlated in environments with yield ≤ 107 g m⁻², and decoupled under more favourable conditions (yield ≥ 170 g m⁻²). Yield associated with phenology under stress but not in favourable conditions. For the combination of lines and environments in this study, broad sense heritability was 0.96 for flowering time, 0.93 for harvest index, 0.89 for yield, 0.87 for crop growth rate and 0.39 for biomass. Selection for harvest index would improve yield across environments whereas selection for growth rate could further improve yield under stress. Agronomic practices to improve the coupling of yield and growth under favourable conditions need to be explored; for example, using precision seeding to reduce rectangularity of crop arrangement and favour penetration of radiation into the canopy and pod set.

1. Introduction

Lentil (*Lens culinaris* Medikus subsp. *culinaris*) is a cool season grain legume grown in Mediterranean, south Asian and temperate regions either as an autumn or winter sown crop (Solanki et al., 2007; Tullu et al., 2011). Driven by demand for affordable, high quality protein (Yadav et al., 2007; Erskine, 2009; Maaz et al., 2018) global lentil production has increased from 3.5 Mt in 2000–2010 to 5.4 Mt in 2011–2018, with annual yield increases of 20 kg ha⁻¹ (FAO, 2020). During the same periods, Australian lentil production increased from 110 000–240 000 t with negligible improvement in yield reflecting the difficult growing conditions and lack of adaptation (Whitehead et al., 2000). Low and unstable yields are a major limitation to the global production of lentil (Siddique and Sykes, 1997; Materne and McNeil,

2007; Akanksha et al., 2021).

The association between yield and crop growth rate in a species-specific critical window has been demonstrated in maize, rice, wheat, canola, sunflower, pea, chickpea and soybean (Tollenaar et al., 1992; Andrade et al., 2002; Guilioni et al., 2003; Andrade et al., 2005; Takai et al., 2006; Sadras et al., 2013; Lake and Sadras, 2016; Zhang and Flottmann, 2016). Yield associated linearly with crop growth rate in chickpea (Lake and Sadras, 2016), soybean (Andrade et al., 2005), and common bean (Scully and Wallace, 1990). It associated linearly in field pea under French conditions (Guilioni et al., 2003), and non-linearly in field pea under Australian conditions (Sadras et al., 2013). A linear relationship indicates a tight coupling between vegetative and reproductive growth whereas non-linearity indicates decoupling related to morphological (e.g., maize, sunflower) or physiological (e.g., field pea)

* Corresponding author at: South Australian Research and Development Institute, Waite Campus, Australia.

E-mail address: lachlan.lake@sa.gov.au (L. Lake).

traits.

The relationship between yield and growth are critical for agronomic and genetic yield improvement and are unclear for lentil. It has been suggested that increasing biomass can increase lentil yield (Hamdi et al., 1991; Whitehead et al., 2000), but the link is unproven and relies on lack of trade-offs between biomass and harvest index. Indeed, conditions that favour prolonged vegetative growth and high biomass can associate with low harvest index, lodging, self-shading and disease (White et al., 1992; Julier et al., 1993; Hay, 1995; Siddique et al., 1998). We aim to establish the relationships between biomass, crop growth rate, harvest index and yield in lentil. Twenty lines were grown under contrasting water and photo-thermal regimes to probe for genotypic and environmental influences on the coupling between vegetative and reproductive growth. A secondary aim was to test high-throughput non-destructive methods to measure biomass and crop growth rate.

2. Methods

2.1. Plant material, environments and experimental design

We established a factorial experiment with 20 lentil lines varying in seed type and phenology (Table 1). Indianhead and Commando are overseas introductions. We included Indianhead because it has been used extensively in local breeding, and Commando for its variation in key traits including phenology and crop growth rate. Crops were grown in eight environments that resulted from the combination of two seasons (2018, 2019), two sowing dates and two water regimes. Early sowings were on the 24th of April 2018 and the 29th April 2019, and the late sowings on the 6th of June 2018 and 24th of June 2019. Early-sown crops were irrigated or rainfed. Rainout shelters were set on early-sown crops to exclude rainfall from 26th June 2018 to harvest and from 1st August 2019 to harvest. Late-sown crops were irrigated or rainfed. The combination of seasons, sowing dates and water regimes generated contrasting photothermal and water conditions (Fig. 1). There were three replicates per treatment with sowing date assigned to main plot, water regime to subplot, and lines randomised within subplots. Each experimental plot comprised six rows, 0.23 m apart, 5 m long, with target plant density 120 plants m⁻².

Crops were sown after barley on calcic luvisol soil at Roseworthy (−34.35, 138.69), South Australia. Seed was pre-treated with P-Pickel T fungicide. At sowing, we added granular Group F inoculant to the seedbed and 80 kg ha⁻¹ monoammonium phosphate. Weeds were controlled with pre-sowing herbicide [mixture of Paraquat (135 g l⁻¹)

and Diquat (115 g l⁻¹)], and a combination of grass herbicide [mixture of Butroxydim (250 g kg⁻¹) and Clethodim (240 g l⁻¹)] and hand weeding during the season. Weekly, we monitored crops for symptoms of fungal diseases and applied 2–3 fungicides during the season (Chlorothalonil, 720 g l⁻¹), ensuring one application before canopy closure to control Botrytis grey mould (*B. cinerea* and *B. fabae*). Crops were treated with insecticide (Omethoate, 290 g l⁻¹) around early podding to prevent damage from *Helicoverpa* spp.

Daily weather data were obtained from the Roseworthy weather station of the Australian Bureau of Meteorology (<https://www.longpaddock.qld.gov.au/silo/>).

2.2. Measurements

2.2.1. Phenology and yield

We scored phenology twice weekly to determine when fifty percent of the plants within the plot had reached flowering and maturity. Phenological stages are expressed on a thermal time scale with a base temperature of 0 °C (Erskine et al., 1990, 1994).

At maturity we harvested 1 m² from the four central rows of the plot to determine grain yield, biomass, seed number and seed size (individual seed weight). Harvest index was derived from total biomass and grain yield.

2.2.2. Biomass and crop growth rate

2.2.2.1. NDVI and green canopy cover calibration. We measured biomass and crop growth rate non-destructively using both Normalised Difference Vegetative Index (NDVI, Greenseeker NTech Industries Inc, California, USA) and green canopy cover measured with the Canopeo app (Patrignani and Ochsner, 2015). We established calibration plots in the same paddock and on the same sowing dates as the main trial, except for the early sowing in 2018. Calibration plots included four morphologically and phenologically different lines (PBA Blitz, Aldinga, Indianhead, PBA Greenfield) with three replicates per time of sowing. We measured NDVI, green canopy cover and plant height every 7–10 days. NDVI was measured by passing the Greenseeker over the four central rows approximately 50 cm above the canopy while Canopeo photographs were taken looking down from 1.4 m. We measured plant height in three sections of each plot, and sampled 1 m² biomass from the centre of the plot. Calibrations were fitted for the relationships between measured biomass and (a) NDVI, (b) green canopy cover, (c) NDVI x plant height and (d) green canopy cover x plant height. The inclusion of height in (c)

Table 1

Seed type, thermal time from sowing to flowering, biomass at maturity, crop growth rate and harvest index of 20 lentil lines. Values are BLUPs ± standard error across eight environments. Crop growth rate is from 900 to 1000 °Cd after sowing.

Line	Seed Type	Thermal time to flowering (°Cd)	Biomass (g m ⁻²)	Crop growth rate (g m ⁻² °Cd ⁻¹)	Harvest Index
PBA Blitz	Red	1095 ± 19.0	519 ± 47.6	0.44 ± 0.056	0.26 ± 0.023
CIPAL1701	Red	1112 ± 23.0	539 ± 47.8	0.45 ± 0.077	0.33 ± 0.025
CIPAL0901	Red	1133 ± 22.5	495 ± 40.7	0.38 ± 0.055	0.31 ± 0.019
PBA Giant	Green	1168 ± 25.0	515 ± 50.3	0.41 ± 0.052	0.18 ± 0.015
PBA Bolt	Red	1199 ± 24.7	563 ± 60.5	0.4 ± 0.059	0.26 ± 0.021
PBA Ace	Red	1208 ± 26.3	545 ± 45.8	0.5 ± 0.066	0.21 ± 0.020
PBA Jumbo2	Red	1221 ± 30.4	509 ± 52.6	0.4 ± 0.057	0.25 ± 0.018
PBA Hurricane	Red	1225 ± 25.9	491 ± 48.2	0.41 ± 0.064	0.25 ± 0.018
PBA Greenfield	Green	1249 ± 28.9	550 ± 57.9	0.42 ± 0.062	0.18 ± 0.022
CIPAL1504	Red	1249 ± 29.4	568 ± 61.2	0.37 ± 0.046	0.23 ± 0.027
Boomer	Green	1259 ± 34.7	539 ± 62.3	0.37 ± 0.040	0.19 ± 0.014
Matilda	Green	1261 ± 36.0	586 ± 79.1	0.32 ± 0.041	0.21 ± 0.022
PBA Jumbo	Red	1274 ± 36.0	520 ± 48.0	0.33 ± 0.042	0.25 ± 0.028
PBA Flash	Red	1281 ± 35.4	564 ± 55.6	0.36 ± 0.047	0.22 ± 0.023
Nugget	Red	1301 ± 42.0	445 ± 42.6	0.3 ± 0.056	0.21 ± 0.023
Aldinga	Red	1325 ± 38.6	508 ± 49.5	0.26 ± 0.041	0.22 ± 0.021
Nipper	Red	1354 ± 44.7	521 ± 60.6	0.24 ± 0.031	0.22 ± 0.025
Northfield	Red	1369 ± 46.8	533 ± 60.0	0.23 ± 0.039	0.20 ± 0.027
Commando	Red	1550 ± 64.9	451 ± 52.5	0.17 ± 0.039	0.09 ± 0.016
Indianhead	Red	1552 ± 48.0	419 ± 43.4	0.22 ± 0.042	0.03 ± 0.010

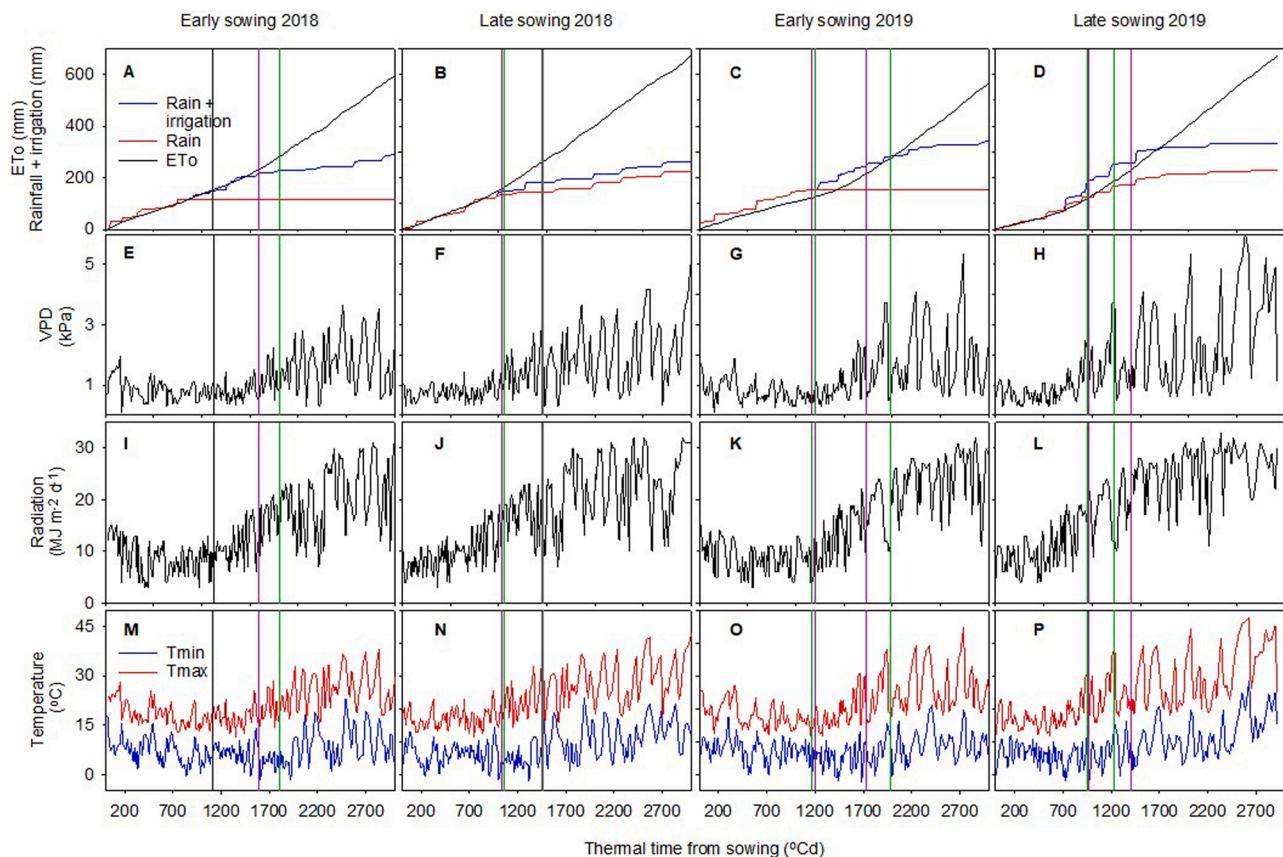


Fig. 1. Growing conditions for early- and late-sown lentil crops during two seasons. (A, B, C, D) Cumulative rainfall, irrigation and reference evapotranspiration. (E, F, G, H) Vapour pressure deficit (VPD). (I, J, K, L) Solar radiation. (M, N, O, P) Maximum and minimum temperature. Vertical lines show the range in flowering time with purple indicating rainfed and green indicating irrigated crops; lines appear black where they overlap.

and (d) seeks to add a third dimension to the 2-D nature of NDVI and green canopy cover.

2.2.2.2. Biomass and growth rate in main trial. Using the calibrations between actual biomass and green canopy cover \times plant height, we determined biomass during the season at 7–10 d intervals.

2.3. Data analyses

We used ANOVA (Genstat 20th edition) to test for the effects of line, environment and their interaction on yield and related traits. Broad sense heritability, phenotypic and genetic correlations (Cheverud, 1988) were calculated with META-R (Multi Environment Trial Analysis with R for Windows) Version 6.0. We report p -value as a continuous quantity, and Shannon information transform [$s = -\log_2(p)$] as a measure of the information against the tested hypothesis (Greenland 2019; Wasserstein et al., 2019).

To test for the degree of coupling between yield and growth, we split yield in five classes: percentile 10th, the most stressful, was yield $\leq 14 \text{ g m}^{-2}$, percentile 25th was $14 \text{ g m}^{-2} < \text{yield} \leq 56 \text{ g m}^{-2}$, percentile 50th was $56 \text{ g m}^{-2} < \text{yield} \leq 107 \text{ g m}^{-2}$, percentile 75th was $107 \text{ g m}^{-2} > \text{yield} \geq 170 \text{ g m}^{-2}$ and percentile 90th, the most favourable condition, was yield $\geq 227 \text{ g m}^{-2}$. Percentiles are commonly used as an objective approach to quantify levels of stress (Alvarez Prado et al., 2014; Sadras et al., 2016; Ciampitti and Salvagiotti, 2018; Ruiz et al., 2019). Brown-Forsythe's test supported equal variance for yield ($p = 0.184$, $s = 2.4$), biomass ($p = 0.084$, $s = 3.6$), harvest index ($p = 0.894$, $s = 0.2$) and crop growth rate ($p = 0.710$, $s = 0.5$). For each percentile, we used Model II (Reduced Maximum Axis) to correlate yield against biomass, growth rate and harvest index. Model II is necessary to account

for error in both x and y , typical of allometric relationships (Niklas, 1994).

3. Results

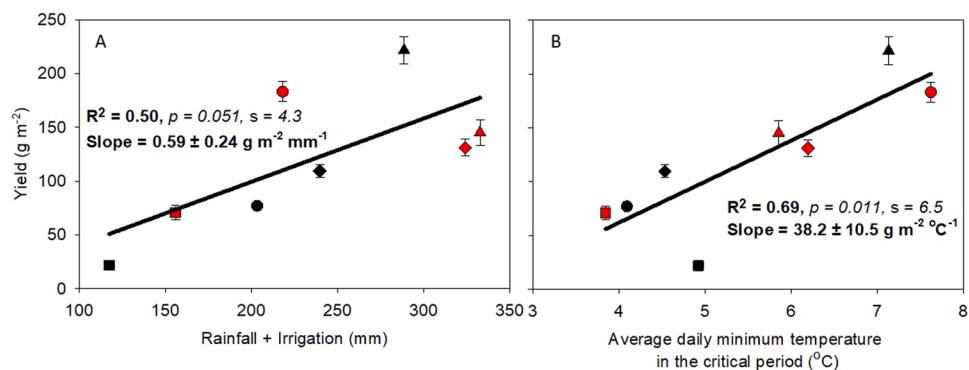
3.1. Environmental conditions

Fig. 1 shows water and photo-thermal regimes during the experiments. Growing-season rainfall + irrigation ranged from 117 mm for the early-sown rainfed crop in 2018 to 332 mm for the early-sown irrigated crop in 2019, and accounted for around 50 % of the variation in site mean yield (Fig. 2A).

The 2018 season was milder than 2019, with five fewer frost events ($< 0^\circ\text{C}$) and seven fewer heat events ($> 34^\circ\text{C}$). Average daily minimum temperature during the critical period accounted for 69 % of the variation in site mean yield (Fig. 2B).

3.2. Crop development

Time to flowering varied with line, environment and their interaction (all $p < 0.0001$, $s > 13.3$) (Tables 1 and 2, Supplementary Table 1). Broad-sense heritability of time to flowering was 0.96. With line, the range was from 1102°Cd in PBA Blitz to 1534°Cd for Indianhead. With environment, time to flowering ranged from 1040°Cd in the late-sown irrigated crop 2019 to 1453°Cd in the early-sown irrigated crop in 2019. Early-sown crops flowered on average 279°Cd later than their late-sown counterparts.

**Table 2**

Genotypic and environmental ranges, and broad-sense heritability of lentil traits measured in 20 lines grown in 8 environments. Thermal time to flowering is from sowing and crop growth rate is from 900 to 1000 °Cd after sowing.

Trait	Genotypic range		Environmental range		Broad sense heritability		
	Min	Max	Min	Max	Pooled	Min	Max
Yield (g m ⁻²)	34	175	21	221	0.89	0.35	0.91
Biomass (g m ⁻²)	480	564	196	891	0.39	0.00	0.72
Crop growth rate (g m ⁻² [°Cd] ⁻¹)	0.22	0.49	0.19	0.83	0.87	0.49	0.76
Harvest Index	0.05	0.33	0.10	0.36	0.93	0.65	0.95
Seeds (m ⁻²)	1178	4215	567.1	5439	0.89	0.56	0.92
Seed size (mg)	0.024	0.057	0.038	0.043	0.98	0.74	0.98
Thermal time to flowering (°Cd)	1102	1534	1040	1453	0.96	0.63	0.98

3.3. Phenotyping crop growth rate

Non-linear relationships between biomass and both NDVI and green canopy cover (Fig. 3AB) were improved with the inclusion of plant height (Fig. 3CD). Green canopy cover x plant height was used for calculations of biomass and crop growth rate. Crop growth rate was calculated for several time windows, and the strongest correlation with

yield was found for the period from 900 to 1000 °Cd after sowing; growth rate refers to this period hereafter.

3.4. Grain yield

Yield varied with environment and line (both *p* < 0.0001, *s* > 13.3) with no effect of interaction (*p* = 0.11, *s* = 3.2) (Supplementary

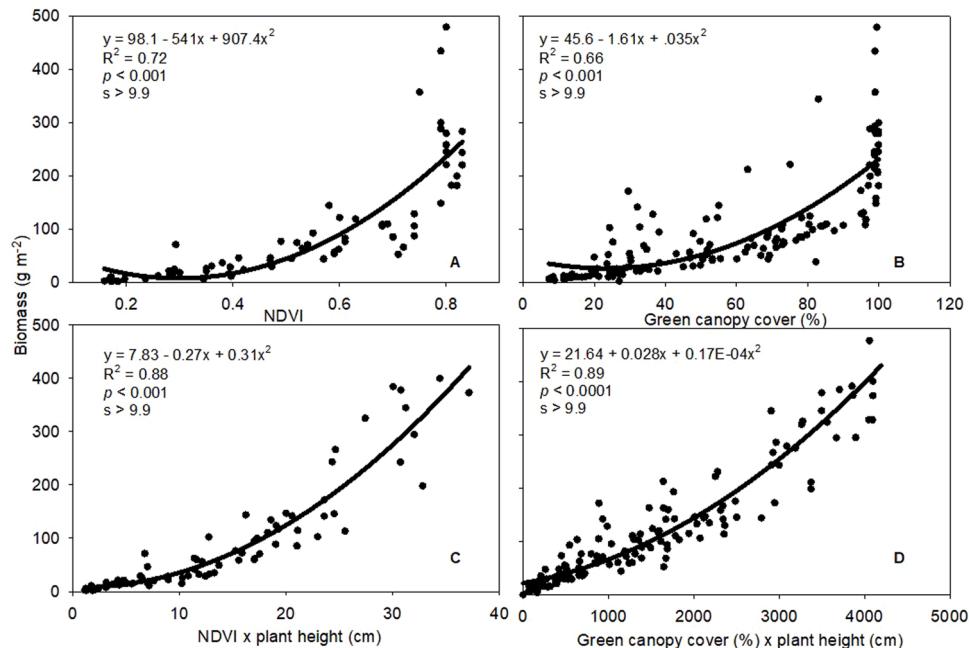


Fig. 3. Relationship between shoot biomass and: (A) NDVI; (B) green canopy cover; (C) NDVI x plant height; (D) green canopy cover x plant height of four lentil varieties grown in six environments in 2018 and 2019.

Table 1). Broad-sense heritability of yield was 0.89 (Table 2). Environmental variation of yield was 10-fold, from 21 g m⁻² in the early-sown rainfed crop in 2018 to 221 g m⁻² in the early sown irrigated crop in 2018 (Fig. 2, Table 2). Variation between lines was 5-fold from 34 g m⁻² for Indianhead to 176 g m⁻² for CIPAL 1701. For the pooled data, yield was strongly associated with seed number, largely unrelated to seed size, and associated with similar strength with both biomass and harvest index (Table 3, Supplementary Fig. 1).

For the pooled data, yield correlated negatively and weakly with time to flowering as late flowering associated with lower harvest index and smaller seed (Table 3, Supplementary Fig. 1). Further analysis showed that the association between yield and time to flowering was stronger, i.e. higher r² and steeper slope, in more stressful environments (Fig. 4A). Delayed flowering associated with a reduction in yield from 0.18 g m⁻² [°Cd]⁻¹ or 0.7 % d⁻¹ in favourable conditions to 0.22–25 g m⁻² [°Cd]⁻¹ or 3.6 % d⁻¹ in the more stressful conditions (Fig. 4A).

Setting an upper limit of 1637 °C d to flowering by exclusion of extremely late lines Indianhead and Commando showed yield declined with late flowering in the most stressful environments (yield ≤ 56 g m⁻²) and was independent of phenology in environments above this threshold (Fig. 4B). Excluding the extremely late flowering lines, yield declined 0.22 g m⁻² [°Cd]⁻¹ or 2.6 % d⁻¹ (10th percentile) and 0.16 g m⁻² [°Cd]⁻¹ or 1.9 % d⁻¹ (25th percentile) (Fig. 4B).

3.5. Environment-dependent coupling of growth and yield

Table 2 shows the ranges of biomass, crop growth rate and harvest index. Environment ($p < 0.0001$, $s > 13.3$), line ($p = 0.0026$, $s = 8.6$) and the interaction ($p = 0.045$, $s = 4.5$) affected biomass and all three sources of variation affected harvest index ($p < 0.0001$, $s = 13.3$) (Supplementary Table 1). Crop growth rate varied with environment and line (both $p < 0.0001$, $s > 13.3$) with no interaction effect. Broad-sense heritability was 0.39 for biomass, 0.87 for crop growth rate and 0.93 for harvest index.

Pooled across sources of variation, yield increased non-linearly with crop growth rate (Fig. 5). The x-intercept was 0.09 g m⁻² [°Cd]⁻¹,

suggesting a minimum plant size for reproduction. A bilinear model fitted to the data returned an inflection point at 0.43 ± 0.042 g m⁻² [°Cd]⁻¹.

To explore the non-linearity between yield and growth, Fig. 6 shows the relationships of yield with biomass, crop growth rate and harvest index; in this analysis where correlations are split by percentiles, the source of variation is line. Yield correlated with biomass except at 90th percentile, and with crop growth rate except at 75th and 90th percentiles. Yield correlated with harvest index in all five conditions, with slopes doubling from 349 g m⁻² in the most stressful environment to 648 g m⁻² in the most favourable condition.

Biomass and harvest index correlated under stress, and the association gradually weakened with more favourable conditions (Fig. 7).

4. Discussion

4.1. Accounting for plant height partially overcomes the limitations of 2-D methods to estimate biomass

Previous studies in morphologically contrasting crops including field pea, chickpea, soybean, rice, sorghum and forages have used NDVI and green canopy cover to estimate either biomass, crop growth rate or yield (Ma et al., 2001; Sadras et al., 2013; Lake and Sadras, 2016; Jáuregui et al., 2019; Phyus et al., 2020). However, the 2-D nature of these measurements leads to saturation after canopy closure. Here we show that including height to capture the third dimension improved the estimate of biomass.

4.2. Phenology was important under stress and neutral under favourable conditions

Early flowering is a typical stress-avoidance trait (Berger et al., 2006; Ludwig and Asseng, 2010). For all 20 lines in our study, early flowering was more strongly associated with yield in stressful environments. This conclusion was reinforced by exclusion of two extremely late lines, showing early flowering was only important in the two most stressful

Table 3

Phenotypic (blue) and genetic (black) correlation between crop traits for 20 lentil lines grown in 8 environments. Each row presents from top to bottom: r (bold), p and s (italics).

	Yield	Biomass	Harvest index	Seeds m ⁻²	Seed size	Time to flowering	Crop growth rate
Yield	0.77 <i>< 0.001</i>	0.74 <i>< 0.001</i>	0.95 <i>< 0.001</i>	0.19 <i>0.019</i>	-0.20 <i>0.012</i>	0.43 <i>< 0.001</i>	
	<i>> 9.9</i>	<i>> 9.9</i>	<i>> 9.9</i>	<i>5.7</i>	<i>6.4</i>		<i>> 9.9</i>
Biomass	0.84 <i>< 0.001</i>	0.24 <i>0.003</i>	0.72 <i>< 0.001</i>	0.12 <i>0.135</i>	0.11 <i>0.169</i>	0.18 <i>0.027</i>	
	<i>> 9.9</i>	<i>8.4</i>	<i>> 9.9</i>	<i>2.9</i>	<i>2.6</i>		<i>5.2</i>
Harvest index		0.78 <i>< 0.001</i>		0.71 <i>< 0.001</i>	0.23 <i>0.004</i>	-0.53 <i>< 0.001</i>	0.50 <i>< 0.001</i>
		<i>> 9.9</i>		<i>> 9.9</i>	<i>8.0</i>	<i>> 9.9</i>	<i>> 9.9</i>
Seeds m ⁻²		0.59 <i>0.005</i>	0.83 <i>< 0.001</i>		-0.05 <i>0.569</i>	-0.13 <i>0.097</i>	0.41 <i>< 0.001</i>
		<i>< 0.001</i>	<i>7.6</i>		<i>0.81</i>	<i>3.4</i>	<i>> 9.9</i>
Seed size		0.69 <i>< 0.001</i>	0.39 <i>0.078</i>	-0.17 <i>0.459</i>		-0.35 <i>< 0.001</i>	0.08 <i>0.321</i>
		<i>> 9.9</i>	<i>3.7</i>	<i>1.1</i>		<i>> 9.9</i>	<i>1.6</i>
Time to flowering	-0.83 <i>< 0.001</i>	-0.85 <i>< 0.001</i>	-0.87 <i>< 0.001</i>	-0.54 <i>0.011</i>	-0.63 <i>0.002</i>		-0.46 <i>< 0.001</i>
	<i>> 9.9</i>	<i>> 9.9</i>	<i>> 9.9</i>	<i>6.5</i>	<i>9.0</i>		<i>> 9.9</i>
Crop growth rate	0.61 <i>0.003</i>	0.70 <i>< 0.001</i>	0.65 <i>0.001</i>	0.28 <i>0.22</i>	0.62 <i>0.002</i>	-0.94 <i>< 0.001</i>	
	<i>> 9.9</i>	<i>10.0</i>	<i>2.2</i>	<i>9.0</i>	<i>> 9.9</i>		

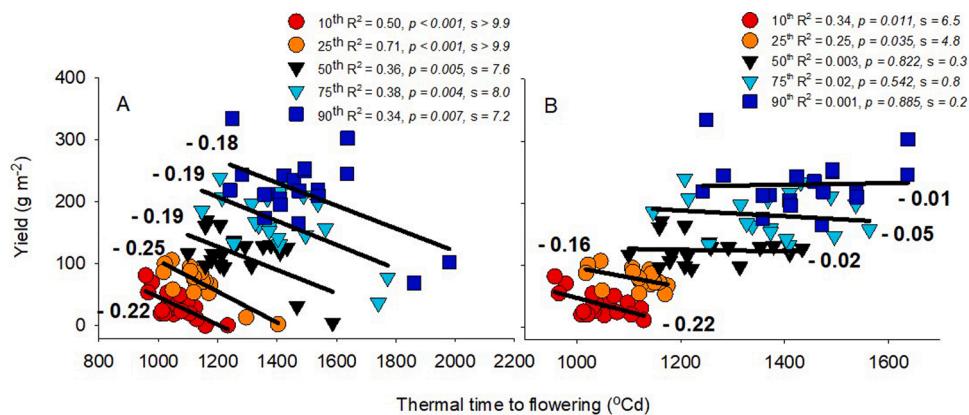


Fig. 4. Relationship between yield and (A) time to flowering of all 20 lines and (B) time to flowering of lines excluding the extremely late flowering Indianhead and Commando. The 10th, 25th, 50th, 75th and 90th percentiles are plotted for both x and y and represent the range from more stressful to more favourable conditions. Lines are least-square regressions, with numbers indicating slopes in $\text{g m}^{-2} [\text{°Cd}]^{-1}$.

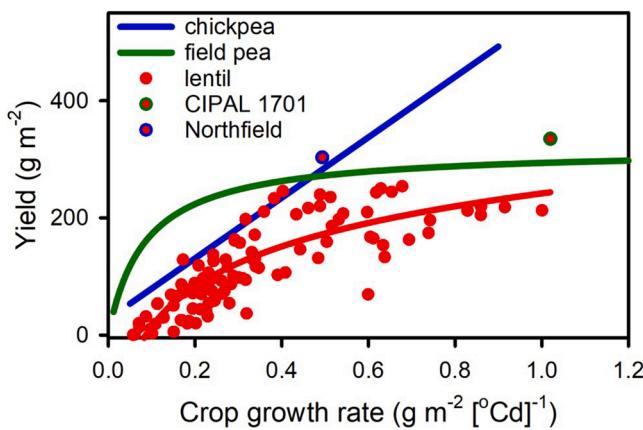


Fig. 5. Relationship between crop growth rate and yield in lentil. The fitted curve is $a + b \ln(x)$, with $a = 241.5 \pm 9.34$ and $b = 98.8 \pm 6.73$, $R^2 = 0.69$, $p < 0.001$, $s > 9.9$). Two high-yielding varieties with contrasting phenotypes are highlighted: CIPAL 1701 and Northfield. Included for comparison are fitted models for chickpea from a factorial of 29 lines x 10 environments (Lake and Sadras, 2016) and for field pea from a factorial of 20 lines x 8 environments (Sadras et al., 2013).

environments where severe water stress limited yield. Importantly, there was no penalty for early flowering lines in favourable conditions. The high heritability of phenology in our sample of lines and environments agrees with Turkish and Indian lentil trials where heritability of time to flowering was 0.94 and 0.92 (Biçer and Şakar, 2008; Singh and Srivastava, 2013).

4.3. Yield was coupled with biomass under stress but not under favourable conditions

Adaptation to drought must not compromise yield potential (Sadras and Richards, 2014), hence the importance of screening genotypes over the whole agronomic range. Here we sampled a 10-fold yield range up to 221 g m^{-2} , which compares with 330 g m^{-2} in the high yield potential environment of Canterbury, New Zealand (McKenzie and Hill, 1990). Our results conform with studies with an average biomass of 380 g m^{-2} and harvest index averaging 0.33 (Shrestha et al., 2005; Unkovich et al., 2010). Published crop growth rates are in days, not thermal time, but compare with ours in the range from 0.96 to $23 \text{ g m}^{-2} \text{ day}$ (McKenzie and Hill, 1990; Shrestha et al., 2005).

We found yield associated with biomass and crop growth rate under stressful conditions, and the relationship weakened in higher yielding

conditions. This was reinforced in 2019 when the late-sown rainfed crop out yielded the early-sown irrigated crop; the high yield of the late-sown crop was partially associated with the strong influence of minimum temperature during the critical period (Fig. 2B).

Experiments with lentil in West Asia with yield between 100 and 320 g m^{-2} concluded that selection for biomass will favour seed yield in all environments (Hamdi et al., 1991). Similar conclusions were formed from observations on lentil progenitors, landraces, older and newer lentil varieties in Western Australian and UK where yields ranged from crop failure to $> 250 \text{ g m}^{-2}$ (Whitehead et al., 2000). However, Whitehead et al. (2000) found that the relationship between biomass and yield became more scattered in the higher yielding environments. In the U.S. Pacific Northwest, yield and biomass correlated in low yielding conditions ($< 70 \text{ g m}^{-2}$), but the relationship weakened and became negative in high yielding environments (230 g m^{-2}) supporting the notion of a decoupling (Kusmenoglu and Muehlbauer, 1998). In southern Australia, a similar decoupling of crop growth rate and yield in favourable conditions was found in both field pea and chickpea (Sadras et al., 2013; Lake and Sadras, 2016).

The decoupling of growth and yield under favourable conditions can be associated with a number of non-mutually exclusive reasons. The higher-biomass, irrigated crops experienced some lodging in our trials with extreme shading in lower parts of the canopy. Radiation penetration may affect pod retention in deeper parts of the canopy – this can be trophic to the extent that pods depend on locally reduced carbon (Hardwick, 1986) or mediated by light quality (Heindl and Brun, 1983; Myers et al., 1987). Contributions of pod photosynthesis to seed yield can be important in legumes, e.g., up to 48 % in alfalfa (Wang et al., 2016) and up to 20 % for faba bean (Austin et al., 1981). We found no reports of pod photosynthesis in lentil. Vigorous crops favour diseases such as botrytis grey mould (*Botrytis fabae* and *B. cinerea*), which thrives in dense canopies (Lindbeck et al., 2008). Despite regular fungicide treatments, sections of our 2018 early-sown irrigated plot matched the conditions needed for disease and experienced severe damage from botrytis, none-the-less returning high yields.

Rapid growth favours canopy cover, photosynthetic capacity and the number of reproductive nodes (Whitehead et al., 2000). However, the indeterminate nature and leaf orientation of lentil may decouple biomass and yield in favourable conditions (Cohen, 1971; Amir and Cohen, 1990). Once canopy closure and maximum radiation interception are reached, continuous vegetative growth can cause shading of reproductive structures, flower and pod abscission (Jiang and Egli, 1993; Ayaz, 2001; Ayaz et al., 2004; Kantolic et al., 2013). A high canopy extinction coefficient due to the planar leaves exacerbates this problem (Thomson and Siddique, 1997; Ayaz, 2001). In New Zealand maximum radiation absorption was reached at leaf area index (LAI) of 7,

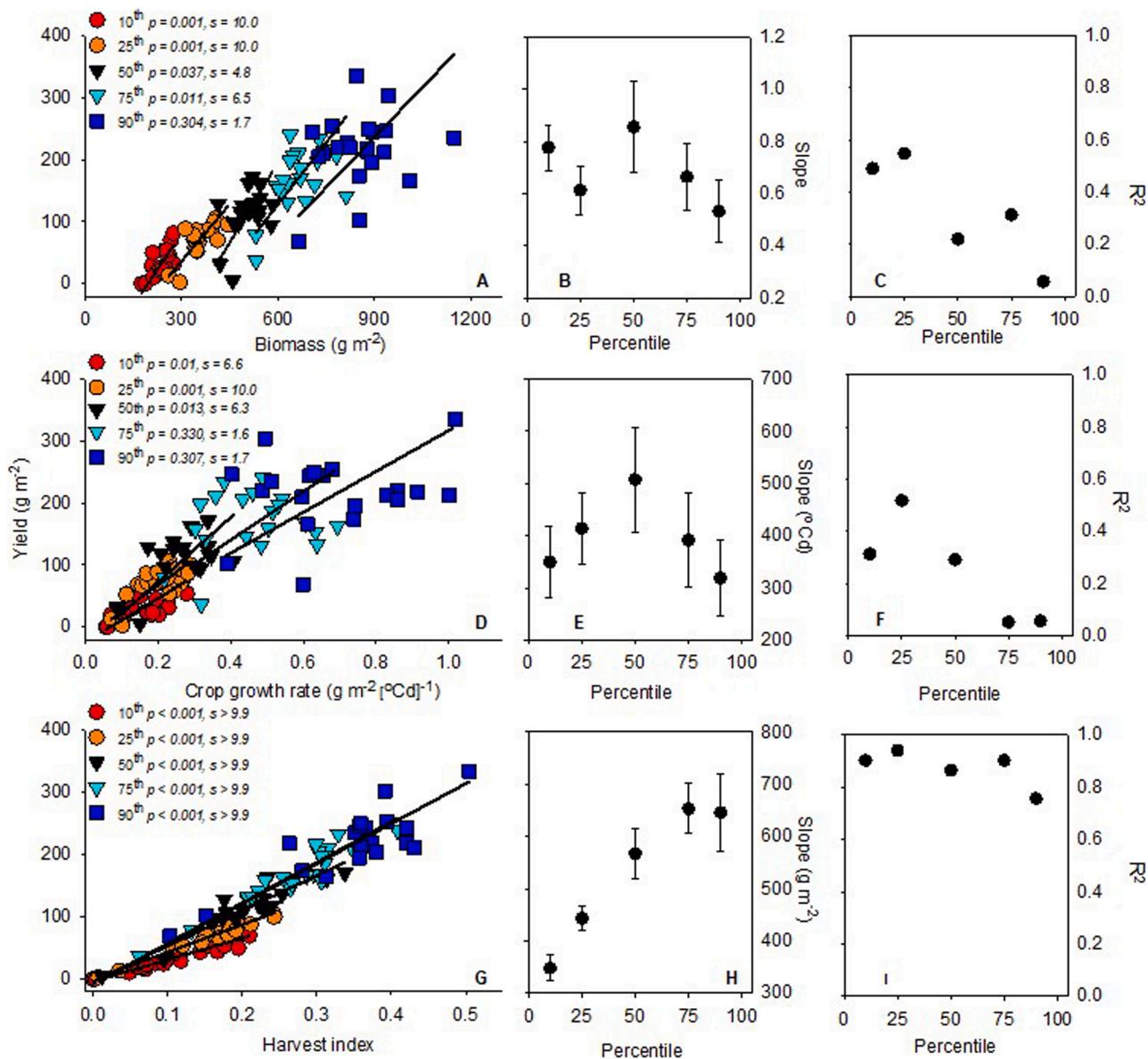


Fig. 6. Relationship between yield and (A) biomass, (D) crop growth rate and (G) harvest index for the combination of 20 lines and 8 environments where the 10th, 25th, 50th, 75th and 90th percentiles are plotted for both x and y and represent a range from more stressful to more favourable conditions. Lines are Model II (Reduced Major Axis) regressions accounting for error in both variables (Ludbrook, 2012). Slope $\pm \text{s.e.}$ of the regression between yield and (B) biomass, (E) crop growth rate and (H) harvest index. The R^2 of the regression between yield and (C) biomass, (F) crop growth rate and (I) harvest index.

but canopies increased up to a LAI of 12 (McKenzie and Hill, 1991). Problems associated with conversion of biomass into yield were reported in a New Zealand study investigating the effects of shade and irrigation on chickpea, which found yield and harvest index were lower in irrigated, vigorous crops compared with unirrigated controls (Verghis et al., 1999).

4.4. Harvest index correlated with biomass under stress but not under favourable conditions

In lentil, there are reports of negative (Hamdi et al., 1991; Scully et al., 1991; Kusmenoglu and Muehlbauer, 1998) or slightly positive correlations (Karadavut, 2009) between biomass and harvest index, and lack of correlation has also been reported (Singh, 1977). Our study explains these inconsistencies whereby the correlation between biomass and harvest index is conditional to the level of stress. For our experimental conditions, an upper limit of harvest index of around 0.4 was

reached when biomass exceeded $\sim 600 \text{ g m}^{-2}$. An upper limit of crop growth rate was also reached at the same biomass, which may indicate the point of maximum radiation interception and the beginning of issues associated with self-shading. For yield $\leq 107 \text{ g m}^{-2}$, lines with higher biomass, such as CIPAL 0901 and CIPAL 1701, also had higher harvest index. However for yield $> 107 \text{ g m}^{-2}$, the relationship between biomass and harvest index disappeared. The lines CIPAL 0901 and CIPAL 1701 were also amongst the highest yielding in favourable conditions and had consistently high harvest index. Indianhead and Commando had consistently low harvest index, which was associated with the late flowering. For our set of lines and environments, harvest index had high heritability as in soybean, common bean and vetch (Schapaugh and Wilcox, 1980; Scully et al., 1991; Atuahene-Amankwa and Michaels, 1997; Cakmakci et al., 2006).

Conceptual models of crop yield often assume the independence of biomass and harvest index. For example in wheat grown under high-yielding conditions, harvest index is reaching its biological limit, and

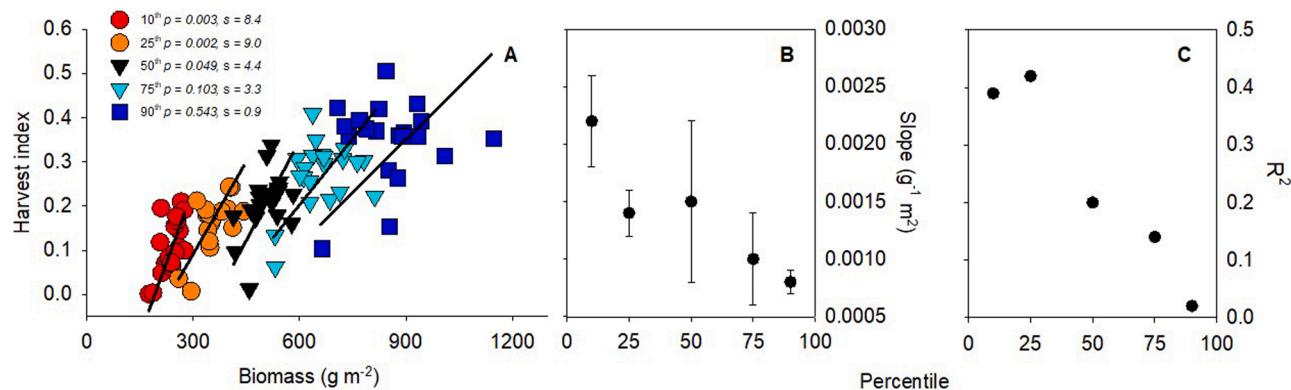


Fig. 7. (A) Relationship between harvest index and biomass for the combination of 20 lines and 8 environments where the 10th, 25th, 50th, 75th and 90th percentiles are plotted for both x and y and represent a range from more stressful to more favourable conditions. Lines are Model II (Reduced Major Axis) regressions accounting for error in both variables (Ludbrook, 2012). (B) Slope \pm s.e. of the regression between harvest index and biomass. (C) The R^2 of the regression between harvest index and biomass.

efforts are placed in improving biomass, under the implicit assumption of independence of these traits (Reynolds et al., 2009, 2012; Deery et al., 2020). At the plant level, harvest index and biomass are not independent; the determinate reproductive strategy of sunflower and maize means that under high availability of resources strong apical dominance limits yield and reduces harvest index, while in crops such as soybean there is a greater capacity to respond to favourable conditions with more stable harvest index (Vega et al., 2000).

4.5. Pea-like and chickpea-like phenotypes could improve lentil yield potential

Fig. 5 compares the yield-growth curves for lentil, chickpea and field pea in similar environments of South Australia, with similar ranges of genotypic and environmental sources of variation. Whereas field pea and chickpea had zero-intercept models, the x-intercept of the model for lentil was $0.09 \text{ g m}^{-2} [{}^\circ\text{Cd}]^{-1}$. This suggests a minimum plant size for reproduction (Weiner et al., 2009) and a greater sensitivity to stress in lentil. Field pea is the fastest-growing crop under stress, with a bilinear model returning an inflection point at a growth rate of $0.29 \pm 0.022 \text{ g m}^{-2} [{}^\circ\text{Cd}]^{-1}$. In comparison, the inflection point was $0.43 \pm 0.042 \text{ g m}^{-2} [{}^\circ\text{Cd}]^{-1}$ for lentil. Overall, field pea and chickpea out-yield lentil at similar growth rates. However, even with a small sample of 20 lines, we identified lentil lines with phenotypes similar to field pea or chickpea, returning higher-than-average yield under favourable conditions. CIPAL 1701 is a fieldpea-like lentil (red symbol with green edge in Fig. 5), with high growth rate and yield as high as field pea. Northfield is a chickpea-like type (red symbol with blue edge in Fig. 5), with substantially lower growth rate than CIPAL 1701 under potential conditions, but a growth-yield coupling comparable to that of chickpea.

5. Conclusions

Our research highlights the decoupling of growth and yield underlying the low yield of lentil in favourable conditions. The similarity between phenotypic and genetic correlation matrices of key crop traits indicates that the effects of genetic and environmental factors are channelled through a common, relatively invariant, developmental system (Cheverud, 1988; Waitt and Levin, 1998). Thus, agronomic and genetic approaches could equally be exploited to improve the coupling of growth and yield of lentil. Harvest index had a robust association with yield across environments and a higher heritability than biomass, hence it should be a profitable breeding target. Pea-like and chickpea-like lentil phenotypes were identified in our small sample, highlighting variability to be exploited. Agronomic practices to improve the coupling of yield and growth under favourable conditions include precision

seeding to reduce rectangularity of crop arrangements (Satorre and Maddonni, 2018) to improve penetration of radiation into the canopy and pod set.

Credit authorship contribution statement

Lachlan Lake was responsible for conceptualisation, methodology, validation, formal analysis, investigation, writing, visualisation, project administration and funding acquisition. Victor Sadras was responsible for conceptualisation, methodology, validation, formal analysis, supervision, writing, visualisation, project administration and funding acquisition

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the Grains Research and Development Corporation of Australia for financial support; Penny Roberts, Phil Rundle, John Nairne and SARDI Clare for the maintenance of crops; Han Chow, Hadtamu Tura, Vy-Price Beck, Annabel O'Dea, Tanja Lenz, Jose Fernandez, Justyn Thompson and Tan Dang for field and laboratory work; Garry Rosewarne, Jason Brand and Arun Shunmugan for seed and information.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.eja.2021.126266>.

References

- Akanksha, S., Kumari, S., Rehman, A., Farooq, M., Kumar, S., Yadav, R., Nayyar, H., Singh, S., Siddique, K.H.M., 2021. Lentil. In: Sadras, V., Calderini, D. (Eds.), *Crop Physiology. Case Studies in Major Crops*.
- Alvarez Prado, S., Sadras, V.O., Borrás, L., 2014. Independent genetic control of maize (*Zea mays L.*) kernel weight determination and its phenotypic plasticity. *J. Exp. Bot.* 65, 4479–4487. <https://doi.org/10.1093/jxb/eru215>.
- Amir, S., Cohen, D., 1990. Optimal reproductive efforts and the timing of reproduction of annual plants in randomly varying environments. *J. Theor. Biol.* 147, 17–42. [https://doi.org/10.1016/S0022-5193\(05\)80250-4](https://doi.org/10.1016/S0022-5193(05)80250-4).
- Andrade, F.H., Calvino, P., Cirilo, A., Barbieri, P., 2002. Yield responses to narrow rows depend on increased radiation interception. *Agron. J.* 94, 975–980. <https://doi.org/10.2134/agronj2002.9750>.
- Andrade, F.H., Sadras, V.O., Vega, C.R.C., Echarte, L., 2005. Physiological determinants of crop growth and yield in maize, sunflower and soybean: their application to crop

- management, modeling and breeding. *J. Crop. Improv.* 14, 51–101. https://doi.org/10.1300/J411v14n01_05.
- Atuahene-Amankwa, G., Michaels, T., 1997. Genetic variances, heritabilities and genetic correlations of grain yield, harvest index and yield components for common bean (*Phaseolus vulgaris* L.) in sole crop and in maize/bean intercrop. *Can. J. Plant Sci.* 77, 533–538. <https://doi.org/10.4141/P96-168>.
- Austin, R., Morgan, C., Ford, M., 1981. A Field Study of the Carbon Economy of Normal and 'topless' Field Beans (*Vicia Faba*). *Vicia faba: Physiology and Breeding*. Springer, pp. 60–79. https://doi.org/10.1007/978-94-009-8308-3_5.
- Ayaz, S., 2001. *Variability of Harvest Index in Four Grain Legume Species*. Lincoln University.
- Ayaz, S., McKenzie, B.A., Hill, G.D., McNeil, D.L., 2004. Variability in yield of four grain legume species in a subhumid temperate environment I. Yields and harvest index. *J. Agric. Sci.* 142, 9–19. <https://doi.org/10.1017/S0021859604004101>.
- Berger, J.D., Ali, M., Basu, P.S., Chaudhary, B.D., Chaturvedi, S.K., Deshmukh, P.S., Dharmaraj, P.S., Dwivedi, S.K., Gangadhar, G.C., Gaur, P.M., Kumar, J., Pannu, R.K., Siddique, K.H.M., Singh, D.N., Singh, D.P., Singh, S.J., Turner, N.C., Yadava, H.S., Yadav, S.S., 2006. Genotype by environment studies demonstrate the critical role of phenology in adaptation of chickpea (*Cicer arietinum* L.) to high and low yielding environments of India. *Field Crop. Res.* 98, 230–244. <https://doi.org/10.1016/j.fcr.2006.02.007>.
- Biçer, B., Şakar, D., 2008. Heritability and path analysis of some economical characteristics in lentil. *J. Cent. Eur. Agric.* 9, 175–180.
- Cakmakci, S., Aydinoglu, B., Karaca, M., Bilgen, M., 2006. Heritability of yield components in common vetch (*Vicia sativa* L.). *Acta Agric. Scand. Section B-Soil Plant Sci.* 56, 54–59. <https://doi.org/10.1080/09064710510008531>.
- Cheverud, J.M., 1988. A comparison of genetic and phenotypic correlations. *Evolution* 42, 958–968. <https://doi.org/10.1111/j.1558-5646.1988.tb02514.x>.
- Ciampitti, I.A., Salvagiotti, F., 2018. New insights into soybean biological nitrogen fixation. *Agron. J.* 110, 1185–1196. <https://doi.org/10.2134/agronj2017.06.0348>.
- Cohen, D., 1971. Maximizing final yield when growth is limited by time or by limiting resources. *J. Theor. Biol.* 33, 299–307. [https://doi.org/10.1016/0022-5193\(71\)90068-3](https://doi.org/10.1016/0022-5193(71)90068-3).
- Deery, D.M., Rebetzke, G.J., Jimenez-Berni, J.A., Condon, A.G., Smith, D.J., Bechaz, K.M., Bovill, W.D., 2020. Ground-based LiDAR improves phenotypic repeatability of above-ground biomass and crop growth rate in wheat. *Plant Phenomics* 2020, 1–11. <https://doi.org/10.34133/2020/8329798>.
- Erskine, W., 2009. *The Lentil: Botany, Production and Uses*. CABI.
- Erskine, W., Ellis, R.H., Summerfield, R.J., Roberts, E.H., Hussain, A., 1990. Characterization of responses to temperature and photoperiod for time to flowering in a world lentil collection. *Theor. Appl. Genet.* 80, 193–199. <https://doi.org/10.1007/bf00224386>.
- Erskine, W., Hussain, A., Tahir, M., Bahksh, A., Ellis, R.H., Summerfield, R.J., Roberts, E.H., 1994. Field evaluation of a model of photothermal flowering responses in a world lentil collection. *Theor. Appl. Genet.* 88, 423–428. <https://doi.org/10.1007/bf00223655>.
- FAO, 2020. FAOSTAT. Food and Agriculture Organization of the United Nations. FAO. <http://www.fao.org/faostat/en/#data/QC>.
- Guilioni, L., Wery, J., Lecoeur, J., 2003. High temperature and water deficit may reduce seed number in field pea purely by decreasing plant growth rate. *Funct. Plant Biol.* 30, 1151–1164. <https://doi.org/10.1071/fp03105>.
- Hamdi, A., Erskine, W., Gates, P., 1991. Relationships among economic characters in lentil. *Euphytica* 57, 109–116. <https://doi.org/10.1007/BF00023068>.
- Hardwick, R., 1986. Physiological consequences of modular growth in plants. *Philos. Trans. R. Soc. Lond. B, Biol. Sci.* 313, 161–173. <https://doi.org/10.1098/rstb.1986.0031>.
- Hay, R., 1995. Harvest index: a review of its use in plant breeding and crop physiology. *Ann. Appl. Biol.* 126, 197–216. <https://doi.org/10.1111/j.1744-7348.1995.tb05015.x>.
- Heindl, J.C., Brun, W.A., 1983. Light and shade effects on abscission and 14C-photoassimilate partitioning among reproductive structures in soybean. *Plant Physiol.* 73, 434–439. <https://doi.org/10.1104/pp.73.2.434>.
- Jáuregui, J.M., Delbino, F.G., Bonvini, M.I.B., Berhongaray, G., 2019. Determining yield of forage crops using the Canopeo mobile phone app. *J. N. Z. Grasslands* 81, 41–46. <https://doi.org/10.33584/jnzg.2019.81.385>.
- Jiang, H.F., Egli, D.B., 1993. Shade induced changes in flower and pod number and flower and fruit abscission in soybean. *Agron. J.* 85, 221–225. <https://doi.org/10.2134/agronj1993.0002196200850002001x>.
- Julier, B., Huyghe, C., Papineau, J., Milford, G., Day, J., Billot, C., Mangin, P., 1993. Seed yield and yield stability of determinate and indeterminate autumn-sown white lupins (*Lupinus albus*) grown at different locations in France and the UK. *J. Agric. Sci.* 121, 177–186. <https://doi.org/10.1017/S0021859600077030>.
- Kantolic, A.G., Peralta, G.E., Slafer, G.A., 2013. Seed number responses to extended photoperiod and shading during reproductive stages in indeterminate soybean. *Eur. J. Agron.* 51, 91–100. <https://doi.org/10.1016/j.eja.2013.07.006>.
- Karadavut, U., 2009. Path analysis for yield and yield components in lentil (*Lens culinaris Medik.*). *Turk. J. Field Crops* 14, 97–104.
- Kusmenoglu, I., Muehlbauer, F.J., 1998. Genetic variation for biomass and residue production in lentil: I. Relation to agronomic traits. *Crop Sci.* 38, 907–910. <https://doi.org/10.2135/cropsci1998.0011183X003800040002x>.
- Lake, L., Sadras, V.O., 2016. Screening chickpea for adaptation to water stress: Associations between yield and crop growth rate. *Eur. J. Agron.* 81, 86–91. <https://doi.org/10.1016/j.eja.2016.09.003>.
- Lindbeck, K.D., Bretag, T.W., Materne, M.A., 2008. Field screening in Australia of lentil germplasm for resistance to botrytis grey mould. *Australas. Plant Pathol.* 37, 373–378. <https://doi.org/10.1071/ap08012>.
- Ludbrook, J., 2012. A primer for biomedical scientists on how to execute Model II linear regression analysis. *Clin. Exp. Pharmacol. Physiol.* 39, 329–335. <https://doi.org/10.1111/j.1440-1681.2011.05643.x>.
- Ludwig, F., Asseng, S., 2010. Potential benefits of early vigor and changes in phenology in wheat to adapt to warmer and drier climates. *Agric. Syst.* 103, 127–136. <https://doi.org/10.1016/j.agrsv.2009.11.001>.
- Ma, B.L., Dwyer, L.M., Costa, C., Cober, E.R., Morrison, M.J., 2001. Early prediction of soybean yield from canopy reflectance measurements ECORC Contrib. no. 11618. *Agron. J.* 93, 1227–1234. <https://doi.org/10.2134/agronj2001.1227>.
- Maaz, T., Wulfforst, J.D., McCracken, V., Kirkegaard, J., Huggins, D.R., Roth, I., Kaur, H., Pan, W., 2018. Economic, policy, and social trends and challenges of introducing oilseed and pulse crops into dryland wheat cropping systems. *Agric. Ecosyst. Environ.* 253, 177–194. <https://doi.org/10.1016/j.agee.2017.03.018>.
- Materne, M., McNeil, D.L., 2007. *Breeding Methods and Achievements*. Lentil. Springer, pp. 241–253.
- McKenzie, B., Hill, G., 1990. Growth, yield and water use of lentils (*Lens culinaris*) in Canterbury, New Zealand. *J. Agric. Sci.* 114, 309–320. <https://doi.org/10.1017/S0021859600072701>.
- McKenzie, B., Hill, G., 1991. Intercepted radiation and yield of lentils (*Lens culinaris*) in Canterbury, New Zealand. *J. Agric. Sci.* 117, 339–346. <https://doi.org/10.1017/S0021859600067083>.
- Myers, R.L., Brun, W.A., Brenner, M.L., 1987. Effects of raceme-localized supplemental light on soybean reproductive abscission. *Crop Sci.* 27, 273–277. <https://doi.org/10.2135/cropsci1987.0011183X002700020031x>.
- Niklas, K.J., 1994. *Plant Allometry: the Scaling of Form and Process*. University of Chicago Press.
- Patrignani, A., Ochsner, T.E., 2015. Canopeo: a powerful new tool for measuring fractional green canopy cover. *Agron. J.* 107, 2312–2320. <https://doi.org/10.2134/agronj15.0150>.
- Reynolds, M., Foulkes, M.J., Slafer, G.A., Berry, P., Parry, M.A., Snape, J.W., Angus, W.J., 2009. Raising yield potential in wheat. *J. Exp. Bot.* 60, 1899–1918. <https://doi.org/10.1093/jxb/erp016>.
- Phyu, P., Islam, M.R., Sta Cruz, P.C., Collard, B.C.Y., Kato, Y., 2020. Use of NDVI for indirect selection of high yield in tropical rice breeding. *Euphytica* 216, 74. <https://doi.org/10.1007/s10681-020-02598-7>.
- Reynolds, M., Foulkes, M.J., Furbank, R., Griffiths, S., King, J., Murchie, E., Parry, M., Slafer, G., 2012. Achieving yield gains in wheat. *Plant Cell Environ.* 35, 1799–1823. <https://doi.org/10.1111/j.1365-3040.2012.02588.x>.
- Ruiz, M.B., D'Andrea, K.E., Otegui, M.E., 2019. Phenotypic plasticity of maize grain yield and related secondary traits: differences between inbreds and hybrids in response to contrasting water and nitrogen regimes. *Field Crop. Res.* 239, 19–29. <https://doi.org/10.1016/j.fcr.2019.04.004>.
- Sadras, V.O., Richards, R.A., 2014. Improvement of crop yield in dry environments: benchmarks, levels of organisation and the role of nitrogen. *J. Exp. Bot.* 65, 1981–1995. <https://doi.org/10.1093/jxb/eru061>.
- Sadras, V.O., Lake, L., Leonforte, A., McMurray, L.S., Paull, J.G., 2013. Screening field pea for adaptation to water and heat stress: associations between yield, crop growth rate and seed abortion. *Field Crop. Res.* 150, 63–73. <https://doi.org/10.1016/j.fcr.2013.05.023>.
- Sadras, V.O., Lake, L., Li, Y., Drew, E., Sutton, T., 2016. Phenotypic plasticity and its genetic regulation for yield, nitrogen fixation and $\delta^{13}\text{C}$ in chickpea crops under varying water regimes. *J. Exp. Bot.* 67, 4339–4351. <https://doi.org/10.1093/jxb/erw221>.
- Satorre, E.H., Maddonni, G.A., 2018. Spatial crop structure in agricultural systems. In: Meyers, R.A. (Ed.), *Encyclopedia of Sustainability Science and Technology*. Springer, New York, New York, NY, pp. 1–17. https://doi.org/10.1007/978-1-4939-2493-6_223-3.
- Schapaugh Jr., W., Wilcox, J., 1980. Relationship between harvest indices and other plant characteristics in soybean 1. *Crop Sci.* 20, 529–533. <https://doi.org/10.2135/cropsci1980.0011183X002000040028x>.
- Scully, B., Wallace, D., 1990. Variation in and relationship of biomass, growth rate, harvest index, and phenology to yield of common bean. *J. Am. Soc. Hortic. Sci.* 115, 218–225. <https://doi.org/10.21273/JASHS.115.2.218>.
- Scully, B., Wallace, D., Viands, D., 1991. Heritability and correlation of biomass, growth rates, harvest index, and phenology to the yield of common beans. *J. Am. Soc. Hortic. Sci.* 116, 127–130. <https://doi.org/10.21273/JASHS.116.1.127>.
- Shrestha, R., Siddique, K., Turner, N., Turner, D., Berger, J., 2005. Growth and seed yield of lentil (*Lens culinaris Medikus*) genotypes of West Asian and South Asian origin and crossbreds between the two under rainfed conditions in Nepal. *Aust. J. Agric. Resour. Econ.* 56, 971–981. <https://doi.org/10.1071/AR05050>.
- Siddique, K., Sykes, J., 1997. Pulse production in Australia past, present and future. *Aust. J. Exp. Agric.* 37, 103–111. <https://doi.org/10.1071/EA96068>.
- Siddique, K., Loss, S., Regan, K., Pritchard, D., 1998. Adaptation of lentil (*Lens culinaris Medik*) to short season Mediterranean-type environments: response to sowing rates. *Aust. J. Agric. Res.* 49, 1057–1066. <https://doi.org/10.1071/A98006>.
- Singh, T.P., 1977. Harvest index in lentil (*Lens culinaris Medik*). *Euphytica* 26, 833–839. <https://doi.org/10.1007/BF00021716>.
- Singh, U., Srivastava, R., 2013. Genetic variability, heritability, interrelationships association and path analysis in lentil (*Lens culinaris Medik*). *Trends Biosci.* 6, 277–280.
- Solanki, I., Yadav, S.S., Bahl, P., 2007. Varietal Adaptation, Participatory Breeding and Plant Type. Lentil. Springer, pp. 255–274. https://doi.org/10.1007/978-1-4020-6313-8_16.
- Takai, T., Matsuura, S., Nishio, T., Ohsumi, A., Shiraiwa, T., Horie, T., 2006. Rice yield potential is closely related to crop growth rate during late reproductive period. *Field Crop. Res.* 96, 328–335. <https://doi.org/10.1016/j.fcr.2005.08.001>.

- Thomson, B., Siddique, K., 1997. Grain legume species in low rainfall Mediterranean-type environments II. Canopy development, radiation interception, and dry-matter production. *Field Crop. Res.* 54, 189–199. [https://doi.org/10.1016/S0378-4290\(97\)00048-8](https://doi.org/10.1016/S0378-4290(97)00048-8).
- Tollenaar, M., Dwyer, L.M., Stewart, D.W., 1992. Ear and kernel formation in maize hybrids representing three decades of grain yield improvement in Ontario. *Crop Sci.* 32, 432–438. <https://doi.org/10.2135/cropsci1992.0011183X003200020030x>.
- Tullu, A., Diederichsen, A., Suvorova, G., Vandenberg, A., 2011. Genetic and genomic resources of lentil: status, use and prospects. *Plant Genet. Resour.* 9, 19–29. <https://doi.org/10.1017/S1479262110000353>.
- Unkovitch, M., Baldock, J., Forbes, M., 2010. Variability in Harvest Index of Grain Crops and Potential Significance for Carbon Accounting: Examples from Australian Agriculture. *Adv. Agron.* Elsevier, pp. 173–219. [https://doi.org/10.1016/S0065-2113\(10\)05005-4](https://doi.org/10.1016/S0065-2113(10)05005-4).
- Vega, C., Sadras, V., Andrade, F., Uhart, S., 2000. Reproductive allometry in soybean, maize and sunflower. *Ann. Bot.* 85, 461–468. <https://doi.org/10.1006/anbo.1999.1084>.
- Verghis, T., McKenzie, B., Hill, G., 1999. Effect of light and soil moisture on yield, yield components, and abortion of reproductive structures of chickpea (*Cicer arietinum*), in Canterbury, New Zealand. *N. Z. J. Crop Hortic. Sci.* 27, 153–161. <https://doi.org/10.1080/01140671.1999.9514091>.
- Waitt, D.E., Levin, D.A., 1998. Genetic and phenotypic correlations in plants: a botanical test of Cheverud's conjecture. *Heredity* 80, 310–319. <https://doi.org/10.1046/j.1365-2540.1998.00298.x>.
- Wang, H., Hou, L., Wang, M., Mao, P., 2016. Contribution of the pod wall to seed grain filling in alfalfa. *Sci. Rep.* 6, 26586. <https://doi.org/10.1038/srep26586>.
- Wasserstein, R.L., Schirm, A.L., Lazar, N.A., 2019. Moving to a World Beyond “ $p < 0.05$ ”. *Taylor & Francis*. <https://doi.org/10.1080/00031305.2019.1583913>.
- Weiner, J., Campbell, L.G., Pino, J., Echarte, L., 2009. The allometry of reproduction within plant populations. *J. Ecol.* 97, 1220–1233. <https://doi.org/10.1111/j.1365-2745.2009.01559.x>.
- White, J., Kornegay, J., Castillo, J., Molano, C., Cajiao, C., Tejada, G., 1992. Effect of growth habit on yield of large-seeded bush cultivars of common bean. *Field Crop. Res.* 29, 151–161. [https://doi.org/10.1016/0378-4290\(92\)90084-M](https://doi.org/10.1016/0378-4290(92)90084-M).
- Whitehead, S., Summerfield, R., Muehlbauer, F., Coyne, C., Ellis, R., Wheeler, T., 2000. Crop improvement and the accumulation and partitioning of biomass and nitrogen in lentil. *Crop Sci.* 40, 110–120. <https://doi.org/10.2135/cropsci2000.401110x>.
- Yadav, S.S., McNeil, D., Stevenson, P.C., 2007. Lentil: an Ancient Crop for Modern Times. Springer.
- Zhang, H., Flottmann, S., 2016. Seed yield of canola (*Brassica napus* L.) is determined primarily by biomass in a high-yielding environment. *Crop Past. Sci.* 67, 369–380. <https://doi.org/10.1071/CP15236>.