Genetic gain in lentil yield between 1988 and 2019 has been larger under stress

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Abstract

The contemporary lentil industry in Australia started in the late 1980s. Yield in farmers' fields averages 1.2 t ha^{-1} nationally and has not increased over three decades. The lack of yield progress can be related to lack of genetic gain in yield; expansion of the crop to low yielding environments; lack of agronomic progress; and lack of adoption of superior technologies. Here we (i) quantify the genetic gain in lentil yield since 1988, (ii) explore the variation in the expression of genetic gain with environment, and (iii) identify shifts in the crop phenotype associated with selection for yield and agronomic adaptation. We grew a historic collection of 19 varieties released between 1988 and 2019 in eight environments resulting from the factorial combination of two sowing dates, two water regimes (rainfed, irrigated) and two seasons. Across environments, yield varied from 0.2 to 2.2 t ha^{-1}. The rate of genetic gain averaged 20 kg ha^{-1} y^{-1} or 1.2 % y^{-1} across environments, and was higher in low yielding environments. This rate is similar to that reported for wheat, despite much lower R&D effort in lentil. Yield increase was associated with substantial shifts in phenology. Newer varieties had shorter time to flowering and pod emergence, and the rate of change in these traits was more pronounced in slow-developing environments (e.g., earlier sowing). Thermal time from sowing to end of flowering and maturity were shorter in newer varieties, and thermal time from pod emergence to maturity was longer in newer varieties; the rate of change in these traits was unrelated to developmental drivers and correlated with environmental mean yield. Despite their shorter time to maturity, newer varieties had similar or slightly higher biomass than their older counterparts because crop growth rate during the critical period increased with year of release. Breeding increased yield over three decades, particularly in low-yield environment, whereas actual farm yield has been stagnant. This suggests an increasing yield gap that requires agronomic solutions. Genetic improvement in high-yield environments requires improved coupling of growth and reproduction.

Keywords

Crop growth rate, biomass, breeding, harvest index, phenology, phenotype, drought

Introduction

Australia currently produces over 300 000 t of lentil annually and contributes to approximately 10% of global trade. The contemporary lentil industry in Australia started in the late 1980s, and after a lag-phase, acreage increased linearly since the mid-1990s. Production increased in parallel to acreage, whereas national average yield remained stagnant at 1.2 t ha^{-1}, with large variation from failed crops to ~2 t ha^{-1}. Lack of progress in lentil average national yield in Australia can be related to several non-mutually exclusive reasons: expansion of the crop to drier, lower yielding environments; lack of genetic improvement in yield; lack of progress in agronomic practices; and lack of adoption of superior technologies. Most of Australian lentil is grown in winter-rainfall regions, with a combination of drought, frost and heat restricting yield of pulses (Lake et al. 2021; Lake et al. 2016; Lake and Sadras 2021; Sadras et al. 2012). Here we focus on genetic improvement using a historic collection of varieties. Our aims were to (i) quantify the genetic gain in lentil yield since 1988, (ii) explore variation in the expression of genetic gain with environment, and (iii) identify shifts in the crop phenotype associated with selection for yield and agronomic adaptation.

Method

We re-analyse results of previously reported experiments (Lake and Sadras 2021), including 19 varieties released and used in the Australian lentil breeding program between 1988 and 2019 (Table 1). Crops were grown in eight environments with a 11-fold variation in yield. Lake and Sadras (2021) emphasised yield components from a physiological perspective; here we focus on yield and phenotypic shifts with year of release. We report *p* as continuous value, and Shannon-s [$s = -\log_2(p)$](Greenland 2019).

Table 1 Seed type (red, green), phenology and yield of 19 lentil varieties. Values are BLUPs ± standard error across eight environments.

Variety	Year of release	Thermal time from sowing to flowering (°Cd)	Yield (g m^{-2})
Indianhead	1988	1546 ±81.0	19 ±6.9
Matilda	1993	1273 ±64.2	120 ±17.1
Aldinga	1995	1315 ±68.7	129 ±16.8
Northfield	1995	1368 ±80.9	129 ±23.7
Nugget	2000	1296 ±70.0	99 ±13.9
Boomer	2008	1251 ±53.3	101 ±10.4
Nipper	2008	1346 ±78.9	128 ±18.7
PBA Flash	2009	1272 ±58.3	140 ±19.5
PBA Blitz	2010	1096 ±31.9	131 ±14.5
PBA Jumbo	2010	1275 ±64.2	146 ±22.7
PBA Ace	2011	1208 ±45.7	116 ±14.2
PBA Bolt	2011	1191 ±44.3	141 ±14.7
CIPAL0901C	2013	1130 ±38.5	153 ±15.2
PBA Hurricane	2013	1225 ±45.6	124 ±16.3
PBA Giant	2014	1168 ±42.5	97 ±11.5
PBA Greenfield	2014	1249 ±49.9	110 ±20.4
PBA Jumbo2	2014	1216 ±57.0	121 ±13.6
CIPAL1504 C	2018	1239 ±51.8	141 ±25.8
CIPAL1701 C	2019	1106 ±41.0	180 ±22.5

Results

Growing-season rainfall + irrigation ranged from 117 mm for the early-sown dry crop in 2018 to 332 mm for the early-sown, wet crop in 2019. Across varieties, yield ranged from 21 g m^{-2} for early-sown, dry treatment in 2018 to 221 g m^{-2} for early-sown, wet treatment in 2018. Across varieties, average yield was positively associated with growing season rainfall ($y = -18.1 + 0.59x$, $R^2 = 0.50$; $p = 0.052$, $s = 4.3$) and with minimum temperature ($y = -90.8 + 38.2x$, $R^2 = 0.69$; $p = 0.010$, $s = 6.6$).

Phenology. Across environments, thermal time from sowing to flowering, pod emergence, end of flowering and maturity all were shortened with year of release (Table 2). Thermal time between pod emergence and maturity and the proportion of the season between pod emergence and maturity both increased with year of release. Fig. 2. shows the rate of change of phenological traits with year of release as a function of a) the environmental mean for the trait, and b) the environmental mean for yield. The environmental mean of the trait captures temperature, photoperiod and water influences on development, empirically defining slow- and fast-developing environments. For example, environmental mean thermal time to flowering ranged from 1039 °Cd in the late-sown wet treatment 2019 to 1451 °Cd in the early-sown wet treatment in 2019 (Table 2). The rate of change in thermal time to flowering and to pod emergence were stronger, i.e., more negative, in environments favouring slower development (Fig. 2AC). The rate of change in thermal time to flowering and maturity were proportional to environmental mean yield (Fig. 2FHJ) and unrelated to the environmental mean of the phenostage (Fig. 2EGI).

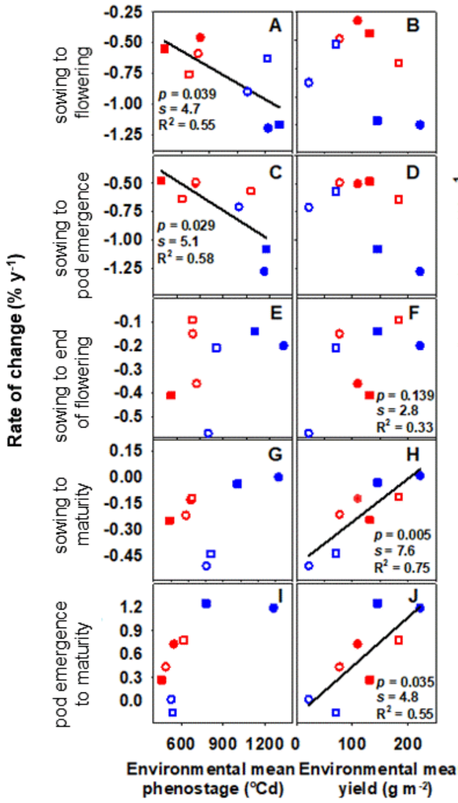
Table 2 The absolute and relative rate of genetic change (± s.e.) for lentil traits in varieties released between 1988 and 2019. Rates are the slope of least-square regressions between trait and year of release for data pooled across eight environments. Relative rate is percentage of the latest variety.

Trait	**Absolute**	**Relative (% y^{-1})**
Yield	20 ± 6.9 kg ha^{-1} y^{-1}	1.23 ± 0.28
Thermal time sowing to flowering	-9 ± 1.6 ^{o}Cd y^{-1}	-0.78 ± 0.08
Thermal time sowing to pod emergence	-9 ± 1.7 ^{o}Cd y^{-1}	-0.72 ± 0.08
Thermal time sowing to end of flowering	-4.9 ± 2.9 ^{o}Cd y^{-1}	-0.27 ± 0.05
Thermal time sowing to maturity	-4.5 ± 3.6 ^{o}Cd y^{-1}	-0.22 ± 0.04
Thermal time pod emergence to maturity	4.9 ± 2.6 ^{o}Cd y^{-1}	0.56 ± 0.13
Ratio thermal time pod emergence-maturity/sowing-maturity	0.003 ± 0.0007 y^{-1}	0.73 ± 0.11
Crop growth rate	0.07 ± 0.02 kg ha^{-1} ^{o}Cd^{-1} y^{-1}	1.46 ± 0.35
Biomass	16 ± 21 kg ha^{-1} y^{-1}	0.38 ± 0.15
Harvest index	0.004 ± 0.001 y^{-1}	1.25 ± 0.25
Grain number	34 ± 18 seeds m^{-2} y^{-1}	0.92 ± 0.31
Grain size	0.40 ± 0.08 mg seed^{-1} y^{-1}	0.96 ± 0.20

Yield and its components. Across environments, yield increased with year of release at 20 kg ha^{-1} y^{-1} or 1.23% y^{-1} (Table 2). The rate of genetic gain in yield declined linearly with increasing environmental mean yield (Fig. 2A). The relatively low yield in high-yielding environments resulted from decoupled reproduction and growth (Lake et al. 2021). Across environments grain number increased with year of release at 34 seed m^{-2} y^{-1} or 0.92 % y^{-1} (Table 2). The rate of change in grain number with year of release was higher in low yielding environments (Fig. 4B). Across environments grain size increased by 0.4 mg seed y^{-1} or 0.96 % y^{-1} (Table 2). The rate of genetic change in grain size was unrelated to environmental mean yield (Fig. 2C). Across environments, the absolute rate of change in biomass with year of release was close to zero and the relative rate was 0.38 % y^{-1} (Table 2). The association between relative rate of change in biomass and environmental mean yield was weak and negative (Fig. 2D). Across environments, crop growth rate increased with year of release at 0.07 kg ha^{-1} ^{o}Cd^{-1} y^{-1} or 1.46 % y^{-1} (Table 2). The rate of change in crop growth rate with year of release was higher in more stressful environments (Fig. 2E). Across environments harvest index increased 0.0042 y^{-1} or 1.25 % y^{-1} (Table 2). The rate of increase in harvest index with year of release almost halved between the lowest and highest yielding environments (Fig. 2F).

Conclusion

Over the three decades of Australian lentil breeding and for our sample of varieties and environments, genetic gain in yield was 20 kg ha^{-1} y^{-1} or 1.23 % y^{-1}. This rate compares well with genetic gains in wheat, despite the significantly smaller allocation of R&D effort to lentil. The estimated genetic gain in yield was larger in lower yielding environments. This genetic gain combined with improved agronomy has allowed the spread of lentil into lower rainfall regions of Australia, increasing rotational options and allowing more diverse cropping. The lack of improvement in the national average yield over this period is partially related to the expansion of the crop to intrinsically lower yielding environments. Further improvements in lentil production require adoption of improved practices to close the gap between water-limited and actual yield, and a stronger focus in breeding for high yield potential.



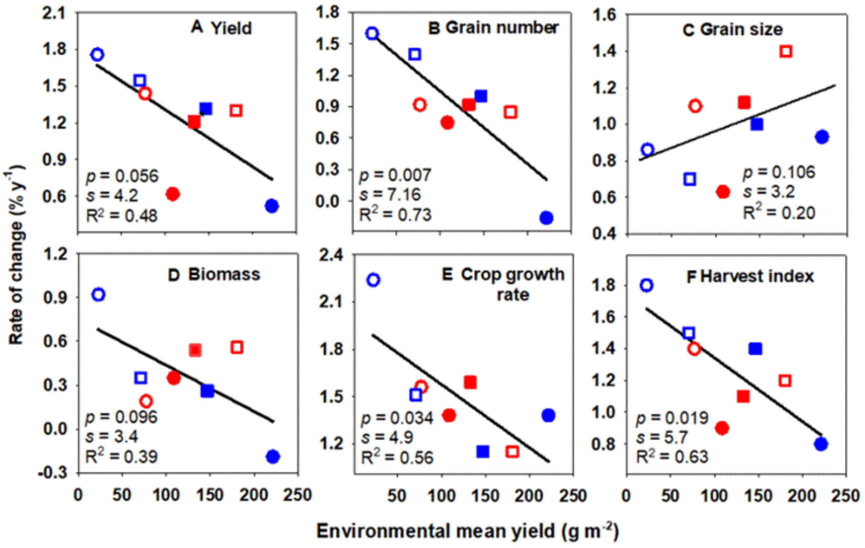


Figure 2. Rate of change of yield and related traits as a function of environmental mean yield. Lines are least-square regressions. Symbols are: blue (2018), red (2019), circles (early sowing), square (late sowing), open (rainfed), closed (irrigated).

Figure 1 Rate of change for thermal time from sowing to (A, B) flowering, (C, D) pod emergence, (E, F) end of flowering, and (G, H) maturity, and (I, J) thermal time between pod emergence and maturity plotted against the environmental mean phenostage (left column) and the environmental mean yield (right column). Lines are least-square regressions and are only presented where p < 0.05, s > 4.3. Symbols are: blue (2018), red (2019), circles (early sowing), square (late sowing), open (rainfed), closed (irrigated).

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