Decoupling of yield and growth means harvest index is more important to lentil yield under favourable conditions

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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 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} [^{o}Cd]$^{-1}$, suggesting a minimum plant size for reproduction. 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. 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.

Keywords
Biomass; canopy; crop growth rate; drought; harvest index; NDVI; phenotyping; stress

Introduction
Lentil is a cool season grain legume grown in Mediterranean, south Asian and temperate regions either as an autumn or winter sown crop. Driven by demand for affordable, high quality protein 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). In Australia and globally low and unstable yields are a major limitation to lentil production.

The association between yield and crop growth rate in a species-specific critical window has been demonstrated in the cereals, oilseeds and grain legumes (Sadras and Dreccer, 2015; Sadras and Calderini, 2021). Yield is 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, Fig 1). 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) 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 a lack of trade-offs between biomass and harvest index. 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.

Methods
We established a factorial experiment with 20 lentil lines varying in seed type and phenology. Crops were grown, in eight environments that resulted from the combination of two seasons (2018, 2019), two sowing dates and two water regimes at Roseworthy (-34.35, 138.69), South Australia. 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 and late sown crops were irrigated or rainfed.

There were three replicates per treatment with sowing date assigned to main plot, water regime to subplot, and lines randomised within subplots; target plant density was 120 plants m^{-2}. Crops were managed in accordance with best local practice. 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 ºC. At maturity we harvested 1 m^2 from the four central rows of the plot to determine grain yield, biomass, harvest index, seed number and seed size. We measured biomass and crop growth rate non-destructively using both NDVI (Greenseeker) 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 with four morphologically and phenologically contrasting lines. We used ANOVA (Genstat 20th edition) to test for the effects of line, environment and their interaction on yield and related traits. 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). To test for the degree of coupling between yield and growth, we split yield in five classes: percentile 10th, the most stressful, was yield ≤ 14 g m^{-2}, percentile 25th was 14 g m^{-2} < yield ≤ 56 g m^{-2}, percentile 50th was 56 g m^{-2} < yield ≤ 107 g m^{-2}, percentile 75th was 107 g m^{-2} > yield ≥ 170 g m^{-2} and percentile 90th, the most favourable condition, was yield ≥ 227 g m^{-2}.

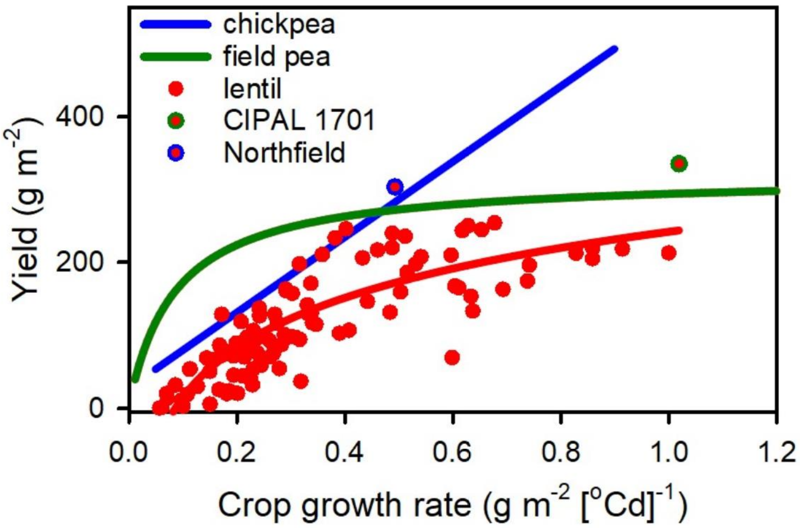


Fig. 1. Relationship between crop growth rate and yield in lentil. The fitted curve is a + b ln (x), with a = 241.5 ± 9.34 and b = 98.8 ± 6.73, R2 = 0.69, p < 0.001, s > 9.9). Two high-yielding varieties with contrasting phenotypes are highlighted: CIPAL 1701 and Northfield. Included for comparison are 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).

Results

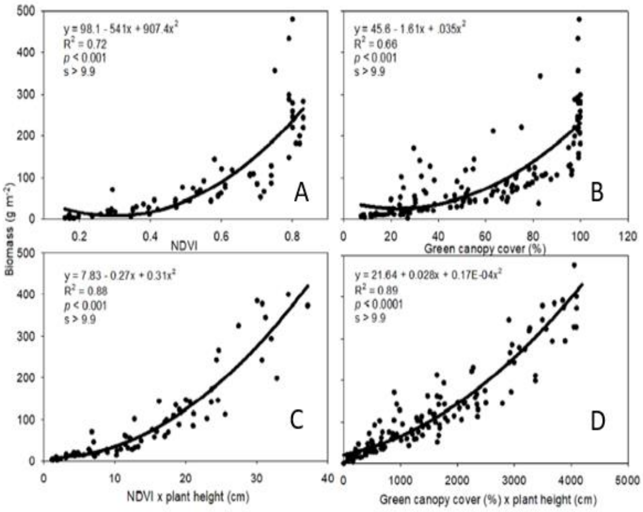
Environmental conditions, crop development and phenotyping crop growth rate

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 (r^2 0.50, p = 0.051, s = 4.3). Environmental mean yield ranged 10-fold from 21 – 221 g m^{-2} while the genotypic range was 5-fold (Table 1). Non-linear relationships between biomass and both NDVI and green canopy cover (Fig. 2AB) were improved with the inclusion of plant height (Fig. 2CD). 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 ºCd after sowing; growth rate refers to this period hereafter.

Table 1. Genotypic and environmental ranges, and broad-sense heritability of lentil traits measured in 20 lines grown in 8 environments.

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

Yield was related to early phenology and biomass under stress but decoupled in higher yielding conditions
The association between yield and time to flowering was stronger, i.e. higher r^2 and steeper slope, in more stressful environments. Delayed flowering associated with a reduction in yield from 0.18 g m^{-2} [$^oCd]^{-1}$ or 0.7 % d^{-1} in favourable conditions to 0.22-25 g m^{-2} [$^oCd]^{-1}$ or 3.6 % d^{-1} in the more stressful conditions. Setting an upper limit of 1637 ^{o}Cd to flowering by exclusion of extremely late lines Indianhead and Commando showed yield declined with late flowering in the most stressful environments (yield $\leq$ 56 g m^{-2}) and was independent of phenology in environments above this threshold. Excluding the extremely late flowering lines, yield declined 0.22 g m^{-2} [$^oCd]^{-1}$ or 2.6 % d^{-1} (10^{th} percentile) and 0.16 g m^{-2} [$^oCd]^{-1}$ or 1.9 % d^{-1} (25^{th} percentile).



Line	Seed Type	Thermal time to flowering (°Cd)
PBA Blitz	Red	1095 ± 19.0
CIPAL1701	Red	1112 ± 23.0
CIPAL0901	Red	1133 ± 22.5
PBA Giant	Green	1168 ± 25.0
PBA Bolt	Red	1199 ± 24.7
PBA Ace	Red	1208 ± 26.3
PBA Jumbo2	Red	1221 ± 30.4
PBA Hurricane	Red	1225 ± 25.9
PBA Greenfield	Green	1249 ± 28.9
CIPAL1504	Red	1249 ± 29.4
Boomer	Green	1259 ± 34.7
Matilda	Green	1261 ± 36.0
PBA Jumbo	Red	1274 ± 36.0
PBA Flash	Red	1281 ± 35.4
Nugget	Red	1301 ± 42.0
Aldinga	Red	1325 ± 38.6
Nipper	Red	1354 ± 44.7
Northfield	Red	1369 ± 46.8
Commando	Red	1550 ± 64.9
Indianhead	Red	1552 ± 48.0

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Fig. 2. Relationship between shoot biomass and: (A) NDVI; (B) green canopy cover; (C) NDVI x plant height; (D) green canopy cover x plant height of a subset of four lentil varieties grown in six environments in 2018 and 2019. (E) experimental lines, seed type and phenology pooled across environments.

Environment ($p < 0.001$, $s > 9.9$), 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 ($p < 0.001$, $s > 9.9$). Crop growth rate varied with environment and line (both $p < 0.001$, $s > 9.9$) with no interaction effect. To explore the non-linearity between yield and growth, Fig. 3 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 90^{th} percentile, and with crop growth rate except at 75^{th} and 90^{th} 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 conditions.

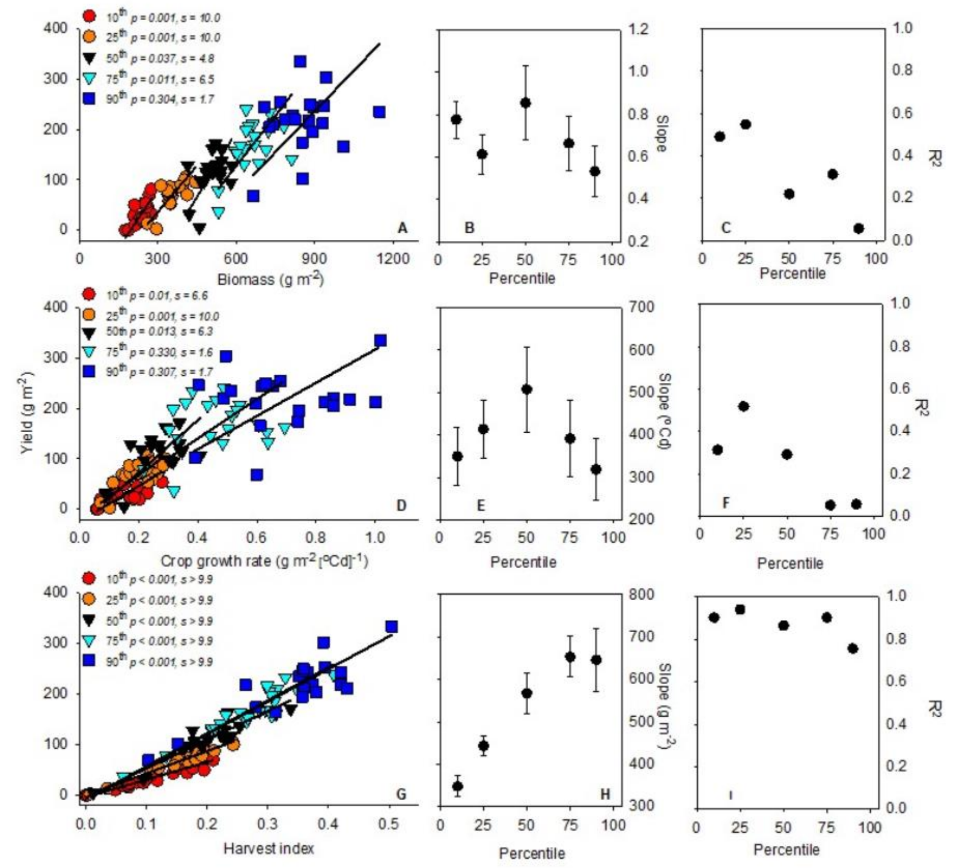

Fig. 3. Relationship between yield and (A) biomass, (D) crop growth rate and (G) harvest index for the combination of 20 lines and 8 environments where the 10th, 25th, 50th, 75th and 90th percentiles are plotted for both x and y and represent a range from more stressful to more favourable conditions. Lines are Model II (Reduced Major Axis) regressions accounting for error in both variables. Slope ± 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.

Conclusion

Our research highlights the decoupling of growth and yield underlying the low yield of lentil in favourable conditions. For this set of lines and environments, 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 such as precision seeding may be used to reduce rectangularity of crop arrangements to improve penetration of radiation into the canopy and pod set.

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References

Andrade et al 2005. Journal of Crop Improvement 14, 51-101.
FAO, 2020. FAOSTAT. http://www.fao.org/faostat/en/#data/QC. FAO.
Guilioni et al 2003. Func. Plant Biol. 30, 1151-1164.
Patrignani et al 2015. Agron. J. 107, 2312-2320.
Lake et al 2016. European Journal of Agronomy. 81:86-91.
Sadras et al 2021. Crop Physiology Case Histories for Major Crops. Academic Press.
Sadras et al 2015. Crop Past. Sci. 66, 1137-1150.
Sadras et al 2013. Field Crop. Res. 150, 63-73.
Scully et al 1990. Journal of the American Society for Horticultural Science 115, 218-225.