



# Benchmarking the response of grain yield to plant population density across environments and management: A case study for faba bean

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## ABSTRACT

Agronomic experiments to establish the relationship between yield and plant population density (PPD) are widespread but remain inconclusive because management and environmental conditions modulate the responses. We analysed and synthesised yield-to-PPD responses in faba bean (*Vicia faba* L.), with a focus on Australia. We compiled a database of 204 yield-to-PPD responses from 77 Australian experiments and included 33 experiments from other regions for comparison. Our framework comprises two steps: 1) estimate the plant population density required to achieve 95% of the grain yield asymptote (critical PPD) in each yield-to-PPD response, 2) explain variation in critical PPD with environmental and agronomic variables. Median critical PPD was 34 plants m<sup>-2</sup>, with an interquartile range of 21 to 49 plants m<sup>-2</sup>. Critical PPD decreased with higher environmental yield, with higher soil pH, and for indeterminate cultivars compared with determinate ones, factors that favour yield, and decreased with hot springs and low in-season rainfall, factors that do not favour yield. Grain yield, seed number, pod number, branch number, and biomass increased to an asymptote with plant population density at the crop-level, and decreased following a power model at the plant-level; seed size, seeds per pod and crop height did not vary with plant population density. Compared to the current standard of 20 plants m<sup>-2</sup>, the profit-to-PPD response for Australian experiments was more negative at 10 and 15 plants m<sup>-2</sup> than positive at 25 and 30 plants m<sup>-2</sup>. This supports the standard recommendation but highlights the risk of reduced profitability when establishment is compromised. Our framework can be used to tailor faba bean plant population density recommendations to local conditions and can be adapted for other crops.

## 1. Introduction

Crop sowing rate is a necessary management choice that sets the upper limit of plant population density and has multiple effects on growth, yield and profitability. Grain yield increases nonlinearly with plant population density, reaching a plateau or declining at higher densities, but the relationship varies with environment (Willey and Heath, 1969). Benchmarking the yield-to-plant population density (yield-to-PPD) response and developing theory to account for management and environmental factors that affect the relationship would provide insights to researchers, breeders, and grain producers.

Crop physiology explains the shape of the yield-to-PPD response curve in annual grain crops. Initially, yield increases with plant

population density because it favours the capture of radiation, water and nutrients, especially in early development (Westgate et al., 1997; Postma et al., 2021). In many growing conditions, crops must achieve full light interception to maximise crop growth rate during the species-specific critical period for grain yield determination, as has been shown in maize, sunflower, soybean and wheat (Andrade, 2002; Fischer et al., 2019). Subsequently, the yield-to-PPD response attenuates or declines for several, non-mutually exclusive reasons: 1) competition for resources between plants in the stand reduces growth of individual plants (Postma et al., 2021); 2) reproduction may be size-dependent (Weiner et al., 2009), hence the lower yield of smaller individuals in denser stands such as in soybean, maize and sunflower (Vega, 2000); 3) populations self-thin or develop hierarchies of dominant and dominated

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plants (Harper, 1977; Novoplansky, 2009), as seen in maize and sunflower (Vega and Sadras, 2003); and 4) high plant population density could favour pests and diseases, compromise the distribution of pesticides through the canopy, and promote lodging (López-Bellido et al., 2005).

The empirical approach to determining a standard plant population density is to repeat plant density experiments in multiple environments, perhaps including interacting factors such as sowing date, cultivar or row spacing (Barry and Storey, 1979; Newton and Hill, 1987; Pratchler, 2019). A brief literature search will return many such studies for most crops on most continents. Usually, however, the effects of growing conditions, coarsely defined, are inferred qualitatively. A recent quantitative method of linking the yield-to-PPD response to the environment has been applied to maize, winter wheat and soybean in North America, where a database is collated, the experiments are divided into higher and lower yield environments and analysed with frequentist or Bayesian methods (Carciochi et al., 2019; Bastos et al., 2020; Lacasa et al., 2020). Grain yield increased linearly with plant population density to a plateau, and the plant population density where the plateau was reached decreased for higher yielding experiments in winter wheat and soybean but increased for maize. In these studies, some variation could be attributed to latitude and relative crop maturity, but the large variation of the yield-to-PPD response was highlighted.

With a focus on profit, French et al. (1994) fitted yield-to-PPD curves for individual experiments, and calculated the economic optimum plant population density as the point where the slope of the response achieved an equilibrium between marginal cost and marginal income. This model has been applied to chickpea (Jettner et al., 1999), lentil (Siddique et al., 1998) and canola (French et al., 2016). These studies showed that economic optimum plant population density increased with the yield asymptote for lupin, chickpea, and canola but was not associated with the asymptote for lentil. This approach addresses both environmental and economic sources of variation, but economic assumptions restrict their contemporary relevance.

Here we present an agronomically useful framework to synthesise data for the yield-to-PPD response. In common with the above studies, we aim at synthesising disparate experimental data, but our approach differs in that we calculate and use the critical PPD (the plant population density that achieves 95% of maximum yield) to explain sources of variation between responses. We develop our framework with faba bean (*Vicia faba*), an indeterminate, winter grain legume prone to lodging and foliar fungal diseases, which varies in branching and plant yield in response to plant population density (López-Bellido et al., 2005). Reviews of faba bean yield-to-PPD response are qualitative (López-Bellido et al., 2005; Gezahegn, 2019). In Australia, the recommended plant population density is 15 to 25 plants m<sup>-2</sup> based on grower experience and field experiments (GRDC, 2017), but this recommendation lacks scientific rigour (Belli et al., 2021). We aim to 1) quantitatively describe crop and plant phenotype responses to plant population density, 2) identify environmental and agronomic variables that affect the critical PPD, and 3) demonstrate the economic implications of our synthesis for Australian faba bean growers.

## 2. Method

### 2.1. Data sources

We compiled a database of faba bean yield-to-PPD responses from published and unpublished small-plot experiments, reporting grain yield and established plant population density with a primary focus in Australia; data from other regions were collected for comparison. Data for each treatment were retrieved from tables or digitalised from figures using WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer/>).

Where available, we compiled seed size, seed number (derived from yield and seed size), shoot biomass at harvest, harvest index (derived from yield and shoot biomass), pod number, branch number, plant

height and percent of crop lodged (Tables S1 and S2). Experimental details were retrieved where provided, including location, year, row spacing, sowing date, cultivar, sowing seed size, topsoil pH (CaCl<sub>2</sub>), topsoil texture, presence of weeds, diseases, and irrigation.

An experiment was included in the database if it met three criteria: 1) plant population density was measured after establishment, 2) it had at least three plant density treatments, and 3) it was generated by a designed experiment with at least three replicates. Within a site-year, we treated each combination of plant population density and variety, row spacing, sowing date or irrigation as a unique yield-to-PPD response. The database consists of 77 Australian experiments (126 yield-to-PPD responses, 576 datapoints) and 33 experiments from the United Kingdom, Ireland, France, Italy, Finland, Canada, Egypt, Sudan, India, and New Zealand (78 yield-to-PPD responses, 398 datapoints) that were conducted from 1974 to 2021 (Tables S1 and S2).

### 2.2. Analysis

#### 2.2.1. Crop and plant phenotype responses to plant population density

We described the response of yield and yield-related traits quantitatively for 204 trait-to-PPD relationships, or subsets in which the trait data was available. We calculated crop-level (m<sup>-2</sup>) and plant-level (plant<sup>-1</sup>) grain yield, shoot biomass, seed number, pod number and branch number. Traits with different units were seed size (mg seed<sup>-1</sup>), seeds pod<sup>-1</sup>, crop height (cm) and percent of crop lodged.

First, to partially account for the effect of growing conditions, we normalised traits to their value at 20 plants m<sup>-2</sup>, the standard in Australia. The trait at 20 plants m<sup>-2</sup> was estimated by regression for each trait-to-PPD response, then the data values were divided by that estimate. Second, we described the normalised trait-to-PPD response with a power model ( $y = a * x^b$ ) for the plant-level, and a Michaelis-Menten model ( $y = a * x / [b + x]$ ) for the crop-level. These were chosen because they are biologically meaningful and returned lower AIC and residual standard error than alternative models; criteria for model selection are further discussed in the next section. For the remaining traits (height, lodging, seed size, seeds per pod), models were selected according to the same criteria.

#### 2.2.2. Modulators of critical plant population density

**2.2.2.1. Model choice.** We fit the Mitscherlich asymptotic model to relate yield (t ha<sup>-1</sup>) and established plant population density (plants m<sup>-2</sup>):

$$\text{Yield} = a * (1 - e^{-c \text{ PPD}})(1)$$

where  $a$  is the grain yield asymptote and  $c$  defines the curvature of the rise to the asymptote. Parabolic models (increasing, then decreasing) are appropriate for some crops in some environments but were not appropriate for our data (see 4.2 for discussion).

The Mitscherlich asymptotic model was preferred to the power model (Marcellos and Constable, 1986) because its parameters link conceptually to resource availability. It was chosen over the hyperbolic model (Helenius and Jokinen, 1994; Loss et al., 1998; Jensen et al., 2023) because it produced more conservative and realistic estimates of the grain yield asymptote, particularly in experiments with a narrow plant population density range. It was preferred to the linear break-point model (Carciochi et al., 2019; Bastos et al., 2020; Lacasa et al., 2020) for two reasons. First, the response for our data was smooth and concave at the experiment-level. Second, theory shows that a breakpoint-type response, implying Leibig's Law of the Minimum, is suited to responses at lower levels of organisation, cell to plant, but the aggregated effect follows a Mitscherlich-type Law of Diminishing Returns at the crop-level (Berck and Helfand, 1990; Sinclair and Park, 1993; Ferreira et al., 2017).

Owing to the large variation in  $c$  with growing conditions and

genotypes, Willey and Heath (1969) argued that the Mitscherlich model is unsuitable to generalise a yield-to-PPD response. Here, we do not produce one prediction for all environments but argue that the variation in  $c$  is informative, provided it can be linked to agronomic and environmental factors.

**2.2.2.2. Data filtering.** We fit the Mitscherlich model to 204 yield-to-PPD responses using the 'nls()' function in the R environment (R Core Team, 2021) and a self-starter routine from the package 'aomisc'. Twenty-one non-Mitscherlich responses were not analysed further for critical PPD; these include: two low-yielding experiments with a positive linear yield-to-PPD response; twelve early-sown experiments in wet years with a negative linear yield-to-PPD response, which also lacked plant population densities below 20 plants  $m^{-2}$ ; and eight experiments that returned no apparent yield-to-PPD response.

For the Mitscherlich-type responses, the data, model, and residuals were plotted and inspected visually. A further fifteen responses were removed because the critical PPD was more than twice the size of the highest plant population density (i.e. the experiment lacked plant population density treatments that were sufficiently high for the growing conditions); three were removed because the critical PPD was smaller than the minimum plant population density treatment (i.e. the experiment lacked sufficiently low plant population density); and two were removed that had a critical PPD greater than 100 plants  $m^{-2}$ , our cut-off value for acceptable values. After these steps, the remaining 163 yield-to-PPD responses were deemed to be agronomically and statistically sound for further analysis. Of these, 103 were from Australia and 60 from other countries.

**2.2.2.3. Analysis of the critical plant population density.** For the 163 yield-to-PPD responses, we retrieved the estimated values of  $a$  (asymptote) and  $c$  (curvature) as well as the predicted critical PPD from the fitted Mitscherlich models. To quantify the effect of the environment on grain yield, that is, the 'environmental yield' (Sadras et al., 2009), we used the grain yield at 20 plants  $m^{-2}$  because 1) it is more meaningful to Australian grain producers than a yield-to-PPD asymptote that may appear unrealistically high or may occur at an impractically high plant population density, and 2) the average grain yield would be confounded by different plant population density treatments across experiments. See Sadras et al. (2009) and references for an overview of this method.

We then related critical PPD to environmental and agronomic variables with linear mixed models, using the 'lmer()' function from the 'lme4' package in the R environment (Bates et al., 2015). The fixed effects were the environmental and agronomic variables, and the random effect was the experiment because multiple yield-to-PPD responses can come from the same site-year, being distinguished by experimental treatments. We applied the model to parameters  $a$  and  $c$  to assist with interpretation of the critical PPD responses.

We quantified the ability of the fixed effects to explain variation in critical PPD with the marginal- $R^2_{LMM}$  (hereon,  $R^2_{LMM}$ ), a coefficient of determination for linear mixed models where 1 means fixed effects entirely describe the data, and 0 means fixed effects do not describe the data at all (Nakagawa and Schielzeth, 2013).

The models were fit to overlapping subsets of the database because most reports provided few, inconsistent agronomic and environmental details. Sowing date was the numeric day of the year, with northern hemisphere day of year converted to the southern hemisphere by adding six months. Various soil classification systems were reported from the database, we classed the descriptions into three categories of texture where 1 is light, 2 is medium, and 3 is heavy. Soil pH ( $CaCl_2$ ) is for the topsoil, up to 20 cm depth.

The effects of weather variables were examined for all Australian yield-to-PPD responses using meteorological data from the nearest Bureau of Meteorology weather station. Some meteorological data were taken from July (before flowering) to November (during or after grain

fill), to focus on the critical period of yield determination for faba bean (Lake et al., 2019). We used 1 °C to count the number of frost events and 28 °C as the threshold to count the number of heat stress events (Bishop et al., 2016). Maximum and minimum temperature, radiation and vapour pressure deficit (VPD) are the average of the daily values, VPD was calculated from daily vapour pressure and maximum and minimum temperatures (Jeffrey et al., 2001). We used monthly rainfall to calculate a rainfall seasonality index (SI), a measure of how concentrated annual rainfall is into wet and dry seasons, where the highest value, 1.83, indicates all rainfall occurs in a single month, and the lowest value, 0, indicates rain falls equally in all months (Walsh and Lawler, 1981).

The standardised coefficients were visualised on dot-and-whisker plots with standard errors and 95% confidence intervals. A coefficient was considered relevant to critical PPD,  $a$  or  $c$  if its 95% confidence interval did not cross zero, and the magnitude of the coefficient was taken as an indicator of its importance relative to other coefficients.

To assist with the agronomic interpretation of models with several parameters, we visualised the marginal effects of the most reliable variables identified from the dot-and-whisker plots. We used the 'ggemmeans()' function from the 'ggeffects' package in R (Lüdtke, 2018) to compute marginal effects of focal terms at their maximum and minimum value on the non-standardised critical PPD,  $a$  and  $c$ . For critical PPD, environmental yield had the largest and most reliable effect, and this has significant agronomic implications, so we illustrate its interaction with the other environmental and agronomic variables. To illustrate changes in  $a$  and  $c$ , we drew the resulting generic yield-to-PPD curves.

### 2.2.3. Profit-to-PPD response in Australia

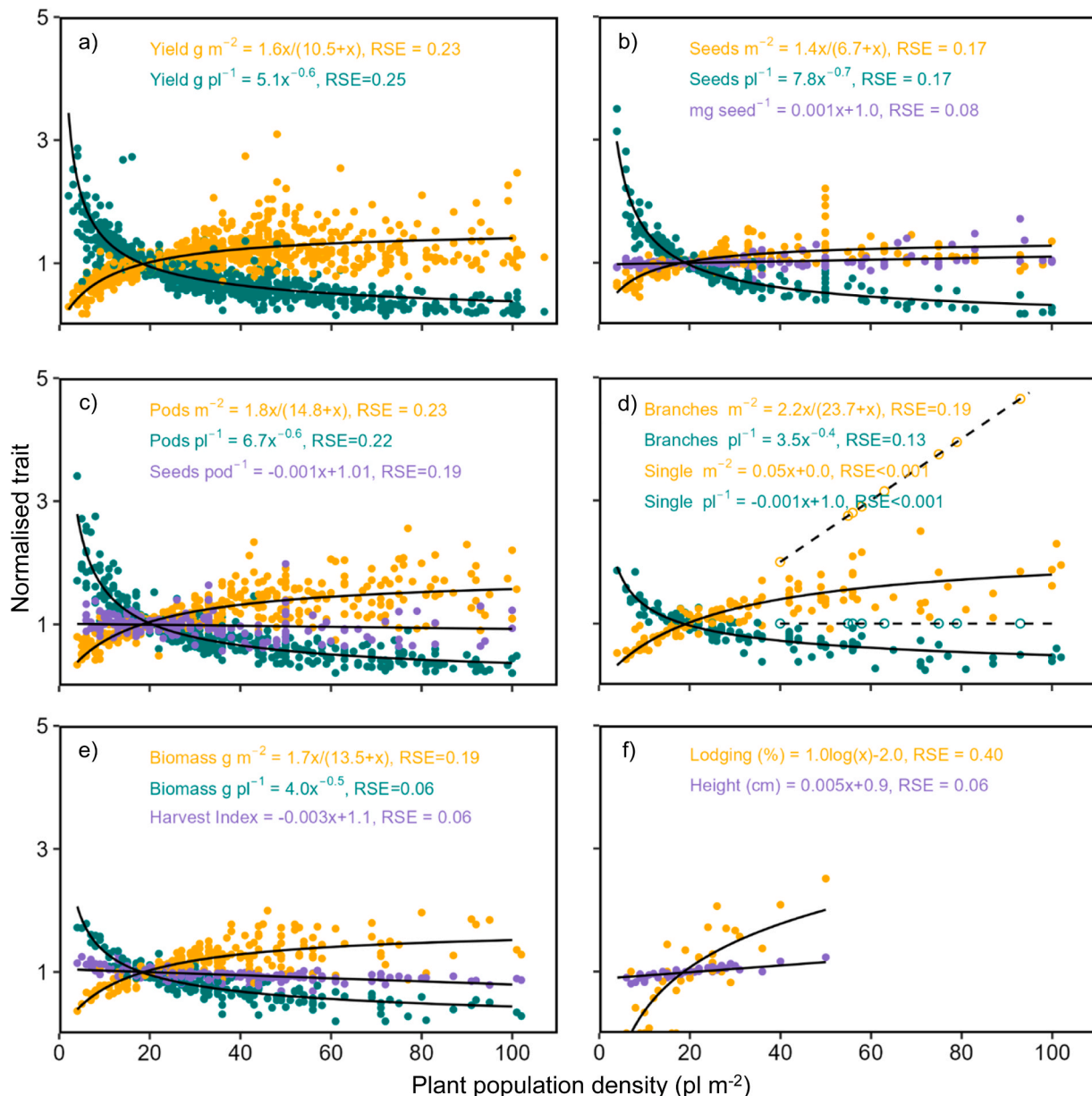
A full economic analysis is beyond the scope of this study. Instead, our aim is to illustrate the application of our findings to inform decisions from an economic perspective. To summarise Australia-wide data, we again plotted critical PPD as a function of environmental yield (grain yield at 20 plants  $m^{-2}$ ) but this time with an exponential decay model ( $y \sim c + [d-c] \cdot \exp[-x/e]$ ) because it has a lower asymptote, interpreted as the lowest critical PPD required for the best environments. This was achieved with the 'drm' function in the 'drm' package in R, using the 'EXD.3()' function to specify our chosen exponential decay formula (Ritz et al., 2015). We fit the exponential decay model to the global data for comparison.

To estimate the effect on profit, we used a partial budget where change in profit is defined as the change in income minus the change in cost, using the current standard of 20 plants  $m^{-2}$  as a reference. We used data from all 126 yield-to-PPD responses in the 77 Australian experiments. First, we modelled grain prices of \$200, \$400 and \$600  $t^{-1}$ ; the median grain price from 2012 to 2022 at Port Adelaide was \$420  $t^{-1}$  and ranged from \$270 to \$900  $t^{-1}$  (PIRSA, 2021). All monetary values are Australian dollars. Second, we estimated the change in grain yield as the difference between grain yield at 20 plants  $m^{-2}$  and yield at 10, 15, 25 or 30  $pl m^{-2}$ . Grain yield was predicted for Australian data using a Mitscherlich model from 103 yield-to-PPD responses and a linear model for 24 yield-to-PPD responses. Third, we calculated the change in income by multiplying the change in grain yield by our chosen grain price. Fourth, marginal costs were estimated at two levels: low and high, using data from the local gross margin guides (PIRSA, 2021). The cost breakdown is summarised in Table S2. Fifth, the change in profit was estimated for the combination of four plant population densities, three grain prices, and two marginal costs.

## 3. Results

### 3.1. Crop and plant phenotype response to plant population density

As plant population density increased, plant yield decreased following a power curve, an approximate mirror image of the increase in crop yield (Fig. 1a). Crop yield increased following a Michaelis-Menten



**Fig. 1.** Faba bean crop and plant phenotype responses to plant population density. Traits are normalised by their value at 20 plants m<sup>-2</sup>. Traits are a) grain yield, b) seed number and seed size, c) pod number and seeds per pod, d) branch number, e) shoot biomass and harvest index, and f) crop height and crop lodging. Yellow symbols are traits with area-based units (m<sup>-2</sup>, % of crop), green symbols have units of plant<sup>-1</sup>, and purple symbols have other units. Curves are Michaelis-Menten models for m<sup>-2</sup> traits, power models for plant<sup>-1</sup> traits, and linear models for other traits, except for lodging (%) that is logarithmic. RSE is residual standard error of the normalised trait. Standard errors for parameters are presented in Table S3.

curve to an asymptote of 1.6, i.e., the response approached a maximum 60% greater than at 20 plants m<sup>-2</sup>. We observed similar crop and plant patterns in seed number (Fig. 1b), pod number (Fig. 1c), branch number (Fig. 1d) and shoot biomass (Fig. 1e). These yield components are highly plastic in response to plant population density, and closely associated with grain yield. An exception was plant branch number that was unresponsive to plant population density in single-branch cultivars and the consequent linear increase in crop branch number (Fig. 1d). Seed size (Fig. 1b), seeds per pod (Fig. 1c) and harvest index (Fig. 1e) were unresponsive to plant population density and did not associate with grain yield. Crop lodging increased with plant population density more markedly than crop height (Fig. 1f).

### 3.2. Critical plant population density

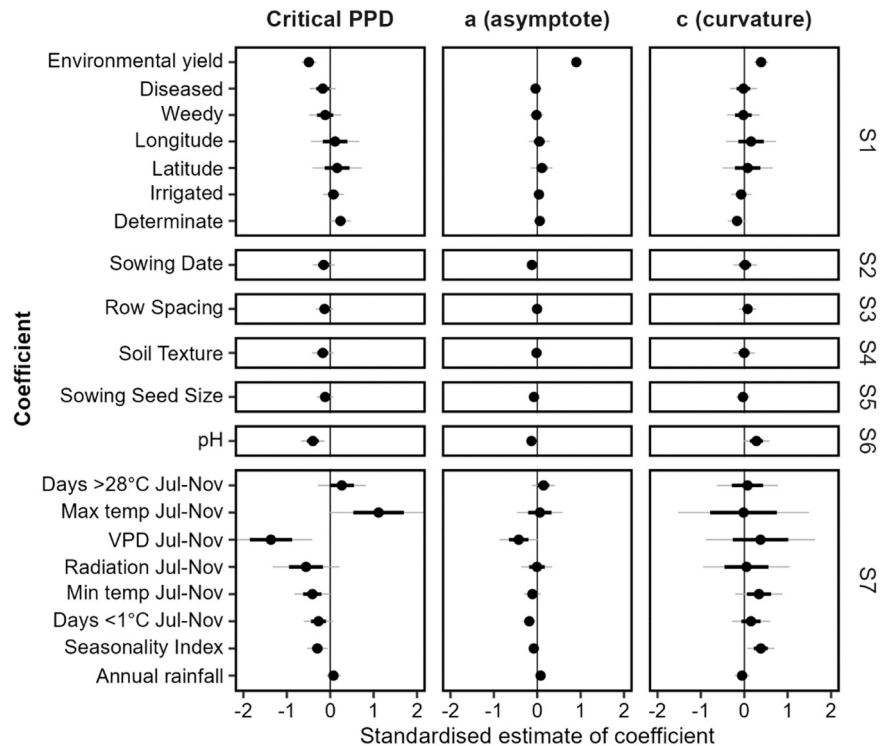
#### 3.2.1. Appropriateness of the Mitscherlich model

Of the 204 yield-to-PPD responses, 90% could be described by the Mitscherlich model, and the exceptions could be attributed to disruptive environmental factors or an experimentally inadequate range in plant population density (see Methods). For the 163 yield-to-PPD responses deemed appropriate for the critical PPD analysis, the residual standard errors of the Mitscherlich models ranged from 0.04 to 0.47 t ha<sup>-1</sup> with a median of 0.14 t ha<sup>-1</sup>.

#### 3.2.2. Modulators of critical plant population density

The variables that more strongly affected critical PPD were environmental yield, genotype determinacy, soil pH, VPD and rainfall seasonality (Fig. 2). Disease, sowing date, row spacing, soil texture, sowing





**Fig. 2.** Standardised coefficients affecting critical PPD and parameters *a* and *c* of the underlying Mitscherlich model in seven data sets. Set S1 contains 163 curves, and S2 to S7 are partially overlapping subsets that introduce unique variables. Only these unique variables are illustrated; the complete model for each subset is in Fig. S1. Thick bars are standard errors, thin bars are 95% confidence intervals.

seed size and most of the weather variables had smaller effects (Fig. 2). In the largest dataset from the widest range of locations (S1), fixed effects explained 25% of the variation in critical PPD (Table 1). For the Australian-only data (S7), the same fixed effects explained 43% of the variation, and increased to 57% with the inclusion of weather data. Soil pH also made a sizeable increase in  $R^2_{\text{LMM}}$  (+11.3%), but sowing date, row spacing, soil texture and sowing seed size did not improve this metric.

For higher environmental yield, the yield-to-PPD asymptote and curvature both increased, and critical PPD decreased with increasing environmental yield (Fig. 3, compare to Fig. 2). Determinate cultivars required a higher critical PPD, accounted for by a lower curvature parameter that produces a more gradual rise to the asymptote. Soils with low pH required a higher critical PPD to compensate for a slow rise to the asymptote (Fig. 2). The asymptote for pH 8 is lower than pH 4.6 (Fig. 3), this may be due to the association of low pH and high rainfall in southwest Victoria. High VPD reduced critical PPD mostly through a

reduction in maximum yield; however, VPD was correlated with temperature and radiation, hence reflecting a syndrome of a hot, sunny spring. High rainfall seasonality decreased critical PPD through a reduction in maximum yield and a steeper yield-to-PPD response. High rainfall seasonality was associated with dry years in which autumn and/or spring rainfall were reduced more than winter rainfall (data not presented).

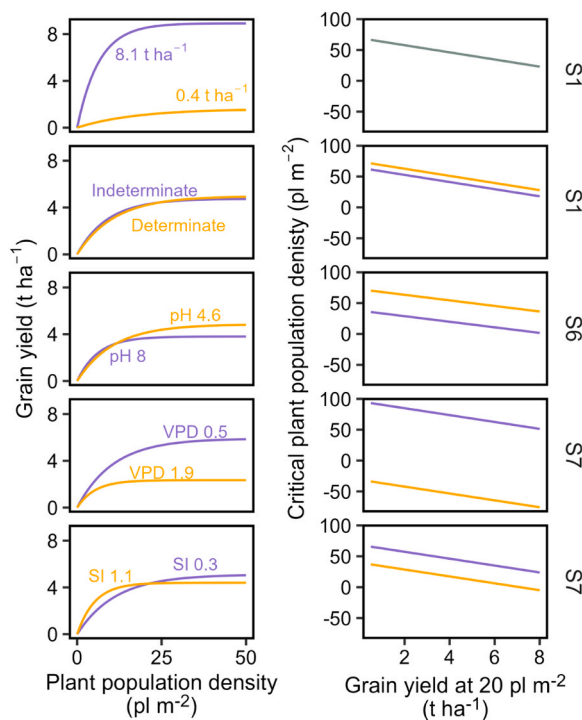
3.3. Profit-to-PPD response in Australia

For benchmarking, we distinguished Australia from other countries because it is our focus region and it represents 60% of our dataset. The critical PPD in Australia and across countries varied from 10 to 100 plants  $\text{m}^{-2}$  (Fig. 4a). When described with an exponential decay model, critical PPD decreased nonlinearly with increasing environmental yield to a minimum of 20 plants  $\text{m}^{-2}$  in Australia (Fig. 4a). For simpler benchmarking, a linear model fit to the data returned: Critical PPD =  $54.9 - 5.1 \times \text{grain yield at } 20 \text{ plants } \text{m}^{-2}$  ( $p < 0.001$ , residual standard error = 17.0  $\text{pl } \text{m}^{-2}$ ). Both functions predict critical PPD much higher than current practice, but the relation between critical PPD and environmental yield was highly scattered, with many environments returning critical PPDs below the curve. The median Australian critical PPD was 30 plants  $\text{m}^{-2}$  with an interquartile range of 20 to 45 plants  $\text{m}^{-2}$ , when calculated for all countries it was 34 plants  $\text{m}^{-2}$  with an interquartile range of 21 to 49 plants  $\text{m}^{-2}$  (Fig. 4b). There is large overlap in the curve parameters (Table S3) between Fig. 4a and b, illustrating that the curves are basically identical.

Comparing grain yield from the yield-to-PPD responses at 10, 15, 20, 25 and 30 plants  $\text{m}^{-2}$  (the range considered by most Australian growers), shows that mean grain yield decreased with plant population density below 20 plants  $\text{m}^{-2}$  and increased with plant population density above this standard (Fig. 5). The response was asymmetric, with higher reduction in grain yield below the standard and flatter responses above it.

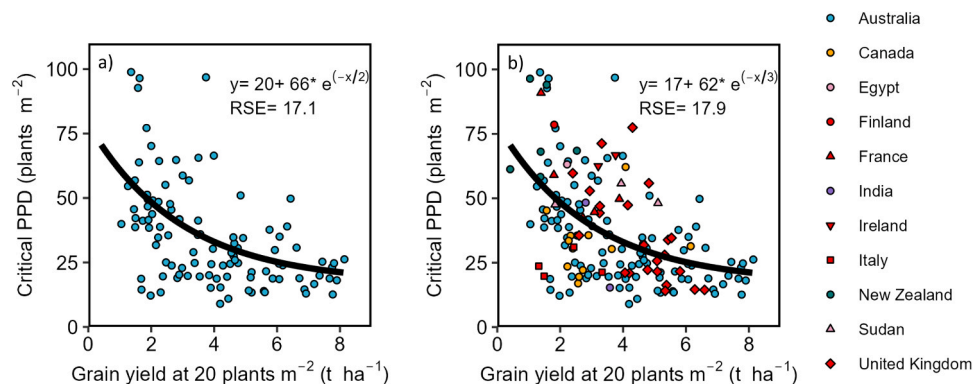
**Table 1**  
 $R^2_{\text{LMM}}$  for the variables explaining critical plant population density, in seven overlapping subsets of the data. For S2–7, “S1 fixed effects only” is the reduced model with only the variables common to all subsets.

Subset	Sample	Description	$R^2_{\text{LMM}}$	+ Unique variable/s	Difference
			S1 fixed effects only		
S1	163	Complete set	0.251	-	-
S2	133	+ Sowing date	0.289	0.294	0.005
S3	108	+ Row spacing	0.285	0.312	0.027
S4	92	+ Soil texture	0.284	0.296	0.012
S5	89	+ Sowing seed size	0.302	0.285	-0.017
S6	61	+ Soil pH	0.327	0.440	0.113
S7	96	+ Australian weather data	0.425	0.574	0.149



**Fig. 3.** (Left column) Effects of selected environmental and agronomic variables on grain yield through the variables' marginal effects on asymptote  $a$  and curvature  $c$  of Eq. 1. (Right column) Marginal effects on critical PPD, as a function of environmental yield, quantified as the yield at 20 pl m<sup>-2</sup>. The values are the maximum and minimum of each variable. Variables are, from top to bottom: environmental yield, genotype determinacy, soil pH, vapour pressure deficit (VPD) and rainfall seasonality index (SI). Purple indicates the value that favours yield, yellow indicates the value that is unfavourable for yield, the grey line in the top left panel is where no interaction is illustrated. S1, S6 and S7 are the sets of data from the database used for the prediction. These do not benchmark plant population density because the predictions are made by holding non-focal variables constant at their average value; rather, they illustrate the direction of change in critical PPD, asymptote and curvature.

The change in profit was larger with higher grain prices, higher yield, and larger changes in plant population density, with a small effect of cost shifting from low to high (Table S4; Fig. 6). As with grain yield, the profit response was asymmetric, being more negative for plant population density reductions than positive for plant population density increases. A specific profit-to-PPD response can be predicted from the data of Fig. 6. For example, for a yield of 4 t ha<sup>-1</sup> at 20 plants m<sup>-2</sup>, grain price of \$400 t<sup>-1</sup> and higher marginal cost, increasing plant population density from 20 to 25 plants m<sup>-2</sup> would increase profit by an average of \$30 ha<sup>-1</sup>.



**Fig. 4.** Critical PPD as a nonlinear function of environmental yield from a) Australia, and b) 11 countries. The fitted curves are an exponential decay model, RSE is residual standard error (pl m<sup>-2</sup>). Standard errors for parameters are in Table S3.

(4 t ha<sup>-1</sup> \* \$7.45 ha<sup>-1</sup> per t ha<sup>-1</sup> = \$30 ha<sup>-1</sup>).

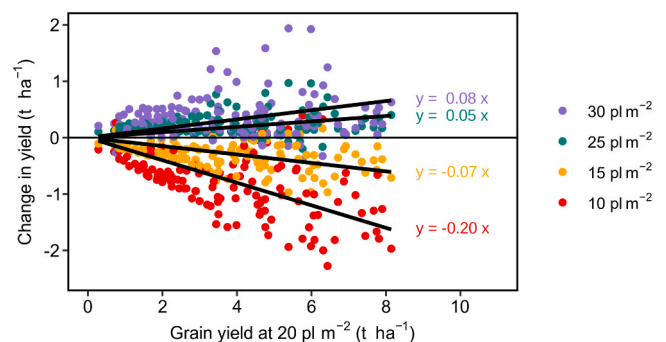
#### 4. Discussion

##### 4.1. Crop and plant phenotype responses to plant population density were nonlinear or close to neutral

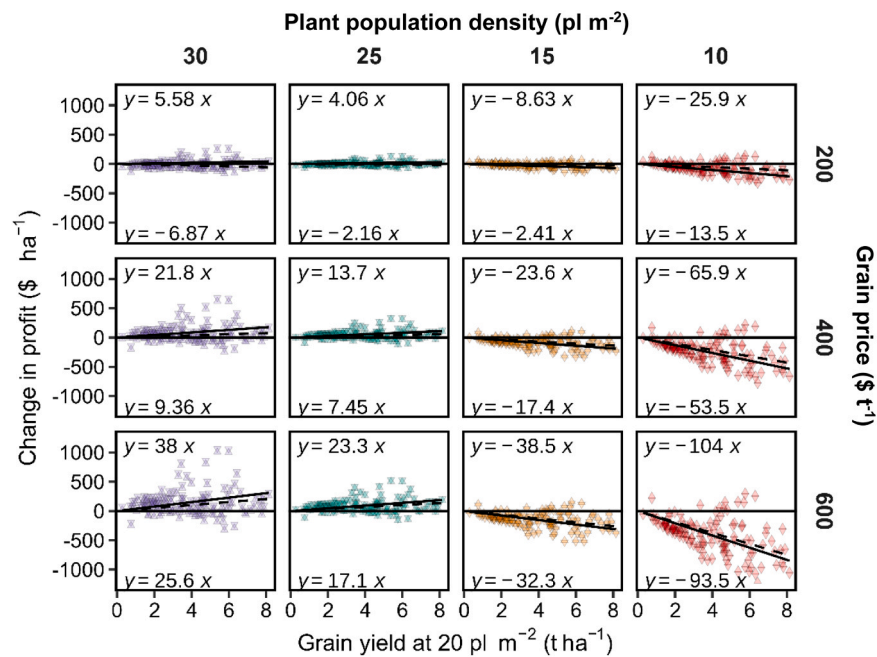
In response to plant population density, crop yield and its components increased nonlinearly to an asymptote 40–80% greater than at 20 plants m<sup>-2</sup>. Asymptotic trait-to-PPD responses are ubiquitous across crops, and have been reported for faba bean in Australia (Marcellos and Constable, 1986; Loss et al., 1998) and elsewhere (López-Bellido et al., 2005).

The crop phenotype responses are asymptotic because competition for light, water and nutrients imposes an upper limit to population-level production (Weiner et al., 2009; Postma et al., 2021). Additionally, plants scale reproduction in response to non-resource signals that forecast environmental conditions, such as the early perception of neighbouring plants mediated by sensing the red:far-red ratio (Aphalo and Sadras, 2021). A controlled-environment study on wheat mini-canopies found that grain yield increased with an artificially increased red:far-red ratio (associated with few neighbours in natural conditions) for the same plant population density and resource supply (Dreccer et al., 2022), suggesting that the realised yield-to-PPD asymptote could be lower than the environmental carrying capacity. An implication for breeding is that a genotype that is unresponsive to neighbours might have a higher asymptote in its trait-to-PPD responses and would therefore exhibit higher yields under crowded conditions.

Plant population density might affect crop growth and yield differently. Growth and yield decoupled at high biomass in lentil (Lake and



**Fig. 5.** Change in grain yield (difference between treatment and yield at 20 pl m<sup>-2</sup>) to changing the plant population density above or below 20 pl m<sup>-2</sup>. Lines and equations are least squares, zero-intercept linear regressions. Data are from 126 yield-to-PPD responses in 77 experiments conducted in Australia.



**Fig. 6.** Profit-to-PPD response (columns) as a function of grain yield at 20 pl m<sup>-2</sup>, depending on grain price (rows) and marginal cost (triangles pointing up and solid lines = high, triangles pointing down and dashed lines = low). The equations are zero-intercept regressions for each treatment, with low cost treatments at the top of each panel and high cost treatments at the bottom of each panel. Monetary values are in Australian dollars.

Sadras, 2021) and field pea (Sadras et al., 2013), where the primary source of variation was the environment. However, in our study where plant population density is the primary source of variation, harvest index was relatively constant. Similarly, the environment but not plant population density affected the harvest index of Australian winter wheat (Porker et al., 2020).

Individual seed weight was insensitive to plant population density, whereas seed number followed the same trend as grain yield. This is predicted by theory, because plants accommodate environmental variation through seed number while maintaining a stable genotype-specific seed weight, partially resulting from the conflict between maternal and offspring fitness (Sadras, 2007, 2021). We found that seeds per pod was insensitive to plant population density, corroborating the conclusion that this trait is stable and heritable in faba bean (López-Bellido et al., 2005).

The larger response of lodging to plant population density compared to the response of plant height is evidence of crowding stress. A relatively small height response was also found in a quantitative review of 163 species (Postma et al., 2021). Genetic variation for yield, and lodging resistance with higher plant population density exists in cereals such as wheat (Austin and Blackwell, 1980; Fischer et al., 2019; Cossani and Sadras, 2021), maize (Carlone and Russell, 1987; Echarte et al., 2000; Tollenaar et al., 2006; Cui et al., 2022; Egli, 2023) and rice (Jennings and Jesus, 1968). In pulses, genetic variation for yield with plant population density has been identified in chickpea (Lake et al., 2016), common bean (Hamblin, 1975) and soybean (Carciochi et al., 2019), but historic selection for yield has not changed the response to density in soybean (De Bruin and Pedersen, 2009; Egli, 2023). Similar genetic resources might be available in faba bean.

Plant-level biomass, yield components and grain yield decreased nonlinearly with increasing plant population density. However, the model with the best fit for the data was not the inverse of the crop-level pattern. A mismatch between population and plant levels was also apparent in a quantitative review of 163 plant species (Postma et al., 2021). Two possible explanations are: 1) resource-use efficiency increased with plant population density, and 2) self-thinning after establishment was not measured and biased the measurements (Postma et al., 2021).

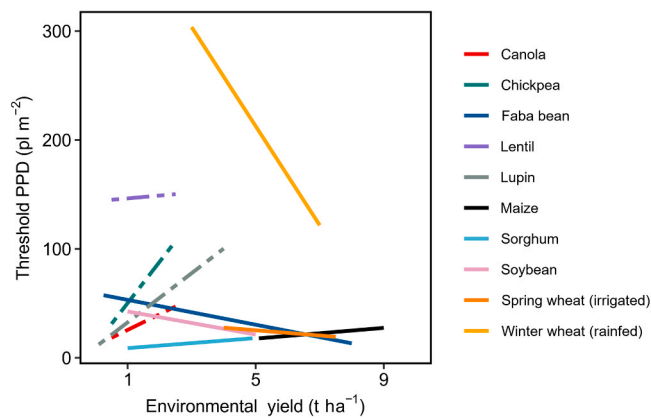
#### 4.2. Some variation in critical plant population density can be described by environmental factors

The most appropriate model for individual yield-to-PPD responses to determine the critical PPD was asymptotic (see Methods, Section 2.2.2, for our rationale in choosing the Mitscherlich model). In the few instances where a parabolic response may have been modelled, a Mitscherlich function performed similarly, and none of the experiments where plant population density was increased to > 100 plants m<sup>-2</sup> had a parabolic yield response. Wheat did not show a parabolic response up to 500 plants m<sup>-2</sup> in one experiment (Fischer et al., 2019), nor did soybean (Andrade et al., 2005). Parabolic responses are common in maize partially due to its high threshold plant size for reproduction (Willey and Heath, 1969; Echarte et al., 2000; Andrade et al., 2005).

The critical PPD declined with environmental yield. This association can be discerned from earlier Australian faba bean studies, such as in Fig. 1 of Marcellos and Constable (Marcellos and Constable, 1986) and Fig. 2 of Loss et al. (1998), but was not found in Adisarwanto and Knight (1997) where the lowest plant population density treatment was 20 plants m<sup>-2</sup> and the mean grain yield was 5 t ha<sup>-1</sup>.

A brief exploration of similar studies in other crops returned contrasting relationships between threshold PPD and environment (Fig. 7). Authors calculated the plant population density where either yield or gross margin (\$ ha<sup>-1</sup>, grain income minus variable costs) were maximised and it appears that a similar plant population density would have been returned with either definition, so we use 'threshold PPD' to describe both approaches. The relationships with environmental yield were either positive, close to neutral or negative (Fig. 7). The relationships for faba bean and soybean were remarkably similar. Contrasting responses between the species are attributable to plant architecture, minimum size for reproduction, responsiveness to space, or other reasons that are beyond the scope of this study.

Faba bean critical PPD was lower for some factors that favour growth or grain yield, primarily captured with environmental yield. Additional factors that reduced critical PPD further were higher soil pH and indeterminate genotypes. Interpreted at the plant-level, fewer plants are required to achieve similar crop-level outcomes under favourable conditions. By contrast, two unfavourable factors also reduced critical PPD,



**Fig. 7.** Threshold PPD (plant population density at which yield or gross margin is maximised, solid lines are yield, dashed lines are gross margin) as a function of environmental yield for ten crops: canola (French et al., 2016), chickpea (Jettner et al., 1999), faba bean (present study), lentil (Siddique et al., 1998), lupin (French et al., 1994), maize (Lacasa et al., 2020), sorghum (Thomas et al., 1981), soybean (Carciochi et al., 2019), irrigated spring wheat (Fischer et al., 2019) and rainfed winter wheat (Bastos et al., 2020). The lines are the estimated response for each crop: chickpea, faba bean, lupin and winter wheat were provided in the papers, the other slopes were estimated from tables or figures.

namely high VPD (indicating hot springs) and high rainfall seasonality (indicating low rainfall concentrated into a few winter months). In the case of VPD, the effect was due to a large reduction in maximum yield, suggesting hot springs could override the yield-to-PPD response, eliminating yield benefits from higher plant population densities. In the case of rainfall seasonality, the effect was due to a slight decrease in maximum yield and a steeper curve in the yield-to-PPD response, which may indicate increased competition for limited moisture, favouring lower critical PPD. This relationship would interact with soil texture, given its effect on curvature in the yield-to-PPD response in a wide range of food plant species through its effect on water uptake (Friedman, 2016). Our results give some indication that heavier soils had a lower critical PPD, but there were no effects found on maximum yield or curvature so it is unclear how the interaction between soil texture and moisture applies to faba bean critical PPD.

The simplest model with the best represented variables in our dataset only explained 25% of variation in critical PPD. Yield-to-PPD responses are highly variable between growing conditions, the motivation for this study, and many papers on yield-to-PPD responses report little information on growing conditions that could be used for further analysis. In the Australian dataset the simple model explained 43% of critical PPD variation, increasing to 57% with weather data. We have identified modulators of critical PPD and increased our understanding of its behaviour in faba bean, but its variation is highly complex and difficult to predict, which needs to be recognised by growers and researchers (Hunt et al., 2019; Lacasa et al., 2020).

#### 4.3. The relationship of critical PPD with environment has implications for breeding

Breeders aim to standardise management, including target plant population density, and the association of critical PPD with environment leads to conflicting selection pressure for low versus high yield environments. For example, in Australia, the network of National Variety Trials (nvt.grdc.com.au/about) is used to benchmark genotypes slated for commercialisation against current standards, and it prescribes a plant population density of 30 plants  $m^{-2}$  for faba bean. The present study indicates that this will protect against a yield limitation imposed by plant population density in 50% of environments, but 1) it differs from current industry practice and so may inhibit the expression of

genetic gain under farm conditions, and 2) it forfeits opportunities to exploit genotype  $\times$  environment  $\times$  management interactions for specific adaptation, such as in very high and very low-yielding environments where contrasting crop architecture and/or plant population density might provide a yield benefit (Hammer et al., 2014).

#### 4.4. Asymmetry in yield- and profit-to-PPD responses has agronomic implications

Our curve relating critical PPD to environmental yield in Australia suggests higher plant population densities than are practiced commercially; reasons for the discrepancy include: 1) the risk of disease that is increased by high population density, 2) the risk of lodging, 3) the risk of an uneconomic response in a dry or hot spring, as reflected in our finding that low in-season rainfall and high VPD reduced critical PPD, and 4) the large seed size of Australian faba bean cultivars (0.6 to 0.8 g seed $^{-1}$ ) that makes it impractical to sow at high rates. A handful of diseased and lodged experiments were included in our dataset, but we expect that points 1 and 2 are only partially accounted for in our study.

The dependence of critical PPD on environmental and agronomic factors can be used to tailor a target PPD to local conditions, but the target PPD also needs to consider the expected yield and profit outcomes. For Australia, grain yield and profit typically increased from 10 to 30  $pl\ m^{-2}$ , but the response was asymmetric (Fig. 5), with a greater negative effect of reducing plant population density below 20 plants  $m^{-2}$  than the positive effect of increasing it. Asymmetric profit responses were also found around the optimum plant population density in canola (French et al., 2016). Our findings support 20 plants  $m^{-2}$  as a target plant population density for most environments at typical grain prices, but the lack of symmetry emphasises that this is a minimum plant population density. Increased sowing rates may be appropriate where crop establishment, growth or yield are constrained, or where the risk of a lack in plant population density response due to hot springs or low rainfall is acceptable. Increased plant population density might not compensate for the plant-to-plant variability caused by staggered plant emergence (Tollenaar et al., 2006; Masino et al., 2018).

#### 4.5. Limitations and advantages of the framework

Limitations of our framework include: 1) it ignores responses that do not have an asymptote or peak, as was the case in a handful of the cases in our database; 2) we use a two-step, frequentist approach, so the error associated with an individual critical PPD estimate is lost in the second stage examining its variation. Furthermore, we cannot quantify the uncertainty in the critical PPD; both shortcomings would be overcome with a Bayesian approach (Carciochi et al., 2019; Lacasa et al., 2020, 2023); 3) the number of studies that can be included is limited by the requirement to have at least three plant population density treatments to generate a nonlinear curve, and by the detail provided in published documents; 4) some of the factors we investigated are unknown or uncontrollable at sowing when the decision for target plant population density is made. A new framework using information at sowing and weather forecasts is able to generate probabilistic predictions of the optimal plant population density, a step forward for risky decisions like sowing rate (Lacasa et al., 2023).

Two advantages of our approach are: 1) the critical PPD integrates the effects of the asymptote and curvature parameters, avoiding the need to decide whether a variable applies to one or both, which is significant because the parameters in nonlinear regression may be theoretically linked and/or empirically correlated, 2) we treat environmental yield as a continuous variable, avoiding the use of arbitrary categories such as low/medium/high yield.

## 5. Conclusions

The immediate application of our findings is to guide local



recommendations of target plant population density for faba bean, and we have provided more detail on economic considerations for Australia. Recommendations must account for the yield potential of the environment and the large spread in the data. The modulators we identified enable some fine-tuning. Local agronomists may be best placed to use our findings to guide recommendations for growers. An important consideration is most responses are described by an asymptotic, not parabolic, relationship, which affects how the profit response is estimated.

Our framework can be adapted to other grain crops. An appropriate model for the experiment-level data must be selected and may differ between crop species and databases. With a brief exploration of the literature, we identified positive, neutral, and negative relationships between threshold plant population density and environmental yield; future research is needed to explain the segregation by species and should account for patterns of resource availability and stress.

Empirical studies are necessary to ensure that theory describes the real world, but the meaning of empirical studies without theory cannot be easily deduced and findings are not easily extrapolated beyond the studied environments. This leads to an endless empiricism, as seen in the proliferation of yield-to-PPD papers published for most crops on most continents, and the lack of specific benchmarks. There is a continued need to develop and apply frameworks to increase research efficiency for greater agricultural outcomes.

#### CRedit authorship contribution statement

**Taylor Julian:** Writing – review & editing, Formal analysis. **Sadras Victor:** Writing – review & editing, Visualization, Conceptualization. **Brand Jason:** Writing – review & editing, Investigation. **Lake Lachlan:** Writing – review & editing, Visualization, Conceptualization. **Denton Matthew:** Writing – review & editing, Visualization. **Manson James:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

#### 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.

#### Data availability

The authors do not have permission to share data.

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#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.eja.2024.127106](https://doi.org/10.1016/j.eja.2024.127106).

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