

# G × E ANALYSIS OF NARROW-LEAFED LUPIN HISTORICAL TRIALS INDICATES LITTLE SPECIFIC ADAPTATION AMONG AUSTRALIAN CULTIVARS

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## ABSTRACT

In order to investigate varietal adaptation and changes over time in Australian lupin breeding, 54 historical variety trials in WA, NSW and Victoria, comprising all narrow-leaved cultivars released since 1967 were subject to G × E analysis. Main effects and interaction were all highly significant ( $P < 0.001$ ), but variance components sequentially from E to G, and G × E, suggesting that interaction was a relatively minor effect. Finlay-Wilkinson (FW) analysis was very effective in capturing the interaction effect, explaining 91.3% of variance, and demonstrated 2 important issues for lupin breeding: There was very little crossover interaction, indicative of extremely limited specific adaptation among Australian narrow leaved lupin varieties.

G × E interaction was manifested as varietal differences in responsiveness to environment quality, as defined by FW slope coefficients.

Genotype responsiveness was curvi-linearly related to yield ( $r^2 = 0.74$ ), with a strong positive linear trend from 800-1200 kg/ha, tailing off in higher yielding genotypes (> 1350 kg/ha). Both mean yield and genotype responsiveness were positively correlated to cultivar release date ( $r^2 = 0.67-0.80$ ), but while the former was linear, the latter curvi-linear, with responsiveness in modern varieties beginning to tail-off. Because genotype responsiveness and mean yield were positively related, and there was little crossover interaction, the instability associated with high FW slope coefficients is a positive attribute because it leads to farmers returning higher yields as conditions become more favourable. However, the lack of specific adaptation among Australian lupin varieties indicates that there is currently insufficient diversity to develop regionally adapted cultivars. This issue must become a research priority in lupin if we are to maximise yield potential among the diverse environments that comprise the Australian grainbelt.

## KEYWORDS

G × E analysis, historical variety change, adaptation, *L. angustifolius*

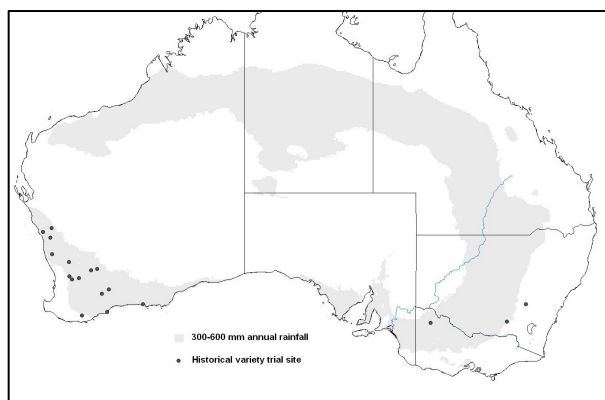
## INTRODUCTION

The genotype by environment (G × E) experimental approach can be a very useful tool for studying plant adaptation, particularly when using a broad range of genotypes and environments. The underlying assumption is that diverse evaluation environments will exert varying selection pressures which will result in differential performance in a diverse group of test genotypes. If environments and genotypes are well characterised by measuring traits associated with differential performance, it becomes possible to use the G × E approach for studying specific adaptation (Berger *et al.* 2007). Questions of interest to breeders and physiologists include-what makes an environment low or high yielding, do genotypes respond differently to different environments, and if so, why? The historical variety trial conducted over multiple environments is a special case of G × E experiment which provides insight into breeding programs by introducing the dimension of time. Thus it becomes possible to assess how varieties changed over time, whether the program has produced specific adaptation to regions or environment types and so on.

In the current paper we investigate varietal adaptation and changes over time in Australian lupin breeding, using 54 historical variety trials conducted throughout the Western Australia grainbelt and a number of locations in NSW and Victoria, comprising all narrow-leaved cultivars released since 1967. Given that narrow leaved lupin is a very recent crop, having been domesticated in Central Europe as late as the 1920-30s (Hondelmann, 1984), and with the Australian breeding program only starting in the 1960s (Gladstones, 1994), we were particularly interested to what extent specific adaptation had been bred into modern Australian lupin varieties.

## MATERIALS AND METHODS

This investigation used 54 site/year combinations of narrow leafed lupin historical variety trials, comprising sites in Western Australia and the east (Fig. 1).



**Fig. 1.** Location of historical variety trial sites in Western Australia ( $n = 44$ ), New South Wales ( $n = 9$ ) and Victoria ( $n = 1$ ). The 300-600 mm annual rainfall distribution is presented to give an approximate location of the southern Australian grainbelt.

**Table 1.** List of narrow leaf lupin varieties evaluated in historical variety trials sorted by balance code (1, evaluated at all 54 sites...7. evaluated at 12 sites) and release year.

Cultivar	Balance	Release date	Notes
Unicrop	1	1973	All 54 sites
Illyarrie	1	1979	All 54 sites
Yandee	1	1980	All 54 sites
Danja	1	1986	All 54 sites
Gungurru	1	1988	All 54 sites
Warrah	1	1989	All 54 sites
Yorrel	1	1989	All 54 sites
Merrit	1	1991	All 54 sites
Myallie	1	1995	All 54 sites
Kalya	1	1996	All 54 sites
Wonga	1	1996	All 54 sites
Belara	1	1997	All 54 sites
Tallerack	1	1997	All 54 sites
Tanjil	1	1998	All 54 sites
Uniharvest	2	1971	48 sites
Marri	2	1976	48 sites
Chittick	2	1982	48 sites
Uniwhite	3	1967	41 sites
Geebung	3	1987	41 sites
Moonah	4	1998	36 sites
Quilinoack	4	1999	42 sites
Jindalee	5	2002	28 sites
Mandelup	5	2004	28 sites
Coromup	6	2006	16 sites
95L256-17-3	7		5 sites

The trials commenced in 1997 with 15 varieties, increasing to 25 varieties by 2006, reflecting ongoing cultivar release over that period. Site-variety balance is presented in Table 1. Trials were grown as randomised complete block designs ( $n = 6$ ), and seed yield measured by machine harvesting entire plots (ca. 12.8 m<sup>2</sup>).

Finlay-Wilkinson (1963) analysis was used to model  $G \times E$  interaction using the site mean yield as an index of environment quality. Variety yields were regressed against site mean yield using general linear regression in Genstat V. 10, fitting block effects separately for each site. Residual plots were used to identify outliers and confirm that the residuals had common variance and were normally and independently distributed. Balance among genotypes and environments is not a formal requirement for linear regression. Nevertheless, because imbalance can introduce bias into the analysis because, by definition, certain genotypes are evaluated under circumstances different to the rest, it is important to assess its impact. With this in mind, the genotypes Coromup and 95L256-17-3, evaluated at only 16 and 5 sites, respectively, were excluded from the analysis, leaving a group of 23 genotypes that had been grown at 28-54 sites (Table 1). Two analyses were performed based on the: 1) completely balanced subset of 28 sites, 2) entire trial, the unbalanced comparison presented in Table 1. Both analyses produced very similar results, with highly correlated Finlay-Wilkinson slope coefficients ( $r = 0.95$ ), suggesting that regression was an appropriate model for estimating missing values in this case. Accordingly, the unbalanced analysis, which uses the entire trial dataset, is presented here. ANOVA was performed on the balanced subset of 28 sites to generate variety means and estimate the relative variances attributed to G, E and their interaction.

## RESULTS AND DISCUSSION

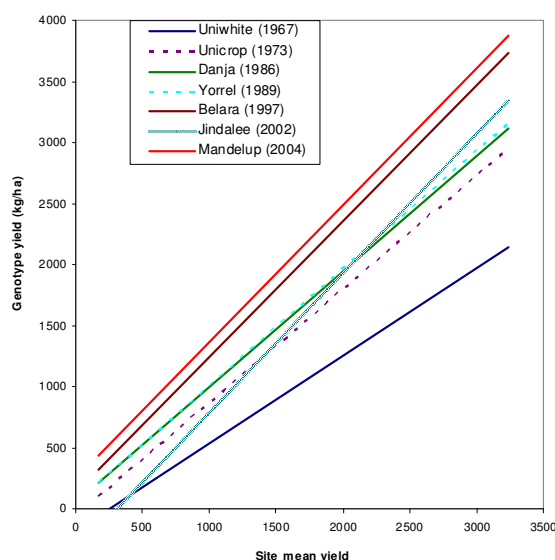
The Finlay-Wilkinson regression model accounted for 91.3% of variance, and while the effects of environment, genotype and their interaction were all highly significant ( $P < 0.001$ ), there was a dramatic diminution in mean square values in the same order, suggesting that differences among main effects, particularly that of environment were considerably more important than interaction. This was confirmed by performing analysis of variance on a balanced subset of 28 sites. This analysis, which does not inflate the effect of environment by regressing against average site mean, returned variety and  $G \times E$  interaction mean squares 16 and 463 times smaller than the environment main effect, respectively. Accordingly, there was a huge range in site yields, from 173 kg/ha at South Carrabin in 2000 to 3243 kg/ha at Cowra Research Station in 2005, and a smaller range of variety yields, from 816-1645 kg/ha, in Uniwhite to Mandelup (Table 2).

**Table 2.** Yield and stability (Finlay-Wilkinson slope coefficients) of narrow leaf lupin varieties evaluated in historical variety trials, sorted in order of productivity and classified by vernalisation response.

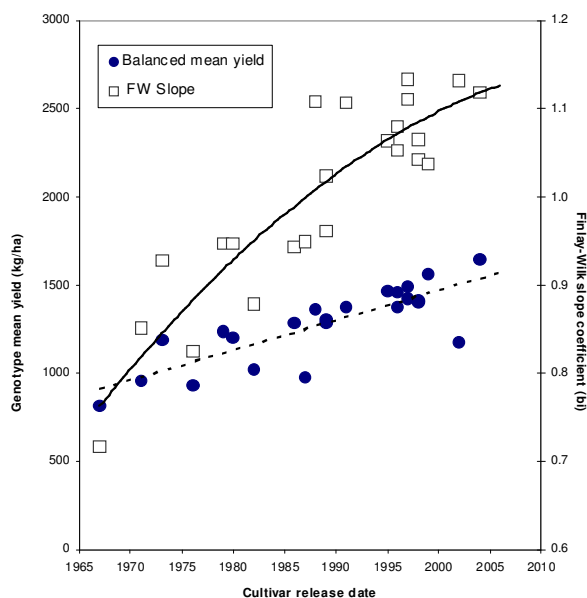
Cultivar	Vernalisation response	Mean yield (kg/ha)	F-W slope
Uniwhite	Obligate	816	0.72
Marri	Obligate	926	0.82
Uniharvest	Obligate	956	0.85
Geebung	Obligate	979	0.95
Chittick	Facultative	1024	0.88
Jindalee	Facultative	1174	1.13
Unicrop	Thermoneutral	1186	0.93
Yandee	Thermoneutral	1200	0.95
Illyarrie	Thermoneutral	1236	0.95
Danja	Thermoneutral	1280	0.94
Yorrel	Thermoneutral	1286	0.96
Warrah	Thermoneutral	1305	1.02
Gungurru	Thermoneutral	1363	1.11
Wonga	Thermoneutral	1373	1.05
Merrit	Thermoneutral	1374	1.11
Moonah	Thermoneutral	1402	1.04
Tanjil	Thermoneutral	1413	1.07
Tallerack	Thermoneutral	1424	1.13
Kalya	Thermoneutral	1459	1.08
Myallie	Thermoneutral	1460	1.06
Belara	Thermoneutral	1489	1.11
Quilinock	Thermoneutral	1561	1.04
Mandelup	Thermoneutral	1645	1.12
LSD		32	0.09

G × E interaction was well modelled by Finlay-Wilkinson slope coefficients, which estimate variety stability, ranging from 0.72 kg/kg site mean in Uniwhite to > 1.1 kg/kg site mean in 6 varieties, including Belara and Mandelup (Table 2). Fig. 2 presents fitted curves from the Finlay-Wilkinson regression model for selected varieties across the response range. With the exception of Jindalee, there is no evidence for cross-over interaction among any of the Australian varieties. This is a very important point because it demonstrates that Australian cultivars differ in their capacity to respond to favourable sites (represented by different slope coefficients), but **not** in their specific adaptation to either low or high yielding environments. Fig. 2 shows that genotype responsiveness and mean yield appear to be positively correlated, low yielding varieties such as Uniwhite having little capacity to respond to favourable environments compared to Mandelup or Belara. In fact there is a curvi-linear relationship between responsiveness and yield among Australian varieties ( $r = 0.86$ ), with a strong positive linear trend from 800-1200 kg/ha, tailing off in higher yielding genotypes (> 1350 kg/ha) (Table 2).

Regressing yield and responsiveness against cultivar release date captures changes over time among Australian varieties (Fig. 3). Whereas yield has linearly increased at  $17 \pm 2.6$  kg/yr since the release of Uniwhite in 1967, the increase in genotype responsiveness is curvi-linear, tailing off after 1990. Table 2 shows that the introduction of the *Ku* gene for thermoneutrality, which rendered flowering time unresponsive to vernalisation (Gladstones, 1994), was a pivotal point in increasing productivity and responsiveness of Australian cultivars.



**Fig. 2.** Fitted curves from the Finlay-Wilkinson regression model for varieties representing the range of responses recorded in the historical variety trials (0.72-1.13 kg/kg site mean, Uniwhite-Jindalee).



**Fig. 3.** Australian cultivar changes over time: mean yield and responsiveness (FW slope coefficients) regressed against release date. (Yield =  $17.0x - 32558$ ,  $r^2 = 0.67$ ; FW slope =  $-0.0001x^2 + 0.536x - 536.3$ ,  $r^2 = 0.80$ ; where  $x$  = cultivar release date).

## SYNTHESIS AND IMPLICATIONS

The absence of cross-over interaction among Australian varieties indicates that breeding programs have **not** developed genotypes specifically adapted to low or high yielding environments. This is likely to be a reflection of the relative immaturity of the Australian lupin breeding program, and an associated lack of depth in the gene pool. Given a high degree of relatedness among Australian cultivars, it is perhaps not surprising that there is no evidence of specific adaptation. In more mature grain legumes, such as chickpea, which has been domesticated for more than 10,000 years, short season, terminally drought-stressed sites select for early phenology, whereas environments with a longer growing season select for later phenology and increased biomass production (Berger *et al.* 2006; Berger *et al.* 2004). This type of specific adaptation allows Indian breeders to produce regionally-adapted material and maximise yield potential (Berger *et al.* 2006). Given the range of rainfall and growing season lengths across the Australian grainbelt, it should be feasible to optimise yield potential in lupin through similar specific adaptation. The current 'one size fits all' approach is unlikely to produce optimal returns in either long or short season environments.

However, phenological variability *per se* is not the issue underlying a lack of specific adaptation among Australian cultivars, which can be classified into 2 types: 1) late flowering, vernalisation responsive; 2) early flowering, thermoneutral. In the present study, vernalisation responsive types were both unproductive, and responsive to favourable long season environments (Table 2). Unpublished data from our laboratory suggests that vernalisation responsive genotypes grow more slowly than thermoneutral types, perhaps as a consequence of unfulfilled vernalisation requirements, and therefore are consistently less productive, even under high rainfall long season environments. If this is correct, matching phenology to growing season lengths in target environments will not be possible until a source of later flowering, thermoneutral germplasm is identified. Our laboratory is currently investigating adaptive strategies of wild germplasm to stress gradients in order to understand the role of vernalisation, how phenology changes across different habitats, and identify promising material (Berger *et al.* 2008).

An unintended consequence of the lack of specific adaptation among Australian varieties is the positive effect of instability. Genotypes with F-W slope coefficients significantly different to the population mean response ( $< 1$  or  $> 1$ ) are formally defined as being unstable (Finlay and Wilkinson, 1963), and normally considered to be undesirable because of the implicit unpredictability. However, because there is no

cross-over interaction among Australian lupin cultivars, the unpredictability associated with *high* FW slope coefficients is a positive trait because it represents increasing responsiveness to high yielding environments without a yield penalty at low yielding sites. In other words, farmers growing responsive genotypes such as Mandelup and Belara are doing as well as is currently possible, in both stressful and benign growing seasons.

## ACKNOWLEDGEMENTS

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