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ORIGINAL PAPER

Domestication bottlenecks limit genetic diversity and constrain adaptation in narrow-leafed lupin (*Lupinus angustifolius* L.)

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Abstract In contrast to most widespread broad-acre crops, the narrow-leafed lupin (*Lupinus angustifolius* L.) was domesticated very recently, in breeding programmes isolated in both space and time. Whereas domestication was initiated in Central Europe in the early twentieth century, the crop was subsequently industrialized in Australia, which now dominates world production. To investigate the ramifications of these bottlenecks, the genetic diversity of wild ($n = 1{,}248$) and domesticated populations ($n = 95$) was characterized using diversity arrays technology, and adaptation studied using G × E trials ($n = 31$) comprising all Australian cultivars released from 1967 to 2004 ($n = 23$). Principal coordinates analysis demonstrates extremely limited genetic diversity in European and Australian breeding material compared to wild stocks. AMMI analysis indicates that G × E interaction is a minor, albeit significant effect, dominated by strong responses to local, Western Australian (WA) optima. Over time Australian cultivars have become increasingly responsive to warm, intermediate rainfall environments in the northern WA grainbelt, but much less so to cool vegetative phase eastern environments, which have considerably more yield potential. G × E interaction is well explained by phenology, and its interaction with seasonal climate, as a result of varying vernalization responses. Yield differences are minimized when vegetative phase temperatures fully satisfy the vernalization requirement (typical of eastern Australia), and maximized when they do not (typical of WA). In breeding for WA optima, the vernalization response has been eliminated and there has been strong selection for terminal drought avoidance through early phenology, which limits yield potential in longer season eastern environments. Conversely, vernalization-responsive cultivars are more yield-responsive in the east, where low temperatures moderately extend the vegetative phase. The confounding of phenology and vernalization response limits adaptation in narrow-leafed lupin, isolates breeding programmes, and should be eliminated by widening the flowering time range in a vernalization-unresponsive background. Concomitantly, breeding strategies that will widen the genetic base of the breeding pool in an ongoing manner should be initiated.

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Introduction

In contrast to the Neolithic founder crops (i.e. wheat, barley, pea) that dominate broad-acre agriculture in Mediterranean climates (Zohary 1999), the narrow-leafed lupin

(*Lupinus angustifolius* L.) is a very recently domesticated crop subject to a series of bottlenecks in breeding programmes isolated in both space and time. A Mediterranean winter-annual (Gladstones 1998), *L. angustifolius* first appeared in an agricultural context as a spring-sown green manure and forage crop in the acid sands of northern Europe in the nineteenth century (Hondelmann 1984; Kurlovich 2002). Systematic breeding was initiated at the start of the twentieth century in Poland, Germany and Russia, and accelerated with a focus on reducing alkaloid levels, pod dehiscence and hard-seededness during the 1920s and 1930s (Hondelmann 1984; Kurlovich 2002). Nevertheless, *L. angustifolius* remained a minor grain legume until further domestication in Western Australia (WA) in the 1950s–1970s, stabilizing pod dehiscence, selecting white flowers and seeds as unlinked domestication markers (cv. Uniwhite 1967), and modifying the vernalization response (cv. Unicrop 1973) (Cowling et al. 1998; Gladstones 1970, 1994). The Australian industry has dominated world production since the mid 1980s (FAO 2010), at which time disease resistance became a major breeding focus (Cowling et al. 1998). Australian dominance notwithstanding, there is considerable global potential for lupins, as illustrated by its previous role in European agricultural systems, and more recent production increase in South America (FAO 2010).

Despite its rather Australian focus to date, lupin has much to offer to crop science as a candidate for examining the ramifications of late domestication in a variable production environment. Australian production systems encompass a wide climatic range, likely to exert contrasting selection pressures on breeding populations, and are therefore of broader interest in the investigation of adaptive traits. The Western Australian (WA) grain belt—responsible for ca. 80% of Australian production (ABARE 2010), has a strongly Mediterranean climate, while the eastern states receive higher summer rainfall (Fig. 1a). Although eastern growing seasons tend to be wetter and cooler than those in WA, there are strong stress gradients within both regions; reproductive phase rainfall decreasing, and seasonal temperature increasing, with latitude and distance from the coast (Fig. 1b).

Variable target environments notwithstanding, crop adaptive potential may be limited early on in domestication by constraining genetic diversity because of drift in small populations, and/or strong directional selection pressure for locally adaptive peaks (Wright 1931). This is particularly pertinent in narrow-leafed lupin because of its short domesticated history of sequential bottlenecks imposed by isolated breeding programmes, and because of small effective population sizes in Australian breeding (Cowling and Gladstones 2000). Given that domestication is a risky venture, there may be a reluctance to dilute elite pools by base-broadening, particularly when there is limited capacity for germplasm exchange from alternative breeding programmes (Cowling et al. 2009). Thus, there is a clear danger of limiting the potential of narrow-leafed lupin, which we examine in the present work.

Therefore, using molecular and genotype by environment (G × E) approaches, we ask how diverse is the domesticated narrow-leafed lupin, based on Australian cultivars released since 1967, and how does it respond across its production environment? Given that selection for specific adaptation is only possible if there is sufficient available diversity, we use diversity arrays technology (DArT^{TM}) to characterize our breeding populations and compare them to their wild progenitors. This methodology has been used extensively among the cereals (Raman et al. 2010; Tinker et al. 2009; Xie et al. 2006), and to a lesser degree among the legumes (Raman et al. 2008; Yang et al. 2006). G × E trials across the production environment are an excellent resource for investigating functional diversity in breeding populations because they demonstrate genotypic responses to real-world stresses, and can be used to study specific adaptation when augmented by yield-related traits (Berger et al. 2007). Multi-environment historical cultivar trials are particularly useful for investigating breeding trends, and therefore in the present study we investigate G × E interaction in all Australian cultivars released between 1967 and 2004, using a multivariate climate analysis to explain interaction behaviour across sites. In a companion paper we focus on genotypic differences to demonstrate which traits are adaptive across the variable production environment and how narrow-leafed lupin cultivars have changed since 1967 (Berger et al. 2012).

Materials and methods

Genetic diversity characterization

Two genetic diversity analyses were undertaken to characterize genetic diversity in narrow-leafed lupin germplasm. In the first analysis, 1,343 narrow-leafed lupin accessions (with 39 individual duplicate and triplicate check replications) were selected from the Australian Lupin Collection (Perth, Australia), comprising a range of origins and type. The bulk of this material ($n = 1{,}248$) was undomesticated, collected from the wild in the Mediterranean basin (Berger et al. 2008b). The domesticated material included all Australian cultivars released since 1967, and 69 European cultivars and advanced breeding lines. DNA was extracted from bulked leaf samples of five plants per accession using Illustra Nucleon Phytopure Genomic DNA extraction kits (GE Healthcare), quantified relative to lambda DNA controls on agarose gels stained with ethidium

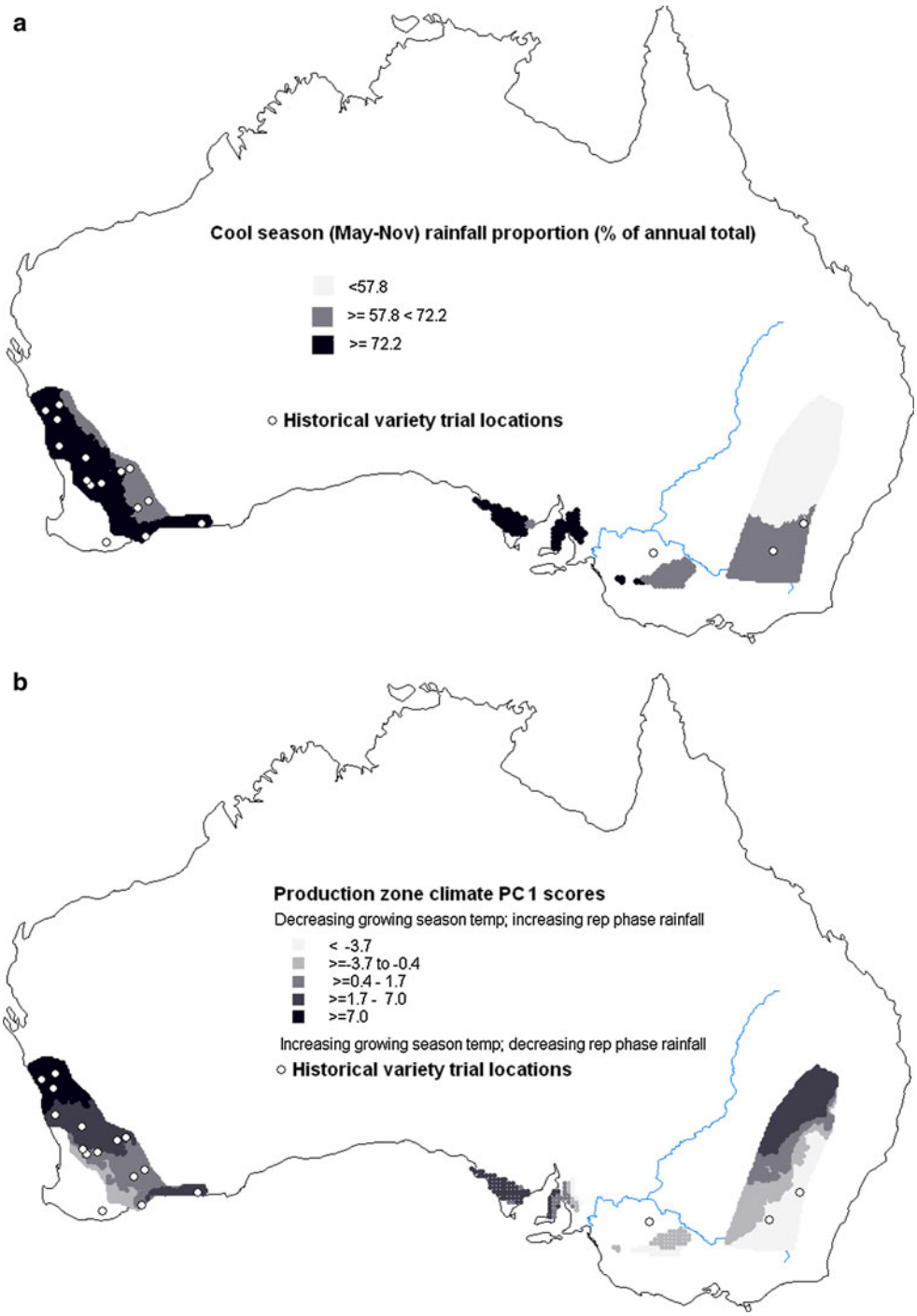

Fig. 1 Historical variety trial locations and climate analysis of Australian potential lupin production regions based on 2.5′ gridded WorldClim data (http://www.worldclim.org/) (Hijmans et al. 2005). **a** Cool season (May–November) rainfall proportion of annual total; **b** mapped principal component 1 scores. [PC1 explains 59.1% of variation; strong positive loadings (>0.76) on May–Aug and Sept–Nov mean, minimum and maximum temperatures; strong negative loading (−0.86) on Sept–Nov cumulative rainfall]

bromide and concentration adjusted to 50–100 ng/μL. All 1,343 accessions were genotyped using 137 polymorphic DArT markers by DArT Pty Ltd (Canberra, Australia). In the second analysis, the 25 Australian cultivars were genotyped at higher resolution using 825 DArT markers. To visualize genetic diversity, similarity matrices were calculated based on Euclidian distance, and principal coordinates analysis (PCO) performed using Genstat, 13th edition.

Multi-environment trials (MET)

The MET comprised 23 narrow-leafed lupin cultivars (Table 1) evaluated in a balanced manner in 31 historical variety trials, grown in the grainbelts of Western Australia ($n = 21$), New South Wales ($n = 9$) and Victoria ($n = 1$) from 2002 to 2007 (Fig. 1). Trials were grown as randomized complete block designs ($n = 6$ in WA and

Table 1 Complete list of Australian narrow-leafed lupin cultivars released between 1967 and 2004, classified by vernalization response and sorted by release date, evaluated in over 31 environments in the present study

Cultivar	Vernalization response[a]	Release date
Uniwhite	Obligate	1967
Uniharvest	Obligate	1971
Marri	Obligate	1976
Geebung	Obligate	1987
Chittick	Facultative	1982
Jindalee	Facultative	2002
Unicrop	Unresponsive	1973
Illyarrie	Unresponsive	1979
Yandee	Unresponsive	1980
Danja	Unresponsive	1986
Gungurru	Unresponsive	1988
Warrah	Unresponsive	1989
Yorrel	Unresponsive	1989
Merrit	Unresponsive	1991
Myallie	Unresponsive	1995
Kalya	Unresponsive	1996
Wonga	Unresponsive	1996
Belara	Unresponsive	1997
Tallerack	Unresponsive	1997
Moonah	Unresponsive	1998
Tanjil	Unresponsive	1998
Quilinock	Unresponsive	1999
Mandelup	Unresponsive	2004

[a] Classification based on the capacity to flower with and without vernalization under very weakly vernalization-inductive temperatures (14.4°C) (Jens Berger, pers. comm.)

$n = 2$–3 in NSW and Victoria), and seed yield measured by machine harvesting entire plots (ca. 12.8 m^2). To investigate cultivar biology additional observations were taken from subsets of trials. Flowering (n trials = 16) and podding dates ($n = 13$) were recorded in WA and NSW. The date of physiological maturity was measured in five contrasting trials in WA. Biomass, harvest index and seed size were estimated from 0.5 m^2 quadrat subsamples harvested at physiological maturity in 13 trials from WA.

ANOVA was performed to generate variety by site means, and estimate the relative variances attributed to G, E and their interaction. Residual plots were used to identify outliers and confirm that the residuals had common variance and were normally and independently distributed. AMMI analysis (Gauch et al. 2008) was used to investigate G × E interaction in Genstat 13th edition, fitting block effects separately for each site. Finlay and Wilkinson (1963) analysis, regressing genotype yield against site mean yield as an index of environment quality, was subsequently used to further investigate the interaction patterns modelled by AMMI analysis, and to present the results in a readily visualized manner (see "Results" for details).

Environment characterization

Western and Eastern Australian potential lupin production climates were mapped with DIVA-GIS (Hijmans et al. 2001) and altitude, and long-term monthly mean rainfall, minimum and maximum temperatures extracted from the 2.5 min WorldClim dataset (ca. 4 km spatial resolution) (Hijmans et al. 2005). The winter growing season was defined as May–November, with September as the start of the reproductive phase. Mean, minimum and maximum temperatures, and cumulative rainfall totals were calculated for vegetative and reproductive phases, respectively. Pre-season rainfall was defined as rainfall totals summed from December to April.

Historical variety trial climate data was extracted from an online database (SILO 2010). Growing seasons were defined by dates of sowing and harvest, and the onset of the reproductive phase estimated by photothermal modelling of flowering time (Berger et al. 2012). In addition to the temperature and rainfall-based bioclimatic variables defined above, a number of other biologically significant criteria were quantified. The number of days with vernalization potential (defined as mean temperature <10°C) was summed over the first 60 days of the growing season. The number of days with rainfall and frost was summed in both vegetative and reproductive phases, while vegetative phase photoperiod was calculated using an Excel macro (Lammi 2007). To characterize potential lupin production and historical variety trial climates in an integrated manner, correlation matrix-based principal components analysis (PCA) was performed on these bioclimatic variables using Genstat 13th edition.

Results

Genetic diversity characterization

Principal coordinates analysis clearly separated domesticated and wild populations, accounting for ~32.3% of variance in 2 dimensions (Fig. 2a). Australian and European cultivars and other breeding material form a single overlapping cluster on the upper-right quadrant of Fig. 2a. This distribution comprises a small subset of the coordinate range expressed by undomesticated Mediterranean germplasm, suggesting that relatively little genetic diversity has been incorporated into the domesticated breeding pool. Concentrating on Australian cultivars only capitalizes on the higher resolution afforded by using 825 DArT markers,

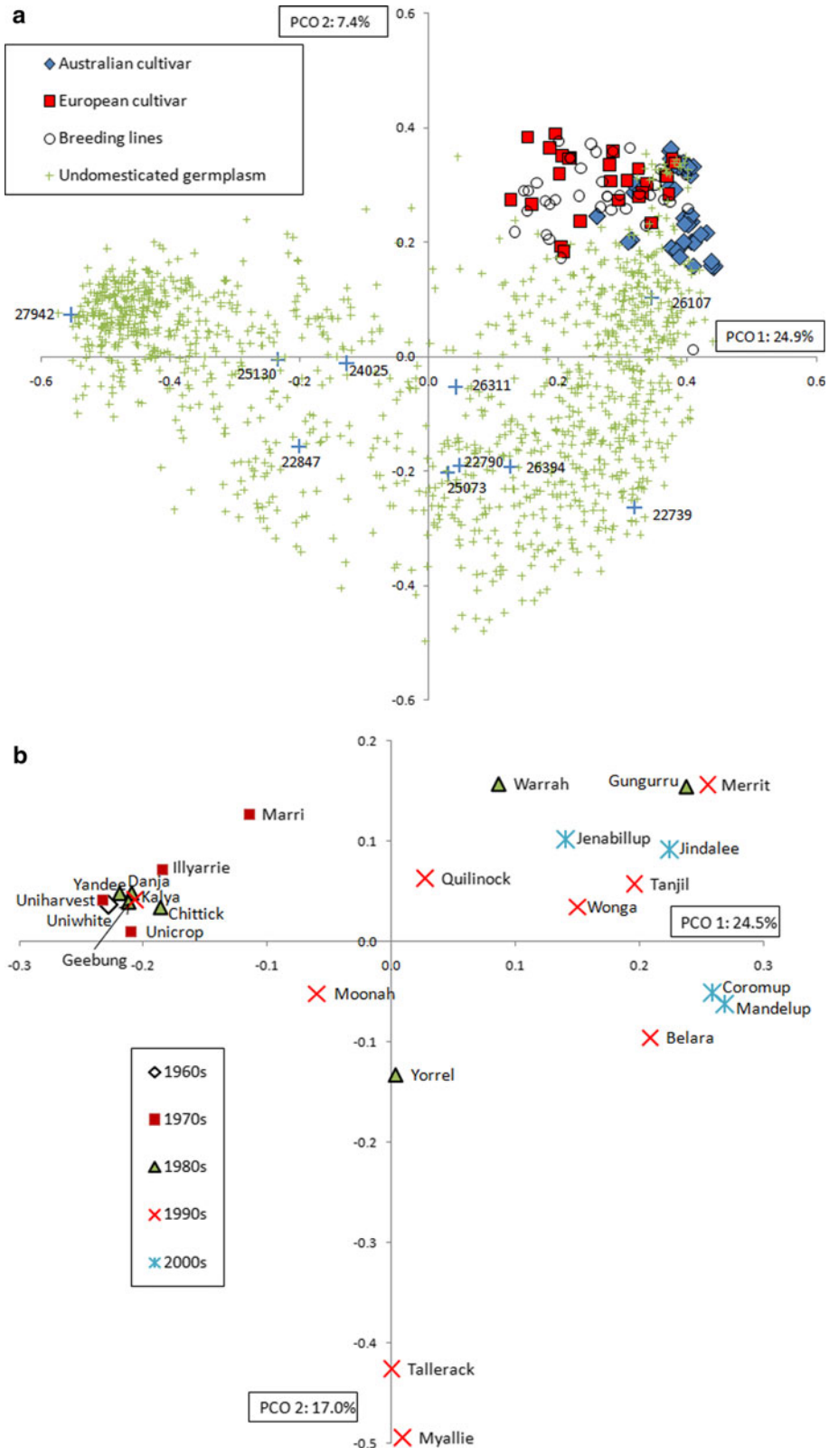

Fig. 2 DArT data principal coordinates ordination of: **a** wild versus domesticated germplasm ($n = 1{,}343$), based on 137 DArT markers, and accounting for 32.3% of variance in 2 dimensions; and **b** all Australian cultivars released since 1967 ($n = 25$), based on 825 DArT markers, and accounting for 41.5% of variance. *Markers* represent genotype coordinates categorized by domestication status and cultivar origin or release date

accounts for increased variance, and shows a clear historical trend within this narrow subset (Fig. 2b). Initially there was very limited diversity in the Australian breeding programme; most cultivars released in the 1960s–1980s are tightly clustered in the upper-left quadrant of Fig. 2b. Cultivars became more diverse from the release of

Gungurru and Warrah in 1988, and Yorrel in 1989, culminating in the most widespread PCO distribution during the 1990s. However, since 2000, cultivar diversity has begun to diminish; all being characterized by high PCO1 and intermediate PCO2 values (Fig. 2b), suggesting that while there has been a considerable change since the 1960s and 1970s, lupin breeding appears to be heading into another bottleneck.

G × E interaction for seed yield

ANOVA of seed yield indicated that while main effects and interaction were all highly significant (Table 2; $P < 0.001$), the environmental variance (E) was 13 times larger than the genotypic variance (G), and 401 times larger than their interaction. Nevertheless, given high statistical significance, an understanding of interaction is essential to put main effects into perspective, and will be addressed below, and then put into an environmental context. [The main effect of G is the focus of a companion paper (Berger et al. 2012).]

AMMI analysis accounted for 66.1% of the interaction sums of squares in 2 highly significant ($P < 0.001$) interaction principal components (IPCA1, 2; Table 2), dominated by contrasting western and eastern environments, respectively. In IPCA1 the majority of sites ($n = 22$) were characterized by interaction loadings close to the origin, while two small subsets with contrasting IPCA1 loadings and productivity drove G × E interaction (circled by solid line in Fig. 3). A low-yielding, positive IPCA1 subset ($n = 4$) largely comprised sites in NSW, while an intermediate-high yielding, negative IPCA1 subset ($n = 5$) consisted exclusively of WA northern grainbelt locations. The strong negative correlation ($r^2 = 0.91$) between genotype IPCA1 score and mean yield (Fig. 3) indicates that low-yielding genotypes performed relatively better at low-yielding, positive IPCA1-loaded sites, and vice versa for high-yielding genotypes, and was consistent with the distribution of vernalization response. Vernalization-responsive (VR) genotypes, particularly obligately responsive types, confined to the upper-left quadrant of Fig. 3, were characterized by positive IPCA1 scores and low mean yield. Among vernalization-unresponsive (VU) cultivars there was a clear historical trend of IPCA1 score decreasing, and yield increasing, as cultivars become more recent (Fig. 3). These interaction patterns are confirmed by classifying both sites and genotypes by mean yield and IPCA1 score (Table 3). Differences between and within vernalization response/release date categories were very small at low-yielding, positive IPCA1-loaded NSW sites, but became very large at the medium-high yielding, negative IPCA1-loaded WA northern grainbelt sites. Here yield increased from obligate to facultative vernalization responses, and again to VU cultivars, and then linearly with release date within this group (Table 3). The highest yielding group, VU cultivars released after 1997, was almost 2.5 times as productive as obligately VR cultivars in IPCA1-loaded sites, a difference of almost 1,120 kg/ha (Table 3).

In contrast to IPCA1, IPCA2 site loadings were strongly negatively correlated with mean site yield ($r = -0.79$), and dominated by high-yielding NSW sites (data not presented). To visualize interaction behaviour across genotypes and sites individually, Finlay and Wilkinson (1963) analysis was performed separately on the subsets of trial sites identified by AMMI analysis as contributing strongly ($n = 9$) or weakly ($n = 22$) to G × E interaction modelled by IPCA1. This was very effective because the genotype

Table 2 ANOVA table for AMMI model of seed yield of 23 narrow-leafed lupin cultivars grown over 31 multi-environment trials

Source	*df*	Sums of squares	Mean squares	*F* ratio	*P* value	% Signal[a]
Total	4,277	3,437,491,913	803,716			
Treatments	712	3,315,349,912	4,656,390	223.23	<0.001	
Genotypes	22	166,311,263	7,559,603	362.42	<0.001	
Environments	30	2,985,053,173	99,501,772	201.39	<0.001	
Block	135	66,699,327	494,069	23.69	<0.001	
Interactions	660	163,985,475	248,463	11.91	<0.001	91.6[b]
IPCA1	51	79,552,248	1,559,848	74.78	<0.001	53.0[c]
IPCA2	49	28,788,781	587,526	28.17	<0.001	19.2[c]
Residuals	560	55,644,446	99,365	4.76	<0.001	
Error	2,658	55,442,674	20,859			

[a] Based on following calculations presented in Gauch and Zobel (1997, #2964}

[b] Interaction signal % = signal SS/Interaction SS × 100, signal SS = interaction SS − noise SS, noise SS = error MS (20,859) × interaction *df* (660)

[c] IPCA 1 or 2 SS/signal SS × 100

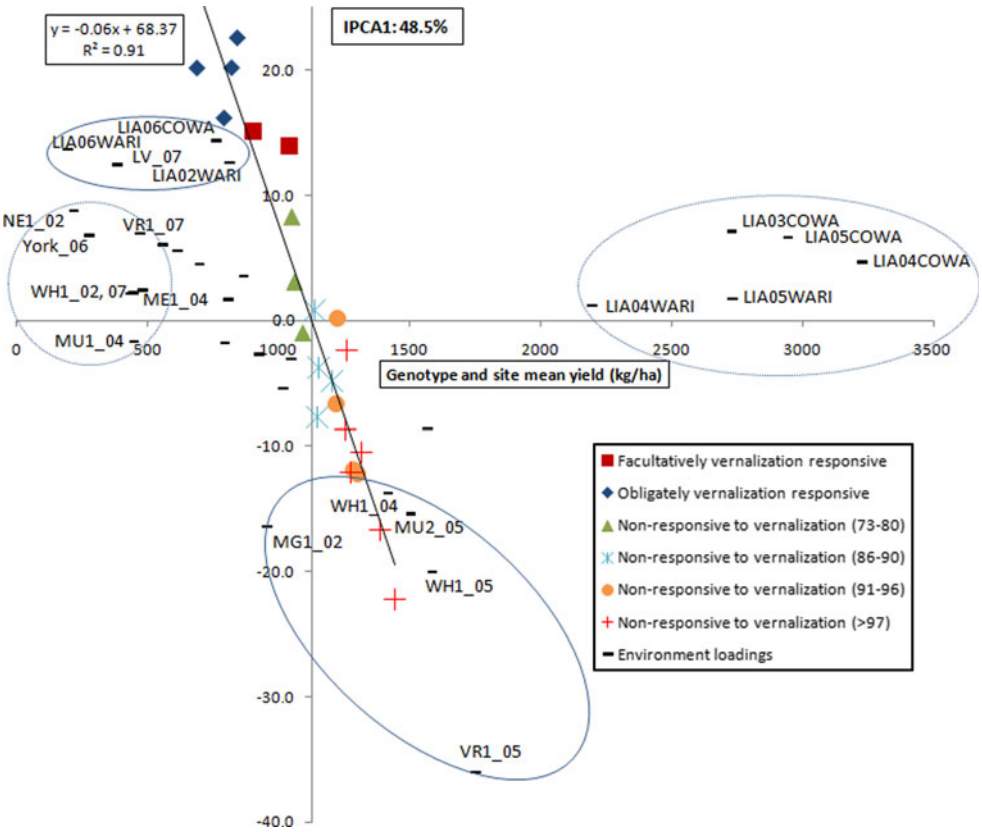

Fig. 3 AMMI analysis of seed yield in Australian historical narrow-leafed lupin trials. Interaction principal component 1 (IPCA1) accounted for 48.5% of interaction sums of squares and is plotted against the corresponding genotype and environment main effects. The *y* axis (IPCA1) crosses the *x* axis at the grand mean (1,126 kg/ha). Environment factor loadings are *circled* to identify named high and low yielding sites contributing strongly (*thick dash*) or weakly (*thin dash*) to G × E interaction modelled by IPCA1. Genotypes are categorized by vernalization response and release date. The regression between IPCA1 and genotype mean yield is highly significant ($P < 0.001$)

Table 3 G × E yield matrix of genotypes grouped by vernalization response and release date, and sites classified by AMMI mean yields and interaction responses (IPCA1 scores)

AMMI site classification	Vernalization responsive		Vernalization unresponsive				LSD (within subsets)
	Obligate	Facultative	1973–1980	1986–1990	1991–1996	>1997	
High yielding, low IPCA1 interaction	2,472	2,852	2,591	2,742	2,909	2,950	44
Med yielding, low IPCA1 interaction	502	650	840	884	974	1,038	44
Low yielding, low IPCA1 interaction	164	278	409	466	503	547	44
Med-high yielding, high −ve IPCA1 interaction	779	1,044	1,323	1,562	1,723	1,897	44
Low yielding, high +ve IPCA1 interaction	492	543	548	524	573	554	44
LSD (between site subsets)	83	83	83	83	83	83	
Mean yield (kg/ha)	785	972	1,061	1,161	1,258	1,323	17
Mean IPCA1 score	19.8	14.6	3.4	−3.9	−7.6	−12.1	8.5

Vernalization response classification based on the capacity to flower with and without vernalization under very weakly vernalization-inductive temperatures (14.4°C) (Jens Berger, pers. comm.)

slope coefficients generated by these 2 regression analyses were very strongly correlated to IPCA1 and 2 scores ($r = -0.99$ and -0.94, respectively), suggesting that AMMI had captured 2 distinct Finlay–Wilkinson type responses, to medium-high yielding western, and high-yielding eastern environments, respectively. Moreover, in both instances Finlay and Wilkinson (1963) analysis accounted for considerable variance (86.7 and 96.6%, respectively).

Western G × E interaction

The 'Western' Finlay–Wilkinson analysis, limited to the nine highly interactive IPCA1 sites captured almost 54% of

the interaction sums of squares, reflecting large genotypic differences in linear responses to site mean yield (Fig. 4a). Genotype responses to increasing site yield were strongly divergent (Fig. 4a), confirming the trends observed across AMMI site categories (Table 3). In low-yielding environments, genotypic differences were relatively small, but grew increasingly large as site mean yield increased, climaxing in the northern WA grainbelt. Crossover interaction was rare and of little consequence. For example, while the fitted curves for Danja, Tallerack and Gungurru cross over at sites yielding ~700 kg/ha, there was no significant yield advantage for Danja over any of the VU cultivars at highly interactive sites below this yield threshold. Therefore, Finlay–Wilkinson analysis of the interactive IPCA1 site subset suggests that G × E interaction among lupin cultivars largely represents differences in the capacity to respond to favourable WA environments, rather than specific adaptation to low-yielding environments. As implied by the strong correlation with IPCA1 ($r = -0.99$), the genotype yield response slopes were linearly related to mean yield ($r = 0.97$), across both VR and unresponsive genotypes. Thus, the highest mean yield and response slopes were recorded in the VU cultivars, starting with Mandelup (not significantly different from Quilinock), followed by Tallerack (alongside Myallie, Kalya, Merrit, Moonah and Belara), Gungurru (alongside Yorrel, Tanjil, Warrah, Wonga and Illyarrie), followed by Danja and Yandee, and finally Unicrop (Fig. 4a). The facultative VR cultivars Chittick and Jindalee follow, but are not significantly different from each other, or from Unicrop. Finally, the lowest mean yield and response slope were recorded in the obligate VR cultivars, starting with Uniwhite (Fig. 4a), followed by Marri (alongside Geebung and Uniharvest). Plotting yield response against cultivar release date (Fig. 5a) demonstrates that while both VR and unresponsive cultivars have become increasingly yield responsive to high-yielding WA environments over time, the rate of progress has been almost twice as high ($P = 0.01$) in the latter group.

Eastern G × E interaction

The 'Eastern' Finlay–Wilkinson analysis, constrained to the 22 weakly interacting IPCA1 sites, captured the IPCA2 trends very effectively ($r = -0.94$), in a readily visualizable manner (Figs. 4b, 5b). In contrast to the previous analysis, genotype response differences to high-yielding eastern environments were very limited (albeit significant at $P < 0.001$). This was confirmed by the relatively minor contribution of the interaction slope term, which only added 0.5% of explained variance to the combined main effects of genotype and yield (96.1% variance explained), representing a regression model of common genotype slopes and different intercepts. As a result, there was no

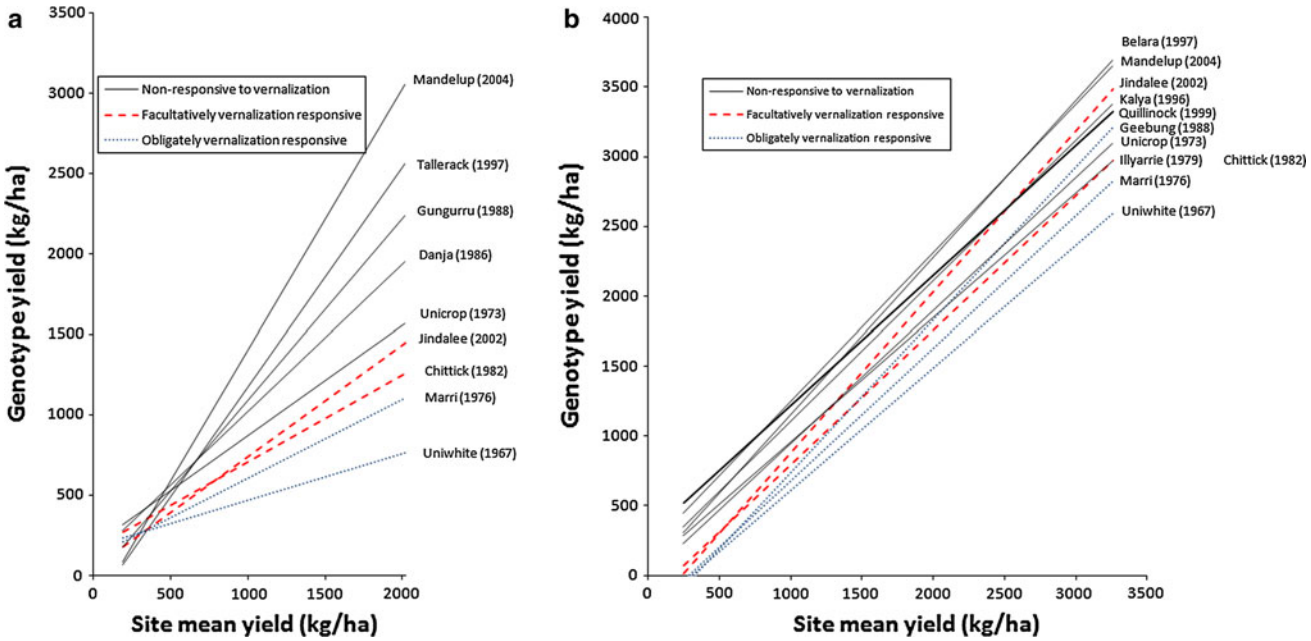

Fig. 4 Finlay and Wilkinson (1963) regression of genotype mean yield against site mean yield performed separately on subsets of trial sites identified by AMMI analysis as contributing: **a** strongly ($n = 9$) or **b** weakly ($n = 22$) to G × E interaction modelled by IPCA1, capturing responses to medium-high and high yielding western and eastern environments, respectively. *Fitted linear curves* are presented for named genotypes (alongside release date) representing the maximum yield response range within each vernalization response category, selected on the basis of significant slope differences. The Quilinock linear curve is *bolded* in **b** to emphasize the combination of high intercept and low response slope

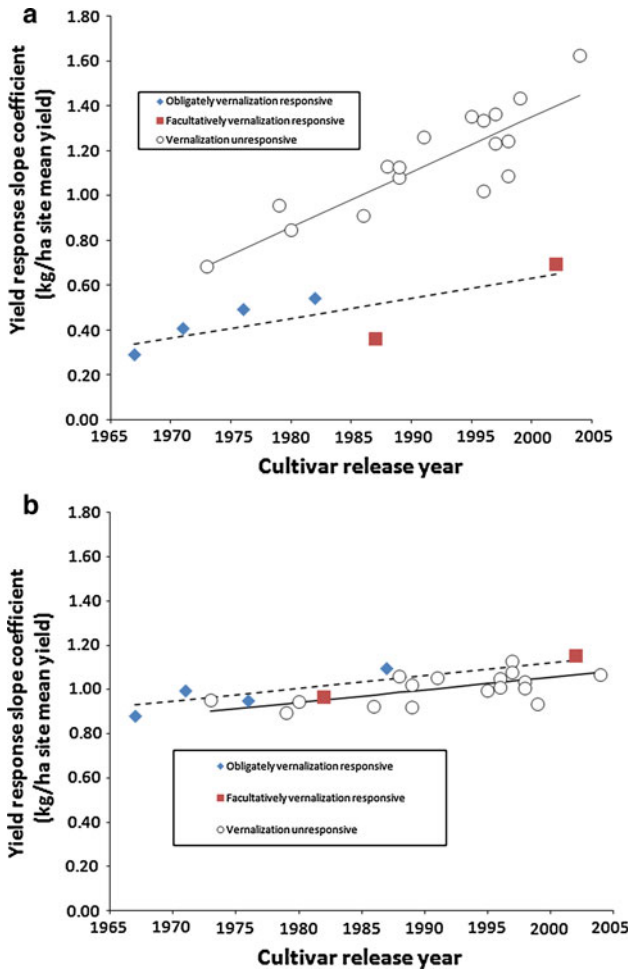

Fig. 5 Changing cultivar responses over time to Western (**a**) and Eastern (**b**) environments, as estimated by Finlay–Wilkinson yield coefficients, respectively, calculated from subsets of trial sites contributing strongly ($n = 9$) or weakly ($n = 22$) to G × E interaction as modelled by IPCA1. The regression model in **a** accounts for 90.2% of variance, with intercepts and slopes for vernalization responsive (*dashed line*) and unresponsive cultivars (*unbroken line*) both significantly different. The regression model in **b** accounts for 46.7% of variance, with common slopes and different intercepts for vernalization responsive and unresponsive cultivars ($P = 0.037$)

G × E interaction in more than half of the cultivars ($n = 12$; from Kalya to Marri in Fig. 4b), characterized by yield response slopes not significantly different ($P < 0.05$) from 1, the definition of the mean genotype response. This is demonstrated by a much reduced divergence among genotype versus site mean yield regressions (Fig. 4b), and the correspondingly limited range of response coefficients (Fig. 5b).

As expected from AMMI analysis, which captures independent patterns in IPCA1 and 2, there was no correlation between yield response slopes between genotypes tested in strongly and weakly interactive IPCA1 environments ($r^2 = 0.06$). This was reflected in some very different genotype yield response rankings, disrupting the simple relationships between yield and yield response, and between vernalization response categories observed in strongly interactive IPCA1 environments (Fig. 3). Thus, in the 'Eastern' Finlay–Wilkinson analysis the VR genotypes Jindalee and Geebung had the first and third highest yield response slopes, respectively, crossing over in high-yielding environments (~2,500 kg/ha) in both cases (Fig. 4b). Jindalee ranked consistently highly in the top 10 yielding varieties in the highest yielding NSW trial sites ($n = 4$, >2,200 kg/ha), significantly outyielding all other varieties in 2 of these trials. At site mean yields <1,100 kg/ha ($n = 16$) the performance of Jindalee and Geebung declined dramatically, and was significantly surpassed by the majority of the VU cultivars in 13 and 16 trial sites, respectively. Conversely, some cultivar behaviour was consistent between strongly and weakly interactive IPCA1 sites (i.e. 'Western' and 'Eastern' Finlay–Wilkinson analysis, respectively). Mandelup was the highest yielding cultivar in both analyses, and remained significantly more responsive than average in the 'Eastern' analysis. Similarly Belara was consistently high yielding and responsive in both strongly and weakly interactive IPCA1 sites, while the opposite was the case for the obligately VR cultivars, Uniwhite and Marri (Fig. 4a, b).

The relationship between cultivar yield response to eastern environments and release date (Fig. 5b) was much weaker than its western counterpart (Fig. 5a; 46.7 and 90.2% variance explained, respectively), and the rate of progress lower. While yield response in both VR and VU cultivar groups increased at the same low rate over time, the former tend to be more responsive than the latter ($P = 0.037$).

The main effect of E: differences between trial sites

To put 'Eastern' and 'Western' interaction behaviour into context, it is important to understand environmental differences, especially given the almost 20-fold differences in site mean yield, from 0.17 t/ha in South Carrabin, WA, in 2000 to 3.24 t/ha in Cowra, NSW, in 2005. Trial site climate varied along long-term regional trends identified in Fig. 1, but also showed considerable rainfall variation across Australia, captured by PC 3 (Fig. 6). PC1 highlighted latitudinal and longitudinal temperature trends, strongly associated with flowering date, accounting for 46.7% of variance (Fig. 6). The south eastern trial sites (VIC, NSW) were significantly cooler, with lower means and minima, and a higher incidence of frost and vernalization inductive days, and therefore later flowering than those in WA (Table 4). Within WA these latitudinal trends were maintained, as temperatures increased from south to north, albeit southern interior sites being colder than southern coastal sites.

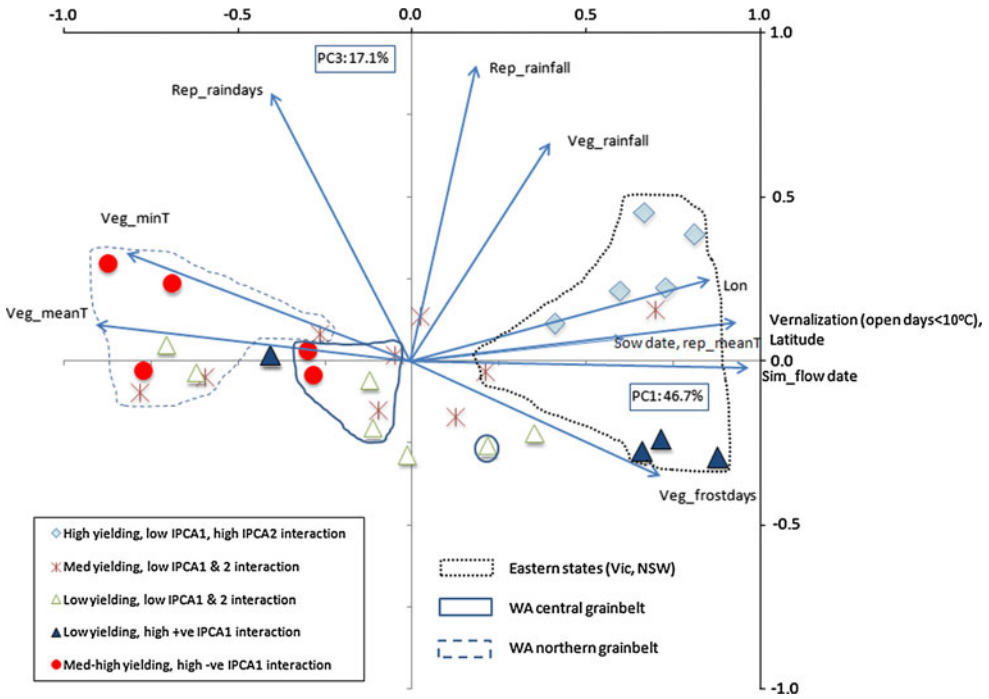

Fig. 6 Principal components analysis of trial site climate. *Markers* represent individual site years; classified by mean yield and IPCA1 scores produced by AMMI analysis. *Vectors* represent variable factor loading coordinates for PC1 and 3, abbreviated as follows: *rep* and *veg* reproductive and vegetative phases, *frostdays* number of days with frost, *Lon* longitude, *MaxT MeanT* and *MinT* maximum, mean and minimum temperature, *raindays* number of rainy days, *Sowdate* date of sowing

Identifying trial sites classified by AMMI analysis of seed yield facilitates a climate-based interpretation of interaction behaviour. Among the 22 weakly IPCA1 interactive sites there was a linear trend of rising PC3 scores with increased yield, reflecting increasing vegetative and reproductive phase rainfall (Table 4). Low-yielding weakly IPCA1 interactive sites were limited to WA, and subject to terminal drought, receiving only 161 mm seasonal rainfall, with 47 mm in the reproductive phase. High-yielding, strongly IPCA2 interactive sites that drive the 'Eastern' Finlay–Wilkinson response were exclusively found in NSW, and confined to the upper-right quadrant of Fig. 6, combining high rainfall with warm reproductive phases, but cool vegetative phases with strong vernalization stimulus (Table 4). Low-yielding, positive IPCA1 sites were also predominantly limited to NSW, and had very similar seasonal temperature profiles (excepting a higher vegetative frost incidence), but received less than half of the seasonal rainfall, with particularly large differences in volume and frequency during the reproductive phase (Table 4). Accordingly, these sites are confined to the lower-right quadrant of Fig. 6. In terms of reproductive phase climate, the positive IPCA1 sites were indistinguishable from their low-yielding, non-interactive counterparts in WA, and can be defined as terminally drought-stressed sites with cool, frosty vegetative phases (Table 4). Medium-high yielding, negative IPCA1 sites that drive the 'Western' Finlay–Wilkinson response were northern and northern-central WA grainbelt locations, largely confined to the upper-left quadrant of Fig. 6. These environments were characterized by the warmest vegetative phases with the lowest vernalization stimulus, cool reproductive phases and intermediate seasonal rainfall, with the highest rainfall frequency during the reproductive phase (Table 4).

Site mean yield was very strongly correlated to biomass production (Fig. 7a). The single outlying site in Fig. 7a has low harvest index as a result of main stem pod abortion due to high frost incidence in the reproductive phase. When this outlier is excluded from the analysis the variance accounted for increases considerably ($r^2 = 0.94$). Seed yield and biomass were both positively correlated to the date of physiological maturity (Fig. 7b).

The interactive role of phenology

Given the significance of the vernalization response in cultivar adaptation and large temperature differences between sites classified by AMMI mean yields and interaction responses, it is important to understand the role of phenology across the lupin production area. Flowering time differences were minimized in high-yielding high IPCA2 sites that drive the 'Eastern' response and in low-yielding, highly positive IPCA1 sites, both characterized by cool vegetative phases with strong vernalization stimulus

Table 4 Seasonal climate data across trial sites classified by region and by AMMI mean yields/interaction responses (IPCA1 scores)

Region/AMMI class	Vegetative phase					Reproductive phase			
	Vernalization inductive days	Frost days	Mean temperature (°C)	Minimum temperature (°C)	Rainfall (mm)	Simulated flowering days	Mean temperature (°C)	Rainfall (mm)	Rain days
Eastern states	15 (8–20)	11 (1–29)	9.7 (8.9–10.7)	−2.4 (−4.0 to −1.0)	157 (91–281)	106 (98–113)	17.6 (16.8–18.8)	106 (29–236)	23 (8–41)
WA, southern interior	8 (2–14)	6 (0–20)	10.8 (10.1–11.7)	−1.3 (−4.8 to 0.4)	117 (85–157)	95 (88–101)	14.8 (13.5–16.4)	69 (35–103)	28 (9–40)
WA, south coastal	6 (0–10)	0	11.8 (11.4–12.5)	1.9 (1.1 to 3.6)	199 (178–225)	90 (84–95)	15.1 (13.7–15.9)	165 (61–238)	45 (37–51)
WA, eastern grainbelt	5 (0–14)	4 (1–9)	11.3 (10.6–11.8)	−1.7 (−2.6 to −0.6)	113 (81–151)	90 (88–97)	15.6 (12.3–17.2)	68 (21–88)	24 (8–37)
WA, central grainbelt	4 (0–10)	2 (0–11)	11.5 (10.9–12.0)	−0.1 (−2.2 to 1.1)	146 (91–216)	89 (82–97)	16.1 (13.6–17.8)	56 (5–96)	22 (6–35)
WA, northern grainbelt	1 (0–8)	0 (0–1)	13.9 (12.2–16.3)	1.7 (−0.8 to 5.4)	118 (70–200)	78 (71–96)	16.5 (13.3–19.2)	77 (7–230)	26 (4–47)
LSD	4	5	0.7	1.3	44	5	1.3	48	10
High yielding, low IPCA1, high IPCA2 interaction	17 (10–20)	6 (4–7)	9.8 (9.0–10.7)	−1.8 (−3.0 to −1.5)	203 (174–281)		17.8 (17.2–18.8)	156 (86–236)	30 (24–41)
Med yielding, low IPCA1 interaction	7 (0–16)	2 (0–12)	11.9 (9.5–14.8)	0.2 (−2.6 to 2.8)	140 (71–209)		16.3 (13.3–17.7)	72 (33–103)	23 (14–37)
Low yielding, low IPCA1 interaction	4 (0–14)	3 (0–9)	12.1 (10.5–15.1)	−0.3 (−2.4 to 3.6)	115 (71–177)		16.3 (12.3–17.5)	47 (5–88)	19 (6–37)
Med-high yielding, high −ve IPCA1 interaction	2 (0–6)	0	13.5 (10.9–16.3)	1.6 (−0.5 to 5.4)	128 (93–174)		14.8 (13.6–16.1)	87 (51–136)	36 (29–47)
Low yielding, high +ve IPCA1 interaction	15 (7–18)	17 (0–29)	10.1 (9.5–11.7)	−2.7 (−4.0 to 0.4)	94 (85–107)		16.5 (13.5–18.3)	44 (29–76)	17 (8–40)
LSD	6	7	2.0	2.4	52		1.8	41	13

Values represent means, data ranges are presented in parentheses

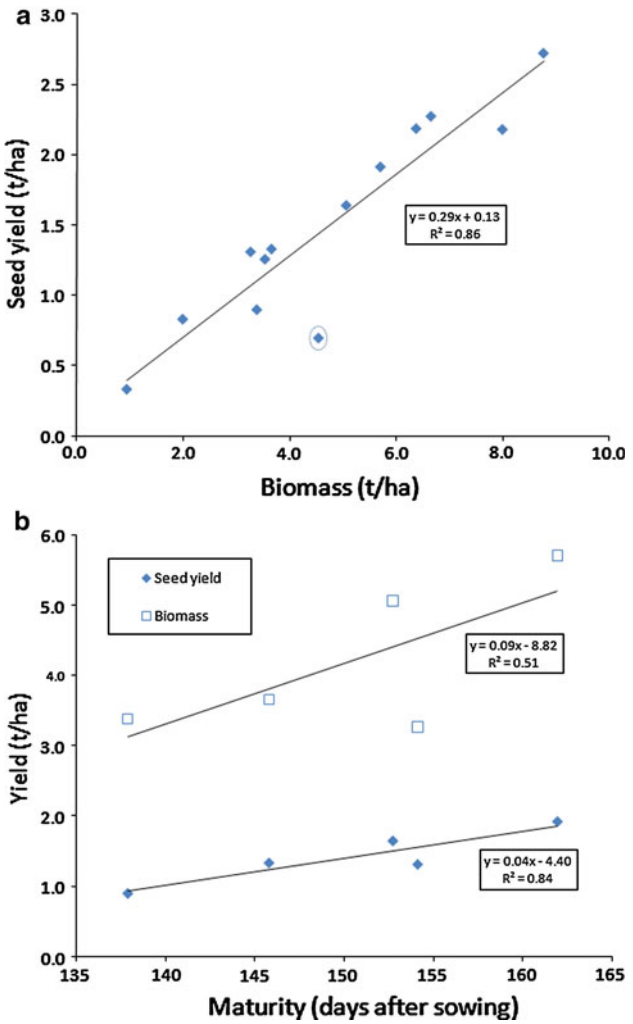

Fig. 7 Trial site productivity: **a** seed yield versus biomass; **b** seed yield and biomass versus physiological maturity. The *outlined point* in **a** represents an outlying site where a high frequency of frost in the reproductive phase caused high main stem pod abortion leading to low harvest index

(Table 4). Under these conditions all genotype categories flowered late, within a 7–9 day period (Table 5), and differences between VR and VU were relatively minor (2–9 days). Note that flowering was more delayed in the low-yielding, highly positive IPCA1 sites, probably reflecting the increased frost incidence during the vegetative phase (Table 4). Conversely, the widest phenological contrast was recorded in medium-high yielding, negative IPCA1 sites that drive the 'Western' response, which experience warm vegetative phases with little vernalization stimulus (Table 4). Under these conditions, VR types flowered at 107–114 days, compared to 76–79 days among VU categories (Table 5). While considerable flowering date differences were also recorded in low and medium yielding, low IPCA1 sites, these were not as large as those in the negative IPCA1 sites (Table 5). Finally, notwithstanding the large differences outlined above, among the VU genotypes there was very little range in flowering time within any given environment, reflected in very minor differences (ca. 3 days) between release date categories in all site types (Table 5).

Discussion

There is little diversity in domesticated narrow-leafed lupin, compared to its wild progenitors (Fig. 2a). While this is a relatively common phenomenon (see references in Spillane and Gepts 2000), and has been observed in other grain legumes such as albus lupin *(L. albus* L.) (Raman et al. 2008), lentil (*Lens culinaris* L.) (Havey and Muehlbauer 1989) and pigeon pea *(Cajanus cajan*) (Yang et al. 2006), we argue that the diversity differential is greater, and the consequences more limiting for narrow-leafed lupin as a crop. Limited genetic diversity in the narrow-leafed lupin may be attributable to a combination of founder effect and subsequent bottlenecks encountered in its short domesticated history; comprising small, relatively isolated breeding populations subjected to strong selection pressure for local optima. While the founder effect is a ubiquitous domestication bottleneck (Abbo et al. 2003; Ladizinsky 1985; Spillane and Gepts 2000; Tanksley and McCouch 1997), millennia of cultivation and dissemination into new habitats have provided considerable opportunity for the generation and/or selection of novel diversity in most crops. For example, a recent core collection microsatellite marker comparison recorded similar levels of genetic diversity in domesticated lentil and its wild relatives (Hamwieh et al. 2009), perhaps due to the fact that lentil is among the oldest of domesticated grain legumes, and the core collection effectively sampled the centres of diversity. Even if many modern cultivars in crops such beans, maize, wheat, barley, etc. have a narrow genetic base (see examples in Spillane and Gepts (2000)), invariably the *domesticated* genetic resources exist to widen the diversity when this becomes limiting. For example, while there is little genetic diversity in American (USA) common bean cultivars, landraces may be almost as diverse as the wild ancestors (Sonnante et al. 1994), facilitating opportunities for base-broadening without leaving the domesticated realm.

Narrow-leafed lupin is an exception. Having been domesticated in the last 100 years there has been insufficient time for the development of variability within the domesticated genepool. There are no exotic landraces to recover diversity from because domestication occurred exclusively in science-based breeding programmes (Gladstones 1994; Hondelmann 1984; Sengbusch and Zimmermann 1937), which were often reproductively

Table 5 G × E days to 50% flowering matrix of genotypes grouped by vernalization response and release date, and sites classified by AMMI mean yields and interaction responses (IPCA1 scores)

AMMI site classification	Vernalization responsive		Vernalization unresponsive				LSD
	Obligate	Facultative	1973–1980	1986–1990	1991–1996	>1997	
High yielding, low IPCA1, high IPCA2 interaction	114	113	110	108	108	107	1
Med yielding, low IPCA1 interaction	106	101	88	87	87	85	1
Low yielding, low IPCA1 interaction	112	108	90	90	89	87	1
Med-high yielding, high −ve IPCA1 interaction	114	107	79	78	77	76	1
Low yielding, high +ve IPCA1 interaction	121	118	116	115	114	112	1

isolated. For example, alkaloid-free 'sweet' lupins, the basis of the modern domesticated crop, were developed independently in Germany and Russia in 1920s and 1930s without germplasm exchange because of an unwillingness to share intellectual property (Gladstones 1970). Indeed, the need to select against high seed alkaloid concentrations, *in addition* to the common domestication traits such as pod indehiscence, permeable seeds, etc., adds an additional founder bottleneck to the domestication of narrow-leafed lupin. Many 100,000s of single plants were screened in the search for 'sweet' lupin, and the search was abandoned as soon as the first alkaloid-free individual was discovered (Sengbusch and Zimmermann 1937). Interestingly, the early lupin breeders recognized this as a mistake which may have limited further development of the crop, and were determined not to make the same error again in the search for pod indehiscence (Sengbusch and Zimmermann 1937). The development of Australian lupin breeding coincided with the decline in European production (Gladstones 1970), and therefore arguably subject to further reproductive isolation. An analysis of pedigree relationships within Australian breeding (Cowling and Gladstones 2000) confirms this to be correct, and explains the high degree of similarity between European and Australian breeding pools (Fig. 2a). The Australian breeding pool is particularly narrow—largely based on two European genotypes, Borre and New Zealand Blue (originally from Europe), and subsequently only occasionally augmented with externally sourced germplasm; using breeding material from USA-based programmes in the 1960s, and wild Mediterranean germplasm in the 1970s and 1980s (Cowling and Gladstones 2000). The only other source of variation used in Australian breeding were natural mutants occurring within previously used parental stocks (Cowling and Gladstones 2000). Therefore, because Australian breeding has largely been based on crosses between closely related parents in the elite cultivar pool, the effective population size is likely to be small, leading to a high risk of gene erosion as a result of genetic drift.

In spite of the above, genetic gain in Australian narrow-leafed lupin breeding has been impressive, returning an 81% yield improvement in 5 breeding cycles over 31 years (i.e. ~16% per cycle) (Stefanova and Buirchell 2010) (compared with 3.2% per breeding cycle for soybean (Mikel et al. 2010)). However, this genetic gain has come from a very low base; elite cultivars such as Mandelup average below 1.5 t/ha (Stefanova and Buirchell 2010), less than the current break-even threshold for growers. Moreover, 16% per breeding cycle may be an overestimation because the data for calculating genetic gain presented by Stefanova and Buirchell (2010) was collected only in WA, the 'local' environment that breeders have optimized the crop for, as discussed below. While the Australian production environment covers a broad range of climates, comprising different seasonal temperatures, rainfall amount and distribution, narrow-leafed lupin breeders have selected very strongly for local optima. The evidence for this is twofold: (a) strong yield responses to warm Mediterranean climates in the northern WA grainbelt dominate the G × E interaction and have been highly directional over time; (b) yield responses to higher yielding, longer season eastern environments are much more limited, play a much smaller role in G × E interaction, and have been far less directional over time. This raises some interesting questions. Is the selection for local optima a natural consequence of late domestication, and does it matter?

We suggest that the answer to both questions is yes, as outlined below. Plant breeders typically assemble elite breeding populations through systematic screening, hybridization and selection, climbing adaptive peaks in their target environment (Wright 1931). In a resource-limited operating environment it behoves breeders to act conservatively, particularly in the early stages of domestication, given the risks associated with introgressing wild material. [Exotic crosses can introduce inferior alleles and disrupt beneficial co-adapted gene complexes in elite material (Spillane and Gepts 2000).] Even with a narrow genetic base it may be possible to make yield improvements by ongoing hybridization within the elite breeding pool, and because wide crosses with unimproved material can disrupt this advance, representing a decline into the valley between adaptive peaks (Wright 1931), there may be

a disincentive against base-broadening (Cooper et al. 2000). This was particularly the case in narrow-leafed lupin because it is such a recently domesticated crop *and* was supported by only a single industrial WA-based breeding programme. In the absence of alternative, large-scale breeding programmes, who was there to exchange elite material with? Lupin breeders interested in base-broadening essentially only had two choices: to introgress undomesticated germplasm, or breeding material from Europe, which our analysis suggests was unlikely to widen the genetic diversity of the Australian breeding pool (Fig. 2a). Hybridization with undomesticated Mediterranean germplasm in the 1970s and 1980s (Cowling et al. 1998) increased the diversity of Australian cultivars subsequently released in the 1980s–1990s (Fig. 2b). However, many wide crosses were not incorporated into the breeding pool because of uncompetitive yield (B. Buirchell, pers. comm.), and later breeding efforts focussed largely crossing within elite material (Stefanova and Buirchell 2010). Accordingly, there has been a reduction in genetic diversity from 2000 onwards (Fig. 2b).

Selection for local optima in short-season WA environments limits lupin yield potential in longer season environments. While the genetic basis of crop adaptation is often poorly understood (Spillane and Gepts 2000), in narrow-leafed lupin G × E interaction for yield is well explained by phenology, and its interaction with seasonal climate—particularly vegetative phase temperatures and reproductive phase rainfall. This is highlighted by the contrasting interaction behaviour in VR and VU cultivars, which is minimized when vegetative phase temperatures fully satisfy the vernalization requirement (typical of eastern Australia), and maximized when they do not (typical of WA). These trends are evident in both 'Western' and 'Eastern' analyses of strongly and weakly interacting IPCA1 sites. The northern grainbelt environments which drive the strong 'Western' response have the warmest, least vernalization inductive vegetative phases and relatively mild reproductive phases with frequent rainfall events (Table 4). In breeding for this local optimum, Australian breeders have eliminated the vernalization response, and selected for early, highly temperature responsive phenology (Berger et al. 2012). As a result, highly yield-responsive cultivars such as Mandelup flower exceedingly early, and are able to exploit the extended reproductive phase, while VR cultivars fail because of extremely late phenology. Interestingly the Australian selection for earliness continues a long-standing trend in lupin domestication. The first attempts to introduce lupin to Central Europe in the eighteenth century failed because of the inability of the crop to ripen in a timely manner (Gladstones 1970). Rapid growth and early maturity remained as key objectives in early European breeding programmes of the twentieth century, attested by cultivar names such as Pflugs Allerfrüheste (plough's earliest) (Gladstones 1970). By contrast, flowering time differences between VU and VR cultivars are minimized in NSW, which is typically fully vernalization inductive, and therefore reflect differences in ambient temperature and photoperiod sensitivity, rather than differences in vernalization response (Berger et al. 2012). Therefore, VR cultivars flower only moderately later than VU types in NSW, minimizing yield differences under terminal drought, but allowing them to better capitalize on the high rainfall, longer season environments which drive the 'Eastern' response.

This contrasting phenology affects growth rates, biomass production, harvest index (Berger et al. 2012), and ultimately yield, and has important implications for the adaptation of narrow-leafed lupin. The current highly temperature responsive, VU elite cultivars are ideally suited to warm, short-season environments, but cannot delay their maturity to capitalize on long-season environments, as demonstrated by the low Finlay–Wilkinson slope coefficients recorded in the 'Eastern' analysis. Within the VU breeding pool there is insufficient ambient temperature response variability to select longer season cultivars (Berger et al. 2012); a clear indicator of limited diversity in flowering response genes. By contrast, the VR cultivars are able to capitalize on long-season environments as a result of their moderate ambient temperature response *only* in the presence of vernalization (Berger et al. 2012). These phenological barriers have isolated the two breeding pools to the disadvantage of the latter, because all Australian narrow-leafed lupin breeding is carried out in WA, where the vernalization response is clearly maladaptive. Phenological barriers have limited gene flow between South Asian and Mediterranean lentil (Erskine et al. 1998) and in soybean across latitudes (Hymowitz and Kaizuma 1981; James and Lawn 2010; Lawn and James 2010). For narrow-leafed lupin the solution to this problem is to identify a wider ambient temperature response range in a VU background, because this will facilitate phenology matching to short- and long-season environments without the need for vernalization-inductive vegetative phase temperatures. Given that lupin is biomass limited and needs to grow for as long as the season will allow, to maximize yield (Fig. 7), this is an important priority for the crop.

G × E analysis indicates that terminal drought is a consistent yield constraint for lupin throughout Australia and that adaptation is largely phenological, implying that there has been little selection for intrinsic drought tolerance. This is consistent with studies exposing Australian lupin cultivars to water deficit, demonstrating that the principal adaptive strategy is drought avoidance through early phenology (Palta et al. 2003, 2007). The narrow-leafed lupin appears to be a profligate water user when

water is freely available, and is very sensitive to drought stress, reducing stomatal conductance even before changes in leaf water potential can be measured (Turner and Henson 1989). Given that all previous work on water relations in narrow-leafed lupin has been based on a very limited number of elite cultivars, studying the variability in genetic resource collections is an important priority. This may pay dividends because lupins have been collected from a range of contrasting drought stress environments (Berger et al. 2008b), which in the case of its close relative, the yellow lupin (*L. luteus* L.), have selected for ecotypes with differing adaptive traits, (Berger et al. 2008a).

We have argued that the narrow genetic base of the narrow-leafed lupin is limiting the adaptive potential of the crop, and advocate the search for a wider range of temperature-responsive phenology, and water-use patterns in response to terminal drought, to facilitate specific adaptation to contrasting environments. The value of specific adaptation in maximizing yield in contrasting temperate and Mediterranean climates has already been established in *L. albus* and to a lesser extent in *L. angustifolius* (Annicchiarico and Carroni 2009). Here we extend this argument to short- and long-season environments within a Mediterranean climate. However, in addition to introducing specific adaptation, it is essential to initiate breeding strategies that will widen the genetic base of the breeding pool in an ongoing manner. Even if the aforementioned adaptive strategies only reside in wild germplasm, and their introgression concomitantly widens the breeding pool, their impact on genetic diversity will only be temporary—akin to the wide crosses of the 1970s and 1980s (Cowling and Gladstones 2000). Base-broadening approaches which seek to capture valuable, but unidentified alleles hidden in otherwise poorly performing exotic germplasm (McCouch et al. 2007; Tanksley and McCouch 1997) may also be useful in the narrow-leafed lupin. Cowling et al. (2009) have described a model for incorporating novel alleles from wild material into elite breeding pools using the narrow-leafed lupin as an example. This methodology is currently being applied in the Australian narrow-leafed lupin breeding programme to develop advanced backcross populations from diverse undomesticated and elite parents, to generate diversity in an adapted background to improve breeding outcomes and the investigation of adaptation in the crop.

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