Phosphorus-use efficiency, growth and yield of spelt wheat (*Triticum aestivum* ssp. *spelta)* compared with standard wheat (*T. aestivum* ssp. *vulgare*) in south-eastern Australia

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Abstract

Experiments were conducted in the glasshouse and the field to assess the phosphorus-use efficiency, yield, and yield components of several spelt wheat genotypes in comparison with standard bread wheats. Spelt genotypes had much lower grain yield than standard bread wheats, in both a well-watered glasshouse and three field situations. The reduction in yield was often as great as 60% and was largest in late-flowering spelt genotypes. Spelt genotypes responded to increasing amounts of applied phosphorus (P) fertiliser, adequately acquired P from soil, and some had higher total amounts in their tissues; however, these P reserves were not as efficiently converted into grain yield as standard bread wheat cultivars, primarily due to the growth of tall, unproductive tillers, and lower kernel number and kernel size. There was no evidence of spelt yielding better than common wheat under conditions of P-deficiency. There is great potential to breed improved spelt genotypes through relatively simple modification of yield components and phenology, but whether this can be achieved while maintaining the grain quality attributes valued highly by the organic industry remains to be seen. Breeding for improved spelt should target reduced height and tiller number, early flowering, and larger kernels.

Keywords: phosphorus-use efficiency, spelt, grain yield, tillering, wheat.

Introduction

Globally, there is increasing interest in using organic farming systems and maximizing grain production in low-input scenarios. Organic residues are being employed as fertilisers (Davari et al., 2012) and plant breeding in being used to develop new cultivars that are specifically adapted to organic and/or low-input systems (Wolfe et al., 2008, Vanaja et al., 2013). Old or 'neglected' crops are receiving more attention from growers and processors seeking a niche product, while consumers are seeking potential nutritional, sensory, and health benefits by eating food from more 'traditional' sources.

Consumer interest in spelt (*Triticum aestivum* ssp. *spelta*) grain is believed to be due to its rich flavour, described as sweet and nutty, agreeable texture in baked products, and good nutritional profile. The grain may have higher contents of protein and fibre (Abdel-Aal et al., 1995, Moudry and Dvoracek, 1999, Escarnot et al., 2012), minerals and P (phosphorus) (Ruibal-Mendieta et al., 2005), and β-carotene and retinol equivalent (Abdel-Aal et al., 2007), than standard bread wheat (*Triticum aestivum* spp. *vulgare*). Spelt is used to make a wide range of consumer products (Neeson, 2011) but mainly leavened bread.

The vast majority of Australian spelt production is organic because the much higher price paid for the organic product offsets the reduced yield (Neeson et al., 2008). The reduced yield is as a result of three factors: 1) poorly-adapted genotypes (i.e. those not specifically bred for local conditions and/or low-input agriculture); 2) the inherently lower-yielding capacity of the organic, low-input system; and 3) spelt produces hulled grain which requires additional processing before flour milling resulting in some losses due to chipping and splitting (Neeson et al., 2008).

Commercially-available spelt in Australia is presently restricted to a few poorly-adapted genotypes. Evidence for poor adaptation is limited but it suggests that the grain yield of current genotypes,

including the predominant commercial genotype 'Kamarah' (a manual mixture of two spelt genotypes that originated from northern Spain), is low relative to standard bread wheats. No direct comparisons between spelt and common bread wheat in organic versus conventional systems have been published. It is known that wheat production under an organic system can yield from 14 to 44% less than under a high-input system (Mäder et al., 2007, Seufert et al., 2012). In our experience the current commercial spelt genotype in Australia, 'Kamarah', yielded 45% less than a common wheat comparator (unpublished data); however, spelt genotypes with only a 28% reduction were also observed (unpublished data).

A significant cost for all cereal production in Australia is P fertiliser, because most grain production is carried out on soils that are highly weathered and inherently low in available P, and the cost of P fertiliser is increasing. Therefore, more efficient utilisation of soil or applied P for grain production is desirable. Several publications have addressed this issue for standard wheat (Horst et al., 1993, Manske et al., 2000, Osborne and Rengel, 2002), but the P efficiency of spelt has not been reported. Current spelt production largely services the organic grain industry. A low P requirement (or a high P-use efficiency) in spelt would be of particular interest to this industry, because organically-managed broad-acre soils are often marginal for available P (Evans, 2005, Cornish, 2009), and such soils are difficult to improve in the short-term using the allowed inputs of rock phosphate or organic compost (Conyers and Moody, 2009, Evans and Condon, 2009). In marginal areas for cereal production, and under low input conditions, the performance of spelt has been claimed to be better than standard bread wheat (Ruegger and Winzeler, 1993), possibly due to better utilisation of the scarce nutrients in low input systems (Moudry and Dvoracek, 1999, Richardson et al., 2009).

Various definitions have been used to describe P efficiency. For example, Osborne and Rengel (2002) described three measures that focus on biological yield; one of these, shoot dry weight relative to shoot P uptake, also known as biological P efficiency, has merit from a climate-warming perspective describing P-use efficiency in relation to C capture via crop photosynthesis. Alternatively, Ortiz-Monasterio (2001) described P-use efficiency as grain yield per unit of applied P, which has merit from an economic perspective. In this study, we compared genotypes for: (i) efficiency of P uptake being the amount of P at flowering obtained by plants from a defined amount of applied P (%),; (ii) shoot P efficiency (g mg^{-1} P) being the weight of shoot tissue dry mass produced at flowering per weight of P applied, and; (iii) grain yield P efficiency (g g^{-1} P) being the weight of grain produced per weight of P applied.

In this study, we compared growth and yield attributes of spelt (using genotypes with a range in maturity) with standard bread wheats, under different regimes of P availability in a glasshouse study and in the field. Our objectives were to quantify the P-use efficiency of spelt relative to standard bread wheat, identify superior yielding lines of spelt, and make recommendations regarding the need to adjust P fertiliser rates for spelt as compared to standard bread wheat.

Materials and methods

Glasshouse study

Spelt genotypes (*Triticum aestivum* ssp. *spelta*), nominally designated SP2, SP10, SP16, SP18, SP19, SP22, SP29, SP40 and SP41 were acquired from a local gene bank: AWCC (Australian Winter Cereals Collection, Industry & Investment NSW, Tamworth, NSW). Two genotypes reputed to be spelt, SP76 and SP77, were sourced from single plant selections taken within a commercial spelt crop. These genotypes, and three standard bread wheat (*Triticum aestivum*) cultivars differing in maturity, namely, Waagan, Gregory, and EGA-Wedgetail (hereafter just Wedgetail), were established in pots and treated with soluble, surface-applied inorganic P fertiliser (KH_2PO_4) at levels equivalent to 6.8 (low), 13.8 (moderately low), 20.3 (moderate), or 33.8 (high) kg P ha^{-1}. The P treatments were allocated to main plots within which the genotypes were randomised. Each genotype was duplicated so that destructive sampling could be performed, firstly for dry matter and P content at flowering and, secondly, for grain yield. Duplicates were adjacent paired pots. There were 3 replicated blocks of the treatments.

Pots were large enough to hold 2 kg of growth medium, which comprised a sand and peat mix (75% sand by volume). Nutrients other than P were supplied in ample amounts and comprised (g kg^{-1}): KNO_3 0.5, urea 0.158, K_2SO_4 0.174, $CaCl_2$ 0.074, $MgSO_4.7H_2O$ 0.029, $FeSO_4.7H_2O$ 0.001, $CuSO_4.5H_2O$ 0.0011, $ZnSO_4.7H_2O$ 0.0024, H_3BO_3 0.0008, $CoSO_4.7H_2O$ 0.000_4, $Na_2MoO_4.2H_2O$ 0.0002, $MnSO_4.H_2O$ 0.01114. The nutrients were dissolved then irrigated into the growth medium.

Five seedlings were established in each pot and were adequately supplied with water through regular irrigation that varied in frequency from once per week to daily as plant biomass increased.

The experiment was sown on 10 May 2007. Days-to-flowering was recorded for each genotype. At flowering, all above-soil biomass was removed, tiller number per plant , was determined and then the material was dried at 80°C and weighed to obtain dry matter per pot (g pot^{-1}). The dried material was digested in Kjeldahl solution, the digest assayed for its P content using a Flame Ionisation Analyser (LACHAT) and these data were then used to estimate tissue P content (mg P pot^{-1}. 'P biological efficiency in dry matter at flowering' was derived from 'dry matter at flowering' divided by 'total P content of shoots at flowering'. 'Efficiency of P uptake at flowering' was calculated from 'total P content of shots at flowering' divided by 'P applied'.

At maturity, grain was recovered using a small grain thresher, then de-hulled manually (if required), and weighed (grain yield, g pot^{-1}). Yield components (kernel number, and kernel weight) were also measured. Grain P content (%) was estimated using the same method as used for dry matter. The remainder of the shoot material at maturity was also dried and weighed, and added to seed weight to give total mature shoot weight (g pot^{-1}). Grain harvest index was calculated as 'grain yield' divided by 'total mature shoot weight'.

Field studies

Wagga Wagga 2008

Three of the higher-yielding spelt genotypes used in the glasshouse study (SP18, SP19, SP40) and the commercial spelt variety 'Kamarah' [non-registered cultivar name, also known as "Brown's Mixture" or "Booth's Mixture"]) and one standard bread wheat cultivar (Wedgetail) were established with four rates of P (0, 4.4, 8.9. 17.8 kg P ha^{-1}) applied as superphosphate, drilled at sowing. The soil was an Oxic Paleustalf (USDA, 1983) or Red Kandosol (Isbell, 1996), with an available P content (Olsen P) (Olsen et al., 1954) of 11 mg P kg^{-1}, located at Wagga Wagga (S 35° 01', E 147° 20'). Sowing rate was 45 kg ha^{-1}. The design consisted of main plots of P rate, split for genotype, with the P treatments randomised in 3 replicate blocks and genotypes randomised within P treatments. Plots were 10 m in length and comprised 8 rows spaced at 0.18 m. Prior to sowing, the soil was cultivated and treated with urea (127 kg N ha^{-1}) and gypsum (200 kg ha^{-1}), which were applied and incorporated with soil on 27 May 2008. Sowing occurred on 5 June 2008. Total rainfall in 2008, 413 mm, was below the long-term yearly average of 525 mm, and growing season rainfall (May to October), 164 mm, was well-below the cumulative long-term average for those months (291 mm).

Days-to-flowering, crop dry matter and P content at flowering, tiller number per plant (fertile and sterile), grain yield, yield components, and grain P content were recorded. Crop dry matter at flowering was estimated from five x 1m sections of row per plot, and tiller number was determined on the plants from 1m of row per plot. Grain yield was estimated from the machine-harvested plot yields. Dry matter and grain yield data were converted to a per hectare unit. For the spelt genotypes, manually dehulled grain was used to estimate grain yield. The cultivar Kamarah was not used in the glasshouse study because it is known to be a mixture of several different genotypes which would have led to deceptive plant-to-plant variation in pots (but not so in plots).

Condobolin 2008

Two of the higher-yielding spelt genotypes used in the glasshouse study (SP18, SP19), two standard bread wheats (Carinya, Ventura), and two barley cultivars (Buloke and Hindmarsh), were used. There were six rates of P (0, 4, 8, 12,16, 24 kg P ha^{-1}) applied as double superphosphate, and the applied P was drilled with the seed at sowing. Information on the barley cultivars is not reported in this manuscript. The site location (S 33° 04', E 147° 14') was on a Calcic Rhodoxeralf (USDA, 1983) or Red Chromosol (Isbell, 1996) soil with an available P content (Colwell P) (Colwell, 1963) of 22 mg P kg^{-1}. The plots were sown on 23 June 2008. Seeding rate was 100 seeds m^{-2} except for SP18, which was only 80 seeds m^{-2} owing to limited seed supply (see Results). Sowing occurred on a cultivated fallow with considerable stored moisture following 140 mm of rain during January to May. Annual rainfall for 2008 was 346 mm compared to a long-term average of 456 mm and growing season rainfall (June-October) was 124 mm, compared to the long-term average of 231 mm. Each factorial combination of genotype and phosphorus rate was randomly allocated within each of three replicated blocks. Plots were 15 m in length and comprised 8 rows at 0.18 m spacing.

Plant establishment (number m^{-2}), dry matter (kg ha^{-1}), tiller number $plant^{-1}$, and plant P content were recorded at flowering time.; Dry matter (kg ha^{-1}), crop height (cm), grain yield (t ha^{-1}), harvest index (t t^{-}

^{1}), 100 seed weight (g), seeds per ear , fertile ears (number m^{-2})], and grain P content (%) were recorded on material harvested at crop maturity. Plant establishment was estimated from four random quadrats per plot, each quadrat was 0.17 m^2. Dry matter was estimated from two quadrats per plot, each quadrat was 0.35 m^2. Grain yield was the machine-harvested plot yield. For the spelt genotypes, a subsample was manually dehulled and used to estimate plot grain yield. Grain yield components were estimated from 50 ears per plot. Plant establishment, dry matter and yield data were converted to per hectare units.

Rutherglen 2008

This field site (S 36^{o} 06', E 146^{o} 31') was certified organic so the use of water soluble P fertiliser was disallowed. Soil type was a Brown Chromosol (Isbell, 1996) with an available P (Olsen P) of 14 mg P kg^{-1}. Four genotypes of spelt (SP18, SP19, SP40, Kamarah) and one standard bread wheat (Wedgetail) were sown with 6 phosphorus treatments (Nil, PL270, PL361, PL480, Guano250 and Guano500). PL is a mixture of ground reactive phosphate rock and finely-divided elemental sulphur (30% by weight) providing 23, 31, or 41 kg P ha^{-1} for PL270, PL361 and PL480, respectively. The guano provided 33 kg P ha^{-1} or 65 kg P ha^{-1} for Guano250 and Guano500, respectively. These products were broadcast and then incorporated with soil on 4 December 2007. The trial was sown on 28 May. The design comprised randomised main plots of the P treatments split for genotypes randomised to the P treatments. The P treatments were randomised within each of 3 replicate blocks. Plot length was 15 m and comprised 6 rows spaced at 0.18 m. Dry matter at flowering was estimated from 4 x 1 m sections of row per plot, and grain yield was determined from the machine-harvested plot yields. These data were converted to per hectare units.

Statistical analysis

Data were analysed using REML (Genstat v. 10.2) to account for spatial effects. Days-to-flowering was used as a covariate in the analysis of all variables (except flowering itself). The covariate was used to increase the analysis precision for each trait by centering across differences in phenology. Differences between the REML-predicted treatment means ($P < 0.05$) were resolved by the least significant difference procedure (LSD) ($P < 0.05$). Fitted curves were calculated and drawn using SigmaPlot v8 software.

Results

While this study was underway, DNA analysis of the putative spelt genotypes was completed (data not presented), and it showed that SP76 and SP77 were not true spelt genotypes but probably unselected common bread wheat genotypes.

Glasshouse study

Genotypic differences between standard bread wheats and spelt

Mean days-to-flowering of spelt genotypes varied widely from 87 to 150 days. Early-, mid-, and late-flowering spelt groups were similar to the three bread wheat controls (Table 1). There was a group of three very late-flowering spelt genotypes that did not match a representative bread wheat cultivar.

Spelt tillered significantly more than the standard bread wheat cultivars (Table 1) except for SP40, and differences between spelt genotypes were also evident. At flowering, in Groups 2 and 3, the dry matter of spelt was greater than the three standard bread wheats (Table 1). Significant variation in dry matter within spelt genotypes was also evident, generally increasing as days-to-flowering increased. Late-flowering spelt genotypes were visually taller than the standard bread wheats.

The highest yielding genotypes (grain yield > 6 g pot^{-1}) were the standard bread wheats (Table 1); only SP40 was not statistically lower yielding than these standard wheats. With the exception of SP40, the lower yields of the spelt wheats were associated with lower mean kernel weights relative to the standard bread wheats (Table 1). Excluding data for the three 'very late flowering' spelt genotypes (SP2, SP22, SP29), higher tiller number was significantly correlated with lower grain yield (R^2 = -0.66). The three excluded spelt genotypes were high tillering but their grain yields fell below the general regression of grain yield on tiller number, suggesting that an additional factor further decreased the grain yield of these spelt wheats (see below). Higher tiller number was also correlated with reduced mean kernel weight (Figure 1).

Table 1. Average effect of genotype on growth parameters of spelt and standard bread wheat genotypes in a glasshouse experiment at Wagga Wagga. Values tabulated are means over all rates of applied phosphorus. Days-to-flowering was used as a covariate in the analysis of all variables (except days-to-flowering itself). The genotypes are shown grouped by their days-to-flowering category. Values followed by a common letter within a column are not significantly different (*P* = 0.05) using an LSD test.

Genotype	Group	Flowering category	Days-to-flowering	Tillers (number plant^{-1})	Dry matter at flowering (g pot^{-1})	Grain yield (g pot^{-1})	Kernel weight (mg seed^{-1})
Waagan	1	Early	82.6 a	6.0 a	12.0 a	6.78 f	41.9 cd
SP10	1	Early	87.8 b	9.2 bc	13.1 a	5.44 cde	34.8 b
Gregory	2	Mid	105.6 c	6.1 a	13.5 a	6.62 f	46.4 e
SP16	2	Mid	101.8 c	8.8 bc	17.1 b	4.51 bcd	35.6 b
SP18	2	Mid	102.8 c	8.9 bc	16.0 b	5.47 cde	37.6 b
SP19	2	Mid	103.8 c	8.8 bc	15.6 b	5.40 cde	42.7 d
Wedgetail	3	Late	119.8 d	6.2 a	16.9 b	6.73 f	44.6 de
SP40	3	Late	126.3 e	5.4 a	26.4 ef	5.77ef	54.3 f
SP41	3	Late	122.1 de	9.7 c	23.3 d	4.79 cde	35.0 b
SP76	3	Late	118.5 d	11.8 d	19.4 c	5.10 cde	37.7 b
SP77	3	Late	118.1 d	12.3 d	19.6 c	4.42 bc	38.0 b
SP2	4	Very late	144.8 fg	8.3 bc	24.6 de	3.66 ab	38.2 bc
SP22	4	Very late	149.4 g	8.0 b	27.8 f	2.89 a	30.4 a
SP29	4	Very late	143.4 f	8.2 b	25.0 de	3.45 ab	37.3 b
LSD (5%)			4.64	1.35	2.08	1.073	3.51

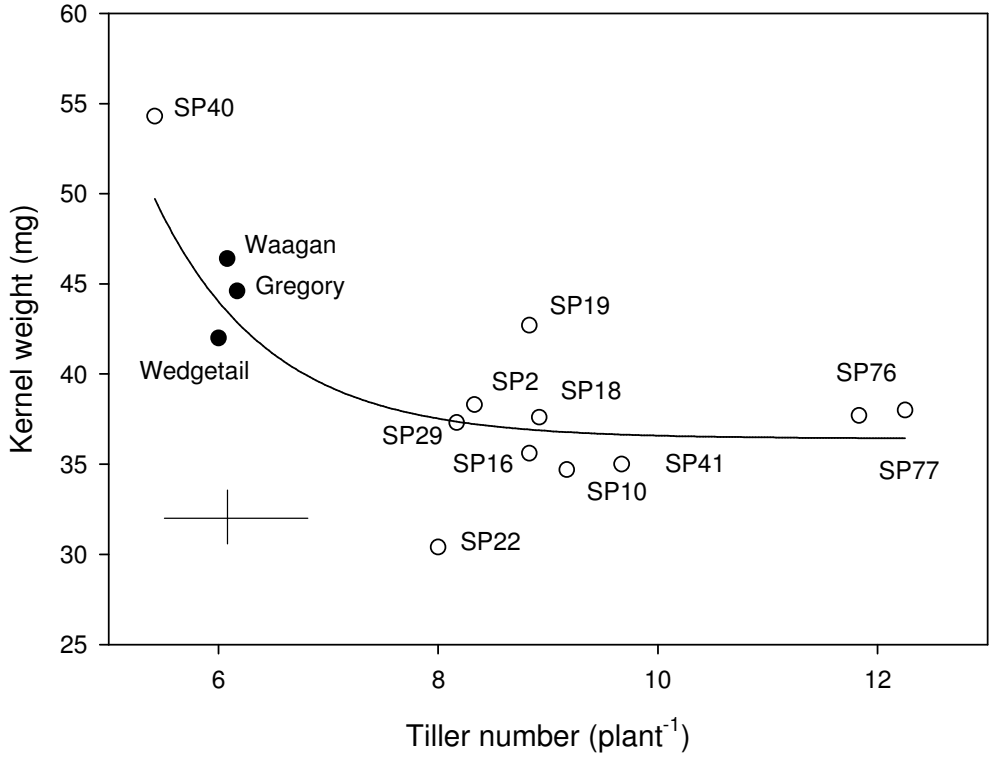

Figure 1. Relationship between mean kernel weight and tiller number . Values are means for genotypes over the applied P treatments. Filled symbols are the standard bread wheat genotypes. Bars indicate the LSD (*P* = 0.05). Kernel weight = 36.4 + 2475 x (1 - e$^{-0.964}$ x tiller number), R^2 = 0.66.

With the exception of SP40, greater dry matter in spelt genotypes was also associated with lower grain yield (Figure 2), because of the negative association of greater dry matter with the other primary grain yield factor, kernel number (Figure 3). Spelt genotypes SP2, SP22 and SP29, and SP40 were particularly reduced for kernel number. Lower kernel number was not generally compensated for by higher kernel weight except with SP40, where lower number was partly offset by higher weight, which helped support the grain yield of this genotype (Table 1).

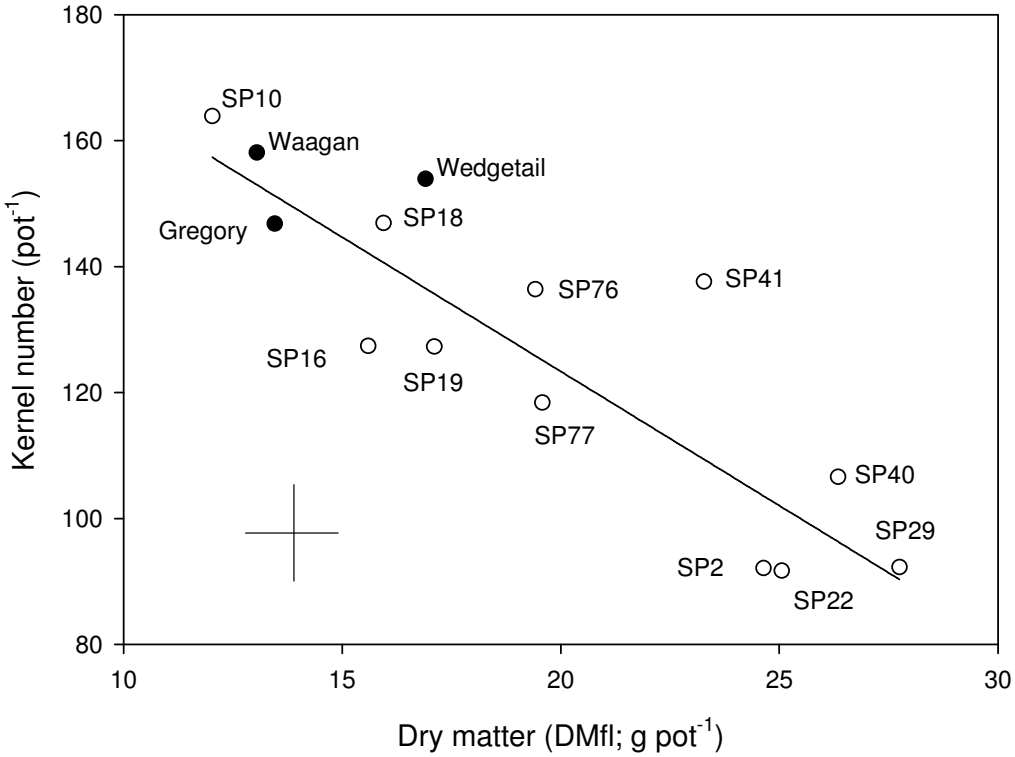

Figure 2. Relationship between kernel number per pot and the amount of plant dry matter present at flowering (DM_{fl}) for a glasshouse experiment in 2007. Values are means of genotypes over all applied P treatments. Filled symbols are the standard bread wheat cultivars. Bars indicate the LSD (*P* = 0.05). Kernel number = 214 - 4.47 x dry matter at flowering, R^2 = 0.78.

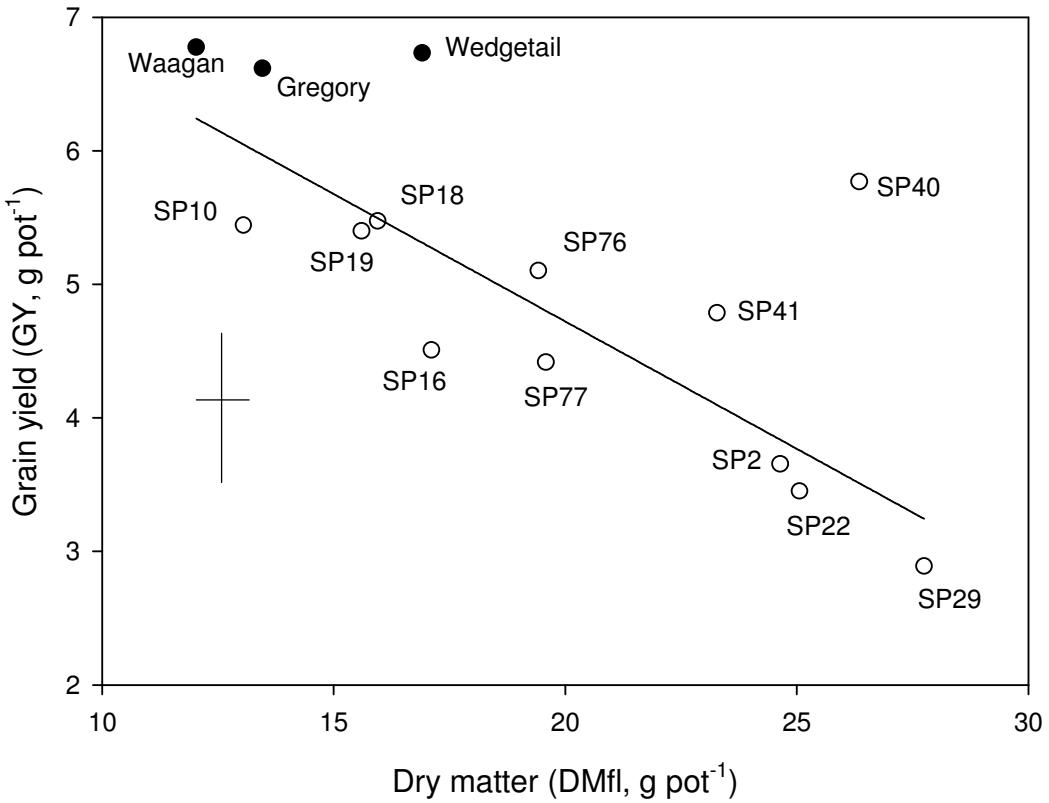

Figure 3. Relationship between grain yield (GY) and dry matter at flowering (DM_{fl}). Values are genotype means over applied P levels. Filled symbols are the standard bread wheat genotypes. Bars indicate the LSD (*P* = 0.05). Grain yield = 8.54 - 1.91 x dry matter at flowering , R^2 = 0.67.

Across all genotypes, higher grain yield was positively associated with higher grain harvest index (grain harvest index = 0.06 x grain yield – 0.09; R^2 = 0.93). The negative impact of a higher dry matter on kernel number and ultimately on grain yield (Figures 2 and 3) therefore resulted in a reduction in

grain harvest index in genotypes with higher total mature shoot dry matter (Figure 4). Particularly at the two highest P levels, the grain harvest index of the commercial bread wheats were much less affected than the spelts because the total mature shoot weight of the commercial wheats was less than that of the spelts (Figure 4). At the lowest P level, despite a similar dry matter in commercial wheats and some spelt genotypes the grain harvest index of the spelts was reduced.

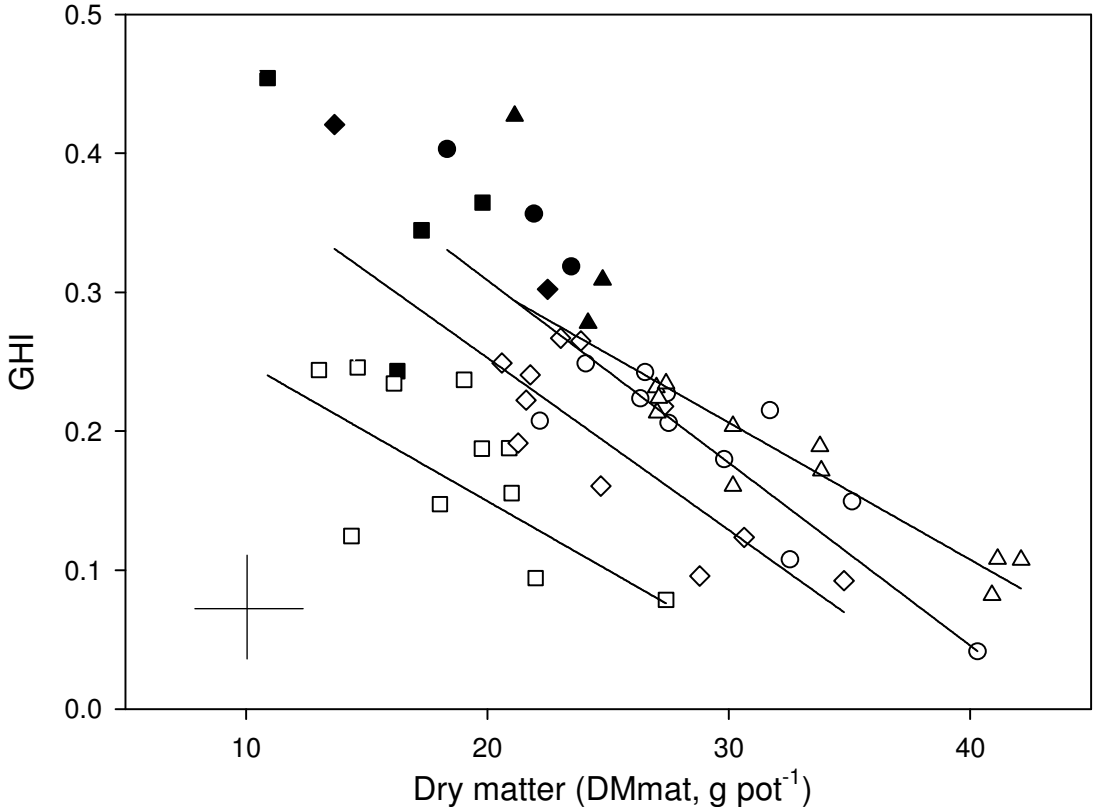

Figure 4. Relationship between total mature shoot dry matter (DM_{mat}) and grain harvest index (GHI). Values are means of genotype within each applied P treatment. Filled symbols are the standard bread wheat genotypes. Bars indicate the LSD ($P = 0.05$). Squares = 11.1 mg P per pot treatment ($R^2 = 0.48$); diamonds = 23.1 mg P per pot ($R^2 = 0.71$); circles = 34.7 mg P per pot ($R^2 = 0.92$); and triangles = 57.6 mg P per pot ($R^2 = 0.89$).

Influences of P nutrition

Plant total P content at flowering (mg P plant^{-1}) increased with higher rate of applied P: means = 6.8, 10.6, 15.0 and 26.1 ($P < 0.001$; LSD = 1.55), for the four levels of P applied, respectively. This occurred as a result of both greater dry matter at flowering: means = 13.0, 18.1, 21.7, and 23.4 ($P < 0.001$; LSD = 1.08), and increased tissue P concentration at flowering: means = 0.056%, 0.066%, 0.076% and 0.120% ($P < 0.001$; LSD = 0.0081), for the four P applied levels, respectively. However, within a P applied level there were no significant differences between genotypes for total P content at flowering or efficiency of P uptake at flowering. Consequently, because spelt genotypes generally produced more dry matter compared to the standard bread wheats, total P content of shots at flowering was usually less in spelt (Table 2) due to a simple dilution effect (total shoot dry matter at flowering vs. total P content of shoots at flowering , R^2 = -0.66, -0.67, -0.83, -0.89 for the four P applied levels, respectively). P biological efficiency in dry matter at flowering of spelt was generally greater than for standard bread wheat cultivars (Table 2).

Grain yield increased with P applied: means = 3.68, 5.23, 5.89 and 6.18 ($P < 0.001$; LSD = 0.554), for the four P applied levels, respectively; explained by a significant increase in kernel number (data not shown) as the supply of P increased. The increase in kernel number was explained by a significant increase in tiller number as the P applied level increased: means = 6.5, 7.6, 8.7, and 10.1 ($P < 0.001$; LSD = 0.70), for the four P applied levels, respectively. However, there was no significant interaction between genotype and P applied for either grain yield or tiller number. Grain harvest index was increased as P applied increased (Figure 4).

Given that plant total P content at maturity was not different between genotypes grown at the same P applied level than the higher yielding standard bread wheats were more efficient in converting P applied into grain yield.

Table 2. Effect of genotype on shoot phosphorus (P) uptake and P biological efficiency at flowering in a glasshouse experiment at Wagga Wagga. Values shown are means pooled across P application rates. Days-to-flowering was used as a covariate in the analysis of both variables. The genotypes are shown grouped by their days-to-flowering category. Values followed by a common letter within a column are not significantly different.

Genotype	Group	Total P content of shoots at flowering (%)	P biological efficiency in dry matter at flowering (g mg P pot^{-1})
Waagan	1	0.13 d	0.88 a
SP10	1	0.11 d	1.03 abc
Gregory	2	0.12 d	0.94 ab
SP16	2	0.09 c	1.26 c
SP18	2	0.09 c	1.25 b
SP19	2	0.09 c	1.25 b
Wedgetail	3	0.09 c	1.21 b
SP40	3	0.06 a	1.81 d
SP41	3	0.06 a	1.84 d
SP76	3	0.07 b	1.57 cd
SP77	3	0.07 b	1.59 d
SP2	4	0.05 a	2.23 e
SP22	4	0.05 a	2.25 e
SP29	4	0.05 a	2.26 e
LSD (5%)		0.016	0.311

Across all treatments, grain yield was significantly (R^2 = 0.53) and positively associated with higher total P content of shoots at flowering (Figure 5). The 95% maximum grain yield level, calculated from the fitted regression equation was 7.89 g pot^{-1}. Using 1 standard error (= 0.825) below this value, as a basis for the minimum critical P concentration to achieve 95% of maximum grain yield, resulted in a threshold estimate of 0.12% total shoot P content at flowering. Only a few spelt treatment combinations achieved this critical value or greater. Therefore, the lower P content in spelt dry matter, compared with standard bread wheat cultivars (Table 2), was a further factor acting against high grain yield in the spelt genotypes.

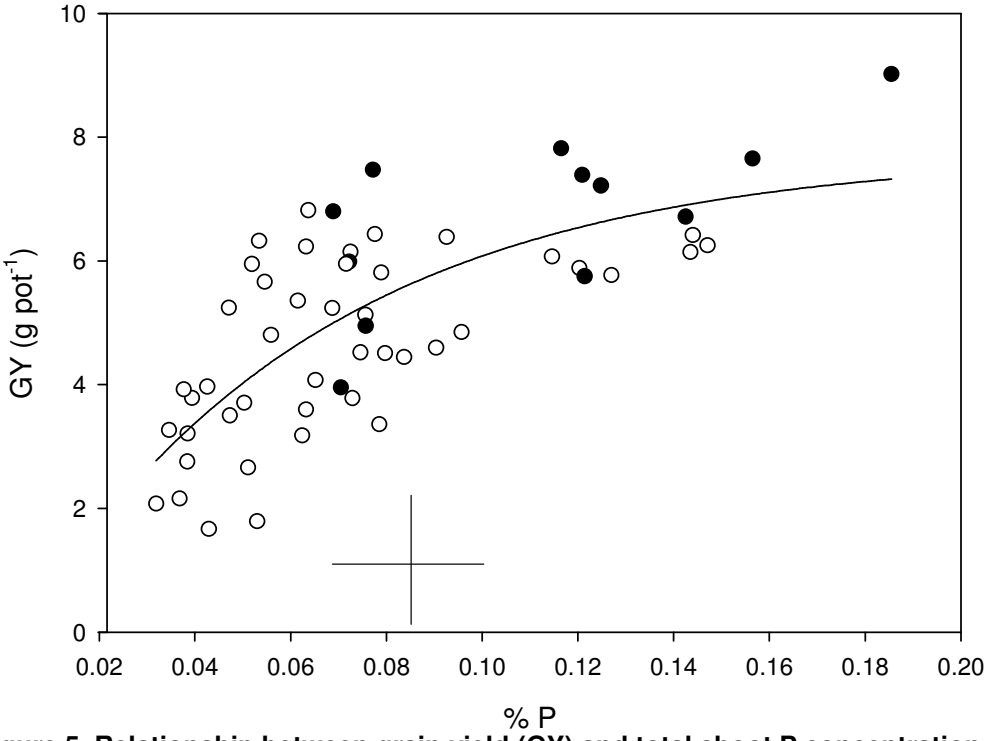

Figure 5. Relationship between grain yield (GY) and total shoot P concentration (%P) at flowering. Values are treatment means; filled symbols indicate the standard bread wheat genotypes. Bars are LSD (P = 0.05). Grain yield = 8.31 x (1-e$^{-16.08 \times \%P}$) - 0.56. R^2 = 0.53.

Grain yields for each of the genotypes at each P applied level are given in Table 3. The grain yield of Gregory and Wedgetail was maximal at the moderately low P level. As compared to these standard bread wheats, the grain yields of SP18 (Group 2), SP40 and SP76 (Group 3), and SP29 (Group 4) were also maximised at the moderately-low P level. These spelt genotypes, therefore, may have a similar fertiliser P requirement for maximal grain yield as some bread wheats, albeit with a lower grain yield potential. Other spelt genotypes, namely SP16, SP19, SP41, SP77 and SP2, had a higher P requirement for maximal grain yield than their comparative bread wheat (Table 3). The grain yield of Waagan may not be maximised at the highest applied P level used here: only SP16 and SP22 were similar in that regard.

When the supply of P was low (mimicking a low P input cropping system) the grain yield of spelt wheats did not differ significantly from the standard bread wheat cultivars (Table 3). However, the apparently larger grain yield of Wedgetail, relative to spelt genotypes with similar days-to-flowering, is consistent with its higher total shoot P concentration (0.07%) as compared to the spelt genotypes (ranging from 0.03% to 0.05%). In this range of total shoot P concentration, grain yield reduces rapidly as P concentration declines (Figure 5).

Table 3. Grain yields (g pot^{-1}) of a range of genotypes of standard bread wheat and spelt in response to four applied P levels in a glasshouse experiment at Wagga Wagga in 2007. Values in bold indicate the statistically significant maximum grain yield for each genotype when compared to the yield at the next lowest P applied level (*P* = 0.05).

Genotype	Group	Applied P level (equivalent kg P ha^{-1})			
		6.8 (low)	*13.8 (moderately low)*	*20.3 (moderate)*	*33.8 (high)*
Waagan	1	4.95	5.75	7.39	**9.02**
SP10	1	4.51	5.13	**5.88**	6.25
Gregory	2	3.78	**7.22**	7.82	7.65
SP16	2	3.60	4.07	4.60	**5.77**
SP18	2	3.18	**6.15**	6.43	6.14
SP19	2	3.96	5.24	**5.99**	6.42
Wedgetail	3	5.95	**6.80**	7.47	6.71
SP40	3	3.92	**5.95**	6.82	6.39
SP41	3	3.71	3.97	**5.66**	5.81
SP76	3	2.66	**6.32**	5.36	6.07
SP77	3	1.79	4.80	**6.23**	4.85
SP2	4	3.26	2.76	**5.24**	3.36
SP22	4	2.16	3.21	1.67	**4.52**
SP29	4	2.08	**3.78**	3.50	4.44

Grain P content (data not shown) was estimated only at the two highest P applied rates. Averaged over these P rates, the grain P content of the standard bread wheat cultivars was significantly less than for some of the spelt genotypes (SP16, SP18, SP40 and SP41), which was partly a dilution effect resulting from the higher grain yield of the standard bread wheats (grain yield = -17.4 x grain P content +11.6; R^2 = 0.49). However, the absolute P content of the grain of the standard bread wheat cultivars, particularly Wedgetail and Waagan, exceeded that of spelts ($P < 0.01$). Furthermore, the total amount of grain P relative to the total amount of P in dry matter at flowering ranged from 0.72 to 0.82 for the standard bread wheat cultivars, exceeding the range for the spelt genotypes: 0.46 to 0.70 (the highest value for spelt occurred with SP19). Across all genotypes and cultivars, grain P content was positively correlated with grain yield (R^2 = 0.91).

Field studies

Wagga Wagga 2008

Flowering of SP18, SP19 and Wedgetail occurred over a similar period (165-172 days after sowing), but before SP40 (165-176 days) and well before Kamarah (182-185 days). Higher P applied reduced the number of days for crops to reach flowering. Therefore, in contrast to the glasshouse study, the days-to-flowering of SP18 and SP19 in the field were similar to Wedgetail.

The site was P-responsive because P applied increased total shoot dry matter at flowering ($P < 0.001$) from 2001 kg ha^{-1} to 3245 kg ha^{-1} between the nil and highest levels of P applied. However, there

were no significant differences in the rate of increase in total shoot dry matter at flowering in response to increased P applied between the genotypes. Averaged over P applied levels, though, Kamarah produced significantly (P < 0.001) less, and SP18 significantly more, dry matter than the other genotypes; therefore, the P efficiency of uptake of SP18 was greater than the standard bread wheat.

The total amount of P in the shots of crops at flowering depended significantly on the genotype and the P applied level (P = 0.02, Figure 6). SP18 and SP40 accumulated more P, more rapidly than SP19, Kamarah or Wedgetail. The superior P response of SP18 and SP40 occurred as a result of significantly (P < 0.001) greater shoot dry matter at flowering compared with SP19 and Wedgetail. Kamarah had the highest total shoot P at flowering but also the least dry matter. The significant genotype x P applied interaction for total P at flowering seen here in the field differed from the findings in the glasshouse study, where there was no such interaction.

Tiller number was increased at the highest P applied level (P = 0.07), though only in genotypes Kamarah and SP18 (P = 0.06), and only by 1 tiller plant^{-1} compared to tillering at nil P applied. Averaged over P levels, Kamarah produced significantly (P < 0.001) more viable tillers (8.0 plant^{-1}) than all other genotypes, and Wedgetail the least (2.5 plant $^{-1}$), with SP18 and SP40 having a similar number (4.6 and 4.9 plant^{-1}, respectively) and significantly more than SP19 (3.6 plant^{-1}). Abortion of tillers was high in Kamarah (70%) and SP40 (53%) compared with a mean of 20% across the other genotypes.

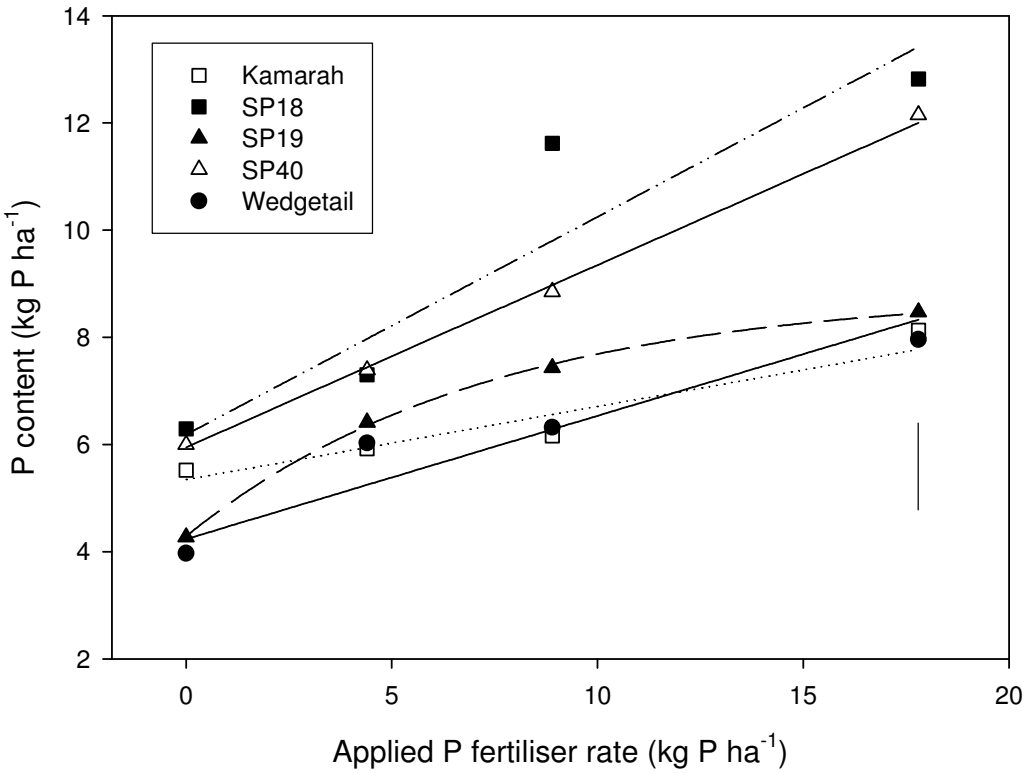

Figure 6. Influence of P applied fertiliser level on the total shoot P content of the dry matter at flowering of standard wheat and spelt genotypes in an experiment at Wagga Wagga in 2008. The vertical bar is the LSD (P = 0.05; genotype x P_{app}). Regression equations:
Wedgetail Total shoot P content at flowering = 4.2 + 0.23 x P applied, R^2 = 0.91,
SP40 Total shoot P content at flowering = 5.9 + 0.34 x P applied, R^2 = 0.99,
SP19 Total shoot P content at flowering = 4.3 + 4.6 x (1 - $e^{-0.14 \times P\ applied}$), R^2 = 0.99,
SP18 Total shoot P content at flowering = 6.46 + 0.39 x P applied, R^2 = 0.87, and
Kamarah Total shoot P content at flowering = 5.29 + 0.15 x P applied, R^2 = 0.93.

Grain was low (< 0.4 t ha^{-1}) and determined only by main factors of P applied (P = 0.02) and genotype (P < 0.001). Increasing P applied significantly increased grain yield (P < 0.001), total shoot P at flowering (P < 0.001) and total P content of grain at maturity (P < 0.001), but these responses were maximal at only the second P applied level, 4.4 kg P ha^{-1}. Therefore, under these field conditions at Wagga Wagga in 2007, all genotypes had a similar requirement for P applied to achieve maximal grain yield. Averaged across P applied levels, grain yield increased in the following order: Kamarah < SP40 = SP18 < SP19 < Wedgetail; and was strongly, and inversely, related to tiller number (Figure 7). Thus, P efficiency in grain yield was greatest in the standard bread wheat, but also differed between

the spelt genotypes, being greatest for SP19. Grain P concentration did not vary between genotypes, but total grain P increased with grain yield (R^2 = 0.98).

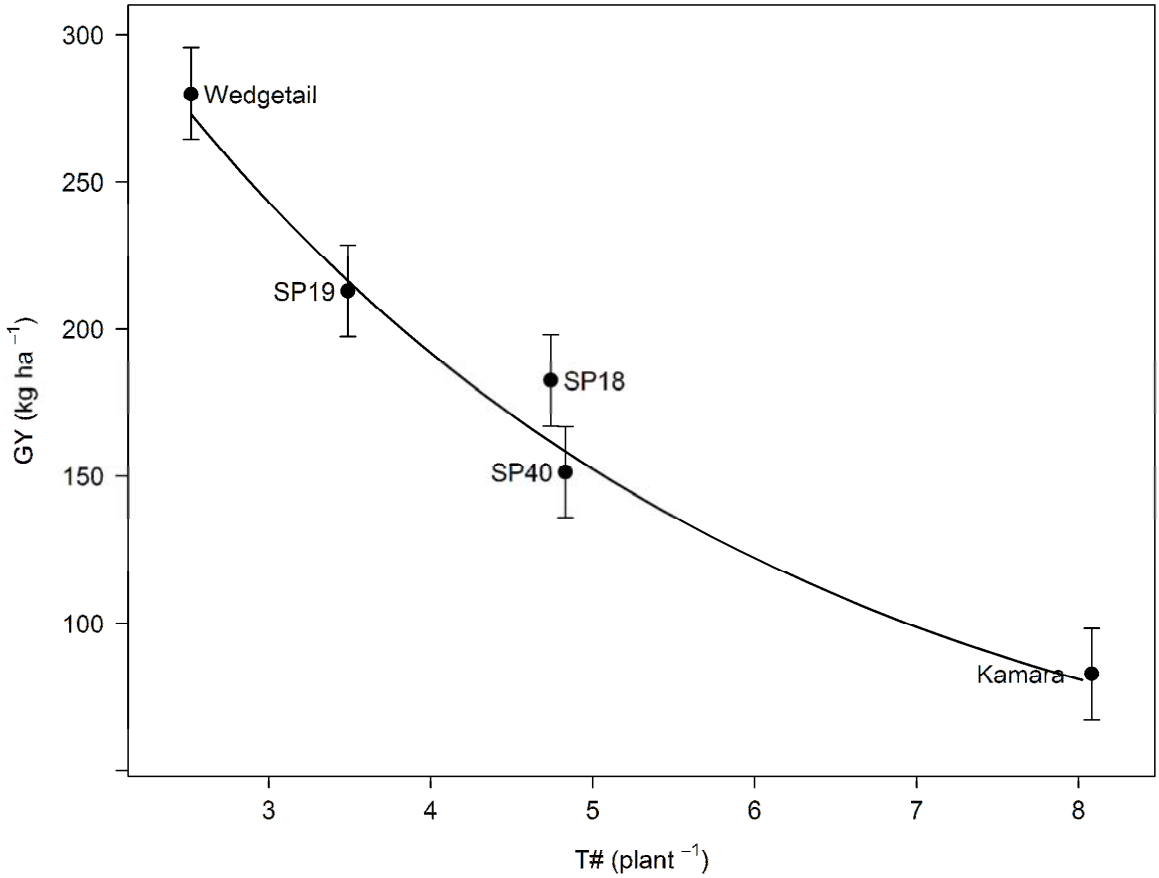

Figure 7. Relationship between grain yield (GY) and tiller number per plant (T#) for five genotypes grown in the field experiment at Wagga Wagga, 2008. Values are means over all applied P levels. Error bars are standard errors for difference of means. Fitted line is: GY = 21.4 + (488 x $e^{-0.263 \times T\#}$), R^2 = 0.97.

Condobolin 2008

Across the range of P applied treatments, the number of plants established in the standard bread wheat genotypes (Carinya and Ventura) significantly exceeded the number in the spelt genotypes (Table 4), and significantly better establishment occurred with SP19 compared to SP18, despite the fact that SP19 was sown at a lower rate, due to limits in seed supply (SP18 sown at 59 kg ha^{-1}; SP19 at 47 kg ha^{-1}).

The site was responsive to P applied with average crop dry matter increasing significantly (P < 0.001) from 2177 kg ha^{-1} to 4880 kg ha^{-1} as P applied increased from 0 to 24 kg P ha^{-1}, with a plateau at 12 kg P ha^{-1}. Total shoot P content at flowering (kg P ha^{-1}), estimated for Carinya, SP18 and SP19, increased linearly over the range of P applied levels (Figure 8), and although it depended on both P applied and genotype (P = 0.02), the data for SP18, the genotype mainly responsible for the interaction, were less reliable as these values were based on only two replicates, because of a shortage of seed of this line. Average total shoot P content at flowering was sustained at 0.11% as total shoot dry matter at flowering increased to the plateau, before increasing to 0.15% at the highest P applied rate.

Averaged over P applied levels, tiller number was significantly higher in the spelt genotypes (Table 4), and crop height (cm) was significantly greater for SP18, compared with the standard bread wheats. Grain yield and grain harvest index of the spelt genotypes were significantly inferior to the standard bread wheats (Table 4). The higher grain yield of the bread wheats did not result from a higher mean kernel weight, or from a higher number of ears per unit area, but from a higher number of seeds per ear (Table 4). Notably, seeds per ear was strongly and inversely related to tiller number (R^2 = 0.94, at the genotype level).

Table 4. Characteristics of two standard bread wheat and two spelt genotypes in a field experiment at Condobolin in 2008. Values are the means over all P applied fertiliser treatments. Values with a common letter, within a column, are not significantly different (*P* = 0.05) using a simple LSD test.

Genotype	Plants m^{-2}	Tillers $plant^{-1}$	Mature crop height (cm)	Shoot dry matter at flowering (t ha^{-1})	Grain Yield (t ha^{-1})	Grain harvest Index	100 Seed weight (g^{-1})	Seeds ear^{-1}	Ears m^{-2}
Carinya	84.2 c	3.05 a	468 a	3.70 b	1.09 c	0.46 c	3.07 c	25.5 c	190 b
Ventura	81.2 c	2.54 a	570 c	3.87 b	0.98 b	0.45 c	2.73 a	27.8 d	145 a
SP18	46.5 a	5.64 c	681 d	3.20 a	0.61 a	0.23 a	2.90 b	13.3 a	165 ab
SP19	68.7 b	4.00 b	520 b	3.55 ab	0.70 a	0.32 b	3.49 d	17.8 b	187 b
LSD (5%)	8.42	0.829	12.0	0.37	0.101	0.017	0.098	1.68	23.4

The initial grain yield response to P applied was greater for the standard bread wheats compared to the spelt genotypes ($P < 0.001$; Figure 8). The reduced response of SP18 and SP19 may be caused by a more rapid but ultimately unproductive tillering response to P applied in these genotypes Thus, the rate of change in tillers $plant^{-1}$ per unit of applied P was 0.26 for SP18 (R^2= 0.80) with a predicted maximum of 9.0 $plant^{-1}$ at 24 kg P ha^{-1}, as compared with 0.08 (R^2 = 0.67) and a corresponding maximum equal to 4.1 $plant^{-1}$ for Carinya; with SP19 intermediate to these [initial rate of change = 0.24 (R^2 = 0.89), with a plateau of 4.6 $plant^{-1}$ occurring at 12 kg P ha^{-1}]. Except for Ventura, no grain yield plateau was reached in response to higher P applied levels (Figure 8). Relative to Ventura, maximum grain yield with SP18, SP19 and Carinya required a greater amount of applied P. In general, P efficiency in grain yield for the standard bread wheat cultivars was superior to the spelt genotypes.

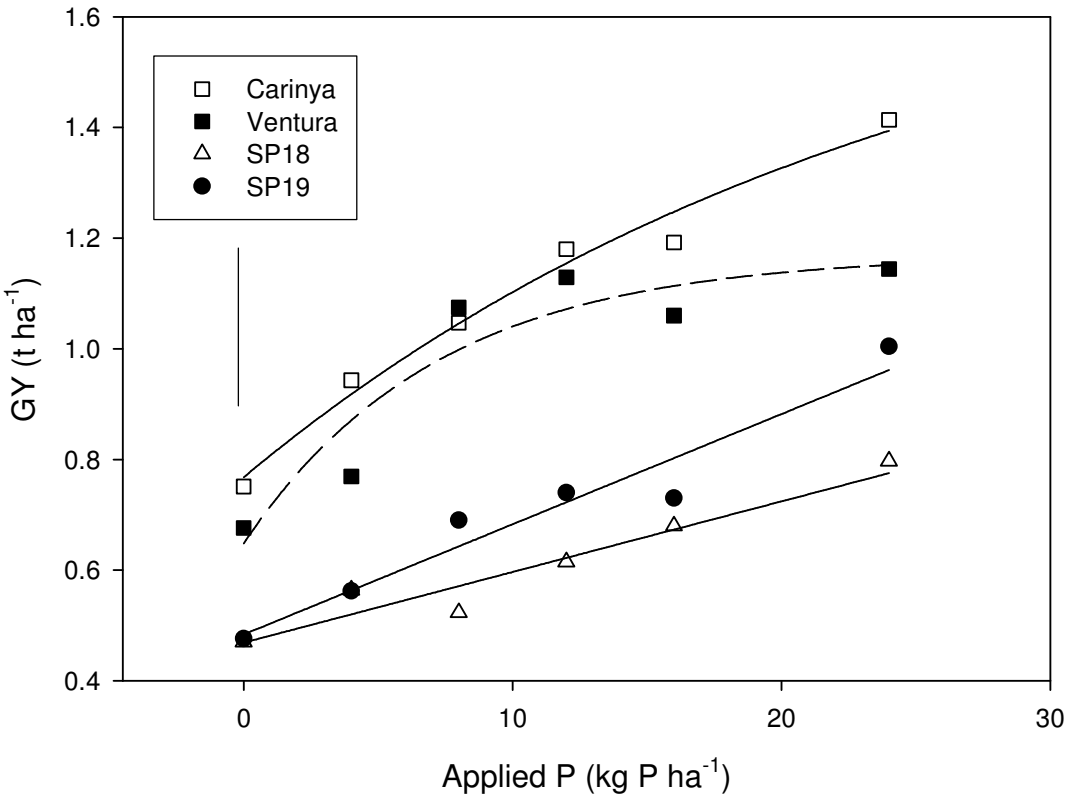

Figure 8. Influence of applied P on the grain yield (GY) of two standard wheats and two spelt genotypes in a field experiment at Condobolin in 2008. Vertical bar is the LSD (*P* = 0.05) for the genotype x applied P interaction (*P* < 0.001). Regression equations:
Carinya Grain yield = 0.77 +1.02 x (1 – $e^{-0\text{-}04 \times P\ applied}$), R^2 = 0.98,
Ventura Grain yield = 0.52 + 0.52 x (1 – $e^{-0.139 \times P\ applied}$), R^2 = 0.88,
SP18 Grain yield = 0.47 + 0.013 x P applied, R^2 = 0.98, and
SP19 Grain yield = 0.48 + 0.02 x P applied, R^2 = 0.94.

Rutherglen 2008

Flowering of SP18, SP19, SP40 and Wedgetail occurred around 19 October 2008, and flowering of Kamarah around 11 November. At this field site there was no effect of the P applied treatments on

either total shoot dry matter at flowering or grain yield, nor any interaction between genotype and P applied. However, averaged over P treatments, the total shoot dry matter at flowering of SP19 and SP40 was similar and significantly (P = 0.002) greater than for Wedgetail and Kamarah, and SP19 significantly greater than SP18. Also averaged over the P applied treatments, the low grain yield (which was very low due to drought conditions) varied significantly (P < 0.001) between genotypes: Kamarah (347 kg ha^{-1}) < SP40 (490 kg ha^{-1}) < SP18 (669 kg ha^{-1}) < SP19 (918 kg ha^{-1}) = Wedgetail (1001 kg ha^{-1}). There was no relationship between total shoot dry matter at flowering and grain yield. The growing season (June-October) rainfall at the Rutherglen site was only 182 mm; compared to a long-term average of 292 mm. The year (2008) was a significant drought with annual rainfall of only 429 mm compared to the long-term mean of 588 mm.

Discussion

After this study was completed, a report on genetic diversity in spelt germplasm using DNA markers (Raman et al., 2009) concluded that the genotypes SP18 and SP19 contained alleles that suggested that these genotypes were derived from crosses between spp. *spelta* and common bread wheat. This is partly evident here in the intermediate response of these genotypes compared to the extremes of the commercial wheat cultivars (e.g. Wedgetail) and the “pure” spelts (e.g. Kamara) (Figures 1, 2, 3 and 7).

Spelt did not show the grain yield potential of the highly-developed and highly-selected standard bread wheat cultivars, either under well-watered glasshouse conditions or under field conditions. In the glasshouse, the average maximum grain yield of spelt (excluding the three late-flowering genotypes: SP2, SP22, SP29) was 77% of the average maximum grain yield of the standard bread wheats, with a range from 56% to 84%. In the field, at Wagga Wagga, the spelt averaged 65% (range of 54-76%) of the grain yield of Wedgetail; at Condobolin, 60% (range of 55-64%) of Carinya; and at Rutherglen, 60% (range of 34-92%) of Wedgetail. Where Kamarah was included in the field experiments, its grain yield was < 55% of Wedgetail, supporting the anecdotal evidence that current commercial crops of spelt yield substantially less than commercially-grown bread wheat. The range of alternative spelt genotypes used in this study also yielded significantly less than standard bread wheats. Furthermore, the P applied requirement to achieve the maximum grain yield of spelt was no less than for bread wheats, suggesting that an economic return from spelt similar to standard bread wheat can only be achieved through the higher market value per tonne of spelt grain.

There was no evidence from our glasshouse or field trials that, in P-deficient soil (low input cropping systems), spelt was capable of higher grain yield than standard bread wheats, indeed in most cases its P uptake and utilisation efficiencies were also lower than bread wheat

The field experiments showed that Kamarah yielded significantly lower than alternative spelt genotypes. Thus, over a range of soil P fertility conditions, the grain yield of Kamarah was only 38% and 39% of the grain yield of SP19 at Rutherglen and Wagga Wagga, respectively. These data suggest that greater economic returns could be achieved through commercialisation of the highest-yielding spelt genotype, SP19, provided that the grain quality attributes valued by the organic spelt industry can be maintained. The long days-to-flowering of Kamarah meant that it was poorly adapted; the plant is also poorly-structured (high tiller number and tall) preventing it from yielding well, at least under moisture-stressed conditions. The glasshouse data also suggested that the minimal P applied requirement for maximal grain yield among the spelt genotypes may differ, so that breeding and selection within spelt may optimise P efficiency for grain yield.

The higher tiller number, total dry matter at flowering, and dry matter at maturity of the spelt genotypes may have value in an organic system for increased competitiveness against weeds, for grazing, or for the production of forage (hay or silage). However, these characteristics were not conducive to high grain yield. Under glasshouse conditions some growth attributes of spelt were negatively correlated to grain yield; including greater dry matter at flowering and greater tiller number. The yield component that appeared to be most adversely influenced by higher dry matter at flowering was kernel number per plant. This yield component is reported to have a major influence on the grain yield of standard wheat (Guitard and Newman, 1961, Shah et al., 1994) as it is a key component of overall sink size. The yield component most adversely influenced by greater tiller number was mean kernel weight., The general conclusion from the glasshouse and field observations reported here is that the greater propensity for tillering and higher dry matter production in spelt render it less able to yield at an equivalent level to standard bread wheats.

Genetic advance in the grain yield of standard winter and spring wheats has shown a correlation with an increase in grain harvest index often through the use of dwarfing genes (Austin et al., 1980, Domnez et al., 2001, Shearman et al., 2005). A reduction in tiller number or plant height in spelt may provide a pathway for increasing its grain harvest index by enabling an increase in mean kernel weight and/or kernel number.

In our glasshouse experiment, greater biomass was not only associated with lower kernel number, but also with a lower total P content at flowering. According to several authors (Boatwright and Viets, 1966, Chapman and Keay, 1971, Batten et al., 1986) the P acquired by wheat up to flowering is usually sufficient for maximal grain yield, because P stored in leaf and stem tissue is re-mobilised to support grain production (Batten et al., 1986). However, at a given level of P applied , the consistency in plant total P between genotypes varying in grain yield, suggested that total P *per se* could not explain grain yield variation. Total shoot P content at flowering was greater in the higher-yielding standard bread wheats than in spelt wheats grown at a fixed level of P applied. Others (Rashid et al., 2005) have reported a strong correlation between total shoot P at flowering and relative grain yield in spring wheat, with a critical concentration of 0.13%; similar to the suggested lower limit (0.12%) estimated here. Tissue that has a higher P concentration, such as that present in the standard bread wheats, may contain a greater fraction of P stored in more readily mobilised compounds which can be used to meet the requirements of grain production. The fact that the mean kernel weight of the standard bread wheat cultivars was significantly superior to nearly all spelt genotypes, and kernel number was lower, suggested that resources for seed growth were in better supply in the standard bread wheat cultivars. As well as carbon (C) (Grafius, 1972), these resources may include mobile P and N that are transported from leaf and stem material to grain (Chapman and Keay, 1971).

Simply enriching plant tissue with P is not likely to be sufficient to maximise the grain yield potential of spelt wheat. In the glasshouse study, applying more P fertiliser increased the tissue concentration of SP18 and SP19 to an adequate maximum value of 0.14 %P, yet these genotypes still did not produce grain yield comparable to the standard bread wheats. A significant amount of P was ‘wasted’ on unnecessary height and unproductive tillers. Despite the significant grain yield differences between standard bread wheats and spelt genotypes in the field at Wagga Wagga and Condobolin, tissue P concentration was similar or greater in the spelt genotypes; and all values exceeded 0.12%. At Wagga Wagga, the significantly higher tissue P concentration in SP18 and SP40 compared to Wedgetail and SP19 occurred in parallel with greater dry matter, which suggests that these spelt genotypes may have greater ability to acquire P from soil, at least under dry soil conditions. This may be due to better root system architecture or functioning (Richardson et al., 2009) and warrants further investigation. From this work it is apparent that tissue P concentration is unlikely to be responsible for determining grain yield differences between spelt and bread wheat, which seems more probably caused by morphological and physiological differences, related to tillering, height, ear size, and seed size.

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