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2 **Comparing the phosphorus requirements of wheat, lupin and canola**

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Abstract. Spring wheat (*Triticum aestivum* L.), lupin (*Lupinus angustifolius* L.), and canola (*Brassica napus* L.) are the major crops species grown in rotation on the predominantly sandy soils of south-western Australia. Comparisons among the species for yield responses to applied phosphorus (P), effects of applied P on growth rates of shoots, P response efficiency for shoot and grain production, and the pattern for accumulation of P into shoots during growth and into grain at maturity, are rare, or are not known, and were quantified in the glasshouse study reported here. Size and P content (P concentration multiplied by yield) of sown seed were in the order canola <wheat <lupin. Therefore, yield responses to applied P were first observed at ~10 days after sowing (DAS) for canola, ~17 DAS for wheat and ~60 DAS for lupin. Lupin shoots showed no yield response to applied P at the first harvest at 51 DAS. Otherwise all species showed large yield, P concentration and P content responses to applied P for all harvests at 51, 78, 87, 101, 121 and 172 DAS. To produce 90% of the maximum grain yield, the relevant data for cropping, lupin required ~67% less P than wheat, canola required ~40% less P than wheat, and canola required ~75% more P than lupin. Growth rates, and P response efficiency, were generally largest for canola, followed by wheat, then lupin. For shoots, P accumulation was in the order lupin >wheat >canola at 51 DAS, canola >wheat >lupin at 78 and 87 DAS, canola >wheat = lupin at 101 DAS, and all 3 species about similar at 121 DAS. For accumulation of P into shoots plus grain at maturity (172 DAS) the order was canola >lupin >wheat, and for grain only was canola >wheat = lupin.

Additional keywords: accumulation of P into shoots and grain, critical tissue test P values, P concentration and content in dried shoots and grain, P response efficiency, P uptake, shoot growth rates.

Introduction

36 When newly cleared about 75% of the almost 18 million hectares used for agriculture
37 in south-western Australia were marginally acidic to neutral sandy soils that were
38 initially acutely phosphorus (P) deficient (McArthur 1991). Spring wheat (*Triticum*
39 *aestivum* L.) has always been the major crop grown on these soils. Since the mid
40 1960s lupin (*Lupinus angustifolius* L.) started to be grown in rotation with wheat on
41 these soils, with canola (*Brassica napus* L.) also being included from the early 1990s.
42 Consequently, numerous experiments have been conducted on most of these soils to
43 determine the P requirements of wheat, fewer have been done on fewer soils for lupin,
44 and fewer still for canola. These experiments involved only one of the crop species
45 and were rate of P field experiments done on P deficient soils. For wheat and lupin,
46 these experiments were conducted when different parts of the region were cleared of
47 native vegetation for agriculture. Grain yield responses to applied P were always
48 measured because these were economically the most relevant data. However,
49 sometimes yield responses of dried shoots to applied P were also quantified before
50 maturity. Most of the data are unpublished, but have been incorporated into decision
51 support systems used for P in the region (Bowden and Bennett 1974; Burgess 1988;
52 Bowden 1989).

53 The limited number of field experiments done in the region to compare the P
54 requirements for grain production of wheat and lupin were on acutely P deficient deep
55 sandy soils (Bolland and Barrow 1991; Bolland 1992a, 1992b, 1992c). Generally,
56 these showed that the relationship between grain yield and the level of P applied was
57 sigmoid for lupin and exponential for wheat. Consequently, at suboptimal levels of P
58 application, lupin required more P than wheat to produce the same yield. However, in
59 the steeply rising part of the response curves, response curves to applied P were

usually steeper for lupin than wheat, so lupin required less applied P to produce near-maximum grain yields.

The limited studies comparing the P requirements of wheat and canola in the same experiment in the region have consistently shown that canola required from ~40 to 60% less applied P than wheat to produce 90% of the maximum yield of dried shoots and grain (Bolland 1997, 1999; Bolland *et al.* 1999, 2006).

The P requirements of wheat, lupin and canola have only been compared in 1 field experiment in the region, when shoot yields were measured at ~120 days after sowing (DAS), and grain yields were measured at maturity (Brennan and Bolland 2001). The amount of applied P required to produce 90% of the maximum yield of dried shoots and grain was similar for wheat and lupin, but was ~50% less for canola than wheat and lupin (Brennan and Bolland 2001).

Consequently, the P requirements of wheat have been determined for most soils and environments used for cropping in south-western Australia. The P requirements for lupin and canola need to be compared to the P requirements for wheat in the same experiment to provide an indication of the different P requirements of lupin and canola relative to wheat. Though this has been done in 1 field experiment in the region (Brennan and Bolland 2001), a more comprehensive study may be required to obtain data during the life cycle of the crop species. Such a comprehensive study, involving glasshouse and field experiments, was undertaken for spring wheat in South Australia to quantify, for different above ground plant parts during the life cycle, yield responses to applied P, and P uptake patterns (Elliott *et al.* 1997*a, b, c, d*). We used a similar approach in a glasshouse experiment for wheat, lupin and canola, and the results are reported in this paper. We did a rate of P glasshouse experiment, using a P deficient sandy soil, to compare among the 3 crop species, plant yield responses to

applied P, and the pattern of P accumulation into shoots during growth and into grain at maturity. The novel data reported are differences among the 3 species for (i) shoot and grain yield responses to applied P, (ii) P accumulation patterns into shoots at different growth stages and into grain at maturity, (iii) growth rates for shoot production between harvests, and (iv) P response efficiency for shoot and grain production up to each harvest.

Materials and methods

Soil

The top 10 cm of a sandy soil was collected from under remnant vegetation on Newdegate Research Station (33°06'S 119°01'E) that had never been fertilised and used for agriculture. The soil was air-dried and passed through a 4-mm sieve before being used for the glasshouse experiment. The soil was a brown sandy loam, classified as a Brown Sodosol (Isbell 2002), and a Typic Natrixeralf (Soil Survey Staff 1987). Some properties of the soil were: pH (1:5 soil:0.01 M CaCl₂, w/v, Rayment and Higginson 1992) 6.1; bicarbonate-extractable P (Colwell 1963) 2 mg/kg; P buffer capacity (P sorbed by soil between 0.25 and 0.35 mg P/L, Ozanne and Shaw 1968) 4 mg/kg; organic carbon (Walkley and Black 1934) 10 g/kg; total nitrogen (Kjeldahl method, as described by McKenzie and Wallace [1954]) 0.14 g/kg; cation exchange capacity (extracted in 1.0 M NH₄Cl at pH 7.0, as described by Piper [1942]) 4 cmol(+)/kg; percentage clay (Day 1965) 7.

Glasshouse experiment

The experiment was conducted from 2 May to 22 October 2006 in a glasshouse near Albany, Western Australia. Temperatures in the glasshouse ranged from 21°C day and 12°C night $\pm$ 2°C.

The experiment was completely randomised, and comprised 3 crop species, 6 harvest dates, and 17 levels of applied P, replicated 2 times. That is, the pots were not blocked into plant species, harvest dates, or replicates, but were all placed completely randomly in the glasshouse. The 3 crop species were spring wheat (*Triticum aestivum* L. cv. Wyalkatchem), lupin (*Lupinus angustifolius* L. cv. Kalya) and canola (*Brassica napus* L. cv. Hyden). The 6 harvest dates were (days after sowing, DAS) 51, 78, 87, 101, 121 and 172 (maturity). So 102 pots (3 plant species x 17 levels of P x 2 replications) were harvested at each of the 6 harvest dates, and after the fifth harvest plants growing in the last 102 pots were harvested at maturity to provide yields of whole tops (dried shoots plus grain) and grain at maturity. The 17 levels of P applied (g P/pot) were 0, 0.005, 0.01, 0.02, 0.04, 0.05, 0.06, 0.07, 0.08, 0.09, 0.1, 0.15, 0.2, 0.25, 0.3, 0.6 and 1.2. The P was applied as powdered single (ordinary) superphosphate (9.1% total P, 80% being water-soluble). A sample of the granulated (0.5-5.0 mm diameter) superphosphate was ground with an agate mortar and pestle until the entire sample passed through a 200- μ m mesh sieve.

Plastic pots (19 cm diameter and 18 cm high), lined with a polyethylene bag, to prevent drainage, were used. Each pot contained 5 kg air-dry soil. To ensure P was the only nutrient element to limit plant yield, nutrient solutions containing the following salts were added to the soil surface in each pot (mg/pot): NH_4NO_3 , 330; K_2SO_4 , 328; $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 85; $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$, 35; $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$, 35; $\text{MnSO}_4 \cdot 5\text{H}_2\text{O}$, 50; $\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$, 52; $\text{CoSO}_4 \cdot 7\text{H}_2\text{O}$, 1.1; $\text{Na}_2\text{MoO}_4 \cdot 2\text{H}_2\text{O}$, 1.1; H_3BO_3 , 1.0. On a surface area basis 284 mg/pot is ~ 100 kg/ha. When the soils had dried after applying the nutrient solutions, finely-powdered calcium sulfate ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$), at 250 mg/pot, and the levels of P as finely-powdered superphosphate, were both applied to the soil surface in each pot. The soil in each pot was then thoroughly shaken in the plastic

bag to mix the applied nutrient elements and P fertiliser through the whole soil. The soil in each pot was then watered to 75% of gravimetric field capacity (11.3 g deionised water per 100 g of soil). Twenty seeds of each crop species were sown 2 cm deep in each pot on 3 May 2006. The plants were thinned to 6 per pot at 14 DAS, by leaving the most uniform plants. Before sowing, seed of the three species was sieved to sow seed of a similar size for each species, being (mg/seed) 43 for wheat, 194 for lupin and 3.8 for canola. Concentrations of P in the sown seed, measured as described below for dried shoots and grain harvested from the experiment, were (g/kg) 3 for both wheat and lupin, and 6 for canola.

For the first 21 DAS soils in each pot were maintained at 75% of field capacity by daily watering to weight. Thereafter soils were maintained at field capacity (15 g deionised water per 100 g soil). Pots were re-randomised at each watering. Pots were watered daily in early growth, increasing up to 3 times daily near maturity.

Nitrogen (NH_4NO_3 , 500 mg/pot) was applied every 10 days for the first 70 DAS.

Measuring shoot and grain yields

At each harvest all 6 plants within each pot were cut at the soil surface and were dried in a forced-draught oven at 80°C for 2 days before weighing. After 87 DAS each pot was placed on a plastic sheet. Leaves that dropped off the plants onto the plastic sheet or into each pot were collected, dried and weighed. The weight of the leaves collected before each harvest was added to the weight of dried shoots measured at that harvest. Few leaves of wheat plants dropped off at any harvest, regardless of the level of P applied. Leaves dropped off lupin and canola plants as a result of P deficiency, increasingly from 87 DAS to maturity. At the final harvest (maturity, 172 DAS), after shoots plus grain cut at ground level were weighed, wheat heads and lupin and canola

159 pods were removed from stems to extract grain to determine grain yields. After
160 removal of grain, the remainder of the wheat heads and lupin and canola pods were
161 included with the rest of shoots to measure yields of the dried shoots and to measure P
162 concentration in the dried shoots.

163 *Measuring P concentrations in shoots and grain*

164 After measuring yields, dried shoots and grain were ground and digested in a mixture
165 of sulphuric acid and hydrogen peroxide (Yuen and Pollard 1954), and the
166 concentration of P in the digest was measured by inductively coupled plasma-atomic
167 emission spectrometry (ICP-AES).

168 *Calculating growth rates of shoots between harvests*

169 For each level of P applied, yields of dried shoots at the first harvest (51 DAS) were
170 divided by 51 to provide growth rates of dried shoot from emergence to the first
171 harvest (mg dried shoots/pot per day). For subsequent harvests, for each level of P
172 applied, yields of dried shoots measured at the previous harvest were subtracted from
173 yields of dried shoots at the present harvest to provide yields of dried shoots grown
174 since the previous harvest. These values were then divided by the number of days
175 since the previous harvest to provide growth rates of dried shoots since the previous
176 harvest (mg dried shoots/pot per day). Note that for the sixth harvest at maturity (172
177 DAS), all above ground growth was harvested at soil level in each pot so growth rates
178 were calculated for dried shoots plus grain (whole tops) from 121 DAS to 172 DAS.

179 *Calculating P response efficiency*

180 P response efficiency was calculated for yields of dried shoots at the first 5 harvests,
181 and for yields of whole tops (dried shoots + grain) and grain at the last (sixth) harvest.
182 At each harvest, yield responses to applied P were calculated by subtracting the yield
183 for the nil-P treatment from yields produced when each level of P was applied. The

yield responses to each level of P applied were then divided by the level of P applied to provide P response efficiency values (kg dried shoot or grain produced/pot per g P applied/pot).

Analysis of data

Yield responses of dried shoots and grain to applied P

Data for the relationship between yield of dried shoots or grain and the level of P applied were adequately described by a rescaled exponential (Mitscherlich) equation (Barrow and Mendoza 1990):

$$y = a - b \exp(-[cx]^n) \quad (1)$$

where y was the yield of dried shoots or grain (g/pot), x was the level of P applied (g P/pot), and a , b , c and n were coefficients. Coefficient a provided an estimate of the asymptote or maximum yield plateau (g/pot). Coefficient b estimated the difference between the asymptote and the intercept on the yield (y) axis at $x = 0$ and so provided an estimate of the maximum yield increase (response) to applied P (g/pot). Coefficient c described the shape of the relationship and governed the rate at which y (yield) approached the asymptote as the value of x (level of P applied) increased (pot/g) (Ratkowsky 1990). Coefficient n also affected the shape of the response curve. When the value of $n = 1$, the response curve was exponential, and as the value of n increased above 1.0, the shape of the yield response curve became increasingly sigmoid (Barrow and Mendoza 1990). Mean data were fitted to the equation by non-linear regression using a computer program written in compiler BASIC (Barrow and Mendoza 1990). The simplex method (Nelder and Mead 1965) was used to locate the least square estimates of the non-linear coefficients.

The level of applied P required to produce 90% of the maximum yield was calculated using the fitted equation to provide P required (PR₉₀) values. The value of

the a coefficient of the fitted equation was used to calculate 90% maximum yield. The larger the value of the c coefficient of Eqn 1 the more rapidly the curve approached the maximum yield plateau, so the steeper the response curve, and a smaller level of applied P was required to produce 90% of the maximum yield. Conversely, the smaller the value of c , the flatter the response curve to applied P and more applied P was required to produce the target yield.

P concentration in dried shoots and grain

Data for the relationship between P concentration measured in dried shoots or grain and the level of P applied were adequately described by an exponential (Mitscherlich) equation (Barrow and Mendoza 1990):

$$y = a - b \exp(-cx) \quad (2)$$

where y was the P concentration in dried shoots or grain (g/kg), x was the level of P applied (g P/pot) and a , b and c are same coefficients described for Eqn 1.

Estimating P uptake between harvests

P content was calculated by multiplying P concentration in dried shoots or grain by yield of dried shoots or grain. Therefore, P content provided an estimate of the amount of P taken up from soil (P uptake) that was accumulated into dried shoots at each harvest or into grain at maturity. At the first harvest (51 DAS) P content was for P taken up from emergence of plants to that harvest. Thereafter, P accumulated into shoots between each harvest was calculated by subtracting P content for the previous harvest from P content for the present harvest. This was done for each level of P applied for each crop species. Finally P accumulated into grain at maturity was calculated by multiplying grain yield by the concentration of P in grain.

Data for the relationship between P accumulated into shoots between harvests, and into grain at maturity, and the level of P applied, were adequately described by

both Eqns 1 and 2, where y was the P content accumulated into dried shoots or grain (mg P/pot), and x was the level of P applied (g P/pot). In most cases Eqn 1 gave significantly lower residual sums of squares than Eqn 2 so all data were fitted to Eqn 1.

Calculating critical diagnostic tissue P test values

For each harvest, data for the relationship between yield of dried shoots or grain (g/pot), as the dependent (y) axis, and P concentration measured in the dried shoots or grain (g/kg), as the independent (x) axis, were adequately described by both Eqns 1 and 2. However, in most cases Eqn 1 gave significantly lower residual sums of squares than Eqn 2 so all data were fitted to Eqn 1. For each harvest, the P concentrations in dried shoots or grain that were related to 90% of the maximum yield was calculated using the fitted Eqn to provide critical diagnostic tissue P test values at each time of sampling below which yield decreases due to P deficiency were likely (Ulrich 1952). The value of the a coefficient of the fitted Eqn was used as the maximum yield to calculate 90% of the maximum yield.

Calculating critical prognostic tissue P test values in dried shoots at early growth for grain production

Concentrations of P in dried shoots that were related to grain yield were confined to the first 3 harvests of shoots because later samplings of shoots are of no practical significance. Data for the relationship between grain yield (g/pot), as the dependent (y) axis, and the P concentration measured in shoots (g/kg) at 51, 78 or 87 DAS, as the independent (x) axis, were adequately described by both Eqns 1 and 2. However, Eqn 1 produced significantly lower residual sums of squares than Eqn 2 so all data were fitted to Eqn 1. For each harvest at 51, 78 or 87 DAS, the P concentration in dried shoots that was related to 90% of the maximum grain yield was

calculated using the fitted Eqn to provide critical prognostic tissue P test values in dried shoots below which grain yield decreases due to P deficiency in the shoots at early growth were likely (Ulrich 1952). The value of the *a* coefficient of the fitted Eqn was used as the maximum grain yield to calculate 90% of the maximum grain yield.

Results

Plant symptoms for P deficiency

Plant P deficiency symptoms of all 3 crop species occurred for the nil-P to about the 0.02 g P/pot (4th) level. The P deficient wheat and lupin plants were stunted with very dark green leaves. Canola deficient plants were very stunted and purple. Lupin leaflets became twisted and eventually dropped off. The deficiency reduced growth at 51 DAS for wheat and canola and 78 DAS for lupin. Thereafter growth progressively worsened for the nil-P and the lowest 4 levels of P applied treatments.

P content of sown seed

Size of sown seed (mg/seed) was largest for lupin (193), followed by wheat (43), and was smallest for canola (3.8). P content (P concentration multiplied by seed mass) in sown seed (mg P/sown seed) was largest for lupin (0.58), followed by wheat (0.129), and was smallest for canola (0.023).

Shoot and grain yield responses to applied P

Responses when no and low levels of P were applied

For the nil-P treatment yields of dried shoots were always largest for lupin, followed by wheat, and smallest for canola (Fig. 1). When shoot yields for the nil-P treatment were expressed as a percentage of the maximum (relative) yield for each crop species at each harvest, relative yields consistently decreased for all 3 crop species for each successive harvest. At maturity, canola produced no grain for the nil-

P treatment, wheat produced no grain for the nil-P and lowest level of P applied treatment (0.005 g P/pot), and lupin produced no grain for the nil-P and the 5 lowest levels of P applied (0.0 to 0.05 g P/pot).

When low levels of P were applied lupin produced much larger shoot yields than the other 2 species up to 121 DAS (Fig. 1). For the last harvest at maturity all 3 crop species produced negligible yields when no P and low levels of P were applied and lupin yield responses became sigmoid, particularly for grain production (Figs. 1f and 1g).

First observation of yield responses to applied P

Visual plant yield responses to applied P were obvious ~10 DAS for canola, ~17 DAS for wheat and ~60 DAS for lupin. Dried lupin shoots showed no response to applied P at the first harvest (51 DAS), whereas both wheat and canola did, with yields being largest for lupin, smaller for wheat, and smallest for canola (Fig. 1a).

Comparing the 3 crop species

For all harvests after 51 DAS, all 3 crop species showed large shoot and grain yield responses to applied P (Fig. 1b-g). After the first harvest, canola consistently produced the largest shoot yields when the larger levels of P were applied, and had larger maximum shoot yield plateaus than wheat and lupin (Fig. 1b-f). The a coefficient of Eqn 1 estimated the maximum yield plateau of the yield response curve. For shoots after the second harvest (after 78 DAS), a was consistently largest for canola, followed by wheat, and was smallest for lupin (Table 1). Likewise, the b coefficient of Eqn 1 estimated the maximum yield response of shoots to applied P. After the first harvest at 51 DAS, b was consistently largest for canola, followed by wheat, and was smallest for lupin (Table 1).

At maturity lupin response curves were sigmoid (n much >1.00) (Table 1), because no lupin grain was produced for nil and the first 5 levels of P applied (Fig. 1g). However, when >0.05 g P/pot was applied, the lupin grain yield response curve was much steeper than the response curve for wheat or canola (Fig. 1g), and lupin had the largest value of c at 172 DAS (Table 1), so lupin required less applied P to produce 90% of the maximum grain yield than the other 2 species (Table 1). Grain data are the most relevant for cropping, and to produce 90% of the maximum grain yield, lupin required ~67% less P than wheat, canola required ~40% less P than wheat, and canola required ~75% more P than lupin (see PR_{90} values in Table 1).

Comparing wheat and canola

For production of dried shoots and grain, canola consistently had a larger c value than wheat (Table 1), indicating that the response curve to applied P was steeper for canola than wheat. Therefore, canola consistently required less applied P than wheat to produce 90% of the maximum yield of dried shoots or grain (PR_{90} values in Table 1). For dried shoots this was so for all harvests, including the first harvest at 51 DAS (Table 1).

Comparing wheat and lupin

For production of both dried shoots and grain, the value of c was always larger for lupin than wheat, except for dried shoots at 101 DAS (Table 1). The level of applied P required to produce 90% of the maximum yield was always smaller for lupin than wheat for production of both dried shoots and grain (Table 1).

Comparing lupin and canola

For production of dried shoots, the value of c was larger for canola than lupin, whereas for grain production, the value of c was larger for lupin than canola (Table 1). Lupin and canola required similar levels of applied P to produce 90% of the

maximum yield of dried shoots at 78 and 87 DAS, and canola required less applied P than lupin to produce 90% of the maximum yields of dried shoots at 101 and 121 DAS (Table 2). However, at maturity (172 DAS), lupin required less applied P than canola to produce 90% of the maximum yield of whole tops (shoots plus grain) and grain (Table 1).

Harvest index

For all 3 crop species at maturity, the harvest index (grain yield divided by yield of shoots plus grain [whole tops]) increased as more P was applied before reaching a plateau (Fig. 2). However, for canola the data were more variable up to about 0.15 g P/pot, with the index first increasing as more P was applied before decreasing then increasing again up to a maximum yield plateau (Fig. 2). Harvest index values on the plateau were similar for wheat and lupin, ranging from ~0.41 to 0.45, compared with ~0.3 for canola (Fig. 2).

Growth rates of dried shoots between harvests

Lupin had the largest growth rate from emergence of seedlings to the first harvest of shoots at 51 DAS (Fig. 3a). However, lupin growth rates were unaffected by the level of P applied because lupin shoots showed no response to applied P at the first harvest (Fig. 1). By contrast, at the first harvest dried shoots of both wheat and canola showed increasing growth rates with increasing levels of P applied until a plateau was reached, with growth rates being smaller for canola than wheat (Fig. 3a).

Between subsequent harvests all 3 species showed increasing growth rates with increasing levels of P applied until a plateau was reached (Fig. 3b-3f). Growth rates were largest for canola from the second to fifth harvests, followed by wheat, and then lupin (Fig. 3b-3e). However, growth rates of lupin and wheat were sometimes larger than for canola at nil-P and low levels of applied P (for example, lupin in Fig. 3b,

wheat in Fig 3d). At maturity (shoots plus grain at 172 DAS) growth rates were about similar for all 3 crop species (Fig. 3f).

Up to 121 DAS, the magnitude of the growth rates between successive harvests generally increased for all 3 crop species (compare values on y axes of Fig. 3a to 3e).

For canola, the relationship between growth rate and the level of P applied first sometimes increased, and then decreased, before increasing again up to a maximum yield plateau (Fig. 3c, 3d and 3e). However, there was no obvious plateau in Fig. 3d because growth decreased as levels of P were increased above 1.5 g P/pot.

P response efficiency up to each harvest

Lupin showed no response to applied P at the first harvest so no P response efficiency values could be determined for lupin at 51 DAS. When lupin produced larger yields than wheat and canola at nil-P and low levels of applied P at 78 and 87 DAS, lupin P response efficiency values started at their largest values for the nil-P treatment, and thereafter decreased as more P was applied, with the decrease flattening off as more P was applied (Fig 4b and 4c). Otherwise, for all 3 species, P response efficiency was negligible for the nil-P treatment and then rapidly increased to a large value for low levels of applied P in the steepest part of the yield v. level of P applied response curve (Fig. 4). Thereafter, P response efficiency decreased as more P was applied, with the decrease tending to flatten off (Fig. 4) as the yield v. level of P applied response curve reached the maximum yield plateau.

P concentration in shoots and grain

All 3 crop species showed large increases (responses) in P concentration measured in dried shoots or grain as the level of P applied was increased (Fig. 5). This was also so for lupin at the first harvest at 51 DAS, even though lupin shoots showed no response to applied P at this harvest (Fig. 1a). Indeed, at the first harvest, P concentrations in

dried shoots were largest for lupin when up to about 0.2 g P/pot was applied (Fig. 5a). P concentration measured in lupin shoots at the first harvest showed larger responses to applied P than wheat or canola, with the value of the c coefficient of Eqn 2 fitted to the data for the relationship between P concentration in shoots and the level of P applied being ~2-5 times larger for lupin than wheat or canola (Table 2). However, for the next 3 harvests (78, 87 and 101 DAS), the P concentrations in lupin shoots were smaller than P concentrations in wheat and canola shoots (Fig. 5b-d), with values of the c coefficient being from 7 to 160% larger for wheat and canola than lupin (Table 2).

For each level of P applied, P concentrations in grain were larger for canola than for wheat and lupin (Fig. 5g). However, for shoots at maturity, after removal of grain, P concentration was largest for wheat, followed by lupin, and was smallest for canola (Fig. 5f).

For all 3 crop species, for each level of P applied, the concentration of P measured in dried shoots tended to decrease as plants matured (Fig. 5).

P uptake pattern at different growth stages

Up to the first harvest (51 DAS), lupin accumulated much more P into shoots than wheat and canola, with canola accumulating the least P (Fig. 6a). The amount of P accumulated into shoots at 51 DAS was calculated by multiplying P concentration in shoots by yield of the shoots at 51 DAS (P content). Thereafter, at each harvest the P accumulated into shoots was calculated by subtracting P content in shoots at the previous harvest from P content in shoots at that harvest. Between 51 to 78 DAS, 78 to 87 DAS, and 87 to 101 DAS, canola consistently accumulated more P into dried shoots than the other 2 species (Fig. 6b, 6c, 6d). Lupin accumulated negligible P into shoots between 51 to 78 DAS and 78 to 87 DAS (Fig. 6b, 6c). Between 87 to 101

DAS, wheat and lupin accumulated similar amounts of P into shoots (Fig. 6d). Between 101 to 121 DAS, all 3 crop species accumulated similar amounts of P into shoots (Fig. 6e). At maturity (172 DAS), canola accumulated larger amounts of P into shoots plus grain, and into grain, than the other 2 species (Fig 6f, g). Lupin accumulating more P into shoots plus grain than wheat (Fig. 6f). Both wheat and lupin accumulated similar amounts of P into grain (Fig. 6g).

Diagnostic tissue testing for P

At each harvest, the relationship between yield of dried shoots or grain and P concentration in shoots or grain at the time of sampling, were mostly very different for each crop species (Fig. 7). Values for coefficients of Eqn 1 fitted to the data were different for the different crop species, with the species at each harvest having different maximum yield plateaus (*a* coefficient), different *b* values, and different values for both the *c* and *n* coefficients (Table 5). Consequently, at each harvest, diagnostic critical P (DCP values listed in Table 5), which is the concentrations of P in shoots or grain that were related to 90% of the maximum yield at each time of sampling, were different for each crop species. For shoot production, DCP values were larger for wheat than canola, and were smallest for lupin, except at 121 and 171 DAS, when values were smaller for canola than lupin (Table 5). In addition, DCP values for each crop species tended to decrease as plants matured (Table 5), because the P concentration in shoots of all 3 species decreased as plants matured (Fig. 5). For grain production, DCP values were largest for canola, followed by wheat, and then lupin (Table 5).

Prognostic tissue testing for P

The relationship between grain yield and P concentration in dried shoots at the first 3 harvests were sigmoid, particularly for lupin, which produced no grain for the nil-P

and first 5 levels of P applied (Fig. 8; and value of n coefficient of Eqn 1 >1.0 in Table 6). Maximum yield plateaus for grain production were largest for wheat and similar for canola and lupin (Fig. 8; see value of a coefficient in Table 6). Critical prognostic P (PCP values in Table 6), which is the P concentration in dried shoots that was related to 90% of the maximum grain yield, were calculated. PCP values were similar for wheat and lupin for shoots harvested at 51 DAS, were consistently larger for wheat than canola for shoots harvest at all 3 harvests, and were smallest for lupin shoots harvested at 78 and 87 DAS (Table 6).

Discussion

Size and P content of sown seed affected seedling results

This study showed that at the first harvest size and P content of sown seed markedly affected seedling responses to applied P of the 3 crop species. At this harvest, lupin, with the largest P content in sown seed, showed no shoot yield responses to applied P, produced the largest shoot yields (Fig. 1), had the largest growth rate between sowing and the first harvest (Fig. 3), and accumulated most P into shoots (Fig. 6). Canola, with the smallest P content in sown seed, showed visual responses to applied P first (~10 DAS), followed by wheat (~17 DAS), then lupin (~60 DAS).

Previous studies in the region, using seed of the same size for each species, showed that, for P deficient soil, increasing P concentration in sown seed increased yields of seedlings grown from seed of wheat (Bolland and Baker 1988) and lupin (Bolland *et al.* 1989; Thomson *et al.* 1992).

Applied P affected subsequent results

After the first harvest, the general order for the following was canola >wheat >lupin: shoot yield responses to applied P (Fig. 1), growth rates of shoots between harvests (Fig. 3), P response efficiency (Fig. 4), and accumulation of P into shoots between

harvests (Fig. 6). For grain production, all 3 species were about similar for all these factors, except canola accumulated most P into grain at maturity (Fig. 6).

Comparing wheat and lupin

In this study, lupin consistently required less applied P than wheat to produce 90% of the maximum shoot and grain yields (Table 1). For grain production, these data support results of the field study of Bolland and Barrow (1991), in which shoot yield responses to applied P were not measured. Though lupin does not form cluster roots, lupin roots have been found to secrete more carboxylate than wheat roots (Pearse *et al.* 2006), which may explain why lupin required less applied P than wheat in this study to produce 90% of the maximum shoot and grain yields.

However, comparisons between wheat and lupin reported in this glasshouse study, and in the field study of Bolland and Barrow (1991), differ from those reported in the field study of Brennan and Bolland (2001). Brennan and Bolland (2001) found that lupin required similar levels of applied P as wheat to produce 90% of the maximum yield of shoots, measured at ~123 DAS, and grain. A possible explanation is that the lupin cultivar (cv. Gungurru) used in the field study of Brennan and Bolland (2001) is susceptible to the fungal pathogen *Pleiochaeta setosa* (Kirchn), which in the region has been shown to infect lupin roots (*Pleiochaeta* root rot) and foliage (brown spot) from resting spores concentrated in the top 50 mm of the soil profile (Sweetingham 1990). Wheat and canola are not infected by *P. setosa*, so both are break crops for the disease (Sweetingham 1990). *P. setosa* has been shown to increase the P requirements of susceptible lupin cultivars for grain production in the region (Bolland *et al.* 2001). This may explain why, relative to wheat, lupin had a higher requirement for P in the field study of Brennan and Bolland (2001) than in this glasshouse study, or in the field study of Bolland and Barrow (1991).

Comparing wheat and canola

This glasshouse study, and our previous glasshouse and field studies (Bolland 1997, 1999; Bolland *et al.* 1999, 2006; Brennan and Bolland 2001), have consistently shown that canola roots are better able to access P from soil than wheat roots and required less applied P to produce near maximum yields. Previous studies have shown that canola plants have fine roots with many root hairs (Brewster *et al.* 1976), and under conditions of P deficiency, canola increases the length and density of root hairs (Foehse and Jungk 1983). Wheat plants also have fibrous roots. However, under conditions of P deficiency, canola plants secrete acid from just behind root tips (Grinsted *et al.* 1982; Hoffland *et al.* 1982a; Moorby *et al.* 1988), enhancing dissolution of P in soil, and increasing P uptake by canola roots (Gerdmann 1968; Hoffland *et al.* 1986a, 1986b; Haynes 1992). Consequently, in P deficient soil, the ability of canola plants to acidify soils near root tips close to plenty of fine root hairs may enable canola plants to take up more P from soil than wheat roots.

Comparing lupin and canola

In this study, to produce 90% of maximum shoot yield, canola required about the same level of applied P as lupin at 78 and 86 DAS, required 50-65% less P than lupin at 101 and 121 DAS, and ~76 more P than lupin to produce 90% of the maximum grain yield (Table 1). In the field study of Brennan and Bolland (2001) it was found that lupin required ~60% more applied P than canola to produce 90% of the maximum shoot yields (measured at ~120 DAS) and grain yields. So the results of Brennan and Bolland (2001) are similar to this study for shoots at ~120 DAS, but differ markedly for grain production. Again, a possible explanation is that the fungal disease *P. setosa* may have increased the P requirements for grain production of the *P. setosa* susceptible lupin cultivar used in the field study of Brennan and Bolland (2001).

Harvest index

In this study, the maximum yield plateau obtained for the harvest index v. level of P applied relationship in Fig. 2, was ~0.43 for wheat and lupin, compared with ~0.30 for canola. The lower harvest index typically found for canola than wheat has been attributed to higher energy requirements for producing oil in canola grain (Thurling 1974; Holmes 1980). The harvest index values obtained on the plateau for the 3 crop species in this study support values obtained in previous studies in the region for wheat (Anderson *et al.* 2000), lupin (Gladstones 1970; Perry *et al.* 1998), and canola, (Gunasekera *et al.* 2006).

Unusual trends in some canola data

For canola, for the relationships between the harvest index and level of P applied (Fig. 2), and in some cases for the relationship between growth rates of shoots and the level of P applied (Fig. 3), there were some unusual trends. For levels of P applied between 0.02 to 0.15 g P/pot, the relationships first increased, then decreased, before increasing again. We can offer no explanation for the dip in these relationships.

Critical tissue P test values

Where published data are available, the critical tissue P test values obtained in this study are within the range of values summarised by Reuter *et al.* (1997) for wheat, lupin and canola.

Plant symptoms for P deficiency

The P deficiency symptoms we described in this study were similar to those described for wheat by Snowball and Robson (1983), for lupin by Snowball and Robson (1986), and for canola by Mason (1991).

Conclusions

There were large differences among the 3 crop species for size and P content of sown seed, which affected early growth of the species. For all subsequent harvest there were large differences in how the species took up P from soil and used the P taken up to produce shoots and grain. Grain production is the relevant data for cropping. To produce 90% of the maximum grain yield, lupin required ~67% less P than wheat, canola required ~40% less P than wheat, and canola required ~75% more P than lupin. To test if the results of this study generally apply to other soil types, further research is required to test if the P requirements among the 3 crop species are similar for different soil types in the region. In addition, we think further research, similar to that of Pearse *et al.* (2006), should be conducted to determine processes in the rhizosphere of the 3 crop species affecting acquisition of P from soil, to help explain results obtained in this study, and in previous glasshouse and field studies, comparing the P requirements among the crop species.

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Table 1. Values for coefficients of the rescaled exponential (Mitscherlich) Eqn 1 fitted to data for the relationship between yield of dried shoots or grain (g/pot) and the level of P applied (g P/pot), and the level of P required to produce 90% of the maximum yield (PR₉₀, g P/pot)
Coefficients of determination (R^2) were >0.980 in all cases, most being >0.990

Crop species ^A	Coefficients				PR ₉₀ (g P/pot) ^B
	<i>a</i> (g/pot)	<i>b</i> (g/pot)	<i>c</i> (pot/g)	<i>n</i>	
<i>Dried shoots 51 days after sowing (DAS)</i>					
Wheat	0.304	0.183	5.9277	1.3310	0.262
Lupin	Lupin showed no shoot yield response to applied P				
Canola	0.133	0.069	14.4922	1.3310	0.100
<i>Dried shoots 78 DAS</i>					
Wheat	2.796	2.509	8.2742	1.1712	0.236
Lupin	3.018	0.968	8.6511	1.2709	0.131
Canola	4.612	4.393	13.3465	1.4440	0.132
<i>Dried shoots 87 DAS</i>					
Wheat	5.414	4.954	9.9943	1.2047	0.194
Lupin	4.906	2.527	13.1702	1.0000	0.124
Canola	8.064	7.466	15.2034	1.3157	0.121
<i>Dried shoots 101 DAS</i>					
Wheat	9.526	8.711	7.8943	0.8125	0.337
Lupin	7.651	4.463	6.2788	1.2498	0.251
Canola	14.168	12.975	13.2300	2.0441	0.112
<i>Dried shoots 121 DAS</i>					
Wheat	20.154	19.751	9.8540	0.8696	0.262
Lupin	15.417	11.588	8.0042	1.2107	0.223
Canola	26.503	26.184	15.6163	1.4941	0.112
<i>Dried shoots and grain (whole tops) at maturity 172 DAS</i>					
Wheat	36.105	34.951	8.4399	1.1040	0.249
Lupin	25.659	25.433	11.7420	2.6584	0.114
Canola	41.892	41.333	12.7937	1.4026	0.141
<i>Grain at maturity 172 DAS</i>					
Wheat	15.860	16.618	6.7403	1.3016	0.280
Lupin	12.116	12.378	12.9536	5.1406	0.091
Canola	12.441	11.939	9.6304	1.8860	0.160

^AWheat, *Triticum aestivum* L. cv. Wyalkatchem; Lupin, *Lupinus angustifolius* L. cv. Kalya; canola, *Brassica napus* L. cv. Hyden.

^BValue of the *a* coefficient of fitted Eqn 1 was used as the maximum yield to calculate PR₉₀ values for each crop species at each harvest.

715 **Table 2. Values of coefficients of exponential (Mitscherlich) Egn 2 fitted to data for the**
716 **relationship between P concentration in dried shoots or grain (g/kg) and the level of P applied (g**
717 **P/pot)**
718 Coefficients of determination (R^2) were >0.869 in all cases, most being >0.940
719

Crop species ^A	Coefficients		
	<i>a</i> (g/kg)	<i>b</i> (g/kg)	<i>c</i>
<i>Dried shoots 51 days after sowing (DAS)</i>			
Wheat	14.327	12.188	2.606
Lupin	9.145	7.387	12.267
Canola	7.426	6.107	6.920
<i>Dried shoots 78 DAS</i>			
Wheat	8.565	6.811	3.435
Lupin	3.656	2.360	3.213
Canola	5.622	2.222	4.015
<i>Dried shoots 87 DAS</i>			
Wheat	8.022	6.684	4.967
Lupin	3.431	2.237	1.834
Canola	7.281	6.047	4.821
<i>Dried shoots 101 DAS</i>			
Wheat	7.955	6.753	2.608
Lupin	5.483	4.621	1.385
Canola	7.108	6.241	3.499
<i>Dried shoots 121 DAS</i>			
Wheat	5.403	4.543	3.279
Lupin	8.279	7.353	0.985
Canola	5.478	4.670	2.745
<i>Dried shoots at maturity after grain removed 172 DAS</i>			
Wheat	2.414	1.946	2.606
Lupin	1.143	0.965	6.520
Canola	1.382	0.865	2.122
<i>Grain at maturity 172 DAS</i>			
Wheat	4.524	3.730	9.540
Lupin	5.739	6.090	6.180
Canola	9.936	8.298	9.325

720 ^AWheat, *Triticum aestivum* L. cv. Wyalkatchem; Lupin, *Lupinus angustifolius* L. cv. Kalya; canola, *Brassica*
721 *napus* L. cv. Hyden.
722

Table 3. Values of coefficients of rescaled exponential (Mitscherlich) Eqn 1 fitted to data for the relationship between P content (P concentration multiplied by yield) accumulated in dried shoots between each harvest, and accumulated in grain (mg P/pot), and the level of P applied (g P/pot)
Coefficients of determination (R^2) were >0.956 in all cases, most being >0.990

Crop species ^A	Coefficients			
	<i>a</i> (g/kg)	<i>b</i> (g/kg)	<i>c</i>	<i>n</i>
<i>P accumulated into dried shoots from emergence to 51 days after sowing (DAS)</i>				
Wheat	4.333	4.162	2.534	1.066
Lupin	7.972	6.819	11.027	0.769
Canola	0.997	0.939	6.704	1.000
<i>P accumulated into dried shoots between 51 to 78 DAS</i>				
Wheat	21.781	22.281	2.820	0.879
Lupin	Did not fit Eqn			
Canola	25.709	26.197	7.510	0.895
<i>P accumulated into dried shoots between 78 to 87 DAS</i>				
Wheat	20.415	19.836	6.052	1.843
Lupin	5.017	4.722	1.776	0.703
Canola	32.548	32.932	4.206	1.281
<i>P accumulated into dried shoots between 87 to 101 DAS</i>				
Wheat	Did not fit Eqn			
Lupin	18.866	19.220	2.182	1.844
Canola	27.259	28.587	5.661	1.671
<i>P accumulated into dried shoots between 101 to 121 DAS</i>				
Wheat	34.442	33.641	5.277	1.766
Lupin	39.407	39.535	3.171	1.093
Canola	56.222	56.274	1.898	1.024
<i>P accumulated into dried shoots between 121 to 172 DAS^B</i>				
Wheat	19.813	20.601	6.031	1.224
Lupin	31.099	31.215	11.900	4.717
Canola	60.369	58.758	9.296	2.304
<i>P accumulated into grain at maturity (172 DAS)</i>				
Wheat	76.697	76.187	4.552	1.450
Lupin	78.017	82.197	4.513	1.128
Canola	121.325	120.829	7.380	2.018

^AWheat, *Triticum aestivum* L. cv. Wyalkatchem; Lupin, *Lupinus angustifolius* L. cv. Kalya; canola, *Brassica napus* L. cv. Hyden.

^BYields are for dried shoots plus grain (whole tops at maturity cut at soil level) and P concentration was for whole tops harvested at maturity after removal of grain.

Table 4. Values of coefficients of rescaled exponential (Mitscherlich) Eqn 1 fitted to data for the relationship between yield of dried shoots or grain (g/pot) and the concentration of P in shoots or grain (g/kg) at the time of sampling, and the concentration of P in shoots or grain that was related to 90% of the maximum shoot or grain yield (diagnostic critical P, DCP, g/kg)

Value of the *a* coefficient of the fitted equation was used as the maximum yield to calculate 90% of the maximum yield, and DCP values were calculated using the fitted equation

Coefficients of determination (R^2) were >0.944 in all cases, most being >0.980

Plant species ^A	Coefficients				DCP (g/kg)
	<i>a</i> (g/kg)	<i>b</i> (g/kg)	<i>c</i>	<i>n</i>	
<i>Dried shoots 51 days after sowing (DAS)</i>					
Wheat	0.331	0.253	0.144	1.452	11.30
Lupin	Lupin showed no yield response to applied P				
Canola	0.142	0.097	0.271	1.452	5.70
<i>Dried shoots 78 DAS</i>					
Wheat	2.842	2.495	0.226	3.438	6.80
Lupin	3.042	1.009	0.463	5.078	2.24
Canola	4.694	5.853	0.253	7.719	4.45
<i>Dried shoots 87 DAS</i>					
Wheat	5.394	5.524	0.273	2.261	5.32
Lupin	4.871	3.035	0.674	4.554	1.69
Canola	8.126	8.162	0.342	2.554	4.06
<i>Dried shoots 101 DAS</i>					
Wheat	10.386	22.989	0.707	0.711	6.94
Lupin	7.572	4.847	0.589	3.122	2.07
Canola	14.234	13.164	0.402	3.566	3.11
<i>Dried shoots 121 DAS</i>					
Wheat	18.636	19.045	0.546	2.601	2.53
Lupin	15.504	12.888	0.541	2.541	2.48
Canola	26.114	41.097	0.800	2.716	1.82
<i>Shoots at maturity 171 DAS^B</i>					
Wheat	35.955	37.220	1.020	2.854	1.32
Lupin	32.926	32.090	1.537	2.002	0.98
Canola	Data did not fit Eqns 1 or 2				0.75 ^C
<i>Grain at maturity 171 DAS</i>					
Wheat	Maximum yield plateau not defined (Fig. 6g)				4.20 ^D
Lupin	11.906	11.954	0.407	13.023	2.62
Canola	Data did not fit Eqns 1 or 2				8.20 ^E

^AWheat, *Triticum aestivum* L. cv. Wyalkatchem; Lupin, *Lupinus angustifolius* L. cv. Kalya; canola, *Brassica napus* L. cv. Hyden.

^BYields are for dried shoots plus grain (whole tops at maturity cut at soil level) and P concentration was for whole tops harvested at maturity after removal of grain.

^CEstimated from hand-fitted curve to canola data shown in Figure 7f.

^DEstimated from hand-fitted curve to wheat grain data shown in Figure 6g using the *a* coefficient for yield versus P applied data for wheat grain yield listed in Table 1 which had a well defined maximum yield plateau (Fig. 1g).

^EEstimated from hand-fitted curve to canola grain data shown in Figure 7g.

Table 5. Values of coefficients of rescaled exponential (Mitscherlich) Eqn 1 fitted to data for the relationship between grain yield (g/pot) and the concentration of P measured in dried shoots at 51, 78 and 87 days after sowing (DAS), and the concentration of P in dried shoots that was related to 90% of the maximum grain yield (prognostic critical P, PCP, g/kg)

Value of the *a* coefficient of the fitted equation was used as the maximum yield to calculate 90% of the maximum yield, and PCP values were calculated using the fitted equation

Coefficients of determination (R^2) were >0.923 in all cases, most being >0.985

Plant species ^A	Coefficients				PCP (g/kg)
	<i>a</i> (g/kg)	<i>b</i> (g/kg)	<i>c</i>	<i>n</i>	
<i>Dried shoots 51 days after sowing (DAS)</i>					
Wheat	15.807	15.753	0.163	2.951	8.15
Lupin		Data did not fit Eqns 1 or 2			8.00 ^B
Canola	12.560	11.971	0.220	4.424	5.47
<i>Dried shoots 78 DAS</i>					
Wheat	16.087	15.443	0.213	4.124	5.73
Lupin	12.267	12.632	0.505	13.623	2.11
Canola	12.577	12.633	0.256	12.866	4.52
<i>Dried shoots 87 DAS</i>					
Wheat		Maximum yield plateau not defined (Fig. 7c)			6.7 ^C
Lupin	11.789	11.796	0.664	88.656	1.75
Canola	12.516	11.932	0.270	4.486	4.44

^AWheat, *Triticum aestivum* L. cv. Wyalkatchem; Lupin, *Lupinus angustifolius* L. cv. Kalya; canola, *Brassica napus* L. cv. Hyden.

^BEstimated from hand-fitted curve to lupin data shown in Fig. 8a.

^CEstimated from hand-fitted curve to wheat data shown in Fig. 8c using the *a* coefficient for yield versus P applied data for wheat grain yield listed in Table 1 which had a well defined maximum yield plateau (Fig. 1g).

765 **Legends for figures**

766 **Fig. 1.** Relationship between yield of dried shoots or grain and the level of P applied at different
767 sampling times during growth of wheat (▲), lupin (■) and canola (◆). Lines are fits of rescaled
768 exponential (Mitscherlich) Eqn 1 to the data and the coefficients of the fitted equations are listed in
769 Table 1. Lupin showed no response to applied P at the first harvest so the line for lupin data in (a) is
770 the mean yield of all the lupin data.

771 **Fig. 2.** Relationship at maturity (172 DAS) between harvest index (yield of grain divided by yield of
772 dried shoots plus grain) and the level of P applied at different sampling times (harvests) for wheat (▲),
773 lupin (■) and canola (◆).

774 **Fig. 3.** Relationship between growth rates of dried shoots and the level of P applied at different
775 sampling times during growth of wheat (▲), lupin (■) and canola (◆). Growth rates were (a) from
776 sowing to the first sampling time at 51 DAS; (b)-(f) from the previous harvest to the present harvest.

777 **Fig. 4.** Relationship between P response efficiency and the level of P applied up to each sampling time
778 during growth of wheat (▲), lupin (■) and canola (◆).

779 **Fig. 5.** Relationship between P concentration measured in dried shoots or grain and the level of P
780 applied at different sampling times during growth of wheat (▲), lupin (■) and canola (◆). Lines are fits
781 of exponential (Mitscherlich) Eqn 2 to the data and the coefficients of the fitted equations are listed in
782 Table 2.

783 **Fig. 6.** Relationship between P content (P concentration multiplied by yield) and the level of P applied
784 for (a) P content accumulated into shoots from emergence to 51 DAS, (b) to (f) P content accumulated
785 into shoots between harvests, calculated, for each level of P applied, by subtracting P content for the
786 previous harvest from P content for the present harvest, and (g) P content accumulated into grain
787 calculated by multiplying grain yield by P concentration in grain. Data are for wheat (▲), lupin (■)
788 and canola (◆). Lines are fits of rescaled exponential (Mitscherlich) Eqn 1 to the data and the
789 coefficients of the fitted equations are listed in Table 3.

790 **Fig. 7.** At each time of sampling, relationship between yield of dried shoots or grain and the
791 concentration of P in shoots or grain, for wheat (▲), lupin (■) and canola (◆). Lines are fits of rescaled
792 exponential (Mitscherlich) Eqn 1 to the data, and the coefficients for the fitted equations are listed in
793 Table 4.

794 **Fig. 8.** Relationship between grain yield and P concentration measured in dried shoots at the first 3
795 sampling dates for wheat (▲), lupin (■) and canola (◆). Lines are fits of rescaled exponential
796 (Mitscherlich) Eqn 1 to the data, and the coefficients for the fitted equations are listed in Table 5.