Strategies and agronomic interventions to improve the phosphorus-use efficiency of temperate farming systems

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Abstract

- Background
  Phosphorus (P)-deficiency is a significant challenge for agricultural productivity on many highly P-sorbing weathered and tropical soils throughout the world. On these soils it can be necessary to apply up to five-fold more P as fertiliser than is exported in products. Given the finite nature of global P resources, it is important that such inefficiencies be addressed. For low P-sorbing soils, P-efficient farming systems will also assist attempts to reduce pollution associated with P losses to the environment.

- Scope
  P-balance inefficiency of farms is associated with loss of P in erosion, runoff or leaching, uneven dispersal of animal excreta, and accumulation of P as sparingly-available phosphate and organic P in the soil. In many cases it is possible to minimise P losses in runoff or erosion. Uneven dispersal of P in excreta typically amounts to ~5% of P-fertiliser inputs. However, the rate of P accumulation in P-sorbing soils is a major contributor to inefficient P-fertiliser use. We discuss the causal edaphic, plant and microbial factors in the context of soil P management, P cycling and productivity goals of farms. Management interventions that can alter P-use efficiency are explored, including better targeted P-fertilisers use, organic amendments, removing other constraints to yield, zone management, use of plants with low critical-P requirements, and modified farming systems.

- Conclusions
  Higher productivity in low-P soils, or lower P inputs in fertilised agricultural systems can be achieved by various interventions, but it is also critically important to understand the agroecology of plant P nutrition within farming systems for improvements in P-use efficiency to be realised.

Keywords: fertiliser, nutrient-use efficiency, organic phosphorus, phosphate fixation, phosphorus efficiency, soil fertility, sparingly-available phosphate
Phosphorus (P) is a primary limitation in most forest, weathered and tropical soils (Walker and Syers 1976; Lynch 2007) and P-deficiency is a significant challenge for agricultural productivity in these soils in many regions of the world. In many developing countries, especially in Africa, fertiliser use is low because it is already a relatively expensive input (World Bank 2004). Development of crops and farming systems that address P limitations in these agroecosystems is contributing to improved food security (Lynch 2007). P-fertilisers are used commonly in intensive agriculture in the developed world to build and replenish soil P reserves. However, P-fertiliser use in agriculture on soils that are moderate to highly P-sorbing, is often relatively inefficient with P-inputs being 2- (cropping systems) to 5-fold (grassland systems) higher than P-export in products (e.g. McLaughlin et al. 1992; Weaver and Wong 2011). High quality rock phosphate reserves are finite and there is an on-going debate about the longevity of global P resources (Cathcart 1980; Stewart et al. 2005; Cordell et al. 2009; Van Kauwenbergh 2010). Given the importance of P to the sustainability of agricultural production and global food security, and to ensure equitable use of scarce P resources, it is important that inefficiencies in P use in agriculture be addressed. The objective is to develop productive farming systems in which P-fertiliser inputs are reduced, and ideally much closer to equalling P-export in products (Helyar 1998; Syers et al. 2008).

P-fertilisers are applied to P-deficient soils to lift or maintain productivity per hectare. The objective is to achieve concentrations of plant-available P in the soil that enhance plant growth and allow the production goals of the farm to be met. The 'logical' upper boundary for soil fertility management is the 'critical P' requirement of the crop-soil system (usually defined as the soil fertility level corresponding to 90% or 95% of maximum yield (e.g. Peverill et al. 1999). Managing soil fertility near the critical P level is expected to maximise productivity. However, it is also legitimate to manage soil fertility at levels below critical P for a variety of farm business or environmental reasons (e.g. business risk mitigation and maintenance of ground cover, Mokany et al. 2010; native perennial grass persistence, Simpson and Langford 1996).
When P-inputs are very low, net extraction of P from soil occurs (Weaver and Wong 2011; McIvor et al. 2011) and production will not be sustained over the longer term. The risk of nutrient exhaustion thus sets a lower 'sustainability' boundary for soil fertility management. Even in low-production farm systems, there is a need for P-inputs that can at least cover the amount of P exported in products. The consequences of nutrient mining have already been observed in temperate Australian agriculture with a widespread decline in productivity of wheat recorded in the era before superphosphate and improved farming practices were adopted (e.g. Donald 1965; Angus 2001; Passioura 2002) and is also observed in some low input farming systems when inadequate amounts of fertiliser are applied (e.g. Burkitt et al. 2007). Similarly the consequence of nutrient depletion and the need to address fertiliser inputs to enhance productive agriculture on tropical African soils has been outlined (Sánchez 2010).

Ideal fertiliser management for a P-deficient soil will typically involve a phase in which soil P-fertility is increased, followed by a soil fertility maintenance phase in which soil P levels are held within a target range (Fig. 1). Variations on this pattern of management which involve periods of soil fertility increase followed by nutrient extraction within the logical and sustainable boundaries are also used for a variety of pragmatic reasons (e.g. unfertilised pasture phases using residual P from a preceding crop phase, Kohn (1974); aerial fertilisation of pasture at multi-year intervals in steep hill country, e.g. Scott 2000).

Although it is highly desirable that the P-fertiliser requirements of a production system are approximately equal to \( P_{\text{export}} \) irrespective of the soil P-fertility level being maintained (Helyar 1998; Syers et al. 2008), this is presently only achieved in farming systems operating with very low productivity, or on soils with low P-sorption capacity (Weaver and Wong 2011; Johnston and Syers 2009) where the risk of P-loss by leaching and lateral flow is often larger. It is a significant challenge to improve the P-balance efficiency of highly productive agricultural systems on soils with moderate to high P-sorption capacity without compromising productivity.
A framework for understanding P-efficiency

Although the reactions of phosphate with soil and the processes leading to P accumulation in soil are very complex (McLaughlin et al. 2011), it is possible to assess the options for improving the P-balance efficiency of a farming system by envisaging the main sources, flows and effective sinks for P in farming systems (Fig. 2). The amount of P held in the cycling pools of soil P (i.e. plant-available P) is the working capital of the soil and it is the concentration of plant-available P in this pool that determines productivity. This is often considerably above the concentration of available P in natural ecosystems because of the yield imperatives imposed by commerce, and the need to use water and land resources efficiently. For agricultural production to be maintained, the cycling pools of P must be maintained by fertiliser applications whenever P is removed or lost from this pool. In a system where plant-available P is being maintained at a stable concentration, the rate at which P must be applied ($P_{\text{fertiliser}}$) and the P-balance efficiency of the system (defined as $100\cdot P_{\text{export}}/P_{\text{fertiliser}}$) are determined by the rates of P removal or loss. This may be summarised as:

$$P_{\text{fertiliser}} = P_{\text{export}} + P_{\text{erosion/leaching}} + P_{\text{waste dispersal}} + P_{\text{soil accum}}$$

Where: $P_{\text{export}} =$ removal of P in products; $P_{\text{erosion/leaching}} = P$ lost by leaching, runoff or soil movement; $P_{\text{waste dispersal}} = P$ accumulated in small areas of farms as a result of uneven dispersal of animal excreta rendering the P less available; $P_{\text{soil accum}} = P$ accumulating as sparingly-available phosphate or organic P compounds that are slowly mineralised.

In a sustainable farming system, improvements in P-balance efficiency and thus long-term reduction in P-fertiliser requirements can ultimately only be achieved when fertiliser technology, agronomic, microbial or plant-based interventions lead to reductions in the P-loss or P-accumulation terms.
The strategies by which significant P-efficiency gains can be made

It is the purpose of this review to examine how management and agronomic interventions may improve the P-efficiency of agricultural systems, with emphasis on strategies that may modify the critical P requirement for optimal productivity. Strategies for direct manipulation of plants or microorganisms that facilitate greater acquisition of P from soil, or extraction of sparingly-available P that accumulates in agricultural soils when P-fertilisers are used are considered in an accompanying review (Richardson et al. 2011). Importantly, strategies that do not reduce the rates of P-loss or P-accumulation in agricultural systems will provide only short-term benefits and will make little difference to the effectiveness with which scarce P resources are used. Briefly, therefore, we first outline the rationale by which agronomic, plant or microbial strategies may minimise P-losses and accumulations enabling improved P-balance efficiencies.

P export in products

The objective of applying P-fertiliser is to increase or maintain agricultural production and it is inevitable that P will be exported in products. The amount of P exported in products sets the minimum amount of P that must be replaced by fertiliser applications if the farming system is to be sustained. In theory, it is feasible to reduce P-fertiliser inputs by selecting for productive plants that have lower internal P concentrations, or by developing farm products that have a lower P content that leads to lower P_{export}. However, it is interesting to note that, currently, agricultural enterprises that export more P-intensive products (e.g. grains, dairy products) tend to be those with higher P-balance efficiency (McLaughlin et al. 1992; Weaver and Wong 2011). P-balance efficiency and economic efficiency ($return per unit P_{fertiliser}$) will also be lifted by any practice that addresses constraints to yield and leads to increased P_{export} per unit of P input. However, attempts to reduce P_{export} by reducing the level of production will be counterproductive because production per hectare will be low, profitability compromised, and the farm system will not be using land or water resources efficiently.
P-losses (erosion, runoff and leaching)

Reducing loss of P from a farm system, other than in farm products, will directly improve P-balance efficiency. In many systems, P loss due to erosion and runoff should be a relatively small component of the P-balance of the farming system when best-practice management is followed (e.g. appropriate forms and placement of fertiliser, appropriate timing of fertiliser in relation to rain and crop growth, use of soil amendments to reduce nutrient transport, use of buffer strips to capture mobilised nutrients and attention to ground cover: Nash and Halliwell 1999; Mathers et al. 2007). Losses due to leaching can vary considerably with soil type, fertiliser management and plant species. Farming systems on soils with moderate to high P-sorption capacity are usually subject to relatively small losses (<0.4% - <5% of applied P, Ridley et al. 2003; McCaskill and Cayley 2000; Melland et al. 2008). However, those on low P-sorbing soils with poor P retention capacity can experience very large P-losses (43% - 69% of applied P: Lewis et al. 1987; Ozanne et al. 1961) which need to be addressed for both financial and environmental reasons.

Waste product dispersal

Accumulation of P within paddocks, or within farm systems due to uneven distribution of excreta is a unique problem of livestock systems which involve grazing. Estimates of the relative size of this accumulation term for grazed paddocks are typically about 5% of the amount of P applied as fertiliser (e.g. Metherell 1994). Adjustment to farm management can address this accumulation to some extent and will make a contribution, albeit sometimes relatively small, to improved P-balance efficiency.

P accumulation in "non-equilibrating" pools in soil

When phosphate is applied to many soils as fertiliser, it is subject to continuing reactions with the soil and incorporation into organic matter that leads ultimately to accumulations of P (e.g. McLaughlin et al. 1990) in sparingly-available phosphate and organic P forms. In low-P soils
the processes leading to P accumulation, also manifest themselves over time as a decline in the residual value of freshly applied fertiliser (Barrow and Carter 1978). In early literature, the pools of sparingly-available phosphate were sometimes referred to as "irreversibly adsorbed" or "fixed", but these descriptors are technically incorrect. Phosphate is initially adsorbed to the surface of soil particles or precipitates with Ca, Al and Fe (Sample et al 1980; Pierzynski et al. 2005; McLaughlin et al. 2011). The continuing reaction of phosphate with the soil may also involve slow diffusion into the reacting soil particles (Barrow 1999). The forward sorption reaction is driven by the phosphate concentration in the soil solution and is considerably faster than the back (desorption) reaction that will occur when the soil solution phosphate concentration is depleted (Barrow 1983a; 1983b). Conceptually, the accumulation of P in slowly cycling organic matter is similar. The various components of organic matter that are returned to soil are mineralised at different rates depending on their chemical and physical protection (Krull et al. 2003). All organic matter, even the more resistant materials (e.g. humus) turnover, albeit sometimes at very slow rates (Krull et al. 2003). However, for a farming system being fertilised annually to maintain soil P fertility, the rate of organic P accumulation will be determined by those components of soil organic matter that take longer than a year to be mineralised.

P is expected to accumulate in an agricultural soil when P-fertiliser is applied to increase soil fertility (e.g. Bünneman et al. 2006; McLaughlin et al. 1990), but there are relatively few reports of the amounts of P that are accumulated in soil maintained under steady-state P-fertility conditions, where accumulation will be the net result of phosphate sorption/desorption reactions and the slowly cycling components of soil organic matter that release phosphate at rates slower than the rate of P supply necessary for commercial agricultural production. Two long-term experiments: a pasture-wheat crop rotation (Wagga Wagga, New South Wales [NSW], Australia; Helyar et al. 1997) which accumulated ~4.6 kg P ha\(^{-1}\) year\(^{-1}\) (P-balance efficiency ~60%), and a permanent pasture (Hall, Australian Capital Territory, Australia; Simpson et al. 2010) which accumulated ~7.3 kg P ha\(^{-1}\) year\(^{-1}\) when managed at near-optimal P fertility (P-balance efficiency ~20%), demonstrate how large the soil P accumulation term of the P-balance equation can be for moderate to high P-sorbing soils under relatively "stable"
soil P-fertility conditions. For accumulation of P to be reduced under these conditions, it would be necessary to shift the balance between phosphate sorption and desorption rates, and/or between the rates of soil organic P input and mineralisation.

Reducing the accumulation of sparingly-available phosphate

Barrow (1980c) cited lack of ability in many agricultural plants to access residual fertiliser phosphate and the very slow rates of phosphate desorption once phosphate had reacted with soil over long periods of time, as reasons for pessimism about the chances of finding plants that can usefully access sparingly-available phosphate. However, a limited number of species can lower the pH of the rhizosphere or are able to exude organic anions to establish the chemical conditions that increase phosphate desorption rates, depending on soil type (Barrow 2002; Gerke 1994). In the case of the much-studied white lupin (Lupinus albus L.), it is evident that citrate exudation from proteoid roots confers the ability to access P-pools that are poorly accessible to many other plant species (Gardner et al. 1983; Dinkelaker et al. 1989; Hocking et al. 1997) and, when grown in close association with other species, enables the companion plant to also access sparingly-available phosphate (Gardner and Boundy 1983; Horst et al. 2001, Cu et al. 2005). On the other hand, buckwheat (Fagopyrum esculentum Moench) which produces exudates with a lower pH in response to low-P conditions (Amann and Amberger 1989), has high P-uptake efficiency in calcareous soils (Zhu et al. 2002) but is less effective in soils dominated by Fe and Al phosphates (Otani and Ae 1996). Nevertheless, the general effectiveness of agronomic strategies intended to enhance phosphate desorption remains unclear as there are relatively few examples of crop species that gain substantial P nutrition benefits by these mechanisms.

It should also be possible to reduce the accumulation of phosphate by slowing the rate at which phosphate continues to react slowly with soil, making it less available for plant growth. The reactions of phosphate with soil are described in more detail by McLaughlin et al. (2011), but it is helpful to consider the empirical relationship between net phosphate sorbed by a soil
Ps = a \cdot c^{b1} \cdot t^{b2}

where: a approximates the amount of sorbing material in a soil, and $b1$ and $b2$ are coefficients that describe the shape of the sorption relationship. The coefficients vary widely between soils; however, $b1$ and $b2$ are reasonably well correlated when compared across a wide range of soils (Barrow 1980a; 1980b). In calcareous soils this equation also applies initially, but precipitation of calcium phosphates decreases the phosphate concentration of the soil solution to levels that are determined by the solubility product (Barrow 1980a).

In practice, Ps is found to vary somewhat between soils that differ in P-sorption capacity (Barrow 1973) and is influenced strongly by the $b1$ and $b2$ exponents that characterise each soil. Because $b1$ and $b2$ values tend to be correlated (Barrow 1980a; 1980b), Ps is expected to be influenced by the phosphate concentration at which soil solution is maintained in the generalised manner shown in Figure 3. This indicates that strategies that allow a farming system to be operated at lower soil phosphate concentrations should reduce the rate at which slow reactions of phosphate and soil lead to P accumulation and should consequently improve P-balance efficiency. The effectiveness of such a strategy will be greatest in soils with high $b1/b2$ values (where continuing sorption reactions with phosphate are slow but persistent) and least in soils with low $b1/b2$ values (where sorption reactions are not as persistent). It is expected that P-inefficiency in soils with low $b1/b2$ values will tend to be associated with other issues such a leaching losses. Field-scale evidence that this strategy can reduce P accumulation in paddocks comes from a study of sheep-grazing systems maintained at contrasting levels of soil P fertility (Simpson et al. 2010). Grazing systems operated at lower plant-available P levels accumulated substantially less P. However, distinctions between P accumulation in sheep camps, as sparingly-available phosphate in the soil, or as organic P were not reported.
Phosphorus application to pastures on low-P soils generally results in accumulation of organic matter and consequently organic P in the soil. The rate of organic matter accumulation in terrestrial systems is directly related to their net primary productivity and the subsequent rate of organic matter return to soil (Grace et al. 1998). Relationships are thus found between soil organic carbon accumulation and factors such as annual rainfall (e.g. Jackson et al. 2002) or P-fertiliser use (e.g. Williams and Donald 1957; Russell 1960a; 1960b; Kohn et al. 1977; Lewis et al. 1987; Chan et al. 2010) when these inputs regulate the net primary productivity of the system.

Rates of net organic P accumulation of the order 1.7 - 4 kg P ha\(^{-1}\) year\(^{-1}\) have been recorded for pastures on P-deficient soils (Williams and Donald 1957; Russell 1960a; 1960b; Barrow 1969; Kohn et al. 1977). Organic P is expected to accumulate in pasture systems when P is being applied at rates intended to increase soil fertility. However, there are few reports of the fate of P in soil in farming systems where plant-available P concentrations of the soil have been maintained at a stable concentration. The pasture-crop rotation experiment of Helyar et al. (1997) was managed in this way for 18 years and organic-P accumulation in the soil (a red earth) accounted for 2.2 - 3.0 kg P ha\(^{-1}\) year\(^{-1}\), or 19%-25% of the P applied annually as fertiliser. The range in accumulation rates was associated with the length of the pasture phase; rotations with shorter pasture phases accumulated less organic P. However, it is notable that accumulation of organic P is not inevitable, and is influenced by the farming system and/or management practices being employed. For instance, Bunneman et al (2006) also measured ~2 kg P ha\(^{-1}\) year\(^{-1}\) accumulating as organic P in soil under a wheat-pasture rotation, but observed no accumulation of organic P in soil under continuous cropping rotations.

When P-fertiliser applications are adjusted to maintain soil plant-available P levels in a steady-state condition, or the available P concentration of soil exceeds the critical P level for plant growth, the rate of organic P return to the soil should stabilise because primary
productivity is stable. However, soil organic carbon (and organic P) may continue to accumulate either because the capacity of the soil to retain organic matter (Baldock and Skjemstadt 2000; Six et al. 2002) has not been saturated, and/or a balance between the input of plant residues and the rate of mineralisation has not been reached (Baldock et al. 2007).

Fractionation of soil organic matter into physical or conceptual classes (Baldock and Skjemstadt 1999; Amelung and Zech 1999) permits the prediction of organic matter accumulation in soil because the organic matter fractions have characteristic turnover rates (Skjemstadt et al. 2004). It is clear that soil organic matter (and consequently organic P) accumulation will equilibrate at some point, but modelling of soil organic matter accumulation for a permanent pasture in southern NSW, Australia predicted that soil organic matter pools would only equilibrate after ~200 years of regular fertiliser applications in this particular farming system (Baldock et al. 2007).

The concept of eventual equilibration of organic P accumulation is supported by empirical data from farming systems fertilised over very long time periods: e.g. Park Grass (Rothamsted, UK) where after 100 years of superphosphate fertilisation, only low proportions of accumulated P (1%-6% topsoil, 10%-18% subsoil layers) were in the form of organic P (Oniani et al. 1973), and from various examples of soil organic carbon stabilisation as cited by Stewart et al. (2007). Unfortunately, the time frame for organic P equilibration may be sufficiently long that relying on the equilibration of soil organic matter concentrations to improve P-balance efficiency will not provide a timely solution to the issue of P-imbalance.

For P-balance efficiency to be improved by reducing the accumulation of organic P in soil, it will be necessary to increase the rates of soil organic matter turnover so that soil organic matter and organic P pools equilibrate at lower concentrations. Inevitably, the objective of reducing organic P accumulations by this route will compete directly with objectives to increase carbon storage in soils (Dalal and Chan 2001; Lal 2004).
The stoichiometric relationship between C:N:S in stabilised soil organic matter (soil humus) is relatively constant across a wide range of soils irrespective of wide variability of the ratio in fresh organic or particulate organic matter fractions. Variation in the latter fractions depends on the source materials and crop and soil management practices. However, C:P and C:organic P ratios of stabilised soil organic matter can vary considerably (Kirkby et al. 2011; Kirkby 2011). Presently, it is unclear whether the variation in C:P ratios of stabilised soil organic matter is a result of differences between analytical methods or reflects real differences in the composition of organic P in soils. If the stoichiometric ratios for C:N:S and C:P in soil organic matter prove not to be tightly coupled, it is possible that enhancing release of phosphate from specific organic-P compounds in soils by release of plant or microbial phosphatases (Richardson et al. 2005) could potentially lower net rates of organic P accumulation independently of effects on soil organic matter accumulation. Orthophosphate monoesters (e.g. phytate) have been identified as a major form of organic P in many soils and are accompanied by lesser amounts of phospholipids, nucleic acids, phosphonates and other compounds (Turner et al. 2005; Smernik and Dougherty 2007). However, large proportions of the soil organic P remain poorly identified as high-molecular-weight material that is intimately associated with the soil humic fraction and this currently limits our understanding of the opportunities for mobilising organic P reserves for plant growth (Guppy and McLaughlin 2009).

**Microbial contributions to organic P mineralisation and the cycling of P in soil**

Several key processes in the P cycle which affect the availability of P to plants are mediated by microbial processes (Oberson and Joner 2005; Turner et al. 2006; Richardson and Simpson 2011). Most significantly microorganisms decompose and mineralise P from organic soil amendments (manures, organic waste composites, plant residues) and soil organic matter. The soil microbial biomass itself represents a P pool containing at least 0.5% to 7.5% of total P in grassland soils, and 0.4% to 2.4% of total P in arable soils (Oberson and Joner 2005). The microbial P pool is highly dynamic because microorganisms react readily to changes in soil temperature, moisture and carbon availability.
Amendment of a soil with a carbon source stimulates microbial growth and this is paralleled by a rapid decrease of soil solution P concentration (Oehl et al. 2001; Bünnemann et al. 2004a; Fig. 4) and the temporary immobilisation of P in microbial biomass. Even under low-P conditions the microbial biomass can grow rapidly and may increase several fold when readily degradable carbon is available (Bünemann et al. 2004a). In the short term, this may occur in competition with plants for available P (Olander and Vitousek 2004). Plants themselves may promote microorganism growth by exuding readily-available organic carbon and nitrogen from the roots (Wichern et al. 2007), indicating that microbial immobilisation of P can be important in the rhizosphere. Moreover, a significant ‘priming-effect’ associated with enhanced mineralisation of soil organic matter has been demonstrated in the rhizosphere (Cheng 2009), suggesting potentially higher turnover of soil organic P around plant roots.

Radiotracer techniques have been used to estimate the recovery of P in microbial biomass from amendments added to soil. The recovery in the microbial biomass of P added as legume residues was 15% (Bünemann et al. 2004c) to 22-28% (McLaughlin et al. 1988). By contrast, only about 5% of mineral fertiliser P was incorporated in microbial biomass (Bünemann et al. 2004c; McLaughlin et al. 1988). This is because soil microorganisms are more likely to be limited by carbon and nitrogen than by P, even in soils with a low plant-available P content (Bünemann et al. 2004b; Ehlers et al. 2010). Studies using low-P soils suggest that microorganisms may also be able to access less-available P pools (Bünemann et al. 2004c; Ehlers et al. 2010), but further work is needed to verify this.

Microbial P is released when sources of readily-available carbon are depleted (Oehl et al. 2001), cells are disrupted, e.g. in response to changes in soil water content (Turner et al. 2003), or as a result of predation (Bonkowski 2004). Microbial P occurs as inorganic orthophosphate, polyphosphates and a range of organic compounds primarily as nucleic acids and phospholipids (Bünemann et al. 2008; Ehlers et al. 2010) that are readily mineralised in soil and are thus potentially available to plants (Macklon et al. 1997). In soil with moderate P-sorption capacity release of microbial P is accompanied by an increase in the water-extractable P (Oehl et al. 2001). On strongly P-sorbing soils the P released from
microbial cells may not remain available to plants, unless mineralisation has occurred in the rhizosphere. Increases in plant-available P follow drying and rewetting of soils are largely explained by release of P from disrupted microbial cells (Blackwell et al. 2009; Butterly et al. 2009; Grierson et al. 1998; Turner and Haygarth 2001). Significant fluctuation in microbial P in response to seasonal conditions and associated changes in plant-available soil P fractions has been observed in a number of field-based studies (e.g. Perrott et al. 1992). The challenge in farming systems for gaining any benefits from release of microbial P under these circumstances is to ensure that microbial P immobilisation and release is in synchrony with the P requirements of a crop or pasture.

Soil organic matter is also mineralised and inorganic P is released without inputs of fresh organic matter and without measurable changes in size of the microbial biomass. This process (basal mineralisation) is associated with continuous microbial P turnover (Oberson et al. 2001; Oehl et al. 2001). Radioisotopic P dilution techniques, corrected for microbial uptake of labelled P, indicate that net basal mineralisation rates across a range of soil types and farming systems are of the order 0.5 to 0.9 mg P kg soil\(^{-1}\) day\(^{-1}\) (Oehl et al. 2004; Bünemann et al. 2007). Higher rates of microbial turnover and net mineralisation occur in more deficient soils, and as such may contribute substantially to plant nutrition in low-input agro-ecosystems and natural ecosystems; this highlights the importance of sustained input and turnover of soil organic matter.

**Management options to improve the P-balance efficiency of agricultural systems**

There are a variety of options for addressing P-balance efficiency in crop and pasture systems. P-fertiliser placements and technology are reviewed by McLaughlin et al. (2011). Here we examine the potential for management interventions that affect the cycling of P, P-availability to plants and the potential for farming with plants known to exhibit P-efficiency attributes.

**Microbial activity and organic P cycling**
P-balance efficiency of many farming systems would be improved if it were possible to increase the rates at which sparingly-available organic P is mineralised and it is sometimes asserted that this may be achieved by enhancing the microbial activity of soil. Farming systems that receive animal manures regularly (i.e. either exclusively organic, or conventional systems that include manure return) maintain higher soil organic carbon levels (Leifeld et al. 2009). Soil microbial biomass and activity is also consistently higher in manured soils as opposed to those managed exclusively with mineral fertilisation (Table 1) (Fliessbach et al. 2007; Joergensen et al. 2010; Mäder et al. 2002). This translates into a higher soil microbial P pool with faster turnover (Oehl et al. 2001) and into higher basal soil organic P mineralisation under organic than conventional cropping with exclusively mineral fertilisation (Oehl et al. 2004) (Table 1). However, the different levels of microbial activity in the soils under the various management regimes (Table 1) were of lesser importance for the recovery of P from fresh manure by ryegrass plants grown in pots (Oberson et al. 2010), because recovery of fresh manure P in ryegrass shoots was lower than recovery of mineral P (24% to 35% for manure P; 37 to 43% for mineral P, Table 1). Recovery of fresh manure P was affected by the available P content of the soil and was lower in soils with higher plant-available P. Uptake of residual P was lower from organically managed soils than from conventionally managed soils. However, this result must be interpreted with care because the total and available P contents of soil were depleted more in organic systems than in the conventional systems as revealed by their P budget deficit (Table 1) (Oehl et al. 2002). Thus, yields in the organic systems were attained partly at the expense of soil P reserves, leaving less residual P in the soils (Oberson et al. 2010). P fractionation of these soils indicated that the more residual P is depleted, the less plant-available the residual P will be (Oberson et al. 1993). Soils under organic and conventional systems did not differ in NaHCO₃-extractable or NaOH-extractable organic P fractions (Oberson et al. 1993). However, total soil organic P was higher in the organic systems (Oehl et al. 2004) and as a consequence the sparingly-available organic P fraction tended to be higher (Oberson et al. 1993).
A series of farming systems studies on high P-sorbing tropical soils have similarly demonstrated how enhancing soil organic P, and consequently microbial activity, can increase the rate of P cycling and the plant-availability of P in grass-legume and grass-only pastures compared with native savannah (Oberson et al. 1999). A beneficial effect of grass-legume pastures on P cycling and P availability was also found in crop-pasture rotations (Gijsman et al. 1997; Oberson et al. 2001). Differences in crop or forage residue decomposition and P release rates suggest that managing the interactions of residue with soil may help to slow strong P sorption reactions (Friesen et al. 1997) and that P held in the soil microbial biomass is also protected, at least temporarily, from sorption. Although these experiments demonstrated that the rates of organic P mineralisation and the size of the microbial P pool could be enhanced in soils under different farming regimes, there was little evidence that higher microbial activity also rendered the sparingly-available soil P fractions more available for crop uptake. This conclusion has parallels to the study of Dann et al. (1996) who found uptake of P from rock phosphate was equally low on soils under organic or conventional cropping, suggesting that P-solubilisation activity was also not enhanced.

Minimising inefficiencies associated with waste and constraints to yield

**Removing constraints to crop yield**

Constraints to crop yield, other than those due to P-availability itself, can influence P-balance efficiency in two ways. In some cases (e.g. an additional nutrient deficiency), addressing the constraint to yield will increase the demand for P and may require additional fertiliser inputs. Additionally, when yield is constrained by factors that limit root growth and soil exploration (e.g. soil acidity, root diseases, soil compaction), alleviating the constraint will increase P export for a given level of P input and will directly improve P-balance efficiency. In reality, it is impractical for the published targets for soil fertility management (e.g. Moody 2007, Gourley et al. 2007) to recognise the existence of other constraints to yield and P will often have been supplied in excess of actual requirements when a yield constraint of any sort exists. Thus, the alleviation of any yield constraint will often improve P-use efficiency.
Acid soils are a clear example of a constraint to root foraging ability, plant yield and P-use efficiency. Acid soils are widespread (von Uexküll and Mutert 1995) and limit plant production when the trivalent aluminium (Al\textsuperscript{3+}) concentration in the soil solution is increased. Al\textsuperscript{3+} inhibits root elongation and reduces the capacity of Al-sensitive genotypes to take up nutrients and water for productive growth. Introduction of Al-resistance genes alone has been shown to increase efficiency of P uptake in barley due primarily to improved root growth and soil exploration (Delhaize et al. 2009). However, the best yield outcomes are achieved when lime applications are combined with the use of Al-resistant cultivars to overcome constraints associated with surface and subsurface soil acidity in cropping (Scott et al. 1997) and pasture systems (Scott et al. 2000). This is most probably because soil acidity inhibits the root-hair and rhizosheath development irrespective of their Al-resistance status (Haling et al. 2010), and this continues to affect the plant’s ability to capture soil nutrients under acid soil conditions.

Root diseases also impact directly on the efficiency with which a plant can capture nutrients. This is demonstrated by the large increase in wheat yields for Australia that accompanied the introduction of canola and improved break crops (Kirkegaard et al. 1997; Angus 2001). Breaking root disease cycles allowed yield responses to N-fertilisers that had previously only given irregular benefits (Passioura 2002). Persistent and widespread root diseases still plague annual crops (Harvey et al. 2001; 2008) and are endemic in perennial farming systems where break crops are not a practical option (Barbetti et al. 2007). Resolving these issues will also improve P-use efficiency.

Many other approaches to increasing productivity per hectare will improve P-use efficiency. New grass cultivars that tolerate high grazing pressure and enable higher stocking rates per hectare (Culvenor et al. 2009) or improved animal genetics (e.g. better feed conversion efficiencies; Arthur et al. 2004; Hegarty et al. 2007) are examples of innovative options for yield improvement, at least one step removed from soil fertility management, that will nevertheless improve P-use efficiency.
Targeted use of P-fertilisers

There are some obvious consequences for efficient agronomic practice revealed by considering typical production responses to fertiliser application. When P-fertilisers are applied to nutrient-poor soil, plant yield increases to a plateau where P no longer determines the yield (e.g. Fig. 5). Accumulation of sparingly-available phosphate, losses due to leaching, erosion and runoff, and accumulations due to uneven distribution of excreta will continue to increase at soil fertility levels beyond critical P, because their rates of accumulation or loss are P-concentration dependent. As there are no additional yield or financial benefits to be achieved at soil P-fertility levels in excess of critical P, there is no justification for operating farming systems at P levels greater than the critical level appropriate to the crop-soil system.

Critical P soil test values for various crop-soil systems have been reviewed and revised recently for southern Australia (Moody 2007; Gourley et al. 2007). These values can be used to demonstrate how well farmer practice aligns with ideal soil P management. The fertility status of soil samples submitted for commercial soil testing by farmers in south-eastern Australia were examined (Fig. 6). This was an imperfect sample of agricultural soils, because soil testing is used by only 40% of southern Australian farms (ABS 2007), but is presumed to reflect the situation for farmers highly motivated to use P-fertilisers. In addition, soil test values do not indicate the management reactions that they may evoke. For example, a high soil test value cannot always be regarded as indicating excessive fertiliser use if the reaction to it is to moderate P-fertiliser inputs. For these reasons we allowed relatively generous margins when interpreting the information in Figure 6, and have focussed on soil test values that are more than 1.5-fold above the expected critical value, or where more than 50% of samples from a district are well above the expected critical P value. Thus, all test averages below or to the left of the dashed lines are assumed to indicate acceptable practice because “high” tests are either close to the ideal for soil fertility management or are in the minority of test results. Although only three farming enterprise types were examined, the data indicated that industry-related cultures may be influencing fertiliser practice. For example, soil tests from all dairy locations showed high proportions of soils testing in the excessive soil P-fertility range, a conclusion supported by other studies (Lawrie et al. 2004; Burkitt and Coad 2006).
Recently, Burkitt et al. (2010) have challenged the trend to excessively elevated soil P concentrations by demonstrating that lower P inputs and short-term cessation of P-fertiliser applications can be viable options when soil fertility is in excess of critical P. However, the analysis of soil test results from all three enterprise types (Fig. 6) indicates that the concept of targeted P fertility management is not understood, or is not being followed on a reasonable proportion of the farms represented by this subsample of agricultural soils. This indicates there is scope to reduce fertiliser input costs and the potential for unnecessary P accumulation in agricultural soils by using existing technology to promote a more targeted approach to P-fertiliser use (e.g. Simpson et al. 2009).

Waste product dispersal

It is long established that nutrient cycling by grazing animals is important to the overall availability of nutrients and productivity of pasture-based systems (Haynes and Williams 1993). However, the tendency of livestock to deposit excreta disproportionately in "camps", under shade, or close to water and feeding points is also a component of poor P-balance efficiency in grazing enterprises. On flat and low slope areas, 25% - 47% of sheep dung, for example, may be deposited in only 5% - 15% of the total area of a paddock (Hilder 1966; Williams and Haynes 1992). A proportion of the P deposited in camps is returned to the rest of the paddock, but over long periods of time the uneven dispersal of P can lead to significant accumulation of P in a small area (Williams and Haynes 1992) effectively rendering this P unavailable for pasture growth. Where P audits of paddocks have been conducted, the accumulations are of the order 1 - 2 kg P ha\(^{-1}\) year\(^{-1}\) (typically 5% - 7% of the annual P input in fertilised systems: Williams and Haynes 1992; Metherell 1994; McCaskill and Cayley 2000).

The absolute rate of accumulation is proportional to the stocking rate and to the rate of P-fertiliser input, because it influences the P concentration of herbage and, consequently, of excreta (Rowarth et al. 1988). On steep hill country, livestock camp predominantly on flat areas of paddocks and substantially higher proportions of P are transferred from steep slopes to flatter areas, because higher proportions of excreta (e.g. 55% - 60% of urine and dung) are deposited in the camp area (Haynes and Williams 1993). Uneven distribution of nutrients across a farm is also not unusual, but is most often associated with regular patterns of stock
movement. This is a particular issue on dairy farms, for example, where nutrient concentrations are often highest in paddocks closer to milking sheds (Lawrie et al. 2004).

Although it has been suggested that rotational grazing instead of continuous grazing can reduce camping effects (Haynes and Williams 1993), there is little evidence that increasing the frequency of rotational grazing has any further benefit on the distribution of nutrient in paddocks (Mathews et al. 1994; 1999) or on the P-balance of the grazing system (Chapman et al. 2003). In contrast, stocking rate does influence the distribution of excreta with lower stocking rates having a disproportionately high deposition of excreta in camps (Hilder 1966; Williams and Haynes 1992). Any impacts of paddock subdivision or rotational grazing on the distribution of excreta will reflect the change in short-term stocking rate achieved by such interventions.

**Zone management and precision agriculture**

Productivity gradients in paddocks, whether a result of nutrient (N, P and K) gradients created by grazing animals (e.g. Matthews et al. 1994; Gillingham and During 1973) or as a result of topography, aspect, botanical composition, grazing preference or differences in soil type and depth (Murray et al. 2007), can result in ineffective use of P when it is applied uniformly across the landscape. The situation is analogous to uneven yield distributions in cropping paddocks which, when managed using variable rate technology, can significantly improve the net profitability of the crop (e.g. Passioura 2002). Hackney (2009) has shown that as P-fertiliser prices increase, differential fertiliser applications combined with grazing management to improve pasture utilisation, will increasingly deliver economic benefits from large paddocks that have uneven productivity (Fig. 7). Whilst yield mapping of crops is now an accessible technology and its use is increasing rapidly, it is more difficult in pasture-based systems to assess the existence of productivity gradients. Where large and easily identified differences in nutrient requirement can be identified (such as camp areas) differential fertilisation is easy and commonplace (e.g. Gillingham and During 1973). However, more complex or fragmented productivity patterns can now also be determined using 'passive' or 'active' ground level, airborne or spaceborne canopy reflectance sensing devices with or without
pasture modelling backup (Hill et al. 1999; Murray et al. 2007; Trotter et al. 2010). The resolution being achieved with these technologies now far exceeds that needed for zone management in pastures (e.g. Berni et al. 2009). When combined with GPS technology, productivity maps should enable variable rate fertiliser delivery in grazed landscapes.

However, because the plant-available nutrient status of soils cannot be mapped remotely, the spatial mapping of nutrient gradients (e.g. Kozar et al. 2002) to underpin variable fertiliser rate decisions is an expensive and rate-limiting step in development of this technology.

Low-P farming systems

The agronomic interventions mentioned so far serve to improve current practice by eliminating waste or unguided use of P-fertilisers. However, these practices will still only bring farming systems up to the levels of P-balance efficiency currently being achieved in the most productive agricultural enterprises, with P export being in the range of 15% (sheep grazing) - 50% (cropping) of P input (McLaughlin et al. 1992; Weaver and Wong 2011). The development of farming systems that are productive at low soil-P concentrations is a strategy likely to provide both environmental (lower P-losses) and efficiency (less P-accumulation) benefits.

Impact of prior fertiliser use

It has been demonstrated that previous applications of phosphate lower the P-sorption capacity of soil (Barrow et al. 1998; Bolland and Allen 2003; Burkitt et al. 2008) and increase the availability of subsequent fertiliser applications (Fig. 8; Bolland and Baker 1998). This phenomenon may have immediate significance for enterprises where there has been a long history of fertiliser use or over-investment in soil P fertility. However, for many soils the amounts of phosphate that need to have been applied previously to achieve a measurable improvement in the current fertiliser requirement of a crop will be relatively large. For the example shown in Figure 8, up to 599 kg P ha\(^{-1}\) had been applied in a single application 20 years previously to a low P-sorbing soil (phosphorus retention index = 35, Bolland and Baker 1998; Bolland and Allen 2003). It is not easy to predict whether applying smaller amounts of
P regularly would elicit the same change in sorption capacity (Barrow et al. 1998). However, at typical rates of P application, it would have taken up to 54 years of continuous fertiliser application to reach this level of P investment in this soil. The quantities of P-investment required to underpin large changes in P buffering capacity mean that this does not appear to be a management path that will achieve a rapid improvement in P-balance efficiency.

Biologically-fixed N versus fertiliser N

Legume-based pastures underpin the productivity of a majority of grazing and cropping enterprises in temperate Australia and New Zealand and are used to a lesser extent elsewhere in the world. Inputs of N via biological N-fixation are economically favourable, particularly in water-limited, extensive agriculture, but tend to be less favoured in well-watered environments with more intensive, high-value production systems (Moore 1970; White et al. 1978; Puckeridge and French 1983). In some farming systems, fertiliser-N has become the preferred N source (e.g. dairying, Mundy 1996; Eckard et al. 2003). The productivity of legume-based pastures depends on adequate nutrition of the legume and in many cases this translates to adequate supply of P. Forage legumes typically have the highest P-requirements of the plants that comprise a pasture system (e.g. Figs 5 & 9; Hill et al. 2005; 2010; Haynes 1980). Figure 5b demonstrates how it would be feasible to shift to N-fertilised pastures to achieve a substantial reduction in the critical soil P fertility levels necessary for pasture production. The final target levels for soil P management would then be determined by the requirements of the major grass species (e.g. Fig 10). A change such as this has already occurred in the dairy industry of southern Australia which was traditionally based on white clover (Trifolium repens L.) -perennial ryegrass (Lolium perenne L.) pastures with N-fixation estimated to provide about 70% of the N necessary to achieve potential production (Mundy 1996). However, as N applications have increased, it is now more likely that white clover will comprise 10-25% of the pasture mix and provide <20 kg N ha\(^{-1}\) year\(^{-1}\) (McKenzie et al. 2003). Unfortunately, the potential improvements in P-use efficiency that could accompany such a major change in nutrient management on dairy farms has not been appreciated, and the indications are that soil P-fertility has often been increased well beyond
where it needs to be for a legume-based system, let alone an N-fed, grass-based system (Fig.
6, Lawrie et al. 2004; Burkitt and Coad 2006).

The feasibility of shifting to N-fertilised pastures to gain improvements in P-balance efficiency
will rest on the future relative costs of P- and N-fertilisers and the prices obtained for
commodities produced in such systems. It is highly likely that N-fertiliser prices will increase
as the costs of energy and compliance with potential carbon emissions constraints rise. In
addition, the use of N-fertilisers will bring new environmental challenges. Losses of N from N-
fertilised dairy systems, for instance, have emerged relatively quickly as a major
environmental issue (Ledgard et al. 1996; Ledgard et al. 1999; Eckard et al. 2003) and have
been a significant issue in N-fertilised systems in Europe and North America for many years
(e.g. Bussink and Oenema 1998).

Farming systems that utilise soil organic P

The cycling of organic P underpins productivity and P-availability on all farms in every year.
For example, the organic P cycle is estimated to contribute ~52% of the P used annually for
pasture growth in a grassland production system in NSW, Australia (Simpson et al. 2007).
Although opportunities to increase the rate of organic P cycling are not easily accommodated
in many agricultural systems, soil organic matter is often used strategically as a nutrient
resource. In ley farming systems, soil organic matter (organic P) levels oscillate between
accumulation and mineralisation across the pasture and crop phases of farming systems
(White et al. 1978). Soil organic matter concentrations are increased during legume-based
pasture phases (e.g. Grace et al. 1995; Dalal et al. 1995; Helyar et al. 1997) and nutrients are
mobilised from soil organic matter and used during crop phases, bare fallows and continuous
cropping (e.g. White et al. 1978; Dalal and Mayer 1986; Dalal and Chan 2001; Bünemann et
al. 2006). Although the focus of soil organic matter management is usually transfer of N from
the pasture (legume) phase to the crop phase, P supply to the crop is also a consequence of
this form of resource management and some part of the generally better P-balance efficiency
of cereal crops (Weaver and Wong 2011) is attributable to net mineralisation of P from soil
organic matter during the crop phase.
Intercropping and phase farming

The ability of particular grain legumes to mobilise sparingly-available P has stimulated research to examine the possibility that P-efficient plants may be used to improve the availability of P from other crops by (i) mixing P-efficient with inefficient species in either crops or pastures (intercropping) or (ii) utilising the residues of the P-efficient crops for subsequent P-inefficient crops (crop rotation). The sorts of species that have been examined in this context include organic anion-exuding crops such as white lupin (Gardner and Boundy 1983; Hocking and Randall 2001; Cu et al. 2005), pigeon pea (Ae et al. 1990), faba bean (Li et al. 2007) and chickpea (Veneklaas et al. 2003), which are considered capable of accessing sparingly-available phosphate, or species thought capable of mobilising P from organic sources, e.g. chickpea (Li et al. 2003; Li et al. 2004) and cowpea (Makoi et al. 2010). The principle that P-mobilising species can enhance growth and P uptake by cereals when intercropped or rotated in P-deficient soil is well established. However, the majority of evidence comes from pot experiments where the crops were not grown to maturity and periods between 'rotations' were short. Enhanced growth and P uptake was demonstrated for wheat in pots intercropped with chickpea (Li et al. 2003), lupin (Cu et al. 2005; Kamh et al. 1999) and faba bean (Song et al. 2007), or by exploiting residues of white lupin and pigeon pea (Hocking and Randall 2001), faba bean and lupin (Nuruzzaman et al. 2005) as if in a rotation. Other evidence of positive responses by cereals in pot experiments include maize (Li et al. 2004) and barley (Gunes et al. 2007) intercropped with chickpea, and maize rotated after groundnut (El Dessougi et al. 2003).

Horst et al. (2001) considered that of the two management options, intercropping should lead to most efficient transfer of P, because the opportunity for re-sorption of mobilised phosphate would be less. However, field results have been mixed. Clear evidence that cereals can gain P that would otherwise not have been accessible has been reported (Gardner and Boundy 1983; Li et al. 2007), but in many cases the component species have poor yields because of interspecific competition (Gardner and Boundy 1983; Härder and Horst 1991; Härder et al. 2001).
In some cases, beneficial outcomes have been attributed to factors other than P-transfer, such as improved N nutrition and reduced allelopathy (Horst and Härdter 1994).

Intercropping is used widely in Africa and Asia, but its application for P nutrition benefits is not obvious in broadacre, highly mechanised cropping systems. Intercropping of lucerne and wheat (Harris et al. 2008), and of summer-active perennial native grasses and wheat (Millar and Badgery 2009) have both received renewed interest and, although feasible, crop yields are nearly always subject to competitive interference (with the possible exception of yields in wet seasons) (Harris et al. 2007a; 2007b). Henry et al. (2010) have examined the impact of 'intercropping' different lines of the same species (i.e. 'multilines' of common bean, Phaseolus vulgaris L) which differed in root architecture as a way of reducing the agronomic challenges of intercropping and achieving improved uptake of P and water. However, they found that root growth in competition varied with both soil treatment and genotype mix. The multilines did not suffer yield penalties but, against expectations, the root architecture differences were often not sustained and differences in P or water uptake, and yield advantages were only observed in a few cases.

Using phase farming to exploit the residues of P-efficient grain legumes for subsequent cereal crop(s) is considered likely to hold more promise (Hocking and Randall 2001; Richardson et al. 2009). However, it is not clear whether P extracted by plants in one phase of a rotation will be transferred successfully to a subsequent crop under field conditions. Positive responses have been reported from rotating maize after high P-efficiency genotypes of cowpea and soybean, but not after less P-efficient genotypes (Jemo et al. 2006). However, gains to maize P nutrition following P-efficient grain legumes in African studies were small and not considered sufficient to substitute for fertiliser application, particularly on high P-fixing soils (Horst et al. 2001; Kamh et al. 2002).

Research is required to extend the promising glasshouse experiments to the field where crops are grown to maturity and translocation of P to the grain occurs. It is necessary to determine the size of any potential P nutrition benefit under practical farming conditions and
how long the residual P benefit from organic anion-exuding crops can persist in the field. Limited work to date has shown that organic anion exudation and P uptake by chickpea and lupin was variable across a range of low P soils from Western Australia (Veneklaas et al. 2003). In another study and contrary to expectation, faba bean and chickpea grown in other low-P soils did not mobilise P from sparingly-soluble soil pools, pointing to a need for a better understanding of how and when these crops gain access to sparingly-available P (Rose et al. 2010).

Pasture and crop varieties with low P requirements
Plants with low critical P requirements have value in farming systems that are operated with widely contrasting soil P fertility regimes. At one end of the spectrum, plants with low P requirements can potentially lift production on soils where P fertility is low and P-fertiliser use is minimal, either through choice (e.g. low-input farms, Cornish 2009), socio-economic circumstance (e.g. subsistence agriculture Lynch 2007; Sánchez 2010), or because other factors are the primary constraint on the productivity of the farming system (e.g. low-rainfall farming, Pang et al. 2010b; extensive grazing systems, McIvor et al. 2011). By contrast, the P-balance efficiency of fertilised farming systems can potentially be improved if it is possible to maintain soils at lower plant-available P concentrations (e.g. Simpson et al. 2010) by using productive plants with low critical P requirements.

The agronomic potential of Australian native herbaceous legumes has been examined in recent years in an effort to harness their natural adaptation to low-P environments prone to drought stress (Table 2; Ryan et al. 2008; Dear and Ewing 2008; Ryan et al. 2009; Suriyagoda et al. 2010; Bennett et al. 2011; Bell et al. 2011). Whilst a number of promising species have been identified, the work showed that native species had few consistent productivity advantages over exotic species in low-P soil and there was no advantage in focusing solely on native plants adapted to low-P environments.

Productive species with low critical P requirements have also been identified for higher rainfall environments. Numerous pasture grasses fit this category of plants, including most of the
productive-volunteer and cultivated grasses used in temperate grasslands (e.g. Hill et al.
2005). Amongst the grasses are a few species with exceptionally low critical P requirements
(e.g. ryegrass (Lolium rigidum Gaud.), silver grass (Vulpia bromoides, V. myuros), Hill et al.
2010), grasses noted for vigorous growth in acid, infertile soils (cocksfoot (Dactylis glomerata
L.), Lolicato and Rumball 1994) and some native perennials with the capacity to capture
phosphate from less soluble sources (e.g. Austrodanthonia spp., Barrett and Gifford (1999);
Austrostipa spp., Marschner et al. (2006)). Unfortunately, P-efficient grasses do not have any
impact on the poor P-balance efficiency of legume-based temperate pasture systems
because they are grown in association with legumes (e.g. subterranean clover (Trifolium
subterraneum L.) and white clover (T. repens L.)) that have coarse roots, short root hairs and
are relatively inefficient with respect to P acquisition (Fig. 9; Ozanne et al. 1969; 1976;
Haynes 1980; Hill et al. 2006; 2010;). The pastures are fertilised to meet the P requirements
of the legume, because N-fixation by the legume drives overall productivity. It will be
necessary to find legumes with lower critical P requirements to improve the P-balance
efficiency of these pasture systems.

Interspecific differences exist in the critical P requirements of some of the keystone temperate
pasture legumes. For example, Medicago polymorpha L. has a higher critical P requirement
than T. subterraneum, which has a higher requirement than Ornithopus compressus L.
(Paynter 1990; Bolland and Paynter 1992; Paynter 1992). Differences in the P requirements
of some annual medic species (e.g. M. truncatula Gaertn, M. murex Willd, M. polymorpha;
Bolland 1997) and for some annual clover species (e.g. T. subterraneum, T. incarnatum L., T.
hirtum All; McKell et al. 1982) have also been reported. However, the results of these and
other studies are sufficiently fragmented that it is difficult to rank species reliably according to
their critical P requirements. A number of alternative pasture legume species have been
released as cultivars in the last 15 years in response to the need for adaptations to difficult
soils and other niche environments, higher levels of hardseededness, deeper root systems,
length of growing season and ease of seed production (e.g. Nichols et al. 2007). A few
appear to have promise for development of more P-efficient pasture systems (Table 2). The
clearest example is yellow serradella (Ornithopus compressus L.), which had a critical P
requirement ~55%-65% of that of subterranean clover (T. subterraneum) in field experiments in Western Australia (Paynter 1990; Bolland and Paynter 1992; Paynter 1992). However, P-fertiliser application rates recommended for serradella do not presently reflect its lower critical P requirement (Paynter and Bolland 2006).

Intraspecific variation in the P requirements of key pasture legumes has been claimed, in a few cases, to be as large as interspecific differences (e.g. Curll 1983; Gartrell and Bolland 1987). However, close examination of the evidence does not support these claims. A number of reports are compromised by comparisons of lines at differing physiological stages of development or at differing herbage yields. Nevertheless, there are a few studies that indicate significant intraspecific variation in the critical P requirements of some pasture legumes (e.g. subterranean clovers when compared at similar shoot weights, Jones et al. 1970; white clover populations from high- and low-P soils, Snaydon and Bradshaw 1962). In general, however, the P requirements of keystone pasture legumes and the newer, alternative species are ill-defined and there have been few demonstrations that pastures can be highly productive at lower soil P fertility levels when P-efficient legumes are used.

There are significant differences in the critical P requirements of some of the mainstream crops used in temperate cropping rotations. Comparisons of wheat (Triticum aestivum L.), narrow-leaf lupin (L. angustifolius L.), canola (Brassica napus L.) and the pasture legume, subterranean clover (T. subterranean L.) indicate that the critical P requirement of the narrow leaf lupin is marginally (10%; Brennan and Bolland 2001) or considerably greater (70%; Ozanne et al, 1976; Bolland 1992) than the critical requirements of wheat and subterranean clover (Ozanne et al. 1976). Wheat and subterranean clover, in turn, have critical P requirements that are 25%-60% larger than that of canola (Bolland 1997; Brennan and Bolland 2001; Brenna

Because the critical P rankings of these crops are reasonably consistent, it is likely that better (targeted) management of soil P-fertility can be achieved across cropping rotations than is practised currently. However, experimental results occasionally indicate wide fluctuations in the critical P requirements of crops (e.g. Bolland 1992) suggesting that other factors such as root diseases, mycorrhizal status or
environmental constraints may alter P-requirements and may need to be considered when developing management guidelines.

Substantial intraspecific variation in P-use efficiency has been reported for a number of major crops: e.g. wheat (*Triticum aestivum* L., Gahoonia and Nielsen 1996; Manske et al. 2000; Osborne and Rengel 2002; Liao et al. 2008), barley (*Hordeum vulgare* L.; Gahoonia and Nielsen, 1996; Górny and Sodkiewicz, 2001), rice (*Oryza sativa* L., Fageria and Baligar 1997a; Wissuwa et al. 2002), maize (*Zea mays* L., Zhu and Lynch 2004; Fageria and Baligar, 1997b), brassicas (*Brassica oleracea*, Hammond et al. 2009), common bean (*Phaseolus vulgaris* L., Yan et al. 1995; Fageria and da Costa 2000) and cowpea (*Vigna unguiculata* L., Krasilnikoff et al. 2003). Most often, P-use efficiency is associated with root traits that enhance root length density, root length, root growth rate and root surface area (e.g. Manske et al. 2000; Lynch 2007, Liao et al. 2008). Indeed, Lynch (2007) has argued that improvement in P-use efficiency will be achieved more effectively by selecting for improved P-acquisition efficiency (i.e. root traits) rather than improved P-utilisation efficiency (yield per unit of internal P). There are several reasons for this argument including the likelihood that shoot traits affecting nutrient-use efficiency will be confounded with other traits of interest to breeders, and because root traits represent an essentially untapped pool of useful phenotypic variation. However, Wang et al. (2010) argue that many crop cultivars already have a relatively high P-uptake capacity but are poor at mobilising and reusing internal P. They argue that improvements in P-utilisation efficiency will be necessary for nutrient efficiency in crops grown under modern intensive cropping systems.

**Ecophysiology of nutrient acquisition in crops, plant communities and the rhizosphere**

There are numerous examples at various levels of system organisation that can be used to illustrate the importance of understanding the ecophysiological context of P nutrition, if P-efficiency gains are to be realised. In many instances, ecophysiological considerations override seemingly reasonable strategies for the use and development of P-efficient plants. For example, it has already been noted when considering the possibility of intercropping white lupins and less P-efficient crops, that interplant competition can negate the potential benefits...
of accessing sparingly-available P in the soil. Similarly, experience tells us that introduction of a new P-efficient species to replace less efficient, but well adapted crop or pasture plants will inevitably be difficult.

An example of the difficulty of capturing the P-efficiency benefits (i.e. access to less soluble P-sources; Barrett and Gifford 1999) by a native Australian perennial grass (*Austrodanthonia* spp.) is illustrated in Figure 10. This grass dominated the botanical composition of a grassland on low-P soil used for fine wool production (Bolger and Garden 2002). However, the subterranean clover content of the pasture (consequently legume N-inputs) and overall production was constrained by P-deficiency. To improve stocking carrying capacity, profitability, water and land-use efficiency the system was fertilised with increased rates of P-fertiliser but competition from annual species that flourish under improved soil fertility, and higher grazing pressure in the more productive systems (e.g. Hill et al. 2005) combined to reduce the *Austrodanthonia* composition of the pasture and negated much of the potential contribution to the P economy of the farming system that *Austrodanthonia* could have made.

The importance of understanding the ecology of nutrient acquisition also extends to the efforts that need to be made to improve the nutrient acquisition efficiency of agricultural species. Plant improvement options fall into three broad categories: (i) strategies for improved soil exploration by roots, (ii) mechanisms that enhance the plant-availability of P from sparingly-available phosphate and/or organic-P sources, and (iii) plants that have high internal P-use efficiency. Plant improvement opportunities are discussed in more detail by Richardson et al. (2011) along with an assessment of how ecophysiological constraints can influence the outcome from plant breeding.

**Conclusions**

It is often asserted that plants with low critical P requirements will reduce the amount of P-fertiliser required in agriculture. This is true for the period in which a farmer is building soil fertility to a target level for long-term management as the soil fertility building phase will be
shorter, but the low critical P requirement does not directly improve P-use efficiency in the longer term. The benefit of low-P plants is derived indirectly because they allow agriculture to be operated at lower plant-available P concentrations. Once a target soil fertility level has been reached (at or below the critical-P requirement of the farming system), fertiliser use is the sum of P exported in products, P lost to the environment and P accumulated through poor distribution of waste products, or in sparingly-available pools of phosphate or organic-P in the soil. Only actions that reduce losses and accumulations of P will reduce the P-balance efficiency of agricultural systems.

Off-farm loss of P can be dealt with directly by implementing best-practice measures to minimise erosion and leaching and is often a small term in the overall farmgate P-balance for farms on soils with a moderate to high P-buffering capacity. However, for farms on soils with an intrinsically low P-sorption capacity (e.g. sands) or where P-buffering capacity is low, because of high soil-P fertility, the options for further reduction in the accumulation terms will be low and potential losses due to leaching will be high. Inefficiencies associated with P-accumulation in stock camps can be improved to some extent by attention to stock movements and by achieving more efficient P-fertiliser use through improved zone management.

In moderate to high P-buffering soils, phosphate accumulation in sparingly-available pools in the soil can be slowed by actions that reduce the concentration of plant-available P at which agriculture is operated. In the first instance, this must be addressed by eliminating the tendency for some farms to be managed at soil P-fertility levels well above the critical P level appropriate to the crop-soil system. Adoption of low critical-P plants and farming systems based on such plants will permit agriculture to be operated at a lower soil P concentration. The long-term benefit of low-P plants will be to reduce the rate at which phosphate continues to react with the soil. There are some crop and pasture plant species that fit this need, but they are limited in number, with only a few options available for immediate trialling and implementation. It is important to improve the P-use efficiency of plant species that are keystone for food and fibre production. Success has been achieved in a limited number of
crops (e.g. Lynch 2007) but there are many key species for which relatively little real progress has been made, mainly through lack of consistent effort. Some success has been achieved by integrate plant species that naturally utilise sparingly-available phosphate and organic-P into conventional farming systems (e.g. intercrops), but success in other farming systems has been limited so far by ecophysiological and agronomic practicalities. Novel agricultural varieties that mimic these species are needed to provide a way to reduce P accumulation in soil by enhancing extraction from, or interception of P destined for accumulation in the sparingly-available P pools in soil. However, it is important that plant improvement activities be focussed on keystone crop and crop rotation species and, for pastures, the species (e.g. legumes) that drive the productivity of the system.

Acknowledgements

The authors thank Mark Conyers, Peter Cornish, Keith Helyar and Peter Randall for critical discussion of the ideas expressed in this paper. FAS and SES wish to acknowledge the Australian Research Council, the South Australian Grain Industry Trust and the Waite Research Institute for research support and AO thanks Else Bünemann and Emmanuel Frossard for stimulating discussions. Preparation of the review was funded in part by Meat and Livestock Australia Ltd and CSIRO's National Research Flagships Program’s Flagship Collaboration Fund which aims to enhance collaboration between CSIRO’s Flagships, Australian universities and other publicly-funded research agencies.
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Table 1. Phosphorus status and indicators of microbial P cycling in soils from a long-term field experiment established in 1978 to study the effects of farming systems on crop performance and soil fertility (Mäder et al. 2002), and the recovery of fresh and residual P in ryegrass grown in soils from the experiment. This trial included two organic systems (bio-dynamic and bio-organic), which were fertilised exclusively with animal manure and received no synthetic pesticides in contrast to the conventional systems. The manure treatments differed with composting of farmyard manure and aeration of slurry in the bio-dynamic system, and application of slightly decomposed manure and slurry in the bio-organic system. The two conventional systems were fertilised either with mixed mineral and organic fertilisation or exclusively with water-soluble mineral fertilisers. The systems also differed in the amounts of P applied, based on system-specific Swiss fertilisation guidelines (Oberson et al. 2010). A non-fertilised control was included. All systems followed the same crop rotation sequence and were ploughed using conventional tillage practices.

<table>
<thead>
<tr>
<th>Cropping system</th>
<th>Control</th>
<th>Bio-dynamic</th>
<th>Bio-organic</th>
<th>Conv. mixed</th>
<th>Conv. mineral</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type of fertilisers</td>
<td>None</td>
<td>Organic</td>
<td>Organic</td>
<td>Organic &amp; mineral</td>
<td>Mineral</td>
</tr>
<tr>
<td>P fertilisation (kg ha⁻¹ yr⁻¹)†</td>
<td>0</td>
<td>24</td>
<td>27</td>
<td>43</td>
<td>28‡ (41)</td>
</tr>
<tr>
<td>P balance (kg ha⁻¹ yr⁻¹)†</td>
<td>-21</td>
<td>-8</td>
<td>-6</td>
<td>+4</td>
<td>-5‡ (+6)</td>
</tr>
<tr>
<td>Water soluble P (mg kg⁻¹) §</td>
<td>0.05 a</td>
<td>0.4 b</td>
<td>0.6 c</td>
<td>1.9 e</td>
<td>1.0 d</td>
</tr>
<tr>
<td>Microbial P (mg kg⁻¹) §</td>
<td>4.7 a</td>
<td>11.8 b</td>
<td>13.0 b</td>
<td>12.1 b</td>
<td>6.6 a</td>
</tr>
<tr>
<td>Organic P (mg kg⁻¹) §</td>
<td>339 ns</td>
<td>379 ns</td>
<td>364 ns</td>
<td>352 ns</td>
<td>349 ns</td>
</tr>
<tr>
<td>Total P (mg kg⁻¹) §</td>
<td>563 a</td>
<td>640 bc</td>
<td>629 b</td>
<td>683 d</td>
<td>658 cd</td>
</tr>
<tr>
<td>Acid phosphatase activity</td>
<td>-</td>
<td>182 a</td>
<td>172 b</td>
<td>-</td>
<td>148 c</td>
</tr>
<tr>
<td>(mg paranitrophenol kg⁻¹ h⁻¹) ¶</td>
<td>-</td>
<td>-</td>
<td>2.5 b</td>
<td>1.7 a</td>
<td>-</td>
</tr>
<tr>
<td>P mineralisation (mg kg⁻¹ d⁻¹) #</td>
<td>-</td>
<td>27.6 a</td>
<td>24.8 a</td>
<td>-</td>
<td>31.8 b</td>
</tr>
<tr>
<td>Exchangeable P (mg kg⁻¹ d⁻¹) ††</td>
<td>-</td>
<td>9.1 b</td>
<td>7.0 ab</td>
<td>-</td>
<td>4.9 a</td>
</tr>
<tr>
<td>Mineral. P/ Exchang. P (%)‡‡</td>
<td>-</td>
<td>6.1 b</td>
<td>3.8 a</td>
<td>-</td>
<td>2.5 a</td>
</tr>
<tr>
<td>³¹P oxidation incorporation (%)§§</td>
<td>-</td>
<td>6.1 b</td>
<td>3.8 a</td>
<td>-</td>
<td>2.5 a</td>
</tr>
<tr>
<td>Manure P recovery in ryegrass ¶¶</td>
<td>35 c</td>
<td>28 ab</td>
<td>30 bc</td>
<td>24 a</td>
<td>29 abc</td>
</tr>
<tr>
<td>Mineral P recovery in ryegrass ¶¶</td>
<td>39 ns</td>
<td>39 ns</td>
<td>43 ns</td>
<td>37 ns</td>
<td>40 ns</td>
</tr>
<tr>
<td>Residual P recovery in ryegrass##</td>
<td>-</td>
<td>9 a</td>
<td>12 b</td>
<td>15 d</td>
<td>13 c</td>
</tr>
</tbody>
</table>

Values within a line followed by different letters are significantly different (Duncan’s multiple range test); ns = not significant.

† Average annual P fertilisation and P balance (difference between P inputs by fertilisers and outputs by harvested products) for 21 years of field experimentation (Oberson et al. 2010)
‡ During the first crop rotation period lasting seven years, the conventional mineral system was used as an unfertilised control. The value in brackets therefore shows the average for the second and third crop rotation periods when it was fertilised as conventional mineral system
§ Data from Oberson et al. (2010)
¶ Data from Oehl et al. (2004)
# Basal organic P mineralisation rate per day assessed using isotopic dilution techniques (data from Oehl et al. 2004).
†† Quantity of inorganic P exchangeable within 1 day determined by isotopic exchange kinetics (data from Oehl et al. 2004).
‡‡ Ratio between quantities of daily mineralised organic P and isotopically exchangeable P.
§§ Percentage of applied $^{33}$PO$_4$ taken up by microorganisms five days after soil labelling; data from Oehl et al. (2001)
¶¶ Percentage of manure P and mineral P, respectively, taken up by four harvest of ryegrass (Oberson et al. 2010)
## Percentage of residual P (composed of plant-available soil P depleted in the non-fertilised control soil but not in the fertilised soils and of residual fertiliser P remaining in the fertilised soils) taken
Table 2. Some niche species recognised for reasonable productivity in low P soils and/or low rainfall environments

<table>
<thead>
<tr>
<th>Species</th>
<th>Herbage type</th>
<th>Attribute(s)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ptilotus polystachyus</em> (Gaudich.) F. Muell.</td>
<td>short-lived native perennial herb</td>
<td>shoot weights greater than chicory (<em>Chicorium intybus</em> L.) in low-P soil</td>
<td>Ryan et al. 2009</td>
</tr>
<tr>
<td><em>Kennedia prorepens</em> F.Muell., <em>K. prostrata</em> R.Br., <em>Glycine canescens</em> F.J.Herm</td>
<td>Australian native legumes</td>
<td>good growth relative to lucerne in low-P soil but does not tolerate high-P soil</td>
<td>Pang et al. 2010a; 2010b</td>
</tr>
<tr>
<td><em>Lotonomis bainesii</em> R.Br. <em>Bituminaria bituminosa</em> (L.) C.H.Stirt. var. <em>albo-marginata</em></td>
<td>exotic legumes</td>
<td>good growth relative to lucerne in low-P soil</td>
<td>Pang et al. 2010a; 2010b</td>
</tr>
<tr>
<td><em>Cullen australasicum</em> (Schltdl.)</td>
<td>Australian native legume</td>
<td>relatively tolerant of dry conditions; presently being developed as pasture species for low-P, low-rainfall cropping soils</td>
<td>Suriyagoda et al. 2010; Dear et al. 2007; Hayes et al. 2009</td>
</tr>
<tr>
<td><em>Lotus uliginosus</em> Schkuhr</td>
<td>exotic legume</td>
<td>good tolerance of low-P soil</td>
<td>Balocchi and Phillips 1997; Kelman 2006</td>
</tr>
<tr>
<td><em>Trifolium ambiguum</em> M.Bieb</td>
<td>Caucasian clover</td>
<td>good tolerance of low-P soil</td>
<td>Virgona and Dear 1996</td>
</tr>
<tr>
<td><em>Biserrula pelecinus</em> L.</td>
<td>exotic legume</td>
<td>deep-rooted species, adapted to acid sandy soils and claimed to tolerate low-P better than subterranean clover (<em>T. suberraneum</em> L.) and burr medic (<em>M. polymorpha</em> L.)</td>
<td>Howieson et al. 2000</td>
</tr>
</tbody>
</table>
Figure legends

Figure 1. (a) Extractable soil P concentration (Olsen et al. 1954) of surface soil (0-10 cm) in paddocks that received P-fertiliser to increase and then maintain soil P fertility (squares) or received no fertiliser (circles) at CSIRO’s Ginninderra Research Station, Hall, ACT, Australia. The target range for soil fertility management in the fertilised grazing system is delineated by the dashed lines and the times that fertiliser was applied are indicated by the arrows. Pastures were grazed continuously by 18 yearling Merino wethers ha\(^{-1}\) (fertilised pasture) or 9 wethers ha\(^{-1}\) (unfertilised pasture). (b) Annual amounts of P applied to the fertilised pasture. Fertiliser amounts were intended to achieve the target soil fertility after each application. The soil fertility build-up phase was characterised by the need for higher but decreasing amounts of P fertiliser; the maintenance phase by a lower more stable P input requirement. Fluctuations in the extractable soil P concentration reflect the consequences of P-fertiliser applications and typical seasonal variations in P availability (from Simpson et al. 2010).

Figure 2. Diagrammatic representation of the inputs, flows and outputs of P in agriculture illustrating the potential components of the P-balance of a farming system (modified from Helyar and Godden 1976).

Figure 3. Generalised relationships between the rate of the continuing reaction of phosphate with soil (Ps) and the concentration of phosphate in soil solution (C) at a given point in time (t), for soils with differing phosphate reaction capacities, where: \( Ps = a.C^{b1}.t^{b2} \) Coefficient a is assumed to be constant, and \( b1 \) and \( b2 \) are assumed to be correlated according to the relationship observed by Barrow (1980b).

Figure 4. Changes in (a) water soluble inorganic P, and in (b) soil microbial P during incubation of soil taken in plots under bio-organic farming. One set of samples was amended with glucose (3 g kg\(^{-1}\)) and NH\(_4\)NO\(_3\) (C:N=10:1) while the other was not amended (modified from Figure 9, Oehl et al. 2001; used with kind permission from Springer Science+Business Media).
Figure 5. Yield responses of (a) silver grass (mixed sward of *Vulpia myuros* and *V. bromoides*) and subterranean clover (*Trifolium subterraneum*) to applications of phosphate in a glasshouse experiment (after Hill et al. 2005) and (b) grass-dominant (nitrogen-fed) and subterranean clover-rich pasture at Bookham, New South Wales, Australia showing critical P levels (corresponding to 90% of yield maximum) for each response function (arrow) (Simpson et al., unpublished).

Figure 6. Proportions of pre-season soil test results (January-April 2010) from 58 farming districts in south-east Australia that exceed the expected critical extractable-P level (Colwell 1963) for each soil sample (determined using the relationship Phosphorus Buffering Index and critical Colwell P; Gourley et al. 2007) and the average levels of excess (-fold) in these 'high' soil test results for beef-sheep, dairy or wheat enterprises. Wheat and legume-based pastures were assumed to have similar critical P requirements (Ozanne et al. 1976). Farming districts were identified by their Australian postcode. Test result numbers for each district ranged between 9-143 results per district (mean = 33) for beef-sheep enterprises; 9-457 results per district (mean = 75) for dairy enterprises and 5-164 results per district (mean = 28) for wheat enterprises. Each district was assigned an arbitrary identification number; where numbers are the same more than one farming enterprise was represented in that district. The results are for soil samples that had been submitted for commercial soil testing. Only results clearly identified by enterprise type and for soils with pH<7(CaCl$_2$) were used. Data supplied by J Laycock and C Walker, Incitec Pivot, Australia.

Figure 7. Anticipated net income from sheep grazing a hilly, 30 ha grassland at Barraga, New South Wales, Australia which had a fragmented productivity distribution due to differences in slope, aspect, soil chemistry and soil depth. Treatments were: superphosphate fertiliser applied uniformly (open bars), fertiliser applied uniformly with fencing to manage grazing patterns (hatched bars), or fertiliser applied differentially according to nutrient responsiveness and fenced to manage grazing patterns (closed bars) (from Hackney 2009; used with permission).
Figure 8. Effect of phosphate applied 20 years earlier on the response of wheat to newly applied phosphate. The original rates were: 0 kg P ha\(^{-1}\) (circles); 86 kg ha\(^{-1}\) (triangles); and 599 kg ha\(^{-1}\) (squares). Lines are fits to the Mitscherlich equation and are extended to the horizontal axis to indicate the amounts of P available from the original application (from Bolland and Baker 1998).

Figure 9. The relationship between critical external P requirement (amount of P applied to achieve 90% of maximum growth rate) and the relative rate of root cylinder development (a measure of root foraging capacity calculated as the volume of soil contacted by the roots from root length and diameter, and root hair length data) of companion species found in many temperate pastures in south-eastern Australia (redrawn from Hill et al. 2010).

Figure 10. Vegetation changes (1998-2001) in a temperate, native grassland after application of differing rates of superphosphate fertiliser to increase production and sheep carrying capacity (redrawn from Bolger and Garden 2002).
Figure 1

Soil fertility build-up phase  Soil fertility maintenance phase

Olsen extractable P
(mg kg⁻¹)

P applied (kg ha⁻¹)


Figure 3

Rate of continuous reaction of phosphate with soil (P_s) 

P concentration in soil solution (C) 
(arbitrary units)
Figure 4

(a) Water soluble P (mg L$^{-1}$) vs. Time (days)

(b) Microbial P (mg kg$^{-1}$) vs. Time (days)

Legend:
- Non amended
- + Glucose + N

LSD
Figure 5.

(a) Relative shoot yield (%) as a function of the amount of phosphate applied (mg P/pot).

(b) Pasture growth rate (kg DM/ha/day) vs. Colwell extractable P (mg P/kg).

Adapted from Hill et al. 2005

Simpson et al. unpublished
Figure 6

Proportion of Colwell P test results from each location that are above the expected critical soil test level

Average level of excess (fold)
Figure 7

[Bar chart showing net income ($) vs. superphosphate price ($ tonne⁻¹) for different fertiliser and subdivision scenarios: uniform fertiliser/no subdivision, uniform fertiliser/subdivision, differential fertiliser/subdivision.]
Figure 8

![Graph showing yield vs. fresh phosphorus applied]
Figure 9

A graph showing the relationship between critical P (mg pot^-1) and the relative rate of potential root cylinder development at low P (cm^3 cm^-3 d^-1). Different species are represented by different markers, including Trifolium subterraneum, Hordeum leporinum, Bromus molliformis, Phalaris aquatica, Microlaena stipoides, Arctotheca calendula, Austrodanthonia richardsonii, Lolium rigidum, and Vulpia spp.
Figure 10

(a) unfertilised; 7.3 wethers ha⁻¹

(b) 62.5 kg superphosphate ha⁻¹ yr⁻¹;
8.7 wethers ha⁻¹

(c) 125 kg superphosphate ha⁻¹ yr⁻¹;
11.5 wethers ha⁻¹

(d) 250 kg superphosphate ha⁻¹ yr⁻¹;
13.6 wethers ha⁻¹

- Perennial grass
(Austrodanthis spp.)
- Legume
(Trifolium subterraneum)
- Annual grasses
- “Other” species