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Review

Management of phosphorus nutrition of beef cattle grazing seasonally dry rangelands: a review

R. M. Dixon[A,E], *S. T. Anderson*[B], *L. J. Kidd*[C] *and M. T. Fletcher*[D]

[A]Queensland Alliance for Agriculture and Food Innovation, Centre for Animal Science, The University of Queensland, PO Box 6014, Rockhampton, Qld 4702, Australia.
[B]School of Biomedical Sciences, The University of Queensland, St Lucia, Qld 4072, Australia.
[C]School of Veterinary Sciences, The University of Queensland, Gatton, Qld 4343, Australia.
[D]Queensland Alliance for Agriculture and Food Innovation, Centre for Animal Science, The University of Queensland, Health and Food Sciences Precinct, Coopers Plains, Qld 4108, Australia.
[E]Corresponding author. Email: r.dixon2@uq.edu.au

Abstract. This review examines the effects of phosphorus (P) deficiency as a major constraint to productivity of cattle grazing rangelands with low-P soils. Nutritional deficiency of P may severely reduce liveweight (LW) gain of growing cattle (e.g. by 20–60 kg/annum) and the productivity of breeder cow herds as weaning rate, mortality and calf growth. In seasonally dry tropical environments, the production responses to supplementary P occur primarily during the rainy season when the nutritional quality of pasture as metabolisable energy (ME) and protein is high and pasture P concentration is limiting, even though the P concentrations are higher than during dry season. When ME and nitrogen of rainy-season pasture are adequate, then P-deficient cattle typically continue to gain LW slowly, but with reduced bone mineralisation (i.e. osteomalacia). In beef breeder herds when diet P is insufficient, cows with high bone P reserves can mobilise bone P reserves during late pregnancy and early lactation. Mobilisation may contribute up to the equivalent of ~7 g diet P/day (one-third of the P requirements) in early lactation, and, thus, allow acutely P-deficient breeders to maintain calf growth for at least several months until depletion of cow body P reserves. However, severe P deficiency in cattle is usually associated with reduced voluntary intake (e.g. by 20–30% per kg LW), severe LW loss and poor reconception rates. When P intake is greater than immediate requirements, breeders can replenish bone P. Replenishment in mature cows occurs slowly when ME intake is sufficient only for slow LW gain, but rapidly at ME intakes sufficient for rapid LW gain. Bone P replenishment also occurs in late-pregnant heifers even when losing maternal LW. Intervals of mobilisation and replenishment of body P reserves will often be important for P nutrition of beef breeder cows through annual cycles. Diagnosis of P deficiency in grazing cattle is difficult and must encompass estimation of both diet P intake and availability of P from body reserves. Cattle behaviour (e.g. pica, osteophagea), low soil P concentrations and low herd productivity provide valuable indicators. Some constituents of blood (plasma inorganic P, calcium, plasma inorganic P : calcium ratios and endocrine markers) are valuable indicators, but the threshold values indicative of P deficiency at various ME intakes are not well established. It is evident that knowledge of both the nutritional physiology and requirements for P provide opportunities to better manage P nutrition to alleviate production losses in low-input systems with beef cattle grazing rangelands.

Additional keywords: body P reserves, P mobilisation, P nutrition, P supplementation.

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Introduction

The importance of phosphorus (P) for numerous metabolic processes and the health and productivity of all animals, including cattle, is well established. Low concentrations of soil P for plant growth usually lead to low P concentrations in pastures and nutritional deficiencies of P in grazing beef cattle. Management of deficiencies of essential minerals, including P, for cattle grazing extensive rangelands is challenging (McCosker and Winks 1994; McDowell 1996; Ferguson and Sklan 2005). It is often difficult to identify unequivocally the cause(s) of poor productivity and to evaluate nutritional deficiencies of minerals, including P, among various classes of cattle through the annual cycle. P deficiency in such environments is usually addressed by P supplementation. However, in practice, it is often difficult to achieve target intakes of low-palatability loose mineral-mix or lick-block P supplements containing the P as calcium phosphates when fed free choice. The generally low productivity and profitability of cattle in extensive rangeland systems leads to generally low adoption of management changes and inputs as P supplements and P fertilisers even though, at least in the northern Australian rangelands, the economic returns from P supplementation of P-deficient cattle are excellent (Bowen *et al.* 2020).

The importance of P deficiencies in the nutrition of beef cattle in some rangelands in southern Africa was established early in the past century (Theiler and Green 1932) and was later recognised in many other rangeland regions (Rose 1954; Ferguson and Sklan 2005; Suttle 2010). Research with sheep, goats and both beef and dairy cattle (e.g. Field *et al.* 1975; Braithwaite 1986; Scott 1986; Breves *et al.* 1995) has extensively investigated the nutrition and physiology of P and its relationship to intakes of metabolisable energy (ME), protein and calcium. The substantial recycling of P to the rumen via saliva is well established (CSIRO 2007; Sathler *et al.* 2017); one consequence is that the supply of P as a substrate for rumen microorganisms appears to rarely constrain rumen microbial synthesis in cattle consuming forage diets. The knowledge and the nutritional requirements for P in relation to the requirements for energy, protein and other nutrients have been developed and described in feeding standards (AFRC 1991; CSIRO 2007). Understanding of the intricacies of P nutrition of cattle grazing seasonally dry extensive rangelands depends primarily on research from southern Africa and northern Australia. The outcomes of early field research with growing cattle in northern Australia were summarised by Kerridge (1990) and by McCosker and Winks (1994). With a paucity of information on the P nutrition of reproducing breeder cows at that time, their recommendations assumed that the nutrition and physiology of P in growing and breeder cattle were similar, except for higher P demands during late pregnancy and lactation. These recommendations were generally supported by studies on breeder cows grazing P-deficient pastures in northern Australia (Ternouth and Coates 1997; Miller *et al.* 1998) and in southern Africa (Read *et al.* 1986*a*, 1986*b*; de Waal *et al.* 1996; De Brouwer *et al.* 2000). More recent investigation of P nutrition in young growing steers through phases of deficiency and subsequent repletion (Bortolussi *et al.* 1996; Quigley *et al.* 2015), and in reproducing breeders (Anderson *et al.* 2017; Dixon *et al.* 2017), has substantially improved understanding of P nutrition of grazing cattle in tropical rangelands. This has established that there are major differences in the physiology of growing cattle and breeders that have important implications for the management of P nutrition in breeder herds.

The present review summarises aspects of P physiology and nutrition that are particularly relevant to management of beef cattle grazing seasonally dry rangelands in the tropics and subtropics, such as in northern Australia, South America and Africa. Seasonally dry environments with distinct rainy and dry seasons, with most cattle growth during the summer rainy season and undernutrition of cattle during the extended winter and spring dry season, create circumstances and demands for cattle management that may be very different from those of environments with more even distribution of rainfall and pasture growth. It is important that research be understood and interpreted with cognizance of the differences and limitations of seasonally dry environments and the consequences on cattle productivity.

P requirements

The P requirements of beef cattle and their wide variation with physiological state have been discussed in numerous reviews (AFRC 1991; CSIRO 2007). The P requirements of cattle losing or only maintaining LW are very low compared with animals with rapid growth of bone and soft tissues, or of cows in late pregnancy or lactation. The requirement of a cow during early lactation (e.g. producing 6 kg milk/day) and gaining LW rapidly (e.g. 0.6 kg/day) during the rainy season is about six times that of the comparable cow when not lactating, only maintaining LW and in mid-pregnancy, such as typically occurs in breeders when grazing mid-dry season pasture. The P required for LW gain (CSIRO 2007) is ~1.2 g P/kg soft tissue gain, but because LW gain will usually be associated with deposition of 6–7 g P in bone/kg LW gain, the total requirement is ~8 g P/kg LW gain (CSIRO 2007). Similarly, since milk contains ~1 g P/kg, substantial additional P is required during lactation.

Availability of P in feedstuffs

Estimation of the availability of P in feedstuffs is clearly essential in evaluation of diets to meet the P requirements of the animal. As Pfeffer *et al.* (2005) comprehensively discussed, several experimental approaches and methods have been used to calculate the proportion of diet P absorbed and available to the animal. Differences in the approaches and nomenclatures to measure and describe P absorption and availability have created confusion in the literature. Difficulties in evaluation are associated with (1) the extensive recycling of P to the rumen in saliva, (2) the excretion primarily in faeces of P surplus to the needs of the animal, (3) the efficiency of P absorption from the small intestine (as the principal site of absorption), which may be affected by the P intake in relation to the needs of the animal, and (4) potential P mobilisation from or deposition into the skeleton. Measurements are best made using a slope ratio-assay approach involving addition of P-containing feedstuffs as supplements to a base diet providing insufficient P for the needs of the animal so that measurements are in diet circumstances where animals will be forced to maximise P absorption (Pfeffer *et al.* 2005; Kiarie and Nyachoti 2010). In the past, radiotracer ^{32}P could be used to measure the endogenous P in faeces, so as to calculate a true rather than an apparent P digestibility; however, this technique can no longer be used. In addition, any mobilisation of P from body reserves during measurement will lead to an over-estimation of the absorption. Availability of P in a feedstuff is usually expressed in terms of the true absorption coefficient (TAC), which is the proportion of diet P that is absorbed from the small intestine during passage through the gastrointestinal tract. When the slope-ratio approach was used by Koddebusch and Pfeffer (1988), the TAC of P in lactating goats in two conventional feedstuffs (a temperate C3 dried grass and wheat bran) and two inorganic P sources (monocalcium phosphate (MCP) and dicalcium phosphate (DCP)) did not differ among the sources, and they were very high, averaging 0.93. As Pfeffer *et al.* (2005) pointed out, this value for net absorption efficiency is much higher than the 0.6–0.8 range reported in most published studies where diet P was often in excess of the animal requirements. The TAC measured using the slope-ratio assay is usually higher than that given in many previous reports and reviews, as summarised by Kiarie and Nyachoti (2010), and a general re-evaluation of the availability of P in feedstuffs for ruminants is needed. The availability of P in feedstuffs has also been investigated from the disappearance of P from feedstuffs in synthetic fibre bags incubated in the rumen. However, as Ibrahim *et al*. (1998) and Bravo *et al*. (2000) pointed out, microbial contamination of the feed residues in the synthetic fibre bag will cause under-estimation, and with forages containing low concentrations of P, potentially serious under-estimation, of the solubilisation and loss of P from the bag. Two additional difficulties are that (1) the loss of P from bags containing forages has generally not been described by first-order kinetics (Zanetti *et al*. 2017), as occurs with most constituents, and (2) there is no measurement of absorption of P from the gastrointestinal tract. This approach of measurement of P availability from incubation of feeds in synthetic fibre bags in the rumen, therefore, appears to be of limited value.

In the context of beef cattle grazing tropical pastures, a series of experiments at several sites in northern Australia are in accord with the hypothesis that the availability of P from such pastures is high. These experiments used ^{32}P tracer to measure the TAC of the P in tropical C4 grasses and grass–legume (*Stylosanthes* spp. or Siratro (*Macroptilium atropurpureum*)) pastures grazed by cattle during various physiological states and seasons. Results for growing cattle were summarised by Ternouth *et al*. (1996) and those for three experiments with pregnant or lactating breeders are given in Table 1. Because the pastures used were usually marginal or deficient in P, the measurements were made in circumstances where low diet-P intakes would likely have led to high net P absorption comparable to the slope-ratio measurements of Pfeffer *et al*. (2005). Ternouth *et al*. (1996) concluded that in growing cattle, when P intake was between 10 and 60 mg P/kg LW, the TAC of P was in the range 0.75–0.85 and averaged 0.79. The results for the breeder experiments (Table 1) were similar, although with a wider range. These TAC values were high compared with AFRC (1991) and led to lower revised estimates of the diet P requirements of cattle grazing tropical pastures (CSIRO 2007). However, these experiments also indicated that the TAC was much lower (~0.50–0.70) with low-quality senesced pastures where low intakes and low P concentrations in the pasture together led to low P intakes (<10 mg P/kg LW). This would occur with pastures containing less than half the P concentration required for LW maintenance and the low TAC would exacerbate P deficiency. Low availability of P might parallel low availability of nitrogen in senesced tropical grasses and may be associated with both the nitrogen and P being closely bound to indigestible fibrous material. The TAC values for tropical forages discussed above are comparable to more recent estimates for a temperate species forages (~0.73–0.77) summarised by Meschy (2003). In conclusion, a TAC of P of ~0.75–0.80 can usually be expected in tropical pastures.

Since calcium (Ca) phosphates and other forms of inorganic P are usually the most economical sources of supplementary P, the availability of the P in these feedstuffs is important. They are manufactured from rock phosphate deposits, but variation in the parent material and processing can produce a wide range of chemical products (e.g. 19 listed by Lima *et al*. 1995, 1999) as mono-, di- and tri- phosphates, and mixtures thereof, in the final product. The availability of P to animals can vary widely among these products. Only P in the phosphate form is absorbed from the small intestine, and the solubilisation of the Ca phosphates is considered to be usually the rate-limiting step for availability. There has been considerable investigation of the utility of *in vitro* measurements of the solubility of Ca phosphates as indicators of the availability of the P to animals. The solubility under standard conditions (e.g. 2 h) in water, in specified concentrations of dilute citric acid or hydrochloric acid (to mimic the low pH conditions of the abomasum), or in

Table 1. True absorption coefficient (TAC) of diet phosphorus (P) measured in three experiments in breeder cattle grazing grass or grass–legume pastures at two sites in a seasonally dry tropical environment in northern Australia

In each experiment, P kinetics were measured with ^{32}P tracer, diet selection and diet *in vitro* dry matter digestibility were measured with samples obtained from oesophageally fistulated animals, and voluntary intake was measured using chromic oxide as an external marker

Experiment	Location	Animal class, pasture and treatment	TAC	
			Mean	Range
Coates and Ternouth (1992)	Lansdown, Townsville	Heifers. Grazing *Urochloa* grass–stylo pastures with four treatments comprising three levels of P fertiliser or P fertiliser with additional supplementary P. Measurements were in the rainy, early dry and late dry seasons in heifers and lactating first-calf cows.	0.79	0.66–0.92
Ternouth and Coates (1997)	Lansdown, Townsville	Heifers were initially pregnant and later as lactating first-calf cows. Three treatments comprised *Urochloa*–stylo (±P fertiliser), or native pasture. Measurements were made in mid and late pregnancy (early and late dry season) and early and late lactation (early and late rainy season).	0.79	0.69–0.86
Miller *et al*. (1998)	Springmount, Mareeba	Reproducing breeders comprising two annual drafts each with six treatments comprising pastures of grass or grass–stylo (±P and non-protein nitrogen supplements). Measurements were in late pregnancy (late dry season), mid-lactation (mid-rainy season) and post-weaning (rainy–dry transition season).	0.78	0.50–1.03

alkaline ammonium citrate, have been investigated. A recent study (Table 2) and other studies lead to the several important conclusions. First, the classes as MCP, DCP and tricalcium phosphate (TCP) can be distinguished by their solubility in the various solutions. Solubilities of MCP, monodicalcium phosphate (MDCP) and hydrated DCP are high and similar in citric acid, but the solubility of hydrated DCP is lower in ammonium citrate. Furthermore, DCP can occur in hydrous or anhydrous forms, which have similar solubility in citric acid, but the anhydrous form is less soluble in ammonium citrate. The two forms can also be distinguished by the P concentrations and their loss of moisture on heating. TCP has moderate solubility in citric acid but is insoluble in ammonium citrate. Second, there may be substantial variation in the P concentration (Lima *et al*. 1995, 1999) and in the solubilities among samples of the same nominal class available as feedstuffs (Table 2). Third, a large number of studies have investigated the relationships between the solubility of the P in various Ca phosphate sources and the rates of increase in bodyweight or of bones or toes in growing chickens or turkey poults. There are large differences in the bioavailability of P among the classes of Ca phosphates, in general accord with the differences in the solubilities. For example, the availability of P in TCP and rock phosphates is very low compared with that in MCP, MDCP or hydrated DCP. Also, the availability for growing chickens of P in anhydrous DCP is much lower than that in hydrated DCP (Gillis *et al*. 1962; Van de Klis and Versteegh 1996). Some studies have reported good correlations and prediction of the biological value of growing birds of the P in MCP, MDCP and DCP from the *in vitro* solubility measurements, while other studies have reported poor relationships inadequate for prediction.

There appear to be no comprehensive studies with ruminants examining the relationships between the *in vitro* solubility of P in Ca phosphate and availability of the P for animal growth rate or performance. Furthermore, solubility of P in citric acid and ammonium citrate has usually been measured over 2 h, but the retention time of digesta in the abomasum in ruminants is 30–60 min; the P solubility over the longer interval may be misleading. The studies that are available generally support the hypothesis that P in mono- and monodi- is highly available, that most hydrous dicalphosphates have reasonable availability, and that the P in anhydrous DCP, TCP and rock phosphate have lower availability. The absence of useful predictive relationships between P absorption and the solubility of P in forage and concentrate feedstuffs in sheep (Field *et al*. 1984) does not support a hypothesis that P solubility in Ca phosphates can be used to accurately predict availability of P in ruminants of samples of the same nominal subclass of Ca phosphates. This is in accord with the conclusions of two recent reviews of the procedures to measure the availability of P in poultry (Shastak and Rodehutscord 2013; Li *et al*. 2016), which both concluded that the *in vitro* solubility procedures are not sufficiently reliable to be used to evaluate the biological availability of P for growing birds and that other approaches should be used. There does seem to be consensus that P availability in subclasses of Ca phosphates as described for monogastrics is also generally applicable to ruminants. In conclusion, the *in vitro* P solubility tests appear to be useful to categorise samples into classes of Ca phosphates, but not sufficiently accurate and reliable to be used to predict the P availability for ruminants from samples of the same class of Ca phosphates (e.g. among samples of hydrated DCP).

The consequences of P deficiency on productivity of growing cattle

Large LW-gain responses by growing cattle grazing P-deficient pastures to P supplements have often been reported (Winks 1990), but the magnitude and duration of such growth responses depend on many animal, pasture and soil factors, and, in particular, the degree of deficiency of soil P for plant growth and the duration of the interval when diet ME and protein are sufficient for an increased growth rate. Rangeland soils in northern Australia have been categorised on the basis of available soil P concentration (measured as P soluble in bicarbonate solution, P_B; Colwell 1963) as ranging from ‘adequate’ (>8 mg P_B/kg) through to ‘acutely deficient’ (<4 mg P_B/kg) in P for grazing cattle (Table 3). The concentrations of P in pasture and in blood of cattle grazing these pastures generally decrease correspondingly with a lower soil P_B (McCosker and Winks 1994). In the context of tropical rangelands, these authors suggested that growing cattle in ‘adequate’ P status are likely to be ingesting rainy-season pasture diets of >2 g P/kg DM. Cattle ranging from ‘acutely

Table 2. The concentration and solubility *in vitro* of phosphorus (P) in monosodium orthophosphate and in various classes of calcium phosphate inorganic P supplements following incubation for 30 or 120 min (mean and standard deviation in parentheses)
The number of samples (*n*) in each class of inorganic P is given (Gonzalez-Rivas 2012)

Source of P	*n*	Total P concentration (g/kg DM)	Solubility after 30 min (g/kg)			Solubility after 120 min (g/kg)		
			Water	Ammonium citrate	Citric acid	Water	Ammonium citrate	Citric acid
Monosodium orthophosphate (MSOP)	1	257 (–)	996 (–)	1000 (–)	991 (–)	1000 (–)	977 (–)	999 (–)
Mono calcium phosphate (MCP)	2	221 (14)	767 (53)	461 (45)	928 (51)	796 (59)	729 (59)	958 (45)
Mono-di-calcium phosphate (MDCP)	8	213 (6)	775 (83)	553 (78)	965 (43)	792 (86)	853 (139)	977 (25)
Dicalcium phosphate (DCP) (hydrated)	5	199 (10)	109 (151)	406 (148)	926 (141)	114 (168)	627 (90)	971 (22)
Dicalcium phosphate (DCP) (anhydrous)	1	195 (–)	15 (–)	232	888 (–)	16 (–)	473 (–)	980 (–)
Tricalcium phosphate (TCP)	2	190 (21)	0 (–)	0 (0)	379 (225)	2 (1)	0 (0)	654 (219)
Rock phosphate (RP)	6	108 (24)	2 (2)	0 (0)	171 (125)	6 (1)	0 (0)	287 (191)

Table 3. Indicative estimates of the concentrations of available phosphorus (P) in soil, of total P in pasture and of blood P in growing steers for the descriptive categories of P deficiency generally used for recommendations in the northern Australian cattle industry

In addition, indicative estimates of the likely liveweight-gain responses of growing cattle on commercial cattle farms to effective rainy-season P supplementation are given and are lower than those often observed in research trials (after McCosker and Winks 1994; Jackson *et al*. 2012). Reported responses to P supplements have ranged up to 140 kg LW/annum. Some extremely deficient soils may be <2 mg P/kg. For such soils, the concentrations of P in forage and blood P are likely to be lower and the animal responses to P supplement greater than for 'acutely deficient' soils. P_B (mg/kg), bicarbonate-extracted P (Colwell 1963) in the top 100 mm of soil. These results are not comparable with some other laboratory measures of available P (e.g. acid extraction). Growing cattle were sampled and measured late in the rainy season. Reported responses to P supplements have ranged up to 140 kg LW/annum

Attribute	Category of P status for grazing cattle			
	Acutely deficient	Deficient	Marginal	Adequate
Indicative soil P ($P_{B\ (mg/kg)}$)	<4	4–6	6–8	>8
Indicative forage-diet P (g/kg)	<0.5	0.5–1.0	1.0–1.5	>2.0
Indicative blood P concentration in growing cattle (mmol/L)	<0.8	0.8–1.1	1.1–1.6	>1.6
Likely liveweight response to P supplements by growing cattle				
Native pasture (kg/annum)	30–40	20–40	0–20	Nil
Stylosantes pasture (kg/annum)	45–70	40–60	0–40	Nil

deficient' to 'marginal' P status would likely be ingesting diets ranging in concentration from <0.5 through to 2.0 g P/kg LW. In circumstances where soil P is much lower than 4 mg P_B/kg, such as occur in some rangelands in southern Africa (<2 mg P/kg; Read *et al*. 1986*a*), and are likely to occur also in some regions of northern Australia, the P deficiency of grazing cattle will be more severe and responses to P supplements larger than is indicated in Table 3. The conclusion that cattle are likely to be adequate in P when soil P is >8 mg P_B/kg implies that cattle should be in adequate P status when grazing pastures on soils that do not require P fertiliser for cereal cropping.

Numerous experiments in northern Australia with growing cattle have reported that the growth responses of cattle grazing native pastures or grass–legume pastures to P supplementation are usually during the rainy season (Fig. 1), even though P concentrations are almost always higher in rainy-season than dry-season pastures. However, this is a consequence of the concentration of P in the diet relative to the availability of other nutrients, especially ME and protein. The key principle is that P is more likely the primary limiting nutrient during the rainy season when diet quality as ME, protein and potential voluntary intake are high. Conversely, in cattle grazing dry-season pastures, the intakes of protein and then of ME are limiting for LW gain and little response to supplementary P can be expected.

In the context of northern Australian rangelands, there is usually little effective rainfall after the end of the rainy season in about March, until the subsequent seasonal break, usually between November and January. The rapidly decreasing nutritive value of the C4 tropical grasses with maturity and senescence leads to little LW gain of cattle after April–May and, therefore, little, if any, response to P supplements as shown in Fig. 1. However, exceptions to this generalisation may occur in P-deficient regions when there is autumn or winter rainfall, with cattle grazing pastures with substantial *Stylosanthes* spp. legumes, or on clay soils with high water-holding capacity where green higher-quality pastures may be maintained into the winter. In these circumstances, dietary ME and protein pasture concentrations are typically above maintenance requirements during the mid-dry season and responses to P supplement often occur (Winter *et al*. 1990; Coates 1994). Under exceptional pasture conditions and in the absence of a 'normal' dry season, the LW-gain responses of cattle to P supplement have continued throughout the entire year (Fig. 2; Coates and Murray 1994), confirming that the P response is associated with pasture quality rather than the dry season *per se*. An additional important consideration is that the *Stylosanthes hamata* cv. Verano and *S. scabra* cv. Seca are unusual, even within the *Stylosanthes* genus (Jones 1974), in that they are productive legumes even when growing on low-P soils. These cultivars provide forage high in protein and ME, but with very low P concentration, into the dry season so that a deficiency of P relative to ME and protein is exacerbated (Fig. 2; Coates *et al*. 2018, 2019). In addition, where soil concentration of Ca is high, there may be a high Ca : P ratio (e.g. often >10 : 1 and up to 25 : 1) in these *Stylosanthes* cultivars when growing on low-P soils and this is likely to contribute to a larger response to P supplements (Coates 1994). This is because high diet Ca : P ratios reduce or prevent mobilisation of bone P, which physiologically would otherwise have alleviated the extent of the P deficiency (Theiler *et al*. 1937; Boxebeld *et al*. 1983; Pfeffer *et al*. 1995). Another tropical legume well adapted and productive when growing on low-P soils is *Cassia rotundifolia* cv. Wynn (Wynn cassia) (Partridge and Wright 1992; Peters *et al*. 1994; Michalk and Zhi-Kai 1995) and, although direct evidence is lacking, may also have low P concentrations in the forage when growing on low-P soils. However, since most sown pasture legume species require at least moderate soil P, it seems unlikely that the very large responses to P supplements

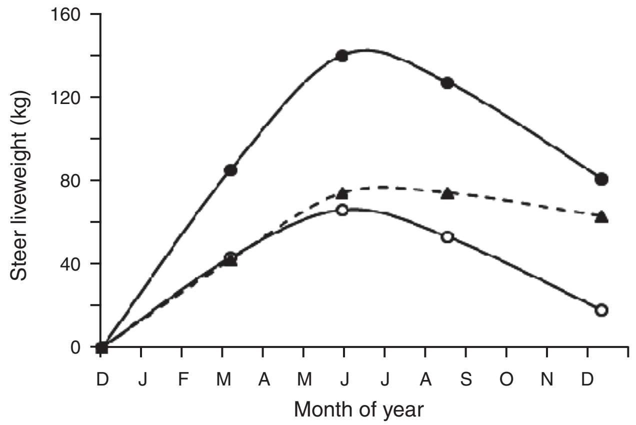

Fig. 1. The mean cumulative liveweight (LW) gain of steers grazing native C4 grass pasture with some legume over four annual cycles in the seasonally dry tropics at Katherine in northern Australia. Bicarbonate soluble soil phosphorus (P_B; Colwell 1963) was ~3 mg P_B/kg. Steers were not supplemented (○) or were given P supplements (●) throughout the year. The difference in LW between the unsupplemented and P-supplemented treatments is also shown (▲). The rainy season was from November–December until March. There was no benefit of the P supplement from May when pasture quality had declined, until the seasonal break in the following December (Winter 1988).

sometimes observed in cattle grazing grass–*Stylosantes* pastures will occur generally on grass–legume pastures.

Cattle supplemented with P through the entire year may lose more LW than do unsupplemented cattle during the dry season. However, this is likely to be a consequence of their higher LW and body condition rather than any adverse effect of P supplements *per se* during this season (Fig. 1; Winter 1988; Winter *et al*. 1990). In addition, some experiments in northern Australia have reported greater dry-season LW loss in P-supplemented than in P-unsupplemented growing cattle (Winks *et al*. 1976, 1979); however, in retrospect, it is likely that this was due to the presence of sulfuric acid as a contaminant in the phosphoric acid used as the source of supplementary P (McMeniman 1973). Also, from several South African studies, McCosker and Winks (1994) concluded that P supplements reduced LW performance of growing animals during the dry season. However, this effect occurred only when the dry-season supplement did not include nitrogen as well as P, and also the reported differences were rarely statistically significant. Thus, the assertion that P supplementation during the dry season is inappropriate is not sound. Furthermore, in the northern Australian rangelands, nitrogen supplements are often fed during the dry season to cattle grazing low-protein senesced pastures and some P is usually included. The evidence from research and producer observations indicates that low intakes of P supplements through the dry season have beneficial effects on cattle performance.

When young growing cattle with high body P reserves have been introduced to P-deficient diets in controlled pen experiments, it has usually required many weeks (typically 5–20 weeks) for plasma inorganic P (PIP) concentrations and voluntary intake to decrease to an extent indicative of severe P deficiency (Gartner *et al*. 1982; Bortolussi *et al*. 1996; Quigley *et al*. 2015; Dixon *et al*. 2019*b*). These observations have established that growing cattle have some capacity to mobilise body reserves of P when introduced to a P-deficient diet and that the magnitude of the P mobilisation is sufficient to usually delay the adverse effects of a diet P deficiency. However, such mobilisation of P in growing cattle appears limited compared with breeder cows, as discussed below. Measurements of the mineral concentrations in the rib and tail bones have shown that growing steers, as well as reproducing females, can partially compensate for a diet P deficiency by reducing the mineral density (and, thus, the P concentration) of the skeleton; these animals may consequently develop rickets (Coates and Murray 1994; Coates *et al*. 2018). In the latter study, the volume of tail bone increased but the total amount of mineral did not change. Thus, there was no net mobilisation of bone minerals but rather a decrease in bone mineral density accompanied by only slow animal growth. Interestingly, in these experiments, the P supplements were fed through the entire annual cycle; an unresolved and related question is whether P supplements fed only during the dry season to P-deficient growing cattle can increase bone P reserves, which can be mobilised during the following rainy season to provide some P and alleviate effects of P-deficient diets. We are not aware of any experiments with growing cattle that have examined this possibility.

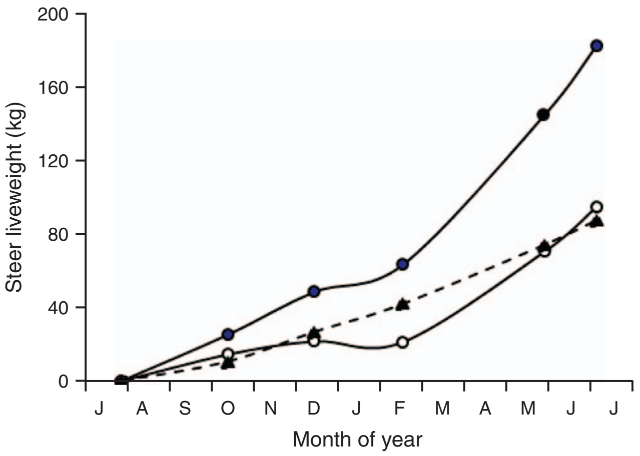

Fig. 2. The cumulative liveweight (LW) gain of steers grazing C4 grass (predominantly *Urochloa*)–*Stylosanthes* pasture at Lansdown, Townsville, in the seasonally dry tropics of northern Australia. Bicarbonate soluble soil phosphorus (P_B) was <4 mg P/kg. Steers were not supplemented (○) or were given P supplements (●) throughout the year. The difference in LW between the two treatments is also shown (▲). The pasture available during the nominal dry season (July–December) was of sufficient quality to maintain moderate LW gain; the paddocks had been destocked for 12 months due to low rainfall and there was some rain from July through to the seasonal break. These were unusual seasonal conditions for the environment (Coates *et al*. 2018).

The responses of cattle to P supplementation are obviously generally greater with pastures that are more P deficient. In pastures of 'marginal' P status, the provision of P supplements will often restore cattle growth to that expected in cattle in P-adequate status and grazing the same pasture. However, the productivity of cattle grazing 'acutely deficient' or 'deficient' pastures and given P supplements will generally be lower than that of cattle grazing comparable P-adequate pastures (Coates *et al*. 1997). This is most likely to be associated with the generally lower nutritional value of pastures growing on soils that are P-deficient and often of low fertility in other respects. Estimates of the likely responses of growing cattle to P supplements under the conditions and management systems typical on commercial farms across northern Australia are given in Table 3. Importantly, these estimated responses are much lower than those observed in many well controlled research trials (Winks 1990), but were deliberatively chosen to be conservative and with the consideration that productivity increases to improved management are usually substantially lower on commercial farms than in research trials (Dillon and Anderson 1990).

Numerous studies (Winks 1990; Bortolussi *et al*. 1996; Quigley *et al*. 2015; Dixon *et al*. 2016*a*) have shown that the voluntary intake of high-ME and -protein diets (representative of rainy-season pastures) is often increased 20–30% per kg LW, and occasionally up to 60% per kg LW, by P supplementation of P-deficient cattle. These increases in intake of DM and ME provide an explanation for increased growth and other productivity from P supplementation. However, there is also evidence from some experiments where P-deficient and P-adequate cattle were ingesting similar amounts of ME but with different LW gains that the efficiency in utilisation of ME may be reduced during severe P deficiency (Gartner *et al*. 1982; Dixon *et al*. 2016*b*). However, this has not always been observed (Ternouth and Sevilla 1990). In general, voluntary intake has not been increased by P supplementation in animals fed diets severely deficient in both P and nitrogen, and, in some experiments, P supplementation has even tended to decrease voluntary intake (Van Niekerk and Jacobs 1985). Negligible LW-change responses to the P supplements have been reported for cattle ingesting low-quality roughage in pens (Van Niekerk and Jacobs 1985) or grazing low-quality dry-season pastures (Winks and Laing 1972; Winks *et al*. 1976, 1979; Winks 1990). Intake and growth responses to P supplement can generally only be expected to occur when P is the first limiting nutrient.

An important consequence of the substantial increases in voluntary intake when P deficiencies are corrected by P supplementation is that the number of animals will have to be reduced to avoid increasing the grazing pressure as animal equivalents (AE) in a paddock and/or on an entire farm. The increase in pasture intake will be associated with both heavier animals and increased growth per annum, and, therefore, an increase in the estimated AE per head. Since the changes in farm productivity due to P supplementation will usually be associated with changes in herd structure the required reduction in animal numbers will vary with circumstances (Bowen *et al*. 2020). However, the required reduction in animal numbers to avoid increasing the total AE on the farm will usually be 10–15% of the herd.

The consequences of P deficiency on productivity of breeder cattle

Where breeders are control mated in seasonally dry environments, calving is usually planned for the late dry season or the early rainy season to take advantage of higher-quality rainy-season pasture for lactation and calf growth. A similar calving pattern tends to occur in continuously mated herds. The high P requirements of breeders, associated with late pregnancy and lactation, will exacerbate low P in relation to ME and protein in rainy-season pastures, so that the greatest responses to P supplementation in breeder cows are, as in growing cattle, also expected during the rainy season. Thus, management recommendations in northern Australia for P-deficient rangelands (McCosker and Winks 1994; Jackson *et al*. 2012) have been to provide P supplements for breeder herds during the rainy season, although some supplementary P will also be required by late-pregnant and lactating cows when they are in this physiological status during the dry season. However, in practice, it is often difficult to effectively P supplement cattle on large commercial farms during the rainy season due to limitations in vehicle access to paddocks for transport, dispersal of cattle and because it is often difficult to achieve satisfactory intakes of low-palatability loose mineral mix or feed-block supplements when cattle are grazing rainy-season pasture.

It is clear that dietary P deficiency can have severe adverse effects on breeder-herd productivity. When breeders are initially in high P status as a consequence of previous adequate P nutrition, the adverse effects of P-deficient pastures are usually small during the first cycle of pregnancy and lactation, but become progressively greater in subsequent years (Read *et al*. 1986*a*, 1986*b*; Spangenberg 1997; Dixon *et al*. 2017). The small effect in Year 1 followed by declining productivity from Year 2 to Year 5 in these experiments provides an explanation for the general absence of large adverse effects of P deficiency in many experiments where P deficiency was imposed for only one annual cycle (Winks 1990). In some other experiments summarised by Winks (1990), it was subsequently understood that the pasture systems were not severely P deficient. As discussed by Dixon *et al*. (2017), the progressive increase in the adverse effects of P deficiency can be attributed to the mobilisation of bone P reserves during the first annual cycle of P deficiency, but, in the absence of replenishment of bone P reserves, there was limited opportunity for bone P mobilisation during subsequent annual cycles. Large effects of P deficiency on breeder-herd productivity have been demonstrated with young *Bos indicus* breeders grazing pastures on soils with very low soil P (~3 mg P_B/kg; Schatz and McCosker 2018, 2019). In this experiment, the P deficiency was imposed on the heifers from when they were weaned at ~6 months rather than from when they were ~2.5 years of age and pregnant as in the experiment of Read *et al*. (1986*a*, 1986*b*). Thus, in the former experiment, the animals as heifers would have been severely P deficient through their post-weaning growth as well as during their first pregnancy, and it is likely that they were calved with very low skeletal P reserves. These breeder cows would not have had sufficient body P reserves and an opportunity to alleviate the effects of diet P deficiency by body P mobilisation, even during their first pregnancy and lactation. After the first mating at ~2 years of age, the P-deficient heifers were 65 kg lighter than were the corresponding P-supplemented heifers, and also a lower proportion was reproductively active (64% versus 87%). Pregnancy rates were reduced in subsequent years from 30% to 5% in Year 3 for first-lactation cows, and from 57% to 20% in Year 4 in second-lactation cows. P deficiency also reduced the average LW of calves at weaning in Year 3 (173 vs 139 kg), breeder LW at the end of the rainy season, and the proportion of deaths and forced withdrawals (due to poor body condition) of breeders increased from 3 to 28% (Schatz and McCosker 2018, 2019).

Recent estimates of the impact of P deficiency on breeder herds in northern Australian commercial farms (Table 4; Bowen *et al*. 2020) considered technical reports and industry surveys where available but, given the paucity of experimental results, were based primarily on opinion of extension officers and animal scientists with lengthy experience in the northern Australian cattle industry. In the absence of P supplementation, 'acute P deficiency' was estimated to reduce weaning rate by 20 percentage units, calf LW at weaning by 32 kg, cull-cow LW at the end of the rainy season by 32 kg, and to increase breeder mortality by 13 percentage units. The latter estimate assumed that herds were vaccinated for botulism; higher mortalities can be expected in cattle grazing P-deficient rangelands in the absence of vaccination due to botulism associated with osteophagia. Effective P supplementation is likely to alleviate these production losses (Table 4), but productivity will still usually be lower than for breeder herds grazing P-adequate pastures. Importantly, experiments in both South Africa (Read *et al*. 1986*a*, 1986*b*; Spangenberg 1997) and northern Australia (Miller *et al.* 1998; Schatz and McCosker 2018, 2019; Coates *et al.* 2019) demonstrated that larger responses to P supplementation than indicated in Table 4 will sometimes occur. Furthermore, the adverse effects of P deficiency on breeder-cow productivity and mortalities are likely to be even larger in subgroups of cows lactating during the dry season or due to the effects of drought on pasture availability and nutritional quality.

The capacity of breeder cows to mobilise body P reserves

From research during the past decade, it is clear that beef-genotype breeder cows, as well as dairy cows, ewes and goats, have a substantial capacity to mobilise bone P during late pregnancy and lactation (Dixon *et al*. 2017) and this P can be utilised for metabolic processes, including conceptus growth and milk synthesis in the pregnant and lactating breeder. The amount of P in the body of cattle is large (e.g. ~3000 g P in a 450-kg breeder cow) in relation to daily P requirements and ~80% of this P is in bone, with the remainder being in soft tissues. Beef-genotype breeders ingesting P-deficient diets can mobilise at least 30% of their bone P reserves during P deficiency (Little 1983; Dixon *et al*. 2016*c*, 2017; Coates *et al*. 2018), while pregnant ewes have been reported to

Table 4. The estimated requirements for phosphorus (P) supplement across three categories of P-deficiency, estimates of productivity of breeder cows in P-adequate status, and the likely productivity with effective P supplementation on commercial cattle farms during the rainy season for each of these categories

Values are estimates from McCosker and Winks (1994) and Jackson *et al*. (2012) and opinion by scientists and beef extension technical staff with extensive knowledge of the northern Australian cattle industry. These estimates are substantially lower than the responses often reported in research trials (adapted from Bowen *et al*. 2020). Categories of soil P deficiency are given in Table 1. The amount of supplement DM will be ~6–12 times the amount of P stated for each supplement P intake. Supplement cost estimate does not include feeding-out costs. Average cow liveweight (LW) is the cow LW in the early dry season. Change is the change in the animal response due to P supplementation. Mortality estimates assumed that management includes vaccination for botulism. Breeder mortality will often be higher in the absence of vaccination

Attribute	(+/−) P supplement	Category of P status for grazing cattle			
		Adequate	Marginal	Deficient	Acutely deficient
		Supplement allocation			
Days of supplementation (per annum)	n.a.	Nil	90	120	120
Supplement P intake (g P/day)	n.a.	Nil	3	7	11
Supplement P intake (kg P/annum)	n.a.	Nil	0.3	0.8	1.3
Supplement cost (US$/annum)	n.a.	Nil	1.3	4.0	6.2
		Estimates of breeder productivity			
Average cow LW (kg)[D]	–P	460	450	435	428
	+P	460	460	450	445
	Change	Nil	+10	+15	+17
Weaning rate (%)	–P	77	72	67	57
	+P	77	77	73	72
	Change	Nil	+5	+6	+15
Calf LW at weaning (kg)	–P	200	190	175	168
	+P	200	200	190	180
	Change	Nil	+10	+15	+12
Expected breeder mortality	–P	2	4	8	15
	+P	2	2	5	7
	Change	Nil	–2	–3	–5

mobilise up to 45% of bone minerals (Benzie *et al*. 1959). Mobilisation of 30% of the skeletal P in a mature 450-kg breeder corresponds to ~700 g P and, because mobilised body P is presumably entirely available, this would be equivalent to ~875 g of diet P. This corresponds to ~7 g P/day or one-third of the P requirements of the breeder for 4 months during late pregnancy and early lactation. Studies with severely P-deficient mature beef cows in early lactation reporting P balances of about –6 g P/day have provided direct measures of the magnitude of mobilisation of body P reserves (Benvenutti *et al*. 2015; Dixon *et al*. 2016*a*) that are remarkably similar to the above calculated estimate. A similar amount of bone P was mobilised by first-calf cows in the experiment of Coates *et al*. (2018), but smaller amounts were reported by Castells *et al*. (2015).

Pen experiments where mature *Bos indicus*-cross breeders calved in high P status and were fed severely P-deficient diets (20–30% of calculated P requirements) or P-adequate diets during early lactation have reported little effect of the diet P deficiency on milk output; calf LW gain during the first 3 months of lactation was not affected ($P > 0.05$) in one experiment (0.69 and 0.64 kg/day; Benvenutti *et al*. 2015) and was reduced ($P < 0.01$) by the P-deficient diet only from 0.93 to 0.76 kg/day in a second experiment (Dixon *et al*. 2016*a*). However, the P deficiency reduced the voluntary intake by ~20% (as g/kg LW) in both experiments, and there was a large effect on cow LW change, with P deficient cows being 55–65 kg lighter after 3 months of lactation (Table 5). The P-deficient cows also lost more rib-bone P than did the P-adequate cows. In summary, mature breeder cows calving in high P status and then fed P-deficient diets could largely maintain milk production in early lactation, but this was associated with adverse effects on voluntary intake, LW and body condition. In another experiment (Castells *et al*. 2014, 2015) first-calf cows calving in high P status had similar responses to P deficiency in early lactation, although having a lower capacity to maintain milk output (Table 6). Furthermore, first-calf cows calving in low P status were more adversely affected than were those calving in P-adequate status. Experiments with both first-calf and mature cows grazing P-deficient *Stylosantes*–grass pastures have shown similar effects where cows without P supplements lost substantial LW but, in general, maintained calf LW gain (Miller *et al*. 1998; Dixon *et al*. 2016*c*; Coates *et al*. 2019).

Where breeders lose extensive LW during lactation, the rates of reconception while still lactating are usually low. However, when a cow with low body P reserves and low body condition does become pregnant and is not able to replace these P and energy reserves, then the capacity of this cow to further mobilise body P and energy reserves during late pregnancy and then lactation will be severely limited. This was clearly demonstrated in the experiments of Read *et al*. (1986*a*, 1986*b*) and Spangenberg (1997) where, in beef-genotype breeders, the adverse effects of P deficiency increased progressively during the five consecutive annual cycles. Similarly, Valk *et al*. (2002) demonstrated that dairy cows fed P-deficient diets largely maintained milk output during the first lactation but, without opportunity for P replenishment, could not maintain the second lactation and had to be withdrawn from the P-deficient diets to avoid mortalities.

Table 5. Measurements in two experiments of mature cows in early lactation that were fed diets of low or high phosphorus (P) concentration (LowP, HighP) during the first 3 months of lactation

Cows had been fed high-P diets during late pregnancy and were expected to have a high P status at calving ($n = 7$ or 8) (Benvenutti *et al*. 2015; Dixon *et al*. 2016*b*). DM, dry matter; LW, liveweight; PIP, plasma inorganic phosphorus

Measurement	Experiment 1			Experiment 2		
	LowP	HighP	Significance	LowP	HighP	Significance
DM intake (g DM/kg LW)	16.6	21.2	***	17.4	21.5	***
PIP (mmol/L)	0.7	1.5	***	0.4	1.7	***
Cow LW change (kg)	–36	+18	**	–	–	–
Cow LW change (kg/day)	–	–	–	–0.34	+0.25	***
Milk production (kg/day)	5.8	4.6	n.s.	–	–	
Calf growth (kg/day)	0.58	0.70	n.s.	0.83	0.92	n.s.

Table 6. Measurements in first-calf cows in early lactation that were fed diets low or high in phosphorus (P) concentration (LowP, HighP) during late pregnancy (preg) or the first 3 months of lactation; thus, the cows had a low or a high P status at calving and were fed low- or high-P diets in lactation ($n = 8$ or 9) (Castells *et al*. 2014, 2015)

LW, liveweight; DM, dry matter; CBT, cortical bone thickness. Values within a row followed by different letters are significantly different (at $P = 0.05$). In a 2 × 2 factorial analysis, the main effect of pregnancy was significant ($P < 0.01$)

Measurement	Low P in preg		High P in preg		s.e.m.	Significance
	LowP	HighP	LowP	HighP		
P intake (g P/day)	3.9	20.6	5.0	24.0	–	–
LW at calving (kg)	373b	357b	407a	416a	13.9	*
LW at weaning (kg)	300b	406a	342b	441a	16.9	*
DM intake (kg DM/day)	4.9b	9.4a	6.3b	10.9a	0.53	*
Milk production (kg/day)	4.9c	7.8ab	6.5b	8.7a	0.58	*
Calf growth (kg/day)	0.57c	0.83a	0.69bc	0.93a	0.052	*
Change in rib CBT (mm)						
Pregnancy	0.66		0.98		0.110	n.s.
Lactation	–1.56	–1.08	–1.13	–0.92	0.249	n.s.

The capacity of breeder cows to replenish body P reserves

If body P reserves are mobilised in the breeder to provide P during late pregnancy and lactation, then these body P reserves will clearly need to be replenished for the breeder to calve annually and to avoid adverse consequences. This will usually require P supplementation, although the likely benefits of grazing P-deficient cattle on high-P land systems for part of the annual cycle have not been investigated. There is evidence from recent experiments that breeder cows have substantial capacity to replenish body P reserves before the next parturition if P intake is high, even when grazing dry-season pastures. When P-depleted recently weaned mature breeders were fed a high-P diet sufficient for slow LW gain (equivalent to dry-season pasture), there was slow replenishment of bone minerals (Dixon *et al*. 2016*b*). Furthermore, bone mineral replenishment occurred much more rapidly when the breeders were fed a high-quality diet (equivalent to rainy-season pasture, and providing for rapid LW gain at >1 kg/day). Breeders losing maternal LW in late pregnancy also have substantial capacity for bone P replenishment (Benvenutti *et al*. 2016). Heifers fed diets high in P but restricted intakes of ME causing up to 50 kg maternal LW loss during the last trimester of pregnancy, nevertheless, deposited substantial amounts of P (~7 g P/day) into bone (Table 7). Presumably, these increased bone P reserves at parturition would have been available to the animal for mobilisation during the lactation. Furthermore, numerous studies have reported extensive replenishment of bone P in sheep, goats and dairy cows during late lactation and in the post-lactation transitional interval (Dixon *et al*. 2017). Thus, the evidence available indicates that appreciable replenishment of the bone P reserves is expected to occur during the dry season when diet P intake exceeds the current requirements of the animal. Such P replenishment is in accord with observations and anecdotes from cattle managers of some benefits from P supplementation of breeders during the dry season. In very harsh and P-deficient environments, where herd calving rate is often only 50–60% and most cows calve each second year, presumably, the alternate rainy season when the breeder is not pregnant or lactating provides the opportunity for replacement of body P reserves, together with body energy soft-tissue reserves as fat and muscle.

A consequence of mobilisation and utilisation of bone P during intervals of diet P insufficiency, or intervals of replenishment of bone P, is that the P requirements calculated from feeding standards may not correctly estimate the amount of diet P that should be provided to avoid adverse effects on the animal or its productivity. Current feeding standards do not include estimates of P derived from mobilisation, or the additional P required for replenishment. This issue of P mobilisation and replenishment is comparable to the estimation of the ME requirements of breeder cows undergoing loss and regain of LW and body energy during intervals of the annual cycle. The nutritional management of breeder herds, especially in harsh environments with seasonally fluctuating quality and quantity of pasture, usually accepts and plans that breeders will lose body fat reserves during late pregnancy and early lactation and that these need to be replenished before the next parturition. A similar approach should be applicable to the management of P nutrition, although implementation will be more difficult in the absence of practical on-farm methods to estimate the bone mineral (i.e. P) reserves of cattle (Dixon *et al*. 2017). Nevertheless, using the knowledge of mobilisation and replenishment of body P reserves should allow improved management of breeder nutrition.

Diagnosis of P status of grazing cattle

Evaluation of P adequacy from soil and pastures

Since the primary cause of diet P deficiencies in cattle grazing rangelands is low concentrations of plant-available soil P, the utility of the P concentrations in soil and pasture have been investigated to evaluate the likelihood of P deficiency in cattle (Kerridge *et al*. 1990; McLean *et al*. 1990). Evaluation of 'average' soil P in a paddock or grazing area is difficult. In rangeland situations, there are often several soil types, high spatial variability within soil types and variation in P with soil depth. The importance of the P at various soil depths and the consequences for plant availability will vary with plant species and seasonal conditions. In the context of northern Australia, soil mapping on a broad scale has been available for many decades (Ahern *et al*. 1994; McCosker and Winks 1994), but is of limited value in regions with heterogeneous soil types. However, the native vegetation often does provide a useful indicator of soil fertility, including of P_B (McCosker and Winks 1994). For cattle management on farms and in paddocks with heterogeneous soils, the use of mapping is likely to be valuable where it is on a sufficiently refined and detailed scale. Ongoing improvements in remote-sensing

Table 7. Measurements in heifers of conceptus-free liveweight (CF-LW) and CF-LW change, metabolisable energy (ME) intake (LowE, MedE and HighE), each with a low (LP) or high (HP) phosphorus concentration during the last 14 weeks of pregnancy (n = 6–8)

Restricted amounts of the diets were fed to provide the three levels of ME (Benvenutti *et al*. 2016). T-LW, total liveweight; PIP, plasma inorganic phosphorus

Measurement	Diet treatment during pregnancy						s.e.m.	Probability		
	LowE-LP	LowE-HP	MedE-LP	MedE-HP	HighE-LP	HighE-HP		E	P	ExP
Initial CF-LW (kg)	403	398	408	418	424	422	–	–	–	–
CF-LW change (kg)	–49	–49	–37	–24	–37	–4	1.97	***	**	*
ME intake (MJ ME/day)	40	40	49	50	53	69	3.9	***	***	***
ME intake (kJ ME/kg T-LW.day)	94.3	97.4	114.3	111.3	113.7	149.0	3.9	***	***	***
PIP (mmol/L)	1.0	2.1	1.0	2.0	0.8	2.1	0.09	n.s.	***	n.s.
Calf birthweight (kg)	26.9	25.4	27.1	30.8	29.3	28.2	1.46	n.s.	n.s.	n.s.

technologies seem likely to allow the development of such detailed mapping and are likely to become much more important in the future.

Natural rangelands often have a wide diversity of plant species with a high variation in the P concentration among pasture species and their morphological components. An additional major difficulty is the high degree of diet selection by grazing cattle through choice of the rangeland areas grazed during any specific period and, usually, high degrees of selection of plant species and morphological components. The latter problem will be exacerbated in extensive rangelands with low stocking rates (e.g. one animal per 10–50 ha) and large paddock areas (e.g. >2000 ha) where P deficiencies most usually occur. In addition, it is clear that P-deficient cattle modify their grazing behaviour to select pasture with a higher P concentration than that selected by P-adequate cattle. Coates and Le Feuvre (1998) showed that P-deficient heifers grazing mixed grass–*Stylosanthes* legume pasture selected the grass rather than the *Stylosantes* when the grass contained higher concentrations of P but lower contents of ME and protein; conversely, P-supplemented heifers in adequate P status selected more of the *Stylosantes* than of the grass in the pasture. A further consideration is that, in a specific paddock, there may be large variation among years (annual cycles) in the responses by breeder cows to P supplementation. P deficiency, as indicated by a lower PIP and animal LW, seems to occur more often and more severely in low-rainfall and drought years, apparently being associated with lower concentrations of P in pasture during such seasonal conditions (Turner *et al*. 1935; Rose 1954; Judkins *et al*. 1985; Ferguson and Sklan 2005; Suttle 2010; Coates *et al*. 2019).

Evaluation of P adequacy from cattle behaviour and production

Pica by cattle in rangelands is considered highly indicative of P deficiency and is a behaviour characterised by seeking out, chewing and ingestion of unusual objects such as sticks, stones, carcasses and old bones (Green 1925). Pica, and also bone chewing (osteophagia), are well recognised and documented as being indicative of a severe nutritional deficiency (Call *et al*. 1987; Shupe *et al*. 1988; Blair-West *et al*. 1992) and, in rangelands, this deficiency is most often of P (Theiler and Green 1932; McCosker and Winks 1994). Osteophagia develops as a learned post-ingestive feedback response following pica in P-deficient cattle and the olfactory constituents of bones probably provide important cues for attraction of the animals to bones (Dixon *et al*. 2019*b*). Most, but not all, cattle cease osteophagia after regaining P adequacy. Another overt behavioural symptom is ‘peg-leg’ characterised by lameness, stiff joints, and a tendency for the standing animal to draw the hind legs forward so that the back is arched (McCosker and Winks 1994). ‘Peg-leg’ is observed most often in young lactating cows. Other indicators of P deficiency include weak and brittle bones, with bone breakages sometimes occurring during handling of cattle, and bone abnormalities at post-mortem. The articular surface of the joint ends of long bones may be eroded and pitted and bones may be light, thin-walled and with a reduced density to the extent they can be cut with a knife. Following severe and prolonged P-deficiency symptoms, such as rickets in younger cattle, osteomalacia, osteoporosis and other bone abnormalities in mature cattle, are often observed. Severe P deficiency in cattle is typically associated with a low LW and body condition, poor growth and a low breeder herd productivity. In situations where cattle are severely P deficient in most years, the identification of the P deficiency is likely to be straight-forward from observations and poor cattle productivity for the region. The more difficult situations to evaluate P deficiency will often be where cattle productivity as growth and reproduction is lower than expected, subclinical P deficiency is suspected, but where low cattle productivity may be associated with other nutritional deficiencies or health problems. The identification of unusual behaviours clearly depends primarily on observation, stockmanship, local knowledge and experience, and expectations of the performance of grazing cattle in relation to the regional environment. These behavioural and observational symptoms, in combination with simple measurements of herd productivity, appear to have received insufficient attention as simple and practical indicators of P deficiency in rangeland cattle.

Faecal measurements

In cattle ingesting forage-only diets, close linear relationships have been observed between diet P concentration and faecal P concentration within many studies (Moir 1960; Cohen 1974; Holechek *et al.* 1985; Dixon and Coates 2011; Dixon *et al*. 2018). If an animal is not mobilising or replenishing bone and estimates are available for the digestibility of the diet and the deposition of P into the body for growth or for milk, then relationships between the P in the diet and in faeces can be expected. From knowledge of the physiology of P in cattle, additional considerations are that (1) diet P surplus to immediate requirements will be excreted in faeces, (2) the ratio of concentrations of P in diet and faeces must partly depend on diet DM digestibility, and (3) there is potentially net deposition or mobilisation of P into or from soft tissues, bone and milk. The effects of these pathways explain why, in at least in some circumstances, diet P concentration is better predicted when measurements of diet N, diet non-grass and faecal N concentrations (measured by faecal near-infrared spectroscopy) are included with faecal P concentration in predictive models (Dixon 2016). Moveover, estimation of diet P from faecal P concentration has provided a useful on-farm estimator of the effects of P deficiency on breeder-herd productivity in northern Australian rangelands (McGowan *et al*. 2014). However, there are limitations in use of faecal P as a diagnostic indicator. Wadsworth *et al*. (1990) reported that faecal P was a poor predictor of the responses of cattle grazing tropical pastures to P supplements. Also, the relationships between diet P concentration and faecal P concentration established in cattle consuming diets of forage alone cannot be applied to cattle ingesting diets containing supplements of inorganic P or concentrate and molasses supplements; these relationships are different (Quigley *et al*. 2015; Dixon *et al*. 2018, 2019*b*).

The different relationship with concentrates is likely to be the result of the concentration of P in faeces being increased by digestion of starch in the large intestine (Rodehutscord *et al*. 2000), and a consequence of increased excretion of microbial debris increasing faecal P concentrations.

The use of faecal P concentration and other measurements in faeces to estimate diet P concentration is likely to be most appropriate in growing cattle that have grazed a specific paddock without any P or concentrate supplements through the rainy season and should, thus, have mobilised or replenished bone P to their potential as limited by the physiology of the animal and the intake of diet P (i.e. be in a new steady-state equilibrium for rainy-season pastures). In this situation, the faecal measurements are likely to provide a useful estimate of diet P concentration and, thus, of diet P intake. If faecal P is less than ~2.0 g P/kg DM, the diet P is likely to be deficient for growing cattle, and if faecal P is greater than ~4 g P/kg DM, the diet P is likely to be adequate for growing cattle. In conclusion, it appears that the faecal P concentration can be useful as a guide to identify very low and very high diet P concentrations.

Markers in blood

Plasma inorganic phosphorus (PIP) concentration is the most widely used indicator of P status in cattle and measures the extracellular-fluid pool that is readily available for metabolism. PIP concentrations reflect diet intake of P, the true absorption of the diet P, losses of P in faeces, P deposited into milk and soft tissues during growth, and transfer of P to and from bone as the major body mineral store. Such characteristics contribute towards making PIP a valuable indicator of P status, but there are fundamental limitations in using PIP, especially as the sole measure of P status in cattle.

An overall important physiological issue is that the control of P in the body is not strictly regulated. As a consequence, PIP concentrations often exhibit variability associated with the normal daily cycles, which lessens the reliability of PIP as a diagnostic marker. Nevertheless, PIP concentrations appear to primarily reflect P intake and, after adaptation to a new diet, are usually stable over intervals of weeks. For a given diet in growing cattle, there are usually linear or curvilinear relationships between P intake and PIP (Wadsworth *et al*. 1990; Coates 1994; Quigley *et al*. 2015). Similar results have been noted in breeder cattle during both pregnancy and lactation, but the relationship changes with physiological state of the cow (Dixon *et al*. 2017; Dixon and Coates 2019*c*). Hence, PIP is often a reliable indicator of P status in the absence of marked changes in dietary P intake, and is particularly useful for diagnosing P deficiency in grazing cattle without P supplementation. A limitation with PIP is that it will be affected, often substantially, by the secretion (loss) of P into body tissues (milk, conceptus) and gain or loss of P into or from soft tissues or bone. Thus, the concentrations of PIP that indicate P status (deficiency or adequacy) will vary with physiological state and ME intake. An additional difficulty in application of PIP as a diagnostic in breeder herds of mixed age and reproductive history is that variation in previous physiological status apparently leads to high variability in PIP among individuals in the herd (Dixon *et al*. 2019*d*).

Plasma inorganic phosphorus (PIP) concentrations have been used to diagnose P status and P intake in growing cattle in the northern Australian rangelands using results from a series of major grazing experiments in growing steers and heifers and Wadsworth *et al*. (1990) concluded that 'PIP successfully diagnosed P deficiency in young, growing cattle in 90–100% of cases' on the basis of the good correlations between PIP concentrations and LW gain, but also noted important caveats that have often been over-looked. These included that there were significant differences among regions, between rainy and dry seasons, and among years, and these differences prevented derivation of a general relationship between LW gain and PIP (Wadsworth *et al*. 1990). There are also other important considerations. First, Coates (1994) reported that PIP concentrations indicative of P adequacy in heifers grazing grass–*Stylosanthes* pastures with LW gain up to ~0.6 kg/day with an increasing diet P were substantially higher than the values concluded by Wadsworth *et al*. (1990). This leads to the hypothesis that the PIP concentration indicative of diet P adequacy increases with growth rates as constrained by other factors such as by energy and protein intake. Second, it is clear that the PIP concentrations of breeders in early or mid-lactation may be much lower than those in non-lactating breeders or growing animals fed the same diet, even though milk production is often maintained due to mobilisation of body P reserves (Dixon *et al*. 2016*c*, 2019*c*; Coates *et al*. 2019). Change in PIP indicative of P adequacy is consistent with the large increases in P requirement with an increasing growth or milk production. Nevertheless, and despite these difficulties associated with physiological state and ME intake, the PIP concentrations late in the rainy season in growing cattle that have not been fed P supplements during the rainy season, in conjunction with estimates of diet quality from faecal analyses, remain the best and most validated marker for diagnosis of P deficiency, at least in growing cattle. In theory, the PIP in P-supplemented cattle should estimate whether the animals are obtaining sufficient diet P from the combined sources of pasture and supplement. However, on current evidence, the use of PIP in this context cannot be recommended due to the well known difficulties associated with large variation among days, and among individual animals in a herd, in intake of loose mineral mix or feed-block supplements.

To better define the P status of cattle, endocrine markers, in addition to PIP, are required to indicate the degree of bone mobilisation. One potential candidate is plasma Ca. In hypophosphatemic animals, plasma Ca concentrations are mildly hypercalcemic, although often still within the normal range. Despite normal physiological responses to excrete any excess Ca, increased plasma total Ca concentrations are observed in P-deficient cattle (Anderson *et al*. 2017). This is because mobilisation of hydroxyapatite from bone during dietary P deficiency releases Ca as well as P and increases extracellular Ca. Studies in sheep and pigs support the hypothesis that concurrent decreases in PIP and increases in Ca are characteristic of dietary P deficiency (Breves *et al*. 1985; Liesegang *et al*. 2002). The ratio of plasma Ca : PIP appears to provide a better diagnosis of P status in cattle than does PIP concentration alone (Anderson *et al*. 2017); however, validation of this hypothesis is required.

Other blood constituents that reflect changes in mobilisation and deposition of bone minerals or altered bone physiology are also likely to be valuable biomarkers of P status in cattle. Markers of bone mobilisation such as hydroxyproline and deoxypyridinoline concentrations in urine have been examined as potential indicators of P deficiency in cattle, but often lack specificity to bone. In at least some circumstances they have been found not to be useful in diagnosis of P deficiency (Wadsworth *et al*. 1990). More contemporary bone-resorption markers for which commercial assay kits are available are potentially more useful (Allen 2003). One such marker is C-terminal telopeptides of Type I collagen (CTX-1) as a marker of bone resorption. Recent evidence in breeders shows that plasma CTX-1 concentrations are valuable to diagnose bone mobilisation in P deficiency (Anderson *et al*. 2016, 2017). Another potential marker of P deficiency is alkaline phosphatase. In P-deficient cattle, defective bone mineralisation causes the development of rickets or osteomalacia. An increase in the circulating bone alkaline phosphatase in blood, measured by an ELISA with reported specificity to the bone isoform, has been observed in P-deficient breeders (Anderson *et al*. 2017). Concentrations of plasma CTX-1 and bone alkaline phosphatase, which together reflect bone mobilisation and defective mineralisation respectively, should aid the diagnosis of bone abnormalities in P-deficient cattle. However, further work is necessary to determine and validate the predictive value of these and other bone markers.

Measurements of bone

Bone obtained by surgical biopsy or at slaughter can provide extensive information of the changes in bone P reserves after substantial intervals of bone mobilisation as a consequence of diet P deficiencies. However, the bone(s) sampled is important. Mobilisation of bone minerals occurs primarily from the axial skeleton (i.e. vertebrae and skull) and to a much lesser extent from the appendicular skeleton. However, the proportional mobilisation of minerals from rib bone and from the entire skeleton in P-deficient cattle are fortuitously similar (Dixon *et al*. 2017) so that rib bone remains an appropriate biopsy-sampling site, while being relatively simple and non-invasive for field experiments. Changes in mineral content of leg bone can be expected to underestimate the change in the entire skeleton.

The most commonly reported measurements of rib bone have been the cortical bone thickness and the concentrations of P and Ca (or ash) in the bone cross-section or in the cortical bone, and they are usually calculated on a volume basis (Dixon *et al*. 2017). An index (P per unit surface area of cortical bone) calculated from the thickness and the specific gravity of the cortical rib bone facilitates comparisons (Dixon *et al*. 2019*a*). Another important recent advance is the development of semi-automated measurements of bone histology, which provide sensitive and informative measurements of changes in bone, including the effects of nutrition (Kidd *et al*. 2016*a*, 2016*b*; Dixon *et al*. 2017).

An alternative simple and economical approach to evaluating bone mineral density as an indicator of P status in field situations has been recently described by a Brazilian research group (Malafaia *et al*. 2018). The test depends on the resistance of the bone in the transverse process of the L2 or L3 vertebrae to insertion by hand of an 18-gauge needle. The resistance was considered in the following three categories comprising: (1) the needle bending rather than penetrating the bone, (2) the bone offering some resistance to penetration, but it was possible for the operator to pierce the bone with the needle, and (3) the needle could be inserted into the bone with minimal resistance. These were considered to represent P-adequate status, subclinical P deficiency and clinical P deficiency respectively, with these categories being established by comparison of the needle-test results with measurements of the rib bone-cortical thickness, specific gravity and mineral density measured by X-rays. Further validation is clearly essential, but this procedure, possibly with modification, appears promising to provide a simple and valuable field evaluation of the bone mineral and, therefore, the P status of cattle.

Many studies have investigated the absorption of photons or X-rays, usually of tail bone or leg bone (Coates *et al*. 2016, 2018), which allows sequential *in vivo* measurements of the changes in mineral content of tail bone due to severe P deficiency. The proportional changes in tail bone and rib bone were similar in young growing cattle and should reflect the changes in the skeleton, but in mature cows the mobilisation of tail-bone mineral was only about half of that from rib bone. Numerous studies have reported the results of X-ray measurements of bones, most often leg bones, obtained at slaughter or occasionally as repeated measurements, and reported measurements of the relative differences among treatments within experiments. However, limitations include that these studies have used a variety of instruments and laboratory procedures and have seldom included examination of the relationships between absorption of radiation and the chemical and/or physical attributes measured in bone biopsies, or addressed the differences in mobilisation and deposition among the bones of the skeleton. The limitations of instrumentation and required skills, and, in many countries, licensing to use radiation technology, seem likely to restrict these technologies and especially for field experimentation and management of cattle in rangelands.

Conclusions

Phosphorus deficiency as a consequence of low soil P_B concentrations can have severe adverse effects on the productivity of beef cattle grazing many rangeland regions. Research has progressed our understanding of many aspects of the nutrition and physiology required to underpin practical management options to alleviate the adverse effects of low P intake in cattle grazing seasonally dry tropical rangelands. The most common management option to address P deficiency is by P supplementation of cattle, preferably during the rainy season and early dry season, when higher pasture quality is sufficient for cattle growth. During late pregnancy and early lactation, breeder cows calving in high P status (i.e. with high

P reserves) have substantial capacity to mobilise these reserves to maintain milk production when the intake of diet P is insufficient. However, because such mobilisation of body P during severe P deficiency has been associated with reduced voluntary intake and rapid losses of LW, there may be adverse effects on cattle productivity depending on bone-P mobilisation rather than P supplementation. Breeder cows have substantial capacity to replenish bone P reserves during the dry season if ingesting diet P surplus to their immediate requirements and such replenishment of bone P reserves is essential in cows calving annually. Diagnosis of the P status and estimation of P intake by grazing cattle remains difficult in situations where the deficiency is subclinical. Large and economically important increases in cattle production can be achieved by P supplementation of P-deficient cattle. However, there are often challenges for management of rangeland cattle production to identify subclinical P deficiency, to estimate the optimal amounts of supplementary P required, and to effectively and efficiently feed P supplements during the rainy season when they are most effective.

Conflicts of interest

The authors declare no conflicts of interest. Dr R. M. Dixon and Dr S. T. Anderson are Associate Editors of *Animal Production Science* but had no role in review or evaluation of the manuscript.

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