Tropical Grasslands-Forrajes Tropicales (2019) Vol. 7(3):223–233
DOI: 10.17138/TGFT(7)223-233

Research Paper

Between-year variation in the effects of phosphorus deficiency in breeder cows grazing tropical pastures in northern Australia

Variación interanual de los efectos de la deficiencia de fósforo en vacas reproductoras en pasturas tropicales del norte de Australia

DAVID B. COATES[1], ROB M. DIXON[2] AND ROBERT J. MAYER[3]

[1]*CSIRO Ecosystems Sciences, ATSIP, Aitkenvale, QLD, Australia.* csiro.au
[2]*Queensland Alliance for Agriculture and Food Innovation (QAAFI), Centre for Animal Science, The University of Queensland, Rockhampton, QLD, Australia.* qaafi.uq.edu.au
[3]*Queensland Department of Agriculture and Fisheries, Maroochy Research Facility, Nambour, QLD, Australia.* daf.qld.gov.au

Abstract

Breeder herd productivity can be severely reduced by dietary phosphorus (P) deficiency. The performance of small groups of P-deficient (P_{defic}) or P-supplemented (P_{supp}) breeder cows was studied over 5 annual cycles while grazing C4 grass-*Stylosanthes* pastures at a site in the seasonally dry tropics of northern Australia. Soils contained c. 4 ppm of bicarbonate extractable P. Plasma inorganic P concentrations (PIP) during the wet season indicated that the P_{defic} cows were deficient in P in 4 years and marginal in one year. Annual liveweight (LW) changes ranged widely between annual cycles from −71 to +13 kg in P_{defic} cows and from +4 to +44 kg/head in P_{supp} cows. The LW responses to increased dietary P ranged from −9 to +115 kg, were greatest in years when LW losses by the P_{defic} cows were greatest, and were associated with low-rainfall years. LW gains of calves suckling P_{supp} cows (mean 0.86 kg/d) tended to be higher (range 0.01–0.17 kg/d; mean 0.09 kg/d) than those of calves suckling P_{defic} cows, but were significantly (P = 0.03) higher in only one year. Reconception appeared to be higher in P_{supp} than P_{defic} cows during the 2 years of lower rainfall. Overall, the results indicated that responses to P supplementation by breeders grazing P-deficient pastures can vary widely between years. Therefore, the response in any one year may not reliably indicate responses in the longer term.

Keywords: Cattle, mineral deficiency, phosphorus responses, phosphorus supplements, seasonal variation.

Resumen

La deficiencia de fósforo (P) en la dieta puede reducir severamente la productividad de las vacas reproductoras. En una zona de clima tropical estacional seco en el norte de Australia, durante cinco ciclos anuales se estudió el rendimiento de este tipo de vacas deficientes en P (P_{defic}) o suplementadas con P (P_{supl}), en pasturas de *Stylosanthes* y gramíneas C4. El suelo tenía una concentración aproximada de 4 ppm de P soluble (bicarbonato). Las concentraciones de P inorgánico en el plasma (PIP) determinadas en época lluviosa indicaron que las vacas P_{defic} presentaron deficiencia de P durante 4 años y suficiencia marginal de P en un año. El cambio anual de peso vivo varió ampliamente entre 4 y 44 kg/animal en las vacas P_{supl} y entre −71 y +13 kg en las vacas P_{defic}. En los años con pocas lluvias la respuesta a la dieta con P_{supl} varió entre −9 y +115 kg, y fue mayor en las vacas P_{defic}. El crecimiento de los terneros amamantados por las vacas P_{supl} (0.86 kg/dia) tendió a ser mayor (rango 0.01–0.17, promedio 0.09 kg/dia) que en aquellos de las vacas $P_{defic,}$ pero esta diferencia fue significativa (P = 0.03) solo en uno de los cinco años experimentales. La reconcepción fue más alta en las vacas P_{supl} que en las P_{defic} durante los dos años de menor precipitación. La amplia variación entre años en las concentraciones de PIP y los efectos de la deficiencia de P estuvieron ligadas a una alta variación en la lluvia anual y estacional. Los resultados mostraron que la respuesta de las vacas en pasturas

---

Correspondence: R.M. Dixon, Queensland Alliance for Agriculture and Food Innovation (QAAFI), Centre for Animal Science, The University of Queensland, PO Box 6014, Rockhampton, QLD 4702, Australia. Email: r.dixon77@uq.edu.au

deficientes en P a suplemento de P puede variar ampliamente entre años. Por lo tanto, la respuesta en un período determinado no garantiza la misma tendencia en el largo plazo.

Palabras clave: Bovinos, deficiencia de P, respuestas de P, suplementación, variación estacional.

Introduction

Phosphorus (P) deficiency is one of the most widespread and economically important mineral deficiencies affecting grazing livestock. For example, based on soil P concentrations, some 70% of northern Australian rangeland pastures are expected to be deficient in P for grazing cattle (McCosker and Winks 1994; CSIRO 2007). P deficiency reduces voluntary pasture intake, leading to adverse effects on liveweight (LW) change and hence live weight in both growing and breeder cattle, lower calving rates and calf growth, and increased breeder mortality (Winks 1990; McCosker and Winks 1994; Suttle 2010). The economic benefits of P supplementation (Dixon et al. 2011) obviously depend on the magnitude and consistency of animal responses in specific regions and paddocks and across years.

Large between-year variability in the amount and distribution of rainfall is typical of many regions in the seasonally dry tropics, and particularly in northern Australia (Weston 1988; Cook and Heerdegen 2001). As a consequence there is generally high between-year variability in pasture quantity and quality (McLennan et al. 1988) and in annual LW gains of growing cattle (McCown 1981; Winks 1984; Jones et al. 1990). The performance of breeder cows in terms of LW, fertility and mortality also varies between years in association with climatic factors. However, the effects of environmental variability on responses to P supplementation in LW and productivity of breeder herds grazing pastures growing on P-deficient soils, and the economic implications of these variable responses, have received little attention. Furthermore, between-year variability in responses by breeder cows to P supplementation is often complicated by carry-over effects through successive annual cycles associated with cow body condition, time of calving and skeletal P reserves (Dixon et al. 2017). The present study examined the magnitude of the variation between years in performance and the responses to providing adequate dietary P in groups of breeder cows grazing pastures growing on severely P-deficient soil at a site in the seasonally dry tropics.

Materials and Methods

General outline and animal cohorts

The study reports results from experiments with breeder cows at the Lansdown Pasture Research Station (19º41' S, 146º51' E), approximately 50 km south of Townsville in north Queensland, Australia. Droughtmaster breeders (*Bos indicus* × *Bos taurus*) grazed an area of pasture growing on soils very low in available P through 4 annual cycles in Experiment 1 (Expt 1), and during an additional fifth annual cycle, when cows grazed similar low-P pasture in an adjacent area (Expt 2). The soils of the experimental site comprised a mixture of yellow earth (Gn 2.64, Northcote 1971), solidic (Dy 3.43) and solodic/solonized-solonetz (Dy 3.43) types (Murtha and Crack 1966; Coates 1994). The low dietary-P treatment (P_{defic}) was imposed by grazing the cattle on the P-deficient pasture without any additional dietary P. The P-supplemented treatment (P_{supp}) was achieved by grazing the cattle on the same P-deficient pasture and providing a P supplement during Expt 1 or by grazing pasture fertilized with P in Expt 2. Since each new group of heifers or cows used in the study (i.e. Expts 1a, 1b and 2) had grazed pastures expected to be adequate in P for at least 2 years before introduction to the experimental treatments, it was expected that the animals would initially have had replete body P reserves. Rainfall was recorded at the Lansdown weather station (Bureau of Meteorology Station #33226) c. 2 km from the experimental site.

Experiment 1

The trial paddocks were in an area of P-deficient soil with bicarbonate extractable P (P_B, Colwell 1963) of c. 4 ppm in the top 100 mm of soil and comprised part of the P-deficient treatment paddock described by Coates et al. (2018). The pasture was a mixture of native grasses (*Heteropogon contortus*, *Chrysopogon fallax*, *Aristida* spp. and naturalized *Bothriochloa pertusa*) plus sown sabi grass (*Urochloa mosambicensis* cv. Nixon) and sown legumes (*Stylosanthes hamata* cv. Verano and *S. scabra* cv. Seca). The 16 ha trial area was divided into 2 paddocks of 8 ha. Each was grazed by a group of 4 breeders, which were allocated to the treatments by stratified randomization according to LW. One group (P_{supp} group) received a P supplement via medication of the drinking water with Monophos (NaH_2PO_4) to provide 0.2 g P/L water. The P_{defic} treatment received no P supplement and both groups had access to salt blocks (sodium chloride). The treatment groups were alternated between the 2 paddocks fortnightly to minimize between-paddock effects. Access to water was arranged to maintain the integrity of the treatments.

Measurements were made throughout 4 annual grazing cycles (Expts 1a, 1b, 1c and 1d). Expt 1a commenced in September 1986 with 3.5-year-old cows pregnant with their second calf (second-calf cows, SCC; calving October–December) and continued until June 1987 when the paddocks were destocked for animal welfare reasons owing to severe drought. The paddocks remained destocked until August 1988, when a new draft of 8 pregnant heifers, initially c. 2.5-year-old, (first-calf cows, FCC; calving October–December) was allocated to the 2 treatments (P_{supp} and P_{defic}) by stratified randomization according to LW. These groups of animals remained in the study and received the same treatments through 3 annual cycles: 1988-89 (Expt 1b, FCC), 1989-90 (Expt 1c, SCC; calving December-January) and 1990-91 (Expt 1d, mature cows; calving December-January). The only exception was that one non-pregnant cow in the P_{supp} group was replaced by a P-replete pregnant cow at the end of the Expt 1c grazing cycle. In Expts 1a, 1b and 1c the cows were joined for at least 3 months with 1 physically sound bull per treatment group after calving was complete. Calves were weaned in early to mid-June of each grazing cycle.

Experiment 2

In Expt 2 measurements were made on P_{defic} and P_{supp} groups of FCC which initially were pregnant heifers c. 2.5 years old in April 1994. The P_{defic} heifers (n = 10) grazed a 20 ha paddock that comprised the area used in Expt 1 plus an adjoining 4 ha of similar low-P pasture. The P_{supp} heifers (n = 10) received no P supplement directly but grazed a nearby 16 ha sabi grass-stylo pasture which had been fertilized annually for >10 years with superphosphate at 10 kg P/ha so that improved dietary P was provided by the pasture. This experiment has been described previously (Coates et al. 2018), where the focus was primarily on the mineral density of tail bone. The heifers calved in November-December 1994 and the calves were weaned on 11 May 1995, when the study was terminated. Both groups of breeders were joined with one bull per group for 3 months after calving was completed.

Measurements

Cows and calves were weighed regularly following an overnight fast, usually at about 4 week intervals. Jugular blood samples from the cows were collected on most weigh days and centrifuged to separate plasma, which was retained for subsequent measurement of plasma inorganic phosphorus (PIP) concentrations. PIP was measured at 4–8 week intervals in Expt 1a, predominantly at 4 week intervals in Expts 1b, 1c and 1d, and at about 8 week intervals in Expt 2, and analyses were as described by Murphy and Riley (1962). Samples of feces were obtained from each cow per rectum when the cows were weighed during Expts 1b, 1c and 1d. The $\delta^{13}C$ in the individual samples of feces was measured by mass spectrometry (LeFeuvre and Jones 1988) and used to calculate the proportion of C3 plants (i.e. non-grass components, comprising predominantly *Stylosanthes* spp.) and C4 tropical grasses in the diet (Jones et al. 1979). In addition the concentrations of total P and total N were measured in feces sampled during Expt 1b and part of Expt 1c. Pregnancy rates were determined at weaning by manual palpation of the uterus via the rectum by an experienced operator to select pregnant animals for each new group, and also of the cows at weaning at the end of each annual cycle.

Animal welfare

All experimental procedures involving the animals were carried out according to the Code of Practice for the Care and Use of Animals for Scientific Purposes and with the approval of the relevant Animal Ethics Committees operating when the experiments were conducted.

Calculations and statistical analyses

Statistical analysis within each grazing cycle was restricted to cows that reared a calf to weaning because of the effects of pregnancy and lactation on cow LW and PIP. Statistical analysis was conducted using GENSTAT (release 16.1 9VSN International Ltd, Hemel Hemstead, UK). There was no paddock replication in either experiment and the differences in measured parameters between the P_{defic} and P_{supp} groups of cows at each measurement date were examined using ANOVA with individual animals considered as the experimental units. As the P_{defic} and P_{supp} treatment groups were rotated between paddocks each fortnight in Expt 1, we considered the effects of any paddock differences on response parameters were minimized. The LW of the cows at the beginning of each grazing cycle, and the individual calving dates, were examined as covariates in the analyses of response variables, and included when there was a greater than 90% probability that the covariates did affect the responses.

Results

Seasonal conditions

Monthly rainfall for the grazing years 1986-87 to 1990-91 (Expt 1) and for 1994-95 (Expt 2) and the dates of the seasonal breaks (the first 3 day interval after June 30 when

≥50 mm rain was received) are shown in Table 1. These data highlight the summer-dominant rainfall pattern and the extreme variability in both total and effective annual rainfall in this environment. The 1986-87 grazing year (Expt 1a) ended in severe drought with insufficient rainfall during any 3 day interval to constitute a seasonal break as defined herein. Rainfall during the 6 months January–June 1987 was only 45% of the long-term mean for that interval and the trial area was destocked during the 1987-88 grazing cycle. In contrast, rainfall for 1988-89 and 1989-90 was high at 128 and 129% of the long-term annual average, while that for 1990-91 was excessive (197% of the long-term average) with particularly high rainfall during January-February 1991. In 1994-95 (Expt 2) rainfall was only 36% of the long-term annual average.

Cow LW and LW change

Mean LWs of cows through each grazing cycle are presented in Figure 1. Differences between grazing cycles in the effects of P treatment on cow LWs and patterns of LW change were unexpectedly large due most likely to the large differences between grazing cycles in the amounts and distribution of rainfall. In Expt 1a, when rainfall was much lower than average (Table 1), the differences in LW between P_{defic} and P_{supp} cows increased progressively from the end of November ($P<0.05$). By the end of the annual cycle the P_{supp} cows had gained 30 kg whereas P_{defic} cows had lost 62 kg, i.e. a difference of 92 kg, which was significant ($P<0.01$). Treatment effects on cow LWs during Expt 1b (1988-89) were in marked contrast to those in Expt 1a. Rainfall was well above average from March to June resulting in an extended green season. In addition, on average, the P_{supp} cows calved 28 days earlier than the P_{defic} cows so were lactating for longer during the grazing cycle; this is the likely reason for the lower mean LW of the P_{supp} cows than that of the P_{defic} cows, although these differences failed to reach significance ($P>0.05$). In Expt 1c (1989-90) rainfall was comparable with that in Expt 1a until the end of February 1990, but there was abnormally high rainfall in March and April (346 and 337 mm, respectively). The differences in mean LW between P_{defic} and P_{supp} cows became progressively greater until mid-January 1990, when P_{supp} cows were 59 kg heavier than P_{defic} cows. From mid-January until the end of the grazing cycle in June 1990, LW changes in both groups were similar and the final LW advantage of P_{supp} cows was 49 kg. When initial LW was used as a covariate in the analysis, treatment differences were significant on all weighing dates from August 1989 to March 1990 ($P<0.05$ to <0.001). When calf birth date was used as a covariate, treatment differences in cow LWs were significant from January to June 1990 ($P<0.05$ to <0.01). During the full annual cycle P_{supp} cows gained 43 kg and P_{defic} cows lost 5 kg with the difference approaching significance ($P=0.07$). There was a carryover effect on cow LW (Figure 1) from Expt 1c to Expt 1d such that the average LW of P_{supp} cows was initially 33 kg greater than that of P_{defic} cows. Changes in LWs during the Expt 1d grazing cycle were similar for the 2 treatment groups. When initial

Table 1. Rainfall (mm) during each of the annual cycles for Expts 1 and 2. In Experiment 1 the area was destocked from 10 June 1987 until 4 August 1988 (1987–88). The long-term (1891–1990) average rainfall (BoM 2019) is also given. The seasonal break was calculated as the first 3 day interval after June 30 when ≥50 mm rain was received.

Month	1986-87 Expt 1a	1987-88 Destocked	1988-89 Expt 1b	1989-90 Expt 1c	1990-91 Expt 1d	1994-95 Expt 2	100 year mean
Jul	8	9	48	55	38	0	16
Aug	19	14	12	9	0	0	13
Sep	4	3	0	0	3	0	11
Oct	105	74	41	7	29	16	21
Nov	32	65	52	131	0	0	41
Dec	21	144	224	68	297	29	96
Jan	102	19	114	28	616	53	227
Feb	73	162	186	23	727	129	221
Mar	79	76	151	346	24	46	148
Apr	35	52	179	337	9	8	51
May	7	47	111	79	17	40	31
Jun	23	1	41	88	18	5	29
Total	507	667	1,157	1,171	1,780	326	906
Seasonal break	None[1]	30–31 Dec	10–12 Dec	21–23 Nov	25–27 Dec	10–12 Feb	

[1] There was not sufficient rain during any 3 day interval to meet the designated criterion for a seasonal break.

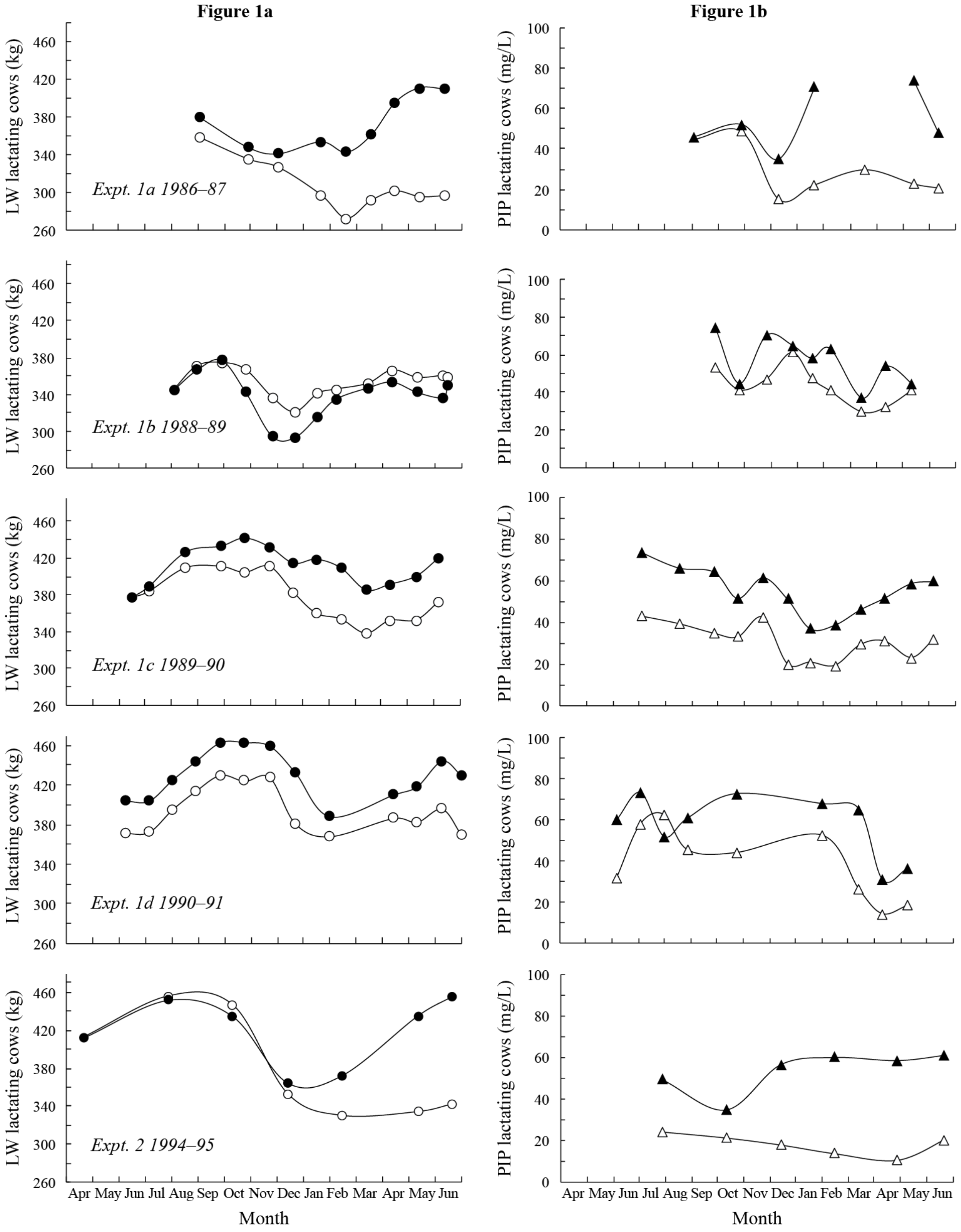


Figure 1a. Treatment mean live weights (LW) of cows grazing P-deficient pasture without (○) or with (●) P supplement through 4 annual cycles (1986–87, 1988–89, 1989–90 and 1990–91), or grazing P-deficient or P-fertilized pasture in 1994-95. **Figure 1b.** Plasma inorganic phosphorus (PIP) concentrations of cows without (Δ) or with (▲) P supplementation or P-fertilizer application through the same annual cycles. Cows in Expt 1 calved in November–December and were weaned in June, while those in Expt 2 calved in December–January and were weaned in mid-May.

LW was included as a covariate in the analysis, differences were not significant ($P=0.14$ to 0.89) except at the end of the grazing cycle in June and July 1991 ($P=0.03$). Through the entire grazing cycle, P_{supp} cows gained 17 kg, while P_{defic} cows lost 5 kg and the difference (22 kg) was significant ($P=0.01$).

In Expt 2 there were no significant differences in LWs between P_{defic} and P_{supp} treatment groups between April and December 1994 by which time calving was complete. Thereafter P_{supp} cows gained LW rapidly while P_{defic} cows virtually maintained LW. The differences between mean LWs of the 2 groups became increasingly greater ($P<0.01$ in February 1995 and $P<0.001$ thereafter). At the end of the annual cycle P_{defic} cows had lost 71 kg LW compared with a 44 kg gain in the P_{supp} group (i.e. a difference of 115 kg LW).

Plasma inorganic phosphorus (PIP) profiles

There were large differences between annual cycles in the effects of treatment on PIP profiles (Figure 1b), with differences apparently related to seasonal rainfall patterns in a similar manner to the differences in the LW profiles. In Expt 1a there were large treatment differences after calving ($P<0.01$) when all cows were lactating. Mean PIP of the P_{defic} cows was only 22 mg/L from December to June, reflecting the effects of low soil P, probably exacerbated by the effects of low rainfall on forage P concentration and the high demand for P during lactation. Over the same interval PIP of P_{supp} cows averaged 57 mg/L, reflecting the increased P intake in this group through supplementation and likely also increased pasture intake. In Expt 1b calving was complete in both groups by the end of December. The PIP of P_{defic} cows for the 6 sampling occasions from December to May averaged 42 mg/L compared with 54 mg/L for the P_{supp} cows, but on no sampling occasion was the difference between groups significant ($P>0.10$). Mean PIP concentrations for all sampling dates in Expt 1c were consistently higher in the P_{supp} treatment than in the P_{defic} group, the differences being significant on all 12 occasions ($P<0.05$ to $P<0.001$). During lactation (December–June), PIP of P_{defic} cows averaged only 26 mg/L, half that of P_{supp} cows (50 mg/L). In Expt 1d, fewer samplings were carried out and PIP in P_{defic} cows remained appreciably lower than in P_{supp} cows for most of the grazing cycle; differences between mean values for the 2 groups between August 1990 and April 1991 were significant on 3 occasions ($P=0.002$ to 0.01) and approached significance on 2 occasions ($P=0.08$). For the 3 sampling occasions conducted during late lactation (March–May 1991) mean PIP of cows in the P_{defic} treatment (20 mg/L) was less than half that of cows in the P_{supp} treatment (44 mg/L). In Expt 2 the PIP in P_{defic} cows for the period July 1994–June 1995 averaged only one-third of the PIP of P_{supp} cows (14 vs. 53 mg/L; $P<0.01$; Figure 1b) and indicated severe and prolonged deficiency of dietary P.

Contribution of Stylosanthes *to the diet and fecal concentrations of P and N*

During the early to mid-wet season (November–January) in Expts 1b, 1c and 1d, when measurements were made, stylo comprised c. 10–30% of the diet selected by both treatment groups of cows (Figure 2). However the proportion of stylo increased progressively from the mid-wet season through to the mid-dry season (February to July), and remained as a high proportion through to the late dry season (August–September). Furthermore, during these latter intervals the P_{supp} cows increased their selection of stylo to a greater extent (to c. 70–85%) than the P_{defic} cows (c. 40–60%).

During the interval from 30 August 1988 to 13 February 1990 (Expt 1b and part of Expt 1c), when measurements were made, the concentration of P in feces of P_{defic} cows averaged 1.93 g P/kg DM, whereas the concentration in P_{supp} cows was consistently higher and averaged 2.41 g P/kg DM (Figure 3a). During Expt 1b fecal P concentration was higher during the wet season (December–April; >2.2 g P/kg DM) than during the following dry season (May–November; 1.5–2.1 g P/kg DM). During the late dry season fecal N concentration was generally 12–14 g N/kg DM in both treatment groups (Figure 3b). However fecal N was generally 14–20 g N/kg DM during the wet season through to the mid dry season (December–July) of Expt 1b, and on average tended to be higher for P_{supp} cows (mean 17.2 g N/kg DM) than for P_{defic} cows (mean 15.1 g N/kg DM).

Calf growth rates and reconception in the cows

Calf growth rates (Table 2) averaged 0.77 kg/d in the P_{defic} treatment groups across the 5 grazing cycles. Calf growth rate was on average 0.09 kg/day higher in the P_{supp} treatment groups, but the difference was significant ($P<0.05$) only for Expt 1a. In Expt 1a, none of the P_{defic} cows, but 3 of the 4 P_{supp} cows, conceived. In Expt 1b, all P_{defic} cows and 3 of the 4 P_{supp} cows conceived. The cow that failed to conceive in the P_{supp} group was comparable in LW and condition with the cows that conceived. All P_{defic} and P_{supp} cows conceived during Expt 1c. Cows were not joined in Expt 1d. In Expt 2, 9 of the 10 P_{supp} cows conceived, while only 1 of the 10 P_{defic} cows conceived.

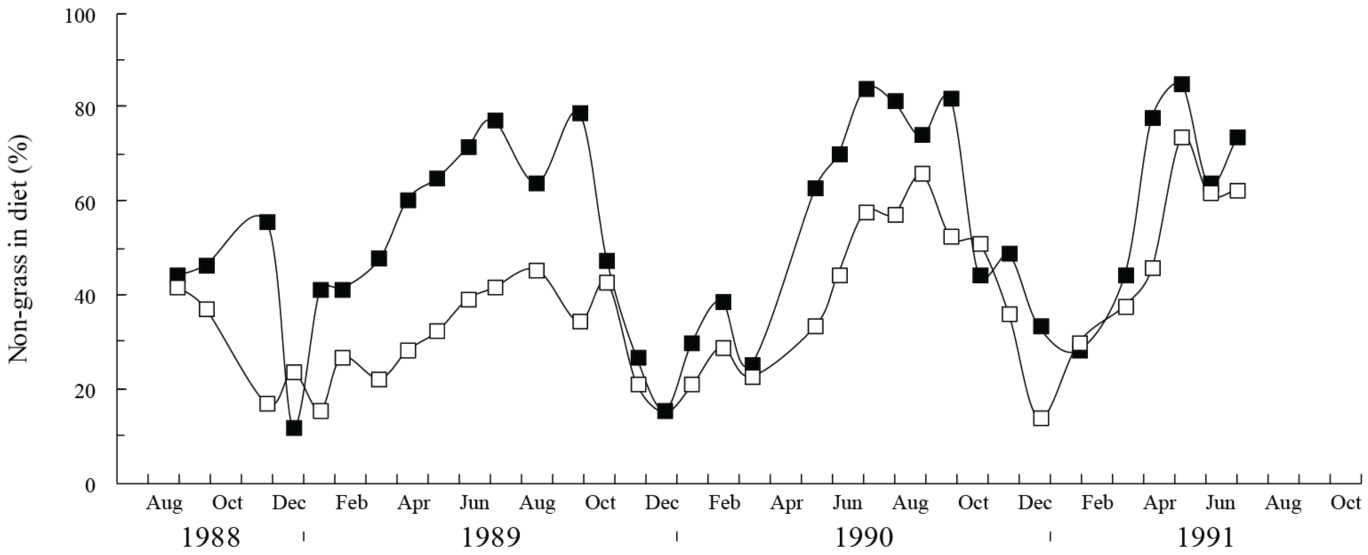
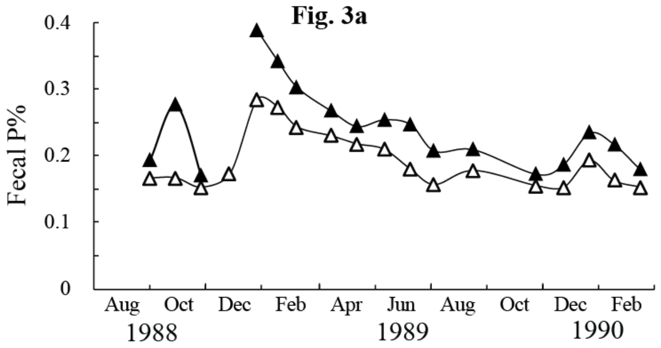


Figure 2. The percentage of non-grass (i.e. principally *Stylosanthes* spp.) in the diet selected by cows not fed P supplement (□) or provided with P supplement (■) from 30 August 1988 until 2 July 1991 during Expts 1b, 1c and 1d. The non-grass in the diet was calculated from the measured $^{13}\delta C$ of feces.



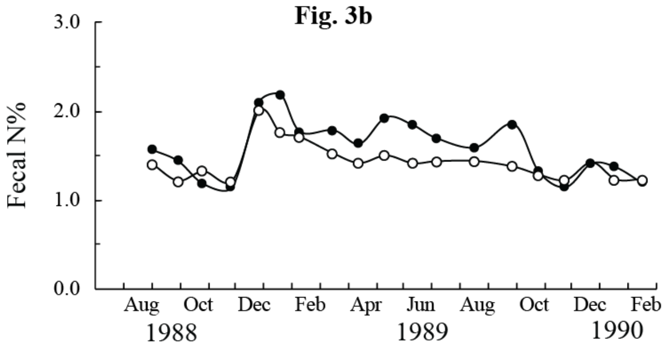


Figure 3a. The concentration of P in feces of cows not fed a P supplement (∆) or provided with P supplement (▲) from 30 August 1988 until 13 February 1990 during Expts 1b and 1c. **Figure 3b**. The concentration of N in feces of cows not fed a P supplement (○) or provided with a P supplement (●) during the same interval.

Table 2. Calf growth rates for Expts 1 and 2. Interval dates and days represent the time from the first weighing after all calves were born through to weaning. Values in parenthesis indicate the number of calves.

Expt	Grazing cycle	Calf growth interval	Days	Calf LW gain (kg/d)		s.e.m.	P
				P_{defic}	P_{supp}		
1a	1986-87	2.12.86–10.6.87	190	0.76 (3)	0.86 (4)	0.026	0.03
1b	1988-89	21.12.88–14.6.89	175	0.73 (3)	0.90 (3)	0.076	0.18
1c	1989-90	16.1.90–6.6.90	141	0.71 (4)	0.74 (4)	0.061	0.48
1d	1990-91	31.1.91–4.6.91	124	0.77 (4)	0.92 (2)	0.051	0.07
2	1994-95	13.12.94–11.5.95	149	0.88 (8)	0.89 (9)	0.026	0.78

Discussion

The most important findings from the study were the large variations between annual cycles in: (i) the performance of breeder cows grazing P-deficient pastures; and (ii) the responses of the breeder cows to the provision of additional dietary P via supplement or fertilizer. The differences between annual cycles in the responses to improved P intake were observed in cow LWs and LW change profiles, PIP profiles, cow conception rates and to some extent calf growth rate, and were associated with large variation in the amount and pattern of rainfall during each annual cycle as shown in Table 1. However, in most inland regions of northern Australia the dry seasons are usually longer, and there is a lower probability of any significant winter rainfall events than at the experimental site. This suggests that the results observed in the present study during the years with the lower rainfall but typical rainfall distribution (Expt 1a and Expt 2) are likely to be most representative of the northern Australian cattle industry.

The large variation between years in the present study was especially apparent with respect to cow LW change. Responses in PIP to improved P intake (Figure 1b) were apparent in 4 of the 5 grazing cycles but were most marked in the 2 years of lower rainfall (Expts 1a and 2). The between-year differences in PIP profiles of the P_{defic} treatment indicated that the severity of dietary P deficiency was not constant across grazing cycles, although PIP concentrations did decline to <20 mg P/L during some intervals in 4 of the 5 annual cycles (the exception being Expt 1b, 1988-89). Thus the breeders in the P_{defic} treatment were often severely deficient in dietary P (Wadsworth et al. 1990; Coates 1994; Anderson et al. 2017), while the PIP concentrations of 50–60 mg P/L in the P_{supp} treatment established that these breeders were ingesting adequate dietary P for their level of production.

The poor LW performance of the P_{defic} cows compared with the P_{supp} cows was most marked in Expts 1a and 2, with mean differences between treatments in annual LW change of 92 and 115 kg, respectively. These large responses to improved dietary P were comparable with large LW responses to P supplement of 62 and 88 kg in breeder cows also grazing grass-stylo pastures during 2 annual cycles in another experiment at a P-deficient site at Springmount, Mareeba, in the seasonally dry tropics of northern Australia (Miller et al. 1998; Dixon et al. 2016; Coates et al. 2018). In Expt 2 additional dietary P was provided via applied P fertilizer, which potentially had additional dietary advantages besides improved P nutrition. However, previous work with similar stylo-grass pastures and low-P soil at the same location showed that annual LW gain was the same for yearling heifers grazing either pasture fertilized annually with superphosphate or grazing unfertilized pasture but supplemented with P (Coates 1994). It therefore appears unlikely that in the present study factors other than dietary P contributed in any substantial way to differences in productivity between the P_{supp} and P_{defic} treatments in Expt 2.

We hypothesize that the variation in responses to additional dietary P between annual cycles was due primarily to variation in the amounts and distribution of rainfall (i.e. seasonal conditions) with consequences for P concentration in the diets selected. The absence of treatment effects on cow LW changes during Expt 1b was most likely due to the favorable seasonal conditions throughout Expt 1b with well-above-average rainfall and an extended period of pasture growth through March and April, i.e. extended green season as defined by McCown (1981). This was in marked contrast to the responses during Expt 1a and Expt 2. Since P concentration is highest in young green leaf and lowest in mature, dry forage, an extended green season will promote higher P intakes through the grazing cycle (Coates 1994). Therefore, favorable seasonal conditions during Expt 1b probably resulted in better-than-average dietary P intakes, especially during lactation. This was supported by the higher PIP concentrations of the P_{defic} cows during Expt 1b, i.e. mean PIP concentration during the December–June lactation interval (41 mg P/L) was appreciably higher than the mean concentrations of 22, 26 and 14 mg P/L for Expts 1a, 1c and Expt 2, respectively (Figure 1b). In Expt 1d the PIP concentrations for the P_{defic} treatment cows remained high (>40 mg P/L, mean 52 mg P/L from July to January) for much of the grazing cycle and declined to much lower levels only late in the grazing cycle. This may have been a consequence of the high rainfall from December 1990 to February 1991 in this experiment (Table 1).

The observation in the present study that the adverse effects of P deficiency in breeder cows were much greater in low-rainfall years is in accord with past observations in the northern Australian rangelands with low-P soils. The symptoms of acute P deficiency such as 'peg-leg' and reduced breeder productivity have been observed to occur most often during droughts and low-rainfall years (Turner et al. 1935; Rose 1954; Barnes and Jephcott 1955, 1959; Ferguson and Sklan 2005). Similarly, a 5-year experiment in semi-arid New Mexico, USA, examining effects of P supplementation on breeder cow performance, reported that the absence of P supplementation had a detrimental effect only when coupled with the effects of drought (Judkins et al. 1985). In 2 studies reported by Holroyd et al. (1977; 1983) with breeders grazing native grass pasture or native grass-stylo pastures, there was relatively low variation among years in the LW responses of breeders to P supplements fed during the wet and early dry seasons at a site in the seasonally dry tropics of northern Australia similar to that at Lansdown. However this was associated with low variation in both total rainfall and the rainfall pattern. We suggest, therefore, that the present study is in accord with these other reported studies in demonstrating a large impact of variable seasonal conditions on the LWs and fertility of breeder cows grazing pastures on low-P soils.

The magnitude of the responses in P_{defic} cows to the provision of additional dietary P in the present study was directly related to the extent of the annual LW losses in the P_{defic} cows (Figure 4). The largest LW responses to additional dietary P occurred during those annual cycles when the P_{defic} cows lost the greatest LW. Furthermore, large LW responses of P_{defic} cows to additional dietary P in 2 drafts of another comparable study with similar genotype breeders in northern Queensland (Miller et al. 1998; Dixon et al. 2016; Coates et al. 2018) were consistent with this relationship. Presumably the annual LW gain of P_{supp} cows in the present study was constrained by the availability of other nutrients such as protein and energy rather than a lack of P through the annual cycle. The magnitude of the cow LW responses to P supplement was also related to the PIP of the P_{defic} cows during lactation; these PIP concentrations were, except for Expt 1b, in the range 14–26 mg P/L indicating severe P deficiency (Wadsworth et al. 1990; Coates 1994; Anderson et al. 2017). The high PIP concentrations (50–59 mg P/L) in the P_{supp} cows in all annual cycles established that the breeders in this treatment were ingesting adequate dietary P. Thus the variations in the responses to P supplement were closely linked to the amount and pattern of rainfall during each annual cycle and to the performance of the P_{defic} breeders. However, the magnitude of the variations in the responses of P_{defic} breeders to P supplements in the present study and in that of Miller et al. (1998), where the breeders also grazed stylo-grass pastures growing on P-deficient soils, may have been greater than would occur with breeders grazing native grass pastures containing little or no legume. Stylo-grass pastures growing on low-P soils are usually higher in protein and metabolizable energy relative to P concentration than grass pastures, and also have a high Ca:P ratio (e.g. often >10:1 and up to 25:1), which reduces bone-P mobilization (Minson 1990; Coates 1994). Consequently, the responses of growing cattle to supplementary P will often be much higher for stylo-grass pastures than for grass pastures. This may also occur with breeders grazing grass-stylo pastures. A lesser variation between annual cycles in the LW response of breeders grazing grass pastures to P supplements would presumably lead to a lesser variation in other measures of breeder herd productivity.

An important observation in the present study was that calf growth was generally similar in both unsupplemented and supplemented groups of breeders. Thus the breeders must have largely maintained milk production, regardless of the dietary P deficiency, even when undergoing substantial LW loss through annual cycles. The LW gain of calves suckling P_{defic} cows was on average only 0.09 kg/day (or c. 10%) lower than that of calves suckling P_{supp} cows, a difference of generally lower economic importance than cow fertility and mortality in rangeland production systems (M. Bowen and F. Chudleigh pers. comm.). The *Bos indicus* × *Bos taurus* genotype cows used in the present study must have been able to mobilize body reserves of both energy and P to maintain lactational output when nutritional intake was insufficient for LW maintenance. However, such mobilization of body reserves by lactating cows must clearly depend on availability of sufficient body reserves for this purpose. The P_{defic} cows in the present study apparently had sufficient body reserves for this purpose but obviously P mobilization can continue only until body P reserves become depleted. The adverse effects of exhaustion of body P reserves with large and severe effects in the second and third years of ongoing P deficiency on intake, LW and milk production have been shown by Read et al. (1986) for Bonsmara crossbred beef cows and by Valk and Sebek (1999) for dairy cows. If the cows used in Expt 1a or Expt 2 had become pregnant and continued for another annual cycle of severe P deficiency, then poor lactational performance and/or cow mortality would probably have occurred. When cows mobilize body P and body energy reserves (as LW and body condition) during early lactation it is obviously essential that the reserves be replaced in late lactation or post-weaning for annual calving in harsh and P-deficient seasonally dry tropical environments (Dixon et al. 2017).

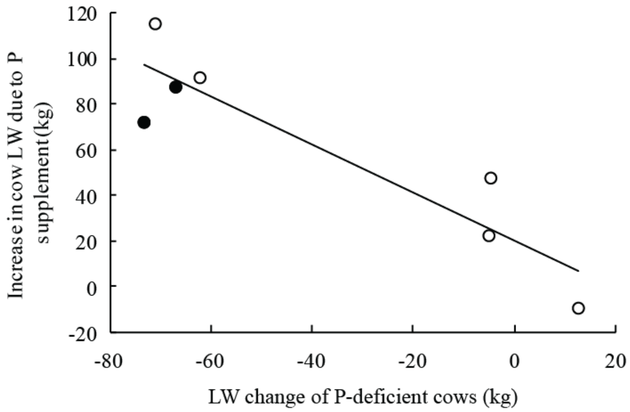


Figure 4. The relationship in paddock groups of cows between the increase in cow LW due to the provision of P supplements and the LW change of the P_{defic} cows during the annual cycle for groups of cows in the present study (o) and for 2 annual drafts of an experiment (●) at Mareeba, north Queensland, Australia, where breeder cows of similar genotype grazed P-deficient pasture and received no supplement or were supplemented with P (Miller et al. 1998). The regression of the results from the present study was: $Y = 19.9 - 1.29 X$ ($R^2 = 0.93$; $P<0.01$). The regression of the pooled results was: $Y = 20.3 - 1.06 X$ ($R^2 = 0.84$; $P<0.01$).

Although the number of cows in each treatment during each annual cycle was small in the present study, the pronounced effects of P_{defic} on pregnancy rates in cows in Expts 1a and 2, but the absence of differences in Expts 1b and 1c (not measured in Expt 1d), indicate the differences likely to occur in commercial herds. The very poor re-conception rates in the P_{defic} cows in Expts 1a and 2 were associated with low cow LW and body condition throughout the mating period. Breeder cows grazing P-deficient pastures are often prone to lactational anoestrus and fail to conceive while lactating, resulting in patterns of either delays in re-conception in consecutive years (i.e. 'slippage') or calving every second year (e.g. Read et al. 1986; McGowan et al. 2014; Dixon et al. 2017). Such a calving pattern was not observed in the P_{defic} cows during the grazing cycles of Expts 1b, 1c and 1d but was probably a consequence of the sequence of annual cycles with well-above-average rainfall (Table 1).

Conclusions

In breeders grazing P-deficient *Stylosanthes*-grass pastures at a site in a seasonally dry environment, there was wide variation among annual cycles in the severity of P deficiency and the LW performance and LW responses of reproducing breeders to provision of adequate dietary P. This was apparently associated with variation in seasonal conditions and dietary P intakes of un-supplemented animals. Thus the assessment of the severity and economic consequences of P deficiency on breeder performance within a given paddock requires cognizance of potential between-year differences and may require diagnostic measurements over a number of annual grazing cycles that encompass a range of seasonal conditions.

Acknowledgments

We thank Michael Breen and Jennifer Stanford for valuable technical assistance and for funding support from Meat and Livestock Australia (formerly the Meat Research Corporation).

References

(Note of the editors: All hyperlinks were verified 11 April 2019.)

Anderson ST; Kidd LJ; Benvenutti MA; Fletcher NT; Dixon RM. 2017. New candidate markers of phosphorus status in beef breeder cows. Animal Production Science 57:2291–2303. doi: 10.1071/AN17363

BoM (Australian Bureau of Meteorology). 2019. BoM, Melbourne, VIC, Australia. www.bom.gov.au.

Barnes JE; Jephcott BR. 1955. Phosphorus deficiency in cattle in the Northern Territory and its control. The Australian Veterinary Journal 31:302–312. doi: 10.1111/j.1751-0813.1955.tb05473.x

Barnes JE; Jephcott BR. 1959. Biochemical studies of cattle in the Northern Territory. Part 1: Seasonal variation of blood phosphorus and haemoglobin levels in the Barkly Tableland. The Australian Veterinary Journal 35:276–279. doi: 10.1111/j.1751-0813.1959.tb08476.x

Coates DB. 1994. Effect of phosphorus as fertilizer or supplement on pasture and cattle productivity in the semi-arid tropics of north Queensland. Tropical Grasslands 28:90–108. bit.ly/2ZqOIIk

Coates DB; Dixon RM; Murray RM; Mayer RJ; Miller CP. 2018. Bone mineral density in the tail-bones of cattle: effect of phosphorus status, liveweight, age and physiological status. Animal Production Science 58:801–810. doi: 10.1071/AN16376

Colwell JD. 1963. The estimation of phosphorus fertilizer requirements of wheat in southern New South Wales by soil analyses. Australian Journal of Experimental Agriculture and Animal Husbandry 3:190–197. doi: 10.1071/EA9630190

Cook GD; Heerdegen RG. 2001. Spatial variation in the duration of the rainy season in monsoonal Australia. International Journal of Climatology 21:1723-1732. doi: 10.1002/joc.704

CSIRO. 2007. Nutrient requirements of domesticated ruminants. CSIRO Publishing, Melbourne, VIC, Australia. bit.ly/31zQw3F

Dixon RM; Coates DB; Holmes W; English B; Rolfe J. 2011. Phosphorus nutrition and management – overcoming constraints to wider adoption. In: Proceedings of the Northern Beef Research Update Conference (NBRUC 2011), Darwin, Australia, 3–4 August 2011. p. 102–109.

Dixon RM; Coates DB; Mayer RJ; Miller CP. 2016. Productivity and phosphorus content of rib and tail bones in reproducing cows ingesting diets deficient or adequate in phosphorus. In: Proceedings of the 31st Biennial Conference of the Australian Society of Animal Production. Glenelg, Australia, 4–7 July 2016. p. 93–94. bit.ly/2ZnBRGH

Dixon RM; Kidd LJ; Coates DB; Anderson ST; Benvenutti MA; Fletcher MT; McNeill DM. 2017. Utilizing mobilization of body reserves to improve the management of phosphorus nutrition of breeder cows. Animal Production Science 57:2280–2290. doi: 10.1071/AN17324

Ferguson JD; Sklan D. 2005. Effects of dietary phosphorus and nitrogen on cattle reproduction. In: Pfeffer E; Hristov AN, eds. Nitrogen and phosphorus nutrition of cattle: reducing the environmental impact of cattle operations. p. 233–253. CAB International, Wallingford, UK. doi: 10.1079/9780851990132.0233

Holroyd RG; Allan PJ; O'Rourke PK. 1977. Effect of pasture type and supplementary feeding on the reproductive performance of cattle in the dry tropics of north Queensland. Australian Journal of Experimental Agriculture and Animal Husbandry 17:197–206. doi: 10.1071/EA9770197

Holroyd RG; O'Rourke PK; Clarke MR; Loxton ID. 1983. Influence of pasture type and supplement on fertility and liveweight of cows, and progeny growth rate in the dry tropics of northern Queensland. Australian Journal of Experimental Agriculture and Animal Husbandry 23:4–13. doi: 10.1071/EA9830004

Jones RJ; Ludlow MM; Troughton JH; Blunt CG. 1979. Estimation of the proportions of C_3 and C_4 plant species in the diet of animals from the ratio of natural ^{12}C and ^{13}C isotopes in the faeces. The Journal of Agricultural Science 92:91–100. doi: 10.1017/S0021859600060536

Jones RJ; Coates DB; McCaskill MR. 1990. Pasture and climatic effects on cattle liveweight gain from stylo-based pastures in the seasonally dry tropics. Proceedings of the Australian Society of Animal Production 18:260–263. livestocklibrary.com.au/handle/1234/8108

Judkins MB; Wallace JD; Parker EE; Wright JD. 1985. Performance and phosphorus status of range cows with and without phosphorus supplementation. Journal of Range Management 38:139–143. doi: 10.2307/3899257

LeFeuvre R; Jones RJ. 1988. Static combustion of biological samples sealed in glass tubes as a preparation for $\delta^{13}C$ determination. The Analyst 13:817–823. doi: 10.1039/AN9881300817

McCosker T; Winks L. 1994. Phosphorus nutrition of beef cattle in Northern Australia. Department of Primary Industries, Brisbane, Australia.

McCown RL. 1981. The climatic potential for beef cattle production in tropical Australia: Part III – Variation in the commencement, cessation and duration of the green season. Agricultural Systems 7:163–178. doi: 10.1016/0308-521X(81)90044-5

McGowan M; McCosker KD; Fordyce G; Smith DR; O'Rourke P; … Jephcott S. 2014. Northern Australian beef fertility project: Cashcow. Final Report B.NBP.0382. Meat & Livestock Australia Ltd., Sydney, Australia. bit.ly/2X4l4XH

McLennan SR; Hendricksen RE; Beale IF; Winks L; Miller CP; Quirk MF. 1988. Nutritive value of native pastures in Queensland. In: Burrows WH; Scanlon JC; Rutherford MT, eds. Native pastures in Queensland. Queensland Department of Primary Industries, Brisbane, Australia. p. 125–159.

Miller CP; Coates DB; Ternouth JH; White SJ. 1998. Phosphorus management for breeding cattle in northern Australia. Final Report Project DAQ093. Meat & Livestock Australia Ltd., Sydney, Australia. bit.ly/2wWTMI1

Minson DJ. 1990. Forage in ruminant nutrition. Academic Press, New York, USA. doi: 10.1016/B978-0-12-498310-6.X5001-9

Murphy GM; Riley JP. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27:31–36. doi: 10.1016/S0003-2670(00)88444-5

Murtha GG; Crack BJ. 1966. Soils of the CSIRO pasture Research Station 'Lansdown', Townsville, Queensland. Divisional Report 1/66. Division of Soils, CSIRO, Melbourne, VIC, Australia.

Northcote KH. 1971. A factual key for the recognition of Australian soils. 3rd Edn. Rellim Technical Publications, Glenside, SA, Australia.

Read MVP; Engels EAN; Smith WA. 1986. Phosphorus and the grazing ruminant. 2. The effects of supplementary P on cattle at Glen and Armoedsvlakte. South African Journal of Animal Science 16:7–12. bit.ly/2wUI6Wh

Rose AL. 1954. Osteomalacia in the Northern Territory. The Australian Veterinary Journal 30:172–177. doi: 10.1111/j.1751-0813.1954.tb07618.x

Suttle NF. 2010. Mineral nutrition of livestock. 4th Edn. p. 122–167. CAB International, Wallingford, UK. bit.ly/2IHOfup

Turner AW; Kelley RB; Dann AT. 1935. Peg-leg of cattle in North Queensland. Journal of the Council for Scientific and Industrial Research 8:120–132. bit.ly/2WIBx3I

Valk H; Sebek LBJ. 1999. Influence of long-term feeding of limited amounts of phosphorus on dry matter intake, milk production and the body weight of dairy cows. Journal of Dairy Science 82:2157–2163. doi: 10.3168/jds.S0022-0302(99)75459-7

Wadsworth JC; McLean RW; Coates DB; Winter WH. 1990. Phosphorus and beef production in northern Australia. 5. Animal phosphorus status and diagnosis. Tropical Grasslands 24:185–196. bit.ly/2ZnVBtN

Weston EJ. 1988. The Queensland environment. In: Burrows WH; Scanlon JC; Rutherford MT, eds. Native pastures in Queensland: The resources and their management. Queensland Department of Primary Industries, Brisbane, Australia. p. 13–20.

Winks L. 1984. Cattle growth in the dry tropics of Australia. Review number 45. Australian Meat Research Committee, Sydney, Australia.

Winks L. 1990. Phosphorus and beef production in northern Australia. 2. Responses to phosphorus by ruminants – a review. Tropical Grasslands 24:140–158. bit.ly/2WLhc2z

(Received for publication 10 December 2017; accepted 1 May 2019; published 30 June 2019)