Calcium and phosphorus requirements of the ewe during pregnancy and lactation

2. Phosphorus

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1. Mineral balance and radioisotope studies have been carried out to test the adequacy of the recent Agricultural Research Council (1980) recommendations for calcium and phosphorus for pregnant and lactating ewes. At the same time, P metabolism was compared throughout pregnancy and lactation in ewes fed according to these recommendations and in ewes fed a plentiful supply of dietary Ca and P.

2. Bone mineral stores were mobilized in late pregnancy and early lactation, irrespective of the rate of P absorption. These stores were then replaced in mid- to late lactation in ewes given the plentiful Ca and P intake but not in the ewes given the restricted intake.

3. Results suggest that these changes in bone stores occurred as a result of changes in Ca requirements rather than in P requirements, and that accretion of P into bone or resorption of P from bone occurred merely as a conseqence of this change in Ca requirements. Immediate demands for P for maintenance and fetal or milk production do not reflect net P demands, which also take into account changes in bone P metabolism.

4. The rate of P absorption was directly related to net demands and the rate of endogenous excretion was inversely related to net demands.

5. Absorption and endogenous faecal loss of P were also both directly related to P intake.

6. A lack of dietary Ca, particularly in mid- to late lactation, makes it impossible to draw conclusions on the adequacy of the Agricultural Research Council (1980) recommendations for P. Results do suggest, however, that P requirements ought to be calculated according to net demands for P rather than immediate demands.

There is concern over the recent drastic reduction by the Agricultral Research Council (ARC, 1980) in recommendations of calcium and, more particularly, of phosphorus requirements for sheep and cows at different stages of growth, pregnancy and lactation (Cooke, 1982; Gueguen, 1982). This reduction highlights the considerable variation in recommendations that is possible by different interpretations of the same research findings. For example, Table 1 shows recommendations for P by the ARC (1965, 1980), the (US) National Research Council (NRC, 1968, 1975) and the Institut National de la Recherche Agronomique (INRA, 1978) for a 50 kg sheep giving an average of 1·36 l milk/d during the first 8–10 weeks of lactation. Whereas the ARC (1980) recently reduced their recommended requirement from 7·0 to 4·1 g/d, the NRC (1975) increased their recommendation from 4·6 to 7·8 g/d. INRA (1978), meanwhile, recommended an intermediate value of 5·8 g/d.

The present work was carried out to test the adequacy of the recent ARC (1980) Ca and P recommendations for pregnant and lactating ewes. At the same time, Ca and P metabolisms were compared throughout pregnancy and lactation in ewes fed according to these ARC (1980) recommendations and in ewes fed a plentiful supply of dietary Ca and P. The results of studies of P metabolism are presented in this paper, and those of Ca metabolism in the preceding paper (Braithwaite, 1983).

Table 1. *Recommendations of phosphorus requirements (g/d) for a 50 kg ewe giving an average of 1·36 l milk/d during the first 8–10 weeks of lactation*

Reference...	ARC		NRC		INRA
	(1965)	(1980)	(1968)	(1975)	(1978)
P recommendation	7·0	4·1	4·6	7·8	5·8

ARC, Agricultural Research Council; NRC, (US) National Research Council; INRA, Institut National de la Recherche Agronomique.
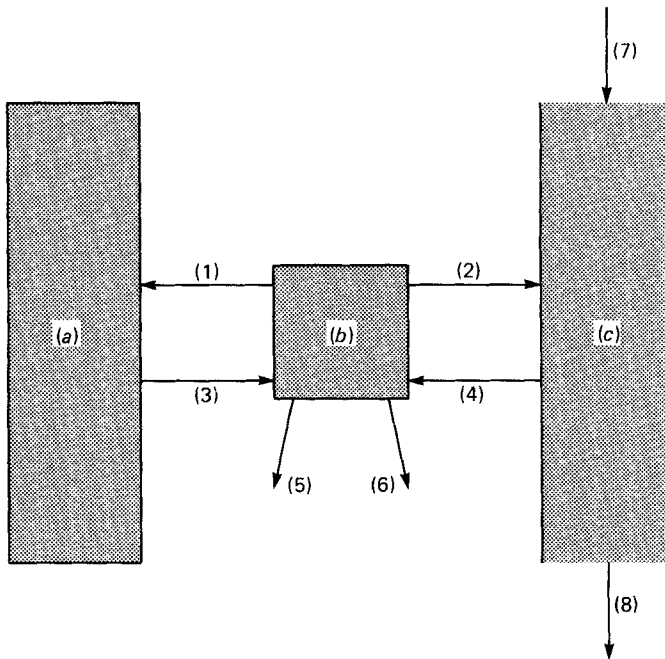

Fig. 1. Scheme of phosphorus metabolism. (*a*) Non-exchangeable P of bone and soft tissues, (*b*) central pool of exchangeable P, (*c*) gut. (1) P accretion into bone (P_{o+}), (2) P secretion in digestive juice (P_{sec}), (3) P resorption from bone (P_{o-}), (4) absorbed dietary P (P_a) and absorbed digestive juice P (P_d), (5) P in milk (P_m), (6) P in urine (P_u), (7) P intake (P_i), (8) unabsorbed dietary P ($P_i - P_a$) and unabsorbed digestive juice P ($P_{sec} - P_d$).

EXPERIMENTAL

Scheme of P metabolism

Fig. 1 shows a diagrammatic representation of the model of P metabolism. This model consists of a central pool of exchangeable P, of which blood inorganic P forms a part, and which P may enter or leave by a limited number of routes. P enters the pool by absorption from the intestine (absorbed dietary P (P_a) and absorbed digestive juice P (P_d)) and by resorption from bone and soft tissues (P_{o-}). It leaves by secretion in digestive juices (P_{sec}), by excretion in the urine (P_u), by accretion into bone and soft tissues (P_{o+}) and by secretion into milk (P_m).

The digestive juice secretion, which in ruminants is considerable, occurs mainly in the

saliva, and this P is then largely reabsorbed in the small intestine. Absorbed P is therefore a mixture of dietary and digestive juice P, whilst endogenous faecal P (P_f) is that portion of the digestive juice P that escapes reabsorption ($P_{sec} - P_d$).

Under steady-state conditions, the size of the exchangeable pool remains constant and the total rate of exit of P is equal to the rate of entry. Hence

$$P_u + P_{sec} + P_{o+} + P_m = P_a + P_d + P_{o-}. \tag{1}$$

Since part (P_d) of the salivary P is reabsorbed into the exchangeable pool from the intestine, the total irreversible loss of P from the pool (P_T) is equal to the total loss minus P_d, i.e.

$$P_T = P_u + P_{sec} + P_{o+} + P_m - P_d \tag{2}$$

but

$$P_{sec} - P_d = P_f, \tag{3}$$

therefore

$$P_T = P_u + P_f + P_{o+} + P_m. \tag{4}$$

The method of kinetic analysis is based on that of Aubert & Milhaud (1960) used in Ca studies. A known amount of radioactive P (^{32}P) is injected intravenously into the experimental animal and measurements done on serial blood samples taken over the next 7 d allow the specific radioactivity–time curve of serum inorganic P to be plotted. The daily intake of dietary P and the daily loss of P in urine, faeces and milk is measured together with the total radioactivity lost in urine, faeces and milk.

The specific radioactivity–time curve is resolved by standard methods of curve analysis into five exponentials. Three are taken to result from exchange of serum inorganic P with sub-compartments of the central pool, one from the irreversible loss of P from the pool and one from the exchange with a slowly exchangeable compartment of bone and soft tissues. The sum of these five exponentials is the equation of the curve.

The size of the exchangeable pools and the rate of total irreversible loss of P from the central pool can be obtained from this equation by the method of Aubert & Milhaud (1960) or by the simplified method of Parsons (1968). The integral of the curve gives, in effect, the mean specific radioactivity of the P in the central pool over the period of the experiment. If it is assumed that P lost from this central pool at any given time has the same specific radioactivity as the inorganic P of the blood, then the amount of endogenous P lost in the urine, faeces or milk can be calculated. Thus

$$P_u = \frac{\text{Total radioactivity in urine (0–7 d)}}{\text{Mean specific radioactivity of blood inorganic P (0–7 d)}}. \tag{5}$$

Both P_u and P_m can also be measured chemically, and values usually agree well with those calculated from measurements of radioactivity. When calculating endogenous faecal P, an allowance is made for the time lag between secretion of radioactivity into the gut and its excretion in the faeces.

Once P_T, P_u, P_f and P_m have been determined, P_{o+}, the rate of accretion of P into bone and soft tissues, can be calculated from eqn (3).

It is not possible with the present methods to distinguish between bone and soft tissue P, and only a combined value for accretion rate can be calculated. It is recognized that this combined value may be subject to error. Calculations are based on the assumption that no radioactivity returns from the non-exchangeable pool during the period of the experiment. Whilst this is probably true of bone, it may not be true for soft tissue P. Nevertheless, previous studies with 1α-hydroxycholecalciferol-treated and control sheep (Braithwaite, 1980) showed similar changes in the bone and soft tissue P metabolism as in

the bone Ca metabolism, which suggests that this value is a useful indicator of changes in bone metabolism, particularly in comparative studies.

The rate of absorption of dietary P from the intestine (P_a), can be obtained from the equation:

$$P_a = P_i - F + P_f, \tag{6}$$

where P_i is the rate of ingestion and F the rate of loss of P in the faeces as measured chemically. The equation takes account of the fact that some of the P present in the faeces is unabsorbed salivary P.

The fractional absorption of dietary P is then given by the equation:

$$\text{Fraction of dietary P absorbed} = \frac{P_a}{P_i}. \tag{7}$$

If the assumption of Young et al. (1966 b) – that salivary and dietary P are completely exchangeable and that salivary P is reabsorbed with the same efficiency as dietary P – is accepted, then the salivary secretion rate (P_{sec}) can be calculated.

$$P_{sec} = \frac{P_f}{1 - \text{Fraction of dietary P absorbed}} \tag{8}$$

The total body retention of P (PΔ) is equal to the difference between the P intake and the total P loss.

$$P\Delta = P_i - (P_u + F + P_m). \tag{9}$$

This P is assumed to be retained only in bone and soft tissues, and changes in retention, which can be positive or negative, are the result of changes in the rate of accretion of P into or resorption of P from bone and soft tissues.

Since P retention is equal to the difference between the rate of accretion (P_{o+}) of P into bone and soft tissues and the rate of resorption (P_{o-}) from these tissues, P_{o-} can be determined.

$$P_{o-} = P_{o+} - P\Delta \tag{10}$$

The definitions of P demands used in this paper are as follows: the immediate P demand of pregnancy or lactation is the requirement for fetal or milk production only (P_m); the net P demand of pregnancy or lactation is the sum of the fetal or milk requirement and the requirement for P retention (the bone and soft tissue requirement), i.e. $P_m + P\Delta$; the retention requirement can be positive or negative depending on whether net deposition or net mobilization of bone and soft tissue is occurring.

Animals, diet and experimental procedure

These are described in the preceding paper (Braithwaite, 1983).

Methods

Total P content of urine and ashed samples of food, faeces, fetuses and milk were determined by the procedure of Fiske & Subbarow (1925) modified (Technicon Instruments Corporation, 1967) for use with an AutoAnalyzer. Serum inorganic P was measured by the same procedure after first precipitating the protein with trichloracetic acid (Manston, 1966).

Radioactivity in the various samples was measured by the methods described in the preceding paper (Braithwaite, 1983).

Table 2. *Phosphorus metabolism in ewes given a plentiful calcium and P intake during pregnancy and lactation*

	At mating	Pregnancy (130–137 d)	Lactation (d)				Post-lactation (d)		Pooled standard deviation (44 df)
			14–21	42–49	63–70	94–99	7–14	28–35	
No. of animals...	3	5	5	6	3	3	3	3	
Rate (mg/d per kg body-wt) of:									
Ingestion of P (P_i)	198·0	193·1	283·6	296·0	316·7	327·3	314·7	312·9	6·53
Loss of P in faeces (F)	195·0	176·9	275·9	270·0	258·9	266·8	287·3	306·2	9·12
Excretion of P in urine (P_u)	2·0	6·6	1·8	3·8	4·3	1·6	14·7	1·2	4·36
Loss of P to fetus or milk (P_m)	—	10·7	40·4	25·9	16·9	12·9	—	—	9·52
Retention of P (PΔ)	+1·0	−1·1	−34·5	−3·7	+36·6	+46·0	+12·7	+5·5	9·62
Endogenous loss of P in faeces (P_f)	63·7	61·6	111·6	103·0	93·9	91·6	94·5	111·6	5·76
Secretion of P in saliva* (P_{sec})	96·1	103·5	184·3	188·4	181·4	171·2	154·2	179·4	23·22
Absorption of P (P_a)	66·7	77·8	119·3	129·0	151·7	152·1	121·9	118·3	8·89
Accretion of P into bone and soft tissues (P_{o+})	46·3	40·9	35·6	35·8	45·9	44·3	29·0	23·6	7·20
Resorption of P from bone and soft tissues (P_{o-})	45·3	42·4	70·1	39·5	9·3	−1·7	16·3	18·1	11·69
Dietary P absorbed (%)	33·7	40·3	42·1	43·6	47·9	46·5	38·7	37·8	4·19
Rapidly exchangeable pool of P (mg/kg body-wt)	29·3	37·0	40·3	35·6	32·2	30·8	27·6	11·6	9·20
Slowly exchangeable pool of P (mg/kg body-wt)	202·0	219·1	222·0	231·1	251·9	224·9	209·1	116·0	23·83
Serum P (mmol/l)	2·44	2·20	1·76	1·80	1·97	1·68	2·25	2·00	0·29
Milk yield (ml/d)	—	—	1610	800	510	460	—	—	—

* Obtained from faecal endogenous loss assuming that salivary P is reabsorbed with the same efficiency as dietary P.
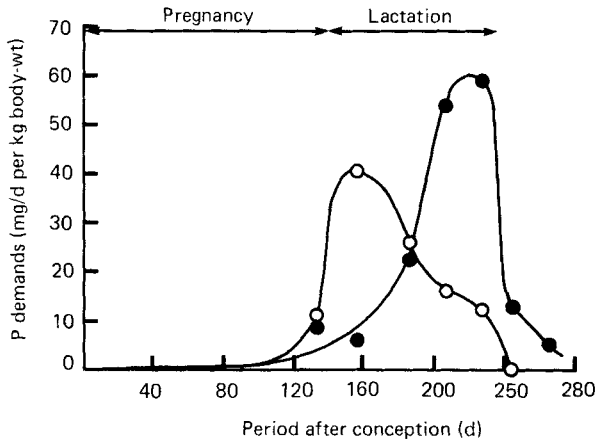
Fig. 2. Variations in immediate (○) and net (●) demands for phosphorus during pregnancy and lactation (mg/d per kg body-weight) in ewes given the plentiful dietary calcium and P intake.
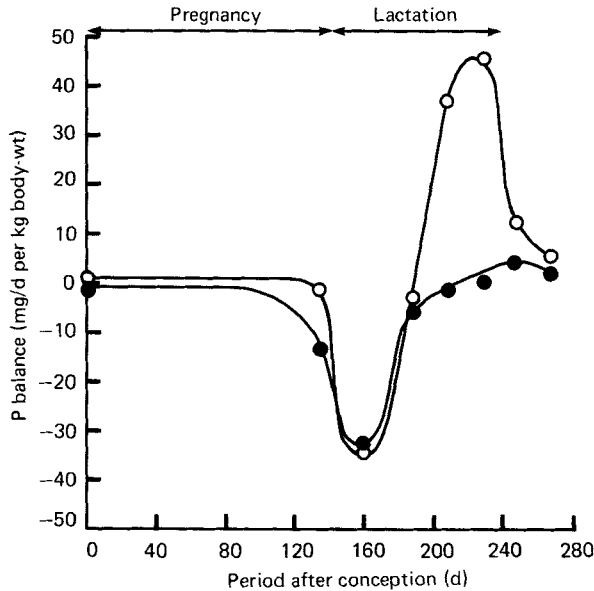

Fig. 3. Phosphorus balance, during pregnancy and lactation, of ewes given the plentiful calcium and P intake (○) and of ewes given the Ca and P intake restricted to Agricultural Research Council (1980) recommendations (●).

RESULTS

Mean values of the various processes of P metabolism at different stages of pregnancy and lactation are shown in Tables 2 and 3. Figs. 2, 3 and 4 show composite curves plotted from these mean values. Although these curves are obtained from many different animals, they do, nevertheless, show the changes which occur throughout the whole of the reproductive cycle.

P metabolism in ewes given a plentiful supply of dietary Ca and P (Table 2)

The additional requirements for P associated with fetal and milk production increased in late pregnancy, reached a peak in early lactation and then slowly decreased (Fig. 2). The rate of absorption of P, which was already high in pregnancy, increased in early lactation as the dietary P intake was increased (Table 2). The efficiency of absorption, however, remained low. In mid- to late lactation, despite the falling demands for milk P (Fig. 2), the amount of P absorbed was increased even further. Since the P intake remained fairly constant, this increase was largely achieved by an increase in absorption efficiency (Table 2).

The endogenous loss of P in the faeces also increased at the onset of lactation but then decreased slightly in mid- to late lactation.

In spite of the plentiful supply of dietary P, P was mobilized from bone and soft tissues in late pregnancy and early lactation when the rate of resorption increased to a high value relative to accretion. At this time, P retention became negative (Fig. 3). Bone and soft tissue stores of P were then replenished in mid- to late lactation when the rate of resorption decreased to a low value relative to accretion. P retention now became positive. Integration of the balance curve (Fig. 3) shows that approximately 65 g of P were lost during pregnancy and early lactation in the plentiful Ca and P intake ewes, and that this P was more than adequately replaced by 5 weeks post-lactation.

P metabolism in ewes given a dietary Ca and P intake restricted to the ARC (1980) recommendations (Table 3)

Although changes in P demands for fetal and milk production (Fig. 4) followed a similar pattern to that found in ewes given the plentiful Ca and P intake (Fig. 2), peak demands were slightly higher. The rate of absorption, which was low during pregnancy, increased to a peak in early lactation and then decreased (Table 3). The efficiency of absorption of P, however, remained high throughout the whole of pregnancy and lactation. This pattern of absorption was different from that in ewes given the plentiful intake and reflected the different pattern of P intake. In fact, in both groups of ewes, the rate of P absorption (P_a) was directly related to the rate of P intake (P_i). However, since the efficiency of absorption of P was very different in the two groups of ewes (70% in the restricted-intake group and 30% in the plentiful-intake group), results did not fit the same regression equation, and separate equations had to be calculated (Fig. 5).

At plentiful Ca and P intake:

$$P_a = -25 \cdot 0 + 0 \cdot 508 \, P_i \quad (r \, 0 \cdot 88, \, P < 0 \cdot 001)$$

At restricted Ca and P intake:

$$P_a = -2 \cdot 60 + 0 \cdot 705 \, P_i \quad (r \, 0 \cdot 98, \, P < 0 \cdot 001)$$

The endogenous loss of P in the faeces of these restricted-intake ewes reflected changes in the P intake, and increased to a high level in early lactation but then decreased throughout the remainder of lactation.

Fig. 6 shows there was a highly significant ($P < 0 \cdot 001$) linear relationship ($r \, 0 \cdot 96$) between endogenous faecal loss of P (P_f) and P intake (P_i) which held for both groups of ewes irrespective of their Ca and P intake:

$$P_f = 11 \cdot 2 + 0 \cdot 29 \, P_i.$$

In late pregnancy and early lactation, P was mobilized from bone and soft tissues in these restricted-intake ewes to a similar extent as in the plentiful-intake ewes and resorption

Table 3. *Phosphorus metabolism in ewes restricted to the Agricultural Research Council (1980) recommendations for dietary Ca and P throughout pregnancy and lactation*

	At mating	Pregnancy (130–137 d)	Lactation (d)				Post-lactation (d)		Pooled standard deviation (44 df)
			14–21	42–49	63–70	94–99	7–14	28–35	
No. of animals...	3	4	5	5	3	3	3	3	
Rate (mg/d per kg body-wt) of:									
Ingestion of P (P_i)	37·7	57·5	106·8	93·9	88·8	57·4	41·9	39·4	6·53
Loss of P in faeces (F)	38·2	49·4	80·6	67·1	61·5	50·4	35·0	36·0	9·12
Excretion of P urine (P_u)	0·2	0·5	1·8	0·7	0·5	0·7	2·0	0·5	4·36
Loss of P to fetus or milk (P_m)	—	20·8	52·6	31·7	28·3	5·8	—	—	9·52
Retention of P (PΔ)	−0·7	−13·2	−28·2	−5·6	−1·5	+0·5	+4·9	+2·9	9·62
Endogenous loss of P in faeces (P_f)	22·7	31·3	41·8	41·4	35·0	30·0	20·6	21·0	5·76
Secretion of P in saliva* (P_{sec})	55·2	97·9	117·7	151·1	117·1	84·5	59·9	55·1	23·22
Absorption of P (P_a)	22·2	39·4	68·0	68·2	62·3	37·0	27·5	24·4	8·89
Accretion of P into bone and soft tissues (P_{o+})	24·0	14·7	27·0	46·3	35·6	31·8	22·8	30·1	7·20
Resorption of P from bone and soft tissues ($P_{o−}$)	24·7	27·9	55·2	51·9	37·1	31·3	17·9	27·2	11·69
Dietary P absorbed (%)	58·9	68·5	64·5	72·6	70·1	64·5	65·6	61·9	4·19
Rapidly exchangeable pool of P (mg/kg body-wt)	19·1	23·1	42·3	53·8	38·4	29·5	14·2	28·6	9·20
Slowly exchangeable pool of P (mg/kg body-wt)	204·0	197·9	229·6	242·9	258·6	249·4	199·5	222·0	23·83
Serum P (mmol/l)	1·80	1·30	1·44	1·56	1·44	1·70	1·86	2·10	0·29
Milk yield (ml/d)	—	—	1750	1100	760	190	—	—	—

* Obtained from faecal endogenous loss assuming that salivary P is reabsorbed with the same efficiency as dietary P.
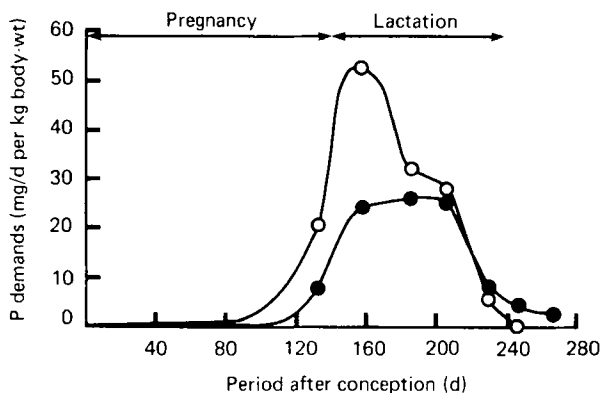
Fig. 4. Variations in immediate (○) and net (●) demands for phosphorus during pregnancy and lactation in ewes given the calcium and P intake restricted to Agricultural Research Council (1980) recommendations.
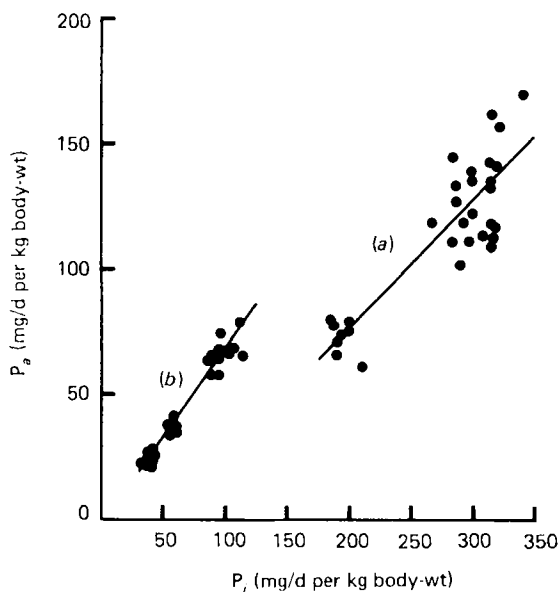

Fig. 5. Relationship between phosphorus intake (P_i) and dietary P absorption (P_a) during pregnancy and lactation in (a) ewes given the plentiful calcium and P intake

$$P_a = -25 \cdot 00 + 0 \cdot 508 \, P_i \quad (r \; 0 \cdot 88, \; P < 0 \cdot 001)$$

and in (b) ewes given the Ca and P intake restricted to the Agricultural Research Council (1980) recommendations

$$P_a = -2 \cdot 60 + 0 \cdot 705 \, P_i \quad (r \; 0 \cdot 98, \; P < 0 \cdot 001).$$

increased to a high level relative to accretion. In contrast to the plentiful-intake ewes, however, the bone and soft tissue stores of P were not replaced in mid- to late lactation, and resorption remained at only a slightly lower level than accretion.

For the sake of comparison, P balance measurements for the restricted-intake ewes are shown together with measurements for the plentiful-intake ewes in Fig. 3. Although in late pregnancy and early lactation both groups of ewes showed a negative P balance, in mid-
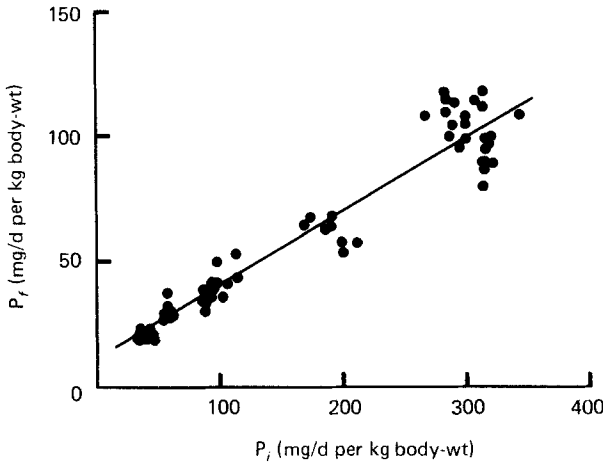
Fig. 6. Relationship between phosphorus intake (P_i) and endogenous faecal loss (P_f) in pregnant and lactating ewes. $P_f = 11\cdot21 + 0\cdot294\ P_i$ ($r\ 0\cdot96$, $P < 0\cdot001$).
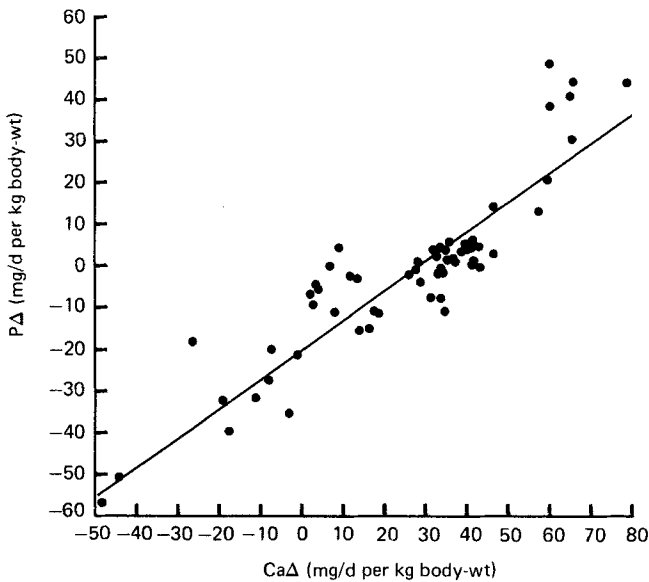

Fig. 7. Relationship between Ca retention (CaΔ) and phosphorus retention (PΔ) in pregnant and lactating ewes. $P\Delta = 1\cdot70 + 0\cdot698\ Ca\Delta$ ($r\ 0\cdot90$, $P < 0\cdot001$).

to late lactation balance in the restricted-intake ewes became only just positive, whereas in the plentiful-intake ewes it was strongly positive.

Integration of the balance curve shows that the restricted-intake group lost on average 75 g P during pregnancy and early lactation (slightly more than the 65 g lost by the plentiful-intake group). At 1 month after the end of lactation, they were still in deficit of 67 g P (90% of their losses) whereas the plentiful-intake group had more than replaced their losses by this time.

Because of the close association of Ca and P in bone and milk, changes in P retention

(PΔ) during pregnancy and lactation were directly related (r 0·90, $P < 0.001$) to changes in Ca retention (CaΔ) and this relationship held for both groups of ewes (Fig. 7):

$$P\Delta = 1.70 + 0.698 \text{ Ca}\Delta.$$

DISCUSSION

Although the rate of absorption of P by the plentiful Ca and P intake ewes was increased to a greater extent between late pregnancy and early lactation than were P demands, the extra P absorbed was not used to meet these demands but was instead excreted in the urine and faeces. Thus, whereas absorption of P increased between late pregnancy and early lactation from 77·8 to 119·3 mg/d per kg body-weight ($+41.5$), and demands for P increased from 10·7 to 40·4 mg/d per kg body-weight ($+29.7$), endogenous loss of P in urine and faeces increased from 68·2 to 113·4 mg/d per kg body-weight ($+45.2$). The additional P demands for milk production were supplied instead from P mobilized from bone and soft tissues.

In view of the high rate of P absorption, it is unlikely that the bone P was mobilized in response to the additional demands for P. In fact, the preceding paper (Braithwaite, 1983) shows that at this time bone mobilization was stimulated in response to a need for more Ca, the low rate of absorption of dietary Ca being insufficient to meet the high demands of peak lactation. Since bone mineral is a complex Ca–P salt, mobilization of bone Ca also results in the release of bone P. In early lactation, therefore, this extra bone P together with the additional supply of absorbed dietary P must result in a surplus of P, which is then excreted. Such an increase in P excretion in response to changes in Ca metabolism has been observed previously in studies with mature sheep given a diet plentiful in P but deficient in Ca (Braithwaite, 1975). These sheep had to mobilize bone Ca in order to supply their maintenance requirements and the accompanying bone P, which was surplus to requirements, was excreted.

Since the rate of absorption of P in the restricted Ca and P intake ewes was lower in late pregnancy and early lactation than in the plentiful-intake ewes, it is possible that the bone and soft tissue mobilization of P, which occurred at this time, was due to a lack of dietary P. It is much more likely, however, that as in the plentiful-intake ewes, this mobilization of P was due to a lack of available Ca.

In mid- to late lactation, the increased efficiency of absorption of dietary P and the decreased endogenous faecal loss of P by the plentiful Ca and P intake ewes coincided with an increase in the rate of Ca absorption to a level well in excess of that needed to meet immediate demands for milk production, and it was at this time that skeletal stores of Ca lost in late pregnancy and early lactation were replaced (Braithwaite, 1983). This replacement of bone Ca stores was accompanied by replacement of bone P, as shown by the decrease in rate of resorption of P from bone and soft tissues relative to that of accretion (Table 2). In contrast, the restricted-intake ewes were unable to replace their lost bone mineral stores at this time. Although this inability might have been due to a lack of available dietary P, it might also be due to a lack of available dietary Ca (see Braithwaite, 1983). It is therefore not possible from the present study to draw any conclusions, particularly in late lactation, about the adequacy of the P requirements recommended by the ARC (1980) for pregnant and lactating ewes. To do so needs a further experiment in which the dietary Ca intake in mid- to late lactation is increased to a level which allows the replacement of bone Ca stores.

Because changes in bone Ca metabolism, which occur as part of the normal Ca homeostatic mechanism of pregnancy and lactation, produce concomitant changes in the supply or demand for bone P, the net P demands of pregnancy and lactation (the sum of fetal or milk requirements and bone requirements) are not the same (Fig. 2) as the immediate demands (fetal or milk requirements only). In late pregnancy and early lactation,
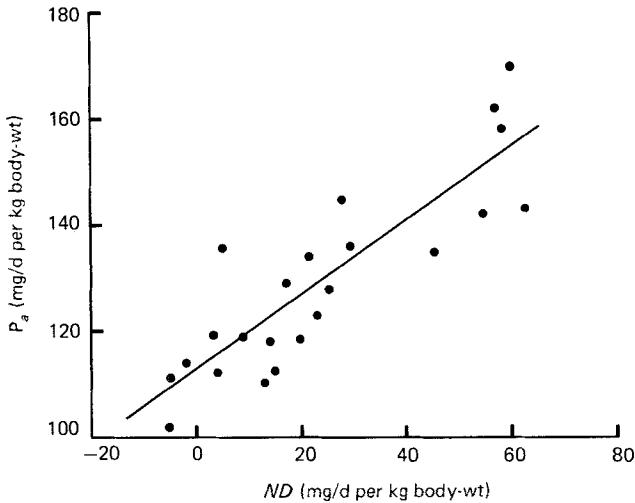
Fig. 8. Relationship between net phosphorus demands (*ND*) and P absorption (P_a) in lactating and dry ewes given the plentiful, but constant, calcium and P intake.

$$P_a = 112{\cdot}98 + 0{\cdot}703\ ND \quad (r\ 0{\cdot}85,\ P < 0{\cdot}001).$$

net demands for P are lower than immediate demands in both groups of ewes because bone stores of P are mobilized in order to release bone Ca. In mid- to late lactation net demands are greatly in excess of immediate demands in the plentiful-intake group because P is used in combination with Ca to replace bone stores, but net demands are roughly the same as immediate demands in the restricted-intake group which failed, because of a lack of Ca or P or both, to replace their bone stores (cf. Figs 2 and 4).

Since the P intake of ewes given the plentiful Ca and P intake was constant throughout lactation and the following dry period, the effect of these changes in immediate and net demands for P on P absorption and endogenous P loss can be examined. Neither absorption, nor endogenous loss was related to immediate demands, but both were related to net demands. Fig. 8 shows that during lactation and the following dry period, the rate of P absorption (P_a) despite the constant P intake, was directly related ($r\ 0{\cdot}85,\ P < 0{\cdot}001$) to net demands (*ND*):

$$P_a = 112{\cdot}98 + 0{\cdot}703\ ND.$$

Furthermore, Fig. 9 shows that the rate of total endogenous excretion of P (in urine and faeces) ($P_u + P_f$) during lactation and the dry period was inversely related ($r = 0{\cdot}60$, $P < 0{\cdot}01$) to *ND*:

$$P_u + P_f = 114{\cdot}80 - 0{\cdot}332\ ND.$$

These relationships suggest that it is by altering both the efficiency of absorption of dietary P and the endogenous loss of P in the urine and faeces that ewes respond to those changes in net P demands of pregnancy and lactation which result largely from the inevitable changes that occur in Ca metabolism (Braithwaite, 1983).

The reason for the difference in efficiency of absorption of P between the two groups of ewes is unclear, especially as it is generally assumed that P is absorbed in direct relation to intake and the surplus P lost in the faeces (Lueker & Lofgreen, 1961; Preston & Pfander, 1964; Young *et al.* 1966 *a*, *b*). It seems unlikely that it was due to the composition of the diets, as many of the ingredients were the same (see Braithwaite, 1983). It is more probable
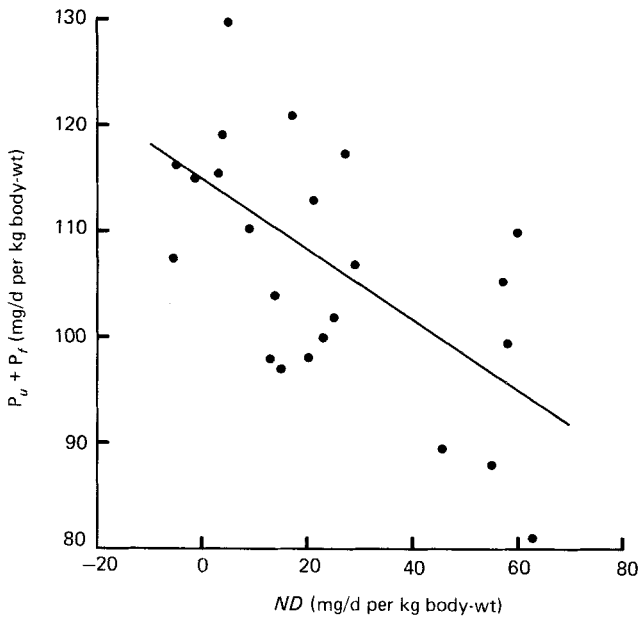
Fig. 9. Relationship between net phosphorus demands (*ND*) and total endogenous excretion in urine and faeces ($P_u + P_f$) in lactating and dry ewes given the plentiful but constant calcium and P intake.

$$P_u + P_f = 114 \cdot 80 - 0 \cdot 332\ ND \quad (r\ 0 \cdot 60,\ P < 0 \cdot 01).$$

that there is some control mechanism which relates efficiency of absorption to intake or demand or both. Some evidence that such a mechanism may exist has been obtained from experiments with 1-α-hydroxycholecalciferol. Administration of this compound – which is rapidly converted into 1,25-dihydroxycholecalciferol, the active metabolite of vitamin D responsible for stimulating active absorption of Ca – to lactating or whether sheep increased the rate of absorption of both Ca and P by increasing their absorption efficiency (Braithwaite, 1978, 1980).

A direct relationship between faecal endogenous P and P intake has been reported previously (ARC, 1980; Grace, 1980) and has been used to predict the endogenous loss of P which would be expected at zero P intake. This minimum value (9–12 mg/d per kg body-weight), with which the value (11·2 mg/d per kg body-weight) obtained in the present study is in good agreement (see Fig. 6), was assumed in calculations of P requirements (ARC, 1980) to represent that inevitable loss which would occur, irrespective of P intake, if sheep were fed just sufficient dietary P to meet their immediate demands (i.e. demands for maintenance plus growth or lactation, or both). Such low endogenous faecal losses of P have only been observed in sheep given P-deficient semi-purified diets (Sykes & Dingwall, 1976) or very poor natural diets (Field *et al.* 1974) and, although the present results (Table 2, Fig. 9) show that the high endogenous faecal loss normally associated with high-P intakes can be reduced to some extent in response to increased P demands, there is, as yet, no conclusive evidence which shows that the inevitable faecal loss does not increase with increased P intake.

Salivary secretion rates for P calculated by the formula of Young *et al.* (1966*b*) (see eqn (8)), which is based on the assumption that endogenous P is absorbed with the same efficiency as dietary P, were directly related to P intake and to P absorption. However, since recent studies with wether sheep show that true salivary secretion rates are much greater than the rates calculated from endogenous faecal losses and suggest that salivary P is

absorbed more efficiently than dietary P (G. D. Braithwaite, unpublished results), these calculated rates probably have little value.

P requirements for pregnancy and lactation

Although it is not possible, for reasons already discussed, to judge the adequacy of the new ARC (1980) recommendations for P for pregnancy and lactation, some observations can be made on the method of calculating these requirements.

The present results show that the net demands of pregnancy and lactation for P are quite different from the immediate demands for fetal and milk production (see Fig. 2). This is because the inevitable mobilization of bone Ca in early lactation and the replacement of this bone Ca in late lactation results in a consequential release and uptake of P.

Requirements calculated according to immediate demands are likely to cause problems of waste in early lactation and deficiency in late lactation. To avoid these problems, requirements should be calculated according to net demands which take account of the inevitable changes in bone metabolism.

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