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# THE ABSORPTION OF PHOSPHATE FROM THE DIGESTIVE TRACT OF RUMINANT ANIMALS

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## SUMMARY

Under normal dietary conditions in which the phosphorus (P) intake of ruminant animals is adequate, the absorption of phosphate (Pi) ions takes place from both the fore-stomachs and the small intestine. The rate of Pi absorption from the latter appears to be at least three times greater than that from the former. When absorption of Pi ions from the reticulorumen is severely reduced, as in dietary P deficiency, the absorption of both calcium and magnesium ions from the reticulorumen becomes impaired. Thus, dietary P deficiency may play a role in the aetiology of acute grass tetany.

KEYWORDS: Phosphate; calcium; magnesium; absorption; ruminants.

## INTRODUCTION

The calculation of the requirements of phosphorus (P) for ruminant animals is based on estimates of their net requirements for production and of the faecal loss of phosphorus of endogenous origin—mainly saliva as the urinary excretion of Pi is usually negligible. The accurate measurement of faecal endogenous loss requires the use of $^{32}P$; attempts have been made to estimate it without using $^{32}P$ which either assume that it is independent of the dietary intake of phosphorus or that there is no net absorption of phosphate (Pi) from the fore-stomachs.

The ARC (1980) recommended a constant absorption efficiency of Pi for mature sheep, but more recent work in both sheep (Braithwaite, 1984a) and ruminant calves (Challa *et al.*, 1989) has shown that the efficiency of P absorption is low when the dietary intake of P is deficient and increases with the intake of P until the requirements are met. A further increase in intake is associated with a reduction in the efficiency of P absorption. This review will examine the physiological background to the absorption of Pi by ruminant animals.

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## SALIVARY SECRETION OF PHOSPHATE

Under grazing conditions, or when forage diets are fed, ruminants usually excrete only negligible amounts of Pi in the urine largely because of a relatively high maximum reabsorptive capacity for Pi in the renal tubules. That is, the salivary glands largely replace the kidneys as a means of removing excess Pi from the circulation. This salivary Pi helps to buffer the production of volatile fatty acids in the rumen and to satisfy the P requirements of the microbial population of the rumen. A reciprocal relationship between renal and salivary secretion of Pi has been demonstrated (Tomas, 1974a).

The daily turnover of Pi in the saliva of ruminants [60–320 mg $kg^{-1}$ $day^{-1}$ bodyweight of sheep (Kay, 1960)] is similar to or greater than the P intake [60–90 mg $kg^{-1}$ $day^{-1}$ (Grace, 1981)]. Almost all the salivary P is in the form of inorganic Pi. This can contribute 80% of the Pi secreted into the digestive tract and represents the major determinant of the endogenous P excretion in faeces [9–32 mg $kg^{-1}$ $day^{-1}$ (Ternouth, 1989)]. There is considerable variation in this endogenous excretion because Pi output in saliva is a function of both concentration and flow and is therefore subject to factors affecting these, as well as to individual variations between animals. For example, for a given diet, the Pi secreted in saliva is proportional to the P intake (Tomas *et al.*, 1967). This is largely because the salivary Pi concentration is proportional to the plasma Pi concentration (Manas-Almendros *et al.*, 1982; Braithwaite, 1984a) and the latter reflects the dietary intake of P. However, a measure of adaptation of salivary concentration of Pi can occur, independent of the plasma Pi concentration, in response to dietary P depletion even in the absence of the parathyroid glands (Manos-Almendros *et al.*, 1982). This aids in the conservation of Pi during dietary P deficiency.

The salivary secretion of Pi generally increases with salivary flow rate (Ternouth *et al.*, 1985) except at low rates of flow when there is an inverse relationship because of a fall in salivary Pi concentration (Bailey & Balch, 1961). Thus when more food is eaten (usually involving the intake of more P) more saliva is secreted and with it more Pi ions, leading to the proportional relationship between Pi secreted in saliva and P intake. The total Pi secreted in saliva is also affected by the physical nature of the diet, the rate of secretion being higher when roughage diets are fed and relatively lower when pelleted or finely ground diets are consumed (Tomas, 1974b).

If the demand for P is increased by a prolonged (12 days) intravenous infusion of calcium to reduce bone resorption and thus promote net bone accretion, this demand is met (Table I) by an increase in the percentage efficiency of absorption of Pi of both dietary and endogenous origin (Braithwaite, 1984b; Rajaratne *et al.*, 1993). The increased secretion of calcitonin caused by the hypercalcaemia has no effect on Pi absorption (Yano *et al.*, 1991). Conversely, if the demand for P is decreased by an intravenous infusion of Pi (Table II) the additional Pi is quantitatively excreted, usually in the faeces (Towns *et al.*, 1978); the increase in excretion in the urine only being significant when the plasma concentration of Pi rose to 2.6 mmol $l^{-1}$.

The increase in phosphataemia increases the secretion of parathyroid hormone

(PTH) (Fischer *et al.*, 1973) which in turn increases the secretion of Pi in the saliva (Wright *et al.*, 1984). Relatively high concentrations of PTH are required to increase the renal excretion of Pi (Barlet & Care, 1972) which presumably accounts for the fact that a phosphaturic effect was observed by Towns *et al.* (1978) only at the highest level of phosphataemia attained. It is concluded that the salivary secretion of Pi is the principal determinant of endogenous faecal P and is largely regulated by the plasma concentration of Pi. Since the latter increases with a rise in dietary P intake, the rate of endogenous faecal excretion of P becomes correlated directly with the dietary intake of P (Scott *et al.*, 1985; Ternouth, 1989).

Because of the relatively large addition of salivary Pi to the rumen contents there is no net absorption of Pi from this region. It is not until the small intestine that the bulk of the net absorption of Pi occurs (Poppi & Ternouth, 1979), although there is also some net absorption of Pi from the large intestine at higher intakes of P.

**Table I**
**Effects of increased demands for phosphorus (P) caused by an intravenous (i.v.) infusion of calcium for 12 days**

| | $mg\ kg^{-1}\ day^{-1}$ | |
|---|---|---|
| | *Control* | *i.v. Calcium* |
| Rate of ingestion of P | 77.2 | 77.1 |
| Rate of endogenous faecal loss of P | 40.1 | 32.1* |
| Rate of absorption of dietary P | 44.1 | 52.2* |
| % efficiency of dietary P absorption | 57.1 | 67.7* |

Adapted from Braithwaite (1984). The daily intakes of P and Ca were 3.09 g and 3.02 g, respectively.
*$P<0.1$.

**Table II**
**Effects of decreased demands for phosphorus (P) caused by an i.v. infusion of phosphate for 11 days at 18 h $day^{-1}$**

| | $mg\ kg^{-1}\ day^{-1}$ | |
|---|---|---|
| | *Control* | *i.v. phosphate* |
| Rate of ingestion of P | 21.6 | 21.6 |
| Rate of salivary P secretion† | 84.0 | 116.0 |
| Rate of intestinal absorption of P† | 86.0 | 90.8 |
| Rate of faecal excretion of P | 18.8 | 43.4* |
| Rate of urinary excretion of P | 0.1 | 2.0 |

Adapted from Towns *et al.* (1978). The daily intakes of P and Ca were 1.08 g and 4.01 g, respectively.
*$P<0.01$.
†Calculated by the authors assessing that these sheep secreted 10 litres saliva per day, that there is a direct relationship between the Pi concentrations in saliva and plasma and that the Pi concentration in saliva is 10 times that in a concurrent sample of plasma (Tomas *et al.*, 1967).

## ABSORPTION OF PHOSPHATE IONS FROM THE FORE-STOMACHS

Controversy still exists as to the existence of significant absorption of Pi from regions of the digestive tract cranial to the duodenum. $^{32}P$ labelled Pi absorption from this region could not be demonstrated in the sheep by Scott & Buchan (1987). In balance studies with sheep, cannulated in the proximal duodenum (Grace *et al.*, 1974), a net secretion of P in excess of the dietary intake amounting to 67 mg $kg^{-1}$ $day^{-1}$ body weight (range 13–99) has been found. This is less than the mean salivary inflow of P (125 mg $kg^{-1}$ $day^{-1}$) obtained in other experiments which could indicate a net absorption of Pi from the ovine stomachs at the rate of approximately 60 mg $kg^{-1}$ $day^{-1}$. In addition, net absorption of Pi from the bovine omasum was found by Edrise & Smith (1986) using a double marker technique. This absorption of Pi amounted to 10–40% of that entering this region. It was shown *in vitro* using omasal epithelium that Pi absorption is a passive process and is thus dependent on the existing electrochemical gradient (Holler *et al.*, 1988).

Since the omasum shares with the reticulo rumen the same type of epithelium (stratified squamous) it is not surprising that the reticulo rumen has also been shown, using the washed reticulo-rumen isolated *in situ* in conscious, unstressed sheep, to be a site for net absorption of Pi (Breves *et al.*, 1988; Beardsworth *et al.*, 1989). That is, the Pi flux in the mucosal to serosal direction exceeded that in the opposite direction. Under short circuit conditions *in vitro* (during which there is no net difference in electrical potential across the epithelium) and the same Pi concentration (3 mmol $l^{-1}$) on both sides there was no net flux of Pi ions in either direction across the ruminal epithelium. When the transmural potential difference (normally approximately 16 mV, serosal side positive) was clamped at either +25 or −25 mV the unidirectional flux of Pi changed according to the electrical gradient but at the same gradient, the unidirectional flux rates for Pi did not differ significantly between the two opposite directions. This indicates that Pi was transferred passively across the ruminal epithelium mainly in the ionized form via the transcellular or paracellular routes (Breves *et al.*, 1988). The ratio of Pi fluxes in either direction at a potential difference of 25 mV (serosa positive) was less than that predicted from the Ussing equation (Ussing & Zerahn, 1951) which may indicate that part of the Pi transfer across the epithelium is electroneutral, e.g. by ion exchange or co-transport.

In *in vivo* studies, net absorption of Pi only occurred from a minimal concentration in excess of approximately 4 mmol Pi $l^{-1}$ (Beardsworth *et al.*, 1989). A linear relationship was shown to exist between the Pi absorption rate and the intraruminal Pi concentration. The gradient of this linear relationship was increased when the animals had been fed a P-depleted diet (Breves *et al.*, 1988) indicating some adaptation of the absorptive mechanism for Pi ions.

The transmural potential difference associated with these ruminal solutions was inversely related to the ruminal Pi concentration (Beardsworth *et al.*, 1989). Since the active absorption of magnesium from the rumen is reduced by an increase in the transepithelial potential difference (Martens *et al.*, 1987), this may account for the increase in both magnesium and calcium absorption rates observed when the intraruminal Pi concentration was increased from 2 to 15 mmol $l^{-1}$. The latter is a concentration within the range found when an adequate P diet is fed (Shirazi-

Beechey *et al.*, 1991). Qualitatively similar increases in the absorption rates of Pi, calcium and magnesium from the rumen also occurred when the intraruminal Pi concentration was increased in the presence of a high intraruminal potassium concentration (90 mmol $l^{-1}$) and the consequent increase in transmural potential difference. This increase in ruminal Pi concentration caused a reduction in the extent of this increase in transmural potential difference induced by the high potassium concentration (Beardsworth *et al.*, 1989). Thus, an intraruminal Pi concentration in the region of 15 mmol $l^{-1}$ should be a factor in the prevention of acute grass tetany associated with the ingestion of heavily fertilized grass. Indeed, under Australian conditions, dietary P deficiency is considered to be a factor in the aetiology of grass tetany (I. W. Caple, Pers. Comm.). However, experimental studies of magnesium absorption in P deficient sheep have not yet been undertaken.

## DIETARY P DEPLETION AND CALCIUM ABSORPTION

In P depleted sheep the mean Pi concentration in ruminal fluid is likely to be about 2 mmol $l^{-1}$. At this concentration of Pi and an accompanying normal intraruminal calcium concentration of 2 mmol $l^{-1}$, five of nine sheep showed net secretion rather than net absorption of calcium from the reticulo-rumen *in vivo* (Beardsworth *et al.*, 1989). All nine sheep showed net absorption of calcium when the Pi concentration in the ruminal fluid was increased to 15 mmol $l^{-1}$, a concentration associated with the ingestion of a P replete diet. This finding could account for the observations made by Young *et al.* (1966) that the efficiency of calcium absorption in P depleted sheep is reduced and that it can be restored by raising the dietary intake of P. This was confirmed by Abdel-Hafeez *et al.* (1982) using $^{47}Ca$.

## PHOSPHATE ABSORPTION FROM THE SMALL INTESTINE

Net absorption of Pi occurs in the small intestine until the pH becomes too high for Pi ions to remain in solution in sufficiently high concentration. Moreover, the absorption of Pi ions from the ruminant small intestine is stimulated by a pH gradient across the brush border membrane of the enterocyte (Shirazi-Beechey *et al.*, 1989). Phosphate absorption from this region has been studied using Thiry-Vella loops of small intestine in conscious, unstressed sheep (Care *et al.*, 1980). Such loops were maintained in an absorptive state for several months by regular perfusion with a nutrient electrolyte solution containing glucose. It was shown that the net rate of Pi absorption from this nutrient solution increased with increasing Pi concentration in the solution up to a concentration of approximately 7 mmol $l^{-1}$. This relationship would be compatible with the saturation of a putative carrier mechanism during an absorptive process involving facilitated diffusion.

At the Pi concentration normally present in an ultrafiltrate of small intestinal contents (3 mmol $l^{-1}$) the Pi absorption rate was 500 $\mu$mol $h^{-1}$ from a 2 metre length of jejunum (Care *et al.*, 1980). Assuming a total length of small intestine of 27 metres in a sheep of weight 50 kg and a consistent rate of absorption of Pi

along its length, the net absorption rate of Pi would amount to 100 mg $kg^{-1}$ $day^{-1}$. Grace *et al.* (1974), using balance studies, showed that the rate of net absorption of P from the small intestine of sheep was 60 mg $kg^{-1}$ $day^{-1}$ to which should be added a further 12 mg $kg^{-1}$ $day^{-1}$ reabsorbed from bile and pancreatic juice and approximately 20 mg $kg^{-1}$ $day^{-1}$ from intestinal juice (Wadsworth & Cohen, 1976), giving a total true absorption of Pi of approximately 90 mg $kg^{-1}$ $day^{-1}$ from the small intestine. This should be compared with a P absorption rate of 36 mg $kg^{-1}$ $day^{-1}$ from the reticulorumen (Breves *et al.*, 1988; Beardsworth *et al.*, 1989) or from the ovine fore-stomachs, 60 mg $kg^{-1}$ $day^{-1}$ (see above).

When sheep are fed a very low calcium diet (0.6 g Ca $kg^{-1}$ DM) (a normal diet would contain approximately 4 g Ca $kg^{-1}$), there is an increase in the efficiency of absorption of both calcium and Pi from the small intestine. This change is accompanied by an increase in the circulating concentration of 1,25-dihydroxy vitamin D. Similarly, the administration of a synthetic analogue (1$\alpha$ hydroxy vitamin D) increased the absorption of both calcium and Pi from the small intestine (Abdel-Hafeez *et al.*, 1982).

Sheep, like non-ruminant animals, adapt their efficiency of Pi absorption from the small intestine in response to dietary P depletion (Care *et al.*, 1980). This is achieved by enhancing the capacity of the brush border membrane to transport Pi ions (Shirazi-Beechey *et al.*, 1991). This absorption of Pi is pH- but not sodium-dependent, as it is in non-ruminants (Murer & Hildmann, 1981). However, unlike non-ruminants, dietary P deficiency does not increase the production rate of 1,25-dihydroxy vitamin D by sheep (Maunder *et al.*, 1986) to achieve this adaptation. Using goats, Schroder *et al.* (1990) showed that dietary P deficiency increases the efficiency of the intestinal receptor for 1,25-dihydroxy vitamin D, thus making the circulating 1,25-dihydroxy vitamin D more effective at the gut level. Whereas vitamin D-stimulated absorption of calcium from the small intestine is generally believed to involve the production of calbindin, a specific calcium-binding protein, the mechanism by which 1,25-dihydroxy vitamin D stimulates the absorption of Pi ions is not understood but probably involves a specific binding protein. Calbindin binding of Pi ions analogous to that of calcium ions, does not appear to be involved.

The above description refers to the healthy digestive tract. When the small intestinal mucosa is damaged by *Trichostrongylus colubriformis* larvae in sheep, the intestinal absorption of Pi becomes reduced (Wilson & Field, 1983).

## PHOSPHATE ABSORPTION FROM THE LARGE INTESTINE

In mature sheep, fitted with re-entrant cannulae in the proximal colon, perfusion of a length of colon with a nutrient electrolyte solution showed that there was slight net secretion of Pi when the perfusion fluid was free of Pi. However, at Pi concentrations between 2.5 and 6.5 mmol $l^{-1}$ net absorption of Pi from the colon was observed (Holler *et al.*, 1988). The significance of this finding in relation to net absorption from the rest of the digestive tract under practical conditions remains to be evaluated.

## CONCLUSION

Unlike the extent of the effort devoted to the study of Pi transport across the renal tubule, much work remains to be done on the mechanisms by which Pi ion absorption from the digestive tract is controlled in ruminant animals. In particular, the structure of the putative phosphate carrier in the brush border of the enterocyte awaits identification and its reaction to dietary P deficiency in the adaptation of the efficiency of Pi absorption to the ingestion of a low P diet requires study. The salivary glands play a very important role in Pi homeostasis in ruminants and more knowledge is required with regard to the control of Pi secretion by these glands using long term rather than acute experimentation *in vivo* coupled with membrane studies *in vitro*.

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