

II. Quantitative aspects of phosphorus absorption in ruminants

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Abstract — Phosphorus absorption in ruminants was analysed from a database described in a previous article. For common values of ingested phosphorus (2.5–5.0 g·kg⁻¹ of DM), 0.73 of dietary phosphorus is absorbed. The remaining variability is probably due to phosphorus quality. Phosphorus absorbed from silage, cereal, cereal by-products and hay differs greatly. The current true absorption coefficient used to calculate daily phosphorus supply is a constant value in the current systems and often it underestimates the true absorption resulting in an excess of phosphorus being supplied in the diets. Adjusting the true absorption coefficient values requires better characterisation of the phosphorus supplied by each feedstuff. Dietary influences (phytate phosphorus, crude fibre, etc.) were investigated but trials assessing the ration effect on phosphorus absorption are lacking. Since rumen microbes have specific phosphorus requirements, particularly for cell-wall degradation, the feedstuff phosphorus availability for the rumen ecosystem is discussed.

absorption / availability / phosphorus / quantitative aspect

1. INTRODUCTION

Up to now, the differences in the quality of dietary phosphorus have not been taken into account for optimising the phosphorus supply in ruminant feeds. Dietary phosphorus is available for absorption since it reaches the absorption sites in an inorganic form [1] pointing out the importance of the digestive solubilisation of this element. Depending on the chemical form of phosphorus in the diet,

digestive phosphorus solubilisation is either a chemical solubilisation (inorganic phosphate), or a release of phosphorus resulting from the digestion of organic matter (phosphorus in nucleotides, in lipids...) or from a specific hydrolysis reaction (phytate phosphorus). In fact, dietary phosphorus is provided partially in inorganic form in forage and mineral supplements. The organic portion includes phytate phosphorus and the phosphorus contained in plant molecules such as

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phospholipids or nucleic acids. The proportions of the different forms of phosphorus vary greatly according to feedstuffs. For example, grains and grain by-products contain 0.50 to 0.70 phosphorus in the form of phytate phosphorus [2], 0.20 to 0.30 as phospholipids, phosphoproteins and nucleic acids and 0.08 to 0.12 as inorganic phosphorus [3]. To improve the understanding of ruminant phosphorus digestion and absorption, the present study analysed the quantitative phosphorus absorption flux and attempted to identify potential limiting factors of digestive solubilisation using a database presented previously [4].

2. MATERIALS AND METHODS

The constitution of the database, the statistical analysis of the data and the abbreviations used in the text are described in a previous article [4]. The term RES[Y(X)] is used for a variable (Y) that was dependent

on a variable X after removal of the variation effect of X.

The following results were obtained by compilation of the information on the flow of phosphorus into the digestive tract according to its source (salivary phosphorus: PSAL; and ingested phosphorus: PING) and on phosphorus absorption from each source (respectively PABS_{SAL} and PABS_{ING}). PABS_{ING} was obtained by radio isotopic dilution and it represents true absorption of phosphorus. PABS_{SAL} was obtained by calculation considering that endogenous faecal phosphorus corresponds to 0.80 of the non-reabsorbed salivary phosphorus: $PABS_{SAL} = PSAL - 0.80 \times PFEC_{ENDO}$.

In the mathematical models, the intercepts between PABS_{SAL} and PSAL; PABS_{ING} and PING; and PABS_{TOT} and PTOT, which were often statistically close to 0, were removed from the models because they have no physiological significance. For instance, salivary phosphorus

Table I. Publications involved in each model. The references are listed in the appendix reference list of [4].

Model number	Publications involved in the models
1	B13, B19, B21, B57, B71, B72, B74, B75, B76
2	B13, B19, B57, B72, B75
3	B13, B19, B57, B75, B76
4	B13, B57, B75, B76, B19
5, 6	B1, B3, B4, B6, B11, B13, B15, B16, B19, B20, B24, B26, B32, B34, B35, B37, B39, B38, B41, B43, B44, B50, B54, B55, B56, B57, B60, B61, B67, B75, B76, B85, B86, B87, B88, B89, B49, B68, B82, B42, B90, B91, B92, B93, B94, B96, B97, B99, B100
7	B1, B6, B13, B14, B16, B19, B26, B37, B39, B38, B34, B35, B42, B55, B54, B57, B56, B61, B67, B68, B75, B76, B84, B85, B87, B90, B91, B94, B99
8	B13, B19, B57, B75, B76
9, 10	B3, B4, B5, B6, B11, B12, B14, B15, B16, B19, B24, B31, B32, B34, B35, B37, B38, B39, B41, B42, B43, B44, B49, B50, B54, B55, B57, B60, B61, B67, B68, B75, B76, B82, B84, B85, B86, B87, B88, B89, B90, B91, B92, B93, B94, B99, B100
11	B4, B5, B11, B12, B14, B15, B16, B19, B24, B32, B34, B35, B37, B38, B39, B42, B43, B49, B50, B54, B55, B57, B61, B68, B75 B76, B82 B86, B88, B89, B90, B91, B94, B99, B100
12	B4, B11, B12, B14, B15, B16, B19, B32, B34, B35, B37, B38, B39, B68, B75, B88, B89, B90, B94

cannot be absorbed when no salivary phosphorus is present in the digestive tract.

For each of the following relationships, the number of observations or treatments (TRT), the number of papers taken into account (EXP), the total number of animals involved (ANIM), the model root mean square error (RMSE), the adjusted square of the correlation coefficients (r^2) and the significant probability level (P) are given. The regression coefficients are followed by their standard errors within brackets. Table I indicates the publications used in each model of the present paper using the code of the variable PUB used in the "References – Appendix" of [4].

3. RESULTS

3.1. Comparison between saliva and ingested phosphorus flows

Total phosphorus entering the digestive tract is provided by salivary and ingested

phosphorus. For high amounts of total phosphorus entering the digestive tract, salivary phosphorus (inorganic phosphorus) becomes lower than ingested phosphorus (mainly organic phosphorus) according to the following relationship:

$$\text{PSAL/DMI} = 5.10 (\pm 0.58) + 0.23 (\pm 0.09) \times \text{PING/DMI}$$

(TRT = 48, EXP = 9, ANIM = 181, RMSE = 2.38, $r^2 = 0.10$, $P = 0.02$, model 1).

According to this equation, for phosphorus intakes higher than $6.62 \text{ g} \cdot \text{kg}^{-1} \text{ DM}$ ($= 5.10 / (1 - 0.23)$), the main origin of phosphorus entering the digestive tract is dietary phosphorus. However, diets containing more than 6.62 g of phosphorus per kg DM are rarely used. In our database, such diets were used in only two trials, one on ewes fed a diet high in calcium and phosphorus [5], and one on sheep fed a 0.88 cereal diet which inhibited saliva production by reducing the chewing activity [6]. Considering only the studies in which the usual, current range of diet phosphorus concentration

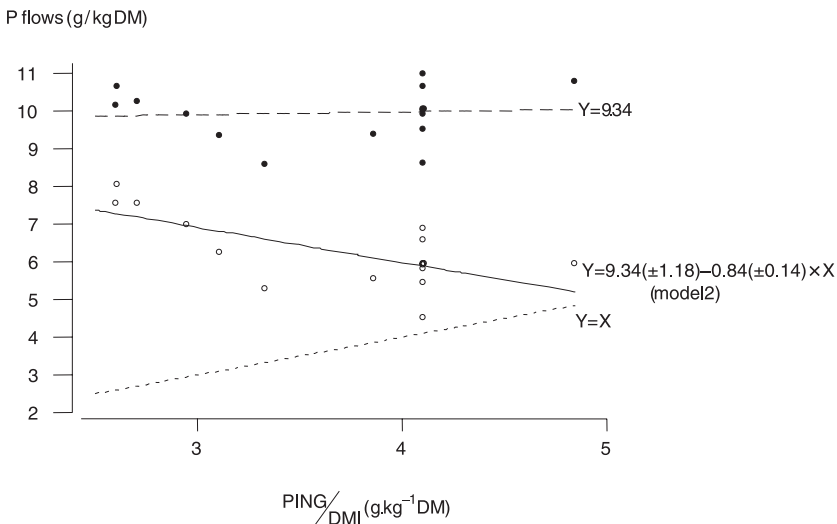


Figure 1. Relationship between salivary phosphorus (\circ , PSAL, $\text{g} \cdot \text{day}^{-1}$), total phosphorus entering the digestive tract (\bullet , PTOT, $\text{g} \cdot \text{day}^{-1}$) and ingested phosphorus (PING, $\text{g} \cdot \text{day}^{-1}$). All the fluxes are normalised according to DM intake ($\text{kg} \cdot \text{day}^{-1}$). The 1 models (solid line and dash line) and the line $Y = X$ (dotted line) are shown.

(between 2.5 and 5.0 g·kg⁻¹ DM) was used, we obtained an alternative model:

$$\text{PSAL/DMI} = 9.34 (\pm 1.18) - 0.84 (\pm 0.14) \times \text{PING/DMI}$$

(TRT = 18, EXP = 5, ANIM = 74, RMSE = 2.19, r² = 0.23, P = 0.02, model 2, Fig. 1).

This model illustrates that for the usual range of dietary phosphorus, the increase of ingested phosphorus corresponds to a salivary phosphorus decrease. For a daily phosphorus intake of 5 g per kg of DM, 5.14 g of salivary phosphorus enters into the rumen.

3.2. Absorption of saliva phosphorus

For the calculation of the salivary phosphorus absorption, we applied the following equation: $\text{PABS}_{\text{SAL}} = \text{PSAL} - k \times \text{PFEC}_{\text{ENDO}}$, with $k = 0.80$, assuming that on average, 0.80 of endogenous phosphorus flow comes from the salivary flow as described by [7].

Salivary phosphorus absorption increased linearly with saliva phosphorus flux as shown by the following equation:

$$\text{PABS}_{\text{SAL}}/\text{DMI} = 0.69 (\pm 0.02) \times \text{PSAL}/\text{DMI}$$

(TRT = 34, EXP = 5, ANIM = 139, RMSE = 2.06, r² = 0.95, P < 0.01, model 3, Fig. 2).

Because the same relationship between salivary phosphorus absorption and saliva phosphorus flux was observed in all the trials (Fig. 2), it appears to be a general relationship. It can also be seen in Figure 2 that, in ewes fed diets high in calcium and phosphorus [5] inducing high values of salivary phosphorus, less than 0.69 of salivary phosphorus was absorbed.

Considering only the diets containing the typical current range of phosphorus concentration (2.5 to 5.0 g·kg⁻¹ of DM intake):

$$\text{PABS}_{\text{SAL}}/\text{DMI} = 0.77 (\pm 0.01) \times \text{PSAL}/\text{DMI}$$

(TRT = 16, EXP = 5, ANIM = 16, RMSE = 2.01, r² = 0.99, P < 0.01, model 4).

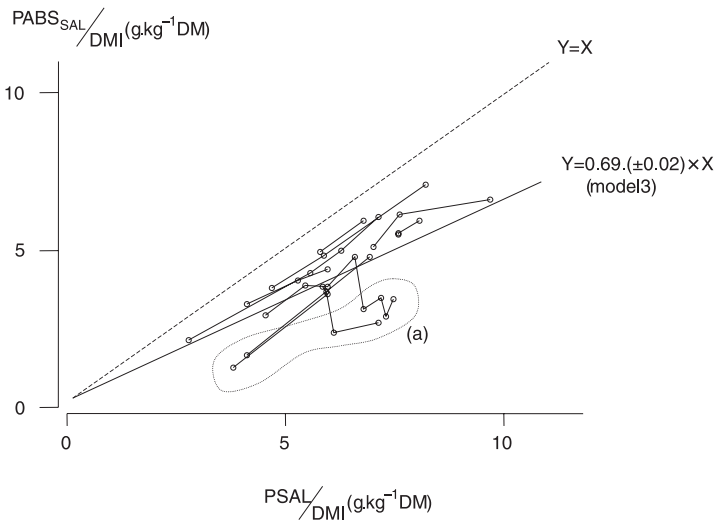


Figure 2. Relationships between the absorption of salivary phosphorus (PABS_{SAL} , g·day⁻¹) and the salivary phosphorus (PSAL , g·day⁻¹) normalised according to DM intake (kg·day⁻¹). The points from the same trial are connected by a solid line. The model (solid line) and the line $Y = X$ (dotted line) are shown. A particular study is also indicated (a: [5]).

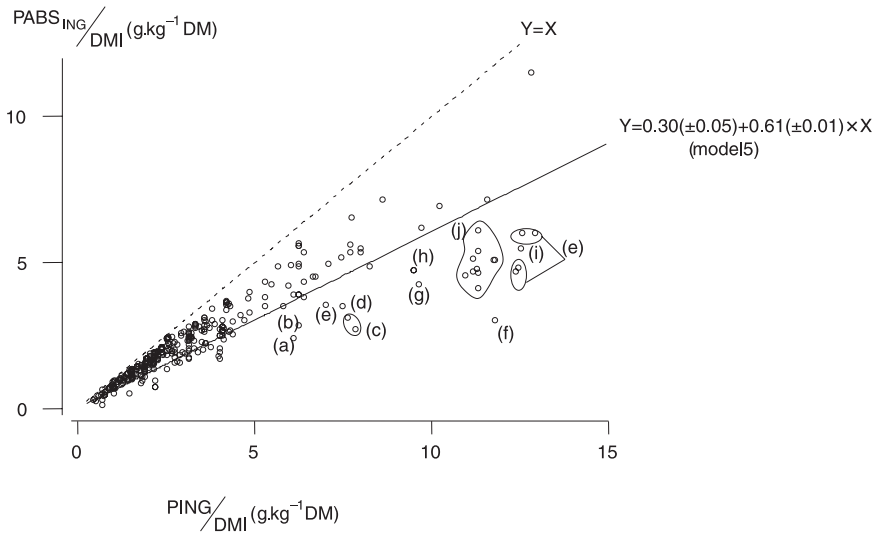


Figure 3. Relationships between the true absorption of ingested phosphorus ($PABS_{ING}$, $g \cdot day^{-1}$) and the ingested phosphorus (PING, $g \cdot day^{-1}$) normalised according to DM intake ($kg \cdot day^{-1}$). The model (solid line) and the line $Y = X$ (dotted line) are shown. Particular studies are also indicated (a: [71]; b: [34]; c: [5]; d: [71]; e: [72]; f: [51]; g: [72]; h: [73]; i: [74]; j: [5, 72, 74, 75]; k: [76]).

According to this last model, ruminants absorb 0.77 of salivary phosphorus versus 0.69 with model 3. The difference illustrates that high phosphorus intake appears to decrease the efficiency of salivary phosphorus absorption (0.69 vs. 0.77).

3.3. Absorption of ingested phosphorus

The other source of phosphorus for the ruminant is the ingested phosphorus, whose true absorption is measured by the ^{32}P radio isotopic dilution. The flow of absorbed ingested phosphorus increases with ingested phosphorus according to either a linear (model 5) or quadratic (model 6) relationship:

$PABS_{ING}/DMI = 0.30 (\pm 0.05) + 0.61 (\pm 0.01) \times PING/DMI$
(TRT = 335, EXP = 49, ANIM = 1228, RMSE = 0.93, $r^2 = 0.84$, $P < 0.01$, model 5, Fig. 3).

$PABS_{ING}/DMI = 0.82 (\pm 0.02) \times PING/DMI - 2.59 \times 10^{-2} (\pm 3.43 \times 10^{-3}) \times [PING/DMI]^2$
(TRT = 335, EXP = 49, ANIM = 1228, RMSE = 0.85, $r^2 = 0.96$, $P < 0.01$, model 6).

The better statistical fit of the quadratic model (RMSE = 0.85 and $r^2 = 0.96$) compared to the linear model (RMSE = 0.93 and $r^2 = 0.84$) would indicate a law of diminishing returns for the absorption of ingested phosphorus efficiency for high phosphorus intake. For this reason, we considered only the diets containing the current range of phosphorus concentration (2.5 to 5.0 $g \cdot kg^{-1}$ of DM intake):

$PABS_{ING}/DMI = 0.72 (\pm 0.01) \times PING/DMI$
(TRT = 113, EXP = 29, ANIM = 418, RMSE = 0.84, $r^2 = 0.97$, $P < 0.01$, model 7, Fig. 4).

The quadratic model did not fit the data and we obtained the linear model probably because in the current range of dietary phosphorus concentration, phosphorus absorption

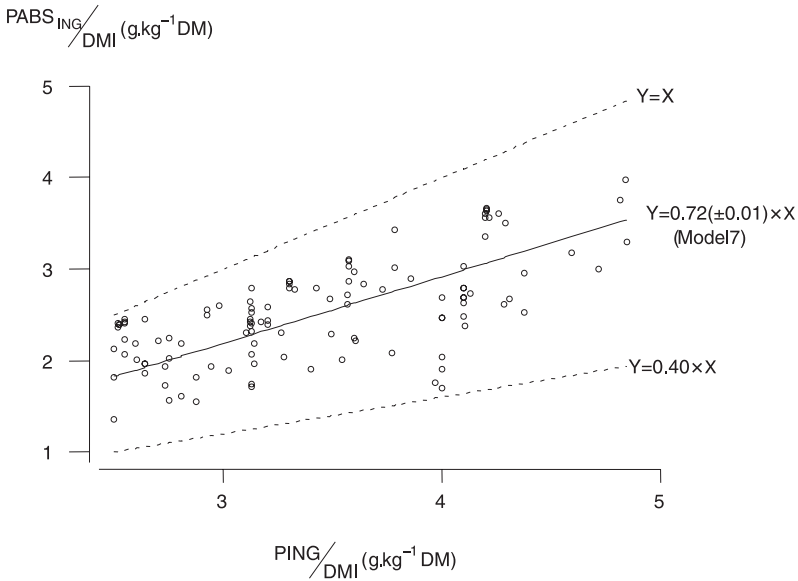


Figure 4. Relationships between the true absorption of ingested phosphorus ($PABS_{ING}$, $g \cdot day^{-1}$) and the ingested phosphorus (PING, $g \cdot day^{-1}$) normalised according to DM intake ($kg \cdot day^{-1}$) on the common scale of dietary phosphorus (between 2.5 and 5.0 $g \cdot kg^{-1}$ DM). The model (solid line) and the line $Y = X$ and $Y = 0.40 \cdot X$ (dot lines) are shown.

efficiency does not decrease with ingested phosphorus.

3.4. Absorption of total phosphorus

Total phosphorus absorption increased with total phosphorus flux into the gut according to the following model:

$$PABS_{TOT}/DMI = 1.01 (\pm 0.05) \times PTOT/DMI - 3.0 \times 10^{-2} (\pm 3.5 \times 10^{-3}) \times [PTOT/DMI]^2$$

(TRT = 34, EXP = 5, ANIM = 139, RMSE = 2.29, $r^2 = 0.97$, $P < 0.01$, model 8, Fig. 5).

The quadratic nature of this regression equation also results from a decrease in the efficiency of total absorption of phosphorus due to the high amount of phosphorus present in the digestive tract.

3.5. Animal and production state effect on the efficiency of phosphorus absorption

The interaction between the species and the physiological state had a significant

effect on the efficiency of phosphorus absorption ($EFFABS_{ING}$, TRT = 405, $r^2 = 0.11$, RMSE = 0.25, $P < 0.01$, Tab. II). Determined on the low number of treatments involved (7, 13, 2, 16 respectively for growing beef, maintenance sheep, gestating sheep and lactating ewes), and the imbalance design, the interaction between species and the production state was not significant for the efficiency of salivary phosphorus absorption ($EFFABS_{SAL}$, $P = 0.28$) and the efficiency of total phosphorus absorption ($EFFABS_{TOT}$, $P = 0.21$).

3.6. Dietary effects on phosphorus absorption

With ingested phosphorus held constant, the dietary content in terms of forage (%FOR), cereals and cereal by-products (%CERBP) and crude fibre (CF) significantly influenced the absorption of phosphorus despite a low correlation for each single variable.

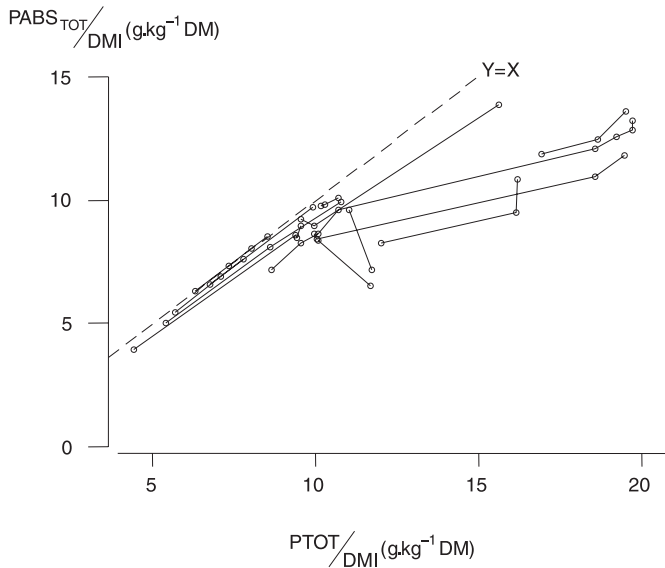


Figure 5. Relationship between the total absorption of phosphorus (PABS_{TOT} , $\text{g}\cdot\text{day}^{-1}$) with total phosphorus entering the digestive tract (PTOT , $\text{g}\cdot\text{day}^{-1}$) normalised according to DM intake ($\text{kg}\cdot\text{day}^{-1}$). The points from the same trial are connected by a solid line. The line $Y = X$ (dotted line) is shown.

Table II. Species and physiological state effect on the efficiency of dietary phosphorus absorption.

SPE	PROD	TRT	Mean (SE)	
Sheep	Growth	100	0.72 (0.01)	B
	Maintenance	201	0.71 (0.01)	B
	Pregnancy	3	0.56 (0.07)	B
	Lactation	32	0.71 (0.02)	B
Cattle	Growth	54	0.76 (0.01)	B
	Maintenance	10	0.42 (0.02)	C
	Lactation	2	0.69 (0.05)	B
Goats	Growth	3	0.87 (0.01)	A
	Lactation		ND	

ABC In the same column, different letters, means different ($P = 0.05$).

$\text{PABS}_{\text{ING}}/\text{DMI} = 1.55 (\pm 0.07) + 2.52 \times 10^{-2}$
 $(\pm 3.13 \times 10^{-3}) \times \% \text{CERBP}$
 (TRT = 301, EXP = 47, ANIM = 1114,
 RMSE = 1.97, $r^2 = 0.18$, $P < 0.01$, model 9).

$\text{PABS}_{\text{ING}}/\text{DMI} = 2.19 (\pm 0.09) + 5.9 \times 10^{-3}$
 $(\pm 1.59 \times 10^{-3}) \times \% \text{FOR}$
 (TRT = 301, EXP = 47, ANIM = 1114,
 RMSE = 2.13, $r^2 = 0.05$, $P < 0.01$, model 10).

$\text{PABS}_{\text{ING}}/\text{DMI} = 3.25 (\pm 0.19) + 6.11 \times 10^{-3}$
 $(\pm 8.73 \times 10^{-4}) \times \text{CF}$
 (TRT = 265, EXP = 35, ANIM = 963,
 RMSE = 1.99, $r^2 = 0.15$, $P < 0.01$, model 11).

In contrast, with ingested phosphorus held constant, dietary phytate phosphorus reduced the true phosphorus absorption:

$\text{RES}[\text{PABS}_{\text{ING}}/\text{DMI}(\text{PING}/\text{DMI})] = -0.374$
 $(\pm 0.07) + 0.11 (\pm 0.02) \times [\text{PHYT}/\text{PDIET}]^{-1}$

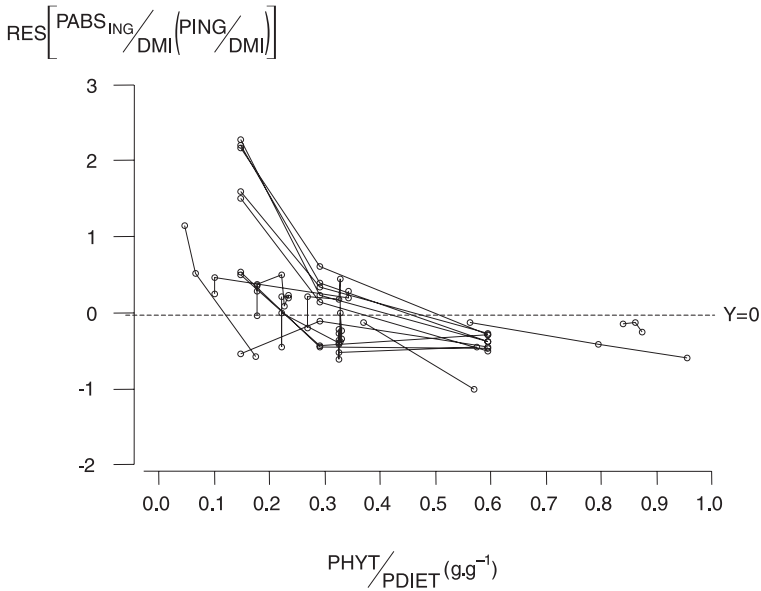


Figure 6. Relationship between the absorption of ingested phosphorus ($PABS_{ING}$, $g \cdot day^{-1}$) and the proportion of phytate phosphorus ($PHYT$, $g \cdot kg^{-1}$ DM) in the total dietary phosphorus content ($PDIET$, $g \cdot kg^{-1}$) with ingested phosphorus ($PING$, $g \cdot kg^{-1}$) held constant. The points from the same trial are connected by a solid line. The line $Y = 0$ (dotted line) is shown.

(TRT = 66, EXP = 19, ANIM = 581, RMSE = 0.87, $r^2 = 0.28$, $P < 0.01$, model 12, Fig. 6).

As shown in Figure 6, in most of the trials with a variation of phytate phosphorus content, a decrease of the absorption of ingested phosphorus was observed. Unfortunately, other specific dietary effects on this absorption were not investigated.

4. DISCUSSION

4.1. The mechanisms and sites of phosphorus absorption

Regarding the mechanisms of phosphorus absorption, few data are available in ruminants, and therefore no conclusion may

be drawn from our database. However, these mechanisms are probably comparable to those of other species [8, 9]. Phosphorus has been reported to be rapidly absorbed as shown in dogs by enrichment of the blood with radioactive phosphorus, 5 minutes after duodenal infusion [10]. The dog intestinal wall is thought to delay phosphorus absorption because 0.20 of radioisotopic phosphorus is still present in the intestinal wall 4h after the duodenal infusion [10], probably in the form of a phospholipid [11]. Absorption was later shown to be maximal 30 minutes after duodenal infusion in rats [12]. Generally, phosphorus absorption combines quickly saturated active absorption and passive diffusion, which predominates when phosphorus concentration in the intestinal lumen is high [13, 14]. Therefore, the efficiency of phosphorus absorption

decreases when the concentration of phosphorus in the digestive tract is high, as observed in our database by the quadratic relationship between phosphorus absorption and ingested phosphorus (model 6). However, within the current range of dietary phosphorus (2.5–5.0 g·kg⁻¹ of DM), phosphorus absorption efficiency appears constant whatever the dietary phosphorus supply.

Increased phosphorus absorption is attributed to regulation of the absorption capacity, several digestive sites being known to absorb phosphorus under restricted conditions. Absorption of phosphorus from the rumen has been discussed [15], and does not appear to be negligible [16–18] even though quantitative data are rare [19]. The abomasum does not absorb phosphorus [9] and the post-rumen absorption sites are distributed in the gut. The main intestinal absorption sites are in the duodenum [20] and jejunum [21–23]. The absorption of phosphorus from the large intestine is controversial: it is either inexistent [22] or very low [21, 23, 24] or substantial [25]. In adult sheep fed balanced phosphorus diets, phosphorus is mainly absorbed in the proximal jejunum. In phosphorus-depleted sheep, the distal colon and even the caecum can absorb phosphorus very efficiently [25]. Consequently, the diversity and potentiality of phosphorus absorption could explain the adjustment capacities of ruminants for phosphorus absorption which is also the case for monogastrics.

4.2. Dietary phosphorus availability

Digestive phosphorus availability, also called the true absorption coefficient, is a main determinant of the daily phosphorus supply calculated by the factorial method. In fact, this availability varies from 0.50 [26] to 0.70 [27], but this value is constant in each system of recommendations, except in [27] where the coefficient is higher for high concentrate diets (0.70) than for high forage diets (0.58). According to

model 7, for common amounts of ingested phosphorus (between 2.5 and 5.0 g·kg⁻¹ of DMI), 0.72 of ingested phosphorus is absorbed on the average. The constant true absorption coefficient values advocated [26, 28] appear to be too low. However, the remaining variations are probably due to feed-stuffs or diets [6, 29, 30], differences in phosphorus digestive availability [31] and also differences among species and physiological state.

Diet effect on apparent mineral availability and retention was not taken into account [32], particularly for phosphorus [33], because variations due to the diet are considered as negligible compared to individual animal variations [34]. Improvement of our knowledge of the mineral content of feedstuff [35] and of phosphorus quality [36] is the two keys for improved supplementation [31] and pollution management [37]. Despite its importance in the calculation of phosphorus supply, few experimental findings on phosphorus availability in ruminants are available. Even though inorganic phosphates have been intensively studied (from 1957 [38] to 1998 [39]), the results are scarce for forages and concentrates. The authors who studied phosphorus digestive availability of forages have reported values of 0.70 [29], of 0.75 [35] and even 0.80 in lactating cows [40] for corn silage. In contrast, true absorption (alfalfa) for hay phosphorus was found to be only 0.55 [41]. A true absorption coefficient value of 0.60 would be suitable for diets with large amounts of hay whereas 0.70 would suit better to silage-based diets. More than 0.70 of the phosphorus in cereals is absorbed [31] and the values reported for cereal by-products are also high: 0.70 in corn gluten meal [31] and 0.90 in wheat bran [42]. For this reason, the main criticism of the current systems is not the level recommended (0.50, 0.55, 0.60 or 0.70) but may concern the constancy of the recommended value. A true absorption coefficient value of 0.60 would be suitable for diets with large amounts of hay whereas 0.70 would better suit silage-

based diets. Only [27] has proposed different true absorption coefficient values whether the diet is rich in forage or rich in concentrate. The precision of phosphorus supply determination should be improved by using a true absorption coefficient differing by feedstuffs or by group of feedstuffs as proposed recently by [43].

4.3. The factors affecting digestive phosphorus availability

The dietary phytate phosphorus content appears to be one factor affecting the digestive availability of phosphorus (model 12, Fig. 6).

In spite of no statistical result and no specific study on dietary effect, another grain component may influence phosphorus absorption. For instance, some minerals, other than phytate, present in the grain could precipitate phosphorus near the absorption sites [34, 44, 45] explaining the results of the model 12. The question of the efficiency of phytase is important since phytate phosphorus, under the IP6 form, escaping the rumen without degradation might not be hydrolysed further in the digestive tract. In fact, the only phytase activity observed in the lower digestive tract is very low phytase activity of enterocytes in pigs [46] or in chyme in the distal ileum [1], probably unable to completely hydrolyse phytate under IP6 form [47]. Undegraded phytate phosphorus, still under IP6 form, is thought to be unabsorbed [1, 48] and phytate decreases the digestibility of other nutrients by inhibiting digestive enzymes [49] or binding with proteins [44] or with dietary minerals [50]. Phytate phosphorus exhibits a highly variable absorption efficiency, from 0.35 to 0.81 in cows [50]. Its digestibility is very low when supplied in excess (0.25 [51]). In current European ruminant diets, phytate phosphorus is increasing with the increasing incorporation of cereals and its influence on phosphorus metabolism has not been investigated up to now in digestibility trials.

4.4. The rumen ecosystem: an additional compartment in phosphorus digestion

Besides saliva and feed origin of phosphorus, another phosphorus source can enter the duodenum, that is rumen microbes.

4.4.1. Phosphorus supply to the rumen ecosystem

Total phosphorus entering the rumen comes from saliva and feed. In common diets (2.5 to 5.0 g·kg⁻¹ of DM), increases in ingested phosphorus decrease saliva phosphorus (model 2, Fig. 2), but the total quantity of phosphorus entering the rumen remains constant since the slope of the model between PTOT and PING is not different from 0. This is important because salivary phosphorus is the main source of rumen inorganic phosphate [52] available for the microbes. Rumen microbes concentrate phosphorus from rumen fluid and from the diet [53] primarily in organic form, as nucleotides [54]. Moreover, since phosphorus requirements for rumen microbes [54] are higher than animal phosphorus requirements [55], care should be taken to meet the microbe requirements [29, 56]. To maintain the concentration of inorganic phosphate in the liquid phase of the rumen contents, dietary phosphorus should be quickly converted into inorganic phosphate. In the rumen, phytate phosphorus is degraded by phytase [57], which is produced by the rumen microbes [58, 59]. Some dietary situations may decrease the efficiency of phytase activity. After formaldehyde and some heat treatments, phytate phosphorus may be inaccessible to phytase [60, 61]. Furthermore, even if when more phytate phosphorus is present in a medium, the higher is the release of inorganic phosphorus, dietary phytate phosphorus may not be broken down in cases of saturation of rumen phytase by large amounts of dietary phytate phosphorus as previously suggested for vegetal phytases [62, 63] and for rumen

phytases [58, 64, 65]. These hypotheses should be verified by new experimental work. Finally, the contact time between the enzyme and the substrate may be limiting. When the rumen turnover rate is increased from $0.02 \cdot \text{h}^{-1}$ to $0.08 \cdot \text{h}^{-1}$, the rumen degradation of phytate phosphorus (from soybean meal) decreases from 0.62 to 0.37 [61]. The rate of conversion of feedstuff phosphorus into inorganic phosphate in the rumen should be investigated. In other words, the question of phosphorus requirements for the rumen ecosystem is raised, owing to the role of phosphorus especially in cell wall degradation [54]. Accordingly, considerations on phosphorus nutrition of ruminants should include a specific, microbial phosphorus compartment that interferes with phosphorus utilisation by the host animal, especially if a decrease in the phosphorus supply is investigated [66] and if the diet fed induces lower salivary phosphorus fluxes.

4.4.2. Rumen microbe phosphorus: a source of phosphorus for the ruminant

Rumen microbes appear to be an intermediary source of phosphorus for the host animal. In fact, since salivary phosphorus is a soluble inorganic form, we expected to find a higher absorption rate for salivary phosphorus than for dietary phosphorus. The models 4 (for PSAL) and 7 (for PING) indicate that, in common diets, 0.77 of salivary phosphorus and 0.72 of ingested phosphorus are absorbed. In both models, the efficiency of absorption of salivary phosphorus was not much higher than the absorption of ingested phosphorus. The protozoa which ingest bacteria, would delay salivary phosphorus utilisation by the animal and would explain why the phosphorus flux in the duodenum is greater in defaunated sheep [67]. Salivary phosphorus incorporated by the microbes requires further digestive solubilisation in order to

be used by the host animal and would be less available than soluble phosphorus [68] or even partly unavailable for the animal [69]. This would explain the lower salivary phosphorus availability compared to dietary phosphate observed by [70].

5. CONCLUSIONS

The current need to decrease pollution requires a better understanding of phosphorus metabolism in ruminants. The first applications of this database study were to analyse digestive phosphorus availability and absorption in ruminants. The present study showed that 0.72 of ingested phosphorus is absorbed on average. In the calculation of the phosphorus supply to ruminants, a high constant value of phosphorus availability should not be used. Instead, different values for groups of feedstuffs should be retained. At present, data is lacking on the phosphorus availability of concentrate meals. Our results also suggest that factors influencing phosphorus availability should be investigated, as well. One of these factors would be dietary phytate phosphorus content. Rumen microbes appear to form an important link in phosphorus nutrition since (i) their own phosphorus requirements are high and essential for rumen cell-wall degradation and (ii) they appear to be an intermediary source of phosphorus that has been underestimated in almost all previous studies. For this reason, more work on phosphorus availability for rumen microbes and the potential utilisation of microbial phosphorus by the host animal is warranted.

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