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Review

Absorption, Availability, Metabolism and Excretion of Phosphorus in Ruminants

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ABSTRACT

This paper describes absorption, metabolism, excretion and availability of phosphorus in ruminants. Phosphorus is an important constituent of various body parts of animals. Deficiency of phosphorus has been reported at global level leading to disorders of skeletal, muscular and nervous systems, decreased efficiency in terms of reproduction and milk production and intravascular hemolysis. Salivary glands having a higher concentration of P compared with the blood plasma play an important role in P homeostasis. Recycling of P is stimulated by parathyroid hormone. Phosphorus may be absorbed from the small intestine via a vitamin D dependent active transport system and/ or passive absorption system. Livestock forages contain an organic form of P (phytate) which must by hydrolyzed to make P available to be absorbed. Absorption of P depends upon its solubility, pH, concentration of available P, forage source, plasma level of Ca, age of animal and genetics. Major route of excretion of P is feces. However, when dietry P is in excess, urinary P excretion is increased. Availability of minerals varies from soil to plansts. In Pakistan, marginal to severe deficiency of P has been documented in Sahiwal and Okara. Berseem (*Trifolium alexandrinum*) has been found notoriously low in phosphorus. To improve the P contents in roughages, superjuice prepared from superphosphate appears the cheapest source of P for livestock feeding in Pakistan.

Key Words: Phosphorus; Absorption; Availability; Metabolism; Excretion; Ruminants

INTRODUCTION

Phosphorus is one of the costliest macronutrients in the diet of animals located in every cell of the body and has more known functions than any other mineral element in the animal body. In addition to being of major importance as a constituent of bone, P is an essential component of organic compounds involved in almost every aspect of metabolism. About 80% of phosphorus in body is found in bones and teeth (Little, 1970; NRC, 2001). Phosphorus plays an important part in muscle, energy, carbohydrate, amino acid, fat, and nerve tissue metabolism and phosphate is an important part of the nucleic acids DNA and RNA. It is also component of many coenzymes and is found in compounds such as adenosine di-and triphosphate.

Its deficiency is wide spread and affects livestock production and health in many parts of world including Indo-Pak subcontinent. Of all mineral deficiencies in cattle, the deficiency of phosphorus is the most common one on a global level (McDowell *et al*., 1993). Extreme phosphorus deficiency leading to the clinical bone disorders is relatively rare under practical conditions in ruminants while moderate to marginal deficiency is undoubtedly very wide spread (Jain & Chopra, 1994). Phosphorous deficiency is intimately associated with the depressed growth rate and generalized impairment of body functions. It is not surprising, therefore, that early effects of P deficiency are unthriftness, inappetence, decreased feed intake, worm infestation, pica, poor growth, reproduction. In lactating animals, P deficiency in diet may lead to 40% reduction in total ash contents (Little, 1972). In heifers, P deficiency leads to depressed fertility and low conception rates (Little *et al*., 1971). Cows fed diet with low phosphorus diet developed an insidious and complex syndrome characterized by weight loss, rough hair coat, abnormal stance, lameness, spontaneous fracture in vertebrae, pelvis and ribs. In severely affected cows the fractures do not heal properly. Bones become demineralized and porous. Bone structure and general health of phosphorus deficient cows improve rapidly when they are fed high phosphorus diet (Shupe *et al*., 1988). Rupturing of Achillus tendon in young bulls may occur as a result of disorder of minerals metabolism when they are fed diet containing low phosphorus and calcium (Illes *et al*., 1966).

Dietary P deficiency is widely believed to be the major predisposing factor of parturient hemoglobinuria, one of the most important diseases of dairy animals particularly in buffalo in Pakistan. It is an acute disease of high yielding buffaloes and is characterized by anemia, jaundice, recumbancy, laboured breathing, inappetance, constipation, intravascular hemolysis, reddish urine and low phosphorus level in blood. The disease can be controlled by feeding phosphate supplements (MacWilliams *et al*., 1982; Raz *et al*., 1988; Habib *et al.*, 2004). Phosphorus deficiency occurs when this nutrient is low in soil or when plant uptake of phosphorus is impaired. Particularly during the dry season, the pasture quality declines.

Metabolism. Metabolism of P in ruminants is complicated (Fig. 1). One reason for this complexity, is that a significant amount of P is incorporated by the rumen microbial population as a component of their nucleic acids and phospholipids. Furthermore, ruminants secrete a large amount of saliva from the salivary glands into the rumen, more than 100 liters per day. The P concentration in cattle saliva is 370-720 mg L^{-1}. These levels are considerably higher than that of bovine blood plasma, which is about 40-80 mg L^{-1}. Therefore, the salivary glands have an important part to play in the regulation and the homeostasis of P (Clark *et al*., 1973). Recycling of P through saliva is more in ruminants than non ruminants and is stimulated by parathyroid hormone. It may serve the two purposes, firstly, it supplies the rumen microbes with the added source of P (Durand & Komisarczuk, 1988) and secondly, it contributes to the total P homeostasis. About 80-85% of P in the body is found in bones and teeth. When dietary P is insufficient; mobilization of stored P becomes important. Bone is an active tissue that undergoes continuous metabolic changes and is remodelled by the activity of osteoblasts and osteoclasts, which form and resorb bone, respectively resulting in a continuous P exchange between bone and blood. Parathyroid hormone and vitamin D are required for maximum bone resorption (Morse *et al*., 1992).

Absorption. Phosphorus occurs in plants in either an inorganic (orthophosphate, pyrophosphate) organic (phospholipids, phosphosugars, ADP/ATP, nucleic acids polymers and phytate) form. Inorganic P sources, which are soluble in water or diluted acids, are available for absorption in ruminants. The solubility of P in organic compounds depends on the ability of the animal to convert P into an inorganic form or by changing the organic P into more acceptable organic forms (Underwood & Suttle, 1999). The absorption of ingested P depends on its solubility at the point of contact with the absorbing membranes (McDowell, 1992). Most of the dietary organic P will be hydrolyzed by the microbes into inorganic forms. The remaining organic P, which has not been hydrolyzed in the rumen, will be soluble in the low pH of the abomasum (Care *et al*., 1980; Breves & Schröder, 1991; Care, 1994). The availability of the microbial P may also depend on pH. Playne (1976) has suggested that if the pH is above 6 then the P may be unavailable. The absorption of P is thus favoured by factors, which operate to hold P in solution, and an acid medium tends to prevent the formation of the insoluble, and thus unobservable, tricalcium phosphate. The term retention is used to denote the amount of P that remains unabsorbed in the body. The current measurements of absorption are the product of the coefficients of availability and absorption. Due to the high amount of P that is recycled in the saliva, salivary secretion to some extent is related to plasma P concentrations and hence to P intake.

The dietary absorption coefficients are homeostatic mechanisms that are not easy to interpret. P is primarily absorbed in the small intestine (Reinhardt & Conrad, 1980), and the absorption is thought to occur mainly in the duodenum and jejunum (Care *et al.,* 1980; Care, 1994). Only small amounts are absorbed from the rumen, omasum, and abomasum, however, little is known about mechanisms and regulation of absorption anterior to the small intestine (Breves & Schröder, 1991). Presumably, P absorption occurs via two distinct mechanisms. A saturable vitamin D dependent active transport system operates when animals are fed low dietary P. Horst (1986) suggests that low plasma P will stimulate 1,25-dihydroxycholecalciferol synthesis that ultimately stimulates the intestine to absorb P more efficiently. Passive absorption predominates when normal to large amounts of potentially absorbable P are consumed, and absorption is thought to be related directly to the amount in the lumen of the small intestine and to the concentrations in blood plasma (Wasserman & Taylor, 1976; Care *et al*., 1980; Care, 1994). However, according to Braithwaite (1983) there is generally an inverse relationship between P intake and the absorption coefficient. When circulating concentrations of P are adequate, the P absorption rate may be reduced by saturation or inhibition in the absorptive mechanism. Morse *et al*. (1992) observed an inverse relationship between P intake and P absorption when non-limiting levels of P were fed. On the other hand, Khorasani *et al*. (1997) found that the relationship between P intake and total absorption of P was curvilinear, suggesting that forage source, due to the NDF-content, had a greater effect on total P absorption than P intake. The effect of P intake on P absorption needs further investigations. Factors which may reduce the coefficient of absorption of P are interactions with other minerals such as, Ca, Mg, Mn, K, Fe, Zn, Mo and Al, due to formation of insoluble and, thus, unabsorbable complexes with P. The desirable Ca:P ratio has for a long time been defined as lying between 1:1 and 2:1, due to the Ca:P ratio of bone. However, several studies suggest that the Ca:P ratio is not critical unless the ratio is greater than 7:1 or less than 1:1 (Wise, 1963; Call *et al*., 1978; McDowell, 1992).

When animals are fed P deficient diets, high levels of Ca may reduce the absorption of P (Schneider *et al*., 1985), due to a reduction in rumen P solubility and also a reduction in dietary P availability at sites further down the gut (Field *et al*., 1985). Therefore, it seems that ruminants can tolerate a wide range of Ca:P ratios as long as the dietary supply of each mineral is adequate and their vitamin D status is adequate. A substantial variation in the coefficient of absorption of P between, but not within, sets of monozygous twin sheep was reported. Thus, variation between animals in their capacity to absorb P appears to be genetically related (Field *et al*., 1985). Phytin P can be hydrolyzed in the rumen of mature ruminants. So in ration formulation for ruminants, phytin P cannot be discounted as is done in case of monogastric animals and young sucklers. The optimum requirement of P in the rumen for the viability of microorganisms has not been determined but addition of P to the P deficient medium enhanced the celluolytic activity. In ruminants effects of phytic on Ca, Zn and other minerals are less due to the degradation in the rumen. Phosphorus can also be made available from intestinal tract due to activity of RNAase and DNAase in ruminants (Preston *et al*., 1977).

Availability. The availability of P may be defined as the proportion of the dietary P which may be absorbed by the animal when it is absorbing P at a maximal rate. The P requirements of livestock are calculated based in part on the availability of P from feeds and supplements (NRC, 1985, 1996). Phosphorus availability is based on the chemical form of P in the feed and various animal factors such as age, stage of production, and overall level of nutrition (Axe, 1998). For ruminants, the NRC (1985, 1996) estimates P availability to be 68%.Most livestock diets are derived from plant-based feedstuffs. These types of feeds contain the organic form of P known as phytate (Tillman & Brethour, 1958). Before P from phytate can be absorbed by the small intestines the phytate molecule must be hydrolyzed by the enzyme phytase (Clark *et al*., 1986). Because phytase is produced by the ruminal microorganisms the general assumption is that there is no difference in the availability of different forms of P to ruminants (Clark *et al*., 1986). However, there have been discrepancies in the literature based on the utilization of different forms of P by ruminants. Tillman and Brethour (1958) reported results from a metabolism trial with sheep comparing inorganic P supplementation (calcium phosphate) to organic P supplementation (calcium phytate). There were no differences in P digestibility, retention, or excretion between the forms of P. According to the results of that study, the P from calcium phytate was 90% as digestible as the P from calcium phosphate. It was also found that for that study 92% of the organic P was hydrolyzed in the rumen and made available for absorption.

Excretion. Practically all P excretion occurs in faeces, and normally urinary excretion of P is of little significance (ARC, 1980; Betteridge *et al*., 1986). The excess of phosphates during the resorption of bone tissues is excreted from the body via kidneys in young ruminants while in adults it is eliminated through the gastrointestinal tract (GIT). Cows excreted 88.2% of P consumed daily, out of which 66.6% in feces, 1% in urine and 30.3% in milk (Morse *et al*., 1992). The excretion of P in monogastric species is mainly in the form of urine. However, in ruminants P excretion occurs mainly via the faeces and it is only under certain conditions that urinary excretion may occur. The P in faeces is either exogenous, which is unabsorbed dietary P (Bromefield & Jones, 1970) or endogenous, which is of bodily origin, mainly from saliva P (Wadsworth & Cohen, 1976) but there is also P from intestinal cells and digestive secretions (Playne, 1976).

Fig. 1. Phosphorus (P) metabolism in the dairy cow

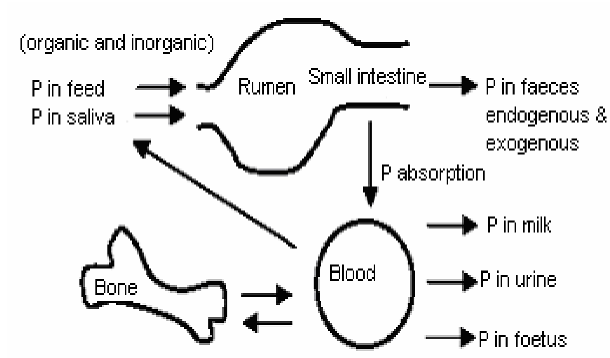
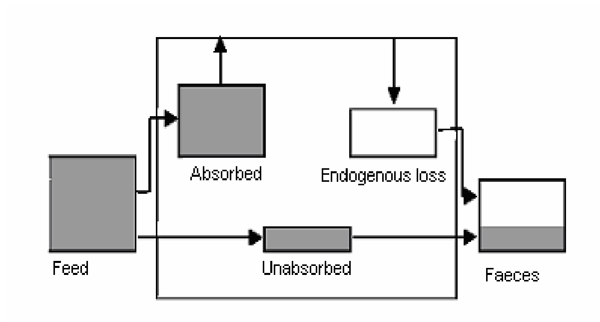


Fig. 2. Block diagrame illustrating the difference between apparent and true digestions of feed (*modified from Playne, 1976*)



Faecal excretion of P may be partitioned into three fractions, namely a) P of dietary origin unavailable for absorption or not absorbed, b) P of endogenous origin that inevitably has to be excreted under actual nutritional and physiological conditions, and c) P of endogenous origin which is excreted to maintain homeostasis (Spiekers *et al*., 1993; NRC, 2001). From investigations using sheep and goats, it was concluded that inevitable faecal losses of P are a function of dry matter intake (DMI) rather than of live weight, as earlier thought (Doyle *et al*., 1982; Field *et al*., 1985). The effects of DMI, of inevitable faecal losses of P, may partly be explained by the large contribution of salivary P to total endogenous P secretion. The total endogenous faecal P may constitute more than 2/3 of the total faecal P in cattle and sheep (Scott *et al*., 1985; Ternouth, 1989; Coates & Ternouth, 1992) and the main sources of faecal P in ruminant animals are illustrated in Fig. 2. "Apparent digestibility", measured by the difference between the amounts of P in the feed and faeces, give no information about the different faecal fractions. The "true digestibility", which is arrived at by correcting for the faecal endogenous loss, is commonly referred to as "availability". However, in most experiments no differentiation has been made between the origins of the faecal P, whether exogenous or endogenous P.

The phosphorus concentrations in products can be measured rather easily, however, the determination of inevitable losses is more critical, and there are no easy and accurate methods available. The amount of endogenous P recycled via saliva must be taken into account and is most appropriately estimated experimentally by quantifying recycling with a tracer (e.g., P_{32}). In addition, P must be fed in an amount less than the animal's true requirement to ensure the maximum efficiency of absorption. Most studies do not satisfy these experimental specifications. Thus, the true absorption coefficient (TAC) is generally unknown and the value given is an underestimation of true absorption (NRC, 2001). It must be kept in mind that the apparent digestibility of P is lower, mainly because of the large endogenous faecal excretion, and not equivalent to the TAC. However, apparent digestibility still provides a lot of information if it is accurately measured. Even though, the apparent digestibility of P is commonly used as a measurement of P digestibility. There are marked differences between studies in the time spent measuring the apparent digestibility (Brintrup *et al*., 1993; Spiekers *et al*., 1993; Valk & Sebek, 1999). The duration in collecting faeces differs from taking spot samples (Wu *et al*., 2000) to total collections for several days (Morse *et al*., 1992), and there is a lack of information about the variations in P excretion over time.

Phosphorus in Pakistan. Pakistan is a land of soils having different agro-climatic regions. The quality and quantity of nutrients of forages mainly depends upon the factors like type of soil, level of fertilization and source of irrigation water. Mineral availability, particularly of trace elements varies to a very great extent from soil to plants. Macronutrients are depleted by more intensive cropping system. Limited research work conducted in the country has indicated marked areas of mineral imbalances and deficiencies in the soil. Mineral composition of soil in the districts of Sahiwal and Okara having higher population of Sahiwal cattle and buffalo has indicated marginal to severe deficiencies of phosphorus, zinc, copper, cobalt and iron (Malik, 1987; Pederson, 1989).

Berseem (*Trifolium alexandrinum*), the most common winter and spring fodder in many parts of Pakistan is notoriously low in phosphorus contents (0.14%) and abundant in calcium (1.44%). Owing to a wide calcium-phosphorus ratio, animals fed predominantly on berseem unless supplemented with some rich source of phosphorus like grains may suffer from phosphorus deficiency syndromes (Ranjhan, 1993). Concentrates and grains, although rich in phosphorus are prohibitively expensive especially for feeding to growing calves. Bone flour, phosphoric acid, sodium and calcium phosphate has been used as sources of phosphorus but from economic stand point, they are expensive especially for feeding to young calves .The value of these compounds in providing phosphorus depends in part upon the biological availability of the phosphorus present (Donovan *et al.,* 1970; McMeniman, 1973).

The nutritional quality (protein & energy) of roughages has been greatly improved through different treatments but no attention has been given to improvement of phosphorus contents while recommending these techniques (Jain & Chopra, 1998). It is mention worthy that the use of super juice is a fairly popular dairy management practice in Australia (Hungerford, 1990; Radostits *et al.,* 2000). Superphosphate or super juice prepared by dissolving superphospate in water appears probably the cheapest source of phosphorus for livestock feeding in Pakistan. The economic value and harmful effects (if any) of feeding super juice or superphosphate fertilizer, however, remains to be investigated under Pakistani dairy farming conditions (Iqbal, 2004).

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