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Invited review: Mineral absorption mechanisms, mineral interactions that affect acid–base and antioxidant status, and diet considerations to improve mineral status

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ABSTRACT

Several minerals are required for life to exist. In animals, 7 elements (Ca, P, Mg, Na, K, Cl, and S) are required to be present in the diet in fairly large amounts (grams to tens of grams each day for the dairy cow) and are termed macrominerals. Several other elements are termed microminerals or trace minerals because they are required in much smaller amounts (milligrams to micrograms each day). In most cases the mineral in the diet must be absorbed across the gastrointestinal mucosa and enter the blood if it is to be of value to the animal. The bulk of this review discusses the paracellular and transcellular mechanisms used by the gastrointestinal tract to absorb each of the various minerals needed. Unfortunately, particularly in ruminants, interactions between minerals and other substances within the diet can occur within the digestive tract that impair mineral absorption. The attributes of organic or chelated minerals that might permit diet minerals to circumvent factors that inhibit absorption of more traditional inorganic forms of these minerals are discussed. Once absorbed, minerals are used in many ways. One focus of this review is the effect macrominerals have on the acid–base status of the animal. Manipulation of dietary cation and anion content is commonly used as a tool in the dry period and during lactation to improve performance. A section on how the strong ion theory can be used to understand these effects is included. Many microminerals play a role in the body as cofactors of enzymes involved in controlling free radicals within the body and are vital to antioxidant capabilities. Those same minerals, when consumed in excess, can become pro-oxidants in the body, generating destructive free radicals. Complex interactions between minerals can compromise the effectiveness of a diet in promoting health and productivity of the cow. The objective of this review is to provide insight into some of these mechanisms.

Key words: fatty acid, adipogenesis, lipogenesis, stromal vascular cell

GENERAL MODELS FOR ABSORPTION OF MINERALS

Minerals in the diet must be absorbed across the epithelial cells that line the gastrointestinal (**GI**) tract to enter the blood for use by the tissues. Minerals can be absorbed from any portion of the GI tract. However, the bulk of absorption for most minerals takes place in the small intestine, so the general processes used for mineral absorption will be illustrated using the small intestine as the model. Both the small and large intestines are lined by a single layer of epithelial cells joined together by proteins such as occludins, claudins, and e-cadherens that form a tight junction between adjacent cells. A portion of the cell membrane of each intestinal epithelial cell is in contact with the lumen of the gut. This is the apical surface of the cell. The apical membrane is thrown into many tiny folds that project out into the lumen. These microvilli, also called the brush border, greatly increase the surface area available for absorption. A thin layer of mucus and glycoproteins known as the glycocalyx overlies the apical membrane, and above this an unstirred water layer adheres to the glycocalyx by surface tension. The remaining surface of the epithelia cell below the tight junctions is in contact with extracellular fluids and is called the basolateral membrane of the cell. The epithelial cells sit on a highly permeable meshwork of protein known as the basement membrane. Beneath this lies the lamina propria. The lamina propria is loose connective tissue with extracellular fluids and a rich vascular and lymphatic network within it. Lymphatic capillaries, known as lacteals, take up absorbed dietary lipids that have been packaged into chylomicrons and recover plasma proteins that may have leaked from the capillary bed. The vascular capillaries are fenestrated, with wide openings between

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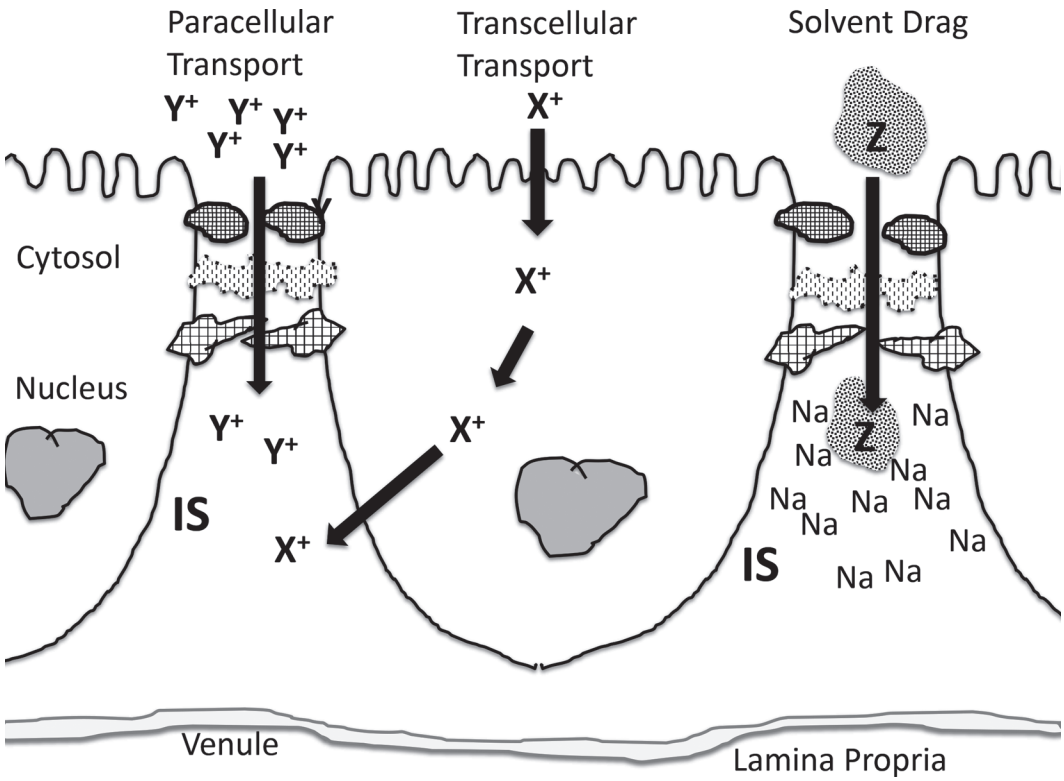

Figure 1. Enterocytes lining the gastrointestinal tract are connected to each other by tight junction proteins. Paracellular absorption involves movement of ions, designated by Y^+, by diffusion down their electrochemical gradient through pores in the tight junction and into the interstitial space (IS) across the tight junctions. Minerals dissolved in water, designated by Z, can move across the tight junction with the bulk flow of water, which is known as solvent drag. Transcellular absorption involves mechanisms that allow minerals, such as X^+, to cross the apical membrane, to move across the cytosol of the cell, and to move the ion across the basolateral cell membrane into the IS and lamina propria for entry into the vasculature.

endothelial cells, to aid absorption of sugars, AA, and minerals into the blood (Goff, 2015). Together the cells and tight junctions form an effective barrier to invasion by most bacteria and large molecules in the lumen that might be toxins (Figure 1). This barrier also typically blocks the passage of sugars, AA, and other large products of digestion.

The tight junctions between cells are not completely solid. There are small fissures, pores, and channels within the protein meshwork forming the tight junction. The tight junction meshwork normally offers resistance to mineral (and water) absorption—that is, the openings are too small for easy penetration by minerals. In addition, there is an electrical potential difference (**PD**) across the tight junctions—about +5 mV (lumen side negative, interstitial space side positive) in the small intestine and as high as +30 mV in the large intestine (Field, 2003)—that offers resistance to absorption of cations across the tight junctions but provides a force that promotes absorption of anions across the tight junctions.

The resistance to movement across the tight junction can be overcome if the concentration of mineral, in a freely ionized state, dissolved in the fluids overlying the luminal side of the tight junction greatly exceeds the ionized concentration of that mineral in the extracellular fluids within the interstitial space (a cleft between adjacent enterocytes) on the other side of the tight junction. Ionized mineral concentration implies that the mineral is in a state where it is not bound to proteins or other large substances and is in solution. The diffusional force created by differences in the ionized mineral concentration on each side of the tight junction can be great enough to push the mineral through the tight junction into the interstitial space, and from there it passes through the openings in the capillary endothelium and into the blood. This process is known as paracellular absorption. It is possible whenever the concentration of a mineral in solution over the tight junction is significantly greater than the concentration of the mineral in the extracellular fluids. Like all processes driven by diffusion, the size of the mineral atom and its electrical charge also determines how easily a mineral will cross the tight junction. Because the driving force to push minerals across the tight junctions is dependent on large concentration gradients, paracellular absorp-