



Review article

Coping with shrub secondary metabolites by ruminants

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ABSTRACT

Rangelands throughout the world contain varying but often substantial proportions of shrubs. Shrubs are generally heavily chemically defended, and herbivores must either contend with their plant secondary metabolites (PSM) or avoid a significant component of the available forage. Browsing ruminants are exposed to thousands of chemicals in infinite combinations and concentrations that are constantly changing both temporally and spatially. The success with which a herbivore navigates this complex environment is in part attributed to its ability to cope with PSM. Plant secondary metabolites can affect a number of physiological and metabolic processes (e.g., altered microbial activity, reduced digestion, compromised acid/base balance, toxicity), although negative consequences to the herbivore range from harmless to lethal, depending factors such as dose, animal species, plane of nutrition, and physiological state. Herbivores have a variety of intertwined mechanisms to cope with consumption of PSM, ranging from physiological (e.g., salivary proteins, detoxification pathways) to behavioral (e.g., avoidance, regulation of intake below critical threshold, cautious sampling, altering size and pattern of feeding bouts, diet switching, consuming diverse and/or complementary diets). Secondary compounds may affect requirements for nutrients (e.g., protein, minerals, and glucose) and water, and may alter basal metabolic rate. Energy requirements may also increase to accommodate increased travel to water and supplementation sites to counter these negative effects, particularly on arid rangelands. A number of management strategies exist for minimizing the negative effects of PSM consumption on livestock. Supplementation to replace nutrients depleted during detoxification (e.g., amino acids and glucose), additives such as PEG and charcoal to reduce absorption and increase excretion of PSM, maintaining animals in good body condition, and behavioral modifications (e.g., diet training) are among the potential management options for enhancing the ability of ruminants to cope with PSM when browsing shrubby ecosystems.

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1. Introduction

About 25% of the world's land surface is used for extensive livestock production, and over a fourth of this grazed land is dominated by shrubs (Asner et al., 2004). Shrubs are generally well defended and have survived and often flourished under systems receiving heavy grazing. These shrubs are typically used by browsing ruminants in low

amounts if at all, even though they often contain an abundance of protein and other nutrients. Secondary chemistry of shrubs across arid and semi-arid regions represents a basic mechanism for plant competitiveness and appears to be especially important for adaptation to harsh, resource-limited environments (Freeland, 1991). Thousands of PSM from numerous structural classes exist in nature, and their presence and concentration in a given plant are influenced by genetics, phenology, and a host of biotic and abiotic environmental factors. Thus, their concentrations vary temporally and spatially among and within species, and their proportions relative to other compounds (both

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primary and secondary) are in constant flux. While there is little doubt that secondary chemistry plays a pivotal role in herbivory, the mechanisms by which ruminants cope with PSM and effect of secondary compounds on livestock production are not well understood.

2. Consequences of PSM consumption

The variable nature of secondary chemistry of plants is the basis for differential use within and among plant species. In one of the first studies to demonstrate differential use of a shrub species by ruminants, Welch et al. (1981) reported varying preference for certain accessions of sagebrush (*Artemisia tridentata*) by mule deer (*Odocoileus hemionus*). Studies conducted at the Jornada Experimental Range (JER) revealed differential use of tarbush (*Flourensia cernua*) by small ruminants. Variable plant to plant defoliation by sheep and goats was related to concentrations of epicuticular wax and specific mono- and sesquiterpenes on the leaf surface (Estell et al., 1994, 1998a). Preference and/or intake of browse species have been negatively related to terpene concentration (either total amount, specific fractions, or individual compounds) in mule deer (Personius et al., 1987; Schwartz et al., 1980b), red deer (*Cervus elaphus*) (Duncan et al., 1994), roe deer (*Capreolus capreolus*) (Vourc'h et al., 2002), sheep (Estell et al., 1998b, 2002; Ngugi et al., 1995), and goats (Riddle et al., 1996). Preference and/or intake of woody browse species have also been negatively related to phenolic and/or tannin concentrations (total phenolics, hydrolyzable tannins, condensed tannins, or individual compounds) in African antelope (*Aepyceros melampus* and *Tragelaphus strepsiceros*) (Owen-Smith and Cooper, 1985), fallow deer (*Dama dama*) (Alm et al., 2002), moose (*Alces alces*) (Stolter et al., 2005), and sheep and/or goats (Degen et al., 2002; Papachristou et al., 2003; Provenza and Malechek, 1984; Silanikove et al., 1996; Woodward and Coppock, 1995). Salem et al. (2006) reported that condensed tannins, total phenolics, saponins, alkaloids, and essential oil were all good predictors of intake by sheep and goats consuming Egyptian browse species.

In addition to effects on intake and dietary preferences, secondary compounds exert other effects ranging from decreasing diet quality to microbial effects to toxicosis. Shrubs containing terpenes, tannins, or phenolics can adversely affect dry matter and/or protein digestibility and nitrogen retention (Hagerman et al., 1992; Kaitho et al., 1998a; Min et al., 1998; Ngugi et al., 1995). Tannins can also shift site of protein digestion (increase ruminal escape protein) and nitrogen excretion (from urine to feces) in ruminants (Kaitho et al., 1998b; Woodward and Reed, 1997), due to their ability to bind and precipitate protein (Mueller-Harvey, 2006). Silanikove et al. (1996) observed reduced serum urea concentration in goats fed shrubs containing tannins, which they attributed to low nitrogen availability. Tannins also bind carbohydrates to some extent (Mueller-Harvey, 2006), which may also have implications for fermentation and nutritional value of some diets.

Secondary compounds also exert indirect effects on microbes that ultimately impact animal status. Phyto-

chemicals that negatively affect rumen bacteria can alter not only extent of digestion, but also fermentation patterns and end products available for metabolism. For example, phenolic acids (including *p*-coumaric acid) can be toxic to ruminal cellulolytic bacteria (Hartley and Akin, 1989), while saponins have been reported to increase microbial nitrogen flow from the rumen and decrease methane production, presumably due to defaunation of ruminal protozoa (Abreu et al., 2004; Babayemi et al., 2004). Terpenes can decrease *in vitro* digestibility in ruminants due to negative microbial effects (Oh et al., 1967; Schwartz et al., 1980a). Broudiscou et al. (2007) reported that with the exception of α -pinene, individual terpenes generally reduced fermentation *in vitro*. However, Malecky et al. (2009) observed no effect of a blend of four monoterpenes on digestion or fermentation in goats and low recovery from the duodenum; they suggested the difference compared to their previous *in vitro* study was due to the long (several weeks) adaptation period. While the mechanisms by which PSM influence digestion and metabolism vary among compounds and classes, some generalizations exist. For example, condensed tannins tend to be poorly absorbed and not particularly toxic, but negatively influence digestion and protein status; conversely, hydrolyzable tannins are more readily absorbed and exert toxic effects at the tissue level.

Once absorbed, mammals rely on a combination of biotransformation enzyme systems (particularly in the liver, kidney, and intestines) for detoxification (e.g., oxidation, reduction, hydrolysis, and conjugation) (Parkinson and Ogilvie, 2008). Although in some cases biotransformation can increase toxicity (Parkinson and Ogilvie, 2008), phase I reactions increase polarity (and water solubility) and typically decrease toxicity of nonpolar lipophilic compounds through addition of functional groups via mixed function oxidases of cytochrome P450 enzymes (e.g., oxidation, hydrolysis, reduction), resulting in production of organic acids for urinary excretion (Dearing et al., 2005; Foley et al., 1999). The resulting decrease in blood pH must be countered by bicarbonate and phosphate buffering systems and elimination of hydrogen ions in the form of ammonium chloride (primarily via ammonia from hepatic glutamine) (Guyton, 1991). Phase II reactions involve detoxification through conjugation of PSM with compounds such as amino acids (e.g., glycine), glucuronic acid, glutathione, and sulfates, producing conjugates for excretion in bile or urine (e.g., glucuronides, hippuric acid); this process is energetically more expensive because of the loss of attached molecules, but avoids the physiological demands of excretion of acidic end products (Dearing et al., 2005; Foley et al., 1999).

The consequences of PSM ingestion at the tissue level are variable and dose dependent, and the degree and site of damage depend on many factors. The physiological implications of ingestion of secondary compounds range from nearly harmless (or even positive) to lethal, depending on the how acutely toxic a compound is and/or whether the quantity ingested is sufficient to overwhelm detoxification systems. For example, saponins are surfactants that can cause cellular membrane damage and red blood cell hemolysis but tend to be poorly absorbed (Majak, 2001; Marston

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