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Review article

Biogenic amines and gamma-amino butyric acid in silages: Formation, occurrence and influence on dry matter intake and ruminant production

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ABSTRACT

The concentration of biogenic amines (mono-, di- and polyamines) in silage and in the rumen, body tissues and body fluids mainly depends on the crop at harvest, the ensiling process, the silage and the digestion in the animal. Both the synthesis and the chemical structure of mono- and diamines are well documented. The basis for their formation is proteolysis, a naturally occurring process during ensilage, comprising the enzymatic decarboxylation of amino acids by the action of plant proteases and peptidases and of enzymes of various lactic acid bacteria (LAB), clostridia and other genera. Recent research has already delivered detailed knowledge about proteolysis, but the biochemical effects of biogenic amines in ruminants, including their impact on dry matter (DM) intake (DMI) by influencing sensory characteristics or post-ingestive feedback of the feed has not been elucidated. Data on effects of biogenic amines on palatability and their possible impacts on animal performance are scarce. However, some studies have been performed concerning the influence of biogenic amines on DMI, mainly with the quantitatively most relevant amines histamine, tyramine, putrescine and cadaverine. Studies differed greatly with regard to type of administration (supplemented to silage, provided orally in capsules or infused in the gastrointestinal tract *via* ruminal cannulas), dosages (2–40 g amine/kg DM) and mixtures (single doses or various combinations of amines; combinations of amines with aldehydes, organic acids or keto-acids). Single doses and low-level doses showed no effect on DMI, whereas higher concentrations naturally not occurring in silage and combinations like histamine and formaldehyde revealed an appetite-reducing effect. Gamma-amino butyric acid (GABA), a non-protein amino acid often classified into the category of amines has also been studied. The conflicting results in terms of the impact of GABA on DMI may result from the administration of non-protected *versus* rumen-protected GABA and the differing modes of action of the two forms in the hypothalamus. In this review the results of research into the effects of different levels of amines in silages from different crops and ensiling treatments including the use of additives as well as the consideration of possible reasons for variation in the concentration of amines in silage are evaluated. Approaches for elucidating

Abbreviations: CCK, cholecystokinin; CE, capillary electrophoresis; CP, crude protein; CZE, capillary zone electrophoresis; DM, dry matter; DMI, DM intake; GABA, gamma-amino butyric acid; GC, gas chromatography; HPLC, high-performance liquid chromatography; IEC, ion exchange chromatography; LAB, lactic acid bacteria; NPY, neuropeptide Y; OM, organic matter; RUP, ruminally undegraded feed CP; SD, standard deviation; TLC, thin layer chromatography; uCP, utilisable CP at the duodenum; VFA, volatile fatty acid(s).

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the possible impact on ruminant feed intake and level of production are also discussed. For an overall understanding of amine formation during ensilage further investigations with emphasis on correlations between the impact of ensiling and storage conditions and extent of amine formation are recommended to reveal relations between cause and effect.

Contents

1. Introduction

Ensiled forage offered to ruminants often results in a lower voluntary dry matter (DM) intake (DMI) as compared to the corresponding fresh (Donaldson and Edwards, 1976) or dried feed (Thiago et al., 1992). Intake may be decreased compared to hay and fresh forage by more than half (Campling, 1966). However, silage is important for productive and efficient ruminant livestock farms, especially in humid and temperate areas, where DM and quality losses in making hay may be excessive due to wet weather between cutting and harvesting the crop (Pahlow et al., 2003). Advantages of silage compared with hay are commonly higher digestible energy and lower hemicellulose concentration in the DM (Thomas et al., 1969). Often this is due to earlier dates of harvest. In general, ensiling is less weather dependent than hay production due to the shorter period of time between cutting and harvesting. A disadvantage of both types of forage conservation is loss of feed value compared to that of the original crop. The extent of the loss depends on the crop management, resulting in large variation in nutritional value and fermentation quality (McDonald et al., 1991). The quality of silage correlates with the pattern of fermentation, which may be the primary cause for decreased DMI in ruminants offered silage-based diets (Eisner et al., 2006). Factors contributing to decreased silage DMI including fermentation acids, pH and ammonia (NH_3), the influence of silage fermentation on utilization of protein and energy by the ruminant and methods for improving voluntary feed intake, protein quality and carbohydrate fermentation were summarized by Charmley (2001). It was presumed that fermentation acids act retrospectively by determining the balance of volatile fatty acids (VFA) produced in the rumen instead of influencing silage intake directly. The same might apply for NH_3 as it is supposed to exert a greater negative influence on silage intake by increasing total nitrogen solubility than by being detrimental *per se* since NH_3 is produced in the rumen by the microbial degradation of protein and amino acids. The most widespread and promising methods to improve silage intake are effective wilting and rapid acidification. A meta-analysis confirmed the significance of digestible organic matter (OM) in DM and the total concentration of fermentation acids in affecting silage intake by dairy cows (Huhtanen et al., 2007). Another meta-analysis found a negative relationship between DMI and the concentration of organic acids, NH_3-N and soluble-N compounds (Südekum and Eisner, 2009). Moreover, the degradation products resulting from proteolysis may impair animal health (Hoedtke et al., 2010); particularly biogenic amines have been given consideration (Křížek, 1995; Saarinen, 2002). Biogenic amines as N-containing compounds of low molecular weight (Křížek, 1993a) have been found in silage and were associated with lowered DMI in sheep (Buchanan-Smith and Phillip, 1986) and acute and subacute toxicity in rats (Til et al., 1997).

Biogenic amines arise from decarboxylation of amino acids (Table 1), based on the action of either plant enzymes or microbial enzymes of various species of lactic acid bacteria (LAB) (*Lactobacillus, Pediococcus* and *Streptococcus*) and species of the genera *Clostridia*, *Bacillus*, *Klebsiella*, *Escherichia*, *Pseudomonas*, *Citrobacter*, *Proteus*, *Salmonella*, *Shigella* and *Photobacterium* (Křížek, 1991, 1993a; Santos, 1996). Determining amine concentrations in silage may help to indicate undesirable changes in forages and could prevent possible toxicity for livestock (Křížek, 1991). However, until now amine analyses are not included in the standard chemical analyses of forages.

This review provides a comprehensive view of likely causes of different levels of amines in silages and approaches for elucidating their possible impact on feed intake and performance of ruminants. Due to conflicting perspectives on functions and effects of gamma-amino butyric acid (GABA) in the metabolism, the current state of research is described and gaps in knowledge are identified. For some time there has been an increase in studies dealing with rumen-protected GABA, arguing