ANTINUTRITIONAL EFFECTS OF CONDENSED AND HYDROLYZABLE TANNINS

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ABSTRACT

Despite major structural differences, hydrolyzable and condensed tannins often produce similar antinutritional effects. The most common effects are diminished weight gains and lowered efficiency of nutrient utilization. The major biochemical basis for these effects appears not to be inhibition of dietary protein digestion but rather a systemic inhibition of the metabolism of digested and absorbed nutrients, particularly protein. In the case of condensed tannins, this inhibition is probably not due to polymeric tannin molecules, which are not absorbed from the digestive tract, but to associated lower MW polyphenols, which are readily absorbed.

INTRODUCTION

Considerable attention is focused at this conference on sometimes subtle structural variations in tannins. These structural distinctions are beginning to be recognized by nutritionists seeking to characterize the nutritional effects of tannins in the diets of herbivores. An outstanding modern example of correlating tannin structural features with biological activity is the work reported by Dr. Tom Clausen at this conference. A further step toward understanding the diverse effects of dietary tannin is the recognition that animals may differ greatly in their response to this nutritional challenge. [1] The wide range of antinutritional effects reported for condensed tannins, as well as metabolic defenses of herbivores against these effects, were reviewed in the first volume of this series.[2] A more recent review addresses nutritional consequences of both condensed and hydrolyzable tannins.[3] This chapter covers recent advances in our understanding of the antinutritional effects of condensed and hydrolyzable tannins.

HYDROLYZABLE TANNINS

Despite the greater abundance of condensed tannins than hydrolyzable tannins in foodstuffs,[3] more nutritional studies have been done with hydrolyzable tannins than with condensed tannins. This is probably because hydrolyzable tannins such as tannic acid have been more readily available in purified forms suitable for feeding trials than have condensed tannins.

Unlike condensed tannins, hydrolyzable tannins are subject to breakdown by hydrolysis due to esterolytic 'tannase' enzymes in the digestive tract.[1] The resulting products include gallic acid, which is readily absorbed and excreted in the urine.[4] Absorbed gallate may cause antinutritional effects. Dietary gallate is reported to depress feed palatability and growth rate in chicks.[5]

Hagerman and coworkers [1] reported that protein digestibility by deer and sheep was reduced by feeding plants containing either condensed or hydrolyzable tannins or by supplementation of the diet with condensed (quebracho) tannin. Supplementation at similar levels with commercial tannic acid, a hydrolyzable (gallo)tannin, had no effect on protein digestibility by these ruminants. No tannin (as gallate) was found in feces after feeding tannic acid, suggesting that this hydrolyzable tannin was degraded in the gut, and the resulting gallic acid was taken up and excreted in the urine. When fireweed containing gallotannin was fed, 27 percent of the ingested gallic acid was found in the feces, indicating that the gallotannin was somehow protected against hydrolysis in the gut, presumably by complexation with protein (see below). The authors suggested that, on the basis of comparison of the molecular weight distributions of the commercial and fireweed gallotannins, differences in molecular weight distribution and consequent affinity for proteins were responsible for the differences in the nutritional effects of two gallotannins. [1] This study illustrates the possibility that differences within one type of tannin (gallotannins) may be as great as those between hydrolyzable tannins and condensed tannins.

BIOCHEMICAL BASIS FOR ANTINUTRITIONAL EFFECTS

Despite their large differences in structure, condensed and hydrolyzable tannins often seem to produce rather similar antinutritional effects, as noted above. The major effects include diminished weight gains and lower efficiency of utilization of dietary dry matter, particularly protein. Food consumption is sometimes, but not always, diminished by dietary tannin, with hydrolyzable tannins usually more effective than condensed tannins. The effects of tannins on food consumption are even less significant when consumption is calculated on a per-weight basis rather than a per-animal basis.[6] Tannin-consuming animals are usually smaller than their counterparts on tannin-free diets and thus consume less food.

It is, of course, tempting to assume that the similar effects of condensed and hydrolyzable tannins on herbivore nutrition are due to the well-recognized shared capacity of these phenol-rich but otherwise dissimilar materials to bind and coagulate proteins. [7,8] This characteristic astringency and associated enzyme inhibition have been proposed to account for various *in vivo* biological activities, including antinutritional properties, of both condensed and hydrolyzable tannins. [9, 10]

Tannins differ greatly in their affinity for proteins, and proteins likewise differ greatly in their affinity for various tannins.[8, 11] Both condensed and hydrolyzable tannins inhibit most *in vitro* enzyme assays, probably because in many assays the enzyme is the only material present that is capable of binding the tannin. In the intestine, many other proteins compete for binding tannins, and inhibition of digestive enzymes may be insignificant. But because the digestive enzymes are the first, and perhaps only, enzymes to be exposed to dietary tannins, the site of the antinutritional effects of tannin is often assumed to be the digestive tract.[12]

The diminished weight gains caused by dietary tannin can usually be overcome by an increase in the level of protein in the diet, although the supplementary protein seems to serve mainly to bind the tannin, rather than as a source of amino acids.[13] The sparing effect of added protein and the increase in the level of fecal nitrogen associated with dietary tannin are in apparent accord with the usual assumption that the underlying basis of the antinutritional effects of tannin is inhibition of the digestion of dietary protein. [12,14, 15] However, there is a growing body of evidence, some of which is presented below, that this perception of tannins primarily as inhibitors of digestion is overly simplistic and inadequate.

ENDOGENOUS VERSUS DIETARY PROTEIN

There was early evidence based on rats fed ^{14}C-casein that the increased fecal protein induced by dietary tannin is not of dietary origin but instead is endogenous protein from the lining and secretions of the digestive tract.[16] The endogenous nature of the tannin-induced increase in fecal protein has now been confirmed by feeding ^{15}N-labelled proteins or ^{14}Cor ^{15}N-amino acids (to label endogenous proteins) along with tannins from tea,[17] beans, [18,19] or quebracho and tannic acid.[20]

The origin of at least some of the tannin-induced endogenous protein in the feces of many tannin-consuming mammals[21,22] is proline-rich salivary proteins, which have an unusually high affinity for tannin (reviewed by Mehansho and coworkers[23]). These specialized tannin-binding proteins are virtually absent from the saliva of rats and mice until induced by dietary tannin.[24] They are induced by either condensed or hydrolyzable tannin but not by monomeric units such as catechin or gallate.[25] In other animals, they appear to be constitutive. In pigs, for example, proline-rich proteins are a major component of the ileal digesta of animals fed diets free of both tannin and protein. [26] These proteins comprise about 70 percent of the total proteins in human saliva.[23]

The strong complex formed between these endogenous proline-rich proteins and dietary tannins is not dissociated by altering the pH (E. Haslam, personal communication} and seems to pass through the digestive tract relatively intact as judged by the high proline content of the fecal protein. [12,27,28] Salivary proline-rich proteins typically contain relatively low amounts of essential amino acids[24] so their loss in the feces as a complex with tannin is a beneficial trade-off if it spares dietary proteins richer in essential amino acids. The proline-rich salivary proteins are an effective defense against dietary tannin, as shown by the heightened vulnerability to tannin of herbivores that cannot produce them.[29]

DIGESTION VERSUS POSTDIGESTIVE METABOLISM - (SYSTEMIC EFFECTS)

'The direct absorption of a whole hydrogen-bonding, nondialyzable, protein precipitating tannin macromolecule seems quite unlikely in the normally functioning animal.'[10] This common sense rationale explains why the location of the antinutritional effects of tannin has almost always been considered to be limited to the nutritional tract.

But now it is recognized that several of the effects of dietary tannin occur in bodily tissue (systemic effects), not just in the intestinal tract. These effects, summarized by Butler,[30] include development of chick leg abnormalities, induction of liver enzymes, increased output of urinary glucuronides, diminished urine volume, and fatalities too rapid to be the result of impaired digestion. These effects were observed on feeding 'high-tannin' sorghums, which contain condensed tannins and associated polyphenolic materials. There were no discernible lesions that could account for apparent uptake of tannins from the digestive tract.[31] Systemic effects, rather than inhibition of digestion, are also apparently mainly responsible for the diminished growth rate associated with dietary tannin. When growth rate impairment of rats by dietary tannin was separated into the effects on food consumption, digestion/ absorption, and post-absorptive metabolism, it was the latter that was the most severely affected by tannin.[28]

It is clear that in the case of 'high-tannin' sorghum, and perhaps for other sources of dietary tannin, toxic materials do get absorbed from the digestive tract. We have recently determined, using ^{14}C-labeled tannin and lower MW polyphenols from sorghum, that the polymeric condensed tannins are not absorbed from the digestive tract of chicks and are completely recovered in the feces. On the other hand, lower MW polyphenols associated with tannin in the sorghum seed were taken up rather efficiently and recovered in serum as well as other tissues (Jimenez Ramsey and co-workers, abstract, this meeting). Like the tannin polymers, these tannin-associated and apparently toxic materials are not present in tannin-free sorghums often used as controls in nutritional studies of sorghum tannins.

It seems likely, at least for high-tannin sorghum, that the antinutritional effects are not due to tannin polymers, but to lower MW, more readily absorbed materials that occur with tannin. The assignment of major antinutritional effects to absorbable tannin-associated materials (possibly tannin precursors) rather than to the tannins themselves helps to explain not only the systemic effects mentioned above, but also other observations not necessarily nutritional in nature. Low MW polyphenols (but not monomeric units such as catechin) from high tannin sorghums are more effective than purified sorghum tannin polymers at inducing production of salivary proline-rich proteins in rats[25] and at repelling birds.[32]

ACKNOWLEDGMENTS

Tannin research in this laboratory is partially supported by USAID Grant No. DAN 1254-G-00-0021 through INTSORMIL, the International Sorghum and Millet CRSP.

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