0273–2289/84/0600–0327$02.00

Microbial Attack on Lignocellulose in the Rumen

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ABSTRACT

The microbial population of the rumen consists of many types and species of anaerobic and facultatively anaerobic microorganisms, often at high population densities, living in symbiosis with the animal. The animal is unable to synthesize enzymes capable of digesting the major structural components of plant cell walls (fiber) and relies on the rumen microbes to ferment this material with the generation of volatile fatty acids and microbial cells that the animal can utilize. The crude fiber fraction of ruminant forages consists mainly of cellulose, hemicellulose, and lignin.

The rumen contents are rich in organic matter, which has a pH of 5.5–6.9, is maintained at about 39°C, and has a low redox potential with little free oxygen in the rumen liquor. When plant material enters the rumen, it is invaded by many species of microorganisms, some of which digest certain structural components of the plant cell walls. Measurable digestion of plant cell walls occurs 4–5 h after ingestion by the animal. The rate and extent of digestion is affected by many factors, including the nature and degree of adaptation of the microbial population to the diet, the species of plant and its lignin content, the form in which it is presented to the animal, the amount consumed, and the rate of passage through the rumen.

Because the rumen contents are anoxic, there is little degradation of lignin. Some solubilization occurs and lignin–hemicellulose complexes are found in rumen liquor, probably released by cellulolytic and hemicellulolytic microorganisms. One species of bacterium isolated from the rumen preferentially attacked highly lignified cell walls and grew on phenolic acids both aerobically and anaerobically (Akin, 1980), but the abundance and distribution of the species is not known. Phenolic acids are also released and further metabolized in the rumen, and methoxyal groups removed from lignin.

Since lignin is covalently bound to cellulose and hemicellulose in the plant cell wall, it probably protects these polysaccharides from microbial attack both physically and chemically. Delignification increases the digestibility of cell wall

polysaccharides several-fold. Cellulose may also be shielded from microbial attack by encrusting xylan or xyloglucans (Albersheim, 1975).

When plant tissues enter the rumen, they are invaded by both cellulolytic and noncellulolytic microorganisms. Initial invasion is by ciliate protozoa and motile bacteria, followed by phycomycete zoospores and, later, nonmotile bacteria, including cellulolytic species. Some species of ciliate protozoa (e.g., *Epidinium ecaudatum*) immediately commence to digest the plant cell walls, but cellulolysis by phycomycete fungi and bacteria is delayed because of preferential metabolism of soluble carbohydrates and the lag before significant attachment of cellulolytic bacteria has occurred. In the predominant cellulolytic rumen bacteria, *Ruminococcus albus, R. flavefasciens,* and *Bacteroides succinogenes* (Forsberg et al., 1981), adhesion is a prerequisite to cellulolysis because the cellulase enzymes are bound to the cell surface, but some strains of *B. succinogenes* also release vesicle-bound enzymes.

Cellulases in some species of protozoa (e.g., *Epidinium ecaudatum, Eudiplodinium maggii,* and *Eremoplastron bovis*) are now considered to be of protozoon origin (Coleman et al., 1976), but ingested bacteria and adsorbed enzymes may contribute to protozoon cellulolysis.

All species of rumen phycomycete fungi examined (Orpin, 1981) have been shown to be cellulolytic and grow on plant cell walls. The cellulase produced by one strain of *Neocallimastix frontalis* was associated in part with membranous vesicles released into the medium. Digestion of plant cell walls by the phycomycete fungi is accompanied by the loss of up to 20% of the lignin as a lignin–hemicellulose complex.

The enzymology of cellulolysis in the rumen is not completely known. It is clear that more than one enzyme is responsible for complete hydrolyses of cellulose to glucose or cellobiose, and endo-1,4-β-glucanases and β-1,4-glucosidases have been found in several species of rumen microorganisms. There is also evidence for a 'swelling factor' being necessary prior to cellulolysis by some rumen species.

All of the cellulolytic rumen microorganisms can also attack, to some degree, the hemicelluloses of the plant cell walls. In some species, cellulase and xylanase activity is associated with the same enzyme complex (e.g., *Bacteroides succinogenes*). Other bacteria may attack hemicelluloses, but not cellulose (e.g., some strains of *Butyrivibrio fibrisolvens*), and others (e.g., *Lachnospira multiparus*) digest pectin which allows plant cells to separate and make more cell wall components available to microbial attack. All these organisms act in a consortium resulting in extensive digestion of the plant cell walls.

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