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DIGESTION OF BLOAT-CAUSING AND BLOAT-SAFE LEGUMES

R.E. HOWARTH, B.P. GOPLEN, J.P. FAY and K.-J. CHENG

Agriculture Canada Research Stations, Saskatoon, Sask. and Lethbridge, Alberta, Canada

Differences among forage legumes, in their potential for causing pasture bloat, have been related to the occurrence of flavolans (tannins) in bloat-safe legumes and the absence of flavolans in bloat-causing legumes. We tested cicer milkvetch (Astragalus cicer L.), a bloat-safe legume of limited use in Canada and the United States, and could not detect flavolans or other protein precipitants. Thus we looked for other differences among the pasture legumes in order to explain this exception to the tannin theory of bloat-safe legumes.

Since the plant proteins, which cause frothy pasture bloat, are intracellular constituents, it seemed that leaf cell rupture might be an important event in the occurrence of pasture bloat because cell rupture should be a prerequisite to release of the intracellular foaming agents into the rumen fluid. Leaf mesophyll cells could be subject to mechanical rupture during chewing, or to rupture by microbial digestion in the rumen.

Howarth et al. (1978) crushed leaves in a mortar and pestle and showed that mesophyll cells in bloat-safe legumes were more resistant to mechanical rupture compared to mesophyll cells in the bloat-causing legumes. In this report we summarize the major findings from a series of recent experiments (Cheng et al., 1979; Brandt et al., 1979; Fay et al., 1979; Howarth et al., 1979) on the digestion of bloat-safe and bloat-causing forage legumes by rumen microorganisms.

Material and Methods

The bloat-causing legumes were alfalfa (Medicago sativa L.), red clover (Trifolium pratense L.), and white clover (Trifolium repens L.). The bloat-safe legumes were sainfoin (Onobrychis viciefolia Scop.), birdsfoot trefoil (Lotus corniculatus L.) and cicer milkvetch (Astragalus cicer L.). Flavolans are present in sainfoin and birdsfoot trefoil, but they do not occur in leaves and stems of the other four species. Leaves or herbage (leaves and stems) were collected during the pre-bud to early-bud stages of growth. Plants were grown in the greenhouse and in the field.

Rates of digestion by rumen microorganisms were measured by in vitro and by nylon bag digestion techniques. Digestion in vitro was measured by gas production and by dry matter (DM) disappearance. Digestion in nylon bags was measured by nitrogen (N) and by DM disappearance. Since pasture bloat typically occurs within 2-3 h after feeding, emphasis was given to events during the early stages of digestion, i.e., up to 10-12 h, with some samples being taken up to 24 h. Leaf samples were withdrawn...
from *in vitro* digestion flasks at similar intervals for examination by light and electron microscopy.

Concentrations of intracellular leaf constituents in sheep rumen ingesta were determined before and after feeding fresh alfalfa, sainfoin, birdsfoot trefoil and cicer milkvetch. The sheep were fed once daily from 9.00-11.00 h, but were allowed voluntary consumption during this period.

**Results**

**Digestion of whole leaves**

Rates of digestion for the three bloat-causing legumes (alfalfa, red clover, and white clover) were very similar. They were consistently digested more rapidly than leaves from the bloat-safe legumes. The typical ranges of values for the bloat-safe legumes after 6-8 h digestion were (as per cent of alfalfa digestion): cicer milkvetch, 50-75%; birdsfoot trefoil, 30-70%; and sainfoin, 15-25%. Differences between the two groups of legumes could be detected as early as 2-4 h, and maximum differences occurred at 6-10 h. Thereafter the digestion rates for bloat-causing legumes diminished. Rates of digestion were quite variable from day to day and among animals in the nylon bag studies.

**Mechanical disruption before digestion**

Chopping leaves into 5 mm segments increased rates of digestion in nylon bags but did not alter the differences among legume species. Homogenization of leaves in a Waring blender prior to digestion *in vitro* obliterated the differences among legume species by increasing the digestion rates of the bloat-safe species.

Herbage (leaves and stems) was ingested by fistulated cows and the boluses were collected at the cardia. When this chewed herbage was digested *in vitro* the differences between bloat-safe and bloat-causing legumes were still apparent, but the differences between the two groups were reduced. Differences in the amount of foaminess in digestion flasks suggested that chewing disrupted bloat-causing legumes to a greater extent than bloat-safe legumes.

**Intracellular leaf constituents in rumen ingesta**

Two hours after feeding fresh herbage the relative concentrations of soluble protein N in sheep rumen fluid were (as per cent of alfalfa-fed sheep): cicer milkvetch, 53%; sainfoin, 23%; and birdsfoot trefoil, 12%. Corresponding values for chlorophyll in a filtrate of rumen contents (pore size 0.12 mm) were: cicer milkvetch, 51%; sainfoin, 28%; and birdsfoot trefoil, 16%. The low values for birdsfoot trefoil were due, in part, to low voluntary feed intake. There were also significant differences among animals.

**Microscopic examination of digested leaves**

The action of the epidermal layer as a barrier to microbial digestion was clearly shown by the invasion of microbes from the cut edges of leaves and by the increased rates of digestion after mechanical disruptions. Although some proliferation of bacteria occurred within the middle lamellae, rapid proliferation did not occur until the bacteria gained access to the interior of the mesophyll cells. The time required for bacteria to invade the interior of mesophyll cells was greater for bloat-safe legumes compared to bloat-causing legumes.

Further studies are in progress to define the relationship between leaf structure or composition and initial rates of digestion of fresh leaves. Leaching of nutrients from cells may be a factor in the different rates of digestion. To date we have not discovered any notable differences among these legume species in chemical composition of the cell walls.

**Breeding a bloat-safe alfalfa cultivar**

High priority is being given to the development of techniques for identifying individual alfalfa plants which have greater mechanical strength of leaf tissue and/or mesophyll cell wall, and slower initial rates of digestion. A two-stage selection process is envisaged with initial screening of a large number of plants by testing for mechanical strength, and with secondary evaluation based upon rates of digestion of fresh leaves by rumen micro-organisms.
Conclusions

A new explanation for the occurrence of bloat-safe forage legumes has been developed from comparisons of bloat-safe and bloat-causing forage legumes. These experiments provide strong evidence that disruption of leaf tissues, rupture of mesophyll cell walls and release of intracellular constituents into the rumen fluid are important events in the etiology of legume pasture bloat. Initial rates of digestion are slower for bloat-safe legumes than for bloat-causing legumes, and these differences result in lower concentrations of intracellular leaf constituents in rumen fluid when bloat-safe legumes are ingested. Resistance to mechanical disruption by chewing and resistance to microbial digestion contribute to the bloat-safe characteristics of some legumes. Mechanical strength of the leaf epidermal layers and of the mesophyll cell walls is important in resistance to damage by chewing. The epidermal layers, the middle lamellae and the mesophyll cell walls are factors in the rates of leaf digestion by rumen microorganisms. These results raise the possibility of reducing the bloat-causing potential of alfalfa, red clover and white clover through plant breeding by selecting for greater mechanical strength of leaf tissue and slower initial rates of digestion.

References


