

Studies on the Alimentary Tract of Merino Sheep in South Africa VIII.—The Pathogenesis of Acute Tympanites (Bloat).

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IN spite of considerable attention devoted to the problem of acute tympanites in ruminants, the aetiology and the pathogenesis of this condition is as yet poorly understood. One of the most commonly accepted views is that it is due to the formation of a food plug in the distal part of the oesophagus, thereby obstructing the normal eructation of gas from the forestomachs. McIntosh in a recent publication refers to two types of acute bloat—

- (a) in which free gas is superimposed on the ruminal mass, its escape being impeded by obstruction in the oesophagus, and
- (b) where the gas remains admixed in the ruminal ingesta as noted after the engorgement with succulent food.

In regard to the actual causes of acute bloat McIntosh admits that these are unknown, but states that chemical factors within the plant are important in view of the experience that the condition is less frequently encountered on lucerne pastures in which fertilization and irrigation have been well maintained, than is the case on neglected pastures growing on poor soil. From analyses conducted on ruminal gas, Dougherty on the other hand concludes that bloat is associated with the appearance of distinct amounts of carbon monoxide and sulphuretted hydrogen which may be the cause of paralysis of the rumen, and thus to its overdistension with gas.

Due to its insidious nature, it is extremely difficult to predict the onset of acute bloat even though it is known that it is usually associated with the feeding of lucerne, or less commonly with other legumes. Moreover, no specific substance has as yet been obtained from lucerne which could be incriminated as the cause of the condition. That this factor is of a very labile character is indicated by the suddenness with which the green plant may become dangerous to ruminants, whereas hay made from it is usually quite harmless. On the other hand, the animal itself may constitute a determining factor as shown by the fact that certain individuals are far more subject to bloat than are others feeding on the same material. Likewise, ravenous feeding, as noted in hungry animals, frequently precipitates the condition.

EXPERIMENTAL PRODUCTION OF BLOAT.

In order to study the pathogenesis of the symptom complex in acute bloat, a series of experiments were undertaken. In the first of these, both cattle and sheep were placed on a diet consisting largely, or in other cases

exclusively, of green lucerne in various stages of growth, the plants being either grazed down or cut and subsequently fed from troughs. Moreover, attention was also paid to the degree of wilting of the lucerne at the time that it was being fed.

The results of the various trials indicated that although lucerne feeding usually led to a rapid filling out of the abdomen, the degree of distension displayed was not accompanied by the characteristic signs of dyspnoea and general distress as noted in cases of acute bloat. Nevertheless, there was definite evidence of an increase in intra-ruminal pressure immediately after a meal of lucerne. This was shown by the forced ejection of ingesta through the ruminal fistula on being opened during this period. No such forced ejection was, however, displayed some hours after the consumption of the lucerne nor when animals were kept on a diet of grass hay supplemented with ground maize.

To ascertain whether the rate of gas production within the rumen could in itself determine the onset of acute bloat, the forestomachs of several sheep were insufflated with air. This was carried out by connecting the ruminal fistula tube to a large pressure cylinder from which a regulated stream of air could be passed into the rumen. In every instance it was found that such animals were capable of belching as much as six litres of air insufflated per minute. Additional raising either of the forequarters or of the hind-quarters or even flooding of the rumen with an extra three litres of water, made very little difference to the ease with which animals were able to expel the large volumes of air constantly rushed into the rumen. These experiments afforded clear evidence that the rate of gas production in the rumen could not in itself determine the onset of bloating. Similarly they served to demonstrate the remarkable mechanism whereby the ruminant animal was safeguarded against overdistension of its forestomachs under normal conditions.

FOAM FORMATION IN THE RUMEN.

Repeated examinations made on fresh ruminal ingesta which was drawn from animals kept on different diets, revealed a definite tendency towards foam formation in those fed on lucerne, whereas in sheep on other diets this was at most only slight and of a transitory nature. Moreover, the foam present in the lucerne ingesta when kept standing at room temperature, required a period of several hours before the gas bubbles collapsed. Similar effects were observed both in pressed lucerne juice and watery extracts made from lucerne hay, which on being vigorously shaken, showed a copious formation of relatively stable foam still evident after a period of 12 hours. Comparative tests conducted on similarly prepared extracts and juice from oats and barley failed to produce this characteristic stable foam which closely resembled that seen in saponin solutions when shaken up. According to the findings of Jacobson, who undertook a series of chemical investigations on lucerne, a saponin with particularly strong foam-producing qualities could be isolated from this plant. This was confirmed in the present investigations undertaken in collaboration with de Waal. As described by Jacobson a characteristic non-haemolytic saponin, but with very strong foam-producing qualities could be isolated from all samples of lucerne analysed. To ascertain whether, in addition to the saponin in lucerne, the presence of certain colloids would aggravate foaming, sugar fermentation tests were conducted on ingesta to which varying amounts

either of egg albumen or gum acacia had been added. There was, however, no definite evidence of a change in foam production following the addition of these colloids.

OBSERVATIONS MADE ON CASES OF CLINICAL BLOAT.

As a result of the difficulties experienced in reproducing cases of clinical bloat under laboratory conditions, the investigations were extended to the Losperfontein Experimental Station where trials were in progress in regard to fat lamb production on different pastures. On various occasions outbreaks of clinical bloat had made their appearance during the period that animals were restricted to lucerne pasture. It was during one of these outbreaks that, in collaboration with Starke, detailed observations were made on the condition. The following represents the main points established during this outbreak:—

1. Cases of rapidly fatal bloat could be definitely caused by the ingestion of fresh green lucerne in an unwilted, unbruised condition and in the preflowering stage.

2. It was associated with a ravenous consumption especially of the green leafy tops, in contrast to the more fibrous stems which were left standing.

3. It was definitely more evident amongst lactating ewes showing a keen appetite than amongst others feeding less greedily.

4. According to analyses made by Louw, the sugar content of the lucerne collected during the actual outbreak increased from 2.5 per cent. in the early morning to 6 per cent. (on dry weight basis) in the late afternoon. Cases of fatal bloat were definitely more numerous in the late afternoon even though actual grazing on lucerne had been restricted to a period of half an hour only.

5. Abdominal distension especially evident in the left flank, was such as to cause complete immobilization of the diaphragm with its dome extending far forward into the thoracic cavity. The resultant asphyxia, combined with obstruction in the return of venous blood from the posterior vena cava, was responsible for the acute death.

6. Opening of the abdominal cavity and of the rumen at the moment of death failed to reveal constriction in the distal part of the oesophagus.

7. The ingesta which was held under great pressure within the rumen consisted of a strongly foaming, frothy mass. Moreover, there was little tendency for free gas to escape from this rapidly fermenting material thus explaining the limited value of ruminal puncture in such cases. Lucerne leaves which comprised the bulk of the solid material showed definite signs of fermentative disintegration.

8. Microscopically, the ingesta from every rumen examined revealed the presence of a dense culture of the pseudo-yeast strain described in the previous report. (Quin, 1943.)

OXIDATIVE ASSIMILATION IN THE FORESTOMACHS IN RELATION TO ACUTE BLOAT.

From the above observations, when considered in conjunction with the investigations previously outlined, the following explanation concerning the aetiology and pathogenesis of acute bloat in ruminants appears to be justified.

Clinically, acute bloat represents an integral part of the normal processes associated with sugar metabolism in the forestomachs of ruminants. Due to the activity of yeast cells (*Schizosaccharomyces species*) in the rumen, a dense culture of which is established on a diet of lucerne, a portion of the ingested plant sugar is immediately assimilated and stored by these cells, mainly as glycogen; the remaining sugar is exposed to a fulminating oxidation and the production of large volumes of gas, comprised chiefly of carbon dioxide. This process, referred to as oxidative assimilation, has been established in the biology of various unrelated micro-organisms and represents a characteristic feature in their carbohydrate metabolism. In acute tympanites, the balance normally established between the rate of gas production in the forestomachs and its escape through the oesophagus may be suddenly disturbed, frequently with fatal consequences. The condition arises through a combination of (a) the presence of characteristic pseudo-yeast cells in the rumen, (b) the rapid consumption of fresh lucerne leaves showing an elevated sugar content, (c) the establishment of an aerobic state in the rumen associated with rapid swallowing of food thus promoting excessive oxidation of sugar and gas formation, (d) the presence of saponin in lucerne which by increasing surface tension and the tendency towards foam formation, impedes the escape of gas from the ruminal mass.

The eructation of foam from the rumen presents serious difficulties, in contrast to the easy escape of free gas. Consequently the excessive frothiness created within the ruminal ingesta leads to unphysiological distension in the forestomachs through which both respiration and circulation are endangered.

CONTROL OF ACUTE BLOAT.

In view of the findings that the pathogenesis of acute bloat is intimately associated with various complicated physiological phenomena in the forestomachs of ruminants, the successful control of this condition depends more upon a rational feeding practice rather than on the administration of remedies calculated to suppress fermentation in the rumen. In a subsequent report consideration will be given to the susceptibility of the ruminal flora to a variety of poisons and other foreign substances.

Due to the fact that starvation readily leads to a depletion of the glycogen reserves within the yeast cells of the rumen, it is essential to safeguard ruminant animals against spells of acute hunger, especially where green succulent lucerne constitutes the major item in their normal diet. Under such conditions the ingestion of green lucerne is immediately associated with an accentuated phase in the assimilation and oxidation of the plant sugars by the starving yeast cells, thus establishing the tendency towards acute bloat. Alternatively, the regular supplementation of carbohydrate rich foods such as grain, molasses or good quality hay, with the lucerne diet, keeps the energy demands of the yeast cells more or less satisfied. Consequently the sugars present in lucerne are not metabolized at the same dangerously high speed, with the result that gas and foam production are kept within physiological bounds.

The same result is achieved in the majority of animals where undisturbed fulltime grazing is allowed on lucerne pastures. Through the cultivation of desirable feeding habits whereby small quantities of lucerne are repeatedly consumed rather than excessive amounts during a single meal, conditions within the forestomachs remain fairly well stabilized, and hence

the dangers of acute bloat are minimized. In this connection attention should be directed to the increased degree of aeration of the ruminal ingesta especially during the hurried consumption of succulent leafy material such as green lucerne. Seeing that the microflora and fauna in the forestomachs are largely aerobic in character, the nature and speed of the metabolic processes occurring within these compartments are influenced by the extent of aeration and thus also by the carbon dioxide tension of the ruminal mass. Likewise, a portion of the stomach contents is periodically aerated in the open mouth during the process of rumination.

Apart from the rôle played by lucerne in the causation of acute bloat, the feeding of ruminants exclusively on fresh green lucerne may be associated with other undesirable consequences. Thus the rapid filling of the rumen with a foaming watery mass, even after the consumption of relatively small amounts of lucerne, would tend to limit the daily intake of total solids to amounts inadequate for normal body requirements. This is a matter of significance especially in the feeding of dairy cows and also of sheep concerned in fat lamb production. Repeated filling of the forestomachs with a foaming mass instead of with solid nutriment, forcibly suppresses appetite until deflation of the rumen has ensued. Alternatively, it may endanger the life of those animals, which, through ravenous feeding, fail to appreciate the first warning of undue distension through foam formation in the forestomachs.

SUMMARY.

Concerning the pathogenesis of acute bloat, this has been shown to be closely associated with the production of gas during the rapid oxidation of sugar mainly by yeast cells as described above. Normal eructation of gas may be impeded as a result of excessive foam production in the forestomachs especially when animals are restricted to a diet of green lucerne. This foaming up of the ruminal mass is directly attributable to the presence of saponin in lucerne which through its action on surface tension retards the breaking of the foam. Undue frothing of the ruminal ingesta can be controlled by resorting to a feeding practice in which green lucerne is supplied to cattle and sheep only after the consumption of other foods.

In a subsequent report attention will be devoted to hydrogen-ion concentration in relation to fermentation in the forestomachs.

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