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ANIMAL FACTORS IN THE AETIOLOGY OF BLOAT

A. T. Johns, J. L. Mangan and C. S. W. Reid*

ONE OF THE FIRST things noticed in a moderate outbreak of bloat in a herd of cows at pasture is that certain animals are more susceptible to the ailment than others. The plant factors are obviously the same for all animals grazing the same field, except that there may be differences in intake between animals and differences in the selection of pasture species. Previous work has shown that the predisposition to bloat is largely an inherited animal characteristic (Knapp *et al.*, 1943; Hancock, 1953; Johns, 1954). Hence it is as important to examine the animal factors concerned with the onset of the condition, as it is to look for "toxic" principles in the herbage.

Bloat is caused by the animal being unable to eliminate by belching the gas produced in its first two stomachs. This gas arises largely from microbial fermentation, but as will be seen later the CO_2 released from bicarbonate of saliva is also of importance.

In the past it has been claimed that it is the greedy eaters which bloat, owing to the too rapid ingestion of succulent herbage. However, it has been found in stall feeding experiments with identical twin cows eating cut red clover, where the opportunity for selective grazing is eliminated, that no correlation existed between the incidence of bloat and the rate or amount of feed eaten (John, 1954). In general, when the animals bloated severely, they had a lower dry matter intake than when they did not.

Rate of eating was thus eliminated as an animal factor in determining susceptibility to bloat.

Another possibility was that anatomical differences could make belching more difficult in some animals than in others. However, the writers have found that the difference between bloat susceptible and non-susceptible animals is not absolute. If bloating conditions are severe enough, all animals in a herd may bloat. Moreover, some animals may bloat at one part of the season and not at others, with members of identical twin sets behaving similarly. Bloating behaviour is thus by no means

**Plant Chemistry Division, Dept. of Scientific and Industrial Research, Private Bag, Palmerston North.*

a constant characteristic. It appears unlikely, therefore, that anatomical variations can explain the differences in animal susceptibility to bloat.

All the evidence obtained over the last four years indicates that the primary cause of uncomplicated pasture bloat is a foaming of the rumen fluid. This is becoming more and more widely accepted by overseas workers. Observations on the condition of rumen contents of stall-fed animals through rumen fistulae show that bloating is closely correlated with the degree of foaming. The difference in appearance of the rumen contents of bloating and non-bloating cows may be quite spectacular. Non-bloating cows may show little or no foam, while bloating cows feeding on the same clover are filled with a mass of viscous, fine-bubbled foam. It is clear that there must be some animal contribution to the foaming system when there can be such a contrast in the condition of the rumen contents of different animals on the same feed.

Johns (1956) and Reid and Johns (1957) have pointed out that the foam in the rumen is of the viscous type such as is formed by proteins and saponins. Mangan (unpublished data) has found that the optimum pH for maximum foam stability in the rumen is in the region of 6. It has also been observed that the pH of rumen contents has to fall to approximately 6.3 before the first signs of bloat are apparent. Hence the amount of acid produced by fermentation and the buffering power of the rumen fluid will be of importance in the formation of a stable foam in the rumen.

The animal factors which can contribute to the formation of a stable foam and the production and elimination of gas in the rumen will be dealt with under the following headings— saliva, microbiological activity, and mechanical activity of reticulo-rumen.

Saliva

According to Colin (1886) the total salivary secretion of a cow is of the order of 60 litres per day and this provides a well-buffered medium for the microbial fermentation in the first two stomachs. There are two properties of this saliva that are of interest in bloat:

(a) The amount of CO_2 evolved when saliva enters the rumen. Saliva is secreted at a pH of 8.2 and passes to the rumen where the pH may be below 6. Kleiber has calculated that, for each litre of saliva entering the rumen at pH 5.7, approximately 2 litres of CO_2 are evolved. Hence the saliva can contribute approximately 120 litres of CO_2 per day to the rumen gases.

(b) The foaming properties of saliva which were first indicated by the surface tension measurements of Reid and Huffman (1949).

Clark and Weiss (1952) demonstrated the existence of a salivary reflex initiated by the stimulation of the membrane of the fore stomachs. Weiss (1953) stressed the importance of saliva as a diluting agent. He believed that bloat on succulent herbage was caused by the formation of a thick viscous rumen ingesta owing to the lack of stimulation of salivary flow. Hay, on the other hand, produced a large flow of saliva. For this reason the suggestion was made that a lack of coarse fodder was the cause of bloat. Weiss (1953) believed that this was due to lack of stimulation of salivary secretion rather than to lack of stimulation of belching as Cole *et al.* (1942) had suggested. That the role of saliva in bloat is not as Weiss has suggested has been demonstrated by Ferguson and Terry (1955) who found that the addition of extra saliva to animals being dosed with lucerne juice did not prevent bloat. The fact also that a number of workers have produced bloat on legume juice would indicate that a lack of liquid is not necessary for the production of the condition.

In considering the role of saliva, research workers have failed to take account of the fact that there are at least three components of mixed saliva with very different properties.

(1) The parotid secretion. This is continuous, high in bicarbonate (0.1M) and buffering power, with very little protein present.

(2) The submaxillary secretion. This is secreted only during the taking of food. The saliva is much lower in bicarbonate (0.01M) and buffering power but is very viscous and contains a considerable amount of mucoprotein with strong foaming properties.

(3) A third secretion (mainly sublingual) which appears to combine the properties of the two mentioned above, being intermediate in protein and bicarbonate level.

A large secretion of saliva could, according to its composition, either assist in preventing bloat by buffering a fall in pH, or increase its severity by adding to the CO_2 evolved and by assisting in foam formation.

Balch (1954) has shown that the amount of saliva secreted varies greatly with the nature of the feed while Phillipson and Reid (1958) found that there is an animal difference in saliva flow in response to pressure in the rumen. The results of acute experiments with sheep and calves can be summarized as follows:

(a) An increase in pressure in the rumen usually caused a marked rise in the rate of parotid and submaxillary secretions and an increase in the residual secretion. Occasionally the submaxillary and residual secretions responded without any effect being found in the parotid secretions.

(b) The pressure producing this effect varied from 8 to 20 mm Hg.

(c) Once stimulation had occurred, further increases in rumen pressure caused an inhibition of salivary secretions.

It could well be with an animal having an increased saliva flow in response to rumen pressure, that, when mildly bloated, the extra CO_2 contributed from saliva could tip the balance in determining whether bloat is severe or not. For it has been found in a five-months-old calf that the amount of CO_2 necessary to raise the pressure 10 mm Hg was much less at higher than at lower pressures as shown below in Table 1.

TABLE 1: PRESSURE INCREASES IN THE RUMEN COMPARED WITH CARBON DIOXIDE VOLUMES

Pressure Increase in Rumen (mm Hg)	Volume of CO_2 Required (l.)
2½ to 10	20.8
10 to 20	4.8
20 to 30	2.7
30 to 40	2.2

Hence at a pressure of 20 mm (slight-moderate bloat) when a markedly increased saliva flow can occur in some animals, this further source of gas, apart from that being formed from bacterial fermentation, could be serious.

There is little change in the composition of pressure stimulated parotid saliva but with submaxillary saliva Mangan (unpublished) has found that a marked increase in the concentration of the foam-producing mucoprotein occurs. This is illustrated in Table 2. Hence an increase in rumen pressure can result in an increased secretion of foaming agent into the rumen.

It appeared that one of the differences between animals in their susceptibility to bloat could be a consequence of dif-

TABLE 2: COMPOSITION OF PRESSURE STIMULATED AND NORMAL PAROTID AND SUBMAXILLARY SALIVAS.

Sample	mg N/100 ml Total N	Protein N	Anions m.e./l. Bicarb.	Phosp.	Chloride	Cations m.e./l. Na	K	Ca
Parotid	14.6	1.5	114.8	11.1	22.1	122	12.2	2.7
Parotid*	14.8	1.6	116.3	13.7	9.2	122	13.7	3.5
Submaxillary	29.2	19.5	19.6	0.6	22.0	12.9	14.2	10.1
Submaxillary*	116.8	96.8	17.2	1.3	49.2	15.8	14.3	7.58

*Rumen pressure stimulated

ferences in saliva composition. Preliminary results obtained by Dr. J. W. Lyttelton at Plant Chemistry Division, D.S.I.R., in a study of the electrophoretic patterns of submaxillary mucoproteins show that there possibly are inherited differences. Similar patterns within a twin set of cows and differences between identical twin sets have been observed.

The realization of the full implications of these saliva studies in the aetiology of bloat, especially with respect to animal differences, must await the results of further work.

Microbiological Factors

The volume of gas (approximately 30 l.) being produced by the microbial fermentation of ingested herbage is of major importance in the production of bloat. However, there is no convincing evidence that bloat is due to any increase in the rate of gas production, provided the complicating factor of foaming is not also present.

Another microbial factor was suggested by Hungate *et al.* (1955) who put forward the idea that slime production by bacteria may be associated with frothy bloat. Since then, Jacobson and Lindahl (1955) in feed-lot bloat studies have calculated the percentage of encapsulated micro-organisms present in the rumen and over an eight-week period obtained a correlation coefficient of 0.94 between the percentage of encapsulation of micro-organisms and the occurrence of bloat.

Bailey and Oxford of the Plant Chemistry Division, D.S.I.R., are working on an organism, *Streptococcus bovis,* which is present in large numbers in the rumen fluid of the cows on legume pasture. This organism has been shown to form a slime in liquid culture only on sucrose and in the presence of CO_2. Bailey has found that the sucrose content of rapidly growing clover is 3.0 to 4.0% of the dry weight of clover leaves and petioles.

Further work is necessary to determine whether there is any difference in slime production between bloating and non-bloating animals.

Mechanical Activity of the Reticulo-Rumen

Changes in Activity During Bloating

Although it is believed that foaming of the rumen contents is the primary cause of bloat, it appears likely that secondary effects due to pressure may be important above a threshold level. Belching ceases almost completely in a severely bloated animal and drenching to destroy the foam will not necessarily mean that the freed gas can be belched. Hence it would be interesting to learn what happens to the rumen movements in bloated animals. However, the pattern of activity in the non-bloated animal must first be established.

A preliminary investigation of the reticulo-rumen in non-bloated cows fed on red clover has been carried out (Phillipson and Reid, in preparation). A variety of techniques has been employed, centring around pressure-recording equipment employing pressure transducers and a modified Sanborn 4 channel recorder (Reid, Melville and Cornwall, in preparation). This has included simultaneous recording of pressures at different points, recording of the mechanical activity of pillars and sacs, and a determination of the sequence of rhythms of activity in relation to feeding, resting and ruminating. Fistulated identical twin cows were available for the work, and it was found that in a number of respects the members of a set showed marked similarities while there were significant differences between sets. This is illustrated in Table 3 showing the average frequency of reticular contractions during feeding, ruminating and resting. (Of the four cows, 293 and 294 are identical twins, the others being unrelated.)

Table 3: Reticulum Contractions per 100 Minutes.
(Means and Standard Errors)

Cow	Resting	Feeding	Ruminating
293	127.8 ± 2.0	170.3 ± 3.7	132.2 ± 4.2
294	130.3 ± 1.2	171.3 ± 2.8	124.3 ± 2.8
48	107.0 ± 1.3	140.2 ± 3.0	135.9 ± 3.6
90	107.7 ± 1.2	150.1 ± 2.8	125.4 ± 3.1
All cows	116.9 ± 0.7	157.1 ± 1.5	128.3 ± 1.7

The investigation of changes that occur during bloating is proceeding. Earlier observations on intact animals using the tympanograph (Reid, 1957) suggested that rhythmic activity of the dorsal sac of the rumen was present at all stages of bloating. The direct recording techniques used have not so far revealed any evidence of inhibition. The frequency of the reticular cycles appears little different from normal, and the strength of the contractions, as judged by the pressure changes they cause, appear to be within the normal range.

Maximum Rumen Pressures

The highest pressures so far observed from recordings in the dorsal rumen have been of the order of 45 to 50 mm Hg. It has been noticeable that in one animal pressures as low as 35 mm Hg caused marked distress. This animal, a Shorthorn, is only moderately susceptible to bloat and has less 'slack' in its body wall than the Jerseys used.

From Dougherty's work with sheep it appears that the pressure that animals can tolerate varies from day to day.

Belching Mechanism

As the level of rumen ingesta is normally above the cardia, the understanding of the mechanism of the clearing of this opening to permit the rumen gases to be eliminated by belching is of considerable importance in a study of factors involved in bloat.

Dougherty and Habel (1955) described a sequence of events occurring during belching in sheep. This was based on cinefluorographic observations of conscious animals, whose fistulated rumens were insufflated with a mixture of CO_2 and CH_4.

The following activity was recorded:

> The reticulum contracted twice, forcing the ingesta back into the rumen. The rumino-reticular fold contracted during the process so that it formed an effective barrier almost cardia high preventing ingesta from running back into the emptied reticulum. At the same time, the rumino-reticular fold was very effective in holding ingesta away from the cardia.
>
> Gas was then forced down into the relaxed and relatively empty reticulum and the belching activity of the oesophagus increased.

Two important points in this work are:

(1) The role of the rumino-reticular fold in the back of the ingesta to keep the cardia clear.

(2) That belching is attendant on reticular activity and occurs during this period that the rumino-reticular fold is contracted.

Observations at the Plant Chemistry Division, with fistulated cows (Reid, unpublished), have not confirmed these findings. It was found that:

(a) Although belching often does occur following the reticular contractions, it may occur at any point during the interval between successive reticular double contractions.

(b) Two distinct belches may occur during the interval between successive reticular double contractions.

Experiments have been carried out with both sheep and cows in which the rumen was insufflated with various gases during recording. Insufflation markedly increased the frequency of belching. It caused an increase in the rate of reticular contractions and it characteristically resulted in the appearance of belching associated with reticular contractions. However, equally characteristic was the occurrence of two, three and even four belches during the interval between successive double reticular contractions.

It is concluded, therefore, that alternative mechanisms for clearing the cardia must exist in addition to that described by Dougherty and Habel.

In a study of belching in the cow the writers have found that the rumino-reticular fold plays at the most only a minor role in belching. Damming back of the ingesta appears to be effected by the anterior pillar. Following a normal reticular contraction this muscular structure contracts—*i.e.*, its free border rises upwards and backwards towards the dorsal sac. If no belch is to occur before the next double contraction, the pillar then sinks back to its former low position. If, however, a belch is to follow, the pillar does not recede completely to its resting level but remains in a state of semi-contraction until just before a belch is to occur when it contracts again. This behaviour of the pillar has been observed on many occasions but is not invariable.

The complete answer of just how the cardia is cleared for all belches has yet to be found.

The Effect of Foam on Belching

The writers assume that one of the main reasons why foam formation in the rumen causes bloat is that it traps the gas in the frothy ingesta and makes it unavailable for belching. However, there are two questions to be answered:

(1) Why does the animal not belch up foam instead of gas?
(2) Has the foam itself any inhibiting effect on the belching reflexes?

Dougherty and Habel (1955) demonstrated in sheep the presence of three sphincters, (a) at the cardia, (b) in the thoracic oesophagus, termed the diaphragmatic sphincter, and (c) a very efficient sphincter at the cranial end of the oesophagus.

Dougherty and co-workers have demonstrated the inhibiting effect of liquid on the opening of this cranial sphincter.

While Dr. Dougherty was at the Plant Chemistry Division, some work was undertaken using his isolated reticular pouch preparation in descrebrate sheep to determine the effect of foam on this sphincter.

Various foams were passed into the pouch and gas passed in after them, and the frequency and size of belches measured. Considerable difficulty was experienced in obtaining a foam of sufficient stability for these experiments, but clear evidence was obtained that the cranial sphincter would not open when foam was passed up the oesophagus. Foam and liquid were immediately swallowed again. Hence the cranial sphincter opens only with the presence of free gas and can hold shut against high pressures when liquid or foam is present.

This explains why an animal does not belch up foam except *in extremis*.

Whether the inhibition of the opening of the cranial sphincter by foam is important in bloat has yet to be determined. The writers have not so far been able to observe in bloated cows the obvious swallowing of foam and liquid seen in the experimental sheep and calves.

Conclusion

The present paper has dealt with only some of the possible animal factors involved in the aetiology of bloat, but enough has been said to indicate how complicated the ailment is. With many animal and plant factors contributing to the condition, it may be that a certain balance of contributing agents is important in certain circumstances, whereas at others a different balance may give the same end result. A study of all the facets of this interesting problem in plant-animal relationship is necessary for the full understanding of the ailment, and at the same time can lead to a marked increase in knowledge of animal physiology, microbial metabolism and plant biochemistry.

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DISCUSSION

Q: : *Have you any information as to why cattle are so much more susceptible to bloat than are sheep?*

A: : The only species difference that we have studied so far is the role of the reticulo-ruminal fold and the anterior pillar. The damming back of the ingesta is carried out in sheep by the former, while the latter is more important in cattle. I believe that bloat in sheep is quite a problem in South Africa though not in New Zealand.

Q: : *Dr. Johns has observed that bloating animals may become non-bloaters and vice versa. Has he associated these trends with any other physiological changes?*

A: : The only state we have correlated these changes with is the degree of foaming of the rumen contents. There does appear to be a definite tendency for cows to be non-bloaters when they are in oestrus. The reason for this is being investigated.

Q: : *Has Dr. Johns any information on the incidence of bloat in beef cattle under New Zealand conditions and could he indicate whether in his opinion this disease might become of importance in Australia with beef cattle grazing on improved pastures? Has Dr. Johns any information which might suggest a method of combating bloat in beef cattle?*

A: : Bloat does occur in beef cattle in New Zealand where legumes are grazed. It appears inevitable that a period of clover dominance will be experienced when the fertility of the land is being improved by the introduction of clovers. It can only be hoped that the farmer can manage his pastures, so that fertility build-up is rapid and the pastures soon become grass dominant. We have control measures for bloat in dairy cows, but these are hardly applicable to beef cattle ranging over a considerable area.