Silage

By P. C. Thomas, N. C. Kelly and D. G. Chamberlain, The Hannah Research Institute, Ayr KA6 5HL

Ensilage as a method of forage conservation was known to the ancient Egyptians around 3000 years ago and throughout recorded history there have been periods when innovative European agriculturalists have enthused about the technique (Schakking, 1976). In Britain, silage-making gained widespread acceptance after the Second World War but as late as 1968 only 12–15% of conserved grass was silage. During the following period, however, the amount of silage made increased sharply; by 1973 it accounted for 28% of conserved forage and the present figure is about 45% (Wilkinson, 1980). Thus, silage is now a conserved grass product of major importance.

This paper deals briefly with technical aspects of the production of grass silage, reviews current information on its feeding value and considers the prospects for the 1980s.

Silage-making

Silage-fermentation. Uncut grass carries low numbers of lactic acid bacteria but the numbers increase during harvesting (McDonald & Whittenburg, 1973), and following the sealing of the silo, when trapped air has been used up and aerobic bacteria inhibited, homofermentative and heterofermentative lactate producing organisms normally become dominant (Woolford, 1972; Beck, 1979). The organisms ferment water-soluble hexose and pentose carbohydrates and there is a partial degradation of hemicellulose (McDonald & Whittenburg, 1973; Edwards & McDonald, 1979; Morrison, 1979). The main fermentation products are lactate and acetate which reduce the pH in the silo to about 4 units, inhibit further fermentation and preserve the crop. Mannitol and ethanol are also produced from sugar fermentation and a range of compounds—lactate, acetate, formate, ethanol, acetoin and 2, 3-butanediol—from fermentation of plant citrate and malate. Saccharolytic and proteolytic clostridial bacteria are also present in the silo. These organisms ferment sugars and lactate to butyrate with small amounts of ethanol, butanol and formate and metabolize amino acids to give acetate, propionate, isobutyrate, isovalerate, phenylacetate, phenylpropionate, indole, indoleacetate, indolepropionate, α-aminobutyrate, γ-aminobutyrate and amines such as histamine, tryptamine, tyramine, cadaverine and putrescine. Their action raises the pH of the silage and if unchecked leads to putrefactive degradation. The clostridial type organisms are discouraged through a combination of the correct moisture conditions and pH in the silo. Their activity is reduced in wilted crops,

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especially when the DM content of the crop is above about 28%, and as the pH in the silo is reduced the clostridia compete increasingly poorly with the lactic acid bacteria.

The rate of fall in pH following ensilage depends on the buffering capacity of the grass, the establishment and maintenance of anaerobiosis in the silo and the availability of sugars for fermentation; these are influenced by the crop and the ensilage technique. Events in the silo can, to a degree, be manipulated through the use of additives which supply soluble carbohydrates or cultures of lactic acid bacteria, or 'regulate' the natural fermentation by ensuring an initial reduction in the pH. Some additives also restrict fermentation through a sterilizing effect or limit protein breakdown by 'protecting' proteins from microbial attack. The additives in most widespread use in Britain are of the 'regulator' type and contain formic acid or mineral acids in some cases with formaldehyde.

Losses in silage-making. Losses in silage-making occur in the field, due to plant respiration, weather damage and inefficiencies in harvesting, and in the silo, due to initial plant and microbial aerobic metabolism, unavoidable and avoidable anaerobic fermentation and loss in effluent. With high DM silages there may also be aerobic deterioration of the silage after the silo has been opened for use (Woolford, 1978).

Losses in silage-making can be measured in chemical terms as yield of constituent in the grass crop minus yield of constituent in the silage removed from the silo; the technical problems in the measurements have been discussed by Watson & Nash (1960) and Norgaard Pedersen (1975). The losses vary between chemical constituents and with the silage-making technique (see Zimmer 1974, 1977; Papendick, 1974). In their classical review of silage experiments Watson & Nash (1960) reported that DM losses could be as high as 40% but were on average 13-19% depending on the ensilage process. Corresponding figures for crude protein and for starch equivalent, calculated from chemical analysis, were 11-20% and 20-30% respectively. Recent studies have shown a similar range of DM loss (Papendick, 1974; Waldo, 1977; Lingvall, 1978) and it appears that even with modern ensilage techniques DM losses are unlikely to be less than 10%. These figures do not of course comment on the true efficiency of the ensilage process since they fail to account in biological terms for difference in nutritional value between the grass and the silage.

Silages as feedingstuffs

There have been a large number of experiments to determine the voluntary intake of silages and to measure growth or milk production in animals given silage diets; the effects of the composition of the crops ensiled, harvesting methods, ensilage procedures and silage additives have received particular attention (see Wilkins, 1974, 1978; Tayler & Wilkins, 1976; Waldo, 1977; Marsh, 1979; Vetter & Von Glan, 1979; Thomas, 1980). These studies have shown that the feeding value of grass is reduced by ensilage partly through effects on voluntary food intake and partly through effects on the nutritive value of the grass. Reductions in feeding

value are especially marked with badly fermented 'clostridial' silages, characterized by high concentrations of butyric acid and ammonia, but they also occur to a greater or lesser extent with silages judged by conventional compositional analysis to be well-fermented (see McCullough, 1979). This raises questions about the mechanisms underlying the regulation of silage intake and about the factors influencing the digestion and utilization of silage energy and protein, and on these topics present knowledge is poor.

Voluntary intake of silages

The intake of silages has been correlated with silage pH and with silage concentrations of ammonia (% in total nitrogen), lactic acid, acetic acid and total acids (% in DM) suggesting that the silage fermentation products are involved in appetite regulation (Wilkins et al. 1971). Studies on the effects of individual fermentation products have not, however, allowed clear-cut conclusions about the agents influencing appetite or their mechanisms of operation. Partial neutralization of silages with sodium bicarbonate has increased intake in some experiments but not others and the responses appear to vary with the species and possibly age of the animal used, with the silage and with the level of supplementation (see Farhan & Thomas, 1978). Likewise, intraruminal infusions of lactic acid or acetic acid have sometimes reduced intake but not invariably (see Wilkins, 1978; Gill & Thomas, 1980). Intake has generally not been reduced by dietary additions of nitrogenous fermentation products, e.g. ammonia, histamine, tryptamine and tyramine (see Vetter & Von Glan, 1979).

Recent work has indicated that the intake of highly digestible silages of high fermentation quality is regulated by a physical 'rumen-fill' mechanism (Farhan & Thomas, 1978). This conclusion is supported by the effects of fine-mincing of silage on its intake (Thomas et al. 1976) and by the differing rates of substitution for silage observed with various supplementary foods. Starchy supplements like barley which reduce the rate of silage cellulose breakdown in the rumen (Thomas, Kelly, Chamberlain & Wait, 1980) and coarse bulky foods like hay produce a more marked reduction in silage intake than low-starch, low-bulk foods like oilseed meals and dried grass cubes (see Thomas & Castle, 1978). The rate of disappearance of silage incubated in Dacron bags in the rumen is similar to that of the parent grass (Smith et al. 1980) suggesting that ensilage does not reduce the susceptibility of grass to microbial attack in the rumen. However, animals receiving silage have low rumination activity and a long 'latency period' after feeding (Deswysen et al. 1978) and this may impose special limitations on the physical breakdown of silages in the rumen. Clancy et al. (1977) showed that intraruminal infusions of lucerne silage juice reduced rumen motility and the rate of eating in sheep and similar results have been obtained with juice from ryegrass silages made with formic acid (E. J. Smith and J. L. Clapperton, unpublished results). This raises the possibility that physical restrictions on silage intake may themselves depend on the products of silage fermentation. Intravenous injections of histamine reduced rumen motility but this compound had no effect on silage

intake when added to the diet (see Vetter & Von Glan, 1979). The physiological activity of other compounds in silage has yet to be explored; in recent experiments (see Barry, Mundell et al. 1978) the intake of lucerne silages varied inversely with their contents of γ -amino butyric acid, a compound well established as a blocking agent for transmission in the nerve synapses.

Digestion of silage organic matter energy and nitrogen

Information on quantitative aspects of digestion is now available for a limited range of untreated, formic acid preserved and formaldehyde preserved silages (Beever et al. 1971; Beever et al. 1977; Brett et al. 1979; Armstrong, 1980; Kelly, Chamberlain et al. 1980; Thomas, Chamberlain et al. 1980; D. J. Thompson, unpublished results).

The relative importance of the rumen, small intestine and caecum and colon as sites of energy and organic matter digestion with silages is broadly the same as that reported for fresh and chopped dried forages. With formic acid silages, for example, the proportions of digested energy disappearing in the rumen, small intestines and caecum and colon are typically 0.64, 0.24 and 0.12; the proportions of organic matter digested are similar although disappearance in the rumen is reduced because of the high energy value of the organic matter of the silage fermentation products. Measurements of ruminal short-chain fatty acid production with silage diets (Beever et al. 1977) indicated that the fatty acids account for 39-43% of the digestible energy in the diet. This value is rather lower than that reported for dried forages (see Leng, 1970) but was consistent with the composition of the mixture of substrates being fermented (Beever et al. 1977).

About 80% of the nitrogen in grass is in protein form but as a result of hydrolysis of grass protein during harvesting and in the silo, and partial deamination and decarboxylation of amino acids during silage-fermentation, silages contain a variable but generally large proportion of non-protein nitrogen (including free amino acids). For well preserved wilted formic acid silages, for example, non-protein nitrogen can often account for 60-65% of the total nitrogen. There have been few determinations of the degradability of silage protein in the rumen but estimates from some of the studies of nitrogen digestion are summarized in Table 1. The beneficial effects of formic acid on protein passage to the small intestine have been referred to in direct comparisons between treated and untreated silages (Hvelplund & Møller, 1976) but the action of the acid is limited, at least at usual rates of application, since only a component of the silage true protein appears to be 'protected' from ruminal attack (see Chamberlain & Thomas, 1980).

Rates of bacterial protein synthesis in the rumen are now generally accepted to be variable but for dried forages they are normally about 30-36 g bacterial nitrogen/kg organic matter apparently digested in the rumen (Hogan & Weston, 1970). With diets consisting solely of silage rates ranging from $10\cdot 3-33\cdot 0$ g N/kg OM have been observed with a mean (with standard error) of $22\cdot 0\pm 1\cdot 7$ (n 17). The reasons for the low figures are not yet clear. Some reduction

Table 1. Estimates of the rumen degradability of dietary crude protein in sheep and cattle given wilted or unwilted silages made with different additives

Additive	Post-cutting treatment	Degradability	
None	Wilted Unwilted Wilted	o·69 [●] § o·88† o·83‡	Brett et al. (1979) Beever et al. (1977) Siddons et al. (1979)
Formic acid	Unwilted	o·69†§	D. J. Thomson (unpublished results)
	Wilted	o·62	Thomas et al. (1980)
	Unwilted	o·58	Thomas et al. (1980)
	Unwilted	o·55	Thomas et al. (1980)
Formaldehyde or	Unwilted	o·52†§	D. J. Thomson (unpublished results)
formaldehyde-	Wilted	o·33‡	Siddons et el. (1979)
formic acid	Unwilted	o·41†	Beever et al. (1977)

^{*}Calculated from the duodenal passage of nitrogenous constituents. Analytical techniques used to fractionate the digesta not given.

§Experiments with dairy cows or growing cattle.

in synthesis rate must result because of the low yield of ATP from ruminal fermentation of silage fermentation products but this is not the complete answer. Nutritional deficiencies in rumen degradable nitrogen can probably be ruled out, except in the case of formaldehyde silages, because rumen ammonia concentrations with silage diets are high. Nutritional limitations on amino acid supply to the rumen bacteria are possible (Maeng & Baldwin, 1976) but intraruminal infusions of sulphur amino acids did not increase bacterial synthesis (Chamberlain & Thomas, 1980) and dietary protein supplements have not consistently given positive responses (Siddons et al. 1979; Armstrong, 1980). There is significant protozoal activity in silage-fed sheep and defaunation reduces rumen ammonia concentration (Chamberlain & Thomas, 1980); effects on bacterial synthesis have yet to be examined.

As a result of the composition of the mixture of dietary and microbial protein passing to the duodenum in silage-fed animals the duodenal digesta contains low proportions of arginine, lysine and especially methionine relative to those observed with many non-silage diets (see Thomas, Chamberlain, Kelly & Wait, 1980). There are few special features of the absorption of amino acids in the small intestine although with formaldehyde silages the absorption of total amino acids

[†]Calculated from the duodenal passage of feed protein as determined by the difference between total amino acid passage and the passage of microbial amino acids (estimated with ³⁵S) and endogenous amino acids (assumed to be 0.11 of total amino acid passage).

[‡]Calculated from the duodenal passage of feed non-ammonia nitrogen (NAN) as determined by the difference between total NAN passage and the passage of microbial nitrogen (estimated with ³⁵S) and endogenous nitrogen (assumed to be 1 · 5 g/d).

 $[\]parallel$ Calculated from the duodenal passage of feed non-ammonia nitrogen (NAN) as determined by the difference between total NAN passage and the passage of bacterial nitrogen (estimated with α - ϵ -diaminopimelic acid) and protozoal and endogenous nitrogen (assumed to be 3 g/d).

and especially lysine may be reduced if the grass protein is 'over-protected' (Beever et al. 1977).

Utilization of silage energy and protein

Calorimetric information on the metabolizable energy (ME) content of grass silages has become available over the last few years (Feedstuffs Evaluation Unit, 1975, 1978; Kelly & Thomas, 1978) but there is still only a limited amount of information on the efficiency of utilization of silage ME. On the basis of the results available the efficiency of utilization of ME for maintenance (k_m) is generally close to that predicted from the metabolizability of the silage using the Agricultural Research Council (1965) equations. However, observed efficiencies of utilization of ME for fattening (k_i) are sometimes substantially lower than those predicted (see Kelly & Thomas, 1978; Sundstøl et al. 1980). Kelly & Thomas (1978) proposed that this might be linked with the presence of high concentrations of D(-) lactic acid in some silages but this was subsequently shown not to be the case (see Thomas, Kelly, Chamberlain & Chalmers, 1980). In a recent experiment with sheep (N. C. Kelly & P. C. Thomas, unpublished results) k_f was substantially higher for a diet of silage and groundnut than for a diet of silage and barley suggesting that the efficiency of utilization may be influenced by dietary protein supply. However, in experiments with growing cattle Waldo & Tyrell (1978) found protein supplements increased the energy retained in the body as protein and reduced the energy retained as fat with no change in total energy retention. In dairy cow experiments too protein supplements to silage diets have in some cases led to an improvement in the calculated efficiency of utilization of ME for lactation (k_{lo}) but in others increases in milk lactose and protein yield have been offset by reduction in fat yield and calculated k_{lo} has been unchanged (Kelly et al. 1980).

Responses in the pattern of efficiency of energy use to dietary protein supplements are likely to operate through changes in amino acid uptake from the small intestine. Infusion studies in sheep given a variety of silage diets have indicated that methionine is the limiting amino acid for tissue synthesis (Kelly & Thomas, 1975; see Barry, Cooke et al. 1978). Similarly, in dairy cows Rogers et al. (1979) have observed increases in milk protein and energy yield in response to intra-abomasal methionine infusions.

Silage in the 1980s

The increased production of silage in Britain in the 1970s was due partly to changes in the economics and management of farming and partly to technical progress in silage-making. Economic pressures are likely to intensify in the 1980s and although silage production is rather more demanding in support energy than hay-making (Joint Consultative Organisation, 1974) the proportion of forage conserved as silage seems likely to increase for some years to come. Alongside this there undoubtedly will be further technical developments. Some of these may be novel; there is current interest in the ensilage of mature grass with alkaline additives which delignify the crop and improve its digestibility. But even allowing

for a successful introduction of new approaches the main emphasis in the future is likely to be directed towards improving present methods of ensilage.

In principle, the silage systems of the future should involve the ensilage of direct cut grass with little effluent loss from the silo and a limited and energetically efficient fermentation. In practice the conflict between direct cutting and low effluent loss and good fermentation quality, is likely to remain a central issue and it may be necessary, as at present, to accept some compromise in ensilage conditions and to rely on additives to regulate the fermentation. Such regulation is designed to minimize deleterious effects on the feeding value of the grass but this objective cannot be approached systematically without a sound appreciation of the factors influencing the intake and nutritive value of silages and it is in this area that advances must initially be made.

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