THE NUTRITIONAL IMPLICATIONS OF DIFFERENTIAL PASSAGE OF PARTICLES THROUGH THE RUMINANT ALIMENTARY TRACT

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INTRODUCTION

Animal production is constrained first by energy supply, and second by the balance of nutrients which affect efficiency of energy use. The optimum nutrient balance will be affected by climatic stress, physiological state, level of production and physical activity. Further, the rumen microbes have nutrient needs separate from those of animal tissues.

Ruminants adapted to grazing poor-quality forages have highly-developed forestomachs which appear to exert a rigorous control over flow of digesta from the reticulo-rumen (RR), in contrast to the simpler anatomical structures found in species which select more-succulent forage (Kay *et al.* 1980). Ruminants consuming forage diets need to balance the advantages of rapid transit of digesta through the gut to maintain high feed intake, against allowing sufficient time for fermentation by rumen microbes of carbohydrate in plant fibre to maximize the yield of energy. In practice, with immature temperate forages, rate of

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fermentation and delay time of digesta in the RR are reasonably-well balanced, and not more than about 10–20% of potentially-degradable fibre passes onward unfermented, while feed intake is maintained at a level consistent with reasonable levels of productivity because constraints to digesta passage are relatively unimportant. As forage matures, especially in the tropics and subtropics, the slow passage of digesta through the gut and the attendant poor fermentation of the refractory fibre result in low voluntary feed consumption and poor body condition. The growing world-wide appreciation of the need to extract more nutrients from very-mature forages and agro-industrial byproducts is focussing attention on the fate of, and the rate of release of nutrients from, the fibrous particulate fraction of rumen digesta; accordingly, the control by the animal of RR motility, the capabilities and requirements of cellulolytic micro-organisms, and the resultant nutritional implications are assuming greater importance. In this review some consequences are considered of the fermentation and passage of digesta particles on the supply to both rumen microbes and the host animal of energy and nitrogen, the digestion of which will have the major impact on nutrition, although the release of minerals from fibrous feeds in the RR may also be determined by residence time in that organ (Playne *et al.* 1978).

Recent reviews have had as their focus the movement of particulate residues through the RR (e.g. Weston & Kennedy, 1984; Faichney, 1986; Grovum, 1986; Martz & Belyea, 1986; Owens & Goetsch, 1986). As a result of the methodological problems involved in studies of kinetics of particulate material, the diversity of techniques in use and subsequent difficulties in data comparison, and the poorly-defined effects on particle kinetics of the over-riding metabolic and endocrine controls of gastrointestinal function and food intake, the data are not adequate for detailed model simulation of fill, flow and fractional disappearance or passage rates (FPR) of digesta constituents from the RR through the reticulo-omasal orifice (Beever *et al.* 1980–81; Murphy *et al.* 1986). Accordingly for accurate prediction of animal performance on all-roughage diets clarification of the processes affecting particulate flow from the RR is an essential ingredient.

The present review seeks to examine the interaction of forage type on particle breakdown, passage and digestion in the gut. In particular we will address the questions: (a) on what basis are rumen particles selected for passage from the RR, (b) what are the nutritional implications of differential passage of particles, (c) how can a modelling framework be developed to facilitate assessment of nutritional implications of the competition between digestion and passage from the RR of particles? The framework applies particularly to ruminants under long-term feeding conditions of forages too mature to permit the animal to achieve its genetic potential to utilize energy and in the absence of gross nutrient deficiencies or imbalances which may restrict intake and digesta content of the RR (Doyle *et al.* 1987).

RETICULO-RUMEN FUNCTION

The complexity of RR function, involving the central nervous system and hormonal influences (Fioramonti & Bueno, 1988) in the integration of gut motility plus considerations of animal and species differences in rumen morphology, physiological state, climatic stress, degree of adaptation to roughage eating and frequency of feeding, produce interactions with the physical and chemical properties of forages which defy easy interpretation or prediction. However, while it is clear that experimental results obtained with one species or breed may not apply quantitatively to another, similar constraints appear to apply to particle passage through the gastrointestinal tract in animals of comparable dietary habits.

Qualitative knowledge exists concerning some aspects of the regulation of RR motility (Wyburn, 1980; Reid, 1984) but we lack the detailed knowledge necessary for construction of a causal quantitative model (Reid, 1984). Techniques of radiographic imaging, involving observations of the movements of boluses of barium sulphate, have permitted the development of a detailed picture of digesta movements in the RR of sheep (Wyburn, 1980). In the ruminant eating *ad lib.*, newly-ingested particles if sufficiently dense, sink in the region of the cardia, but more usually float until the next contraction of the reticulum pushes them into the dorsal sac of the rumen. Movement of digesta within the RR of sheep has been described as following two streams; one which circulates in the dorsal sac as the raft of floating particles, the other with counter circulation operating in the ventral sac. Using an endoscope technique, A. Lirette & L. P. Milligan (personal communication) could find evidence only of the first stream in the dorsal sac of cattle. Evans *et al.* (1973) concluded that newly-ingested feed was retained in the dorsal sac of the RR of cattle, and that particles entered the reticulum from the ventral sac. Reid (1986) considered that subsequent movement of particles could be summarized into four processes: the first, the concentration of particles eligible for passage and delivery to the reticulum; the second, selection of appropriate material in the reticulum and its presentation to the reticulo-omasal orifice; the third, factors affecting entry of digesta into the omasum; and finally the motility of the omasum and digesta flow therein.

Concentration of particles in the RR varies with diet, which will affect passage of particles. Thus Weston (1989) reported a correlation (r 0·92) between organic matter (OM) content of digesta leaving the reticulum and that of reticulum digesta, the average content of outflow being 55 (SE 12) % that of reticulum digesta. For sheep fed on lucerne (*Medicago sativa*) hay, grinding increased digesta OM concentration in the reticulum by 81 % in the study of Weston *et al.* (1989) and would therefore encourage faster passage rate of particles unless counteracted by a greater depression of digesta flow.

Sorting of digesta particles in the RR after ingestion of chopped diets is a time-dependent process. The segregation of coarse, light particles in a 'raft' by flotation in the dorsal sac will reduce passage into the reticulum, comminution during rumination, and perhaps opportunities for bacterial colonization. Sutherland (1987) found that raft particles were almost entirely of stalk origin in sheep fed lucerne hay once daily, and that the relative enrichment of particles in the raft compared to their concentration in the ventral sac was positively related to particle size. The raft entraps small particles which would otherwise sink into the ventral sac, thereby delaying their entry to the pool which can pass from the RR (Sutherland, 1987). Welch (1982) reported that placing of plastic particles at the top of the 'raft' impeded their time of arrival at the reticulum by only 20–44 min compared to particles placed below the raft. Feed particles, however, would pass through the 'raft' in a less-predictable manner owing to the entanglement of the rough particle surfaces, and to the opposing effects on buoyancy of hydration of particles and the fermentative activities of rumen micro-organisms, which generate gas bubbles. It might be expected that when the 'raft' is reduced by grinding the feed, entrapment might also be reduced; however Faichney (1986) reported increased entrapment when a lucerne diet was ground and pelleted. This result would tend to indicate that increased dry matter concentration in RR digesta from ruminants given pelleted diets may mimic the entrapment within 'rafts', or that factors other than physical entanglement, e.g. rumen motility, were responsible for entrapment.

There is discrimination against movement from the ventral rumen to the reticulum which increases markedly with increasing particle size for sheep given roughage in the chopped form, but not for the ground and pelleted form (Weston, 1989). This discrimination, the reasons for which are poorly understood (Reid, 1984), appears less important than that responsible for selective flow of particles, during contraction of the reticulum, to the post-

rumen tract (Weston, 1989). The particle spectrum in faeces indicates that large particles (up to 10 mm in length; McLeod, 1986) may flow from the RR but at a rate substantially less than that of smaller particles, leading to the suggestion (Poppi et al. 1980) that particles can be divided into at least two fractions, large particles that exhibit a high resistance to flow from the RR, and smaller particles that exit relatively readily from the RR. The probability of passage is inversely related to particle size (e.g. Poppi et al. 1980, 1985), but even the finest particles flow from the RR more slowly than fluid (Faichney, 1986). Discrimination against passage of large particles appears to be somewhat less for animals of large body size (Poppi et al. 1985; Weston et al. 1989), but does not appear to result from inhibition of movement of large particles from the reticulum to the omasum or from preferential return of large particles from the omasum (McBride et al. 1984; Welch, 1987). However Welch (1987) reported that light particles were more likely to be returned to the reticulum from the omasum than were heavier particles. Thus the resistance to flow of large particles from the reticulum and acceptance by the omasum may relate more to their high buoyancy (Evans et al. 1973; Wyburn, 1980) and to the spilling of lighter material from the reticulum into the cranial rumen during contraction (Reid, 1984) than to size per se. This discrimination against large, buoyant particles functions to prevent a 'log-jam' of particles in the reticulo-omasal orifice and omasum.

Movement of digesta through the reticulo-omasal orifice presumably is affected by the frequency and amplitude of contractions of the RR, the pressure differential between reticulum and omasum, and the presence of a receptive space in the omasum. These factors are modulated by the degree of tactile stimulation afforded by the digesta to tension receptors in the wall of the RR (Reid, 1984). Physical properties of diets, e.g. particle size (Pharr et al. 1967), clearly affect tactile stimulation although there is little quantitative information on other pertinent attributes of particles. When diets are ground and pelleted tactile stimulation is reduced, as evidenced by reduced rumination despite often higher fill of fluid plus dry matter in the RR (Weston & Kennedy, 1984; Faichney, 1986), and consistency of digesta is markedly decreased (Welch, 1982). Weston (1989) suggested that the fractional passage rate (FPR; rate of flow out of the RR per unit fill or pool) of particulate dry matter would be affected by differences between diets in concentration and load of particles in the RR. Increased motility of the reticulum with cold stress led to greater flow of plant fibre from the RR although the amount flowing per contraction decreased (Kennedy, 1985b). In contrast, greater amplitude, but not frequency of contractions of the forestomach, appeared to be responsible for enhanced flow of digesta from the RR observed in swamp buffaloes (Bubalus bubalis) compared to cattle (McSweeney & Kennedy, 1987).

Chewing during rumination aids in clearing feed residues from the RR and is intimately involved in the physical reduction of particle size of rumen digesta (Pearce & Moir, 1964; Ulyatt et al. 1986). Particle size reduction by microbial action alone is minor (Murphy & Nicoletti, 1984; Kennedy, 1985a) but may be relatively more important for smaller particles (Ehle & Stern, 1984). Chai et al. (1984) suggested that fragmentation by ruminating chewing was enhanced by prolonged microbial attack on plant residues. The limited quantitative information on the movement and comminution of particles during rumination chewing has been reviewed by Ulyatt et al. (1986). The pertinent features appear to be aspiration of a bolus into the oesophagus and mouth, followed by return within 1 s of the fine particulate material. The material retained in the mouth is thus enhanced in content of large particulate material and is chewed for a length of time apparently determined by the fragility of the large particles (Kennedy, 1985a) and swallowed after about 1 min, thereby locating freshly-generated small particles close to the reticulo-omasal orifice (see Wyburn, 1980). Duration of rumination per unit intake is

apparently inversely related to level of intake and to body size, and time spent ruminating is positively related to rumen load (Weston, 1984; Weston & Kennedy, 1984). Rumen digesta load in some circumstances is apparently determined by the degree to which energy supplied by the diet satisfies the energy demand by body tissues (Weston, 1982).

DETERMINANTS OF PARTICLE PASSAGE

PARTICLE SIZE MEASUREMENTS AND KINETICS

In interpreting the literature on particle size of feed and digesta in ruminants, the reader should be aware that, until recent advances using computer technology facilitated direct measurements of particle dimensions (Luginbuhl *et al.* 1984), estimates of particle size relied on use of various wet- or dry-sieving techniques. Separation on a size basis thus achieved is somewhat arbitary, and may not be based purely on size characteristics. Shape is also important and McLeod (1986) found that the 1·18 mm (linear aperture) sieve, used to discriminate large and small particles, retained faecal particles measuring up to 10 mm in length, while allowing passage of 'small' particles, some exceeding 5 mm in length.

Many studies have employed kinetic analysis of the behaviour of administered markers, either applied generally to the rumen to encourage adsorption by all digesta particles (e.g. Dixon *et al.* 1983) or dosed attached to specific particles (Ellis *et al.* 1979). Such markers may alter the properties of passage and digestion of the particles to which they are attached, rendering them at best only qualitatively useful (e.g. Ehle, 1984), or may translocate to the fluid phase or to other particles. Furthermore, studies on the faecal excretion of markers cannot be relied on to provide accurate information on the passage of particles from the rumen, largely because of inadequacies in mathematical approaches used to describe marker excretion (Faichney, 1986). Accordingly, preferred techniques to calculate FPR are those yielding direct estimates of rumen-pool sizes of particles by emptying the RR or by the double-marker method, combined with estimates of flow of particle fractions from the RR with appropriate corrections for digestion of particulate dry matter (Faichney, 1986).

EFFECT OF PARTICLE SIZE AND SPECIFIC GRAVITY ON PARTICULATE PASSAGE RATES

The previous discussion has emphasized the relation between particle size and probability of passage from the RR. Other factors which modify particle dynamics in the rumen also need consideration. The most important of these appears to be buoyancy or functional specific gravity (FSG) (Ehle & Stern, 1986; Welch, 1986; Sutherland, 1987); the evidence is unequivocal for differential passage of plastic particles identical in length and diameter but differing in specific gravity (King & Moore, 1957; Campling & Freer, 1962; desBordes & Welch, 1984; Ehle & Stern, 1984). Maximal passage rates from the RR were observed with plastic particles of specific gravity of 1·2–1·4 (Welch, 1986). FSG may be defined as effective density, with contributions from the solid, liquid and gaseous components of the particle (Sutherland, 1987). Measurements of FSG need to be made quickly and in a suitable environment in order to maintain microbial activity and gas content of particles. Separation techniques designed to characterize buoyancy of particles without inhibiting microbial fermentation have been recently described (A. Lirette, L. P. Milligan, N. Cyr & R. M. Elofson, personal communication; Sutherland, 1987). For sheep given lucerne once daily, the proportions of buoyant particles (FSG less than that of artificial saliva) from sieves of 4·0, 2·0, 1·0, 0·5 and 0·25 mm aperture, sampled 3–6 h after feeding were 89·5, 85·5, 52·9, 20·1 and 7·4 % (Sutherland, 1987).

The effects of microbial digestion of forages on FSG of material contained in porous synthetic fibre bags, and therefore largely unaffected by normal comminution processes in the rumen, were illustrated by Nocek & Kohn (1987) for lucerne and timothy (*Phleum pratense*) hay which had been chopped through a forage harvester (theoretical length of cut, 6·4 mm) and further ground through a 5·0 mm screen or dry sieved into two fractions, that retained on or having passed a 3·2 mm sieve. FSG of samples of lucerne after they had been incubated within bags in the RR for intervals of 1–100 h, was measured by progressive immersion of particles in solutions of known specific gravity but of unknown effects on gas formation. FSG was inversely related to particle size of lucerne, with 14–60 % of the four fractions having a FSG of 1·3 or more before incubation in the rumen, increasing by 12–24 % to achieve maximal values of FSG after 52–76 h of incubation. By contrast, practically none of the timothy had an initial FSG exceeding 1·3, but FSG increased by 28–47 % to maximal values after 76–100 h of incubation. It is uncertain whether these differences between forages obtained with porous bags are typical of legumes and grasses, but the findings indicate the existence of differing FSG–time relationships between forages. Similar changes occur when forages are soaked in vitro in the absence of rumen microbes (Hooper & Welch, 1985). Calculations made from values presented by Hooper (1984) showed that the FSG of hay fractions ground through screens of aperture 1, 2, 4 and 6 mm was inversely related to rumen particle size. The predicted asymptotic FSG achieved after soaking in water was 31–35 % higher than the initial value in all fractions, and was 1·40, 1·28, 1·10 and 0·94 respectively. These results agree with the relationships presented by Sutherland (1987), which indicate that smaller particles have higher intrinsic maximum densities because of their characteristics of poor gas entrapment and high surface area : volume ratio.

PARTICLE SIZE AND SPECIFIC GRAVITY INTERACTIONS

When there is a close correlation between particle size and FSG, as for example in the studies of Evans *et al.* (1973) and Sutherland (1987), measurements of both factors will not distinguish between those characteristics of particles that affect their FPR. However, when physical and chemical properties of feeds are altered by mechanical or chemical treatment, such distinctions may be possible. Thus, differences in FPR between particles of similar size from chopped and pelleted lucerne (Faichney, 1986) might be partially attributable to differences in FSG caused by depressed microbial activity in animals given pellets (Faichney, 1986; Udén, 1988) or perhaps to differential incorporation of stem into pellets due to loss of leaf during mechanical processing. Again, Gates *et al.* (1987) observed an apparently increased FPR of particulate grass hay residues with ammonia treatment and attributed this to an increased rate of hydration and higher FSG of the ammonia-treated material. Most direct evidence is available from the results for sheep of Davis & Weston (1986; personal communication) who found that treatment of wheaten straw with alkali increased straw intake by 53 %. FPR were increased through alkali treatment, the relative increase being positively related to particle size (Table 1), but not to content in the RR of the various particle fractions. The absolute change in FPR due to alkali treatment for all fractions excepting the < 0·15 mm fraction, which included soluble as well as microbial dry matter, was negatively related to screen size. Thus, the effects of alkali treatment on FPR were highly related to particle size in a situation where rumination time and particle pool sizes were not substantially affected by treatment. While the results of Berger *et al.* (1980) and of Egan & Doyle (1985) suggest that some of the response might be caused by increased cation load, increased feed intake and rumen digestion, the relative increase in FPR was well correlated (r^2 0·98) with increases in specific gravity (measured in the absence of

Table 1. *Fractional passage rates (FPR/h) of particle fractions from the rumen and relative change in specific gravity of particles isolated from the large intestine of sheep given wheaten straw with or without alkali treatment*

Sieve aperture (mm)	FPR		Relative increase (%)	
	Control	Alkali	FPR	Specific gravity*
4·8	0	0		
2·4	0·0006	0·0022	266	—
1·2	0·0015	0·0052	247	24·5
0·6	0·0061	0·0131	114	14·6
0·3	0·0225	0·0322	43	11·1
0·15	0·0370	0·0485	30	10·6
< 0·15	0·0337	0·0381	13	—

Values from Davis & Weston, 1986; R. H. Weston & P. M. Kennedy, unpublished results)
* Results from measurements of specific gravity of dried, sieved samples (following pycnometer method of Hooper (1984)).

fermentation) of material which had escaped from the rumen (Table 1). The practical importance of this interaction of specific gravity with size of particle can be deduced from the experiment of Hunt *et al.* (1984), who fed lambs wheat straw which had been treated with alkali and ground through a screen of either 25 or 100 mm. Alkali treatment increased fibre digestion by comparable amounts in both finely- and coarsely-ground diets, but relatively-more digestion of treated straw occurred in the rumen for the coarsely-ground diet. This result was associated with a reduction in retention time of rumen digesta in lambs given the finely-ground diet, but not the coarsely-ground diet. Such interactions may be partly responsible for the variable responses to alkali treatment (Thiago *et al.* 1979).

DIETARY PARTICLE SIZE
The effect of particle size of ingested material on rate of digestion is variable, perhaps in part because of differential enhancement between forages of microbial attack on tissues exposed by fracture and disruption of over-laying structures. If dietary material is sieved, it is found that chemical composition may vary with particle size (Jaster & Murphy, 1983; Emanuele & Staples, 1987), perhaps a result of segregation of leaf from stem fractions. In particular, lignin content, and the attendant protection of otherwise-available cell wall carbohydrate, is likely to vary with particle size (Jaster & Murphy, 1983; Pond *et al.* 1987). However, when forages are processed by milling to produce different particle sizes of similar chemical composition, results are variable. For example, Nocek & Kohn (1987) compared lucerne, chopped through a forage harvester (6·4 mm theoretical cut) with lucerne that had been further ground through a 7 mm screen. The disappearance rate of the latter from a porous synthetic fibre bag suspended in the sheep rumen was approximately 30 % greater than the former. No comparable effect was evident from timothy hay. Again, Robles *et al.* (1980) found that the estimated rate of digestion of orchard grass (*Dactylis glomerata*) was unaffected, but that of lucerne doubled, by grinding through a screen of 1 or 4 mm when compared to material ground through 8–12 mm screens. Differences between forages in the ease with which cuticle and lignified structures are removed by grinding may determine effects of particle size on fermentation. In this respect, the ability of rumen microbes to colonize plant material is pertinent. Thus Gerson *et al.* (1988) found

that the rate of gas production and density of microbial population per surface area of particle was 600 % higher in large than in small particles of meadow hay.

Fine grinding may increase the rate of digestion of protein-rich supplements (Freer & Dove, 1984) but such digestion is usually rapid and extensive, irrespective of particle size. Digestion of nitrogen is usually more rapid than that of dry matter in forages (Beever & Siddons, 1986), with the difference becoming smaller with increasing maturity (Lindberg, 1985; Beever & Siddons, 1986).

Dietary particle size affects chewing behaviour, voluntary feed consumption, nutrient yield and rumen conditions (Weston & Kennedy, 1984), as demonstrated by comparison of digestion in animals given ground and pelleted diets compared to long, stemmy mature forages. Time spent eating is less likely to be affected by fatigue (Campling & Balch, 1961), although the physiological limit to eating time is undefined, than by the ease with which the feed is compressed to form a bolus for swallowing (Fujihara, 1980). Eating time of green forages decreases with advancing maturity, but due to a decreasing intake, eating time per unit intake increased gradually and was higher in grasses than in legume diets (Dulphy & Demarquilly, 1974).

The degree of chewing in relation to reduction in particle size is variable. Lee & Pearce (1984) could not demonstrate a relationship between particle size reduction and content of refractory components of cell walls, perhaps according to M. N. McLeod, P. M. Kennedy & D. J. Minson (unpublished results), because of differing fragility of leaf and stem fractions. Lee & Pearce (1984) did identify differences between animals in the extent and efficiency of breakdown. The particle spectrum of feed entering the rumen is likely to be somewhat variable due to different fracture patterns of dietary components (Pond *et al.* 1984). Despite particle comminution during eating, the majority of swallowed particles of most forage diets requires further reduction in size before easy passage from the RR is possible (Weston & Kennedy, 1984).

PARTICLE FLOW AND DIGESTION DISTAL TO THE RETICULO-RUMEN

Large particles may be preferentially retained in both the omasum and abomasum (Sutherland, 1987), but there is no good evidence for differential passage of particles distal to the pylorus in ruminants. In sheep given a pelleted diet, particulate digesta passed at rates of about 60, 20 and 100 % that of a fluid marker in the rumen, abomasum and caecum–colon respectively (Faichney & Boston, 1983). Post-omasal passage rate of inert particles was not affected by length (1–10 mm) but showed an optimum at specific gravity of 1·2 (Siciliano-Jones & Murphy, 1986*a*).

Digestion in the caecum–colon of potentially-fermentable cell-wall constituents which escape the RR is variably efficient. Thus the escape from the RR of an additional 7–100 % of potentially-digestible fibre caused by grinding and pelleting of Italian ryegrass (*Lolium multiflorum*), timothy and lucerne, was accompanied by digestion in the caecum–colon of 60–100 % of this fibre (Beever *et al.* 1981). Conversely, no such compensation was observed in sheep following increased flow of potentially-digestible fibre due to cold-exposure (Kennedy *et al.* 1986).

MICROBIAL ATTACHMENT TO PARTICLES

Passage of microbial protein to the intestines is considered to be a function of the energy-limited growth of microbes, and the extent of microbial turnover within the RR. From in vitro relationships showing positive relationships between net efficiency of microbial growth and turnover rate, it would be expected that higher FPR of rumen digesta would

be accompanied by greater flow of microbes from the RR if not counteracted by depression of fermentation. However, although FPR of fluid and particles from the RR are generally positively correlated, Sniffen & Robinson (1987) concluded that increased particulate passage was more important than fluid passage alone in increasing microbial yield. These authors supported the suggestion by Van Soest (1982) that more rapid FPR of particles would lead to increased outflow of more-heavily-colonized particles at an earlier stage of digestion.

While colonization of plant cell walls by microbes starts within 30 min of ingestion of temperate feeds (Orpin, 1980), maximal concentrations of adherent microbes were not seen until 6, 24, 96 h after exposure to rumen microbes for lucerne, orchard-grass and bermuda-grass (*Cynodon dactylon*) hays, respectively (Olubobokun *et al.* 1987). A comparable value of 24 h was reported for ground preparations of cell walls (Elliott *et al.* 1985). As the average time for breakdown of large particles is of the order of 12–24 h (Poppi *et al.* 1981; Moseley & Jones, 1984; Worrell *et al.* 1986), maximal colonization and rate of digestion may not necessarily be confined to large particles.

Microbes which adhere to rumen particulate digesta may comprise 70–80 % of microbial OM (Forsberg & Lam, 1977; Craig *et al.* 1987) and this proportion increases with rumen fluid turnover (Faichney & White, 1988). The adherent microbial population will be dependent on the species composition and numbers of microbes, the availability of attachment sites and the ability of the microbes to colonize the fibre. At 1 h after feeding, microbes associated with particles represented 30 % of microbial plus particle dry matter, but this value progressively reduced to 19 % in samples taken 10 h after feeding (Craig *et al.* 1987). There is little information on distribution of microbes relative to particle size. Bauchart *et al.* (1987) found that microbial content of digesta particles generally decreased with size, but markedly increased by 58 % for the smallest particles (passing a 0·1 mm sieve) compared to the next larger category (passing 0·4 mm, retained on 0·1 mm sieves). Using dietary material of differing particle size, Gerson *et al.* (1988) reported a contrary trend with increase microbial content per g particles with smaller particle size. In a theoretical appraisal of microbial degradation of particles, Hobson (1987) considered that a homogeneous particle covered by bacteria would be degraded at a constant rate per unit area of surface, leading to an exponential relationship between loss by digestion per unit time and particle size. However, Czerkawski (1986) calculated that a single layer of bacteria on the exterior of a large stem particle would account for only 0·2 % of actual microbial content, indicating that internal as well as external surfaces were colonized. Bauchart *et al.* (1987) reported low (< 7 %) values of microbial attachment for cows given a 500 g concentrate/kg diet, in agreement with evidence of depressed attachment to particles from animals given a grain diet (Forsberg & Lam, 1977), and the close relationship between rate of digestion of fibre and quantity of adherent bacteria (Robinson *et al.* 1987; Gerson *et al.* 1988).

Given favourable conditions of rumen pH, we may assume that particle content of firmly-adherent microbes after colonization will reflect the amount of accessible and potentially-fermentable cell-wall carbohydrate. Microbial autolysis associated with progressive depletion of nutrients would be expected. In contrast, microbes which are loosely associated with particulate matter are likely to decrease in numbers following the early stages of digestion and removal of soluble and readily-available carbohydrate. Squeezing and chewing of boluses during rumination may also dissociate this population from particles (Czerkawski, 1986). Therefore, within a particle population of given size, the origin of particles, i.e. whether derived directly from the diet, or after residence and digestion in the RR as larger particles, is likely to determine protein present as firmly-attached microbes. Findings from an experiment in which leaf and stem fractions of a grass

and legume were given to cattle, indicated a curvilinear relationship between size of particles taken from the rumen and in vitro digestion by cellulase of their cell wall (P. M. Kennedy & M. N. McLeod, unpublished results). One interpretation of these relationships would be that they reflect the fermentation history of particles, and therefore that the speed of fragmentation of large particles differed between diets. In this experiment, for particles that passed a sieve of 0·50 mm aperture during wet sieving, there was a positive relationship between cellulase digestibility and content of neutral-detergent solubles. It was concluded that the latter component in small, water-extracted particles might approximate dry matter of adherent microbes. The relationship supported the conclusion that content of firmly-associated microbes follows the amount of degradable carbohydrate in the cell wall, and therefore detachment or lysis of microbes occurs as substrate is depleted.

If content of neutral-detergent solubles in small and medium particles is correlated to content of attached microbes, the findings of Worrell et al. (1986) indicate that more microbes adhere to small than to medium particles. In addition, attachment of microbes appeared to increase for several hours after feeding, and thereafter decreased, in agreement with the observations of cellulolytic bacteria in rumen fluid after feeding (Leedle et al. 1982). Similar estimates of microbial content from the experiments of P. M. Kennedy & M. N. McLeod (unpublished results) indicate that fewer microbes adhered to particles in cattle given stem compared with leaf diets, with more microbes adhering to legume than to grass with both fractions. On the same basis, microbial content of particles of different size from the rumen of sheep given lucerne at hourly intervals did not differ appreciably (Waghorn et al. 1986). While these conclusions remain speculative until confirmed using a specific microbial marker, they indicate that across forages, microbial content of particles escaping from the RR may vary. In addition, leaf:stem ratios in forage diets may markedly alter the patterns of passage of adherent microbes.

Condition or diets which promote proliferation of the rumen fungal population are likely to increase fragmentation rate of particles (Orpin, 1983–1984; R. H. Weston, personal communication) through the invasive effects of hyphae on integrity of plant fibre and by accelerating the access by bacteria to plant structures such as vascular bundle sheaths.

NUTRITIONAL IMPLICATIONS OF DIFFERENTIAL PASSAGE OF PARTICLES

The preceding discussion and that of Allen & Mertens (1988) highlight the heterogeneous processes in fibre digestion and the importance of defining the time-course of colonization and digestion of various particle pools in the RR. Reduction in time available for fibre digestion following accelerated comminution and passage will be of less significance with immature than mature forages, as the former contain a greater proportion of more-readily-fermentable carbohydrate. Accelerated passage from the RR of residues of mature forages could lead to increased intake of dry matter but not of digestible OM. Accordingly, enhanced rumen fill and prolonged rumen digestion of fibre associated with slow digesta passage is a common feature of ruminants constrained to eat mature diets.

In contrast, because protein supply to the intestines comprises microbial and, to a lesser extent, undegraded dietary protein, the amount of crude protein digested in the small intestine (DCPi) depends largely on efficiency of microbial synthesis which depends on rumen availability of N from digested dietary protein and endogenous sources and its synchrony with fermented energy. Greater comminution and passage of small particles from the RR may reduce microbial protein yield if the small particles are derived by chewing directly from the diet and pass from the rumen with much of their degradable fibre
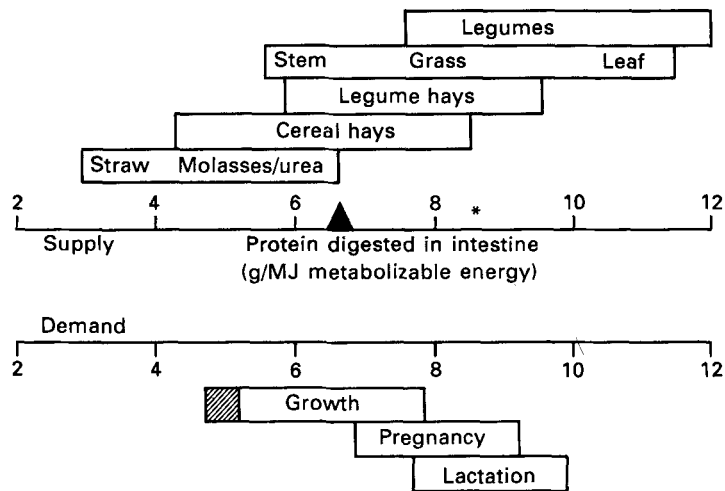
Fig. 1. Relationship between protein:energy supply from a range of temperate feedstuffs, and the demand to be met in producing-ruminants (from Egan, 1985). ▲, Average provision of microbial protein to protein digested in small intestine; *, highest values recorded for microbial protein for temperate feedstuffs; ▨, maintenance requirement.

unfermented. Conversely, of course, an increased dilution rate of liquid in the rumen should enhance the yield of non-attached bacteria (Harrison & McAllan, 1980).

The nutrient supply of protein (DCPi) relative to metabolizable energy (ME) varies substantially between diet classes (Fig. 1). Enhanced digesta passage and improvement of the ratio, DCPi:ME may allow greater growth or satisfaction of requirements for pregnancy or lactation only if ME supply is not limiting. Therefore the possibility exists for improvements of productivity of ruminants by selection of plant species or other means to provide fragmentation patterns which optimize both DCPi and ME. In the absence of appropriate experimental information, we have used a modelling approach to estimate the nutritional benefits of variations in ease of fragmentation or passage of plant residues.

MODEL OF PARTICLE DIGESTION AND PASSAGE

A mathematical model incorporating first-order kinetics was constructed. Comparable approaches were taken by Poppi *et al.* (1981) and Mertens & Ely (1982), and simple mathematical models have been discussed by Allen & Mertens (1988). The present model, although narrowly focussed, is based on concepts developed in more-comprehensive models of rumen function (Murphy *et al.* 1986; Baldwin *et al.* 1987), and incorporates several new features, i.e., recognition that buoyancy or FSG influences FPR of particles of given size, and that large particle fragmentation is determined mainly by chewing during eating and rumination. In addition, three rumen particle pools plus one soluble-dry-matter pool were incorporated into the present model, in contrast to three or two pools in the models of Mertens & Ely (1979), Poppi *et al.* (1981) and Faichney (1986). The pools chosen represented those of large (LP)-, medium (MP)- and small (SP)-particle size based on the findings of Egan & Doyle (1984) which indicated that these discontinuous groupings would approximate patterns of particle passage as determined from wet-sieving techniques in sheep fed on chopped oaten hay.

MODEL DESCRIPTION

Particle pools were described by separations achieved by wet sieving, with LP (those retained on a sieve of 1 mm linear aperture), MP (particles passing the 1 mm screen but retained on a sieve of 0·5 mm aperture), SP (particles recovered on a sieve of less than 0·5 mm aperture or after centrifugation at 333 g), and soluble material (SOL). FPR of these pools were fixed at 5, 20, 55 and 100 % that of rumen fluid, respectively (Egan & Doyle, 1984). The effects of changes in FPR of particles were simulated by varying the FPR of fluid by ±25 %, i.e. from 0·101 to 0·0754 and 0·1257/h.

Comminution during eating and rumination was described by considering the particle size distribution of boluses swallowed after eating or rumination (see Ulyatt et al. 1986), using values for sheep given chopped lucerne hay (39·5 g dry matter) at hourly intervals (Ulyatt et al. 1984; Waghorn et al. 1986; M. J. Ulyatt, personal communication). The particle spectrum of these boluses was fixed for all simulations. Effects of varying the rate of fragmentation of particulate digesta by ±25 % were studied by changing the proportion of dry matter chewed during rumination from 0·25 to 0·1875 or 0·3125/h.

To incorporate the concept that FSG affected the probability of particles passing from the rumen, LP and MP pools were divided into 'new' and 'old' subpools. Only material in the 'old' subpools which had attained a functional specific gravity of 1·3, was considered eligible to pass from the RR. Findings of Siciliano-Jones & Murphy (1986 b; unpublished results), has shown that of the 'new' material, 70 % of LP and 75 % of MP attained a FSG of 1·3 in 7 and 4 h from initial values of 0·98 and 1·14 respectively. These values were used to fix fractional rates of flow between 'new' and 'old' pools at 0·15 and 0·30/h for LP and MP in the first series of simulations. A second series of simulations was made of a 'fibrous' diet of which LP and MP had initial specific gravities of 0·52 and 1·07 respectively (values for wheat straw, J. Siciliano-Jones & M R Murphy, unpublished results) and in which rate of entry into 'old' LP and MP pools was arbitrarily fixed at 0·075 and 0·15/h respectively. It was assumed that LP of specific gravity < 0·9 ('lag phase' LP) was not fermented, nor ruminated, until it entered the 'new' pool on reaching a specific gravity of 0·9. Other conditions were kept identical to the first simulation series.

For all simulations, entry of dry matter into LP, MP, SP and SOL pools was 23·5, 3·01, 4·08 and 9·02 g/h respectively. Fractional rates of fermentation (g/g dry matter per h) for the various particle pools were considered to be equal on the basis of content of the neutral-detergent-soluble fraction (Waghorn et al. 1986) as previously discussed, with 37·2 % of feed dry matter being fermented in the RR for the control ('lucerne') simulation in series 1 (Ulyatt et al. 1986). Apparent rate of digestion of dry matter was accordingly 0·023/h for each pool for all simulations. For comparison, the effect of a doubling of the fractional fermentation rate with each subsequent pool of smaller particles was simulated, following the preferred suggestion of Hobson (1987) that rate of fermentation should theoretically show an exponential relationship to particle size. For this simulation, rates of chewing during rumination of rumen digesta and of fluid passage were identical to the control simulation.

Representative block diagrams within the model are presented in Fig. 2. The program was written in ACSL and run on a 3081 GX computer (IBM) until a steady-state was reached.

Several specific questions were addressed through sensitivity analysis. These questions were: (a) to what extent do changes in particle comminution and passage affect amount and size spectrum of particles in the RR and the intake potential of the animal; (b) how might an inverse relationship between fermentation rate and particle size affect fermentation in, and passage from the rumen of particles and adherent microbes, (c) is initial FSG of feed particles likely to contribute to effects on rumen fill?
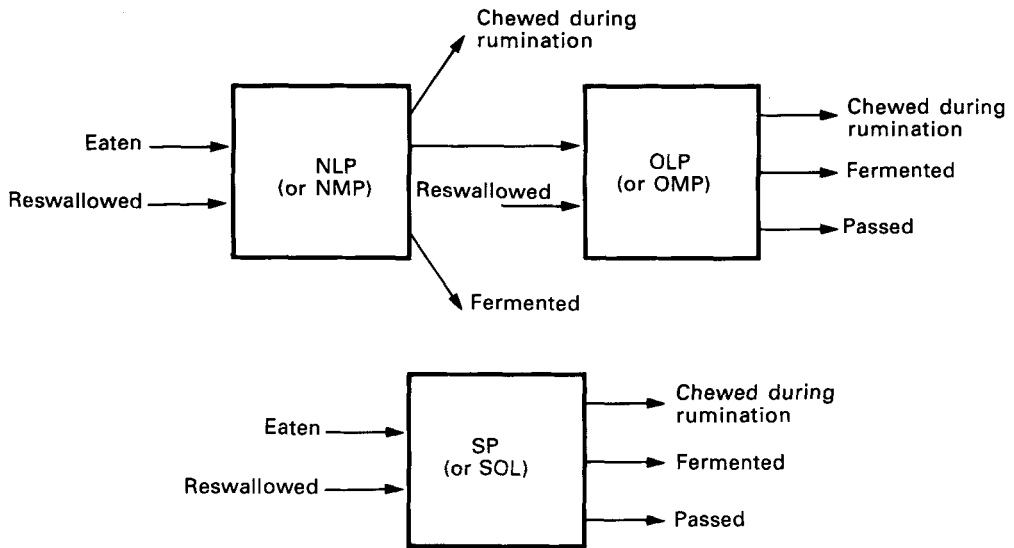
Fig. 2. Representative block diagrams of model used to simulate particle kinetics in the reticulo-rumen. Large (LP) and medium (MP) particles entered the old (O) from new (N) pools on the achievement of a functional specific gravity of 1·3. Small particles (SP) and soluble dry matter (SOL) were derived from inputs during eating or after comminution of LP or MP during rumination.

RESULTS OF SIMULATION

In both simulation series, simulated rumen load (Table 2) was slightly more sensitive to changes in particle comminution (-10% to $+10\%$) than to the same proportional change in digesta passage rate (-8% to $+6\%$). In contrast, the existence of 197 g of 'lag phase' LP in simulation series 2 increased dry matter load in the RR by about 25%, and reduced the proportion of LP in the 'old' subpool by about 65% compared to simulation series 1. Fermentation patterns (Table 3) showed substantial differences between simulations within series, with the majority of fermentation being derived from the SP plus SOL pools when rates of comminution or digesta flow were fixed at $+25\%$ or -25% respectively. With reduced comminution and increased digesta passage rates, the significance of fermentation from LP was greatly enhanced at the expense of that from SP plus SOL pools. This was due principally to variation in LP pool size, because the proportion of dry matter fermented within pools was little affected between simulations, in contrast to the substantial reduction with smaller particle size (Table 4).

The second question regarding ways in which differential fermentation rates might affect RR dynamics can be approached by examining the comparison between control and variable digestion simulations in series 1 (Tables 2–4). The increased dry matter load ($+89$ g) was attributable to increases of 33 and 41% respectively in 'old' LP and MP pools, with a 15% reduction in the SOL pool. These patterns were caused by competition between passage and digestion, evident in Table 4.

The very-marked effects of degree of comminution before passage from the RR occurs, on the time available for microbes to colonize and digest fibre is shown in Table 5. Although we assumed no fermentation in 'lag phase' LP in simulation 2, colonization of that material would markedly enhance LP fermentation compared to that of simulation 1. Particles which entered as 'new' MP and passed from the RR as 'old' MP or after comminution to SP were retained for only 5·3–6·9 h and 8·0–10·5 h in all simulations.

Table 2. *Summary of simulation of dry matter (DM) pools (g) of large (LP), small (SP) and soluble (SOL) material* in the reticulo-rumen as affected by rates at which digesta is chewed during rumination or with which digesta flows from the rumen*

(Simulations 1 and 2 refer to entry of LP of specific gravity greater than, or less than 0·9 respectively)

		Rumination		Digesta flow		Variable digestion†
	Control	−25%	+25%	−25%	+25%	
Simulation series 1						
Total DM	638	709	579	692	601	727
Total LP	211	320	120	158	243	257
Old: total LP	0·57	0·67	0·43	0·50	0·60	0·62
(SP + SOL): total DM	0·44	0·36	0·52	0·52	0·38	0·37
Simulation series 2						
Total DM	842	916	780	893	805	948
Total LP	394	520	315	353	440	458
Old: total LP	0·20	0·31	0·10	0·14	0·24	0·26
(SP + SOL): total DM	0·33	0·28	0·39	0·41	0·28	0·29

* For details see p. 200.
† Rate of digestion followed exponential increase with smaller particle size.

Table 3. *Summary of simulation of fermentation (g dry matter (DM)/h) in the reticulo-rumen in total DM pool, and the proportion derived from large particles (LP) or small particles plus soluble (SP + SOL) pools**

(Simulations 1 and 2 refer to entry of LP of specific gravity greater than, or less than 0·9 respectively)

		Rumination		Digesta flow		Variable digestion†
	Control	−25%	+25%	−25%	+25%	
Simulation series 1						
Total DM	14·7	16·4	13·4	15·9	13·8	14·7
LP: total	0·33	0·45	0·21	0·23	0·41	0·12
(SP + SOL): total	0·46	0·36	0·52	0·52	0·38	0·69
Simulation series 2						
Total DM	14·9	16·6	13·5	16·1	14·1	
LP: total	0·32	0·45	0·20	0·22	0·40	
(SP + SOL): total	0·44	0·35	0·52	0·53	0·38	

* For details, see p. 200.
† Rate of digestion followed exponential increase with smaller particle size.

Undoubtedly, severe limitations on time for microbial fermentation may follow if much of the diet is in the MP or SP form.

Approximations of passage of microbial protein to the intestines relative to fermentation in the RR may be made if it is assumed that microbial attachment per g particles was independent of particle size, or increased in parallel with digestion rate in the variable digestion simulation. Ignoring undegraded dietary protein and post-rumen digestion of OM, DCPi:DE would be approximated by the ratio, dry matter passage:fermentation.

Table 4. *Simulation (series 1) of the ratio, dry matter (DM) fermented: that passed from the rumen plus fermented as affected by the rates at which rumen DM is chewed during rumination, fluid flow from the rumen, or by an exponential increase in the rate of digestion with smaller particle size (variable digestion)*

| | Control | Rumination | | Digesta flow | | Variable digestion |
		−25%	+25%	−25%	+25%	
Total DM	0·37	0·42	0·34	0·40	0·35	0·37
Old LP	0·82	0·82	0·80	0·86	0·79	0·58
Old MP	0·53	0·54	0·58	0·60	0·53	0·39
SP	0·30	0·29	0·33	0·35	0·25	0·32
SOL	0·19	0·20	0·20	0·23	0·16	0·34

LP, large particles; MP, medium particles; SP, small particles; SOL, soluble pool; for details of particle pools, see p. 200.

Table 5. *Simulation of mean retention time* (h) in the reticulo-rumen of particles† entering the rumen as new LP (large particles) for series 1 or 'lag phase' LP for series 2, and passing from the rumen as old LP (1), old medium particles (MP) (2), or small particles (SP) (3), as affected by the rates at which rumen digesta is chewed during rumination, digesta flow from the rumen, or by an exponential increase in the rate of digestion with smaller particle size (variable digestion)*

| | Control | Rumination | | Digesta flow | | Variable digestion |
		−25%	+25%	−25%	+25%	
Simulation 1						
Route 1	9·1	13·5	5·5	7·1	10·4	10·5
2	12·9	17·6	9·1	11·2	13·9	15·1
3	16·0	20·8	12·0	14·8	16·6	18·0
Simulation 2						
Route 1	18·4	24·0	14·3	16·1	20·3	
2	22·2	28·2	18·0	20·2	23·9	
3	25·4	31·4	21·0	24·0	26·5	

* Calculated as sum of the inverse of fractional flux rate for dry matter of pools involved.
† For details, see p. 200.

Thus, in series 1, changing rumination chewing by −25% or +25% would result in a change of DCPi:DE of −19% and +16%, while values for a change in fluid passage rate of −25% or +25% were −12% and +10% respectively (Table 4). Comparable changes with the variable-digestion model were not as marked as this model, but were still significant, and averaged 40 and 80% of the changes predicted from the fixed-digestion model (M. R. Murphy, unpublished).

CONCLUSIONS FROM MODELLING EXERCISE

The unvalidated model of particulate digestion and passage has been presented to permit speculation on possible nutrient implications of differential particle digestion and passage, but undoubtedly does not adequately represent the complexities likely to be of importance

in the RR of ruminants given a range of forage diets. In particular it does not distinguish between potentially-digestible and indigestible fibre, and is unlikely to describe the effect of plant chemical composition and anatomy on microbial attachment and digestion. Better description is required of: relationships of FSG and particle size with probability of rumination or passage; changes with time of FSG; the relationships between FPR of particle pools to that of fluid, and the importance of the 'raft' in the dorsal rumen in modifying the 'distribution coefficients' (Sutherland, 1987) which describe the sequestration of particles in the raft. Several general points are pertinent. First, increased rumination chewing and gut motility to enhance particle passage may be comparable in their effects on voluntary feed consumption, but will increase supply of digestible energy only if the rate of digestion is sufficiently high relative to FPR, so that particles flowing to the intestines have a low content of potentially-available fibre, unless enhanced fibre fermentation occurs in the caecum and colon. Intake may be substantially reduced by the presence of 'lag phase' LP of low specific gravity. Second, the value for animal production of mature forages with differing fragmentation patterns as described by rates of comminution of LP, extent of comminution, and passage rate of SP from the RR, is very dependent on the digestion rate applying to different particle pools. Thus the nutritive value of a forage that could be comminuted with some difficulty but which readily passed from the rumen after comminution would be determined largely by the rate of colonization and digestion of LP. Conversely, if the physical structure of LP impeded microbial colonization and fermentation, a forage which was rapidly comminuted during rumination but which slowly passed from the RR as MP and SP would be of greater nutritive value providing microbial colonization of SP was sufficient. The effect of fragmentation pattern on time available for microbial fermentation of lucerne (Table 5) highlights the importance of determining relevant physical and chemical factors which control rate and extent of particle breakdown. For roughage diets marginal in protein content, animals able to comminute the diet more rapidly and remove SP from the RR (such as the swamp buffalo (McSweeney & Kennedy, 1987)) may benefit from a greater digestible protein:energy ratio, despite perhaps a depression of fibre digestibility.

GENERAL CONCLUSIONS

The slow progress in achieving an adequate description of determinants of passage of particles from the RR stems from inadequate techniques for describing key particle characteristics, such as dimensions, buoyancy and 'age', together with an inadequate appreciation of the control of gut function by the central nervous system and the role of nutrient imbalances.

An increasing number of reports appearing in the literature is providing information pertinent to description of particle passage from the RR, but frequently these fail to include key factors such as FSG, fluid turnover rates, available cell-wall content of particles, or concentration of adherent microbes. It is hoped that growing awareness of such factors will encourage researchers to make appropriate measurements in future experiments or even to re-examine samples from previous experiments. In this way information could accumulate that would facilitate greater understanding of particle digestion and passage.

Such a search is not merely an academic exercise. Compounders of rations have already benefited from information indicating the increased availability of protein from soya-bean meal subjected to fine grinding to accelerate passage of protein to the small intestine (Netemeyer et al. 1980), and the potential to alter passage rate of digestion from the RR pharmacologically has been recently demonstrated (Froetschel et al. 1987).

However the greatest benefit can be expected to come in the development of a major new

research area: the tailoring of rumen microbes by genetic engineering to colonize and ferment plant fibre more rapidly. It is a common experience with ruminants fed on mature roughage that supplementary feeding, while increasing feed intake, depresses digestibility of the roughage. Any enhanced rate of fibre fermentation by superior microbes will presumably accelerate both rate of weakening of fibre and propulsion from the rumen. It is therefore clear that such research efforts must consider and achieve appropriate measurements on RR loads and passage rates of particles affected by superior microbes, and the reverse effect. Accordingly, more appropriate techniques and better characterization of particle kinetics should be given a high research priority.

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