

Factors affecting the nutritive value of kikuyu grass (*Pennisetum clandestinum*) — a review

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Abstract

Kikuyu grass, which occurs naturally on the highland plateau of east and central Africa, has been introduced to many countries, where it forms highly productive pastures. However, in many instances, its growth is restricted by a lack of cold and drought tolerance. The grass reproduces vegetatively and by means of seed. Since kikuyu produces stem material throughout the growing season its nutritive value is highly influenced by stage of regrowth. Kikuyu grows well when heavily fertilised with N, but accumulates nitrogenous compounds far in excess of animal requirements. These substances can have a negative impact on digestion and animal performance. Energy is a major limiting factor for milk production on kikuyu, due to a lack of readily digestible non-structural carbohydrates and a low digestibility of structural components. Kikuyu grass contains oxalic acid, which binds calcium, rendering it largely unavailable to the grazing animal. Kikuyu is deficient in sodium and prone to calcium: phosphate imbalances, and also to potassium: calcium plus magnesium imbalances. The grass produces allelopathic substances which may have a detrimental effect on the persistence of mixed pastures in which kikuyu is a component. Kikuyu poisoning and the correction of nutritional limitations by supplementation, manipulation of growth conditions and ecotype selection are discussed.

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Introduction

The nutritive value of a forage, as related to ruminants, may be regarded as the product of the intake of the forage and its digestibility, with intake being the more important of the two parameters (Mott and Moore 1969). Grasses have co-evolved with herbivores over a vast period of time, and their structure and chemical composition are the result of evolutionary pressure to survive as components of a specific ecosystem. In fact, most plants have developed structures and mechanisms which impede predation, and kikuyu grass (*Pennisetum clandestinum*) is no exception. The nutritive quality of kikuyu is unacceptably low, giving milk yields below 11 kg/cow/d (Reeves 1997) and is dictated by its unique morphology, physiology and chemical composition which could vary, to a greater or lesser extent, according to the growth stage and environmental conditions during growth. The effect of anti-predatory or anti-quality factors can, therefore, often be reduced by optimising grazing conditions through improved pasture management practices, by supplementing the grazing animal to correct deficiencies, or by breeding and selection. Selection against anti-quality factors may reduce the plant's ability to compete or survive in its normal habitat, but the benefits of the removal of anti-quality factors usually far outweigh the negative effect of reduced competitiveness, especially when the grass is grown in monoculture as a cultivated pasture. The present review aims to highlight those factors which reduce the nutritive value of kikuyu and discusses ways of correcting these limitations.

Origin and distribution

Kikuyu occurs naturally as a forest margin species on the highland plateau of central and east Africa (Kenya, Ethiopia, Uganda, Rwanda,

Zaire, Tanzania and the Congo) at altitudes of 1950–2700 m and a mean annual rainfall of 1000–1600 mm (Mears 1970). Its natural habitat consists of many elevated, high-moisture and low-temperature areas, separated by lower lying regions of dissimilar climate (Edwards 1937). Varying climatic conditions within its habitat, and in the marginal regions around it, are conducive to ecotype development. Edwards (1937) recognised 3 distinct landraces from Kenya, but many more races, differing in morphology and chemical composition, are likely to exist within its distribution range.

From its natural habitat, introductions were made to various countries where highly productive pastures have been established mainly for milk production. In 1910, Forbes collected a single stolon on the banks of Lake Naivasha, the highest of the lakes in the eastern part of the rift system in Kenya, and sent it to the Botanic Gardens in Pretoria. To the present author's knowledge, this material formed the basis of all kikuyu pastures in South Africa prior to the introduction of the seeding variety, Whittet. Lake Naivasha, situated about 100 km north-west of Nairobi, lies on an alluvium-covered plain in the valley floor, 1884 m above sea-level. The mean annual temperature is 18°C, with little fluctuation throughout the year. South African kikuyu therefore originated from a landrace at a relatively low, warm altitude.

Initially, kikuyu was introduced to Australia by means of seed obtained from the Congo (Breakwell 1923), but later introductions were made from Kenya (Mears 1970). Kikuyu was introduced into New Zealand, directly from east Africa or via Australia, during the early part of the 20th century. A comparison of the original naturalised kikuyu with high-altitude (1900–2800 m) ecotypes later imported from Kenya, showed that all the high-altitude Kenyan ecotypes were more vigorous than the original lines (Rumball and Lambert 1985). Introductions were also made to other countries such as Colombia and Hawaii.

Reproduction and genetics

Kikuyu grass is readily propagated vegetatively, forming long, vigorously growing stolons. Decapitation of the stolons gives rise to secondary stolons or, under certain circumstances, to short

culms bearing terminal spikes, each consisting of 2–5 sessile or shortly stalked spikelets. Due to the sessile nature of the inflorescence, it remains concealed within the leaf sheath of the terminal leaf of the culm. Only the long stigmas and anthers become exposed, usually at night, but soon wither in the heat of day. Due to their inconspicuous nature, kikuyu flowers may easily be overlooked.

The chromosome number of kikuyu is $2n = 36$ (Mears 1970). Conflicting views exist regarding its mode of reproduction. In many countries, the perception exists that kikuyu is reproduced only vegetatively, but the existence of bisexual and male-sterile (stamen absent) races has been established (Youngner 1961). A strong possibility of apomictic reproduction (the formation of viable seed without fertilisation) also exists. Apomixis is often unstable, causing apomictic species to be variable. As kikuyu originated in equatorial regions, it is unlikely that flower initiation is influenced by day length or temperature. Flowering is controlled by apical dominance, but ecotypes appear to vary in sensitivity to auxin. South African kikuyu appears to be highly apical-dominant and does not appear to flower in the pasture situation. However, an ecotype which readily sets viable seed was described from the Estcourt region in KwaZulu-Natal in 1956 (Edwards 1961). Similar ecotypes may exist unnoticed elsewhere in South Africa. In auxin-sensitive races, flowering can be induced by severe grazing or defoliation (Carr and Eng Kok Ng 1956). The kikuyu variety, Whittet, appears to be less sensitive to apical auxin production and flowers readily. Although most kikuyu in New Zealand has been assumed to be male-sterile, seed which is readily spread by means of the dung of grazing ruminants (Rethman 1989; Gardener *et al.* 1993), appears to have played a greater role in the spread of kikuyu than previously anticipated (Piggot and Morgan 1985). This may also be true of South African kikuyu, which raises questions about the diversity of indigenous kikuyu pastures.

Relatively few attempts have been made to improve kikuyu by breeding and selection. The agronomic performance of naturally occurring ecotypes can therefore be as good as, or even better in many respects than, the few ecotypes and commercial cultivars available at present. Kikuyu grass has spread over a wide range of extreme and stressful habitats and material from these areas can be expected to be rich in genes

for stress tolerance and other desirable characters which could be usefully employed in pasture improvement.

Soil and climate

Soil

In its natural habitat, kikuyu usually occurs on deep, lateritic red loams of volcanic origin (Mears 1970). Kikuyu thrives on well drained, fertile soils with a high nitrogen level, but can tolerate a moderate degree of water-logging and high salinity (Russel 1976). It does poorly on shallow, infertile soils and appears to be very sensitive to a lack of magnesium, phosphorus, potassium, sulphur, iron, copper and manganese, but less sensitive to a lack of calcium, boron, molybdenum and zinc (Cassidy 1972). Kikuyu is highly efficient in utilising soil phosphorus, but on virgin soils requires liberal amounts of phosphorus for pasture establishment (Miles 1986). It is tolerant of high soil acidity, with soil acid saturations of 60% having no significant effect on grass yield (Miles 1998). However, under these conditions, calcium uptake is impaired. If available, vast quantities of potassium are absorbed from the soil. Potassium in the growth medium has been shown to stimulate nitrate uptake in kikuyu (Marais *et al.* 1987). For optimum dry matter production, the annual nitrogen requirement of kikuyu ranges from 300–500 kg/ha, and should be applied as split dressings throughout the growing season.

Temperature

Low temperature has a marked beneficial effect on the nutritive value of temperate grasses by increasing the non-structural carbohydrate content of the plant. However, tropical species accumulate less non-structural carbohydrates, the concentration of which is also little affected by temperature variations. High temperature affects the maturation processes, leading to an increase in acid detergent fibre, cellulose, lignin and silica (Henderson and Robinson 1982) and, therefore, has a marked negative effect on digestibility. Low day temperatures (15°C) and high night temperatures (up to 30°C) decrease the growth rate and improve the digestibility of kikuyu (Ivory *et al.* 1974). The digestibility of kikuyu leaves appears to decrease

faster with increased growth rate than that of stems. Due to the high altitude of its natural habitat, the optimum growth temperature for kikuyu ranges from 16–21°C, which is lower than for most tropical grasses (Morrison 1969; Russel and Webb 1976). Metabolic processes in kikuyu grass are very sensitive to low temperatures. At temperatures below 10°C, photosynthesis is more severely suppressed than in tropical grasses such as *Panicum maximum*, *P. coloratum*, *P. milioides*, *P. repens* and *Setaria anceps* (Ito and Numaguchi 1989). Moderate frost will kill top growth, but stolons will remain unaffected. Growth of kikuyu is restricted if the maximum temperature drops below 21°C or the minimum temperature is less than 8°C (Ivory 1976; Colman and O'Neill 1978; Wilson 1985). According to Colman and O'Neill (1978) active growth of kikuyu still occurs at temperatures well below the accepted optimum for tropical grasses of 30–35°C. Growth in excess of 20 kg DM/ha/d was recorded at a mean day temperature of 13°C. However, in many situations, animal production on kikuyu is restricted in late autumn and early spring by a lack of herbage due to restricted growth at sub-optimal temperatures (Ivory and Whiteman 1978), emphasising the need for cold-tolerant ecotypes.

Moisture

A major advantage of C₄ over C₃ plants is their better drought resistance and water-use efficiency (Brown and Simmons 1979). Most C₄ plants also have a better heat tolerance, probably due to reduced photorespiration (Treharne and Nelson 1975). Kikuyu, however, evolved in a high rainfall region. South African kikuyu, in particular, developed on the banks of a lake. The annual rainfall requirement of kikuyu is estimated at 850–1269 mm (Russel and Webb 1976; Whiteman 1980), but conflicting data are available on its drought tolerance. Due to its deep root system in well drained soils, its drought resistance is often regarded as good. However, moisture stress is an important determinant of growth when temperature is non-limiting, and even a high evaporative demand can greatly reduce the growth rate of kikuyu. At low evaporative demands, of the order of 2 mm/day, 50% of the total available water in the upper soil horizon can be removed before growth is impaired. However, growth can be reduced by 61%, even on a wet soil, if the evaporative demand is only medium-

high (5 mm per day) (Murtagh 1988). In many instances, kikuyu production systems will benefit from more drought-tolerant kikuyu landraces.

Solar radiation

Kikuyu is less shade-tolerant than many other grasses and contains less leaf chlorophyll on a fresh weight basis than *Panicum maximum*, *Axonopus compressus* and *Stenotaphrum secundatum* (Ludlow *et al.* 1988). Although the conversion efficiency of solar energy to fixed carbon dioxide is usually higher for C₄ than for C₃ plants, the annual light energy conversion under field conditions for kikuyu has been estimated at 1.7%, compared with about 2.4% for perennial ryegrass (Cooper 1970).

Plant morphology

Kikuyu grass is a stoloniferous perennial producing stem material throughout the growing season, rooting strongly at the nodes. The proportion of green leaf declines, while the proportion of stem and dead material increases, after the 4.5 leaf per tiller growth stage (Reeves *et al.* 1996). Leaf-blade tissue of grasses is usually of higher nutritive value than stem tissue and is consumed in larger quantities by both sheep and cattle. Grass leaves appear to have a faster rate of passage than stem tissue, even if their digestibilities are the same (Poppi *et al.* 1980). Plant maturity is therefore a major factor affecting the leaf:stem ratio and nutritive value, which normally declines as the leaf:stem ratio decreases. The nutritive value of immature grass stems is usually high (Minson 1990), but the quality tends to decrease rapidly as the plant matures. Low digestibility can be attributed to the lignification of xylem cells and a high concentration of sclerenchyma cells and vascular bundles. Although stem parenchyma cells are readily digestible, the surrounding lignified ring poses the greatest limitation to breakdown in the rumen (Akin *et al.* 1990). Since the nutritive quality of the stem tissue of warm-season grasses is much more variable than the quality of leaf-blade material, there is merit in focussing on the stem in forage quality improvement programs (Nelson and Moser 1994).

Henning *et al.* (1995) found a 30-day grazing cycle on kikuyu to give optimal milk yields. However, milk yields per cow declined between

December and May by 38%. The milk potential of kikuyu pasture appears to range from about 12 kg/cow/d during spring to 5–8 kg/cow/d in autumn (Bredon and Stewart 1979). Henning *et al.* (1995) suggested that the decline could be due to a drop in digestibility and voluntary intake, while Dugmore and Du Toit (1988) suggested that factors such as a high non-protein nitrogen content or mineral imbalances could be involved. Due to the decline in quality of kikuyu during autumn, kikuyu foggage is, at best, a maintenance feed for dry animals (Barnes and Dempsey 1993). Since the growth rate of kikuyu is controlled by climatic conditions, the grazing cycle should be based on the morphological stage of regrowth and not on a fixed regrowth period (Reeves *et al.* 1996).

A comparison of New Zealand lines and the Australian seeding cultivars, Whittet, Breakwell and Noonan, showed that Whittet was the highest yielding cultivar in terms of both total dry matter and leaf material (Piggot and Morgan 1985) and was more palatable to sheep than New Zealand ecotypes (Dalebrook *et al.* 1985).

Chemical composition

Nitrogenous compounds

High producing dairy cows have a requirement for protein at the small intestine greater than that which can be supplied by microbial protein synthesis in the rumen (Clark 1975). This high requirement is usually only met by a supply of rumen non-degradable protein. Forage leaf protein is highly soluble and is readily deaminated in the rumen to form ammonia, much of which is absorbed into the bloodstream, and subsequently excreted as urea. Important prerequisites for satisfactory protein metabolism are the presence of readily available energy in the rumen and adequate amino acid pools for meat, milk or wool production. Ideally, 1kg of feed should contain 10–11 MJ of metabolisable energy and not more than 22–26 g of nitrogen or 138–161 g of crude protein. If this ratio is exceeded, milk production is reduced (Emmans 1994) and the animal is adversely affected due to the loss of energy used in the liberation of excess ammonia in the rumen and its detoxification in the liver (Figure 1). Kikuyu appears not to contain condensed tannins which could reduce ammonia formation in the rumen (Jackson *et al.* 1996a).

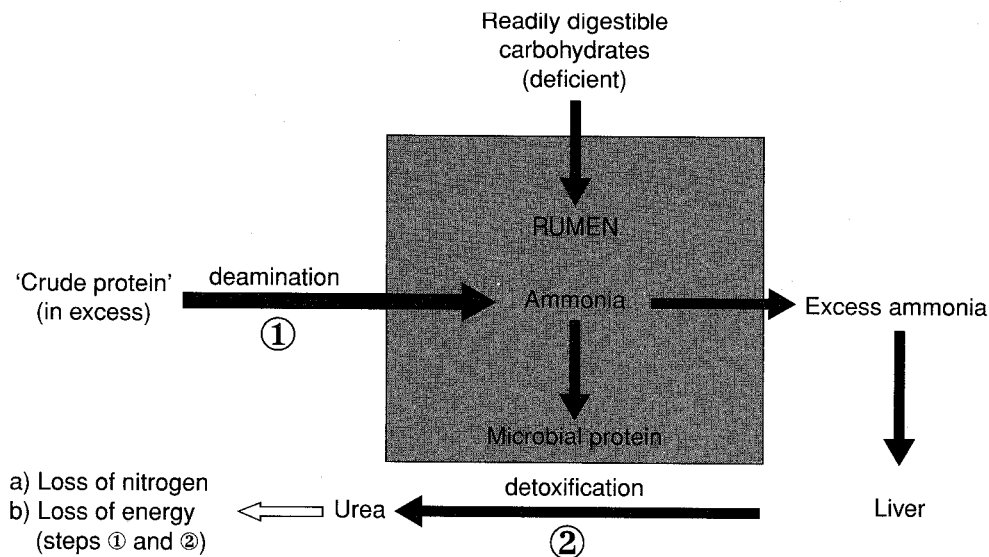


Figure 1. Fate of excessive nitrogen in the rumen.

The dry matter yield of kikuyu shows an upward trend, even at annual nitrogen applications exceeding 900 kg/ha (Marot and Miles 1999). Kikuyu is therefore often heavily fertilised with nitrogen in order to increase DM yield, leading to nitrogen concentrations ('crude protein') far in excess of animal requirements (Van der Grinten *et al.* 1992). The nitrogen concentration in the last fully-expanded lamina from a well fertilised kikuyu sward increased significantly with increasing temperature and growth rate and varied from 37–53 g/kg DM (Murtagh 1990). Nitrogen concentration is also affected by plant maturity. Total nitrogen concentrations ranging from 13.6–41.1 g/kg DM have been reported (Table 1). The nitrogen concentration of kikuyu has been shown often to be higher than that of other grass species. Kemp (1975) recorded concentrations of 24.8 g/kg DM in kikuyu compared with 22.2 and 23.1 g/kg DM in *Setaria* and *Paspalum*, respectively, at comparable nitrogen fertiliser levels and conditions of growth. In a comparative study of 14 grasses of tropical origin and 6 grasses of temperate origin which ranged in nitrogen concentration from 22.8–32.9 g/kg DM, kikuyu had the highest nitrogen content (Forde *et al.* 1976). Furthermore, a study of the response of 9 tropical grasses to nitrogen fertiliser showed that the mean seasonal nitrogen concentration was highest (243 g/kg DM) in kikuyu grass and lowest (191 g/kg DM) in *Chloris gayana*, with inter-

mediate concentrations in *Digitaria decumbens*, *Setaria sphacelata*, *Panicum maximum*, *Brachiaria decumbens* and *Paspalum plicatulum* (Cook and Mulder 1984). High nitrogen levels in kikuyu give rise to poor protein metabolism and animal production (Marais *et al.* 1990).

The voluntary intake of digestible organic matter is lower on kikuyu fertilised with high (230 kg/ha) than with low (57.5 kg/ha) nitrogen applications (Minson 1973). Steers on kikuyu pasture appear to select herbage according to its protein concentration (Dugmore *et al.* 1991). At low nitrogen concentrations, animals tend to select herbage of higher nitrogen concentration, while at average nitrogen concentrations above about 22.4 g/kg DM, animals select for lower concentrations of nitrogen in the herbage. Soto *et al.* (1980) showed that the dry matter intake of kikuyu grown in Colombia was positively correlated with level of nitrogen application and plant nitrogen concentration, which ranged from 21.4–23.2 g/kg DM. Kikuyu pasture grazed 29, 30 and 40 days after nitrogen fertilisation had nitrogen concentrations of 46.4, 40.0 and 38.4 g/kg DM, respectively, with corresponding crude protein degradability in the rumen of 74, 55 and 57% (van der Merwe *et al.* 1998). This suggests that high concentrations of nitrogen in young kikuyu regrowth may result in excessive rumen ammonia which could be lost as urea via the urine and milk.

Table 1. Published values for nutrient composition of plant fractions of kikuyu grass.

Regrowth age/ plant fraction	Composition ¹							Reference
	N	TNC	NDF	ADF	Lignin	Nitrate-N	Oxalate	
	(g/kg DM)							
49-day regrowth	27.0			303				Jeffery (1971)
51-87-day								
leaf	15.4		680	323	29			Laredo and Minson (1973)
stem	13.6		706	360	50			
80-130 mm	17.1	40.3		330				Joyce (1974)
200-300mm	27.0	27.4		329				
Late season regrowth	23.0		590	310	60			Johnson and Pezo (1975)
40-day, hay	19.0				47			Laas <i>et al.</i> (1981)
42-65-day								Ishizaki <i>et al.</i> (1981)
oesophageal	23.5		635	296				
plucked sample	17.8		688	326				
clipped sample	15.8		710	344				
21-day								Marais <i>et al.</i> (1987)
low N	15.2					0.6		
high N	20.0					8.0		
28-day								Marais (1990a)
leaf	41.1					1.7	13.3	
stem	30.0					6.8	3.9	
28-day regrowth	25.3	66.7			48	4.0		Marais (1990b)
21-day								Marais and Figenschou (1990)
leaf		102.9						
stem		112.6						
Leaf	26.6	53.0	581					Jackson <i>et al.</i> (1996b)
Plucked sample	33.3	53.7	603	231		0.3	6.8	Reeves <i>et al.</i> (1996)
42-day								Marais <i>et al.</i> (1997)
leaf							24.4	
stem							9.8	
28-day plucked sample	32.0	59.0						Fulkerson <i>et al.</i> (1998)
Oesophageal sample	29.3		741	378				Brand <i>et al.</i> (1999)
Range	13.6-41.1	27.4-112.6	581-741	231-378	29-60	0.3-8.0	3.9-24.4	

¹N — nitrogen; TNC — total non-structural carbohydrates; NDF — neutral detergent fibre; ADF — acid detergent fibre.

The degradability of nitrogen may be linked to its solubility in the rumen. Aii and Stobbs (1980) showed that kikuyu had a nitrogen solubility of 35.1% compared with 26.3% and 43.3% for *Setaria anceps* and *Brachiaria mutica*, respectively.

The amino acid concentrations in kikuyu grass are similar to those in ryegrass, except for methionine and cysteine, which are 68 and 57% lower in kikuyu (Reeves *et al.* 1996). After rumen digestion, histidine is regarded as the first limiting amino acid for milk production on kikuyu, followed by lysine and methionine (Dennison and Phillips 1983). The rumen degradability of protein in forage grasses and the loss of amino nitrogen can be reduced by selecting for plants with a higher-than-average sulphur amino acid content. Sulphur amino acids form disulphide bridges, increasing the stability of proteins and reducing their digestibility in the rumen.

The nitrate concentration of kikuyu increases rapidly with an increase in the total nitrogen of the plant (Whitney 1974; Marais 1990b; Reeves *et al.*

1996). It accumulates when uptake exceeds its assimilation into proteins. Since accumulation occurs mainly in stem tissue (Marais *et al.* 1987), plants with a high leaf: stem ratio are less likely to contain excessive amounts of nitrate. Concentrations of nitrate nitrogen in high-nitrogen kikuyu may reach 8.0 g/kg DM (Table 1). Nitrate, as such, is relatively non-toxic, but is readily reduced to ammonia by microbial action in the rumen, with toxic nitrite as an intermediate (Figure 2). Nitrite absorbed into the blood stream reacts with haemoglobin to form methaemoglobin which is unable to bind oxygen, resulting in oxygen starvation (cyanosis) of the tissue and, in severe cases, death (Marais 1997). On prolonged nitrate intake (over several weeks) by ruminants, methaemoglobin concentrations gradually decline, indicating the adaptation of the rumen microbial population to a more efficient reduction of nitrite. The presence of readily digestible carbohydrates in the digest also tends to ameliorate the harmful effects of nitrite (Wright and Davison 1964). Kikuyu, with its low carbohydrate reserves, would therefore provide

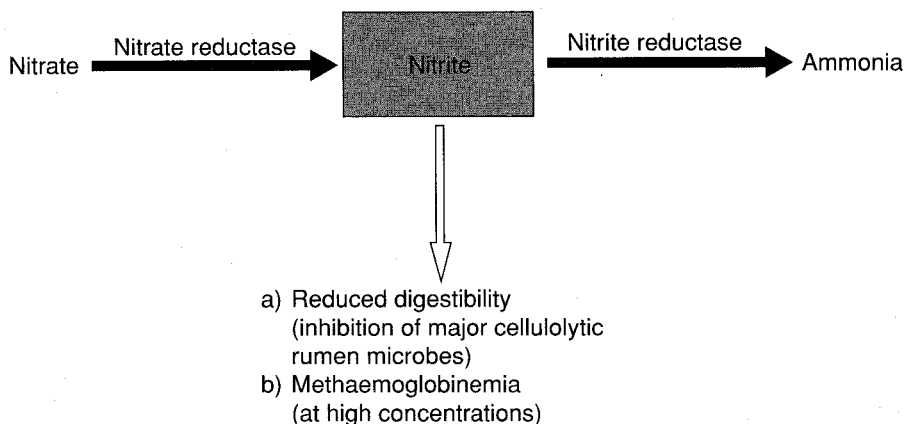


Figure 2. Reduction of nitrate in the rumen.

little protection in this respect. Nitrite derived from high-nitrate pastures markedly reduces digestibility *in vitro* (Marais *et al.* 1988). The growth in pure culture of 3 of the 4 major cellulolytic bacteria found in the rumen, *viz.* *Ruminococcus flavefaciens*, *Butyrivibrio fibrisolvens* and *Bacteroides succinogenes*, is reduced in the presence of nitrite. Due to the extreme sensitivity to nitrite of these key microbes in the rumen, animal performance could be affected long before clinical symptoms of nitrite toxicity in the animal become apparent. Few deaths attributable to nitrite poisoning on kikuyu have been reported. However, the impact of subclinical concentrations of nitrite on digestion and animal performance may be large, but is difficult to assess.

The accumulation of excess concentrations of nitrate in kikuyu pastures can readily be prevented by applying more moderate levels of nitrogen fertiliser and avoiding large single applications, especially to grazed pastures subjected to the recycling of nitrogen through urine and faeces.

Carbohydrates

The grazing ruminant derives energy mainly from non-structural and structural carbohydrates in forage. Energy is often the first limiting factor for milk production in dairy cows, even under ideal conditions (Moir *et al.* 1979; Van Vuuren 1993). According to Fulkerson *et al.* (1998), the metabolisable energy requirement for maintenance of a 600 kg Friesian cow with a milk production of 23 L/d is 208 MJ/d. At an estimated intake of 17.5 kg DM/cow/d, a metabolisable energy

concentration in the ration of 11.9 MJ/kg DM is required. However, these workers reported a mean metabolisable energy value for kikuyu of only 8.5 MJ/kg DM, based on an organic matter digestibility of 645 g/kg DM. Reported organic matter digestibility values for kikuyu are often lower than 645g/kg DM (Table 2).

Animal production on kikuyu can be improved by energy supplementation. Even on well-managed kikuyu pasture, milk production is restricted to 13–16 L/Friesian cow/d (Reeves *et al.* 1996). Milk production of Jersey cows grazing kikuyu at a stocking rate of 4.94/ha can be increased by up to 20% by supplementing the animals with crushed oats as an energy source (Colman and Kaiser 1974). Similarly, Friesian cows grazing kikuyu pasture and supplemented with barley grain at 3 kg/cow/d had a milk production of 17.9 kg/d, compared with 14.7 kg/d for control animals on kikuyu pasture only (Hamilton *et al.* 1992). Maize or molasses supplementation significantly increased the growth rate and final carcass mass of lambs (Van Ryssen *et al.* 1976) and Hereford cross calves (Kaiser 1975) on kikuyu pasture. A limitation of energy supplementation is that ruminants tend to substitute supplement for grass, thus depressing forage intake (Campbell *et al.* 1969; Minson 1990). Ideally, the non-structural carbohydrate content of kikuyu should be increased, thereby improving the palatability and intake of the grass.

Chemical analysis of kikuyu indicates a severe protein: energy imbalance, caused by a lack of readily digestible energy in the form of non-structural carbohydrates (Joyce 1974; Mears and

Table 2. Published digestibility and dry matter intake values of kikuyu grass.

Regrowth age	Plant fraction	DM intake (g/kg W ^{0.75} /d)	OMD ¹ (g/kg DM)	DMD ² (g/kg DM)	Reference
52-day	Chaff			619	Minson and Milford (1968)
Not specified				633	Katiyar and Ranjhan (1969)
Not specified			498–535		Campbell <i>et al.</i> (1971)
49-day & older	Regrowth			646	Jeffery (1971)
28-day	Regrowth	48.0	623	620	Minson (1972)
98-day	Regrowth	45.2	484	474	
51-day	Leaf	63.1		574	Laredo and Minson (1973)
	Stem	45.9		577	
87-day	Leaf	44.3		450	
	Stem	29.0		503	
21-day	Leaf			686	Ivory <i>et al.</i> (1974)
	Stem			671	
80–130 mm	Regrowth	54.3		614	Joyce (1974)
200–300 mm	Regrowth	53.5		614	
Not specified				716	Van Ryssen <i>et al.</i> (1976)
42-day	Regrowth		595		Andrews and Crofts (1979)
39-day	Regrowth			475	Soto <i>et al.</i> (1980)
50-day	Regrowth			562	
78-day	Regrowth			604	
42–65-day	Oesophageal		729	749	Ishizaki <i>et al.</i> (1981)
	Plucked sample		628	650	
	Clipped sample		600	626	
21–28-day	Regrowth		607		Dugmore and Du Toit (1988)
Not specified	Leaf		671		Jackson <i>et al.</i> (1996b)
Not specified	Plucked sample		734		Reeves <i>et al.</i> (1996)
Not specified	Oesophageal sample	20.7	623		Brand <i>et al.</i> (1999)
Range		20.7–63.1	484–734	450–749	

¹OMD — organic matter digestibility.²DMD — dry matter digestibility.

Humphreys 1974). The optimal non-structural carbohydrate: degradable protein ratio in the diet for rumen microbial synthesis is about 2:1 (Hoover and Stokes 1991). A ratio of only 0.6:1 was obtained for kikuyu (Fulkerson *et al.* 1998). Non-structural carbohydrates, forming part of the plant cell content, range from 27.4–112.6 g/kg DM in kikuyu (Table 1). The soluble sugar concentration in 14 grasses of tropical and 6 of temperate origin ranged from 28.3–88.5 g/kg DM (Forde *et al.* 1976). Values for temperate grasses were generally higher than for the tropical grasses. Kikuyu grass had a soluble sugar concentration of only 38.2 g/kg DM. Non-structural carbohydrates in kikuyu leaves consist mainly of sucrose (99 g/kg DM), with small amounts of glucose (2.0 g/kg DM) and fructose (2.3 g/kg DM) (Marais and Figenschou 1990). The deficiency in readily digestible carbohydrates is likely to be aggravated by diurnal fluctuations in the plant. Marais and Figenschou (1990) reported a day to night variation in non-structural carbohydrate concentration for 3-week kikuyu leaf regrowth from about 100 g/kg to 60 g/kg DM, while 3-week stem tissue varied diurnally from 126 g/kg to 90 g/kg DM. Similar trends were

obtained by Reeves *et al.* (1996). These results show that kikuyu grass, and the leaf material in particular, is very low in non-structural carbohydrates for a large part of the day, *i.e.* from after sunset to mid-morning, during which a considerable amount of grazing can be expected, especially when day temperatures are high.

Non-structural carbohydrates also have a marked effect on the regrowth potential (Alberda 1966), sward persistency (Thomas and Norris 1981) and palatability of grasses (Bailey 1965; Beever *et al.* 1978) and may reduce the plant's susceptibility to drought stress (Munns and Weir 1981). An improvement in the non-structural carbohydrate status of kikuyu grass should therefore benefit the plant and have a positive effect on intake and protein metabolism in the rumen.

Plant cell walls are an important source of energy for the ruminant and consist mainly of the structural carbohydrates, cellulose and hemicellulose, and a smaller amount of lignin. Digestibility of structural carbohydrates and the amount of energy released depend largely on the degree of lignification of the tissue and tend to decline as plant age increases (Said 1971). The digestibility of kikuyu leaf is generally higher than that of

stem tissue (Marais *et al.* 1992). A relatively small amount of lignin can render a large amount of cell wall carbohydrate indigestible. A strong, negative correlation exists between lignin concentration and digestibility of tropical forages (Ford *et al.* 1979). The lignin levels in kikuyu can be as high as 60 g/kg DM in stemmy late-season kikuyu (Table 1). In contrast, the lignin concentration in *Lolium perenne* ranges from 28–35 g/kg DM (Butler and Bailey 1973). The *in vitro* digestibility of 14 grasses of tropical and 6 of temperate origin ranged from 576–749 g/kg DM (Forde *et al.* 1976). *Lolium perenne* was the most digestible, while kikuyu had a digestibility of 673 g/kg DM. The apparent digestion of organic matter in the digestive tract and microbial nitrogen flow from the rumen decrease with increasing maturity of kikuyu (Hart and Leibholz 1990). Colombian-grown kikuyu showed an increase in voluntary dry matter intake and digestibility with a decrease in lignin concentration (Soto *et al.* 1980). Brown-midrib mutations, effectively reducing the lignin level in plants, have been introduced in *Pennisetum glaucum*, suggesting that it might be possible to reduce the lignin in kikuyu in a similar way. Unfortunately, the brown-midrib trait appeared to be linked to reduced plant yield (Cherney *et al.* 1991). Hacker (1982) improved the digestibility of leaf material of *Digitaria milanjiana* by 5 digestibility units by selecting for a higher digestibility, which was correlated with reduced lignin and cell wall concentrations. By screening kikuyu landraces for reduced lignin, it should be possible to improve the digestibility and energy production in the rumen.

A strong, negative correlation often exists between neutral detergent fibre (NDF), or cell wall concentration, and digestibility of grasses (Moore and Mott 1972). Tropical grasses generally have higher NDF levels than temperate grasses. The NDF concentration in *Lolium perenne* was 546 g/kg DM, compared with 657 and 572 g/kg DM in the tropical grasses, *Chloris gayana* and *Setaria splendida*, respectively, grown under similar conditions (McLeod and Minson 1974). The NDF concentrations in kikuyu grass range from 581–741 g/kg DM (Table 1). According to Wilson *et al.* (1976), kikuyu resembles temperate species in having relatively low NDF concentrations and should, theoretically, have digestibilities similar to those of temperate grasses. However, the dry matter

digestibility was found to be similar to those of other tropical grasses (Butterworth 1967), and lower than that of temperate species at equivalent stages of growth (Mears 1970). The dry matter digestibility of kikuyu ranges from 450 g/kg DM in the leaves of 87-day regrowth to 749 g/kg DM in an oesophageal sample of 42–65-day regrowth (Table 2).

NDF concentration is considered to be the laboratory measure most closely correlated with voluntary intake by the ruminant. Voluntary dry matter intake of kikuyu does not appear to exceed 63 g/kg $W^{0.75}$ per day (Table 2), while that of perennial ryegrass ranges from 62–78 g/kg $W^{0.75}$ per day (Minson 1990). The NDF concentration in low quality forages such as kikuyu is considered to be an important factor restricting dry matter intake of cows on pasture. Milk production is maximised when NDF intake is equivalent to 1.2% of the live mass of the animal (Mertens 1985). The NDF intake for kikuyu was shown to be as high as 1.4%, and that of a ryegrass-clover pasture only 1.0% of the live mass (Fulkerson *et al.* 1998). However, these authors pointed out that the interpretation of the results is complicated by the fact that the chemical composition of the NDF fractions may have differed.

Many regressions have been published for predicting dry matter digestibility and organic matter digestibility of grasses from acid detergent fibre (ADF) values. Negative correlations are usually found, but the prediction error is often large (Minson 1982). An ADF concentration of 210 g/kg DM in the ration is recommended for high-producing dairy cows (NRC 1989). McLeod and Minson (1974) reported an ADF concentration in *Lolium perenne* of 258 g/kg DM. However, ADF levels in existing kikuyu pastures are usually much higher, reaching values of 378 g/kg DM (Table 1). Although kikuyu grass contained significantly lower concentrations of NDF and ADF than bana grass (*Pennisetum purpureum* × *P. americanum*), its NDF disappearance from nylon bags in the rumen and *in vitro* digestible organic matter did not differ from that of bana grass (Köster *et al.* 1992). Organic matter intake of kikuyu was also significantly lower than that of bana grass.

The hemicellulose concentrations in *Lolium perenne* and *Pennisetum typhoides* are 30–40% lower than the cellulose concentrations, which is typical for both panicoid and festucoid grasses. However, in this respect, kikuyu is atypical, in that hemicellulose is equal to, or slightly lower

than the cellulose (Kamstra *et al.* 1966; Bailey and Hunt 1973). Soto *et al.* (1980) obtained hemicellulose values 20–50% higher than the cellulose in kikuyu grown in Colombia and showed that these hemicellulose values increased with increasing nitrogen applications and stage of regrowth, while cellulose concentrations showed less variation. These workers also showed that the digestibility of the hemicellulose was 15–23% higher than that of the cellulose and that the digestibility of the hemicellulose increased with increasing nitrogen application and stage of regrowth. Similarly, high hemicellulose values were obtained for kikuyu grown in Peru (Johnson and Pezo 1975). Hemicellulose concentration could, therefore, be an important parameter for selection or screening landraces for improved digestibility.

Oxalic acid — calcium interaction

Kikuyu grass belongs to one of the genera of tropical panicoid grasses accumulating oxalic acid (Marais 1997). Due to its interference with energy metabolism (Young and James 1988), and the precipitation of oxalate crystals in renal tubes, oxalic acid has been shown to cause acute toxicity in cattle consuming pasture with a high oxalate concentration (69 g/kg DM) (Seawright *et al.* 1970) (Figure 3). However, ruminants readily adapt to oxalate-containing forage due to the proliferation of a rumen obligate anaerobe,

Oxalobacter formigenes, which converts oxalate to harmless formate and carbon dioxide (Allison *et al.* 1977). Acute toxicity of adapted ruminants on kikuyu is therefore unlikely, as the oxalate level in kikuyu is a relatively low 3.9–24.4 g/kg DM (Table 1).

A more insidious effect of oxalic acid is to render forage calcium unavailable to the grazing animal. Oxalic acid forms complexes with many elements to form oxalates. Soluble salts are formed with monovalent metals such as potassium and sodium, but divalent cations form highly insoluble salts due to their 5-membered chelate ring structures (Figure 3). Of all the divalent cations, calcium forms the most stable and least soluble chelate (solubility 0.0086 g/L at 25°C) (Hodgkinson 1977). Most forages contain sufficient calcium for animal production (Minson 1990). However, due to the low solubility of calcium oxalate, extremely little soluble calcium can exist in forages in the presence of oxalic acid. Because of its low solubility, the calcium in calcium oxalate is poorly available to the grazing herbivore, passes through the digestive tract and is eliminated in the faeces. Cymbaluk *et al.* (1986) pointed out that certain prairie forages with moderate amounts of oxalate (13–18 g/kg DM) could cause subclinical bone diseases. Oxalate-producing tropical grasses such as kikuyu have been responsible for many of the reported incidences of hypocalcaemia in herbivores (Elphinstone 1981; McKenzie 1985). The

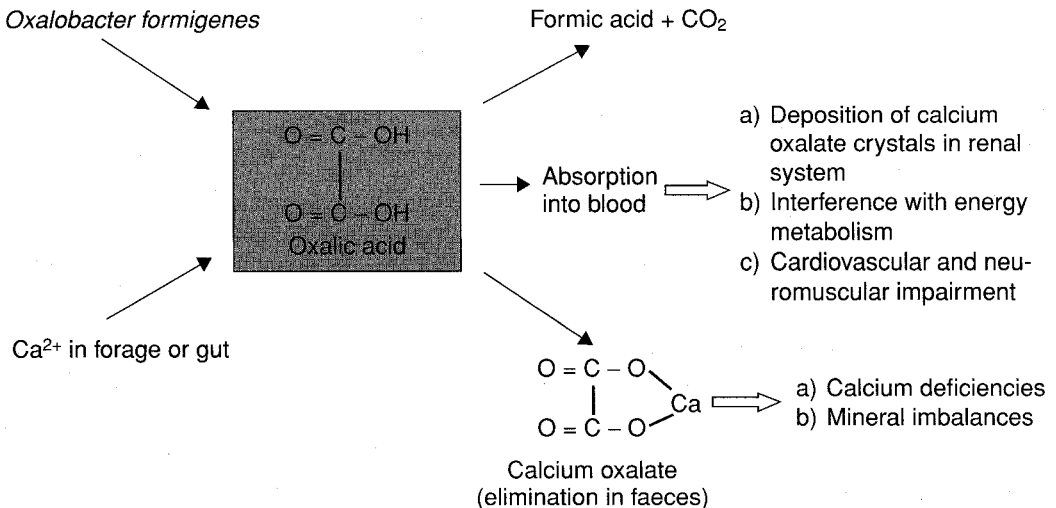


Figure 3. Fate of oxalic acid in the digestive tract.

oxalate in kikuyu could, theoretically, bind all the calcium in the grass (Marais 1990a). The availability of calcium from calcium oxalate crystals in kikuyu and other plants is further reduced by the crystals' specific association with poorly digestible tissue, such as the xylem, phloem, cambium, mesophyll or epidermis (Franceschi and Horner 1980; McKenzie and Schultz 1983). The availability to animals of the calcium in calcium oxalate also depends on the type of animal. Pigs appear to be able to utilise up to 80% of the calcium (Brune and Bredehorn 1961). However, horses appear to be unable to utilise calcium bound to oxalic acid in grasses (Blaney *et al.* 1981; McKenzie and Schultz 1983) and readily contract nutritional secondary hyperparathyroidism, a well known calcium deficiency disease, if confined to oxalate-containing pastures for a period of several months.

The total oxalate content of kikuyu appears to vary considerably, but the factors affecting the concentration are not known. Increasing the calcium concentration in the growth medium increased the insoluble: soluble oxalate ratio only, while the total oxalate content remained relatively constant (Marais *et al.* 1997). Minerals such as sodium, potassium and nitrogen in the growth medium do not appear to affect oxalate concentrations (Williams 1987). Observed differences in oxalate content are likely to be genetically controlled.

Minerals

It is generally assumed that if the soil mineral status is adequate for forage production, forages should contain sufficient minerals for animal production. This does not apply to sodium and calcium in kikuyu pasture and can lead to serious mineral imbalances in ruminants grazing kikuyu.

Most of the calcium in the body is present in the form of bone, which acts as a reserve to maintain a relatively uniform blood calcium concentration. Only 0.33% of total body calcium occurs in the blood and is involved in vital functions such as blood clotting, neuromuscular excitability, enzyme activity and membrane permeability (Minson 1990). A prolonged calcium deficiency causes a softening and weakening of the bone structure, due to the remobilisation of calcium reserves (Miller 1979), and reduces voluntary feed intake (Field *et al.* 1975), growth (Benzie *et al.* 1960) and milk production

(McDowell 1992). The recommended calcium and phosphorus concentrations in the feed consumed by a 600 kg cow producing 23 L of milk per day are 5.4 g/kg and 3.4 g/kg DM, respectively (NRC 1989), giving a calcium: phosphorus ratio of 1.6:1. Fulkerson *et al.* (1998) reported Ca: P ratios in kikuyu of 0.9:1 in summer-autumn and 2.5:1 in early spring, not considering the binding of calcium by oxalate. It is noteworthy that the reproductive performance of a number of commercial dairy herds on kikuyu pastures in Australia has been reduced as a result of calcium deficiencies (Reason *et al.* 1989).

In South Africa, the growth of kikuyu is insensitive to liming and near-maximum yields can be obtained under extreme soil acidity (Miles 1986). Although kikuyu grass grows well on acidic soils, calcium deficiencies are aggravated by the antagonistic effect of soluble aluminium on calcium uptake and translocation (Awad *et al.* 1976). In the North Coast region of New South Wales, liming increased kikuyu dry matter yields and the concentrations of calcium, phosphorus and nitrogen in plant tops (Awad and Edwards 1977). Recorded values for calcium in kikuyu range from 0.9–5.4 g/kg DM (Table 3). The calcium concentration in kikuyu leaf lamina was shown to be about twice that in stem tissue (Marais *et al.* 1992). As kikuyu matures and the leaf: stem ratio decreases, the calcium level in the plant can be expected to decline. Under acidic soil conditions the calcium concentration in kikuyu is rarely above 2 g/kg DM, all of which is likely to be bound by the oxalic acid in the grass.

Sodium is the main cation in the extracellular fluid of ruminants and not only plays a major role in the maintenance of membrane potentials, osmotic pressure and the transmission of nerve impulses, but is also required for the maintenance of a healthy rumen microbial population. A sodium: potassium ratio in excess of 15:1 in the saliva is essential for normal health. The sodium level in the blood is kept static by control mechanisms regulating sodium loss in the urine and faeces, or by drawing on the large sodium pool in the rumen, which is usually sufficient to meet the sodium requirements of the animal for many months. A sodium concentration of 1.5 g/kg DM of dry forage should meet the production requirements of most ruminants (ARC 1980). Plants differ greatly in their capacity to absorb and transport sodium to their leaves and are accordingly classified as natrophiles and natrophobes.

Table 3. Published macro-mineral composition of kikuyu grass.

Regrowth age	Plant fraction	Composition ¹ (g/kg DM)					Reference
		P	Ca	K	Mg	Na	
28-day		2.4	5.0	15.0	4.1		Gomide <i>et al.</i> (1969)
84-day		2.1	4.3	9.3	3.4		
80–130-day		3.6	4.4	21.8	2.5	3.5	Joyce (1974)
200–300-day		3.8	4.9	19.0	3.2	4.7	
Not specified		3.1	3.5	36.6	4.0	0.3	Kaiser (1975)
70 days after planting		1.5–4.0	0.9–6.6		2.7–4.1		Awad <i>et al.</i> (1976)
28-day			1.5–6.2	16.5–37.0	1.6–2.6		Awad <i>et al.</i> (1979)
42–65-day	Oesophageal	3.5	3.4	26.3	2.4	5.4	Ishizaki <i>et al.</i> (1981)
	Plucked sample	2.9	3.3	26.5	3.1	1.3	
	Clipped sample	2.9	3.3	28.7	3.3	1.2	
Not specified						0.4	Smith (1981)
Not specified			5.1–7.9				Laredo <i>et al.</i> (1983)
Not specified	Short grass	2.7	3.6		3.6		Hughes <i>et al.</i> (1988)
	Long grass	2.8	3.9		3.8		
Not specified	Rainy season	2.6	3.2	28.1	2.2	0.3	Pastrana <i>et al.</i> (1990)
	Dry season	1.7	3.7	16.8	2.3	0.2	
21–28-day		3.2–3.7	2.3–3.1	33.8–42.4	2.5–3.3	0.2–0.5	Miles <i>et al.</i> (1995)
Plucked sample		3.1	3.1	30.7	2.2	0.2	Reeves <i>et al.</i> (1996)
28-day		2.8	4.2	29.0	2.9	0.9	Fulkerson <i>et al.</i> (1998)
Range		1.5–4.0	0.9–5.4	9.3–42.4	1.6–4.7	0.2–5.4	

¹P = phosphorus; Ca = calcium; K = potassium; Mg = magnesium; Na = sodium.

Kikuyu, a natrophobe, is incapable of providing enough sodium for grazing animals, even when the soil contains sufficient sodium (Smith 1981).

The sodium concentration in grasses ranges from 0.05–21.3 g/kg DM with a mean of 2.2 g/kg DM for values cited in the scientific literature (Minson 1990), while that of kikuyu usually ranges from 0.2–5.4 g/kg DM (Table 3). Since the sodium concentration in milk is maintained at a constant level, regardless of dietary sodium intake (Murphy and Plasto 1973), lactating animals are more susceptible to sodium deficiencies in the diet than non-lactating animals. A sodium deficiency depresses the appetite, growth rate and milk production of the ruminant (Minson 1990) and is implicated with bloat, due to the buffering properties of sodium in the rumen. Supplementing cows on kikuyu pasture with sodium chloride increased milk production by 1.2 kg per cow per day (Davison *et al.* 1980). The improvement in milk production has been attributed to the direct effect of sodium, or through its effect of increasing dry matter intake.

Tropical grasses exhibit a greater genetic variation in sodium concentration than temperate species (Minson 1990). Lines low in sodium appear to have evolved in arid regions, while high-sodium ecotypes are found in coastal areas

with a high rainfall (Hacker *et al.* 1985). Joyce (1974) reported sodium values of 3.5–4.7 g/kg DM in kikuyu grass grown on Te Kopuru sandy soils at Dargaville Experimental Station in New Zealand. These extremely high values could indicate a high-sodium ecotype of kikuyu.

Mineral imbalances may seriously affect animal performance, especially during lactation, when animals have high mineral demands (Spears 1991). Phosphate and magnesium in kikuyu grass range from 1.5–4.0 g/kg and 1.6–4.7 g/kg DM, respectively (Table 3). Miles *et al.* (1995) showed that the calcium concentration decreased while phosphate increased in mid-summer, often giving calcium:phosphorus ratios of 0.4:1–0.5:1, which are well below the critical limits (2:1–1:1). Potassium concentrations in kikuyu are well in excess of animal requirements (0.9% of dietary DM) and range from 9.3–42.4 g/kg DM (Table 3) and could seriously inhibit calcium and magnesium uptake by the plant. This results in potassium:calcium plus magnesium molar ratios ranging from 2.19–3.15. The safety threshold of 2.2 is therefore often exceeded, making animals on kikuyu vulnerable to milk fever or hypomagnesaemic tetany, a serious disease of ruminants caused by a deficiency of magnesium and/or an excess of

potassium in the herbage (Kemp and t'Hart 1957). Similar results were obtained by Awad *et al.* (1979). Since the potassium: calcium plus magnesium ratio of kikuyu tends to fall with regrowth time, it is recommended that kikuyu be grazed at the 4 to 5-leaf growth stage (Reeves *et al.* 1996). The potassium: sodium ratio of forage appears to affect the fertility of the grazing animal. A ratio of less than 20:1 is recommended, with the calving interval increasing by 5 days for every 10:1 increase of the ratio above a ratio of 30:1 (Berringer 1988).

When the requirements of growing animals for sodium, calcium and phosphorus are considered (ARC 1980), it is unlikely that sufficient quantities to support rapid growth can be ingested from kikuyu pastures. By supplementing calves on kikuyu pasture with calcium, sodium, and phosphorus in the ratio, 3.5:0.3:3.3, respectively, live-mass gain was increased by 27% and carcass mass by 16% (Kaiser 1975).

Allelopathy

Allelopathy, the detrimental or beneficial interaction among organisms, is an important mechanism influencing plant dominance and crop productivity and is mediated largely by phenolic compounds exuded by plants. Phenolic compounds such as *m*-coumaric acid, *p*-coumaric acid, vanillic acid and gallic acid, and many unidentified flavonoids, have been found in kikuyu grass (Chou *et al.* 1987). These allelopathic substances, derived mainly from decaying stoloniferous material, reduce seed germination and the growth of many plants associated with kikuyu, thus giving kikuyu an ecological advantage, but could be a disadvantage in attempts to establish mixed pastures involving kikuyu. Root washings of kikuyu also reduce the nodulation of certain legumes (Philpotts 1981) and may have a detrimental effect on the persistence of pastures consisting of kikuyu and certain legumes.

Attempts to maintain white clover (*Trifolium repens*) in co-existence with kikuyu in Australia have been largely unsuccessful, due to the vigour of kikuyu in summer (Fulkerson and Reeves 1996). The dominance of kikuyu might be partly due to allelopathic effects, suggesting that forages grown in combination with kikuyu should be tested for resistance to allelopathic compounds.

Much more research is needed into the problem of legume persistence in association with kikuyu.

Kikuyu poisoning

The cause of the sporadic deaths of ruminants grazing lush kikuyu pasture in South Africa (Van Heerden *et al.* 1978), Australia (Wong *et al.* 1987) and New Zealand (Cordes *et al.* 1969; Smith 1972) remains an enigma. It has been suggested that periods of hot, dry weather, followed by rain and subsequent rapid growth, predispose conditions to sudden outbreaks of poisoning (Wong *et al.* 1987). The army worm caterpillar, *Mythimna convecta* or *Spodoptera exempta*, has also been incriminated in kikuyu poisoning (van Heerden *et al.* 1978). Since 1972 the disease has become rare in the Northlands of New Zealand due to the successful control of the army worm caterpillar by means of an introduced parasitic wasp (Black 1979). The possibility of cytotoxicity of fungal origin, such as from *Myrothesium* species, has largely been eliminated (Di Menna *et al.* 1973; Wong *et al.* 1987; Peet *et al.* 1990).

Several incidences of kikuyu poisoning have been described (Gabbedy *et al.* 1974; Wong *et al.* 1987; Peet *et al.* 1990). Clinical signs of the condition include ataxia, recumbency, abdominal distension and excessive salivation. Necropsy reveals large amounts of sloppy, green rumen contents, some separation of the rumen epithelium from the submucosa and a relatively empty abomasum and distal intestinal tract. The kidneys may be swollen. Histopathology reveals severe necrosis of the rumen epithelium, with marked neutrophil infiltration and under-running of the stratum corneum, separating it from the basal layers. Similar, but less severe, focal necrotising inflammation may be seen in the reticulum and omasum. Tubular nephrosis of the kidneys is evident. Although tissue damage resembled that of severe ruminal acidosis or grain poisoning, rumen pH ranges from 7–8 (Peet *et al.* 1990). These workers detected abundant calcium oxalate crystals on and in the damaged epithelium tissue and in the kidneys, but oxalate poisoning was not suspected since the observed lesions were not consistent with conventional acute oxalate poisoning.

Plants are known to produce chemical defence substances in response to herbivore damage or pathogenic attack, which are not formed in response to normal mechanical injury to the plant

(Stowe *et al.* 1995). Changes in the plant's physiology and biochemistry appear to lead to the active release of substances such as indole, terpenes and sesquiterpenes in response to herbivore feeding and continue to be released many hours (> 16 h) after their induction. It is noteworthy that the response is systemic, in that the entire plant produces and releases these volatile compounds, even when only one or a few leaves are attacked. An extremely rapid (< 8 min) plant defence response to a variety of exogenously added compounds is derived from the rapid production of hydrogen peroxide and its subsequent utilisation by endogenous cell wall peroxidases to oxidise susceptible substrates (Apostol *et al.* 1989). By virtue of its oxidising properties, hydrogen peroxide alone, or in combination with peroxidases, forms a potent bacteriocidal agent. Hydrogen peroxide production is greatly enhanced in the presence of salicylic acid. It was suggested that salicylic acid, accumulating in the plant in a systemic manner due to previous infection, may enhance hydrogen peroxide production during subsequent infection (Krauss and Jeblick 1995). Drought, in turn, causes a decrease in the activity of catalase (25%), ascorbate peroxidase (18%) and superoxide dismutase (30%) in pea nodules (Gogorcena *et al.* 1995).

Hydrogen peroxide is readily formed from oxalic acid in the presence of oxalate oxidase in plant tissue (Pundir and Nath 1984) and in fungi (Espejo and Agosin 1991). In the presence of iron (Fe^{2+}), hydrogen peroxide can give rise to hydroxyl radicals by means of the Fenton reaction (Cohen 1985). Furthermore, superoxide radicals can be generated by the oxidation of hydrogenase and nitrogenase by molecular oxygen (Dalton 1995). These highly reactive radicals combine with virtually any molecule at their site of formation, causing severe tissue damage. The formation of free radicals appears to be involved in the destruction of infected lung tissue by oxalate-producing fungi of the *Aspergillus* group (Ghio *et al.* 1992).

The compound N-(17-hydroxylinolenoyl)-L-glutamine, a constituent of the oral secretions of the beet army caterpillar or lesser army worm (*Spodoptera exigua*), elicits the emission of volatile compounds from maize seedlings it feeds on. These substances attract parasitic wasps, the natural enemy of the caterpillar (Alborn *et al.* 1997). Mechanical damage to the plant in the absence of the oral secretions does not trigger the release of the wasp attractants. The African army

worm caterpillar (*Spodoptera exempta*) is indigenous to east and central Africa. Regular seasonal outbreaks occur usually every 6–8 months, between November–December and May–June. The young larvae have a preference for indigenous grasses (Brown *et al.* 1970), and it is quite likely that they have co-evolved with kikuyu for a vast period of time. It is therefore conceivable that, due to the continual exposure to army worm, oxalate-containing kikuyu grass could have developed the ability to produce characteristic chemical substances capable of destroying the anaerobic nature of the rumen and causing severe tissue damage in the digestive tract, in response to the secretions of the phytophagous caterpillar.

Conclusion

Leng (1991) stated: 'To optimize ruminant production from forages, the need is to optimize digestibility and intake, maximize microbial growth efficiency and adjust the nutrients so that they closely correspond to the quantities and balances required for the productive function.' Kikuyu has been used for pasturage by dairy cattle in many countries for almost a century, but milk production on kikuyu alone has been restricted by various deficiencies. Due to the morphology of kikuyu and the large difference in nutritive value of leaf and stem tissue, management practices should be aimed at optimising the leaf: stem ratio of the grass on offer and preventing the accumulation of large amounts of stem material. The nutritive value of kikuyu regrowth appears to be optimised at the 4.5 leaves per tiller growth stage. Due to the variation in growth rate over the growing season, the grazing cycle should be based on growth stage rather than on a fixed regrowth period.

Due to the tendency of kikuyu to accumulate excessive amounts of nitrate and other nitrogenous compounds which could affect the rumen microbial population or which require energy to be detoxified and eliminated in the urine of the grazing animal, levels in the plant should be closely monitored. Large single applications of nitrogen fertiliser should be avoided. Nitrogen applications in excess of 50 kg/ha/month appear to be undesirable (Reeves 1997).

The main nutritional limitation of kikuyu grass is a lack of readily digestible energy and a relatively low digestibility of structural carbo-

hydrates. Due to the large diurnal fluctuation in non-structural carbohydrate content, reaching maximum levels during the afternoons, some nutritional benefit could be obtained by ensuring that the animals are exposed to the pasture during these peak periods. However, attempts should be made to select ecotypes containing higher levels of non-structural carbohydrates and better digestibilities of structural components.

At present, supplementary nutrients are necessary in most production settings to obtain acceptable levels of performance from animals fed on kikuyu. The most important of these are cereal grain supplements. However, the poor absorption of calcium by kikuyu, especially under conditions of high soil acidity and the presence of oxalic acid in the plant tissue which drastically reduces the availability of calcium to the grazing animal, makes calcium supplementation also essential. Calcium supplementation also prevents serious clinical conditions caused by imbalances between calcium, potassium, phosphate and magnesium. Furthermore, due to the poor absorption of sodium from the soil, supplementation of sodium is important for optimal animal production on kikuyu pasture.

Other strategies for improving animal production on kikuyu, such as using kikuyu in combination with, or over-sowing it with, other grasses or legumes for winter production, are hampered by difficulties regarding establishment and persistency of species. Less vigorous kikuyu ecotypes or races with a more compatible growth pattern or allelopathic composition may be required.

Nutrient supplementation is costly and requires certain skills to execute successfully. In some third world countries, neither funds nor skills are available, making the genetic improvement of kikuyu an attractive option. Apart from the selection of the seeding variety, Whittet, which was mainly based on improved DM yield, little attention has been given to the screening of kikuyu ecotypes for plants with a more favourable chemical composition and nutritive value. Drought resistance or cold tolerance can be improved only by the introduction of more suitable genetic material. Due to the unique anatomy and inconspicuous nature of the kikuyu inflorescence, conventional breeding and selection techniques are difficult to execute. Furthermore, the gene pool of existing commercial kikuyu pastures could be relatively small. Exploiting the naturally occurring diversity

of kikuyu in its broad natural habitat appears to be a logical and feasible alternative.

Preventing animal losses due to kikuyu poisoning appears to depend on the successful control of army worm infestations.

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