PROSPECTS FOR IMPROVING THE DIGESTIBILITY AND INTAKE OF TROPICAL GRASSES

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ABSTRACT

Constraints on quality of tropical forage imposed by enviroment and by plant growth, physiological, morphological and anatomical characteristics are reviewed. Emphasis is given to grasses because their low quality problem is most acute. Prospects are assessed for increasing the proportion of usable energy in the dry matter produced.

INTRODUCTION

Substantial gains in animal production can be obtained by replacing native species with sown grass-legume pastures. These improved pastures still have low dry matter digestibilities (DMD) and voluntary intakes which limit the proportion of energy in the dry matter that is usable for animal production (Stobbs 1971, 1974). Since species currently used have mainly been selected for high yield and survival, there is no reason to expect that they will naturally have a high nutritive value which offers no ecological or competitive advantage

When cut and fed to animals in pens, tropical grasses are on average 13% units less digestible than temperate species (Minson and McLeod 1970) and intake is 25% lower (Minson 1981). Contrasting with this, tropical legumes are on average 4% units lower in DMD than temperate legumes (D. J. Minson and J. R. Wilson, unpublished data). The low intake of tropical grasses is caused by their high cell wall and low crude protein % (Minson 1981). One quarter of all crude protein values reported for tropical grasses in the literature are less than 6% (Minson 1976), a value below which intake is seriously restricted by a protein deficiency (Minson and Milford 1967).

The low quality of tropical forage is caused by environmental and plant factors. These will be described together with ways for increasing the proportion of energy in the pasture that can be converted into animal product. Emphasis is given to grasses because their quality problems are more severe than those of the legumes and because they contribute the highest proportion of the energy even in mixed swards.

FACTORS CONTRIBUTING TO LOW HERBAGE QUALITY

Tropical environment

High insolation (Sakurai 1963) and water stress (French 1957) are believed to lower herbage quality, while DMD is negatively correlated with temperature (Minson and McLeod 1970).

The direct influence of the first two factors appears minor; and in contrast to some beliefs, high irradiance actually increases DMD (Deinum *et al.* 1968, Wong 1978) and plants water-stressed for relatively short periods are usually higher or similar in DMD to plants kept well watered (Vough and Marten 1971, Carlson 1974, Pesant and Dionne 1976). Naturally, a long, severe drought will eventually lead to dead herbage of low quality. Differences in evaporation rate or relative humidity do not appear to change DMD (Wilson *et al.* 1976).

Controlled enviroment studies confirm that high temperature is a serious constraint on herbage quality (Table 1). High temperature increases the proportion of

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cell wall and decreases its digestibility in both leaf and stem (Deinum and Dirven 1976, Wilson *et al.* 1976, Moir *et al.* 1977). The detrimental effect of high temperature arises partly from the higher growth rate (Ivory *et al.* 1974) and greater stem development (Deinum and Dirven 1975). Stem DMD is more affected by temperature than leaf DMD (Deinum and Dirven 1975, see also Table 1). The collated data in Table 1 show that DMD decreases at 0.60 (tropical grasses), 0.56 (temperate grasses), 0.28 (tropical legumes) and 0.21 (temperate legumes) units for each °C rise in growth rate. Comparison of mean spring and summer temperatures for Samford (19.1 and 23.5°C) and Townsville (24.7 and 27.4°C), Australia with Aberystwyth, U.K. (8.9 and 15.3°C) indicates the possible magnitude of the temperature effect. The 8–16°C differences could account for 5–10% units of the 13 units difference in DMD of tropical and temperate grasses reported by Minson and McLeod (1970) and 2–4% units of the 4% units difference between the legume groups. Miaki *et al.* (1973) and Forde *et al.* (1976) reported differences in DMD between tropical and temperate grasses even when grown side by side in the same field but McLeod and Minson (1974) found that ryegrass grown under sub-tropical conditions had a similar DMD to that of Setaria and Rhodes grass grown in the same environment. Direct effects of temperature on DMD are often outweighed by other factors, e.g. in autumn the potential improvement in DMD due to lower temperature is offset by slow development of new leaf and frost damage (Wilson and Mannetje 1978). Although temperature is a major factor contributing to the low quality of tropical species other factors as discussed below are also important.

TABLE 1

Effect of temperature on dry matter digestibility (data collated from a survey of published controlled environment studies).

	Average change in DMD (% units) per °C increase in growth temperature		
	Tops	Leaf	Stem
Tropical grasses	−0·60	−0·57	−0·86
Temperate grasses	−0·56	−0·64	−0·76
Tropical legumes	−0·28	+0·19	−0·27
Temperate legumes	−0·21	−0·09	−0·22

Plant growth potential and nitrogen utilization

The yield potential for tropical grasses is extremely high (35–85 t ha^{-1} $year^{-1}$ of dry matter) compared with the temperate grasses (20–27 t ha^{-1} $year^{-1}$) (Roberts and Carbon 1969, Cooper 1970, Strickland 1974). This high growth potential is accompanied by efficient nitrogen utilization (Brown 1978) which enables tropical grasses to grow at a higher rate than temperate grasses even at low tissue %N (Wilson 1975a). This leads to low levels of protein and other nutrients which may reduce intake. This is particularly evident in the far north of Australia where in the growing season green leaf may have as little as 0.7% N and 0.06% P (R. McLean, pers. comm.).

Whilst N deficient tropical grasses may often be of low quality (Bryan and Evans 1971), applying fertilizer nitrogen generally has little effect on DMD and only increases intake when the nitrogen level is below about 1% (Minson 1967, 1973). This lack of response is because leaf senescence is accelerated (Wilson and Mannetje 1978), larger stems are produced (Deinum and Dirven 1976), and with long growth intervals N-fertilized pasture may even reach lower % N than unfertilized grass

(Henzell 1963). Because N effects on quality strongly interact with growth stage (Gomide *et al.* 1969, Perry and Baltensperger 1979) higher digestibility will be gained from N fertilizer only if pastures are grazed at a young stage of growth.

The seasonal nature of the high growth rate of tropical grasses in Northern Australia leads to a need for conservative stocking rates. During the growing season pasture available is therefore well in excess of animal requirement if sufficient feed is to be available for the dry season (Table 2). This practice leads to an accumulation of mature, stemmy material with a high rate of tissue death and low DMD and intake (Chacon *et al.* 1978). In the growing season cattle may gain 0.5–0.7 kg head^{-1} day^{-1} but this is low compared with 1–1.2 kg found on temperate pastures (Nicol *et al.* 1976). The problem of mature forage may be accentuated in a wet year, for example at Narayen (S.E. Queensland) rate of liveweight gain in a year of especially high rainfall was 36% lower than in a dry year despite a much higher pasture yield (see Table 2). The accumulation of herbage for winter feeding is obviously necessary but the levels shown in Table 2 may be higher than necessary, particularly since some plant growth may be expected in the cool season. Blaxter and Wilson (1963) studied the interaction between quality and yield or stage of growth of temperate grasses. They found that, although grass at a young age of growth gave only half the yield of dry matter, the animal liveweight gain was five times greater than could be achieved from a much higher yield cut at a more mature growth stage.

TABLE 2

Pasture yield in relation to animal requirement and productivity, (data for sites in S.E. Queensland from T. R. Evans (Beerwah), R. M. Jones (Samford) and L. 't Mannetje (Narayen)).

Pasture	Beerwah		Samford		Narayen	
	Setaria +448kgN	Pangola +448kgN	Setaria +300kgN	Setaria/ Siratro	Buffel/Siratro Wet year	Buffel/Siratro Dry year
Stocking rate (beasts ha^{-1})	4·0	4·2	5·0	1·0	1·1	1·1
Ratio herbage available/ animal requirement*	2·5–5	2·8–4	2·0–3·5	10–20	22–25	10–16
Liveweight gain (Jan-May, kg beast^{-1} day^{-1})	0·5	0·5	0·7	0·7	0·45	0·7
Herbage available in May (kg ha^{-1})	4520	4700	5000	6500	8650	3890

*Values represent grazing months of herbage ahead of the animal throughout the growing season between January and May. Herbage available is yield on offer and animal requirements are based on 2.4% body weight.

Leaf morphology and anatomy

Leaf has a higher DMD and intake than stem and its proportion, especially in the top of the sward, significantly influences animal performance (Chacon *et al.* 1978). Leaf is selectively grazed by animals and, in mature tropical grasses, the small and widely dispersed upper leaves on the tall flowering stems lead to small bite size and limit intake. Intake is restricted when bite size is < 0.3 g OM (Stobbs 1973) and bite sizes may be as low as 0.17 g in mature tropical grass compared with 0.34 g for immature tropical grass and 0.43 for immature temperate grass (Munro 1978). Some upper leaves on green panic weigh only 0.03 g DM and even 50 cm long leaves weigh only 0.25 g (Wilson 1976) so small bite size appears inevitable. Lower tiller densities of many tropical grasses (Dirven 1977) also accentuate bite size problems. The leaves of highest DMD are the earliest formed leaves at the base of the tiller (Wilson 1976) and in mature swards tall, thick stems prevent easy access by the animal.

The leaf midrib is poorly digested and in maize grown at 30°C it was 32% units lower in DMD than the rest of the blade (Deinum 1976). The midrib comprises 25% of the leaf weight in maize, and in other tropical grasses the values appear comparable *e.g.* 26% in green panic and guinea grass, 27% in Pioneer Rhodes and 18% in Signal grass (J. R. Wilson, unpublished data).

Different cell tissues are digested at varying rates and to a different extent (Akin 1979), hence leaf anatomy influences DMD and probably intake. Tropical grasses differ markedly in leaf anatomy from temperate grasses (Laetsch 1974) and have less of the readily digested mesophyll and more of the less digesetible epidermis, vascular and sclerenchyma tissues (Table 3). The mesophyll is more densely packed in tropical grasses than in temperate grasses (Carolin *et al.* 1973); air space occupying 3–12% and 10–35% respectively of leaf volume (Byott 1976). These air spaces appear to allow rumen micro-organisms quicker access to a larger surface area (Hanna *et al.* 1973), and differences between pearl millets in rate of digestion have been associated with packing density of mesophyll cells (*loc cit.*).

TABLE 3

Percentage of different tissues in cross-sectional area (CSA) of grass leaf blades (data collated from literature).

	Epidermis	Mesophyll	Bundle sheath	Vascular bundle	Sclerenchyma
Temperate (C_3)	28·7±1·5	61·0†	—	5·5±0·4	3·4±0·4
Tropical (C_4)	33·0±2·1	34·6±2·4	19·3±2·1	7·6±0·4	5·0±1·1

†Includes parenchyma sheath (*c.* 6% of CSA).

The specialized bundle sheath of tropical grasses has thick, suberized outer walls (O'Brien and Carr 1970) resistant to mechanical breakdown (Pheloung and Brady 1979), and there are no intercellular spaces (Laetsch 1974). These features hinder digestion of the sheath and enclosed vascular tissue (Akin and Burdick 1975). The larger number of vascular bundles in leaves of tropical than temperate grasses and their tough sheath may account for the longer time tropical feeds are retained in the rumen and hence their lower intake compared with temperate forages (Minson 1966).

Stem development and sward structure

The higher the proportion of stem in the pasture the lower will be the proportion of energy transferred to meat, milk or wool. Stem DMD declines rapidly with age and in mature herbage stem DMD is much lower than that of leaf. The long upper internodes of grasses have the lowest DMD (Stobbs 1973) due to extreme lignification and degeneration of the central parenchyma (Steppler 1951). They also support leaves with a high proportion of sheath (Borrill 1961) which is of low DMD, especially after internode elongation exposes it to the atmosphere (Wilson 1976).

Indoor studies have shown that stem is eaten in much smaller quantities than leaf even when at the same digestibility. The lower intake of stem is due to structural features which slow its rate of passage through the rumen (Laredo and Minson 1973). The tropical environment accentuates the problem because high temperature promotes the development of stem (Deinum and Dirven 1976) and its lignification (Ehara and Tanaka 1961).

Quality problems caused by stem are much greater in most tropical grasses because, unlike temperate grasses, the tropical grasses have no specific environmental requirements for flowering and elongated culms are produced continually over the growing season (Barnes 1960, Boonman 1973). Tropical grasses also have more vascular bundles in their stems than temperate grasses (Stiff and Powell 1974), and Schank *et al.* (1973) found a negative correlation between DMD and proportion of stem vascular tissue for a range of *Hemathria* lines.

PROSPECTS FOR IMPROVING THE USABLE ENERGY IN HERBAGE

Environmental and growth potential constraints

High growing temperatures are unavoidable but the detrimental effects of temperature would be lessened if swards could be managed to prevent mature growth and excessive stem. More legume should help because the decrease in DMD with high temperature in legumes is less than half that of grasses and legumes will also improve the intake of low protein grass.

Because of the seasonal nature of pasture growth, stocking rates sufficiently high to keep grass in a young growth stage are usually not possible. In the temperate zone this problem is usually overcome by conserving the excess. This does not at present seem a viable option for tropical grasses because there are difficulties in making silage from them (Catchpoole and Henzell 1971), the weather is usually unsuitable for haymaking, and more especially the quality of conserved product is poor. DMD and intake can be increased by chemical treatment of hay (e.g. caustic soda or ammonia) but the improvement does not usually warrant the expenditure.

Some reduction in the potential yield of grasses might actually increase the level of animal production per hectare since there is usually an inverse relation in grasses between yield and quality attributes (Clements 1970, Bray and Pritchard 1976, van Bogaert 1977). The opportunity thus exists to manipulate the present yield/quality balance, especially if the lower yield is primarily due to less stem. One new possibility of manipulating yield is with the growth regulant "mefluidide" which has been found to maintain higher DMD in tall fescue (Glenn *et al.* 1976). Studies are required on the use of this chemical with tropical forages.

Modification of stem and leaf characteristics

Breeding for more digestible stem offers scope because variation between genotypes in stem DMD is apparent in many species (Mowat *et al.* 1965, Lovelace *et al.* 1972, Bhat and Christie 1975, Marum and Hovin 1979). Pasture DMD and intake should also be increased by reducing stem elongation, especially of the upper internodes, and this can be readily accomplished in grasses as instanced by the dwarf cereals. The possible gain in production is illustrated for dwarf versus tall millets (Johnson *et al.* 1968). In an indoor feeding trial the dwarf gave 22% less total yield but had 6.8% higher DMD, 21% greater intake and gave 49% more daily weight gain. Tall stems may have conferred competitive advantage in the native habitats of our sown grasses but are probably of little ecological significance in grazed pastures.

Stobbs (1973) modified stem elongation by growth regulators. The shorter sward was higher in protein and DMD, and animals ate more per bite because of higher sward bulk density. Compression of the sward apparently does not alter canopy photosynthesis and hence the potential for yield (M. M. Ludlow and T. H. Stobbs, unpublished data).

Restricted flowering would reduce the stem problem. Boonman (1973) suggests that little can be done by selection for a more specific environment requirement in tropical grasses, but certainly there is considerable variation in flowering between ecotypes of various species (Mott and Popenhoe 1977) which could be exploited.

Modification of stem anatomy may improve intake and in this respect there appears to be substantial variation in vascular bundle numbers in tropical grasses (McWhorter 1971, Schank *et al.* 1973, Stiff and Powell 1974). Thick, succulent stems have been a feature of genotypes selected for high DMD, e.g. bermudagrass (Hanna *et al.* 1976), often associated with higher soluble carbohydrate (Jones *et al.* 1974). It would seem advantageous if mature stems of tropical grasses did not hay-off but remained succulent. There is variation within genera for stem succulence, e.g. within *Setaria,* but for reasons outlined elsewhere (Wilson 1975b) the potential for tropical forage grasses to accumulate sugar appears limited. Obviously plants such as sugarcane and sweet sorghum can store sugar which may be associated with specialized stem anatomy (Burns *et al.* 1970).

Modification of leaf characteristics is less urgent. Genetic variation in DMD is usually small and the basic anatomy is an integral part of the C_4 photosynthetic system and hence not easily manipulated. Although, a reduction in midrib size may be one method of improving the DMD and intake of leaf. Also there is variation in bundle sheath characteristics (Carolin *et al.* 1973, Akin 1979) and within some genera *e.g. Panicum* there are C_4, C_3 and intermediate types of leaf anatomy (Morgan and Brown 1979). Hybridization of C_4 and C_3 types is possible, *e.g. Atriplex* (Bjorkman *et al.* 1971). The higher quality of Coastcross 1, the bred line of *Cynodon,* is partly associated with quicker digestion of mesophyll and bundle sheath (Akin *et al.* 1974).

Selection for DMD or chemical attributes

DMD and intake have been improved by selection of less cutinized lines of sorghum (Hanna *et al.* 1973) and low lignin lines of corn (Muller *et al.* 1972). A low cellulose selection of ryegrass has increased liveweight gain by 3–7% (Lancashire and Ulyatt 1975). Improvements in DMD are probably best approached directly using the *in vitro* DMD procedure rather than selection for specific tissue chemical attributes (Minson 1971). Coastcross 1 *Cynodon* is a prime example of a successful breeding programme with an improvement of 6.6 units in DMD and 30% in daily animal weight gain (Lowrey *et al.* 1968). Similar prospects for improving herbage quality are illustrated in a recent study comparing *Digitaria decumbens* and *D. setivalva* at five different stages of growth (D. J. Minson, unpublished data). The latter species was 4.5 units higher in DMD, 8% higher in dry matter intake, 18% higher in intake of digestible energy and this was calculated to improve animal production by 38%.

CONCLUSIONS

It should be possible to select grasses with smaller rates of decline in DMD and crude protein, despite the rapid rate of growth and development under high temperatures. Herbage intake is probably the most critical factor limiting animal production from tropical forages. Stem is the main problem and restructuring tropical grasses in relation to flowering, stem morphology, anatomy and chemical composition offers the prospect of substantial gains. Selection for higher digestibility can lead to increased intake and substantial improvement in animal production.

Positive steps are needed to seek higher quality grasses but these may not be the highest yielding lines.

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