The influence of polyphenolics on the nutritive value of browse: A summary of research conducted at ILCA

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SUMMARY

MANY AFRICAN *browse species contain high levels of polyphenolic compounds (including tannins) which have a large effect on protein digestibility and nitrogen metabolism in ruminants. A brief discussion of tannin chemistry and methods of tannin analysis is presented. Results from research on the nutritive value of African browse species are reviewed. The nutritive value of tanniferous browse cannot be easily predicted from chemical analyses because tannins can have both negative and positive effects on nitrogen metabolism. Examples of both types of effect are presented and the implications for feeding browse to ruminants are discussed.*

INTRODUCTION

In arid, semi-arid and subhumid areas, where cropping is impossible or unreliable, man depends on ruminants for sustenance. Ruminants produce food for human consumption by feeding on plants or plant parts that have no nutritive value for man. Trees and shrubs survive harsh climatic conditions and are an important source of browse feed in drier parts of Africa.

Because of its high content of protein, browse has been suggested as a solution to feeding tropical animals: woody species are more drought-tolerant than grasses and may be a more reliable feed resource. Browse trees benefit soils by protecting them from erosion and may increase soil fertility. They also benefit crops and animals with shade, and provide people with fuel, medicines and building materials.

Browse is particularly important in areas where increasing human population has necessitated the cultivation of grazing land. The larger areas cultivated produce more crop residues whose nutritive value can then be enhanced by nitrogen supplementation in the form of browse. Although tree leaves have a high protein content, tannins and other secondary compounds may bind this protein, thus rendering it unavailable to the animal. Tannins and related polyphenolics may have negative effects on palatability and digestibility, and many are also poisonous.

One research priority for the study of browse is to determine the effect of tannins on protein availability and other aspects of digestion. This is a complex problem because the term 'tannin' refers to a heterogeneous group of phenolic compounds which precipitate protein to varying degrees, depending on the type of phenolic and protein present as well as the chemical environment. The nutritional effects of these compounds must be fully understood before the

economic value of browse as a component of an animal management system can be realistically determined.

Scientists in ILCA's Nutrition Unit have attempted to determine the effects of tannins in woody species on feed intake and the growth, digestion and nitrogen metabolism of ruminants. The research was conducted in Ethiopia using local browse species, mainly *Acacia,* which are widely distributed in Africa. This paper summarises ILCA's findings over several years of research. Nitrogen metabolism in ruminants and tannin chemistry are briefly discussed to give background information on the work reported.

NITROGEN METABOLISM

In ruminants, feed is mainly digested in the rumen, which causes the growth of a microbial population, which, in turn, is digested in the lower tract, thereby benefiting the host animal. Nitrogen metabolism in ruminants has been reviewed by Ørskov (1982), Van Soest (1982) and NRC (1985), and is briefly described below.

The primary source of nitrogen for rumen microbes is either protein or non-protein nitrogen from feed. Most of this is converted to ammonia and then incorporated into microbial cells (Ørskov, 1982). The ability of rumen organisms to use ammonia depends on an adequate supply of energy. The energy must be available at the same time as the ammonia, otherwise the ammonia will not be effectively utilised. Excess ammonia in the rumen is absorbed into the blood and converted to urea by the liver.

A secondary source of nitrogen for the rumen microbes is urea recycled from the blood directly through the rumen wall or in saliva (Kennedy and Milligan, 1980). Urea diffuses from blood to rumen, while rumen ammonia diffuses in the reverse direction (Houpt, 1970). The amount of urea recycled is fairly constant and independent of dietary nitrogen (Van Soest, 1982). Recycled urea is more important for animals on low nitrogen intake, because recycling prevents the loss of endogenous nitrogen to excretion in urine and allows its use by nitrogen-deficient rumen microbes.

The rumen microorganisms convert nitrogen into microbial cells, irrespective of whether the nitrogen originated as protein or as non-protein nitrogen unusable by the host. The conversion of feed nitrogen into microbial cells is obviously an advantage to the animal in the case of non-protein nitrogen. However, it is detrimental if the nitrogen source is high-quality protein because most nitrogen in bacterial cell walls is indigestible (Ørskov, 1982), resulting in a net loss of N available to the host.

Available microbial protein does not vary in amino-acid composition in response to diet (Storm, 1981). A comparison of the amino-acid composition of microbes and animal tissue shows that microbial protein may be deficient in some amino acids necessary for wool production but not in those required for growth and milk production (Ørskov, 1982; Van Soest, 1982).

Some protein escapes ruminal digestion to undergo peptic digestion in the abomasum. The rate of protein escape is increased by high rates of passage, low protein solubility, small particle size and high level of intake (Van Soest, 1982). Efforts have been made to encourage protein to escape from the rumen by chemical or physical treatment which alters protein solubility or degradability. These methods need to protect protein from ruminal but not peptic digestion.

Previous research suggests that treating protein with tannins may increase protein escape (Driedger and Hatfield, 1972). Some tannins may bind proteins in the neutral pH of the rumen and release them in the acidic abomasum (Barry and Forss, 1983). This seems to occur with feeds treated with hydrolysable tannins (Driedger and Hatfield, 1972) because they contain ester linkages (Haslam, 1966) which hydrolyse in gastric acid, thus releasing the protein. However, it is unlikely that proanthocyanidins will have the same effect (Zelter et al, 1970) because they have an acid-resistant biphenyl structure (Haslam, 1966). Most naturally occurring forage tannins are proanthocyanidins (McLeod, 1974).

Microbial and escape protein from the rumen may be digested in the lower tract and absorbed by the host. Protein bound in plant cell walls or in chemical complexes is not absorbed. The unabsorbed protein, as well as endogenous nitrogen from the digestive tract and recycled urea, may be available to microorganisms in the large intestine (Visek, 1968; Beever et al, 1974; Nolan, 1975). The incorporation of nitrogen into microorganisms in the lower tract depends on the energy source which escapes absorption (Beever et al, 1974; Van Soest, 1982).

Faecal nitrogen is composed of undegraded feed nitrogen, microbial nitrogen from the rumen and large intestine, and endogenous nitrogen from the digestive tract (Mason, 1969). The size of these fractions depends on the content of protein and energy in the diet, rate of passage, and the nutritional status of the host (Mason, 1979). Faecal material originating from microbial and endogenous sources can be separated from other faecal material by its solubility in neutral detergent (Mason, 1969).

TANNINS

Chemistry of tannins

Tannins are a subset of plant polyphenols found in leaves, twigs, flowers, fruit and tree bark. Long after Fischer's (1919) work on the chemistry of the so-called 'vegetable tannins', the subject remained "one of the untidy corners of organic chemistry" (Gupta and Haslam, 1980), and even at present, the chemical classification of some phenolic compounds may prove difficult.

The original definition of tannin as 'a compound able to convert hide to leather' was unclear, because while all tannins contain phenolic groups, not all phenolics can cross-link collagen fibres in animal hides to form leather. Nevertheless, the ability of tannins to precipitate proteins is one of their most important biological properties.

Precipitation can be the result of hydrogen bonding (Loomis and Battaile, 1966), covalent bonding (Swain, 1979), ionic bonding (Gustavson, 1956) or hydrophilic bonding (Oh et al, 1980). The ability of tannins to precipitate proteins depends on their molecular weight, water solubility, conformation and other factors. A definition with enough generality to include all tannins was given by Horvath (1981):

Tannins are any phenolic compound of sufficiently high molecular weight and containing sufficient phenolic hydroxyls and other suitable groups (i.e. carboxyls) to form effectively strong complexes with protein and other macro-molecules under the particular environmental conditions being studied.

This definition allows for the fact that tannins may form complexes with starch and cellulose, as well as protein. It also underscores the difficulty in precisely defining the chemistry of tannins.

Tannins are usually subdivided into two major groups: hydrolysable and condensed tannins. Hydrolysable tannins split into sugars and phenolic carboxylic acids in acid and alkaline conditions (White, 1957). They are further classified according to the products of hydrolysis into gallo-tannins (gallic acid and glucose) and ellagi-tannins (ellagic acid and glucose) (McLeod, 1974). Two other categories, tara-gallo-tannins (gallic and quinic acid plus glucose) and caffe-tannins (caffeic acid arid quinic acid plus glucose) have also been suggested (Haslam, 1966).

The condensed tannins are often referred to as proanthocyanidins because they produce red anthocyanidins when heated in acid (Haslam, 1982). Proanthocyanidins are phenylpropanoid polyphenols and are categorised by the type of monomer they contain - either flavan-3-ols or flavan-3, 4-diols - into catechins or leucoanthocyanidins (Horvath, 1981).

The term leucoanthocyanidin was originally used to name the whole group of condensed tannins (Haslam, 1982); the literature must, therefore, be read carefully to avoid misinterpretation. Furthermore, since condensation is a reaction which hydrolysable tannins can also undergo, the term 'proanthocyanidin' is preferred to 'condensed tannin'.

Besides hydrolysable tannins and proanthocyanidins, a group called the beta-tannins can be added (Swain, 1979; Horvath, 1981). Beta-tannins are protein-precipitating compounds which are insoluble in water. They form very stable bonds with protein, and they can have lower molecular weight than other tannins and still be effective.

However, as more is learned about tannin chemistry in relation to animal nutrition, the less useful this classification system is likely to be because there are some compounds, such as catechin gallates, which have properties of both the hydrolysable and condensed tannins. Catechin gallates are important nutritionally because they are toxic to some rumen bacteria (Mueller-Harvey et al, 1988).

The interaction between tannins and proteins is very specific (Hagerman and Butler, 1981) and depends on the characteristics of both tannin and protein, such as molecular weight, tertiary structure, isoelectric point and compatibility of binding sites. It also depends on the properties of the solvent, especially its pH. Proanthocyanidins seem to be more important than hydrolysable tannins in forming complexes in feed (Reed et al, 1985).

Tannin assays

Using fresh samples to determine tannin content is best, but if storage is necessary, freezing is preferred. In some situations, drying is the only means of preserving material. However, at low drying temperatures (<40° C), enzymes may still function, thereby leading to oxidation. At temperatures above 60° C, heat damage (Van Soest, 1965) and polymerisation (Haslam, 1966) may occur.

There is no definitive assay for tannins because they are heterogeneous compounds, but there are many methods for assaying tannins, each with its own specificity, which have been reviewed in literature (e.g. Swain and Hillis, 1959; Maxson and Rooney, 1972; Horvath, 1981). The International Livestock Centre for Africa (ILCA) developed two assays, one to quantify

insoluble proanthocyanidins and one for soluble phenolics, including proanthocyanidins and other phenolics which may be nutritionally important by having effects other than precipitating protein. These methods are briefly described below.

Insoluble proanthocyanidins. These are determined by heating a sample of neutral-detergent fibre in a solution of n-butanol and concentrated hydrochloric acid. The solution turns red as proanthocyanidins are converted to anthocyanidins. Absorbance is read at 550 nm (Bate-Smith, 1973; Reed et al, 1982).

Initial treatment of the sample by extraction with aqueous acetone and by neutral detergent removes soluble phenolic compounds that may polymerise under acidic conditions, thus avoiding the exaggeration of the content of insoluble proanthocyanidins. Results are presented as absorbance per gram of neutral-detergent fibre. One problem with this procedure is that not all of the proanthocyanidins dissolve, as evidenced by the red colour remaining in the fibre after the analysis.

Soluble phenolics. Total polyphenolics soluble in acetone are determined in a gravimetric assay, by precipitating them from solution with trivalent ytterbium (Reed et al, 1985). The major advantage of the assay is that, unlike in colorimetric assays, standards are not required. Precipitated phenolics may be recovered for qualitative analysis, enzymatic assay, and for assays of protein precipitation and effects on in vitro digestibility. Therefore, potential anti-nutritional effects can be related to the amount of soluble phenolics.

The two assays described give general indications of the size of different phenolic fractions in a feed. The complex tannin chemistry makes it necessary to identify the individual compounds present in the fractions before the effects of each one can be determined. High-performance liquid chromatography and thin-layer chromatography, which separate compounds according to their differential solubility in appropriate solvents, are suitable methods for separating individual phenolic compounds in browse.

Chromatography has been applied by ILCA in the study of phenolic compounds in African browses (Mueller-Harvey et al, 1987; Rittner. 1987; Tanner, 1988). It is hoped that in time, it will be possible to attribute nutritional effects to specific compounds, and then develop simpler assays for the effective compounds.

EFFECT OF BROWSE ON ANIMALS

Below is a synthesis of studies conducted at ILCA in recent years to investigate the behavioural and physiological effects of browse on small ruminants. Most of these studies compared the performance and/or physiological parameters of animals fed browse with the performance and physiological parameters of animals fed standard, non-tanniferous high-protein feeds. Browses and other high-protein feeds were each fed in combination with a low-protein roughage. Both browse and traditional feeds were fed at isonitrogenous levels designed to achieve a pre-determined performance goal. The contents of soluble phenolics and insoluble proanthocyanidins of the browse species included in these studies are shown in Table 1.

Table 1. *Contents of soluble phenolics and insoluble proanthocyanidins of eight browse species used in ILCA studies.*

Browse[1]	Soluble phenolics (% DM)	Insoluble proanthocyanidins (A_{550})	Source
Acacia brevispica (1)	23.9	0.37	Woodward and Reed (in press)
Acacia cyanophylla (1)	38.9	0.45	Reed et al (in press)
Acacia sieberiana (f)	41.8	0.12	Reed et al (in press)
	40.6	0.37	Tanner (1988)
Acacia seyal (1)	40.0	0.14	Reed et al (in press)
	30.0	0.55	ILCA (1988b)
	29.5	0.40	Rittner (1987)
Sesbania sesban (1)	17.9	0.06	Reed et al (in press)
	18.0	0.01	Woodward and Reed (in press)
	16.0	0.06	ILCA (1988b)
	15.7	0.11	Ritmer (1987)
Acacia nilotica (1)	34.0	0.15	ILCA (1988b)
	33.8	0.21	Ritmer (1987)
Acacia nilotica (f)	43.6	0.89	Tanner (1988)
Acacia tortilis (f)	37.3	0.31	Tanner (1988)
Acacia albida (f)	36.5	0.27	Tanner (1988)

[1] The plant parts used were leaves (1) and fruit (f).

Intake

Tannins may reduce intake and palatability of feeds by causing an astringent (Bate-Smith, 1973) or dry feeling in the mouth (Goldstein and Swain, 1963), or by negatively affecting digestion. ILCA data both support and contradict the hypothesis that polyphenolics have a negative effect on feed intake (Table 2).

Table 2. *Browse and roughage intakes and growth rate recorded in three experiments with sheep.*

Browse	Intake (g/d)				
	Browse	Roughage	Total	Growth	Source
Acacia cyanophylla (1)	170	318*	488*	–11*	Reed et al (in press)
Acacia sieberiana (f)	195	269 *	464*	20*	Reed et al (in press)
Acacia seyal (1)	193	285 *	478*	21*	Reed et al (in press)
Sesbania sesban (1)	157	473	630	48	Reed et al (in press)
Acacia tortilis (f)	336	423	759	53	ILCA (1988a)
Acacia brevispica (1)	237	510	747	53	ILCA (1988a)
Acacia tortilis (f)	206	430*	636	32	Tanner (1988)
Acacia albida (f)	194	401*	595	22	Tanner (1988)
Acacia nilotica (f)	204	347*	551	16*	Tanner (1988)
Acacia sieberiana (f)	212	320*	532	0*	Tanner (1988)

Notes: Animal performance with browse was compared to performance obtained with a standard protein supplement. Browse offered varied with experiment but was calculated to provide the same amount of nitrogen in each experiment. The roughages used were grass hay (ILCA, 1988a), maize stover (Tanner, 1988) and teff straw (Reed et al, in press). Standard supplements were cowpea hay and lucerne (ILCA, 1988a), noug cake (Tanner, 1988; Reed et al, in press) and vetch hay (Reed et al, in press). The browse parts were leaves (1) and fruits (f). *= significantly ($P<0.05$) lower than the value obtained in the same trial for the standard supplement.

In a study (Reed et al, in press) comparing three browses high in polyphenolics (leaves of *Acacia cyanophylla* and A. *seyal* and fruits of *A. sieberiana)* with *Sesbania sesban* (low in polyphenolics) and three standard protein supplements *(Vicia dasycarpa* and *noug* or urea), all of which were fed in combination with teff straw *(bragrostis abyssinica),* tannins appeared to reduce total feed intake.

The amount of browse on offer was determined by its protein content. *Sesbania sesban* has a high content of protein, and was, therefore, fed at a lower amount (180 g/d) than, for example, *A. cyanophylla* (330 g/d) which is low in protein. Sheep consumed almost all of the *S. sesban* offered but only about half of the *A. cyanophylla* offered. Compared with the other two acacias, intake of *A. cyanophylla* was lowest, due to its very high content of insoluble proanthocyanidins. Intake of *A. seyal* was initially also very low, but it increased after the animals got used to the browse.

In an experiment where *A. brevispica* and *S. sesban* were each fed in combination with vetch and teff straw at three levels, intake differed between sheep and goats. Feed refusal by sheep increased as the proportion of *A. brevispica* increased in the diet, suggesting a negative response to tannins. In comparison, goats rejected portions of diets which included both *A. brevispica* and vetch, which might be a negative response to fibre (Woodward and Reed, in press).

The effect of browse on the intake of roughage fed concurrently is an important consideration. When *S. sesban* was fed with teff straw, its high content of nitrogen and low content of fibre and proanthocyanidins caused an increase in teff intake over diets including vetch (Reed et al, in press; Woodward and Reed, in press). Compared with roughage intake obtained with standard supplements, browses with high contents of proanthocyanidins (such as *A. cyanophylla* leaves and fruits of *A. sieberiana* and *A. nilotica)* caused a reduction in roughage intake (Tanner, 1988; Reed et al, in press) (Table 2). Browses with moderate levels of proanthocyanidins led to either improved roughage intake (Woodward and Reed, in press) or intake comparable to that with standard supplements (ILCA, 1988a).

Growth

Animal growth rates reflect total intake and the availability of nutrients in the diet. When there was a reduction in total intake due to the fibre or phenolic content of browse, growth rate was low compared with that obtained with non-tanniferous supplements (Table 2).

Low growth rates were observed in animals fed fruits of *A. sieberiana* and *A. nilotica* (Tanner, 1988) although total feed intake was not very low. Reed et al (in press) found that animals fed *A. sieberiana* fruits and *A. seyal* leaves had low total intake and low growth rates, while feeding *A. cyanophylla* resulted in a negative growth rate. The growth rates of animals fed diets with *A. seyal*improved after a period of adaptation to the browse. The negative effect of tannins in *A. cyanophylla* on growth rate was caused by a reduction in nitrogen availability.

Digestion of fibre fractions

Tannins may reduce cell-wall digestibility by binding bacterial enzymes and/or forming indigestible complexes with cell-wall carbohydrates (Barry and Manley, 1984; Barry et al, 1986; Reed, 1986). The digestibilities of organic matter and the fibre fractions of sheep diets comprising *A. cyanophylla* were depressed (Table 3) because of high contents of proanthocyanidins and soluble phenolics. Neutral-detergent fibre digestibility was also depressed in diets containing two other tanniferous browses, *A. sieberiana* fruits and *A. seyal* leaves.

Table 3. *Digestibility of organic matter (OM), neutral-detergent fibre (NDF) and acid-detergent lignin for sheep fed six diets.*

	Digestibilty (%)			
Browse	Apparent OM	True OM	NDF	Lignin
Acacia cyanophylla	41.0a	54.4a	29.0a	–61.1a
Acacia sieberiana fruits	54.0b	64.0b	37.0b	–35.8b
Acacia seyal	54.0b	70.1d	41.9b	–3.7c
Sesbania sesban	54.0b	66.4c	51.7cd	15.4c
Vetch hay	53.1b	63.6b	49.0c	0.6c
Noug cake	57.3b	67.1c	57.1d	14.9c

Notes: The diets consisted of the browse, teff straw and other supplements fed to provide nitrogen for weight gain of 50 g/d. Values in the same column followed by different letters are

significantly different (P<0.05).
Source: Reed et al (in press).

The digestibility of lignin was negative for all the three acacias used in the trial (Reed et al, in press) (Table 3). In most common feeds, the true digestibility of lignin is not different from zero. However, tannin-protein complexes formed in the digestive tract were recovered as faecal lignin (Reed, 1986), which led to an apparent negative digestibility of lignin.

The interference of tannins with the lignin fraction is further emphasised by a comparison between true dry-matter digestibility and digestibility predicted by the summative equation of Goering and Van Soest (1970) which penalises digestibility for lignin in the feed. However, the penalty for lignin in *A. brevispica* was too high, because digestibility was increasingly underpredicted as *A. brevispica* was added to the diet (Table 4). This suggests that the lignin fraction measured in *A. brevispica* was not true lignin but may have been contaminated by phenolics.

Table 4. *Apparent, true and predicted digestibilities of dry matter and the difference between the true and predicted digestibilities for seven diets fed to sheep and goats.*

Dry-matter digestibility	Diet[1]							SE[2]
	B3	B2VI	B1V2	V3	SlV2	S2V1	S3	
	——————————%——————————							
Apparent	58.7	59.0	58.5	60.4	62.4	61.7	62.7	0.8
True	73.4	73.8	73.6	74.6	77.0	76.0	78.4	0.6
Predicted	61.8	65.3	69.0	73.2	73.7	74.4	75.1	0.1
True-predicted	11.7	8.6	4.6	1.5	3.3	1.6	3.2	0.6

[1] Numbers in diet designations refer to proportions of nitrogen provided by *Acacia brevispica* (B), *Sesbania sesba* (S) and *Vicia dasycarpa* (V). Teff straw was fed *ad libitum.*
[2] SE = standard error. Source: Woodward and Reed (in press).
Source: Woodward and Reed (in press).

Tannin interference with fibre fractions makes it impossible to determine the nutritive value of browse from chemical analysis, as is done for other forages. The issue will, therefore, be discussed again in terms of determining nitrogen availability.

Utilisation of nitrogen

Tannins can form complexes with protein, and thus their greatest potential negative effect is on nitrogen metabolism. This can be seen when tanniferous browses are compared with non-tanniferous feeds. Tannins have large effects on nitrogen utilisation at each stage of digestion, as is shown below using four parameters.

Rumen ammonia, plasma urea nitrogen and urinary nitrogen. These are the most accessible pools with which to describe nitrogen available to and incorporated into animal tissues. They have been described for both sheep and goats fed diets made up of combinations

of either *A. brevispica* or *S. sesban* plus vetch plus teff straw *ad libitum* (Woodward, 1988) (Table 5), and for sheep given diets composed of *S. sesban, A. nilotica* or *A. seyal* (Rittner, 1987).

Table 5*. Rumen ammonia and plasma urea nitrogen concentrations and daily, urinary, nitrogen loss for goats and sheep fed seven diets.*

	Diet[1]							
	B3	B2V1	BlV2	V3	SlV2	S2V1	S3	SE[2]
Rumen ammonia (mg/dl)	10.6	17.5	24.7	21.8	32.2	29.9	32.0	5.0
Plasma urea nitrogen (mg/dl)	23.2	26.7	30.6	31.9	33.1	36.7	37.1	1.8
Urinary nitrogen (g/d)	4.9	4.8	4.8	5.3	5.7	6.0	6.6	0.2

[1] Numbers in diet designations refer to proportions of nitrogen supplied by *Acacia brevispica* (B), *Sesbania sesban* (S) and *Vicia dasycarpa* (V). Teff straw was fed *ad libitum.* Values shown are averages from samples taken 3, 6, 12 and *24* hours after feeding.
[2] SE = standard error.
Source: Woodward (1988).

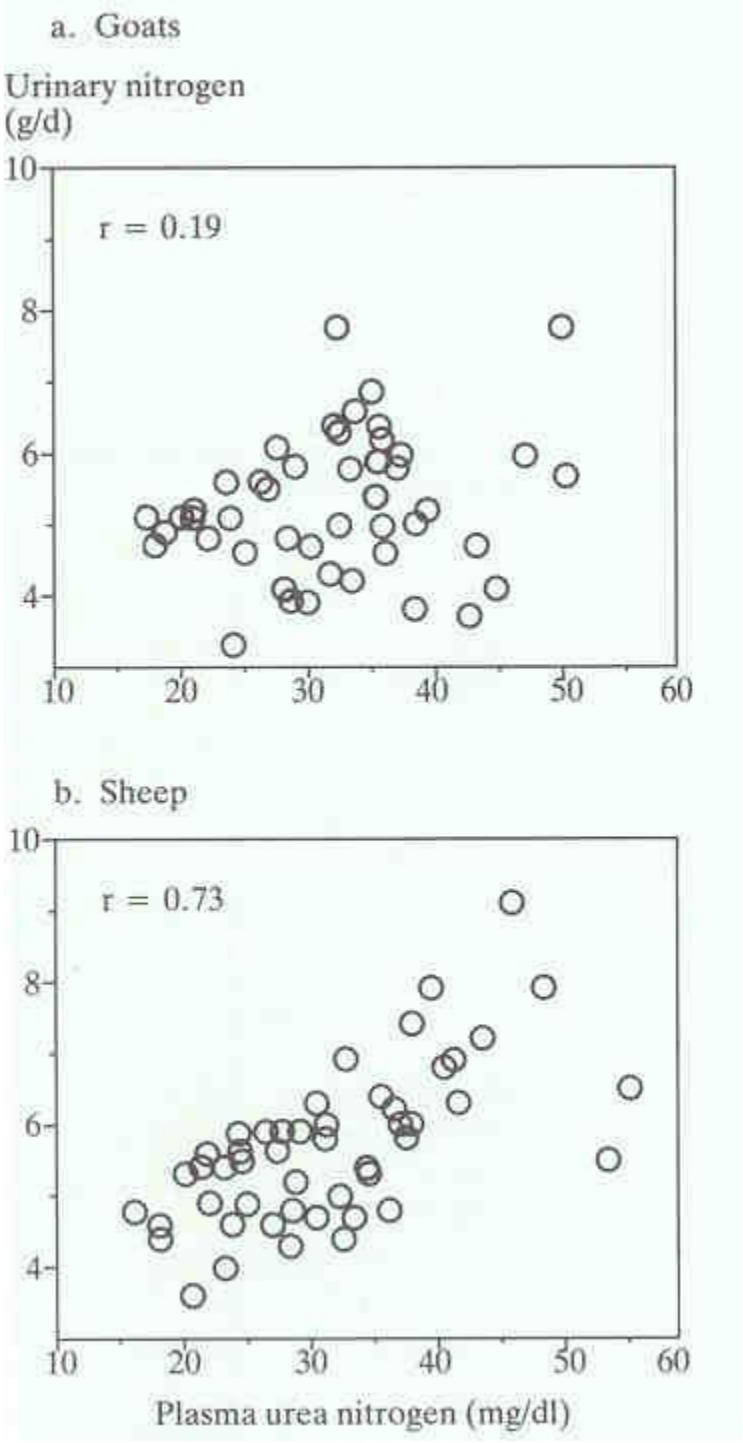
Proteolytic activity in the rumen is indicated by ammonia concentration. Rumen ammonia was highest for diets including *S. sesban* and lowest for diets with increasing amounts of *A. brevispica,*reflecting the rapid fermentation rate of *S. sesban* due to low phenolic and fibre contents (Table 5). Diets with *S. sesban* also had higher concentration of rumen ammonia than diets with *A. nilotica* or*A. seyal* (Rittner, 1987).

Rumen ammonia enters the plasma urea pool after it has been absorbed into the blood and converted to urea by the liver. Endogenous loss from tissue also enters this pool. Excess plasma urea nitrogen is excreted in urine, preventing toxicity in the animal. High values of plasma urea nitrogen indicate an inability of the animal to utilise nitrogen made available by digestion. As with rumen ammonia, plasma urea nitrogen was higher in animals fed diets including *S. sesban* than in those fed diets with *A. brevispica* (Woodward, 1988). Similar results were obtained when diets containing*S. sesban* were compared with diets including *A. seyal* or *A. nilotica* (Rittner, 1987).

When levels of plasma urea nitrogen were compared with levels of urinary nitrogen, a difference was observed between sheep and goats (Figure 1). The correlation between plasma urea nitrogen and urinary nitrogen was high in sheep (r = 0.73), but low in goats (r = 0.19). Also, urinary nitrogen was markedly lower in goats, which suggests that goats may be able to recycle more urea to the rumen than sheep at high levels of plasma urea nitrogen.

Figure 1*. Correlations between urinary nitrogen and plasma urea nitrogen for sheep and goats fed diets containing* Acacia brevispica *or* Sesbania sesban *combined with vetch hay and teff*

straw.



Source: Woodward (1988).

Faecal nitrogen. This is composed of indigestible feed nitrogen, microbial nitrogen from the rumen, and lower-tract and endogenous (metabolic) nitrogen secreted into the digestive tract but not incorporated into microbial nitrogen (Mason, 1969; Van Soest, 1982). Indigestible feed nitrogen in the faeces is insoluble in neutral detergent and can be estimated by the amount of

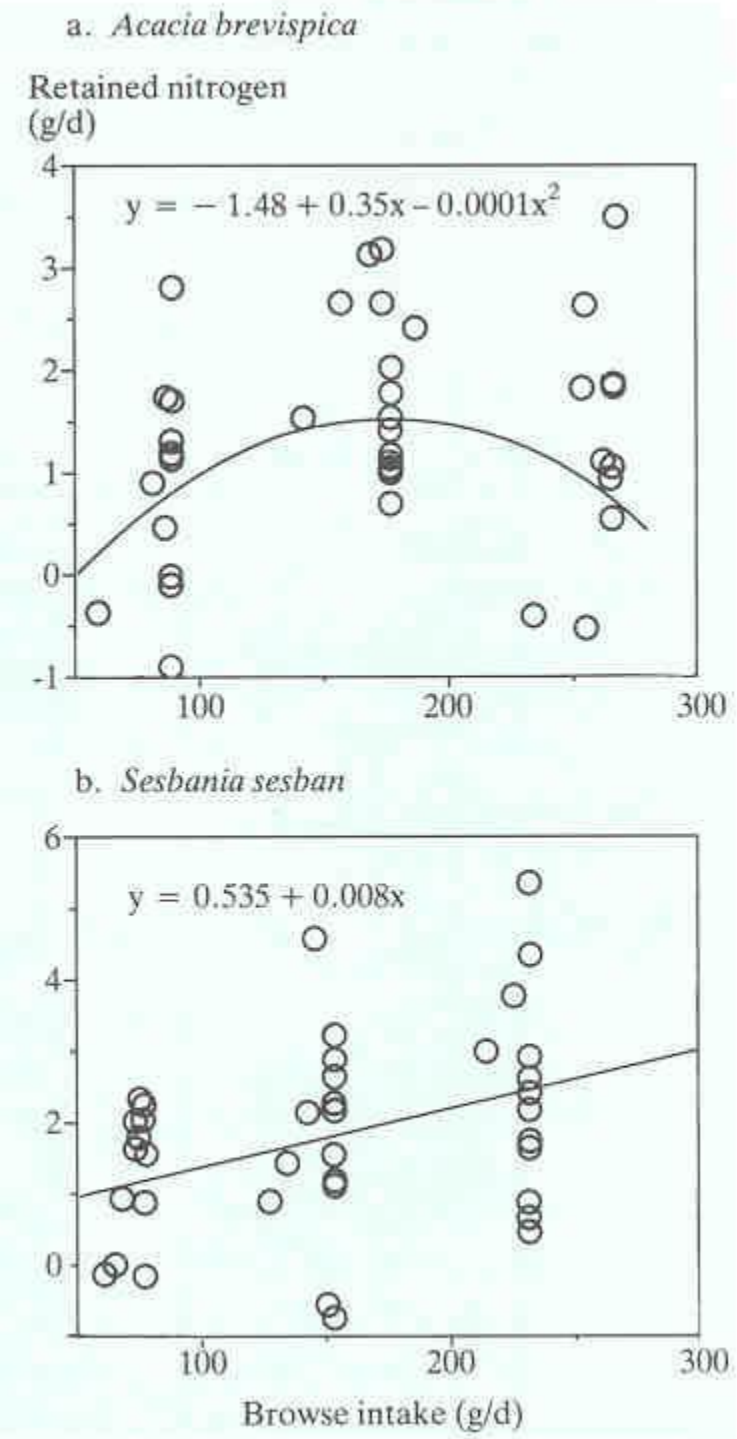
nitrogen in neutral-detergent fibre (NDF-N) (Mason, 1969). Faecal NDF-N may also include indigestible tannin-protein complexes (Reed, 1986).

Higher total faecal nitrogen (which could be accounted for by higher faecal NDF-N) was observed for all diets containing tanniferous feeds (Rittner, 1987; ILCA, 19886; Tanner, 1988; Woodward, 1988; Reed et al, in press). The higher faecal NDF-N values can be attributed to indigestible tannin-protein complexes.

Sheep fed diets containing *A. seyal* had high levels of faecal nitrogen (Reed and Soller, 1987; ILCA, 1988b). This fraction, also called the metabolic increment, is nitrogenous material of endogenous origin, and may result from a higher production of rumen microbes as a consequence of greater recycling of urea from blood to rumen.

Nitrogen retention. This parameter summarises the value of a feed as a source of nitrogen. When *A. brevispica* and *S. sesban* were each fed at three levels in combination with vetch and teff straw, the amount of retained nitrogen was higher for all diets containing browse than for vetch alone (Woodward, 1988) (Figure 2). Nitrogen retention increased as a linear function of intake of *S. sesban,*but increased then decreased as a function of intake of *A. brevispica.* The quadratic term in the regression of retained nitrogen on intake of *A. brevispica* was significant ($P<0.05$).

Figure 2. *Retained nitrogen as a function of intake of* Acacia brevispica *or* Sesbania sesban, *each fed at three levels with vetch arid teff straw.*

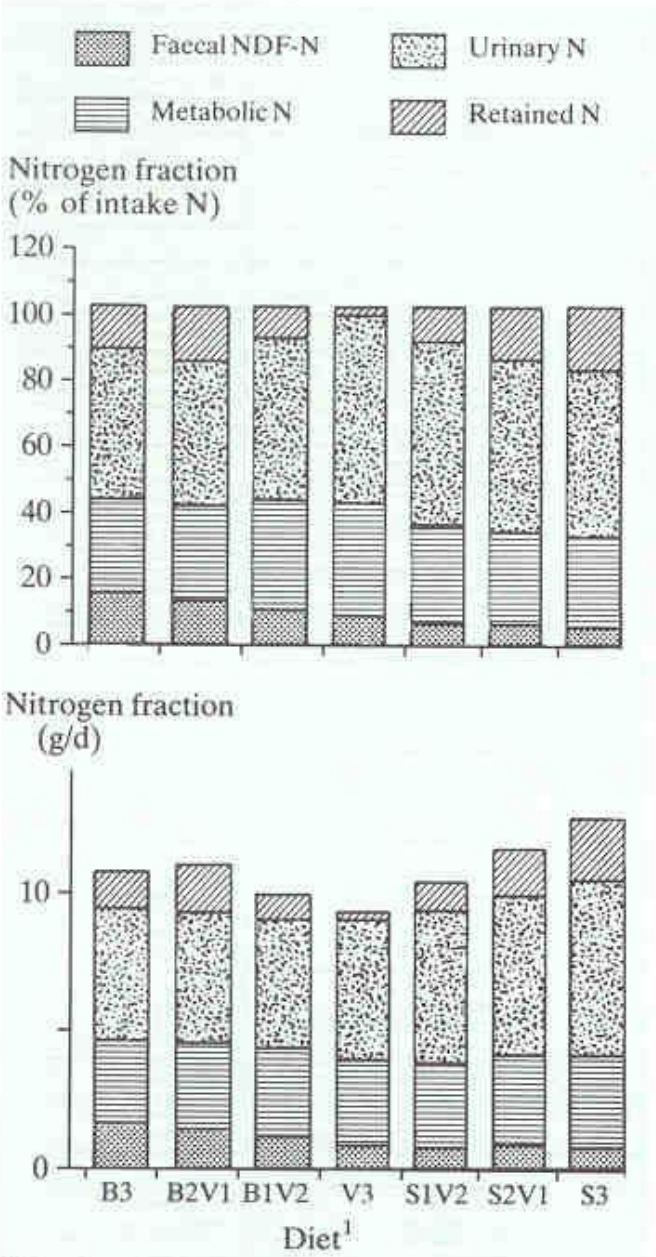


Source: Woodward (1988).

Partioning of intake nitrogen among faeces, urinary and retained nitrogen explains the difference between *S. sesban* and *A. brevispica* (Woodward, 1988) (Figure 3). For diets

including *S. sesban,* urinary nitrogen increased with increasing proportion of browse in the feed, but remained a constant fraction of intake nitrogen. Also, metabolic nitrogen (expressed in g/d) did not vary but decreased as a fraction of intake (Figure 3). Therefore, nitrogen retention increased steadily.

Figure 3. *Partitioning of intake nitrogen (N) for seven diets fed to intact animals.*



[1] Numbers in diet designations refer to proportions of nitrogen provided by *Acacia brevispica* (B), *Sesbania sesban* (S) and *Vicia dasycarpa* (V).

Source: Woodward (1988).

For diets including *A. brevispica,* faecal NDF-N increased by 2% of intake nitrogen with each incremental increase in *A. brevispica.* The loss of nitrogen in urine was much lower for *A. brevispica* than for *S. sesban,* but it was not significantly different between a diet of *A. brevispica plus* vetch and a diet of *A. brevispica* alone. The lower urinary nitrogen loss offset the increased faecal NDF-N loss sufficiently to increase nitrogen retention with the *A. brevispica* and vetch mixture but not with the browse alone. The ability to compensate for a higher loss of faecal nitrogen with a lower loss of urinary nitrogen was observed also by Rittner (1987), ILCA (1988b) and Reed et al (in press).

Digestibility of nitrogen. In non-tanniferous feeds, the true digestibility of nitrogen is approximately 93% (Van Soest, 1982). For browses used in ILCA's experiments, the true digestibility of nitrogen ranged from 52 to 94% (Table 6). Browses with high contents of proanthocyanidins typically had low nitrogen digestibilities, reflecting the ability of these chemicals to bind protein, thereby reducing its availability to the animal.

Table 6*. Nitrogen digestibilities and contents of soluble phenolics and insoluble proanthocyanidins for nine browses.*

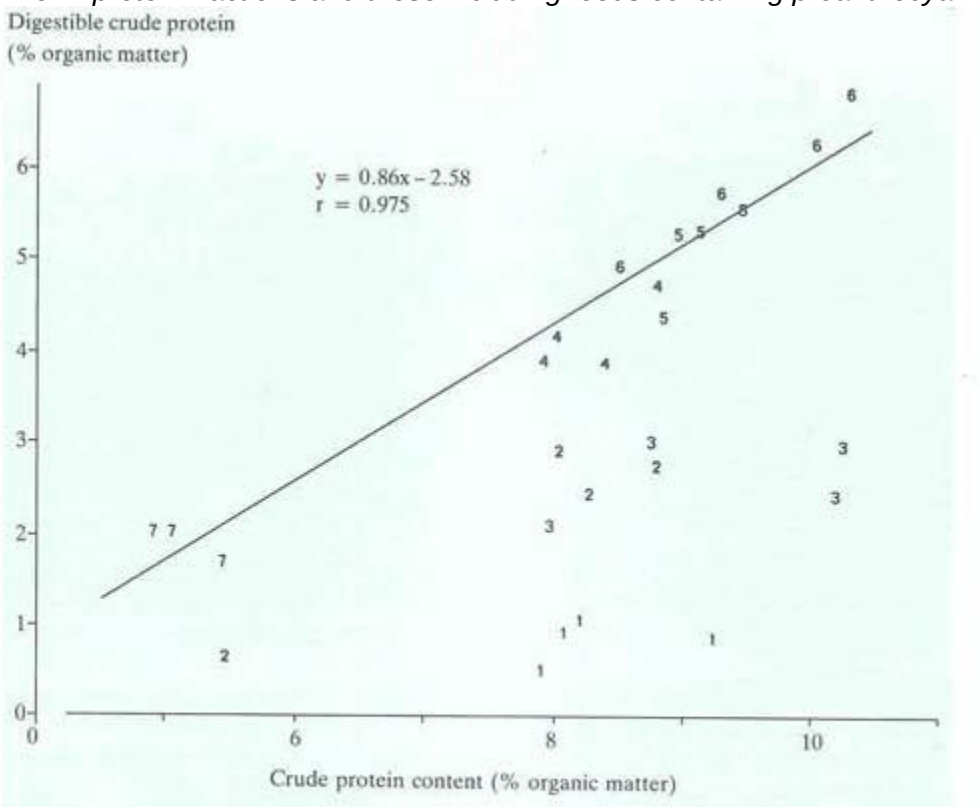
Browse[1]	Nitrogen digestibility (%)							Soluble phenolics (% DM)	Insoluble proanthocyandins (A_{550})
	Source[2]:	Ri	T	I	Re	W	Mean		
Sesbania sesban(l)		92	–[3]	94	90	94	92	17	0.06
Acacia nilotica (l)		90	–	93	–	–	92	34	0.18
Acacia brevispica(l)		–	–	–	–	85	n.a.[4]	24	0.37
Acacia seyal (l)		86	–	84	84	–	85	30	0.30
Acacia tortilis (f)		–	81	–	–	–	n. a.	37	0.31
Acacia albida (f)		–	80	–	–	–	n. a.	36	0.27
Acacia nilotica (f)		–	80	–	–	–	n. a.	44	0.89
Acacia sieberiana(f)		–	70	–	74	–	72	42	0.12
Acacia cyanophylla (l)		–	–	–	52	–	n. a.	39	0.45

[1] Plant parts used were leaves (l) and fruits (f).
[2] Ri = Rittner (1987); T = Tanner (1988); I = ILCA (1988b); Re = Reed et al (in press); W = Woodward and Reed (in press).
[3] Dash (–) indicates that the browse was not studied.
[4] n. a. = not applicable, since only one value is available.

Uniform feed fractions are those fractions for which the digestible amount of the fraction can be related to feed content by a linear regression, with the y-intercept indicating the amount of the fraction which is produced metabolically and appears in faeces (Van Soest, 1982). The true digestibility of uniform feed fractions can be predicted from chemical analysis of the feed, without conducting a feeding trial.

When three tanniferous browses were compared with one non-tanniferous browse and three traditional supplements, the four non-tanniferous feeds fell on a regression line typical of protein (Reed et al, in press) (Figure 4). The three diets including acacias fell below the line, describing non-uniform behaviour caused by the complexing of protein with tannins. The non-uniform behaviour of the protein in browse causes a problem for their use as sources of protein and emphasises the need to understand the chemistry of tannin-protein interactions.

Figure 4. *Regression of digestible amount of protein on protein content, for diets[1] having uniform protein fractions and those including feeds containing proanthocyanidins[2].*



[1] Includes four diets (4, 5, 6 and 7) with non-tanniferous protein supplements.

[2] Refers to diets 1, 2 and 3 which included *Acacia cyanophylla* and fruits of *A. sieberiana* and *A. seyal*, respectively.

Source: Reed et al (in press).

FACTORS AFFECTING THE USE OF BROWSE

Browse is a readily available feed resource and has a role to play in agroforestry. In cropped areas, browse can supplement crop residues, providing animal feed at the cost of the labour needed to harvest it. Most other supplements must be purchased. In grazing areas, browse can provide feed in dry seasons when grass has low nutritional value. The experiments conducted

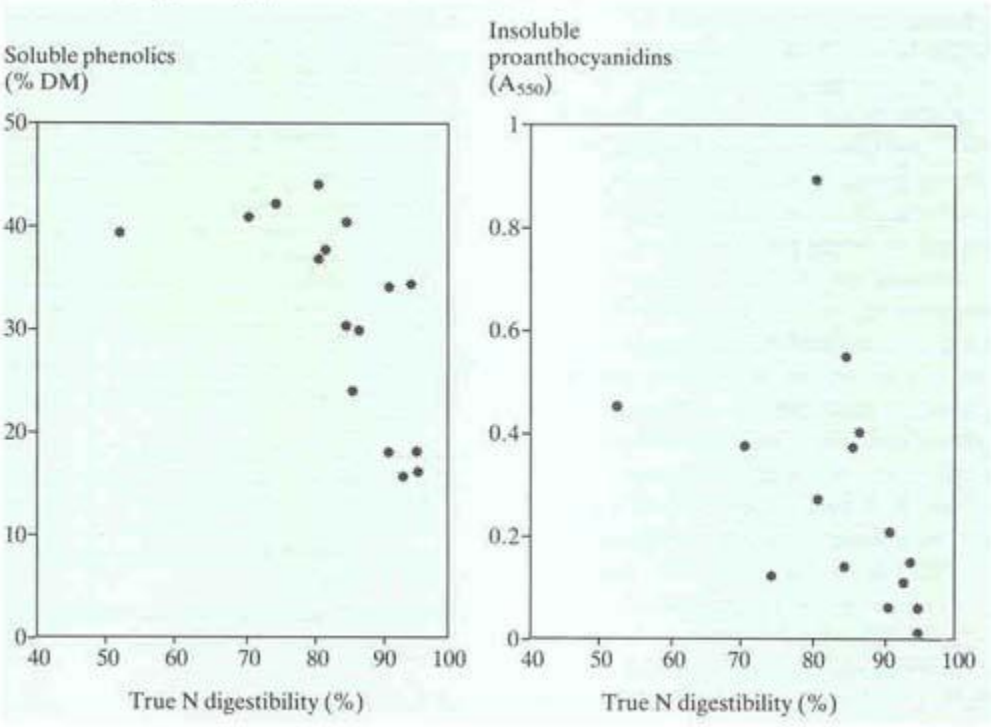
at ILCA highlighted factors that must be considered when evaluating browses for use in livestock systems.

Chemistry of browse

Research at ILCA has shown that polyphenolics in browse, especially proanthocyanidins, affect the availability of protein to, and the nitrogen metabolism of, ruminants. The complexity of tannin chemistry has made it difficult to define chemical fractions that have predictable effects.

The two fractions measured at ILCA, acetone-soluble phenolics and neutra-detergent insoluble proanthocyanidins, have nutritional relevance. However, their effect on nitrogen digestibility, for example, is variable (Figure 5). Hence, it is necessary to look at the effects of individual compounds. This can be accomplished using chromatographic techniques in combination with animal experiments. ILCA has conducted such research, but the determination of the effects of individual compounds is still in the early stages.

Figure 5. *Relationship between soluble phenolics or insoluble proanthocyanidins and the true nitrogen (N) digestibility for browses used in ILCA trials.*



Sources: ILCA (1988b); Tanner (1988); Reed et al (in press); Woodword and Reed (in press).

Effects of browse on ruminants

The studies of browse species at ILCA showed the formation of tannin-protein complexes to be the major effect of polyphenolics in browse, leading to reduced digestibility of nitrogen. The consequences for the animal were an increased faecal nitrogen excretion and a lower rumen fermentation rate.

When an extreme amount of nitrogen was bound, as was the case with *A*. *cyanophylla*, the animal could not achieve positive nitrogen balance and would eventually starve. When the phenolic content was very low (as with *S. sesban*, for instance), fermentation was so rapid that excess ammonia had to be excreted as urea in urine. This represented loss of nitrogen as well as of the energy required for detoxification.

Most of the other species evaluated in ILCA's studies had effects which were between the extremes described above. Their moderate levels of proanthocyanidins reduced nitrogen availability enough to slow rumen fermentation, thereby resulting in little excess ammonia. The consequently lower plasma urea nitrogen reduced loss of nitrogen in urine. More efficient recycling of plasma urea nitrogen to the rumen may also have contributed to a lower loss of nitrogen in urine. Thus in animals eating feeds with moderate levels of proanthocyanidins, higher faecal nitrogen loss was offset by lower urinary loss. Another advantage of such browses is that the lower fermentation rate of their nitrogen helps improve the utilisation of fibrous crop residues, which also ferment slowly.

The disadvantage is that proanthocyanidins bind protein into complexes, which lowers both the digestibility of crude protein and its availability to animals. The amount of browse offered must, therefore, take into account the lower digestibility of protein. The additional browse needed to provide an adequate amount of protein will depend on the degree to which protein availability is reduced by proanthocyanidins.

Finally, the possibility of animals becoming adapted to browse must be considered. This appears to occur with animals eating *A*. *seyal*, whose feed intake and performance improved after 7 weeks. Adaptation may be possible with other browses as well, although the mechanism is not understood.

CONSIDERATIONS FOR EVALUATION AND MANAGEMENT OF BROWSES

The concentrations of soluble phenolics and insoluble proanthoeyanidins in browses vary with season (Woodward, 1988), site (Le Houérou, 1980) and individual plant. *Acacia cyanophylla* is an example of regional variation. It has been fed to small ruminants with good results in West Africa (Dumancic and Le Houerou, 1980) but in East Africa, it has proved to be a poor feed (Reed et al, in press).

Evidence for the variation in phenolic concentrations within species and among the collections made for ILCA's experiments is given in Table 1. The reasons for the different concentrations found may have to do with plant strategy for defence against herbivores (Janzen, 1979) or with response to soil and climate (Le Houérou, 1980). In either case, variation must be considered when selecting species and individuals for propagation or when generalising results obtained in one region to another.

In some management systems, browse may be harvested and stored for feeding during the dry season. Rittner (1987) has shown that the effect of storage on phenolic concentration varies with species: the phenolic content of *A*. *nilotica* was not influenced by storage, but it shifted from the insoluble to the soluble fraction in *A*. *seyal*. Once again, the need to evaluate individual species is apparent.

With respect to fruits, Tanner (1988) observed that in some cases it may be advantageous to process them to reduce bulk and mechanical damage to the rumen. He also found variation between species in the number of seeds which escape digestion. He suggested that scarification or other treatment may increase the utilisation of fruits from tanniferous browse.

CONCLUSION

The International Livestock Centre for Africa has made good progress in under-standing the positive and negative effects of browse on the nitrogen metabolism of ruminants. Although there is still much to be learned before the nutritive value of browse can be predicted from chemical analysis alone, nutritionally important fractions have been identified. ILCA's research shows that the contents of insoluble proanthocyanidins and soluble phenolics in feed are related to nitrogen digestibility.

Browses with moderate levels of phenolic compounds, such as leaves of *A. brevispica, A. seyal* and *A. nilotica* and fruits of *A. albida* and *A. tortilis,* are promising protein supplements. Although the phenolics in these species reduce nitrogen availability, the negative effect is partially offset by lower urinary loss of nitrogen, allowing adequate animal performance.

Sesbania sesban has low levels of phenolics, typical of such standard high-protein leguminous forages as lucerne *(Medicago sativa). Acacia seyal* is a potentially useful feed if animals are allowed to adapt to it. Animals did not perform well with *A. cyanophylla* leaves and fruits of *A. sieberiana* and *A. nilotaca.* These conclusions cannot automatically be generalised to other areas, but knowledge of the phenolic content of these species from other regions would make it possible to predict performance.

The use of browse can improve animal feeding systems but individual browse species must be evaluated according to their effects on the metabolism of individual animals.

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