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Use of Trees by Livestock

ANTI-NUTRITIVE FACTORS

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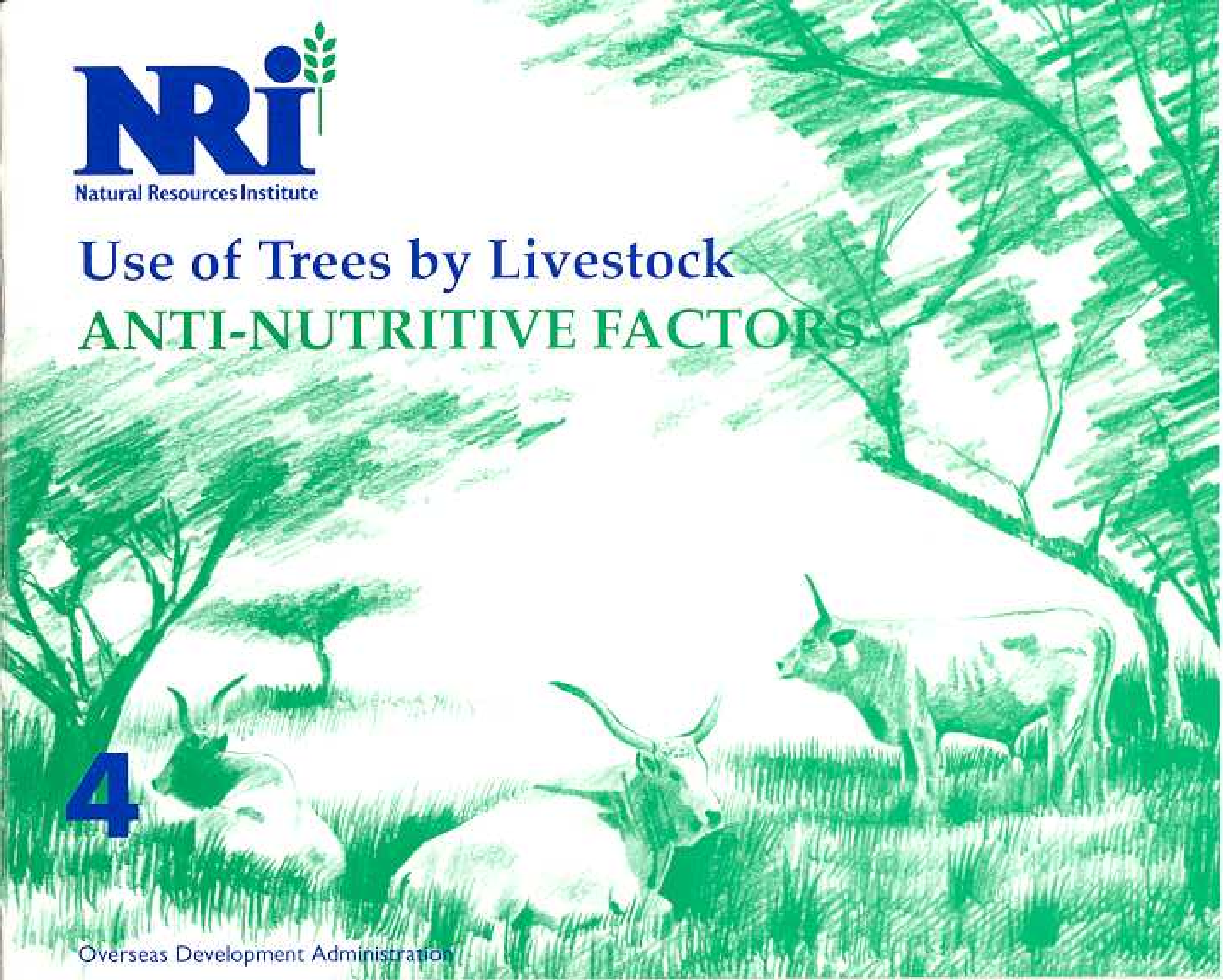

Overseas Development Administration

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Use of Trees by Livestock
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R.T. Paterson

Natural Resources Institute

The scientific arm of the
Overseas Development Administration

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Foreword

The importance of trees and shrubs in the feeding of animals in the tropics and sub-tropics has long been recognized by livestock owners. In arid areas where the growth of herbaceous plants is limited by lack of moisture, leaves and edible twigs of trees and shrubs can constitute well over 50% of the biomass production of rangeland. At high altitudes, tree foliage may provide over 50% of the feed available to ruminants in the dry season, branches being harvested and carried to the animals. Even in regions of higher rainfall where grass supplies the major proportion of the dry matter eaten by ruminants, tree leaves and fruits can form an important constituent of the diet, particularly for small ruminants.

In the last two decades interest in the planting of trees as a source of feed for livestock has been encouraged by workers in research and development, but in contrast to the hundreds of indigenous species which are used as fodder, attention has focussed on a limited number of introduced species. Thus there are many publications reporting the chemical composition of *Leucaena leucocephala* leaves and suggesting management strategies for utilization of the tree for fodder, but it is more difficult to find information on alternative genera which might be equally, or more, appropriate.

The aim of this series of publications is to bring together published information on selected genera of trees which have the potential to increase the supply of fodder for ruminants. Each booklet summarizes published information on the fodder characteristics and nutritive value of one genus, with recommendations on management strategies, where available. Since the leaves of woody species frequently contain secondary compounds which may have an anti-nutritional or toxic effect, this booklet summarizes the effects of a number of these compounds. It is hoped that the booklets will provide useful resource material for students, research and extension workers, interested in promoting the use of trees as a source of fodder for ruminants

Further copies of this booklet or others in the series can be obtained by writing to Publishing and Publicity Services at the Natural Resources Institute.

Margaret Gill
Livestock Production Programme

Summary

Woody plants contain a wide array of anti-nutritive factors which can have either repellant or adverse effects on livestock. While physical features of plants will serve only to limit intake and hence production, chemical components may lead to stock losses through poisoning. Manifestations of toxicity will depend on the level of toxin in the plant (which itself varies with the plant part, the variety, the species, the season of the year and the conditions under which it has grown), the level of intake of the feed and the extent and rate of metabolism of the toxic constituents within the animal. The simultaneous occurrence of several toxic substances in the same feed creates difficulties in establishing a hierarchical order of potency and complicates attempts to detoxify the feed by simple, cost-effective means.

There is a need for further research to elucidate some of the problems involved in the utilization of foliage from trees and shrubs. At present, perhaps the greatest need is for the development of laboratory tests which accurately reflect animal performance in the presence of anti-nutritional factors such as tannins and alkaloids. This will require extensive collaboration between chemists, agronomists and animal nutritionists in order to establish correlations under a wide range of conditions of both plant and animal growth.

Introduction

Anti-nutritive factors are those physical and chemical features of plants potentially available for grazing or browsing, which result in lower levels of animal productivity than would be expected from proximate and mineral analyses of the foliage. In general, they serve to protect the plants from excessive damage by being feeding deterrents to herbivores. Many factors appear to be the natural result of co-evolution of the plants with herbivorous animals (Levin and York, 1978; Brewbaker, 1989). Others have probably evolved as protection mechanisms against insect pests and plant diseases (D'Mello, 1982), in which case their effects on higher animals may be coincidental.

Many features of plants are capable of reducing their acceptability to animals and they range from the

purely physical, to symbiotic relations and chemical reactions. Plants can be rendered unattractive as forage by virtue of their effects on any of the senses of the animal. *Acacia lysiphloia* has sticky foliage, and *A. coriacea* gives off an offensive odour, both of which are repellent to livestock and result in reduced acceptance of the feed (Fox, 1987). Alternatively, physiological effects on digestion and metabolism can also reduce voluntary intake by the grazing animal, with a consequent loss of productivity. Many of the chemical effects are caused by potentially toxic substances. Under normal grazing conditions intake may be insufficient to result in stock losses, but animal productivity is often reduced even in the absence of physical symptoms of toxicity. Deaths usually occur in such cases only when animals are hungry and access to alternative fodder is limited.

The study of anti-nutritive factors is complicated by the frequent occurrence of more than one toxic compound in a single feed source. This creates difficulty in the establishment of a hierarchical order of potency. The toxic principles may also act synergistically. The levels of deleterious substances vary with plant part, species, cultivar, growing conditions and season of the year and post-harvest treatments such as drying, soaking, autoclaving and germination of seed material. Extrapolation from case to case must therefore be made only with great care.

Shrubs and trees exist which are highly toxic at all times of the year and under almost all circumstances. They contain phytotoxins, sometimes known as toxalbumins (Kingsbury, 1964). These complex molecules, similar in both structure and physiological reaction to bacterial toxins, can kill at extremely low levels of intake, as with *Robinia pseudoacacia* (black locust) and *Rinicus communis* (castor bean). These plants are generally avoided by livestock, except when severe nutritional stress makes feed selection difficult, or when toxic plants are cut and mixed with other, acceptable fodder. Animals which have never been exposed to the poisonous plants are at greater risk than those which are accustomed to them.

Such plants and their toxic principles are beyond the scope of this review, which deals only with those anti-nutritive factors commonly found in shrubs and trees with potential for feeding domestic livestock.

Acceptability of plants

Physical features

Physical features of plants generally affect their acceptability to livestock and consequently the level of voluntary feed intake. Several aspects of the acceptability of fodder are purely physical in nature and are considered below.

Growth form

This is the most obvious physical deterrent to consumption by herbivores. Many herbaceous species avoid being grazed through a creeping growth habit. While animals such as horses and sheep can graze close to ground level, cattle are limited in their ability to defoliate prostrate plants such as *Desmodium triflorum*. Most trees will rapidly grow out of the reach of domestic grazing animals unless they are suitably managed. Species such as *Leucaena leucocephala* will readily regrow after severe cutting or defoliation, even to ground level, while others such as *Sesbania* spp. are much less tolerant of complete defoliation (Skerman *et al.*, 1988).

Thorns and spines

Within any given genus there may be both armed and unarmed species, but *Acacia, Caesalpinia, Erythrina, Mimosa* and *Prosopis* are all recognized for their dangerous thorns and spines (Allen and Allen, 1981). The presence of these features and their distribution on the plant are of great importance in determining their usefulness as a browse species for different classes of livestock.

Selective grazers such as goats and camels can consume foliage that is unacceptable to cattle and sheep; and while sheep make use mainly of fallen leaves and pods of *Prosopis tamarugo* in Chile, goats are, to some extent, able to avoid the spines while browsing the green foliage (Habit *et al.*, 1981). In Australia, *Acacia polyacantha* has spines that protect it from most grazing animals (Skerman *et al.*, 1988), while in Africa, species such as *A. detinens, A. karoo* and *A. tortilis* form impenetrable thickets which can impale game (Allen and Allen, 1981).

Myrmecophily is an obligatory, symbiotic association between ants and plants, the best known example being the habitation of swollen, stipular *Acacia* thorns by ants of the genus *Pseudomyrmex*. The

ants feed on the enlarged foliar nectaries and modified leaflet tips of the plant. In return, they protect it from defoliation by insects and herbivorous animals by swarming to attack when the tree is disturbed. Approximately nine neotropical species of *Acacia* share non-specific, obligatory relationships with some five ant species (Allen and Allen, 1981). The ants, amongst the most ferocious in the world, present a formidable defensive barrier to the grazing animal.

Other

Cattle generally show a marked preference for grass and soft herbage rather than tough, sclerophyllous leaves. This characteristic is shared, to some extent by sheep but probably not by goats. Such a preference, however, often assumes importance only when animals are presented with a choice. In arid and semi-arid regions, or at particularly dry times of the year, the choice is often between consuming unattractive leaf material or going hungry. Foran (1984) noted that in central Australia, *Acacia aneura* and *A. kempeana* contributed up to 40% of the diet for cattle during the hardest times of the year, but when grass was abundant, the level normally fell to less than 20%. Thus, while the shrubs are clearly not the favourite cattle forage in this region, they are consumed in large quantities when the preferred species are not available.

Chemical features

The leaves of woody plants tend to contain more anti-nutritive components (plant secondary compounds) than those of herbaceous plants. This is particularly true of phenolics (Bate-Smith, 1962), although there is a wide range of chemical components capable of having adverse effects on herbiverous animals.

Phenolic compounds

Plant materials contain a wide range of phenolics from low molecular weight, metabolizable phenols to the much larger polyphenols, a group which, with molecular weights in the approximate range of 500-3000, includes the tannins. Phenolic compounds are commonly found in the leaves, bark, fruit and twigs of trees and are thought to confer resistance to both insect and fungal attack (D'Mello, 1982). Much has been written about the anti-nutritional effect of tannins on herbivores including recent reviews from McLeod (1974), Kumar and Singh (1984), Mangan (1988) and Kumar and Vaithiyanathan (1990).

Chemically, tannins are complex phenolic polymers containing aliphatic and phenolic hydroxyl groups and in some cases, carboxyl groups. The term tannin comes from the use of plant extracts in the tanning of leather which bind protein to form insoluble tannin-protein complexes. They are generally classified into two structural types, depending on their chemical properties.

Hydrolyzable tannins are mainly found in fruit pods and plant galls (Liener, 1980). They have a central carbohydrate core and can be degraded by chemicals or enzymes into a sugar residue and a phenol-carboxylic acid which can then be absorbed through the gut wall of the animal. These can be further subdivided depending on the nature of the phenol-carboxylic acid component into, for example, gallotannins and ellagitannins, which can influence feed intake by affecting the palatability of the feed. They may also have a toxic effect on animals (Mangan, 1988).

Condensed tannins (procyanidins or proanthocyanidins) have no carbohydrate core and are usually derived from condensation of flavonoid precursors. They cannot be degraded by enzymes and are therefore unlikely to pass through the gut wall. They are the principal tannins of forage legumes and they usually exist in the plant as leucoanthocyanins. The formation of protein-tannin complexes may depress the nutritive value of fodder by reducing both voluntary feed intake and digestibility. The acceptability of browse is clearly a complex matter but it appears to be related to the concentration of condensed tannins although there may be a threshold possibly at about 5%, below which there is no measurable effect (McNaughton, 1987).

Tannins mainly affect livestock by forming complexes with, and thus precipitating, proteins in the gut. Lower molecular weight polyphenolics in feeds, or products of tannin degradation, could also have an effect. Tannins provoke an astringent reaction in the mouth of the animal (Bate-Smith, 1973), probably by reacting with proteins in the saliva and the mucous epithelium, to impair lubrication in both the mouth and the oesophagus. They may inhibit digestibility by forming relatively indigestible

protein-tannin complexes and by directly inhibiting digestive enzymes and micro-organisms. The effect on rumen microflora appears to be a result of the formation of complexes with proteins in the cell wall.

Tannins are assumed to reduce voluntary feed intake, either by their astringent effect, or by reducing protein digestibility and absorption but the exact mechanism is poorly understood and results are conflicting. Tannic acid added to the feed does not always produce the results ascribed to natural tannins. However, many factors interact to control voluntary intake (Forbes, 1986) and thus the response to individual factors will vary according to the specific circumstances.

There is a mechanism which protects animals from the potentially toxic effects of tannins and this is demonstrated by greater tolerance when either tannic acid or naturally occuring tannins are ingested orally rather than when administered by subcutaneous injection. At high levels of feed intake, tannins react with both muco-proteins and the outer cellular layer of the digestive tract. This appears to alter the permeability of the gut wall resulting in gastritis, intestinal irritation and constipation. Under such conditions, tannins may be absorbed by the animal and result in liver and kidney damage if the physiological detoxication mechanisms are inadequate to cope with the influx.

The tolerance to tannins varies between animal species. The saliva of some species such as deer, rodents and goats, appears to contain proline-rich proteins, which may constitute a first line of defence against tannins. Cattle, sheep and chickens appear to have less, or possibly no capacity to secrete these proteins (D'Mello, 1992). Poultry and horses have been shown to develop symptoms of toxicity when fed tannic acid at levels of about 2% of diet (dry matter basis) under experimental conditions, while ruminants are able to handle higher levels of the acid without adverse effects.

Although deaths in sheep and cattle have been attributed to the high levels of tannins found in the foliage of trees such as *Quercus* spp., McLeod, (1974) concluded: 'there is no evidence that forage tannins have any detrimental effect upon the grazing ruminant, even though tannins have been shown to reduce protein digestibility.' A more recent review (Kumar and Singh, 1984), however, implicated tannins in: low milk yields; a reduction in available sulphur; in toxic, degenerative changes in the intestine, liver, spleen and kidney; and the appearance of mucus in urine and fatal constipation. These authors suggested that tannin-rich fodder for ruminants should be restricted or fed with caution. They also pointed out that the risk to unconfined animals was generally small, since given a choice they will seldom consume enough tannin to suffer harm.

The literature abounds with conflicting reports on the effects of tannin content on animal performance. There are several possible explanations for the apparent contradictions.

(a) The choice of assay. There are a number of analytical techniques which have been used to estimate tannin content and these have been critically reviewed by Hagerman and Butler (1989). They are based on measures of either chemical groups and structures (e.g. based on Folin, or Prussian blue reagents, vanillin or butanol) or biochemical activity (e.g. protein precipitation tests). Different assays can result in widely varying estimates of tannin content, since they are designed to measure different characteristics. Ahn *et al.*, (1989) reported that leaf dry matter of *Acacia angustissima* contained up to 6.5% tannin when assayed by the vanillin-HCl method, whereas no tannins could be detected by the butanol-HCl technique. There was also poor correlation in some browse species between nitrogen digestion and total condensed tannin content as measured by either vanillin or butanol-HCl assays. Clearly determinations made using different techniques are not necessarily comparable. Hagerman and Butler (1981) noted evidence that the protein binding capacity of tannins could be highly specific to certain proteins.

(b) The presence of other factors. More than one anti-nutritive factor can be present in a single feed and this can confound results. Tanner *et al.*, (1990) suggested that the poor performance of sheep fed on pods of *Acacia sieberiana* was due to the presence of both tannins and cyanogenic glycosides.

(c) Seasonal variation. Both the concentration and the type of phenolic compounds within the plant are subject to continual change. Van Hoven (1985)

described the rapid mobilization of phytochemicals in response to defoliation by animals. As leaves and fruits mature, phenolic compounds polymerize, resulting in a decrease in the protein precipitating capacity (Makkar *et al.*, 1988).

(d) Individual variation. The levels of anti-nutritive factors vary considerably between different parts of the same plant and there can be wide variation between individual trees of the same species (Joshi *et al.*, 1985). This is true even of trees grown at the same site. With reports from different sites, it is not known to what extent observed variations are due to either environment or heredity.

In addition to the deleterious effects noted above, condensed tannins are generally, but not universally, considered to have two beneficial effects in ruminant nutrition. Firstly, they may protect labile plant proteins from microbial degradation in the rumen, thereby increasing the supply of high quality protein entering the duodenum and becoming available for absorption by the animal. Secondly, tannins appear to be implicated in the prevention of bloat in sheep and cattle by hindering the formation of stable protein foams in the rumen.

Since tannins occur in many valuable sources of animal feed, including forage crops, agricultural wastes and by-products, and tree foliage, it has been suggested that the digestibility of feeds could be improved by breeding programmes to develop low-tannin crop lines. Given the protective function of tannins in the plant, however, such a procedure could lead to a loss of resistance to pests and diseases, thereby replacing a nutritional problem with an agronomic one (D'Mello, 1982).

Other approaches to the problem of tannins include water or alkali treatment or addition of adsorbents to remove tannins, or reaction with formalin to convert them to nonreactive resins. These processes all increase the cost of the feed and some lead to substantial losses of dry matter. As far as ruminants are concerned, it seems likely that the best approach would be to develop feeding systems to optimize the use of high tannin fodder in conjunction with other feed sources.

Toxic amino acids

Free, non-protein amino acids have been detected, principally in the leaves and seeds of many plant species, including a number of grain, pasture and browse legumes. They are capable of interfering with the normal metabolic processes of animals as a result of their effects on either amino acid biosynthesis and transport, or on activation and incorporation of amino acids into protein molecules (Hammond, 1987). They influence the rate of protein synthesis, cause the formation of aberrant proteins and affect RNA and DNA metabolism. Manifestations of toxicity range from simple reductions of food and nutrient utilization to lethal neurological disorders (D'Mello, 1992). The best known of these compounds are mimosine and canavanine. Mimosine is found at high concentrations in *Leucaena* and *Mimosa* spp. where it acts as a natural fungicide. Canavanine occurs in some tropical species of *Canavalia* and *Sesbania*, as well as in the temperate legumes *Medicago sativa* (lucerne) and *Trifolium* spp. (clovers), where it appears to have insecticidal properties.

Mimosine is typically found in foliage of mature *Leucaena leucocephala* at concentrations in the range of 2-5% (Brewbaker and Hylin, 1965), with higher levels of up to 10% in young, expanding leaves (Skerman *et al.*, 1988). There is considerable variation in mimosine content between species of *Leucaena* and much attention has been paid to the production of inter-specific hybrids, often of *L. leucocephala* with either *L. diversifolia*, *L. pallida* or *L. pulverulenta*, to combine low levels of mimosine with high forage production (e.g. Gupta *et al.*, 1991). This approach could lead to reduced resistance to plant pests (D'Mello, 1982) and so may be inappropriate for general use.

It has long been recognized that *Leucaena* could cause depilation, growth reduction, general ill-health and reproductive disorders when fed to non-ruminants at levels in the range of 5-15% of the diet on a dry matter basis (Hutton and Gray, 1957). Ruminants show tolerance to higher dietary levels but for the sake of safety, it has frequently been suggested that cattle should not consume more than 30% of their diet as *Leucaena* (Jones and Hegarty, 1984).

In non-ruminants, mimosine is absorbed directly into the blood stream where it acts as a protease inhibitor (Liener, 1980). In ruminants, however, rumen

bacteria convert the mimosine to 3,4-dihydroxy-pyridine (DHP) which is then absorbed, acting as a goitrogenic agent to reduce the production of thyroxine.

In areas of the world such as Indonesia and Hawaii, where *Leucaena* is naturalized and animals have been fed it for many years, rumen bacteria have evolved which are capable of degrading DHP to non-toxic metabolites (Jones and Megarrity, 1983). In such areas, ruminants can be maintained on diets of 100% *Leucaena* for months at a time without showing symptoms of toxicity (Quintyne, 1987). The capacity to degrade DHP was transferred from goats in Hawaii to other goats and subsequently to cattle in Australia by inoculation with imported rumen liquor (Jones, 1985). Under normal grazing conditions, the rumen bacteria are able to move readily from one animal to another (Hammond, 1987), resulting in the rapid transfer throughout the herd, of the ability to utilize high levels of potentially toxic *Leucaena*. For a modest cost, ruminant resistance to mimosine toxicity can be introduced into areas where it does not occur naturally.

In Jamaica, a patented, anaerobic fermentation process has been developed which detoxifies ground *Leucaena* leaf meal for use in rations for non-ruminants (Lewis, 1987). The process produces three major fractions:

- fermented leaf meal with negligible mimosine and DHP content, which can be used at high levels in diets for pigs and poultry;
- fuel gas, containing about 70% of methane and hydrogen; and
- liquid organic fertilizer with an approximate N:P:K ratio of 13:4:35 on a dry basis.

This process offers a useful technique to utilize the productive potential of *Leucaena* forage for feeding to non-ruminants.

Canavanine is a water-soluble, heat-resistant structural analogue of arginine and as such is capable of radical interference in the metabolic pathways of livestock. Mammals are considered to be more tolerant of canavanine than are birds and the productive potential of *C. ensiformis* could be utilized to feed pigs, provided that the meal is subjected to heat treatment to deactivate the lectins that are also present in the beans (D'Mello, 1992). Cattle consuming more than 30% of their diet as seed or meal of *Canavalia ensiformis* are at risk (Skerman *et al.*, 1988). Symptoms of toxicity include a low body temperature, a clear nasal discharge, frequent passing of clear urine, lameness, prostration and death. Skerman *et al.*, (1988) recommended heat treatment to remove the toxicity, although Parra *et al.*, (1988) indicated only a 50% reduction of canavanine content as a result of autoclaving. Treatment for 10 days with either 6% urea or 3% urea and 3% sodium hydroxide, led to complete elimination of the amino acid. The canavanine levels of beans of six cultivars of *C. ensiformis* ranged from 2.73-5.37%, suggesting that there may be scope for breeding to produce less toxic lines (Parra *et al.*, 1988), although this may reduce plant pest resistance (D'Mello, 1992).

Cyanogenic glycosides

Hydrogen cyanide (HCN) is potentially the most serious anti-nutritional factor in fodder trees, since rapid absorption of the toxin can lead to the death of the animal. Symptoms of HCN poisoning are due to oxygen starvation at the cellular level and include laboured breathing (dyspnoea), intense red conjunctiva, frothing at the mouth, bloat, convulsions and a staggering gait. Post-mortem examination often reveals a characteristic smell of almonds from the stomach contents.

Cyanogenic substrates, usually glycosides, react in the digestive tract of the animal with a hydrolyzing enzyme, often also found in the plant, to produce HCN. When HCN production is low, little threat is posed to the animal. Maslin *et al.*, (1987) suggested that plants producing HCN at levels above 20 mg/100g (7.5 μmol/g) fresh weight could be considered as dangerous to livestock. The stomach contents tend to buffer the absorption of cyanide in ruminants (Goodchild and McMeniman, 1987), possibly due to its reaction with sugars or with sulphur compounds, to form harmless cyanhydrins or sulphocyanides respectively (Steyn and Rimington, 1935). Plants containing both large amounts of cyanogenic glycosides and an endogenous hydrolytic enzyme have the highest potential for toxicity (Maslin *et al.*, 1987), although broad spectrum enzymes present in other fractions of the diet could react with the cyanogenic compounds

to release HCN. In South African *Acacia* spp., leaves and immature pods produced higher levels of HCN than mature pods (Steyn and Rimington, 1935). *A. robusta* contained the glycoside but not the hydrolyzing enzyme and so was considered to be less dangerous than other species.

HCN poisoning usually occurs only in sporadic outbreaks. A number of factors appear to be implicated, including the species and variety of browse consumed, the rate of ingestion and the availability of alternative feeds. It is more likely to occur during periods of drought or feed scarcity, when hungry animals consume large amounts of feed over a short period of time. Practical control measures can be taken to avoid cyanide poisoning:

- restrict the access to potentially poisonous plants and limit the grazing time during periods of feed scarcity;
- avoid feeding pods that are wet. Physically separate potentially dangerous feeds from water sources, since cold water appears to encourage the release of HCN;
- mix potentially toxic feeds with sulphur or molasses, or feed them in conjunction with licks containing these substances.

Alkaloids

The alkaloids are a heterogeneous group, with diverse chemical structures and this leads to problems of definition of both the group and their effects on livestock. Essentially they are complex compounds containing nitrogen, usually in heterocyclic and/or aromatic ring structures. They are basic in reaction, forming salts in the presence of acids. They are generally insoluble in water but extractable in organic solvents. Often they are poisonous to livestock but there are many examples of alkaloids with medicinal properties. Many are derived from amino acids and they have been described under headings that correspond to the amino acid unit (Southon and Buckingham, 1989). They are almost universally bitter in taste and while their role in plants has been variously ascribed, for example, as possible mechanisms of defence against plant pests (Levin, 1976), they are commonly held to represent evolutionary aberrations of nitrogen metabolism (Kingsbury, 1964).

Alkaloids are found in some 5-10% of all plants, being more common in tropical than in temperate species. Plant families such as Leguminosae, Amaryllidaceae and Compositae are noted for high levels of these compounds. Kingsbury (1964) indicated that more than 5000 alkaloids had been named and at least partially characterized. The alkaloid content of a plant is usually a feature of the cultivar, varying little with ecological factors such as climate, season and availability of water, although there can be wide differences between varieties of the same species. Unlike some other anti-nutritive factors such as tannins and amino acids which tend to be concentrated in certain plant parts, alkaloids are often uniformly distributed throughout the plant, all parts being equally dangerous (or beneficial) to livestock. The reaction of a given alkaloid in a given organism is usually quite specific, although there may be considerable variation between different alkaloids in the same animal species, or with the same alkaloid in different animals (Kingsbury, 1964).

One important subgroup in this category is that known as the pyrrolizidine alkaloids. These have a world-wide distribution, being present in both Leguminosae and Compositae (Smith and Culvenor, 1981). They are hepatotoxins which will cause fatal liver failure if ingested in sufficient quantities over a period of time (Molyneux and Ralphs, 1992). There is, however, a range of susceptibility to these compounds. Sheep are able to graze pastures considered dangerous to cattle, because of either better detoxification of the alkaloid in the rumen or through differences in hepatic activity (Hooper, 1978).

Clearly, shrub and tree species which contain appreciable quantities of alkaloids should be treated with caution where it is intended to utilize them as browse or fodder and they should be evaluated with a range of animal species before being recommended for general use. Nevertheless, the literature is not without its contradictions where alkaloids are concerned. *Erythrina*, a genus noted as a source of alkaloids, is attracting attention in Africa and South America as a multi-purpose tree suitable for use as fodder, and also for windbreaks, shade, fences and fuel (Brewbaker, 1989). Insufficient information is available to draw general conclusions regarding the effects of these compounds on animal production.

Differences in acceptability

There are many contradictions in the literature regarding the acceptibility of fodder from trees and shrubs, which may, or may not be of practical importance in commercial animal production. Reasons for the reported differences may be physical, chemical, or a combination of both. Some possible explanations are noted below.

(a) Acceptability can change during the year under the influence of season. Rodriguez *et al.*, (1987) showed that with milking goats, consumption of dry matter from fresh, young *Gliricidia* foliage was less than with older, mature leaves. As the growing season progresses, the proportion of mature foliage on the tree will increase which should lead to improved utilization by goats.

(b) In some cases, it may take several days for animals to accept a new feed but once accustomed to it, they may then consume it readily (e.g. Atta-Krah and Sumberg, 1987, for *Gliricidia).*

(c) Preference for one feed over another does not necessarily imply poor acceptability of the latter when the former is absent. Observations from 'cafeteria' type trials where animals are given simultaneous access to a range of fodders, must be interpreted with care, since they reflect preferences rather than absolute acceptance or rejection, and then only at the time of the trial. A species which is rejected in favour of another may be well accepted if it is offered as the sole feed, or at a different time of the year.

(d) Within a single species, differences in acceptability can exist between varieties, accessions or provenances, individual trees, and even between parts of the same tree. There is much scope through selection and possibly even breeding to enhance the desirable characteristics of woody plants (e.g. Habit *et al.*, 1981 for *Prosopis tamarugo*) and make them more available as fodder species.

(e) Within a single accession, acceptability can be influenced by edaphic and climatic conditions at the production site. The acceptability by animals of the same varieties of shrubby *Stylosanthes* spp. in Australia varies greatly between the sandy, infertile soils of the Cape York Peninsula and the more fertile soils of the Katherine region of the Northern Territory (W. Winter, Pers. Comm.)

References and further reading

ALLEN, O.N. and ALLEN, E.K. (1981) *The Leguminosae: A Source Book of Characteristics, Uses and Nodulation.* London: MacMillan Scientific and Medical Division.

AHN, J.H., ROBERTSON, B.M., ELLIOT, R., GUTTERIDGE, R.C. and FORD, C.W. (1989) Quality assessment of tropical browse legumes: tannin content and protein degradation. *Animal Feed Science and Technology,* **27:** 147-156.

ATTA-KRAH, A.N. and SUMBERG, J.E. (1987) Studies with Gliricidia sepium for crop-livestock production systems in West Africa. In: *Gliricidia sepium* (Jacq.) Walp: *Management and Improvement. Proceedings, Workshop held at CATIE, Turrialba, Costa Rica, June 1987.* Special Pub. 87-01. pp31-43. Hawaii, USA: Nitrogen Fixing Tree Association.

BATE-SMITH, E.C. (1962) The phenolic constituents of plants and their taxonomic significance. I Dicotyledons. *Journal of the Linnean Society (Botany)* **58:** 95-173.

BATE-SMITH, E.C. (1973) Haemanalysis of tannins: the concept of relative astringency. *Phytochemistry,* **12:** 907-912.

BREWBAKER, J.L. (1989) Nitrogen-fixing trees for fodder and browse in Africa. In: *Alley Farming in the Humid Tropics.* KANG, B.T. and REYNOLDS, L. (eds. *Proceedings, International Workshop held at Ibadan, Nigeria, March 1986.* pp 55-70. Ottowa, Canada: International Development Research Centre.

BREWBAKER, J.L. and HYLIN, J.W. (1965) Variations in mimosine content among *Leucaena* species and related Mimosaceae. *Crop Science,* **5(4):** 348-349.

D'MELLO, J.P.F. (1982) Toxic factors in tropical legumes. *World Review of Animal Production,* **18(4):** 41-46.

D'MELLO, J.P.F. (1992) Chemical constraints to the use of tropical legumes in animal nutrition. *Animal*

Feed Science and Technology, **38:** 237-261.
FORAN, B.D. (1984) Central arid woodlands. In: *Management of Australia's Rangelands*. HARRINGTON, G.N., WILSON, A.D. and YOUNG, M.D. (eds). pp 299-315. Canberra, Australia: Commonwealth Industrial and Scientific Research Organization.

FORBES, M. (1986) The Voluntary Intake of Farm Animals. Stoneham, USA: Butterworths.

FOX, J.E.D. (1987) Potential of Australian *Acacias* from arid and semi-arid zones. In: *Australian Acacias in 18 Developing Countries*. TURNBULL, J.W. (ed). *Proceedings, International Workshop held at Gympie, Australia, August 1986*. ACIAR Proceedings No.16. pp 17-28. Canberra, Australia: ACIAR.

GOODCHILD, A.V. and McMENIMAN, N.P. (1987) Nutritive value of Acacia foliage and pods for animal feeding. In: *Australian Acacias in Developing Countries*. TURNBULL, J.W. (ed.) *Proceedings, International Workshop held at Gympie, Australia, August 1896*. ACIAR Proceedings No.16. pp1 01-106. Canberra, Australia: ACIAR.

GUPTA, B.K., AHUJA, A.K. and KHEJURIA, H.N. (1991) Fodder analysis of new *Leucaena* varieties. *Leucaena Research Reports*, **12:** 40-41.

HABIT, M.A., CONTRERAS, D.T. and GONZALEZ, R.H. (1981) *Prosopis tamarugo:* fodder tree for the arid zones. FAO *Plant Production and Protection Paper* No.25. Rome: Food and Agricultural Organization.

HAGERMAN, A.E. and BUTLER, L.G. (1981) The specificity of proanthocyanidin-protein interactions. *Journal of Biological Chemistry*. **256:** 4494-4497.

HAGERMAN, A.E. and BUTLER, L.G. (1989) Choosing appropriate methods and standards for assaying tannin. *Journal of Chemical Ecology*, **15(6):** 1795-1810.

HAMMOND, A.C. (1987) Chemical, anatomical and other antiquality factors limiting forage utilization. In: *Forage Livestock Research Needs for the Caribbean Basin*. MOORE, J.E., QUESENBERRY, K.H. and MICHAUD, M.W. (eds) *Proceedings, Workshop held at Tampa, USA. February, 1987*. pp 59-69. Gainsville, USA: Caribbean Basin Advisory Group/University of Florida.

HOOPER, P.T. (1978) Pyrrolizidine alkaloid poisoning: pathology with particular reference to differences in animal and plant species. In: *Effects of Poisonous Plants on Livestock*. KEELER, R.F., VAN KAMPEN, K.R. and JAMES, L.F. (eds). New York: Academic Press.

HUTTON, E.M. and GRAY, S.G. (1957) Problems in adapting *Leucaena glauca* as a forage for the Australian tropics. *Empire Journal of Experimental Agriculture*, **27:** 187-196.

JONES, R.J. (1985) Leucaena toxicity and ruminal degradation of mimosine. In: *Plant Toxicology*. SEAWRIGHT, A.A., HEGARTY, M.P., JAMES, L.F. and KEELER, R.F. (eds.) *Proceedings, Australia-USA Poisonous Plants Symposium, held at Brisbane, Australia, May 1984*. pp. 111-119. Yeerongpilly, Australia: Queensland Poisonous Plants Committee.

JONES, R.J. and HEGARTY, M.P. (1984) The effect of different proportions of *Leucaena* in the diet of cattle on the growth, feed intake, thyroid function and secretion of DHP. *Australian Journal of Agricultural Research*, **35(2):** 317-325.

JONES, R.J. and MEGARRITY, R.G. (1983) Comparitive toxicity responses of goats fed on *Leucaena leucocephala* in Australia and Hawaii. *Australian Journal of Agricultural Research*, **35:** 781-790.
JOSHI, U.N., ARORA, S.K., PARODA, R.S., JATASARA, D.S. and RANA, D.S. (1985) Chemical composition of *Prosopis* leaves to show the presence of anti-nutritive factors responsible for low in vitro dry matter digestibility. *Nitrogen Fixing Tree Research Reports*, **3:** 20-21.

KINGSBURY, J.M. (1964) *Poisonous Plants of the United States and Canada*. Englewood Cliffs, USA: Prentice Hall Inc.

KUMAR, R. and SINGH, M. (1984) Tannins: their adverse role in ruminant nutrition. *Journal of Agricultural Food Chemistry*, **32(3):** 447-453.

KUMAR, R. and VAITHIYANATHAN, S. (1990) Occurrence, nutritional significance and effect on animal productivity of tannins in tree leaves. *Animal Feed Science and Technology*, **30:** 21-38.

LEVIN, D.A. (1976) Alkaloid-bearing plants: an ecogeographic perspective. *American Naturalist*, **110:** 261-274.

LEVIN, D.A. and YORK, B.M. (1978) The toxicity of plant alkaloids: an ecogeographic perspective. *Biochemical Systems and Ecology*, **6:** 61-76.

LEWIS, C.E. (1987) (ed.) *Proceedings, First Caribbean Leucaena Industries Symposium, held at Kingston, Jamaica, August, 1987*. Kingston, Jamaica: Enerplan Ltd.

LIENER, I.E. (1980) *Toxic Constituents of Plant Foodstuffs*. London: Academic Press.

MAKKAR, H.P.S., DAWRA, R.K. and SINGH, B. (1988) Changes in tannin content, polymerization and protein precipitation capacity in oak (*Quercus incana*) leaves with maturity. *Journal of Science of Food and Agriculture*, **44:** 301-307.

MANGAN, J.L. (1988) Nutritional effects of tannins in animal feeds. *Nutrition Research Reviews*, **1:** 209-231.

MASLIN. B.R., CONN, E.E. and DUNN, J.E. (1987) Cyanogenic Australian species of *Acacia:* a preliminary account of their toxicity potential. In: *Australian Acacias in Developing Countries.* TURNBULL, J.W. (ed) *Proceedings, International Workshop held at Gympie, Australia, August* 1986. ACIAR Proceedings No.16. pp107-111. Canberra, Australia: ACIAR.

McLEOD, M.N. (1974) Plant tannins - their role in forage quality. *Nutrition Abstracts and Reviews*, **44:** 803-815.

McNAUGHTON, S.J. (1987) Adaptation of herbivores to seasonal changes in nutrient supply. In: *Nutrition of Herbivores*. HACKER, J.B. and TERNMOUTH, J.H. (eds.) pp391-408. Sydney, Australia: Academic Press.

MOLYNEUX, R.J. and RALPHS, M.H. (1992) Plant toxins and palatability to herbivores. *Journal of Range Management*, **45:** 13-18.

PARRA, R., ESCOBAR, A., de VIERMA, C., VARGAS, R., VIERA, J., DOMINGUEZ, M.G. and MORA, M. 1988. The potential and constraints to *Canavalia* spp. as an animal feed resource. In: *Forage*

Legumes and Other Local Protein Sources as Subsitutes for Imported Protein Meals. WALMSLEY, D (ed.) *Proceedings CTA/CARDI Seminar, Kingston, Jamaica, December 1987.* pp154-180. Port of Spain, Trinidad: CARDI.

QUINTYNE, R.C. (1987) Utilization of *Leucaena leucocephala* as a livestock feed in Barbados. In: *First Caribbean Leucaena Industries Symposium.* LEWIS, C.E. (ed.) *Proceedings, Workshop held at Kingston, Jamaica.* pp.10-14. Kingston, Jamaica: Enerplan Ltd.

RODRIGUEZ, Z., BENAVIDES, J.E., CHAVES, C. and SANCHEZ, G. (1987) Produccion de leche de cabras estabuladas alimentadas con foliaje de madero negro (*Gliricidia sepium*) y de poro (*Erythrina poeppigiana*) y suplementadas con platano pelipita (*Musa* sp. cv. Pelipita) In: *Gliricidia sepium* (Jacq.) Walp: *Management and Improvement. Proceedings, Workshop held at CATIE, Turrialba, Costa Rica, June 1987.* Special Pub. 87-01. pp 212-216. Hawaii, USA: Nitrogen Fixing Tree Association.

SKERMAN, P.J., CAMERON, D.G. and RIVEROS, F. (1988) *Tropical Forage Legumes.* 2nd edn. Rome: Food and Agriculture Organization.

SMITH, L.W. and CULVENOR, C.C.J. (1981) Plant sources of hepatotoxic pyrrolizidine alkaloids. *Journal of Natural Products,* **44(1):** 129-152.

SOUTHON, I.W. and BUCKINGHAM, J. (1989) *Dictionary of Alkaloids.* London, UK: Chapman and Hall. 2 vols.

STEYN, D.G. and RIMINGTON, C. (1935) The occurrence of cyanogenetic glycosides in South African species of *Acacia. Onderstepoort Journal of Veterinary Science and Animal Industry,* **4(1):** 51-73.

TANNER, J.C., REED, J.D. and OWEN, E. (1990) The nutritive value of fruits (pods with seeds) from four *Acacia* spp. compared with extracted noug (*Guizotia abyssinica*) meal as supplements to maize stover for Ethiopian highland sheep. *Animal Production,* **51:** 127-133.

VAN HOVEN, W. (1985) The tree's secret weapon. *South African Panorama,* **30(3):** 34-37.