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

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 occurring 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.