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## Opportunities to use secondary plant compounds to manage diet selection and gut health of grazing herbivores

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### Key points :

1. Grazing herbivores and plants have co-evolved such that plant chemistry and animal metabolism are intimately linked.
2. Whilst conventionally-measured traits of plant nutritive value provide invaluable information to help predict animal performance, there are many situations where knowledge of secondary plant compounds can provide insights into the interactions between plants and herbivores.
3. Secondary compounds can affect diet selection and, sometimes, longer-term feed intake.
4. Secondary compounds can interact with rumen microbes to alter fermentation profiles and can be toxic towards nematode parasites in the gastrointestinal tract thereby providing a natural means to help control these important pests.
5. Combining plant traits with knowledge of animal behaviour can aid our design and management of mixed plant assemblies that address both animal production and natural resource management goals.

**Key words :** Secondary plant compounds, diet selection, gut health

### Introduction

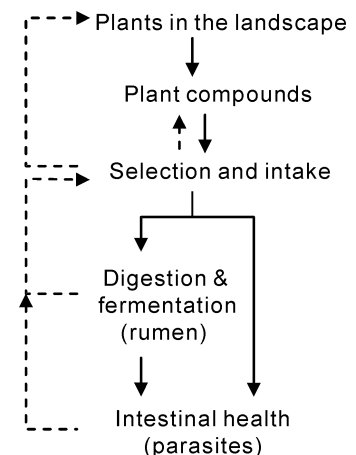
Grazing herbivores and the plants they consume interact with each other. The interactions are complex, based on hundreds of plant compounds and plant physical characteristics and the sensory and metabolic systems of animals. The ultimate goal of animals is to consume an optimal combination of nutrients that promotes survival, growth and reproduction. To select an optimal diet, herbivores must find a balance between over- and under-consumption of particular plant species and plant parts. Plants similarly need to find a balance between encouraging and discouraging herbivory. Animals can assist in pollination, seed dispersal, reducing inter-plant competition, and nutrient cycling, but excessive herbivory can severely reduce plant growth. Herbivores and plants have co-evolved, and a complex biological system has emerged to control the interactions (Figure 1). In the following paper, we discuss and provide examples of how plant compounds can influence diet selection, feed intake and gut health of animals, and comment on the implications to designing and managing grazing systems.

### Plant compounds, diet selection and voluntary feed intake

Plants vary both spatially and temporally in their chemical and physical composition. Consequently, for grazing herbivores to meet their nutritional requirements and avoid the over-consumption of toxins, they must continuously assess characteristics of what they eat, link this to the post-ingestive consequences of eating the plant, and modify their selectivity for particular plants (Provenza et al., 2007).

A critical factor in animal production is the regulation of feed intake. Plant secondary compounds play an important role in regulating intake and influencing diet selection (Villalba et al., 2002; Mote et al., 2007). Animals use sensory perception to discriminate among different plants, and the metabolic feedback from ingested nutrients and/or toxins calibrates the smell, flavour, sight and texture sensations with the positive and negative consequences of eating the food. This enables an animal to acquire preferences for foods that are nutritious and become averse to foods that are either deficient in nutrients or toxic (Provenza 1995).

Although our capacity to measure diet selection and intake is less than ideal, particularly in extensive grazing systems, there is some evidence of sensory discrimination during grazing. For example, when Thomas (2005) offered sheep 20 genotypes of annual plants across three stages of plant phenology, a standard set of measured traits (nitrogen, sulphur, neutral detergent fibre, acid detergent fibre, water soluble carbohydrates, *in vitro* digestibility, shear and compression energy) accounted for up to 60% of the variation in relative preference values. However, during the vegetative stage, only 20% of the variation could be accounted for by these particular traits. Principal component analysis showed that, at the senesced phase, the legumes that were preferred by the sheep had higher nitrogen content and digestibility, but this trend was not apparent when the pastures were at the vegetative phase. At the reproductive and senesced stages, the nutritive value, or digestibility, of annual plants decline, and hence animals are motivated to select plants with higher than average digestibility. But during the vegetative phase when there was a uniformly high digestibility across all 20 genotypes, other characteristics of the plants were used to



**Figure 1** Schematic representation of the interactions between the landscape, plants and herbivores.

discriminate between genotypes . Hence there is the possibility that secondary plant compounds may provide important distinguishing features of the different plant species to the animals . Such a conclusion has been reached with folivorous marsupials offered Eucalyptus leaves (Lawler et al . , 1998) , where no correlation was found between feeding and several measures of nutritional quality , total phenolics or condensed tannins . However , terpenes and a particular group of phenolic compounds ( diformylphloroglucinols ) did appear to alter feeding behaviour by acting as deterrents , with the latter being more important .

Another example of how conventional nutritive value traits cannot always account for differences in selection comes from a series of experiment with sheep grazing *Atriplex* spp ( saltbush ) . The selection of saltbush by sheep is known to differ between individual plants ( Maywald et al . , 1998 ; Norman et al . , 2004 ) . For example , Norman et al . , ( 2004 ) found distinct preferences for specific saltbushes by young Merino sheep , both within and between species ( old man saltbush , *A . nummularia* , and river saltbush *A . amnicola* ) . The basis for the strong preferences could not be explained by conventional measures of nutritional composition ( digestibility or content of fibre , crude protein or minerals ) . Preferences between individual old man saltbush plants was positively associated with nitrate concentration ( 250 v 98 mg/kg for most preferred v least preferred plants ) , whilst preferences for individual river saltbush plants was positively related to crude tannin content ( 0 . 12 v 0 . 09% for most preferred v least preferred plants ) .

Sensory assessment of a food is achieved through sight , smell and taste . The odour of a plant can be a powerful signal to herbivores , but it is an aspect that has not received much attention in livestock production . Livestock species ( sheep , goats , cattle and horses ) have a more sensitive olfactory system than humans , and hence the power of olfaction in determining intake can easily go unnoticed . Detecting odours can be beneficial in the process of food selection for at least four interrelated reasons . First , odour can be rapidly detected and thereby provides a means to influence feeding behaviour in the short term . Rapid decision-making may be important if a feed source is only temporarily available , as in a competitive feeding situation . Second , the decision to select or reject a particular feedstuff can be made without actually consuming the feed , and thereby avoid toxicosis . For example roe deer used odour to recognise and avoid undesirable plants once they learnt the consequences of eating these plants ( Tixier et al . , 1998 ) . Conversely , once smelled , preferred plants are rarely refused . Third , the physiology of odour detection allows animals to integrate a complex suite of odours that may reflect the biochemical composition of the food . This may be important in identifying whether a novel species is likely to be of low nutritive value , or toxic , prior to sampling . Although animals can detect individual odorants , the way in which the olfactory system processes information also allows animals to ' generalise ' the inputs to the central nervous system from a mixture of odours . Thus , the olfactory sense is able to distinguish among a practically infinite number of chemical compounds at very low concentrations ( Leffingwell 2002 ) . Fourth , neural processes link the detection of odour with memory , and hence the odour profile of a feedstuff can be used in learning and demonstration of learnt behaviour . The links between olfaction and memory allows animals to develop learnt behaviours based on associations between the sensory characteristics of feedstuffs and metabolic experiences ; in other words , a characteristic odour profile can trigger memory processes , and thus help an animal assess whether a familiar feedstuff is associated with favourable or unfavourable metabolic consequences following its ingestion .

Examples of volatile plant compounds affecting feed intake include : ( i ) Preferences in cattle being strongly correlated (  $r^2=0 . 97$  ) with 6-methyl-5-hepten-2-one , ( Z )-3-hexenyl propionate and acetic acid emitted from fresh tall fescue cultivars ( Mayland et al . , 1997 ) ; ( ii ) Preferences of horses for particular oaten hays being strongly related to the abundance of two volatile compounds released from the hay . One of the volatile compounds was negatively correlated (  $r^2=0 . 77$  ) to both preference and crude protein content of the hays , suggesting that the horses may have used the odorant to identify and avoid low protein hays . Such a phenomenon would be consistent with the finding that rats can self-select for dietary protein based on olfactory stimuli ( Heinrichs et al . , 1990 ) . Cox ( 2004 ) did not identify the compound unambiguously , but based on preliminary gas chromatography analysis , it appeared to be a naphthalene compound . The second volatile compound was positively related to hay preference in horses (  $r^2=0 . 83$  ) , with preliminary analysis suggesting this compound was a decane , a class of compounds that have been linked to the odours from peaches that attract insects ( Natale et al . , 2003 ) . It is conceivable that horses also found the odour attractive , or it was positively associated with a favourable nutritional trait of the hay ; ( iii ) Individual volatile compounds accounting for 25-40% of the variation in preferences between different batches of oaten or lucerne hays offered to dairy cows or horses ( preliminary data reported in Pain and Revell , 2007 ) . The abundance of particular volatile compounds may be particularly useful in explaining ' outlier hays ' - i . e . , those for which animals select considerably more or less than predicted from nutritive value alone .

### Secondary compounds and microflora of the gastrointestinal tract

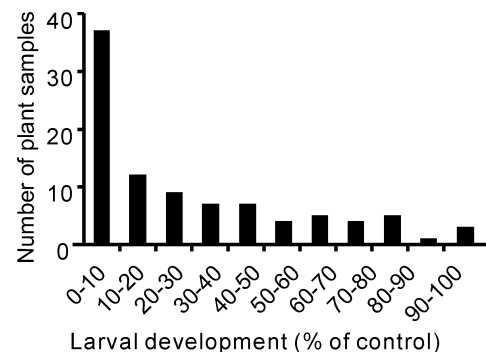
Once ingested , plant compounds interact with the microbes of the gastrointestinal tract . Phytochemicals that can affect rumen fermentation include tannins , saponins and essential oils ( Źliwiński et al . , 2002 ; Kamra et al . , 2006 ) . Much of the literature has focussed on toxins and anti-nutritional factors that limit the use of plants as feedstuffs ( see review of McSweeney et al . , 2002 ) . However , secondary compounds may have desirable effects on rumen fermentation by possessing specific antimicrobial , antiproteolytic , antiprotozoal or antimethanogenic properties that positively impact rumen ecology . For example , oral administration of an aqueous extract of saponin from *Biophytum petersianum* reduced ruminal ammonia and increased volatile

fatty acid concentrations in goats (Santoso et al . , 2007) . Similarly , a modest intake of *Acacia cyanophylla* leaves (100 g) consumed before the ingestion of 200 g of soybean meal reduced the ruminal digestion of crude protein and increased the growth rate of lambs (Ben Salem et al . , 2005) . Plant compounds also have the potential to reduce lactic acidosis , methane production , or influence ruminal biohydrogenation ( Vercoe et al . , 2007) .

Plants with anthelmintic properties are of special interest because of a growing problem of nematode resistance to the chemical anthelmintics in many countries (Besier and Love 2003) . Condensed tannins have received the most attention (e.g . , Iqbal et al . , 2007) but many other active compounds have been identified (Githiori et al . , 2006) . Condensed tannins are a good example of how a plant compound (or group of plant compounds) can be detrimental at high doses (Makkar 2003 ; Min et al . , 2003) , but beneficial at lower doses by protecting fermentable protein from degradation in the rumen (Barry and McNabb , 1999 , Ben Salem et al . , 2005) or by controlling gastrointestinal parasites (Aerts et al . , 1999 ; Iqbal et al . , 2007) . Whilst there has been some research on the use of plant extracts to control intestinal parasites , there remains the need to further investigate the use of particular plants under commercial conditions to control parasite burdens . Such research has been initiated by Ramírez-Restrepo et al . . (2004) with sheep grazing either tannin-containing pasture species (*Lotus corniculatus* , birdsfoot trefoil) or perennial ryegrass/white clover pasture . More is required as specific environmental conditions and production systems (e.g . , grazing rotations) may impact on responses , and there is a need to ensure that antinutritional effects to the host animals do not out-weigh benefits from parasite control (Athanasiadou et al . , 2007) .

Compounds besides condensed tannins could also be exploited . For example , phytoecdysteroids have been detected in about 6% of all plant species (Dinan 1995) . These compounds induce abnormal moulting in many arthropods with lethal effects . Nematodes have a similar hormonal regulation of ecdysis , and phytoecdysteroids may provide a means of defence against free living , plant or animal nematodes (see summary by Soriano et al . , 2004) . Another class of plant compounds that may have a role in controlling gastrointestinal nematodes are the cysteine proteases (Stepek et al . , 2004) . These are known to digest nematode cuticles and are inducible by environmental stressors such as salinity (Forsthoefel et al . , 1998 ; Jones and Mullet , 1995) and invertebrate herbivory (Lopez et al . , 2007) .

We are currently screening about 100 native shrub species for a range of characteristics , including *in vitro* inhibition of parasite larvae as a measure of anthelmintic activity . About 20% of the plants under evaluation reduce larval development to < 40% of controls (A . Kotze and J . O'Grady , unpublished data) . As these plant species have not been through any plant improvement program , there is potentially a high degree of variation between individual plants within a species ; i.e . different chemotypes . For example , we have tested 100 individual plants of one species growing at one location . Most but not all plants possessed anthelmintic properties (Figure 2) . The plants have been scored for morphological traits , and plants toxic to parasites tended to be bigger , more upright in structure , with larger , thicker and darker green leaves—but none of these traits on their own were significantly different between toxic and non-toxic plants . The aim is to further quantify between-plant variation across sites and with plant phenology or maturity .



**Figure 2** Variation in the inhibition of parasite larval development in an *in vitro* screening test of 100 individual plants of one plant species .

#### Putting it all together : how plant compounds can influence the design and use of diverse plant mixtures

The nature of interactions between plants and animals influences ecosystem function (Foley and Moore , 2005) . There are many examples from non-agricultural systems that have explored aspects of these interactions (e.g . , Crone and Jones 1999 ; Smallegange et al . , 2007 ; Staudt and Lhoutellier , 2007) , but there is great scope to build knowledge of interactions between secondary compounds and livestock to design and manage forage systems for the simultaneous benefit of livestock and the environment . In particular , when benefits of secondary plant compounds to herbivores can be combined with other desirable traits of the plants , such as a capacity to tolerate dry conditions and low soil fertility , provide ground cover on soils prone to erosion , or provide out-of-season feed , then we have an exciting proposition to re-design plant assemblies for grazing systems that take into account animal health and landscape function . The challenge is to ensure we optimise both the animals' long term performance and health and the persistence of the desired plant mixture . How can we best incorporate plants with bioactive compounds into grazing systems ? This is a particularly pertinent question when one considers that beneficial plant compounds are often detrimental at higher concentrations in the diet , but there are signs it can be done . Frutos et al . ( 2007) recently reported that grazing goats supplemented *ad libitum* with freshly cut heather were able to self-select the plant such that beneficial effects of the condensed tannins in heather (reduced nematode eggs in faeces , reduced ruminal ammonia and increased VFA concentrations) were not accompanied by anti-nutritional effects often associated with condensed tannins . Indeed , Villalba

et al. (2006) have shown that, with conditioning, sheep are able to self-medicate by consuming an appropriate remedy to a specific malaise. Despite the capacity of livestock to self-regulate and possibly self-medicate, livestock managers still have a crucial role to play. Even in low-input systems, there is the opportunity to intervene relatively easily by designing or modifying the plant combinations on offer, the spatial layout of plants, the duration or intensity of grazing. Here, some interrelated basic principles can be used to inform our decisions:

(i) *The combinations of plants made available to animals will influence intake and diet selection.*

Palatability, so often considered a fixed trait for a particular plant, is very much a dynamic phenomenon that depends on the combinations of food on offer and the previous experience the animals have had with them (Provenza 1995). When animals are offered two or more feeds simultaneously (usually the case with grazing herbivores), there are at least two levels at which the contrasts between the options can be interpreted by the animal (see Bergvall et al., 2007). First, the animals compare the options on offer in 'real time', without relying on memory or expectations of the future. Second, the reward (e.g., nutrient supply) or penalty (e.g., metabolic discomfort) of consuming one of the feeds is compared with the memory of a previously experienced.

(ii) *The combinations of secondary plant compounds affect animal responses.*

Experiences of secondary plant compounds are strongly influenced by the degree of complementarity or antagonism between compounds (Lyman et al., 2008a). Furthermore, the sequence of offering bioactive plants or secondary compounds can influence the response of animals (Lyman et al., 2008b). So when considering the impact of plants and their secondary compounds, we need to be mindful that different circumstances may yield different outcomes. If a particular plant is considered to have high concentrations of an undesirable compound, the plant may still be a valuable component of the feedbase if it can be coupled with complementary species. Issues relating to 'duty of care' (Revell and Revell, 2006) become important here to avoid undesirable outcomes whilst maximising the chances of beneficial effects of incorporating particular plants into the mixture.

(iii) *The experiences of animals can strongly influence diet selection.*

If we want animals to eat a particular species in the pasture mix on offer, a situation should be created where the animals sample the plant little by little and have a positive experience of doing so. The positive experience may be achieved easily if a plant is nutritious, or it may require intervention such as the provision of a supplement (or a complementary plant species) to overcome a nutrient deficiency or avoid toxicosis. A positive experience usually leads to a situation where animals eventually choose to include the plant into their regular diet. An example of the influence of previous experience on selection was shown by Thomas (2005). In this study, the intake of three pasture species (*Trifolium incarnatum* L., *Biserrula pelecinus* L., and *Lolium rigidum* Gaud.) offered simultaneously to sheep was heavily dependent on what species and what combinations had been offered to the animals in the past.



**Figure 3** Relative preference in sheep that had grazed plots for 4 weeks previously sown with either *B. pelecinus* (BIS) or *T. incarnatum* (CRI) or *L. rigidum* (RYE) or *B. pelecinus* and *L. rigidum* (BIS/RYE) or *T. incarnatum* and *L. rigidum* (CRI/RYE). During the preference testing, the sheep were offered all three species simultaneously: open bars, BIS; hatched bars, CRI and closed bars, RYE.

For example, in some cases, animals selected for *B. pelecinus* whilst others almost completely avoid it (Figure 3). Learnt feeding responses can be developed not only through trial and error, but also by animals observing others. The most powerful example is that of young animals learning from their mother. The offspring observe and mimic the eating behaviours of the older flock or herd members. Young animals tend to be more willing to experiment with novel feeds, so exposing young animals to new foods is more likely to lead to those foods being voluntarily incorporated into their diet (even many years later) than offering novel foods to older animals. The management of grazing herbivores should take into account the capacity of animals to learn about the plants on offer to ensure dietary preferences include a broad range of the plants on offer and to create the opportunity for animals to optimise their nutrition and/or self-medicate.

### Capitalising on designed or naturally diverse plant combinations

Livestock production systems must address multiple challenges associated with economic, environmental and social issues. To meet multiple goals there is a need to embrace the challenges of using plant diversity across the landscape. No single plant will achieve all purposes, from the timely provision of nutrients and other benefits to livestock through to managing the natural resources of soil and water. In an attempt to simplify management, we have tended to reduce biological complexity and plant diversity in grazing systems. Yet simplified systems are inevitably incomplete systems that ultimately require more inputs to be sustained. Building in plant diversity across a landscape not only offers opportunities to improve flexibility and meet diverse challenges in land management, but it is consistent with the design of grazing animals. An enormous opportunity exists to capitalise on emerging knowledge of the role of secondary plant compounds, and in particular their role in the regulation of diet selection, feed intake and gut health. This knowledge should help uncover new opportunities to manage livestock and diverse plant mixtures to improve economic, animal health and environmental outcomes.

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