DEER FORAGE PALATABILITY, DIGESTIBILITY AND MANAGEMENT IMPLICATIONS

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Abstract: To be palatable, deer forage plants must also be digestible. Digestibility in turn has been found to depend to a large extent on the balance between nutrients which favor the growth of rumen microbes and any inhibitory substances which plants may contain that depress microbial growth. Deer select their forage primarily by olfaction and secondarily to taste and sight. The inhibitory substances which have been isolated thus far fall into two general groups of chemicals, essential oils and phenolic compounds. However, only a few compounds in these large groups have been found to be inhibitory. Soil fertility, particularly the level of nitrogen available to plants, seems to have a marked effect on palatability, however, this is thought to result from an improvement in the nutrient level accumulated in the plants. Deer can tolerate the inhibitors in unpalatable plants if they only eat a small amount at a time, and they appear to thrive best on a mixed diet. The development and accumulation of microbial inhibitors in plants is considered to be a form of physiological defense against animal use that has had a bearing on natural selection. Conversely, natural selection has operated to favor strains of deer that are able to make the best use of the available plants. An understanding of these relationships should be useful in planning management programs.

In recent years documentation has been provided for some of the fundamental relationships governing the selection and utilization of forage by deer. Following up on the work of Nagy *et al* (1964), Longhurst *et al* (1968) and Oh *et al* (1967, 1968) have shown that deer (*Odocoileus hemionus columbianus*)

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select forage not only for its nutritive value, but likewise for its digestibility by their rumen bacteria.

Deer like other ruminants tend to avoid plants which contain substances which are inhibitory to the growth of their rumen bacteria. Even though they do select plants which contain high nutrient values (Swift 1948, Weir and Torell 1959), nutrient value is not the only controlling factor. A number of unpalatable species have been found which are exceptionally high in nutrients, but usually they contain some overriding inhibitory substances which depress growth of rumen bacteria. Actually, palatability and commensurate digestibility appear to depend upon the balance between the amount of available nutrients such as protein and carbohydrates including cellulose which promote growth of rumen organisms and the effects of any inhibitors which may be present.

The question naturally arises as to how deer select palatable plants over those which are unpalatable. Our observations of both wild and captive animals indicate that they depend largely on their sense of olfaction and secondarily upon taste and sight. If a plant smells favorable, they taste it and with experience learn to recognize palatable plants by sight so they do not then follow the more lengthy procedure of first smelling and then tasting before eating. We do not as yet know, however, whether deer are selecting directly against the smell of inhibitory substances in plants or whether they are recognizing other associated "indicator" compounds.

Since deer appear to place great emphasis upon the odor of plants, we have devoted considerable attention to the volatile substances which they contain. These compounds are classified under the general term essential oils. Thus far the species which we have studied most exhaustively is Douglas fir (Psuedo Tsuga menziesii) and to date some 38 of the major individual compounds have been identified out of approximately 200 which appear to be present. For these identifications we used ultrasensitive gas chromatography coupled with infrared spectroscopy (Sakai et al, 1967). These volatiles in Douglas fir have fallen into three broad groups, the monoterpene hydrocarbons, oxygenated monoterpenes, and sesquiterpenes. Of these only the oxygenated monoterpenes have been found to inhibit rumen organisms.

Both in vivo and in vitro techniques have been employed to determine the relationships between forage palatability and digestibility. However, the Warburg apparatus which measures gas production manometrically from digestion flasks into which rumen fluid is placed with ground samples of the fresh plants has proven most useful for obtaining quantitative comparisons.

We have observed that a large proportion of the most unpalatable plants are highly aromatic, but aromatic compounds are not the only ones which inhibit rumen bacteria. In addition to the oxygenated monoterpenes a wide array of phenolic compounds appears to have varying degrees of inhibitory effects. Many of these may be only transitionally present in plants associated with certain growth stages. Because of the complex chemical changes which take place in the biogenesis of plant tissues and their contained fluids, it is difficult to generalize. With some plants it seems that precursors of the chemicals found in the mature growth may be more inhibitory than the final forms and in other cases the final chemical products may be more inhibitory than the precursors. Such changes may explain part of the observed differences in palatability which are correlated with forage growth stages. However, as pointed out earlier it is the balance between the relative concentrations of nutrients and inhibitors at any given time that is important.

It is of interest to note that not all unpalatable plants inhibit rumen bacteria. Compared to alfalfa (Medicago sativa) which we have used as a standard in our Warburg in vitro digestion trials, some of the known toxic plants are more digestible. These plants frequently contain systemic toxins such as alkaloids or glucocides which affect the host ruminant adversely but do not produce effects directly on the rumen bacteria. The reason why deer avoid such plants is not entirely clear, but it is doubtful that they do so because of prior individual experience. Since fawns which have been bottle reared exhibit very nearly the same preferences as deer trapped on the range when they are first exposed to various plants during penned cafeteria feeding trials, it would appear that these innate preferences are inherited. Perhaps these deer which tend to prefer plants which are nutritious, noninhibitory on their rumen bacteria, and nontoxic have a selective survival advantage and pass these traits on to their progeny.

Soil fertility, especially the level of nitrogen available to plants, seems to have marked effects on palatability. When commercial nitrogen fertilizer is added to nitrogen deficient soil, protein levels in plants are increased along with palatability. While the precise effects on inhibitors of rumen bacteria have not as yet been fully determined, nutrient changes appear to be of greater magnitude. Again, the observed palatability increase even in only moderately palatable plants such as fertilized Douglas fir may result from the improved balance between protein and the inhibitory oxygenated monoterpenes. If soil contains adequate levels of nutrients for a particular plant species, the addition of commerical fertilizer produces negligible effects.

Even though ingestion of unpalatable plants frequently produces inhibitory effects on rumen bacteria, the overall effect on the rumen culture as a whole depends on the concentration of inhibitors in the plants and the amount eaten. When eaten in relatively small amounts, deer can tolerate unpalatable plants. Pressure to eat unpalatable species is usually a function of range competition. On heavily stocked ranges where competition is severe, animals are forced to take a higher proportion of unpalatable species in their diet with consequent lowering of overall digestibility and often of nutritive intake as well.

Deer seem to thrive best on a mixed diet and where they are forced to utilize too much of any one species, they have digestive troubles. Familiar examples in California are sagebrush (Artemisia tridentata) on winter ranges in the Great Basin and bear clover (Chamaebatia foliolosa) on winter ranges on the west side of the Sierras. Both these plants are good "fillers", but are not good for deer if they do not have other better species to go along with them. Bay (Umbellularia californica) trees are often heavily browsed in the north coast ranges even though bay oil is extremely inhibitory. This appears to be a manifestation of severe competition with many deer consuming only a small amount at a time.

Different species of ruminants are known to possess markedly different kinds of rumen bacteria. These bacteria, many species of which are normally present at any one time, are known to have varying tolerances for different species of plants (Kistner 1965). Therefore, numbers and kinds of bacteria are constantly shifting in response to variations in diet as well as time after feeding. This is an extremely dynamic process, but full adjustment to any marked and sustained change of diet does not occur immediately. On controlled feeding trials, for example, we usually allow two to three weeks to assure complete adaptation. These differences in the bacterial complement between species of ruminants possibly account, in part, for their varying food preferences.

Previously we advanced the hypothesis that the accumulation of inhibitory compounds in plants was in effect, a type of physiological defense against animal use (Longhurst et al., 1968). Evidence was cited in terms of better digestion by deer of introduced plants as compared with indigenous species. In other words, we have reason to believe that in evolutionary terms plants are continually selecting against being eaten by herbivorous animals while animals are selecting to take advantage of available plants. Time does not permit exploration of these points in depth at this meeting, but we feel that when plants and animals have been exposed to each other over a long period of time, they tend to strike a balance. Dramatic effects of animals on plants are usually achieved when animals are introduced into areas where there is a different flora. Conversely, introduced plants are often much more vulnerable than native species.

Pursuing this line of reasoning, it follows that within a plant or animal species evidence of genetic variation should be present. Certain strains of herbivores should be better adapted than others to make use of particular plants. Likewise, some strains of plants should be more or even less usable for herbivorous animals. To date we have not been able to collect sufficient quantitative evidence to confirm this with deer even though there is some indication of individual variation in food preferences. With livestock, however, particularly domestic sheep (Ovis aries), documentation during carefully controlled supplemental feeding trials points strongly in this direction. On the plant side we have found significant differences in digestibility of two nursery strains of Douglas fir using in vitro techniques. Careful observation of browsed young fir trees in the field has indicated individuals which were virtually untouched. This could be genetically related resistance to deer use through higher accumulation of oxygenated monoterpenes. At present we are in the process of testing this point with gas chromatography using samples of essential oil from paired browsed and unbrowsed trees. Smith (1950), found much the same situation in junipers (Juniperus spp.) in Utah but only related deer use to total essential oil content which was higher in the unbrowsed trees.

A very comparable situation has been recognized recently in other conifers where individual trees exhibit special resistance to certain insect pests. It is thought that these trees are producing a substance called juvabione, analogous to the insect juvenile hormone which controls metamorphasis in Lepidoptera (Lessing 1969). Basically all of these studies have attempted to provide a better understanding of the role of naturally occurring compounds in protecting plants from use by herbivorous animals and destructive insects.

Management Implications

Much more study will be required to explore the many avenues which these investigations have opened up, but already certain management possibilities are evident. Obviously deer range should be managed to produce a maximum of palatable forage species which are advantageous both for their better digestibility and nutritive value. This is not always easily accomplished because deer tend to use the most palatable species first often leaving a large residue of unpalatable plants which are unusable. Proper stocking rates are therefore exceedingly important to maintain desirable plant species composition. It is likewise advantageous to manage for a mixture of palatable species and to diversify extensive monotypic stands of vegetation.

A manager should be aware that micro differences in site such as soil type and fertility as well as slope exposure can affect photosynthetic efficiency and palatability. Nitrogen fertilizers are now being spread on large areas of forests and rangelands. Consequent improvement of palatability and overall productivity should raise carrying capacities of rangelands for both livestock and deer, but such results may not be desirable for uniform age crops of young conifers until they grow beyond the reach of deer.

If possible, abrupt dietary changes which will upset an orderly change in their complement of rumen bacteria should not be forced upon deer. Attempts at supplemental feeding during severe weather on overcrowded winter ranges would fall in this category.

Introduction of new plant species into a deer area may be an open invitation to damage as they are likely to be more palatable and digestible than the native flora. Many agricultural crops are good examples of this relationship.

With both agricultural crops and commercial forest trees there is some possibility of reducing their attractiveness to deer if plant breeders will select strains that not only have good commercial qualities but also accumulate high levels of rumen bacterial inhibitors or other naturally occurring repellents.

Whether some of the compounds which inhibit rumen bacteria could be applied directly to other plants as repellents has not yet been demonstrated. However, in addition to selecting strains of plants for their repellency as described above, it may be found that certain cultural practices may enhance this effect.

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