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Plant toxins and palatability to herbivores

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Abstract

A complex relationship exists between the presence of toxins in a plant species and the palatability of that plant. The nature of the toxin and its concentration within the plant can generally be precisely defined, given a reasonable amount of research commitment, but the measurement of palatability, especially in livestock, is much more difficult to achieve.

We hypothesize that analysis of possible roles of toxins in plants, their metabolic activity in animals, and physical and temporal distribution within the plant can be used to examine whether or not such compounds may significantly increase or reduce palatability to mammalian herbivores. Thus, if the toxin is effective in preventing predation of the plant or plant part by insect herbivores, or if it provides the plant with a competitive advantage versus other species, but does not produce adverse effects upon large mammals until significant quantities of biomass are consumed, then the toxin-palatability relationship is not significant. This concept is illustrated by examination of the toxicity produced in livestock by consumption of alkaloid-containing groundsel *(Senecio)* and locoweed (*Astragalus* and *Oxytropis)* species. The prevention of predation by localization of the toxin, mobilization to the site of attack, or production at a particular stage of growth provides opportunities for the application of management techniques designed to reduce exposure of livestock to natural plant toxicants.

Key words: toxin, palatability, groundsel, locoweed

The relationship between toxins in plants and the palatability of such plants to herbivores, especially livestock, is exceptionally complex. As a consequence, very little research has been done to correlate the presence or absence of a specific toxin in a plant with the acceptability of that plant as a food source for mammalian herbivores. Nevertheless, a considerable body of knowledge exists as to the specific phytochemicals responsible for the toxicity of particular plant species, especially those responsible for either human poisonings or for animal poisonings causing major economic losses to livestock producers (Kingsbury 1964, Keeler et al. 1978, Seawright et al. 1985, James et al. 1988). In the United States such losses of livestock are most prevalent on the arid rangelands of the Western states.

Research conducted on these problems for the better part of a century has yielded empirical observations, which have established the relative palatability to livestock of particular plant species co-existing in a given rangeland habitat. The problem to be confronted is the establishment of a definitive relationship between toxin occurrence, which can be unequivocally documented and quantified, and palatability, which is a behavioral response dependent upon a multitude of factors varying in significance with each specific situation.

The great variety of plant toxin structural types, plant species available for grazing, and livestock species of concern, renders a general discussion of the toxin-palatability phenomenon highly problematic. Substantive conclusions can only be drawn from consideration of individual toxic plant-livestock interactions, specifically those that have resulted in significant losses. The difficulty of defining the palatability side of the equation with precision requires that the nature of the toxin be clearly defined. Its chemical structure must therefore be known, a method must be available for its detection and analysis, and its mode of action upon the animal must be well-established.

The natural chemical metabolites produced by plants may be either acutely or chronically toxic to animals. Acutely toxic compounds are very limited in number, and for these there can be little relationship with palatability. The mere act of sampling the plant may in such cases be sufficient to kill the animal. On the other hand, toxic compounds may be either aversive or repellent, or they may be neutral or attractive (Provenza et al. 1991). From a practical viewpoint, if a plant toxin correlates with repellency, then animal losses should be small or nonexistent. Greatest attention must therefore be paid to those situations in which the toxin is undetectable by the animal or in which it is attractive or addictive.

The present discussion will consider in general terms the role of toxins in plants, analyze the possible relationship of the role to palatability, and examine specific livestock toxicity problems in terms of such an interaction.

Toxins and Their Role in Plants

A plant grows in a highly competitive environment. It is continually threatened by other plants encroaching upon the space from which it draws its sustenance, by micro-organisms, by insects, and by both large and small mammalian, avian, or reptilian herbivores. In order to survive, each plant must draw upon a complex of defenses, which may be physical, such as spines or leathery leaves, or chemical (Rosenthal and Janzen 1979). In general, these defenses are passive, coming into action only when the plant is actually attacked, although in certain cases volatile chemicals may be released which repel insects, or chemicals may be exuded into the soil which suppress micro-organisms or which prevent germination and effective growth of competitive plants, a phenomenon known as allelopathy.

Many predators either tolerate or circumvent the physical defenses of plants. Thus the ultimate protection resides in the chemicals which a plant can produce. Certain of these chemicals are amino acids which cannot be utilized because they are not among the 20 or so essential to the well-being of the herbivore. These are therefore not incorporated into protein and provide no nutritional advantage, or if incorporated, are detrimental to the animal (Rosenthal and Bell 1979). Examples of the latter are the selenoamino acids, occurring in selenium-accumulating plants such as certain *Astragalus* species, which replace sulfur-containing amino acids, resulting in consequent disruption of normal hoof and hair growth. Inorganic toxicants such as nitrites, nitrates, selenium salts, oxalates, and fluoracetates also occur, on soils

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having high concentrations of these particular substances.

More commonly, the toxic agents are natural organic chemicals, encompassing a great variety of structural types, which are biosynthesized *de novo* by the plants. These compounds are of most interest because they are often specific to a particular species or genera and must, therefore, have been designed to serve a particular protective function. Among the most prevalent are numerous classes of phenolics, terpenes and steroids, cyanogenic compounds, and alkaloids. The alkaloids are by far the most predominant of the plant toxins, and because of their enormous structural diversity and various modes of action, examples may be chosen from among them to serve as paradigms for virtually every type of plant-herbivore interaction. In order to make comparisons of the toxin-palatability relationship as consistent as possible, the examples presented in this discussion will be limited to situations in which the toxins are known to be alkaloids. Nevertheless, the concepts dealt with may be extrapolated to other toxin classes.

A great deal of discussion and speculation has been devoted to the role of toxins in plants (Rosenthal and Janzen 1979). Experimental evidence for the evolution of their biosynthetic pathways is extremely difficult or impossible to obtain, even though numerous studies have elucidated presently operational biosynthetic routes for individual natural products. Many of these routes have similar features and such commonalities have been classified as pathways leading from primary metabolites of the plant such as acetate, shikimic acid, lysine, tryptophan, etc.

Regardless of the structure of a particular toxin, it is likely to have evolved and been elaborated biosynthetically under pressure from a specific predator or limited group of predators. The vast majority of herbivorous stress encountered by plants is from insects and not mammals. Moreover, insects are capable of subjecting a plant population to selective pressures by feeding upon virtually all of the members within that population, whereas mammalian herbivores are most likely to eliminate individual plants while leaving others unaffected, even though they may be equally susceptible. The surviving plants, therefore, have not been subjected to selective pressures which might influence them to produce toxins. Plants that are attacked but not obliterated may respond by producing potential toxins, which can be evaluated for their deterrent efficiency against the usually large numbers of subsequent insect generations in a relatively short period of time. It is now generally accepted that in the rangeland situations of the Western U.S.A., the native plants evolved during a period when large mammals were absent and the toxins present must have developed primarily in response to insect herbivores (Cronin et al. 1978, Laycock 1978).

Poisoning of livestock, even when common, should therefore be regarded as an unfortunate accident caused by placing mammalian herbivores in juxtaposition with such plants. Ironically, a poisoned cow, sheep or horse may be an indicator of an extremely effective natural insecticide within the plant. Conversely, there may be many native plants which, although well-protected against insect attack, are nontoxic to livestock because of their vastly different metabolic processes. If this were not so, the rangelands would be essentially unusable for grazing since virtually every plant would be toxic to a greater or lesser extent to mammals.

Concentration of Toxins

The axiom of Paracelsus: "Sola dosis facit venenum" ("Only the dose makes the poison") is particularly appropriate in the case of natural toxins. Insect attack upon a plant may cause it to mobilize its defensive toxins in such a way that they are concentrated at the most threatened site, whether it be leaf tissue, flower, root, or seed. The generally small size of insects ensures that sufficient metabolite can be produced to kill, injure, or deter the attacker. On the other hand, the relatively large size of mammalian herbivores, and their less selective feeding habits, means that a plant population may be seriously threatened or even obliterated before the predator is sufficiently affected to cease feeding. Most plant toxins are therefore not effective deterrents to mammalian herbivory unless they are concentrated enough to precipitate an immediate response. While acute toxicity might effectively protect a plant population from serious depredation, delayed responses such as chronic toxicity, reduced reproductive success, and poor nutritional quality would be inadequate to provide any significant measure of protection.

The cost to the plant of producing its chemical weapons in the arms-race against its rapidly evolving insect enemies is extremely high. Valuable resources of water, nutrients, and energy must be utilized in the frequently complex biosynthetic route to an effective toxin. It is obviously advantageous to the plant if it can survive by producing either a minimal amount of a compound which is especially toxic to its particular predator or is localized at the point of attack. The metabolic processes of insects and mammals are often vastly different. Only when the toxin affects fundamental biological processes common to all animals, and is present in sufficient concentration in the plant parts eaten, will it kill or injure a large herbivore. If this threshold is not exceeded, the animal can generally feed upon the plant with relative impunity.

Deliberate attempts have often been made in breeding cultivated plants to ensure lower levels of natural toxicants in human foodstuffs. Unfortunately, such varieties frequently lose their ability to resist insect or microbial attack and consequently become uneconomical to produce. Commercial crops for human food usage must therefore have optimal concentration of biologically active natural products, low enough to be nontoxic to the consumer (at least when eaten in reasonable quantities) but sufficiently great to repel or limit pests. Similar considerations must be applied to the production of feed and forage for livestock. Concentration and location of the toxin are the primary considerations in evaluating the toxicity of poisonous plants.

Palatability

Palatability is extremely difficult to define in terms of the biological processes involved in food selection. As commonly used the term implies acceptability but not necessarily desirability. Thus, a foodstuff that is palatable may be essentially neutral with regard to preference, being neither attractive nor repellant to the taste. In terms of nutritional needs, a great proportion of an animal's food supply may be comprised of plants that are nonattractive or bland to the taste. The physiological phenomenon of taste is itself exceedingly complex, encompassing not only stimulation of taste buds but also mouth feel and aroma. Odors alone can produce such a marked response that many individuals will refuse to sample the item, while others will disregard this facet of flavor even though well aware of it. The best example of this in human experience is probably the durian *(Durio zibethinus)* fruit of Southeast Asia, which has been said to taste like heaven and smell like hell!

Unfortunately, any assessment of palatability of plants to animals is necessarily founded upon anthropomorphic arguments. Although scientists may be able to make observations as to selection or preference for particular plants, they can never determine the taste experienced by the animal on which such choice is based. Moreover, preferences vary greatly with individuals, the selection offered, hunger, and peer group or herd leader influence.

Scientists studying palatability in insects are in an enviable position relative to those investigating mammals. They can work with large groups; feed relatively simple controlled diets; add specific amounts of individual components; and accurately measure responses such as refusal to feed, reduced growth rate, and disrupted maturity. It is even possible to measure specific physiological responses with instruments such as antennograms. It is probably futile to expect to perform analogous experiments on large animals. Even if large enough groups could be used, the quantities of individual compounds that would need to be isolated or synthesized for testing would probably be prohibitive. Information about palatability to livestock must therefore rely almost entirely on careful human observations in feeding trials and grazing studies.

Phytochemicals and Palatability

Specific plant natural products, which may or may not be toxic, have an important influence upon palatability, although not necessarily in a manner that might be expected from the taste to humans of the individual compounds. Humans often regard bitterness as undesirable, yet certain ethnic groups consume with relish intensely bitter foodstuffs such as bitter melons *(Momordica charantia)*, which contain the steroidal cucurbitacins. Other foods and condiments such as chocolate and coffee require a certain degree of bitterness to confer palatability upon them. A particular example is beer, to which hops *(Humulus lupulus)* are added during the brewing process to produce a desirable bitter character which confers upon the finished product the property known in the industry as "drinkability". The varieties of hops used introduce distinctly different characters of bitterness, which are readily distinguishable by the experienced taster. In contrast, sweetness is usually regarded as a pleasant and attractive taste sensation, yet in juxtaposition with inappropriate foods, or when consumed to excess, it may be decidedly nauseating.

Not all flavor components are nontoxic and in fact a sufficient level of toxic compounds is necessary for certain foodstuffs to be acceptable to humans. For example the glucosinolates in Cruciferae generate toxic nitriles, thiocyanates, and goitrogenic compounds upon hydrolysis; yet low, nontoxic levels are essential for vegetables and condiments (cabbages, radishes, turnips, mustards, etc.) in this plant family to possess the pungent, biting flavors that are appealing to humans. Even a staple in human diets, potatoes *(Solanum tuberosum)*, must have a low level of toxic and possibly teratogenic steroidal alkaloids in order to have generally acceptable flavor.

Aversion

Consideration of palatability or unpalatability of foods generally leads to considerations of aversion. The reaction to a particular taste, or the consequences of consuming a foodstuff associated with a particular taste, must be extraordinarily profound for aversion to develop. Aversion requires not only an intense response but also a remembered response. Initial attempts at smoking are almost always unpleasant, but this response is not sufficient to override the (presumably) pleasurable physiological changes resulting from nicotine ingestion.

A striking example of aversion in nature is that of the larvae of monarch butterflies *(Danaus plexippus)*. These larvae feed exclusively upon the milkweed *(Asclepias curassavica)* from which they absorb and sequester considerable amounts of toxic cardiac glycosides. Young blue jays initially attempt to eat these larvae, which are highly visible and warningly (aposematically) colored, but they soon find them distasteful and capable of inducing vomiting if consumed. This results in a conditioned response in which experienced jays avoid the larvae, together with larvae of other species which are similarly colored but do not use the same food plant or accumulate the toxins (Brower 1969).

Unfortunately, an analogous conditioned response does not operate in the poisoning of sheep by sneezeweed *(Helenium hoopesii)*, pingue (*Hymenoxys richardsoni* var. *floribunda*) or bitter rubberweed (*Hymenoxys odorata)* (Kingsbury 1964). Although these plants are generally unpalatable they are eaten when other green forage is unavailable. A consistent sign of poisoning by these plants is chronic vomiting (James et al. 1980). In contrast to the blue jay example, however, this does not serve a protective function because the poisonous substances, sesquiterpene lactones, have a cumulative effect and vomition frequently develops only after a lethal quantity of plant has been consumed. The concentration of toxin needed to produce the physical response is therefore higher than the toxic dose and cannot produce a learned response.

It has been hypothesized that natural aversions are uncommon, because large generalist herbivores graze many different plants over an extended feeding period (Zahoric and Houpt 1977, 1981). The delayed effects caused by most plant toxins makes it difficult for animals to relate illness to a specific plant that may have been consumed. However, aversions in sheep have been experimentally created to many common foods (Provenza and Balph 1987, 1988). Aversions are effective if a single taste is paired with a rapid illness, i.e., 1–4 hours. The association declines after 4 hours. If other foods are consumed, the animals cannot distinguish which one has made them ill. Aversion to tall larkspur *(Delphinium barbeyi)* in cattle has been induced using lithium chloride, an inorganic emetic, and an extract of larkspur alkaloids has successfully created aversion to alfalfa pellets (Ralphs and Olsen 1990). An apparent negative correlation exists between total alkaloid content and palatability of larkspurs. Alkaloid concentrations are generally high during early growth stages of larkspurs, when cattle refuse to graze them, and levels decline as the plant matures, leading to increased grazing (Ralphs et al. 1989). Nevertheless, many of the individual alkaloids present in the extract, including the major components, are quite nontoxic to cattle. Until the precise toxin is identified it may be premature to conclude that a negative correlation exists between toxicity and palatability (Manners et al. 1992).

Alkaloidal Toxins

Compounds classified as alkaloids encompass an enormously diverse group of chemical structures. Although any competent organic chemist should be capable of recognizing a particular chemical structure as that of an alkaloid, a succinct definition is difficult to derive. Probably the best is that of Pelletier (1983) namely:

> "An alkaloid is a cyclic organic compound containing nitrogen in a negative oxidation state, which is of limited distribution among living organisms."

In developing this definition Pelletier specifically eliminated any requirement for pharmacological activity, even though most alkaloids manifest some such activity. In the context of a discussion of palatability this is an important point, since alkaloids are frequently referred to as substances that taste bitter to humans (Laycock 1978). Although some are well known for their bitter taste (e.g., quinine), many do not taste bitter. For example, neither the pyrrolizidine nor the indolizidine alkaloids induce any bitter sensation when tasted in their pure forms (R.J. Molyneux, personal observation). On the other hand, many nonalkaloids are intensely bitter. Examples are certain flavonoids from citrus, as well as the cardenolides and cucurbitacins mentioned above.

A direct relationship between particular structural classes and palatability or unpalatability cannot therefore be advanced. Each example of livestock intoxication must be evaluated on the basis of the individual toxin, its concentration and localization within the plant, correlated with observations of the ecological situation pertaining at the time the plant is consumed. These factors are illustrated by the following examples of alkaloidal toxins affecting livestock.

Pyrrolizidine Alkaloids of Senecio

Pyrrolizidine alkaloids (PAs) occur worldwide in many plant species and genera (Smith and Culvenor 1981, Mattocks 1986). In the western USA, serious livestock poisoning episodes are caused by *Senecio* species, especially the native species Riddell's groundsel *(S. riddellii)* and threadleaf grounsel *(S. douglasii* var. *longilobus)*, and the introduced species tansy ragwort *(S. jacobaea)* The PAs found in these plants are all of the macrocyclic diester type, but there are considerable differences in the number and concentration of individual alkaloids (Molyneux et al. 1979, Johnson et al. 1985a).

These PAs can all be considered as derivatives of senecionine, exhibiting varying degrees of oxidation of the latter. However, whereas Riddell's groundsel produces the single PA, riddelliine, threadleaf groundsel produces 4 structurally similar PAs, and tansy ragwort contains not only these 4 but 5 additional alkaloids. In general the alkaloid concentration in the plant peaks at the bud stage of growth, attaining exceptionally high levels (as much as 18% of the dry weight) in *S. riddellii* (Molyneux and Johnson 1984). Nevertheless, the PA content of *S. jacobaea* rarely exceeds 0.35% (Johnsen et al. 1985a).

If, as discussed earlier, the alkaloid production evolved to protect the plant from insect attack, then the maximum alkaloid concentration of *Senecio* species appears timed to ensure that seed production is not interrupted. The biosynthesis of differing numbers of alkaloids is more difficult to explain. Either each PA is produced in response to a different insect predator, or the primary predator may be confronted with either high concentrations of a single alkaloid or lower concentrations of a number of structurally similar alkaloids, each of which must be overcome. In any event, the cost to the plant of producing these alkaloids is considerable, involving a complex biosynthetic pathway with numerous steps under enzymatic regulation. The advantage of producing an alkaloid is that the compound can be catabolized to scavenge the nitrogen, an element essential to growth of the plant. In the *Senecio* species the PA level drops precipitously following flowering and seed production.

At present, the role of PAs as insect feeding deterrents is not well established. Riddelliine and related PAs have been shown to be moderately effective feeding inhibitors to the pea aphid, although much less so than certain quinolizidine and indolizidine alkaloids, which are generally found in the Leguminosae (Dreyer et al. 1985). However, there is evidence for a long period of evolutionary interaction between insects and PAs since a considerable number, especially moths and butterflies of the family Danainae, use metabolites of the alkaloids obtained from plants as sex attractants (pheromones), kairomones etc. (Boppré 1990).

There is compelling evidence that the toxicity of PAs to livestock is coincidental. The plant alkaloids *per se* are nontoxic to mammals, whatever their effect upon insects might be. Only after oxidation in the liver by the multifunction oxidases (MFOs), do they become hepatotoxic. Rarely is the toxicity acute; more commonly the prepatent period is extended, sometimes up to 18 months (Molyneux et al. 1988). Experimental PA feedings to cattle have shown that a threshold level must be exceeded for toxicity to occur (Johnson and Molyneux 1984, Johnson et al. 1985b). Under such circumstances no advantage accrues to the plant by virtue of its toxicity to livestock because the animals may continue to consume large quantities of plant material before ceasing to feed and subsequently succumbing to liver failure. Moreover, it has been observed that cattle may graze the flower heads selectively (A.E. Johnson, personal observation), thereby destroying the reproductive part of the plant essential to survival of the species.

Senecio plants commonly appear early in the grazing season and may therefore be especially attractive to animals and consequently destroyed before the flower buds are even formed, while PA levels are low. *S. riddellii* exhibits regrowth in response to occasional rainfall after periods of drought and then may be readily consumed because little other green forage is available. Such circumstances impose considerable grazing pressure upon plant species that are not otherwise very competitive, and thus can be fairly easily displaced from their ecological niche. The foregoing evidence suggests that the presence of PAs, at least in *Senecio* species, provides the plant with no protective advantage against mammalian herbivores and has no discernable effect on palatability.

Another PA-containing plant responsible for livestock poisoning is hound's-tongue *(Cynoglossum officinale)*, a member of the family Boraginaceae, introduced from Europe. Livestock generally avoid grazing hound's-tongue on the range, possibly because other forage is frequently available, but when the plant is dried and mixed with other forage it is readily consumed. Cases of calves being poisoned and succumbing to PA intoxication have been documented in such situations (Baker et al. 1989). Deaths of 2 horses from hepatic failure caused by consumption of hound's-tongue in baled hay has also been reported (Knight et al. 1984). The plant has a distinctive, unpleasant odor when green, which deters grazing animals, but this is lost upon drying and the plant becomes quite palatable. Similar palatability assessments have been made of tansy ragwort. It is unlikely that the odor bears any relationship to PA content because the pure alkaloids are odorless.

The Locoweed Alkaloid, Swainsonine

In contrast to *Senecio* toxicosis, which produces essentially a single syndrome, the locoweeds produce many different syndromes. These include neurological lesions, abortion, birth defects, sexual disfunction, emaciation, and congestive right-heart failure at high altitudes. The plants historically classified as locoweeds are specific species of the genera *Astragalus* and *Oxytropis*, which are capable of producing the neurological syndrome known as "locoism" in mammals consuming them (Molyneux et al. 1985).

Recent research has shown that the neurological lesion responsible for locoism is caused by the alkaloid swainsonine, which generally occurs in the plant together with its N-oxide (Molyneux and James 1982). Swainsonine has been detected in all *Astragalus* and *Oxytropis* species historically regarded as locoweeds. The alkaloid is toxic by virtue of its potent inhibition of α-mannosidase, an enzyme essential to the proper functioning of mammalian cells (Elbein and Molyneux 1987). In view of this general property, it is probable that it is responsible for many of the syndromes attributable to locoweed consumption.

The etiology of the locoweed disease was established by C.D. Marsh in the early years of this century. Previous field observations had indicated that the locoweeds had an addictive property but Marsh's research (1909) qualified this assessment, and he stated that while livestock initially find it distasteful they subsequently acquire a taste or habit for it. The term "habituation" has generally been adopted for this behavior, rejecting the implication of physiological dependency implied by "addiction."

The question of habituation to locoweeds has been investigated by controlled grazing and feeding trials (Ralphs and Molyneux 1989). In controlled feeding trials, spotted locoweed *(Astragalus lentiginosus)* was not innately palatable to sheep. As the sheep became progressively intoxicated, most continued to reject locoweed when a choice was offered, suggesting that there is no physiological or psychological addiction to locoweeds. A few of the sheep habituated to locoweed, or learned to accept it, but it was never preferred (Ralphs et al. 1990). Following recovery from intoxication in the pen feeding trials, all sheep rejected locoweed when grazed on locoweed-infested rangeland (Ralphs et al. 1991).

Cattle grazed dry, senescent stalks of Wahweap milkvetch *(Astragalus lentiginosus* var. *wahweapensis)* on desert and foothill winter ranges in the Henry mountain area of southeastern Utah in proportion to its availability (Ralphs et al. 1988). Although pathological syndromes developed (abortion and water belly) cattle did not cease to eat locoweed. Furthermore, there was no difference in acceptability between the one-year-old stalks (0.005% swainsonine) and two-year-old blackened stalks (0.023% swainsonine), indicating that swainsonine level did not influence palatability. Additional grazing studies on white locoweed *(O. sericea)* (Ralphs and Molyneux 1989) showed that the only plant part consistently chosen by the cattle was immature seed pods. Locoweed leaves were rarely selected and the flowers were consumed only when grass was depleted. Swainonine content is greatest in the immature pods, yet this was the plant part preferred by cattle. Swainsonine was only slightly lower in the blooms and mature pods, which were not selected. It must be concluded that swainsonine does not decrease palatability and is unlikely to account for selection of particular plant parts since the differences in content are not great and vary much more significantly from year to year, without apparently affecting choice. The palatability is far more closely correlated with crude protein content.

Consideration of swainsonine content in general indicates that it is unlikely to be a determinant of palatability. In comparison with the alkaloid content of most plants, the levels are extremely low. The highet level so far recorded has been 0.36% in the seeds of *A. lentiginosus,* levels in other plant parts being an order of magnitude less. This suggests that swainsonine biosynthesis is advantageous in deterring seed predation by insects. The low alkaloid level in succulent parts of the plant requires that considerable amounts of plant material must be consumed by mammals before even minimal clinical signs of toxicity are observed. The work of Marsh (1909) indicated that this quantity was of the order of 50–100% of the body weight of the animal. Swainsonine cannot therefore be regarded as a toxin which protects the plant against predation by large herbivores. In fact, if it were not for its extraordinary potency as an enzyme inhibitor, it is probable that it could be consumed with impunity.

An additional minor alkaloid, named lentiginosine, has recently been discovered in the spotted locoweed, *A. lentiginosus* var. *diphysus* (Pastuszak et al. 1990). The compound is structurally related to swainsonine but rather than inhibiting α-mannosidase it is instead a good inhibitor of several α-glucosidases. This property may be responsible for the emaciation syndrome, due to suppression of the digestive enzymes. If this is indeed the case, lentiginosine confers no advantage to the plant because animals continue to consume it despite their emaciation.

Conclusions

Examples of significant plant toxins that fail to confer deterrency to predation of the plants by mammalian herbivores have been provided. The pyrrolizidines, although occurring at very high levels, fail to protect the plant because their toxic effects are greatly delayed. In contrast the locoweed toxin, swainsonine, occurs at very low concentrations and only produces significant toxicity when large quantities of plant material have been consumed.

Such examples illustrate some points that are generally applicable to most plant toxin-livestock interactions:

1. Plant toxins confer a competitive advantage to the plant, and especially protect it from insect attack or plant pathogens. Poisoning of livestock is coincidental to this function.
2. There is poor correlation between toxin presence and either increased or decreased palatability.
3. Since plant toxins seem specifically targeted on insects, either by concentration in a particular plant part or by production at concentrations sufficient to intoxicate the insect, livestock poisonings may be avoidable. Careful management plans should be developed so that consumption of the toxic plant parts are avoided and so that the animals are not forced to consume large quantities of a toxic plant because more desirable forages are not present.

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