The capability of several toxic plants to condition taste aversions in sheep


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ABSTRACT

Grazing livestock frequently ingest toxic plants, occasionally with fatal results. Behavioral adjustments by livestock may reduce toxin intake; for example they can develop food aversions which may protect animals from over-ingestion of toxic plants. The purpose of this study was to evaluate three plants with different mechanisms of toxicity for their efficacy in conditioning a taste aversion: (1) a seleniferous plant, Xylorhiza glabriuscula, (2) an indolizidine alkaloid-containing plant, Astragalus lentiginosus, and (3) a diterpene acid-containing plant, Gutierrezia sarothrae. For each plant species, 15 sheep were divided into 3 treatment groups and periodically tested for consumption of a novel food, whole corn: (1) controls – given 200 g of ground alfalfa hay by oral gavage, (2) averted – given lithium chloride (LiCl) at 175 mg/kg BW via oral gavage, and (3) given the specific target plant by oral gavage. X. glabriuscula was given at a dose equivalent to 3 mg Se/kg BW; A. lentiginosus was given at a dose equivalent to 3 mg/kg of the toxic alkaloid, swainsonine; freshly thawed G. sarothrae was dosed at 5 g/kg body weight (BW). Both LiCl and Xylorhiza conditioned an aversion to corn, with sheep eating 1.6 and 0.6% of offered corn during the final test; controls were not averted, eating 93% of the corn (P<0.01). Sheep were partially averted by Xylorhiza after a single dose, and the aversion was complete after the second dose. Sheep were not averted by A. lentiginosus or G. sarothrae. Of the three toxic plants used in this study, only Xylorhiza conditioned a taste aversion. These results likely reflect differing mechanisms of action of the plant toxin(s) on brain and gut structures important for forming conditioned taste aversions. These results suggest that conditioned aversions to Se-containing plants may help to deter consumption of such plants by grazing ruminants on rangelands.

1. Introduction

Poisonous plants are an integral component of many rangelands and pastures worldwide. Although livestock losses from toxic plants can be severe (Burrows and Tyrl, 2001), most wild or domestic animals grazing on rangelands do not die from ingesting toxic plants. Grazing animals use a number of interrelated behavioral and physiological strategies to reduce the risk of fatal poisoning, including avoiding or reducing toxin intake through changes in diet selection (Provenza et al., 1992; Pfister, 1999; Iason and Villalba, 2006). When grazing animals reject toxic plants in favor of less toxic or nontoxic species, learning is usually involved (Provenza, 1995, 1996). Learning is not a perfect avoidance mechanism, however, behavioral adjustments by livestock may greatly reduce toxin intake (Provenza et al., 1992). Aversions conditioned while foraging are an important learning mechanism pro-
tecting grazing animals from over-ingestion of toxic plants (Provenza et al., 1992; Pfister et al., 1997).

Conditioned taste aversions (CTAs) deliberately induced by livestock producers may also be a practical means to keep livestock from eating poisonous plants such as Delphinium (larkspur, Ralphs, 1997), Astragalus and Oxytropis (locoweeds, Ralphs et al., 1997), or Pinus ponderosa (pine needles, Pfister, 2000). Conditioned aversions have been shown with a number of plant toxins, including alkaloids, tannins, cyanogenic glycosides, terpenes, and glucosinolates (Provenza et al., 1992). Conditioned food aversions may be mild and transient (Pfister et al., 1997; Kyriazakis et al., 1998) or strong and long-lasting (Ralphs, 1997) depending on the dose of the toxin (Rappold et al., 1984), and when and how the toxin affects the gut and central nervous system (e.g., parabrachial nucleus; Bernstein, 1999).

Further, CTAs may be apparent before pathological lesions are formed, or at doses sufficiently low that lesions are not produced (Wellman et al., 1989).

The purpose of this study was to evaluate three plants with three different toxins for their efficacy in conditioning a taste aversion using sheep as a model animal: (1) a seleniumiferous plant, Xylorhiza glabriuscula (woody aster), (2) an indolizidine alkaloid-containing plant, Astragalus lentiginosus (locoweed), and (3) a diterpene acid-containing plant, Gutierrezia sarothrae (broom snakeweed).

X. glabriuscula is a selenium-accumulating plant that is native to western North America. Although considered unpalatable, cases of intoxication from Se-accumulating plants, including woody aster, are increasing because of land sub-division and increased grazing pressure on many western U.S. rangelands (Davis et al., 2000). A. lentiginosus is widespread across the southwestern U.S.; locoweed causes serious economic losses to livestock producers because the plant is palatable and is often the major source of green feed when other forage is dormant (Pfister et al., 2003). G. sarothrae is an invasive half-shrub that causes substantial losses to the livestock industry across the western U.S. from reduced rangeland productivity and toxicity (Carpenter et al., 1990). Broom snakeweed can be toxic to sheep, goats, and cattle particularly during winter, spring, or during drought, when poor forage availability influences animals to consume large quantities.

2. Materials and methods

2.1. Animal management and feeding

Sheep were individually penned (2 x 2 m pens) indoors at 10 °C, and provided water and trace mineral salt at all times. Each afternoon, animals were individually fed a basal diet of pelleted alfalfa hay at 2% of BW for 4 h. Animals typically consumed their allotment with no uneaten residues throughout the trials. All procedures were approved by the Institutional Animal Care and Use Committee at Utah State University, and conducted under veterinary supervision.

2.2. Plant chemistry

Selenium was analyzed in X. glabriuscula using inductively coupled plasma mass spectroscopy (ICP-MS) (Heard et al., 2008). Plant tissue was digested via a modification of EPA method 3050 (Kingston and Walter, 1992). Digestions were performed in screw-cap teflon tubes, using 0.5 g of ground plant material in 10 ml of trace metal grade nitric acid at 90 °C for 2 h. The plant digests were diluted 1:20 with 18.3 M ultrapure water to 5% nitric acid prior to analysis. Standard curves consisted of five concentrations between 10 and 500 ng ml⁻¹. Standard curves and quality control samples were analyzed every five samples.

A. lentiginosus var. dypsis was analyzed for swainsonine concentration using the method of Gardner et al. (2001). Ground plant samples were extracted using a small-scale liquid/liquid extraction procedure followed by isolation of the swainsonine by solid phase extraction with a cation-exchange resin. Detection and quantitation of the swainsonine were accomplished using reversed phase high-performance liquid chromatography coupled to atmospheric pressure chemical ionization tandem mass spectrometry.

No chemical analysis was conducted on broom snakeweed because of the extremely complex mix of phytochemicals contained in the plant (Roitman et al., 1994); it is unknown which class or individual compounds might cause toxicity (Dollahite et al., 1962), or condition an aversion.

2.3. Lithium chloride as a control

Lithium chloride (LiCl) given orally in water was used as a negative control in all trials; LiCl is a standard drug in many CTA experiments (Reilly and Schachtman, 2009). Oral doses of LiCl reliably and quickly produce gastrointestinal emesis and CTA (Provenza et al., 1994) when paired with novel foods.

2.4. X. glabriuscula (selenium) trial

X. glabriuscula was collected (whole plants) at maturity near Soda Springs, Idaho (N lat. 42°43' W long. 111°31') from a site with traditionally high soil selenium concentrations. Plants were air-dried, ground to pass a 2 mm screen with a Wiley mill, and stored in plastic bags. Fifteen white-faced yearling male sheep (mean weight 68 ± 3.2 kg) were randomly divided into three treatment groups (n = 5): (1) controls – given 200 g of ground alfalfa hay in a volume of 2 L tap water by oral gavage, (2) averted – given LiCl at 175 mg/kg BW via oral gavage in a volume of 2 L tap water, and (3) selenium (Se) – given ground X. glabriuscula by oral gavage in 2 L tap water at a dose equivalent to 3 mg of Se/kg BW. All dosing was done at 08:00 h, and all testing was carried out at the same time on different days as detailed below.

Whole corn was used as the novel food, and all sheep were naive to whole corn. Sheep were briefly exposed twice to the novel food during the 2 days before the trial began. This exposure consisted of two, 5-min opportunities to consume 20 g of corn at 08:00 h before being fed their daily ration. On Day 1 (test 1) all sheep were offered 100 g of corn for 10 min at 08:00 h after an overnight fast, intakes recorded, and animals were dosed with their respective treatments after ingesting corn. Days 2–6 were recovery days. On Day 3 one sheep in the Se treatment died overnight from apparent cardiac failure from Se toxicity. On Day 7 (test 2) all sheep were offered 100 g of corn for 10 min after an overnight fast. If any animal ate any amount of corn during this test, it was immediately dosed according to the treatment regimen. Three of the four remaining animals in the Se group ate a small amount of corn and were dosed with Se-containing plant for the second time. However, the Se dose was reduced to 2 mg/kg BW to decrease the risk of intoxication. Days 8–13 were recovery days, and animals were tested as noted above on Day 14 (test 3); no plant or LiCl was dosed to any animal.

2.5. A. lentiginosus var. dypsis (indolizidine alkaloid swainsonine) trial

Locoweed (A. lentiginosus var. dypsis) was collected near St. Johns, Arizona (N lat. 34°25', W long. 109°9') while in the flower stage (whole plants), air-dried to pass a 2 mm screen in a Wiley mill, then stored at 10 °C in plastic bags. Subjects were fifteen white-faced yearling male sheep weighing 65 ± 2.7 kg. Animals were treated and tested as detailed in the Se trial. Five sheep were controls dosed with 300 g of ground alfalfa hay, 5 were dosed with LiCl at 175 mg/kg BW, and 5 were orally gavaged with ground locoweed plant at a dose equivalent to 3 mg/kg BW of the toxic alkaloid, swainsonine. Swainsonine is the primary toxic alkaloid in locoweeds, and daily swainsonine doses ≥0.2 mg/kg BW are considered toxic (Pfister et al., 1996; Stegelmeier et al., 1999). All animals in the locoweed treatment were given a second dose immediately after the second test (Day 7), as all ate some corn during that test. No dosing was done on test day 3 (Day 14).
northern Utah (N lat. 41°51′, W long. 111°57′) and immediately frozen until use. To dose snakeweed, frozen plant was thawed for 15 min, placed with a small amount of water in a blender, and macerated. Fourteen white-faced male sheep were used in the snakeweed trial (mean body weight 74 ± 3.0 kg). The macerated snakeweed mixture (liquid and solids) was immediately dosed to 6 treated sheep via oral gavage at 5 g/kg b.w. (frozen plant weight). This dose was chosen based on an earlier pilot study using four sheep indicating that this was the maximum volume of macerated material that could be given by oral gavage in one pulse dose. Four sheep were used as controls, and given only ground alfalfa hay at 5 g/kg BW in 2 L tap water; 4 other sheep were dosed with LiCl at 175 mg/kg BW in 2 L tap water. Animals that ate some test food during the second test, and they were dosed a second time with woody aster immediately after the 2nd test concluded.

2. G. sarothrae (diterpene acids) trial

Procedures for this trial were similar to those for locoweed and woody aster except that an extra testing day (Day 3) was added. Thus, after the initial dosing day (Day 1), animals were tested on Days 3, 7, and 14. Snakeweed contains a complex mixture of diterpene acids, flavones, and saponins (Dollahite et al., 1962; Roitman et al., 1994), some of which may be volatile, therefore frozen plant was used. Fresh plant was collected from northern Utah (N lat. 41°51′, W long. 111°57′) and immediately frozen when collected. For each test day, treatments with different lowercase superscript letters (within a column) differ ($P < 0.01$). Within each treatment, means with different uppercase superscript letters (within a row) differ ($P < 0.01$). On test day 1, animals were offered the test food, then immediately dosed with the respective treatments. Test days 2 and 3 were 7 and 14 days, respectively, after the initial test day. One animal died after the first dose; 3 of 4 animals ate some test food during the second test, and they were given a second dose of locoweed immediately after the 2nd test concluded.

2.7. Statistical analysis

The dependent variable was amount of corn consumed (% of offered) on test days. Data were transformed using an arcsine transformation as is typical for percentages. All data shown are untransformed means and errors. A mixed linear model (Proc Mixed) was used in SAS (2004) with a Tukey adjustment to control experiment wise error rates.

3. Results

3.1. X. glabriuscula

*X. glabriuscula* contained 940 mg/kg Se (dry weight basis). There was a day × treatment interaction ($P < 0.001$) for intake of the test food in the Se aversion trial (Table 1). Control animals did not differ ($P = 0.55$) in consumption of the test food on the 3 test days. However, both LiCl and Se treatment groups showed differences in intake ($P < 0.001$) over time (Table 1). None of the treatments differed ($P > 0.90$) on test day 1, but did thereafter ($P < 0.001$; Table 1). During the 2nd and 3rd test days, the Se group ate less than did controls ($P = 0.001$) as did the LiCl group ($P = 0.001$). Sheep were partially averted by woody aster after a single dose, and the aversion appeared to be complete after the second dose (Table 1).

The fatally intoxicated animal died suddenly from presumptive cardiac failure, showing few clinical signs as is typically the case in acute selenosis in sheep (Morrow, 1982). Because the animal died during the night, no necropsy was performed.

3.2. A. lentiginusos

*A. lentiginusos* contained 0.36 mg/g (dry weight basis) of swainsonine. Locoweed was completely ineffective at conditioning an aversion. The locoweed treatment did not differ ($P = 0.001$) from controls on any test day (Table 2). The LiCl treatment group differed ($P < 0.001$) from controls and the locoweed groups on each test day except for the initial, pre-dose test day.

3.3. G. sarothrae

*G. sarothrae* was not effective at conditioning an aversion (Table 3). Sheep treated with snakeweed did not differ ($P > 0.9$) in intake of the test food from control animals. Sheep dosed with LiCl had reduced ($P < 0.01$) consumption of the test food compared to the other two treatments.

Table 1

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Intake (% of offered)</th>
<th>Test 1</th>
<th>Test 2</th>
<th>Test 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control alfalfa (5 g/kg BW)</td>
<td>100 κA</td>
<td>93.3 ± 6.7 κΑ</td>
<td>92.5 ± 4.6 κΑ</td>
<td></td>
</tr>
<tr>
<td>Lithium chloride (175 mg/kg BW)</td>
<td>100 κA</td>
<td>7.6 ± 7.2 κΑ</td>
<td>1.8 ± 1.7 κΑ</td>
<td></td>
</tr>
<tr>
<td>Woody aster (3 mg Se/kg BW)</td>
<td>100 κA</td>
<td>31.6 ± 14.2 κΑ</td>
<td>0.6 ± 0.5 κΑ</td>
<td></td>
</tr>
</tbody>
</table>

For each test day, treatments with different lowercase superscript letters (within a column) differ ($P < 0.01$). Within each treatment, means with different uppercase superscript letters for the 3 test days (within a row) differ ($P < 0.01$). On test day 1, animals were offered the test food, then immediately dosed with the respective treatments. Test days 2 and 3 were 7 and 14 days, respectively, after the initial test day. All animals in the locoweed treatment ate some test food during the second test, and they were given a second dose of locoweed immediately after the test concluded.

Table 2

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Intake (% of offered)</th>
<th>Test 1 (Day 1)</th>
<th>Test 2 (Day 7)</th>
<th>Test 3 (Day 14)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control alfalfa (5 g/kg BW)</td>
<td>100 κA</td>
<td>93.8 ± 6.2 κΑ</td>
<td>94.0 ± 6.0 κΑ</td>
<td>100 κΑ</td>
</tr>
<tr>
<td>Lithium chloride (175 g/kg BW)</td>
<td>100 κA</td>
<td>6.3 ± 3.7 κΑ</td>
<td>0.9 κΑ</td>
<td></td>
</tr>
<tr>
<td>Locoweed (3 mg swainsonine/kg BW)</td>
<td>100 κA</td>
<td>100 κΑ</td>
<td>100 κΑ</td>
<td>100 κΑ</td>
</tr>
</tbody>
</table>

For each test day, treatments with different lowercase superscript letters (within a column) differ ($P < 0.01$). Within each treatment, means with different uppercase superscript letters for the 3 test days (within a row) differ ($P < 0.01$). On test day 1, animals were offered the test food, then immediately dosed with the respective treatments. Test days 2 and 3 were 7 and 14 days, respectively, after the initial test day. All animals in the locoweed treatment ate some test food during the second test, and they were given a second dose of locoweed immediately after the test concluded.
after 16 days of locoweed dosing. At very high swainsonine effects, and metencephalon, and in cerebellar neurons developed lesions in the neurons of the basal ganglia, mesencephalon, and in cerebellar neurons and glia (Steigelmeier et al., 1999); clinical signs were noted after 16 days of locoweed dosing. At very high swainsonine doses (e.g., 8 mg/kg BW) aberrant behaviors were apparent in goats within 4 days of dosing (Furlan et al., 2007). We used a swainsonine dose (3 mg/kg BW) that was 15× the dose normally required to induce chronic toxicity. However, at the dose and duration used in this study, locoweed did not appear to stimulate adverse post-ingestion feedback (Garcia et al., 1985) necessary to condition an aversion. This could be due to the delayed clinical effects of swainsonine and these effects not being directly associated with the test food by the sheep.

4. Discussion

Neither locoweed nor broom snakeweed were effective at conditioning a food aversion, whereas the seleniferous woody aster conditioned an aversion to a novel food. This was a very conservative test in that whole corn is a very palatable food with positive postingestive consequences, thus these results indicate that a Se-containing plant can condition strong aversions after two pairings.

These results with three different plants could reflect differing mechanisms of action of the various toxin(s), or alternatively could reflect doses that were too low for a specific toxin in the case of locoweed and broom snakeweed. A number of brain structures are involved in acquisition of taste aversions (Garcia et al., 1985), including the area postrema, the nucleus of the solitary tract (NST), and the parabrachial nucleus (PBN). Current evidence suggests that the PBN is essential for CTA acquisition (Reilly and Schachtman, 2009), whereas other brain structures (e.g., amygdala) may (Yamamoto et al., 1994) or may not (Reilly and Bornova1ova, 2005) be essential for taste aversion learning (Reilly et al., 1993; Grigson et al., 1997; Bernstein, 1999). It appears that in the absence of such CNS activation, other biochemical and physiological lesions will not condition aversions (Yamamoto et al., 1998). The CNS and gut receptors are linked so that physiological information on noxious stimuli is transmitted to the brain. For example, noxious distension of the colon results in increases in C-Fos expression in hypothalamic and thalamic areas of the limbic system (Monnikes et al., 2003). Similarly, administration of LiCl has been shown to induce C-Fos expression in the brain (Sakai and Yamamoto, 1997; St. Andre et al., 1999). It appears that in the absence of such CNS activation, other biochemical and physiological lesions will not condition aversions (Yamamoto et al., 1998). The CNS and gut receptors are linked so that physiological information on noxious stimuli is transmitted to the brain. For example, noxious distension of the colon results in increases in C-Fos expression in hypothalamic and thalamic areas of the limbic system (Monnikes et al., 2003). Similarly, administration of LiCl has been shown to induce C-Fos expression in the brain (Sakai and Yamamoto, 1997; St. Andre et al., 1999). Additionally, although nausea is not essential for acquisition of CTA, nausea may greatly potentiate dislike of a specific food (Pelchat and Rozin, 1982).

The locoweed toxin, swainsonine, inhibits essential glycosidase enzymes, particularly lysosomal α-mannosidase and mannosidase II (Dorling et al., 1980). Ingestion by livestock causes depression, proprioceptive deficits, intention tremors, and nervousness (Steigelmeier et al., 1999). Swainsonine affects the CNS, causing numerous brain lesions that appear 5–8 days after ingestion (Van Kampen and James, 1972). Sheep dosed with 0.4–0.8 mg/kg swainsonine developed lesions in the neurons of the basal ganglia, mesencephalon, and metencephalon, and in cerebellar neurons and glia (Steigelmeier et al., 1999); clinical signs were noted after 16 days of locoweed dosing.

Table 3

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Intake (% of offered)</th>
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</thead>
<tbody>
<tr>
<td>Control alfalfa (5 g/kg BW)</td>
<td>97.7 ± 1.8aA</td>
</tr>
<tr>
<td>LiCl (175 g/kg BW)</td>
<td>100aA</td>
</tr>
<tr>
<td>Broom snakeweed (5 g/kg BW)</td>
<td>100aA</td>
</tr>
<tr>
<td></td>
<td>100aA</td>
</tr>
<tr>
<td></td>
<td>98 ± 2.0aA</td>
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<td></td>
<td>100aA</td>
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<td>100aA</td>
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<td></td>
<td>4.3aA</td>
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<tr>
<td></td>
<td>93.2 ± 4.3aA</td>
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<tr>
<td></td>
<td>16.3 ± 8.1ab</td>
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<tr>
<td></td>
<td>100aA</td>
</tr>
<tr>
<td></td>
<td>10.3 ± 2.2ab</td>
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</tbody>
</table>

For each test day, treatments with different lowercase superscript letters (within a column) differ (P<0.01). Within each treatment, means with different uppercase superscript letters for the 4 test days (within a row) differ (P<0.01). On test day 1, animals were offered the test food, then immediately dosed with the respective treatments. Test days 2, 3 and 4 were 3, 7, and 14 days, respectively, after the initial test day. Animals that ate the test food on Day 3 were also dosed with their respective treatment. For LiCl, the Day 3 vs. Day 14 comparison approached significance (P=0.06); other non-significant P values were >0.15.

Selenium is an essential element of the antioxidant enzyme glutathione-peroxidase utilized to convert oxidation products and intracellular free radicals into less reactive compounds. Other biological functions of Se include regulation of thyroid hormones and regulation of the status of vitamin C (Beckett and Arthur, 2005). Selenium is also toxic and has complex effects on many cellular processes, including inhibition of enzyme redox reactions, particularly those involving sulphur-containing amino acids (Aitken, 2001). The exact mechanism of Se intoxication is not clear, although Se may cause glutathione depletion and lipid peroxidation (Spallholz, 1994). The margin between safe and toxic levels is slight. Forages containing <0.1 mg/kg cause deficiency (Mayland et al., 1989), whereas concentrations >5 mg/kg result in toxicosis (National Research Council, 2005).
Clinical signs of Se toxicity include abnormal movement, severe diarrhea, and respiratory failure (Raisbeck and O'Toole, 2000; Fessler et al., 2003). Selenium dosed to pigs in plant form (Astragalus bisulcatus) resulted in neurological dysfunction and extensive and severe CNS lesions within 4 days of exposure (Panter et al., 1996). Ingestion of excess selenium in humans has been reported to cause severe abdominal pain and gastroenteritis (Gasmī et al., 1997; Lech, 2002). The parenteral injection of a single dose of sodium selenite resulted in lesions in the cerebellum, cerebrum, midbrain and medulla in cattle (MacDonald et al., 1981).

Hyperaccumulator plants such as X. glabriuscula take up Se as selenate, selenite, and organic Se. Selenomethionine and selenate appear to be the dominant Se species found in X. glabriuscula (Zane Davis, unpublished data), consistent with Se species found in other hyperaccumulator species (Freeman et al., 2006). The toxicity of this species of Se is probably at least as high as other forms; toxicity to rats occurred at doses >0.5 mg/kg BW (Johnson et al., 2008).

Typically, the maximum tolerated level of Se for sheep and cattle is given as 5 mg/kg diet dry matter (NRC, 2005). We initially used a Se dose of 3 mg/kg BW based partially on the work of Davis et al. (2006), who fed sheep 4–12 mg inorganic Se/kg BW with no clinical signs, and current research work (J. Hall, personal communication). Four of five sheep tolerated this dose with no clinical signs of toxicosis, but this dose was fatal to one animal. This result indicates that susceptibility to Se varies greatly among animals.

Grazing animals occasionally ingest large and fatal amounts of seleniferous plants when other forage is scarce (Fessler et al., 2003). More typically, anecdotal information suggests that grazing animals do not consume substantial amounts of plants with high Se concentrations (Burrows and Tyrl, 2001) because of the taste or odor. Not coincidentally, acute Se toxicity is reported to occur in naive livestock, as experienced animals are rarely tolerated this dose with no clinical signs of toxicosis, but current research may reflect differing mechanisms of action of the plant toxin(s) on gut and neural structures important for forming conditioned taste aversions. Alternatively, the doses of locoweed and/or snakeweed may not have been high enough to condition an aversion. These results suggest that conditioned aversions to Se-containing plants may help to deter consumption of such plants by grazing ruminants on rangelands.

Acknowledgements

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References

Franke, K.W., Potter, V.R., 1936. The ability of rats to discriminate between foods containing differing amounts of Se. Raisbeck et al. (1993), at least in part because animals find Se hyperaccumulator plants distasteful. Franke and Potter (1936) reported that rats are able to distinguish between foods containing differing amounts of Se. Raisbeck et al. (1993) noted that virtually all cases of selenium toxicity in Wyoming livestock occur in naive livestock, as experienced animals are rarely intoxicated. Further, Raisbeck et al. (1993, 1996) reported conditioned aversions in cattle and pronghorn antelope when animals were given Se diets. Some cattle fed Se developed such a strong aversion to the experimental diets that they starved rather than consume it (Raisbeck et al., 1996). Selenium as the chemical form(s) found in woody aster appears to be a potent aversive agent for sheep, and likely all ruminant livestock.

5. Conclusion

One potential management tool to reduce livestock losses from toxic plants is conditioned food aversion. In addition, understanding factors that influence consumption of toxic plants by grazing livestock can provide information to refine management schemes to prevent toxicosis and death. Three problematic toxic plants on U.S. rangelands were used to determine their efficacy in conditioning a taste aversion. Of the three toxic plants with differing toxins, and mechanisms of action, used in this study (X. glabriuscula – selenium; A. lentiginosus – swainsonine; G. sarothrae – diterpene acids), only the seleniferous woody aster conditioned a taste aversion. It was also the only acutely toxic plant used in this study. These results may reflect differing mechanisms of action of the plant toxin(s) on gut and neural structures important for forming conditioned taste aversions. Alternatively, the doses of locoweed and/or snakeweed may not have been high enough to condition an aversion. These results suggest that conditioned aversions to Se-containing plants may help to deter consumption of such plants by grazing ruminants on rangelands.


Mathews, F.P., 1936. The toxicity of broomweed (Gutierrezia microlopa) to locoweed in naïve and familiar cattle. J. Range Manage. 50, 367–370.

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