# Interactions between Woody Plants and Browsing Mammals Mediated by Secondary Metabolites

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# INTERACTIONS BETWEEN WOODY PLANTS AND BROWSING MAMMALS MEDIATED BY SECONDARY METABOLITES

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## INTRODUCTION

Mammals must overcome several challenges to exploit woody plants; these include variation among plant species, individuals, growth stages, and parts in their nutritional value and mechanical and chemical defenses (91). The latter are especially significant because woody plants produce a variety of secondary metabolites (56), many of which are chemical defenses against browsing by mammals and some of which appear to be an evolutionary

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response to browsing by mammals (12a). Not all secondary metabolites are equally effective as defenses against browsing, and none provides complete protection (98), because mammals have evolved anatomical, physiological, and behavioral counters to plant defenses (27, 61, 91). As a result, some woody plants are browsed more than others.

The effects of secondary metabolites occur at different hierarchical scales, ranging from individual plants to ecosystems. There are recent reviews of the evolutionary and environmental controls of chemical defenses against browsing, and of the physiological and biochemical mechanisms mammals use to counter these defenses (61, 81). This review concerns three aspects of chemically mediated interactions between woody plants and browsing mammals: (i) chemical specificity and toxicity, (ii) learning as a counter to chemical defense, and (iii) the effects of chemical defense on plant communities and ecosystems.

## MODES OF CHEMICAL DEFENSE AGAINST MAMMALS

### Specificity of Chemical Defenses Against Mammals

Until about a decade ago, knowledge of the chemical defenses of plants against mammals was limited to an understanding that the concentrations of several classes of secondary metabolites (e.g. resins, phenolics, tannins, alkaloids) were often inversely correlated with the use of plants by herbivores (11, 34, 102, 119). The potential role of toxins in the defense of plants against mammals was also recognized (34), and correlative evidence existed for the defensive roles of some individual plant metabolites (55, 103).

During the last decade, chemists have furthered our understanding of phytochemical defenses against mammals in two ways (98). First, they have identified specific chemical substances, rather than general classes of substances, that are responsible for a mammal's response. Second, they have linked avoidance or rejection of a plant to: (i) some fundamental nutritional deficiency in the plant, or (ii) phytochemicals that are unpalatable and adversely affect the mammal's physiology. This chemically oriented approach has increased interest in individual substances that mediate plant-mammal interactions.

One of the most intensively studied chemically mediated interactions involves snowshoe hares *(Lepus americanus)* and winter-dormant woody plants (9, 11, 12, 61, 110). In winter, snowshoe hares discriminate among woody plants based on species, growth forms (evergreen vs deciduous), developmental stages (juvenile vs adult), and plant parts. Much of this discrimination is related to secondary metabolites, and boreal woody plants contain a diversity of low molecular weight metabolites that serve as "antifeedents." Individual monoterpenes (97, 110), triterpenes (96, 98), and phe-

nols (19, 52) deter feeding by hares, as do other substances of unknown biosynthetic origins (95). Three generalities arise from examining the relationship between hares and secondary metabolites in woody plants.

The first generalization is that phytochemicals belonging to similar biosynthetic classes do not necessarily have similar activities. For example, camphor contributes to the defense of white spruce *(Picea glauca),* but the structurally related monoterpene bornyl acetate does not (110). Similarly, Reichardt et al (97) identified six monoterpenes in the buds of balsam poplar *(Populus balsamifera),* of which only cineol was significantly unpalatable to hares. Analogue studies confirm the relationship between chemical structure and activity for defensive chemicals. For example, pinosylvin is a strong feeding deterrent, pinosylvin methyl ether is effective but less potent, and pinosylvin dimethyl ether is virtually inactive (19). Similarly, 2,4,6-trihydroxydihydrochalcone in juvenile balsam popular deters feeding by hares (52), but the structurally similar pinostrobin in green alder *(Alnus crispa)* does not (19).

Another generalization concerning the chemical defenses of woody plants is that deterrence varies with the concentrations and potencies of individual metabolites, but the situation within a plant can be quite complex. For example, Jogia et al (52) consider differences in the concentrations of 2,4,6-trihydroxydihydrochalcone to be primarily responsible for the low palatability to hares of juvenile as compared to mature balsam poplar. Reichardt et al (97), on the other hand, argue that the difference in palatability is largely due to different concentrations of salicaldehyde and 6-hydroxycyclohexenone in the two growth stages. These two studies suggest that the chemical defense of juvenile poplar against hares involves different phytochemicals and the additive and (or) synergistic effects of different metabolites.

The final generalization is that the chemical defenses of woody plants vary by growth stage and by plant parts within growth stages. For example, the internodes of the juvenile and adult stages of Alaska paper birch *(Betula resinifera)* differ qualitatively in chemical defenses, as do the chemical defenses of buds and internodes (96). Hares reject balsam poplar buds because of the presence of high levels of metabolites that are not even detectable in the internodes (97). Similarly, hares reject green alder buds because of high concentrations of metabolites that are found only in low concentrations in the internodes (19).

## Dynamic Aspects of Chemical Defense

Although it has long been recognized that disruption of plant tissue by herbivores during ingestion may release harmful substances (e.g. cyanogenic glycosides; 23), the concept of "dynamic defenses" has not been extensively applied to mammals. However, recent reports indicate that dynamic defenses

against mammals may be common (21, 97). For example, phenol glycosides are transformed enzymatically to substances (trichcoparpogenin and 6-hydroxycyclohexenone) that deter feeding by hares on quaking aspen *(Populus tremuloides)* and balsam poplar (97).

## Relationship of Feeding Deterrence to Antibiosis

Chemical defenses have been classified as either toxins or generalized digestion inhibitors, although some overlap between the categories has been recognized (32, 100). There is growing evidence, however, that food selection and ingestion are regulated by toxins rather than by inhibition of protein or carbohydrate digestion. Studies of domestic and wild mammals fed unpalatable browse normally available to them, or artificial diets treated with extracts from this browse, confirm the importance of toxicity. For instance, condensed tannins supposedly limit intake by inhibiting ruminant digestion (102, 119), but deterrence of goat browsing is associated with toxicity, not digestion inhibition (27, 93). Indeed, most phytotoxins deter feeding by domestic mammals (93, 114). Moreover, snowshoe hares (95–97), microtine rodents (3, 53), and bushy tailed woodrats *(Neotoma lepida)* (74) voluntarily reduce food intake to well below maintenance when fed browse containing high concentrations of secondary metabolites or when fed artificial diets treated with extracts from this browse. Creosote brush *(Larrea tridentata)* resin that deters feeding by woodrats forms a complex with protein in vitro (100), but it does not affect protein digestion by woodrats that normally eat creosote brush (75). Hares that eat birch and evergreen conifers containing high concentrations of feeding deterrents lose more nitrogen in feces (96, 109), but the associated large losses of sodium and nitrogen in urine indicate that detoxification increased and that renal function was disrupted (86, 87, 96). Finally, essentially all known feeding deterrents extracted from food that could be browsed by snowshoe hares are lipid soluble low molecular weight substances that are toxic to mammals, insects, and microbes (Table 1).

## Tannins as Defenses Against Mammals

Tannins are generally defined as water-soluble, high molecular weight (>500 amu) polyphenols capable of precipitating proteins. Only condensed and hydrolyzable tannins were considered in ecological studies at the beginning of the last decade, because tanning quantity was considered more important than tannin quality (32, 100). However, the importance of low molecular weight metabolites as chemical defenses against mammals is changing the view of tannins.

It is questionable that tannins deter browsing primarily by inhibiting digestion of proteins or carbohydrates. Instead, mammals may reject tannin-containing plants because they cause internal malaise (27, 92). Condensed

**Table 1** Toxicity to mammals, insects, and microbes of substances that deter feeding by snowshoe hares (Numbers in parentheses are references)

| Compound | Deterrent to mammals | Toxic to mammals | Toxic to insects | Toxic to microbes |
|---|---|---|---|---|
| Cineole | Yes (97) | Yes (43) | Yes (25) | Yes (1) |
| Alpha Bisabolol | Yes (97) | Yes (41) | Yes (2) | Yes (29) |
| Pinosylvin | Yes (19) | Yes (35) | Yes (123) | Yes (35) |
| Pinosylvin Methyl Ether | Yes (19) | ? | Yes (123) | Yes (35) |
| Germaerone | Yes (95) | ? | ? | ? |
| Campher | Yes (110) | Yes (99) | ? | Yes (24) |
| Papyriferic Acid | Yes (96) | Yes (19, 96) | ? | ? |
| Condensed Tannins | Yes (20, 92) | ? | ? (5) | Yes (122) |

tannins, particularly procyanidins (46), readily depolymerize under acidic conditions similar to those in portions of the digestive tract of most mammalian herbivores (16, 21). Hence, some condensed tannins may be toxic (16, 58, 70). In addition, hydrolyzable tannins in some plant species cause severe necrosis and ulceration of the epithelium of the esophagus, stomach, intestines, and proximal renal tubules (28, 70).

It is also clear that the effectiveness of condensed tannins as deterrents to browsing depends on tannin structure (20). Tannin structures are now routinely elucidated, and tannins are readily isolated even on a large scale (92). As a result, the use of commercially available tannins for bioassays, or as standards for analytical procedures, is being replaced by partially characterized tannins isolated from plants of interest (42).

# LEARNING AS A MAMMALIAN COUNTER TO CHEMICAL DEFENSE

## Evolutionary Considerations

Some aspects of plant defense theory assume that mammals have the innate ability to detect secondary metabolites and to avoid intoxification, but there is increasing evidence that mammals learn to avoid poisoning. Mammalian herbivores are generally long lived, many are social, their home ranges frequently encompass entire landscapes, and their diets are commonly catholic (108). Such conditions should confer a selective advantage to individuals whose diet selection is flexible (6, 90, 91). Learning provides the flexibility necessary for mammalian herbivores to maintain homeostasis in environments where the nutrient content and toxicity of potential foods change temporally and spatially. While some nutritious foods do not contain toxins, nearly all

woody species contain potentially toxic secondary metabolites whose concentrations vary with environment, season, plant developmental phase, plant physiological age, and plant part (9, 12, 69).

In what follows, we must refer to the results of studies involving domestic herbivores such as sheep and goats because the role of learning in diet selection for most mammalian species is not known. While learning in diet selection has not been studied in many mammals, the mechanisms that different species of mammals use to learn about foods should be qualitatively similar (37, 90, 91) and are likely important in the feeding behavior of wild mammalian herbivores (61). From a theoretical standpoint, evolutionary processes create a match between environmental exigencies and behavior such as foraging (94, 111). Even in domestic herbivores the match should still exist because the behavioral changes brought about through domestication are more quantitative than qualitative (89).

## Learning from Postingestive Consequences

One way animals can learn about foods is through postingestive feedback from nutrients and toxins. Animals learn about the postingestive consequences of foods through two interrelated systems, affective and cognitive (36). Taste plays an essential role in both systems. The affective system integrates the taste of food and its postingestive consequences, and changes the amount of food the animal will ingest, depending on whether the postingestive consequences are aversive or positive. Thus, the affective system provides feedback so mammals can learn to ingest nutritious foods and to avoid intoxification. The cognitive system integrates the taste of food with its odor and sight. Mammals use the senses of smell and sight to select or to avoid particular foods.

Research on conditioned food preferences and aversions shows that voluntary intake depends on postingestive consequences. If the food is nutritious (positive postingestive consequences), intake of the food increases. If toxicity ensues (aversive postingestive consequences), intake of the food is limited. For example, bitter and sweet are often considered feeding deterrents and attractants, respectively. However, intake of bitter substances increases when they are paired with positive postingestive consequences, and intake of sweet substances decreases when they are paired with aversive postingestive consequences (38).

Mammalian herbivores apparently learn to prefer foods with positive postingestive consequences, as demonstrated by lambs' strong preference for nonnutritive flavors paired with glucose over nonnutritive flavors paired with the nonnutritive sweetener saccharine (15). The amount ingested by other species of mammals is also increased by pairing nonnutritive foods or flavors with calories, recovery from nutritional deficiencies, and recovery from postingestive distress (93).

Animals also regulate their intake of potentially toxic foods by associating the taste of the foods with aversive postingestive consequences (36, 93). For example, current season's growth (CSG) of blackbrush *(Coleogyne ramosissima)* is rich in condensed tannin, while older growth (OG) is not. In less than four hours, goats switch from a diet largely composed of CSG to a diet largely composed of OG. Aversive feedback from condensed tannin in CSG causes this rapid dietary shift (27, 92). When purified condensed tannin from CSG is incorporated into OG pellets, goats eat until they experience aversive feedback, which sets an upper limit to the mass of OG that goats will eat (27, 92). In these studies, the taste of condensed tannin per se did not regulate goat feeding. Rather, goats associate the taste of the food (i.e. CSG or OG) with the degree of postingestive malaise caused by condensed tannin to determine how much to eat.

Odor is an important signal mammals use to avoid foods that elicit negative feedback (93), and many of the secondary metabolites that deter feeding by snowshoe hares in winter are volatile even at low temperatures (95–97, 110; Table 1). However, mammals require taste as well as odor to assess the quality of food (36). For example, animals that become ill after only smelling a novel food will later ingest that food, unless they have also tasted the food. Persistent sampling of foods, which is characteristic of mammalian herbivores (34), lets mammals determine when the association between odor, taste, and food quality have changed (60).

Mammalian herbivores have physiological and biochemical mechanisms to detoxify secondary metabolites (61, 67), and if the capacity of these detoxification systems is exceeded mammals becomes ill and may die. However, mammals usually adjust intake to avoid intoxification. To do so, they must sample foods to determine when the concentrations of nutrients and toxins change as a result of growth processes and previous herbivory (9). Sheep (13, 31, 60, 116), goats (27, 92), and cattle (88) sample foods and regulate their intake of nutritious plants that contain toxins. If toxicity decreases, the taste of the plant is no longer paired with aversive postingestive consequences. Any nutritional value that plant provides will constitute positive feedback, and subsequently cause intake of the plant to increase. In contrast, intake decreases as the toxicity of the plant increases.

## Learning from Mother

Learning by trial and error, based solely on postingestive feedback, is one way to determine which foods to eat and which foods to avoid, but it can be inefficient and risky (6, 90, 91, 93). This could provide additional selective pressure for herbivores that feed in mixed-generation groups to rely on social learning, where information is passed from experienced to inexperienced foragers, generally from a mother to her offspring.

Learning from mother increases learning efficiency. For example, if a ewe has learned to avoid a food that causes postingestive distress, its lamb also learns to avoid that food much sooner than a lamb reared without its mother (13, 76–78). Likewise, a lamb learns to eat food preferred by its mother much sooner than a lamb not reared with its mother (64, 76–78, 117). Such socially mediated feeding behavior leads to foraging traditions (48, 54, 63, 101).

Learning from social models also decreases the risks of trial and error learning, provided young mammals remember what they ate and sample novel foods cautiously. Young mammalian herbivores can remember, for at least one to three years, specific foods with either aversive (14, 27, 59) or positive (27, 39, 113) postingestive consequences. They identify novel foods and sample them cautiously (13, 92, 116). Animals that experience either unpleasant or pronounced positive postingestive consequences attribute those consequences to the novel food, even when it has eaten several familiar foods and the consequences occur six to eight hours after ingestion (13, 15, 92).

## EFFECTS OF SELECTIVE BROWSING ON COMMUNITIES AND ECOSYSTEMS

Differences in the chemical defenses of woody species, and in the abilities of mammalian herbivores to learn to distinguish among food items with different levels of defenses, have consequences for plant communities and ecosystems.

### Consequences of Functional Responses to Toxin Satiation

Selective browsing can change the composition of woody plant communities (62). In biomes as diverse as boreal forests (8, 84, 85), arid shrublands of western North America (114), African savannas (49), and the tropical woodlands of Sri Lanka (Ceylon) (80), selective browsing increases the abundance of unpalatable species. These unpalatable species are often heavily defended chemically (8). For example, in the boreal forest of Isle Royale National Park (57, 68, 112) and the Alaskan taiga (65), browsing of poorly defended deciduous species such as willow *(Salix spp.)*, quaking aspen, and birch by snowshoe hare, beaver *(Castor canadensis)*, and moose *(Alces alces)* favors domination by more chemically defended evergreens such as white spruce and Labrador tea *(Ledum groenlandicum)* (11, 95, 109).

Selective browsing does not always favor dominance by chemically defended species, however, because browsing intensity depends on the relative abundance of the woody species in the vegetation. On Isle Royale (7) and in Newfoundland (4), browsing by moose removes balsam fir *(Abies balsamea)* from areas where it is not abundant (7), even though balsam fir is rich in terpenes that are potentially toxic to mammals (121). In contrast, in areas where fir density is high, enough young fir escape to ensure that it persists.

Similarly, although chemicals defend green alder against browsing by boreal mammals (11, 19), snowshoe hares browse green alder heavily when it grows in areas dominated by palatable species such as feltleaf willow *(Salix alaxensis)* (10); they browse it lightly in areas where it is moderately abundant. More intense browsing of a woody species when it is rare has been reported for other biomes as well (45).

Bryant & Fox (10) suggest that the inverse relationship between relative abundance and browsing intensity represents a functional response of a predator to its prey (47). A functional response assumes that at some prey biomass predators become satiated and allow some prey to escape. When applied to interactions between woody plants and mammals, the functional response relates the percent of the plant's biomass eaten (browsing intensity) to the relative biomass of the plant in the vegetation. Such a graph shows that a woody species is more likely to be browsed severely when it is rare than when it is abundant.

Intoxification apparently causes the functional response (10). When a woody species is so rare that its mass of toxins does not exceed the detoxification capacity of the browsing mammals, all of the individuals of the species can be eaten. If the biomass of the species exceeds the detoxification capacity of its predators, however, the average browsing intensity decreases. Thus, because the satiation biomass of the heavily defended species is less than that of poorly defended species, selective browsing is more likely to favor an increase in the abundance of a heavily defended species. This increase is less likely to occur if the heavily defended species is rare.

## Effects of Selective Browsing on Nutrient Cycling in Ecosystems

The link between tissue secondary chemistry, selective foraging by mammals, and the abilities of woody species to survive selective browsing has important consequences for nutrient cycling in ecosystems. These consequences arise for two reasons. First, forage selection and litter decomposition are determined not only by nutrients, structural carbohydrates, and lignins, but also by secondary metabolites (8, 33, 72, 73, 82, 83, 85, 115); broad spectrum phytotoxins that affect mammals are also toxic to microbes (Table 1). Second, the chemical defenses of many woody species are directly correlated with their ability to tolerate nutrient stress (9, 22).

The selective foraging of mammals involves both positive and negative feedbacks in ecosystems. Positive feedbacks occur when selective foraging causes the rate of nutrient cycling to increase or decrease. This is especially true of nitrogen because its mineralization limits the net primary production in many terrestrial ecosystems (120), and the nitrogen content of plant tissues may determine herbivore feeding rates (66), as well as the kinds and amounts

of chemical defenses (9). Negative feedbacks occur when physical dis-
turbances (e.g. wildfires or outbreaks of pathogens or specialized insects)
destroy woody plant species that are not browsed by mammals. Negative
feedbacks appear to be exceptions to the correlation of feeding preferences,
tissue chemistry, and litter decay rates.

Invasion and ultimate dominance by unpalatable, slowly growing species is
apparently a more common response of woody vegetation to selective brows-
ing (8, 82–85). The limited evidence for this hypothesis comes primarily from
boreal forests and south African savanna-woodlands. On Isle Royale in
Michigan and in interior Alaska, browsing by moose on willow, aspen, birch,
and other palatable hardwoods increases the abundance of white spruce (57,
65, 68, 112). White spruce is a poor quality food for moose and other boreal
mammals (11); it is also a low quality litter (33, 79, 82, 83, 85). The same
chemical properties that reduce its food quality also reduce its value for soil
microbes; those properties include high concentrations of toxic secondary
metabolites, lignins, waxes, and cutins that are indigestible by mammals
(102) and slow to decompose (115), and a low concentration of nitrogen (33).
Likewise, in the dystrophic savanna woodlands of southern Africa, browsing
by mammals apparently influences vegetation composition in the same way
and may have similar effects on nutrient cycling (30).

Palatable species are browsed more intensively as chemically defended
species become dominant, primarily because they represent a declining sup-
ply of good food (8, 83), and secondarily because of the functional response
described above. Thus begins a decrease in nutrient cycling that leads to the
establishment of pure stands of chemically defended species beneath which
nitrogen availability is low (8, 30, 82–85). This sequence of events has been
confirmed in exclosures on Isle Royale National Park in Minnesota (83, 85)
and is suggested by the reduction in soil nutrients outside exclosures in
African savanna ecosystems with high populations of mammalian browsers
(44). It also occurs in exclosures in central Washington (118).

Soil fertility declines as the biomass of unpalatable species such as spruce
comes to contain increasing amounts of nutrients, and as decomposition
declines because of low litter quality (8, 82–85). Slowly growing species such
as spruce, however, can persist in nutrient-deficient soils (17, 40), and a
decline in soil fertility associated with increasing abundance of such species
may actually enhance their dominance relative to species that require more
nutrients (18).

In contrast to ecosystems dominated by woody plants, selective foraging
can enhance nutrient cycles in grassland ecosystems such as the Serengeti of
tropical East Africa and the Great Plains of temperate North America. In these
ecosystems, grazing by mammals can stimulate grass regrowth and the rapid
recycling of nutrients in urine, feces, and carrion (26, 71, 104, 106, 107). In

the Hudson Bay lowlands, grazing by lesser snow geese also accelerates nutrient cycling and the growth of preferred graminoids through fecal deposition (50, 51, 105).

In grasslands, the enhancement of nutrient cycles through deposition of feces and urine depends on continued grazing of preferred species. In contrast, reduced nutrient cycling and decreased ecosystem productivity following the invasion of unpalatable woody species can continue even after browsers abandon an area, if the invading woody species have low nutrient demands (8, 18, 83). Moreover, selective browsing of less palatable species is unlikely to change the dominance of species that are heavily defended against browsing. Palatable species will proliferate, and ecosystem productivity will increase, only following negative feedback from physical disturbances (e.g. wildfires or outbreaks of pathogens or specialized insects) that destroy species that are not browsed.

## CONCLUSIONS

Woody plants apparently rely on a chemically diverse array of specific secondary metabolites (rather than classes of secondary metabolites) as defenses against browsing by mammals. The effectiveness of these substances is primarily due to toxicity rather than digestion inhibition.

A mammal's most flexible counter to phytotoxins is to learn to avoid intoxification through trial and error and from social models like mother. Through learning, mammals can determine which foods to eat and which to avoid, and how much food they can safely ingest. The amount of each food they can safely ingest is usually lower than the mammal's maintenance food requirement, so browsing mammals usually starve before they eat enough browse to be poisoned.

The limits of food intake set by toxins suggest that interactions between woody plants and mammals can be analyzed as a functional response of a predator to its prey; the mammal is satiated when it is intoxified by the prey's chemical defenses. According to this hypothesis, a woody species should be most intensively browsed when it is rare. Heavily defended species should be more likely than poorly defended species to increase, because the detoxification capacity of mammals would be satiated sooner by heavily defended species. However, browsing does not always result in dominance by heavily defended species. If the biomass of a heavily defended species is too low to satiate the detoxification systems of mammals, browsing can eliminate the species.

Selective browsing by mammals can greatly affect the composition of plant communities. Browsing usually favors an increase in unpalatable species that are heavily defended chemically. Moreover, once selective browsing encour-

ages invasion by chemically defended species, invasion is likely to continue because the low nutrient requirements of these woody species let them persist in a nutrient-deficient environment.

Selective browsing can slow nutrient cycling in ecosystems dominated by woody plants, but it can accelerate nutrient cycling in ecosystems dominated by graminoids. A major reason for this difference is that woody plants have more chemical defenses than grasses do against mammalian herbivores. The chemical defenses that decrease the quality of woody species as food also make their litter poor quality as a substrate for decomposers.

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