Chemically mediated interactions between woody plants and browsing mammals

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Abstract

A diverse array of secondary metabolites deters feeding by mammals on woody plants. However, not all secondary metabolites are equally deterrent and the potencies of these substances as antifeeds is related to their structures. Although the physiological reason underlying deterrence by secondary metabolites is not well understood, the available evidence indicates that toxicity is more important than digestion inhibition.

Resource limitation influences the production of secondary metabolites by woody plants. Species that are adapted to unproductive habitats are more chemically defended than species that are adapted to productive habitats. Resource limitation also affects the phenotypic expression of chemical defense with nutrient stress favoring increased production of carbon-based secondary metabolites and reduced production of nitrogen-containing secondary metabolites. Light stress has the opposite effects on the production of these substances.

Herbivory by mammals also affects the chemical defenses of woody plants. In some cases browsing results in increased defense and in others decreased defense. Three circumstances under which browsing by mammals can change the chemical defenses of woody plants are discussed.

Explanations of diet selection by mammalian herbivores have emphasized optimization of nutrient or energy intake (Westoby 1974, Belovsky 1978). This theoretical framework is useful for interpreting interactions between graminoids and grazing mammals (Sinclair et al. 1975). However, it cannot explain why browsing mammals feed more on some woody plants than others (Bryant and Kuropat 1980, Owen-Smith and Novellie 1982). This insufficiency is caused by relatively high concentrations of secondary metabolites in woody plants in comparison to graminoids (Bryant et al. 1991b). In biomes from the arctic to the tropics avoidance of defensive secondary metabolites is a more important cause of selective browsing by mammals than is selection for nutrients or energy (reviews in Palo and Robbins 1991).

Future attempts to explain selective browsing by mammals on woody plants must include chemical antiherbivore defense. This will require identification of defensive substances and clarification of their modes of action. It will also require an understanding of factors that influence the production of defensive substances. Here we consider these aspects of chemically mediated interactions between woody plants and browsing mammals.

Modes of Chemical Defense Against Mammalian Herbivores

Specificity of Chemical Defense

About a decade ago knowledge of chemical defense of plants against mammalian herbivory was limited to the understanding that concentrations of several classes of secondary metabolites (e.g., resins, phenolics, alkaloids) often inversely correlated with the herbivores' use of plants (Freeland and Janzen 1974, Bryant and Kuropat 1980, Van Soest 1982, Robbins 1983). In addition, the potential role of toxins in the defense of plants against mammals was recognized (Freeland and Janzen 1974) and correlative evidence existed for the defensive roles of some individual plant metabolites (Rosenthal and Janzen 1979).

In the last decade chemists, with their orientation toward molecular-based processes, have in 2 ways made a major impact on this conceptualization of chemical defenses against mammalian herbivory (Reichardt et al. 1987). First, a mammal's response to chemical attributes of a plant must be based upon specific chemical substances rather than general classes of substances. Second, a mammal's avoidance or rejection of a plant must be based upon (1) some fundamental nutritional deficiency in the plant's tissues or (2) the presence of specific phytochemicals which are unpalatable or adversely affect the mammal's physiology. Furthermore, these 2 aspects of chemical defense may or may not reside in the same substance. This chemically oriented thinking has shifted the focus of research away from classes of phytochemicals to the search for individual substances that mediate plant/mammal interactions.

Probably the best studied or the chemically mediated plant/-mammal interactions is between winter-dormant boreal woody plants and the snowshoe hare *(Lepus americanus)*. It is now clear that snowshoe hares are very discriminating in their use of woody plants in winter with respect to growth forms (evergreen vs. deciduous), species, developmental stages (juvenile vs. adult), and plant parts (Bryant and Kuropat 1980). Many aspects of this discriminatory use have been related to secondary metabolites, and it is useful to examine the generalities resulting from these relationships.

The most striking feature of the chemical defenses of woody plants against snowshoe hares is the diversity of low molecular weight phytochemical which serve as feeding deterrents. Individual monoterpenes (Sinclair et al. 1988a, Reichardt et al. 1990b), triterpenes (Reichardt et al. 1984), and phenols (Clausen et al. 1986, Jogia et al. 1989) deter hare feeding as do other substances with obscure biosynthetic origins (Reichardt et al. 1990a).

However, it is also clear that not all phytochemicals which belong to these general biosynthetic classes have similar activities. For example, camphor contributes to the defense of white spruce (*Picea glauca;* Moench, Voss), but the structurally related monoterpene bornyl acetate does not (Sinclair et al. 1988a). Similarly, Reichardt et al. (1990b) reported that of 6 monoterpenes identified in buds of balsam poplar (*Populus balsamifera* L.) only cineol contributes significantly to their unpalatability to hares. The notion of a close structure-activity relationship for defensive chemicals is further indicated by analogue studies. For example, pinosylvin is a strong feeding deterrent, pinosylvin methyl ether is effective but less potent, and pinosylvin dimethyl ether is virtually inactive (Clausen et al. 1986). Similarly, 2,4,6-trihydroxydi-hydrochalcone in juvenile balsam poplar deters hare feeding (Jogia et al. 1989), but the structurally similar pinostrobin in green alder (*Alnus crispa* subsp. *crispa;* Ait., Pursh) does not (Clausen et al. 1986).

Although the emerging view is that chemical defense of woody plants against browsing results from the concentrations and poten-cies of individual metabolites, the situation in a given plant can be quite complex. A case in point is the chemical defense of balsam poplar against hares. Jogia et al. (1989) consider 2,4,6-trihydroxy-dihydrochalcone to be primarily responsible for defense of juvenile, relative to mature, plants. Reichardt et al. (1990b), on the other hand, have argued that the palatability difference between juvenile and mature poplar resides principally in the concentration differences of salicaldehyde and 6-hydroxycyclohexenone in the 2 growth stages. Taken together, the 2 studies suggest that although individual phytochemicals are involved, the chemical defense of juvenile poplar is a result of the additive and/or synergistic effects of a suite of metabolites.

Physiological Effects of Low Molecular Weight Defenses

An important issue is the relationship of deterrence to the underlying physiological reason for selective feeding. Chemical defenses have been grouped into specific toxins and generalized digestion inhibitors although overlap has been recognized (Feeny 1976, Rhoades and Cates 1976). The experimental evidence indicates that low molecular weight metabolites that deter feeding by mammals are toxins. For example, when snowshoe hares (Reichardt et al. 1984, 1990a,b); microtine rodents (Bazli and Jung 1980, Jung and Batzli 1981); and bushy tailed woodrats *(Neotoma lepida)* (Meyer and Karazov 1989), are fed unpalatable browse that contains high concentrations of these substances or artificial diets treated with extracts of this browse, voluntary food intake is reduced to well below maintenance. These results indicate avoidance of intoxification by reduced food intake rather than inhibition of protein carbohydrate digestion (Bryant et al. 1991c, Meyer and Karazov 1991). This conclusion is strengthened by Meyer and Karazov's (1989) study of feeding deterrent phenolic resins of creosote brush (*Larrea tridentata;* Moc. Ses. ExDC., Vail.). Although, these resins complex with protein in vitro (Rhoades and Cates 1976), they do not affect in vivo digestion of protein by woodrats that normally eat creosote brush. When hares eat twigs of birch and evergreen conifers that contain high concentrations of feeding deterrents, increased loss of nitrogen in faeces occurs (Reichardt et al. 1984, Sinclair et al. 1988b); but the associated large losses of sodium and nitrogen in urine (Pehrson 1983a,b,; Reichardt et al. 1984) also indicate toxic disruption of kidney function and increased detoxification.

Tannins as Defenses against Mammals

As the importance of low molecular weight metabolites as chemical defense against mammals has become clear, the view of tannins as defenses has begun to change. Tannins are generally defined as water-soluble, high molecular weight (>500 amu) polyphenols capable of precipitating proteins. At the beginning of the last decade, 2 general types of tannins were known: condensed and hydrolyzable. At that time, however, structural elements of tannins, other than condensed vs. hydrolyzable, were seldom considered in ecological studies, because tannin quantity was considered more important than tannin quality (Feeny 1976, Rhoades and Cates 1976).

Elements of tannin structure, however, are now routinely elucidated. Tannin isolations, once considered laborious, are now readily performed even on large scales (Provenza et al. 1991). As a result, the use of commercial bioassays or standards for analytical procedures is being replaced (Haggerman and Butler 1989) by partially characterized tannins isolated from plants of interest. This approach has demonstrated that structurally different condensed tannins vary in their effectiveness as deterrents to browsing (Clausen et al. 1990).

For mammals the proposal that tannins act primarily by inhibiting digestion is questionable. Decreased voluntary intake of plants that contain condensed tannins is not necessarily related to digestion inhibition. Indeed, mammals may reject tannin-containing plants because they cause internal malaise, not because tannins are bound with protein or cell wall constituents (Provenza et al. 1991). Depolymerization of condensed tannins, particularly procyanidins (Hemingway and McGraw 1983), readily occurs under acidic conditions similar to those in portions of the digestive tract of most mammalian herbivores (Butler et al. 1986, Clausen et al. 1990). Hence, some condensed tannins appear to be toxic to mammals (Butler et al. 1986, Provenza et al. 1991).

Evolutionary Responses by Woody Plants to Resource Limitation and Disturbance

Inherently Slow Growth

Plants typical of resource limited habitats (infertile soil, dry soil, shade) generally cannot acquire sufficient resources to support rapid growth. The primary evolutionary response by plants to resource limitation has been a low maximum potential growth rate (Grime 1977, Chapin 1980). Additionally, slowly growing species usually have a low nutrient absorption capacity that limits their ability to acquire mineral nutrients (Chapin 1980) and a low photosynthetic rate that limits their ability to acquire carbon (Pearcy et al. 1987).

While a low maximum potential growth rate is selectively advantageous when resources are scarce (Grime 1977, Chapin 1980), it is disadvantageous when herbivory occurs. A given rate of herbivory removes more of the capital resources and net production of a slowly growing species than a rapidly growing species (Coley et al. 1985). Moreover, the limited ability of slowly growing species to absorb nutrients and to fix carbon reduces their ability to acquire the resources needed for regrowth after herbivory (Bryant et al. 1983). As a result, selection for defenses to deter herbivory increases as resources become limiting to growth (Bryant et al. 1983, Coley et al. 1985).

In contrast, species that have evolved in productive habitats have been selected for rapid growth so as to outcompete their neighbors and dominate available resources (Grime 1977, Chapin 1980). In these habitats there is strong selection to invest carbon directly in growth rather than energetically expensive chemical defenses. Rapidly growing species usually have high leaf and twig turnover rates. The inevitable loss of nutrients and carbon associated with rapid leaf and twig turnover (Chapin and Kedrowski 1983) is not a strong selective pressure on these plants in comparison to plants adapted to growth in infertile soil or shade, because nutrients and light are more available. Furthermore, rapid growth, a high nutrient absorption capacity, and high photosynthetic rate all enable rapid regrowth after herbivory so that there is less need for defenses that deter herbivory (Bryant et al. 1983).

The Evergreen Growth Form

The evergreen growth form is frequently associated with unproductive habitats and low digestibility and palatability to mammals (Bryant and Kuropat 1980, Bryant et al. 1983, Coley et al. 1985). Slow leaf turnover is advantageous in a low-nutrient habitat, because each time a leaf is shed it carries with it approximately half the nitrogen and phosphorus contained in it at mid-growing season (Chapin and Kedrowski 1983). Similarly, in deep shade where the potential for carbon (energy) acquisition is low, carbon loss can be minimized by slow leaf turnover (Grime 1977). However, greater leaf longevity also carries with it certain disadvantages. A long-lived leaf is more likely to encounter unfavorable physical conditions than a short-lived leaf. The high fiber content, low water content, and thick cuticle of many evergreens are adaptations to

unfavorable conditions such as winter dessication or summer drought (Levitt 1972). Fiber, wax, and cutin are comparatively indigestible by mammals and dilute the concentrations of more digestible nutrients and energy in leaves (Van Soest 1982, Robbins, 1983).

Evergreen species also differ from deciduous species in that they store more of their carbon and nutrient reserves in leaves (Chapin 1980). As a result, browsing is usually more damaging to an evergreen than to a deciduous species (Garrison 1972, Bryant and Chapin 1986). Thus, mature leaves of evergreens are usually more defended chemically against browsing than are mature leaves of decidious species (Bryant et al. 1983, Coley et al. 1985).

Adaptations to Disturbance

In many ecosystems productive habitats are associated with disturbances such as wildfire that open the canopy and provide a pulse of nutrients (Chapin and Van Cleve 1981). As a result, rapidly growing woody species that dominate early in secondary succession are often selected for traits that enable rapid regrowth of destroyed above-ground parts (Kramer and Kozlowski 1979). These adaptations also enable regrowth after herbivory with the result that they reduce the need for antiherbivore defense (Bryant et al. 1983).

The Regrowth-Defense Continuum

To summarize, through evolution plants have developed different life forms that are specialized to constraints imposed by the spatial and temporal variation in resource availability and disturbance (Fig. 1). When the return time of disturbance is very short (less than about 10 yr) so that nutrients become available in short pulses and growth is more water- than nutrient- or light-limited, the vegetation is dominated by fast growing graminoids that have a high capacity for regrowth and poor chemical defenses (Chapin and Van Cleve 1981, Schultze and Chapin 1987). Productive grassland ecosystems dominated by such species, for example the Serengeti Plains of East Africa, support a large biomass of mammalian herbivores dominated by grazers (Bell 1982, McNaughton and Georgiadis 1986). As the return time of disturbance increases, woody species progressively become more important in the vegetation. In savannas and caatinga where severe seasonal drought limits the abundance of evergreens, deciduous species predominate. In these biomes rapidly growing species that are poorly defended chemically characterize eutrophic habitats and more chemically defended vegetation such as miombo characterizes dystrophic habitats. Thus, eutrophic savannas are characterized by woody vegetation that is good food for browsing mammals and dystrophic savannas are characterized by woody vegetation that is poor food for browsing mammals (Bell 1982). As water becomes less limiting to growth, nutrient deficient and/or shaded habitats become progressively more dominated by well-defended evergreens. Thus, in arctic tundra, boreal forests (Bryant and Kuropat 1980), and tropical rainforests (Janzen 1974), the vegetation of the most nutrient deficient soils and shaded habitats is dominated by inherently slowly growing evergreens that are so defended against herbivory that the biomass of mammalian herbivores is low.

Phenotyic Responses by Woody Plants to Resource Limitation

All plants adjust physiologically to a low resource supply in basically the same way: through a decline in growth rate and in the rate of resource acquisition (Chaplin 1991). This centralized stress response is hormonally mediated but also involves integrated changes in nutrient, water, and carbon balances. These balances strongly affect the allocation of resources by plants to secondary metabolism (Bryant et al. 1983).
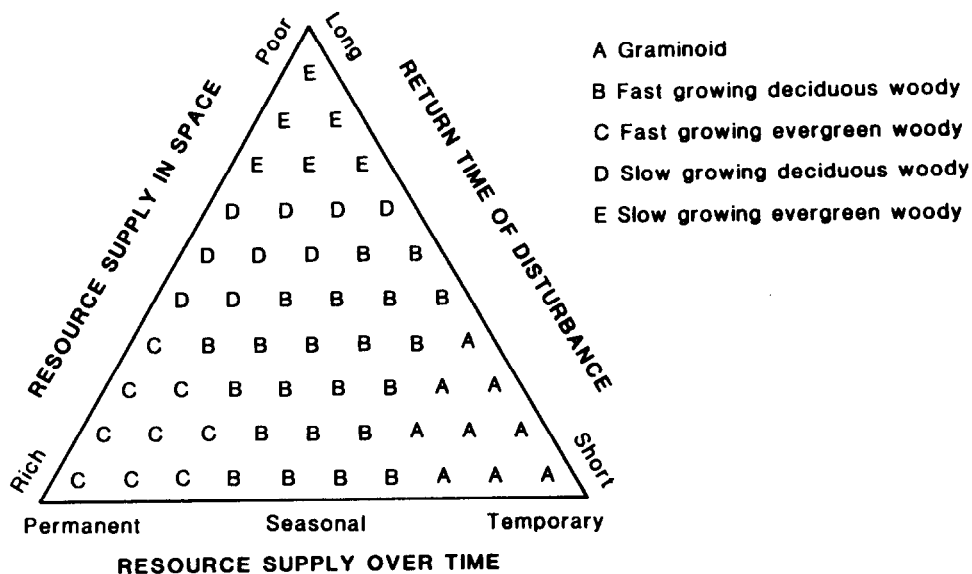
Fig. 1. Distribution of plant life forms on gradients of resource supply over time and space and the return time of disturbance.

Nutrient Limitation

When nutrients are less available in the soil, less nutrients are absorbed. A reduction in nutrient concentration reduces photosynthesis rate directly by reducing RuBP carboxylase, chlorophyll, and phospholipid contents and indirectly by decreasing the growth of leaf area (Moony 1972, Ingestad and Lund 1979). However, under conditions of nutrient stress, growth of the whole plant is usually more restricted by mineral nutrition than is photosynthesis, so in nutrient-stressed plants carbohydrates accumulate in excess of growth demands (Chapin 1980, 1991). This surplus carbohydrate is available for increased production of carbon-based secondary metabolites that contain no nitrogen, for example the phenolics and terpenes (Bryant et al. 1983). As a result, when woody plant growth is nutrient-limited, concentrations of carbon-based secondary metabolites usually increase (Wong 1973, Bryant et al. 1983, Gershenzon 1984). Furthermore, when plants are nitrogen stressed, production of nitrogen-containing secondary metabolites such as alkaloids (Culvenor 1973) often declines (Bryant et al. 1983).

Fertilization with nitrogen often stimulates plant growth more than photosynthesis (Chapin 1980). When this happens, concentrations of carbohydrates decline and as a result synthesis of carbon-based secondary metabolites becomes substrate limited (Wong 1973, Bryant et al. 1983). However, when N-supply exceeds N-demand, tissue nitrogen rises allowing increased synthesis of N-containing secondary metabolites (Culvenor 1973, Bryant et al. 1983).

Light Limitation

The plant phenotypic response to carbon stress due to insufficient light is essentially the converse of that described above. Photosynthesis declines and as a result carbohydrate concentrations decline so that growth becomes relatively carbon-limited. In general the decline in growth rate is greater than declines in the nutrient absorption (Chapin 1980). Thus, the concentration of nitrogen in leaves and shoots accumulates above levels necessary to support growth. Under these conditions one often finds a reduction in carbon-based secondary metabolite concentrations and a rise in the concentrations of N-containing secondary metabolites, because under such circumstances nitrogen is relatively "cheap" in comparison to carbon (Bryant et al. 1983).

Water Limitation

The response of woody plant secondary metabolism to water limitation is complex and poorly understood (Gershenzon 1984). When water stress is mild, concentrations of carbon-based secondary metabolites may rise, but severe drought usually results in a decline (Lorio 1986). This variation may indicate that mild drought reduces growth more than photosynthesis while severe water limitation results in a relatively greater decline in photosynthesis than in growth. Water limitation also affects production of nitrogen-containing secondary metabolites (Culvenor 1973), but the direction of change in a particular situation cannot be predicted.

Responses of Static and Dynamic Secondary Metabolites

Not all secondary metabolites respond equally to resource limitation (Reichardt et al. 1991). This is because substrate supply is more likely to affect the production of metabolic end products such as static secondary metabolites than production of dynamic secondary metabolites that are part of the metabolic pool. For example, concentrations of dynamic secondary metabolites such as the phenolic glycosides, monoterpenes, and diterpenes that are part of metabolic pools are less affected by nutrient- or light-limitation of growth than are concentrations of static metabolites, for example lignin, condensed tannin polymers, or triterpenes that are deposited on the plant's surface.

Responses to Browsing by Mammals

Browsing by mammals affects the chemical defense of woody plants. In some cases browsing results in increased defense of the browse supply and in other cases browsing decreases defense as a result of browsing (Bryant et al. 1991a,b). Here we discuss 3 ways browsing can alter the chemical defenses of woody plants.

Twigs: Juvenile Reversion

Pruning of a mature-stage woody plant as occurs when it is severely browsed by mammals throws a genetic switch causing it to revert to the juvenile-stage (Kozlowski 1971). Because the juvenile-stage of many woody plants is more heavily defended chemically than the mature-stage, juvenile reversion also results in an increase in the chemical defense of twigs available to browsing mammals (Bryant et al. 1983, 1991a,b). This increase is greatest in the dormant season when growth demands for carbon are low and in

woody plant populations that have been strongly selected for chemical defense of the juvenile-stage (Bryant et al. 1983, 1989).

In contrast, browsing of the juvenile-stage results in a carbon stress that can reduce juvenile-stage chemical defenses (Bryant et al. 1983). Browsing induced amelioration of juvenile-phase chemical defense is most likely to occur in plants with limited below-ground carbon reserves, for example evergreen conifers and young saplings. The large below-ground carbon reserves of established, disturbance-adapted species enable them to be more heavily browsed before amelioration of defense begins.

Twigs: Change in the Average Age of Internodes

The current-annual-growth (CAG) of many woody species contains higher concentrations of defensive secondary metabolites than does older-growth (OG) (Bryant et al. 1991a,b). As a result, browsing mammals that have small enough mouth parts to feed selectively on OG often do so. For example, goats feed selectively on the OG of blackbrush (*Cologyne ramosissima* Torr.) because OG contains a lower concentration condensed tannin than does CAG (Provenza and Malechek 1983, Provenza et al. 1991) and sheep feed selectively on OG of big sage (*Artemisia tridentata* Nutt.) because big sage OG contains a lower concentration monoterpenes than does CAG (Yabann et al. 1987). Woodrats eat less CAG of creosote brush than OG, because the CAG of creosote brush contains a higher concentration phenolic resin than does OG (Meyer and Karazov 1989). In boreal forests snowshoe hares and mountain hares feed on the OG and reject the CAG of a wide variety of woody species because the CAG of these species contains higher concentrations of chemical defenses than the OG (Bryant et al. 1991a,b).

Regrowth after severe browsing must result in an increase in the proportion of twig biomass that is CAG. If this CAG contains higher concentrations of chemical defenses than OG, then severe browsing must also result in an increase in the chemical defense of the browse supply (Bryant et al. 1991a,b). Increased defense resulting from an increase in the proportion of twig biomass that is CAG can occur in woody plants of both growth stages. However, it is greatest in the juvenile-stage, because the CAG of the juvenile-stage is more defended than the CAG of the mature-stage (Bryant et al. 1983, 1991a,b).

Leaves: Reversal of Aging

When the shoot tips of woody plants are eaten by mammals apical dominance is broken and growing points are removed. As a result competition for nutrients among the remaining growing points is decreased and leaf growth increases (Moorby and Waring 1963) resulting in a carbohydrate demand that can limit production of carbon-based secondary metabolites by leaves (Bryant et al. 1991a,b). For example, browsing of birch by moose (Danell and Huss-Danell 1984) and browsing of *Acacia nigrescens* (Oliver) by giraffe and impala (du Toit et al. 1990) both resulted in an increase in leaf nitrogen, an increase in leaf growth, and a decline in leaf tannin. As a result, herbivory of the leaves of browsed plants increased in comparison to leaves of unbrowsed plants.

Conclusions

Management of rangelands and wildlife habitat requires an understanding of factors that affect the quality of forage (Heady 1975, Stoddart et al. 1975). Forage quality has usually been equated with the digestibility of nutrients or energy (Van Soest 1982, Robbins 1983). Thus, attempts to understand the chemical basis of forage quality have emphasized measurement of concentrations of fiber or nutrients. When secondary metabolites have been considered, it is their potential to inhibit digestion that has received the most attention. For example, tannins are widely perceived as important because they may reduce the digestion of

protein and fiber (e.g., Robbins et al. 1987, Lindroth 1988) and monoterpenes have received attention because they may inhibit fiber degradation by gut microbes (e.g., Nagy et al. 1964; Oh et al. 1967; Schwartz et al. 1980a).

Less attention has been paid to feeding deterrence and toxicity even though these modes of action of secondary metabolites have been recognized (Arnold and Hill 1972, Stoddart et al. 1975, Laycock 1978, Schwartz 1980b). However, over the past decade collaboration between ecologists and chemists has begun to indicate that many secondary metabolites, including the tannins and the monoterpenes, influence mammalian herbivory by a combination of deterrence and toxicity (Bryant et al. 1991c, Meyer and Karazov 1991).

This hypothesis indicates that current foraging theory cannot explain why mammals selectively feed on some woody species, growth stages, and parts and reject others. This is because, from the perspective of a mammal feeding on woody vegetation, optimization of foraging time or optimization of intake of nutrients or energy is probably less important than avoidance of intoxification.

To be useful management tools, models of browsing systems foraging models must include realistic constraints imposed by deterrence and toxicity. The accuracy of these constraints will require identification of the secondary metabolites that actually defend woody plants against browsing and their modes of activity. It will also require an in-depth understanding of the biochemical, physiological, and behavioral mechanisms mammals use to counter these defenses. However, at the present time such information is extremely limited. Thus, an increased attempt to obtain this information by experimental studies of chemically mediated interactions between woody plants and browsing mammals is critical to better management of browsing ecosystems.

Another generalization to emerge out of the last decade of research in chemical ecology is the link between resource limitation and the chemical defenses of woody plants (Bryant et al. 1983, Coley et al. 1985). We suggest that this generalization also has important implications for ecosystem management.

Throughout the world an increasing demand for food has resulted in use of the most productive habitats for production of resource-demanding crops. As a result, livestock and wildlife are forced to feed in the least productive habitats. The vegetation of these habitats usually contains some low resource adapted woody species that have effective chemical antiherbivore defenses. In this habitat selective feeding by mammalian herbivores on the more palatable woody species can result in domination of the vegetation by the chemically defended woody species (Bryant and Chapin 1986, Malechek et al. 1986, Bryant et al. 1991c). An immediate result of this change in vegetation induced by browsing is a decline in the habitat's potential to produce livestock and wildlife biomass. When browsing mammals are forced to feed on unproductive vegetation that is so chemically defended that is almost unusable as food, both their numbers and biomass decline (Bell 1984, Bryant and Chapin 1986).

Such a browsing-induced change in vegetation also produces feedbacks that further degrade ecosystem productivity (Bryant and Chapin 1986, Pastor et al. 1989, Bryant et al. 1991c). This is because low resource adapted woody species that are chemically defended against browsing also produce litter that is slow to decompose. As a result, selective browsing that results in domination of the vegetation by chemically defended species is also likely to result in a reduced rate at which nutrients (especially nitrogen) cycle through the ecosystem. In turn, a reduced rate of nutrient cycling causes nutrient-limitation of the growth of woody vegetation with the further result that production of carbon-based secondary metabolites increases. As concentrations of these substances rise in leaves, the quality of leaves as food for mammals declines

further and so does the rate of litter decomposition. Moreover, reduced soil fertility further favors the persistence of low resource adapted woody species so that their dominance of the vegetation is insured unless they are destroyed by wildfire or outbreaks of high specialized insects that can eat them. This feedback degrades the soil and vegetation resources of ecosystems and the ability of ecosystems to support livestock and wildlife.

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SRM Election Results

The Elections Committee counted the ballots for new officers at the Society for Range Management headquarters. Elected officers are:

Second Vice President—**David A. Fischbach**
Directors (1992–1994)—**Dennis R. Phillippi** and **Lamar Smith**

Directors Dennis Phillippi and Lamar Smith will replace retiring Directors Charles Jordan and Phillip Sims in February 1992.

The Bylaws Amendment passed.

Ballots and tally sheets are retained in the Denver office for one year for review. Approximately 33% of the membership voted.