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The Chemistry of Plant/Animal Interactions

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ABSTRACT

Chemical approaches to studying plant/animal interactions have led to an appreciation that plant chemistry strongly influences patterns of herbivory. Although this chemistry is often rather complex, two basic factors have emerged: plant chemistry influences herbivores in both positive and negative ways by determining dietary quality of plants and by providing feeding cues. Examination of the results from numerous studies addressing these issues has led to the development of three working hypotheses: (1) there is a molecular basis for chemical cues; (2) the molecular diversity of chemical signals implies specific mechanisms for plant-initiated attraction or repellence of herbivores; and (3) there are dynamic elements to many plant chemical defenses.

KEY WORDS

chemistry, herbivore, birch, chemical, snowshoe hare (Lepus americanus), mountain hare (L. *timidus*), *salicorten, tremulacin, papyriferic acid*

INTRODUCTION

Herbivory has substantial and lasting effects on both natural and agricultural ecosystems. Crawley (1983), for example, estimates that on average about 10% of net primary productivity in natural ecosystems is taken by herbivores on an annual basis. By way of illustration, it is estimated that there are about 5,000 moose *(Alces alces)* in the Tanana River flats in interior Alaska, an area of about 13,000 km^2 between the Tanana River and the northern foothills of the Alaska Range. These moose each consume about 20 kg of vegetation each day, for an annual total of about 4×10^7 kg of forage! On average, this means that for each hectare, about 30 kg of vegetation is removed just by moose each year. However, variations from this estimated average and the selectivity with which vegetation are removed are at least as important as the average itself.

Some herbivores are extremely selective in what they consume, to the extent that many specialists have been named based upon what they eat—e.g., the spruce budworm *(Choristoneura fumiferana)* [Clem.] and the large aspen tortrix *(C. conflictana)* [Walker]. While the set of plants which make up the specialists' diet is severely restricted, the extent to which these herbivores consume their host plants can vary dramatically from year to year due to fluctuations in herbivore populations. For example, the larch budmoth *(Zeiraphera diniana)* has been estimated to consume 2% to 100% of new growth of larch *(Larix decidua)* buds in the same ecosystem in different years (Crawley 1983, Baltensweiler 1985).

In contrast to the specialists, generalists are herbivores with more varied diets. However, the distinction is most often one of degree of dietary variety rather than strict adherence to use of a single host plant as opposed to an all-inclusive smorgasbord. The impact of this foraging does not fall uniformly on all plants nor is the distribution uniform for a given plant species across all ecosystems. For example, data (Table 1) from MacAvinchey's (1991) study of winter herbivory by snowshoe hares *(Lepus americanus)* on the Tanana River floodplain indicates that while these herbivores have preferred (e.g., most willows) and unpreferred (e.g., alder) browse, their selection of browse is, in part, dependent upon the ecosystem in which they are feeding.

Table 1. MacAvinchey's (1991) Analysis of Percent of Available Twigs Browsed by Moose and Hares in Four Stands on the Tanana River Floodplain; Mean (Standard Error)

Plant Species	Alder Successional Stage	White Spruce Successional
Salix alaxensis	29 (17)	17[a]
	44 (9)	38[a]
Salix nova-angliae	16 (16)	36[a]
Salix interior	33 (8)	0[a]
	3 (10)	6 (2)
Populus balsamifera	23 (9)	4 (3)
Alnus tenuifolia		
Picea glauca		

[a] Only a single stand was analyzed.

These general observations about herbivory—extensive impact but moderately to highly selective choice of vegetation by herbivores—are consistent with the view that plant chemistry strongly influences plant/animal interactions. There are two fundamental components to the role that plant chemicals may play in the mediation of these interactions: definition of the plant's nutritional value to the herbivore and formation of, or at least contribution to, the cues upon which the herbivore's sensory perception of the plant is based. A given plant metabolite could contribute either positively or negatively to the plant's nutritional value (e.g., as a component of the plant's protein, vitamin, or mineral content or as a toxin or digestion inhibitor) to the herbivore or it could function as a cue, or signal, on which the herbivore would rely in making its dietary choices (i.e., attractant or repellent). While it is clear that in the long run an herbivore must choose a diet in which its minimal nutritional requirements are met, every plant included in its diet probably contains metabolites which are positive from a nutritional standpoint as well as some which are negative. Furthermore, the chemicals which determine an individual plant's status in this respect need not be the basis of the signals or cues which the herbivore employs in making its dietary decisions.

The potential distinction between "cues" and "underlying reasons" associated with "defended plants" is particularly important if one attempts to employ natural feeding deterrents as pesticides. In particular, it is not clear if the presence of only a "signaling" substance is sufficient to provide long-term deterrence for an artificially defended plant.

There are a number of empirical protocols which have been utilized for detecting and identifying plant metabolites which deter herbivory. In our own studies, we have focused on chemical comparisons of plant tissues with different patterns of use by herbivores coupled with bioassays of the effects of key plant metabolites on palatability of adulterated artificial diets. Using this approach, we have, for example, rationalized snowshoe hares' selective use of parts of green alder *(Alnus crispa)* twigs based upon their concentrations of pinosylvin and pinosylvin methyl ether (Bryant et al. 1983), hares' preference for mature over juvenile paper birch *(Betula papyrifera* ssp. *humilis)* twigs (Reichardt et al. 1984) as well as twigs of eastern North American birches over those of Alaskan birches based upon their concentrations of papyriferic acid (Bryant et al. 1994), and the effects of fertilizer on plant palatability (Bryant et al. 1987). While correlations between patterns of herbivory and concentrations of plant metabolites are key pieces of data in these studies, the causative relationships can only be determined by also considering data from relevant bioassays.

As our research group has considered the results of our studies (as well as those of others) conducted over the past 15 years, we have developed some working hypotheses or principles which define the framework within which we interpret the role of chemicals in plant/animal interactions. Some aspects of these principles are quite clear to us while others are less precisely defined; but they all seem relevant to future studies of plant/animal interactions as well as to the potential application of what we have learned to wildlife management.

Molecular Basis for Signals or Cues That Herbivores Use to Make Dietary Choices

There is a molecular basis for the signals or cues that herbivores use in making dietary choices. The set of plant metabolites (all of which have been shown to mediate or influence plant/herbivore interactions) shown in Figure 1 illustrates several relevant points. First, it is apparent that molecules from a variety of structural classes play key roles in plant/animal interactions. Thus there is no general structural feature or functional group which characterizes deterrents or attractants. Second, structural details are important. For example, while pinosylvin and pinosylvin methyl ether are deterrent to snowshoe hares' consumption of both alder and oatmeal coated with these substances, the corresponding pinosylvin dimethyl ether has almost no effect on hares' preferences in feeding trials using oatmeal (Clausen et al. 1986).

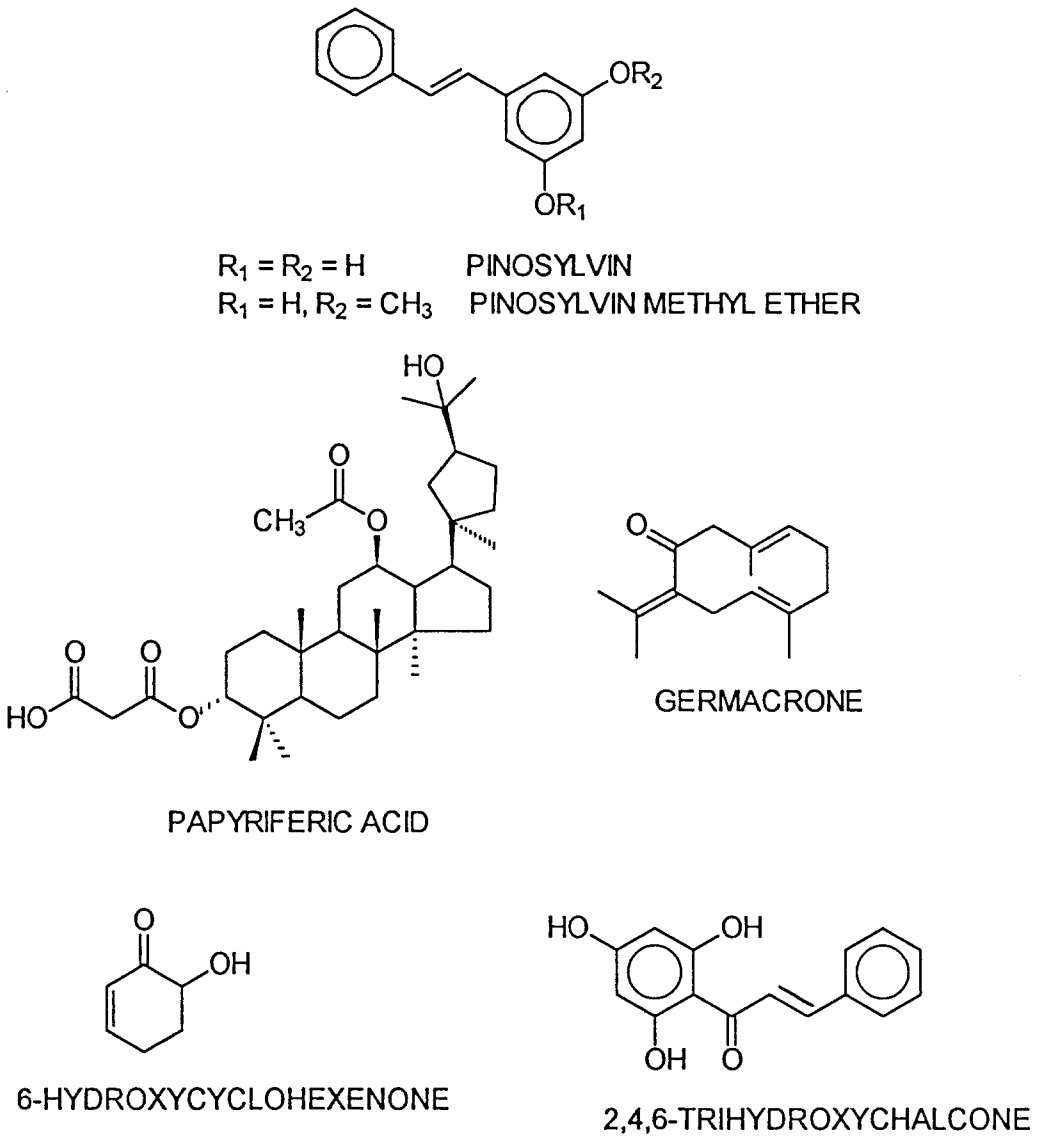

FIGURE 1. Examples of allelochemicals involved in plant/animal interactions.

Perhaps the best recent evidence for the relationship between structure and function for feeding deterrents comes from a study of condensed tannins (Figure 2). Clausen et al. (1990) determined that condensed tannin from blackbrush *(Coleogyne ramosissima)* inhibited food (oatmeal) ingestion by snowshoe hares much more effectively than did condensed tannin from bitterbrush *(Purshia tridentata)* and that, rather surprisingly, the blackbrush tannin was slightly less astringent than the bitterbrush tannin. These tannins have similar molecular weights, corresponding to chains of about five monomeric units, and differ only with respect to stereochemistry (ratio of catechin to epi-catechin monomers). Thus, even in polymeric materials, minor structural differences can impart very different biological properties.

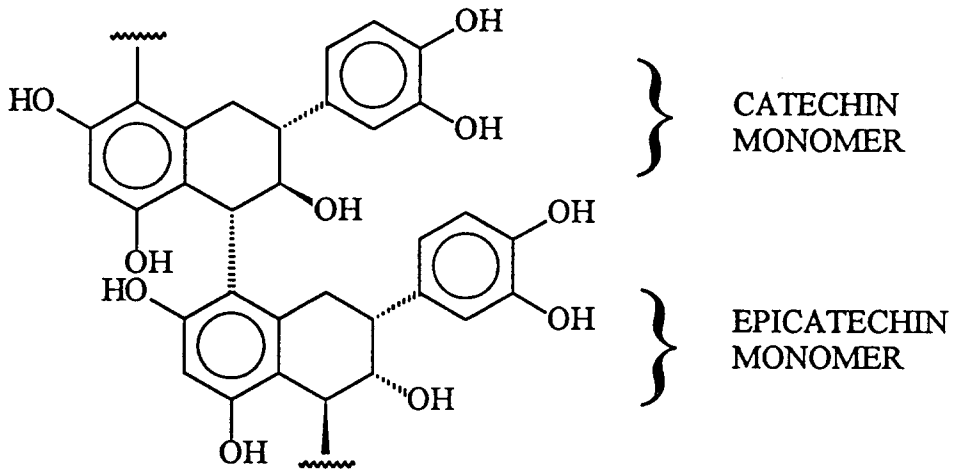

FIGURE 2. Schematic representation of condensed tannin structures.

Molecular Diversity in Chemicals That Mediate Plant/Animal Interactions

The molecular diversity observed in chemicals that mediate plant/animal interactions implies the existence of specific mechanisms by which they act. While bromides like "tannins are feeding deterrents due to their astringency," "phenol glycosides render plants unpalatable because they have a bitter taste," and "phenols are defensive substances because of phenolic-protein interactions" may provide useful guidelines for thinking about chemical mediation of plant/animal interactions, the diverse structures and functional groups represented by even the limited set of substances shown in Figure 1 imply that there are a variety of mechanisms by which deterrent substances act. At a minimum, a deterrent substance must be detectable by herbivores, and there is a rather large body of research which indicates that molecular structure plays an important role in the ways in which animals perceive secondary chemicals (Frazier 1992). However, for a perceived substance to act as a deterrent, its occurrence must be coupled with some deleterious factor. Obviously, the best deterrent would be one which incorporates both "signal" and "deleterious property." Some insight into the potential for both attributes to reside in the same molecule can be gleaned from examining the biological properties of some known feeding deterrents (Table 2). Although this limited data set implies that feeding deterrents often have toxic

Table 2. Reported Biological Properties of Several Phytochemical Defensive Substances

Substance	Biological Property	Reference
pinosylvin		
methyl ether	feeding deterrent to hares	Bryant et al. 1983
	toxicity to mice	Frykholm 1945
	fungicidal	Lyr 1969
	bacteriocidal	Frykholm 1945
	insecticidal	Wolcott 1953
papyriferic acid	feeding deterrent to hares and moose	Reichardt et al. 1984
	toxicity to mice	NIH (pers. comm.)
bisabolol	feeding deterrent to hares	Reichardt et al. 1990
	bacteriocidal	Dull et al. 1957
	fungicidal	Szalonkai et al. 1976
	insecticidal	Bar-Zeev 1980
	toxicity to mammals	Habersang et al. 1979

properties, it is not clear that their toxic properties are necessarily germane to the situations in which they act as deterrents. Nevertheless, the overall impression is that plant-derived feeding deterrents have properties which allow them to be uniquely perceived by an herbivore and that they often have at least the potential for adversely affecting the herbivore.

A good example of our present level of understanding of this proposal comes from birch and its use by snowshoe hares and mountain hares *(Lepus timidus)*. It is known that: (1) papyriferic acid (Figure 1) is a feeding deterrent to hares (Reichardt et al. 1984), (2) papyriferic acid concentrations in various birches and birch parts explains hares' selective use of birch in their diets (Reichardt et al. 1984), (3) prolonged consumption of fine twigs of birch, which have high concentrations of papyriferic acid, cause excessive loss of sodium by mountain hares (Pehrson 1983), and (4) papyriferic acid is toxic (50 mg/kg) to laboratory mice (M. Suffness, National Cancer Institute, unpublished results). It is tempting to conclude that hares avoid birch that has high concentrations of papyriferic acid because of its toxic effects. However, it is clear that some key pieces of missing data do not presently allow one to reach this conclusion.

Existence of a Dynamic Element to Many Plant Defenses

There is a dynamic element to many plant defenses, even some which traditionally have been considered to be static. The most obvious examples of dynamic plant defenses are those classified as induced defenses in which a plant's response to damage is either de novo synthesis of defensive substances (e.g., Wolfson 1991) or increased synthesis and storage of toxins (Tallamy and McCloud 1991). There are also examples of response to herbivore damage in which a previously existing substance is converted into another substance, or set of substances, which are repellent and deleterious to herbivores. For example, damage of plant tissue from either quaking aspen *(Populus tremuloides)* or balsam poplar *(Populus balsamifera)* initiates an enzymatic process (Figure 3) which converts salicortin and tremulacin to 6-hydroxy-cyclohexenone (6-HCH) and catechol (Clausen et al. 1991). Since there is evidence that all these substances have negative effects upon herbivores and since the conversions of salicortin and/or tremulacin to 6-HCH and catechol occur rapidly upon damage to plant tissue, it is not clear which of these substances can actually be classified as having "deterrent" properties.

There are other examples of dynamic elements of plant defenses which are not directly related to damage of plant tissue. In some cases, the concentrations of defensive chemicals in juvenile plants are significantly higher than those in mature plants (Reichardt et al. 1984). In these cases, at least the level of defense diminishes as an individual plant matures, and the level of defense provided by these deterrents for a given species can greatly increase throughout an entire ecosystem if the plants respond to intense browsing by a juvenile reversion (Bryant et al. 1991). Finally, there are examples of fluctuating levels of plant defensive substances which are totally unrelated to herbivory, for example, the seasonal variations in concentrations of salicortin and tremulacin in balsam poplar leaves (Lindroth et al. 1987).

Chemical mediation of plant/animal interactions is a fascinating and complex phenomenon. A complete appreciation of the role played by a plant metabolite that functions as a repellent of an herbivore requires the documentation of a correlative relationship between the concentrations of the metabolite in vegetation and patterns of herbivory, a demonstration that the metabolite has

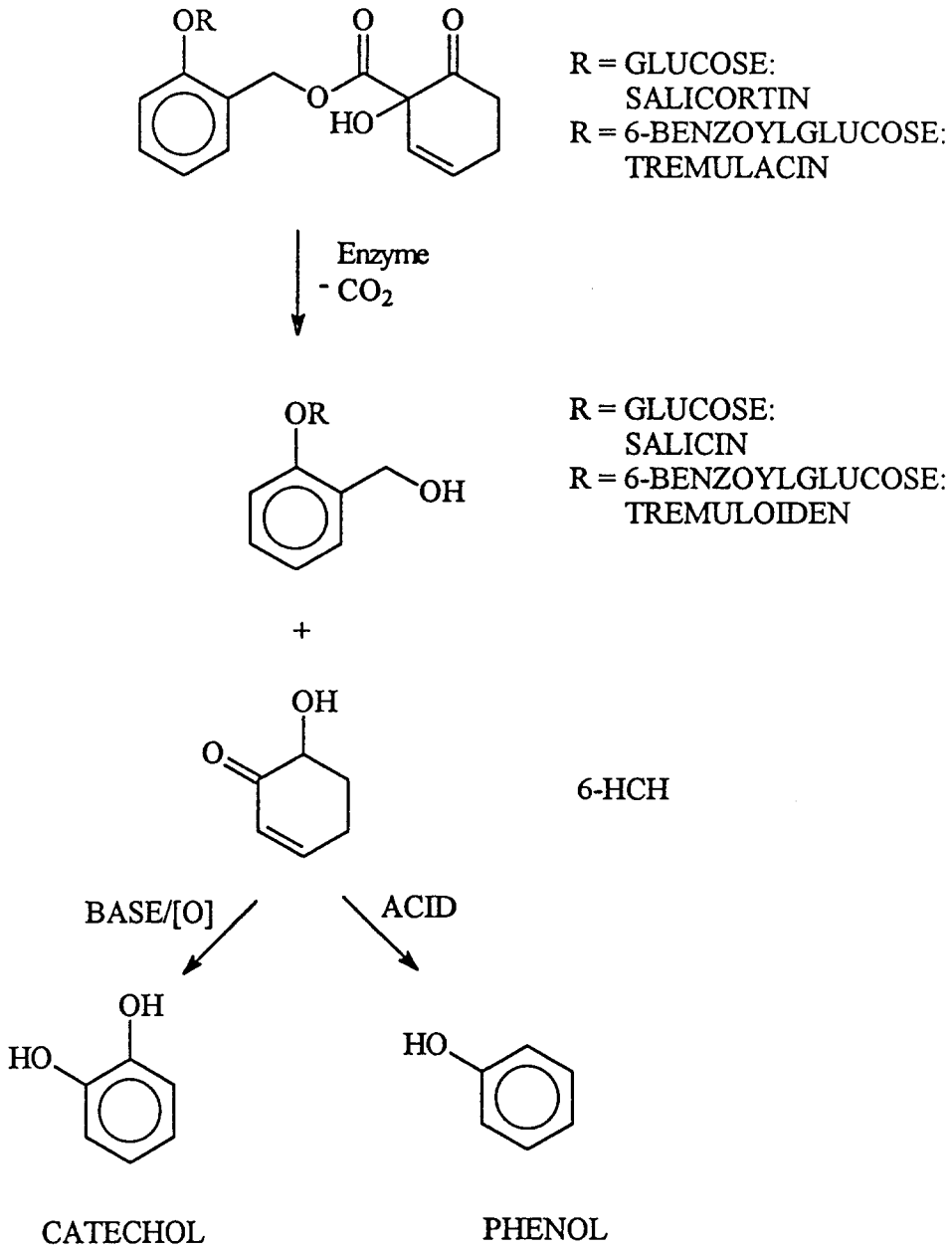

FIGURE 3. Hypothetical mechanism for the formation of 6–hydroxycyclohexenone and catechol from salicortin and/or tremulacin.

inherent deterrent properties at the relevant concentrations, and an understanding of how the metabolite is perceived by and biologically affects the herbivore. While the first two of these three conditions have now been met in a variety of studies of plant/herbivore interactions, our understanding of the third is in its infancy.

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