

Adaptations of Quaking Aspen for Defense Against Damage by Herbivores and Related Environmental Agents

Richard L. Lindroth¹

Abstract—*Quaking aspen* (*Populus tremuloides*) employs two major systems of defense against damage by environmental agents: chemical defense and tolerance. Aspen accumulates appreciable quantities of phenolic glycosides (salicylates) and condensed tannins in most tissues and accumulates coniferyl benzoate in flower buds. Phenolic glycosides are toxic and/or deterrent to pathogens, insects, and small mammals, and coniferyl benzoate is toxic to ruffed grouse, but the functional significance of tannins remains unclear. Levels of secondary compounds are influenced by both genetic and environmental (e.g., resource availability) factors. Tolerance is less well understood but may play an important role as an adaptation to extensive damage during herbivore outbreaks. Critically needed is an assessment of the roles of chemical defense and tolerance in relation to the foraging ecology of large mammals such as cervids.

Introduction

If geographic range, population density, and capacity to flourish in a diversity of habitat types are indicators of “ecological success,” then quaking aspen (*Populus tremuloides* Michx.) must be considered one of the most successful of extant tree species. A primary contributor to such success has been the evolution of chemical and physiological defense systems that afford resistance or tolerance to a host of biotic and abiotic factors. The purpose of this paper is to provide a succinct summary of the defensive adaptations of aspen and how they are influenced by genetic and environmental factors, and to discuss implications for their efficacy against harmful environmental agents, particularly herbivores. (For more detailed information, refer to the review by Lindroth and Hwang [1996a].) One caveat must be stated up front: Nearly everything known about the defense systems of aspen is based on research conducted in Eastern North America. The same systems are likely important to Western aspen, although particular contexts will vary.

Plants have evolved arrays of chemical, physiological, and physical defenses against damage by environmental agents. For aspen, a growing body of literature has unveiled the critical importance of chemical defense mechanisms. Physiological defenses, such as tolerance, are less well understood but are generating increased interest. Physical defenses (associated with physical characteristics such as spines and silica) are unlikely of importance in aspen. In the context of this paper, secondary plant metabolites with demonstrated or putative protective roles will be considered “chemical defenses.” Tolerance—the capacity to sustain growth and reproduction following damage—will be considered a “physiological defense.”

¹University of Wisconsin, Madison, WI.

Chemical Defense

Secondary Metabolites

The dominant secondary metabolites of aspen are phenolic compounds, produced via the shikimic acid pathway. These include phenolic glycosides and condensed tannins, which occur in leaf, bark, and root tissues, and coniferyl benzoate, which occurs only in flower buds.

The signature secondary metabolites of aspen comprise a suite of salicylates generally known as phenolic glycosides (Lindroth et al. 1987; Palo 1984). The exact biosynthetic pathway is unknown, but the compounds are most likely derivatives of salicylic acid. They vary according to the type and position of benzoyl and similar functional groups, and these groups confer tremendous variation in terms of biological activity (Lindroth and Peterson 1988; Lindroth et al. 1988). Quaking aspen contains four phenolic glycosides, including salicin, salicortin, tremuloidin, and tremulacin (figure 1). Of these, salicin and tremuloidin generally occur in concentrations <1% leaf dry weight. Levels of salicortin and tremulacin, however, are much higher, typically 1 to 8% each, and occasionally attain 15% (Hemming and Lindroth 1995; Lindroth and Hwang 1996b; Osier et al. 2000a).

A second major class of phenolics produced in aspen is condensed tannins. These compounds are derived from 4-coumaric acid and accumulate to appreciable levels, up to nearly 30% of leaf dry weight (Hemming and Lindroth 1995; Lindroth and Hwang 1996b; Osier et al. 2000a). Aspen does not produce hydrolyzable tannins.

Coniferyl benzoate is a phenylpropanoid ester, also derived from 4-coumaric acid. Concentrations of this compound range from 0 to 7% dry weight in flower buds (Jakubas et al. 1993a,b).

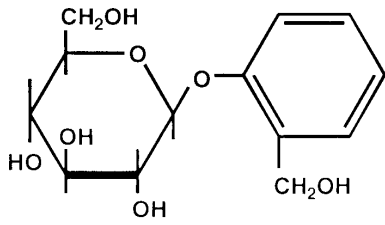
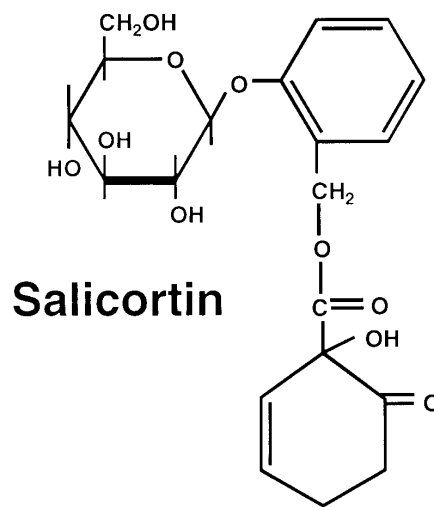
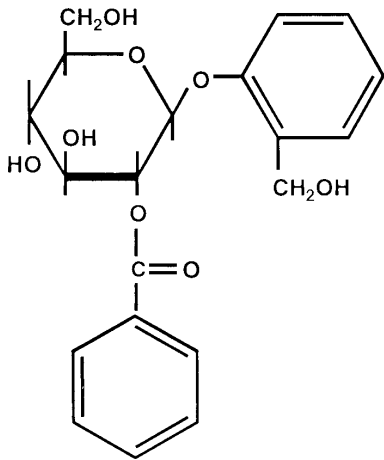
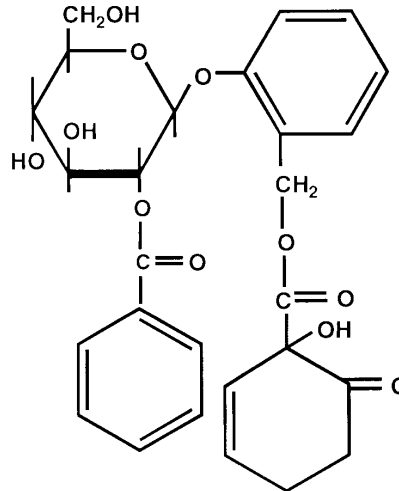
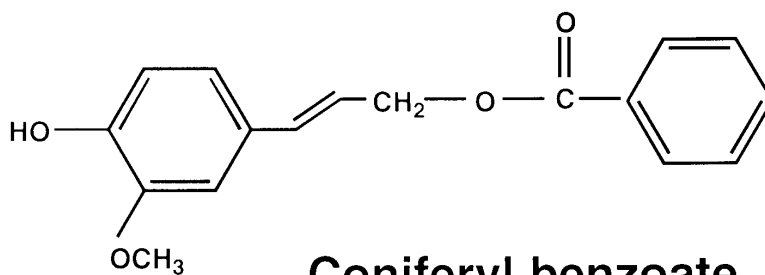
Phytochemical Variation

Aspen exhibits tremendous variation in levels of foliar chemical defenses (Lindroth and Hwang 1996a). Research over the last 10 years has identified a complex of genetic and environmental factors, and interactions among them, that contribute to such variation. Moreover, the magnitude of influence of genetics and environment varies among different secondary metabolites. In contrast to a large accumulated literature for leaves, we know almost nothing about quantitative chemical variation in stem, bark, or root tissues.

Genetic variation

Striking genetic variation among clones is a hallmark characteristic of aspen, and no less so for levels of foliar secondary metabolites. Among clones in a common field habitat, levels of total phenolic glycosides vary from <1 to 16% dry weight, whereas levels of condensed tannins vary from 3 to nearly 30% dry weight (Hemming 1998; Lindroth and Hwang 1996a,b; Osier et al. 2000a). Measurements of chemical variation among clones in the field do not indicate true genotypic variation, however, as they may be confounded with differences among local (clone) environments. Sorting out true genotypic variation requires growing trees in a common environment.

To that end, we have conducted several common garden experiments with trees propagated from root cuttings of field clones. Quantification of phenolic glycoside and condensed tannin concentrations revealed virtually the entire range of concentrations reported for field clones (Hwang and Lindroth 1997, 1998).

**Salicin****Salicortin****Tremuloidin****Tremulacin****Coniferyl benzoate****Figure 1**—Phenolic glycosides and coniferyl benzoate, characteristic secondary compounds of quaking aspen.

Interestingly, levels of secondary metabolites appear to be much more variable among aspen genotypes than are those of primary metabolites or mineral nutrients. Our studies have generally shown that although concentrations of water, carbohydrates, and nitrogen (an index of protein) may differ significantly among clones, the magnitude of variation (both relative and absolute) is minimal in comparison with that of secondary metabolites (Hwang and Lindroth 1997, 1998). We have not evaluated levels of macronutrients in aspen foliage. Jelinski and Fisher (1991), however, assessed nutrient content of winter twigs and reported similar low levels of clonal variation for all macronutrients except calcium. If aspen secondary metabolites are effective deterrents to feeding by particular herbivores, these results suggest that clonal variation in herbivore preference or performance may be more strongly determined by secondary than primary chemical composition.

Temporal variation

Levels of foliar defense compounds exhibit temporal variation with respect to both development (ontogeny) and seasonal progression (phenology). A preliminary survey of foliar defense chemistry in seedling, juvenile (burned or browsed), and mature aspen in Yellowstone National Park suggested that levels of phenolic glycosides decline as aspen mature (Erwin et al. 2000). These results are consistent with the hypothesis of ontogenetic development of chemical defense against herbivores, which purports that early successional trees have evolutionarily adapted to substantial herbivory during juvenile stages by the expression of high levels of constitutive defenses (Bryant and Julkunen-Tiitto 1995).

Within a growing season, changes in levels of foliar phenolic glycosides differ among clones; increases, decreases, and no significant changes have been reported (Hemming 1998; Hwang and Lindroth 1998; Lindroth and Hwang 1996a; Osier et al. 2000a). In contrast, levels of condensed tannins generally increase during a growing season, with the most pronounced increases occurring during the period of leaf expansion (Hemming 1998; Hwang and Lindroth 1998; Lindroth and Hwang 1996a; Osier et al. 2000a).

Resource availability

Numerous studies have investigated the effects of resource (light, water, nutrients, carbon dioxide) availability on the chemical composition of aspen. As would be expected for a fast-growing species (Bryant et al. 1987a), aspen exhibits considerable plasticity in chemical response to changes in nutrient availability. In general, these changes accord well with predictions of the carbon-nutrient balance (Bryant et al. 1983) and growth-differentiation balance (Herms and Mattson 1992) hypotheses. According to these hypotheses, environmental conditions that increase carbon availability (e.g., high light, high CO₂) or decrease nutrient availability (e.g., low soil fertility) lead to a relative excess of carbohydrates and an increase in C-based secondary or storage compounds.

Indeed, levels of phenolic glycosides, condensed tannins, and starch generally increase in aspen grown under conditions of high light, high CO₂, and/or low nutrient availability (Hemming and Lindroth 1999; Lindroth et al. 1993; McDonald et al. 1999). The various compounds are not, however, similarly responsive to changes in resource availability. Concentrations of condensed tannins respond much more strongly to environmental changes than do concentrations of phenolic glycosides. Moreover, the magnitudes of chemical responses differ among clones (significant gene x environment effects).

Induction

Damage by herbivores or pathogens can elicit a host of plant responses that alter the susceptibility of remaining tissues to further damage (Karban and Baldwin 1997). Several research groups have investigated short-term induction of chemical defenses in aspen leaves. Mattson and Palmer (1988) reported an 18% increase in total phenolics following artificial defoliation of 50% leaf area. Clausen et al. (1989) found that levels of salicortin and tremulacin, but not salicin and tremuloidin, increased (slightly) within 24 hours of mechanical defoliation. Work by my research group has shown slight to no increases in phenolic glycoside levels immediately following mechanical or natural defoliation (Lindroth and Kinney 1998; Roth et al. 1998; Osier and Lindroth 2000). In contrast, levels of condensed tannins generally increase following natural or artificial defoliation, and the magnitude of increase is influenced by resource availability (Lindroth and Kinney 1998; Roth et al. 1998; Osier and Lindroth 2000).

Less is known about long-term (interannual) induced defenses in aspen. Clausen et al. (1991) reported increases in only one (tremulacin) of four phenolic glycosides 1 year after 50 and 100% defoliation. Osier and Lindroth (unpublished data) investigated the effects of 90% defoliation on several aspen genotypes grown in nutrient-deficient or nutrient-rich soil. We found no increases in phenolic glycoside concentrations and a slight increase in condensed tannin concentrations 1 year after defoliation. Responses did not differ significantly across clones or nutrient treatments.

To date, virtually all work with induced defenses in aspen has focused on folivory. Almost nothing is known about the impacts of browsing on expression of foliar defense traits in aspen. According to the resource-based model of Bryant et al. (1991), however, defoliation and browsing may cause very different outcomes for the quality of subsequent leaf tissue. Severe defoliation contributes to mortality of fine roots, leading to reduced nutrient absorption, reduced nutrient concentration per leaf, decreased leaf growth, increased leaf carbohydrate pools, and an increase in carbon-based secondary metabolites. In contrast, browsing reduces leaf numbers, leading to increased nutrient concentration per leaf, increased leaf growth, decreased carbohydrate pools, and a decrease in carbon-based secondary metabolites. This model suggests that insect outbreaks on aspen may elicit changes in foliar quality very different from those of browsing mammals.

Costs of Chemical Defense

If levels of aspen defense compounds are strongly genetically determined, and if the compounds are effective deterrents against herbivores, the question arises as to why genetic variation persists in field populations. The classic answer to this evolutionary problem is that costs of defense must exist, such that expression of defense is not advantageous in all environments at all times.

Recent research by Osier and Lindroth (unpublished data) documented significant costs of resistance in aspen. These were exhibited as tradeoffs (negative genotypic correlations) between growth and phenolic glycoside concentrations among aspen genotypes. The tradeoffs were strongest in low-resource (low light, low nutrient availability) environments. In high-resource environments, however, the tradeoff disappeared. Thus, expression of high levels of constitutive defense (phenolic glycosides) appears to exact a cost in terms of plant growth, except in high-resource environments.

Tolerance

Historically, investigations of defensive strategies of plants have focused on chemical systems. Recently the concept of tolerance has begun to generate theoretical and empirical attention. Tolerance refers to the capacity of plants to maintain fitness through growth and reproduction after herbivore damage (Rosenthal and Kotanen 1994; Strauss and Agrawal 1999). Tolerance is considered to be an especially viable form of defense in plants with high intrinsic growth rates, large storage capacity, and substantial physiological (e.g., photosynthetic) plasticity. All such traits are characteristic of aspen. Tolerance is advantageous in situations where herbivore damage is so uniform and severe that even chemically resistant genotypes are heavily damaged. Under such conditions, tolerance would confer a fitness advantage even though resistance does not. Tolerance may be selectively advantageous in forest ecosystems in which outbreak folivores cause extensive and uniform damage during peak periods of defoliation (Mattson et al. 1991). Examples include outbreaks of forest tent caterpillars (*Malacosoma disstria*), gypsy moths (*Lymantria dispar*), and large aspen tortrix (*Choristoneura conflictana*) on aspen.

Results from studies by Osier and Lindroth (unpublished data) suggest that aspen does exhibit tolerance to defoliation and that tolerance differs among aspen genotypes and resource environments. Under low nutrient availability, defoliation suppressed growth in each of four genotypes. Under high nutrient availability, however, two of the genotypes compensated nearly entirely for damage.

Defense Against Abiotic Agents

Lindroth and Hwang (1996a) reported that exceedingly little is known about the roles of aspen secondary metabolites with respect to protection from physical factors. Five years later, the same holds true. Phenolic glycosides may confer protection from ultraviolet (UV) radiation (Lindroth and Hwang 1996). Evidence in support of that function includes the fact that phenolic glycosides absorb UV radiation (especially at 200-320 nm) and that several clones of aspen propagated from cuttings collected in alpine environments in Colorado (high incident UV) continued to express very high levels of phenolic glycosides when grown in a common garden in Wisconsin.

Defense Against Biotic Agents

That the defense systems of aspen are based on fairly simple phenolic chemicals, coupled with physiological adaptations for tolerance, seem all the more remarkable given their apparent efficacy against a host of potentially damaging organisms. The phenolic glycosides, in particular, appear to have broad-spectrum activity, reducing the performance of organisms as variable as fungi, insects, and vertebrates (table 1).

Pathogens

Aspen is subject to diseases caused by viruses, bacteria, and most importantly, fungi (Ostry et al. 1988; Perala 1990). Although the nature of the defense mechanisms mounted against these pathogens is mostly unknown, secondary metabolites play a role in some cases.

Hypoxyylon mammatum stem canker is a serious fungal pathogen of aspen, particularly east of the Rocky Mountains (Perala 1990). Initially, Flores and Hubbes (1979, 1980) showed that phenolic glycoside “phytoalexins” (identity

Table 1—Organisms affected by secondary metabolites of aspen.

Species	Metabolite	Reference
Pathogenic fungi		
<i>Hypoxylon</i> (ascospores)	Unidentified “phytoalexin,” phenolic glycosides	Flores and Hubbes 1979, 1980; Kruger and Manion 1994
<i>Alternaria</i> (conidia and mycelia)	Unidentified “phytoalexin”	Flores and Hubbes 1979, 1980
Insects		
Gypsy moth (<i>Lymantria dispar</i>)	Phenolic glycosides	Hemming and Lindroth 1995; Lindroth and Hemming 1990; Hwang and Lindroth 1997; Osier et al. 2000b
Forest tent caterpillar (<i>Malacosoma disstria</i>)	Phenolic glycosides	Hemming and Lindroth 1995, 1999; Lindroth and Bloomer 1991; Lindroth et al. 1993
White-marked tussock moth (<i>Orgyia leucostigma</i>)	Phenolic glycosides	McDonald et al. 1999
Canadian tiger swallowtail (<i>Papilio canadensis</i>)	Phenolic glycosides	Hwang and Lindroth 1998
Big poplar sphinx moth (<i>Pachysphinx modesta</i>)	Phenolic glycosides	Hwang and Lindroth 1998
Large aspen tortrix (<i>Choristoneura conflictana</i>)	Phenolic glycosides	Bryant et al. 1987b
Aspen blotch leafminer (<i>Phyllonorycter tremuloidiella</i>)	Phenolic glycosides (?; marginal effect)	Auerbach and Alberts 1992
Vertebrates		
Ruffed grouse (<i>Bonasa umbellus</i>)	Coniferyl benzoate	Jakubas et al. 1993a,b
Snowshoe hare (<i>Lepus americanus</i>)	Unidentified “phenolic and terpene resin”	Bryant 1981
Beaver (<i>Castor canadensis</i>)	Unidentified “phenolic”	Basey et al. 1990

unknown) could be isolated from aspen twigs following inoculation with *Hypoxylon*; these compounds inhibited germination of *Hypoxylon* ascospores and *Alternaria* conidia, and growth of *Alternaria* mycelia. Later, Kruger and Manion (1994) showed that the phenolic glycosides salicin and salicortin, and the simple phenolic catechol, inhibit *Hypoxylon* ascospore germination.

Insects

Aspen serves as a host to over a hundred species of insects, including nine species of expansive outbreak folivores (Baker 1972; Furniss and Carolin 1977; Mattson et al. 1991; Perala 1990). Some of the latter defoliate trees on a scale rarely seen for other insect pests in North America. For example, annual defoliation by the forest tent caterpillar (*Malacosoma disstria*) and large aspen tortrix (*Choristoneura conflictana*) for the period 1957–1987 averaged 935,000 and 246,000 ha, respectively, with tent caterpillar outbreaks as large as 13.5 million ha observed (Mattson et al. 1991). With the exception of the gypsy moth (*Lymantria dispar*), all the major insect pests of aspen are native species.

Numerous studies have evaluated the role of chemistry pertaining to the performance of aspen-feeding insects (table 1). These studies have included specialists and generalists, as well as outbreak and nonoutbreak species, and have been conducted under laboratory and field conditions. In nearly every instance, phenolic glycosides were of singular importance with respect to influence on insect performance (survival, development, growth, feeding, reproduction). Phenolic glycoside concentrations typically account for 60 to 98% of the

variation in insect performance parameters. Results from correlative studies have been substantiated by experimental studies in which purified phenolic glycosides were incorporated into insect diets (Hemming and Lindroth 1995; Lindroth and Bloomer 1991; Lindroth and Hemming 1990). The only study published to date that does not suggest a major role of phenolic glycosides in insect resistance in aspen is that of Auerbach and Alberts (1992) for aspen blotch leafminers (*Phyllonorycter tremuloidiella*).

Surprisingly, several studies have shown that condensed tannins have no deleterious effect on the performance of aspen-adapted insects (Ayres et al. 1997; Bryant et al. 1987b; Hemming and Lindroth 1995; Hwang and Lindroth 1997, 1998). Indeed, presence of moderate to high levels of tannins can actually increase consumption rates, perhaps as a consequence of the dilution of critical foliar nutrients (Osier and Lindroth 2000).

The efficacy of chemical defense appears to change during the course of insect (e.g., gypsy moth, forest tent caterpillar) outbreaks on aspen. At moderate to high insect population densities, aspen clones are not uniformly susceptible to defoliation; rates may vary from 20 to 90% of leaf area removed for clones in a common habitat (Lindroth, personal observation). Differential defoliation is likely due to genotypic differences in levels of phenolic glycosides, although this has yet to be confirmed experimentally. At very high population densities, however, all aspen are heavily defoliated, apparently irrespective of chemical variation. Traits conferring tolerance to damage would be particularly beneficial in these situations.

Vertebrates

Given the importance of aspen as a food source for a variety of vertebrate species, surprisingly little is known about the role of particular defense characteristics in mediating those interactions. The most detailed assessment of the impact of aspen chemistry on a vertebrate herbivore was conducted for ruffed grouse (*Bonasa umbellus*). A series of studies by Jakubas and colleagues (Jakubas and Gullion 1991; Jakubas et al. 1989, 1993a,b) revealed that coniferyl benzoate, rather than phenolic glycosides or tannins, strongly influences selection of buds and catkins. These tissues can comprise from much to nearly all of the diet of grouse during winter and spring. Ingestion of high levels of coniferyl benzoate causes loss of nitrogen, reductions in metabolizable energy, and acidosis from production of acidic detoxication products.

Less is known about the roles of aspen defenses with respect to herbivory by mammals. Winter browsing by snowshoe hares (*Lepus americanus*) may be influenced by aspen chemical composition, as adventitious shoots contain high levels of phenolic and terpene resins and are unpalatable to hares (Bryant 1981). 6-Hydroxycyclohex-2-ene-1-one and salicylaldehyde, derivatives of phenolic glycosides such as salicortin and tremulacin, protect internodes of juvenile balsam poplar (*Populus balsamifera*) from browsing by hares (Reichardt et al. 1990). Related work with other poplars and willows has shown that phenolic glycosides deter feeding by opossums (*Trichosurus vulpecula*) in New Zealand (Edwards 1978) and mountain hares (*Lepus timidus*) in Scandinavia (Tahvanainen et al. 1985).

Aspen chemistry also appears to play a role in defense against feeding by beaver (*Castor canadensis*). Aspen trees cut by beaver will resprout with a juvenile growth form, which is avoided by beaver when mature growth-form plants are available (Basey et al. 1990). Food selection is not influenced by phenolic glycoside levels, but by levels of an unknown phenolic constituent that occurs in high concentrations in juvenile tissue.

Almost nothing is known about the effects of aspen chemical composition on foraging by cervids. Given the importance of aspen as a browse species for deer (*Odocoileus hemionus*, *O. virginianus*), elk (*Cervus elaphis*), and moose (*Alces alces*), this represents a significant gap in our understanding of cervid foraging ecology. Because accessible aspen are heavily browsed by cattle and cervids (especially elk) throughout much of Western North America, the argument could be made that chemical defenses are ineffective in reducing herbivore damage. Although such may be the case now, it is likely an artifact of artificially sustained high densities of browsing mammals. Such high densities were likely rare throughout most of the evolutionary history of aspen (C. Kay, this proceedings). The potential error of the deduction of “ineffective defense” becomes clear as one considers the analogous situation with outbreak insects. At low to moderately high herbivore densities, marked differences in susceptibility to defoliation exist (advantages of chemical defense are obvious), but these differences disappear under conditions of exceptionally high herbivore feeding pressure. In situations during which chemical defenses are rendered ineffective, aspen likely relies on tolerance. But tolerance is a relatively short-term defense. It cannot be sustained during extended periods of heavy browsing, as now exist throughout much of the western range of aspen. Clearly, much remains to be learned about the roles of chemical and physiological mechanisms as mediators of aspen-mammal interactions in Western North America.

Conclusions

Much of the ecological success of aspen can be attributed to the defense systems it employs against potentially damaging agents in the environment. The dominant defense system is chemical, and phenolic glycosides are the signature compounds. Tolerance is also likely to be an important defense system, although less is known about this system than is known about chemical defenses. Commitment to chemical defense varies strikingly among aspen genotypes. Such variation is likely maintained due to the “costs” of defense; negative genetic correlations exist between growth and defense, and these are strongest under conditions of low resource availability. Chemical defense systems have been demonstrated to negatively affect the performance of a variety of aspen pathogens and herbivores. That work focused, however, on interactions between aspen and insect herbivores in the Great Lakes region. Critically needed is an evaluation of (1) the relevance of chemical defense and tolerance to herbivory by large browsing mammals and (2) implications thereof for the long-term health of aspen in Western North America.

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