

# Tree Defenses Against Insects

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## 12.1 Introduction

Our understanding of individual resistance mechanisms against insects, and especially against pathogens, has improved tremendously during the last decade (Heath and Boller, 2002). This progress has largely been achieved by studying plants (such as cotton, tomato, or *Arabidopsis*) with suitable traits for experimental work. Trees share just the opposite characteristics: long life span, large size, architectural complexity, and an often short and distinct period of leaf growth. Only saplings can be studied effectively under experimental laboratory conditions; it is not clear, however, to what extent the defenses of saplings are similar to those of mature trees. Hence the defenses of woody plants are not well known; presumably, trees employ mechanisms that are widespread in the plant kingdom. The specific features, compared to herbs, also offer opportunities to study mechanisms of plant defense, and their interactions, that are not obvious in short-lived hosts.

In explaining tree resistance against insects, the traditional emphasis in forest entomology has been to pay attention to secondary compounds, such as phenolics and terpenoids, and—especially in the older literature—to foliar proteins and sugars. A major problem is that plant phenolics and terpenoids are not likely to serve for insect defense alone. Nevertheless, they may strongly modify insect performance and consumption, thus linking them to plant defense. Some recent observations indicate that tree defense may involve cascades of defense reactions, induced for instance by products of the octadecanoid pathway or ethylene. What we know less about is to what extent the effects of defensive cascades are based on the specific end products of these pathways, to what extent on interactions of compounds in the pathways with “traditional” defenses such as phenols or with nutritive compounds. In any case, tree defenses are probably fundamentally multigenic.

Variance in individual defense mechanisms, and the relative importance of these mechanisms, is poorly known in all plants, including trees. The use of genetically uniform plants under standardized conditions is likely to eliminate variance in defense expressions that depends on environmental conditions or on plant biochemical variation, leading easily to an overestimation of the role of single mechanisms behind plant resistance. Accordingly, individual, potentially defensive mechanisms may or may not be important under field conditions, where their

importance has to be judged against all the factors that contribute to a reduction in damage. This problem is especially relevant in the defense of long-lived plants against insects, simply because the longer the plant lifespan, the more diverse the herbivore types and environmental conditions the plant is likely to encounter. Possible interactions may take place among specific defense cascades, secondary compounds, and nutritive plant traits. All this means that trees need multiple means to handle the diversity of insects and environmental situations.

In this chapter I deal with certain major ecological issues involved in tree defenses, by emphasizing the complications that emerge when we try to include insect traits in the picture (Haukioja, 2003; for another recent review of tree defenses against insects, see Larsson, 2002). My emphasis comes from birch studies, and biases the discussion toward birches and other deciduous trees. I will deal with the defenses of conifer foliage, but not, for instance, with defenses against bark beetles (Raffa, 1991). I will first review the ecological aspects relating to traits creating resistance in woody plants. I will then discuss the problem of how long-lived plants such as trees can remain resistant against short-lived pests that have numerous generations during the lifetime of a single host. Finally, I will discuss some general practical and theoretical problems encountered in research into tree resistance.

## 12.2 Constitutive versus Induced Resistance

Ecologically the most relevant classification of tree resistance is that of constitutive versus induced resistance. The levels of constitutive defenses do not depend on prior contacts with herbivores. The boundary between constitutive and induced resistance, however, is not sharp. For instance, the efficiency of typical constitutive defenses, such as phenolic compounds, may depend critically on polyphenol oxidases (PPOs) that are activated when insect feeding crushes the leaf cells and allows plant oxidases to react with phenolics (Felton et al., 1992). This leads to the formation of quinones, which are regarded as more toxic than phenols. Although PPOs are known to be inducible by insect damage and jasmonic acid (Constabel et al., 2000; Tschardt et al., 2001), constitutive PPOs also function as very rapidly inducible defenses.

Constitutive defenses may contribute to the average levels of pest populations, but unlike herbivore-induced responses they are not good candidates in explaining temporal variation in insect population densities (e.g., Larsson, 2002). The most spectacular and economically important effects of forest insects relate to their multiannual population outbreaks or cycles, which often lead to large-scale defoliations. Herbivore-induced responses can in theory modify pest populations, and because of their variable time lags they have gained much attention in woody plant research.

### *12.2.1 Constitutive Tree Defenses*

Constitutive defenses have been studied in forest entomology for a long time, and in particular secondary compounds have received much attention. Defense is usually

credited to phenolics or terpenoids, the main groups of secondary compounds in the foliage of deciduous and coniferous trees, respectively. Sugars and proteins may also be important contributors to variance in the success of forest pests, as emphasized in the older German forest-entomological literature (e.g., Schwenke, 1968). Similarly, the stress hypothesis by White (1974) is based on the importance of temporal variance in soluble nitrogen.

Although the levels of constitutive defenses do not depend on previous encounters with insects, the concentrations of constitutive secondary compounds show very dynamic variation, both temporal (Zou and Cates, 1995; Nerg et al., 1994; Habermann, 2000; Riipi et al., 2002) and spatial (Suomela et al., 1995a,b). In birch, the seasonal succession in dominant groups of foliar phenolics takes place very rapidly during leaf development: from phenolic aglycons via galloylglucoses, phenolic glycosides, and ellagitannins to proanthocyanidins (condensed tannins) (Nurmi et al., 1996; Kause et al., 1999b; Salminen et al., 2001; Haukioja, 2003; Valkama et al., 2003). Together with the simultaneous rapid decline in protein contents and the hump-backed seasonal trend in foliar sugars (Riipi et al., 2002), this rapid succession may explain why young and mature leaves represent very different diets for leaf chewers (Haukioja et al., 2002). At different times of leaf development, the same trees may represent such different diets that even specialized species of sawflies experience strongly reduced growth and increased mortality on birch leaves not matching the typical leaf age at that developmental stage of the larva (Martel et al., 2001). These observations suggest that the level of “tree defense” may be an elusive concept.

Compared to studies emphasizing the effects of phenolics on insects (Feeny, 1970; Rossiter et al., 1988; Bryant et al., 1993; Julkunen-Tiitto et al., 1996; Keinänen et al., 1999; Ossipov et al., 2001; Salminen and Lempa, 2002), much less attention has been paid to proteins and sugars as determinants of tree defense and insect performance (see Mattson and Scriber, 1987; Slansky, 1993; Clancy, 1992; Zou and Cates, 1994; Haukioja et al., 2002). Interestingly, different foliar sugars may have different effects on insects. High levels of galactose (Zou and Cates, 1994) and sucrose (Clancy, 1992) may retard insect growth on artificial diets. These sugars also displayed negative correlations with insect growth in birch leaves, contrary to the positive correlations shown by glucose and fructose, even at the time of peaking leaf sugars (Haukioja et al., 2002; Henriksson et al., 2003).

The effects of individual amino acids in tree foliage on insects are not well understood, and seem to show variable correlations with insect growth, perhaps because of rapid changes in the concentrations and ratios of individual foliar amino acids, and high intra-tree variation (Suomela et al., 1995b; Riipi et al., 2002). The stress hypothesis by White (1974) claims that insect outbreaks are caused by the increased availability of soluble nitrogen in stressed trees. There exist no good data to demonstrate the validity of this claim, but in birch we found no consistent correlations between soluble amino acids and the performance of an outbreaking lepidopteran (Haukioja et al., 2002; Henriksson et al., 2003). Actually, in several birch-insect data sets the best correlate with insect growth is the amount of water ingested with consumed leaf mass. Leaf water content was found to be correlated with soluble and cell-wall bound proteins, but correlations between insect growth

and these groups of proteins were not as high as those with water (Haukioja et al., 2002; Henriksson et al., 2003).

It is increasingly obvious that defensive secondary compounds do not function independently of the nutritional background of tree leaves (Schopf, 1986, Jensen, 1989; Haukioja et al., 2002). Simpson and Raubenheimer (2001) demonstrated that gallic acid had a strong effect on locusts only when combined with extreme protein:carbohydrate ratios in the diet. Haukioja et al. (2002) found that while 7 out of the 35 individual phenolic compounds displayed a significant correlation with the growth or consumption of a geometrid moth, 17 more compounds showed significant interactive (insect trait \* phenolic trait \* leaf trait) effects with three seasonally changing leaf traits: water content, sugar:protein ratio, and toughness. In these data sets, the sugar:protein ratio was not a more important covariate than water content or toughness, perhaps because only two (glucose and fructose) of the four dominant birch leaf sugars (Riipi et al., 2002) displayed consistent positive correlations with insect growth.

Another reason relates to the logic of insect feeding (Haukioja, 2003). The goal of insect feeding is to obtain a sufficient amount of those nutritive compounds that limit its performance, in forest insects usually larval growth. On high nutritive diets insects have their demands satisfied with less consumption than on diets containing low concentrations of nutritive compounds (Haukioja et al., 2002). Low consumption on high nutritive diets naturally means a simultaneous limited intake of potentially defensive compounds. On low quality birch leaves, late-season sawfly species strongly increase their consumption (Kause et al., 1999a). This increase in consumption with declining leaf nutrition is truly dramatic: the ratio of leaf mass consumed relative to larval growth (in terms of dry matter) for a lepidopteran larva feeding on the nutritious leaves of mid-June was below 3, but in late summer sawflies it was as high as 15 (Haukioja, 2003).

All in all, foliar nutrient and phenolic contents interact strongly in their effects on insects, just as in mammals (Villalba et al., 2002). Maintaining a low nutritive value sounds like an appealing solution for plant defense, and in evolutionary time it may be so. But it can also easily lead to high loss of leaf mass to adapted herbivore species (Moran and Hamilton, 1980). The critical question is what really sets a limit to further consumption before the insect's nutritive demands are satisfied. Surprisingly, the answer to this question is not well known, presumably for several reasons. First, due to compensatory feeding, the amounts of single allelochemicals or groups of physiologically related allelochemicals consumed may be so high that the insect cannot handle any more. This is especially likely on low nutritive diets (Slansky and Wheeler, 1992). Second, due to low concentrations of growth-limiting compounds, the feeding rate needed may be so high that the insect simply cannot consume and process that much plant mass. This is because moving the leaf mass consumed through the gut demands metabolic work, due to the active construction of peritrophic membranes that separate the gut contents from the gut walls, for example (Barbehenn, 2001). In this case, there may be no single compound responsible for the cessation of feeding; it may simply become impossible to continue feeding. Third, the ratios of different nutritive compounds

(particularly carbohydrates vs. proteins) may be so far from optimal that the elimination of nonlimiting nutrients puts an end to insect feeding (Raubenheimer and Simpson, 1994). This is a complex question because different nutritive compounds demand different elimination processes (surplus sugars are respired, proteins are excreted as ammonium), and because of interactive effects between nutrient ratios and secondary compounds (Simpson and Raubenheimer, 2001).

### 12.2.2 *Herbivore-Induced Responses in Trees*

Plant responses are regarded as defenses due to their end result, which is reduced damage. The term “induced defense” therefore pools together heterogeneous mechanisms (Karban and Kuć, 1999). Some of these undoubtedly are true defenses, designed by natural selection for that purpose. Induced defenses may also be inclusive and occur even when no specific defense pathways are activated. In other words, the null hypothesis is not that no change in plant quality takes place after herbivore damage. The drying up of partially consumed leaves is an example. Since plants are modular organisms, any damage to hormonally active plant meristems is bound to rearrange resource flows within the plant (Haukioja et al., 1990; Dyer et al., 1991), and this may lead to drastic changes in the suitability of adjacent plant parts for insects. Consistent with the multiple ways whereby induced resistance against insects can emerge is the pronounced variance between the results of individual experiments; for birch see Ruohomäki et al. (1992), for pines Watt (1990), Lyytikäinen (1994), Trewhella et al. (1997), Raffa et al. (1998) and Smits et al. (2001). Unlike many of the mechanisms activated by defense pathways, such as the octadecanoid cascade, responses based on mechanical damage via altered sink-source relations seem to be local (Tuomi et al., 1988, Långström et al., 1990; Henriksson, 2001, Henriksson et al., 2003).

Some herbivore-induced responses may occur immediately after the damage; the long lifespan of trees, however, also allows carry-over responses of damage into foliage produced in the growth season(s) following the damage. Due to variation in the duration of induced responses relative to insect generation time, induced plant responses can cause different and even opposite pressures on insect population densities (Haukioja, 1982; 1990). I therefore deal separately with rapid induced (RIR) and delayed induced resistance (DIR).

#### Rapid Induced Defenses

RIR is experienced by the same generation of herbivores that triggered the response with adverse effects on the insect. RIR is likely to dampen out fluctuations in insect population density: the higher the insect density, the more likely it becomes that induced responses will be expressed and will detrimentally affect the insect. There are numerous observations of rapid induced systems against insects in the foliage of various woody plants, such as birch (Haukioja and Niemelä, 1977; Edwards and Wratten, 1982; Wratten et al., 1984; Fowler and MacGarvin, 1986; Hanhimäki and Senn, 1992), oak (Schultz and Baldwin, 1982; Rossiter et al., 1988), poplar (Havill

and Raffa, 1999), larch (Krause and Raffa, 1992), pine (Litvak and Monson, 1998), fir (Litvak and Monson, 1998), and alder (Seldal et al., 1994; Dolch and Tschardtke, 2000).

A key challenge in explaining rapid induced tree defenses is to understand interactions between specific defense pathways (such as cascades induced by octadecanoid compounds, salicylic acid and by ethylene), phenolic metabolism, and primary leaf nutrients. Changes in tree nutrient levels in connection with RIR are poorly known (Beardmore et al., 2000). An induced resistance response is often characterized by an accumulation of phenolics in deciduous species, and of terpenoids in conifers. The role of jasmonic acid in the increased synthesis of terpenoids has been demonstrated by Martin et al. (2002). Jasmonate treatments did not induce higher levels of phenolic synthesis in alder (Tschardtke et al., 2001) or birch leaves (Ossipov, unpublished observations), but a response was found in poplar sink leaves (Arnold and Schultz, 2002). Since jasmonates are implemental in the activation of plant enzymes, such as PPOs, they may still control the efficacy of phenolic compounds on insects (Constabel et al., 2000; Tschardtke et al., 2001). The cascade induced by ethylene was found to induce increased production of phenolics (Tschardtke et al., 2001), reiterating the old observation in eucalypts (Hillis, 1975).

Tschardtke et al. (2001) demonstrated no increase in predator densities after induction of defense in alder, but, in general, the possible role of parasitoids in RIR in woody plants is not known. This is a promising area, since the spread of herbivore-induced volatiles (Dolch and Tschardtke, 2000) may have an even forest-wide effect on predation.

### Delayed Induced Defenses

Multiannual, large-scale insect outbreaks are characteristic of many woody plants. Induced defenses offer a potential explanation for the collapse of peak populations; in order to lead to a low population level, however, they would have to severely impair insect performance over several generations, i.e., lead to delayed negative feedbacks. The increased resistance associated with DIR has been shown to last for one to four years after manual defoliations in birch (Neuvonen and Haukioja, 1991; Kaitaniemi et al., 1999) and after natural defoliation in larch (Benz, 1974; Omlin, 1980). Thus DIR—unlike RIR—offers a potential factor for the decline and the low phase of insect populations after outbreaks of forest insects.

The chemical basis of DIR is not well understood. The simplest explanation is that defoliations reduce tree nutrient reserves. In the years following defoliations the trees actually tend to be low in nutritive compounds, especially nitrogen and water (Valentine et al., 1983; Kaitaniemi et al., 1998). Honkanen and Haukioja (1998) presented a physiological null hypothesis for DIR, based on the observation that primordial leaves within short shoot buds are initiated the year before their flush. Early damage to the leaves supporting the buds weakens the sink strength of the buds, and the following year reduces their ability to draw resources from the common pool. Such leaves are therefore likely to remain small, low in nutrients,

and high in phenolics. Levels of phenolics in the leaves of trees defoliated the previous year have been found to be higher than in undefoliated control trees. Most early studies refer to the consequences of manual defoliations (Tuomi et al., 1984; Hartley and Lawton, 1990; Bryant et al., 1993; Ruohomäki et al., 1996; Kaitaniemi et al., 1999), and their relevance to field conditions is not clear. Benz (1974) reported a drop in both consumption and efficiency of larval growth in larch trees that had been naturally defoliated in previous year; these measures were associated with low nitrogen and high fiber contents in needles. Kaitaniemi et al. (1998) demonstrated increased levels of phenolics (and lower levels of sugars and proteins) in trees naturally defoliated by moth larvae during previous years, compared to trees that had been protected from defoliations by pyrethrin spraying. They also found more seasonal overlap between the peaks of hydrolyzable and condensed tannins in birch leaves after natural defoliation (Kaitaniemi et al., 1998).

Whether DIR operates via the third trophic level in trees is not known, and clearly deserves more attention, as does the use of larval-produced rather than manual defoliation. Kaitaniemi and Ruohomäki (2001) experimentally introduced few geometrid larvae on individual trees (leading to negligible consumption at the whole-tree level). The following year they found that larvae disappeared at a significantly faster rate from these trees than from trees without caterpillars the year before. Although the experiment did not reveal whether the larvae disappeared due to predation or dispersal, the study suggests that natural larval damage, unlike manual damage (Tuomi et al., 1984), leads to systemic DIR.

### Induced Susceptibility

It is easy to interpret induced resistance as an evolved mechanism of plant defense. The dangers of that approach are indicated by observations showing that plant responses to herbivory may also make further herbivory more likely. It is actually very easy to manipulate trees so as to improve the quality of their foliage for herbivores: one simply breaks the apical dominance by removing the most apical meristems. After that the previously suppressed meristems start to grow actively, becoming rich in nutrients and low in tannins. After mammalian browsing, plants may become better for insects (Danell and Huss-Danell, 1985); insect feeding can lead to a similar outcome (Bryant et al., 1991). Since responses to the breaking of apical dominance are of a very general nature, it is not surprising that induced susceptibility has been found in many types of woody plants, including eucalypts (Landsberg, 1990), birch (Haukioja et al., 1990), oak (Hunter and West, 1990), alder (Williams and Myers, 1984), willows (Hjälten and Price, 1996), and pines (Trewella et al., 1997; Raffa et al., 1998).

The chemical changes that describe induced susceptibility have not been studied in detail. In birch they seem to be just the opposite of DIR—an increase in nutrients and a decline in phenolics (Danell et al., 1997); better insect performance, however, may also follow even though some chemical traits may indicate poor foliage quality (Wagner and Evans, 1985; Raffa et al., 1998).

Induced susceptibility pinpoints certain unconsidered possibilities with regard to the origin of population cycles. If insects are able to manipulate the plant hormonal system for their own benefit, this may improve the foliage; hypothetically, this could create positive feedbacks into population numbers. This might be reflected in an improved reproductive capacity in insects during the increase phase. A further hypothetical possibility is that during the increase phase of the population, insects could sabotage the expression of defensive cascades and reduce the effects of possible indirect defenses (Dicke and van Poecke, 2002). The sabotage of indirect defenses (Edwards, 1989; Krause and Raffa, 1995; Kaitaniemi et al., 1997) might even contribute to a low rate of parasitism during the years of population build-up, a necessary prerequisite for increasing insect populations.

### 12.3 Resistance of Long-Lived Hosts Against Short-Lived Pests

Defoliating forest insects have short generation times compared to their hosts. This creates a potential evolutionary dilemma: the numerous generations of herbivores during the lifetime of a single host suggest the insect should easily develop genotypes that exactly match the genotypes of the host (Edmunds and Alstad, 1978), perhaps at the cost of being able to live on other host individuals. In studying the idea of adaptive deme formation, van Zandt and Mopper (1998) found evidence for locally adapted insect populations; however, it did not correlate in any simple way with the herbivore dispersal rate, feeding type, or mode of reproduction.

An obvious answer to the question of why short-lived herbivores are not able to completely breach the genetic resistance system of their long-lived trees is that insects interact with tree phenotypes, not genotypes, and that the same tree genotype is able to express vastly different resistance mechanisms. Induced defenses represent an important source of variance in plant defense (Denno and McClure, 1983), which insects try to overcome by moving around or by compensatory feeding. In birch sawflies these alternatives seem to be mutually exclusive (Kause et al., 1999a).

By no means do induced defenses represent the only source of variability. The architectural complexity of trees also promotes spatial heterogeneity within canopies (Lawton, 1983). In mountain birch, Suomela and Nilson (1994) showed that most of the variance in insect performance in birch canopies was within, not among, trees, mainly between ramets and between branches. Actually the largest component of variance in tree foliage probably is seasonal. Since secondary compounds function interactively with other leaf traits (water content, sugar/protein ratio, toughness) (Schopf, 1986; Haukioja et al., 2002), this creates rich phenotypic variation in foliage quality of the same tree genotypes.

From the viewpoint of insect adaptation to a single host, a critical point is that during its development an insect may encounter successive qualities of leaves from the same tree so different that the tree simply does not represent a single target

for the insect to adapt to (Adler and Karban, 1994). This is especially likely in insects that feed on growing leaves, and is obviously less likely in sucking insects. Interestingly, none of the examples of adaptive deme formation in van Zandt and Mopper (1998) referred to foliage-chewing insects.

Pronounced changes in diet quality during the lifetime of an arboreal chewing insect take place during the time of most intense leaf development. Because of the large seasonal variation in the main nutritive, phenolic, and terpenoids compounds, individual insect genotypes may not be optimally adapted to handle each successive defensive trait. The interactive actions of phenolics with nutritive leaf traits (Haukioja et al., 2002) further enhance the challenge of dealing with the foliage of an individual tree, as suggested by the observation that most of the variance in sugars and amino acids fell within and not among trees (Suomela et al., 1995b).

Accordingly, in birch it has been common not to find significant correlations when spring-feeding insects have been repeatedly tested on leaves of the same trees. On young, nutritious leaves the lack of correlation may result from compensatory feeding on poorer quality trees producing similar growth on different host individuals, but also from the rapid developmental switching of main foliar defenses. Still, each larva that survived to pupation on a single host had to be able to handle all the seasonally switching defenses. Ruusila et al. (2005) tested autumnal moth larvae at different instars in the same trees; in accordance with the above logic, they did not find significant difference among trees but did find tree \* instar interactions. In other words, different trees were best for different instars. Major switches in tree suitability seemed to take place between the third instar and later ones (i.e., at the time when gallotannin contents declined, Riipi et al., 2002). Brood-specific larval growth, on the other hand, was similar in the fourth and fifth instars (see also Ayres et al., 1987). The results suggest that one component of the defensive strategy of mountain birch against *Epirrita autumnata*, its most important herbivore, may be to minimize the probability of the evolution of well adaptive insect genotypes. Birch leaf quality remains relatively invariant in mid and late season, allowing insects to adapt to certain developmental phases of the host (Hanhimäki et al., 1995; Kause et al., 2001). Martel et al. (2001) found that birch sawflies did manage poorly when they were experimentally exposed to younger (and more nutritious) leaves or to more mature (nutritionally inferior) ones than those that they typically consume. This suggests that mid- to late-season sawfly species were specialized to certain phases of birch leaf development, not to host trees per se.

## 12.4 Discussion

Low consumption, the final outcome of successful defense, can be achieved by numerous different combinations of defensive solutions, and we lack a holistic understanding of the plant traits that prevent consumption by insects or that curtail it to values less than optimal for insect development. This, however, is the

critical problem in explaining how plant defenses lead to the ultimate goal, reduced consumption. It is important to realize that a trait with adverse effects on a herbivore may or may not be an important component of plant defense. A fundamental task in identifying crucial plant defenses is thus to determine the contribution of different plant traits to consumption (the inverse of defense); in other words, we should concentrate on how much these traits explain of the variance ( $r^2$ ) in consumption. This is more important for a holistic understanding than whether a certain trait makes a defensive contribution (i.e., whether it correlates with consumption), or whether it is detrimental for a herbivore. Scriber and Feeny (1979) demonstrated the importance of water for arboreal insects, and Haukioja et al. (2002) showed that in most cases leaf water content explained more of the variance in growth and to some extent in consumption of a defoliator than any phenolic compound measured.

### 12.4.1 Possibilities for General Theories

Within the ecological paradigm of plant defense, research on tree defenses has long concentrated on measuring the levels of those compounds that are likely to be defensive, such as phenolics and terpenoids. The most popular general theories (the carbon-nutrient balance and the growth-differentiation balance hypotheses) have stressed the importance of trade-offs between plant growth and defense, and the defense level has often been measured as the concentration of phenolic compounds (see e.g., Herms and Mattson, 1992; Hamilton et al., 2001). In woody plants there are actually strong negative correlations between nutrient levels (high values characterizing rapidly growing plant parts) and total phenolics, or their usually largest component, condensed tannins. This has traditionally been explained by the passive accumulation of carbon in defensive compounds after carbon demands for plant growth have been met. However, the key point may not be in plant growth versus defense, since other types of putative defenses (hydrolyzable tannins, terpenoids) of woody plants do not respond to variable carbon availability in the same way as condensed tannins (Haukioja et al., 1998; Koricheva et al., 1998). Furthermore, correlations between the synthesis of putatively defensive compounds and the growth of other plant tissues may not be generally inversely related, as indicated by an analysis of the accumulation of phenolic compounds in growing birch leaves and shoots (Riipi et al., 2002). As such this does not refute trade-offs at the whole-plant level; the synthesis of leaf phenolics in mountain birch, however, depends on local and not whole-tree carbon resources, as shown by experiments shading whole canopies or individual branches only (Henriksson et al., 2003).

I have elsewhere introduced an alternative, adaptive explanation for the strong trade-off between leaf nutritive quality and its “quantitative” (sensu Feeny, 1975) defenses, such as condensed tannins (Haukioja, 2003). Quantitative defenses are obviously targeted against adapted species of herbivores, which are well equipped to handle single defensive compounds in their host. Quantitative defenses would not be effective against such species if the plant were rich in nutrients; this is because on nutrient-rich diets insects can satisfy their requirements for nutritive compounds with such low consumption that the *amounts* of tannins ingested are

inconsequential. Accordingly, quantitative defenses can be effective only if plant nutrient content is low, and if compensatory feeding leads to increased consumption of defensive compounds. This scenario predicts a tight negative correlation between plant nutrient content and quantitative defenses such as condensed tannins. The explanation is not sensitive to the matter of whether the reason for high nutrition is nitrogen fertilization, shade or seasonal schedules.

Quite obviously, possibilities for the creation of new general theories as broad as the carbon-nutrient balance hypothesis are limited (see e.g., Lerdau and Coley, 2002, Nitao et al., 2002, Koricheva, 2002). This is because of the emerging picture of plant defenses as the outcomes of complex and probably idiosyncratic interactions between secondary compounds, nutritive plant traits and specific defense cascades.

### 12.4.2 *What Next?*

During recent years specific defense pathways have been shown to operate in trees, such as poplars (Constabel et al., 2000), alder (Tscharntke et al., 2001), and spruce (Martin et al., 2002). In birch as well, strong negative correlations between insect growth and leaf fatty acids of the octadecanoid pathway suggest the importance of this pathway (Haukioja et al., unpublished data). The emerging genetic maps of woody plants and the use of microarrays for trees too will offer new tools for the study of specific defense systems with the same accuracy as for well-known herbs (e.g., Chiron et al., 2000). At that point we will have the tools to start to unravel the specific and relative roles of particular defense pathways, of constitutive secondary compounds, and of nutritive compounds as codeterminants of tree defenses. Several major problems still remain. Experimentation with trees is easy only with saplings, while the most dramatic incidents of herbivory tend to occur in mature or overmature stands (e.g., Ruohomäki et al., 1997). The context-dependence and interactive functions of defenses suggest that generalizations about defenses may be risky, and we have to keep in mind possible species-specific effects of plant defense responses.

Particular interest should be accorded to the idea that trees may utilize indirect defenses, i.e., recruit parasitoids as part of tree defense, presumably via volatile exudates luring parasitoids. This idea is really worth testing; it is well known that trees release huge amounts of volatiles into the atmosphere (Rhoades, 1985; Hakola et al., 1998; Monson and Holland, 2001). Yet a further source of complexity is the possibility that some of these mechanisms may interact with “traditional” plant defenses, producing unanticipated results; dietary phenolics, for instance, may increase larval resistance against viral diseases (Hunter and Schultz, 1993).

## *References*

- Adler, F.R., and Karban, R. 1994. Defended fortresses or moving targets? Another model of inducible defenses inspired by military metaphors. *Am. Nat.* 144:813–832.
- Arnold, T.M., and Schultz, J.C. 2002. Induced sink strength as a prerequisite for induced tannin biosynthesis in developing leaves of *Populus*. *Oecologia* 130:585–593.

- Ayres, M.P., Suomela, J., and MacLean, S.F., Jr. 1987. Growth performance of *Epirrita autumnata* (Lepidoptera: Geometridae) on mountain birch: trees, broods, and tree\*brood interactions. *Oecologia* 74:450–457.
- Barbehenn, R.V. 2001. Roles of peritrophic membranes in protecting herbivorous insects from ingested plant allelochemicals. *Arch. Insect Biochem. Physiol.* 47:86–99.
- Beardmore, T., Wetzel, S., and Kalous, M. 2000. Interactions of airborne methyl jasmonate with vegetative storage protein gene and protein accumulation and biomass partitioning in *Populus* plants. *Can. J. For. Res.* 30:1106–1113.
- Benz, G. 1974. Negative Rückkoppelung durch Raum- und Nahrungskonkurrenz sowie zyklische Veränderung der Nahrungsgrundlage als Regelprinzip in der Populationsdynamik des Grauen Lärchenwicklers, *Zeiraphera diniana* (Guenée) (Lep., Tortricidae). *Z. Ang. Ent.* 76:196–228.
- Bryant, J.P., Heitkoning, I., Kuropat, P., and Owen-Smith, N. 1991. Effects of severe defoliation on the long-term resistance to insect attack and on leaf chemistry in six woody species of the southern African savanna. *Am. Nat.* 137:50–63.
- Bryant, J.P., Reichardt, P.B., Clausen, T.P., and Werner, R.A. 1993. Effects of mineral nutrition on delayed inducible resistance in Alaska paper birch. *Ecology* 74:2072–2084.
- Chiron, H., Drouet, A., Lieutier, F., Payer, H.D., Ernst, D., and Sandermann, H. 2000. Gene induction of stilbene biosynthesis in Scots pine in response to ozone treatment, wounding, and fungal infection. *Plant Physiol.* 124:865–872.
- Clancy, K.M. 1992. The role of sugars in western spruce budworm nutritional ecology. *Ecol. Entomol.* 17:189–197.
- Constabel, C.P., Yip, L., Patton, J.J., and Christopher, M.E. 2000. Polyphenol oxidase from hybrid poplar. Cloning and expression in response to wounding and herbivory. *Plant Physiol.* 124:285–295.
- Danell, K., Haukioja, E., and Huss-Danell, K. 1997. Morphological and chemical responses of birch leaves and twigs to winter browsing along a gradient of plant productivity. *Écoscience* 4:296–303.
- Danell, K., and Huss-Danell, K. 1985. Feeding by insects and hares on birches earlier affected by moose browsing. *Oikos* 44:75–81.
- Denno, R.F., and McClure, M.S. eds. 1983. *Variable Plants and Herbivores*. New York: Academic Press
- Dicke, M., and van Poecke, R.M.P. 2002. Signaling in plant-insect interactions: signal transduction in direct and indirect plant defence. In *Plant Signal Transduction*, eds. D. Scheel, and C. Wasternack, pp. 289–316. Oxford: Oxford University Press
- Dolch, R., and Tscharnatke, T. 2000. Defoliation of alders (*Alnus glutinosa*) affects herbivory by leaf beetles on undamaged neighbours. *Oecologia* 125:504–511.
- Dyer, M.I., Acra, M.A., Wang, G.M., Coleman, D.C., Freckman, D.W., McNaughton, S.J., and Strain, B.R. 1991. Source-sink carbon relations in two *Panicum coloratum* ecotypes in response to herbivory. *Ecology* 72:1472–1483.
- Edmunds, G.F., and Alstad, D.N. 1978. Coevolution in insect herbivores and conifers. *Science* 199:941.
- Edwards, P.J. 1989. Insect herbivory and plant defence theory. In *Towards a More Exact Ecology*, eds. P.J. Grubb, and J.B. Whittaker, pp. 275–297. Oxford: Blackwell.
- Edwards, P.J., and Wratten, S.D. 1982. Wound-induced changes in palatability in birch (*Betula pubescens* Ehr. ssp. *pubescens*). *Am. Nat.* 120:816–818.
- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51:565–581.

- Feeny, P. 1975. Biochemical coevolution between plants and their insect herbivores. In *Coevolution of Animals and Plants*, eds. L.E. Gilbert, and P.H. Raven, pp. 3–19. Austin: University of Texas Press.
- Felton, G.W., Donato, K.K., Broadway, R.M., and Duffey, S.S. 1992. Impact of oxidized plant phenolics on the nutritional quality of dietary protein to a noctuid herbivore, *Spodoptera exigua*. *J. Insect Physiol.* 38:277–285.
- Fowler, S.V., and MacGarvin, M. 1986. The effects of leaf damage on the performance of insect herbivores on birch, *Betula pubescens*. *J. Anim. Ecol.* 55:565–573.
- Habermann, M. 2000. The larch casebearer and its host tree II. Changes in needle physiology of the infested trees. *For. Ecol. Manage.* 136:23–34.
- Hakola, H., Rinne, J., and Laurila, T. 1998. The hydrocarbon emission rates of tea-leaved willow (*Salix phylicifolia*), silver birch (*Betula pendula*) and European aspen (*Populus tremula*). *Atmosph. Environ.* 32:1825–1833.
- Hamilton, J.G., Zangerl, A.R., DeLucia, E.H., and Berenbaum, M.R. 2001. The carbon-nutrient balance hypothesis: its rise and fall. *Ecol. Lett.* 4:86–95.
- Hanhimäki, S., and Senn, J. 1992. Sources of variation in rapidly inducible responses to leaf damage in the mountain birch-insect herbivore system. *Oecologia* 91:318–331.
- Hanhimäki, S., Senn, J., and Haukioja, E. 1995. The convergence in growth of foliage-chewing insect species on individual mountain birch trees. *J. Anim. Ecol.* 64:543–552.
- Hartley, S.E. and Lawton, J.H. 1990. Damage-induced changes in birch foliage: mechanisms and effects on insect herbivores. In *Population Dynamics of Forest Insects*, eds. A.D. Watt, S.R. Leather, M.D. Hunter, and N.A.C. Kidd, pp. 147–155. Andover, Hampshire: Intercept.
- Haukioja, E. 1982. Inducible defences of white birch to a geometrid defoliator, *Epirrita autumnata*. In *Insect-Plant Relationships*, eds. J.H. Visser, and A.K. Minks, pp. 199–203. Wageningen, The Netherlands: Pudoc.
- Haukioja, E. 1990. Induction of defenses in trees. *Annu. Rev. Entomol.* 36:25–42.
- Haukioja, E. 2003. Putting the insect into the birch-insect interaction. *Oecologia* 136:161–168.
- Haukioja, E., and Niemelä, P. 1977. Retarded growth of a geometrid larva after mechanical damage to leaves of its host tree. *Ann. Zool. Fennici* 14:48–52.
- Haukioja, E., Ossipov, V., Koricheva, J., Honkanen, T., Larsson, S., and Lempa, K. 1998. Biosynthetic origin of carbon-based secondary compounds: cause of variable responses of woody plants to fertilization? *Chemoecology* 8:133–139.
- Haukioja, E., Ossipov, V., and Lempa, K. 2002. Interactive effects of leaf maturation and phenolics on consumption and growth of a geometrid moth. *Entomol. Exp. Appl.* 104:125–136.
- Haukioja, E., Ruohomäki, K., Senn, J., Suomela, J., and Walls, M. 1990. Consequences of herbivory in the mountain birch (*Betula pubescens* ssp. *tortuosa*): importance of the functional organization of the tree. *Oecologia* 82:238–247.
- Havill, N.P., and Raffa, K.F. 1999. Effects of elicitation treatment and genotypic variation on induced resistance in *Populus*: impacts on gypsy moth (Lepidoptera: Lymantriidae) development and feeding behavior. *Oecologia* 120:295–303.
- Heath, M.C. and Boller, T. 2002. Biotic interactions levels of complexity in plant interactions with herbivores, pathogens and mutualists. *Curr. Opin. Plant Biol.* 5:277–278.
- Henriksson, J. 2001. Differential shading of branches or whole trees: survival, growth, and reproduction. *Oecologia* 126:482–486.
- Henriksson, J., Haukioja, E., Ossipov, V., Ossipova, S., Sillanpää, S., Kapari, L., and Pihlaja, K. 2003. Effects of host shading on consumption and growth of the geometrid *Epirrita autumnata*: interactive roles of water, primary and secondary compounds. *Oikos* 103:3–16.

- Hermes, D.A., and Mattson, W.J. 1992. The dilemma of plants: to grow or defend. *Quart. Rev. Biol.* 67:283–335.
- Hillis, W.E. 1975. Ethylene and extraneous material formation in woody tissues. *Phytochemistry* 14:2559–2562.
- Hjältén, J., and Price, P.W. 1996. The effects of pruning on willow growth and sawfly population densities. *Oikos* 77:549–555.
- Honkanen, T., and Haukioja, E. 1998. Intraplant regulation and plant/herbivore interactions. *Écoscience* 5:470–479.
- Hunter, M.D., and Schultz, J.C. 1993. Induced plant defenses breached? Phytochemical induction protects a herbivore from disease. *Oecologia* 94:195–203.
- Hunter, M.D., and West, C. 1990. Variation in the effects of spring defoliation on the late season phytophagous insects of *Quercus robur*. In *Population Dynamics of Forest Insects*, eds. A.D. Watt, S.R. Leather, M.D. Hunter, and N.A.C. Kidd, pp. 123–135. Andover, Hampshire: Intercept.
- Julkunen-Tiitto, R., Rousi, M., Bryant, J.P., Sorsa, S., Keinänen, M., and Sikanen, H. 1996. Chemical diversity of several Betulaceae species: comparison of phenolics and terpenoids in northern birch stems. *Trees* 11:16–22.
- Kaitaniemi, P., Neuvonen, S., and Nyssönen, T. 1999. Effects of cumulative defoliations on growth, reproduction, and insect resistance in the mountain birch. *Ecology* 80:524–532.
- Kaitaniemi, P., and Ruohomäki, K. 2001. Sources of variability in plant resistance against insects: free caterpillars show strongest effects. *Oikos* 95:461–470.
- Kaitaniemi, P., Ruohomäki, K., and Haukioja, E. 1997. Consumption of apical buds as a mechanism of alleviating host plant resistance for *Epirrita autumnata* larvae. *Oikos* 78:230–238.
- Kaitaniemi, P., Ruohomäki, K., Ossipov, V., Haukioja, E., and Pihlaja, K. 1998. Delayed induced changes in the biochemical composition of host plant leaves during an insect outbreak. *Oecologia* 116:182–190.
- Karban, R., and Kuč, J. 1999. Induced resistance against pathogens and herbivores: an overview. In *Induced Plant Defenses Against Pathogens and Herbivores*, eds. A.A. Agrawal, S. Tuzun, and E. Bent, pp. 1–16. St. Paul, MN: APS Press.
- Kause, A., Haukioja, E., and Hanhimäki, S. 1999a. Phenotypic plasticity in foraging behavior of sawfly larvae. *Ecology* 80:1230–1241.
- Kause, A., Ossipov, V., Haukioja, E., Lempa, K., and Hanhimäki, S. 1999b. Multiplicity of biochemical factors determining quality of growing birch leaves. *Oecologia* 120:102–112.
- Kause, A., Saloniemi, I., Morin, J.P., Haukioja, E., Hanhimäki, S., and Ruohomäki, K. 2001. Seasonally varying diet quality and the quantitative genetics of development time and body size in birch feeding insects. *Evolution* 55:1992–2001.
- Keinänen, M., Julkunen-Tiitto, R., Mutikainen, P., Walls, M., Ovaska, J., and Vapaavuori, E. 1999. Trade-offs in secondary metabolism: effects of fertilization, defoliation, and genotype on birch leaf phenolics. *Ecology* 80:1970–1986.
- Koricheva, J. 2002. Meta-analysis of sources of variation in fitness costs of plant antiherbivore defenses. *Ecology* 83:176–190.
- Koricheva, J., Larsson, S., Haukioja, E., and Keinänen, M. 1998. Regulation of woody plant secondary metabolism by resource availability: hypothesis testing by means of meta-analysis. *Oikos* 83:212–226.
- Krause, S.C., and Raffa, K.F. 1992. Comparison of insect, fungal, and mechanically induced defoliation of larch—effects on plant productivity and subsequent host susceptibility. *Oecologia* 90:411–416.

- Landsberg, J. 1990. Dieback of rural eucalypts: response of foliar dietary quality and herbivory to defoliation. *Aust. J. Ecol.* 15:89–96.
- Långström, B., Tenow, O., Ericsson, A., Hellqvist, C., and Larsson, S. 1990. Effects of shoot pruning on stem growth, needle biomass, and dynamics of carbohydrates and nitrogen in Scots pine as related to season and tree age. *Can. J. For. Res.* 20:514–523.
- Larsson, S. 2002. Resistance in trees to insects—an overview of mechanisms and interactions. In *Mechanisms and Deployment of Resistance in Trees to Insects*, eds. M.R. Wagner, K.M. Clancy, F. Lieutier, and T.D. Paine, pp. 1–29. Dordrecht, The Netherlands: Kluwer Academic Press.
- Lawton, J.H. 1983. Plant architecture and the diversity of phytophagous insects. *Annu. Rev. Entomol.* 28:23–39.
- Lerdau, M., and Coley, P.D. 2002. Benefits of the carbon-nutrient balance hypothesis. *Oikos* 98:533–535.
- Litvak, M.E., and Monson, R.K. 1998. Patterns of induced and constitutive monoterpene production in conifer needles in relation to insect herbivory. *Oecologia* 114:531–540.
- Lyytikäinen, P. 1994. Effects of natural and artificial defoliations on sawfly performance and foliar chemistry of Scots pine saplings. *Ann. Zool. Fennici* 31:307–318.
- Martel, J., Hanhimäki, S., Kause, A., and Haukioja, E. 2001. Diversity of birch sawfly responses to seasonally atypical diets across a seasonal gradient of larval feeding periods. *Entomol. Exp. Appl.* 100:301–309.
- Martin, D., Tholl, D., Gershenzon, J., and Bohlmann, J. 2002. Methyl jasmonate induces traumatic resin ducts, terpenoid resin biosynthesis, and terpenoid accumulation in developing xylem of Norway spruce stems. *Plant Physiol.* 129:1003–1018.
- Mattson, W.J., and Scriber, J.M. 1987. Nutritional ecology of insect folivores of woody plants: nitrogen, water, fiber, and mineral considerations. In *Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates*, eds. F. Slansky, Jr., and J.G. Rodriguez, pp. 105–146. New York: John Wiley.
- Monson, R.K., and Holland, E.A. 2001. Biospheric trace gas fluxes and their control over tropospheric chemistry. *Annu. Rev. Ecol. Syst.* 32:547–576.
- Moran, N., and Hamilton, W.D. 1980. Low nutritive quality as defence against herbivores. *J. Theor. Biol.* 86:247–254.
- Nerg, A., Kainulainen, P., Vuorinen, M., Hanso, M., Holopainen, J.K., and Kurkela, T. 1994. Seasonal and geographical variation of terpenes, resin acids and total phenolics in nursery grown seedlings of Scots pine (*Pinus sylvestris* L.). *New Phytol.* 128:703–713.
- Neuvonen, S., and Haukioja, E. 1991. The effects of inducible resistance in host foliage on birch-feeding herbivores. In *Phytochemical Induction by Herbivores*, eds. D.W. Tallamy, and M.J. Raupp, pp. 277–291. New York: John Wiley & Sons.
- Nitao, J.K., Hamilton, J.G., Zangerl, A.R., DeLucia, E.H., and Berenbaum, M. 2002. CNB: requiescat in pace? *Oikos* 98:539–545.
- Nurmi, K., Ossipov, V., Haukioja, E., and Pihlaja, K. 1996. Variation of total phenolic content and low-molecular-weight phenolics in foliage of the mountain birch trees (*Betula pubescens* ssp. *tortuosa*). *J. Chem. Ecol.* 22:2033–2050.
- Omlin, F.X. 1980. Aspekte zum wechselweisen Beziehungsgefüge Lärchenwickler (*Zeiraphera diniana* GN.) und Lärche (*Larix decidua* MILL.). 1. Teil: Einflussnahme des Lärchenwicklers auf die Lärche. *Mitt. Schweiz. Entomol. Ges.* 53:379–399.
- Ossipov, V., Haukioja, E., Hanhimäki, S., and Pihlaja, K. 2001. Phenolic and phenolic-related factors as determinants of suitability of mountain birch leaves to an herbivorous insect. *Biochem. Syst. Ecol.* 29:223–240.

- Raffa, K.F. 1991. Induced defensive reactions in conifer-bark beetle systems. In *Phytochemical Induction by Herbivores*, eds. D.W. Tallamy, and M.J. Raupp, pp. 245–276. New York: John Wiley.
- Raffa, K.F., Krause, S.C., and Reich, P.B. 1998. Long-term effects of defoliation on red pine suitability to insects feeding on diverse plant tissues. *Ecology* 79:2352–2364.
- Raubenheimer, D., and Simpson, S.J. 1994. The analysis of nutrient budgets. *Funct. Ecol.* 8:783–791.
- Rhoades, D.F. 1985. Offensive-defensive interactions between herbivores and plants: their relevance to herbivore population dynamics and community theory. *Am. Nat.* 125:205–238.
- Riipi, M., Ossipov, V., Lempa, K., Haukioja, E., Koricheva, J., Ossipova, S., and Pihlaja, K. 2002. Seasonal changes in birch leaf chemistry: are there trade-offs between leaf growth and accumulation of phenolics? *Oecologia* 130:380–390.
- Rossiter, M.C., Schultz, J.C., and Baldwin, I.T. 1988. Relationships among defoliation, red oak phenolics, and gypsy moth growth and reproduction. *Ecology* 69:267–277.
- Ruohomäki, K., Chapin, F.S., III, Haukioja, E., Neuvonen, S., and Suomela, J. 1996. Delayed inducible resistance in mountain birch in response to fertilization and shade. *Ecology* 77:2302–2311.
- Ruohomäki, K., Hanhimäki, S., Haukioja, E., Iso-Iivari, L., Neuvonen, S., Niemelä, P., and Suomela, J. 1992. Variability in the efficacy of delayed inducible resistance in mountain birch. *Entomol. Exp. Appl.* 62:107–115.
- Ruohomäki, K., Virtanen, T., Kaitaniemi, P., and Tammaru, T. 1997. Old mountain birches at high altitudes are prone to outbreaks of *Epirrita autumnata* (Lepidoptera: Geometridae). *Environ. Entomol.* 26:1096–1104.
- Ruusila, V., Morin, J.P., van Oik, T., Saloniemi, I., Ossipov, V., and Haukioja, E. 2005. A short-lived herbivore on a long lived host: tree resistance to herbivory depends of leaf age. *Oikos* 108:99–104.
- Salminen, J.-P., and Lempa, K. 2002. Effects of hydrolysable tannins on an herbivorous insect: fate of individual tannins in insect digestive tract. *Chemoecology* 12:203–211.
- Salminen, J.P., Ossipov, V., Haukioja, E., and Pihlaja, K. 2001. Seasonal variation in the content of hydrolysable tannins in leaves of *Betula pubescens*. *Phytochemistry* 57:15–22.
- Schopf, R. 1986. The effect of secondary needle compounds on the development of phytophagous insects. *For. Ecol. Manage.* 15:55–64.
- Schultz, J.C., and Baldwin, I.T. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. *Science* 217:149–151.
- Scriber, J.M., and Feeny, P. 1979. Growth of herbivorous caterpillars in relation to feeding specialization and to the growth form of their food plants. *Ecology* 60:829–850.
- Schwenke, W. 1968. Neue Hinweise auf eine Abhängigkeit der Vermehrung blatt- und nadelfressender Forstinsekten vom Zuckergehalt ihrer Nahrung. *Z. Ang. Ent.* 61:365–369.
- Seldal, T., Dybwad, E., Andersen, K., and Högstedt, G. 1994. Wound-induced proteinase inhibitors in grey alder (*Alnus incana*): a defence mechanism against attacking insects. *Oikos* 71:239–245.
- Simpson, S.J., and Raubenheimer, D. 2001. The geometric analysis of nutrient-allelochemical interactions: a case study using locusts. *Ecology* 82:422–439.
- Slansky, F., Jr. 1993. Nutritional ecology: the fundamental quest for nutrients. In *Caterpillars. Ecological and Evolutionary Constraints on Foraging*, eds. N.E. Stamp, and T.M. Casey, pp. 29–91. New York: Chapman and Hall.
- Slansky, F., Jr., and Wheeler, G.S. 1992. Caterpillars' compensatory feeding response to diluted nutrients leads to toxic allelochemical dose. *Entomol. Exp. Appl.* 65:171–186.

- Smits, A., Larsson, S., and Hopkins, R. 2001. Reduced realised fecundity in the pine looper *Bupalus piniarius* caused by host plant defoliation. *Ecol. Entomol.* 26:417–424.
- Suomela, J., Kaitaniemi, P., and Nilson, A. 1995a. Systematic within-tree variation in mountain birch leaf quality for a geometrid, *Epirrita autumnata*. *Ecol. Entomol.* 20:283–292.
- Suomela, J., and Nilson, A. 1994. Within-tree and among-tree variation in growth of *Epirrita autumnata* on mountain birch leaves. *Ecol. Entomol.* 19:45–56.
- Suomela, J., Ossipov, V., and Haukioja, E. 1995b. Variation among and within mountain birch trees in foliage phenols, carbohydrates and amino acids, and in growth of *Epirrita autumnata* larvae. *J. Chem. Ecol.* 21:1421–1446.
- Trewhella, K.E., Leather, S.R., and Day, K.R. 1997. Insect induced resistance in lodgepole pine: Effects on two pine feeding insects. *J. Appl. Entomol.* 121:129–136.
- Tschantke, T., Thiessen, S., Dolch, R., and Boland, W. 2001. Herbivory, induced resistance, and interplant signal transfer in *Alnus glutinosa*. *Biochem. Syst. Ecol.* 29:1025–1047.
- Tuomi, J., Niemelä, P., Haukioja, E., Sirén, S., and Neuvonen, S. 1984. Nutrient stress: an explanation for plant anti-herbivore responses to defoliation. *Oecologia* 61:208–210.
- Tuomi, J., Niemelä, P., Rousi, M., Sirén, S., and Vuorisalo, T. 1988. Induced accumulation of foliage phenols in mountain birch: branch response to defoliation? *Am. Nat.* 132:602–608.
- Valentine, H.T., Wallner, W.E., and Wargo, P.M. 1983. Nutritional changes in host foliage during and after defoliation, and their relation to the weight of gypsy moth pupae. *Oecologia* 57:298–302.
- Valkama, E., Salminen, J.P., Koricheva, J., and Pihlaja, K. 2003. Comparative analysis of leaf trichome structure and composition of epicuticular flavonoids in Finnish birch species. *Ann. Bot.* 91:643–655.
- van Zandt, P.A., and Mopper, S. 1998. A meta-analysis of adaptive deme foundation in phytophagous insect populations. *Am. Nat.* 152:595–604.
- Villalba, J.J., Provenza, F.D., and Bryant, J.P. 2002. Consequences of the interaction between nutrients and plant secondary metabolites on herbivore selectivity: benefits or detriments for plants? *Oikos* 97:282–292.
- Wagner, M.R., and Evans, P.D. 1985. Defoliation increases nutritional quality and allelochemicals of pine seedlings. *Oecologia* 67:235–237.
- Watt, A.D. 1990. The consequences of natural, stress-induced and damage-induced differences in tree foliage on the population dynamics of the pine beauty moth. In *Population Dynamics of Forest Insects*, eds. A.D. Watt, S.R. Leather, M.D. Hunter, and N.A.C. Kidd, pp. 157–168. Andover, Hampshire: Intercept.
- White, T.C.R. 1974. A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. *Oecologia* 16:279–301.
- Williams, K.S., and Myers, J.H. 1984. Previous herbivore attack of red alder may improve food quality for fall webworm larvae. *Oecologia* 63:166–170.
- Wratten, S.D., Edwards, P.J., and Dunn, I. 1984. Wound-induced changes in the palatability of *Betula pubescens* and *Betula pendula*. *Oecologia* 61:372–375.
- Zou, J., and Cates, R.G. 1994. Role of Douglas fir (*Pseudotsuga menziesii*) carbohydrates in resistance to budworm (*Choristoneura occidentalis*). *J. Chem. Ecol.* 20:395–405.
- Zou, J.P., and Cates, R.G. 1995. Foliage constituents of Douglas-fir (*Pseudotsuga menziesii* (Mirb)) Franco (Pinaceae)—their seasonal variation and potential role in Douglas-fir resistance and silvicultural management. *J. Chem. Ecol.* 21:387–402.