

Monoterpenes and Herbivores: plant resistance and insect adaptation

Sheryl Costello

sherylc@lamar.colostate.edu

Plant oleoresins, often referred to as resins, are sticky plant secretions synthesized in large quantities by about 10 % of plant families. Resin is secreted when a plant is disturbed and the sticky substances produced contain many toxic compounds used to defend the plant from herbivores and pathogens. A major component of resin is the terpenoid compounds. Although terpenoid compounds can be quite complex, they are all composed of five-carbon units, with an isoprene unit as the base. The simplest of these terpenes are the monoterpenes that possess 10-carbon atoms derived from two fused isoprene units. Monoterpenes are an important component of the volatile portion of terpenes and often emit very strong odors. Monoterpenes are chemicals that accumulate in resin ducts, secretory cavities, and epidermal glands and are considered secondary chemicals because they lack a role in basic plant processes. The specific monoterpenes present between species is highly variable, and in many cases are also different within a species due environmental conditions and herbivory pressures.

Monoterpenes have been shown to repel plant herbivores and in many cases cause herbivore death. Toxicity in some cases is due to the monoterpene vapors and not direct contact. In response, many insect plant herbivores have developed detoxifying mechanisms that allow them to feed on the plant parts containing monoterpenes. Over time this coevolutionary “arms race” has resulted in further adaptations including insect species that have adapted the use of monoterpenes as chemical cues to sense plant health. Additionally, many species of bark beetles can utilize components of the host resin to create pheromones promoting aggregation. Herein, I will examine the basic evolution and synthesis of terpenes, the role of monoterpenes in plant defense, and the extraordinary adaptations herbivores have evolved.

Plant resin is a complex chemically diverse mixture of terpenoids that serve many functions. All living organisms contain terpenoids, but plants contain the highest diversity of terpenoids. Many terpenoids are considered secondary metabolites because they appear to lack direct function in basic growth and defense. These secondary metabolites of terpenes contain insect and microbial toxins and other agents that act to deter insect herbivory. Terpenes also act as band aids by sealing a plant wound. Once plant tissue is exposed to the air, the volatile terpene portion evaporates leaving a semi-hardened mass (Phillips & Croteau 1999). Even though terpenoids are chemically diverse and perform many functions they are all made up of fusion of a five-carbon unit, known as isoprene. Production of terpenes takes place via similar chemical pathways and terpenes are then stored for defense. The amount of terpenes produced and released depends on several factors, such as drought and fire. Furthermore, the same

terpenes that are produced for defense, can be used by plant herbivores in host location and selection. The review that follows is a brief overview of terpene production, terpene variation, and herbivore response.

Terpene Synthesis, Location and Evolution

Terpenoid compounds are synthesized by two known chemical pathways within plants. The traditional acetate-mevalonate pathway was long believed to produce the precursors to all terpenes. Recently it has been shown that this pathway produces sesquiterpenes (C_{15}) and triterpenes (C_{30}), but not monoterpenes. An alternative pathway is now known to produce monoterpenes, diterpenes (C_{20}) and tetraterpenes (C_{40}) in conifers. This pathway utilizes pyruvate and glyceraldehydes-3-phosphate, which are converted to deoxyxylulose phosphate that forms isopentenyl pyrophosphate (IPP) (Fig. 1). Once IPP is formed, the action of the terpenoid synthases catalyze several reactions. Monoterpene precursors are formed by the reaction between IPP and its isomer. A further condensation between IPP and its isomer forms the precursor of most sesquiterpenes. Additions and reactions of IPP lead to all other terpenes. The precursors then undergo a series of reactions, including the formation of double bonds, which create the enormous diversity of terpenes and stabilize the internal structure (Gershenzon & Croteau 1991).

Fossils from the Carboniferous tropical forests demonstrate the earliest evidence of resin synthesis as well as the internal storage of resin in secretory canals. During this period resin was not produced in large amounts like current species (Langenheim 1990). Based on phylogenetic analysis it seems that all plant terpene synthases share a common evolutionary origin and it has been suggested that the gene for multiple monoterpene synthase arose by gene duplication. Moreover, one copy of the gene remained conserved in structure and function. The second copy diverged to form the gene superfamily of terpene synthases involved in secondary metabolic pathways such as those that act on IPP. This is further supported by terpene synthase genomic

intron/exon organization, which demonstrates that certain introns have been conserved over time. Protein-based phylogenetics and intron/exon organization also indicate that the separation between primary and secondary metabolites occurred before the separation of angiosperms and gymnosperms (Trapp & Croteau 2001).

Primary terpenes are produced by the secretory epithelial cells and accumulate in resin cells. The complexity of the resin cells depends on the plant species. In conifers, resin cells can be isolated, as in cedars (*Thuja* sp.), or they can form blisters, as in true firs (*Abies* sp.). The most complex systems are those of pines (*Pinus* sp.) that form a highly complex network of branched canals capable of transporting resin many meters. When this network is severed, resin ducts will exude large amounts of resin. In addition to primary terpene production, conifers also possess an inducible terpene defense system that is produced by the parenchyma cells when injury occurs. This defense system leads to the formation of new traumatic resin ducts and increased resin flow in the area surrounding the injury (Theis & Lerdau 2003, Trapp & Croteau 2001).

Monoterpenes and Plant Defense

The simplest of the terpenes are the monoterpenes which consist of a ten-carbon unit. Similar to other terpenes, monoterpenes have been demonstrated to act as toxins, feeding deterrents, or oviposition deterrents to a large variety of insects. Thus it has been hypothesized that they play an important role in herbivore deterrence. A well-studied example is the pyrethroids, that are monoterpene esters, found in certain *Chrysanthemum* species leaves and flowers. The toxin causes disturbance in the nervous system and leads to paralysis (Gershenzon & Croteau 1991). A study performed by Raffa et al. (1985) demonstrated that vapors from monoterpenes also cause mortality. They exposed the fir engraver, *Scolytus ventralis* LeConte, to various monoterpenes found in quantities similar to their host grand fir, *Abies grandis* (Douglas) Lindley. They were careful that the monoterpenes did not come in contact with the

beetle. Results showed that all monoterpene vapors were toxic at both levels tested and some compounds were more toxic than others. In the laboratory, the beetle can be observed retreating from resin flow. Furthermore, monoterpenes slowed the growth of the beetle-fungal symbiont, *Trichosporium symbioticum* Wright, that is also responsible for tree death. These results indicate that monoterpenes play a major role in plant defense.

Attack behavior by tiger moth larvae, *Halisdota ingens* Hy. Edwards, also indicates a monoterpene role in plant defense. The tiger moth larvae feeds on ponderosa pine needles and consumes 1/2-2/3 of the needle, but not the base. Analysis revealed that a concentration and diversity of monoterpenes is greatest at the base of the needle, indicating that foraging maybe reduced by increases in monoterpenes (Litvak & Monson 1998). However, authors caution that plant morphology may also play a role in moth feeding behavior. Tiger moth larvae also have been shown to induce secondary monoterpene production. Induction of monoterpene production by moth larvae was two-fold higher than just mechanically wounding the plant and large increases in monoterpene volatilization were observed (Litvak & Monson 1998). Recently, herbivory by the white pine weevil, *Pissodes strobi* Peck., has been shown to directly induce gene expression in Sitka spruce, *Picea sitchensis* [Bong.] Carriere. By subjecting branches to weevil attack and then harvesting and extracting RNA a two-fold increase in the monoterpene synthase gene transcripts was observed. This evidence demonstrates a direct link between herbivory and monoterpene production (Mckay et al. 2003). Although the mechanisms are not always the same, these studies suggest that monoterpenes can affect insect herbivores.

Variation in Conifer Monoterpenes

Not only do plants contain and produce monoterpenes for plant defense, the composition of monoterpenes has also been shown to vary in relation to insect herbivory and in response to stresses such as drought or fire. The composition of monoterpenes seems to affect the trees ability to resist insect attack. A study by Cates and Redak (1988) determined that Douglas-fir,

Pseudotsuga menziesii var. *glauca* (Beisn.) Franco, trees differ in their resistance ability.

Douglas-fir trees were found to produce different levels of terpenes and these levels conferred different levels of resistance to western spruce budworm, *Choristoneura occidentalis* Freeman. Trees that were resistant in the first year of the study were retested the second year and most remained resistant, even though the terpenes that conferred the resistance changed between years. The most important components that conferred resistance were the individual terpenoid, the acetate fraction, and the terpene evenness (Cates & Redak 1988). This study also determined that the trees that were susceptible remained susceptible in following years and were not able to switch to resistant modes. Interestingly, preliminary data seemed to indicate that induction of secondary metabolites in Douglas-fir did not take place. Mechanical injury did not produce long-term induction of terpene production.

Studies by Sadof and Grant (1997) also support the work by Cates and Redak (1998). Scotch pine trees, *Pinus sylvestris* L., of resistant and susceptible varieties were exposed to herbivory by the Zimmerman pine moth, *Dioryctria zimmermani* (Grote), and monoterpene responses were measured. The presence of wounding did not change the proportion or ratio of monoterpenes of each variety. This is consistent with many previous studies that demonstrate that mechanical wounding does not change the monoterpene composition. However, the monoterpene composition varied significantly among varieties. Limonene was the only monoterpene that was consistently higher in both resistant varieties. Limonene acts as an oviposition stimulant for at least three members of the pine moth genera. However, for many other herbivores limonene acts as an oviposition deterrent and is toxic to many herbivore species. Therefore, the authors suggest that it may confer resistance against other herbivorous species than the pine moth.

Even though many studies have shown a lack of induced secondary monoterpenes in conifers, there are some studies that do demonstrate a change of terpene composition in response

to herbivory. Monoterpene content in *Pinus caribaea* Morelet needles was found to change after attack by *Atta laevigata* (Smith), leafcutter ants. Newly defoliated pines differed from undefoliated pines in both an increase and decrease of some monoterpenes. Furthermore, four months after defoliation the increases and decreases of monoterpene concentrations were greater than after the initial defoliation. This change was accompanied by the observation that no further signs of defoliation were present after the initial defoliation event. In this system it is possible that changes in terpenes are a direct defense mechanism (Barnola et al. 1994).

Based on the evidence that differences in monoterpenes affect herbivore survival, studies began to examine if herbivores are a selective force on the evolution of monoterpene concentrations. Evidence provided by Sturgeon (1979) suggests that western pine beetle, *Dendroctonus brevicomis* LeConte, predation has caused variation in ponderosa pine, *Pinus ponderosa* Laws., xylem resin. For example limonene, which is toxic to the pine beetle and its fungal symbionts, was found in higher concentrations in areas where pine beetle predation was continuous. Additionally, higher proportions of myrcene (needed for beetle pheromone production) and beta-pinene (the least toxic terpene) were found in populations with more destructive beetle damage. However, Latta and Linhart (1997) provide evidence that herbivores are not a selective force on the evolution of monoterpene concentrations. By examining cone production, resin flow rate, monoterpene composition, and herbivory with multiple regression analysis, they found that resin characteristics were not correlated with herbivory attack. Instead, the pattern between resin characteristics and fitness components suggest that other factors than herbivory are causing the association.

Other factors in addition too herbivory are also known to change plant resin composition. Water stress is one of these important factors that has been studied well. Water stress in trees reduces the resin exudation pressure and thus the rate of resin flow is lowered (Mattson & Haack 1987). Many hypothesized that this event renders the tree more susceptible to herbivores.

Therefore, drought stressed trees should produce more constitutive defenses. This is also in support of the carbon-nutrient balance hypothesis that states that excess carbon not used for growth is allocated for defense. Constitutive defenses were measured after exposing Scots pine, and Norway spruce, *Picea abies* (L.) Karst., to medium and severe drought stress for two growing seasons. Concentrations of total monoterpenes and resin acids were significantly higher in the severely drought stressed trees. More specifically drought increased the concentrations of abietane-type resin acids, which are known to be strongly toxic to wood rotting fungi (Turtola et al. 2003). Studies on loblolly pine, *Pinus taeda* L., have also demonstrated an increase monoterpenes in response to drought stress (Hodges & Lorio 1975). A more recent study by Lombardero et al. (2000) determined that constitutive resin flow was least during periods of rapid tree growth and most under drought conditions. However, not all plant systems fit these exact patterns. Johnson et al. (1997) demonstrated that constitutive defenses in ponderosa pine increased not only in the water stressed plants, but also in the artificially watered plants as compared to the controls (non-watered, non-stressed). Changes in constitutive defenses of water stressed loblolly pines also demonstrated an increase in some monoterpenes and a decrease in others (Gilmore 1977).

In addition to constitutive defenses, inducible defenses also play a major role in herbivore resistance. Significant changes in inducible defenses under drought conditions have been shown to exist in several conifers. Inducible defenses in drought stressed Scots pine exposed to bark beetle-associated fungus were measured two weeks after the exposure to the pathogen. Inducible defenses, including the length and resin quantity, were significantly less in drought stressed trees (Croise & Lieutier 1993). Wagner (1986) found similar results in drought stressed ponderosa pine seedlings that produced significantly lower levels of phenols, needle nitrogen, and tannins than non-stressed seedlings. These findings support theories that stressed plants are unable to produce the level of inducible plant defense that un-stressed plants can produce. Thus, the

previously discussed increase in constitutive defenses in water stressed plants serves an important role to compensate for the reduction in inducible defenses.

Fire is another factor known to change plant resin composition, but has been studied far less. Measurements of resin flow on red pines, *Pinus resinosa* Ait., following a prescribed burn showed a significant increase in resin flow. Other conifers that are a subject to frequent fires also exhibit an increase in resin flow (Santoro et al. 2001). The response of increased resin flow after a fire may be an evolved defensive response due to the increased probability of attack by some bark beetles. Alternatively, the response could be due to the wounding by the fire. Further studies of plant species, historically exposed and not exposed to fire, need to be performed to demonstrate the actual defensive mechanisms.

Insect Detoxification and Adaptations

Many insect herbivores have evolved mechanisms to detoxify toxins they encounter. Herbivores can convert toxins into less toxic chemical compounds, sequester the toxin for its own defense or in some cases secrete the chemical compound. For instance, the weevil, *Oxyops vitiosa* (Pascoe), produces a secretion of terpenoids from its host *Melaleuca quinquenervia* (Cav.). This secretion covers the larval integument and provides defense from generalist predators (Wheeler et al. 2002). A common example of detoxification is in the Lepidopteran family. Larvae contain cytochrome P-450-dependent oxygenases in their guts and are able to convert monoterpenes to more polar metabolites that allows conjugation and excretion. In many cases cytochrome P-450 oxygenase activity is present in low levels, but is induced by ingestion of monoterpenes (Gershenson & Croteau 1991).

Bark beetles in the family Scolytidae and the interaction with their host trees have been studied in detail due to their destructive capacity to bore into trees. Along with their symbiotic fungi, the beetles feed on the cambium of the tree and oviposit under the bark, but it is not clear if bark beetles detoxify the resin they encounter when attacking a tree. It is clear that they use

monoterpenes in chemical host location and selection. Beetles in a certain area will converge upon newly exposed resin. Bark beetles use olfactory, gustatory, and visual signals to locate a suitable host. Once they locate a host, they may begin boring or decide the tree is unsuitable and take flight in search of another host. While the bark beetle is boring into the tree, it may encounter a resin duct and if the resin flow is strong enough the insect will be overcome by the resin and die. This process called “pitching-out” is one of the most important defenses a tree has against bark beetles (Gijzen et al. 1993).

Once a suitable host tree is located, the bark beetle will produce an aggregation pheromone. The aggregation of many beetles over comes the trees defenses and allows successful colonization. Aggregation pheromones are usually derivatives of monoterpenes. *cis*-Verbenol, (+)-ipsdienol and (-)-ipsdienol were the first scolytid aggregation pheromones identified from *Ips paraconfusus* Lanier. *I. paraconfusus* converts the acyclic monoterpene myrcene to either (+) or (-) enantiomer of ipsdienol. In this species (+)-ipsdienol elicits an aggregation response. Interestingly, (-)-ipsdienol elicits the opposite response and signals that the tree has sufficient numbers of individuals and directs colonization towards adjacent trees (Trapp & Croteau 2001). Monoterpene pheromones are also important as sex attractants. This indicates that beetles many have evolved the use of tree defensive compounds into a sophisticated communication system.

Until recently the common belief was that free-living fungal symbionts and beetle gut bacteria converted tree monoterpenes such as alpha-pinene and myrcene to the corresponding pheromones. Studies showed the conversion of labeled monoterpene precursors to the corresponding pheromones (Gijzen et al. 1993). However, a new study by Martin et al. (2003) clearly supports the recent findings of de novo synthesis of ipsdienol and ipsenol. They report the first known monoterpene synthase activity in animals found in the bark beetle *Ips pini* (Say). Furthermore, they reject that the monoterpene synthase enzyme activity is sequestered from the

host tree. A biosynthetic pathway is proposed in which the insect is able to synthesize ipdienol and ipsenol via a mevalonate pathway similar to the pathway previously described in plants. Because the pathways arose through independent functional evolution in plants and animals, they expect further work to reveal that the synthases from plants will be substantially different than those found in animals. This research has exciting implications including the possibilities that other insects possess similar enzymes capable of synthesizing their own pheromones de novo.

Many other insects besides bark beetles respond to monoterpenes emitted from trees. The beetle family Cerambycidae, known as longhorned woodborers are attracted to dead or dying trees. Trees that have been stressed by events such as fire or logging will emit volatile monoterpenes. *Monochamus carolinensis* (Oliver) and *M. titillator* (F.) both responded to a terpentine solution distilled from mixed resins of slash and longleaf pines (Phillips et al. 1988). More specifically, *M. alternatus* Hope demonstrated a strong attractiveness to alpha-pinene, beta-pinene and beta-phellandrene, which are monoterpenes components of pine trees (Ikeda et al. 1980). Several other herbivores such as weevils, are also attracted to monoterpenes emitted from trees (Phillips et al. 1988).

Lastly, monoterpenes emitted from trees not only attract herbivores to the trees, but also attract insect herbivore predators. Induced plant volatiles are known to attract parasitoid wasps and predatory mites (Dicke & van Loon 2000). Simple oxygenated monoterpenes produce long-range attraction of predators such as clerid beetles or *Rhizophagus* predator beetles (Phillips & Croteau 1999). The attraction of predators demonstrates the complexity of plant-herbivore-predator systems.

Until recently experiments examining the tree-beetle-fungus-predator/parasitoid association and the biochemistry of resin formation in conifers have largely been neglected (Gijzen et al. 1993). This neglect is probably due to the vast scope of the topic. The examples presented in this review article clearly demonstrate many interactions take place between

herbivores, environmental conditions and plant resin formation. Furthermore, the plant resin formation plays a direct role in host selection and predator attraction. By understanding these interactions exciting possibilities exist for genetic manipulation of resin composition. For example, it may be possible to increase the levels of resin compounds toxic to invaders by recombinant DNA methods (Gijzen et al. 1993). Whatever the outcome, future studies will no doubt bring a better understanding to the mechanisms of resin production and regulation that confer susceptibility and resistance in conifers.

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