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Chapter 18

Leaves as Islands of Spatial and Temporal Variation: Consequences for Plant Herbivores, Pathogens, Communities and Ecosystems

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Introduction

From an evolutionary perspective there is a major conundrum in understanding how long-lived plants can cope with their rapidly evolving pests and pathogens. In agriculture, it has been well established that monocultures in space are susceptible to rapidly evolving pests. The same logic applies to long-lived plants, as they are essentially monocultures in time. Plants that form large clones are especially important to consider as they may be exposed in both space and time. The obvious answer to this conundrum is that long-lived plants are not monocultures; an individual tree or clone is effectively a polyculture of leaf islands in time and space. Just as polycultures in agriculture create severe evolutionary problems for pests and pathogens, so would variation within individual plants make it more difficult for their pests and pathogens to ecologically and evolutionarily track their long-lived hosts. Although this logic is not new (see reviews by Whitham, 1981; 1983; Whitham et al., 1984), advances in techniques and newer studies have greatly advanced our understanding of both the mechanistic origins of variation within plants and its ecological consequences. Throughout this chapter, we argue that the variation one finds within an individual plant or genet (i.e. the genetic individual derived from sexual reproduction) can be as great as the variation one finds between different genets in the population. Although such variation appears to contradict the view that plants are uniform throughout (i.e., the daughter cells of somatically derived divisions are identical), the fields of developmental biology and embryology are based upon differential gene expression, which causes different tissues to perform different functions. Thus, it should be expected that individual plants represent highly variable resources for pests and pathogens, and that enhanced variation could be evolutionarily favored if it confers greater resistance to important agents of selection.

Plants exhibit ecologically important variation at all levels; they differ within a leaf, among leaves, among shoots, among branches, and among ramets or sexually derived plants of the same clone. This variation is caused by diverse processes, such as development (i.e., ontogenetic and physiological aging; Diggle and Endress, 1999), induction (i.e., pest induced responses; Karban and Baldwin, 1997), phyllotaxy and sink-source relationships (e.g., Jones et al., 1993; Larson and Whitham, 1997), somatic mutations (e.g., Gill et al., 1995), and/or modular structure (Andrews, 1998). These processes can then interact with the environment to produce variation within genets that
can be as great as the variation among genets. Here we explore both the mechanisms and the ecological consequences of this variation.

Resource quality between and among leaves on an individual plant is due to natural levels of variation in both primary nutrients and secondary compounds, which is further enhanced by pest-induced compounds. Variation in carbon and nitrogen partitioning is partly controlled by genetics and partly controlled by source-sink dynamics, a very plastic mechanism that allows for much heterogeneity within a plant module (Schlichting, 1986; DeKroon and Hutchings, 1995). Since Denno and McClure’s (1983) “Variable plants and herbivores in natural and managed systems”, considerable work has been done in this area documenting examples of natural variation between leaves of different age, plant development, growth rate and environmental variables such as shading (Whitham et al., 1984; Coley, 1988a; Bowers and Stamp, 1992; Basey and Jenkins, 1993; Winn, 1996; Nilsson et al., 1998; Crone and Jones, 1999). Recent studies further illustrate that leaves may vary in N and other primary compounds as well as defensive or resistance traits such as phenolics, terpenes and other secondary compounds (Haukioja et al., 1991; Bingaman and Hart, 1993; Berenbaum, 1994a; Waits et al., 1995b). The resultant mosaics in leaf quality created by these factors are hypothesized to reduce the success of herbivores and pathogens, which may lead to increased fitness of individual plants (Whitham et al., 1984; Edwards et al., 1990; Stockhoff, 1993; Suomela and Ayres, 1994).

Induced variation in response to pathogen attack or feeding by herbivores, acts to further increase the variation within an individual plant. The rate, specificity, duration and timing of induced responses may introduce more variation into leaves because the formation of secondary compounds is very species and herbivore specific (Honkanen and Haukioja, 1994; Stout et al., 1996; Kaitaniemi et al., 1998; Agrawal et al., 1999a; Agrawal, 2000). Phytochemical induction by pathogens and herbivores shows a range of responses at the leaf, branch and clone level (see comprehensive reviews in Tallamy and Raupp, 1991; Karban and Baldwin, 1997; Agrawal et al., 1999b). Together, variation in constitutive and induced chemical responses, act to create a very heterogeneous environment of “islands” within individual trees.

Although there are numerous mechanisms that cause plants to become mosaics in space and time, here we focus on two mechanisms that have received more recent attention, plant development and induction. We examine how these mechanisms affect the distributions and performance of plant pests and then go on to explore their community and ecosystem-level consequences. Recent advances suggest that within-plant variation can have important consequences, such as affecting keystone species, trophic interactions, leaf litter decomposition and nutrient cycling (Findlay et al., 1996; Waltz and Whitham, 1997).

Plant Development

Developmental processes in plants, which are defined as ordered, directional changes in shoot behavior, can be generalized into two broad categories, ontogenetic and physiological or environmental (e.g., Lawson and Poethig, 1995). Ontogenetic changes arise from changes in gene expression in plant meristems (e.g., genes are turned on or off; Poethig, 1990). For example, heteroblasty commonly refers to changes in vegetative structures across whole plant gradients (Jones, 1999). Such changes can be quite striking. In the Eucalyptus risdonii-E. tenuifolius hybrid complex, adult leaves produced in the upper canopy are lanceolate and alternate, whereas the juvenile leaves at the base of the
tree are opposite and connate (Wiltshire et al., 1998). These leaves are so strikingly different that they appear to be from different species. Rather than a gradual shift in leaf morphology with height, there can be an abrupt shift in leaf types over just a few centimeters. Importantly, experimental crosses and heritability studies show that the height and age of this shift in leaf morphology is under strong genetic control (Wiltshire et al., 1998). Because these morphological traits and their associated physiological and biochemical attributes are genetically based, they are likely to be subject to natural selection and have important evolutionary consequences.

In contrast to ontogenetic processes, physiological caused changes can result from alteration in the meristem environment by shading, water and nutrient relations and other factors associated with the local environment of shoots. Such environmental factors can produce morphological variation within a single plant (e.g., sun and shade leaves or leaves in the canopy being morphologically different because the leaves of the canopy are under greater water stress than leaves at the base of the tree).

An important distinction between these two developmental processes is that with asexual propagation (i.e., cuttings taken from different portions of a plant), the ontogenetic traits tend to remain stable, whereas traits derived from physiological changes do not. For example, Zagory and Libby (1985) found that mature radiata pine, *Pinus radiata*, is resistant to western gall rust, *Endocronartium harknessii*, whereas, juvenile trees are susceptible. They first established that hedged or pruned donor trees expressed juvenile traits, whereas non-hedged donors expressed mature traits. By collecting cuttings from hedged and non-hedged donors of the same clone, they could hold genotype and chronological age constant and examine how differences in juvenile and mature traits affected resistance to western gall rust. These derivative clones were then planted near heavily infected trees. They found that the clones derived from mature donors were approximately twice as resistant to western gall rust than those derived from juvenile donors. Importantly, these differences in resistance traits of clones derived from juvenile and mature tissues remained stable over 7 years of study and led the authors to conclude that the differences were ontogenetically based rather than physiologically based. This study emphasizes how different portions of the same plant can express islands of different phenotypes, which affect the distribution and performance of a major pathogen.

Likewise, both ontogenetic and environmental processes can be acting within the same plant. Cavender-Bares and Bazzaz (2000) used common garden studies of seedlings, juvenile and mature red oak, *Quercus rubra*, to separate the environmental and ontogenetic components of drought responses. Their experiment demonstrated that the difference in photosynthetic capacity between seedlings and mature trees was ~50% due to an environmental component and ~50% due to an ontogenetic component. Another example showing mixed contributions of plant ontogeny and environment is by Winn (1996), who showed significant additive genetic variation for within-individual variation in leaf traits of the annual plant, *Dicerandra linearifolia*. Thus, some plants are programmed to be more variable than others and the trait is heritable.

Both ontogenetic and physiological processes work in ways that cause modules further from the root crown to express more mature phenotypes (Poethig, 1990). For example, Kearsley and Whitham (1998) showed that with increasing distance from the base of narrowleaf cottonwoods to their upper canopy, leaf morphology and reproduction were greatly altered. Lower branches produced small leaves and were not reproductive,
whereas, upper branches produced large leaves and were highly reproductive. Furthermore, defensive chemistry varied predictably over the developmental gradient. Analyses showed that relative to leaves expressing juvenile traits at the base of the tree, mature leaves in the canopy contained 43% higher concentrations of condensed tannins and 72% lower concentrations of phenolic glycosides (Whitham et al., unpub. data). Such differences among modules of the same plant have been quantified in other systems. For example, Suomela and Ayers (1994) showed that the within-tree variation could equal the between-tree variation in chemical and physical traits of mountain birch, *Betula pubescens*. In a hierarchical analysis, they found that within-tree variation (i.e., different ramets, branches or shoots of the same genet) accounted for 40 to 44% of the total variance in traits measured. In contrast, between-tree variation (i.e., among genets) accounted for 12 to 64% of the total variance. For specific traits of water content and toughness, within-tree variation was actually greater than between-tree variation.

This developmental variation within individual plants can have a great effect on diverse organisms. For example, Karban and Thaler (1999) found that spider mites, *Tetranychus urticae*, performed very differently on cotton leaves expressing different developmental stages and similar patterns have been observed with the pathogen, *Colletotrichum graminicola*, on corn (Leonard and Thompson, 1976). Figure 1 shows that the gall aphid, *Pemphigus betae*, is ~100 times more abundant on leaves expressing mature traits than on leaves expressing juvenile traits of narrowleaf cottonwood, *Populus angustifolia*. Transfer experiments showed that aphid preference for mature leaves in the upper canopy is closely associated with performance; aphids realized 80% greater reproduction on mature leaves than on juvenile leaves (Kearsley and Whitham, 1998). Although these aphids prefer mature leaves, other insects exhibit equally strong preferences for juvenile leaves that are associated with their increased performance on juvenile leaves (*ibid.*). Importantly, the island mosaic results in only a portion of the leaves of a tree being available to any one herbivore.

Having demonstrated these developmental patterns, a major question remains. Are they ontogenetic (i.e., turning on and off of genes) or physiological (i.e., environmental based, not genetic)? To answer this question, we tested whether or not the traits were stable. Dormant cuttings from 4 different clones were collected from the trunk at different heights and developmental zones (i.e., <1.5m in height, 2 to 4m and 4.5 to 7m) and rooted in the greenhouse. In the spring, one year later when the stocklings were 1.5m tall, they were randomly planted out in a common garden and grown for two more years. At the beginning of the 4th growing season, colonizing aphids were transferred onto each of the stocklings and their survival, fecundity, and expected fitness recorded. We found that aphid survivorship averaged ~60% higher on stocklings derived from 4.5 to 7m on the tree relative to those collected from <1.5m in height, and those collected from intermediate heights had intermediate survival (Kearsley and Whitham, unpub. data). These results supported the hypothesis that plant ontogeny rather than physiological processes have a major influence on aphid performance.

Not only does plant ontogeny result in different portions of a plant expressing different traits, there is great variation among trees in the expression of these traits. Figure 2 shows aphid survival on the juvenile and mature zones of 12 different genets in which the juvenile and mature zones of each genet are connected by a solid line. Note that the slope and intercepts of aphid survival vary greatly from one genet to another. This suggests that plant ontogeny is being expressed differently in different genets.
Zagory and Libby (1985) found similar intra-genet effects in their studies of ontogeny and genotype effects of western gall rust on radiata pine.

Figure 1 shows that the gall aphid, *Pemphigus betae*, on narrowleaf cottonwood, *Populus angustifolia*, is ~100 times more abundant on trees and leaves expressing mature traits than on trees and leaves expressing juvenile traits. A tree <1.5 m tall produces only juvenile leaves and is rarely attacked by gall aphids. However, trees >10 m in height produce mature leaves in the upper canopy that are heavily attacked, whereas juvenile leaves at the base of the tree are only lightly attacked. Trees of intermediate height (i.e., 2 to 5 m) can express juvenile only traits or may have recently shifted to become reproductively mature in their upper canopy (adapted from Kearsley and Whitham, 1989).

While the above studies have emphasized how developmental variation affects insects, vertebrates are also affected. Bryant et al. (1992) argued that the juvenile growth of plants were most likely to suffer from herbivory and should be more heavily defended than mature growth. In support of this hypothesis, they found that papyriferic acid and salicylaldehyde were much more abundant in the juvenile growth of Alaska paper birch, *Betula resinifera*, and balsam poplar, *Populus balsamifera*, respectively, than in mature growth. Because these secondary compounds effectively deter feeding by a major herbivore (snowshoe hare, *Lepus americanus*), and show their greatest concentrations in regions of North America where hares and their forage plants have a long evolutionary history, Bryant et al. (1994) argued that the increased defenses of the juvenile zone has been selected by mammals. In their review, Bryant et al. (1992) argued that similar effects of plant development affect the feeding of diverse vertebrates including microtine rodents, deer, moose and elephants.
Figure 2 shows aphid survival differs greatly in the juvenile and mature zones of 12 different genets of *Populus angustifolia* (the juvenile and mature zones of each genet are connected by a solid line, adapted from Kearsley and Whitham, 1998). For each genet, aphid survival is generally much greater in the mature zone than in the juvenile zone. There is also great variation among genets in which some are more susceptible than others and the trajectories (i.e., the differences between juvenile and mature zones) differ greatly. Such variation results in aphids encountering a mosaic of habitat qualities both within and among genets.

Although the effects of developmental variation on plant-animal interactions are under-studied, the fact that the developmental variation within a plant can be as great as the variation among genets in the population suggests that much more research is needed to understand the mechanisms and consequences of this process.

**Induction**

Many plants are known to exhibit changes in nutrient quality, chemical defenses, phenology, morphology and other traits following pest or pathogen attack (Karban and Baldwin, 1997; Pennazio and Roggero, 1998; Tollrian and Harvell, 1999). Induction of defensive compounds commonly occurs after pest attack, and can have both short and long-term impacts on leaf chemistry which can structure insect communities on both live and senesced leaves (Schultz and Baldwin, 1982; Baldwin, 1988; Choudhury, 1988; Karban and Baldwin, 1997). Alterations in plant morphology and phenology are other mechanisms that allow plants to reduce the impact of herbivores and pathogens by allowing plants to “cut their losses”. Variation in the strength of these responses is commonly recognized and is hypothesized to have important ecological and evolutionary implications for plants as it allows plants to be “moving targets” in space and time.
(Haukioja, 1990; Hartley and Lawton, 1991; Berenbaum, 1995b; Karban and Baldwin, 1997). Qualitative and spatial variation in induced responses creates island mosaics within a plant that may lessen the damage by future pests (Coley, 1988b; Stout et al., 1996; Agrawal, 2000).

An example of how induction creates island mosaics is illustrated by the gall-forming aphid, *Pemphigus betae* (Williams and Whitham, 1986). When these aphids colonize the leaves of narrowleaf cottonwood, *Populus angustifolia*, premature leaf abscission is often triggered. Galloled leaves are selectively dropped before they mature and the average tree loses 25% of its parasite load. The effectiveness of the premature leaf abscission response depends upon two major factors. Galls on small leaves are much more likely to be abscised than large leaves, and leaves with multiple galls are much more likely to be abscised than leaves with single galls. Because large leaves are relatively rare, the combination of these two factors forces aphids to pile up on large leaves where they will then trigger the induced response of the host plant. For example, Williams and Whitham (1986) found that a leaf with 4 galls had a 54% chance of being abscised, whereas a leaf with only one gall had a 10% chance of being dropped. Because leaves with no gall had only a 2% probability of being dropped, these data show that abscission was highly selective and that the plant could selectively drop unproductive leaves.

Within-plant variation in this induced response may be the single most important factor in the evolution of territoriality in these aphids; sharing leaves with other aphids is almost certain to trigger the induced premature leaf drop which will kill all the aphid colonies on those leaves. Such territorial behavior would not likely have evolved if all the leaves of a plant were uniform in quality. It is important to consider how variation within plants in resource quality has affected the evolution of behaviors in their pest organisms that can potentially be manipulated by the host plant to its own benefit.

Mammalian herbivory can also induce changes in leaf tissue quality within a single genet that can impact associated community members. Martinsen et al. (1998) showed that the leaf-feeding beetle, *Chrysomela confluens*, is strongly associated with beavers (Figure 3); as the density of beaver-felled trees increases, so does the density of beetles. This surprising association is caused by the variation in resource quality among ramets of the same clone that results from beavers felling some ramets, but not others. When a beaver fells a tree, it generally does not kill the tree as it often resprouts from the stump or from its roots. This resprout growth is approximately two times higher in phenolic glycosides than foliage from undamaged ramets in the same clone. Although phenolic glycosides play a defensive role against many herbivores, for this specialized insect, the plant defense is an attractant and the beetle sequesters the phenolic glycosides into their own defensive system (Pasteels et al., 1983). Thus, beaver felling of some ramets but not others of the same clone creates a mosaic of varying tissue quality that greatly affects the distribution of this common insect.

In addition to organisms such as beavers inducing chemical responses in leaves, herbivores must also contend with variable patterns of induction that are caused by the host plant's phyllotaxy or the patterns of vascular connections between leaves. Jones et al. (1993) showed that patterns of vascular connections greatly affect the magnitude of the systemically induced host response. First, they demonstrated that induction was a factor in this system. The tip of an eastern cottonwood leaf, *Populus deltoides*, was damaged and then undamaged portions of the leaf were fed to adult *Plagiodera versicolora* at different time intervals after the leaf was initially damaged. Relative to control leaves, they found that beetles were detered from feeding on previously damaged
leaves. This argues that beetle feeding triggers a locally induced response that creates an island of increased defense that negatively affects subsequent feeding.

![Graph showing number of beetle larvae clutches vs. number of tree stumps per 4 m diameter plot.](image)

Figure 3 shows how a keystone herbivore, beaver (*Castor canadensis*) can create variation within a clone, which greatly affects the distribution of the leaf-feeding beetle, *Chrysomela confluens*. When beavers fell a tree, resprout growth from the stump and roots is much higher in phenolic glycosides than leaves from control trees. Because these beetles sequester their defenses from their host trees, this beetle is positively associated with beavers (adapted from Martinsen et al., 1998).

Having shown that leaf damage induces a defensive response, they then examined the role of phyllotaxy in affecting the patterns of induction. Because induction often involves changes in plant defensive chemistry that are mobilized through the vascular system, it is important to know how the leaves of plants are connected. Because of the anatomy research of Dickson and Isebrands (1991), we know how the vascular traces are interconnected among leaves of a cottonwood shoot. When the leaves from the youngest to the oldest leaves on a stem are counted, their studies show that adjacent leaves are not as intimately connected as leaves farther apart (see Figure 4). For example, the vascular connections between leaves #5 and #10 are stronger than the vascular connections between adjacent leaves #5 and #4. Similarly, the vascular connections between leaves #6 and #11 are stronger than the vascular connections between adjacent leaves #6 and #5.

Because of the patterns of vascular connections, Jones et al. (1993) predicted that if induction is important in this system, damage to leaf #5 should show a stronger induction response in leaf #10 than in leaves #6 or #9. This was shown to be the case. More distally, but directly connected leaves exhibited a stronger induced response than adjacent, but less directly connected leaves. When the reverse experiment was performed,
they found that the pattern was bi-directional. This example demonstrates that phyllotaxy can play a major role in creating leaf islands for other colonizing herbivores.

The effects of induction have the potential to be long-term and transferred from one generation to the next. Agrawal et al. (1999a) examined transgenerational induction of the wild radish, *Raphanus raphanistrum*, in response to damage caused by caterpillars of *Pieris rapae*. Relative to control plants, induced plants produced 10x higher concentrations of indole glucosinolates (mustard oil glycosides) and 30% higher densities of setose trichomes on newly formed leaves. After induction, these plants suffered 50% less chewing damage and had 60% higher lifetime seed production than control plants that had not been induced.

![Adapted from Dickson & Isebrands 1991](image)

Figure 4 shows that the patterns of vascular connections among leaves vary predictably in which adjacent leaves (e.g., LPI 4 and LPI 5) share fewer vascular connections than leaves farther apart that share direct vascular connections (e.g., LPI 5 and LPI 10; adapted from Dickson and Isebrands, 1991). These patterns have been shown to affect systemically induced defenses to produce islands of variable leaf quality on the same shoot (Jones et al., 1993).

Feeding by caterpillars not only induced a chemical defense in the damaged plant, but also caused attacked plants to produce offspring that were better defended than offspring from unthreatened parents. To examine the consequences of herbivory for the next generation, they grew induced and unmanipulated control plants, and then collected seeds from both groups. No differences in carbon or nitrogen between the seeds of either group were detected. However, the seeds from induced plants were higher than the controls in some defensive glucosinolates. Seeds germinated from both groups were exposed to caterpillars. Caterpillars gained 20% less weight on seedlings from induced parents than
when raised on seedlings from the controls (Figure 5). Thus, induction of plant defenses can persist in the progeny of induced plants, but the mechanisms of transgenerational induction are not known.

![Bar graph showing caterpillar mass (mg) for Control and Herbivory conditions.](image)

**Maternal environment**

Figure 5 shows transgenerational induction in which caterpillar feeding on wild radish, *Raphanus raphanistrum*, induces high levels of induced defenses in the offspring (adapted from Agrawal et al., 1999a). Caterpillars fed on seedlings from undamaged maternal controls were significantly heavier than caterpillars fed on seedlings produced by maternal plants that had been damaged.

In summary, these few examples illustrate how induction can operate across space and time to affect resource quality within individual plants or clones. The following section examines how such variation affects the distribution of common and/or keystone herbivores and may structure entire communities.

**Community-Level Consequences**

Although few studies have examined the community-level consequences of plant development and induction, the few studies conducted to date suggest that these impacts are significant and are likely to be widespread. The community consequences are likely to be most important when plant development and/or induction affects the abundance and distribution of a keystone species. Relative to their abundances, keystone species have large impacts on communities (Power et al., 1996). Examples of the impacts of keystone species include predators whose removal from a system alters the density of prey, thus affecting a wide array of species (Paine, 1966; Bond, 1993; Mills et al., 1993), and herbivores that alter the condition of plant resources, thereby affecting other herbivores (Hunter, 1992; Bond, 1993). Some species are also considered to be ecosystem engineers due to their modifications of the environment that affect other species (Jones et al., 1994; 1997). Dam building beavers (Naiman et al., 1986), and gall-forming insects (Martinsen et al., 2000) exemplify some of the extremes in taxa that have such impacts on communities.

At the individual shoot level, some herbivores create islands of habitat that affect many other species. For example, Martinsen et al., (2000) found that the habitat created
by the leafroller, *Anacampsis niveopulvella*, supported 4 times more species of arthropods that reached 7 times greater abundance than adjacent shoots that had no leaf rolls (Figure 6). Thus, on a very local scale of adjacent shoots of the same branches, the rolled leaves created by this insect resulted in islands of increased biodiversity. Even different guilds of arthropods showed positive responses to rolled leaves. Shoots with leaf rolls contained 7 times as many species of predators and 17 times as many predators as adjacent shoots without leaf rolls. Similarly, shoots with leaf rolls contained 4 times as many species of herbivores and 7 times as many herbivores as shoots without leaf rolls.

Other experiments showed that many of these organisms are attracted to leaf rolls for the shelter they provide. When artificial leaf rolls were constructed, both species richness and abundance increased ~2 fold. This result argues that this shelter-building Lepidoptera is actually an “ecosystem engineer” because the leaf roll that it constructs modifies the habitat to affect the distributions of diverse species. Because adjacent shoots with and without leaf rolls have different associated communities, this example clearly demonstrates how a single insect can create habitat islands within a single host plant that subsequently affects the rest of the community. The fact that many common plant pests and pathogens are not uniformly distributed across their hosts increases the probability that they will alter their local host environment in ways that affect other species.

![Graph showing species richness and abundance](image)

Figure 6 shows that the leaf-rolling Lepidopteran, *Anacampsis niveopulvella*, creates sheltered islands of habitat that result in increased local biodiversity (adapted from Martinsen et al., 2000). Shoots with leaf rolls supported 4 times more species and 7 times greater abundances of arthropods than adjacent shoots without leaf rolls. Both predators and other herbivores were affected.

Although the above study did not examine how plant development, induction or any of the other mechanisms that cause within-plant variation might have affected the
distribution of leaf rollers, if this additional tie had been made, then the resulting island mosaic could have been much more complex. We are aware of only one study in which this chain of interactions has been established (Waltz and Whitham, 1997). We have found that the gall-producing aphid, *Pemphigus betae*, is largely restricted to the adult leaves in the upper canopy of cottonwood trees (*Populus fremontii, P. angustifolia,* and their natural hybrids) and the leaf-feeding beetle, *Chrysomela confluentes*, is largely restricted to the juvenile leaves at the base of the tree and to juvenile suckers that sprout from the roots. Because plant development affects the distributions of these two insects, we hypothesized that the impacts of plant development on these two putative keystone herbivores would result in the mature zone in the upper canopy of trees having a different arthropod community than the juvenile zone at the base of trees or the juvenile suckers that had sprouted from the roots. As a test of the indirect effects of plant development on community structure, aphids were experimentally removed from mature zones of trees where they are most abundant, and beetles were experimentally removed from juvenile zones of trees where they predominate.

In comparison with their respective controls, the presence of each insect had a dramatic, but opposite, impact on biodiversity. Aphid removal decreased species richness and relative abundance by 32% and 55%, respectively in mature zones, whereas beetle removal increased species richness and relative abundance by 120% and 75%, respectively in juvenile zones. These opposite results are probably due to the different feeding modes and lifestyles of these two insects. Leaf beetles defoliate and destroy the ability of cottonwoods to support other leaf-feeding herbivores. For example, Lepidopteran miners were completely eliminated, and leafhoppers (Cicadellidae), Lepidopteran leaf rollers and Hymenopteran leaf folders were reduced to 1/3rd their normal levels. Also, these beetles are chemically defended by salicylaldehyde, so they generally attract fewer predators and parasites (Kearsley and Whitham, 1992). In contrast with the beetles, phloem-feeding aphids do not defoliate trees and are not chemically defended. These aphids also attract diverse predators and parasites that range from birds to wasps, and they apparently modify the host plant in ways that attract other herbivores. For example, when gall aphids were removed, leaf rollers completely disappeared, and leafhoppers and leaf folders declined by half. Because the arthropod community of this study consisted of 42 taxa (herbivores, predators, parasites) from 8 arthropod orders, these removal experiments illustrate community-wide responses. Even vertebrates and fungi were affected by the presence of aphids (Dickson and Whitham, 1996). With the experimental removal of aphids, the foraging of Black-capped Chickadees, which open galls and consume the aphid colony, declined three fold. Similarly, the mold, *Cladosporium cladosporioides*, which lives on the honeydew and may kill the entire aphid colony, declined two fold.

In combining the above studies we found that the interaction of developmental variation and induction subsequently affect the distributions of many other species and the greater habitat complexity brought about by within-plant variation ultimately supports greater biodiversity. Developmental variation results in aphids being found in the mature zone of cottonwoods and beetles being found in the juvenile zone. Induced impacts of beavers trigger resprout growth after trees are felled, which results in aphids being found on mature ramets and beetles being found on juvenile resprout growth. Because the distributions of these two keystone insects are determined by plant development and induction, the rest of the community is also affected and overall biodiversity is greatest when both are present. These results show that plant development and induction have both direct and indirect impacts on species, communities and biodiversity.
We believe that such chains of interactions are just the beginning of even larger community-wide interactions. For example, the impacts of plant development on gall aphids should also affect the distribution and abundance of the microbial community of the phyllosphere. Stadler and Muller (2000) found that the honeydew excreted by aphids had a pronounced effect on epiphytic microorganisms. Bacteria, yeasts and other fungi always thrived better on spruce, beech and oak in the presence of honeydew producing aphids than in their absence. Such studies argue that we are only beginning to appreciate the complexity of interactions that occur due to within-plant variation, the effects of which are likely to ripple through communities to have potentially important ecosystem consequences.

Ecosystem-Level Consequences

Variation in leaf chemical traits due to ontogeny, induction or environment affect leaf litter quality, which can then affect leaf litter decomposition, nutrient retention and nutrient cycling at both the individual tree and stand levels. Because carbon to nitrogen ratios and secondary compounds influence the rate of leaf litter colonization by the microbial community and subsequent decomposition, within-plant variation in leaf quality and phenology can enhance or delay rates of decay and nutrient release. At a population or stand level, plants that exhibit high variation in litter quality, due either to natural or pest-induced variation, could contribute to nutrient mosaics in the rhizosphere by altering rates of decomposition and mineralization. Nutrient mosaics in the rhizosphere could have important implications for site productivity and feedback to the community composition as a whole. In this section we first review some of the general literature on the importance of leaf litter and variation in litter quality in ecosystem processing. We then describe how plant development and pest-induced variation in leaf litter quality can create mosaics on the forest floor using Populus as a model system.

Variation in the quality of leaf tissue can alter ecosystem-level processes such as leaf litter decomposition, nitrification, mineralization and nutrient release (e.g., Rice and Pancholy, 1973; Lindroth et al., 1993; Lindroth and Huang, 1996; Harborne, 1997; Scott and Binkley, 1997). Plant phenolics, especially tannins, have been shown to inhibit litter decomposition by reducing litter palatability to decomposers and by rendering enzymes inactive (Benoit and Starkey, 1968; Harrison, 1971; Horner et al., 1988; Northup et al., 1995; Aerts and Caluwe, 1997; Hattenschwiler and Vitousek, 2000). For example, condensed tannins in leaf litter explain ~65% of the variation in decomposition in cottonwoods (Populus fremontii, P. angustifolia and their natural hybrids; Driese and Whitham, 2000). Other studies have also found negative relationships between plant phenolics and both decomposition and rate of nitrogen release, indicating that litter quality measures (specifically plant phenolics) can be important predictors of ecosystem-level processes (Nicolai, 1988; Palm and Sanchez, 1991; Northup et al., 1995; Aerts and Caluwe, 1997). For example, Northup et al. (1995) found that polyphenols in pine litter control the rate of nitrogen loss by binding with the nitrogen to form protein-tannin complexes in the soil. These complexes effectively immobilize the nitrogen into a form that is utilized almost exclusively by the plant's mycorrhiza, whose rapid uptake minimizes losses that would otherwise occur due to leaching. Furthermore, the feedback between leaf litter and soil processes is commonly recognized and may be more important to leaf litter decomposition than climate in many systems (Scott and Binkley, 1997), indicating that variation in litter quality traits within a site could impact the rate of turnover and the retention of plant available nutrients at both local and larger scales.
Because high quality litter (i.e., low C:N and low levels of secondary compounds) rapidly decomposes, while poor quality litter (i.e., high C:N and high levels of secondary compounds) has slow decay rates and mineralization (Hobbie, 1992; Couteaux et al., 1995; Scott and Binkley, 1997; Hattenschwiler and Vitousek, 2000), we hypothesize that soil nutrient mosaics, under and adjacent to the plant, are related to within-plant variation in litter quality. Specifically, plants with high variation in litter quality originating from the mosaic of leaf islands caused by (plant development, induction, phenology, or environmental variation), would have the effect of extending decomposition and nutrient release, because high quality litter would decompose rapidly while the more recalcitrant litter would decay more slowly. Variation in microbial immobilization of the mixture of decaying litter could extend the time of nutrient release and create resource islands in the rhizosphere, possibly reducing nutrient loss from the system (Blair et al., 1990). Likewise, plants with low variation in leaf traits would have more specific patterns of nutrient release (i.e., slow or fast). Therefore, on a local level, soil nutrients are a reflection of the variation within the overhead canopy, because the recycling of nutrients from trees to the rhizosphere via leaf litter is the primary source of internal cycling in many systems (Hobbie, 1992; Finzi et al., 1998; Scott, 1998).

The “after-life” effects of herbivory on leaf litter quality are seldom factored into the models of herbivores and energy flow, but may represent an important mechanism for nutrient turnover in many systems (Loreau, 1995; Findlay et al. 1996; Grime et al., 1996; Pastor and Cohen, 1997). As we demonstrated in earlier sections, the concentration of secondary compounds can be induced by pathogens and herbivores at the individual leaf level (Zucker, 1982; Taper and Case, 1987; Orians and Fritz, 1995). Because herbivory can trigger increased phenolics and can reduce or bind up nitrogen, induced defenses that are retained in leaf litter may have the opposite effect of greenfall and herbivore waste products. Reduced litter quality slows nutrient release, which promotes greater uptake by plants and reduced nutrient loss from the system (Lodge et al., 1994; Loreau, 1995; Pastor and Cohen, 1997).

Induced defenses, retained in the leaf litter, can impact decomposition and provide a link between aboveground and belowground processes mediated through leaf litter quality. A recent survey of chemical defense and leaf litter decomposition for 54 plant species revealed a negative relationship between level of anti-herbivore defense and rate of leaf decay (Grime et al., 1996). Similarly, Findlay et al., (1996) found that leaf litter that had been damaged by mites and/or ozone, decomposed at rates ~50% slower than controls. They attributed this slower rate of decomposition to induced polyphenols in the living leaves that were retained with senescence, which effectively bound up the nitrogen in leaf litter making it unavailable to decomposers (Figure 7). In our studies, we found that leaves galled by P. beta have nearly 7 times the amount of condensed tannins in the leaf litter than non-galled leaves from the same tree. This variation in leaf litter quality translates into a 40% reduction in decomposition on the forest floor for galled litter compared to non-galled leaf litter (Schweitzer and Whitham, unpub. data). These examples demonstrate that variation in leaf resource traits can be carried over to the leaf litter to affect decomposition and the rate of nutrient release.

Variation within and between plants in their litter traits at any given site could help explain the nutrient heterogeneity of soils. Because plants vary in their physiological activity depending on the local environment as well as their genetic programming (e.g., resistance and susceptibility to herbivory), different plants of the same species can exhibit large variation in leaf/litter quality (Adler et al., 1995; Hemming and Lindroth, 1995;
Lindroth and Hwang, 1996). At a stand level, trees having low and high variation in leaf/litter traits could create a forest floor with "hot spots" of plant available nutrients immediately adjacent to patches with low nutrients.

![Bar graph showing % Bound Phenolics](image)

Figure 7 shows that ecosystem-level processes can be affected by local induction. Leaves that have been damaged by either pollution (i.e., ozone) or herbivorous mites produced higher concentrations of induced polyphenols than control leaves. Because decomposition is closely tied to the concentrations of polyphenols in leaf litter, the induced effects of either mites and/or ozone resulted in ~50% slower decomposition than controls (adapted from Findlay et al., 1996).

To illustrate the above points we will demonstrate how within-plant variation in *Populus* leaf traits, due to plant development and induction, can translate to variation in ecosystem-level processes through variation in decomposition. First, analyses of cottonwood leaf chemical traits in a common garden have shown that plant development affects leaf quality. Condensed tannins in mature foliage are, on average, 41% higher than juvenile foliage on the same tree. Thus, independent of herbivory, *Populus* naturally produces at least two types of leaves that differ in their secondary chemistry, creating two distinct types of leaf litter.

Second, overlaid upon the developmental variation in leaf chemistry, herbivores interact with the host plant to induce further variation in leaf litter that affects decomposition. Cottonwoods exhibit great variation in genetic resistance to the gall-forming aphid, *P. betae* (Whitham, 1989; Paige and Capman, 1993). Because 70% of the leaves on a susceptible tree can have at least one gall (Whitham, 1989) and galls induce high levels of condensed tannins in leaves, its presence on susceptible trees further expands the range of litter types under these trees. For example, in aphid susceptible trees, galled leaves have much higher levels of condensed tannins than non-galled leaves and decompose at much slower rates (Schweitzer unpub. data). Both aphid-resistant and aphid-susceptible tree types can occur side-by-side in the field so that a tree with high variation in leaf litter traits (i.e., aphid susceptible) can grow adjacent to a tree with
relatively low variation in leaf litter traits (i.e., aphid resistant). The effect of herbivory alone results in a 22% difference in mean residence time (MRT) of galled and non-galled leaves on the forest floor, because galled leaf litter decomposes much more slowly (Schweitzer unpub. data). Differences in MRT within a site are good predictors of how palatable the litter is to the decomposer community and indicates the rate of soil humus formation (Waring and Running, 1998).

The net result of the variation caused by plant development and induction is that a susceptible tree has a wider range of litter decay and nutrient release rates than a resistant tree. For example, an aphid resistant tree can produce leaf litter that varies three-fold in polyphenol concentrations based on the variation of juvenile foliage and mature foliage. In contrast, aphid susceptible trees can produce leaf litter that varies six-fold due to the presence of juvenile and mature foliage as well as having both galled and ungalled leaf litter. From our previous studies we estimate that differences in the range of variation can result in a 20 to 40% difference in rates of decomposition within a site for resistant and susceptible trees, respectively. Because of this range of variation we predict that the mosaic of leaf/litter traits within a tree can then be reflected in the rhizosphere, creating patches of nutrient availability at the stand level due to variation in mineralization. Nutrient mosaics due to within-tree variation in leaf litter quality could be one mechanism for variation in growth rates and productivity of trees within a single stand.

Future work on the consequences of within-tree variation on nutrient turnover should focus on the rhizosphere response to variation in litter decomposition. Variation aboveground should be reflected in variation belowground such that the decomposer community would also respond to differences in substrate quality, further enhancing the variation in nutrient availability (Seastedt, 1984). Examining the effects of variation within a tree at this level is rarely done. We believe that in order to untangle the factors impacting ecosystem-level processes and functioning, we have to examine plant traits at finer scales. The relationship between aboveground and belowground processes is complex and difficult to examine but we must begin to factor intra-plant variation and plant genotype into our models to understand the patterns in nature that we observe and hope to conserve (Mooney et al., 1995).

Conclusions

At the onset of our paper we raised the central issue “How can long-lived plants, especially clonal ones, resist their rapidly evolving pests and pathogens?” Here we argue that plants are heterogeneous environments that exhibit ecologically important variation in morphology, nutrition and defenses at all levels (e.g., from different leaves of the same shoot to different ramets of the same clone). This variation causes an individual plant to effectively become an island mosaic or polyculture of different phenotypes, rather than a monoculture as has often been assumed. We suggest that this variation reduces their exposure to rapidly evolving pests and pathogens and show how this variation can have major impacts on pest populations, keystone species, community structure, and ecosystem dynamics. Mechanisms that generate this variation include plant development (i.e., ontogenetic and physiological aging), induction (e.g., pest induced responses), sink-source relationships, and/or somatic mutations. These processes can then interact with the environment to produce variation within a genet that can be as great as the variation among genets. To illustrate these mechanisms and their consequences, our review concentrated on poplars, a system where the effects of within-plant scaling from
individual leaves to different ramets of the same clone have been extensively studied. Based on these findings, three major predictions are made. First, plants that exhibit little internal variation should be more susceptible to rapidly evolving pests than plants that exhibit high variability. Second, variation within a plant results in greater habitat complexity, which in turn supports greater biodiversity. Third, chemical variation within dominant plants results in dispersed nutrient release at a stand level, which in turn supports greater stability in nutrient pools than a pulse of nutrient release. We predict that higher productivity will be achieved with more stable nutrient pools than with pulsing nutrient pools. Although the community and ecosystem consequences of within-plant variation are just beginning to be examined, we believe the variation within individual plants represents an important key to the understanding of large-scale processes and interactions that have both basic and applied value.

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Literature Cited


