Chapter 7
Influence of Tree Ontogeny on Plant-Herbivore Interactions

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Abstract As trees develop, they undergo morphological and physiological changes that can influence not only their performance, but also their interactions with herbivores. The expression of their defenses is influenced by changes in the selective pressures exerted by herbivores and by the plant's tradeoffs in resource allocation, and can result in ontogenetic trajectories that show increases, decreases, or mixed trends in the expression of anti-herbivory traits. In some species, these trajectories occur as gradual transitions among ontogenetic stages, but in other species there are pronounced phase changes marked by heterophylly or by abrupt changes in chemical, physical, or biotic defenses. This chapter discusses the patterns of such trajectories and the multiple factors that can influence them, including the specific herbivores feeding on trees, the activities of herbivores' natural enemies, the switches among the different defensive mechanisms that trees can express to reduce herbivory, the particular ecosystem in which they grow, and the influence of phylogenetic constraints that restrict or allow the evolution of ontogenetic trajectories in plant defense. Studies that integrate the role of ontogeny into evolutionary ecology theory will advance our understanding of how natural selection can target the ontogenetic trajectories of plant defense. Such research will also have application for targeting pest control onto vulnerable ontogenetic stages, and for selection of lines

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with improved defensive mechanisms to protect rare and endangered species as well as promote productivity in commercial stands.

1 Why Is Plant Ontogeny Influential for Plant-Herbivore Interactions?

As plants develop, they undergo important morphological and physiological changes. These changes, defining their ontogenetic trajectories (Fusco 2001), can be particularly striking for trees, given that they develop from small seedlings to very large and long-lived individuals. Such morphological and physiological changes are likely to influence not only the performance of individual trees, but also their interactions with many species, for example, their herbivores. Overall, as trees develop, changes in the selective pressures exerted by herbivores, together with plant resource allocation tradeoffs, influence the expression of plant defense. Thus, the ontogenetic trajectories in anti-herbivory traits can be characterized by increases, decreases, or mixed trends in the expression of such traits. In some species, these ontogenetic trajectories occur with pronounced phase changes marked by heterophylly or abrupt changes in chemical, physical, or biotic defenses (e.g. *Eucalyptus globulus*, and many ant plants), while most other tree species show more gradual transitions among ontogenetic stages. As we will discuss in this chapter, the patterns of such trajectories can be influenced by multiple factors, including the specific herbivores feeding on trees, the activities of herbivores' natural enemies, the switches among the different defensive mechanisms that trees can express to reduce herbivory, the particular ecosystem in which they grow, and the influence of phylogenetic constraints that restrict or allow the evolution of ontogenetic trajectories in plant defense.

2 External and Internal Factors Driving Ontogeny-Related Changes in the Quality of Trees as Food for Herbivores

Herbivory has been identified as a biotic interaction that usually has negative impacts on plant fitness (Harper 1977; Dirzo 1984; Crawley 1997). Such impacts however, may depend on the ontogenetic stage at which trees are attacked (Ehrlén 1995; Weiner 2004). Seeds and seedlings, for example, are particularly vulnerable to herbivore attack and they commonly get killed, especially when eaten by mammalian herbivores (Dirzo et al. 2007). As trees develop and acquire more biomass, the impacts of herbivore damage are less drastic but can still cause important reductions in their growth rates, survival and reproduction (Marquis 1984; Domínguez and Dirzo 1994; Boege 2005b). These negative impacts commonly represent an important selective force that has favored the evolution of defensive mechanisms that

allow plants to deal with their consumers. Defenses have been classified into (i) resistance traits that reduce the amount of damage received, which can be physical (e.g., spines, thorns or leaf toughness), chemical (secondary metabolites), or biotic (e.g., traits maintaining or enhancing the activity of natural enemies of herbivores); (ii) tolerance mechanisms that reduce the impact of herbivore damage once it has occurred, and (iii) escape strategies that reduce the probability of plants to be found by their consumers (Lubchenco and Gaines 1981; Dirzo 1984; Rosenthal and Kotanen 1994; Crawley 1997). Because the most dramatic impacts of herbivores on plant fitness occur during the youngest stages (Dirzo 1984; Marquis 1984), natural selection by herbivores is predicted to promote trees to have higher levels of any of these defensive mechanisms early than later during their development (Spiegel and Price 1996; Boege and Marquis 2005; Barton and Koricheva 2010).

However, despite the selective pressure of herbivores and the adaptive value of defensive mechanisms, plants are likely to optimize their levels of defense throughout ontogeny, depending on the priorities of other functions that also can influence plant fitness, such as growth, reproduction or maintenance, which commonly compete for the limited resources available for plants (Herms and Mattson 1992). The amount of resources allocated to each function, and in particular to defense against herbivores, depends on the physiological priorities at each ontogenetic stage and on resources available for plants at that particular moment of their lives. For example, in young plants it may be a priority to express high growth rates to establish and outcompete their neighbors; in contrast, when entering into their mature phase, reproduction may become a priority for resource use. In the specific case of trees, resource allocation to different functions during ontogeny also depends on the type of ecosystem and particular conditions in which they grow (e.g., open areas vs. forests, tree gaps vs. understory, and nutrient-poor vs. nutrient-rich soils). For instance, after producing the primary root system, seedlings growing in the understory of forests soon deplete the carbon stored in cotyledons, so further growth depends on the accumulation of new photosynthetic tissue (Swaine and Whitmore 1988; Martínez-Ramos et al. 1989; Bryant et al. 1991). Because in closed forests understory growth is constrained until a light gap is opened, saplings may remain in the same stage for many years, and allocate the few resources they can acquire to prevent herbivore attack on their limited amount of leaf area. As soon as light becomes available (after, for example, a branch or tree fall), growth can resume and is likely to have a priority over other functions, allowing plants to balance their root:shoot ratio and acquire enough above-ground biomass to reach the canopy (Blundell and Peart 2001). However, during such growth, as trees become larger and are able to accumulate resources, they can also start allocating them to other functions, such as defense or storage. Finally, when trees reach the canopy and enter into their mature stage, reproductive structures may compete for resources with defensive traits (Bryant et al. 1991; Boege and Marquis 2005). Thus, from the resource allocation perspective, two peaks of increased plant defense are likely to occur as plants develop: one at the seedling stage, when plants have enough maternal resources to defend their developing tissues, and a second one after they have reached a balance in their root:shoot ratio and before reproduction commences

(Bryant et al. 1991, and see Boege and Marquis 2005, Fig. 1). In contrast, in open areas or treefall gaps within forests, tradeoffs between growth and defense are likely to be defined by nutrient or water availability rather than by light limitation, and tolerance is likely to have a priority over the production of resistance traits (Coley 1983). For example, pioneer species in tree fall gaps of forests have a priority to grow fast to outcompete their neighbors (Blundell and Peart 2001). Having enough light and resources, their rapid intrinsic growth rates allow them to tolerate herbivore damage, by efficiently replacing the tissues lost to herbivores with no need to produce high levels of resistant traits. Once trees have reached the canopy, they are likely to keep compensating but also to allocate some resources to resistance and reproduction. Nevertheless, there are no available studies assessing switches in defensive strategies of pioneer species and this warrants further investigation. In the particular case of environments where water availability is the limiting factor for growth, distinct ontogenetic patterns in defense expression may be absent or weak if the same traits function for both water conservation and defense, as is the case with sclerophyllous leaves (Turner 1994). However, the specific role of water availability on the ontogeny of defense has not received much attention and remains unclear.

Interestingly, if we consider the magnitude of the impacts of herbivores throughout ontogeny, one would expect to observe a decline in the quantity or quality of defensive traits as plants develop, given that the young stages are more vulnerable, and thus should be better defended than old stages. In contrast, when considering resource allocation tradeoffs between defense and growth or reproduction, and the resources available for plants to produce defenses, the opposite pattern is expected (Barton and Koricheva 2010). As we will describe in the rest of the chapter, empirical evidence suggests that a combination of both mechanisms drives the ontogenetic trajectories of defense observed in trees. Furthermore, ontogenetic patterns in defense vary among tree species depending on the particular guild and abundance of herbivores feeding on them, on the type of defenses expressed, as well as on the ecosystem in which the trees grow.

3   Changes in the Quality of Trees as Food for Herbivores: Ontogenetic Patterns in Resistance

Several studies have detected that the number of herbivores feeding on trees and the amount of damage they produce are strongly dependent on the age of trees. In some cases herbivore abundance, performance and/or damage has been reported to increase with tree age (Tahvanainen et al. 1985; Jachmann 1989; Jogia et al. 1989; Kearsley and Witham 1989; Swihart and Bryant 2001; Boege and Marquis 2006), but in many others the opposite pattern has been found (Zagory and Libby 1985; Price et al. 1987; Kearsley and Witham 1989; Karban 1990; Fritz et al. 2001; Van Bael et al. 2003). In fact, a recent meta-analysis has detected that the overall pattern is that mammalian herbivores prefer to consume more tissue from mature than from juvenile trees, but the patterns of abundance and preference of insect herbivores is

rather more variable and presents no general trend (Barton and Koricheva 2010). Plant quality as food for herbivores is highly dependent on the type and amount of resistance traits they produce, and on the expression of other defensive strategies, such as tolerance or escape. Thus, changes in the defensive strategies during the development of trees are likely to be responsible for the observed patterns in herbivore preference and performance. Only two studies have examined developmental trajectories of defense throughout the entire ontogeny of trees, and these reveal differences among kinds of plant resistance. In *Ryparosa kurrangii* (Achariaceae), levels of cyanogenic glycosides decrease from the cotyledon to the autonomous seedling stage, and further decrease from the juvenile to mature tree stage (Webber and Woodrow 2009). Interestingly, the decrease in cyanogenic glycosides occurs simultaneously with an increase in leaf mass per area, measured as a proxy for leaf toughness, suggesting an ontogenetic switch from chemical resistance during early ontogeny to physical resistance in late ontogeny (Webber and Woodrow 2009). This study, however, did not explore other possible defensive traits that might also have changed during ontogeny. An ontogenetic switch has also been observed in *Populus tremuloides* (Salicaceae), although in this case it is a switch among classes of secondary compounds (Donaldson et al. 2006). As ramets age from 0 to 25+ years, concentrations of condensed tannins increase while concentrations of phenolic glycosides decrease significantly (Donaldson et al. 2006). Neither of these studies examined herbivore damage, and so the relationships between the ontogenetic switches observed and herbivore performance and damage remain unclear.

Although general conclusions about whole-ontogeny patterns cannot be drawn from only two studies, additional insights can be gained by considering studies focusing on patterns of resistance within a single or across two ontogenetic stages. For example, the few studies comparing tree seedlings of different ages in different species show a consistent increase in plant defense with developmental age, specifically for phenolics (Close et al. 2001; Fritz et al. 2001) and terpenoids (Bryant and Julkunen-Tiitto 1995). A single study examining the pattern in chemical resistance from the seedling to the juvenile stage reports a decrease in levels of leaf resin terpenoids (Feibert and Langenheim 1988). Within the juvenile stage, consistent increases have been observed for physical defenses (Nomura et al. 2001; del-Val and Dirzo 2003), while chemical resistance shows no clear pattern. Comparing saplings of different ages, it has been shown that concentrations of cyanogenic glycosides increase with plant age (Goodger et al. 2007), that alkaloids decrease (Liu et al. 1998), and that the levels of phenolics may increase or decrease, depending on the tree species (Bonell and Selander 1974; Basey et al. 1988; Laitinen et al. 2005). These patterns suggest that in trees, plant defense increases via secondary chemistry in seedlings and then via physical defenses in saplings. Developmental patterns in secondary chemistry during the sapling stage vary among species and among classes of secondary compounds. However, it should be noted that these patterns rely on data from relatively few species; additional studies are needed to ascertain their generality.

In contrast, many more studies have examined the expression of defense traits across the transition from the juvenile to the mature stages of trees, revealing again that the ontogenetic pattern varies among species and among defense traits.

As a measure of physical defense, leaf toughness tends to increase from the juvenile to the mature stage of trees (Kearsley and Witham 1989; Macedo and Langenheim 1989; Loney et al. 2006; but see Boege 2005b). Ontogenetic patterns in phenolics are variable: some species show increases from the juvenile to mature stage (Eck et al. 2001; Erwin et al. 2001; del-Val and Dirzo 2003; Gowda and Palo 2003; Boege 2005a, b; Boege and Marquis 2006; Goodger et al. 2006; Neilson et al. 2006), while other species show a decrease (Rousi et al. 1987; Basey et al. 1988; Loney et al. 2006; Neilson et al. 2006). Similarly, a general pattern fails to emerge for terpenoids, given the increases (Sinclair and Smith 1984; Goralka and Langenheim 1996; Loney et al. 2006) and decreases (Reichardt et al. 1984; Sinclair and Smith 1984; Langenheim et al. 1986; Macedo and Langenheim 1989) that have been reported. The single study we found comparing the induction of total phenolics in juveniles versus mature trees reports a greater inducibility in mature trees of the tropical deciduous *Casearia nitida* (Salicaceae; Boege 2005b). In addition, considering that cyanogenic glycosides are regarded as inducible defenses (Karban and Baldwin 1997), there is existing evidence of an increase of these compounds from the juvenile to the mature transition of several species of the genus *Eucalyptus*, (Gleadow and Woodrow 2000; Goodger et al. 2004; Goodger et al. 2006; Neilson et al. 2006), although *Eucalyptus cladocalyx* var. *nana* is a striking exception to this general pattern (Goodger et al. 2006). Considering the vast diversity of compounds within the broad classes of phenolics and terpenoids, it is perhaps not surprising that we do not detect general ontogenetic patterns for these classes (Barton and Koricheva 2010). Furthermore, investigations into the ontogeny of induced defense will need to consider how plant architecture changes as plants grow and develop. The transmission of signaling compounds within small juvenile plants is likely to result in a more synchronized induced response to herbivory, while the modularity and limited connectivity among branches within large mature trees may limit induction or even lead to induced susceptibility (Nykänen and Koricheva 2004). Additional studies on more species including several defensive traits may help clarify these ontogenetic trajectories. Moreover, variability among patterns can be explained by additional factors, such as the guild of herbivores feeding on trees, the particular habitat where tree species grow, life history strategies, and tradeoffs between types of defense (e.g., direct vs. indirect defense strategies), as we will discuss below.

4   Tree Ontogeny and the Impact of the Natural Enemies of Herbivores: Indirect Defenses

Traits facilitating the visitation or colonization of mutualistic animals that defend the plants against herbivores, such as plant food rewards, nesting space or chemical cues that attract herbivores' natural enemies (predators and parasitoids) are defined as indirect defenses. As we discuss below, these defensive strategies can include the interaction with mutualistic or non-mutualistic animals, and can change during the development of trees.

4.1   Indirect Defenses Involving Defensive Mutualisms

The most commonly documented indirect defense, myrmecophytism (Janzen 1966, 1969), involves plant-ant mutualisms, whereby the myrmecophytic plant provides nesting space in structures known as domatia, and sometimes offers food rewards directly, in the form of extrafloral nectar and/or nutritious food bodies (Fiala and Maschwitz 1992), or indirectly, via, for example, coccoid-produced honeydew (Gaume et al. 1998). In turn, ants protect host plants from herbivores (Janzen 1966; Schupp 1986; Fiala et al. 1994; Heil and McKey 2003). Additionally, in a few documented cases, such defensive mutualisms occur between wasps and plants, and in these cases the plant provides a reward in the form of floral nectar (Domínguez et al. 1989; Narbona and Dirzo 2010).

The fundamental driver of the ontogenetic shifts observed in plants with defensive mutualistic relationships is an ontogenetic constraint imposed by the fact that mutualistic plants do not start their lives associated with their defending insects. Instead, they have to acquire their defenders in the course of their ontogeny. Typically, a mutualistic plant starts with a size and morphology that cannot maintain a colony of ants, given that young (uncolonized) plants have not developed functional domatia, nor structures for the production of food bodies or nectar (extrafloral nectar in the case of myrmecophytic plants, or floral nectar in the case of wasp-mutualistic plants). This, coupled with the fact that young stages of the myrmecophytic plant are particularly vulnerable to the impacts of herbivory, leads to the hypothesis that in the absence of defenders during this critical stage of their ontogeny, uncolonized plants may be more dependent upon direct defenses than older (colonized) plants (del-Val and Dirzo 2003; Heil and McKey 2003). Assuming that colonized plants are sufficiently defended against herbivores, we might then expect to see a reduction in direct defenses upon colonization by ants or wasps. This would lead to an ontogenetic switch from direct defenses in young uncolonized plants to indirect defenses in older colonized plants.

Only a handful of studies are available to assess these expectations. Table 7.1 summarizes the results derived from seven independent studies involving seven different tree (with one exception, *Croton suberosus*, a shrubby plant) species. In six of these species, biotic, indirect defense has been found to be present in the older (colonized) plants, while younger stages lack such biotic defense. In most of these studies, plant palatability has been measured as a proxy of direct (chemical or physical) defense (eight comparisons, Table 7.1), while four comparisons examined natural herbivory in the field. Only one study (del-Val and Dirzo 2003) examined, in addition to herbivory and palatability, direct defenses in terms of plant phenolics, tannin concentration, and pubescence in colonized and uncolonized plants of the myrmecophyte *Cecropia peltata*. One study also compared herbivore survival in young and old plants (also a proxy of direct defenses) of the myrmecophyte *Macaranga* under controlled conditions with captive animals (Nomura et al. 2001).

The specific hypotheses for the comparisons of Table 7.1 are that, in contrast with old plants, young plants should be: (i) less palatable, (ii) have higher levels of direct defenses (phenolics and tannin concentrations, and pubescence), and (iii) should cause

Table 7.1 Studies that have examined ontogenetic changes in defense strategy among tree species with indirect defenses involving mutualistic animals (ants, or wasps) present in the old but not young ontogenetic stages

Plant species	Indirect defense	Variable measured	Comparison young vs. old plants	Source
Macaranga myrmecophytes	Ants	Palatability Herbivore survival	Young < old Young < old	Nomura et al. (2001)
Cordia alliodora	Ants	Palatability	Young ~ old	Trager and Bruna (2006)
Cecropia peltata	Ants	Palatability Herbivory Chemical defense Physical defense	Young > old Young > old Young < old Young < old	del-Val and Dirzo (2003)
Omphalea oleifera	Ants	Palatability Herbivory	Young ~ old Young ~ old	R. Dirzo, unpublished
Cordia alliodora *Croton suberosus*	Ants Wasps	Palatability Palatability Herbivory	Young < old Young < old Young ~ old	Llandres et al. (2010); Narbona and Dirzo (2010)
Acacia cornigera	Ants	Palatability Herbivory	Young < old Young ~ old	R. Dirzo, unpublished
Populus tremuloides	Ants	Extrafloral Nectaries Chemical defense	Young > old Young > old	Wooley et al. (2007)

lower survival of captive generalist herbivores. Only five out of eight tests found that uncolonized young plants were less palatable than older plants. The other three studies found the opposite pattern or no difference between young and old plants. Survival of generalist herbivores was lower on young plants than in older plants, supporting the prediction that direct defense decreases with plant age. Finally, patterns of herbivore damage were generally similar across ontogenetic stages, suggesting that direct and indirect defense provide similar levels of protection against herbivores. A striking exception to these results was observed in *Cecropia peltata*, in which young plants lack direct defenses (chemical and physical) as well as indirect defenses (ants). This resulted in higher palatability and levels of herbivore damage of young plants compared to older plants (del-Val and Dirzo 2003). Clearly, young *C. peltata* plants lack resistance against herbivory, and the authors suggest that perhaps they rely instead on tolerance (del-Val and Dirzo 2003). Although tolerance has not been tested in *C. peltata*, a study with a related species, *C. obtusifolia*, found that artificial defoliation during the uncolonized stage had no effect on plant survival or growth compared to undamaged control plants (Frías 1996), suggesting that tolerance may be indeed important in *Cecropia* juveniles.

As mentioned above, our predictions about ontogenetic switches in direct and indirect defense were only partially supported by the evidence presented in Table 7.1. In some cases, the inconsistency of the results can be explained on the grounds of methodological differences. For example, it has been found that young

Cordia alliodora plants are either less palatable (Llandres et al. 2010) or similarly palatable (Trager and Bruna 2006), when compared to older plants. Such discrepancy could be due to the facts that in Trager and Bruna's (2006) study, their young (1 year-old) plants included saplings that had domatia already occupied by ants, while in the other study all young plants were uncolonized. The young but occupied saplings of the former study might have already foregone direct defenses (see Llandres et al. 2010). In addition, the palatability trials in Trager and Bruna's study were performed using the *Cordia*-specialized beetle *Coptocyla leprosa*, while the other study used a generalist herbivore, the larvae of the lepidopteran *Hypercombe* sp. Conceivably, the specialized beetle might be more capable of dealing with the secondary compounds of *C. alliodora* than the larvae of the generalist herbivore, thus rendering the palatability of plants from the two stages indistinguishable. A similar interpretation can be applicable in the case of the Neotropical tree *Omphalea oleifera* (Table 7.1) in which only the old trees produce extrafloral nectar that attracts a variety of ants, while the young plants do not produce such a reward. In contrast, in the case of *Populous tremuloides,* the density of extrafloral nectaries is actually greater in young trees (1 year old) than in 4- and 10-year-old trees (Wooley et al. 2007), and there is no detectable trade-off between this indirect defense and direct chemical defenses or tolerance (Sugiura et al. 2006; Wooley et al. 2007).

Limited as it is, this set of studies collectively suggests that young uncolonized trees may invest in direct defenses to reduce herbivory, and then relax these defenses upon colonization by their animal defenders. Future studies measuring chemical, physical, and tolerance traits in young uncolonized and old colonized plants are needed and will provide key new insights into ontogenetic switches and trade-offs between direct and indirect defense. Furthermore, explicit comparisons of generalist and specialist herbivores will reveal whether direct and indirect defenses are in fact redundant, and thus involved in an ontogenetic switch, or whether they may act in synergy to defend plants against a wide range of herbivores.

4.2 Indirect, But Non-mututalistic Defense and Ontogeny

In some cases, plant species are defended by animals that are not engaged in mutualistic interactions with the plant. Such indirect defense is known in herbaceous plants and some trees, but knowledge is extremely scarce as to whether this exhibits any kind of ontogenetic trajectory. One relevant study (Van Bael et al. 2003) investigated how predators affected herbivore abundance and levels of herbivory in saplings and adult trees in three tropical tree species. Using cages to prevent access to bird predators, they found that caging dramatically increased herbivore abundance and levels of herbivory on trees but had no effect on saplings. Although a variety of factors could potentially account for these results, a proximate interpretation is that the third trophic level has a greater impact on the plant's herbivores at the older but not younger ontogenetic stages and that the levels of herbivory on adult trees would be significantly higher in the absence of predatory, top-down controls.

The consequences of such patterns on ontogenetic trajectories of plant defense and on plant fitness remain to be investigated.

Further evidence for the importance of tritrophic interactions on the ontogeny of plant defense and herbivory comes from studies on the dry forest deciduous tree species, *Casearia nitida*. Comparisons of caged and non-caged saplings and mature trees found that the foraging intensity of bird predators was significantly higher in mature trees (Boege and Marquis 2006). Moreover, foraging of parasitoid wasps was restricted to the canopies of mature trees, and they did not forage in saplings (Boege 2005a). Together with ontogenetic increases in total leaf phenolics, these patterns of indirect and direct defense led to significantly higher herbivore densities and levels of damage in saplings compared to mature trees (Boege 2005a). Determining whether the ontogenetic increases in predation and parasitism observed in these studies reflect general patterns requires further tests in additional species. Particular focus on the potential ontogenetic change in expression of plant volatile organic compounds (VOC's) may reveal a mechanism by which tritrophic interactions change during plant development. Although VOC release has been shown to decrease with plant age in cultivated herbs (Cole 1980), information about their ontogenetic patterns in trees remains unknown.

5   Ontogenetic Patterns in Escape and the Influence of Biogeography

Developmental patterns in herbivory may occur for reasons other than top-down (i.e. indirect) or bottom-up (i.e. defensive chemistry) forces. Specifically, apparency to herbivores (Feeny 1976) may change as plants grow and develop, leading either to ontogenetic increases or decreases in escape from herbivores. Several different mechanisms can drive developmental patterns in apparency to and escape from herbivores, including associational resistance, distance from conspecific trees, lag time in the herbivore colonization of young trees, phenology, and limited access to trees as they grow. Furthermore, these developmental patterns often show biogeographical variation.

There is a strong spatial component to developmental patterns in apparency and escape, evidenced by the importance of plant neighbors and distance from conspecific trees. Associational resistance occurs when susceptible plants escape from herbivory by growing in close proximity to well-defended plants. Typically, it is small and/or young plants that gain associational resistance from neighbors, sometimes called nurse plants (Niering et al. 1963). Associational resistance is often provided by nurse plants with physical defenses that effectively protect seedlings from mammalian herbivores (Rousset and Lepart 2000; Baraza et al. 2006; Vandenberghe et al. 2009), but can also be mediated by secondary chemistry (Smit et al. 2006). Although it has rarely been compared among species, associational resistance seems to be especially important for seedlings that lack their own resistance or tolerance to herbivory (Vandenberghe et al. 2009).

Spatial relationships of individuals within species are also important for escape from herbivory. In this case, it is distance from, rather than proximity to, an adult tree that provides a benefit to young and small plants. As proposed by the Janzen-Connell hypothesis (Janzen 1970; Connell 1971), seedlings and juveniles growing near conspecific adults receive high loads of specialist herbivores from nearby adult trees, leading to relatively high mortality near adults and a decrease in herbivory and mortality with distance from conspecific adults. A meta-analysis of 23 studies testing the Janzen-Connell hypothesis in seedlings confirmed that distance from conspecific adults increases seedling survival (Hyatt et al. 2003), but that this pattern is more common in tropical forests. In contrast, temperate species tend to show higher survival near conspecific adults, perhaps indicating that suitable establishment sites are limited (and associated with conspecific adults) and that the distribution of individuals from the same species is more homogeneous in temperate forests, in contrast with tropical forests. Like escape by associational resistance, distance from conspecific adults provides only an ephemeral defense against herbivory. As trees grow, herbivores will undoubtedly locate and colonize them, but by that time, the plants are likely to have started expressing their own resistance and tolerance traits.

To our knowledge, only two studies have explicitly linked ontogenetic patterns in defense traits with Janzen-Connell patterns of herbivory and mortality (Langenheim and Stubblebine 1983; Sánchez-Hidalgo et al. 1999). Both studies examined tropical tree species showing relatively high seedling survival beneath parental trees, notable exceptions to the Janzen-Connell hypothesis. Furthermore, in both studies, it was demonstrated that the surviving seedlings had distinct secondary chemical profiles compared to the adult trees. It was concluded that parent trees produced genetically variable offspring and that herbivores consumed only those seedlings with profiles similar to the parent trees, leaving chemically differentiated seedlings to survive. By consuming a specific subset of the seedling pool, these herbivores would be selecting for ontogenetic patterns in plant secondary chemistry, thereby creating a moving-target (*sensu* Adler and Karban 1994) and allowing seedlings to escape from herbivory.

Associational resistance and the Janzen-Connell hypothesis illustrate how space affects herbivore-seeking behavior, thereby driving developmental patterns of escape. Time is similarly important for escape from herbivory, and can lead to ontogenetic differences in herbivory resulting in the simple observation that herbivore loads increase over time, as trees develop, and more herbivores find and colonize them. Temporal increases are most commonly reported for insect herbivores (Guedes et al. 2000; Fonseca and Benson 2003; Campos et al. 2006) and may also apply to other invertebrate herbivores, such as slugs and snails, but have not been explicitly tested. In addition, phenological changes are also involved in the ability of plants to escape from herbivory. For example, young saplings of *Acer mono* flush their leaves earlier than their adult relatives, increasing their probabilities of escaping from predators and pathogens (Seiwa 1999).

In contrast to the previous examples showing how seedlings and juvenile plants escape from herbivory, some species escape from herbivory as adults. In particular, trees are able to escape from ground-dwelling mammalian herbivores only when they

outgrow the reach of these browsers. Due to the high densities of ground-dwelling mammalian herbivores, this phenomenon is especially common and well-documented in boreal forests (Swihart and Bryant 2001). Intense herbivory on juvenile, but not on adult plants, results in an ontogenetic decrease in the selection pressure on resistance traits. Indeed, feeding trials with the relevant ground-dwelling browsers (hares, deer, voles) reveal that juvenile plant tissue is much less palatable than adult plant tissue (reviewed in Swihart and Bryant 2001), and the limited evidence from studies examining plant resistance traits indicates that levels of secondary compounds can be as much as 96% higher in juvenile plants than in conspecific adults (Reichardt et al. 1984). For these species, escape from ground-dwelling herbivores occurs with a concomitant ontogenetic shift away from chemical defense in adult trees.

Interestingly, developmental patterns in escape and associated ontogenetic switches in defense vary biogeographically. In boreal forests, seedlings and juveniles experience herbivory by mammals and express high levels of chemical defense, while adults show lower levels of chemical defense and escape from mammalian herbivores. Unlike boreal trees, temperate and tropical species show weak ontogenetic patterns in herbivory and tend to increase chemical defense across ontogeny (Barton and Koricheva 2010). Biogeographical trends in key herbivores may explain this difference. In temperate and tropical forests, insects (Coley and Barone 1996) and mollusks are the most important herbivores, and these taxa are not limited by tree height in the same way that boreal mammals are. Ontogenetic increases in chemical defense of temperate and tropical species (Barton and Koricheva 2010) may reflect allocation constraints during development that limit production of secondary chemicals and physical defenses in seedlings (Herms and Mattson 1992). Future research explicitly measuring ontogenetic patterns in herbivore selection pressure and growth-defense trade-offs in temperate and tropical tree species would shed light on this striking biogeographical pattern.

Although still under-studied, these examples illustrate how escape from herbivory can change as trees grow and develop. Future research should further explore the mechanisms driving developmental patterns in escape with particular focus on biogeography, the role of herbivore feeding guild (mammalian browsers vs. insect defoliators, etc.), and how escape is involved in ontogenetic switches among defense traits. Studies of non-model tree species, particularly in the temperate and tropical forests, are needed to ascertain the generality of these patterns.

6   Ontogenetic Patterns in Tolerance to Herbivory

For many plants, resistant traits reduce levels of herbivory but are unable to completely eliminate damage. In these cases, tolerance can become an important plant defense strategy. Tolerance occurs when herbivore damage induces changes in plant traits that allow for compensation, or replacement of lost tissues, and the maintenance of fitness levels comparable to undamaged conspecifics. Although it remains unclear which mechanisms are most important, commonly studied tolerance

traits include increases in photosynthesis rates, activation of dormant meristems, utilization of stored reserves, shifts in allocation patterns, and changes in phenology (Tiffin 2000). Considering the small size of seedlings with their limited photosynthetic area, minimal stored reserves, and nearly non-existent bud bank, we would predict that tolerance increases dramatically during plant ontogeny. Interestingly, the relatively few studies examining the ontogeny of tolerance in trees suggest that the pattern is actually more complex than this simple prediction.

Only four studies have explicitly tested how tolerance changes with plant age or ontogeny in woody plants (Weltzin et al. 1998; Warner and Cushman 2002; Boege 2005b; Hódar et al. 2008), but our synthesis can be expanded if we include a recent meta-analysis that compared studies that separately measured compensation in seedlings, saplings, and mature trees (Nykänen and Koricheva 2004). In general, seedlings experience significant reductions in growth following herbivory and are unable to compensate for lost tissues (Weltzin et al. 1998). Demonstrating the importance of even small differences in age (and, probably more importantly, size) during early ontogeny is the observation that 5-week-old honey mesquite (*Prosopis glandulosa*, Fabaceae) seedlings compensate for defoliation significantly better than 3-week-old seedlings. However, 3-week-old seedlings show higher survival after ten successive defoliations than 5 week old seedlings (Weltzin et al. 1998), demonstrating that the fitness currency used (survival vs. growth) can influence interpretations of tolerance.

As juveniles develop from seedlings to saplings, they show significant increases in compensation for herbivory (Nykänen and Koricheva 2004; Hódar et al. 2008), presumably due to increases in photosynthetic area, stored reserves, and bud bank. Following a peak at the sapling stage, compensation appears to decrease as plants mature (Warner and Cushman 2002; Nykänen and Koricheva 2004; Boege 2005b). This is likely due to a combination of factors, including shifts in allocation priorities, increased sectoriality of large trees, and senescence. During the vegetative juvenile stage, resources for growth are allocated entirely to vegetative tissues. After the onset of reproduction, however, allocation patterns shift, and reproductive tissues may be produced at the expense of vegetative growth. Following herbivory, these resource allocation shifts can limit compensation in mature plants. Thus, under-compensating mature plants may actually have high tolerance if they are preferentially allocating resources to reproduction at the expense of growth.

Compensation may decrease from the sapling to mature tree stage because sectoriality increases with plant size, so that large trees have few physiological connections among branches. As a result, herbivore-induced tolerance traits are localized on the damaged branch, and whole-plant measures of compensation are low (Haukioja and Koricheva 2000). Moreover, gradual activation of dormant buds due to release from apical dominance may reduce the bud bank in mature trees compared to saplings, further limiting compensatory growth following herbivory (Lehtilä 2000).

Finally, mature plants may experience lower compensation for herbivory than saplings because they have relatively more senescent leaves. As Nykänen and Koricheva (2004) demonstrated, trees are more responsive to herbivory early in the season when leaves are more "vigorous" (sensu Price 1991). As the season progresses,

leaves begin to senesce and show limited responses to herbivory. This is consistent with the general observation that actively growing leaf tissue can better detect and respond to herbivory than older, inactive leaves (Herms and Mattson 1992; Karban and Baldwin 1997).

Determining whether the observed non-linearity in the ontogeny of compensation and tolerance is the result of shifts in allocation priorities, sectoriality, senescence, or some combination of these factors, requires further research. Additional questions that will shed light on the ontogeny of compensation and tolerance include the following: (1) Does tolerance to invertebrate vs. vertebrate herbivory differ in seedlings vs. mature trees? Mammals and mollusks account for most of seedling herbivory, while insects cause most of the damage experienced by mature trees. Because tolerance mechanisms are likely to differ for vertebrates versus invertebrates (Haukioja and Koricheva 2000), it is important to test these responses separately at each stage. (2) Do deciduous and evergreen trees differ in their ontogenetic patterns? Herbivory tends to reduce growth in evergreens more than in deciduous trees (Nykänen and Koricheva 2004), but it remains unclear whether this response is consistent across ontogenetic stages. (3) Do the mechanisms of tolerance differ among ontogenetic stages? Despite the general assumption that compensatory growth increases fitness, there are very few tests of the relationship between compensation and reproductive output (Tiffin 2000). Thus, it remains unclear whether compensatory growth actually acts as a mechanism by which plants tolerate herbivory. Furthermore, plant responses to herbivory can be confusing. In their meta-analysis, Nykänen and Koricheva (2004) found that herbivory increases the rate of photosynthesis, concentrations of carbon and phenolics, but decreases concentrations of carbohydrates, terpenes, and plant growth. Apparently, damaged plants were unable to achieve growth rates comparable to undamaged control trees despite increases in photosynthesis. Examination of other putative tolerance traits in seedlings, saplings, and mature plants would provide new insights into how trees compensate for defoliation and would elucidate how tolerance changes across ontogeny.

7   Mixed Strategies: Switching Between Defensive Mechanisms During Ontogeny

During their prolonged life span trees are usually attacked by several species of herbivores, which have different impacts on their performance. On the other hand, resource allocation constraints and costs of defense are also likely to change during plant development. Hence, because the efficiency and the benefit:cost ratios of the different defensive mechanisms are likely to vary throughout tree development, it is not surprising to find that plants can switch from one defensive strategy to another as they develop. However, few studies have examined suites of defense traits across plant ontogeny (Boege et al. 2007), and only one has formally assessed such switches for the particular case of trees. Webber and Woodrow (2009) demonstrated that cyanogenesis decreases during ontogeny while a proxy of physical defense

(leaf weight per unit area) increases in the tropical understory tree *Ryparosa kurrangii* (Achariaceae). Additional data from independent studies and observations suggest that ontogenetic switches in plant defense are an important aspect of plant-herbivore interactions. For example, as explained above, it is well known that trees can be defended through associational resistance as seedlings, and then switch from escape to secondary chemistry, physical defenses or tolerance later in development. In addition, when seedlings then become juveniles and mature trees, switches between tolerance and chemical defense are also likely to occur, driven by the risk of attack and resource allocation trade-offs between growth and defense (Boege 2005b). For example, saplings of the tropical tree *Casearia nitida* show greater ability to compensate for intense levels of herbivory (75% of leaf damage) but present lower concentrations of secondary metabolites (phenolic compounds) than mature trees, which show a lower ability to compensate damage but have higher concentration of phenolics (Boege 2005a, b). In addition, as discussed in Sect. 4, trees may shift from direct to indirect (biotic) defense as they age, particularly in the case of tropical trees where defensive mutualisms are particularly prominent.

An additional case of switches in defensive mechanisms occurs in systems where mammalian herbivores cannot climb or reach the canopy of trees (e.g., rabbits in boreal zones, deer in temperate and tropical zones). In those systems, it is common that physical defenses such as spines and thorns, which are effective largely against mammalian herbivores (Hanley et al. 2007), are expressed only early in ontogeny, when these herbivores have access to the branches of young trees. Once trees outgrow the reach of these herbivores, the expression of such defensive traits is likely to decrease, as they do not provide further benefits to plants (Gowda and Palo 2003). Hence, a switch in defensive strategies is likely if damage in older ontogenetic stages is performed by insects that can reach high canopies. In this case, the expression of tolerance or other resistance traits (e.g., trichomes, secondary metabolites, etc.) or indirect, biotic defense could be expected. Nevertheless, such expected switches have not been assessed and deserve further research.

8   Ecological and Evolutionary Implications of Ontogenetic Changes in Plant Defense

As mentioned in previous sections, ontogenetic changes in plant defense are likely to be promoted by resource allocation adjustments to physiological priorities of trees during their development, but also by the relative impact and intensity of herbivore attack as trees grow and mature. Overall, ontogenetic changes in defense should allow plants to reduce the costs of defense by restricting their production to only those stages in which (a) defenses have reduced physiological or ecological costs and/or (b) fitness is severely reduced by herbivore damage. Because reducing the costs of defense should be translated into greater plant fitness, natural selection should favor genotypes whose ontogenetic patterns of defense minimize the cost:benefit ratio of defense production. This adds a level of complexity to the traditional approach to

study the evolution of plant defense, which has implicitly focused on investigating how natural selection targets different defensive traits at a given ontogenetic stage of trees (Latta and Linhart 1997; Andrew et al. 2007; Bailey et al. 2007, Donaldson and Lindroth 2007). In contrast, here we propose that natural selection could target directly the ontogenetic trajectories in plant defense. However, for this to be possible, the variation in ontogenetic trajectories in a population should have a genetic component. That is, some plant genotypes should present greater degree of ontogenetic change than others, and this variation should have relevant impacts on plant fitness. Genetic variation in ontogenetic trajectories has been detected for some herbs and shrubs (Bowers and Stamp 1993; Schappert and Shore 2000; Barton 2007), and only for two tree species (Donaldson et al. 2006, Rehill et al. 2006). Thus, exploring the genetic component of the ontogenetic trajectories in trees warrants further research, as a starting point to understand the microevolutionary patterns of the ontogenetic trajectories of defense in plants.

9   Phylogenetic Signal

Studies documenting genetic variation in and natural selection on developmental trajectories of defense traits would inform us about the microevolution of the ontogeny of defense. To understand macroevolutionary patterns in the ontogeny of defense, we must adopt a phylogenetic context for these studies. Phylogenetics is typically applied to plant defense research in the following ways: (i) to avoid pseudoreplication in tests of trade-offs among defense traits across species (Rudgers 2004; Agrawal and Fishbein 2008), (ii) as phylogenetic contrasts for testing a specific hypothesis, such as the growth rate hypothesis (Van Zandt 2007), and (iii) to examine within-lineage patterns of evolution, such as escalation (Agrawal et al. 2008; Agrawal et al. 2009). Of these three areas, the use of phylogenetic contrasts for testing hypotheses is likely to be the most useful for understanding the ontogeny of plant defense.

A recent meta-analysis on the ontogeny of plant defense and herbivory revealed several key questions that could benefit from a phylogenetic contrast approach (Barton and Koricheva 2010). First, as discussed in Sect. 5 of this chapter, developmental patterns in herbivory suggest that the ontogeny of defense varies biogeographically. Herbivores in boreal forests show a strong preference for adult plant foliage compared to juvenile foliage, while herbivores in temperate and tropical forests tend to show the opposite pattern, preferring juvenile foliage (Barton and Koricheva 2010). However, this result is confounded by herbivore type: studies in boreal forests focused on mammalian herbivores, but studies in the temperate and tropics were limited to insect and mollusk herbivores. Phylogenetic contrasts could be used to separately test how latitude and herbivore type influence the ontogeny of plant defense. In the first case, a single replicate would consist of a phylogenetic trio (related species from each of a tropical, temperate, and boreal forests), and ontogenetic patterns would be compared among the three geographical regions for as

many phylogenetic replicates as possible. Similarly, phylogenetic replicates could be used to compare ontogenetic patterns in defense traits in species experiencing herbivory by different herbivores (mammals vs. mollusks vs. insects). Typically, phylogenetic replicates consist of congeners (e.g. Rudgers et al. 2004; Van Zandt 2007), but in the case of the ontogeny of defense, it will be important to consider phylogenetic patterns at the plant family level in addition to the generic level, considering the evidence that the ontogeny of defense varies significantly among plant families (Barton and Koricheva 2010).

A key insight from previous research on the macroevolution of plant defense that is relevant to the study of the ontogeny is the general failure to detect trade-offs among defense traits, as evidenced by a lack of negative correlations among them (reviewed in Agrawal 2007). However, some trade-offs become apparent when multivariate analyses are conducted on suites of traits or "defense syndromes" (*sensu* Agrawal and Fishbein 2006). Because plants encounter different herbivores and express different defense traits across ontogeny, multivariate analysis provides a method for simultaneously examining these factors.

10 Conclusions

Ontogenetic patterns in plant defense and herbivory are complex, involving shifting suites of herbivores, switches among defense traits, and changing resource allocation priorities. Yet, many studies continue to overlook this key aspect of plant ecology. Integrating the role of ontogeny into evolutionary ecology theory provides new perspectives to our understanding of the interaction of trees with their herbivores, and in particular on how natural selection can target the ontogenetic trajectories of plant defense. Furthermore, this perspective can have important applications for forest management. For example, identifying when trees are most susceptible to be attacked by herbivores, and when they are likely to express particular defensive traits could help to concentrate pest control efforts on the ontogenetic stages that are not able to resist or tolerate herbivore damage, or on those stages with greater risk of attack. If genetic variation in ontogenetic trajectories in plant defense is found, selection of lines which best optimize the expression of defensive mechanisms throughout ontogeny could enhance productivity of commercial stands and help conserve rare and endangered species suffering from stage-specific herbivory. In the near future, it is imperative as well to incorporate the insights of emerging fields such as functional genomics, to understand the epigenetic regulation of developmental changes in trees (Brunner et al. 2004), in particular, to identify the genes responsible for the ontogenetic trajectories of plant defense traits. Within this framework, evo-devo research offers new avenues to determine how environmental factors affect developmental processes at a mechanistic level and how they influence the expression of phenotypes during the life history of plants. In particular, the understanding of the genetic bases and transduction patterns of ontogenetic changes will help to understand their ecological and evolutionary consequences (Sultan 2005).

References

Adler FR, Karban R (1994) Defended fortresses or moving targets? Another model of inducible defenses inspired by military metaphors. Am Nat 144:813–832

Agrawal AA, Fishbein M (2006) Plant defense syndromes. Ecology 87:S132–S149

Agrawal AA (2007) Macroevolution of plant defense strategies. Trends Ecol Evol 22:103–109

Agrawal AA, Fishbein M (2008) Phylogenetic escalation and decline of plant defense strategies. P Indian Acad Sci 105:10057–10060

Agrawal AA, Lajeunesse MJ, Fishbein M (2008) Evolution of latex and its constituent defensive chemistry in milkweeds (*Asclepias*): a phylogenetic test of plant defense escalation. Entomol Exp Appl 128:126–138

Agrawal AA, Salminen JP, Fishbein M (2009) Phylogenetic trends in phenolic metabolism of milkweeds (*Asclepias*): evidence for escalation. Evolution 63:663–673

Andrew RL, Wallis IR, Harwood CE, Henson M, Foley WJ (2007) Heritable variation in the foliar secondary metabolite sideroxylonal in *Eucalyptus* confers cross-resistance to herbivores. Oecologia 153:891–901

Bailey JK, Schweitzer JA, Rehill BJ, Irschick DJ, Whitham TG, Lindroth RL (2007) Rapid shifts in the chemical composition of aspen forests: an introduced herbivore as an agent of natural selection. Biol Invasions 9:715–722

Baraza E, Zamora R, Hódar JA (2006) Conditional outcomes in plant-herbivore interaction: neighbors matter. Oikos 113:148–156

Barton EK (2007) Early ontogenetic patterns in chemical defense in *Plantago* (Plantaginaceae): genetic variation and trade-offs. Am J Bot 94:56–66

Barton EK, Koricheva J (2010) The ontogeny of plant defense and herbivory: characterizing general patterns using meta-analysis. Am Nat 175:481–493

Basey JM, Jenkings SW, Busher PE (1988) Optimal central place foraging by beavers: tree size selection in relation to defensive chemicals of quaking aspen. Oecologia 76:278–282

Blundell AG, Peart DR (2001) Growth strategies of a shade-tolerant tropical tree: the interactive effects of canopy gaps and simulated herbivory. J Ecol 89:608–615

Boege K (2005a) Herbivore attack in *Casearia nitida* influenced by plant ontogenetic variation in foliage quality and plant architecture. Oecologia 143:117–125

Boege K (2005b) Influence of plant ontogeny on compensation to leaf damage. Am J Bot 92:1632–1640

Boege K, Marquis RJ (2005) Facing herbivory as you grow up: the ontogeny of resistance in plants. Trends Ecol Evol 20:441–448

Boege K, Marquis RJ (2006) Plant quality and predation risk mediated by plant ontogeny: consequences for herbivores and plants. Oikos 115:559–572

Boege K, Dirzo R, Siemens DH, Brown P (2007) Ontogenetic switches from plant resistance to tolerance: minimizing costs with age? Ecol Lett 10:177–187

Bonell ML, Selander RK (1974) Elephant seals: genetic variation and near extinction. Science 184:908–909

Bowers MD, Stamp NE (1993) Effects of plant age, genotype and herbivory on *Plantago* performance and chemistry. Ecology 76:1778–1791

Brunner AM, Busov VB, Strauss SH (2004) Poplar genome sequence: functional genomics in an ecologically dominant plant species. Trends Plant Sci 9:49–56

Bryant JP, Julkunen-Tiitto R (1995) Ontogenetic development of chemical defense by seedling resin birch: energy cost of defense production. J Chem Ecol 21:883–896

Bryant JP, Kuropat PJ, Reichardt PB, Clausen TP (1991) Controls over the allocation of resources by woody plants to chemical antiherbivore defense. In: Palo RT, Robbins CT (eds) Plant defenses against mammalian herbivory. CRC Press, Boca Raton, pp 83–103

Campos RI, Vasconcelos HL, Ribeiro SP, Neves FS, Soares JP (2006) Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*. Ecography 29:442–450

Close DC, Davies NW, Beadle CL (2001) Temporal variation of tannins (galloylglucoses), flavonols and anthocyanins in leaves of *Eucalyptus nitens* seedlings: implications for light attenuation and antioxidant activities. Aust J Plant Physiol 28:269–278

Cole RA (1980) Volatile components produced during ontogeny of cultivated crucifers. J Sci Food Agr 31:549–557

Coley PD (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecol Monogr 53:209–233

Coley PD, Barone JA (1996) Herbivory and plant defenses in tropical forests. Annu Rev Ecol Syst 27:305–335

Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals andin rain forest trees. In: den Boer PJ, Gradwell GR (eds) Dynamics of populations. Wageningen, Pudoc, pp 298–312

Crawley MJ (1997) Plant herbivore dynamics. In: Crawley MJ (ed) Plant ecology. Blackwell Science, Cambridge, pp 401–475

del-Val E, Dirzo R (2003) Does ontogeny cause changes in the defensive strategies of the myrme-cophyte *Cecropia peltata*? Plant Ecol 169:35–41

Dirzo R (1984) Herbivory: a phytocentric overview. In: Dirzo R, Sarukhan J (eds) Perspectives on plant ecology. Sinauer, Sunderland, pp 141–165

Dirzo R, Mendoza E, Ortíz P (2007) Size-related differential seed predation in a heavily defaunated Neotropical rain forest. Biotropica 39:355–362

Domínguez CA, Dirzo R (1994) Effects of defoliation on *Erythroxylum havanense*, a tropical proleptic species. Ecology 75:1896–1902

Domínguez CA, Dirzo R, Bullock SH (1989) On the function of floral nectar in *Croton suberosus* Euphorbiaceae. Oikos 56:109–114

Donaldson JR, Stevens MT, Barnhill HR, Lindroth RL (2006) Age-related shifts in leaf chemistry of clonal aspen (*Populus tremuloides*). J Chem Ecol 32:1415–1429

Donaldson JR, Lindroth RL (2007) Genetics, environment, and their interaction determine efficacy of chemical defense in trembling Aspen. Ecology 88:729–739

Eck G, Fiala B, Linsenmair KE, Bin Hashim R, Proksch P (2001) Trade-off between chemical and biotic antiherbivore defense in the southeast Asian plant genus *Macaranga*. J Chem Ecol 27:1979–1996

Ehrlén J (1995) Demography of the perennial herb *Lathyrus vernus*. I. Herbivory and individual performance. J Ecol 83:287–295

Erwin EA, Turner MG, Lindroth RL, Romme WH (2001) Secondary plant compounds in seedling and mature aspen (*Populus tremuloides*) in Yellowstone National Park, Wyoming. Am Midl Nat 145:299–308

Feeny PP (1976) Plant apparency and chemical defense. In: Wallace JW, Mansell RL (eds) Biochemical interactions between plants and insects. Plenum, New York, pp 1–40

Feibert EB, Langenheim JH (1988) Leaf resin variation in *Copaifera langsdorfii*: relation to irradiance and herbivory. Phytochemistry 27:2527–2532

Fiala B, Maschwitz U (1992) Food bodies and their significance for obligate ant-association in the tree genus *Macaranga* (Euphorbiaceae). Bot J Linn Soc 110:61–75

Fiala B, Grunsky H, Mashwitz U, Linsenmair KE (1994) Diversity of ant-plant interactions: protective efficacy in *Macaranga* species with different degrees of ant association. Oecologia 97:186–192

Fonseca F, Benson WW (2003) Ontogenetic succession in Amazonian ant trees. Oikos 202:407–412

Frías R (1996) Ecología del mutualismo entre *Cecropia obtusifolia* y hormigas *Azteca* en la selva de Los Tuxtlas. Universidad Nacional Autónoma de México, Mexico City

Fritz RS, Hochwender CG, Lewkiewicz DA, Bothwell S, Orians CM (2001) Seedling herbivory by slugs in a willow hybrid system: developmental changes in damage, chemical defense, and plant performance. Oecologia 129:87–97

Fusco G (2001) How many processes are responsible for phenotypic evolution? Evol Dev 3:279–286

Gaume L, McKay D, Terrin S (1998) Ant-planr momopteran mutualism: how the third partner affects the interaction between a plant-specialist ant and its myrmecophyte host. Proc R Entomol Soc B 265:569–575

Gleadow RM, Woodrow IE (2000) Temporal and spatial variation in cyanogenic glycosides in *Eucalyptus cladocalyx*. Tree Physiol 20:591–598

Goodger JQD, Ades PK, Woodrow IE (2004) Cyanogenesis in *Eucalyptus plynthemos* seedlings: heritability, ontogeny and effect of soil nitrogen. Tree Physiol 24:681–688

Goodger JQD, Gleadow RM, Woodrow IE (2006) Growth cost and ontogenetic expression patterns of defence in cyanogenic *Eucalyptus* spp. Trees 20:757–765

Goodger JQD, Choo TYS, Woodrow IE (2007) Ontogenetic and temporal trajectories of chemical defence in a cyanogenic eucalypt. Oecologia 153:799–808

Goralka RJL, Langenheim JH (1996) Implications of foliar monoterpenoid variation among ontogenetic stages of California bay tree (*Umbellularia californica*) for deer herbivory. Biochem Syst Ecol 24:13–23

Gowda JH, Palo RT (2003) Age-related changes in defensive traits of *Acacia tortilis* Hayne. Afr J Ecol 41:218–223

Guedes RNC, Zanuncio TV, Medeiros GB (2000) Species richness and fluctuation of defoliator Lepidoptera populations in Brazilian plantations of *Eucalyptus grandis* as affected by plant age and weather factors. For Ecol Manag 137:179–184

Hanley ME, Lamont BB, Fairbanks MM, Rafferty CM (2007) Plant structural traits and their role in anti-herbivore defence. Perspect Plant Ecol 8:157–178

Harper JL (1977) Population biology of plants. Academic, New York

Haukioja E, Koricheva J (2000) Tolerance to herbivory in woody vs. herbaceous plants. Evol Ecol 14:551–562

Heil M, McKey D (2003) Protective ant-plant interactions as model systems in ecological and evokutionary research. Annu Rev Ecol Syst 34:425–453

Herms DA, Mattson WJ (1992) The dilemma of plants: to grow or to defend. Quart Rev Biol 62:186–202

Hódar JA, Zamora R, Castro J, Gómez JM, García D (2008) Biomass allocation and growth responses of Scots pine saplings to simulated herbivory depend on plant age and light availability. Plant Ecol 197:229–238

Hyatt LA, Rosenberg MS, Howard TG, Bole G, Fang W, Anastasia J, Brown K, Grella R, Hinman K, Kurdziel JP, Gurevitch J (2003) The distance dependence prediction of the Janzen-Connell hypothesis: a meta-analysis. Oikos 103:590–602

Jachmann H (1989) Food selection by elephants in the Miobbo biome, in relation to leaf chemistry. Biochem Syst Ecol 17:15–24

Janzen DH (1966) Coevolution of mutualism between antes and *Acacias* in Central America. Evolution 20:249–275

Janzen DH (1969) Allelopathy by myrmecophytes: the ant *Azteca* as an allelopathic agent of *Cecropia*. Ecology 50:147–153

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–527

Jogia MK, Sinclair ARE, Andersen RJ RJ (1989) An antifeedant in balsam poplar inhibits browsing by snowshoe hares. Oecologia 79:189–192

Karban R (1990) Herbivore outbreaks on only trees: testing hypotheses about aging and induced resistance. Oikos 59:27–32

Karban R, Baldwin IT (1997) Induced responses to herbivory. University of Chicago Press, Chicago

Kearsley MJ, Witham TG (1989) Developmental changes in resistance to herbivory: implication for individuals and populations. Ecology 70:422–434

Laitinen J, Julkunen-Tiitto R, Rousi M, Heinonen J, Tahvanainen J (2005) Ontogeny and environment as determinants of the secondary chemistry of three species of white birch. J Chem Ecol 31:2243–2262

Langenheim JH, Stubblebine WH (1983) Variation in leaf resin composition between parent tree and progeny in *Hymenea:* implications for herbivory in the humid tropics. Biochem Syst Ecol 11:97–106

Langenheim JH, Convis CL, Macedo CA, Stubblebine WH (1986) *Hymenaea* and *Copaifera* leaf sesquiterpenes in relation to lepidopteran herbivory in southeastern Brazil. Biochem Syst Ecol 14:41–49

Latta RG, Linhart YB (1997) Path analysis of natural selection on plant chemistry: the xylem resin of ponderosa pine. Oecologia 109:251–258

Lehtilä K (2000) Modeling compensatory regrowth with bud dormancy and gradual activation of buds. Evol Ecol 14:315–330

Liu Z, Stanley BC, Wayne JB, Ying Y, Roysell JC, Matthew JF, John CA (1998) Variations in the secondary metabolite camptothecin in relation to tissue age and season in Camptotheca acuminata. Tree Physio 18:265–270

Llandres LA, Rodríguez-Gironés MA, Dirzo R (2010) Tropical dry forest plants and plant stages with bodyguards are more palatable and suffer less herbivory than their undefended counterparts. Biol J Linn Soc 101:536–543

Loney PE, McArthur C, Potts BM, Jordan GJ (2006) How does ontogeny in a *Eucalyptus* species affect patterns of herbivory by Brushtail Possums? Funct Ecol 20:982–988

Lubchenco J, Gaines SD (1981) A unified approach to marine plant-herbivore interactions. I. Populations and communities. Ann Rev Ecol Syst 12:405–437

Macedo CA, Langenheim JH (1989) Microlepidopteran herbivory in relation to leaf sesquiterpens in *Copaifera langsdorfii* adult trees and their seedling progeny in a brazilian woodland. Biochem Syst Ecol 17:217–224

Marquis RJ (1984) Leaf herbivores decrease fitness of a tropical plant. Science 226:537–539

Martínez-Ramos M, Álvarez-Buylla E, Sarukhán J (1989) Tree demography and gap dynamics in a tropical rain forest. Ecology 70:555–558

Narbona E, Dirzo R (2010) A reassessment of the function of floral nectar in *Croton suberosus* (Euphorbiaceae): a reward for plant defenders and pollinators. Am J Bot 97:672–679

Neilson EH, Goodger JQD, Woodrow IE (2006) Novel aspects of cyanogenesis in *Eucalyptus camphora* subsp. *humeana*. Funct Plant Biol 33:487–496

Niering WA, Whittaker RH, Lowe CH (1963) The saguaro: a population in relation to environment. Science 142:15–23

Nomura M, Itioka T, Murase K (2001) Non-ant antiherbivore defenses before plant-ant colonization in *Macaranga* myrmecophytes. Pop Ecol 43:207–212

Nykänen H, Koricheva J (2004) Damage-induced changes in woody plants and their effects on insect herbivore performance: a meta-analysis. Oikos 104:247–268

Price PW (1991) The plant vigor hypothesis and herbivore attack. Oikos 62:244–251

Price PW, Roinen H, Tahvanainen J (1987) Plant age and attack by the bud galler, *Euura mucronata*. Oecologia 73:334–337

Rehill BJ, Whitham TG, Martinsen GD, Schweitzer JA, Bailey JK, Lindroth RL (2006) Developmental trajectories in cottonwood phytochemistry. J Chem Ecol 32:2269–2285

Reichardt PB, Bryant JP, Clausen TP, Wieland GD (1984) Defense of winter-dormant Alaska paper birch against snowshoe hares. Oecologia 65:58–69

Rosenthal JP, Kotanen PM (1994) Terrestrial plant tolerance to herbivory. Trends Ecol Evol 9:145–148

Rousi M, Häggman J, Bryant JP (1987) The effect of bark phenols upon mountain hare barking of winter-dormant Scots pine. Holarctic Ecol 10:60–64

Rousset O, Lepart J (2000) Positive and negative interactions at different life stages of a colonizing species (*Quercus humilis*). J Ecol 88:407–412

Rudgers JA (2004) Enemies of herbivores can shape plant traits: selection in a facultative ant-plant mutualism. Ecology 85:192–205

Rudgers JA, Strauss SY, Wendel JE (2004) Trade-offs among anti-herbivore resistance traits: insights from Gossypieae (Malvaceae). Am J Bot 91:871–880

Sánchez-Hidalgo ME, Martínez-Ramos M, Espinoza-García F (1999) Chemical differentiation between leaves of seedlings and spatially close adult trees from the tropical rainforest species *Nectandra ambigens* (Lauraceae): an alternative test of the Janzen-Connell model. Funct Ecol 13:725–732

Schappert PJ, Shore JS (2000) Cyanogenesis in *Turnera ulmifolia* L. (Turneraceae): II. Developmental expression, heritability and cost of cyanogenesis. Evol Ecol Res 2:337–352

Schupp EW (1986) *Azteca* protection of *Cecropia:* ant occupation benefits juvenile trees. Oecologia 70:379–385

Seiwa K (1999) Changes in leaf phenology are dependent on tree height in *Acer mono*, a deciduous broad-leaved tree. Ann Bot 83:355–631

Sinclair ARE, Smith JNM (1984) Do plant secondary compounds determine feeding preferences of snowshoe hares? Oecologia 61:403–410

Smit C, Den Ouden J, Müller-Schärer H (2006) Unpalatable plants facilitate tree sapling survival in wooded pastures. J Appl Ecol 43:305–312

Spiegel LH, Price PW (1996) Plant aging and the distribution of *Rhyaciona neomexicana* (Lepidoptera: Tortricidae). Environ Entomol 25:359–365

Sugiura S, Abe T, Makino S (2006) Loss of extrafl oral nectary on an oceanic island plant and its consequences for herbivory. Am J Bot 93:491–495

Sultan SE (2005) An emerging focus on plant ecological development. New Phytol 166:1–5

Swaine MD, Whitmore TC (1988) On the definition of ecological species groups in tropical rain forests. Vegetatio 75:81–86

Swihart RK, Bryant JP (2001) Importance of biogeography and ontogeny of woody plants in winter herbivory by mammals. J Mammal 82:1–21

Tahvanainen J, Helle E, Julkunen-Tiitto R, Lavola A (1985) Phenolic compounds of willow bark as deterrents against feeding by mountain hare. Oecologia 65:319–323

Tiffin P (2000) Mechanisms of tolerance to herbivore damage: what do we know? Evol Ecol 14:523–536

Trager MD, Bruna EM (2006) Effects of plant age, experimental nutrient addition and ant occupancy on herbivory in a neotrpical myrmecophyte. J Ecol 94:1156–1163

Turner IM (1994) Sclerophylly: primarily protective? Funct Ecol 8:669–675

Van Bael SA, Brawn JD, Robinson SK (2003) Birds defend trees from herbivores in a Neotropical forest canopy. P Natl Acad Sci USA 100:8304–8307

Van Zandt P (2007) Plant defense, growth, and habitat: a comparative assessment of constitutive and induced resistance. Ecology 88:1984–1993

Vandenberghe C, Smit C, Pohl M, Buttler A, Freléchoux F (2009) Does the strength of facilitation by nurse shrubs depend on grazing resistance of tree saplings? Basic Appl Ecol 10:427–436

Warner PJ, Cushman JH (2002) Influence of herbivores on a perennial plant: variation with life history stage and herbivore species. Oecologia 132:77–85

Webber BL, Woodrow IE (2009) Chemical and physical plant defence across multiple ontogenetic stages in a tropical rainforest understorey tree. J Ecol 97:761–771

Weiner J (2004) Allocation, plasticity and allometry in plants. Perspect Plant Ecol Evol Syst 6:207–215

Weltzin JF, Archer SR, Heischmidt RK (1998) Defoliation and woody plant (*Prosopis glandulosai*) seedling regeneration: potential *vs* realized herbivory tolerance. Plant Ecol 138:127–135

Wooley SC, Donaldson JR, Gusse AC, Lindroth RL, Stevens ML (2007) Extrafloral nectaries in aspen (Populus tremuloides): heritable genetic variation and herbivore-induced expression. Ann Bot 100:1337–1346

Zagory D, Libby WJ (1985) Maturation-related resistance of *Pinus radiata* to western gall rust. Phytopathology 75:1443–1447