

Chapter 7

Forest Insect—Plant Interactions



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7.1 The Ecology of Insect—Plant Interactions in Forests

Insects and plants dominate terrestrial ecosystems in terms of both species numbers and biomass. Ecological relationships between insects and plants are ubiquitous and insect-plant interactions are important for ecosystem structuring and functioning. Insects probably contain more species than any other group of organisms with an estimated 5.5 million species (Stork et al. 2015). They can affect plants positively, for example as pollinators, or negatively, as consumers of plant tissues and vectors of disease. Herbivorous species that consume living plant tissues make up nearly half of all known insect species. In this chapter, we describe the negative effects herbivorous insects can have on plant fitness and the mechanisms plants use to counter these effects.

Forests cover about 31% of the Earth's land surface (FAO UNEP 2020). A great diversity of forest types, with over 60,000 tree species, support ~ 80% of the planet's biodiversity and provide many vital ecosystem services (Bliss 2011; Beech et al. 2017). Trees exhibit considerable morphological diversity but typically have elongated stems, secondary (woody) growth, and long life spans. Healthy forests deliver global ecosystem services such as carbon storage, biodiversity, and natural climate regulation, while providing humans with building and other industrial materials, energy, and food (Raffa et al. 2009; Trumbore et al. 2015). Healthy forests are adapted

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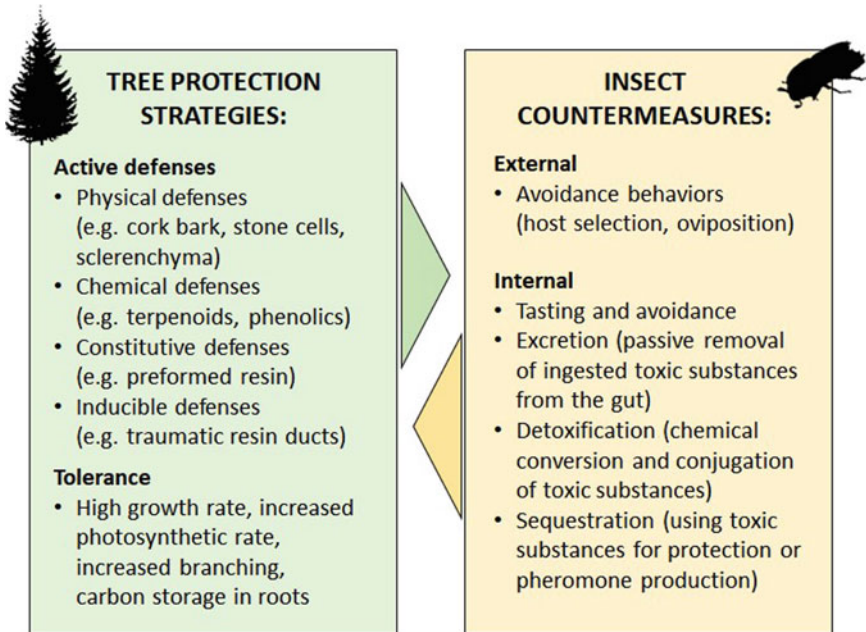


Fig. 7.1 Overview of tree protection strategies to minimize consumption by insects and insect countermeasures to avoid or tolerate tree defenses. The different strategies and countermeasures are presented in depth in the subchapters ‘7.2. The plant side—tree defenses against insects’ and ‘7.3. The insect side—how insects cope with tree defenses’. © Justin Whitehill and Paal Krokene

to tolerate some level of stress caused by pests, pathogens and climate. A major challenge to forest health now and in the future is global climate change and mitigating the effects of climate change will be essential to maintaining healthy, resilient forests for future generations.

In this chapter, we describe insect-tree interactions from the perspective of both insects and trees (Fig. 7.1). We focus on interactions where insects use living trees as a food source and have to overcome or tolerate tree defenses. We first describe tree defense adaptations that minimize consumption by insects, including anatomical, mechanical, biochemical and molecular defenses. Then we explore how insects may counteract these defenses by different mechanisms that detoxify or provide tolerance against tree defenses, using examples of insects that feed internally and externally on both conifers and deciduous trees.

7.2 The Plant Side—Tree Defenses Against Insects

Co-evolution between plants and insects has driven the evolution of specialized plant defense mechanisms as well as insect counter-adaptations (Fraenkel 1959;

Janzen 1966; Walling 2000). Insect herbivory has thus been a major selection force behind species diversification in both plants and insects (Ehrlich and Raven 1964). Plant defenses can reduce the growth, survival, and fertility of attacking insects by disrupting insect feeding and oviposition preferences (Harborne 1993; Walling 2000). Plant defense traits are sometimes discussed without precise knowledge of specific traits, their ecological function, or the mechanisms through which they provide resistance against a pest. However, from an ecological perspective, a defense mechanism can be defined by how specific defense traits interact with and impact specific insect pests. Plants are said to be resistant to a specific insect species when plant defenses inhibit the insect's ability to utilize plant tissues for growth and survival.

Several previous reviews comprehensively explore the various aspects and intricacies of plant defenses against insects in both herbaceous and woody plant systems (Walling 2000; Franceschi et al. 2005; Howe and Jander 2008; Krokene 2015). We discuss the various terminologies associated with tree-insect interaction studies, while providing a conceptual framework to organize how different tree defense traits interact with insect herbivores (Fig. 7.2). This classification framework could be applied to describe any plant defense trait under investigation.

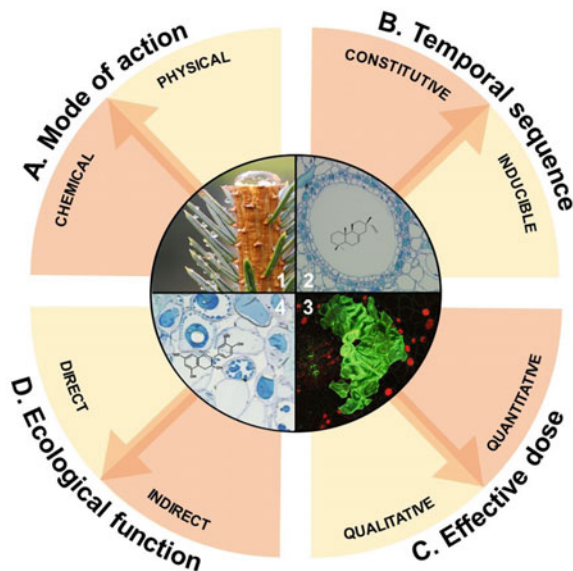


Fig. 7.2 A conceptual overview of plant defense traits within a context of plant–insect interactions. Plant defense traits against insects are categorized according to four different levels of organization. These include: (A) mode of action (plant-side); (B) temporal sequence (interaction between plant and insect); (C) effective dose (insect-side); and (D) ecological function (tritrophic interactions). Individual defense traits can be classified according to any of these categories and examples include: (1) oleoresin, (2) resin ducts and associated metabolites; (3) stone cells and other sclerified cell types; and (4) polyphenolic cells and associated metabolites. © Justin Whitehill and Paal Krokene

Tree defenses against insect pests are highly varied and combine chemical, physical, and molecular traits to resist attack (Franceschi et al. 2005; Krokene 2015; Whitehill et al. 2019). Tree defenses can be categorized in various ways, based on the compounds or structures by which they interfere with insects (physical versus chemical defenses), their effective doses (qualitative versus quantitative defenses), their ecological function (direct versus indirect defenses), or when they become active relative to insect attack (constitutive versus induced defenses) (Fig. 7.2). For example, categorizing tree defense traits by their mode of action contrasts structural and morphological traits that add toughness to tissues (physical defenses), and specialized (or secondary) metabolites that interfere with insect feeding and oviposition through toxic effects (chemical defenses).

7.2.1 *Plant Defense Hypotheses*

The theoretical framework of plant defense theory encompasses several independent but partially overlapping hypotheses. These include the *Optimal Defense (OD)* hypothesis, the *Carbon:Nutrient Balance (CNB)* hypothesis, the *Growth Rate (GR)* hypothesis, and the *Growth-Differentiation Balance (GDB)* hypothesis (Stamp 2003). The expanded *Growth-Differentiation Balance* hypothesis (Loomis 1932; Herms and Mattson 1992) may represent the most mature plant defense hypothesis, as it incorporates all the other hypotheses into its conceptual framework.

The GDB hypothesis provides a framework for predicting how plants balance resource allocation between differentiation-related and growth-related processes over a range of environments. Growth refers to the production of roots, stems and leaves, while differentiation is the process by which cells and tissues take on different functions. These functions can be transport of water and photosynthates or production of specialized metabolites and physical structures involved in defense against herbivory. The production of carbohydrates through photosynthesis represents the inflection point between growth and differentiation/defense. The GDB hypothesis predicts a trade-off in allocation to growth and defense that depends on resource availability (Stamp 2003).

Rigorously testing the GDB hypothesis in trees has proven difficult because trees have long lifespans and engage in complex ecological interactions. The diverse responses observed in tree chemical defenses to various nutrient levels in field studies suggest there is a need for comprehensive, multi-faceted experiments to test the GDB hypothesis. Such experiments should incorporate molecular, biochemical and ecological approaches to fully understand the subtle complexities of interactions that occur between herbivores and trees (Glynn et al. 2007; Kleczewski et al. 2010). Additionally, induced plant defenses play a critical role in many plant–insect interactions, but induced defenses have yet to be adequately incorporated into plant defense theories.

7.2.2 *Defense, Resistance, Tolerance*

Forestry and ecology are broad fields of study that each overlap with other disciplines. Each field approaches research questions from many angles and as a result can develop similar terminologies with very different meanings. The exact meaning of a term can vary based on the questions being explored, the lens through which the researcher studying these traits is viewing them, and the level of biological organization at which an interaction is being studied. For example, ecologists refer to quantitative and qualitative defense traits from the perspective of a trait and its dose-dependent direct impact on an insect, such as the effective lethal dose of a chemical required for mortality. Conversely, forest geneticists refer to quantitative and qualitative defense traits from the perspective of tree genetics. A quantitative defense ‘trait’ from the perspective of a geneticist refers to a phenotypic trait controlled through multiple genetic loci or nucleotides. We attempt to provide context to the area of tree defense traits and the intersection of terminologies across the major disciplines that study tree-insect interactions.

In this chapter, we distinguish between tree defense and tree resistance, although these terms are often used vaguely interchangeably. ‘Defense’ generally refers to the ways in which a tree defends itself from for example an insect attack. But just because defenses are present when an insect attacks, they may not be effective at protecting the tree. The absence of an effect may be due to insect counter-adaptations shaped through a shared co-evolutionary history with the tree. ‘Resistance’ is an observable phenotype that results from the interaction between the tree and an insect pest. Tree resistance occurs when one or several defense traits, working alone or together, provide complete or nearly complete protection from insect attack. For example, the resistance phenotype of Sitka spruce (*Picea sitchensis*) against spruce weevil (*Pissodes strobi*) is a result of multiple physical and chemical defense traits working together to provide resistance (Whitehill et al. 2019). However, while most Sitka spruce trees have chemical defense traits resembling those of resistant trees, the absence or reduction in a single physical defense trait may lead to susceptibility to insect attack (Whitehill et al. 2019). When multiple defense traits work together to provide resistance against an insect pest, the synergism between the traits is defined as a defense syndrome (Agrawal and Fishbein 2006; Raffa et al. 2017; Whitehill et al. 2019).

There is often no clear-cut line that separates resistance and susceptibility. Rather, complete resistance and complete susceptibility represent extremes along a continuum of tree phenotypes. To describe phenotypes that are neither completely resistant nor completely susceptible, the term tolerance is sometimes used. However, such intermediate phenotypes are usually categorized as partially resistant. Partial (or quantitative) resistance would describe a phenotype where a plant may not succumb completely to insect attack, but suffers a significant reduction in biomass compared to resistant genotypes. This type of resistance is typically due to many genes with small individual effects and appears to be the norm in insect-plant interactions (Kliebenstein 2014; French et al. 2016). For instance, induced terpene accumulation in Norway

spruce (*Picea abies*) trees showed a negative relationship with attack success by the Eurasian spruce bark beetle (*Ips typographus*) (Zhao et al. 2011). Trees with high induced terpene levels had fewer and less successful beetle attacks than trees with low terpene levels. This example highlights the dose-dependent nature of plant defense traits against insects, because the level of resistance in individual spruce trees depended on the concentration of defensive terpenes in the attacked tissues.

The term tolerance is usually reserved for a clearly defined plant phenotype with compensatory responses to insect attack. Tolerance is achieved through mechanisms that modulate the plants' primary metabolism and is thus a distinct plant protection strategy that differs from the active defense strategies described above. Plants that are tolerant to herbivory are characterized by having: (1) high relative growth rates; (2) increased net photosynthetic rate after damage; (3) increased branching or tillering after release of apical dominance; (4) pre-existing high levels of carbon storage in roots available for allocation to above-ground reproduction; and (5) the ability to shunt carbon stores from roots to shoots after damage (Strauss and Agrawal 1999). Tolerance mechanisms thus involve changes in primary metabolism that mitigate negative effects of herbivore attack. We will not discuss tolerance further in this chapter, but rather focus on defense traits that actively protect trees against herbivory.

7.2.3 Mode of Action: Chemical and Physical Defenses in Trees

Plant defense traits can be distinguished by their mode of action of interfering with insects. Modes of action include chemical traits that have, for example, toxic effects and physical traits that provide a mechanical barrier, as well as traits that combine both modes (Fig. 7.2). Chemical and physical defense traits are considered the major components of a plant's defense system (Painter 1951; Gatehouse 2002).

Defensive plant chemicals may be species-specific and expressed in certain tissues or cell types (Walling, 2000). Chemical defense traits have received much attention since Gottfried Fraenkel's seminal 1959 paper 'The *raison d'être* of secondary substances'. Fraenkel (1959) documented the defense chemistry of several common plant families and how these chemicals interact with known herbivore pests. He correctly highlighted that while many scientists had studied phytochemicals for their own purposes and applications, no one had accurately stated their intrinsic biological function and reason for existing—their *raison d'être*. Several reviews have been published on the topic of chemical diversity, ecological function, and mechanisms of chemical defense in forest trees, including poplar (Phillippe and Bohlmann 2007), ash (Kostova and Iossifova 2007), oak (Salminen and Karonen 2011), eucalyptus (Naidoo et al. 2014), pine (Gijzen et al. 1993), and spruce (Keeling and Bohlmann 2006; Celedon and Bohlmann 2019). Well-studied defense chemicals in trees include terpenoids and phenolics.

Terpenoids make up the largest group of plant chemicals with tens of thousands of known compounds (Celedon and Bohlmann 2019; Fig. 7.3). They are structurally diverse, metabolically costly to produce, may occur in large quantities or as minor compounds, and can be toxic or inhibitory to a variety of insects and microorganisms (Raffa et al. 1985; Gershenzon 1994; Celedon and Bohlmann 2019). Terpenoids play important defensive roles in many conifers (Keeling and Bohlmann 2006). They are biosynthesized from five-carbon building blocks to produce monoterpenes (10 carbons), sesquiterpenes (15 carbons), diterpenes (20 carbons), and higher-order terpenes. Conifer resin typically consists predominantly of monoterpenes and diterpenes, and often-smaller amounts of sesquiterpenes and other compounds (Keeling and Bohlmann 2006). Different conifer species produce diverse resin mixtures containing dozens of individual terpenes (Schiebe et al. 2012). These compounds are produced by terpene synthases and cytochrome P450s that often make multiple products. A single terpene synthase (γ -humulene synthase) in grand fir (*Abies grandis*) can for example make 52 different sesquiterpene products (Steele et al. 1998). Such multiproduct enzymes contribute to the high biochemical diversity of conifer resin, and maintaining this chemical diversity seems to be an important part of the defense strategy of conifers (Ro et al. 2005; Keeling and Bohlmann 2006).

Phenolics in plants total several thousand compounds, including many with toxic or repellent effects towards insects and microorganisms (Lindroth and Hwang 1996; Zeneli et al. 2006; Fig. 7.3). Phenylalanine is a common precursor for the formation of

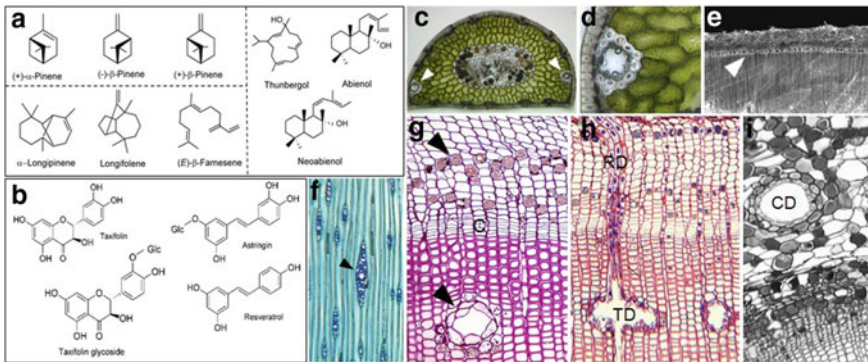


Fig. 7.3 Examples of chemical defenses in trees. (a) Monoterpenes (top left), sesquiterpenes (bottom left) and diterpenes (right) are the main constituents of conifer resin. (b) Soluble phenolics like flavonoids (left) and stilbenes (right) are important chemical defenses in many tree species. (c) Cross-section of a mountain pine (*Pinus mugo*) needle showing two resin ducts, with a close-up of one duct (d). (e) Cross-section of Norway spruce (*Picea abies*) stem showing a ring of traumatic resin ducts formed in response to external stress. (f) Tangential section of Scots pine (*Pinus sylvestris*) latewood showing a large radial ray with a resin canal in the center. (g) Cross-section of Scots pine stem showing an axial resin duct in the young sapwood and phenol-containing parenchyma cells in the young phloem (C: vascular cambium). (h) Cross-section of Norway spruce stem showing axially oriented traumatic resin ducts (TD) in the sapwood, interconnected with a radial resin duct (RD). (i) Cross-section of a balsam fir (*Abies balsamea*) stem showing a large cortical resin duct (CD) in the phloem surrounded by dark phenol-rich cells. © Justin Whitehill and Paal Krokene

phenolics, including flavonoids, stilbenes, condensed tannins and other polyphenolics, as well as the structural polymer lignin (Dixon et al. 2001). Beyond lignin, which is the major phenolic in all trees, some tree species invest considerable resources into phenolic defenses. For example, 35% of leaf dry weight in poplar may consist of condensed tannins and other phenolics (Lindroth and Hwang 1996). So-called soluble phenolics, which include stilbenes and flavonoids (Fig. 7.3), are abundant in conifer bark and have been studied extensively. Stilbene production is inducible but stilbene levels do not appear to increase following bark beetle attack or fungal infection (Zeneli et al. 2006; Schiebe et al. 2012), probably because the fungi metabolize stilbenes at a faster rate than the tree can produce them (Hammerbacher et al. 2013).

Defense traits such as terpenoid resins, latexes and gums play well-documented chemical roles in tree-insect interactions, but these traits can also be considered physical defenses. The mechanical properties of these toxic substances can physically trap or expel insects that attempt to bore into a tree. As an example, terpenoid resin is stored under pressure in specialized resin ducts in many conifers. Tunneling insects that rupture these ducts may be flushed out by the resin flow and trapped in the sticky, toxic substance (Christiansen et al. 1987; Franceschi et al. 2005).

Some of the classical literature on plant-insect interactions emphasized physical defenses, noting that ‘repellent factors [...] are very frequently physical in nature’ and that these factors influence feeding patterns of insects and other herbivores (Dethier 1941). Trees have several cell types and anatomical structures that reduce insect feeding by providing physical toughness or thickness to tissues. Physical defense traits may reside inside tissues and cells or they may be structures exposed on the plant surface. They include spines, thorns, trichomes on leaf surfaces, bark texture, leaf toughness, granular minerals incorporated into tissues, and increased quantities of specialized sclerenchyma cells (Wainhouse et al. 1990; Franceschi et al. 2005; Ferrenberg and Mitton 2014; Whitehill et al. 2016a, 2016b, 2019). The mode of action of these traits is to disrupt feeding and tunneling of adult insects and larvae by wearing down their mouthparts or interfering with digestion (Raupp, 1985; Wainhouse et al. 1990; Whitehill et al. 2016b). A number of studies have highlighted that physical plant defenses play similarly important roles as chemical traits, depending on the species under investigation (Massey and Hartley 2006; Hanley et al. 2007; Carmona et al. 2011; Ferrenberg and Mitton 2014; Lopresti and Karban 2016).

The periderm, the tough outer surface of the bark, is the first line of physical and chemical protection against insects and also protects trees against desiccation and fire (Krokene 2015). The outermost part of the periderm is the cork, the dry bark layer that is paper thin in young trees, but may be more than 30 cm thick in older conifer trees. The cork consists of mostly dead cells reinforced with lignin and lipophilic suberin polymers (Franceschi et al. 2005). The texture of the outer bark surface may also serve as a physical defense. Trees with smooth, slippery bark have been observed to have fewer bark beetle attacks compared to trees with rough bark. Lower brood production under smooth outer bark that is more difficult for beetles to grip suggests reduced oviposition on such slippery bark surfaces (Ferrenberg and Mitton 2014).

Inside the periderm there are other more localized physical defenses, such as stone cells, fiber cells and calcium oxalate crystals. Stone cells are tough, highly lignified cells that function as a dose-dependent physical defense against insects (Wainhouse et al. 1990; Whitehill et al. 2016a, 2016b, 2019; Fig. 7.2). Fiber cells are lignified sclerenchyma cells that form densely spaced concentric sheets in the inner bark of many conifers. These sheets appear to be an effective barrier to bark beetles and other insects that attempt to penetrate the bark (Franceschi et al. 2005). Granular minerals such as calcium oxalate crystals are also interspersed throughout the bark of both angiosperm and conifer trees. These crystals are tough, pointed physical structures found inside and outside the cell walls in different plant tissues (Franceschi et al. 2005; Massey et al. 2007). The crystals are thought to provide protection from chewing insects.

While insects may adapt to chemical defenses, for example through mechanisms of secretion or detoxification (Despres et al. 2007), resistance based on anatomical defenses may be more difficult for insects to overcome (Whitehill et al. 2019). In conifers for example, stone cells have been recognized as a substantial determinant of resistance in different spruce species against several destructive forest pests, such as bark beetles and weevils (Wainhouse et al. 1990; Whitehill et al. 2016a, 2019; Whitehill & Bohlmann, 2019). Stone cells can provide resistance against phloem feeding weevils through at least three mechanisms: (i) they form a physical barrier that prevents establishment and movement of neonate larvae, (ii) they physically displace more nutritious host tissue and thereby reduce larval development, and (iii) they cause mandible damage to young larvae which affects feeding. By acting as a physical barrier that slows larval development, stone cells also increase larval exposure to other defenses such as resin (Whitehill et al. 2019). Such synergism between stone cells and resin-based defenses constitutes a robust defense syndrome that is difficult for insects to overcome (Whitehill and Bohlmann 2019).

7.2.4 Temporal Sequence: Constitutive, Induced and Primed Defenses in Trees

The distinguishing feature of constitutive and induced defenses is the time when they are deployed. Constitutive defenses are always present, even in the absence of insect attack. They can be viewed as an insurance against the attacks that almost inevitably will come during the long life of a tree (Franceschi et al. 2005). Examples of constitutive defenses in conifers are polyphenolic cells in the phloem that store phenolic metabolites, which are released upon insect feeding (Franceschi et al. 1998; Nagy et al. 2014), (ii) resin ducts filled with terpene-rich oleoresin (Celedon and Bohlmann 2019), and (iii) stone cells functioning as physical barriers (Whitehill et al. 2016a, 2019; Whitehill and Bohlmann 2019). In contrast, induced defenses are mobilized in response to an attack (Eyles et al. 2010). Examples of induced defenses are the formation of traumatic resin ducts in conifer wood and the hypersensitive

response in foliage. Constitutive and induced plant defenses can be both physical and chemical in nature.

The concepts of constitutive and induced defenses play central roles in plant defense theory. Plant survival and competitive success require that plants optimize how they allocate the resources they have available. Resource allocation is primarily dependent upon carbon availability (i.e. photosynthate), which is used for two major purposes: growth or defense (Herms and Mattson 1992; Stamp 2003). Defense theory predicts that plant defense responses to insect attack are largely determined by the resources the plant has access to and how those resources are allocated within the plant. When resources are allocated to physical and chemical defenses, less are available to grow new leaves and other vegetative structures. This trade-off concept is crucial to understanding both the nature of present-day plant defenses and the evolutionary history of plant defense mechanisms. Inducible defenses are thought to have evolved as a means to reduce the overall costs associated with defense, since inducible defenses only are activated when they are needed, i.e. after an attack has occurred (Steppuhn and Baldwin 2007). Induction of plant defenses reduces the amount of resources diverted to specialized metabolism and facilitates a return to growth-dominated activities once a threat from an invading pest has been removed. Additionally, induced defenses can be targeted to the site of an ongoing attack and thereby further reduce resource allocation to defense, since the plant does not invest in defending tissues that are not being attacked.

In some cases, trees can trigger systemic defense responses in unattacked tissues following insect attack (Philippe and Bohlmann 2007; Eyles et al. 2010; Krokene 2015). Systemic induction of defense prepares plants for insect attack through signaling cascades involving the octadecanoid pathway, the plant hormone ethylene, or small peptides that induce defenses throughout the plant (Philippe and Bohlmann 2007; Eyles et al. 2010). Trees can also activate a form of delayed induced defense known as defense priming. Delayed or long-term defenses in trees are based on two, non-mutually exclusive mechanisms of induced defenses: prolonged up-regulation of induced defenses and defense priming (Wilkinson et al. 2019). Prolonged up-regulation of induced defenses simply means that defenses induced by insect attack or fungal infection remain up-regulated for weeks or months and thus provide resistance to subsequent attacks. Because resources are diverted away from growth to defenses for a long time, prolonged up-regulation of induced defenses may be a costly defense strategy. A more cost-efficient mechanism of long-term induced defense is defense priming. When a plant is primed, induced defenses are sensitized in a way that provides faster and/or stronger activation of induced defenses in response to future attacks (Conrath et al. 2015). Following a priming stimulus, defenses are maintained at constitutive or weakly induced levels, but are then rapidly activated upon subsequent attack (Pastor et al. 2013). The priming stimuli may be wounding, colonization by insects, pathogens or beneficial organisms, or treatment with chemical compounds (Mauch-Mani et al. 2017).

Defense priming can provide very effective protection of forest trees. For example, Norway spruce trees in an area with epidemic bark beetle populations became almost completely resistant to attack when they had been treated with the wound hormone

methyl jasmonate as a priming stimulus (Mageroy et al. 2020a). The molecular mechanisms responsible for defense priming in Norway spruce and other trees are still unclear, but many defense-related gene transcripts in spruce bark showed a primed response after methyl jasmonate treatment, including transcripts for Pathogenesis-Related (PR) proteins and epigenetic regulators (Mageroy et al. 2020b).

7.2.5 Effective Dose: Qualitative and Quantitative Defenses in Trees

Historically, the terms qualitative and quantitative defenses have been used mostly for chemical traits and refer to the dosage required for specific compounds to negatively affect a feeding insect. Toxic compounds that are effective in low amounts are said to be qualitative and compounds that must be ingested in high amounts to have an effect are considered quantitative. The terms were established and popularized by Feeny (1976) and Rhoades & Cates (1976) to explain the evolution of plant defenses based on plant apparency, i.e. how likely a plant is to be found by an herbivore. Large and long-lived plants that are easily found by herbivores are ‘apparent’, and small or ephemeral plants that are less likely to be found are ‘unapparent’. Qualitative defense traits were predicted to be dominant in unapparent plants while quantitative defense traits were predicted to be dominant in apparent plants.

Qualitative chemical defenses are potent toxins that are effective at very small doses against most insect species, i.e. against generalist pests without co-evolved countermeasures. Examples of qualitative plant chemicals are small toxic molecules such as certain alkaloids and cyanogenic compounds. Insects that have co-evolved with their host plant may have adapted countermeasures to such qualitative defenses. Such specialist insects may for example sequester qualitative defense metabolites and use them for their own protection against predators and parasites (Rhoades and Cates 1976; Agrawal and Kurashige 2003). Strong selection pressures and short generation times may allow insect pests to rapidly evolve counter-adaptations and overcome tree defenses through specialization (Despres et al. 2007). Therefore, qualitative defenses in forest trees typically do not provide robust resistance against adapted insect pests, and the application of qualitative defenses for long-term pest management is not a viable strategy.

Quantitative chemical defenses, on the other hand, involve specialized metabolites such as tannins, with a dose-dependent effect and are generally effective against an herbivore only in high amounts. Due to the basic mechanisms by which quantitative defenses interfere with the physiology of an insect, it is difficult for insect pests to evolve countermeasures against these traits. Quantitative defenses thus tend to be effective against both specialist and generalist species. However, quantitative defenses may come at a high cost: because they are most effective in high concentrations they are energetically costly to produce and maintain.

Interestingly, in contrast to chemical defenses, physical defense traits have received less attention in plant defense hypotheses dealing with quantitative versus qualitative defense. Hay (2016) points out limitations of the plant apparency model and makes the case that ‘plants are rarely defended by one compound or even by chemistry alone’. We propose that existing plant defense hypotheses incorporate physical defenses as an integral part of a synergistic plant defense system. As an example of a synergy between chemical and physical defense in trees, stone cells are a constitutive, quantitative and physical defense in Sitka spruce against the spruce weevil (Whitehill and Bohlmann 2019). Stone cells provide a robust resistance that synergizes the effect of a physical defense with terpenoid chemical defenses, which are both constitutive and induced and may be either quantitative or qualitative (Whitehill and Bohlmann 2019).

7.2.6 Ecological Function: Direct and Indirect Defenses in Trees and Tri-Trophic Interactions

Tree defenses that directly affect the physiology or behavior of an insect, and thus impair its growth, survival or reproduction, are defined as direct defenses (Fig. 7.2). However, a tree can also attract species in its environment to protect it against attackers. Such indirect defenses can involve the release of volatile metabolites, which may attract predators and parasitoids of plant-feeding insects. Such volatiles may be induced locally or systemically by activity of the insect and are then called herbivore-induced plant volatiles (HIPVs) (Turlings and Erb 2018; Wilkinson et al. 2019). When plants attract natural enemies of plant-feeding insects they engage in tri-trophic interactions, i.e. interactions with reciprocal ecological impacts between three trophic levels: a primary producer, a herbivore, and the herbivore’s natural enemy. By engaging in tri-trophic interactions, plants can benefit from the vulnerability of plant-feeding insects to natural enemies. This is the premise for the tri-trophic niche concept, which states that certain plants may be an enemy-sparse or enemy-dense space for herbivores (Singer and Stireman 2005). Plants can increase or reduce the predation risk of an herbivore by releasing HIPVs or providing toxic plant metabolites that the herbivore can sequester and use in their anti-predator defense.

Tri-trophic interactions involving HIPV signaling have been mostly studied in herbaceous angiosperms but are also known from both angiosperm and gymnosperm trees (Turlings and Erb 2018). When Scots pine (*Pinus sylvestris*) needles are attacked by ovipositing sawflies, their foliage emits the sesquiterpene (*E*)- β -farnesene. This HIPV attracts a specialized egg parasitoid, which oviposits inside the sawfly eggs, thereby reducing the growth and ultimately survival of the sawfly larvae (Hilker et al. 2002). Similarly, black poplar (*Populus nigra*) responds to feeding by spongy moth (*Lymantria dispar*) larvae by releasing HIPVs that attract the spongy moth parasitoid *Glyptapanteles liparidis* (Clavijo-McCormick et al. 2014). Tri-trophic interactions have also been demonstrated belowground, at least in angiosperm systems. When

insect larvae are feeding upon maize (*Zea mays*) roots, they emit a sesquiterpene that attracts nematodes, which then infect the larvae (Rasmann et al. 2005). Because indirect defenses involving tri-trophic interactions are found across the plant kingdom this is probably an ancient plant defense strategy that emerged early in the evolution of land plants (Mumm and Dicke 2010).

7.3 The Insect Side—How Insects Cope with Tree Defenses

Insect and host tree populations usually exist in some sort of equilibrium, where insect attacks are countered by tree defenses. Most insect herbivores subsist at low levels where they are rarely noticed, whereas others go through boom and bust cycles as part of their normal ‘outbreak’ behavior. Outbreak species are often referred to as ‘pests’, particularly if they damage economically important tree species. The delicate balances that regulate insect populations around an equilibrium are sometimes disrupted, for example if trees are suffering due to anthropogenic factors such as movement of species and climate change. Insect populations that are out of balance—because they are introduced into new environments or are favored by changing climates—often become pests.

Interactions between herbivorous insects and trees are highly variable. This diversity is a product of the enormous number of insect species that feed on trees and the many different ways that trees can be exploited by insects. Because of their large dimensions, long life cycles, and complex architecture, trees provide numerous niches that can be exploited by insects with many different lifestyles. Much of a tree consists of lignified organs and tissues, both above ground (main stems, branches, twigs) and below ground (roots in many different diameter classes). Wood may contain living cells, like the water-conducting sapwood, or consist mostly of dead cells, such as the heartwood. Bark, needles and leaves also offer a large and apparent array of living tissues that support many different insects. Tree-feeding insects subsist on their hosts by utilizing various feeding strategies and can be grouped into so-called feeding guilds. Feeding guild largely dictates the mechanisms by which different insects may cope with tree defenses. The oldest known fossil record of insects feeding on plants dates back approximately 400 million years and consists of fossilized insect guts or feces and feeding damage on fossilized plants (Labandeira 1998). Insect herbivory presumably originated as generalist feeding on foliage and diversified into specialized feeding guilds. The earliest fossils of insects feeding on living woody or wood-like tissues are 350 million years old. Wood-boring is considered a primitive life habit for beetles and their immediate ancestors have evolved into some of the most destructive present-day forest pests (Vega and Hofstetter 2015).

7.3.1 A Note on Generalist and Specialist Insect Herbivores

The mechanisms trees use to defend themselves are usually effective against most herbivorous insect species in the trees' natural environment. However, some insects have co-evolved with their host tree to overcome tree defenses. Such co-evolved species can successfully colonize unique niches that are not readily available to non-adapted competitors (Despres et al. 2007). Based on their host relationships herbivorous insects are often categorized as either specialist or generalist species. These terms are usually used within the context of chemical defenses as opposed to physical defenses. Specialist insects have evolved mechanisms that allow them to feed on a select set of plant species with a high concentration of a particular type of chemical defense, while these plants would not be suitable hosts for most other insects. In extreme cases, while increasing the insect's fitness on its preferred host(s), this specialization may have reduced its fitness on other plants. Generalist insects are species that have a much wider host range than specialists and are able to deal with more diverse chemical defenses, at least at low to moderate concentrations. The terms 'generalist' and 'specialist' are widely used in the literature but there are no defined set of criteria that clearly differentiates generalists from specialists (Ali and Agrawal 2012).

7.3.2 Insect Feeding Guilds and Their Interaction with Tree Defenses

Herbivore feeding or trophic guilds are groups of species that exploit the same kinds of plant resources in comparable ways. The major feeding guilds of insects that live on trees include foliage feeders (Chapter 9), bark beetles (Chapter 10), woodborers (Chapter 12), sucking insects (Chapter 13), and insects feeding on reproductive structures (Chapter 16). Here we briefly address how the major feeding guilds interact with tree defenses.

Insect-tree interactions are largely constrained by the physical and chemical properties of the tissues the insects feed upon and the physical closeness of the insect-tree association. Many insects live and feed inside trees and may thus remain in close contact with tree defenses for long periods. This is true for woodborers (Chapter 12) and bark beetles (Chapter 10) that feed and oviposit in tunnels in the bark or sapwood, and for ambrosia beetles (Chapter 11) that tunnel in the sapwood. Weevils feeding on tips, shoots, roots and reproductive organs (Chapter 15) and insects feeding on cones and seeds (Chapter 16) also spend most of their lives inside their host. The same is true for some foliage feeders, such as gall insects (Chapter 14) and leaf miners (Chapter 9). Most other foliage feeders feed externally in the canopy, such as sucking insects (Chapter 13) and some weevils feeding on tips, shoots and young plants. These external feeders have a looser physical association with their host tree

and are exposed to tree defenses largely through the tissues they ingest. The herbivorous insects that tend to be the least exposed to tree defenses are sucking or piercing insects that ingest sap or xylem fluids.

7.3.3 Insect Strategies to Cope with Tree Defenses

Insects can overcome plant defenses through counter-adaptations that are genetically determined or due to behavioral plasticity (Fox et al. 2004). Insect strategies to cope with plant defenses can be classified as external or internal (Despres et al. 2007), depending on whether they operate before or after ingestion of plant tissues, respectively. Some insects, such as galling insects, actively suppress tree defenses prior to ingestion by manipulating host tissues externally (Samsone et al. 2012). Once an insect has ingested host tissues, it can excrete, sequester or detoxify chemical defenses internally. Such internal, post-ingestive counter-adaptations are well studied, especially against chemical defenses, and may involve the action of enzymes in the insect midgut, such as cytochromes P450 and glutathione S-transferases (Enyati et al. 2005; Feyereisen 2006; Despres et al. 2007; Che-Mendoza et al. 2009; Chiu et al. 2019). Insect counter-adaptations to physical defense traits, on the other hand, are not well studied.

7.3.3.1 External Strategies of Insects to Cope with Tree Defenses

Prior to feeding, an insect can respond to plant defense traits through behavioral avoidance mechanisms. These behaviors can reduce or completely bypass negative impacts of tree defenses. Insects actively evade defenses through avoidance in time (phenology) or by feeding on tissues that are less well defended. For example, many moths and butterflies that feed on leaves closely synchronize larval emergence with bud burst because emerging young leaves are less well defended chemically and physically than older leaves (Feeny 1970). Also, some leaf feeding insects cut through a primary leaf vein to reduce turgor pressure before they start to feed. This trenching behavior has been observed in insects feeding on plants that store highly toxic latex within specialized defense structures called laticifers (Doussard and Eisner 1987). Plant latexes and resins represent both chemical and physical defenses, as these fluids often contain toxic metabolites that are also highly viscous and sticky.

Insects use visual, olfactory or tactile cues from plant defense traits, volatile emissions or nutritional quality to avoid feeding or laying eggs on toxic plant tissues. Young larvae usually feed on the tissues where oviposition occurred and brood survival will thus be higher if optimal substrates are selected for oviposition. This is the premise for the “mother knows best” hypothesis which predicts that insects oviposit on hosts where their progeny will perform optimally (Bernays and Graham 1988). The use of chemical cues to avoid chemical defenses is often intertwined with the use of visual cues. For instance, woodboring beetles tend to rely first on

visual cues to select potential host trees, before switching to tactile and olfactory cues when they land on the host. Ambrosia beetles also integrate visual and olfactory cues to differentiate host species from non-host species (Campbell and Borden 2009). The role of olfactory cues in host selection behaviors of bark beetles have been particularly well studied, since tree-killing bark beetles are important forest pests. Bark beetles utilize tree chemistry to identify suitable hosts for oviposition and brood development. Specifically, these beetles have evolved complex mechanisms to modify terpenes in the trees' chemical defenses for use in their own pheromone biosynthesis (Chiu et al. 2017). Instead of attempting to summarize the vast literature on this topic in a short paragraph, we refer the reader to some of the relevant literature that explores these well-documented interactions (Wood 1982; Raffa 2001; Zhang and Schlyter 2004; Blomquist et al. 2010).

Although we are not aware of studies that demonstrated active avoidance behaviors in forest pests to physical defense traits, observations of the spruce weevil have suggested that adult maturation feeding on spruce shoots prior to oviposition may improve brood fitness (Whitehill and Bohlmann 2019). Adult maturation feeding drains resin canals on the apical shoot and is hypothesized to reduce exposure of eggs and larvae to the toxic effects of oleoresin. This probably improves survival of young weevil larvae, although further experimental evidence is required to support this hypothesis. This behavior resembles the trenching behavior of insects that feed on herbaceous plants with toxic latex.

7.3.3.2 Internal Strategies of Insects to Cope with Tree Defenses

Insects have various internal mechanisms to circumvent the toxic effects of specialized plant metabolites. These mechanisms include tasting (gustation) and subsequent avoidance of toxic food, as well as excretion, detoxification, and sequestration of toxic plant metabolites after ingestion. In herbaceous systems, gustatory cues can deter continued insect feeding on plant tissues. For instance, cyanogenic glycosides deter further feeding by the alfalfa weevil (*Hypera brunneipennis*) even when glycoside levels are below the threshold of toxicity (Bernays and Cornelius 1992). In poplar (genus *Populus*), deterrents of insect feeding such as phenolic glycosides and salicynoids (glycosides of salicylic acid) are important for defense (Hwang and Lindroth 1997). Tasting and avoidance strategies are challenging behaviors to unravel, as they require careful observation combined with targeted bioassays of individual plant metabolites. The avoidance responses of insects to toxic metabolites are very simple: move on and feed on a different plant or tissue. Since avoidance is conceptually straightforward, we focus here instead on the more complex internal metabolic mechanisms insects use to cope with toxic plant compounds. Using forest insects as examples, we present the three non-behavioral metabolic coping mechanisms: excretion, detoxification, and sequestration of toxic plant metabolites.

Excretion—In the context of insect-plant interactions, excretion refers to the simple removal of ingested toxic plant metabolites from the insect gut with the feces

(Zagrobelny et al. 2004). Insects that are adapted to feed on plants with diverse chemical defenses tend to rely on excretion as their main mechanism to avoid potentially toxic metabolites. For instance, case moth (*Hyalarcta huebneri*) larvae that feed on chemically well-defended eucalyptus leaves excrete most of the toxic metabolites they ingest unchanged (Cooper 2001). Some ingested plant toxins are stopped by the peritrophic matrix in the insect midgut, acting as a barrier that prevents toxins from reaching the gut epithelium. The polarity of ingested compounds and the pH of the midgut can also influence the toxicity of certain plant metabolites. For instance, many lipophilic compounds do not interact readily with the insect midgut and therefore are passively excreted following ingestion (Barbehenn 1999). Conversely, hydrophilic compounds must be modified enzymatically in the midgut to reduce their toxicity and ease their removal from the digestive tract.

Detoxification—Detoxification involves biochemical processes to remove toxic compounds that have been ingested. Insect detoxification of plant defense compounds may involve variations and combinations of compounds being oxidized, hydrolyzed, or reduced, as well as conjugated to molecules that can be readily cleared from the insect body (Despres et al. 2007). Detoxification of plant metabolites by herbivorous insects has been described to involve a variety of different enzymes such as cytochrome P450 monooxygenases (CYP450s), glutathione-S-transferases, and carboxylesterases. Of these, CYP450s are perhaps the best studied and appear to play a key role in many plant–insect interactions (Feyereisen 2005). CYP450s are a diverse group of enzymes that are found throughout the animal and plant kingdoms (Li et al. 2007). In insects, CYP450s are essential to the function of certain organs such as antennae, where they clear old odorant molecules from the odorant receptors (Maibèche-Coisne et al. 2005). CYP450s are also critical to insect metabolism and tolerance of anthropogenic chemicals such as insecticides (Petersen et al. 2001; Wondji et al. 2007). The important functions CYP450s have in detoxification are reflected in the large diversity and number of CYP450s in insect genomes. Glutathione-S-transferases are involved in detoxification of glucosinolates by making them more soluble and thus more easily excreted (Enayati et al. 2005). Insect carboxylesterases detoxify chemical insecticides and are therefore also thought to be involved in detoxification of other toxic substances, such as plant specialized metabolites (Yang et al. 2005).

Sequestration—Sequestration in insects is the process of utilizing plant metabolites for protection against predators or as precursors for pheromone production. Sequestration of plant metabolites is a highly specialized counter-adaptation to plant chemical defenses. The process may appear complex but only requires a few modifications of conserved molecular processes. Insect sequestration requires a selective import system that targets potentially harmful compounds, a safe transport mechanism through the body so the toxic metabolites do not harm the insect, and a site for safe, long-term storage (Kuhn et al. 2004). Sequestration processes are best documented in leaf beetles (Chrysomelidae) where the juvenile stages use sequestered plant compounds to defend themselves against predation (Meinwald et al. 1977; Pasteels et al. 1990; Gillespie et al. 2003). In trees, the poplar leaf beetle (*Chrysomela populii*) sequesters salicin in specialized defensive glands and excretes the toxin for

its own protection (Strauss et al. 2013). Similarly, sawfly larvae feeding on pine foliage sequester diterpenes from the needles as a defense against predators (Eisner et al. 1974).

Sequestration versus detoxification: a closer look at the mountain pine beetle - The mountain pine beetle (*Dendroctonus ponderosae*) is a devastating forest pest with unique mechanisms to cope with the terpene-rich resin defenses of its host trees. Females initiate mass attacks on trees by releasing the aggregation pheromone *trans*-verbenol as they enter the bark. *Trans*-verbenol is formed by the hydroxylation of α -pinene, an abundant monoterpene in pine resin. This hydroxylation is catalyzed by a specific CYP450 in the beetle (Chiu et al. 2019). For attacking females it is essential to rapidly initiate mass attacks in order to overcome tree defenses and successfully colonize trees. Earlier, it was believed that females hydroxylated α -pinene into *trans*-verbenol immediately upon entering the bark. However, Chiu et al. (2019) found that the beetles lay the foundation for rapid pheromone production much earlier in life. As the larvae develop in the bark, they detoxify α -pinene and store it as monoterpenyl esters inside their body. These pheromone precursors are most abundant in female larvae around the time of pupation and are retained through to adult emergence and host finding. Detoxification of α -pinene and sequestration of pheromone precursors thus appears to provide a reservoir for the rapid female-specific release of *trans*-verbenol upon tree attack (Chiu et al. 2018). The mountain pine beetle example shows that sequestration and detoxification are not necessarily mutually exclusive mechanisms, but can be context dependent and open to interpretation; α -pinene is first detoxified, then sequestered as monoterpenyl ester pheromone precursors, and finally converted to the aggregation pheromone *trans*-verbenol.

7.3.4 *The Role of Symbiotic Microorganisms in Insect-Tree Interactions*

Many herbivorous insects benefit from microorganisms in obtaining resources from well-defended and nutrient-poor tree tissues. It would therefore be oversimplified to consider insect-plant interactions as two-species interactions, as in reality they are likely complex insect-plant-microbiome interactions (Geib et al. 2008; Berasategui and Salem 2020; Frago et al. 2020). The insect microbiome includes the endo-microbiome (organisms living inside the insect, including in the gut) and the exo-microbiome (organisms living on the external surface of the insect). Bacteria and fungi in insect microbiomes may play essential roles in the breakdown of food (Scully et al. 2014; Lee et al. 2015; Berasategui and Salem 2020), defense against pathogens (Cardoza et al. 2006), and protection against plant defenses (Ceja-Navarro et al. 2015; Howe and Herde 2015; Frago et al. 2020). In the context of insect-tree interactions, the microbiome may significantly increase insect fitness by detoxifying tree defense metabolites and otherwise make plant tissues more suitable for feeding and reproduction. Large-scale mapping of insect microbiomes can be achieved by

targeted sequencing of DNA barcoding regions of major microbial groups, such as bacteria, archaea, and fungi (Caporaso et al. 2012). Here, we present two examples that illustrate the intricate ways microbial symbionts may influence insect-tree interactions. First, we describe how fungal and bacterial symbionts may help bark beetles to colonize well-defended conifer trees, and secondly, how endosymbiotic bacteria are involved in a highly specialized nutritional mutualism with aphids.

7.3.4.1 Bark Beetles, Bluestain Fungi and Bacteria

A century-old paradigm in bark beetle ecology holds that fungi vectored by tree-killing bark beetles are critical for overwhelming host tree defenses and ultimately killing the tree (Six and Wingfield 2011; Krokene 2015). As early as 1928, F.C. Craighead suggested that ascomycete bluestain fungi carried by the beetles were important in tree killing (Craighead 1928), and historically most research on microorganisms involved in overwhelming tree defenses has focused on these fungi (Kirisits 2004). It has proved difficult to demonstrate experimentally that bluestain fungi are crucial for tree-killing, partly because it is difficult to separate the contribution of the fungi from that of the beetle itself. Even though it is hard to prove conclusively that microbionts are essential for tree-killing, fungi and bacteria have been shown to metabolize tree secondary metabolites and thus help detoxify tree defenses. In some North American bark beetle species, bacteria in the endo-microbiome have been demonstrated to help digest plant tissues and break down plant defenses (Adams et al. 2009, 2013; Boone et al. 2013). Also, bluestain fungi associated with the Eurasian spruce bark beetle rapidly break down phenolics in spruce bark and make the phloem more attractive to tunneling beetles (Hammerbacher et al. 2013; Kandasamy et al. 2019; Zhao et al. 2019a). Bluestain fungi may also produce components of bark beetle aggregation pheromones, suggesting that these fungi have a long co-evolutionary history with the beetle (Zhao et al. 2019b).

7.3.4.2 Aphids and Endosymbiotic Bacteria

Aphids are sap-sucking insects that feed externally on trees and other plants. Sap provides a very unbalanced diet consisting mostly of carbohydrates. It contains little nitrogen, and is a poor source of specific amino acids such as methionine and leucine (Sandström and Moran 1999). To overcome the nutritional deficiency of their diet, aphids harbor different species of endosymbiotic bacteria inside their cells. One species that is carried by almost all aphids is the endosymbiotic bacterium *Buchnera aphidicola*. This obligate intracellular endosymbiont provides essential amino acids that allow the aphids to survive on their carbohydrate-rich but nutrient-poor diet. In return, the bacterium receives all its other essential nutrients from its aphid host. The bacterium lives inside large specialized cells known as bacteriocytes and is vertically transmitted from mother to offspring with the egg. Since the bacterium cannot survive

outside the cells of its aphid host, it essentially functions like an organelle. The aphid-*Buchnera* symbiosis is ancient and dates back at least 180 million years (Moran et al. 2008). Due to its obligatory endosymbiotic lifestyle the bacterium has lost many key genes for metabolic pathways and extracellular structures present in free-living bacteria. Because of this gene loss, the genome size of *Buchnera aphidicola* is only 15% of that of its close free-living relative *Escherichia coli* (Shigenobu et al. 2000). In addition to *Buchnera*, aphids harbor other bacteria such as *Hamiltonella defensa*, which may improve aphid fitness by providing protection against parasitic wasps and other natural enemies (Dion et al. 2011).

7.4 Case Studies: Major Forest Pest Issues Worldwide

Here we present examples of some major forest pest challenges. The selected insect-tree interactions highlight many of the tree defense mechanisms and insect adaptations described above. We present insect species with varied lifestyles and belonging to different feeding guilds, including species that feed internally or externally in conifer and broadleaved trees (Fig. 7.4). Also, since co-evolution between insect herbivores and trees is important in shaping insect-tree interactions, we present examples of both native and invasive forest pests.

7.4.1 Native Pests Living on Co-Evolved Host Trees

Interactions between native insects and their co-evolved host trees tend to be much more stable and predictable than interactions between invasive insects and evolutionary naïve tree species. Still, native insects such as sawflies and bark beetles may be opportunistic pests that go through boom-and-bust cycles and can have large-scale and long-lasting outbreaks.

7.4.1.1 The European Pine Sawfly: An Eruptive Defoliator with a Co-Evolved Tri-Trophic Niche

The European pine sawfly (*Neodiprion sertifer*) is native to Eurasia where it feeds on the needles of Scots pine and other two-needle pines. It is an early-season defoliator that occasionally undergoes short-lived outbreaks that may cover tens of thousands of hectares (Chorbadjian et al. 2019). The larvae feed on pine needles, starting with 1-year-old and older needles and only feeding on current-year needles if they run out of older needles. Larval development is completed relatively early in the summer and the mature larvae move down the stem and pupate in the forest litter. Adults emerge in the autumn and females lay eggs on current-year needles. Since the larvae rarely defoliate trees completely, tree mortality is low, but heavy attacks may cause

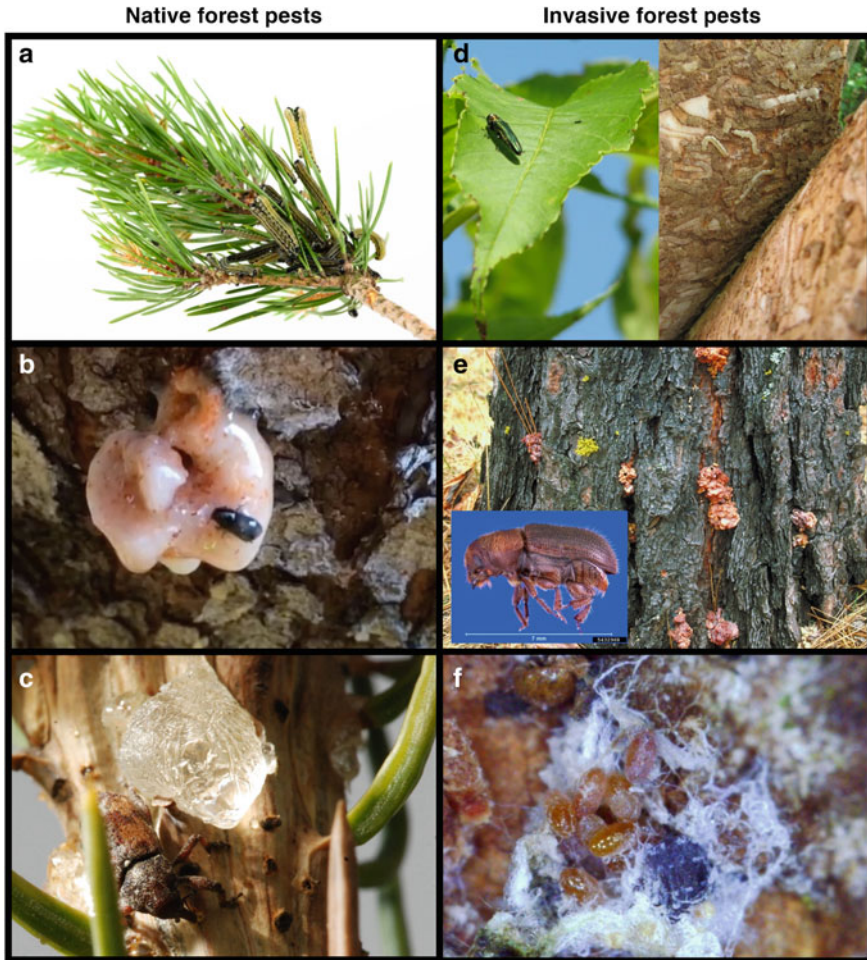


Fig. 7.4 Examples of native and invasive forest pests worldwide. Native insects living on co-evolved host trees: (a) the European pine sawfly (*Neodiprion sertifer*) is a native defoliator of pines in Europe and Asia; (b) a mountain pine beetle (*Dendroctonus ponderosae*) female is swimming through resin to enter and colonize a pine host in its native range in western North America; (c) the spruce weevil (*Pissodes strobi*) is a native regeneration pest across North America, ovipositing in the apical shoot of different spruce and pine species. Invasive insects attacking evolutionary naïve host trees: (d) the bark and wood boring emerald ash borer (*Agrilus planipennis*) is native to Asia but has invaded eastern North America where it is killing native ash trees; (e) the red turpentine beetle (*Dendroctonus valens*) is native to North America and has been introduced into China where it is killing millions of native pine trees; (f) the balsam woolly adelgid (*Adelges piceae*) is a small sap sucking insect of European origin that has been introduced into North America where it is killing native fir species. Photo credits: a © Erling Fløistad, Norwegian Institute of Bioeconomy Research; b © Christine Chiu, Natural Resources Canada; c and d © Justin Whitehill; e © (inset) Erich G. Vallery, USDA Forest Service—SRS-4552, <https://doi.org/Bugwood.org> and (damage) Bob Oakes, UGA1241449, USDA Forest Service, <https://doi.org/Bugwood.org>; f © Brad Edwards, North Carolina Cooperative Extension

significant growth losses. A complex relationship exists between the trees' chemical defenses, survival of sawfly larvae, and predation risk. As they feed, the larvae ingest diterpene resin acids stored in resin canals in the needles (Niemelä et al. 1982; Fig. 7.3). High concentrations of resin acids in the diet reduce larval growth, but resin acids may also improve larval survival. Larvae protect themselves against predators by sequestering ingested resin acids and storing them in specialized pouches in the foregut (Eisner et al. 1974). When challenged by birds or other predators, the larvae startle the attackers by synchronously waving their bodies and discharging a bubble of resin acid through their mouth. Ingestion of diterpene resin acids thus represents a trade-off for the larvae: in the absence of predation diterpenes negatively affect larval growth and survival, but diterpenes may increase larval survival when predators are present. This complex relationship between pine defenses and sawfly survival illustrates the tri-trophic niche concept and the intricate relationships that may exist between plants, herbivores and predators. As described above ('Plant side') the tri-trophic niche concept states that toxic specialized compounds and other plant characteristics may increase or decrease a herbivore's vulnerability to natural enemies by making the plant an enemy-sparse or enemy-dense space for the herbivore (Singer and Stireman 2005).

7.4.1.2 The Mountain Pine Beetle: Rapid Range Expansion by a Native Tree-Killing Bark Beetle

The mountain pine beetle is native to western North America, colonizing lodgepole pine (*Pinus contorta*) and other pine species throughout its large geographical range (Six and Bracewell 2015). The mountain pine beetle epitomizes the devastating effects tree-killing bark beetles can have on forest ecosystems, having killed 55% of all merchantable lodgepole pine over a 25 million hectare area since the 1990's (Meddens et al. 2012). Most of the time beetle population levels are low and oviposition occurs in the stem bark of weakened and dying trees. Following disturbances and favorable climatic conditions, beetle populations build up and massive outbreaks can occur, with an explosive increase in abundance over a short period of time. Beetle outbreaks may last several years, and during outbreaks the beetles are able to overwhelm the resistance of even healthy trees through mass-attacks coordinated by aggregation pheromones (Raffa et al. 2008; Boone et al. 2011). The last 20 years, climate change has been driving range expansions of this pest into higher altitudes and eastwards across the Rocky Mountains in Canada (Cudmore et al. 2010; Buotte et al. 2016). Warming temperatures have also favored beetle population growth and outbreak development by reducing winter mortality and causing drought stress that lowers tree defenses. The beetles vector a pathogenic fungal symbiont, the bluestain fungus *Grosmannia clavigera*, that colonizes the phloem and sapwood of attacked trees following beetle colonization. The combined effect of beetle mass-attacks and fungal infection ultimately overwhelms tree defenses and kills the trees. In an effort to mitigate the impacts of beetle outbreaks researchers are dissecting the complex three-way interactions between beetles, fungal symbionts and trees. This work has been

facilitated by the development of genomic resources for both the fungal pathogen (DiGuistini et al. 2011) and the beetle (Keeling et al. 2013).

7.4.1.3 The Spruce Weevil: A Shoot-Feeding Reforestation Pest of North American Conifers

Pissodes strobi is a ‘snout beetle’ (family Curculionidae) colonizing various spruce and pine species across its wide range in North America. In western forests it attacks various spruce species and is known as the spruce weevil (Ebata 1991), whereas in the east it attacks primarily eastern white pine (*Pinus strobus*) and is referred to as white pine weevil. The beetles cause damage when females oviposit near the top of the apical shoot of young trees. The developing larvae tunnel downwards in the phloem, destroying the shoot in the process. Because of its abundance, wide geographical range, and ability to disrupt the height growth of young trees, the spruce weevil is considered the most important threat to reforestation of commercial spruce forests in western North America. Sitka spruce is particularly susceptible and very little reforestation has historically been attempted with this species, despite its intrinsically high economic value (King and Alfaro 2009). However, extensive research has identified weevil-resistant spruce genotypes that are now used actively in forest regeneration programs (Kiss and Yanchuk 1991; King and Alfaro 2009; King et al. 2011). Weevil-resistance in Sitka spruce results from a complex defense syndrome with synergism between chemical and physical defense traits that are both constitutively present and induced following insect attack. Specifically, resistant trees have more stone cells in the upper part of the shoot where the young larvae start their development. The stone cells slow down larval growth and increase larval exposure to the chemical toxicity and physical aspects of oleoresin (Whitehill et al. 2019). Resistant spruce genotypes have co-evolved with the insect in areas with high weevil densities (King et al. 2011). In contrast, a highly susceptible genotype was found on the remote Haida Gwaii Islands that have historically been free from weevils (King et al. 2011). Plants propagated from resistant and susceptible spruce genotypes have been used for detailed mechanistic studies of tree resistance (Robert and Bohlmann 2010; Robert et al. 2010; Hall et al. 2011; Whitehill et al. 2016a, 2016b, 2019). This research has generated important tools and resources, including one of the first sequenced conifer genomes that has been the basis for several genomic and gene sequence-based mechanistic studies (Birol et al. 2013; Celedon et al. 2017; Whitehill et al. 2019).

7.4.2 Invasive Pests Attacking Evolutionary Naïve Host Trees

Some of the most devastating insect-tree interactions involve insects that have been accidentally introduced into new areas where they interact with local tree species that lack effective defenses (Gandhi and Herms 2010). International trade with live

plants, such as plants for planting, and the use of infested wood packaging materials are the main sources for the introduction of invasive tree pests to new areas (Aukema et al. 2010). Novel insect-tree associations may result in unpredictable and surprising outcomes due to the lack or reciprocal adaptations between insects and trees (Ploetz et al. 2013).

7.4.2.1 Emerald Ash Borer: An Invasive Stem Borer Ravaging Non-Adapted American Ash Species

The emerald ash borer (*Agrilus planipennis*) is an invasive bark- and wood-boring insect causing widespread mortality of ash (genus *Fraxinus*) in eastern North American forests. The beetle originates from East Asia and was accidentally introduced into North America in the 1990s (Herms and McCullough 2014). In its invasive range the beetle colonizes healthy ash trees and kills them within 2–3 years. The damage is done by the larvae as they feed on the inner bark and sapwood of the main stem, ultimately killing the trees by disrupting the flow of water and nutrients (McCullough and Katovich 2004). All North American ash species are susceptible to attack (Cappaert, et al. 2005; Poland and McCullough 2006). Detailed studies of the interaction between ash defenses and tunneling beetle larvae have shown that North American ash species are unable to confine and kill the young larvae. Thus, the evolutionary naïve ashes of North America lack effective defenses against this invasive pest. In contrast, Manchurian ash (*F. mandshurica*) native to Asia is resistant to attack, likely because it has targeted defenses developed over its co-evolutionary history with the insect (Bryant, et al. 1994; Rebek et al. 2008). Manchurian ash is less preferred for adult feeding and oviposition than susceptible ash species (Rebek et al. 2008), is more resistant to larval feeding (Chakraborty et al. 2014), and has higher constitutive concentrations of specialized metabolites and defensive proteins in the bark (Eyles et al. 2007; Whitehill et al. 2011, 2012, 2014; Hill et al. 2012). Interestingly, normally susceptible North American ash species can be made resistant to attack following external application of the wound hormone methyl jasmonate on the stem bark (Whitehill et al. 2014). Methyl jasmonate application increased the activity of trypsin inhibitors and concentrations of phenolics and lignin in the bark and decreased larval survival. This shows that even susceptible ash species have the defense machinery to prevent beetle infection, but they apparently are unable to induce these defenses under natural conditions, perhaps because they fail to recognize the feeding larvae or respond quickly enough to attack.

7.4.2.2 Red Turpentine Beetle: Novel Insect-Fungus Partnerships Are Invading Chinese Forests

Like the emerald ash borer, the red turpentine beetle (*Dendroctonus valens*) is mostly a secondary colonizer of weakened trees in its native range, but is a serious tree-killer in its invasive range. The red turpentine beetle is the largest and most widespread

bark beetle in North America. It can breed in more than 40 conifer species in North America but is most common in different pine species. Although it normally colonizes weakened trees or trees attacked by other bark beetles, it may occasionally attack and kill apparently healthy trees in its native range (Sun et al. 2013). Unlike most other bark beetles, the larvae of the red turpentine beetle feed gregariously in groups of up to 100 larvae that excavate a large cave-like gallery in the bark of the lower stem. The beetle was accidentally introduced into China in the early 1980s, probably through import of unprocessed conifer logs from the western United States, and has killed millions of pine trees in China since its first outbreak in 1999 (Yan et al. 2005; Sun et al. 2013). The beetle's success in China appears to be due to a combination of naïve host trees, few natural enemies, and an ability to partner with new species of mutualistic symbiotic microorganisms (Sun et al. 2013). In its invasive range the beetle mainly attacks Chinese pine (*Pinus tabulaeformis*) and sometimes Chinese white pine (*Pinus armandii*). It attacks both healthy trees and trees that have been stressed by drought, fire or root disturbance. The beetle naturally vectors different species of bluestain fungi and some of these were introduced in China together with the beetle. In addition, the beetle has picked up several native Chinese bluestain fungi and this appears to have contributed to the beetle's impact in China (Lu et al. 2009). The beetle's potential geographic range in China is much larger than its current range, suggesting there is a high risk of future range expansion (Tang et al. 2008; He et al. 2015). Chinese pine is a widely planted reforestation tree used to reduce soil erosion and further expansion of the red turpentine beetle in China will probably have severe ecological impacts.

7.4.2.3 Balsam Woolly Adelgid: An Invasive Sucking Insect Killing North American Firs

The balsam woolly adelgid (*Adelges piceae*) is an invasive piercing-sucking insect that has devastated most naturally occurring populations of the premier Christmas tree species in North America, Fraser fir (*Abies fraseri*). Since its accidental introduction into North America from Europe around 1900, the adelgid has killed thousands of hectares of Fraser fir, its main host in North America. The adelgid has also spread west across the continent and reached most areas where suitable host trees occur. All North American fir species are highly susceptible to the pest, while European firs tolerate infestation for several years with little symptoms (Newton et al. 2011). In its invasive North American range, the balsam woolly adelgid reproduces strictly through parthenogenesis and completes two or more generations per year (Arthur and Hain 1984). The adults are wingless and the only mobile life stage is the early phase of the first larval instar (the crawler), which disperses from tree to tree primarily by wind or gravity. When the crawler finds a suitable feeding site on a branch or trunk it inserts its mouthparts into the bark and remains attached at that site for the rest of its life (Balch and Carroll 1956). The formation of 'rotholz' (red wood) around feeding sites is a characteristic symptom of balsam woolly adelgid feeding in Fraser fir (Mester et al. 2016). This abnormal wood formation resembles compression wood

and is considered to be a major cause of decline in infested trees (Timell 1986). Fraser fir is a specialty crop conifer and the most valuable Christmas tree species in the US. Christmas tree revenues total more than 2 billion USD annually. Both the entire natural range and the largest production region of Fraser fir are located in small rural communities in the Southern Appalachian Mountains of the southeastern US. Here, the balsam wooly adelgid has killed 80% of the mature Fraser fir trees across the very restricted natural range, reducing Fraser fir to an endangered species (White et al. 2012). Tree resistance mechanisms to infestation are not well understood but probably involve a combination of physical and chemical defenses at the infestation site (Hain et al. 1991; Newton et al. 2011). Methodologies to screen for genetic resistance in Fraser fir to the adelgid have been developed (Newton et al. 2011) and the ultimate goal is to develop tolerant or resistant Fraser fir genotypes through genetic improvement and thus support the Christmas tree industry for future generations.

7.5 Conclusions and Future Prospects

Climate change is expected to reduce forest health and amplify damage from native and invasive insect pests (Allen et al. 2010; Bentz et al. 2010). Ecological constraints tend to keep insect populations more or less stable and prevent large-scale pest eruptions. However, increasing temperatures alter species interactions and remove natural climatic barriers that have historically prevented population growth and range expansion of forest pests. Warming temperatures over the last several decades have already resulted in some of the most severe forest insect outbreaks reported in the literature. These include outbreaks of well-known pests such as mountain pine beetle, spruce budworm (*Christoneura occidentalis*), and Eurasian spruce bark beetle. In addition, new invasive forest pests have emerged, such as emerald ash borer in North America, red turpentine beetle in China, and redbay ambrosia beetle (*Xyleborus glabratus*) in the south-eastern United States. The combination of warmer temperatures, leading to increased stress and decreased resilience of forest ecosystems, and so-called naïve host trees without co-evolved defenses provide invasive species with a favorable, potentially defense-free environment. Expansion of invasive pests into novel environments may cause extirpation of other species and disruption of ecosystems in the process (Klooster et al. 2014).

Climatic and other environmental change may favor insect pests over their host trees, because insects have much shorter life cycles and can adapt more rapidly than trees to changing conditions. As human populations continue to affect the planet through climate change and homogenization of the world's biota we will increasingly see dramatic effects of interactions between insects and trees. It is therefore more important than ever to understand the mechanisms of tree resistance to herbivore attack, in order to promote tree resistance through optimized forest management and development of resistant cultivars. Natural variability in tree defense traits, as a result of co-evolutionary history between trees and insects, can provide robust

defenses against forest pests. The most effective tree defense mechanisms fend off or stop insect attack despite continual exposure to a pest.

While much is known about some of the traits that contribute to tree defense, little is known regarding how these defense traits function ecologically, or how the underlying genomic mechanisms function to control tree defenses. Researchers who study tree-insect interactions face several challenges and limitations compared with those who study annual plants and model species like *Arabidopsis thaliana*, tobacco and tomato. However, these challenges also pose opportunities for the development of novel and innovative approaches to elucidate the complex interactions between forest trees and insects. Genomics tools are opening new avenues of research in notoriously difficult-to-study non-model tree species. The marriage between ecological and genomic approaches will help to streamline the identification of genetic markers that associate with complex resistance mechanisms in tree-insect interactions and rapidly increase tree health through genetic improvement. To keep pace with the rapid impacts of climate change and prepare trees for expected future climates, the application of modern genomic technologies may be crucial to the survival of forest tree ecosystems.

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