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Insect and Pathogen Influences on Tree-Ring Stable Isotopes

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Chapter 25
Insect and Pathogen Influences on Tree-Ring Stable Isotopes



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Abstract Understanding long-term insect and pathogen effects on host tree physiology can help forest managers respond to insect and pathogen outbreaks, and understand when insect and pathogen effects on tree physiology will be exacerbated by climate change. Leaf-level physiological processes modify the carbon (C) and oxygen (O) stable isotopic composition of elements taken up from the environment, and these modifications are recorded in tree-rings (see Chaps. 9, 10, 16 and 17). Therefore, tree-ring stable isotopes are affected by both the tree's environment and the tree's physiological responses to the environment, including insects and pathogens. Tree-ring stable isotopes provide unique insights into the long-term effects of insects and pathogens on host tree physiology. However, insect and pathogen impacts on tree-ring stable isotopes are often overlooked, yet can substantially alter interpretations of tree-ring stable isotopes for reconstructions of climate and physiology. In this chapter, we discuss (1) the effects of insects (defoliators, wood-boring, leaf-feeding), pests (parasitic plants), and pathogens (root and foliar fungi) on host physiology (growth, hormonal regulation, gas exchange, water relations, and carbon and nutrient use) as they relate to signals possibly recorded by C and O stable isotopes in tree-rings, (2) how tree-ring stable isotopes reveal insect and pathogen impacts and the interacting effects of pathogens and climate on host physiology, and (3) the importance of considering insect and pathogen impacts for interpreting tree-ring stable isotopes to reconstruct past climate or physiology.

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25.1 Introduction

Harmful insects, pathogenic fungi, and parasitic plants can alter host tree physiology, reduce tree health, and contribute to tree mortality. Native and introduced insects and pathogens influence forest structure, composition, biodiversity, and carbon dynamics (Castello et al. 1995; Clark et al. 2010). Environmental stress can increase biological challenges to tree health and create a greater likelihood of host tree mortality by either insect pests (Waring and Pitman 1985; Fettig et al. 2007; Anderegg et al. 2015) or pathogens (Manion 1991; Marçais and Bréda 2006; Voelker et al. 2008). Forest-pathogen interactions with amplified climate variability have been cited as the primary cause of the widespread forest mortality observed in recent decades (Allen et al. 2010; Hubbart et al. 2016; Hartmann et al. 2018). Mitigating and predicting future mortality events requires understanding the physiological mechanisms underlying interactions among insects and pathogens and trees, and the influence of climate variability on forests (Hartmann et al. 2018). However, the interacting effects of insects and pathogens, and climate on tree physiology are poorly understood, partly due to the long timescales over which all of these impact tree function. Furthermore, separating the effects of insects and pathogens, and climate on tree function is challenging. Therefore, combining annually resolved tree-ring stable isotopes and ring width chronologies that record information over decades to centuries are ideal tools to reconstruct insect and pathogen, and climate impacts on host physiology and to help predict future effects of insects and pathogens on forests.

Tree-rings record both the tree's environmental conditions, and the tree's physiological responses to the environment. Insects and pathogens can alter host physiology (i.e. growth, hormonal regulation, gas exchange, water relations, carbon and nutrient relations), and therefore pathogen effects can be recorded in the tree-ring record. Many studies have used tree-ring widths and growth to reconstruct climate and tree vigor (Fritts 1971; Fritts and Swetnam 1989). However, ring widths have limited use for reconstructing key aspects of tree physiology. In contrast, tree-ring stable isotopes can be used to more precisely infer certain physiological and ecological processes because they can provide more specific and additional information about trees' responses to their environment compared to tree-ring widths alone (Cernusak and English 2015; see Chaps. 16, 17). The carbon (C) from carbon dioxide (CO_2) in the atmosphere and oxygen (O) from water taken up by the tree reflect climatic conditions, and are then altered by physiological processes before eventually being incorporated into each tree-ring (see Chaps. 9, 10). The stable isotopic composition of the cellulose of each tree-ring can be analyzed over the lifespan of a tree to reveal temporal shifts in physiological responses. Because forest insects and pathogens can affect host physiology, tree-ring stable isotopes combined with ring widths are well-suited to investigate past and long-term impacts of insects and pathogens on host tree physiology.

Here, we synthesize and review how tree-ring stable isotopes record the impacts of insects and pathogens on host physiology over seasonal to multi-decadal timescales and the interacting effects of climate and pathogens on host physiology. First, we

discuss the effects of insects and pathogens on host physiology (focusing primarily on insects and pathogens that have been investigated with tree-ring stable isotopes), and briefly relate that to the isotope theory presented in Chaps. 9, 10, 16, and 17. Second, we discuss how tree-ring stable isotopes can be used to reveal the aforementioned insect and pathogen impacts and to help separate the interacting effects of insects and pathogens, and climate on host physiology. Finally, we conclude by discussing the importance of considering insect and pathogen impacts when interpreting tree-ring stable isotopes to reconstruct past climate or physiology.

25.2 Effects of Pathogens on Host Physiology

Forest insects and pathogens have diverse effects on host tree physiology, including alterations in growth, hormonal regulation, gas exchange, water relations, and carbon and nutrient use, many of which can alter the isotopic composition of cellulose in tree-rings. The detrimental effects of forest insects and pathogens on host tree functions often contribute to host tree mortality. Here, we focus on the physiological impacts of insects and pathogens that have also been investigated using tree-ring stable isotope approaches.

Many forest insects and pathogens reduce growth and biomass via partial defoliation and branch dieback. Leaf-feeding, defoliating insects, such as spruce budworm (*Choristoneura*), jack pine budworm (*Choristoneura pinus*), web-spinning sawfly (*Cephalcia*), larch budmoth (*Zeiraphera diniana* Gn), aspen leaf miner (*Phyllocnistis populiella*), and pandora moth (*Coloradia pandora* Blake) cause changes in leaf area (per tree and/or per leaf), photosynthetic capacity, water relations, and photosynthate allocation, often resulting in reduced radial growth (Kozlowski 1969). Artificial defoliation studies have also demonstrated defoliation-induced reductions in phloem sieve tube diameter, reducing C transport capability (Hillabrand et al. 2019), and defoliation-induced increases in C allocation to storage over growth (Wiley et al. 2013; Puri et al. 2015). The reduction in photosynthetic tissue can result in very narrow or one or more locally absent growth rings. This means that a physiological process or climate signal detectable by tree-ring stable isotopes may not be available because cell division is inhibited, phloem transport is disrupted, or recent photosynthetic C uptake is not sufficient to supply sugars to produce tree rings. In some such situations, narrow rings can form if stored C reserves are mobilized for growth (Kozlowski et al. 1991; Helle and Schleser 2004; Kagawa et al. 2006). Utilization of stored starch can alter the tree-ring stable isotope composition of newly synthesized plant compounds because the C stable isotope composition of photosynthetic products stored as starch is relatively enriched compared to that of triose-phosphates (Brugnoli et al. 1988; Cernusak et al. 2009; McKellar et al. 2011). Additionally, the isotopic composition of stored compounds is a mixture from previous photosynthetic activity and will not reflect the current physiological processes within the plant (Sohn et al. 2014). Consequently, plant structural compounds, such as cellulose in tree-rings could potentially be enriched and the intra- or inter-annual variance muted if those

tissues were derived in part from stored starch. Enriched C isotope signals have been observed in early-forming parts of growth rings of some hardwood species (Helle and Schleser 2004). However, to our knowledge, changes in inter-annual C isotope variability due to stress modifying the proportion of C derived from storage has not yet been demonstrated (Sohn et al. 2014). Leaf lifespan also can influence how defoliation events are recorded in the tree-ring record with deciduous species responding more quickly than evergreen species. For example, the larch web-spinning sawfly (*Cephalcia lariciphila* (Wachtl)) reduced radial growth of European larch (*Larix decidua* Mill.) by 67% during the same year as defoliation (Vejpustková and Holuša 2006). In contrast, in evergreen species, substantial radial growth reductions were often observed during the second consecutive year of heavy defoliation. Spruce web-spinning sawfly (*Cephalcia arvensis* Panzer) reduced growth only in the second year of defoliation of Norway spruce (*Picea abies* (L.) Karst.) (Gori et al. 2014a) and similar results were also found for defoliation of white pine (*Pinus strobus* (L.)) by pine false webworm (*Acantholyda erythrocephala* (L.)) (Mayfield et al. 2005). The slower response of evergreen species compared to deciduous species is consistent with a strong legacy effect due to cohorts of evergreen leaves remaining functional for multiple years, as opposed to only months for deciduous species (Zweifel and Sterck 2018). However, sometimes the timing of radial growth reduction in response to defoliation is more variable, such as in *L. decidua* that exhibited radial growth reductions for four years after defoliation by larch budmoth (*Z. diniana*) (Peters et al. 2017). Similarly, growth reductions in balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss.) were observed 1–4 years after defoliation by spruce budworm (*Choristoneura fumiferana* (Clem.)) (Blais 1958; Krause 1997). Furthermore, leaf lifespan can influence foliage quality for insects, and thus can affect the severity of the insect's impact on tree physiology, how defoliation may be recorded in tree-rings (but not always, see below Sect. 25.2 and also Kress et al. 2009), and consequently the magnitude and/or duration of isotopic departures signaling variations in insect outbreak cycles. For example, in the European Alps during spring, larch budmoth (LBM) has defoliated European larch on a cyclic pattern every 8–10 years (Baltensweiler et al. 2008). After defoliation events, larch will refoliate in early August if the leaf mass loss exceeds 50% (Baltensweiler et al. 2008). This second flush of short needles is often killed in early frosts in October, preventing defoliated larch trees from accumulating assimilates and nutrients, so resource-deprived trees again produce short needles the following spring. In addition to short needles, resource-deprived trees also produce needles with low nitrogen (N) content and high raw fiber. These alterations in LBM food quality trigger the collapse of the LBM population and create the remarkably regular 8–10 year periodicity of LBM outbreaks that had been observed for 1200 years. Switzerland's forest service had documented regular LBM outbreaks since 1864 (Baltensweiler 1993; Baltensweiler et al. 2008). However, since the 1980s, no alpine-wide synchronized LBM outbreak event has occurred. As a result, tree-ring stable isotopes have been used to reveal that an increase in summer temperatures may explain why no LBM outbreak has occurred since the 1980s (Kress et al. 2009; and for more details, see below Sect. 25.2).

Growth perturbations also have been attributed to insect- and pathogen-induced alterations in host tree hormonal regulation, as is the case with the parasitic plant, dwarf mistletoe (*Arceuthobium* spp.). Dwarf mistletoe, a relative of Christmas mistletoe (*Phoradendron*, *Loranthus, Viscum* spp.), is a vascular, obligate, hemiparasitic plant that relies primarily on the host tree for water and nutrients. Dwarf mistletoes, native to and found throughout North America, include 42 species that infect species of *Abies*, *Picea*, *Tsuga*, *Larix*, *Pseudotsuga*, *Keteleeria*, and *Juniperus*, and 95% of the species in *Pinus* (Hawksworth and Wiens 1998; Nickrent et al. 2004). Dwarf mistletoes divert host tree water and nutrients by developing an endophytic system within the host xylem and phloem (Geils and Hawksworth 2002; Mathiasen et al. 2008; Glatzel and Geils 2009). In contrast to Christmas mistletoes, dwarf mistletoe eventually kills its host and instead of leafy shoots, has small diminutive aerial shoots that are essentially leafless. Needles on host branches infected with dwarf mistletoe possessed lower abscisic acid and greater total cytokinin contents than needles on uninfected branches (Logan et al. 2013). Cytokinins are known to delay senescence, promote resource mobilization, and increase the frequency of branching (Mok 1994; Davies 2010). This is likely the cause of a classic symptom of the infection known as a witches' broom, a dense disorganized mass of host tree branches. The self-shaded witches' brooms reduce host light capture and photosynthetic C gain (Logan et al. 2013). The dwarf mistletoe-induced alterations in cytokinins may explain why resources are continuously allocated to self-shaded witches' brooms. The alterations in hormone levels and witches' broom formations also may underlie significantly greater leaf area:sapwood area ratios in infected trees compared to uninfected trees (Sala et al. 2001). These hormonal influences and morphological effects would be expected to alter $\delta^{13}C$ and $\delta^{18}O$ of infected plant tissues.

Forest insects and pathogens induce alterations in gas exchange, either directly or indirectly. Swiss needle cast is caused by a fungus (*Phaeocryptopus gaeumannii* (T. Rohde) Petr.) that blocks stomata by either the fungal fruiting bodies (pseudothecia) or hyphae. This physical blockage of stomata restricts leaf gas exchange, reducing the CO_2 assimilation rate (A) and stomatal conductance (g_s) by 50% and 37%, respectively (Manter et al. 2000). Some insects and pathogens can also restrict leaf gas exchange by interrupting water transport in stems (Parke et al. 2007). Alternatively, forest insects and pathogens can alter gas exchange indirectly. For example, defoliating insects such as spruce budworm induce needle loss which has been shown to have a compensatory effect on the remaining needles where A of remaining needles increases, possibly due to increased allocation of mineral nutrients to remaining foliage (Reich et al. 1993; Lavigne et al. 2001; Little et al. 2003). In western hemlock trees infected with dwarf mistletoe, photosynthetic capacity was significantly reduced due to sequestration of host N by dwarf mistletoe (Meinzer et al. 2004). White spruce infected with dwarf mistletoe exhibited greater transpiration (E) rates than uninfected trees, due to the dwarf mistletoe-induced perturbations in hormonal regulation where needles on infected likely branches possessed lower abscisic acid and greater total cytokinin contents than needles on uninfected branches (Logan et al. 2013). Because abscisic acid promotes stomatal closure (Mittelheuser and Van Steveninck 1969),

whereas cytokinins promote stomatal opening and decrease sensitivity of stomata to abscisic acid (Acharya and Assmann 2009), these combined alterations in hormone levels likely underlie the increase in host *E* (Logan et al. 2013). The dwarf mistletoe infection also reduces stomatal limitations on gas exchange, as shown by significant reductions in intrinsic water use efficiency in infected trees compared to uninfected trees (Meinzer et al. 2004; Logan et al. 2013).

Forest insects and pathogens influence host tree water relations. For example, *Heterobasidion parvidporum* (white rot fungus) and *Phytophthera quercina* are fungal root pathogens of conifers and oaks, respectively. These fungal infections result in root mortality and consequently reduced water and nutrient uptake, hydraulic failure, and increased susceptibility to windthrow, wood decay, and mortality (Filip 1999). Host trees of mistletoes and dwarf mistletoes adjust their hydraulic system and water relations to accommodate these parasitic plants that sequester host water, C, and nutrients (Geils and Hawksworth 2002; Mathiasen et al. 2008; Glatzel and Geils 2009). Some mistletoes have leafy shoots that provide a greater surface area for transpiration (*E*), which can result in significant additional water loss from the host tree (Flanagan et al. 1993; Cernusak et al. 2004). Mistletoes can transpire up to 9 times more per unit leaf area and maintain 72% greater rates of g_s than their hosts (Ullmann et al. 1985; Marshall et al. 1994). This results in significant additional water loss, lowers host tree water potentials, and increases risk for hydraulic failure. To compensate, host trees close their stomata, significantly reducing C assimilation and resulting in a negative host tree C balance (Zweifel et al. 2012). The mistletoe-induced 'leak' in the hydraulic system is intensified under drought conditions (Zweifel et al. 2012). In contrast to leafy mistletoes, dwarf mistletoes have reduced aerial shoots with less leaf area from which water can be lost. Needles of host trees infected with dwarf mistletoe have exhibited greater rates of g_s and *E*, reduced water use efficiency, and consequently more negative $\delta^{13}C_{leaf}$ (Sala et al. 2001; Meinzer et al. 2004; Logan et al. 2013). The vascular occlusions caused by dwarf mistletoe's sinkers tapping into host xylem lead to branch swellings and restrictions in water flow that can either reduce needle size (Logan et al. 2002; Reblin et al. 2006) or cause needle loss (Meinzer et al. 2004). Infected trees exhibited significantly reduced sapwood-area specific hydraulic conductivity (K_s) compared to uninfected trees, yet leaf-specific hydraulic conductivity (K_L) did not significantly differ between infected and uninfected trees (Meinzer et al. 2004; Logan et al. 2013). The maintenance of K_L but not K_s of infected branches was the result of two different infection symptoms: reduced needle size (Logan et al. 2002; Reblin et al. 2006) and needle loss (Meinzer et al. 2004). Due to these differences, Logan et al. (2013) observed significantly greater *E* in infected branches while Meinzer et al. (2004) observed no significant differences in g_s between infected and uninfected trees. Due to significant needle loss and reductions in photosynthetic capacity, infected trees exhibited significantly lower water use and inferred significantly lower C use on the whole tree level compared to controls (Meinzer et al. 2004).

Forest insects and pathogens also disrupt host tree C and nutrient relations. By establishing an endophytic system within the host phloem and xylem, dwarf mistletoes and mistletoes sequester photosynthates and nutrients. As stated above, trees

infected with dwarf mistletoe and mistletoe exhibited significantly reduced leaf N content compared to non-infected trees, presumably due to the sequestration of N by the parasite (Meinzer et al. 2004; Galiano et al. 2011). This contributes to the significantly reduced photosynthetic capacity of infected tree needles compared to uninfected tree needles (Meinzer et al. 2004). Insects such as bark beetles (Coleoptera: Curculionidae, Scolytinae) and the red oak borer (*Enaphalodes rufulus* (Haldeman); Coleoptera: Polyphaga, Cerambycidae) nest in and feed on phloem, impeding photosynthate transport. Bark beetles such as the mountain pine beetle (*Dendroctonus ponderosae* Hopk.) are native forest disturbance agents that infest and kill *Pinus* species. Although tree-ring width records show that bark beetles have been associated with western North American forests for hundreds of years, current outbreaks have increased in duration, intensity, and geographic area affected due to rising temperatures and decreasing precipitation throughout western North America (Samman and Logan 2000; Bentz et al. 2009, 2010). Bark beetles overwinter as larvae and attack trees in the summer (July–August). Females bore through the bark to the phloem and construct egg galleries. Trees can defend themselves by releasing resin, a defense mechanism to "pitch out" and resist beetle attack (Amman et al. 1985). This requires that a tree be healthy enough to allocate current photosynthates and/or stored nonstructural carbon to create this resin and healthy enough to transport photosythate and resin to sites of attack. The first beetles to attack a tree release aggregating pheromones to attract additional beetles to overcome the tree's defense. In addition to phloem, bark beetles can also injure the xylem because bark beetles vector various fungi that can disrupt xylem functionality (Dysthe et al. 2015), and inhibit water transport and also resin production. The bark beetle-induced, and fungal-enhanced, combination of phloem and xylem dysfunction kills the tree. With longer summers and shorter winters, some bark beetle species like *D. ponderosae* are not killed off by cold temperatures as they generally have been in the past, and can produce more than one generation per year, increasing the duration, intensity, and geographic area of outbreaks (Bentz et al. 2010). However, other species like *D. ruffipennis* are more cold-adapted, and rarely experience winter kill events (Miller and Werner 1987). In addition, warming and drought has stressed trees and weakened their capacity to fend off insects like bark beetles (Raffa et al. 2008; Anderegg et al. 2015).

Red oak borer is another native wood-boring insect that has recently experienced outbreaks of unprecedented magnitude that contribute to oak mortality observed in the Ozark Mountains of Arkansas and Missouri, USA (Crook et al. 2004). Episodic oak mortality in this region and elsewhere have been attributed to "oak decline," which is often incited by drought, late frosts, or insect defoliation, but is also influenced by a combination of predisposing factors such as tree age, competition, soil quality, and a number of insect pests and pathogens that are effective at contributing to the death of weakened trees, including red oak borer (Manion 1991; Thomas et al. 2002; Crook et al. 2004; Voelker et al. 2008; Gagen et al. 2019). The red oak borer has a two-year cycle with adults emerging in only odd numbered years. Larvae chew through bark into the phloem, sapwood, and heartwood where they build a gallery, feed, and overwinter twice. At low numbers, trees tolerate red oak borer but at extremely high infestation levels, mortality occurs. These physiological effects of

insects and pathogens can all impact the stable C and O isotopic composition within host trees, but because of the diversity of influences described above, each insect- and pathogen-host isotopic pattern can vary substantially (Cernusak et al. 2004).

25.3 Tree-Ring Stable Isotopes Record Physiological Impacts of Insects and Pathogens

Although numerous dendrochronological studies have examined outbreak cycles of pathogens and insects (Lynch 2012), fewer have used tree-ring stable isotopes to investigate host physiological impacts and interactions with climate. Any factors that affect leaf gas exchange (A, g_s) can influence the tree-ring stable isotope record (see Chaps. 16, 17). The enhanced insight into physiological impacts of insects and pathogens has led to research using tree-ring stable isotopes combined with ring widths to identify physiological outbreak signatures, outbreak cycles, and infestation dynamics. Correlations between the C and O stable isotopic composition of tree-rings and climate variables reveal the bidirectional interactions between climate, and the severity and susceptibility of insect and pathogen infection: how climate affects host susceptibility to insect and pathogen infestation, and how insect and pathogen infestation influences sensitivity to climate. Tree-ring stable isotope records can improve efforts by forest managers to combat insect and pathogen outbreaks by providing early detection of insect or pathogen infection and improving predictions of outbreaks and mortality events under future climate regimes as a result of synergistic insect and pathogen and climate influences. Tree-ring stable isotopes have helped elucidate this interaction between pathogen and climate. Below, we describe how tree-ring stable isotopes have been used to investigate (1) the impacts of insects and pathogens on host tree physiology (growth, hormonal regulation, gas exchange, water relations, and carbon and nutrient use), (2) the effects of climate on insect and pathogen infestation severity levels and host tree susceptibility to infestation, and (3) the effects of insect and pathogen infestation on host tree sensitivity to climate.

25.3.1 Tree-Ring Stable Isotopes Reveal Insect and Pathogen Impacts on Host Physiology

Given the potential for greater insights into host tree physiological impacts of insects and pathogens, tree-ring stable isotopes have been used to more precisely identify physiological impacts to reveal infection ‘signatures’ and onset of infection. For example, Marias et al. (2014) used tree-ring growth and $\delta^{13}C$ over 100 years and also tree-ring $\delta^{18}O$ during 20 years of severe infection to investigate the impacts of hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones ssp. *tsugense*) on the physiology of host western hemlock (*Tsuga heterophylla* (raf.)

Sarg.). Radial growth of infected trees was initially greater than that of uninfected trees in 1886–90 but then declined more rapidly and became significantly lower than uninfected trees in 2006–10 as the infection became severe, suggesting that infected trees were growing faster than uninfected trees prior to becoming infected. During the advanced stage of the infection, infected trees exhibited significantly lower tree-ring $\delta^{13}C$ and $\delta^{18}O$ than uninfected trees regardless of annual precipitation (drier versus wetter years). The lower $\delta^{13}C$ of infected trees supports previous work that the dwarf mistletoe infection reduces host photosynthetic capacity, due to the parasite's sequestration of N from the host tree (Meinzer et al. 2004). Because the impacts on radial growth and $\delta^{13}C$ were evident only when the infection became severe, the authors concluded that tree-ring growth and stable isotopes could not be used to identify precisely when trees became infected. However, this information suggests that western hemlock can live for decades with the dwarf mistletoe infection. The lower $\delta^{18}O$ of infected trees was unexpected because g_s and environmental variables, expected to influence $\delta^{18}O$ (see Chap. 10), were similar for both infected and uninfected groups of trees. However, estimates of lower mesophyll conductance (g_m) in leaves of infected trees from A-C_i curves led the authors to conclude that effective path length (L) estimated from the Peclet effect model (Barbour 2007) was higher in leaves of infected trees, leading to their lower tree-ring $\delta^{18}O$. Although the anatomical causes of the Peclet effect have been debated (Roden et al. 2015), these unexpected findings pointed to limitations in the dual isotope approach (Scheidegger et al. 2000; Roden and Siegwolf 2012) often used to interpret tree-ring $\delta^{13}C$ and $\delta^{18}O$ because it does not account for changes in traits related to leaf anatomical characteristics such as g_m and L that alter gas exchange and may underlie the observed $\delta^{18}O$ patterns.

Tree-ring stable isotopes have been used to investigate the long-term impacts of insect-induced defoliation and leaf herbivory on host physiology and tree growth-climate relationships (Leavitt and Long 1986; Simard et al. 2008, 2012; Kress et al. 2009; Gori et al. 2014a). Defoliation and herbivory can be recorded in tree-ring cellulose because they directly influence gas exchange by damaging stomata and photosynthetic machinery (Weidner et al. 2010) and indirectly by increasing A in remaining leaves (Simard et al. 2008) and reducing stand-level E and associated competition for water during dry periods. Simard et al. (2008) investigated the effects of western spruce budworm (SBW) (*Choristoneura fumiferana* Clem.) by comparing the C and O tree-ring stable isotope records of SBW's primary host balsam fir (*Abies balsamea*), secondary host black spruce (*Pinus mariana*), and a non-host tree species *Pinus banksiana* (Lamb.). Severe infestations of the leaf-feeding SBW are recorded in the tree-ring record as reduced radial growth lasting 5 years or more (Swetnam et al. 1985). Light to moderate infestation effects on radial growth are less pronounced. SBW-induced defoliation appeared to cause a compensatory increase in A of the remaining needles with a relatively smaller concurrent increase in g_s, exhibited by increased tree-ring $\delta^{13}C$ (i.e. decreased tree-ring $\Delta^{13}C$) and reduced radial growth not observed in the non-host species and concurrent with documented SBW outbreaks in the area. The compensatory increase in A may have resulted from an increase in allocation of mineral nutrients to remaining leaves (Lavigne et al. 2001). In contrast,

the tree-ring $\delta^{18}O$ trajectories were synchronous among host and non-host species, supporting that the $\delta^{13}C$ signal is most likely due to a compensatory increase in *A* (rather than shifts in g_s) in remaining needles and suggesting that the tree-ring $\delta^{18}O$ signal is driven primarily by climate, rather than SBW.

Compensatory increases in *A* in response to defoliation by the web-spinning sawfly also have been recorded in tree-ring stable isotopes of host Norway spruce. Gori et al. (2014a) compared tree-ring growth, $\delta^{13}C$, and $\delta^{18}O$ in healthy and defoliated Norway spruce in the southern Alps of Italy. Defoliated trees exhibited significantly greater tree-ring $\delta^{13}C$ and lower $\delta^{18}O$ values than control trees, suggesting that defoliated trees may have increased the photosynthetic capacity of remaining foliage according to the dual isotope model (Scheidegger et al. 2000). Interestingly, the $\delta^{13}C$ and $\delta^{18}O$ isotope patterns of defoliated trees began 2 years and 1 year, respectively before defoliation. Using the Scheidegger et al. (2000) model, the authors hypothesized that the isotope patterns observed before defoliation were due to reduced g_s, suggesting defoliated trees may have been responding to drought stress, which likely contributed to the outbreak. The drought-stressed trees may have mobilized stored starch into tree-ring cellulose, known to have greater $\delta^{13}C$ values (Brugnoli et al. 1988; Helle and Schleser 2004; Cernusak et al. 2009).

In contrast to the findings of Gori et al. (2014a) and Simard et al. (2008), other studies have not found evidence for compensatory increases in *A* as a result of defoliating insects and pathogens. Leavitt and Long (1986) did not observe a tree-ring $\delta^{13}C$ signal of SBW outbreak in infested stands of host species white fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*) and non-host ponderosa pine (*Pinus ponderosa*). Furthermore, Ellsworth et al. (1994) observed a decline in instantaneous measures of *A* and no change in leaf $\delta^{13}C$ of sugar maple (*Acer saccharum* Marsh.) heavily defoliated by pear thrips (*Taeniothrips inconsequens* Uzel), a piercing-sucking insect. Artificially defoliated balsam fir (*Abies balsamea* Mill.) saplings exhibited an increase in tree-ring $\delta^{13}C$ but the lack of significant correlations among gas exchange parameters (*A*, g_s, c_i/c_a) and tree-ring $\delta^{13}C$ did not support a compensatory increase in *A* (Simard et al. 2012). Instead, the authors attributed the increase in tree-ring $\delta^{13}C$ to mobilization of stored carbohydrates enriched in ^{13}C (Brugnoli et al. 1988; Helle and Schleser 2004; Cernusak et al. 2009).

25.3.2 *Tree-Ring Stable Isotopes Inform Effects of Climate on Insect and Pathogen Infestation Severity Levels and Host Tree Susceptibility to infestation*

Climate-induced alterations in host physiology have been shown to both decrease and increase the severity of and susceptibility to insect and pathogen infections. As mentioned earlier, larch budmoth (LBM) defoliates larch in the European Alps, and had occurred with a regular 8–10-year periodicity for at least 1200 years until

the 1980s after which no regular outbreaks have been observed (Baltensweiler et al. 2008). Tree-ring stable isotopes have been used to determine if climate variables may explain why no LBM outbreak has occurred since the 1980s. Because LBM infestation results in needle loss or damaged, dysfunctional needles, no tree-ring cellulose is formed during an outbreak, and the C isotope signature of outbreak years reflects the cellulose formed either before or after defoliation occurs when normally functioning needles have replaced damaged needles in the second half of the growing season (Baltensweiler et al. 2008). Indeed, the tree-ring $\delta^{13}C$ in outbreak years appeared to be dominated by latewood formation due to the second flush of needles because $\delta^{13}C$ correlated strongly with summer (July–August) temperatures (Kress et al. 2009; Weidner et al. 2010). Cooler summer temperatures were positively related with severe LBM outbreaks, suggesting that the 1980s halt in infestation may have been due to increasing summer temperatures (Kress et al. 2009). This is likely because winters of sufficient duration (120 days below 2 °C) are required to successfully induce diapause and protect overwintering insects from low temperatures. However, warmer spring and summer temperatures may lead to an early diapause with fewer frost days, leading to egg mortality (Baltensweiler et al. 1977). Additionally, above-average summer temperatures could influence maturation of needles, the main food source for LBM and result in poor food quality, leading to larval and pupal mortality. Both tree-ring $\delta^{13}C$ and $\delta^{18}O$ were unaffected by LBM but $\delta^{18}O$ was strongly correlated with the $\delta^{18}O$ of previous winter (December–March) precipitation, consistent with a winter recharge of the soil (Daux et al. 2011). Because of LBM, the potential for larch, a long-lived (850 + years) economically valuable species, to be used to reconstruct climate was questioned. However, strong correlations between climate and the tree-ring stable isotope record and not LBM suggest that the tree-ring stable isotope record of LBM-infected larch can be used for climate reconstructions (Kress et al. 2009; Weidner et al. 2010; Daux et al. 2011). In contrast, tree-ring widths can be used to track LBM outbreaks but potentially not climate, making radial growth unsuitable for climate reconstructions (Kress et al. 2009; Weidner et al. 2010), unless corrections are made and/or comparison with a non-host species is included (e.g. King et al. 2013; Konter et al. 2015; see Sect. 25.3). Comparison of these LBM studies with other studies on defoliating insects highlights that leaf lifespan and phenology may govern whether insect-induced defoliation is recorded in tree-ring stable isotopes (Simard et al. 2008; Gori et al. 2014a) or not (Kress et al. 2009; Weidner et al. 2010). Because deciduous larch refoliates after defoliation, the tree-ring stable isotope record reflects the physiology of the second flush of foliage. In contrast, evergreen species that are defoliated for multiple years may remobilize stored C reserves to maintain function (e.g. Simard et al. 2012) or exhibit a compensatory increase in A (Simard et al. 2008; Gori et al. 2014a), both of which influence tree-ring $\delta^{13}C$.

Tree-ring stable isotopes have also revealed how climate variables such as relative humidity increase the severity of fungal pathogens such as Swiss Needle Cast (SNC). The fruiting bodies (pseudothecia) of the fungus *Phaeocryptopus gaeumannii* (T. Rohde) Petr.) that causes SNC physically occlude stomata, restricting gas exchange and resulting in premature needle loss in host Douglas-fir (*Pseudotsuga menziesii*) (Manter et al. 2000). In spring, spores land on foliage and colonize needles to the

extent that environmental conditions promote germination and hyphal growth into stomata. Warm winter and spring temperatures and spring/summer leaf wetness may facilitate fungal growth and reproduction (Manter et al. 2005; Stone et al. 2008). Saffell et al. (2014) compared tree-ring growth, $\Delta^{13}C$, and $\delta^{18}O$ in SNC-infected Douglas-fir treated and not treated with a fungicide to remove SNC to examine whether $\Delta^{13}C$ and $\delta^{18}O$ can serve as a tool for detecting past SNC infection and the influence of climate on SNC disease severity. Given the pseudothecia-induced restrictions in gas exchange, SNC reduced $\Delta^{13}C$ as expected, suggesting that $\Delta^{13}C$ can be used to detect past SNC infection. In contrast, tree-ring $\delta^{18}O$ did not differ between treated and untreated trees likely because high humidity masked any effect of SNC on O isotope fractionation (see Chapter 10). High humidity can mask O isotope fractionation because high humidity reduces evaporative enrichment of leaf water and vapor exchange with leaf water is high, reducing physiological $\delta^{18}O$ signals within the leaf (Barbour and Farquhar 2000). In diseased trees, a significant negative correlation between $\Delta^{13}C$ and relative humidity during the spring sporulation period of antecedent years suggested that high humidity, conditions that promoted fungal growth and reproduction, increased SNC disease severity (Saffell et al. 2014). Other favorable climate conditions for the fungus, including warmer winter temperatures at coastal (relatively cool, wet) sites, and increased summer precipitation at inland (relatively warm, dry) sites, are likely to increase SNC disease severity (Lee et al. 2013, 2017).

Tree-ring $\delta^{13}C$ and $\delta^{18}O$ have revealed in what situations climate-induced stress may have increased susceptibility to insect-induced mortality. Recent increases in temperature and decreases in precipitation in western North America have promoted unprecedented outbreaks of bark beetles (Samman and Logan 2000; Bentz et al. 2009, 2010). Bark beetle outbreaks have affected tens of millions of hectares in western North America since 1990 (Raffa et al. 2008) and have led to widespread forest mortality and economic timber loss (Corbett et al. 2016). Tree-ring growth has been used to identify bark beetle outbreaks because surviving trees experience prolonged periods of release visible in the tree-ring record (e.g. Alfaro et al. 2004). However, tree-ring stable isotopes provide the physiological information needed to determine if drought may predispose host trees to bark beetle-induced mortality (Gaylord et al. 2013). In south central Alaska, Csank et al. (2016) used tree-ring $\delta^{13}C$ and $\delta^{18}O$ from live and dead trees to examine whether white spruce (*Picea glauca*) killed by spruce bark beetle (*Dendroctonus rufipennis* Kirby) showed greater evidence of drought stress prior to mortality compared to trees that survived the beetle outbreak. Compared to live trees, dead trees exhibited significantly greater correlation coefficients describing relationships between $\delta^{13}C$ and spring/summer temperature; however, the isotopic record in dead trees had no correlation with precipitation, whereas in live trees, $\delta^{18}O$ was highly correlated with spring precipitation. As a result, the authors inferred that trees that succumbed to beetle attack were more drought-stressed than those that survived. However, the authors could not determine how drought stress contributes to the development of epidemic outbreaks because they could not determine the stable isotope sensitivity to these climate variables among live versus dead. To more robustly test whether drought stress has a role in

allowing incipient spruce bark beetle populations to build toward epidemic outbreak conditions, mixed-effect modeling of tree-ring stable isotopes is useful (Pettit et al. in prep.; Pettit 2018). Pettit et al. (in prep) sampled tree-ring $\Delta^{13}C$ from Engelmann spruce (*P. engelmannii*) trees from six stands in montane forests of southern Utah that died either early or late during an outbreak that killed >95% of overstory spruce trees across the region. As expected, tree-ring $\Delta^{13}C$ was consistently lower during progressively more severe droughts across stands, but mixed-effect modeling of $\Delta^{13}C$ response to summer drought detected no significant differences between early- and late-dying trees. The lack of a difference in $\Delta^{13}C$ sensitivity to drought between early- and late-dying trees indicates that incipient spruce beetle populations did not build into an epidemic outbreak by selecting hosts that were more sensitive to drought stress, but rather that warmer growing season temperatures during this time were the most important direct driver of the spruce beetle outbreak.

Another recent study conducted in California, used tree-ring $\Delta^{13}C$ and $\delta^{18}O$ to investigate whether paired surviving versus dead ponderosa pines (*Pinus ponderosa* Dougl. ex Laws.) killed by western pine beetle (*Dendroctonus brevicomis*) differed in drought sensitivity prior to the outbreak (Keen 2019). The authors found that although drought sensitivity of growth and $\Delta^{13}C$ had increased dramatically since 1900, there were no significant differences between surviving and dead trees in climate sensitivity of $\Delta^{13}C$ or $\delta^{18}O$ in response to temperature, precipitation, and various drought metrics. Surviving trees grew faster than the paired dead trees and much faster than randomly sampled ponderosa pines from the same region, and were located in stands with more conspecific stem basal area. In this case, tree-ring stable isotopes indicated that drought sensitivity had increased about five-fold between 1900 and the initiation of the bark beetle outbreak, but that tree drought sensitivity did not determine local-scale selection of hosts by bark beetles at sites where at least one overstory tree survived. Overall, increases in drought sensitivity preceded the western pine beetle outbreak that killed >95% of overstory ponderosa pines across the region, and surviving overstory ponderosa pines tended to be the fastest growing and more isolated from conspecifics.

The aforementioned studies using tree-ring stable isotopes to investigate the effect of drought on host susceptibility to insect attack highlight an underexplored line of research: determining the relative contributions of drought-induced stomatal closure versus stress-induced shifts in C allocation to the tree-ring $\delta^{13}C$ signal. During drought, stomatal closure restricts gas exchange and is reflected by increased tree-ring $\delta^{13}C$. During insect attack, stressed trees may allocate more current year photosynthate to defense and less to growth, and/or allocate more stored photosynthate to tree-ring growth (Kozlowski et al. 1991; Helle and Schleser 2004; Kagawa et al. 2006; Sohn et al. 2014). This can increase tree-ring $\delta^{13}C$ due to more stored C, enriched during remobilization from starch, being allocated to tree-ring growth and/or less current year C being allocated to tree-ring growth. More broadly, drought-induced negative water potentials more strictly constrain cell division and expansive growth of plants compared to leaf gas exchange (Hsiao 1973; Muller et al. 2011). This concept was recently demonstrated for stem radial growth and stomatal conductance in isohydric and anisohydric conifer species adapted to an arid region of Utah,

USA (Voelker et al. 2018). The predictable ordering of these processes governing key aspects of C fixation and allocation to growth make it likely that tree-ring isotope signals will be somewhat lagged and muted during droughts that cause trees to cease growth but maintain low but significant levels of photosynthesis. Overall, it can often remain unclear to what extent the tree-ring $\delta^{13}C$ signal is driven by drought-induced growth inhibition, drought-induced stomatal closure, defense-induced shifts in C allocation, or a combination of these effects.

25.3.3 Tree-Ring Stable Isotopes Inform Effects of Insect and Pathogen Infestation on Host Tree Sensitivity to Climate

Insect- and pathogen-induced alterations in host physiology have been shown to both increase and decrease host tree sensitivity to climate variables. Fungal pathogens such as Armillaria root disease (*Armillaria*) and *Heterobasidion parviporum* cause root and butt rot, needle loss, reduced uptake of water and nutrients, and predisposition of trees to drought-induced decline and mortality (Marçais and Bréda 2006; Colangelo et al. 2018). The tree-ring growth, $\delta^{13}C$, and $\delta^{18}O$ of *H. parviporum*-infected and uninfected Norway spruce were compared across three different elevation sites (850, 1300, 1900 m) in the eastern Alps of Italy (Gori et al. 2013, 2014b). Infected trees exhibited the greatest reductions in radial growth, $\delta^{13}C$, and $\delta^{18}O$ relative to control trees at the low elevation site compared to the higher elevation sites. This suggests that the infection was most severe at low elevation, likely because conditions were less favorable for the fungus at higher elevations (Gori et al. 2013, 2014b). At higher elevation, the growing season is shorter, and temperatures and water availability are also lower, which makes the fungus less aggressive. Other observational and modeling studies have found similar elevational gradients in insect outbreak intensity (Johnson et al. 2010; Peters et al. 2017). The tree-ring stable isotope data suggested that infection induced an increase in g_s according to the Scheidegger et al. (2000) model (see Chap. 16). Increased g_s may compensate for reduced foliage observed in infected trees. Radial growth of low elevation infected trees was the most sensitive to drought stress, as shown by a significant correlation between the Palmer Drought Severity Index (PDSI) and infected tree radial growth that was not observed in low elevation control trees nor in infected or control trees at higher elevation sites.

Just as relative humidity was shown to influence SNC severity (Saffell et al. 2014), SNC severity has also been shown to influence Douglas-fir sensitivity to climate in western Oregon (Lee et al. in review). Consistent with Saffell et al. (2014), Lee et al. (in review) found that the coastal site with greater relative humidity exhibited greater SNC severity compared to the inland sites with lower relative humidity. At the inland sites where SNC severity was low, $\Delta^{13}C$ and $\delta^{18}O$ in Douglas-fir tree-rings were more sensitive to climate variation than to SNC severity. Growth reductions of trees at the inland sites were primarily attributed to stomatal response to high VPD, consistent

with (Barnard et al. 2012). In contrast, at the coastal site where SNC severity was high, $\Delta^{13}C$ and $\delta^{18}O$ were less variable over time, showing muted and lagged responses to past climate and suggesting a greater reliance on stored carbohydrates. Growth reductions of trees at the coastal site were primarily attributed to a reduction in *A* through an SNC-induced loss of foliage. Growth response to high summer VPD was greater in years with high SNC severity than in years with low disease severity (Lee et al. 2017).

Defoliating insects such as pandora moth (*Coloradia pandora* Blake) can modify co-occurring host and non-host tree sensitivity to PDSI for up to two decades after defoliation events. This has been observed in a dry mixed-conifer landscape in central Oregon where old-growth ponderosa pines were defoliated four times by pandora moth for at least 2–6 years per event at local scales, between the 1850s and the 1990s (Voelker et al. 2019). More comprehensive regional information on defoliations extends back over 600 years (Speer et al. 2001). At this site, historic suppression of wildfire has led to increased sensitivity of leaf gas exchange to drought, which has likely made trees more susceptible to insects and pathogens (Keen et al. in prep, Voelker et al. 2019). Compared to the period prior to defoliation, tree-ring $\Delta^{13}C$ during and after defoliation was less sensitive to PDSI (Fig. 25.1). This defoliation-induced reduction in drought sensitivity lasted for 15–20 years, with a

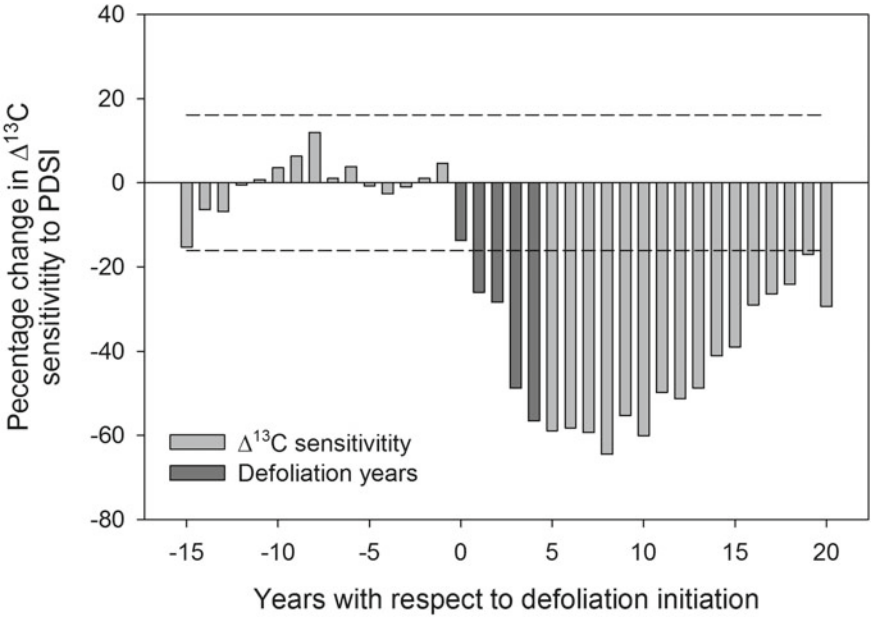


Fig. 25.1 Percentage change in ponderosa pine tree-ring $\Delta^{13}C$ sensitivity to Palmer Drought Severity Index (PDSI) before and after defoliation by pandora moth (*C. pandora*). Dashed lines indicate the percentage change in drought sensitivity that would be considered significantly different than 0 at $P < 0.01$ ($\pm 16.16\%$)

broad peak extending from near the end of the defoliation to about six years thereafter. In Fig. 25.1, both host and non-host trees were included. It is notable that non-host trees were reduced in drought sensitivity to an equal or greater magnitude compared to the host trees (data not shown), suggesting that the greatest effect of defoliation in these dry conifer forests was a reduction in competition for water at the stand-level due to a loss of leaf area and associated *E*. This application of tree-ring $\Delta^{13}C$ demonstrates that (1) defoliation can affect climate sensitivity of trees for up to two decades, and (2) although no significant changes in absolute $\Delta^{13}C$ were detected in host or non-host trees associated with defoliation, if used in a drought reconstruction, tree-ring $\Delta^{13}C$ of host or non-host trees would tend to underestimate drought severity for up to twenty years after a defoliation event.

Other tree-ring stable isotope records also have revealed loss of sensitivity to climate variables with increased severity of pathogen infection or insect herbivory. The aspen leaf miner (*Phyllocnistis populiella* Cham.) is responsible for widespread herbivory of trembling aspen since its first recorded outbreak in the early 2000s (Boyd et al. 2019). The aspen leaf miner feeds on leaf epidermal cells during summer months, decreases *A*, g_s, and growth, and has resulted in increased leaf $\delta^{13}C$ due to damaged stomata (Wagner et al. 2008). In contrast to leaf-level measurements of gas exchange and leaf $\delta^{13}C$, under low soil moisture conditions, tree-ring wood $\delta^{13}C$ decreased with increasing intensity of leaf mining (Boyd et al. 2019). When leaf mining intensity was low, trees responded as expected to low soil moisture, exhibiting increased tree-ring $\delta^{13}C$ and suggesting reduced g_s. In contrast, when leaf mining was severe, trees did not respond as expected to low soil moisture, exhibiting reduced tree-ring $\delta^{13}C$ and suggesting increased g_s and/or decreased *A* relative to any shifts in g_s. This leaf mining-induced de-coupling of tree-ring $\delta^{13}C$-climate sensitivity may reflect a compensatory response of increased g_s in remaining leaves due to premature leaf-mining-induced leaf area reductions. Hence, severe leaf mining may override the influence of climate on tree-ring stable isotopes in trembling aspen (Boyd et al. 2019).

An insect-induced reduction in host tree climate sensitivity has also been observed in northern red oak (*Quercus rubra* L. (Fagaceae)) infested with red oak borer, a wood boring insect. “Oak decline” is a widespread phenomenon that is believed to be triggered by a combination of factors including tree age, drought, and soil quality (Manion 1991; Thomas et al. 2002; Crook et al. 2004; Voelker et al. 2008; Gagen et al. 2019). The oak decline episode of the early 2000s in the Ozark forests of central USA was unique because it coincided with drought and red oak borer activity (Muzika and Guyette 2004; Voelker et al. 2008; Haavik et al. 2008). From ~1950–2000, infested trees reduced radial growth more rapidly compared to control trees as red oak borer infestation became severe. However, the tree-ring $\delta^{13}C$ signal of infected and healthy trees only diverged during the most advanced stage of infestation when reductions in radial growth were greatest (Haavik et al. 2008; Billings et al. 2016). In both studies, tree-ring $\delta^{13}C$ was sensitive to drought early in the study period but not when infestation became severe (Haavik et al. 2008; Billings et al. 2016). This is consistent with the observation that before infestation, trees that

eventually became severely infested exhibited a 20% lower radial growth immediately following a severe drought compared to trees that only became lightly infested. Similar to western hemlock infected with dwarf mistletoe (Marias et al. 2014), it appears that oak can support high levels of wood boring insects for ~17 years without measurable impacts on the tree-ring $\delta^{13}C$ record (Haavik et al. 2008). Oaks stricken by drought-induced dieback have reduced C resources available for defense (sensu Voelker et al. 2008) but increased tissue N concentrations (Billings et al. 2016) after remobilization—both of which would presumably benefit red oak borer fitness. In oaks suffering dieback, live tree crowns (i.e. leaf area) are smaller and made up of more epicormic branches (Voelker et al. 2008). If these tree-level N resources are concentrated in fewer leaves and result in greater leaf-level *A*, higher tree-ring $\delta^{13}C$ would be expected in dying trees. Unexpectedly however, Billings et al. (2016) found that dying trees exhibited lower tree-ring $\delta^{13}C$ than healthy trees, which contrasted with the dying trees' greater N concentration than healthy trees. Although dying trees were characterized by greater N concentration, the difference in tree-ring $\delta^{13}C$ during later stages of oak decline were apparently more influenced by proportionally greater increases in stomatal conductance as a product of an unbalanced hydraulic system—whereby extensive branch dieback caused large decreases in leaf area and preserved much of the pre-dieback xylem functionality of stems and roots supplying the leaves water. In summary, tree-ring stable isotopes have revealed that infestation by insects and pathogens with diverse impacts on host physiology can increase or decrease the sensitivity of host trees to climate.

25.4 Considering Insect and Pathogen Influences on Tree-Ring Stable Isotopes in Future Work

Because tree-ring stable isotopes reflect both the environment and tree physiological responses to the environment, they provide invaluable insights about past climate and physiology, yet can be complicated to interpret (Barbour and Song 2014). The fact that the effect of insects and pathogens on host physiology can be recorded in tree-rings and potentially mask climate signals (e.g. Simard et al. 2008; Marias et al. 2014; Saffell et al. 2014) and also that climate signals can potentially mask insect and pathogen impacts, needs to be considered when using the tree-ring record to reconstruct past climate, climate-growth relationships, and physiological responses to the environment. Moreover, the potential for pests or pathogens to affect both hosts or non-hosts may not be detectable in absolute isotopic values but only in isotopic sensitivity to climate (Fig. 25.1). Insect/pathogen impacts are not always reflected in tree-ring stable isotopes (Kress et al. 2009) and, with proper consideration, tree-ring stable isotopes can often still be useful for reconstruction of climate and physiology. Here, we highlight the importance of considering the limitations to interpreting tree-ring stable isotope signals and ways to address these limitations in future research studies.

The effect of an insect or pathogen can be significant enough to shift tree-ring isotope signals and can confound interpretations of tree-rings to reconstruct climate if it is unknown whether the tree was infected or not. Paleoclimate studies that use dated tree-rings from dead or sub-fossil logs or buildings may in some cases include trees infected with a pathogen or insect (Krause 1997). For example, if the tree-ring $\Delta^{13}C$ record of Pandora moth-defoliated Douglas-fir were to have been used to reconstruct climate, one could gain the erroneous inference that climate variability was relatively quiescent for one to two decades after each defoliation event (e.g., Fig. 25.1). To address this issue, corrections can be made to the tree-ring record to properly reconstruct climate if insect or pathogen presence is known. For example, growth rings during LBM events have been removed and replaced with variance-adjusted values obtained from unaffected rings (Esper et al. 2006; Büntgen et al. 2006). Experimental study design can also be used to reduce the confounding effects of climate and insects/pathogens on tree-ring stable isotopes. Studies can be designed where uninfected and infected sets of trees are exposed to the same environmental conditions by sampling trees in a relatively small area (e.g. Marias et al. 2014). Another approach to separate the effect of climate and insects/pathogens is to also sample and compare the tree-ring record of a non-host species that grows in the same area or region to identify climate shifts not associated with insect/pathogen physiological impacts (e.g. Simard et al. 2008; King et al. 2013; Saffell et al. 2014; Konter et al. 2015).

Insect and pathogen influences also challenge traditional isotope theory. For example, Marias et al. (2014) found that the differences in tree-ring $\delta^{18}O$ between uninfected and infected trees could not be explained by climate or g_s alone—the traditional interpretations using the dual isotope approach (Scheidegger et al. 2000). The dual isotope approach does not necessarily incorporate parameters related to leaf anatomy such as g_m and L, which appeared to have significantly affected tree-ring $\delta^{18}O$ in the study of Marias et al. (2014). Therefore, future research using the dual isotope approach must properly account for its assumptions and consider its limitations, especially in potential insect- and pathogen-infected systems (Roden and Siegwolf 2012).

Research on insect and pathogen effects on tree-ring stable isotopes also sheds light on variation in isotope signals. The competing influences of climate and plant physiological responses to environment or insects and pathogens on tree-ring cellulose may be responsible for discrepancies among studies in how and if insect and pathogen influences are recorded in tree-ring cellulose. For example, defoliation by SBW has been recorded in tree-ring stable isotopes in some studies (Simard et al. 2012), but not in others (Leavitt and Long 1986). This variability in how and if insect/pathogen impacts are recorded in the tree-ring stable isotope record in different systems makes it critical to consider the potential effect of insects and pathogens on host physiology and the tree-ring stable isotope record when using tree-rings to reconstruct past climate and physiology. Insect- and pathogen-induced reductions in radial growth also contribute to discrepancies among studies because many pathogens result in narrow or missing rings, inhibiting the development of cellulose in which C and O stable isotopes can be recorded. In addition, insects and

pathogens, and other stressors can increase the reliance on stored C reserves which would dampen or mute the tree-ring record to the actual climate or physiological responses during any particular year (Kozlowski et al. 1991; Helle and Schleser 2004; Kagawa et al. 2006; Sohn et al. 2014). Other factors that contribute to the variability in results across insect- and pathogen-infested systems include the intensity, frequency, and distribution of the infestation or disturbance, and whether the history of infestation is known or unknown, which varies by type of insect/pathogen. It is clear that when designing experiments and when interpreting tree-ring stable isotope chronologies to reconstruct past climate or physiology, consideration of insect and pathogen impacts is as essential as considering the more well-studied effects of tree age and size on tree-ring $\delta^{13}C$ and $\delta^{18}O$ (McDowell et al. 2011; Klesse et al. 2018).

Despite challenges to interpreting tree-ring stable isotope signatures, their application to examine the physiological impacts of insects and pathogens can provide valuable information to forest managers on tree responses to insects and pathogens in light of intensifying outbreaks due to climate change. Tree-ring stable isotopes enable examination of spatial and temporal variation in host-insect/pathogen dynamics to inform management plans for the future and in diverse systems. For example, findings that insect/pathogen effects are more severe and result in increased drought stress at low elevation compared to higher elevations highlights that the insect or pathogen could become more aggressive at currently colder high elevation sites as climates become warmer (e.g. Gori et al. 2014b).

25.5 Conclusion

Tree-ring stable isotope analyses are a powerful tool because they reveal long-term physiological effects of insects and pathogens on the host tree that would not otherwise be observable in ring widths alone. More detailed information on the impacts of insects and pathogens on host physiology and the bidirectional interacting effects of insects/pathogens and climate on host physiology should increasingly be leveraged to improve predictions of future outbreaks and forest mortality events that can guide forest management. However, interpretation of tree-ring stable isotope ratios may not be straightforward given that they record both climate and physiological responses to abiotic and biotic environmental factors. Therefore, the potential for insect/pathogen impacts on host physiology should be critically evaluated when designing experiments or research that employs tree-ring stable isotopes to reconstruct past plant physiological responses or climate variability.

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