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REVIEW

From Colonization to Collapse: a Mechanistic Perspective on Tree Mortality by Bark Beetles

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Abstract

Purpose of Review Bark beetle outbreaks are intensifying under climate change, yet the links among drought stress, beetle attack and colonization, rapid tree mortality, and tree physiology, remain poorly integrated across disciplines. This review provides a comprehensive, mechanistic synthesis of recent advances in tree physiology, bark beetle ecology, and microbial interactions to examine how drought alters xylem–phloem function, carbon allocation, and defense capacity, how these changes affect beetle host selection and reproductive success, and how associated microbes accelerate host decline.

Recent Findings Drought-driven declines in xylem water potential constrain phloem transport through reduced turgor and increased sap viscosity, reshaping carbon distribution and defense deployment. Moderate drought may transiently enhance some defenses, whereas severe or prolonged drought depletes non-structural carbohydrates, impairs resin flow, and increases phloem nutritional suitability for beetles. Beetle attacks cause spatially complex phloem disruption and local carbon depletion together with their associated fungi, which also contribute to pit membrane degradation, increasing vulnerability to embolism. The altered bark and phloem microenvironments, including gas exchange and moisture conditions within bark beetle galleries, may further influence microbial activity and host responses.

Summary We propose a cross-disciplinary, integrated mechanistic framework in which drought-induced physiological destabilization predisposes trees to beetle attack, after which phloem disruption and microbial activity amplify carbon limitation and hydraulic dysfunction. Hydraulic failure may represent a convergence point among interacting stressors, underscoring the complex multi-trophic feedbacks driving infestation expansion. Key gaps remain in quantifying phloem dynamics, bark permeability, and subcortical microclimates during attack, limiting predictions of forest vulnerability under increasing drought and bark beetle pressure.

Keywords Bark beetles · Drought stress · Phloem physiology · Hydraulic failure · Tree defenses · Tree mortality

Introduction

Bark beetle outbreaks are a leading cause of forest mortality worldwide, with profound ecological and economic consequences [1]. In recent decades, the frequency and severity of these disturbances have risen markedly, primarily due to climate warming and the associated increase in extreme weather events such as windstorms and droughts [2–4].

The intensification of drought events, characterized by greater severity and longer duration, together with rising temperatures, is increasing water stress in trees and enhancing the number of scolytid generations per year (voltinism), thereby posing a substantial threat to the long-term sustainability of forest ecosystems globally [2, 5–7]. However, the effects of drought duration on forest susceptibility to the bark beetle species capable of entering epidemic population

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Extended author information available on the last page of the article phases (mainly of the genera *Ips* and *Dendroctonus*) are not uniform. For example, acute droughts, defined as strong reductions in soil water availability, in mesic environments have been associated with increased scolytid activity, whereas trees acclimated to chronically dry habitats often do not exhibit heightened vulnerability during drought events [8]. These findings indicate that certain bark beetle species may employ a selective colonization strategy, preferentially attacking moderately stressed trees while avoiding both unstressed and severely stressed individuals [9].

Drought stress induces stomatal closure and reduces photosynthetic carbon assimilation, progressively constraining the carbohydrate pool available for metabolism, storage, growth and the biosynthesis of new carbon-based defence compounds. This reduced carbon budget is thought to limit both the formation of structural defenses (e.g., lignification, resin ducts) and the synthesis of bioactive secondary metabolites involved in plant defense (e.g., phenolics, terpenoids), ultimately increasing tree susceptibility to bark beetle colonization [10, 11]. Beyond weakening defenses, depletion of stored carbon reserves may also alter phloem nutritional quality by changing concentrations of soluble sugars, amino acids, and other metabolites essential for larval development, with potential consequences for beetle fecundity and brood viability [12, 13].

Bark beetles colonize the phloem of host trees and facilitate the establishment of a complex microbiome, including associated fungi and bacteria, which can synergistically accelerate host mortality. Ophiostomatoid fungi, a group of ascomycete fungi commonly associated with bark beetles, are frequently implicated in tree death due to their capacity to detoxify tree defense compounds and disrupt xylem hydraulic conductivity [14]. A key mechanism underlying this disruption is the enzymatic degradation of pit structures connecting xylem conduits [15], which increases wood porosity [16] and compromises the pits' capacity to prevent the entry of air into water-filled xylem conduits (a process known as air seeding). This process directly elevates vulnerability to drought-induced embolism across the hydraulic system [16–18]. Some ophiostomatoid fungi can colonize not only the vascular elements of sapwood, but also the phloem and ray parenchyma tissues [19]. Although bark beetle–fungus associations are often host-specific [20], they share core physiological mechanisms across systems. Well-studied pathosystems, such as *Dendroctonus ponderosae – Pinus contorta*, *D. frontalis* – southern pine species, and *Ips typographus – Picea abies*, illustrate the tight ecological coupling among beetles, host trees, and microbial consortia [21–23].

Despite broad recognition that tree mortality emerges from complex interactions among host trees, bark beetles, and their associated fungal symbionts [21], critical knowledge gaps remain regarding the physiological factors that predispose trees to infestation and the mechanistic pathways leading to decline and mortality. In particular, the links between physiological destabilization in conifer hosts and the underlying biochemical and molecular processes, both prior to and following bark beetle attack, remain poorly understood [24]. Notably, the dynamics of phloem transport during different phases of bark beetle attack have received limited attention. Moreover, it is increasingly evident that these pathosystems extend beyond binary host–beetle interactions to encompass diverse microbial communities of both agents, including aerobic and anaerobic taxa [13, 25].

We argue that an important pathway to mortality may be represented by hydraulic failure, defined as the inability of the xylem to supply sufficient water to offset leaf transpirational losses due to the formation and spread of air embolisms. This condition may be triggered, potentially synergistically, by multiple factors, including drought, beetle-induced phloem disruption, and fungal weakening of the xylem via pit membrane degradation.

To capture the multifaceted nature of bark beetle pathosystems, we propose an integrative framework encompassing the physiological, biochemical, and ecological dimensions of interactions among host trees, beetles, and their associated microbiota. We outline a conceptual model describing a sequential and empirically testable cascade of events initiated by climate-induced environmental stressors. These stressors trigger physiological responses in host trees that increase susceptibility to beetle colonization, followed by mechanical and biochemical disruption of host tissues and the establishment of a restructured internal microenvironment shaped by symbiotic fungi and bacteria. Together, these processes drive profound alterations in host physiology, ultimately culminating in tree mortality, potentially further accelerated by additional pathogens (Fig. 1).

Phloem Physiology is Dependent on Xylem Physiology

Bark beetles primarily exploit the inner phloem, a vascular tissue specialized for the long-distance translocation of aqueous solutions enriched in soluble carbohydrates [26]. This transport system is essential for distributing energy-rich compounds to non-photosynthetic tissues (known as sink tissues) throughout the plant, thereby sustaining cellular metabolism. Among these sink tissues, roots have particularly high and dynamic metabolic demands. The plasma membranes of root cells are densely populated with specialized transport proteins, such as aquaporins that facilitate water movement and ion channels that mediate nutrient uptake. Maintaining these transport processes requires

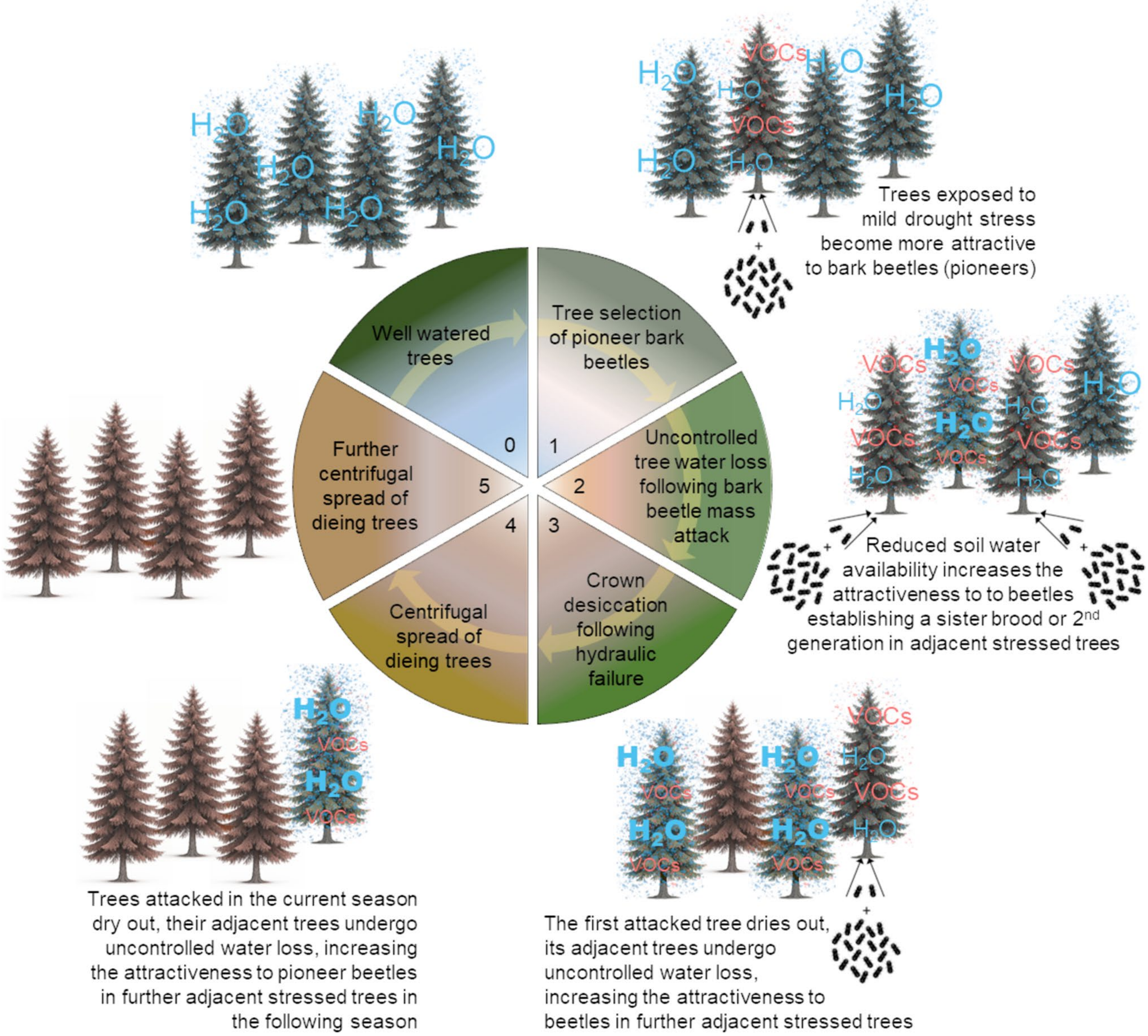

Fig. 1 Schematic development of bark beetle attack (e.g., *Ips typographus*) on specific host trees. Phase 0: Trees are healthy, with no physiological limitations from soil water availability or vapor pressure deficit (VPD) affecting their physiology. Tissues are well hydrated, and resin exhibits low viscosity. Phase 1: Drought-stressed trees begin to reduce the osmotic potential of their living tissues, making them vulnerable to colonization by pioneer bark beetle adults. These pioneers emit aggregation pheromones, initiating mass attack. Phase 2: During mass colonization (establishment of first offspring generation), damage to bark tissue leads to increased water loss, which intensifies competition for soil water among neighboring trees. As water availability declines, neighboring trees also lower the osmotic potential of their tissues, becoming susceptible to colonization by beetles establishing a sister brood or second generation. Phase 3: Excessive water loss causes a sharp decline in xylem water potential, surpassing the threshold for embolism formation. Extensive embolism (hydraulic failure) rapidly impairs xylem water transport, leading to tree death. Trees undergoing mass colonization further increase bark water loss, imposing additional stress on adjacent trees, which may then be colonized in the current or next season. Phases 4 and 5: Trees affected during previous mass colonization phases progressively die from hydraulic failure

substantial metabolic energy to support rapid protein turnover and to preserve the electrochemical gradients (differences in ion concentration and charge across membranes) that are critical for cellular function [27].

Phloem transport is driven by a hydrostatic pressure gradient between sieve elements at source tissues (e.g., leaves and storage parenchyma) and sieve elements at sink tissues (i.e., heterotrophic tissues such as roots), as described by Münch's pressure-flow theory [28, 29]. This transport mechanism is intrinsically dependent on xylem water potential. Turgor pressure in sieve elements develops when sugar loading lowers phloem water potential below that of the adjacent xylem, inducing passive water influx from the xylem into the phloem. The resulting expansion of sieve elements generates the turgor pressure required to drive bulk flow along the phloem pathway.

A key physical constraint on phloem transport is sap viscosity, which increases nonlinearly with rising sugar concentrations. Elevated viscosity increases hydraulic resistance to flow, as described by the Hagen–Poiseuille relationship [30], thereby reducing transport efficiency. This constraint becomes especially pronounced under declining xylem water potentials, such as during drought events. Living tissues may acclimate to reduced water availability either through passive dehydration, where cells lose water and osmotic potential decreases without maintaining turgor, or through active osmotic adjustment, where sugar accumulation helps retain water and sustain turgor pressure. Passive dehydration ultimately leads to phloem transport failure due to insufficient turgor, while active sugar accumulation can maintain turgor but at the cost of increased sap viscosity, which imposes a physical limit on transport capacity.

These physiological dynamics of phloem transport and tissue hydration may have important consequences for bark beetle development. Variations in phloem sap sugar composition, concentration, and water content [31, 32] are likely to influence the nutritional quality of phloem tissues, thereby affecting host suitability, colonization success, and reproductive performance of pioneer beetles [33]. Despite this potential relevance, the mechanistic links between phloem physiology and bark beetle ecology remain poorly understood and warrant targeted investigation.

Phloem dynamics under drought conditions are tightly coupled to concurrent physiological responses driven by changes in xylem water potential resulting from soil water deficits. Under conditions of adequate soil moisture and moderate atmospheric evaporative demand (Fig. 1, phase 0), xylem water potential remains relatively high, supporting sustained stomatal conductance and maximizing photosynthetic carbon assimilation. This favorable hydraulic status maintains comparatively low concentrations of soluble carbohydrates in both phloem sap and adjacent living tissues, thereby minimizing sap viscosity, optimizing phloem hydraulic conductivity, and supporting efficient long-distance carbohydrate transport as well as adequate hydration of metabolically active cells.

Under such well-hydrated conditions, corresponding to higher xylem water potentials, the relatively diluted phloem sap [32] may offer limited nutritional value for organisms feeding on phloem tissues, such as sap-feeding insects or phloeophagous bark beetles. In healthy trees, low concentrations of sugars and other nutrients (assimilates) may act additively with tree defenses to limit larval growth, survival, and reproductive success, thereby reducing host suitability [33]. In addition, bark water losses in healthy trees are typically low, as the bark functions as an effective insulating layer. Well-hydrated and fully expanded bark tissues protect living cells and functional xylem from direct atmospheric exposure, further contributing to hydraulic stability and resistance to biotic invasion [34].

Constitutive and Inducible Tree Defenses Against Bark Beetles

Tree defense mechanisms against bark beetle colonization comprise both constitutive and inducible components. Constitutive defenses provide pre-formed protection against potential invaders, whereas inducible defenses are activated or amplified in response to attack, reinforcing both physical and chemical barriers [35, 36].

A central component of conifer defense is the secretion of oleoresin from axial and radial resin ducts damaged during beetle penetration beneath the bark. Exuded resin can physically repel or entomb invading insects while simultaneously isolating beetle-associated fungi, thereby restricting pathogen spread within host tissues [37]. In many conifers, including *Picea* and *Pinus* species, resin ducts form an extensive three-dimensional network filled with oleoresin, a hydrophobic mixture dominated by volatile monoterpenes and non-volatile diterpene acids [38–40]. High monoterpene concentrations are associated with low resin viscosity [11], facilitating rapid resin mobilization and enhancing the tree's ability to deter beetle entry during the initial phases of attack [37].

Effective defense requires resin to flow at sufficiently high rates to inundate and immobilize invading beetles. Resin is a viscous fluid, and its flow rate is therefore inversely related to viscosity (Hagen–Poiseuille law [41]), making it highly sensitive to oleoresin composition and tissue hydration. Upon exposure to air, volatile terpenes evaporate, causing resin hardening by polymerization, while dehydration further accelerates solidification. In addition, volatile organic compounds may diffuse from resin ducts into adjacent xylem tissues, driven by concentration gradients and facilitated by negative xylem water potentials [42].

Well-hydrated bark tissues help maintain low resin viscosity by preserving oleoresin composition and tissue hydration, thereby ensuring rapid resin mobilization during beetle attacks [11]. Suberized bark layers and adequate hydration also act as physical barriers limiting monoterpene volatilization and preserving the chemical efficacy of oleoresin at entry points [34]. Under these conditions, resin is rapidly mobilized and solidifies around the beetle body, forming both physical and chemical barriers that restrict beetle advancement and fungal inoculation.

Under drought conditions, however, these defensive processes become compromised. Water deficits increase resin viscosity and reduce its flow rates [11], impairing the tree's capacity to repel bark beetles. Prolonged or severe drought further exacerbates this vulnerability by markedly reducing resin secretion rates [11, 22], thereby diminishing overall defensive potential [43].

While constitutive defenses provide initial resistance, inducible defenses can enhance resin synthesis and flow following recognition of biotic threats, including the formation of traumatic resin ducts [35, 36, 44, 45]. Trees also activate a range of chemical defense pathways in response to biotic and abiotic stressors. Fungal infection, for instance, induces hypersensitive wound responses in bark tissues characterized by localized cell death and the accumulation of secondary metabolites such as phenolics and terpenoids [43, 46, 47].

The impact of drought on tree susceptibility to bark beetle infestation depends strongly on tree water status and the availability of stored carbon reserves that sustain investment in both constitutive and inducible defenses. Carbon allocation to defense inevitably trades off with other demands, including the accumulation of osmotically active compounds (substances that help retain water in tissues) to maintain tissue hydration [48] and the production of new biomass [49].

Most conifers exhibit tight stomatal regulation under water-limiting conditions [50], reducing carbon assimilation and increasing reliance on stored non-structural carbohydrates (NSCs) to sustain metabolism and hydration. Under mild to moderate drought, concentrations of soluble NSCs often increase in phloem and bark parenchyma [10], partly offsetting declines in xylem water potential. This condition may transiently stimulate certain defense responses, such as stilbenes, flavonoids, and diterpenes, particularly following fungal infection [43]. However, experimental evidence indicates that elevated soluble carbohydrate concentrations do not necessarily translate into increased terpene biosynthesis [51–53], despite the high toxicity of these compounds to bark beetles and their fungal symbionts [54, 55].

As drought intensifies, the combined effects of carbon depletion and increasingly negative xylem water potentials elevate the risk of hydraulic failure due to embolism formation, while simultaneously constraining carbon availability for the biosynthesis of new defensive compounds [19, 56]. Tissue dehydration in the outer bark layers reduces cell turgor, potentially creating gaps between dehydrated cells [57], thereby compromising the bark's insulating function [58]. These structural changes may facilitate the diffusion of hydrophobic monoterpenes into the atmosphere, reducing their local concentration within resin ducts, especially in the longer term [51]. The decline in monoterpene content to be expected after extended, severe drought, increases resin viscosity and limits resin mobility, undermining one of the primary defense mechanisms against pioneer bark beetles [11]. Collectively, these physiological changes may increase the risk of bark beetle infestation [11, 59, 60].

In parallel, higher osmolality, the concentration of dissolved solutes, in bark and phloem tissues under drought conditions [32, 48] may provide a more favorable nutritional substrate for bark beetles and their fungal associates [61]. Osmoregulatory adjustments, together with drought-induced accumulation of phenolic compounds, suggest that water stress fundamentally reshapes the nutritional and chemical landscape of bark tissues [51].

Consistent with this hypothetical framework, model outcomes and monitoring data clearly demonstrate that drought events leading to acute tree water deficits are correlated with outbreaks of *I. typographus* [8].

Despite these advances, current understanding remains fragmented. The physiological regulation of defense responses has not yet been fully integrated with phloem transport dynamics and drought-induced shifts in osmotic potential, which together govern carbon redistribution within stressed trees. Furthermore, bark beetle-associated fungi exacerbate defense depletion by consuming host-derived sugars [47, 62] and metabolizing phenolic compounds [63–65], further weakening chemical defenses. Emissions of volatile terpenoids and ethanol, through both bark diffusion and xylem transport to the canopy, are strongly modulated by temperature, soil moisture, and resin quality [66, 67]. While moderate drought often enhances volatile organic compound emissions, severe drought suppresses emissions and alters their chemical composition, reflecting metabolic constraints and substrate limitation [68]. These biochemical and physical signals may enable pioneer bark beetles to identify hosts with compromised defensive capacity and optimal conditions for colonization.

Host Tree Selection

Osmotic adjustment in drought-stressed trees can alter the performance and development of bark-feeding organisms by reshaping the nutritional and chemical properties of phloem and bark tissues. These drought-induced changes may also affect host suitability for colonizing beetles and, importantly, may provide cues that allow insects to discriminate between stressed and healthy trees through a combination of olfactory, gustatory, visual, and potentially vibrational (auditory/tactile) signals [69] (Fig. 1, phase 1).

Olfactory and Gustatory Cues

The volatile fraction of conifer resin has long been hypothesized to contribute to the primary attraction of bark beetles [9]. Bark beetles exhibit high olfactory sensitivity not only to aggregation pheromones but also to volatiles emitted by host and non-host trees [70], as well as to compounds associated with symbiotic fungi [71]. In principle, drought-induced shifts in resin chemistry and emission rates could modify these olfactory landscapes, enabling beetles to assess host condition at distance. However, despite strong mechanistic plausibility, definitive field evidence that pioneer beetles reliably orient toward "high-quality" stressed hosts based solely on host volatiles remains limited [9].

By contrast, gustatory mechanisms remain comparatively poorly understood. Once a beetle contacts the bark surface, short-range cues likely become increasingly important. Pioneer beetles are thought to detect and avoid non-hosts partly via characteristic volatile blends [72] and emissions may differ between healthy and vulnerable trees [9]. Individual compounds, including camphor, trans-4-thujanol, and other oxygenated monoterpenoids, can act as attractants or repellents in beetle and fungal bioassays. This suggests that host selection may depend on a balance between cues that indicate susceptibility and those that signal toxicity or active defense [24, 73].

In addition to terpenoids, ethanol has been proposed as a potential indicator of physiological stress. Increased ethanol emissions from drought-stressed bark could signal altered carbon status and enhanced availability of soluble substrates in inner bark tissues, potentially increasing host attractiveness under certain conditions [74]. In fact, ethanol has been shown to be an effective attractant for most species of bark and wood boring scolytids, yet not for economically important species such as *I. typographus* [75].

Radiative and Thermal Cues

Drought-induced hydraulic constraints reduce stomatal conductance, weakening transpirational cooling of needles and potentially also of stems. At the same time, lower sap flow rates reduce the supply of relatively cool water from deeper soil layers to the canopy. Together, these processes can alter the thermal regime of both stems and crowns, shifting their long-wave radiative signatures relative to well-watered trees [7, 76]. Such temperature contrasts may provide radiative and thermal information, directly or indirectly, at short distances, particularly under conditions where canopy thermal properties covary with physiological stress and reduced defensive capacity.

Auditory, Tactile, and Vibrational Cues

As xylem water potential becomes increasingly negative and crosses species-specific thresholds, air can enter water-filled conduits and spread through the xylem network as pit membranes fail to contain air seeding, leading to embolism formation (i.e., the blockage of water transport by air bubbles). The rapid release of tension during embolism events generates ultrasonic acoustic emissions [77]. Although such emissions can be masked by other ultrasound sources in natural environments [78], they may still produce airborne or substrate-borne vibrations detectable by insects when in close proximity or when walking on the bark surface. If detectable, embolism-generated vibrations could serve as a highly proximate indicator of acute hydraulic stress and declining host function, potentially contributing to host assessment during the final stages of selection.

The Mass Attack Phase: Much More than Just Girdling

Once pioneering adults (males in *Ips*) start boring into tree bark, they release aggregation pheromones that attract additional male and female conspecifics and promote rapid colonization. As larvae hatch, they excavate feeding galleries along the inner phloem. During successful outbreaks, gallery densities can become extremely high and extend over several meters of the bole, producing extensive damage across large stem areas [5].

Phloem Disruption is Spatially Complex, Not a Simple "Ring Cut"

During colonization, bark beetles mechanically disrupt the phloem tissue responsible for long-distance assimilate transport. This damage reduces the longitudinal continuity of sieve elements and impairs the redistribution of carbohydrates from sources to sinks, thereby weakening the whole-plant carbon economy. Functionally, this resembles girdling in that phloem transport is interrupted; however, beetle injury cannot be treated as equivalent to a continuous girdle.

Unlike a circumferential cut that fully severs phloem transport, beetle galleries create a heterogeneous and discontinuous mosaic of lesions, with highly variable spatial arrangement and degrees of vascular interruption along and around the stem [5]. This spatial complexity likely results in areas where phloem transport fails in some regions but not others, leading to localized carbohydrate accumulation above damaged areas and carbon starvation below them, conditions that are difficult to capture with classical girdling analogies.

Carbon Depletion and Altered Xylem–Phloem Coupling

Beyond mechanical disruption, larval feeding directly consumes soluble sugars in the phloem and non-structural carbohydrates stored in bark parenchyma [53, 79, 80]. The combination of (i) disrupted transport pathways and (ii) local carbohydrate removal is expected to destabilize xylem–phloem coupling by altering both the availability of osmotically active solutes and the capacity to maintain phloem turgor. Because phloem transport depends on water exchange with the xylem [28, 29], this disruption can amplify existing drought stress by impairing the dynamic coordination of water and carbon fluxes, especially under low xylem water potentials.

Induced Defenses are Costly, Spatially Constrained, and May be Short-Lived

Mass attack also triggers strong host responses. Beetle-associated fungi elicit hypersensitive wound reactions [44, 46], which are accompanied by localized accumulation of secondary metabolites, including mono-, sesqui-, and diterpenes in bark tissues [47]. In drought-stressed trees, elevated local sugar concentrations, initially accumulated for osmotic adjustment, may temporarily provide substrates for defense biosynthesis, potentially intensifying chemical responses near attack sites. However, these defenses are inherently spatially constrained and energetically expensive. As the attacked surface area expands rapidly during mass colonization, host capacity to sustain effective inducible defenses may be outpaced by the scale and speed of tissue invasion, especially if carbon supply and phloem transport are already compromised.

Why Beetle-Attacked Trees Die Faster than Girdled Trees

Phloem disruption has well-characterized whole-plant consequences. Carbohydrate accumulation above phloem blockages can increase respiratory activity in stems and branches and alter leaf traits such as leaf mass per area [81]. In girdling experiments, sugar accumulation has been used to explain declines in leaf photosynthesis via end-product inhibition [82]. In parallel, reduced carbon supply to root sinks can decrease stomatal conductance and transpiration, increase leaf abscisic acid, and raise leaf water potential [83, 84]. Severe phloem disruption can therefore impair carbohydrate supply to the lower stem and roots, compromising maintenance respiration, nutrient uptake, and other essential functions [61].

Yet, while artificially girdled trees (e.g., removal of a ~ 10 cm-wide bark strip) can survive for years [85], trees subjected to mass bark beetle attack often die within weeks to months [13, 43]. This discrepancy suggests that mortality may be driven by more than phloem interruption alone. A key difference could be the simultaneous action of multiple stressors: (i) widespread, spatially complex phloem damage and carbohydrate depletion, (ii) intense metabolic costs of defense and wound responses, and (iii) fungal-mediated impairment of xylem function. In particular, beetle-associated fungi may accelerate hydraulic collapse by increasing xylem vulnerability, e.g., through mechanisms such as pit membrane degradation, thereby amplifying drought-induced embolism risk and pushing the tree toward rapid hydraulic failure. Together, these interacting processes may help explain why mass attack can produce much faster mortality than girdling alone.

The Pathway to Crown Desiccation and Tree Death

Following a successful attack, oviposition and brood development begin within days, whereas fungal proliferation typically proceeds over longer timescales, with extensive sapwood colonization often developing over months [5, 16, 21]. Importantly, however, the *physiological* impacts of the first fungal inoculations can be immediate. Ophiostomatoid fungi associated with *I. typographus* (e.g. *Grosmannia penicillata* and *Endoconidiophora polonica*) challenge tree defenses by inducing the accumulation of monoterpenes and diterpene resin acids, while simultaneously consuming NSCs and degrading phenolic compounds in the necrotic areas [43, 47]. Even before external symptoms such as needle discoloration become visible, *E. polonica* can trigger rapid vertical expansion of dehydrated sapwood “dry zones”, often extending ~ 20–40 cm within weeks of inoculation [16]. The speed of this response is suggestive of an embolism-driven mechanism, whereby fungal activity at numerous inoculation points may initiate localized hydraulic dysfunction that can rapidly propagate along the stem. During mass attacks, multiple dry zones may coalesce, increasingly constraining sap flow until whole-tree transport becomes critically impaired and systemic hydraulic failure ensues [16]. In parallel, fungal growth into phloem tissues may further suppress photosynthate transport, compounding carbon limitation already imposed by gallery formation [21].

The Subcortical Microenvironment as a Driver of Multi-Trophic Feedbacks

Bark beetles are aerobic and rely on ventilation holes to support gas exchange between the atmosphere and their galleries beneath the bark. Within these galleries, beetle respiration and altered water relations likely generate microenvironments with strongly fluctuating oxygen availability and humidity, creating spatial and temporal mosaics of aerobic and anaerobic conditions. Such heterogeneity may promote the establishment of diverse microbial communities, including aerobic and anaerobic taxa, that are symbiotically associated with beetles or introduced by other vectors [86–88]. Within this expanding microbiome, ophiostomatoid fungi, as well as associated bacteria/yeasts can contribute to host decline by depleting non-structural carbohydrates in phloem, bark, and living xylem cells [47, 62]. Some of these microbial associates may damage parenchyma cells (the living cells in wood and bark) [89], even though they generally do not decompose the structural wood polymers characteristic of classical wood-decay fungi [18, 90]. In addition, nitrogen-fixing bacteria may be strategically important for supporting beetle development, given the low nitrogen content of phloem tissues that constitute the primary larval substrate [91, 92].

From Gallery Aeration to Bark Water Loss and Escalating Hydraulic Stress

Bark beetle galleries under the bark create networks of tunnels that breach the protective barrier of the bark and phloem [36], exposing subcortical tissues to the atmosphere and altering the normal gas and vapor exchange pathways. These tunnels and the structural changes in the wood increase permeability of the affected tissues, likely enhancing oxygen supply to the galleries but also increasing evaporative water loss from subcortical tissues [34, 93] (Fig. 1, phase 2). Increased bark dehydration would further depress xylem water potential and could transiently intensify sap flow demands. However, as xylem water potential becomes progressively more negative, declining xylem conductance and increasing embolism frequency should ultimately curtail water transport, pushing the tree toward critical thresholds (Fig. 1, phase 3).

At this stage, beetle-infested trees are likely to experience extensive xylem hydraulic failure, characterized by widespread embolism formation and reduced water reserves in bark tissues, particularly under severe drought [94, 95]. While embolism-driven mortality can occur in the absence of beetles and fungi, their presence introduces additional, synergistic pathways that promote embolism formation at less negative water potentials and accelerate system-wide collapse. Beetle galleries can increase water loss, whereas ophiostomatoid fungi can directly increase xylem vulnerability. In particular, fungal degradation of pit membranes weakens the xylem's capacity to prevent air seeding, and may also release surface-active compounds into the sap stream that reduce xylem sap surface tension, both mechanisms that promote embolism spread under comparatively milder tensions [16, 96]. These interacting mechanisms provide a plausible explanation for the rapid sapwood desiccation commonly observed in beetle-killed trees [95]. A sapwood dominated by air-filled vascular conduits may then become more permissive to colonization by aerobic fungi, potentially helping to explain why blue stain development in sapwood often becomes conspicuous after crown desiccation.

Spatial Contagion: Why Infestations Expand

Within this framework, the expanded microbiome that develops in susceptible trees may accelerate the depletion of carbon and nitrogen resources stored in bark tissues, thereby driving overall tree decline. An additional, intriguing implication of the "high bark water loss" hypothesis is that attacked trees could temporarily increase their uptake of local soil water, potentially affecting water availability for neighboring trees. If surrounding trees experience more negative water potentials, osmotic adjustment may increase the concentration of soluble compounds in phloem and bark tissues, potentially shifting them into a more "attractive" or "susceptible" physiological state for pioneer beetles (Fig. 1, phase 2). Such neighborhood-scale feedbacks could contribute to the characteristic spatial expansion of infestation nuclei observed in some pathosystems, including *Picea abies–Ips typographus* (Fig. 1, phases 4–5).

Conclusions

This synthesis integrates plant hydraulics, phloem transport, carbon allocation, defense chemistry, insect behavior, and microbial ecology to develop a mechanistically grounded framework for understanding bark beetle–associated tree mortality under drought. By explicitly linking well-established physiological responses of host trees to beetle colonization dynamics and the modifying role of symbiotic microorganisms, the framework highlights interactions that are often examined in isolation. Central to this perspective is the coupling between xylem and phloem function: drought-induced declines in water potential, changes in osmoregulation, and shifts in carbohydrate allocation constrain transport efficiency and defensive capacity, thereby shaping host susceptibility prior to attack.

Following successful colonization, mass attacks disrupt phloem integrity in a spatially complex manner, reducing assimilate transport, depleting local carbon reserves, and destabilizing xylem–phloem coordination. In parallel, fungal and bacterial associates amplify host decline by consuming stored resources, detoxifying chemical defenses, and impairing xylem function through processes such as pit membrane degradation. Together, these interacting mechanisms can accelerate hydraulic dysfunction and increase vulnerability to embolism, positioning hydraulic failure as a potential convergence point among multiple stressors rather than as a single, universal cause of mortality.

At the same time, several elements of the proposed cascade remain supported primarily by indirect evidence. In particular, the magnitude and ecological relevance of changes in bark permeability, subcortical gas and vapor exchange, microbial microenvironmental heterogeneity, and sensory cues guiding beetle behavior remain poorly quantified. Moreover, the relative importance of hydraulic failure, carbon limitation, and metabolic disruption as terminal processes likely varies across species, environments, and disturbance regimes. These unresolved aspects primarily reflect gaps in empirical observation and therefore identify priorities for future research rather than shortcomings of the integrative approach.

By clearly delineating both established mechanisms and unresolved questions, this framework provides a foundation for targeted experimentation and model development aimed at improving predictions of forest responses to increasingly frequent and severe drought and bark beetle outbreaks under ongoing climate change.

Key References

- Baños-Quintana AP, Gershenzon J, Kaltenpoth M (2024) The Eurasian spruce bark beetle *Ips typographus* shapes the microbial communities of its offspring and the gallery environment. Front Microbiol 15:1,367,127

  A study investigating the microbial communities associated with *Ips typographus*, and how these communities are shaped by the beetle's life stages and maternal behaviors.

- Basile S, Střîbrská B, Kalyniukova A, Hradecký J, Synek J, Gershenzon J, Jirošová A (2024) Physiological and biochemical changes of *Picea abies* (L.) during acute drought stress and their correlation with susceptibility to *Ips typographus* (L.) and *I. duplicatus* (Sahlberg). Front For Glob Change 7:1,436,110.

  A study reporting that acute drought alters Norway spruce physiology (reduced growth, changed carbohydrates) while chemical defenses remain largely stable. Despite this, *Ips typographus* more readily colonizes drought-stressed trees, indicating short-term water stress can increase susceptibility even without major defensive changes.

- Junttila S, Yrttimaa T, Blomqvist M, Paljakka T, Pelto-Arvo M, Vastaranta M (2025) Influence of bark beetle infestation on stem diameter dynamics. Trees For People 19:100,777

  A study investigating the seasonal dynamics of stem growth in Norway spruce trees, particularly focusing on the negative impact of bark beetle infestation.

- Lehmanski LMA, Kandasamy D, Andersson MN, Netherer S, Alves EG, Huang J, Hartmann H (2023) Addressing a century-old hypothesis – do pioneer beetles of *Ips typographus* use volatile cues to find suitable host trees? New Phytol 238:1762–1770

  A review of the existing literature on the roles of volatile and visual cues in guiding pioneer beetles during the search for suitable host trees, with identification of key knowledge gaps.

- Malone SC, Thompson RA, Chow PS, de Oliveira Jr. CR, Landhäusser SM, Six DL, McCulloh KA, Adams HD, Trowbridge AM (2025) Water, not carbon, drives drought-constraints on stem terpene defense against simulated bark beetle attack in *Pinus edulis*. New Phytol 245:318–331

  A study addressing the relationships and dynamics between non-structural carbohydrate (NSC) levels and terpenes in *Pinus edulis*, investigating how drought and phloem connectivity influence induced terpene responses and NSC concentrations.

- Masch D, Buscot F, Rohe W, Goldmann K (2025) Bark beetle infestation alters mycobiomes in wood, litter, and soil associated with Norway spruce. FEMS Microbiol Ecol 101:fiaf015

  A study investigating the impact of bark beetle infestations on the mycobiome associated with Norway spruce trees, focusing on variations from soil to wood, and highlighting differences between habitats (soil, litter, and stem wood) and the progression of infestation stages (early and late).

- Netherer S, Lehmanski L, Bachlehner A, et al. (2024) Drought increases Norway spruce susceptibility to the Eurasian spruce bark beetle and its associated fungi. New Phytol 242:1000–1017

  A pioneer study on the effect of drought on Norway spruce physiology and vulnerability to *Ips typographus* and associated fungi using an artificial drought manipulation.

- Siegert C, Clay N, Pace K, Vissa S, Hofstetter RW, Leverón O, Riggins JJ (2024) Bark beetle-driven community and biogeochemical impacts in forest ecosystems: a review. Ann Entomol Soc Am 117:163–183

  A review of interactions between bark beetles and their associated fungi, emphasizing how these relationships reshape microbial and detrital communities and influence biogeochemical processes such as carbon and nitrogen cycling.

- Singh VV, Naseer A, Mogilicherla K, Trubin A, Zabihi K, Roy A, Jakuš R, Erbilgin N (2024) Understanding bark beetle outbreaks: exploring the impact of changing temperature regimes, droughts, forest structure, and prospects for future forest pest management. Rev Environ Sci Biotechnol 23:257–290

  A review of the factors influencing bark beetle outbreaks, particularly *Ips typographus*, in the context of climate change, highlighting how shifting temperature regimes, drought stress, and altered forest structure increase forest ecosystem susceptibility to infestation.

- Six DL, Hammerbacher A, Trowbridge A, Bullington L (2026) From beginning to end: the synecology of tree-killing bark beetles, fungi, and trees. Biological Reviews 101:314–335.

  A review synthesizing decades of research on tree-killing bark beetles, showing how behavioural, physiological, and microbial processes drive beetle success and tree mortality. It highlights climate and stress as key modulators and frames outbreaks as complex multi-trophic ecological systems.

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Declarations

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References

1. Morris JL, Cottrell S, Fettig CJ, Hansen WD, Sherriff RL, Carter VA, et al. Managing bark beetle impacts on ecosystems and society: priority questions to motivate future research. J Appl Ecol. 2017;54:750–60. https://doi.org/10.1111/1365-2664.12782
2. Seidl R, Rammer W. Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. Landsc Ecol. 2017;32:1485–98. https://doi.org/10.1007/s10980-016-0396-4.
3. Marini L, Økland B, Jönsson AM, Bentz B, Carroll A, Forster B, et al. Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. Ecography. John Wiley & Sons, Ltd; 2017:40:1426–35. https://doi.org/10.1111/ecog.02769
4. Rodman KC, Andrus RA, Carlson AR, Carter TA, Chapman TB, Coop JD, et al. Rocky mountain forests are poised to recover following bark beetle outbreaks but with altered composition. J Ecol. 2022;110:2929–49. https://doi.org/10.1111/1365-2745.13999
5. Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, et al. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience. 2008;58:501–17. https://doi.org/10.1641/B580607.
6. Seidl R, Müller J, Hothorn T, Bässler C, Heurich M, Kautz M. Small beetle, large-scale drivers: how regional and landscape factors affect outbreaks of the European spruce bark beetle. J Appl Ecol. 2016;53:530–40. https://doi.org/10.1111/1365-2664.12540
7. Trubin A, Kozhoridze G, Zabihi K, Modlinger R, Singh VV, Surový P, et al. Detection of green attack and bark beetle susceptibility in Norway spruce: utilizing planetscope multispectral imagery for tri-stage spectral separability analysis. For Ecol Manage. 2024;560:121838. https://doi.org/10.1016/j.foreco.2024.121838.
8. Netherer S, Panassiti B, Pennerstorfer J, Matthews B. Acute drought is an important driver of bark beetle infestation in Austrian Norway spruce stands. Front For Glob Change. 2019;2. https://doi.org/10.3389/ffgc.2019.00039
9. Lehmanski LMA, Kandasamy D, Andersson MN, Netherer S, Alves EG, Huang J, et al. Addressing a century-old hypothesis – do pioneer beetles of *Ips typographus* use volatile cues to find suitable host trees? New Phytol. 2023;238:1762–70. https://doi.org/10.1111/nph.18865.

10. Tomasella M, Beikircher B, Häberle K-H, Hesse B, Kallenbach C, Matyssek R, et al. Acclimation of branch and leaf hydraulics in adult *Fagus sylvatica* and *Picea abies* in a forest through-fall exclusion experiment. Tree Physiol. 2018;38:198–211. https://doi.org/10.1093/treephys/tpx140.
11. Rissanen K, Hölttä T, Bäck J, Rigling A, Wermelinger B, Gessler A. Drought effects on carbon allocation to resin defences and on resin dynamics in old-grown Scots pine. Environ Exp Bot. 2021;185:104410. https://doi.org/10.1016/j.envexpbot.2021.104410.
12. Gely C, Laurance SGW, Stork NE. How do herbivorous insects respond to drought stress in trees? Biol Rev Camb Philos Soc. 2020;95:434–48. https://doi.org/10.1111/brv.12571.
13. Six DL, Hammerbacher A, Trowbridge A, Bullington L. From beginning to end: the synecology of tree-killing bark beetles, fungi, and trees. Biol Rev Camb Philos Soc. 2026;101:314–35. https://doi.org/10.1111/brv.70084
14. Kirisits T, Offenthaler I. Xylem sap flow of Norway spruce after inoculation with the blue-stain fungus *Ceratocystis polonica*. Plant Pathol. 2002;51:359–64. https://doi.org/10.1046/j.1365-3059.2002.00722.x
15. Jansen S, Lamy J-B, Burlett R, Cochard H, Gasson P, Delzon S. Plasmodesmatal pores in the torus of bordered pit membranes affect cavitation resistance of conifer xylem. Plant Cell Environ. 2012;35:1109–20. https://doi.org/10.1111/j.1365-3040.2011.02476.x
16. Kuroda K. Xylem dysfunction in Yezo spruce (*Picea jezoensis*) after inoculation with the blue-stain fungus *Ceratocystis polonica*. For Pathol. 2005;35:346–58. https://doi.org/10.1111/j.1439-0329.2005.00424.x
17. Little NS, McConnell TE, Irby NE, Shi SQ, Riggins JJ. Surface free energy of blue-stained southern pine sapwood from bark beetle-attacked treesitle. Wood Fiber Sci. 2013;45:206–14.
18. Siegert C, Clay N, Pace K, Vissa S, Hofstetter RW, Leverón O, et al. Bark beetle-driven community and biogeochemical impacts in forest ecosystems: a review. Ann Entomol Soc Am. 2024;117:163–83. https://doi.org/10.1093/aesa/saae009.
19. Franceschi VR, Krekling T, Berryman AA, Christiansen E. Specialized phloem parenchyma cells in Norway spruce (Pinaceae) bark are an important site of defense reactions. Am J Bot. 1998;85:601–15. https://doi.org/10.2307/2446529
20. Kirisits T. Fungal associates of European bark beetles with special emphasis on the ophiostomatoid fungi. 2007. https://api.semanticscholar.org/CorpusID:86348734
21. Six DL, Wingfield MJ. The role of phytopathogenicity in bark beetle–fungus symbioses: a challenge to the classic paradigm. Annu Rev Entomol Annual Reviews. 2011;56:255–72. https://doi.org/10.1146/annurev-ento-120709-144839.
22. Netherer S, Matthews B, Katzensteiner K, Blackwell E, Henschke P, Hietz P, et al. Do water-limiting conditions predispose Norway spruce to bark beetle attack? New Phytol. 2015;205:1128–41. https://doi.org/10.1111/nph.13166.
23. Singh VV, Naseer A, Mogilicherla K, Trubin A, Zabihi K, Roy A, et al. Understanding bark beetle outbreaks: exploring the impact of changing temperature regimes, droughts, forest structure, and prospects for future forest pest management. Rev Environ Sci Biotechnol. 2024;23:257–90. https://doi.org/10.1007/s11157-024-09692-5.
24. Netherer S, Kandasamy D, Jirosová A, Kalinová B, Schebeck M, Schlyter F. Interactions among Norway spruce, the bark beetle *Ips typographus* and its fungal symbionts in times of drought. J Pest Sci. 2004;2021(94):591–614. https://doi.org/10.1007/s10340-021-01341-y.
25. Six DL. The bark beetle holobiont: Why microbes matter. J Chem Ecol. 2013;39:989–1002. https://doi.org/10.1007/s10886-013-0318-8.
26. Ryan MG, Asao S. Phloem transport in trees. Tree Physiol. 2014;34:1–4. https://doi.org/10.1093/treephys/tpt123.
27. Hodge A, Berta G, Doussan C, Merchan F, Crespi M. Plant root growth, architecture and function. Plant Soil. 2009;321:153–87. https://doi.org/10.1007/s11104-009-9929-9.
28. Hölttä T, Vesala T, Sevanto S, Perämäki M, Nikinmaa E. Modeling xylem and phloem water flows in trees according to cohesion theory and Münch hypothesis. Trees. 2006;20:67–78. https://doi.org/10.1007/s00468-005-0014-6.
29. De Schepper V, De Swaef T, Bauweraerts I, Steppe K. Phloem transport: a review of mechanisms and controls. J Exp Bot. 2013;64:4839–50. https://doi.org/10.1093/jxb/ert302.
30. Woodruff DR. The impacts of water stress on phloem transport in Douglas-fir trees. Tree Physiol. 2014;34:5–14. https://doi.org/10.1093/treephys/tpt106.
31. Salmon Y, Dietrich L, Sevanto S, Hölttä T, Dannoura M, Epron D. Drought impacts on tree phloem: from cell-level responses to ecological significance. Tree Physiol. 2019;39:173–91. https://doi.org/10.1093/treephys/tpy153.
32. Sevanto S. Drought impacts on phloem transport. Curr Opin Plant Biol. 2018;43:76–81. https://doi.org/10.1016/j.pbi.2018.01.002.
33. White TCR. Are outbreaks of cambium-feeding beetles generated by nutritionally enhanced phloem of drought-stressed trees? J Appl Entomol. 2015;139:567–78. https://doi.org/10.1111/jen.12195.
34. Lintunen A, Preisler Y, Oz I, Yakir D, Vesala T, Hölttä T. Bark transpiration rates can reach needle transpiration rates under dry conditions in a semi-arid forest. Front Plant Sci. 2021;12:790684. https://doi.org/10.3389/fpls.2021.790684.
35. Christiansen E, Horntvedt R. Combined *Ips/Ceratocystis* attack on Norway spruce, and defensive mechanisms of the trees. Z Angew Entomol. 1983;96:110–8. https://doi.org/10.1111/j.1439-0418.1983.tb03650.x
36. Franceschi VR, Krokene P, Christiansen E, Krekling T. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New Phytologist. 2005;167:353–76. https://doi.org/10.1111/j.1469-8137.2005.01436.x
37. Trapp S, Croteau R. Defensive resin biosynthesis in conifers. Annu Rev Plant Biol Annual Reviews. 2001;52:689–724. https://doi.org/10.1146/annurev.arplant.52.1.689.
38. Ferrenberg S, Kane JM, Mitton JB. Resin duct characteristics associated with tree resistance to bark beetles across lodgepole and limber pines. Oecologia. 2014;174:1283–92. https://doi.org/10.1007/s00442-013-2841-2.
39. Phillips MA, Croteau RB. Resin-based defenses in conifers. Trends Plant Sci. 1999;4:184–90. https://doi.org/10.1016/S1360-1385(99)01401-6.
40. Kane JM, Kolb TE. Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. Oecologia. 2010;164:601–9. https://doi.org/10.1007/s00442-010-1683-4
41. Tyree MT, Ewers FW. The hydraulic architecture of trees and other woody plants. New Phytol. 1991;119:345–60. https://doi.org/10.1111/j.1469-8137.1991.tb00035.x
42. Vanhatalo A, Chan T, Aalto J, Korhonen JF, Kolari P, Hölttä T, et al. Tree water relations can trigger monoterpene emissions from Scots pine stems during spring recovery. Biogeosciences. 2015;12:5353–63. https://doi.org/10.5194/bg-12-5353-2015.
43. Netherer S, Lehmanski L, Bachlehner A, Rosner S, Savi T, Schmidt A, et al. Drought increases Norway spruce susceptibility to the Eurasian spruce bark beetle and its associated fungi. New Phytol. 2024;242:1000–17. https://doi.org/10.1111/nph.19635
44. Nagy NE, Franceschi VR, Solheim H, Krekling T, Christiansen E. Wound-induced traumatic resin duct development in stems of Norway spruce (Pinaceae): anatomy and cytochemical traits. Am J Bot. 2000;87:302–13. https://doi.org/10.2307/2656626

45. Baier P, Führer E, Kirisits T, Rosner S. Defence reactions of Norway spruce against bark beetles and the associated fungus *Ceratocystis polonica* in secondary pure and mixed species stands. For Ecol Manage. 2002;159:73–86. https://doi.org/10.1016/S0378-1127(01)00711-3.
46. Christiansen E, Krokene P, Berryman AA, Franceschi VR, Krekling T, Lieutier F, et al. Mechanical injury and fungal infection induce acquired resistance in Norway spruce. Tree Physiol. 1999;19:399–403. https://doi.org/10.1093/treephys/19.6.399.
47. Viiri H, Annila E, Kitunen V, Niemelä P. Induced responses in stilbenes and terpenes in fertilized Norway spruce after inoculation with blue-stain fungus. Ceratocystis polonica Trees. 2001;15:112–22. https://doi.org/10.1007/s004680000082.
48. Lintunen A, Paljakka T, Jyske T, Peltoniemi M, Sterck F, von Arx G, et al. Osmolality and non-structural carbohydrate composition in the secondary phloem of trees across a latitudinal gradient in Europe. Front Plant Sci. 2016;7:726. https://doi.org/10.3389/fpls.2016.00726.
49. Herms DA, Mattson WJ. The dilemma of plants: To grow or defend. Q Rev Biol. The University of Chicago Press. 1992;67:283–335. http://www.jstor.org/stable/2830650
50. Martínez-Vilalta J, Garcia-Forner N. Water potential regulation, stomatal behaviour and hydraulic transport under drought: deconstructing the iso/anisohydric concept. Plant Cell Environ. 2017;40:962–76. https://doi.org/10.1111/pce.12846
51. Basile S, Stříbrská B, Kalyniukova A, Hradecký J, Synek J, Gershenzon J, et al. Physiological and biochemical changes of *Picea abies* (L.) during acute drought stress and their correlation with susceptibility to *Ips typographus* (L.) and *I. duplicatus* (Sahlberg). Front For Glob Change. 2024;7:1436110. https://doi.org/10.3389/ffgc.2024.1436110
52. Malone SC, Simonpietri A, Knighton WB, Trowbridge AM. Drought impairs herbivore-induced volatile terpene emissions by ponderosa pine but not through constraints on newly assimilated carbon. Tree Physiol. 2023;43:938–51. https://doi.org/10.1093/treephys/tpad016.
53. Erbilgin N, Zanganeh L, Klutsch JG, Chen S, Zhao S, Ishangulyyeva G, et al. Combined drought and bark beetle attacks deplete non-structural carbohydrates and promote death of mature pine trees. Plant Cell Environ. 2021;44:3866–81. https://doi.org/10.1111/pce.14197
54. Wallin KF, Raffa KF. Prior encounters modulate subsequent choices in host acceptance behavior by the bark beetle *Ips pini*. Entomol Exp Appl. 2002;103:205–18. https://doi.org/10.1046/j.1570-7458.2002.00975.x
55. Novak M, Krajnc AU, Lah L, Zupanec N, Kraševec N, Križman M, et al. Low-density Ceratocystis polonica inoculation of Norway spruce (*Picea abies*) triggers accumulation of monoterpenes with antifungal properties. Eur J For Res. 2014;133:573–83. https://doi.org/10.1007/s10342-013-0772-4.
56. Muller B, Pantin F, Génard M, Turc O, Freixes S, Piques M, et al. Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. J Exp Bot. 2011;62:1715–29. https://doi.org/10.1093/jxb/erq438.
57. Tomasella M, Jansen S, Giacomin C, Boccato E, Nardini A. Turgor loss in vessel-associated parenchyma cells increases xylem vulnerability to embolism. J Exp Bot. 2026;77:1279–92. https://doi.org/10.1093/jxb/eraf470.
58. Lachenbruch B, McCulloh KA. Traits, properties, and performance: how woody plants combine hydraulic and mechanical functions in a cell, tissue, or whole plant. New Phytologist. 2014;204:747–64. https://doi.org/10.1111/nph.13035
59. Hart SJ, Veblen TT, Eisenhart KS, Jarvis D, Kulakowski D. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. Ecology. 2014;95:930–9. https://doi.org/10.1890/13-0230.1
60. Tomasella M, Petrussa E, Petruzzellis F, Nardini A, Casolo V. The possible role of non-structural carbohydrates in the regulation of tree hydraulics. Int J Mol Sci. 2020;21. https://doi.org/10.3390/ijms21010144
61. Huang J, Kautz M, Trowbridge AM, Hammerbacher A, Raffa KF, Adams HD, et al. Tree defence and bark beetles in a drying world: carbon partitioning, functioning and modelling. New Phytol. 2020;225:26–36. https://doi.org/10.1111/nph.16173
62. Lahr EC, Krokene P. Conifer stored resources and resistance to a fungus associated with the spruce bark beetle *Ips typographus*. PLoS One. Public Library of Science. 2013;8:e72405-. https://doi.org/10.1371/journal.pone.0072405
63. Wadke N, Kandasamy D, Vogel H, Lah L, Wingfield BD, Paetz C, et al. The bark-beetle-associated fungus, *Endoconidiophora polonica*, utilizes the phenolic defense compounds of its host as a carbon source. Plant Physiol. 2016;171:914–31. https://doi.org/10.1104/pp.15.01916.
64. Hammerbacher A, Kandasamy D, Ullah C, Schmidt A, Wright LP, Gershenzon J. Flavanone-3-hydroxylase plays an important role in the biosynthesis of spruce phenolic defenses against bark beetles and their fungal associates. Front Plant Sci. 2019;10. https://doi.org/10.3389/fpls.2019.00208
65. Zhao T, Kandasamy D, Krokene P, Chen J, Gershenzon J, Hammerbacher A. Fungal associates of the tree-killing bark beetle, *Ips typographus*, vary in virulence, ability to degrade conifer phenolics and influence bark beetle tunneling behavior. Fungal Ecol. 2019;38:71–9. https://doi.org/10.1016/j.funeco.2018.06.003.
66. Holopainen JK, Virjamo V, Ghimire RP, Blande JD, Julkunen-Tiitto R, Kivimäenpää M. Climate change effects on secondary compounds of forest trees in the Northern hemisphere. Front Plant Sci. 2018;9:1445. https://doi.org/10.3389/fpls.2018.01445.
67. Malone SC, Thompson RA, Chow PS, de Oliveira Jr. CR, Landhäusser SM, Six DL, et al. Water, not carbon, drives drought-constraints on stem terpene defense against simulated bark beetle attack in *Pinus edulis*. New Phytol. 2025;245:318–31. https://doi.org/10.1111/nph.20218
68. Loreto F, Schnitzler J-P. Abiotic stresses and induced BVOCs. Trends Plant Sci. 2010;15:154–66. https://doi.org/10.1016/j.tplants.2009.12.006.
69. Raffa KF, Andersson MN, Schlyter F. Chapter one - Host selection by bark beetles: Playing the odds in a high-stakes game. In: Tittiger C, Blomquist GJ, editors. Adv In Insect Phys. Academic Press; 2016. p. 1–74. https://doi.org/10.1016/bs.aiip.2016.02.001
70. Andersson MN, Grosse-Wilde E, Keeling CI, Bengtsson JM, Yuen MMS, Li M, et al. Antennal transcriptome analysis of the chemosensory gene families in the tree killing bark beetles, Ips typographus and *Dendroctonus ponderosae* (Coleoptera: Curculionidae: Scolytinae). BMC Genomics. 2013;14:198. https://doi.org/10.1186/1471-2164-14-198.
71. Kandasamy D, Zaman R, Nakamura Y, Zhao T, Hartmann H, Andersson MN, et al. Conifer-killing bark beetles locate fungal symbionts by detecting volatile fungal metabolites of host tree resin monoterpenes. PLoS Biol. Public Library of Science; 2023:21:e3001887-. https://doi.org/10.1371/journal.pbio.3001887
72. Zhang Q-H, Schlyter F. Redundancy, synergism, and active inhibitory range of non-host volatiles in reducing pheromone attraction in European spruce bark beetle *Ips typographus*. Oikos. John Wiley & Sons, Ltd; 2003:101:299–310. https://doi.org/10.1034/j.1600-0706.2003.111595.x
73. Jirošová A, Kalinová B, Modlinger R, Jakuš R, Unelius CR, Blaženec M, et al. Anti-attractant activity of (+)-trans-4-thujanol for Eurasian spruce bark beetle *Ips typographus*: Novel

potency for females. Pest Manag Sci. John Wiley & Sons, Ltd; 2022:78:1992–9. https://doi.org/10.1002/ps.6819
74. Kelsey RG, Gallego D, Sánchez-García FJ, Pajares JA. Ethanol accumulation during severe drought may signal tree vulnerability to detection and attack by bark beetles. Canadian Journal of Forest Research. NRC Research Press; 2014:44:554–61. https://doi.org/10.1139/cjfr-2013-0428
75. Fiala T, Pyszko P, Holuša J. Using ethanol and other lures to monitor invasive ambrosia beetles in endemic populations: case study from the Czech Republic. Frontiers in Forests and Global Change. 2023:6. https://doi.org/10.3389/ffgc.2023.1258729
76. Kozhoridze G, Korolyova N, Jakuš R. Norway spruce susceptibility to bark beetles is associated with increased canopy surface temperature in a year prior disturbance. For Ecol Manage. 2023;547:121400. https://doi.org/10.1016/j.foreco.2023.121400.
77. Tyree MT, Sperry JS. Vulnerability of xylem to cavitation and embolism. Annu Rev Plant Biol Annual Reviews. 1989;40:19–36. https://doi.org/10.1146/annurev.pp.40.060189.000315.
78. Nardini A, Cochard H, Mayr S. Talk is cheap: rediscovering sounds made by plants. Trends Plant Sci. 2024;29:662–7. https://doi.org/10.1016/j.tplants.2023.11.023.
79. Rosell JA, Piper FI, Jiménez-Vera C, Vergílio PCB, Marcati CR, Castorena M, et al. Inner bark as a crucial tissue for non-structural carbohydrate storage across three tropical woody plant communities. Plant Cell Environ. John Wiley & Sons, Ltd; 2021:44:156–70. https://doi.org/10.1111/pce.13903
80. Gargiulo S, Boscutti F, Carrer M, Prendin AL, Unterholzner L, Dibona R, et al. Snowpack permanence shapes the growth and dynamic of non-structural carbohydrates in *Juniperus communis* in alpine tundra. Sci Total Environ. 2024;948:174891. https://doi.org/10.1016/j.scitotenv.2024.174891.
81. Domec J-C, Pruyn ML. Bole girdling affects metabolic properties and root, trunk and branch hydraulics of young ponderosa pine trees. Tree Physiol. 2008;28:1493–504. https://doi.org/10.1093/treephys/28.10.1493.
82. Iglesias DJ, Lliso I, Tadeo FR, Talon M. Regulation of photosynthesis through source: sink imbalance in citrus is mediated by carbohydrate content in leaves. Physiol Plant. John Wiley & Sons, Ltd; 2002:116:563–72. https://doi.org/10.1034/j.1399-3054.2002.1160416.x
83. Setter TL, Brun WA, Brenner ML. Stomatal closure and photosynthetic inhibition in soybean leaves induced by petiole girdling and pod removal. Plant Physiol. 1980;65:884–7. https://doi.org/10.1104/pp.65.5.884.
84. Williams LE, Retzlaff WA, Yang W, Biscay PJ, Ebisuda N. Effect of girdling on leaf gas exchange, water status, and non-structural carbohydrates of field-grown *Vitis vinifera* L. (cv. Flame Seedless). Am J Enol Vitic. 2000:51:49. https://doi.org/10.5344/ajev.2000.51.1.49
85. Hornslein NJ, Siegert CM, Renninger HJ. Changes in Physiological Functioning in Loblolly Pine Trees Undergoing Bark Beetle Simulated Mortality. Forest Science. 2019;65:312–23. https://doi.org/10.1093/forsci/fxy060.
86. Baños-Quintana AP, Gershenzon J, Kaltenpoth M. The Eurasian spruce bark beetle *Ips typographus* shapes the microbial communities of its offspring and the gallery environment. Front Microbiol. 2024;15:1367127. https://doi.org/10.3389/fmicb.2024.1367127.
87. Moussa A, Nones S, Vannucchi PE, Shahzad G-R, Dittmer J, Corretto E, et al. The bacterial community of the European spruce bark beetle in space and time. Entomologia Generalis. Stuttgart, Germany: Schweizerbart Science Publishers; 2024:44:211–22. https://doi.org/10.1127/entomologia/2023/2114
88. Masch D, Buscot F, Rohe W, Goldmann K. Bark beetle infestation alters mycobiomes in wood, litter, and soil associated with Norway spruce. FEMS Microbiol Ecol. 2025:101:fiaf015. https://doi.org/10.1093/femsec/fiaf015
89. Hammerbacher A, Schmidt A, Wadke N, Wright LP, Schneider B, Bohlmann J, et al. A common fungal associate of the spruce bark beetle metabolizes the stilbene defenses of Norway spruce. Plant Physiol. 2013;162:1324–36. https://doi.org/10.1104/pp.113.218610.
90. Seifert KA. Sapstain of commercial lumber by species of *Ophiostoma* and *Ceratocystis*. In: Wingfield MJ, Seifert KA, Webber JF, editors. Ceratocystis and Ophiostoma: Taxonomy, ecology, and pathogenicity. St. Paul: The American Phytopathological Society Press; 1993. p. 141–51.
91. Mifsud IEJ, Akana PR, Bytnerowicz TA, Davis SR, Menge DNL. Nitrogen fixation in the stag beetle, *Ceruchus piceus* (Coleoptera: Lucanidae): could insects contribute more to ecosystem nitrogen budgets than previously thought? Environ Entomol. 2023;52:618–26. https://doi.org/10.1093/ee/nvad053.
92. Johnston E, Okada S, Gregg CM, Warden AC, Rolland V, Gillespie V, et al. The structural components of the Azotobacter vinelandii iron-only nitrogenase, AnfDKG, form a protein complex within the plant mitochondrial matrix. Plant Mol Biol. 2023;112:279–91. https://doi.org/10.1007/s11103-023-01363-3.
93. Hýsek Š, Löwe R, Turčáni M. What happens to wood after a tree is attacked by a bark beetle? Forests. 2021:12. https://doi.org/10.3390/f12091163
94. Preisler Y, Tatarinov F, Grünzweig JM, Yakir D. Seeking the "point of no return" in the sequence of events leading to mortality of mature trees. Plant Cell Environ. 2021;44:1315–28. https://doi.org/10.1111/pce.13942
95. Junttila S, Yrttimaa T, Blomqvist M, Paljakka T, Pelto-Arvo M, Vastaranta M. Influence of bark beetle infestation on stem diameter dynamics. Trees, Forests and People. 2025;19:100777. https://doi.org/10.1016/j.tfp.2025.100777.
96. Paljakka T, Rissanen K, Vanhatalo A, Salmon Y, Jyske T, Prisle NL, et al. Is decreased xylem sap surface tension associated with embolism and loss of xylem hydraulic conductivity in pathogen-infected Norway spruce saplings? Front Plant Sci. 2020;11. https://doi.org/10.3389/fpls.2020.01090

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