



## Fallen trees' last stand against bark beetles

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### ABSTRACT

The weakened or suppressed hosts targeted by tree-killing conifer bark beetles during endemic phases are considered to be poorly defended and available to several competing species. Hosts face trade-offs in the allocation of resources in growth and reproduction or in defense, and the defense/resources status varies with time after host's death or weakening event. Tree-killing bark beetles at endemic levels must choose along a spectrum, compromising between encountering minimal defense and facing high competition, or benefiting from high nutritional quality but facing high host defense.

The relationships between resources and defenses in dead/dying trees have not been quantitatively assessed to date, because most studies focus on epidemic conditions. We measured the changes in constitutive and induced defenses in the phloem of spruce trees artificially uprooted at different times (up to 17 months prior to experiment initiation) and treated with methyl-jasmonate (MeJ) in order to induce chemical defense. We measured the effect of these changes on different steps of the host selection process and brood success of a major forest pest in Eurasia, *Ips typographus* (Coleoptera, Curculionidae).

Our results show that uprooted trees maintain some level of constitutive defenses, in particular monoterpenes, that decrease with time after uprooting. Moreover, the trees maintain some inducibility and can produce monoterpenes in response to MeJ treatment up to 7 months after uprooting. These defenses are correlated in part with the energy available in the phloem, but are likely too weak to exert pressure on the beetles' success and selection, the latter being related to the amount of energy available.

Our results confirm that wind-felled trees are poorly defended, consistent with the hypothesis of the evolution of the tree-killing behavior from saprophagy in response to an overwhelming interspecific competition on undefended hosts. Wind-felled trees still represent a useful resource, exposing endemic populations of aggressive beetles to low defense levels while facilitating reproduction, growth and development. The constraint on the beetles' populations then becomes the ability to locate these scattered and unpredictable resources.

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## 1. Introduction

Tree-killing conifer bark beetles have evolved the ability to mass-attack healthy living trees (Wood, 1982). Aggregation pheromones and complex associations with microorganisms facilitate this process which results in overcoming the constitutive defenses (the defenses strategies present in the tree without any challenge) and induced defenses (the defense strategies elicited in response to foreign aggression) of the conifers (Wood, 1982; Seybold et al., 2006; Six and Wingfield, 2011; Raffa et al., 2015).

However, this tree-killing behavior is only observed during epidemic phases of the population dynamics of aggressive species, outside of which attacks are restricted to less defended, weakened or suppressed hosts (Raffa et al., 1993; Franceschi et al., 2005;

Bleiker et al., 2014). The transition between the two phases depends on biotic and abiotic factors that influence host susceptibility and/or beetle population density, in particular catastrophic events that provide large amounts of susceptible hosts (droughts, storms, etc.) (Bouget and Duelli, 2004; Gandhi et al., 2007). When population density exceeds a certain threshold (dependent upon host resistance), the beetles acquire the capacity to collectively overwhelm healthy trees (Raffa and Berryman, 1983; Aukema et al., 2008; Kausrud et al., 2011; Lindgren and Raffa, 2013; Raffa et al., 2015).

It has been speculated that collective tree-killing has evolved from saprophagy, under the pressure of interspecific competition, the trade-off being to evolve mechanisms for bypassing or tolerating the host defenses (Seybold et al., 2000; Lindgren and Raffa, 2013). This evolutionary scenario is based on the assumption that the weakened trees targeted during endemic phases are less defended or undefended, therefore also available to a number of

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competing species. However, a spectrum of defense levels exists between the two extreme situations of a healthy living, highly protected host and a completely undefended dead tree. Furthermore, even after death, the defense/resources status of a potential host still varies with time. Tree-killing bark beetles at endemic levels must choose their resources along this continuum, maximizing their brood success in a compromise between encountering minimal defense and facing high competition, or benefiting from high nutritional quality but facing high host defense. In living trees, according to the growth-differentiation balance framework developed by [Herms and Mattson \(1992\)](#), production of defense components is costly, demanding resources that will then not be allocated to other physiological processes connected to plant growth and development. Secondary metabolites such as the terpenoids implicated in defense mechanisms, also share common precursors and “compete” with the metabolic pathways leading to the production of protein and carbohydrates necessary to the host’s growth, maintenance and storage ([Gill, 1986](#)). Consequently, there are strong trade-offs and inverse relationships between the allocation of resources to growth and reproduction and to defense ([Chapin, 1991](#); [Herms and Mattson, 1992](#)), and a gradient of defense mechanisms is to be expected according to the health status and vigor of the trees. In dead trees, defense and resources start decreasing after the event leading to death. The mechanisms guiding bark beetles to fallen trees are still largely unexplored. [Saint-Germain et al. \(2007\)](#) showed that secondary bark beetles use primary attractants to locate suitable patches, but then land at random on individual trees. Ethanol, produced by fire- or water-stressed trees have been shown to elicit positive response from bark beetles ([Joseph et al., 2001](#); [Kelsey and Joseph, 2003](#)), although [Klimetzek et al. \(1986\)](#) contend that the most aggressive beetles tend to avoid ethanol as it may indicate high inter-specific competition. Finally, visual cues may play a role in the selection process: some “visual specialists” show strong preferences toward the silhouette of their host (standing vs. fallen tree) and most beetles show some capacity to visually discriminate traps of different shape and color ([Byers, 1993](#); [Strom et al., 1999](#)). This choice is further complicated in endemic conditions by the fact that the potential resources are scattered and unpredictable and, to date, little is known about the discovery and exploitation of such resources by endemic bark beetle population even though both steps are critical for population maintenance. In particular, the relationships between resources and defenses in dead trees have not been quantitatively assessed to date, as most studies focus on epidemic conditions with high ecological and economic impact.

The Eurasian spruce engraver, *Ips typographus* L., provides an example of a bark beetle able to attack and kill living trees during epidemic phases, classifying it as a major forest pest in Eurasia ([Grégoire and Evans, 2004](#); [Grégoire et al., 2015](#)). At endemic levels in Europe, it is primarily confined to wind-felled Norway spruce, *Picea abies* (L.) Karst. Location and selection of these resources are poorly understood for this bark beetle because there is no strong evidence of primary attraction ([Austarå et al., 1986](#); [Erbilgin et al., 2007](#)) and visual cues seem to be weak or even absent ([Niemeier, 1985](#); [Sanders, 1987](#); [Byers, 1993](#)). The defenses of living *P. abies* have been well studied, showing constitutive and induced, mechanical and chemical defense mechanisms ([Franceschi et al., 2005](#)), developed during millions of years of co-evolution with bark beetles ([Wood, 1982](#); [Sequeira et al., 2000](#); [Seybold et al., 2000](#)). The terpenoids are the most extensively studied constituents of this arsenal ([Seybold et al., 2006](#)). They act as mechanical barriers (resin exudation) and as chemical repellents or toxins against the beetles or their fungal associates ([Franceschi et al., 2005](#); [Boone et al., 2013](#)). Monoterpenes (MT) are usually highly toxic to insects and their associated symbionts ([Langenheim, 1994](#); [Lieutier, 2002](#)), they are toxic to *I. typographus*

([Everaerts et al., 1988](#)) and tunneling by *I. pini* in phloem-based medium is reported to be inversely proportional to MT concentration ([Wallin and Raffa, 2000](#)). Sesquiterpenes (ST) are the largest group of terpenoids with well-known antifeeding activity ([Ryan, 2002](#)). Diterpenes (DT) are well known as antifeedants, and are also known to decrease larval growth, development and survival ([Ryan, 2002](#)). Finally, DT indirectly influence bark beetles’ success by reducing the growth of their fungal and bacterial associates that are involved in the defenses overcoming and beetles’ nutrition ([Boone et al., 2013](#); [Mason et al., 2015](#)).

A previous study has shown that artificially uprooted trees maintain their energetic budget and nutritional quality over 17 months, allowing sufficient time for the development of *I. typographus* ([Louis et al., 2014](#)). Here we report how the constitutive defenses and defense inducibility (elicited by localized treatment with the defense hormone methyl jasmonate (MeJ)) of the same artificially uprooted trees varied in time after uprooting, and how bark-beetles responded to these changes.

## 2. Materials and methods

A detailed account of the materials and methods used here has been provided in [Louis et al. \(2014\)](#). The experiment was conducted in Winenne, province of Namur, Belgium, in a mixed conifer and deciduous forest plantation on a south-oriented slope constituted of apparently healthy Norway spruce of very similar age (50 years), and size (DBH:  $24.5 \pm 1$  cm). Eight randomly chosen trees were artificially uprooted, at intervals, on 01/01/2012, 04/06/2012, 23/10/2012, 28/03/2013 to create uprooting time classes of 2.1, 7.2, 12 and 17 months, respectively. The trees were protected against potential insect attacks until the first flight period of 2013 by a polyethylene ultra-fine mesh (Harrod Horticultural, Lowestoft, Suffolk, UK) hermetically sealed around the lower 9 m of the bole. The unprotected crowns and stem bases were sprayed with a broad spectrum pyrethroid insecticide (Karate Zeon, Syngenta, 0.3% lambda-cyhalothrin).

### 2.1. Attack density

The mesh was removed and all trees were baited with pheromone dispensers (sealed polyethylene bags containing each 1.64 g of 2-methyl-3-buten-2-ol (MB) (Sigma–Aldrich, 98% chemical purity) and 0.08 g of (S)-*cis*-verbenol (cV) (Sigma–Aldrich, 95% chemical purity;  $\geq 50\%$  optical purity) ([Bakke et al., 1977](#))) on 4 June 2013 to facilitate colonization by local bark beetles. The boles were divided into eight observation sections on which new entrance holes were marked with date-specific pins twice a day during the flight period, from June 6 to July 19.

### 2.2. Beetles’ success

Each observation section was debarked 1 month after the first attack and various measurements of bark beetle success were made, including maternal gallery length, number of larval galleries for each female, number of living pupae and teneral adults in four 1 dm<sup>2</sup> phloem disks collected at each section, and fresh weight of sampled teneral adults. Furthermore, we quantified the nutrients acquired by the progeny using the colorimetric methods described in [Louis et al. \(2014\)](#).

### 2.3. Bark nutrients quantification

We quantified the nutrients present in one half of phloem samples (diameter: 1 cm) taken along the bole at 1, 3, 5 and 8 m (B) ([Fig. 1](#)) using colorimetric methods ([Giron et al., 2007](#)). The total

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