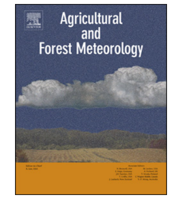
Agricultural and Forest Meteorology 263 (2018) 69–89

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet



Transpiration deficits increase host susceptibility to bark beetle attack: Experimental observations and practical outcomes for *Ips typographus* hazard assessment

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A R T I C L E I N F O

Keywords:
Ips typographus
Drought stress
Picea abies
Ecosystem modelling
Bark beetles
Infestation hazard assessment

A B S T R A C T

The projected increase in the frequency and severity with which bark beetle disturbances occur is forecasted to be partially driven by increases in drought episodes. Drought is widely considered to predispose host conifer trees to bark beetle attack; however, experimental data supporting this hypothesis are scarce. This study revisits the Rosalia Roof Project, the first throughfall manipulation experiment to investigate how attack by the Eurasian spruce bark beetle (*Ips typographus*) on mature Norway spruce (*Picea abies*) trees is affected by drought stress. Using the *in situ* "attack box" method, this study explores whether increased host acceptance by *I. typographus* and/or reduced host defense against attack coincide with increased tree transpiration deficits (i.e. the reduction from a potential transpiration caused by soil water limitation). To estimate transpiration deficits of the respective control and drought stress-induced (full-cover) trees, sap flow measurements were combined with simulations from a simple forest water balance routine. The model, which was calibrated against *in situ* hydrological measurements, has been developed for a hazard rating tool (PHENIPS-TDEF) which simulates both potential *I. typographus* phenology and tree drought stress in Norway spruce stands. While host acceptance appeared unaffected by tree transpiration deficits, acute and chronic transpiration deficits did lead to reduced host defense. Full cover trees for instance, which experienced an estimated 93 mm transpiration deficit in the previous May-Sep, could only defend against < 10% of the total individual attack attempts between spring and midsummer compared to the control trees which experienced a corresponding deficit of 9 mm and defended > 70% of attacks. However, similar defended attack percentages on the full-cover and control trees during late summer demonstrate the difficulty in deriving simple stress proxy-infestation risk relationships. The experiment therefore highlights the utility and limitations of transpiration deficits within *I. typographus* disturbance models and hazard assessment tools, such as PHENIPS-TDEF.

1. Introduction

Bark beetles belonging to the genus *Ips* and *Dendroctonus* are arguably the most important biotic agents of forest natural disturbance in the northern hemisphere (Bentz et al., 2010; Marini et al., 2017; Raffa et al., 2008; Schelhaas et al., 2003). From an ecological perspective, these natural disturbance regimes are simply inherent ecosystem phenomena (Chapin et al., 2011); however, in socioeconomic terms they can complicate the provision of important ecosystem goods and services (Kautz et al., 2018; Thom and Seidl, 2016). As with other disturbance agents, infestations by these forest insects cause sudden changes in ecosystem structure and function, subsequently altering the trajectories of these properties (Turner, 2010). While adult bark beetles and their larvae can destroy phloem and cambium tissue, physiological

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https://doi.org/10.1016/j.agrformet.2018.08.004
Received 3 May 2017; Received in revised form 12 June 2018; Accepted 11 August 2018
Available online 22 August 2018

deterioration and subsequent mortality of the host is often accelerated by blue stain fungi, which are vectored by bark beetles and rapidly disrupt xylem water flow (Hubbard et al., 2013; Urbanek Krajnc, 2009). Due to these initial impacts on host physiology, the resulting mortality, and subsequent secondary succession, bark beetle outbreaks can have a number of deleterious effects over a range of temporal and spatial scales. For instance, the associated consequences for forest biogeochemical cycling (Edburg et al., 2012; Frank et al., 2014; Hicke et al., 2012) can negatively impact drinking water quality within forested catchments (Mikkelson et al., 2013) and may limit regional forest carbon sequestration (Kurz et al., 2008; Seidl et al., 2014). Furthermore, the subsequent regional pulse in salvage logging puts an acute strain on the resources of forest enterprises at a time when markets prices for timber are reduced by surplus supply (Hanewinkel et al., 2011). With climate change set to further amplify the severity and frequency of bark beetle infestations, a comprehensive understanding of these biotic disturbance regimes is crucial (Bentz et al., 2010; Marini et al., 2017).

In Europe, the volume of timber salvaged from Norway spruce (*Picea abies*) forests due to infestations by the Eurasian spruce bark beetle *Ips typographus* has been increasing since the 1950s (Schelhaas et al., 2003; Seidl et al., 2014). Though peaks in these records often followed spikes in salvage logging due to windthrow occurrence (due to the pulses in breeding material), trends in these data also indicated a stimulatory effect of both changes in the European forest landscape (e.g. increased stand age and growing stock) and regional climate change (e.g. increased mean annual air temperatures, reduced summer precipitation) (Seidl et al., 2011b). Indeed, in addition to discrete increases in breeding material caused by windthrow, scolytid population dynamics are strongly influenced by spatial/temporal variations in forest stand structure (e.g. tree species, age, stand density) and variations in climate, which influence both the ecophysiology of scolytids directly and that of their tree hosts (Fettig et al., 2007; Jactel et al., 2009; Raffa et al., 2008). As such, combinations of spatial and temporal descriptions of stand characteristics and weather variables are often used as input variables in hazard risk assessment frameworks for modelling outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) (Coops et al., 2012; Safranyik et al., 2010) and *I. typographus* (Netherer and Nopp-Mayr, 2005; Stadelmann et al., 2013). However, as highlighted by Kautz et al. (2014), the extent to which the underlying assumptions and functions are validated by experimental data varies between the numerous processes modelled within such assessment frameworks.

In the case of *I. typographus*, the increase of stand susceptibility to infestation with increasing Norway spruce abundance and stand age and/or occurrence of windthrow is well documented (Wermelinger, 2004) and has been incorporated in spatial assessments of potential stand predisposition to infestation (Netherer and Nopp-Mayr, 2005; Stadelmann et al., 2013). Furthermore, the influence of temperature on *I. typographus* flight and generation development has been rigorously investigated (Annila, 1969; Lobinger, 1994; Wermelinger and Seifert, 1998, 1999) which has facilitated the development of robust temperature-based models simulating *I. typographus* phenology such as PHENIPS (Baier et al., 2007) and the model of Jönsson et al. (2007). Combinations of these and other models have been subsequently applied to evaluate of how future climate change may affect this particular coniferbark beetle relationship in various regional contexts (Hlásny et al., 2011; Jönsson and Bärring, 2011; Jönsson et al., 2011; Temperli et al., 2013). However, a key limitation of such scenario analyses has been the model assumptions (or lack thereof) describing the influence of drought events on host susceptibility to infestation. Drought stress of host trees is considered key trigger of *I. typographus* outbreaks (Marini et al., 2013, 2017); yet, experimental data underpinning model assumptions in respective risk assessment frameworks are scarce.

In ecosystem modelling, drought stress is often conceptualised in hydrological modules by comparing the difference between potential (evapo-)transpiration, simulated under non-limiting soil moisture, and the *actual* (evapo)transpiration, simulated under prevailing soil moisture conditions (Seidl et al., 2011a). Normally, these potential and actual fluxes are calculated using Penman-Monteith type equations (Monteith and Unsworth, 2008). This (evapo)transpiration deficit is often expressed in relative terms over a season and can be used in general regional assessments of forest health (Katzensteiner et al., 2007; Schwärzel et al., 2009; Zierl, 2001), or in explicit bark beetle risk assessment systems looking to explain temporal and spatial infestation dynamics of *I. typographus* (Seidl et al., 2007; Temperli et al., 2013) and other pests e.g. *D. ponderosae* (Coops et al., 2012). Drought stress has long been considered an important factor in coniferbark beetle relationships, hypothesised to increase conifer vulnerability by compromising host defense (Berryman, 1972; Christiansen et al., 1987). During periods of severely reduced precipitation, low soil water potentials and high vapor pressure deficits, isohydric conifers such as Norway spruce typically decelerate the decrease in xylem water potential by increasing the stomatal regulation of transpiration (Bréda et al., 2006). While the degree of stomatal control can vary significantly between individuals of the same stand (Hentschel et al., 2014), the strategy can help to avoid embolism in the xylem. However, the resulting restrictions in photosynthesis may reduce the synthesis of constitutive and induced defense compounds (e.g. resin, terpenes and phenols) due to net depletion of carbon resources with on-going respiratory consumption (McDowell et al., 2008) and/or impaired carbon mobilization and transport (Sala et al., 2010). The deficit between potential and actual transpiration (or evapotranspiration) thus represents a physiologically meaningful stress index in modelling *I. typographus* infestations. However, the sigmoidal function of seasonal evapotranspiration deficit used in model frameworks to describe Norway spruce predisposition to bark beetle attack (Seidl et al., 2007; Temperli et al., 2013) is yet to be validated by physiological experiments on mature host trees.

While statistical analyses of Norway spruce salvage trends have repeatedly confirmed other drought indices (e.g. precipitations deficits) as significant explanatory variables of *I. typographus* damage (Faccoli, 2009; Marini et al., 2013; Seidl et al., 2011b), links between tree transpiration deficits of Norway spruce or other conifers to bark beetle attack have yet to be demonstrated experimentally. Moreover, the hypotheses that drought stress increases Norway spruce susceptibility to successful attack (Christiansen et al., 1987; Lieutier, 2004), and that susceptible hosts are more attractive to pioneer *I. typographus* beetles (Wermelinger, 2004), have only been partially tested in experiments with mature trees (Netherer et al., 2015). The utility of monotonic stress-predisposition functions as well as definitions of drought intensity furthermore need to be reconsidered given the growth-differentiation-balance hypothesis (Herms and Mattson, 1992), which predicts that moderate drought stress enhances host resistance against insect pests. A case in point is the evidently less frequent and severe drought-induced forest dieback further triggered by bark beetle outbreaks in the eastern regions of the US compared to the more water-limited western forests that have consistently undergone periods of intense drought; warm temperatures positively acting upon beetle development and survival have added to attack risks in drought-prone areas (Kolb et al., 2016). Hence, *in situ* physiological studies of drought stress and coniferbark beetle relationships (Gaylord et al., 2013; Lorio et al., 1995; Lusebrink et al., 2016; Netherer et al., 2015) are essential for improving mechanistic understanding and modelling of bark beetle disturbances (Ryan et al., 2015), yet, still pose substantial methodological challenges (Kausrud et al., 2012).

This study presents new insights and outcomes from the Rosalia Roof Project, the first *in situ* throughfall manipulation experiment to demonstrate the impacts of drought stress on the susceptibility of mature Norway spruce trees to attack by *I. typographus* (Netherer et al., 2015). The paper here describes how variations in experimental bark beetle attack were influenced by treatment and prevailing weather