Applied Soil Ecology 105 (2016) 25–30

Contents lists available at ScienceDirect

Applied Soil Ecology

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

Bark coverage and insects influence wood decomposition: Direct and indirect effects

Michael D. Ulyshen[a,*], Jörg Müller[b,c], Sebastian Seibold[b,c]

[a] USDA Forest Service, Southern Research Station, 320 Green Street, Athens, GA 30602, USA
[b] Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany
[c] Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Center for Food and Life Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

ARTICLE INFO

Article history:
Received 28 December 2015
Received in revised form 16 March 2016
Accepted 21 March 2016
Available online 14 April 2016

Keywords:
Blattodea
Ecosystem services
Isoptera
Saproxylic

ABSTRACT

Rates of terrestrial wood decomposition are known to vary widely depending on regional and local climatic conditions, substrate characteristics and the organisms involved but the influence of many factors remain poorly quantified. We sought to determine how bark and insects contribute to decomposition in a southeastern U.S. forest. Open-topped stainless steel pans with screened bottoms were used to prevent subterranean termite (Rhinotermitidae: *Reticulitermes* spp.) colonization from "protected" logs. After a 20-month study period, we compared mass loss and lignin content between these and logs assigned to "unprotected" treatments that permitted termite colonization. The experiment was repeated for 1) logs from which bark had or had not been initially removed and 2) logs with sealed or unsealed ends. Logs with bark lost significantly (~2.4-fold) more mass than those without bark, likely due to the moisture-conserving properties of bark. Logs with unsealed ends lost significantly more mass than those with sealed ends. There was no significant difference in mass loss between protected and unprotected logs but logs with visible termite activity lost significantly more mass than those without termite damage. Few differences in lignin content were detected in this study but when logs with bark were analyzed separately, those with visible damage from long-horned beetles (Coleoptera: Cerambycidae) had lower lignin content than those without cerambycid activity. This suggests that cerambycids may promote decomposition indirectly through interactions with fungi or other organisms capable of degrading lignin. Our results suggest that insects can have significant direct and indirect effects on wood decomposition and clearly demonstrate the importance of bark in determining wood decay rates and insect activity.

Published by Elsevier B.V.

1. Introduction

Although woody debris represents a major terrestrial carbon store (Cornwell et al., 2009) and supports at least one fifth of forest insect biodiversity (Elton, 1966; Stokland et al., 2012), the importance of insects to its decomposition remains poorly understood. Insects associated with dead wood can be assigned to various functional groups including phloem and wood feeders, fungus and detritus feeders and predators. Different species are active at different stages of decomposition and all taxa have the potential to influence decomposition either directly or indirectly through interactions with other species (Ulyshen, 2016). Many of the first insects to colonize recently dead wood are known to vector spores or mycelia of rot fungi or facilitate the movement of fungi into logs, for example, with the potential to thereby indirectly affect decomposition and alter the composition of future fungal communities (Jacobsen et al., 2015; Leach et al., 1937; Persson et al., 2009; Strid et al., 2014). Social insects (ants and termites) commonly dominate saproxylic insect communities and may exert considerable influence on wood decomposition and related processes. In warmer climates, for example, termites are often among the most numerous insects found within dead wood (King et al., 2013) and have been shown to consume larger volumes of wood than all other insects combined (Ulyshen et al., 2014). While termites continue to receive a great deal of attention from researchers as important structural pests in urban areas, little is known about their ecology in forested systems (Maynard et al., 2015) and only a handful of studies have attempted to quantify their contributions to the decomposition of naturally-occurring woody substrates (Ulyshen, 2016).

* Corresponding author.
E-mail address: mulyshen@fs.fed.us (M.D. Ulyshen).

http://dx.doi.org/10.1016/j.apsoil.2016.03.017
0929-1393/Published by Elsevier B.V.

Methodological issues continue to impede efforts to quantify the role of insects in terrestrial decomposition. The most critical of these is the persistent challenge of excluding invertebrates without otherwise affecting microclimatic conditions known to influence microbial decomposers. According to Kampichler and Bruckner (2009), for example, this methodological issue renders more than 50 years of litterbag research inconclusive. Studies aimed at quantifying the contributions of insects to wood decomposition suffer from the same problem, with mesh bags, insecticides and other insect-exclusion methods known to alter microbial activity compared to unprotected substrates (Stoklosa et al., 2016; Ulyshen and Wagner, 2013). Differences in microclimate between treatments in such studies may be minimized by focusing on select taxa instead of attempting to exclude all invertebrates. In Finland, for example, Müller et al. (2002) showed that bark beetles promoted decomposition in spruce logs by only briefly exposing one set of logs to colonization by these insects. For the rest of the experiment, these logs were enclosed within cages identical to those used in the control treatment. In Malaysia, Takamura and Kirton (1999) and Takamura (2001) excluded termites by placing sections of wood in small trays with screened bottoms. The open-topped design allowed other insects to colonize the logs, thereby underestimating the total insect effect, but minimized differences in microclimate between treatments.

Wooden stakes or blocks of standardized dimensions have long-been used in applied termite research as a way to compare feeding preferences among tree species or chemical treatments (Bultman and Southwell, 1976). Wooden blocks have also been used to study the role of termites in decomposition but are not representative of naturally-occurring substrates (Ulyshen and Wagner, 2013; and references therein). Most importantly, wooden blocks lack the cambium and bark layers which are required by a diverse assemblage of phloem- and wood-feeding insects as a food resource and oviposition substrate (Stokland et al., 2012). In addition to their tunneling activities, these species are known to play an important role in facilitating fungal colonization (Leach et al., 1937) and can have lasting priority effects (Weslien et al., 2011). Whether or not bark is present may also influence microbially-driven decomposition, either positively or negatively. As suggested by Cornwell et al. (2009), bark may limit microbial access to wood during the initial stages of decomposition but may ultimately have a positive effect by enhancing moisture retention. To our knowledge, the role of bark in determining wood decay rates remains untested. Cut surfaces are a typical trait of dead wood in managed forests resulting from harvesting. These open areas may allow colonization of certain wood-decaying fungal species and reduce the importance of insects for vectoring and giving access to fungi. At the same time, such logs may dry out more quickly which may negatively influence microbial activity. The overall effect of cut ends on wood decomposition remains unclear.

Here we present the results from the fourth study in a series of experiments aimed at estimating the contributions of insects to wood decomposition in the southeastern United States. In the first study, termites were found to consume 15–20% of wood volume from pine logs over a several year period but unexpectedly had no effect on mass loss (Ulyshen et al., 2014). These results may either reflect an inhibition of microbial decomposers by insects or a stimulatory effect of the insecticide used to exclude termites. The second study, using stainless steel mesh bags to exclude insects, found insects to be responsible for ~14–20% wood loss in unflooded and seasonally flooded forests (Ulyshen, 2014). Due to uncertainties about how the mesh bags may have affected these results, a third study sought to specifically test for the mesh effect while measuring the contributions of insects to fine woody debris loss. Because the mesh bags were found to increase moisture levels and speed up wood decomposition, it was concluded that insects contribute more to the process than the observed value of 9–10% (Stoklosa et al. 2016). These findings support the notion that insects contribute importantly to decomposition but also underscore the need for alternative exclusion methods less likely to alter microclimatic conditions.

In the current study, we tested a modification of the open-topped tray first used by Takamura and Kirton (1999) for excluding termites from experimental logs. Because logs placed in such trays are completely exposed from above to flying insects, this approach can only speak to the effects of termites and other excluded soil invertebrates on decomposition. By largely eliminating any microclimatic differences between treatments, however, this approach has the potential to produce reliable estimates on how termites affect decomposition. In a subtropical southeastern U.S. forest, we tested the hypotheses that (i) termites significantly accelerate wood decomposition; (ii) wood with bark decomposes significantly faster than wood without bark; (iii) bark coverage and termites interact to affect decay rates, with bark coverage stimulating termite activity; and (iv) termites more strongly affect the decomposition of logs with sealed ends relative to those with unsealed ends. Two metrics were used to measure decomposition in this study. The first was mass loss which is commonly used in developing decay models. The second was lignin content. Lignin is largely responsible for the strength of the lignocellulose complex comprising wood and constrains decay rates. The degradation of lignin is thought to be largely driven by fungi and other microbes but the activities of these organisms can potentially be impacted by interactions with wood-dwelling insects (Ulyshen, 2016).

2. Materials and methods

2.1. Study location and design

The experiment took place in a mixed pine/hardwood forest on the Noxubee Wildlife Refuge, Noxubee Co., Mississippi, U.S.A. (33°14′56.1″N 88°46′07.3″W). The climate of the region is classified as humid subtropical with annual precipitation and temperature averaging 140 cm and 16.9 °C, respectively (usclimatedata.com, accessed 3-Nov-2015). The 72 logs used in this study came from 14 sweetgum (*Liquidambar styraciflua* L.) trees felled for this purpose at a single Mississippi location on 28 May 2013. The logs were 35 cm in length and were, on average, 8.5 ± 0.2 cm in wood diameter (not including bark). Immediately preceding and following each log, 10-cm-thick disks were cut. Measurements made on these subsamples were used to estimate the initial dry weight (without bark), initial cross sectional area and initial specific gravity of each log (see Section 2.2). In order to test the role of bark in decomposition, bark was removed from half the logs at the beginning of the experiment. In addition, the ends of half the logs with bark and half of those without bark were sealed with three layers of black plastic and secured in place with wire to test how this would affect the observed effect of termites on decomposition.

A row of six locations (replicate blocks) was established approximately 100 m from and parallel to the forest edge, with locations separated from one another by ~10 m. Six plots were established at each location, arranged in two rows and three columns and separated from one another by about 1 m. The six plots at each location were randomly assigned to one of six treatments consisting of a pan/termite factor with three levels and a bark factor with two levels (i.e., with or without bark). Regarding the pan factor, two plots received a stainless steel pan (Vollrath Super Pan V item number 30022, $52.7 \times 32.4 \times 6.5$ cm) with closed mesh bottoms ("closed pans") to prevent colonization by termites. Two other plots received identical pans with open mesh bottoms ("open pans") to permit termite access. The remaining two plots