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Understory plant functional groups and litter species identity are stronger drivers of litter decomposition than warming along a boreal forest post-fire successional gradient

Jonathan R. De Long [a, *], Ellen Dorrepaal [b], Paul Kardol [a], Marie-Charlotte Nilsson [a], Laurenz M. Teuber [b], David A. Wardle [a]

[a] Department of Forest Ecology & Management, Swedish University of Agricultural Sciences, SE-901 83, Umeå, Sweden
[b] Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, SE-981 07, Abisko, Sweden

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ABSTRACT

Increasing surface temperatures due to climate change have the potential to alter plant litter mass loss and nutrient release during decomposition. However, a great deal of uncertainty remains concerning how ecosystem functioning may be affected by interactions between warming and other drivers, such as plant functional group composition and environmental context. In this study, we investigated how vascular plant litter decomposition and nutrient release were affected by experimental warming, moss removal and shrub removal along a post-fire boreal forest successional gradient. Our results show that litter decomposition and nutrient loss were primarily driven by understory plant functional group removal. The removal of mosses generally reduced litter mass loss and increased litter phosphorus (P) loss, while shrub removal typically increased litter mass loss and in one litter species reduced immobilization of P. Litter nitrogen (N) loss was unaffected by plant functional group removal. Warming interacted with successional stage and species identity of the litter decomposed, but these effects were uncommon and generally weak. As climate change advances, moss cover is expected to decrease, while shrub cover is expected to increase. Taken together with our results, this suggests that lower moss cover will decrease leaf litter decomposition rates and increase P release from litter, while increasing shrub cover will decrease decomposition rates and may reduce P release from litter. Our results demonstrate that in the short term, the direct effects of warming and successional stage will play a relatively minor role in driving litter decomposition processes in the boreal forest. In the long term, as the climate warms, temperature and its indirect effects via changes in the understory vegetation will play an important role in driving litter decomposition, thereby potentially altering C storage and nutrient cycling.

1. Introduction

Global temperatures are expected to rise by 1–3 °C during the next century (IPCC, 2013), which will impact upon litter decomposition and thus carbon (C) storage (Kirschbaum, 1995) and nutrient cycling (Kalbitz et al., 2000). One paradigm proposes that increasing temperatures will enhance decomposition rates (Hobbie, 1996), thereby potentially creating a positive feedback between soil-atmosphere C exchange with climatic warming if the total amount of plant litter transferred to the soil C pool is reduced (Cox et al., 2000). However, contrary evidence suggests that warming may decrease soil water availability, thereby negatively impacting upon decomposer organisms and consequently inhibiting decomposition (Sjögersten and Wookey, 2004; Pries et al., 2013; Blok et al., 2015). Resultantly, a great deal of uncertainty remains concerning how other environmental conditions such as substrate quality or biotic interactions might modify the effects of increased temperature on decomposition (Davidson and Janssens, 2006; Schmidt et al., 2011). Plant functional groups may generate different microclimate effects on litter decomposition rates, which can impact upon ecosystem C storage and nutrient cycling (Aerts, 2006). Further, plant functional groups may vary in their responses to changing climate (Chapin et al., 1995; Hollister et al., 2005). Therefore, investigating the direct effects of warming on litter decomposition, together with its interaction with plant

* Corresponding author.
E-mail address: jonathan.de.long@slu.se (J.R. De Long).

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functional groups, is essential to understanding how decomposition and the processes it controls (i.e., C loss and nutrient cycling) will be altered as climate change advances.

Feather mosses and ericaceous dwarf shrubs are the main plant functional groups in the boreal forest understory. Mosses contribute significantly to ecosystem primary productivity (Benscoter and Vitt, 2007) and produce recalcitrant litter (Lang et al., 2009) that can affect decomposition rates and C sequestration (Jonsson et al., 2015). Presence of mosses can enhance decomposition of freshly fallen vascular plant litter (Jackson et al., 2013) by generating more favorable temperature and moisture conditions for microbial activity (Turetsky, 2003; Turetsky et al., 2012). Additionally, shading caused by the understory shrub canopy decreases soil temperatures (Myers-Smith et al., 2011) and controls soil moisture regimes via changes to evapotranspiration (Wahren et al., 2005; Bond-Lamberty et al., 2011), which may impact upon decomposition rates. Further, understory shrubs can produce high quantities of litter, but the quality of this litter varies between species and therefore can affect decomposition rates by influencing decomposer microbial activity (Bradley et al., 2000; Wardle et al., 2003b; Myers-Smith et al., 2011). Given the ubiquitous presence of mosses and shrubs in the boreal forest understory (Nilsson and Wardle, 2005), understanding how changes to the environment and microclimate generated by these two plant functional groups affect decomposition is vital.

The effects of increasing temperatures on mosses and shrubs and the consequences of these effects for ecosystem functioning have been gaining considerable recent attention (Myers-Smith et al., 2011; Turetsky et al., 2012; Lindo et al., 2013). Increasing air temperatures often reduce moss cover (Rixen and Mulder, 2009; Sorensen et al., 2012), which may in turn increase decomposition rates through generating warmer soil conditions (O'Neill et al., 2006; Gornall et al., 2007). On the other hand, increasing temperatures generally increase shrub productivity (DeMarco et al., 2014) and belowground C-transfer between individual shrubs (Deslippe and Simard, 2011), leading to increased shrub dominance. Greater shrub productivity as a result of warming can stimulate decomposer organisms through enhanced resource availability. However, increases in shrub cover associated with warming may reduce decomposition rates due to soil cooling via increased shading (Blok et al., 2010; Myers-Smith and Hik, 2013). Further, the increased production of recalcitrant litter by certain shrub species may also provide negative feedbacks to decomposition (Cornelissen et al., 2007). Nevertheless, there is a scarcity of knowledge concerning how the impact of warming on decomposition depends upon interactions with plant functional groups (Davidson and Janssens, 2006; Schmidt et al., 2011).

Wildfire caused by lightning strike is one of the most influential abiotic drivers of boreal forest ecosystem function on decadal to centennial timescales (Zackrisson, 1977; Niklasson and Granström, 2000; Bergeron et al., 2001). Fire suppression in Fennoscandia over the past two centuries has decreased wildfire prevalence (Zackrisson, 1977), although fire frequency is expected to increase in unpopulated boreal regions as global climate change advances (IPCC, 2013). Advancing post-fire succession in the boreal forest is associated with lower plant-available nitrogen (N) and shifts in the vegetation from faster growing, nutrient acquisitive species with fast decomposing litter to slower growing, nutrient conservative species with slow decomposing litter (DeLuca et al., 2002; Hart and Chen, 2006). For example, in Fennoscandia the early successional shrub *Vaccinium myrtillus* produces readily decomposable litter high in N. On the other hand, *Empetrum hermaphroditum* and feather mosses (which both become more dominant in late succession) produce recalcitrant, slow decomposing litter (DeLuca et al., 2002; Wardle et al., 2003a), which can lead to greater C storage in old-growth boreal forests (Wardle et al., 2003a).

Plant removal experiments performed across post-fire chronosequences show that the effect of mosses on microclimate on leaf litter decomposition is sometimes independent of successional stage (Jackson et al., 2013). However, other work has shown that higher moss abundance associated with advancing post-fire succession slows decomposition due to decreased soil temperature (O'Neill et al., 2006). Additionally, the removal of dwarf shrubs has been shown to reduce litter decomposition in early successional stages, due to the loss of high quality C from shrub litter input (Wardle and Zackrisson, 2005). As such, removal experiments reveal that the length of time following fire, and the understory vegetation that develops during post-fire succession, can serve as important drivers of decomposition and nutrient cycling in the boreal forest.

We conducted an experiment along an established 368-year post-fire boreal chronosequence in northern Sweden (DeLuca et al., 2002; Jackson et al., 2013; Bokhorst et al., 2014). We decomposed vascular plant litter of contrasting qualities in plots across the chronosequence subjected to warming, moss removal and shrub removal treatments in a full factorial design. We measured litter mass and nutrient loss to test the following hypotheses: 1) Negative effects of moss removal on litter mass and nutrient loss will be greater in late successional stages, while negative effects of shrub removal will be greater in early successional stages; 2) Moss and shrub removal will both have a greater effect on litter mass and nutrient loss in warmed plots; 3) The effect of moss and shrub removal (singly or in combination) on litter mass and nutrient loss will be determined by interactive effects between successional stage and warming because the effect of moss removal will be greater in warmed plots in late successional stages, while the effect of shrub removal will be greater in warmed plots in early successional stages. Further, we measured a number of soil properties in order to elucidate how the mechanisms controlling leaf litter decomposition were affected by the experimental treatments.

Investigating how litter decomposition and nutrient loss respond to interactions between plant functional group removal and warming along a successional gradient will allow us to better anticipate how leaf litter decomposition, a key driver of ecosystem nutrient and C flux, responds to global climate change under varying environmental conditions.

2. Methods

2.1. Study site and experimental design

We used ten sites along a fire-driven boreal forest successional chronosequence near Arvidsjaur in northern Sweden (65°35′–66°07′N, 17°15′–19°26′E). Chronosequences are important tools for answering ecological questions based upon "space for time substitution" over large time scales that are not possible through other experimental approaches (Fukami and Wardle, 2005; Walker et al., 2010). Along this successional chronosequence, time since last stand-replacing fire varies from 48 to 368 years. The sites used in this experiment are divided into early, mid and late successional stages, with time since last fire of <100 years (three sites), 100–260 years (four sites), and >260 years (three sites), respectively (Jackson et al., 2013). With advancing post-fire succession, the *Pinus sylvestris* overstory generally becomes increasingly dominated by *Picea abies* while *E. hermaphroditum* generally replaces *V. myrtillus* in the understory (Appendix 1). Additionally, moss cover and biomass increases as this chronosequence proceeds, while nutrient availability and vascular plant litter decomposition rates tend to decrease (DeLuca et al., 2002; Jackson et al., 2013). The climate is cold temperate humid with