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Original article

Climate change triggers effects of fungal pathogens and insect herbivores on litter decomposition

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ABSTRACT

Increasing infestation by insect herbivores and pathogenic fungi in response to climate change will inevitably impact the amount and quality of leaf litter inputs into the soil. However, little is known on the interactive effect of infestation severity and climate change on litter decomposition, and no such study has been published for deciduous forests in Central Europe. We assessed changes in initial chemical quality of beech (*Fagus sylvatica* L.) and maple litter (*Acer platanoides* L.) in response to infestation by the gall midge *Mikiola fagi* Hart. and the pathogenic fungus *Sawadaea tulasnei* Fuckel, respectively, and investigated interactive effects of infestation severity, changes in temperature and soil moisture on carbon mineralization in a short-term laboratory study. We found that infestation by the gall midge *M. fagi* and the pathogenic fungus *S. tulasnei* significantly changed the chemical quality of beech and maple litter. Changes in element concentrations were generally positive and more pronounced, and if negative less pronounced for maple than beech litter most likely due to high quality fungal tissue remaining on litter after abscission. More importantly, alterations in litter chemical quality did not translate to distinct patterns of carbon mineralization at ambient conditions, but even low amounts of infested litter accelerated carbon mineralization at moderately increased soil moisture and in particular at higher temperature. Our results indicate that insect herbivores and fungal pathogens can markedly alter initial litter chemical quality, but that afterlife effects on carbon mineralization depend on soil moisture and temperature, suggesting that increased infestation severity under projected climate change potentially increases soil carbon release in deciduous forests in Central Europe.

1. Introduction

Insect herbivores and pathogenic fungi are important components of forest ecosystem, exerting essential impacts on ecosystem structure and functioning by cascading direct and indirect effects on ecological processes and interactions (Hunter, 2001). The devastating impacts of mass outbreak insect herbivores and epidemic pathogenic fungi on forest trees and their widespread threats for long-term ecosystem functioning are well documented (Malmström and Raffa, 2000; Barbosa et al., 2012). For instance, mass outbreaks of the mountain pine beetle and the eastern spruce budworm have dramatically reduced plant growth and increased tree mortality over large areas, and turned forests from carbon sinks to carbon sources (Kurz et al., 2008; Dymond et al., 2010). Similarly, epidemics of pathogenic fungi, including the Asian chestnut blight or the Dutch elm disease have caused severe die-offs and extinctions in forest ecosystems around the world (Anagnostakis, 1987; Fisher et al., 2012).

Mass outbreak insect herbivores and epidemic fungal pathogens, however, constitute only a minor proportion of all phytophagous insects and plant associated fungi in forests. More frequently trees are infested by endemic (non-outbreak) herbivores and fungal pathogens, which generally cause low levels of damage, but nevertheless can profoundly impact major ecosystem processes by a diverse set of mechanisms. For instance, insect herbivores can remove 15% of primary production in terrestrial ecosystems (Cyr and Pace, 1993) and defoliation has been shown to change throughfall chemistry (Stadler and Michalzik, 2000), soil microclimatic conditions (Classen et al., 2005), root exudation (Bardgett et al., 1998) and rhizosphere interactions (Fu and Cheng, 2004). Moreover, insect herbivores deposit significant quantities of nutrient rich fecal material and increase the amount of high quality greenfall (Fonte and Schowalter, 2004; Frost and Hunter, 2004). More importantly, trees respond to infestation by changing the composition and concentration of foliar nutrients and

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secondary compounds and alterations of foliar chemistry can persist into leaf litter subsequently changing the quality of organic matter inputs into the soil (Choudhury, 1988; Allison and Schultz, 2005; Schweitzer et al., 2005; Chapman et al., 2006; Crutsinger et al., 2008).

Changes in leaf litter quality in response to infestation can profoundly impact decomposition processes in forest ecosystems. It is widely accepted that decomposition rates are controlled by climate, resource quality and consumer community composition, but the importance of each of these factors varies at local and global scales (Couteaux et al., 1995; Aerts, 1997). At the global scale climate is the most important controlling factor (Gholz et al., 2000; Liski et al., 2003), whereas variation in leaf litter quality generally surpass climate in driving litter decomposition at local scales (Cornwell et al., 2008). Given the major importance of leaf litter decomposition for nutrient recycling, net primary productivity and the global carbon cycle (Chapin et al., 2011) considerable attention has been paid to the consequences of insect herbivore and fungal pathogen infestation for leaf litter chemical quality and subsequent decomposition. However, previous studies have found variable effects and whereas in some cases infestation accelerated decomposition (Chapman et al., 2003; Crutsinger et al., 2008; Purahong and Hyde, 2011) some studies found negative or neutral effects (Schweitzer et al., 2005; Frost et al., 2012), suggesting that effects of insect herbivores and pathogenic fungi are context dependent and species specific.

Changes in temperature and precipitation due to anthropogenic climate change is expected to exacerbate the impacts of many herbivores and fungal pathogens on forest ecosystems (Ayres and Lombardero, 2000; Bale et al., 2002; Dukes et al., 2009; Jactel et al., 2012). During the last century the global average terrestrial surface temperature has increased by 0.74 °C and climate models project an additional 1.8°—5.8 °C increase by the end of this century relative to 1990 (IPCC, 2007). This will most likely shift precipitation regimes and atmospheric water, and due to changes in evaporation, the frequency of extreme hydrologic events will increase (IPCC, 2007). The impact of climate change on insect herbivores and fungal pathogens can be direct, by climate induced changes in the performance of insects and fungi, or indirect, resulting from modifications of host tree physiology (Ayres and Lombardero, 2000; Bale et al., 2002; Harvell et al., 2002; Netherer and Schopf, 2010; Jactel et al., 2012). As ectotherms, insects are highly sensitive to changes in temperature, with warming potentially speeding up growth rate, fecundity and overwintering survival, resulting in higher population densities and more generations per growing season (Bale et al., 2002). Although fungi have a large temperature tolerance, overwintering survival and dispersal in subsequent seasons also has been shown to increase with temperature (Dukes et al., 2009). Moreover, foliar fungal pathogens require high levels of humidity for successfully penetrating plant tissue, suggesting that increasing precipitation will result in more frequent and severe infestations (Magarey et al., 2005). Prolonged drought therefore may have adverse impacts on insect herbivores and pathogenic fungi, but may in turn accelerate infestation of stressed tree hosts due to drought induced carbon starvation that reduces the physiological ability of host trees to defend against insect herbivores and fungal pathogens (Ayres and Lombardero, 2000). Moreover, divergent sensitivities to variation in temperature or precipitation can result in phenological asynchrony between insect herbivores or fungal pathogens and their host trees, which may have major impacts for population viability and infestation severity (Singer and Parmesan, 2010; Schwartzberg et al., 2014).

In addition to indirectly altering decomposition processes via herbivore and fungal induced changes of leaf litter quality, climate change may directly affect litter decomposition via altering soil microbial activity and community composition (Bardgett et al., 2008; Butenschoen et al., 2011). Generally, microbial biomass changes only little in response to alterations of temperature (Zhang et al., 2005), whereas moderate warming has been documented to modify microbial community composition and to increase metabolic process rates and extracellular enzyme production (Schindlbacher et al., 2011). Moreover, soil moisture is a critical factor controlling the diffusion of substrates and extracellular enzymes, suggesting that spatiotemporal changes in precipitation regimes will strongly affect litter decomposition and element cycling (Schimel et al., 1999).

Considering the expected climate change mediated alterations in the quality of leaf litter in response to increased herbivore and fungal infestation as well as temperature and moisture mediated changes in microbial activity, surprisingly little is known on their interactive effects on litter decomposition. This limits predictions on how effects of fungi and insect herbivores on litter decomposition will change with alterations in climate. To contribute to filling this gap, we investigated the effects of increased temperature, altered moisture conditions and herbivore- or fungal-induced changes in leaf litter quality on carbon mineralization in a microcosm study. We used litter of maple (*Acer platanoides* L.) and beech (*Fagus sylvatica* L.) as model species as both are common tree species in deciduous forests in Central Europe, and are frequently infested by the ectoparasitic fungus *Sawadaea tulasnei* Fuckel (maple) and the galling insect *Mikiola fagi* Hart. (beech). To assess the interactive effect of climate change agents and fungal infestation or herbivore attack on litter decomposition, infested and uninfested litter was homogenously mixed with forest soil and incubated at three temperatures and three soil moisture conditions for 110 days. Carbon mineralization rates were measured at regular intervals and used to calculate cumulative carbon mineralization representing litter decomposition. The aims of the current study were to test the hypotheses that (1) infestation by *S. tulasnei* and *M. fagi* changes the chemical quality of maple and beech litter, respectively, which (2) translates into divergent decay rates interactively affected by moderately increased temperature and soil water content. Despite the large number of studies comparing decay rates of infested and uninfested litter (e.g. Chapman et al., 2003; Schweitzer et al., 2005; Crutsinger et al., 2008; Frost et al., 2012), infestation severity has received surprisingly little attention, although in natural ecosystems infested and uninfested litter decomposes in mixtures rather than isolated, which may impact litter decay rates (Hättenschwiler et al., 2005; Gessner et al., 2010; Handa et al., 2014). Consequently, previous studies likely overestimate effects of herbivory and fungal infestation and we suggest that dynamics of infested and uninfested litter need to be investigated in mixture to reliably predict the effect of herbivores and fungal infestation on litter decomposition rates. Therefore we incubated two additional litter mixtures containing intermediate amounts of infested leaf litter (40 and 80% infested leaf litter) and hypothesized that (3) the threshold concentration of infested leaf litter in mixtures is negatively related to the relative disparity between litter decay rates of infested and uninfested litter. In other words, the higher the differences in litter decomposition between infested and uninfested litter, the lesser infested litter is needed to significantly modify litter decomposition and carbon release of litter mixtures. This, however, might be further interactively affected by global change factors.

2. Material and methods

2.1. Litter and soil collection

Soil sampling was carried out in autumn 2011 in a 140 year old deciduous forest in the vicinity of Göttingen (51°32′4″ N, 10°3′5″ O, 420 m a.s.l., Lower Saxony, Germany). The region has a continental