Acta Oecologica 70 (2016) 79–86

Contents lists available at ScienceDirect

Acta Oecologica

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

Original article

Mixing effects on litter decomposition rates in a young tree diversity experiment

Nuri Nurlaila Setiawan [a, *], Margot Vanhellemont [a], An De Schrijver [a, b], Stephanie Schelfhout [a, c], Lander Baeten [a], Kris Verheyen [a]

[a] Forest & Nature Lab, Department of Forest and Water Management, Ghent University, Geraardsbergsesteenweg 267, 9090 Gontrode, Belgium
[b] Department of Biosciences and Food Sciences, University College Ghent, Valentin Vaerwyckweg 1, 9000 Ghent, Belgium
[c] Department of Applied Biosciences, Ghent University, Valentin Vaerwyckweg 1, 9000 Ghent, Belgium

ARTICLE INFO

Article history:
Received 5 July 2015
Received in revised form
2 December 2015
Accepted 15 December 2015
Available online 28 December 2015

Keywords:
FORBIO
Biodiversity–ecosystem functioning
Temperate forest
Post-agricultural forest

ABSTRACT

Litter decomposition is an essential process for biogeochemical cycling and for the formation of new soil organic matter. Mixing litter from different tree species has been reported to increase litter decomposition rates through synergistic effects. We assessed the decomposition rates of leaf litter from five tree species in a recently established tree diversity experiment on a post-agriculture site in Belgium. We used 20 different leaf litter compositions with diversity levels ranging from 1 up to 4 species. Litter mass loss in litterbags was assessed 10, 20, 25, 35, and 60 weeks after installation in the field. We found that litter decomposition rates were higher for high-quality litters, i.e., with high nitrogen content and low lignin content. The decomposition rates of mixed litter were more affected by the identity of the litter species within the mixture than by the diversity of the litter *per se*, but the variability in litter decomposition rates decreased as the litter diversity increased. Among the 15 different mixed litter compositions in our study, only three litter combinations showed synergistic effects. Our study suggests that admixing tree species with high-quality litter in post-agricultural plantations helps in increasing the mixture's early-stage litter decomposition rate.

1. Introduction

Every ecosystem in the world depends on decomposition to convert dead organic matter to inorganic nutrients and CO_2 usable for plant and microbial production (Chapin et al., 2011). Decomposition is an essential process in the ecosystem, next to photosynthesis, since only a small part of the produced plant biomass will enter the trophic system. During decomposition, litter changes physically and chemically through several processes that vary in duration, i.e., leaching, fragmentation, and degradation of simple molecules (early decomposition stages), and degradation of large molecules such as lignin (later decomposition stages) (Adl, 2003; Berg and Matzner, 1997). The overall decomposition rate is controlled by three main factors, i.e., the physicochemical environment, the litter quality, and the composition of the decomposer community (Daubenmire and Prusso, 1963; Swift et al., 1979).

In forest ecosystems, tree leaves are the main component of the aboveground plant litter (Berg and McClaugherty, 2008; Gessner et al., 2010). As tree species differ in their leaf litter quality, the tree species composition of a forest influences the overall quality of the litter that reaches the forest floor (Hättenschwiler, 2005; Hobbie, 1992). In general, high decomposition rates are expected for high-quality litter: litter with a low carbon:nitrogen (C:N) and low lignin:nitrogen (L:N) ratio, which promotes microbial decomposer activity, and high calcium (Ca) concentration, which promotes earthworm activity (Gartner and Cardon, 2004; Reich et al., 2005; Hobbie et al., 2006; Gessner et al., 2010). The quality and structure of mixed-species litter can differ from monospecific litter, which may affect the physicochemical environment (e.g., soil chemical composition) as well as the decomposer abundance, composition, and activity (Blair et al., 1990; Chapman and Newman, 2010; Chapman et al., 2013), and thus the decomposition rate. Numerous studies do indeed show significant tree diversity effects

* Corresponding author. Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, 9090 Gontrode, Belgium.

E-mail addresses: NuriNurlaila.Setiawan@UGent.be (N.N. Setiawan), Margot.Vanhellemont@UGent.be (M. Vanhellemont), An.DeSchrijver@UGent.be (A. De Schrijver), Stephanie.Schelfhout@UGent.be (S. Schelfhout), Lander.Baeten@UGent.be (L. Baeten), Kris.Verheyen@UGent.be (K. Verheyen).

http://dx.doi.org/10.1016/j.actao.2015.12.003
1146-609X/

on the rate of litter decomposition (Gartner and Cardon, 2006, 2004; Gessner et al., 2010; Handa et al., 2014; Jacob et al., 2010; Vivanco and Austin, 2008; Vos et al., 2013). Higher decomposition rates in mixed litter compared to monospecific litter were more commonly found than the opposite (Cuchietti et al., 2014; Gartner and Cardon, 2004; Hättenschwiler and Gasser, 2005). However, litter mixture effects on decomposition rates are not yet predictable in forests (Hättenschwiler, 2005) and inconsistent among ecosystems (Cardinale et al., 2011). Recent research in forests suggests that the identity of the litter species within the mixture affects the decomposition rate of mixed litter more than the diversity of the litter per se (Cuchietti et al., 2014; Wu et al., 2013).

Mixing litter of different species may have an additive or non-additive effect on the decomposition rate. Purely additive effects occur when the decomposition rate of a litter species is not affected by the other litter species present in the mixture. The decomposition rate of the litter mixture can then be predicted from the monospecific decomposition rates of the component litter species. Non-additive effects, on the other hand, occur when different litter species do influence each other, which leads to a higher (synergistic effects) or lower (antagonistic effects) decomposition rate in the mixed litter than expected based on the decomposition rates of the component species (Hättenschwiler, 2005). These non-additive effects may be the result of chemical effects brought about by one or more of the litter species in the mixture, which will affect the decomposer activity. A transfer of nitrogen (N) from litter of nitrogen-fixing plants to the co-occurring litter will accelerate decomposition (Hobbie, 2000; Schimel and Hättenschwiler, 2007); a release of inhibitory compounds such as phenols and tannins by one of the litter species will dampen the decomposition rate of the adjacent litter (Gartner and Cardon, 2004; Salamanca et al., 1998).

Tree species diversity experiments (cf. the global network TreeDivNet, see www.treedivnet.ugent.be and Verheyen et al., 2015) are promising platforms to study the effects of tree species diversity and composition on ecosystem functioning, e.g., the leaf litter decomposition rate. Up till now, most studies about tree diversity effects on litter decomposition have focused on mature forest. Yet, litter decomposition rates may differ between forest development stages (Coleman and Crossley, 2004). The early stages of forest development, especially in post-agricultural forests, are important in producing soil organic matter and nutrient input into the soil (Chapin et al., 2011). In addition, the soil nutrient concentrations (e.g., N, phosphorus) and the soil pH are generally much higher and less limiting in young post-agricultural forests than in mature forests. Hence, differences in the effects of litter mixing on decomposition rates can be expected between young and mature forests. We focus on a young plantation of the FORBIO experiment in Belgium (see Verheyen et al., 2013), established in 2010. To investigate the relation between leaf litter diversity and decomposition, we assessed the decomposition rate for 20 different leaf litter compositions with diversity levels ranging from 1 to 4 species. In the present paper, we address three main questions: (1) Are there differences between the litter decomposition rates of the tree species in the FORBIO experiment and is there a link with chemical litter quality?; (2) Are there differences in litter decomposition rate between litter mixtures and are these differences related to litter diversity and composition?; (3) Do the observed decomposition rates of the litter mixtures differ from the decomposition rates predicted based on the component litter species, i.e., is there evidence for non-additive effects? We hypothesize that: (1) high-quality leaf litter (high in N and Ca, and with low C:N ratio and lignin content) will decompose faster than low-quality leaf litter; (2) the decomposition rate will differ between leaf litter mixtures, and the composition of the leaf litter mixture will be more important than the number of species in the litter mixture; (3) litter mixtures that include high-quality leaf litter will decompose faster than predicted based on the abundances of the component species and their monospecific (unmixed) decomposition rates. We will discuss possible mechanisms underlying the observed patterns in decomposition and translate our results into recommendations for planting or managing mixed forests with an eye to good litter decomposition.

2. Materials and methods

2.1. Study site

Our study was conducted at one plantation of the Belgian FORBIO experiment (see www.treedivbelgium.ugent.be, Verheyen et al., 2013), located in the municipality of Zedelgem (51°9′N 3°7′E). The site was previously an agricultural field, which was intensively fertilized. Extensive soil sampling prior to planting (152 sampling points covering the entire site) showed high mean values of initial total P (1110 ± 175 mg/kg SD) and a low initial C:N ratio (13.50 ± 1.62) in the soil (Verheyen et al., 2010). The site was planted with five site-adapted tree species (*Betula pendula* Roth, *Fagus sylvatica* L., *Quercus robur* L., *Tilia cordata* Mill., and *Pinus sylvestris* L.) in spring 2010. The species differ, among other things, considerably in their leaf chemistry (see, e.g., Table 1). The design of the FORBIO plantations follows a classical synthetic community approach. Monocultures and mixtures of two up to four tree species were planted on an environmentally homogeneous site. For more detailed information about the design of the experiment and the planted species and provenances, we refer to Verheyen et al. (2013).

2.2. Leaf litter collection

Litter was collected from the five different tree species at the site in November 2011. Since the trees were still young, with small crowns, we could not collect enough freshly fallen litter. We used senescing leaves (i.e., withering-yellowish leaves that were still attached to the trees) for the broadleaved species and green needles formed during the last growing season for *P. sylvestris* (no brown needles were present yet). Thus, the nutrient reabsorption was probably not yet completed for the leaves and needles we used as litter in our litter bags. For each tree species, leaves were collected throughout the site (in both monocultures and mixtures) and then mixed. The collected litter was first air-dried for 1–2 weeks and then dried in a forced air oven at room temperature (25 °C) for 24 h.

For each species, the collected litter was analysed for its chemical composition: from each big bag, we randomly took three samples to analyse for total concentrations of C, N, P, Ca, Mg, and K; one sample per species was analysed for concentrations of lignin, cellulose, and hemicellulose. Prior to the chemical analysis, the litter was oven-dried (70 °C) until it reached constant weight and then ground using a centrifugal mill (Retsch ZM1, Germany). The Ca, K, and Mg concentrations were measured with flame atomic absorption spectrophotometry (Varian SpectrAA-240) after digestion with $HClO_4$ (65%) and HNO_3 (70%) in Teflon bombs for 4 h at 140 °C. The concentrations of C and N were measured by combustion at 1150 °C using an elemental analyser (Vario MACRO cube CNS, Elementar, Germany). The lignin, cellulose, and hemicellulose contents were determined using acid detergent fibre analysis (Van Soest et al., 1991).

2.3. Litterbags

The litterbags used in this experiment were constructed from 50 cm × 20 cm nylon nets with a 0.7 cm × 0.7 cm mesh size. This