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Is there a tree economics spectrum of decomposability?

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ABSTRACT

The plant economics spectrum (PES) integrates trade-offs and coordination in resource traits among species within and between organs, and affects ecosystem processes such as litter decomposition. This PES is currently based on trait variation among a wide range of plant types and growth forms. Here we ask whether the PES also features within the same growth form, i.e. within and between organs among temperate tree species. If so, is there a tree economics spectrum (TES) of decomposability driving the decomposition rates across the coarse branches, twigs and leaves of different species? And how robust would this TES of decomposability be to different environmental conditions?

To investigate these questions, we conducted a “common garden decomposition experiment” with ten temperate tree species in two contrasting forest environments in the Netherlands for 47 months. We evaluated the effects of functional traits of leaves, twigs, branch wood and branch bark on the decomposition rates of those organs. We measured the same resource traits for all those organs of the ten tree species and assessed whether there was a multivariate axis of functional traits explaining decomposition rates in both environments.

We report three key findings. First, tree organ specific economics spectra were significantly correlated with each other for the studied tree species. Second, tree organs differ significantly in decomposition rates, i.e. leaves were consistently more decomposable than twigs and twigs more than coarse branches. Third, we found some evidence of a TES with important afterlife effects driving coordinated decomposability of twigs and leaves but not of coarse branches across the tree species, and the effects of this TES on decomposition rates strongly depended on local forest environment.

The consistent contrasting decomposability between tree organs across species confirms an important role of plant litter inputs of different organs in forest biogeochemistry and carbon storage. There is also substantial coordination of interspecific trait variation between the finer tree organs. Knowledge about relationships of the TES and decomposability taking interactions with environmental variation into account can help for predicting whole-tree carbon and nutrient turnover as dependent on forest and soil type, even within the same climate zone.

1. Introduction

Plant litter decomposition is a major driver of carbon and nutrient cycling in terrestrial ecosystems (Parton et al., 2007), and affects local soil formation and global atmospheric composition (Canadell et al., 2007). Decomposition of plant material is strongly determined by climate (Berg et al., 1993; Parton et al., 2007), substrate quality (Aerts, 1997; Cornwell et al., 2008), and activity of soil organisms (Lavelle

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et al., 2006; Swift et al., 1979). These controls operate hierarchically to influence the decomposition. At regional to global scales, climate and litter quality were found as co-dominant factors (Cornwell et al., 2008; Wall et al., 2008; Bradford et al., 2016). Bradford et al. (2017) found decomposers strongly regulate decomposition at regional scales. Within biomes, climate often fails to predict decomposition rates (Bradford et al., 2014), while local environmental parameters, such as soil fertility, decomposer activity, and litter quality are strong predictors of the decomposition rates. On the plot scale, litter quality is known to explain much of the variation in decomposition rates, especially when measured as plant functional traits associated with plant acquisitive or conservative resource strategies (Chambers et al., 2000; Cornelissen et al., 2004; Cornwell et al., 2008; Weedon et al., 2009; Pietsch et al., 2014). Plant litter derives from different plant parts such as leaves, flowers, seeds, wood and bark. A wealth of information exists on leaf litter decomposition and the factors that drive their decay rates (e.g. Cornelissen et al., 1999; Cornwell et al., 2008; Makkonen et al., 2012). However, much less is known about the decomposition of twigs and coarse branches, although these woody plant components represent a substantial proportion of total litter fall and organically bound elements in forest soils (Harmon et al., 1986; Dearden et al., 2006; Chave et al., 2009; Cornwell et al., 2009). Moreover, the question arises if species with rapidly decaying leaf litter also have rapidly decaying twigs and branches; in other words whether organ specific decomposability within species covaries. Understanding the variation of decomposition within and between plant organs across species is of vital importance for predicting biogeochemical cycles under global change (Chapin et al., 2009; Brovkin et al., 2012; Pietsch et al., 2014).

Plant organs have marked differences in function, morphology, physiology and microenvironment, which imply a large variation in ecology and associated functional traits. If traits are coordinated among plant organs and affect decomposability, there might be a cross-species economics spectrum driving parallel decomposition relationships across plant organs. In one of the few studies on coordinated traits for litter decomposition, Freschet et al. (2012a) found a plant economics spectrum (PES) of litter decomposability which integrates trade-offs and coordination in resource traits among species within and between organs. They demonstrated that the PES had important afterlife effects on carbon turnover by driving coordinated decomposition rates of different organs (leaves, stem, roots) across a wide range of subarctic plants. However, this PES was investigated across a wide range of growth forms, from small herbaceous plants to large trees. Whether resource economic traits are also coordinated and affect decomposability across organs within a single growth form, as hypothesised by Reich (2014), has not been proven yet. Recent studies have not shown any convincing evidence in support of a PES within growth forms (Jackson et al., 2013; Pietsch et al., 2014; Zanne et al., 2015). For example, Zanne et al. (2015) found endogenous factors, including species identity and tissue construction, had stronger control on decay rates than exogenous factors across plant tissues. Perhaps one source of deviation from a general PES of decomposability is that it may manifest itself differently in different sites varying in other biotic (e.g. decomposer communities) and abiotic (e.g. soil, micro- and macroclimatic) drivers. Local forest environment may vary in both abiotic and biological parameters that determine decomposition. Trees can respond to abiotic conditions physiologically and biochemically and, as a consequence, produce litter of different qualities (Flanagan and Van Cleve, 1983; Hobbie, 1992). Soil moisture, and composition of both microbial and faunal decomposer communities, can directly influence the decomposition process (Bradford et al., 2002). The interactions with environment can confound the decomposition drivers.

The aim of this study was therefore to assess the effects of multiple abiotic and biotic factors, tree species, organ type and incubation environment, on decomposition rates across the three tree organs, i.e. leaves, twigs, and coarse branches, varying in resource trait values. We asked whether the PES also exists within the dominant growth form in forest ecosystems, as a tree economics spectrum (TES) in temperate forests. We hypothesise that if economics spectra are coordinated in dead tree crown organs, then the TES combining these organs might drive coordinated interspecific variation in the decomposabilities of different organs but this coordination might interact with environment. We expect, (1) leaves, twigs and branches of species with trait values reflecting an acquisitive resource strategy would decompose faster than those of species with a conservative resource strategy (*sensu* Freschet et al., 2012a; Reich, 2014; Diaz et al., 2016). Therefore, the predictive power of TES for decomposition will be consistent with each organ's specific economics spectrum. (2) At a local scale, decomposition is controlled by plant functional trait variation determining litter quality, heterogeneity in soil, microclimate and the decomposer community and their interactions (Hättenschwiler et al., 2005; Cornelissen et al., 2012; Freschet et al., 2012b; Bradford et al., 2014), however the effect strengths of functional traits and TES′ predictive power of decomposability will be robust to such interactions.

To test the hypothesis and predictions, we carried out a “common garden decomposition experiment” sensu Cornelissen (1996) studying the traits of different plant organs, i.e. leaves, twigs, branches (wood and bark), and the decomposition rates of those organs for 47 months, among ten co-occurring tree species in two contrasting temperate forest types and their environments on infertile sandy soil and fertile clayey soil.

2. Materials and methods

2.1. Study area and tree species

To test the impact of soil environment on decomposition of different plant organs, two environmentally contrasting sites were selected to represent two predominant temperate forest types and soils in NW Europe: (1) the Hollandse Hout forest plantation in Flevoland (hereafter site F) (Lat. 52.46 N, Long. 5.42 E) and (2) the forest estate Schovenhorst in the Veluwe region (hereafter site S) (Lat. 52.25 N, Long. 5.63 E). Both sites are located in the central part of the Netherlands. Site F was reclaimed from the former Zuiderzee in the 1960s; it has a relatively young marine clay soil, and is calcareous, moist and fertile, with a pH close to neutrality. This site mainly consists of monospecific plantations used for commercial forestry. In contrast, site S is much older and has a sandy and podzolic soil that is well-drained. The soil is acidic and has low fertility. Further site details are given in Cornelissen et al. (2012).

The incubation plot at site F was a relatively light-open *Populus x canadensis* Moench stand with a dense herb layer dominated by the nitrophylic herbs *Urtica dioica* L. and *Galium aparine* L. The incubation plot at site S was *a Larix kaempferi* (Lambert) Carriere stand that was also relatively light-open. It had a low and dense ground layer of predominantly the acidophilic grass *Deschampsia flexuosa* (L.) Trin. intermingled with mosses and patches of the dwarf shrub *Vaccinium myrtillus* L. More information about the incubation sites can be found above and in Cornelissen et al. (2012).

2.2. Sampling

Six tree species were sampled per site, with two species overlapping, giving in the two sites combined a total of ten species, i.e. six broadleaved and four coniferous species (see tree species list, extraction site and abbreviations in Table 1). All selected species are important and representative for NW European forests or forestry plantations. *Quercus robur* L. and *Picea abies* (L.) Karst. were sampled from both sites in order to compare the effects of growing conditions on intraspecific variability in plant organ functional traits and decomposability. Because the collection site had a significant effect on traits (Fig. S1, Supplementary material) and litter mass loss for *Q. robur* and *P. abies* (Table S1, Supplementary material), we treated the same species collected from two