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Litter decomposition in fynbos vegetation, South Africa

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ABSTRACT

The Western Cape of South Africa is characterized by the hyperdiverse vegetation of the Fynbos biome. Typical fynbos vegetation is a fire-adapted sclerophyllous Mediterranean-type ecosystem on poor, sandy or stony soils. It is characterized by plants with low nutrient content producing slowly decomposing litter. Fire is recognized as a major factor for carbon and nutrient cycling in this vegetation type. However, knowledge of biological decomposition processes in this biome is limited. We used litter-bags to measure mass loss and changes in chemical composition in litter from three species representing characteristic taxa in fynbos, a *Protea exima* hybrid, *Erica multumbellifera*, and *Restio multiflorus*, during approximately 180 days. In addition, we used a standard litter of a species with high nutrient content, *Galenia africana*, and a mixture of *Protea* and *Erica*. We compare our results with a previous study from renosterveld including the geophyte *Watsonia borbonica*, which occurs in both vegetation types and occurs commonly in the study area. We found that decomposition rate among the true fynbos plant species *P. exima*, *E. multumbellifera*, *R. multiflorus* and *W. borbonica* varied almost eight-fold. Litter decomposition was strongly correlated to litter stoichiometry, i.e. C/N and C/P-ratios. Most litters accumulated one or several nutrients during the study period. The mixture of litters decomposed faster than expected from the results of each litter separately. Our study indicates that biological decomposition may be more important for carbon and nutrient cycling in fynbos than previously thought. These results are in accordance with recent studies showing large variation in plant litter quality within vegetation types and biomes. Such large variation in litter quality and decomposition rate suggests that some generalisations about ecosystem processes in the fynbos may need reevaluation.

1. Introduction

Decomposition of plant litter is affected by variation in the substrate quality of litter, environmental conditions, and the composition of decomposer communities (Parton et al., 2007; Osler and Sommerkorn, 2007; Cornwell et al., 2008; Jonsson and Wardle, 2008; Carrillo et al., 2011). In contrast to what has previously been thought, recent studies have shown that decomposition rates appear to be more strongly affected by plant quality than by variation caused by environmental factors. Cornwell et al. (2008) found a 10.5-fold average difference in species decomposition rates within climate zones, which is twice as large as the variation in decomposition rate of common substrates attributable to different climate conditions. Large variation in leaf litter quality or decomposition among plant taxa has also been found locally within vegetation types and climate zones (e.g. Hättenschwiler et al., 2008; Kazakou et al., 2009; Wardle et al., 2009; Bengtsson et al., 2011). This variation in decomposition rates among plant species has been attributed to variation in ecological traits, such as leaf nutrient composition, associated with different plant strategies and phylogenetic groups (Cornwell et al., 2008). The dominant role of plant leaf and litter traits implies that previous generalisations about decomposition processes may need reevaluation in a variety of vegetation types and climatic regions.

The Western Cape of South Africa is characterized by the hyperdiverse vegetation of the Fynbos biome (Cowling and Lombard, 2002; Linder, 2003; Mucina and Rutherford, 2006). Typical fynbos vegetation is fire-adapted, sclerophyllous and occurs on poor, sandy or stony soils (Mucina and Rutherford, 2006). It is characterized by Proteaceae and Ericaceae shrubs, and the reed-like Restionaceae, but it also contains a diversity of geophytes, and in drier areas short-lived annuals (Manning, 2007). Several other vegetation types are found in the Fynbos biome, one of which is the renosterveld, which occurs on richer soils and is also fire-prone (Rebelo et al., 2006). In a previous

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study, we found a 20-fold difference in decomposition rate between three representative plant species from renosterveld (Bengtsson et al., 2011). Here we extend these results to the true fynbos vegetation. Biological decomposition of typical fynbos plant species has previously been suggested to be very low, and carbon and nutrient dynamics dependent upon the periodic fires characteristic of fynbos (Mitchell et al., 1986; Witkowski, 1991; Stock and Allsopp, 1992). However, the considerable diversity of plant species and functional types within a given area of fynbos (e.g. Cowling et al., 1997; Cowling and Lombard, 2002) suggests that plant litter quality and hence biological decomposition may vary between functional types of plants within sites, in a way similar to that found in renosterveld (Bengtsson et al., 2011). As a consequence, biological decomposition by soil fauna and microbial communities may have been underestimated and deserve more attention. For example, nutrient turnover of plant litter with higher nutrient content may be much faster and less dependent on fire than is the case for the previously studied nutrient-poor species in the Proteaceae and Restionaceae (e.g. Mitchell et al., 1986; Mitchell and Coley, 1987; Witkowski, 1991).

In this paper, we examine whether species-specific differences in first-year decomposition rates of three representatives of major fynbos taxa, as measured by organic matter mass loss, are related to their nutrient content (carbon-to-nutrient ratios), as an indicator of plant litter quality. The species we studied represent the natural range of litter nutrient content and life forms in this biome (see below and van Wilgen and le Maitre, 1981; Mucina and Rutherford, 2006). We also investigate changes in nutrient content of the different plant litters during decomposition, and whether litter from different plant species decomposes faster when placed in vegetation dominated by their own functional type rather than vegetation dominated by another functional type, i.e. if a home field advantage (Ayres et al., 2009) exists. We compare these results with a standard litter used previously (*Galenia africana*) in our investigations of decomposition in renosterveld (Bengtsson et al., 2011). Finally, because plant litter seldomly occurs as a monoculture in the diverse fynbos vegetation, we determine whether a mixture of litters from two characteristic fynbos taxa with different quality decomposes at rates different to those expected from the single species litters. Increased decomposition would be expected if, for example, nutrients such as nitrogen from the more nutrient-rich litter is used by decomposers utilizing the nutrient-poor litter (e.g. Gartner and Cardon, 2004).

2. Materials and methods

2.1. Study site, plant species and sampling methods

The study was carried out from mid-March to mid-September 2008, during the South African winter, using methods described in detail in Bengtsson et al. (2011). This part of South Africa has a Mediterranean climate with cool, wet winters and hot, dry summers. While studying springtail (Collembola) abundance and diversity, we also recorded mass loss and changes in chemical composition of litter of four plant species placed in litter-bags. Three of the species represented three major components of the fynbos vegetation type in the Western Cape, South Africa, viz. Ericaceae, Proteaceae and Restionaceae. In addition we used a shrub species characteristic of disturbed areas, *G. africana*, and a litter mixture of the Ericaceae and Proteaceae species.

The four plant species used were: (1) The hybrid *Protea exima* × *Protea susannae*, var. 'silva' and 'cardinal'; (2) *Erica multumbellifera*. For conservation reasons, as the study was carried out in a nature reserve, and to obtain litter of standard quality, *E. multumbellifera* was collected from Heuningkloof farm in Kleinmond, while the *Protea* was obtained from Flower Valley Farm, Gansbaai. The plants from which we derived the litter may have received some fertilizer in a previous growing season, although no clear information on this was available; (3) *Restio multiflorus*, which was collected from a field site on Whitewater Lodge estate close to Stanford; (4) *G. africana* (Aizoaceae), which is a common shrub in the Western Cape, and an indicator of disturbance such as overgrazing (Allsopp, 1999; Todd and Hoffmann, 1999). It is toxic to sheep and goats (Van der Lugt et al., 1992; Vries et al., 2005) and has been argued to enrich soils under its canopy with nitrogen and phosphorus (Allsopp, 1999; Simons and Allsopp, 2007). This species was collected from an overgrazed rangeland west of the Paarl mountain. *G. africana* is usually not found in true fynbos, but we used it for two reasons: First, we wanted to have a standard litter to be able to compare decomposition across sites and between years, and second because we wanted to include a nutrient-rich litter in the fynbos study, in a similar way as done previously in renosterveld (Bengtsson et al., 2011). All litters were obtained from live plants at the end of the dry season, and hence partly senescent; for practical reasons it was not possible to gather litter by litterfall traps over an extended period.

The study site consisted of three plots in the Jonkershoek Nature Reserve close to Stellenbosch, South Africa (S33° 58.809′, E18° 56.862′). All plots were situated in natural fynbos vegetation, but in different vegetation types, viz. proteoid, ericoid or restioid, respectively. The proteoid plot was dominated by *Protea nitida*, the ericoid by *Erica hirta*, *and* the restioid plot by *Elegia capensis*. In each plot we selected 10 shrubs or tufts along an L-shaped transect with approximately 10 m between each shrub. Under each shrub (tuft) 5 litter-bag traps filled with different litters were placed – four with single species and one with the mixture. The traps were placed in the soil with the top of the trap at ground level, within 3–4 cm from each other and less than 40 cm from the shrub base on the south-west to south-east side to minimise sun exposure.

The litter-bags were individually numbered cylindrical plastic containers with a height of 4 cm and a diameter of 7.5 cm (Bengtsson et al., 2011). The bottom consisted of a steel net with mesh size 0.5 mm. The traps had a removable lid with 1.6 mm mesh size to allow animals to enter the trap. In the laboratory they were filled with well-mixed air-dried litter up to approx. 3.5 cm, which had been weighed to nearest 0.1 mg on an electronic balance (FA304T, Avery Berkel, Fairmont, USA). The litter was not compressed and was allowed to maintain its normal volume and density.

The litter-bag traps were placed in the field on 10 March 2008 and were collected on 8 or 17 September 2008, i.e. after 182 and 191 days respectively. Trap sets 1–5 from each of the sites were sampled on the first date, and sets 6–10 on the second date. This was done for extraction capacity reasons, because soil fauna was also collected. The traps were brought into the laboratory and treated as in Bengtsson et al. (2011). Total C and N concentrations were determined using a Carlo-Erba NA 1500 Elemental Analyzer, while P, K, Na, Mg and Ca were measured by Inductively Coupled Plasma Atomic Spectroscopy (see Bengtsson et al., 2011). Two samples were accidentally mislabelled during the chemical analyses and therefore excluded from the data set.

2.2. Statistics

We measured mass loss as the loss of organic matter from each litter-bag. Mass loss was determined using ash free dry weight measurements. To compare our results with other studies, we also calculated the decomposition constant k assuming the exponential decomposition model (Olson, 1963), i.e. $W_t = W_0\, e^{-kt}$, where W_0 is the mass of organic matter at the start of the experiment and W_t is the mass of organic matter at the end (t = 182 or 191 days). The constant k has unit day^{-1} and was calculated for each litter-bag.