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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.

Carbon-to-nutrient ratios were calculated on a weight basis using the data from the chemical analyses. All variables were square-root-transformed before statistical analysis.

The data were analysed with a split-plot analysis of variance, with Vegetation Type (Proteoid, Ericaceaous or Restioid) as whole plots, with the error term Vegetation Type*Shrub ID, and Litter Type (5 levels) as the split-plot factor with the residual as error term. The interaction between Litter Type and Vegetation Type was included in all models, with the residual as error term. The approximately balanced design of the present study ($n = 29$ or 30 in all litter treatments) means that the split-plot model gives essentially the same results as a mixed model (GLMM). The analyses were undertaken with the SuperAnova program for Macintosh (Abacus inc., 1918 Bonita Ave. Berkeley, CA). To examine relationships between mass loss and C/nutrient ratios in the original litter, we used Microsoft Excel spreadsheet functions.

2.3. Analysis of decomposition of mixed vs. single species litter

To determine whether mixed Protea–Erica litter had higher mass loss than expected from the mass loss from the two single litters, we employed a randomization test using Microsoft Excel spreadsheets. The procedure assumed that there was no effect of vegetation type on decomposition, an assumption that is fulfilled in our case (Table 2a). From the 29 single litter litter-bags of each species we randomly chose 29 combinations of mass loss values, and calculated the expected mass loss in the mixed litter-bags based on the average initial proportion of Erica litter in the mixed litter-bags, which was 55.7%. From these values we calculated the expected mean mass loss and its standard deviation. The expected and the observed mass loss in mixed litter-bags was compared using a t-test with df $= 2*(29 - 1) = 56$ and $t_{0.05,56} = 2.01$ (following Sokal and Rohlf, 1991). It was noted if the difference between expected and observed mass loss was significant at the $p = 0.05$ level. This procedure was repeated 100 times, each time with a new set of randomly selected combinations of single litters, and the proportion of significant t-tests was used as an indicator whether mass loss was higher from mixed litters than expected from single species litter-bags. In our case, there were no instances when the t-test was non-significant, so we stopped the randomization test after 100 iterations.

3. Results

Mass loss during the six month period (≈ 185 days) differed almost 7-fold between the four species (Table 1). Litter type (including the mixture) explained most of the variation in decomposition (Table 2). All differences between single species litters were significant (Tukey–Kramer tests, $p < 0.05$). There was no significant effect of vegetation type or the litter type*vegetation type interaction (Table 2a). Hence we found no support for different litter types decomposing faster when placed in vegetation dominated by their own plant functional type.

The standard litter of the non-fynbos species G. africana decomposed the quickest, losing almost 70% of its organic matter mass during the study period. The Protea hybrid decomposed fastest of the fynbos plants, losing approximately 35% of the initial mass. R. multiflorus decomposed the slowest, with only about 10% of the initial mass disappearing, while E. multumbellifera was intermediate with a mass loss of 25% (Table 1). The decomposition constant k showed similar variation, with an almost 4-fold difference between the three true fynbos species (Fig. 1; black dots). These values correspond to litter half-lives (calculated as $0.693*k^{-1}$; Olson, 1963) of 108, 297, 462 and 1136 days for Galenia, Protea, Erica and Restio, respectively.

Decomposition was 14.6% faster in the mixed Protea/Erica litter than expected from the two single species litters (Table 1; Fig. 1). This difference is statistically significant, as shown by the randomization test. We found a significant difference between the observed and expected mass loss (as examined with t-tests) in all of the 100 randomizations. In the split-plot ANOVA, mass loss of the mixed litter was significantly higher than that of Erica litter (Table 1; Tukey–Kramer test, $p < 0.05$), but did not differ significantly from the slightly faster decomposing Protea litter (Table 1; Tukey–Kramer test, ns).

Combining the present data with previous results from renosterveld (Bengtsson et al., 2011), a strong negative relationship was found between decomposition rate k and initial C/N-ratio (Fig. 1), which was well described by the equation $k = 0.0095 \, e^{-0.0225 \, (C/N\text{-ratio})}$ ($r^2 = 0.87$). Similar negative relationships were found between k and initial C/P ratio, as well as for C/Mg and C/Na. However, it was not meaningful to calculate separate relationships between k and the other nutrients because the concentrations of different nutrients and consequently C/nutrient ratios in the initial litter were highly collinear (e.g. N and P content, $r = 0.987$, $n = 8$, $p < 0.001$; Appendix 3 for other nutrients). Because of this high collinearity it is not possible to examine the relative importance of the different nutrients for decomposition rate.

Significant effects were found of plant litter type on carbon-to-nutrient ratios at the end of the study (Tables 2 and 3; Appendix 1 and 2). C/N-ratios differed significantly between all litters (Tukey–Kramer tests, $p < 0.05$) while C/P-ratios did not differ

Table 1

Mass loss (proportion organic matter mass lost from litter-bags during ≈ 185 days) of plant litter of four species, the standard litter Galenia africana, three representatives of major components of fynbos vegetation (Erica, Protea and Restio), and the mixture of Protea and Erica. See Fig. 1 for k-values. $n = 30$ (29 for Erica and Protea). *Mass loss data for the species Watsonia borbonica placed in the renosterveld for 182 days, from Bengtsson et al. (2011), has been added for comparison but is not included in the statistical tests.

Species	Mass loss	SE
Galenia africana	0.6904	0.00792
Erica multumbellifera	0.2420	0.00810
Protea exima × susannae	0.3503	0.00810
Mixture Protea/Erica	0.3234	0.00792
Restio multiflorus	0.1072	0.00792
Watsonia borbonica*	0.0950	0.00952

All differences between litters were significant (Tukey–Kramer tests $p < 0.05$) except the difference between Protea and the mixture. The effects of vegetation type and the interaction between litter type and vegetation were not significant (See Table 2 for statistics).

Table 2

Results from split-plot ANOVAs of effects of plant litter type and vegetation type on (a) mass loss and (b) final litter C/N-ratio. The dependent variables were square-root-transformed prior to analysis. Vegetation type was used as whole plot, with the error term Vegetation Type*Shrub ID, while Litter Type was the split-plot factor with the residual as error term.

| Factor	df	SS	F	p <
(a) Mass loss				
Vegetation type	2	0.02213	2.10	0.135 ns
Vegetation type*Shrub ID	27	0.13816		
Litter type	4	4.10127	559.1	0.0001
Litter type*Vegetation Type	8	0.01838	1.253	0.28 ns
Residual	106	0.19440		
(b) Final C/N-ratio				
Vegetation type	2	2.601	5.099	0.013
Vegetation type*Shrub ID	27	6.885		
Litter type	4	545.4	1120	0.0001
Litter type*Vegetation Type	8	2.544	2.611	0.012
Residual	106	12.91		
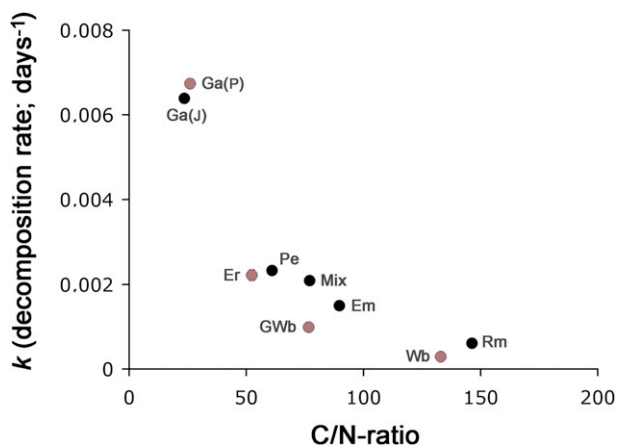
Fig. 1. Relationship between initial litter quality, measured as C/N-ratio, and decomposition rate *k* in litters from the experiment in fynbos vegetation in Jonkershoek (this study; black dots; J) and in litters from renosterveld near Piketberg, South Africa (Bengtsson et al., 2011; red dots; P). Standard errors of the means are smaller than the size of the dots. Litters are the standard litter of *Galenia africana*, Ga(J) and Ga(P), *Elytropappus rhinocerotis*, Er (P), *Protea exima* × *susannae*, Pe (J), green *Watsonia borbonica*, GWb (P), mixture of Pe and Em (J), *Erica multumbellifera*, Em (J), brown *W. borbonica* leaves Wb (P), and *Restio multiflorus*, Rm (J). The exponentially decreasing relationship is described by the equation $k = 0.0095\,e^{-0.0225\,(C/N-ratio)}$ ($r^2 = 0.87$). Data for green Watsonia (GWb) from J. Bengtsson, C. Janion, S.L. Chown, H.P. Leinaas (unpublished). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significantly between *Protea*, *Erica* and the mixture. Both *Galenia* and *Restio* differed from all the other species. C/N-ratios had decreased in all litters, while C/P-ratio showed a different pattern, with decreases in the *Protea*, mixture and *Restio* but no clear changes in *Galenia* and *Erica* litter (Table 3; this table also contains nutrient concentrations of N and P, which changed as a consequence of the changes in C/N and C/P-ratios). There was a significant effect of vegetation type on final C/N-ratio, which became slightly lower at the *Protea* site than at the two other sites. Nevertheless, litter type was by far the most important factor explaining variation in this ratio, *F*-values differing more than 200-fold (Table 2). The total amount of nitrogen at the end of the study period had increased by 7–31 % in all litters except *Galenia*, from which 64% of the N had been lost from the litter-bags during decomposition. By contrast, the total amount of P had increased only in *Restio* litter-bags, and there by almost 100%.

Final C/Ca and C/Mg-ratios differed significantly between all litters (Tukey–Kramer tests, $p < 0.05$), while C/K and C/Na mainly differed between *Galenia* and the other species, but also between *Erica* and *Restio*. C/K and C/Na-ratios showed large increases over time in all litters. In contrast, C/Mg-ratio increased in *Galenia* but decreased in the other litters, and C/Ca decreased in all litters (Appendix 1 and 2). The other nutrients than N and P had usually

been lost from all litter-bags, with the exception of Ca and Mg in the *Restio* litter-bags.

4. Discussion

Many characteristic plant species of the fynbos decompose slowly (Stock and Allsopp, 1992). Indeed, earlier decomposition studies from the fynbos found low decomposition rates (*k*-values<0.001 day⁻¹) and low nutrient content of plants (usually C/N > 80 and C/P > 1000; Mitchell et al., 1986; Mitchell and Coley, 1987; Witkowski, 1991). By contrast, recent studies have indicated large differences in decomposition rate between plant species within vegetation types and climatic regions (biomes) (e.g. Cornwell et al., 2008; Kazakou et al., 2009; Wardle et al., 2009; Bengtsson et al., 2011). Several of the plant species we used had both higher nutrient content and faster decomposition rates than those in previous studies of decomposition in fynbos. Thus our studies show a substantially wider range in decomposition rates of plants from the Fynbos biome than previous studies have suggested (references above; Bengtsson et al., 2011). Although some of the differences between our study and previous ones may be due to the fact that we collected *Protea* and *Erica* leaf litter at a nursery, our results provide evidence for substantial variation in decomposition rates within the fynbos vegetation type, and differ from previous results showing generally slow decomposition rates in fynbos. In particular, if we include the decomposition rate of *Watsonia borbonica* from Bengtsson et al. (2011), which is a species occurring in both fynbos and renosterveld, the difference between fynbos plants found by us is almost 8-fold (*k*-values from 0.0003 to 0.0023 day⁻¹) (Note: This comparison is justified because the decomposition rate of the standard litter *G. africana* was so similar between the years and sites; Fig. 1). Nutrient levels in fynbos plants have been found to vary both among plant species and with soil conditions (van Wilgen and le Maitre, 1981). Our study spans the range of nutrient concentrations and life forms included in previous studies, and can hence be considered representative in a general sense. For example, recalculated values of C/N-ratios derived from van Wilgen and le Maitre (1981, Table 2) vary 3.6-fold, and the species studied by us are distributed over most of this range. Nonetheless, it is clear that further studies on a wider range of species and sites are needed to assess the degree to which decomposition rates vary in the Fynbos biome. The large variation in decomposition rate among species from fynbos vegetation found by us, as well as the large variation in fynbos plant nutrient concentrations found by van Wilgen and le Maitre (1981), suggests that previous generalisations about decomposition processes in the Fynbos biome may need reconsideration. It also highlights the importance of understanding the ways in which plant leaf and litter traits result in different rates of decomposition, based on an understanding of plant strategies and plant functional types (Lavorel and Garnier, 2002; Cornwell et al., 2008).

Table 3
Initial and final C/N and C/P-ratios, and N and P concentrations as % of organic matter, in four plant litter types and a mixture of *Protea* and *Erica* after ≈185 days. The initial litter was well-mixed, while for final values ± SE represent the variation between litter-bags. See Table 1 for *n*-values and species names, *p*-values refer to an overall difference in C/nutrient ratios between plant litters after 185 days (Table 2 and Appendix 2).

Variable	Litter type					$p <$
	Galenia	Erica	Protea	Mixture	Restio	
Initial C/N	23.6	89.7	61.0	77.0	146.4	
% N	2.12	0.557	0.820	0.649	0.342	
Final C/N	21.0 ± 1.16	66.5 ± 1.19	34.7 ± 1.19	46.5 ± 1.16	103.7 ± 1.16	0.001
% N	2.41 ± 0.057	0.76 ± 0.012	1.44 ± 0.021	1.08 ± 0.008	0.49 ± 0.015	
Initial C/P	295.5	1390.9	1274.6	1339.4	6956.5	
% P	0.169	0.0359	0.0392	0.0373	0.00719	
Final C/P	326.3 ± 96.0	1237 ± 98.2	1057 ± 98.2	1139 ± 96.0	3682 ± 96.0	0.001
% P	0.164 ± 0.0087	0.041 ± 0.0009	0.047 ± 0.0111	0.044 ± 0.0010	0.016 ± 0.0014	

A strong relationship was found here between plant stoichiometry, i.e. C/N or C/P-ratio, and decomposition rate during the first-year wet season in our combined data (Fig. 1). Whether decomposition rates are best related to nutrient concentrations in the litter, environmental conditions, or the carbon fractions in the litter has been the subject of much discussion (e.g. Enríquéz et al., 1993; Aerts, 1997; Joffre and Ågren, 2001). The meta-analysis of Cornwell et al. (2008) suggested that litter nutrient content as well as carbon fractions are important for explaining variation in decomposition rate, and that the role of environmental conditions related to climate may have been overemphasised relative to plant traits. In the fynbos, nutrient limitation of plant growth is pervasive, although it is unclear which nutrients are most limiting (e.g. Witkowski, 1989; Richards et al., 1997). In any case, until more detailed studies are carried out it seems reasonable to use a measure of nutrient content, e.g. C/N-ratio, as an indicator of decomposition rate in this biome. Hence, the high diversity of species in fynbos may lead to a larger variation of decomposition rates than previously thought.

The mixed litter decomposed faster than expected from the single *Protea* and *Erica* litters. Although by no means ubiquitous, increased decomposition of litter mixtures has often been observed (Gartner and Cardon, 2004; Chapman and Koch, 2007; Jonsson and Wardle, 2008; Wardle et al., 2009); approximately 65% of the studies reviewed by Gartner and Cardon (2004) found this pattern. One possible mechanism for such an effect is the movement of nutrients among litters, with the higher quality litter stimulating the decomposition of the lower quality one, either by biological processes or by leaching (Gartner and Cardon, 2004). For example, nitrogen-limited decomposer fungi may use nitrogen from the more nutrient-rich *Protea* litter when acquiring energy from the *Erica* litter. The observation that mixing of litter may increase decomposition suggests that interactions between co-occurring litters may need to be taken into account when examining soil biological processes in fynbos.

To conclude, our studies from fynbos and renosterveld in the Fynbos biome in South Africa found 8- to 20-fold differences, respectively, in first-year decomposition rates between plant species representing several important taxa and functional types in these vegetation types (this study, Bengtsson et al., 2011). Both vegetation types are fire-prone, with fire intervals of 10–20 years in natural fynbos (on average 11 years; van Wilgen, 2009). Hence fires are clearly important for ecosystem processes in this biome, as shown by previous authors (e.g. Stock and Allsopp, 1992). However, the observed variation in litter quality and decomposition rates found in the present study (see also van Wilgen and le Maitre, 1981) suggests that biological decomposition may still be important for carbon and nutrient cycling between fire events. Biological decomposition is especially likely for plants with higher nutrient contents, such as *G. africana*, renosterbos *Elytropappus rhinocerotis* and the *Protea* species used here, which had litter half-lives of less than one year. Biological carbon and nutrient cycling may be most important in the years immediately after fires, when fynbos vegetation shows many adaptations that result in rapid regrowth and recovery after fire (e.g. Richardson and van Wilgen, 1992) and nutrient levels in the soil are likely to be higher (Stock and Lewis, 1986). Long-term studies examining a larger set of species during succession after fire are needed for a better understanding of the relative roles of fire and biological decomposition as well as other ecosystem processes in this biome.

Acknowledgements

Appendix. Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.soilbio.2011.11.023.

References

Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79, 439–449.

Allsopp, N., 1999. Effects of grazing and cultivation on soil patterns and processes in the Paulshoek area of Namaqualand. Plant Ecology 142, 179–187.

Ayres, E., Steltzer, H., Simmons, B.L., Simpson, R.T., Steinweg, J.M., Wallenstein, M.D., Mellor, N., Parton, W.J., Moore, J.C., Wall, D.H., 2009. Home-field advantage accelerates leaf litter decomposition in forests. Soil Biology and Biochememistry 41, 606–610.

Bengtsson, J., Janion, C., Chown, S.L., Leinaas, H.P., 2011. Variation in decomposition rates in the Fynbos biome, South Africa: the role of plant species and plant stoichiometry. Oecologia 165, 225–235.

Carrillo, Y., Ball, B.A., Bradford, M.A., Jordan, C.F., Molina, M., 2011. Soil fauna alter the effects of litter composition on nitrogen cycling in a mineral soil. Soil Biology and Biochemistry 43, 1440–1449.

Chapman, S.K., Koch, G.W., 2007. What type of diversity yields synergy during mixed litter decomposition in a natural forest ecosystem? Plant and Soil 299, 153–162.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.H., Hoorens, B., Kurokawa, H., Perez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., can Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Diaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.N., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11, 1065–1071.

Cowling, R.M., Lombard, A.T., 2002. Heterogeneity, speciation/extinction history and climate, explaining regional plant diversity patterns in the Cape Floristic Region. Diversity and Distributions 8, 163–179.

Cowling, R.M., Richardson, D.M., Muster, P.J., 1997. Fynbos. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), The Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp. 99–130.

Enríquéz, S., Duarte, C.M., Sand-Jensen, K., 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia 94, 457–471.

Gartner, T.B., Cardon, Z.G., 2004. Decomposition dynamics in mixed-species leaf litter. Oikos 104, 230–246.

Hättenschwiler, S., Aeschlimann, B., Coûteaux, M.-M., Roy, J., Bonal, D., 2008. High variation in foliage and leaf litter chemistry among 45 tree species of a neotropical rainforest community. New Phytologist 179, 165–175.

Joffre, R., Ågren, G.I., 2001. From plant to soil: litter production and decomposition. In: Roy, J., Saugier, B., Mooney, H.A. (Eds.), Terrestrial Global Productivity. Academic Press, pp. 83–99.

Jonsson, M., Wardle, D.A., 2008. Context-dependency of litter-mixing effects on decomposition and nutrient release across a long-term chronosequence. Oikos 117, 1674–1682.

Kazakou, E., Violle, C., Roumet, C., Pintor, C., Gimenez, O., Garnier, E., 2009. Litter quality and decomposability of species from a Mediterranean succession depend on leaf traits but not on nitrogen supply. Annals of Botany 104, 1151–1161.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16, 545–556.

Linder, H.P., 2003. The radiation of the Cape flora, southern Africa. Biological Reviews 78, 597–638.

Manning, J., 2007. Field Guide to Fynbos. Struik, Cape Town, South Africa.

Mitchell, D.T., Coley, P.G.F., 1987. Litter production and decomposition from shrubs of *Protea repens* growing in sand plain lowland and mountain fynbos, south-western Cape. South African Journal of Botany 53, 25–31.

Mitchell, D.T., Coley, P.G.F., Webb, S., Allsopp, N., 1986. Litter fall and decomposition processes in the coastal fynbos vegetation, south-western Cape, South Africa. Journal of Ecology 74, 977–993.

Mucina, L., Rutherford, M.C. (Eds.), 2006. The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African national Biodiversity Institute, Pretoria.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322–331.

Osler, G.H.R., Sommerkorn, M., 2007. Toward a complete soil C and N cycle: incorporating the soil fauna. Ecology 88, 1611–1621.

Parton, W., Silver, W.L., Burke, I.C., Grassens, L., Harmon, M.E., Currie, W.S., King, J.Y., Adair, E.C., Brandt, L.A., Hart, S.C., Fasth, B., 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315, 361–364.

Rebelo, A.G., Boucher, C., Helme, N., Mucina, L., Rutherford, M.C., 2006. Fynbos biome. In: Mucina, L., Rutherford, M.C. (Eds.), The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria, pp. 52–219.

Richards, M.B., Stock, W.D., Cowling, R.M., 1997. Soil nutrient dynamics and community boundaries in the Fynbos vegetation of South Africa. Plant Ecology 130, 143–153.

Richardson, D.M., van Wilgen, B.W., 1992. Ecosystem, community and species response to fire in mountain fynbos: conclusions from the Swartboskloof experiment. In: Van Wilgen, B.W., Richardson,, D.M., Kruger, F.J., Hensbergen, H.J. (Eds.), Fire in South African Fynbos. Springer, pp. 273–284.

Simons, L., Allsopp, N., 2007. Rehabilitation of rangelands in Paulshoek, Namaqualand: understanding vegetation change using biophysical manipulations. Journal of Arid Environments 70, 755–766.

Sokal, R.R., Rohlf, F.J., 1991. Biometry, second ed. Freeman, New York.

Stock, W.D., Allsopp, N., 1992. Functional perspective of ecosystems. In: Cowling, R.M. (Ed.), The Ecology of Fynbos: Nutrients, Fire and Diversity. Oxford University Press, Cape Town, pp. 241–259.

Stock, W.D., Lewis, O.A.M., 1986. Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. Journal of Ecology 74, 317–328.

Todd, S.W., Hoffmann, M.T., 1999. A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. Plant Ecology 142, 169–178.

Van der Lugt, J.J., Schultz, R.A., Fourie, N., Hon, L.J., Jordaan, P., Labuschagne, L., 1992. *Galenia africana* L. poisoning in sheep and goats: hepatic and cardiac changes. Journal of Veterinary Research 59, 323–333.

van Wilgen, B.W., le Maitre, D.C., 1981. Preliminary estimates of nutrient levels in fynbos vegetation and the role of fire in nutrient cycling. South African Forestry Journal 119, 24–28.

van Wilgen, B.W., 2009. The evolution of fire and invasive alien plant management practices in fynbos. South African Journal of Science 105, 335–342.

Vries, F.A., El Bitar, H., Green, L.R., Klaasen, J.A., Mabulesa, W.T., Bodo, B., Johnson, Q., 2005. An antifungal active extract from the aerial parts of *Galenia africana*. In: Midiwo, J.O., Yenesew, A., Derese, S. (Eds.), 11th NAPRECA Symposium Book of Proceedings, Antananarivo, Madagascar, 2005. Napreca, Nairobi, Kenya, pp. 123–131. www.napreca.net.

Wardle, D.A., Bardgett, R.A., Walker, L.R., Bonner, K.I., 2009. Among and within plant species variation in plant litter decomposition in contrasting long-term chronosequences. Functional Ecology 23, 442–453.

Witkowski, E.T.F., 1989. Effects of nutrient additions on litter production and nutrient return in a nutrient-poor Cape fynbos ecosystem. Plant and Soil 117, 227–235.

Witkowski, E.T.F., 1991. Effects of invasive alien acacias on nutrient cycling in the coastal lowlands of the Cape fynbos. Journal of Applied Ecology 28, 1–15.