Plant traits relate to whole-community litter quality and decomposition following land use change

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Summary

1. Given the speed and extent of changes in vegetation as a result of human activity, there is a need to investigate ways in which individual species’ impacts on ecosystem processes can be generalized and scaled-up to the community level.
2. We focus on linking community functional parameters (mean of the traits of the plants in the community, weighted using four different methods) with litter chemistry and decomposition, in a chronosequence of currently managed and abandoned semi-natural grasslands in southern Sweden.
3. Changes in plant community composition with age since abandonment were reflected in community functional parameters: as expected, aggregated specific leaf area (SLA) declined, and aggregated leaf dry matter content (LDMC) and leaf carbon : nitrogen ratio (C : N) increased with plot age.
4. Several litter chemistry indices were closely linked with plant traits at the community level; in particular, community aggregated LDMC was correlated with the lignin and fibre content of the community litter.
5. Aggregated LDMC stood out as the trait most closely linked to community litter decomposition. This relationship was consistent across all three incubation periods (by which time up to c. 70% mass loss had occurred) and as strong as that between the best single chemical index of litter quality (lignin : N ratio) and litter mass loss.
6. Mass loss of whole community litter, incubated in its plot of origin, was related to mass loss of the same litter incubated under standard conditions, but not to decomposition of a standard substrate, indicating dominant substrate quality control over decomposition.
7. This study demonstrates the potential of the traits of living plants as a tool to link changes in species composition with ecosystem processes at the community level.

Key-words: specific leaf area, leaf dry matter content, nitrogen, lignin, ecosystem process

Introduction

A major goal in ecology is to understand and predict the impacts of (human induced) changes in the structure, diversity and composition of plant communities on ecosystem processes. Although the impacts of individual species, via their functional characteristics or traits, on processes such as decomposition, nutrient cycling and productivity are becoming well established (Zinke 1962; Pastor & Post 1988; Wedin & Tilman 1990; Hobbie 1992; Wardle et al. 1997; Eviner 2004), there are very few tests of the links between species’ traits and ecosystem processes at the level of whole, natural plant communities (Garnier et al. 2004, 2006).

Here, we focus on the consequences of shifts in vegetation as a result of land use change for decomposition processes. Land use change is one of the most important elements of anthropogenic impacts on the earth’s ecosystems (Vitousek et al. 1997). Specifically, in southern Sweden, abandonment of former grazing areas has been substantial, resulting in an estimated 90% reduction in the area of semi-natural grasslands over the last 80 years, with associated changes in species composition (Cousins 2001; Eriksson & Ehrlén 2001; Eriksson, Cousins & Bruun 2002). We consider the implications of these plant community changes for decomposition, a key ecosystem process determining...
stocks and fluxes of carbon and nutrients in ecosystems (Swift, Heal & Anderson 1979), with important consequences for feedbacks to the atmosphere and the global climate (Grace 2004).

Biochemical indices such as contents of lignin, nitrogen and phenolics have long been known to be a major control on rates of litter decomposition, determining the quality of the substrate as a resource for decomposer organisms (Swift et al. 1979; McClaugherty et al. 1985; Berg & Ekbohm 1991; Heal, Anderson & Swift 1997; Wardle 2002). These links have been extended over the past 10 years in comparative studies connecting the litter quality and decomposition of single species litters to the functional traits of living plants. Traits investigated to date include specific leaf area (SLA; leaf area divided by dry mass) (Cornelissen & Thompson 1997; Cornelissen et al. 2006), leaf dry matter content (LDMC; dry mass divided by fresh mass) (Kazakou et al. 2006), and measures of the physical strength of leaves (e.g. leaf toughness, i.e. the pressure required to puncture a leaf (Gallardo & Merino 1993) or leaf tensile strength, that is, resistance to tearing (Cornelissen & Thompson 1997). The primary goals of these studies are to connect the functioning of living vegetation (including the growth–defence trade-off) with effects on the decomposer system and biogeochemical cycles, and to find simple and cost-effective correlates for intra-specific variation in decomposition.

In this study, we build on these findings, and assess whether functional trait–decomposition relationships can be useful for understanding changes in in-situ ecosystem processes. The ‘biomass ratio hypothesis’ provides a key to linking the traits of individual species to ecosystem processes, and proposes simply that the proximate effect of a species’ traits on an ecosystem property is likely to be strongly related to the contribution of the species to the total biomass of the community (Grime 1998). Thus, a mean of the traits of the species present, weighted by their contribution to the community (‘community functional parameter’, Violle et al. 2007), should be related to ecosystem processes (Lavorel & Garnier 2002; Garnier et al. 2004). This approach requires that the traits chosen adequately represent the species’ immediate effects on the ecosystem process in question, and that non-additive interactions are unimportant. To date the biomass ratio hypothesis has not been extensively tested (but see Garnier et al. 2004, 2006), and important questions remain regarding its applicability in a range of systems, and the relative roles of litter quality and the decomposition environment. Plant species can influence decomposition processes not only via variation in substrate quality (e.g. Cornelissen 1996), but also via effects on the physico-chemical environment or the soil decomposer community (Eviner & Chapin 2003; Wardle et al. 2003; Hobbie et al. 2006). In order to test the extent to which a single suite of litter quality related traits can be a useful indicator of changes in decomposition, it is necessary to separate the relative roles of substrate quality and the decomposition environment.

The aim of this study is to test links between a key ecosystem process (decomposition of whole-community, above-ground plant material) and the traits of the species present, in the context of land abandonment in southern Sweden. We focus on three plant leaf functional traits: SLA, LDMC, and the C : N ratio of living leaves. This selection is based on links to the roles of plant species in processes determining biogeochemical cycles, including production (Reich, Walters & Ellsworth 1992; Cornelissen, Diez & Hunt 1996; Shipley et al. 2005) and decomposition (Cornelissen et al. 2006; Kazakou et al. 2006). To separate the relative contributions of litter quality and the decomposition environment and/or organisms we take a three part approach (e.g. Austin & Vitousek 2000; Hobbie et al. 2006): (i) the above-ground vascular plant litter produced by communities along an inferred chronosequence was incubated in its plot of origin (‘Home Plot’ experiment); (ii) a standard litter was incubated in-situ in each plot (‘Standard Litter’ experiment); and (iii) community litter was decomposed under standard conditions (‘Common Garden’ experiment).

Methods

STUDY SYSTEM

The study was carried out in Nynäsh Nature Reserve, South East Sweden (60°50’N : 17°24’E). The highest monthly average temperature is 16·1 °C, and the lowest −3·3 °C. Annual precipitation is 551 mm (Trosa and Västerljung Weather Stations, 1961–1990, Swedish Meteorological and Hydrological Institute). Twenty plots (current or former management units), consisting of five replicates in each of four categories (currently managed semi-natural grassland, and former semi-natural grassland abandoned 5–15 years ago, 15–60 years ago, or more than 60 years ago) were identified using interpretation of historical maps, aerial photographs and local knowledge. Site selection was based partly on the historical analysis developed in Cousins (2001), with the limits of the four age class categories determined by the chronological resolution of historical maps and aerial photos. The current and former semi-natural grasslands in this study have been used for cattle grazing during their recent history, although mowing was also frequent up to c. 100 years ago. They have been continuously managed for at least 200 years, and there is no evidence of ploughing or use of artificial fertilizers (see Eriksson et al. 2002 for further details).

Studies employing a space- for time-substitution of this kind will always have a degree of uncertainty in their assumptions, that is, the similarity of the starting point and the abiotic and biotic factors operating during succession at each of the plots. In Nynäsh Nature Reserve the landscape undulates gently, and plots were
selected to differ little in altitude or slope position. There is some variation in soil type among the plots, but there was no substantial systematic difference between plots in the different age categories. Patterns of land abandonment at this site are probably more closely related to physical location (closeness to the farm, or belonging to farms completely abandoned) rather than productivity or soil type.

The maximum and minimum distances between the plots were 7 km and 200 m, respectively. The dimensions of each plot varied between c. 100 x 100 m and 500 x 500 m, with sampling and litter incubation occurring in the central area. Two plots were lost during the course of the study in the 5–15 year age category, due to reintroduction of mowing or grazing.

SOIL SAMPLING

Samples were taken on the 8 and 12 May 2003. At each plot, at least 10 cores (5 cm depth) were mixed to form a bulk sample, which was subsequently air dried for 1 week, and sieved (2 mm mesh). Soil C and N content were determined by the Dumas method (combustion) at the ‘Laboratoire d’Analyses des Sols’ of the National Institute for Agronomic Research (INRA, 62000 Arras, France).

SPECIES ABUNDANCE AND BIOMASS

The field layer and taller vegetation (> 50 cm in height) were sampled using different methods. Abundance of vascular plant species in the field layer vegetation was estimated during late June 2003, as the mean number of occupied 10 x 10 cm squares in haphazardly placed 50 x 50 cm quadrats. Nine quadrats were inventoried in each abandoned plot, and three in each grazed plot. The semi-natural grasslands considered here have a very high species density and the majority of species present can be found at a small spatial scale (Eriksson & Eriksson 1997) such that sampling additional quadrats in grazed plots would have added very little additional information. Field layer above-ground live biomass was estimated in mid-July 2003, approximately the period of peak biomass. Vegetation was cut at ground level in six 20 x 20 cm quadrats per plot, sorted into live and dead material, dried at 60 °C for 4 days and weighed. Biomass of woody plants was estimated in three haphazardly placed quadrats per plot (5 x 5 m). For shrubs, the stem diameter, main stem length and number of main branches were measured, and relationships between these and biomass were developed using a subsample of harvested material. Biomass of trees was estimated based on diameter at breast height, using pre-existing allometric relationships (Marklund 1988).

TRAIT MEASUREMENTS

Traits were measured for species whose cumulative abundance made up at least 80% of the field layer at each plot (Table 1), giving a total of 79 species. In addition, traits were measured for all the common woody species occurring in the plots (19 species). Material for measurement of LDMC, SLA and leaf nitrogen and carbon content (LNC and LCC) was collected during the first 2 weeks of July 2003. The majority of species were collected from at least three different plots in different classes of time since abandonment. Collection of material and trait measurements followed standard methods (Cornelissen et al. 2003). Briefly, leaves were placed in sealed plastic bags together with moist paper tissue, transported to the laboratory in a cooling box and measured within 12 h. Leaves were blotted dry and weighed. Fresh leaves (including petioles) were scanned and leaf area calculated using image analysis software (UTHSCSA ImageTool, San Antonio, TX, USA). Leaves were then oven dried (60 °C, 4 days) and weighed. The one-sided area of each fresh leaf was divided by its oven-dry mass to give SLA expressed in m² kg⁻¹. The oven-dry mass of each leaf was divided by its fresh mass, to give LDMC expressed in mg g⁻¹. SLA and LDMC values for some species were taken from a data base (R. Lindborg, unpublished data) of data from plants collected within Nynäs Nature Reserve, using identical methods. LNC and LCC were analyzed on dried ground leaves using a CHONS microanalyser (Carlo Erba 1500). All trait calculations were based on mean values per species.

**Table 1.** Plot characteristics of the 18 plots in different stages since abandonment of semi-natural grassland. Means and standard errors are shown

<table>
<thead>
<tr>
<th>Plot Type</th>
<th>n</th>
<th>Number of species*</th>
<th>Number of species, top 80%*</th>
<th>Dead biomass at senescence (g m⁻²)†</th>
<th>Woody biomass (kg m⁻²)</th>
<th>Field layer live biomass (g m⁻²)</th>
<th>Soil C : N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Semi-natural grassland</td>
<td>5</td>
<td>698 (6-3)</td>
<td>21-8 (2-0)</td>
<td>93-0 (11-1)</td>
<td>0-65 (0-37)</td>
<td>152-0 (16-8)</td>
<td>13-9 (0-61)</td>
</tr>
<tr>
<td>Abandoned 5–15 years</td>
<td>3</td>
<td>698 (7-9)</td>
<td>18-0 (1-5)</td>
<td>251-6 (54-7)</td>
<td>3-5 (1-76)</td>
<td>225-6 (20-4)</td>
<td>13-8 (0-77)</td>
</tr>
<tr>
<td>Abandoned 15–60 years</td>
<td>5</td>
<td>668 (5-5)</td>
<td>14-8 (0-8)</td>
<td>187-2 (41-7)</td>
<td>12-4 (2-41)</td>
<td>133-1 (16-4)</td>
<td>15-3 (0-60)</td>
</tr>
<tr>
<td>Abandoned 60+ years</td>
<td>5</td>
<td>394 (7-0)</td>
<td>8-8 (1-6)</td>
<td>179-9 (18-3)</td>
<td>19-1 (4-67)</td>
<td>119-0 (5-8)</td>
<td>21-0 (1-59)</td>
</tr>
</tbody>
</table>

*Number of species refers to the field layer only.
†Fine litter, excluding woody material over 5 mm diameter.
aggregation of traits was performed using four methods: (1) the weighted mean of the traits of species making up 80% of the field layer, according to Garnier et al. (2004):

$$\text{trait}_{agg} = \sum_{i=1}^{n} p_i \times \text{trait}_i,$$

where $p_i$ is the relative abundance of species $i$ (in this study from quadrat based abundance data, see above), $n$ is the number of species, and trait $i$ is the trait value of species $i$. This is referred to as the Field Layer basis; (2) As in method 1 but including woody species weighted by their contribution to the total biomass (referred to as Complete Vegetation Biomass basis); (3) the unweighted mean of the traits of the species making up to 80% of the field layer and the woody species (Complete Vegetation Unweighted basis); and (4) on the basis of the contribution of plant groups to the litter layer, to take account of the differences in proportional input of litter from different plant types (Litter basis). Method 4 was calculated in two stages. First, for each plot, the weighted mean of the trait for each plant type (herbaceous, graminoid, N-fixing species, see ‘Collection of community litter’ section, below) was calculated according to eqn 1, to give a weighted mean trait value for each plant type for each plot. Second, these weighted mean traits were themselves aggregated using eqn 1 but with $p_i$ representing the relative contribution of each litter type to the total (Fig. 1), resulting in a single weighted mean trait value (community functional parameter) per plot.

**COLLECTION OF COMMUNITY LITTER**

Whole community, above-ground vascular plant litter consisting of a mixture of leaves, stems and other plant parts was collected during the peak of autumn senescence (e.g. Hector et al. 2000). All naturally senesced, current year litter was taken from several (between 5 and 16) haphazardly placed 30 $\times$ 30 cm quadrats per plot, during early November 2003. Seed heads and seeds were removed, along with cones and twigs larger than 5 mm diameter. All litter was well mixed and air dried at room temperature in the laboratory. Larger litter (e.g. stems) was cut to c. 5 cm lengths in order to fit in the litterbags and ensure...
each bag contained a representative mixture of plant parts and species (Dukes & Field 2000). Above-ground dead biomass at the time of senescence was estimated from the number of quadrats and the total dry mass of litter collected. To determine the composition of the community litter, a subsample from each plot was sorted into species (for the commonest trees, shrubs and subshrubs) and broad plant groups (for herbaceous litter, grass litter and N-fixer litter), oven dried (60 °C, 3 days) and weighed.

**STANDARD LITTER**

Hay from a nearby site just outside the nature reserve was used as a standard litter. This was treated in the same way as community litter. The hay had an N concentration of 1-21%, C concentration of 46-3% and C : N ratio of 38.5. Under standard conditions (see below), this material lost 43% (±2.4) mass over 6 months of incubation.

**LITTER QUALITY (NIRS)**

A 5 g subsample of the initial litter from each plot was ground to pass through a 1 mm mesh in a cyclone mill (Cyclotec Sample Mill 1093), then scanned by near infrared reflectance spectrometry (NIRSystem 6500). Data analysis was conducted with the ISI software system (Shenk & Westerhaus 1991). Calibrations between initial litter spectral data and litter decomposability were calculated using the cross-validated partial least square (PLS) method (Shenk & Westerhaus 1991). Four commonly used litter quality indices were determined from initial litter spectral data following the method described by Joffre et al. (1992) and Gillon et al. (1999): nitrogen, lignin, cellulose and hemicellulose contents. In addition, three indices of litter chemistry, relating to the proportions of labile and non-labile compounds in the litter, were calculated (Berg et al. 1984; McClaugherty & Berg 1987; Gillon et al. 1994; Cortez et al. 1996; Cornelissen et al. 2004): the lignin : N ratio (LIG : N), the holocellulose-to-hemicellulose ratio (HLQ = (CEL + HEM)/(LIG + CEL + HEM)) and the litter fibre component or sum of non-labile compounds (LCH = LIG + CEL + HEM).

**INCUBATION IN-SITU (HOME PLOT AND STANDARD LITTER EXPERIMENTS)**

Two grams (±0.1 g) of community litter or standard litter were weighed into litterbags made of a double layer of plastic coated glass fibre 1-1 mm mesh (internal area c. 10 × 7 cm). Twenty-one litterbags containing community litter and 21 litterbags containing hay were made for each plot, that is, seven replicate bags for each litter type in each of three harvests (after 6, 12 and 18 months). Litter that fell out of the bags during filling was collected, re-weighed and subtracted from the mass in the litterbags. The mean spillage loss was c. 0.5%. Subsamples were oven dried (60 °C, 3 days) for conversion between air dry and oven dry masses.

Litterbags were placed in the field on the 17–20 November 2003. Bags containing community litter were incubated in the plot from which the litter had been collected. The position of litterbags within each plot was chosen haphazardly. Each bag was attached to the soil surface using plastic cable ties. To mimic the natural conditions for decomposing litter at each plot, the litterbags was covered with a thin (c. 1 cm) layer of litter from within 100 m. In the grazed plots, litterbags were placed inside exclosures. Throughout the incubation period, vegetation in exclosures was regularly cut back to the same height as the surrounding vegetation. The litterbags in the grazed plot were not covered, since there is no substantial deep layer of surface litter at these plots. Proximate, direct effects of grazing animals on litter decomposition (e.g. trampling, inputs of urine) are missing from the decomposition estimates produced within exclosures. We may thus underestimate the ‘true’ decomposition in grazed plots, although such effects are likely to be small as the plots are not intensively grazed. Six ‘dummy’ litterbags from each of these treatments were placed in the field and immediately harvested, in order to estimate spillage losses during handling, transport and field placement. Seven litterbags from each litter type (community or standard) and plot were collected after 6, 12 and 18 months of incubation in the field.

**Incubation in standard conditions (Common Garden Experiment):** The litterbed approach used here should be seen as an ‘outdoor laboratory’ incubation, and does not attempt to replicate field decomposition, but provides an assessment of relative decomposability under standard conditions (Cornelissen 1996). The decomposability ranking of different litters has been shown to be remarkably robust to methodological factors such as mesh size, burial, climate, incubation medium or length of incubation (Cornelissen 1996; Cornelissen et al. 1999). Litterbags to be incubated in the litterbed were constructed from 0.3 mm nylon mesh. Five replicate bags with community litter were made per plot, plus five litterbags containing standard litter, each containing 1 g (±0.1 g) air dried litter. A litterbed was constructed in a fenced garden at the Department of Botany, Stockholm University, and consisted of a series of 1-60 x 1-0 m wooden frames sunk into the ground. A layer of nylon fibre material was placed in the bottom of each frame, over the underlying sand, to prevent weed growth. A 5 cm deep layer of well mixed leaf and needle litter was placed in the frames. The litter bed was divided into five blocks. On the 25 November 2003, one replicate litterbag from each plot was placed in each block, and all bags were covered with c. 3 cm of the same litter. The whole bed was covered with nylon mesh (c. 2 cm mesh size). All litterbags were harvested after 6 months of incubation in the litter bed.
LITTERBAG COLLECTION AND PROCESSING

Litterbags were collected, placed in plastic bags in a cool box, and stored at 5°C for a maximum of 4 days, or frozen. Litterbags were opened, any extraneous material removed, the contents oven dried at 60°C for 4 days, then weighed.

DATA ANALYSIS

Mean litter mass loss values from each plot and harvest were calculated, and analyses performed treating each of the 18 plots as a replicate. All percent litter mass loss data were arcsine square-root transformed before analysis. Data analyses were carried out in R 2.1.1 (R core development team).

Differences in community functional parameters and Common Garden decomposition among age categories were assessed using one-way ANOVA. In order to account for the repeated harvests in the Home Plot and Standard Litter experiments, litter mass loss differences among age classes were analyzed using linear mixed effects models, with harvests nested within plots as a random factor (Crawley 2002). The fixed effects of age class and harvest, and their interaction were included in the model. Test statistics and \( P \) values are reported for the change in model prediction upon deletion of the term in question from the model (Crawley 2002). Relationships between mass loss in the Home Plot experiment and mass loss in the Common Garden or Standard Litter experiments was tested using similar mixed effects models, with Home Plot as the dependent variable, harvest and Common Garden or Standard Litter mass loss as fixed predictor variables, and harvests nested within plots as a random factor. Relationships between traits, litter chemistry and mass loss were assessed with correlation analyses, followed by sequential Bonferroni corrections (Simes 1986).

Results

VEGETATION AND COMMUNITY FUNCTIONAL PARAMETER CHANGE

The composition and structure of the vegetation differed markedly between plots in different age classes (Table 1), and these changes were reflected in the composition of the litter input (Fig. 1). Notably, the proportion of litter from herbs was highest in the semi-natural grassland plots, with a progressive increase in the litter of the dominant tree species (Betula spp. and Pinus sylvestris) with time since abandonment, whilst grass litter was most abundant in the early successional plots. These changes were reflected in the community functional parameters (presented for Litter method; Table 2); as expected, aggregated SLA decreased with age since abandonment, whilst aggregated LDMC and the aggregated leaf C : N ratio both increased.

DECOMPOSITION OF COMMUNITY AND STANDARD LITTER

Mass loss from community litter declined significantly with age since abandonment in both the Common Garden (Table 2) and Home Plot experiments (Fig. 2a, mixed effect model, effect of deleting age class main effect \( L = 22.5, P < 0.001 \)). The mass loss of the Standard Litter also differed significantly with age since abandonment (Fig. 2b), but showed a different pattern. The effect of age class differed over the three harvests (mixed effect model, effect of deleting age class × harvest interaction, \( L = 16.7, P = 0.01 \)). In the 12- and 18-month incubations only, mass loss from the standard litter was greatest in plots abandoned 5–15 years ago, and slowest in the semi-natural grassland plots.

Mass loss in the Common Garden and Home Plot experiments were strongly positively related to each other in all three harvests (mixed effect model, effect of deleting Common Garden mass loss, \( L = 17.5, P < 0.001 \)), whilst mass loss in the Standard Litter experiment was not significantly related to mass loss in the Home Plot experiment (\( L = 2.5, P = 0.11 \)), suggesting that much of the observed variation in mass loss in the Home Plot experiment was due to differences in substrate quality rather than changes in the decomposition environment and organisms. Further, including in-situ mass loss from standard litter in a model already containing community litter mass loss under standard conditions did not improve prediction of in-situ community litter mass loss (mixed effect model, effect of deleting standard litter mass loss \( L = 2.9, P = 0.086 \)).

Table 2. Community functional parameters (Litter Basis) and mass loss after 6 months in the Common Garden experiment for 18 plots in different stages since abandonment of semi-natural grassland

<table>
<thead>
<tr>
<th>Category</th>
<th>SLA (m² kg⁻¹)</th>
<th>LDMC (mg g⁻¹)</th>
<th>Leaf N (mg g⁻¹)</th>
<th>Leaf C (mg g⁻¹)</th>
<th>Leaf C : N ratio</th>
<th>Common Garden Mass loss (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Semi-natural grassland</td>
<td>21.5 (0.7) a</td>
<td>414 (16.1) a</td>
<td>21.1 (0.3) a</td>
<td>470 (2.1) a</td>
<td>22.3 (0.4) a</td>
<td>21.3 (0.69) a</td>
</tr>
<tr>
<td>Abandoned 5–15 years</td>
<td>21.7 (0.6) a</td>
<td>434 (9.6) ab</td>
<td>18.6 (1.1) ab</td>
<td>469 (2.0) a</td>
<td>25.4 (1.5) a</td>
<td>19.0 (1.9) ab</td>
</tr>
<tr>
<td>Abandoned 15–60 years</td>
<td>20.0 (1.2) a</td>
<td>403 (13.5) b</td>
<td>20.2 (0.9) a</td>
<td>487 (4.3) b</td>
<td>24.3 (0.9) a</td>
<td>17.6 (0.77) ab</td>
</tr>
<tr>
<td>Abandoned 60+ years</td>
<td>13.0 (0.8) b</td>
<td>545 (8.7) c</td>
<td>16.9 (0.6) b</td>
<td>500 (2.6) c</td>
<td>29.8 (1.0) b</td>
<td>15.3 (0.75) b</td>
</tr>
<tr>
<td>One-way ANOVA, ( F )</td>
<td>21.2***</td>
<td>21.4***</td>
<td>7.36***</td>
<td>23.31***</td>
<td>12.8***</td>
<td>7.25***</td>
</tr>
</tbody>
</table>

Means and standard errors are given. The final row gives the results of one-way ANOVA with plot age class as a factor: * \( P < 0.05 \), ** \( P < 0.01 \), *** \( P < 0.005 \). Means not sharing a common letter (a, b, c, ab) differ significantly (Tukey’s test, \( P < 0.05 \)).
There were clear links between litter mass loss and community functional parameters calculated on the basis of contribution to the litter layer in both the Common Garden and Home Plot experiments (Table 3, Fig. 3a). LDMC stood out as the trait most closely related to mass loss, and the relationship persisted through all three incubation periods.

Of the four methods used for calculating community functional parameters, the Litter method was, as expected, most closely related to decomposition processes (data presented for LDMC only, Table 4). The Complete Vegetation Biomass method did not produce aggregated traits that were significantly correlated with either decomposition rates or to the other methods of calculation, most likely because in some plots woody species make up 90% of the biomass but do not the litter layer to the same extent. The Field Layer and Complete Vegetation Unweighted methods were both significantly correlated with decomposition and with the Litter method (Table 4).

Of the litter chemistry parameters measured, the Lignin : N ratio stood out as the index most closely related to mass loss in both the Common Garden and Home Plot experiments (Fig. 3b, Table 5). Several of the measured litter chemistry parameters were strongly related to the community functional parameters of the communities (Table 6). In particular, LDMC was related to the lignin concentration, Lignin N ratio, and non-labile compounds (LCH).

### Discussion

Community functional parameters varied with time since abandonment of semi-natural grasslands, as a result of changing species abundance and composition. Species with lower SLA, and greater LDMC and leaf C : N ratio dominate in later stages of succession, in line with the general picture of a shift from species acquiring resources rapidly in the early stages of succession to slow growing species with more conservative resource use strategies later in succession (Grime 1979; Reich, Ellsworth & Uhl 1995; Wardle et al. 1997; Kazakou et al. 2006).

### Table 3

<table>
<thead>
<tr>
<th></th>
<th>Common Garden</th>
<th>Home Plot 6 months</th>
<th>Home Plot 12 months</th>
<th>Home Plot 18 months</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLA</td>
<td>0.676***</td>
<td>0.403</td>
<td>0.439</td>
<td>0.492</td>
</tr>
<tr>
<td>LDMC</td>
<td>-0.814***</td>
<td>-0.669**</td>
<td>-0.684**</td>
<td>-0.715**</td>
</tr>
<tr>
<td>Leaf [N]</td>
<td>0.433</td>
<td>0.568*</td>
<td>0.368</td>
<td>0.539*</td>
</tr>
<tr>
<td>Leaf [C]</td>
<td>-0.752***</td>
<td>-0.556*</td>
<td>-0.558*</td>
<td>-0.486</td>
</tr>
<tr>
<td>Leaf [C] : [N]</td>
<td>-0.577*</td>
<td>-0.621*</td>
<td>-0.454</td>
<td>-0.591*</td>
</tr>
</tbody>
</table>

Significance levels corrected by the sequential Bonferroni procedure (Simes 1986): *P < 0.05, **P < 0.01, ***P < 0.005.

### Table 4

<table>
<thead>
<tr>
<th></th>
<th>Decomposition (% mass loss)</th>
<th>Aggregation method</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Common Garden</td>
<td>Home Plot 6 months</td>
</tr>
<tr>
<td>Field Layer</td>
<td>-0.60*</td>
<td>-0.66**</td>
</tr>
<tr>
<td>Complete Vegetation Biomass</td>
<td>-0.43</td>
<td>-0.41</td>
</tr>
<tr>
<td>Complete Vegetation Unweighted</td>
<td>-0.67**</td>
<td>-0.64**</td>
</tr>
<tr>
<td>Litter</td>
<td>-0.81***</td>
<td>-0.67**</td>
</tr>
</tbody>
</table>

Relationships among the different aggregation methods are also shown. Significance levels corrected by the sequential Bonferroni procedure (Simes 1986): *P < 0.05, **P < 0.01, ***P < 0.005.
A central finding of this study is that these shifts in plant community composition, reflected in the weighted mean of simple functional traits of the living community, can be explicitly linked with changes in in-situ decomposition processes. This extends and develops the trait-decomposition links apparent at the species level (e.g. Cornelissen & Thompson 1997; Vaieretti et al. 2005; Cornelissen et al. 2006; Kazakou et al. 2006), indicating the applicability of such results to the community level. Encouragingly, in both the current study and that of Garnier et al. (2004) conducted in abandoned vineyards in the Mediterranean, LDMC stood out as the trait most closely linked to community litter decomposition, despite the contrasting ecological constraints and evolutionary histories of the two study systems. Further, the strength of the relationship between LDMC and litter mass loss was consistent across all three incubation periods (by which time up to c. 70% mass loss had occurred) and roughly equal to that between the best single chemical index of litter quality (lignin : N ratio) and litter mass loss. Clearly, further work is warranted to test the generality and applicability of these findings, but should they prove consistent, community aggregated LDMC may be a useful indicator for shifts in decomposition processes during vegetation change.

This study provides important lines of evidence supporting the causal role of shifts in the measured community functional parameters in driving changes in decomposition processes. First, it is clear from our results that the changes in community litter decomposition with age since abandonment are primarily driven by declining litter quality, rather than by changes in the decomposition environment and/or soil organisms. The mass loss of the standard litter differed between plots in different age classes, and we suggest that the faster decomposition of the standard litter in the recently abandoned plots is a result of more favourable moisture and temperature regime for decomposition within the dense layer of grass litter characteristic of these plots. It is also possible that these plots support a larger or more active soil decomposer community. However, this was not reflected in the mass loss of community litter in the Home Plot experiment, which was closely related to mass loss of community litter under standard conditions. The key role of litter quality in determining in-situ decomposition is in line with a number of studies which have identified a link between increasing successional age and the presence or abundance of plant

---

**Table 5.** Relationships (Pearson’s correlation coefficients) between decomposition of community litter under standard conditions (Common Garden experiment) or in-situ (Home Plot experiment) and litter chemistry

<table>
<thead>
<tr>
<th></th>
<th>Common Garden</th>
<th>Home Plot 6 months</th>
<th>Home Plot 12 months</th>
<th>Home Plot 18 months</th>
</tr>
</thead>
<tbody>
<tr>
<td>[N]</td>
<td>0.521</td>
<td>0.599*</td>
<td>0.266</td>
<td>0.437</td>
</tr>
<tr>
<td>[Lignin]</td>
<td>−0.594*</td>
<td>−0.400</td>
<td>−0.582*</td>
<td>−0.436</td>
</tr>
<tr>
<td>[Lignin] : [N]</td>
<td>−0.808*</td>
<td>−0.644*</td>
<td>−0.609*</td>
<td>−0.606*</td>
</tr>
<tr>
<td>[Cellulose]</td>
<td>−0.281</td>
<td>−0.450</td>
<td>−0.115</td>
<td>−0.385</td>
</tr>
<tr>
<td>[Hemicellulose]</td>
<td>0.377</td>
<td>0.055</td>
<td>0.479</td>
<td>0.305</td>
</tr>
<tr>
<td>[LCH]</td>
<td>−0.632*</td>
<td>−0.686*</td>
<td>−0.468</td>
<td>−0.542</td>
</tr>
<tr>
<td>[HLQ]</td>
<td>0.459</td>
<td>0.204</td>
<td>0.503</td>
<td>0.296</td>
</tr>
</tbody>
</table>

Significance levels corrected by the sequential Bonferroni procedure (Simes 1986): *P < 0.05, **P < 0.01, ***P < 0.005.

**Table 6.** Relationships (Pearson’s correlation coefficients) between community functional parameters and litter chemistry

<table>
<thead>
<tr>
<th></th>
<th>SLA</th>
<th>LDMC</th>
<th>Leaf [N]</th>
<th>Leaf [C]</th>
<th>Leaf C : N</th>
</tr>
</thead>
<tbody>
<tr>
<td>[N]</td>
<td>0.504</td>
<td>−0.489</td>
<td>0.637*</td>
<td>−0.264</td>
<td>−0.621*</td>
</tr>
<tr>
<td>[Lignin]</td>
<td>−0.640*</td>
<td>0.707***</td>
<td>−0.172</td>
<td>0.881***</td>
<td>0.367</td>
</tr>
<tr>
<td>[Lignin] : [N]</td>
<td>−0.890***</td>
<td>0.877***</td>
<td>−0.581*</td>
<td>0.869***</td>
<td>0.726***</td>
</tr>
<tr>
<td>[Cellulose]</td>
<td>−0.149</td>
<td>0.285</td>
<td>−0.515</td>
<td>−0.028</td>
<td>0.467</td>
</tr>
<tr>
<td>[Hemicellulose]</td>
<td>0.639*</td>
<td>−0.543*</td>
<td>0.107</td>
<td>−0.689**</td>
<td>−0.245</td>
</tr>
<tr>
<td>[LCH]</td>
<td>−0.458</td>
<td>0.670**</td>
<td>−0.416</td>
<td>0.622**</td>
<td>0.539*</td>
</tr>
<tr>
<td>[HLQ]</td>
<td>0.571*</td>
<td>−0.571*</td>
<td>0.026</td>
<td>−0.798***</td>
<td>−0.211</td>
</tr>
</tbody>
</table>

Significance levels corrected by the sequential Bonferroni procedure (Simes 1986): *P < 0.05, **P < 0.01, ***P < 0.005.
species which produce low quality litter (Wardle et al. 1997; Garnier et al. 2004; Kazakou et al. 2006), and supports the contention that at a landscape or regional level, litter quality is the dominant control on decomposition (Lavelle et al. 1993; Aerts 1997).

Second, there is a clear mechanistic link between the measured traits and the quality of the litter as a resource for decomposer organisms. Both SLA and LDMC reflect leaf structural characteristics, which are likely to survive through senescence and influence litter structure and chemistry. LDMC depends on tissue density (Garnier & Laurent 1994; Shipley & Vu 2002), which is in turn determined by the proportions of mesophyll vs. vessels and fibres (Garnier & Laurent 1994; van Arendonk & Poorter 1994). At the species level, LDMC has been related to lignin concentration in litter (Kazakou et al. 2006). Indeed, in this study, community aggregated LDMC was linked to key chemical litter quality indices, including the lignin concentration of the community litter. SLA has been linked in a range of studies to leaf life span, and structural and chemical defence against herbivores and the abiotic environment (Reich et al. 1992; Grime et al. 1996). Neither leaf nor litter N concentrations alone were particularly good correlates for decomposition.

This study provides evidence that relationships between traits and processes apparent using comparative approaches at the leaf- and species-level (Cornelissen 1996; Cornelissen & Thompson 1997; Cornelissen et al. 1999, 2004, 2006; Pérez-Harguindeguy et al. 2000; Gurvich et al. 2003; Kazakou et al. 2006) are applicable to whole communities. This is noteworthy since the community litter consisted of a considerable quantity of other plant parts including stems (varying from 16% to 34% depending on site age), which differ from leaves in their decomposition dynamics. Also of note is that within species variation in litter quality (e.g. Austin & Vitousek 2000; Madrich & Hunter 2005; Sariylidiz, Anderson & Kucuk 2005) and complex interactions between the environment and litter quality (e.g. Hobbie & Gough 2004; Couteaux 1995) do not alter the broad community level relationships observed here. Further, our results indicate that non-additive interactions between different litter types (reviewed by Gartner & Cardon 2004) do not disrupt the overall pattern of trait-decomposition links. Our results also illustrate the rather obvious importance of selecting a relevant weighting for the calculation of community functional parameters. In vegetation consisting of different life-forms, the relationship between biomass and litter input is not necessarily straightforward (cf. Garnier et al. 2004). The correspondence between the community functional parameters calculated on the basis of field layer abundance or the unweighted mean of the species present suggests that the latter two methods may be useful indicators in situations where litter proportions are unavailable, although the generality of this result clearly requires testing in other contexts.

Conclusions

Implications for longer term ecosystem processes are hard to predict from litterbag studies, and more work is needed to elucidate the roles of plant traits in driving processes such as N-cycling and soil organic matter formation. However, the data presented here build on previous work and emphasise the potential of plant traits, particularly LDMC, as a tool to link changes in species composition with ecosystem processes at the community level.

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References


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