Plant traits, litter quality and decomposition in a Mediterranean old-field succession

Jacques Cortez · Eric Garnier · Natalia Pérez-Harguindeguy · Max Debussche · Dominique Gillon

Abstract Human-induced changes in land use lead to major changes in plant community composition which have strong effects on ecosystem processes. Here, we tested the hypothesis that changes in traits of living plants induced by such changes resulted in changes in the quality and decay properties of the litter produced by the different communities. This was done in the context of a secondary succession following land abandonment in the Mediterranean region of Southern France.

During the course of succession, species with high specific leaf area (the ratio of leaf area to leaf mass), low leaf dry matter content (the ratio of leaf dry mass to leaf fresh mass) and high leaf nitrogen concentration were progressively replaced by species with opposite characteristics. Accordingly, the initial litter concentrations of carbon (C) and nitrogen (N) decreased, while their C:N ratio and their hemicellulose concentration increased with time after abandonment.

Early-successional communities had faster rates of litter decay and N release from litter, but these differences damped out with decomposition time. Nitrogen release from litter was related to initial litter chemical composition, particularly to its N concentration. This also held for litter decay rate, but only during the first 18 months of decomposition.

Community functional parameters (i.e. trait values weighed according to the relative abundance of species) were tightly linked to initial litter N concentration, and thereby to litter decay and N loss rates. The strongest correlations were found with leaf dry matter content, which therefore appears as a powerful marker of litter properties. This provides further evidence that characteristics of living leaves persist in litter, and that some ecosystem processes can be inferred from plant functional traits.

Keywords Biogeochemical cycles · Ecosystem functioning · Functional markers · Initial litter chemical composition · Leaf dry matter content · Litter mass and nitrogen loss

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Introduction

Human-induced changes in land use and climate lead to major changes in plant community composition (Boyle and Boyle 1994; Huntley et al. 1997), which have strong effects on ecosystem processes (Díaz and Cabido 2001; Chapin et al. 2000) such as litter

decomposition and nutrient cycling (Anderson 1991; Vitousek et al. 1997). Mechanistic approaches have demonstrated that at a local scale, litter decomposition rate depends on the structural and biochemical components of litter (Cadish and Giller 1997), which depend, to some extent, on features of the living plants and their leaves. For example, life-form and deciduous versus evergreen habit (Cornelissen 1996; Pérez-Harguindeguy et al. 2000; Quested et al. 2003; Dorrepaal et al. 2005), leaf life span, foliar nutrient content, components of leaf structure (Gillon et al. 1994; Cornelissen and Thompson 1997; Kazakou et al. 2006), plant defences (Grime et al. 1996; Wardle et al. 1998; Cornelissen et al. 2004) were all found to relate to leaf decomposition rate. More generally, fast growing, poorly defended species produce litter with a high decomposability whereas slower-growing, better defended species produce poor-quality litter with low decomposition rates (Cornelissen et al. 1999).

The aim of the present study is to understand how changes in land use, one of the most important anthropogenic effects on Earth's ecosystems (Vitousek et al. 1997), affect litter quality and decomposition rate, and how this relates to changes in functional characteristics of the living vegetation. In the Mediterranean region of Southern France, the continuous decrease of human impact during the course of the twentieth century has induced dramatic changes in vegetation type and cover through successional dynamics (Debussche et al. 1999). A previous study conducted in this context of land abandonment has shown that such changes corresponded to the replacement of species with high specific leaf area (SLA: the ratio of leaf area to leaf dry mass) and leaf nitrogen concentration (LNC), and low leaf dry matter content (LDMC: the ratio of leaf dry mass to saturated fresh mass) in the first stages following abandonment, by species with opposite characteristics as succession proceeds (Garnier et al. 2004). These traits, which are involved in a fundamental trade-off between fast resource acquisition and efficient resource conservation (cf. Grime et al. 1997; Poorter and Garnier 1999; Wright et al. 2004), have been identified as key traits to scale-up from plant to ecosystem functioning (Lavorel and Garnier 2002; Eviner and Chapin 2003; Quétier et al. 2007). In the post-cultural succession studied, these have indeed been shown to correlate with several

ecosystem properties, including rates of biomass production, litter mass loss and soil organic matter, provided that, according to the biomass ratio hypothesis (Grime 1998), species traits were weighed by the relative abundance of species (Garnier et al. 2004).

The objectives of the present study are to address more detailed questions pertaining to litter quality and decomposition in the context of the same successional sere. These are: (i) what are the controls over litter decay rates and nitrogen release from litter during succession? (ii) how do these controls change during the course of the decomposition process? and (iii) what are the relationships between litter quality, decomposition, and the leaf traits of the dominant species from the different communities found along the succession?

Material and methods

Study site

Fourteen old-fields located in southern France (43°51′N, 3°56′E, 100–160 m asl) under a sub-humid Mediterranean climate were selected for this study. The mean annual temperature and rainfall over the 1972–2002 period at the meteorological station closest to the plots (Saint-Martin-de-Londres, approximately 18 km south-west of the plots) were 13.2°C and 994 mm, respectively. Figure 1 shows the daily temperature and rainfall during the period of study at

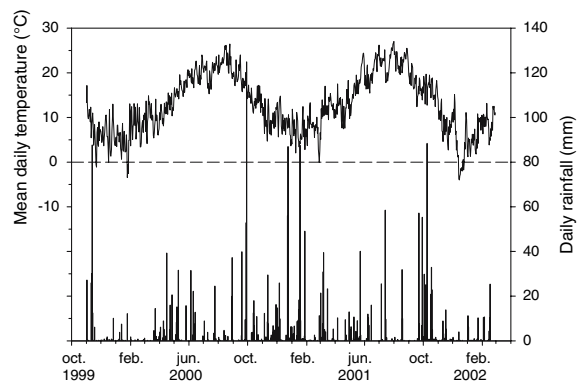

Fig. 1 Daily temperature (top) and rainfall (bottom) during the period of study (November 1999–February 2002), at the Saint-Martin-de-Londres meteorological station, 18 km south-west of the plots. The *horizontal dashed line* is the 0°C line

the same meteorological station. Plots were located within a 4×4 km^2, on brown calcareous soils (calcic cambisol). Although there was some variation in soil texture and physico-chemical properties among plots (Appendix 1), there was no systematic trend with field age, except for total soil carbon and nitrogen concentrations (Garnier et al. 2004), which reflects a built-up of organic matter as succession proceeds. These old-fields (''plots'' hereafter) were all previously vineyards which, following removal of the vines, were abandoned 7–42 years prior to our study (Table 1). In all the fields, the herbaceous layer always represented at least 70% of total plant cover (cf. Appendix 2). The similarities in soil characteristics, climate and plant species pool, make these fourteen old-fields a good model of a chronosequence to study successional patterns and mechanisms. Further details can be found in Garnier et al. (2004).

Characteristics of plant communities and species traits

In the 14 study plots, species frequency was recorded at spring maximum biomass, using a 1-m long needle placed successively at 50 points, 50 cm apart along a 25 m transect-line. All species whose parts touched the needle were recorded. The relative frequency of each species was computed as the ratio between species frequency and the sum of all recorded species' frequencies along a particular line. These relative frequencies were used as approximations of relative species cover.

The three following leaf traits, previously shown to relate to field age and litter mass loss (Garnier et al. 2004) were measured: specific leaf area (SLA) representing the light-intercepting area per dry mass of leaf, leaf dry matter content (LDMC), an approximation of leaf tissue density, and leaf nitrogen

Table 1 Age since abandonment, community functional parameters and initial litter chemical composition in the 14 old-fields studied

Field age (years)	Community functional parameters			Initial litter chemical composition					
	SLA (m^2 kg^{-1})	LDMC (mg g^{-1})	LNC (mg g^{-1})	LitC (mg g^{-1})	LitN (mg g^{-1})	LitC:N	Hemi (mg g^{-1})	Cell (mg g^{-1})	Lign (mg g^{-1})
7	23.99	272	24.1	436	11.6	37.71	219	299	183
8(†)	13.75	400	11.6	400	5.62	71.14	277	358	115
8	22.38	247	23.6	438	12.8	34.13	244	326	118
11	22.33	249	26.3	409	14.2	28.80	232	344	153
12	24.08	243	29.2	425	12.6	33.87	240	311	136
22	15.81	377	16.2	411	7.34	55.92	280	350	128
26	19.26	320	18.9	417	7.95	52.50	282	358	129
26	13.27	402	11.5	404	5.10	79.13	293	358	123
26(†)	20.62	277	20.7	426	14.0	30.50	248	302	70.3
29	13.10	411	10.9	401	5.08	78.84	277	344	122
35	13.24	409	10.7	413	5.00	82.63	270	308	152
40	13.85	398	10.1	409	5.78	70.71	282	337	134
40	14.45	388	9.39	415	7.03	59.06	256	311	118
42	18.46	440	17.0	402	4.88	82.32	286	369	133
Pearson									
All sites	−0.59*	0.71**	−0.66*	−0.45	−0.63	0.64*	0.60	0.14	−0.20
(†) Excluded	−0.78**	0.90***	−0.83**	−0.68*	−0.87**	0.84**	0.73*	0.30	−0.38

The two last lines show the Pearson correlation coefficients between field age and each community parameter or initial litter chemical compound calculated with all plots and with two plots excluded (marked †: see text). SLA, specific leaf area; LDMC, leaf dry matter content, LNC, leaf nitrogen concentration. LitC, LitN, Lit C:N: carbon, nitrogen concentrations and carbon:nitrogen ratio of litter, respectively. Hemi, Cell and Lign refer to the initial litter concentrations of hemicellulose, cellulose and lignin, respectively

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$ (significance levels corrected by the improved Bonferroni procedure)

concentration (LNC). These traits were measured on green leaves of individuals sampled in the old-fields at the spring peak of growth, following standardized protocols (Garnier et al. 2001; Cornelissen et al. 2003).

Community functional parameters (cf. Violle et al. 2007) were calculated according to the biomass ratio hypothesis (Grime 1998), as:

$$\text{Community functional parameter} = \sum_{i=1}^{n} p_i \times \text{trait}_i \tag{1}$$

where trait_i is the trait value of species i, and p_i is the proportion of species i in the community. Equation 1 was applied to the species that accounted for at least 70% of the total plant presence registered along the transect-line of each plot (Appendix 2).

Litter decomposition experiments

The main experiment was carried out using 14 different litters collected from each of the 14 study plots and each decomposing in its own plot (''native'' litter hereafter). At the time of the major peak of natural senescence (August 1999), undecomposed

litter of all plant parts of all vascular plant species was collected in the proportions in which it was naturally shed in the plots. Each litter was then assumed to represent the average litter characteristics of the community present at each plot. Eighty samples from each well mixed, air-dried litter were weighed and placed into polyester net litterbags (16 × 12 cm, 5 mm mesh) and left to decompose on the soil surface of the plots for 836 days. Five additional samples of each litter were oven-dried at 40°C to constant mass to determine the initial litter water content. Ten litterbags were sampled every 3 months in each plot (last two sampling dates missing for two of the plots: cf. Table 2). The recovered litter samples were oven-dried at 40°C to constant mass, and weighed after soil particles were carefully removed by hand.

An additional experiment was carried out to test the influence of plot local conditions (i.e. soil, soil decomposer community and physico-chemical influence of the living plants) on litter decomposition. Thirty-two samples of the same air-dried litter (''standard'' litter hereafter) taken from the 11-year-old plot (Table 1) were placed in litterbags and left to decompose on the soil surface of four plots of different ages (7, 11, 26 and 42 years) for 384 days.

Table 2 Field age, litter mass remaining at first sampling date (132 days after the beginning of the experiment), litter decay rate (K) at three sampling times and annual N loss rate in g kg^{-1} initial litter year^{-1}

The two last lines show the Pearson correlation coefficients between field age, litter mass loss, K or N loss rate calculated with all plots and with two sites excluded (marked †: see text). nd, not determined

*P < 0.05; **P < 0.01; ***P < 0.001 (significance levels corrected by the improved Bonferroni procedure)

Field age (years)	Mass remaining after 132 days (%)	K (g kg^{-1} year^{-1}) 222 days	598 days	836 days	QN_0 (g)	Annual N loss rate (g kg^{-1} year^{-1})
7	80.2	623	621	618	11.6	3.18
8(†)	86.8	402	532	592	5.6	1.50
8	72.0	746	681	nd	12.8	4.46
11	76.0	723	682	695	14.2	5.10
12	74.5	738	669	633	12.6	3.86
22	83.5	543	606	620	7.3	1.91
26	87.1	394	452	511	7.9	2.21
26	88.9	323	367	435	5.1	1.19
26(†)	75.3	633	569	556	14.0	4.57
29	83.9	498	647	687	5.1	1.51
35	86.4	363	405	nd	5.0	0.12
40	86.6	375	437	451	5.8	0.62
40	84.4	442	484	495	7.0	0.70
42	88.0	346	421	460	4.9	0.99
Pearson						
All sites	0.60*	−0.73*	−0.71*	−0.68*	−0.63*	−0.71*
(†) excluded	0.81**	−0.88***	−0.77**	−0.70*	−0.87***	−0.90***

Eight litterbags were sampled every 3 months and were treated as described for the main experiment.

NIRS determination of litter chemical composition

A subset (618 out of 1,080) of the litter samples from the main experiment representative of the litter collected in each plot at the different dates were ground in a cyclone mill (Cyclotec Sample Mill, Tecator, Höganäs, Sweden) and scanned using a near infrared reflectance spectrophotometer (NIRSystems 6500, Foss NIRSystems, Raamsdonksveer, The Netherlands). For these samples, carbon (C), nitrogen (N), hemicellulose, cellulose and lignin concentrations were determined according to the method described by Joffre et al. (1992). The measured values were obtained with standard errors of calibration of 0.9% for C, 0.07% for N, 1.7% for hemicellulose and cellulose, and 2.8% for lignin. Phenolic compounds were not assessed in this study, since these have been shown to play only a minor role in the decomposition rate of the dominant species of this successional sere (Kazakou et al. 2006).

Determination of litter decay rate constants (K) and litter N release

From the dry mass data during field decomposition, percentage of litter mass remaining (X_i) was calculated for each sample i. The X values for each litter were fitted to the Olson model (1963):

$$X_t = X_0 e^{-Kt} \tag{2}$$

where X_0 was the litter dry mass at the beginning of decomposition (=100), X_t was the percentage of litter mass remaining at time t, expressed in years; rate constants K were multiplied by 10^3 and expressed in g kg^{-1} year^{-1}. Correlation coefficients for the different fits obtained at various times during the experiment are given in Appendix 3.

At the beginning of the field incubation, the quantity of N in each initial litter (QN_0) was equal to its mass ($X_0 = 100$) multiplied by its initial N concentration (N_0). The remaining N quantity (QN_i) in each sample i of decomposing litter was calculated as:

$$QN_i = X_i \times N_i \tag{3}$$

where X_i was the percentage of litter mass remaining of sample i and N_i its N concentration. In all plots, an initial period of rapid leaching was observed between the start of the experiment and the first sampling date after 132 days of decomposition. QN decreased rapidly during this period, while it decreased more slowly and linearly with time afterwards (cf. Fig. 1b), except for some of the older plots. A linear regression was thus fitted to the QN data excluding the QN_0 value, as:

$$QN_t = a - b \times t \tag{4}$$

where QN_t was the quantity of N at time t, t was expressed in years, b was the annual N loss rate expressed in g kg^{-1} of initial litter year^{-1}, and a is QN after the initial period of rapid leaching. The parameters and correlation coefficients for the different plots are given in Appendix 4.

Data analyses

The multiple comparisons between the fitted decay rate constants K and between the annual N loss rates b was carried out using the T'-method (Sokal and Rohlf 1995, pp. 240–260). In a first set of analyses, the plots were grouped into one of three successional stages (cf. Table 1), corresponding to 7–12 years after abandonment (''early'' successional plots), 22–29 years after abandonment (''intermediate'' plots) and 35–42 years after abandonment (''advanced'' plots). The effects of succesional stage and decomposition time on litter mass loss and nitrogen release were then tested using two-ways analyses of variance (ANOVAs). Correlations between field age, functional parameters of the communities, initial litter chemical composition, litter decomposition rate and annual N loss rate were evaluated with Pearson product-moment correlation coefficients. In all analyses significance levels were corrected by the improved Bonferroni procedure (Simes 1986; Sokal and Rohlf 1995, pp. 229–240).

Results

Field age, plant community and leaf litter

Plant community composition changed with field age (Appendix 2): early successional plots were generally

dominated by annual or biennial species (e.g. *Avena barbata*, *Bromus madritensis*, *Medicago minima*), while older plots were usually dominated by perennial species: the grasses *Brachypodium phoenicoides* and *Bromus erectus* were dominant in many plots, but other species such as e.g. *Rubus caesius* or *Picris hieracioides* could also contribute significantly. As a consequence of this shift in species composition, community functional parameters changed with field age: LDMC significantly increased whereas SLA and LNC decreased during the course of succession (Table 1). The species composition and trait values of two of the plots (one 8-year-old and one 26-year-old: ''atypical plots'' hereafter) differed substantially from the other plots of comparable ages (cf. Appendix 2). When these two plots were excluded from the analysis, correlations with field age were stronger (Table 1).

The chemical properties of the leaf litter produced in these plots also changed with field age (Table 1): litter C and N decreased while litter C:N and hemicellulose increased as succession proceeds. Note that the difference between the C:N ratio and lignin concentrations of the two 40-year-old plots can probably be related to the different proportions of the two grasses that are dominant in these plots: *Brachypodium phoenicoides* (58 and 20% respectively in each plot) and *Bromus erectus* (44 and 88%, respectively). Trends for litter cellulose and lignin concentrations were not significant. All these correlations were stronger when the two ''atypical plots'' were excluded from the analyses.

Decay rate of standard litter in four plots of different ages

The mean (±standard error) decay rate constants of the standard litter in the 7, 11, 26 and 42-year-old plots were 571 (±33), 581 (±34), 506 (±26) and 584 (±43) g g^{-1} year^{-1}, respectively. These values were not significantly different, except that for the 26-year-old plot ($P < 0.05$).

Decay rate and nitrogen release of native litters in the 14 plots

Mass loss of all litters fitted the exponential model of decay during field decomposition (r^2 from 0.70 to 0.94, degree of freedom from 20 at 222 days to 80 at

836 days: see Appendix 3 and cf. Fig. 2a). At the second sampling date (after 222 days of decomposition), K varied 2.3-fold among the different plots, while at the last sampling date (after 836 days), K varied only 1.6-fold (Table 2). This was reflected in the significant decrease in the coefficient of variation (CV: Appendix 3) of K among plots with time of decomposition ($r = -0.96$, $P < 0.001$, $n = 8$). ANOVAs showed significant differences in litter mass remaining among plots differing in successional stages (Fig. 2a). At all dates, K decreased significantly with field age, but the longer the decomposition time, the weaker the trend (Table 2).

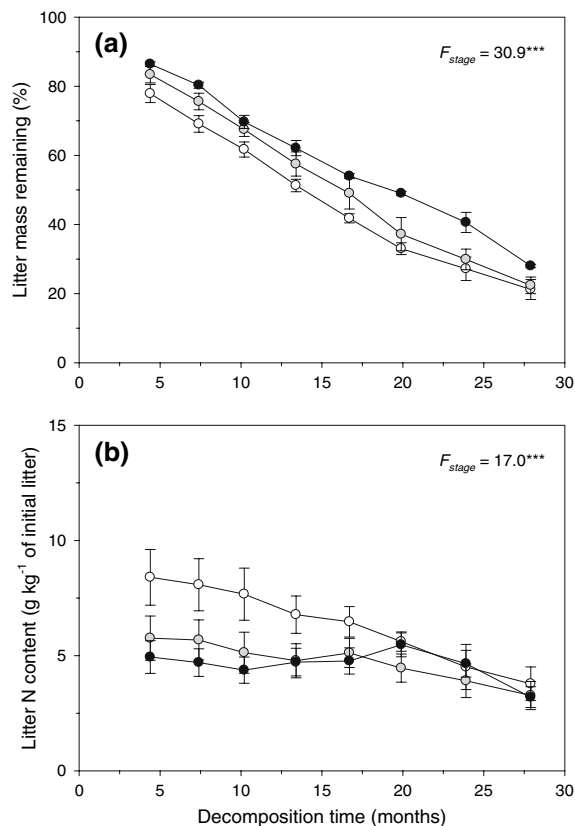The quantity of N contained in 1 kg of each initial native litter (QN_0) ranged from 4.9 to 14.2 g, and

Fig. 2 Litter mass remaining (**a**) and nitrogen content (**b**) as a function of decomposition time in litters from early (*white symbols*), intermediate (*grey symbols*) and advanced (*black symbols*) successional stages. Means and standard errors are shown for four to five replicate plots per successional stage (see Table 1). *F* values from two-way (decomposition time and successional stage) analyses of variance testing for the effect of successional stage are given (decomposition time is always significant); ***$P < 0.001$

decreased significantly with field age (Table 2). Between 21% and 75% of this initial N was lost during the course of the experiment. The initial differences in litter N content (CV of 43%) tended to decrease with decomposition time (CV of 22% after 598 days of decomposition) (Fig. 2b). Litter N content was significantly different among plots differing in successional stage (Fig. 2b), and annual N loss rate decreased significantly with field age (Table 2).

All correlations with field age were stronger when the two ''atypical plots'' were removed from the analyses (Table 2).

Initial litter chemical composition, litter decay rate and N release

During the first year of decomposition, mass loss and decay rate were strongly correlated to the initial content in C, N, C:N and hemicellulose concentration of the litter (Table 3; Fig. 3a, c). With increasing time of decomposition, the strength of the relationships between litter chemical composition and decay rate decreased until they reached a threshold after 17–19 months when they became non significant.

The annual N loss rate was significantly correlated to the litter decay rate, more strongly at the beginning of the decomposition ($r = 0.90$, $P < 0.01$ at 222 days) than at the last sampling time ($r = 0.61$, $P = 0.03$). It closely depended on the initial litter N content (Fig. 2b) and secondarily on the initial C and hemicellulose contents (Table 3; Fig. 3d).

Community functional parameters and litter decomposition

Litter C, N, C:N and hemicellulose were significantly related to the three parameters calculated at the community level (Table 4). Consequently, since litter decomposition directly depended on its initial chemical composition, all parameters related to both litter decomposition in the first year and N release were correlated to the characteristics of the living plant community (Table 4). Community-average LDMC was the parameter most closely related to the different litter properties assessed (Table 4; Fig. 4).

Discussion

Succession, plant traits and litter

The replacement of species during the course of succession led to changes in the functional parameters of the plant community: communities composed of fast-growing species with high specific leaf area (SLA) and leaf nitrogen concentration (LNC) and low leaf dry matter content (LDMC) in early succession were progressively replaced by communities composed of slow-growing species with low SLA and LNC and high LDMC (see also Garnier et al. 2004, who studied ten of the plots used in the present work). Comparable trends along successional gradients were found across Europe, in sites where abandonment is

Table 3 Pearson correlations between litter mass remaining (LMR) at first decomposition sampling date (132 days after the beginning of the experiment), litter decay rate (K), annual N loss rate and the initial litter chemical composition ($n = 14$, except for K 717 and 836 days $n = 12$)

	LitC	LitN	LitC:N	Hemicellulose	Cellulose	Lignin
LMR 132 days	−0.71**	−0.92***	0.88***	0.81***	0.54	0.11
K 222 days	0.67*	0.91***	−0.89***	−0.83***	−0.47	0.03
K 307 days	0.70**	0.89***	−0.89***	−0.89***	−0.55*	0.12
K 402 days	0.59*	0.84***	−0.84***	−0.83***	−0.47	0.10
K 500 days	0.55	0.78**	−0.78**	−0.78**	−0.43	0.07
K 598 days	0.45	0.72*	−0.72*	−0.70*	−0.29	0.06
K 717 days	0.23	0.57	−0.55	−0.62	−0.31	0.23
K 836 days	0.16	0.50	−0.50	−0.56	−0.23	0.24
Annual N loss rate	0.60*	0.96***	−0.92***	−0.73**	−0.28	−0.10

LitC, LitN, Lit C:N: carbon, nitrogen and carbon:nitrogen ratio of litter, respectively. Hemicellulose, Cellulose and Lignin refer to the initial concentrations of these compounds in litter

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$ (significance levels corrected by the improved Bonferroni procedure)
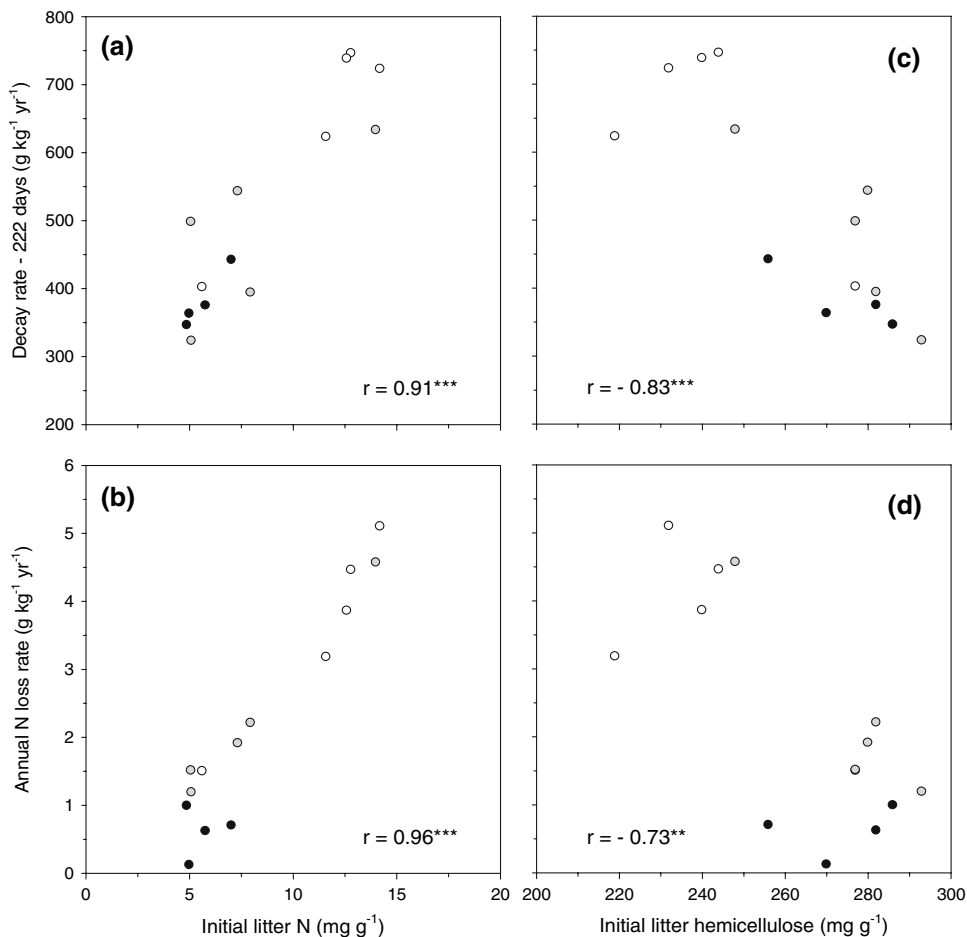
Fig. 3 (**a** and **b**) Relationships between initial litter nitrogen (N) concentration and (**a**) litter decay rate constant after 222 days of decomposition and (**b**) annual N loss rate in the 14 native litters decomposing in the 14 plots studied. (**c** and **d**) Relationships between initial litter hemicellulose concentration and (**c**) litter decay rate constant after 222 days of decomposition and (**d**) annual N loss rate of the 14 native litters decomposing in the 14 plots studied. *White*, *grey* and *black* symbols are for early, intermediate and advanced successional stages, respectively (see Table 1)

the main driver of vegetation dynamics (Garnier et al. 2007).

The trends described here (as well as those concerning litter properties) were stronger when two of the plots were removed from the analyses. The species composition of these plots actually differed substantially from that of plots of comparable age: the 8-year-old plot was dominated by species more typical of later stages (e.g. the perennial grass *Brachypodium phoenicoides*), while the 26-year-old plot was dominated by species more typical of earlier stages (e.g. the short-live perennial Asteraceae *Picris hieracioides*). This may be due to several reasons: (i) incorrect dating of age of abandonment; (ii) particular

propagule sources and/or initial floristic conditions; (iii) particular micro-climatic and/or edaphic conditions not taken into account in the study. Unfortunately, we have not enough information to choose from these different possibilities. The range of variation in decay rate of the standard litter decomposing in the four different plots was small compared to that observed among the native litters decomposing in the same plots: the coefficient of variation of K of the standard litter was only 7% whereas it was 29% at the equivalent sampling time (402 days) for the native litters. We therefore conclude that differences in local climatic and edaphic conditions had only little impact on the regulation of the decay

Table 4 Pearson correlations between community functional parameters and (i) initial litter chemical composition, (ii) litter decay parameters and (iii) litter N release (n = 14, except for K 417 and 836 days n = 12)

	SLA	LDMC	LNC
Initial litter composition			
LitC	0.74**	−0.78**	0.64*
LitN	0.87***	−0.96***	0.87***
LitC:N	−0.86***	0.96***	−0.85***
Hemicellulose	−0.79**	0.83***	−0.74**
Cellulose	−0.35	0.48	−0.27
Lignin	0.22	−0.08	0.21
Litter decay			
LMR 132 days	−0.78**	0.89***	−0.79**
K 222 days	0.80**	−0.90***	0.84**
K 307 days	0.79**	−0.88***	0.80**
K 402 days	0.72**	−0.81***	0.75**
K 500 days	0.68*	−0.75**	0.72**
K 598 days	0.62*	−0.71**	0.67*
K 717 days	0.45	−0.57	0.56
K 836 days	0.39	−0.51	0.50
Litter N release			
Annual N loss rate	0.85***	−0.93***	0.88***

LMR 132 days is the litter mass remaining at the first sampling date (132 days after the beginning of the experiment). SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf nitrogen content. LitC, LitN, Lit C:N: carbon, nitrogen and carbon:nitrogen ratio of litter, respectively. Hemicellulose, cellulose and lignin refer to the initial concentrations of these compounds in the litter

*P < 0.05; **P < 0.01; ***P < 0.001 (significance levels corrected by the improved Bonferroni procedure)

process among plots. Differences observed in the main experiment using the 14 native litters could therefore be attributed to the differences in plant composition and consequently to the corresponding physical and chemical differences among litters.

The changes in community composition resulted in variations of litter properties with age of abandonment: litter N (both concentration and initial content) decreased and hemicellulose increased, while decay rate and N release decreased as succession proceeds. Such a gradual replacement of species along succession with decreasing litter quality and decomposition rates was already and ingeniously demonstrated by Wardle et al. (1997b) who studied litter decomposition in 50 boreal islands that varied in successional

stage, owing to increasing lightning frequency with island size. Lower decomposition and N mineralization rates corresponded to smaller island size and older successional stages. This was explained by the decline in leaf and litter quality as later-successional species replaced earlier ones.

Trends in decomposition with field age obtained here on ''average'' community litters were also found for litters produced by the different species composing these communities: the litter produced by species from early stages tends to decompose more rapidly than that produced by species from later stages (Kazakou et al. 2006). Combining these findings shows that the patterns of litter decay rate observed along the succession were robust enough to scale-up from species to community levels, in spite of potential mixing effects in the pluri-specific litters on which decomposition was assessed (cf. Hättenschwiler et al. 2005).

Which initial chemical compounds controlled litter decomposition?

The initial chemical composition of the litter appeared to control the decay processes for about 1 year and then its impact progressively decreased to become insignificant. Decomposition is a gradual change in litter quality (Joffre et al. 2001) and the effects of initial litter quality on decomposition rate depend on the age of the litter (Cortez et al. 1996; Chapin et al. 2002). The most easily decomposable compounds are lost first, leaving the most resistant fractions, while polymerized compounds may also be synthesized (Minderman 1968). The factors controlling decomposition therefore change with time. For example, Berg and Staaf (1980) showed that nutrients controlled the first stages of decomposition of the litter of *Pinus sylvestris*, whereas the lignin content controlled decomposition in the later stages. Along the same lines, Berg (1986) developed a conceptual model connecting litter quality to the decomposition of a selection of organic compounds, in which litter decay is divided in two parts. The first one corresponds to the decomposition of labile fractions (hydrosolubles, non lignified-cellulose and hemicellulose) which are controlled by nutrient concentration, while the second one corresponds to the decomposition of lignified carbohydrates in which carbohydrates are chemically bound to native lignin.
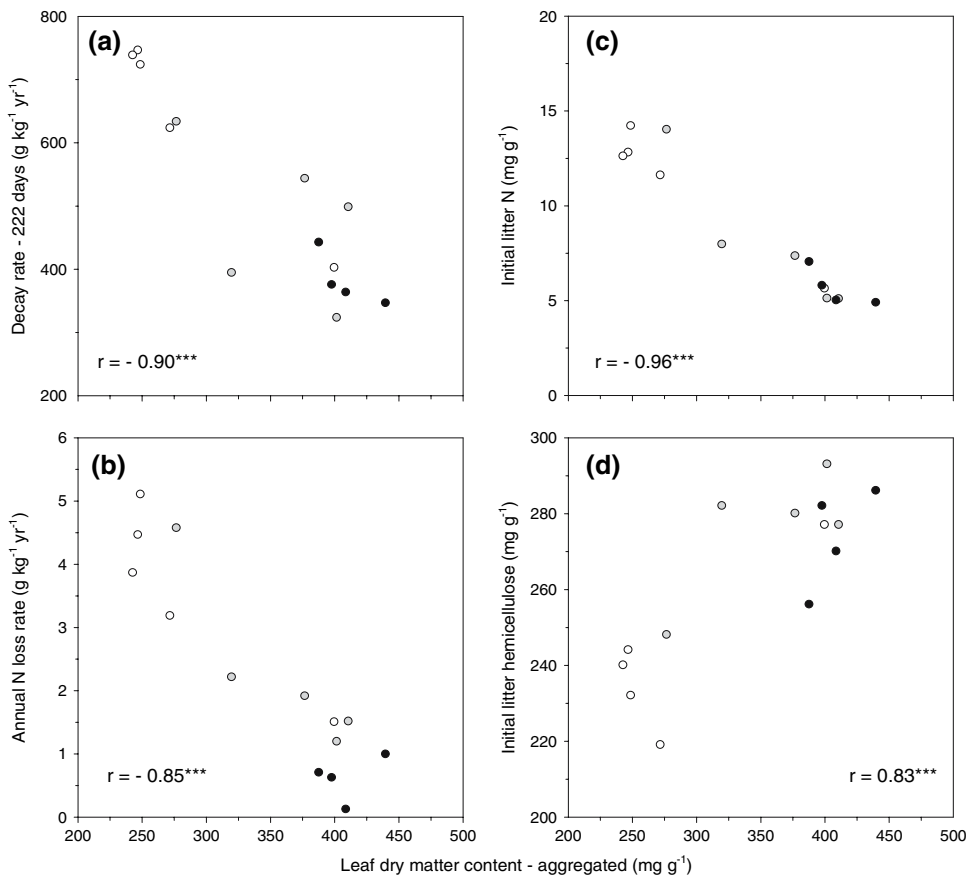
Fig. 4 Relationships between leaf dry matter content (LDMC) of the living plant community and (**a**) litter decay rate constant after 222 days of decomposition, (**b**) annual N loss rate, (**c**) initial litter N concentration and (**d**) initial litter hemicellulose concentration of the 14 native litters decomposing in the 14 plots studied. *White*, *grey* and *black symbols* are for early, intermediate and advanced successional stages, respectively (see Table 1)

Similarly, Aerts and De Caluwe (1997) demonstrated that the initial mass loss of *Carex* litter was controlled by phosphorus related quality parameters; this control decreased with time, as nitrogen control of litter decay became progressively more important. In our study no relations were found between the measured litter chemical compounds at each sampling time and the next rate of decay (data not shown). This study confirms that the links found between the initial litter characteristics and the early stages of decomposition cannot be extrapolated to long-term decomposition.

In the present study, the richer in C and N and the poorer in hemicellulose the initial litter, the faster its mass loss during the first year. N loss rate from litter, which was related to the decay process, depended on the same litter chemical compounds

(cf. Parton et al. 2007). The initial litter N concentration, and its corollary its C:N ratio, were the best predictors of the rate of litter decay, as often observed in decomposition studies (see for example Aber and Melillo 1980; Aerts et al. 1997; Heal et al. 1997; Güsewell and Verhoeven 2006). Initial hemicellulose also played a role here, although less important. It is noteworthy that the initial lignin content of the litter, often found to be an important factor controlling decomposition (see for example Meentemeyer 1978; Berendse et al. 1987; Aber et al. 1990; Aerts et al. 1997), did not appear as an effective predictor in this study. This is probably due to the fact that litter from the old-fields was mainly herbaceous, relatively poor in lignin and showed a low range of variation among plots (not shown).

Relationships between litter properties and traits of the living plant community

Initial litter chemical composition was strongly related to the functional parameters of the living plant community: those communities with high SLA and LNC and with low LDMC provided N-rich and hemicellulose-poor litters which decomposed and released their nitrogen rapidly; conversely, those with low SLA and LNC and with high LDMC provided a litter poor in N and rich in hemicellulose which decomposed more slowly. Therefore, the rates of litter decomposition and N release were related to the traits of the living plant community via litter quality. Comparable results have been found at the species level: leaf mass *per* area—the inverse of SLA—(Gillon et al. 1994), LDMC (Kazakou et al. 2006), tissue nitrogen concentration (Wardle et al. 1998) and leaf toughness (Cornelissen et al. 1999, Pérez-Harguindeguy et al. 2000) have been found to correlate with litter decomposition.

Our results demonstrate that among these different traits, LDMC was the best predictor of litter chemical composition and decomposability. LDMC reflects the proportion of mesophyll versus sclerenchyma and vascular tissues of the leaves (Garnier and Laurent 1994), and relates to the hemicellulose content of the litter (Fig. 4). These results provide further insights into the mechanistic link between the properties of the living leaves and those of litter, and shows that LDMC can be considered as an indicator of the structural and physical attributes of both leaves and litter. LDMC therefore appears as a powerful functional marker (sensu Garnier at al. 2004) of litter decomposition, which was also found in other ecological contexts (Quétier et al. 2007). Further studies should challenge the generality of this conclusion, and evaluate how the predictive power of LDMC compares to other approaches using e.g. growth forms of species as predictors of litter decomposition (e.g. Dorrepaal et al. 2005).

Overall, this study further corroborates the idea that some attributes associated with the functioning of living leaves have an impact on the properties of senescent leaves and on their decomposition rate, therefore contributing to the so-called ''afterlife''

effect (Grime et al. 1996; Wardle et al. 1998; Cornelissen et al. 1999, 2004). A major finding of the present study is that this effect, previously observed at the species level, actually scales up to the community level.

Conclusions

In the present study, land abandonment was the main driver of changes in plant community composition. Along the successional sere, species with low LDMC and high LNC and SLA were progressively replaced by species with opposite characteristics. These changes in leaf traits led to drastic changes in litter quality, and consequently in litter decay rates and nitrogen release. In early stages of succession, species produced litter that decomposed quickly while in later stages the plant communities were dominated by species producing poor-quality litter that decomposed more slowly. Among the traits measured, leaf dry matter content was the best functional marker of litter decomposition and nitrogen release, both of which are fundamental components of ecosystem function. This study provides further support to the hypotheses put forward by Hobbie (1992), Grime (1998) and Wardle et al. (1998), stating that species differences in plant traits and litter quality make up important factors by which plant species affect ecosystem processes.

Appendix

Appendix 1 Means and standard errors (between brackets) of physical and chemical properties in each of the plots studied

Field age (years)	pH (H_2O)	CEC (mol kg^{-1})	Clay (g kg^{-1})	Fine silt (g kg^{-1})	Coarse silt (g kg^{-1})	Fine sand (g kg^{-1})	Coarse sand (g kg^{-1})
7	8.1 (0.1)	12	246 (11)	92 (8)	105 (3)	32 (5)	1 (0.3)
8[†]	8.3 (0.1)	8.3	287 (6)	215 (5)	144 (3)	66 (2)	6 (1.5)
8	8.2 (0.1)	15.7	278 (10)	144 (2)	107 (2)	29 (1)	2 (0.7)
11	8.3 (0.1)	10.5	228 (5)	175 (8)	114 (2)	96 (4)	7 (0.9)
12	8.3 (0.1)	–	184 (5)	74 (2)	61 (2)	33 (2)	6 (0.6)
22	8.3 (0.1)	11.2	230 (7)	139 (4)	177 (3)	65 (4)	6 (0.5)
26	8.3 (0.1)	11.9	274 (5)	168 (4)	102 (2)	57 (2)	3 (0.1)
26[†]	8.2 (0.1)	14.8	249 (9)	264 (5)	110 (3)	39 (3)	23 (1.6)
29	8.2 (0.1)	10.7	209 (8)	253 (5)	327 (5)	125 (5)	14 (1.1)
35	8.3 (0.1)	13.2	278 (4)	158 (9)	101 (2)	64 (5)	6 (1.9)
40	8.1 (0.1)	12.2	123 (5)	173 (6)	136 (4)	138 (2)	50 (3.2)
40	8.1 (0.1)	11.8	203 (12)	80 (5)	71 (2)	23 (1)	1 (0.0)
42	8.2 (0.1)	15.7	314 (16)	164 (3)	99 (4)	33 (1)	3 (0.6)
Pearson	ns	ns	ns	ns	ns	ns	ns

Data are for the upper 10 cm of soil on three batches taken in April 2000, each composed of a mixture of 10 samples taken randomly in each field. CEC is the cation exchange capacity. The last line shows the significance levels of the Pearson correlations between field age and the different soil properties: ns, not significant ($P > 0.05$). –, missing value

[†] Denotes the two ''atypical'' plots (see text)

Appendix 2 List of species (nomenclature follows Tutin et al. 1968–1980, 1993) accounting for at least 70% of the total plant presence recorded along the transect-line in each plot

Species	Field age (years)													
	7	8	8	11	12	22	26	26	26	29	35	40	40	42
Arenaria serpyllifolia	X													
Avena barbata	X		⊗	⊗	X				X					
Avena sterilis			X											
Brachypodium phoenicoides		⊗				⊗	⊗	⊗	X	⊗	⊗	⊗	⊗	⊗
Bromus erectus						⊗					⊗	⊗	⊗	
Bromus lanceolatus	X													
Bromus madritensis	X		X	⊗	⊗		X		X					
Bromus hordeaceus	X													
Calamintha nepeta				X	X		X							⊗
Clematis vitalba			X											
Convolvulus arvensis			X		X		X							
Crepis foetida					X									
Crepis taraxacifolia	X													
Cynodon dactylon	X		X						X					
Dactylis glomerata	X						X							
Daucus carota	X		X	X			X		X					
Dipsacus fullonum			X											
Holcus lanatus			X											
Lotus corniculatus			X											
Medicago lupulina	⊗		X	X	X									
Medicago minima					⊗									
Medicago orbicularis	X													
Picris hieracioides	X		X	X	X		X		⊗					
Potentilla reptans	X		X					⊗						
Prunus spinosa							⊗							
Rubus caesius	⊗	⊗	X	X	X		X		⊗	⊗				
Tordylium maximum			X											
Torilis japonicus	X		⊗				X							
Trifolium angustifolium	X			X										
Vicia angustifolia	X				X									
Vicia heterophylla				X										
Vicia hybrida			X			X	X							
Xeranthemum inapertum							X							
% Herbaceous species	77	98	99	86	70	100	76	95	74	91	99	98	98	99

Circled crosses denote the two dominant species of each field. All species are herbaceous but *Clematis vitalba*, *Prunus spinosa* and *Rubus caesius*. The last line shows the percentage cover of herbaceous species in each plot

Appendix 3 Litter decay rate K in g kg^{-1} year^{-1} (fitted value of K, standard error (SE) and r^2 of the regression) at each sampling time in the different plots

Field age (years)	222 days n = 20		307 days n = 30		402 days n = 40		500 days n = 50		598 days n = 60		717 days n = 70		836 days n = 80	
	K (SE)	r^2	K (SE)	r^2	K (SE)	r^2	K (SE)	r^2	K (SE)	r^2	K (SE)	r^2	K (SE)	r^2
7	623 (24)	0.81	652 (18)	0.88	625 (15)	0.89	626 (12)	0.92	621 (11)	0.93	611 (11)	0.93	618 (10)	0.94
8[†]	402 (14)	0.85	415 (12)	0.87	453 (15)	0.84	492 (16)	0.86	532 (17)	0.87	562 (17)	0.88	592 (18)	0.89
8	746 (40)	0.75	678 (30)	0.70	652 (21)	0.81	671 (17)	0.89	681 (15)	0.91	nd		nd	
11	723 (24)	0.84	665 (20)	0.79	672 (17)	0.86	654 (15)	0.88	682 (15)	0.90	690 (15)	0.91	695 (13)	0.93
12	738 (28)	0.78	682 (20)	0.78	678 (17)	0.86	679 (16)	0.88	669 (14)	0.90	649 (13)	0.89	633 (13)	0.89
22	543 (19)	0.87	531 (15)	0.87	564 (14)	0.90	596 (14)	0.92	606 (12)	0.94	604 (10)	0.95	620 (10)	0.96
26	394 (12)	0.87	399 (9)	0.92	402 (11)	0.86	405 (11)	0.86	452 (14)	0.86	483 (15)	0.86	511 (15)	0.88
26	323 (12)	0.80	350 (10)	0.88	350 (12)	0.80	349 (11)	0.81	367 (11)	0.84	414 (15)	0.82	435 (14)	0.85
26[†]	633 (24)	0.79	588 (16)	0.81	573 (13)	0.86	578 (12)	0.90	569 (10)	0.92	554 (9)	0.92	556 (9)	0.93
29	498 (21)	0.79	501 (16)	0.84	548 (20)	0.82	579 (19)	0.85	647 (26)	0.82	674 (24)	0.85	687 (22)	0.88
35	363 (14)	0.70	387 (12)	0.84	379 (10)	0.85	402 (9)	0.90	405 (8)	0.91	nd		nd	
40	375 (16)	0.73	410 (12)	0.86	435 (12)	0.88	442 (10)	0.90	437 (10)	0.89	427 (9)	0.91	451 (10)	0.90
40	442 (14)	0.82	490 (14)	0.88	500 (12)	0.91	494 (11)	0.91	484 (10)	0.91	485 (11)	0.90	495 (10)	0.92
42	346 (11)	0.83	362 (10)	0.88	381 (15)	0.78	415 (16)	0.79	421 (14)	0.82	441 (13)	0.86	460 (13)	0.88
CV (%)	30		25		23		21		21		18		16	

The last line shows the coefficient of variation (CV) of the decay rate constant at each sampling date. nd, not determined

[†] Denotes the two "atypical" plots (see text)

Appendix 4 Parameters of the linear regressions of litter N content (QN in g kg^{-1} of initial litter) on decomposition time (QN = $a - b \times$ t) for each plot

Field age (years)	a	b	r^2	P
7	10.82	2.72	0.84	<0.001
8[†]	4.08	0.32	0.16	=0.15
8	10.36	2.26	0.59	<0.001
11	12.13	3.76	0.83	<0.001
12	9.06	1.71	0.66	<0.001
22	6.20	1.11	0.54	<0.001
26	6.77	1.47	0.61	<0.001
26	4.15	0.53	0.25	< 0.01
26[†]	9.88	1.97	0.69	<0.001
29	4.31	0.93	0.50	<0.001
35	3.51	−1.21	0.47	<0.001
40	5.34	0.34	0.09	<0.05
40	6.64	0.41	0.10	=0.06
42	3.61	0.22	0.06	=0.09

b, annual N loss rate (g kg^{-1} of initial litter year^{-1}).
Correlation coefficients (r^2) and significance levels (P) are also given

[†] Denotes the two "atypical" plots (see text)

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