

Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe

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Abstract. Land use and climate changes induce shifts in plant functional diversity and community structure, thereby modifying ecosystem processes. This is particularly true for litter decomposition, an essential process in the biogeochemical cycles of carbon and nutrients. In this study, we asked whether changes in functional traits of living leaves in response to changes in land use and climate were related to rates of litter potential decomposition, hereafter denoted litter decomposability, across a range of 10 contrasting sites.

To disentangle the different control factors on litter decomposition, we conducted a microcosm experiment to determine the decomposability under standard conditions of litters collected in herbaceous communities from Europe and Israel. We tested how environmental factors (disturbance and climate) affected functional traits of living leaves and how these traits then modified litter quality and subsequent litter decomposability.

Litter decomposability appeared proximately linked to initial litter quality, with particularly clear negative correlations with lignin-dependent indices (litter lignin concentration, lignin: nitrogen ratio, and fiber component).

Litter quality was directly related to community-weighted mean traits. Lignin-dependent indices of litter quality were positively correlated with community-weighted mean leaf dry matter content (LDMC), and negatively correlated with community-weighted mean leaf nitrogen concentration (LNC). Consequently, litter decomposability was correlated negatively with community-weighted mean LDMC, and positively with community-weighted mean LNC.

Environmental factors (disturbance and climate) influenced community-weighted mean traits. Plant communities experiencing less frequent or less intense disturbance exhibited higher community-weighted mean LDMC, and therefore higher litter lignin content and slower litter decomposability. LDMC therefore appears as a powerful marker of both changes in land use and of the pace of nutrient cycling across 10 contrasting sites.

Key words: climate; community functional parameters; disturbance; leaf traits; litter decomposability; litter quality.

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INTRODUCTION

Human activities alter terrestrial ecosystems, both directly and indirectly, by converting land use, modifying global biogeochemical cycles and altering the number and identity of species present (Vitousek et al. 1997, Foley et al. 2005). In Europe, land use change is driven by substantial urbanization and agricultural

policies that lead to the concentration of agricultural food production in easily accessible productive zones (Bouma et al. 1998) resulting in the marginalization of entire rural areas (Mendras 1984, MacDonald et al. 2000). Land abandonment and management changes modify community functional composition, and consequently contribute to variations in stocks and fluxes of carbon and nitrogen in ecosystems (Chapin et al. 2000). Decomposition of dead plant material is a key component of these fluxes in most terrestrial ecosystems (Swift et al. 1979, Couteaux et al. 1995, Chapin et al. 2002), since it determines the rate at which carbon and nutrients are mineralized from plant litter. It is thus essential to understand how shifts in plant communities due to land use change can modify litter decomposition.

Changes in plant diversity along environmental gradients can be assessed through shifts in species richness and abundance or through variations in functional diversity (Hooper et al. 2005). In the quest for general rules linking environmental factors and species characteristics, functional traits offer a method for going beyond botanical complexity (McGill et al. 2006). They have been proposed as a means of directly predicting changes in ecosystem processes from shifts in plant communities in response to global change factors (Chapin et al. 2000, Diaz and Cabido 2001, Lavorel and Garnier 2002, Lavorel et al. 2007). At the species level, some studies have shown that the rate of ecosystem processes can be either semi-mechanistically (primary productivity; Chapin 1993) or correlatively (litter decomposition; Cornelissen et al. 1999) linked to a small number of functional traits, such as leaf dry matter content or leaf life span.

In the present study, we tested the biomass ratio hypothesis, which postulates that the traits of individual species, combined with their biomass proportion in the community, and not the species number alone, determine the impacts of plant communities on ecosystem processes (Grime 1998, Diaz and Cabido 2001, Garnier et al. 2004). We explicitly tested whether variations in functional parameters of plant communities (*sensu* Violle et al. 2007) resulting from disturbance and climate differences affect litter potential decomposition (litter decomposability hereafter). So far, the biomass ratio hypothesis as applied to decomposition has only been tested within sites (Cortez et al. 2007, Quedsted et al. 2007, Quétier et al. 2007). Here, its validity will be assessed using the broad range of environmental conditions sampled in the European project VISTA ("Vulnerability of Ecosystem Services to Land Use Change in Traditional Agricultural Landscapes"). The VISTA sites represent a variety of situations in Europe where abandonment or decrease in grassland management intensity have resulted in substantial changes in plant communities (Garnier et al. 2007).

Litter decomposition rate is influenced by the litter quality, the decomposer community and the physico-chemical environment (Swift et al. 1979), with the

relative importance of these three factors varying across ecosystems (Lavelle et al. 1993, Pérez-Harguindeguy et al. 2000). Climate appears to be, with some exceptions (e.g., Hobbie 1996), the main direct factor in areas with unfavorable climatic conditions, whereas litter quality seems to prevail when local conditions are favorable (Swift et al. 1979, Lavelle et al. 1993, Couteaux et al. 1995, Pérez-Harguindeguy et al. 2007). In this study, we experimentally tested the influence of litter quality on decomposition rate under standardized conditions by keeping all other environmental factors constant, thus studying the effect of litter quality alone on litter decomposability.

The traditional approach of linking litter decomposability to common predictors of litter quality (e.g., lignin/nutrient ratios) can be extended by linking litter decomposability to functional traits of living leaves (Cornelissen and Thompson 1997, Pérez-Harguindeguy et al. 2000, Kazakou et al. 2006). Structural traits, such as leaf dry matter content, reflect structural support and defense against herbivores, and are thus potentially linked to litter lignin concentration and fiber component. Chemical traits, such as leaf carbon, nitrogen, and phosphorus concentrations, are likely to be related to litter nitrogen concentration or lignin:nitrogen ratio (Cornelissen et al. 2004), albeit modified by resorption of nutrients during senescence (Quedsted et al. 2003). Variations in functional traits of living leaves can thus be expected to have subsequent effects on litter quality and hence on litter decomposability (Pérez-Harguindeguy et al. 2000, Cornelissen et al. 2004, Kazakou et al. 2006, Quedsted et al. 2007). These functional traits could provide easy-to-measure predictive tools of litter decomposability without requiring any detailed knowledge of individual species biology.

To summarize, the hypotheses of our study were that (1) disturbance and climate influence the functional composition and structure of herbaceous communities, whose shifts can be detected by variations in the leaf functional parameters of the plant communities. These modifications in leaf functional parameters subsequently (2) alter the initial leaf litter quality produced by these communities, which ultimately (3) affect the rate of litter decomposability.

MATERIALS AND METHODS

The VISTA experimental design

The study was conducted on the living leaves and the litter of plant communities from nine sites across Europe and one site in Israel (Table 1). Given the geographical range, these sites exhibited contrasting climatic conditions. Mean annual temperature (°C) and mean annual rainfall (mm) were obtained using monthly data from the meteorological stations closest to each site (Garnier et al. 2007). We also used synthetic climate indices, such as the aridity index (as suggested in Garnier et al. 2007), to test the effects of climate on community functional parameters, but it did not improve the analyses of

TABLE 1. Geography, topography, and climate characteristics and land use changes of the 10 VISTA sites selected for this study (adapted from Garnier et al. [2007]).

Country	Locality	Abbreviation	Coordinates	Altitude range (m above sea level)
Czech Republic	Ohrazení	CZ-OHR	48°57' N, 14°36' E	510–510
France	Ercé/Angladure	FR-ERC	42°50' N, 1°17' E	600–1000
France	Hautes Garrigues du Montpelliérais	FR-HGM	43°51' N, 3°56' E	100–160
France	Col du Lautaret	FR-LAU	45°02' N, 6°21' E	1900–2100
Germany	Müritz National Park	GE-MNP	53°27' N, 12°44' E	65–65
Greece	Lagadas	GR-LAG	40°47' N, 23°12' E	450–550
Israel	Karei Deshe	IS-KDE	32°55' N, 32°35' E	150–150
Portugal	Mértola/Castro Verde	PT-MER	37°40' N, 8°00' W	100–150
Scotland	South Uist (Staoinebrig)	SC-SUT	57°16' N, 7°24' W	0–100
Sweden	South East Baltic Sea	SE-BAL	58°50' N, 17°24' N	0–50

responses of functional parameters to climate (results not shown).

The sites also experienced different land use changes: extensification of agricultural practices such as reduction of grazing pressure, decrease in fertilizer input, or complete land abandonment (see details in Appendix A). For each land use treatment at each site, replicate plots were selected in the landscape, providing a total number of 136 plots. The disturbance regimes in each plot were characterized by disturbance intensity (percentage of biomass removed) and return interval of disturbance (year) (see White and Pickett 1985, Kleyer 1999, White and Jensch 2001). In case of rotational disturbances, each disturbance was parameterized separately and the rotation was characterized by aggregating the single values.

Within each plot, sampling areas were selected to collect data pertaining to community composition, species traits, and ecosystem properties. Further details can be found in Garnier et al. (2007).

Leaf traits of the species constituting the plant communities

Five leaf traits known to affect components of the carbon and/or nitrogen cycles at the leaf, entire plant, and ecosystem levels (Reich et al. 1992, Cornelissen et al. 1999, Lavorel and Garnier 2002) were measured in each plot following standardized procedures (Garnier et al. 2001, Cornelissen et al. 2003): leaf dry matter content (LDMC, the oven-dry mass of a leaf divided by its water-saturated fresh mass), specific leaf area (SLA, the ratio of the one-sided area of a fresh leaf by its oven-dry mass), leaf carbon concentration (LCC, total amount of C per unit of dry leaf mass), leaf nitrogen concentration (LNC), and leaf phosphorus concentration (LPC).

Within each plot, traits were measured at peak biomass on the youngest, fully expanded, and well-lit leaves for the most abundant species, i.e., species whose cumulated biomass reached at least 80% of community maximum standing biomass (Garnier et al. 2004).

To test the biomass ratio hypothesis (Grime 1998), leaf functional parameters at the community level were calculated as follows:

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

where p_i is the relative contribution of species i to the maximum biomass of the community, trait_i is the trait value of species i , and n the number of species included in the calculation (Garnier et al. 2004, Violle et al. 2007). These community functional parameters take explicitly into account the number, relative abundance, and identity (in terms of quantitative traits) of species present.

Aboveground “average” litter of plant communities

The aboveground litter of the plant communities was collected at the peak of senescence in each plot of the ten sites. Only the aboveground litter (consisting of dead leaves and stems) of the current growing season was kept for the experiment. The seeds were removed so as to avoid any effect of germination on mass loss measurements under standardized conditions. It was assumed that each litter sample contained the litter of each species in the proportions produced by the plant communities in each plot at a given time. After collection, the litter samples were air dried at ambient temperature (20°C) for three to four days and then stored in the laboratory.

Aboveground “average” litters of plant communities were subjected to two types of experiments (Appendix A): (1) the determination of their decomposability by incubation in microcosms under standardized conditions in the laboratory; to keep a manageable sample size for the lab work, this was done on 86 community litters corresponding to a subsample of three replicate plots for two to four selected treatments per site (Appendix A); and (2) the measurement of their spectral properties by near-infrared reflectance spectroscopy (NIRS); this was done for litters from all communities sampled (Appendix A).

Litter decomposition experiment

Microcosms, as simplified analogues of natural ecosystems, allow the study of litter decomposition under controlled temperature and humidity, with similar soil conditions and decomposer populations. As microcosms exclude the influence of biotic and abiotic factors

TABLE 1. Extended.

Type of climate	Temperature (°C)	Rainfall (mm/year)	Land use change	No. treatments/plots
central European temperate	8.2	583	experimental regimes	3/6
mountain humid	10.0	1079	extensification	6/18
Mediterranean subhumid	13.2	994	abandonment	3/12
subalpine	3.0	902	extensification	5/15
temperate	8.7	639	extensification/abandonment	8/21
Mediterranean semiarid	12.1	586	extensification/abandonment	4/12
Mediterranean semiarid	19.6	572	abandonment/extensification	4/12
Mediterranean	16.6	538	extensification/abandonment	4/12
oceanic	8.4	1275	abandonment	3/9
cold temperate	6.0	551	abandonment/extensification	4/19

that can play a role in situ, they solely reveal the effect of initial litter quality on the decomposition process.

The microcosm type used for this experiment was described by Taylor and Parkinson (1988). Each microcosm chamber, 15 cm high, was made out of a 15 cm diameter polyvinylchloride pipe, fitted with a lid and a sealed bottom. The lid could be opened to allow gas exchange and the plug at the bottom could be removed to drain excess water. A grid, 2 cm above the bottom, divided the chamber into two unequal parts: a usable space of 1.5-L capacity and a drainage compartment of 300 mL. One kilogram of soil, of previously known water holding capacity, was placed on the grid. The soil was a mixture (3:1) of mineral soil and surface organic horizon from an experimental field (Kazakou et al. 2006).

For each replicate plot of the two to four selected treatments per site ($n = 86$; Appendix A), five litter samples of 3 g were sealed in a nylon litter bag of 1 mm mesh (Northern Mesh, Oldham, UK). Each litter sample was soaked for 24 h in 0.1 L of water, and then placed on the surface of the microcosm soil. In order to keep all the soluble nutrients in the system, the soaking water was poured into the microcosm. The soil was subsequently moistened up to 80% of field capacity. The microcosms were kept in the dark at 22°C throughout the experiment and watered once a week to maintain constant soil moisture during incubation. For each replicate plot, one litter sample was removed from the microcosms at the end of 1, 2, 4, 6, and 8 weeks. Soil particles were carefully removed from the litter bags and the litter samples were weighed after drying for 48 h at 55°C. Prior to the experiment, two litter samples of 2 g from each replicate plot were weighed, dried in an oven for 48 h at 55°C and weighed again in order to correct the initial mass for the water content of the litter. We then calculated the percentage of litter mass remaining, which will be denoted %LMR hereafter.

To compare the decomposability of the different litters, the single negative exponential model proposed by Olson (1963) was fitted to the %LMR of each litter during the course of the experiment: $\%LMR = DM_0 \times e^{-kt}$, where DM_0 is the dry mass at time = 0 and k is the litter decomposability rate over time t in days.

Near-infrared reflectance spectroscopy calibrations and predictions

Near infrared reflectance spectroscopy (NIRS) is a nondestructive and highly precise physical method based on the selective absorption of near infrared electromagnetic waves by organic molecules (Birth and Hecht 1987). NIRS has proved useful to relate the spectra of samples to their laboratory biochemical values in a number of litter decomposition studies (McLellan et al. 1991, Joffre et al. 1992, 2001, Gillon et al. 1993, 1994, 1999b).

In the present study, spectral properties of the initial litter were established for each replicate plot of each treatment at each site ($n = 136$; Appendix A). For each initial litter, a 5-g subsample was ground in a cyclone mill (Cyclotec Sample Mill 1093; Tecator, Hogånäs, Sweden) with a filter mesh of 1 mm aperture diameter, and then scanned by a near-infrared reflectance spectrometer (NIRSystem 6500) so as to produce an average spectrum with 1050 data points. Data analysis was conducted with the ISI software system (Shenk and Westerhaus 1991).

NIRS was first used to develop calibration equations between the spectral properties and the decomposability rate (k) of the 86 litters studied in the microcosm experiment (see Appendix A). Calibration equations were calculated using cross-validated partial least square (PLS) method (Shenk and Westerhaus 1991) (Appendix B; Table B1). As measured and predicted litter decomposability rates were strongly positively correlated ($k_{\text{micr}} = 1.02k_{\text{NIRS}} - 0.19$, $R^2 = 0.85$, $P < 0.0001$; Fig. 1), the NIRS method proved to allow a precise prediction of litter decomposability from its spectral data. Consequently the established calibration equations were used to predict litter decomposability (hereafter NIRS-predicted litter decomposability) of all the plots, including those that were not studied in microcosms, from their spectral properties (Appendix A).

Furthermore, using calibration equations between initial litter spectral properties and its chemistry (Appendix B, Table B2) that were established previously on a large set of initial litters encompassing a very large array of species (Joffre et al. 1992, Gillon et al. 1993, 1999a), indices of initial quality were predicted for all

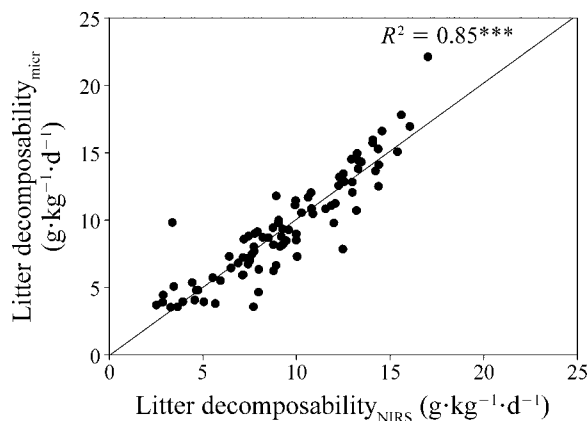


FIG. 1. Regression between near infrared reflectance spectroscopy (NIRS) predicted litter decomposability and microcosm-measured litter decomposability. Regression R^2 and probability are indicated.

*** $P < 0.001$.

litters from their spectral properties: nitrogen (N), lignin (LIG), cellulose (CEL), and hemicellulose (HEM) concentrations. Three litter quality indices relating to the proportions of labile and non-labile compounds in the plant organic matter were calculated to test their relevance as litter decomposability indicators (Berg et al. 1984, McClaugherty and Berg 1987, Gillon et al. 1994, Cortez et al. 1996, Cornelissen et al. 2004): lignin: nitrogen ratio (LIG:N), holocellulose:hemicellulose ratio (HLQ = (CEL + HEM)/(LIG + CEL + HEM)), and litter fiber component or sum of non-labile compounds (LCH = LIG + CEL + HEM).

Statistical analyses

As the set of litter samples used to develop calibration equations of litter decomposability by the NIRS method encompassed the set of litter samples whose decomposability were predicted (PCA, results not shown), we legitimately used NIRS-predicted litter decomposability to conduct the statistical analyses on all replicate plots.

To test the influence of disturbance on litter decomposability at the intra-site level, a two-way ANOVA was carried out at each site using disturbance intensity and return interval of disturbance as explanatory factors in the analysis (Whittingham et al. 2006).

As our experimental design was unbalanced between sites, the relative influence of disturbance and climate parameters, as well as their interactions, on litter decomposability at the inter-site level was tested using residual maximum likelihood methods (REML), with disturbance and climate parameters as fixed effects and site as a random effect (Whittingham et al. 2006). The REML algorithm actually estimates the parameters effects and variance components in a linear mixed model (with both fixed and random effects). Like regression, it can be used in unbalanced designs; but unlike regression, it can account for more than one source of variation in the data, providing an estimate of the variance components associated with the random terms in the model. The same REML analysis was subsequently used to test the effects of disturbance and climate on community functional parameters at the inter-site level.

Correlations among community functional parameters, indices of initial litter quality and litter decomposability at the inter-site level were tested using Pearson's rank coefficients. Pearson's rank coefficients were also used to establish the links between community functional parameters and indices of initial litter quality at the intra-site level.

The statistical analyses were conducted on the 86 litter decomposability rates measured in microcosm and the 136 litter decomposability rates predicted by NIRS. We present only the results for NIRS-predicted litter decomposability hereafter, the results for litter decomposability measured in microcosm being qualitatively similar (see Appendix C).

The statistical tests were run using the SAS system, Version 9.1 (SAS Institute 2003) and Genstat 8.1 (VSN International, Hemel Hempstead, UK).

TABLE 2. Intra-site ANOVA results of the influence of disturbance parameters on near-infrared reflectance spectroscopy (NIRS) predicted litter decomposability.

Site	No. plots	Disturbance intensity (% biomass removed)			Return interval of disturbance (yr)		
		Variation	<i>F</i>	df	Variation	<i>F</i>	df
CZ-OHR	6	[0; 50]	9.32*	1, 4	[1; 15]	9.32*	1, 4
FR-ERC	18	[32.3; 51.9]	1.68 ns	1, 16	[0.33; 0.33]	‡	
FR-HGM	12	[0; 0]	‡		[2; 42]	4.20†	1, 10
FR-LAU	15	[8; 31]	1.42 ns	1, 13	[1; 1]		
GE-MNP	21	[0; 47.9]	7.13*	1, 18	[0.003; 50]	4.13†	1, 18
GR-LAG	12	[10; 20]	0.02 ns	1, 10	[0; 0]	‡	
IS-KDE	12	[0; 65]	37.49***	1, 9	[0.005; 30]	0.31 ns	1, 9
PT-MER	12	[0; 110]	2.44 ns	1, 8	[2; 20]	15.16***	1, 8
SC-SUT	9	[40; 100]	0.21 ns	1, 7	[0.005; 0.01]	0.21 ns	1, 7
SE-BAL	19	[0; 20]	3.05 ns	1, 16	[0.01; 60]	15.12**	1, 16

Notes: Intervals (minimum and maximum) and *F* values with their probabilities are indicated. See Table 1 for site abbreviations.

† $0.05 < P < 0.07$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, nonsignificant.

‡ Because the range of variation of the factor is null, the statistical test cannot detect any effect of this factor on the variable.

TABLE 3. Inter-site residual maximum likelihood (REML) results of the influence of disturbance and climate parameters on factors.

Environmental factor	k_{NIRS} ($\text{g}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$)	LDMC (mg/g)	SLA (m^2/kg)	LCC (mg/g)	LNC (mg/g)	LPC (mg/g)
Rainfall (mm)	0.003 ns	-0.123 ns	0.000 ns	0.027 ns	0.003 ns	0.002 ns
Temperature ($^{\circ}\text{C}$)	0.004***	-9.809*	0.040 ns	-0.544 ns	0.970 ns	0.173**
Disturbance intensity (%)	0.148***	-0.754***	0.013***	-0.158†	-0.393 ns	0.029***
Return interval of disturbance (year)	-0.484***	0.505***	0.030†	-0.541 ns	-1.419***	0.099 ns
Rainfall \times temperature	-0.002†	-0.001 ns	0.000 ns	0.125 ns	0.002 ns	0.000 ns
Rainfall \times intensity	-0.000 ns	-0.000 ns	-0.001 ns	-0.000 ns	-0.000 ns	0.000*
Rainfall \times frequency	-0.000 ns	0.006***	0.001 ns	-0.002 ns	-0.001***	-0.000 ns
Temperature \times intensity	-0.000 ns	-0.085 0	0.000 ns	-0.016 ns	0.002 ns	0.000 ns
Temperature \times frequency	0.003 ns	0.114 ns	-0.001***	0.087 ns	0.201*	-0.000 ns
Intensity \times frequency	-0.019 ns	-0.074 ns	0.001 ns	-0.011 ns	-0.051**	0.004 ns

Notes: Slopes and χ^2 probabilities are indicated. Factors are NIRS-predicted litter decomposability (k_{NIRS}), community-weighted mean leaf dry matter content (LDMC), specific leaf area (SLA), and leaf carbon, nitrogen, and phosphorus concentrations (LCC, LNC, and LPC, respectively).

† $0.05 < P < 0.07$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, nonsignificant).

RESULTS

Disturbance and climate effects on litter decomposability

At the intra-site level, disturbance intensity drove litter decomposability in three sites (Czech Republic, Germany, and Israel), while return interval of disturbance drove it in five sites (Czech Republic, France-Montpellier, Germany, Portugal, and Sweden; Table 2). However, in some sites, the small range of variation or the small number of replicates for a given disturbance parameter prevented detecting its effects on litter decomposability (Appendix D). This was the case in most sites for disturbance intensity and in four sites (France-Ercé, France-Lautaret, Greece, and Scotland) for return interval of disturbance.

At the inter-site level, disturbance parameters significantly influenced litter decomposability (Table 3). A 10-fold increase in disturbance intensity led to a 12.8%

increase in litter decomposability, while a 10-year increase in return interval of disturbance led to a 48.4% decrease in litter decomposability (Fig. 2). Moreover the significant interaction between disturbance intensity and return interval of disturbance suggested that disturbance intensity enhanced the effect of return interval of disturbance, further decreasing litter decomposability. Return interval of disturbance corresponds to time since last disturbance, thus reflecting succession length. Litter decomposability was lowest on late successional plots, such as those at France-Montpellier and Sweden. The effect of climate at the inter-site level was less clear (Table 3), which might arise because we only had 10 different sites for the statistical analysis. Only the interaction between rainfall and temperature showed marginally significant effect on litter decomposability.

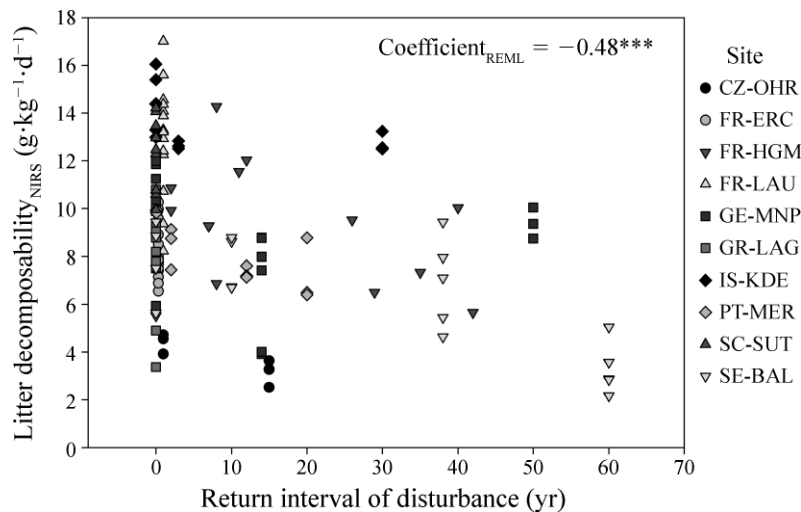


FIG. 2. Relationship between NIRS-predicted litter decomposability and return interval of disturbance. Residual maximum likelihood (REML) coefficient and probability are indicated. See Table 1 for site abbreviations.

*** $P < 0.001$.

TABLE 4. Intra-site correlation between NIRS-predicted litter decomposability and community-weighted mean leaf dry matter content (LDMC), specific leaf area (SLA), and leaf carbon, nitrogen, and phosphorus concentrations (LCC, LNC, and LPC, respectively).

Site	No. plots	LDMC (mg/g)		SLA (m ² /kg)		LCC (mg/g)	
		Variation	<i>r</i>	Variation	<i>r</i>	Variation	<i>r</i>
CZ-OHR	6	[301.46; 360.80]	0.562 ns	[12.95; 14.94]	0.027 ns	[430.13; 443.60]	0.001 ns
FR-ERC	18	[201.31; 250.83]	-0.427 ns	[17.07; 34.67]	0.291 ns	[480.12; 519.85]	-0.410 ns
FR-HGM	12	[192.40; 410.40]	-0.818 **	[13.10; 23.60]	0.710**	[430.00; 453.00]	0.171 ns
FR-LAU	15	[281.08; 383.35]	-0.226 ns	[9.81; 21.76]	0.623*	[438.02; 456.21]	0.196 ns
GE-MNP	21	[170.55; 310.50]	-0.137 ns	[18.58; 65.36]	0.184 ns	[290.54; 471.48]	-0.172 ns
GR-LAG	12	[216.91; 317.88]	0.141 ns	[17.58; 26.19]	-0.237 ns	[430.13; 473.08]	0.242 ns
IS-KDE	12	[147.96; 242.48]	-0.395 ns	[25.66; 34.28]	0.596*	[371.19; 407.50]	-0.434 ns
PT-MER	12	[222.34; 529.19]	-0.690*	[6.18; 31.38]	0.589*	[422.03; 482.02]	-0.724**
SC-SUT	9	[182.10; 226.22]	0.254 ns	[18.98; 34.17]	-0.605 ns	[420.49; 456.44]	0.225 ns
SE-BAL	19	[373.46; 507.51]	-0.465 *	[19.66; 30.09]	-0.165 ns	[459.89; 497.87]	-0.336 ns

Notes: Intervals (minimum and maximum) and Pearson correlation coefficients with their probabilities are indicated. See Table 1 for site abbreviations; nd, no data.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, nonsignificant.

Disturbance parameters appeared as drivers of litter decomposability both within and among sites in our study. To analyze their effects with more detail, we identified two groups: successional sites (with current zero disturbance intensity, thus characterized by the time since abandonment) and managed sites (with a range of positive disturbance intensities). Among successional sites, litter decomposability significantly decreased with increasing time since last disturbance (slope = -0.034 , $P < 0.05$) while it showed no response to climate (slope = -0.001 , not significant [ns], for rainfall and slope = 0.649 , ns, for temperature). Among managed sites, there was no effect of disturbance intensity on litter decomposability (slope = 0.044 , ns). However, with increasing rainfall, litter decomposability decreased significantly more at higher mean temperatures (slope = -0.004 , $P < 0.01$). For example, France-Ercé and France-Lautaret have similar and relatively

high mean annual rainfall (around 1000 mm), but France-Ercé has higher mean annual temperature and substantially lower litter decomposability than France-Lautaret.

Disturbance and climate effects on community functional parameters

Disturbance parameters significantly influenced community functional parameters at the inter-site level (Table 3). With increasing disturbance intensity, LDMC decreased while SLA and LPC increased. With increasing return interval of disturbance, LDMC increased whereas LNC decreased. Moreover, higher intensity of disturbance enhanced the effect of time since last disturbance, further decreasing LNC.

Concerning climate parameters, only temperature had direct effects on two community functional parameters

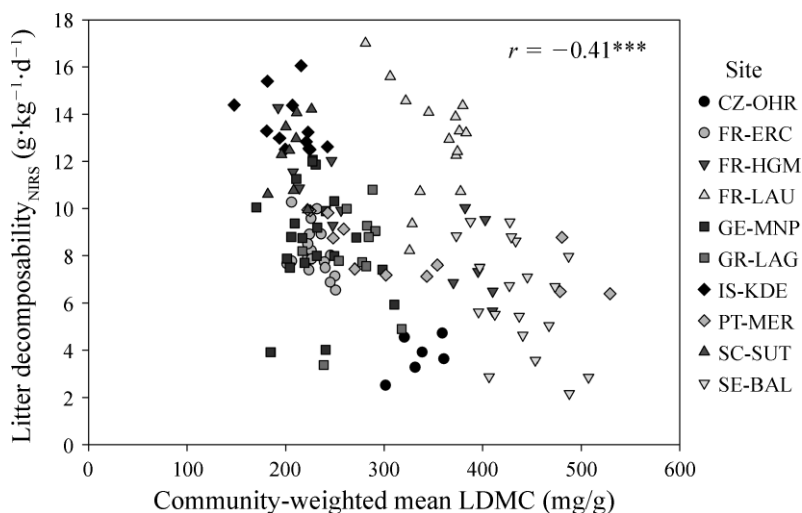


FIG. 3. Correlation between NIRS-predicted litter decomposability and community-weighted mean leaf dry matter content (LDMC). Pearson correlation coefficient and probability are indicated. See Table 1 for site abbreviations.

*** $P < 0.001$.

TABLE 4. Extended.

LNC (mg/g)		LPC (mg/g)	
Variation	<i>r</i>	Variation	<i>r</i>
[1.88; 2.14]	-0.715 ns	[1.42; 2.02]	-0.815*
[21.71; 42.26]	0.040 ns	[1.34; 4.59]	0.232 ns
[9.98; 28.70]	0.632*	[1.90; 2.99]	0.693*
[12.65; 24.32]	0.780***	[0.74; 2.18]	0.823***
[15.29; 33.12]	0.371 ns	[0.10; 0.32]	-0.092 ns
[16.46; 23.00]	-0.462 ns	[1.20; 2.39]	-0.648*
[21.57; 29.02]	0.197 ns	[2.25; 4.47]	-0.052 ns
[18.54; 23.58]	0.268 ns	[1.17; 2.40]	0.200 ns
[19.22; 32.94]	-0.390 ns	[1.15; 3.55]	0.302 ns
[13.86; 23.56]	0.629***	nd	nd

at the inter-site level (Table 3): LDMC decreased while LPC increased with increasing temperature.

Climate effects on community functional parameters were often detected when in interaction with disturbance parameters (Table 3). At higher temperature, LDMC decreased more as disturbance intensity increased while SLA and LNC decreased more with increasing return interval of disturbance. Higher rainfall exaggerated the effect of return interval of disturbance, further promoting LDMC and reducing LNC. It appeared that disturbance was the major driver of changes in community functional parameters, while climate only modulated these effects.

Links between community functional parameters, litter quality, and litter decomposability

At the intra-site level, the links between community functional parameters and litter decomposability were not easy to disentangle. For example, only three sites, all undergoing land abandonment, exhibited a negative relationship between litter decomposability and LDMC (Table 4). The lack of significant relationships in the other sites was probably the consequence of the small range in trait value or sample size in some sites (e.g., the Czech site, Fig. 3, and Appendix D).

At the inter-site level, litter decomposability was strongly correlated with community functional param-

eters (Table 5), notably with LDMC (Fig. 3). Litter decomposability decreased with increasing LDMC and LCC, whereas it increased with increasing LNC and LPC. Conversely it showed no correlation with SLA.

Among sites, community functional parameters were significantly correlated to litter quality indices (Table 5). LDMC was positively correlated with LIG, LCH, and especially with LIG:N (Fig. 4), but was negatively correlated with CEL, HEM, and HLQ. LCC related positively to LIG and LIG:N, but negatively to N. LNC was positively correlated with N but related negatively to LIG and LIG:N.

Accordingly, when we could detect a significant correlation within sites, we found that litter decomposability decreased with LIG, LIG:N, and LCH (Table 6). Analyses among sites confirmed these links between litter decomposability and litter chemistry (Table 5), notably the strong negative correlation between litter decomposability and LIG:N (Fig. 5).

At the intra- and inter-site levels, we found that a plant community with a high LDMC produced a litter with higher LIG:N that decomposed more slowly. A closer examination of the link between LDMC and LIG:N (Fig. 4) showed that the three late-successional plots in Portugal (PT-MER) were outliers. When removing them from the analysis, the correlation between LDMC and LIG:N increased (Pearson product-moment correlation coefficient, *r*, increasing from 0.34 [*P* < 0.001] to 0.46 [*P* < 0.001]). Still, at a given LIG:N, we observed a variation that was due to the discrepancy of some sites: SE-BAL, FR-LAU, and three plots from FR-HGM. These sites were characterized by a very low percentage of annuals (<1.5%). Litter decomposability appeared positively correlated with the percentage of annuals (*r* = 0.26, *P* < 0.01). Annuals generally have lower LDMC and higher SLA and LNC than perennials (Garnier et al. 1997). A multiple regression of LIG:N with LDMC, SLA, and LNC as explanatory factors showed that LIG:N = 0.03LDMC + 0.46SLA - 0.46LNC + 8.94 (*R*² = 0.17, *P* < 0.001). The corresponding equation for NIRS-predicted litter decomposability was: *k*_{NIRS} = -0.02LDMC - 0.11SLA +

TABLE 5. Inter-site Pearson correlation test between NIRS-predicted litter decomposability (*k*_{NIRS}) and both community functional parameters and initial litter quality indices.

Parameter	<i>k</i> _{NIRS} (<i>n</i> = 136)	LDMC (<i>n</i> = 136)	SLA (<i>n</i> = 134)	LCC (<i>n</i> = 135)	LNC (<i>n</i> = 135)	LPC (<i>n</i> = 116)
<i>k</i> _{NIRS}		-0.409***	0.124 ns	-0.299***	0.313***	0.277**
Nitrogen concentration	0.122 ns	-0.086 ns	0.11 ns	0.270**	0.200*	-0.339***
Lignin concentration	-0.482***	0.287***	0.15 ns	0.457***	-0.168†	-0.263**
Cellulose concentration	-0.126 ns	-0.291***	0.06 ns	0.093 ns	0.090 ns	0.309***
Hemicellulose concentration	0.071 ns	-0.105***	-0.01 ns	-0.117 ns	0.181*	0.163 ns
Lignin: nitrogen ratio	-0.656***	0.342***	0.05 ns	0.269***	-0.318***	0.030 ns
HLQ	0.354***	-0.356***	-0.12 ns	-0.433***	0.183*	0.339***
LCH	-0.390***	-0.184*	0.12 ns	0.190*	0.051 ns	0.081 ns

Notes: Pearson correlation coefficients and probabilities are indicated. Abbreviations: LDMC, leaf dry matter content; SLA, specific leaf area; LCC, leaf carbon concentration; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; HLQ, holocellulose : hemicellulose ratio; LCH, litter fiber component.

† 0.05 < *P* < 0.07; * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001; ns, nonsignificant.

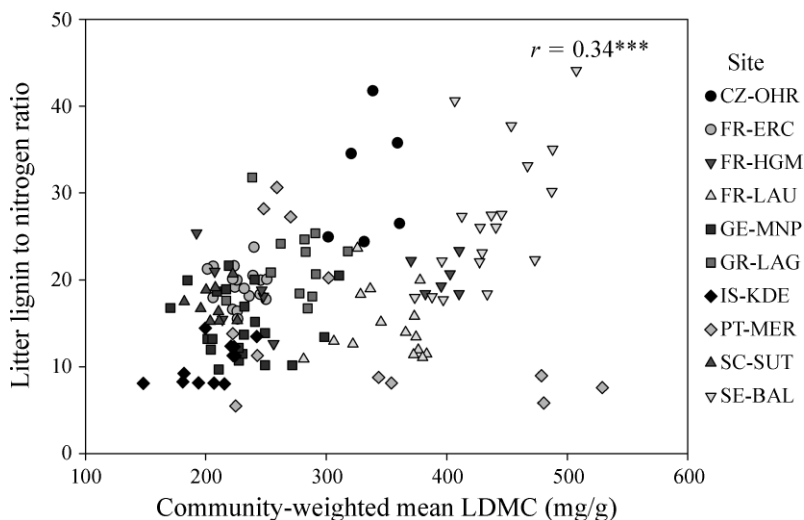


FIG. 4. Correlation between initial litter lignin to nitrogen ratio and community-weighted mean leaf dry matter content (LDMC). Pearson correlation coefficient and probability are indicated. See Table 1 for site abbreviations. *** $P < 0.001$.

0.11LNC + 13.74 ($R^2 = 0.22$, $P < 0.001$). LDMC was thus not the only factor controlling litter quality and subsequent litter decomposability.

DISCUSSION

Methodological considerations

The litter used in this study is a community “average” litter in the sense that all the senescent parts of the species present in the community at senescence peak were collected, similarly to other studies (e.g., Aerts and de Caluwe 1997a, Hector et al. 2000, Knops et al. 2001). It is thus likely that litter quality and decomposability of plant communities with a high proportion of early senescing species was underestimated, since this litter would already be somewhat decomposed at the time of collection. However collecting litter from each species at its peak of litter production (which would demand fine monitoring of each species phenology) was deemed too labor intensive to be appropriate for a multisite

screening study and would introduce other artifacts due to altered relative starting times of decomposition for different species. The method used here produces litter samples which are representative of the real substrate for the decomposition process at the peak of senescence in a given plant community.

An important consideration when assessing the microcosm experiment is whether the results, obtained using the same soil with associated decomposer organisms for all samples, gives a robust indication of decomposition processes. However there is evidence that species ranking in terms of litter decomposition rates is robust to methodological and environmental factors (Cornelissen et al. 1996, 1999, Gillon et al. 1999b, Pérez-Harguindeguy et al. 2000, Joffre et al. 2001, Queded et al. 2003, 2007). Even though climate conditions and soil decomposer communities strongly influence in situ decomposition, there is a good correlation between in situ litter decomposition and microcosm litter decomposability (Aerts and de Caluwe

TABLE 6. Intra-site Pearson correlation test between NIRS-predicted litter decomposability and initial litter quality.

Sites	No. plots	Nitrogen concentration		Lignin concentration		Cellulose concentration	
		Variation	r	Variation	r	Variation	r
CZ-OHR	6	[0.49; 0.69]	-0.727 ns	[16.15; 20.30]	0.661 ns	[27.79; 32.02]	-0.090 ns
FR-ERC	18	[0.64; 0.95]	0.228 ns	[11.95; 17.34]	0.096 ns	[25.36; 37.56]	-0.552*
FR-HGM	12	[0.58; 1.07]	0.287 ns	[12.25; 17.61]	0.583*	[25.21; 33.54]	-0.545 ns
FR-LAU	15	[0.54; 1.09]	0.568*	[7.66; 16.49]	-0.504†	[20.79; 32.75]	-0.809***
GE-MNP	21	[0.81; 1.85]	0.685***	[13.44; 26.57]	0.045 ns	[18.74; 32.19]	-0.552**
GR-LAG	12	[0.56; 1.01]	0.169 ns	[10.14; 20.40]	-0.343 ns	[30.11; 39.52]	0.022 ns
IS-KDE	12	[0.49; 0.75]	0.737**	[4.54; 7.49]	-0.418 ns	[27.79; 34.12]	-0.874***
PT-MER	12	[0.35; 0.94]	-0.64*	[1.92; 15.31]	-0.242 ns	[13.20; 34.35]	0.734**
SC-SUT	9	[0.95; 1.78]	0.012 ns	[15.80; 29.78]	-0.366 ns	[17.89; 27.02]	-0.650†
SE-BAL	19	[0.70; 1.26]	0.501*	[15.02; 33.00]	-0.592**	[19.17; 27.11]	-0.323 ns

Notes: Intervals (minimum and maximum) and Pearson correlation coefficients with their probabilities are indicated. Abbreviations: HLQ, holo cellulose : hemicellulose ratio; LCH, litter fiber component. See Table 1 for site abbreviations.

† $0.05 < P < 0.07$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, nonsignificant.

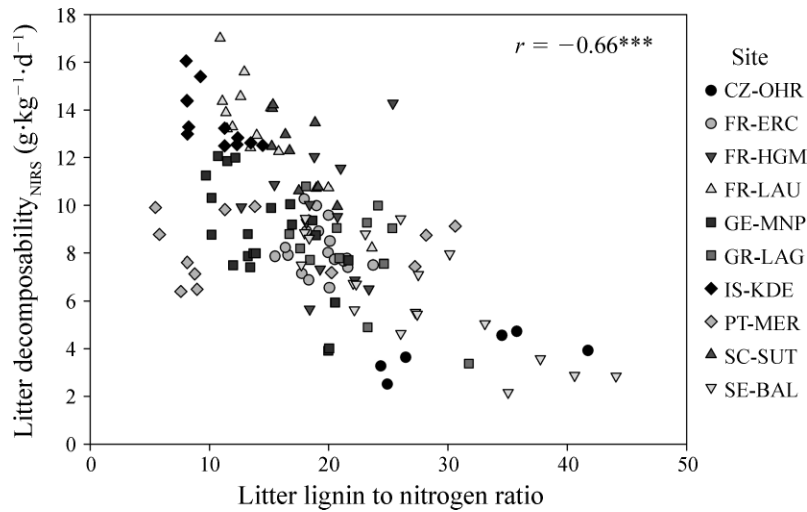


FIG. 5. Correlation between NIRS-predicted litter decomposability and initial litter lignin to nitrogen ratio. Pearson correlation coefficient and probability are indicated. See Table 1 for site abbreviations.
 *** $P < 0.001$.

1997b). Besides, the aim of our study was to investigate the effects of land use change and climate on litter quality and decomposition under standard conditions rather than to measure in situ decomposition rates, which are influenced by each site’s inherent factors.

The present study supports previous evidence that NIRS is a reliable method to predict litter decomposability rate from litter spectral data (Joffre et al. 1992, 2001, Gillon et al. 1993, 1999b). Moreover NIRS has so far mostly been used at the species level. Here, we emphasize that the approach remains valid when scaling up from the species level to the ecosystem level, which broadens the application possibilities of the NIRS method.

Disturbance and climate effects on litter decomposability captured by community functional parameters

In this study, we showed that disturbance and climate could modify litter decomposability via changes in functional traits of living leaves of the plant community,

variations that will afterwards affect the litter properties. We demonstrated that a plant community experiencing lower disturbance intensity or longer time since last disturbance had higher community-weighted mean LDMC and lower community-weighted mean LNC. We confirmed other studies conducted at the intra-site level on the effect of variations of anthropogenic pressure on community functional parameters. These include a 12-year manipulation of montane grassland management (Louault et al. 2005) that showed community functional parameters, including LDMC and LNC, responded significantly to management intensity. Consistent with our study, LDMC increased with decreasing management. Likewise, Garnier et al. (2004) found that vegetation changes along a Mediterranean post-cultural succession corresponded to shifts from species with traits allowing rapid resource acquisition to species with traits conferring efficient resource conservation: community-weighted mean LDMC significantly increased

TABLE 6. Extended.

Hemicellulose concentration		Lignin : nitrogen ratio		HLQ		LCH	
Variation	<i>r</i>	Variation	<i>r</i>	Variation	<i>r</i>	Variation	<i>r</i>
[26.11; 28.42]	-0.639 ns	[24.37; 41.75]	0.700 ns	[0.74; 0.79]	-0.689 ns	[70.82; 77.78]	0.171 ns
[21.22; 29.91]	-0.680**	[15.49; 23.72]	-0.192 ns	[0.73; 0.84]	-0.395 ns	[63.85; 81.55]	-0.636**
[17.62; 28.41]	-0.748**	[12.67; 25.37]	0.070 ns	[0.73; 0.82]	-0.756**	[57.76; 76.93]	-0.537 ns
[17.24; 27.03]	-0.832***	[10.88; 23.62]	-0.873***	[0.74; 0.87]	-0.040 ns	[48.12; 76.26]	-0.901***
[11.44; 27.37]	-0.498*	[9.69; 21.63]	-0.636**	[0.55; 0.78]	-0.301 ns	[53.40; 77.28]	-0.641**
[20.92; 30.86]	-0.393 ns	[16.71; 31.75]	-0.587*	[0.73; 0.86]	0.224 ns	[68.59; 85.76]	-0.326 ns
[20.99; 26.73]	-0.911***	[8.04; 14.47]	-0.684*	[0.88; 0.92]	0.089 ns	[54.85; 68.30]	-0.863***
[9.10; 28.50]	0.722**	[5.48; 30.61]	0.088 ns	[0.72; 0.97]	0.796**	[30.56; 73.65]	0.634*
[17.23; 20.91]	0.186 ns	[15.23; 20.71]	-0.721*	[0.57; 0.74]	0.159 ns	[55.34; 70.43]	-0.695*
[11.21; 22.81]	0.378 ns	[17.72; 44.09]	-0.805***	[0.50; 0.76]	0.440†	[55.64; 71.70]	-0.619**

with successional stage, whereas community-weighted mean LNC decreased.

Moreover, we found that community-weighted mean LDMC decreased with increasing temperature. This pattern can be related to the decrease in litter LIG:N with increasing temperature that Murphy et al. (2002) found in grassland species, though it stands in contradiction with Niinemets (2001) who showed that leaf density increased with temperature in a set of shrubs and trees. Conversely, we found no effect of rainfall on the community functional parameters we investigated, in agreement with Wright et al. (2004). These latter studies used traits of individual species as data points, whereas we used community-weighted averages. A further analysis will be carried out to test if the impact of environmental factors on leaf traits differs between species- and community-based analyses (see Garnier et al. 2004, Cingolani et al. 2007, Pakeman et al. 2008). Community functional parameters, and the ensuing rate of litter decomposability, thus appeared mostly driven by disturbance, whose effects were modulated by climate. For example, community-weighted mean LDMC decreased more with increasing disturbance intensity at higher temperature, while it increased more with time since last disturbance at higher rainfall.

Effects of community functional parameters and litter quality indices on litter decomposability

This inter-site study demonstrated that shifts in community functional parameters were strongly related to variations in litter decomposability, which is in agreement with results from individual site studies (Garnier et al. 2004, Cortez et al. 2007, Queded et al. 2007). We showed that litter decomposability of herbaceous communities was negatively correlated with community-weighted mean LDMC and LCC, and positively correlated with community-weighted mean LNC. Similarly to these individual site studies, LDMC was the measured trait most closely linked to litter decomposability.

Our results support the hypothesis of “afterlife” effects of functional traits of living leaves on litter quality and decomposability (Hobbie 1996, Cornelissen and Thompson 1997, Wardle et al. 1998, Pérez-Harguindeguy et al. 2000, Queded et al. 2003, Cornelissen et al. 2004). Grime et al. (1996) suggested litter decomposability to be partly a consequence of adaptive features of living leaves affecting their palatability. Unpalatable leaves have low LNC and high leaf tensile strength, which depends on LDMC, these traits determining high LIG, LIG:N, and LCH (Heal et al. 1997, Cornelissen et al. 1999, Pérez-Harguindeguy et al. 2000, Wardle et al. 2002). Carbon-rich structural compounds, particularly lignin, strengthen leaves significantly (Choong et al. 1992, Wright and Illius 1995) and determine leaf digestibility and litter decomposition (Swift et al. 1979, Melillo et al. 1982, Schädler et al. 2003).

We confirmed the negative correlation between litter decomposability and litter LIG, LIG:N ratio, and LCH (e.g., Fogel and Cromack 1977, Aber and Melillo 1980, Melillo et al. 1982, Taylor et al. 1989, Gallardo and Merino 1993, Prescott et al. 2004, Queded et al. 2007). Litter N only played a role as a component of LIG:N to predict litter decomposability, in line with the findings of Cornelissen et al. (2004).

LIG:N was a better predictor of litter decomposability than LDMC (Figs. 3 and 5). Two reasons could partly explain why: first, LDMC was measured on living leaves whereas LIG:N was measured on the leaf litter itself and, second, LDMC was assessed for each species of the community and the community average was then calculated, while LIG:N was determined on mixed species litter. Moreover we found that LIG:N was better explained by LDMC, SLA, and LNC than by LDMC alone. Litter N evidently depends on LNC through the degree of nutrient resorption (e.g., Hättenschwiler et al. 2008), and Cornelissen et al. (1999) showed that leaf tensile strength, which relates to litter LIG, depends on both LDMC and SLA. This can be related to the community composition: plant communities with few annual species, thus exhibiting low SLA and LNC, but high LDMC, produced leaf litters with higher LIG:N that decomposed more slowly.

Causal pathway controlling litter decomposability

The simultaneous study of several plant communities under standardized conditions (a “screening” approach advocated for by, e.g., Keddy [1992] and Grime [2001]) allowed us to identify a causal pathway from environmental factors to litter decomposability through leaf traits and litter quality. Lower disturbance intensity or longer time since last disturbance induced higher community-weighted mean LDMC that was closely linked to higher litter LIG and LIG:N, which led to slower litter decomposition rate under standard conditions. Shifts in plant species assemblages following disturbance variations reflect different strategies along the resource acquisition-conservation trade-off (Grime 2001, Prach et al. 2001, Kahmen and Poschlod 2004). Species in intensely disturbed habitat or from early succession grow faster, have lower LDMC (Garnier et al. 2004, Louault et al. 2005) and produce a litter of better quality that consequently decomposes faster than the litter of species in less disturbed habitat or from late succession (Garnier et al. 2004, Kazakou et al. 2006, Queded et al. 2007). This represents a positive feedback between plant growth rate and ecosystem productivity on one hand, and organic matter breakdown and mineralization on the other hand (Hobbie 1992, Berendse 1994, Aerts and Chapin 2000).

Wardle et al. (1998) pointed out that multiple combinations of ecophysiological traits are likely to have significant effects at the ecosystem level since they involve modification of the environment in terms of soil processes, nutrient dynamics and plant succession. Here,

we further validate the biomass ratio hypothesis, which emphasizes the importance of community functional parameters in understanding the effects of plant species on ecosystem processes (Lavorel and Garnier 2002, Garnier et al. 2004, Brooker et al. 2008). Community-weighted mean LDMC, a trait affecting the trade-off between fast-growth vs. physical or chemical protection of herbaceous species, was a good predictor of litter decomposability (Grime et al. 1996, Cornelissen et al. 1999, Cortez et al. 2007, Quedsted et al. 2007), related to initial litter chemical composition (lignin:nitrogen ratio). As an integrator of the effects of disturbance and climate on the functional structure of plant communities, LDMC proved a powerful functional marker (*sensu* Garnier et al. 2004) of plant control on the pace of nutrient cycling in terrestrial ecosystems.

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APPENDIX A

List of selected treatments at each site (*Ecological Archives* E090-042-A1).

APPENDIX B

Near-infrared reflectance spectroscopy calibrations between initial litter spectral properties and (a) litter decomposability and (b) litter quality (*Ecological Archives* E090-042-A2).

APPENDIX C

Results of the statistical analyses for the 86 community litters used for the microcosm experiment (*Ecological Archives* E090-042-A3).

APPENDIX D

Patterning of factor relationships with litter decomposability fitted within individual sites in relation to the range of factor variation and sample size at the study sites (*Ecological Archives* E090-042-A4).