

PLANT FUNCTIONAL MARKERS CAPTURE ECOSYSTEM PROPERTIES DURING SECONDARY SUCCESSION

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Abstract. Although the structure and composition of plant communities is known to influence the functioning of ecosystems, there is as yet no agreement as to how these should be described from a functional perspective. We tested the biomass ratio hypothesis, which postulates that ecosystem properties should depend on species traits and on species contribution to the total biomass of the community, in a successional sere following vineyard abandonment in the Mediterranean region of France. Ecosystem-specific net primary productivity, litter decomposition rate, and total soil carbon and nitrogen varied significantly with field age, and correlated with community-aggregated (i.e., weighed according to the relative abundance of species) functional leaf traits. The three easily measurable traits tested, specific leaf area, leaf dry matter content, and nitrogen concentration, provide a simple means to scale up from organ to ecosystem functioning in complex plant communities. We propose that they be called “functional markers,” and be used to assess the impacts of community changes on ecosystem properties induced, in particular, by global change drivers.

Key words: biodiversity; ecosystem functioning; functional effect groups; functional leaf traits; litter decomposition; net primary productivity; secondary succession; soil carbon and nitrogen.

INTRODUCTION

The urgent need to assess the impacts of global change factors on the functioning of ecosystems has renewed the question of how the structure and composition of communities affect ecosystem processes (Jones and Lawton 1995, Vitousek et al. 1997, Chapin et al. 2000). The number, relative abundance, and identity of plant species, the primary producers, all potentially influence these processes (Grime 1998, Chapin et al. 2002). A major difficulty is that the factors involved are not of comparable nature: numbers, relative abundances of species, and processes are quantitative variables, while the identity of a species is usually described by a latin binomial, which is purely qualitative. Hence the recurrent attempts to describe species from a functional, rather than a taxonomic, perspective (reviews in Lavorel et al. 1997, Weiher et al. 1999, Grime 2001, Westoby et al. 2002). A first possibility is to categorize species into discrete groups displaying a similar way of performing a particular process

(species with C₃ vs. C₄ photosynthetic pathway, nitrogen fixers vs. non-fixers, etc.) into so-called “functional groups” (Woodward and Cramer 1996, Lavorel et al. 1997). However, the use of quantitative traits, i.e., characters measurable on an individual, to which continuous numeric values can be assigned, rather than discrete groups, has recently been advocated to assess the influence of species composition and identity on ecosystem processes (Díaz and Cabido 2001, Lavorel and Garnier 2002).

The “biomass ratio hypothesis” proposed by Grime (1998) integrates these different attributes of plant communities. It postulates that “the extent to which the traits of a species affect ecosystem properties is likely to be strongly related to the contributions of the species [. . .]” to the total biomass of the community, and therefore takes explicitly into account the number, relative abundance, and identity (through quantitative traits) of the species present. It implies that the instantaneous functioning of ecosystems is determined to a large extent by the trait values of the dominant contributors to the plant biomass. The challenge that remains is to identify some key traits of the organisms that have significant effects on ecosys-

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TABLE 1. Definitions of abbreviations, acronyms, and units of variables.

Abbreviation	Definition	Units
Agg	aggregated	
ANPP	aboveground net primary productivity	$\text{g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$
BIOmax	green (live) biomass measured at peak standing biomass (May 2000)	g/m^2
Csoil	total soil organic carbon concentration	g/kg
dom	dominant	
LDMC	leaf dry matter content	mg/g
LNC	leaf nitrogen concentration	mg/g
NbSp	number of species accounting for at least 80% of the maximum standing biomass of each field	
Nsoil	total soil nitrogen concentration	g/kg
PCA	principal components analysis	
SANPP	specific aboveground net primary productivity	$\text{g}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$
SLA	specific leaf area	m^2/kg
SMLoss	specific rate of litter mass loss	$\text{g}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$

tems (Díaz and Cabido 2001, Grime 2001, Chapin et al. 2002).

The main aim of this study is to test the biomass ratio hypothesis for some components of carbon and nitrogen cycles in ecosystems: primary productivity, decomposition of leaf litter, and soil carbon and nitrogen stocks. The species traits selected therefore pertain to the processing of these resources at the plant level, with the underlying assumption that these would scale up to ecosystem functioning (Chapin et al. 2000, Lavorel and Garnier 2002). We chose three leaf traits, known to affect components of the carbon and/or nitrogen cycles at the leaf, whole-plant, and ecosystem levels (Reich et al. 1992, Cornelissen et al. 1999, Lavorel and Garnier 2002): specific leaf area (SLA, the ratio of water-saturated leaf area to leaf dry mass), leaf dry matter content (LDMC, the ratio of leaf dry mass to water-saturated fresh mass) and leaf nitrogen concentration (LNC) (see Table 1).

This test will be conducted in the context of land use change, one of the most important anthropogenic effects on Earth's ecosystems (Vitousek et al. 1997). In the case of many Mediterranean regions, 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 conceptual framework of succession involving ecosystem functioning, plant communities, and species characteristics was formulated more than three decades ago (Odum 1969), but most observational and experimental studies have approached these different aspects separately (see Huston and Smith [1987], Tilman [1990], and Bazzaz [1996] for species traits; Vitousek et al. [1989], Berendse [1990], and Knops and Tilman [2000] for ecosystem properties). In several instances, various combinations of species and ecosystem properties were determined: in some cases, the aim was to understand how changes in the environment (e.g., soil nutrient availability) during succession affect the distribution of species (Inouye et al. 1987, Gleeson and Tilman 1990, Reich et al. 1995), while in others, the effects of plant species

on ecosystem properties were explicitly formulated (Meltinger and McNaughton 1975, Wardle et al. 1997, Berendse 1998) but not formally tested. Here we report correlated changes in several aspects of biogeochemical cycles and plant species traits in a Mediterranean postcultural succession, within a framework which integrates ecophysiology, community, and ecosystem ecology.

METHODS

Study sites

Twelve old fields located in southern France (43°51' N, 3°56' E, 100–160 m above sea level) in a subhumid Mediterranean climate (Daget 1977) were selected for study. They were located within a 4 × 4 km square, on soils of similar texture and physico-chemical properties: brown calcareous or calcic cambisol (FAO 1974); pH (H₂O) between 8.1 and 8.6. These fields were all previously vineyards, which, following removal of the vines, were abandoned 2–42 years prior to our study (Table 2). Age since abandonment in 1999 was determined from (1) chronological series of aerial photographs (scale:1:25000), available at an approximate frequency of five years since 1956, and (2) age of the largest (supposedly the oldest) individuals of woody species found in each field, assessed by counting the number of visible annual growth rings. Except for these few large individuals, herbaceous species were dominant in all plots (Appendix). The similarities in soil type, climate, and plant species pool make these 12 old fields a good model of chronosequence to study successional patterns.

Ecosystem properties

Sampling was conducted in herbaceous areas, where only small woody species were present in the oldest fields (see Appendix). Total aboveground standing biomass was harvested in February and May 2000 (minimum and maximum yearly values, respectively) on four 0.5 × 0.5 m plots per field at each date. This sampling surface area (1 m² per harvest) is suitable for herbaceous vegetation

TABLE 2. Age since abandonment, ecosystem-level properties, and community attributes for the 12 old fields studied.

Age (years)	BIOmax (g/m ²)	ANPP (g·m ⁻² ·d ⁻¹)	SANPP (g·kg ⁻¹ ·d ⁻¹)	SMLoss (g·kg ⁻¹ ·d ⁻¹)	Csoil (g/kg)	Nsoil (g/kg)	NbSp (% 2 dom.)†	SLA _{agg} (m ² /kg)	LDMC _{agg} (mg/g)	LNC _{agg} (mg/g)
2	104	0.83	7.54	NA	12.1	1.08	6 (62)	19.6	218	28.0
2	64	0.54	8.76	NA	6.4	0.96	4 (54)	21.2	216	25.2
7	222	1.69	6.67	1.8	11.9	1.47	9 (37)	21.4	251	24.4
8	247	1.78	5.84	1.2	12.9	1.41	2 (80)	14.3	377	13.5
8	183	1.29	5.54	1.5	8.88	1.17	6 (48)	21.9	182	27.0
11	221	1.54	5.41	1.7	12.2	1.32	12 (37)	17.7	200	20.6
12	137	1.03	6.49	1.7	15.3	1.44	5 (39)	19.8	227	24.5
26	121	0.73	4.18	1.1	24.8	2.37	2 (83)	13.3	402	11.3
29	246	1.54	4.43	1.4	23.8	2.06	2 (99)	13.3	405	11.7
35	167	1.08	4.71	1.1	31.7	2.94	2 (94)	13.9	398	10.1
40	184	0.83	2.64	1.4	22.1	2.32	2 (95)	14.7	385	9.5
42	286	1.50	3.32	1.0	24.7	2.60	2 (95)	13.0	411	10.9
Pearson	0.52‡	0.09 ^{NS}	-0.91 ^{***}	-0.72 [*]	0.89 ^{***}	0.94 ^{***}	-0.59 [*]	-0.80 ^{**}	0.82 ^{**}	-0.87 ^{***}

Notes: See Table 1 for definitions of acronyms and abbreviations. Species are identified in the Appendix. ANPP and SANPP were calculated between February and May 2000. SLA_{agg}, LDMC_{agg}, and LNC_{agg} are each the community-aggregated trait values (see *Methods: Leaf traits* for method of calculation). The bottom line shows the Pearson correlation coefficients between field age and each ecosystem property.

† (% 2 dom.) is the percentage of the maximum standing biomass the two most abundant (“dominant” hereafter) species represent.

‡ $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = not significant; NA = not available.

(cf. Wiegert 1962), and we found a good interannual reproducibility of data ($r = 0.79$, $P < 0.01$ for the relationship between May 2000 and May 2001 harvests). After separating live and dead plant parts, live biomass was sorted by species and oven dried, in order to calculate the dry mass proportion of species in the communities. Aboveground net primary productivity (ANPP) was calculated between May and February, the period of maximum production under the Mediterranean climate of southern France (Daget 1977), as

$$\frac{(\text{live biomass in May}) - (\text{live biomass in February})}{t_{\text{May}} - t_{\text{Feb}}} \quad (1)$$

where t_{May} and t_{Feb} are the harvest dates. Specific aboveground net primary productivity (SANPP) was calculated as

$$\frac{\log_e(\text{live biomass in May}) - \log_e(\text{live biomass in February})}{t_{\text{May}} - t_{\text{Feb}}} \quad (2)$$

SANPP, also called “ecosystem efficiency” (Reich et al. 1997), expresses ANPP on a per gram of green biomass basis instead of a ground area basis.

Litter mass loss was determined in a litter bag experiment. Undecomposed litters were collected in each field in August 1999, without separating the litters of the species present. They were air-dried, cut into small pieces (2–3 cm²), placed in polyester net litter bags (16 × 12 cm ; 0.5 cm mesh) and left to decompose on the soil surface for 307 days in the field they had been taken from. Ten litter bags were sampled every three months in each field. The recovered material was air-dried for 2–3 weeks,

then dried at 40°C to constant mass, separated by hand from soil particles, and weighed. The percentage mass of each sample that remains in the litter bag relative to its initial mass was calculated for each sampling date and plotted against time since the beginning of the experiment. The resulting curve was fitted with an equation of the form $Y = Y_0 e^{-kt}$ (Olson 1963), where Y_0 and Y are the percentage mass in the litter bag at the beginning of the experiment (100%) and at time t , respectively. The parameter k is the specific rate of litter mass loss (SMLoss) given in Table 2; as SANPP, it expresses the rate of the process per unit biomass, and has the same units (grams per kilogram per day).

Total soil carbon and nitrogen concentrations were measured 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. The soil of each batch was then homogenized, and its total organic carbon (Csoil; Anne method: Duchaufour 1970) and nitrogen concentrations (Nsoil with an element analyzer EA1108, Carlo Erba, Milan, Italy) were determined after decarbonating the samples.

Leaf traits

The traits measured were: (1) SLA, which represents the light-intercepting area of a leaf per unit dry mass, related to net assimilation rate (Reich et al. 1992, 1997) and plant relative growth rate (RGR: Reich et al. 1997, Poorter and Garnier 1999), (2) LDMC, an approximation of leaf tissue density, related to nutrient retention within the plant (Poorter and Garnier 1999, Ryser and Urbas 2000), and (3) LNC, strongly correlated to the concentrations of leaf nitrogen compounds (RuBP carboxylase

and chlorophyll in particular) involved in photosynthesis (Evans 1989). SLA, LDMC, and LNC (Carlo Erba elemental analyzer, Model EA1108) were measured as described in Garnier et al. (2001a, b). Measurements were conducted at spring peak of growth (April–May), on the youngest, fully expanded, well-lit leaves of species whose cumulated individual biomass makes up at least 80% of the maximum standing biomass of these communities (“most abundant species” hereafter). A total of 29 species were selected, which gives 54 data points for the whole sere (Fig. 1), since some species were present in more than one field (Appendix). The exact number of species measured in each field (NbSp) is given in Table 2. NbSp is closely related to the species richness (total number of species) of the different fields: species richness = $2.6 \times \text{NbSp} + 7.4$ ($r^2 = 0.83$, $P < 0.001$).

Treatment of data

To test the biomass ratio hypothesis, aggregated values of leaf traits ($\text{trait}_{\text{agg}}$) were calculated using data from the most abundant species as follows:

$$\text{trait}_{\text{agg}} = \sum_{i=1}^n p_i \times \text{trait}_i \quad (3)$$

where p_i is the relative contribution of species i to the maximum biomass of the community (May 2000 harvest), n is the number of most abundant species (NbSp), and trait_i is the trait value of species i .

Correlations between field age and ecosystem properties on the one hand and leaf traits on the other hand, and between aggregated trait values and ecosystem properties, were tested using Pearson correlation coefficients. A principal component analysis (PCA) on standardized data was conducted to analyze the overall pattern of correlations between ecosystem properties and aggregated trait values. All statistical analyses were carried out with the *Statgraphics Plus* software (Manugistics 1999).

RESULTS

Maximum standing biomass was low in the first years following abandonment, but did not show any significant trend with field age after seven years (Table 2). ANPP showed a threefold variation among the 12 old fields, but this was not significantly correlated with age. By contrast, SANPP and SMLoss significantly decreased with field age, while total soil carbon and nitrogen concentrations showed a significant, threefold increase over the course of succession (Table 2).

At the species level, both SLA and LNC showed a significant decrease with field age, while LDMC showed the opposite trend (Fig. 1). Correlations were stronger when only the two dominant species of each field were taken into account (Fig. 1). This is mainly due to the tendency of younger fields to be more species rich than older ones (cf. Table 2). This higher species richness induces a higher but not significant trait variance in younger fields (trend not shown). Correlations with field age were

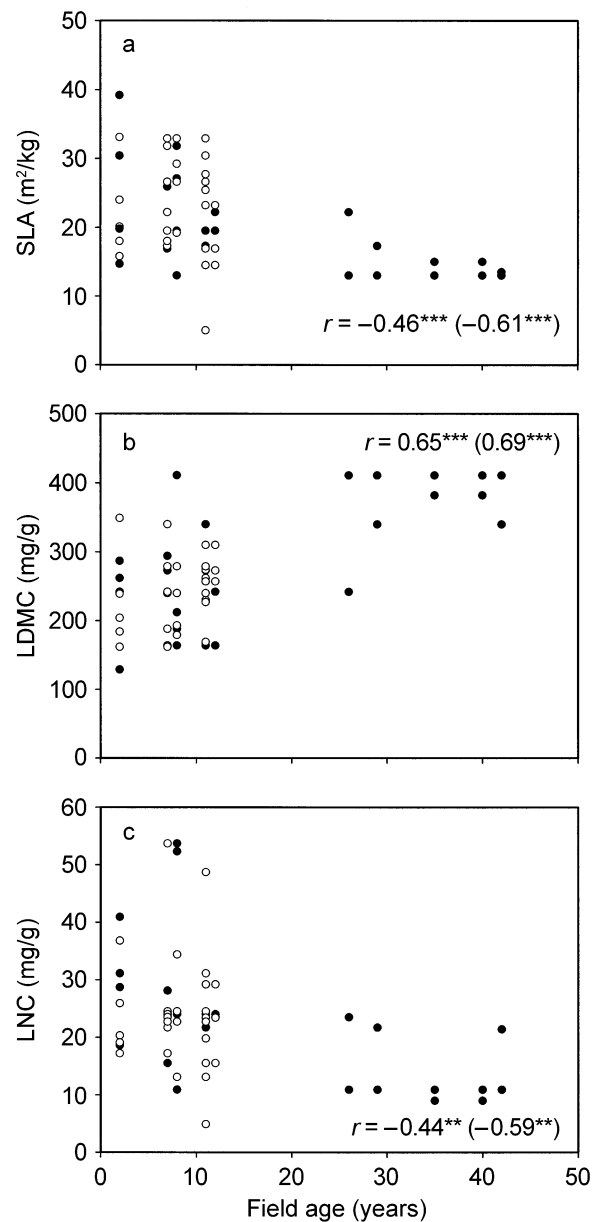


FIG. 1. Relationships between field age and leaf traits of the most abundant species of the communities: (a) SLA, specific leaf area; (b) LDMC, leaf dry matter content; (c) LNC, leaf nitrogen concentration. Pearson correlation coefficients are given in the figures: on each graph, the first value is for all species ($n = 54$), and the values in parentheses are for the two dominant species of the communities ($n = 24$). Solid symbols represent these two dominant species; open symbols represent the other species. Levels of significance: ** $P < 0.01$; *** $P < 0.001$.

TABLE 3. Pearson correlation coefficients between ecosystem properties and (1) trait values aggregated at the community level (subscript agg), (2) mean trait values of the two dominant species in the communities (subscript dom; species names in the Appendix), and (3) number of species accounting for at least 80% of the maximum standing biomass of the communities (NbSp).

	Community-aggregated			Two dominant species			NbSp
	SLA _{agg}	LDMC _{agg}	LNC _{agg}	SLA _{dom}	LDMC _{dom}	LNC _{dom}	
SANPP	0.78**	-0.71**	0.87***	0.88***	-0.70**	0.69**	0.41 ^{NS}
SMLoss	0.78**	-0.81**	0.74*	0.55†	-0.64*	0.33 ^{NS}	0.80**
Csoil	-0.88***	0.84***	-0.96***	-0.89***	0.84***	-0.90***	-0.61*
Nsoil	-0.84***	0.83***	-0.93***	-0.90***	0.87***	-0.87***	-0.59*

Notes: See Table 1 for definitions of acronyms and abbreviations. Correlations between trait values and either maximum standing biomass or ANPP were not significant (coefficients not shown, P values between 0.14 and 0.96); $n = 12$ for all correlations except those involving the rate of litter mass loss ($n = 10$; cf. Table 2). Stepwise multiple regressions of ecosystem processes vs. community-aggregated leaf traits improved only marginally the percentage of variance explained compared to the best correlation shown here; results are thus not shown.

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = not significant.

even stronger when community-aggregated trait values were calculated (Table 2).

To what extent does this replacement of species with contrasting characteristics relate to the changes presented above at the ecosystem level? To answer this question and test the biomass ratio hypothesis (Grime 1998), simple correlations and a PCA combining data on ecosystem properties and species traits aggregated at the community level were conducted. The analyses reveal significant correlations between aggregated-trait values and SANPP, SMLoss, Csoil, and Nsoil (Table 3), while relationships between traits and either BIOmax or ANPP were not sig-

nificant (not shown). Fig. 2 shows how these different variables are associated in the multivariate analysis. The first axis differentiates communities according to age since abandonment: "old" communities show high C and N in soil and high LDMC_{agg}, while "young" communities are characterized by high SLA_{agg} and LNC_{agg}, and high process rates when expressed per unit mass (SANPP and SMLoss). The second axis is mostly defined by ANPP, which thus appears unrelated to both the other ecosystem properties and the community-aggregated trait values. The outcome of the PCA is only weakly modified (not shown) and most simple correlations are conserved (Table 3), except for SMLoss, if the mean values of the two dominant species of each community are taken instead of the aggregated values for the communities.

DISCUSSION

Decreases in rates of processes per unit biomass (SANPP and SMLoss) with age of the communities found here (Table 2) have been observed in different types of successions, but such changes do not always go with increases in carbon stocks in vegetation and/or soils (Mellinger and McNaughton 1975, Wardle et al. 1997). At the species level, changes in plant traits with field age (Fig. 1) point to the replacement of fast-growing species (high SLA and LNC, low LDMC) acquiring external resources rapidly, which dominate the early stages following abandonment, by slower growing species (low SLA and LNC, high LDMC), which tend to conserve internal resources more efficiently as succession proceeds (Huston and Smith 1987, Bazzaz 1996). This overall picture is consistent with the pattern predicted by Odum (1969) for plant succession.

Collecting information simultaneously at the ecosystem and species levels allowed us to connect explicitly plant and ecosystem functioning. This was done through the use of quantitative structural and biochemical plant traits, which bear direct relationships with photosynthesis (leaf process) and plant growth (whole-plant process). It

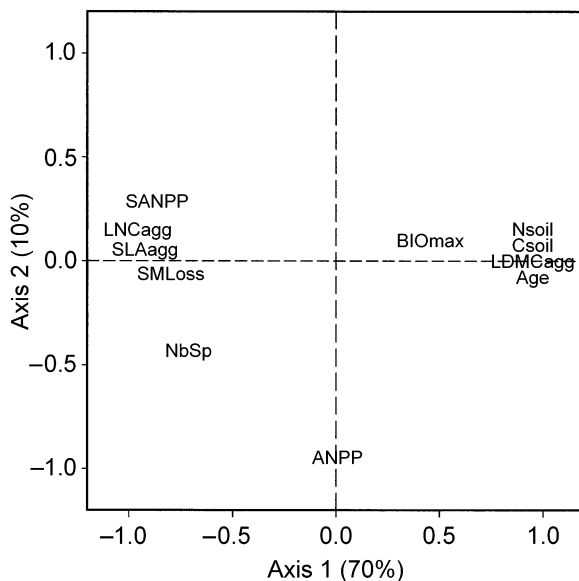


FIG. 2. Principal components analysis combining data on ecosystem properties (data from Table 1) and community-aggregated values of leaf traits ("agg"). Only the first two axes, which account for 80% of the total inertia, are retained here. (The third and fourth axes account for 9 and 4%, respectively.) Abbreviations are as in Tables 1 and 2.

is shown here that, provided trait values are weighed by the relative abundance of the species in the community, these specific traits also correlate with ecosystem-level properties (see also Reich et al. 1992, 1997). Our results are thus in agreement with the biomass ratio hypothesis (Grime 1998). Ecosystems composed of fast-growing plant species found in early successional stages tend to have high rates of resource processing per unit biomass (SANPP and SMLoss), while the reverse is true for ecosystems composed of slow-growing species in more advanced stages.

Changes in the values of community-aggregated traits may be due to the replacement of species with different trait values (interspecific variation), to changes in trait values within a species (intraspecific variation), or to a combination of these two. Here, the three traits measured showed a certain degree of intraspecific variability, but there was no systematic trend along the succession. Taking SLA as an example, some species show an increase with field age (e.g., *Brachypodium phoenicoides*, range: 11.1–13.8 m²/kg), others a decrease (e.g., *Picris hieracioides*, range: 19.7–17.9 m²/kg), while others show no particular trend (e.g., *Calamintha nepeta*). Furthermore, intraspecific variability in trait values was found to be much lower than interspecific variability, as shown elsewhere for the same traits (e.g., Jurik 1986, Ellsworth and Reich 1996, Garnier et al. 2001a). We therefore conclude that changes in community-aggregated values were mainly due to the replacement of species with different trait values during succession.

Are the observed relationships between species traits and ecosystem functioning causal or are these mere correlations? Building on Chapin's (1993) approach and its development by Lavorel and Garnier (2002) as applied to Eq. 2, SANPP can be written as:

$$\text{SANPP} = \frac{\log_e \left[\sum_{i=1}^n p_i \times e^{\text{RGR}_i \times (tf - to)_i} \right]}{\Delta T} \quad (4)$$

where n is the number of species, p_i is the relative contribution of species i to the biomass of the community, RGR_i and $(tf - to)_i$ are the aboveground relative growth rate and period of active growth, respectively, of species i (to is the time of onset of growth, and tf the time when growth stops, either because of a scheduled ontogeny [e.g., seed set in annuals] or of unfavorable environmental conditions [drought, cold temperatures, etc.]). ΔT is the period over which SANPP is assessed. Eq. 4 suggests that the relationships between SANPP and species traits related to RGR and phenology are causal rather than being simply correlative. In the present study, phenological differences among species are likely to have only a small impact on productivity, since the latter was assessed between February and May, when most species undergo sustained active growth. SLA, LDMC, and LNC, all traits related to RGR (Reich et al. 1992, Poorter and Garnier

1999) are therefore expected to have a mechanistic effect on SANPP, provided that they are weighed by the relative abundance of the species in the communities (compare Eqs. 3 and 4).

Is this likely also to be the case for the other ecosystem properties studied here? At a local scale, litter decomposition is mainly controlled by litter characteristics such as fiber concentration, C:N and/or lignin:N ratios (Heal et al. 1997, Wardle 2002). These characteristics have been shown to depend on the physical and chemical properties of living organs such as leaf toughness (Cornelissen et al. 1999, Pérez-Harguindeguy et al. 2000) or tissue nitrogen concentration (Wardle et al. 1998). Since leaf toughness depends both on SLA and LDMC (cf. Cornelissen et al. 1999, Wright and Westoby 2002), it can be predicted that ecosystems composed of species with low SLA and LNC but high LDMC will show slow decomposition rates, as actually found here (Fig. 2, Table 3). The low rate of litter mass loss of high LDMC leaves was further confirmed in a recent experiment on six herbaceous species, where the LDMC of living leaves was found to be related to the concentration of nonlabile compounds in litter (N. Pérez-Harguindeguy, J. Cortez, E. Garnier, and D. Gillon, *unpublished manuscript*). A striking result of the present study is that the same plant traits also strongly correlate with carbon and nitrogen stocks in soils, and thus with their organic matter content. Increases in soil C, N, and/or organic matter during the course of succession are well documented (Berendse 1990, Gleeson and Tilman 1990, Knops and Tilman 2000, but see Mellinger and McNaughton 1975). In our system, it is probably due to a combination of an increase in the rate of litter input per unit ground area as the standing biomass of the communities increases (up to 7–10 years following abandonment: Table 2), and a decrease in the rates of litter decomposition, as fast-growing species that produce high-quality litter are progressively replaced by slow-growing species producing a litter of lower quality (Fig. 1). Ecosystem process models such as BIOME-BGC (Running and Hunt 1993) or CENTURY (Parton et al. 1993) explicitly incorporate one or several of the traits (or close correlates) measured in the present study, which further suggests that SLA, LDMC, and LNC constitute *functional effect traits* (Díaz and Cabido 2001, Lavorel and Garnier 2002), i.e., species traits that affect ecosystem properties.

The fact that most relationships still hold when traits of the two dominant species only are considered (Table 3) has important implications. First, it suggests that the traits of these particular species are good indicators of the community-aggregated values. If additional tests on a larger number of communities confirm these results, this would indicate that, even in species-rich systems, ecosystem properties could be assessed from the measurement of relevant traits on a limited number of species. Second, it means that the two- to threefold variations of ecosystem properties (Table 2) can be accounted for by

the two- to fourfold changes in trait values of a constant number of dominant species. We also found weaker (or nonsignificant) associations between number of species and ecosystem properties than between community-aggregated values of traits and ecosystem properties (Fig. 2, Table 3). These findings are in line with the idea that ecosystem properties depend more on species traits than on species number (Tilman et al. 1997, Díaz and Cabido 2001, Grime 2001). A further step is to assess which components of functional diversity, defined as the values and range in the values of organismal traits found at a given site (Tilman 2001), are important to ecosystem functioning. In the present study, we did not find any significant relationship between any of the ecosystem properties measured and the within-field coefficient of variations of the three traits (data not shown). We therefore conclude that community-average trait values have more impact on ecosystem functioning than within-community trait variation. Manipulative experiments with artificial communities could be designed (Naeem 2002) to disentangle possible confounding effects inherent to the correlative approach adopted here, and further test the generality of these findings with a higher replication level.

Our study has demonstrated that simple, quantitative, easily measurable plant traits (Hodgson et al. 1999, Weiher et al. 1999) could yield relevant information on key aspects of ecosystem functioning. This was shown here in the context of land use change, but the approach can be generalized to other situations involving changes in community structure and/or composition, induced by, for example, other drivers of global change (climate, nitrogen deposition, species invasions and/or extinctions, etc.). We have also shown that the particular traits selected here, specific leaf area, leaf dry matter content, and leaf nitrogen concentration, could be used to capture the functioning of plant species and communities. As such, we propose that they be called “functional markers.” Such markers hold great promise as powerful quantitative tools with which to describe and predict fluxes of matter across several scales, from the plant organ to the ecosystem.

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APPENDIX

A list of species accounting for 80% of the maximum standing biomass of the different fields is available in ESA's Electronic Data Archive: *Ecological Archives* E085-079-A1.