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How does the nature of living and dead roots affect the residence time of carbon in the root litter continuum?

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Abstract

Root litter transformation is an important determinant of the carbon cycle in grassland ecosystems. Litter quality and rhizosphere activity are species-dependent factors which depend on the attributes of the dead and living roots respectively. These factors were tested, using non-disturbed soil monoliths of *Dactylis glomerata* L. and *Lolium perenne* L. monocultures. ^{13}C-labelled root litter from these monoliths was obtained from a first stand of each crop, cultivated under very δ^{13}C-depleted atmospheric CO_2 (S1). In a factorial design, ^{13}C-labelled root litter of each species was submitted to a second, non ^{13}C-labelled, living stand of each species (S2). Carbon derived from S1 and from S2 was measured during an 18-month incubation in the root phytomass and in three particulate organic matter fractions (POM). The decay rate of each particle size fraction was fitted to the experimental data in a mechanistic model of litter transformation, whose outputs were mineralisation and stabilisation of the litter-C. Few differences were found between species, in the amount and biochemical composition of the initial root litter, but *Dactylis* roots showed a greater C:N ratio, a lower mean root diameter and a greater specific root length compared to *Lolium*. A transient accumulation of litter residues arose successively in POM fractions of decreasing particle size. The litter-continuum hypothesis was validated, i.e. that the attributes of the compartments (C:N, chemical composition and residence time) depended mainly on their particle size. The S1 species influenced the rate of litter decay while the S2 species controlled the efficiency of litter-C stabilisation versus mineralisation: *Dactylis* litter decomposed faster and *Lolium* rhizosphere allowed a greater proportion of litter C stabilisation. Discussions focus on the processes responsible of species strategy in relation with the morphological root traits, and the implication of strategy diversity for rich grassland communities.

Introduction

Transformation of plant litter is a key process of the carbon and nutrient cycles, which drives C-mineralisation and C-accumulation in the soil organic matter (Tateno and Chapin, 1997), and soil N availability through N mineralisation and immobilisation. The decomposition of organic returns from dead plant parts has been widely studied for aboveground organs (Cornelissen, 1996; Jenkinson, 1977). In perennial grasslands, the root turnover provides the major part of the litter input to the soil, because most of the aboveground biomass is removed before senescence at grazing or haymaking. This process of root turnover determines N availability, species growth and botanical composition, that in turn influence the amount and quality of the root litter, thereby governing the ecosystem dynamics (Aerts et al., 1992; Berendse, 1994; Wedin and Tilman, 1990).

From root litter production to carbon accumulation in soil organic matter, a transient accumulation of litter-C occurs in successive particle size fractions. Using the measurement of litter-derived particulate organic matter (POM), the residence time of the POM-C has been shown to decrease with decreasing particle

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size (Balabane and Balesdent, 1992; Loiseau and Soussana, 1999). At the same time, N concentration of the POM increases, as a result of carbon mineralisation and nitrogen immobilisation (Blair, 1988). Hence, the process of litter transformation can be considered as a continuum (Bosatta and Agren, 1991; Melillo et al., 1989).

In a given climate, litter transformation is controlled by two groups of factors: litter quality and the conditions that occur during litter incubation. On the one hand, the rate of litter transformation depends on the quality of the fresh litter. Initial nitrogen concentration and the C:N ratio have commonly been used as predictors for plant litter decomposition rate (Moorhead, 1998; Seastedt et al., 1992). In addition, the chemical composition has been taken in consideration, because soluble carbohydrates, cellulose and lignin have been shown to decompose more slowly in that descending order (Larsson and Steen, 1988). Consistently, the lignin concentration and the lignin:N ratio have been found to predict the decomposition rate (Berendse, 1994; Melillo et al., 1984). In addition, other litter components such as phenols and tannins may slow down root decomposition (Kalburtji et al., 1999). The morphological characteristics of the dead organs, such as the specific root length, that determine the contact area with the microbial biomass, could also condition the residence time of the root phytomass and residues.

On the other hand, the rhizosphere determines litter environment during litter incubation *in situ*, because root activity modifies soil moisture, the inorganic nitrogen concentration of the soil solution, and the supply of fermentable-substrates through root exudates and rhizodeposits. High nitrogen availability in soil may enhance decomposition (Melillo et al., 1984; Prescott et al., 1992), or have no effect (Dukes and Field, 2000; Fog, 1988). Rhizodeposition and exudation of easily fermentable substrates stimulate microbial activity and SOM decomposition (Bottner et al., 1999; Cheng and Coleman, 1990). Moreover, the priming effect of fermentable C on SOM mineralisation was shown to depend on nitrogen availability (Cheng and Coleman, 1990; Fontaine et al., 2001). However, no evidence has yet been found of such a priming effect of exudates on litter decay in natural, undisturbed soil-sward ecosystems.

The theory of plant strategy towards the carbon and nutrient cycles points to the existence of competitive and conservative species (Tilman, 1990) and this theory was used to account for the dynamic aspects of the C and N cycles at the ecosystem level. A faster litter decomposition rate of the competitive species is expected from a higher litter N concentration, due to a slower rate of N resorption within the plant at senescence (Cornelissen and Thompson, 1997). With a constant, non-optimal, fertiliser supply, nitrogen availability in the rhizosphere may depend on the plant strategy, because the critical N concentration of the soil solution which determines the absorption of inorganic N is higher in competitive than in conservative species (Tilman, 1990).

Hence, a better understanding of litter transformation in grassland may consider two factors, the litter quality and living root activity, now referred as the litter and the rhizosphere effects. These two species-dependent factors involved in the carbon fluxes during litter transformation should be dissociated in controlled experiments (Berendse, 1994). The question here addressed is whether, in grassland species, root litter quality and rhizosphere activity have similar or opposite effects on the rate of transformation of the root litter.

Two common and contrasting grass species, present together in species rich meadows and pastures, were chosen to examine the rhizosphere and root litter effects on root litter transformation. Undisturbed grassland monoliths with intact root systems were used to measure the residence time of carbon in successive compartments of the litter decay continuum. For this purpose, differential ^{13}C-labelling of two successive stands, dead and living respectively, allowed the carbon derived from the root litter to be distinguished from that derived from the rhizosphere.

Materials and methods

Experimental design

Two grass species were chosen that occur in nutrient rich grasslands managed for grazing and hay making at a sub-optimal level of N-availability: *Dactylis glomerata* and *Lolium perenne*, subsequently referred to as *Dactylis* and *Lolium*. Although they have similar habitat preferences, these species have been shown to differ in both leaf and root traits and are therefore opposed as regards the strategy concept (Tilman, 1990). Greater leaf life span, leaf lamina size and thickness (Ryser and Urbas, 2000), lower SLA (Hunt and Cornelissen, 1997) greater nutrient resorption efficiency and residence time of N in the leaves (Eckstein et al., 1999)

and greater nitrogen use efficiency in *Dactylis* than in *Lolium* imply that *Dactylis* is more conservative and *Lolium* more competitive.

The experimental design involved two grass monocultures, referred as S1 and S2, that were cultivated successively on the same soil monoliths. S1 was first cultivated to produce root litter *in situ*, and destroyed by application of glyphosate. S2 was then grown on the monoliths containing the S1 root litter, to measure the transformations of the S1 litter under the living stand S2. Both S1 and S2 consisted of pure *Dactylis* and pure *Lolium* stands. In a factorial design, root-litter monoliths of *Dactylis* and *Lolium* (S1) were submitted to the root activity of each living stands (S2). Controls consisted of S1 monoliths without S2, referred as 'bare soils'. The acronym of the treatments used two letters, which symbolised S1 and S2, respectively: DD, DL, DB, LD, LL and LB, where D is for *Dactylis*, L for *Lolium* and B for Bare.

Soil

A loamy soil was collected under a semi-natural grassland in the granitic region of Theix (850 m a.s.l, Massif Central, France), at a depth of 10–30 cm in order to minimise its organic matter content. After sieving through a 2-mm mesh, the soil consisted of 48% sand, 36% loam and 16% clay, with 2.7% OM at a C:N ratio of 9.3. The pH (water) was 6.6 and the CEC was 15.9 meq per 100 g dry soil. This soil was used to fill plastic containers of 39 × 31 cm area and 26 cm depth. Phosphorus and potassium sulphate were applied before sowing at 5 and 15 g m^{-2}, respectively, to ensure that these nutrients did not limit plant growth, litter quality, or microbial activity, and the soils were watered to field capacity.

Production of labelled root litter monoliths (S1)

On 23 March 2000, 33 pure stands of *Dactylis glomerata* (cv. Lupré) and 33 pure stands of *Lolium perenne* (cv. Fennema) were sown broadcast at 3 g seed m^{-2}. Sand was then spread to a depth of 1 cm onto the soil surface of the containers. All containers were immediately placed in a transparent plastic tunnel. CO_2 enrichment to a concentration of 700 μL L^{-1} (700 ppm) enabled labelling the tunnel's atmospheric CO_2-C at a $\delta^{13}C$ of $-28‰$ by addition of fossil-fuel derived, very ^{13}C-depleted, CO_2 (Loiseau and Soussana, 1999). Average CO_2 concentration, measured every 15 min by IRGA, were within ±5% of the concentration setpoint over 94% of the time (Casella et al., 1996). The climate in the tunnel was regulated in order to restore outdoor conditions of temperature and vapour pressure. The average temperature per regrowth period was within ±10% of the temperature setpoint over 84% of the time and the mean vapour pressure was not significantly different from the outdoors (Casella et al., 1996).

The grassland monoliths were grown for seven months until 12 October 2000. The swards were cut four times during the cultivation period. Nitrogen fertilisation with ammonium nitrate was applied after sowing at 3 g N m^{-2} and at the same rate after each cut. Two containers of each stand were weighed every day. The water loss was compensated by an equal supply to all the monoliths of the same stands. In this way, the water content was kept near field capacity during the whole cultivation period (24% w/w). On 12 October 2000, plants were destroyed with glyphosate, the watering was stopped and the monoliths allowed to dry. Two weeks later, all leaves and stubble were cut and removed. The monoliths containing dead root systems were then placed indoors during seven months prior to sowing and kept dry (humidity less than 5% w/w) to avoid any microbial activity.

Decomposition experiment under stand S2

The decomposition experiment ran from 23 April 2001 until 24 September 2002. The soil monoliths were rewatered for three days in order to reach field capacity. Pure stands of *Dactylis* and *Lolium* from the same cultivars as S1 were sown broadcast at the same seed density as S1 on the soil surface, without disturbance of the soil surface. Mineral sand to a depth of 1 cm was added onto the soil surface to ensure germination. Phosphorus and potash were applied at the same rate as for S1. All monoliths were kept outdoors in ambient atmospheric conditions. A randomised block design was used with three replicates.

During S2 cultivation, the soil moisture conditions were maintained at field capacity. In each block, soil temperature at 10 cm depth was recorded every hour in one monolith of each treatment. The swards were cut four times per year for two years, the cuts being numbered 1 to 8. The mean duration of a regrowth period was five weeks. Fertiliser N was applied as a solution of ammonium nitrate at 15 g N m^{-2} y^{-1}, in split applications, 3.75 g m^{-2} at sowing and 3.75 g m^{-2} at the beginning of each of the 7 regrowth periods. At this rate of fertiliser supply, sward growth was limited by N availability, as shown by the

N nutrition index of 40% calculated from the DM and N concentration of the harvests (Lemaire and Gastal, 1997). For each monolith, the aboveground material harvested at each cut was dried at 60 °C for 48 hours, weighed and ground. Total C and N concentration and δ^{13}C were determined with a Fisons isochrom mass spectrometer coupled with a Fisons ANA 1500 elemental analyser.

Soil sampling, SOM fractionation and analysis

Soils were first sampled in February 2001, before the start of the decomposition experiment. During the experiment, destructive measurements with three replicates per treatment were performed at cuts 1 to 5 and at cut 8 in June, July, August and October 2001; June and September 2002. The soil from 5 cm around the edges was discarded. One sample of 8 × 12 × 15 cm (1800–2000 g DW) was stored at 5 °C prior to soil measurements.

Four soil organic fractions were obtained by wet sieving (Loiseau and Soussana, 1999): the root phytomass (RP), the coarse particulate organic matter between 1 and 10 mm (POM_c), the fine POM between 0.2 and 1 mm (POM_f) and the lightest part of the coarse organo-mineral fraction between 0.05 and 0.2 mm (AOM_c). The soil sample was shaken rotationally in water for 10 min in a plastic cylinder (21 cm diam.; 25 cm length), then poured through a series of three brass sieves with successive mesh sizes of 1, 0.2 and 0.05 mm. The material recovered on each sieve was washed under a continuous water flow, until the water ran clear. The organic material was separated from the mineral sands by density flotation in water. In the fraction above 1 mm, the residues greater than 10 mm were separated by hand. This fraction, only composed of living and intact dead roots, was called root phytomass (RP). The fraction 1–10 mm was composed of free plant residues derived from dead roots and called POM_c. The light fraction recovered on the 200 μ-mesh size sieve was composed of free root residues derived from root litter and called POM_f. The lightest part of the fraction recovered on the 50 μ-mesh size sieve, mostly composed of aggregates and of some pure light minerals (micas), was called AOM_c.

The four particle-size fractions were dried at 60 °C for 48 h, weighed, ground and analysed for total organic C, total N, and δ^{13}C. In addition, those separated at the initial sampling date were analysed for water soluble components (WSC), hemicellulose (Hcell), cellulose (Cell) and lignin (Li) content by the method of successive hydrolysis, according to Jarrige (1961). At the same time, total phenolics in the root phytomass was analysed by colorimetric measurement after methanol extraction (Bernhard-Reversat et al., 2003).

Five 0.2 g-root phytomass subsamples of each S1 species at t_0 were scanned on Win Mac LA 1600 (Regent Instruments INC, Québec, Canada). The total length and the mean diameter were measured using the WinRHIZO software. The sub-samples scanned were weighed after drying at 60 °C for 2 days, to calculate the specific root length (m g^{-1}). The root tissue density (mg mm^{-3}) and the exchange area (m^2 g^{-1}) were calculated, assuming cylindrical roots.

Carbon derived from S1 and S2

The carbon derived from S1 (C_1) and from S2 (C_2) in each soil fraction (i) was calculated according to the isotope mass balance as done in Balesdent et al. (1988)

$$C_{1i} = C_i(\delta_i - \delta_2)/(\delta_{1i} - \delta_2) \qquad C_1 + C_2 = C \tag{1}$$

$$C_{2i} = C_i(\delta_{1i} - \delta_i)/(\delta_{1i} - \delta_2) \qquad C_1 = 0 \Leftrightarrow \delta = \delta_2$$

$$C_2 = 0 \Leftrightarrow \delta = \delta, \tag{2}$$

where δ_1 and δ_2 are the δ of C_1 and C_2 of a given fraction i. In any treatment, δ_1 was assumed to be equal to that measured in the bare soil monoliths at each date of sampling and calculated as the mean value of three replicates per litter species and per fraction. δ_2 was the mean of six replicates measurements per species on the S2 harvest at the end of each regrowth period. The initial soil used to fill the containers did not contain coarser organic particles (Root Phytomass) but contained POM_c fraction (1 g C m^{-2}) and POM_f fraction (8.9 g C m^{-2}), that corresponded respectively to 2.5% and 14% of the total C in each fraction during the experiment. This initial carbon source had the same δ^{13}C-signature as S_2. Some minor underestimation could therefore occur in C_2 calculations without consequences on C_1 calculations.

The C_1 and C_2 contents of the soil fractions were analysed by ANOVA with the cut number, the S1 species and the S2 species as factors. In order to characterise the transformations of the root litter, the decay dynamics of C_1 was first fitted to an exponential model. The time constant of C_1 was estimated, successively for the fractions: RP (> 1 cm), RP+POM_c (> 1 mm) and RP+POM_c+POM_f (> 0.2 mm). During the two-year incubation with regular restoration of

the soil water reserve, microbial activity was little limited by soil moisture, but presumably mostly driven by temperature. Therefore, in the non-linear fitting procedure, time was expressed in degree-days, using the cumulative mean daily temperature measured in the soil during the experiment.

In a second approach, a representation of the litter transformation continuum was implemented in a mechanistic compartment model, using the Model Maker software. In this model, root litter was represented with three compartments in order of decreasing particle size (successively indexed RP, POM_c and POM_f). During decay of each compartment, C was partly assimilated by the microbial biomass and loss in CO_2. The remaining C was simultaneously transformed into one unique fraction, whose size was immediately lower. Each compartment was characterised by two parameters: the constant rate: k (dd^{-1}) of the compartment and the yield in the subsequent fraction: y (%). The carbon leaving the POM_f compartment was assumed to be entirely stabilised in the AOM fraction ($y = 100\%$). The model included 3 decay rates and 2 yields (4 degrees of freedom). For each treatment, these parameters were optimised to produce the best fit to the experimental mean values of C in RP, POM_c and POM_f at 6 times (17 degrees of freedom).

Results

Litter amounts and quality

At the end of the S1 cultivation, just before the start of the decomposition experiment, there was no significant difference due to the S1 species on the carbon accumulated in all measured below-ground fraction. The C amount of the RP fraction (168 g C m^{-2}) was three times greater than that of POM_c (35.5 g m^{-2}) and POM_f (51 g m^{-2}) (Table 1). The carbon in the litter continuum represented $9.9 \pm 2.0\%$ of the total soil carbon.

Most of the variation in the C:N ratio of the litter fractions (70%) was due to the particle size. The C:N ratio was highest in the root phytomass (Table 1). The C:N ratio of the POM_c, the POM_f and the AOM_c decreased in that order with decreasing particle size, to mean values of 33, 26 and 10, respectively. Only 6% of the variation in the C:N ratio of the litter fractions depended on the species. At t_0, the C:N ratio of the RP was lower for *Lolium* (38.7 ± 1.0) than for *Dactylis* (48.1 ± 1.0), although the N concentration did not differ significantly between species. On the contrary, the C:N ratio of the POM_f was lower in *Dactylis* while the C:N ratio of POM_c and AOM_c were similar in both species. After t_0, there was no more significant effect of the species on the C:N ratio of any litter fraction.

The chemical composition of the root litter was not significantly different between the S1 species, except that *Lolium* was one point richer in WSC (Table 1). However, WSC represented only a small proportion of the chemical composition (3.8%) as the major chemical components of the root phytomass were hemicellulose (40%), lignin (29%) and cellulose (26%) (Table 1). From RP to POM_f, WSC and cellulose concentration decreased while N concentration increased and the concentration of hemicellulose was similar in each fraction.

The root morphology differed significantly between *Dactylis* and *Lolium* (Table 2). A lower mean diameter of the roots was recorded in *Dactylis* (Table 2), where 90% of the root length belonged to the diameter class < 0.4 mm, compared to 46% in *Lolium* (data not shown). This was responsible for a greater specific root length of *Dactylis* (93.14 m g^{-1}), compared to *Lolium* (58.85 m g^{-1}). The exchange area per root mass unit was not affected by the species, despite higher tissue density in *Dactylis* roots (0.15 compared to 0.12 mg mm^{-3}). However, from the SRL, *Dactylis* roots were more uniformly distributed in the volume of the soil monoliths than those of *Lolium*.

$\delta^{13}C$-labelling

At the end of S1 cultivation (t_0), the $\delta^{13}C$ in the AOM_c was $-28.4 \pm 0.6‰$ (Table 1), which was not significantly different from the initial value. This indicated that little labelled carbon from S1 had entered in the AOM_c before t_0. The study therefore only focused on the other compartments of the litter continuum (RP, POM_c, POM_f). The $\delta^{13}C$ of the S1 root phytomass was very negative ($-43.3‰$) and not significantly different from that in the harvest (data not shown). The $\delta^{13}C$ of the root litter depended on the species and on the particle size fraction (Table 1): significantly less negative $\delta^{13}C$ values were recorded in *Dactylis* than in *Lolium* in the RP and POM_c and a mean positive isotopic deviation was recorded from RP to POM_c ($+1.6‰$) and from POM_c to POM_f ($+2.8‰$). In the bare monoliths, whose carbon was entirely derived from S1, $\delta^{13}C$ varied with time during the course of the experiment. A positive deviation occurred from t_0 to t_1, in each fraction and species, at monolith

Table 1. General characteristics and biochemical composition of the S1 root litter at t_o. Data are means for three replicates per species calculated in ANOVA with species and fraction as factors. Statistical groups were affected by the same letter. Numbers subscripted by the same upper cases letters do not differ between species; numbers subscripted by the same lower case letters do not differ between particle size fractions. $\delta^{13}C$ (‰), initial quantity (gDM m^{-2}), C:N: Carbon to Nitrogen ratio and %N: nitrogen concentration (% of DM), WSC: water soluble compounds, Hcell : hemi-cellulose, Cell: cellulose, Li: lignin. Data are expressed in percent of the total C of the sample. PP: Total phenolics (mg g^{-1} DM). RP: root phytomass (> 10 mm); POM_c: coarse particulate organic matter between 1 and 10 mm; POM_f: fine POM between 0.2 and 1 mm; AOM_c: aggregated OM between 0.05 and 0.2 mm. Significant level at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***); NS, non significant.

	$\delta^{13}C$ (‰)	Quantity (g m^{-2})	C :N	%N (%)	WSC	Hcell	Cell	Li	PP (mg g^{-1})
						(% of total C)			
Dactylis									
RP	-41.93_{Aa}	161_{Ab}	48_{Bd}	0.7_{Ab}	3.1_{Aa}	37.7_{Aa}	28.6_{Ab}	30.6_{Aa}	2.26_A
POM_c	-40.47_{Aa}	36_{Aa}	34_{Ac}	1.0_{Ac}	2.7_{Aa}	41.8_{Aa}	26.1_{Ab}	29.3_{Aa}	
POM_f	-35.85_{Ab}	47_{Aa}	22_{Ab}	0.8_{Ab}	2.8_{Aa}	34.9_{Aa}	22.8_{Aa}	39.5_{Ab}	
AOM_c	-28.07_{Ac}		10_{Aa}	0.2_{Aa}					
Lolium									
RP	−44.64Ba	174_{Ab}	39_{Ac}	0.9_{Bb}	4.4_{Bb}	43.3_{Aa}	24.3_{Ab}	28.0_{Aa}	2.79_A
POM_c	−43.90Ba	35_{Aa}	33_{Aa}b	1.1_{Ac}	3.1_{Aa}	39.1_{Aa}	26.8_{Ab}	31.0_{Aa}	
POM_f	−37.94Bb	55_{Aa}	29_{Bb}	0.9_{Ab}	2.5_{Aa}	38.7_{Aa}	21.5_{Aa}	37.2_{Ab}	
AOM_c	-28.79_{Ac}		11_{Aa}	0.2_{Aa}					
Significance level									
Species	***	NS	NS	NS	NS	NS	NS	NS	NS
(AB) Fraction	***	***	***	***	**	NS	*	*	
(abc) Interaction	NS	NS	*	NS	*	NS	NS	NS	

re-watering (Figure 1). The $\delta^{13}C$ of S2 was not significantly different between harvest and stubble, but depended on species and time. The mean value of the $\delta^{13}C$ was -25.9 ± 0.1‰ for *Dactylis* and -27.3 ± 0.1‰ for *Lolium* and was not affected by the nature of S1 (data not shown).

As a consequence, the data used to calculate the amounts of C_1 and C_2 by equation (1) and (2) were: (i) the values of δ_1 observed in each fraction at each sampling date in the control treatments, maintained bare during S2, assuming that δ_1 was similar in the presence of any species in S2; (ii) the values of δ_2 in the harvests at each cut and for each species S2, before soil sampling.

Carbon accumulation and decomposition

During the course of the experiment, new carbon from S2 accumulated exponentially in each particle size fraction. In an exponential model, neither the rate nor the potential accumulation of new carbon differed according to the nature of the root litter (S1) or the growing species (S2) (Table 3).

In the same time, old carbon from S1 disappeared exponentially from the particle size fractions. The rate of C decay was calculated for the root phytomass (RP > 10 mm), for the sum of RP and POM_c (> 1 mm) and for the sum of RP, POM_c and POM_f (> 0.2 mm). In all treatments, the decay rate decreased from the RP fraction to the sum of RP and POM_c and to the sum of RP, POM_c and POM_f (Table 4).

The decay rate was greatly affected by the nature of the root litter (Table 4). That of *Dactylis* litter was faster for all particle size fractions, with respective values for *Dactylis* and *Lolium* of 14.10^{-4} dd^{-1} and 8.10^{-4} dd^{-1} in the RP fraction, 9.10^{-4} and 4.10^{-4} dd^{-1} in the RP + POM_c, and 5.10^{-4} and 2.10^{-4} dd^{-1} in the total litter continuum. In addition, the presence of a living sward during litter incubation accelerated the decay rate of the RP+POM_c and that of the total litter continuum (Table 4), as compared with the bare soil.

Table 2. Dead root morphology at t_0. Means of 5 replicates per root species for the morphological characteristics of the dead roots at t_0, start of incubation experiment. Mean root diameter (mm), root density (mg mm^{-3}), specific root length (SRL, m g^{-1}); exchange area per root mass unit : EA (m^2 g^{-1}). The average sample mass was 0.2 g. Significant level at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***); NS, non significant.

	Diameter (mm)	Density (mg mm^{-3})	SRL (m g^{-1})	EA (m^2 g^{-1})
Dactylis	0.30	0.15	93.14	0.88
Lolium	0.43	0.12	58.85	0.80
Significance level	***	***	***	NS

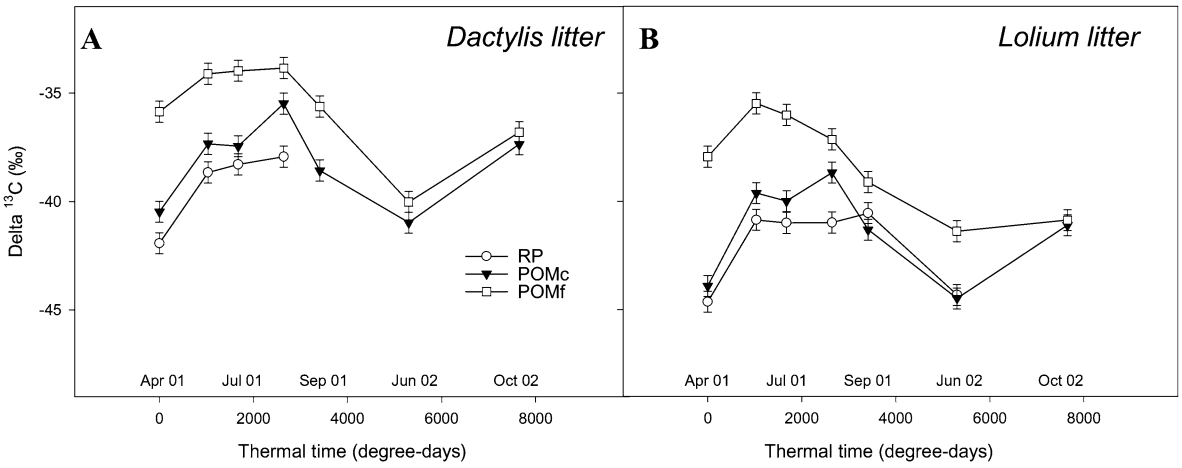

Figure 1. Seasonal variation $\delta^{13}C$ of the root litter fractions from S1. $\delta^{13}C$ in the three different litter fractions of S1 (RP, POM_c and POM_f) is given at seven sampling dates over two years of incubation. δ_1 values are the means ± SE of 3 replicates for the monoliths taken bare during S2 RP: root phytomass (> 10 mm); POM_c: coarse particulate organic matter between 1 and 10 mm; POM_f: fine POM between 0.2 and 1 mm. Treatments: A: *Dactylis* litter; B: *Lolium* litter. Lack of some data at the end of the experiment is caused by the total decay of the RP. Time was expressed in degree-days, using the cumulative mean daily temperature measured in the soil during the experiment.

Table 3. Accumulation dynamics of carbon in the root system of S2. The accumulation rate (a) and the potential accumulation (y_o) are calculated according to exponential regression models ($y = y_o{}^*(1 - \exp(-a^*\text{time}))$) for the RP fraction, the sum of RP+POM_c and the sum of RP+POM_c+POM_f. Data ± (SE). Time was expressed in degree-days, using the cumulative mean daily temperature measured in the soil during the experiment. The accumulation rate (a) is expressed in degree-day^{-1}*10^{-4} and the potential (y_o) in gC m^{-2}. Treatments: D=*Dactylis* and L=*Lolium*. The first letter designates root litter (S1) and the second letter rhizosphere species (S2).RP: root phytomass (> 10 mm); POM_c: coarse particulate organic matter between 1 and 10 mm; POM_f: fine POM between 0.2 and 1 mm. Significant level at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***)

	Rate of accumulation(a)						Potential accumulation (y_0)					
	RP		RP+POM_c		RP+POM_c+POM_f		RP		RP+POM_c		RP+POM_c+POM_f	
	Mean ±SE	P	Mean ±SE	P	Mean ±SE	P	Mean ±SE	P	Mean ±SE	P	Mean ±SE	P
DD	6.0 ± 2.0	*	6.6 ± 2.1	*	2.9 ± 0.4	***	84 ± 10	**	98 ± 10	***	186 ± 12	***
DL	7.9 ± 2.2	*	6.5 ± 1.9	*	2.6 ± 0.4	***	87 ± 7	***	120 ± 11	***	239 ± 18	***
LD	6.7 ± 1.5	**	6.1 ± 1.4	**	3.5 ± 0.6	**	90 ± 6	***	115 ± 9	***	188 ± 14	***
LL	6.0 ± 0.8	**	5.6 ± 1.9	*	3.7 ± 1.0	*	100 ± 5	***	145 ± 19	**	202 ± 23	***

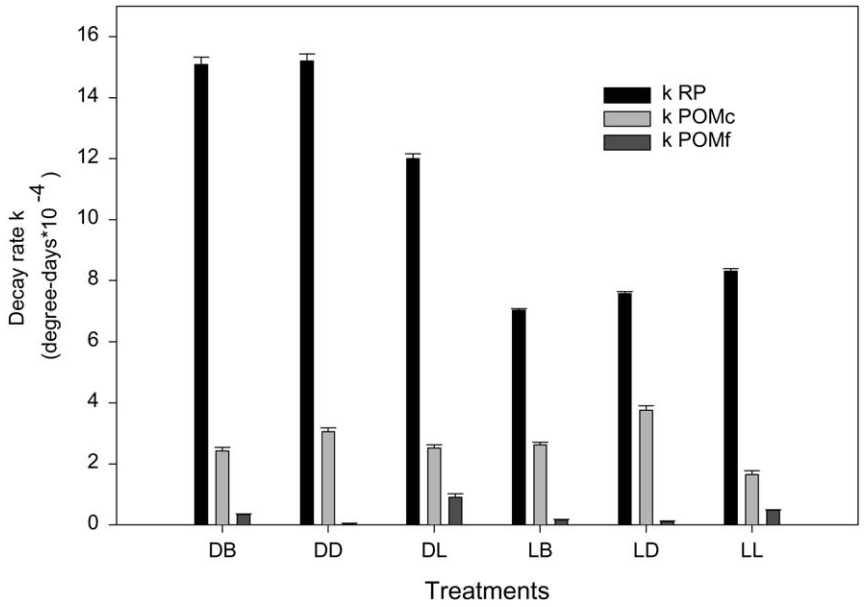

Figure 2. Decay rates (k) for three compartments of the litter continuum. Data are values ± SE (in degree-day^{-1}*10^{-4}) calculated in the mechanistic model of litter continuum decomposition. In each treatment, k values are calculated from experimental values of C_1 in three particle size fractions at 6 occurrences. Time was expressed in degree-days, using the cumulative mean daily temperature measured in the soil during the experiment. Significance of the model $P < 0.01$, $r^2 = 0.95$ for the 6 treatments. The degrees of freedom were 4 for the model, 17 for the data and 13 for the residual. Treatments: the first letter indicates the nature of the litter (S1), the second letter, the nature of the rhizosphere (S2) during root litter incubation. D: *Dactylis*, L: *Lolium* and B: bare soil. RP: root phytomass (> 10 mm); POM_c: coarse particulate organic matter between 1 and 10 mm; POM_f: fine POM between 0.2 and 1 mm.

Modelling the continuum of litter transformation

The mechanistic model allowed more accurate estimations of the decay rate for individual particle size fractions (Figure 2). The mean rate of litter transformation decreased from $(10.9 \pm 0.2)\ 10^{-4}$ to $(2.7 \pm 0.1)\ 10^{-4}$ and to $(0.2 \pm 0.04)\ 10^{-4}$ dd^{-1} as particle size decreased from RP to POM_c and to POM_f. The particle size factor explained 84% of the variance of the rate constants, while only 14% of this variation was due to the treatments (ANOVA for 3 fractions and 6 treatments).

Most of the variation in the rate constants of the RP fraction was due to the nature of the root litter: the decay rate was faster for the *Dactylis* (14.1 ± 0.3) than for the *Lolium* litter $(7.6 \pm 0.1\ 10^{-4}$ dd$^{-1})$ (Figure 2). Therefore, more carbon remained in the root litter continuum of *Lolium* than in that of *Dactylis*, at any time during root litter incubation (Figure 3A). There was also a significant effect of the growing species on the litter decay rate. The *Lolium* dead root phytomass decayed significantly faster in the presence of a living stand (LD and LL treatment), than under the bare soil (LB treatment). The dead root phytomass of *Dactylis* decayed significantly faster when incubated in the rhizosphere of *Dactylis* (DD treatment) than in the rhizosphere of *Lolium* (DL treatment) (Figure 2).

From the mechanistic model, C in the root litter continuum decreased exponentially to 25–40% of the initial litter–C content at the end of the first growing period, depending on the treatment, and to 20% after 18 months of incubation in all treatments (Figure 3A). The dynamics of the decayed-C stabilised in the AOM fraction was linear (Figure 3B). The cumulated amount of C stabilised after 18 months incubation varied between 1 and 14% of the initial litter-C, according to the treatment. At any time of litter incubation, a greater part of the litter-C was accumulated in the soil under the *Lolium* than under the *Dactylis* rhizosphere (Figure 3B).

Hence, the mechanistic model characterised not only the litter-C decay rate but also the efficiency of C stabilisation, defined as the percentage of litter-C stabilised in the AOM at a given stage of litter decay (Figure 4). The proportion of C stabilised increased exponentially at the later stage of litter transformation. It was much influenced by the living stand, more carbon being stabilised under the *Lolium* than under the *Dactylis* stands. Compared to the bare soil,

Table 4. Decay rate of root litter C from S1. The relative decay rate (k) is calculated according to the exponential regression model: $y = y_o{}^* \exp(-k^*\text{time})$ for RP, for the sum of RP+POM_c and for the sum of RP+POM_c+POM_f. y_0 is the initial carbon content at t_0. Time was expressed in degree-days, using the cumulative mean daily temperature measured in the soil during the experiment. Data are calculated values ± SE and are expressed in degree-day$^{-1*}10^{-4}$. Treatments: B=Bare soil, D=*Dactylis* and L=*Lolium*. The first letter designates root litter (S1) and the second letter rhizosphere species (S2). RP: root phytomass (> 10 mm); POM_c: coarse particulate organic matter between 1 and 10 mm; POM_f: fine POM between 0.2 and 1 mm. Significant level at $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***)

Rate of decay (k)

	RP			RP+POM_c			RP+POM_c+POM_f		
	Mean	SE	P	Mean	SE	P	Mean	SE	P
DD	15.2	±0.4	***	10.6	±0.7	***	5.9	±0.7	**
DB	15.2	±1.7	***	7.0	±1.2	***	3.8	±1.0	*
DL	12.0	±1.2	**	8.6	±1.1	***	4.6	±0.6	***
LD	7.6	±1.0	**	4.1	±0.5	***	2.3	±0.4	**
LB	7.0	±0.3	***	3.3	±0.2	***	2.1	±0.3	***
LL	8.2	±1.1	***	4.5	±0.7	**	2.7	±0.3	***

Lolium increased, whereas *Dactylis* decreased litter C stabilisation in the soil (Figure 4).

Finally, two significant factors were the nature of the litter and the nature of the growing species, and two meaningful variables were litter decay rate and the efficiency of carbon stabilisation. The decay rate was particularly influenced by the nature of the root litter, whereas the efficiency of stabilisation was particularly influenced by the growing species. *Lolium* favoured litter C conservation through slower litter decay rate and greater stabilisation of the litter-C. On the contrary, both the nature of the litter and the rhizosphere activity of *Dactylis* induced greater loss of litter C.

Discussion

Methods

The decomposition of grassland root litter occurs in conditions that are markedly different from those of above-ground crop residues, either buried or submitted to decomposition on the soil surface (Dukes and Field, 2000). It has been previously shown that roots decompose more slowly than leaves when placed in the same laboratory conditions (Bending et al., 1998, Gorissen and Cotrufo, 2000). Nevertheless, due to sward longevity, grassland root litter experiences particular conditions during incubation in the soil. Our experimental conditions allowed the fate of the root litter C to be measured for a realistic distribution in the soil and contact with the growing species, that would not have been possible with the litter bag method (Wieder and Lang, 1982). Observing up to 80% of the decay in the litter-continuum during an 18-month experiment enables the medium-term litter dynamics to be addressed, whereas litter incubation experiments often focus on the first stage of litter decomposition.

Initial litter

At the start of the decomposition experiment, root litter quantity was similar between both S1 species (Table 1). Hence, any S1 effect on root litter decomposition can only be due to qualitative attributes of the root litter. The few differences in the chemical composition of the root litter would rather indicate a greater litter quality and fermentability in *Lolium*, that should increase its root litter decay. Species differ more in root morphology, *Dactylis* roots being finer and more uniformly distributed in the soil than those of *Lolium*.

Litter continuum

The C:N ratio of the RP, POM_c, POM_f and AOM_c decreases in that order, with respective mean values of 46, 33, 26 and 10. N enrichment of the litter residues during decomposition can be explained by two processes. First, C mineralisation results in an increased N concentration (Prescott et al., 1992). Secondly, microbes of low C:N ratio surround the litter residues of

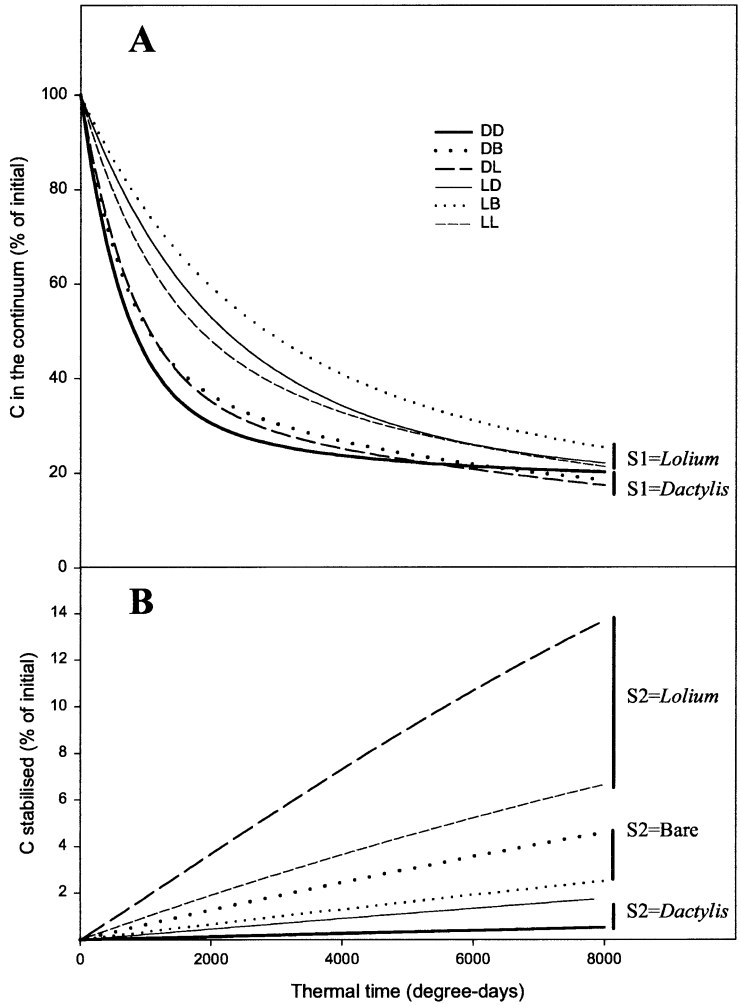

Figure 3. Dynamics of C in the litter continuum. A: C remaining in the litter continuum (RP+POM_c+POM_f) over two years of incubation (8000 degree-days). B: C stabilised in the AOM during the same time. Data are calculated from the mechanistic model and expressed in percent of the initial C in the litter continuum at t_0. Time was expressed in degree-days, using the cumulative mean daily temperature measured in the soil during the experiment. Treatments: the first letter indicates the nature of the litter (S1), the second letter, the nature of the rhizosphere (S2) during root litter incubation. D: *Dactylis*, L: *Lolium* and B: bare soil.

higher C:N ratio (Fahey, 1983) and the relative size of this microbial film may increase with decreasing particle size of the root debris. In any way, a continuous N enrichment with decreasing particle size argues for the existence of a continuum of transformation.

The chemical composition of the POM fractions is in accord with our conceptual model of litter transformation. First, POM chemical composition only depends on the particle size fraction and does not depend on the species. Secondly, the chemical components disappear in the order of their fermentability in the POM of decreasing particle size: WSC decomposes from RP to POM_c, and cellulose from POM_c to POM_f resulting in an increase of lignin concentration.

The decay rates in the litter continuum also depends mostly (84%) on the particle size and decreases from RP to POM_f. Finally, few experimental results refute the conceptual model of a litter continuum, in which the attributes of the particle size compartments (C:N ratio, chemical composition and decay rate) are constants depending mainly on the particle size. Some results, as variable C:N ratios of the POM_c, seem to refute this conception, but could as well validate the model, because discrete fractions of the litter continuum would not have exactly the same mean

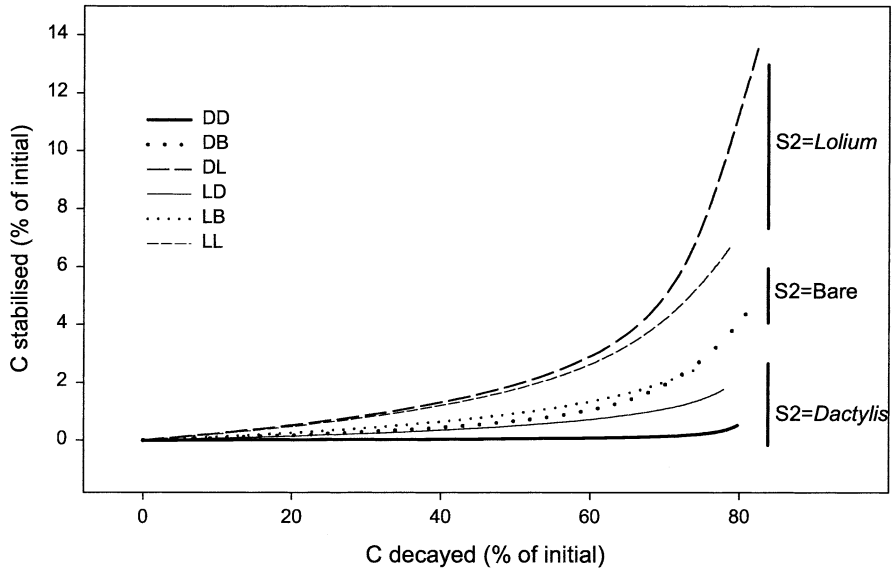

Figure 4. Efficiency of carbon stabilisation versus litter decay rate. For each treatment, the amount of litter-C stabilised is plotted against the total amount of decayed litter-C (leaving the litter continuum) during an incubation period of 8000 degree-days. Data are calculated from the mechanistic model and expressed in percent of the initial C in the litter continuum at t_0. Time was expressed in degree-days, using the cumulative mean daily temperature measured in the soil during the experiment. Treatments: the first letter indicates the nature of the litter (S1), the second letter, the nature of the rhizosphere (S2) during root litter incubation. D: *Dactylis*, L: *Lolium* and B: bare soil.

particle size in different systems which are not at equilibrium. Nevertheless, the nature of the initial litter and of the rhizosphere induced different dynamics and modalities of litter transformation of this continuum.

Litter effect (S1 factor)

The exponential regressions (Table 4) and the mechanistic model (Figure 2) show that the decay rate of the litter continuum depends on the nature of the initial litter even if it explains only a few part of the variability in the decay rates of individual particle size fractions (14%). Higher decay rates are measured for *Dactylis* than for *Lolium* litter, despite little difference in root quality. The only significant differences in the C:N ratio and WSC concentration should have rather favoured the decay of *Lolium* litter, because of higher N concentration and fermentability. As chemical composition or C:N ratio cannot explain the faster rate of the *Dactylis* root litter, factors governing the litter decay rate should therefore be sought in the morphological features of the roots and in the distribution of the root litter within the soil.

As the SRL explained 95% of the variability in the transformation rate of similar amount of root phytomass ($k = -3.5 + 0.19SRL$, $P < 0.01$, $n = 6$) root morphology could be the major factor of the litter effect. A longer total root length per unit soil volume may have accelerated the decay of the root litter by more efficient contact with soil micro-organism and the smaller mean diameter of the *Dactylis* roots may have favoured splitting and N enrichment of the root fragments. Finally, the decay rate of the particle size fractions depended mostly on two aspects of litter particle morphology: the length ('particle size') and the width ('SRL'). As might be expected, the role of the width was limited to the greatest particle size fractions.

Rhizosphere effect (S2 factor)

The presence of a sward during litter incubation accelerates the decay rate of the litter continuum as compared with the bare soil. Such an acceleration of the decay rate can be due to the presence of living roots, confirming the rhizosphere activity as a factor that stimulates litter decomposition (Billès and Bottner, 1981; Van Ginkel et al., 1996). The decay rate of the *Dactylis* litter is faster in the presence of a *Dactylis* than of a *Lolium* rhizosphere. From similar carbon accumulation in the living roots for both S2 stands and greater SRL in *Dactylis*, this result is consistent with better soil prospecting by the *Dactylis* roots. The maximum litter decay rate is obtained with

Dactylis litter incubated in the presence of a *Dactylis* sward, probably because this situation maximises the chances of conjunction between the living roots and root litter in the soil volume.

The amount of litter-C, from any species, that is stabilised in the AOM is greater in the presence of *Lolium* rhizosphere than of *Dactylis* one (Figure 3B). The living stand also determines the efficiency of litter-C stabilisation: for similar amount of carbon leaving the litter continuum, more is stabilised under *Lolium*, while proportionally more is mineralised under *Dactylis* (Figure 4). More litter-C is therefore presumably sequestered for a longer term under *Lolium*, whereas more litter-C is lost under *Dactylis*. Such a result is in agreement with Bardgett (1999), who showed microbial biomass (fungi and bacteria) lower under *Lolium* than under other grasses.

Species strategy

In this experiment, *Dactylis* demonstrates both a 'fast' root litter decay and a rhizosphere activity more able to stimulate C mineralisation. By contrast, *Lolium* associates a 'slow' litter decay with a rhizosphere activity able to stabilise a greater part of the litter-C. Therefore, both root traits, relative to the root litter and to the rhizosphere, distinguish two divergent species strategies, toward more carbon sequestration with *Lolium* and more carbon turnover and loss with *Dactylis*. The ability of *Dactylis* to accelerate the turnover of its own litter-C is probably able to ensure better availability of the nutrients present in the root litter, whereas *Lolium* strategy may allow longer conservation of litter C and N in the soil. Therefore, from the root traits influencing the soil C-N cycle (Tilman, 1990), *Dactylis* should be more competitive than *Lolium*.

This result is unexpected, because numerous leaf traits tend to indicate *Dactylis* to be more nutrient conservative than *Lolium*: e.g. greater leaf size (Ryser and Urbas, 2000), lower SLA (Hunt and Cornelissen, 1997), and greater nutrient resorption efficiency (Eckstein et al., 1999). Finally, relative to each other, each species associates competitive with conservative traits: *Dactylis* is rather leaf-conservative and root-competitive, whereas *Lolium* is leaf-competitive and root-conservative. This result is in accordance with Gorissen and Cotrufo (2000), who observed no positive correlation between leaf and root decomposition rates. In addition, in *Lolium*, a fast leaf litter decomposition rate was associated with a slow root litter decomposition rate.

The competitive strategy is usually considered as typical of species from fertile habitats, whereas the conservative strategy is considered typical of poor ones (Chapin, 1980). At the ecosystem level, one species strategy tends to differentiate the habitat in a sense that excludes the opposite strategy (Tateno and Chapin, 1997). Here, we looked at two species, which demonstrate similar high nutrient requirements (Ellenberg et al., 1992) and that usually grow together in the same community. The association of traits that are opposite for roots and leaves in a manner that is also opposite for *Dactylis* and *Lolium* could explain why they do not exclude each other. Species strategies acting differently on the C and N cycles seem able to ensure the conservation of mixed species community and ecosystems.

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