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REGULAR ARTICLE

Decomposition rates of fine roots from three herbaceous perennial species: combined effect of root mixture composition and living plant community

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Abstract
Aims In most ecosystems, plant roots from different species decompose in mixtures and in the presence of living roots; however much root decomposition research has focused on how roots of individual species or artificial mixtures decompose in the absence of living plants. We thus examined two poorly studied components of root litter decomposition: 1) whether decomposition of root mixtures can be predicted from the sum of the decomposition rates of each component species and 2) how living plants influence rates of root decomposition.
Methods Decomposition rates of roots from three perennial herbaceous Mediterranean species grown in monocultures and in two- and three-species mixtures were determined after a one-year incubation period under their living community and in non-vegetated soil (bare soil). Soil respiration in the presence of glucose (substrate induced respiration, SIR) was measured in each plant community and in bare soil.
Results Decomposition rates of root mixtures cannot be predicted from decomposition rates of the component species, both additive and non-additive effects were observed; the presence of low quality roots of *Carex humilis* in mixtures strongly negatively influenced root decomposition. The presence of living plants stimulated root decomposition in monocultures and two-species communities, likely through an enhanced microbial activity (SIR) under plant communities.
Conclusion This study highlights that root decomposition cannot be predicted from decomposition rates of the component species and is more influenced by endogenous factors or root litter functional composition than by plant community composition.

Keywords Living plant effects · Mediterranean species · Microbial activity · Non-additivity · Root decomposition · Root mixtures

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Introduction

Plant roots are critical organs for soil functioning since they represent the main direct inputs of C and nutrients in soil through root decomposition (Clemmensen et al. 2013). Despite their importance, only 2% of studies on decomposition have focused on roots (Zhang et al. 2008). Moreover, in plant communities roots of different species are frequently intermingled; they grow, interact and decompose in mixtures rather than isolated and they do so in the presence of living roots, a factor that largely affects root decomposition (Van Der Krift et al. 2002; Personeni and Loiseau 2004). Despite this evidence, most studies on root decomposition have considered roots from individual plant species that were left to decompose under controlled laboratory conditions (Van Der Krift et al. 2002; Personeni and Loiseau 2004) and in bare soil or that used artifitial root mixtures (Robinson et al. 1999; Cong et al. 2015; Guerrero-Ramírez et al. 2016). It thus becomes crucial to understand processes regulating root decomposition in experiments where root litter of different species and from species mixtures interact and decompose in the presence of living plants.

Root litter decomposition is controlled by two main groups of factors: endogenous factors, i.e. the chemical composition and morphology of roots (Van Der Krift et al. 2002; Zhang et al. 2008; Zanne et al. 2015) and exogenous factors, i.e. the conditions where incubation takes place. On one hand, the rate of decomposition depends on endogenous factors such as the quality of the root litter decomposing, which in the case of root mixtures is influenced by the number, the identity and the quality of each component species. Both at the species or community levels, root decomposition is influenced by root morphology and chemistry (Zhang et al. 2008). Roots characterized by high lignin concentrations or high C: N and lignin: N ratios are associated with low rates of decomposition (Silver and Miya 2001; Vivanco and Austin 2006; Hobbie et al. 2010; Freschet et al. 2012; Birouste et al. 2012; Roumet et al. 2016) whereas roots with high N concentrations decompose faster (Prieto et al. 2016; Roumet et al. 2016). On the other hand, in a given climate and soil, exogenous factors are affected by the presence of living plants that alter resource availability, the soil micro-environment (i.e. soil moisture, pH, O_2), and the supply of easily metabolized carbon compounds in the soil through root exudates (Van Der Krift et al. 2002; Personeni and Loiseau 2004; Austin and Zanne 2015). Living plants are expected to enhance root decomposition by stimulating microbial activity. However, evidence for such effects is contradictory since both negative and positive effects have been reported (Sparling et al. 1982; Nicolardot et al. 1995; Van Der Krift et al. 2002). Negative effects were generally associated with soil desiccation under living plants resulting from plant water uptake (Jenkinson 1977) whereas positive effects have been associated to stimulation of soil microbial growth (Van Der Krift et al. 2002). The composition of the living plant community may affect root decomposition since plant species differ in their rhizospheric activities (pH, resources acquisition, quantity and quality of exudates released to the soil) (Hinsinger et al. 2009; Jones et al. 2009), which may influence the activity and the diversity of the microbial community. Recent studies suggest that soil microbial communities found below a particular plant community are specialized in the degradation of the substrates derived directly from the plant community above it (home-field advantage hypothesis; Gholz et al. 2000; Ayres et al. 2009; Freschet et al. 2012; Perez et al. 2013). This hypothesis suggests that decomposition is enhanced if litter decomposed in the habitat from where it derives as compared to if it decomposed in another environment.

Mechanisms underlying patterns of decomposition in leaf and root litter mixtures are still debated and unclear (Robinson et al. 1999; Gartner and Cardon 2004; Hättenschwiler et al. 2005; Lecerf et al. 2011; Coq et al. 2011; Makkonen et al. 2013; Cong et al. 2015). According to the mass ratio hypothesis (Grime 1998), within a given mixture, the effect of each species is proportional to its relative abundance and the decomposition rates can be calculated through the decomposition rates of each component species separately (hereby refered to as additivity; Tardif and Shipley 2013). However, other studies on leaf litter decomposition evidenced that non-additive effects are predominant over additivity since decomposition of a mixture may be increased or decreased due to synergistic or antagonistic interactions (Gartner and Cardon 2004; Pérez Harguindeguy et al. 2008; Makkonen et al. 2013). For example, possible interactions between litter from different species include nutrient transfer from litter-rich to nutrient-poor litter increasing overall decomposition rates of litter mixtures (Salamanca et al. 1998; Liu et al. 2009). Other examples include amelioration of micro-environmental conditions or positive interactions

across trophic levels that increase litter decomposition rates, or negative effects of particular secondary compounds on decomposition of litter mixtures (Hättenschwiler and Gasser 2005; Hättenschwiler et al. 2005). Additionally, an increase in the number of species in a mixture could increase the diversity of habitats and type of litter available for soil biota increasing rates of microbial activity and decomposition. However, there is growing evidence that identity of species and functional diversity of leaf litter in mixtures are more important than the number of species *per se* for decomposition processes (Wardle et al. 1997; Downing and Leibold 2002). For example, the presence of species with leaves having low N and high lignin concentrations may slow down the overall decomposition of the mixture (Pérez Harguindeguy et al. 2008). Similarly, the presence of roots with these characteristics in a mixture may slow down the overall decay rates although this remains to be tested experimentally. To the best of our knowledge, a handful of studies have dealt with decomposition of root mixtures (Robinson et al. 1999; Carrera et al. 2008; de Graaff et al. 2011; Shi et al. 2012; Cong et al. 2015; Guerrero-Ramírez et al. 2016), but none of them have tested the combined effect of root mixture composition and of living plant presence on root decomposition rates.

In this study, our main aims were to investigate whether decomposition of root mixtures can be predicted from the decomposition of the component species and whether root decomposition is affected by the presence of living plants and by the composition of the plant community under which root litter decomposed. The few studies that have dealt with root mixture decomposition (Robinson et al. 1999; de Graaff et al. 2011; Shi et al. 2012; Guerrero-Ramírez et al. 2016) used artificial root mixtures (i.e. obtained by mixing a known proportion of roots from each single species previously harvested from monocultures or single individuals) that decomposed in the absence of living roots. In this study, we compared root decomposition of three perennial herbaceous species of Mediterranean rangelands differing in their root morphology and chemistry (Pérez-Ramos et al. 2013): *Bromus erectus*, *Festuca christiani-bernardii* and *Carex humilis*. These species were cultivated in monocultures and in mixtures with all possible combinations of pairs of species and the combination of the three species (Fig. S1). Fine roots were harvested from each monoculture and mixed community and incubated during 1 year in bare soil (soil with no vegetation) and underneath its own plant community, i.e. in presence of living roots. We hypothesized that i) decomposition of root mixtures cannot be predicted from the decomposition rates of the individual component species within the root litter mixture (non-additivity hypothesis) since the presence in the mixtures of individual root litter quality (e.g. roots with low N and high C: N ratios and tissue density) would affect the decomposition rate of the root mixtures in a non-additive way and that ii) roots will decompose faster when incubated under plant communities, in the presence of living roots, than under bare soils due to a stimulation of microbial activity under plant communities. We also hypothesized that root decomposition is influenced by the species composition of the plant community under which it decomposes and will be stimulated in more diverse pant communities.

Material and methods

Experimental design

The study was performed in a common garden experiment located at the Centre d'Ecologie Fonctionnelle et Evolutive in Montpellier, France (43°59′N, 3°51′E). Climate is Mediterranean sub humid (Daget 1977). The mean annual temperature and the mean annual precipitation were 14.4 °C and 769 mm, respectively, and the mean deficit between precipitations and reference evapotranspiration (P-ET_0) was 382 mm for the spring and summer period comprised between March and end of August (INRA Lavalette meteorological station; period: 1990–2013; Barkaoui et al. 2016). The soil was 1.20 m deep and the topsoil (0–20 cm) contained 44.8 ± 3.6% clay (mean ± standard error), 33.7 ± 3.7% silt and 21.5 ± 2.7% sand with pH = 7.8, total organic C = 14.5 g Kg^{-1}, N = 1.38 g Kg^{-1} and C: N = 10.5. During the experiment, each plot received 277 mm of water by irrigation to compensate for substantial precipitation deficit and to provide proper plant development conditions.

Three perennial graminoid species, abundant in Mediterranean rangelands, *Bromus erectus* Huds., 1762 (B), *Festuca christiani-bernardii* Kerguélen., 1979 (F) and *Carex humilis* Leyss., 1758 (C), were selected according to their contrasted root chemistry and morphology (Pérez-Ramos et al. 2013; Barkaoui et al. 2016). Ramets of each species were collected in January 2011 at La

Fage INRA experimental site (see Bernard-Verdier et al. 2012; Pérez-Ramos et al. 2012 for site details) and were grown for 3 months in a glasshouse. When plants were well rooted, they were transplanted into a common garden in March 2011. Seven plant communities were established (treatments from now on) in 1 × 1.2 m plots (Fig. S1, S2): three monocultures (B, C, F), three bi-species mixtures (CF, BC, BF) and a tri-specific mixture (BCF). The 7 treatments were contiguous forming a block; they were repeated in four blocks, each treatment was randomly assigned within the four replicated blocks. Within each treatment, plants were transplanted every 10 cm in order to ensure a plant density of 100 individuals m^{-2}. In mixtures, individuals of each species were intermingled to ensure interactions between the different species; they were planted alternatively, 50 and 33% of each species for bi- and tri-specific mixtures respectively. Additionally, four plots (1 × 1.20 m) without vegetation (bare soils thereafter), one per block, were used as a litter bed. All plots were weeded regularly by hand. The first year after planting (from March 2011 to March 2012) allowed plants to reach full establishment (Fig. S2).

Above- and belowground biomass

Above and belowground biomass were determined in May 2012 (i.e. 1 year after plant establishment), at the peak of vegetative growth. At that time the foliar cover ranged from 90 to 100% (Fig. S2). In order to minimize border effects, shoots of the 24 most central plants (e.g. a central plot of 0.24 m^2 surface with its borders located 25 cm away from the plot borders) were harvested in each plot. Individual plants were clipped three centimeters above soil surface (24 plants for monocultures, 12 plants of each species in bi-specific mixtures and 8 plants of each species in the tri-specific mixture). Shoots were sorted by species, oven dried at 60 °C for 72 h and weighed. The abundance of each species in the mixtures was calculated as the ratio between the shoot dry mass of each species divided and the total shoot dry mass of the 24 individuals from the mixtures.

For belowground biomass, one soil core (5 cm diameter, 20 cm deep) collected between two healthy plants was taken from each monoculture and bi-specific mixture plot. When root material was insufficient for decomposition and root trait determinations, an additional soil core from the same plot was collected and roots from the two cores were pooled and used as a single replicate. For the tri-specific mixtures (BCF), three soil cores were collected between each species and pooled into one single replicate. Immediately after soil coring, soil and roots were carefully separated by hand and roots were gently washed with water. Using a digital caliper, we selected fine roots only, defined in this study as roots with a diameter ≤ 2 mm. Fine roots were split into four homogeneous subsamples; one subsample was kept in water at 4 °C and used to determine root morphology, one was oven-dried at 40 °C for 72 h and used to determine its chemical composition, the remaining two subsamples were spread on filter paper after washing, air-dried for a week and used for the decomposition experiment (one subsample incubated in the litter bed and one incubated in the plots where they were collected). We selected fine roots with no sign of senescence since it was very difficult to identify and collect large quantities of dead roots. Nonetheless, the features of living and decomposing roots form a continuum (Hobbie et al. 2010), and most studies have reported little or no difference in nutrient concentration between live and dead roots (McClaugherty et al. 1982; Nambiar 1987; Aerts 1990; Freschet et al. 2010). Root biomass was calculated on a per area basis as the total root dry mass in each core(s) divided by the core(s) area (g m^{-2}). The root: shoot ratio (R: S) was calculated for each species in monocultures as the ratio between root and shoot biomass (g m^{-2}). Assessing root biomass for each species in mixtures was extremely difficult due to strong similarities in root morphology among the three graminoid species studied so for each mixture and block, we used the method described in Mueller et al. (2013) to calculate the root biomass of each component species as the shoot biomass of each species in the mixture multiplied by the R: S ratio of each species in monocultures. The calculated root biomass of each component species was summed to produce an "expected" total root biomass, which was compared to the total observed biomass to evaluate the accuracy of root biomass prediction (Fig. S3). The relationship between observed and expected root biomass was highly significant with an $R^2 = 0.90$ and a slope = 0.94. These results are consistent with those of Mueller et al. (2013) showing that species do not differ on their belowground biomass allocation whether grown in monocultures or in species mixtures with up to eight species. We then calculated the root relative abundance for each species of the mixtures as the root biomass of each species divided by the observed total root biomass.

Root morphology and chemistry

Root morphology and root chemistry were determined for each species growing in monocultures (4 replicates per species). For root morphology, prior to scanning, roots were sponged carefully to remove all excess water and weighted to determine their saturated mass (SM, mg) and then stained by a 2-min immersion in methyl violet (0.5 g L^{-1}) to increase contrast. Roots were then rinsed and spread out in water onto a mesh tray, transferred onto a transparent acetate sheet and scanned at 400 dpi. The Winrhizo software (v. 2009, Regent Instrument, Quebec, Canada) was used to determine root length (L, cm), volume (V, cm^{-3}) and average diameter (D_m, mm). Subsequently, roots were oven-dried at 60 °C for 72 h and weighed to determine their dry mass (DM, g). Root dry matter content (RMDC, mg g^{-1}) was calculated as the ratio between DM/SM, root tissue density (RTD, g cm^{-3}) as the ratio DM/V and specific root length (SRL, m g^{-1}) as the ratio L/DM. Root length density (RLD, cm cm^{-2}) was calculated as the root dry mass per m^2 multiplied by the SRL.

Root chemistry was determined on four oven-dried (40 °C for 48 h) replicates per treatment. Root material was ground in a cyclone mill (Cyclotec Sample Mill 1093; Tecator, Hogänäs, Sweden) with a filter mesh of 1 mm diameter. The water-soluble compounds (soluble hereafter), cellulose and lignin concentrations (mg g^{-1}) were obtained by the Van Soest method (Van Soest 1963) using a Fibersac analyzer (Ankom, Macedon, NJ, USA). Root carbon (C) and nitrogen (N) concentrations (%) were determined on four finely ground root replicates (ball mill) by dry combustion using an elemental analyzer (Thermo-Finnigan EA1112, Milan, Italy).

Decomposition experiments

Root decomposition was determined as the root mass loss after a one-year incubation period in litterbags buried in soil. In June 2012, two sets of litterbags were buried to test the different hypotheses (Fig. S1). One set of litterbags ($n = 28$) with roots collected from each plot were buried and incubated in their own plots. The second set of litterbags contained roots from the 7 treatments ($n = 28$) that were incubated in the associated litter bed (bare soil with no plants). For each litterbag, air-dried roots were weighed (301 ± 1 mg, mean ± SE) and enclosed in a polyamide tissue litterbag (Diatex, Villeurbanne, France; inner size of 4 × 10 cm). Litterbags had a mesh size of 50 μm and were closed on one side with staples. Four additional sub-samples of air-dried roots were oven-dried at 60 °C for 72 h to determine the air-dried: oven-dried mass ratio to correct the initial root mass. Subsequently, these roots were burned at 500 °C to determine their initial ash content. All litterbags ($n = 56$) were buried vertically between 10 and 15 cm depth in the bare soils and in the different plots. They were buried between two randomly selected healthy plants in monocultures or between two or three healthy plants from different species in the mixtures. After a one-year incubation period, litterbags were gently retrieved, opened and all the remaining roots inside litterbags were extracted. Roots were washed to eliminate adhered soil particles, dried at 60 °C for 72 h, weighed and then burned at 500 °C for ash content determination. The initial (M_0) and remaining (M_f) root dry mass in the litterbags were expressed on an ash-free basis. Mass loss (ML; %) was calculated as followed: $ML = (M_f/M_0) \times 100$.

For each mixture, we calculated its expected mass loss (ML_{exp}) as the sum of the ML of each component species in monocultures weighed by the root abundance of these species in the mixture (see Above- and below-ground biomass section). The deviation from additivity was assessed as proposed by Wardle et al. (1997) as:

$$\text{Deviation from additivity} = \left(\frac{ML}{ML_{\text{exp}}}\right) - 1,$$

where ML and ML_{exp} are the observed and expected mass losses of root mixtures. A null value not different from zero indicates additivity (i.e. the expected and observed mass losses are equal), a positive value indicates a synergetic effect (i.e. a greater observed mass loss than expected) and a negative value an antagonist effect (i.e. a lower observed mass loss than expected).

Soil substrate-induced respiration (SIR)

Soil substrate-induced respiration (SIR), a proxy for microbial biomass, which measures the overall potential soil microbial respiration was determined following Beare et al. (1990). For each plot, air-dried soil collected from the 0 to 20 cm soil cores was sieved at 2 mm. Soil was placed in a plasma flask and a solution of C-glucose (1.5 mg C g^{-1} dry soil) was added to achieve 80% of field capacity. Flasks were sealed and incubated in the dark at 25 °C. Headspace gas samples were analyzed

after 2 and 6 h incubation for CO_2 concentration using a microcatharometer (VARIAN GC4900, Varian, Walnut Creek, USA) and the amount of CO_2 produced was used to calculate SIR rates (μg C-CO_2 g^{-1} dry soil h^{-1}).

Soil water content

Soil water content (SWC, mm m^{-2}) was measured in each plant community and in bare soil from March 2012 to April 2013 with a 1.5-month interval between two consecutive measurements (Fig. S4). Soil water content was monitored in the top 20 cm using a neutron probe through an aluminum access tube inserted to a depth of 120 cm. Total transpirable soil water (TTSW, mm) for each plant community and for bare soil was estimated as the difference between SWC at field capacity (SWC_{fc}, as measured in January 2013 after the winter rainfalls) and the minimum SWC (SWC_{min}, as measured in July 2012 before the summer storms). Total transpirable soil water is a good proxy of the overall water status of the soil in the top 20 cm throughout the study period.

Statistical analysis

To test differences in plant variables (*above- or belowground biomass, root: shoot ratio, root traits*) between treatments (B, C, F for monocultures or CF, BC, BF, BCF for mixtures) we used general linear mixed models (LMM). We conducted separate analyses for monocultures and mixtures and in both cases, for each model, we used each variable under study as the dependent variable and treatment as the fixed factor. Differences between mass loss in litterbags incubated in bare soil and samples incubated under living plants were evaluated with a LMM using *mass loss* as the dependent variable and *treatment* and *site* (bare soil or under living plants) and their interaction as the fixed factors. The same model was used to test for these differences in SIR and TTSW. For all LMMs we included *block* as a random factor to account for potential spatial differences between the plots. The significance of the fixed factors in the LMMs was tested with type-II analysis of variance and Chi-square Wald tests (χ^2). Post-hoc differences were tested using the simultaneous inference method for linear mixed models described in Hothorn et al. (2008).

We assessed whether the deviation of root mass loss from additivity was different from zero with a Student's t-test against a constant value (zero). Spearman's rank correlation tests were performed to test the relationship between *mass loss under living plants* and *mass loss in bare soil*. We tested the influence of SIR, TTSW and root biomass on mass loss underneath plant communities with a general linear mixed regression model using *mass loss* as the dependent variable and either SIR, TTSW or root biomass as the independent variables. The relationship between the total observed and total expected belowground biomass in mixed communities was tested with a linear regression model with the intercept forced to zero.

All calculations and statistical analyses were performed with the R software (v. 2.15.3, R Development Core Team 2013) using the packages ade4 (Chessel et al. 2004), effects (Fox et al. 2014), Hmisc (Harell 2015), lme4 (Bates et al. 2015), nlme (Pinheiro et al. 2014) and multcomp (Hothorn et al. 2008). Data presented in the text are mean ± SE.

Results

Total transpirable soil water (TTSW) did not differ between species within monocultures (Fig. S5, *treatment* effect $X^2 = 2.032$, $P = 0.36$) and was higher under monocultures than in bare soil (24.20 ± 0.63 vs. 22.19 ± 0.88 mm, respectively, $X^2 = 5.47$, $P < 0.05$). Within mixed cultures, TTSW differed between plant communities (Fig. S4, $X^2 = 6.93$, $P = 0.07$) being on average 7.4% higher under CF. TTSW was not higher in mixed plant communities than in bare soil (23.00 ± 0.52 vs. 22.19 ± 0.88 mm, respectively, $X^2 = 0.92$, $P = 0.33$).

The three monocultures strongly differed in terms of aboveground biomass (Table 1, Fig S6), root morphology and chemistry (Table 1). *F. christiani-bernardii* (F) had the highest standing biomass, with an aboveground biomass 1.9 and 2.8 times higher than *B. erectus* (B) and *C. humilis* (C), respectively (Table 1, Fig S6). The belowground biomass (0–20 cm depth) did not differ among monocultures and averaged 325 g m^{-2}; as a consequence, *C. humilis* and *B. erectus* had higher root: shoot ratio than *F. christiani-bernardii*. Roots of *B. erectus* had significantly larger diameters and higher concentration of water-soluble compounds (Table 1) than *C. humilis* and *F. christiani-bernardii* whereas *F. christiani-bernardii* was characterized by the highest specific root length (SRL), hemicellulose concentration and root length density (RLD). On the other hand, roots of *C. humilis* presented trait values associated with a poorer root quality with significantly higher root tissue

density (RTD), C:N ratio, cellulose concentration and lower root nitrogen concentration (RNC) than the other two species (Table 1). Among the four mixtures, the highest total aboveground biomass was found for CF communities while observed belowground biomass did not vary significantly between plant mixtures (Fig. S6). After 1 year of growth the mixtures were strongly dominated by one of the species. The CF mixture was dominated by *F. christiani-bernardii* whose aboveground biomass represented 95% of the aboveground biomass of the mixture while the BC, BF and BCF mixtures were dominated by *B. erectus* whose aboveground biomass represented 95, 86 and 77% of the aboveground biomass of each mixture respectively. The calculated root abundance was on average 86% for *F. christiani-bernardii* in the CF mixture and exceeded 90% for *B. erectus* in BC, BF and BCF mixtures.

Comparing roots collected in monocultures and incubated in bare soil, *C. humilis* roots decomposed significantly slower (31% mass loss) than roots from *F. christiani-bernardii* or *B. erectus* (41 and 47% mass loss, respectively) (Fig. 1). Comparing roots collected in mixed communities and incubated in bare soil, litterbags with roots from CF had significantly lower mass loss than roots from mixtures where *B. erectus* was present (BC, BF and BCF; $X^2 = 17.7$; $P < 0.01$) (Fig. 1). The mass loss of root mixtures deviated significantly from the expected values (additivity) in three of the four mixtures (Fig. 2). In roots from the CF and BC root mixtures, the deviation from additivity was negative, i.e. the observed mass loss was lower than expected indicating an antagonist effect. Conversely, BCF deviated positively from additivity indicating a synergetic effect, whereas roots from the BF mixture did not deviate from additivity significantly (Fig. 2).

Roots of all treatments, except BCF, decomposed faster under their living plant communities than when incubated in bare soil (Fig. 3; *site* effect, $X^2 = 6.66$,

Table 1 Plant biomass, root morphological and chemical trait values (Mean ± SE) of the three species grown in monocultures

	Bromus erectus	*Carex humilis*	*Festuca christiani-bernardii*	X^2	*P*
Plant biomass					
Aboveground biomass (g m^{-2})	219 ± 5.3a	146 ± 35a	416 ± 50b	43.8	***
Belowground biomass (g m^{-2}) (0–20 cm)	370 ± 49	304 ± 77	301 ± 32		ns
Root: shoot ratio	1.68 ± 0.20a	1.89 ± 0.44a	0.76 ± 0.12b	11.2	**
Root length density (cm cm^{-2})	288 ± 66a	171 ± 32b	418 ± 96a	14.4	***
Morphological root traits					
Diameter (mm)	0.32 ± 0.01a	0.27 ± 0.25b	0.25 ± 0.00b	39.4	***
RDMC (mg g^{-1})	312 ± 30	366 ± 20	374 ± 98		ns
SRL (m g^{-1})	75.3 ± 6.5a	59.8 ± 5.3a	133 ± 21b	18.6	***
Root tissue density (g m^{-3})	0.17 ± 0.01a	0.27 ± 0.01b	0.17 ± 0.01a	24.3	***
Chemical root traits					
RNC (%)	0.95 ± 0.09a	0.65 ± 0.14b	0.92 ± 0.05a	6.6	*
RCC (%)	35.1 ± 2.6a	45.1 ± 0.8b	39.1 ± 3.5ab	7.6	*
C: N	37.5 ± 2.9a	79.3 ± 4.6b	42.6 ± 2.9a	11.6	**
Lignin (mg g^{-1})	131 ± 5	121 ± 4	136 ± 8		ns
Hemicellulose (mg g^{-1})	350 ± 8a	367 ± 3a	403 ± 12.4b	10.1	*
Cellulose (mg g^{-1})	257 ± 7a	299 ± 10b	267 ± 7.02ab	7.3	*
Water-soluble compounds (mg g^{-1})	263 ± 16a	212 ± 9b	194 ± 3b	10.4	*
Lignin: N	134 ± 10	267 ± 5	148 ± 4.4		ns

Results of a mixed model with species as fixed factor and block as the random factor (X^2 - and P-value) were given. Different letters indicate significant differences between species (Orthogonal tests, ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$)

Trait abbreviations are as follows: *Diameter* mean root diameter, *RDMC* root dry matter content, *SRL* specific root length, *RNC* root nitrogen concentration, *RCC* root carbon concentration

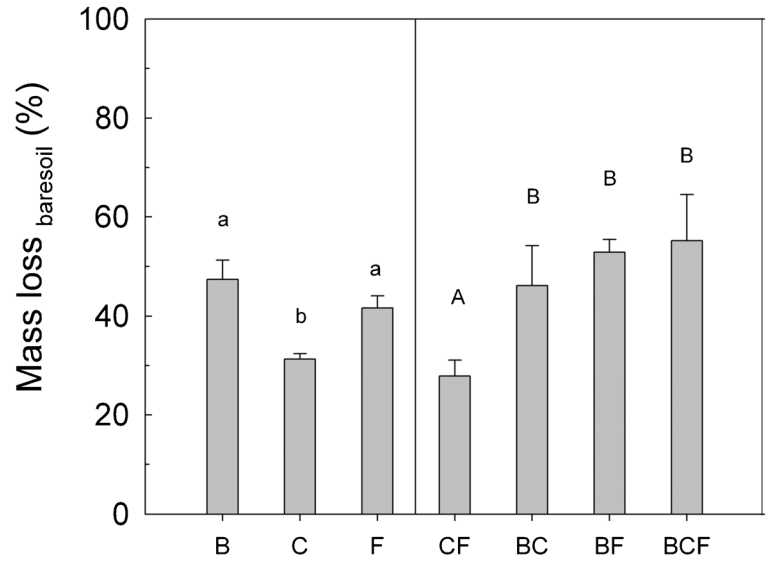

Fig. 1 Percentage of mass loss (mean ± SE) of roots collected from monocultures (B, C, F; *left* panel) and mixtures (CF, BC, BF and BCF; *right* panel) incubated in bare soil (e.g. soil with no plants). Root litter species: B, *Bromus erectus*; F, *Festuca christiani-bernardi*; C, *Carex humilis*. Different lowercase letters indicate significant differences between monocultures and different capital letters indicate differences between mixtures (simultaneous inference post-hoc contrasts, $P < 0.05$). Separate tests were performed for monocultures and mixtures

$P < 0.01$ and $X^2 = 2.85$, $P < 0.01$ for monocultures and mixtures, respectively). The interaction between incubation *site* × *treatment* was not significant in either monocultures or mixtures ($X^2 = 0.76$, $P = 0.68$ and $X^2 = 0.54$, $P = 0.91$) indicating similar effects of the plant community composition (treatment) regardless

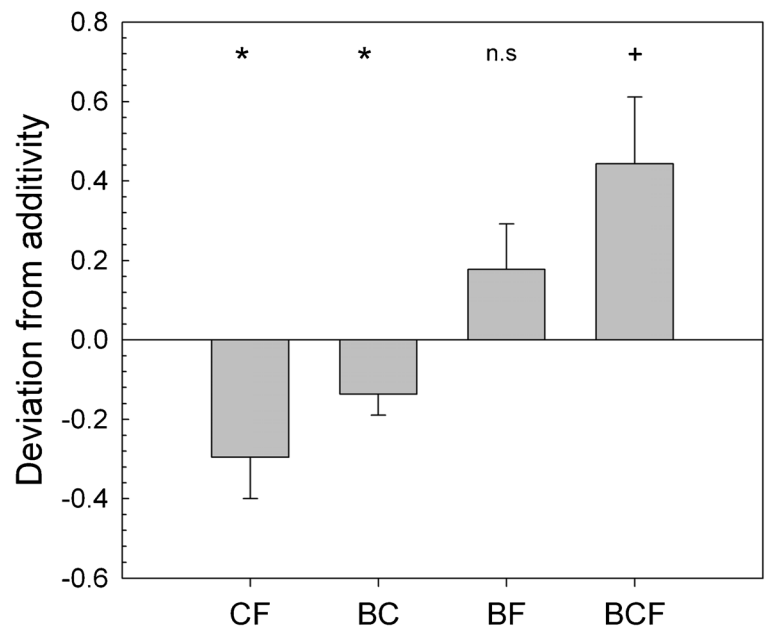

Fig. 2 Average deviation from additivity in mass loss of roots incubated in bare soil (mean ± SE). Positive values indicate synergistic (i.e. greater observed mass loss than expected from monocultures) and negative values indicate antagonistic effects (i.e. lower observed mass loss than expected from monocultures) on root decomposition. Root litter species: B, *Bromus erectus*; F, *Festuca christiani-bernardi*; C, *Carex humilis*. Statistical results are from a Student-t test against a constant value (zero); *$P < 0.05$, +$P < 0.06$)

of the incubation site (bare soil or under living plants). Overall, mass loss of roots decomposing under their living plant communities was 8.2% higher than mass loss in bare soil (11 and 6% for monocultures and mixtures respectively). The ranking of mass loss in the different plant communities and monocultures (treatments) was conserved except for roots under BCF that decomposed at slower rates under its living plant community (Fig. 3).

In line with these results, after one year of growth, soil substrate induced respiration rate (SIR) from all treatments was twice higher than the SIR rate in bare soils (Fig. 4, $X^2 = 5.85$, $P < 0.05$ and $X^2 = 6.32$, $P < 0.001$ for monocultures and mixtures respectively). Within monocultures, SIR rate was the lowest in soils from *C. humilis* plots (Fig. 3, *treatment* effect $X^2 = 14.87$, $P < 0.001$). Within mixtures, SIR rate was lower under CF than under BC but did not differ from BF or BCF (Fig. 3, *treatment* effect $X^2 = 10.37$, $P < 0.05$).

Across plant communities, root mass loss in the litterbags underneath living plants was not correlated to SIR ($X^2 = 0.326$, $P = 0.57$), belowground biomass ($X^2 = 0.064$, $P = 0.80$), TTSW ($P > 0.31$) or SWC on any date ($P > 0.81$).

Discussion

Our results show that the decomposition rate of root mixtures cannot be predicted from the decomposition rates of each component species and that the presence of living plants stimulated root decomposition in relation with a stimulation of substrate induced microbial respiration under living plant communities.

In bare soil, effects of root litter mixing were either additive (BF) or non-additive with both antagonistic (CF, BC) and synergistic (BCF) effects suggesting that root litters of different species grown together have the potential to interact with contrasted effects on decomposition of root mixtures. These results are in line with a review of 30 studies demonstrating that only 30% of the leaf litter mixtures decomposed additively, whereas synergetic and antagonist non-additive effects were observed in the remaining 70% of litter mixtures (Gartner and Cardon 2004).

In leaf litter mixtures, non-additivity has been reported when one component of the mixture was of low quality material (Liu et al. 2009). For root mixtures, however, the mechanisms remain unclear; based on leaf studies we hypothesize that the antagonist effects observed for CF and BC may result from the presence of

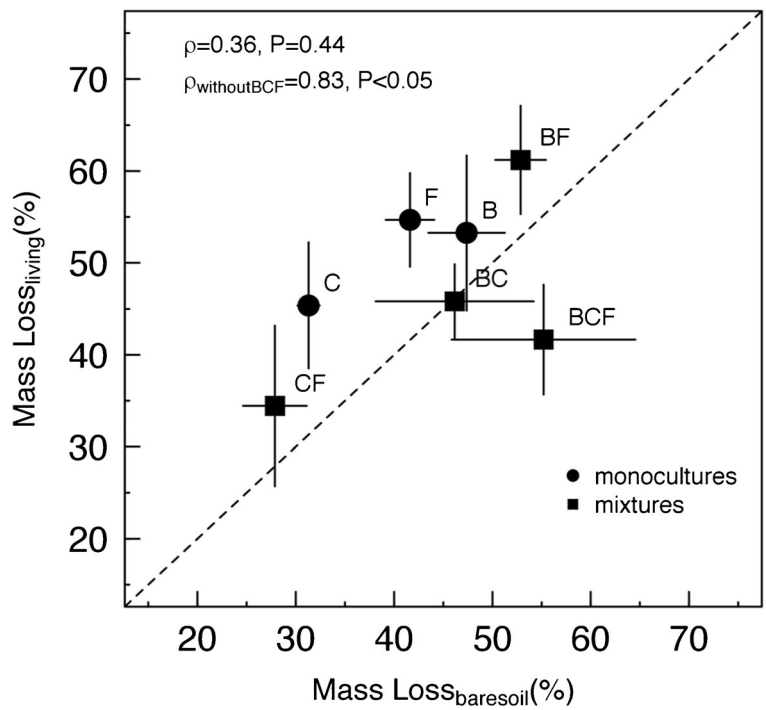

Fig. 3 Relationship between mass losses of roots incubated under living plants (ML_{living}) and in bare soil (with no plants, $ML_{baresoil}$). Each point represents the mean mass loss for a given monoculture (B: *Bromus erectus*; C: *Carex humilis*; F: *Festuca christiani-bernardi*) or mixture (CF, BC, BF, BCF) with their correspondent SE (bars). The *dashed line* depicts the 1:1 line. Spearman correlation coefficients were calculated for all plant communities (ρ) and without the tri-specific mixture BCF ($\rho_{without\ BCF}$)

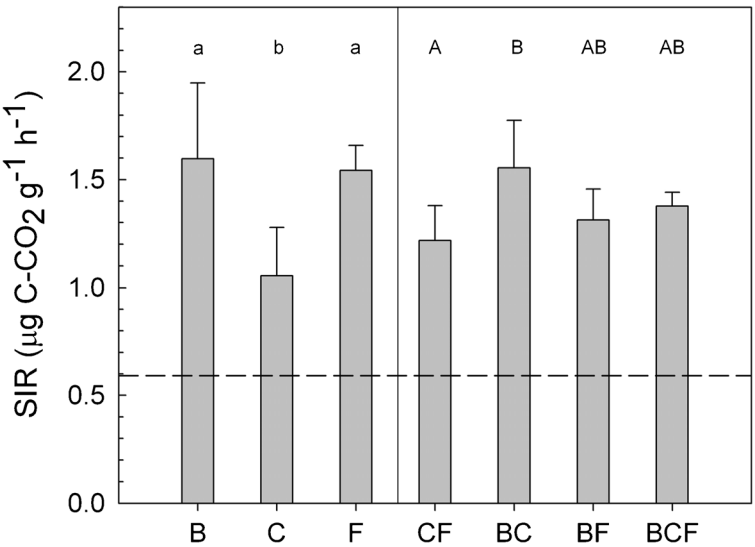

Fig. 4 Soil substrate induced respiration (SIR) rates measured under monocultures (*left* panel) and mixtures (*right* panel). Values are mean ± SE. The dashed line depicts the average SIR in the bare (soil with no plants; 0.57 ± 0.05; mean ± SE). Soil was collected from the top 20 cm in monocultures (B, *Bromus erectus*; F, *Festuca christiani-bernardi*; C, *Carex humilis*) and mixed communities (CF, BC, BF, BCF). Different *letters* indicate significant differences between treatments (Simultaneous inference post-hoc contrasts, $P < 0.05$). Separate tests were performed for monocultures and mixed cultures

roots from *C. humilis*, whose quality is low in comparison with the other two species *F. christiani-bernardii* or *B. erectus*. Roots of *C. humilis* have traits known to limit decomposition, i.e. they have high tissue density, C:N and lignin: N ratios, along with low N concentrations (Zhang et al. 2008; Birouste et al. 2012; Prieto et al. 2016; Roumet et al. 2016). In addition, most species of the *Carex* genus do not establish mycorrhizal symbioses (Miller 2005), and may contain alkaloids that are a microorganism deterrent, thereby exerting a potential negative effect on decomposition (Martijn Bezemer et al. 2013), which may be another reason for the low decomposition rates observed in *C. humilis* roots. In any case, whether mediated by root litter quality, decreased mycorrhizal colonization or both, it appears that the presence of *C. humilis* in root mixtures is likely to have slowed down the decomposition of the other component root species, reducing the overall decomposition of the mixture. Although the proportion of *C. humilis* in mixtures was relatively low (<13%), a slight increase in the proportion might have changed the effects from synergistic (BCF, 6% of *C. humilis*) to little (BC, 9% of *C. humilis*) or moderately antagonist (CF, 13% of *C. humilis*). The synergistic effect observed in BCF suggests that the negative effect of *C. humilis* may be overcome by the nearly significant positive interaction between *B. erectus* and *F. christiani-bernardinii* or by the number of species present in the mixture (i.e. diversity effect, Gessner et al. 2010) since more diverse litter mixtures could improve the microclimatic conditions and thus habitat and resource availability for decomposers (Wardle et al. 2004).

However, we acknowledge that other factors besides root litter quality or mycorrhizal colonization, for example a reduced ratio of bacterial-feeding to fungal-feeding communities with increased root litter diversity (Wardle et al. 2006), may have influenced decomposition of root mixtures. Thus, we believe further experiments manipulating the proportion of *C. humilis* in root mixtures and accurately describing the microbial community composition would be necessary to confirm these mechanisms. The observed non-additivity might also result from potential changes in the root quality of component species in response to competition between species and/or from our estimation of the root biomass of each species in mixtures, which is based on the root: shoot ratio of species in monocultures. Although our estimation of the proportion of root biomass for each species in the mixture was validated ($R^2 = 0.90$), there is always a proportion of error in the estimation in each mixture and the effect of competition on root: shoot ratios might vary among species as reported by Robinson et al. (2010) and Casper and Jackson (1997). Thus, a more accurate estimation of root biomass of each component

species using molecular (Mommer et al. 2008) or near infrared spectroscopy (Roumet et al. 2006; Lei and Bauhus 2010) approaches would help improving our understanding of the effect of root litter mixing on decomposition. We underline that variability in the observed non-additivity was large and the limited number of perennial species (three) belonging to two close families (Cyperaceae and Poaceae) likely narrowed the range in decay rates (30–47%) limiting the extent of our conclusions. These results should be further tested with studies using a greater number of species of contrasting families with more divergent functional traits and a larger range in decomposition rates.

In this study, the presence of living plants induced an average 8% increase in root decomposition in all plant communities except the three-species communities. Such an increase occurred in relation with a close to 50% stimulation of substrate induced microbial respiration whereas soil water availability was not strongly affected. These results are in line with previous studies reporting a stimulating effect of living plants on root decomposition of single species (Van Der Krift et al. 2002; Personeni and Loiseau 2004), but in contrast with other studies reporting that living plants could inhibit decomposition rates due to lower soil moisture under living plants as a result of plant water uptake and transpiration (Jenkinson 1977; Sparling et al. 1982). Our results thus support the hypothesis that the presence of living plants has a positive effect on root decomposition rates likely through the release of root exudates that increase microbial activity rather than through changes in soil moisture beneath plant communities. Despite the effect of living plants on root decomposition, the ranking of root decomposition rates in the different plant communities remained conserved in both bare soil and underneath plant communities (with the exception of the three-species community), indicating that the living plant effect was low as compared to the effect of endogenous factors.

We did not find support that root decomposition is consistently influenced by the plant community composition under which roots decomposed and that more diverse plant communities will increase root decomposition through microbial activity mediated effects. Living monocultures enhance root decomposition (11%), yet rates of root decomposition underneath species mixtures are more complicated since they increased (6%) in two-species mixtures but decreased (13%) in three-species mixtures. The causes of variations in root decomposition rates under different living plant communities remained unclear since we found no significant relationship between root decomposition rates and SIR, water availability or the root biomass of the plant community that is expected to reflect the amount of exudates released in soil.

Contrary to our hypothesis that more diverse plant communities will increase root decomposition through a higher substrate availability for microbial communities, we observed a negative effect of living plant in the more diverse plant communities (three-species plant communities) that occurred despite a high microbial activity (high SIR rates) and in the absence of water availability limitation. Although soils were re-wetted when conducting SIR measurements, we cannot rule out that air-drying the soil before SIR determination could have affected the microbial activity (Hawkes et al. 2011; de Vries and Shade 2013; Romanowicz et al. 2016). Also, other factors besides microbial activity or soil moisture (i.e. soil temperature) may have negatively influenced root decomposition rates underneath three-species plant communities. Possible mechanisms whereby living plants can decrease the decomposition rates are, i) soil microorganisms may preferentially use exudates released from the living roots rather than root litter compounds (Reid and Goss 1982; Nicolardot et al. 1995; Van Der Krift et al. 2002), ii) some plant species release root exudates that may inhibit decomposers or iii) a higher plant diversity might increase competition for N between plants and microorganisms inhibiting root litter decomposition.

These results suggest that the effect of living plant community composition or the decomposition environment is weaker than the effect of root litter endogenous factors (e.g. litter quality), as reported at local (Aulen et al. 2012; Smith et al. 2014; Guerrero-Ramírez et al. 2016; García-Palacios et al. 2016, but see McLaren and Turkington 2010) and global scales (Zhang et al. 2008). In addition, the reduced decomposition rates observed under three-species communities suggest that rates of root decomposition may be reduced under grassland swards where more than three species coexist. Whether our conclusions obtained in a common garden approach apply in natural communities still need to be tested.

Conclusion

Our study demonstrated that decomposition of root mixtures cannot be predicted from decomposition rates of component species. The significant non-additivity appeared to be related to the species identity through the presence of *Carex* roots in the mixture. In this respect, endogenous factors seem to have a greater influence on fine root decomposition than the composition of the plant community under which roots decomposed (i.e. the species present in the community). The presence of living plants slightly stimulated root decomposition in monocultures and two-species communities, likely through an enhanced microbial activity under plant communities. Our results highlight the importance of microbial activity on root decomposition and the complex interactive effects of species identity depending on their quality.

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