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RESEARCH PAPER

Short life–fast death: decomposition rates of woody plants leaf- and herb-litter

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Abstract

• ***Key message*** **Decomposition of forest herb species litter was not always completed in less than a year and was not always faster than decomposition of tree leaf litter in an oak-hornbeam forest in Western Poland. Litter decomposition of herbaceous plants is connected with their life strategy and functional traits of their leaves.**
• ***Context*** Forest understories are frequently ignored in ecological research on decomposition, although they play an important role in biomass and nutrient cycling in forest ecosystems.
• ***Aims*** We hypothesized that the decomposition process of herbaceous species was completed in less than a year, as opposed to tree leaf litter. The second aim of our study was to determine if life strategy affects the rate of litter decomposition.
• ***Methods*** We performed the decomposition experiment in the oak-hornbeam forest in Czmoń (Western Poland) using the litter bag method to determine decay constants (k) for all species studied. The influence of species identity, functional group, and functional traits of leaves and other effects on the decomposition process was assessed.
• ***Results*** The decomposition process was significantly dependent on the functional group of plants, time of exposure in the field, species identity, and precipitation. We found a significant correlation between leaf traits and decay rates of the species studied.
• ***Conclusion*** Litter decomposition of herbaceous plants is connected with their life strategy and functional traits of their leaves in an oak-hornbeam forests.

Keywords Ecosystem processes · Decomposition · Functional groups · Leaf litter · Life strategy · Understory vegetation

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Contribution of the co-authors Katarzyna Rawlik: designed the research, formulated research problem and developed the methodology; collected the data; analyzed the data and wrote the first draft of the manuscript; contributed critically to the drafts and gave final approval for publication.
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1 Introduction

Forest understories are frequently ignored in ecological research on productivity, probably due to their relatively small (ca. 1–2%) contribution to total plant biomass of ecosystems. However, herbaceous species have great importance for forest nutrient retention (Bormann et al. 1968; Muller and Bormann 1976; Muller 2014). The herb layer can provide up to 16% of annual litter fall in forests (Gilliam 2007; Muller 2014). Moreover, in temperate deciduous forests herbaceous species supply litter to the litter horizon continuously during the growing season, thus not only in an autumnal pulse like tree leaf litter (Wise and Shaefer 1994). Additionally, foliar concentrations of some nutrients (N, P, K, Mg) are higher in herbaceous than in tree species (Gilliam 2007). It is particularly important that, on average, the herbaceous layer contains 80% of forest plant species biodiversity and rare herb species can be useful as indicators of biodiversity or site quality (Gilliam 2007;

Spyreas and Matthews 2006). Moreover, by competition with natural woody plant species regeneration, the herb layer influences or even determines overstory composition (Baraloto et al. 2005). The biomass of herb species is also an important source of food for animals (Dzięciołowski 1970).

The decomposition of organic matter is a crucial process in ecosystem functioning because it is responsible for replenishing the pool of soil nutrients available to plants, returning huge amounts of carbon dioxide to the atmosphere, and creating long-term storage of carbon as soil organic matter (Berg and McClaugherty 2014). In recent decades, the number of studies describing organic matter decomposition has increased rapidly. An important subset of those studies has been experiments comparing decomposition rates of litter from different species in common garden conditions (e.g., Hobbie 1996; Hobbie et al. 2006). These kinds of studies are keys for estimating species effects on litter decomposition and to create ecosystem models that help to illuminate their inner organization (Hobbie et al. 2006). Moreover, they are crucial for understanding the consequences of changes in plant biodiversity for ecosystem functioning (Chapin 2003; Handa et al. 2014; Liang et al. 2016). The majority of decomposition experiments in forest ecosystems have focused on woody species foliage (e.g., Dziadowiec 1987, 1990; Hobbie et al. 2006; Horodecki and Jagodziński 2017, 2019; Horodecki et al. 2019; Jackson et al. 2013; Jurkšienė et al. 2017) and wood (e.g., Bantle et al. 2014; Harmon et al. 2000). The limited studies available on decomposition in deciduous forests have focused on herb species decomposition rates (Halabuk and Gerhátová 2011; Mayer 2008; Rodgers et al. 2008; Wise and Shaefer 1994) and interactions with soil organisms (Wise and Shaefer 1994). Most of those studies noted that herb species litter in temperate deciduous forests was fully decomposed within 6 months after senescence (Halabuk and Gerhátová 2011; Mayer 2008; Muller 2014; Rodgers et al. 2008). Only herb species biomass dominated by sedges, shrubs, and mosses (Hobbie 1996) or ferns and shrubs (MacLean and Wein 1978) required more than 1 year to decompose completely.

Decomposition rates depend on climate, litter quality, and communities of soil organisms (Berg and McClaugherty 2014; Cornwell et al. 2008; Kamczyc et al. 2019; Urbanowski et al. 2018). Microclimates in temperate deciduous forest understories vary during the growing season, due to changing solar zenith angle and canopy phenology (Noda et al. 2015). Seasonal changes in the availability of light in the understory of deciduous forests are strictly connected with changes in other microclimatic conditions, like temperature and moisture (Graves 1990). This seasonality results in the occurrence of different phenological strategies among herb species in deciduous forests, including spring ephemeral, summer-green, winter-green, and evergreen species (Neufeld and Young 2014; Uemura 1994). These strategies represent a kind of niche separation, which allows the species to utilize habitat resources efficiently and avoid competition (Díaz and Cabido 2001; Jagodziński et al. 2016; Scherer-Lorenzen 2008).

Plant adaptations to variation in the physical environment is reflected in plant biological traits and connected with their different functions within an ecosystem. They determine the potential of a given species to establish or persist under any given set of environmental conditions (Díaz and Cabido 2001). The connection between plant adaptation strategies and decomposability is crucial for understanding vegetation–soil feedbacks. There is a general concept that functional traits of leaves (Leaf Economic Spectrum; Wright et al. 2005) influence leaf litter decomposition and nutrient release (Cornelissen and Thompson 1997; Zukswert and Prescott 2017). According to this concept species of plants with conservative resource strategies (high leaf dry matter contents (LDMC)), low nutrient concentrations, and low specific leaf area (SLA), decompose slower than fast-growing, acquisitive species (Díaz et al. 2016; Freschett et al. 2010, 2012; Wright et al. 2005). Studies that conceptualize decomposition within the tradeoff between defense and photosynthetic production have been frequently conducted for leaves of trees (Makkonen et al. 2012; Melilo et al. 1982; Zukswert and Prescott 2017) or herbaceous species of grasslands (Cornelissen and Thompson 1997; Cornwell et al. 2008). Previous research indicated that spring ephemerals have typical short-lived, sun-type leaves. They have the greatest metabolic activity, the highest rates of photosynthesis, and leaf N contents among all phenological groups of herbs (Muller 2014; Rothstein and Zak 2001). Generally, foliar nutrient concentrations of herbs are higher than overstory species (Muller 2014). In many previous studies, it was found that decomposition rate was strongly positively correlated with leaf N concentration and negatively with leaf life span (Bakker et al. 2011; Cornwell et al. 2008; Wright et al. 2005). To our knowledge, there is no information about differences in decomposition rates among species representing different life strategies of forest understory plant species in a temperate deciduous forest. Although functional traits of plants are nowadays widely accepted as potentially powerful indicators of the ecology of species, only a few forest understory species have been included in studies (Ma et al. 2010; Poorter and De Jong 1999; Rawlik and Jagodziński 2020; Rawlik et al. 2018; Rothstein and Zak 2001; Wang et al. 2010), and most frequently these species were pooled with other herbaceous plants. Many studies have demonstrated that plant traits have afterlife effects via their impacts on decomposition rates, however, it is still not clear whether patterns found on a global scale are reproducible at local scales, in specific growth forms (Kleyer et al. 2018), or different organs (Hobbie 2015).

Many studies researching correlations among plant traits or their correlations with decomposition included only one organ (e.g., stems or leaves), avoiding a whole-plant perspective (Kleyer and Minden 2015). These studies concerned homogeneous components of plants, usually focused on leaves (Hobbie 1992), even though a large part of herbaceous litter comes from stems or roots. Differences in structural and physiological traits between organs, connected with their different biological functions, might cause differential decomposability (Freschet et al. 2012). In this study, we wanted to know the true biological rate of biomass decomposition of the species included; therefore, we used mixed aboveground biomass (including leaves and shoots). Moreover, we decided to compare decomposition rates of leaves and blooming shoots (material dominated by shoots) of one herb species (*Aegopodium podagraria*) to assess differences in decomposition rates of different organs.

Our primary objective was to compare decomposition rates of oak-hornbeam forest herb species with different ecological requirements, phenology, and life-history traits. The second aim of our study was to compare the decomposition rates of these plants with leaf litter of tree species occurring in the overstory. We hypothesized that (1) biomass of herbaceous plants in a temperate deciduous forest decomposes completely in less than a year (decomposition constants $k > 1$) (Muller 2014 and literature cited therein). We also hypothesized that (2) spring ephemerals decompose faster than summer and autumn species (Jagodziński et al. 2016; Neufeld and Young 2014), and (3) herb species biomass decomposes faster than that of tree leaves (Mayer 2008; Muller 2014).

2 Materials and methods

2.1 Study area

This study was conducted in the Czmoń Forest (Babki Forest District, W Poland; 52° 09′ 05.76″ N, 17° 03′ 00.68″ E; 76 m a.s.l.), in the temperate climatic zone. Mean annual temperature in this area was 8.7 °C, and mean annual precipitation was 514 mm in 1971–2010, and 9.2 °C and 535 mm in 2001–2010 (Central Statistical Office 2020). According to meteorological data from a nearby meteorological station (Institute of Dendrology, Polish Academy of Sciences, Kórnik; 52° 14′ 41″ N, 17° 06′ 03″ E; 10.5 km from the study area) the mean annual temperature in 2011–2013 was 9.1 °C (Fig. 6a in the Appendix) and mean annual precipitation was 573 mm (Fig. 7 in the Appendix). In the year preceding the experiment (2011), the mean annual temperature was 9.5 °C, which was higher than during a typical year in the study area. More specifically, during the 12 months preceding the experiment (June 2011–May 2012), the average monthly temperature was as follows: 19.0 °C in June, 18.2 °C in July, 19.7 °C in August, 14.7 °C in September, 9.1 °C in October, 3.2 °C in November, 3.3 °C in December, 0.4 °C in January, − 4.6 °C in February, 5.8 °C in March, 9.0 °C in April, 15.2 °C in May. In the year preceding the experiment (2011), the annual precipitation was 431 mm, which was less than during a typical year in the study area. In the 12 months preceding the experiment (June 2011–May 2012), the monthly sum of precipitation was as follows: 59.3 mm in June, 108.1 mm in July, 78.8 mm in August, 24.7 in September, 26.8 mm in October, 0.7 mm in November, 48.0 mm in December, 74.5 mm in January, 44.2 mm in February, 10.3 mm in March, 30.5 mm in April, 40.8 mm in May. Air temperature at the meteorological station was measured at the level of 2 m. During the experiment (28 May 2012–26 October 2013), we also measured temperatures at the ground level every hour using four data loggers evenly distributed within the stand (HOBO U23-001 Pro v2 Temperature/Relative Humidity, Onset Computer Corporation, Bourne, Massachusetts, USA) (Fig. 6b in the Appendix). Since we compared the decomposition rates of the species studied after ca. 6 months from the beginning of the experiment, we show detailed temperature and precipitation conditions for this period (Table 4 in the Appendix). There were differences in average air temperatures, ground temperatures, and total precipitation among the five dates of the field experiment.

The study area was located in a deciduous forest complex, covered by a 97-year-old oak-hornbeam stand (Table 5 in the Appendix). Detailed descriptions of the study area were given by Horodecki et al. (2014), Rawlik et al. (2015), and Wiczyńska et al. (2013).

We determined soil particle-size distribution, soil pH in H_2O and in 1 M KCl, physicochemical soil characteristic (Table 6 in the Appendix). These properties were measured in two soil samples collected in October 2013.

The number of sample plots and growing seasons included in the study was limited by the high labor demand for sampling senescent herbaceous plants and preparing the litter bag experiment. We are aware that chances to generalize results from our study are limited by the low replicability (one sample plot and one growing season). However, despite the lack of replications, our assessments of the effects of life-history traits on biomass decomposition, inclusion of stem and leaf biomass to estimate ecologically relevant decomposition of aboveground herbaceous biomass, and comparisons of herbaceous biomass with tree leaf litter decomposition, gives unique insight into the complexity of decomposition at this site. In addition, our study provides novel data that could be used in designing further studies.

2.2 Species studied

We chose 14 vascular plant species, which are the most abundant in the understories of fertile deciduous forests in Central Europe and present within the research site (Ellenberg 1988), i.e., *Adoxa moschatellina* L., *Aegopodium podagraria* L., *Alliaria petiolata* (Bieb.) Cav. et Grande, *Anemone nemorosa* L., *Anemone ranunculoides* L., *Asarum europaeum* L., *Corydalis cava* L. (Schweigger et Koerte), *Ficaria verna* Huds., *Galeobdolon luteum* Hudson, *Maianthemum bifolium* L. (F.W. Schmidt), *Mercurialis perennis* L., *Paris quadrifolia* L., *Stachys sylvatica* L., and *Urtica dioica* L. Additionally, we studied the five most abundant tree and shrub species in the overstory and undergrowth of the forest stand, i.e., *Acer pseudoplatanus* L., *Carpinus betulus* L., *Corylus avellana* L., *Fraxinus excelsior* L., and *Quercus robur* L. We chose these herb and woody plant species because they have a strong influence on ecosystem functioning, due to the fact that abundance of species is correlated with their importance to ecosystem function (Grime 2001), and because these species differ in their ecological requirements, phenology, and life-history traits (Table 1).

2.3 Methods

We harvested herbaceous plants during one growing season (2012) at the time when most of the plants within each population began senescing. In most cases, we collected senescent aboveground biomass (mixed leaves and stems). In the case of *A. podagraria*, we collected leaves and blooming shoots separately. During autumn 2012, we collected freshly fallen leaves of the mentioned tree species from stands in the vicinity of the sample plot. After collection material was dried in the laboratory at 65 °C to a constant weight in a dryer with forced air circulation (UFE 600, Memmert GmbH+Co.KG, Germany). Dried litter was weighed using BP 210 S (http://www.sartorius.dataweigh.com) and Mettler Toledo PG 1003-S (http://www.mt.com) scales with an accuracy of 0.001 g and placed into "litter bags" made of fiberglass netting (15 cm × 15 cm) with a mesh size of 1 mm.

Those bags were filled with 3.9–4.2 g (*U. dioica*), 1.9–3.2 (the remaining herb species), or 8.0–8.3 g (tree leaves) of litter and labeled. In total, 2658 litter bags were placed in the forest at five dates, according to the time of senescence of most plants of the particular taxon (Table 1). The decision on mesh size for our experiment took into account that it can modify activities of mesofauna and macrofauna, microclimatic conditions, and material leaching out of litter bags. Results of choosing different mesh sizes were shown by many previous methodological studies (Bradford et al. 2002; Harmon et al. 1999; Slade and Riutta 2012; Wise and Shaefer 1994). Thus, our choice was a compromise. The masses put in litter bags differed for particular species to avoid excessive compaction of the material. Moreover, the amount of material was adjusted to each material type, to standardize litter densities and textures inside the bags. For all herbaceous species, we placed a mix of leaves and shoots in litter bags, in proportions similar to what occurs in specimens in the field.

For *A. europaeum*, we decided to start the experiment according to the time of senescence of most of last-year's leaves. For *G. luteum*, we decided to start the experiment according to the time of senescence of most of the current year's leaves. Our main criterion (time of senescence of most plants of the particular taxon) was used to separate spring ephemerals and summer-green plants. Summer-green plants were further separated into two groups, mid-summer, and autumn-senescing plants. We decided to use different starting times of the experiment for particular groups of plants because the aim of our studies was to find real, biological rates of decomposition of the species studied. We established one research plot (ca. 0.25 ha in total). Litter bags were randomly placed on this research plot in six sets of samples. Distance between every set of samples was ca. 10 m. On the research plot we established samples of all species harvested in each term of collection (six samples per collection term).

Six randomly selected litter bags of each species were collected every week for herb species or every 2 weeks for tree species (Rawlik et al. 2020). The time of exposition in the field was generally about one half year (175 or 182 days) for herb species and 364 days for leaves of trees. After drying at 65 °C to a constant weight in a dryer with forced air circulation (UFE 600, Memmert GmbH+Co.KG, Germany), litter was removed from bags, and cleaned to remove sand, fungi and roots, and then weighed. The mass loss of the plant material was determined systematically during the experiment. For some species, we noticed that the decomposition rate was lower than previously assumed, and thus, we decided to extend the period of litter collection (see Table 7 in the Appendix). Thus, we decided to continue the experiment for longer durations for blooming shoots of *A. podagraria* (406 days) and *M. bifolium* (238 days), and leaves of *A. podagraria* (203 days), *M. perennis* (203 days), *S. sylvatica* (203 days), and *U. dioica* (203 days).

We are aware of the limitations of the litter bag method, due to artifacts the method has compared to real biological decomposition rates. Mainly, drying plant material can slow the decomposition rate because the chemical composition of samples may be changed, making dried material less attractive for consumers. Secondly, putting material into litter bags influences decomposition. In this context chosen mesh size is important. Mesh size is important because of the exclusion of macrofauna and different impacts of

microclimate, and thus biological activity and control on handling effects and increased exposure to abiotic factors (Bradford et al. 2002). The litter bag mesh size chosen for our experiment was a compromise between the smallest mesh, which inhibits meso- and macrofauna from entering litter bags, and the largest mesh, which leads to material leaching out of the bags. Moreover, in our studies, it was important to treat all samples in the same way, to enable making comparisons among them.

2.4 Data analysis

For each litter bag, we determined the proportion of initial litter mass remaining. We analyzed decay constants (k) by fitting the data for each species (the proportion of initial mass remaining was calculated by dividing the mass at each harvest date by the initial mass) with a negative exponential decay model. We used linear regressions of log-transformed proportions of initial mass remaining against time (Berg and McClaugherty 2014; Hobbie 1996; Olson 1963) using the following formula:

$$X = e^{-kt},$$

where X is the proportion of remaining biomass at time t and k is the decay rate.

Differences in the rates of decomposition among the species studied were assessed using a one-way analysis of variance (ANOVA), followed by Tukey's test. After that, we used Bonferroni correction, meaning that we tested hypotheses at $\alpha = 0.000877$. We used the Bonferroni correction to control the family-wise error rate (FWER). The FWER is the probability of rejecting at least one true H_i, that means making at least one type I error. The Bonferroni correction rejects the null hypothesis for each $p_i = \alpha/m$, thereby controlling the FWER at $\leq \alpha$. The influence of the studied factors (species, time of exposure in the field, their interaction) on litter decomposition rates was assessed using two-way ANOVA. We checked the normality and homogeneity of the distribution of variables in each group compared by ANOVA. The assumptions of normality and homogeneity were not always valid; however, we decided to assume a normal distribution of data, as due to high sample size we may assume that with increasing sample size distribution of a variable in the whole population tends to a normal distribution, according to the central limit theorem.

Functional trait data were obtained from BiolFlor (Klotz et al. 2002), the LEDA trait database (Kleyer et al. 2008), and the TRY database (Kattge et al. 2011). We focused on morphological and chemical traits of living leaves known to affect components of the carbon and/or nitrogen cycles at the leaf, whole-plant, and ecosystem levels (Cornelissen et al. 1999; Reich et al. 1999): specific leaf area (SLA), leaf nitrogen (N) content per leaf dry mass (LNC), and leaf dry matter content (LDMC). The traits involved in this study were chosen to represent the trade-off between fast acquisition and conservation of resources. Moreover, these traits are correlated with leaf litter traits, traits of other organs, as well as with decomposition rates of leaves and decomposition rates of other organs (Freschet et al. 2012). Four species (*A. moschatellina*, *A. ranunculoides*, *C. cava*, *P. quadrifolia*) were excluded from the analysis of LNC impact on the decay process because of a lack of data. We evaluated simple linear regression models of species-specific k and the above-mentioned plant traits as independent variables. Moreover, we used principal components analysis (PCA) to assess the correlations between plant traits and decomposition rates. We performed an analysis of variance of a mixed-effects linear model, describing differences in mass loss as a function of functional group, exposition time, temperature, and precipitation. To account for species-dependence of samples representing particular species we treated species as random factors with random slopes (we expected different trajectories of decomposition rates for each species).

All analyses were conducted in JMP Pro 14.0 (SAS Institute Inc. Cary, NC. USA; http://www.sas.com).

3 Results

3.1 Litter decomposition of understory herb species

We found statistically significant effects of herb species ($p < 0.0001$, $df = 14$, $F = 350.6065$), time ($p < 0.0001$, $df = 1$, $F = 1707.408$) and interaction of species × time ($p < 0.0001$, $df = 14$, $F = 36.503$) on litter decomposition. After ca. 2 months of incubation, spring ephemeral species (*A. moschatellina* and *C. cava*) reached 95% biomass losses. After the same time of decomposition in the forest, losses of biomass were the highest for the second group of spring ephemerals, i.e. *A. moschatellina*, *P. quadrifolia*; on average 95 % of litter decayed. At the same time, ca. 92 % of the first group of spring ephemerals (*C. cava*, *A. ranunculoides*, *F. verna*, and *A.nemorosa*), 69% of winter-green plants (*A. europaeum* and *G. luteum*), 35% of mid-summer senescing plants (*M. bifolium*, *A. podagraria* (blooming shoots), *A. petiolata*) and 30.5% of autumn-senescing plants (*A. podagraria* (leaves), *M. perennis*, *U. dioica*, and *S. sylvatica*) decomposed. Later, after ca. 6 months of incubation, rates of decomposition of litter for most of the herb species were considerably slower than at the start of the process. Six-month decay constants of spring ephemerals decreased, with the lowest value for *A. moschatellina* ($k = 4.7$) and the highest for *A. ranunculoides* ($k = 6.9$).

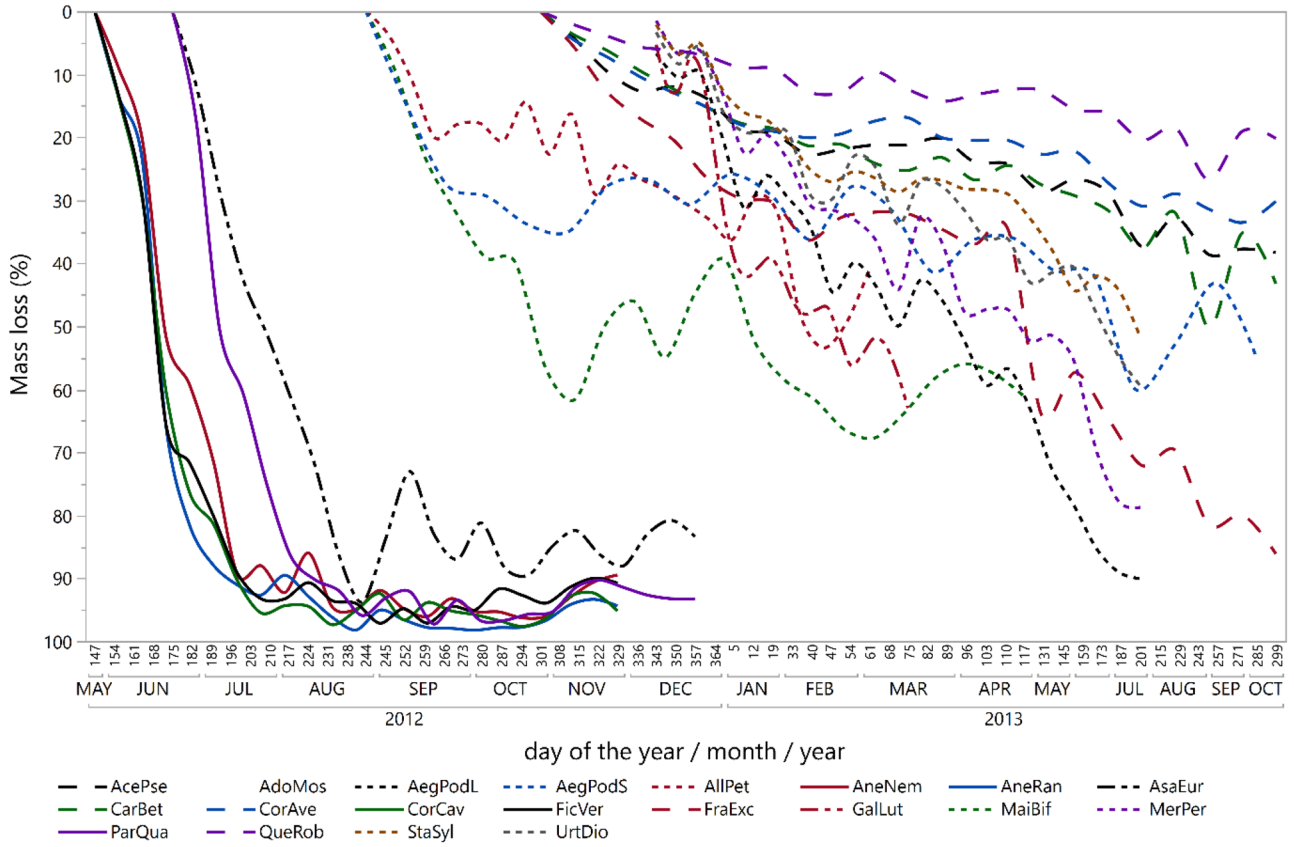

Fig. 1 Decomposition (percentage of mass loss) for all plant species studied during the experiment by date during the years 2012 and 2013. Explanations of abbreviations: AcePse - *Acer pseudoplatanus*; AdoMos - *Adoxa moschatellina*; AegPodL - *Aegopodium podagraria* leaves; AegPodS - *Aegopodium podagraria* shoots; AllPet - *Alliaria petiolata*; AneNem - *Anemone nemorosa*; AneRan - *Anemone ranunculoides*; AsaEur - *Asarum europaeum*; CarBet - *Carpinus betulus*; CorAve - *Corylus avellana*; CorCav - *Corydalis cava*; FicVer - *Ficaria verna*; FraExc - *Fraxinus excelsior*; GalLut - *Galeobdolon luteum*; MaiBif - *Maianthemum bifolium*; MerPer - *Mercurialis perennis*; ParQua - *Paris quadrifolia*; QueRob - *Quercus robur*; StaSyl - *Stachys sylvatica*; UrtDio - *Urtica dioica*

Mid-summer senescing plants decomposed the slowest (*k* range 0.2–3.2). During 182 days (ca. 6 months) of the experiment 95% of the biomass of all spring ephemeral species decomposed (Table 2). Plants that senesced during the mid-summer (*M. bifolium*, *A. petiolata*, *A. podagraria* (blooming shoots)) decomposed the slowest (Figs. 1 and 2). Biomass losses of *A. moschatellina* and *C. cava* were the most rapid—96% and 95% of the initial litter mass decayed during 63 days, respectively. After the same time of decomposition, 94% of *P. quadrifolia* and *F. verna*, 91% of *A. ranunculoides*, 90% of *A. europaeum*, 88% of *A. nemorosa*, 54% of *M. bifolium*, 48% of *G. luteum*, 34% of *A. podagraria* (leaves), 33% of *A. podagraria* (blooming shoots), 33% of *M. perennis*, 30% of *U. dioica*, 25% of *S. sylvatica*, and 18% of *A. petiolata* litter decomposed (Fig. 1). During ca. 6 months of the experiment, 95% of the biomass of *C. cava*, 94% of *A. ranunculoides*, 93% of *P. quadrifolia*, 91% of *F. verna*, and *A. moschatellina* decomposed (Table 2). After the same time of decomposition, 89% of the biomass of *A. nemorosa*, 87% of leaves of *A. podagraria*, 81% of *A. europaeum*, and 73% of *M. perennis* decomposed. Biomass of *M. bifolium*, *U. dioica*, *S. sylvatica*, and *A. petiolata* were 68, 50, 42, and 41% decomposed, respectively, whereas 28% of blooming shoots of *A. podagraria* decomposed.

3.2 Litter decomposition of the overstory species

We found statistically significant influence of woody plant species ($p < 0.0001$, $df = 4$, $F = 616.6597$), time ($p < 0.0001$, $df = 1$, $F = 916.3222$), and interaction of species × time ($p < 0.0001$, $df = 4$, $F = 70.108$) on litter decomposition. After ca. 6 months in the field decay rates of decomposition of tree foliage litter ranged from 0.2 to 0.8. *Q. robur* litter had the lowest decomposition rate (12%). At the same time, 21% of *C. avellana* leaf biomass, 24% of *C. betulus*, 25% of *A. pseudoplatanus*, and 43% of *F. excelsior*

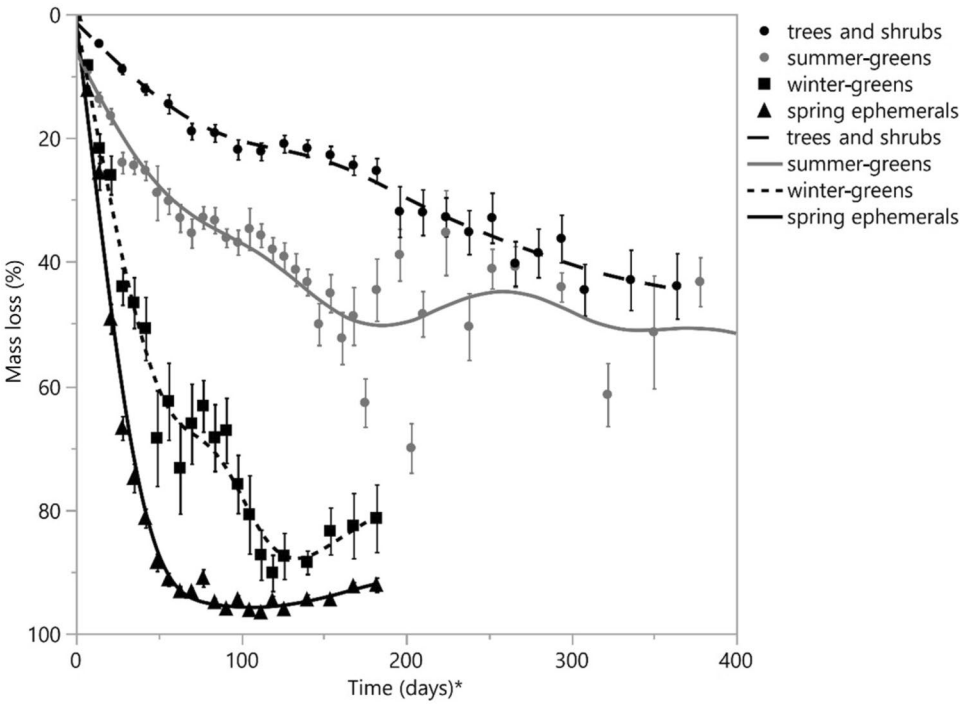

Fig. 2 Decomposition (mean percentage of initial mass loss) of all functional groups of plants studied during the experiment. *Time of the exposition in the field = time from the start of the experiment, which varied in time of the year for different functional groups as shown in Fig. 1

decomposed (Fig. 1). After 1 year of exposure in the field, 20% of *Q. robur*, 30% of *C. avellana*, 38% of *A. pseudoplatanus*, 43% of *C. betulus*, and 86% of *F. excelsior* decomposed. The foliage of trees had decay rates ranging from 0.2 to 1.9 during the first year of decomposition. *F. excelsior* leaf biomass decomposed significantly faster than leaves of other tree species (Table 7 in the Appendix).

3.3 Herbs vs. deciduous tree species litter decomposition

In general, litter decomposition for woody plant species was distinctly lower than for herbaceous species. The decay rates calculated for 6 months ranged from 0.2 to 0.8 and 0.2 to 6.9, respectively. *F. excelsior* leaf biomass did not decompose significantly slower than *A. podagraria* (both leaves and blooming shoots), *A. petiolata*, *M. perennis*, *U. dioica*, or *S. sylvatica* litter during ca. 2 months and *A. petiolata*, *A. podagraria* (blooming shoots), *U. dioica*, or *S. sylvatica* litter during 6 months of exposure in the field (Figs. 1 and 2; Table 7 in the Appendix). The value of mass remaining after ca. 6 months of the study reached by this tree species foliage was more similar to values reached by *A. petiolata*, *S. sylvatica*, and *U. dioica* than to the other woody species studied.

The species studied may be arranged from the fastest to slowest decomposition rate determined after ca. 6 months of the study: *A. ranunculoides*, *C. cava*, *A. nemorosa*, *F. verna*, *P. quadrifolia*, *A. moschatellina*, *A. europaeum*, *A. podagraria* leaves, *M. perennis*, *M. bifolium*, *U. dioica*, *S. sylvatica*, *A. petiolata*, *F. excelsior*, *C. betulus*, *A. pseudoplatanus*, *C. avellana*, *Q. robur*, and *A. podagraria* blooming shoots (Table 2).

3.4 Predictors of decay

We found significant regressions between morphological (SLA and LDMC) or chemical (LNC) leaf traits and decay rates of the species studied after six months of the experiment (Fig. 3, Table 3). Moreover, LDMC was a stronger predictor of decay rates than SLA and LNC. The regressions between *k*-values and traits are visualized in Fig. 3. Variation among traits studied was effectively captured by PCA. The principal ordination axis (PC1) accounted for 65.2% of the total trait variation, and together with the first two principal axes, accounted for 85.8% (Fig. 4). *K* decay and SLA contributed to the first axis, as well as LDMC, but in opposite directions, whereas LNC was correlated with the second axis. The decomposition process depended on fixed effects (time of exposition in the field, the functional group of plants, and mean total daily precipitation during 6 months of the experiment), as well as on species identity (random intercept) (Table 3). Impact of the other fixed effect (mean temperature during 6 months of the experiment) on the decay process was not statistically significant (Table 3). We found statistically significant differences in the rate of litter decomposition among all functional groups studied (Fig. 5).

Table 1 Description and life history traits of the species included in the study

Species	Life form[1]	Life span	Functional group[2]	Strategy[3]	Leaf persistence[4]	LDMC (mg g^{-1})	SLA (cm^2 g^{-1})	LNC (mg g^{-1})	Date of the start of the experiment	Number of litter bags
Anemone nemorosa	G	Perennial	se	CSR	V	205.0	277.1	26.77	26.05.2012	132
Anemone ranunculoides	G	Perennial	se	CSR	V	184.1	365.3	-	26.05.2012	132
Corydalis cava	G	Perennial	se	CSR	V	139.9	510.0	-	26.05.2012	132
Ficaria verna	G/H	Perennial	se	CSR	V	117.5	317.9	33.00	26.05.2012	132
Asarum europaeum	H	Perennial	wg	CS	I	145.8	275.2	31.80	23.06.2012	132
Adoxa moschatellina	G	Perennial	se	CSR	V	136.7	384.5	-	23.06.2012	132
Paris quadrifolia	G	Perennial	se	CSR	S	176.0	350.0	-	23.06.2012	132
Alliaria petiolata	C/H	Annual/perennial	ms	CR	I	161.3	404.4	37.22	01.09.2012	126
Maianthemum bifolium	G	Perennial	ms	S	S	238.6	331.4	24.90	01.09.2012	144
*Aegopodium podagraria*S	H	Perennial	ms	C	S	230.0	297.7	21.49	01.09.2012	198
*Aegopodium podagraria*L	H	Perennial	as	C	S	230.0	297.7	21.49	08.12.2012	132
Galeobdolon luteum	C	Perennial	as	CS	I	270.0	253.5	18.19	08.12.2012	78
Mercurialis perennis	G	Perennial	as	CS	S	224.5	256.8	24.74	08.12.2012	132
Stachys sylvatica	H	Perennial	as	CS	S	207.0	421.2	22.89	08.12.2012	132
Urtica dioica	C	Perennial	as	C	S	212.5	261.6	40.53	08.12.2012	132
Corylus avellana	N	Perennial	ts	C	S	283.8	205.4	24.20	27.10.2012	132
Acer pseudoplatanus	M	Perennial	ts	C	S	262.5	167.6	23.80	27.10.2012	132
Carpinus betulus	M	Perennial	ts	C	S	254.4	236.7	20.85	27.10.2012	132
Fraxinus excelsior	M	Perennial	ts	C	S	256.5	135.6	22.61	27.10.2012	132
Quercus robur	M	Perennial	ts	C	S	280.0	153.4	21.99	27.10.2012	132
Source[5]:	1	1		1	1	2	2	3		

*Aegopodium podagraria*S - *Aegopodium podagraria* blooming shoots; *Aegopodium podagraria*L - *Aegopodium podagraria* leaves

[1]Life forms: H - hemicryptophytes; C - chamaephytes; G - geophytes; T - therophytes

[2]Functional group: se - spring ephemerals; wg - winter-green plants; ms - mid-summer senescing plants; as - autumn-senescing plants; ts - trees and shrubs

[3]Life strategies: C - competitive; CR - competitive/ruderal; CSR - competitive/stress-tolerant/ruderal; CS - competitive/stress-tolerant; S - stress-tolerant

[4]Leaf persistence: S - summer green; I - persistent green; V - spring green

[5]Source of data: 1 - BiolFlor (Klotz et al. 2002); 2 - LEDA trait database (Kleyer et al. 2008), 3 - TRY database (Kattge et al. 2011)

Table 2 Results of the exponential decay model during 6 months of decomposition in the field. k_6 is the decay rate assessed after 6 months of the experiment in the field and r_6 is Pearson's correlation coefficient—values marked with the same letter do not differ significantly at $p < 0.0001$, based on one-way ANOVA and Tukey's a posteriori test. The last three columns show a decay time for 50%, 90%, and 95% litter mass loss

Species	Parameter					
	k_6 (years^{-1})	r_6		Decay time (days)		
				50%	90%	95%
Corydalis cava	6.4	− 0.68	a	28	56	63
Anemone ranunculoides	6.9	− 0.74	a	28	56	84
Anemone nemorosa	6.2	− 0.75	ab	28	70	91
Adoxa moschatellina	4.7	− 0.54	cd	14	63	63
Ficaria verna	5.4	− 0.63	bc	28	56	98
Paris quadrifolia	5.0	− 0.60	cd	21	49	84
Maianthemum bifolium	1.4	− 0.57	fg	56	-	-
*Aegopodium podagraria*L	3.2	− 0.87	e	98	203	-
Mercurialis perennis	2.1	− 0.87	f	140	-	-
*Aegopodium podagraria*S	0.2	− 0.18	h	322	-	-
Stachys sylvatica	0.9	− 0.84	gh	203	-	-
Asarum europaeum	4.1	− 0.58	de	35	63	-
Urtica dioica	1.1	− 0.82	fgh	203	-	-
Galeodbolon luteum	-	-	-	77	-	-
Alliaria petiolata	0.9	− 0.78	gh	-	-	-
Fraxinus excelsior	0.8	− 0.80	gh	196	-	-
Carpinus betulus	0.5	− 0.86	gh	-	-	-
Corylus avellana	0.3	− 0.76	gh	-	-	-
Acer pseudoplatanus	0.4	− 0.82	gh	-	-	-
Quercus robur	0.2	− 0.79	h	-	-	-

*Aegopodium podagraria*S - *Aegopodium podagraria* shoots; *Aegopodium podagraria*L - *Aegopodium podagraria* leaves

4 Discussion

Our hypotheses were only partially supported by the results of the experiment. We found statistically significant differences in litter decomposition among the plant species studied. Our study revealed that: (1) decomposition of herbaceous plants (including stems) was not always completed in less than a year, (2) spring ephemerals had higher decomposition rates than species which dominate the understory during summer and autumn, and (3) decomposition rates of herb species biomass were not always higher than that of tree leaves.

Few published papers on biomass and nutrient cycling of forests have addressed the dynamics of herbaceous material decomposition. Most of them suggest that decay rates (k) for herbaceous plants are higher than one, being in some cases considerably higher (Muller 2014). Exceptions are tundra vegetation dominated by mosses, sedges, or woody understory species (Hobbie 1996), and bulked herbaceous litter, dominated by ferns and woody understory species in a mixed hardwood stand in Canada (MacLean and Wein 1978). This is not in accordance with our study. In most cases, decomposition of herb litter biomass was completed much faster than within 1 year. During our experiment (ca. 6 months) decomposition

Table 3 Linear mixed model analysis of plant functional group effects on decomposition. Time of exposure in the field (duration of the experiment), mean temperature during 6 months of the experiment, and mean total daily precipitation during 6 months of the experiment were fixed effects and plant species were random effects (random intercepts and slopes among species) on the decay process

Variable	Sum of squares	Mean square	NumDF	DenDF	F	Pr(> F)
Functional group of plants	*1017*	*338.93*	*3*	*10.6*	*7.3*	*0.006*
Time of exposure in the field	*92,448*	*2254.82*	*41*	*594.9*	*48.3*	*< 0.0001*
Mean temperature	1	0.68	1	10.5	0.01	0.91
Mean total daily precipitation	*259*	*259.28*	*1*	*10.5*	*5.5*	0.04
Random effect–intercept	SD = 3.75	Random effect–slope	SD = 0.07			

Parameters in italics are statistically significant

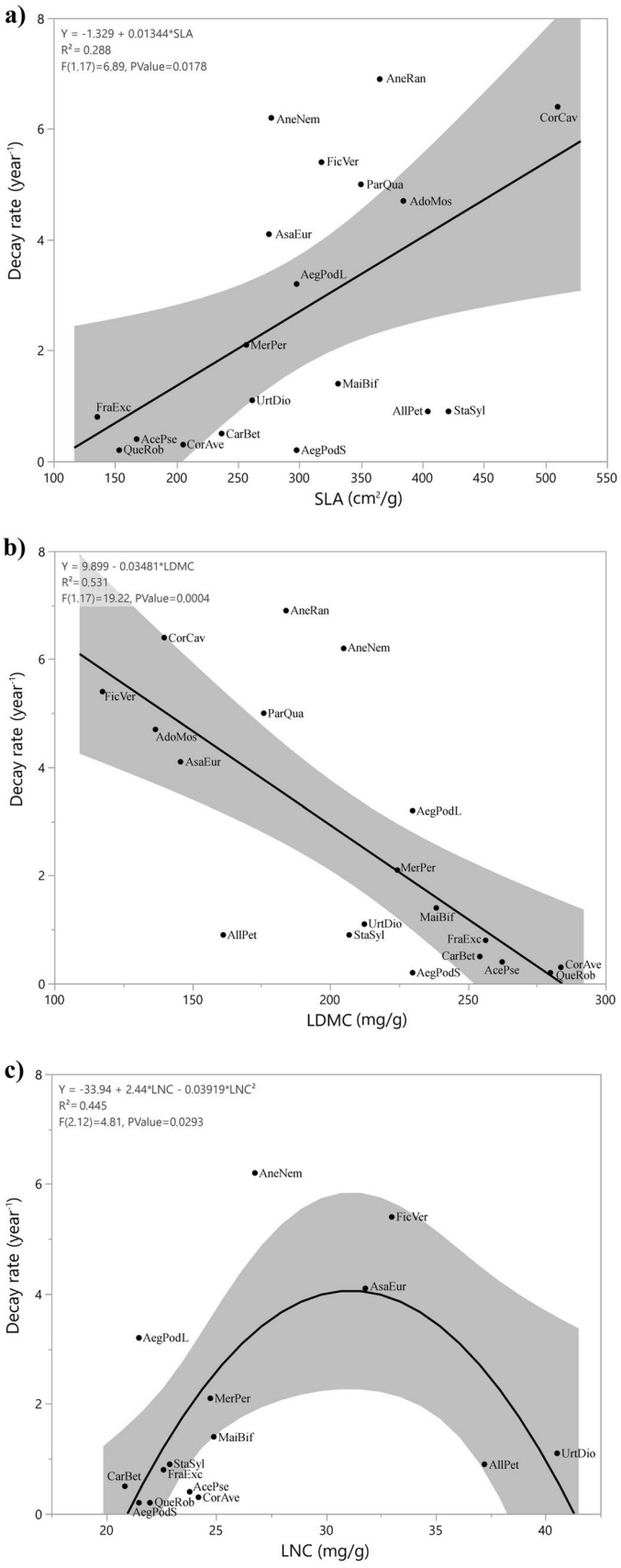

Fig. 3 Results of regressions of the decay rate (decay constant after 6 months of decay) of each litter species with functional traits: **a** SLA vs. decay rates; **b** LDMC vs. decay rates; **c** LNC vs. decay rates. The gray area shows 95% confidence intervals for the predicted values. Explanations of abbreviations: AcePse - *Acer pseudoplatanus;* AdoMos - *Adoxa moschatellina*; AegPodL - *Aegopodium podagraria* leaves; AegPodS - *Aegopodium podagraria* shoots; AllPet - *Alliaria petiolata*; AneNem - *Anemone nemorosa*; AneRan - *Anemone ranunculoides*; AsaEur - *Asarum europaeum*; CarBet - *Carpinus betulus*; CorAve - *Corylus avellana*; CorCav - *Corydalis cava*; FicVer - *Ficaria verna*; FraExc - *Fraxinus excelsior*; GalLut - *Galeobdolon luteum*; MaiBif - *Maianthemum bifolium*; MerPer - *Mercurialis perennis*; ParQua - *Paris quadrifolia*; QueRob - *Quercus robur*; StaSyl - *Stachys sylvatica*; UrtDio - *Urtica dioica*

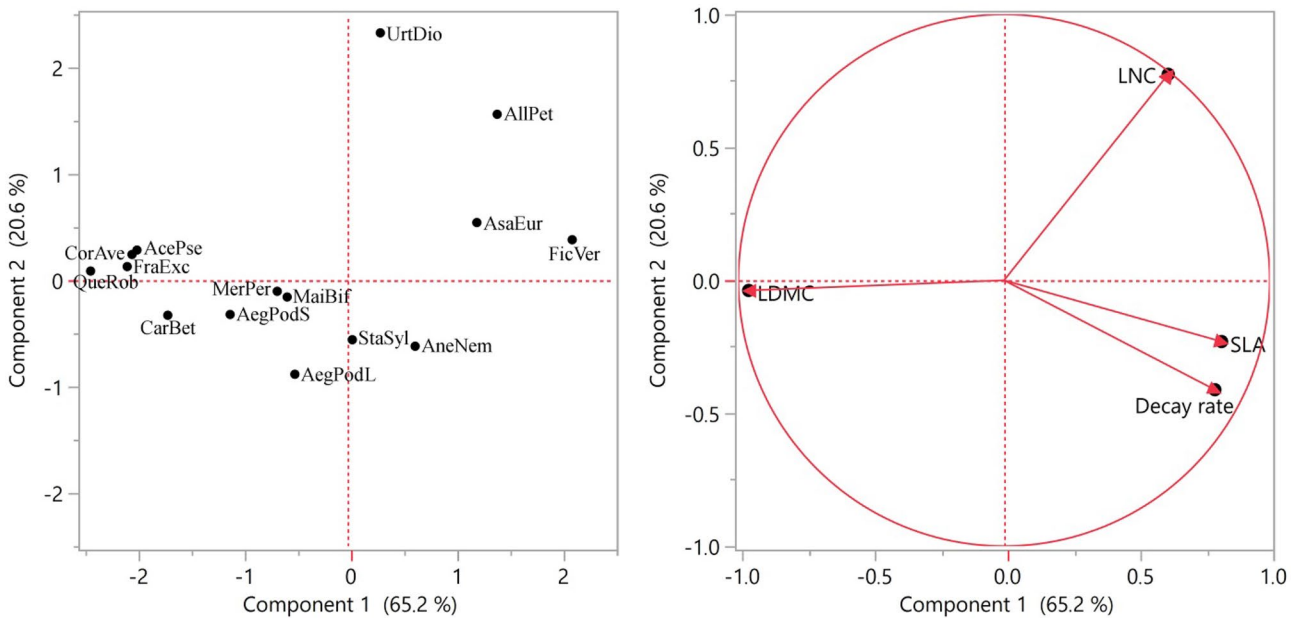

Fig. 4 Results of principal components analysis. Explanations of abbreviations: AcePse - *Acer pseudoplatanus*; AdoMos - *Adoxa moschatellina*; AegPodL - *Aegopodium podagraria* leaves; AegPodS - *Aegopodium podagraria* shoots; AllPet - *Alliaria petiolata*; AneNem - *Anemone nemorosa*; AneRan - *Anemone ranunculoides*; AsaEur - *Asarum europaeum*; CarBet - *Carpinus betulus*; CorAve - *Corylus avellana*; CorCav - *Corydalis cava*; FicVer - *Ficaria verna*; FraExc - *Fraxinus excelsior*; GalLut - *Galeobdolon luteum*; MaiBif - *Maianthemum bifolium*; MerPer - *Mercurialis perennis*; ParQua - *Paris quadrifolia*; QueRob - *Quercus robur*; StaSyl - *Stachys sylvatica*; UrtDio - *Urtica dioica*

rates of six species included in the spring ephemeral group reached *k* values in the range of 4.7–6.9, while mid-summer senescing summer-green plants (three species) ranged from 0.2–1.4, autumn-senescing summer-green plants (four species) ranged from 0.9 to 3.2, and winter-green *A. europaeum* reached 4.1. According to Muller (2014), the decomposition

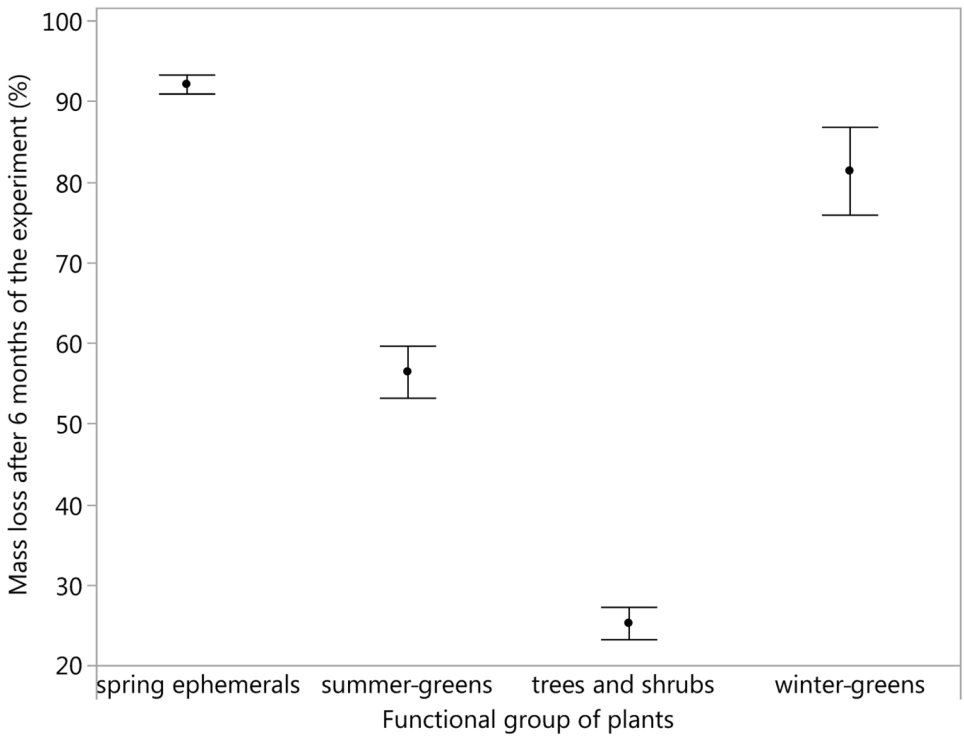

Fig. 5 Differences among functional groups of plants based on the Tukey HSD test ($p < 0.0001$)

rates of herbaceous species during 12 months of field exposure reached values in the range of 0.61–3.31. This was likely related to the species taken into account in Muller's (2014) review, as only two species are in common between that study and our study, namely, *A. nemorosa* and *M. perennis*. Data about these species were obtained from Wise and Shaefer (1994), who found statistically significant differences between decomposition rates of these species connected with three litter bag mesh sizes used in their experiment. In the treatment similar to ours (1 mm mesh size), they found 12-month decomposition constants *k* of 13.99 and 10.58 for *A. nemorosa* and *M. perennis*, respectively. Our study had 6-month decomposition constants of 6.2 and 2.1 for *A. nemorosa* and *M. perennis*, respectively. However, the results cited were obtained in beech forests on mull soils, where mean annual temperatures during the period of the study, were 6, 6.7, and 6 °C, and mean annual precipitation was 706, 726, and 717 mm. We conducted our studies in drier and warmer conditions, which may have significantly influenced *k* constants since mean temperature and precipitation are key factors determining decomposition rate (Aerts 1997; Hobbie 1996; Trofymow et al. 2002). In contrast, Halabuk and Gerhátová (2011) in SW Slovakia found results similar to our study, in similar environmental and climatic conditions (an ecotone of the hornbeam-oak forest situated in a region with a mean annual temperature of 9.3 °C and total annual precipitation of 580 mm). They found decomposition rates of $k = 2.41$ for *M. perennis* and $k = 2.44$ for *A. petiolata* during a 324-day experiment. In an experiment conducted in North America by Rodgers et al. (2008), green rosettes of *A. petiolata* decomposed in about 6 months, and senesced litter of *A. petiolata* decomposed in about one year. These results are very close to our 0.9 decomposition rate for *A. petiolata*, although those studies were conducted at five different sites including deciduous, coniferous, and mixed forests. In our study, decomposition constants of *A. petiolata* and blooming shoots of *A. podagraria* were lower than one. These species (especially *A. podagraria* blooming shoots) decomposed as slowly as tree leaves during our experiment. These two plant species had the highest contributions of stems to aboveground biomass among the species studied (Paź-Dyderska et al. 2020). For these two species, the decomposition rate visibly decreased during decomposition. In our opinion, this is connected with the differences in organ-specific decomposition rate *k*. Every sample is a mix of leaves and shoots in proportions similar to what occurs in specimens in the field. After the first stage of decomposition, when leaves have decomposed, the process slows down, and rates of mass losses between dates of sample collection are stable or even decreasing. Biomass allocation to organs that differ in the way that they decompose (e.g., stems and leaves) affects decomposition itself (Hobbie 1996). However, this has not been confirmed by studies of Bumb et al. (2018), which showed the same leaf and shoot decomposability of sixteen Mediterranean species. More in-depth studies are needed to understand how the decomposability of different plant organs is correlated and if these processes are controlled by the same functional traits (Freschet et al. 2012; Hobbie 2015). The duration of our experiment was only half of a year for most of the species. In the case of spring ephemerals, this was enough time to complete decomposition, but in other cases, we considered only part of the process that included decay of the labile part of the plant material.

Cornwell et al. (2008) found that decomposition and nutrient cycling processes across biomes were affected by the functional group of plant species. This has been described for a wide range of temperate plant species (Cornelissen and Thompson 1997), in Alaskan tundra (Hobbie 1996), lowland tropical forest (Santiago 2010), Mediterranean forests (De la Riva et al. 2019), rainforests (Jackson et al. 2013), experimental grasslands (Scherer-Lorenzen 2008), old-fields (Kazakou et al. 2006), alpine meadow (Jiang et al. 2013), alpine snow beds (Carbognani et al. 2014), and post-mining sites (Rawlik et al. 2019). There is little information available about tradeoffs between plant traits (Kleyer et al. 2018), and between plant functional traits and decomposition, in forest herb species. Plant functional groups were also connected with similar SLA, LDMC, and LNC (Cornwell et al. 2008). It was previously reported that these traits have an "after-life effect" on decomposition (Freschet et al. 2010, 2012; Jackrel and Wootton 2015; Santiago 2010). Freschet et al. (2012) reported that structural (lignin, DMC) and chemical (N) traits together were better predictors for decomposition rates of several high-turnover organs (leaves, fine stems, and reproductive parts) than structural traits alone, whereas leaf nitrogen content influenced leaf decomposition, but this relationship was not apparent in any other organs. Results of our studies focused on the decomposition of aboveground biomass of herbaceous plants, confirmed patterns reported by Freschet (2012). The best predictor for decomposition rates in our studies was LDMC. The results obtained were similar to those reported in previous studies, although we decided to use values obtained from global databases of functional traits. This method has limitations, as it is known that measurements of traits and decay rates on the same species, conducted at different sites, can potentially add noise to the analyses (Zanne et al. 2015).

In temperate deciduous forests, light availability is a major factor that determines leaf structure, with spring ephemeral species exhibiting nutrient-rich leaves with higher SLA relative to other herb species groups or late-successional canopy tree species (Jagodziński et al. 2016; Muller 2014; Rothstein and Zak 2001). Therefore, leaf traits associated with canopy openness determine litter decomposition rates. This is in accordance with our results showing decreasing decay rates in this order: spring ephemerals (high N concentration, high SLA), mid-summer, and autumn-senescing summer-green

herbaceous species. Our study further confirmed that fast decomposition rates were related to fast growth and can be generally predicted from functional plant group. Higher decomposition rates for spring ephemerals are supposedly connected with their traits as well as with ecological function in forest ecosystems. Results of previously published papers suggest that the spring ephemeral group of plants act as a "vernal dam" for nutrients. According to this theory spring ephemerals, by nutrient uptake and storage before canopy leaf-out, prevent nutrient losses by spring flow of soil water (Muller and Bormann 1976; Muller 2014; Rothstein and Zak 2001). Fast decomposition of the litter of this phenological group of herbaceous species may be the main part of their function in nutrient cycling, because it allows a huge pool of nutrients to be returned to the soil, making them available for trees at the time of their most intensive physiological activity. The remaining herb species with lower decomposition rates can be very important for nutrient storage in plant biomass. However, a broader study is needed to understand the function of herbaceous species in nutrient cycling in deciduous forest systems.

Most recent research results suggest that decomposition of tree leaf litter requires longer than one year for completion. Moreover, for leaves of woody species, decomposition rates have most often been reported in the range from 0.3 to 0.8 (see Muller 2014 and literature cited therein). This is generally in accordance with our studies showing that ca. 6-month decomposition rates of four oak-hornbeam tree species were in the range cited above (*F. excelsior* $k = 0.8$, *C. betulus* $k = 0.5$, *A. pseudoplatanus* $k = 0.4$, *C. avellana* $k = 0.3$, and *Q. robur* $k = 0.2$).

Our results are similar to previous estimates of tree foliage decomposition in areas of similar climatic and environmental conditions, although the variability of values is high because decay processes are sensitive to even small microclimatic and climatic fluctuations. In the experiment provided by Dziadowiec (1987) in an oak-linden-hornbeam forest in the Białowieża Forest, 65% of the initial biomass of *A. pseudoplatanus* and 36.5% of *Q. robur* leaves decomposed after 1 year in the field. This author also reported similar results from an oak-hornbeam forest near Toruń in Poland (Dziadowiec 1990). After 1 year of the experiment, 46% of the initial biomass of *C. betulus* leaf litter and 36% of *Q. robur* leaves decomposed. For those species, we found 43.3% and 20.2% of biomass decomposed, respectively, at the same time. Faster decomposition in Białowieża can be connected with bigger litter bag mesh size (2 mm) and more humid climatic conditions (Dziadowiec 1987). Hobbie et al. (2006) reported decomposition results for *Q. robur* leaves in central Poland similar to our results (k range after 1 year of exposure in the field of 0.21–0.24 vs. 0.23). However, in the case of the experiment cited above, decomposition constants were lower than in our experiment for *A. pseudoplatanus* (0.29 vs. 0.47) and *C. betulus* (0.30 vs. 0.54). Although several studies described tree leaf litter decomposition rates much higher than for herbaceous litter, research focused on oak-hornbeam forest tree species from other parts of those species geographical distributions are still limited (Jacob et al. 2009; Slade and Riutta 2012).

One of the key certainties in decomposition in forest ecosystems is the faster decomposition of herb litter than tree leaf biomass (Halabuk and Gerhátová 2011; Mayer 2008; Muller 2014), as most reported tree foliage has decomposition rates of $k < 1$ and most herbaceous litter of $k > 1$. We did not find significant differences between the decomposition of tree leaves and summer-green herb species after six months of the study. This is particularly important because it shows that not all herb species litter is part of the labile litter fraction. Some parts of those plant materials should be categorized as more resistant to decomposition—this seems to be a fact for species with a higher allocation of biomass to stems or with more lignified stems. In contrast, our study indicated that *F. excelsior* leaf litter can be included in the labile pool of litter which decomposes and returns nutrients to available nutrient pools quickly. Unfortunately, our studies focused on the first stages of the decomposition process, and differences between decomposition of herb and tree species foliage may be more visible in the later stages of decomposition.

Previous studies recognized that climatic factors such as mean annual temperature, mean annual precipitation and annual actual evapotranspiration regulate litter decomposition rate (Berg and McClaugherty 2014; Zhang et al. 2008). Generally, higher temperatures and precipitation stimulate mass loss during decomposition (Hobbie 1996; Mueller et al. 2016; Trofymow et al. 2002). In this context, reported differences in decomposition rates of the species we studied can be partly explained by changes in microclimatic conditions, and by their life history traits. At the same time, climate conditions have impacts on both litter quality (Coûteaux et al. 1995) and plant traits. Moreover, it is difficult to separate the influence of climate from the influence of litter quality on decomposition processes (Berg and McClaugherty 2014). As summarized by Aerts (1997), climate, litter chemistry, and litter decomposition are connected by a triangular relationship. As we mentioned above (introduction), we found differences between average air temperatures, ground temperatures, and total precipitation during the field incubation of litter for different groups of plants, e.g., during the 6-month experiment for the 1st group of plants mean ground temperature was more than 10 °C higher than during the 6-month experiment

for tree leaves. Total precipitation also differed for the periods of field experiments for different groups of plants. Our results indicated that microclimatic conditions stimulated decomposition when spring ephemeral litter decays in forest ecosystems and precipitation had a statistically significant impact on the decay process. Our study seemed to suffer because different times of incubation, which made it impossible to disentangle the influences of different climatic conditions and litter quality on the decomposition process. However, our studies aimed to find real, biological rates of decomposition of the species studied. Generally, we conducted our study with weather conditions similar to average conditions of the last decade (mean annual temperature: 9.1 °C in 2011–2013 vs. 9.2 in 2001–2010 and mean annual precipitation: 573 mm vs. 535 in the same periods of time, respectively). Moreover, we included microclimatic conditions as fixed effects into linear mixed models, to assess the impact of technical limitations of our studies on the results obtained.

In our studies, we make an effort to find real biological rates of decomposition of the species studied. However, we are aware of the limitations of research methods used in decomposition research. Kurz-Besson et al. (2005) compared the results of litter bag and direct observation methods and found higher mass losses measured by litter bags than by direct observation. These results were in agreement with previous results (De Santo et al. 1993) and were probably connected with a higher and more stable moisture content of litter in litter bags than in surrounding litter. In light of these findings, our results could overestimate decomposition rates; however, the studies mentioned took place with different material (Scots pine needles) and habitat. On the other hand, taking into account the results obtained by Bradford et al. (2002), our results could underestimate decomposition rates. According to these results, using litter bags of 1 mm mesh size decreased decomposition by 20% at 35 days because of macrofauna exclusion. Despite these limitations, the litter bag method is highly repeatable, relatively inexpensive, and widely used in decomposition studies (Harmon et al. 1999).

5 Conclusions

1. The decomposition process was dependent on the functional group of plants, time of exposure in the field, species identity, and precipitation.
2. Spring ephemerals had higher decomposition rates than species that dominate the understory of oak-hornbeam forest during summer and autumn.
3. The decomposition of herbaceous plants was not always completed in less than a year—not all litter of herbaceous species is part of the labile litter fraction.
4. Functional traits of leaves of herbaceous plants were correlated with their decomposition. The best predictor for decomposition rates in our studies was leaf dry matter content (LDMC).

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Data availability The datasets generated and analyzed during the current study are available in the FigShare repository, https://doi.org/10.6084/m9.figshare.12987410.v3.

Appendix

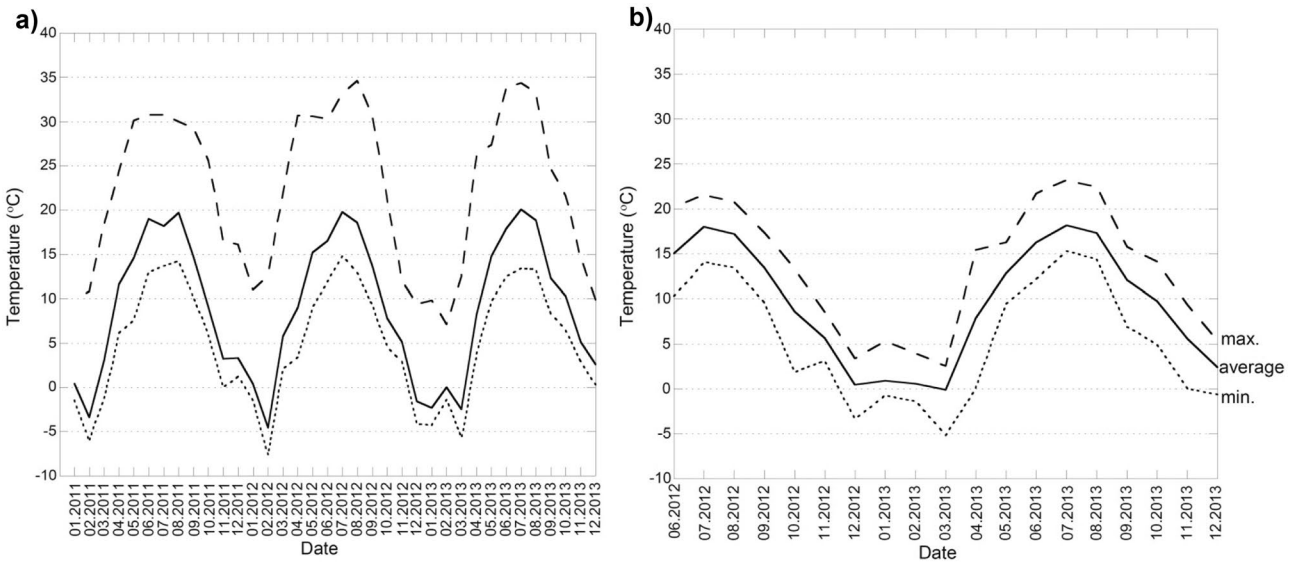

Fig. 6 Temperatures during the course of the research. **a** Air temperature data from the meteorological station in Kórnik including the year prior to start of the research and the 2 years during the research project. **b** Temperature of the ground surface on sample plots measured by HOBO data-loggers

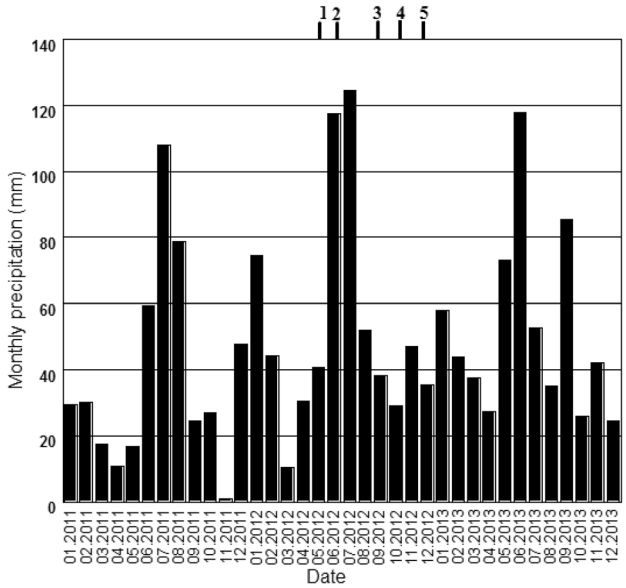

Fig. 7 Monthly precipitation during the course of the research. Data was from the meteorological station in Kórnik including the year prior to start of the research and the 2 years during the research project: 1- beginning of the experiment for the first group of plants; 2- beginning of the experiment for the second group of plants; 3- beginning of the experiment for the third group of plants; 4- beginning of the experiment for the fourth group of plants; 5- beginning of the experiment for the fifth group of plants

Table 4 Meteorological characteristics during the experiment. Ranges and mean values were given for 2- and 6-month periods from the beginning of the experiments, where leaf litter in litterbags was placed in the forest (5 terms)

Date	Air temperature (°C) at the meteorological station								Ground temperature (°C) in the forest								Total daily precipitation (mm) at the meteorological station							
	During 2 months				During 6 months				During 2 months				During 6 months				During 2 months				During 6 months			
	Range	Mean	SD	SE	Range	Mean	SD	SE	Range	Mean	SD	SE	Range	Mean	SD	SE	Range	Mean	SD	SE	Range	Mean	SD	SE
26.05.2012	10.0–24.4	17.5	3.5	0.5	− 1.8–24.7	13.9	6.0	0.4	10.3–21.1	16.0	2.8	0.4	1.9–21.6	13.3	4.8	0.4	0–40.5	4.0	7.6	1.0	0–40.5	2.2	5.0	0.4
23.06.2012	14.4–24.7	19.1	3.1	0.4	− 9.9–24.7	11.3	8.1	0.6	13.8–21.6	17.4	2.4	0.3	− 3.3–21.6	11.3	6.3	0.5	0–22.2	3.0	5.4	0.7	0–22.2	1.8	3.6	0.3
01.09.2012	1.4–19.1	11.3	3.5	0.5	− 9.9–19.1	3.8	6.8	0.5	3.6–17.3	11.5	2.8	0.4	− 3.3–17.3	4.9	5.2	0.4	0–10.7	1.2	2.4	0.3	0–13.4	1.5	2.3	0.2
27.10.2012	-9.9–8.7	1.6	4.8	0.6	− 10.8–16.8	1.0	5.6	0.4	− 3.3–8.5	3.4	2.9	0.4	− 5.2–15.4	2.5	3.8	0.3	0–13.4	1.2	2.2	0.3	0–13.4	1.7	2.4	0.2
08.12.2012	-9.9–6.5	-1.6	5.2	0.7	− 10.8–25.7	4.8	8.1	0.6	− 3.3–5.3	0.8	1.7	0.2	− 5.2–21.7	5.4	5.9	0.4	0–8.6	1.9	2.2	0.3	0–24.7	2.3	3.3	0.3

Table 5 Description of study site

Main plant communities	*Galio sylvatici-Carpinetum typicum*, *Galio sylvatici-Carpinetum corydaletosum*
Most common herb species	*Adoxa moschatellina*, *Anemone nemorosa*, *A. ranunculoides*, *Aegopodium podagraria*, *Asarum europaeum*, *Corydalis cava*, *Ficaria verna*, *Galeobdolon luteum*, *Milium effusum*
Most common tree species	*Fraxinus excelsior*, *Quercus robur*, *Carpinus betulus*
Most common shrub species	*Corylus avellana*
Mean height of trees	20.2 m (the highest trees reach 31.8 m)
Density of trees	230 specimens per hectare
Soil type	Gleyic Umbrisol (Arenic), Epidistric Gleyic Cambisol (Humic, Arenic)

Table 6 Physicochemical properties of the soil on the sample plot

Profile no.	Soil horizon	Depth (cm)	Percentage content of fractions with particle diameter (mm)			Granulometric group	C_{org}	N_{tot}	C/N	Humus content	pH reaction	
			Sand (0.05–2 mm)	Silt (0.002–0.05 mm)	Clay (< 0.002 mm)		%			%	In H_2O	In KCl
1	Ol	3–1(0)	-	-	-	-	43.191	1.686	25.6	74.46	5.45	5.02
	Ofh	1–0	-	-	-	-	42.285	1.675	25.2	72.90	5.98	5.51
	Au	0–30	77	18	5	LoSa	2.558	0.248	10.3	4.41	4.31	3.47
	AC	30–48	83	14	3	LoSa	0.598	0.057	10.5	1.03	4.95	3.93
	C1g	48–61	89	6	5	Sa	0.116	0.008	14.5	0.20	5.79	4.26
	C2g	61–150	92	7	1	Sa	0.065	0.006	10.8	0.11	6.90	5.18
2	Ol	3–1(0)	-	-	-	-	45.920	1.444	31.8	79.17	4.90	4.47
	Ofh	1–0	-	-	-	-	34.422	1.400	24.6	59.34	5.65	5.12
	A	0–26	77	19	4	LoSa	1.353	0.092	14.7	2.33	4.33	3.46
	Bw	26–60	81	12	7	LoSa	0.463	0.044	10.5	0.80	5.01	3.95
	BC	60–80	89	7	4	Sa	0.145	0.013	11.2	0.25	6.02	4.32
	Cg	80–150	96	3	1	Sa	0.116	0.011	10.5	0.20	6.83	5.27

LoSa - loamy sand; Sa - sand; C_{org} (%) - organic carbon content determined using the Tiurin method (in accordance with the PN-ISO 14235:2003 standard); N_{tot} (%) - total nitrogen content determined using the modified Kjeldahl method (in accordance with the PN:ISO 11261:2002 standard); C:N - C_{org} to N_{tot} ratio; pH H_2O, measured in 1:5 soil suspension in H_2O obtained by the potentiometric method in distilled water (in accordance with the ISO 10390:2005 standard)

Table 7 Decomposition (percentage of initial mass remaining) during the time of the experiment

Interval (days)	Species	Mean rest of litter (%)	SE (%)	Results of ANOVA
7	CorCav	13.82	1.44	a
	AneNem	9.19	1.07	abcd
	AneRan	12.88	2.29	ab
	FicVer	12.08	1.35	ab
	AsaEur	6.7	1.07	bcd
	ParQua	11.59	1.26	abc
	AdoMos	13.7	2.57	ab
	MaiBif	13.76	0.88	a
	AegPodS	13.77	1.36	a
	AllPet	8.16	0.83	abcd
	MerPer	4.68	0.66	d
	UrtDio	6.91	0.96	abcd
	AegPodL	11.33	1.83	abc
	StaSyl	5.29	1.03	cd
	GalLut	9.76	1.49	abcd
14	CorCav	16.53	2.87	def
	AneNem	10.68	2.33	efg
	AneRan	15.89	0.96	def
	FicVer	19.35	3.92	cde
	AsaEur	27.73	1.92	bc
	ParQua	39.63	4.04	ab
	AdoMos	51.36	2.68	a
	MaiBif	23.27	1.2	cd
	AegPodS.	23.26	2.21	cd
	AllPet	16.09	1.61	cdef
	MerPer	7.97	1.07	fgh
	UrtDio	9.38	1.33	fg
	AegPodL	9.9	0.91	efg
	StaSyl	7.73	0.98	fgh
	GalLut	15.49	2.49	def
	CorAve	5.1	0.63	gh
	FraExc	6.66	1.09	gh
	CarBet	4.2	0.36	gh
	AcePse	5.03	1.46	gh
	QueRob	2.44	0.18	h
21	CorCav	48.5	6.35	abc
	AneNem	36.1	3.43	cdef
	AneRan	39.79	4.53	cde
	FicVer	45.61	5.33	bcd
	AsaEur	29.34	5.91	def
	ParQua	58.7	1.74	ab
	AdoMos	66.21	2.00	a
	MaiBif	25.21	1.67	efg
	AegPodS	26.44	2.92	efg
	AllPet	21.28	1.71	fgh
	MerPer	8.00	1.51	i
	UrtDio	10.85	1.22	hi
	AegPodL	12.7	0.87	ghi
	StaSyl	10.26	1.13	hi
	GalLut	22.54	1.85	efgh
28	CorCav	63.94	3.15	abc
	AneNem	56.04	5.61	bcd
	AneRan	75.29	2.25	a

Table 7 (continued)

Interval (days)	Species	Mean rest of litter (%)	SE (%)	Results of ANOVA
	FicVer	71.49	4.65	ab
	AsaEur	48.82	4.88	cde
	ParQua	62.16	5.34	abc
	AdoMos	71.63	2.86	ab
	MaiBif	35.56	6.6	efg
	AegPodS	31.13	2.92	efgh
	AllPet	16.63	2.81	hijk
	MerPer	18.76	1.75	ghijk
	UrtDio	20.67	2.23	ghij
	AegPodL	30.24	3.56	fghi
	StaSyl	14.47	1.25	ijkl
	GalLut	39.05	2.45	def
	CorAve	8.09	0.7	jkl
	FraExc	14.69	2.24	hijkl
	CarBet	7.08	0.51	kl
	AcePse	10.97	1.12	jkl
	QueRob	4.49	0.74	l
35	CorCav	77.45	4.55	ab
	AneNem	59.57	5.85	bcd
	AneRan	81.65	3.66	a
	FicVer	71.47	5.00	abc
	AsaEur	51.4	7.66	cde
	ParQua	76.75	2.72	ab
	AdoMos	82.39	6.93	a
	MaiBif	38.07	2.37	defg
	AegPodS	29.63	3.94	efgh
	AllPet	18.26	0.56	gh
	MerPer	21.76	1.52	fgh
	UrtDio	17.21	1.75	h
	AegPodL	28.74	1.28	fgh
	StaSyl	16.93	0.6	h
	GalLut	41.68	2.49	def
42	CorCav	80.76	2.28	ab
	AneNem	69.04	3.91	bc
	AneRan	87.62	1.00	a
	FicVer	78.80	1.71	ab
	AsaEur	60.31	6.83	c
	ParQua	85.56	2.68	a
	AdoMos	86.12	4.3	a
	MaiBif	42.52	2.84	d
	AegPodS	29.85	2.73	def
	AllPet	21.48	1.78	fg
	MerPer	18.67	0.86	fg
	UrtDio	20.00	2.26	fg
	AegPodL	26.08	1.57	ef

Table 7 (continued)

Interval (days)	Species	Mean rest of litter (%)	SE (%)	Results of ANOVA
	StaSyl	17.55	1.12	fg
	GalLut	39.19	3.7	de
	CorAve	11.94	1.46	gh
	FraExc	18.38	1.4	fg
	CarBet	11.11	1.01	gh
	AcePse	12.77	1.12	gh
	QueRob	6.2	0.37	h
49	CorCav	87.55	3.2	a
	AneNem	86.8	3.06	a
	AneRan	89.25	2.31	a
	FicVer	87.52	2.55	a
	AsaEur	68.41	7.72	a
	ParQua	90.63	2.75	a
	AdoMos	88.91	6.48	a
	MaiBif	40.56	10.03	b
	AegPodS	33.71	1.66	bc
	AllPet	12.09	2.14	c
56	CorCav	94.19	1.99	a
	AneNem	89.33	1.77	ab
	AneRan	93.83	0.60	a
	FicVer	91.12	1.55	ab
	AsaEur	79.18	7.19	b
	ParQua	89.31	4.23	ab
	AdoMos	89.44	3.67	ab
	MaiBif	56.56	3.45	c
	AegPodS	33.47	1.23	de
	AllPet	23.77	2.03	efg
	MerPer	25.37	3.06	efg
	UrtDio	19.82	2.62	efgh
	AegPodL	30.56	1.34	def
	StaSyl	21.32	1.57	efg
	GalLut	45.75	2.69	cd
	CorAve	14.17	0.90	fgh
	FraExc	24.05	4.22	efg
	CarBet	13.99	1.11	fgh
	AcePse	12.17	1.15	gh
	QueRob	6.4	0.54	h
63	CorCav	95.46	0.91	a
	AneNem	88.22	1.97	a
	AneRan	90.95	2.99	a
	FicVer	94.23	1.10	a
	AsaEur	90.13	2.52	a
	ParQua	94.27	1.50	a
	AdoMos	95.87	1.58	a
	MaiBif	53.80	3.28	b
	AegPodS	33.50	5.48	cde

Table 7 (continued)

Interval (days)	Species	Mean rest of litter (%)	SE (%)	Results of ANOVA
	AllPet	17.81	2.13	e
	MerPer	32.96	3.23	cde
	UrtDio	29.64	5.90	cde
	AegPodL	34.40	2.91	cd
	StaSyl	25.34	2.69	de
	GalLut	47.98	5.62	bc
70	CorCav	94.11	0.85	ab
	AneNem	92.45	1.36	ab
	AneRan	89.66	1.57	ab
	FicVer	92.73	1.17	ab
	AsaEur	84.53	4.92	b
	ParQua	93.27	1.55	ab
	AdoMos	96.96	0.55	a
	MaiBif	62.38	5.70	c
	AegPodS	35.41	3.55	def
	AllPet	18.67	1.97	ghi
	MerPer	32.36	3.36	defg
	UrtDio	30.26	1.92	efgh
	AegPodL	44.64	3.30	de
	StaSyl	27.08	2.93	fgh
	GalLut	47.63	4.71	cd
	CorAve	17.64	1.26	hi
	FraExc	29.95	1.68	efgh
	CarBet	17.66	1.43	hi
	AcePse	18.30	0.91	ghi
	QueRob	8.92	0.52	i
77	CorCav	94.34	1.53	a
	AneNem	85.76	4.96	ab
	AneRan	92.81	1.39	a
	FicVer	90.56	5.46	a
	AsaEur	70.32	6.88	bc
	ParQua	91.15	2.96	a
	AdoMos	91.23	2.45	a
	MaiBif	48.92	5.38	cde
	AegPodS	26.32	4.15	ef
	AllPet	30.20	3.95	ef
	MerPer	32.77	4.07	ef
	UrtDio	24.07	2.47	f
	AegPodL	40.06	1.22	def
	StaSyl	26.03	2.41	f
	GalLut	56.11	3.05	cd
84	CorCav	97.09	0.77	a
	AneNem	92.99	0.97	ab
	AneRan	95.17	1.06	ab
	FicVer	93.50	2.36	ab
	AsaEur	84.13	3.40	b

Table 7 (continued)

Interval (days)	Species	Mean rest of litter (%)	SE (%)	Results of ANOVA
	ParQua	95.94	1.25	a
	AdoMos	94.79	2.07	ab
	MaiBif	53.52	2.54	c
	AegPodS	30.28	3.14	de
	AllPet	24.19	2.01	de
	MerPer	34.78	3.71	cde
	UrtDio	22.62	4.44	ef
	AegPodL	42.33	6.18	cd
	StaSyl	24.91	3.50	de
	GalLut	52.56	4.09	c
	CorAve	19.02	1.74	ef
	FraExc	29.87	2.44	de
	CarBet	18.43	1.30	ef
	AcePse	19.25	1.13	ef
	QueRob	9.05	0.91	f
91	CorCav	96.65	1.10	a
	AneNem	95.81	0.47	a
	AneRan	98.46	0.21	a
	FicVer	93.08	3.47	a
	AsaEur	80.49	6.87	b
	ParQua	96.72	0.90	a
	AdoMos	95.00	2.02	a
	MaiBif	45.43	3.10	cd
	AegPodS	33.10	1.88	de
	AllPet	26.48	2.68	e
	MerPer	40.68	2.63	cde
	UrtDio	30.59	3.30	de
	AegPodL	46.68	2.92	cd
	StaSyl	29.48	2.57	de
	GalLut	53.86	1.88	c
98	CorCav	92.85	2.32	ab
	AneNem	91.90	2.54	ab
	AneRan	94.78	0.75	ab
	FicVer	97.08	0.46	a
	AsaEur	88.67	2.56	b
	ParQua	92.88	1.88	ab
	AdoMos	97.18	0.79	a
	MaiBif	53.27	3.10	cd
	AegPodS	23.32	3.53	gh
	AllPet	26.79	3.37	gh
	MerPer	43.43	2.65	def
	UrtDio	33.60	1.72	fgh
	AegPodL	50.24	3.48	cde
	StaSyl	27.03	1.47	gh
	GalLut	62.99	4.95	c

Table 7 (continued)

Interval (days)	Species	Mean rest of litter (%)	SE (%)	Results of ANOVA
	CorAve	19.74	1.30	hi
	FraExc	35.56	1.88	efg
	CarBet	21.00	1.29	ghi
	AcePse	21.81	1.01	ghi
	QueRob	10.87	0.67	i
105	CorCav	96.74	0.44	a
	AneNem	94.98	0.60	a
	AneRan	96.70	0.56	a
	FicVer	94.72	1.42	a
	AsaEur	80.76	6.32	b
	ParQua	97.01	0.59	a
	AdoMos	96.92	0.15	a
	MaiBif	52.63	4.34	c
	AegPodS	26.27	2.86	d
	AllPet	27.96	2.42	d
112	CorCav	93.96	1.54	ab
	AneNem	96.62	0.49	ab
	AneRan	97.79	0.65	a
	FicVer	97.48	0.25	a
	AsaEur	87.26	4.07	b
	ParQua	97.06	0.61	ab
	AdoMos	96.43	1.40	ab
	MaiBif	46.81	2.51	c
	AegPodS	30.88	9.31	cde
	AllPet	30.95	2.04	cde
	MerPer	38.62	4.13	cd
	UrtDio	28.61	1.46	de
	AegPodL	47.00	3.44	c
	StaSyl	26.96	1.35	def
	CorAve	19.90	0.51	ef
	FraExc	33.64	2.38	cde
	CarBet	20.77	2.86	ef
	AcePse	22.33	1.31	ef
	QueRob	13.90	1.43	f
119	CorCav	94.78	2.64	a
	AneNem	93.66	1.98	a
	AneRan	97.77	0.33	a
	FicVer	94.21	1.74	a
	AsaEur	90.17	2.92	a
	ParQua	95.33	0.89	a
	AdoMos	92.76	1.98	a
	MaiBif	37.46	9.17	bc
	AegPodS	33.06	2.88	bc
	AllPet	34.45	2.42	bc
	MerPer	47.90	2.81	bc
	UrtDio	31.74	1.33	c
	AegPodL	52.61	2.46	b

Table 7 (continued)

Interval (days)	Species	Mean rest of litter (%)	SE (%)	Results of ANOVA
	StaSyl	28.33	2.65	c
126	CorCav	95.45	0.86	ab
	AneNem	94.52	0.76	ab
	AneRan	98.23	0.26	a
	FicVer	95.69	0.44	ab
	AsaEur	87.44	3.70	b
	ParQua	96.29	0.50	ab
	AdoMos	96.07	0.95	ab
	MaiBif	43.18	8.15	de
	AegPodS	24.16	3.23	fg
	AllPet	36.12	1.78	def
	MerPer	47.47	3.24	cd
	UrtDio	36.25	4.54	def
	AegPodL	59.38	1.77	c
	StaSyl	28.42	1.95	efg
	CorAve	17.93	0.86	gh
	FraExc	31.97	1.46	defg
	CarBet	23.63	0.78	fg
	AcePse	21.22	0.38	fgh
	QueRob	9.65	0.81	h
133	MerPer	46.80	2.07	ab
	UrtDio	35.42	2.95	bc
	AegPodL	56.85	2.78	a
	StaSyl	28.39	3.38	c
140	CorCav	96.82	0.39	ab
	AneNem	95.36	0.77	abc
	AneRan	97.79	0.22	a
	FicVer	91.50	4.13	abc
	AsaEur	88.44	1.90	c
	ParQua	91.07	1.92	bc
	AdoMos	94.43	1.44	abc
	MaiBif	57.58	3.30	d
	AegPodS	29.74	1.55	fg
	AllPet	29.11	2.35	fg
	MerPer	51.31	2.77	de
	UrtDio	41.74	2.58	ef
	AegPodL	60.18	3.10	d
	StaSyl	32.65	2.21	fg
	CorAve	16.89	0.40	hi
	FraExc	32.15	1.49	fg
	CarBet	25.31	1.21	gh
	AcePse	21.23	1.96	ghi
	QueRob	12.42	0.99	i
147	MerPer	52.61	3.91	b
	UrtDio	43.21	2.52	bc
	AegPodL	69.98	3.51	a
	StaSyl	34.23	3.00	c
154	CorCav	97.04	1.24	a

Table 7 (continued)

Interval (days)	Species	Mean rest of litter (%)	SE (%)	Results of ANOVA
	AneNem	96.414	0.574	a
	AneRan	97.18	0.77	a
	FicVer	94.08	1.85	a
	AsaEur	83.40	3.76	b
	ParQua	91.10	1.81	ab
	AdoMos	92.52	2.36	ab
	MaiBif	58.82	3.20	c
	AegPodS	33.08	2.99	def
	AllPet	43.11	2.75	d
	CorAve	20.44	1.11	fg
	FraExc	35.08	1.92	de
	CarBet	23.30	1.80	efg
	AcePse	20.42	2.30	fg
	QueRob	14.32	1.63	g
161	MerPer	51.38	9.75	ab
	UrtDio	39.71	7.45	b
	AegPodL	75.24	2.80	a
	StaSyl	42.76	3.35	b
168	CorCav	92.09	2.20	ab
	AneNem	91.91	0.95	ab
	AneRan	93.55	1.96	a
	FicVer	90.51	2.24	ab
	AsaEur	82.55	5.26	b
	ParQua	92.97	1.78	a
	AdoMos	93.10	1.65	a
	MaiBif	64.33	2.32	c
	AegPodS	35.66	1.16	d
	CorAve	20.31	1.43	ef
	FraExc	36.44	1.50	d
	CarBet	27.31	1.72	de
	AcePse	24.88	0.58	de
	QueRob	12.84	1.20	f
175	MerPer	72.65	1.87	b
	UrtDio	49.83	1.92	c
	AegPodL	86.53	2.78	a
	StaSyl	41.76	3.90	c
182	CorCav	95.19	0.35	ab
	AneNem	89.47	4.77	ab
	AneRan	94.38	0.92	a
	FicVer	90.76	2.38	ab
	AsaEur	81.35	5.45	bc
	ParQua	93.26	1.79	ab
	AdoMos	90.62	3.84	ab
	MaiBif	67.94	2.85	c
	AegPodS	27.90	2.95	def
	AllPet	41.00	2.42	de

Table 7 (continued)

Interval (days)	Species	Mean rest of litter (%)	SE (%)	Results of ANOVA
	CorAve	21.32	0.74	fg
	FraExc	42.88	2.81	d
	CarBet	23.89	1.09	efg
	AcePse	25.10	1.27	efg
	QueRob	12.36	0.84	g
196	AegPodS	38.81	4.17	b
	CorAve	22.77	0.62	bc
	FraExc	66.20	10.77	a
	CarBet	28.05	1.34	bc
	AcePse	29.05	1.21	bc
	QueRob	12.62	1.59	c
203	MerPer	78.72	7.71	ab
	UrtDio	59.45	4.15	bc
	AegPodL	90.05	3.37	a
	StaSyl	51.78	4.74	c
210	MaiBif	56.79	2.94	a
	AegPodS	39.93	4.03	b
	CorAve	23.38	0.48	cd
	FraExc	64.03	4.15	a
	CarBet	28.57	2.27	bc
	AcePse	26.54	1.24	c
	QueRob	15.50	0.73	d
224	AegPodS	41.73	4.17	b
	CorAve	22.57	0.61	cd
	FraExc	55.47	2.49	a
	CarBet	29.89	2.28	c
	AcePse	27.43	1.38	c
	QueRob	15.78	2.84	d
238	MaiBif	61.13	2.6	a
	AegPodS	44.41	6.57	ab
	CorAve	29.60	2.33	bc
	FraExc	65.49	8.60	a
	CarBet	31.33	1.25	bc
	AcePse	30.13	1.55	bc
	QueRob	18.32	2.54	d
252	AegPodS	41.05	3.18	b
	CorAve	23.12	1.84	cd
	FraExc	63.07	6.41	a
	CarBet	32.73	2.03	bc
	AcePse	27.94	3.89	bcd
	QueRob	13.22	1.23	d
266	AegPodS	40.74	3.31	b
	CorAve	30.88	3.73	bc
	FraExc	72.40	5.25	a
	CarBet	36.79	1.49	b
	AcePse	37.31	2.88	b
	QueRob	20.39	2.94	c
280	CorAve	30.69	2.73	bc
	FraExc	69.41	5.63	a
	CarBet	40.99	2.87	b

Table 7 (continued)

Interval (days)	Species	Mean rest of litter (%)	SE (%)	Results of ANOVA
	AcePse	36.25	5.54	bc
	QueRob	20.31	3.03	c
294	AegPodS	44.01	2.37	b
	CorAve	28.77	2.60	cd
	FraExc	70.48	3.74	a
	CarBet	30.77	1.91	bcd
	AcePse	32.33	4.22	bc
	QueRob	18.63	2.28	d
308	CorAve	30.16	3.73	b
	FraExc	79.76	4.69	a
	CarBet	48.78	5.98	b
	AcePse	37.27	7.34	b
	QueRob	26.41	3.60	b
322	AegPodS	61.38	5.10	
336	CorAve	33.64	1.73	b
	FraExc	79.79	3.57	a
	CarBet	36.33	5.50	b
	AcePse	37.88	11.14	b
	QueRob	19.82	4.39	b
350	AegPodS	51.29	9.11	
364	CorAve	30.16	3.13	bc
	FraExc	86.13	3.09	a
	CarBet	43.32	7.15	b
	AcePse	38.32	7.02	bc
	QueRob	20.23	5.47	c
378	AegPodS	43.18	3.94	
406	AegPodS	55.01	4.94	

AcePse - *Acer pseudoplatanus*; AdoMos - *Adoxa moschatellina*; AegPodL - *Aegopodium podagraria* leaves; AegPodS - *Aegopodium podagraria* shoots; AllPet - *Alliaria petiolata*; AneNem - *Anemone nemorosa*; AneRan - *Anemone ranunculoides*; AsaEur - *Asarum europaeum*; CarBet - *Carpinus betulus*; CorAve - *Corylus avellana*; CorCav - *Corydalis cava*; FicVer - *Ficaria verna*; FraExc - *Fraxinus excelsior*; GalLut - *Galeobdolon luteum*; MaiBif - *Maianthemum bifolium*; MerPer - *Mercurialis perennis*; ParQua - *Paris quadrifolia*; QueRob - *Quercus robur*; StaSyl - *Stachys sylvatica*; UrtDio - *Urtica dioica*

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