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The effect of lignin photodegradation on decomposability of *Calamagrostis epigeios* grass litter

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Abstract The common grass *Calamagrostis epigeions* produces a large amount of dead biomass, which remain above the soil surface for many months. In this study, we determined how exposure of dead biomass above the soil affects its subsequent decomposition in soil. Collected dead standing biomass was divided in two parts, the first one (initial litter) was stored in a dark, dry place. The other part was placed in litterbags in the field. The litterbags were located in soil, on the soil surface, or hanging in the air without contact with soil but exposed to the sun and rain. After 1 year of field exposure, litter mass loss and C and N content were measured, and changes in litter chemistry were explored using NMR and thermochemolysis-GC–MS. The potential decomposability of the litter was quantified by burying the litter from the litterbags and the initial litter in soil microcosms and measuring soil respiration. Soil respiration was greater with litter that had been hanging in air than with all other kinds of litter. These finding could not be explained by changes in litter mass or C:N ratio. NMR indicated a decrease in polysaccharides relative to lignin in litter that was buried in soil but not in litter that was placed on soil surface or that was hanging in the air. Thermochemolysis indicated that the syringyl units of the litter lignin were decomposed when the litter was exposed to light. We postulate that photochemical decay of lignin increase decomposability of dead standing biomass.

Keywords Thermochemolysis-GC–MS · ^{13}C NMR · Decomposition · Plant litter · Post mining sites · Light

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Introduction

Litter decomposition plays an important role in carbon (C) turnover at both local and global scales. The major drivers of litter decomposition are generally water availability and litter chemical composition as indicated by its C:N ratio or the N:lignin ratio (Mellilo et al. 1982). Other factors can also affect the rate of decomposition, and these include the composition of biota and photochemical degradation (Whitford et al. 1981; Wall et al. 2008; Austin and Vivanco 2006; Austin and Ballaré 2010).

Solar radiation can affect litter decomposition in several ways. In aquatic ecosystems, light in general

and UV radiation in particular can accelerate the breakdown of complex aromatic compounds (Rozema et al. 2002; Moorhead and Callaghan 1994). In terrestrial ecosystems, the photochemical degradation of litter has received the most attention in polar and arid areas (Gehrke et al. 1995; Pancotto et al. 2005; Gallo et al. 2006; Moody et al. 2001; Austin and Vivanco 2006; Brandt et al. 2007), where photochemical degradation of litter may be a major driver of litter decomposition (Gallo et al. 2006; Austin and Vivanco 2006). Elevated UV radiation, however, could also slow litter decomposition by altering the chemistry of plants (and therefore of litter) and by adversely affecting the decomposer organisms (Gehrke et al. 1995; Pancotto et al. 2003, 2005). Also here photodegradation targets mostly lignin and whereas increasing lignin content reduce biological decomposition it may enhance mass loss by photodegradation (Austin and Ballaré 2010).

Although photodegradation of lignin has been repeatedly reported as a major driver of litter decomposition in arid ecosystems (Gallo et al. 2006; Austin and Vivanco 2006), little is known about the effect of photochemical degradation of lignin on litter degradation in temperate zones and about changes in composition of aromatic compounds of litter caused by photodegradation. We expect that post-senescent exposure to light could significantly affect litter decomposition and that the response of litter to light could differ depending on the source plant. In some species, litter moves into the soil or onto the litter layer soon after senescence and is protected from light by incorporation into soil or by shading from the plant community. In other species, a substantial part of the dead biomass remains standing for several months and therefore can be exposed to solar radiation. In this contribution, we asked two questions. First, how does post-senescent exposure to light affect subsequent decomposition of *Calamagrostis epigeios* grass litter? Second, how do changes in decomposability caused by light exposure correspond to changes in litter chemistry and especially to changes in the composition of aromatic compounds?

Calamagrostis epigeios is common grass that occurs usually in disturbed habitats at young and intermediate succession stages. It is a strong competitor that often outcompetes most other plant species. It can also complicate tree establishment (Rebele and Lehmann 2001). *Calamagrostis epigeios* often retains a large proportion of the litter it produces as dead standing biomass (Rebele and Lehmann 2001), while a smaller portion of its litter falls to the soil. *Calamagrostis epigeios* thus represents a useful model for studying how the initial location of litter, and therefore its exposure to light, affects its future rate of decomposition.

Materials and methods

Study sites

A field decomposition experiment was performed in unreclaimed sites at heaps created by the dumping of alkaline tertialry clay material after brown coal mining near Sokolov, Czech Republic. The study area was located at an altitude of 500–600 m a.s.l., with mean annual precipitation of 650 mm and mean annual temperature of 6.8°C (Frouz and Novakova 2005; Frouz et al. 2008). Over time, the vegetation at these sites changes from herbs to shrubs and forests, but the grass *C. epigeios* is common at all succession stages (Frouz et al. 2008). Two sites were used. One site was about 15 years old (i.e., the heaps had been formed 15 years earlier) and is referred to as the young site. The other site, the old site, was 45 years old. The young site was dominated *by C. epigeios* with individual *Salix caprea* shrubs. At the old site, a birch and aspen (*Betula pendula* and *Populus tremula*) forest had developed but *C. epigeios* was the dominant understory species.

Experiment and data collection

At both sites, dead standing biomass of *C. epigeios* was collected in September 2006, dried, cut in pieces about 5 cm long, mixed (from each site separately), and placed in litterbags (5 g of dry litter per bag). Collected litter was yellow which is typical for fresh litter produced in the same growing season, while older litter which was half standing or laying on soil surface was gray. Litterbags were 10 × 15 cm and with 0.2 mm openings, the open space area of the mesh is about 52% of total area and thickness of the material is 80 μm. Mesh was made from nylon which is generally translucent for UV radiation (Alvarez and Lipp-Symonowicz 2003). Litterbags were placed in the field sites by the end of September, with litter

from the young and old sites placed at the young and old sites, respectively. At each site, the litterbags were placed in three locations: in the soil (4 cm deep), on the soil surface, and hanging in the air on the rope about 1 m above the soil surface. There were five replicate litterbags for each location (exposure treatment) at each site. These exposure treatments (hereafter referred to as soil, surface, and hanging) mimicked litter that was immediately incorporated into soil, that remained on the soil surface, or that remained as dead standing biomass. A portion of litter used in the litterbag experiment was stored in a dark and dry cabinet at room temperature; this litter is referred to as "initial litter."

After 1 year of exposure (the end of September 2007), the litterbags were collected and dried, and the litter inside the bags was weighed. Because of some soil penetration into the buried bags, about 1.5 g of remaining material from each bag (and five 1.5 g samples of initial litter from each site) was used to establish litter mass loss after ignition at 550°C for 6 h. The mass lost with ignition was assumed to represent the organic matter portion of the litter and was used to calculate loss of organic matter (or litter mass loss) during exposure.

Rate of microbial decomposition of the litter (initial or from the litterbags exposed in one of three locations at the field sites) was estimated with a laboratory microcosm experiment. Topsoil (0–4 cm depth) was collected from both sites (when the litterbags were collected), passed through a 2 mm sieve, and stored in a refrigerator for 2 weeks. The soil, litter, and water were mixed and placed in 250 ml glass bottles, hereafter referred to as microcosms (5 g of soil, 1 g of litter, and 2 ml of water per microcosm). The litter added to each microcosm came from one of the litterbags collected from the field (30 microcosms) or from the initial litter (five microcosms per site), giving 40 bottles in total. Each bottle also received small vial with 3 ml of 1 M NaOH, and bottles were sealed to prevent gas exchange and incubated at 20°C for 3 days. After incubation, CO_2 trapped by the NaOH was determined by titration by 0.05 M NaOH with BaCl addition.

Remaining litter from three randomly chosen litterbags from each treatment and site as well as three replicates of initial litter (about 1 g each) from each site was separately ground with a Mixer mill MM 200 (Reich, Germany). This ground material was used to determine C and N content with a CN 2100 soil analyzer (Thermoquest, Italy) and was then used for pyrolysis (TMAH-Py-GC MS). The remaining ground material was pooled to yield one replicate for each combination of site and treatment; this material was used for ^{13}C NMR.

TMAH-Py-GC MS analyses were performed as previously described (Sampedro et al. 2009). Briefly, 1 mg samples of ground litter were treated with an excess of tetramethylammonium hydroxide (25% aqueous solution), placed on Wolfram wire spirals, and then dried in a desiccator overnight at room temperature.

Pyrolysis was performed with a PYR-01 pyrolyzer (Labio, Czech Republic). Pyrolysis was performed directly in the injector of a GC/MS system (Varian 3400/Finnigan ITS 40 ion trap detector). The GC instrument was equipped with a split injector (split ratio 1/40); an HP-5 column was used for separation (30 m, inner diameter 0.25 mm, 0.25 mm film thickness); and the carrier gas was helium (1 ml min^{-1}). The temperature program started at 45°C and the oven was heated to 240°C at a rate of 5°C min^{-1}. The detector delay time was 2 min. The injector and transfer line temperature was set to 240°C. Mass spectra were recorded at 1 scan s^{-1} under an electron impact at 70 eV, mass range 50–450 amu. Pyrolysis products were identified both by comparing mass spectra with data in the NIST02 library and by interpreting the fragmentation pattern. Values presented are the means of triplicate runs, and the percentages of pyrolysis products were calculated from the relative areas of the peaks after recalculation according to the exact weight of samples. Reproducibility of the sample introduction exceeded 95%. The individual chromatograms were integrated, and the peaks representing lignin-related structures were used for PCA analysis for p-hydroxyphenyl, guaiacyl (3-methoxy-4-hydroxyphenyl), and syringyl (3,5-dimethoxy-4-hydroxyphenyl) derivatives.

NMR spectra were measured on fine grounded material, with a Bruker Avance 500 WB/US NMR spectrometer (Karlsruhe, Germany, 2003) in a 4 mm ZrO_2 rotor. Magic angle spinning (MAS) speed was 9 kHz in all cases, with a nutation frequency of $B_1(^1H)$ and $B_1(^{13}C)$ fields for cross-polarization $\omega_1/2\pi = 62.5$ kHz. Repetition delay and number of scans was 4 s and 1024, respectively. TPPM (two-

pulse phase-modulated) decoupling was applied during evolution and both detection periods. The phase modulation angle was 15°, and the flip-pulse length was 4.8–4.9 μs. Applied nutation frequency of $B_1(^1H)$ field was $\omega_1/2\pi = 89.3$ kHz. ^{13}C scale was calibrated with glycine as the external standard (176.03 ppm; low-field carbonyl signal).

Resulting ^{13}C NMR spectra were used to quantify three basic fractions (aromatic, alifatic, and polysacharidic) according to Wilson (1987) and Keeler and Maciel (2000), and based on the area of the appropriate peak relative to the total area.

Data analysis

For individual treatments within each site, litter mass loss (expressed as a percentage) and C:N from field-exposed litterbags, and soil respiration data from the laboratory microcosms were compared by a one-way ANOVA (analysis of variance) followed by an LSD post hoc test which can indicated differences between individual means. Additionally, a two-way ANOVA was applied to determine the effect of both site and treatment. For NMR results, only a one-way ANOVA was used to compare treatments using data from both sites pooled. Computation was done using SPSS 10.0.

Principal component analysis was used to describe the relationship of individual aromatic compounds to particular treatments and to light and soil. Light and soil were included as dummy variables and were coded as 1 and 0, 0.5 and 0.5, and 0 and 1 for soil, surface, and hanging treatments, respectively. For the initial litter, soil and light were coded as 0 and 0. Computation was done using CANOCO 4.0 software (Ter Braak and Šmilauer 1998).

Results

Based on one-way ANOVAs, in which each site was analyzed separately, the N content was lower in litter at the beginning of the experiment (initial litter) than in litter exposed in the field in litterbags at the young site (Table 1). At the old site, the N content was lower in the initial litter and in litter in the hanging treatment than in litter in the soil or surface treatments (Table 1). At both the young and old sites, the C content tended to be higher in the initial litter than in the litter exposed in the field (Table 1). At both the young and old sites, the C:N ratio was higher in the initial litter than in the soil or surface treatments (Table 1). The C:N ratio also was higher in the initial litter than in the hanging treatment at the old site but not at the young site.

The C:N ratio was analyzed further with a two-way ANOVA, which indicated no significant effect of site ($F = 1.5$, ns) but a significant effect of treatment ($F = 25.4$, $P > 0.0001$). In this analysis, the C:N ratio was higher in the initial litter than in the three treatments and was higher in the hanging treatment than in the soil or surface treatments.

Based on one-way ANOVAs, litter mass loss at the old site was greatest in the soil treatment, intermediate in the surface treatment, and lowest in the hanging treatment (Table 2). Although litter mass loss tended to be greater in the soil than in the other two treatments at the young site, mass loss did not statistically differ between soil and hanging treatments or between hanging and surface treatments (Table 2). Two-way ANOVA indicate no significant effect of site ($F = 0.15$, ns) but significant effect of treatment ($F = 16.4$, $P > 0.0001$). Post hock test show that soil exposed litter decomposed fasted than bot hanging litter and litter on soil surface without significant differences between latter two. There was significant interaction between treatment and site ($F = 3.5$, $P = 0.0469$, $df = 3$) connected with inverse behavior of hanging and soil surface treatments in old and young sites.

Based on one-way ANOVAs for each site, decomposition (as measured by release of CO_2 from the soil in the laboratory microcosms) at both sites was greater with litter that had been hanging than with initial litter or litter that had been buried in soil or placed on the soil surface (Fig. 1). The same result was obtained with a two-way ANOVA, in which both site and treatment were significant ($F = 78.4$ and 22.4, for site and treatment, respectively, and $P > 0.0001$ and $df = 32$ in both cases). Decomposition was significantly greater in soil from the older than the younger site, and was greater with litter that had been hanging than with initial litter or litter that had been buried in soil or placed on the soil surface (LSD post hoc test $P > 0.05$).

Th effect of light and soil burial on individual aromatic derivatives of pyrolysis was studied using principal component analysis (PCA) (Fig. 2). To read relationship between individual environmental

Table 1 The changes in the carbon and nitrogen contents of *Calamagrostis epigeios*

	Young site			Old site		
Litter treatment	N (%)	C (%)	C:N	N (%)	C (%)	C:A
Initial	0.44 ± 0.01a	43.79 ± 0.75c	98.6 ± 3.1a	0.47 ± 0.10a	43.58 ± 0.36b	97.5 ± 19.6a
Surface	0.72 ± 0.17b	37.30 ± 4.23a	56.3 ± 19.0b	0.81 ± 0.13b	40.17 ± 0.47b	50.8 ± 8.7bc
Soil	0.64 ± 0.01b	39.40 ± 0.89ab	61.7 ± 2.6b	0.80 ± 0.03b	36.46 ± 3.72a	45.6 ± 6.2c
Hanging	0.63 ± 0.04b	42.52 ± 0.30bc	67.4 ± 5.0a	0.62 ± 0.01a	42.34 ± 0.01b	68.7 ± 0.6b

C N content and ratio of dead standing biomass at the initial stage (Initial) and after 1 year exposure on the soil surface (Surface), buried in the soil (Soil), or hanging above the soil (Hanging) at a young and old site. Values are the means (±SE) of five replicates. Values in a column followed by the same letter are not statistically different (one-way ANOVA, LSD post hoc test $P < 0.05$)

Table 2 The changes in litter mass of *Calamagrostis epigeios*

Litter treatment	Young site	Old site
Soil	40.4 ± 10.8a	44.4 ± 3.8a
Surface	22.4 ± 5.2b	28.8 ± 4.6b
Hanging	27.5 ± 11.1ab	16.1 ± 2.3c

Mass loss (percent) of dead standing biomass after 1 year of exposure in litterbags buried in the soil (soil), on the soil surface (surface), or hanging above the soil (hanging) at a young and old site. Values are the means (±SE) of five replicates. Values in a column followed by the same letter are not statistically different (one-way ANOVA, LSD post hoc test $P < 0.05$)

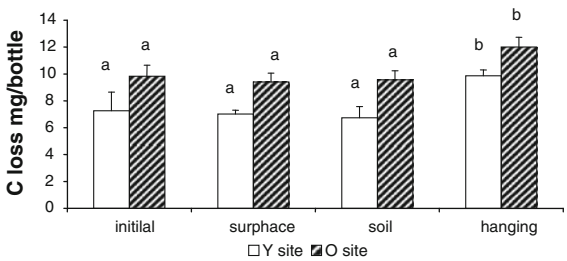

Fig. 1 Respiration of *Calamagrostis epigeios* litter. Soil respiration in laboratory microcosms containing soil from young and old sites and litter that had not been exposed in the field (Initial) or had been exposed in litterbags on the soil surface (Surface), buried in the soil (Soil), or hanging in the air above the soil (Hanging). *Bars* with the same fill pattern and marked by the same letter are not statistically different (ANOVA, LSD post hoc test $P < 0.05$)

factors and individual derivatives on PCA diagram, angle between them is important. More narrow is angle between environmental factor and particular derivative, more stronger is positive relationships between them. Similarly more obtuse angle means stronger negative relationship. Right angle between particular derivatives and environmental factor means no relationship. For examples 2 methoxi 4 vinilphenol is strongly negatively affected by soil burial (arrows goes just opposite to soil arrow), and in inserted table one can see that its occurrence is much lover in soil treatment than in initial litter or hanging treatment. On the other hand 3.4-dimethoxibenzaldehide show strong negative relationships with light, and inserted table shows that its occurrence in light exposed hanging treatments is much lower than in other treatment (Fig. 2) PCA showed that most derivatives were depleted in litter that was buried in soil. Some deviates, particularly trimethoxy benzaldehyde and trimethoxy benzoic acid, were depleted in litter that was placed on the soil surface or that was hanging above the soil surface (Fig. 2).

When NMR was used to determine the composition of litter buried in soil relative to the initial litter, there was a reduction of peaks in 60–90 and 90–110 ppm, which are characteristic of polysaccharides, and an increase of peaks in 110–160 ppm, which is characteristic of aromatic compounds (Fig. 3). This was confirmed by relative areas of peaks associated with the major group of compounds. In litter buried in soil relative to the initial litter, the percentage of polysaccharides significantly decreased while the percentages of aliphatic and aromatic compounds significantly increased (Table 3). In contrast, NMR data did not indicate a change in composition of litter that was placed on the soil surface or that was hung above the soil (Fig. 3, Table 3).

Discussion

After 1 year of exposure in the field, litter that had been hanging in the air decomposed faster (supported greater soil respiration in laboratory microcosms) than

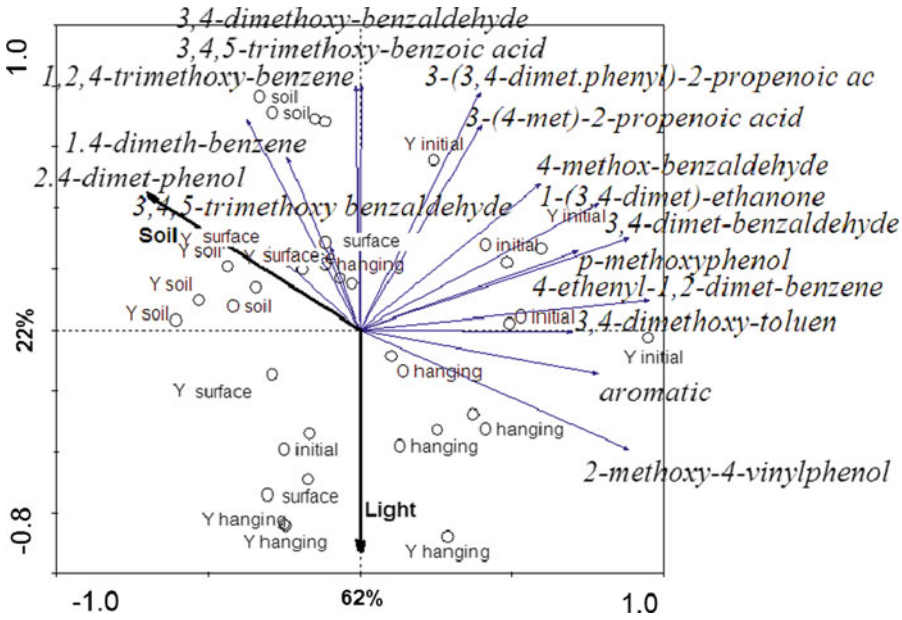

Fig. 2 Principal component analysis of aromatic derivatives of *Calamagrostie epigeios* litter. Litter had not been exposed in the field (Initial) or had been exposed in litterbags for 1 year on the soil surface (surface), buried in the soil (soil), or hanging in the air above the soil (hanging) at a young site (Y) or an old site (O). Positions of individual derivatives are marked by *arrows*; *bold arrows* indicate influence of environmental factors, soil or light. Inserted table show peaks height of individual derivatives, standardized according to sample mass

plot	Young				Old			
treatment	initial	hanging	surface	soil	initial	hanging	surface	soil
2 methoxi 4 vinilphenol	31 ±11	25 ±8	9 ±0	3 ±1	26 ±9	20 ±14	17 ±2	5 ±2
3.4-dimethoxibenzaldehide	14 ±1	8 ±1	12 ±0	15 ±1	13 ±1	9 ±1	11 ±1	15 ±2

litter that had been buried in the soil or placed on the soil surface. The litter that had been hanging in the air also decomposed faster than the initial litter. This is in agreement with previous reports that sun exposure increases the rate litter decomposition (Gallo et al. 2006; Austin and Vivanco 2006). Hanging litter had a lower C:N ratio than the initial litter, which might explain its faster rate of decomposition when subsequently placed in the soil (Aerts 1997). In the other treatments, however, similar or even greater decreases in the C:N ratio were not followed by increases in decomposition, and so we conclude that change in C:N ratio was not a major factor causing an increase in decomposability of hanging litter.

Based on NMR, litter buried in soil had reduced levels of polysaccharides, which is in agreement with the literature (Parfitt and Newman 2000; Sjoberg et al. 2004) and which indicates the preferential decomposition of polysaccharides and preservation of lignin in buried litter. In contrast, hanging litter and litter on the soil surface did not show preferential decomposition of polysaccharides. Although this might be explained by a lack of decomposition, some mass loss was detected (Table 2), and we therefore conclude that aromatic and aliphatic components decomposed at the same speed as polysaccharides when litter was hanging in the air or on the soil surface. In other words, sun exposure caused lignin to be decomposed faster when litter was on or above the soil than when litter was in the soil. Similar observations were made in a desert ecosystem (Day et al. 2007).

Moreover, pyrolysis indicated that trimethoxy groups representing syringyl derivatives decomposed most in the presence of light. Hence, we conclude that photochemical degradation of the most resistant component of litter, lignin, is the best explanation for the increased decomposability of the hanging litter.

Thermolysis may be another potential explanation but we do not thing temperatures are so extreme that thermolysis would be important. Even if thermolysis would be the case, it would be much more likely to occur in soil surface, where the highest temperature fluctuation are usually found, and not in hanging material.

The detection of syringyl derivatives after thermochemolysis of grass litter was surprising because these structures are representative of hardwood,

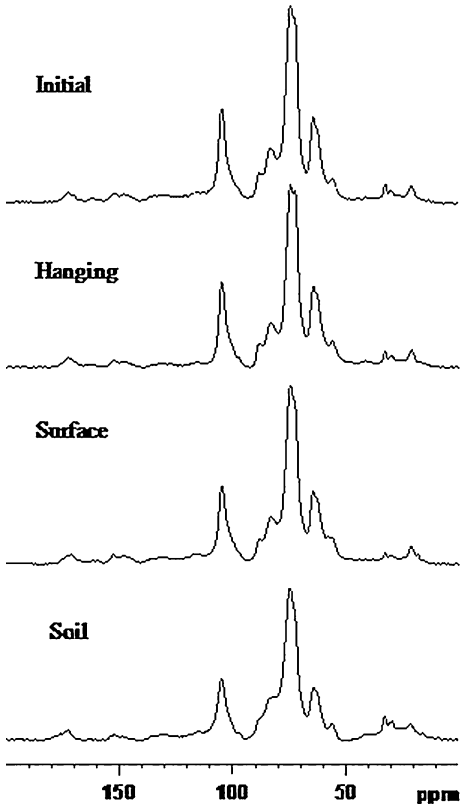

Fig. 3 ^{13}C NMR spectra of *Calamagrostie epigeios* litter. Litter had not been exposed in the field (Initial) or had been exposed for 1 year in litterbags hanging in the air above the soil (Hanging), on the soil surface (Surface), or buried in the soil (Soil)

angiosperm lignin (Simoneit et al. 1993; Martinez et al. 2005). These compounds, however, have also been found in humus from a field without trees (Gryndler et al. 2009); the authors considered fungi to be the source of the syringyl structures, but in our case a more likely explanation is that the grass lignin contained a low amount of syringyls.

The preferential decomposition of syringyl lignin by light is possible because of the predominance of ether inter unit C_4 linkages comparing to guayacyl lignin that can contain higher portion of C–C bonds at C_5. In the case of syringyl unit, this position is occupied by methoxy group. Guayacyl C–C bonds at C_5 lead to a higher degree of condensation resulting generally in increased resistance of guayacyl lignin units. The same degradation pattern of wood lignin by fungi also was found by other authors (Steffen et al. 2007).

Table 3 ^{13}C NMR spectra in *Calanagrostis epigeios* litter

Litter treatment	Compounds and site					
	Polysaccharides		Aliphatic		Aromatic	
	Young	Old	Young	Old	Young	Old
Initial	83.8	90.4a	9.7	4.1a	6.5	5.5a
Hanging	87.3	87.8a	6.5	7.1a	6.2	5.1a
Surface	89.0	90.4a	6.8	4.2a	4.2	5.1a
Soil	71.6	77.4b	18.2	14.5b	10.2	8.1b

Percentage of aromatic aliphatic and polysaccharide compounds in litter after 1 year of exposure in litterbags buried in the soil (soil), on the soil surface (surface), or hanging above the soil (hanging) at a young and old site. Values for a compound category followed by the same letter are not statistically different (ANOVA, LSD post hoc test $P < 0.05$, individual sites used as replicates)

Our study suggests that lignin breakdown resulting from solar radiation of litter before it is incorporated into soil can increase the subsequent decomposition of litter in the soil. Here it should be underlined that join action of microflora and phototegradation takes place in this process rather than photodegradation per se. Lignin decomposition could hardly explain the total changes in the lignino-celluloses material observed in hanging bags. However, possible abiotic decomposition of syringyl and other parts of lignin could lead to release easily bioavailable carbon in celluloses and hemicelluloses. In fact the same strategy is used by ligninolytic fungi, that co-metabolically degrade aromatic structures in lignin, in order to gain an access to polysaccharide parts of wood (Steffen et al. 2007).

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