Controls of litter chemistry over early lignin decomposition in beech litter

Lukas Kohl[1], Wolfgang Wanek[1], Katharina Keiblinger[2,3], Sonja Leitner[1,3], Maria Mooshammer[1], Ieda Hämmerle[1], Lucia Fuchslueger[1], Jörg Schnecker[1], Sophie Zechmeister-Boltenstern[2,3], Andreas Richter[1],

1 Department of Chemical Ecology and Ecosystem Research, University of Vienna, Althanstraße 14, A-1090 Vienna, Austria

2 ederal Research and Training Centre for Forests, Natural Hazards and Landscape, Department of Soil Biology, Seckendorff-Gudent-Weg 8, A-1131 Vienna, Austria

3 Current adress: Institute for Soil Science, University of Natural Resources and Life Sciences, Peter Jordan-Straße 82, A-1190, Vienna, Austria

∗ **E-mail: Corresponding author@institute.edu**

Abstract

Lignin is considered the most recalcitrant component of plant litter, accumulated during early decomposition and degraded only during late decomposition stages when its concentration limits litter decomposition rates. A recent study based on the more specific methods challenges this concept, reporting highest lignin decomposition rates during early litter decomposition. Until now, no further studies exploring early lignin decomposition were published, and its potential controls remain unknown.

We follow lignin and carbohydrate decomposition during early litter decay with analytical pyrolysis in a climate-chamber decomposition experiment, focusing on resource control over microbial carbon substrate preferences. Beech litter with different C:N:P stoichiometry but identical initial microbial communities was incubated to identify the control of litter chemistry on the developing microbial community and its decomposition activity.

During the first 6 month fundamental differences in lignin degrading activities were found between sites. Lignin discrimination in litter decomposition ranges from insignificant amounts of lignin decomposed to lignin decomposition at the same rate bulk litter, leading to different niveaus of lignin accumulation. Between 6 and 15 month, no lignin discrimination was found, but different lignin contents aquired earlier reminded.

[results]

Introduction

Plant litter biomass is dominated by macromolecular compounds. Together, lignin, carbohydrate and protein polymers make up xx% of litter dry mass, while leachable substances in litter account for only xx %.

Litter decomposition models [lit] follow the concept that macromolecules in litter form three independent carbon pools of increasing recalcitrance attributed to (1) soluble compounds, (2) cellulose and hemicelluloses and (3) lignin. During decomposition, soluble compounds are most accessible to microbes and consumed first, followed by carbohydrates (i.e. cellulose). Lignin can be decomposed only by specialists and is not degraded until accumulated to a certain, critical level when it inhibits the degradation of less recalcitrant compounds [1–3].[1] Most common methods to quantify these carbon pools gravimatrically determine cellulose, hemi-celluloses and lignin contents after sequential extractions with selective solvents. These methods were repeatedly criticize as unspecific for lignin determination [4]. When analyzed with alternative methods (NMR, CuO-oxidation, Pyrolysis-GC/MS), extracted lignin fractions contain many other than the proclaimed substances. (i.e. [5] [2].

Recent studies based on specific methods to determine litter lignin content (CuO - oxidation, Pyrolysis-GC/MS, NMR) question the assumed intrinsic recalcitrance of lignin. Experiments using isotope labeling used to calculate mean residence times for lignin in soils and litter/soil mixtures in both laboratory and outdoor incubation reported lignin residence times no longer than that of other carbon compounds or bulk SOM [6, 7][3].

For leaf litter, lignin depletion during early decomposition and decreasing lignin decomposition rates were recently by [8]. Based on their results, the authors proposed a new concept for lignin degradation in which fastest lignin degradation occurs during early litter decomposition. Lignin decomposition during late decomposition is limited by (dissolved organic) carbon availability, a pulsed input of labile carbon (during litterfall or experimental manipulations like drying and rewetting) causes higher lignin degradation rates for a limited time period. The authors also suggest, that lignin decomposition is hampered in late decomposition stage, when labile (soluble) carbon source are limited.

[8] do not elaborate the of stoecheometric constrains on lignin decomposition. In isolated lignin fractions from fresh beech litter, N contents twice as high as bulk litter were found [4]. It was argued that, while yielding little C and energy, lignin decomposition makes occluded cell wall protein accessable to decomposers, and

[1] more lit.
[2] [lit CuO], lit[Pyr]
[3] more lit?
[4] cit

lignin decompostion is driven not by carbon but by nitrogen demand ("Nitrogen mining theory", [9]).

Nitrogen fertilization experiments on litter and soils indicate a that litter N contents are important controls of lignin degradation: N addition increases mass loss rates in low-lignin litter while slowing down decomposition in lignin-rich litter [10]. High nitrogen levels were reported to inhibit lignolytic enzyme in forest soils [11]. Cellulose triggered higher priming effect in fertilized than in unfertilized soils indicating that the mineralization of recalcitrant C is controlled by an interaction of labile C and N availability [12].

N fertilization has different effects on litter decomposition than different nutrient levels in litter, as leaf litter N is stored in protein and lignin structures and not directly availeable to microorganisms. N-fertilization experiments can simulate increased N-deposition rates. To simulate variations litter C:N ratios, our approach is preferable, because potential variations in litter N content occur in complex substrates.

In this study we analyze samples from climate-chamber incubated beech litter varying in N and P content with pyrolysis-GC/MS (pyr-GC/MS). The experiment was designed to study the effect of resource stroichiometry on microbial decomposition, exclude decomposing fauna and keep climatic conditions constant.

We test several proposed mechanisms, by which lignin degradation is affected by litter chemistry:

(1) High lignin contents inhibit the degradation of other carbon sources, and trigger lignin decomposition [1].

(2) Lignin degradation is inhibited, when the availability of cofactors for oxidative enzymes (mainly Mn) is low [5].

(3) Lignin degradation is directed to degrade N, therefore less lignin is decomposed in litter with narrow C:N ratios where more lignin is available [9].

-(4) The availability of dissolved carbon limits lignin decomposition, and lignin decomposition is inhibited when DOC content becomes rate limiting (and therefore correlated to) carbon respiration rates [8].

Results

Mass loss, respiration and extractable organic carbon

Litter mass loss was not significant after 2 weeks and 3 month, significant for 2 litter types after 6 month. After 15 month, litter mass loss was significant for all litter types, and strongly correlated to litter N content (R=0.794, p=***). Detailed results were reported by [13]. After 15 month, between 5 and 12% of the initial

[5] cit

dry mass was lost. This is less than reported in litter decomposition studies on other species, but in a similar range as recently reported for beech litter from an in-situ litterbag-study [14] .

Highest respiration rates were measured after 14 days incubation (150-350 µg CO_2-C d-1 g-1 litter-C), dropped to rates between between 75 and 100 µg CO_2-C d-1 g-1 litter-C after 97 days. After 181 and 375 days, respiration rates for AK and OS further decreased, while SW and KL show a second maximal respiration after 181 days.

Soluble organic carbon content decreased between the first three harvests (14 to 181 days), to strongly increase after 475 days (0.1 to 0.7 mg C g $^{-1}$ d.w. were found after 14, 97 and 181 days, and increased to amounts between 1.5 and 4 mg/g after 375 days. After 14 and 97 days, the highest C content was found in SW litter followed by AK (see fig. **??**. DOC content was loosely correlated to litter N content after 14 ($R=0.69$, $p<0.001$) and 97 days ($R = 0.65$, $p =<0.01$), they were strictly correlated after 181 days ($R = 0.85$, $p=<0.001$) and 375 days ($R=0.90$, $p=<0.001$).

Microbial biomass abundance and stoichiometry

Microbial biomass contents ranged from 0.5 to 6 mg C, 0.05 to 5.5mg N and 0.05 to 3.5 mg P per g litter (d.w.). In KL and OS biomass buildup reaches a plateau after 3 month, AK and SW show further growth reaching a maximum of microbial C and N contents after 6 month (AK also for P). Microbial C:N ratios measured range between 1:6 and 1:18, C:P ratios between 1:8 abd 1:35, and N:P ratios between 1:0.5 and 1:3.5. Microbial C:N ratios (Fig. 1).

Litter microbial biomass is homeostatic during the first 6 month (no or marginally negative correlation between microbial stoichiometry and litter stoichiometry) [13], but not after 15 month, when all three ratios show correlations (R 0.53 - 0.64, all $p <0.002$, $H_{C:N}=2.01$, $H_{C:P}=1.68$, $H_{N:P}=2.29$). Microbial C:N ratios are tighly constrained after 3 (1:14.5 - 1:18.2) and 6 month (1:6.9 - 1:9.0), but significantly different between the two time points. C:P and N:P ratios are less constrained, with the highest variance between litter from different sites after 3 month incubation (Fig. 1).

Potential enzyme activities

Absolute potential enzyme activities were correlated to litter N, respiration and other other decomposition processes (all $R >0.8$, $p <0.001$). For all enzymes and at all time points, SW showed the highest and AK the lowest activity. Cellulase was below detecten limit after 14 days, oxidatitve enzymes after 15 month. Cellulases activity is highest after 3 month and decreases between 97 and 181 days. Peroxidase and Peroxidase activities reach their maximum after 181 (fig. 2). After between 6 and 15 month, cellulase activity strongly increased. After 475 days, the activity of oxidative enzymes was below the detection limit [data not shown]

The ratio between the potential activities of cellulases and oxidative enzymes was lowest for AK at all time points. Microbial communities in AK litter invest more energy and nitrogen into degrading lignin and less into degrading carbohydrates than other litter types. (fig. 2)

Pyrolysis-GC/MS and Lignin content

Litter pyrolysis products and different sites are reported in detail elsewhere (Kohl, in preparation). We found only minor changes during pyrograms during decomposition, differences between sites were were small but well preserved during decomposition. The high similarity allowed tracind small changes in lignin and carbohydrate abundance during decomposition.

When measured by pyr-GC/MS, lignin derrived compounds make up between 29 and 31 %TIC in the initial litter, with an increase of up to 3 %TIC over the first 3 month. Carbohydrate derrived pyrolysis products account for 26 to 29 %TIC in initial litter and decrease by up to 2.6 % during litter decomposition. Carbohydrate depletion and lignin accumulation were coorelated ($R = 0.47$, $p < 0.01$) in all samples measured. The initial (pyrolysis-) LCI index (applied to excludes influences of changes in the abundance of other pyrolysis products) ranges between 0.517 and 0.533. During decomposition, it increases by up to 8.7% of the initial value, with SW showing the highest and KL the lowest increase. This increase almost completely occurs over the first 6 month, with insignificant changes in both directions between 6 and 15 month incubation. Figure **??**[6] shows changes in the relative abundance of in pyrolysis products versus incubation time and accumulated respiration. Lignin to carbohydrate ratios in a similar range (increasing from 0.565 to 0.588 over 24 month) were reported for in situ oak litter decomposition by [15] using thermochemolysis. [7]

During the first 6 month of litter decomposition, between one and 6% of the initial lignin pool and between 4 and 17% of the initial carbohydrate pool were degraded. Lignin decomposition was highest in AK and KL litter, while KL and SW decomposed the highest part of their carbohydrate pools. Lignin discimination (compared to carbohydrates) was highest in SW and lowest in AK litter. In AK litter, lignin molecules were 50% more likely to be decomposed than carbohydrates, while in SW litter carbohydrates were 10 times more likely to be decomposed (fig. 4).

Between 6 and 15 month, no further discrimination occurs, lignin and carbohydrate are degraded at the

[6] check fig.

[7] I converted the L:C ratio stated by Snajdr to L/(L+C). This demonstrates a surprising coherence between quite different analytical methods, different peaks analyzed.

same rates and their content in pyrograms remains constant (fig. ??).

Correlation between litter chemistry, lignin decomposition, other processes

Table 2 provides linear regressions found between lignin and carbohydrate degradation, litter chemistry, microbial biomass and decomposition processes after 6 month incubation including data presented by [13] and [16]. We found The lignin to cellulose degradation ratio was correlated to phenoloxidase to cellulase and peroxidase to cellulase enzymatic activity ratios (R=0.729 and R=0.863, p=?). Lignin accumulation and carbohydrate depletion were found to increase with enzymatic activities measured (including lignolytic enzymes) N, and P gross depolymerization rates but not with glucan depolymerization.

While carbohydrate degradation and depletion was correlated litter N content, C:N ratio and C:N imbalances. lignin degradation and accumulation were correlated to litter P, litter C:P and N:P ratios, C:P and N:P imbalances and extractable organic C and PO_4. High lignin accumulation and carbohydrate depletion were also connected to wide C:N, C:P and N:P ratios.

Discussion

Our experimental approach allows to single out litter quality and it's influence on the microbial decomposer community as the only source of the differences in decomposition processes found, while we can excluding fauna, climate and the initial microbial community as controlling factors. By exploiting intra-specific differences in beech litter stoichiometry, we were able to minimize differences in the composition of initial litter while exploring the effect of different litter nutrient contents on lignin and carbohydrate decomposition. Therefore, we can attribute different levels of carbohydrate-over-lignin preference encountered to the intrinsic qualities of different litter types used.

Contradicting traditional concepts of litter decomposition, our results demonstrate that relevant amounts of lignin are degraded during the the first 6 month of litter decomposition. Lignin decomposition rates found during this early stage depend on litter quality and ranges from non-significant amounts decomposed to degradation at bulk carbon mineralization rates (i.e. no discrimination against lignin). We can therefore confirm that early lignin decomposition rates are by far underestimated, as proposed by [8], with complementary analytic approach. Contrasting their results, we found no significant decreases in lignin contents and constant or increasing lignin degradation rates during early decomposition. Additionally, we found a change in controls over lignin discrimination after this initial period. While the preference of carbohydrate over lignin decomposition was controlled by litter chemistry over the first 6 month, all components of litter were degraded at similar rates thereafter.

In the search of the control over this early lignin decomposision, we can descard hypothesis (1) and (2): Differences in initial lignin contents were below 10%, and lignin contents of sites with high initial lignin decomposition rates were not higher than that of sites with low rates. Mn and Fe contents strongly vary between litter collected at different sites, but both Mn and Fe contents are lowest in the litter with the highest lignin decomposition (AK, see tab. 1). Low contents of these Elements would explain inhibited, not enhance lignin decomposition. Hypothesis (3) can be excluded because we found highest amounts of soluble carbon in litter from two different sites who show the highest and the lowest lignin degradation.

We did find strong evidence that C:N:P stoichiometric ratios wield key control over the extend of lignin accumulation during this first decomposition stage. While carbohydrate decomposition was correlated to litter N contents (as were a majority of decomposition processes found, from respiration to enzymatic activities), relative decomposition rates of Lignin were strictly correlated to C:P imbalances and a number of P pools analyzed. Correlation was highest when lignin decomposition was compared to resource:consumer C:P ratios.

Strong evidence exists that labile carbon and nitrogen availability control (late) lignin decomposition. Cultivation studies show that lignin decomposition in fungi is triggered by nitrogen starvation, and that lignin does not provide sufficient energy to maintain the decomposer's metabolism without the use of other carbon sources [8]. Lignin decomposition was found in wild-type A. thaliana litter, but not in a low-cellulose mutant during 12 month incubation in a boreal forest [17]. However, a stimulation of lignin decomposition by a high P imbalance or a delay of lignin decomposition under high P availability, as indicated by the high correlation to P pools we found, was not reported yet. In the N- and P- co-limited situation during early litter decomposition, in which lignin is degraded either to access additional nutrients or as a mean to use a C surplus in a N/P co-limited situation.

[17] also suggests that lignin decomposition might be interpreted a k-strategy used by microbes to be able to colonize more lignin-rich and nutrient-poor substrates. Low nutrient availability might favor this strategy, as the high P- demands of a fast growing microbial community can not be met under such conditions.

While we found different levels of lignin degredation during the first 6 month, lignin contents remained constant in all litter types between 6 and 15 month. This indicates that lignin is not degraded slower than other litter compounds, but differences in lignin contents acquired during the first 6 month remain in place.

[8] citation

The controls which lead to differences in the extend of lignin discrimination over the first six month are no longer predominant between 6 and 15 month.

This change in decomposition dynamics corresponds to change in soluble carbon. While during the first 3 month, extractable carbon contents were not or to a lesser extend correlated to litter N, soluble carbon is strictly correlated to litter N and actual respiration after 6 and 15 month[9]. [8] suggests a change in decomposition dynamics after 100 to 200 days of incubation, after which lignin decomposition rates decrease due to lack of labile carbon. They also report a correlation between respiration rates and extractable carbon after this change. The authors interprets this correlation as carbon limited respiration, and suggest that lignin decomposition is inhibited under such a limitation. We can confirm the correlation between extractable carbon and respiration after 181 days, but not the inhibition of lignin decomposition. Also, we found that both respiration and the production of soluble carbon are controled by litter N content. The process of degrading macromolecular compounds into soluble molecules is conducted by extracellular enzymes and is therefore N intensive that the mineralization of labile carbon, de-polymerization is the point in the decomposition process where a N limitation would be most likely to become effective.

Another notable change occurs in the homeostasis of the microbial community. While is was strictly homeostatic during the first 6 month, substrate stoichiometry had a minor, but significant influence on microbial stoichiometry after 15 month. Together, those changes indicate that the microbial community is able to compensate for differences in substrate quality (on the expense of community growth and overall decomposition speed) and can select preferred compounds during the first 6 month. However, this compensation is limited and imbalances can not be upheld at the same intensity after the first 200 days.

Our results further question the concept that lignin decomposition is inhibited until late decomposition. While traditional litter decomposition concepts locate lignin decomposition only during late decomposition, we find substancial amounts of lignin decomposed over the first six month. The extend, to which lignin is decomposed, was controlled by litter chemistry over the first 6 month. However, we did not find lignin decomposition rates controlled by litter quality thereafter. Soluble carbon contents were not restrictive to lignin decomposition.

While carbohydrate decomposition was stimulated by high N contents, early lignin decomposition rates were highly correlated C:P ratio and resource:consumer imbalances. High lignin contents accumulated during this stages remained in place during later decomposition. For further studies, this raises the question, to which extend late decomposition is influenced by this early, stoichiometry-controlled accumulation of recalcitrant

[9] stats

compounds.

Material and methods

Litter decomposition experiment

A detailed description of our litter decomposition experiment was published in [18]. Briefly, beech litter was collected at four different sites in Austria (Achenkirch (AK), Klausenleopoldsdorf(KL), Ossiach(OS), and Schottenwald(SW); refered to as litter types) in October 2008. Litter was cut to pieces of approximately 0.25cm^2, homogenized, sterilized twice by gamma[10] radiation (35 kGy, 7 days between irradiations) and inoculated (1.5% w/w) with a mixture of litter and soil to assure that all litter types share the same initial microbial community. From each type, four samples of litter were taken after inoculation and stored dried at room temperature. Samples of 60g litter (fresh weight) were incubated at 15 °C and 60% water content in mesocosms for a duration between 2 weeks to 15 month. For each litter type 5 replicas were removed and analyzed after 14, 97, 181 and 475 days.

Litter chemistry as analyzed 14 days after incubation is listed in table 1. C:N ratios between 1:41 and 1:58 and C:P ratios between 1:700 and 1:1300 were found, N:P ratios ranged between 1:15 and 1:30. No significant changes occurred during litter incubation except a slight decrease of the C:N ratio (1:41.8 to 1:37.4) found in the most active litter type (SW) after 15 month. Fe content were more than twice as high for OS (approx. 450 ppm) than for other litter types (approx. 200 ppm). Litter Mn also was highly variable between litter types, ranging between 170 and 2130 ppm. Changes of micro-nutrient concentrations during litter incubation were significant, but in all cases $<$15% of the initial concentration.

Bulk litter, extractable, and microbial biomass nutrient content

To calculate litter mass loss, litter dry mass content was measurement in 5 g litter (fresh weight) after 48 h at 80 °C. Dried litter was ball-milled for further chemical analysis. Litter C and N content were determined using an elemental analyzer (Leco CN2000, Leco Corp., St. Joseph, MI, USA). Litter phosphorus content was measured with ICP-AES (Vista-Pro, Varian, Darmstadt, Germany) after acid digestion [19]).

To determine soluble C, N, and P contents, 1.8g litter (fresh weight) were extracted with 50 ml 0.5M K_2SO_4. Samples were shaken on a reciprocal shaker with the extractant for 30 minutes, filtered with ash-free filters and frozen at -20 °C until analysis. To quantify microbial biomass C, N and P pools, sample were

[10] greek gamma here

extracted under the same conditions after chloroform fumigation. Microbial biomass was determined as the difference between fumigated and non-fumigated extractions [20]. C and N concentration in extracts were determined with a TOC/TN analyzer (TOC-VCPH and TNM, Schimadzu), Phosphorous was determined photometrically.[11]

Substrate to consumer stoichiometric imbalances $X{:}Y_{inbal}$ were calculated as

$$X : Y_{inbal} = \frac{X : Y_{litter}}{X : Y_{microbial}} \tag{1}$$

where X and Y stand for one of the elements C, N, or P.

Microbial Respiration

Respiration was monitored weekly during the entire incubation in mesocosms removed after 6 month and on the last incubation day for all mesocosms using an infrared gas analyzer (IRGA, EGM4 with SRC1, PPSystems, USA). CO2 concentration was measured over 70 seconds and increase per second was calculated based on initial dry mass. Measurements of ambient air were performed before and after each measurement to assess possible leaks or base-line drifts IRGA. Accumulated respiration after 6 month was calculated assuming linear transition between measurements, accumulated respiration after 15 month was estimated from respiration rates after 181 and 475 days.

Enzyme activities

Measurements of potential exo-enzyme activities for cellulases, peroxidases and phenoloxidase were described by [16]. Activities were determined with a series of micro-plate assays based on the hydrolysis of 4-methyl-β-D-cellobioside (cellulase) and L-3,4-dihydroxyphenylalanin (oxidative enzymes). Products of enzyme catalyzed reactions were detected photometrically (oxidative enzymes) or flourometrically (cellulase) [21–23].

Pyrolysis-GC/MS

Pyrolysis-GC/MS was performed with a Pyroprobe 5250 pyrolysis system (CDS Analytical) coupled to a Thermo Trace gas chromatograph and a DSQ II MS detector (both Thermo Scientific) equipped with a carbowax colomn (Supelcowax 10, Sigma-Aldrich).

[11] lit!!

Litter analyzed was sampled immediately after inoculation and after 3, 6, and 15 month incubation. 2-300 µg dried and finely ball-milled litter were heated to 600°C for 10 seconds in helium atmosphere. GC oven temperature was constant at 50 °C for 2 minutes, followed by an increase of 7°C/min to a final temperature of 260 °C, which was held for 15 minutes. The MS detector was set for electron ionization at 70 EV cycling between m/z 20 and 300.[12]

Peaks were assignment was based on NiSt 05 MS library after comparison with reference material measured. 128 peaks were identified and selected for integration due to their hight abundance or diagnostic value, including 28 lignin and 45 carbohydrate derrived substances. For each peak between one and four dominant mass fragments selected for high abundance and specificity were integrated and converted to TIC peak areas by a multiplication with a MS response coefficient [24, 25]. For principal component analysis, unconverted areas were used. Peak areas are stated as % of the sum of all integrated peaks of a sample.

Relative peak areas are different from weight%, but allow tracing of accumulation/depletion of substance classes during decomposition [24].

We use the terms "accumulation" and depletion to refer to changes in litter composition and "degradation" to refer to the amount of lignin and carbohydrates decomposed.

A lignin to carbohydrates index was calculated to measure the ratio between these two substance classes without influences of changes in the abundance of other compounds

$$LCI = \frac{Lignin}{Lignin + Carbohydrates} \tag{2}$$

Accounting for carbon loss, we estimate % lignin and cellulose degraded during decomposition according to equation 3, where TIC_{init} and TIC_{act} stand for initial and actual %TIC area of lignin or cellulose pyrolysis products, C_{init} for the initial amount of C and R_{acc} for the accumulated CO_2-C respired by a mesocosm.

$$\%_{loss} = 100 \cdot \frac{TIC_{init} - TIC_{act}}{TIC_{init}} \cdot \frac{(1 - R_{acc})}{C_{init}} \tag{3}$$

We provide % of initial lignin and carbohydrate pools decomposed, % decomposed per % litter carbon mineralized and the ratio between the twodecomposition rates.

[12] maybe cite other paper for method?

Statistical analysis

All statistical analyses were performed with the software and statistical computing environment R using the package "vegan" [26]. If not mentioned otherwise, results were considered significant when $p < 0.05$. Due to the frequent of variance inhomogenities Welch anova and paired Welch's t-tests with Bonferroni corrected p limits were used. Principal component analysis was performed using vegan function "rda" scaling variables. All correlations refer to Pearson correlations. We calculated correlations between depletion and degradation rates found in this study with litter chemistry parametres and process data reported by [13] and [16].

Acknowledgments

References

1. Berg B, Staaf H (1980) Decomposition rate and chemical changes of Scots pine needle litter. II. Influence of chemical composition. Ecological Bulletins : 373–390.

2. Coûteaux MM, Bottner P, Berg B (1995) Litter decomposition, climate and liter quality. Trends in ecology & evolution (Personal edition) 10: 63–66.

3. Moorhead DL, Sinsabaugh RL (2006) A theoretical model of litter decay and microbial interaction. Ecological Monographs 76: 151–174.

4. Hatfield RD, Romualdo SF (2005) Can Lignin Be Accurately Measured? Crop Science 45: 832–839.

5. Preston CM, Trofymow JA, Sayer BG, Niu J (1997) 13C nuclear magnetic resonance spectroscopy with cross-polarization and magicâĂŞangle spinning investigation of the proximate analysis fractions used to assess litter quality in decomposition studies. Canadian Journal of Botany 75: 1601–1613.

6. Thevenot M, Dignac MF, Rumpel C (2010) Fate of lignins in soils: A review. Soil Biology and Biochemistry 42: 1200–1211.

7. Bol R, Poirier N, Balesdent J, Gleixner G (2009) Molecular turnover time of soil organic matter in particleâĂŘsize fractions of an arable soil. Rapid Communications in Mass Spectrometry 23: 2551–2558.

8. Klotzbücher T, Kaiser K, Guggenberger G, Gatzek C, Kalbitz K (2011) A new conceptual model for the fate of lignin in decomposing plant litter. America 92: 1052–1062.

9. Craine JM, Morrow C, Fierer N (2007) Microbial nitrogen limitation increases decomposition. Ecology 88: 2105–13.

10. Knorr M, Frey S, Curtis P (2005) Nitrogen addition and litter decomposition : A meta-analysis. Ecology 86: 3252–3257.

11. Sinsabaugh RL (2010) Phenol oxidase, peroxidase and organic matter dynamics of soil. Soil Biology and Biochemistry 42: 391–404.

12. Fontaine S, Henault C, Aamor a, Bdioui N, Bloor J, et al. (2011) Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect. Soil Biology and Biochemistry 43: 86–96.

13. Mooshammer M, , the Crew (2011) Marias paper. ecosystems .

14. Kalbitz K, Kaiser K, Bargholz J, Dardenne P (2006) Lignin degradation controls the production of dissolved organic matter in decomposing foliar litter. European Journal of Soil Science 57: 504–516.

15. Snajdr J, Cajthaml T, Valášková V, Merhautová V, Petránková M, et al. (2011) Transformation of Quercus petraea litter: successive changes in litter chemistry are reflected in differential enzyme activity and changes in the microbial community composition. FEMS microbiology ecology 75: 291–303.

16. Leitner S, Wanek W, Wild B, Haemmerle I, Kohl L, et al. (2011) Linking resource quality to decomposition processes: Influence iof litter chemistry and stoichiometry on glucan depolymerization during decomposition of beech (Fagus silvatica L.) litter. Soil Biology and Biochemistry .

17. Talbot JM, Treseder KK (2011) Interactions between lignin, cellulose, and nitrogem drive litter chemistry - decay relationships. Ecology [preprint].

18. Wanek W, Mooshammer M, Blöchl A, Hanreich A, Richter A (2010) Determination of gross rates of amino acid production and immobilization in decomposing leaf litter by a novel N-15 isotope pool dilution technique. Soil Biology and Biochemistry 42: 1293–1302.

19. Henschler G (1988) Analysen im biologischen Material. Weinheim: VCH Verlagsgesellschaft mbH.

20. Schinner (1996) chloroform fumigation method (dummy) .

21. Marx M (2001) A microplate fluorimetric assay for the study of enzyme diversity in soils. Soil Biology and Biochemistry 33: 1633–1640.

22. Sinsabaugh RL (1999) Characterizing soil microbial communities. Standard Soil Methods for Long-Term Ecological Research 2: 318–348.

23. Kaiser C, Koranda M, Kitzler B, Fuchslueger L, Schnecker J, et al. (2010) Belowground carbon allocation by trees drives seasonal patterns of extracellular enzyme activities by altering microbial community composition in a beech forest soil. New Phytologist 187: 843–858.

24. Schellekens J, Buurman P, Pontevedra-Pombal X (2009) Selecting parameters for the environmental interpretation of peat molecular chemistry âĂŞ A pyrolysis-GC/MS study. Organic Geochemistry 40: 678–691.

25. Kuder T, Kruge MA (1998) Preservation of biomolecules in sub-fossil plants from raised peat bogs âĂŤ a potential paleoenvironmental proxy. Organic Geochemistry 29: 1355–1368.

26. Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara R, et al. (2011). vegan: Community Ecology Package. R packge version 1.17-9. URL `http://cran.r-project.org/package=vegan`.

Figure Legends

Tables

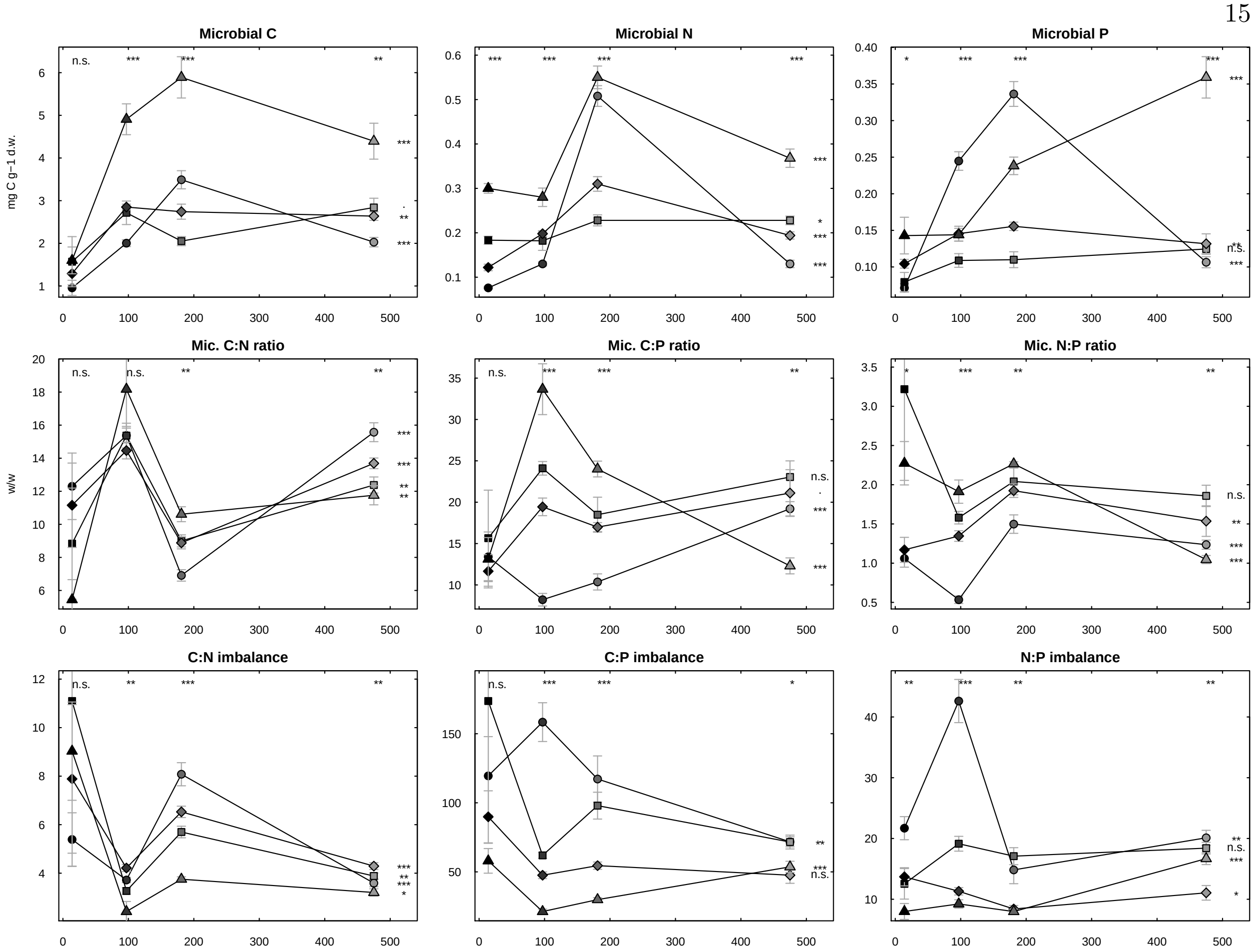


Figure 1. Microbial biomassm, microbial stoichiometry and resource:consumer stoichiometric imbalance. Error bars indicate standard errors (n=5).

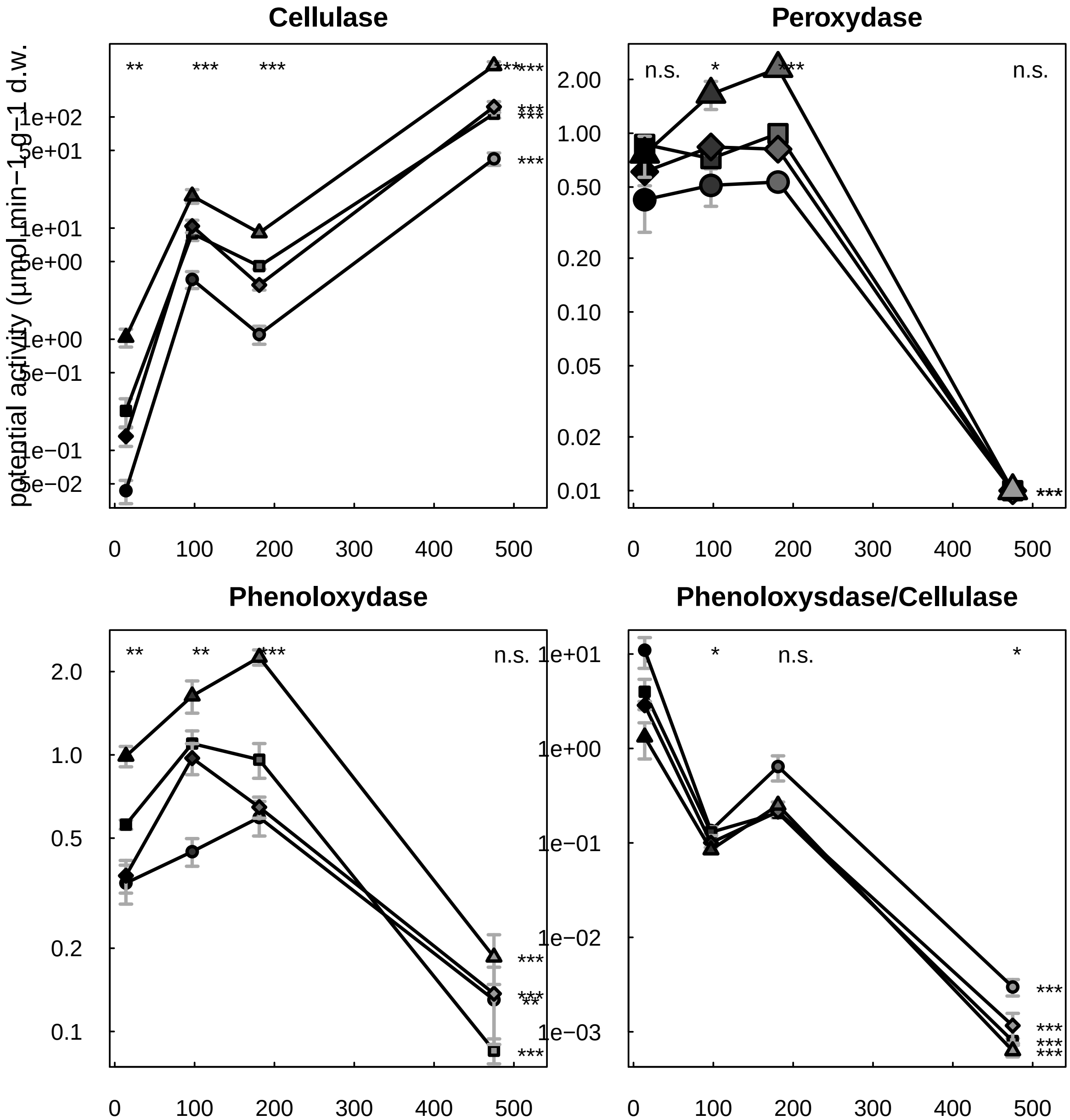


Figure 2. Potential eco-enzyme activities

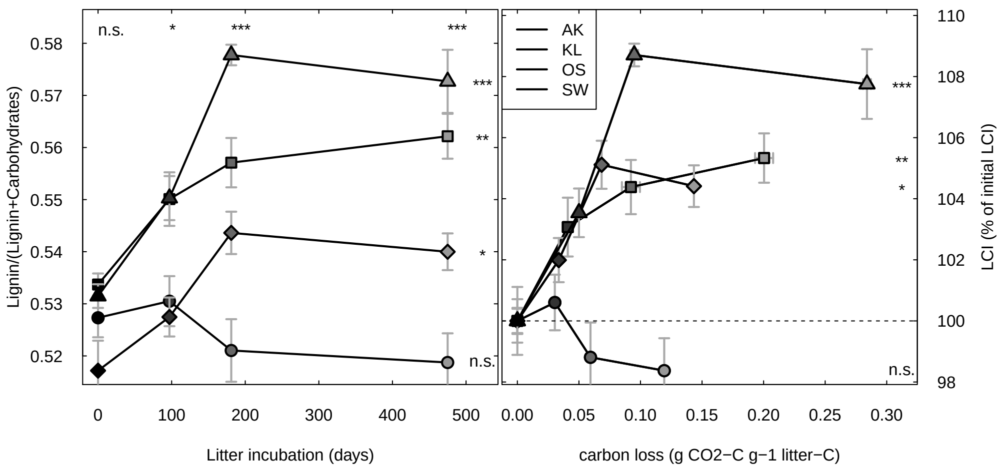


Figure 3. Develoment of the LCI (lignin/(lignin+carbohydrates)). Errorbars indicate standard errors (n=4-5). The dashed line indicates a constant ratio between lignin and carbohydrates (i.e. no preferential decomposition of carbohydrates.)

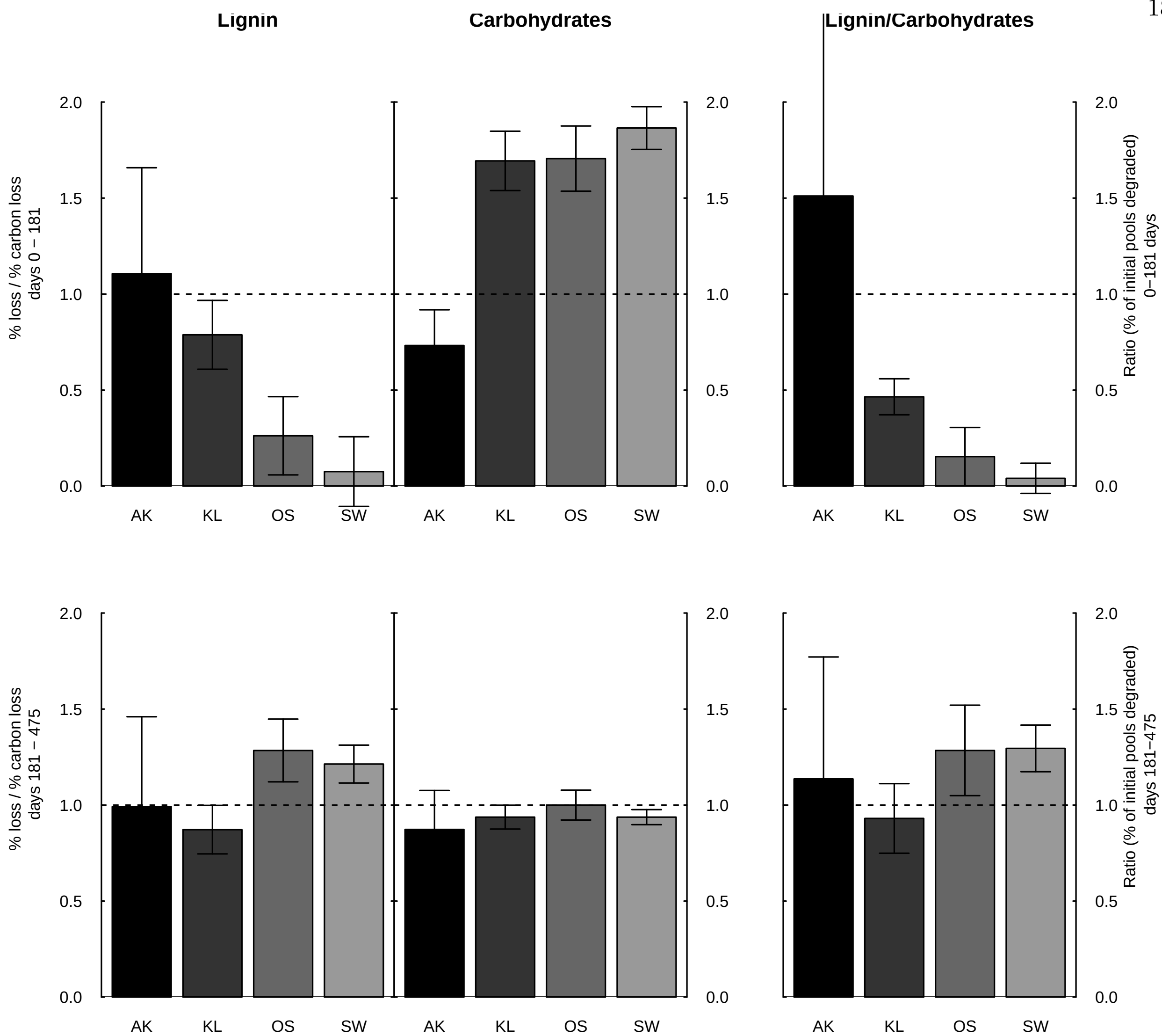


Figure 4. Carbon loss corrected amounts of lignin and carbohydrates degraded. Carbon loss was calculated based on accumulated respiration. Error bars indicate standard errors (n=4-5). The dashed line marks no discrination between lignin, carbohydrates and bulk carbon loss.

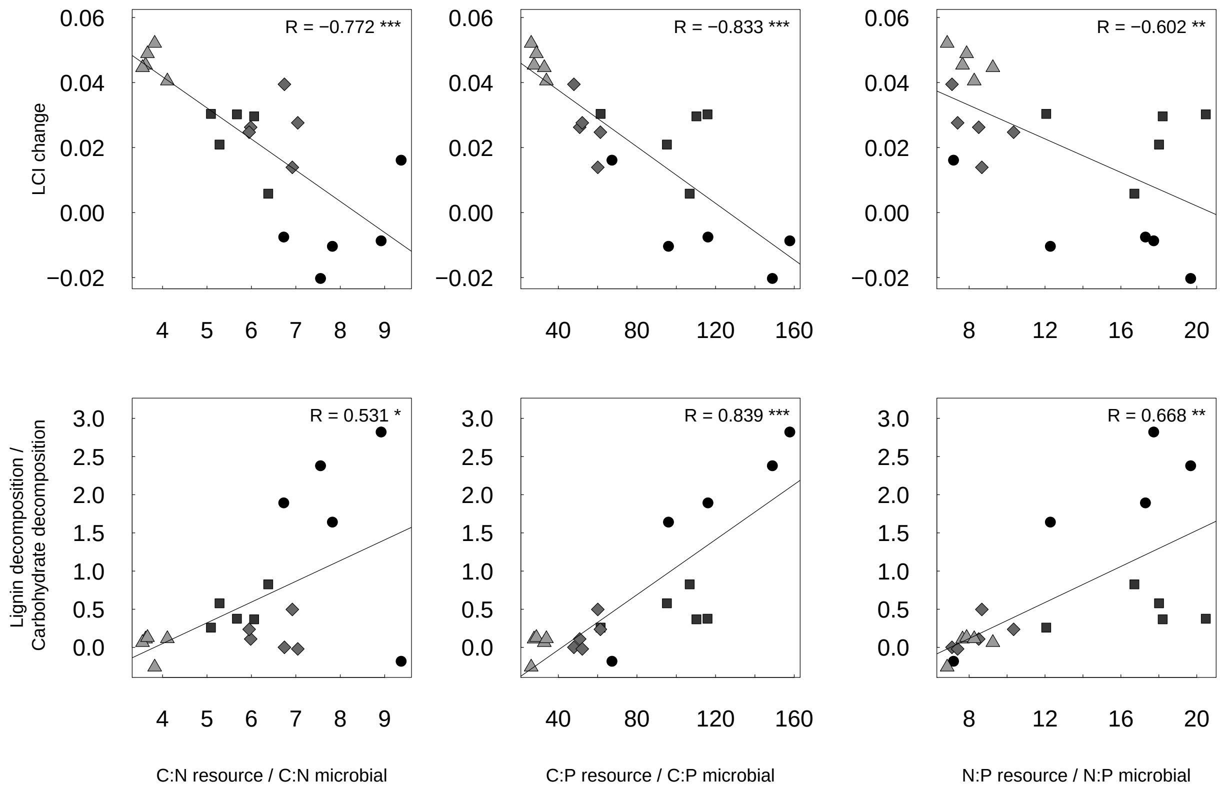


Figure 5. Correlations between Lignin accumulation during the first 6 month of litter incubation and stoichiometric resource:consumer imbalances

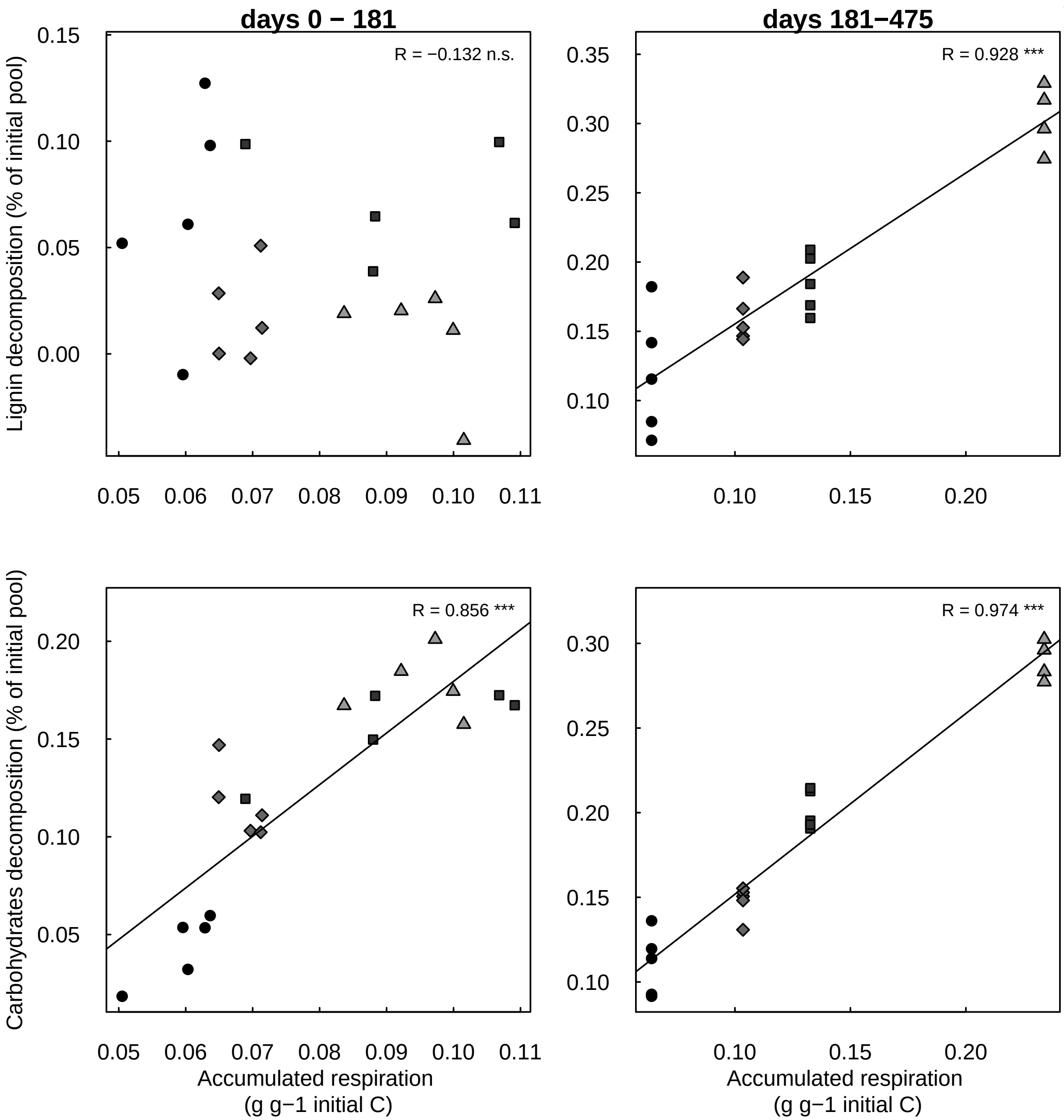


Figure 6. caption

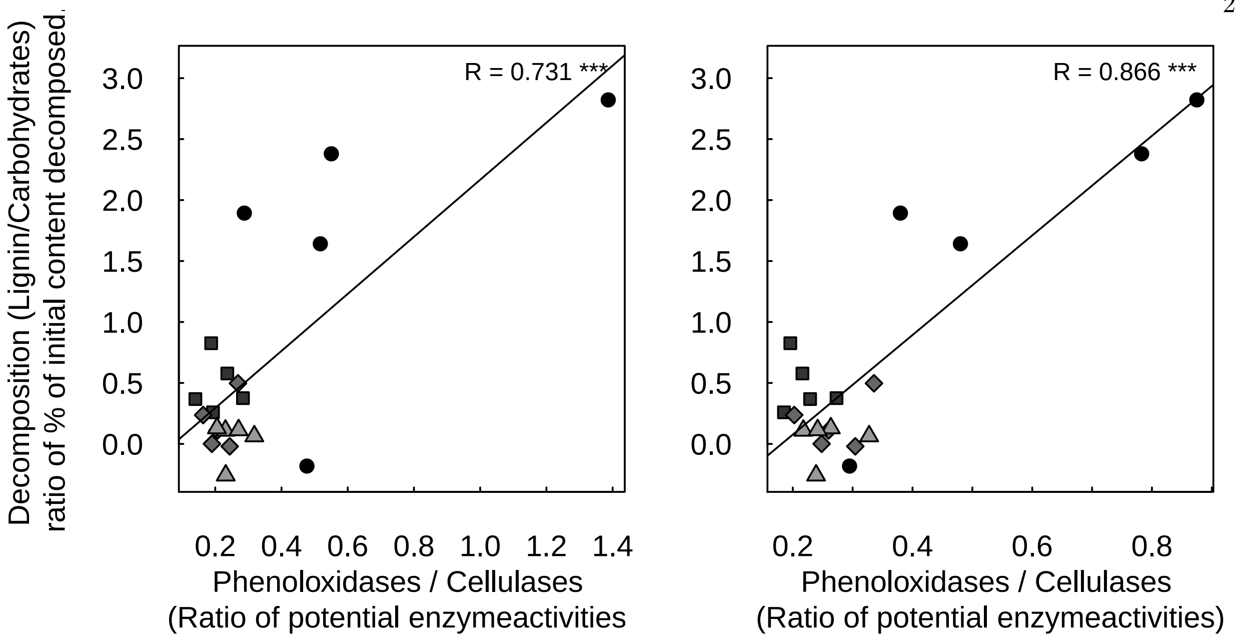


Figure 7. caption

Table 1. Litter stoichiometry and mineral elemental contents measured after 14 days incubation. Standard errors are stated in brackets (n=5). C extr stands for extractable carbon.

	AK	(SE)	KL	(SE)	OS	(SE)	SW	(SE)	p value
C (% d.w.)	50.86	(0.39)	49.41	(0.53)	48.15	(0.39)	48.90	(0.34)	0.002
C extr (mg g-1)	0.46	(0.03)	0.14	(0.01)	0.21	(0.01)	0.64	(0.03)	0.002
N (% d.w.)	0.878	(0.012)	0.938	(0.012)	0.806	(0.013)	1.172	(0.016)	<0.001
P (% d.w.)	0.040	(0.000)	0.030	(0.000)	0.052	(0.002)	0.070	(0.000)	<0.001
C:N (w/w)	57.86	(0.57)	52.60	(0.49)	59.97	(0.72)	41.78	(0.76)	<0.001
C:P (w/w)	1282	(21)	1548	(25)	905	(15)	699	(9)	<0.001
N:P (w/w)	22.17	(0.47)	29.45	(0.60)	15.10	(0.29)	16.75	(0.39)	<0.001
K (mg g-1)	0.26	(0.00)	0.54	(0.00)	0.21	(0.00)	0.55	(0.00)	<0.001
Ca (mg g-1)	1.33	(0.01)	1.26	(0.01)	1.63	(0.01)	1.23	(0.01)	<0.001
Mg (mg g-1)	0.27	(0.00)	0.14	(0.00)	0.20	(0.00)	0.15	(0.00)	<0.001
Fe (ppm)	210	(2)	208	(4)	453	(12)	192	(4)	<0.001
Mn (ppm)	172	(2)	1430	(10)	776	(9)	2137	(51)	<0.001
Zn (ppm)	30.8	(0.4)	33.0	(0.3)	36.0	(1.0)	42.4	(0.7)	<0.001

Table 2. Correlation (R) between Lignin and Carbohydrate degration with litter chemistry, microbial community and decomposition processes. Significant ($p<0.05$) correlations are printed bold. Data taken from [13, 16]. Differences in litter chemistry were calculaten between 0 and 181 days, process rates were measured after 181 days.

	L acc	Ch acc	LCI diff	L dec	C dec	L resp	C resp	L/C dec	Per/Cell	Phen/Cell
Massloss	0.291	-0.15	0.245	-0.328	0.106	-0.201	0.125	-0.081	0.048	0.0534
Actual respiration	0.333	**-0.723**	**0.606**	-0.0822	**0.771**	-0.195	**0.594**	-0.368	-0.268	-0.362
Accumulated Respiration	**0.494**	**-0.704**	**0.688**	-0.132	**0.856**	-0.332	**0.557**	**-0.525**	**-0.506**	**-0.534**
Cellulase activity	**0.657**	**-0.76**	**0.803**	-0.431	**0.801**	**-0.497**	**0.664**	**-0.589**	-0.436	**-0.539**
Protease activity	0.186	-0.296	0.264	-0.132	0.274	-0.157	0.301	-0.27	-0.26	-0.18
Chitinase activity	0.409	**-0.749**	**0.663**	-0.17	**0.795**	-0.312	**0.677**	**-0.559**	**-0.49**	**-0.607**
Phosphatase activity	**0.549**	**-0.813**	**0.776**	-0.302	**0.851**	-0.407	**0.702**	**-0.556**	-0.418	**-0.522**
Phenoloxidase activity	**0.632**	**-0.669**	**0.737**	-0.415	**0.719**	**-0.449**	**0.552**	**-0.484**	-0.305	-0.356
Peroxidase activity	**0.599**	**-0.588**	**0.677**	-0.412	**0.639**	-0.438	**0.47**	-0.435	-0.173	-0.302
N mineralization	**0.466**	**-0.664**	**0.65**	-0.167	**0.739**	-0.299	**0.527**	-0.387	-0.282	-0.367
Nitrification	**0.587**	**-0.707**	**0.732**	-0.38	**0.74**	-0.432	**0.621**	**-0.499**	-0.369	-0.45
P mineralization	**0.665**	**-0.55**	**0.684**	**-0.544**	**0.596**	**-0.576**	0.414	**-0.478**	-0.212	-0.255
C litter	**-0.545**	**0.506**	**-0.578**	**0.604**	-0.368	**0.643**	**-0.618**	**0.698**	**0.525**	**0.581**
extractable C	**0.609**	**-0.766**	**0.782**	-0.37	**0.814**	**-0.446**	**0.658**	**-0.54**	-0.392	**-0.484**
N litter	0.354	**-0.517**	**0.503**	-0.14	**0.587**	-0.187	0.366	-0.203	-0.119	-0.159
P litter	**0.682**	-0.222	**0.517**	**-0.747**	0.175	**-0.68**	0.188	**-0.491**	-0.0728	-0.16
C:N litter	-0.405	**0.586**	**-0.57**	0.175	**-0.654**	0.234	-0.44	0.273	0.195	0.242
C:P litter	**-0.636**	0.174	**-0.453**	**0.754**	-0.0823	**0.649**	-0.176	0.418	0.049	0.0805
N:P litter	**-0.512**	-0.0287	-0.264	**0.714**	0.147	**0.577**	-0.0202	0.316	-0.0316	-0.0192
C:N mic	**0.666**	**-0.758**	**0.799**	-0.43	**0.798**	**-0.515**	**0.678**	**-0.609**	**-0.584**	**-0.596**
C:P mic	**0.692**	**-0.787**	**0.834**	**-0.476**	**0.814**	**-0.562**	**0.726**	**-0.672**	**-0.564**	**-0.648**
N:P mic	**0.582**	**-0.729**	**0.74**	-0.415	**0.729**	**-0.508**	**0.715**	**-0.67**	**-0.545**	**-0.671**
C:N imbalance	**-0.56**	**0.81**	**-0.772**	0.288	**-0.859**	0.391	**-0.71**	**0.531**	**0.564**	**0.56**
C:P imbalance	**-0.817**	**0.663**	**-0.833**	**0.757**	**-0.61**	**0.799**	**-0.668**	**0.839**	**0.575**	**0.67**
N:P imbalance	**-0.724**	0.351	**-0.602**	**0.81**	-0.253	**0.764**	-0.397	**0.668**	0.301	0.41

Table 3. Correlation (R) between Lignin and Carbohydrate degration with litter chemistry, microbial community and decomposition processes. Significant ($p<0.05$) correlations are printed bold. Data taken from [13, 16]. Differences in litter chemistry were calculaten between 181 and 475 days, process rates were measured after 475 days.

	L acc	Ch acc	LCI diff	L dec	C dec	L resp	C resp	L/C dec	Per/Cell	Phen/Cell
Massloss	-0.0455	-0.264	0.0665	**0.623**	**0.71**	**0.505**	**0.496**	-0.118	-0.444	0.403
Actual respiration	-0.374	-0.22	-0.213	**0.86**	**0.83**	**0.837**	**0.809**	0.0279	-0.403	0.29
Accumulated Respiration	-0.165	-0.29	-0.0113	**0.909**	**0.981**	**0.753**	**0.825**	-0.119	**-0.608**	**0.486**
Cellulase activity	-0.317	-0.307	-0.137	**0.861**	**0.863**	**0.805**	**0.91**	-0.00551	**-0.575**	0.414
Protease activity	-0.229	-0.271	-0.086	0.455	0.447	0.434	**0.645**	-0.0269	**-0.456**	0.381
Phosphatase activity	0.0425	-0.0182	0.0685	0.334	0.39	0.259	**0.487**	-0.0904	-0.152	0.0167
Chitinase activity	-0.221	-0.228	-0.0874	**0.695**	**0.7**	**0.578**	**0.78**	0.0348	**-0.58**	0.395
Phenoloxidase activity	0.34	-0.436	0.435	-0.196	0.0177	-0.338	-0.121	**-0.456**	**-0.483**	**0.692**
Peroxidase activity	-0.274	0.452	-0.385	0.126	-0.067	0.261	0.0631	0.397	**0.546**	**-0.708**
N mineralization	0.175	0.195	0.0757	0.0631	0.111	-0.0805	-0.142	-0.145	0.0624	0.0892
Nitrification	-0.289	0.23	-0.321	**0.645**	**0.573**	**0.574**	0.407	0.164	-0.105	-0.0234
P mineralization	-0.164	0.0616	-0.137	**0.475**	**0.461**	**0.516**	0.402	-0.0877	0.0433	-0.0273
C litter	0.33	0.231	0.176	-0.329	-0.269	-0.358	**-0.654**	-0.0539	**0.501**	-0.348
extractable C	-0.205	-0.188	-0.0882	**0.884**	**0.912**	**0.727**	**0.774**	-0.0383	**-0.538**	0.409
N litter	-0.17	-0.166	-0.0672	**0.854**	**0.896**	**0.722**	**0.644**	-0.0751	-0.431	0.349
P litter	-0.4	-0.369	-0.181	**0.727**	**0.701**	**0.786**	**0.883**	-0.00155	**-0.464**	0.325
C:N litter	0.124	0.196	0.018	**-0.846**	**-0.912**	**-0.683**	**-0.643**	0.113	**0.49**	-0.404
C:P litter	**0.508**	0.277	0.313	**-0.572**	**-0.463**	**-0.721**	**-0.765**	-0.144	0.283	-0.162
N:P litter	**0.477**	0.189	0.325	-0.233	-0.0883	**-0.466**	**-0.5**	-0.205	0.048	0.0338
C:N mic	0.216	0.186	0.095	**-0.723**	**-0.745**	**-0.568**	**-0.693**	0.136	**0.57**	**-0.513**
C:P mic	0.395	0.0762	0.312	**-0.559**	-0.453	**-0.599**	-0.45	-0.122	0.233	-0.223
N:P mic	0.333	0.0142	0.288	-0.288	-0.169	-0.409	-0.207	-0.174	-0.00191	-0.00931
C:N imbalance	-0.0522	0.084	-0.0756	-0.348	-0.412	-0.311	-0.132	0.00942	0.0273	0.0196
C:P imbalance	0.0913	0.335	-0.0757	-0.114	-0.16	-0.218	**-0.499**	0.0773	0.16	-0.0317
N:P imbalance	0.0576	0.293	-0.0865	0.0497	0.0088	-0.0352	-0.392	0.128	0.16	-0.0803

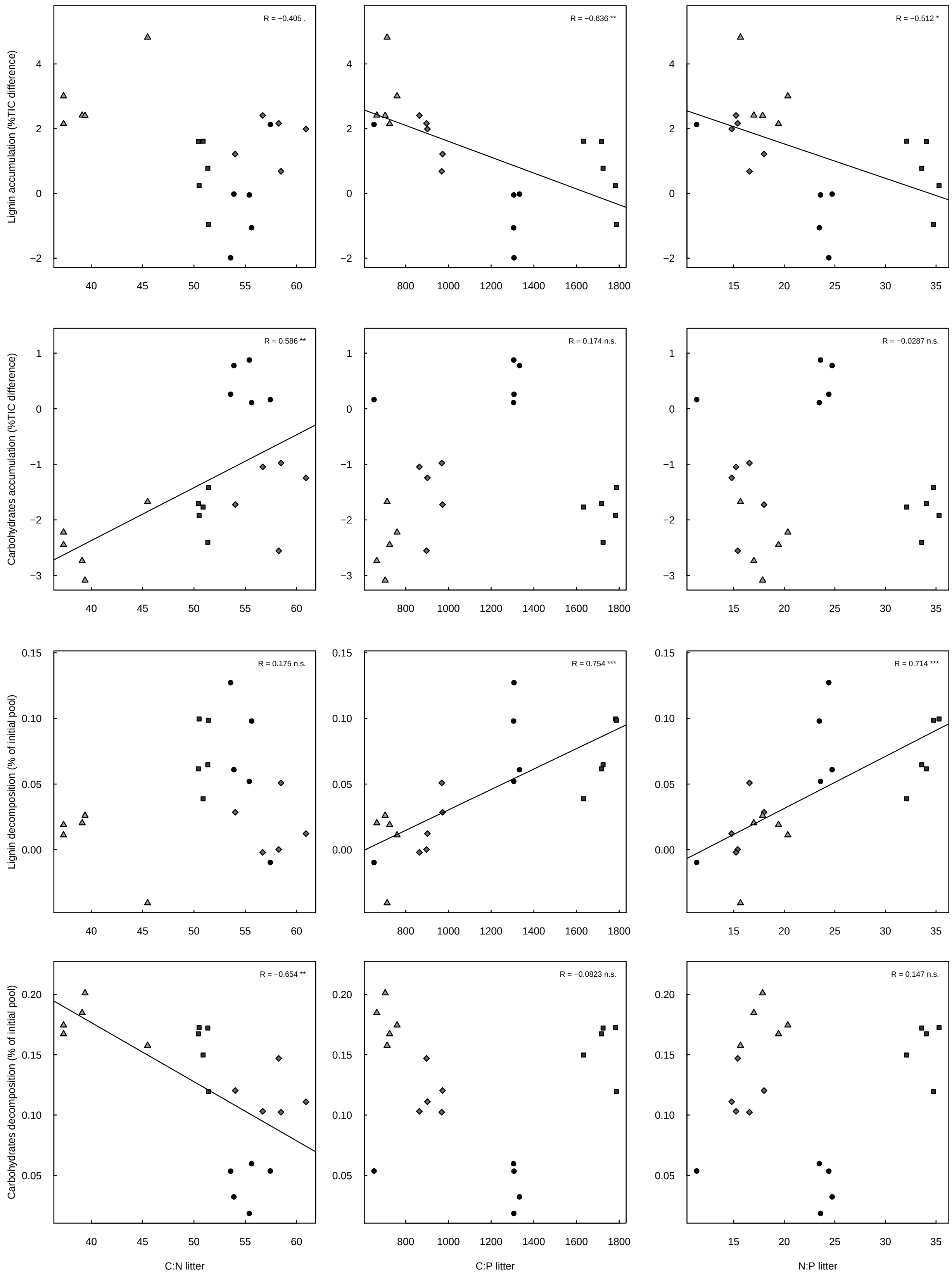


Figure 8. Correlations between Lignin and Carbohydrates accumulation and decomposition during the first 6 month of litter incubation and litter C:N:P ratios

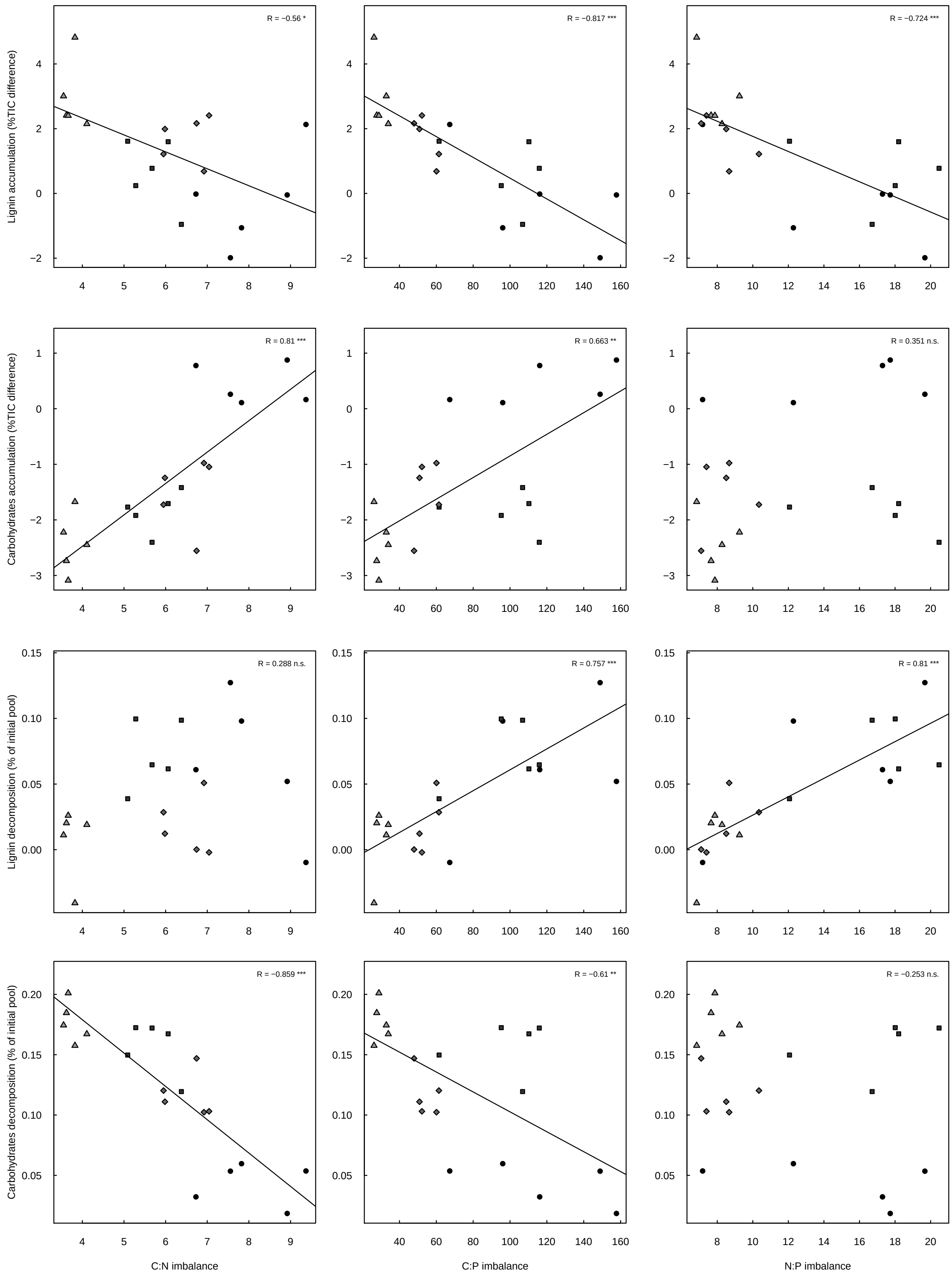


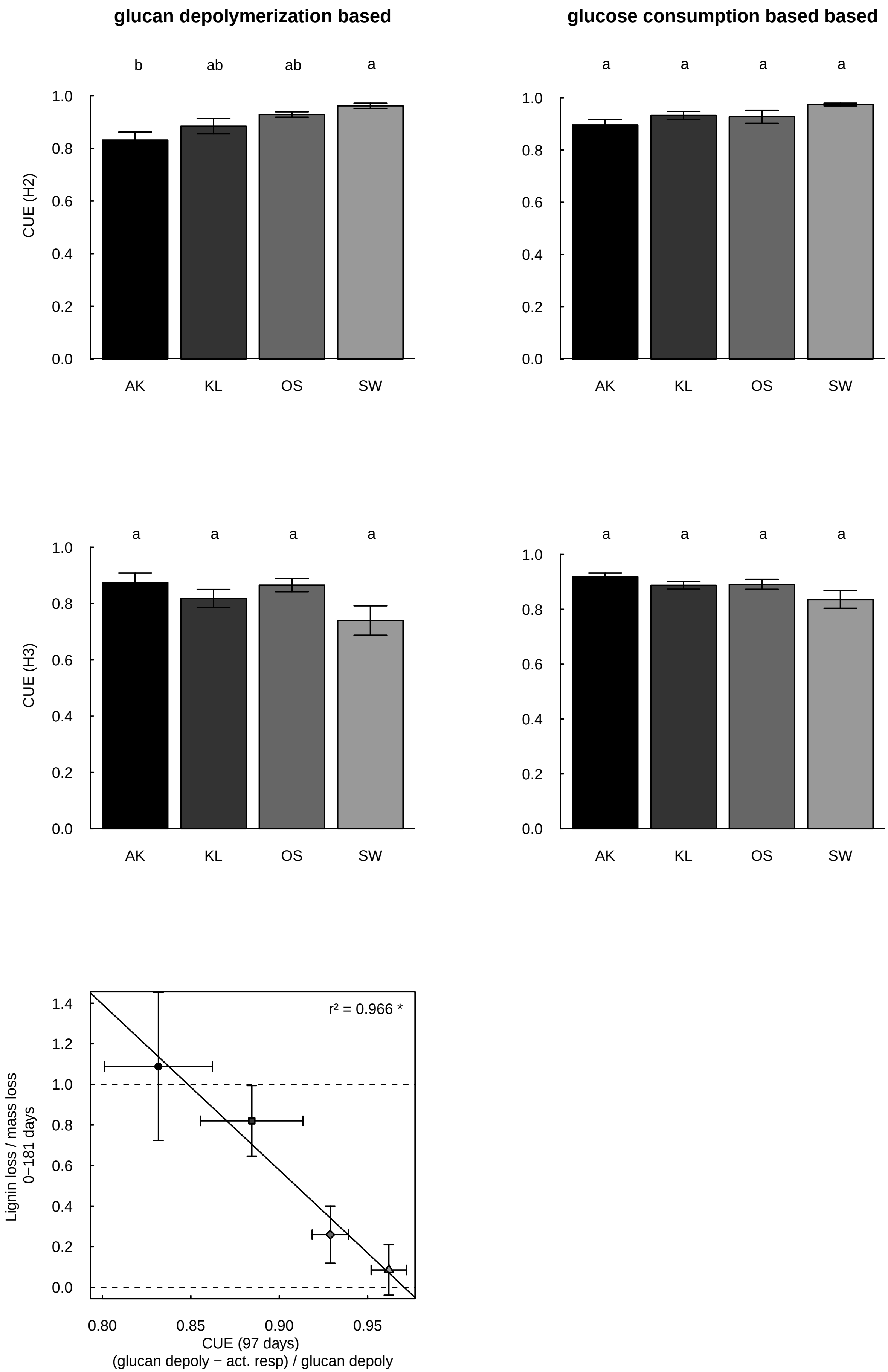
Figure 9. Correlations between Lignin and Carbohydrates accumulation and decomposition during the first 6 month of litter incubation and stoichiometric resource:consumer imbalances

Table 4. Correlations between C25/27/29 alkanes and alkenes, 14:0, 16:0 and 18:0 fatty acids and phytol. Differences between 0 and 181 days.

	alkanacc	alkenacc	faacc	phytolacc	alkandeg	alkendeg	fadeg	phytoldeg	alkanresp	alkenresp	faresp	phytolresp
Massloss	0.17	**0.49**	-0.0933	0.226	-0.15	-0.348	-0.00722	**-0.462**	-0.189	-0.227	-0.0146	-0.291
Actual respiration	**0.752**	0.428	**0.701**	**0.792**	-0.357	0.163	**-0.656**	**-0.867**	0.119	0.349	**-0.767**	**-0.863**
Accumulated Respiration	**0.703**	0.0679	**0.703**	**0.781**	-0.221	**0.545**	**-0.507**	**-0.714**	0.431	**0.673**	**-0.792**	**-0.87**
Cellulase activity	**0.665**	**0.548**	**0.673**	**0.894**	-0.154	0.112	**-0.531**	**-0.905**	0.308	0.332	**-0.719**	**-0.903**
Protease activity	0.027	0.0541	0.139	0.304	0.245	0.178	0.09	-0.172	0.344	0.3	-0.0935	-0.21
Phosphatase activity	**0.673**	0.169	**0.756**	**0.778**	-0.229	0.405	**-0.574**	**-0.691**	0.231	**0.574**	**-0.75**	**-0.774**
Chitinase activity	**0.744**	**0.519**	**0.748**	**0.916**	-0.234	0.157	**-0.617**	**-0.931**	0.27	0.382	**-0.78**	**-0.93**
Phenoloxidase activity	**0.626**	**0.601**	**0.574**	**0.838**	-0.157	0.0178	**-0.482**	**-0.911**	0.286	0.238	**-0.653**	**-0.87**
Peroxidase activity	**0.535**	**0.614**	**0.478**	**0.79**	-0.0898	-0.0474	-0.426	**-0.917**	0.282	0.155	**-0.581**	**-0.843**
N mineralization	**0.724**	0.453	**0.662**	**0.828**	-0.327	0.132	**-0.625**	**-0.941**	0.197	0.298	**-0.74**	**-0.923**
Nitrification	**0.654**	**0.487**	**0.551**	**0.836**	-0.223	0.121	-0.43	**-0.912**	0.19	0.319	**-0.615**	**-0.876**
P mineralization	0.438	**0.695**	0.368	**0.652**	-0.052	-0.174	-0.317	**-0.762**	0.353	0.0259	-0.437	**-0.712**
C litter	-0.0337	-0.192	-0.284	-0.369	-0.244	-0.0544	-0.0979	0.0362	-0.303	-0.155	0.0115	0.0999
extractable C	**0.715**	**0.496**	**0.688**	**0.906**	-0.225	0.17	**-0.562**	**-0.944**	0.263	0.374	**-0.741**	**-0.937**
N litter	**0.688**	**0.65**	**0.502**	**0.7**	-0.376	-0.13	**-0.579**	**-0.92**	0.0454	0.0547	**-0.645**	**-0.829**
P litter	0.0781	**0.728**	0.076	0.317	0.133	**-0.494**	-0.107	-0.429	0.197	-0.334	-0.0955	-0.294
C:N litter	**-0.728**	**-0.636**	**-0.562**	**-0.759**	0.38	0.0768	**0.598**	**0.943**	-0.0723	-0.113	**0.689**	**0.87**
C:P litter	0.054	**-0.734**	0.0372	-0.219	-0.216	**0.57**	-0.0572	0.273	-0.185	0.418	-0.0817	0.135
N:P litter	0.305	**-0.561**	0.24	0.0377	-0.348	**0.584**	-0.263	-0.0351	-0.156	**0.49**	-0.324	-0.159
C:N mic	**0.535**	0.398	**0.62**	**0.826**	0.00763	0.226	-0.345	**-0.704**	**0.48**	0.439	**-0.609**	**-0.782**
C:P mic	**0.557**	0.397	**0.647**	**0.864**	-0.00386	0.246	-0.38	**-0.762**	**0.458**	**0.469**	**-0.624**	**-0.821**
N:P mic	**0.486**	0.28	**0.613**	**0.773**	0.0068	0.288	-0.358	**-0.661**	0.396	**0.487**	**-0.554**	**-0.717**
C:N imbalance	**-0.695**	**-0.486**	**-0.713**	**-0.91**	0.167	-0.193	**0.507**	**0.87**	-0.367	-0.42	**0.738**	**0.915**
C:P imbalance	-0.289	**-0.576**	**-0.46**	**-0.684**	-0.196	0.0683	0.213	**0.566**	**-0.487**	-0.164	0.375	**0.574**
N:P imbalance	0.0124	**-0.566**	-0.155	-0.356	-0.31	0.303	-0.00124	0.271	-0.354	0.128	0.0428	0.216

Table 5. Correlations between C25/27/29 alkanes and alkenes, 14:0, 16:0 and 18:0 fatty acids and phytol. Differences between 181 and 475 days.

	alkanacc	alkenacc	faacc	phytolacc	alkandeg	alkendeg	fadeg	phytoldeg	alkanresp	alkenresp	faresp	phytolresp
Massloss	**-0.634**	-0.289	0.0683	**0.709**	0.448	**0.557**	0.344	**-0.478**	0.152	**0.525**	**-0.535**	**-0.731**
Actual respiration	**-0.471**	-0.301	0.432	**0.676**	0.313	**0.638**	0.0176	-0.253	0.157	**0.464**	-0.326	**-0.584**
Accumulated Respiration	**-0.795**	-0.35	0.324	**0.835**	**0.53**	**0.764**	0.242	-0.402	0.241	**0.77**	**-0.63**	**-0.829**
Cellulase activity	**-0.596**	-0.244	**0.562**	**0.784**	0.386	**0.613**	-0.0828	-0.288	0.317	**0.5**	-0.274	**-0.547**
Protease activity	-0.38	-0.00818	**0.659**	0.439	0.12	0.196	-0.394	-0.0506	0.264	0.194	-0.011	-0.0894
Phosphatase activity	-0.451	0.0332	**0.461**	0.323	0.25	0.194	-0.224	-0.000321	0.28	0.255	-0.178	-0.192
Chitinase activity	**-0.633**	-0.104	**0.589**	**0.611**	0.3	0.44	-0.189	-0.186	0.244	**0.536**	-0.353	-0.4
Phenoloxidase activity	-0.0256	0.134	-0.345	-0.134	-0.0858	-0.13	0.379	0.137	-0.184	0.0737	-0.0468	-0.0142
Peroxidase activity	0.0627	-0.106	0.343	0.127	0.028	0.0833	-0.401	-0.172	0.119	-0.106	0.0258	0.0264
N mineralization	-0.0379	0.0275	-0.156	0.236	-0.0981	0.0926	0.259	-0.395	-0.397	0.283	**-0.569**	-0.421
Nitrification	**-0.496**	-0.451	0.253	**0.663**	0.417	**0.628**	0.112	-0.424	0.179	**0.535**	**-0.57**	**-0.657**
P mineralization	-0.303	**-0.466**	0.206	**0.473**	0.333	**0.543**	0.0642	-0.249	0.235	0.211	-0.182	-0.447
C litter	0.0444	-0.336	**-0.825**	-0.0325	0.223	0.145	**0.685**	-0.412	-0.0238	0.0415	-0.212	-0.3
extractable C	**-0.733**	-0.294	0.398	**0.876**	0.452	**0.701**	0.14	**-0.5**	0.174	**0.735**	**-0.666**	**-0.809**
N litter	**-0.76**	**-0.548**	0.116	**0.836**	**0.618**	**0.862**	0.415	**-0.52**	0.28	**0.764**	**-0.652**	**-0.909**
P litter	-0.354	-0.181	**0.597**	**0.575**	0.254	0.448	-0.246	-0.0722	0.345	0.17	0.0983	-0.261
C:N litter	**0.784**	**0.503**	-0.0977	**-0.818**	**-0.614**	**-0.843**	-0.448	**0.494**	-0.248	**-0.804**	**0.701**	**0.922**
C:P litter	0.0939	0.0836	**-0.682**	-0.422	-0.0492	-0.249	**0.48**	-0.000689	-0.281	0.0934	-0.341	-0.0041
N:P litter	-0.241	-0.0878	**-0.627**	-0.0957	0.187	0.0732	**0.654**	-0.191	-0.202	0.445	**-0.659**	-0.377
C:N mic	**0.549**	0.241	**-0.502**	**-0.611**	-0.18	**-0.547**	0.04	0.245	0.0205	**-0.687**	**0.589**	**0.55**
C:P mic	0.206	0.413	-0.218	**-0.503**	-0.241	**-0.508**	-0.0471	0.26	-0.217	-0.175	0.0327	0.355
N:P mic	-0.0201	0.326	-0.054	-0.273	-0.175	-0.297	-0.028	0.156	-0.253	0.13	-0.243	0.124
C:N imbalance	0.429	0.393	0.363	-0.443	**-0.586**	**-0.515**	**-0.584**	0.403	-0.335	-0.297	0.27	**0.611**
C:P imbalance	-0.0373	-0.357	**-0.544**	0.0137	0.13	0.208	**0.535**	-0.327	-0.143	0.262	-0.427	-0.324
N:P imbalance	-0.2	**-0.486**	**-0.619**	0.199	0.37	0.391	**0.687**	**-0.468**	0.045	0.324	**-0.457**	**-0.522**


glucan depolymerization based
glucose consumption based based
b
ab
ab
a
CUE (H2)
CUE (H3)
AK
KL
OS
SW
Lignin loss / mass loss
0−181 days
r² = 0.966 *
CUE (97 days)
(glucan depoly − act. resp) / glucan depoly