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Strakova, Petra

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# Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: Consequences for accumulation of organic matter in boreal peatlands.

Petra Straková[1,2], Timo Penttilä[2], Jukka Laine[3] and Raija Laiho[1]

[1]Peatland Ecology Group, Department of Forest Sciences, University of Helsinki, Finland (petra.strakova@helsinki.fi, raija.laiho@helsinki.fi)
[2]Finnish Forest Research Institute, Vantaa Research Unit, Finland
[3]Finnish Forest Research Institute, Parkano Research Unit, Finland

**Key words:**

Climate change, decomposition, litter quality, peatlands, plant litter, organic matter accumulation, temperature, water table drawdown.

**Abstract**

Pristine peatlands are carbon (C) accumulating wetland ecosystems sustained by a high water table (WT) and consequent anoxia that slows down decomposition. Persistent WT drawdown as a response to climate and/or land-use change affects decomposition either directly through environmental factors such as increased oxygenation, or indirectly through changes in plant community composition. This study attempts to disentangle the direct and indirect effects of WT drawdown by measuring the relative importance of environmental parameters (WT depth, temperature, soil chemistry) and litter type and/or litter chemical quality on the 2-year decomposition rates of above- and belowground litter (altogether 39 litter types). Consequences for organic matter accumulation were estimated based on the annual litter production. The study sites were chosen to form a three stage chronosequence from pristine (undrained) to short-term (years) and long-term (decades) WT drawdown conditions at three nutrient regimes.

The direct effects of WT drawdown were overruled by the indirect effects via changes in litter type composition and production. Short-term responses to WT drawdown were small. In long-term, dramatically increased litter inputs resulted in large accumulation of organic matter in spite of increased decomposition rates. Further, the quality of the accumulated matter greatly changed from that accumulated in pristine conditions.

Our results show that the shift in vegetation composition as a response to climate and/or land-use change is the main factor affecting peatland ecosystem C cycle and thus dynamic vegetation is a necessity in any models applied for estimating responses of C fluxes to changing environment. We provide possible grouping of litter types into plant functional types that the models could utilize. Further, our results clearly show a drop in soil summer temperature as a response to WT drawdown when an initially open peatland converts into a forest ecosystem, which has not yet been considered in the existing models.

## 1. Introduction

Decomposition is one of the key processes in element cycling in most ecosystems. In peatlands, there has been a long-term imbalance between litter production and decomposition caused by high water tables (WT) and consequent anoxia. This has resulted in peatlands being a significant sink of carbon (C) from the atmosphere (e.g., Gorham 1991; Schulze & Freibauer, 2005).

Lowering of the WT, because of climatic or land-use changes, promotes several changes in peatland environmental conditions that have direct effects on decomposition (Laiho *et al.* 2006). Increased soil aeration has a positive effect, while increased peat compaction, lowering of soil pH and drop in temperature may, in turn, have a negative effect. Yet, there is increasing evidence that the indirect effects on decomposition via changes in the structure of plant communities may have much more impact on ecosystem C cycling than any direct effects of environmental changes (Straková *et al.* 2010).

Lowering of WT induces changes in the plant community structure (Weltzin *et al.* 2000; 2003; Robroek *et al.* 2007; Breeuwer *et al.* 2009), that can eventually lead to a complete replacement with species adapted to the new conditions (Laine *et al.* 1995). Such changes tend to be more pronounced in sites with more nutrients, and intensify over time since the WT drawdown (Laine *et al.* 1995). Following that, quantity and quality of the above- and belowground litter produced after the WT drawdown, as well as the location (depth distribution) of the belowground litter, greatly differ from that produced in pristine conditions (Laiho *et al.* 2003; Straková *et al.* 2010, Murphy *et al.* 2009 ). Litter quality (relative proportions of soluble and recalcitrant compounds and nutrients) is a key factor in C cycle, for it determines the quality of the substrate as a source of energy and nutrients for decomposer microorganisms. Thus, different litter materials may have vastly differing rates of decomposition (e.g., Hobbie 1996; Thormann *et al.* 2001; Cornwell *et al.* 2008). Changes in vegetation composition following a persistent WT drawdown may therefore result in overall shifts in litter quality and decomposability in peatlands (Dorrepaal *et al.* 2005; Straková *et al*. 2010). In addition to the "fate" of the existing peat deposit, the C balance of fresh litter inputs affects the C sink/source function of peatlands following persistent water table drawdown (Laiho 2006). The extent of the role of the changed litter inputs and their decomposition rates on the C balance of different peatland types have not been explored yet, in spite of their significance.

The aim of this study was to evaluate the effect of WT drawdown (at different time scales: years and decades after the persistent WT drawdown) on plant litter decomposition. We determined decomposition rates of the litter types typical of boreal peatland sites with varying nutrient and WT regimes, and estimated the relative importance of environmental parameters and litter type and/or litter chemical quality on the decomposition dynamics. Further, we described the short-term accumulation rate of organic matter at the different WT regimes. To estimate C sink/source behaviour of drained peatlands, we compared our results with literature data on heterotrophic soil respiration.

We postulated that WT drawdown has dual effects on plant litter decomposition:

(1) direct, made by improved environmental conditions for aerobic decomposers, that will be reflected as an increase in litter decomposition rate at plant species level, and

(2) indirect, through changes in plant community structure, that will be reflected in the decomposition rate at the community level and/or in the short-term accumulation rate of organic matter.

We presumed that the direct effects will dominate in the short-term (no big changes in vegetation yet), while the indirect effects will dominate in the long-term (dramatic changes in vegetation composition, additional effects of the vegetation changes on soil properties). Further, we expected the effects be more pronounced in nutrient-rich (fen) than nutrient-poor (bog) sites, in line with changes in vegetation composition (e.g., Laine *et al.* 1995), tree stand development (Minkkinen *et al*. 2001), litter quality and inputs (Straková *et al*. 2010), microbial community composition and activity (Peltoniemi *et al*. 2010; Straková *et al*. 2011). We assume N and P be more readily available at the minerotrophic fen sites (nutrient-rich) compared to the bog (nutrient-poor), enhancing microbial activities and thus instigating greater mass loss (McClaugherty *et al.* 1985; Taylor *et al.* 1989; Vávřová *et al.* 2009).

This article focuses on the first two years of the decomposition process, what is, for most litter types, a decadal movement from litter to soil organic matter. In a peatland ecosystem the first two years are very much still the initial stage of litter decomposition, and may not reflect the long-term C accumulation accurately. We will validate the further behaviour of the accumulated organic matter at the different WT regimes after obtaining longer-term data from the continuation of this study.

## 2. Materials and methods

### *2.1. Study sites*

The research was carried out at Lakkasuo, a raised bog complex in Central Finland (61°48'N, 24°19'E, c. 150 m.a.s.l.). Annual precipitation in this area is 710 mm, of which about one-third falls as snow. The average annual temperature sum (threshold value 5°C) is 1160 degree days and average temperatures for January and July are −8.9 and 15.3°C, respectively (Finnish Meteorological Institute, Juupajoki weather station 1961-1990).

We had three study sites with differing nutrient regimes: bog (ombrotrophic, i.e. fed solely by precipitation; nutrient-poor), oligotrophic fen (minerotrophic, i.e. additionally fed by groundwater inputs; moderate nutrient regime) and mesotrophic fen (minerotrophic; nutrient-rich). Each of those consisted of a pristine control plot, a plot with short-term, c. 4 years, water table drawdown (STD), and a plot with long-term, c. 40 years, water table drawdown (LTD) (Laine *et al.* 2004). Together, these plots formed a gradient from a wet pristine peatland to a drying system and finally to a peatland forest ecosystem (Laiho *et al.* 2003. Within each site, all plots supported the same plant community and had similar soil composition and structure before the WT drawdown. The pristine and LTD plots covered about 900 $m^2$, and the STD plots about 500 $m^2$.

The water tables in the manipulated plots were lowered by ditching. LTD had been achieved with practical-scale drainage for forestry in 1961 (i.e., to improve tree growth), and STD with new ditches for this experimental purpose in 2001. Short-term WT drawdown had led to the average WT being 10 cm (bog) to 20 cm (fen) deeper than in the corresponding pristine plots, which is close to the estimate given by Roulet *et al.* (1992) for the short-term impact of climate change on WT in northern peatlands. In the LTD plots, the average WT was 15 (bog) to 40 (fen) cm deeper than in the pristine plots. We assume that the initial post-drainage drop in WT was close to that observed in our STD plots, and that the further lowering was caused by increased evapotranspiration by the growing tree stands (Sarkkola *et al.* 2010). The difference between fen and bog also largely derives from the higher tree stand evapotranspiration in fens where the tree stands develop faster (Minkkinen *et al*. 2001). As the WT depth is clearly different (usually lower) next to a drainage ditch than is the average of the drained area (Grieve *et al.* 1995; Schlotzhauer & Price 1999), no measurements were made next to the ditches (minimum distance > 1 m for STD and 10 m for LTD).

Short-term, four-year WT drawdown had a rather small effect on vegetation composition: *Sphagnum* moss and sedges had suffered while shrubs had flourished together with pine (*Pinus sylvestris*) and birch (*Betula pubescens*) (Straková *et al.* 2010; Jukka Laine, Eeva-Stiina Tuittila and Harri Vasander, unpublished data). In long-term, 40 years, the changes in vegetation composition were dramatic: WT drawdown had resulted in conversion of an open peatland dominated by *Sphagnum* and graminoids into a forest ecosystem dominated by pine and birch. The vegetation change was associated, besides a decrease in WT, with a drop in pH and increase in nutrient concentration of surface peat (Straková *et al.* 2010).

*2.2. The litter material*

We collected altogether 39 litter types (plant species and part/organ) that included foliar litter, roots and woody parts of vascular plants, and mosses (Appendix 1), and reflected the dominant species at the different nutrient and WT regimes, as well as different plant groups with distinctive chemical composition (Straková *et al.* 2010). Litter of *Betula nana*, *Eriophorum vaginatum* and *P. sylvestris* (altogether 6 types) was present at all plots ("common litter"), and could be used to evaluate the direct effect of WT drawdown on litter decomposition, including a possible change in litter quality at the litter type level. The other litter types included were typical of certain nutrient and WT regimes ("specific litter") (Appendix 1; Anttila 2008), and thus reflected the indirect effects. Vascular plant litter was collected by harvesting senescent leaves, needles or dead branches from living plants. As young green stem parts of *Sphagnum* moss were shown to decay at faster rate than litter (recently dead stem parts, Limpens & Berendse 2003), we collected moss litter by cutting a 3-5 cm thick layer beyond the living moss with scissors (thus, excluding both the upper green and the lower, already decomposing, layers). The collected litter was further sorted and any green or visually decomposing parts were removed. Harvesting took place in September and October 2004 or 2005 during the highest natural litter fall at our sites (Anttila 2008).

For the belowground litter of *Carex lasiocarpa*, *C. rostrata*, *E. vaginatum* and *B. nana*, whole living plants were collected at the study sites and cultivated in containers filled with expanded clay and water from May to October 2005. To simulate the natural variation in nutrient regimes between the different peatland sites, fertilizer was added to the containers monthly at two concentration levels. Higher concentration was used for plants from the nutrient-rich mesotrophic fen, lower concentration for the plants from the nutrient-poor bog and oligotrophic fen. Roots that were used to represent belowground litter were harvested from the plants at the end of the cultivation period. Pine roots were harvested from 3 years old Scots pines, cultivated at a tree-nursery, and divided into two size classes: 0-2 mm and 2-10 mm.

Each litter type was air-dried at the room temperature (20 °C) to constant mass (about 92-94% dry mass) and gently mixed. Sub-samples were withdrawn to determine initial litter quality and dry mass content (Straková *et al*. 2010). Detailed chemical characterization of the different litter types is presented by Straková *et al.* (2010). In short, non-graminoid foliar litters had a high concentration of nutrients and extractives. Graminoids and mosses were rich in holocellulose-comprising sugars and lignin-like compounds (Klason lignin, CuO oxidation phenolic products). *Sphagnum* species of sections Acutifolia and Palustria (mostly hummock species) displayed a higher concentration of cellulose and lignin-like compounds and lower concentration of hemicellulose than the species of section Cuspidata (mostly lawn-level and hollow species). Woody litters were marked by a high concentration of Klason lignin.

*2.3. Litter decomposition*

Litter decomposition rates were determined in the natural environment. This means that each specific litter type was decomposing at the plot where it had been produced and collected (except for pine roots that originated from a tree-nursery), in conditions where that kind of litter would fall and naturally be decomposing. We used the litterbag method, which, in spite of some known sources of inaccuracy (Domisch *et al.* 2000; Taylor 1998, Kurz-Besson *et al.* 2005) is the most useful and widely used method for determining mass loss rates of different materials *in situ*. To minimize the negative effect of air-drying on litter decomposition (Taylor 1998), litterbags were remoistened with surface water of the given site before installation. We assume that this helped the microbial communities typical of the site to re-colonize the litter. Also, the mesh size of the nylon bags used was 1 x 1 mm to prevent physical losses of the material but to allow small mesofauna typical of the sites (Silvan *et al.* 2000) to enter the bags. There are generally not bigger decomposers at our sites and thus the mesh size 1 x 1 mm did not prevent their effects on litter fragmentation, which was the concern of Cotrufo *et al.* (2010). For each plot, mostly 4-5 replicates were prepared per each litter type for annual recovery; the number of replicates was lower for some litter types or plots due to limitations in litter amounts (Appendix 1).

For the litterbag incubation, locations were selected following the given plant species abundance, i.e. each litterbag was installed in the conditions where the given litter type would naturally decompose. Litterbags containing moss litter were installed under the living parts of moss shoots of the given species, where fresh moss litter is naturally formed and begins to decompose. The other aboveground litters were placed horizontally on the litter layer surface where the litters naturally fall, always in touch with some fallen litter of the given litter type. As the decomposition process may be affected by interactions (either positive or negative) between different litter types when decomposing as mixtures (Gartner & Cardon 2004), contact with other typically associated litters was also ensured. Belowground litterbags were installed vertically in the peat profile at the given depth (0-10 to 20-30 cm below the soil surface, see Appendix 1) near living plants of the species in question. Installation took place in October-November 2004. To capture for possible between-year variation in litter decomposition rates, another set of litterbags was installed in October 2005 for a 1-year period. Some litterbags with belowground litter were installed in October 2005 and 2006 (see Appendix 1). Incubation periods presented in here are 1 and 2 years: the first recovery cohort was collected 12 months after installation and the second one 24 months. The samples are a subset from an ongoing long-term study.

After each recovery, litterbags were transported to a laboratory where the content was cleaned by removing all additional (ingrowth) materials, weighted to determine the remaining mass and gently homogenized before sub-sampling. Dry mass content was determined by drying two sub-samples at 105 °C overnight. Decomposition rates were expressed as dry mass loss after each incubation period (Appendix 1).

*2.4. Environmental parameters*

This section describes measurements of environmental parameters that were tested in this study as potential predictors of variation in litter decomposition rates.

WT depth was continuously recorded at all pristine and LTD plots using Ott (Kempten, Germany) WT recorders. Position of the decomposing litter relative to the WT was estimated based on those continuous measurements, and monthly measurements at the exact locations where litterbags were installed.

Temperature was monitored in 2-4 hour intervals using temperature loggers (i-Button DS1921G, MaximIntegrated Products) at the same locations where the studied litter was decomposing. The loggers were thus installed in soil at 10 and 20 cm depth for the belowground litters, in moss patches about 5 cm from the surface for the moss litters, and in the surface litter layer for the other litter types in which case they were protected from direct sunlight by a thin layer of litter. *Daily mean temperatures* and the *cumulative temperature sums over 0 ºC threshold* for the specific incubation periods were calculated from these local measurements. If local data were not available for some dates or locations, mean daily soil temperature values were estimated from the values of adjacent measurements or the closest locations of the same plot and litter type. *Daily variation in temperature* was calculated as standard deviation of the temperature records within a day.

Soil samples were collected at all plots using a box sampler from the 0-30 cm surface peat layer. The peat-cores were cut into 10-cm layers, and element concentrations were analyzed as for the litter materials (Straková *et al.* 2010).

To capture purely environmental effects on decomposition we used pine cellulose as a standard material. Unlike common litter the quality of which may change as a response to WT drawdown, cellulose had identical chemical composition at all nutrient and WT regimes. Mesh bags with cellulose strips were installed at the same locations as the litterbags and the mass loss rates were measured for the same periods as that for litters. After each recovery, the cellulose strips were gently cleaned, dried at 105 °C overnight and weighted to determine the dry mass loss.

### *2.5. Data analyses*

#### 2.5.1. Direct effects of WT drawdown and site nutrient regime on litter decomposition

The direct effects (i.e., induced mainly by the environmental changes and reflected at plant species level) of WT drawdown and site nutrient regime on litter decomposition were estimated using 1) decomposition rates of the common litter (litter types common to all WT and nutrient regimes), 2) decomposition rates of cellulose as a standard material, and 3) the relative effect of environmental factors in the models of litter decomposition (described in detail later).

Factorial ANOVA followed by Tukey´s post-hoc comparison was carried out using Statistica for Windows version 6.1 (StatSoft, 2003). Mass loss of the common litter was used as a single continuous response variable, and site nutrient and WT regime, litter type, incubation layer and incubation period (1 or 2 years) were used as categorical predictors (factors). Separate tests were performed for aboveground and belowground litter. Correspondingly, to estimate the direct effects of site nutrient and WT regime and their interactions on cellulose decomposition, mass loss of cellulose was used as a single continuous variable, and site nutrient and WT regime, incubation layer and incubation period (1 or 2 years) as factors.

#### 2.5.2. Indirect effects of WT drawdown on litter decomposition

To estimate the indirect effects of WT drawdown we calculated litter decomposition rates at the community level that are mediated by changes in plant community structure. Decomposition rates of different litter types were weighted by their inputs presented by Straková *et al.* 2010. Further, we calculated the relative effect of litter type (PFT) in the models of litter decomposition (described in detail later).

2.5.3. Models of litter decomposition

Models were constructed to identify factors controlling the variation in the litter mass loss. Because of the hierarchical data structure, a mixed (multilevel) model approach was used (Goldstein 1995). We identified three hierarchical levels, or levels of clustering, in the data: (1) site, (2) incubation location, (3) recovery cohort (year 1 and year 2; this made the model follow a repeated measures design). The models thus had the following form:

$$y_{ijk}=\alpha_{ijk}+\beta_1 x_{1ijk}+\beta_2 x_{2ijk}+\ldots+\beta_n x_{nijk}+ v_k+u_{jk}+\varepsilon_{ijk} \quad (1)$$

where $y_{ijk}$ is the cumulative mass loss for the incubation period $i$ within incubation location $j$ in site $k$. The fixed part consists of intercept $\alpha$, and site, weather and litter quality characteristics $x_{1ijk}$–$x_{nijk}$ with parameters $\beta_1$–$\beta_n$. In the random part, $v_k$ is the variance derived from site $k$, $u_{jk}$ is the variance associated with different incubation locations $j$, and $\varepsilon_{ijk}$ accounts for the within-incubation location variation between different incubation periods (1 or 2 years; recovery cohort).

The estimation was done using MLwiN software (Rasbash *et al.* 2004), which estimates the fixed and random parameters simultaneously. We applied the restricted iterative generalized least square (RIGLS) method. The significance of the variables was evaluated based on their parameter standard error (parameter value should be at least twice its SE).

The parameter SE was also used to group different litter types into plant functional types (PFTs, Box 1996). Litter types whose mass loss rates did not significantly differ (based on SE) were grouped into a PFT so that the different PFTs significantly differed from each other.

The value of −2×log-likelihood was used to compare models of increasing complexity. The factors included in the final models were selected based on the amount of explained total variation in litter mass loss and the value of −2×log-likelihood. The goodness of fit was further evaluated based on residuals. Different models were constructed for the belowground litters and for the aboveground litters that included mosses.

Simple decomposition rate coefficients were estimated for the different litter types using the exponential decay function (Olson 1963) as described in Vávřová *et al*. (2009). The goodness of fit was evaluated based on residuals. The fit of our litter materials was generally poor and thus the percentage of dry mass loss after each incubation period will be used to express the decomposition dynamics.

2.5.4. Temperature patterns in the decomposing litter

To estimate the effects of site nutrient and WT regime, their interactions, litter type and incubation layer on variation in temperature patterns in the decomposing litter, variation partitioning was performed by redundancy analysis (RDA) using Canoco for Windows version 4.5 (ter Braak & Šmilauer 2002). Measured values of daily mean temperature or daily variation in temperature in the decomposing litter were used as response variables (a separate variable for each day). A group of binary variables describing either site nutrient or WT regime, their interaction term, litter type or incubation layer was kept at a time as explanatory variables, while the other groups were used as covariables (see Table 1).

*2.6. Simulation of organic matter accumulation*

To calculate short-term accumulation of organic matter (amounts of different litter types remaining at the sites after 2 years of decomposition), the measured litter mass loss rates were applied to the litter inputs presented by Straková *et al.* (2010).

## 3. Results

### *3.1. Variation in environmental conditions for decomposition*

#### 3.1.1. Water table

In pristine conditions, fens had higher WT with smaller variation during the vegetation season compared to the bog (Fig. 1). Ditching had greater impact on WT in the initially wetter fens compared to the bog. At fens, the ditching had resulted in average WT being 20 (years) to 40 (decades) cm deeper than in the pristine plots. At the bog, the WT was only 10 (years) to 15 (decades) cm deeper following the ditching compared to the pristine plot (Fig. 1).

#### 3.1.2. Litter temperature

WT drawdown influenced temperature patterns in the decomposing litter. Daily mean temperature, cumulative temperature sums as well as variation in temperature within a day (estimated for mid May - mid October) decreased following the long-term WT drawdown (Table 2; see also Fig. 2). The decrease in daily mean temperature following the long-term WT drawdown was greatest in the spring and summer months (April - July): by 1-2 ºC for the surface litter layer and by 3-4 ºC for the soil layers. Only in the autumn months (September-October) the daily mean temperature of the decomposing litter at the pristine plots was somewhat lower compared to that at the long-term drained plots, the difference was generally less than 1 ºC.

There was a strong effect of litter type and/or incubation layer on temperature patterns in the litter (Table 1). Daily mean temperature during summer and daily variation in temperature generally decreased in the direction: surface > moss > soil 10 cm > soil 20 cm (Table 2; see also Fig. 2). Opposite pattern was found for daily mean temperature during winter (not shown).

#### 3.1.3. Cellulose decomposition

Decomposition of cellulose (standard material) was used to capture for purely environmental effects on the decomposition process. The best environmental conditions for decomposition were generally in moss patches and soil 0-10 cm layer; worst on the surface litter layer of the pristine plots, in hollows of the pristine bog, and in the deepest (20-30 cm) soil layer (Appendix 4).

WT drawdown had a positive effect on cellulose decomposition ($p < 0.001$), and the effect was more pronounced in the long-term (decades) WT drawdown conditions. The effect of WT regime on cellulose decomposition was greatest in the surface and 0-10 cm soil layer, and decreased with increasing soil depth. In the surface layer, site nutrient regime had a positive effect on decomposition ($p < 0.01$) that was highest at the mesotrophic fen and lowest at the bog.

### *3.2. Litter decomposition*

#### 3.2.1. General

Decomposition rates varied considerably between the different litter types (Appendix 1-3). For the aboveground litters, mass loss rates decreased in the direction: 1) foliar litter (broad-leaved arboreal plants > minerotrophic graminoids > needle-leaved arboreal plants > ombrotrophic graminoids), 2) moss (feather moss > lawn species of *Sphagnum* > hummock species of *Sphagnum*), 3) woody litters. For the belowground litters, mass loss rates decreased in the direction: 1) minerotrophic graminoids, 2) fine roots (< 2 mm) of trees and shrubs, 3) ombrotrophic graminoids, 4) thicker roots (2-10 mm) of trees.

There was no between-year variation in 1-year decomposition rates.

### 3.2.2. Direct effects of WT drawdown

WT drawdown had a direct positive effect on litter decomposition ($p < 0.001$): the mass loss of common litter increased following the short-term WT drawdown, and increased further following the long-term WT drawdown. The effect of WT drawdown on belowground litter decomposition decreased with increasing soil depth ($p < 0.001$).

The effect of WT drawdown on aboveground litter had different patterns at sites with different nutrient regimes ($p < 0.01$). At the nutrient-rich mesotrophic fen the effect appeared already after the short-term WT drawdown, while at the nutrient-poor bog and the oligotrophic fen it appeared only after the long-term WT drawdown. Such differences were not observed for the belowground litter.

Of the site environmental parameters, soil N concentration and WT drawdown (STD, LTD) for aboveground litters (positive correlations) and installation depth for belowground litters (negative correlation; effect decreases with increasing soil depth) proved to be the best predictors of litter decomposition rates (Table 3). However, these parameters accounted for only less than 2% of the total variation in litter decomposition rates.

### 3.2.3. Indirect effects of WT drawdown

Litter decomposition rates at the community level (decomposition rates of different litter types weighted by their input) increased following WT drawdown (Fig. 3). At the fen sites the increase appeared already after the short-term WT drawdown, being most dramatic at the nutrient-rich mesotrophic fen, there the rates were even higher than those in the long-term drained conditions. At the nutrient-poor bog site the increase appeared only after the long-term WT drawdown.

Litter type accounted for about 65% of the total variation in litter decomposition rate, which was far more than what was the effect of site environment (less than 2%). Litter type as such (39 types) captured for all the variation in initial litter quality in relation to variation in litter decomposition rates. For aboveground litters, our grouping of litter types into PFTs based on their decomposition rates (Table 4, 5 types; see also Fig. 4) required further inclusion of the concentration of extractable compounds and holocellulose to lignin ratio in the litter to the model (Table 3). These litter quality parameters showed positive correlation with the decomposition rates. When litter types or PFTs were not included in the model, the litter quality parameters that were most related to mass loss rates included concentration of total extractives and N (positive correlation with mass loss), Klason lignin and p-hydoxyphenols (lignin-like compounds, negative correlation with mass loss). These parameters accounted for about 40% of the total variation in aboveground litter mass loss (not shown).

### 3.2.4. Effects of site nutrient regime

Site nutrient regime had an effect on litter decomposition at the surface litter layer and at the 0-10 cm soil depth ($p < 0.001$). Within the fens, the decomposition increased with increasing nutrient availability, being higher at the nutrient-rich mesotrophic fen. However, at the nutrient-poor bog the decomposition was as high as at the mesotrophic fen (surface litter layer) or even higher (0-10 cm soil depth).

In pristine conditions and after the short-term WT drawdown, decomposition rates at the community level were higher at the mesotrophic fen compared to the nutrient-poorer bog and the oligotrophic fen. After the long-term WT drawdown, the rates were very similar at all three sites.

### *3.3. Accumulation of organic matter*

Following changes in litter inputs (Fig. 3 in Straková *et al.* 2010), the amount of accumulated organic matter increased dramatically after the long-term WT drawdown and its composition greatly changed (Fig. 5). The clearest effect was an increase in remains of tree litters (leaves, needles, branches, cones) following the long-term WT drawdown. The accumulated organic matter consisted mainly of *Sphagnum* and graminoids at the pristine plots and after the short-term WT drawdown. Those materials were reduced after long-term WT drawdown and other moss species, mostly *P. schreberi* increased in amounts.

## 4. Discussion

There are three main factors that influence decomposition dynamics *in situ*: (1) quality of litter as the substrate for decomposing organisms, (2) the type and abundance of the decomposers, and (3) the environmental conditions (e.g., temperature, moisture, oxygen and nutrient availability, pH) under which the decomposers live and assimilate the litter (Belyea 1996; Laiho 2006). In this study we focused on the effects of changing peatland hydrology on litter decomposition at plant species (i.e. affected mainly by the environmental changes; direct effects) and community levels (i.e. additionally affected by the successional changes in vegetation community; indirect effects) at sites with different nutrient regimes. As peatlands contain a major proportion of the terrestrial C pool, predictions of their C cycle under a changing climate and/or land-use are of great importance.

### *4.1. Direct effects of WT drawdown overruled by the indirect effects*

As hypothesized, WT drawdown had direct positive effects on litter decomposition rates, but in the long-term (decades) they were overruled by the indirect effects via changes in plant community composition and production. This resulted in large accumulation of organic matter at the long-term drained plots, in spite of increased decomposition rates of the litter.

Our results show that litter type or PFT as such may predict, to a large extent, the variation in litter decomposability. This finding is supported by earlier studies (e.g., Hobbie 1996; Thormann *et al.* 2001; Dorrepaal *et al.* 2005; Bragazza *et al.* 2007; Cornwell *et al.* 2008). We propose that the variation in litter quality between the different materials (Straková *et al.* 2010) and consequent differences in activity and composition of microbial communities (Thormann *et al.* 2004; Peltoniemi 2010; Straková *et al.* 2011) are largely responsible for the variation in decomposition rates; the litter type/litter quality effect is, in the active surface layers, stronger than the effect of the environment. For example, the specific chemical quality of *Sphagnum* moss suppresses its decomposition (e.g., Bragazza *et al.* 2007), in spite of favourable environmental conditions for decomposition provided by moss patches as shown by our results on cellulose decomposition.

Though no single chemical parameter could predict the variability in decomposition dynamics associated with such different materials as included in this study (see also Bragazza *et al.* 2007), reasonable predictions were obtained with a few chemical parameters: concentrations of total extractives and N (positive correlation with mass loss), Klason lignin and p-hydoxyphenols (lignin-like compounds, negative correlation with mass loss). This gives the general characteristic of a substrate that the decomposers prefer to utilize: rich in nutrients, with high proportion of easily degradable compounds relative to the recalcitrant fraction.

We found total extractives (i.e. sum of nonpolar- (dichloromethane-) and polar- (acetone-, ethanol- water-) extractives) being somewhat better related to litter mass loss than water extractives used in earlier decomposition studies (Gholz *et al.* 2000; Preston & Trofymow 2000; Trofymow *et al.* 2002; Vávřová *et al.* 2009) or in decomposition models predicting litter mass loss (e.g., Moorhead *et al.* 1999; Liski *et al.* 2005). This finding may be influenced by the number of different materials used in this study, which was higher than in any earlier studies.

It is noteworthy that besides the increased soil aeration (direct effect of WT drawdown), environmental conditions for decomposition are in long-term further changed through the changes in vegetation (indirect effect of WT drawdown). The litter layer might, together with increasing tree canopy, serve as protection against UV-B radiation that has negative effects on litter decomposers (Gehrke *et al.* 1995; Duguay & Klironomos 2000), as well as insulation keeping favourable moisture conditions. Such effects were not explicitly measured in this study and thus cannot be separated from the direct effects of WL drawdown.

This study shows a drop in temperature associated with the site forestation, possibly due to tree canopy shading and evaporative cooling effect of trees. We did not find any negative effect of such decrease in temperature on litter decomposition rates (cf. Dorrepaal *et al.* 2009). The temperature effect was possibly overruled by other effects, i.e. litter type and soil characteristics, as those also changed following WT drawdown. Also, fresh litter represents the youngest, most easily decomposable organic matter that has low temperature sensitivity (Karhu *et al.* 2010).

### *4.2. Effects of site nutrient regime and soil depth*

As expected, litter decomposition rates at the community level correlated positively with site nutrient regime. Contrary to that, decomposition of the common litter at the nutrient-poor bog was not slower compared to that at the fens, even though environmental conditions for decomposition were indeed worse at the bog, as shown by our results on cellulose decomposition. One possible explanation of this finding is adaptation and specialization of decomposers to plant species characteristic of a given community, a “home field advantage” (Hunt *et al.* 1988; Gholz *et al.* 2000; Bragazza *et al.* 2007). Litter types included here in common litter represent plant species more typical of bogs: *B. nana*, *E. vaginatum* and *P. sylvestris*. Such litters then decompose more slowly in communities that have lower abundance of comparable plant and associated microbial decomposers, independent of favourable environmental conditions. This mechanism may in fact be also included in the increase of decomposition rates of common litter following WT drawdown as the species are also more typical of the drained plots (indirect effect of WT drawdown).

Decomposition rates of belowground litter decreased with depth. It is noteworthy that it was the distance from the soil surface that determined decomposition rates, rather than the distance from the WT. Soil compaction with associated change in the soil pore size distribution towards higher proportion of small pores that may protect litter against microbial attack (Breland & Hansen 1996), as well as decrease in litter summer temperature with soil depth (see Table 2) may slow down the decomposition process in deeper soil layers, independently of the WT position.

### *4.3. Accumulation of organic matter*

In long-term, dramatically increased litter inputs (Straková *et al.* 2010) resulted in large accumulation of organic matter in spite of increased decomposition rates. This emphasizes the significance of litter production: if the inputs are high, organic matter accumulates at a site despite the high litter decomposition rates.

The C balance of a drained peatland depends on 1) the rate of decomposition of the ‘‘old C’’ (peat accumulated before the WT drawdown), and 2) the rates of inputs and decomposition of the ‘‘new C’’ (biomass produced by the changed vegetation after the WT drawdown) under the new environmental conditions (Laiho 2006). If the accumulation (inputs – decomposition losses) of the new organic matter exceeds the decomposition losses from the old peat, the peatland will remain a sink of C. If not, then the peatland will become a source of C to the atmosphere. The estimated annual C loss via heterotrophic soil respiration ranges from 145-670 g $m^{-2}$ in boreal forestry-drained peatlands (Ojanen *et al.* 2010). The annual C inputs via litter production estimated in this study ranged from 190 to 200 g $m^{-2}$ for the forestry-drained (LTD) plots, and from such inputs 110-130 g $m^{-2}$ remained after 2 years. Considering that relatively large part of the measured litter losses (10-30%) may still be retained in the soil (Domish *et al.* 2000), it seems that a drained peat soil may, under certain conditions defined mainly by the site nutrient regime (Ojanen *et al.* 2010), still act as a sink of atmospheric C. When the whole ecosystem C balance is estimated, tree biomass accumulation must be included in the calculations. In our study sites the tree stand retained 1300-5300 g $m^{-2}$ C in the forestry-drained plots compared to 40-80 g $m^{-2}$ C in the pristine (undrained) plots (Anttila 2008).

Our assumptions are based on 2-year decomposition data only, however. Longer-term decomposition results are needed to validate the further behaviour of the accumulated organic matter at the different WT regimes. Also, the measured “old C” loss may not include the possible priming effect of litter inputs on peat decomposition, as litter was removed from the sites before each measurement (Ojanen *et al.* 2010). The possible role of this should also be investigated.

### *4.4. Time-scale of the effects*

As presumed, the indirect effects of WT drawdown on litter decomposition, via changes in plant community structure, dominated in the long-term (decades) relative to short-term (years). The short-term changes reflect transient conditions where the direct effects of WT drawdown are dominant: improved conditions for aerobic decomposition are linked with unchanged or lowered amounts of organic matter inputs, most likely facilitating a net C loss from the soil. In contrast, the long-term changes reflect a longer-lasting situation as the ecosystem becomes adapted to the new conditions and the indirect effects of WT drawdown get dominance: the increased litter inputs may at least partly compensate for the increased rates of peat decomposition. So far, too few studies have considered the long-term aspect.

### *4.5. Implications for soil C modelling*

Our results demonstrate that the shift in vegetation composition as a response to climate and/or land-use change is the main factor affecting the peatland ecosystem C cycle (see also Straková *et al.* 2010). Thus, dynamic vegetation is a necessity in any models applied for estimating responses of C fluxes to changes in environmental conditions. It is noteworthy that the time scale for vegetation changes caused by hydrological changes needs to extend to decades.

We provide possible grouping of litter types into plant functional types based on their decomposition rates (Table 4; 5 types for aboveground litter and 3 types for belowground litter) that the models could directly utilize. As litter types within these groups may still significantly vary in their quality, the PFT grouping suggested by Straková *et al.* (2010) based on detailed chemical characterization of litter would probably provide even better performance when the models allow for a narrower grouping.

Of the existing models, the dynamic global vegetation model LPJ-Why (Wania *et al.* 2009) includes 5 PFTs applicable for boreal peatlands: graminoids, *Sphagnum*, herbs, broad-leaved and needle-leaved boreal plants, which compares rather well to our grouping.

Distinguishing the different sections of *Sphagnum*, and minerotrophic versus ombrotrophic graminoids, would probably increase the accuracy of the model. The same holds for, e.g., the ecosystem-level models by Zhang *et al.* (2002) and Bauer (2004). An updated version of the Holocene Peat Model (HPM) uses 12 PFTs based on productivity and rooting characteristics (Frolking *et al.* 2010). HPM now distinguishes within vascular PFT's whether they are minerotrophic or ombrotrophic, and within Sphagna their preference of microform, which corresponds to our grouping. However, this model does not distinguish trees or belowground litter. Since trees are an integral part of many present-day peatlands, and based on palaeoecological studies characterized several currently wet treeless sites during a drier climate period, they should be considered also in peatland models even if the general perception of a peatland is wet, treeless, and *Sphagnum*-dominated. With trees, especially, comes also the need to distinguish different litter types, since woody materials decompose at rates different from the foliar litters of the same species.

The clear evidence of lowered soil temperature as a response to WT drawdown when an initially open peatland converts into a forest ecosystem is another outcome of our study that the models could directly utilize. In the existing models the possible lowering of soil temperature as the long-term response of a peatland ecosystem to climatic warming has not yet been considered.

Our materials generally showed a non-linear mass loss over the 2-year study period: most of the mass was lost during the first year and further decomposition slowed down. Decomposition of organic matter has often been described with the exponential decay, i.e. negative exponential function, following Olson (1963), which implies that decomposition approaches zero with time. This function may be suitable for the initial phase of decomposition, but may not fit the later phases when decomposition gets slow while considerable proportion of litter still remains (Latter *et al.* 1998). The fit of the negative exponential function to our litter materials was generally poor, and especially so for belowground litter. This suggests lower applicability of the negative exponential function in peatlands where decomposition is generally suppressed by waterlogged conditions, compared to mineral soil sites.

## 5. Conclusions

The study demonstrates that the direct effects of changing climate and/or land-use on decomposition and C accumulation in peatlands are in long-term (decades) overruled by the indirect effects via changes in vegetation community composition. Even though plant litter decomposition rates increase following WT drawdown, the accumulation of new organic matter also increases due to proportionally more increased litter inputs. The accumulation may even exceed decomposition of the old peat at the nutrient-poor (bog) sites. Some boreal peatlands may thus still act as a sink of atmospheric C under changing climate and/or land-use, but the quality (chemical composition) of accumulated C will greatly differ from that accumulated in pristine conditions. Longer-term decomposition results are needed to validate the further behaviour of the accumulated organic matter at the different WT regimes.

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**Table 1** Variation partitioning by redundancy analysis (RDA) showing the percentage of the total variation in litter temperature explained by litter type, incubation layer, site nutrient and water table regime. All effects are significant at $p < 0.002$.

| | daily mean T | | daily variation in T | |
|---|---|---|---|---|
| Main effect | F-ratio | explanatory power (%) | F-ratio | explanatory power (%) |
| litter type [1,2,3] | 14.4 | 22.4 | 42.5 | 37.9 |
| incubation layer [1,2,3] | 54.9 | 15.2 | 201.7 | 32.5 |
| nutrient regime [2,4,5] | 23.4 | 4.2 | 36.4 | 4.3 |
| WT regime [1,4,5] | 69.9 | 12.6 | 128.3 | 15.1 |
| interaction of nutrient and WT regime [1,2,4,5] | 15.7 | 5.1 | 40.1 | 7.5 |

T, temperature; WT, water table. Covariables used in the test: [1] nutrient regime; [2] WT regime; [3] interaction of nutrient and WT regime; [4] incubation layer; [5] litter type.

**Table 2** Average mean air temperature and cumulative temperature sum at the different litter incubation layers and site water table regimes. Data from the oligotrophic fen site and the year 2005.

| | pristine | | short-term WT drawdown | | long-term WT drawdown | |
|---|---|---|---|---|---|---|
| | T sums, d.d. > 0 ºC annual (summer) | mean T, ºC annual (summer) | T sums, d.d. > 0 ºC annual (summer) | mean T, ºC annual (summer) | T sums, d.d. > 0 ºC annual (summer) | mean T, ºC annual (summer) |
| surface | 2244 (1976) | 6.1 (12.9) | 2268 (1998) | 6.2 (13.1) | 2079 (1832) | 5.7 (12.0) |
| moss | 2273 (1957) | 6.2 (12.8) | 2129 (1856) | 5.8 (12.1) | 2042 (1777) | 5.6 (11.6) |
| soil 10 cm | 2243 (1911) | 6.1 (12.5) | 2188 (1849) | 6.0 (12.1) | 1947 (1651) | 5.3 (10.8) |
| soil 20 cm | 2205 (1834) | 6.0 (12.0) | 2263 (1812) | 6.2 (11.8) | 2007 (1560) | 5.5 (10.2) |

d.d.; degree days over 0 ºC threshold; summer, mid May-mid October; T, temperature

**Table 3** Hierarchical linear models showing parameters most related to variation in litter decomposition rates. The models accounted for 72.2% and 63.7% of the total variation in litter decomposition rates for the aboveground (including mosses) and belowground litter, respectively.

| Fixed part<br>Effect | Coefficient | Random part<br>Effect | Variance<br>component |
|---|---|---|---|
| **Aboveground litter** | | | |
| Constant | -9.665 (1.572) | Site | *2.020 (1.704)* |
| Time | 9.238 (0.376) | Incubation location | 15.941 (2. 090) |
| PFT 1 | 39.644 (1.783) | Recovery cohort | 46.720 (2.072) |
| PFT 2 | 20.257 (1.316) | | |
| PFT 3 | 12.600 (0.994) | | |
| PFT 4 | 4.123 (1.095) | | |
| PFT 5 used as reference | | | |
| Soil N | 3.224 (0.727) | | |
| Water table drawdown | 2.261 (0.570) | | |
| Pristine plots used as reference | | | |
| Litter hol:lig ratio | 0.462 (0.202) | | |
| Litter TE | 0.252 (0.051) | | |
| **Belowground litter** | | | |
| Constant | 5.045 (1.445) | Site | *9.925 (5.580)* |
| Time | 7.097 (0.418) | Incubation location | 24.501 (3.541) |
| PFT 6 | 28.798 (1.798) | Recovery cohort | 39.909 (2.067) |
| PFT7 | 16.122 (1.070) | | |
| PFT 8 used as reference | | | |
| Depth 0-10 cm | 4.799 (0.457) | | |
| Deeper layers (10-30 cm) used as reference | | | |

Standard errors in parentheses, nonsignificant effect terms in italics.

Litter hol:lig ratio, holocellulose to lignin ratio in the litter; Litter TE, concentration of total extractives in the litter; Soil N, N concentration in the soil. See Table 4 for the grouping of litter types into PFT 1-8.

**Table 4** Recommended separation of plant functional types (PFT) and litter types within PFTs for modelling peatland C dynamics, based on litter decomposition rates.

| PFTs and litter types to be distinguished | Species representing the PFTs in our material |
|---|---|
| **Aboveground litter** | |
| 1. Herbs | *Rubus chamaemorus* |
| 2. Broad-leaved and needle-leaved arboreal plants, minerotrophic graminoids: foliar litter | *Betula nana, B. pubescens, Ledum palustre, Vaccinium uliginosum, Pinus sylvestris, Carex lasiocarpa, C. rostrata* |
| 3. Ombrotrophic graminoids: foliar litter, feather moss, *Sphagnum* moss: section Cuspidata | *Eriophorum vaginatum, Trichophorum cespitosum, Pleurozium schreberi, S. fallax, S. angustifolium* |
| 4. *Sphagnum* moss: sections Acutifolia and Palustria | *S. russowii, S. magellanicum, S. fuscum, S. papillosum; S.balticum (section Cuspidata) grouped with these species* |
| 5. Woody litter (FWD, cones) | *B. nana, B. pubescens, P. sylvestris, V. uliginosum* |
| **Belowground litter** | |
| 6. Minerotrophic graminoids | *C. lasiocarpa, C. rostrata* |
| 7. Fine roots (< 2 mm) of trees and shrubs | *B. nana, P. sylvestris* |
| 8. Ombrotrophic graminoids and thicker (2-10 mm) tree roots | *E. vaginatum, P. sylvestris* |

FWD; fine woody debris with diameter up to 25 mm.

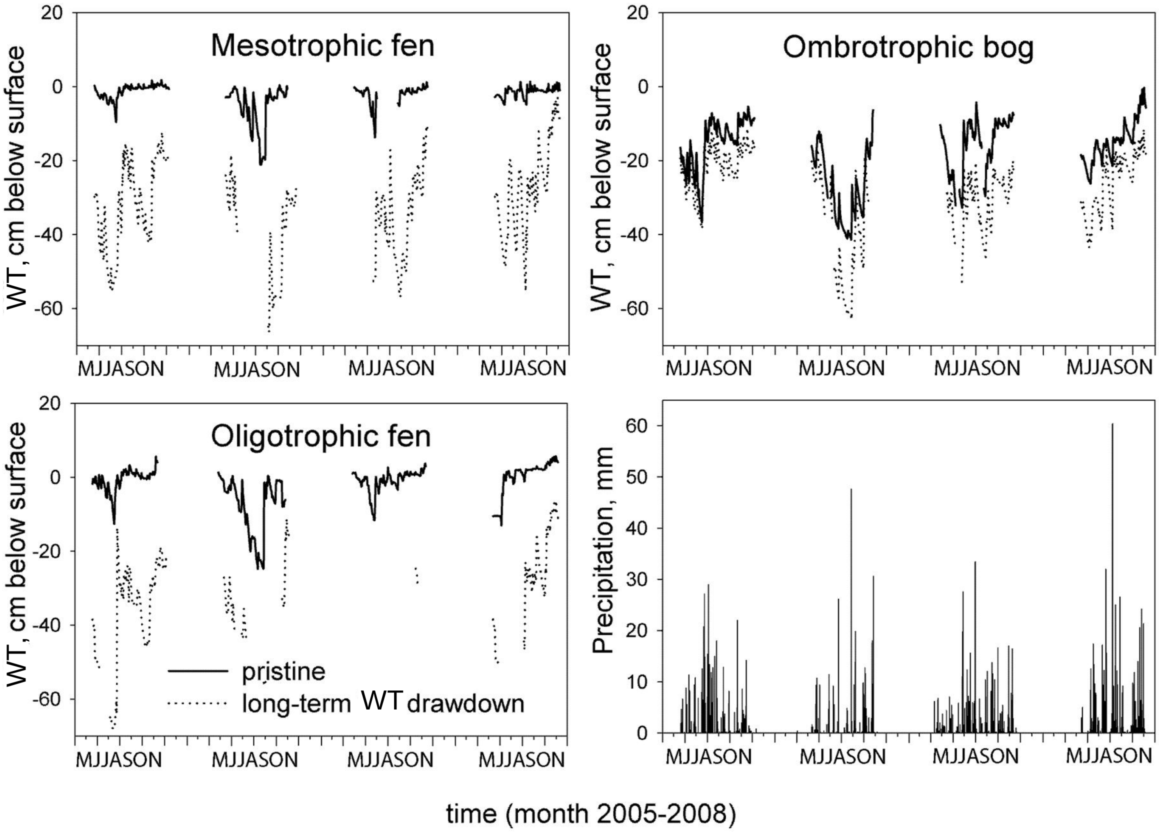



**Fig. 1** Variation in water table (WT) in pristine conditions and after the long-term WT drawdown during May - November 2005-2008.

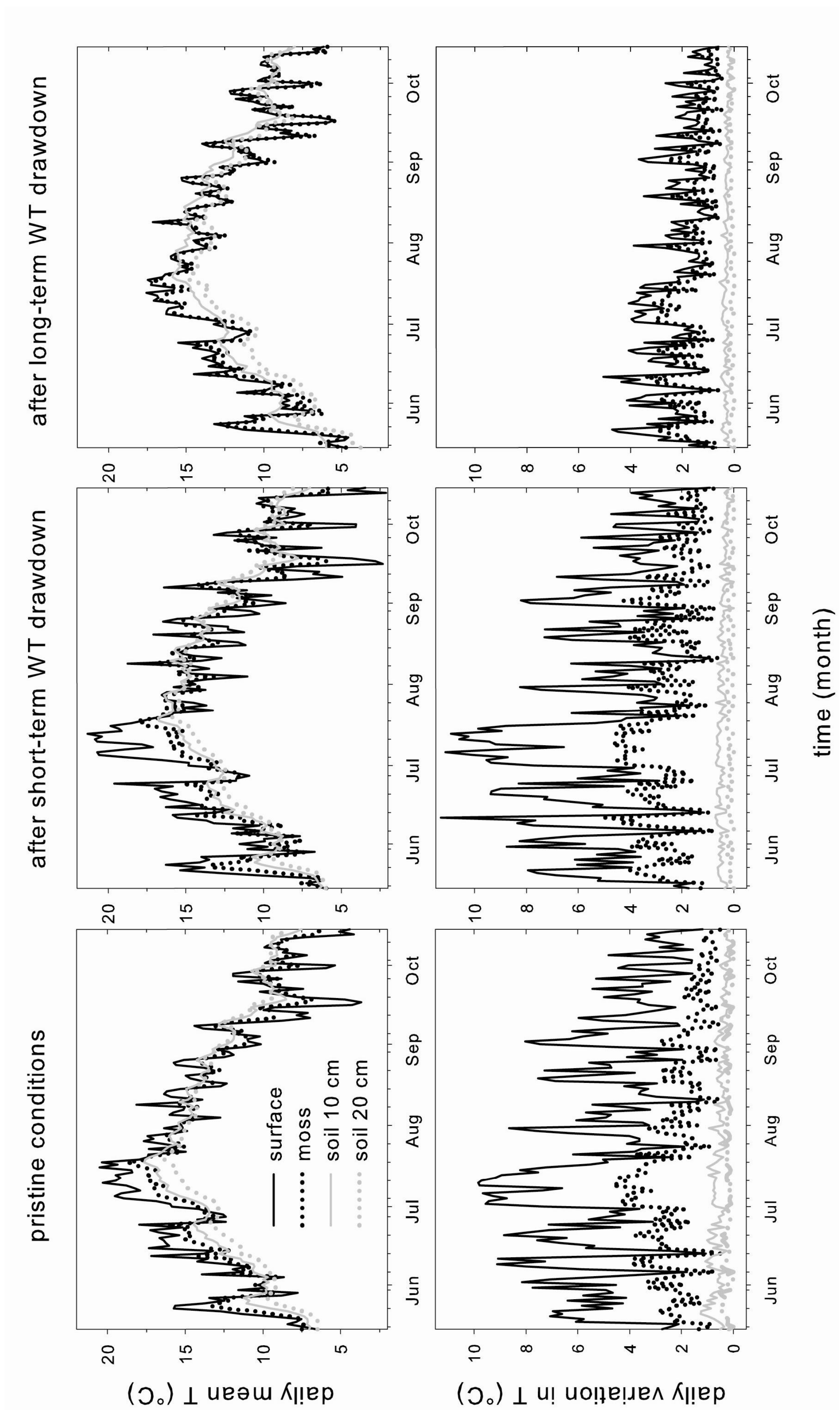



**Fig. 2** Effect of incubation layer and site water table regime on temperature patterns during one vegetation season (mid May-mid October 2005). Data from the oligotrophic fen site. T, temperature; WT, water table.

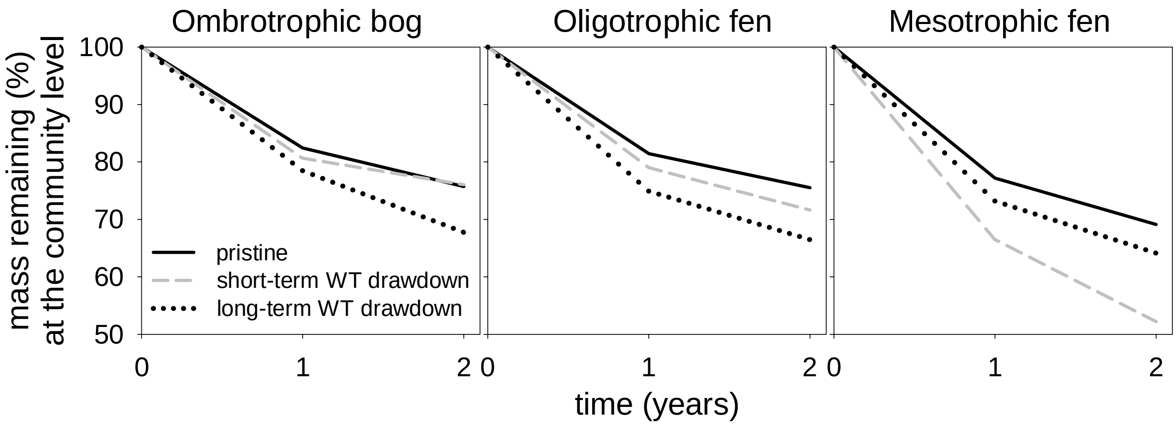



**Fig. 3** Decomposition rates at the community level (weighted average of decomposition rates of the litter types present at the given nutrient and WT regime plot; annual input of each litter type (g $m^{-2}$) in year 1 and year 2 used as the weight).

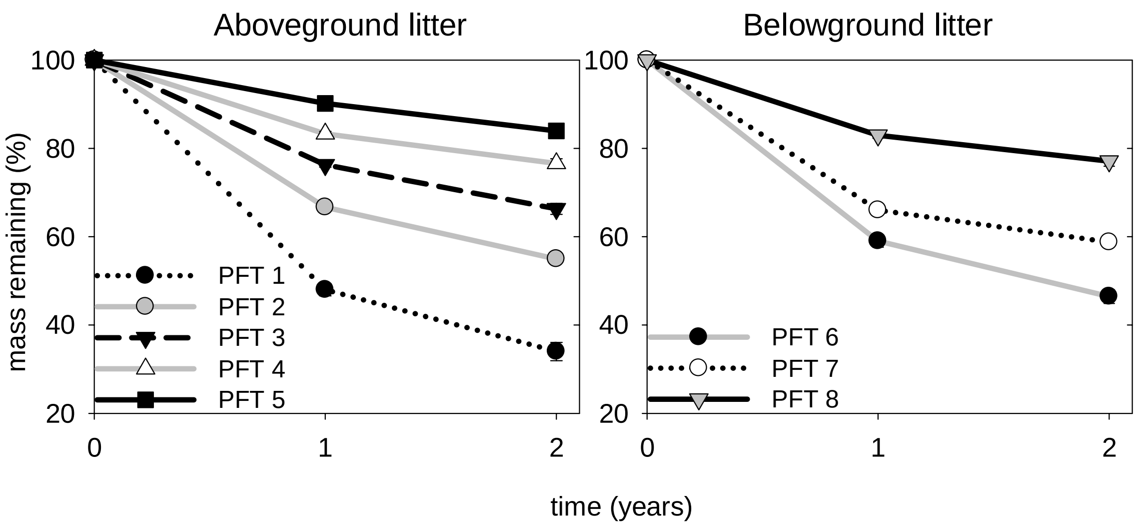



**Fig. 4** Remaining litter mass following decomposition. Data are presented as means ± S.E. per plant functional type (PFT); data for belowground litter include only the topmost (0-10 cm below soil surface) installation layer. See Table 4 for litter types included in PFT 1-8.

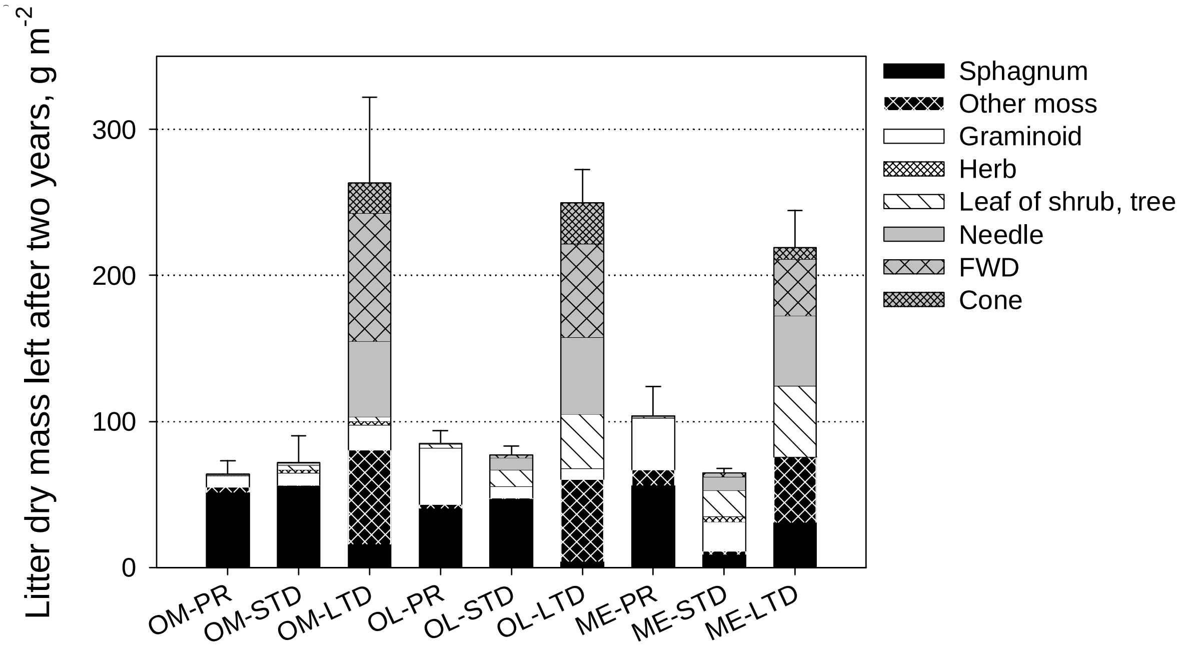



**Fig. 5** Accumulation of organic matter: remains of annual litter inputs after two years of decomposition. The error bars show standard errors for the total mass. FWD, fine woody debris (twigs, branches, bark).

Site nutrient regimes: OM, bog (ombrotrophic); OL, oligotrophic fen (minerotrophic); ME, mesotrophic fen (minerotrophic). Site water table (WT) regimes: PR, pristine; STD short-term WT drawdown; LTD long-term WT drawdown.

**Appendix 1.** Litter mass loss (% of initial dry mass) per litter type and nutrient and water table regime after 1 and 2 years of field decomposition with standard error of mean in parentheses.

| litter type | PFT | *n* | *OM-PR* year 1 | *n* | year 2 | *n* | *OM-STD* year 1 | *n* | year 2 | *n* | *OM-LTD* year 1 | *n* | year 2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| RC-L[a] | 1 | *10* | 49.06 (2.61) | *5* | 68.57 (5.32) | *8* | 50.89 (3.73) | *5* | 70.88 (3.14) | *10* | 56.64 (1.52) | *5* | 67.63 (2.49) |
| BN-L[a] | 2 | *10* | 37.79 (2.10) | *5* | 49.18 (6.07) | *10* | 42.39 (1.77) | *5* | 58.65 (4.97) | *10* | 42.86 (2.77) | *5* | 50.86 (2.52) |
| BP-L[a] | 2 | | | | | | | | | *10* | 42.62 (2.81) | *5* | 62.38 (4.10) |
| LP-L | 2 | *4* | 30.65 (1.14) | *4* | 47.79 (3.68) | *4* | 30.05 (2.25) | *4* | 46.27 (1.55) | *5* | 34.34 (2.18) | *5* | 46.36 (3.51) |
| P-N[a] | 2 | *10* | 31.79 (0.79) | *5* | 47.96 (2.62) | *10* | 29.2 (1.11) | *5* | 44.02 (2.14) | *10* | 34.47 (1.6) | *5* | 50.76 (2.76) |
| VUL-L | 2 | *5* | 31.15 (1.79) | *5* | 43.82 (2.32) | *5* | 31.00 (1.9) | *4* | 47.49 (6.15) | *5* | 28.97 (3.67) | *5* | 37.10 (3.99) |
| EV-L[a] | 3 | *10* | 21.37 (1.63) | *5* | 37.08 (10.71) | *10* | 19.15 (1.60) | *5* | 30.57 (6.30) | *10* | 24.65 (2.72) | *5* | 34.84 (4.89) |
| PLS[a] | 3 | | | | | | | | | *8* | 23.6 (2.05) | *3* | 37.56 (4.10) |
| SA[a] | 3 | *4* | 40.49 (4.99) | *1* | 47.21 | *4* | 20.95 (3.06) | *1* | 36.61 | *8* | 25.52 (1.22) | *4* | 40.20 (2.93) |
| TRC-L[a] | 3 | *8* | 25.96 (2.13) | *4* | 34.03 (3.11) | *5* | 24.53 (0.95) | *3* | 29.24 (0.53) | | | | |
| SB[a] | 4 | *8* | 14.37 (1.13) | *4* | 17.83 (2.53) | *9* | 20.21 (1.97) | *4* | 25.47 (2.15) | | | | |
| SFC[a] | 4 | *10* | 12.25 (1.35) | *5* | 17.20 (2.63) | *10* | 15.78 (0.85) | *5* | 17.66 (2.82) | *10* | 16.73 (2.05) | *5* | 24.23 (1.58) |
| SMG[a] | 4 | | | | | | | | | *10* | 20.11 (1.80) | *5* | 27.73 (4.20) |
| SR[a] | 4 | | | | | | | | | *9* | 24.58 (2.48) | *3* | 35.51 (3.74) |
| BN-B I | 5 | *3* | 7.26 (1.13) | *3* | 14.57 (0.93) | *3* | 8.17 (0.40) | *3* | 13.09 (1.57) | *3* | 9.27 (1.30) | *3* | 11.55 (5.26) |
| BN-B II | 5 | *1* | 4.83 | *2* | 11.49 (0.57) | *2* | 6.54 (0.46) | *2* | 8.41 (1.32) | | | | |
| BN-B III | 5 | *3* | 5.73 (0.31) | *3* | 11.67 (2.15) | *3* | 3.77 (2.14) | *3* | 10.55 (3.87) | *3* | 4.25 (0.75) | *3* | 11.52 (9.24) |
| BP-B I | 5 | | | | | | | | | *10* | 11.59 (0.35) | *5* | 21.63 (1.36) |
| BP-B II | 5 | | | | | | | | | *10* | 9.06 (2.43) | *5* | 10.14 (1.87) |
| P-B I[a] | 5 | *10* | 10.65 (0.53) | *5* | 15.07 (1.05) | *9* | 8.28 (1.47) | *5* | 13.39 (0.51) | *10* | 13.24 (1.10) | *5* | 19.01 (1.40) |
| P-B II[a] | 5 | *10* | 8.68 (0.75) | *5* | 14.08 (1.66) | *10* | 11.02 (1.76) | *5* | 15.66 (3.18) | *10* | 12.49 (1.31) | *5* | 21.14 (1.30) |
| P-B III | 5 | | | | | | | | | *4* | 4.07 (1.27) | *4* | 10.42 (1.40) |
| P-C | 5 | *4* | 7.94 (1.62) | *4* | 12.63 (0.73) | *4* | 6.77 (0.48) | *4* | 7.93 (0.87) | *5* | 7.14 (1.14) | *5* | 16.69 (2.05) |
| VUL-B I | 5 | *3* | 12.54 (0.36) | *3* | 24.68 (2.98) | *3* | 12.70 (0.55) | *3* | 23.16 (0.62) | *3* | 18.14 (0.44) | *3* | 28.19 (2.86) |
| VUL-B II | 5 | *2* | 6.23 (0.23) | *2* | 17.38 (4.73) | *1* | 7.98 | *1* | 15.43 | *5* | 8.47 (0.52) | *5* | 17.88 (2.09) |
| VUL-B III | 5 | *3* | 0 (0) | *3* | 11.86 (2.54) | *3* | 4.99 (0.47) | *3* | 9.65 (2.05) | *3* | 5.23 (0.54) | *3* | 15.02 (0.53) |
| BN-R 0-10[b] | 7 | | | | | | | | | *3* | 28.43 (2.05) | *3* | 39.68 (2.87) |
| P-R I 0-10[c] | 7 | *5* | 33.29 (1.12) | *5* | 39.20 (3.08) | *5* | 36.95 (2.85) | *5* | 47.00 (1.45) | *5* | 32.88 (1.64) | *5* | 48.76 (2.74) |
| P-R I 10-20[c] | 7 | *5* | 30.49 (1.35) | *5* | 30.13 (0.90) | *5* | 32.22 (3.95) | *5* | 38.68 (2.44) | *5* | 29.86 (1.13) | *5* | 38.89 (1.50) |
| P-R I 20-30[c] | 7 | *5* | 30.85 (0.88) | *5* | 30.21 (1.57) | *5* | 25.76 (5.35) | *5* | 31.95 (3.12) | *5* | 30.07 (1.85) | *5* | 34.52 (1.29) |
| EV-B 0-10[a] | 8 | *6* | 19.65 (1.29) | *3* | 22.09 (2.11) | *6* | 24.86 (1.09) | *3* | 22.46 (1.49) | *6* | 25.26 (0.45) | *3* | 26.23 (1.29) |
| EV-R 0-10[b] | 8 | *4* | 15.63 (2.74) | *4* | 37.00 (5.41) | *4* | 20.86 (2.77) | *4* | 39.50 (3.26) | *4* | 22.54 (4.59) | *4* | 30.50 (3.34) |
| EV-R 10-20[b] | 8 | *4* | 16.83 (2.15) | *4* | 27.07 (2.71) | *4* | 8.47 (3.86) | *4* | 32.90 (3.10) | *4* | 12.60 (3.24) | *4* | 26.18 (2.87) |
| EV-R 20-30[b] | 8 | *3* | 10.45 (1.70) | *3* | 24.02 (3.79) | *3* | 2.51 (1.47) | *3* | 32.03 (4.06) | *3* | 7.76 (0.89) | *3* | 21.76 (5.80) |
| P-R II 0-10[c] | 8 | *5* | 14.41 (0.82) | *5* | 13.83 (0.74) | *5* | 14.27 (0.54) | *5* | 17.33 (0.46) | *5* | 15.42 (1.42) | *5* | 26.70 (3.76) |
| P-R II 10-20[c] | 8 | *5* | 13.17 (1.17) | *5* | 14.17 (0.88) | *5* | 13.01 (0.78) | *5* | 13.66 (1.44) | *5* | 13.27 (0.59) | *5* | 20.03 (0.36) |
| P-R II 20-30[c] | 8 | *5* | 17.83 (1.25) | *5* | 18.82 (1.54) | *5* | 18.34 (0.90) | *5* | 16.99 (1.81) | *5* | 16.20 (1.18) | *5* | 20.85 (0.98) |

[a] extra 1 year set of litter bags installed in 2005; [b] installed in 2005; [c] installed in 2006; others installed in 2004. *n*, number of samples per litter type, nutrient and water level (WT) regime and year. Nutrient and WT regimes: LTD long-term WT drawdown; ME, mesotrophic fen (minerotrophic); OL, oligotrophic fen (minerotrophic); OM, bog (ombrotrophic); PR pristine; STD short-term WT drawdown. Litter types: BN-L, *Betula nana* leaves; BN-B, *B. nana* branches (diameter I, < 2mm; diameter II, 2-5 mm; diameter III, 5-10 mm); BN-R, *B. nana* roots; BP-L, *B. pubescens* leaves; BP-B, *B. pubescens* branches (diameter I, < 5mm; diameter II, 5-10 mm; diameter III, 10-25 mm); CL-L, *Carex. lasiocarpa* leaves; CL-R, *C. lasiocarpa* roots; CL-S, *C. lasiocarpa* rhizome (underground stem); CR-L, *C. rostrata* leaves; CR-R, *C. rostrata* roots; EV-L, *Eriophorum vaginatum* leaves; EV-B, *E. vaginatum* basal sheaths; EV-R, *E. vaginatum* roots; LP-L, *Ledum palustre* leaves; P-B, *Pinus sylvestris* branches (diameter I, < 5 mm; diameter II, 5-10 mm; diameter III, 10-25 mm); P-C, *P. sylvestris* cones; P-N, *P. sylvestris* needles; P-R, *P. sylvestris* roots (diameter I, < 2 mm; diameter II, 2-10 mm); PLS, *Pleurozium schreberi;* RC-L, *Rubus chamaemorus* leaves*;* SA, *Sphagnum angustifolium*; SB, *S. balticum*; SCU, *S. cuspidatum*; SFA, *S. fallax*; SFC, *S. fuscum*; SMG, *S. magellanicum*; SP, *S. papillosum*; SR, *S. russowii*; TRC-L, *Trichophorum cespitosum;* VU-B, *Vaccinium uliginosum* branches (diameter I, < 2mm; diameter II, 2-5 mm; diameter III, 5-10 mm); VU-L, *V. uliginosum* leaves. Instalation layer for belowground litters: 0-10, 0-10 cm below soil surface; 10-20 below soil surface, 10-20 cm; 20-30, 20-30 cm below soil surface.

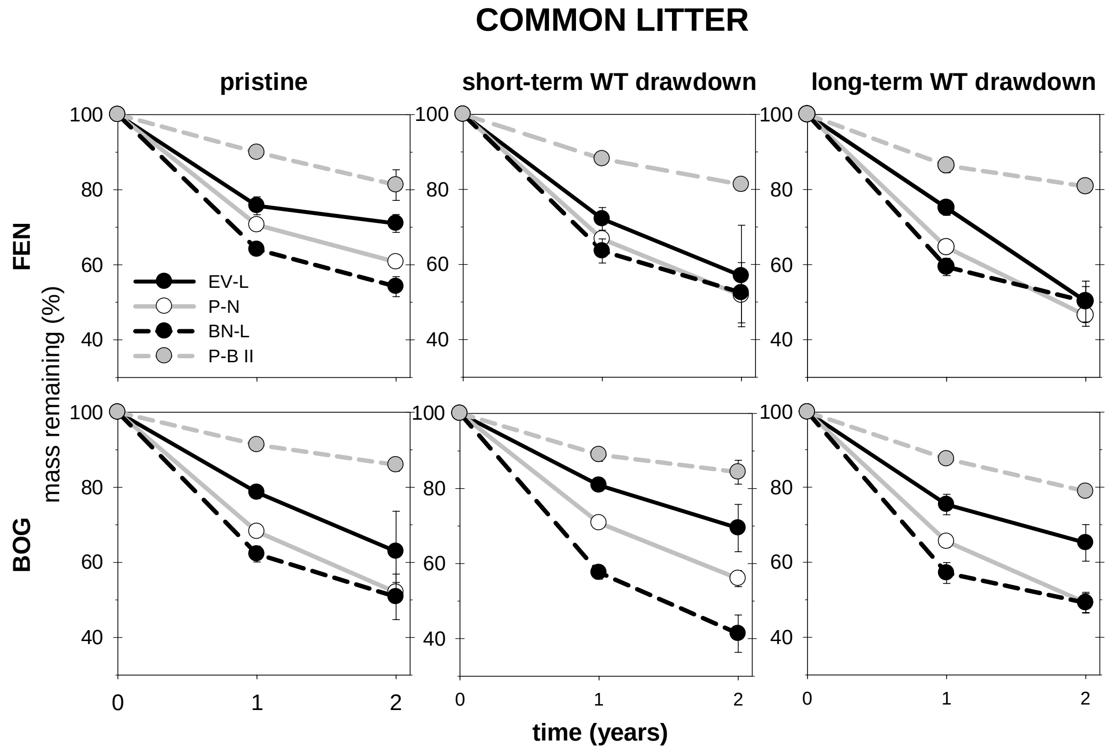
## **Appendix 1.** continued

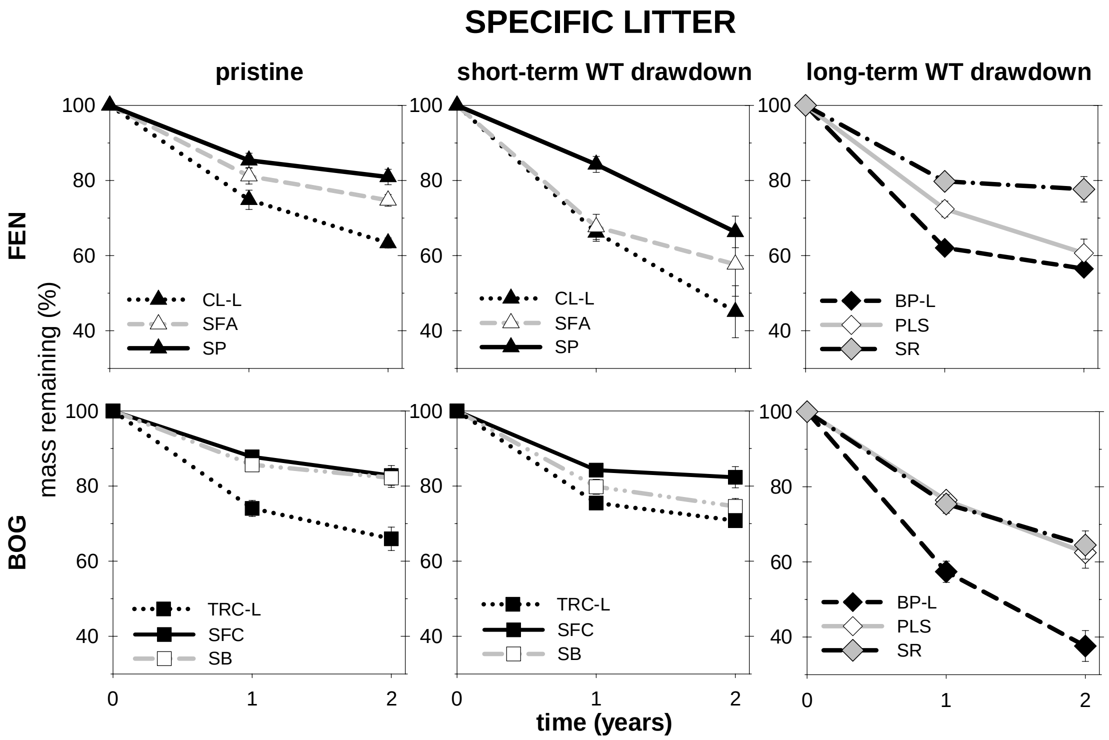
| litter type | PFT | *n* | *OL-PR* year 1 | *n* | year 2 | *n* | *OL-STD* year 1 | *n* | year 2 | *n* | *OL-LTD* year 1 | *n* | year 2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| EV-L[a] | 3 | 8 | 15.05 (1.76) | 4 | 21.06 (4.45) | 8 | 16.29 (2.20) | 4 | 45.63 (8.66) | 7 | 26.3 (2.40) | 3 | 33.31 (2.65) |
| CL-L[a] | 2 | 10 | 23.69 (1.17) | 5 | 32.14 (1.26) | 9 | 24.16 (0.99) | 5 | 42.22 (8.35) | | | | |
| CR-L[a] | 2 | 10 | 28.68 (1.09) | 5 | 36.45 (1.66) | 4 | 30.77 (1.81) | 4 | 43.36 (4.13) | | | | |
| TRC-L[a] | 3 | 9 | 23.03 (1.60) | 5 | 24.43 (0.95) | 9 | 28.31 (2.24) | 5 | 37.4 (2.78) | | | | |
| P-N[a] | 2 | 10 | 27.05 (0.52) | 5 | 35.56 (1.02) | 10 | 26.65 (0.74) | 5 | 38.12 (0.96) | 10 | 37.66 (1.11) | 5 | 53.13 (1.19) |
| BP-L[a] | 2 | | | | | | | | | 10 | 35.54 (0.95) | 5 | 49.61 (4.54) |
| BN-L[a] | 2 | 10 | 31.81 (1.98) | 5 | 41.44 (5.19) | 10 | 37.82 (7.11) | 5 | 42.4 (3.43) | 10 | 34.06 (2.95) | 5 | 43.35 (5.71) |
| VUL-L[a] | 2 | | | | | | | | | 5 | 30.74 (5.72) | 5 | 37.6 (7.46) |
| P-B I[a] | 5 | 10 | 15.35 (5.29) | 5 | 12.46 (0.30) | 10 | 8.34 (0.38) | 5 | 16.63 (3.97) | 10 | 18.71 (0.93) | 5 | 29.02 (2.30) |
| P-B II[a] | 5 | 10 | 7.93 (0.70) | 4 | 9.8 (2.01) | 9 | 6.29 (0.58) | 5 | 7.74 (0.70) | 9 | 11.61 (1.36) | 5 | 16.33 (1.80) |
| P-B III | 5 | | | | | | | | | 4 | 7.69 (3.02) | 4 | 22.28 (5.79) |
| P-C | 5 | 4 | 7.51 (0.57) | 4 | 10.92 (1.10) | 3 | 6.55 (0.99) | 4 | 10.84 (1.32) | 5 | 12.50 (4.50) | 4 | 17.04 (3.13) |
| BP-B I | 5 | | | | | | | | | 9 | 10.62 (1.65) | 5 | 17.26 (1.14) |
| BP-B II | 5 | | | | | | | | | 10 | 11.97 (2.27) | 5 | 20.85 (4.68) |
| BN-B I | 5 | 5 | 8.77 (0.84) | 5 | 11.83 (0.63) | 5 | 8.29 (1.04) | 5 | 11.49 (3.68) | 5 | 11.08 (1.21) | 5 | 18.17 (1.50) |
| BN-B II | 5 | 2 | 5.35 (0.24) | 2 | 8.90 (1.37) | 2 | 5.96 (1.48) | 2 | 19.21(5.86) | 2 | 7.44 (0.93) | 2 | 14.11 (2.38) |
| BN-B III | 5 | 5 | 6.48 (1.77) | 5 | 10.70 (0.75) | 5 | 5.29 (0.64) | 5 | 9.75 (2.01) | 3 | 10.83 (2.37) | 5 | 18.54 (2.33) |
| VUL-B I | 5 | | | | | | | | | 3 | 19.76 (0.58) | 3 | 31.28 (5.09) |
| VUL-B II | 5 | | | | | | | | | 2 | 10.05 (3.95) | 2 | 25.20 (2.78) |
| VUL-B III | 5 | | | | | | | | | 3 | 5.59 (0.69) | 3 | 27.73(14.72) |
| PLS[a] | 3 | | | | | | | | | 8 | 22.34 (2.23) | 4 | 29.11 (2.26) |
| SFA[a] | 3 | 8 | 21.56 (5.96) | 4 | 9.49 (2.56) | 8 | 13.93 (1.19) | 4 | 22.64 (3.18) | | | | |
| SA[a] | 3 | 2 | 33.51 (0.82) | 1 | 28.09 | 4 | 17.57 (1.38) | 1 | 21.68 | 8 | 19.32 (1.52) | 4 | 32.29 (1.41) |
| SP[a] | 4 | 9 | 8.17 (1.50) | 4 | 11.97 (0.37) | 8 | 14.05 (3.17) | 3 | 20.20 (3.45) | | | | |
| SMG[a] | 4 | | | | | | | | | 10 | 15.92 (1.47) | 5 | 24.69 (4.07) |
| SR[a] | 4 | | | | | | | | | 9 | 18.05 (1.47) | 4 | 25.7 (4.96) |
| EV-B 0-10[a] | 8 | 4 | 9.01 (4.63) | 2 | 6.85 (3.28) | 4 | 9.15 (3.02) | 2 | 9.50 (3.03) | 4 | 9.07 (4.04) | 2 | 12.41 (4.43) |
| EV-R 0-10 | 8 | 1 | 28.73 | 1 | 36.82 | 1 | 24.77 | 1 | 13.23 | | | | |
| EV-R 10-20 | 8 | 1 | 23.6 | 1 | 15.05 | 1 | 24.41 | 1 | 6.2 | | | | |
| CL-S 0-10[b] | 6 | 4 | 48.03 (3.55) | 4 | 55.39 (1.59) | 4 | 41.23 (2.84) | 4 | 64.45 (2.18) | | | | |
| CL-R 0-10[b] | 6 | 4 | 28.76 (1.62) | 4 | 40.52 (1.83) | 4 | 26.25 (4.89) | 4 | 45.06 (3.57) | | | | |
| CL-R 10-20[b] | 6 | 4 | 28.93 (1.67) | 4 | 36.49 (0.85) | 4 | 16.37 (4.46) | 4 | 38.53 (2.58) | | | | |
| CL-R 20-30[b] | 6 | 4 | 27.22 (1.43) | 4 | 34.02 (0.63) | 4 | 11.38 (6.98) | 4 | 36.53 (4.70) | | | | |
| CR-R 0-10[b] | 6 | 5 | 43.87 (2.99) | 5 | 57.46 (0.65) | 4 | 47.01 (3.63) | 4 | 51.82 (4.95) | | | | |
| CR-R 10-20[b] | 6 | 5 | 42.11 (3.77) | 5 | 54.06 (1.60) | 4 | 44.89 (8.97) | 4 | 46.55 (8.38) | | | | |
| CR-R 20-30[b] | 6 | 4 | 41.00 (4.05) | 4 | 48.32 (1.41) | 3 | 31.78 (8.98) | 3 | 50.33 (2.00) | | | | |
| P-R I 0-10[c] | 7 | 5 | 31.32 (1.24) | 5 | 36.88 (1.68) | 5 | 33.81 (1.18) | 5 | 41.96 (1.58) | 5 | 38.28 (1.67) | 5 | 46.03 (1.72) |
| P-R I 10-20[c] | 7 | 5 | 27.79 (1.77) | 5 | 32.78 (1.54) | 5 | 30.79 (1.51) | 5 | 34.58 (3.02) | 5 | 31.88 (1.70) | 5 | 36.90 (1.48) |
| P-R I 20-30[c] | 7 | 5 | 28.85 (1.06) | 5 | 33.81 (1.07) | 5 | 28.65 (0.97) | 5 | 33.77 (1.99) | 5 | 28.71 (1.47) | 5 | 33.60 (3.23) |
| P-R II 0-10[c] | 8 | 5 | 15.00 (0.95) | 5 | 17.34 (0.81) | 5 | 15.66 (1.90) | 5 | 25.24 (3.75) | 5 | 17.93 (0.95) | 5 | 35.57 (8.41) |
| P-R II 10-20[c] | 8 | 5 | 16.09 (0.76) | 5 | 17.24 (0.49) | 5 | 12.65 (0.88) | 5 | 15.60 (0.86) | 5 | 14.91 (1.06) | 5 | 20.00 (2.10) |
| P-R II 20-30[c] | 8 | 5 | 16.49 (1.66) | 5 | 19.51 (0.78) | 5 | 17.11 (1.50) | 5 | 20.34 (1.20) | 5 | 19.22 (1.08) | 5 | 18.80 (1.59) |

## **Appendix 1.** continued

| litter type | PFT | *n* | *ME-PR* year 1 | *n* | year 2 | *n* | *ME-STD* year 1 | *n* | year 2 | *n* | *ME-LTD* year 1 | *n* | year 2 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| EV-L[a] | 3 | 8 | 24.29 (2.37) | 4 | 29.00 (2.38) | 8 | 27.86 (3.02) | 4 | 43.04 (13.52) | 8 | 24.92 (1.94) | 4 | 49.76 (3.93) |
| CL-L[a] | 2 | 10 | 25.13 (2.57) | 5 | 36.64 (1.34) | 10 | 33.84 (2.37) | 5 | 54.94 (6.91) | | | | |
| CR-L[a] | 2 | 8 | 34.54 (2.19) | 5 | 41.38 (1.54) | 8 | 37.10 (2.15) | 4 | 43.98 (4.75) | | | | |
| TRC-L[a] | 3 | 8 | 27.67 (3.24) | 4 | 33.04 (2.98) | 8 | 30.73 (1.45) | 4 | 38.38 (4.52) | | | | |
| RC-L | 1 | | | | | | | | | 5 | 50.41 (2.26) | 5 | 56.95 (2.98) |
| P-N[a] | 2 | 10 | 29.38 (1.64) | 5 | 39.26 (1.59) | 10 | 33.25 (1.32) | 5 | 48.24 (0.91) | 10 | 35.41 (1.62) | 5 | 53.53 (2.89) |
| BP-L[a] | 2 | | | | | | | | | 10 | 37.95 (1.00) | 5 | 43.51 (0.88) |
| BN-L[a] | 2 | 10 | 35.92 (1.28) | 5 | 45.80 (2.66) | 10 | 36.40 (3.20) | 5 | 47.53 (8.03) | 10 | 40.63 (2.30) | 5 | 49.82 (5.45) |
| VUL-L | 2 | | | | | | | | | 2 | 24.17 (1.93) | 2 | 28.46 (0.40) |
| LP-L | 2 | | | | | | | | | 5 | 26.03 (3.11) | 5 | 41.82 (5.31) |
| P-B I[a] | 5 | 10 | 8.34 (0.52) | 5 | 12.06 (1.39) | 10 | 11.32 (0.73) | 5 | 14.04 (1.67) | 10 | 13.47 (1.05) | 4 | 18.65 (2.08) |
| P-B II[a] | 5 | 10 | 10.08 (1.09) | 5 | 18.76 (4.08) | 10 | 11.86 (1.43) | 5 | 18.73 (1.59) | 10 | 13.64 (1.85) | 5 | 19.20 (1.66) |
| P-B III | 5 | | | | | | | | | 4 | 6.48 (1.17) | 4 | 18.21 (2.75) |
| P-C | 5 | 4 | 7.5 (0.38) | 4 | 12.82 (1.90) | 4 | 9.09 (0.97) | 4 | 17.90 (1.68) | 5 | 8.16 (1.04) | 5 | 15.17 (1.83) |
| BP-B I[a] | 5 | | | | | | | | | 10 | 9.38 (0.74) | 5 | 16.87 (1.35) |
| BP-B II[a] | 5 | | | | | | | | | 10 | 7.11 (0.87) | 5 | 13.83 (2.88) |
| BP-B III | 5 | | | | | | | | | 3 | 8.87 (6.81) | 3 | 23.29 (9.87) |
| VUL-B I | 5 | | | | | | | | | 3 | 15.66 (2.62) | 3 | 28.65 (4.49) |
| VUL-B II | 5 | | | | | | | | | 2 | 9.47 (1.41) | 3 | 19.63 (5.27) |
| VUL-B III | 5 | | | | | | | | | 3 | 6.64 (0.97) | 2 | 20.28 (9.61) |
| PLS[a] | 3 | | | | | | | | | 8 | 27.59 (2.09) | 4 | 39.35 (3.75) |
| SFA[a] | 3 | 8 | 18.85 (2.10) | 3 | 25.3 (1.55) | 7 | 32.36 (3.37) | 3 | 42.32 (8.48) | | | | |
| SA[a] | 3 | 4 | 24.40 (1.56) | 2 | 45.52 (8.24) | 4 | 25.68 (1.79) | 1 | 59.26 | 8 | 23.01 (3.69) | 4 | 32.55 (4.64) |
| SP[a] | 4 | 9 | 14.65 (1.92) | 4 | 19.06 (2.06) | 8 | 15.72 (2.11) | 3 | 33.69 (4.19) | | | | |
| SMG[a] | 4 | | | | | | | | | 10 | 19.07 (1.62) | 5 | 32.03 (3.42) |
| SR[a] | 4 | | | | | | | | | 9 | 20.23 (1.78) | 4 | 22.33 (3.38) |
| EV-B 0-10[a] | 8 | 4 | 17.41 (0.83) | 2 | 17.81 (0.59) | 4 | 10.85 (1.65) | 2 | 13.56 (0.36) | 4 | 16.85 (2.15) | 2 | 16.89 (2.48) |
| EV-R 0-10 | 8 | 1 | 32.76 | 1 | 35.59 | 1 | 37.62 | 1 | 19.84 | | | | |
| EV-R 10-20 | 8 | 1 | 32.68 | 1 | 31.63 | 1 | 29.8 | 1 | 7.96 | | | | |
| CL-S 0-10[b] | 6 | 4 | 47.61 (0.29) | 4 | 54.77 (0.76) | 4 | 41.95 (1.53) | 4 | 58.11 (2.84) | | | | |
| CL-R 0-10[b] | 6 | 3 | 29.72 (1.56) | 3 | 35.55 (6.00) | 3 | 28.37 (2.29) | 3 | 42.37 (1.85) | | | | |
| CL-R 10-20[b] | 6 | 3 | 24.64 (0.71) | 3 | 32.73 (4.10) | 3 | 25.90 (2.11) | 3 | 33.96 (2.04) | | | | |
| CL-R 20-30[b] | 6 | 3 | 25.83 (1.44) | 3 | 31.57 (1.91) | 3 | 23.05 (1.46) | 3 | 32.85 (3.54) | | | | |
| CR-R 0-10[b] | 6 | 5 | 51.1 (2.34) | 5 | 64.45 (7.13) | 5 | 47.04 (1.89) | 5 | 60.17 (1.23) | | | | |
| CR-R 10-20[b] | 6 | 5 | 48.93 (4.40) | 5 | 54.88 (0.78) | 5 | 48.07 (3.41) | 5 | 56.47 (1.28) | | | | |
| CR-R 20-30[b] | 6 | 4 | 39.59 (1.60) | 4 | 50.35 (1.67) | 4 | 40.96 (3.83) | 4 | 51.40 (2.10) | | | | |
| P-R I 0-10[c] | 7 | 5 | 31.79 (0.81) | 5 | 38.41 (3.42) | 5 | 38.93 (1.59) | 5 | 39.49 (3.05) | 5 | 36.04 (2.99) | 5 | 39.12 (1.14) |
| P-R I 10-20[c] | 7 | 5 | 20.99 (3.29) | 5 | 35.35 (1.18) | 5 | 32.45 (2.96) | 5 | 33.17 (0.95) | 5 | 30.99 (3.41) | 5 | 39.56 (3.75) |
| P-R I 20-30[c] | 7 | 5 | 23.36 (2.21) | 5 | 34.64 (1.32) | 5 | 30.97 (2.32) | 5 | 34.23 (2.52) | 5 | 29.09 (2.81) | 5 | 31.59 (4.59) |
| P-R II 0-10[c] | 8 | 5 | 12.74 (0.71) | 5 | 17.57 (0.87) | 5 | 16.17 (1.41) | 5 | 20.01 (1.30) | 5 | 15.98 (0.84) | 5 | 22.06 (1.40) |
| P-R II 10-20[c] | 8 | 5 | 11.48 (0.77) | 5 | 17.22 (0.88) | 5 | 15.95 (0.38) | 5 | 18.29 (2.04) | 5 | 13.86 (1.24) | 5 | 16.43 (1.02) |
| P-R II 20-30[c] | 8 | 5 | 18.48 (2.14) | 5 | 23.63 (1.66) | 5 | 15.84 (0.93) | 5 | 20.76 (0.81) | 5 | 23.62 (5.78) | 5 | 18.86 (1.12) |
| BN-R 0-10[b] | 7 | 3 | 35.22 (0.57) | 3 | 30.11 (1.68) | 3 | 28.40 (2.69) | 3 | 36.24 (1.68) | 3 | 32.01 (3.58) | 3 | 49.22 (2.82) |

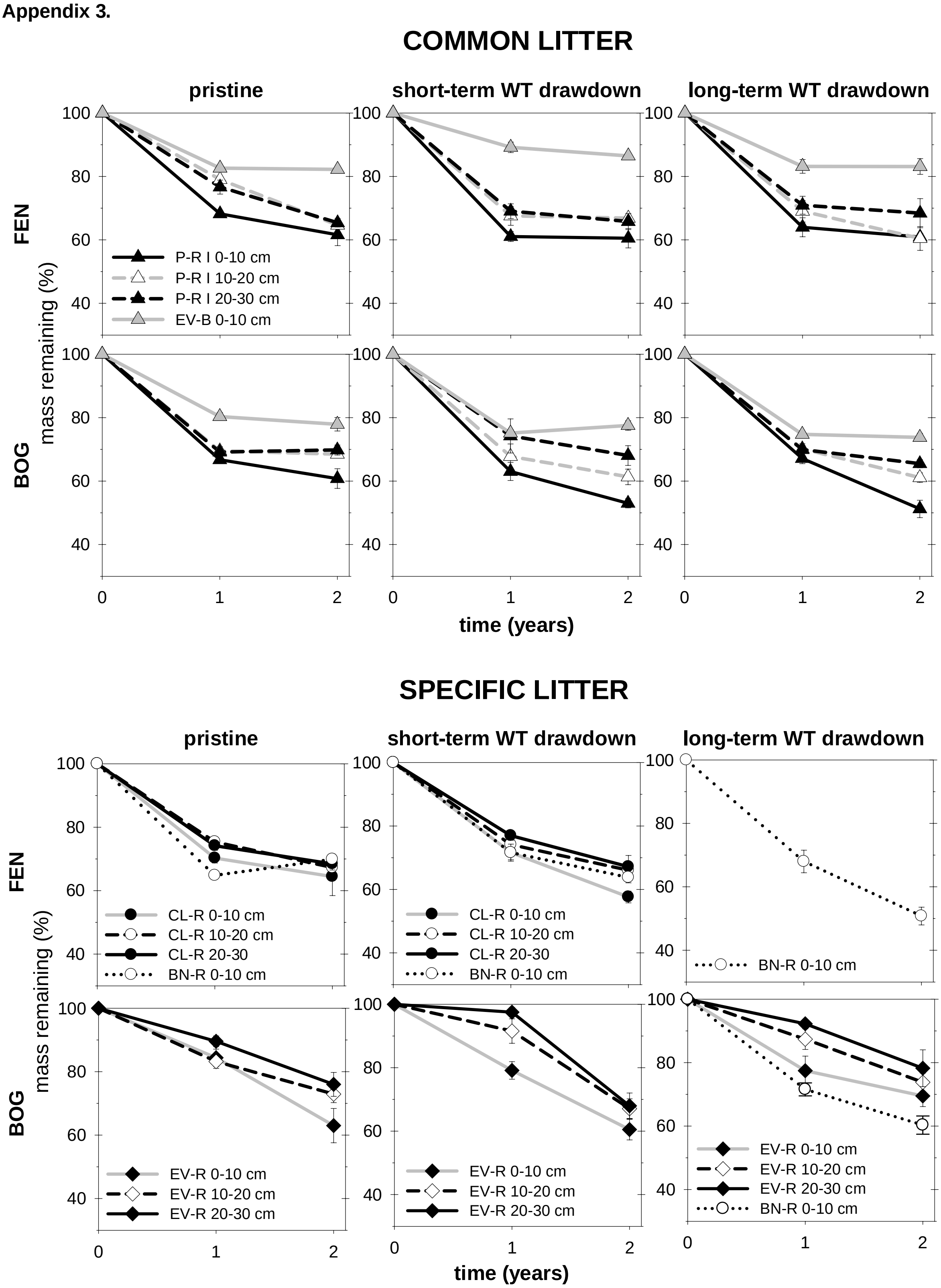
**Appendix 2.**



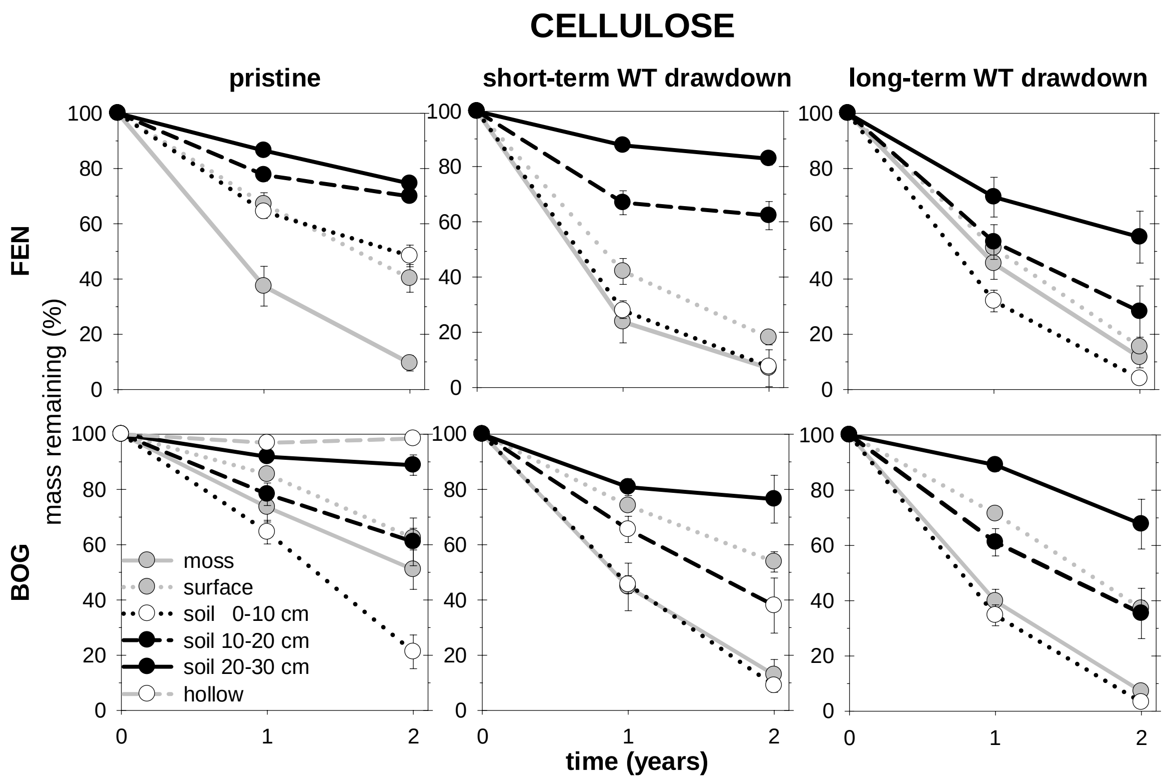

Remaining litter mass following decomposition, examples for common (common to all plots) and specific (typical of only certain nutrient and WT regimes) aboveground litter types. Data are presented as means ± S.E. BOG, ombrotrophic bog; FEN, mesotrophic fen; WT, water table. Litter types: BN-L, *Betula nana* leaves; BP-L, *B. pubescens* leaves; CL-L, *Carex. lasiocarpa* leaves; EV-L, *Eriophorum vaginatum* leaves; P-B II, *Pinus sylvestris* branches (diameter 5-10 mm); P-N, *P. sylvestris* needles; PLS, *Pleurozium schreberi*; SB, *Sphagnum balticum*; SFA, *S. fallax*; SFC, *S. fuscum*; SP, *S. papillosum*; SR, *S. russowii*; TRC-L, *Trichophorum cespitosum* leaves.

**Appendix 3.**




Remaining litter mass following decomposition, examples for common (common to all plots) and specific (typical of only certain nutrient and WT regimes) belowground litter types. Data are presented as means ± S.E. BOG, ombrotrophic bog; FEN, mesotrophic fen; WT, water table. Litter types: BN-R, *Betula nana* roots; CL-R, *Carex lasiocarpa* roots; EV-B, *Eriophorum vaginatum* basal sheaths; EV-R, *E. vaginatum* roots; P-R I, *Pinus sylvestris* roots (diameter < 2 mm).

**Appendix 4.**




Remaining cellulose mass following decomposition. Data are presented as means ± S.E. BOG, ombrotrophic bog; FEN, mesotrophic fen; WT, water table.