Long-Term Monitoring of Scots Pine Litter Decomposition Rates Throughout Sweden Indicates Formation of a More Recalcitrant Litter in the South

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Abstract Decomposition studies were carried out at sites throughout Sweden, including the four Integrated Monitoring sites. Scots pine needle litterbag weight loss measurements over 3 or 5 years were determined at 26 sites and repeated up to 27 times, depending on the site. Humus layer respiration rates were determined for 20 sites in 1987–1989 and repeated in 2007–2008. Partial Least Squares (PLS) regression was used to elucidate the relative importance of climatic and soil factors. Annual needle weight losses decreased only slowly (20–10%) over 3–5 years for all northern ($>60^{\circ}\text{N}$) sites but decreased sharply from 30 to 10% in the third year in southern ($<60^{\circ}\text{N}$) sites. Respiration rates of southern sites were less (40% on average) than those of northern sites. Humus layer N was positively correlated to needle weight loss during the first and the second years, but negatively correlated in the third year and to respiration rates. The results indicated that litter formed in southern Sweden became more recalcitrant in later stages of decomposition compared to litter produced in northern Sweden.

Keywords Integrated monitoring · Scots pine litter · Annual decomposition rates · Standard respiration · Recalcitrant · Humus quality · Soil nitrogen · Partial Least Squares (PLS) regression

INTRODUCTION

Many studies have been carried out concerning the early stages of litter decomposition dynamics using the litterbag incubation method (see overview in Berg and McClaugherty 2008; Kang et al. 2009). Several studies (e.g. Edmonds 1979; Melillo et al. 1982; Berg et al. 1993; Johansson 1994) have stressed the importance of substrate quality in controlling the turnover rate of organic matter

and the release of nutrient elements, while others have stressed the importance of climatic factors in addition to substrate quality (Berg et al. 2010).

While these studies have increased our basic understanding of the processes of decomposition and transformation of litter in boreal and temperate forest ecosystems, they only deal with the early stages of litter decomposition. The factors governing the later stages of litter decomposition are known to differ from those governing the earlier stages of the decomposition process. For example, nitrogen (N) is a dominant nutrient factor that appears to stimulate decomposition in the early stages and inhibit it in later stages (Berg and Staaf 1980; Berg and Meentemeyer 2002). Furthermore, the relative contributions of different types of litter to the maintenance of soil organic matter and nitrogen levels cannot be determined with the standard litterbag weight loss method alone (Aber and Melillo 1980). Soil respiration rates are used to describe the later stages of decomposition rates of in situ soil organic matter.

Relationships between humus layer respiration rates and environmental factors have been found to be contrary to what one might have expected. For example, in a previous study (Bringmark and Bringmark 1991), it was found that the respiration of humus layer samples measured in the laboratory and sampled from throughout Sweden, but from the same forest type, increased rather than decreased with the latitude of the sampling site. The respiration rates increased northward by a factor of two. Similar results have been found for untreated reference samples taken from experimental trials also located along a north-to-south gradient in Sweden (Torstensson et al. 1989; Åkerblom et al. 2010). Together these observations led us to hypothesize that there is a difference in the rate of decomposition of forest litter between the south and north of the boreal zone and that more recalcitrant humus material is formed in the south than in the north.

In this article, we investigate these hypotheses by using needle litterbag weight loss measurements and soil (humus layer) respiration rates that have been repeated over a long time period for several sites forming a latitudinal gradient throughout Sweden, including the Swedish IM sites (Fig. 1a). The needle litterbag weight loss measurements

describe the early stage of litter decomposition, and soil respiration rates represent the later stage of litter decomposition. Our specific aims were to test if the decomposition of litter under site conditions that initially favor the process (southerly latitudes) slow down more abruptly than in sites that start out with more moderate decomposition rates

Fig. 1 **a** Sites of litter decomposition studies in Sweden, showing location north or south of latitude 60°N. More information about stands is found in Table 1. **b** Sites of humus respiration studies in Sweden, showing location north or south of latitude 60°N

(northerly latitudes). We looked for indications of latitudinal differences in the kinetics that would indicate a reduced decomposition rate. In addition, we used the multivariate analysis technique of Partial Least Squares (PLS) regression (Carrascal et al. 2009) to relate annual decomposition rates to different climatic parameters, as well as to humus layer nitrogen, sulfur, calcium, aluminum, and potassium concentrations. PLS is particularly well suited for such analysis and for elucidating the relative importance of a large array of correlated variables.

MATERIALS AND METHODS

The decomposition of organic material in Norway spruce or mixed Norway spruce-Scots pine stands and, in one case, alpine downy birch was studied in a north–south climatic gradient over Sweden covering the boreonemoral and boreal zones (National Atlas of Sweden 1996). All sites had acid podzolic soils with well-defined humus (mor) layers.

The data consist of two pine needle litterbag studies and one microbial respiration study of the mor layers. Most of the data were collected as part of the former long-term National Environmental Monitoring program (PMK) and the ongoing IM monitoring program, and hereafter is collectively referred to as PMK/IM data. One of the PMK sites, Aneboda, continued as an IM site. In addition, data from temporary research efforts in several pine forest sites and litterbag data from the study by Johansson (1986, 1994) have been included.

The PMK/IM Litterbag Study (3-Year Study)

The decomposition of standard brown pine-needle litter was measured in 19 PMK/IM sites (Table 1; Fig. 1a). The litterbags (10 × 17 cm) were made of terylene net with a mesh size of about 1 mm and filled with 0.6–1.0 g (exact weighted recorded) of Scots pine needles. The needles originated from one Scots pine stand in Central Sweden (Jädraås, 60°52'N). At each PMK/IM forest site, litterbags were placed on the forest floor at 18–25 locations with 10-m spacing, which is known to ensure spatial independence (Bringmark and Bringmark 1998). The bags were fixed in place using 10–15 cm long stainless steel pegs. Each autumn, litterbags that had been incubated for 1, 2, and 3 years were retrieved at each location and replaced with a new set of litterbags. In the laboratory, the litterbags were carefully rinsed, dried at 85°C, and weighed individually. The needle weight losses for each incubation period and for each year were calculated. This procedure was repeated for between 7 (Stormyrän and Tyresta) and 27 years (Aneboda).

The JOH Litterbag Study (5-Year Study)

In the second litterbag study, the weight loss of local Scots pine needles was followed in several stands located throughout Sweden (Johansson 1986). The data from 10 stands were used in this study, and are hereafter referred to as JOH (Table 1; Fig. 1a). The decomposition of the pine needles was followed for 5 years, with no repeated measurements. Altogether, 125 terylene-net litterbags (11 × 13 cm) per site were placed out in 1983. The bags contained exactly about 1.5 g and fixed in place using 10–15-cm-long metal pegs. Twenty-five of the litterbags per site were collected each year over the 5-year study period (Johansson et al. 1995). In the laboratory, the litterbags were carefully rinsed, dried at 85°C, and weighed individually. The annual weight loss was calculated.

In addition to using local pine-needle litter, standard pine-needle litter was also used at a southern site. A significant correlation between the weight losses of local and standard litters was found ($r = 0.993^{***}$), enabling a comparison between the PMK/IM and JOH data.

The PMK/IM Microbial Respiration Study on Humus Layers

Microbial respiration was measured from 12 humus layer samples per stand taken at 10-m intervals, ensuring spatial independence. In the laboratory, the samples were sieved, and respirations were measured after 12 days of incubation at 20°C and 70% moisture contents. CO₂ developing overnight in closed vessels was trapped in 0.2 M NaOH solution. After precipitation of carbonate with BaCl₂, any remaining alkali was determined by titration with 0.50 M HCl acid. The results were expressed as mg CO₂-evolved per hour per gram of dry matter (Bringmark and Bringmark 1993, 1998). This titrimetric method for analysis of CO₂ trapped in alkali, although old, is not only simple but has a high degree of sensitivity (Anderson 1982).

The stands in the study formed a north–south gradient throughout Sweden. In addition to some of the PMK/IM stands, a few supplementary pine forest sites were included to make the north–south gradient more complete (Fig. 1b). The study was performed twice, once in 1987–1989 (no. of stands, $n = 20$; Bringmark and Bringmark 1991) and repeated in 2007–2008 ($n = 22$).

Chemical Analysis

Contents of C, S, and N in the humus layers were determined by dry combustion and detection using a LECO analyzer. Contents of P, Ca, and Al were determined by digestion in nitric acid and analyzed using Inductively Coupled Plasma.

Table 1 Geographical location and properties of the sites in the PMK/IM litterbag study together with the sites from the JOH 5-year research study

Site	Abbreviation	Pro-gramme	North or south, >60°N	Latitude, °N	Altitude, m a s l	Dominant tree species	Litterbag weight loss				
							Study period	No. of years	Weight loss (%) Year 1	Weight loss (%) Year 2	Weight loss (%) Year 3
Gammtratten	GAMM	IM	N	63°51'	510	Norway spruce	2000–2009	10	24–32	41–58	60–73
Kindla	KIND	IM	S	59°45'	325	Norway spruce	1995–2009	15	21–36	52–63	69–80
Gårdsjön	GÅRD	IM	S	58°03'	125	Norway spruce	1995–2009	15	26–41	55–70	66–82
Aneboda	ANEB	IM	S	57°07'	230	Norway spruce, Scots pine	1995–2009	15	24–42	54–71	63–79
Reivo-Laxtjärn	REIV-L	PMK	N	65°48'	510	Norway spruce	1986–1996	11	17–30	32–48	43–61
Reivo-Rutjebäcken	REIV-R	PMK	N	65°47'	450	Scots pine, Norway spruce	1985–1993	9	14–27	24–40	37–51
Vindeln-Svartberget	VIND-S	PMK	N	64°15'	285	Norway spruce, Scots pine	1984–1994	11	21–35	41–51	52–65
Vindeln-Kulbäcksliden	VIND-K	PMK	N	64°10'	270	Norway spruce	1983–1993	11	24–34	38–55	52–74
Sandnäset	SAND	PMK	N	63°45'	440	Norway spruce, downy birch ^b	1984–1993	10	27–36	46–58	61–70
Stormyran	STOR	PMK	N	62°15'	490	Norway spruce	1987–1993	7	21–33	39–53	56–68
Grimsö	GRIM	PMK	S	59°38'	90	Norway spruce	1985–1997	13	22–37	46–69	62–77
Tyresta	TYRE	PMK	S	59°10'	45	Norway spruce	1987–1993	7	28–37	49–59	60–72
Tresticklan	TRES	PMK	S	59°00'	210	Norway spruce, Scots pine	1983–1993	11	21–33	39–61	58–64
Tiveden	TIVE	PMK	S	58°43'	215	Norway spruce, Scots pine	1983–1993	11	29–39	48–60	60–67
Svartedalen	SVAD	PMK	S	58°02'	140	Norway spruce, Scots pine	1983–1996	14	27–38	51–67	57–77
Norra Kvill	NKVI	PMK	S	57°46'	185	Norway spruce, Scots pine	1983–1993	11	26–38	39–59	53–65
Aneboda	ANEB	PMK	S	57°07'	230	Norway spruce, Scots pine	1983–1994	12	30–42	53–70	65–73
Berg	BERG	PMK	S	57°05'	120	Norway spruce, Scots pine	1983–1993	11	35–43	51–63	59–71
Sännen	SÄNN	PMK	S	56°20'	90	Norway spruce, Scots pine	1985–1993	9	31–41	52–65	63–75
Skällarimsheden	SKÄL	JOH	N	66°32'	280	Scots pine	1983–1986	1	18	35	48
Haradsheden	HARA	JOH	N	66°08'	58	Scots pine	1983–1988 ^a	1	11	20	34
Manjärvi N	MANJN	JOH	N	65°47'	135	Scots pine	1983–1988 ^a	1	20	36	50
Manjärvi S	MANJS	JOH	N	65°47'	135	Scots pine	1983–1988 ^a	1	26	43	61
Manjärvi	MANJ	JOH	N	65°47'	135	Scots pine	1983–1988 ^a	1	31	48	64
Grensholm	GREN	JOH	S	58°33'	58	Scots pine	1983–1988	1	38	60	67
Hökensås	HÖKE	JOH	S	58°05'	245	Scots pine	1983–1988	1	34	59	67
Kullavägen	KULL	JOH	S	56°36'	135	Scots pine	1983–1988	1	36	59	67
Kungs-Husby	KUNG	JOH	S	59°31'	30	Scots pine	1983–1987	1	30	47	58
Tveten	TVET	JOH	S	58°07'	170	Scots pine	1983–1987	1	42	63	69

Annual mass loss in litter of 1, 2 and 3 years of age

Sampling period: ^ayear 4 missing, ^b *Betula pubescens*, subspecies *turtosa*

Statistical Analysis

A nested ANOVA test (Zar 2009) was used to identify if there was any significant difference in the development of decomposition between north and south Sweden in the PMK/IM litterbag study. The latitude of 60°N was used to delimit between north and south Sweden, which roughly coincides with the limit of the boreal forest zone in Scandinavia (Lundmark 1986; National Atlas of Sweden 1996). The yr1/yr2, yr1/yr3, and yr2/yr3 weight loss ratios were used to describe the change in decomposition rates. Five northern sites (VIND-S, VIND-K, SAND, STOR, and GAMM) and five southern sites (TIVE, SVAD, ANEB, NKVI, and BERG) were selected for the ANOVA test. Measurements of 7 subsequent years were included. No ANOVA was made for the 5-year JOH litterbag study because of a lack of repetition.

The importance of various environmental variables on PMK/IM litterbag weight loss and humus layer respiration data were examined by applying PLS regression (Carrascal et al. 2009). PLS can be seen as a regression extension of principal component analysis, and particularly suitable for such multicollinear data. For the analysis of the litterbag weight loss data, environmental variables used were: latitude, altitude (m above sea level), mean of annual precipitation (MAP 1951–1980, mm), precipitation (mm) during the vegetation period, mean annual temperature (MAT 1951–1980 and 1961–1990, °C), length of vegetation period (days), humidity (defined as precipitation minus evapotranspiration during vegetation period, mm), and humus layer sulfur, S (%), nitrogen, N (%) and carbon, C (%) contents. Spatial climate data for the period 1951–1980 were obtained from the National Atlas of Sweden (1992), while MAT 1961–1990 were obtained separately to test the importance of period. The analysis for the litterbag data was performed using 18 PMK/IM forest stands.

The PLS regression of the microbial respiration in humus layers (stand mean) in 2007 was performed using 16 forest stands, including eight PMK/IM stands. In addition to the environmental variables listed above, the following soil properties were included in the analysis: humus layer concentrations of calcium (mg Ca kg⁻¹), phosphorus (mg P kg⁻¹), and aluminum (mg Al kg⁻¹).

RESULTS

Needle Litter Decomposition

Examples of the cumulative decomposition of needle litter at 1, 2, and 3 years of decomposition (green, blue, and orange, respectively) for a northern stand (REIV-L, 65°48'N) and for a southern stand (ANEB, 57°07'N) are

shown, respectively, in Figs. 2a and b. Annual values of cumulated needle weight losses with moving averages as lines are displayed. The Aneboda site has the longest continuous data series (27 years spanning 1983–2009) and that for the Reivo site was 11 years (1986–1996) (Table 1).

While the decomposition (needle weight loss) was higher for the southern site, reflecting the warmer and wetter climate, there was a marked slowing down of decomposition during the third year compared to the northern site (REIV-L). At the REIV-L site, the weight loss after first year of decomposition was approximately 23% of the initial weight, increasing to 38% in the second year and to 51% in the third year. The additional weight losses during the second and third years were similar, 15 and 13%, respectively. However, cumulated needle weight loss at the southern site (ANEB) during the third year of decomposition had only increased by a further 10% compared to the 27% annual loss during the second year.

This same pattern was found for all sites. That is, almost the same rate of annual litter decomposition over the 3 years was found for the northern sites compared to a decreasing annual decomposition rate from year 1 to year 3 for the southern sites. Differences in needle weight loss between sites in north and south Sweden were tested using a nested ANOVA design (Zar 2009). The results showed a significant north–south difference for yr1/yr3 weight loss ratios ($F_{1, 12} = 19.53$, $p < 0.01$) and for yr2/yr3 ratios ($F_{1, 12} = 60.2$, $p < 0.001$), but no significant differences for yr1/yr2 ratios ($F_{1, 12} = 1.03$, n.s.).

To compare the kinetics of needle weight loss at comparable stages of the process, it is appropriate to use the accumulated weight loss rather than time as an indicator of the progress of decomposition. Then, the rate of weight loss can be shown for comparable stages of the process in the north and south. Such results are presented for individual sites in Fig. 3a and for the PMK/IM and JOH materials in Fig. 3b. It is of special interest that the slowing of decomposition was not only a matter of the stage reached in the process, but at a comparable degree of decomposition, there was a more intense slowing down in the southern sites than in the northern sites (Fig. 3a). The JOH material showed a similar tendency (Fig. 3b).

Respiration of Humus Layers

The relationship between humus layer respiration rates and latitude is shown in Fig. 4a (1987–1989, $n = 20$) and Fig. 4b (2007–2008, $n = 22$). The pattern was the same on both measuring occasions: the respiration rates of the southern sites were lower than those of the northern sites (40% lower on average) and increased with latitude, while those of the northern sites did not vary with latitude and remained stable at about 0.06 mg CO₂ g dw⁻¹ h⁻¹.

Fig. 2 **a** Cumulative litter decomposition for individual years in the northern PMK-site Reivo-Laxtjärnen. Materials of one (*green*), two (*blue*), and three (*orange*) years of age. *Lines* indicate 3 years moving averages. **b** Cumulative litter decomposition for individual years in the southern PMK/IM-site Aneboda. Materials of one (*green*), two (*blue*), and three (*orange*) years of age. *Lines* indicate 3 years moving averages

Another difference in the respiration values between northern and southern Sweden was the amount of within-site variation. The standard deviation of the respiration values for the northern sites was twice that of the southern sites.

Environmental Factors

The PLS score plot of the sites from the PMK/IM litterbag study (Fig. 5a) shows a clear separation of the northern and southern sites. The strong mutual correlations between the environmental variables and pine needle decomposition variables were also clear (Fig. 5b).

Decomposition in the first year (yr1) was strongly and positively correlated to MAT (1951–1980, $r = 0.854^{***}$

and 1961–1990, $r = 0.835^{***}$), length of vegetation (veg.) period ($r = 0.796^{***}$) as well as temperature sum during the vegetation period ($r = 0.755^{***}$) and amount of precipitation during the vegetation period ($r = 0.772^{***}$). Positive but weaker correlations with yr1 decomposition rates were found for MAP, and humus layer nitrogen and sulfur concentrations ($r = 0.486^*$, 0.663^{**} , and 0.558^* , respectively). High, negative correlations were found with latitude and altitude ($r = -0.831^{***}$ and -0.759^{***} , respectively).

The corresponding correlations of litter decomposition in the second year of incubation (yr2) were similar to those of the first year's decomposition correlations, but had lower degrees of significance, except for sulfur content ($r = 0.589^{**}$).

Fig. 3 a Average for all years of annual litter decomposition (%) against average for all years of accumulated mass loss (%) in three northern and three southern sites in the PMK/IM data set. Northern sites; REIV-L, VIND-K and SAND. Southern sites; SVAD, ANEB and NKVI. Latitudes of sites indicated. **b** Average for all years of

annual litter decomposition (%) against average for all years of accumulated mass loss (%) with all northern stands and all southern stands pooled. Both the PMK/IM 3-years study and the JOH 5-years study are represented in the figure

Fig. 4 Relationships between standard respiration at 20°C in humus layers and latitude. Site mean values and standard deviation 1987–1989 (a) and 2007–2008 (b)

Decomposition in the third year (yr3) was, however, negatively correlated with MAT (1951–1980, $r = -0.624^{**}$ and 1961–1990, $r = -0.635^{**}$), length of vegetation period ($r = -0.631^{**}$) as well as to temperature sum during the vegetation period ($r = -0.632^{**}$) and to precipitation during the vegetation period ($r = -0.532^{*}$). Positive correlations for yr3 decomposition rates, although not so strong, were found for latitude ($r = 0.640^{**}$) and altitude ($r = 0.701^{**}$). Decomposition rates during the third year of incubation were negatively correlated to humus layer nitrogen concentrations ($r = -0.481^{*}$). The different periods chosen for MAT had no influence on the spatial PLS analysis of decomposition, neither in the first nor in the third year of decomposition.

Humidity during the vegetation period and carbon concentration of the humus layer was not significantly

correlated with any of the three annual litterbag decomposition values and displayed non-significant positions in the plot (as illustrated by the short vector for humidity and the divergent direction for carbon, see Fig. 5b).

The PLS score plot of sites in the respiration study (Fig. 6a) showed a clear separation between sites in the north and those in the south of Sweden. In the PLS loading plot of environmental variables (Fig. 6b), strong positive relationships between respiration and latitude ($r = 0.884^{***}$), phosphorous ($r = 0.651^{**}$) and calcium ($r = 0.736^{**}$) were found. Altitude was also correlated with respiration, although not strongly ($r = 0.547^{*}$). Strong negative correlations with the length of vegetation period ($r = -0.847^{***}$), MAT (1950–1980, $r = -0.859^{***}$), temperature sum during the vegetation period ($r = -0.777^{***}$), MAP, precipitation during the vegetation

Fig. 5 **a** Display of sites in the Partial Least Square regression on litterbag degradation in 7 northern PMK/IM-sites (in blue) and 11 southern PMK/IM-sites (in red). See Fig. 1a for geographical location. The ellipse illustrates the Hotelling's T², a multivariate

generalization of the student's *t* distribution. **b.** Display of variables in the Partial Least square regression on litterbag degradation. For abbreviation of variables, see text in Results

period and humidity during the vegetation period ($r = -0.713^{**}$, $r = -0.722^{**}$ and $r = -0.571^{*}$; respectively), and with humus layer sulfur and nitrogen concentrations ($r = -0.952^{***}$ and $r = -0.759^{*}$, respectively) were clearly found. Humus layer carbon and aluminum concentrations, however, were not significantly correlated with respiration ($r = -0.329$, n.s. and $r = -0.191$, n.s.; respectively).

DISCUSSION

The weight loss of Scots pine needles for up to 5 years of incubation in field conditions, which represents the early stage of litter decomposition, and the microbial respiration of the humus layer, which represents the later stage of litter decomposition, were followed in nearly natural and mature

Fig. 6 **a** Display of sites in Partial Least Square regression on humus respiration in 9 southern sites (in red) and 7 northern sites (in blue). See **1b** for geographical location. **b** Display of variables in the Partial

Least square regression on humus respiration. For abbreviation of variables, see text in [Results](#). The ellipse illustrates the Hotelling's T², a multivariate generalization of the student's *t* distribution

mesic spruce and spruce/pine forest stands located throughout Sweden. Humus layers are mixed materials of various ages and stages of decomposition. Results of a ¹⁴C measurement study by Fröberg et al. 2011 on carbon residence time in the humus layer along a climatic gradient in

Scandinavia did not find large differences in the average age of humus layers between northern (ca. 41 years old), middle (ca. 36 years old) to southwestern Sweden (ca. 40 years old), although a somewhat lower mean age was found in another central region. The age of the humus

layers used in our soil respiration study can be assumed to be of a similar mean age. Thus, the average age of the humus layer material is about 8 (JOH) to 13 (PMK/IM) times the age of the pine needle litter used in this study.

In Berg et al. (2010), climate variables, such as MAP and MAT, together with substrate-chemistry variables, explained the pine-needle litter decomposition in later stages. Nitrogen in the substrate has been found to have a stimulating influence during early decomposition stages, but later it became inhibitory (Berg and Staaf 1980; Berg and Meentemeyer 2002; Berg et al. 1995; Johansson et al. 1995). In the early stages of litter development, there is an influx of nitrogen into the litter mainly from the soil, which helps to meet the microbial demand of nitrogen (Staaf and Berg 1977, 1982). The nutrient status of the forest site and its consequences for microbiological processes are conserved for a long time, even in situations of reduced nitrogen deposition, which can be attributed to the mobilization of the large stores of organic nitrogen in the system (Dörr et al. 2010). A large number of well-documented studies have identified a negative influence of nitrogen on decomposition in the later stages of decomposition (e.g. Berg and Matzner 1997; Berg and Meentemeyer 2002; Berg et al. 1995, 2010; Hyvönen et al. 2007). Prescott (2010) argued that nitrogen addition frequently leads to a greater stabilization of organic matter and increased humification. On the other hand, Dalías et al. (2001) showed in a laboratory experiment that exposure to higher temperature (raised from 4–10°C up to 23–30°C) during a period can lead to a similar stabilization of the material.

There is often a high degree of covariation among chemical variables in litter and humus materials and microbiological variables (Taylor et al. 1991; Parton et al. 1994; Prescott 2005), and microbiological activity is seldom explained by a single factor. In this study, we made use of PLS regression to explain the needle litter weight loss and humus layer respiration rates. Although we are not able to separate the influence of soil nitrogen from the influence of climate or humus layer sulfur content in this study, the PLS results brought out some interesting results. Thus, the patterns and environmental relationships found for the third years of litter decomposition (PMK/IM and JOH litterbag data, Fig. 3b) differed from those during the first and second years of decomposition and instead were more similar to those found for the microbial respiration study (PMK/IM), which represents the later stage of decomposition. The negative correlations to climate variables MAT, MAP, and the length of vegetation period, and also to humus layer nitrogen contents were discernible in the third year of the litterbag weight loss material (Fig. 5b) and in the soil respiration material (Fig. 6b), but not in the first- and second-year litterbag weight loss results. The patterns of influence by environmental factors were clearly reversed during the

decomposition process. However, limitations of empirical correlation studies should be born in mind (Prescott 2005). The magnitude of observed effects of different factors is a result not only of their functional influence but also of the range of the variation encountered by the studied populations.

Together the results show that there is a striking difference in the litter decomposition dynamics between northern and southern Sweden, indicating that organic material produced in such conditions initially favoring decomposition, but later it becomes more recalcitrant. Since our litterbag studies are based on 7–27 years of monitoring measurements, and the soil respiration is based on repeated measurements at a 20-year interval, the results are considered reliable. The opposite tendencies in early and later stages of the decomposition process make the long-term result on soil carbon storage and carbon circulation less evident. Relatively similar humus layer mean ages were reported for the Swedish North and South as calculated from C¹⁴ determinations (Fröberg et al. 2011). This indicates that the heterogeneous humus layer materials have reached similar degrees of decomposition in this geographical range in spite of geographic differences in both early and late phases of decomposition. Thus, the magnitude of litter inputs rather than decay will be decisive for the soil carbon store, as also suggested by Prescott (2005); Fröberg et al. (2011).

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