Plant and Soil (2006) 283:187–201
DOI 10.1007/s11104-006-0010-7

Linking foliar chemistry to forest floor solid and solution phase organic C and N in *Picea abies* [L.] Karst stands in northern Bohemia

Jacqueline A. Aitkenhead-Peterson[1,6], Jess E. Alexander[2], Jana Albrechtová[3], Pavel Krám[5], Barrett Rock[2], Pavel Cudlín[4], Jakub Hruška[5], Zuzana Lhotaková[3], Ryan Huntley[2], Filip Oulehle[5], Tomáš Polák[3] & William H. McDowell[1]

[1]*Department of Natural Resources, University of New Hampshire, Durham, NH, 03824, USA.* [2]*Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, NH, 03824, USA.* [3]*Department of Plant Physiology, Faculty of Science, Charles University, Viničná 5, 12844, Prague 2, Czech Republic.* [4]*Institute of Landscape Ecology, Academy of Sciences of the Czech Republic, 37005, České Budějovice, Czech Republic.* [5]*Department of Environmental Geochemistry, Czech Geological Survey, Klárov 3, 11821, Prague 1, Czech Republic.* [6]*Corresponding author**

Received 17 October 2005. Accepted in revised form 9 January 2006

Key words: cellulose and nitrogen, dissolved organic carbon, dissolved organic nitrogen, forest floor C:N, foliar lignin, *Picea abies* [L.] Karst

Abstract

Dissolved organic carbon and nitrogen (DOC and DON) produced in the forest floor are important for ecosystem functions such as microbial metabolism, pedogenesis and pollutant transport. Past work has shown that both DOC and DON production are related to litterfall and standing stocks of C and N in the forest floor. This study, conducted in spring, 2003, investigated variation in forest floor water extractable DOC (WEDOC) and DON (WEDON) and forest floor C and N as a function of lignin, cellulose and N contained in live canopy foliage across eight *Picea abies* [L.] Karst stands in northern Bohemia. Based on Near Infrared Spectroscopy (NIR) analysis of foliar materials, lignin:N and cellulose:N content of the youngest needles (those produced in 2002) were positively and significantly related to WEDOC ($R^2 = 0.82$–0.97; $P < 0.01$) and to forest floor C:N ratio ($R = 0.72$–0.78; $P < 0.01$). Foliar N was strongly and negatively related to WEDOC and C:N ratio ($R = -0.91$ and 0.72; $P < 0.05$) among our study sites. WEDON was positively correlated to foliar lignin:N ($R = 0.48$; $P < 0.05$; $n = 40$). Forest floor C pools were not positively correlated with foliar lignin and cellulose and forest floor N pools were not positively correlated with foliar N. Instead, a significant negative correlation was found between forest floor N pools and foliar cellulose ($R = -0.41$; $P < 0.05$), and between forest floor C pools and foliar N ($R = -0.44$; $P < 0.05$). From a remote sensing standpoint, our results are important because canopy reflectance properties are primarily influenced by the most recent foliage, and it was the chemistry of the most recently produced needles that showed a stronger relationship with forest floor WEDOC and C:N ratio suggesting forest floor production of WEDOC can be calculated regionally with remote sensing.

Introduction

Dissolved organic carbon (DOC) in the forest floor plays an important role in the transport of pollutants (Kalbitz et al., 1997), pedogenesis (Dawson et al., 1978) and microbial metabolism (Yano et al., 1998). A multitude of studies spanning several decades have examined relationships between DOC in forest floor and soil solution and solid phase organic and mineral horizons (e.g. Kalbitz et al., 2000 review). The

* FAX No: + 1-603-862-4976.
E-mail: jaa@cisunix.unh.edu

largest internal ecosystem flux of DOC occurs as percolate from the forest floor (Aitkenhead-Peterson et al., 2003; Michalzik and Matzner, 1999). While recent litter and humus are postulated to constitute the major source of DOC, root death and rhizodeposition may also contribute to DOC production (Aitkenhead-Peterson and Kalbitz, 2005; Lajtha et al., 2005). Gundersen et al. (1998) observed that DOC flux was correlated to litterfall amount and concluded that across several European sites C supply and turnover rate determined DOC leaching from the forest floor. Yet loss of DOC from the forest floor of a hardwood stand in Germany represented only 8% of annual litterfall C input and removal of annual litter decreased DOC flux only slightly in the Oi but not at all in the Oe + Oa horizons (Park and Matzner, 2003). Furthermore, only 5–8% of DOC collected at 5–10 cm depth in a forest floor was derived from new ^{13}C labeled carbon, even though new C sources accounted for 17–22% of total soil organic matter at 0–10 cm depth after a growing season of labeling (Hagedorn et al., 2002). These studies suggest that older materials in the forest floor, particularly those in the lower Oe and Oa horizons, are major contributors to DOC flux. Leaching losses of DOC from the forest floor are related to organic matter content as well as forest floor C:N in coniferous stands (Aitkenhead and McDowell, 2000; Tipping et al., 1999). Higher organic C mass and forest floor C:N ratios reflect the amount of refractory C, which is determined by vegetation type. A link between refractory C and substrate C:N is supported by the work of Schimel and Weintraub (2003) who report that 'left-over' or non-utilized DOC after exposure to microbes is significantly related to substrate C:N ratio.

Forest foliage and the forest floor are unequivocally linked because above-ground litterfall is its major contributor but below-ground fine roots and associated macro- and micro flora and fauna are also an integral part. Several studies have investigated the relationship between foliar and forest floor C and N. A significant relationship exists between foliar lignin:N ratios and soil C:N ratios for a variety of tree species across the White Mountains of New Hampshire, USA (McNulty et al., 1991; Ollinger et al., 2002). Individual tree species also have an effect on underlying soil C:N ratio (Lovett et al., 2002, 2004). The effect of tree species on the underlying forest floor likely relates to the proportion of refractory C contained within foliage, as these materials are most likely to accumulate in soil organic matter C pools thus affecting the ratio of C:N in the forest floor.

The Krušné Hory (Ore Mountains) in the Czech Republic (Figure 1) have been studied over the past several decades as a site of forest decline caused by a range of factors, including exposure to high levels of air pollution (Albrechtová et al., 2001; Ardo et al., 1997; Campbell et al., 2004). Forest stands from previous studies were selected for the present study because of uniform litter input from the *Picea abies* [L.] Karst monoculture stands, and extensive on-going vegetation assessment studies at six of the eight sites included in this study. The two remaining forest stands, in the Slavkov Forest, were included in the study because of well-documented catchment biogeochemistry (Hruška and Krám, 2003; Krám et al., 1997).

The major objective of this study was to examine links between the chemistry of forest floor solid and water-extractable C and N and fresh foliage across eight monocultural stands of *Picea abies* [L.] Karst in the Czech Republic. We hypothesized that the oldest needles, which will shed sooner, would most affect forest floor composition and its chemistry.

Materials and methods

Site descriptions

At six sites in the Krušné Hory Mountains and two sites in the Slavkov Forest we established 30×30 m^2 plots (Figure 1.). Of these eight sites, five were used previously in investigations of variation in *Picea abies* [L.] Karst health because of their location along a historical sulfate deposition gradient (Albrechtová et al., 2001; Ardo et al., 1997; Campbell et al., 2004; Rock et al., 1994; Soukupova et al., 2000). Three of the five represent healthy stands located near the village of Přebuz (PZ) and two represent previously heavily damaged sites at Kovářská (KV) and Cerny

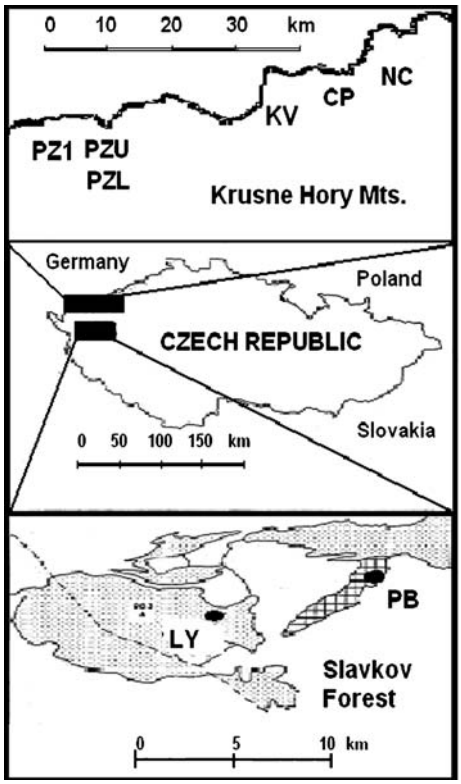

Figure 1. Location of the eight stands of Norway spruce used in this study from the Slavkov Forest in the west through the Krušné Hory Mountains to the east.

Potak (CP). Two of the eight sites represent intensively monitored catchments (Lysina-LY, Pluhuv Bor-PB) of the Czech Geological Survey (Cudlín unpublished data; Hruška and Krám 2003; Krám et al., 1997). The eighth site, (Načetín – NC) is an intensively monitored site of the Czech Geological Survey and Czech Academy of Sciences (e.g. Dambrine et al., 1993; Oulehle and Hruška 2005). A gradient of sulfate deposition occurred between the Slavkov Forest and Krušné Hory Mountains from Lysina in the west to Načetín in the east up until the early 1990s. Sulfate deposition (Hruška et al., 2002) and drainage water concentrations of sulfate (Majer et al., 2005) decreased significantly in the 1990s. The recovery of trees in the Krušné Hory Mountains, interpreted by chlorophyll content measured by hyperspectral red edge inflection point (REIP) values, characterized the trees at the PZ, KV, and CP sites as relatively healthy in 1997–1998 (Albrechtová et al., 2001; Campbell et al., 2004).

Six of the stands have similar aspects, facing a general southern direction. Načetín and Lysina have a northeasterly aspect. Stand elevation ranges from 740 to 947 m and meteorological conditions at all sites are comparable (Table 1). The dominant forest type for the five central sites is a *Picea abies* [L.] Karst monoculture of at least 60 years in age (Albrechtová et al., 2001). *Picea abies* [L.] Karst at Pluhuv Bor is approximately 120 and at Lysina 50 years of age (Krám et al., 2000). Each site is underlain by base cation-poor crystalline bedrock with the exception of Pluhuv Bor, which is underlain by magnesium-rich serpentinite. None of the study sites were glaciated.

Foliar collection and analysis

During late May to early June 2003 five trees that have been sampled in previous years for biochemical, histochemical and spectral analysis (Albrechtová et al., 2001; Campbell et al., 2004) and five trees from new plots (LY, PB and NC) established in 2002, were sampled at each of the eight sites (Table 1). Upper limbs, from the mid-third of the live canopy, which are exposed to the sun, were removed from the tree using a pruning pole. Two limbs were taken from each tree. Once on the ground the limbs were separated into sections, with youngest and oldest needles separated and kept in sealed plastic bags until processed in the evening. Needles were then separated into five age classes spanning the most recent three years of needle production in 2002, 2001 and 2000, as well as the oldest (x-year old), and next oldest ($x-1$-year old) needles. The oldest and next oldest needles varied in age, depending on the number of needle age classes retained on each tree and at each site (Table 1). Oldest needles ranged in age from 9.8 ± 0.8 at PZ1 to 6 ± 0 years at KV representing needles produced in 1992–1996 respectively (Table 1.). The 2003 needles were not fully developed in the spring of 2003 and therefore not collected. Needles from each tree and for each age class were air dried for two weeks and then removed from the stem and ground in a Wiley Mill (<1 mm). The air-dried, ground needles were dried for a further 48 h at 70 °C prior to Near Infrared Spectroscopy (NIR System 6500). The mass (dry weight) of foliar N, lignin and cellulose were analyzed by NIR, which is based upon the spectral properties

Table 1. Characteristics of the eight stands of Norway spruce used in this study

Site name	Site code	Stand elevation (m)	GPS coordinates	Soil type	Mean needle retention (*y*)	Mean annual temperature (°C)	Annual precipitation (mm)
Lysina	LY	867	50°02′7″ N 12°40′14″ E	Spodo-distric cambisol	8.8 ± 1.3	[a]5.0	[a]953
Pluhuv Bor	PB	740	50°03′47″ N 12°47′22″ E	Inceptisol	8.2 ± 1.9	[a]6.0	[a]783
Přebuz 1	PZ1	924	50°21′50″ N 12°34′48″ E	Entic spodozol	9.8 ± 0.8	[e]5.5	[d]1325
Přebuz lower	PZL	926	50°21′34″ N 12°38′16″ E	Entic spodozol	8.6 ± 1.5	[e]5.5	[d]1325
Přebuz upper	PZU	937	50°21′29″ N 12°38′19″ E	Entic spodozol	9.0 ± 1.0	[e]5.5	[d]1325
Kovářská	KV	790	50°29′53″ N 13°07′20″ E	Entic spodozol	6.0 ± 0	[c]6.3	[c]1024
Cerny Potok	CP	771	50°28′09″ N 13°03′54″ E	Distric cambisol	7.0 ± 0	[c]6.3	[c]1024
Načetín	NC	780	50°35′21″ N 13°15′16″ E	Distric cambisol	7.8 ± 0.8	[b]6.3	[b]842

Site codes relate to the stand position on Figure 1.
Source of data: [a]Hruška and Krám (2003); [b]CHMI; Mean annual temperature and precipitation were not measured at Přebuz sites, Kovářská and Cerny Potok. Shown data refer to [c]Climate station Měděnec in vicinity of Kovářská and Cerny Potok; [d]Meteorology and Climatology Division of Czech Hydrometeorological Institute in the vicinity of Přebuz; [e]Estimate using the mean air temperature change with altitude (0.56 °C) in the Czech Republic (Kalvová, 1996).

of total lignin, cellulose and N. Sub-samples of ground needles were scanned a minimum of three times each until QA/QC values were <5%. An equation generated from a partial least squares regression (Bolster et al., 1996) was used to determine lignin, cellulose and N content of our samples. Within each of the eight sites foliar lignin, cellulose, N and their ratios were compared between each of the age classes of needles.

Forest floor collection and analysis

Samples of forest floor (Oe and Oa material) were collected around each of five trees at each of the eight sites using a tulip bulb corer. Two samples were taken from the forest floor at opposite sides of the tree approximately 30–45 cm away from the base of the trunk and bulked. The organic material was air dried prior to sieving (2 mm), sub-sampling and grinding. Visible roots were removed and discarded during sieving. Ground sub-samples were saturated with a 2 *M* HCl solution for 48 h to remove any inorganic C. This step was particularly important, as the five central sites were fertilized with aerial applications of dolomitic limestone by the Czech government. Lysina, Pluhuv Bor and Načetín stands were not fertilized. The samples were then dried at 70 °C for 48 h and analyzed for total organic C and N (Perkin Elmer CHN analyzer). Most methods to remove carbonate from soil samples involve treatment with strong mineral acid to convert carbonates to CO_2. The residue is then analyzed to provide an estimate of the organic C. However, the acid may solubilize organic as well as carbonate C, and so the solution must be evaporated and the soil completely dried to fully measure the organic C fraction. Of the acids commonly used to remove carbonates, H_2SO_4 is not recommended because it is too strong an oxidant, cannot easily be removed by evaporation, and may damage CN analyzers (Sollins et al., 1999). HCl can be removed by evaporation, but the residual Cl^- may also damage CN analyzers (Sollins et al., 1999). Some researchers remove the Cl^- by washing, but this may also remove water-soluble organic C particularly if the sample has a high organic C con-

tent. Van Kessel et al. (2005) found no loss of organic C using the HCl carbonate removal method. At present the simplest solution is to use phosphoric acid which evaporates well and is not thought to damage CN analyzers (Sollins et al., 1999). Another useful method to remove carbonates is to use acid fumigation (Harris et al., 2001). To examine whether there was any loss of organic C or N using the HCl method we saturated five samples from the LY plot (known not to have carbonates) with 2 *M* HCl and analyzed in duplicate, the five HCl treated plus five HCl untreated for organic C and N. We found no significant difference between untreated and HCl-treated samples for either C or N.

Water extractions of DOC (WEDOC) and DON (WEDON) with a forest floor:water mass ratio of 1:10 were performed on sieved (2 mm) sub-samples. Extracts were shaken on an automated shaker at 60 rpm for 48 h and filtered using ashed (500 °C for 4 h) GF/F filters prior to acidification and analysis of DOC and total dissolved N (Shimadzu TOC 5000; Merriam et al., 1996). Inorganic N ($NH_4^+ + NO_3^-$) was measured using automated colorimetry (Lachat Quik Chem; phenol hypochlorite and Cd–Cu reduction methods, respectively). Dissolved organic N was measured as the difference between inorganic and total N.

There are limitations to the experimental design of this study. Factors such as differences in bedrock, stand aspect, soil order, land use history (stand age), elevation, precipitation and historical sulfate deposition could not be controlled for in a regional study such as this one.

Statistical analysis

Data were analyzed within stand level ($n = 5$) and among stands ($n = 40$). For foliar chemistry, needles were separated into five needle age classes for each of five trees at each of the eight sites. Pearson bivariate correlations were used to determine relationships between foliar and forest floor chemistry. One-way analysis of variance (ANOVA) with a Tukey's honestly significant difference *post hoc* comparison was used to determine if there were significant differences in foliar lignin, cellulose and N within and among sites for needle ages classes and for forest floor solid and solution phase C and N. All statistical analysis was performed using SPSS 11.

Results

Variation in foliar and forest floor C and N

We observed considerable variation in foliar chemistry within and among our sites despite constant forest species (*Picea abies* [L.] Karst) composition (Table 2 and Figure 2). There was a significant difference in foliar N, lignin and cellulose within individual sites (Figure 2) and among sites in needles produced in all needle-age class (Table 2). Although there was a trend of increasing foliar lignin between the oldest needles and those produced in 2002 within most sites, only one site (KV) had a significant increase in foliar lignin content in 2002 compared to its oldest needles (Figure 2). Five of the eight stands had significant increases in cellulose between their oldest and 2002 needles (NC, KV, PZL, PZ1, and LY; Figure 2). Foliar N increased between the oldest and 2002 needles at two sites (CP and PZ1) and 2000 needles at five sites (NC, PZU, PZL, LY, and CP), but this increase was only significant for three out of the eight stands (CP, PZ1, and LY; Figure 2).

Among the eight stands, there was a significant difference in lignin, cellulose and N in recent (2002) needles. Foliar lignin was highest in 2002 needles at the PZ1 site and was significantly greater than lignin content at the LY, PB, CP and NC sites. There was no significant difference in lignin content among sites in the oldest needles (Table 2). Foliar N was significantly reduced in both age classes of needles at the PB stand compared to PZI, PZL, PZU, KV and CP stands (Table 2). Highest foliar N in 2002 needles was found at the PZ1 site where it was significantly greater than LY, PB and NC. The spruce stand at PZ1 had significantly increased foliar cellulose in 2002 needles compared to CP, PZU and PB (Table 2), but in the oldest needles, cellulose was significantly increased relative to PZL, PZU, KV and CP.

Depth of the forest floor differed significantly among sites (ANOVA $P < 0.0001$), ranging from $7.75 \pm$ SD 1.96 cm to $13.3 \pm$ SD 1.6 cm (Table 3.).

Table 2. Significant differences among sites for foliar N and cellulose in 2002 and oldest needles

	Mean	2002 needles	Mean	Oldest needles
Nitrogen				
LY	0.01	bc	0.009	bc
PB	0.007	b	0.007	b
PZ1	0.013	a	0.011	a
PZL	0.012	ac	0.011	a
PZU	0.011	ac	0.01	ac
KV	0.012	ac	0.011	ac
CP	0.012	ac	0.01	ac
NC	0.01	bc	0.009	abc
Lignin				
LY	0.230	a	0.245	a
PB	0.226	a	0.224	a
PZ1	0.265	bc	0.234	a
PZL	0.234	ac	0.222	a
PZU	0.259	bc	0.223	a
KV	0.253	ac	0.219	a
CP	0.227	a	0.217	a
NC	0.229	a	0.238	a
Cellulose				
LY	0.39	ad	0.34	abcd
PB	0.36	bd	0.36	ac
PZ1	0.41	a	0.37	a
PZL	0.37	ad	0.32	be
PZU	0.33	bc	0.30	e
KV	0.37	abd	0.33	bce
CP	0.35	bd	0.33	bce
NC	0.39	ad	0.34	abcd

Site abbreviations are described in Table 1. Different letters indicate a significant difference among sites. (Tukey's HSD *post hoc*; $P < 0.05$; $n = 40$).

Deepest forest floors occurred at PZ1 and KV sites where they were significantly deeper than the forest floor at LY, PZU, and NC. Forest floor depth was inversely related to foliar lignin content in the oldest needles among the eight sites (Figure 3). Forest floor C ranged from $0.43 \pm$ SD 0.015 to $0.24 \pm$ SD 0.04 g g^{-1} soil (Table 3) and it was significantly different among stands (ANOVA $P < 0.01$). Highest forest floor C occurred at PB where it was significantly higher than all the other sites. Forest floor N ranged from $0.02 \pm$ SD 0.002 to $0.01 \pm$ SD 0.002 g g^{-1} soil (Table 3) and was significantly different among stands (ANOVA $P < 0.01$). Highest forest floor N occurred at PZL where it was significantly higher than at sites LY, PZ1, KV, CP and NC. Water extractable DOC and DON ranged from $14.4 \pm$ SD 3.0 to $34.9 \pm$ SD 7.9 mg C g $soil^{-1}$ and $85.4 \pm$ SD 15.5 to $156.5 \pm$ SD 33.5 μg N g $soil^{-1}$ and showed significant differences among stands (Table 3). Highest WEDOC was found at the PB sites where it was significantly higher than all the other sites. WEDON was significantly higher at the PB and PZU sites compared to the other sites.

Figure 2. Mean foliar lignin, cellulose and N for each of the eight stands used in this study (mg per mg dry weight foliage). Error bars are one standard deviation of the mean. Significant differences in foliar chemistry *within* each stand are shown by the *P*-value derived from a one-way analysis of variance. NSD = no significant difference. "Older" needles = those needles one year younger than the oldest needles. Site abbreviations are described in Table 1. For significant differences in oldest and newest needle-age-class *among* these stands refer to Table 2. Data source: Alexander (2005).

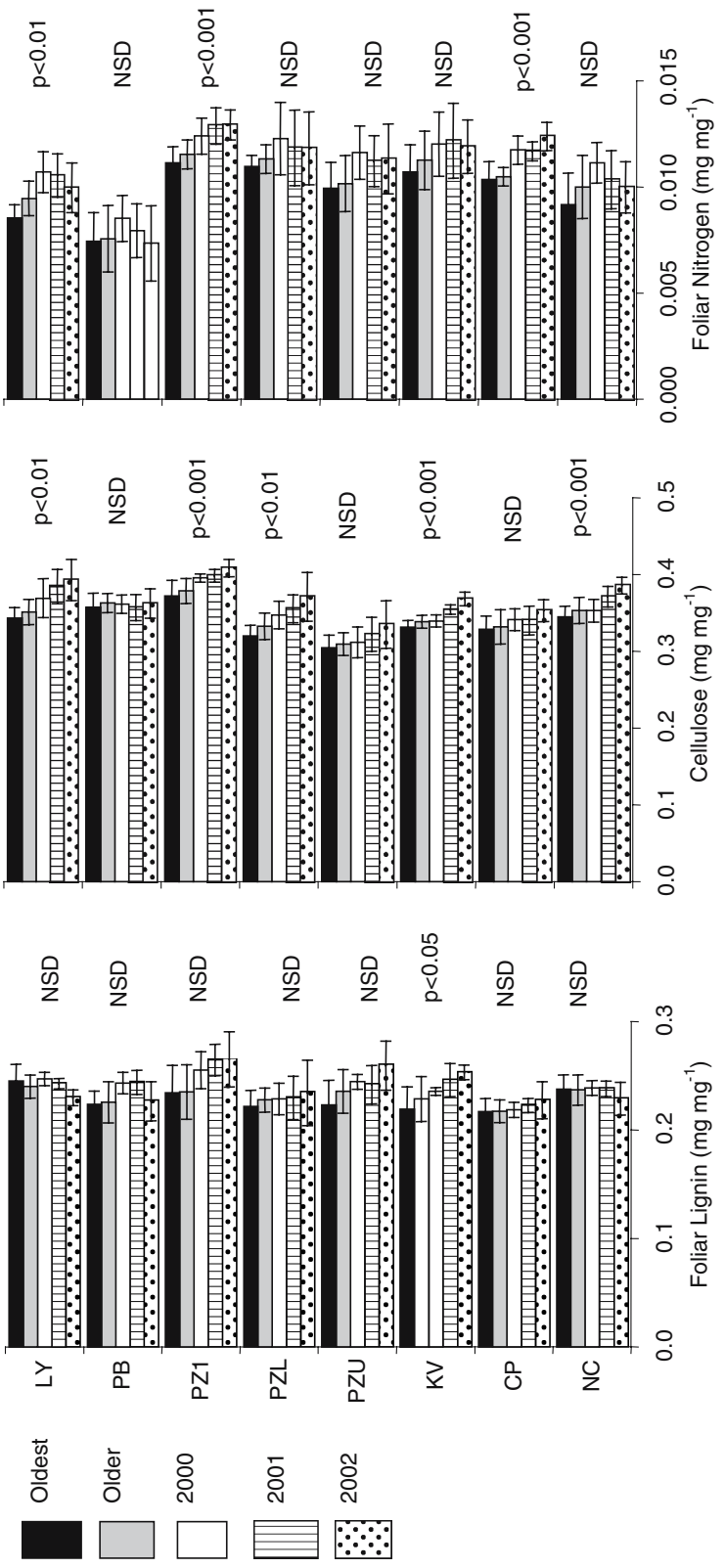
Oldest
Older
2000
2001
2002
LY
PB
PZ1
PZL
PZU
KV
CP
NC
NSD
NSD
NSD
NSD
NSD
p<0.05
NSD
NSD
p<0.01
NSD
p<0.001
p<0.01
NSD
p<0.001
NSD
p<0.001
p<0.01
NSD
NSD
NSD
p<0.001
NSD
0.0
0.1
0.2
0.3
Foliar Lignin (mg mg-1)
0.0
0.1
0.2
0.3
0.4
0.5
Cellulose (mg mg-1)
0.000
0.005
0.010
0.015
Foliar Nitrogen (mg mg-1)

Table 3. Forest floor solid and water extractable (1:10 soil:water extraction) organic C and N

	Solid phase			Solution phase	
	Depth (cm)	Carbon (g g soil^{-1})	Nitrogen (g g soil^{-1})	WEDOC (mg g soil^{-1})	WEDON (μg g soil^{-1})
LY	^{b}7.7	^{a}0.286	^{a}0.011	^{b}20.6	^{a}91.5
	2.0	*0.05*	*0.002*	*4.1*	*35.5*
PB	^{a}12.5	^{c}0.431	^{bc}0.014	^{c}34.9	^{b}156.5
	3.6	*0.01*	*0.004*	*7.9*	*33.5*
PZ1	^{a}13.3	^{a}0.260	^{a}0.011	^{a}15.3	^{a}91.9
	4.8	*0.06*	*0.002*	*1.6*	*19.1*
PZL	^{a}11.9	^{b}0.362	^{b}0.016	^{a}16.6	^{a}85.4
	2.9	*0.004*	*0.003*	*1.7*	*15.5*
PZU	^{b}9.9	^{b}0.336	^{b}0.015	^{b}21.0	^{b}141.3
	3.7	*0.07*	*0.003*	*3.8*	*61.6*
KV	^{a}13.3	^{a}0.255	^{ac}0.012	^{a}17.8	^{a}90.2
	1.6	*0.004*	*0.002*	*0.8*	*7.3*
CP	^{a}12.0	^{a}0.243	^{a}0.012	^{a}14.4	^{a}86.0
	4.2	*0.004*	*0.002*	*3.0*	*23.8*
NC	^{b}9.7	^{a}0.260	^{a}0.012	^{b}22.7	^{a}108.9
	2.5	*0.05*	*0.002*	*5.6*	*31.0*

Values in italics are 1 standard deviation of the mean ($n = 5$). Superscript letters represent significant difference between stands derived by Tukey's HSD *post hoc* at a 95% confidence interval. Data source: Alexander (2005).

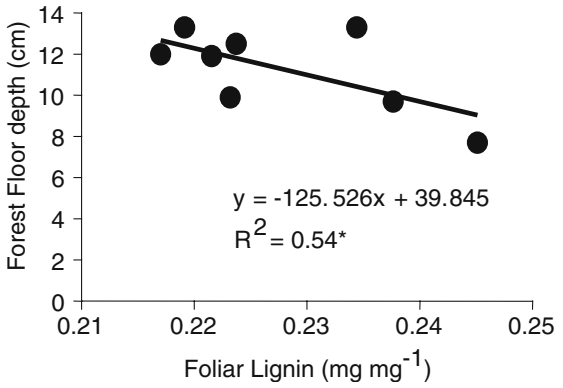

Figure 3. Relationship between forest floor depth and lignin content of the oldest needles.

Relationships between forest floor C:N, WEDOC, WEDON and foliar chemistry

Among the eight sites, strong and significant positive relationships were found between forest floor C:N ratio and WEDOC and foliar lignin:N and cellulose:N and strong and significant negative relationships between the forest floor C:N and WEDOC and foliar N in the recent and oldest needles.(Figures 4 and 5). The PB site had high statistical leverage and so data is presented with and without the inclusion of this site. The strong positive relationship between WEDOC and foliar lignin:N and the strong negative relationship between WEDOC and foliar N is not affected with the removal of site PB in the newest needles (Figure 4). For the oldest needles, the only relationship to remain significant with the removal of site PB is the negative relationship between WEDOC and foliar N (Figure 5). The relationship between WEDOC and C:N and foliar chemistry is much stronger with the newest needle-age-class than with the oldest needles (Figures 4 and 5).

Water-extractable DON was negatively correlated to foliar N and positively correlated to foliar lignin:N in both 2002 and the oldest needles but these correlation's disappeared with the removal of site PB. The ratio of WEDOC:WEDON, was significantly and negatively correlated to foliar lignin and N and positively correlated to foliar cellulose:N in the newest needles with and without the inclusion of site PB (Table 4). In the oldest needles, WEDOC:WEDON was positively correlated to foliar cellulose and cellulose:N and negatively correlated to foliar N. The relationships between these variables was lost when PB

was removed from statistical analysis except for the positive correlation between WEDOC:WEDON and foliar cellulose:N. (Table 4).

Forest floor C pools were not related to foliar lignin or cellulose for any needle age classes in this study, instead, they displayed a significant negative relationship with foliar N in the newest and oldest needles (Table 4). Whereas forest floor N pools had a significant negative relationship with foliar cellulose in newest and oldest needles (Table 4).

As might be expected from other studies, forest floor WEDOC was significantly and positively related to forest floor C:N ratio ($R^2 = 0.79$; $P < 0.01$; $n = 8$) and percentage of forest floor C ($R^2 = 0.55$; $P < 0.05$; $n = 8$). Water extractable DOC explained 73 percent of the variance in WEDON ($P < 0.01$; $n = 8$). WEDON was significantly related to forest floor C ($R^2 = 0.51$; $P < 0.05$; $n = 8$) but not forest floor N or C:N ratio. Depth of forest floor explained none of the variance in WEDOC and WEDON in this study.

Discussion

Foliar and solid phase forest floor C and N

The forest floor is an organic horizon with its major constituents derived from leaf and root litter. One would expect, then, that refractory litter inputs high in foliar lignin would result in a deeper forest floor and increased C pools. Yet our results show the opposite pattern, with a negative relationship between lignin content of our oldest needles and forest floor depth. This observation may in part be explained by the stands used in this study, five of which were once part of a much larger study investigating the effects of sulfate deposition on forest health. Lignin content

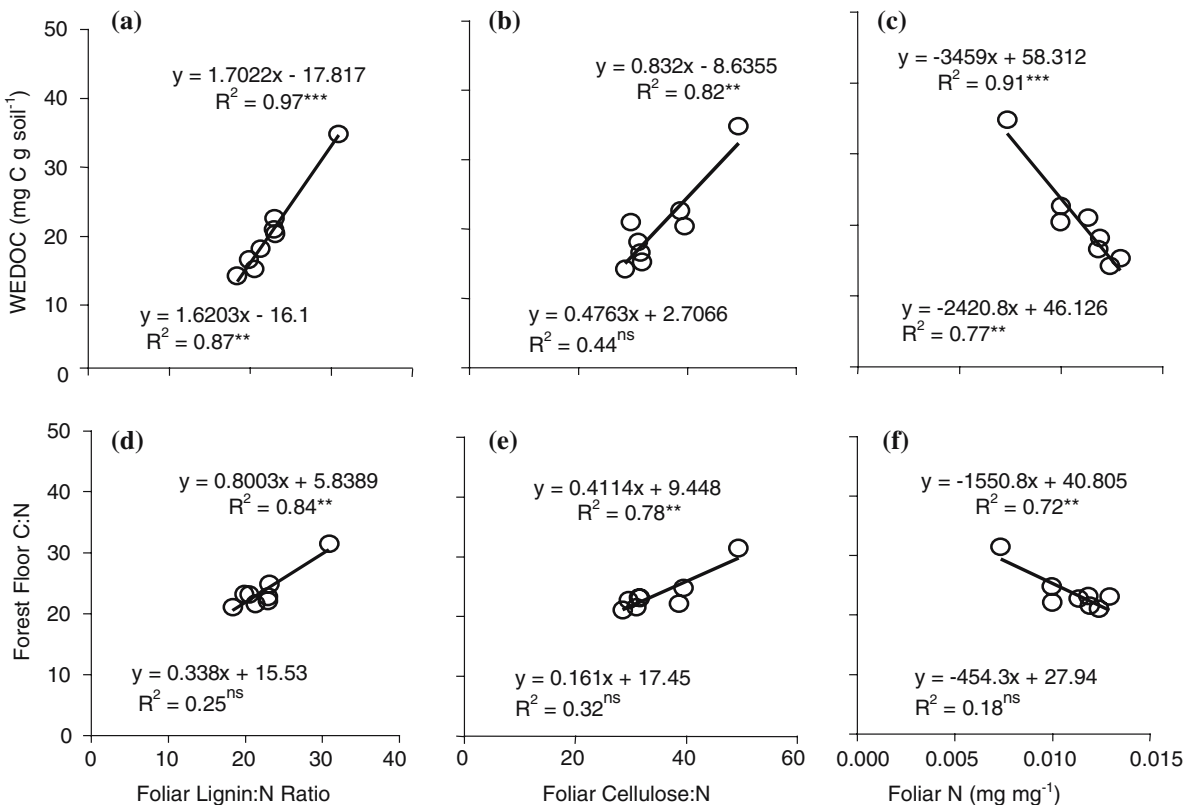

Figure 4. Relationships between mean forest floor WEDOC (mg C g soil^{-1}) and mean foliar chemistry for needles produced in 2002. Data points represent one site ($n = 5$). The top regression equation represents all eight sites and the bottom equation represents the seven sites on granitic bedrock (i.e. removal of the serpentine PB site). Relationships are significant at $^{**}P < 0.01$ and $^{***}P < 0.001$. Superscript ^{ns} is a non-significant relationship.

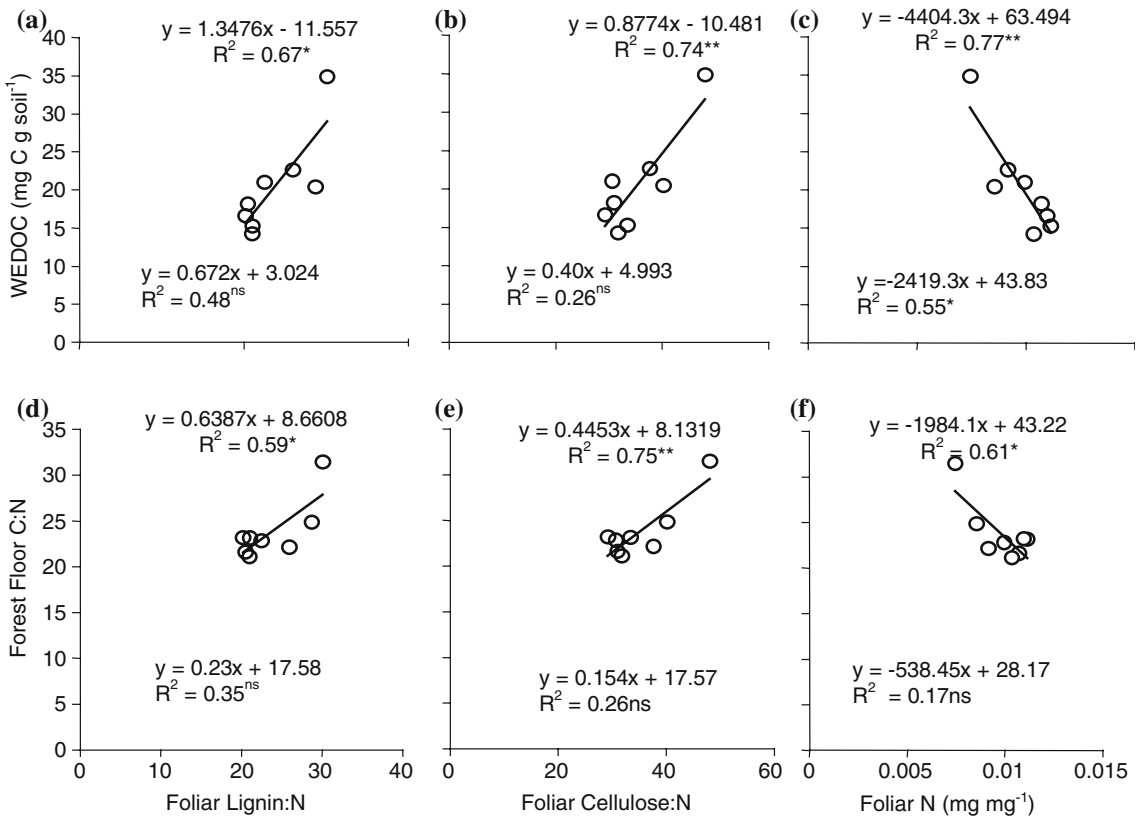

Figure 5. Relationships between mean forest floor WEDOC (mg C g soil^{-1}) and mean foliar chemistry for the oldest needles. Data points represent one site ($n = 5$). The top regression equation represents all eight sites and the bottom equation represents the seven sites on granitic bedrock (i.e. removal of the serpentine PB site). Relationships are significant at $^{**}P < 0.01$ and $^{***}P < 0.001$. Superscript ^{ns} is a non-significant relationship.

of *Picea abies* [L.] Karst needles was reduced in damaged forest stands across a gradient of damaged forest sites in the Czech Republic (Albrechtová et al., 2001; Campbell et al., 2004) and yet it is generally accepted that increased cell wall lignification is a non-specific reaction of plants to stresses (Lewis and Yamamoto, 1990). Although we saw a trend of increasing foliar lignin with younger needle age it was only significant at one of our stands (KV) which was previously considered to be one of the most heavily damaged sites in a study initiated in 1995 (B. Rock, unpublished). We suspect that reduced lignin content in our oldest needles compared to 2002 needles reflects forest recovery in the area studied and deeper forest floors are likely attributable to low lignin, necrotic needle fall prior to 1992. Lignin and cellulose are static and not capable of being transported from one needle age class to another unlike N which is a highly mobile nutrient frequently moved from older tissues to newer tissues such as foliage. Therefore, while N content in current foliage may reflect current growing conditions, lignin and cellulose levels in a given age class of needles reflect the growing conditions at the time of needle production.

Lignin is the most resistant of plant residues entering the soil C pool. It is a complex, non-uniform polymer and that produced in coniferous species tends to have an abundance of methoxyl groups with an estimated turnover time of 500 days (Killham, 1994). Furthermore, decomposition of litter to soil organic matter (SOM) is determined by the degradation rate of lignin which may, in the late stages of decomposition, be retarded by raised N concentrations (Fog, 1988; Magill and Aber, 1998). Forest floor N pools were not correlated to N content of any needle age class in this study, supporting the findings of studies in alpine ecosystems (Bowman

Table 4. Pearson bivariate correlation's for 2002 needles and oldest needles with and without the inclusion of the serpentine site (PB)

	Forest floor			
	WEDON	WEDOC:WEDON	Carbon	Nitrogen
Foliage removed from tree canopy				
2002 needles				
With site PB				
Lignin	0.14	**−0.43**	−0.08	0.02
Cellulose	−0.31	−0.32	−0.31	**−0.4**
Nitrogen	**−0.38**	**−0.51**	**−0.44**	−0.07
Lignin:N	**0.48**	**0.37**	**0.46**	0.06
Cellulose:N	0.28	**0.59**	**0.35**	−0.07
Without site PB				
Lignin	0.24	**−0.39**	0.06	0.05
Cellulose	−0.33	**0.36**	−0.29	**−0.41**
Nitrogen	−0.07	**−0.45**	−0.05	0.02
Lignin:N	0.18	0.26	0.02	−0.07
Cellulose:N	−0.17	**0.66**	−0.15	−0.29
Oldest needles				
With site PB				
Lignin	0.17	−0.08	−0.06	−0.09
Cellulose	−0.12	**0.35**	−0.07	**−0.33**
Nitrogen	**−0.44**	**−0.33**	**−0.4**	−0.06
Lignin:N	**0.45**	0.27	**0.34**	0.005
Cellulose:N	**0.36**	**0.44**	**0.36**	−0.06
Without site PB				
Foliar lignin	0.23	−0.04	−0.02	−0.09
Foliar cellulose	−0.33	0.27	**−0.36**	**−0.39**
Foliar nitrogen	−0.18	−0.21	−0.05	0.02
Foliar lignin:N	0.22	0.16	0.02	−0.07
Foliar cellulose:N	−0.04	**0.38**	−0.16	−0.25

Values are *R*-values showing the strength of correlation between the two variables, bold numbers are significant at $P < 0.05$, $n = 40$ with the PB site and $n = 35$ without the PB site.

et al., 2003). However, across 30 forested stands in New Hampshire, USA, forest floor N mineralization rates and foliar N are positively correlated suggesting a positive feedback between foliar chemistry and forest floor N status (Ollinger et al., 2002). What we did find in this study was that forest floor C was significantly but inversely correlated to foliar N and that forest floor N was inversely correlated to foliar cellulose, albeit a weak correlation. Furthermore, the significance of these correlation's were not lost with the removal of site PB which had high statistical leverage. We cannot rule out the effect of N deposition or fertilization and its effect on foliar N (e.g. Berg and Matzner, 1997; Pitcairn et al., 1998) and forest floor C (e.g. Berg and Matzner, 1997; Fog, 1988; Waldrop et al., 2004). Thus our observation of an inverse relationship between forest floor C pools and foliar N may also be an effect of N deposition causing increased decomposition of less recalcitrant C. For example, decay rates for lignified material are slowed with added N (Fog, 1988; Magill and Aber, 1998). The inverse correlation between forest floor N and foliar cellulose and is difficult to interpret. Cellulosic plant material decomposes faster with added N (Fog, 1988). Our results suggest that low forest floor N is linked to high foliar cellulose. Degradation of cellulose and the production of cellulase may often be limited by N availability. For example, a recent study in Oa material under *Piceas abies* report no response of

endoglucanase and β-glucosidase (both involved in cellulose degradation) to N addition in sites characterized by a low C:N ratio of 17.9 (Michel and Matzner, 2003). However, in sites characterized by wide C:N ratio (>21.1 or low N content), endoglucanase activity was increased by N-addition (Michel and Matzner, 2003). All of our sites with the exception of CP had forest floor C:N ratios of more than 21.1. We might also assume that high forest floor N results in lower NPP and cellulose storage. However, the effect of past pollutant loading (SO_2 and H_2SO_4 deposition) prior to 1989 on cellulose production and storage may well be confounding our results and this is illustrated by the significant increase in foliar cellulose at 5 of our 8 sites between circa.1993 and 2000.

Solid and solute phase forest floor C and N

Our data confirm previous work suggesting that foliar and forest floor chemistry are important controllers of DOC flux in forest soils. Many studies have examined factors that may control DOC production or leaching in forest floor material (see Kalbitz et al., 2000 review). The hypothesized controls are extremely variable and tend to be based upon solid phase properties of the forest floor. For example, some studies suggest that forest floor DOC is a product of photosynthate in recent litterfall material (Qualls and Haines, 1991) or of high litterfall fluxes (Currie and Aber, 1997). Other studies suggest that the leaching and microbial decay of humus rather than recent litter is largely responsible for forest floor DOC production (e.g. McDowell and Likens, 1988; Zsolnay, 1996). Soils with higher organic matter content export more DOC (Tipping et al., 1999), and related to this, organic horizons with higher C:N ratios experience higher DOC concentrations under field conditions (Aitkenhead and McDowell, 2000) and laboratory studies (Gödde et al., 1996; Kalbitz and Knappe, 1997). In contrast, a study synthesizing fluxes of DOC in temperate forests reported no relationship between DOC leaching and soil solid phase C or N or their ratio, but a positive correlation between DOC and forest floor pH (Michalzik et al., 2001). Our study shows that the pool of water extractable DOC in these Czech coniferous forest floors is significantly related to forest floor C:N, percentage C and water-extractable DON as well as foliar chemistry among eight sites.

Much less is known about forest floor DON, although there has been a plethora of studies over the last decade (McDowell, 2003). While there is little consensus on the production of DON some notable findings have been reported. Dissolved organic N is a larger fraction of total dissolved N in older soils than younger soils (Yu et al., 2003). This finding may be attributed to differences in forest age or species composition that affect N availability and DON production, as the older soils in this study supported dwarf conifer and ericaceous species while the younger soils supported grasslands and mixed conifer. Yet forest species do not appear to influence differences in DON concentration and flux among temperate coniferous and deciduous stands (Michalzik et al., 2001) even though species type is known to affect soil C:N and inorganic N (Lovett et al., 2004). Neither does stand age affect DON leaching within old growth and second growth northern hardwoods (Fisk et al., 2002). Climate does appear to affect DON release from forest floors. Throughfall intensity during the growing season (Michalzik and Matzner, 1999) and temperature (Andersson et al., 2000) result in increased DON concentration and flux. The forest floor at PB yielded the highest in WEDON of the eight sites (Table 3), and yet all age classes of needles from PB trees exhibit the lowest foliar N content (Figure 2), this may be due to the serpentine nature of the soils at the site. The limited amount of Ca available in soils derived from serpentinized bedrock is known to reduce nutrient uptake by vegetation by reducing root membrane permeability (Bidwell, 1979; Epstein, 1961; Goetz et al., 1983).

Far more studies have investigated anthropogenic effects on DON, but the results are mixed. For example, DON increased in the forest floor of *Pinus resinosa* [Ait.] stands that have been fertilized (McDowell et al., 2004), showed no increase in laboratory or field fertilization studies of *Picea abies* [L.] Karst forest floor (Raastad and Mulder 1999; Sjöberg et al., 2003) but enhanced the release of DON in an incubation of deciduous forest floor (Park et al., 2002).

The link between foliar C and N and forest floor solid and water-extractable C and N was evident in both recently produced and the oldest

needles. This may be due to newer-age-class-needles reflecting the C and N status of the forest floor as well as the expected forest floor reflection of the C and N status of the older needles. This is a particularly exciting finding given that growing conditions have changed dramatically in recent years, such as the observed forest recovery in the 1990s (Albrechtová et al., 2001).

Despite the link between DOC and forest floor C:N (Aitkenhead and McDowell, 2000) and between forest floor C:N and foliar lignin:N (Ollinger et al., 2002; McNulty et al., 1991), to our knowledge little research has examined the control that foliar lignin, cellulose and N might have on water extractable forest floor DOC and DON. Several studies have, however, investigated forest floor litter lignin and N in conjunction with DOC, forest floor DON and inorganic N (e.g. Lovett et al., 2004; Madritch and Hunter, 2003). We believe that our empirical relationships between water extractable DOC, DON and foliar chemistry may be indirect and that several abiotic and biotic variables interact to determine forest floor C:N, DOC and DON. Forest vegetation and its associated micro-organisms, climate (precipitation and temperature), topography, age of soil and bedrock are all likely interrelated contributing in various proportions to forest floor C:N ratio, DOC and DON.

Our hypothesis that the oldest needles, which are shed sooner, most affect the forest floor and its chemistry was not supported by our results. In many cases we noted a stronger, significant correlation with recently produced needles than with older needles. More research on foliar chemistry and its link with forest floor DOC and DON using differing forest species is needed to support or counter the findings of this study. Additional studies are also needed which compare spectral reflectance data from fresh foliage and dried, ground foliage (the NIR results reported in this study), in order to improve our understanding of the best remote sensing methods to be used in characterizing foliar chemistry. The results of this study illustrate a link between foliar chemistry and forest floor solid phase C:N, WEDOC and WEDON suggesting that the potential exists for extrapolation to watershed scales through remotely sensed foliar lignin, cellulose and N in order to aid modeling of aquatic DOC and DON exports.

Although we have attempted to interpret our results from correlation and regression analysis, we have to reiterate that this study was completed on a single forest species in stands across a historical gradient of sulfate deposition that may have confounded our findings. Furthermore, not all soil orders or bedrock were the same for the eight sites and five out of the eight sites had some history of dolomite application. As such we were unable to control for this wide variety of variables that might also influence foliar and forest floor chemistry. We do not state nor believe that foliar chemistry explicitly controls production of DOC and DON in the forest floor. However, we do believe that we have shown that a link between foliar chemistry and forest floor WEDOC and WEDON exists which, in terms of remote sensing is an important advance for modeling forest floor DOC and DON production across regions.

Acknowledgements

Funding for research, analysis and manuscript preparation was provided by a grant from the U. S. National Science Foundation (DEB 01108385) awarded to W. H. McDowell and J. A. Aitkenhead-Peterson, and for participant support from Kontakt/NSF ME658 of the Ministry of Education of the Czech Republic awarded to J. Albrechtová of Charles University, Prague. This is a contribution of the Agricultural Experiment Station of the University of New Hampshire. We thank Zdeněk Seidl, Matyáš Fendrych and Sandor Forczek (Charles University, Prague) and Brian Pellerin (University of New Hampshire) for stimulating discussions and assistance in the field.

References

Aitkenhead J A and McDowell W H 2000 Soil C:N ratio as a predictor of annual riverine DOC flux at local and global scales. Global Biogeochem. Cycles 14, 127–138.

Aitkenhead-Peterson J A, McDowell W H and Neff J C 2003 Sources, production and regulation of allochthonous dissolved organic matter inputs to surface water. *In* Aquatic Ecosystems: Interactivity of Dissolved Organic Matter. Eds. S E G Findlay and R L Sinsabaugh. pp. 25–70. Academic Press, San Diego.

Aitkenhead-Peterson J A and Kalbitz K 2005 Short-term response on the quantity and quality of rhizo-deposited carbon from Norway spruce exposed to low and high N inputs. J. Plant Nutr. Soil Sci. 168, 687–693.

Albrechtová J, Rock B N, Soukupová J, Entcheva Campbell P, Solcová B and Polák T 2001 Biochemical, histochemical, structural and reflectance markers of damage in Norway spruce from the Krušné hory Mts. used for the interpretation of remote sensing data. J. For. Sci. 47, 26–33.

Alexander J E 2005 Linking foliar and soil chemistry in northern Bohemia. MS Thesis, University of New Hampshire.

Andersson S, Nilsson S I and Saetre P 2000 Leaching of dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) in mor humus as affected by temperature and pH. Soil Biol. Biochem. 32, 1–10.

Ardo J, Lambert N, Henzlik V and Rock B N 1997 Satellite-based estimations of coniferous forest changes: Krusne hory, Czech Republic 1972–1989. Ambio 26, 158–166.

Berg B and Matzner E 1997 Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environ. Rev. 5, 1–25.

Bidwell R G S 1979 Plant Physiology. 2nd edn. MacMillon, New York 726 pp.

Bolster K L, Martin M E and Aber J D 1996 Interactions between precision and generality in the development of calibrations for the determination of carbon fraction and nitrogen concentration in foliage by near infrared reflectance. Can. J. For. Res. 26, 590–600.

Bowman W D, Bahnj L and Damm M 2003 Alpine landscape variation in foliar nitrogen and phosphorus concentrations and the relation to soil nitrogen and phosphorus availability. Arct. Antarc. Alp. Res. 35, 144–149.

Campbell P K E, Rock B N, Martin M E, Neefus C D, Irons J R, Middleton E M and Albrechtová J 2004 Detection of initial damage in Norway spruce canopies using hyperspectral airborne data. Int. J. Remote Sens. 25, 5557–5583.

Currie W S and Aber J D 1997 Modeling leaching as a decomposition process in humid montane forests. Ecology 78, 1844–1860.

Dambrine E, Kinkor V, Jehlička J and Gelhaye D 1993 Fluxes of dissolved mineral elements through a forest ecosystem submitted to extremely high atmospheric-pollution inputs (Czech Republic). Ann. Sci. Forest. 50, 147–157.

Dawson H J, Ugolini F C, Hrutfiord B F and Zachara J 1978 Role of soluble organics in the soil processes of a podzol, Central Cascades, Washington. Soil Sci. 126, 290–296.

Epstein E 1961 The essential role of calcium in selective cation transport in plant cells. Plant Physiol. 36, 437–444.

Fisk M C, Zak D R and Crow T R 2002 Nitrogen storage and cycling in old- and second-growth northern hardwood forests. Ecology 83, 73–87.

Fog K 1988 The effect of added nitrogen on the rate of decomposition of organic matter. Biol. Rev. 63, 433–462.

Gödde M, David M B, Christ M J, Kaupenjohann M and Vance G F 1996 Carbon mobilization from the forest floor under red spruce in the northeastern USA. Soil Biol. Biochem. 28, 1181–1189.

Goetz A F H, Rock B N and Rowen L C 1983 Remote sensing exploration: an overview. Econ. Geol. 78, 573–590.

Gundersen P, Emmett B A, Kjonaas O J, Koopmans C J and Tietema A 1998 Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data. For. Ecol. Manage. 101, 37–55.

Hagedorn F, Blaser B and Siegwolf R 2002 Elevated atmospheric CO_2 and increased N deposition effects on dissolved organic carbon – clues from $\delta^{13}C$ signature. Soil Biol. Biochem. 34, 355–366.

Harris D, Horwath W R and van Kessel C 2001 Acid fumigation of soils to remove carbonates prior to total organic carbon or carbon-13 isotopic analysis. J. Soil Sci. Soc. Am. 65, 1853–1856.

Hruška J and Krám P 2003 Modelling long-term changes of streamwater chemistry in catchments with contrasting vulnerability to acidification (Lysina and Pluhuv Bor, Czech Republic). Hydrol. Earth Syst. Sci. 7, 525–539.

Hruška J, Moldan F and Krám P 2002 Recovery from acidification in central Europe – observed and predicted changes of soil and streamwater chemistry in the Lysina catchment, Czech Republic. Environ. Pollut. 120, 261–274.

Kalbitz K and Knappe S 1997 Einfluß der Bodeneigenschaften auf die Friesetzung der gelösten organischen Substanz (DOM) aus dem Oberboden. Z. Pflanzenernahr. Bodenk 160, 475–483.

Kalbitz K, Popp P, Geyer W and Hanschmann G 1997 HCH mobilization in polluted wetland soils as influenced by dissolved organic matter. Sci. Total Environ. 204, 37–48.

Kalbitz K, Solinger S, Park J H, Michalzik B and Matzner E 2000 Controls on the dynamics of dissolved organic matter in soils: a review. Soil Sci. 164, 277–304.

Kalvová J Ed. 1996 Climate change scenarios for the Czech Republic. Country study of climate change for the Czech Republic. National Climatic Program of the Czech Republic, No 24, Czech Hydrometeorological Institute, Prague.

Killham K 1994 Soil Ecology. University Press, Cambridge.

Krám P, Hruška J and Driscoll C T 2000 Biogeochemistry of forest catchments with contrasting geology. Technical Documents in Hydrology, UNESCO, Paris 37, 65–72.

Krám P, Hruška J, Wenner B S, Driscoll C T and Johnson C E 1997 The biogeochemistry of basic cations in two forest catchments with contrasting lithology in the Czech Republic. Biogeochemistry 37, 173–202.

Lajtha K, Crow S, Yano Y, Kaushal S S, Sulzman E W and Spears J D H 2005 Detrital controls on dissolved organic matter in soils: a field experiment. Biogeochemistry 76, 261–281.

Lewis N G and Yamamoto E 1990 Lignin: occurrence, biogenesis and biodegradation. Ann. Rev. Plant Physiol. Plant Mol. Biol. 41, 455–496.

Lovett G M, Weathers K C and Arthur M A 2002 Control of nitrogen loss from forested watersheds by soil carbon:nitrogen ratio and tree species composition. Ecosystems 5, 712–718.

Lovett G M, Weathers K C, Arthur M A and Schultz J C 2004 Nitrogen cycling in a northern hardwood forest: do species matter? Biogeochemistry 67, 289–308.

Madritch M D and Hunter M D 2003 Intraspecific litter diversity and nitrogen deposition affect nutrient dynamics and soil respiration. Oecologia 136, 124–128.

Magill A H and Aber J D 1998 Long-term effects of experimental nitrogen additions on foliar litter decay and humus formation in forest ecosystems. Plant Soil 203, 301–311.

Majer V, Krám P and Shanley J B 2005 Rapid regional recovery from sulfate and nitrate pollution in streams of the western Czech Republic – comparison to the other recovering areas. Environ. Pollut. 135, 17–28.

McDowell W H 2003 Dissolved organic matter in soils – future directions and unanswered questions. Geoderma 113, 179–186.

McDowell W H and Likens G E 1988 Origin, composition and flux of dissolved organic carbon in the Hubbard Brook valley. Ecol. Monogr. 58, 177–195.

McDowell W H, Magill A, Aitkenhead-Peterson J A, Aber J D, Merriam J and Kaushal S S 2004 Effects of chronic nitrogen amendment on dissolved organic matter and inorganic nitrogen in soil solution. For. Ecol. Manage. 196, 29–41.

McNulty S G, Aber J D and Boone R D 1991 Spatial changes in forest floor and foliar chemistry of spruce-fir forests across New England. Biogeochemistry 14, 13–29.

Merriam J, McDowell W H and Currie W S 1996 A high-temperature catalytic oxidation technique for determining total dissolved nitrogen. Soil Sci. Soc. Am. J. 60, 1050–1055.

Michalzik B, Kalbitz K, Park J H, Solinger S and Matzner E 2001 Fluxes and concentrations of dissolved organic carbon and nitrogen – a synthesis for temperate forests. Biogeochemistry 52, 173–205.

Michalzik B and Matzner E 1999 Dynamics of dissolved organic nitrogen and carbon in a Central European Norway spruce ecosystem. Eur. J. Soil Sci. 50, 579–590.

Michel K and Matzner E 2003 Response of enzyme activities to nitrogen addition in forest floors of different C-to-N ratios. Biol. Fertil. Soils 38, 102–109.

Ollinger S V, Smith M L, Martin M E, Hallett R A, Goodale C L and Aber J D 2002 Regional variation in foliar chemistry and soil nitrogen status among forests of diverse history and composition. Ecology 83, 339–355.

Oulehle F and Hruška J 2005 Tree species (*Picea abies* and *Fagus sylvatica*) effects on soil water acidification and aluminium chemistry at sites subjected to long-term acidification in the Ore Mts., Czech Republic. *J. Inorg. Biochem.* 99, 1822–1829.

Park J H, Kalbitz K and Matzner E 2002 Resource control on the production of dissolved organic carbon and nitrogen in a deciduous forest floor. Soil Biol. Biochem. 34, 813–822.

Park J H and Matzner E 2003 Controls on the release of dissolved organic carbon and nitrogen from a deciduous forest floor investigated by manipulations of aboveground litter inputs and water flux. Biogeochemistry 66, 265–286.

Pitcairn C E R, Leith D, Sheppard L J, Sutton M A, Fowler D, Munro R C, Tang S and Wilson D 1998 The relationship between nitrogen deposition, species composition and foliar nitrogen concentrations in woodland flora in the vicinity of livestock farms. Environ. Pollut. 102(Suppl. 1), 41–48.

Qualls R G and Haines B L 1991 Geochemistry of dissolved organic nutrients in water percolating through a forest ecosystem. Soil Sci. Soc. Am. J. 55, 1112–1123.

Raastad I A and Mulder J 1999 Dissolved organic matter (DOM) in acid forest soils at Gardsjon (Sweden): natural variabilities and effects of increased input of nitrogen and of reversal of acidification. Water Air Soil Pollut. 114, 199–219.

Rock B N, Lambert N, Ardo J and Henzlik V 1994 The use of satellite remote sensing for forest monitoring. *In* Optical Methods in Biomedical and Environmental Sciences. Eds. H Ohzu and S Komatsu. pp. 261–264. Elsevier Science, Amsterdam.

Schimel J P and Weintraub M N 2003 The implication of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biol. Biochem. 35, 549–563.

Sjöberg G, Bergkvist B, Berggren D and Nilsson S I 2003 Long term N addition effects on the C mineralization and DOC production in mor humus under spruce. Soil Biol. Biochem. 35, 1305–1315.

Sollins P, Glassman C, Paul E A, Swanston C, Lajtha K, Heil J W and Elliott E T 1999 Soil carbon and nitrogen-pools and fractions. *In* Standard Soil Methods for Long-Term Ecological Research. Eds. G Philip Robertson, C Coleman David, S Bledsoe Caroline and Sollins Phillip. pp. 89–105. Oxford University Press.

Soukupova J, Cvikrova J, Albrechtová J, Rock B N and Eder J 2000 Histochemical and biochemical approaches to the study of phenolic compounds and peroxidases in needles of Norway spruce (*Picea abies*). New Phytol. 146, 403–414.

Tipping E, Woof C, Rigg E, Harrison A F, Ineson P, Taylor K, Benham D, Poskitt J, Rowland A P, Bol R and Harkness D D 1999 Climatic influences on the leaching of dissolved organic matter from upland UK moorland soils, investigated by a field manipulation experiment. Environ. Int. 25, 83–95.

van Kessell C, Nitschelm J, Horwath W R, Harris D, Walley F, Luscher A and Hartwig U 2005 Carbon-13 input and turnover in a pasture soil exposed to long-term elevated atmospheric CO_2. Global Change Biol. 6, 123–135.

Waldrop M P, Zak D R, Sinsabaugh R L, Gallo M and Lauber C 2004 Nitrogen deposition modifies soil carbon storage through changes in microbial enzymatic activity. Ecol. Appl. 14, 1172–1177.

Yano Y, McDowell W H and Kinner N E 1998 Quantification of biodegradable dissolved organic carbon in soil solution with flow-through bioreactors. Soil Sci. Soc. Am. J. 62, 1556–1564.

Yu Z S, Kraus T E C, Dahlgren R A, Horwath W R and Zasoski R J 2003 Mineral and dissolved organic nitrogen dynamics along a acidity-fertility gradient. Soil Sci. Soc. Am. J. 67, 878–888.

Zsolnay A 1996 Dissolved humus in soil waters. *In* Humic Substances in Terrestrial Ecosystems. Ed. A Piccolo. pp. 171–224. Elsevier Science, Amsterdam.

Section editor: C. Neill