

Soil organic carbon dynamics along a climatic gradient in a southern Appalachian spruce–fir forest

C.E. Tewksbury and H. Van Miegroet

Abstract: A field study was conducted in a high-elevation spruce–fir (*Picea rubens* Sarg. – *Abies fraseri* (Pursh.) Poir) forest in the Great Smoky Mountains National Park to assess the effect of temperature on soil C storage and dynamics. In eight plots along an elevation gradient (1500–1900 m), we measured soil temperature, forest floor and mineral soil C, litter decomposition, soil respiration, and forest floor mean residence time. Mean annual soil temperature and annual degree-days above 5 °C were inversely correlated with elevation. Total soil C (166–241 Mg·ha⁻¹) showed no trend with elevation, while forest floor C accumulation (16.3–35.9 Mg·ha⁻¹) decreased significantly with elevation. Carbon dynamics did not follow a consistent elevation pattern; however, the cooler upper elevations showed the lowest C turnover as indicated by the lowest needle decomposition rate ($k = 0.0231 \cdot \text{year}^{-1}$) and the longest mean residence time of forest floor C (22 years). Mean annual CO₂ efflux from the soil (1020–1830 kg C·ha⁻¹·year⁻¹) was negatively correlated with mean annual soil temperatures and annual degree-days above 5 °C. This gradient study offers useful insights into C release patterns under future warming scenarios, and suggests that the highest elevation may be most susceptible to global warming.

Résumé : Une étude de terrain a été entreprise dans une forêt en haute altitude composée d'épinette et de sapin (*Picea rubens* Sarg. et *Abies fraseri* (Pursh.) Poir) située dans le parc national de Great Smoky Mountains pour évaluer l'effet de la température sur l'entreposage et la dynamique du C dans le sol. Dans huit parcelles établies le long d'un gradient altitudinal (1500 à 1900 m), nous avons mesuré la température du sol, la teneur en C de la couverture morte et du sol minéral, la décomposition de la litière, la respiration du sol et le temps de résidence moyen de la couverture morte. La température annuelle moyenne du sol et le nombre de degrés-jours au-dessus de 5 °C étaient inversement corrélés à l'altitude. La teneur totale en C du sol (166 à 241 Mg·ha⁻¹) n'a montré aucune tendance avec l'altitude alors que l'accumulation de C dans la couverture morte (16,3 à 35,9 Mg·ha⁻¹) diminuait de façon significative avec l'altitude. La dynamique du carbone ne suivait pas un patron altitudinal cohérent. Cependant, les températures froides des altitudes plus élevées étaient associées à un plus faible taux de renouvellement du C comme l'indiquent le taux de décomposition des aiguilles le plus faible ($k = 0,0231 \cdot \text{an}^{-1}$) et le temps de résidence moyen du C de la couverture morte le plus long (22 ans). Le débit annuel moyen de CO₂ en provenance du sol (1020 à 1830 kg C·ha⁻¹·an⁻¹) était négativement corrélé à la température annuelle moyenne du sol et au nombre de degrés-jours au-dessus de 5 °C. Cette étude de gradient donne un aperçu utile des patrons de libération de C en fonction de scénarios futurs de réchauffement et indique que les altitudes élevées peuvent être davantage affectées par le réchauffement global.

[Traduit par la Rédaction]

Introduction

In the coming century, atmospheric concentrations of CO₂ are expected to double, and global average temperature may increase by 1.8 to 5.8 °C (Albritton et al. 2001). Admundson (2001) postulates that any increase in global temperatures will undoubtedly affect soil organic carbon (SOC) storage. Global C reserves in soils are large, so small changes in SOC storage may significantly affect atmospheric CO₂ concentrations (Kirschbaum 2000). However, both the direction and magnitude of the feedbacks between SOC and atmospheric CO₂ remain subject to substantial uncertainties. Davidson and Janssens (2006) suggest that much of soil-mediated feedback between climate change and the global

C cycle will greatly depend on the temperature sensitivity of decomposition.

Liski et al. (1999) and Giardina and Ryan (2000) have postulated that only decomposition of young litter and labile C (i.e., forest floor) accelerates with increasing temperature, while older, more stable C in the mineral soil is far less responsive to temperature changes. Subsequent studies have refuted this assertion, and have provided evidence that even relatively resistant SOC pools are temperature sensitive (Knorr et al. 2005).

A meta-analysis of 32 ecosystem warming experiments indicates that higher soil temperatures stimulate CO₂ emission from soils (Rustad et al. 2001). Yet, concurrent in-

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creases in nutrient availability and higher atmospheric CO₂ levels may enhance net primary productivity and C input to the soils (Kirschbaum 1995; Melillo et al. 2002), possibly counteracting the soil response (Kirschbaum 2000). An increase in soil C storage due to accelerated net primary productivity is limited by the extent to which C additions are partitioned into pools with slow turnover rates (Trumbore 2000; Schlesinger and Lichter 2001).

Temperate and boreal forest ecosystems have relatively large reservoirs of organic C in the form of forest floors (Post et al. 1982; Vogt et al. 1996). Some have suggested that soil respiration rates are generally more responsive to warming than productivity in these cool, high-latitude ecosystems (Schleser 1982; Kirschbaum 1995). Although the quality and quantity of inputs affect the storage of C in forest floor, abiotic factors controlling C loss may be more important in determining C storage in temperate ecosystems (Simmons et al. 1996; Vogt et al. 1996). Cool climate forest ecosystems are expected to experience the largest and earliest effects of warming (Zolbrod and Peterson 1999; Prichard et al. 2000). Considering current evidence, these ecosystems may represent significant net sources of CO₂ to the atmosphere.

The cool temperate, high-elevation red spruce – Fraser fir (*Picea rubens* Sarg. – *Abies fraseri* (Pursh.) Poir) forests in the southern Appalachians are an example of coniferous forests with large accumulations of organic C in the forest floor and surface soil horizons. Although the geographic extent of this forest type is relatively small, ~27 000 ha, ~74% of which occurs in the Great Smoky Mountain National Park (GSMNP) (Dull et al. 1988), the spruce–fir forest occupies a unique area of forest soil types within the southeastern United States (Fernandez 1992). Steepness of the terrain and difficulties in access has limited much soils research in this forest type (Bolstad and Vose 2001; Miller et al. 2004). The majority of this area has not experienced severe, stand-replacing disturbances such as fire or logging (Pyle and Schafale 1988). The prevalence of old unglaciated landscapes with a legacy of soil C and limited fire history (Pyle and Schafale 1988) has resulted in significant C accumulation in soils (Johnson et al. 1991; Joslin et al. 1992) and aboveground biomass (Van Miegroet et al. 2007). More recently, the spruce–fir forest has been impacted by the balsam woolly adelgid (*Adelges piceae* (Ratz.)) (BWA), causing dieback of mature Fraser fir and spatial heterogeneity of coarse woody debris on the forest floor (Nicholas et al. 1992; Rose 2000). Because the spruce–fir forest type is at the southern edge of its distribution occupying the highest and coolest available mountain ranges; and because large pools of organic matter in the forest floor and upper mineral horizons have developed under a cool, moist temperate climatic regime; this ecosystem may be particularly sensitive to climatic warming. Garten et al. (1999) predicted substantial losses (~42%–46%) of organic C from high-elevation spruce–fir soils under future regional warming scenarios, especially since a high proportion of C in these forest soils is thought to be associated with unprotected pool or labile organic matter, highly susceptible to enhanced mineralization with increase in temperature (Garten et al. 1999, 2000).

This research focuses on the mature high-elevation spruce–fir forest type in the GSMNP, because it presents the opportunity to study the influence of climate on storage and

dynamics of soil C in a distinctive and highly valued forest in the southern Appalachians that may be particularly sensitive to climate-induced changes in ecosystem structure and function. The objectives of this study were to quantify and characterize soil organic C storage and dynamics along an elevation gradient of the spruce–fir zone within the GSMNP, with elevation as a predicted surrogate for temperature. It was predicted: (i) that a significant negative correlation would exist between elevation and temperature; and (ii) that the different temperature regimes along the elevation gradient would result in a predictable trend in SOC storage and dynamics, with lower soil C storage and faster C turnover at lower elevations characterized by a warmer climate, and slower turnover and larger C storage in upper elevations characterized by a cooler climate. The warmer conditions in the lower elevations of this gradient study may give indications of how future climatic trajectories may affect soil C processes at higher elevations.

Materials and methods

Study site

The study was conducted in the high-elevation spruce–fir zone of GSMNP in the proximity of Clingman's Dome, on the North Carolina and Tennessee border. It capitalized on existing infrastructure and available data from prior and ongoing research on forest dynamics (Nicholas et al. 1992), nutrient cycling (Johnson et al. 1991), soil processes (Garten and Van Miegroet 1994), and watershed dynamics (Nodvin et al. 1995; Van Miegroet et al. 2001) in high-elevation spruce–fir forests. This is an uneven-aged forest, with red spruce and Fraser fir as the dominant overstory species. Species distribution follows an elevational gradient. The overstory is dominated by mature red spruce in the lower elevations (1370–1650 m), and the understory consists mainly of hardwoods including yellow birch (*Betula lutea* Michaux f.), mountain ash (*Sorbus americana* Marshall), and mountain maple (*Acer spicatum* Lam.). At middle elevations (1675–1890 m), red spruce and Fraser fir codominate. At higher elevations (>1890 m), the forest has undergone canopy decline because of Fraser fir mortality caused by the infestation of the BWA and the overstory is dominated by young and standing dead Fraser fir with a component of red spruce (Nicholas et al. 1992; Pauley et al. 1996).

The soils are Inceptisols with spodic characteristics classified as Dystrichrepts or Haplumbrepts, typified by relatively thick O-horizons (5–10 cm) that overlie organic matter rich A-horizons (Kelly and Mays 1989; Joslin et al. 1992; Van Miegroet et al. 1993). Soils are underlain by Thunderhead sandstone of the Great Smoky Group (King and Stupka 1950; Feldman et al. 1991). They are relatively shallow with estimates of total depth ranging from ~50 cm (Van Miegroet et al. 2001) to ~60–65 cm (Johnson and Lindberg 1992) and have a silt loam to sandy loam texture. Despite the relatively old landscapes that dominate the southeastern US, the soils in this ecosystem are genetically young and developmentally immature because of slope instability and soil mixing associated with frequent landslides on steeper slopes and windthrow of shallow-rooted trees (Wolfe 1967; Fernandez 1992; White and Cogbill 1992). Soils are acidic, characterized by high organic matter content and low base

saturation, as well as high nitrogen (N) mineralization and nitrification capacity (Johnson et al. 1991; Garten and Van Miegroet 1994).

Mean annual temperature at the study site is 8.5 °C, ranging from -2 °C in January to 18 °C in July, with a frost-free period from May through September (Johnson et al. 1991). Mean annual precipitation is 230 cm, with annual variations of 150–300 cm, with 10% as snow (Van Miegroet et al. 2001). Precipitation generally exceeds evapotranspiration (Shanks 1954), although some moisture stress occurs in summer and early fall (Pauley 1989). These climatic conditions result in a relatively short growing season (100–150 days), combined with frequent cloud immersion and high winds (White and Cogbill 1992; Johnson et al. 1991).

Experimental design

The core measurements were conducted in selected plots in the Noland Divide Watershed (NDW), a small (17.4 ha), high-elevation (1700–1900 m) forested catchment, and from an adjacent network of plots established in the mid-1980s as part of the National Acid Precipitation Assessment Program (NAPAP) (Nicholas et al. 1992). To encompass the full spruce–fir elevation range within the GSMNP (Nicholas et al. 1992), eight 20 m × 20 m plots were included in our design: four NAPAP plots, two above NDW at an elevation of ~2000 m near Clingman's Dome, and two below the catchment outlet at an elevation of ~1530 m; and four plots within the NDW, two in the upper catchment at ~1850 m, and two in the lower catchment at ~1700 m ("intensive plots", Fig. 1). Selection criteria for the eight plots were as follows: stratification along the full elevation range of the spruce–fir forest within the GSMNP (1450–2000 m); proximity to one another and similar aspect (east) to minimize possible differences in geology and climate; relatively intact forest structure to minimize the confounding effect of recent gaps on soil microclimate and C dynamics; and overstory species composition and live basal area (LBA) representative of that particular elevation band (Nicholas et al. 1992). Some plot characteristics are summarized in Table 1.

Soil temperature

Stowaway Tidbit dataloggers (Onset Computer Corporation, Pocasset, Massachusetts) were placed at ~10 cm soil depth in the center of each plot and programmed to measure soil temperature every 2 h over a 2 year period (2001–2003). Mean annual soil temperatures were calculated as the average of the minimum and maximum daily temperature readings during the year. An annual soil heat index was expressed as annual soil degree-days (ADD) and calculated as the sum of mean daily soil temperatures above 5 °C over the year. Five degrees and higher was chosen as a threshold for microbial activity (Alexander 1977). Additional soil temperature readings for the NDW were obtained between 1998 and 2003 using dataloggers placed along a central elevation transect (H. Van Miegroet, unpublished data) ("temperature transect", Fig. 1).

Soil organic carbon pools

Carbon content of the forest floor (Oi, Oa, and Oe) in the plots was determined in October 2003 by excavating a 15 cm × 15 cm area at four random locations at the periph-

ery of each plot using a sampling frame. All samples were oven-dried (65 °C), weighed, ground in a Wiley mill (No. 40 mesh screen; 0.85 mm mesh), and subsamples were analyzed for C concentration using a LECO CN analyzer (CHN 1000; Leco Corp., St. Joseph, Michigan).

Mineral soil cores were taken at four locations at the periphery of each plot in summer 2004 and were sampled from 0–15 cm and then in 10 cm sections to a depth of 50 cm or until bedrock. The 0–15 cm section represented a combination of O- and A-horizons; therefore, the organic horizon was removed and only the mineral soil was further analyzed. Because mineral soils were high in organic matter, all samples were oven-dried at 65 °C, which is appropriate for organic-rich substrates, sieved (2 mm mesh), and homogenized with a mortar and pestle, composited per depth increment and plot, and analyzed for total C on a LECO CN analyzer. Bulk density and percent gravel for mineral soil was determined using the core method (Blake and Hartge 1986) in the eight plots (four replicate cores per plot). In addition to these mineral and forest floor estimates, ecosystem overstory and coarse woody debris pools were determined as part of the larger C budget project (Van Miegroet et al. 2007).

Soil organic carbon dynamics

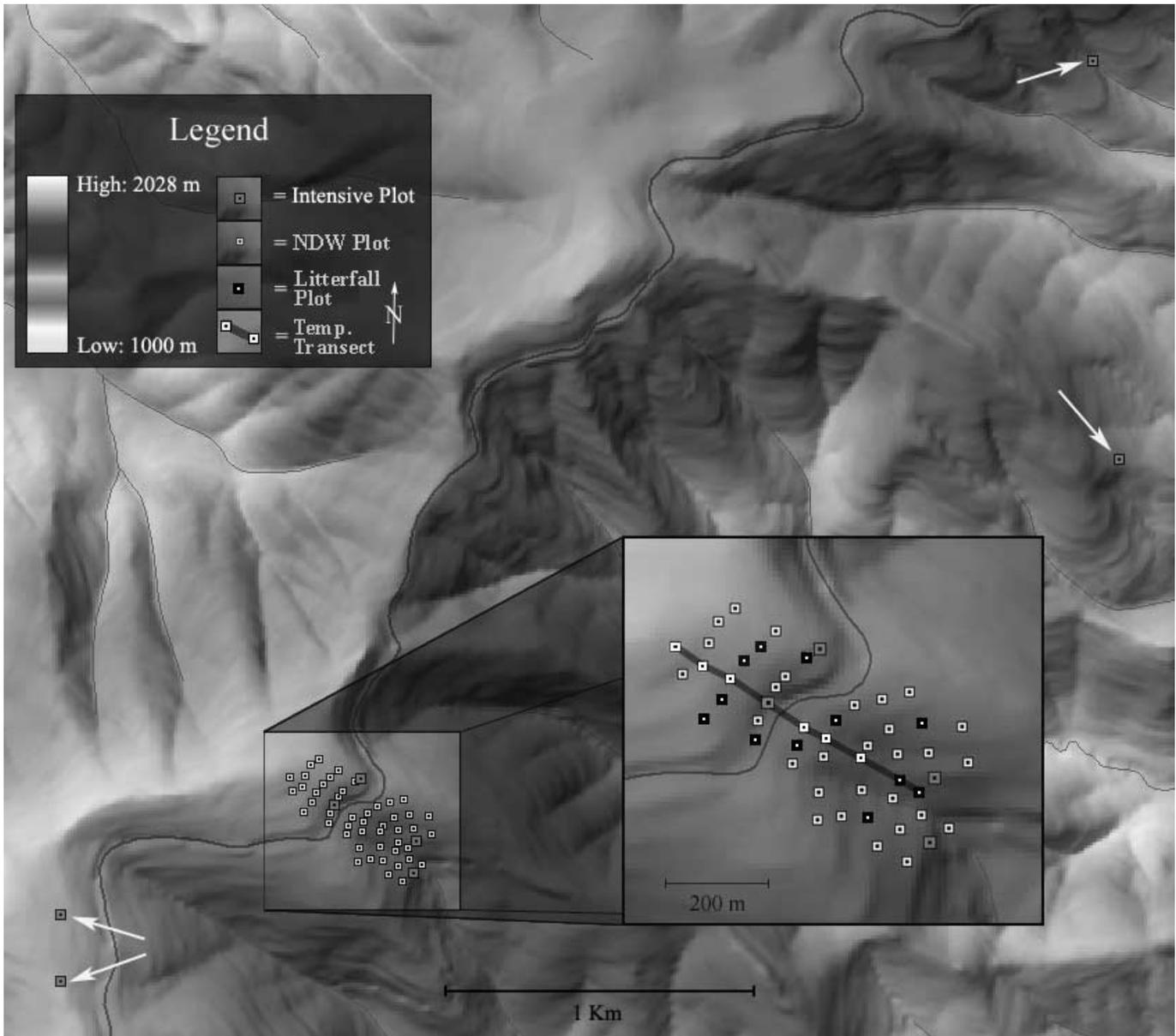
To analyze the effects of temperature on organic C dynamics, we quantified the turnover of various SOC cohorts. We measured litter decomposition rates as an indicator of the turnover of a single cohort of needle fall; mean residence time of forest floor C pools as an indicator of the dynamics of a mixed organic layer cohort; and CO₂ efflux rates from the soil as an indicator of total belowground C dynamics.

Litter decomposition rates

Litter decomposition rates were determined from litterbags with a homogeneous substrate of air-dried spruce needles, obtained earlier from littertraps and fallen trees. Using the same substrate across all plots allowed us to explicitly test the influence of soil microclimate on litter decomposition without the confounding effect of litter chemical composition. Litterbags (17 cm × 17 cm) were constructed using fine sport utility nylon on the bottom and 1 mm mesh cloth on the top, allowing access by invertebrate decomposers without losing sample from the bottom. All litterbags, containing approximately 15 g of initial air-dried litter, were assembled, weighed, transported to the field in individual plastic bags, and anchored into the forest floor at random locations (30 bags per plot; 240 bags total) in May of 2002. The mass of needles lost from the litterbags in transport and collected in the plastic bags was subtracted from the initial substrate mass. At 6, 12, 18, 24, and 36 months (October 2002 – June 2005), five litterbags were collected from each plot, oven-dried at 65 °C until thoroughly dried, and litter remaining was weighed. Subsamples were ground with a Wiley mill (No. 40 mesh screen, 0.85 mm mesh) and analyzed for C using a LECO CN analyzer. Litter C concentrations were corrected for ash content via loss-on-ignition, to account for possible contamination of the litter samples with mineral soil.

Forest floor mean residence time

In addition to the forest floor measurements described

Fig. 1. Map of study site and plot layout in the Great Smoky Mountains National Park.**Table 1.** Spruce–fir plot characteristics.

Plot	Elevation (m)	Elevation band (m)	Aspect	Slope (%)	Live basal area ($\text{m}^2 \cdot \text{ha}^{-1}$)	Mean annual soil temperature ($^{\circ}\text{C}$)	Annual degree-days (days)
1	1524	Lower (~1550)	SE	40	60.9	8.86	1660
2	1536		E	45	59.2	9.29	1756
3	1701	Lower–mid (~1700)	E	49	36.6	7.89	1430
4	1701		S	50	41.4	7.34	1263
5	1835	Upper–mid (~1850)	SE	40	49.0	7.01	1283
6	1835		SE	40	63.0	8.97	1695
7	1966	Upper (~2000)	NE	27	38.7	5.64	1064
8	1966		E	27	53.5	6.91	1180
Overall mean						7.74	1417

earlier, forest floor C content of 12 NDW plots was calculated from dry mass measurements from four replicate cores (inside diameter 4.1 cm) per plot taken in summer 1998 and

1999, as part of another study initiated earlier in the NDW (H. Van Miegroet, unpublished data). The plots were located along three elevation bands composed of four plots each

(low, 1705–1768 m; medium, 1798–1828 m; and high, 1859–1920 m) representing the elevation range of the watershed (Barker et al. 2002) (Fig. 1). Litterfall was collected in the four NAPAP plots and the 12 NDW plots (“litterfall plots”, Fig. 1) using round litterfall collection traps (0.07 m²) located at the four corners of the plot quadrants. Samples were collected from each of the four NAPAP plots in May, August, October for 2 years (2001–2003), and for the NDW during the same months over 5 years (1998–2003) as part of another study (Barker et al. 2002). All samples were oven-dried at 65 °C and weighed; composited by plot; sorted into four fractions: (1) needles, (2) foliage, (3) twigs and bark, and (4) other; ground in a Wiley mill (No. 40 mesh screen; 0.85 mm mesh); and analyzed for C using a LECO CN analyzer. In this study, mean residence time (MRT) of forest floor C was calculated for the four NAPAP plots and 12 NDW plots as

$$\text{MRT (years)} = \frac{\text{Forest floor C biomass (kg C}\cdot\text{ha}^{-1})}{\text{annual litterfall (kg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1})}$$

Data for the NDW plots are presented as means by elevation band ($n = 4$), using average elevation within each band in the analysis of elevation patterns.

Soil respiration

Soil respiration was measured in summer and fall in the eight plots over a 2 year period for a total of 10 measurements between May 2002 and May 2004. At four locations in each plot, CO₂ efflux from the soil surface was measured over a 24 h period using the static chamber technique with 2 mol·L⁻¹ NaOH as the trapping agent (Cropper et al. 1985; Raich et al. 1990), followed by back titration with 0.75 mol·L⁻¹ HCl in the laboratory. Soil respiration measurements were not taken during the winter because of limited accessibility, and average daily winter respiration rates were estimated for each plot from measured summer rates and average soil temperatures using the equation (Zak et al. 1993)

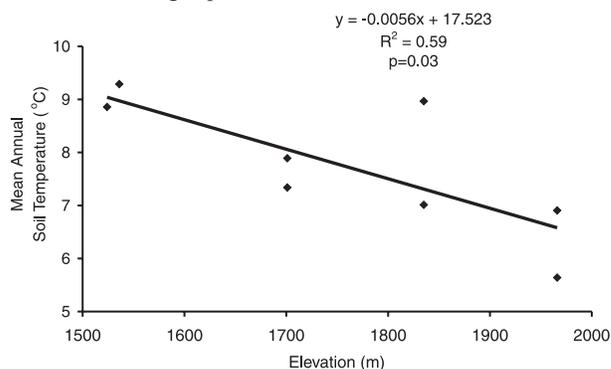
$$k_1 = k_2 e^{(t_1 - t_2)/10 \times \ln Q_{10}}$$

where k_1 is calculated daily winter respiration rate, k_2 is mean measured daily summer respiration rate, t_1 is average winter soil temperature, t_2 is average summer soil temperature, and $Q_{10} = 2$. Data were organized into three periods: summer, 15 May – 31 August; fall, 1 September – 15 November; winter, 15 November – 15 May. For each period, average daily respiration rate was multiplied by the number of days (summer, 107 d; fall, 76 d; winter, 181 d), and annual CO₂ emission from the soil was calculated as the sum of the seasonal values.

Statistical analysis

We used linear regression to analyze relationships between the response variables (soil C pools and dynamics) and indices of temperature regime, represented by the elevation gradient in this study. In some of the linear regression analyses, data were analyzed by elevation band with two plot replicates per band. Litter decomposition data were analyzed using one-way ANOVA to test significant differences in decomposition rates with time followed by a t test (LSD,

Fig. 2. Relationship between mean annual soil temperature and elevation across the eight plots.



least significant difference) to determine significant differences between the elevation bands. The decomposition of litter was also described by a simple single-exponential decay model

$$X_t = X_0 e^{-kt}$$

where X_0 is the initial mass of litter, X_t is the mass of litter at time t , and k is the decay rate constant (Olson 1963; Swift et al. 1979). Decay constants for each elevation band were derived from all decomposition data for the 3 year period using curve-fitting nonlinear regression. Multiple linear regression was used to investigate the effects of independent climate variables on respiration rates. We considered model parameters to be significant if: $R^2 \geq 0.40$ and $p \leq 0.1$. All data were analyzed using SAS (version 8.1 edition, SAS Institute, Inc. 2002).

Results and discussion

Elevation and soil temperature

Plot differences in soil temperature regime are summarized in Table 1. Mean annual soil temperature (MAST) across the eight spruce–fir plots was 7.7 °C at 10 cm soil depth, similar to the value of 7.4 °C at 10 cm soil depth reported by Garten et al. (1999) for two nearby high-elevation spruce–fir sites. Average annual soil temperatures ranged from 5.6 °C in the upper elevations to 9.3 °C in the lower elevations, with corresponding annual degree-days (ADD) above 5 °C ranging from 1064 to 1756 (Table 1). There was a significant negative correlation between elevation and MAST (Fig. 2), corresponding to a mean lapse rate of 0.56 °C per 100 m rise in elevation. The calculated soil heat index (ADD) was also negatively correlated with elevation ($R^2 = 0.56$, $p = 0.03$; $y = -1.118x + 3382$). These results confirmed our assertion that elevation could serve as a proxy for temperature in our experimental design, which allowed for investigation of the effect of temperature on C dynamics.

Soil organic carbon pools

Total ecosystem C storage across the plots was approximately 400 ± 87 Mg·ha⁻¹. Overstory biomass averaged 139.7 Mg C·ha⁻¹, ranging from 101 to 175 Mg C·ha⁻¹, and represented 36% of total ecosystem C storage. Coarse woody debris averaged 38.5 Mg C·ha⁻¹ or 10% of total ecosystem C storage, but was highly variable, ranging from 2.6

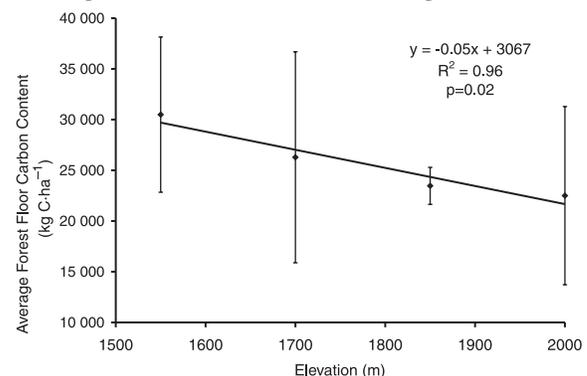
Table 2. Total organic carbon storage in spruce–fir soils to a depth of 50 cm.

Plot	Elevation (m)	Forest floor (O-horizon) (Mg C·ha ⁻¹)	A-horizon (to 15 cm) (Mg C·ha ⁻¹)	Mineral soil (15–50 cm) (Mg C·ha ⁻¹)	Total (0–50 cm) (Mg C·ha ⁻¹)
1	1524	25.1	30.1	152.1	207.3
2	1536	35.9	16.2	180.9	233.0
3	1701	18.9	81.4	136.6	237.0
4	1701	33.6	21.9	149.0	204.5
5	1835	22.2	41.5	122.2	185.9
6	1835	24.8	35.4	105.7	165.8
7	1966	16.3	52.8	172.4	241.5
8	1966	28.7	29.8	156.2	214.8
Average		25.7	38.6	146.9	211.2

to 127.7 Mg C·ha⁻¹ (Tewksbury 2005; Van Miegroet et al. 2007). The SOC storage to a depth of 50 cm averaged 211 Mg·ha⁻¹, ranging from 166 to 241.5 Mg·ha⁻¹, which represented 54% of total ecosystem C storage (Table 2). Average C storage in the spruce–fir forest floor was 25.7 Mg C·ha⁻¹, ranging from 16.3 to 35.9 Mg C·ha⁻¹, and accounted for 12% of total soil organic C storage to a depth of 50 cm. The A-horizon to 15 cm averaged 38.6 Mg C·ha⁻¹, ranging from 16.2 to 52 Mg C·ha⁻¹, and accounted for 18% of the total soil organic C. Between 15 and 50 cm depth, an additional 146.9 Mg C·ha⁻¹ was stored in the mineral soil, ranging from 105.7 to 180.9 Mg C·ha⁻¹ (Table 2). In some sampling points, we were not able to take soil cores to a depth of 50 cm, consistent with earlier observations of a relatively shallow soil (Johnson et al. 1991; Van Miegroet et al. 2001) because of a layer of dense subsurface gravel and fractured rock documented by Feldman et al. (1991).

Our total soil C pool sizes are higher than the mean calculated by Miller et al. (2004) for well-drained soils in southwestern Virginia (112 Mg·ha⁻¹), but closely correspond to the average of 201 Mg C·ha⁻¹ estimated by Kern (1994) for Haplumbrepts, the dominant soil classification in the spruce–fir. They are similar to the worldwide average for wet boreal forests (Post et al. 1982; Callesen et al. 2003). Forest floor C pools are at the low end of estimates for other montane conifer forests in North America (Van Miegroet et al. 2007), and fall in between the worldwide averages for temperate and cold temperate coniferous forests (Cole and Rapp 1982; Vogt et al. 1986). Our forest floor C estimates are lower, and soil C estimates are higher compared with other studies in the Southern Appalachians. Johnson and Lindberg (1992) estimated that the forest floor and mineral soil (0–49 and 0–64 cm) contained, respectively, 41 and 112 Mg C·ha⁻¹, while Garten et al. (1999) reported an average of 35 Mg C·ha⁻¹ for forest floor C and an average of 72 Mg C·ha⁻¹ for mineral soil C storage (0–30 cm) in two high-elevation spruce–fir plots. The lack of consistent results from southern Appalachian spruce–fir zone studies may be attributable to sampling methodology and because it is sometimes difficult to discern purely organic forest floor from organic-rich mineral soils, especially in ecosystems like the spruce–fir where mixing of layers has occurred (Federer 1982; Ryan et al. 1992).

Contrary to our hypothesis, total C storage in the soil showed no relationship with elevation; if any trend was present, it indicated lowest soil C storage in the mid-elevation plots relative to the lower- and higher-elevations plots

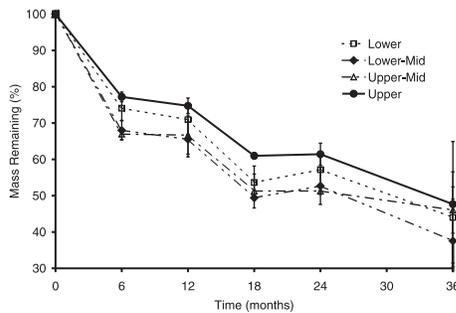
Fig. 3. Relationship between forest floor carbon content and elevation; bars represent standard deviation ($n = 2$) per elevation band.

(Table 2). When plots were combined into elevation bands, only average forest floor C exhibited a significant negative correlation with elevation ($R^2 = 0.96$, $p = 0.02$; $y = -0.05x + 3067$) (Fig. 3). This pattern in forest floor C accumulation was likely driven by a decline in overstory production and litterfall with elevation. Indeed, average litterfall inputs for lower-elevation NAPAP plots were 1790 kg C·ha⁻¹·year⁻¹ compared with a mean of 1500 kg C·ha⁻¹·year⁻¹ for the mid-elevation NDW plots, and only 1000 kg C·ha⁻¹·year⁻¹ in the upper-elevation NAPAP plots. Litterfall corresponded to average live basal area (LBA) of 60 m²·ha⁻¹ in the lower NAPAP plots, 37 m²·ha⁻¹ in the NDW plots, and 52 m²·ha⁻¹ in the upper NAPAP plots (Table 2). Differences in litterfall alone could not explain forest floor accumulation patterns, as forest floor C pools at the lower elevation were only 1.4 times those of the upper-elevation plots, despite almost double the amount of C input via litterfall. This suggests differences in C turnover rates with elevation.

Litter decomposition rates

Overall, decomposition rates of spruce needles were relatively high, with only 43% of substrate remaining after 3 years (Fig. 4; Table 3). Decomposition rates were always lower over winter months (October–June) corresponding to the relative plateau of decomposition between 6 and 12 months and between 18 and 24 months. Decomposition rates did not vary consistently with elevation, and plot differences were not statistically significant at all measurement dates. Throughout the 3 year study, the lowest decomposition rates were measured at the upper-elevation plots, consistent with lower mean temperature; and the highest decomposition

Fig. 4. Relative weight loss of decomposing litter over a 3 year period by elevation band.



rates were measured in the mid-elevation plots (Fig. 4; Table 3). However, there were never statistically significant differences between the lower- and upper-elevation plots or between the lower-mid and upper-mid elevation plots. At the end of the 3 years, differences among elevation bands had dissipated, partly because of greater within-plot variability (Fig. 4).

Litter decay constants (k) (Olson 1963; Swift et al. 1979), calculated for each elevation band based on 3 years of decomposition (mass loss) data also supported slower decomposition in the upper-elevation band, with the lowest $k = 0.0231 \cdot \text{year}^{-1}$, followed by $k = 0.0272 \cdot \text{year}^{-1}$ in the lower-elevation band. The highest decay constants were calculated for the lower-mid and upper-mid elevation bands, with $k = 0.0326 \cdot \text{year}^{-1}$ and $0.0301 \cdot \text{year}^{-1}$, respectively. While not calculated directly, k values for C loss would have been quite similar, as C concentrations remained fairly stable during decomposition (average 52% between 6 and 24 months, average 50% at 36 months).

The overall mass loss estimates in our study closely parallel those published for the initial 3 years in the cool temperate forest site (Port McNeill, British Columbia) within the long-term Canadian Intersite Decomposition Experiment (CIDET), where only 47% of the mass of all litter types remained after the 3 years (Moore et al. 1999), similar to the 43% observed in our study. Trofymow et al. (2002) published mass loss results from the same study after 6 years, with 35% of the mass of all litter types remaining in the cool temperate climate. This indicates a progressive decline in decomposition rates over time, and suggests that a 3 year study is likely to capture major trends and differences in litter turnover. Our estimates of spruce needle decomposition rates are similar to the first-year values published by Johansson (1995) for spruce needle along a climatic transect from the Arctic Circle in Scandinavia to northern continental Europe (81%–66% mass remaining after 1 year), but higher than those reported by Gholz et al. (2000) for pine (*Pinus resinosa* Soland.) leaves in five temperate coniferous forests in North America as part of the Long-Term Intersite Decomposition Experiment (LIDET) (82% and 46% of pine needle mass remaining after 1 and 5 years, respectively).

No direct correlation between soil temperature and decomposition rates was found in our study, although the cooler upper-elevation plots consistently had lower rates of decomposition. This suggests that other factors besides temperature may have influenced C turnover at our sites, such

as precipitation input and soil moisture; litter quality (e.g., lignin content) or chemistry (e.g., N content). In the CIDET study, decomposition was strongly related to mean annual temperature and precipitation accounting for 72%–87% of the variance (Moore et al. 1999). Gholz et al. (2000) also found significant positive correlations between mean annual temperature and litter decomposition rates. No significant correlation between mass loss of spruce needle litter and climate factors was reported by Johansson (1995). However, in that study, mass loss was significantly correlated with substrate quality factors (Mn and lignin concentrations).

Forest floor mean residence time

Overall mean residence time (MRT) of the forest floor across the 16 spruce–fir plots (four NAPAP, 12 NDW) was 17 years, ranging from 7 to 23 years. The forest floor had an average MRT of 17 years in lower-elevation NAPAP plots; 14 years in the mid-elevation NDW plots; and 22 years in the upper NAPAP plots. This elevation pattern was consistent with findings from the litterbag study, with the highest turnover in the mid-elevation plots and lowest turnover in the cooler upper plots. To analyze correlations between soil temperature and MRT, the MRT of the 12 NDW plots (“litterfall plots”, Fig. 1) was averaged to represent three elevation bands, with corresponding soil temperature data collected along an elevation transect within the watershed (“temperature transect”, Fig. 1) also averaged by elevation band. Individual plot-level data were used for the two lower-elevation and upper-elevation NAPAP plots, because plot-specific soil temperature data were available. Across this combined data set, MRT was negatively correlated with MAST (Fig. 5), and ADD ($R^2 = 0.85$, $p = 0.08$; $y = -0.282x + 46.59$), indicating that the observed differences in forest floor C accumulation with elevation (Fig. 3) reflected the differences in litterfall (decline with elevation; Van Miegroet et al. 2007) modified by organic matter turnover (slower at higher and cooler sites).

Our calculated MRT values are well within the range of published data for spruce–fir and conifer forests. Garten et al. (1999) estimated average forest floor MRT of high-elevation spruce–fir at around 15 years, while Johnson and Lindberg (1992) reported forest floor C inventories for the same area that range from 44 000 to 67 000 kg C·ha⁻¹ and litterfall inputs that range from 885 to 2700 kg C·ha⁻¹·year⁻¹, with corresponding MRT between 16 and 76 years. In the spruce-dominated northern region of Maine, Simmons et al. (1996) estimated MRT of the forest floor to be 11 years. A MRT for the forest floor organic matter was estimated at 17 years for temperate coniferous forests (Cole and Rapp 1982), and at 14 years for cold temperate needleleaf evergreen forests (Vogt et al. 1986) and cool temperate forests (Admundson 2001). The average decomposition rate of forest floor C ($1/\text{MRT}$) is $0.0588 \cdot \text{year}^{-1}$, close to the decay constants ($k = 0.0583 \cdot \text{year}^{-1}$ and $0.0610 \cdot \text{year}^{-1}$) derived by Garten et al. (1999) for unprotected SOC at two high-elevation spruce–fir sites in the GSMNP.

Soil respiration

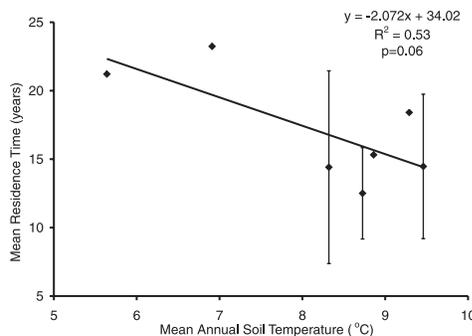
Mean annual soil respiration across the eight plots was 1460 kg C·ha⁻¹·year⁻¹, ranging from 1020 to 1830 kg C·ha⁻¹·year⁻¹ (Table 4). Annual rates were posi-

Table 3. Analysis of variance of needle mass remaining over 3 years of decomposition.

Month	<i>p</i>	Mean mass remaining (%)*	df	MS	<i>n</i>	Elevation band
6	0.03	74.10±3.36ab	3	48.2	2	Lower
		60.95±2.64c				Lower-mid
		68.00±1.52bc				Upper-mid
		77.21±1.33a				Upper
12	0.26	70.93±4.12	3	35.7	2	Lower
		65.51±4.82				Lower-mid
		66.68±5.26				Upper-mid
		74.75±2.14				Upper
18	0.08	53.64±4.53ab	3	51.4	2	Lower
		49.42±0.71b				Lower-mid
		51.29±4.67b				Upper-mid
		60.98±0.90a				Upper
24	0.14	57.17±4.07	3	42.3	2	Lower
		51.30±5.09				Lower-mid
		52.68±0.95				Upper-mid
		61.43±3.03				Upper
36	0.86	46.65±12.56	3	39.3	2	Lower
		37.56±11.52				Lower-mid
		44.02±6.37				Upper-mid
		47.66±17.28				Upper

*Means with different letters are significantly different at $p \leq 0.1$.

Fig. 5. Relationship between calculated mean residence time of the forest floor and average annual soil temperature. Diamonds, individual National Acid Precitation Assessment Program (NAPAP) plots; triangles, Noland Divide Watershed (NDW) elevation bands ($n = 4$). Bars represent standard deviation ($n = 4$) per elevation band in NDW.



tively correlated with corresponding plot soil temperature regime expressed as MAST ($R^2 = 0.44$, $p = 0.07$; $y = 0.003x + 2.97$) or ADD (Fig. 6).

In this study, average respiration rates during the fall period were higher than summer respiration rates ($5.15 \text{ kg CO}_2\text{-C}\cdot\text{ha}^{-1}\cdot\text{day}^{-1}$ in summer versus $5.23 \text{ kg CO}_2\text{-C}\cdot\text{ha}^{-1}\cdot\text{day}^{-1}$ in fall), even though soil temperatures in summer were 2–3 °C higher. This is counter to the accepted norm that C dynamics are mostly temperature driven. The higher CO_2 efflux rates in fall may be due to input of a fresh decomposable C source with litterfall. It may also reflect the confounding effect of other factors, such as substrate moisture content and (or) quality. Soil temperature and moisture often interact to control the rate of soil respiration, but their effect is difficult to separate, as their interaction may be temporally and spatially variable and possibly site-specific (e.g., Davidson et al. 1998). Our data do suggest

that soil temperature may not be the sole driver for soil CO_2 efflux in this system.

Annual CO_2 efflux rates for the spruce–fir, even when corrected for systematic methodological bias ($2600\text{--}3900 \text{ C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, Van Miegroet et al. 2007), are lower than the values for some common temperate coniferous forests reported by Kane et al. (2003) ($5000\text{--}7000 \text{ kg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$), Rustad et al. (2001) ($3000\text{--}12\,000 \text{ kg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$), and Davidson et al. (2002) ($6500\text{--}9900 \text{ kg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$). They are more comparable to CO_2 efflux rates for spruce in Alaska summarized by Raich and Tufekcioglu (2000) ($3100 \text{ kg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$), and Vogel et al. (2005) ($3100\text{--}6000 \text{ kg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$). One potential reason for the difference between our results and published annual respiration rates is that winter CO_2 efflux rates were estimated from summer rates and temperatures, assuming a $Q_{10} = 2$, rather than being measured directly. The actual Q_{10} factor can vary significantly across a wide range of climatic conditions (Schleser 1982; Raich and Schlesinger 1992; Peterjohn et al. 1994), ranging from 1.6 to 3.2 (Schlesinger 1977; Singh and Gupta 1979; Kirschbaum 1995; Grogan et al. 2000). Applying this range of possible Q_{10} values to our data would have yielded daily winter rates between 1.87 ($Q_{10} = 3.2$) and $3.42 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$ ($Q_{10} = 1.6$), compared with the $2.82 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$ ($Q_{10} = 2$), used in our flux calculation. This would have translated into annual CO_2 efflux rates that were either 7.5% higher ($Q_{10} = 1.6$) or 12% lower ($Q_{10} = 3.2$) than our current estimates. Total belowground C allocation (TBCA) in this system has been estimated at $\sim 1700 \text{ kg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ (possibly as high as $2100 \text{ kg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$), assuming belowground steady state conditions (Van Miegroet et al. 2007). The latter assumption seems reasonable, given the mature stage of the forest and the shallow soil depth ($<50 \text{ cm}$), which allows for limited expansion of the roots. Using an average methodological correction factor of 47% to our total annual soil CO_2 efflux rates (Knoepp and Vose 2002), and

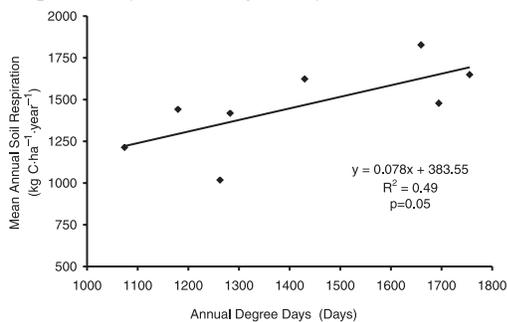
Table 4. Seasonal soil respiration rates.

Plot	Summer (kg C·ha ⁻¹)	Fall (kg C·ha ⁻¹)	Winter (kg C·ha ⁻¹)*	Annual (kg C·ha ⁻¹ ·year ⁻¹)
1	651±183 [†]	567±95 [‡]	610	1828
2	586±91	500±268	565	1650
3	618±228	411±177	594	1624
4	362±124	313±19	343	1018
5	591±235	318±4	510	1419
6	589±285	332±82	558	1478
7	448±139	404±58	362	1214
8	574±155	334±192	534	1442
Average	552	397	510	1459

*Calculated from average daily summer respiration rates, based on seasonal soil temperatures and assuming a $Q_{10} = 2$.

[†]Standard deviation, calculated from standard deviation on daily average rates ($n = 8$) multiplied by 107.

[‡]Standard deviation, calculated from standard deviation on daily average rates ($n = 2$) multiplied by 76.

Fig. 6. Relationship between mean annual respiration and soil heat index as expressed by annual degree-days over 5 °C.

above TBCA values (Van Miegroet et al. 2007), annual heterotrophic respiration rates are estimated at ~1450 kg C·ha⁻¹·year⁻¹ or lower. This corresponds to ~45% of the total soil CO₂ efflux, compared with ~30% reported for mature boreal and cold temperate forests in Bond-Lamberty et al. (2004). Our estimate of heterotrophic respiration closely resembles average annual litterfall C inputs of 1400 ± 280 kg C·ha⁻¹·year⁻¹ for the NDW (5 year mean) and 1200 ± 520 kg C·ha⁻¹·year⁻¹ for the four NAPAP plots (2 year mean). It substantiates near steady-state conditions of the forest floor (inputs equal outputs) and suggests that heterotrophic C efflux is mainly derived from the decomposition of fresh litter, conditions which underly our calculation of forest floor MRT.

Conclusions

Significant differences in temperature existed along the elevation gradient in the high-elevation spruce–fir, providing us with an opportunity to test temperature as a driver of soil C storage and dynamics. As predicted, indices of the temperature regime, including mean annual soil temperature and annual degree-days, were inversely correlated with elevation. Differences in soil temperature along the elevation gradient resulted in significant differences in forest floor C pools, litter decomposition rates, forest floor mean residence time, and soil respiration. However, SOC pool and flux patterns did not always follow clean and consistent trends with elevation, possibly reflecting confounding factors such as stand structure and growth patterns (Van Miegroet et al. 2007), soil moisture, and litter quality. Nevertheless, the SOC dynamics in this spruce–fir ecosystem appeared re-

sponsive to soil temperatures, and soil warming will likely result in greater CO₂ releases because of accelerated turnover of the C-rich soil substrates.

The mid-elevation plots consistently emerged as having the most rapid SOC turnover, also reflected by lower total SOC storage. The cooler upper-elevation plots were consistently characterized by slower C turnover, indicated by lower litter decomposition rates, lower soil respiration rates, and higher mean residence times of forest floor C. Laboratory incubations further indicated that organic and mineral horizons in the upper-elevation band contained more labile C than lower- and mid-elevation sites (Tewksbury 2005). Larger residual active C pools in the upper elevation suggests incomplete decomposition, limited by cooler temperatures, compared with the depletion of active C pools in the lower elevations where decomposition rates are generally higher. A clear temperature limitation of C dynamics at the highest elevations combined with resultant SOC quality shifts towards higher concentrations of active C, thus suggests that higher-elevation zones in these ecosystem sites may experience the largest impacts of future warming scenarios, and may in fact become net sources of CO₂, if soil C dynamics in the lower elevations are indicative of how future climatic trajectories may affect upper elevations. Mid- and lower-elevation sites would appear less sensitive to global warming. At this point it is still unclear how the concurrent change in potentially confounding factors, such as soil moisture and litter quality, may affect future temperature responses of this ecosystem, or how long temperature-driven C release pulses could be sustained.

An additional confounding factor in predicting SOC response to global change is that in addition to warming, there may be a change in precipitation form, timing, and amount (Weltzin et al. 2003). Many high-elevation forests are located in areas that receive substantial amounts of precipitation as snow, and the reduction or disappearance of an insulating snow pack may affect soil C turnover in winter (Bubier et al. 2002). In the southern Appalachians, however, a very thick and persistent snow pack rarely accumulates throughout the winter, soils are often frozen, and C dynamics are generally slow in winter. Changes in snow accumulation and retention may therefore have less impact on overall C dynamics than future changes in the soil temperature and moisture regime during summer, and especially in fall when fresh needle fall stimulates decomposer activity. While this

elevation gradient is not a perfect proxy for future climate change scenarios, it nevertheless provides us with some useful insights into patterns of SOC accumulation and dynamics that help identify those areas that are most likely to respond to changes in global climate.

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