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Soil carbon fluxes and stocks in a Great Lakes forest chronosequence

Running title: Soil carbon in a chronosequence

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Abstract

We measured soil respiration and soil carbon stocks, as well as micrometeorological variables in a chronosequence of deciduous forests in Wisconsin and Michigan. The chronosequence consisted of (1) four recently disturbed stands, including a clearcut and repeatedly burned stand (burn), a blowdown and partial salvage stand (blowdown), a clearcut with sparse residual overstory (residual), and a regenerated stand from a complete clearcut (regenerated); (2) four young aspen (*Populus tremuloides*) stands in average age of 10 years; (3) four intermediate aspen stands in average age of 26 years; (4) four mature northern hardwood stands in average age of 73 years; and (5) an old-growth stand approximately 350 years old. We fitted site-based models and used continuous measurements of soil temperature to estimate cumulative soil respiration for the growing season of 2005 (days 133 to 295). Cumulative soil respiration in the growing season was estimated to be 513, 680, 747, 747, 794, 802, 690, and 571 gC m⁻² in the burn, blowdown, residual, regenerated, young, intermediate, mature, and old-growth stands, respectively. The measured apparent temperature sensitivity of soil respiration was the highest in the regenerated stand, and declined from the young stands to the old-growth. Both cumulative soil respiration and basal soil respiration at 10°C increased during stand establishment, peaked at intermediate age, and then decreased with age. Total soil carbon at 0-60 cm initially decreased after harvest, and increased after stands established. The old-growth stand accumulated carbon in deep layers of soils, but not in the surface soils. Our study suggests a complexity of long-term soil carbon dynamics, both in vertical depth and temporal scale.

Key words: chronosequence, succession, soil respiration, CO₂ flux, soil carbon, old-growth

Introduction

Soil respiration is the second largest terrestrial carbon flux and is sensitive to climate, vegetation type, and soil properties (Raich and Potter 1995; IPCC 2001). Soils contain more than twice as much carbon as the atmosphere or terrestrial vegetation (IPCC 2001). Soil respiration affects the soil carbon stock in that the stock is determined primarily by the long-term balance between soil respiration (outputs) and detrital carbon inputs from vegetations (Turner and Lambert 2000; Guo and Gifford 2002). This balance may change with stand age and natural and human disturbances. Thus there is a potential for soils to sequester carbon and mitigate climate change (Lal 2004; Goh 2004), or lose carbon and exacerbate rising atmospheric CO₂ concentration. To model the long-term forest carbon dynamics and its coupling with the climate system, we need to understand not only the responses of forest ecosystems to the changing climate, but also the role of stand age and successional status on carbon dynamics.

Ecosystem respiration, photosynthesis and carbon allocation change with forest succession, yielding changes in net ecosystem production (NEP). Generally, forests lose carbon immediately after severe disturbances as ecosystem respiration is larger than production, but gradually revert to net carbon sinks if allowed to re-grow, and then approach to carbon neutral (Kira and Shidei 1967; Odum 1969). Currently, most forests in North America are re-growing from abandoned farmland or previously logged forests, acting as carbon sinks (Fan *et al.* 1998; Myneni *et al.* 2001). However, the duration and

future change of the net carbon sinks is unknown, primarily due to scarcity of older stands that act as a reference for current second-growth forests. Of the few old-growth forests that have been studied, none appear to be carbon neutral (Law *et al.* 2003; Paw U *et al.* 2004; Desai *et al.* 2005), possibly due to ongoing climate change and the fertilization effects of increasing atmospheric CO₂ concentration and nitrogen deposition (Grace *et al.* 1995).

Our knowledge of the effects of forest succession on carbon fluxes is limited. It has been long accepted that respiration continuously increases as stems and detritus accumulate in older forests, and eventually balance decreasing photosynthesis when forests age (Kira and Shidei 1967; Odum 1969). However, there is substantial uncertainty regarding this conceptual model (Ryan and Waring 1992; Ryan *et al.* 2004). For example, Law *et al.* (2003) found that net primary production (NPP), heterotrophic respiration and NEP in ponderosa pine stands in Oregon increased with forest age, and then decreased in the oldest stands (190-316 years). Tang *et al.* (2008) recently reported a decrease in soil respiration and total ecosystem respiration in an old-growth forest in upper Midwest of the U.S. In contrast, Litvak *et al.* (2003) found that ecosystem respiration consistently increased with age in a Canadian boreal forest chronosequence spanning from 11 to 130 years, but soil respiration decreased across these ages (Wang *et al.* 2002). As a result of our limited knowledge in forest succession and carbon cycles, most large-scale ecosystem carbon models have not taken into account the change of forest metabolic rates with age (e.g., Parton *et al.* 1993; Peng *et al.* 1998).

Trajectories of soil carbon stocks with stand age are also uncertain. Despite the relative ease in measuring soil carbon stocks compared with carbon fluxes, the

mechanisms determining the change of mineral soil carbon stocks is still unclear (Thuille and Schulze 2006). Generally, soil carbon in forest ecosystems change slowly, but the slow rate over long time periods may yield substantial sums. Covington (1981) has concluded that forest floor organic matter decreased by 50% in the first 20 years after harvest, and then increased asymptotically, a finding soon verified by Federer (1984). Despite the factor that the Covington study was conducted in northern forests for forest floor organic matter (O horizon), the curve has been widely used to describe the effect of harvest on forest floor and mineral soil carbon storage in various ecosystems (e.g., Cooper 1983; Houghton *et al.* 1983; Pastor and Post 1986; Harmon *et al.* 1990). However, Yanai *et al.* (2000; 2003) found that the Covington curve based on chronosequence studies may not be valid by resampling the chronosequence of stands 15 years later. Zhou *et al.* (2006) recently reported that old-growth forests can accumulate carbon in soils based on 24 years of measurements of carbon stocks in the top 20-cm soil layer in a old-growth forest in southern China. More studies have indicated that the effects of forest harvest, disturbance, afforestation, or reforestation on soil carbon storage are complex and uncertain (Johnson 1992; Johnson and Curtis 2001; Rothstein *et al.* 2004; Guo and Gifford 2002; Paul *et al.* 2002).

Chronosequence studies provide a “space-for-time substitution” approach to estimate time series of forest succession by examining spatially different stands within the same period. Here we report soil carbon fluxes and stocks across a chronosequence of deciduous forests in the Great Lakes region of the United States. We sampled a broader range of ages than previous studies in the northern deciduous forests and used four replicates of three major age classes to estimate potential long-term trajectories in soil

carbon. By sampling many stands across ages under the chronosequence assumption that the primary difference between sites is age, and that species, geology, climate, or other site differences are small relative to age effects, we intend to better define carbon dynamics across age.

Materials and Methods

Site description

The study sites were located in the Chequamegon-Nicolet National Forest in northern Wisconsin (45°48' N, 90°05' W) and the Sylvania Wilderness and Recreation Area of the Ottawa National Forest in the upper peninsula of Michigan (46°15' N, 89°21' W). Average elevation was 540 m. The climate is northern continental, characterized by short growing seasons and long, cold winters. Annual average precipitation and air temperature measured in a nearby weather station over 1961-1990 was 896 mm and 3.9°C, respectively. Precipitation was evenly distributed in all seasons. Upland soils were dominated by sandy loam spodosols. All sites are within a circle with the diameter of 50 km. The landscape is characterized by glacial outwash and moraine with an average slope of 10% over short distances (Pastor and Broschart 1990).

We established 16 measurement plots surrounding an eddy covariance flux measurement tower near Willow Creek in northern Wisconsin (Cook *et al.* 2004), and one measurement plot adjacent to an eddy covariance flux measurement tower in the Sylvania Wilderness and Recreation Area in Michigan (Desai *et al.* 2005). The chronosequence of stands covered age classes from one year old (recent clearcut) to approximately 350 years old (old-growth) as of year 2005. The old-growth stand (old-

growth, or OG) was a hardwood-dominated stand in an undisturbed hemlock-northern hardwood old-growth forest, dominated by sugar maple (*Acer saccharum*) with yellow birch (*Betula alleghaniensis*) and eastern hemlock (*Tsuga canadensis*) present (Tang *et al.* 2008). The 16 second-growth stands consisted of (1) four recently disturbed sites, including a clearcut and repeatedly burned stand (burned, or CB) with very short and sparse grass and shrubs, a blowdown and partial salvage stand (blowdown, or BS) with dense woody debris and shrubs, a clearcut with sparse residual overstory (residual, or CR, $< 3 \text{ m}^2 \text{ ha}^{-1}$), and a regenerated stand from complete clearcutting (regenerated, or RG); (2) four young aspen (*Populus tremuloides*) stands (young, or YA) with complete canopy closure in average age of 10 years; (3) four intermediate aspen stands (intermediate, or IA) in average age of 26 years; and (4) four mature northern hardwood stands (mature, or MH) in average age of 73 years. The stands were selected following forest management or disturbance history. A common set of stand attributes were summarized in Table 1. In addition to dominant species of aspen and sugar maple, other tree species include yellow birch and basswood (*Tilia americana*). Stand age was obtained from forest management records. Each stand typically covered more than one hectare. Tree diameter at breast height (DBH) was measured from each tree in a circle with diameter of 40 m in each stand. Leaf area index (LAI) was measured in summer along a 50 m transect in the stands with LAI-2000 (LI-COR, Inc., Lincoln, NE, USA). Because of similar climate and soil properties among these stands, they form an ideal chronosequence to study the age effect (years after a major disturbance, namely, clearcut or natural blowdown) on carbon cycles.

Soil respiration

We measured soil respiration in snow-free seasons (approximately from day 100 to day 300 of the year) using an LI6400-09 soil chamber connected to an LI-6400 portable photosynthesis system (LI-COR, Inc., Lincoln, NE, USA). Eight soil collars, each with a height of 4.4 cm and a diameter of 11 cm, were inserted into the soil in each stand in 2004 and 2005 for soil respiration measurement, except for the old-growth stand. The collars were randomly placed in a 20-meter-diameter circle. In the old-growth stand, we installed 20 collars and measured soil respiration in 2002 and 2003 (Tang *et al.* 2008). Soil temperature at 10 cm was measured adjacent to each respiration collar with a portable temperature probe provided with the LI-6400. Soil volumetric water content at 0-20 cm was measured by a portable time domain reflectometer (Hydrosense, Campbell Scientific, Inc., Logan, UT, USA) installed vertically. The measurements were made every 3-4 weeks in the growing seasons.

In addition to periodic measurements of soil temperature and moisture coincident with respiration measurements, continuous soil temperatures (every 30 minutes) were measured at 10 cm in each plot in 2005 using temperature sensors (Omega Engineering, Inc., Stamford, CT, USA) stored to a datalogger (CR10X, Campbell Scientific, Inc., Logan, UT, USA) in the old-growth stand, and using integrated temperature-dataloggers (HOBO datalogger, Onset Computer Corp., Pocasset, MA, USA) in all other stands. A full suite of micrometeorological measurements were made at the two eddy covariance flux measurement sites in Willow Creek and the Sylvania old-growth stand, including

soil moisture, air temperature, humidity, precipitation, and solar radiation (Cook *et al.* 2004; Desai *et al.* 2005).

Due to non-simultaneous and periodic cross-stand soil respiration measurement, which may change diurnally and seasonally, we relied on modeling results to compare soil respiration among stands across the seasons. We did not directly compare soil respiration in stand OG measured in years 2002 and 2003 with other stands measured in 2004 and 2005, but we compared temperature response functions and cumulative soil respiration, which was estimated from temperature response functions and soil temperature, among all stands in 2005.

We used an exponential equation (Eq. 1) to describe the relationship between respiration and temperature (Tang *et al.* 2008), given a consistently high soil moisture condition (mean 27.7%, minimum 11.8% at a half-hour measurement interval in 2005) and thus insensitivity of soil respiration to moisture in these forests:

$$R = R_0 e^{\beta T} \quad (1)$$

where R is the soil respiration, T is the soil temperature, and R_0 and β are fitted parameters. The temperature sensitivity parameter, Q_{10} , can be derived as $Q_{10} = \exp(10\beta)$. Estimated parameters were used to estimate soil respiration every half-hour in the 2005 growing season based on continuous soil temperature measurements at 10 cm in each stand.

To test the moisture effect on soil respiration, we added soil moisture or log-transformed soil moisture as a term to log-transformed Eq. (1), and conduct multilinear regression (soil temperature and moisture as two independent variables). By statistically

testing the moisture term (t-tests), we determined if the moisture term was significant in predicting soil respiration.

Soil carbon contents and root biomass

We cored nine soil samples close to the location where we measured soil respiration at each stand with the diameter of 7.6 cm at 0-10 cm, 10-30 cm, and 30-60 cm of soils in summer 2006. Roots were manually separated from soils, and dry biomass (fine and coarse roots) was measured. We measured mass-based soil carbon content (%) and bulk density (g m^{-3}), and calculated soil carbon stocks (g m^{-2}) for each soil sample at 3 layers across the chronosequence. Soil carbon contents were measured with a PerkinElmer CHN analyzer (PerkinElmer Inc., Wellesley, MA, USA) according to standard methods applied by the University of Georgia's Coweeta Hydrologic Laboratory, Otto, NC, USA.

Regression analyses and other statistical analyses were mainly conducted with the statistical package Stata (Stata Corporation, Texas, USA).

Results

Soil temperature

Soil temperature varied among stands. Fig. 1 shows daily mean soil temperature at 10 cm in 8 types of stands in the 2005 growing season (from leaf expansion to senescence), from day of year (DOY) 133 to DOY 295. Temperatures in all stands increased from 6-7°C in mid-May to 19-26°C in mid-July, and then gradually declined, with high day-to-day variations. Within the four recently disturbed stands (Fig.1a), the burn stand had the highest soil temperature, followed by the residual, blowdown and

regenerated stands. The soil temperature in the blowdown stand was lower than that in the regenerated in mid-May to mid-June, but higher in September–October. Among the four established stands (Fig. 1b), the young stands had the highest soil temperature, followed by the mature, intermediate, and old-growth stands.

Measurements of soil respiration

The seasonal patterns of soil respiration in 7 types of stands were similar to those of soil temperature (Fig. 2). Soil respiration increased in spring, peaked in June-July, and declined in autumn. Among the 4 disturbed stands (Fig. 2a), the rank order of soil respiration changed over the season. There was a spike of soil respiration on day 209 in the regenerated stand, which is likely driven by root respiration during the fast growth period in this stand. Among the three types of established stands (Fig. 2b), soil respiration in the intermediate stands was generally highest while soil respiration in the mature was relatively lowest. The difference of soil respiration among the three stands was not significant in spring and autumn, but in summer (June-August), soil respiration in the intermediate stands was significantly higher (ANOVA, $p < 0.05$) than that in the mature with the young stands falling between the intermediate and mature.

The variations of soil respiration measurement within a stand (8 samples) were higher than among stand replicates (4 replications for the young, intermediate, and mature). The averages of coefficient of variation (CV) within a stand across the season were 19%, 20%, 28%, and 22% for the burn, blowdown, residual, and regenerated stands, respectively, and were 18%, 14%, and 21% for the young, intermediate, and mature, respectively. However, the coefficients of variation among replicated stands were

averaged across the season to be 6%, 6%, and 5% for the young, intermediate, and mature, respectively (Fig. 2b).

Soil respiration strongly correlated with soil temperature when we plotted all measurements of soil respiration (spatially averaged, two years of data) against soil temperature at 10 cm, and the correlations were significant ($r^2 > 0.6$, $p < 0.01$ over all sites). Table 2 summarizes the parameters for the exponential function (Eq. 1) fit from the datasets with replicate stands pooled to increase the sample size. Among the 4 disturbed stands, the temperature sensitivity in the regenerated was the highest, with $Q_{10} = 5.49$, followed by the blowdown, burn, and residual. The residual stand had the lowest Q_{10} value of 1.92. Among the 4 age classes of established stands, the magnitude of Q_{10} was in a reverse order to the age of the stands, with the highest Q_{10} (3.12) in the young stands, and the lowest Q_{10} (2.31) in the old-growth. However, soil respiration in the intermediate stands was higher than that in the young, with higher basal respiration (R_0) in the intermediate.

We did not find significant correlation between soil respiration and soil moisture, as reported by a previous study in the region (Tang *et al.* 2008). In all stands, r^2 for soil respiration and soil moisture measured at 0-20 cm was less than 0.2. Multilinear regression (soil respiration vs. soil temperature and moisture) indicated that the moisture term was not significant in predicting soil respiration (t-tests, $p > 0.1$). Therefore, we used solely soil temperature to estimate soil respiration across the growing season.

Chronosequence of soil respiration

Cumulative soil respiration in the growing season of 2005 (DOY 133-295) was estimated to be 513, 680, 747, 747, 794, 802, 690, and 571 gC m⁻² in the burn, blowdown, residual, regenerated, young, intermediate, mature, and old-growth stands, respectively. Fig. 3 shows soil mean temperature, temperature sensitivity (Q_{10}), soil respiration normalized to 10°C (R_{10}), and cumulative soil respiration over the growing season across the age chronosequence. The solid lines link the regenerated, young, intermediate, mature, and old-growth stands to indicate the trajectory implied by the chronosequence, as the regenerated represents the early stage of stand development. Mean growing season soil temperature was the highest in the burn stand, and lowest in the old-growth (Fig. 3a). ANOVA tests indicated that the differences in soil temperature between the young, intermediate, and mature are significantly different ($p < 0.05$). Q_{10} was low in the burn and residual stands, but high in the regenerated, and slightly declined from the young to old-growth (Fig. 3b). After adjusted for soil temperature, R_{10} increased from the regenerated stand at the age of 3 years to maximum respiration rates in the intermediate stand at the age of 26 years, and then decreased with age to lower rates in the old-growth (Fig. 3c). Cumulative soil respiration had a similar pattern to soil respiration at 10°C. Soil respiration increased with age until 26 years old, and then gradually declined with age (Fig. 3d). The differences in soil respiration between the young and intermediate, and between the intermediate and mature are statistically significant (ANOVA, $p < 0.05$), tested with replicated stands. Soil respiration in the single regenerated stand or old-growth is out of the variation range of the young, intermediate, or mature, indicating the trend (Fig. 3d) from the regenerated to old-growth

is significant. Within these age classes, soil respiration peaked at 802 gC m^{-2} over the growing season in the intermediate stands. The lowest soil respiration was in the burn stand, which was summed as 513 gC m^{-2} over the growing season.

Chronosequence of soil carbon stocks

Changes of soil carbon stocks across age had different patterns among three layers of soils. Fig. 4 shows soil carbon chronosequence from the three-year-old stand to the old-growth stand. Soil carbon decreased from the mature stands to old-growth at 0-10 cm soils but increased at 30-60 cm soils, both statistically significantly (ANOVA, $p < 0.05$). The low soil carbon in the regenerated at 0-10 cm suggests a quick loss of carbon at the soil surface after harvest (Fig. 4a). At 10-30 cm soil, soil carbon increased from the regenerated to the intermediate, slightly decreased in the mature, and then slightly increased to the old-growth (Fig. 4b). However, the variation of soil carbon at 10-30 cm among the intermediate, mature, and old-growth stands are not statistically significant (ANOVA, $p > 0.05$). At 30-60 cm of soils, the soil carbon pattern was complicated, but increased from the mature to old-growth (Fig. 4c).

After summing up soil carbon over 0-60 cm, we found a chronosequence pattern (Fig. 4d) similar to that reported by Covington (1981), though we did not find this pattern in the surface layer at 0-10 cm. Soil carbon at 0-60 cm decreased from the regenerated stand to the young, recovered in the intermediate, and continuously increased from the mature to the old-growth stand at an average rate of $3.6 \text{ gC m}^{-2} \text{ yr}^{-1}$.

Discussion

Chronosequence of soil respiration and controls

The variations in soil temperature (T), temperature sensitivity (Q_{10}), and basal respiration (R_0 at $T = 0^\circ\text{C}$, or R_{10} at $T = 10^\circ\text{C}$) among stands jointly drive the chronosequence pattern of soil respiration, as indicated in Eq. 1. However, to understand the mechanism of soil respiration across the age, we have to partition soil respiration into microbial decomposition and root respiration. We did not directly measure the rates of microbial decomposition and root respiration in this study, but we found that root biomass, a proxy of basal root respiration, indicated a similar pattern to soil respiration across the age (Fig. 5a). Root biomass increased from the regenerated stand to the intermediate stands, peaked in the intermediate, and decreased to the old-growth. This pattern is also consistent with expected growth rates of forest ecosystems (Ryan *et al.* 2004) along this chronosequence. We speculated that basal microbial decomposition, which is determined by carbon availability, shows a similar pattern to root biomass and forest growth, because labile carbon is primarily sourced from plant debris, root exudates and turnover.

The soil respiration pattern across the age is not consistent with the pattern of LAI in that soil respiration peaked at the intermediate age while LAI peaked at the mature age (Fig. 5b). The difference in timing between the peak of root biomass and of LAI may indicate the change in the allocation pattern during stand development (Ryan *et al.* 1997): more photosynthate is allocated to roots than to leaves during the early stage. Although LAI-correlated gross primary production (GPP) may drive respiration over a short period

of time (days to months) (Hogberg *et al.* 2001; Tang *et al.* 2005a), root biomass has more influences on soil respiration than LAI does.

Changes in soil temperature with age may be explained by canopy shading and surface litter shading, which affects soil exposure to solar radiation and the transfer of sensible heat to latent heat. Within the four recently disturbed stands (Fig. 1a), the decreasing order of soil temperature is probably determined by the decreasing order of soil exposure across the same sequence. The shift of soil temperature in the blowdown and regenerated stands across the growing season is probably caused by more debris shading in the blowdown than regenerated in spring before leaves are fully generated, while the shading in the regenerated substantially increased when leaves expanded.

In addition to T and R_0 , temperature sensitivity (Q_{10}) also affects cumulative soil respiration across the stands. Estimated Q_{10} values were quite variable at the early establishment of stands. After stands were established starting in the young stands, Q_{10} consistently and linearly decreased with age. This negative linear correlation between Q_{10} and stand age is statistically significant ($r^2 = 0.98$, $p < 0.05$).

Temperature sensitivity (Q_{10}) discussed here is the measured “apparent seasonal temperature sensitivity,” which may be different from the intrinsic temperature sensitivity (Davidson and Janssens 2006), a kinetic response of soil microbes or roots to temperature increase. In this study, Q_{10} was calculated over the season, and thus not only reflects intrinsic temperature sensitivity but also include the effects of seasonal phenology (root growth and photosynthate supplies) and carbon availability constraints (e.g., moisture limitation), which may co-vary with T (Davidson *et al.* 2006). Q_{10} here also combined temperature sensitivity of root respiration and microbial decomposition, which are

functionally different processes. However, the Q_{10} function is still a valid empirical method to simulate soil respiration in a specific site which is not limited by water content, particularly when the simulation is made through interpolation rather than extrapolation. A caveat is suggested when the Q_{10} function is used as a constant value across ecosystems (Tjoelker *et al.* 2001), to predict the response of respiration to future climate change (Curiel Yuste *et al.* 2004), or to estimate respiration in arid or semiarid ecosystems where soil moisture is an important determinant (Tang *et al.* 2005a; Tang *et al.* 2005b).

The soil respiration results in this paper cover a broader range of age classes than previous studies conducted in this area. Consistently, Bolstad *et al.* (2004) found that soil respiration increased in aspen stands from 24-27 years to 42-48 years old, but decreased in mature northern hardwood stands (67-72 years). Martin and Bolstad (2005) estimated the annual sums of soil respiration in 1998-1999 of 965, 950 and 895 in young aspen, intermediate aspen, and mature northern hardwood stands, respectively, the numbers higher than this study that reports soil respiration in the growing season. Consistently, all of previous studies in this area found lower soil respiration in mature northern hardwood stands. However, this study adds more younger stands and older stands so that we have a substantially broader chronosequence to show the successional pattern of soil respiration.

Soil respiration peaking at intermediate age and declining in the old-growth reported in this study is consistent with a few studies in other ecosystems in the limited literature on this topic. For example, it is consistent with the study of Law *et al.* (2003) that reported that heterotrophic respiration in ponderosa pine stands in Oregon increased with forest age, and then decreased in the oldest stands (190-316 years). Wang *et al.*

(2002) also found soil respiration in a Canadian boreal forest decreased when the stands age (130 years). Recently, Saiz et al. (2006) reported that soil respiration in central Ireland decreased with stand age but leveled out in the older stands (47 years) with peak respiration in 10-year-old stands.

The successional pattern of soil respiration may suggest a similar pattern of ecosystem respiration. Tang et al. (2008) have reported that soil respiration accounted for a majority part of ecosystem respiration in northern forests in this area, and the decline of soil respiration in old-growth forests was consistent with the decline of ecosystem respiration. Thus, this study supports the hypothesis that in general, respiration may decrease with forest age (Ryan *et al.* 2004; Ryan and Waring 1992), which disagrees with the conceptual model that respiration increases continuously with forest age (Odum 1969; Kira and Shidei 1967).

Chronosequence of soil carbon

The complex behavior of soil carbon dynamics over time and depth suggests that the soil carbon stock is a delicate balance between carbon inputs (litterfall, root mortality and exudates, and transport of dissolved organic carbon) and outputs (decomposition) (Turner and Lambert 2000; Guo and Gifford 2002). Soil carbon decomposes more slowly in the deeper soil probably due to low soil temperature in the growing season, low oxygen availability, and high soil aggregation (Six *et al.* 2002). Soil carbon inputs from roots may peak at the age of 10-30 years when we observed fastest stem growth rates in these stands. As a result, soil carbon in the regenerated stand at 0-10 cm was lower than the young stands probably due to fast post-harvest decomposition of soil carbon in the

surface accumulated from the pre-harvest stand; at 30-60 cm, soil carbon in the regenerated stand remained higher than the young stands probably due to continuous loss of post-harvest carbon in the young, which was not timely offset by the accumulation of carbon. In the old-growth stand, more carbon was accumulated in the deep soils than the mature. Although we have observed the chronosequence pattern based on the limited number of stands across age, our knowledge in understanding the mechanism of soil carbon dynamics is still limited (Thuille and Schulze 2006; Peichl and Arain 2006).

Our chronosequence study covering a broad range of stand age and different depths of soils suggests that soil carbon dynamics may be more complex than previously reported (Covington 1981; Johnson and Curtis 2001; Zhou *et al.* 2006). Soils continuously accumulated carbon in deep layers in the old-growth stand, which remained non-steady-state in carbon balance. Total soil carbon (0-60 cm) initially decreased after harvest, and then increased after stands established, compensating the loss of carbon during harvest. The patterns of total soil carbon (0-60 cm) shown in this study are consistent with Covington (1981) on forest floor and Zhou *et al.* (2006) on surface soils (0-20 cm), albeit a different pattern of surface soils in this study. The change of soil carbon in the study is within the range of reported long-term soil carbon accumulation (Schlesinger 1990) but much lower than the rate reported recently by Zhou *et al.* (2006). These empirical results suggest that it may take long time (hundreds of years) for ecosystems to recover to its original carbon storage after a major disturbance (such as harvest), as was reported by a published model result (Harmon *et al.* 1990); ecosystems will lose soil carbon if old-growth forests are harvested or converted to young forests.

Chronosequence approach

This study uses the chronosequence, a space-for-time substitution approach, to study age succession of soil carbon fluxes and stocks. As with all chronosequence designs we assume age is the primary difference among sites by neglecting other factors. This is largely justified under the observed conditions because all stands were established on similar well-drained, glacially derived soils, experiencing essentially the same climate. The species effect on soil carbon could also be neglected because old aspen stands are often replaced by maple-birch-hemlock if left undisturbed as a stand successional pathway in northern Wisconsin (Kotar *et al.* 1988). As a result, there are few pure maple-birch-hemlock stands younger than 40 years old and few aspen stands older than 40 years. However, the detailed effect of species shifts on soil respiration and other biogeochemical cycles is still uncertain. Chronosequence studies need to be complemented by long-term observation studies and may be not consistent with long-term studies (Yanai *et al.* 2003), because long-term observation studies may also suffer from errors associated with random disturbance and human-induced disturbance. This study highlights the complexity of soil carbon dynamics, the importance of soil depth in carbon storage, and the research need to study long-time soil carbon sequestration capacity and mechanism.

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Table 1 Summary of stand characteristics measured in summer 2005. Age since clear cutting or major disturbance.

Stand	Description	Dominant species	Age (years)	DBH (\pm SD, cm)	LAI (\pm SD)	Coordinate ($^{\circ}$ W)	Coordinate ($^{\circ}$ N)
CB	Clearcut and repeated burns	--	1	--	--	90.17537	45.87090
BS	Blowdown and partial salvage	--	1	--	--	90.07699	45.87017
CR	Clearcut with residual trees	<i>P. tremuloides</i>	1	--	--	90.16995	45.87421
RG	Regeneration from clearcut	<i>P. tremuloides</i>	3	1.1 \pm 0.4	--	90.11872	45.89176
YA1	Young aspen	<i>P. tremuloides</i>	10	6.3 \pm 2.3	2.4 \pm 0.1	90.07977	45.83021
YA2	Young aspen	<i>P. tremuloides</i>	10	7.5 \pm 2.0	1.5 \pm 0.2	90.15335	45.78203
YA3	Young aspen	<i>P. tremuloides</i>	10	6.9 \pm 1.4	1.5 \pm 0.1	90.10920	45.79335
YA4	Young aspen	<i>P. tremuloides</i>	10	7.3 \pm 1.6	1.8 \pm 0.1	90.24637	45.92729
IA1	Intermediate aspen	<i>P. tremuloides</i>	26	22.0 \pm 7.3	3.8 \pm 0.2	90.27376	45.94281
IA2	Intermediate aspen	<i>P. tremuloides</i>	26	21.1 \pm 6.8	2.2 \pm 0.3	90.23641	45.88991
IA3	Intermediate aspen	<i>P. tremuloides</i>	26	22.2 \pm 5.1	3.6 \pm 0.4	90.14531	45.78197
IA4	Intermediate aspen	<i>P. tremuloides</i>	26	21.9 \pm 5.0	2.5 \pm 0.4	90.23845	45.93764
MH1	Mature northern hardwood	<i>A. saccharum</i>	73	21.5 \pm 7.0	4.7 \pm 0.2	90.08473	45.81753
MH2	Mature northern hardwood	<i>A. saccharum</i>	73	24.4 \pm 8.0	5.3 \pm 0.5	90.15481	45.79547
MH3	Mature northern hardwood	<i>A. saccharum</i>	73	24.0 \pm 6.7	5.6 \pm 0.4	90.12313	45.76018
MH4	Mature northern hardwood	<i>A. saccharum</i>	73	23.3 \pm 7.4	5.6 \pm 0.4	90.10093	45.77812
OG	Old-growth northern hardwood	<i>A. saccharum</i>	~350	25.9 \pm 11.2	4.1 \pm 0.2	89.34765	46.24202

Table 2 Parameters estimated for the temperature response function, $R = R_0 \exp(\beta T)$

Stand	R_0	β	Q_{10}	r^2	p value	Sample size
CB	0.621	0.085	2.34	0.792	0.0001	12
BS	0.627	0.122	3.40	0.853	< 0.0001	12
CR	1.351	0.065	1.92	0.636	0.0019	12
RG	0.327	0.170	5.49	0.880	< 0.0001	12
YA	0.744	0.114	3.12	0.729	< 0.0001	34
IA	0.839	0.113	3.09	0.785	< 0.0001	34
MH	0.780	0.106	2.87	0.704	< 0.0001	34
OG	0.967	0.084	2.31	0.868	< 0.0001	18

Figure captions:

Fig. 1 daily mean soil temperature at 10 cm in 8 types of stands in DOY 133- 295 in 2005. Abbreviation: CB = clearcut and repeatedly burned, BS = blowdown and partial salvage, CR = clearcut with sparse residual overstory, RG = regeneration from clearcut, YA = young aspen, IA = intermediate aspen, MH = mature northern hardwood, OG = old-growth.

Fig. 2 Measurements of soil respiration in 7 types of stands in 2005. The error bars in b indicate standard deviations among stands.

Fig. 3 Chronosequence of soil mean temperature (a), temperature sensitivity (Q_{10}) (b), soil respiration normalized to 10°C (c), and cumulative soil respiration (d) over the growing season. The solid lines link stands RG, YA, IA, MH, and OG to indicate the trajectory implied by the age chronosequence. Error bars indicate standard deviations among replicated stands

Fig. 4 Chronosequence of soil carbon stocks at 0-10 cm (a), 10-30 cm (b), 30-60 cm (c), and 0-60 cm (d) of soils. Error bars indicate standard deviations among replicated stands.

Fig. 5 Chronosequence of root biomass (in dry biomass) at 0-20 cm in soil (a) and of LAI (b). Error bars indicate standard deviations among replicated stands.

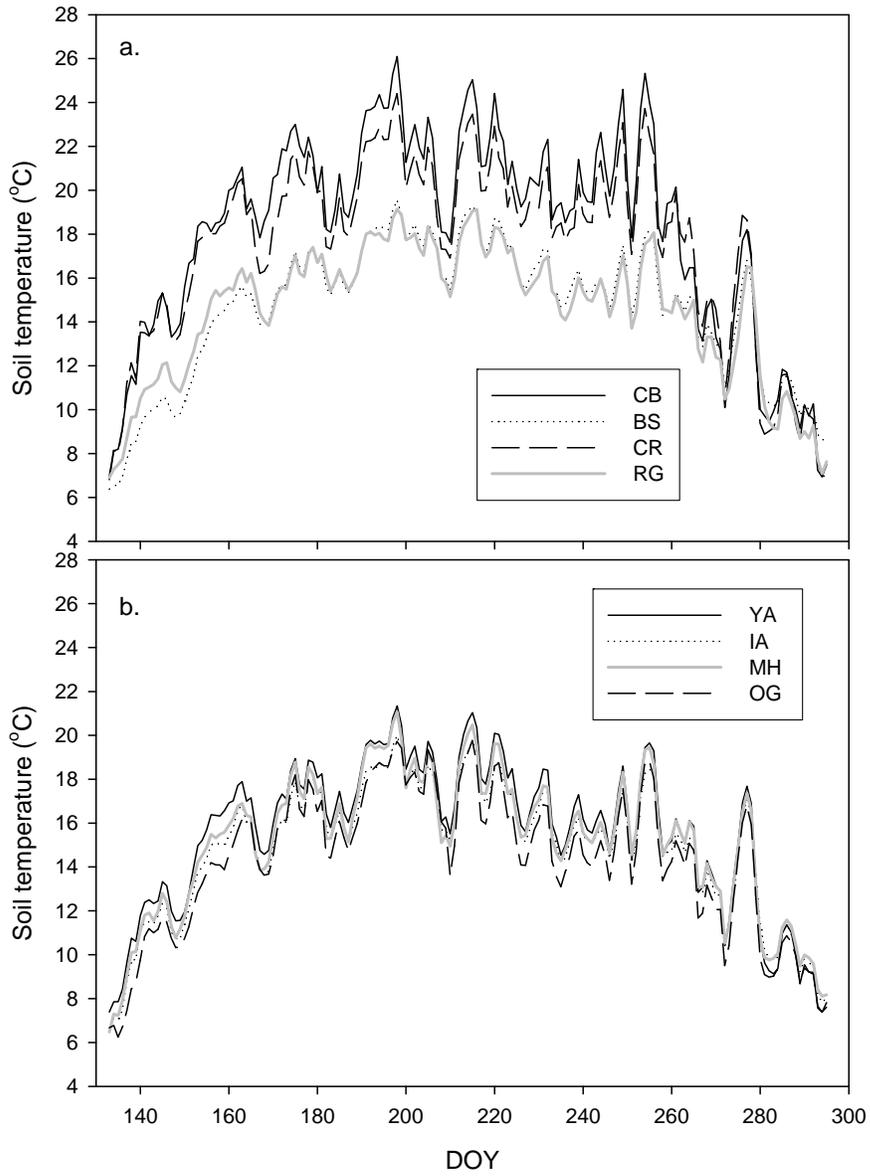


Fig. 1

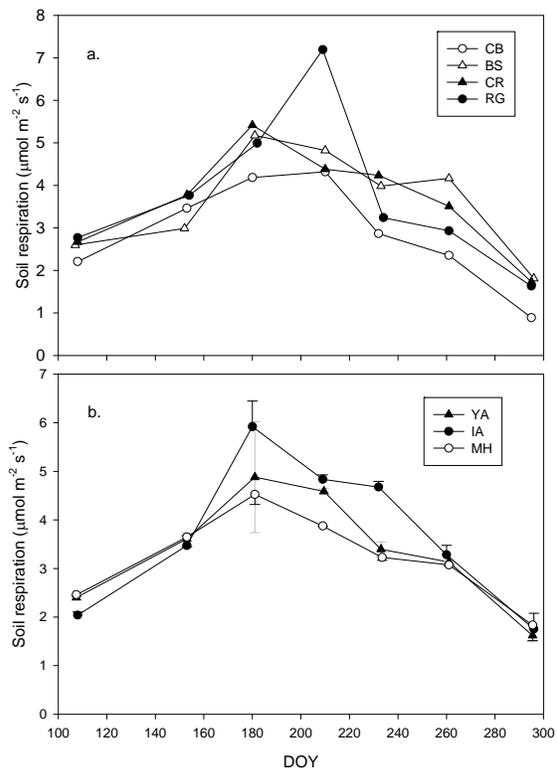


Fig. 2

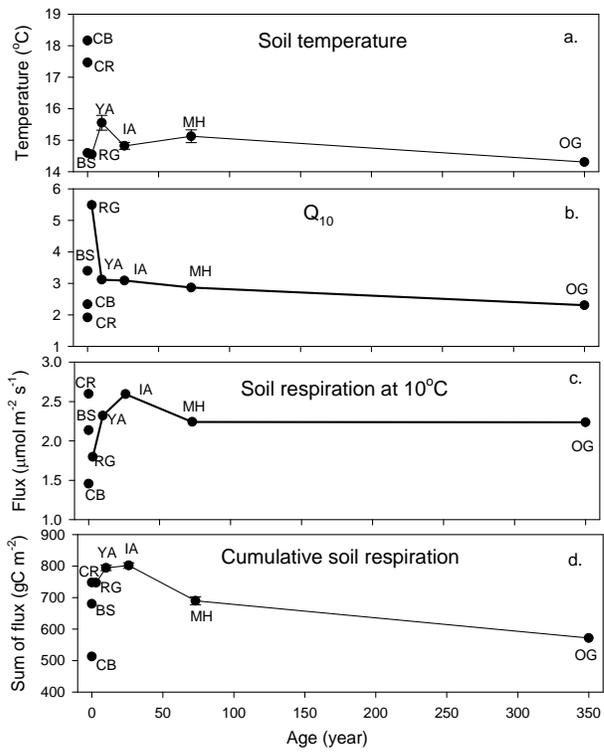


Fig. 3

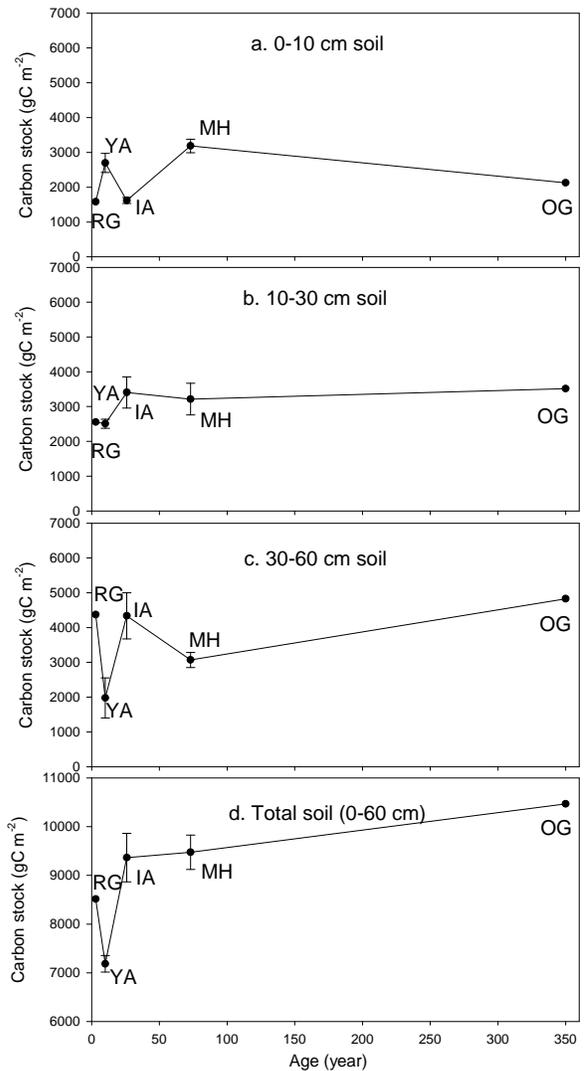


Fig. 4

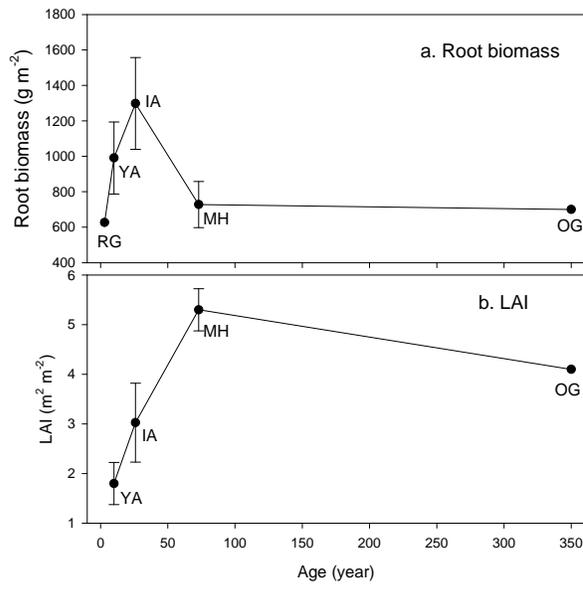


Fig. 5