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Review

Harvest impacts on soil carbon storage in temperate forests

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ABSTRACT

Forest soil carbon (C) storage is a significant component of the global C cycle, and is important for sustaining forest productivity. Although forest management may have substantial impacts on soil C storage, experimental data from forest harvesting studies have not been synthesized recently. To quantify the effects of harvesting on soil C, and to identify sources of variation in soil C responses to harvest, we used meta-analysis to test a database of 432 soil C response ratios drawn from temperate forest harvest studies around the world. Harvesting reduced soil C by an average of 8 ± 3% (95% CI), although numerous sources of variation mediated this significant, overall effect. In particular, we found that C concentrations and C pool sizes responded differently to harvesting, and forest floors were more likely to lose C than mineral soils. Harvesting caused forest floor C storage to decline by a remarkably consistent 30 ± 6%, but losses were significantly smaller in coniferous/mixed stands (−20%) than hardwoods (−36%). Mineral soils showed no significant, overall change in C storage due to harvest, and variation among mineral soils was best explained by soil taxonomy. Alfisols and Spodosols exhibited no significant changes, and Inceptisols and Ultisols lost mineral soil C (−13% and −7%, respectively). However, these C losses were neither permanent nor unavoidable. Controls on variation within orders were not consistent, but included species composition, time, and sampling depth. Temporal patterns and soil C budgets suggest that forest floor C losses probably have a lesser impact on total soil C storage on Alfisols, Inceptisols, and Ultisols than on Spodosols, which store proportionately large amounts of C in forest floors with long C recovery times (50–70 years). Mineral soil C losses on Inceptisols and Ultisols indicate that these orders are vulnerable to significant harvest-induced changes in total soil C storage, but alternative residue management and site preparation techniques, and the passage of time, may mitigate or negate these losses. Key findings of this analysis, including the dependence of forest floor and mineral soil C storage changes on species composition and soil taxonomic order, suggest that further primary research may make it possible to create predictive maps of forest harvesting effects on soil C storage.

Contents

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1. Introduction

Forest soils contain a globally significant amount of carbon (C). Approximately half of Earth's terrestrial C is in forests (1146×10^{15} g), and of this amount, about two-thirds is retained in soil pools (Dixon et al., 1994; Goodale et al., 2002; Johnson and Curtis, 2001). On an annual basis, detrital C inputs (61.4×10^{15} g) slightly exceed respiratory C losses (60×10^{15} g) from soils, suggesting that soil C storage may contribute to the 'missing C sink' implicated in the global C budget (Schimel, 1995). Since the net C balance of forest soils (whether sequestering or losing C) generally is a small difference between two large fluxes, a relatively minor change in either term could have major impacts on the forest C budget.

Soil C storage is important not only because of its role in the global C cycle (Kirschbaum, 1995), but also because it affects forest productivity (Jurgensen et al., 1997; Grigal and Vance, 2000). Since soil C is a principal source of energy for the nutrient-recycling activities of heterotrophic soil organisms, the maintenance of soil C stocks is vital for sustaining forest productivity (Attiwill and Adams, 1993; Vance, 2000). Furthermore, soil C is one of the principal components of soil organic matter (SOM), which also contains significant amounts of water and nitrogen—all of which are exchanged between the biosphere and the atmosphere to affect Earth's atmospheric chemistry, energy and water budgets, and climate (Conrad, 1996; Raich and Schlesinger, 1992). Therefore, improving our understanding of the factors that affect forest soil C storage is fundamentally important for anticipating changes in ecosystem goods and services ranging from forest products, to water resources, to greenhouse gas mitigation.

Forest management, especially the harvesting of biomass for forest products, can significantly affect soil C storage. Forest harvesting may shift the soil C balance by many mechanisms, including altering the quantity and quantity of detrital C inputs, changing soil microbial community composition, and affecting the climatic conditions that drive plant and microbial processes (Chen et al., 1995; Covington, 1981; Gray et al., 2002; Hassett and Zak, 2005; Zogg et al., 1997). However, soil C measurements frequently have high levels of spatial and temporal variability, making it difficult to detect the effects of management on soil C storage within an individual site (Homann et al., 2001, 2008; Magrini et al., 2000). Fortunately, the statistical technique of meta-analysis can be used to find underlying patterns that are broadly consistent across studies, even when such patterns are so obscured by variability as to be rendered undetectable within each individual study. In meta-analysis, the results of many individual experiments are synthesized by compiling a distribution of responses to a treatment applied at multiple locations, or at different times. Analysis then proceeds by testing this distribution for an overall effect of the treatment, and by identifying the sources of variation among responses to that treatment. We collected soil C data from experiments that compared harvested and unharvested temperate forest sites, and used meta-analysis to answer the following questions. First, is there a consistent, overall effect of forest harvesting on soil C storage? Second, what factors control variation in soil C responses to harvest? Third, is it possible to identify soil C pools that exhibit different levels of vulnerability to harvest-induced change? Finally, how much does soil C storage change in response to harvest and site preparation techniques commonly practiced in temperate forests?

2. Methods

We conducted this meta-analysis following the general methods of Curtis (1996) and Johnson and Curtis (2001). We searched the peer-reviewed literature using keyword searches within the online reference databases ISI Web of Science, BIOSIS, Agricola, and CAB Direct. Keyword search strings were combinations of terms such as: forest, timber, logging, harvest, clearcut, thinning, coppice, residue, management, and soil C. In the process of inspecting over 6500 references returned by our literature searches, we found 75 publications that met our inclusion criteria of: (1) reporting control (unharvested) and treatment (harvested) soil C values, and (2) being conducted in a temperate forest (4–8 months of mean air temperature >10 °C; Köppen, 1931). Acceptable controls for harvested forest soils were either pretreatment soil C values, or soil C observations from nearby reference stands that were not harvested. The latter type of control value included both simultaneous measurements of harvested and unharvested soils, and chronosequences, in which case the oldest stand was treated as the control. As a minimum, control stands were those which had not been harvested within the past 30 years, although some publications had control stands that had not been harvested for 1–2 centuries. Therefore, our meta-analysis does not bear specifically on either old-growth conversions or short-rotation plantation forestry, but rather a mix of many different harvest regimes practiced across time scales. Although they did not meet the temperate climate requirement, we included several publications from the southeast United States due to the importance of this region to forestry in the U.S. We accepted soil C concentrations and pool sizes as metrics of soil C, and used meta-analysis to determine whether concentrations and pool sizes significantly differed in their responses to harvest. Among publications that reported both concentrations and pool sizes, we chose pool sizes as the response parameter, and we calculated soil C pool sizes for publications that reported concentrations and bulk densities. The term 'C storage' as used in this study denotes C pool sizes only; we use the more general term 'soil C' when referring to soil C estimates that encompass both types of reporting units.

We extracted meta-data (potentially useful predictor variables) from each publication, including temporal, climatic, soil chemical and physical data, measurement units, and treatment and analytical methods. One pertinent distinction in the soil physical data category was the soil layer sampled. We extracted data for organic and mineral soil layers separately, and coded the data so that we could test for differences between soil layers defined as forest floor (mostly organic horizons), surface mineral soil (5–20 cm deep), deep mineral soil (20–100 cm), and whole mineral soil profile. Inconsistencies among the soil layers reported in primary publications are considered in the Discussion. Regarding our classification of harvest, residue management, and site preparation techniques, we categorized studies as follows, provided meta-data were descriptive enough to ascertain the specific practices used. First, each response ratio was classified according to its harvest type as a clearcut, in which all overstory trees were cut down, or a thinning, if some proportion of the overstory was left intact. If possible, we then categorized each response ratio according to harvest intensity, a categorical variable to distinguish whole-tree and stem-only harvests. Finally, for each response ratio, we noted the residue management and site

Table 1
Categorical factors tested as potential predictor variables in the meta-analysis.

Factor	Levels
Reporting units	Pool size, concentration
Soil layer	Forest floor, surface mineral soil (<20 cm), deep mineral soil (>20 cm), whole mineral soil profile
Species composition	Hardwood, coniferous/mixed
Soil taxonomic order	Alfisol, Andisol, Inceptisol, Mollisol, Spodosol, Ultisol
Geographic group	NE U.S., NW U.S., SE U.S., SW U.S., Europe, Australia, Asia
Harvest type	Thin, clearcut
Harvest intensity	Stem only, whole-tree
Residue management/site preparation methods	None, residue removed, residue spread, broadcast burn, intensive (tillage)
Time since harvest	0–5, 6–20, 21–40, >40 years
Soil texture[a]	Coarse (mostly sand), fine (mostly silt or clay)

The levels listed within each factor define the response ratio groups used for Q_b analysis in Table 2.
[a] Mineral soils only.

preparation methods employed after harvest. We defined residue management as the manipulation of the unused portions of harvested forest biomass, such as tops, limbs, and leaves. We defined site preparation as any process employed with the aim of improving tree regeneration (natural or planted) on the post-harvest landscape. The complete list of factors by which we categorized the response ratios in the database may be found in Table 1.

Meta-analysis estimates the magnitude of change in a parameter (i.e., the 'effect size') in response to an experimental treatment, which may be applied across a wide range of experimental systems and conditions. We used the ln-transformed response ratio R to estimate treatment effect size:

$$\ln(R) = \ln\left(\frac{\bar{X}^E}{\bar{X}^C}\right) \qquad (1)$$

where $\bar{X}^E$ is the mean soil C value of treatment (harvested) observations, and $\bar{X}^C$ is the mean soil C value of control observations for a given set of experimental conditions. The number of response ratios (k) from a given publication depends on how many sets of experimental conditions are imposed. For example, one publication with soil C storage data from a control soil and from four different levels of thinning would yield $k = 4$ response ratios, or 'studies'. Because it is unitless, the effect size R is a standardized metric that allows comparison of data between experiments reporting responses in different units (Hedges et al., 1999). After back transformation ($e^{\ln(R)}$), R can be conceptualized as the proportional or per cent change in soil C relative to its control value. When error terms and sample sizes are reported for each $\bar{X}^E$ and $\bar{X}^C$, a parametric, weighted meta-analysis is possible, but many publications we found did not report these data. Therefore, in order to include as many studies as possible, we used an unweighted meta-analysis, in which confidence intervals around mean effect sizes are generated with nonparametric resampling techniques (bootstrapping; Adams et al., 1997). We performed analyses using MetaWin software (Sinauer Associates, Sunderland, MA, USA).

One of our principal goals in this analysis was to identify the categorical variables that were the best predictors of variation in soil C responses to harvest. Accomplishing this task with meta-analysis is similar to using analysis of variance to partition the total variance of a group of observations (Q_t, the total heterogeneity) into two components: within- and between-group heterogeneity (Q_w and Q_b, respectively; Hedges and Olkin, 1985). In such a Q_b analysis, a categorical variable that defines a group of response ratios with a large Q_b is a better predictor of variation (or heterogeneity) than a categorical variable associated with small response-group Q_b. In order to determine which categorical variables were the 'best' predictors of variation, we followed the hierarchical approach detailed in Curtis (1996) and Jablonski et al. (2002). Briefly, we ran meta-analysis on the entire database to determine which categorical variable had the lowest P value, and then divided the database into the categorical groups defined by that variable. Then, within each of these groups, we ran meta-analyses again for each categorical variable, and split the studies into the groups defined by the categorical variable with the lowest P value. We performed this variance-partitioning exercise for a total of three iterations, at which point we felt it prudent to go no further due to limited sample sizes and possible confounding relationships. When, during the course of these Q_b iterations, we found multiple categorical variables with the same P value, we selected the one with the highest Q_b. In Q_b analyses, and all other meta-analyses, we accepted tests with $P < 0.05$ as statistically significant.

While our literature search was not exhaustive, the database we developed for this analysis is quite large, comprising 432 soil C response ratios from 75 papers published between 1979 and 2008. These publications correspond to forest harvests conducted in temperate forests around the world, and the full dataset is available at <http://nrs.fs.fed.us/carbon/data>. Publications included in the analysis are denoted in the References section with a (*), and basic information is provided for each publication in Appendix A.

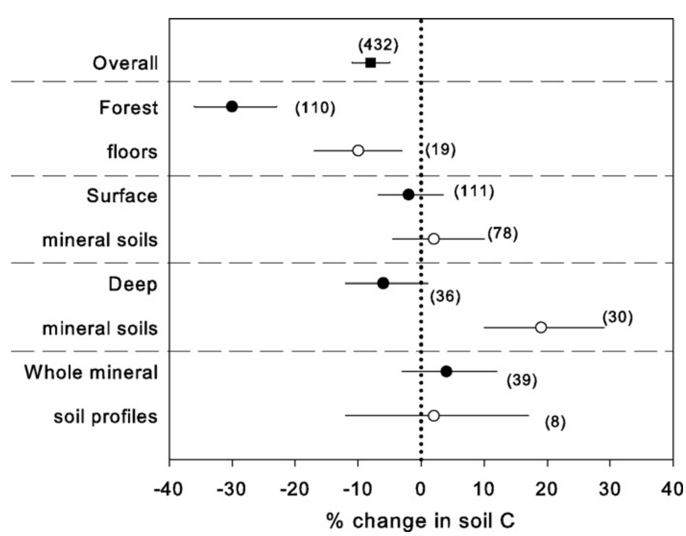

Fig. 1. Soil C changes due to forest harvesting, overall and by soil layer. All points are mean effect sizes ± bootstrapped 95% confidence intervals, with the number of studies (k) in parentheses. Groups with confidence intervals overlapping the dotted reference line (0% change) show no significant change in soil C due to harvest. The filled square at the top shows the overall effect of harvesting on soil C, including C pool sizes and concentrations from forest floors and mineral soils. Within each soil layer, mean effect sizes are shown separately for C pool sizes (C storage; filled circles) and C concentrations (open circles).

Table 2
Between-group heterogeneity (Q_b) among the k studies comprising each response parameter.

Response parameter	k	Reporting units	Soil layer	Species composition	Soil taxonomic order	Geographic group	Harvest type	Harvest intensity	Residue management/ site prep	Time since harvest	Soil texture
Overall soil C	432	2.95**	10.12**	4.38**	3.85**	4.71**	<0.01	0.17	0.33	0.70	–
Forest floor C storage	110	–	–	1.40*	2.27	3.64*	0.37	1.00	0.82	1.52	–
Coniferous/mixed	48	–	–	–	1.38	1.42	<0.01	0.81	0.86	0.40	–
Hardwood	62	–	–	–	0.25	2.32**	<0.01	0.21	0.42	0.65	–
Mineral soil C storage	186	–	0.17	0.56**	1.90**	0.96*	0.09	0.26	0.40	0.29	0.12
Alfisols	32	–	0.03	1.01**	–	0.57	<0.01	0.06	0.01	0.44	0.24
Inceptisols	28	–	0.15	0.31	–	0.14	0.10	0.09	0.91**	0.81**	NA
Spodosols	57	–	0.35*	0.04	–	0.20	0.08	<0.01	0.12	0.14	<0.01
Ultisols	37	–	0.27*	<0.01	–	<0.01	0.06	<0.01	0.21	0.14	NA

The overall soil C response to harvest includes all studies in the database, and is separated into forest floor and mineral soil groups. Forest floor and mineral soil C storage response ratios include only pool sizes, which were significantly different from concentrations in the overall analysis. Within forest floors and mineral soils, Q_b is shown separately for response ratio groups defined by the categorical variable with the lowest P value (species composition for forest floors; soil order for mineral soils). See Table 1 for the levels that comprise each factor (categorical group) included in the Q_b analysis.
* Statistical significance of Q_b is denoted by $P < 0.05$.
** Statistical significance of Q_b is denoted by $P < 0.01$.

3. Results

3.1. Overall effects and primary sources of variation

Averaged across all studies, forest harvesting resulted in a small, but significant reduction in soil C (−8%, Fig. 1). Our meta-analysis revealed several important sources of variation underlying this overall effect, however (Table 2). The two most significant categorical factors accounting for among-study variation in harvest impacts were the soil layer sampled (forest floor vs. mineral soil) and the reporting units (concentration vs. pool size). Specifically, the forest floor was the only soil layer to show an overall, significant change in C storage following harvest (Fig. 1; −30%), an effect which was paralleled by a much smaller impact on forest floor soil C concentration (−10%). Harvesting had no overall effect on surface, deep, or whole mineral soil C storage, but deep mineral soil C concentrations increased by an average of 19%. The significant difference between harvest impact results reported as C concentrations compared to those reported as C pool size, or storage, led us to restrict all further analyses to results reported as C storage.

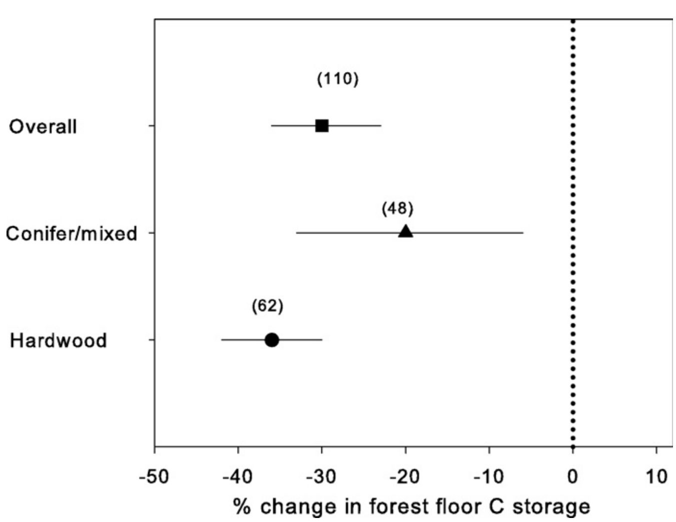

Fig. 2. The effects of harvesting on forest floor C storage, overall and by species composition. Plots show means ± bootstrapped 95% confidence intervals, with number of studies (k) in parentheses.

3.2. Variation within soil layers in harvest impacts

3.2.1. Forest floors

The overall effect of harvest on forest floor C storage was remarkably consistent among studies, with little variation due to differences in soil taxonomic order, time since harvest, or harvest intensity (Table 2). The principal predictor of variation in harvest impacts on C storage was tree species composition, with coniferous/mixed forests losing less forest floor C than do hardwood forests (Fig. 2; −20% and −36%, respectively). Geographic location also accounted for significant between study variation (Table 2), but this was due to two studies from the southeast U.S. that showed a 50% increase in forest floor C storage, both of which were from Mattson and Swank (1989).

In forests growing on Spodosols, forest floor C storage after harvest showed a lengthy, but relatively well-constrained recovery period, on the order of 50–70 years (Fig. 3A). Long-term studies of forest floor C recovery on other soil orders are lacking (Fig. 3B).

3.2.2. Mineral soils

Soil order was the most important predictor of between-study variation in harvest impacts on mineral soil C storage (Table 2). When all layers were analyzed together, mineral soils from Inceptisols and Ultisols had significant declines in C storage following harvest (−13% and −7%, respectively), while Spodosols and Alfisols were not significantly affected (Fig. 4). Among Inceptisol mineral soils, time since harvest was the principal source of between-study variation, with C storage declining by 25% within 5 years of harvest, but recovering to control values within 6–20 years. Both Ultisols and Spodosols showed significant differences in response to harvest between surface and deep mineral soil layers (Fig. 4). Among Ultisols, surface mineral soils lost significant C (−7%, $P = 0.016$), while deep mineral soils were unchanged. Spodosols showed the opposite pattern, with no loss in surface mineral soil C storage but a significant decline in deep mineral soil C (−9%, $P = 0.031$). Species composition was a significant predictor of variation among Alfisols, with hardwoods exhibiting a decline in C storage in response to harvest (−36%, $P = 0.001$) but with no harvest effect seen in coniferous and mixed forests (Fig. 4).

In contrast to forest floors, species composition and geographic factors were of secondary importance in accounting for variation in

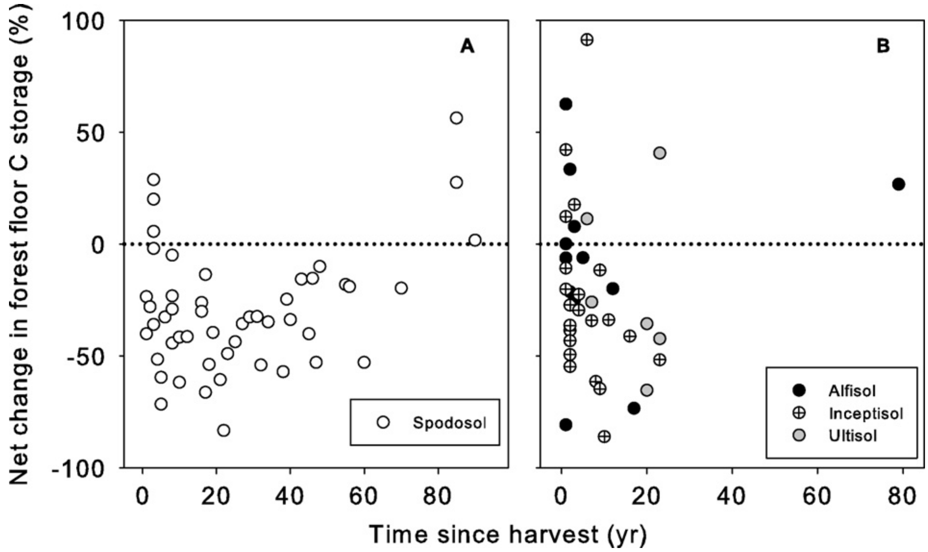

Fig. 3. Temporal patterns in forest floor C storage following harvest for Spodosols (A) and all other soil orders (B; Alfisols, Inceptisols, and Ultisols). Each point represents one response ratio. While the trajectory of post-harvest forest floor C storage is evident for Spodosols, more long-term data are needed to predict forest floor C recovery for other soil orders.

mineral soil response to harvest (Table 2). Overall, coniferous/mixed forests showed no significant change in mineral soil C storage following harvest (+2%, NS) while hardwoods lost C (−9%). Studies from the southeast U.S. showed a significant reduction in mineral soil C (−7%), while those from other geographic groups exhibited no significant change.

3.3. Soil C budgets

Harvest impacts on forest floor and mineral soil C storage have different consequences for forest soil C budgets because of differences in the magnitude of C pools among the different soil layers (Fig. 5). While forest floors can lose a substantial proportion of their C stocks following harvest, the magnitude

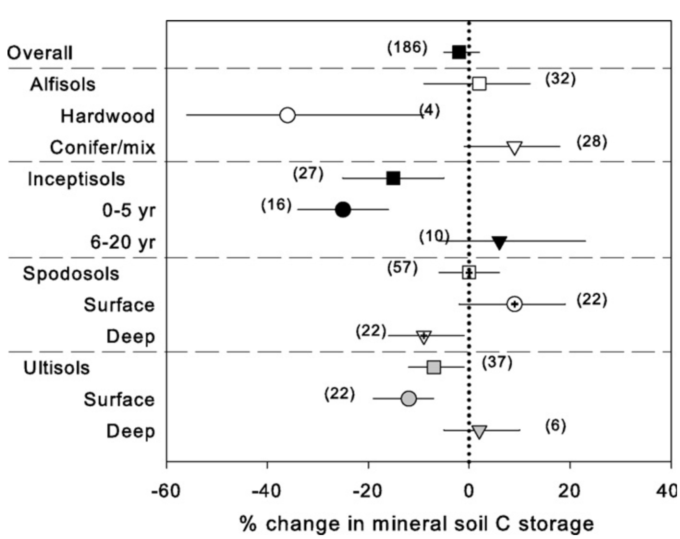

Fig. 4. The effects of forest harvesting on mineral soil C storage, by soil taxonomic order. All points are mean effect sizes ± bootstrapped 95% confidence intervals, with the number of studies (k) in parentheses. The filled square at the top of the figure represents the overall harvest effect on mineral soil C storage, including surface, deep and whole mineral soils from all orders. Within each soil order, the effect of harvest on mineral soil C storage across all layers is represented by a square, while the circle and inverted triangle designate significantly different groups.

of these losses is tempered by the relatively small amount of C stored in the forest floor compared to the mineral soil in most soil orders. Among Alfisols, Inceptisols, and Ultisols, forest floor C storage in unharvested stands generally ranged from 5 to 20 Mg ha^{-1}, while mineral soils held 20–80 Mg C ha^{-1}. Spodosols were an exception to this general pattern, as forest floors and mineral soils contained a similar range of amounts of C (5–50 Mg ha^{-1}).

4. Discussion

4.1. Overall harvest effects and sources of between study variation

Our results show that, across studies, there is a significant effect of forest harvesting on soil C (−8 ± 3% overall, −13 ± 4% for C storage only). This statistically robust conclusion is in spite of the frequently high levels of spatial and temporal variability in forest soil C measurements, which often make it difficult to quantify the effects of management on soil and whole-ecosystem C budgets from a single study (Homann et al., 2001, 2008; Magrini et al., 2000). Fortunately, many factors responsible for variation in soil C responses to harvest, such as species composition and soil order, are typically recorded as meta-data within the experimental design.

Soil layer was the strongest predictor of soil C storage shifts due to harvest in the overall meta-analysis, despite variable sampling depths among studies. For example, forest floor material from some studies (e.g., Yanai et al., 2000, and references therein) included mineral soil, and the depth of the surface and deep mineral soil categories varied substantially across studies (5–20 and 25–100 cm, respectively). Nonetheless, forest floor C storage was significantly more vulnerable to decline following harvest than was mineral soil C storage. There may be several reasons for this difference in sensitivity to disturbance. First, there are significant differences in pool sizes, turnover times, and molecular characteristics of C stored at different depths in forest soils, which may cause the forest floor to be more responsive to disturbance or management than the mineral soil (Currie, 1999; Cromack et al., 1999; Dai et al., 2001; Trumbore, 2000). For example, the smaller C pool size of the forest floor means that even a modest C loss in absolute terms

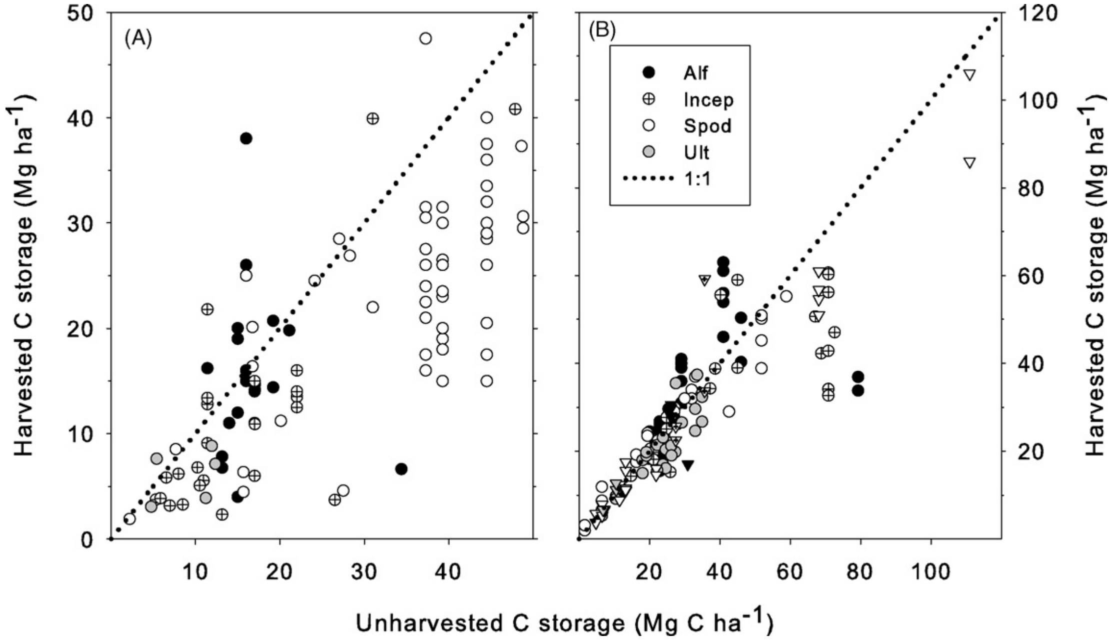

Fig. 5. Absolute changes in C storage due to harvest, for forest floors (A) and mineral soils (B), by soil taxonomic order. In panel B, surface mineral soils are represented by circles; deep mineral soils are triangles. Forest floor and soil C storage values for some points were estimated from loss on ignition data (C = 0.5 × LOI). The 1:1 reference line in each panel denotes no difference in C storage between unharvested and harvested stands; points below represent decreases, while points above are C storage increases. Points from unidentified or under-represented soil orders (Andisols, Entisols, Mollisols) are not plotted.

can cause a large proportional reduction, compared to the mineral soil. Forest soil C generally has longer turnover times and increasing molecular complexity with depth in the profile, and the abundance of labile organic matter in the forest floor may promote a more rapid microbial response following disturbance. The physical effects of harvesting on the forest floor, where machinery can directly disturb organic matter through mixing and fragmentation, also are different from those on the mineral soil, which is generally protected from the direct physical effects of harvesting. Forest floor C losses during harvest may be due to mixing and incorporation of surface organic matter into the upper mineral soil as suggested by several studies of whole-tree harvesting in northern hardwoods (Mroz et al., 1985; Ryan et al., 1992). However, our results indicate that this is generally not the case, since, in our meta-analysis, surface mineral soil C storage decreased significantly (−8%) in the time category immediately following harvesting (0–5 years).

4.2. Variation within soil layers

Although forest floors lose C after harvest regardless of species composition, the smaller C storage declines in forest floors from coniferous/mixed forests compared to hardwood forests may reflect the greater recalcitrance of coniferous residue. Generally, coniferous detritus and forest floor materials have higher C/N and lignin/N, slower decomposition and N-mineralization rates, and longer organic matter residence times than hardwood detritus/forest floor materials (Currie, 1999; Finzi et al., 1998; Silver and Miya, 2001). Although forest floor C losses were substantial, temporal trends suggest that these losses were not permanent: on Spodosols forest floors appear to recover after 50–70 years. This estimate supports the seminal study by Covington (1981), even when his data are removed from Fig. 3A (13 of 59 response ratios). It may be that forest floor C recovers more slowly in Spodosols than in other soil orders since Spodosols tend to have larger forest floor C pools, such that a similar proportional reduction in forest floor C corresponds to a greater absolute amount of C in Spodosols than in other soil orders. In addition, productivity of forests growing on Spodosols generally is less than on Alfisols and Ultisols, and approximately equal to Inceptisols (Vogt et al., 1995). Therefore, Spodosols might also require a longer recovery period than Alfisols or Ultisols due to lower rates of litter inputs. To fill the knowledge gap that exists for most temperate forest soil taxonomic orders, there clearly is a need for additional long-term forest harvest–forest floor C studies. Chronosequences, such as those surveyed in Yanai et al. (2000) and Covington (1981), yield large amounts of data, but are a weaker experimental design than long-term monitoring of control and treatment stands. Namely, it may be impossible to distinguish whether forest floor C loss was due to changes in treatment over time or time since treatment based on chronosequence studies.

Harvest impacts on mineral soil C varied among soil orders, suggesting that order-specific properties or soil-forming factors mediate management effects on soil C storage. Within each soil order, a dominant soil forming process mediates the physical and chemical properties of that soil's horizons, including accumulation and distribution of soil C (Shaw et al., 2008). For example, Spodosols form through the process of podzolization, which occurs as soluble organic compounds are eluviated from forest floors and surface mineral soils, and illuviated at deeper depths in the mineral soil. Results from our meta-analysis suggest that this process may be responsible for the impacts of forest harvesting on Spodosol mineral soil C storage. While Spodosol surface mineral soils showed no changes following harvest, a significant increase in C *concentration* accompanied a significant decrease in C *storage* in the deep mineral soil. This suggests that a downward redistribution of soil C, perhaps due to accelerated podzolization, changed the organic matter chemistry of the deep mineral soil. Ussiri et al. (2007) reached a similar conclusion in their study of 15-year changes in soil organic matter in a paired-watershed clearcut experiment at Hubbard Brook. They used nuclear magnetic resonance to show that changes in organic matter composition accompanied the downward redistribution of soil C after harvest, such that biogeochemically stable forms of organic matter were lost and replaced with less stable compounds. If shifting the balance of soil organic matter towards less stable compounds results in faster overall decomposition, this change in organic matter chemistry may explain why Spodosols lost significant amounts of deep mineral soil C stocks in our meta-analysis.

An additional factor accounting for differences among soil orders in their sensitivity to harvesting could be the specific management techniques most commonly practiced on them. For example, intensive site preparation (tillage) following harvest caused a significant decline in surface mineral soil C storage (−20%) but was practiced almost exclusively on Inceptisols and Ultisols (e.g., Carter et al., 2002; Merino and Edeso, 1999). Other post-harvest residue management and site preparation methods, such as broadcast burning or complete residue retention, did not reduce Inceptisol/Ultisol surface mineral C storage (e.g., Mattson and Smith, 1993; Shelburne et al., 2004). This suggests that C losses on these two soil orders may be mitigated, or even prevented, through the use of management practices that minimize physical disturbance to the soil profile.

Significant sources of variation in sensitivity to mineral soil C loss in Alfisols and Inceptisols also were good predictors of harvest impacts on mineral soil C storage of all orders. This is in contrast to Spodosols and Ultisols, which had controls on mineral soil C variation that were not present in the overall mineral soil analysis. Across all soil orders, and specifically within Alfisols, hardwoods lost mineral soil C and coniferous/mixed stands showed no change. This may reflect a general effect of differential residue quality, as hypothesized for forest floor C responses to harvest. Time since harvest affected the magnitude of mineral soil C losses on Inceptisols (and mineral soils in general, although it was not a significant predictor), which declined significantly 0–5 years post-harvest, but recovered after 6–20 years.

Although mineral soils across orders showed no significant harvest impact on surface or deep mineral soil C storage, Spodosols and Ultisols lost C from deep and surface layers, respectively. Thus, at what layer soil C was lost following harvest varied with soil order, perhaps due to differences in the dominant soil-forming processes among orders. Despite our large overall sample size, the relatively small number of studies conducted on specific soil orders precludes a full understanding of mechanisms responsible for variation within and between soil orders. Our meta-analysis has helped underscore the need to better describe relationships between soil taxonomy and variation in mineral soil C responses to harvest.

4.3. Soil C budgets

We found that forest floor C storage was more sensitive to harvest impacts than was mineral soil C storage, but the long-term implications of this differential sensitivity on forest productivity are difficult to predict. On one hand, the smaller amount of C stored in forest floors compared to mineral soils, and the shorter residence times of forest floor C pools suggests that C lost from the forest floor will be more readily replaced than C lost from the mineral soil. Forest floor C losses therefore may have only modest effects on total soil C storage, especially over long rotations or C accounting intervals. Alternatively, forest floor C reductions may have large impacts on forest productivity because forest floor organic matter plays important roles in nutrient cycling and water retention (Attiwill and Adams, 1993; Currie, 1999; Schaap et al., 1997; Tietema et al., 1992). Forest floor C losses could have a great impact on forest productivity when recovery times are multidecadal, as is the case on Spodosols. Due to their greater C pool sizes, changes in mineral soil C are capable of causing greater changes to soil C budgets than losses from forest floors. However, since mineral soils showed no overall response to harvest, forest floors probably have a greater general effect on the soil C budgets of harvested forests. It is also worth noting that, among most studies we analyzed, residues such as coarse woody debris were not sampled as a component of the forest floor. Therefore, while forest floor C stocks did decline significantly, harvesting presumably increased the amount of C stored in woody debris pools, which promote nutrient and water retention and also have a significant impact on whole-ecosystem C budgets (Eisenbies et al., 2009; Janisch and Harmon, 2002).

An additional finding of this analysis related to soil C budgets pertains to the choice of units used for measuring and reporting soil C values. We found that soil C concentration and soil C storage responded differently to harvest in the overall analysis, or when examining forest floor and deep mineral soil layers individually. Measurements of soil C concentrations and soil C pool sizes are appropriate for different situations. For example, if microbial processes are the topic of study, then soil C concentrations may be relevant. However, if soil or whole-ecosystem C budgets are to be assessed, then soil C pool sizes are necessary. At the very least, bulk density links C concentration with C storage, and should be more widely reported in primary research articles focusing on all aspects of soil C. The significant difference between reporting units indicates that measurements of soil C concentrations are not adequate for soil C accounting purposes.

4.4. Conclusions

We analyzed 432 studies of soil C responses to harvest drawn from temperate forests around the world. We found a significant overall impact of harvesting on soil C storage, and determined that variation among harvest impacts was best explained by variation in species composition, soil taxonomic order, and time since harvest. One of the most important overall findings of this analysis was that C stored in forest floors is more vulnerable to harvest-induced loss (−30% on average) than mineral soil C (no significant change). Species composition (hardwood vs. coniferous/mixed) had a significant effect on forest floor C storage responses to harvest, with hardwoods generally losing more forest floor C than coniferous/mixed stands. Reductions in forest floor C storage probably have a greater impact on the soil C budgets of Spodosols than on other soil orders, since Spodosols store large amounts of C in forest floors relative to mineral soils, and require 50–70 years to recover lost forest floor C. Harvesting caused significant mineral soil C losses on Inceptisols and Ultisols, but not on Alfisols or Spodosols. Mineral soil C losses on Inceptisols were temporary, with C stocks recovering within 6–20 years after harvest. Ultisol mineral soil C losses were restricted to the surface mineral layer. The effects of species composition and soil taxonomic order on harvest-induced changes in forest floor and mineral soil C storage suggest that further research may allow development of predictive maps of forest management effects on soil C storage.

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Appendix A

References providing response ratios for the present analysis. The full citation for each is denoted with a (*) in the references section.

Reference	Soil layers sampled	Dominant canopy genera	Locations
Alban and Perala (1992)	WM	*Populus*	MN, USA
Bauhus et al. (2004)	FF, SM, DM	*Fagus*	Germany
Black and Harden (1995)	FF, SM	*Abies*, *Calocedrus*	CA, USA
Boerner et al. (2006)	SM	*Pinus*	SC, USA
Borchers and Perry (1992)	SM	*Abies*, *Pseudotsuga*	OR, USA
Cade-Menun et al. (2000)	FF, SM	*Thuja*, *Tsuga*	BC, Canada
Carter et al. (2002)	SM	*Pinus*	LA, TX, USA
Cromack et al. (1999)	FF	*Pseudotsuga*, *Tsuga*	OR, USA
Dai et al. (2001)	FF, SM	*Fagus*, *Acer*	NH, USA
DeByle (1980)	SM	*Pinus*	WY, USA
DeLuca and Zouhar (2000)	SM	*Pinus*	MT, USA
Edmonds and McColl (1989)	SM	*Pinus*	Australia
Edwards and Ross-Todd (1983)	SM, DM	*Quercus*, *Liriodendron*	TN, USA
Elliott and Knoepp (2005)	SM	*Quercus*	NC, USA
Ellis and Graley (1983)	SM	*Eucalyptus*	Tasmania
Ellis et al. (1982)	SM	*Eucalyptus*	Tasmania
Esquilin et al. (2008)	SM	*Pinus*	CO, USA
Fraterrigo et al. (2005)	SM	*Liriodendron*, *Acer*	NC, USA
Frazer et al. (1990)	SM	*Pinus*, *Abies*	CA, USA
Gillon et al. (1999)	FF	*Pinus*	France
Goh and Phillips (1991)	FF	*Nothofagus*	New Zealand
Goodale and Aber (2001)	FF, SM	*Fagus*, *Acer*	NH, USA
Gough et al. (2007)	SM, DM	*Populus*	MI, USA
Grady and Hart (2006)	SM	*Pinus*	AZ, USA
Gresham (2002)	WM	*Pinus*	SC, USA
Griffiths and Swanson (2001)	SM	*Pseudotsuga*	OR, USA
Gundale et al. (2005)	FF, SM	*Pinus*	MT, USA
Hart et al. (2006)	FF, SM	*Pinus*	AZ, USA
Hendrickson et al. (1989)	FF, SM	*Pinus*, *Populus*	ON, Canada
Herman et al. (2003)	SM	*Quercus*	CA, USA
Holscher et al. (2001)	FF, SM	*Fagus*, *Betula*	Germany
Hwang and Son (2006)	WM	*Pinus*, *Larix*	Korea
Johnson (1995)	FF, SM, DM, WM	*Fagus*, *Acer*	NH, USA
Johnson and Todd (1998)	SM, DM	*Quercus*, *Liriodendron*	TN, USA
Johnson et al. (1991)	FF, SM	*Fagus*, *Acer*	NH, USA
Johnson et al. (1997)	FF, SM, DM	*Fagus*, *Acer*	NH, USA
Kaye and Hart (1998)	FF, SM	*Pinus*	AZ, USA
Keenan et al. (1994)	SM	*Thuja*, *Tsuga*	BC, Canada
Kelliher et al. (2004)	FF, SM, DM	*Pinus*	OR, USA
Klopatek (2002)	FF, SM	*Pseudotsuga*, *Tsuga*	WA, USA
Knoepp and Swank (1997)	SM, DM	*Quercus*, *Acer*	NC, USA
Korb et al. (2004)	SM	*Pinus*	AZ, USA
Kraemer and Hermann (1979)	SM	*Pseudotsuga*	WA, USA
Laiho et al. (2003)	SM, WM	*Pinus*	NC, LA, USA
Latty et al. (2004)	FF, SM	*Fagus*, *Acer*	NY, USA
Law et al. (2001)	SM, DM	*Pinus*	OR, USA
Law et al. (2003)	WM	*Pinus*	OR, USA
Leduc and Rothstein (2007)	FF + SM	*Pinus*	MI, USA
Maassen and Wirth (2004)	FF, SM	*Pinus*	Germany
Mattson and Smith (1993)	FF, SM	*Quercus*, *Acer*	WV, USA
Mattson and Swank (1989)	FF, SM, DM	*Quercus*, *Carya*	NC, USA
May and Attiwill (2003)	SM	*Eucalyptus*	Australia
McLaughlin and Phillips (2006)	FF, WM	*Picea*, *Abies*	ME, USA
McLaughlin et al. (1996)	FF, SM, DM	*Picea*	MI, USA
Merino and Edeso (1999)	SM	*Pinus*	Spain
Murphy et al. (2006)	FF, SM, DM	*Pinus*, *Abies*	CA, USA
Neher et al. (2003)	SM	*Pinus*	NC, USA
O'Brien et al. (2003)	WM	*Eucalyptus*, *Pinus*	Australia
Prietzel et al. (2004)	FF	*Pseudotsuga*	WA, USA
Rab (1996)	WM	*Eucalyptus*	Australia
Riley and Jones (2003)	SM	*Pinus*	SC, USA
Sanchez et al. (2007)	SM, DM	*Pinus*	SC, USA
Sanscrainte et al. (2003)	FF, WM	*Abies*, *Tsuga*	WA, USA
Selig et al. (2008)	SM, DM	*Pinus*	VA, USA
Shelburne et al. (2004)	FF, SM	*Pinus*	SC, USA
Skovsgaard et al. (2006)	FF, SM, DM	*Picea*	Denmark
Small and McCarthy (2005)	SM	*Quercus*	OH, USA
Stone and Eliof (1998)	FF, SM	*Populus*	MN, USA
Stone et al. (1999)	SM	*Pinus*	AZ, USA
Strong (1997)	SM, DM	*Acer*, *Tsuga*	MN, USA
Ussiri and Johnson (2007)	FF, SM, DM	*Fagus*, *Acer*	NH, USA
Vesterdal et al. (1995)	FF	*Picea*	Denmark
Waldrop et al. (2003)	FF	*Pinus*, *Libocedrus*	CA, USA
Yanai et al. (2000)	FF	*Fagus*, *Betula*	NH, USA
Zhong and Makeschin (2003)	FF, SM	*Picea*	Germany

Soil layer abbreviations: FF, forest floor; SM, surface mineral; DM, deep mineral; WM, whole mineral.

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