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Afforestation Effects on Soil Carbon Storage in the United States: A Synthesis

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Afforestation (tree establishment on nonforested land) is a management option for increasing terrestrial C sequestration and mitigating rising atmospheric carbon dioxide because, compared to nonforested land uses, afforestation increases C storage in aboveground pools. However, because terrestrial ecosystems typically store most of their C in soils, afforestation impacts on soil organic carbon (SOC) storage are critical components of ecosystem C budgets. We applied synthesis methods to identify the magnitude and drivers of afforestation impacts on SOC, and the temporal and vertical distributions of SOC change during afforestation in the United States. Meta-analysis of 39 papers from 1957 to 2010 indicated that previous land use drives afforestation impacts on SOC in mineral soils (overall average = +21%), but mined and other industrial lands (+173%) and wildlands (+31%) were the only groups that specifically showed categorically significant increases. Temporal patterns of SOC increase were statistically significant on former industrial and agricultural lands (assessed by continuous meta-analysis), and suggested that meaningful SOC increases require ≥15 and 30 yr of afforestation, respectively. Meta-analysis of ^{13}C data demonstrated the greatest SOC changes occur at the surface soil of the profile, although partial replacement of C stocks derived from previous land uses was frequently detectable below 1 m. A geospatial analysis of 409 profiles from the National Soil Carbon Network database supported ^{13}C meta-analysis results, indicating that transition from cultivation to forest increased A horizon SOC by 32%. In sum, our findings demonstrate that afforestation has significant, positive effects on SOC sequestration in the United States, although these effects require decades to manifest and primarily occur in the uppermost (and perhaps most vulnerable) portion of the mineral soil profile.

Abbreviations: BD, bulk density; CI, confidence interval; MAP, mean annual precipitation; MAT, mean annual temperature; SOC, soil organic carbon.

Scientifically informed prediction, projection, and management of soil and related ecosystem resources in the United States require accurate accounting of SOC stocks under diverse land use and management practices. This is not only because terrestrial ecosystems store the bulk of their C in soils (Jobbágy and Jackson, 2000), but also because SOC is a fundamental driver of critical ecosystem processes and services including nutrient cycling, water retention, and biological carbon sequestration (Lal, 2004; Post et al., 2004). Furthermore, while the general and broad-scale effects of basic management activities (e.g., fertilization or biomass removal) on C production and storage in aboveground ecosystem pools are fairly well understood (Birdsey et al., 2006; Fox, 2000; Ludwig et al., 2011; Vance, 2000), management impacts on belowground C stocks (including SOC) at

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similarly broad conceptual and spatial scales are much less understood. Recent reviews have demonstrated measureable impacts of fertilization (Alvarez, 2005; Ladha et al., 2011; Nave et al., 2009) or biomass removal (Nave et al., 2010; Thiffault et al., 2011; Wilhelm et al., 2004) on SOC in a variety of ecosystems, and others have addressed questions of SOC change when management involves land use transitions including afforestation (Guo and Gifford, 2002, Post and Kwon, 2000; Berthrong et al., 2009; Laganiere et al., 2010). During afforestation, increases in aboveground C stocks can be expected, owing to the establishment and growth of trees on lands that previously lacked significant woody biomass, and trajectories of C accumulation in forest biomass are precisely quantified for afforesting lands in the United States. (Smith et al., 2006). However, scientific understanding of SOC changes for C accounting purposes lags behind knowledge of aboveground C accumulation, and in the midst of this need for information that is specific to the United States the global scope of afforestation-SOC synthesis papers makes their direct application to the C balance of U.S. lands uncertain. Furthermore, existing global afforestation-SOC reviews are mostly restricted to intentionally established forests, while in the United States a large amount of forest regrowth has occurred on lands managed for natural regeneration of forest cover (Birdsey et al., 2006).

Global-scale quantitative reviews of SOC change during afforestation have demonstrated some consistent patterns. First, all such work reveals that previous land use significantly impacts the amount or rate of SOC change during afforestation. Second, coniferous species tend to decrease SOC in mineral soils, while broadleaf trees show no effect or an increase (Laganiere et al., 2010; Berthrong et al., 2009; Guo and Gifford, 2002). These large-scale reviews have also revealed relationships between SOC change and soil or environmental factors that are logically consistent with understanding of the factors controlling SOC accumulation. For example, the amount of SOC accumulation during forest regrowth tends to approximate the quantity lost to cultivation on agricultural afforestations (Guo and Gifford, 2002), and the amount of change in SOC during afforestation is typically a function of time elapsed since the prior land use (Guo and Gifford, 2002; Post and Kwon, 2000). Such relationships are logical if it is expected that in SOC stocks in a given location equilibrate over time in response to factors such as the productivity and architecture of vegetation, climate, and the physical characteristics of the soil. Further examples come from reviews indicating that climatic factors modulate SOC responses to afforestation, and that the capacity for SOC accumulation during afforestation is positively related to soil clay content (Guo and Gifford, 2002; Laganiere et al., 2010). In light of this diversity of drivers, and the rarely reported result in the review literature that most of the variability in SOC change during afforestation is unattributed, a quantitative review of afforestation studies directly relevant to the United States is necessary for accurate C accounting. To close this geographic knowledge gap and produce a set of products for land managers and policymakers concerned with C accounting, we compiled relevant information from academic and agency sources and then applied synthesis methods (meta-analysis and a community soil C database) to the question of SOC changes following afforestation. We address four primary questions in our analyses: (i) What factors drive variation in the effects of afforestation on SOC? (ii) What temporal patterns underlie SOC responses to afforestation? (iii) How are afforestation effects on SOC distributed throughout the soil profile? (iv) Do point-based, national-scale data indicate that afforestation has increased SOC in formerly agricultural soils?

METHODS

Meta-Analysis: Literature Searching and Inclusion Criteria

The meta-analysis portion of this synthesis followed the methods of Nave et al. (2010). We searched the peer-reviewed and gray literature via the online databases ISI Web of Science, BIOSIS, Agricola, and CAB Direct with keywords such as forest management, afforestation, agroforest, plantation, and soil carbon. We also checked references of papers on afforestation and soil change. By inspecting >7500 references returned by literature searches and reference checking, we found 39 publications that met our inclusion criteria of reporting control (nonafforested) and treatment (afforested) mineral soil C values, and being conducted in the United States (or adjacent Canadian provinces, to increase data availability). Acceptable control–treatment comparisons were (i) time series measurements (pre- vs. post-afforestation), (ii) paired plot designs in which some plots were and others were not afforested, and (iii) chronosequences. In the case of most chronosequences, the control plot was a year-zero plot with no afforestation in progress. However, to maximize data availability for this analysis, we included several publications in which the "control" plot of the chronosequence had been undergoing afforestation for 1 to 10 yr. Calculating soil C response ratios relative to a non-zero baseline may underestimate the overall effects of afforestation, but since a primary goal of this meta-analysis was to assess changes in soil C over time following afforestation, we corrected for non-zero controls by expressing the age of the treatment (afforested) plots relative to the youngest plot. For example, for one paper with chronosequence plot ages of 1, 3, 7, and 14 yr since agricultural abandonment (Markewitz et al., 2002), we used the 1-yr plot as the control condition and coded the others as treatment plots with 2, 6, and 13 yr elapsed since afforestation began. Thus, while the overall effect of afforestation on soil C change may be underestimated for this example, we assume that the temporal pattern of that change over 13 to 14 yr is robust whether the initial control plot had been under afforestation for 0 or 1 yr. Note that for tests not explicitly applied to temporal questions, afforestation effect sizes were derived from studies spanning a wide temporal scale, from short-term (several years) to long-term (decades or even >100 yr).

To the degree possible, we used published estimates of soil C pool size (C storage; SOC) as the response variable for this analysis. When papers reported only soil C concentrations and bulk densities, we calculated the SOC stock from these terms.

For a small number of papers that reported soil %C but no bulk density, we used the gap-filling approach of Post and Kwon (2000) to estimate soil bulk density and subsequently calculated the SOC stock. Finally, for the small number of papers that reported soil organic matter rather than SOC, we assumed that 50% of the soil organic matter was C and adjusted the reported values accordingly.

In an effort to identify sources of variation in the effects of afforestation on SOC, we extracted metadata (predictor variables) from each publication, including temporal and climatic data, soil properties, and treatment and analytical methods. One important distinction in the soil properties category was the soil layer sampled. As we did not include data from O horizons in this analysis, we extracted data for every mineral soil layer reported in each publication, and coded the data so that we could test for differences between layers we coded in the database as surface, middle, and deep mineral soil. Soil layers were coded according to the midpoints of their sampling depths; surface mineral soils had midpoints $\leq$10 cm, middle soil layers had sampling midpoints of 11- to 20-cm depth, and deep soil layers had midpoints >20 cm. Regarding our classification of previous land use, we categorized studies if metadata were descriptive enough to ascertain which land use occurred before afforestation. Land use categories were (i) cultivated agricultural lands, (ii) agricultural lands actively used for livestock forage production (whether grazed pasture or mowed hayland), (iii) agricultural lands whose specific history was unknown, (iv) industrial substrates (slag, mine spoils, overburden, and barrens), and (v) wildlands (wild grasslands without intensive grazing or haying). The complete list of factors by which we categorized the response ratios in the database appears in Table 1.

Meta-Analysis: Statistical Approach

Meta-analysis quantifies 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:

$$\ln(R) = \ln\left(\overline{X}^{\mathrm{T}} / \overline{X}^{\mathrm{C}}\right) \qquad [1]$$

where $\overline{X}^{\mathrm{T}}$ is the mean SOC value of treatment (afforested) observations and $\overline{X}^{\mathrm{C}}$ is the mean SOC value of control observations for a given set of experimental conditions. The number of response ratios (k) in a paper depends on how many sets of experimental conditions are imposed. For example, one publication with SOC data from a control plot and from plantations of two different ages would yield $k = 2$ response ratios, or "studies." Because it has no units, the effect size R can be used to compare experiments reporting data in different units (Hedges et al., 1999). After back transformation [$e^{\ln(R)}$], R can be conceptualized as the proportional or percentage change in SOC relative to its control value. When error terms and sample sizes are reported for each $\overline{X}^{\mathrm{T}}$ and $\overline{X}^{\mathrm{C}}$, a parametric, weighted meta-analysis is possible, but many publications did not report these data. Therefore, to include as many as possible, we used unweighted meta-analysis, in which all studies in the data set are assigned an equal variance. In an unweighted meta-analysis, distributional statistics (mean effect sizes and confidence intervals) are generated by bootstrapping, which estimates distributional statistics by iteratively permuting and resampling the data set. Since it makes no parametric assumptions and generates distributional statistics from the available data, bootstrapping typically produces wider, more conservative confidence intervals (Adams et al., 1997). We performed meta-analyses using MetaWin (Sinauer Associates, Sunderland, MA USA), with 999 iterations.

Meta-analysis is useful for identifying factors that drive variation in SOC responses to afforestation. Similar to ANOVA, meta-analysis partitions the total variance (Q_t, the total heterogeneity) of a distribution of observations into its within- and between-group components (Q_w and Q_b, respectively) according to groups defined by any categorical factor (Hedges and Olkin, 1985). A categorical factor that defines groups of response ratios with large Q_b is a better predictor of variation than a categorical factor with low Q_b, and accordingly has a lower P value. If sample sizes and data structure permit, Q_b assessments can be conducted hierarchically by identifying the best predictor of variation in the entire dataset, splitting the dataset into the groups defined by that predictor, and then repeating the process within each group to elucidate underlying sources of variation (Nave et al., 2010). In the present study, we used Q_b and P statistics to iden-

Table 1. Predictor variables tested using meta-analysis.

Factor	Levels
Woody establishment type	natural; planted
Previous land use	agriculture- cultivated, ag- forage, ag- unknown, industrial, wildland
Forest type	conifer; hardwood; mixed
Soil layer	surface; middle; deep
Soil texture†	coarse; fine
Analytical method	dry combustion; loss on ignition; wet oxidation
Soil taxonomic order	Alfisol; Andisol; Aridisol; Entisol; Inceptisol; Mollisol; Spodosol; Ultisol
Region‡	Hawai'i; Northeast; Northern Lakes; Northern Prairie; Pacific Northwest; Rocky Mountain North; Rocky Mountain South; South Central, Southeast
Time category	<5, 5–14, 15–24, 25–34, 35–44, 45–54, 55–64, 65–74, 75–84, 85–94, 95–104, 105–114, 115–124, 125–135 yr
Time	continuous (range: 1–131 yr)
Mean annual temperature	continuous (range: 2.7–22.4°)
Mean annual precipitation	continuous (range: 219–4600 mm)
Control soil C pool size§	continuous (range: 0.3–229 Mg C ha^{-1})
Soil sample depth midpoint	continuous (range: 1–200 cm)

† Coarse- mostly sand; Fine- mostly silt and/or clay.
‡ From Smith et al. (2006).
§ Eq. [1], $\overline{X}^{\mathrm{C}}$ across all studies.

tify the best predictor of variation in the overall meta-analysis (previous land use), then conducted further meta-analyses on each significantly different land use category. Because the three previous agricultural land uses (cultivated, forage, unknown agricultural use) had the same overall response to afforestation (no net change in SOC), they were grouped and analyzed together as a single, well-replicated previous land use category, permitting full Q_b analysis without confounded data structure. However, to avoid outlier bias, it was necessary to remove 12 response ratios from this category (>2σ criterion; <6% of observations) before continuing into hierarchical Q_b analysis. Hierarchical Q_b analysis was not performed for industrial or wildland previous land uses due to confounded data structure.

In addition to identifying categorical variables that influenced soil C responses to afforestation, we tested several continuously varying factors (Table 1) as predictors of variation using continuous meta-analyses. Continuous meta-analysis is similar to the variance-partitioning process of Q_b analysis, in that the heterogeneity among k observations is partitioned into that which is explained by a linear model (Q_m) and that which constitutes the residual error variance (Q_e). In this way, continuous meta-analysis is the same as the ANOVA F-test for significance of linear regression models (Hedges and Olkin, 1985). Because MetaWin calculates its slope and intercept terms for continuous meta-analysis using the same matrices as simple linear regression (Rosenberg et al., 2000) but does not have the capability to add confidence or prediction bands, we used linear regression in SigmaPlot (SYSTAT Software, San Jose, CA) to obtain confidence intervals for point estimates that were calculated from continuous meta-analytic models. In all tests, including overall, Q_b, and continuous meta-analyses, we accepted results with $P < .05$ as statistically significant, and effect sizes were considered significant for groups with 95% confidence intervals that did not overlap 0% change in SOC.

Our data synthesis generated 282 SOC response ratios from 39 papers published between 1957 and 2010. The full dataset is available on the National Soil Carbon Network website (http://www.soilcarb.net). Publications that were used as data sources for this meta-analysis are identified in Appendix A.

Meta-Analysis of Soil δ^{13}C

To resolve the depth distribution of SOC change following afforestation, we conducted a supplementary meta-analysis using data from afforestations on lands previously dominated by C4 vegetation. Because the C4 photosynthetic pathway produces fixed-C ranging from -13 to -11 ‰ δ^{13}C, soils under C4 vegetation tend to have similarly enriched δ^{13}C, which becomes more depleted when trees are established and begin adding C3 detritus with δ^{13}C of −30 to −24 ‰ to the soil (Boutton et al., 1998). The exact proportions of C3 vs. C4-derived SOC in a soil are calculated using site-specific δ^{13}C values for C3 vs. C4 soils or detritus inputs (i.e., end-members) and a mass balance equation which generally takes the form:

$$pSOC_3 = (d - \delta_0)/(\delta_c - \delta_0) \qquad [2]$$

where, for any soil sample, $pSOC_3$ is the proportion of SOC derived from C3 vegetation, d is the d^{13}C of the soil sample, d_0 is the d^{13}C of a soil under C4 vegetation, and d_c is the d^{13}C of the C3 (forest) detritus inputs. The publications we gathered for this portion of the meta-analysis used structurally different but conceptually identical versions of this equation, all of which are based on the same assumptions and share a common method of estimating, by difference, the proportion of SOC derived from either type of vegetation. For greater detail on these mixing-model equations, including assumptions and input values, refer to Balesdent et al. (1988), Boutton et al. (1998), Vitorello et al. (1989), or any of the references in Appendix B. To conduct this portion of the meta-analysis, using the publications in Appendix B, we chose $pSOC_3$ as the response parameter of interest and extracted this value from the control soil and from the afforested soil in each paper. Therefore, the response ratio in this part of the analysis (R_{SOC3}) corresponds to the net change in $pSOC_3$ due to afforestation. In all other methodological regards, including metadata and study categorization, this portion of the meta-analysis follows the procedures outlined in the above sections Meta-analysis: Literature Searching and Inclusion Criteria and Meta-analysis: Statistical Approach.

Geospatial Analysis: Assumptions and Initial Data Filtering

To interpret and assess the accuracy of our meta-analysis results, we conducted hypothesis testing using the spatially explicit soil C database of the National Soil Carbon Network (NSCN), which integrates soils information with land cover data from the National Land Cover Database 2001 (Multi-Resolution Land Characteristics Consortium, 2011). We hypothesized that afforestation of cultivated agricultural lands would significantly increase C storage in the surface mineral horizons of the soil profile, and we tested this hypothesis by comparing Ap horizons from recently forested vs. cultivated soils. Ap horizons are plowed mineral surface soil layers that reflect past homogenization and mixing of surface organic and upper mineral soil layers. Because they tend to originate from mechanical cultivation, Ap horizons usually have a fairly uniform depth, and may remain conspicuous for decades or even centuries after cultivation has ended (Compton and Boone, 2000). Therefore, when an Ap horizon is found in a forest setting, we assumed for this analysis that the forest was established on land that was formerly cultivated. Comparing SOC in these forested vs. cultivated Ap horizons is thus a validation of our meta-analysis results that constrain afforestation effects on former agricultural soils. To ensure comparability across Ap horizons, we selected from the NSCN database only Ap horizons from the United States that were at the surface layer in their profile (i.e., layer top = 0 cm) and did not extend any deeper than 50 cm (layer bottom ≤50 cm). This pair of criteria assured that the selected Ap horizons originated from soil profiles without O horizons (which were not considered in

Table 2. Linear models derived from the NSCN database for gap-filling Ap horizons that were missing either %OC or BD_{samp}. Input variables were chosen using best subsets regression with adjusted r^2 and C-p statistics as criteria.

Predicted variable (Y)	Input variables (X)	Equation	n	r^2	P
%OC	X_1 = %$CaCO_3$ X_2 = %C_{tot}	$Y = -0.00911 - (0.111X_1) + (1.020X_2)$	184	0.88	<0.001
%OC	X_1 = %C_{tot}	$Y = 0.132 + (0.930X_1)$	493	0.94	<0.001
BD_{samp}	$X_1 = BD_{other}$ X_2 = %silt X_3 = %clay X_4 = %c.frag	$Y = 0.137 + (.914X_1) - (.000791X_2) + (0.0069X_3) - (0.000706X_4)$	3742	0.87	<0.001
BD_{samp}	$X_1 = BD_{whole}$ X_2 = %silt X_3 = %clay X_4 = %c.frag	$Y = 0.167 + (.898X_1) - (.000871X_2) + (0.00662X_3) - (0.00824X_4)$	3900	0.81	<0.001

this paper) and did not come from buried horizons or other deep soil layers. Furthermore, we did not include soils from Alaska in this analysis.

Geospatial Analysis: Gap-Filling and Criteria for Landcover Analysis

The two key variables necessary to compute SOC stocks in the geospatial analysis (soil C concentration and bulk density) were not always available for each Ap horizon, leading to gap-filling exercises to estimate them. The final equations for the gap-filling exercises described below are presented in Table 2. Using the 12,375 Ap horizons from the NSCN Database that met the criteria in section 2.4, we derived regression functions to gap-fill % organic C (%OC) and root-free fine earth bulk density (BD_{samp}) values for each Ap that was missing one of these measurements. Ap horizons missing both of these variables were excluded from the analysis. We chose %OC instead of total C concentration (%C_{tot}) because the former was more commonly reported, and more accurate for assessing afforestation effects on SOC. For all Ap horizons with measures of %C_{tot} and inorganic C concentration, we used linear regression to model %OC as a function of these two predictors. The organic C concentrations of Ap horizons lacking inorganic C concentration data were predicted as a simple linear function of %C_{tot}. For bulk densities, we chose BD_{samp} (root-free, <2 mm) rather than BD_{whole} or BD_{other} (see NSCN database for full definitions), because the latter two metrics are based on subjective estimation and variable methods, respectively. When BD_{samp} was not available, we used best subsets regression to predict BD_{samp} from a combination of BD_{whole} or BD_{other} and the soil's particle-size distribution (% sand, silt, clay, and coarse fragments).

After applying the gap-filling equations (Table 2) to the Ap horizons with missing data, we filtered all Ap horizons according to two criteria before assessing land cover effects: (i) each Ap horizon had to originate from one of the Northern Prairie States (ND, SD, NE, KS, IA, MO, IL, IN [Smith et al., 2006]), and (ii) each Ap horizon had to have been sampled between 1995 and 2009. The first criterion was established to mitigate potential sources of inter-regional variation, such as climate, historic trends of land use change or demographic shifts, while the second criterion ensured that all Ap horizons used in the land cover analysis were sampled within 10 yr of the National Land Cover Database classifications (Multi-Resolution Land Characteristics Consortium, 2011) contained in the NSCN database.

Geospatial Analysis: Statistical Methods

The final Northern Prairie States Ap horizon dataset developed in the previous section Geospatial Analysis: Gap-Filling and Criteria for Landcover Analysis included 386 observations from currently cultivated soils and 23 from afforested soils. We used %OC, BD_{samp}, and a horizon thickness of 5 cm to calculate the SOC pool size of each of these Ap horizons to a standardized, surficial depth. This approach assumes that each Ap horizon had homogenous properties throughout its vertical extent, which we considered to be a reasonable assumption given that these horizons tend to originate from mechanical mixing. Soil organic carbon pool sizes (as well as %OC and BD_{samp}) were analyzed by

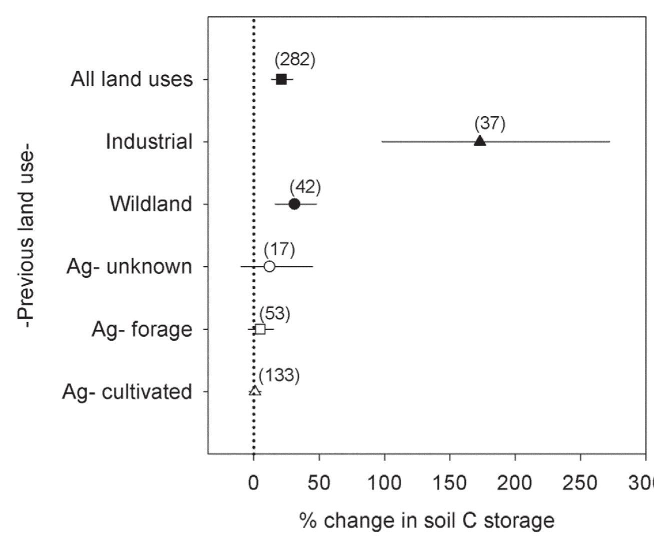

Fig. 1. Effects of afforestation on soil organic carbon (SOC) storage overall and for each previous land use, as calculated using meta-analysis. Points are means with bootstrapped 95% confidence intervals (CIs) and number of response ratios. Groups with CIs overlapping the dotted reference line show no overall significant change in SOC due to afforestation.

Table 3. Between-group (Qb) and total heterogeneity (Qt), sample sizes, and *P* values for the predictor variables tested in the overall meta-analysis of SOC responses to afforestation.

Factors	Qb	Qt	*k*	*P*
Categorical factors				
Previous land use	30.3	89.9	265	0.001
Establishment type	12.4	93.8	276	0.001
Time category	10.8	93.2	265	0.006
Region	5.3	94.3	276	0.053
Forest type	4.5	94.3	279	0.002
Soil texture	3.9	91.3	257	0.001
Soil layer	2.0	94.4	282	0.050
Analytical method	1.9	52.7	266	0.034
Soil taxon. order	1.1	28.5	223	0.282
Continuous factors				
Initial pool size	6.8	94.4	282	0.001
Time	6.0	93.9	265	1.000
Sampling midpoint	1.0	94.4	282	0.028
MAT†	0.4	93.7	272	0.157
MAP	0.2	93.7	272	0.233

† MAT, mean annual temperature; MAP, mean annual precipitation.

t test to determine whether and by what amount these properties changed due to afforestation on formerly cultivated soils.

RESULTS

Meta-Analysis: Overall Results

Our meta-analysis of the literature showed that afforestation significantly increased SOC, although the overall increase (averaging 21% across all studies) was driven by large SOC increases associated with specific previous land uses (Fig. 1). Accordingly, previous land use was the most significant source of variation among studies (Table 3), with afforestation increasing SOC on industrial substrates (+173%) and wildlands (+31%).

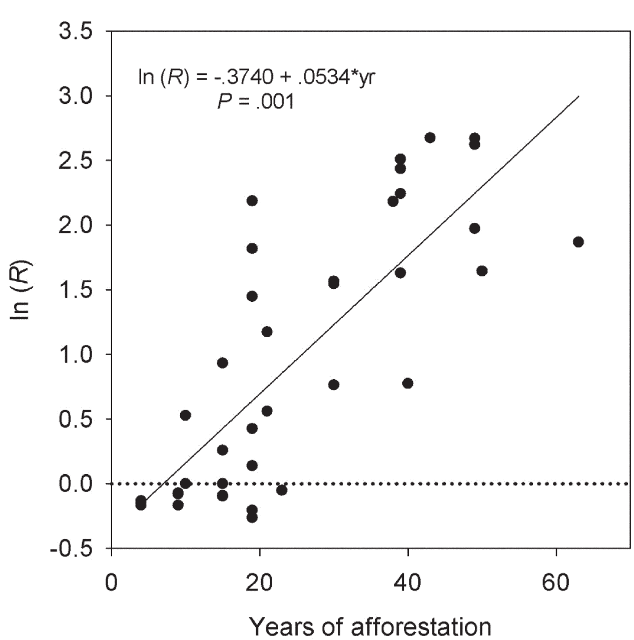

Fig. 2. Net change in C storage of industrial substrates as a function of time. Points plotted are individual, ln-transformed response ratios. The dotted reference line indicates no net change in soil carbon storage due to afforestation. Best-fit line statistics correspond to continuous meta-analysis results.

Table 4. Table showing soil organic carbon (SOC) changes over time during afforestation of industrial substrates.†

Time interval	Mean change	95% confidence interval
yr	%	
<5	−21.4	(−47.1, 26.4)
5–15	17.4	(−14.0, 60.4)
15–25	100.2	(59.3, 152.0)
25–35	241.4	(173.4, 327.4)
35–45	482.4	(333.5, 685.5)
45–55	893.4	(564.0, 1393.9)
55–65	1594.5	(895.2, 2802.6)

† Mean changes (relative to nonafforested baseline) and 95% confidence intervals are calculated for the midpoint of each time interval from continuous meta-analysis linear model outputs.

Lands previously under the three agricultural use categories (cultivation, forage, unknown) showed no generalized, significant overall change in SOC and were thus bulked into a single group for further tests aimed at partitioning underlying sources of variation. Partitioning sources of variation within these agricultural studies, as well as the studies within industrial and wildland previous land uses provided further insight into the generalized effects of afforestation on each of the previous land use categories.

Meta-Analysis: Variation within Land Uses

Afforestation on barren industrial lands caused extremely large, statistically significant increases in SOC. However, aside from the highly significant effect of time (P = .001 [Fig. 2]), variation in SOC change during industrial land afforestations was not attributable to any predictors because of a limited sample size (k = 37) and confounded data structure. Inspecting the 95% confidence intervals for the amount of SOC change across the discrete time periods in Table 4, it is apparent that approximately 15 yr of afforestation are required to significantly increase SOC on industrial substrates, with very large, continued SOC increases continuing through subsequent decades (Table 4). For wildland afforestations, which mostly corresponded to woody encroachment in native grasslands, categorical sources of variation were not testable because of confounded data structure. However, continuous meta-analysis indicated that there was a negative relationship between mean annual precipitation (MAP) and SOC change in the deeper portions of the soil profile (Fig. 3a). On the contrary, afforestation-induced SOC changes in surface soils did not vary with MAP but instead increased significantly with the duration of woody encroachment (Fig. 3b). On former agricultural lands, time was the only significant predictor of afforestation effects on SOC (Table 5). The large scatter of data points around the significant positive slope of the time relationship (Fig. 4) indicates major, additional sources of variation that could not be quantified in this meta-analysis. Across all agricultural afforestations, confidence intervals for discrete time periods suggest at least 35 yr are required to significantly increase SOC, with modest decadal increases thereafter culminating in a ~15% net increase in SOC storage by the end of the first century (Table 6).

Meta-Analysis of ^{13}C Data

Synthesis of ^{13}C isotopic data revealed a consistent pattern in the depth distribution of SOC changes following afforestation. All of the papers that used ^{13}C to quantify variation in tree-derived SOC with depth showed the same pattern, with four of six studies showing significant, negative linear relationships with sampling depth (Fig. 5a). Continuous meta-analysis using the entire set of R_{SOC3} values indicated that sampling depth was also a highly significant predictor of variation across studies ($P < .001$ [Fig. 5b]). Across the range of sampled depths, the continuous meta-analysis linear fit explained 24% of the variation (Q_m/Q_t) in R_{SOC3}. A nonlinear regression model (exponential decay) explained more variation in R_{SOC3} across depths (33%), although qualitatively both best-fit models yielded the same result: afforestation causes large net increases in pSOC$_3$ in surface soils, while deeper layers are less responsive.

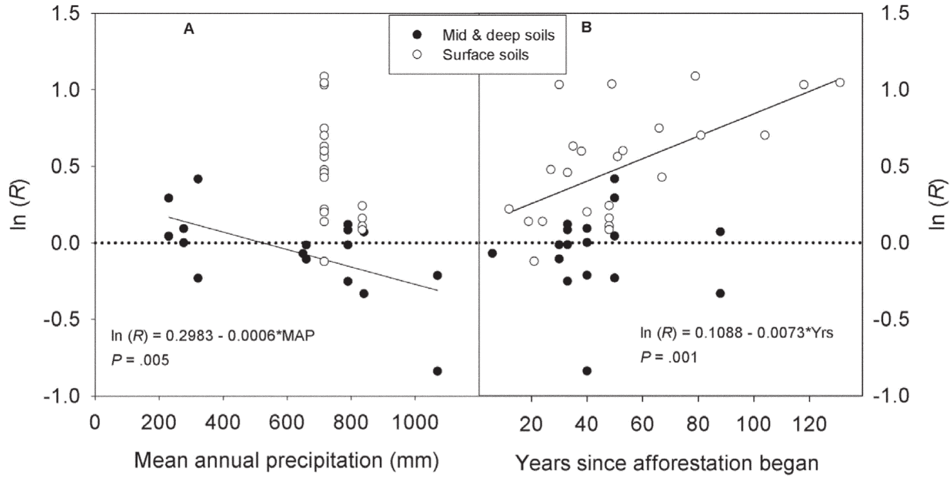

Fig. 3. Net change in wildland soil organic carbon (SOC) as a function of (a) precipitation or (b) time. In both panels, the points plotted are individual, ln-transformed response ratios. The dotted reference line indicates no net change in SOC due to afforestation. Best-fit line statistics correspond to continuous meta-analysis results. The best-fit line in Fig. 3a is for mid and deep soils only, while the best-fit line in Fig. 3b corresponds to surface soils only.

Geospatial Analysis

In support of meta-analysis results indicating SOC increases over time on former agricultural lands (Fig. 4 and Table 6), geospatial analysis using the NSCN database indicated that afforestation has caused measureable changes on surface soil properties and SOC stocks in the Northern Prairie states. Soil C concentration was significantly higher in afforested Ap horizons than Ap horizons from cultivated soils, with the difference in means (2.4 vs. 1.7%) corresponding to a relative increase of 38% (Fig. 6, left). Ap horizon bulk density significantly declined during afforestation, with the two land uses differing by 0.06 g cm^{-3}, or 4% (Fig. 6, right). These shifts in Ap horizon properties translated into an average increase of 4.3 Mg C ha^{-1} in the top 5 cm of Ap horizons following transition from cultivation to forest cover (a 32% increase [Fig. 7]).

DISCUSSION

Our synthesis indicates that afforestation has significantly increased SOC sequestration throughout the United States, with substantial potential for continuing this trend. This record of change and evidence for continued sequestration potential comes from (i) large meta-analytic effect sizes for industrial and wildland afforestations; (ii) temporally resolved SOC increases during afforestation of former industrial and agricultural lands; (iii) consistent ^{13}C patterns indicating a highly responsive surface soil zone where incorporation of forest-derived detritus into the native SOC pool is nearly always large, and often rapid; and (iv) significantly greater SOC in afforested than cultivated Ap horizons distributed across the agricultural midsection of the United States. However, while these results show that afforestation has a positive impact on SOC sequestration, knowledge gaps identified in this synthesis are evidence that far more work is needed for comprehensive SOC accounting of this type of land use change at all spatial scales.

Afforestation on lands made barren by mineral mining or processing offers substantial opportunities for SOC sequestration. Over the course of the half century of experimental data reported in the literature, forest establishment on these industrial soils increased their SOC stocks by 15-fold. Where such lands occur, they hold great potential for sequestering SOC and providing attendant soil ecosystem services. However, it is necessary to contextualize this potential in light of our definition for the "control" condition for meta-analysis of industrial afforestations, which we established to maximize data availability and consistency across publications and to ensure the most straightforward interpretation of results: we treated the barren postindustrial

Table 5. Between-group (Qb) and total heterogeneity (Qt), sample sizes, and *P* values for the predictor variables tested among afforestations on former agricultural land.

Factors	Qb	Qt	k	P
Categorical Factors				
Time category	0.6	8.4	174	0.148
Region	0.5	8.5	185	0.140
Analytical method	0.3	8.6	191	0.114
Soil taxon. order	0.1	7.0	152	0.910
Previous land use	<0.1	7.7	177	0.348
Establishment type	<0.1	8.3	185	0.402
Soil texture	<0.1	8.5	185	0.818
Forest type	<0.1	8.5	188	0.555
Soil layer	<0.1	8.6	191	0.832
Continuous factors				
Time	0.2	8.4	175	0.016
MAT†	<0.1	8.3	181	0.703
MAP	<0.1	8.3	181	0.661
Initial pool size	<0.1	8.6	191	0.249
Sampling midpoint	<0.1	8.6	191	0.467

† MAT, mean annual temperature; MAP, mean annual precipitation.

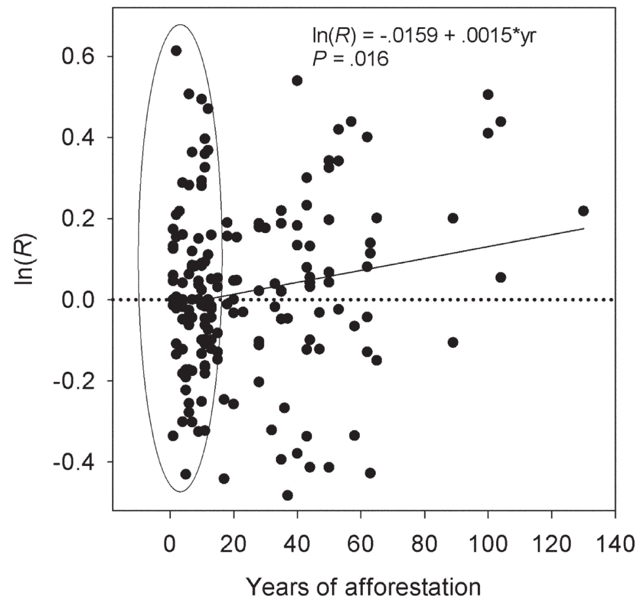

Fig. 4. Net change in carbon storage of former agricultural soils as a function of time. Points plotted are individual, ln-transformed response ratios. Note the large amount of variability among response ratios <15 yr old, denoted by the ellipse surrounding these points on the figure.

substrates created by the removal of native vegetation and soil as the control or starting points for industrial afforestations. Because deconstructing a native ecosystem in this manner releases C stored in soils and biomass (Amichev et al., 2008), SOC increases during afforestation on such lands do not represent net SOC gains but rather recoveries of lost C.

Our overall meta-analysis results suggest that woody vegetation encroachment into native grasslands of the United States (which we termed "wildland afforestation") generally causes large SOC increases in these ecosystems. However, divergent controls on the SOC responses of wildland soils at different depths and a lack of data for exploring the broader applicability of these controls preclude strong inferences for this previous land use category. Our findings suggest that precipitation affects SOC change in deep soils during woody plant invasion, with drier sites (MAP < 500 mm yr^{-1}) increasing, and wetter sites decreasing SOC storage. This finding supports and is partly based on data synthesized by Jackson et al. (2002), who observed the same relationship and proposed that the dependency of SOC shifts on precipitation during land use change were related to changes in the rooting depth of dominant vegetation. This portion of our meta-analysis highlights that the SOC response of deep soils is in contrast with that of surface soils, where precipitation had no effect on SOC changes during woody encroachment. This inconsistency indicates that expanded data collection with a focus on SOC controls across depths is needed in such systems. Because this type of land use change has occurred on millions of hectares in the United States over the last 150 yr (Van Auken, 2000), the effects on SOC stocks may be quite large, and data collections that close this knowledge gap will be important for accurate SOC accounting at the national scale.

Table 6. Table showing soil carbon changes during afforestation of former agricultural lands.†

Time interval	Mean change	95% confidence interval
yr	%	
<5	−1.2	(−5.4, 3.2)
5–15	−0.1	(−3.9, 3.7)
15–25	1.4	(−2.0, 4.7)
25–35	3.0	(−0.4, 6.5)
35–45	4.5	(0.6, 8.6)
45–55	6.1	(1.1, 10.8)
55–65	7.7	(1.7, 14.1)
65–75	9.3	(1.9, 16.5)
75–85	11.0	(1.7, 20.1)
85–95	12.6	(2.2, 23.1)
95–105	14.4	(2.6, 26.2)
105–115	16.1	(2.9, 30.9)
115–125	17.8	(3.2, 34.5)

† Mean changes (relative to nonafforested baseline) and confidence intervals are presented for the midpoint of each time interval.

Temporal patterns of SOC increase indicate the potential for significant C sequestration over decadal timescales on former industrial or agricultural lands, but large uncertainties within the time categories we adopted for this meta-analysis belie major underlying sources of variation. On agricultural lands, the effect size within each time category is much smaller than the 95% confidence interval (1/2 to 1/5 the magnitude), indicating that the average rate of accumulation across studies is small relative to the variation among the studies. Conversely, industrial lands show fast rates of SOC increase and have effect sizes similar in magnitude to the variation across studies. The net effect of this difference between land use types is that while both do show quantitative increases in SOC over time, afforestation causes significant SOC increases much sooner on industrial than agricultural lands (15–25 vs. 35–45 yr). However, even for the large distribution of agricultural response ratios, our meta-analysis could not identify predictive factors that drive variation in SOC change over time, indicating that site-specific data collection is more effective than literature synthesis for accurate SOC accounting of agricultural afforestations. In light of this result, it is important to consider the distribution of stand ages among agricultural afforestations and how this distribution affects the overall results of the meta-analysis described in the section *Meta-analysis: Overall Results*. Specifically, because >35 yr are required for significant, detectable increases in SOC during agricultural afforestation, but a large share of the response ratios tested in the meta-analysis had not yet reached this threshold, the effect of afforestation on SOC in agricultural soils was significant as a temporal trend rather than a categorical effect.

We used a new approach to quantify the depth distribution of SOC changes during afforestation: meta-analysis of ^{13}C mixing model data. This combination of research approaches produced results largely confirmatory of other methods. For instance, quantitative and qualitative literature reviews of basic SOC stock data have showed that superficial layers of the soil profile respond to land use changes more rapidly and to a greater degree than deeper soils (Guo and Gifford, 2002; Jandl et al., 2007). Our findings based on meta-analysis of isotope data thus add to prior work in affirming the widely held methodological assumption that management effects on SOC are most detectable near the top of the soil profile. At the same time, the distribution of R_{SOC3} values assembled here indicates that SOC stocks in deep soils are not static—significant isotopic shifts regularly occur well below depths typically sampled by designs that emphasize change detection through shallow sampling. Although not explicitly tested in this analysis, C storage in organic horizons may be expected to be the most responsive of any portion of the soil profile, as afforestation will often lead to the development of litter, woody debris, and other surface organic matter pools that did not exist before the establishment of forest vegetation. In that regard, results of the SOC_3 meta-analysis component of this work (as well as the other components) would likely show an even greater potential for increased SOC sequestration (in relative terms) than the mineral soils assessed here. Setting aside sampling considerations, the R_{SOC3} values we tested in this meta-analysis were nearly all positive and most were rather large. Because $pSOC_3$ is the net balance of two opposing gross fluxes (new forest detritus inputs and "native" SOC_4 losses), R_{SOC3} indicates the *relative* change in this *net* balance with afforestation—and the two gross fluxes that drive the net change in $pSOC_3$ can simultaneously affect the absolute size of the total SOC pool. For example, $pSOC_3$ could increase rapidly because of large new inputs and equally large losses of existing stocks, and these balanced fluxes would result in no net change in total SOC. Alternately, $pSOC_3$ could be very small and positive as new SOC is added to the soil, but a large background of native SOC remains stable, resulting in a small net accumulation of SOC. Ultimately, the $pSOC_3$ response ratios are a metric of how pervasive and rapid the SOC changes are in the studied soils.

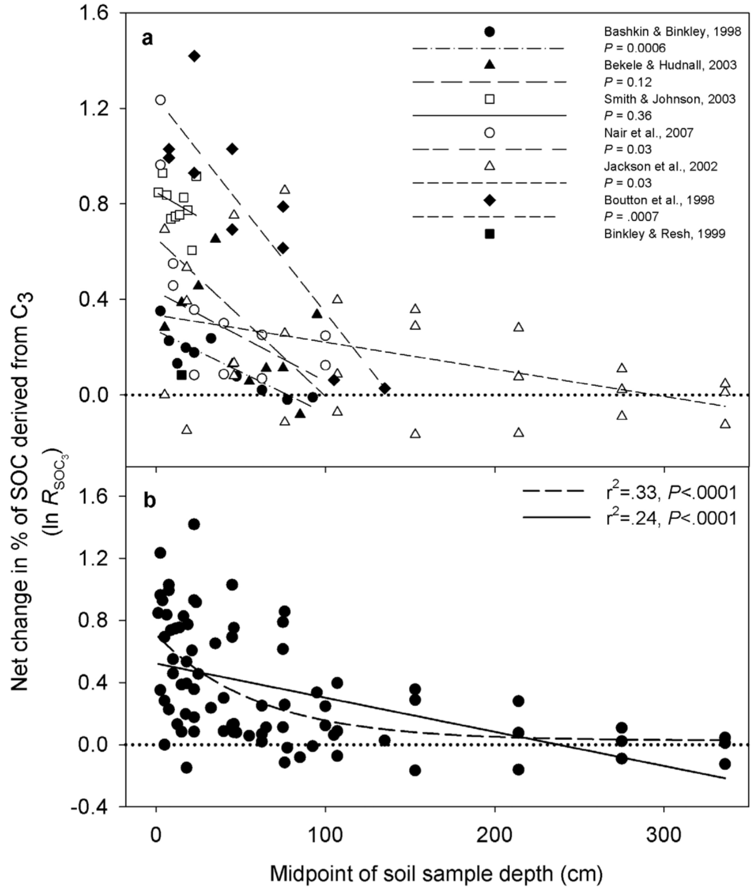

Fig. 5. Change in the fraction of SOC derived from forest (C3) inputs as a function of soil depth during afforestation of lands formerly under C4 vegetation. Points plotted are individual, ln-transformed response ratios. (a) Response ratios and best-fit statistics for the individual papers included in this part of the analysis (see Appendix B). (b) Distribution of response ratios across all papers, with best-fit statistics for continuous meta-analytic and nonlinear regression models.

If comprehensive SOC pool size data had been published for more of the ^{13}C depth profiles we synthesized in this analysis, it would have been possible to calculate gross input and output fluxes for the SOC_3 and SOC_4 pools and assess the SOC budgets of these soils. However, even without such an assessment, synthesis of ^{13}C depth profiles furthers our broader understanding of management and C dynamics in soils by indicating a surface soil zone where C cycling processes are consistently most affected by afforestation. This affirms the potential of afforesting soils to play a significant role in C sequestration, especially if the type, production rate, and stabilization mechanisms acting on C inputs to highly responsive surface soil can be simultaneously managed—and findings from both primary studies and quantitative reviews inform how these factors could be manipulated to promote SOC accumulation during afforestation. For example, research consistently indicates that coniferous trees decrease SOC in mineral soils during afforestation while broad-leaved hardwoods have neutral or positive effects (Guo and Gifford, 2002; Laganiere et al., 2010), perhaps through relationships between vegetation composition and structure and the amount, chemical and physical properties, and location of detritus inputs to soil (Lorenz and Lal, 2005; Sarkhot et al., 2008; Shan et al., 2001). However, even if coniferous trees release native SOC from deeper portions of the profile, these species tend to drive surface organic layer accumulation, a process which can dramatically affect the C balance of an afforestating ecosystem (Laganiere et al., 2010). In the context of the responsive surface soil zone identified by our meta-analysis of SOC_3 data, the generalized difference between coniferous and broadleaved trees could be used to target SOC accumulation in particular portions of the soil profile, depending on the goals of the afforestation project. Laganiere et al. (2010) also found in their global meta-analysis that soils with higher clay content had higher capacity for SOC increase, congruent with the important role of organo-mineral interactions in forming stabilized SOC from plant- and microbe-derived C inputs (Kleber et al., 2010; Schmidt et al., 2011). Because interactions with microbial biomass can also promote the growth of stabilized SOC pools through aggregation and physical protection mechanisms (Godbold et al., 2006; Langley and Hungate, 2003; Rillig, 2004; Rillig et al., 2001), forest establishment on fine-textured soils or the use of mycorrhizal inoculation could be used to accelerate SOC accumulation during afforestation.

One of the principal justifications for the meta-analysis portion of this synthesis paper is that the global scope of existing affor-

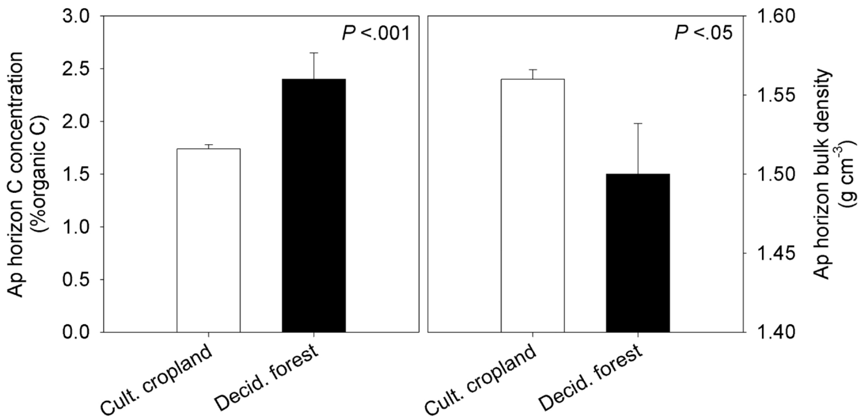

Fig. 6. Carbon concentrations (left panel) and bulk densities (right panel) of Ap horizons from cultivated vs. forested land cover types. Bars are means with errors expressed as SE.

estation–SOC meta-analyses makes their direct application to the United States uncertain. Qualitatively, our meta-analysis reaffirmed the findings of global reviews in that (i) previous land use was the major driver of SOC change and (ii) changes in SOC are greatest near the top of the soil profile. However, our meta-analysis did not confirm other important findings of global reviews, such as a difference between coniferous and broadleaved tree species or any covariance between SOC change and soil texture during afforestation. This could indicate that, within the geographic scope of the United States, such factors do not vary sufficiently to drive significant variation in SOC change but is more likely due to a limited availability of data from widely distributed sites. With 282 response ratios from 39 papers, the database we tested in the present meta-analysis was not insubstantial and indeed was still sufficient to constrain significant temporal trajectories of SOC change for several previous land uses. Nonetheless, it is clear from the abundant unexplained variability and site specificity in this analysis that more data are needed for tightly constrained estimates of SOC change during afforestation or balanced comparisons with other reviews.

Our geospatial analysis of SOC contents from forested vs. cultivated Ap horizons indicates that afforestation has increased SOC sequestration at locations throughout the Northern Prairie region of the United States. In once-plowed A horizons now under forest cover, higher %C and SOC likely indicate locations where new detritus inputs have augmented SOC stocks depleted during cultivation. Widespread conversion of agricultural land to forests is currently unlikely, but there is potential to introduce limited afforestation into active agricultural lands. Importantly, afforestation need not occur at the expense of crop production, because approaches like alley cropping, shelterbelt planting, and afforestation of buffer strips can incorporate trees into agricultural landscapes with no loss, or even gains in crop or livestock production (Bird, 1998; Garrett et al., 2004; Jose et al., 2000; Miller and Pallardy, 2001; Mize et al., 2005). At the same time, however, such limited-scale afforestation approaches are not likely to produce the same degree of ecosystem C sequestration as larger-scale projects, such as the wholesale establishment of plantations on large areas of degraded lands. Afforestation of depleted croplands for soil quality remediation requires a longer-term concept of crop rotation but could also be used to increase SOC in locations that have suffered extreme losses of soil productivity (Wilde, 1964; Richter et al., 1999). Regardless of how afforestation is incorporated into agricultural settings, our geospatial and meta-analysis results indicate that this management decision will typically increase SOC. These results are contextualized by the geographically broader meta-analysis of Guo and Gifford (2002), which revealed that the net SOC increase due to afforesting agricultural land approximates the net SOC loss observed when forests are converted to agriculture. In this sense, the benefit of afforestation on former U.S. agricultural lands from a soil C perspective appears to be the recovery of soil C stocks that have been lost since forest clearing began 1 to 2 centuries ago across much of the country (Birdsey et al., 2006).

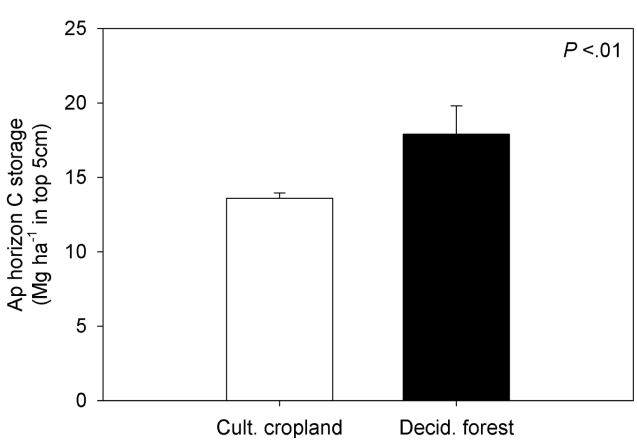

Fig. 7. Soil C stocks in the upper 5 cm of Ap horizons from cultivated vs. forested soils. Means and SEs plotted.

CONCLUSION

The results of our synthesis indicate that, in general, soils undergoing afforestation in the United States are increasing their SOC stocks, especially in surficial layers. However, this result must be considered in the context of several findings of our meta-analysis. First, categorically significant SOC increases were associated with afforestation on reclaimed industrial lands or unmanaged wildlands invaded by woody vegetation but not on former agricultural lands. Temporal patterns of SOC change during afforestation indicate that agricultural lands do increase SOC storage, but that several decades are typically required to reach significant, detectable levels (as is also the case with reclaimed industrial lands). Lastly, significant, unexplained variability in soil C responses to afforestation (especially on agricultural or unmanaged lands) indicates substantial site-specificity in the effects of afforestation on soil C storage. This argues strongly for project-specific SOC measurements whenever possible, both for C accounting of land use changes and for the sake of increasing data availability for future modeling and meta-analysis.

APPENDIX A.

Data sources used in the overall meta-analysis of afforestation impacts on SOC.

Reference	Dominant canopy genera	Locations
Akala and Lal, 2000	*Pinus, Acer*	OH (USA)
Arevalo et al., 2009	*Populus*	AB (CA)
Bambrick et al., 2010	*Picea, Populus*	ON, QC (CA)
Bashkin and Binkley, 1998	*Eucalyptus*	HI (USA)
Binkley and Resh, 1999	*Eucalyptus*	HI (USA)
Christenson and MacAller, 1985	*Pinus*	NC (USA)
Coleman et al., 2004	*Populus*	MN, WI, IA, ND (USA)
De Gryze et al., 2004	*Populus, Pinus*	MI (USA)
Dowell et al., 2009	*Populus*	MO (USA)
Grigal and Berguson, 1998	*Populus*	MN (USA)
Hamburg, 1984	*Acer, Picea*	NH (USA)
Hansen, 1993	*Populus*	MN, WI, IA, ND (USA)
Hooker and Compton, 2003	*Pinus*	RI (USA)
Hosner and Graney, 1970	*Pinus*	VA (USA)
Jackson et al., 2002	*Prosopis, Larrea*	TX, NM, CO (USA)
Leisman, 1957	*Populus, Prunus*	MN (USA)
Liao et al., 2006	*Prosopis*	TX (USA)
Markewitz et al., 2002	*Pinus*	GA (USA)
Martens et al., 2003	*Prunus, Robinia*	NE (USA)
McKinley and Blair, 2008	*Juniperus*	KS (USA)
Montes and Christenson, 1979	*Pinus, Liquidambar*	NC (USA)
Morris et al., 2007	*Acer, Quercus*	MI (USA)
Nair et al., 2007	*Pinus*	FL (USA)
Neff et al., 2009	*Pinus, Juniperus*	UT (USA)
Paul et al., 2003	*Acer, Pinus*	OH (USA), ON (CA)
Peichl and Arain, 2006	*Pinus*	ON (CA)
Pregitzer and Palik, 1997	*Pinus*	WI (USA)
Richter et al., 1999	*Pinus*	SC (USA)
Rolfe and Boggess, 1973	*Pinus*	IL (USA)
Sartori et al., 2007	*Populus*	OR (USA)
Sauer et al., 2007	*Juniperus, Pinus*	NE (USA)
Scharenbroch et al., 2010	*Quercus, Pinus*	WI (USA)
Schiffman and Johnson, 1989	*Pinus*	VA (USA)
Sharrow and Ismail, 2004	*Pseudotsuga*	OR (USA)
Sherman and Beckett	*Pinus*	ON (CA)
Smith et al., 1997	*Pinus, Betula*	CT (USA)
Springsteen et al., 2010	*Amelanchier, Sheperdia*	ND (USA)
Zou and Bashkin, 1998	*Eucalyptus*	HI (USA)

APPENDIX B.

Data sources used in the meta-analysis of soil ^{13}C data.

Reference	Previous land use	Locations
Bashkin and Binkley, 1998	Cultivated	HI (USA)
Bekele and Hudnall, 2003	Unmanaged	LA (USA)
Binkley and Resh, 1999	Cultivated	HI (USA)
Boutton et al., 1998	Unmanaged	TX (USA)
Jackson et al., 2002	Unmanaged	CO, NM, TX (USA)
Nair et al., 2007	Forage	FL (USA)
Smith and Johnson, 2003	Unmanaged	KS (USA)

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