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Carbon fluxes, storage and harvest removals through 60 years of stand development in red pine plantations and mixed hardwood stands in Northern Michigan, USA

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ABSTRACT

The storage and flow of carbon (C) into and out of forests can differ under the influence of dominant tree species because of species-based variation in C production, decomposition, retention, and harvest-based export. Following abandonment of agricultural activities in the first half of the 20th century, many landscapes of the Great Lakes region (USA) were planted to red pine (*Pinus resinosa*) or naturally regenerated to northern hardwood species including sugar maple (*Acer saccharum*), red oak (*Quercus rubra*) and red maple (*Acer rubrum*). We located eight pairs of adjacent, similarly aged (~60 yr) stands of planted red pine and naturally regenerated hardwood forests on previous agricultural fields. We found that the hardwood forests stored more C than pine stands (255 *vs.* 201 Mg C ha^{-1}), with both storing substantially more than an adjacent area maintained as pasture (107 Mg C ha^{-1}). The greater accumulation of C in the hardwood stands occurred mostly in living biomass. No significant differences for soil C (to 1 m depth) were found between forest types, despite significantly higher belowground inputs and aboveground litterfall in hardwood stands. Notably, both forest types had about 18% more soil C than the pasture, with O horizon C accounting for about one-third of the increase under trees. Forest type had no significant effect on estimated amount of exported C despite fairly large differences in projected end uses (solid wood products, land-fills, bioenergy). Using adjacent pasture as our baseline condition, we combined estimated on-site accumulation rates with estimates of exported C, and found that average total C sequestration rates were higher for hardwood (2.9 Mg C ha^{-1} yr^{-1}) than red pine plots (2.3 Mg C ha^{-1} yr^{-1}). The modeled potential contribution of exported C to these sequestration rate estimates did not differ between species, but the fate of modeled post-harvest off-site C may exert a large influence on sequestration rate estimates depending on actual displacement actions, including product longevity. These results show that tree species selection has the potential to impact C sequestration rates but effects vary by ecosystem component and could not be predicted from previous species effects studies.

1. Introduction

The storage of carbon (C) in soils (Jobbagy and Jackson, 2000) and forest biomass (Dixon et al., 1994) is highly variable, with a portion of local variation due to the diverse influences of dominant tree species on production, decomposition, and the suite of processes that stabilize C in forests (Binkley and Fisher, 2013; Laurent et al., 2014). This variation has led to the idea that tree species could be chosen with a goal of high C sequestration rates, but current knowledge about the mechanisms that might underlie C storage and sequestration rates in ecosystems is too limited for routine application (Lal, 2005; Ryan et al., 2010; Laurent et al., 2014). The effects of tree species on soils have been the topic of many reviews (e.g., Binkley and Giardina, 1998; Johnson and Curtis, 2001; Binkley and Menyailo, 2005; Laurent et al., 2014).

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Despite very large and widely appreciated differences in growth rates across tree species, these differences do not easily translate into an understanding of how species vary in their effects on ecosystem C storage, harvested removals, and sequestration rates. For example, Berger et al. (2002) found that monocultures of Norway spruce (*Picea abies*) had about 20% more soil C (to 50 cm depth) than mixed stands of Norway spruce and beech (*Fagus sylvatica*), and that differences varied with soil parent material. In contrast, Li et al. (2005) found no soil organic C (SOC) differences between tropical pine plantations and secondary hardwood forests on similar soils following similar changes in land-use.

Increasingly, the fate of harvested C is a focus of carbon studies, because changes to both on-site C storage and off-site C exports influence the global warming potential of a forestry activity (Harmon et al., 1990). Therefore, both need to be considered when quantifying land-use and land-cover change effects on C sequestration rates. For example, a mixed oak/beech forest stored more on-site C than short rotation coppice poplar stands, but because of potential off-site biomass energy substitution for fossil fuels, the poplar stands were overall more effective at reducing [CO_2] of the atmosphere (Deckmyn et al., 2004). In contrast, Harmon et al. (1990) found that more than two centuries of plantation based fossil fuels displacement would be required to offset carbon losses caused by harvesting old-growth forest of the northwestern USA. While many studies have examined species effects on mineral soil C content or O horizon mass, and much is known about forest productivity in temperate forests (e.g., Reich and Bolstad, 2001), few studies have compared tree species effects on ecosystem C cycling, harvested C, and long-term sequestration rates for industrial forest lands.

Comparisons of stands of different species at individual locations (common gardens) can identify the likely magnitude and timing of C storage effects, and allow underlying mechanisms to be identified (Laurent et al., 2014). Our objectives were to quantify the effects of forest type effects on C pools and to explore mechanisms that may drive differences. This study is a long-term, common garden experiment with paired, adjacent red pine and mixed northern hardwood stands all occurring on similar soils (Fig. 1). All stands were actively managed by the forest products industry, and both forest types are widespread in north central and north east USA. We measured all C pools in paired hardwood and pine stands – from the canopy to 1 m depth in soil. We measured aboveground net primary production (ANPP) and total belowground C flux (TBCF), the later typically a large proportion of gross primary production (GPP) in forests (Law et al., 1999; Litton et al., 2007). We also combined measurements of total ecosystem C storage with off-site estimates of C storage from harvested materials to develop forest-type specific C sequestration rates. Further, we examined soil nutrient, canopy leaf area and light capture based controls on production ecology (Laurent et al., 2014). In this experimental context, we used these 8 paired forests to test the hypothesis that hardwood stands would store and sequester more carbon than red pine stands. We reasoned that: (1) hardwood stands would have higher LAI, higher light interception values, higher nutrient availability and carbon quality, and so higher ANPP and biomass increment; and (2) TBCF and litterfall inputs would be higher in hardwood plots, leading to higher soil C.

2. Site description and methods

2.1. Study site

The research site is located near Atlantic Mine, MI (47° 06′–N, 88° 52′–W), and has been previously described (55 yr old red pine site in King et al., 2007). The climate is characterized by long cold winters and substantial snowfall. The growing season spans late-May to early-October. Mean annual temperature is 5 °C and mean annual precipitation is 860 mm, with roughly 42% of total precipitation falling during the growing season (National Climate Data Center). The site is on a Keweenaw–Kalkaska soil complex, with sandy soils that are moderately well drained to somewhat excessively drained. The study site had been previously used for grazing, but abandoned in 1925, as determined from aerial photographs of the area. Hardwood trees established soon after, and developed for about 25 years when portions of the landscape were planted with red pines (1950 planting date was verified with tree cores). The oldest hardwood tree encountered in our biomass sampling was 81 years, while 83% of hardwood stems were younger than 60 years (average age 43 years). The longer period of development of the hardwood stands may have had some influence on the total accumulation of ecosystem C, though we expect that natural

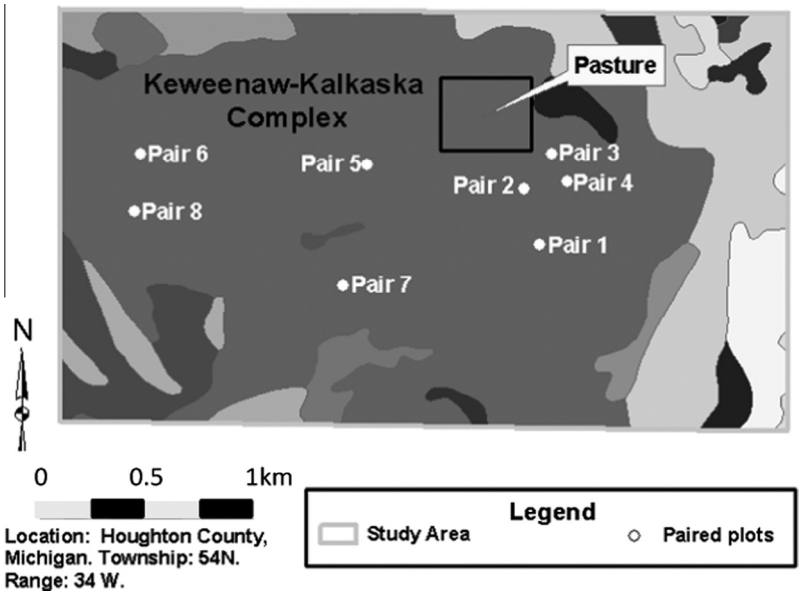

Fig. 1. Soil mapping units within our study area (Houghton County Soil Survey) and locations of the paired plots near Atlantic Mine, in Michigan, USA.

regeneration was slow, which led to slow rates of change prior to pine plantation establishment in 1950. Soils, climate, and topography were constant across our two forest types, but thinning regimes differed: two entries for red pine stands, one entry for hardwood stands. The soil type examined here is common across the region and typically supports the forest management practices studied here.

We identified eight locations where plantations of red pine were adjacent to hardwood stands. We installed a 30 × 30 m plot in each of the 16 stands (Fig. 1). The major tree species in the hardwoods plots were sugar maple (*Acer saccharum*, mean 56% of basal area), red oak (*Quercus rubra*, 26% of basal area) and red maple (*Acer rubrum*, 14% of basal area). The red pine overstory was made up entirely of red pine with a few red maple and red oak saplings in the understory. A 15 × 15 m area was established in the center of each plot for carbon flux and nutrient measurements. Across all plots, 50–100 cm depth soils were ⩾98% sand. We sampled one actively managed, grass-dominated pasture (<200 m to the nearest forest plot in this study) on the same soil type that had been in pasture since before plantation establishment. We used this remnant pasture as the baseline condition for prior non-forest land-use against which forested land-uses were compared. We recognize that changes in pasture soils may have occurred since 1950, and that a single reference site may not represent initial conditions for the 8 pairs of forested plots.

2.2. Ecosystem carbon storage

Diameter at breast height (DBH) was measured to within 0.1 cm for all trees >2.5 cm DBH in the 225 m^2 measurement plots, and bole and branch biomass was estimated with allometric equations (Jenkins et al., 2004; Table 1). For the hardwoods, a single equation was used for sugar maple and red oak, and two additional equations were used for red maple and "other hardwoods". Biomass estimates for sugar maple from the sugar maple/red oak allometric equation were corrected using tree harvest data from an adjacent hardwood excavation site (see live root carbon below). Allometrically determined biomass values were highly correlated with measured values, but predicted values were 14% lower than observed values measured on harvested whole trees (r^2 = 0.99), and so aboveground biomass estimates for sugar maple and red oak were corrected upwards by 14%. Biomass estimates were converted to C assuming aboveground biomass was 48% C (King et al., 2007). Pine biomass was estimated using a red pine allometric equation (Jenkins et al., 2004). As with maple, allometrically predicted biomass values for harvest red pine trees were highly correlated with (r^2 = 0.94) but 10% lower than measured biomass of harvested trees, and so plot-level aboveground biomass values for red pine were adjusted upward by 10% from regression predicted values. Three other pine allometric equations (Ker, 1980; Perala and Alban, 1994; Young et al., 1980) were examined but were inferior to Jenkins et al., 2004).

A single plot in each forest type was used to determine the ratio of belowground biomass to aboveground biomass (root to shoot ratio) as described in King et al. (2007). All trees within a 12 × 12 m plot in a 60-year-old hardwood stand were measured for DBH, height, and age. Six of the felled trees were separated into aboveground components (foliage, live branches, dead branches, and bole) and weighed fresh. Sub-samples (3–4) of each component were taken to determine concentrations of moisture, ash, and %C. The same approach was used in a one 55-year-old 15 × 15 m plot of red pine. For the hardwood plot, the entire soil of the plot was excavated to one meter after aboveground tree portions were removed. The central 7.5 × 7.5 m of the plot was then excavated to two meters. Coarse roots were sieved and weighed following methods in King et al. (2007). Sieved soils were checked for collection efficiency, and we found that >95% of all roots >1 mm were being collected as found for red pine by King et al. (2007). Our estimates of live root biomass also include tree stumps to a height of 30 cm, the height at which boles were cut. Sub-samples of roots were taken to determine concentrations of moisture, ash, and %C. Because so few roots were encountered in the second meter of sampling for the hardwood site, we did not sample below 2 m. The root to shoot ratio used for our red pine plots came from the 55-year-old red pine excavation site described in King et al. (2007), which was located <200 m from the nearest red pine plot in this study. Excavations were completed as with the hardwood excavation site except the plot was 15 × 15 m and an additional 1/16 of the plot was excavated to 3 m. Most belowground biomass was associated with stump and attached roots. The pool of non-attached roots was assigned to individual trees based on tree size (King et al., 2007). Dead root mass was associated almost entirely with thinned trees, and was excluded.

All plots were selected so that they occurred on the same soil series (Fig. 1). Soil physical and chemical properties were examined by depth (Table 2), including soil C for the O horizon and three

Table 2
Soil properties (±SE; n = 8) for various soil depths at our site in Michigan, USA.

Stand type	Horizon	Soil C (Mg C ha^{-1})	Bulk density (Mg m^{-3})	[C] (mg/kg)
Hardwood	O horizon	3.7 (0.2)		
	0–15 cm	26 (1)	0.98 (0.02)	18 (1)
	15–50 cm	42 (1)	1.07 (0.04)	13 (0.4)
	50–100 cm	41 (5)	1.31 (0.04)	6 (0.4)
	Total	113 (5)		
Red pine	O horizon	8.1 (0.4)		
	0–15 cm	25 (2)	1.07 (0.03)	16 (1)
	15–50 cm	49 (4)	1.13 (0.4)	12 (1)
	50–100 cm	35 (4)	1.41 (0.4)	5 (0.4)
	Total	117 (5)		
Pasture	O horizon	0		
	0–15 cm	30	0.82	25
	15–50 cm	32	0.61	16
	50–100 cm	34		
	Total	97		

Table 1
Parameters and equation used to estimate aboveground biomass (from Jenkins et al., 2004) for our sites near Atlantic Mine in Michigan, USA.

Species group	Parameter		Data points	Max DBH (cm)	RMSE (log units)	R^2
	β_0	β_1				
Hard maple/oak	2.0127	2.4342	485	73	0.236483	0.988
Soft maple	1.9123	2.3651	316	66	0.491685	0.958
Mixed hardwood	2.4800	2.4835	289	56	0.360458	0.980
Pine	2.5356	2.4349	331	180	0.253781	0.987

Equation: $bm = \mathrm{Exp}(\beta_0 + \beta_1 * \ln \mathrm{DBH})$
Where bm = total aboveground biomass (kg) for trees with DBH ⩾ 2.5 cm

depths in mineral soil. The O horizon material was collected in four stratified 1 × 1 m sub-plots per plot (32 sub-plots per forest type), oven-dried to constant mass, sub-sampled by plot, and plot composites finely ground for %C on an element analyzer (Fisons Instruments, NA 1500 NC series 2, Milan, Italy). Three mineral soil cores (8 cm diameter) were taken at three random points within the 15 × 15 m measurement plots, with one taken to a depth of 1 m and two more cores taken to 50 cm. Plastic sleeves held cores intact; sleeves were cut and soils processed at 0–15 cm (24 estimates per species), 15–50 cm (24 estimates per species), and 50–100 cm (8 estimates per species) depths. Soils were sieved (2 mm) to remove rocks and roots. Live and dead roots in the cores were not separated because the vast majority of roots were live. Soils and roots were separated and oven dried (105 °C) to constant mass in order to calculate bulk density and a second measure of root biomass. The <2 mm soil fraction was sub-sampled and ground using an 8000 M mixer/mill (Spex Certiprep, Metuchen, NJ). The %C of these sub-samples was determined as above. Bulk density and %C were used to determine C mass. Texture was determined on 50–100 cm soils from four pairs of hardwood and pine cores by hydrometer (Carter, 1993).

In the pasture site we collected 10 soil cores (6 cm diameter) every 10 m along a single transect through the center of the pasture. Cores were taken to a depth of 50 cm, and were processed as above for forest soil cores, with the exception that aboveground standing dead (winter sampling) and O horizon material were collected and separated in the lab to calculate aboveground biomass. To estimate pasture mineral soil C in the 50–100 cm depth and compare pasture and forest plots, we assumed that the proportion of total mineral soil C in pasture plots for 50–100 cm depth soils was the same as that measured for forest plots (34% of the C in 0–100 cm soils). Given low %C and similarly sandy soil, we expect this assumption was reasonable.

Because of the young age of the forests, and previous land-use, we encountered little aboveground coarse woody material >2 cm diameter in the forest plots, which we collected using two 2 × 2 m sub-plots, placed off of the southwest (randomly selected) corner of each interior 15 × 15 m. Samples were weighed and subsampled, and subsamples were oven-dried (105 °C) to determine dry weights. Dead root mass was estimated from aboveground harvested wood mass (see harvested wood below) and transformed to belowground dead root mass using root to shoot ratios described above. Following a harvest thinning, dead coarse root mass was assumed to decompose following simple 1st order (single pool) exponential decay (Paul and Clark, 1996) with a turnover time of 15 yr. This turnover time is based on our observations that belowground root biomass in harvested red pine stands can disappear within 20 years of harvest (personal observation from work in King et al., 2007). This contrasts with our observations of excavated white pine root mass and stumps, which can remain largely intact 50+ yr after harvest. These assumptions represent a source of uncertainty but the contribution of dead coarse roots to our budgets is small and unlikely to affect overall patterns. Dead root C storage was not estimated during belowground harvesting of plots (only live roots were measured), and so is not included in our root to shoot ratio estimates. We calculated dead root C contribution to C sequestration rate as storage at the time of thinning less loss due to decomposition since thinning.

2.3. Carbon fluxes

We estimated aboveground net primary production (ANPP) as the sum of current annual increment for stem wood + branches ($ANPP_W$) plus foliage production ($ANPP_F$). Understory biomass was insignificant in both stand types and so was not measured. Current annual increment was determined from DBH measurements made in early spring of 2005 and two growing-seasons later in the late fall of 2006. The locations of diameter measurements were marked on each tree to ensure accurate measurement. A few small trees showed a decline in diameter, and their increments were assumed to be zero. One hardwood plot had 3 larger trees with negative diameter increments, so we took increment cores to estimate growth for these trees. Aboveground woody biomass from spring 2005 was subtracted from fall 2006 biomass and divided by two to determine $ANPP_W$. There was no mortality in our plots during the study period.

Foliage production was estimated at a plot-scale. We collected leaf litterfall using six 28 × 56 cm trays per plot. Four trays were placed at each corner of the central 15 × 15 m plot, and two were placed between two randomly selected corners of the same plot. Litter was collected every 2 weeks during the heavy leaf drop period in the late summer and fall of 2005 and 2006. Samples were oven-dried at 105 °C to constant mass. An average of the two years of litterfall was used to calculate average $ANPP_F$ for the study period.

We examined belowground production by estimating total belowground C flux (TBCF) as annual soil respiration – ($ANPP_F$ + estimated coarse root decomposition) + coarse root increment + Δ mineral soil C (Giardina and Ryan, 2002). Annual soil respiration was determined from measurements taken during the 2005 and 2006 growing seasons. During the first 3 months of the study we used a PP system EGM-3 with 10 cm collars (PPSystems, Haverhill, MA, USA). In the middle of the 2005 growing season, we began using the Li-Cor 8100 soil respiration system with 20 cm collars (Li-Cor, Lincoln, NE, USA). Plot level estimates of soil respiration were taken at two different dates with both systems to develop a relationship between the two systems (60 measurements with the EGM-3; 20 measurements with the Li-Cor 8100), from which a conversion factor of 0.58 ($R^2 = 0.89$) was obtained to convert EGM-3 measurements, in line with findings by Pregitzer et al. (2006). With the EGM-3 (10 cm diameter chamber), two transects of seven measurements each were taken across the 15 × 15 m plot. With the Li-Cor 8100 (20 cm diameter chamber), four 20 cm collars per plot were installed to a predetermined and constant depth (5 cm) across collars and plots. Collars were in place for 2 weeks before measurements were taken. In 2005 measurements were taken approximately every 10–14 days from May 26 to November 3, while in 2006 measurements were taken at 3–4 week intervals from April 16 to December 3. Frequency was higher during the growing season.

Annual soil respiration was determined by scaling up instantaneous growing season measurements to represent the number of days between the halfway point of the previous and subsequent measurements. Our modeling of non-growing season flux relied on fewer flux measurements coupled with continuous soil temperature and moisture data collected with soil sensors and microloggers (Decagon Devices, Pullman, Washington) in 2 red pine and 2 hardwood plots. Continuous data from 2006 showed no notable temperature or moisture fluctuations between December and April, and so the December respiration rate was used to estimate winter efflux. The very low rates for December and April indicate that our assumption is reasonable. Amount of coarse root matter that decomposed during each sampling year was calculated as [dead root C (beginning of sampling year) dead root C (end of sampling year)] and subtracted from annual soil respiration for TBCF estimates.

Coarse root increment was determined from changes in aboveground biomass and whole stand root to shoot ratio. The difference between total live root C at spring 2005 and fall 2006 measurements was assumed to equal coarse root increment for two years. For change in total mineral soil C, we estimated annual change (Δ mineral soil C) as: (forest mineral soil C pasture mineral soil C)/stand age, which assumes a constant rate over stand development.

Basal diameter of all stumps was measured in each 30 × 30 m plot to determine harvested biomass. The ratio of diameters at breast height and stump height were measured on a sub-sample of 25 red pine (0.77, $r^2 = 0.96$) and 76 hardwood trees (0.82, $r^2 = 0.95$). For decomposition calculations, age of harvested material was determined for each plot. On the hardwood plots, stump sprouts were used to determine that the time since the last (and only) harvest was six years prior to the study. For the red pine sites, growth rings were counted on intact stumps to determine that two thinnings occurred at stand ages 25 and 40. The red pine stumps that could not be read were separated into these two categories by taking the median DBH of all stumps, based on basal diameter, and putting all diameters that could not be read and below the median in the 25 year category and all diameters that could not be read and larger than the median in the 40 year category. Based on typical landowner preferences for the region and on-site assessments of potential end uses for harvested materials, we assumed 50% of the harvested hardwood material had been used as sawtimber and 50% as pulp. Based on discussions with land ownership (MeadWestVaCo), we assumed 100% of the harvested red pine material had been used as pulp. Potential amounts of harvested wood remaining (not decomposed) at the time of sampling was estimated from Birdsey (1996) and Row and Phelps (1996), including species specific information on proportion of wood directed to solid products, pulp-based products and bioenergy offsets. This approach provides only potential displacement benefits of the potential offset activity, however the detailed tracking of off-site carbon products required to construct actual offset budgets was beyond the scope of this study.

Annual sequestration rate was calculated as total ecosystem C in forest plus C remaining in harvested wood or allocated to bioenergy, less the C stored in the pasture, which was then divided by stand age. We followed accounting rules and guidelines for two land management alternatives, in our case afforestation to red pine or to northern mixed hardwood species, against a base case, in our case pasture management (Smith et al., 2006). These averages reflect long-term stand level growth, whereas our annual estimates of ANPP and TBCF represent short-term stand-level growth.

2.4. Factors that influence C fluxes

To understand forest type effects on nutrient cycling and carbon storage, we estimate soil organic C quality. One composite soil sample (three subsamples taken from a 1 m^2 area) from the 0–15 cm depth of each plot was used in 39 day laboratory incubations to assess soil carbon quality difference between the two forest types. Sub-samples from soil cores were dried at 30 °C to constant moisture, and 30 g of soil from each plot were: placed into a 120 mL specimen cup; brought to 60% water holding capacity (WHC); incubated at 21 °C in 1 L mason jars; and head space [CO_2] determined at 1, 3, 10 and 39 days after Fissore et al. (2008) on an Agilent 6890 Gas Chromatograph (Agilent, Inc. Palo Alto, CA). Scaling to g C kg^{-1} soil C to calculate SOC decomposition rates followed Fissore et al. (2008). Water was added periodically to maintain 60% WHC throughout the 39 day period.

Light interception was measured with a Ceptometer (AccuPAR LP-80, Decagon Devices, Pullman, WA). Seven above–canopy and 24 below-canopy light measurements were taken for each plot on three dates in 2005 (early July, early August and late August), and within a 3 h period (1100–1400) on cloudless days. Estimated light interception under conditions of clear skies can be used to determine leaf area index (LAI) as:

$$\mathrm{LAI} = \frac{[(1 \quad 1/2K) * \mathrm{fb} \quad 1] * \ln \tau}{A * (1 \quad 0.47 * \mathrm{fb}) \leftarrow} \tag{1}$$

where K is the light extinction coefficient, fb = the fraction of incident PAR that is direct beam, τ is the ratio of above and below canopy PAR, and A is a constant that approximates the absorptivity of leaves at our site (Decagon Devices AccuPAR LP-80 Manual, 2003).

Soil nitrogen supply was evaluated with ion exchange resin bags (Binkley and Matson, 1983; Binkley et al., 2000). Resin bags were inserted into soils in June of 2005 in transects that spanned from the center of one plot across the plot boundary to the center of the paired plot. This design allowed comparison of the influence of each species in monoculture as well as any interacting effect of species near the boundaries. Resin bags (4 × 4 cm) were prepared by adding 14 mL of cation resins (C-251 cation resin, Sybron Chemicals, Inc, Pittsburgh, PA, USA) plus 14 mL of anion resins (ASB-1 POH anion resins, Sybron Chemicals, Inc.) to nylon stockings, and sealing with heat. In each plot, three transects received 11 bags per transect, with 4 bags placed 5 m apart in red pine and hardwood plots and 3 bags located 5 m apart in the transition zone. We sampled the transition zone to understand how mixture of litter might affect soil N availability. A spade was used to diagonally cut through the O horizon and into the mineral soil. The bag was placed flat on the mineral soil, the spade removed, and the soil and O horizon above gently pressed down. The location of each bag was marked with a pin flag. The bags were re-located in September after the 2005 growing season, sealed in individual Ziplock bags, and sent to Colorado State University for individual extraction along with time zero blanks with 100 mL of 1 M KCl. Colorimetric analyses for nitrate and ammonium concentrations were completed on a continuous flow autoanalyzer (Alpkem Corporation, College Station, TX, USA).

2.5. Statistical analyses

Differences between the red pine and hardwood plots were examined with paired sample t-tests with an alpha of 0.05 (SPSS Version 9). The standard error of the mean is based on 8 plots for each forest type. We had only a single pasture plot, and so do not have a measure of variation for how pastures perform in the area of this study. The patterns of resin-captured N along transects were analyzed with orthogonal contrasts (SYSTAT 11) revealed within: (1) the pine and hardwood ends of each transect (linear and quadratic); (2) within each of the four positions within each tree species type (linear and quadratic); and (3) within the three transition positions (linear).

3. Results

3.1. Ecosystem carbon storage

Aboveground biomass C was 33% higher in hardwood (80 ± 6 Mg C ha^{-1}; Fig. 2) than red pine plots (60 ± 4 Mg C ha^{-1}), with both exceeding the pasture (2 Mg C ha^{-1}). The hardwood plot root to shoot ratio (0.54) was higher than that of red pine (0.30). Similar to red pine (King et al., 2007), a very small fraction of the total hardwood root biomass was found below one meter depth. Higher hardwood aboveground biomass and root to shoot ratio resulted in much higher ($P < 0.001$) live root C in hardwood (44 ± 3 Mg C ha^{-1}) than the red pine plots (18 ± 1 Mg C ha^{-1}). The pasture contained 8.1 Mg C ha^{-1} in roots. The plots contained low amounts of coarse woody material: 8.0 ± 3.0 Mg C ha^{-1} for hardwood plots and 2.8 ± 0.8 Mg C ha^{-1} for red pine plots, but the difference was not significant. The soil O horizon was also small for both forest types, though significantly higher for red pine (8.1 ± 0.4 *vs.* 3.7 ± 0.2 Mg C ha^{-1}; Table 2). Mineral soils comprised the largest C pool, with no differences between forest types (109 ± 5 Mg C ha^{-1} for both; Table 2). The adjacent pasture had

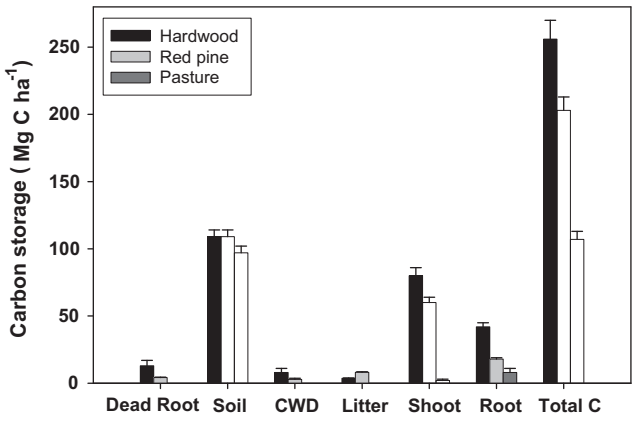

Fig. 2. Ecosystem C storage (with standard error bars; $n = 8$) for both forest types and an adjacent pasture (mean of 10 subsamples with standard error for the mean) at our Michigan, USA field site, by component: dead roots, mineral soil (soil), coarse woody debris (CWD), O horizon (litter), aboveground biomass (shoot), belowground biomass (root) and whole ecosystem carbon (total C).

about 10% less C in the mineral soil. There was no significant difference between stand types in the total quantity of dead root C that was produced during the two red pine thinnings (14 ± 1 Mg C ha $^{-1}$) compared to the single entry in the hardwood plots (19 ± 5 Mg C ha $^{-1}$; $P = 0.361$). However, as dead roots decomposed, estimated dead root C remaining at the time of sampling was significantly higher in hardwood (12 ± 4 Mg C ha $^{-1}$) than red pine plots (4.2 ± 0.3 Mg C ha $^{-1}$, $P = 0.053$; Fig. 2). Average total ecosystem C storage was significantly higher for hardwood plots (255 ± 14 Mg C ha $^{-1}$) than red pine plots (203 ± 10 Mg C ha $^{-1}$; $P = 0.004$, Fig. 3), and both species were higher than the pasture (107 Mg C ha $^{-1}$). The range was 211–314 Mg C ha $^{-1}$ for the hardwood plots and 154–229 Mg C ha $^{-1}$ for the red pine plots.

3.2. Production ecology

There were no significant differences between stands for ANPP (red pine: 319 ± 15 g C m $^{-2}$ yr $^{-1}$; hardwoods: 349 ± 31 g C m $^{-2}$ yr $^{-1}$) or $ANPP_W$ (red pine: 165 ± 24; hardwoods: 175 ± 16). There also were no differences in TBCF (red pine: 625 ± 22 g C m $^{-2}$ yr $^{-1}$; hardwoods: 596 ± 38 g C m $^{-2}$ yr $^{-1}$) or the components of TBCF (Table 3). Nitrogen availability showed no pattern between forest types (Fig. 3) or across transects. However, light interception was

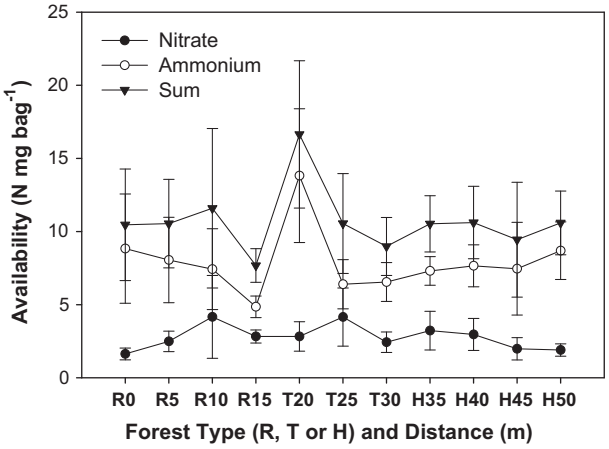

Fig. 3. Nutrient availability from resin bag transects at the Atlantic Mine site ($n = 24$ for each transect location). Transect forest types; R = red pine; T = transition; H = hardwoods.

Table 3
Annual and growing season means (±SE; $n = 8$) for soil surface CO_2 efflux, soil moisture and soil temperature (0–10 cm mineral soils) for hardwood and red pine forest types at our Michigan, USA field site.

Variable	Year	Growing season		Annual	
		Hardwoods	Red pine	Hardwoods	Red pine
Soil CO_2 efflux (g C m $^{-2}$ yr $^{-1}$)	2005	472 (38)	433 (35)	715 (449)	700 (45)
	2006	645 (73)	489 (38)	870 (84)	750 (48)
Soil moisture (%)	2005	11.8 (0.4)	7.9 (0.6)	13.9 (0.2)	10 (0.4)
	2006	13.2 (0.9)	6.8 (0.5)	14.2 (0.4)	8.9 (0.2)
Soil temperature (°C)	2005	16.5 (0.1)	16.6 (0.2)	9.2 (0.1)	9.2 (0.1)
	2006	16.4 (0.3)	17.0 (0.3)	9.1 (0.1)	9.1 (0.3)

substantially higher ($P < 0.001$) in hardwood (91 ± 2%) than red pine plots (67 ± 6%). Lower light interception by pines combined with similar C fluxes for pine indicates that the pine plots produced 40–50% more C per unit of light interception than hardwood plots, although pine canopies may be able to photosynthesize for 2–3 additional months when the hardwood stands do not display leaves. There were no differences in mineral soil C decomposition rates and quality. Decomposition rates on day one of the incubations were 2.1 ± 0.3 and 2.2 ± 0.5 g C kg $^{-1}$ soil C d $^{-1}$ for hardwood and red pine soils, respectively. Rates declined similarly over the 39 day incubation, and total release did not differ ($P = 0.723$) between hardwood (34.2 ± 1.6 g C kg $^{-1}$ soil C) and pine (35.5 ± 3.0 g C kg $^{-1}$ soil C).

3.3. Modeled potential fate of harvested wood

There was no significant difference in the amount of harvested wood during the two thinnings in the red pine at stand ages 25 and 40 (a combined 48 ± 3 Mg C ha $^{-1}$) compared to the single entry in the hardwood plots (37 ± 11 Mg C ha $^{-1}$) at age 50 ($P = 0.318$). Estimated C content at the time of sampling in harvested wood products or modeled potential bioenergy offset were similar ($P = 0.607$) for red pine (29 ± 2 Mg C ha $^{-1}$) and hardwood plots (25 ± 7 Mg C ha $^{-1}$).

4. Discussion

Globally, landscapes previously supporting forest cover are being returned to forest through commercial establishment of forest plantations, restoration efforts to re-establish native forest cover, and natural succession (Ryan et al., 2010). Tree species composition is often managed during afforestation and reforestation of converted lands, but the impacts of these choices on ecosystem C cycling, storage and sequestration rates remain poorly understood. However, strong trends for forest type effects on storage, processes and biogeochemistry are emerging (Laurent et al., 2014). Results from our comparison of adjacent northern hardwood stands and red pine plantations – all on lands managed for forest products – suggest that choices about tree species composition can influence ecosystem C cycling and storage, but differences did not consistently match our hypotheses. While both forest types enhanced storage and sequestration rates relative to the pasture baseline, differences between forest types were more subtle and dependent on ecosystem component.

4.1. Ecosystem carbon storage

Our live shoot C estimates and associated standard errors for the hardwood plots are consistent with estimates for other second-growth stands in the region supporting relatively low basal area (Crow, 1978; Martin and Bailey, 1999; Zavitkovski, 1976). In

line with our first hypothesis, live shoot C was significantly higher in hardwood than red pine plots (Fig. 2). Total light interception is often positively correlated with productivity (Landsberg, 1997), so species differences in live C storage may relate to the higher growing season light interception measured for hardwood plots. The higher growing season LAI of the hardwood plots (5.0 ± 0.4 m^2 m^{-2} and 2.5 ± 0.3 m^2 m^{-2}; $P < 0.001$) explains the light interception patterns, but higher light use efficiency and longer period of canopy photosynthesis in the pine plots partly offset differences. While LAI was a poor predictor of ANPP in our hardwood plots ($R^2 = 0.27$), LAI explained 41% of the variation in red pine ANPP. Thinning and removal of trees from the red pine plots explain about 20% of standing biomass difference with hardwoods.

The hardwood root to shoot ratio is similar to previous estimates for hardwood stands (e.g., Millikin and Bledsoe, 1999), but this value is higher than average values for temperate deciduous forests (Jackson et al., 1996; Giardina et al., 2005). Similarly, our root biomass estimates (88 Mg ha^{-1}) are higher than those found for 56 yr old (25 Mg ha^{-1}) and 121 yr old (29 Mg ha^{-1}) northern hardwood stands (Yanai et al., 2006; Park and Yanai, 2007). Because few data exist, interpreting this variation is not possible. The root to shoot ratio for the red pine excavation site was above the mean of values reported for temperate coniferous forests (Jackson et al., 1996), but was comparable to other studies investigating belowground root biomass of coniferous forest (Comeau and Kimmins, 1989; Albaugh et al., 1998; Helmisaari et al., 2002; Li et al., 2003; Giardina et al., 2005). Our findings are consistent with differing above- and belowground allocation strategies found between species. For example, our site is characterized by nutrient poor soils, and Comeau and Kimmins (1989) found that lodgepole pine had a larger root to shoot ratio on a xeric site (0.34) compared to a mesic site (0.25), while also allocating a much larger proportion of NPP belowground.

Amounts of coarse woody material for our hardwood plots are within the range reported by Muller and Liu (1991) for young to mature managed hardwood forests of the region (2.5–14 Mg C ha^{-1}), but they found that coarse woody material to living aboveground biomass ratio ranged between 13% and 26%, which is substantially higher than the 3% we found for hardwood plots. The red pine coarse woody material values are within the range presented by Duvall and Grigal (1999) for 30 and 90 yr old managed red pine stands (3.3–10.1 Mg C ha^{-1}). Two thinnings in the red pine plots and one thinning in hardwood plots, combined with high utilization, likely explain the lower coarse woody material values for our sites.

Our O horizon results for hardwood plots are within the range of findings by McClaugherty et al. (1985), who compared five forest types, and Fassnacht and Gower (1999), who compared dominant upland forest ecosystems in northern Wisconsin. They are lower, however, than those reported in earlier forest floor studies (Gosz et al., 1976; Covington, 1981; Federer, 1984), perhaps due to variation in the quality and quantity of inputs, climate, and the activity of earthworms. At our site, the higher O horizon C in red pine was due to both higher mass and higher %C ($47 \pm 2\%$ *vs.* $40 \pm 2\%$) – highlighting the role of litter quality as hardwood litterfall rates and litter turnover were much higher. These are not unusual findings (Laurent et al., 2014). McClaugherty et al. (1985) found a 2:1 relation between white pine and sugar maple O horizon mass, but similar hemlock and white pine O horizon mass despite more than two times greater litterfall in white pine than in hemlock stands.

We had hypothesized that soil C content would be higher in the hardwood plots (Hypothesis 2). Instead, we found no difference in mineral soil C content or quality between species, despite higher coarse root production, $ANPP_F$, coarse woody material and TBCF in hardwood plots. These findings point to limited capacity for tree species management on low quality sites to impact soil C quantity or quality at century time scales. Li et al. (2005) also found no species effect of species on soil C to a depth of 25 cm in a comparison of a tropical pine plantation (56 ± 1.6 Mg C ha^{-1}) and a naturally regenerated secondary forest (57 ± 0.9 Mg C ha^{-1}). Similarly, Finzi et al. (1998) for American species reported little difference in SOC for 0–15 mineral soils while Vesterdal et al. (2008) reported minor differences for European species to 30 cm despite for both studies strongly differing rates of litter production, litter quality, and O horizon mass. Overall, boreal angiosperm and gymnosperm species may differ minimally in their effects on soil C (Laurent et al., 2014). Notably, Perala and Alban (1982) found that afforestation effects on organic matter varied with soil fertility.

Our estimates of total ecosystem C storage are comparable with those for temperate forests on sandy soils (Perala and Alban, 1982). While few other estimates are available for the region, we expect that, depending on management, biomass C storage of these young forests will continue to increase with stand age to some maximum (Law et al., 2001; Litton et al., 2004; Pregitzer and Euskirchen, 2004).

4.2. Ecosystem carbon fluxes and controls

We hypothesized that wood net primary production ($ANPP_W$) would be higher in the hardwood plots (Hypothesis 1), but differences were not significant. These results were surprising given that: (i) foliage net primary production ($ANPP_F$) was higher in the hardwood stands, in line with a recent synthesis for boreal species (Laurent et al., 2014); and (ii) components of gross primary production are often tightly coupled (Litton et al., 2007). Our hardwood $ANPP_W$ and $ANPP_F$ values are similar to previously reported values for sugar maple dominated hardwood forests on soils of intermediate texture (Burrows et al., 2003; Reed et al., 1994; Benzie, 1977; Crow, 1978; Gower et al., 1993; Martin and Bolstad, 2005). As with previous findings, our study shows that $ANPP_F$ for hardwood forests can equal or exceed $ANPP_W$. The differences in duration of leaf area display, and estimated light use efficiency between forest types clearly complicate efforts to model forest growth as a simple function of intercepted light. That $ANPP_W$ during the observation period was less than mean $ANPP_W$ over stand development for both hardwood (165 ± 24 *vs.* 201 ± 23 g C m^{-2} yr^{-1}, $P = 0.059$) and red pine plots (175 ± 16 *vs.* 204 ± 11 g C m^{-2} yr^{-1}, $P = 0.052$) is to be expected given reduced LAI and light interception during thinning events and age-related declines in productivity (Pregitzer and Euskirchen, 2004; Ryan et al., 2004).

4.2.1. Total belowground C flux

We hypothesized that TBCF would be higher in the hardwood plots because of greater root inputs, as reflected in hypothesized higher soil CO_2 efflux rates (Hypothesis 2). Instead, we found a more complicated story. The significantly higher hardwood soil CO_2 efflux for the 2006 growing season and higher litterfall inputs for the hardwood stands did not translate into higher total annual flux for either 2006 or 2005 (Table 4). Soil water content (SWC) is an important driver of belowground processes, and varied between years and species. The 2005 growing season (May–August) was drier (30 mm less rainfall) than the 2006 growing season, as well as the long term average (King et al., 2007), but for red pine plots,

Table 4
Means in g C m^{-2} yr^{-1} (±SE; $n = 8$) for TBCF and components for the calculation (soil CO_2 efflux, $ANPP_F$, coarse root increment, and Δ Soil C) at our site in Michigan, USA.

Forest type	Average annual soil CO_2 efflux	$ANPP_F$	Coarse root increment	Δ Soil C	TBCF
Hardwood	672 (42)	184 (10)	88 (13)	19 (9)	596 (38)
Red pine	695 (12)	144 (8)	52 (5)	22 (10)	625 (22)

annual and growing season SWC in 2005 were higher than in 2006 – opposite the pattern for hardwoods. This indicates that both total precipitation and factors that regulate interception losses such as canopy structure, winter foliage and O horizon thickness may exert an influence over soil moisture, with implications for ecosystem processes (Laurent et al., 2014). For example, given that fine roots at shallow depth respire more than coarse or deep roots (Pregitzer et al., 1998), higher overall SWC may explain higher efflux rates in hardwood plots for 2006, whereas the stronger SWC response in hardwood plots to reduced rainfall in 2005 may explain the larger absolute and proportional difference in efflux from 2006 compared with the difference for hardwood plots. In line with this interpretation, Burton et al. (1998) reported that drought substantially reduced root respiration rates in sugar maple forests, while Lee et al. (2004) concluded that hardwood O horizons are sensitive to moisture changes, exhibiting large rain-driven pulses of C release. At the stand scale, Brzostek et al. (2014) reported whole ecosystem reductions in carbon processes due to drought, with hardwood forest types potentially being more sensitive to drought than pine. In a review of boreal species effects, Laurent et al. (2014) reported that evergreen gymnosperms generally have lower water inputs to soils compared to deciduous angiosperms, and so that the red pine forest type may be better adapted to lower water availability than northern hardwoods.

Overall, soil CO_2 effluxes are similar to previous studies of northern hardwood and pine forests (Davidson et al., 1998; Gower et al. 1996; Hibbard et al., 2005; Bolstad et al., 2004; Martin and Bolstad, 2005). However, Wang et al. (2006) did report annual respiration rates that were 72% higher in temperate broadleaved forests compared to coniferous. Clearly species level controls over soil respiration are not well characterized, and we speculate that red pine soils were able to support soil CO_2 efflux rates that are comparable to hardwood plots because of enhanced root and microbial activity in red pine stands despite drier conditions. Coleman et al. (2000) found a higher density of fungal hyphae on minirhizotron surfaces in pine compared to poplar forest. Similarly, Giardina et al. (2001) reported higher active fungal and total bacterial biomass in lodgepole pine *vs*. aspen forest soils paired by texture across a range of textures. Along these lines, wet season microbial biomass in tropical secondary forest was twice that in the dry season, but there was no pattern in adjacent pine plantations (Li et al., 2005).

We had hypothesized that TBCF would be higher in hardwood plots due to higher root and mycorrhizal production (Hypothesis 2). Instead, we found mean TBCF across the two year period did not differ ($P = 0.502$) between stand types (Table 3), despite significantly ($P = 0.011$) higher coarse root increment for hardwood plots (88 ± 13 g C m^{-2} yr^{-1}) than red pine plots (52 ± 5 g C m^{-2} yr^{-1}). Our estimates of TBCF for pine are within the wide range of values reported by Haynes and Gower (1995) for Wisconsin red pine forest (TBCF from 253 to 791 g C m^{-2} yr^{-1}), and within the range for the sites characterized by similar MAT (Litton and Giardina, 2008). Haynes and Gower (1995) observed an average coarse root production of 90 ± 7 g C m^{-2} yr^{-1}, which is higher than our rates perhaps, because basal area in their stands was nearly twice those in our pine plots (42 *vs*. 25 m^2 ha^{-1}). Overall, our data highlight the important contributions of aboveground litterfall and decomposition to variation in soil respiration. Taken together, even strongly contrasting ecosystems may allocate C aboveground and belowground similarly ([TBCF/(TBCF + ANPP)] = 0.65 for hardwood and 0.66 for red pine plots).

4.2.2. Mineral soil C decomposition rates and nutrient availability

The lack of species differences over our 39 day incubations indicates that over short time periods, species do not affect even the labile fraction of soil organic C. These findings support the TBCF findings for these plots, and are in line with long-term incubation results for paired pine and hardwood forests across North America (Fissore et al., 2008). Similarly, Van Miegroet et al. (2005) reported no difference for SOC losses from conifer (fir and spruce) and aspen soils. Further, this lack of SOC quality difference was matched by a lack of difference between species for nitrate or ammonium availability and similar 0–10 cm mineral soil pH (4.59 *vs*. 4.43 for hardwood and pine soils, respectively; $P = 0.180$), which to some extent conflicts with trends in a broad comparison of boreal angiosperms and gymnosperms (Laurent et al., 2014). We have no explanation for the observed transition zone spike in ammonium availability (Fig. 3).

The lack of nutrient availability differences between our hardwood and pine plots is consistent with the overall lack of productivity difference between stand types, and countless observations that nutrient availability exerts a strong influence on aboveground (Binkley and Fisher, 2013) and belowground process rates (Giardina et al., 2004; Litton et al., 2007). In contrast to findings of Fassnacht and Gower (1997), however, the greater LAI and litter inputs in our hardwood plots did not lead to increased nutrient availability. Our findings also contrast with Washburn and Arthur (2003) who found that *Pinus echinata* and *Pinus rigida* individuals maintained lower soil pH and extractable cations than adjacent red maple (*Acer rubrum*) and chestnut oak (*Quercus prinus*) individuals in mixed species forests. While the literature is rich with studies examining species effects on soil properties, generalizations are complicated by the diversity of methods, as well as the confounding effects of site differences that select for certain tree species (Binkley and Menyailo, 2005), and so it is not surprising that results from our common garden study would differ from studies of naturally occurring stands.

4.3. Afforestation options and carbon sequestration rates

During 60 yr of stand development, and using adjacent pasture site as a baseline, hardwood plots sequestered more C than red pine plots (2.9 ± 0.3 *vs*. 2.3 ± 0.2 Mg C ha^{-1} yr^{-1}), and this difference was nearly significant ($P = 0.069$; Fig. 4). The maximum sequestration rate for a single plot was higher for the hardwood plots (4.3 Mg C ha^{-1} yr^{-1}) than red pine plots (2.9 Mg C ha^{-1} yr^{-1}), and intercepted light and total basal area were positively correlated with sequestration rate for the red pine plots ($R^2 = 0.73$ and $R^2 = 0.66$, respectively), but not for hardwood plots ($R^2 = 0.19$ and $R^2 = 0.26$, respectively). Our annual sequestration rates are within the range of carbon flow model for plantations in the UK (Dewar and Cannell, 1992), but we caution that these average rates over stand development do not accurately capture rates for any given year because stands were likely dynamic over the 60 years of stand

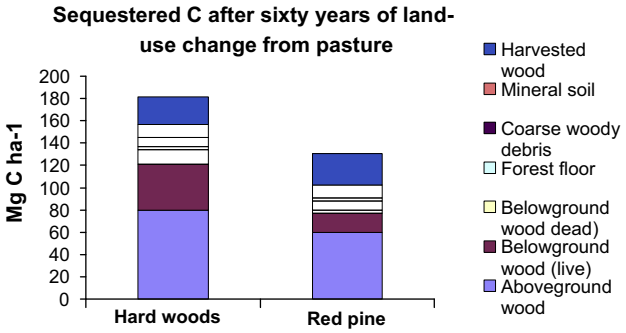

Fig. 4. Carbon sequestration for adjacent hardwood and pine stands relative to a pasture baseline at the Atlantic Mine site in Upper Peninsula, Michigan. Over 60 years of stand development, the hardwood stands sequestered approximately 2.9 Mg C ha^{-1} yr^{-1}, compared with 2.3 Mg C ha^{-1} yr^{-1} for the red pine stands.

development with respect to productivity and losses of detrital carbon.

We anticipate that stands will continue to be dynamic, and our estimates of average annual sequestered C unlikely to accurately predict future patterns of C sequestration rates, as these should change – even dramatically. Mature red pine stands are often harvested for utility poles, which shifts sequestered C off site into long-lived pools. In contrast, hardwood stands are typically managed in an uneven-aged system with a stand improvement cutting cycle of 10–15 yr, which maintains some level of C storage on site as well as continued exports of C for potential offsite offsets such as bioenergy. While the fates and longevities of off-site material will exert an impact on sequestration rate potential of these forests, effects of this shift on sequestration rate cannot be predicted.

5. Conclusion

Our findings show that land-use change from pasture to forest leads to an increase in on-site C storage – primarily through increases in above- and below-ground biomass, coarse woody material and O horizon mass, and to a much smaller extent through increases in mineral soil C. Further, while management of tree species composition can alter aspects of ecosystem C cycling, as well as some components of C storage and sequestration, differences are likely to be small relative to large changes accompanying afforestation. Despite similar aboveground production rates and amounts of harvested material, the hardwood plots stored more C in wood, especially belowground, and showed higher rates of belowground production. While hardwood plots produced more aboveground litter, both forest types stored similar amounts of mineral soil C, with both accumulating more mineral soil C than the pasture site. Finally, potential sequestration rates for off-site carbon (modeled offsets) represented a large fraction of the sequestration rate budget, but differences between species were minor.

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References

Albaugh, T.J., Allen, H.L., Dougherty, P.M., et al., 1998. Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. For. Sci. 44, 317–328.

Benzie, J.W., 1977. Manager's handbook for red pine in the north-central states. General Technical Report NC-33. U.S. Department of Agriculture, Forest Service, North Central Research Station. 18pp.

Berger, T.W., Neubauer, C., Glatzel, G., 2002. Factors controlling soil carbon and nitrogen stores in pure stands of Norway spruce (*Picea abies*) and mixed stands in Austria. For. Ecol. Manage. 159, 3–14.

Binkley, D., Fisher, R.F., 2013. Ecology and Management of Forest Soils. Wiley-Blackwell, Chichester.

Binkley, D., Giardina, C.P., 1998. Why trees affect soils in temperate and tropical forests: the warp and woof of tree/soil interactions. Biogeochemistry 42, 89–106.

Binkley, D., Matson, P., 1983. Ion exchange resin bag method for assessing forest soil N availability. Soil Sci. Soc. Am. J. 47, 1050–1052.

Binkley, D., Menyailo, O., 2005. Gaining insights on the effects of tree species on soils. Chapter 1. In: Binkley, D., Menyailo, O. (Eds.), The Impacts of Global Climate Change on Plant – Soil Interactions. NATO Science Series, Kluwer Academic Press.

Binkley, D., Giardina, C.P., Bashkin, M., 2000. Soil phosphorus pools and supply under the influence of *Eucalyptus saligna* and nitrogen-fixing *Albizia falcataria*. For. Ecol. Manage. 128, 241–247.

Birdsey, R.A., 1996. Carbon storage for major forest types and regions in the conterminous United States. In: Sampson, R. Neil, Hair, Dwight (Eds.), Forests and Global Change Volume Two – Forest Management Opportunities, American Forests, Washington, DC, pp. 1–26.

Bolstad, P.V., Davis, K.J., Marting, J., et al., 2004. Component and whole-system respiration fluxes in northern deciduous forests. Tree Physiol. 24, 493–504.

Brzostek, E.R., Dragoni, D., Schmid, H.P., Rahman, A.F., Sims, D., Wayson, C.A., Johnson, D.J., Phillips, R.P., 2014. Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. Global Change Biol. 20, 2531–2539.

Burrows, S.N., Gower, S.T., Norman, J.M., et al., 2003. Spatial variability of aboveground net primary production for a forested landscape in northern Wisconsin. Can. J. For. Res. 33, 2007–2018.

Burton, A.J., Pregitzer, K.S., Zogg, G.P., et al., 1998. Drought reduces root respiration in sugar maple forests. Ecol. Appl. 8, 771–778.

Carter, M.R., 1993. Soil sampling and methods of analysis. Can. J. Soil Sci., 508.

Coleman, M.D., Dickson, R.E., Isebrands, J.G., 2000. Contrasting fine-root production survival and soil CO_2 efflux in pine and poplar plantations. Plant Soil 225, 129–139.

Comeau, P., Kimmins, J., 1989. Above- and below-ground biomass and production of lodgepole pine on sites with differing soil moisture regimes. Can. J. For. Res. 19, 447–454.

Covington, W.W., 1981. Changes in O horizon organic matter and nutrient content following clear cutting in northern hardwoods. Ecology 62, 41–48.

Crow, T.R., 1978. Biomass and production in three contiguous forests in northern Wisconsin. Ecology 59, 265–273.

Davidson, E., Belk, E., Boone, R., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biol. 4, 217–227.

Deckmyn, G., Muys, B., Quijano, J., et al., 2004. Carbon sequestration following afforestation of agricultural soils: comparing oak/beech forests to short-rotation poplar coppice combing a process and a carbon accounting model. Global Change Biol. 12, 1482–1491.

Dewar, R.C., Cannell, M.G., 1992. Carbon sequestration in the trees, products and soils of forest plantations: an analysis using UK examples. Tree Physiol. 11, 49–71.

Dixon, R.K., Brown, S., Houghton, R.A., et al., 1994. Carbon pools and flux of global forest ecosystems. Science 263, 185–189.

Duvall, M.D., Grigal, D.F., 1999. Effects of timber harvesting on coarse woody debris in red pine forests across the Great Lakes states, U.S.A. Can. J. For. Res. 29, 1926–1934.

Fassnacht, K.S., Gower, S.T., 1997. Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin. Can. J. For. Res. 27, 1058–1067.

Fassnacht, K.S., Gower, S.T., 1999. Comparison of the litterfall and O horizon organic matter and nitrogen dynamics of upland forest ecosystems in north central Wisconsin. Biogeochemistry 45, 265–284.

Federer, C.A., 1984. Organic matter and nitrogen content of the O horizon in even-aged northern hardwoods. Can. J. For. Res. 14, 763–767.

Finzi, A.D., Breemen, N.V., Canham, C.D., 1998. Canopy tree-soil interactions within temperate forests: specie effects on soil carbon and nitrogen. Ecol. Appl. 8, 440–446.

Fissore, C., Giardina, C.P., Kolka, R., Trettin, C., King, G.M., Jurgensen, M.F., Barton, C., McDowell, S.D., 2008. Temperature and vegetation effects on soil organic carbon quality along a forested mean annual temperature gradient in North America. Global Change Biol. 14, 193–205.

Giardina, C.P., Ryan, M.G., 2002. Total belowground carbon allocation in a fast-growing Eucalyptus plantation estimated using a carbon balance approach. Ecosystems 5, 487–499.

Giardina, C.P., Ryan, M.G., Hubbard, R.M., et al., 2001. Tree species and soil textural controls on carbon and nitrogen mineralization rates. Soil Sci. Soc. Am. J. 65, 1272–1279.

Giardina, C.P., Binkley, D., Ryan, M.G., et al., 2004. Belowground carbon cycling in a humid tropical forest decreases with fertilization. Oecologia 139, 545–550.

Giardina, C.P., Coleman, M., Hancock, J., et al., 2005. The effects of global change on belowground carbon allocation in forests. Chapter 7. In: Binkley, D., Menyailo, O., (Eds.), The Impacts of Global Climate Change on Plant – Soil Interactions. NATO Science Series, Kluwer Academic Press.

Gosz, J.R., Likens, G.E., Bormann, F.H., 1976. Organic matter and nutrient dynamics of the forest and O horizon in the Hubbard Brook forest. Oecologia 22, 305–320.

Gower, S.T., Reich, P.B., Son, Y., 1993. Canopy dynamics and aboveground production of five tree species with different leaf longevities. Tree Physiol. 12, 327–345.

Gower, S.T., Pongracic, S., Landsberg, J., 1996. A global trend in belowground carbon allocation: can we use the relationship at smaller scales? Ecology 77, 1750–1755.

Harmon, M., Ferrel, W.K., Franklin, J.F., 1990. Effects of carbon storage of conversion of old-growth forests to young forests. Science 247, 699–704.
Haynes, B.E., Gower, S.T., 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiol. 15, 317–325.
Helmisaari, H.S., Makkonen, K., Kellomaki, S., et al., 2002. Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. For. Ecol. Manage. 165, 317–326.
Hibbard, K.A., Lae, B.E., Reichstein, M., et al., 2005. An analysis of soil respiration across northern hemisphere temperate ecosystems. Biogeochemistry 73, 29–70.
Jackson, R.B., Canadell, J., Ehleringer, J.R., et al., 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108, 389–411.
Jenkins, J.C., Chojnacky, D.C., Heath, L.C., Birdsey, R.A., et al., 2004. Comprehensive Database of Diameter-based Biomass Regressions for North American Tree Species. General Technical Report NE-319. U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 45p.
Jobbagy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol. Appl. 10, 423–436.
Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta-analysis. For. Ecol. Manage. 140, 227–238.
Ker, M.F., 1980. Tree biomass equations for ten major species in Cumberland County, Nova Scotia. Can. For. Serv. Marit. For. Res. Cent. Inf. Rep., M-X-108, 26.
King, J.S., Giardina, C.P., Pregitzer, K.S., et al., 2007. Biomass partitioning in red pine (*Pinus resinosa*) along a chronosequence in the Upper Peninsula of Michigan. Can. J. For. Res. 37, 93–102.
Lal, R., 2005. Forest soils and carbon sequestration. For. Ecol. Manage. 220, 242–258.
Landsberg, J., 1997. The biophysical environment. In: Nambiar, E.K.S., Brown, A.G. (Eds.), Management of soil, nutrients and water in tropical plantation forests. ACIAR/CSIRO/CIFOR Monograph No. 43, Canberra, Australia, pp 65–96.
Laurent, A., De Schrijver, D., Vesterdal, L., Smolander, A., Prescott, C., Ranger, J., 2014. Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. Biol. Rev. 5. http://dx.doi.org/10.1111/brv.12119.
Law, B.L., Ryan, M.G., Anthoni, P.M., 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. Glob. Change Biol. 5, 169–182.
Law, B.E., Thornton, P.E., Irvin, J., et al., 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Glob. Change Biol. 7, 755–777.
Lee, X., Wu, H.J., Oishi, C., et al., 2004. Rapid and transient response of soil respiration to rain. Glob. Change Biol. 10, 1017–1026.
Li, Z., Kurz, W., Apps, M., et al., 2003. Belowground biomass dynamics in the Carbon Budget Model of the Canadian Forest Sector: recent improvements and implications for the estimation of NPP and NEP. Can. J. For. Res. 33, 126–136.
Li, Y., Xu, M., Zou, X., et al., 2005. Comparing soil organic carbon dynamics in plantation and secondary forest in wet tropics in Puerto Rico. Glob. Change Biol. 11, 239–248.
Litton, C.M., Giardina, C.P., 2008. Belowground carbon flux and partitioning: global patterns and response to temperature. Funct. Ecol. 22, 941–954.
Litton, C.M., Ryan, M.G., Knight, D.H., 2004. Effects of tree density and stand age on carbon allocation patterns in postfire lodgepole pine. Ecol. Appl. 14, 460–475.
Litton, C.M., Ryan, M.G., Raich, J.W., 2007. Review: carbon allocation patterns in forest ecosystems. Glob. Change Biol. 13, 2089–2109.
Martin, C.W., Bailey, A.S., 1999. Twenty years of change in a northern hardwood forests. For. Ecol. Manage. 123, 253–260.
Martin, J.G., Bolstad, P.V., 2005. Annual soil respiration in broadleaf forests of northern Wisconsin: influence of moisture and site biological, chemical, and physical characteristics. Biogeochemistry 73, 149–182.
McClaugherty, C.A., Pastor, J., Aber, J.D., et al., 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66, 266–275.
Millikin, C.S., Bledsoe, C.S., 1999. Biomass and distribution of fine and coarse roots from blue oak (*Quercus douglasii*) trees in the northern Sierra Nevada foothills of California. Plant Soil 214, 27–38.
Muller, R.N., Liu, Y., 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Can. J. For. Res. 21, 1567–1572.
Park, B.B., Yanai, R.D., 2007. Estimating root biomass in rocky soils using pits, cores, and allometric equations. Soil Sci. Soc. Am. J. 71, 206–213.
Paul, E.A., Clark, F.E., 1996. Soil Microbiology and Biochemistry. Academic Press, New York.
Perala, D.A., Alban, D.H., 1982. Biomass, nutrient distribution and litterfall in Populus, Pinus and Picea stands on two different soils in Minnesota. Plant Soil 64, 177–192.
Perala, D.A., Alban, D.H., 1994. Allometric biomass estimators for aspen-dominated ecosystems in the Upper Great Lakes. U.S. Forest Service Research Paper NC-134, 38. U.S. Department of Agriculture, Forest Service, Northcentral Research Station. 216p.
Pregitzer, K.S., Euskirchen, E., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Glob. Change Biol. 10, 2052–2077.
Pregitzer, K.S., Laskowski, M.J., Burton, A.J., et al., 1998. Variation in sugar maple root respiration with root diameter and soil depth. Tree Physiol. 18, 665–670.
Pregitzer, K.S., Loya, W., Kubiske, M., et al., 2006. Soil respiration in northern forests exposed to elevated atmospheric carbon dioxide and ozone. Oecologia 148, 503–516.
Reed, D.D., Pregitzer, K.S., Liechty, H.O., et al., 1994. Productivity and growth efficiency in sugar maple forests. For. Ecol. Manage. 70, 319–327.
Reich, P.B., Bolstad, P., 2001. Productivity of evergreen and deciduous temperate forests. In: Roy, J., Saugier, B., Mooney, H.A. (Eds.), Terrestrial Global Productivity. Academic Press, San Diego, CA, pp. 245–283.
Row, C., Phelps, R.B., 1996. Wood carbon flows after timber harvest. In: Neil Sampson, R., Hair, Dwight (Eds.), Forests and Global Change Volume Two – Forest Management Opportunities, American Forests, Washington, DC, pp. 27–58.
Ryan, M.G., Binkley, D., Fownes, J., Giardina, C.P., Senock, R., 2004. An experimental test of the causes of forest growth decline with stand age. Ecol. Monogr. 74, 393–414.
Ryan, M.G., Harmon, M.E., Birdsey, R.A., Giardina, C.P., et al., 2010a. A Synthesis of the Science on Forests and Carbon for US Forests. Issues in Ecology, Report number 13.
Smith, J.E., Heath, L.S., Skog, K.E., Birdsey, R.A., 2006. Methods for calculating forest ecosystem and harvested carbon with standard estimates for forest types of the United States. General Technical Report NE-343. U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 216p.
Van Miegroet, H.V., Boettinger, J.L., Baker, M.A., et al., 2005. Soil carbon distribution and quality in montane rangeland-forest mosaic in northern Utah. For. Ecol. Manage. 220, 284–299.
Vesterdal, L., Schmidt, I.K., Callesen, I., Nilsson, L.O., Gundersen, P., 2008. Carbon and nitrogen in O horizon and mineral soil under six common European tree species. For. Ecol. Manage. 255, 35–48.
Wang, C., Yang, J., Zhang, Q., 2006. Soil respiration in six temperate forests in China.
Washburn, C.M., Arthur, M.A., 2003. Spatial variability in soil nutrient availability in a oak-pine forest: potential effects of tree species. Can. J. For. Res. 33, 2321–2330.
Yanai, R.D., Park, B.B., Hamburg, S.P., 2006. The vertical and horizontal distribution of roots in northern hardwood stands of varying age. Can. J. For. Res. 36, 450–459.
Young, H.E., Ribe, J.H., Wainwright, K. 1980. Weight tables for tree and shrub species in Maine. Life Sciences and Agriculture Experiment Station, University of Maine at Orono, Miscellaneous Report 230, 84.
Zavitkovski, J., 1976. Ground vegetation biomass, production, and efficiency of energy utilization in some northern Wisconsin forest ecosystems. Ecology 57, 694–706.