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Current and Future Carbon Storage Capacity in a Southeastern Pennsylvania Forest

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ABSTRACT

Temperate forests have a strong carbon sink capacity, although the future of this ecosystem service is uncertain in the eastern United States in light of widespread changes affecting succession. This study quantified aboveground carbon accumulation and storage in a southeastern Pennsylvania forest fragment, while assessing whether carbon storage capacity will be supported in the future. Six 0.2 ha plots were censused in 2013 and 2018 for living tree and dead wood carbon storage, as well as tree species composition. Three plots were in a 100-year-old forest, while the remainder were in a 200-year-old forest. Living tree carbon storage increased significantly over time ($p < 0.05$), although dead wood carbon storage did not. Living tree carbon storage, basal area, and stem density were significantly higher in the younger forest ($p < 0.05$). The 200-year-old forest lacked small-diameter stems (<30 cm), relative to the younger forest, although both areas contained many large-diameter trees (>60 cm). Compositional data suggest decreased future canopy tree diversity, with the native *Fagus grandifolia* and nonnative *Acer platanoides* dominating forest understories. While there is high living tree carbon storage capacity, the dead wood pool will increase over time as many large trees die. Intervention to augment regeneration and maintain sink strength in the 200-year-old forest is needed. Action to limit the spread of *A. platanoides* and increase native regeneration throughout the forest will support forest resilience and long-term carbon storage capacity. Assessments of understory conditions are critical in supporting forests' carbon sink capacity into the future.

Index terms: forest age; forest carbon storage; forest composition; mid-Atlantic U.S; temperate forest

INTRODUCTION

Temperate forests play a key role in the global carbon cycle, containing ~14% of global forest carbon stocks and contributing nearly 30% of the global forest carbon sink capacity (Pan et al. 2011a). Within temperate forests of the northern and northeastern United States, much of this sink capacity can be attributed to the legacy of agricultural land clearing and timber extraction, followed by forest regrowth (Birdsey et al. 2006). At present, forests of the region range in age up to ~250 y, although the majority of forest land area is occupied by regrowing forests <100 y old (Pan et al. 2011b). Given its significance to the global carbon cycle, the influence of temperate forest age on productivity and patterns of carbon storage has been a focal area of recent research (Luyssaert et al. 2008; Gough et al. 2016; Curtis and Gough 2018).

It has long been thought that forest productivity, thus carbon sequestration, plateaus during mid-succession, followed by a decline in later succession that eventually leads to carbon-neutral late-successional forests (Kira and Shidei 1967; Odum 1969; Curtis and Gough 2018). Recent evidence contradicts these long-held ideas, particularly as data have become available for temperate deciduous forests (Luyssaert et al. 2008; Gough et al. 2016; Curtis and Gough 2018). Both biometric and eddy covariance data show that these forests continue to accrue carbon after 100+ y of succession, and there is evidence that most late-successional temperate forests continue to act as carbon sinks (Luyssaert et al. 2008; Gough et al. 2016). In addition, late-successional forests serve as important reservoirs

of carbon following centuries of forest growth (Luyssaert et al. 2008; McGarvey et al. 2015). As a whole, the maintenance of temperate forest carbon reservoirs and their associated storage capacity is of critical importance in lessening the intensity of future climate change.

Despite the important contribution of temperate forests to the global carbon sink, the scientific community often fails to address potential threats to this sink capacity. For instance, it is assumed that older forests are structurally complex, with well-developed sub-canopy tree strata, and this structural complexity will continue to support carbon accumulation as older canopy trees die (Luyssaert et al. 2008). This assumption requires investigation, particularly in the United States's temperate deciduous forests, as several agents of change have altered the growing environments in which successional processes are proceeding. Over the past century, once frequent fires have been suppressed and the climate has shifted toward increased moisture availability in the eastern United States (Nowacki and Abrams 2008; McEwan et al. 2011). Additionally, biotic changes including increased abundance of white-tailed deer (*Odocoileus virginianus*), introduction of nonnative, invasive species, and loss of the American chestnut (*Castanea dentata* (Marshall) Borkh.) are transforming many forest ecosystems (Côté et al. 2004; Nowacki and Abrams 2008; McEwan et al. 2011). Therefore, determination of a forest's long-term carbon sink capacity must include assessments of understory forest structure and composition, as typical successional trajectories may be disrupted by these alterations to the growing environment.

The present study sought to determine whether older temperate deciduous forests can maintain relatively high carbon storage capacity and continue to accumulate carbon over time. This study was carried out in a ~36.5 ha forest fragment in southeastern Pennsylvania. Despite its small size, this forest has a mixed land-use history and contains a ~100-year-old forest surrounded by forest ~200 y old. Within this context, the following research questions were addressed: (1) Has above-ground carbon storage in living and dead tree biomass increased over a 5 y period, and do these changes vary with forest age? (2) How have forest structural parameters changed over a 5 y period in the 100-year-old vs. 200-year-old areas of the forest? (3) Is current forest structure and composition likely to support future carbon storage capacity? Because the study area contains a managed natural area, findings will inform future management actions to support the forest's carbon sink capacity.

METHODS

Study Site

Research was carried out in the Gordon Natural Area (GNA; 39°56'8.52"N, 75°35'55.68"W, 107 m a.s.l.), a deciduous forest located in southeastern Pennsylvania on the West Chester University of Pennsylvania campus. The GNA has been protected since 1971, and its 32.4 ha forested core is part of a larger 36.4 ha forest fragment. Aerial photos from 1937 show an 8.1 ha patch of forest in early succession, as evidenced by tightly spaced tree crowns of equal size (Penn Pilot 2019). This area was likely clearcut in the early 1900s, as large trees cored at a height of 1–1.2 m have maximum ages of ~100 y. Soils in this 8.1 ha area show no evidence of a plow horizon. The forest surrounding the 100 y forest to the north and east had an uneven canopy structure in 1937, with large tree crowns interspersed among small and medium-sized crowns (Penn Pilot 2019). Tree cores collected from the largest trees in this area have maximum ages of ~200 y, and, again, there is no evidence of a plow horizon.

The GNA's modern-day forest fragment is surrounded by athletic fields and suburban development. Mean annual temperature is 11.8 °C, with a mean monthly minimum of 0.0 °C in February and a mean monthly maximum of 24.2 °C in July (NOAA 2018). Total annual precipitation averages 1277 mm and is evenly distributed throughout the year (NOAA 2018). Plots censused for this study are distributed across the following soil series: Gladstone (Typic Hapludults), Parker (Typic Dystrudepts), and Califon (Typic Fragiudults) (Helmke et al. 2014; SSS 2018). The GNA contains hiking trails that are cleared when obstructed by debris.

Field Data Collection

Six circular 0.2 ha plots, three in the 100-year-old forest and three in the 200-year-old forest, were established in 2013 and re-censused in 2018. Plot centers are permanently marked with rebar, and two of the six plots encompass short portions of hiking trails. All measurements described below were made in both 2013 and 2018. In each plot, living woody stems ≥10 cm diameter at breast height (dbh, 1.37 m above the ground) were measured for dbh and identified to species or genus in the case

of *Carya* species (twigs and leaves could not be collected for identification). All individuals were categorized as occupying either the canopy or understory environment, where canopy trees were those with leaves exposed to direct overhead sunlight. Naming authority for all species follows the PLANTS Database (USDA NRCS 2019).

Measurements of dead wood were made in each plot. All down (on the forest floor) dead trees ≥10 cm in diameter at the widest point and at least 2 m in length were measured. The length of each down wood segment was measured, and diameter measurements parallel to the forest floor were made at the base (above root flare, if present), midpoint, and top. Because two plots contained trails, some large dead wood had been cut into short logs. Any log ≥1 m in length and 20 cm in diameter was measured for total length, as well as diameter at the base and top. Standing dead trees were also measured; trees with snapped crowns were measured for dbh and bole height, while those with intact crowns were identified to species and dbh was measured. Leaning dead wood was included in the standing wood pool and was measured for dbh and total length. All dead wood was categorized as hollow or solid, and a decay class based on visual inspection was assigned after Harmon et al. (2011).

Data Processing and Analyses

Data collected in 2013 and 2018 were processed identically with the following procedures. Within each plot, stem density and basal area were calculated for all trees ≥10 cm dbh. Aboveground biomass (AGBM) for each measured tree was calculated using allometric equations for North American tree species. Separate equations grouped species by taxonomy (family or genus) and wood-specific gravity to determine AGBM as

$$\ln(\text{AGBM}) = \beta_0 + \beta_1 \ln(\text{dbh}) \quad (\text{Eq.1})$$

where AGBM is dry biomass (kg) and β_0 and β_1 are constants (Chojnacki et al. 2014). One shrub species (*Lonicera maackii* (Rupr.) Herder) occurred in the dataset, so a species-specific allometric equation was used to determine its biomass as

$$\ln(\text{AGBM}) = 3.7992 + 1.7880 * \ln(\text{dbh}) \quad (\text{Eq.2})$$

where AGBM is dry biomass (g; Dickinson and Zenner 2010). Carbon content of AGBM was determined by halving biomass measurements.

Volume for down dead wood was calculated with the equation

$$V = L/12 \left[5A_b + 5A_u + 2\sqrt{(A_b A_u)} \right] \quad (\text{Eq.3})$$

where V is volume (m^3), L is total length of the measured segment (m), A_b (cm^2) is cross-sectional area at the base, and A_u (cm^2) is cross sectional area at the top (Fraver et al. 2007). This calculation was performed independently for the top and bottom segments of CWD ≥2 m in length. The equation for a cylinder was used to determine cut log volume (using mean diameter) and leaning or standing dead tree volume (using dbh). Biomass for dead wood with volume measurements was determined as the product of wood volume and mean density associated with the assigned decay class (Harmon et al. 2011). The biomass of standing dead trees with intact crowns was

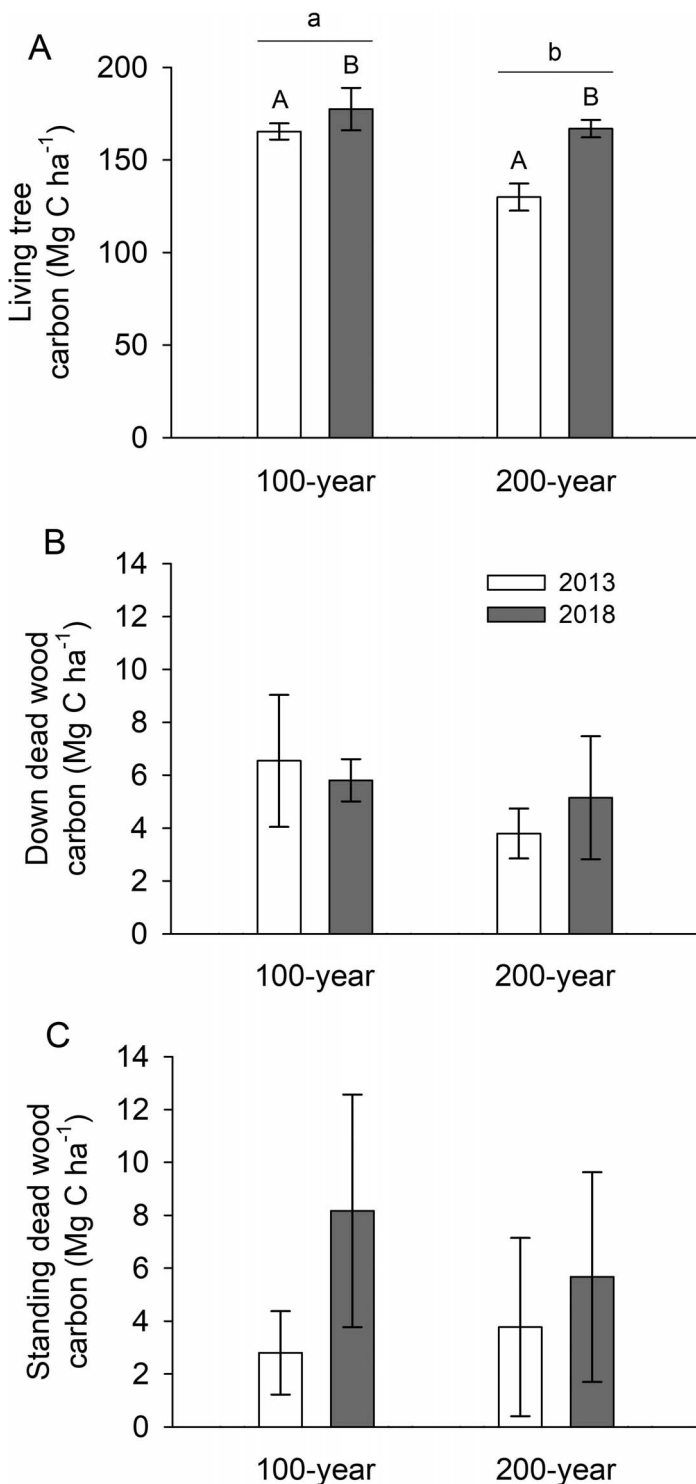


Figure 1.—(A) Mean $\pm$ one standard error of living tree carbon (Mg C ha⁻¹), (B) down dead wood carbon (Mg C ha⁻¹), and (C) standing dead wood carbon (Mg C ha⁻¹) by site age (100 or 200 y) and year (2013 or 2018). Lowercase letters indicate significant differences ($p < 0.05$) in site age, while capital letters indicate significant differences in year.

calculated with Eq. 1 and was then subject to a density reduction by decay class (Harmon et al. 2011). Carbon content of down and standing dead wood was determined by decay class after Harmon et al. (2013).

Linear mixed-effects models with the fixed effects year (2013 or 2018), site age (100 or 200 y), and the year $\times$ site age interaction and the random effect plot were used to examine the variables: living tree carbon content, down dead wood carbon content, standing dead wood carbon content, stem density, and basal area. Living tree carbon content and stem density data were also divided into five dbh size classes (10–15, 15.1–20, 20.1–30, 30.1–60, and 60.1+ cm), and data for each size class were analyzed as above to examine living tree carbon content and stem density in greater detail. An ANOVA was performed for each model, and all data were examined for normality and equal variance. The open-source statistical computing software R (v. 3.5.1; R Core Development Team 2018) and the *nlme* package (Pinheiro et al. 2019) were used for these analyses.

Compositional attributes of the plots in 2018 were examined by calculating tree species importance values, composed of relative density, relative dominance, and relative frequency (Curtis and McIntosh 1951). These calculations were performed separately for canopy and understory trees in both the 100 and 200 y plots. Importance values were divided by 3 to express the data on a 0–100 scale. The 2018 data were also used to determine the number of stems in 5 cm dbh classes by species and site age. Species included in this analysis were those with ≥ 5 stems present in either the 100 or 200 y plots, and data were pooled for all plots within a given site age.

RESULTS

Aboveground Carbon Storage

Carbon stored in living tree biomass increased significantly between 2013 and 2018 ($p = 0.0279$; Figure 1A, Table 1) and was significantly higher in the 100 y plots relative to the 200 y plots ($p = 0.0418$; Figure 1A, Table 1). Living trees were divided into dbh classes to examine which size classes were important in determining overall patterns in this carbon pool. These analyses showed that the largest trees (60.1+ cm dbh) were responsible for driving much of the temporal increase in carbon storage, as they exhibited a significant increase in stored carbon between 2013 and 2018 ($p = 0.0026$; Figure 2, Table 1). The four smaller dbh classes showed no significant change in carbon storage over this time period ($p > 0.05$; Figure 2, Table 2). In the two smallest dbh classes (10–15 and 15.1–20 cm), living tree carbon storage was significantly higher in the 100 y plots relative to the 200 y plots ($p = 0.0148$ and 0.0089 , respectively; Figure 2, Table 2). While this pattern was mirrored in the 20.1–30 and 30.1–60 cm dbh classes, no significant differences were detected due to high variance ($p > 0.05$; Figure 2, Table 2). Additionally, site age did not differentially affect living tree carbon storage in the largest (60.1+ cm) dbh class ($p > 0.05$; Figure 2, Table 2).

Carbon storage for both down and standing dead wood did not vary by year or site age ($p > 0.05$; Figure 1B, 1C; Table 1). Variance, particularly for standing dead wood, was high, suggesting substantial spatial heterogeneity in the GNA's dead wood carbon pools (Figure 1B, 1C). Mean carbon storage in both down and standing dead wood, pooled by site age, was 8.46 Mg C ha⁻¹ in 2013 and 12.40 Mg C ha⁻¹ in 2018.

Table 1.—Results of mixed-effects model analyses to examine whether year (2013 or 2018), site age (100 or 200 y), or their interaction affected living tree carbon storage, down dead wood carbon storage, standing dead wood carbon storage, stem density, or basal area.

Statistic	Year	Site age	Year × Site age
Living tree carbon			
<i>F</i>	11.3989	8.7271	2.9124
<i>p</i>	0.0279	0.0418	0.1631
Down dead wood			
<i>F</i>	0.0519	0.6079	0.5985
<i>p</i>	0.8310	0.4791	0.4823
Standing dead wood			
<i>F</i>	1.4626	0.0377	0.3340
<i>p</i>	0.2931	0.8555	0.5943
Stem density			
<i>F</i>	0.5590	38.4522	0.0786
<i>p</i>	0.4962	0.0034	0.7931
Basal area			
<i>F</i>	10.6299	17.1539	4.4378
<i>p</i>	0.0311	0.0144	0.1029

Forest Structure

In terms of overall patterns in forest structure, stem density did not change significantly over time ($p > 0.05$; Figure 3A, Table 1), although basal area increased significantly from 2013 to 2018 ($p = 0.0311$; Figure 3B, Table 1). Both stem density and basal area were significantly higher in the 100 y plots relative to the 200 y plots ($p = 0.0034$ and 0.0144 , respectively; Figure 3A, 3B; Table 1). Stem density data were also examined by dbh class, in part to assess the future growth potential of these forests. The four smallest dbh classes exhibited no significant change in stem density over the 5 y study period ($p > 0.05$; Figure 4, Table 3), but there was a significant increase in the number of large (60.1+ cm) stems over this time period ($p = 0.0033$; Figure 4, Table 3).

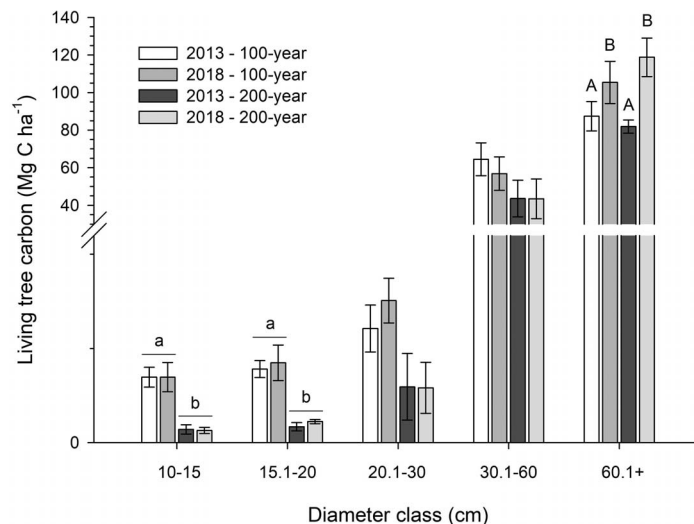


Figure 2.—Mean $\pm$ one standard error of living tree carbon (Mg C ha^{-1}) within five separate diameter classes (cm) by site age (100 or 200 y) and year (2013 or 2018). Analyses were performed separately within each diameter class. Lowercase letters indicate significant differences ($p < 0.05$) in site age, while capital letters indicate significant differences in year for each diameter class.

Table 2.—Results of mixed-effects model analyses to examine whether year (2013 or 2018), site age (100 or 200 y), or their interaction affected living tree carbon storage when data were divided into five tree diameter classes (10–15, 15.1–20, 20.1–30, 30–60, and 60.1+ cm). Analyses were performed separately for each diameter class.

Statistic	Year	Site age	Year × Site age
10–15 cm			
<i>F</i>	0.0354	16.8719	0.0393
<i>p</i>	0.8599	0.0148	0.8525
15.1–20 cm			
<i>F</i>	0.6030	22.6424	0.0048
<i>p</i>	0.4808	0.0089	0.9484
20.1–30 cm			
<i>F</i>	4.0745	3.8881	4.6775
<i>p</i>	0.1137	0.1199	0.0966
30.1–60 cm			
<i>F</i>	0.5606	1.9081	0.5220
<i>p</i>	0.4956	0.2393	0.5100
60.1+ cm			
<i>F</i>	44.8330	0.1132	5.3305
<i>p</i>	0.0026	0.7534	0.0821

The significantly higher overall stem density observed for the 100 y plots (Figure 3A) was largely driven by significantly higher stem density in the two smallest dbh classes (10–15 and 15.1–20 cm, $p = 0.0120$ and 0.0161 , respectively; Figure 4, Table 3). As was the case with aboveground carbon storage, this pattern was reflected in the next two largest dbh classes (20.1–30 and 30.1–60 cm), but was not significant due to high variance, nor was there any difference observed in the largest dbh class ($p > 0.05$; Figure 4, Table 3). Overall, the 100 y plots had the largest number of stems in the smallest dbh class, while the 200 y plots had the lowest stem density in the three smallest diameter classes (Figure 4).

Canopy and Understory Tree Species: Composition and Structure

Analyses of tree species composition focused on the most recently collected data from 2018. At this time, 100% of trees with a dbh ≤ 30.0 cm were classified as understory trees, while 35.8% of trees from 30.1 to 60 cm and 1.4% of trees 60.1+ cm were understory trees (data not shown). Fifteen tree species or genera (in the case of *Carya* sp.) and one shrub species were observed at the study sites, although their distribution varied by canopy position (i.e., understory vs. canopy) and site age (Table 4). While 11 canopy species were found in the 200 y plots, only four occurred in the 100 y plots. Dominant canopy tree species in the 200 y plots, with importance values over 40, included *Carya* sp., *Fagus grandifolia* Ehrh., and *Liriodendron tulipifera* L. (Table 4). While *L. tulipifera* was also dominant in the 100 y plots' canopy, its co-dominant was *Quercus rubra* L. (Table 4). Collectively, *Quercus* sp. represented an important component of the canopy in both the 100 and 200 y plots (Table 4). Two nonnative, invasive species, *Ailanthus altissima* (Mill.) Swingle and *Paulownia tomentosa* (Thunb.) Siebold and Zucc. ex Steud., were found in the canopy of the 200 y plots, though both were relatively uncommon (Table 4).

The understory environments of these forests were more similar, in terms of number of species, with eight in the 100 y

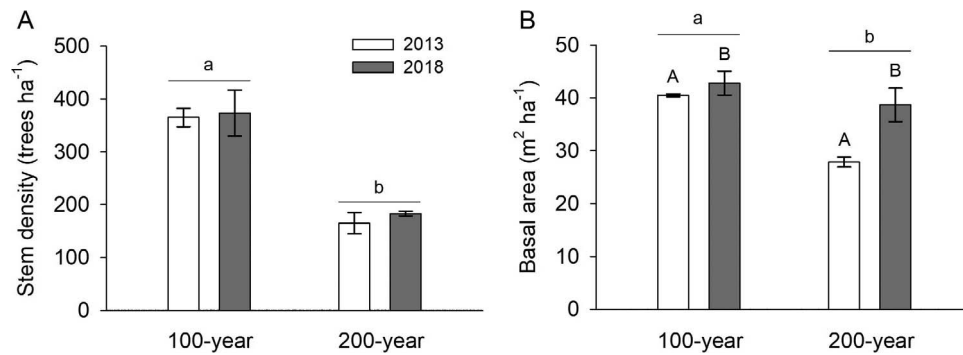


Figure 3.—(A) Mean $\pm$ one standard error of stem density (trees ha⁻¹) and (B) basal area (m² ha⁻¹) by site age (100 or 200 y) and year (2013 or 2018). Lowercase letters indicate significant differences ($p < 0.05$) in site age, while capital letters indicate significant differences in year.

plots and nine in the 200 y plots. Six species occurred in both sets of plots. *Fagus grandifolia* had the highest importance value in both forest types (72 and 71, in the 100 and 200 y plots, respectively), followed by the nonnative, invasive *Acer platanoides* L. with importance values in the 40s (Table 4). It should be noted that no *A. platanoides* trees occurred in the canopies of the 100 or 200 y plots, but this species represented $>18\%$ of the understory stem density in both areas and occupied 18.8% (100 y) and 6.1% (200 y) of the understory basal area (Table 4). The only other nonnative species observed was the invasive shrub *L. maackii*, which occurred with low frequency in the understory of the 200 y plots (Table 4).

Notable differences in composition between the canopy and understory environments were observed for *Quercus* sp., which were rare in the understory with low importance values, and *Acer rubrum* L., which had higher importance values in the understory than the canopy, particularly in the 100 y plots (Table 4). Also, while *L. tulipifera* were present in both understory environments, the species had lower importance

values relative to the canopy (Table 4). These observations were also reflected in tree species diameter distribution data (Figure 5). *Quercus* sp. were almost entirely lacking from dbh classes below 40 cm across site ages (Figure 5). The four smallest diameter classes (<30 cm dbh, representing only understory trees) in the 100 y plots were dominated by *F. grandifolia*, *A. platanoides*, *Carya* sp., and *A. rubrum*, in descending order of total number of stems (Figure 5). In the 200 y plots, only *F. grandifolia* and *A. platanoides* had more than five stems present in the four smallest dbh classes (Figure 5). Small-diameter (<30 cm) *L. tulipifera* trees were rare in the understory, regardless of forest age (Figure 5).

DISCUSSION

Consistent with recently reported findings for temperate deciduous forests (Luyssaert et al. 2008; Gough et al. 2016; Curtis and Gough 2018) and more locally for mid-Atlantic forests (Pan et al. 2009), a significant increase in the GNA's living tree carbon storage was found over the 5 y study period (Figure 1A). Despite the short study duration, this demonstrates

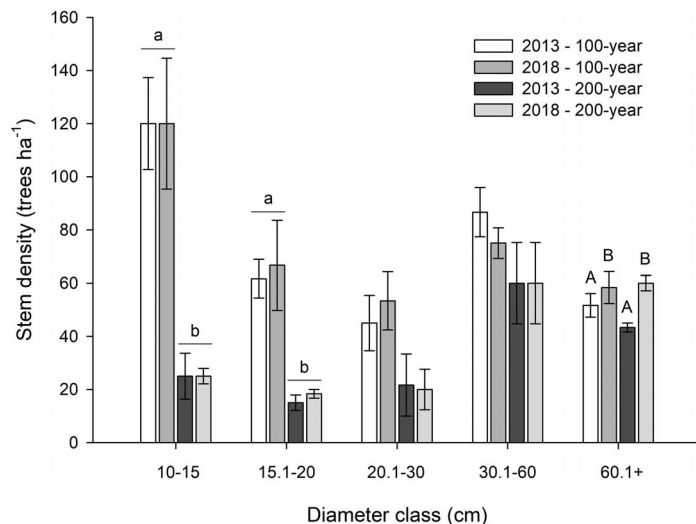


Figure 4.—Mean $\pm$ one standard error of stem density (trees ha⁻¹) within five separate diameter classes (cm) by site age (100 or 200 y) and year (2013 or 2018). Analyses were performed separately within each diameter class. Lowercase letters indicate significant differences ($p < 0.05$) in site age, while capital letters indicate significant differences in year for each diameter class.

Table 3.—Results of mixed-effects model analyses to examine whether year (2013 or 2018), site age (100 or 200 y), or their interaction affected stem density when data were divided into five tree diameter classes (10–15, 15.1–20, 20.1–30, 30–60, and 60.1+ cm). Analyses were performed separately for each diameter class.

Statistic	Year	Site age	Year $\times$ Site age
10–15 cm			
<i>F</i>	0.0000	19.0837	0.0000
<i>p</i>	1.0000	0.0120	1.0000
15.1–20 cm			
<i>F</i>	0.5102	16.0049	0.0204
<i>p</i>	0.5145	0.0161	0.8933
20.1–30 cm			
<i>F</i>	1.1429	3.9862	2.5714
<i>p</i>	0.3453	0.1166	0.1841
30.1–60 cm			
<i>F</i>	0.6712	1.7908	0.6712
<i>p</i>	0.4586	0.2518	0.4586
60.1+ cm			
<i>F</i>	39.1994	0.3721	7.1999
<i>p</i>	0.0033	0.5748	0.0550

Table 4.—Importance values (relative density, relative dominance, and relative frequency summed and divided by 3 to express values on a 0–100 scale) for all woody stems ≥ 10 cm diameter at breast height. Data were divided by canopy and understory growing environments, as well as site age (100 or 200 y). The presence of a dash indicates that a given species was not found. Species designated with (NN) indicate nonnative invasives. Summary data for stem density, basal area, and the percent contribution of invasive species to these categories are also reported.

Species	Canopy		Understory	
	100-year	200-year	100-year	200-year
<i>Acer negundo</i>	–	–	–	12
<i>Acer platanoides</i> (NN)	–	–	46	41
<i>Acer rubrum</i>	–	12	39	14
<i>Ailanthus altissima</i> (NN)	–	12	–	–
<i>Carya</i> sp.	–	45	38	27
<i>Fagus grandifolia</i>	–	48	72	71
<i>Fraxinus americana</i>	35	–	13	–
<i>Fraxinus pennsylvanica</i>	–	–	–	12
<i>Juglans nigra</i>	–	12	–	–
<i>Liriodendron tulipifera</i>	77	57	24	31
<i>Lonicera maackii</i> (NN)	–	–	–	12
<i>Nyssa sylvatica</i>	–	13	11	–
<i>Paulownia tomentosa</i> (NN)	–	12	–	–
<i>Quercus alba</i>	–	31	–	–
<i>Quercus rubra</i>	53	12	13	12
<i>Quercus velutina</i>	24	12	–	–
Parameter				
Stem density (trees ha ⁻¹)	120	83	253	100
Basal area (m ² ha ⁻¹)	35.77	27.45	7.02	7.83
Density of invasives (%)	0	4.0	20.4	21.7
Basal area of invasives (%)	0	2.5	18.8	6.5

that both the younger (100 y) and older (200 y) portions of the GNA's forest continued to accumulate carbon in living aboveground biomass. The significant contribution of large-diameter trees (60.1+ cm) to this increase in carbon storage (Figures 2, 4) reflects a relatively new understanding of the important role of large trees in continued forest carbon accumulation over time (Stephenson et al. 2014). While the magnitude of the increase in total carbon storage over the 5 y study period was greatest in the GNA's 200 y plots, overall living tree carbon storage was significantly higher in the 100 y plots (Figure 1A). This pattern was largely explained by structural differences between the two forest types, as the 100 y plots contained many more small-diameter stems than the 200 y plots (Figure 4). Collectively, these small stems contributed to higher overall living tree carbon storage in the 100 y forest (Figure 2). In the 200 y plots, the increase in living tree carbon storage was driven almost entirely by the growth of large-diameter trees (Figure 2).

As eastern deciduous forests mature and canopy gaps created by windthrow or tree death become common, the general expectation is that new canopy openings will facilitate release of advance regeneration and recruitment of new trees into the canopy (Runkle 1982). Such a low-intensity, high-frequency disturbance regime typically maintains a structurally diverse forest capable of supporting continued carbon accumulation (Luyssaert et al. 2008). In the GNA, forest structure in the 100 y plots aligns with this paradigm, but this is not the case for the

200 y plots. In comparison with a global dataset for deciduous broadleaf forests reporting on both mature and old-growth forests, it is evident that the GNA's 200 y plots have lower than typical stem density despite near-average basal area and living aboveground biomass (Burrascano et al. 2013). The paucity of stems ≤ 30 cm dbh and the increased number of large-diameter stems over the 5 y study period suggests that intervention may be required to augment regeneration and maintain the sink strength of the GNA's 200-year-old forest as larger trees begin to die (Figures 4 and 5). The underlying cause of such poor regeneration is unknown, but may be related to low canopy tree mortality and/or gap closure dominated by lateral tree growth (i.e., small gaps).

Because of the mid-Atlantic region's land-use history, most forests in the area are relatively young (< 100 y; Pan et al. 2011b), with much lower basal area and living tree carbon stocks (Jenkins et al. 2001) than found in the GNA's forests. However, a recent summary of carbon storage capacity in remaining old-growth forests of the mid-Atlantic provides an approximate upper limit on aboveground carbon storage for living and dead tree biomass of 154 ± 47 (SD) and 46 ± 30 Mg C ha⁻¹, respectively (McGarvey et al. 2015). Living tree carbon storage from the GNA fell within this range, but carbon stored in the GNA's dead wood was considerably lower, regardless of forest age (Figure 1). These findings demonstrate substantial carbon storage capacity in live trees, but suggest that with time, the dead wood pool is likely to increase throughout the GNA. These changes are likely imminent, as there are many large-diameter (> 60 cm) stems across both forest ages (59.2 ± 3.0 stems ha⁻¹, mean $\pm$ SE), and the quantity of standing dead wood in the GNA is relatively low.

While forest structural data raise concerns about the future growth potential and carbon storage capacity of the GNA's 200-year-old forest, differences in tree species composition between the canopy and understory are cause for concern in both the younger and older forest areas. The GNA's forest shows some evidence of a widely reported pattern throughout eastern North America in which *Quercus* sp. in the canopy are replaced by *Acer* sp. throughout the understory (Lorimer 1984; McEwan et al. 2011). Both the 100- and 200-year-old forests in the GNA have canopies in which *Quercus* sp. are an important component, but the genus is largely absent from the forest understory (Figure 5, Table 4). The rise in importance of *Acer* sp. in the understory has occurred throughout the forest, despite a lack of *Acer* sp. in the canopy of the censused plots. A combination of factors, including changing fire dynamics, climate, and herbivore populations, as well as progressive forest mesophication and loss of the American chestnut likely influenced this shift in species composition (Nowacki and Abrams 2008; McEwan et al. 2011). The *Quercus* to *Acer* transition is typically characterized by increased regeneration of *A. rubrum* and *Acer saccharum* (e.g., Lorimer 1984; McCarthy et al. 1987; Dodge 1997), although in the GNA, it is *A. rubrum*, and to a greater extent the nonnative, invasive *A. platanoides* that have increased in understory abundance. *Acer platanoides* can increase height growth faster than native tree species, inhibit survival of natives growing beneath its canopy, and is not known to be browsed by deer (Munger 2003; Galbraith-Kent and Handel 2008; Martin et al.

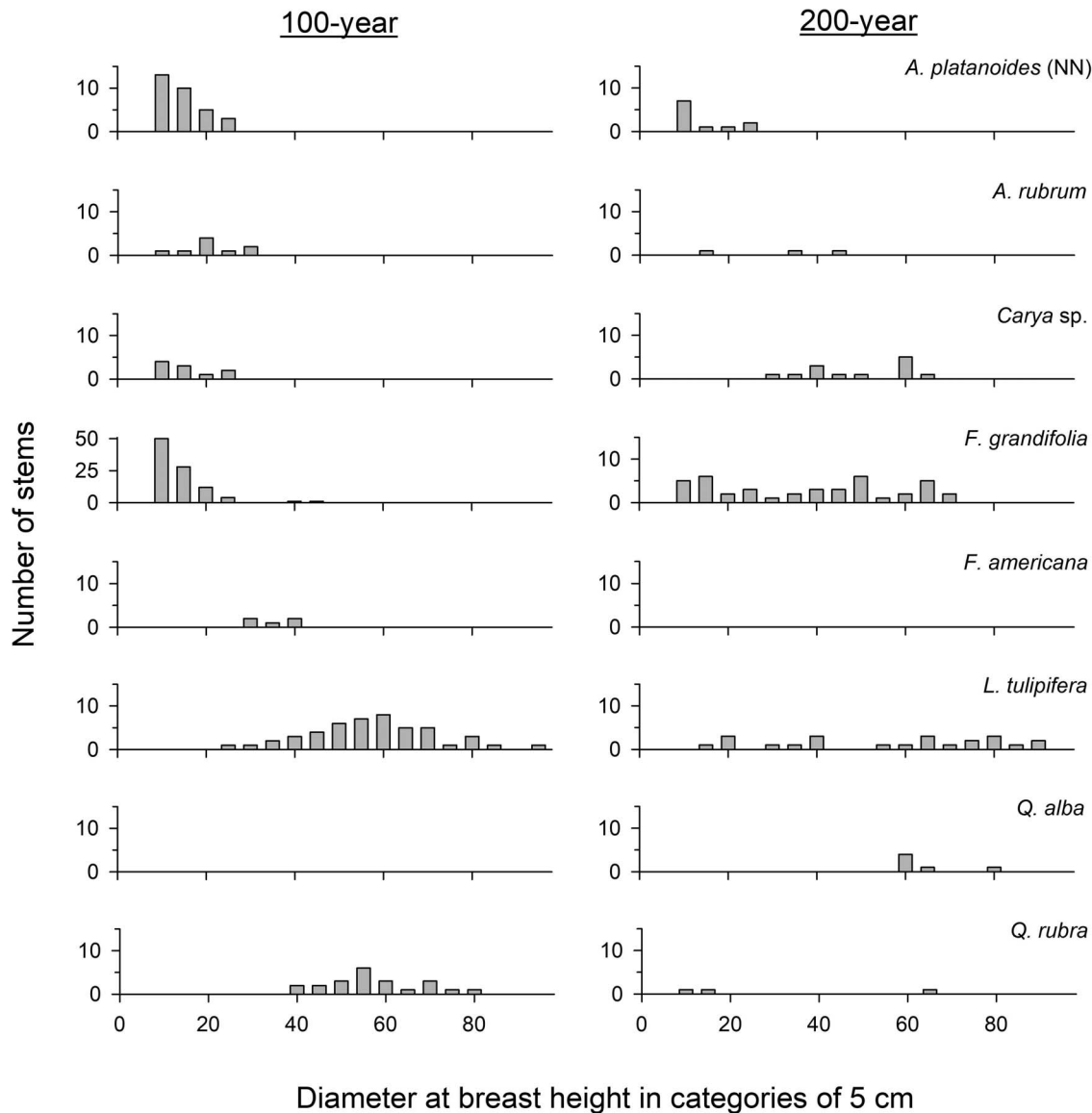


Figure 5.—Number of tree stems per 5 cm diameter at breast height (dbh) category for species represented by at least five stems in the 100 or 200 y plots during the 2018 sampling period. Presented data were pooled across the three 0.2 ha plots per site age. Species designated with (NN) indicate nonnative invasives. Note the large magnitude *y*-axis for the 100 y *F. grandifolia* panel, relative to other panels.

2010, Paquette et al. 2012). The presence of this species throughout the GNA's understory has the potential to limit future native tree species regeneration and may require active management to constrain its spread.

The understory composition of the 100 y plots indicates that this forest, although adjacent to the 200-year-old tract of forest, is developing along a different successional trajectory. While *F. grandifolia* and *Carya* sp. are likely to be important future canopy species in the 100 y forest, similar to the current 200 y forest, points of divergence emerge, as it is probable that *A. rubrum* and *A. platanooides* will become canopy species and *L. tulipifera* may decline in the canopy over the next 100 y (Figure 5, Table 4). Several of these likely future dominants have been identified as those playing a role in the progressive mesophication of eastern forests (Nowacki and Abrams 2008). This process

excludes more fire-resistant and less shade-tolerant trees, including *Quercus* sp., and also leads to a self-reinforcing feedback loop favoring mesophytic species (Nowacki and Abrams 2008). Mesophication has likely been bolstered by a changing climate with more infrequent droughts and greater moisture availability, as well as changes in herbivore populations affecting *Quercus* sp. recruitment (McEwan et al. 2011). Included in the latter agent of forest change is increased white-tailed deer populations, which often favors the regeneration of species with known deer browse resistance, including *F. grandifolia*, *A. platanooides*, and several *Carya* species (Tubbs and Houston 1990; Munger 2003; Tripler et al. 2005; Krueger et al. 2009; Bressette et al. 2012; McGarvey et al. 2013). These are three of the more common understory species/genera in the GNA's

forests (Figure 5), and the site is known to have high deer density (D'Angelo 2009).

Overall, variation in successional trajectories between adjacent forests of varying age in the GNA is perhaps unsurprising given the suite of modern pressures on these forests. As described above, today's growing environment contrasts considerably with that present 100–200 y ago. In fact, despite low understory stem density in the 200 y plots, this forest may experience changes in tree species composition similar to those likely in the 100 y forest (Figure 5, Table 4). Similar findings demonstrating divergent successional trajectories by forest age but convergent understory composition have been reported in other eastern deciduous forests (Drury and Runkle 2006). The present study suggests that pressures including mesophication and increased deer density are contributing to the high importance values and abundance of *F. grandifolia*, *A. platanoides*, and *Carya* sp. in the understory. With time, both the younger and older forests of the GNA may come to be dominated by a fairly homogenous suite of tree species. This is cause for concern, as maintenance of diversity supports ecosystem resilience and provisioning of ecosystem services, including carbon storage (Elmqvist et al. 2003).

Conclusions

Although the present-day forests of the GNA support aboveground carbon accumulation and substantial living tree carbon pools, maintenance of these conditions is uncertain. Management action to augment regeneration in the 200-year-old areas of the forest will likely be required to support the forest's carbon sink strength into the future. Further, while the rise of *A. platanoides* throughout the GNA's understory may not threaten carbon storage capacity directly, it has the potential to limit native tree regeneration (Galbraith-Kent and Handel 2008). When coupled with the dominance of only a few species in diameter classes below 30 cm, the prospect of a more compositionally homogeneous forest canopy seems probable. As ecosystem resilience to change declines with decreased diversity, and these forests are currently beset by change, action to limit the spread of *A. platanoides* and support native regeneration throughout the understory is likely merited. Because the pressures experienced by the GNA are not uncommon in the United States's temperate deciduous forests (Côté et al. 2004; Webster et al. 2006; Nowacki and Abrams 2008), the present study suggests that forest managers should be attuned to understory tree species density and composition. While forest recovery from prior land-use history in the northern and northeastern United States has supported considerable carbon sequestration to date (Birdsey et al. 2006), intervention may be necessary to sustain this important ecosystem service and support forest resilience in the future.

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