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Aboveground carbon biomass of plantation-grown American chestnut (*Castanea dentata*) in absence of blight

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ABSTRACT

Forest management activities may help reduce global net CO_2 concentrations by capturing and storing atmospheric CO_2. Research related to carbon sequestration potential of plantations in North America has focused predominantly on conifers, with relatively little emphasis thus far on temperate deciduous forest tree species. American chestnut (*Castanea dentata* (Marsh.) Borkh.), a former dominant tree species in eastern North America until its demise associated with the introduced chestnut blight (*Cryphonectria parasitica* (Murr.) Barr.), is a temperate deciduous species that holds promise for future carbon sequestration programs with expected availability of blight-resistant backcross hybrids. We quantified aboveground biomass and bole carbon of American chestnut interplanted with black walnut (*Juglans nirga* L.) and northern red oak (*Quercus rubra* L.) across four blight-free experimental sites varying in site quality and/or age (8, 8, 12, and 19 years) isolated from the native American chestnut range in the Coulee Region of southwestern Wisconsin, USA. American chestnut exhibited more rapid growth and greater aboveground biomass and bole carbon than either of the other interplanted species. Aboveground biomass ranged from 46.9, 60.7, 55.0, and 179.9 Mg ha^{-1} for the 8-, 8-, 12-, and 19-year-old sites, respectively, while bole carbon content ranged from 13.6, 18.6, 14.1, and 60.1 Mg ha^{-1} for the 8-, 8-, 12-, and 19-year-old sites, respectively. Cross-referencing our data to studies conducted within this same physiographic region using other important forestry species (i.e., *Populus tremuloides* Michx., *Pinus resinosa* Ait., and *Pinus strobus* L.) showed that American chestnut compared favorably in growth and carbon uptake. Incorporating American chestnut into carbon sequestration plantations provides additional ecological and economic benefits associated with consistent production of quality nuts for wildlife, valuable timber, and contribution toward species restoration. Our data lend support to building evidence demonstrating rapid and sustained growth of American chestnut and the potential role of plantation-grown American chestnut in helping to mitigate climate change through carbon sequestration.

1. Introduction

Recent trends in greenhouse gas concentrations have created concern associated with climate change. Warming of the climate system is unequivocal, as is now evident from observations of increased global air and ocean temperatures, widespread melting of snow and ice, and rising global average sea level (IPCC, 2007). Land use changes from forestry to other uses, as well as greenhouse gas emissions associated with exploitation of fossil fuels have disrupted the planet's fragile carbon balance (Wigley and Schimel, 2000).

Forested ecosystems may help contribute toward carbon sequestration by capturing and storing atmospheric CO_2 where it is not immediately re-emitted to the atmosphere. Globally, concentrations of CO_2 in the atmosphere are rising by only 3.2 Pg C $year^{-1}$, while fossil fuel emissions release 6.3 Pg C $year^{-1}$, reflecting an apparent carbon sink of 2.7–3.1 Pg C $year^{-1}$ (Prentice et al., 2001; Gurney et al., 2002). Between 1988 and 1992, there was a net terrestrial uptake of CO_2 of magnitude 1.7 ± 0.5 Pg C $year^{-1}$ in North America (Fan et al., 1998). Forests are the primary source of terrestrial carbon uptake, storing approximately two-thirds of Earth's terrestrial carbon (Brown et al., 1993). Woodbury et al. (2007) estimated that the conterminous U.S. annually sequesters 149–330 Tg C $year^{-1}$, with forests, urban trees, and wood products being responsible for 65–91% of this sink. These trends have created increased interest in managing forests for carbon sequestration.

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The Kyoto Protocol, regional greenhouse gas programs, and a burgeoning voluntary carbon market currently offer financial incentives for reducing atmospheric CO_2 concentrations. This can be done by reducing actual emissions or by increasing the amount of carbon sequestered by the environment (UNFCCC, 1997). Although the U.S. is not a Party to the Kyoto Protocol, there are numerous other carbon-based markets that recognize a wide variety of terrestrial carbon sequestration activities as potentially viable means for reducing atmospheric CO_2 concentrations (Niu and Duiker, 2006). Additionally, the U.S. Congress is expected to pass federal climate change legislation that is likely to include a comprehensive cap-and-trade program, which will allow regulated entities to use carbon offsets to meet their greenhouse gas emission obligations. The utilization of existing carbon markets and anticipation of future regulation has spurred U.S. companies to actively sequester carbon to create tradable carbon offsets.

Forest management practices offer a unique means of offsetting greenhouse gas emissions (Marland and Schlamadinger, 1997). Among forest management options for carbon sequestration, afforestation (i.e., establishment of trees on land not previously forested) has been recognized as a cost-effective and environmentally beneficial strategy for carbon sequestration (see citations in Niu and Duiker, 2006). Under the established greenhouse gas programs and markets, carbon sequestered through afforestation may be used to create tradable offsets that regulated entities can use to meet their greenhouse gas emission reduction commitments (Watson et al., 2000). Although research related to carbon sequestration of forests in North America has focused predominantly on conifers, afforestation of temperate deciduous species also represents a potential means of carbon sequestration, particularly in regions with an abundance of marginal agricultural lands, such as the Midwestern U.S. (Niu and Duiker, 2006).

American chestnut (*Castanea dentata* (Marsh.) Borkh.) is a temperate deciduous species that may hold promise for future carbon sequestration programs. American chestnut was once one of North America's most important trees (Braun, 1950), representing 40–45% of the forest canopy in portions of its native range (Keever, 1953). In all but a few isolated areas, however, chestnut blight (*Cryphonectria parasitica* (Murr.) Barr.) destroyed the range of American chestnut in North America (Hepting, 1974; McCormick and Platt, 1980; Anagnostakis, 1987; Youngs, 2000). The blight fungus was first discovered in New York City in 1904 (Roane et al., 1986) and spread rapidly through the American chestnut range (Hepting, 1974). Within four decades, nearly every American chestnut tree had been infected and the species was eliminated as a dominant forest tree. Identifying trees with demonstrated resistance to the fungus has been futile (Hepting, 1974) and early attempts at hybridizing the tree with blight resistant chestnut species were abandoned because hybridized trees failed to demonstrate desired characteristics of pure American chestnuts. Burnham (1988) recognized design flaws of earlier hybridization techniques and initiated a new breeding program in association with the non-profit group, The American Chestnut Foundation (TACF). The current TACF breeding program structure is summarized in Hebard (2001, 2006). Briefly, American chestnut was initially hybridized with blight resistant Chinese chestnut (*Castanea mollissima* Blume) and then "backcrossed" three times to American chestnut (leading to BC3F1) with the objective of increasing the proportion of American chestnut alleles while maintaining blight resistance conferred by Chinese chestnut. Progeny from subsequent crosses (BC3F2, BC3F3) are experimentally inoculated with blight and selected for degree of resistance as well as American chestnut phenotype. The BC3F3 trees, which represent the final cross for reintroduction, should average 94% American chestnut and 6% Chinese chestnut. Putatively resistant BC3F3 seed was first harvested by TACF in 2005 (Diskin et al., 2006), and BC3F3 trees should be available for reintroduction within the next decade (Griffin, 2000; Ronderos, 2000).

Although recent studies (Paillet and Rutter, 1989; Jacobs and Severeid, 2004; McEwan et al., 2006) have reported superior growth of American chestnut relative to other temperate deciduous forest tree species, many other basic ecological and silvical attributes of the species have yet to be quantified (Jacobs, 2007). This oversight includes studies of biomass and carbon uptake at the whole tree and stand level. American chestnut has potential as a future species option for carbon sequestration through afforestation programs (Jacobs and Severeid, 2004; Jacobs, 2007), and for long-term carbon storage in the form of forest products associated with the relatively high value and decay resistance of the timber (Youngs, 2000). However, rates of carbon storage and biomass accumulation for this species are unknown. Thus, the objectives of this study were to (i) evaluate aboveground allocation of biomass and carbon storage of plantation-grown American chestnut on four different plantation sites of varying age (i.e., 8–19 years) and/or site characteristics in the Coulee region of southwestern Wisconsin, USA, and (ii) compare observed trends to other important forest tree species of this region growing on the same experimental sites or through cross-reference to published literature. Our study sites provided a unique opportunity to accomplish these objectives as the plantations were isolated from the natural range and exhibited no evidence of blight.

2. Materials and methods

2.1. Study area and climatic conditions

The Coulee region of southwestern Wisconsin, USA is not part of the natural range of American chestnut (Fig. 1), but the tree has thrived in that region where it has been planted (Paillet and Rutter, 1989; Jacobs and Severeid, 2004; McEwan et al., 2006). In the late 1800s and early 1900s, settlers from eastern U.S. forests introduced American chestnut to the region and these trees largely escaped blight infection due to their isolation from the native range (Paillet and Rutter, 1989). There are refuges of American chestnut trees in

Fig. 1. The range of American chestnut (*Castanea dentata* (Marsh.) Borkh.), adapted from Little (1977), and approximate location of the Rockland and La Crosse, Wisconsin experimental plantation sites.

Table 1
Environmental parameters of experimental sites.

Site	Soil series	Taxonomic description	Site index (m)	Slope (%)	Aspect (°)
8 yr – site 1	Urne	Fine-silty, mixed, mesic Mollic Hapludalf	18.3[a]	12	255
8 yr – site 2	Council	Coarse-loamy, mixed, mesic Fluvaquentic Hapludoll	20.1[a]	17	40
12 yr	Coffeen	Coarse-silty, mixed, mesic Fluvaquentic Hapludoll	19.8[b]	4	30
19 yr	Fayette	Fine-silty, mixed, mesic Typic Hapludalf	19.2–22.9[a]	24	85

[a] Determined for northern red oak (*Quercus rubra* L.), reference age = 50 yr.
[b] Determined for white ash (*Fraxinus americana* L.), reference age = 50 yr.

Vernon, La Crosse, Trempealeau, and Monroe counties of Wisconsin. A site near West Salem contains the largest known remaining stand of American chestnuts in the U.S. A few seeds were planted around the turn of the century and have since naturalized to about 20 ha of woodland (Paillet and Rutter, 1989).

This project was conducted on three different sites (two 8-year-old and one 12-year-old) located near Rockland, WI, and a site (19-year-old) near West Salem, WI. All sites differed from each other in terms of aspect, slope, soil series and site index (Table 1), but conditions were relatively homogeneous within each site. For all sites, American chestnut seeds were collected from the aforementioned stand near West Salem, WI, believed to have been established from seed of Pennsylvania, USA origin (Paillet and Rutter, 1989) and from a stand near Trempealeau, WI.

Historically, the Rockland study area was intensively cultivated and grazed, but these activities were abandoned on the property as of 1978. Three species were interplanted to establish the study sites: American chestnut, northern red oak (*Quercus rubra* L.), and black walnut (*Juglans nigra* L.). The 8-year-old sites were planted via direct seeding at 1.52 m × 1.83 m. The 12-year-old site was planted using a mixture of direct seeding and seedlings at 3.05 m × 3.66 m. At time of sampling, the Rockland property had approximately 450 American chestnut trees.

The West Salem stand was established in 1985 using interplanted American chestnut, black walnut, and white spruce (*Picea glauca* (Moench) Voss) seedlings at 2.13 m × 2.44 m with white spruce interplanted. Northern red oak was not established in this stand. The white spruce died soon after planting in the black walnut plantings and was outcompeted in the chestnut plantings. Thus, actual density at the time of the study was 2.44 m × 4.27 m, as the white spruce was no longer significant. At time of sampling, the West Salem property had approximately 45 American chestnuts of age 19 years.

In all stands, herbicide applications (1.7 kg ha^{-1} simazine and 3.4 kg ha^{-1} glyphosate) using a backpack sprayer were made in the spring of each year, prior to budbreak, for the first 3 years following sowing or planting to control competing vegetation. Mechanical cutting to remove woody vegetation and stump sprouts was also performed once per year for the first 3 years following sowing or planting. On the Rockland sites, a chemical deer repellent (Bitrex®) was applied to terminal buds of all seedlings each fall for the first 3 years following sowing or planting. All trees in every stand were pruned regularly but only shaded branches were removed; therefore, effects on growth rates were likely minimal. No fertilizer was ever applied.

2.2. Field measurements

Growth, biomass, and carbon sequestration were quantified in July 2004 using five randomly selected trees from each species at each site (i.e., a total of 20 American chestnuts, 20 black walnuts, and 15 northern red oaks). Basal diameter (5 cm above groundline), diameter at breast height (1.37 m above groundline) (DBH), and crown diameter were measured on standing trees. To determine crown diameter, the crown span of individual trees was measured in four cardinal directions and averaged.

Trees were then felled for processing and total height to terminal leader and crown height were obtained. Based on field observations of form for the three species, crown volume was estimated using the equation for the volume of a cone ($V = 0.2618D^2H$), where V = crown volume D = crown diameter, and H = crown height. Aboveground portions were separated into two components: bole (i.e., main stem and primary branches ≥ 20 cm diameter) and canopy (i.e., remaining branches and leaves). Component mass was collected in the field using a tripod, hanging scale, and pulley hoisting system. Samples (100–800 g), consisting of cross-sections of boles or branches and collections of multiple leaves with petioles, were also collected and weighed in the field on a digital balance for use in carbon analysis.

2.3. Biomass and carbon analysis

Component samples were oven-dried (96 h, 70 °C) and resulting samples were weighed to determine moisture content and dry matter coefficients. Coefficients were applied to the field mass of respective components and tree biomass was estimated. Component samples were then ground and passed through a 20-mesh filter to prepare for carbon analysis. Carbon concentration of bole, branch, and leaf samples was analyzed using a Carlo Erba NA 1500 Series II elemental analyzer (Carlo Erba Strumentazione, Rodano, Italy). Resultant carbon percentages were multiplied by estimated biomass of respective components to calculate carbon content. Bole, crown, and total biomass data were used to assess aboveground biomass production among species in this study and for comparisons to published results with other species in this region. We focused on bole components for evaluations of aboveground carbon content because this reflects long-term carbon storage in the form of wood products in managed forest plantations. Canopy components (i.e., smaller branches and leaves) represent short-term aboveground sites of carbon storage, contributing primarily to forest floor and soil organic carbon pools (Jobbágy and Jackson, 2000; Johnson and Curtis, 2001).

2.4. Statistical analysis

Each site was analyzed as a separate experiment using a completely randomized design to compare American chestnut to the interplanted species at a given age. Individual trees were used as experimental units in an analysis of variance (ANOVA). When $P \leq 0.05$ in the ANOVA, Tukey's HSD procedure was used to determine significant differences among species at $\alpha = 0.05$.

Biomass and carbon estimation equations were developed using linear regression based on data from individual trees among the various sites, which can be used to predict tree and stand biomass on an individual-tree basis (Verwijst and Telenius, 1999) or an area basis (e.g., Heilman et al., 1994). A Log transformation of DBH was used as the predictor variable and Log transformations of biomass and carbon were used as response variables. The model was chosen based on its high R^2 and appropriateness of fit

Table 2
Mean values (±SE) for measured morphological characteristics of American chestnut (*Castanea dentata* (Marsh.) Borkh.), black walnut (*Juglans nigra* L.), and northern red oak (*Quercus rubra* L.) trees across different ages and experimental sites. For each parameter and planting year group, species with the same letter are not significantly different at $\alpha = 0.05$.

Site	Species	Basal diameter (cm)	DBH (cm)	Height (m)	Crown volume (m^3)
8 yr – site 1	*C. dentata*	12.9 (0.4)a	9.3 (0.9)a	8.8 (0.3)a	12.4 (1.9)a
	J. nigra	11.8 (0.6)a	8.5 (0.9)a	8.2 (0.4)a	10.0 (1.9)a
	Q. rubra	6.1 (0.6)b	4.3 (0.2)b	5.1 (0.5)b	2.9 (0.5)b
8 yr – site 2	*C. dentata*	12.4 (0.4)a	7.9 (0.4)a	8.5 (0.2)a	14.3 (1.4)a
	J. nigra	6.1 (0.3)b	4.2 (0.5)b	5.7 (0.4)b	4.1 (0.9)b
	Q. rubra	5.6 (0.7)b	3.8 (1.0)b	5.2 (0.6)b	4.8 (1.3)b
12 yr	*C. dentata*	20.7 (1.7)a	14.8 (2.4)a	9.5 (0.8)a	38.8 (8.8)a
	J. nigra	17.2 (1.6)a	12.4 (1.8)a	8.0 (0.5)a	24.1 (5.0)a
	Q. rubra	14.3 (1.6)a	9.4 (2.4)a	8.6 (0.5)a	15.4 (3.6)a
19 yr	*C. dentata*	35.0 (1.3)a	25.6 (1.8)a	13.6 (0.3)a	97.0 (17.6)a
	J. nigra	27.1 (1.5)b	22.0 (1.7)a	13.9 (0.4)a	76.5 (19.1)a

compared to actual means. JMP IN® statistical software (SAS Institute Inc., Cary, NC, USA) was used for all data analysis.

3. Results

American chestnut consistently exhibited the largest mean size in almost every category at every age on every site (Table 2). Species differed significantly ($P < 0.05$) in DBH on both 8-year-old sites, with American chestnut DBH significantly greater than that of northern red oak on both 8-year-old sites and significantly greater than black walnut on site 2 (Table 2). Similar results occurred for basal diameter, though species also differed significantly ($P < 0.05$) on the 19-year-old site, with basal diameter of American chestnut being significantly greater than that of black walnut (Table 2). Species also differed significantly ($P < 0.05$) for height on both 8-year-old sites, with American chestnut having significantly greater height than northern red oak on both 8-year-old sites and black walnut on site 2. Similarly, the only significant ($P < 0.05$) species differences in crown volume were in the 8-year-old sites, with American chestnut having significantly greater crown volume than northern red oak on both sites and black walnut on site 2.

Biomass was calculated as a product of the field mass of tree components and respective dry matter coefficients, and is reported as bole mass, crown mass, and total biomass (Table 3). American chestnut consistently had greater mean biomass for all components for every age and site except for one of the 8-year-old sites (site 1) where black walnut had a higher mean bole mass. Species differed significantly ($P < 0.05$) for all three components on both 8-year-old sites, with American chestnut having significantly greater biomass than northern red oak on both 8-year-old sites and significantly greater biomass than black walnut on site 2.

Table 3
Mean values (±SE) of bole, crown, and total biomass for American chestnut (*Castanea dentata* (Marsh.) Borkh.), black walnut (*Juglans nigra* L.), and northern red oak (*Quercus rubra* L.) trees across different ages and experimental sites. For each parameter and planting year group, species with the same letter are not significantly different at $\alpha = 0.05$.

Site	Species	Bole (kg)	Crown (kg)	Total (kg)
8 yr – site 1	*C. dentata*	11.2 (1.1)a	5.7 (0.5)a	16.9 (1.4)a
	J. nigra	12.2 (2.6)a	4.1 (0.9)a	16.3 (3.4)a
	Q. rubra	2.2 (0.4)b	1.1 (0.2)b	3.3 (0.5)b
8 yr – site 2	*C. dentata*	8.2 (1.3)a	4.9 (0.8)a	13.1 (1.5)a
	J. nigra	2.0 (0.5)b	1.1 (0.2)b	3.1 (0.7)b
	Q. rubra	2.5 (1.3)b	1.4 (0.8)b	3.9 (2.1)b
12 yr	*C. dentata*	33.8 (7.8)a	27.5 (8.7)a	61.3 (16.1)a
	J. nigra	25.7 (7.0)a	15.2 (4.7)a	40.9 (11.6)a
	Q. rubra	21.3 (8.4)a	11.4 (3.9)a	32.7 (12.1)a
19 yr	*C. dentata*	134.1 (14.4)a	53.5 (6.9)a	187.6 (20.6)a
	J. nigra	125.1 (22.6)a	40.6 (8.6)a	165.7 (31.0)a

There were no significant differences in carbon concentration among species. Values for carbon content were scaled to an area basis (Table 4). Estimated values were then compared to other studies of different species, conducted within this same physiographic region of Wisconsin (Table 4), suggesting that American chestnut compares favorably in carbon sequestration ability with any other species in this region.

Prediction equations were developed for determining total aboveground biomass and carbon content of bole wood on an individual tree level (Fig. 2). Log transformations were used to allow for a linear fit. All equations are in the form Log $Y = b + m$(Log X), where Y is aboveground biomass (kg) or carbon in bole wood (kg) and X is DBH (cm). DBH alone provided an adequate predictor of both aboveground biomass and bole carbon with R^2 values of 0.986 and 0.976, respectively (Fig. 2).

4. Discussion

In the near future, a blight-resistant hybrid of American chestnut will be available for reintroduction and will likely be incorporated into mixed hardwood plantings both within and beyond its native range (Jacobs, 2007). Concurrently, programs are

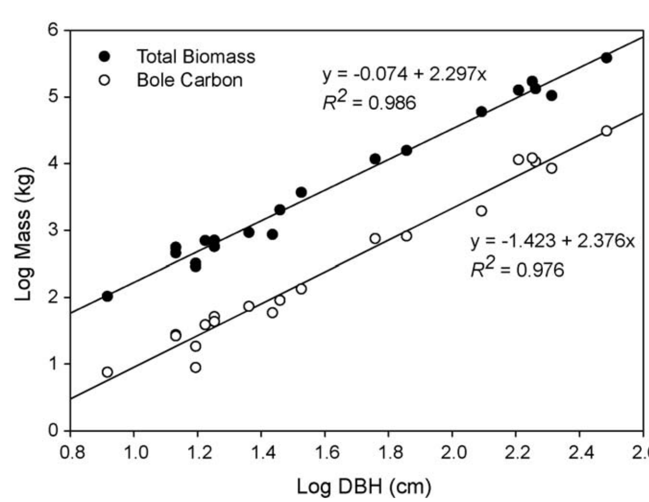

Fig. 2. Relationships between total biomass, bole carbon, and diameter at breast height (DBH) for American chestnut (*Castanea dentata* (Marsh.) Borkh.). All equations are in the form Log $Y = b + m$(Log X), where Y is aboveground biomass (kg) or carbon in bole wood (kg) and X is DBH (cm).

Table 4
Bole, crown, and total biomass and bole carbon for American chestnut (*Castanea dentata* (Marsh.) Borkh.), black walnut (*Juglans nigra* L.), and northern red oak (*Quercus rubra* L.) trees across different ages and experimental sites in this study. Also provided is a comparison of data from other studies using different species (i.e., quaking aspen (*Populus tremuloides* Michx.), red pine (*Pinus resinosa* Ait.), and white pine (*Pinus strobus* L.)), in the same physiographic region of Wisconsin.

	Species	Trees (ha^{-1})	Biomass ($Mg\ ha^{-1}$)			Bole carbon	
			Bole	Crown	Total	(%)	($Mg\ ha^{-1}$)
8 yr – site 1	*C. dentata*	3588	40.3	20.4	60.7	46.22	18.6
	J. nigra	3588	43.7	14.9	58.6	46.20	20.2
	Q. rubra	3588	7.9	4.0	11.9	46.49	3.7
8 yr – site 2	*C. dentata*	3588	29.4	17.5	46.9	46.15	13.6
	J. nigra	3588	9.1	4.9	14.0	46.33	4.2
	Q. rubra	3588	7.3	3.8	11.1	46.45	3.4
8 yr	*P. tremuloides*[a]	12670	19.4	6.0	25.4	47.09[c]	9.1
12 yr	*C. dentata*	897	30.3	24.7	55.0	46.37	14.1
	J. nigra	897	23.0	13.6	36.7	46.37	10.7
	Q. rubra	897	19.1	10.2	29.3	46.61	8.9
14 yr	*P. tremuloides*[a]	6600	33.4	9.2	42.6	47.09[c]	15.7
18 yr	*P. tremuloides*[a]	6495	39.6	10.9	50.5	47.09[c]	18.6
19 yr	*C. dentata*	960	128.6	51.3	179.9	46.73	60.1
	J. nigra	960	119.9	38.9	158.8	46.59	55.9
27 yr	*P. resinosa*[b]	2000	127.8	–	–	53.28[c]	68.1
	P. strobus[b]	1260	126.0	–	–	49.74[c]	62.7

[a] Adapted from Ruark and Bockheim (1988).
[b] Adapted from Gower et al. (1991).
[c] Adapted from Lamlom and Savidge (2003).

developing that provide financial incentives to individuals conducting forest management practices that increase the amount of carbon sequestered by their forest plantations. Afforestation of marginal agricultural lands offers great potential for carbon sequestration. For example, Niu and Duiker (2006) estimated that about 52.0 Mg C ha^{-1} could be sequestered in aboveground tree biomass 20 years after afforestation in the Midwestern U.S.

Although not always statistically significant (likely due to limited sample size associated with intensity of sampling), American chestnut exhibited consistent trends of more rapid growth (Tables 2 and 3) and greater aboveground biomass and bole carbon (Table 4) than either of the other interplanted species. These trends correspond with results of Jacobs and Severeid (2004), also in southwestern Wisconsin, who reported American chestnut had more rapid height (47–77%) and diameter (50–140%) growth compared to interplanted black walnut and northern red oak. The biomass and carbon prediction equations developed in this study (Fig. 2) provide a means for estimating these attributes in other stands. For example, the strong relationship between DBH and tree biomass and bole carbon content should provide confident estimations of these parameters using DBH, a simple and non-destructive measurement.

Comparing our data to studies conducted within the same physiographic region of Wisconsin using other commercially important forest tree species (Table 4), the within species influence of planting density and site quality on productivity and corresponding rates of carbon uptake is evident. As with any other attempt to evaluate rates of terrestrial carbon sequestration between tree species or regions, variation in both planting density and site quality make direct comparisons regarding carbon uptake and storage difficult. This type of extrapolation often occurs, however, due to the logistical challenge and cost of collecting biomass information (Zabek and Prescott, 2006). Regardless of these limitations, our study results suggest that American chestnut may compare favorably in carbon sequestration ability with many other species available for planting in this region (Table 4). For example, Gower et al. (1991) destructively harvested 27-year-old red pine (*Pinus resinosa* Ait.) (2000 stems ha^{-1}) and white pine (*Pinus strobus* L.) (1260 stems ha^{-1}) plantation trees from southwestern Wisconsin to determine stem biomass. Extrapolating bole carbon concentration results from Lamlom and Savidge (2003) resulted in estimated bole carbon of 68.1 and 62.7 Mg ha^{-1} for red and white pine, respectively, compared to 60.1 Mg ha^{-1} for 19-year-old American chestnut (960 trees ha^{-1}) in our study (Table 4). Similarly, Ruark and Bockheim (1988) examined quaking aspen (*Populus tremuloides* Michx.) stands in north-central Wisconsin representing a variety of age classes that regenerated naturally after clearcutting. For an 8-year-old stand (12670 stems ha^{-1}), total aboveground biomass was reported at 25.4 Mg ha^{-1}, compared to a range of 46.9–60.7 Mg ha^{-1} for the same-aged American chestnut in our study (Table 4). Extrapolating results of Lamlom and Savidge (2003) resulted in bole carbon of 9.1 Mg ha^{-1}, compared to a range of 13.6–18.6 Mg ha^{-1} in our study (Table 4). Similarly, 14- and 18-year-old stands (6600 and 6495 stems ha^{-1}, respectively) contained ranges of 42.6–50.5 Mg ha^{-1} for total aboveground biomass and 15.7–18.6 Mg ha^{-1} 1 for bole carbon, compared to values of 55.0 and 14.1 Mg ha^{-1} for total aboveground biomass and bole carbon, respectively, in our 12-year-old (897 stems ha^{-1}) American chestnut stand (Table 4). Given the former dominance of American chestnut in eastern U.S. forests, similar patterns of high carbon sequestration ability of American chestnut may be observed across other regions.

Our study did not quantify root biomass or soil carbon pools associated with afforestation of American chestnut. However, Niu and Duiker (2006) found that aboveground tree biomass accounts for about two thirds of the total carbon sequestration potential of afforestation plantations in the Midwestern U.S. The other one third of carbon capacity was approximately equally distributed over carbon in roots, forest floor, and soil organic carbon pools (Niu and Duiker, 2006). Grigal and Berguson (1998) noted that biomass of structural roots for mature trees is commonly in the range of 20% of aboveground biomass. From literature reviews, Niu and Duiker (2006) used a value of 0.21 (range 0.19–0.25) for estimates of root:shoot in deciduous trees in modeling potential carbon sequestration from afforestation plantations. Assuming this range, belowground biomass likely varied from 8.9–15.2, 10.5–13.8, and 34.2–45.0 Mg ha^{-1}

for our 8-, 12-, and 19-year-old American chestnut trees, respectively.

Many short-rotation woody crop species, such as hybrid poplar (e.g., *Populus trichocarpa* Torr. and Gray × *P. deltoides* Marsh.), grow faster than American chestnut and likely sequester more carbon over a shorter time frame, but are generally limited in commercial value to lower grade forest products. In contrast, American chestnut supplies high value, decay resistant timber (Youngs, 2000) in a relatively short rotation length. For example, mean annual diameter growth for various aged American chestnuts in the Coulee region of Wisconsin has been consistently measured at nearly 1 cm per year (Paillet and Rutter, 1989; Jacobs and Severeid, 2004; McEwan et al., 2006). This suggests that American chestnut could provide 30-cm saw logs in just over 30 years, a rate currently unachievable with most other high quality hardwood tree species. American chestnut also provides an exceptional source of wildlife food, producing good nut crops nearly every year (Diamond et al., 2000). The economic and ecological desirability of this species, combined with current evidence implicating its potential as a plantation species to help offset increasing CO_2 emissions, makes American chestnut an extremely attractive tree for carbon sequestration. Furthermore, integrating American chestnut into carbon sequestration projects will help contribute to the restoration of the species, a cause that has garnered extensive public support (Ronderos, 2000; Jacobs, 2007).

5. Conclusions

Our data lends credence to the growing body of literature (Paillet and Rutter, 1989; Jacobs and Severeid, 2004; McEwan et al., 2006; Jacobs, 2007) demonstrating rapid and sustained growth of American chestnut and the potential role of plantation-grown American chestnut in helping to mitigate climate change through carbon sequestration. Rapid growth capacity of American chestnut coupled with high-quality, decay-resistant wood offers further advantage for carbon storage by securing carbon in long-term forest products. The hybrid tree for reintroduction is expected to exhibit predominantly American chestnut characteristics (Burnham, 1981; Hebard, 2002) and therefore performance of the hybrid tree may be fairly well correlated with that of American chestnut as reported here. Our data substantiate investments in breeding of blight-resistant American chestnut for reintroduction. Future research is needed across a wider range of regions and site types to further improve our knowledge of American chestnut silvics (i.e., growth, reproduction, response to management and environmental changes) to help develop effective guidelines for plantation establishment.

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