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Developing Woody Crops for the Enhancement of Ecosystem Services under Changing Climates in the North Central United States

Ronald S. Zalesny Jr.[1,*] and William L. Headlee[2]

[1]*Institute for Applied Ecosystem Studies, Northern Research Station, U.S. Forest Service, Rhinelander, WI 54501, USA*
[2]*Department of Natural Resource Ecology and Management, Iowa State University, Ames, IA 50011, USA*

Abstract

Short rotation woody crops belonging to the genera *Populus* L., *Salix* L., *Pinus* L., and *Eucalyptus* L'Hér. have provided broad economic and ecological benefits throughout the world, including afforestation and reforestation along urban to rural gradients. Within the genus *Populus*, cottonwoods, poplars, aspens, and their hybrids (hereafter referred to as poplars) have been shown to exhibit favorable genotype × environment interactions, especially in the face of changing climates. Similar growth responses have been reported for *Pinus*, especially with white pine (*Pinus strobus* L.) in the North Central United States. This has led to current research priorities focused on ecosystem services for both genera. The Millennium Ecosystem Assessment (2005) defines cultural, supporting, provisioning, and regulating ecosystem services. The overarching objective of this paper was to synthesize information about the potential of poplars to provide multiple ecosystem services when grown at sites with varying soil and climate conditions across landscape gradients from urban to rural areas. Specific objectives included: 1) providing background of the United States Forest Service and its Research and Development branch, 2) integrating knowledge of current poplar breeding and development with biomass provisioning and carbon regulating ecosystem services as they relate to changing climates in the North Central United States, and 3) providing a case study illustrating this integration through comparisons of poplar with white pine. Our results were evaluated in the context of climate change mitigation, with specific focus on selection of favorable genotypes for sequestering atmospheric carbon and reducing fossil fuel carbon emissions.

Key Words: Biomass, Carbon Sequestration, *Pinus strobus* L., Poplar, *Populus*, White pine

Introduction

Approximately 304 million ha of forestland exist in the United States, with 56% under private ownership and 44% that is publicly owned. The majority of private forestlands are located in the eastern United States, while their public counterparts are mostly in the West. Of all public forests in the country, 76% (102 million ha) are owned by the federal government, followed by 21% (28 million ha) having state ownership and 3% (4 million ha) under local control (Northern Research Station 2008; Nelson et al. 2010). The U.S. Forest Service (hereafter referred to as Forest Service), whose mission is to *sustain the health, diversity, and productivity of the Nation's forests and grasslands to meet the needs of present and future generations*, manages an extensive amount of this federal ownership. Specifically, there are 155 national forests and 20 national grasslands constituting 78 million ha (i.e., 76% of all public forests). In addition to an

International Programs group that works to enhance economic development and environmental sustainability worldwide, the Forest Service has three branches. First, the National Forest System manages the national forests and grasslands. Second, State and Private Forestry works with state, local, and private forest owners to manage their forests. Third, Research and Development (FS R&D) produces technologies that improve the health and use of our Nation's forests and grasslands. Forest Service R&D is the largest forestry research organization in the world with nearly 550 scientists and over 2,100 employees, all of which work in a range of biological, physical, and social science fields to promote sustainable ecosystem management. In addition to National Headquarters in Washington, DC, FS R&D is comprised of the Forest Products Laboratory, International Institute of Tropical Forestry, and five research stations (Pacific Northwest, Pacific Southwest, Southern, Rocky Mountain, and Northern) based on geographic regions of the country (United States Forest Service 2014; Fig. 1).

The Northern Research Station is the largest unit within FS R&D, covering 20 states, 69 million ha of forests, 40% of U.S. inhabitants, and many of the largest U.S. cities (e.g., Chicago, Philadelphia, New York) (Fig. 2). The station has a multidisciplinary cadre of approximately 140 scientists belonging to 15 research work units conducting both applied and basic research relating to five science themes:
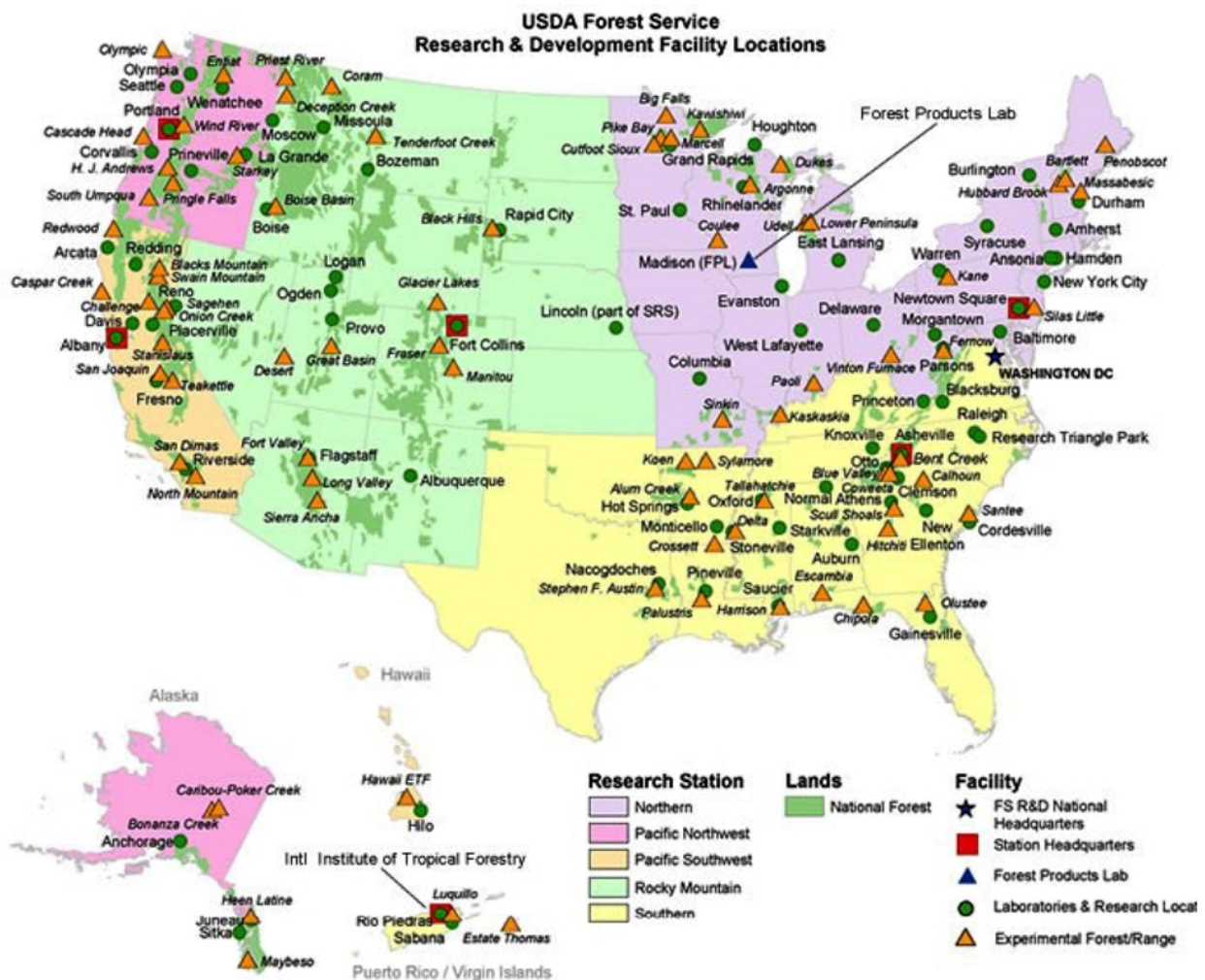
1. Sustaining forests,

Fig. 1. USDA Forest Service Research and Development facility locations.

Fig. 2. USDA Forest Service Northern Research Station locations.

2. Forest disturbance processes,

3. Providing clean air and water,

4. Urban natural resource stewardship, and

5. Natural resources inventory, monitoring, and assessment.

One of those units, the Institute for Applied Ecosystem Studies (IAES) located in Rhinelander, WI (Fig. 2), has collectively addressed all science themes throughout its history, which dates back to the 1960s. The North Central United States (i.e., the area surrounding Lake Superior and Lake Michigan) was heavily logged throughout the late 1800s and early 1900s and the genetics and tree improvement research of the IAES (which was previously known as the Northern Institute of Forest Genetics) was pivotal in providing planting stock and silvicultural recommendations for reforestation in the region. In addition to silviculture research, early priorities in Rhinelander consisted of range-wide/regional provenance tests and common garden tests of all major conifer species.

The Middle East oil embargo of the 1970s prompted a shift away from the historical, conifer-dominated regional tree improvement programs to the development of productive and sustainable short rotation woody crop (SRWC) production systems (Dickmann 2006). Given their eco-

nomic and ecological benefits throughout North America and the world (Dickmann 2001), along with their breeding and productivity potential throughout the region (Zalesny et al. 2009; Mahama et al. 2011; Headlee et al. 2013), *Populus* species and hybrids (i.e., poplars) were selected as the SRWC of choice in the North Central United States (Dickmann 2006; Vance et al. 2010).

Overall, *Populus* is the most-studied tree genus in the world, resulting in its genome being the first woody species to be sequenced (Tuskan et al. 2006). Poplar species and their associated base populations in breeding programs exhibit tremendous genetic diversity (Rajora and Zsuffa 1990; Eckenwalder 1996), which often results in heterosis and significant gains from selection (Riemenschneider et al. 2001). From a practical standpoint, poplars are ideal for multiple end uses given that they grow fast (Headlee et al. 2013), exhibit extensive root systems (Zalesny and Zalesny 2009), and have elevated water usage for hydraulic control (the benefits of which may decrease under future drier environments) (Zalesny et al. 2006). In addition, they can be stored on the stump until harvest, which can take place throughout the year (Johnson et al. 2007), and require relatively minimal fertilization and other cropping inputs (Stanturf et al. 2001). Starting in the 1970s, the IAES has

become a world leader in poplar development for multiple end uses, including but not limited to: phytotechnologies (Zalesny and Bauer 2007), energy (Wang et al. 2012), and fiber (Lazarus et al. 2011). This has led to current research priorities focused on ecosystem services, which are generally defined as the benefits people obtain from ecosystems (http://www.greenfacts.org).

More specifically, the Millennium Ecosystem Assessment (2005) defines four categories of ecosystem services: 1) *cultural* (the nonmaterial benefits obtained from ecosystems, e.g. values), 2) *supporting* (the natural processes that maintain other services, e.g. nitrogen cycle), 3) *provisioning* (the goods or products obtained from ecosystems, e.g. freshwater), and 4) *regulating* (the benefits obtained from an ecosystem's control of natural processes, e.g. soil quality). An overarching objective of current poplar research in the North Central United States is to enhance aboveground biomass production (provisioning services) and carbon sequestration (regulating services) of the purpose-grown trees at afforestation and reforestation sites in urban and rural areas (Headlee et al. 2014; Zalesny et al. 2014a). While the attention placed on urban to rural gradients is somewhat recent for poplar deployment strategies, the concept has been around for decades. For example, McDonnell and Pickett (1990) defined the gradient as an ordering of sites based on the predominance of buildings and infrastructure, coupled with dense human population (urban), in contrast with sites having sparse infrastructure and low human population density (rural). In addition to ecosystem services and urban to rural gradients, the results of these current studies can be evaluated in the context of climate change mitigation, with specific focus on selection of favorable genotypes for sequestering atmospheric carbon and reducing fossil fuel carbon emissions.

Climate change is expected to have profound effects on forest cover and species composition worldwide. Some research suggests that droughts associated with climate change may already be impacting certain forest ecosystems globally via increased mortality rates (Allen et al. 2010). In addition, the predicted increases in temperature are also expected to intensify the frequency and severity of outbreaks of forest pests including bark beetles (Bentz et al. 2010), aphids (Banfield-Zanin and Leather 2014), and leaf rusts (Pinkard et al. 2014). These responses are especially evi-

dent in the eastern United States (Rustad et al. 2012). In this region, for example, research has suggested that spruce-fir and aspen-birch forest types will shrink by more than 90% in land area by the end of the current century, with optimal climatic conditions for some species shifting up to 500 km north of their current locations (Hansen et al. 2001). Conditions in the North Central United States are expected to follow similar trends (Kling et al. 2003; Handler et al. 2014). For example, Kling et al. (2003) described four changes: 1) shorter winters, 2) warmer annual average temperatures, 3) decreased duration of ice cover on lakes, and 4) more frequent heavy rainstorms, which were most recently corroborated by Handler et al. (2014). Specific potential impacts on regional forests included: 1) increased stress for boreal species, 2) increased adaptability for southern species, 3) altered forest community compositions across the landscape, and 4) increased productivity (Handler et al. 2014).

To some degree, the resilience of forests to climate change may be enhanced through silviculture, such as by adjusting planting practices (Magruder et al. 2012), harvesting practices (D'Amato et al. 2011), or both (Duveneck et al. 2014). Beyond these coping strategies, however, deployment of SRWCs can help address the root cause of climate change by removing large amounts of carbon dioxide from the atmosphere over relatively short timeframes (Tuskan and Walsh 2001) with greater energy-use-efficiency (i.e., energy output per unit input) than annual and other perennial herbaceous crops (Boehmel et al. 2008). This can help alleviate climate change both in the near-term by reducing atmospheric carbon and in the long-term by displacing fossil fuels, especially if the biomass is converted to biofuels or bioenergy under a comprehensive strategy to reduce fossil carbon emissions (Pacala and Socolow 2004). Thus, short-rotation woody crops can provide multiple ecosystem services including carbon regulating services and fuel/energy provisioning services to enhance overall sustainability in the process of addressing climate change (Gopalakrishnan et al. 2009).

Among short-rotation woody crops, poplars and their hybrids are well-suited for mitigating climate change via sequestering atmospheric carbon and displacing fossil fuels. Previous research comparing poplars to other sources of biomass indicates that poplars have greater potential for dis-

placing fossil carbon emissions (600 kg C Mg^{-1} of biomass) than willow (550 kg C Mg^{-1}), switchgrass (400 kg C Mg^{-1}), corn (300 kg C Mg^{-1}), or native forests (30 to 140 kg C Mg^{-1}) in the USA (Cook and Beyea 2000). In addition, poplars have a long history of breeding research and development which has resulted in the production and testing of an array of genotypes in region-wide networks (Zalesny et al. 2009), offering the opportunity to maximize carbon sequestration and renewable fuel/energy production by matching genotypes to current and future climate and soil conditions (Chhin et al. 2010).

One recent example of enhancing these ecosystem services includes an ongoing poplar carbon study in the North Central United States (Headlee et al. 2013). The overall objective of the study is to identify genotype × environment interactions that simultaneously enhance both aboveground biomass production and carbon sequestration. In total, 13 genotypes grown across 17 sites exhibited annual biomass production ranging from 2.0 to 24.4 Mg ha^{-1} yr^{-1}, with associated stand-level carbon sequestration ranging from 0.9 to 13.2 Mg C ha^{-1} yr^{-1}. Carbon concentrations varied by genotype and ranged from 45.3 to 47.2%, resulting in the ability to choose high-yielding clones with favorable combinations of biomass provisioning and carbon regulating services. In addition, more northern latitudes were associated with higher mean carbon concentrations and differences among clones, even those from similar genomic groups. Overall, understanding these genotype and site effects will help to adapt deployment strategies as the regional climate continues to warm (Headlee et al. 2014).

Similarly, examples of current phytotechnologies research include a collection of two rural afforestation projects (riparian buffer system; phytoremediation), one rural reforestation site (surface-mine reclamation), and three urban afforestation locations [brownfields remediation (×2); city park development] (Zalesny et al. 2014a). In total, over 150 poplar genotypes belonging to eight genomic groups were (or are being) tested. Given the variability in soil and climate conditions, along with contamination at some sites, biomass provisioning and carbon regulating services were within the range of expected values compared to production plantings. Specific genotype × environment interactions resulted in similar (or greater) productivity from the phytotechnologies sites than production plantings. Overall, geno-

type selection was critical for success, especially when considering changing climates.

In this paper, we further assess the potential enhancement of ecosystem services provided by purpose-grown poplars, using information from the above poplar studies as a basis for comparison with another plantation-grown species in the North Central United States. Specifically, we integrate results from the aforementioned poplar carbon study with an ongoing eastern white pine (*Pinus strobus L.*) project (Zalesny et al. 2014b) to directly compare biomass provisioning and carbon regulating ecosystem services. In doing so, we will also discuss the importance of genotype, environment, and their interactions on the biomass production and carbon sequestration abilities of each crop.

Eastern white pine (*Pinus strobus L.*) is the premiere softwood species throughout much of eastern North America (Wendel and Smith 1990), both in terms of economic values such as biomass for lumber, millwork, and specialized products (e.g., masts for sailing ships) and ecological values including carbon sequestration, mine reclamation, and wildlife habitat. While adaptable and valuable, further reductions in the range and abundance of white pine dominated forests are projected to result from climate change (McKenney et al. 2007; Iverson et al. 2008).

Eastern white pine is threatened by a number of biotic and abiotic factors (Wendel and Smith 1990). White pine weevil and white pine blister rust are serious insect and disease pests. Eastern white pine is vulnerable to a range of pollutants, such as acidic deposition and road salt. The shifts in suitable habitats predicted by climate change models represent a serious threat to white pine throughout the North Central United States, especially as changes in the climate will likely interact with other stressors (Millar et al. 2007). Thus, it is imperative to identify specific eastern white pine provenances that are genetically adapted to local and regional environmental conditions.

Case Study: Biomass and Carbon of Poplar Versus White Pine

Rationale

Although both *Populus* and *Pinus* exhibit economic and ecological importance throughout North America, there are few comparisons highlighting the differences in potential

ecosystem services between intensively-managed poplar and plantation-grown white pine. It is clear both species groups share related silvicultural needs during establishment yet exhibit contrasting growth rates and lifespans, with poplars growing faster and white pine living longer. A consistent thread across genera is that reports for biomass productivity are more prevalent than for carbon sequestration. In fact, aside from soil-related carbon (Grigal and Berguson 1998; Coleman et al. 2004), there is a paucity of peer-reviewed literature for either genus pertaining to aboveground carbon sequestration, and equally-limited direct comparisons highlighting variability in their potential for providing any type of ecosystem services (Coleman et al. 2000). Therefore, the goal of our case study was to evaluate differences in aboveground biomass and carbon sequestration potential of poplars at rotation age (10 yr) and stand decline (20 yr) with mid-rotation white pine (48 yr) in the North Central United States. In doing so, our primary objective was to determine the ages where potential ecosystem services for white pine were comparable to that of poplar in the region.

Methods

Site and clone selection

Headlee et al. (2013) provided a detailed description of the sites and genotypes associated with the poplar carbon study summarized above, which is the basis for the current analyses. For this case study, growth ring data were used from two separate plantation networks: 1) 10-year-olds, and 2) 20-year-olds. The 10-year-old plantings were comprised of seven clones belonging to three genomic groups grown at three sites, and the 20-year-old plantings consisted of two clones from a single genomic group grown at nine sites (Table 1). Furthermore, King and Nienstaedt (1969) provided a detailed description of the sites and provenances tested in a range-wide white pine study, from which growth ring data were collected during the 49th growing season. Here, we present data from 48 years after planting, as this represents the last complete year of growth available.

Table 1. Poplar genomic groups and clones from two plantation networks in the North Central United States

Age group	Genomic group[a]	Clone
10-yr-old	*P. deltoides*	C916000
	P. nigra × *P. suaveolens* subsp. *maximowiczii*	NM2
	(*P. trichocarpa* × *P. deltoides*) × *P. deltoides*	NC13624, NC13649, NC13563
20-yr-old	*P. deltoides* × *P. nigra*	DN34, DN182

[a]Authorities for the aforementioned species are: *P. deltoides* Bartr. ex Marsh; *P. maximowiczii* A. Henry; *P. nigra* L.; *P. trichocarpa* Torr. & Gray.

Table 2. White pine provenances grown at four sites in the North Central United States

Canada[a]	United States[a]	Location of Origin	Latitude (°N)	Longitude (°W)
1	1633	Union County, Georgia, USA	34.08	84.00
2	1634	Greene County, Tennessee, USA	36.00	82.08
3	1640	Monroe County, Pennsylvania, USA	41.02	75.05
4	1639	Franklin County, New York, USA	44.05	74.03
6	1632	Ashland County, Ohio, USA	40.08	82.03
7	1624	Allamakee County, Iowa, USA	43.03	91.03
8	1622	Cass County, Minnesota, USA	47.03	94.05
9	1623	Forest County, Wisconsin, USA	45.08	88.08
10	1637	Luneborg County, Nova Scotia, Canada	44.05	64.07
11	1635	Pontiac District, Quebec, Canada	47.05	77.00
12	1636	Algoma District, Ontario, Canada	46.02	82.07
13	1670	Newaygo County, Michigan, USA	43.05	85.07

[a]Columns for Canada and United States indicate differences in nomenclature for the genotypes.

Table 3. Mean stand height, latitude, longitude, and soil texture of sixteen sites in the North Central United States where 10- and 20-year-old poplar are being compared to 48-year-old white pine for biomass provisioning and carbon regulating ecosystem services

Group	State	Site	Height (m)	Latitude (°N)	Longitude (°W)	Soil Texture
Poplar (10 yr)	IA	Ames	15.1±0.4	42.05	93.66	Fine Sandy Loam
	MI	Escanaba	12.5±0.2	45.77	87.20	Fine Sandy Loam
	MN	Waseca	16.3±0.4	44.06	93.54	Clay Loam
Poplar (20 yr)	MN	Belgrade	17.2±0.4	45.67	95.11	Loam
	MN	Bemidji	17.9±0.3	47.58	94.93	Loamy Sand
	MN	Fairmont	18.7±0.2	43.69	94.35	Clay Loam
	MN	Granite Falls	21.4±0.8	44.80	95.52	Loam
	MN	Lamberton	18.7±0.9	44.25	95.29	Clay Loam
	MN	Milaca	19.4±0.3	45.78	93.63	Silt Loam
	MN	Warren	20.8±0.7	48.14	96.65	Fine Loamy Sand
	WI	Mondovi	19.3±0.3	44.52	91.65	Silt Loam
	WI	Rhinelander	21.5±0.6	45.63	89.46	Loamy Sand
White Pine (48 yr)	MI	Manistique	20.3±0.2	46.00	86.41	Fine Sandy Loam
	MI	Newaygo	13.3±0.1	43.47	85.66	Sand
	MI	Pine River	19.4±0.3	44.23	85.76	Sand
	WI	Wabeno	18.8±0.2	45.43	88.51	Silt Loam

Table 2 lists thirteen white pine provenances grown across seven sites from north central Wisconsin to northeast Maine. The case study uses data from four of those sites, one located in Wisconsin and three in Michigan. Table 3 is a description of all sixteen sites in the case study, including their average stand height, latitude, longitude, and soil texture.

Experimental design, data collection, and data analysis

The original experimental design for both genera was randomized complete blocks with site and genotype (poplar=clone; white pine=provenance) main effects. For 10-year-old poplar, trees were planted in five blocks with two trees per clone per block at a spacing of 3.05×3.05 m (Zalesny et al. 2009), whereas a narrower spacing of 2.44×2.44 m was used for the 20-year-old trees (Netzer et al. 2002). For white pine, two original field designs were used. The Wabeno, WI; Manistique, MI; and Pine River, MI sites were planted in 24 blocks with one tree per provenance per block at a spacing of 2.13×2.13 m, while trees at the Newaygo, MI site were planted in 4 blocks with 81 trees per provenance per block at similar spacing as the other three sites (King and Nienstaedt 1969). For the current study, 3 to 4 poplar trees and 2 to 28 white pine trees were

sampled for each combination of site and genotype.

Poplar trees were harvested during the leafless period. At harvest, tree height and diameter were measured to the nearest cm, trees were felled, and cross-sectional disks were collected at diameter at breast height (dbh; 1.4 m), one-third tree height, and two-thirds tree height. Fresh weight of all aboveground woody biomass was recorded, and sub-samples of boles and branches, along with the cross-sectional disks, were brought to the analytical laboratory at the IAES in Rhinelander, WI for processing. The subsamples and disks were dried at 55°C until constant mass. Using calculated moisture content from fresh and dry material, aboveground dry biomass was estimated for each tree. Disks were cut in half, and a wafer was extracted along a plane extending through the pith. From this wafer, three subsamples were harvested from each growth ring. All sub-samples were analyzed for total carbon content using a Flash EA1112 N-C analyzer with a model MAS 200 auto-sampler (Thermo Electron, via CE Elantech, Inc., Lakewood, NJ, USA). Carbon sequestration estimates were calculated based on the formula:

$$\text{Carbon sequestration} = \text{biomass} \times \frac{(\%C)}{100}.$$

White pine trees were cored during the 49th growing season. Height and dbh were measured and two incre-

ment cores were collected from each tree at $0°$ (north) and $90°$ (east), with $180°$ (south) and $270°$ (west) being used in cases where previous cores were of poor quality. Cores were sent to the analytical laboratory at the Ontario Ministry of Natural Resources in Sault Ste. Marie, Ontario, Canada where they were processed and analyzed with WinDENDRO software (Regent Instruments, Inc., Sainte-Foy-Sillery-Cap-Rouge, Quebec, Canada) to determine annual growth ring widths. The WinDENDRO data were then used to estimate annual diameters; those from 40 to 48 years were used in the current study. Based on these annual diameter data, aboveground dry biomass for each tree was estimated according to Jenkins et al.

(2003) using the following expression that was developed explicitly for a variety pine species:

$$Biomass = Exp[-2.5356 + 2.4349 \ln(dbh)].$$

In addition, a constant carbon concentration of 49.74% was assumed, according to Lamlom and Savidge (2003). Aboveground carbon sequestration was then estimated from biomass and carbon concentration, as with poplar.

For both genera, individual-tree biomass data were multiplied by genus-specific stocking rates (10-year-old poplar=1,075 trees ha^{-1}; 20-year-old poplar=1,680 trees ha^{-1}; white pine=2,205 trees ha^{-1}; assuming 100% survival)

Table 4. Probability values from analyses of variance testing the effects of site and genotype on biomass$_{MAI}$ (Mg ha^{-1} yr^{-1}) and carbon$_{MAI}$ (Mg C ha^{-1} yr^{-1}) of poplar at rotation age (10-yr) and stand decline (20-y) along with white pine at mid-rotation (48-yr) when grown in the North Central United States. Except for genotype main effects for 20-year-old poplar, all main effects and interactions were significant

Source	Poplar (10-yr)		Poplar (20-yr)		White Pine (48-yr)	
	Biomass$_{MAI}$	Carbon$_{MAI}$	Biomass$_{MAI}$	Carbon$_{MAI}$	Biomass$_{MAI}$	Carbon$_{MAI}$
Site	0.0007	0.0007	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Genotype[a]	< 0.0001	< 0.0001	0.0807	0.0946	< 0.0001	< 0.0001
Site × Genotype	0.0134	0.0123	< 0.0001	0.0001	< 0.0001	< 0.0001

[a]Poplar clones; white pine provenances.
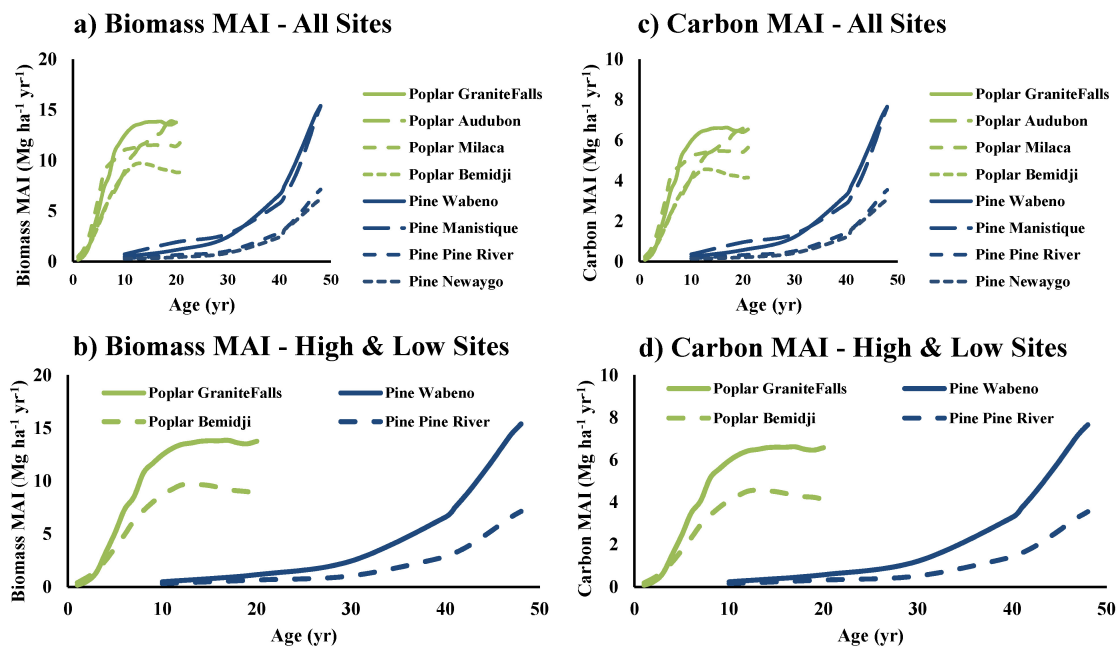
Fig. 3. Biomass$_{MAI}$ (a, b) and carbon$_{MAI}$ (c, d) production curves throughout plantation development for poplar at four sites in Minnesota, USA through age 20 years and white pine in Wisconsin, USA (one site) and Michigan, USA (three sites) through age 48 years.
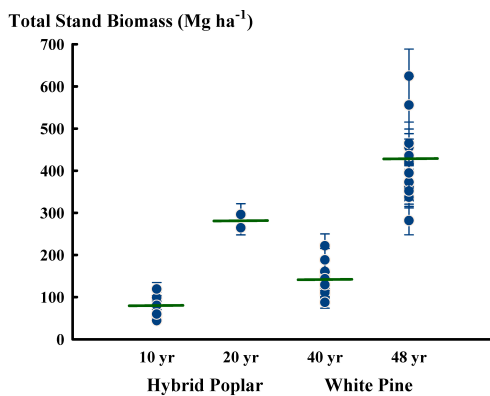
and their product was divided by the age of the trees to calculate biomass (and carbon) per unit land area per year (i.e., mean annual increment, $_{MAI}$). Thus, biomassTOTAL (Mg ha^{-1}), biomass$_{MAI}$ (Mg ha^{-1} yr^{-1}), and carbon$_{MAI}$ (Mg C ha^{-1} yr^{-1}) were the data compared in all of the analyses. The data were analyzed independently by genus using analyses of variance (PROC GLM; SAS Institute, Inc. 2011) assuming a completely random design with site and genotype main effects, as described above. Means were considered different at probability values of $P < 0.05$, according to Fisher's protected Least Significant Difference (LSD).

Results and Discussion

Site effects

Despite minimal differences in probability values, overall trends in analyses of variance results were identical for biomass$_{MAI}$ and carbon$_{MAI}$ (Table 4). With the exception of genotype main effects for 20-year-old poplar, all site and genotype main effects were significant for poplar and white pine, regardless of stand age. Interactions among sites and genotypes determined specific changes in rank and magnitude across clones and sites; thus, specific results are described in the Site × Genotype Effects section below.

An evaluation of biomass$_{MAI}$ and carbon$_{MAI}$ curves throughout plantation development indicated comparable biomass productivity and carbon sequestration of white pine relative to poplar began to occur at approximately 40 years after planting (Fig. 3). The advantage of the site with greatest biomass and carbon over that with the least is more

prevalent with white pine (116%) relative to 10- (45%) and 20-year-old (57%) poplar, which is likely a result of the broad variation in geographic origins of the provenances and how those provenances responded to site and climate conditions that were much different than their own (Joyce and Rehfeldt 2013). In contrast, although the poplars segregated into generalist and specialist genotypes, they were all previously selected for testing (and possible deployment)
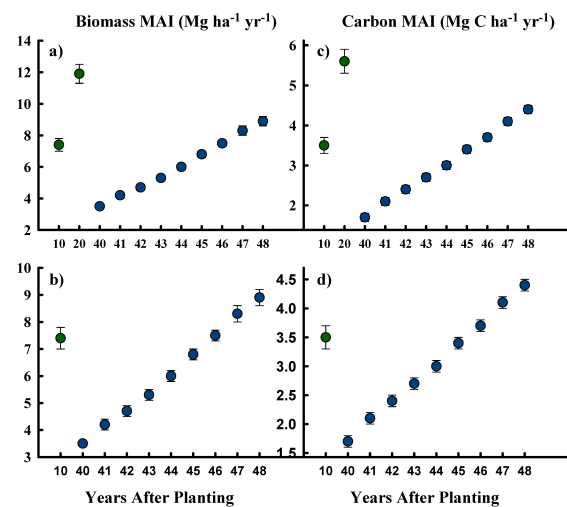
Fig. 5. Biomass$_{MAI}$ (a, b) and carbon$_{MAI}$ (c, d) of poplar at rotation age (10 yr) and stand decline (20 yr) along with mid-rotation white pine (40 to 48 yr) in the North Central United States. Error bars represent one standard error of the mean.
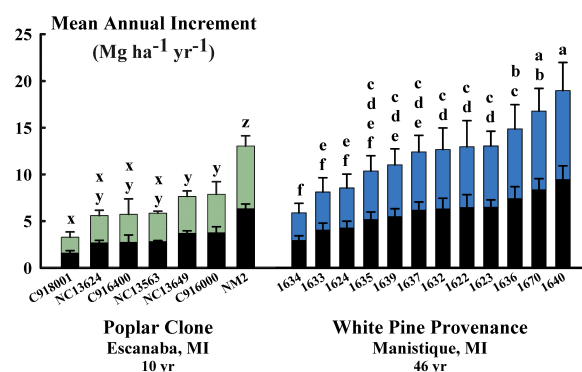
Fig. 6. Biomass$_{MAI}$ (tall green bars, poplar; tall blue bars, white pine) and carbon$_{MAI}$ (short black bars) of 7, 10-year-old poplar clones grown in Escanaba, Michigan, USA and 12, 46-year-old white pine provenances grown in Manistique, Michigan, USA. Mean comparisons with different letters within genera were different, according to Fisher's protected least significant difference at $P < 0.05$. Results for carbon$_{MAI}$ were identical to those for biomass$_{MAI}$ and are not shown. Error bars represent one standard error of the mean.

Fig. 4. Total stand biomass of poplar and white pine genotypes at respective stand ages. Error bars represent one standard error of the mean.

within the region (Riemenschneider et al. 2001; Zalesny et al. 2009), resulting in less overall variability in performance across sites relative to the white pine.

Genotype effects

Fig. 4 depicts the range in genotypic means for total stand biomass at 10 (poplar), 20 (poplar), 40 (white pine), and 48 (white pine) years after planting. Trends described above relating to the broad variation in performance of white pine provenances relative to that of poplar clones are further illustrated. While relative differences in total stand yield among the four groups favored 48-year-old white pine, standardizing the biomass on an annual basis showed that white pine productivity between the ages of 40 and 48 years was not comparable to 20-year-old poplar (Fig. 5). However, 45- to 47-year-old white pine exhibited comparable biomass$_{MAI}$ as 10-yr-old poplar. Both trends were similar for carbon$_{MAI}$, with 20-year-old poplar outperforming white pine yet its carbon sequestration being similar to 10-year-old poplar between 45 and 46 years after planting.

Site × Genotype Effects

Combinations of site and genotype were assessed to interpret the comparable ages identified in the previous section. Given their similar latitudes (Escanaba 45.77 $^{\circ}$N; Manistique 46.00 $^{\circ}$N), climates, and soil textures (fine sandy loam for both), biomass$_{MAI}$ and carbon$_{MAI}$ were evaluated for 10-year-old poplar at Escanaba versus 46-year- old white pine at Manistique. Overall, ranges across genotypes were comparable, while mean biomass$_{MAI}$ and carbon$_{MAI}$ of poplar was 55% of white pine (Fig. 6). In addition, distinct site × genotype effects existed within genera. For example, NM2 exhibited significantly greater biomass$_{MAI}$ and carbon$_{MAI}$ than all other poplar clones, which corroborated previous reports of NM2 and its sibling NM6 being more adapted to northern latitudes (Zalesny et al. 2009). For white pine, the three bottom-ranked provenances were all from southern origins (Iowa, Tennessee, Georgia) while the three top-ranked provenances were from northern sources (Pennsylvania, Michigan, Ontario), thus corroborating expected genecological responses in the species (Joyce and Rehfeldt 2013).

For 10-year-old poplar, biomass$_{MAI}$ ranged from 3.1± 1.1 to 14.0±2.0 Mg ha^{-1} yr^{-1} for NC13624 at Waseca

and NM2 at Waseca, respectively. The overall mean across sites was 7.4±0.4 Mg ha^{-1} yr^{-1}, which was 80% of the Waseca average yet 23% greater than Ames and 4% greater than Escanaba. NM2 exhibited the greatest biomass$_{MAI}$ across sites, which was 159% greater than the overall mean. These biomass$_{MAI}$ values were in the range of those previously reported for the region (Zalesny et al. 2009; Riemenschneider et al. 2001; Headlee et al. 2013). In addition, the identification of generalist and specialist genotypes was consistent with those reported in Ames and Waseca (Zalesny et al. 2009). For example, in the current study NC13624 was a generalist having similar biomass$_{MAI}$ across all three sites, ranging in values by 2.5 Mg ha^{-1} yr^{-1}. In contrast, its sibling NC13563 was a specialist exhibiting nearly identical biomass$_{MAI}$ at Ames and Escanaba that was nearly 4.6 Mg ha^{-1} yr^{-1} less than that at Waseca. The implications for genotype selection, therefore, are that NC13624 can be selected across the region, while NC13563 is better-adapted to soil, climate and/or cultural conditions of southern Minnesota.

For 20-year-old poplar, the non-significant clone effects were not surprising, however, given the similarity of productivity between these clones during establishment (Netzer et al. 2002). Across sites and clones, biomass$_{MAI}$ ranged from 5.8±0.7 to 21.7±1.3 Mg ha^{-1} yr^{-1} for DN34 at Bemidji and DN182 at Rhinelander, respectively. The overall mean was 11.9±0.6 Mg ha^{-1} yr^{-1}.

For white pine, biomass$_{MAI}$ ranged from 3.1±0.7 to 32.7±7.5 Mg ha^{-1} yr^{-1} for provenance 1635 at Pine River and 1640 at Wabeno, respectively. The overall mean was 8.9±0.3 Mg ha^{-1} yr^{-1}, which was 58% (Manistique) and 57% (Wabeno) of two of the sites yet 44% greater than Newaygo and 25% greater than Pine River. Provenance 1640 exhibited the greatest biomass$_{MAI}$ across sites, which was 46% greater than the overall mean. While 1640 was an average provenance during initial testing and selection across sites (King and Nienstaedt 1969), overall site rankings are similar to their previous report: Wabeno > Manistique > Pine River (Newaygo was not included given the different experimental design described above). A more detailed analysis of the interactions among sites, provenances, and climate is currently underway at Michigan State University, with collaboration from the United States Forest Service and Ontario Ministry of Natural Resources.

Conclusions and Practical Implications

An array of technologies and policies will be needed to reduce atmospheric carbon levels and mitigate climate change in the coming decades (Pacala and Socolow 2004). Among available technologies, afforestation and reforestation along urban to rural gradients using fast-growing woody crops such as poplars and longer-lived species such as white pine offer the opportunity to sequester atmospheric carbon during stand growth as well as reduce carbon emissions after harvest via the displacement of fossil fuels. In this case study, we evaluated the timing and magnitude of the delivery of carbon regulating services and biomass provisioning services for poplars and white pine in the North Central United States. In general, biomass and carbon sequestration rates comparable to 10-year poplars were not achieved for white pine until 45 years after planting. Specifically, mean biomass$_{MAI}$ was comparable from 45 to 47 years and mean carbon$_{MAI}$ from 45 to 46 years. While unique site $\times$ genotype interactions resulted in white pine exceeding 10-year-old poplar at ages younger than 45 years, white pine at 48 years averaged much lower than the 20-year-old poplars. Thus, poplars are favorable for achieving rapid biomass production and carbon sequestration, although the longer lifespan of white pine may provide additional advantages in terms of long-term carbon storage. Therefore, to the extent that these genera and their provenances are adapted to various growing conditions and may provide auxiliary benefits such as wildlife habitat and species diversity, a balanced approach using both crops should be employed for the purpose of maximizing ecosystem services across the landscape while also mitigating global climate change.

Acknowledgements

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