# An Afforestation System for Restoring Bottomland Hardwood Forests: Biomass Accumulation of Nuttall Oak Seedlings Interplanted Beneath Eastern Cottonwood

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## Abstract

**Bottomland hardwood forests of the southeastern United States have declined in extent since European settlement. Forest restoration activities over the past decade, however, have driven recent changes in land use through an intensified afforestation effort on former agricultural land. This intense afforestation effort, particularly in the Lower Mississippi Alluvial Valley, has generated a demand for alternative afforestation systems that accommodate various landowner objectives through restoration of sustainable forests. We are currently studying an afforestation system that involves initial establishment of the rapidly growing native species eastern cottonwood *(Populus deltoides* Bartr. ex Marsh.), followed by enrichment of the plantation understory with Nuttall oak *(Quercus nuttallii* Palm.). In this article, we examine the growth and biomass accumulation by Nuttall oak seedlings to determine whether this species can be established and whether it will develop beneath the cottonwood overstory. After 3 years of growth beneath cottonwood canopies, Nuttall oak seedlings were similar in height (126 cm), but were 20% smaller in root-collar diameter than seedlings established in open fields. Seedlings established in the open accumulated more than twice the biomass of seedlings growing beneath a cottonwood canopy. However, the relative distribution of accumulated biomass in seedlings did not differ in the two environments. Ten percent of total seedling biomass was maintained in leaf tissue, 42% was maintained in stem tissue, and 48% was maintained in root tissue on open-grown seedlings and seedlings established in the understory of cottonwood plantations. Though establishment in the more shaded understory environment reduced Nuttall oak growth, seedling function was not limited enough to induce changes in plant morphology. Our results suggest that an afforestation system involving rapid establishment of forest cover with a quick-growing plantation species, followed by understory enrichment with species of later succession, may provide an alternative method of forest restoration on bottomland hardwood sites and perhaps other sites degraded by agriculture throughout temperate regions.**

Key words: **forest restoration, *Populus deltoides, Quercus nuttallii,* regeneration, wetland forest.**

## Introduction

Forest restoration activities have become prevalent around the globe as marked by an afforestation rate of about 1.6 million hectares per year between 1990 and 2000 (FAO 2001). Of critical importance to forest conservation and sustainability in the temperate zone of North America is the restoration of bottomland hardwood forest ecosystems. Bottomland hardwood forests are deciduous and associated with alluvial soils on the floodplains of rivers and streams that dissect the southern and eastern United States. The largest contiguous area of bottomland hardwood forest originally occurred in the Lower Mississippi Alluvial Valley (LMAV), but forest cover in this region has been reduced to an estimated 26% of the former 10.1 million-ha forest (Stanturf et al. 2000; Gardiner & Oliver, in press). In the last decade, a concentrated forest restoration effort has developed in the LMAV where afforestation activities have reestablished native tree species on more than 193,000 ha of degraded agricultural land marginally suited for crop production (Stanturf et al. 1998; Schoenholtz et al. 2001; Gardiner & Oliver, in press). The ultimate success of this massive forest restoration effort will be determined by the basic implementation of sound afforestation practices.

Interests in carbon sequestration, game habitat enhancement, timber production, water quality protection, and conservation of biological diversity are among the driving forces behind afforestation activities in the LMAV (King

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& Keeland 1999). Basic silvicultural practices for afforestation of bottomland hardwood forests were developed and have been applied since the 1960s (Allen 1990; Newling 1990). Conventional practices, which generally evolved from earlier techniques for establishing single-species plantations, have proven successful for some afforestation needs, but there is a need for alternative afforestation practices that provide additional options for achieving various resource management objectives (Gardiner et al. 2002). Development of afforestation systems that quickly produce complex vertical forest structure will provide alternative pathways to attain various restoration objectives.

Recently, plantations have been used effectively to restore and conserve tropical forests (Parrotta et al. 1997). Some of these systems have demonstrated value for restoring particular ecological processes or ecosystem functions. Several authors, including Parrotta (1995), Lugo (1997). and Powers et al. (1997), provide examples of plantations catalyzing natural forest regeneration and tree species richness on degraded sites. Plantations are often used to facilitate restoration of native forest cover on degraded tropical sites because they provide rapid development of forest structure attractive to wildlife species, and an associated understory microenvironment favorable to germination and establishment of native tree species (Parrotta 1992; Keenan et al. 1997; Lugo 1997). Other workers have extended the application of plantations for forest restoration by establishing rapidly growing species that develop an understory microenvironment favorable to establishment of planted seedlings of late-successional species (Ashton et al. 1997, 199X). Application of similar plantation establishment approaches involving fast-growing canopy species and understory enrichment plantings has not been widely studied or used for forest restoration in temperate regions (Ashton et al. 1997).

We are currently investigating the development and application of an interplanting system for restoration of bottomland hardwood forests on former agricultural fields in the LMAV. This restoration sequence is initiated by establishing the native species eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) to rapidly develop forest structure on the site. Following the establishment of the cottonwood plantation, the understory is enriched by planting Nuttall oak (*Quercus nuttallii* Palm.), a hard-mast-producing, disturbance-dependent species of later successional seres. Initial results indicate that this interplanting system has potential as an alternative afforestation practice that can address multiple forest restoration objectives, for example, rapid forest biomass production and quick assembly of bird species richness (Hamel 2003). However, the ability of Nuttall oak to establish and grow in the understory of eastern cottonwood remains an uncertainty. In the current study, we examine biomass accumulation of Nuttall oak seedlings established under two contrasting afforestation techniques (interplanted beneath eastern cottonwood vs. planted in the open). The purpose of this investigation was to gain knowledge on the early morphological development and biomass distribution of Nuttall oak seedlings that may be incorporated into future afforestation and forest restoration practices.

## Methods

### Study Site

The study was established in the LMAV on a former agricultural site located in Sharkey County, Mississippi, U.S.A. (32°58′ N, 90°44′ W). The site is situated in the humid, subtropical region of the temperate zone where the mean annual precipitation is 1,318 mm, and air temperature averages from 27.8 "C in July to 7.5°C in February (Scott & Carter 1962). Sharkey Clay, a very fine, smectitic, thermic, chromic Epiaquerts, is the predominant soil on the site. Core samples collected across the study site indicated that texture of this alluvial soil ranges from 7 to 12% sand, 22 to 42% silt, and 46 to 71% clay in the surface horizon (O-7.5 cm).

### Establishment of Experimental Stands

More than 25 years of agricultural production ended on the study site with the harvest of a soybean *(Clycine max* [L.] Merrill) crop in the fall of 1994. We initiated this experiment in March 1995 by establishing a replicated eastern cottonwood plantation. Three 8.1-ha cottonwood stands were established according to methods used by Crown Vantage paper company as previously described by Gardiner et al. (2001). Cottonwood cuttings were hand-planted on a 3.7 × 3.7-m spacing, and each stand replication received mechanical cultivation for competition control during the first two growing seasons. After the second growing season (February 1997), l-0, bare-root Nuttall oak seedlings were interplanted between every other cottonwood row (3.7 x 7.3-m spacing). Additionally, a Nuttall oak stand was established immediately adjacent to each of the three interplanted cottonwood stands for the purpose of providing open-grown seedlings that would serve as experimental controls for morphology and growth measurements. Thus, the experiment included three replicated stands of Nuttall oak seedlings interplanted beneath eastern cottonwood and three replicated stands of open-grown Nuttall oak seedlings. The three Nuttall oak stands were hand-planted on a 3.7 x 3.7-m spacing with the same stock material used for interplanting the cottonwood stands. Fifty experimental seedlings were selected in each stand and protected from small mammal herbivory with 0.6-m tall and 0.6-m diameter wire mesh shelters.

### Experimental Stand Conditions

Sampling for this investigation began after oak seedlings completed three growing seasons. Table 1 provides a summary of the early stand characteristics that developed under each afforestation treatment. The eastern cottonwood nurse crop developed rapidly on this former

**Tablel.** Stand characteristics of open-grown Nuttall oak and eastern cottonwood interplanted with Nuttall oak established on former agricultural land in Sharkey County, MS, U.S.A.

| | Stand Type | |
|---|---|---|
| | *Open-Grown Nuttall Oak* | *Cottonwood Interplanted with Oak* |
| Eastern cottonwood density (stems/ha) | — | 716 |
| Eastern cottonwood basal area ($m^2$/ha) | | 8.3 |
| Nuttall oak density (stems/ha) | 405 | 272 |
| Herbaceous competition (kg/ha) | 4,230 | 1,480 |
| Light availability ($\mu$mol $m^{-2} s^{-1}$)* | 1,047 | 32.5 |

The open-grown Nuttall oak stands were 3 years old, eastern cottonwood stands were 5 years old, and interplanted Nuttall oaks were 3 years old.
*Light availability data arc the mean photosynthetic photon flux density from a cloud-free day (10 July 1998) in the middle of the second growing season for Nuttall oak seedlings

agricultural site providing a forest structure that appeared to reach maximum leaf area index 3 years after establishment. The cottonwood canopy reduced light availability to interplanted oak seedlings (approximately 30% of light available in the open), but the amount of herbaceous competition in the understory of cottonwood plantations was less than 35% of that in the open (Table 1). It should be noted that growth and productivity of eastern cottonwood is very site specific. Bottomland soils that are excessively flooded, for example, are not appropriate for establishment of eastern cottonwood.

### Measurements and Statistical Procedures

After the third growing season for Nuttall oak, six randomly chosen oak seedlings were destructively sampled from each treatment combination (36 total). Height (cm) and root-collar diameter (mm) were measured, then each sample seedling was excavated from the soil and separated into leaf, stem, and root tissues. The number of leaves on each seedling was counted, then total leaf area was measured with an area meter (LI-COR, Lincoln, NE, U.S.A.). Average blade area was determined by dividing the total leaf area of the seedling by the number of leaves. Roots were washed to remove adhering soil particles then seedling biomass components were oven-dried at 50°C until completely desiccated. Oven-dried tissues were weighed, and proportional biomass accumulation by tissue type was computed according to the following formulae: leaf weight ratio (LWR) = leaf weight/total seedling weight; stem weight ratio (SWR) = stem weight/total seedling weight; and root weight ratio (RWR) = root weight/total seedling weight. Analyses of variance (ANOVA) according to a randomized block design (three levels of block, two levels of treatment) were conducted to test for a treatment effect on 12 response variables. Response variables tested included seedling height, root-collar diameter, leaf weight, stem weight, root weight, total seedling weight, number of leaves, blade area, total leaf area, LWR, SWR, and RWR. Individual tests were conducted on each response variable at an alpha level of 0.05.

## Results

### Stem Growth

Three years after establishment, Nuttall oak height was not influenced by the presence of the eastern cottonwood canopy, as seedlings averaged approximately 126cm tall regardless of afforestation treatment (Table 2). Mean heights observed on sampled seedlings represent positive growth of more than two times the height of seedlings at planting. Seedling root-collar diameter also showed positive growth during the 3-year establishment period (Table 2), but the magnitude of this response was influenced by the afforestation treatment. Nuttall oak seedlings interplanted in the understory of cottonwood stands were 20% smaller in root-collar diameter compared to those established in the open (Table2).

### Biomass Accumulation

After 3 years of establishment on former agricultural land, accumulation of Nuttall oak seedling biomass was greatest in stems and roots (Fig. 1). However, the amount of biomass accumulated by seedlings differed according to the afforestation treatments. Seedlings established in the understory of eastern cottonwood accumulated less biomass than open-grown seedlings (Fig. 1). This reduction was observed for all plant components such that interplanted seedlings accumulated 54% less leaf mass ($p = 0.0096$), 59% less stem mass ($p = 0.0242$), and 50%

**Table 2.** Initial and third-year height and root-collar diameter of Nuttall oak seedlings planted on a former agricultural field in Sharkey County, MS, U.S.A.

| *Variable* | *Open-Grown* | *Interplanted* | *p-Value* |
|---|---|---|---|
| Initial | | | |
| Height (cm) | 50.4 ± 2.8 | 53.6 ± 2.6 | 0.4117 |
| Root-collar diameter (mm) | 8.1 ± 0.5 | 7.4 ± 0.5 | 0.3707 |
| Year 3 | | | |
| Height (cm) | 128.4 ± 11.9 | 123.9 ± 14.1 | 0.7285 |
| Root-collar diameter (mm) | 26.7 ± 2.2 | 21.4 ± 1.3 | 0.0135 |

Values are expressed as mean ± standard error.

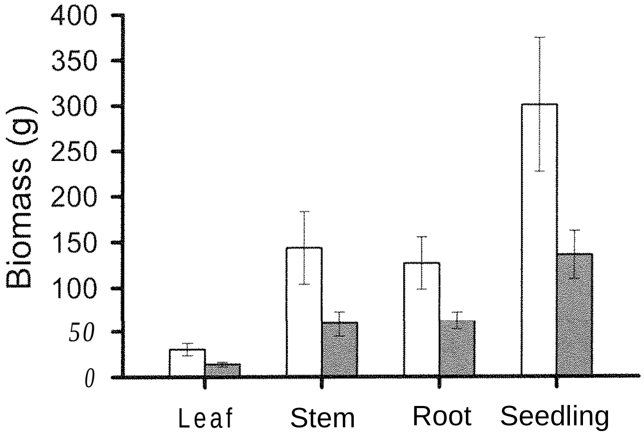

Figure 1. Biomass accumulation of Nuttall oak seedlings established in the open and in the understory of an eastern cottonwood stand in Sharkey County, MS, U.S.A. The seedlings were established 3 years prior to excavation. Light bars represent open-grown seedlings, dark bars represent underplanted seedlings, and error bars are ± standard error of the mean.

($p = 0.0113$) less root mass relative to seedlings established in the open. Accordingly, Nuttall oak seedlings established in the open developed a total mass more than two times the mass of seedlings established beneath eastern cottonwood ($p = 0.0148$) (Fig. 1).

### Biomass Distribution in Leaf Tissue

The comparatively greater amount of leaf biomass observed on open-grown Nuttall oak seedlings is partially attributed to a larger number of leaves (250% more) relative to interplanted seedlings (Table 3). Leaf blades of open-grown seedlings, however, were generally smaller in area (52%) than those of the interplanted treatment (Table3). Despite the greater number of leaves observed on open-grown seedlings, we were unable to detect a treatment effect on total leaf area (Table3). Thus, the photosynthetic surface area of interplanted seedlings did not differ from that maintained by open-grown seedlings.

### Biomass Distribution in Seedlings

Three years after establishment, Nuttall oak seedlings accumulated the smallest proportion of fixed carbon in leaf tissue (10%) (Fig. 2). Stem tissue comprised 42% whereas root tissue comprised about 48% of total seedling biomass (Fig.2). Irrespective of the large differences observed for biomass accumulation, the proportional distribution of biomass within seedlings was not altered by stand environment (Fig.2). Interplanted Nuttall oak seedlings accumulated leaf ($p = 0.9736$), stem ($p = 0.0847$), and root ($p$ -0.1042) biomass in equal proportions to open-grown seedlings.

**Table 3.** The number of leaves, mean blade area, and mean total leaf area observed on 3-year-old Nuttall oak seedlings planted on a former agricultural field in Sharkey County, MS. U.S.A.

| *Variable* | *Open-Grown* | *Interplanted* | *p-Value* |
|---|---|---|---|
| Number of leaves | 345 ± 83 | 98 ± 16 | 0.0023 |
| Blade area (cm’) | 10.4 ± 0.88 | 21.5 ± 1.98 | <0.0001 |
| Leaf area (cm’) | 3,259 ± 734 | 2,157 ± 402 | 0.0953 |

Values are expressed as mean ± standard error.

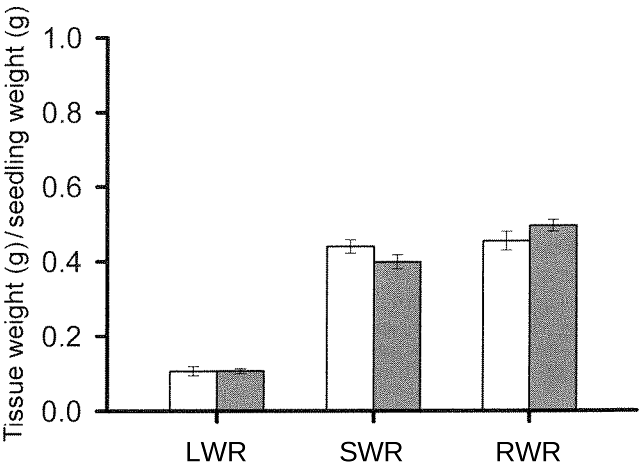

Figure 2. Proportional biomass accumulation of Nuttall oak seedlings established in the open and in the understory of an eastern cottonwood stand in Sharkey County, MS, U.S.A. The seedlings were established 3 years prior to excavation. LWR = leaf weight ratio. SWR = stem weight ratio, RWR = root weight ratio. Light bars represent open-grown seedlings, dark bars represent underplanted seedlings, and error bars are ± standard error of the mean.

## Discussion

Seedlings planted on former agricultural fields in the LMAV are prone to encounter numerous stress agents including vigorous herbaceous weed competition, mammal and insect herbivory, and drought and flooding (Allen et al. 2001). Small seedlings of poor vigor are generally more vulnerable to some of these environmental stresses than are vigorous large seedlings and saplings (Allen et al. 2001). For example, large seedlings and saplings have an advantage over smaller seedlings in the event of shallow flooding because the crown of the taller seedling is at a lower inundation risk. Thus, it is critical for establishment success that seedlings planted on former agricultural fields in the LMAV exhibit vigorous early growth. Irrespective of establishment treatment, Nuttall oak seedlings examined in this study averaged nearly 25 cm of annual height growth during the 3-year establishment period. This growth rate was within the expected range for bare-root, bottomland oak seedlings established on former agricultural fields without the use of competition control (Kennedy 1981, 1993). The presence of the eastern cottonwood canopy did not reduce average seedling height 3 years after establishment. In contrast, root-collar diameter was larger on seedlings established and grown in the open.

Though root-collar growth was not maximized when seedlings were established in the understory of eastern cottonwood, the root-collar growth we observed on interplanted seedlings appeared as good or better than other published observations for open-grown Nuttall oak planted on similar soils (Kennedy 1981; Patterson & Adams 2003). However, it is not known whether these interplanted seedlings with relatively smaller stem diameters will be prone to wind damage when released.

Our research may be the first to examine oak seedling growth and development in the understory of another broadleaf species established on former agricultural land. Studies examining oak seedling height and diameter growth in relation to establishment beneath partial overstories of natural broadleaf species stands have demonstrated mixed results. Teclaw and Isebrands (1993), who worked in natural stands in Wisconsin, demonstrated that northern red oak (Quercus *rubra* L.) seedlings may exhibit better height growth under a partial canopy than in the open, particularly where open sites are subject to vigorous competition and late spring frosts. Truax et al. (2000), who compared development of northern red oak and bur oak Michx.) growing in open fields and beneath natural aspen (*Populus tremuloides* Michx.) stands in Canada, observed contrasting results for these two species. They observed a better height and diameter growth increment for northern red oak established beneath aspen, whereas bur oak exhibited a better height and diameter growth increment when established in the open (Truax et al. 2000). Results from our study were most closely in line with those presented by Gcmmcl et al. (1996), who studied the development of pedunculate oak ***(Quercus** robur* L.) under different canopy densities of natural stands in southern Sweden. In their study, seedlings established beneath the partial canopies grew to the same height as those established in the open, but root-collar diameter was less than that of open-grown seedlings. It is obvious that the range of responses documented in the literature precludes generalizations on how oak seedling height and diameter will respond to an understory environment as responses appear specific to species, forest environment, and silvicultural system.

Biomass accumulation by Nuttall oak, particularly whole plant biomass for seedlings growing on former agricultural land in the LMAV, has not been well documented (Schlaegel & Willson 1983). In the current study, Nuttall oak seedlings established under two different afforestation treatments showed positive biomass accumulation over the 3-year study period, but biomass accumulation rate was determined by the environment in which seedlings were established. Our findings indicate that Nuttall oak seedlings established in the understory of eastern cottonwood plantations will maintain a positive accumulation of leaf, stem, and root biomass, but the accumulation rate will be less than for seedlings established in the open. This observation is in line with the decrease in root-collar diameter we observed on interplanted seedlings. This finding conflicts with observations on oak seedling biomass accumulation beneath artificial shade cloth. Biomass accumulation by cherrybark oak ***(Quercus pagoda*** Raf.) and pedunculate oak seedlings established under moderate levels of light availability can be as high or greater than for seedlings established under full sunlight (Ziegenhagen & Kausch 1995; Gardiner & Hodges 1998), because the artificial shade is thought to reduce seedling water stress. However, our finding is consistent with that of Gemmel et al. (1996), who reported greater biomass accumulation by pedunculate oak seedlings established in the open versus beneath partial canopies in southern Sweden. Moderating light availability with the use of partial overstories in natural stands or sparse canopies of plantation species does not appear to benefit oak seedling biomass accumulation to the same extent observed when seedlings are cultured under artificial shade.

Nuttall oak seedlings established in the understory of eastern cottonwood stands produced fewer leaves than those seedlings grown in the open, but they produced leaves with a blade area twice the size of those on open-grown seedlings. Because of these characteristics, seedlings from both afforestation treatments showed similar leaf areas. Oak seedlings studied by other workers exhibited a wide range in leaf number, blade size, and total leaf area responses along light gradients. Pedunculate oak, black oak ***(Quercus velutina*** Lam.), and banj oak ***(Quercus** leucotrichophora* A. Camus) showed a higher number of leaves in high light environments than in low light environments (Gottschalk 1994; Thadani & Ashton 1995; Welander & Ottosson 1998). Some oak species increase blade size under low irradiance, whereas others do not exhibit this characteristic (Callaway 1992). Valley oak ***(Quercus lohata*** Nee) and blue oak ***(Quercus douglasii*** H. & A.) did not alter total leaf area when grown under a range of light availability, but coast live oak ***(Quercus** agrifolia* Nee) seedlings did respond to increased light availability by decreasing blade area, which led to a decrease in total leaf area (Callaway 1992). Most species of oak will probably decrease leaf area under low light availability, but this response is typically not observed until extremely low levels of light are experienced (Gottschalk 1994; Ziegenhagen & Kausch 1995). The light levels observed in this study (approximately 30% of light available in the open) along with the ability of seedlings to maintain appreciable leaf area in the understory of eastern cottonwood are consistent with our premise that the understory environment in eastern cottonwood plantations appears suitable for Nuttall oak seedling establishment and growth.

Though establishment beneath the cottonwood canopy reduced total biomass accumulation by Nuttall oak seedlings, it is interesting that the relative distribution of accumulated biomass in seedlings was similar for both treatments. For the open and the understory environment, leaf tissue comprised 10%, stem tissue comprised 42%, and root tissue comprised 48% of total seedling biomass.

These results illustrate that Nuttall oak seedlings accumulated near equal proportions of biomass above- and belowground 3 years after establishment on a former agricultural field.

Several studies conducted on various oak species indicate that oak seedlings acclimate morphologically to environmental stresses through proportional biomass accumulation rates (Kolb et al. 1990; Thadani & Ashton 1995; Ashton & Larson 1996; Gardiner & Hodges 1998). For example, Kolb and Steiner (1990) demonstrated that northern red oak seedlings acclimated to belowground competition by increasing the proportion of biomass accumulated in roots. Welander and Ottosson (1998) reported a decrease in the root-to-shoot ratio of pedunculate oak seedlings with decreasing light availability. This response favors biomass accumulation in aboveground components to improve light gathering in low light environments (Welander & Ottosson 1998). The fact that seedlings established beneath eastern cottonwood accumulated less biomass than those established in the open indicates that light, soil moisture, or another factor were not sufficiently available in the understory to maximize Nuttall oak seedling growth. Though growth was not maximized, proportional accumulation of biomass indicates that resource availability in the eastern cottonwood understory did not limit seedling function substantially enough to alter Nuttall oak seedling morphology.

Stanturf et al. (2001) argued that afforestation is a necessary first step toward ecological restoration of bottomland hardwood ecosystems on former agricultural land. Conventional afforestation practices have generally targeted the establishment of mast-producing overstory species such as bottomland oaks (Allen 1997; Schoenholtz et al. 2001). Bottomland oaks have been favored because of their high value as a component of wildlife habitat and their limited dispersal; it is also thought that light-seeded species will establish naturally (Allen 1997; King & Keeland 1999). A primary criticism of conventional afforestation practices employed on bottomland sites centers on their effectiveness at initiating restoration of ecological functions of bottomland hardwood ecosystems. For example, Allen (1997), who studied woody plant invasion on 10 afforestation sites in the LMAV, expressed concern that conventional afforestation practices were leading to stands with low woody species diversity relative to natural bottomland hardwood stands. He observed a limited amount of natural invasion and inferior growth by light-seeded species in oak plantations, especially if stands were not immediately adjacent to a seed source (Allen 1997). Likewise, Ouchley et al. (2000) examined the composition of a historic bottomland hardwood forest, concluding that current silvicultural and afforestation practices foster a higher component of oak species than what was characteristic of historic bottomland hardwood forests. Allen (1997) and Ouchley et al. (2000) provide arguments that support establishment of more complex plantations with a higher component of light-seeded species to facilitate restoration of tree species diversity on bottomland hardwood afforestation sites. Their arguments and observations by others illustrate a clear need to identify and implement afforestation practices that will provide pathways toward catalyzing development of biodiversity components in bottomland ecosystems.

The eastern cottonwood–Nuttall oak interplanting system examined in this manuscript is a unique alternative for establishing bottomland hardwood forests because it quickly develops a forest cover, which may facilitate restoration of some ecological functions more rapidly than conventional afforestation. For example, results from this study indicate the understory microenvironment of eastern cottonwood stands is sufficient for establishment of the shade-intolerant Nuttall oak; hence it is likely that other bottomland hardwood species can invade the understory. Indeed, Hodges (1997) reported that shade-intolerant species such as American sycamore (*Platanus occidentalis* L.), sweet pecan (*Curyu illinoensis* [Wang.] K. Koch), green ash (*Fraxinus pennsylvanica* Marshall), and sweetgum (*Liquidambar styraciflua* L.) are often present in the understory of natural eastern cottonwood stands. Our own observations indicate that given a seed source, numerous bottomland hardwood species readily become established in the understory of eastern cottonwood plantations. Thus, use of a plantation system such as this may serve to catalyze invasion by other bottomland hardwood species, thereby increasing species richness on the site as is the case for similar plantation systems studied in the tropics (Parrotta 1992; Lugo 1997; Powers et al. 1997).

Hamel (2003), who studied winter bird use on afforestation sites, described another example of how the eastern cottonwood-Nuttall oak interplanting system can provide a swift trajectory toward developing attributes of a natural ecosystem. He observed a more rapid assemblage of forest canopy-dwelling birds on sites receiving the eastern cottonwood–Nuttall oak interplanting system relative to sites receiving afforestation with oak alone (Hamel 2003). Hamel (2003) attributed this rapid assemblage of forest canopy birds to the quick development of forest cover by eastern cottonwood. Similarly, Twedt and Portwood (1997) found a it-fold increase in the number of bird species that established breeding territories in 5- to 7-year-old eastern cottonwood stands versus 4- to 6-year-old oak plantings. As our research efforts continue to focus on this eastern cottonwood-Nuttall oak afforestation system, we are encouraged that additional benefits to restoration of bottomland hardwood ecosystem functions will be revealed. Future work with this afforestation system will concentrate on the developmental trajectory of various biodiversity components in bottomland hardwood ecosystems, including understory flora, soil arthropods, small mammals, and insect assemblages.

## Management implications

Several management implications of practical significance to forest restoration practitioners working in the LMAV and other temperate regions may be drawn from this work. First, we documented substantial height growth and positive biomass accumulation for the 3-year period Nuttall oak seedlings were established in the understory of eastern cottonwood stands. We are encouraged that these interplanted seedlings are rapidly developing into large saplings that should respond quickly to release and are at a lower risk of sustaining damage from herbivory or flooding. We also noted similar morphologies between seedlings established in the open and beneath eastern cottonwood, indicating that resources, that is, light, water, and nutrients, required for growth by interplanted seedlings were sufficiently available to maintain seedling function. These findings complement earlier work on leaf-level photosynthetic characteristics of Nuttall oak seedlings established beneath eastern cottonwood (Gardiner et al. 2001) and support the application of this interplanting system as an alternative method of establishing Nuttall oak as a component in restored bottomland hardwood stands on former agricultural land in the LMAV.

Second, we present favorable results from an experimental afforestation system that begins with rapid development of forest cover on former agricultural land through the establishment of a fast-growing, native plantation species (eastern cottonwood). After the establishment of forest cover, the plantation understory is enriched with a slower-growing, disturbance-dependent species (Nuttall oak) that is generally considered mid-successional. The promising application of this interplanting system in the LMAV provides a forest restoration model that can be tried with other species in other temperate regions. Advantages of this afforestation model include, but are not limited to, a speedy transition from cleared land to forest structure and associated forest functions (Hamel 2003), the potential to realize an early financial return on the restoration investment (Stanturf & Portwood 1999), and the opportunity to establish complex forest structure through enrichment of the understory with slower-growing, desirable species.

Finally, the magnitude of the afforestation effort currently concentrated in the LMAV presents a considerable opportunity for forest restoration, particularly for bottomland hardwood ecosystems. Because of biological and social factors inherent to the LMAV, for example, site heterogeneity, tree species diversity, ownership characteristics, landowner objectives, and restoration project scale, there is a strong need to provide alternative mechanisms for achieving restoration of sustainable forest ecosystems. We demonstrate that research aimed at understanding basic plant processes can aid in the development of biologically feasible afforestation systems that will provide the foundation for advancing sustainable forest restoration practices.

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