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Restoration of bottomland hardwood forests across a treatment intensity gradient

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ABSTRACT

Large-scale restoration of bottomland hardwood forests in the Lower Mississippi Alluvial Valley (USA) under federal incentive programs, begun in the 1990s, initially achieved mixed results. We report here on a comparison of four restoration techniques in terms of survival, accretion of vertical structure, and woody species diversity. The range of treatment intensity allowed us to compare native recolonization to direct seeding and planting of *Quercus nuttallii* Palmer, and to an intensive treatment of interplanting two species that differed in successional status (early successional *Populus deltoides* Bartram ex Marsh. ssp. *deltoides*, with the mid-successional *Q. nuttallii*). Native recolonization varied in effectiveness by block but overall provided few woody plants. All active restoration methods (planting and direct seeding) were successful in terms of stocking. *Populus* grew larger than *Quercus*, reaching canopy closure after 2 years and heights after 2 and 5 years of 6 and 12.7 m, respectively. Planted *Quercus* were significantly larger than direct seeded *Quercus* in all years, but only averaged 1.4 m in height after 5 years. Interplanting did not seem to facilitate development of the *Quercus* seedlings. The early success of the interplanting technique demonstrated that environmental benefits can be obtained quickly by more intensive efforts. Native recolonization can augment active interventions if limitations to dispersal distance are recognized. These results should provide landowners and managers with the confidence to use techniques of varying intensity to restore ecosystem functions.

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1. Introduction

Reconstruction (*sensu* Stanturf, 2005) of forest conditions on former agricultural land is occurring in all forested regions of the world through passive (native recolonization) or active (afforestation) restoration. In the decade 1990–2000, global afforestation proceeded at the rate of 1.6 million ha annually (FAO, 2001). Recolonization by woody species into idle pasture and cropland was widespread especially in the Tropics and Eastern Europe (FAO, 2001). Afforestation in Europe and the United States is driven primarily by agricultural policy (Stanturf et al., 2000; Weber, 2005). There is ample evidence that if left alone abandoned agricultural land will develop into secondary forest although it may take considerable time (up to decades to develop a closed canopy) and could result in species composition that fails to meet management objectives. The literature on old field succession (cf. Cramer and Hobbs, 2007) is large and venerable and theories of old field succession informed much of the development of ideas about ecosystem dynamics, especially in North America (Cramer, 2007). Nevertheless, the considerable diversity in dispersal patterns (Nuttle and Haefner, 2005), the relative importance of abiotic and biotic barriers to seedling establishment (Grubb, 1977; Young et al., 2005), and the long-term effects of founder and filter species (Grime, 1998; Battaglia et al., 2007) all affect the composition of the forest that results. Most work on old field succession has been in upland systems; bottomland systems differ significantly in the effective dispersal of propagules by floodwaters, in addition to dispersal by wind and animals (Bonck and Penfound, 1945; Hopkins and Wilson, 1974; Battaglia et al., 2002) and by the interactive effect of microtopography and inundation regime on seedling establishment (Gardiner and Oliver, 2005).

In the last decade of the 20th Century, over 193,000 ha of cropland were afforested in the LMAV (Schoenholtz et al., 2001;

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Gardiner and Oliver, 2005), mostly on land cleared in the 1960s and 1970s primarily for soybean (*Glycine max* (L.) Merr.) production (Sternitzke, 1976). Cleared during a drought period, this land remained at risk for late spring and early summer flooding, and is returning to trees (Amacher et al., 1998; Stanturf et al., 2000; Schoenholtz et al., 2001). The decision by many landowners to afforest these lands has been aided in part by the increased availability of public incentive programs such as the Conservation Reserve (CRP) and Wetlands Reserve (WRP) Programs (Stanturf et al., 2000). Private programs have developed recently in anticipation of trading in carbon offset credits, led by the electric power industry (e.g., PowerTree Carbon Company, 2004). To date, the WRP has funded afforestation of the most hectares (Schoenholtz et al., 2005) using technology developed in the 1960s to establish commercial timber plantations (Allen, 1990; Newling, 1990; Allen et al., 2001).

Early results from the WRP were discouraging (Stanturf et al., 2001a); seedling survival rates were low, despite much available information on planting and direct seeding techniques (Stanturf et al., 1998; Allen et al., 2001; Gardiner and Oliver, 2005). Previous research work showed great promise but was done on small experimental plots and scaling up operationally to the landscape level was challenging. In response to questions from managers, we undertook a study to compare operational techniques for afforesting bottomland hardwoods. Although the basic techniques for afforesting native hardwood species have been worked out (Allen et al., 2001), few studies have directly compared several techniques on the same site in order to determine efficacy (Lockhart et al., 2003). We designed our study to examine four levels of restoration intensity in order to address both applied and more theoretical questions. Besides the standard approaches of direct seeding acorns and planting bare-root seedlings, we included a more intensive operation interplanting a fast-growing, native species eastern cottonwood (*Populus deltoides* Bartram ex Marsh. ssp. *deltoides*) with Nuttall oak (*Quercus nuttallii* Palmer), and the least intensive treatment of doing nothing and depending upon native recolonization. This restoration intensity gradient allowed us to look at the trade-off between effort and benefit from restored ecosystem functions (Hamel, 2003; Ciccarese et al., 2005). The objectives of the study were to compare four restoration techniques in terms of survival, accretion of vertical structure, and woody species diversity. Hypotheses tested included the test of no differences in woody plant stocking density and growth among alternative afforestation techniques and no difference in Nuttall oak growth in the open versus beneath the cottonwood overstory. Because we planted four cottonwood clones with different phenology, we included the hypothesis of no difference in Nuttall oak growth beneath the four cottonwood clones.

2. Methods

2.1. Study site

The study was located in Sharkey County, MS (lat 32°58′N long 90°44′W). The study site was in the Big Sunflower River drainage, part of the Yazoo River Basin. Historically the area was part of the floodplain of the Mississippi River. The study site was 2.5 km east of the town of Anguilla, immediately north of the Delta National Forest. The site was privately owned until acquired by the Federal government Farmers Home Administration through foreclosure. The tract was transferred to the U.S. Department of Interior Fish and Wildlife Service (FWS) in 1993 and is administered by the Yazoo National Wildlife Refuge (since rededicated as part of the Theodore Roosevelt National Wildlife Refuge Complex). The land was actively cropped until the study was established; cultivation for soybean production ended in the fall of 1994. Annual rainfall in Sharkey County averages 1318 mm, and mean temperatures range from 7.5 °C in January to 27.8 °C in July (Scott and Carter, 1962).

The hydrologic and edaphic conditions of the study site were typical of land available for restoration in the LMAV. Soils were mapped as the Sharkey series of very-fine, smectitic, thermic chromic Epiaquerts (Pettry and Switzer, 1996), by staff of the Natural Resources Conservation Service in 1994. Sharkey soils consist of poorly drained clays formed in fine textured sediment in slack water areas in the Mississippi River floodplain. The Sharkey series is one of the most extensively mapped soils in the United States, accounting for more than 1.5 million ha (Pettry and Switzer, 1996). The shrink-swell nature of these Vertisols result in 2–10-cm wide cracks up to 1.5-m deep that form under dry conditions, and close when saturated, Surface soils (0–7.5 cm) contained 42–71% clay; subsoil clay content typically ranges from 60 to 90% in the Sharkey series (Pettry and Switzer, 1996).

2.2. Experimental design

The experiment was a randomized complete block design with three replicates located to avoid minor depressions in different portions of the tract. The blocks were based on observed slight differences in elevation. During the study we observed backwater flooding in some years of portions of the site during the winter and early spring prior to leaf out. This occurs when drainage from the site is impeded by high water levels in the receiving water (streams and the Big Sunflower River) and may involve some overbank flooding from nearby drainage ways. In general, Block I was the driest and Block III the wettest. Treatment plots were 8.1 ha and approximately rectangular. Treatments were chosen to represent a gradient in restoration treatment intensity, from native recolonization, direct seeding Nuttall oak, planting Nuttall oak, to interplanting Nuttall with eastern cottonwood. The interplanting technique combined a fast growing species, eastern cottonwood, as a nurse crop for the slower growing Nuttall oak. Within the cottonwood plots, four clones were planted in clonal subplots, 2-ha in size. Cottonwood is very intolerant of shading and intensive competition control is required to insure survival (Stanturf et al., 2001b). Thus, oak interplanting was delayed until after the cottonwood's second growing season. This planting pattern left an interrow without oak seedlings, which will allow directional felling and removal of the cottonwood with minimal damage to the oak seedlings, as the cottonwood can be harvested in as little as 10 years, providing an opportunity to manipulate canopy structure and a financial return to the landowner.

In a separate experiment, we examined the effect on cottonwood growth and survival of disking 1 year versus 2 years after planting by splitting each clonal subplot; one sub-sub-plot was disked twice during summer 1995 and the other sub-sub-plot was disked twice in each of the 1995 and 1996 growing seasons.

2.3. Establishment

All treatment plots were site prepared by disking. Two blocks (II and III) were disked in November 1994 but Block I became too wet for machines. Blocks III and I were disked in February 1995, just before planting. Locally grown bareroot 1–0 Nuttall oak seedlings (Fratesi Nursery, Leland, MS) were machine planted by FWS staff in March 1995 at 3.7 by 3.7-m spacing (730 seedlings/ha). Viable acorns that had been collected from nearby natural stands were machine sown by Fish and Wildlife Service staff in May 1995. Spacing was 1.1 by 3.7 m (2457 acorns/ha), with one acorn placed at each planting spot. No additional site preparation or tending was applied to the direct seeding, seedling planting, or native recolonization treatments, following standard practice under the WRP.

Eastern cottonwood cuttings were hand planted in March 1995 by Crown Vantage (now Tembec) crews. Site preparation and establishment procedures for the cottonwood were similar to those used operationally by forest industry (Stanturf et al., 2001b). Four commercially available clones were planted at 3.7 by 3.7-m spacing (730 cuttings/ha). Three clones had been selected from native populations along the Mississippi River (ST66, ST72, and ST75) and one was from an east Texas population (S7C1); all four clones are used operationally. Clonal material was provided by Crown Vantage and grown in their nursery at Fitler, MS. These clones were selected because they are adapted to the site, are in widespread use, and are available commercially. The material designated ST was collected from open pollinated progeny of phenotypically superior trees found in Issaquena County, MS (lat 32°37′N long 91°W). The clones ST66 and ST75 are male; ST72 is a female clone (Mohn et al., 1970). The material from the East Texas population (S7C1) is a male clone (Eckenwalder, 2001) collected from a site on the Brazos River.

Two growing seasons later (March 1997), Nuttall oak seedlings were interplanted under the cottonwood. Oaks were planted between every other cottonwood row, with spacing for the oak seedlings of 3.7 by 7.4-m (365 seedlings/ha). Approximately 300 additional oak seedlings were planted at the same spacing in an open field adjacent to each cottonwood plot to provide experimental controls for morphology and growth measurements (Gardiner et al., 2001).

2.4. Measurements

Four permanent measurement plots were installed in each treatment plot (except the native recolonization treatment) in fall 1995. For the direct seeded and planted treatments, measurement plots were rectangular, approximately 0.2 ha in size. Measurement plots for the cottonwood were also 0.2 ha, placed in each clonal subplot with two plots each in the split–split plots disked 1 and 2 years after establishment. The native recolonization plots were sampled differently but at comparable intensity. A total of 64 circular measurement plots of 6.45-m radius were established, totaling 0.85-ha for each treatment plot. This compares to the total area sampled (0.8 ha) in each of the direct seeded and planted plots. The native recolonization plots are larger than would be used to detect natural regeneration (i.e., larger than would be occupied by a mature tree) in a forested stand and represent a trade-off between sampling intensity, the time needed to visit plots, and our expectation that there would be few woody plants establishing by this method.

Herbaceous biomass was sampled in each treatment to determine the intensity of competition, which can be severe on these sites. For the native recolonization, direct-seeded, and planted treatments, each measurement plot was divided into quadrants and two randomly located herbaceous samples were taken in each quadrant for a total of eight samples per treatment plot. For the cottonwood treatment, herbaceous samples were taken in each clonal sub-plot; two samples were located in each disking treatment sub-sub-plot for a total of 16 herbaceous samples in each treatment plot. In all treatments, sampling consisted of randomly placing 1-m^2 plastic frames, removing all non-woody aboveground biomass by clipping at ground level, and returning the samples to the laboratory where they were held in cold storage for further processing. Samples were sorted by species and dried at 50 °C to constant mass; only biomass totals are reported here.

Height and diameter were measured of all woody stems that were detected in the native recolonization treatment annually beginning with the second growing season (1996). The number of plots containing at least one woody stem was used to determine the percentage of stocked plots. Distance from the plots to the nearest seed sources was measured by pacing; species of potential tree seed sources were noted. This does not account for all potential sources for water-borne or animal dispersed seeds, merely the closest sources. Survival, height and diameter growth were measured in the active restoration treatments annually through the fifth growing season. Tree heights were measured to the nearest cm with a height pole if 2 m or less, then to the nearest 3 cm with a tripod-mounted Criterion 400 Survey Laser (Laser Technology Inc., Englewood, CO) if taller than 2 m. Diameter at 15 cm or 1.37 m was measured to the nearest 2.5 mm with calipers. When multiple stems originated from the same cottonwood cutting, the largest stem was measured.

The interplanted oak seedlings were measured as above, annually beginning in 1997. A subset of these seedlings (105 in each disking treatment sub-sub-plot) was measured in March 1997 for initial height after planting. We found evidence of herbivory by deer and small mammals, i.e., clipped or torn seedlings. Because counting only the damaged seedlings would not account for seedlings clipped at ground level or torn from the ground, we derived an index of herbivory by comparing heights at the beginning and end of the first growing season. Negative height growth was attributed to herbivory but since other factors such as moisture deficit could have caused top dieback, this probably overestimates herbivory.

Soils were systematically sampled for chemical analysis at four depths in multiple locations in each plot. Generally, surface soil (0–7.5-cm depth) was sampled at nine locations and the 7.5–15-cm depth sampled at five of these locations per plot. Samples for bulk density measurement were taken later from five locations within each plot. Bulk density of the surface 15 cm was sampled at each location using a hammer-driven split-core sampler with an inner sleeve; of the 15–30 cm-depth at two locations; and the 30–45-cm depth at one location per plot. Samples were taken from nearby stands of red oak-sweetgum (*Liquidambar styraciflua* L.) overstory, on Sharkey soils in a similar topographic position for comparison to natural forests (S. Schoenholtz, 1998, Virginia Tech, Blacksburg, VA, unpublished data). Soils were analyzed for nutrients (total nitrogen, total carbon, total organic carbon, total inorganic carbon, available phosphorus, and extractable potassium, calcium, magnesium, and sodium) at Mississippi State University Soil and Hydrology Laboratory. Extractions for cations were by a 1 M NH_4Oac and available phosphorus was by Mehlich III (Janet Dewey, 2002, Mississippi State University, Mississippi State, MS, personal communication).

Photosynthetic photon flux density (PPFD) was measured in a randomly selected cottonwood plot and an adjacent open area throughout the 1997 growing season and in July 1998. A LI-COR® LI-190SA (LI-COR, Lincoln, NE) quantum sensor placed in the open and a LI-191SA line quantum sensor placed under the cottonwood overstory measured PPFD on a 15-min interval.

2.5. Statistical analyses

All data were analyzed as Analyses of Variance for randomized complete blocks designs using PROC MIXED for repeated measures in SAS for Windows Release 8.01 (SAS Institute, 1994; Littell et al., 1996). Effects of treatment on survival, stocking density, and growth of woody stems over five growing seasons were tested. Prior to analysis, an angular transformation of survival data was applied to ensure normality of residual variances (Snedecor and Cochran, 1974). Similarly, height and diameter were logarithmically transformed. Annual survival, height, and diameter were analyzed ($\alpha = 0.05$) as repeated measures ANOVA with time as the repeated measure, treatment as a fixed factor, and blocks as a random factor using PROC MIXED (Littell et al., 1996). Degrees of

Table 1
Soil chemical characteristics of former agricultural land and nearby natural forest stands at the Sharkey Restoration Site, Sharkey County, MS by nutrient concentration and depth; all values are expressed as mg/kg except for C:N ratio; means are followed by standard error in parentheses.

Treatment	Total N	Total C	Total organic C	C:N	P	K	Ca	Mg	Na
0–7.5 cm depth									
Forest	2.54a (0.226)	28.78a (2.253)	27.39a (2.165)	10.8	33.0a (7.17)	405a (22)	4115a (410)	1207a (75)	33.4a (3.67)
Native recolonization	1.77b (0.110)	20.08b (1.070)	18.56b (1.144)	10.5	50.6b (7.78)	313b (19)	3564a (154)	845b (80)	25.8a (2.90)
Direct seeded	1.70b (0.109)	19.50b (0.916)	17.86b (1.345)	10.5	46.2ab (5.03)	305b (20)	3629a (61)	867b (2)	25.5a (4.67)
Planted	1.70b (0.234)	19.91b (2.158)	18.37b (1.878)	10.8	50.0ab (7.48)	325b (28)	3535a (155)	860b (33)	30.0a (2.65)
Interplanted	1.58b (0.065)	17.41b (0.112)	16.50b (0.556)	10.4	50.3b (7.28)	313b (13)	3707a (223)	926b (26)	25.7a (4.98)
7.5–15 cm depth									
Forest	1.21a (0.250)	11.94a (1.842)	11.79a (1.730)	9.7	30.2a (8.21)	400a (48)	3992a (709)	1342a (138)	54.2a (9.07)
Native recolonization	1.07a (0.107)	11.58a (1.186)	11.13a (1.120)	10.4	40.2a (9.34)	275b (27)	3780a (78)	948b (95)	47.9a (10.11)
Direct seeded	1.03a (0.077)	10.42a (0.484)	10.42a (0.484)	10.2	33.5a (3.65)	264b (16)	3709a (67)	934b (35)	41.5a (10.87)
Planted	1.00a (0.118)	11.34a (1.950)	11.34a (1.903)	11.3	43.0a (8.18)	278b (26)	3741a (207)	944b (59)	44.0a (2.52)
Interplanted	1.06a (0.070)	10.41a (0.164)	10.41a (0.180)	9.8	35.0a (5.73)	274b (8)	3894a (181)	1020b (30)	43.1a (8.35)

Means in a column followed by the same letter are not significantly different at the $p = 0.05$ level.

freedom were adjusted by the Satterthwaite method. We evaluated several covariance structures for each repeated measures analysis, including autoregressive order one, Huynh-Feldt, unstructured, compound symmetry, and Toeplitz (Milliken and Johnson, 1992). Akaike's Information Criterion and Schwartz' Bayesian Criterion (Milliken and Johnson, 1992) were used to determine the appropriate variance structure. Where time by treatment interaction was significant, means were separated using the LSMEANS option in PROC MIXED and planned comparisons of treatment means were tested ($\alpha = 0.05$) using pair-wise comparisons of means obtained by the PDIFF option of LSMEANS. Soils data were analyzed as a randomized complete blocks repeated measures ANOVA with depth as the repeated measure, treatment as a fixed factor, and blocks as a random factor using PROC MIXED. Degrees of freedom were adjusted and variance structure chosen as described above.

We examined two questions in the interplanting that were not pertinent to the other treatments: were there differences in growth of the oaks under the four cottonwood clones with different phenology, and did disking for only one versus the standard two growing seasons affect the growth of herbaceous plants or the interplanted oak? The effect of cottonwood clone on growth of the interplanted oak was tested with clone as the fixed treatment factor and year as the repeated measure. The effect of 1 year versus 2 years disking on herbaceous biomass was similarly tested (disking as the fixed factor, year as the repeated measure). The effect of the disking treatment on interplanted oak was tested as a split-plot repeated measure with clone as fixed and disking as the repeated factor.

3. Results

3.1. Soils

Soil chemical properties did not differ significantly among the four restoration treatments at any depth (Table 1) but they differed significantly from soils of nearby forests in most respects. Compared to the natural forest the soils of the restoration treatments had lower carbon (C), nitrogen (N), and potassium (K) concentrations in the surface soil (0–7.5-cm depth) but higher phosphorus (P; Table 1) at the beginning of the experiment. Soil bulk density was not significantly different among treatments (Table 2) but was higher than in comparable forest soils. There was no evidence of a plow pan in any treatment, as bulk density did not significantly increase between the 0–15 and 15–30-cm depths (Table 2). Despite the lower C and N concentrations of the soils in the experimental area, the higher bulk density of the upper 15-cm of mineral soil offset this effect such that C and N mass was similar to natural forests (Tables 1 and 2). During the study, we observed that Block I was better drained than the other blocks and water often ponded at the surface in portions of Block III.

3.2. Herbaceous biomass

All treatments, including the native recolonization, were disked at the start of the experiment, before the 1995 growing season. Herbaceous biomass, an indicator of herbaceous competition, changed over time and differed significantly among treatments (Fig. 1). We found no significant differences in herbaceous biomass due to disking in the cottonwood treatment therefore we used the mean data for comparison to other treatments. Increasing biomass over time on all treatments reflects the response to the cessation of disking. Herbaceous biomass under the interplanting treatment was significantly less than the direct seeded treatment in 1996 and was less than all other treatments in 1998. The cottonwood crowns in the interplanting treatment closed in the second growing season (1996), shading the herbaceous layer. By the fourth growing season (1998), light availability under the cottonwood canopy was reduced to 35% of that in the open (Gardiner et al., 2001, 2004).

3.3. Competition growth and stocking in passive restoration

The abandoned soybean field was colonized over time by woody species usually disseminated by wind, mammals, birds, and possibly backwater flooding (Table 3). The woody species swamp dogwood (*Cornus stricta* L.), common persimmon (*Diospyros virginiana* L.), green ash (*Fraxinus pennsylvanica* Marsh.), sugarberry (*Celtis laevigata* Willd.), elm species (*Ulmus americana* L. and *U. crassifolia* Nutt.), hawthorns (*Craetaegus* species), honeylocust (*Gleditsia triacanthos* L.), and deciduous holly (*Ilex decidua* Walter) were found in the measurement plots (Table 3). All these species except *Gleditsia triacanthos* and *Craetaegus* spp. occurred in ditch banks within 100 m of Blocks 1 and III. In Block II, the closest seed sources for woody species were 500 m away. Four species that

Table 2
Bulk density (Mg/m^3) of the Sharkey soils at three depths by blocks at the beginning of the restoration treatments as compared to soils from natural forest; data for the natural forest are averages of four sites from).

Treatment	Depth (cm)		
	0–15	15–30	30–45
Forest	0.88 (0.050)	1.05 (0.036)	1.13 (0.041)
Native recolonization	1.43 (0.034)	1.44 (0.039)	1.27 (0.092)
Direct seeded	1.38 (0.040)	1.44 (0.049)	1.31 (0.085)
Planted	1.46 (0.027)	1.52 (0.021)	1.43 (0.008)
Interplanted	1.47 (0.030)	1.41 (0.038)	1.50 (0.030)

Means are followed by standard error.

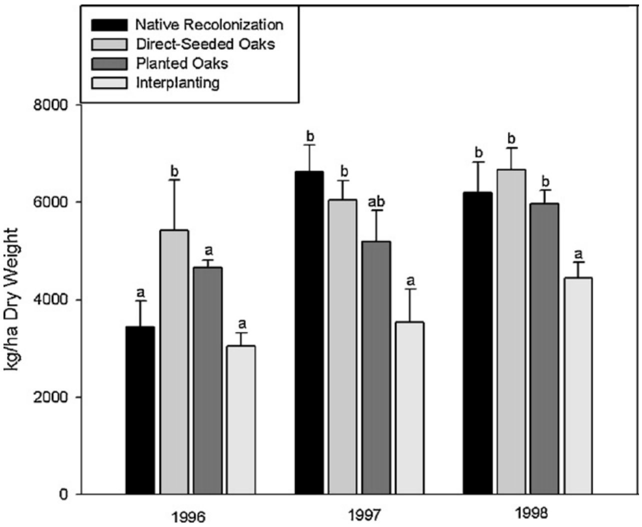

Fig. 1. Herbaceous biomass (kg/ha dry weight) in four restoration treatments over 3 years, measured annually beginning in the second season after cessation of active agriculture. Values are means of three replicates; bars indicate standard error of the mean. Different letters over bars within a year indicate significant differences at the $p = .05$ level.

occurred in nearby ditch banks were absent from the measurement plots: red maple (*Acer rubrum* L.), black willow (*Salix nigra* Marsh.), sweetgum, and water oak (*Quercus nigra* L.).

The earliest invaders were *Cornus stricta*, *Fraxinus pennsylvanica*, and *Ulmus* spp., all with local seed sources. *Cornus stricta* attained a greater average stocking than any other species by the third year (1997). Stocking overall averaged 118 stems/ha of woody species after 5 years. Colonization varied considerably among the blocks (Fig. 2); the greatest numbers of woody colonizers occurred in Block I, the driest block. By the fourth growing season (1998), over 73% of the plots in Block I were stocked with at least one woody stem; as the measurement plots were systematically placed throughout the treatment plot, this indicates the colonizers had penetrated the entire area. By far the most numerous species of colonizers was swamp dogwood (Table 3), which occurred in all blocks. Established stems grew rapidly; after two growing seasons some stems were already over 1-m tall (Fig. 2) and above the average height of the herbaceous species (1.3 m; Hamel, 2003). At the end of the fifth year, stems of seven woody species were over 1-m tall and two species, *Fraxinus pennsylvanica* and *Gleditsia triacanthos*, averaged more than 2-m tall.

3.4. Survival and stocking in active restoration treatments

Survival of the direct seeded acorns was significantly lower than the other treatments, less than 12% (Fig. 3). Cottonwood survival was uniformly high, over 90%; effects of disking 1 year versus 2 years on cottonwood survival were not significant, hence these data were combined. There was no effect of clone on survival or growth of the interplanted oaks; therefore we used the clonal means in each block for comparing the treatments. Survival of planted oak was intermediate, ranging from 56 to 64%. Survival of the interplanted oak did not differ significantly from the planted oak in any year (1997–1999), even though the interplanted oak was younger. Oak seedlings planted in the open at the same time as the interplanted oak (1997), for the physiology measurements (Gardiner et al., 2001, 2004), appeared to have the same survival rate (data not shown). Year-to-year differences in survival within a treatment were insignificant, except for direct seeding. Direct seeded oak stocking fluctuated annually over the first four growing seasons (1995 vs. 1996, $p = 0.0001$; 1996 vs. 1997, $p = 0.0003$; 1997 vs. 1998, $p = 0.0147$; 1998 vs. 1999, $p = 0.9069$). Such variability is often observed for operationally planted sites and is variously attributed to delayed germination, herbivory and re-sprouting, and the low visibility of new oak germinants and small seedlings in a heavy herbaceous cover (Gardiner and Oliver, 2005).

The low survival rate of direct seeded oak is usually expected; to compensate, more acorns are sown than seedlings are planted. In our study, three-times as many acorns were directly seeded as seedlings were planted. Despite the year-to-year variability in survival of the direct seeded oak, this compensatory measure appeared to be successful. By the end of the fifth year, stocking in the direct seeded and planted treatments did not differ significantly. Stocking of the interplanted oak was significantly less than the planted oak, reflecting the lower planting rate (365 stems/ha vs. 730 stems/ha). Herbivory on the interplanted oak was significantly related to the prior year's disking treatment. Thus seedlings planted after disking in the previous summer were damaged more than seedlings in the undisked plots (39% vs. 29%, respectively). Cottonwood stocking after 5 years was almost double the rate of the planted oak due to greater survival. After 5 years, the direct seeding and planting treatments did not differ in stocking but the interplanted treatment (cottonwood and oak together) was over 2.5 times as densely stocked as the other active restoration treatments.

3.5. Growth in active restoration treatments

The main effects of treatment and year, as well as their interaction, were significant for both height and diameter (Table 4) in all active restoration treatments. In each of the five growing seasons, the cottonwood was significantly taller and had larger diameter than the oak in any treatment (Fig. 4). Planted oak were significantly larger (both height and diameter) than direct seeded oak in all years. After five growing seasons, planted oak averaged almost 1.4-m in height. The interplanted oak was significantly taller than the direct seeded oak in 1997 and 1998; by 1999, they were not significantly different in height and they were half as tall as the planted oaks.

Table 3
Average stocking and height of woody species over 4 years for the passive restoration treatment (native recolonization).

Species	Average stocking (stems/ha)				Average height (cm)				Seed source nearby	Dispersal mechanism
	1996	1997	1998	1999	1996	1997	1998	1999		
Celtis laevigata	0	5	11	10		136.6	132.1	175.4	Yes	Birds and water
Cornus stricta	1	52	71	85	157.5	104.4	132.0	173.4	Yes	Birds and mammals
Diospyros virginiana	0	3	7	9		144.4	126.3	168.1	Yes	Birds, mammals; water
Fraxinus pennsylvanica	4	11	13	12	109.4	145.5	178.3	211.1	Yes	Wind, possibly water
Gleditsia triacanthos	0	<1	<1	<1		97	193.0	290.0	No	Birds and mammals
Craetaegus spp.	0	0	2	<1			75.7	117.0	No	Birds and mammals
Ilex decidua	0	0	0	1				63.3	Yes	Birds and mammals
Ulmus spp.	3	10	10	7	114.3	102.0	110.2	163.6	Yes	Wind

Nearby seed sources were within 500 m of the treatment plots.

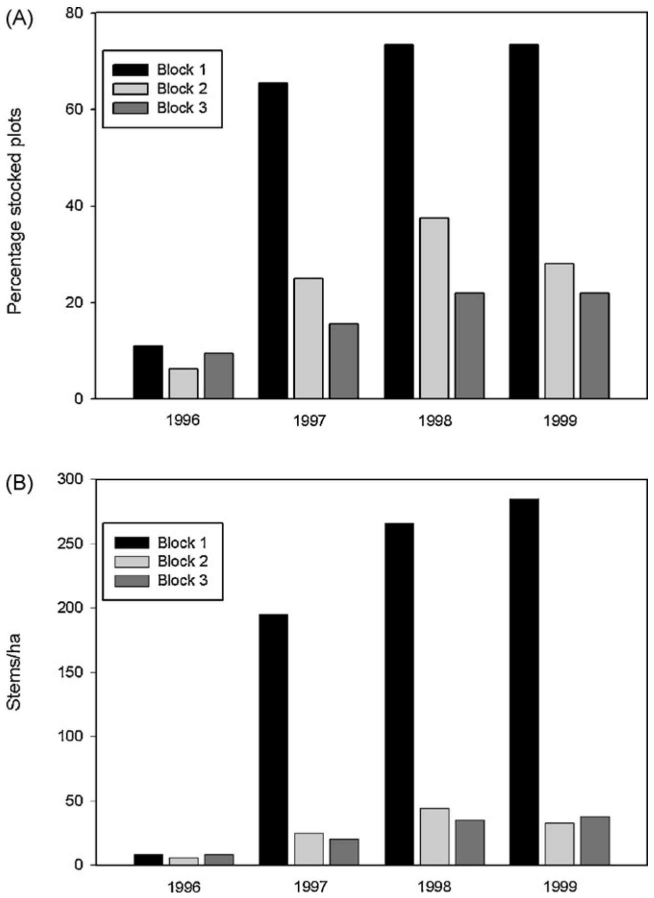

Fig. 2. Effectiveness of native recolonization on the Sharkey Site, illustrated by the variability among blocks in (A) percentage of stocked plots and (B) number of woody stems per hectare. A plot was considered stocked if it contained at least one woody stem of any species.

Diameter growth differences among treatments were similar to the pattern of height differences. Diameter of cottonwood was significantly greater than oaks in all treatments, despite being measured at 1.37 m rather than 15 cm. The mean diameter of the planted oak was significantly greater than the direct seeded oak in all years. The interplanted and direct seeded oak seedlings were the same diameter, even though the direct seeded oak seedlings were 2 years older (Fig. 4).

3.6. *Passive versus active restoration*

After five growing seasons, cottonwood was the tallest tree on the restoration site (Fig. 5). Significant block differences in growth of the cottonwood and native recolonizers followed the wetness gradient (Block 1 drier > Block 2 > Block 3), as indicated by the height of the tallest stems. Thus, the tallest cottonwood stems were in the drier Block 1. For the planted and direct seeded Nuttall oak seedlings, the trend was in the reverse direction; the tallest stems were in the wettest Block 3. After five growing seasons, both passive and active restoration treatments produced individual stems taller than the average height of the herbaceous vegetation (1.3-m), except the tallest direct seeded oak in Blocks 1 and 2 were not taller than the herbaceous competition. The direct seeded oak and the recolonizing species all originated from seed at about the same time but the tallest stems of the recolonizers were taller than the sown oak in all blocks, and approached (Block 2) or exceeded (Block 1) the height of planted oak seedlings. The tallest recolonizer species were green ash and honey locust.

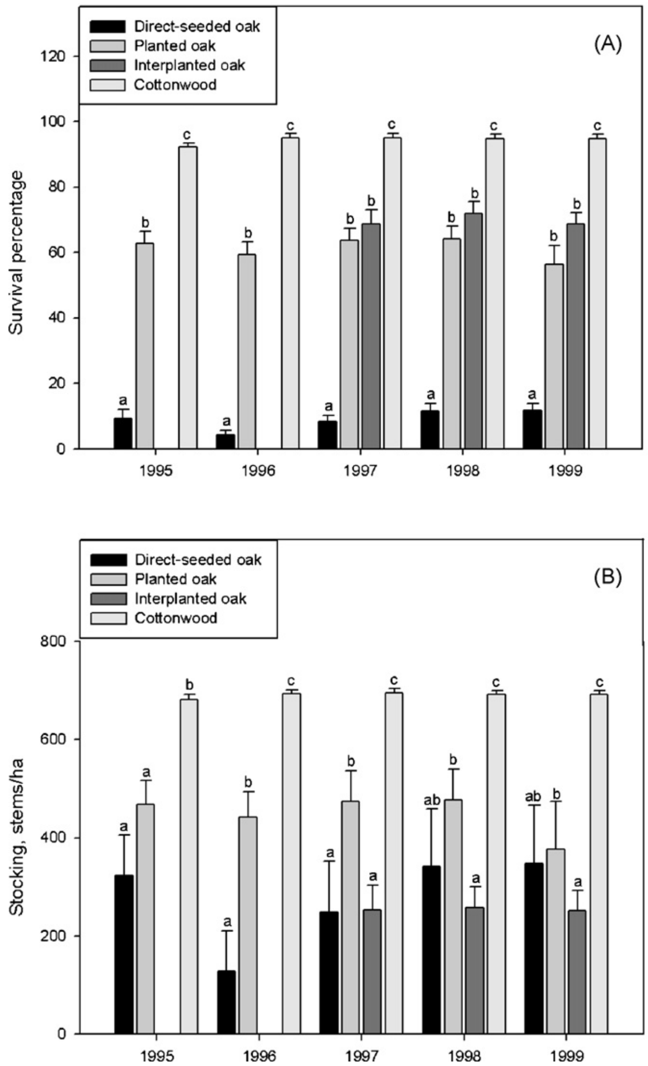

Fig. 3. Effectiveness of active restoration treatments in terms of (A) average percentage survival, and (B) average stocking of all active restoration treatments by year over the first five growing seasons; values are means of three replicates; error bars indicate standard error of the mean. Different letters over bars within a year indicate significant differences at the $p = .05$ level.

Table 4

ANOVA mixed model of repeated measures, Type 3 sums of squares test for fixed effects of height and diameter in the active restoration treatments (direct seeding and planting oak; interplanting cottonwood; height and diameter log-transformed).

	Numerator d.f.	Denominator d.f.	*F* value	Pr > *F*
Effect for height				
Treatment	2	9	5902.64	<0.001
Year	4	154	705.52	<0.001
Treatment × Year	8	154	112.56	<0.001
Effect for diameter				
Treatment	2	9	5396.27	<0.001
Year	4	154	560.84	<0.001
Treatment × Year	8	154	74.84	<0.001

4. Discussion

Land degradation from agriculture has long been a concern (Hudson and Alcántara-Ayala, 2006) and the effects of deforestation and conversion to agricultural land use can persist for considerable time (Hedman et al., 2000; Bossuyt and Hermy, 2001;

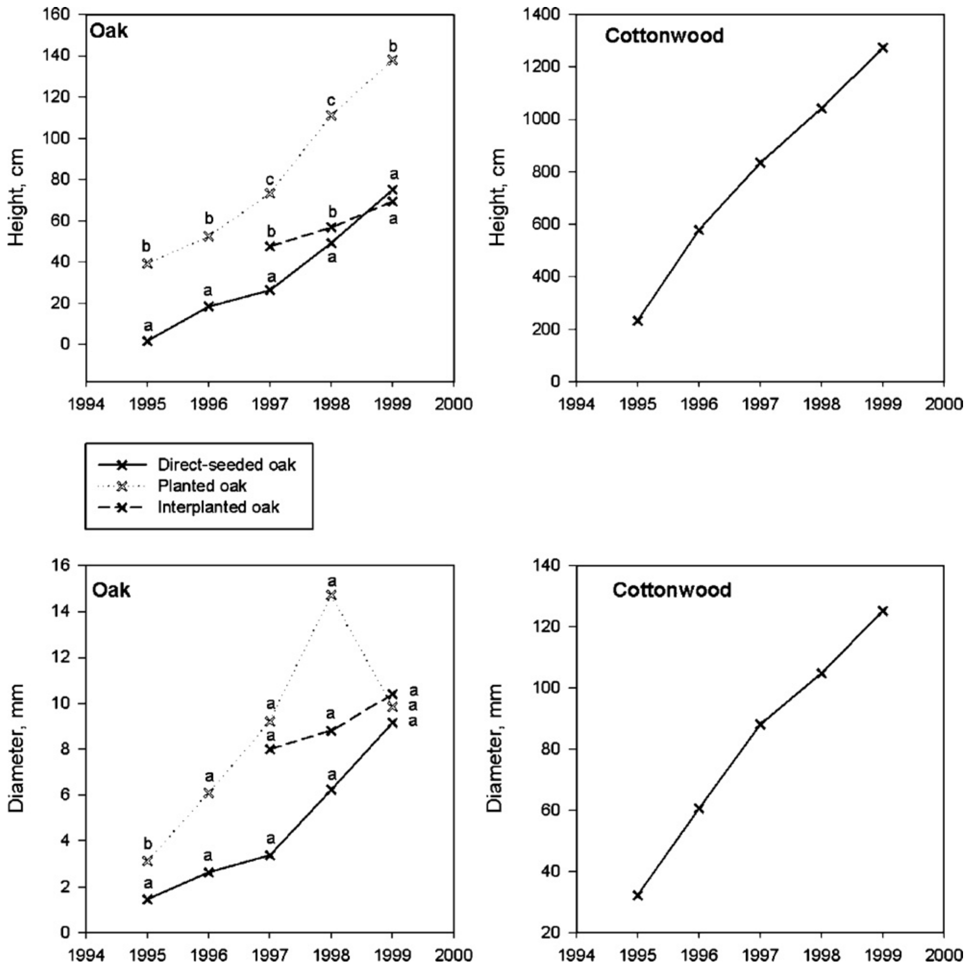

Fig. 4. Mean annual height (cm) and diameter (mm) of oak and cottonwood in all active restoration treatments over the first 5 years (the interplanted oak are only for three growing seasons). Diameter was measured at 15 cm for oaks, at 1.37 m for cottonwood. Different letters within a year indicate significant differences at the $p = .05$ level for the height and diameter of the oaks; the cottonwood differed from the oaks in all years.

Bellemare et al., 2002; Callaham et al., 2006; Flinn and Marks, 2007). The wave of conversion of forests to agriculture in the LMAV during the 1970s (Sternitzke, 1976) involved removal of the woody overstory followed by clearing tree stumps and roots with heavy machinery. Annual plowing and disking to prepare the seedbed for row crops over a 20–30-year period further affected soil physical and chemical properties, as well as changing the composition of microbial communities and herbaceous species. The lingering effects of agricultural use can be seen in the surface compaction (0–45 cm; Table 2) and enhanced P content from fertilizing the surface soil (0–15 cm; Table 1). Although former agricultural fields often exhibit low levels of soil C and N, C and N content at the Sharkey site was equal to that found under secondary forests. The story may be more complicated, however, because N content in the soil alone is a poor predictor of plant available N except under conditions of extreme deficiency. Gardiner et al. (2001) found a two-fold range in variation in foliar N levels in the interplanted and open planted oak and sensitivity of net photosynthesis to foliar N; they suggested this indicated sub-optimal carbon assimilation on these soils due to sub-optimal N uptake (Gardiner et al., 2001).

Hydrological characteristics of the study area were altered at several scales; levees and other flood control structures on the mainline of the Mississippi River and smaller structures on the Little Sunflower River prevent major floods (Harmar et al., 2005) although backwater flooding is a regular occurrence. Local drainage ditches to provide surface drainage are widespread throughout the LMAV, further altering hydroperiod on the site. There is no evidence, however, for land leveling in the study area, a common practice especially for rice cultivation; recent aerial photography indicates the presence of ridge and swale topography on the study site. Nevertheless, the repeated disturbance of the surface soil removed the microtopography characteristic of forest soils (Stone, 1975; Beatty and Stone, 1986) and possibly reduced safe sites for many recolonizing species.

Matching species to site is critical to restoration success (Baker and Broadfoot, 1979; Allen et al., 2001). The problem observed in the early days of the WRP, severe mortality, was attributed primarily to inattention to site adaptation of species, in particular tolerance to inundation (C.J. Schweitzer, 2004, US Forest Service, Normal, AL, unpublished data). Even so, seedlings often faced severe physical conditions as illustrated by the shrink-swell soil characteristics of our site. The variability in wetness among blocks in our study is typical and there are even wetter phases of the Sharkey series (Pettry and Switzer, 1996).

The frequent failure of direct seeding has led to much speculation about seed predation by small mammals and certainly the competing vegetation that developed in the absence of competition control (Fig. 1) provided ample cover to protect rodents from predators. The significantly greater herbaceous vegetation on the direct seeded treatment in the first growing season after establishment was due to variability unrelated to the treatments. In 3 years, the amount of herbaceous vegetation was the same for all treatments except the interplanted, where development of the herbaceous understory was retarded by

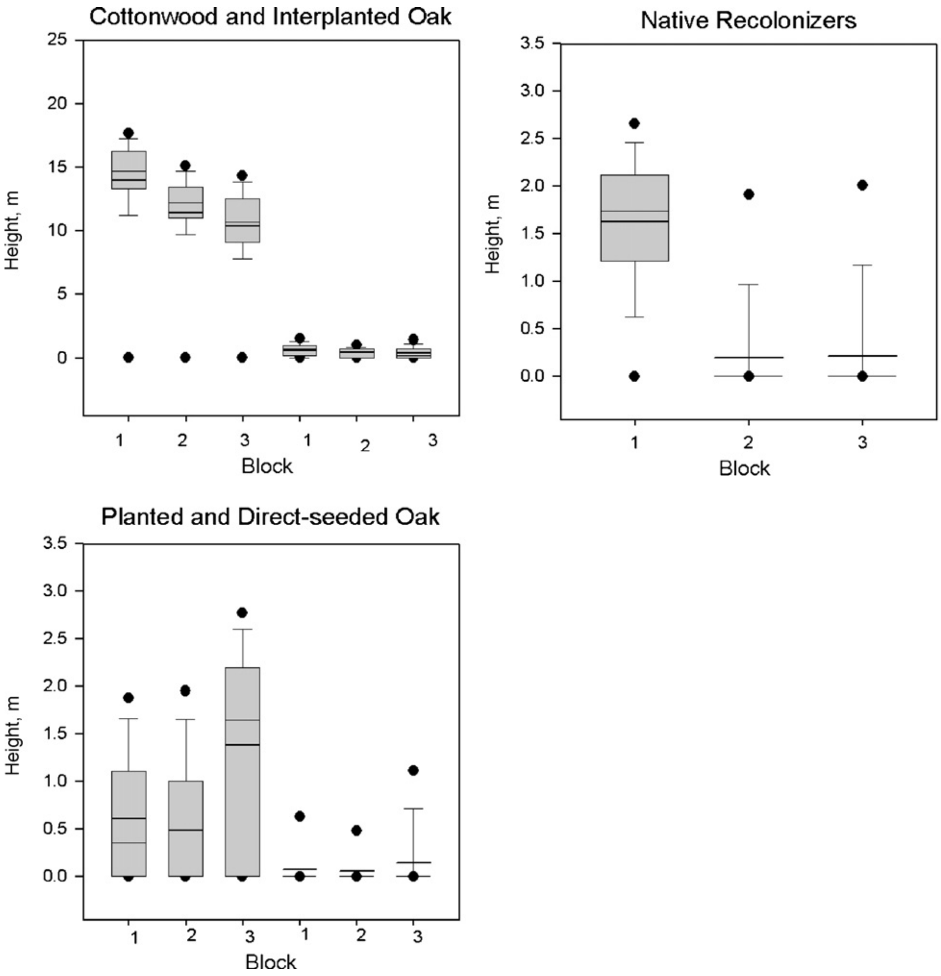

Fig. 5. Box plots of the heights in each treatment after five growing seasons (1999). The lower and upper boundaries of each box represent the 25th and 75th percentiles, respectively. Lines within the box mark the mean and median. Error bars above and below each box indicate the 90th and 10th percentiles and the dots are outliers.

continued competition control into the second growing season and thereafter by lowered light levels from the closing of the overstory crowns. In addition to suitable habitat, other work on the site has found that small mammal populations exploded in the early years (P.B. Hamel, 1996, US Forest Service, Stoneville, MS, unpublished data). This suggests that seed predation was likely although other factors likely contributed to the low survival of the direct-seeding treatment. The decline in survival of the direct-seeded oak in the second growing season and subsequent rebound thereafter (Fig. 3) we attribute to herbivory (clipping and resprouting); although some contribution from delayed germination cannot be discounted.

4.1. Passive to active comparison

Along with the reduction in microsite diversity noted above, repeated soil disturbance under row crop agriculture would have destroyed much of the seed bank of woody species developed under the original forest, further limiting potential compositional diversity (Beatty, 1991; Bossuyt and Hermy, 2001; Meadows et al., 2006). There is some evidence that herbaceous species live longer in the seed bank (Middleton, 2003; but see Bellemare et al., 2002) and populations of some woody vines persist even under annual plowing and become serious competitors on some bottomland sites (Stanturf et al., 2004). On many sites, the rapidly developing community of herbaceous competitors (e.g., Baer and Groninger, 2004) would have posed a biotic barrier to establishment of trees.

The location, size, and configuration of abandoned agriculture fields relative to mature forests are important. Allen (1997) found that large, relatively isolated fields had much lower densities of woody colonizers than long, narrow fields or especially fields with mature forest on more than one edge (Shear et al., 1996; Allen, 1997). Nevertheless, we found that even narrow strips of vegetation along ditch banks can provide seed, and noticeable dispersal occurs even when sources are more than 0.5 km distant (Fig. 2). The effectiveness of native recolonization varied considerably among the blocks in our study and only in Block I did they occur in abundance. The low numbers of stems and stocked plots in Blocks II and III were similar, despite that seed sources were more distant from Block II than Block III (Fig. 2), suggesting a critical role for wetter microsite conditions in Block III. We observed what is locally termed backwater flooding caused by impeded drainage from the site. The effective dispersal of some native recolonizers may have been aided by water dispersal in Blocks II and III that were the farthest from seed sources.

Of the species occurring on banks of nearby drainage ditches, four (black willow, sweetgum, water oak, and red maple) were absent from the restoration stands. The failure of the light-seeded black willow to establish is consistent with our observations in natural stands where black willow requires very moist soil conditions to establish and timing is critical for seedfall to coincide with flooding and subsequent recession of water. Most of the species present on the ditch banks produce seed by the age of 15 years; however sweetgum and water oak typically require 20 years or more (Kormanik, 1990; Vozzo, 1990). It is possible that insufficient time had elapsed since clearing and draining in the 1970s for these species to mature to seed-bearing age. Water oak acorns would have faced additional dispersal obstacles from their large size (Battaglia et al., 2007). Sweetgum produces many small seeds that develop within a large head, but generally the seeds readily disperse. That the light-seeded red maple did not colonize the restoration treatments is puzzling, as it begins bearing seed as young as 4-year of age (Walters and Yawney, 1990).

4.2. Planting to direct seeding oak comparison

Direct seeding has been successful (Wittwer, 1991; Stanturf et al., 1998) and can be less expensive than other methods (Bullard et al., 1992). In this study, the strategy of planting more seed than seedlings to compensate for lower survival was successful. After four growing seasons, the stocking from direct seeding was not significantly less than from planting seedlings (Fig. 3). After three growing seasons, the planted oak seedlings were significantly taller (73.2 cm) than the directed seeded plants (26.3 cm) and by the fourth season, the planted oak was even with the herbaceous competition (1.3 m; Hamel, 2003). The lack of significant differences between planted and direct seeded oak in the first 2 years could have been due in part to clipping by small mammals and deer, which we observed. Twedt and Wilson (2002) found the height advantage for planted oak persisted for at least 18 years. It should be noted that Nuttall oak seems to be more robust than other oaks and seeding rates should be higher for other species or under more severe site conditions (Stanturf et al., 2004). Lockhart et al. (2003), for example, found that direct seeded Nuttall oak survived better than willow oak or water oak following direct comparisons on two sites in Louisiana with clay soils.

4.3. Operational to innovative comparison

In addition to comparing operational planting techniques on the same site, we tested the performance of interplanting. Kelty (2006) reviewed the experience with species mixtures in plantations for timber production and for restoration, specifically mined land reclamation. He concluded that strategies based on either relay or initial floristic succession models can be used, but generally at least two sequential planting stages would be needed to approach the species composition of native forest. Ashton et al. (2001) drew primarily on work in the Tropics and advocated mixing shade-intolerant with shade-tolerant species in mixtures or species of different successional status because species of similar shade tolerance planted in mixtures fail to stratify their canopies.

Interplanting has been used in the Tropics to restore degraded sites (Ashton et al., 1997; Lamb et al., 2005) and to jump-start forest succession (Parrotta et al., 1997) but mostly with exotic species as the nurse crop. The interplanting technique as we used it appears to mimic natural stand development processes of riverfront hardwoods (stands on better-drained ridge and front sites in major alluvial floodplains) but within a compressed time frame (Hodges, 1997; Meadows and Stanturf, 1997). In this pathway, cottonwood establishes in mostly pure stands. Over time (40–50 years), other species establish under the cottonwood and are released after disturbance or senescence removes the overstory. Cottonwood is a typical shade intolerant species with rapid height growth that develops a crown with low leaf area, allowing substantial light to penetrate to the ground. In naturally regenerated cottonwood stands this allows substantial variation in the stand composition that follows (Hodges, 1997).

The interplanting technique was designed to rapidly develop vertical structure. The early growth of cottonwood allowed for the rapid establishment of forested conditions, with canopy closure attained by the end of the second growing season. Interplanting produced a two-layered stratified stand; the cottonwood canopy averaged over 10 m tall after 5 years, with an understory of oak seedlings and herbaceous competitors around 1 m tall. The other plantings were essentially single-layered with some emergent oak seedlings in the planted treatment (Fig. 4). Vegetation structure and avian occurrence are closely related (Twedt and Wilson, 2002; Twedt et al., 2002) and tree height appears to be positively correlated with colonization of restored forests by birds (Twedt et al., 2002; Twedt and Best, 2004). These relationships appeared to apply to our stands: Hamel (2003) observed twice the mean species richness of birds in the winter on the interplanted plots in this study as compared to the other treatments. We anticipated the interplanting treatment would attract bird and mammal seed dispersers (McClanahan and Wolfe, 1993; Myers et al., 2004) as well as trapping wind-blown seed and that the relatively open crowns of the cottonwood would not only permit light but also seeds to reach the forest floor, such as we observed in industrial cottonwood plantations and documented by Twedt and Portwood (1997). Early observations suggested that native recolonizers were establishing within the stands on the edges but not yet penetrating to the interior of all restoration treatments.

Facilitative interactions are increasingly recognized in the ecological literature with reference to niche concepts (Callaway and Walker, 1997; Bruno et al., 2003) and in restoration (e.g., Castro et al., 2002; Gómez-Aparicio et al., 2004). We hypothesized that the cottonwood would facilitate the development of the interplanted Nuttall oak seedlings by ameliorating microclimate. Facilitation involves one species directly benefiting the growth of another (Bruno et al., 2003) without harm to either. Foresters have recognized this kind of interaction and mixed nitrogen-fixing species with commercial timber species or used nurse trees to ameliorate microsite conditions (Kelty, 2006). The interplanted and planted oaks developed similarly when comparing seedlings of the same age (Fig. 4). Despite the greater herbivory on the seedlings in the plots that were disked both years before the oak seedlings were planted, the interplanted oak out-performed the older direct seeded plants. There is no evidence that interplanting beneath the cottonwood retarded the growth of the oak seedlings. In a separate study, Gardiner et al. (2004) compared the interplanted oak to seedlings planted in the same year in the open and found that after 3 years, height growth was comparable but the open-grown seedlings accumulated twice as much biomass, primarily due to greater diameter. Nevertheless, the interplanted oak seedlings did not change their morphology, which would have signaled a stress adaptation. A thorough evaluation of the facilitation hypothesis must await the removal of the cottonwood overstory; the critical test will be how the interplanted oak responds to release and whether or not it outperforms the open grown oak.

4.4. Implications for management and policy

The experience in the LMAV can be extrapolated to other programs for restoration of large areas and we identify three general results from this study: the difficulty of extrapolating from small-scale research studies and controlled pilot projects to operational restoration, differing objectives for restoration in a public–private ownership context, and the value of focusing on restoring functional forested ecosystems.

Operational restoration—The problems that emerged when restoration efforts in the LMAV moved from small experimental plots to large-scale afforestation and from controlled planting on public land to operational planting on private land were typical of the issues that surface when scaling up from research to practice. Early experience with the WRP in the Delta Region of the state of Mississippi further underscored the criticality of nearby seed sources: only those restoration sites adjacent to natural stands achieved successful stocking levels because of problems with the restoration prescriptions (C.J. Schweitzer, US Forest Service, Normal, AL, unpublished data). Other factors included inattention to site adaptations of species and the complex but subtle relationship of topography to growing season inundation that resulted in off-site plantings; and the failures of direct seeding and planting that were likely due to contractor crews experienced with planting pines but not hardwoods. These problems motivated our study and our decision to establish it using operational crews. The success of each of the treatments under operational conditions provides managers and landowners with assurance that these techniques can be used (Gardiner et al., 2008).

Variable objectives over time in mixed ownership landscapes—The restoration strategy developed by the FWS and adopted in the early days of the Wetlands Reserve Program (Haynes, 2004) was one of broadening the dispersal niche by translocating propagules of heavy-seeded species facing a physical dispersal barrier (*sensu* Young et al., 2005). The initial objectives of FWS restoration were to plant as many hectares as possible with the limited funds available, concentrating on establishing the heavy-seeded species that were difficult to establish and were important to wildlife, and relying on native recolonization to add diversity and increase stocking. Examination of the earliest plantings (Allen, 1990) indicated that mortality often was less than anticipated and the resulting oak stands gave other natives little opportunity to recolonize. To facilitate colonizer establishment and enhance biodiversity, Allen (1990) recommended direct seeding because of the gaps left by mortality. Native recolonization remained a critical element of the WRP approach to restoration. Departing from the guidelines used by the FWS, planting density in the WRP was lowered to produce widely spaced oak in order to improve opportunities for other woody species to establish. Effective dispersal distance became recognized as a problem for restoring small patches within a large matrix of active agricultural land with few sources for seeds of forest trees. Absent effective native recolonization, the resulting stands would be understocked and of low quality for timber management (Stanturf et al., 2001a).

Restoration practices attractive to landowners may not be acceptable to agency personnel or appropriate to public land. The interplanting technique met with resistance from the agencies responsible for the WRP and their objections were based on programmatic difficulty with the intensive measures required to establish cottonwood and the potential to harvest a commercial timber crop. The treatments needed to establish the cottonwood, herbicides and disking, were said to reduce herbaceous diversity and thus wildlife value. The need to continue establishment treatments (disking but also planting the oak) beyond the first year presented procedural problems with how payments to the landowner were structured (Floyd Woods 1996, Natural Resources Conservation Service, Jackson, MS, personal communications). Nevertheless, interested landowners have instituted the interplanting scheme under the CRP program (Conservation Practice 31) and 13,000 ha were enrolled for this treatment in the Continuous Sign-Up CRP program from 2003 to 2005 (Theodor Leininger 2006, US Forest Service, Stoneville, MS, personal communication).

Focus on restoring functions—Ecological restoration guidelines measure success in terms of attaining the structure and composition of reference stands (Society for Ecological Restoration, 2004). Although there are numerous drawbacks to using reference stands to measure success (Clewell and Lea, 1990), they are useful in defining goals and realistic expectations (Anderson and Dugger, 1998). Alluvial floodplain forests exhibit high species richness and spatial diversity of vegetation communities (Wharton et al., 1982; Kellison et al., 1998). More than 70 tree species are endemic to bottomland hardwood forests along with numerous vines, shrubs and herbaceous species (Putnam et al., 1960). In restoring large areas of former agricultural land, managers can intervene to restore only a few species due to financial and other constraints so that complete restoration will require effective natural dispersal and long time periods (e.g., McLachlan and Bazely, 2003; Battaglia et al., 2007). Using reference sites to define restoration success in highly modified landscapes faces other problems: in areas of drainage and levee construction such as the LMAV, regional hydrology has changed substantially within the lifetime of mature stands and the conditions under which reference stands established may be quite different from current conditions. Because much of the extensive floodplain of the Mississippi River has been isolated from most flood events of the river, sites are now "drier" and oaks have been planted in greater proportion than they may have been prior to European settlement (Ouchley et al., 2000). Nevertheless, natural regeneration of oak is problematic (Oliver et al., 2005), supporting the emphasis of restoration programs on establishing oak and other heavy-seeded species as the initial intervention. Experience suggests that complete restoration of species-rich forests with complex structures will require multiple interventions over time (Ashton et al., 2001; Kelty, 2006), but substantial functionality can be obtained in a short time using innovative techniques such as interplanting, especially if interventions are sequenced to take advantage of native recolonization and stand development processes.

The early success of the interplanting technique in rapidly developing forested conditions and vertical structure demonstrated that environmental benefits can be obtained quickly by more intensive efforts. Native recolonization can be utilized to augment active interventions if limitations to dispersal distance are clearly recognized. The results from this study should provide landowners and managers with the confidence to use techniques of varying intensity that restore ecosystem functions over time. The necessity of trading off costs with time needed to achieve desirable levels of environmental benefits underscores the importance of clearly defining at the outset restoration objectives and measures of success.

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