Plant Ecology **172:** 251–263, 2004.

Stand development on reforested bottomlands in the Mississippi Alluvial Valley

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Received 20 August 2002; accepted in revised form 4 July 2003

Key words: Afforestation, Bottomland Hardwood Forest, Plantations, Mississippi Alluvial Valley, Oaks, Reforestation, Tree Establishment

Abstract

Reforestation of bottomland hardwood sites in the southeastern United States has markedly increased in recent years due, in part, to financial incentives provided by conservation programs. Currently $>250{,}000$ ha of marginal farmland have been returned to hardwood forests. I observed establishment of trees and shrubs on 205 reforested bottomlands: 133 sites were planted primarily with oak species (*Quercus* spp.), 60 sites were planted with pulpwood producing species (*Populus deltoides*, *Liquidambar styraciflua*, or *Platanus occidentalis*), and 12 sites were not planted (i.e., passive regeneration). Although oak sites were planted with more species, sites planted with pulpwood species were more rapidly colonized by additional species. The density of naturally colonizing species exceeded that of planted species but density of invaders decreased rapidly with distance from forest edge. Trees were shorter in height on sites planted with oaks than on sites planted with pulpwood species but within a site, planted trees attained greater heights than did colonizing species. Thus, planted trees dominated the canopy of reforested sites as they matured. Planted species acted in concert with natural invasion to influence the current condition of woody vegetation on reforested sites. Cluster analysis of species importance values distinguished three woody vegetation conditions: (1) *Populus deltoides* stands (2) oak stands with little natural invasion by other tree species, and (3) stands dominated by planted or naturally invading species other than oaks. Increased diversity on reforested sites would likely result from (a) greater diversity of planted species, particularly when sites are far from existing forest edges and (b) thinning of planted trees as they attain closed canopies.

Introduction

Over 10 million ha of bottomland hardwood forest once covered the Mississippi Alluvial Valley. Currently, only 24% (2.6 million ha) of this vast forest remain within a highly fragmented landscape dominated by agriculture (Rudis 1995; Twedt and Loesch 1999). Altered hydrology and unwise forest management have degraded many of the forest fragments (Gosselink and Lee 1989).

Government (e.g., U. S. Department of Agriculture, U. S. Fish and Wildlife Service, and state wildlife agencies) and private organizations (e.g., Ducks Unlimited and The Nature Conservancy) have increased public awareness of the ecological and economic benefits of bottomland hardwood forests. Increased value placed on forested wetlands has led to government programs, particularly the Wetland Reserve Program (U. S. Department of Agriculture), that provide financial incentives to restore forested wetlands. Some reforestation has targeted wildlife habitat under the auspices of conservation agencies, whereas other reforestation has been undertaken to provide forest products or to sequester carbon. As of 2002, $>250{,}000$ ha have been reforested (Stanturf et al. 1998; updated by R. Wilson, Lower Mississippi Valley Joint Venture) with additional reforestation likely to add $>100{,}000$ ha to this total (Stanturf et al. 2001).

The objectives of reforestation vary among landowners and among target sites; reforestation methods are influenced by these restoration objectives. Although reforestation of bottomland hardwoods is uniquely undertaken on each site, I categorized initial establishment of reforested sites among three methods: (1) passive reforestation, (2) planting predominately heavy-seeded tree species – either as seeds (acorns) or seedlings, and (3) planting predominately fast-growing, early-successional tree species – either as stem cuttings or seedlings.

In passive reforestation, managers simply restrict future disturbance on the site – usually by terminating agricultural practices. On these sites, managers depend upon the vagility of colonizing species and therefore they cannot dictate the initial composition of the forest. This inability to influence species composition likely contributes to the rarity of passive reforestation on bottomland sites. Passive reforestation is usually restricted to sites where managers deem existing seed banks or nearby seed sources are sufficient (both in species and numbers) to ensure adequate colonization of the site. Although passive reforestation is initially less expensive than "active" reforestation, economic considerations have not encouraged passive reforestation. Indeed, in some cases, managers setback advanced regeneration of woody species obtained through passive reforestation by mowing, disking, or herbicide application and plant propagules of different species on these sites (pers. obs.).

The most common reforestation method on bottomland sites has been to plant seedlings (or seeds) of heavy-seeded trees (King and Keeland 1999). The species planted were predominately oaks (*Quercus* spp.), although on some sites additional planted species included: *Carya illinoensis*, *Taxodium distichum*, *Fraxinus pennsylvanica*, or *Diospyros virginiana*. These species were emphasized at planting due to their: (1) presumed limited dispersal capabilities, (2) importance to wildlife species (e.g., mast crops), and (3) high timber value (Allen and Kennedy 1989). Furthermore, managers have assumed that light-seeded tree species will naturally establish in these "heavy-seeded" plantations and ultimately result in a diverse forest.

Reforestation using fast-growing, "pulpwood producing" tree species, such as *Populus deltoides* or *Platanus occidentalis*, has most often occurred on sites managed by private timber companies (Twedt and Portwood 1997). After thorough site preparation, these sites are planted at densities as high or higher than when reforesting with heavy-seed species. Rapid development of planted pulpwood species is encouraged by chemical (Ezell and Chachot 1998) and mechanical (Kennedy and Henderson 1976) weed suppression during the first one or two years after planting.

Reforested bottomland hardwood sites have different habitat qualities and species compositions at different seral stages. Thus, their contribution to conservation goals is dynamic (Hamel et al. 2001; Twedt et al. 2002). Despite the importance of understanding this process, no long-term monitoring program documents the temporal changes in forest structure on variously forested sites. Thus, as a first step toward assessing forest development on reforested bottomlands, I used a chronosequence approach to assess tree and shrub colonization on reforested sites of different ages within the Mississippi Alluvial Valley and its adjacent minor river bottomlands. My objectives were to: (1) quantify density and development of planted species, (2) determine the extent of tree and shrub colonization on reforested bottomland sites by naturally invading species, and (3) contrast forest development and diversity among different methods of reforestation.

Methods

Study areas

I surveyed 205 reforested sites in six states: Arkansas ($n = 21$), Kentucky ($n = 25$), Louisiana ($n = 36$), Mississippi ($n = 113$), Missouri ($n = 6$), and Tennessee ($n = 4$). Ten reforested sites in Louisiana and Mississippi were surveyed during 1997. During 1998, I surveyed an additional 150 sites randomly selected from databases maintained by USGS Patuxent Wildlife Research Center, Lower Mississippi Valley Joint Venture, and Yazoo National Wildlife Refuge Complex. Even though I sought to ensure a diversity of stand ages by stratifying selections between older (>7 years old) and younger (≤ 7 years old) stands, most stands surveyed during 1998 were oak-dominated plantations that were ≤ 10 years old. Therefore, during 1999, I sought help from public and private land managers to locate older-aged stands and sites planted with species other than oaks. As a result

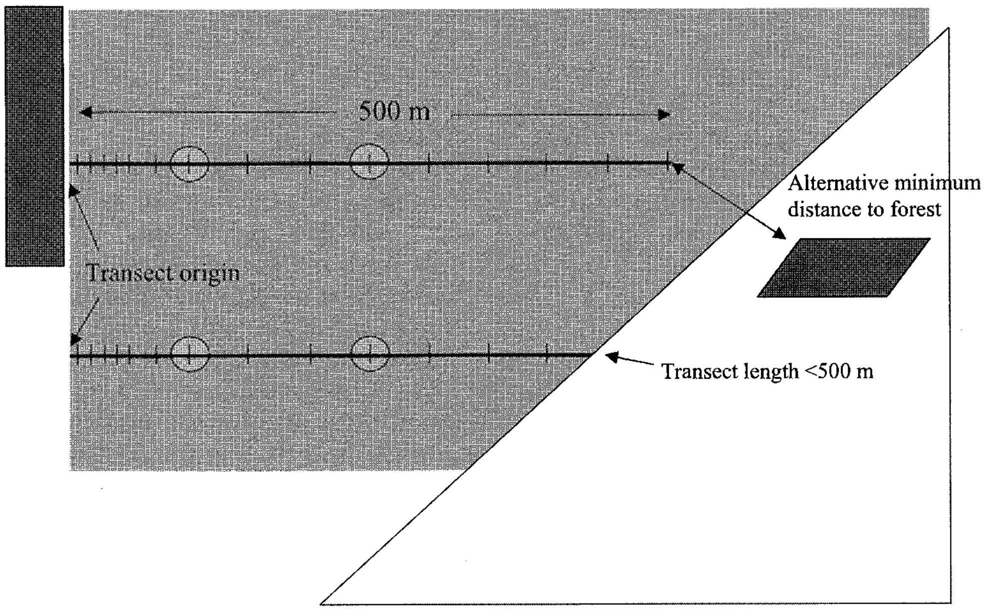

Figure 1. An example of transect and sample point locations used to survey reforested sites. Note transect conformity to site configuration and distance to nearest mature forest.

of these solicitations, I surveyed an additional 45 sites during 1999.

The method of reforestation used on each study site was determined by a land manager based on reforestation objectives and local site conditions (e.g., soil, hydrology, etc.). Therefore, reforestation methods were not randomly applied to study sites. Because reforestation methods were applied, in part, based on local conditions, readers should use caution when extrapolating these findings to other reforestation sites.

Sampling

While trees had leaves (Apr – Oct), I sampled tree and shrub abundance along transects that ran from the edge nearest mature forest into the interior of reforested sites (Figure 1). Usually, two transects 500 m long and ≥ 200 m apart were established, but this required sites > 30 ha. Some sites were < 30 ha or had dimensions (e.g., sites < 500 m in length) that resulted in variation in the number and length of transects (Figure 1). Thus, the total area surveyed varied slightly on some sites.

Along each transect, I measured vegetation in 0.002-ha (2.5 m radius) circular plots at distances of 10, 20, 30, 40, 50, 75, and 100 m, and at 50 m intervals thereafter, to 500 m. Additional vegetation measurements were obtained within 0.04-ha (11.3 m radius) circular plots at distances of 100 m and 250 m along each transect. Because I was interested in colonization relative to distance from seed source, I estimated and recorded the distance to the nearest forest edge at each vegetation plot: usually this was the point of transect origin (Figure 1).

Within all circular plots, I identified, counted, and measured the height of all trees and shrubs (woody stems) ≥ 0.5 m in height. I did not count or measure heights of vines. Instead, within each 0.04-ha plot I categorically ranked, from 0 (none) to 4 (dense), the cover of five common vines (*Campsis radicans, Ampelopsis arborea, Toxicodendron radicans, Parthenocissus quinquefolia*, and *Bignonia capreolata*), and the combined cover of all other woody vines. Similarly, I ranked the cover of three herbaceous species: coffeeweed (*Sesbania exaltata*), goldenrod (*Solidago* species), and broom sedge (*Andropogon virginiana*). I was interested in these herbaceous species, as well as vines, because they may be abundant and form seeming monocultures on reforested bottomlands. Dense herbaceous cover may inhibit recruitment and development of woody species through allelopathy (Rice 1972; Bramble et al. 1996) or competition (e.g., light, water, or nutrients).

I obtained data on the species planted and the density of planting for each reforested site from land managers. Considering each site independently, all species not planted were considered 'natural colonizers' whereas trees were categorized as 'planted' if they were of the same species as planted on the site. An exception was that all trees < 2 m tall on sites > 12 years old were categorized as natural colonizers. Based on the species planted, I assigned each reforested site to one of three reforestation methods: passive, oak dominated planting, or pulpwood dominated planting.

Statistical analysis

Because the total area surveyed varied among reforested sites, I used rarefaction analysis (Krebs 1989) as implemented using program PAST (Hammer et al. 2001) to predict the number of species expected with equal sampling. Rarefaction analysis produces distribution-free measures of species richness, that are standardized to a specified sample size. This provided richness estimates, unbiased by sample size, that allowed for direct comparisons between methods (Birks and Line 1992). I compared the number of woody species observed within each method of reforestation with the predicted number of species based on the number of individuals surveyed.

Mean species richness (S), Shannon diversity ($H' = -\sum[p_i \bullet \ln p_i]$, Greig-Smith 1983), and evenness($E = H'/\ln[S]$) of woody species were compared among methods of reforestation using analysis of covariance (ANCOVA) with stand age as the covariate. Using ANCOVA, I also compared differences in height of woody stems and stem densities between planted and natural colonizing species. I was most interested in assessing the height of the dominant canopy trees, not the average height of all trees nor the height of the tallest tree. Therefore, I compared the tree heights at which 10% of all sampled trees were taller (i.e., the 90^{th} percentile). Because distance from seed source was expected to influence recruitment of woody stems, I used linear regression to relate distance from seed source to density of naturally colonizing tree species.

An importance value (IV) was determined for each species within each reforested site and used in cluster analysis (Gauch 1982) to group sites with similar woody species characteristics. Importance values were calculated from each species' relative frequency (rf), relative density (rd), and relative height (rh) as: IV = (rf + rd + rh) x 100 (modified from Curtis and McIntosh 1951). The proportion of the total (frequency, density, or height) for each site that was contributed by a species was that species relative value. For example, if *Quercus nigra* was encountered on 10 sample plots out of 30 total plots, it's relative frequency was 0.33.

I used indicator species analysis (Dufréne and Legendre 1997) to identify species that characterized each of three groups identified by cluster analysis. This procedure assigned an indicator value to each species based on its frequency of occurrence (i.e., the number of sites on which it was detected) and the number of individuals recorded (i.e., density). Species were considered indicative of a group when the observed indicator value exceeded the indicator value from less than 1% of randomized trials ($p \leq 0.01$).

Results

Planted species

Reforested sites ranged in age from 2 to 34 years. Average area of reforested sites was 33 $\pm$ 3 ha (mean $\pm$ SE). Twelve sites were passively reforested with no trees planted, 60 sites were planted predominately with pulpwood species, and 133 sites were planted primarily with oaks. Although 28 species were used in reforestation, oaks (*Quercus* spp.) were most commonly planted (Table 1). Of 133 sites planted predominately to oaks, *Q. nuttallii* was planted on 106 sites, *Q. nigra* on 99 sites, and *Q. phellos* on 87 sites. Two other heavy-seeded species, *Q. pagoda* and *Carya illinoensis* were planted on 42 and 33 sites, respectively. Eight additional oak species were each planted on ≤ 10 sites. Three non-oak species were planted on ≥ 10 oak dominated sites: *Fraxinus pennsylvanica* (20 sites), *Diospyros virginiana* (12 sites), and *Taxodium distichum* (10 sites). Eleven other species were each planted on ≤ 5 sites (Table 1).

Of the 60 sites planted predominately with light-seeded, pulpwood producing species, most were planted with a single species: *Populus deltoides* (30 sites), *Platanus occidentalis* (18 sites), and *Liquidambar styraciflua* (13 sites). Surprisingly, *Q. nuttallii* was also planted on nine of these sites. On some sites, *Q. nuttallii* was included within a mix of species planted during initial establishment, whereas on other sites it was "under-planted" 1 or 2 years after the stand was established (Twedt and Portwood 1997). Five other species were planted on ≤ 4 sites (Table

Table 1. Number of sites on which each tree species was planted from 133 sites planted predominately with oaks and 60 sites planted with pulpwood producing species in the Mississippi Alluvial Valley. Passive reforestation, where no trees were planted, was undertaken on 12 additional study sites.

Species	Common Name	Oak sites n = 133	Pulpwood sites n = 60
Carya illinoensis	Sweet pecan	33	1
Cercis canadensis	Redbud	1	0
Celtis laevigata	Sugarberry	5	0
Diospyros virginiana	Persimmon	12	0
Fraxinus pennsylvanica	Green ash	20	4
Liquidambar styraciflua	Sweetgum	3	13
Morus rubra	Red mulberry	1	0
Nyssa aquatica	Swamp Tupelo	3	1
Nyssa sylvatica	Blackgum	3	0
Platanus occidentalis	American sycamore	2	18
Populus deltoides	Eastern cottonwood	1	30
Prunus serotina	Black cherry	1	0
Quercus acutissima	Sawtooth oak	6	0
Quercus alba	White oak	3	0
Quercus pagoda	Cherrybark oak	42	0
Quercus lyrata	Overcup oak	9	1
Quercus michauxii	Swamp chestnut oak	4	0
Quercus nigra	Water oak	99	0
Quercus nuttallii	Nuttall oak	106	9
Quercus palustris	Pin oak	6	0
Quercus phellos	Willow oak	87	0
Quercus shumardii	Shumard oak	10	0
Quercus stellata	Post oak	1	0
Quercus virginiana	Live oak	1	0
Taxodium distichum	Baldcypress	10	2
Ulmus americana	American elm	1	0
Ulmus crassifolia	Cedar elm	1	0

1), usually as a site specific compliment to the more numerous pulpwood species.

Species richness

Over all surveyed sites, I found 64 species of trees and shrubs (Table 2). Similar numbers of species were on sites planted with pulpwood species (52 species) and oaks (54 species), despite surveying over twice as many sites planted with oaks. Only 25 species were encountered on the sparsely surveyed passive reforestation sites.

Because the study area ranged widely in latitude, species were not ubiquitous across the study area. Thus, woody species were not random colonizers on these sites. Indeed, rarefaction analysis indicated fewer species than expected were encountered on sites of all three reforestation types. Based on the number of individuals sampled, a random distribution of species should have resulted in detection of 62 ± 1 species on both oak sites and pulpwood sites and 49 ± 2 species on passively reforested sites.

The number of species detected on individual reforested sites ranged from 1 to 20. Because, the number of woody species detected increased with stand age ($r^2 = 0.22$, $P < 0.01$), I used age as a covariate when comparing species richness among the three reforestation methods. After adjustment for age, fewer species of trees and shrubs ($F_{2, 201} = 7.04$, $P < 0.01$) were detected within pulpwood sites (8.1 ± 0.5) than within oak sites (10.5 ± 0.3). However, species richness increased by only 1.7 ± 0.7 ($t = 2.31$, $P = 0.03$) species every 10 years on oak sites, whereas on pulpwood sites 4.4 ± 0.9 ($t = 5.10$, $P < 0.01$) species were added every 10 years (Figure 2). When adjusted for age, both Shannon diversity ($F_{2, 201} = 17.9$, $P < 0.01$) and species evenness ($F_{2, 201} = 23.1$, $P < 0.01$) were greater within oak sites (H' = 1.74 ± 0.04; E = 0.78 ± 0.01) than within pulpwood sites (H' = 1.26 ± 0.07; E = 0.61 ± 0.02).

Table 2. Trees and shrubs found on 205 reforested bottomland hardwood sites within the Mississippi Alluvial Valley and it's adjacent minor bottomlands.

Species	Percent of sites			Percent of trees			Mean importance value (IV)[1]
	Oak sites	Pulpwood sites	Passive sites	Oak sites	Pulpwood sites	Passive sites	
	n = 133	n = 60	n = 12	n = 31687	n = 26762	n = 2371	
Acer negundo	42.1	61.7	16.7	7.4	6.3	0.3	20.4
Acer rubrum	32.3	28.3	16.7	1.6	13.1	0.1	11.3
Acer saccharinum	5.3	21.7	0.0	2.7	3.2	0.0	5.4
Acer saccharum	0.8	1.7	0.0	< 0.1	< 0.1	0.0	0.2
Albizia julibrissin [2]	0.8	0.0	0.0	< 0.1	0.0	0.0	0.1
Alnus serrulata	0.0	1.7	0.0	0.0	0.4	0.0	0.3
Amorpha fruticosa [2,4]	3.0	0.0	0.0	0.1	0.0	0.0	0.2
Asimina triloba	0.0	3.3	0.0	0.0	0.1	0.0	0.2
Baccharis halimifolia [2]	32.3	3.3	33.3	1.9	< 0.1	4.8	8.6
Betula nigra	2.3	15.0	0.0	0.5	0.4	0.0	1.6
Broussonetia papyrifera [4]	0.0	1.7	0.0	0.0	< 0.1	0.0	0.1
Callicarpa americana [2,4]	0.0	1.7	0.0	0.0	< 0.1	0.0	0.1
Carpinus caroliniana	0.0	3.3	0.0	0.0	0.1	0.0	0.2
Carya aquatica	5.3	11.7	0.0	0.1	0.1	0.0	0.2
Carya illinoensis	32.3	25.0	41.7	1.1	0.8	0.8	6.7
Carya species	2.3	18.4	0.0	< 0.1	0.1	0.0	0.1
Cercis canadensis	0.0	1.7	0.0	0.0	< 0.1	0.0	0.1
Celtis laevigata [4]	52.6	65.0	58.3	5.5	9.6	5.9	24.4
Cephalanthus occidentalis [2]	27.1	21.7	16.7	1.4	1.9	0.2	6.6
Cornus florida [2,4]	0.0	6.7	0.0	0.0	0.1	0.0	0.3
Cornus species [2,4]	18.8	31.7	0.0	1.4	1.2	0.0	5.2
Crataegus species [2,4]	28.6	21.7	41.7	1.6	0.2	1.4	2.5
Diospyros virginiana	68.4	35.0	83.3	2.5	0.6	1.8	13.8
Forestiera acuminata [2,4]	4.5	6.7	0.0	0.4	0.5	0.0	1.2
Fraxinus pennsylvanica	81.2	75.0	100.0	17.9	10.6	68.9	60.7
Gleditsia aquatica	1.5	0.0	0.0	< 0.1	0.0	0.0	0.1
Gleditsia triacanthos	29.3	25.0	41.7	0.8	0.6	0.4	1.2
Ilex decidua [2,4]	27.1	46.7	16.7	1.5	1.4	0.4	4.7
Juniperus virginiana [4]	4.5	6.7	16.7	0.1	0.2	0.1	1.0
Liquidambar styraciflua	50.4	58.3	41.7	7.9	14.8	2.5	31.2
Liriodendron tulipifera	0.0	8.3	0.0	0.0	0.1	0.0	0.4
Morus rubra [2,4]	1.5	11.7	0.0	< 0.1	0.1	0.0	0.5
Myrica cerifera [2,4]	0.8	0.0	0.0	0.2	0.0	0.0	0.3
Nyssa aquatica [4]	0.8	0.0	0.0	< 0.1	0.0	0.0	0.1
Nyssa sylvatica [4]	2.3	6.7	0.0	< 0.1	< 0.1	0.0	0.3
Pinus taeda	3.0	3.3	0.0	< 0.1	0.3	0.0	0.5
Planera aquatica	0.8	3.3	0.0	0.3	0.1	0.0	0.7
Platanus occidentalis	15.0	60.0	25.0	0.9	7.7	0.4	18.7
Populus deltoides	18.8	60.0	8.3	2.6	14.3	< 0.1	37.8
Prunus serotina [4]	0.0	6.7	0.0	0.0	< 0.1	0.0	0.2
Quercus acutissima [3]	1.5	0.0	0.0	< 0.1	0.0	0.0	0.1
Quercus alba	0.8	0.0	0.0	< 0.1	0.0	0.0	0.1
Quercus pagoda	23.3	1.7	0.0	1.3	0.0	0.0	8.6
Quercus lyrata	13.5	15.0	0.0	0.2	0.2	0.0	1.6
Quercus michauxii	4.5	0.0	0.0	0.1	0.0	0.0	0.3
Quercus nigra	65.4	18.3	41.7	7.2	0.5	0.4	25.2
Quercus nuttallii	79.7	28.3	33.3	10.2	1.1	1.1	40.7
Quercus palustris	4.5	8.3	0.0	0.6	0.1	0.0	4.6
Quercus phellos	59.4	13.3	25.0	3.0	0.2	0.2	13.7
Quercus rubra	0.0	5.0	0.0	0.0	0.1	0.0	0.2
Quercus shumardii	3.0	0.0	0.0	0.1	0.0	0.0	0.7
Quercus stellata	2.3	3.3	0.0	0.1	< 0.1	0.0	7.7
Rhus species [2,4]	3.0	13.3	8.3	0.3	1.5	1.0	2.0

Table 2. Continued.

Species	Percent of sites			Percent of trees			Mean importance value (IV)[1]
	Oak sites	Pulpwood sites	Passive sites	Oak sites	Pulpwood sites	Passive sites	
	n = 133	n = 60	n = 12	n = 31687	n = 26762	n = 2371	
Robinia pseudo-acacia	6.8	0.0	8.3	0.1	0.0	0.1	0.5
Sabal minor [2]	6.8	0.0	0.0	0.7	0.0	0.0	1.4
Salix nigra	32.3	18.3	16.7	9.3	0.4	0.2	8.7
Sambucus canadensis [2,4]	0.8	0.0	0.0	0.1	0.0	0.0	0.1
Sapium sebiferum [3,4]	4.5	0.0	0.0	0.3	0.0	0.0	0.6
Styrax americana [2]	0.8	1.7	0.0	<0.1	<0.1	0.0	0.1
Taxodium distichum	12.8	10.0	0.0	0.5	0.4	0.0	3.7
Ulmus alata	0.8	11.7	16.7	<0.1	0.4	0.2	1.2
Ulmus americana	51.9	60.0	75.0	4.6	6.3	8.7	23.3
Ulmus crassifolia	6.0	3.3	8.3	1.5	<0.1	0.1	2.9
Ulmus rubra	0.0	1.7	0.0	0.0	0.1	0.0	0.1

[1]IV = (relative frequency + relative density + relative height) x 100 (modified from Curtis and McIntosh 1951); [2]Shrub species; [3]Exotic (non-native) species; [4]Bird-dispersed species

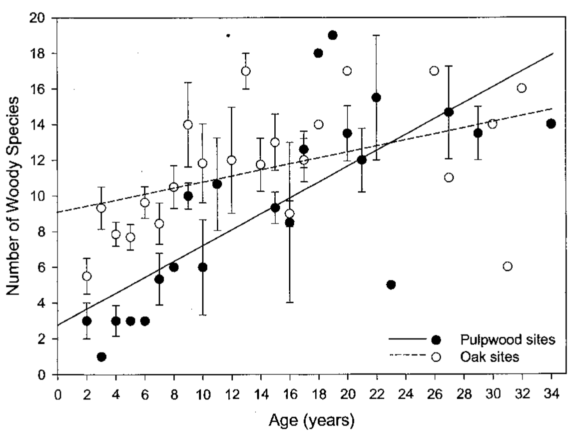

Figure 2. Mean (± SE) number of woody species (excluding vines) encountered on Mississippi Alluvial Valley bottomlands that were reforested by planting predominately oaks or predominately pulpwood producing trees.

The three most commonly planted oaks (*Q. nuttallii*, *Q. nigra*, and *Q. phellos*) were each encountered on ≥60% of sites planted predominately with oaks (Table 2). Together these three oaks accounted for 20% of all woody stems on these sites. Four other species (*Celtis laevigata*, *Ulmus americana*, *Liquidambar styraciflua*, and *Acer negundo*) were each detected on >42% of oak-planted sites with each species accounting for >4% of all woody stems.

Pulpwood planted sites were usually planted with a single species. Even so, the three most commonly planted species (*Populus deltoides*, *Platanus occidentalis*, and *Liquidambar styraciflua*) were each encountered on 60% of these sites (Table 2). Together, these three species accounted for 36% of all woody stems on these sites. Three other species (*Celtis laevigata*, *Ulmus americana*, and *Acer negundo)* were encountered on as many sites as were the planted pulpwood species; these three species accounted for an additional 22% of all woody stems. Two other maples (*Acer rubrum* and *Acer saccharinum*) were present on fewer than 30% of the pulpwood sites but together accounted for 16% of all woody stems.

Although rarely planted, *Fraxinus pennsylvanica* was the most commonly encountered tree regardless of the method of reforestation (Table 2). *Fraxinus pennsylvanica* was encountered on all passive reforestation sites and accounted for 69% of all woody stems (excluding vines) on these sites. *Fraxinus pennsylvanica* occurred on 81% and 75% of oak-planted and pulpwood sites and accounted for 18% and 10% of woody stems on these sites, respectively.

Diospyros virginiana was present on most sites that were passively reforested (83%) and on sites planted with oaks (68%) but it only accounted for 2% of woody stems. Only two other species, *Ulmus americana* and *Celtis laevigata,* were encountered on >50% of passively reforested sites and they accounted for 9% and 6% of woody stems on these sites.

Stem density

Over all reforested sites, mean stem density of planted trees was 494 ± 37 stems•ha^{-1}. Because sites planted with pulpwood were usually planted at a higher density and because their survival was enhanced by cultivation when young, these sites had nearly three times the planted stem density (944 ± 86) compared to sites planted with oaks (335 ± 27).

The median number of natural colonizers was 644 stems•ha^{-1}. Because mean stem density of naturally colonizing species was inflated by a very high number of colonizers on a few sites (maximum = 15,052 stems•ha^{-1}), naturally colonizing species averaged 1640 ± 171 stems•ha^{-1} and far exceeded the densities of planted species.

Stem density declined (t = 7.96, P < 0.01) with distance from seed sources (i.e., mature trees adjacent to reforested sites). However, this relationship varied with time and differed between planted and colonizing species. For example, during the first decade after planting, the density of planted trees was constant with distance from seed source (t = 1.24, P = 0.21). Conversely, during the first decade, stem density of natural colonizers declined by 51 stems•ha^{-1} with every 100 m from seed source (t = 7.80, P < 0.01, Figure 3a). During the second decade after planting (Figure 3b), stem density of woody colonizers declined 186 stems•ha^{-1} with every 100 m from forest edge (t = 7.17, P < 0.01) and planted species declined 41 stems•ha^{-1} (t = 1.97, P = 0.05, Figure 3b). After 20 years, this relationship was no longer discernable, either for planted (t = 0.80, P = 0.42) or colonizing species (t = 0.96, P = 0.35).

Decreased natural colonization with distance from forest edge occurred regardless of the method of initial reforestation but varied among colonizing species (Figure 4). The most abundant colonizing species had winged-seeded and the density of these anemochoric species was greatest near forest edges (Figure 4a). Conversely, species with bird dispersed seeds (e.g., *Celtis laevigata*) exhibited little relationship between stem density and distance from forest edge (Figure 4b).

Ground cover

On sites planted predominately with oak, ground cover by herbaceous species and woody vines was nearly complete from time of establishment through the first 15 years – thereafter ground cover declined.

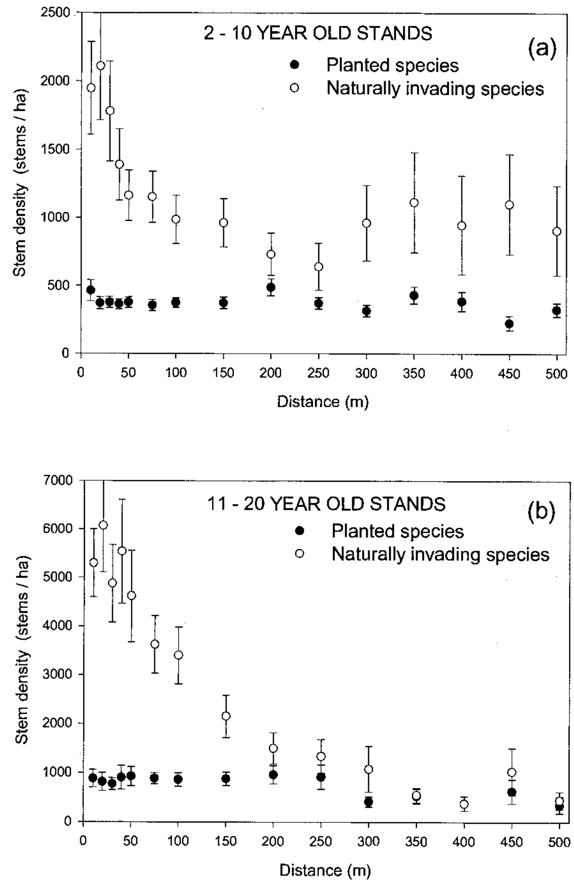

Figure 3. Mean density of woody species (excluding vines) as a function of the distance from nearest forest edge on Mississippi Alluvial Valley bottomlands that were reforested by planting predominately oaks or predominately pulpwood producing trees: (a) depicts densities on sites ≤ 10 years post-planting. (b) depicts densities on sites between 11 and 20 years post-planting.

Vine cover on these oak-dominated sites increased over time (Figure 5a). Thus, herbaceous plants accounted for most ground cover during the early development of these stands (Figure 5a). Ground cover on sites dominated by pulpwood species was also high during the first 10 years (Figure 5b). Vine cover on pulpwood sites varied over time and was low during the first 4 years. Herbaceous cover declined on pulpwood sites earlier than it did on oak sites (Figure 5b).

Tree height

Planted species grew more rapidly than invaders for all reforestation methods. However, trees on reforested sites planted with oaks grew more slowly than trees on sites planted with pulpwood species (Figure

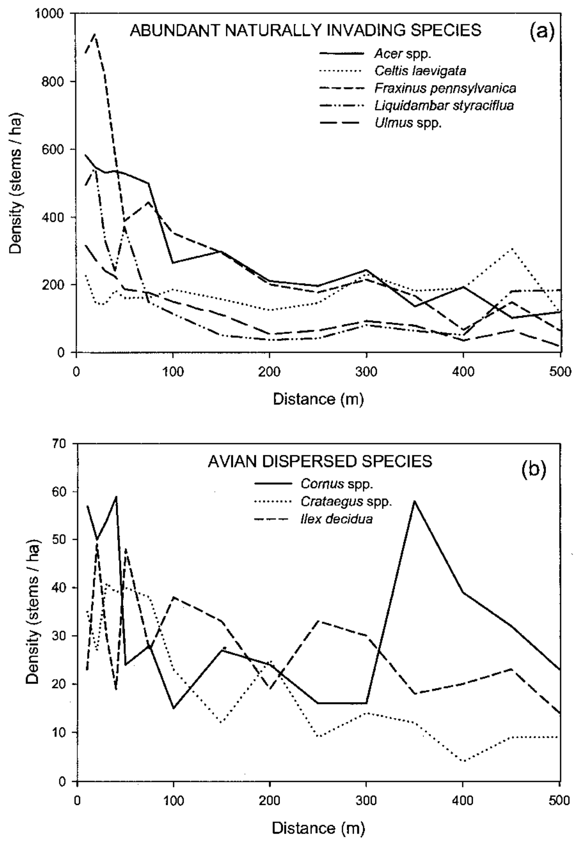

Figure 4. Density of the (a) most common woody species invading Mississippi Alluvial Valley bottomlands as a function of the distance from nearest forest edge and (b) density of invading species that are generally dispersed by birds.

6). Within oak-planted sites, the heights of naturally colonizing species were similar to those of planted species for the first 10 years (Figure 6a) with most trees < 5 m tall. Despite relatively slow growth (0.65 m per year), after 10 years, heights of planted oaks were markedly greater than those of naturally colonizing species: 90% of colonizing trees were < 10 m tall through 20 years.

On pulpwood sites, planted species attained a height advantage over natural colonizers shortly after planting and the height difference increased with time (Figure 6b). Planted pulpwood species grew an average of 1.2 m per year. Most of this increase, however, was accounted for on sites planted with *Populus deltoides* where heights of ≥ 5 m were achieved within 2 years and growth averaged 2.2 m per year for the next 10 years (Figure 8).

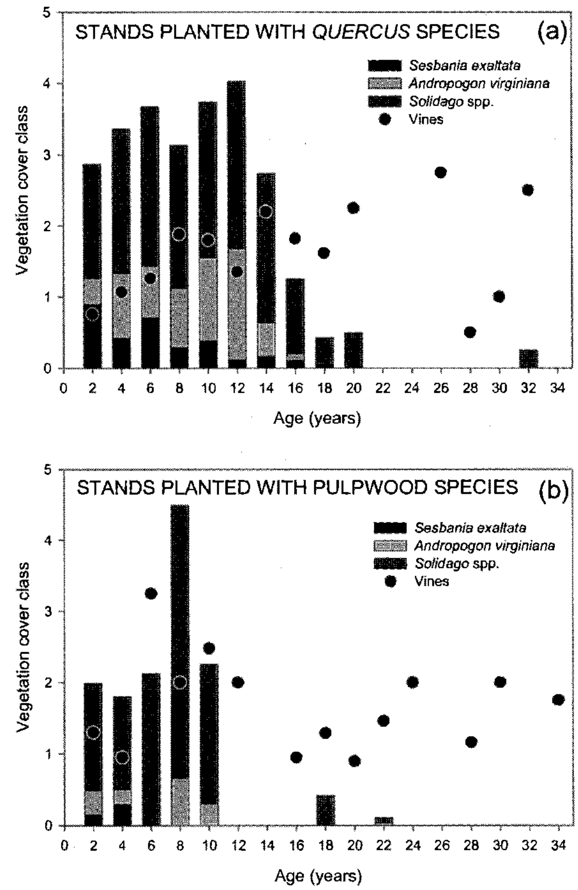

Figure 5. Relative cover (0 – 4; where 0 = absent, 4 = dense) of vines and selected herbaceous species on Mississippi Alluvial Valley bottomlands that were reforested by planting (a) predominately oaks or (b) predominately pulpwood producing trees. Sites are grouped in 2-year intervals.

Cluster analysis

Cluster analysis of the importance values of woody species provided insight into the similarity of vegetative conditions on reforested sites. Three groups were identified, but these clusters conformed poorly with the three methods of establishment. The first group contained 25 stands planted with cottonwood (*Populus deltoides)* and one site with extensive natural *P. deltoides* colonization. All stands were ≤ 12 years old and *Populus deltoides* was the only indicative species for these "cottonwood stands".

A second group of 91 sites contained passively reforested sites, sites planted with pulpwood species other than cottonwood, cottonwood stands that were > 12 years old and partially harvested (i.e., thinned),

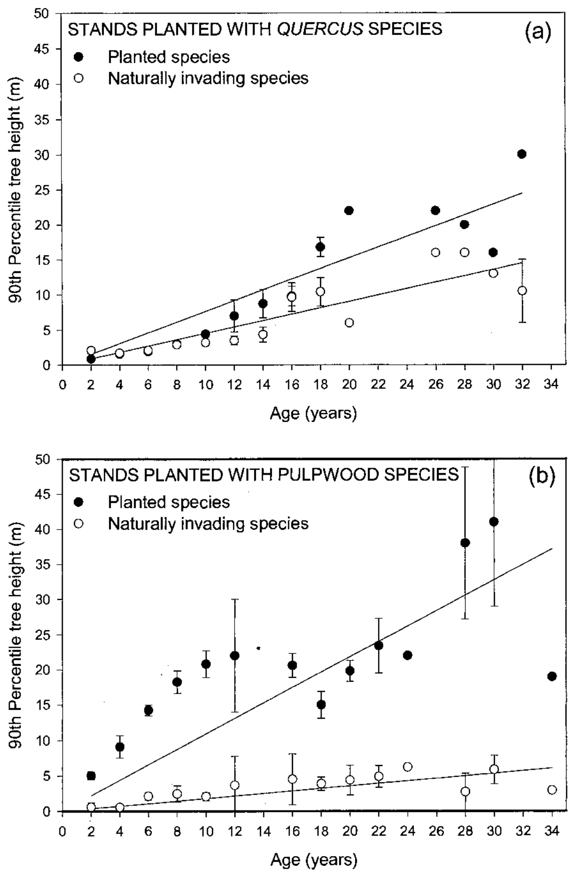

Figure 6. Heights (90th percentile) of trees on Mississippi Alluvial Valley bottomlands that were reforested by planting (a) predominately oaks or (b) planting predominately pulpwood producing trees. Sites are grouped in 2-year intervals.

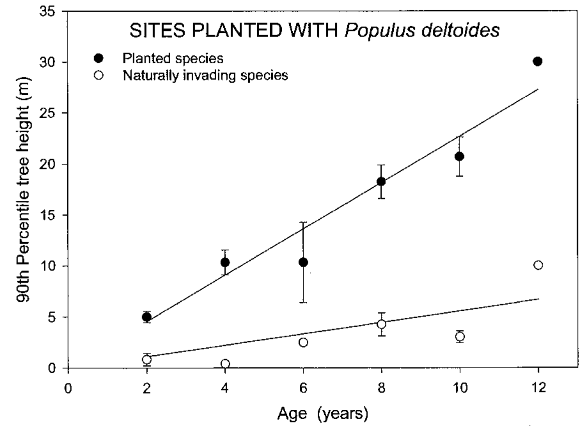

Figure 7. Heights (90th percentile) of trees on Mississippi Alluvial Valley bottomlands that were planted with *Populus deltoides*.

and oak-planted sites with extensive natural colonization. These "older" cottonwood sites were the only stands in this study that had been subjected to harvest. Six species were indicative of these "mixed-species stands": *Celtis laevigata*, *Liquidambar styraciflua*, *Ulmus americana*, *Fraxinus pennsylvanica*, *Platanus occidentalis*, and *Acer rubrum*.

The third group contained 88 sites planted with oaks and had little natural colonization. These "oak stands" accounted for 66% of the sites planted with oaks. The three most commonly planted oaks (*Q. nuttallii*, *Q. nigra*, and *Q. phellos*) were indicative of these sites, as was a shrubby invader, *Baccharis halimifolia*.

Examination of stem densities within the groups defined by cluster analysis revealed differences in the distribution of stems among these groups. Stem density of naturally colonizing species on "oak stands" declined 44 stems•ha^{-1} with every 100 m from the edge ($t = 3.57$, $P < 0.01$) but was constant for planted species ($t = 0.63$, $P = 0.53$; Figure 7a). In contrast, stem densities on "mixed-species stands" declined 129 stems•ha^{-1} for colonizing species and 23 stems•ha^{-1} for planted species per 100 m from a forest edge ($t > 3.94$, $P < 0.01$; Figure 7b). Neither stem densities of planted nor invading species varied with distance from forest edge on *Populus deltoides* stands (t < 1.13, $P > 0.25$).

Discussion

Planting either predominately oak or pulpwood species resulted in stands that exceeded a stated goal of 500 stems•ha^{-1} (Strader et al. 1994; Figure 3). At 494 $\pm$ 37 stems•ha^{-1}, the mean number of planted species alone met this objective. Densities of naturally colonizing species varied widely among study sites but were more numerous than planted species. Thus, the assumption that light-seeded trees invade reforested sites appears justified. However, natural invasion was highly dependent on distance from seed sources (Figures 3, 4, and 8) and distance dependence remained evident for up to 20 years (Figure 3). Furthermore, even when reforested sites are near seed sources, diaspores of light-seeded, wind-dispersed species vary considerably with respect to their wind dispersal potential (Tackenberg et al. 2003).

A decline in the density of naturally colonizing woody species with distance from forested edge has also been found in other studies (Allen 1997; Allen et al. 1998). This suggests that sites far from existing

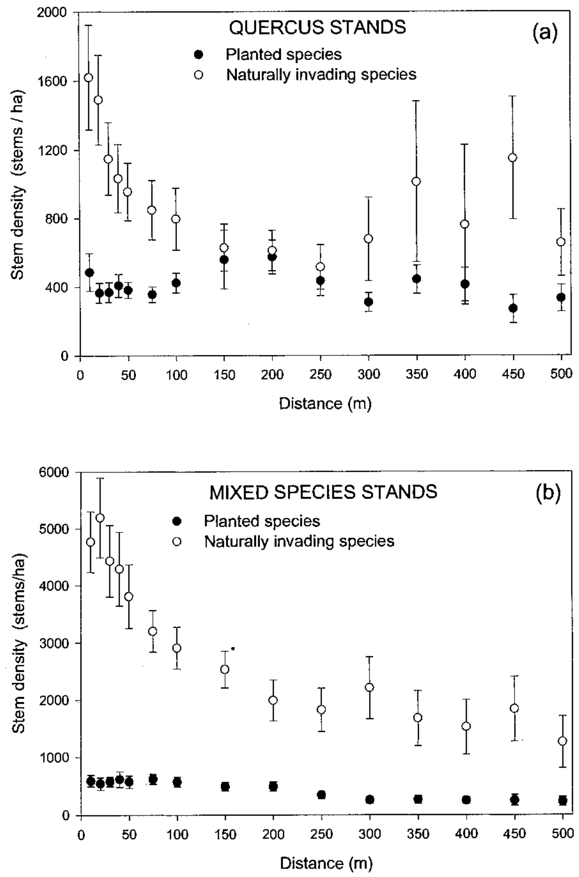

Figure 8. Mean density of woody species (excluding vines) within two of the groups identified by cluster analysis as a function of the distance from nearest forest edge on reforested Mississippi Alluvial Valley bottomlands: (a) densities on sites characterized by *Quercus nigra, Q. phellos*, or *Q. nuttallii* and little natural colonization except for *Baccharis halimifolia*, (b) densities on sites characteristically planted with *Liquidambar styraciflua* or *Platanus occidentalis* or naturally colonized by *Celtis laevigata, Fraxinus pennsylvanica, Acer rubrum*, or *Ulmus americana.*

forests receive few propagules thereby limiting natural colonization. Poor seed recruitment may account for 25% of study sites having < 208 stems•ha^{-1} of naturally colonizing woody species. Thus, land managers should consider the proximity and species composition of adjacent forests when making decisions on the appropriate species to plant. When reforestation sites are far from potential seed sources, additional woody species, including light-seeded species, should be planted.

Higher density of planted species near forest edges (Figure 3b, Figure 6b) suggests natural supplementation of planted species. However, this is uncertain as natural colonizers could not be reliably distinguished from planted individuals of the same species.

Initial species richness was low on pulpwood sites because they were often planted as monocultures. As a result, young pulpwood stands had lower diversity and species were less evenly distributed than they were on stands planted with multiple species of oak. However, pulpwood forests may act as catalysts for colonization as they had greater density of colonizing species (2665 $\pm$ 440 stems•ha^{-1}) compared with oak-planted sites (1190 $\pm$ 152 stems•ha^{-1}; Figure 6). Taller trees may facilitate zoochory by providing perch sites and cover for animal vectors of seeds (McClanahan and Wolfe 1993; Robinson and Handel 2000). In addition, rapid maturation of pulpwood species may supplement seed recruitment by producing viable seeds. Increased species diversity should remain on these sites if pulpwood stands are partially harvested, coppiced after complete harvest (Twedt and Portwood 1997), or allowed to undergo natural succession. However, if site preparation is undertaken following pulpwood harvest in anticipation of replanting, natural recruitment of woody species within these sites will likely be eliminated.

Site-specific estimates of tree species richness may be biased because the number of vegetation plots varied slightly among study sites and species richness is positively correlated with area surveyed. The mean area sampled on pulpwood sites (0.167 $\pm$ 0.009 ha) was less ($P < 0.01$) than the mean area sampled on oak-planted sites (0.209 $\pm$ 0.004 ha) but neither differed ($P \geq 0.10$) from the area surveyed on passively reforested sites (0.197 $\pm$ 0.013 ha). Even so, I found no relationship between the number of species detected within reforested sites and the area sampled ($r^2 = -0.001$, $P = 0.40$), suggesting that sampling effort was sufficient for comparison of species richness among methods of initial establishment.

Bottomland reforestation within the Mississippi Alluvial Valley has been extensive rather than an intensive. That is, managers have focused on maximizing the area planted while limiting the cost of reforestation. As a result, reforestation often consisted of planting 3-5 heavy-seeded species without weed control. Light-seeded species were rarely planted and usually limited to *Fraxinus pennsylvanica* and *Taxodium distichum.* This homogeneity of plantings was reported by King and Keeland (1999) who found that oaks, *Carya illinoensis*, and *Taxodium distichum* comprised 87% of all trees planted in the Mississippi Alluvial Valley. The mix of species planted on reforested sites that I surveyed was highly skewed towards 3 oak species (*Quercus nuttallii*, *Q. nigra*, and *Q. phellos*) with 2 additional species, *Q. pagoda* and *Carya illinoensis*, also planted on about a third of these sites. Sites planted with pulpwood species were usually on lands owned by timber or paper companies.

On some sites planted with oaks where managers did not control weeds, competition acted in concert with herbivory to maintain tree heights under 5 m for up to 15 years (Figure 6a). Because reforested sites initially lack canopy cover, they support a high percentage of ground cover (>90%; Figure 5). Dense herbaceous ground cover likely inhibited growth of developing trees through competition for light, water, and nutrients. Similarly, abundant ground cover provided cover for rodents and lagomorphs that reduced woody invaders and stunted planted trees by consuming seeds and girdling seedlings (Savage et al. 1996).

Even though natural colonizers outnumbered planted species, they were significantly shorter than planted species (Figure 6). Thus, despite the larger number of natural colonizers, their relegation to subdominance within the forest canopy often resulted in older reforested sites looking like plantation monocultures. Notable exceptions were those few sites that had been subjected to silvicultural manipulation (e.g., thinning). Thinning planted trees promoted increased diversity of co-dominate canopy trees within reforested stands by releasing naturally colonizing species within canopy gaps. In addition, thinning enhanced the growth of the remaining planted species, thereby promoting their emergence above the primary canopy. Thus, on reforested sites with high survival rates (i.e., dense stocking rates) I recommend post-planting management (e.g., 'thinning') of these stands to increase within-stand heterogeneity of vegetation structure. Silvicultural manipulations should be undertaken to create canopy gaps for the development of woody understory vegetation and concurrently provide access to the canopy for colonizing tree species.

Acknowledgments

I am grateful to Randy Wilson, Jared Mott, and Gaddis Guider for their assistance in surveying reforested sites. Seth Mott, Lower Mississippi Valley Joint Venture (U. S. Fish and Wildlife Service [USFWS]) and Lamar Dorris, Yazoo National Wildlife Refuge Complex (USFWS) graciously allowed access to their reforestation databases for selection of sites. I am indebted to the following for their assistance and access to land under their management: Jeff Portwood, Crown Vantage; Lisa Gericke, Westvaco; Arel Simpson, Seterria; Mark Monroe, Anderson Tully Company; Sidney Montgomery, Tara Wildlife; Jim Johnson, Felsenthal National Wildlife Refuge (NWR); Howard Poitevint, Southeast Louisiana Refuges (USFWS); Randy Cook, Reelfoot NWR, Don Orr (USFWS); Mike Kennedy, University of Memphis; Eric Smith, Lake Ophelia NWR; Rick Huffines, Clarks River NWR; Kelby Ouchley, Louisiana Wetland Management District (USFWS); Jon Wessman, Tensas River NWR; Kenney Ribbeck, Louisiana Department of Wildlife and Fisheries; Dennis Sharp, Cache River NWR; Glen Miller, Wapanocca NWR; Joe Garvey, Missouri Department of Conservation; Johnny Kiser, U. S. Army Corps of Engineers; Larry Moore, U. S. Forest Service; Stephen Gard, Mississippi Wetlands Management District (USFWS); and Rayford Hancock. This study was funded by the U. S. Fish and Wildlife Service and USGS Patuxent Wildlife Research Center. Sammy King and Randy Wilson provide helpful comments on a draft manuscript.

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