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Development of oak plantations established for wildlife

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Abstract

Extensive areas that are currently in agricultural production within the Mississippi Alluvial Valley are being restored to bottomland hardwood forests. Oaks (*Quercus* sp.), sown as seeds (acorns) or planted as seedlings, are the predominant trees established on most afforested sites. To compare stand development and natural invasion on sites afforested by planting seedlings or by sowing acorns, we sampled woody vegetation on ten 14- to 18-year-old oak plantations established to provide wildlife habitat. Stem densities of about 900 oaks/ha were comparable between stands established by sowing 4000 acorns/ha and stands established by planting 900 seedlings/ha. Densities of oaks in stands established from seedlings increased 38% from densities detected when these stands were 4- to 8-year-old. Densities of oaks established from field-sown acorns increased >100% during this same 10-year span. Oaks that were planted as seedlings were larger than those established from acorns, but trees resulting from either afforestation method were larger than trees naturally colonizing these sites. Natural invasion of woody species varied greatly among afforested sites, but was greater and more diverse on sites sown with acorns. Afforested stands were dominated by planted species, whereas naturally invading species were rare among dominant canopy trees. When afforestation objectives are primarily to provide wildlife habitat, we recommend, sowing acorns rather than planting seedlings. Additionally, planting fewer seeds or seedlings, diversifying the species planted, and leaving non-planted gaps will increase diversity of woody species and promote a more complex forest structure that enhances the suitability of afforested sites for wildlife. Published by Elsevier Science B.V.

Keywords: Afforestation; Bareroot seedling; Direct seeding; Mississippi; National Wildlife Refuge; Oak plantation; *Quercus*; Reforestation; Tree invasion; Wildlife habitat

1. Introduction

Flood control and favorable commodity prices previously prompted the conversion of extensive areas of forested wetlands in the Mississippi Alluvial Valley to agricultural production (Galloway, 1980; Twedt and Loesch, 1999). However, irregular but persistent flooding and fluctuating commodity prices have decreased profitability of agricultural production and recently, government incentive programs (e.g. USDA Wetland Reserve Program) have encouraged extensive afforestation of marginal agricultural lands. Indeed, >180 000 ha of afforestation are anticipated within the Mississippi Alluvial Valley by 2005 (Stanturf et al., 1998). Afforestation of sites formerly occupied by bottomland hardwood forest has historically focused on heavy-seeded species, such as oaks (*Quercus* sp.) and sweet pecan (*Carya illinoensis*). These species are favored because of: (1) perceived limitations of their seed dispersal; (2) the value of their mast crop to wildlife; (3) their potential timber value; and (4) an assumption that light-seeded species will

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naturally invade afforested sites (Strader et al., 1994). As a result of this focus, King and Keeland (1999) reported 78% of the trees planted on afforested sites in the Mississippi Alluvial Valley were oaks.

Most afforested sites have been established by directly sowing seeds (i.e. acorns) or by planting 1-year-old bareroot seedlings. Both sowing acorns (Johnson, 1981) and planting seedlings (Krinard and Kennedy, 1987) successfully regenerate stands of these heavy-seeded species. Further, it has been assumed that neither height growth (Johnson, 1983) nor eventual yield (Bullard et al., 1992) of trees differ between these two afforestation methods. However, planting seedlings is more expensive than directly sowing acorns (Bullard et al., 1992; Stanturf et al., 2000). Even so, because of greater likelihood of survival, and to extend limited seed supplies, planting seedlings has become the more common method of afforestation (King and Keeland, 1999). Regardless of afforestation method, there is typically limited site preparation and no post-planting weed control.

Because reliable methods for regeneration of light-seeded species are only now being developed, regeneration of these species has usually been limited to planting seedlings or left to natural invasion (Allen et al., 2001). Colonization of afforested sites by naturally invading trees is influenced by the distance and direction to seed sources (Allen et al., 1998), such that most natural regeneration is within 100 m of forested edges (Allen, 1997; Wilson and Twedt, 2001). Thus, invading species have reduced capability to establish on sites far from extant forests.

Allen (1997) suggested that as sites planted with oaks mature and experience mortality, other species (i.e. natural invaders) will occupy significant portions of these stands. Additionally, Allen (1997) hypothesized that sites sown with acorns develop more diverse forests upon maturity than sites planted with seedlings. This hypothesis was based on his observation of slow initial development of trees planted from acorns, which he reasoned would lengthen the time to crown closure and allow increased opportunity for establishment and development of invading species.

Because different forest conditions provide habitat for different fauna, we are loath to describe what constitutes optimal wildlife habitat. However, forests with a diversity of tree species interspersed with small gaps of herbaceous vegetation provide greater foraging opportunities and greater availability of habitat niches than do monotypic forests of uniform density (Kilgo et al., 1999). Indeed, current management recommendations for bottomland hardwood forests encourage development of structurally complex forests with multiple canopy layers and small openings (e.g. tree-fall gaps) to support more diverse and abundant avifauna than structurally deficient forests with uniform, closed canopies (Willson, 1974; Swift et al., 1984). As such, concern over the slow growth of oaks, the uniformity of resultant canopies, and a lack of species diversity on afforested sites has encouraged planting a more diversified mix of tree species on afforested sites. To further improve planting recommendations for future afforestation in the Mississippi Alluvial Valley, the forest structure on afforested sites must be assessed as these stands mature. Because the initial phase of widespread bottomland afforestation was undertaken circa 20 years ago, evaluation of the composition of woody species and their structural complexity is only now becoming possible on these maturing forest stands.

To assess forest development and natural invasion on afforested sites, we evaluated ten oak plantations 14–18 years after planting. Five of these sites were established by sowing acorns, whereas the other five were established by planting seedlings. These afforested sites were the same ten sites visited by Allen (1990) when they were 4- to 8-year-old and from which he formulated his hypotheses regarding predicted forest composition. Our objectives in reassessing these sites were: (1) to compare density and growth of trees resulting from planted seedlings and field-sown acorns; (2) to compare natural invasion of woody species between these two afforestation methods; and (3) to relate stand conditions on 4- to 8-year-old stands to stand conditions observed 10 years later.

2. Study sites

Study sites were all within the Mississippi Alluvial Valley in west-central Mississippi. Four sites were on Yazoo National Wildlife Refuge (NWR), four sites were on Hillside NWR, and two sites were on Panther Swamp NWR. Between November 1981 and November 1985, five of these 10 sites were planted

Table 1
Characteristics of study sites afforested from planted seedlings (S) or field-sown acorns (A) on bottomland sites at Hillside, Panther Swamp, and Yazoo National Wildlife Refuges in west-central Mississippi, USA[a]

Stand	Origin	Date planted	Planting density (number/ha)	Stand area (ha)	Species planted[b]	Density in 1989 (stems/ha)
1	S	2/1984	890	5.2	*Q. nuttallii*	741
2	S	3/1982	890	12.8	*Q. phellos*	509
					Q. nigra	0
					Q. pagoda	148
3	S	1/1984	890	3.6	*Q. nuttallii*	613
4	S	2/1982	890	6.4	*Q. phellos*	279
					Q. nigra	415
					Q. pagoda	87
5	S	3/1982	890	4.4	*Q. phellos*	17
					Q. nigra	437
					Q. pagoda	40
6	A	4/1984	3950	11.2	*Q. nuttallii*	496
7	A	11/1981	6670	4.8	*Q. phellos*	1146
					Q. nigra	1082
					Q. nuttallii	30
8	A	2/1984	3950	2.5	*Q. shumardii*	395
9	A	3/1985	3950	3.2	*Q. shumardii*	252
10	A	11/1985	3950	3.6	*Q. nigra*	215

[a] Stand identification number and 1989 stem densities are from Allen (1990).
[b] Nuttall oak (*Quercus nuttallii*), willow oak (*Q. phellos*), water oak (*Q. nigra*), cherrybark oak (*Q. pagoda*), Shumard oak (*Q. shumardii*).

with seedlings and the other five sites were sown with acorns (Table 1). Overall, five species of oak were planted on these sites, but no more three species were planted on a single site (Table 1). Additional, site specific, characteristics were presented by Allen (1990).

3. Methods

Following the sampling methods used by Allen (1990), we established transects perpendicular to the nearest mature forest and sampled vegetation within 0.0202 ha (1/20 ac) circular sample plots along these transects. However, Allen (1990) sampled at 30.5 m (100 ft) intervals, whereas we established sample plots 50 m apart—this resulted in sampling about 5% of the area on sites <10 ha and about 2% of the area on sites >10 ha (Table 1).

Whereas Allen recorded only trees and shrubs >1.0 m tall, we recorded all trees and shrubs with heights $\geq$0.5 m. Diameter at breast height (dbh) was recorded for all stems with $\geq$1 cm dbh. Additionally, we estimated the coverage of woody vines and dominant herbaceous cover within each sample plot. Some individuals of the stocked species (either planted or sown) may have naturally invaded these sites. Likewise, a few individuals of other species may have contaminated the stock that was planted or sown on these sites. Even so, we classified all trees of species that were not intentionally planted on a site as natural invaders. Invaders included non-planted species of oaks. Finally, although, we recognize that woody species can have multiple vectors for seed dissemination, we categorized all invading species by their most likely method of seed dissemination: wind or water dispersed, bird dispersed, or mammal dispersed.

We compared stem densities, heights, and diameters of oaks planted from seedlings with oaks sown from acorns. We controlled for differences in these parameters that resulted from stand age by using analysis of covariance (ANCOVA) with stand age as the covariate.

We also tested Allen's (1990) hypothesis of greater diversity of naturally invading trees in stands that develop from sown acorns. Because data on invading trees were not normally distributed, we tested this hypothesis using one-tailed, Mann–Whitney U-tests to compare stem density, species richness (S), and Shannon diversity indices (H) on sites sown with acorns with those same parameters on sites planted with seedlings. Diversity indices were calculated as $H = -\sum(p_i - \ln(p_i))$.

We compared heights and diameters between stocked and naturally invading trees using paired t-tests. Finally, to assess differences in the mechanisms through which afforested stands were colonized by invading woody species, we graphically compared the structure of invading species between afforestation methods. Comparisons were made within seed dispersal categories and height class categories.

4. Results

4.1. Planted species

Planting seedlings resulted in a mean density of 771 ± 78 oak stems/ha ($\bar{x} \pm$ S.E.) which was less than ($F_{1,7} = 8.33, P = 0.02$) the density of 1 480± 599 oak stems/ha that resulted from sowing acorns (Table 2). However, when data from the lone site that was sown with 6670 acorns/ha is ignored, mean oak density on the four sites sown with 4000 acorns/ha (895 ± 161 stems/ha) was nearly identical to that on sites planted with seedlings ($F_{1,6} = 2.48\, P = 0.16$. Greater tree heights ($F_{1,7} = 13.4, P < 0.01$) were attained from planted seedlings (11.5 ± 0.6 m) than from sown acorns (7.9 ± 0.6 m). Likewise, greater diameters ($F_{1,7} = 24.6, P < 0.01$) were attained by trees planted from seedlings (14.8 ± 1.6 cm) than from those sown as acorns (6.7 ± 1.0 cm; Table 2).

Height classes of field-sown oaks were approximately normally distributed, whereas oaks planted from seedlings were negatively skewed with most trees >10 m tall (Fig. 1). Stem densities that resulted from planting seedlings were comparatively homogeneous among stands, but increased from 657 ± 50 stems/ha in 1989 (Table 1) to 908 ± 137 in 1999 (Table 2). Conversely, stem densities that resulted from field-sown acorns varied markedly among stands (Table 2), although, maximum stem density (3824 stems/ha) was attributed to the high number of acorns sown on site #7. Even so, the mean density of oaks on sites sown with acorns doubled from 723 ± 386 stems/ha in 1989 to 1494 ± 593 stems/ha in 1999. Whether their origin was planted seedlings or field-sown acorns, stocked oaks were significantly ($t = 8.02, P < 0.01$) taller (9.7 ± 0.7 m) than naturally

Table 2
Mean (±S.E.) density, height, and diameter (dbh) of stocked oaks on sites originating from planted seedlings (S) or field-sown acorns (A) on afforested bottomland sites on Hillside, Panther Swamp, and Yazoo National Wildlife Refuges in Mississippi during 1999

Stand	Origin	Species[a]	Stems/ha	Height (m)	Diameter (cm)
1	S	*Q. nuttallii*	827 ± 72	13.3 ± 0.5	12.6 ± 0.8
2	S	*Q. phellos*	656 ± 38	11.7 ± 0.3	14.5 ± 0.6
		Q. nigra	28 ± 4	10.6 ± 1.0	17.7 ± 4.3
3	S	*Q. nuttallii*	550 ± 38	9.7 ± 0.2	20.6 ± 0.6
4	S	*Q. phellos*	121 ± 42	11.4 ± 0.6	14.5 ± 1.0
		Q. nigra	715 ± 92	12.1 ± 0.2	15.4 ± 0.5
		Q. pagoda	187 ± 39	11.7 ± 0.4	10.6 ± 0.6
5	S	*Q. phellos*	15 ± 11	7.0 ± 2.0	6.8 ± 2.8
		Q. nigra	614 ± 68	11.8 ± 0.4	12.9 ± 0.5
		Q. pagoda	144 ± 40	7.4 ± 1.2	4.9 ± 1.6
6	A	*Q. nuttallii*	1219 ± 88	8.5 ± 0.4	7.4 ± 0.6
7	A	*Q. phellos*	2756 ± 394	6.6 ± 0.3	2.7 ± 0.4
		Q. nigra	1062 ± 277	6.7 ± 0.3	3.0 ± 0.5
		Q. nuttallii	6 ± 6	1.0 ± 1.0	0.5 ± 0.5
8	A	*Q. shumardii*	1064 ± 101	9.7 ± 0.4	8.6 ± 0.7
9	A	*Q. shumardii*	483 ± 132	7.2 ± 0.8	7.3 ± 1.0
10	A	*Q. nigra*	813 ± 80	7.3 ± 0.4	7.1 ± 0.4

[a] Nuttall oak (*Quercus nuttallii*), willow oak (*Q. phellos*), water oak (*Q. nigra*), cherrybark oak (*Q. pagoda*), Shumard oak (*Q. shumardii*).

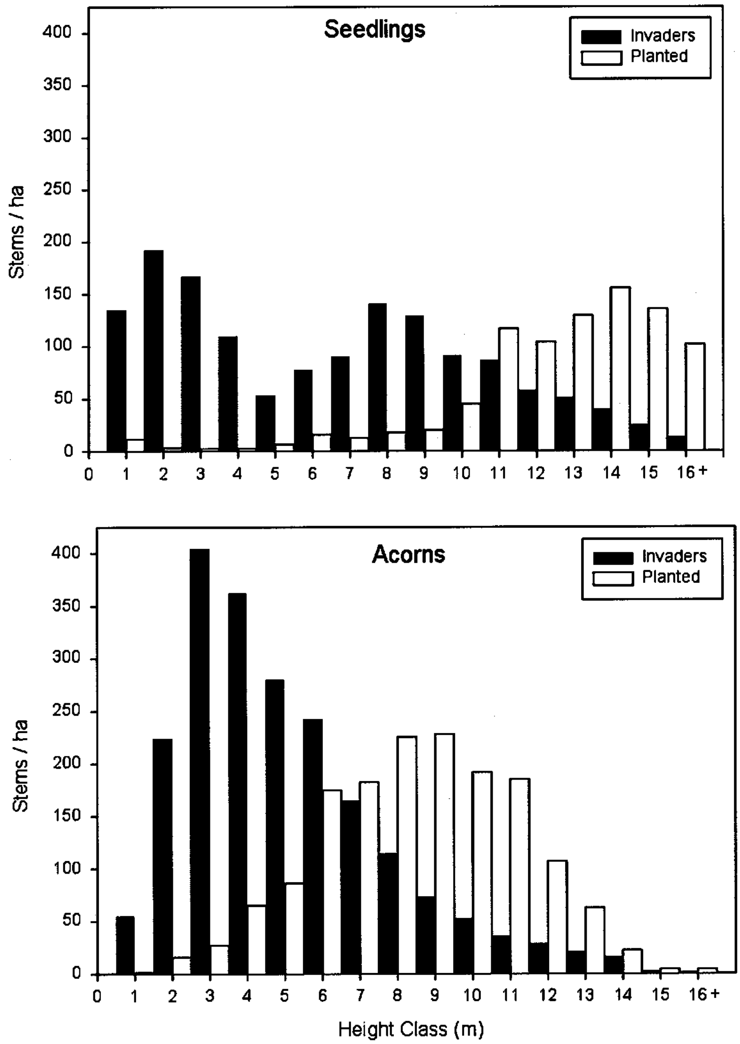

Fig. 1. Mean stem density, within 1 m height class intervals, of oaks planted as seedlings or sown as acorns and naturally invading woody species on 14- to 18-year-old oak plantations, west-central Mississippi, USA.

invading trees (height $= 4.2 \pm 0.5$ m; Fig. 1). Similarly, planted trees had greater ($t = 4.71, P < 0.01$) diameters at breast height (10.7 ± 1.6 cm) than natural invaders (dbh $= 2.6 \pm 0.4$ cm).

4.2. Invading species

Because densities of invading woody species (Table 3) varied widely among study sites (range = 555–3843 stems/ha), the difference we detected in the density of invaders on sites sown with acorns (2078 ± 458 stems/ha) and on sites planted with seedlings (1302 ± 576 stems/ha) was not deemed statistically significant ($z = -1.6, P = 0.05$). Even so, this observed difference in density was likely biologically significant. Particularly noteworthy, were the differences within the shorter height classes where stem densities of invading species on sites sown with acorns were twice as dense as those found on sites planted with seedlings (Fig. 1). Similarly, species richness of naturally invading species was greater ($z = -1.6$, $P = 0.05$) on sites sown with acorns ($S = 14.8 \pm 0.5$) than on sites planted with seedlings ($S = 12.0 \pm 0.8$). Likewise, the mean diversity on sites sown with acorns

Table 3
Mean (±S.E.) stem density, height, and diameter (dbh) of woody species invading bottomland sites afforested using oak seedlings or field-sown acorns, 14–18 years after afforestation in relation to densities previously observed (Allen, 1990) on the same sites 4–8 years after afforestation[a]

	Seedlings ($n = 5$)				Acorns ($n = 5$)			
	1989	1999			1989	1999		
	Stems/ha	Stems/ha	Height (m)	Diameter (cm)	Stems/ha	Stems/ha	Height (m)	Diameter (cm)
Acer negundo (w)	11 ± 7	18 ± 12	2.2 ± 1.0	1.3 ± 0.6	54 ± 36	203 ± 85	5.5 ± 0.8	4.9 ± 1.5
Acer rubrum (w)	3 ± 2	0	–	–	2 ± 1	75 ± 66	3.9 ± 0.2	2.0 ± 0.1
Carya sp. (m)	0 ± 0	3 ± 2	0.5 ± 0.0	1.0 ± 0.5	3 ± 2	16 ± 12	3.9 ± 2.2	2.5 ± 2.0
Celtis laevigata (b)	31 ± 20	78 ± 35	2.9 ± 0.5	1.7 ± 0.5	3 ± 3	52 ± 44	3.3 ± 1.0	2.1 ± 1.0
Diospyros virginiana (m)	48 ± 29	101 ± 50	3.9 ± 0.7	2.0 ± 0.5	29 ± 8	146 ± 70	4.8 ± 1.1	3.5 ± 1.0
Fraxinus pennsylvanica (w)	73 ± 45	93 ± 49	2.8 ± 1.0	2.3 ± 0.8	71 ± 46	188 ± 86	4.8 ± 0.3	3.2 ± 1.0
Gleditsia sp. (m)	13 ± 5	25 ± 15	3.0 ± 1.6	1.2 ± 0.5	29 ± 8	57 ± 38	4.2 ± 1.2	1.7 ± 1.0
Liquidambar styraciflua (w)	2914 ± 2896	606 ± 561	6.2 ± 1.6	5.9 ± 1.9	39 ± 26	137 ± 32	6.0 ± 0.8	5.5 ± 1.7
Quercus sp. (m)	6 ± 6	22 ± 17	3.4 ± 2.1	2.1 ± 1.5	4 ± 2	15 ± 7	4.8 ± 0.5	4.1 ± 1.3
Platanus occidentalis (w)	88 ± 83	10 ± 6	11.4 ±1.9	7.6 ± 1.1	0	0	–	–
Ulmus americana (w)	74 ± 27	127 ± 51	4.5 ± 0.4	2.0 ± 0.5	27 ± 14	126 ± 75	4.8 ± 1.0	3.3 ± 1.5
Snags	–	229 ± 161	4.0 ± 0.6	5.9 ± 1.1	–	271 ± 210	2.6 ± 0.7	1.6 ± 0.6
Other tree sp.	4 ± 2	332 ± 150	3.2 ± 0.8	2.7 ± 1.2	2 ± 1	1192 ± 598	3.3 ± 0.2	1.8 ± 0.2
Cornus stricta (b)	–	42 ± 28	2.5 ± 1.0	1.1 ± 0.5	–	138 ± 83	3.2 ± 0.5	2.2 ± 0.5
Crataegus sp. (b)	–	4 ± 4	3.7	2.0	–	213 ± 146	3.1 ± 0.1	1.3 ± 0.1
Forestiera acuminata (b)	–	0	–	–	–	201 ± 194	3.4 ± 0.1	1.7 ± 0.2
Ilex decidua (b)	–	34 ± 13	1.7 ± 0.3	0.6 ± 0.1	–	284 ± 107	3.2 ± 0.3	1.5 ± 0.5
Juniperus virginiana (b)	–	9 ± 4	2.6 ± 1.2	2.9 ± 2.0	–	17 ± 17	3.5	3.2
Morus rubra (b)	–	2 ± 1	5.2 ± 4.7	4.2 ± 3.7	–	2 ± 2	4.0	3.0
Pinus taeda (w)	–	0	–	–	–	5 ± 5	2.1	2.3
Populus deltoides (w)	–	2 ± 2	18.5	15.5	–	0	–	–
Salix nigra (w)	–	0	–	–	–	4 ± 2	6.2 ± 4.2	4.5 ± 4
Taxodium distichum (w)	–	0	–	–	–	2 ± 2	2.0	0.5
Ulmus alata (w)	–	0	–	–	–	52 ± 34	3.1 ± 0.6	1.8 ± 0.7
Ulmus crassifolia (w)	–	0	–	–	–	5 ± 5	3.1	0.7
Shrubs	7 ± 5	100 ± 99	2.7 ± 1.3	2.8 ± 2.3	40 ± 22	132 ± 94	2.8 ± 0.6	1.0 ± 0.3
Amorpha fruticosa (b)	–	0	–	–	–	107	1.4	0.5
Callicarpa americana (b)	–	1	1.0	0.5	–	2	2.5	1.0
Cephalanthus occidentalis (w)	–	1	4.0	5.0	–	1	1.5	0.5
Prunus angustifolia (b)	–	98	1.7	0.5	–	7	2.9	1.8
Rhus sp. (b)	–	0	–	–	–	23	4.2	1.6
Sambucus canadensis (b)	–	33	1.6	0.5	–	4	2.0	1.0

[a] w: wind or water dispersed seeds; b: bird dispersed seeds; m: mammal dispersed seeds.

($H = 2.03 \pm 0.06$) was greater than ($z = -1.9$, $P = 0.03$), the diversity on sites planted with seedlings ($H = 1.55 \pm 0.22$). Finally, sites sown with acorns had more ground cover, retained a higher proportion of cover by early-successional herbaceous species, and had more vine cover than did sites planted with seedlings (Table 4).

Species with light seeds (wind or water dispersed) dominated the taller height classes of invading trees, especially on sites planted with seedlings (Fig. 2). Surprisingly, the height class distribution of these light-seeded invaders shifted towards smaller height classes on sites sown with acorns. Species with seeds dispersed by birds were distributed primarily among the shorter height classes, but were markedly more abundant on sites sown with acorns. Invading species that use mammals as the primary vector of seed dispersal were not abundant regardless of afforestation

Table 4
Percent cover of selected herbaceous species and woody vines on afforested bottomland sites on Hillside, Panther Swamp, and Yazoo National Wildlife Refuges in Mississippi, planted to oaks (*Quercus* sp.) using seedlings or field-sown acorns

Cover type	Seedlings	Acorns
Campsis radicans	11.8 ± 4.5	31.6 ± 10.1
Ampelopsis arborea	6.8 ± 3.3	3.1 ± 3.1
Toxicodendron radicans	40.0 ± 8.5	35.5 ± 9.9
Parthenocissus quinquefolia	9.0 ± 3.8	3.3 ± 3.3
Other vines	10.6 ± 2.0	38.2 ± 11.8
Sesbania exaltata	0.0 ± 0.0	0.6 ± 0.6
Solidago altissima	5.5 ± 3.2	12.9 ± 7.3
Andropogon virginicus	2.3 ± 1.4	4.8 ± 4.1
Total ground cover	51.6 ± 13.3	74.0 ± 4.2

method, but these invaders increased in density among smaller height classes.

5. Discussion

Stem density of stocked oaks increased markedly from 1989 to 1999—38% on sites planted with bareroot seedlings and >100% on sites sown with acorns. Although, dense herbaceous vegetation (up to 87% cover by goldenrod (*Solidago* sp.) and Johnson grass (*Sorghum halepense*) present during 1989 (Allen, 1990) made it difficult to detect all seedlings present, we believe it unlikely that many trees >1.0 m were overlooked. It is more likely that numerous oak seedlings were <1.0 m tall at age 4–8 years. Short tree stature may have resulted from competition with the dense herbaceous cover or it may have been a consequence of clipping of stems by rodents (Burkett and Williams, 1997; Ostfeld et al., 1997). Rodents, particularly hispid cotton rat (*Sigmodon hispidus*) can achieve high densities (Hawthorne, 1994; 373 individuals/ha) within the herbaceous cover present during the first few years of plantation establishment (P. Hamel, US Forest Service, personal communication). Thus, assessment of only trees >1.0 m tall, 4–8 years after afforestation, is likely insufficient to determine the ultimate stand density, particularly on sites sown with acorns.

Johnson (1983) indicated that "height growth of Nuttall oak trees starting from seed appears comparable over the first 10 years to that of 1-0 planted stock", and Bullard et al. (1992) concluded "that planted oaks do not have a significant 'head start' in growth and eventual yield". However, we found that planted seedlings do have a growth advantage over field-sown acorns. Notably, this advantage persists even as these stands approach 18-year-old.

Although densities of trees colonizing sites by natural invasion was nearly twice that of planted or sown oaks, the oaks were more than twice as tall and had four times the diameter of invading trees. Thus, naturally invading trees were not an obvious component of these stands and they were rare among dominant canopy trees.

In addition to dependence on distance from seed sources (Allen, 1990; Wilson and Twedt, 2001), natural invasion of afforested sites is related to the invading species' mode of dispersal (Wolfe, 1990; Wunderle, 1997). The low frequency and broad distribution of mammalian dispersed species among height classes indicates that these species are slow, but constant immigrants to these sites. Conversely, invading species transported by other vectors, such as wind or birds, were by comparison normally distributed among height classes. This distribution among size classes is indicative of pulsed or periodic establishment.

When all invading species are considered concurrently, their distribution among size classes revealed a marked decrease in stem densities between 3 and 6 m in height on sites planted with seedlings. This anomaly is partly explained by the reduction of wind-dispersed species in shorter height classes. However, this contrasts sharply with the distribution pattern of these species groups on sites sown with acorns where invading species attained maximum stem densities within the 3–6 m height classes. We suspect that the patterns of invasion we observed were directly influenced by the structural development of stocked oaks.

In South Africa, Geldenhuys (1997) found that species richness, stem density, mean dbh, and mean height of woody invaders were greater in plantations with greater clean bole lengths. Although, seemingly contradictory to our findings. These South African plantations were comprised of fast-growing pine (*Pinus* sp.) and eucalypt (*Eucalyptus saligna*) that may grow >3 m annually and rapidly develop

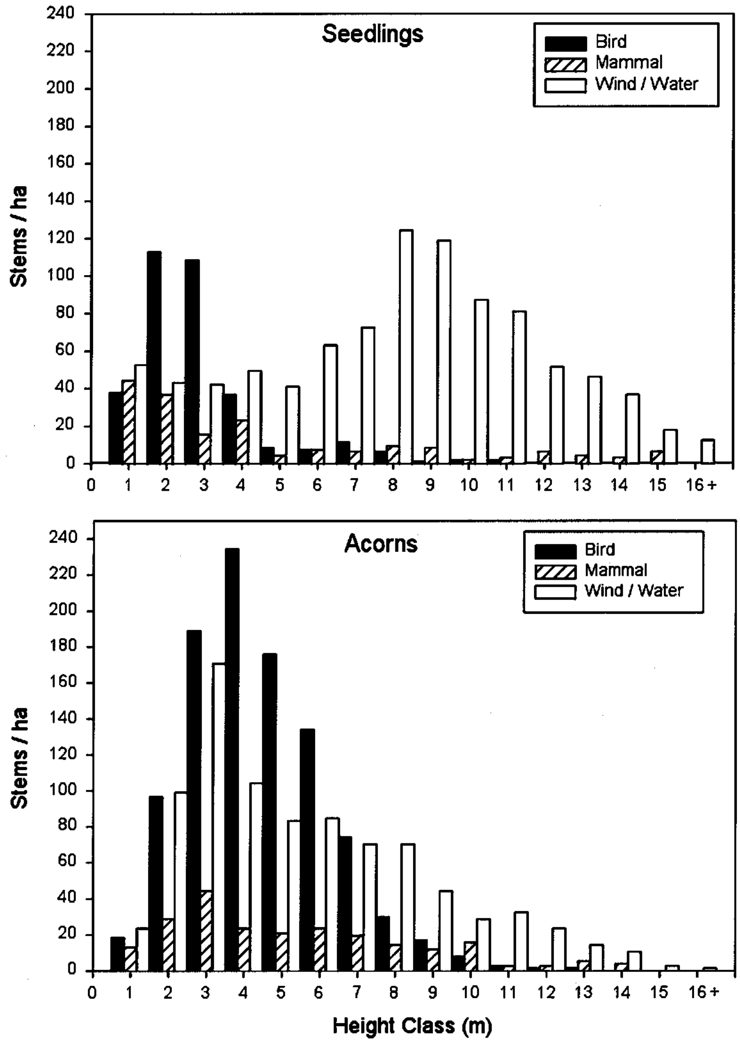

Fig. 2. Mean stem density, within 1 m height class intervals, of naturally invading trees likely dispersed via wind or water, deposited by birds, or transported by mammals within 14- to 18-year-old oak plantations established from seedlings or from field-sown acorns, west-central Mississippi, USA.

limb-free boles. The tall vegetation structure within fast-growing plantations provides ample perch sites for seed dispersing birds (Wunderle, 1997) and stands with 'long clean boles' likely allowed sufficient light penetration within these plantations to ensure development of germinated seeds. Conversely, we found the mean height of oaks planted from seedlings was only 11.5 m after 14–18 years with self-pruning of lower limbs just beginning. Furthermore, although we did not quantify the uniformity of spacing on sites planted with seedlings, these sites retained their row structure and had a consistent intra-row spacing of trees (Fig. 3). This homogeneous stand structure and heavily limbed tree boles resulted in relatively closed canopies that allowed seed dispersed by birds to germinate, but not to develop beyond the shorter height classes.

Although stands originating from sown acorns were shorter, these stands were less uniformly distributed. Numerous canopy gaps allowed bird-dispersed species the opportunity to compete for dominance in the canopy (Fig. 4). The resultant increase in woody species richness and diversity supports Allen's (1990)

Fig. 3. Homogeneous stem density, marked row structure, and sparse understory within an 16-year-old oak plantation (stand #3) established using 1-0 bareroot seedlings, Hillside National Wildlife Refuge, Mississippi, USA.

hypothesis of greater diversity on sites afforested with acorns.

Notably, fast-growing early-successional species (e.g. *Populus deltoides*, *Platanus occidentalis*, and *Salix nigra*) were absent or occurred at very low densities within these afforested sites. Those few present, however, attained heights equal to or surpassing the heights of trees planted as seedlings (Table 3). This finding confirms our previous advocacy for including fast-growing species among planted trees (Twedt and Portwood, 1997; Twedt et al., 2001).

One relatively fast-growing invader, sweetgum (*Liquidambar styraciflua)*, was found at high densities (612 $\pm$ 560 stems/ha) on sites planted with seedlings. However, this high density, and its associate large variance, was attributable to extremely high density on one site that was partially burned shortly after planting (Allen, 1990). When this aberrant site is ignored, density of *L. styraciflua* was reduced to 52 $\pm$ 23 stems/ha on planted sites.

Because sites planted with bareroot seedlings have retained the systematic row structure and within row spacing established during planting (Fig. 3), these stands will likely require silvicultural manipulations, such as thinning, to maximize their suitability for wildlife (Allen, 1997; L. Dorris, pers. commun.). Conversely, sites sown with acorns (Fig. 4) developed a more random distribution of oaks and had greater species diversity as a result of natural invasion.

Fig. 4. *Ilex decidua* (left-center) invading a canopy gap that resulted from spatially heterogeneous survival of acorns used to establish this 14-year-old oak plantation (stand #10). Although, row structure persists, note the irregular and clumped distribution of trees within rows that resulted from afforestation using field-sown acorns, Hillside National Wildlife Refuge, Mississippi, USA.

Even so, we believe that the high stand density of oaks on sites sown at rates ≥4000 acorns/ha will also require thinning to enhance their suitability for wildlife. Because many of these afforested sites are small and the market for oak pulpwood is not well developed, commercial thinning of these stands may not be economical. Thus, optimizing habitat on these afforested sites for wildlife may require active participation by managers or monetary expenditures.

Because of increased stand diversity and more heterogeneous stand development, we recommend sowing acorns, instead of planting seedlings, when the primary objective of afforestation is to provide wildlife habitat. This recommendation is bolstered by the greatly reduced cost of afforestation associated with sowing acorns compared to planting seedlings (Bullard et al., 1992; Stanturf et al., 2000). To reduce the likelihood of requisite silvicultural management to enhance the wildlife value of these afforested stands, we recommend using fewer than 4000 acorns/ha. A rate as low as 1000 acorns/ha may be sufficient for stand regeneration, particularly if multiple species are included in the mix of sown seeds. Sowing multiple species will provide increased evenness between artificially and naturally regenerated species.

If afforestation for wildlife habitat is undertaken by planting seedlings, we recommend planting multiple species, including a high proportion of fast-growing species, at a planting rate that is substantially less than 900 seedlings/ha. Furthermore, when restoring wildlife habitat, seedlings should be planted in irregular and clustered patches with non-planted openings dispersed throughout the afforested site. These recommendations should result in restored bottomland forests that have increased species diversity and are structurally more complex than the stands surveyed in this study. Providing increased structural and floristic diversity within afforested stands will provide suitable habitat for a variety of wildlife species that depend on bottomland hardwood forests.

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