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SIMULATION OF WIND DISPERSAL OF TREE SEEDS, TREE COLONIZATION, AND GROWTH OF BOTTOMLAND HARDWOOD REFORESTATION SITES OF THE MISSISSIPPI ALLUVIAL VALLEY

by

Timothy James Nuttle

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

James W. Haefner Major Professor	Eugene W. Schupp Committee Member
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UTAH STATE UNIVERSITY
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ABSTRACT

Simulation of Wind Dispersal of Tree Seeds, Tree Colonization, and Growth of Bottomland Hardwood Reforestation Sites of the Mississippi Alluvial Valley

by

Timothy James Nuttle, Doctor of Philosophy

Utah State University, 2003

Major Professor: Dr. James W. Haefner
Program: Ecology

Tree community composition in bottomland hardwood reforestation sites is considerably less diverse than natural bottomland hardwood forests. This study sought to understand the mechanisms behind failure to develop diverse tree communities. First, I developed a mechanistic model of seed dispersal by wind in spatially variable environments. Second, I developed a spatially explicit simulation model of forest dynamics that includes this wind-dispersal model to investigate whether diversity is limited by dispersal or interactions among species and individuals. Finally, I performed model experiments to determine if manipulations of stand structure might help improve conditions for colonization of various species, thus enhancing diversity of reforestation sites. The wind dispersal model was unbiased and accurate for predicting seed dispersal patterns of four species of wind-dispersed trees, demonstrating the utility of my algorithm for making predictions of seed arrival in a forest simulation model. The forest simulation model accurately predicted basal area growth and general patterns of species relative abundance in natural and reforested bottomland hardwoods, and predicted that reforestation sites will probably never attain diversity levels of natural forests under the current management scenario. Development of diversity was hindered by competition from the species planted and limited dispersal from forests. Hence, the only reasonably successful option to enhance diversity is probably to establish sites with mixed-species plantings at the outset. However, if stands are thinned at relatively young ages (15 yr for acorn-established stands, 25 yr for seedling-established stands), before canopy closure from planted individuals results in mortality of colonizing individuals, diversity may be enhanced if adequate numbers of colonizers are able to disperse to the site. Further research is necessary on mechanistic dispersal by animals, transition rates from seeds to seedlings, and the factors that affect such transitions in order to more accurately predict forest community development.

(162 pages)

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Tim Nuttle

CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Understanding processes affecting composition of forests is an extremely active research area in ecology. Within this research area, especially active topics have been understanding long-term dynamics in temperate hardwood forests, particularly those of the Northeastern United States (e.g., Shugart 1984, Botkin 1993, Pacala and Deutschman 1996) and mechanisms for maintenance of diversity in tropical forests (e.g., Hubbell 1979, 2001, Kelly and Bowler 2002, Porté and Bartelink 2002).

Bottomland hardwoods are wetland forests of the Southeastern United States. They are in a way transitional between the two widely studied forest types mentioned above. They share many characteristics (and a few species) with hardwood forests of the Northeastern United States, but they have higher tree species diversity than their Northeastern counterparts, though not as high as lowland tropical forests. However, there is comparatively very little theoretical research on bottomland hardwood forests, perhaps because they are located at less convenient distances from prestigious universities or research stations. There is also less silvicultural or forestry research on these forests, compared to high-yield pine forests that dominate uplands in the Southeast, and what exists is aimed almost exclusively at promoting growth of high-market-value species.

There is a need, however, to understand development of bottomland hardwood forests because these ecosystems have on the one hand suffered tremendous losses and on the other are undergoing restoration at such unusually large spatial scales (see Schoenholtz et al. 2001). The desire to restore diversity to levels found in natural bottomland hardwood forests has come into conflict with the need to rapidly reforest hundreds of thousands of hectares with limited resources. It is within the context of this bottomland hardwood reforestation, and possible restoration, that I submit this dissertation.

The overall aim of this dissertation is to understand what factors limit bottomland hardwood reforestation sites' ability to attain levels of tree species diversity similar to natural bottomland hardwood forest. One possible explanation is that seeds of various species are not able to reach reforestation sites. The first step in addressing this question is to be able to accurately predict the number of seeds that arrive. Chapter 2 thus describes a model to predict dispersal patterns of wind-dispersed seeds in spatially variable environments. Another possible explanation is that seeds that arrive are unable to become members of the canopy tree community because they are out-competed by other species that arrived in greater abundance (either via dispersal or because they were planted) or that have higher growth rates. Chapter 3 seeks to understand the relative influence of these factors by incorporating the mechanistic dispersal model with a model of forest dynamics, and compares model predictions to observed forest composition in both natural bottomland hardwood forests and reforestation sites. Chapter 4 elaborates on this validation with expanded data sets and site-establishment scenarios. Chapter 5 uses the model to assess whether thinning at different ages can increase site diversity. Finally, the concluding chapter briefly summarizes results and provides some recommendations for further work.

CHAPTER 2

A MECHANISTIC MODEL FOR WIND-DISPERSED SEEDS IN HETEROGENEOUS ENVIRONMENTS: DESIGN AND VALIDATION

Abstract.—Seed dispersal is an important determinant of local and regional community composition. I present a mechanistic model of seed dispersal by wind that incorporates heterogeneous vegetation structure within the model landscape. Such vegetation heterogeneity is important because it affects the horizontal wind profile, which is one of the primary determinants of seed dispersal distance. The model was developed for bottomland hardwood forests in the Mississippi Alluvial Valley, but is applicable to any forest community for which the requisite data are available. The model moves each seed in 3-dimensional space from the parent tree until it reaches the ground, by combining local wind speed and terminal fall velocity of seeds. The model differs from other mechanistic seed-dispersal models in that vegetation, and thus wind speed, may vary along the trajectory of each seed. The model was validated using source populations of trees in forests and seed-trap data in adjacent reforestation sites of two distinct vegetation structures (younger, open reforestation sites and older, closed-canopy reforestation sites). The model was replicatively and predictively valid for all species and vegetation types, even though patterns of seed density differed greatly between the two vegetation types. The model's sensitivity to vegetation structure, and its ability to accurately predict seed arrival when this structure is incorporated, demonstrates its utility for modeling seed dispersal in heterogeneous environments, and its potential utility for incorporating mechanistic seed dispersal in a forest simulation model.

INTRODUCTION

Seed dispersal is widely recognized to be of paramount importance for a complete understanding of plant ecology, shaping all subsequent ecological interactions (e.g., Schupp and Fuentes 1995) and determining to a large extent local and regional patterns of community composition (Hubbell 2001, Tuomisto et al. 2003). Forests are important plant communities for many ecological and socio-economic reasons, and many forest systems have been well studied. Despite seed dispersal's fundamental importance for plant ecology, published models that have been developed to simulate forest development either disregard or greatly simplify seed dispersal, focusing on interactions between sapling and adult trees (e.g., Botkin 1993, Shugart 1994, and derivatives, Pacala et al. 1996, Chave 1999). These studies explicitly assume that seed and seedling stages are unimportant because seeds are ubiquitous and the vast majority of seeds never germinate, or die after germinating as seedlings. The seemingly illogical conclusion of these assumptions, that seeds and seedlings are simultaneously unlimited and rare, boils down to the assumption that establishment of new individuals is largely stochastic compared to processes affecting their later growth and survival. Clark et al. (1999) discussed the relative merits of the competing views about which processes, seed or adult, are most important in determining forest composition. Briefly, the influence of seed dispersal on subsequent population processes depends on the transition of seeds to later stages. However, without knowing rates of transition, the importance of seed dispersal cannot be judged (Schupp 1995, Nathan et al. 2002b). More importantly, however, seed dispersal determines the pool of potential species, from which a subset emerges, via the vagaries of chance and abiotic and biotic factors, to form the forest community (Hubbell 1979, 2001). Thus, without assessing dispersal, one cannot predict which species will be present to interact as adults, making predictions of community development that fail to include dispersal fundamentally flawed.

Hence, omission of seed dispersal has necessarily limited application of forest simulation models to relatively small areas of forest, where seed sources can be assumed to be nearby and thus saplings constantly available. However, even when source populations of adult trees are nearby, seed dispersal and subsequent colonization can decline sharply within as little as 30 m depending on dispersal mode and direction of the source (Allen 1997, Allen et al. 1998, Ingle 2003). Limited attempts to implicitly include seed dispersal have included linking nonspatially explicit (i.e., "gap") simulations with an assumed external source of saplings (Johnson et al. 1981). Another method has been to link several forest gap simulations, where the location of trees within gaps is not explicit but location of gaps relative to each other is, so that adult trees in one gap contribute saplings to other gaps depending on inter-gap distance (e.g., Clark and Ji 1995). Pacala et al. (1996) explicitly included dispersal in their forest simulation model SORTIE by using a probabilistic dispersal kernel based on the distribution of seedlings and saplings around adult trees, rather than on actual seed deposition. A disadvantage to this approach is that it confounds seed dispersal with germination, establishment, and early survival of seedlings and saplings, so the importance of seed dispersal relative to these other processes cannot be determined.

With these limitations in mind, several studies have focused on quantifying seed distributions around parent plants, especially in trees. Models relevant to wind-dispersed seeds can be grouped into two basic categories: phenomenological and mechanistic. Nathan et al. (2001) discussed the various models in more detail. Briefly, phenomenological models describe the probability density function of seed arrival with distance from a source (e.g., parent plant, forest edge) based on observed patterns of seed deposition around parent trees (e.g., Clark et al. 1998a, Clark et al. 1998b). Alternatively, the greatest development in mechanistic models of wind dispersal has been the micrometeorological approach, which combines seed terminal fall velocity and horizontal wind speed (Sharpe and Fields 1982, Greene and Johnson 1989, 1996, Nathan et al. 2001, 2002a). Horizontal wind speed increases with height above ground, and the nature of this effect depends on the nature of the vegetation the wind is flowing above or within. Extant models incorporate the change in wind speed with height by calculating the average wind speed (U) experienced by each seed, from release height (z) to the ground, which determines its horizontal displacement (Δx) during the time it takes the seed to reach the ground:

$$\Delta x = (z \cdot U)/f \tag{2.1}$$

where f is the fall velocity. A variation on this theme incorporates vertical wind updrafts, which permits a small proportion of seeds to travel extremely long distances (several kilometers, Nathan et al. 2002b). However, it is the relatively short distances within a few hundred meters of existing populations of trees that I consider because of their direct relevance to forest simulations.

Although forest modeling studies have begun to call for increased realism in quantifying recruitment patterns around parent trees (Ribbens et al. 1994, Clark and Ji 1995, Pacala et al. 1996, Clark et al. 1998b), and seed dispersal studies have frequently included justifications to that effect (e.g., Clark et al. 1998b, Nathan et al. 2001, 2002a, 2002b), to my knowledge, no model linking seed dispersal mechanisms and forest dynamics has yet been presented.

The main limitation preventing such a linkage is that existing mechanistic and probabilistic seed dispersal models assume a homogeneous dispersing environment. This assumption is clearly not valid for many potential applications of forest simulation models, precisely because they are designed to portray vegetation dynamics, i.e., heterogeneity. For mechanistic wind-dispersal models, the homogeneity assumption is necessary to calculate U. Because it is known that vegetation profoundly influences wind speed and therefore dispersal of wind-dispersed seed (Nathan et al. 2002a), one also cannot simply ignore differences in vegetation and use probabilistic dispersal kernels (which also ignore effects of wind direction). Greene and Johnson (1996) relaxed the homogeneity assumption by calculating U in two steps.

They modeled seed dispersal from forest into clearings, and calculate *U* from seed origin to forest edge and then from height of the seed at the edge to the ground within the clearing. They assumed two discrete, internally homogeneous vegetation types with a defined edge between types. This approach holds promise for incorporating wind dispersal into a forest simulation model, but must be modified to characterize the dynamic nature of vegetation in space and time. Hence, an analytical solution of dispersal distance within discrete vegetation types is not tractable; incorporating an algorithm to map edges between vegetation types would require many questionable assumptions regarding what constitutes an edge and the behavior of wind at edges.

To circumvent the limitations of current mechanistic and probabilistic approaches, I created a mechanistic wind dispersal model that allows any amount of vegetation heterogeneity and does not require determination or mapping of edges between differing vegetation environments. Rather, my model tracks the three-dimensional movement of seeds from their parent tree to the ground; movement of each seed is determined by whatever vegetation, and hence wind speed, it encounters along its dispersal path. Tackenburg (2003) described a similar approach that allows some vegetation heterogeneity, but is not appropriate for forest systems. My spatially explicit, individual-based model of forest colonization of abandoned agricultural fields, YAFSIM, incorporates the wind-dispersal model herein described. Complete details of YAFSIM are contained in Chapter 3. The focus of this paper is to more fully describe the wind dispersal model, assess the model's performance relative to observed seed arrival from a field study, and discuss the merits of my approach for incorporating seed dispersal into a forest simulation model.

METHODS

My algorithm is a numerical adaptation of the analytical model described by Greene and Johnson (1996), where wind-dispersed species are dispersed mechanistically using an algorithm that combines empirical seed fall velocities, wind speed, and vertical wind distribution to calculate the movement of each seed in three-dimensional space. The model focuses on Phase I dispersal (i.e., movement of the seed from the parent to the ground, sensu Chambers and MacMahon 1994) because in dense vegetation or on rough surfaces, subsequent seed movements (Phase II dispersal) are comparatively shorter and hence less significant (Chambers and MacMahon 1994). Greene and Johnson (1996) calculated each seed's eventual dispersal distance by analytically integrating the wind environment over the trajectory of seeds that originated in a forest and dispersed over a clearing. This approach assumes that the horizontal wind speed is homogeneous at any given height within each habitat (i.e., the forest is homogeneous and so is the field). Because the horizontal wind environment is modified by vegetation, one can only assume a homogeneous wind environment if the vegetation is homogeneous. Furthermore, this approach requires identification of the edge of each habitat type (forest or clearing). This approach seems adequate for modeling seed dispersal during single growing season, in low-diversity systems, when it can be assumed that the vegetation is relatively homogeneous and static, and edges can be easily identified. However, this approach is inadequate for modeling large space and time scales such as a model of succession or reforestation where seeds may pass over or through any combination of forest, open field, clumped colonizing trees, or young reforestation sites, all of which have dynamic vegetation environments. Furthermore, in order to accomplish an analytical solution for wind speeds, and the eventual dispersal distance, many simplifying assumptions are required that would limit application of the model to narrow circumstances (as is the case for Greene and Johnson 1996).

Design, structure, and parameterization of wind dispersal algorithm

The algorithm calculates the seed's dispersal distance numerically. First, it determines the number of seeds originating at each parent that is of reproductive size (i.e., its fecundity). I assumed that fecundity was linear with basal area for all trees > 15 cm diameter at breast height (following Nathan et al. 2002):

$$F_{ij} = a_{ij} \cdot \beta_i \tag{2.2}$$

where F_{ij} is the fecundity of tree j of species i, a_{ij} is its basal area (cm^2), and β_i (cm^{-2}) is a normally distributed constant for the species i (see below for how β_i was fitted).

Next, based on the tree map that is input into the model, the model determines the starting position of each seed (x and y coordinates of parent). The vertical position, z, of each seed is normally distributed with a mean of 0.8 parent's height and a standard deviation of 0.2 parent's height (following Nathan et al. 2002b, see also Greene and Johnson 1989). The height of the parent tree is calculated allometrically from tree radius, based on the function and parameters in Fulton (1999):

$$H = 1.4 + (H_{\max} - 1.4)[1 - \exp(-S \cdot 2r)] \tag{2.3}$$

where H has units of m, H_{max} is the asymptotic tree height (m), 1.4 is the height (m) at which the radius r (cm) is measured, and S is an allometry parameter with units cm^{-1}.

Once released from the tree, the seed's descent is a function of its terminal fall velocity, which I determined in the laboratory under still air conditions by dropping 100 seeds of each species and timing their descent. These data are approximately normally distributed, but the model draws a random element in a lookup table of the raw data (see Fig. 2.1). The descent of the seed is either accelerated or decelerated by vertical winds. Vertical wind speed (w) is normally distributed with mean of -0.1 m/s and standard deviation of 0.25 m/s (i.e., there is a slight updraft on average; parameters from Nathan et al. 2001). These values are from savannah vegetation in Israel, but Tackenburg (2003 fig. 2) reported similar values for open vegetation in Germany. Therefore, lacking locally measured vertical wind data, I used the same vertical wind distribution for all vegetation types. The resulting realized seed fall velocity ($f - w$) controls the amount of time the seed is in the air. Values of $(f - w) > z / (\Delta t\,(\mathbf{a} - 1))$, where Δt is the time step for the dispersal algorithm, would exceed the storage capacity of the array **a**, which is currently set at 1000 values. For $\Delta t = 3$ s and $z = 24$ m, this excludes $(f - w) > -0.008$ m/s (i.e., taking > 8 hr to fall to the ground; $\Delta t = 1$ s was also tried, but this did not strongly affect dispersal patterns, so $\Delta t = 3$ s was used to save computation time and memory). Because of their extremely slow fall velocity, such seeds are assumed to eventually fall outside the landscape and are not tracked. In model tests, $(f - w)$ values slower than -0.008 m/s were extremely rare.

Each seed experiences a unique wind direction and horizontal reference wind speed, which is drawn from species-appropriate dates (based on the species' dispersal season, from Young and Young 1992) in a lookup table of paired wind directions and velocities from a nearby reference station (Greenville Airport, weather station GLH, National Weather Service). The data represent 162,259 instantaneous wind observations recorded hourly from 1973 to 2002. The model scales the horizontal wind speed (u) from the reference height (10 m) up to 80 m above ground using a power-function wind profile,

$$u_{80} = u_{10} \cdot \left(\frac{80}{10}\right)^{0.14} \tag{2.4}$$

adapted from Greene and Johnson (1996). They used 2 z_h instead of a fixed 80 m, reasoning that at that height the atmospheric drag of the canopy would be insignificant. However, because in my model canopy height is variable I used a constant value, coinciding with approximately twice the height of the tallest canopy trees in my system.

The model calculates the wind speed at the top of the canopy (z_h) for the current location, using a logarithmic wind profile (from Greene and Johnson 1996, but with functional form consistent with most other authors, e.g., Nathan et al. 2001):

$$u_{zh} = u_{80} \frac{\ln[(z_h - d) / z_0]}{\ln[(80 - d) / z_0]} \tag{2.5}$$

where d and z_0 are roughness parameters that describe how vegetation affects wind speed above it. Following Greene and Johnson (1996; see also Tackenburg 2003), I have assumed that $d = 0.667z_h$ and $z_0 = 0.105z_h$ for forests with a full canopy of leaves (from Oke 1978).

After computing u_{zh}, the model calculates the horizontal wind speed along the seed's trajectory (the wind direction), by first determining the vegetation height at the seed's starting position. Vegetation height is determined for all locations at the start of a simulation as the highest point of any overlapping tree crowns. Thus, each tree contributes its height (from Eq. 2.3) to all cells within its crown radius, unless the cell has already been determined to have a taller height from a different tree. The crown radius ρ is calculated allometrically from the tree's radius at breast height, r (mm):

$$\rho = 0.01 \cdot r \tag{2.6}$$

where the scalar 0.01 has units m/mm (from Pacala et al. 1996). If no tree influences a cell, or if its height is < 1 m, the algorithm assigns a value of 1 m to the cell to account for the height of herbaceous vegetation.

Next, the model calculates the wind profile along the seed's trajectory. Using a fourth-order Runge-Kutte solver, the model numerically integrates wind velocity between the current height and the next height (determined by $f{\cdot}\Delta t$). The equation solved depends on position within or above the vegetation and height of the vegetation. Thus, the effect of vegetation on horizontal wind speed differs within the canopy of leaves, below the canopy, or above the canopy (following Greene and Johnson 1996). Within the canopy (assumed to be between 0.5 z_h and z_h), the algorithm uses the intracanopy model to estimate the wind speed at height z:

$$u_z = u_{zh} \cdot \exp\left(\alpha\left[\frac{z}{z_h} - 1\right]\right) \tag{2.7}$$

where u is the wind speed at current height z and $\alpha = 4$ for full-leafed canopies. This equation simplifies to

$$u_z = u_{zh} \cdot \exp(-\alpha/2) \tag{2.8}$$

below the canopy (i.e., $z < 0.5\ z_h$), which is independent of height z. If the current location is above the canopy, the algorithm uses the supracanopy model (Eq. 2.5, substituting the current height z for z_h). This process is repeated for each x, y point along the seed's trajectory from its starting position until either the ground or the edge of the landscape is reached. The resulting wind profile is stored in a 2-dimensional array of the distance along the seed's trajectory and height above ground.

Note that the procedure thus far described has been to calculate the horizontal wind profile, and the seed has not yet begun to disperse. Before the seed disperses, the wind profile is recalculated along the seed's trajectory at all heights by averaging each value in the array of wind speeds with value 1 m before, to dampen abrupt changes in wind speed that would otherwise result from abrupt changes in vegetation. This method is based on the concept that wind speed at a given location is the result of both winds above the current position, and winds blowing into the current position. Fig. 2.3 shows wind speed vectors as a function of vegetation and height along a hypothetical trajectory. The resulting wind speed profile is comparable to that assumed by Greene and Johnson (1996), but is flexible for any combination of vegetation heights (e.g., wind blowing from shorter into taller vegetation and vice versa), whereas the fitted relationship used by Greene and Johnson (1996) is only suitable for wind blowing from a specific type of forest into clearings (and specifically not vice versa).

Finally, once the wind profile along the seed's trajectory has been calculated, the seed begins to disperse. From its starting location on the parent tree, the seed moves horizontally by incrementing its current location, in the direction of its trajectory, by the product of u_z at the current location (as integrated and averaged above) and Δt. Next, the seed is moved vertically by $(f - w) \cdot \Delta t$. This process is repeated until $z \leq 0$.

Wind-speed profiles are calculated *de novo* for each dispersing seed because there is an infinitesimal probability that any two seeds experience the same combination of starting position, f, u_{10}, w, and wind direction. Whereas the algorithm as written is extremely computationally intensive, storing a reasonable representation of possible starting positions, f, u_{10}, w, and wind directions for possible use for subsequent seeds would require an enormous amount of storage space, negating any advantages in algorithm speed.

Study sites and species

To estimate some of the required parameters and validate the dispersal algorithm, I studied dispersal of seeds within and originating from bottomland hardwood forest and adjacent reforestation sites. All sites were on the main and Brown Tract units of Yazoo National Wildlife Refuge (NWR) in west-central Mississippi, in the Mississippi Alluvial Valley (MAV; 33°10'N, 90°51'W, elevation 35 m). Because the long growing season and fertile soils make the region well suited for crop production, Yazoo NWR and most other public lands in the MAV exist as forested islands within an agricultural landscape. The predominant geomorphic feature of Yazoo NWR's main unit is Swan Lake, an old (ca. 800 yr) oxbow of the Mississippi River, and much of the topography consists of ridge and swale formations from the Mississippi River and other, minor streams' meanderings. The 5,200-ha main unit consists of a mosaic of seasonally flooded bottomland hardwood forests; bottomland hardwood reforestation sites; intermittently drained cypress swamps; share-cropped agricultural fields; moist-soil impoundments; and sloughs, bayous, and small lakes with open water and aquatic herbs and shrubs. Both forests and adjacent reforestation sites at Yazoo NWR's main unit were entirely contained within the refuge boundaries. The Brown Tract consists of former agricultural fields near the northern edge of

Delta National Forest. The topography is less varied than on the main unit, with flats being the predominant formation. Though reforestation sites studied on the Brown Tract were on lands owned by Yazoo NWR, the forests adjacent to them were on Delta National Forest, private property, or a tract managed by the Mississippi Forestry Commission.

Bottomland hardwoods are species- and structurally diverse, seasonally flooded, broadleaf-deciduous, forested wetlands. Dominant tree species include Nuttall oak (Qu*ercus nuttallii*), water oak (*Q. nigra*), willow oak (*Q. phellos*), American elm (*Ulmus americana*), sugarberry (*Celtis laevigata*), green ash (*Fraxinus americana*), and sweetgum (*Liquidambar styraciflua*). Additionally, at my study sites, cedar elm (*Ulmus crassifolia*) were prevalent as small codominant trees. Mature trees may reach up to 33 m in height, with a multi-layered canopy and an abundance of shrubs and woody vines (Kennedy and Nowacki 1997). Bottomland-hardwood reforestation sites are considerably less species- and structurally diverse than their counterparts of similar age that have regenerated naturally from cutover forests.

The primary goal of bottomland hardwood reforestation is to restore a diverse forest system similar in species composition and structure as that found in naturally regenerated, second-growth bottomland hardwood forests in the MAV (Schoenholtz et al. 2001). However, the restoration process at these sites has been limited primarily to ceasing agricultural crop production with subsequent planting of two or three species of trees, usually Nuttall, cherrybark (*Q. pagoda*), willow, or water oak. All of the reforestation sites in the current study were established as plantations with seedlings of these species. Seedlings were planted in rows 4 to 5 m apart, with 2 to 3 m spacing within the row (Yazoo NWR Reforestation Plan). It was hoped that other species would colonize plantations through their own means, though this has proven unreliable and is, in fact, an unrealistic assumption. To date, other manipulations of these reforestation sites, such as restoration of historic flooding regimes, have been impractical due to constraints of surrounding land ownership and management. Furthermore, no supplemental planting of trees or shrubs has been attempted as of 2002. The majority of other reforestation sites in the MAV were established and subsequently managed similarly to those of Yazoo NWR, although limited attempts have been made to increase species diversity of plantings (usually including green ash and baldcypress, *Taxodium distichum,* on wetter sites).

Validation data

I placed seed traps in mature bottomland hardwood forest and adjacent reforestation sites to fit fecundity parameters for each species and provide a validation data set to assess model performance. I located sites to test the model's validity in different vegetation environments. I chose sites that had a reforestation site adjacent to a forest that might serve as source population of seeds. Sites also had to allow establishment of a transect that could emanate from the forest edge to the interior of the plantation and be > 300 m from all forested areas except the forest from which it emanated (so I could be more certain of the origin of seeds). Based on these criteria, I was able to locate seven paired plantation-forest sites: four with reforestation sites $\leq$ 3 yr post-establishment in approximately each cardinal direction from forest, and three with reforestation sites 17 to 18 yr post-establishment in each cardinal direction (except west) from forest. Vegetation was 1-2 m tall in younger reforestation sites, 12-15 m tall in older reforestation sites, and 20-23 m tall in adjacent forests (Fig. 2.4). Table 2.1 shows the composition of each forest stand and the position of modeled reforestation sites relative to each stand.

To assess seed arrival at each site, I placed 10 or 11 seed traps along each transect beginning ca. 5 m from the forest edge and continuing into the reforestation site perpendicular to the forest edge. In addition, I place 12 seed traps inside the forest in a grid pattern (except one site, which had only four traps within the forest). I chose trap spacing along the transects to best characterize the regions where the most change in seed arrival with distance occurred along a series of model runs with hypothesized seed fall velocities and wind speeds. Thus, I placed traps within reforestation sites 5-130 m from the forest edge, with spacing between traps 5 m near the forest edge increasing to up to 30 m for traps far from the edge; traps inside the forest were ca.10 m apart in a grid ca. 10 m from the edge (Fig. 2.5).

Seed traps were 0.5 m^2 (0.71 m on a side) fiberglass or nylon window screen that sagged to ca. 10 cm deep, mounted on a PVC frame ca. 1 m above ground on three galvanized steel poles. Seed traps were emptied and repaired approximately monthly between March 2000 and April 2002 . All tree and shrub seeds found within seed traps were identified to species using Young and Young (1992), herbarium specimens, or advice from experts whose opinions were solicited via email and a website hosted by the Intermountain Herbarium (Utah State University, Logan, Utah).

To assess seed loss from seed traps, in November 2002 I placed a known quantity of marked American elm seeds in a random sample of seed traps in each of the three vegetation types investigated (forest, younger reforestation sites, older reforestation sites). I chose American elm at this time of year because marked seeds could be identified as such even if marks were lost because American elm does not disperse in autumn. Furthermore, American elm is likely to be the species that suffers the most severe losses because it is light and might easily blow out of traps. Seed trap contents were subsequently collected as usual in December, and I compared the number of "dummy" seeds returned to the number originally placed in traps.

To assess the population of trees contributing seeds to seed traps, I mapped all trees ≥ 8 cm dbh in the vicinity of the seed traps within each forest site. For six of the sites, this was accomplished by surveying locations within a 40- × 60-m rectangular plot along two perpendicular transects using right-angle prisms to line up the tree with its position along each transect. I mapped seed traps within the forest similarly. I also mapped all seed trap locations with a Trimble Surveyor® global positioning system (GPS) so I could georeference the surveyed locations. For the remaining site (which was also the one with only four seed traps within the forest), I used the GPS to map all trees within ca. 20 m of seed traps, because understory vegetation was too dense to permit sighting along transects. I also used the GPS to map all trees within reforestation sites that I deemed likely to be reproductively mature and contribute seeds to seed traps (these were mostly green ash and sweetgum in 17- to 18-yr-old sites).

Model analysis

I used seed-trap data and trap and tree locations as simulation model input. Because forests were more extensive than my sample of trees, I needed to simulate trees in the forest beyond to create a more extensive population of trees both as seed sources and as modifiers of the wind environment. Forest composition and structure outside of mapped plots was similar to that inside mapped plots (personal observation). Therefore, I filled the remaining forest model space by resampling the population of mapped trees and copying trees randomly, though with the same density as the original sample, within that space.

Fitting the fecundity parameter β_i .—To compare model predictions with seed-trap data, I needed to estimate the number of seeds produced per tree. Because I was interested mainly in predicting seed dispersal into reforestation sites, and wanted to reserve those data and model predictions for model validation rather than parameter fitting, I used seed arrival in forest seed traps to estimate β_i. For each of the seven sites (k) I numerically fit β_{ik} to the seed trap data. I used estimates from Clark et al. (1998b) as starting values, and iterated the model using 10 different values β_{i*}, with three replicate runs per β_{i*} value. Each run simulated 1 yr of seed dispersal. I calculated the deviance (D) between the model's predicted seed arrival at each trap (seeds/m^2 averaged over an area of radius 2 m around each trap location) to the average total yearly seed arrival actually observed in each seed trap:

$$D = \text{predicted} - \text{observed}. \qquad (2.9)$$

I estimated β_{ik} by plotting β_{i*} against D^2 to find the value of β_{ik} that produced the smallest D^2. Where possible, I estimated β_{ik} by quadratic interpolation to solve for the minimum (i.e., best-fit value); otherwise, I estimated β_{ik} visually. Finally, I calculated the mean (β_i) and standard deviation ($\sigma_{\beta i}$) from β_{ik}.

Validation.—I used the remaining model output (i.e., those not used to fit β_i) to calculate the distribution of predicted seed arrival for each species in each seed trap. I weighted predicted seed arrival for each trap × β_{i*} combination by the expected frequency of each β_{i*} using 10 random deviates from $\sigma_{\beta i}$. I used the resulting mean predicted seed arrival per trap to assess model performance for replicative and predictive validation. A model is replicatively valid if model output matches data used to formulate and parameterize the model, whereas it is predictively valid if model output matches data that were not used in its formulation and parameterization (Power 1993). Model validity for both replicative and predictive senses can be assessed regarding model bias (i.e., the mean difference between model prediction and observed data) and model accuracy (i.e., the magnitude of absolute or squared differences). Following Power (1993), I assessed model bias (W) for n paired observed and predicted values as:

$$W = \frac{\sqrt{n}\sum_{i=1}^{n} D_i}{n \cdot s} \tag{2.10}$$

where s is the standard deviation of the sample data used to fit β_i (i.e., the forest seed-trap data). I assessed the significance of W by referring it to a t-table with $n - 1$ degrees of freedom. Also following Power (1993), I assessed model accuracy (Q) as:

$$Q = \frac{\sum_{i=1}^{n} D_i^2}{n \cdot s^2} \tag{2.11}$$

and assessed its significance by referring Q to an F-table with n and $n - 1$ degrees of freedom. Another method of assessing model bias and accuracy is by regressing observed values against model predictions and testing the simultaneous null hypothesis that the slope of this relationship is unity and the intercept is zero (i.e., there is a one-to-one relationship between model predictions and observed values). Although Power (1993) considered the above measures *W* and *Q* superior to linear regression, I also performed regression analysis (using PROC REG in SAS, SAS Institute 2001) so I could compare model performance with results present in Nathan et al. (2001).

I tested *W*, *Q*, and regression slope/intercept for significance for all species combined and all species separately for each of the three distinct vegetation physiognomies: forest, younger reforestation site, and older reforestation site. I assessed model performance in forests to test the model's replicative validity, and in younger and older reforestation sites to see whether predictive validity differed between the two distinct vegetation physiognomies. For all statistics, significant test statistics indicate a significant departure of model predictions from reality. Before computing statistics, I screened the data for outliers. Outliers were defined as values that would have violated the parametric assumptions of the test statistics. In all cases, biological explanations for outlying values are provided in the Discussion. For *W* and *Q*, I examined histograms of *D* for values in the tails of the distribution. *D* was approximately normally distributed for all species by vegetation combinations, and this screening removed two green ash, three American elm, and three cedar elm prediction-observation pairs from the forest dataset. I also screened the data for extreme values for regression analysis because regression is heavily influence by extreme values. I therefore removed one data point each from younger and older sweetgum datasets because they were far outside the range of the majority of the data.

RESULTS

On average, ca. 50% of marked American elm seeds were collected in subsequent seed-trap samples. Seed loss appeared to be random with respect to vegetation type and distance from forest, except that seed loss was negligible in forest seed traps. Thus, I did not correct observed seed arrival based on measured seed loss for the purpose of fitting β_i, which relied on forest seed-trap data. However, for the regression analysis I corrected observed American elm seed arrival by multiplying the actual value by two (I also did this for Q and W, though results presented here are uncorrected because correction did not affect conclusions). I did not correct other species for possible seed loss because I did not assess seed loss for other species, and I judged other species to be less vulnerable to seed loss based on their morphology (e.g., green ash had pointed tips that stuck to the seed-trap mesh, and sweetgum were small and frequently collected in crevices).

Of the six wind-dispersed species investigated, my estimation procedure allowed determination of β_i for four species (Table 2.2). The model predicted very low seed arrival for cedar elm in several younger reforestation sites, but none were observed in seed traps. Cedar elm was neither observed nor predicted in older reforestation sites. Therefore, I did not carry out regression analysis for cedar elm in reforestation sites.

Replicative validity.—Values of the bias statistic W revealed that the model was replicatively unbiased for all species and values of the Q statistic revealed that the model was replicatively accurate for all species except cedar elm. However, I rejected the null hypothesis of unity slope and zero intercept for the regression analysis for all species (Table 2.3). For low predicted values for each species, there was a wide range in observed values, resulting in significant positive intercepts and slopes < 1 (Fig. 2.6).

Predictive validity.—The model was predictively unbiased and accurate for all species in both younger and older reforestation sites (Table 2.3). I failed to reject the null hypothesis of a one-to-one relationship between predicted and observed seed arrival for American elm in younger and older sites and green ash in older sites. Of these, the strength of the straight-line relationship (measured by r^2) was best for older sites compared to younger sites. Values of r^2 for these species and sites were approximately 0.70. Green ash in younger sites had a strong linear relationship (r^2

= 0.901) between predicted and observed values, but the one-to-one relationship was rejected because of a high slope. Sweetgum had a fairly good straight-line relationship for older sites (r^2 = 0.714) but the one-to-one relationship was narrowly rejected because the intercept was marginally too high (Table 2.3).

DISCUSSION

Validation

Replicative validity.—Results concerning replicative validity of the model differ markedly between the bias (W) and accuracy (Q) statistics versus regression analysis. Assessing model validity with these different measures is very instructive in determining what constitutes a valid model and what does not. The relevant difference between W and Q versus regression analysis stems from the way the statistics use variation in the observed values (s). Because W and Q are scaled by the s or s^2, highly variable observational datasets decrease the potential to demonstrate bias or inaccuracy. Thus, W and Q were reduced by large s, but in regression analysis, increasing s, especially at low predicted values, simply increases the estimate of the intercept if s is not explained by the model or balanced by similar variation in predicted values. Hence, analysis of W and Q in opposition to regression analysis clarifies that the model is unbiased and accurate, relative to the variability in the estimation data set. Furthermore, examination of scatter plots of predicted versus observed values reveals that observed values are especially variable for low predicted seed arrival. The most likely reason for this result is an inadequacy of my assumptions regarding maturity diameter threshold and linearity of fecundity with basal area (Eq. 2.2). Though the assumption that fecundity is linear with basal area seems reasonable and has been used by others (e.g., Clark et al. 1998b, Nathan et al. 2002b), it is obviously a gross simplification and a potential source of much error in model predictions. It is possible that some trees that were predicted to produce few or no seeds in reality were highly fecund, and that trees predicted to produce many seeds actually produced none. Many factors could be responsible for these errors, including competitive position in the stand, microsite quality, individual variation, annual variation outside the range studied (e.g., masting behavior) or that fecundity and basal area are related but nonlinearly. Lowering the maturity diameter threshold from 15 cm would not likely change model predictions drastically, as trees ≥15 cm comprised most of the basal area of modeled trees (compare basal area of all trees measured, those ≥ 8.0 cm, with basal area ≥15.0 cm, Table 2.1), but could have large effects for particular seed traps if a small, fecund tree were nearby. A more realistic alternative to Eq. 2.2 would probably reduce absolute errors between observations and predictions, but such an alternative is currently unavailable due to a lack of data. Additional research on the factors that affect tree fecundity would therefore be highly desirable.

Predictive validity.— Although the null hypothesis of unity slope and zero intercept was rejected for regression analysis of sweetgum in both habitats and green ash in younger reforestation sites, according to bias (W) and accuracy (Q) statistics, the model is predictively valid for all species in both younger and older reforestation sites (Table 2.3). W and Q result in different conclusions than regression because deviations from the one-to-one relationship (Fig. 2.7) were small compared to the variation in the estimation data set (i.e., s and s^2). Hence, W and Q can be considered better indices of model validity than regression because regression fails to account for natural variability in the modeled system. Even when W and Q were calculated using variation in the validation data for each species in each habitat, the model was still accurate for all species and habitats and unbiased for sweetgum and green ash in both habitats, though biased for American elm in both habitats in the direction of model overprediction (agreeing with regression results).

Because seed traps in reforestation sites had a distinct linear spatial arrangement, model predictive accuracy can also be examined with respect to the model's ability to predict spatial patterns. In this regard, the model also appears valid. Although Allen et al. (1998) attributed the significant effect of direction on tree colonization of abandoned fields in the MAV to prevailing wind patterns, we could not demonstrate the effect of direction on seed arrival because source populations of trees among sites were so different, making sites incomparable (Table 2.1). However, the model does accurately predict some interesting within-site patterns. For example, the model accurately predicts the bimodal distribution of American elm at sites Y24 and Y27, and mode away from the forest edge for green ash at Y27, American elm at Y27 and B22, and sweetgum at Y39. At other sites and species, the model correctly predicts the observed monotonic decrease in seed arrival with distance from forest (Fig. 2.8). Upon examination of each stand's tree map, it appears that a few isolated sweetgum trees produced the outlying peaks of predicted sweetgum seed deposition in stands Y27 (at 100 m) and Y39 (at 15 and 50 m; Fig. 2.8). As noted under the discussion of replicative validity, these errors likely reflect departures from the assumptions of linear fecundity with basal area (Eq. 2.2), and the basal area threshold for maturity. Conversely, observed sweetgum seed density at the 5-m trap at Y111 was over 10 times that predicted by the model. This was most likely the result of one or two whole sweetgum fruits falling into the trap, rather than usual wind dispersal of seeds from fruits still attached to the parent tree. Whole sweetgum fruits were frequently collected, though usually in forest seed traps; there were frequently > 50 seeds/fruit, though number of seeds/fruit was highly variable and not recorded.

Other deviances between observed and predicted seed arrival for the various species could have occurred for several reasons. Sweetgum and green ash were somewhat underpredicted in younger reforestation sites, especially in traps near the forest edge (Fig. 2.6; note that in several cases, relative deviances are high, but absolute deviance in terms of seeds/m^2 are quite low). If there are downdrafts caused by the abrupt change in vegetation height as wind flowing over the forest canopy suddenly encounters the shorter vegetation of the young reforestation site, seed deposition at the edge would be higher than predicted by my model. An additional source of error could be contribution of seeds from trees that were not included in the tree map because they were outside the boundaries of the sample. Such omissions would result in largest errors if the overlooked tree were large and near the forest edge. A source of error specific to green ash is that it is dioecious; because I did not identify green ash to sex on tree maps, its β_i is an average of the true β_i for females and the β_i for males, which is 0. Such unaccounted variation is especially important because green ash is extremely fecund (high β_i, see Table 2.2), and thus this parameter has a potentially large effect.

Furthermore, I did not include any effect of wind speed or other climatic factors on seed release—seeds simply experience winds in proportion to there representation in the 29 yr of instantaneous, hourly wind data. Greene and Johnson (1989) and Nathan et al. (2001, 2002a, 2002b) also did not include nonrandom seed release with respect to wind speed, but Greene and Johnson (1995, 1996) did, whereas Nathan et al. (2001) included effect of humidity and temperature on seed release. If seed release is not random with respect to wind speed, but more likely at higher wind speeds, then dispersal distance (and thus seed arrival in reforestation sites) would be higher. Sudden changes in wind speed, whether increases or decreases, are also more likely result in seed abscission, though how this would affect seed dispersal distance on average is not clear. Nathan et al. (2002a) asserted that such effects are probably not important for short-distance dispersal. However, sweetgum seeds are contained in clustered capsules and therefore might require substantial wind speeds to abscise. Thus, nonrandom seed release might be important for short-distance dispersal in certain situations.

In contrast to sweetgum and green ash, American elm was generally slightly overpredicted (Fig. 2.6–2.8), and adjusting for observed seed loss lead to a failure to reject the one-to-one relationship between predicted and observed seed arrival for both vegetation types and overall. Cedar elm was generally overpredicted—I did not collect any cedar elm seeds in traps in reforestation sites. Nevertheless, the model predicted extremely low densities of cedar elm, based on their small size and low density in source forests, so their absence in seed traps could have been an artifact of insufficient seed-trap sampling to detect such low densities.

Comparison to other models

I did not assess predicted seed arrival using any of the previously reported models to compare fits to those of my model, because Nathan et al. (2002a) have already shown that the shape of the wind profile has pronounced effects on dispersal distance. Hence, applying a model that assumes vegetation homogeneity would not be instructive. Tackenburg (2003) did compare predictions of his spatially variable wind-dispersal model to those of other, non–spatially variable models, but both his model and the competing models all shared the same functional form of the wind profile, and differences in vegetation heights were small compared to those I investigated.

Other models of seed dispersal using the same basic micrometeorological approach but without heterogeneous wind profiles produced comparable fits for the homogeneous systems they investigated. Quantitative comparison of the various studies is difficult because measures of fecundity, validation criteria, and validation test statistics differ. Generally, however, as the realism of the system to which the model was applied and independence of validation and parameterization data sets has increased, so has the goodness-of-fit between predicted and observed values decreased. For example, Greene and Johnson (1989) reported quite good results (their analysis was primarily qualitative and graphical), and showed the utility of the basic micrometeorological approach for modeling wind dispersal in controlled conditions. However, the total number of dispersing seeds was controlled in one case and validation was only replicative in the other. Greene and Johnson (1996) further refined the micrometeorological wind-dispersal approach by considering how wind speed changed from one vegetation type to another. They assessed the decline in seed deposition with distance from a forest edge relative to the seed deposition at the edge. Observed seed deposition fell within the 95% confidence intervals of the dispersal curve predicted from their model for some species and sites, but other species/sites were either over- or underpredicted. Once again, validation was mainly replicative, because their predictions were not independent of observed seed deposition, the fecundity parameter being based on the observed seed density at forest edge. Nathan et al. (2001) is perhaps most comparable to the current study, as they investigated the micrometeorological model for seed dispersal within *Pinus halepensis* stands. Using independent data, they determined the effect of climatic variables on seed release, and tested the one-to-one relationship between predicted and observed seed deposition. They predictively validated their model using regression analysis and failed to reject the one-to-one relationship for all seasons at both study sites they investigated. They obtained R^2 values of between 0.670 and 0.897 for the fit of observed to predicted seed arrival, depending on season and study site. My results (see Table 2.3) for American elm and green ash for older reforestation sites were comparable to those reported by Nathan et al. (2001) for *Pinus halepensis*, even given my lack of climatic detail and somewhat less rigorous seed-trap sampling used to collect the validation dataset.

This brief discussion can be understood better when one considers the two primary purposes of models: understanding mechanisms and making accurate predictions. The majority of studies on wind dispersal of plant diaspores (Greene and Johnson 1989, Nathan et al. 2001, 2002a, 2002b, Tackenberg 2003, etc.) have been primarily concerned with understanding mechanisms, i.e., determining which processes were most important in determining dispersal distance. As such, they chose relatively simple systems that allowed them to control extrinsic factors as much as possible. Making accurate predictions was the means to assess the importance of the various factors included in their models; they were not interested in the values of the predictions *per se*. Hence, one cannot expect the predictions of these models to be accurate if the models are applied to systems that are not similarly simple. The current study builds from these models by synthesizing the various processes that were previously modeled separately into a single model that can track seed dispersal in continuously heterogeneous environments. Hence, my model contributes to understanding mechanisms by showing how processes previously modeled in simple environments affect seed dispersal when included in complex environments. Furthermore, my model is fundamentally interested in the second use of models, namely, the making of accurate predictions. Having demonstrated the model's robustness for use in complex environments, the algorithm can then be confidently applied to predict seed arrival for other purposes.

Application to forest simulation models

The mechanistic model of seed dispersal by wind presented here provides a sound basis for incorporating seed dispersal into a forest simulation model, because it applies the micrometeorological wind-dispersal model to mixed stands and tracks seed dispersal out of the stand, across heterogeneous vegetation. Specifically, my approach expands on Greene and Johnson (1996) and Nathan et al. (2002a) by allowing any configuration of vegetation heights in the model landscape, rather than discrete *a priori*, definitions of differing patch types (Greene and Johnson 1996), or separate models for different vegetation types (Nathan et al. 2002a). My distinction between forest and reforestation-site habitats was merely a convenience for grouping the results; my model allows every 1-m^2 cell in the model landscape to have a different vegetation height. Nathan et al. (2001) suggested such a refinement, but did not implement it. Tackenburg (2003) implemented spatial variability on a much coarser scale and did not model wind speed below the top of vegetation, making that model invalid in tall vegetation like forests (his focus was on long-distance dispersal of herbaceous species in open habitats). By accounting for heterogeneity in the model algorithm (rather than averaging heterogeneity over the model landscape), I was able to accurately predict seed arrival within the various heterogeneous regions of the landscape. Indeed, it is likely that my model would perform substantially better if I were to apply it to a more homogeneous study area, with fecundity parameters fit from data in more similar stands. However, as stated earlier, that was not the goal of this exercise.

Rather, the goal of this study was to parameterize a model of wind dispersal that captured the important mechanisms determining seed arrival across heterogeneous and dynamic landscapes. The wind dataset used in this paper represents nearly 20 years of hourly wind observations, and though they are from a single location, Greene and Johnson (1989, 1995, 1996) pointed out that long-term wind conditions over flat areas are fairly stable in North America (indeed, the MAV is probably one of the flattest regions in North America). Furthermore, I estimated the fecundity parameter β_i from several sites at two distinct study areas with different geomorphic origins (thus perhaps affecting plant traits), using seed data collected over a 2-yr period. Thus, I expect that my estimates incorporate a large amount of the natural variation present, and importantly, the algorithm described herein makes use of that variation (via $\sigma_{\beta i}$). Thus, by incorporating such sources of variation, I have likely prevented the model from being over fit to my specific sites and time period. This fact is confirmed because the model was both replicatively valid and predictively valid for areas of differing vegetation physiognomy and spatially removed from the source population of trees. The fact that patterns of seed arrival differed between vegetation types, and that the model predicted the observed patterns accurately (Fig. 2.6–2.8; Table 2.3) further demonstrates its validity and generality. Furthermore, like other mechanistic seed dispersal models, parameters for my model are either easily measured or available from local weather stations. Therefore, there is great flexibility in applying my model to virtually any system (Greene and Johnson 1996).

In summary, my method of numerically calculating the effect of vegetation on wind speed was valid and effective for predicting seed arrival in vegetation types with drastically different and heterogeneous vegetation heights. Additionally, the method's flexibility to heterogeneous and dynamic vegetation demonstrates its utility for incorporating seed dispersal in spatially explicit forest succession models. Given that the behavior of animal dispersers is also influenced by vegetation (Schupp 1993), incorporation of mechanistic algorithms for animal-dispersed species would be helpful for similar reasons.

Table 2.1. Basal area (m^2/ha) of trees ≥ 8 cm dbh (diameter at breast height, 1.4 m; first number in column) and ≥ 15 cm dbh (second number in column) in forests adjacent to reforestation sites.

		Sites 0–3 yr-old		Sites 17–18 yr old				
		south*	north	east	west	north	south	east
Species	Common name	B22	B24	B3	Y111	Y24	Y27	Y39
Fraxinus pennsylvanica	Green ash	0.32	4.51	2.09	–	1.83	1.51	–
		0.25[¶]	3.85	1.70	–	1.79	1.51	–
Liquidambar styraciflua	Sweetgum	6.13	1.42	–	7.95	14.80	2.38	–
		5.77	1.26	–	7.82	14.41	2.38	–
Ulmus americana	American elm	4.40	0.75	3.37	1.69	2.63	0.44	0.67
		4.12	0.41	2.46	1.07	2.04	0.33	0.58
Ulmus crassifolia	Cedar elm	0.75	0.18	0.33	0.22	0.19	0.07	–
		0.20	–	0.11	0.09	–	–	–
Total other species [§]		17.58	22.69	3.58	27.63	22.70	27.23	28.33
		15.99	21.16	2.65	25.99	21.29	24.80	26.49
Total all species		**29.18**	**29.55**	**9.37**	**37.49**	**42.12**	**31.63**	**29.00**
		26.33	**26.68**	**6.92**	**34.97**	**39.53**	**29.02**	**27.07**

* Direction of reforestation site relative to forest.

[¶] Basal area of trees ≥ 8 cm followed by those ≥ 15 cm. The 8-cm limit includes all trees mapped and the 15-cm limit includes only trees assumed to be reproductively mature. A dash (–) indicates a zero value.

[§] Species included *Acer negundo, Acer rubrum, Carya aquatica, Carya illinoensis, Celtis laevigata, Cercis canadensis, Cornus drummondii, Crataegus viridis, Diospyros virginiana, Forestiera segregata , Fraxinus pennsylvanica, Gleditsia triacanthos, Melia azederach, Morus rubra, Populus deltoids, Quercus lyrata, Quercus nigra, Quercus nuttallii, Quercus pagoda, Quercus phellos, Robinia pseudoacacia, Salix nigra, Sassafras albidum, Taxodium distichum, Ulmus alata,* and *Ulmus rubra.*

Table 2.2. Mean number of seeds per cm^2 basal area (β_i, see Table 2.4), its standard deviation ($\sigma_{\beta i}$) and number of sites (n) on which mean and standard deviation are based.

Species (*i*)[a]	β_i	$\sigma_{\beta i}$	n
American elm	45.8	19.1	7
Cedar elm	23.0	1.5	2
Green ash	112.6	55.6	5
Sweetgum	21.7	9.9	6

[a] I also attempted to simulate red maple (*Acer rubrum*) and boxelder (*A. negundo*), but parent trees and seed arrival in traps were too infrequent to determine β_i.

Table 2.3. Statistical tests of model performance, where values with asterisk indicate model predictions deviate from observed seed arrival in seed traps (*F* and *P* values for regression pertain to H_0: slope = 1 and intercept = 0).

				Regression results									
						slope			intercept (seeds/m^2)				
	n	Bias (*W*)	Accuracy (*Q*)	df	r^2	Lower 95% CI	Mean	Upper 95% CI	Lower 95% CI	Mean	Upper 95% CI	*F*	*P*
Forest													
American elm[¶]	73	1.52	1.18	2, 74	0.257	0.175	0.289	0.403	12.2	24.3	36.3	85.3*	< 0.001
Cedar elm	61	1.61	5.19*	2, 62	0.001	-0.0313	-0.0039	0.0235	0.0816	0.176	0.270	2830*	< 0.001
Green ash	73	-0.723	0.473	2, 74	0.207	0.141	0.258	0.375	24.8	66.9	109	81.4*	< 0.001
Sweetgum	72	-0.950	0.994	2, 70	0.423	0.362	0.502	0.641	46.6	85.0	123	26.08*	< 0.001
Older plantations													
American elm[¶]	30	0.0955	0.000986	2, 28	0.711	0.707	0.939	1.17	-0.736	-0.136	0.465	0.59	0.561
Cedar elm	20	0	0										
Green ash	30	-1.14	1.16	2, 18	0.671	0.746	1.14	1.54	-86.6	41.9	170.4	0.83	0.451
Sweetgum	30	-0.143	0.0126	2, 27	0.714	0.846	1.12	1.39	0.566	6.79	13.0	3.71*	0.038
Younger plantations													
American elm[¶]	40	0.113	0.00212	2, 38	0.330	0.492	0.925	1.36	-0.925	0.469	1.86	0.24	0.789
Cedar elm	40	0.568	0.0357										
Green ash	40	-0.0466	0.000492	2, 38	0.901	1.75	1.96	2.17	-1.331	-0.487	0.356	49.3*	< 0.001
Sweetgum	30	-0.0921	0.00412	2, 27	0.312	1.25	3.02	4.79	-0.767	0.295	1.356	6.02*	0.007

[¶] For regression analysis, observed values were corrected for 50% seed loss from seed traps by multiplying actual observed value by 2.

Table 2.4. Definition of symbols used and default values

Symbol	Definition	Default value	Units
D	deviance between model predicted and observed seed arrival		m^{-1}
d	displacement height—a parameter for the logarithmic wind profile	$0.667 \cdot z_h$	m
Δt	time step of the seed dispersal algorithm	3.0	s
f	realized seed fall velocity (change in vertical position of seed at each time step)		m/s
F	fecundity of a tree (number of seeds produced/year)	$a_{ij} \cdot \beta_i$	seeds
H	tree height		m
H_{max}	asymptotic tree height		m
Q	model accuracy (Eq. 2.11)		
r	radius at breast height		cm
s	standard deviation of seed arrival in forest seed traps		
S	parameter defining allometry between r and H		cm^{-1}
U	average wind speed over some horizontal and vertical plane		m/s
u_z	wind velocity at height z		m/s
u_{zh}	wind velocity at the top of the canopy		m/s
w	vertical wind speed—mean and standard deviation (in parentheses)	0.1 (0.25)	m/s
W	model bias (Eq. 2.10)		
z	height of a seed above ground		m
z_0	roughness length—a parameter for the logarithmic wind profile	$0.105 \cdot z_h$	m
z_h	height of the top of the canopy		m
α	canopy flow index—a constant for the exponential wind profile	4.0	
β_i	fecundity per unit basal area of species i		$seeds/cm^2$
Δx	change in horizontal position of a seed		m
ρ	crown radius		m

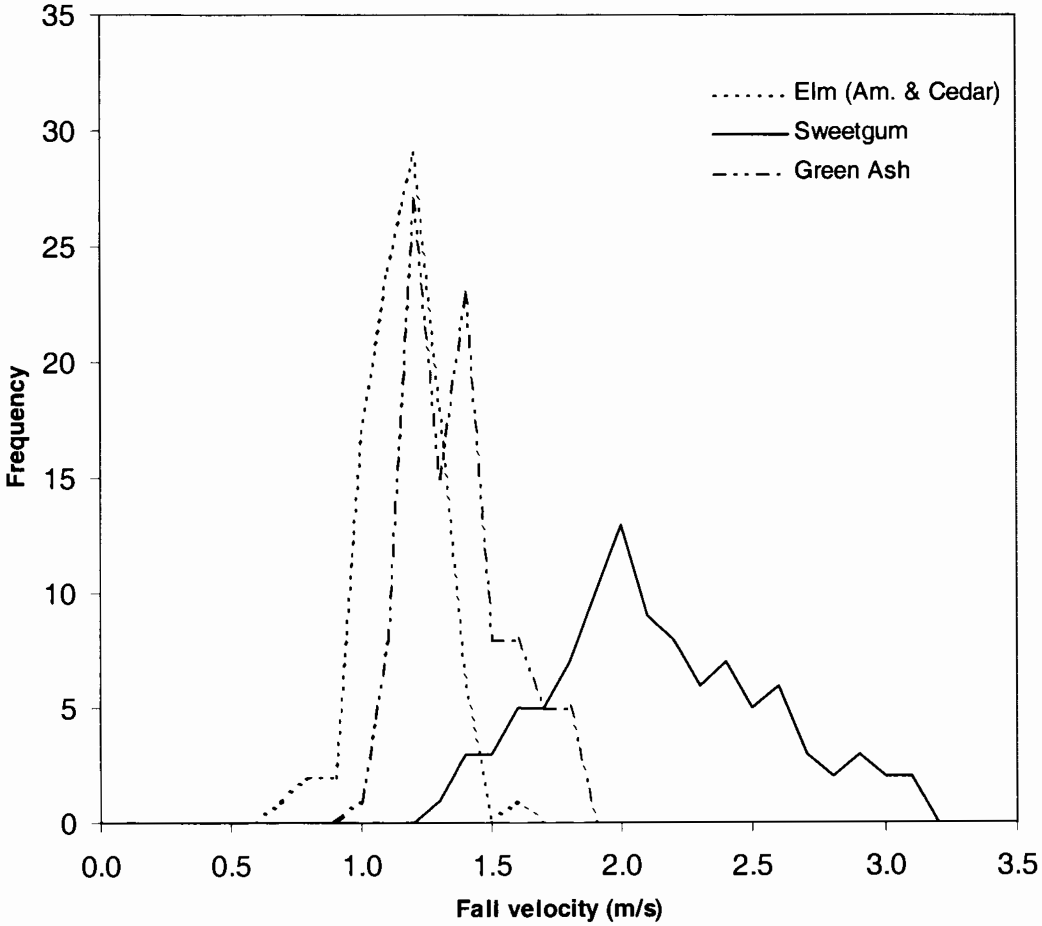


Fig. 2.1. Seed fall velocities of seeds as determined by timing the descent of 100 seeds of each species from a height of 1.7 m in still-air conditions in the lab. American elm and cedar elm seeds are similar morphologically, so were assumed to comprise a single population of seed fall velocities.

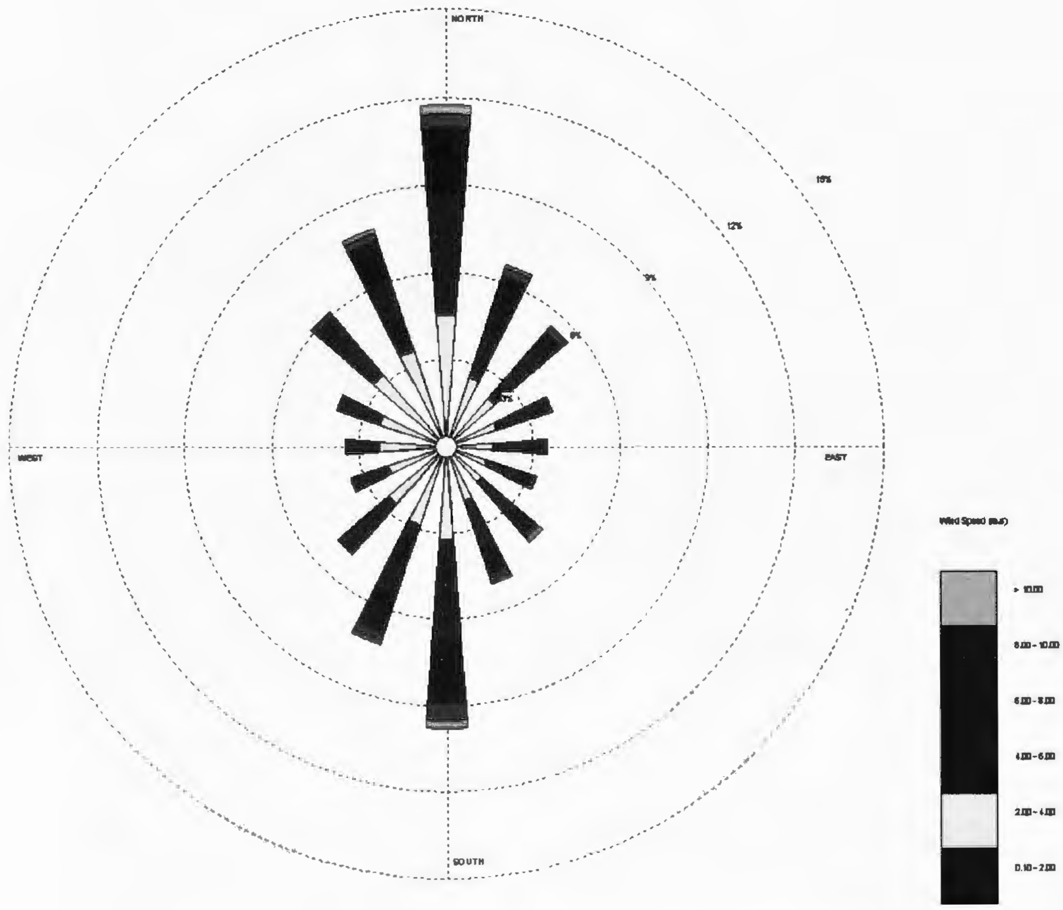


Fig. 2.2. Wind rose for hourly wind observations between 1 January 1973 and 31 July 2002 at Greenville, Mississippi, showing the distribution of wind flow vectors. Wind roses for particular months and seasons differ considerably, so the overall wind rose is not a good indication of patterns of seed dispersal.

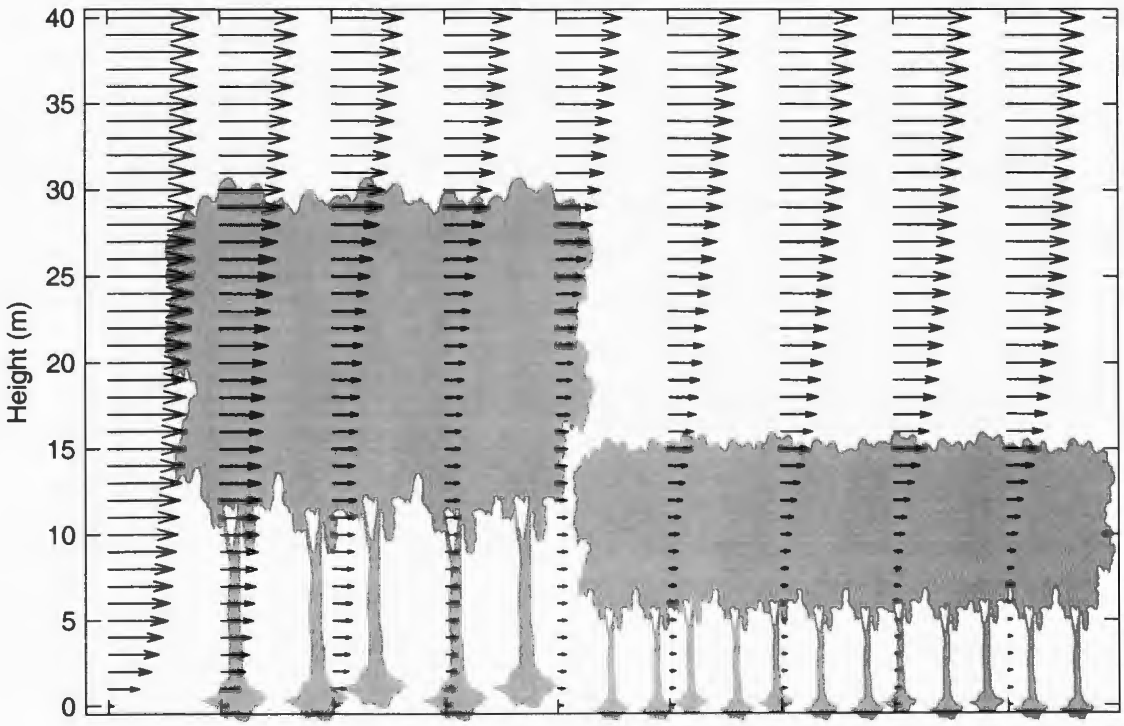


Fig. 2.3. Simulated wind speed vectors above and within vegetation, based on logarithmic profile above vegetation and exponential wind profile within vegetation. Vectors are running average of wind speed at the current location and previous location. Wind vectors are based on a reference wind speed of 4 m/s at 10 m above bare ground (the size of the wind vector nearest the 10 m tic on the vertical dimension).

Fig. 2.4. A younger (3-year-old, above) and older (18-year-old, below) reforestation site and adjacent, naturally regenerated bottomland hardwood forest.

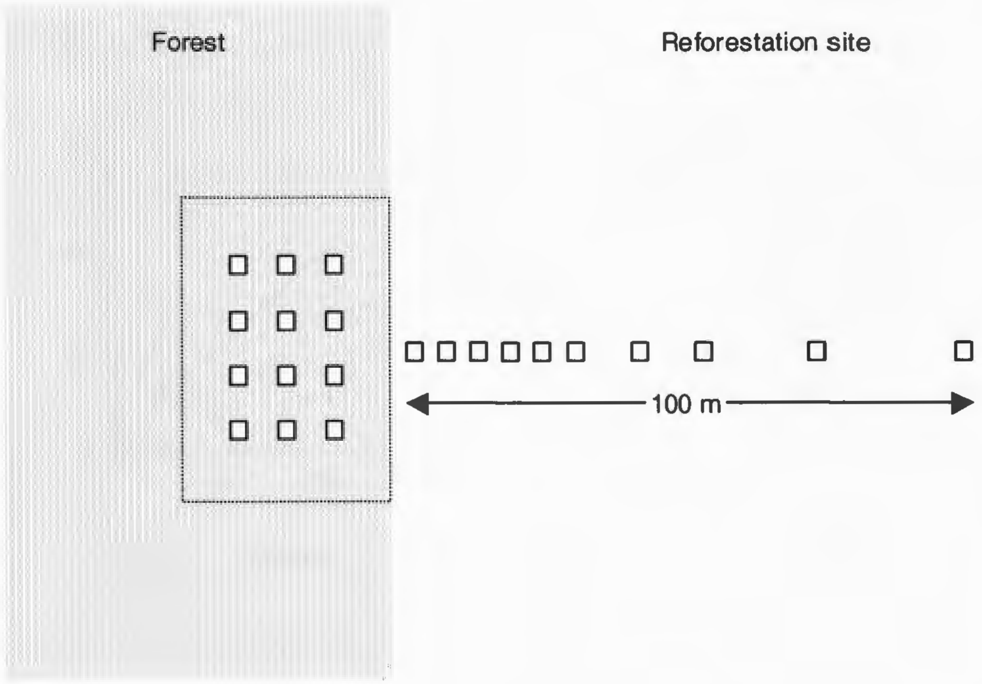


Fig. 2.5. Seed trap (small squares) sampling design in forest and adjacent reforestation sites. Traps in forest were ca. 10 m apart, and those in adjacent reforestation sites were 5-30 m apart. Outlined area in forest indicates placement of plot wherein all trees > 8 cm dbh were mapped. Forests were more extensive than is apparent on figure.

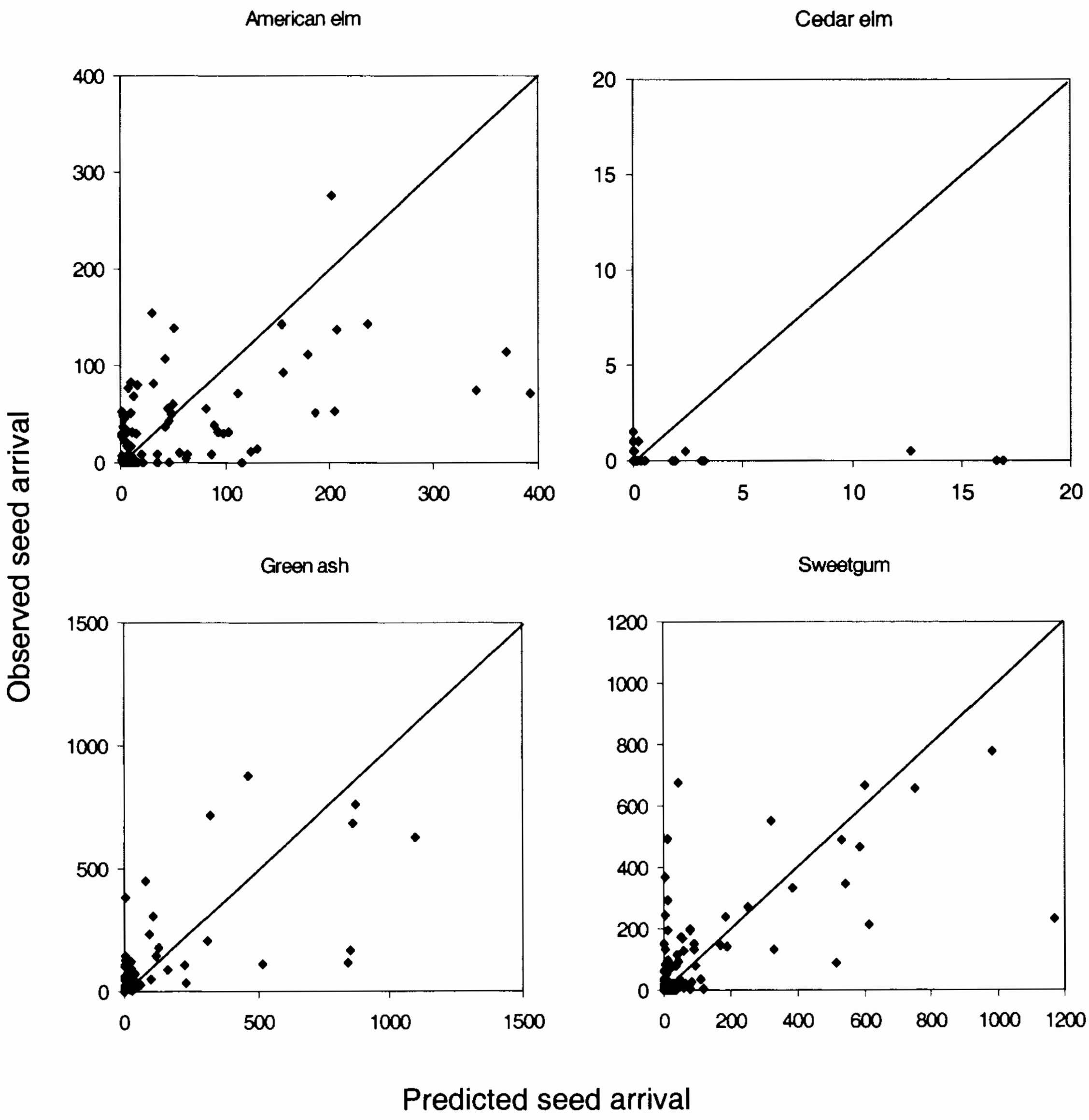


Fig. 2.6. Observed versus predicted seed arrival (seeds/m^2) in forest seed traps at Yazoo NWR. One green ash data point at (2191, 31) is not shown. The diagonal line is the 1:1 line.

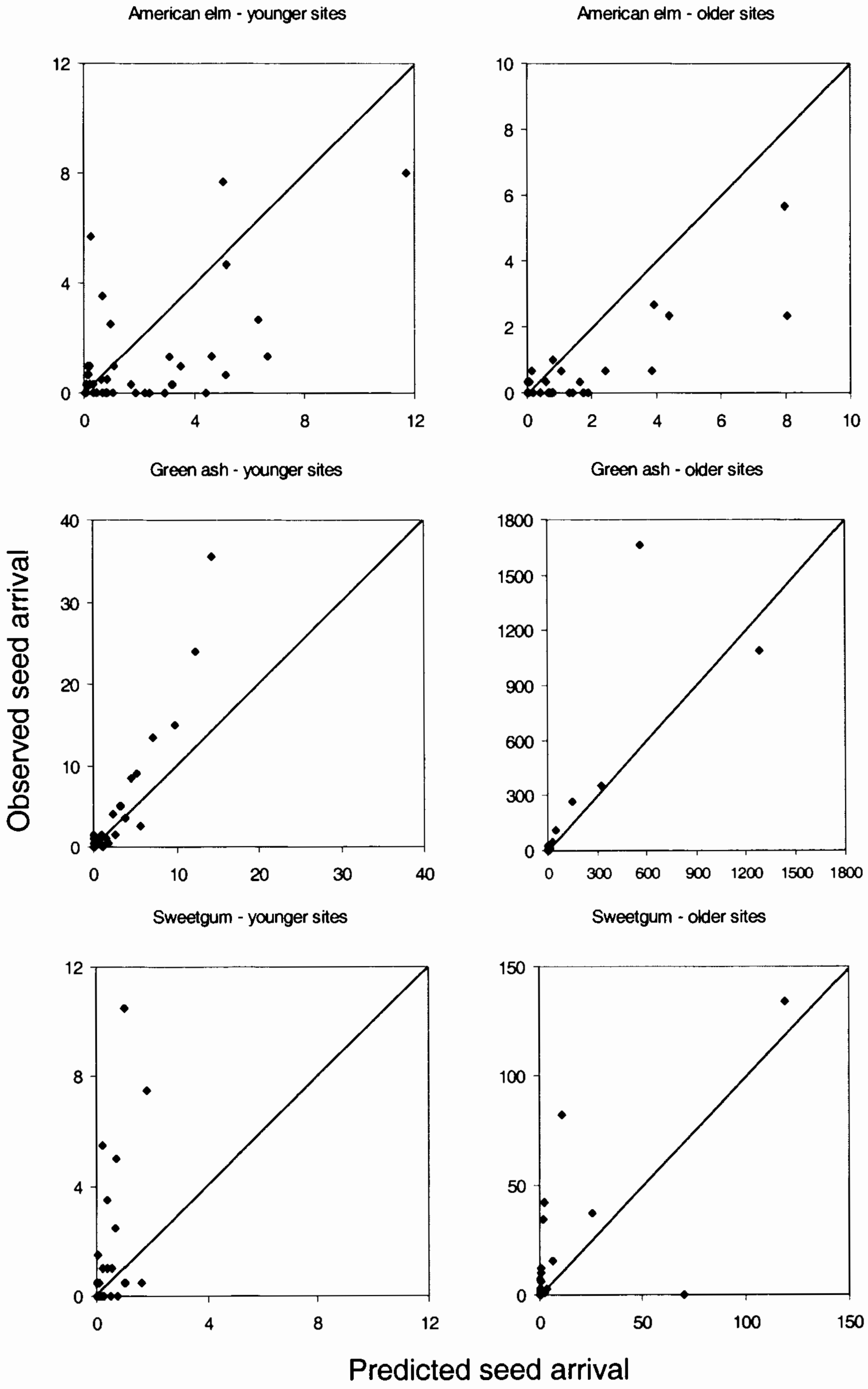


Fig. 2.7. Observed versus predicted seed arrival (seeds/m^2) in reforestation site seed traps at Yazoo NWR. One sweetgum data point (at 7, 72) is outside the displayed range and not shown. The diagonal line is the 1:1 line.

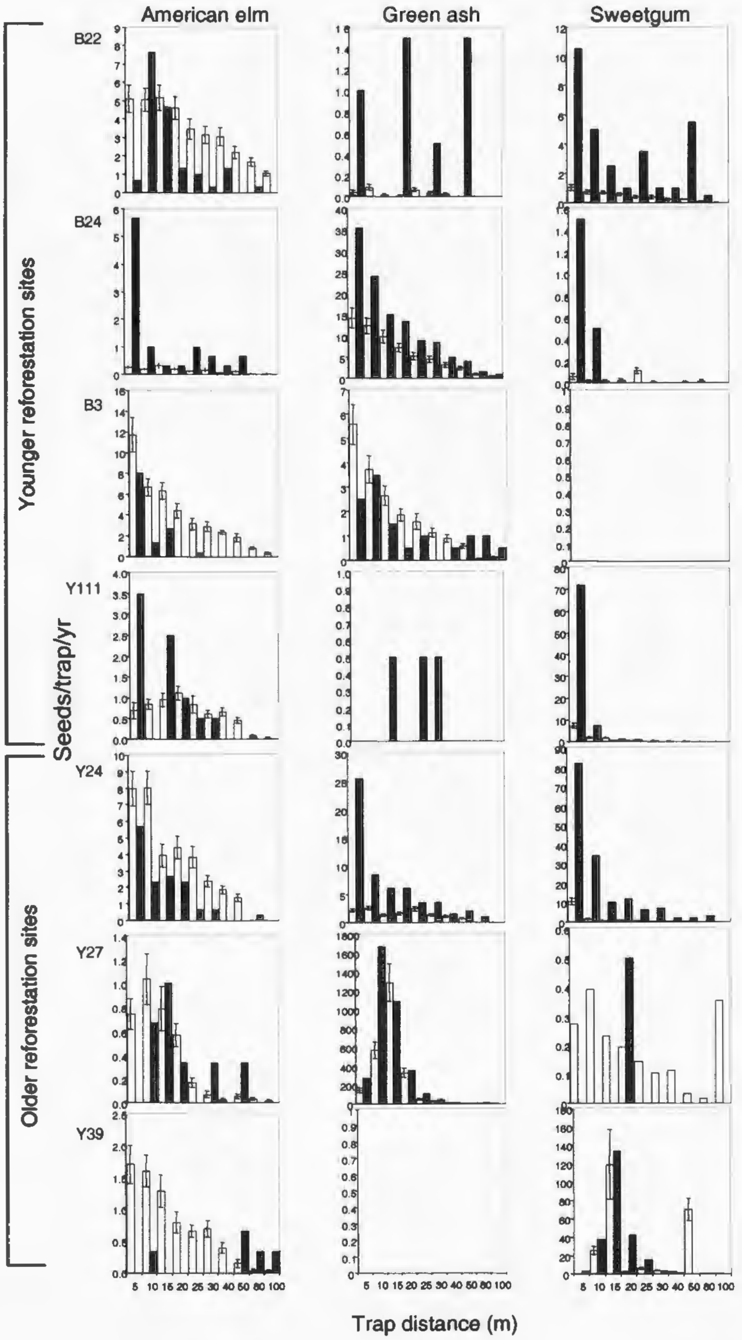


Fig. 2.8. Seed densities (seeds/trap/yr, traps were 0.5 m^2) from simulated (open bars) and real (shaded bars) seed traps in younger ($\leq$ 3-yr post-establishment) and older (17-18 yr post-establishment) reforestation sites. Observed (real) values are from seed traps sampled monthly from March 2000 to April 2002 at Yazoo NWR. Standard error bars (1 SE) around simulated values show variation from model replicates that used different random-number seeds and incorporate variation in fecundity. Trap distance from forest edge is approximate, but all trees and traps were georeferenced, so the model made use of actual distances. Note that scales on Y axis vary over 5 orders of magnitude, depending on species and site.

CHAPTER 3

THE IMPORTANCE OF DISPERSAL AND COMPETITION ON FOREST SUCCESSION: A SIMULATION STUDY OF BOTTOMLAND HARDWOOD REFORESTATION

Abstract.—YAFSIM is an individual-based, spatially explicit forest simulator that combines mechanistic seed dispersal with growth and mortality of trees. I describe the basic structure of the model and its application to forested wetland restoration sites in the Mississippi Alluvial Valley. Basal areas and stem densities of trees in larger strata predicted by YAFSIM are similar to values from real restoration sites, and species composition is similar to real sites. I performed sensitivity analysis on dispersal and establishment parameters and alternative establishment scenarios for restoration sites to assess their relative importance in driving successional dynamics. The model predicts that seed dispersal limits colonization far from forests, but even when colonization is plentiful, trees planted as part of conventional reforestation scenarios inhibit recruitment of colonizers into larger size classes. After 100 yr, ca. 90% of canopy trees in simulated reforestation sites belonged to the species initially planted. Monodominance of planted species is multigenerational and lasts at least 500 yr, becoming more extreme with time. Diverse forests did not develop under any of the scenarios examined, and may require incorporation of spatial heterogeneity in flooding and its effects on seedlings. Alternatively, diversity of extant, natural forests may be a legacy of site history, and as such, new reforestation projects must make concerted efforts to ensure diversity if that is a goal.

INTRODUCTION

How ecological communities can be diverse despite limited environmental heterogeneity and large niche overlap between species is a central question in ecology. Composition of ecological communities is shaped by a combination of random events, species environmental tolerances, and interactions among individuals. Hubbell (2001) attempted to reconcile the various competing ideas and identified two paradigms about how ecological communities are organized: the niche-assembly paradigm and the dispersal-assembly paradigm. The niche-assembly paradigm has dominated ecological thought since formulated by Grinnell (1917), even though many of the patterns in community composition that have previously been attributed to niche-assembly processes can more parsimoniously be explained by the vagaries of random mortality, recruitment, and migration, i.e., by dispersal-assembly processes (Hubbell 1979, 2001). Hubbell developed his neutral theory to explain how tropical forests can maintain high tree species diversity. However, the majority of forest simulation models (e.g., Shugart 1984 and derivatives, Botkin 1993, Pacala et al. 1996, Chave 1999) continue to focus almost exclusively on niche-based, resource-mediated interactions among established trees.

In contrast to the niche-assembly paradigm, the dispersal-assembly paradigm seeks explanations for observed patterns of species coexistence by focusing on factors determining what species are available to occupy a position in the community. Only available species can have a chance at interacting via their niche relationships, so determining what factors influence species availability is of primary importance. The growing literature on seed dispersal, including phenomenological and mechanistic models, thus arises from the dispersal assembly paradigm (e.g., Chapter 2, Barrows 1975, Greene and Johnson 1989, Okubo and Levin 1989, Greene and Johnson 1995, 1996, Clark et al. 1998a, Clark et al. 1998b, Nathan et al. 2001, Nathan et al. 2002a, Nathan et al. 2002b).

It seems obvious that forest community composition is a product of both dispersal and niche assembly processes (a fact recognized by Hubbell repeatedly in his 2001 book, though overlooked by such critics as McGill 2003). Perhaps not so obvious is that the effect of limited dispersal on species assemblages can be seen at very large regional scales, not only in regions still responding to changing climates (e.g., temperate forests, see Davis et al. 1994), but also in climates that have been relatively stable for eons (e.g., tropical forests, see Tuomisto et al. 2003).

Though ever changing, the existence of dispersal-dependant patterns is essentially permanent because of time scales involved in site occupancy. In shorter time scales, dispersal-assembly processes may completely overshadow niche-assembly processes during the initial several hundred years following colonization of newly available sites. Hence, it is possible that much of the focus on interactions among individuals (e.g., competition) is unfounded and has produced misleading conclusions about processes important for forest development. The magnitude of the influence of dispersal on subsequent population processes depends on the transition rates of seeds to later stages (Clark et al. 1999).

In an attempt to address some of these issues, at least on a local scale, several forest simulation models have implemented spatial mechanisms such as dispersal. One such approach has been to expand plot- or stand-level models to landscapes by linking several such models and making recruitment of new individuals (always as established saplings) dependent on presence of adult conspecifics in adjacent plots or stands (e.g., Smith and Urban 1988, Clark and Ji 1995). In contrast to single or linked stand-level models, in spatially continuous models (e.g., Pacala et al. 1996, Chave 1999) fates of individuals depend not on average conditions over the stand, but on conditions immediately surrounding each individual. Such models describe well the mechanistic basis of competition for light, but currently rely on simple probability functions to disperse seedlings or saplings (not seeds) in space, an improvement over the stand-level approach, but one that still ignores the early stages of seed dispersal and seedling establishment, including their mechanisms. Thus far, no forest simulation model has incorporated mechanistic dispersal. Without this mechanism, the ability to analyze larger-scale patterns like reforestation is limited.

Because spatial patterns of seed deposition eventually determine the number of adult trees added to the population, vegetation dynamics cannot be understood without considering seed dispersal (Schupp and Fuentes 1995). To investigate patterns of species colonization and what factors and conditions limit colonization, it is therefore necessary to incorporate seed dispersal into a spatially explicit forest simulation model, because one must not only determine where seeds go, but also what happens to them after they arrive (Nathan et al. 2002b).

To address this need, I created a spatially explicit, individual-based model of tree colonization of abandoned agricultural fields, YAFSIM (YAzoo Forest SIMulator, or Yet Another Forest SIMulator). YAFSIM disperses wind-dispersed species using a mechanistic algorithm and other, primarily animal-dispersed species using probabilistic kernels. To transform seeds into saplings, YAFSIM incorporates estimates of germination and seedling survival. Growth of individuals is based on the effect of crowding on empirically derived growth rates, adapted from a gap model for bottomland hardwoods (Phipps 1979), which I have scaled to individualized neighborhoods (ecological fields, sensu Walker et al. 1989) surrounding each tree. Mortality for saplings and adult trees is based on annual increment growth and tree size.

Thus, currently, YAFSIM is the only forest simulator to track forest development starting from estimates of numbers of seeds produced by adults, through dispersal, establishment, and growth, without forcing density of resulting seedlings to agree with some predefined limit (e.g., total number of surviving seedlings, Pacala et al. 1996, or maximum of 1 seedling/m^2 regardless of species, Chave 1999). This distinction is important because relying on such predefined limits prevents assessment of the importance of underlying mechanisms. Thus, explicitly incorporating processes that affect density of seedlings forms a hypothesis about the validity of our understanding of such processes.

The system to which I apply the model is former agricultural fields undergoing restoration to bottomland hardwood forests in the Mississippi Alluvial Valley (MAV). Bottomland hardwood forests were once the predominant vegetation in the region, but today the MAV is largely deforested (Fig. 3.1). The first step in restoration of these systems is reforestation (Allen et al. 2001, Schoenholtz et al. 2001). There are currently > 78,000 ha of such reforestation sites on both private and public lands in the MAV—a figure that is expected to more than double by 2005 (Stanturf et al. 2000). Hence, application of YAFSIM to this system is fruitful not only from a theoretical but also a management perspective. Reforestation of these sites has emphasized the importance of natural tree invasion to augment plant diversity, but data show that such invasion is unreliable (e.g., Allen 1997, Stanturf et al. 2000). Therefore, accurate prediction of the degree of success at a given site requires understanding processes that limit natural tree invasion, which will elucidate whether substantive changes in the restoration paradigm need to be considered to avoid producing low-diversity systems that resist invasion indefinitely.

Given this theoretical and practical background, I used YAFSIM to address questions related to the role of dispersal and competition in development of forests on abandoned fields. The first question was: can diverse communities develop on new sites when seed sources are spatially distant from the site of interest? This question was assessed for sites undergoing natural succession and those established with a few species of trees (i.e., with a plantation, as is the normal practice). The second question is: do established trees suppress colonizers, thereby inhibiting development of diverse forests? Tracking forest development in simulated sites that were planted at different densities and with different species or not planted at all, to see if trees that invaded after the first cohort were able to recruit into larger strata, assessed this question. Finally, I compare insights from these analyses to other studies and ecological theory, and discuss limitations of the current modeling approach.

METHODS

Design, structure, and parameterization of the model YAFSIM

YAFSIM is a spatially explicit individual-based model in continuous two-dimensional space that models the full life cycle of trees, incorporating seed, seedling, sapling, and adult stages. Individual tree dynamics are modeled using a discrete time step of one year. In YAFSIM, the population of trees is overlaid on a habitat matrix made up of discrete 1-m^2 cells containing information on tree stocking and vegetation height.

Tree stocking, defined in terms of basal area, influences tree growth, which affects mortality. Pacala et al. (1996) modeled individual trees in continuous space without creating a discretized habitat matrix, by identifying for every tree in the population every other tree that affected its light environment. I did not use this approach because of its computational demands and because parameters for light extinction, effect of various light intensities on growth, etc., were not available for the species in my system. Instead, I used a discrete habitat matrix to store stocking information for trees modeled in continuous space to make use of published parameter estimates for tree growth and crowding developed for a stand-level model of bottomland hardwood forest dynamics in the MAV (program SWAMP, Phipps 1979). Other modeling approaches create landscapes linking several plot or stand-level models (e.g., Urban and Smith 1989, Clark and Ji 1995). In these models, all trees within the plot contribute to and experience identical conditions regardless of their proximity to other trees or plot edges. Instead, I mapped the landscape onto a matrix of 1-m^2 cells, wherein trees experience and contribute to the demographic conditions of surrounding cells. This approach is based on ecological field theory (Walker et al. 1989), where organisms are influenced most by conditions nearest them, and both their influence on the environment and the environment they experience are defined by their own resource demands (reflected in their size). Thus, in YAFSIM, trees contribute their stocking to cells around them, and experience the stocking contributed to those cells by themselves and other trees, in effect creating an individualized plot of relevant size centered on each tree.

Vegetation height is stored in another layer of the 1-m^2 habitat matrix. Vegetation height affects the wind environment experienced by dispersing seeds. In YAFSIM, vegetation height is updated every year of the simulation to reflect growth and death of trees. Thus, dispersing seeds experience wind environments modified by vegetation along their trajectory (see Chapter 2).

In addition to overlaying a continuous tree population on a discrete habitat matrix of stocking and vegetation height, this structure allows flexibility in expanding the model to include such factors as fine-scale environmental heterogeneity. Such heterogeneity may include features of microtopography that are known to be important in structuring bottomland hardwood forests (Putnam et al. 1960). Including microtography in the habitat matrix would allow inclusion of algorithms to calculate the effects of such factors as variable flooding regimes across the model landscape, as was addressed for the discrete case in SWAMP (Phipps 1979).

Initial populations of trees.—The simulated landscape is initially populated with trees from a two-dimensional raster habitat map of the model landscape (a grid of 1-m^2 cells) and samples of trees for each habitat (e.g., natural forest and reforestation site), along with the amount of area each sample represents. The forest is created by randomly drawing trees according to observed densities in each habitat. At the start of each simulation, trees thus selected are read into a linked list that contains all information for each tree.

Initialization.—Each time step (one year) begins with an initialization of the stocking and vegetation height of each cell in the landscape, to reflect changes due to growth and mortality the previous year. Vegetation height affects the wind environment, which affects dispersal of wind-dispersed seeds (Chapter 2). Stocking affects the growth algorithm, so is discussed later.

Seed dispersal.—Reproduction is species- and size-dependent. Each tree > 15 cm diameter at breast height (dbh, 1.4 m) is reproductively mature (following Nathan et al. 2002b). The number of seeds produced per tree is linear with the tree's basal area (following Clark et al. 1998b and Nathan et al. 2002b; see β, Table 3.1). Seed viability is based on the species' germination rate (Table 3.1). To reduce computations, only germinating seeds are dispersed; nongerminating seeds die (i.e., there is no seed bank). The absence of a seed bank in the model reflects the biology of the modeled species (see Young and Young 1992). Determining whether a seed will germinate before it disperses does not allow for the microenvironment to affect seed germination, but currently there exists insufficient data to develop a more realistic germination algorithm. Until such data are available, my approach saves considerable computational time, especially for wind-dispersed species, which produce high numbers of seeds but have low germination rates. All seeds that disperse to a point inside the model landscape are then established as seedlings with an initial radius at breast height (r) = 0.5 mm, height (H) calculated allometrically from Eq. 3.7, height growth increment (used for mortality function, below) $\Delta H = H$ and radial growth increment $g = r$ (used for mortality function, below), and age of 0 yr. Although it is obvious that real newly established seedlings are shorter than breast height (1.4 m, making $r = 0$), this assumption is necessary for the allometric height relationship and mortality function that depends on it (described later). The algorithm for dispersing individual seeds differs depending on whether the species is wind-dispersed or animal-dispersed.

Wind-dispersed seeds.—The wind-dispersal algorithm is described in further detail in Chapter 2. Briefly, each individual seed produced by a parent tree is moved in three-dimensional space from a starting position in the tree crown until it reaches the ground. The seed's rate of descent is determined by its fall velocity, which is based on an empirical distribution, and vertical winds. The wind environment determines the seed's horizontal movement, which is a function of the distribution of wind speeds at a reference location and the vegetation along the trajectory of the seed.

Non-wind dispersal.—If the species is not wind-dispersed, I rely on phenomenological dispersal kernels to disperse seeds. Individual seeds leave each tree in a random direction and travel a distance determined by a probability distribution. I use the composite dispersal kernel described by Clark et al. (1998a):

$$k_f = \exp\left[\left(\frac{D}{\alpha_f}\right)^{c_f}\right] \cdot \frac{1}{N} \tag{3.1}$$

where k_f is the probability of dispersing distance D from the source, α_f is the mean dispersal distance, c_f is a shape parameter, N is a normalizing constant, and $f = (1, 2)$ determines which of two sets of parameters the function takes. The composite kernel specifies that a proportion p of the total seeds produced by an individual are dispersed by a function that describes primary dispersal, which is Gaussian with $c_1 = 2$. The remainder $(1 - p)$ are dispersed by a function that describes secondary dispersal and dispersal by rare, long-distance dispersal events, which is fat-tailed with $c_2 = 0.5$. Estimates of the mean dispersal distance for Gaussian dispersal, α_1, are derived from Clark et al. (1998b) and reported in Table 3.1. Estimates of the mean dispersal distance for fat-tailed dispersal are $\alpha_2 = 200$ m and $p = 0.99$ from Clark et al. (1998a).

For each species, an initialization algorithm builds lookup tables of the cumulative probability K_f of a seed dispersing up to distance D from the source based on parameters for each species for the two component dispersal kernels. The algorithm increments D from 0 to 5000 m, calculating Eq. 3.1 for each D with $N = 1$. The values K_f are generally asymptotic at $D << 5000$ m, and these asymptotic values are then used as N in Eq. 3. Dispersal distance is a random deviate from the cumulative distribution K_f. For each dispersing seed, if a uniform random deviate v_1 is less than p, the seed is dispersed with the Gaussian dispersal kernel ($f = 1$); otherwise, it is dispersed with the fat-tailed kernel ($f = 2$).

Growth.—I have adapted growth functions from Phipps (1979). He used a stand-level approach to model growth and survival of post-seedling stages of bottomland hardwood species in response to environmental conditions (including soil and flooding conditions, shading, and crowding). Currently, my model does not address flooding, but rather focuses on crowding to modify growth. Thus, the growth function for each tree is:

$$g_t = \min\left(1, \frac{r_{t-1}}{P}\right) \cdot \sqrt{r_{t-1}^2 + B \cdot C} - r_{t-1} \tag{3.2}$$

where g_t is the radial growth increment, r_{t-1} is the radius during the previous time step, P is a parameter (21 mm) that modifies growth of small trees.(see Phipps 1979), B is the basic growth rate (mm^2), and C is the crowding factor. Basic growth rate is the mean annual growth increment multiplied by *pi* (see Table 3.1) and describes the species' growth rate when the site is fully occupied (see Phipps 1979).

The crowding factor C is based on stocking in a tree's vicinity (rather than stand means of stocking as in Phipps 1979). Stocking is calculated for each cell based on trees that influence that cell. The total influence of a tree is calculated as its basal area, and is distributed to all cells within $0.25H$ m around it based on the following formula:

$$S_i = \frac{10000r^2}{(0.25H)^2} \tag{3}$$

where S_i is the stocking of cell i in $\mathrm{mm}^2\mathrm{ha}^{-1}$ and H is tree height (see Eq. 3.7). The stocking from each tree at each cell is assigned to one of three strata based on the tree's r (following Phipps 1979). This is done so that small trees are affected by large trees, but not vice versa (as for competition for light, which Pacala et al. 1996 determined to be most limiting). Trees with $r < 50$ mm contribute to the small tree stratum (stratum 1), trees with $50 \leq r < 100$ mm contribute to the subcanopy (stratum 2), and trees with $r > 100$ mm contribute to the canopy (stratum 3). This algorithm is repeated for all trees in the population, with each tree's contribution to the stocking at each cell in each stratum added to the stocking already calculated for that cell and stratum.

The stocking in each stratum l in the vicinity of each tree is the average of the stocking in all cells within $0.25H$ of the tree (henceforth, $\overline{S}_l$). These stocking values are then used to calculate the crowding experienced by the tree. Crowding in each stratum l is calculated based on the ratio of stocking in each stratum to a reference level R_l of stocking determined by Phipps (1979) to represent a fully stocked site (Table 3.2). The crowding factor, C_l, for each stratum is:

$$C_l = \left(\frac{R_l}{\overline{S}_l}\right)^2 \quad \text{if} \quad \overline{S}_l \geq R_l$$
$$C_l = 2 - \left(\frac{\overline{S}_l}{R_l}\right)^2 \quad \text{if} \quad \overline{S}_l < R_l. \tag{3.4}$$

Thus, C_l is unity when $R_l = S_l$, 2 when $S_l = 0$, and asymptotes to zero when $S_l >> R_l$. I calculate the crowding a tree experiences (C) as the product of the C_l values for whatever stratum the tree is in and the maximum of C_l values for larger strata. Phipps (1979) used the product of the current stratum and all larger strata rather than the maximum, but this resulted in unrealistically high growth values for small trees early in the simulation when subcanopy and canopy strata were vacant (the two methods are identical for trees in the middle and upper strata). Additionally, I multiplied C for the small tree stratum by an effect of herbaceous vegetation, C_h:

$$C_h = 1 - 0.75\exp\left(-0.05\left(\frac{\overline{S}_3}{R_3} + \frac{\overline{S}_2}{R_2}\right)\right) \tag{3.5}$$

where the term inside the exponent is the sum of the relative stocking in the subcanopy and canopy strata (analogous to overhead canopy cover) multiplied by a scaling factor (0.05). The effect is that less stocking in higher strata results in an increase in competition from herbaceous vegetation.

Finally, shade-intolerant species were affected more by crowding than shade-tolerant species. Thus, for shade-intolerant species (Table 3.1), for $C < 1.0$, C was further multiplied by 0.8 to further suppress growth, and for $C \geq 1.0$, C was further multiplied by 1.2 to reflect shade-intolerant species' abilities to more fully capitalize on available resources (following Phipps 1979).

Mortality.—After each tree's radial increment growth has been determined, it is subjected to mortality. Phipps' (1979) model of mortality assumed that all species had the same mortality response to low growth rate (a common assumption shared by most gap models, e.g., Shugart 1984, Botkin 1993). However, better estimates of growth effects on mortality are currently available, and YAFSIM incorporates such estimates from two sources (Pacala et al. 1996 and Fulton and Harcombe public communication, Ecological Society of America 85th Annual Meeting, Snowbird, Utah, August 2000). I used these two sources to cover the full range of tree sizes and to make use of estimates for tree species that occur in my study area. Both approaches are based on carbon balance, where trees allocate resources to maintenance before growth. Hence, trees with low growth increment are assumed to be barely meeting their maintenance needs and are more susceptible to mortality (Phipps 1979). Furthermore, Fulton and Harcombe's approach assumes that larger trees have larger pools of stored resources to withstand short periods of stress, and are thus less likely to die than smaller trees. Additionally, Pacala et al. (1996) recognized that their mortality functions did not produce sufficient self thinning to accurately model early stages of stand growth which I hypothesize are most important in determining stand dynamics.

Fulton and Harcombe derived mortality functions from growth and mortality measured at 3-yr intervals on adult trees and a subsample of saplings. They include many of the species in the current study; where they did not provide parameters for a species in the current study, I substituted values from similar species (Table 3.1). Fulton and Harcombe's equation is a logistic function of a tree's height and height increment growth relative to its asymptotic height H_{max}:

$$m = \frac{1}{1 + \exp\left(-\left[M_a + \left(\frac{M_b H + M_c \Delta H}{H_{\max}}\right)\right]\right)} \tag{3.6}$$

where ΔH is the change in height from the previous time step, M_a sets the mortality probability at zero height and growth, M_b specifies the effect of tree height (H) and M_c specifies the effect of growth. Tree height is calculated allometrically from r based on relationships from Fulton (1999):

$$H = 1.4 + (H_{\max} - 1.4)\left[1 - \exp\left(\frac{-q}{10} \cdot 2r\right)\right] \tag{3.7}$$

where H is in m, 1.4 is the height at which the r is measured, and q is an allometry with units cm^{-1} (converted to mm by dividing by 10 mm/cm).

Eq. 3.6 flattens out at extremely low growth rates (as expected from a logistic function). Especially for small seedlings, I reasoned that a more severe mortality function was necessary at low growth rates, because of the potentially large number of seedlings produced. Hence, I used the negative exponential function reported by Pacala et al. (1996), which does not flatten out at low growth rates. I used the average value of mortality parameters reported for species that were most similar to the species in the current study. Although using one average value fails to account for species differences in mortality rates, I used the average because reported parameter values for relevant species were very similar to each other. Pacala et al. (1996) developed their equation from mortality probabilities of saplings (trees > 25 cm tall and < 10 cm dbh) over a 2.5-yr period, and is a function of a tree's radial growth increment:

$$m = M_1 \exp(-M_2 g) \tag{3.8}$$

where m is the mortality probability, g is radial growth in cm, M_2 is the decay of the function (cm^{-1}), and M_1 is the mortality probability when $g = 0$.

Pacala et al. (1996) recognized that their mortality functions did not produce sufficient self thinning to accurately model early stages of stand growth . Hence, mortality of seedlings ≤ 2 yr old is subject to an additional growth-independent mortality, based on survival probability estimates from studies of seedling survival (Table 3.1; trees > 2 yr old received a mortality probability of zero for this factor). Where estimates for a species could not be found, estimates from a similar species were substituted. Additionally, all trees are exposed to a growth-independent, constant mortality probability of 0.01 yr^{-1} to account for background disturbance (following Pacala et al. 1996). Thus, the algorithm calculates each of the two growth-dependent probabilities, and chooses the highest among these and the constant growth-independent probabilities as the mortality probability for the individual:

$$m = \max(m_1, m_2, 1 - s, 0.01) \tag{3.9}$$

where m_1 and m_2 are the mortality probabilities from Eqs. 6 and 8, respectively, adjusted to annual probabilities, and s is the seedling survival rate for that species (Table 3.1).

Model landscape, the nominal model, and sensitivity to parameters

Model landscape.—The purpose of these analyses was to evaluate model behavior under the nominal (best estimate) conditions to validate model predictions with data from a range of forests and reforestation sites; and to assess the theoretical impacts of parameters, initial conditions, and assumptions to the model system. Model validation under specific field conditions and model experiments with various manipulations at different times are the subjects of Chapters 4 and 5. For the current chapter, I created a hypothetical landscape that would provide the greatest insight with few model runs. The hypothetical model landscape was a 350×350-m region with a 50×50-m forest in the center and four reforestation sites located in 50×150-m strips emanating in each cardinal direction from the forest (Fig. 3.2). The rest of the landscape was considered barren, and no trees were allowed to establish in those areas (as if they were active agricultural fields).

The nominal model.—I limited the nominal set of simulations primarily to the first 200 yr of reforestation because I was primarily interested in colonization processes and the effects of initial conditions on forest dynamics. For the purposes of analysis of model results, I define colonization as the processes of dispersal and establishment (including germination and seedling survival for the first 2 yr) of trees that are descended from trees located in a naturally regenerated forest, excluding those individuals initially planted. I performed 20 200-yr runs of the model using the nominal parameter values of Table 3.1. For three of these runs, I continued the simulations for an additional 300 yr (for a total of 500 yr) to assess how initial conditions might affect longer-term dynamics; much longer runs (e.g., 2000 yr in Pacala et al. 1996) are unrealistic situations for the system investigated, which experiences major landform changes relatively frequently due to alluvial action (Hodges 1994). The same random number seed was used for each simulation because the enormous number of stochastic processes operating on differing starting conditions would overwhelm any effect of differing the random number seed. Differing starting conditions consisted of different initial populations of trees (see above), with each initial population drawn randomly from sample data. For the source forest, trees were selected at random from a list of trees from 108 0.04-ha plots in naturally regenerated, second-growth bottomland hardwood forest at Yazoo NWR. Reforestation sites contained a random arrangement of 2-yr-old Nuttall oak seedlings at a density consistent with real reforestation sites (1 tree/15 m^2, or 667 seedlings/ha).

Sensitivity analysis.—I focused sensitivity analysis on parameters dealing with dispersal and establishment, because I was primarily interested in assessing whether colonization of trees in reforestation sites was dispersal or establishment limited. The model's sensitivity to these parameters gives an indication as to the relative importance of these processes in the model system. Dynamic model behavior was assessed for elevated (×1.5) and decremented (×0.667) values, for all species simultaneously, of each of the following parameters: germination probability, seedling survival, and seed fall velocity. For the proportion of non-wind-dispersed seeds dispersed by the fat-tailed dispersal kernel (p), I assessed model behaviour for $p = 0.95$ and $p = 1.00$. See Table 3.1 for nominal values). Each replicate was initialized with one of three initial tree populations chosen from those used for the nominal runs, and simulated for 100 yr.

Because Nuttall oak is one of the fastest growing trees in the study area (see Table 3.1), I also wished to investigate whether suppression of colonization by planted trees was less severe if reforestation site were planted with other species of oaks in mixed culture. I ran three replicates using the nominal parameter values, but with reforestation sites in the simulated landscape being initialized with equal proportions of Nuttall oak, willow oak, and water oak at the same density as the Nuttall oak-only situation of the nominal runs (willow oak and water oak are also commonly planted in reforestation sites).

To assess the degree to which planted oaks within reforestation sites inhibited colonization or subsequent recruitment by other species, I ran three simulations using the nominal parameter values, but with reforestation sites in the simulated landscape not being initialized with Nuttall oak or any other trees. Additionally, I ran the same three simulations with Nuttall oak plantings at half the nominal density (i.e., 333 seedlings/ha). I plotted planting density (0, 333, or 667 seedlings/ha) against proportion of canopy trees (those ≥ 200 mm dbh) that were Nuttall oak at year 100. If colonization were more important than competition from planted Nuttall oaks, one would expect proportion in the canopy to be proportional to planting density (i.e., a straight-line relationship). If planted trees suppress colonization, then a convex relationship would be expected (i.e., reducing planting density would not have much effect on proportional species composition). A convex curve would also be produced if dispersal were limiting colonization, but the difference between the two conclusions can be assessed by seeing if colonization rates affect the eventual density in the overstory. If colonizing trees actually were better competitors than the planted trees, then a concave relationship would result (i.e., reducing planting density has a disproportionate effect on reducing proportion of Nuttall oak in the overstory).

For each of the three replicates, a different initial population of trees was used, though the initial population of trees in the source forest (at center) was identical for a given replicate (i.e., the source forest was the same for replicate 1 of nominal, nonplanted, half-density-planted, and mixed planted runs). Each scenario was simulated for 200 yr.

Assessing spatial and temporal dynamics produced by YAFSIM

Because I was explicitly interested in investigating processes that lead to spatially variable tree colonization, it was necessary to design a system to produce model output at locations at various distances and directions from the source population of trees. Therefore, I generated output for 0.04-ha (11.28-m radius) plots located at the center of the source forest, and with plot centers at 12.5, 37.5, 62.5, 87.5, 112.5, and 137.5 m from the edge of the forest into reforestation sites, in each of the four cardinal directions from the source forest (indicated by circles on Fig. 3.2).

Model validation and study site

I compared model prediction to data on real bottomland hardwood forests and reforestation sites in the MAV. The main study area was Yazoo National Wildlife Refuge (NWR) in west-central Mississippi (33°10'N, 90°51'W, elevation 35 m) (Fig. 3.1). Because the long growing season and fertile soils make the region well suited for crop production, Yazoo NWR and most other public lands in the region exist as forested islands within an agricultural landscape. Most of the following study site information comes from the Yazoo NWR Reforestation Plan (unpublished report on file at Yazoo NWR). Yazoo NWR was established in 1936 under the authority of the Migratory Bird Treaty Act and the Migratory Bird Stamp Act, to provide winter habitat for migratory waterfowl; this remains its primary purpose. The predominant geomorphic feature of Yazoo NWR is Swan Lake, a ca. 800-year-old oxbow of the Mississippi River, and much of the topography consists of ridge and swale formations from the Mississippi River and other, minor streams' meanderings. Yazoo NWR's 5,200 ha consist of a mosaic of semi-permanently to seasonally flooded cypress swamp, shrub swamp, green-tree reservoirs, and bottomland hardwood forests (1,895 ha); bottomland hardwood forests that are not normally flooded (364 ha); bottomland hardwood reforestation sites (435 ha); share-cropped agricultural fields (1,511 ha); and sloughs, bayous, and small lakes with open water (591 ha).

Reforestation of bottomland hardwood forest on some of Yazoo NWR's former agricultural croplands began in 1968 with the planting of two ca. 10-ha plots to cherrybark oak (*Quercus pagoda* Raf.) and Nuttall oak (*Q. nuttallii* Palmer). In 1973, two other plantings were made, one ca. 15-ha plot of cherrybark and Nuttall oak, and one 4-ha plot of swamp-chestnut oak (*Q. michauxii* Nutt.; Yazoo NWR Reforestation Plan). To my knowledge, these are the oldest oak plantations in existence that were established for bottomland hardwood reforestation. Although conversion of forest to cropland has ceased on the refuge, agricultural crop production continues on existing fields. Reforestation efforts escalated in 1980, and several hundred hectares have subsequently been planted annually for reforestation. A primary goal of bottomland hardwood reforestation is to restore a diverse forest system similar in species composition and structure as that found in naturally regenerated, second growth bottomland hardwood forests in the region, while also increasing hard mast-producing species (especially oaks) to provide additional food for wildlife (especially migratory waterfowl, Yazoo NWR Reforestation Plan). Current plantings tend to be near (< 300 m) or adjacent to established bottomland hardwood forest. Species most commonly planted are red oaks (either as seedlings or acorns), including cherrybark oak, Nuttall oak, water oak (*Q. nigra* L.), and willow oak (*Q. phellos* L.). Several tree species occasionally volunteer, including green ash (*Fraxinus pennsylvanica* Marsh.), sweetgum (*Liquidambar styraciflua* L.), common persimmon (*Diospyros virginicus* L.), American elm (*Ulmus americana* L.), cedar elm (*U. crassifolia* Nutt.) and sugarberry (*Celtis laevigata* Willd.).

The restoration process at these sites has focused primarily on ceasing agricultural crop production with subsequent reforestation. All of the reforestation sites in the current study were established with seedlings of the species listed above. Seedlings were planted in rows 4 to 5 m apart, with 2- to 3-m spacing within the row (the Reforestation Plan calls for 5-m spacing between rows and 3- to 5-m spacing within rows, but personal observations indicate spacing is usually closer). To date, other manipulation of these sites, such as restoration of historic flooding regimes, has been impractical due to constraints of surrounding land ownership and management. Furthermore, no supplemental planting of trees or shrubs has been attempted as of September 2002. The majority of other reforestation sites in the MAV were established and subsequently managed similarly to those of Yazoo NWR, although limited attempts have been made to increase species diversity of plantings (usually including green ash and baldcypress, *Taxodium distichum* (L.) L. C. Rich., on wetter sites).

I compared model predictions to vegetation observed in real restoration sites at Yazoo NWR, based on data collected in 1995 and 1996. I measured dbh of all trees with dbh > 25 mm and counted all other trees > 1 m tall in 0.04-ha square plots in restoration sites of various ages. I located 94 plots in restoration sites 3- to 5-yr-old, 91 plots in restoration sites 11- to 13-yr-old, and 65 plots in restoration sites 22- to 28-yr-old. Additionally, I located 108 plots in nearby naturally regenerated, second growth bottomland hardwood forest. I used data from naturally regenerated forest plots to provide data for initializing the source forests of the simulation runs. Data from restoration-site plots were not used for model formulation or initialization, and thus serve as an independent validation data set.

RESULTS

Baseline dynamics

Forest dynamics —I first describe dynamics within the forest only (Fig. 3.3, column "Forest"; NB: Fig. 3.4 and Fig. 3.7–3.8 show slightly different dynamics in the forest because they represent a subset of modeled initial populations, each with their own stochastic history). Mean basal area for the source forests at initialization was ca. 22 m^2/ha. Mean basal area increased to about 31 m^2/ha at year 100 (Fig. 3.3A); increases in basal area were associated with recruitment of trees into the canopy stratum (i.e., trees $\geq$ 200-mm dbh; Fig. 3.3B). Basal area started to decline after year 100, and reached a low at year 200 (Fig. 3.3A, 3.4A), where it climbed again to 32.5 m^2/ha in about year 480 before an abrupt decrease to 18 m^2/ha at year 500 (Fig. 3.4A). These changes in basal area reflect the effects of model process on forest input data, with its randomized species composition and individual tree locations, and subsequent recruitment and growth processes. The initial rise in basal area was associated with recruitment of midstory (Fig. 3.3C, 100–200-mm dbh) trees into the overstory (> 200-mm dbh, Fig. 3.3B), until the overstory was nearly 100% occupied and few trees remained in the midstory to recruit. At that point (around year 100), the dominant process became density-dependent and -independent mortality, which can be seen in the decline of overstory tree density between years 50 and 200 (Fig. 3.3B). Basal area declined less dramatically than overstory density, because resulting canopy gaps stimulated growth of remaining trees (compare Fig. 3.3A–B). Although as a group, animal-dispersed species dominated the overstory and basal area throughout the 500 yr of simulation, American elm (wind-dispersed) was the single most dominant species for the first two centuries of simulation. With continued mortality and the canopy opening up (Fig. 3.4B), water oak (animal-dispersed) began to overtake American elm as the dominant canopy tree, both in terms of basal area and density in the overstory (though species identities are not shown in Fig. 3.4A, the shift in dominance coincides with the observed minimum of basal area at yr 190). This change in dominance occurred because American elm is classified as shade tolerant, and therefore does not have the ability to respond as rapidly to canopy gaps as water oak, which is intolerant (Table 3.1). The number of species represented in the canopy and by basal area declined from 15 to 3 species in 500 yr of simulation (data not shown). This decline occurred because the total number of trees in the overstory decreased from a median high of ca. 210 stems/ha to a median low of ca. 35 stems/ha (Fig. 3.3B), which was fairly stable from year 200 to 500 (Fig. 3.4B). As the number of individuals sampled decreases, so does the probability of including more species. It is possible that more species were still represented in the forest surrounding the sampled plot. However, it is also probable that the community was on a random walk towards monodominance, an inevitability for small, isolated communities; if the modeled forest were larger or connected via dispersal to other forest patches, the random walk to monodominance would take longer, and perhaps not be apparent in the timeframe analyzed (Hubbell 2001).

Reforestation dynamics.— Reforestation dynamics are shown as the dynamics of sampling plots located 12.5 m to 137.5 m from the forest (Fig. 3.3, four rightmost columns show results to the north of forest). I will discuss dynamics of tree communities in these plots in order from the smallest size class to the largest, followed by a discussion of dynamics of basal area. References between size classes are made as they are relevant.

Many species with wind-dispersed seeds, and several with animal-dispersed seeds, successfully colonized (i.e., individuals that dispersed and established) the simulated reforestation plots. The smaller half of the small tree stratum (i.e., stems < 50 mm dbh, Fig. 3.3E) shows that wind-dispersed species were the most abundant colonizers in all distances from forest (both to the north, as shown in Fig. 3.3, and in other directions). Of these, American elm was the most abundant because it both produces many seeds per unit basal area (Table 3.1) and was well represented in the source forest. Initial colonization of American elm during the first 20 yr of simulation, when all American elm seeds originated in the source forest and not from previous colonizers (because no colonizers were of reproductive size, Fig. 3.3B–C), was 10 times greater in plots 12.5 m from forest compared to plots 137.5 m from forest (see also Fig. 3.5). Other, less abundant, wind-dispersed colonizers followed similar patterns to American elm, and included green ash, sweetgum, cedar elm, and boxelder (Fig. 3.5). This distance effect was actually a tapering off pattern with distance, similar to the tail of a dispersal kernel (e.g., Willson 1993, Clark et al. 1998a). Colonization to the west and east, away from prevailing winds, was less abundant than to the north and south, especially in plots far from forest (e.g., 87.5 and 137.5 m from forest; Fig. 3.5).

Animal-dispersed species were very uncommon colonizers of simulated reforestation sites, and included water hickory, sugarberry, willow oak, and cherrybark oak, but only in plots adjacent to forest (12.5 m, density is so low that they are not apparent in Fig. 3.3). At ca. year 10, the first planted Nuttall oaks became reproductively mature, causing a large influx of Nuttall oak seedlings into the < 50-mm dbh stratum (Fig. 3.3E). Concomitantly, seedlings of other species continued to colonize, but few died or recruited into larger strata, resulting in high stem densities in this stratum. Such high stem densities are unrealistic and probably the result of the failure of my basal-area-based competition function to adequately control mortality, because such stems have almost no basal area.

Despite high densities in < 50-mm-dbh stems (Fig. 3.3E), few individuals were able to recruit into 50–100-mm-dbh stems (compare Fig. 3.3D–E). Planted Nuttall oak began to recruit into this stratum beginning at about year five, followed about 5 yr later by wind-dispersed colonizers in plots nearer the forest (Fig. 3.3D; American elm colonized first, followed by small numbers of sweetgum, green ash, and cedar elm). No other species recruited beyond the initial colonizing size class (< 50 mm; Fig. 3.3E). American elm did not start recruiting into the 50–100-mm stratum until after year 20 in plots farthest from forest to the east, south, and west because of lower colonization there. Beginning in ca. year 10, density of planted oaks dropped because of recruitment of the initial planted cohort into larger strata ("Planted" line declines in Fig. 3.3D while concomitantly increasing in Fig. 3.3C). This recruitment-related decline in 50–100-mm-dbh planted-oak density continued through ca. year 50 in plots farther from forest (87.5 and 137.5 m), but took until ca. year 100 in plots nearer the forest because growth of oaks was slowed by competition from other colonizing individuals. After this decline, oak densities began to build up again because additional seedlings that recruited into the stratum were not able to recruit into larger strata, which had become fully stocked (Fig. 3.3B–C, year 50–80). Wind-dispersed colonizers (mostly American elm) peaked in density at about year 50, but thereafter gradually started to decline (Fig. 3.3D). In contrast to planted oaks, there was very little recruitment of colonizers out of the 50–100-mm stratum (Fig. 3.3C–D), so densities accumulated until upper canopy strata became fully stocked (Fig. 3.3A–B), at which point densities began to decline because of increased mortality (Fig. 3.3D). This decline in colonizer density continued until after the peak in total basal area was reached (Fig. 3.3A, ca. year 100), when colonizer density began to increase because of the opening of the canopy (Fig. 3.3B and 3.3D, around year 150). This second increase in colonizer density only occurred for American elm. Because American elm was almost exclusively the only species to successfully recruit into reproductive sizes, the second wave of American elm colonists was probably from reproduction by American elm trees that had earlier colonized in the vicinity.

The difference in stem densities of seedlings and small saplings between near and far plots (Fig. 3.3D–E and Fig. 3.5) supports the hypothesis that colonization is dispersal limited at scales relevant to real reforestation sites. Specifically, the direction and distance effect evident for wind-dispersed species supports a mechanistic explanation of the effect of wind direction and velocity on dispersal distance and subsequent colonization.

The 100–200-mm-dbh stratum was primarily a transition stage, where trees did not remain long—generally 5–10 yr—before dying or recruiting into the upper canopy (the ≥ 200-mm stratum). Some wind-dispersed colonizers (American elm, cedar elm, sweetgum, and green ash) were able to recruit into this stratum in addition to the planted (Nuttall) oaks. Densities in this stratum were somewhat lower in plots adjacent to forest (Fig. 3.3C, 12.5-m plot) because individuals' growth rates were hampered by competition from higher rates of colonization and also from competition from canopy trees in the forest. Occurrence of individuals in this stratum tapered off after year 100 because opportunities to recruit into the canopy became increasing rare and dependant on death of a canopy tree. After year 200, when the canopy began to break up (Fig. 3.4B), individual trees recruited rapidly through this stratum whenever a canopy tree died, creating short-term but frequent pulses of occurrence (Fig. 3.4C).

Recruitment of trees (mainly Nuttall oak) continued to be slower in the canopy stratum (≥ 200-mm dbh) in plots adjacent to the forest compared to those ≥ 37.5 m from forest (Fig. 3.3B). Density peaked between years 40–60 at median values of 250–350 stems/ha, with larger densities being farthest from forest (Fig. 3.4B, 137.5-m plot). The high density in far plots resulted from these plots being located on the edge of the landscape, and thus having fewer trees to compete with, as would be the case for trees on the edge of an open field (a frequent situation in the MAV and other agricultural landscapes). Peak densities correspond almost exactly to the density of Nuttall oaks originally planted to initiate the simulations, with minimal density-dependent mortality. From the peak, canopy tree density declined steadily through year 200 to ca. 80 stems/ha (still somewhat higher in the farthest plots, Fig. 3.4B). This pattern follows the constant 1% annual density-independent mortality offset by occasional recruitment from below, indicating that density-dependent mortality was relatively unimportant (a result consistent with poor self-thinning in oak plantations, see Meadows and Goelz 1999, 2001). Other than Nuttall oak, American elm was the only major species present in the canopy, although at densities generally < 10% of Nuttall oak densities (Fig. 3.3B and 3.4B). Occasionally, cedar elm, sweetgum, or green ash was represented, but in very low density (data not shown).

Finally, by examining basal area of the plots, we can get an idea of what happened to the surviving trees as other trees in the canopy were dying. Although density of stems in the canopy stratum declined ca. 75% from year 60 to year 200 (Fig. 3.3B), basal area showed much more sporadic behavior (Fig. 3.3A). Declines in basal area associated with death of canopy trees were offset initially by continued growth of surviving trees—mortality in the canopy meant more opportunity for growth of surviving trees, causing basal area to rise again after the low experienced ca. year 200 (Fig. 3.4A, plots 37.5–137.5 m from forest). Wide fluctuations in basal area then began to dominate basal-area behavior (Fig. 3.4A). As remaining canopy trees grew bigger with each death of a neighbor, their own deaths produced ever-greater losses of basal area. Such gaps allowed recruitment from the subcanopy when it was no longer possible for surrounding canopy trees to fill the gap themselves (notice recruitment pulses in Fig. 3.4C followed within 5 yr by a decline in Fig. 3.4C corresponding to an increase in Fig. 3.4B). Which species, Nuttall oak or American elm, replaced dead canopy trees appears random (Fig. 3.4B) and probably depends on whichever species was in the most favorable position relative to the canopy gap. Nevertheless, it appears that reforestation sites are also on a random walk to monodominance by Nuttall oak, as expected by their overwhelming initial advantage.

Model validation

Forest dynamics.—The initial populations of trees in source forests had median stem densities that were indistinguishable from the samples used to generate them, although the range in basal area in simulation plots was biased slightly low compared to my sample data (Fig. 3.6A, column "Forest"). Simulated plots had lower basal area than sample plots because sample data contained some minor species (mostly shrubs) that were not modeled by YAFSIM. Nevertheless, by year 30, the distribution of simulated basal areas became indistinguishable from the distribution of sample basal areas (Fig. 3.6A).

Whereas the data for source forest plots do not constitute an independent validation data set, such convergence of simulated and sample data does verify that YAFSIM's short-term dynamics are reasonable. Furthermore, the baseline dynamics described above are similar with respect to basal area and stem dynamics to those described for development of old-growth in forests in general (Oliver 1981) and for bottomland hardwoods specifically (Meadows and Nowacki 1996, Kennedy and Nowacki 1997). Reported basal areas for old-growth bottomland hardwoods are 10–50 m^2/ha, which agrees well with model predictions (Fig. 3.4A). Stem densities predicted by YAFSIM in old growth are also within the reported range (79–506 stems/ha of trees ≥ 100 mm dbh, Meadows and Nowacki 1996, Kennedy and Nowacki 1997, compare with Fig. 3.4B–C;). It is important to note that not much is known about old-growth conditions in bottomland hardwood forests, and the figures presented here come from only 4–5 stands with overstory trees 58–150 yr old (Meadows and Nowacki 1996, Kennedy and Nowacki 1997). Due to frequent natural and anthropogenic, large-scale-disturbances, it is possible that old-growth conditions never truly develop in real bottomland hardwood forests (Meadows 1994). Such disturbances were not included in the current analysis; therefore, YAFSIM eventually develops a multi-aged structure. An even-age structure is considered typical of bottomland hardwood forests (Hodges 1994, Meadows 1994).

Reforestation dynamics.—Because I used none of the sample data from restoration sites in model formulation or initialization, these data do constitute an independent validation data set. Model agreement with sample data for all ages of restoration sites was excellent (Fig. 3.6A, four panels on right). I do not have sample data from real restoration sites > 28 yr post-establishment, as at the time the data were collected no sites > 28 yr old were in existence. Sample data showed more variation in basal area than YAFSIM predictions for the 12-year-old age class of restoration sites, although medians from the two datasets were very close. Real restoration sites are composed of more species than just Nuttall oak (see study site description), so would have different growth rates and thus exhibit greater variation in basal area. There are also site differences in real restoration sites not included in these analyses. For restoration sites in the 26-year-old age class, distributions of sample data and model predictions were quite similar for all plots > 12.5 m from forest (Fig. 3.6A). YAFSIM predicts considerably lower basal area in plots adjacent to the forest (plot center 12.5 m from edge). Validation data are pooled from a variety of distances, though there does appear to be a narrow region of low growth and colonization adjacent to the forest edge (Allen et al. 1998 and personal observations).

YAFSIM predicted that American elm was the predominant colonizer of reforestation sites. YAFSIM also predicts that cedar elm, sweetgum, green ash, and boxelder colonize sites near forest well, with some additional colonization by sugarberry, willow oak, cherrybark oak, and water hickory. These predictions are supported by my data for American elm, cedar elm, and sugarberry, with stem densities in each stratum on the order of those predicted by YAFSIM, except for < 50-mm dbh stems, for which I have incomplete data. However, I rarely observed oak seedlings or saplings outside the planted rows of oaks in real restoration sites; this fact indicates that in reality oak colonization is not as prevalent as predicted by the model. Although having high establishment rates even under closed-canopy forests, oaks generally die within 3 yr if not released from competition (Putnam et al. 1960). I assumed that growth-dependent mortality would accomplish this in YAFSIM, but because the 3-yr die-off is more related to depletion of stored reserves in the acorn than inherent growth ability, inclusion of this effect for oaks (and water hickory) may be able to help restrict oak seedlings to realistic densities. Another factor that could limit establishment of seedlings in real reforestation sites is the deep and recalcitrant litter layer created under oak trees. The effect of litter on germination and establishment is not currently included in YAFSIM, but perhaps could be included in future versions. Importantly, regardless of seedling density, model predictions agree with sample data that colonizing trees have very low recruitment into the canopy, and tend to become relegated to smaller size classes.

Alternative establishment scenarios: planted trees inhibit colonization

Diversifying plantations by planting willow oak and water oak in addition to Nuttall oak increased recruitment of wind-dispersed colonizers in restoration sites (Fig. 3.7E), but only for

American elm. Such mixed-species plantings resulted in marginally lower total basal areas through year 30 (Fig. 3.6B and compare Fig. 3.3A and Fig. 3.7A), because water oak and willow oak have lower growth rates than Nuttall oak, bringing down total growth. Ranking of species basal areas of planted oaks followed ranking of their respective growth rates (B values in Table 3.1). Because of lower basal areas of planted oaks, there was more opportunity for recruitment of colonizing species into the canopy compared to the baseline model runs with only Nuttall oak planted (compare Fig. 3.3B and Fig. 3.7B). American elm and cedar elm (to a more limited extent) were the only species able to take advantage of increased recruitment opportunity, because of their relatively high growth rate and numerical advantage as seedlings. Conversely, other colonizing species did not recruit into the canopy because of slower growth rates and lower colonization rates.

In contrast to diversifying plantations, initializing restoration sites without a plantation provided much more opportunity for development of diverse tree assemblages by allowing more opportunity for colonizers to recruit into the subcanopy and canopy (Fig. 3.8B–C). Because of its greater dispersal ability, American elm tended to be the predominate colonizer in all plots, but especially in farther plots. Other wind-dispersed species colonized well, including sweetgum, green ash, cedar elm, and boxelder. The only animal-dispersed species to colonize were Nuttall oak and sugarberry, and then only to the east 12.5-m plot. Recruitment of stems into the 50–100-mm stratum was twice as abundant as in the nominal model runs (Fig. 3.8D), because there lacked a pre-established, dominating canopy of planted oaks. Growth in the 100–200-mm stratum was more transient than in the baseline model runs (compare Fig. 3.3C and Fig. 3.8C) because there lacked a single cohort of uniform-sized trees growing together. After the initial cohort of colonizers, recruitment into the subcanopy and canopy was always associated with the death of a canopy tree; presence of individuals in the subcanopy (100–200-mm stratum) was brief (ca. 5 yr) because trees quickly recruited into the canopy. Such gap-phase dynamics, where the subcanopy primarily acts as a brief transition stage following release of suppressed individuals (Oliver 1981), were more prevalent in non-planted model runs compared to nominal runs (compare Fig. 3.3C and Fig. 3.8C). Gap-phase dynamics took longer to emerge in the baseline runs because planted oaks formed a single cohort that effectively suppressed smaller trees. Growth into the canopy in the non-planted scenario was also more gradual compared to the baseline model runs, and density and basal area did not peak as high because trees were not overstocked (compare Fig. 3.3A–B and Fig. 3.8A–B). Additionally, because of lower growth rates of colonizing trees compared to trees planted in nominal model runs, trees were not as able to rapidly take advantage of canopy gaps created by death of overstory trees, resulting in less dramatic fluctuations in basal area and lower basal area and density in the canopy (Fig. 3.8A–B). The first and most abundant species colonizing a plot were those that came to dominate the community at the plot, in terms of both basal area and density of canopy trees. For nominal runs this was Nuttall oak; for non-planted runs, it was American elm. Thus, the rank order of colonization, not the absolute abundance of colonizing stems, determined community composition for the first 200 yr.

Although initializing restoration sites without planting any species promoted recruitment of colonizers, it caused a delay in accrual of basal area compared to the nominal runs (Fig. 3.6C), with a more pronounced delay in plots adjacent to and farthest from forest compared to plots of intermediate distance (Fig. 3.9). The effect occurs in all directions from forest because although adjacent plots receive more colonization initially, large trees in the forest (as in nominal runs) suppressed seedlings there. Conversely, plots of intermediate distances still had high seed arrival but were not impacted by large forest trees and grew better. Finally, the farthest plots were dispersal limited, so there were insufficient colonizing trees to stock the plots fully, especially in directions away from prevailing winds (Fig. 3.5, Fig. 3.9 east and west). The colonization effect was temporary, as far non-planted sites away from prevailing winds had similar basal areas and overstory density to nearer sites by year 100; suppression of trees near the source forest, however, was more permanent (Fig. 3.8A–B). These results demonstrate that both dispersal and competition limit forest growth.

Plotting Nuttall oak planting density against proportion of Nuttall oak in the canopy provided further evidence for the importance of competition from planted trees in limiting tree colonization. The relationship between density of Nuttall oak seedlings planted and the proportion of canopy trees that were Nuttall oak at year 100 was convex, regardless of distance or direction from the source forest, though convexity was more pronounced for far plots away from the prevailing winds (i.e., west and east, Fig. 3.10). Reducing planting density by half had almost no effect on the proportion of Nuttall oak in the overstory, even when colonization was abundant (compare Figures 3.5 and 3.10). The fact that the relationship between planting density and proportion in the canopy was convex regardless of arrival of colonizers indicates that competition from planted Nuttall oak was more important than colonization in determining relative species abundance.

Sensitivity analysis: insensitivity reveals bottleneck

Seed dispersal.—Increasing seed fall velocity by a factor of 1.5 resulted in much lower colonization of American elm and almost no colonization by other species to plots farthest (137.5 m) from the forest. Conversely, closer plots had higher colonization of all wind-dispersed species because a higher proportion of seeds landed in them. Higher colonization by American elm in near plots resulted in slightly higher American elm representation in the canopy in near plots, but fewer to none in far plots. Decreasing seed fall velocity by a factor of 0.667 had the opposite effect: there was much greater colonization to far plots by many wind-dispersed species, including cedar elm, sweetgum, green ash, boxelder, and American elm, whereas at least initially, there was much lower colonization by these species in near plots. The shift in colonization caused by decreasing seed fall velocity resulted in more recruitment of American elm in far plots, and no American elm recruitment in some near plots.

In contrast to wind-dispersed seeds, changing the proportion (p) of seeds of animal-dispersed species that dispersed via the fat-tailed dispersal kernel had virtually no effect on model outcome. Eliminating the fat-tailed kernel by dispersing 100% of seeds via Gaussian dispersal resulted in some colonization of water oak, which was absent in baseline model runs, and increased colonization of willow oak to the 12.5-m east plot, resulting in somewhat higher density in the < 50-mm stratum. However, these did not recruit into larger strata. Increasing proportion of seeds in the fat-tailed kernel had no apparent effect, probably because any changes in density were too low to detect or make a difference in overall dynamics. Proportion of seeds in the fat-tailed dispersal kernel did not affect model results because it did not affect the rank order of seedling abundance, because of low fecundities of animal-dispersed species compared to wind-dispersed species (see β values in Table 3.1).

Germination.—Decreasing germination probability by a factor of 0.667 reduced the total density of seedlings in the < 50-mm stratum: instead of leveling off at ca. 60 stems/m^2, it leveled off at about 45 stems/m^2. There was no effect on recruitment to higher strata. Increasing germination probability by a factor of 1.5 resulted in a higher leveling off (80 stems/m^2), and higher recruitment of colonizers to higher strata in some far plots. There was lower recruitment of planted and colonizing trees in near plots, though, because seedlings were overcrowded and stunted.

Seedling survival.—Decreasing seedling survival by a factor of 0.667 resulted in significantly lower leveling-off densities in the < 50-mm stratum (30–40 versus 60 stems/m^2). This reduction carried over into reduced density in the 50–100-mm stratum that was maintained for the first 50 yr of the simulation. Reducing seedling survival resulted in better overall recruitment into 100–200-mm and ≥ 200-mm strata especially for American elm, but also for planted Nuttall oak, because of reduced crowding in the lower strata producing increased growth rates. Increasing seedling survival by a factor of 1.5 had no great effect, however, except for marginally higher densities in the < 50-mm stratum, because density-dependent mortality compensated for reduced density-independent mortality. Another effect of increasing seedling survival was a slight reduction of American elm recruitment into the canopy, caused by overcrowding and reduced growth in the smaller strata.

Results of sensitivity analyses are summarized in Table 3.3. None of the parameters adjusted had a large effect on basal area or densities in subcanopy or canopy trees. As discussed previously, rank order of density, not absolute density, of seedlings affected what species became dominant or codominant. Changes in parameter values were insufficient to change the rank order of colonization, because, having been planted, Nuttall oak was always the most abundant species in the small-tree stratum. Thus, the establishment of a single-species plantation of Nuttall oak created a bottleneck where other species were unable to recruit, regardless of their dispersal or establishment abilities.

DISCUSSION

One theoretical question that also has implications for management is whether seed dispersal limits colonization of tree species in restoration sites. In my model system, there is no doubt that seed dispersal limits colonization, because plots far from the source forest had lower colonization rates than those of intermediate distance; no other mechanism in the model could create this pattern. However, plots adjacent to the source forest had lower recruitment than those of intermediate distance, and planted oaks inhibited recruitment in all plots. Implications are that reforestation sites located near source populations of trees may be restored more effectively if competition from established individuals can be alleviated, perhaps through thinning (see Chapter 5).

The result that species initiated at higher densities (e.g., in a plantation) inhibited colonization by other species is consistent with results from Pacala et al. (1996), who predicted that species composition of forests was heavily influenced for > 300 yr by the initial cohort of trees established during model initialization. In my model system, in oak plantations, planted oaks and American elm were virtually the only species able to take advantage of canopy gaps because of their prevalence in the understory. American elm was relegated to a secondary position, however, because of the oaks' greater growth rate and greater survival probability as seedlings. Other species with lower growth rates or fecundities were not able to occupy much of the canopy because American elm and Nuttall oak were ubiquitous. In the nonplanted model runs, where oaks were absent, American elm was able to occupy the majority of space in the canopy because of its greater dispersal ability, fecundity, and prevalence in the source forest. Species with higher basic growth rates (e.g., cherrybark, Nuttall, willow, and water oak, Table 3.1) were unable to colonize because of low fecundity and dispersal abilities and because they are shade intolerant and their growth was suppressed under competition from shade-tolerant species like American elm. In real forests, as in YAFSIM, American elm is seldom overtaken by other species once it becomes dominant in the canopy (Bey 1990).

Because American elm has a lower basic growth rate than most oaks (Table 3.1), my results agree in part with predictions from the competition-colonization tradeoff model (Tilman et al. 1997, Pacala and Rees 1998) where inferior competitors persist in communities by colonizing patches not yet reached by superior competitors. However, the competition-colonization tradeoff assumes that superior competitors exclude inferior competitors by reducing resources below levels tolerated by inferior competitors, either immediately (e.g., Tilman 1994, Tilman et al. 1997) or gradually (Pacala and Rees 1998). Gradual reduction of resources in Pacala and Rees (1998) was an implementation of the successional niche concept, where early-arriving inferior competitors have high growth rates in the relatively uncrowded conditions before superior competitors arrive and reduce resource levels, e.g., by overtopping inferior competitors. After superior competitors reduce resource levels, inferior competitors die out. However, in YAFSIM, both ability to reduce resources (via growth rate) and responses to resource levels (shade tolerance) differ among species. A simple ranking of species with respect to competitive ability is impossible because competitive ability depends on size, which depends on growth rate interacting with resource levels. Furthermore, according to the empirical estimates of basic growth rate (*B*) and dispersal parameters in YAFSIM, the best colonizers are shade-tolerant, not shade-intolerant, and thus do not have especially high growth rates in uncrowded conditions. There is no reason to assume that a species that produces small seeds should be shade-intolerant after those seeds become established as seedlings, just as there is no reason to assume that a species that produces large seeds should be shade-tolerant after its seed resources are used up. Thus, neither the competition-colonization tradeoff nor the successional niche operates in a straightforward way in YAFSIM, or in the bottomland hardwood forests it simulates (Hodges and Switzer 1979, Hodges 1994).

Pacala et al. (1996) invoked the competition-colonization tradeoff concept as the main theoretical basis for explaining dynamics in SORTIE. The competition-colonization tradeoff in SORTIE was assumed to operate via dispersal and shade production (resource reduction) so that better dispersers cast less shade and are thus inferior competitors (Pacala and Rees 1998). However, rankings of dispersal distance and shade produced by each species were only marginally significant and other correlations between dispersal and competitive ability were similarly bad or worse (Pacala et al. 1996). Therefore the generalization that better dispersers are worse competitors is tenuous.

Furthermore, there is ample evidence that the primary assumption upon which the competition-colonization tradeoff is based, namely that species can be ranked with respect to competitive ability (i.e., the resource competition hypothesis, Tilman 1982) is fundamentally flawed for trees because there is no basis to formulate such a ranking that holds throughout their life. According to Connell and Slatyer's (1977) inhibition model of succession, any early-arriving species can prevent other species from establishing for time scales relevant to most forest systems. Another alternative, also ignored by resource competition, is the widely known phenomenon where dominant species create environments more suitable for their own regeneration than for regeneration of other species (e.g., by rapid or slow nutrient cycling; Waring and Schlesinger 1985, Perry 1994). An example of such a positive feedback loop is northern hemlock–sugar maple dynamics in northern hardwood forests (Davis et al. 1994). Hemlock patches established 100–200 yr following range expansion into the area, and hemlock and sugar maple have remained continuously monodominant in their respective patches for > 3000 yr. There is no evidence for a soil- or dispersal-related cause for species segregation (Davis et al. 1994), so that the resource competition hypothesis would predict that one of the two species would eventually dominate all sites. The fact that this has not happened suggests that the competition-colonization tradeoff is not valid for describing vegetation dynamics in the hemlock–sugar maple system, and also may not be valid for other systems such as bottomland hardwood forests modeled by YAFSIM. In fact, in a review of trade-offs between dispersal and other plant traits, Thompson et al. (2002) found little evidence or theoretical justification for the competition-colonization tradeoff (or either of the other tradeoffs examined) that could be generalized beyond specific studies.

Predictions from resource competition models and YAFSIM notwithstanding, real bottomland hardwood forests are quite diverse and, at least historically, not particularly dominated by oaks or American elm, but rather by sugarberry, sweetgum, and green ash (Tingle et al. 2001). Maintenance of diversity in natural systems has been a topic of considerable interest for ecologists, both in general (Hutchinson 1961, Tilman et al. 1997) and in forests particularly (e.g., Hubbell 1979, Glitzenstein et al. 1986, Hunter 1999, Hubbell 2001). Large-scale disturbance has been determined to be important in maintaining species diversity in forests, with the timing and intensity of disturbance determining which species are favored (Oliver 1981, Glitzenstein et al. 1986). Large-scale disturbances relevant to bottomland hardwood forests in the MAV include logging, tornadoes, and prolonged flooding (with fire also important historically).

Even when not constituting a major disturbance, depth and duration of flooding has a large influence on species composition by altering growth, survival, and regeneration (Tharp 1978, Hodges and Switzer 1979, Phipps 1979). Variation in flooding within a stand is caused by microsite variation, which is created primarily by alluvial action (Putnam et al. 1960). Microsite also influences depth to water table, which affects growth rates of trees differently because of differing species' optima (Phipps 1979), although this effect is insufficient to substantially change the ranking of species growth rates and thus would not change species dominance. Rather, flooding affects species composition primarily by affecting establishment and survival of seedlings, with some species' seedlings more tolerant of flooding than others (Tharp 1978, Hodges and Switzer 1979, Phipps 1979). Thus, incorporating spatially heterogeneous flooding in YAFSIM would increase species diversity because it would change the ranking in small tree abundances at different sites, interacting with dispersal in the short term and preventing some species from ever establishing in the long term. Flooding tolerance of seedlings thus appears to be the most likely mechanism by which niche-assembly processes could modify dispersal assembly processes that currently dominate dynamics of YAFSIM. Invoking such a niche-assembly explanation for the failure of dispersal-assembly mechanisms to create diverse forests may at first smack of the kind of "facile" supposition of environmental heterogeneity criticized by Hubbell (2001: page 25). However, the difference here is that the proposed environmental heterogeneity is not only measurable, but its effect on plant survival has been well established and the mechanism is known (e.g., Streng et al. 1989). Incorporating spatially variable flooding in YAFSIM, however, would be a major modelling challenge, because its effects would be difficult to assess in combination with various other spatial processes.

Whatever species are favored by local flooding regimes, it is possible that they will remain dominant for very long time periods (Oliver 1981, Davis et al. 1994). It may take hundreds of years for other species to effectively recruit into the canopy once the canopy has been first occupied, which was most likely by the dominant initially colonizing species. Such recruitment apparently is largely a function of chance, with success a function of flood tolerance of seedlings (Tharp 1978, Phipps 1979) and their proportions in the understory (Hubbell 2001). Thus, the failure of YAFSIM to produce diverse stands at a given location may accurately reflect dynamics of uniform, nonflooded site (despite YAFSIM's prediction of relative homogeneity in community composition, tree density was heterogeneous, reflecting spatial effects on dispersal). Extant second-growth bottomland hardwood stands in the study area originated not from colonization of abandoned fields, but from regeneration of logged sites. Advance regeneration (seedlings and saplings present before the disturbance that survive the disturbance) is the most likely form of regeneration for most bottomland species discussed here (Burns and Hankala 1990), so dispersal would not be very important in determining composition of these sites. Therefore, if a diverse forest was present prior to logging, it is likely that a similarly diverse forest would develop after logging. Other forest simulation models for the MAV (Tharp 1978, Phipps 1979) more accurately describe such a situation, and in these models a diverse forest is perpetuated, though regeneration processes are greatly simplified, so diversity maintenance is virtually guaranteed.

YAFSIM's current lack of microsite variation has little bearing on predictions for development of oak plantations as restoration sites, however, because by establishing plantations with seedlings, site-specific establishment limitation is largely circumvented. YAFSIM predictions match my validation data (and results reported in Allen 1997, Allen et al. 1998) from real reforestation sites that show that management goals of restoring a diverse forest community (Stanturf et al. 2000) usually are not well met. Furthermore, YAFSIM predicts that the situation improves only marginally over time, as overstocked, planted oaks eventually decline in density and basal area to relatively stable levels after year 200. Planted trees continue to inhibit recruitment by other species, preventing their long-term persistence by stunting colonizers in non-reproductive sizes, with oak mortality rates insufficient for release and recruitment. Thus, while the predominant restoration practice has been effective in providing forest cover relatively quickly, the properties of selected species that promoted forest growth are also those that will prevent development of diversity unless some remedial action is undertaken. Such remedial action will likely involve large-scale removal of overstory trees before oaks become dominant in the understory and therefore have a greater chance of occupying canopy gaps than colonizing species (see Chapter 5).

In conclusion, the mechanisms and assumptions incorporated in YAFSIM are consistent with the observation that dispersal, growth rate, and inhibition by established individuals interact to affect species colonization and recruitment in forests developing on newly available sites. Specifically, dispersal and planting affect the initial ranking of species inhabiting a site, and this ranking determines community dominance for at least as long as most temperate forests have been in existence. Furthermore, I have demonstrated that inclusion of mechanistic algorithms for dispersal of seeds by wind is important to realistically forecast the spatial distribution of species colonization. Specifically, distance and directional effects on colonization by various species depended on wind distribution and source strength (number of seeds produced). The importance of differing colonization with distance and direction depended on whether the site was initialized with a plantation: planted oaks sequestered the canopy and prevented almost all colonization stems from recruiting. When oaks were not planted, the first and most abundant colonizers sequestered most of the canopy, but recruitment of other species was higher than in plantations.

Although YAFSIM failed to produce diverse forests, these findings are entirely consistent with Hubbell's (2001) unified neutral theory because only a few species were available to occupy the sites. Neutrality in the unified neutral theory is a simplifying assumption, not an assumed reality (as e.g., McGill 2003 seems to believe); hence different species do in fact have different characteristics, among them dispersal ability.

Inclusion of mechanistic algorithms for long-distance dispersal would be helpful to describe colonization at larger spatial scales, especially considering Nathan et al.'s (2002b) finding that, for wind-dispersed species, the usually assumed fat-tailed kernel erroneously places the mode of long-distance dispersal. I have shown that such rare long-distance dispersal events are not important for affecting tree colonization and forest development at sites relatively near (< 150 m from) source populations of trees because of the overwhelming influence of local dispersal (also, the mode for long-distance dispersal is far outside the distance range examined here). However, long-distance dispersal could be important in affecting species composition at sites very far from forest. If forests originated by rare, long-distance dispersal events, unique forest communities could develop and persist despite subsequent arrival of species with higher growth rates.

Along similar lines, I have assumed that colonization by animal-dispersed species is unaffected by vegetation type. It is unlikely that this assumption is true, because not only do animal dispersers have habitat preferences, so seeds are more likely to be move from and to certain vegetation types than others, but the caching behavior of some animal dispersers is likely to affect germination and seedling survival in non-random ways. Therefore, development and inclusion of mechanistic algorithms for dispersal and establishment of animal-dispersed tree species would allow more realistic predictions to be made for these species.

If YAFSIM predicts reforestation sites will never develop diverse tree communities, and in fact forests will continue to lose species, how then did the diversity of existing bottomland hardwood forest ever develop in the first place? Maintenance of diversity in large tracts of forest that start out diverse is not so much the issue (see Hubbell 2001 for elaboration on effect of community size on diversity maintenance). Rather, the results presented here suggest that there must have been some mechanism that ensured more diverse cohorts of seedlings were able to colonize the sites. Inclusion of environmental heterogeneity, where its effect on germination and establishment are known, would allow more realistic limits to be placed on species colonization and resulting communities. Hence, development of diverse forests could have reflected historic hydrologic heterogeneity that no longer exists. Nevertheless, inclusion of such niche-assembly constraints is likely to have only a small effect on community composition except in the most extreme environments. Given YAFSIM's relative insensitivity to alterations other than initial density (either via planting or colonization), it is likely that the composition of the source population of trees will have the greatest effect on community composition of newly available sites. For historical or environmental reasons, for example, many forests lack American elm; thus, other species that do occur in the forest, especially highly fecund ones, will likely dominate newly available sites in the vicinity.

YAFSIM and the ecological theory and empirical data on which it is based, however, all point to one conclusion of extreme ecological importance: concerted efforts need to be made to ensure a diverse tree community is established from the outset, because natural colonization is unreliable and the legacy of a low-diversity initial community will remain for a very long time. This effect has the potential to amplify with time, as low-diversity reforestation sites become the "seed source" for the next generation of sites in a shifting mosaic of ever-lower diversity. Therefore, new reforestation sites must always be established with a full complement of desired species from the outset, especially in sites that are > ca. 50 m from populations of desired species. Even in sites located close to such populations, surveys must be made within the first few years after site establishment to ascertain whether supplemental plantings need to be made, or if thinning needs to be carried out to release overtopped colonizers and reduce stagnation of planted species (see Chapter 5).

Table 3.1. Parameter values and properties of species used in YAFSIM (extended on next page).

Species	Common name	Dispersal mode	germination rate*	s*	H_{max}[§]	q[†]
Acer rubrum	Red maple	wind	0.0894	0.218	31	0.043
Acer negundo	Boxelder	wind	0.0894	0.218	15	0.044
Carya aquatica	Water hickory	animal	0.1529	0.802	25	0.044
Celtis laevigata	Sugarberry	animal	0.0379	0.489	24	0.044
Diospyros virginiana	Common persimmon	animal	0.0379	0.489	24	0.044
Fraxinus pennsylvanica	Green ash	wind	0.0106	0.525	30	0.044
Liquidambar styraciflua	Sweetgum	wind	0.0405	0.328	36	0.035
Quercus pagoda	Cherrybark oak	animal	0.1529	0.802	27	0.042
Quercus lyrata	Overcup oak	animal	0.1529	0.802	30	0.044
Quercus nigra	Water oak	animal	0.1529	0.802	35	0.035
Quercus nuttallii	Nuttall oak	animal	0.1529	0.802	40	0.044
Quercus phellos	Willow oak	animal	0.1529	0.802	37	0.044
Ulmus americana	American elm	wind	0.0175	0.391	38	0.044
Ulmus crassifolia	Cedar elm	wind	0.0175	0.391	38	0.044

* estimates from Streng et al. (1989) and DeSteven (1991a); *s* is survival probability of seedlings ≤ 2 yr old.

[§] maximum height, from Iverson et al. (1999) and Fulton and Harcombe (public communication, Ecological Society of America 85th Annual Meeting, Snowbird, Utah, August 2000).

[†] shape parameter for diameter-height relationship (Eq. 3.7), from Fulton (1999).

Table 3.1 (extended from previous page).

Species	Tolerance[‡]	B[¶]	M_a**	M_b**	M_c**	β^	α_l^^	Dispersal months[@]
Acer rubrum	1	500	-0.79	-3.02	-343.88	45.8(19.1)	-	Apr-Jun
Acer negundo	2	500	-0.77	-5.75	-403.50	45.8(19.1)	-	Sep-Mar
Carya aquatica	2	375	-0.21	-2.93	-528.45	3.20(1.68)	10.8	Sep-Dec
Celtis laevigata	1	358	-0.77	-5.75	-403.50	3.23(1.49)	16.9	Oct-Dec
Diospyros virginiana	2	120	-1.97	-2.97	-49.98	3.2(1.68)	11.8	Sep-Mar
Fraxinus pennsylvanica	2	500	-0.21	-2.93	-528.45	112.6(55.6)	-	Oct-Apr
Liquidambar styraciflua	1	450	-0.56	-4.75	-525.40	21.7(9.93)	-	Sep-Nov
Quercus pagoda	2	1380	-0.23	-3.53	-485.26	3.20(1.68)	11.8	Aug-Dec
Quercus lyrata	2	490	-0.21	-2.93	-528.45	3.20(1.68)	11.8	Aug-Dec
Quercus nigra	2	652	-1.07	-0.94	-304.11	3.20(1.68)	11.8	Aug-Dec
Quercus nuttallii	2	831	-0.23	-3.53	-485.26	3.20(1.68)	11.8	Aug-Dec
Quercus phellos	2	685	-0.23	-3.53	-485.26	3.20(1.68)	11.8	Aug-Dec
Ulmus americana	1	499	-0.21	-2.93	-528.45	45.8(19.1)	-	Mar-Apr
Ulmus crassifolia	1	343	-0.77	-5.75	-403.50	23.0(1.48)	-	Oct

[‡] from Phipps (1979); tolerant = 1, intolerant = 2.

[¶] basic growth rate (mm^2/yr) from Phipps (1979) and empirical estimates from tree cores and remeasured trees at Yazoo NWR.

** mortality parameters (see text, Eq. 3.6, and Table 3.2) from Fulton and Harcombe (public communication, Ecological Society of America 85th Annual Meeting, Snowbird, Utah, August 2000).

^ seeds produced per unit basal area (cm^{-2}); empirical estimates and surrogates with standard error in parentheses (see Chapter 2).

^^ mean dispersal distance (m) for animal-dispersed species; adapted from Clark et al. (1998b).

[@] from Young and Young (1992).

Table 3.2. Definition of symbols and default values (continued on next page).

Symbol	definition	default value	units
A	basal area of a tree	πr^2	mm^2
B	basic growth rate of trees, the annual area increment	see Table 3.1	mm^2
C	crowding factor		
c_1	shape parameter for Gaussian dispersal kernel	2.0	
c_2	shape parameter for fat-tailed dispersal kernel	0.5	
D	seed dispersal distance		m
d_i	distance of cell *i* from the current tree		m
f	index of parameter set for dispersal kernels: Gaussian (f =1) or fat-tailed (f = 2)		
g	annual radial growth increment		mm
H	tree height		m
H_{max}	asymptotic tree height	see Table 3.1	m
k_f	probability of a seed dispersing distance D based on parameter set f		
K_f	cumulative probability of dispersing distance D based on parameter set f		
l	canopy stratum, based on r	≤ 50 mm	
		50–100 mm	
		≥ 100 mm	
m_1	mortality probability calculated over 2.5 yr from Pacala et al. (1996)		
M_1	m_1 when $g = 0$; from Pacala et al. (1996)	0.964	
M_2	mortality decay parameter from Pacala et al. (1996)	-6.92	mm^{-1}
m_2	mortality probability calculated over 3 yr from Fulton and Harcombe (public communication, Ecological Society of America 85th Annual Meeting, Snowbird, Utah, August 2000)		
M_a	mortality parameter from Fulton and Harcombe; m_2 when $g = 0$ and $H = 1.4$ m	see Table 3.1	
M_b	mortality parameter from Fulton and Harcombe; scales H	see Table 3.1	
M_c	mortality parameter from Fulton and Harcombe; scales ΔH	see Table 3.1	
p	proportion of seeds dispersed using Gaussian dispersal	0.98	
P	parameter that determines whether radial growth calculation follows paraboloidal form	21.0	mm

Table 3.2 (continued from previous page).

Symbol	Definition	default value	units
r	radius at breast height		mm
R_l	reference stocking for the three strata based on r:		
	≤50-cm stratum:	200	mm^2/m
	50 to 100-cm stratum:	375	
	>100-cm stratum:	3750	
q	parameter defining allometry between r and H	see Table 3.1	cm^{-1}
S_l	stocking of a cell in each of three strata based on r		mm^2/m
s	seedling survival probability, applied over first 2 yr of seedling's life	see Table 3.1	
α_1	mean dispersal distance of dispersal kernel based on Gaussian dispersal	see Table 3.1	m
α_2	mean dispersal distance of dispersal kernel based on fat-tailed dispersal	200.0	m
ρ	crown radius		m

Table 3.3. Relative effects of altering parameter values for sensitivity analysis in YAFSIM. Nominal values are listed in Table 3.1 and the amount decreased and increased is discussed in Methods.

Parameter	Effect of decreasing parameter	Effect of increasing parameter
Seed fall velocity	Higher colonization to far plots, lower colonization to near plots, greater diversity of colonization in far plots; small but corresponding difference in larger strata.	Lower colonization to far plots, higher colonization to near plots; small but corresponding difference in larger strata.
Proportion of seeds in fat-tailed kernel (*p*)	Higher colonization to near plots; no effect on larger strata.	No effect.
Germination rate	Lower density of seedlings; no effect on larger strata.	Higher density of seedlings; higher recruitment far but lower recruitment near from overcrowding.
Seedling survival	Lower density of seedlings; higher density in larger strata.	No effect.

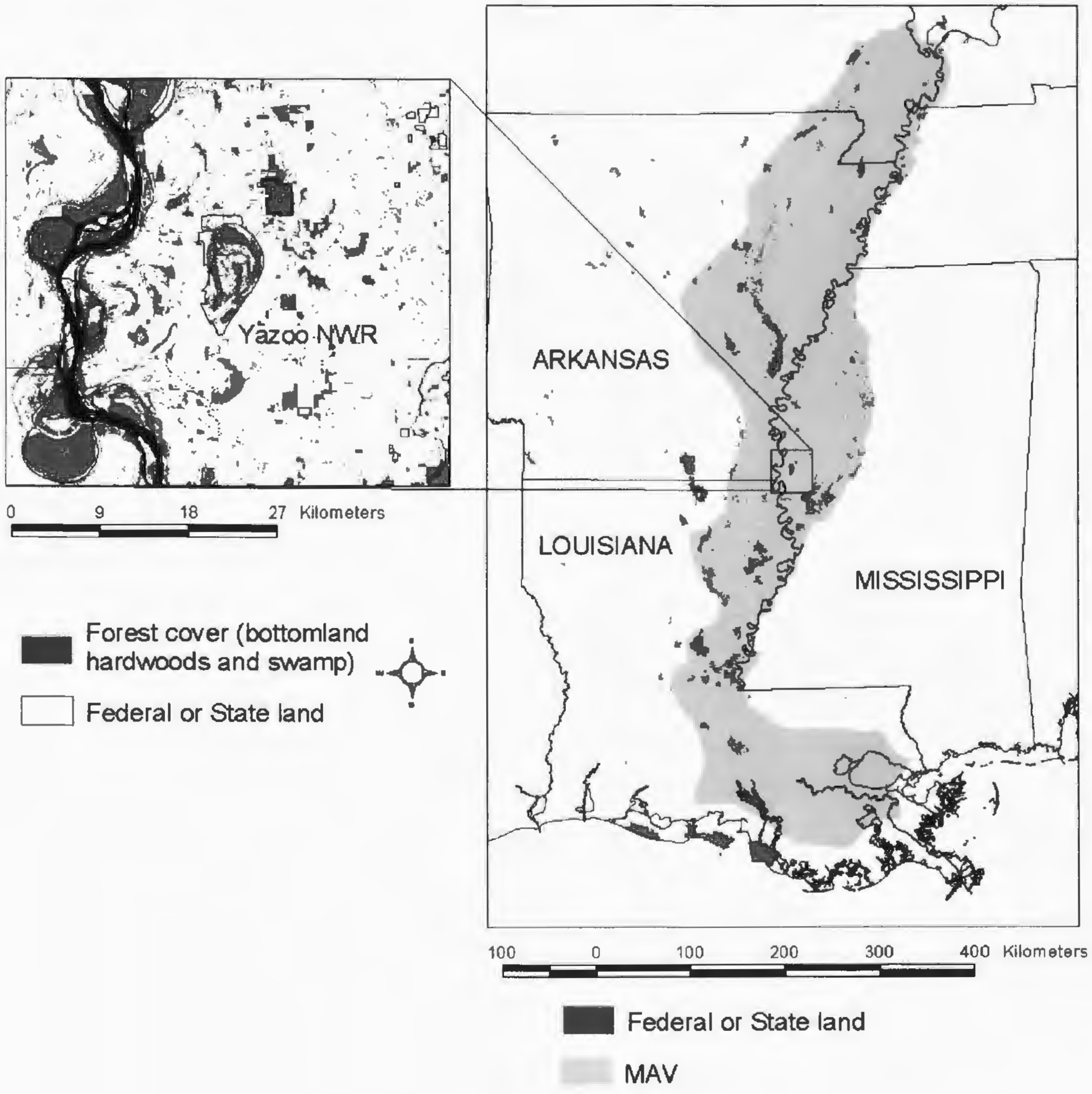


Fig. 3.1. Location of the study site, Yazoo National Wildlife Refuge, within the Mississippi Alluvial Valley (MAV). Excepting small, isolated blocks, virtually all forest in the MAV is either between the mainline Mississippi River levees or on federal or state land (boundaries shown in inset; white in general indicates nonforested land).

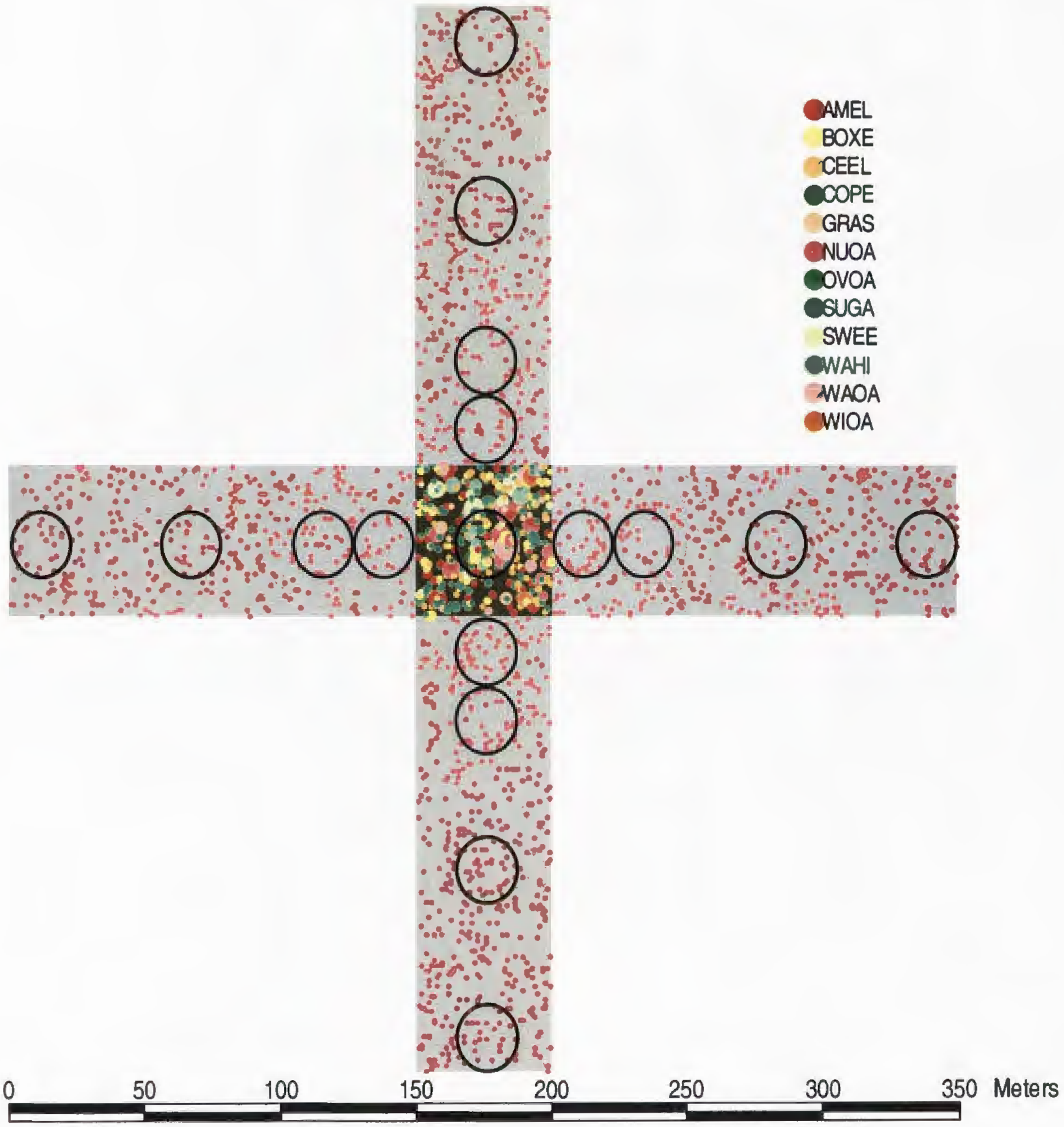


Fig. 3.2. Hypothetical model system with source forest in center and restoration sites planted with Nuttall oak seedlings in the four cardinal directions. Symbol size is proportional to diameter at breast height.

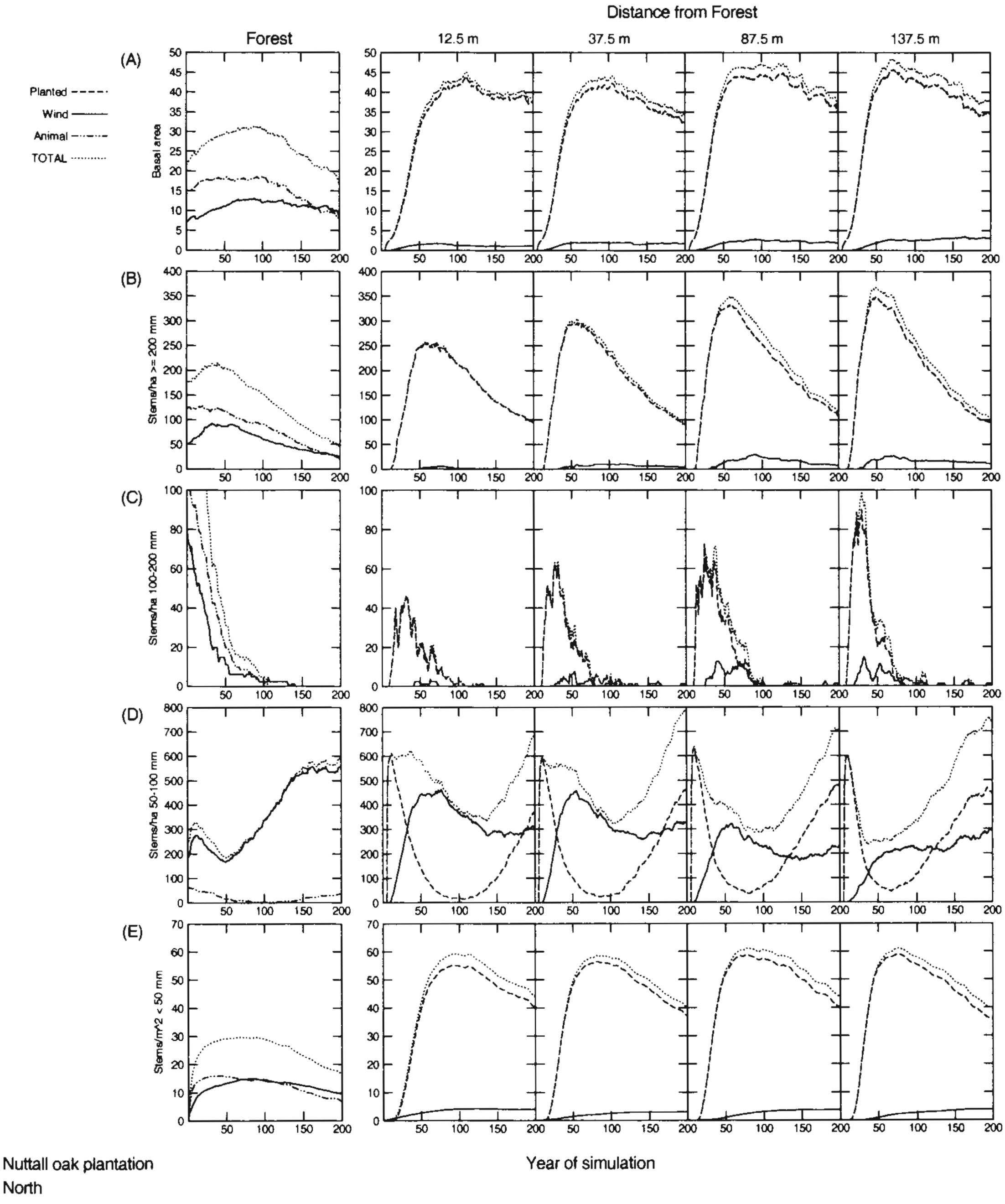


Fig. 3.3. Nominal output: 200-yr simulated time series for plots at the center of the source forest and to the north of the source forest in reforestation sites planted with Nuttall oak. Values are medians of density or basal area for each species group from 20 model runs of Yafsim. A, basal area per species; B, stem density (ha^{-1}) in the canopy (dbh ≥ 200 mm); C, subcanopy (100–200 mm); D small tree (50–100 mm); E, small tree (≤ 50 mm; m^{-2}) strata. Data for each species is grouped for display by dispersal mechanism.

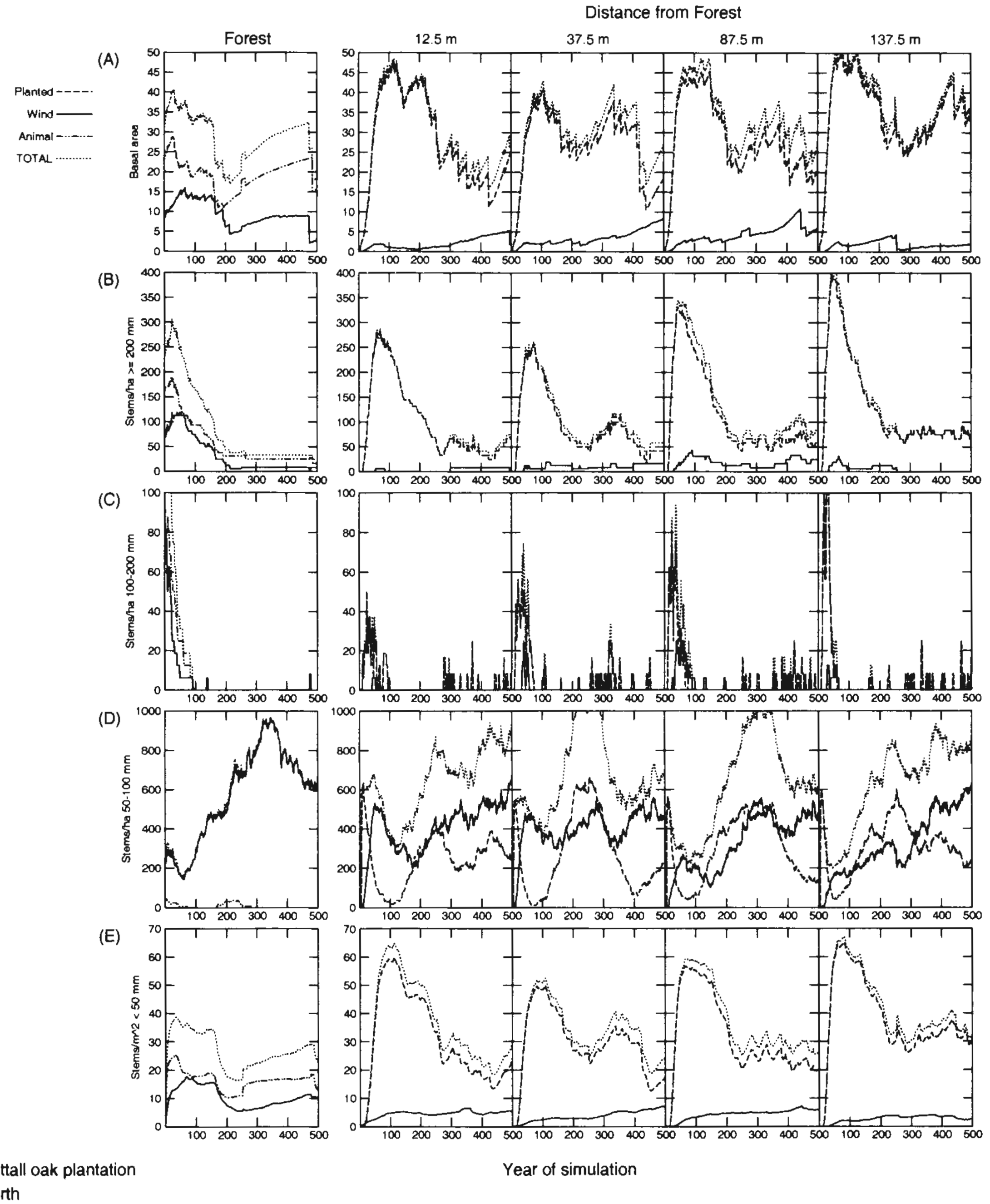


Fig. 3.4. Nominal output: 500-yr simulated time series for plots at the center of the source forest and to the north of the source forest in reforestation sites planted with Nuttall oak. Values are medians of density or basal area for each species group from 4 model runs of Yafsim. A, basal area per species group; B, stem density (ha^{-1}) in the canopy (dbh ≥ 200 mm); C, subcanopy (100–200 mm); D small tree (50–100 mm); E, small tree (≤ 50 mm; m^{-2}) strata. Data for each species is grouped for display by dispersal mechanism.

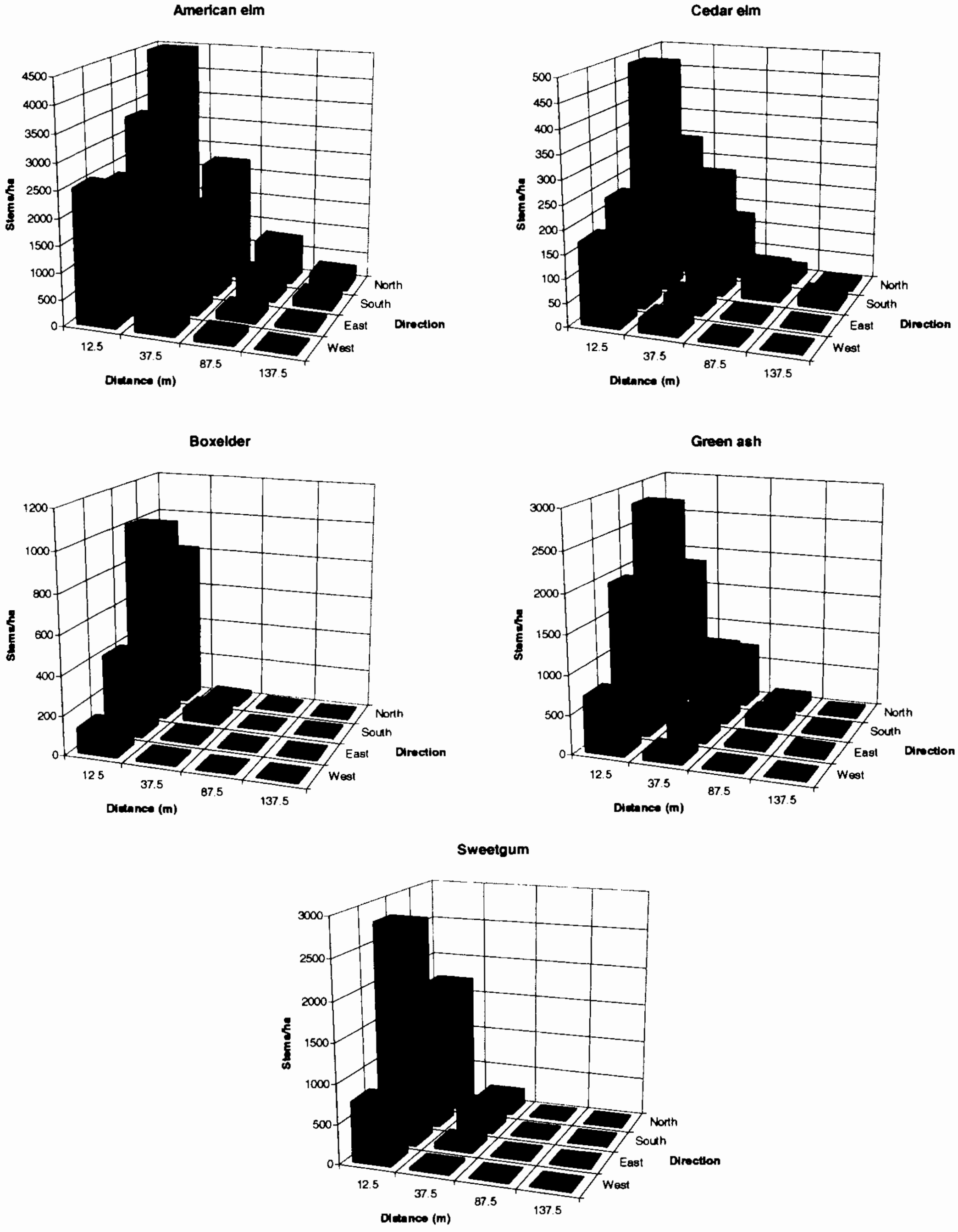
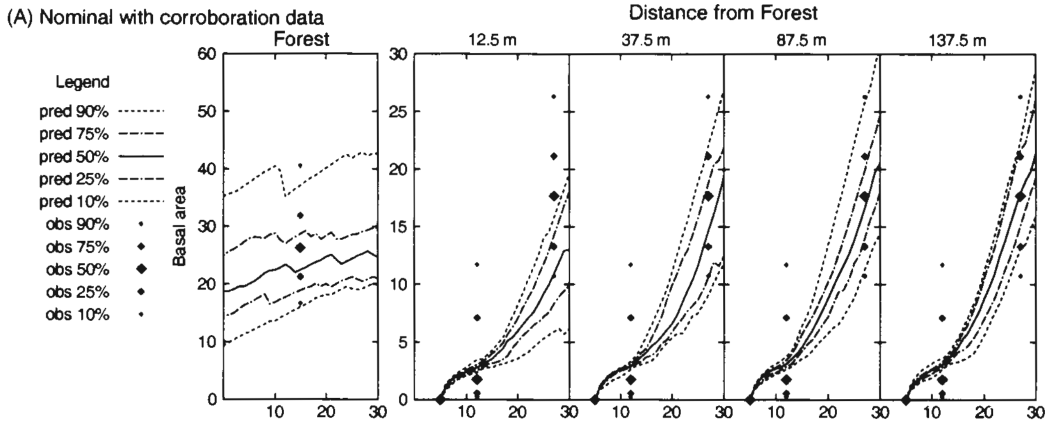
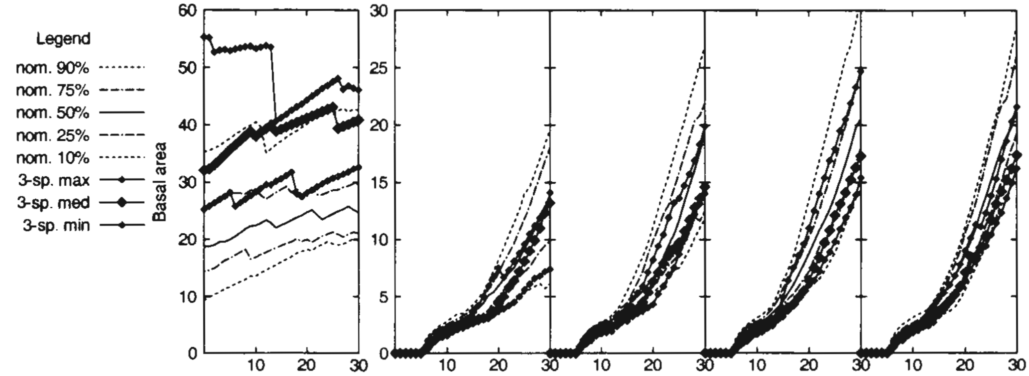


Fig. 3.5. Histogram of colonization of wind-dispersed species at year 15 at different distances and directions form forest. Differences in distributions among species are caused by differing seed fall velocities, densities of trees in the forest, and dispersal season (winds vary seasonally).

(A) Nominal with corroboration data



(B) Nominal with 3-spp. planting runs



(C) Nominal with non-planted runs

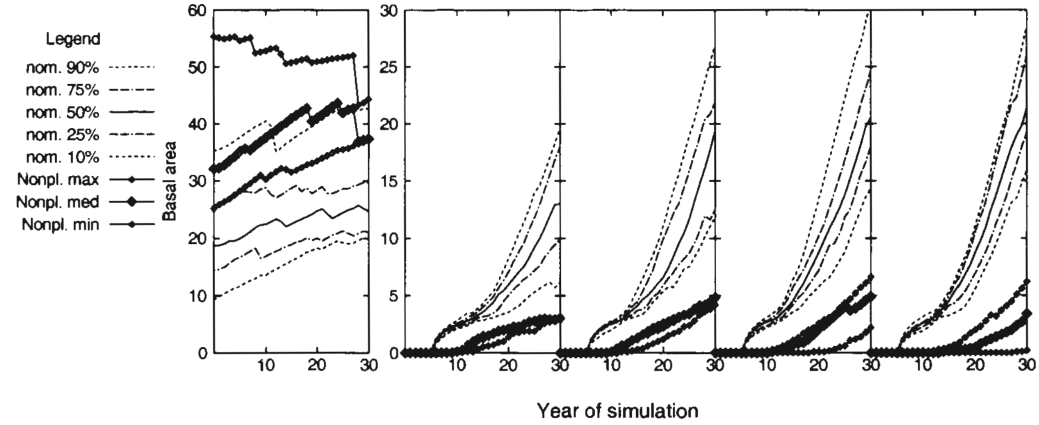


Fig. 3.6. Distribution of basal area in nominal runs, validation data, and alternative initialization scenarios. (A) Quantiles of 20 simulations using nominal parameter values and one species (Nuttall oak) planted in restoration sites ("pred." in legend) and quantiles of validation data ("obs." in legend) show that YAFSIM accurately predicts basal area distributions of restoration sites. (B) Simulations initialized with 3-species plantations (minimum, median, and maximum of 3 simulations shown: "3-sp.") have basal areas indistinguishable from single-species plantations ("nom."). (C) Simulations initialized without planting trees (i.e., natural succession; minimum, median, and maximum of 3 runs shown: "Nonpl.") had slower basal area accumulation than nominal runs ("nom.").

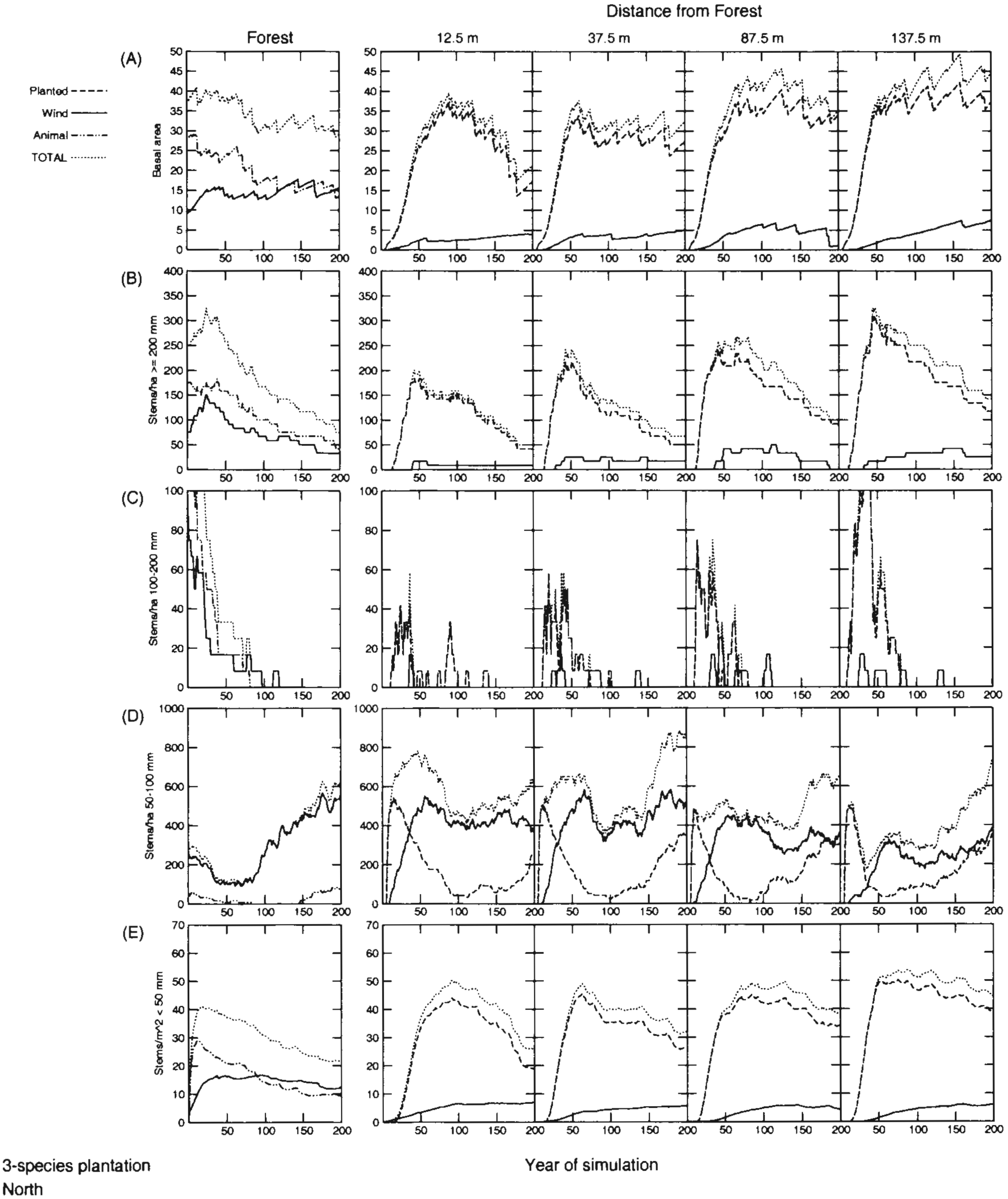


Fig. 3.7. Three-species plantation: 200-yr simulated time series for plots at the center of the source forest and to the north of the source forest in restoration sites planted with seedlings of willow oak, water oak, and Nuttall oak. Values are medians of density or basal area for each species group from 3 model runs of Yafsim. A, basal area of stems ≥ 50 mm dbh; B, stem density (ha^{-1}) in the canopy (dbh ≥ 200 mm); C, subcanopy (100–200 mm); D, small tree (50–100 mm); and E, small tree (≤ 50-mm; m^{-2}) strata. Data for each species is grouped for display by dispersal mechanism

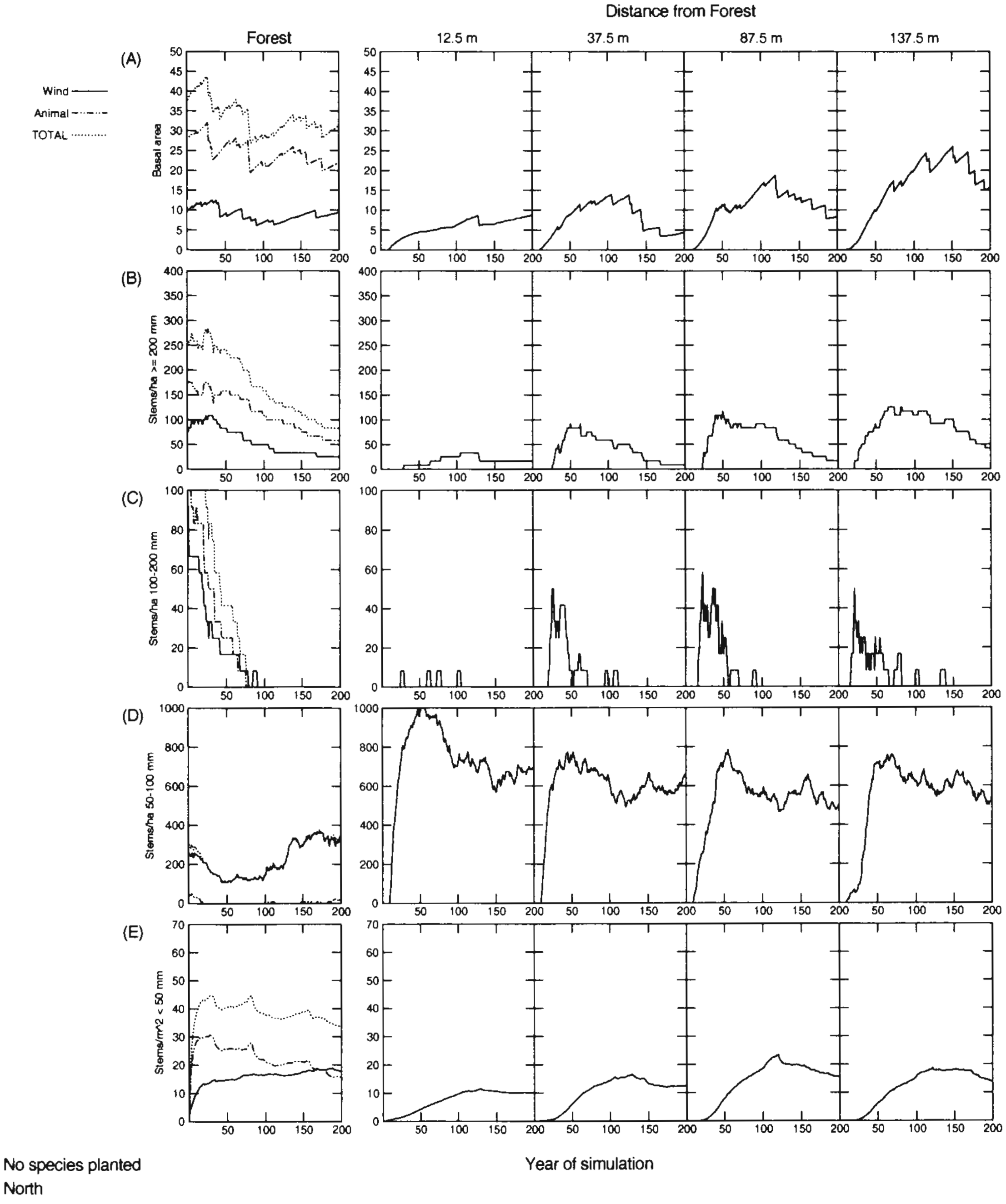


Fig. 3.8. Non-planted: 200-yr simulated time series for plots at the center of the source forest and to the north of the source forest in restoration sites not planted with any seedlings. Values are medians of density or basal area for each species group from 3 model runs of Yafsim. A, basal area of stems ≥ 50 mm dbh; B, stem density (ha^{-1}) in the canopy (dbh ≥ 200 mm); C, subcanopy (100–200 mm); D, small tree (50–100 mm); and E, small tree (≤ 50-mm; m^{-2}) strata. Data for each species is grouped for display by dispersal mechanism.

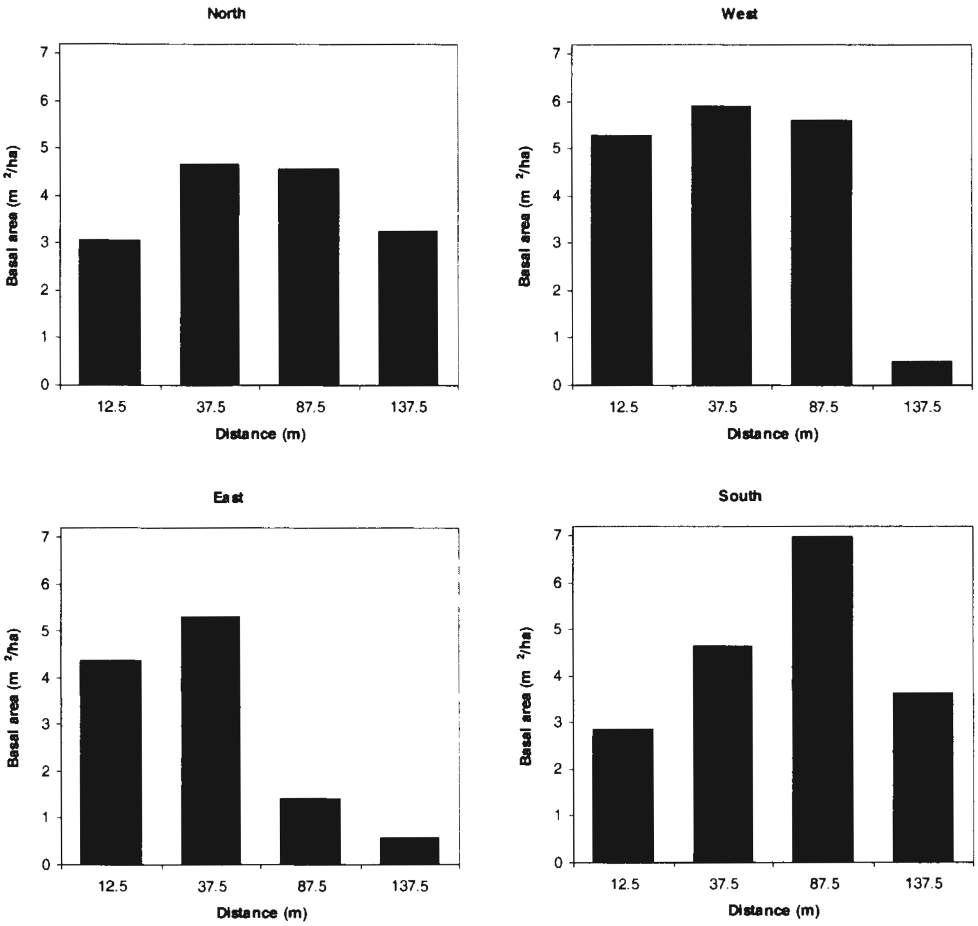


Fig. 3.9. Basal area at different distances and directions from forest at year 30 in non-planted model runs. Plots of intermediate distance (37.5 and 87.5 m) had higher basal area because colonizing trees were neither suppressed by large trees in the forest or by high density of competing colonists (as for near plots at 12.5 m to the north and south) nor limited by dispersal of seeds (as for plots at 137.5 m to the west and east).

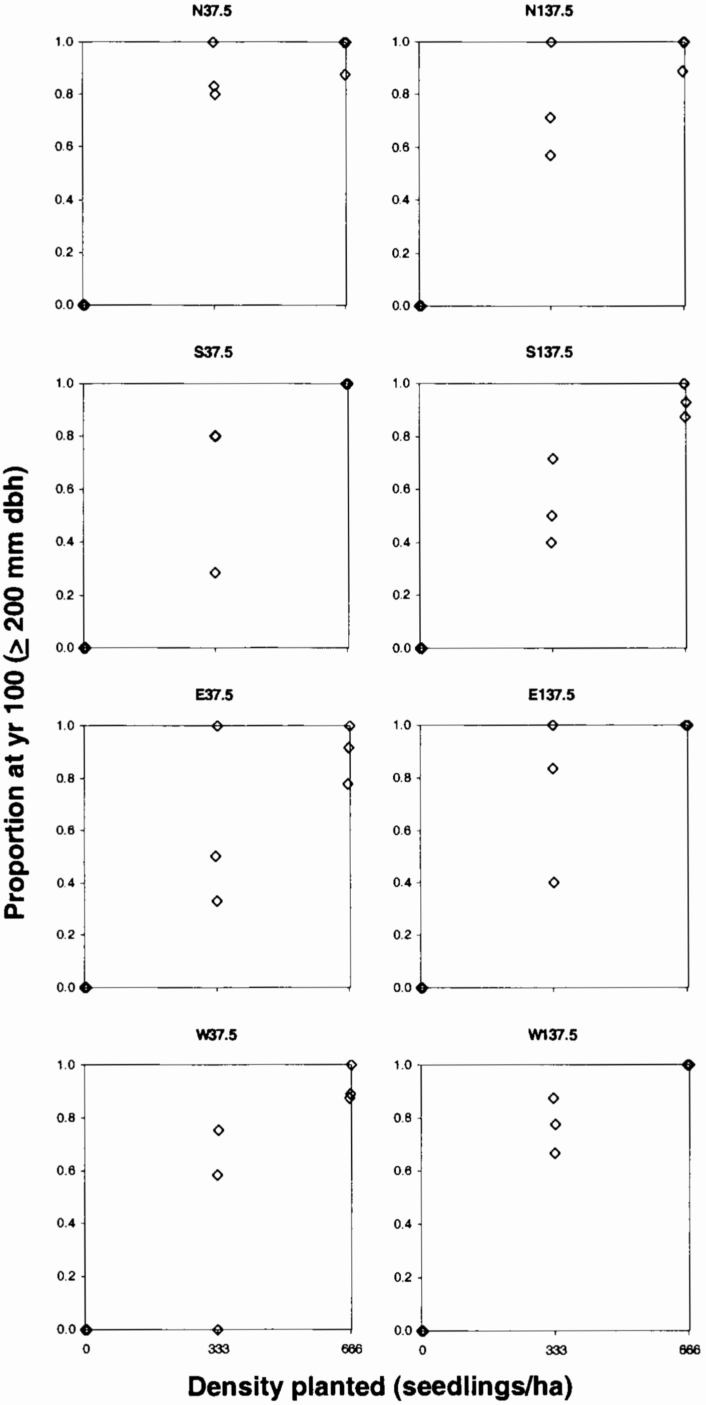


Fig. 3.10. Simulated proportion of trees ≥ 200 mm dbh at year 100 that are Nuttall oak, versus density of Nuttall oak seedlings planted at year 0, at various distances and directions from a source population of trees. The general concavity of the relationship shows that competition is more important than colonization in determining tree communities, even when colonization is plentiful as in nearer plots in the direction of prevailing winds (i.e., north and south).

CHAPTER 4

FURTHER VALIDATION OF A SPATIALLY EXPLICIT FOREST SIMULATOR FOR ALTERNATIVE ESTABLISHMENT SCENARIOS FOR BOTTOMLAND HARDWOOD REFORESTATION SITES

Abstract.—I evaluated the validity of a spatially explicit forest simulator,YAFSIM, for predicting size distributions of colonizing and planted or sown trees in bottomland hardwood reforestation sites. For tree height distributions, YAFSIM performed better on sown versus planted sites, and for tree diameter distributions YAFSIM tended to underpredict diameter growth of planted trees. Colonizing trees were limited to wind-dispersed species in YAFSIM, but real sites also had several animal-dispersed colonizing species. Improved estimates of germination and establishment of seedlings are needed to model a fuller range of species.

INTRODUCTION

When establishing oak plantations for bottomland hardwood reforestation and restoration, a choice can be made between planting oak seedlings or sowing acorns. There are various logistical, economic, and ecological considerations that influence this decision. Logistical and economic considerations are addressed by Allen et al. (2001). Two of the main ecological issues are a desire for both good growth and survival of planted or sown oaks and attainment of high tree-species diversity levels, similar to natural bottomland hardwood forests, via colonization of non-oak species from such forests that are located in the vicinity. At present, these two ecological goals seem to be in conflict with each other, because planted oaks are preventing colonizing species from establishing and recruiting into canopy positions (see Chapter 3).

Oak plantations established for bottomland hardwood reforestation and restoration occupy > 78,000 ha in the Mississippi Alluvial Valley (MAV), with 205,000 ha expected by 2005

(Stanturf et al. 2000, Schoenholtz et al. 2001). Restoration goals for these sites included restoring a diverse tree community, but establishment has consisted primarily of ceasing agricultural crop production and planting or sowing one to three species of oaks. However, the expected natural colonization in the vast majority of cases has been extremely limited, restricted mostly to regions immediately adjacent to existing forests, and especially in the direction of prevailing winds (north and east; Allen 1997). Development of diverse forests at these sites is limited not only by dispersal of seeds from the adjacent or nearby forests, but also from competitive exclusion from the oak trees that were planted to initiate the restoration site (see Chapter 3). Allen (1997), Stanturf et al. (2000), and Twedt and Wilson (2002) elaborate on the reforestation context and problems encountered.

Allen (1997) hypothesized that natural mortality of planted oaks would provide canopy gaps where colonizing trees could recruit. However, survival of planted oaks is very high (15-yr survival of 81% for Nuttall oak, *Quercus nuttallii*, Krinard and Johnson 1988); as a result, such canopy gaps are not common. Alternatively, it is reasoned that the more patchy germination and establishment of acorns will result in a more heterogeneous pattern of oak recruitment and therefore create patches where colonizers can recruit (Allen 1997). Indeed, reforestation sites established with acorns had slightly higher numbers of colonizers 14 to 18 yr post-establishment than those established with seedlings, though these were mainly restricted to the smallest size classes of saplings and colonizers in seedling-established sites were larger on average (see figs. 2 and 3 in Twedt and Wilson 2002).

It is not known whether this initially promising diversity in sites established with acorns will be maintained or even enhanced in older sites, because there are no acorn-established sites > ca. 20 yr old. In the very few seedling-established stands that are currently 30–35 yr old, most colonizing trees were eventually suppressed and killed by overtopping, planted oaks by around yr 25 (Nuttle 1997 and personal observations of chronosequences).

Based on these observations, I investigated the development of reforestation sites established under simulated planting of seedlings or sowing of acorns using the spatially explicit forest simulation model, YAFSIM (see Chapter 3). YAFSIM has already been shown to be valid for predicting basal area growth in bottomland hardwood forests and reforestation sites established with seedlings, as well as forecasting long-term dynamics that are consistent with known patterns in both bottomland hardwoods and eastern deciduous forests generally (Chapter 3). Here, I compare model predictions to observed data from real reforestation sites of various ages and under the two establishment scenarios to assess model validity for predicting size distributions of plantation and colonizing species.

METHODS

YAFSIM simulation model.—Details of the simulation model YAFSIM are in Chapter 3, and its mechanistic seed dispersal algorithm is described and analyzed in Chapter 2. Briefly, YAFSIM tracks the dispersal, establishment, growth, and survival of bottomland hardwood forests in simulated three-dimensional space. Dispersal is modeled mechanistically for wind-dispersed species and probabilistically for animal-dispersed species (Fig. 4.1 shows species and dispersal mechanisms). Seedling germination and establishment is a probabilistic function dependent only on species, whereas survival and growth are functions of species and crowding in the vicinity of each individual. Specifically, crowding affects growth, which in turn affects survival probability (better growth results in higher survival probability). Species that grow large enough (≥ 15 cm dbh) become reproductively mature and disperse seeds of their own. YAFSIM tracks dispersal and subsequent processes at any point in the model landscape, and results of size distributions by species are reported for user-specified assessment plots.

I simulated tree colonization, growth, and mortality in restoration sites initialized with seedlings or acorns in an equal proportion of willow oak (*Q. phellos*), water oak (*Q. nigra*), Nuttall oak, and cherrybark oak (*Q. pagoda*), the most commonly used species for real reforestation sites (Schoenholtz et al. 2001). To simulate reforestation sites established with seedlings, sites were initialized at a density of 890 seedlings/ha (based on values reported in Twedt and Wilson 2002), 2 mm diameter and age of 2 yr (to bypass density-independent seedling survival in YAFSIM). To simulate reforestation sites established with acorns, sites were initialized at a density of 3950 acorns/ha (based on values reported in Twedt and Wilson 2002) and 0 yr old. Because acorns were sown in the soil and not simply scattered on the soil surface (as YAFSIM assumes), I adjusted the germination rate of sown acorns to reflect observed germination and first year survival estimates (from Johnson and Krinard 1985); thus, to reflect the resulting germination rate, I multiplied acorn sowing density by a germination rate of 0.625. Germinating acorns then received an initial diameter of 1 mm, as did all other germinating seeds in the model.

I simulated each scenario for 50 yr with 5 runs, each with a different random arrangement of trees in reforestation sites. Simulated reforestation sites were located around a square 50 × 50–m forest. Trees in the forest were selected at random from sample data (see next section). Simulation output was summarized in and averaged among 24 0.4-ha (11.3-m radius) sample plots with centers from 12.5–137.5 m from forest edge at 25-m intervals in each cardinal direction within simulated reforestation sites.

Model validation data collection and study area.—Validation data for tree height distributions were extracted from Twedt and Wilson (2002, figures 2 and 3), who pooled data from several 14–18-year-old sites in the MAV into histograms of tree heights for planted or sown and colonizing species according to dispersal agent. Species planted or sown in the sites assessed by Twedt and Wilson (2002) included a subset of one to all of those simulated, except two sown sites were established with Shumard oak (*Q. shumardii*). Although I did not model Shumard oak, it has the same growth rate as willow oak (Phipps 1979), so I assumed results would be comparable.

Validation data for tree diameter distributions came from data collected in 1995 and 1996 at Yazoo National Wildlife Refuge (NWR, west-central Mississippi, USA, 33°10'N, 90°51'W, elevation 35 m; Chapter 3 contains a full description of the study area). Sampled reforestation sites were established with seedlings of the species listed above. The Yazoo NWR Reforestation Plan called for planting seedlings in rows 5 m apart with 3- to 5-m spacing within rows (which would result in ca. 400–667 seedling/ha), but actual planting density for each stand was not recorded, and personal observations suggested within-row distances were somewhat closer, resulting in higher density. I measured dbh (diameter at breast height, 1.3 m above ground) of all trees with dbh > 2.5 cm and counted all other trees > 1 m tall in 0.04-ha square plots in reforestation sites of various ages. All reforestation sites sampled were established with two or three of the four modeled oak species. I measured 91 plots in restoration sites 11–13 yr old and 65 plots in restoration sites 22–28 yr old.

In addition to reforestation sites, I measured 108 plots in nearby bottomland hardwood forest stands. All plots were in mixed-species, even-aged stands initiated ca. 60 yr previously by logging followed by unassisted, natural regeneration. I used data from these naturally regenerated forest plots to provide data to construct the source forest at the center of each model landscape; data from reforestation-site plots were not used for model formulation or initialization in any way, and thus serve as an independent validation data set.

Model validation data analysis.—I compared the distributions of tree heights and diameters between model predictions and observed values for planted/sown and colonizing trees by comparing histograms of tree-size distributions. I assessed goodness-of-fit semi-quantitatively by visual inspection of the histograms because the form of both predicted and observed data violate assumptions of parametric and nonparametric goodness-of-fit tests. I excluded the smallest size category of height (< 2 m) or diameter (< 2.5 cm) because not all trees in these categories were counted in validation data sets. For tree height comparisons, predicted height distributions came from simulations of restoration sites initialized with either acorns or seedlings. I compared model predictions of tree height at year 16 to those of reforestation sites 14–18 yr old reported by Twedt and Wilson (2002). For tree diameter comparisons, I compared sampled data from real reforestation sites to model predictions of seedling-established simulations of similar age. Thus, analyzed years from YAFSIM were the mean age of sampled sites within each age class, weighted by age of plots within an age class. Thus, I compared model predictions at year 12 to data pooled from sites 11–13 yr old, and at yr 26 to data pooled from sites 22-28 yr old. The use of height versus diameter in validation was dictated by the nature of the validation data: I did not measure tree height except on a few individuals in each plot and Twedt and Wilson (2002) only reported distribution of tree heights, not diameters.

RESULTS

Model validation.—Fig. 4.1 shows the diameter distributions of planted and colonizing trees in 11–13- and 22–28-yr-old reforestation sites and natural forest at Yazoo NWR. Although low densities of bird-dispersed and mammal-dispersed colonizers were observed in real reforestation sites of all ages for which data are available (see Fig. 4.1 and Twedt and Wilson 2002), YAFSIM predicted 0 colonization of non-wind-dispersed species. Fig. 4.2 shows height distributions of planted or sown oaks and colonizing wind-dispersed species for both predicted and observed data; Fig. 4.3 is analogous for tree diameters.

Fig. 4.2 and 4.3 show some interesting patterns regarding variation in stem densities both in simulated and real reforestation sites. The variation apparent in YAFSIM predictions for small height classes, especially for wind-dispersed colonizers, probably reflects the variation that occurs because of differential colonization across the model landscape (a function of distance and direction to source forests, see Chapter 3 for elaboration) and model stochasticity. As deterministic controls on density begin to compensate for stochastic or landscape differences in initial density, this variation is reduced in larger height classes. The same general pattern is evident for wind-dispersed colonizers in real reforestation sites (Fig. 4.3), though variation is even greater in smaller size classes because of site differences that are not included in YAFSIM.

Agreement between YAFSIM predictions and observed data were good for height distributions ca. 16-yr post-establishment of sites established with acorns, for both sown and colonizing species (Fig. 4.2, right two graphs). For seedling-established stands, YAFSIM predicted shorter heights than were observed, but the shape of the distribution was basically correct for planted oaks (top left of Fig. 4.2). However, for wind-dispersed colonizers in seedling-established sites, YAFSIM predicted an incorrect height distribution: real sites had an interior mode but simulated sites had a mode at the smallest height category. The difference in height distributions between acorn-and seedling-established stands is probably because canopy closure occurred at an earlier age in seedling-established stands, resulting in suppressed colonization (Twedt and Wilson 2002). The only mechanism in YAFSIM for suppressing colonization is density-dependent mortality, which is insufficient to stop colonization (see Chapter 3).

Agreement between YAFSIM predictions and validation was not as good for diameter distributions in seedling-established sites, either at 12 or 26 yr post-establishment. For 12-year-old sites, the modes for planted and wind-dispersed colonizers were approximately in the correct location (right two graphs in Fig. 4.3). However, for planted species, the model predicted much higher density overall, but there were fewer trees in larger diameter classes compared to real sites. The converse was true for wind-dispersed colonizers: the model predicted much lower colonization than was observed in real sites. In hindsight, it appears that the simulated planting density was probably higher than the density at which real sites were planted (recall from the Methods section that Yazoo NWR's Reforestation Plan specified a lower planting density than I assumed). Such a higher planting density would result not only in higher density of planted trees, but also their diminished growth; stagnation of low-diversity oak stands at high density is a phenomenon known for real oak forests and plantations (Meadows and Goelz 1999, 2001). There would also be less room for any wind-dispersed colonizers to become established and grow. As these same simulated sites continued development to year 26, oaks remained stagnated in small diameter classes, though densities in the largest diameter classes are quite close (Fig. 4.3, top right graph). Wind-dispersed colonizers at year 26 were much more common in the model than in reality, probably for similar reasons as discussed above for height distributions; colonizers remain stunted in lower diameter classes because high total densities suppressed their growth, but not enough to reduce density through increased mortality.

DISCUSSION

YAFSIM appears reasonably valid for predicting stem size distributions for bottomland hardwood reforestation sites established with both acorns and seedlings of oaks and experiencing natural colonization from nearby forests. YAFSIM predicted basal area distributions of seedling-established sites (Chapter 3) more accurately than it predicted diameter distributions of similar stands, although simulated sites for basal area predictions were initialized at a density closer to that specified in the Yazoo NWR Reforestation Plan (i.e., 667 seedlings/ha).

The main failure of YAFSIM appears to be its failure to allow adequate colonization of animal-dispersed species, and colonization of wind-dispersed species is largely restricted to the most fecund species (i.e., American elm). It is likely that this problem is caused by a combination of inadequate fecundity estimates (for example, failure to include masting behavior of some species) and inadequate germination and survival rates of animal-dispersed seeds. Additionally, the assumed dispersal kernel for animal-dispersed species may be inappropriate. Consider, for example, sugarberry (*Celtis laevigata*), which is nearly ubiquitous in reforestation sites of all ages and distances from forest, but very rare in simulated reforestation sites, and then only in plots adjacent to forest (see Chapter 3). It may be possible that modifying parameters for sugarberry's dispersal kernel could account for such a pattern, but perhaps mechanistic algorithms for animal-dispersed species could also be fruitfully included to understand these processes better.

Compounding such poor performance of animal-dispersed species is the high germination and establishment rates of wind-dispersed and planted species. On a strictly probabilistic level, there is virtually no chance of successful colonization of animal-dispersed individuals, or individuals that do not descend from planted individuals, because of the enormous numbers of individuals of these species to compete with. The degree of validity of these seedling densities is difficult to assess because of the very poor quantitative data on small seedlings in bottomland hardwood forests and reforestation sites. However, personal observations of seedling densities are not nearly as high as the 40–80 seedlings per square meter sometimes predicted by YAFSIM (see Fig. 3.5).

Porté and Bartelink (2002), in their review of models of mixed forest growth, recognized that recruitment (i.e., regeneration) sub-models of almost all forest models, regardless of type, were inadequate (they did not mention exceptions). All forest models except YAFSIM model the distributions of seedlings around parent trees instead of seeds; that is, "seed dispersal," if included at all, affects only the spatial distribution of seedlings, not their total number. Even with seedling density controlled in such a manner (e.g., by making final numbers of seedlings or saplings fit empirical data or some theoretical maximum) most forest simulators poorly predicted seedling density. Errors in predicting seedling density had large and long-lasting effects on stand basal area and species composition for periods of > 200 simulated years (Porté and Bartelink 2002, see also Pacala et al. 1996). For YAFSIM to more accurately predict seedling density, it is therefore necessary to include better estimates of seed germination and establishment and the processes that affect these parameters for all species modeled. For example, such mechanisms would allow more realistic constraints to be placed on colonization under closed-canopy conditions, that was problematic for predicting densities of colonizers in seedling-established sites at 16 and 26 yr post-establishment (Figures 4.2–4.3).

In conclusion, this paper has further demonstrated the general validity of YAFSIM for predicting colonization patterns and growth of trees in bottomland-hardwood reforestation sites. I suggest that further modifications of YAFSIM's regeneration algorithm and parameter estimates are necessary to more accurately represent the full diversity of colonization potential of sites.

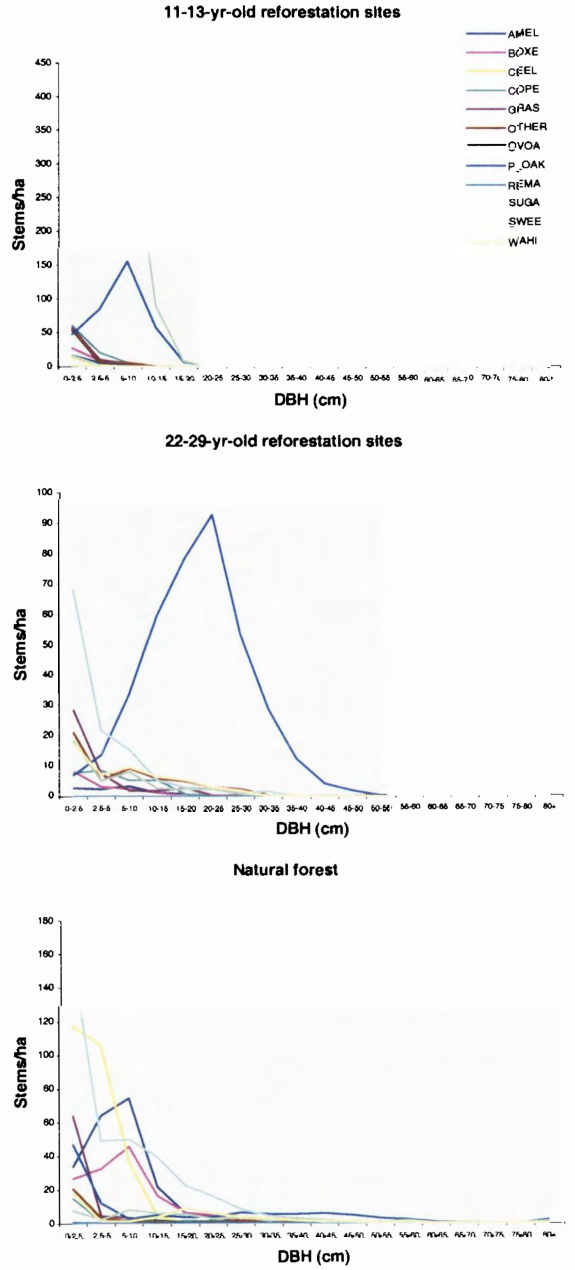


Fig. 4.1.Diameter distributions of trees in bottomland hardwood reforestation sites (11–13-yr- old and 22–28-yr-old) and natural stands (ca. 60-yr-old) at Yazoo NWR (1995-1996). Reforestation sites were established with seedlings of cherrybark oak, Nuttall oak, willow oak, or water oak (P_OAK in key, for "planted oak", see text for Latin names.). Wind-dispersed colonizers are: American elm (AMEL, *Ulmus americana*), boxelder (BOXE, *Acer negundo*), cedar elm (CEEL, *U. crassifolia*), green ash (GRAS, *Fraxinus pennsylvanica*), red maple (REMA, *A. rubrum*), and sweetgum (SWEE, *Liquidambar styraciflua*). Animal-dispersed species are: common persimmon (COPE, *Diospyros virginiana*), overcup oak (*Q. lyrata*), sugarberry (SUGA, *Celtis laevigata*), and water hickory or pecan (WAHI, *Carya aquatica* or *C. illinoensis*).

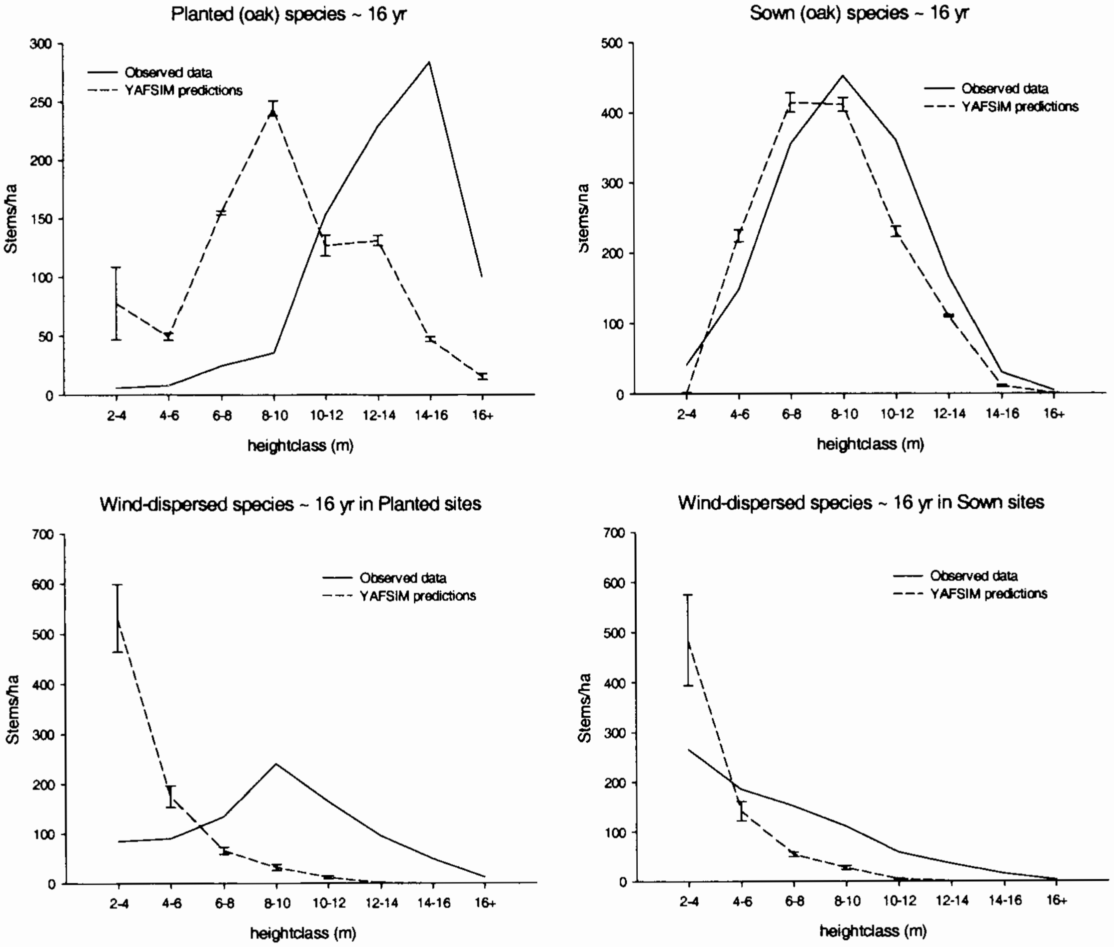


Fig. 4.2. Height distributions of planted/sown and wind-dispersed colonizing trees in real and simulated bottomland hardwood reforestation sites, established with oak seedlings or acorns. Simulated sites were 16 yr old and real sites were 14–18 yr old. Error bars for YAFSIM predictions are 1 standard error. Observed data are from Twedt and Wilson (2002; they did not report variation associated with height distributions).

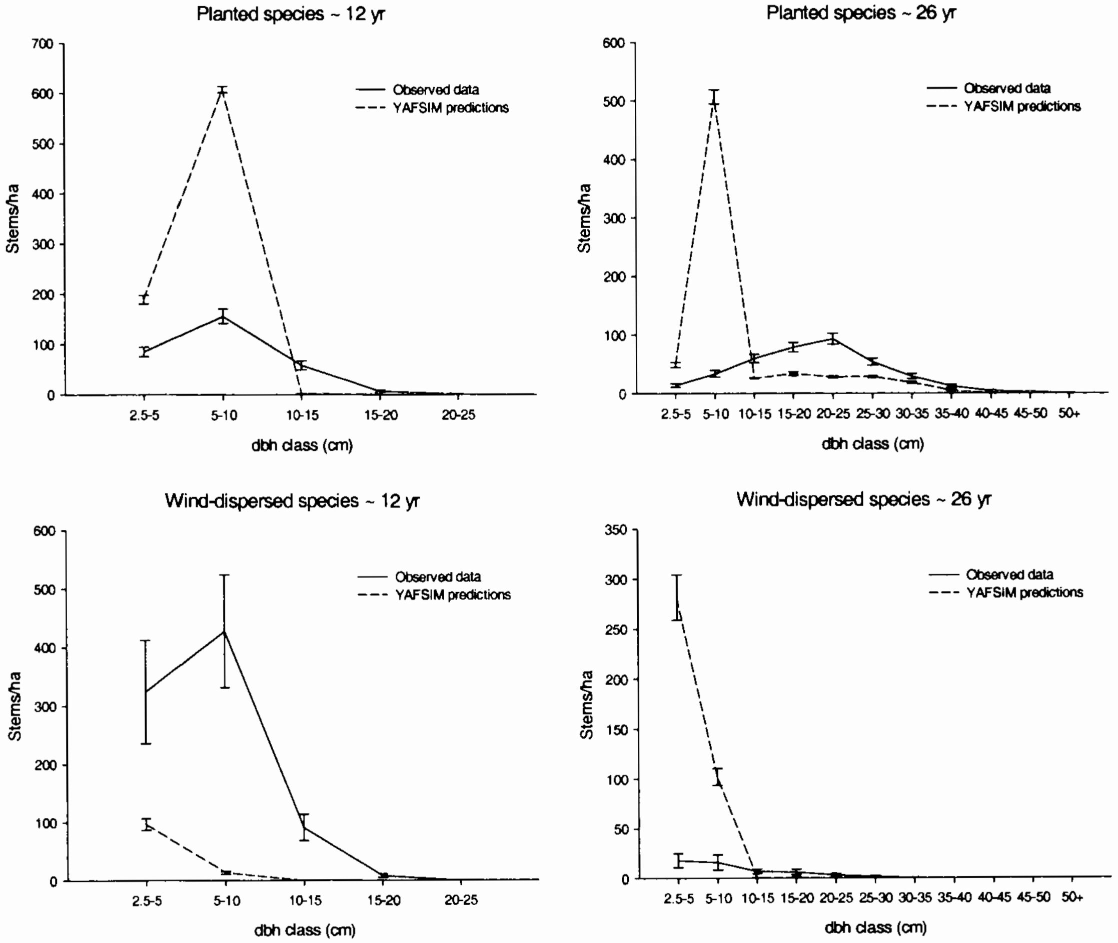


Fig. 4.3. Diameter distributions of planted and wind-dispersed colonizing trees in real and simulated bottomland hardwood reforestation sites, established with oak seedlings. Simulated sites were 12 yr old and 26 yr old and real sites were 11–13 yr old and 22–28 yr old. Error bars are 1 standard error.

CHAPTER 5

THINNING STRATEGIES FOR BOTTOMLAND HARDWOOD FORESTS: APPLICATIONS OF A FOREST SIMULATOR

Abstract.—I evaluated alternative establishment and thinning strategies for bottomland hardwood reforestation sites using the spatially explicit forest simulator YAFSIM. Unthinned stands had virtually no recruitment of colonizing trees over 50 yr of simulation. Thinning understory and midstory planted or sown trees increased recruitment of wind-dispersed species in simulations, though optimal thinning levels and timings differed depending on whether the site was established with acorns or seedlings. Thinning acorn-established stands at 15 yr and seedling-established stands at 25 yr produced the best combinations of colonizer recruitment and density of large trees.

INTRODUCTION

Oak plantations established for bottomland hardwood reforestation and restoration almost never achieve desired levels of tree species diversity (Chapter 3 and 4, Allen 1997, Allen et al. 1998, Stanturf et al. 2000). Currently, such oak plantations occupy > 78,000 ha in the Mississippi Alluvial Valley (MAV), with 205,000 ha expected by 2005 (Stanturf et al. 2000, Schoenholtz et al. 2001). Sites are generally established with seedlings or acorns of one to three species of oaks for two reasons: first, these species have high socio-economic importance and second, it was reasoned that they would not disperse to sites in sufficient quantities by their own mechanisms. Conversely, it was expected that these oak plantations would accumulate diverse tree communities from dispersal of wind- and bird-dispersed seeds from natural forests in the vicinity. However, this natural colonization is largely restricted to locations adjacent to natural forest (Allen 1997, Allen et al. 1998).

Even where natural colonization is abundant, plantation trees eventually overtop, suppress, and kill colonizers. In 18-year-old reforestation sites, non-planted trees had substantially smaller diameters than planted trees, even though the non-planted trees were only one to three years younger than the planted trees (based on tree ring data); evidence of past colonization was largely absent in older (23- to 28-year old) plantations, suggesting that by that age any colonizers had died out (personal observations, see also Fig. 4.1). Results from a spatially explicit simulation model of this system, YAFSIM, suggest that likely mechanisms for this phenomenon are a combination of oaks' high growth and survival rates and high initial planting density (Chapter 3). In an alternative model scenario, in the absence of planted populations of oaks, other species were able to recruit into codominant and dominant canopy positions. Thus, it appears that the establishment of oak plantations actually hinders restoration of diverse forests. Nevertheless, although modeled non-planted restoration sites were more diverse, density and basal area of trees were lower compared to planted sites. Thus, given the current management practice of site establishment and waiting, there appears to be a tradeoff between tree community diversity and rapid reforestation.

These empirical and modelling results reflect the fact that oaks do not self-thin very well when grown only with other oaks, and thus produce stagnated, low-vigor stands (Meadows and Goelz 1999). Under a more active management scenario it may be possible to enhance both growth of plantation and colonizing trees by thinning. Achievement of both restoration goals—reforestation and diversity—may thus be possible if the correct level of thinning can be determined. Thinning should be heavy enough to permit recruitment of colonizers, but not so heavy as to substantially reduce basal area or density of overstory trees for the long-term.

Published thinning guidelines for natural bottomland hardwood forests are not appropriate for bottomland reforestation sites, because they focus on enhancing development of the oak component at the expense of other species (Meadows 1996 and Goelz and Meadows

1997). Thus, applying these thinning guidelines to reforestation sites would likely make the diversity situation worse, not better. Their focus on enhancing oaks is driven by the usual goals of production of timber and game wildlife, which eat oak mast, and because ensuring an adequate oak component for these purposes in natural regeneration of cutover bottomland hardwoods is considered the most difficult challenge for regenerating the stand (Meadows 1996, Goelz and Meadows 1997). Reforestation plantations circumvent the regeneration problems experienced by oaks in mixed forests, but reforestation guidelines were formulated based on the expectation of poor oak survival, and so also initially emphasized planting oaks (e.g., Allen 1989 and Yazoo NWR reforestation plan, unpublished report). Despite the growing body of evidence that oak plantations often fail to produce diverse forests, the latest restoration guide (Allen et al. 2001) still recommends planting mainly oaks and hickories.

Given the evidence, however, such a narrow focus on establishing oaks is shortsighted, as oaks almost always dominate reforestation sites established under these protocols. Thus, managers are currently faced with the opposite problem from naturally regenerated bottomland hardwoods: how to encourage colonization and recruitment of non-oak trees in oak plantations, while also maintaining an oak component adequate for timber and game production goals?

Currently, there are no published thinning guidelines for bottomland hardwood reforestation and restoration sites. To date, only one such site has received a thinning treatment, at Yazoo National Wildlife Refuge (NWR), Mississippi, USA. In addition, a 28-year-old water oak (*Quercus nigra*) plantation in northern Louisiana was experimentally thinned but the site was upland and not in the MAV; non-planted (colonizing) species were rare and their dynamics were not assessed (Meadows and Goelz 1999, 2001). Prior to being thinned, the site at Yazoo NWR was completely dominated by planted Nuttall oak (*Quercus nuttallii*) and cherrybark oak (*Q. pagoda*; see Fig. 4.1, which shows data from this and two other sites). The site was thinned at approximately 29 yr post-establishment, and has had noticeably enhanced overstory tree, understory shrub, and small tree growth compared to a portion of the same site that was not thinned (Yazoo NWR internal report and personal observations). Although the thinning did not result in recruitment of non-planted trees into the overstory, it is possible that mortality of suppressed individuals was abated by increased light availability before remaining overstory trees again attained canopy closure (within ca. 2 yr). Evidence from other sites of different ages suggests that perhaps the thinning occurred too late and most colonizing trees had already died. Thus, perhaps if sites were thinned earlier, there would be more opportunity for colonizing trees to recruit before they suffer substantial mortality or become so suppressed that they are unable to recruit into the canopy during the short time between thinning and canopy closure.

Based on these observations, I investigated the effects of different levels and timings of thinning on tree species composition and abundance in the overstory of simulated reforestation plantations. I assessed effects of thinning in reforestation sites established under simulated planting of seedlings or sowing of acorns. Results from these analyses can be interpreted as hypotheses for optimal thinning prescriptions in real restoration sites established under the two scenarios.

METHODS

YAFSIM simulation model.—Details of the simulation model YAFSIM are in Chapter 3, and its mechanistic seed dispersal algorithm is described and analyzed in Chapter 2. Briefly, YAFSIM tracks the dispersal, establishment, growth, and survival of bottomland hardwood forests in simulated 3-dimensional space. Dispersal is modeled mechanistically for wind-dispersed species and probabilistically for animal-dispersed species (Fig. 4.1 shows species and dispersal agents). Seedling germination and establishment is a probabilistic function dependent only on species, whereas survival and growth are functions of species and crowding in the vicinity of each individual. Specifically, crowding affects growth, which in turn affects survival probability (better growth results in higher survival probability). Species that grow large enough (≥ 15 cm dbh [diameter at breast height, 1.4 m]) become reproductively mature and disperse seeds of their own. YAFSIM tracks dispersal and subsequent processes at any point in the model landscape, and results of size distributions by species are reported for user-specified assessment plots.

I simulated tree colonization, growth, and mortality in restoration sites initialized with seedlings or acorns in an equal proportion of willow oak (*Q. phellos*), water oak (*Q. nigra*), Nuttall oak, and cherrybark oak, the most commonly used species for real reforestation sites (Schoenholtz et al. 2001). To simulate reforestation sites established with seedlings, sites were initialized at a density of 890 seedlings/ha (based on values reported in Twedt and Wilson 2002), 2 mm diameter and age of 2 yr (to bypass density-independent seedling survival in YAFSIM). To simulate reforestation sites established with acorns, sites were initialized at a density of 3950 acorns/ha (based on values reported in Twedt and Wilson 2002) and 0 yr old. Because acorns were sown in the soil and not simply scattered on the soil surface (as YAFSIM assumes), I adjusted the germination rate of sown acorns to reflect observed germination and first year survival estimates (from Johnson and Krinard 1985); thus, to reflect the resulting germination rate, I multiplied acorn sowing density by a germination rate of 0.625. Germinating acorns then received an initial diameter of 1 mm, as did all other germinating seeds in the model.

I simulated each scenario for 50 yr with 5 runs, each with a different random arrangement of trees in reforestation sites. Simulated reforestation sites were located around a square 50 × 50–m forest. Trees in the forest were selected at random from sample data (see next section). Simulation output was summarized in and averaged among 24 0.4-ha (11.3-m radius) sample plots with centers from 12.5–137.5 m from forest edge at 25-m intervals in cardinal direction within simulated reforestation sites.

Simulated effects of thinning.—Thinning was simulated by specifying a diameter interval and species to cull at a specific time. I chose thinning levels and timings by comparing diameter distributions of trees in real and simulated reforestation sites to a stocking guide for bottomland hardwoods (Goelz 1995; Fig. 5.1). My goals for thinning were to encourage growth of both planted and colonizing trees. Therefore, a "low thinning" of planted species was performed in all cases, where trees were culled in the lower size classes, leaving trees in upper size classes free to grow (as recommended by Meadows 1996 and Goelz and Meadows 1997). However, in contrast to the usual goal of bottomland hardwood forestry to encourage growth of oaks at the expense of other species, my goal was the opposite: to encourage recruitment of species other than oaks, while maintaining a large degree of forest cover. Therefore, whereas Meadows (1996) and Goelz and Meadows (1997) recommend frequent, light thinnings to encourage growth of dominant oaks, I wanted thinnings to be heavy enough so that understory colonizing trees would have a chance to recruit into the overstory. Therefore, I selected diameters to cull so that the expected average residual diameter and tree density would correspond to stocking levels just below the residual stocking level recommended by Putnam et al. (1960; see "B"-line in Fig. 5.1).

Based on these considerations, I investigated effects of thinning at different times and different diameter classes (see Table 5.1). I investigated effects of thinning on both planted and colonizing trees by comparing diameter and height distributions of thinned stands at various time intervals after thinning to distributions for unthinned stands of the same age.

RESULTS

Figs. 5.2–5.7 show size distributions (height and dbh) averaged among plots within each model run and among model runs for thinned and unthinned sites for each scenario. Model stochasticity did not result in much variability (i.e., standard errors were < 5% of means) among model runs within the various dbh and height classes; thus any differences in stem densities that are apparent in Fig. 5.2–5.7 are real, and error bars are not shown to reduce clutter.

As expected, culling 0–7.5-cm planted (from seedlings) trees at year 15 resulted in stem distributions somewhat below the "B"-line (Fig. 5.1, 5.2A-B). Five years after thinning, there was a large increase in stem densities of colonizers in small dbh classes, and increased numbers of planted trees in mid dbh classes, but not much change in tree height distributions compared to unthinned runs of the same age, except that there were fewer planted species in mid-height ranges (Fig. 5.3C–D). By year 25 (10 yr after thinning), there were still more colonizing stems in small dbh classes, but not in larger classes compared to unthinned runs (Fig. 5.2E-F). There were increased numbers of planted species in larger dbh classes (Fig. 5.2E–F), though, and increased height growth of both planted and colonizing trees (Fig. 5.3E-F). By year 50 (25 yr after thinning), thinning in year 15 resulted in more colonizing trees reaching the tallest height class, but few of these were in larger dbh classes; there were also fewer planted trees in the largest height class (Fig. 5.2G-H, 5.3G–H). Also, compared to unthinned stands at year 50, which were highly overstocked (stocking > 110%), stands of this age that were thinned at year 15 had ca. 90–100% stocking (Fig. 5.1, 5.2G–H).

Culling 0–7.5-cm sown (from acorns) trees at year 15 also resulted in stem distributions below the "B"-line (Fig. 5.1, 5.4A–B). Five years after thinning, there were more colonizing trees in small dbh classes, and many more planted trees in mid-dbh classes (Fig. 5.4C–D). Height distributions 5 yr after thinning were markedly affected by thinning: there were far fewer planted trees overall, but more in the tallest height class, and slightly more colonizing trees in mid height classes (Fig. 5.5C–D). By year 25, there were still more small-dbh colonizers compared to unthinned runs, but these had not grown into larger classes; there was more growth of planted trees, however, into larger dbh classes, and over 3 times more planted trees in the largest height class compared to unthinned runs of the same age (Fig. 5.5E–F). By year 50 (15 yr after thinning), thinned stands had more trees in the highest height class than unthinned stands (Fig. 5.5G–H), but these were all relatively small diameter compared to sown trees (Fig. 5.4H), and there were fewer sown trees in the highest height class compared to unthinned stands (Fig. 5.5G–H). Thinned stands had almost no sown trees but good densities of colonizers in intermediate height classes (Fig. 5.5H). Also, compared to overstocked, unthinned stands at year 50, stands of this age that were thinned at year 15 had ca. 90–100% stocking, similar to stands initiated with seedlings, but thinned stands initiated with acorns and thinned at year 15 had higher colonizer density than similarly thinned stands established with seedlings (Fig. 5.2H, 5.4H).

Comparing unthinned stands established with seedlings versus those established with acorns, stands established with seedlings had more colonizers through year 50 than those established with acorns, though in both cases colonizers occurred only in the smallest dbh classes (left columns of Fig. 5.2 and 5.4). Despite the higher numbers of colonizers in seedling-established stands, sites established with acorns responded better to thinning at year 15 than those established with seedlings, in terms of numbers of colonizers in all dbh and height classes at year 50 (Fig. 5.2H–5.5H).

Both thinning treatments on seedling-established stands at year 25 produced stem distributions near or slightly below the "B"-line (Fig. 5.1, 5.6B–C). Whether seedling-established stands were thinned at 0–12.5 cm or 0–17.5 cm dbh did not make much difference; both thinning levels similarly enhanced recruitment of colonizers into larger dbh classes and into the tallest height class by year 50, compared to unthinned runs of the same age (Fig. 5.6D–F, J–L). The lighter thinning treatment (0–12.5 cm) resulted in slightly more trees in the tallest height class compared to the heavier thinning, but both had fewer total trees in the higher height classes than the overstocked unthinned stands (Fig. 5.6J–L). In contrast, thinned stands were ca. 90 – 100% stocked (Fig. 5.1). Both thinning treatments at year 25 resulted in better colonizer recruitment compared to the thinning treatment at year 15 (Fig. 5.2, 5.3, 5.6).

Both thinning treatments on acorn-established runs produced stem distributions quite a bit below the "B"-line (Fig. 5.1, 5.7B–C). Virtually the only sown trees remaining after thinning were in the tallest height class. By year 50, there were more colonizing trees than sown trees in all dbh (Fig. 5.7D–F) and height (Fig. 5.7J–L) classes. There were far fewer trees overall in the tallest height class for thinned versus unthinned runs, although for unthinned runs, there were no colonizing trees except in the smaller dbh and height classes. Thus, both thinning levels for sown runs at year 25 produced marked improvements in colonizing recruitment compared to unthinned sites, and compared to sites that were thinned at year 15. Though the precise stocking level is difficult to determine from Fig. 5.1 and 5.7 because stem distributions were not unimodal, it is clear that both thinning levels at year 25 on stands established with acorns resulted in very poor stocking through year 50.

DISCUSSION

Thinning stands established with seedlings of oaks enhanced colonizer recruitment in both thinning ages. Sites thinned at year 25 had good recruitment of colonizers by year 50 into mid dbh and height ranges and into the tallest height class. There was very little difference between the two thinning levels at year 25; hence, the lighter thinning level (0–12.5 cm) was adequate. In contrast, sites thinned at year 15 had good colonizer recruitment through year 25, but very little of this recruitment made it into mid to high dbh classes by year 50, and there were only a few colonizers in the tallest height classes. Therefore, if only one thinning is made on such stands, it appears that the 25-year thinning is better because of the greater numbers of large colonizers at year 50 (Fig. 5.8). However, another thinning at yr 25 of sites previously thinned at year 15 might effectively enhance colonizer recruitment, especially if a low thinning of colonizers were also done to encourage recruitment of residual colonizers, while not severely lowering density of large trees. Such a thinning would reduced crowding in the smaller size classes, allowing recruitment into larger size classes.

Both thinning treatments at year 25 were too heavy for acorn-established sites, resulting in very few residual oaks, almost all of which were in the largest dbh and height class. The largest height class at year 50 had > 4 times more colonizers than oaks, but total density was low (ca. 100 stems/ha); thus both thinning treatments at year 25 failed to meet the goal of maintaining a high number of large overstory trees (Fig. 5.8). Unthinned sites established with acorns did not start to self thin until after year 25; prior to year 25, all trees appeared stunted in small diameter classes. The high sowing density in combination with the high survival of oaks explains why colonizing species were less abundant in unthinned acorn-established sites than in unthinned seedling-established sites, contrary to Allen's (1997) expectations (see also Chapter 4). The simulated thinning levels investigated were not effective because most stems were in very small size classes, and thus there were not enough large oak trees remaining after thinning to recruit into higher dbh and height classes. Perhaps an even lower thinning limit might be effective. However, sites responded very well to thinning at year 15, because thinning released suppressed trees from competition and resulted in both increased growth of oaks and of colonizers. By year 50, the tallest height class had ca. 2 times more oaks than colonizers, but colonizers were well represented; total density in larger diameter and height classes was higher than in stands thinned at year 25 (Fig. 5.8). Thinning at year 15 also produced a multi-layer canopy at intermediate age, which was absent in stands thinned at year 25. Therefore, in sites established with acorns, thinning at year 15 produced better results both with respect to diversity and growth of sown species.

Comparing the different establishment and thinning options, it appears that establishing sites with seedlings and thinning at year 25 produced similar size distributions of both oaks and colonizers as establishing sites with acorns and thinning at year 15. Thinning at an earlier age was necessary for acorn-established stands because of their high sowing density and high oak survival rates; they thus needed to be thinned earlier to make room for colonizers, whereas in seedling-established stands, which were planted at lower density, colonizing trees had more room to grow for more time. Total density of trees > 25 cm dbh was higher in acorn-established sites thinned at yr 15 than in seedling-established stands thinned in year 25 (Fig. 5.8). It is also clear from Fig. 5.8 that not thinning stands at all, regardless of establishment protocol, results in very low colonization. The choice of thinning regime will depend on which method of site establishment was used, so a clear recommendation about whether colonization is better in sites established with acorns or seedlings cannot be made from this study. However, thinning at year 15 for acorn-established sites and the lighter thinning (0–12.5-cm) for seedling-established sites produced the best results in terms of total density of large trees and density of large colonizers (Fig. 5.8).

Meadows and Goelz (1999, 2001) observed similar responses to thinning an upland water oak plantation (established with seedlings) at 28 yr post establishment compared to my simulated thinnings in seedling-established stands thinned at year 25, regarding response of residual oak trees. They observed unthinned stands to be stagnating because of a lack of opportunity for trees to gain competitive advantages over neighbors, and thus grow, as occurs in YAFSIM. Stands assessed by Meadows and Goelz (1999, 2001) did not respond as well to thinning as expected because residual trees were of low vigor. They also observed that heavy thinning, below the "B"-line, resulted in underutilization of the site because residual trees were not able to fully occupy the available growing space. Thus, it appears that for oak plantations, thinning to enhance diversity and maintaining full site occupancy (and thus optimal growth) are incompatible goals. However, if colonizers like American elm are present (i.e., they colonized and have not already been killed by competition), they might be able to compensate for oaks' inability to respond to thinning (American elm has been noted to respond well to release after suppression, Bey 1990). Nevertheless, for sites already established as oak plantations and without many colonizers in the understory or midstory, managers may need to decide which goal is more important: full site occupancy or diversity.

An alternative establishment scenario was recommended by Meadows and Goelz (1999, 2001) to obviate the need for thinning and allow development of high-quality oak trees for timber production, while also ensuring diversity: establishing plantations in a mixture of oaks and other species. In mixed red oak–sweetgum (*Liquidambar styraciflua*) stands (a subtype of bottomland hardwoods), oaks eventually gain a competitive advantage over sweetgum, but the presence of sweetgum enhances height growth of oaks and prevents formation of epicormic branches, which lower log quality (Clatterbuck and Hodges 1988, Johnson and Krinard 1988). I have also observed such a phenomenon in oak plantations where sweetgum invaded naturally. Thus, Meadows and Goelz (2001) recommend that for new reforestation sites, oaks should be planted in combination with other species, especially sweetgum, for the sole purpose of enhancing quality of planted oaks. Additionally, this practice would ensure at least some measure of diversity that does not rely on proximity to natural seed sources. Because of the uncertainty of whether thinning will be successful in promoting growth and diversity, the unreliability of natural colonization, and the uncertainty of whether thinning will actually be carried out as planned, establishing reforestation sites as mixed plantations of oaks and other species from the outset appears to be the most reasonable option for new sites. Additional modeling studies with YAFSIM under such mixed plantations are therefore warranted.

Validity of YAFSIM predictions about the effects of thinning (or mixed plantings) cannot currently be assessed because data on stem size distributions of thinned bottomland reforestation sites are not available; indeed, only one such site has been thinned, though at a much lower level of thinning than examined here. Thinnings on an upland water oak plantation were also lighter than those investigated here; they produced increased growth of residual trees, but not as much as expected because the thinned stand was of low vigor from years of suppression (Meadows and

Goelz 1999, 2001). Thinnings simulated in this study were intended to stimulate both growth of residual trees and recruitment of suppressed seedlings and saplings of colonizers. Therefore, it seems likely that YAFSIM's ability to accurately predict effects of thinning would depend to a large degree on accurate prediction of density of such seedlings and saplings.

However, despite the large influence of seedling density on stand dynamics (Porté and Bartelink 2002), the combined effects of errors in recruitment estimation and effects of thinning have not been assessed for this or any other model. More generally, models designed to assess impacts of perturbations, such as thinning, have not been validated under the perturbations assessed: i.e., model dynamics that were valid under unperturbed conditions (e.g., unthinned conditions) were assumed to also be valid under perturbed conditions (Porté and Bartelink 2002).

Thus, this paper presents a set of hypotheses of potential effects of thinning at different ages, levels, and under different establishment regimes. I recommend that such thinnings be carried out experimentally to determine the extent to which YAFSIM's predictions are valid.

Table 5.1. Timing and diameter class of thinning in simulated bottomland hardwood reforestation sites; thinning levels and timings were investigated for sites established with acorns and for sites established with seedlings of equal proportions of willow oak, water oak, and Nuttall oak.

Year of thinning	Diameter class culled*
15	0–7.5 cm
25	0–17.5 cm ("thinning A")
25	0–12.5 cm ("thinning B")

* Only planted species were culled.

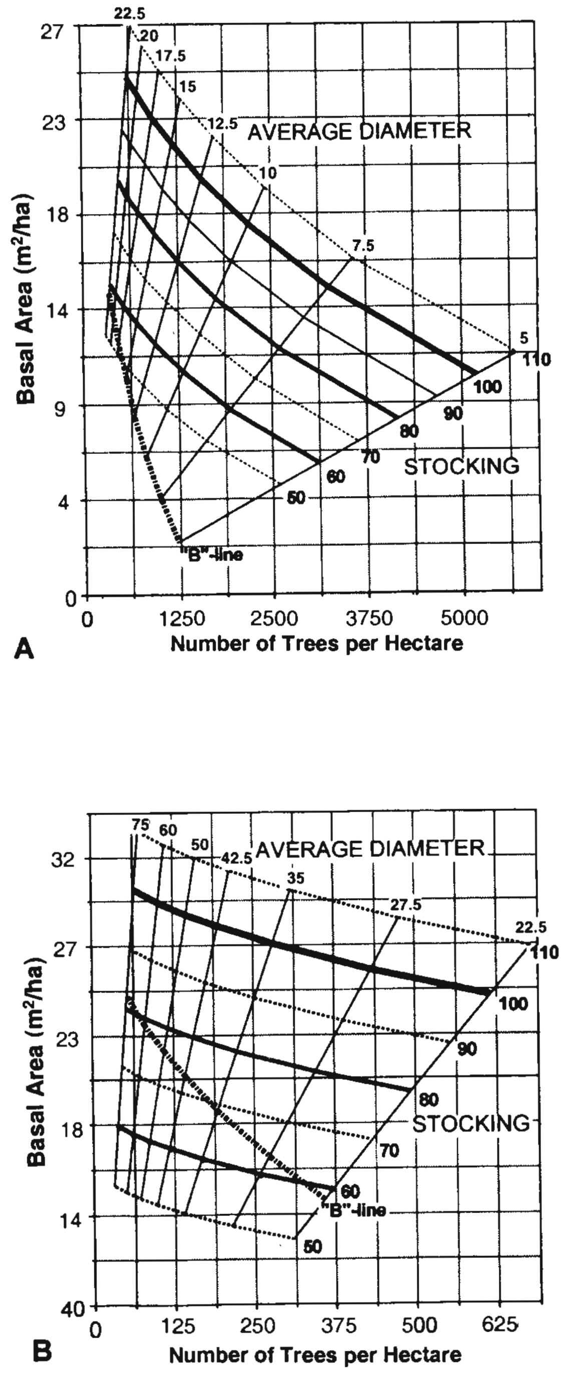


Fig. 5.1. Stocking guide for southern bottomland hardwood forests. The "B"-line represents the suggestion of Putnam et al. (1960) for desirable stocking after thinning for stands of small (A) and large (B) average diameter (quadratic mean diameter, shown in cm). Stocking is in percent. Adapted from Goelz (1995, figure 1).

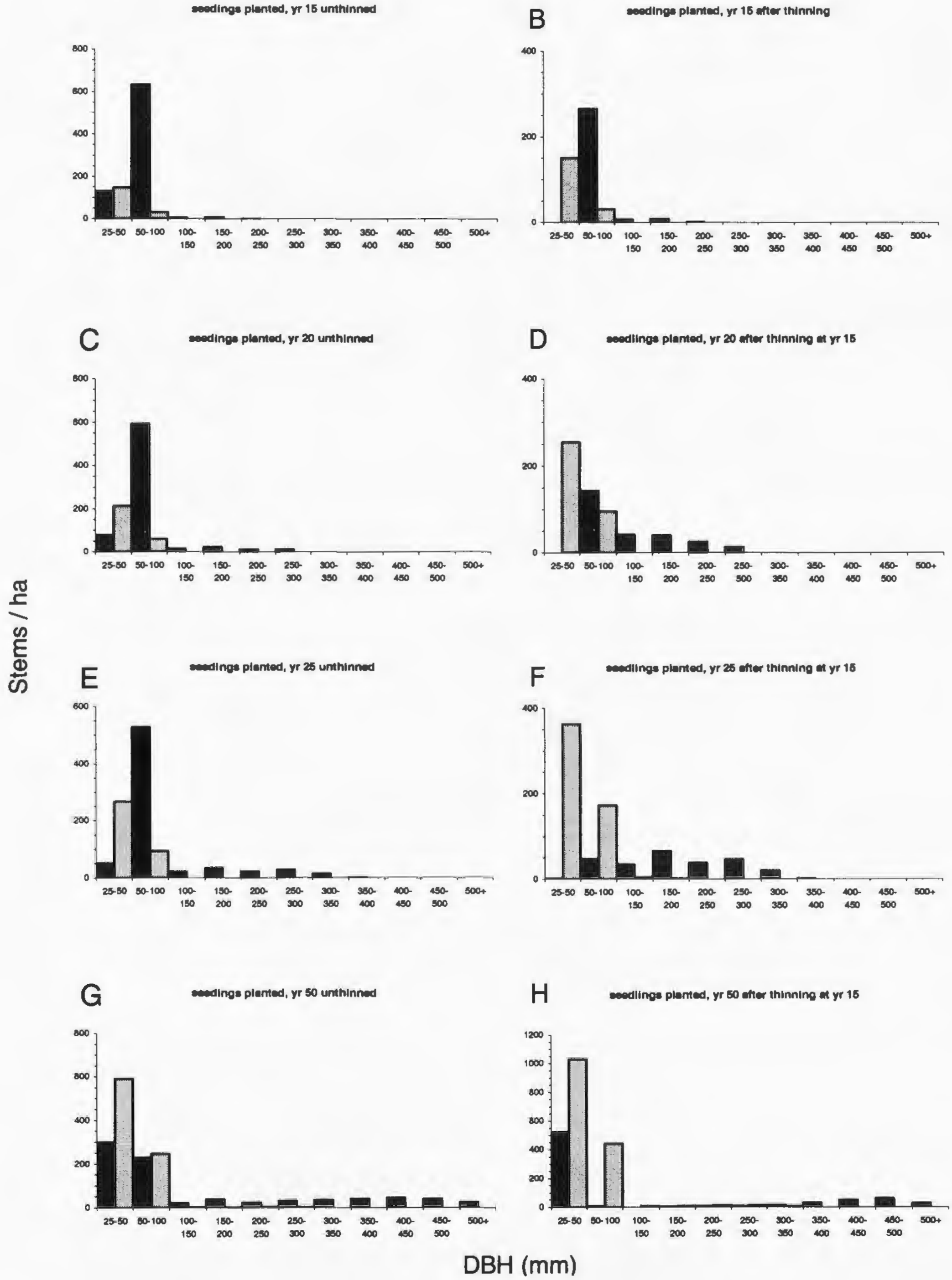


Fig. 5.2. Effects on diameter distributions of thinning 0–7.5-cm dbh planted (as seedlings) species at year 15 versus not thinning, through year 50 in simulated bottomland hardwood reforestation sites. Dark bars are planted species, light bars are colonizers.

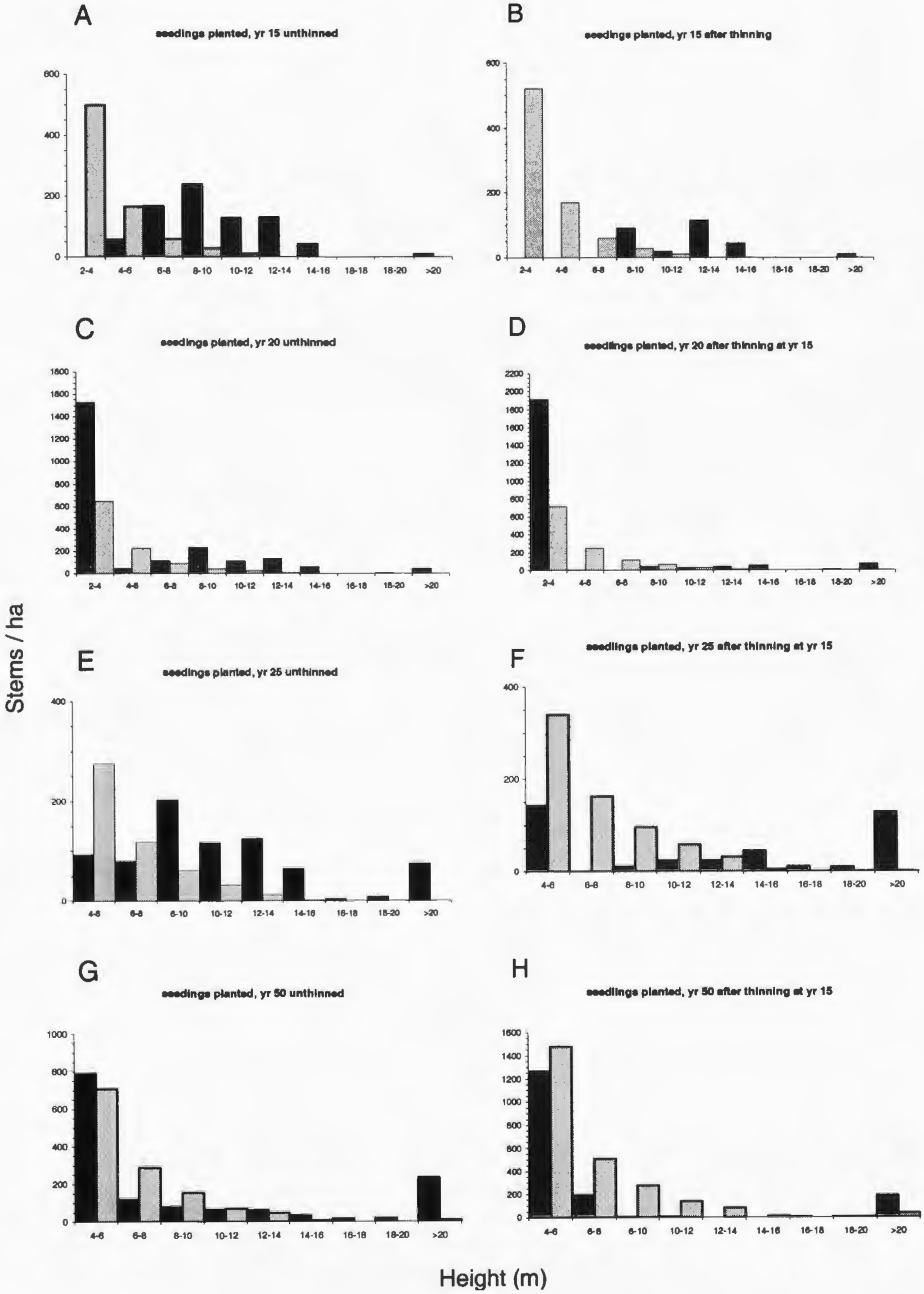


Fig. 5.3. Effects on height distributions of thinning 0–7.5-cm dbh planted (as seedlings) species at year 15 versus not thinning, through year 50 in simulated bottomland hardwood reforestation sites. Dark bars are planted species, light bars are colonizers.

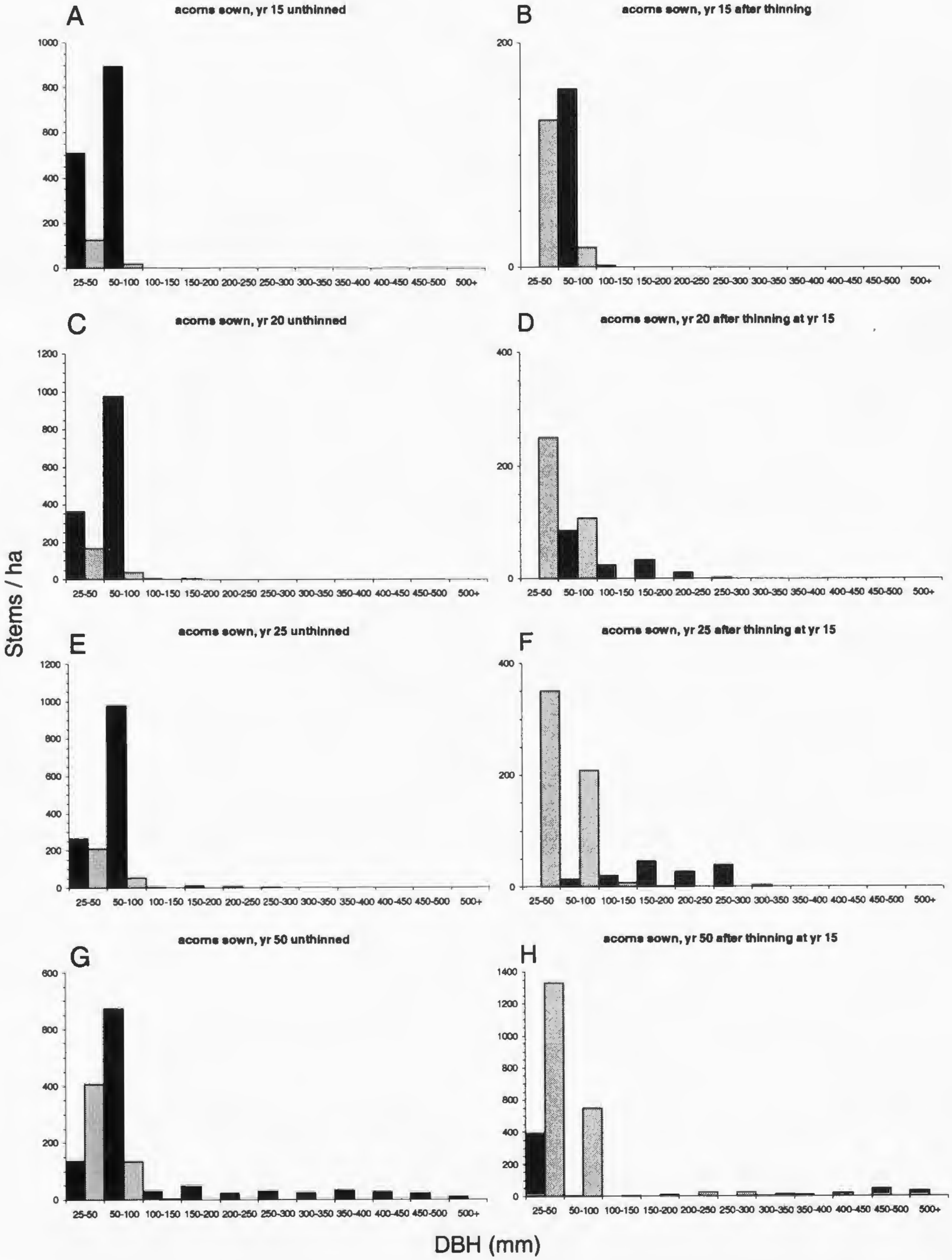


Fig. 5.4. Effects on diameter distributions of thinning 0–7.5-cm dbh sown (as acorns) species at year 15 versus not thinning, through year 50 in simulated bottomland hardwood reforestation sites. Dark bars are sown species, light bars are colonizers.

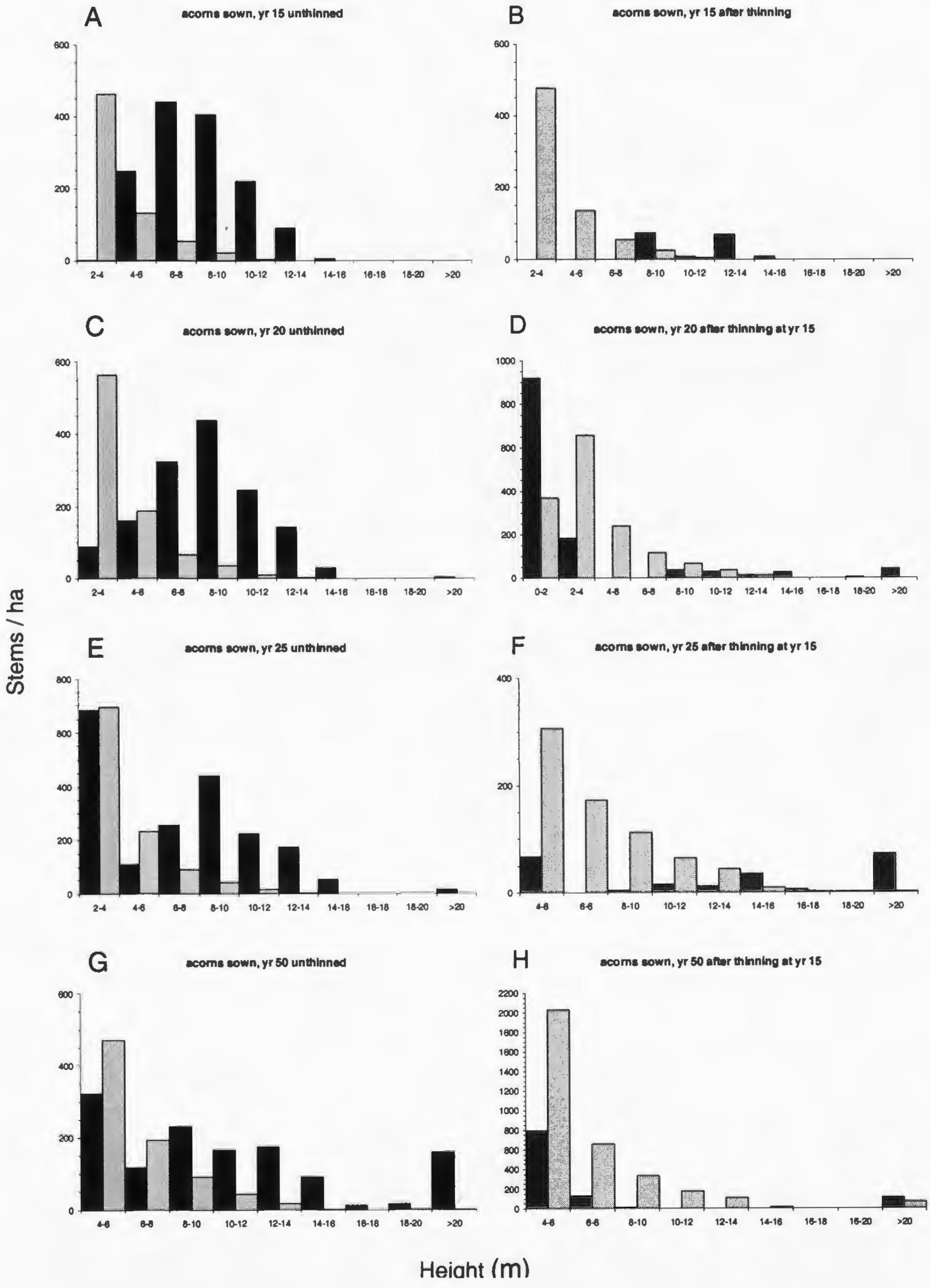


Fig. 5.5. Effects on height distributions of thinning 0–7.5-cm dbh sown (as acorns) species at year 15 versus not thinning, through year 50 in simulated bottomland hardwood reforestation sites. Dark bars are sown species, light bars are colonizers.

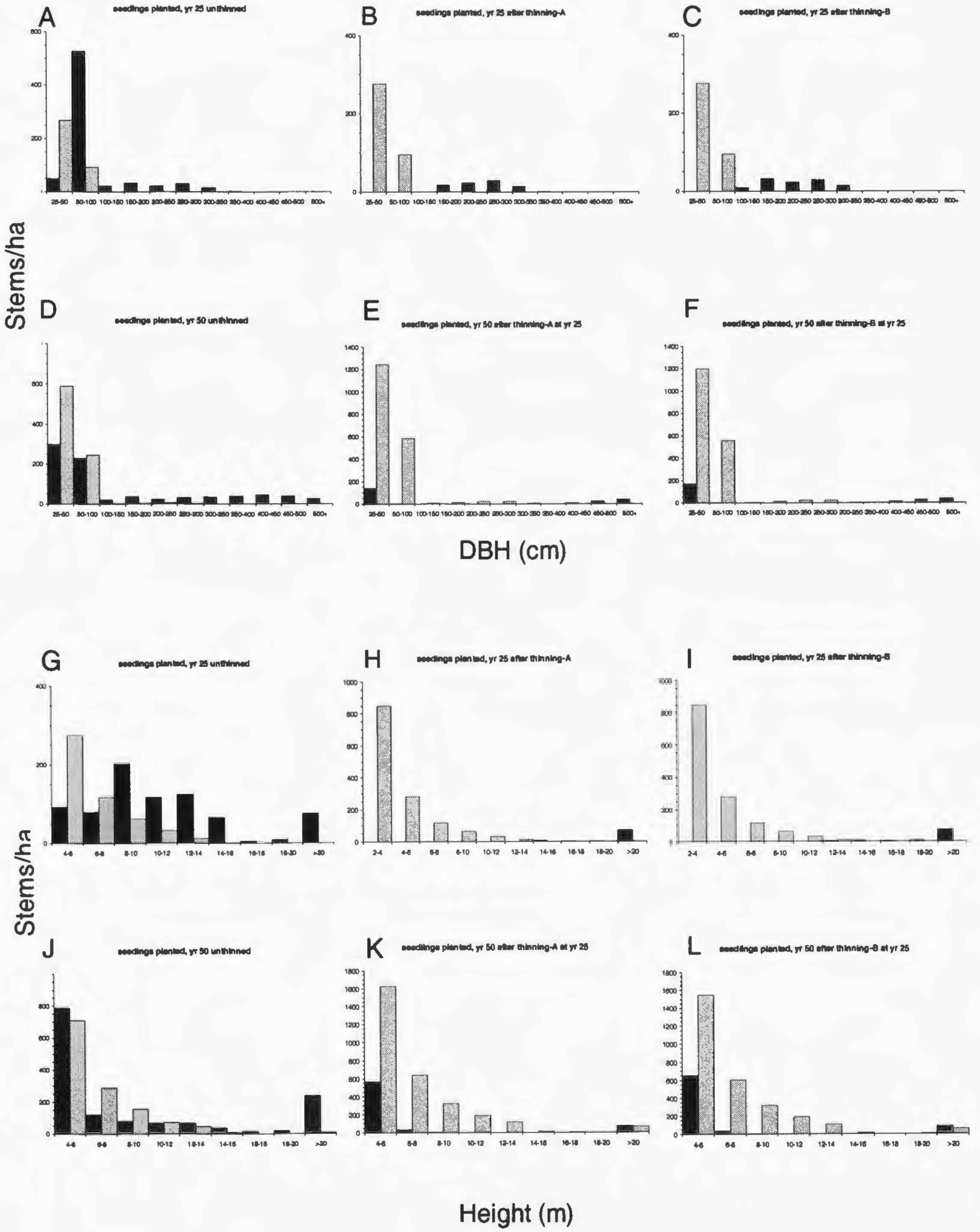


Fig. 5.6. Effects on diameter and height distributions of thinning 0–17.5-cm dbh (thinning-A) or 0–12.5-cm dbh (thinning-B) planted (as seedlings) species at year 25 versus not thinning, through year 50 in simulated bottomland hardwood reforestation sites. Dark bars are planted species, light bars are colonizers.

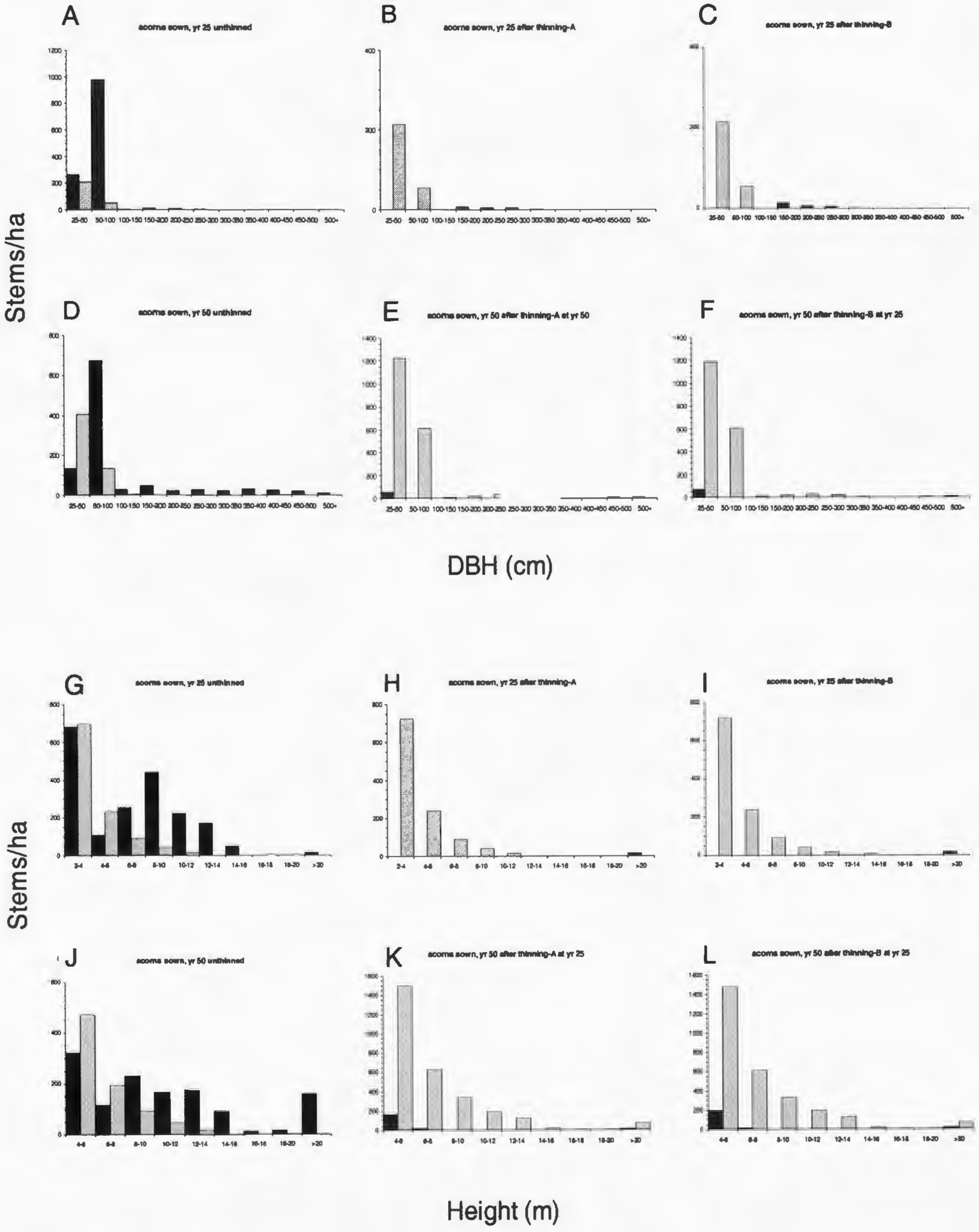


Fig. 5.7. Effects on diameter and height distributions of thinning 0–17.5-cm dbh (thinning-A) or 0–12.5-cm dbh (thinning-B) sown (as acorns) species at year 25 versus not thinning, through year 50 in simulated bottomland hardwood reforestation sites. Dark bars are sown species, shaded bars are colonizers.

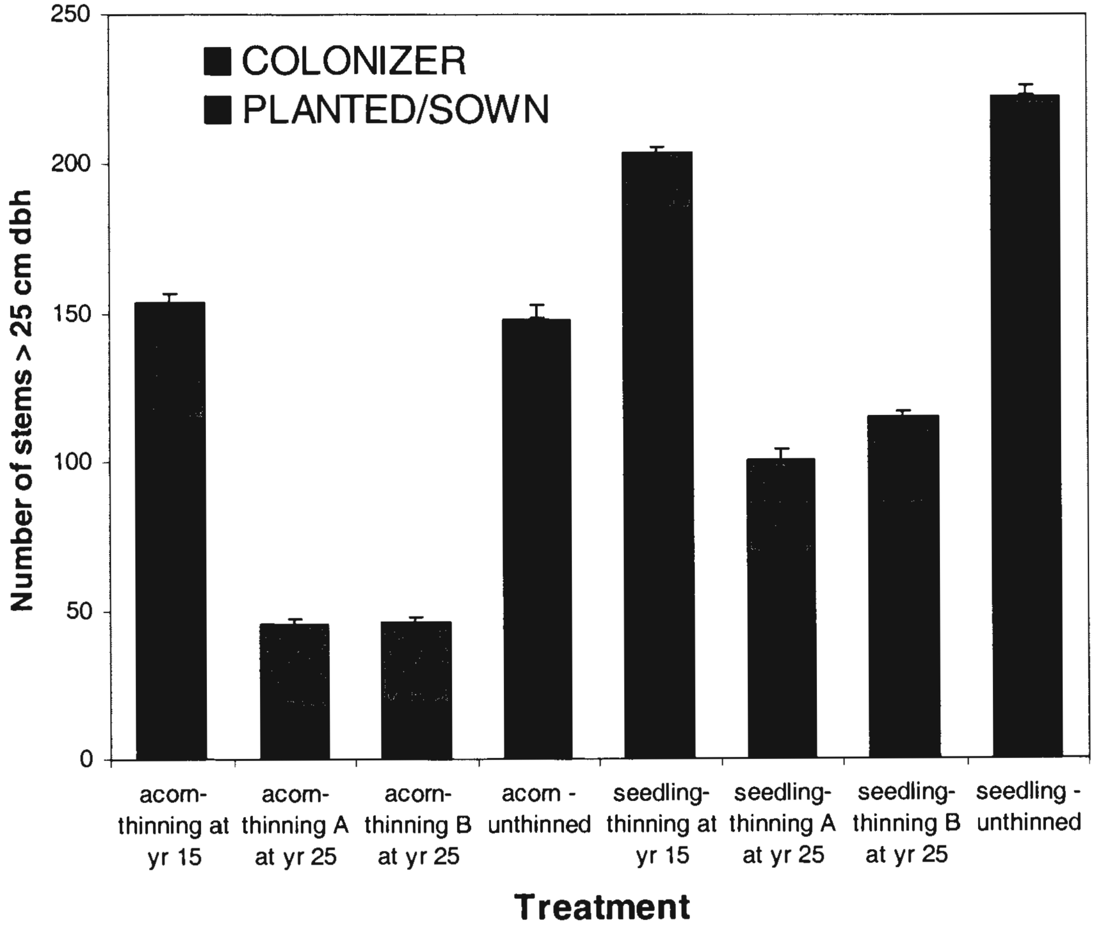


Fig. 5.8. Summary of effects (stem density/ha) at year 50 of different thinning treatments on bottomland reforestation sites established with acorns or with seedlings of oaks. Thinning treatments are defined in Table 5.1. Error bars show ±1 SE.

CHAPTER 6

CONCLUSION

This dissertation had the primary goal of explaining what factors limit development of diverse forests, with special application to bottomland hardwood reforestation sites in the Mississippi Alluvial Valley. Implicit in this goal was the expectation that by understanding limiting factors, changes in management scenarios aimed at relieving limitations might be suggested, and thus better realization of the goal of restoring diverse forest communities.

In the end, I have achieved the explicit goal of identifying limiting factors, but the implicit goal of coming up with simple ways of dealing with these limiting factors remains an enigma. Factors limiting development of diverse forests consist of limited dispersal and limited ability of dispersing species to recruit in the face of inhibition from other species that arrived first either because of superior dispersal abilities or because they were planted. Thus, my modeling study suggests that short of making sure that reforestation sites are located near diverse forests to start with or, failing that, establishing reforestation sites with more species of trees planted, there is no way to overcome dispersal limitation. Thinning oak plantations to alleviate recruitment limitation, however, was moderately successful: more opportunities were created for colonizers' recruitment into the canopy, but colonizers still represented a small subset of tree species present in the source forest.

There are two potential ways of interpreting these results. The first is that the assumptions on which YAFSIM is based, i.e., its algorithms and parameter values, must be incorrect, because diverse forests really do exist but are not produced by YAFSIM, at least not in the current context. The second interpretation is that YAFSIM is essentially correct, and hence so are its predictions; reforestation sites are destined to be low-diversity systems unless substantial changes are made, and that the current levels of diversity found in real, natural forests are present for various historical reasons that are beyond the scope of explanation afforded by YAFSIM.

But other forest simulation models do produce and maintain diverse forest communities. So why doesn't YAFSIM? There are numerous very good reasons, as numerous perhaps as the individual models themselves. But most important is that all other forest simulators, from JABOWA (Botkin 1993) to the Unified Neutral Theory of Biodiversity and Biogeography (UNTBB, Hubbell 2001) start with diverse communities throughout the area of interest. I have started from a quite different scenario: the diverse community is spatially separated from the area of primary interest, and species must disperse to the area of interest to have a chance at becoming a member of the community. Therefore, resultant communities were shaped first by what species arrived in high abundance early in the simulation. This point brings up the issue of species differences in dispersal ability. Not only do all other models start out diverse, but diversity in gap models is further ensured because all species have universal dispersal and the potential source population is infinite. Some gap models have modified this assumption slightly but all species have the same dispersal abilities and fecundities. Hence, these models are neutral with respect to dispersal, as of course is the UNTBB. So because in each of these models the forest starts off diverse, and all species have identical dispersal properties, the only mechanism left for reducing diversity are stochastic processes and niche-assembly interactions, which can take a very long time to exert themselves (e.g., 500–1000 yr in SORTIE, Pacala et al. 1996). Even in models that do include species differences in dispersal, species differences are not large, and once again, the communities start out diverse (see Pacala et al. 1996, Chave 1999).

So the fact that YAFSIM fails to produce diverse forests in reforestation sites under any scenario should not be surprising. But let's return to the issue how YAFSIM might fail to be a realistic model. It remains somewhat disconcerting that the species that ends up dominating simulated reforestation sites, either as the overall dominant in nonplanted sites or as the dominant colonizing species in planted sites, is always the same (namely, American elm). Simulated source forests were an amalgam of all sampled forests, so site differences with respect to species composition were eliminated. Real reforestation sites of course do not receive colonists from an amalgamated source forest, but from real forests that are not homogeneous. Hence, one would expect differences in species composition of source forests to be reflected to some degree in composition of nearby reforestation sites. This is a question that could be addressed with additional model runs that are initiated with specified forest compositions in the source forest, although it is obvious that in the extreme of total absence of American elm in the source forest, reforestation sites will be dominated by some other species.

Another issue that has the potential to greatly affect model results is the assumed shape of the dispersal functions for animal-dispersed seeds. In the current analyses, animal-dispersed species were universally rare colonists, restricted to reforestation plots adjacent to the source forest (unless they were planted in the reforestation site). There are several problems with the way I modeled animal dispersal. First, the mechanisms of animal dispersal are varied and complex, so I used a phenomenological function with shape parameters and mean dispersal distances borrowed from other systems, and sometimes from other, similar species (Clark et al. 1998b). The problem with this approach is that it fails to account for differences between the system for which the functions were fit and the system to which I applied them; these differences could be many and are unknown. Another problem is that my fecundity-parameter fits to these functions, based on my empirical seed dispersal data, were generally poor, in part because of small sample sizes to estimate the parameters, although it could be that the functional form itself is not a good choice (as for long-distance wind dispersal, see Nathan et al. 2002b); without more data, it is hard to tell. It would therefore be interesting to develop a mechanistic algorithm for animal dispersal of the relevant species (perhaps building from Johnson et al. 1981).

Yet another issue is that even once good models of seed dispersal for all species are developed, there is still a general lack of data on transitions from seeds to adults, including the mechanisms behind these transitions. I used simple transition probabilities between seeds and seedlings, based on published data, and hence did not include any mechanism for germination or establishment. As mentioned in Chapter 3, flooding effects on establishment of the species modeled here has been addressed in other models (Tharp 1978, Phipps 1979), and YAFSIM could easily be modified to assume different flooding depths and frequencies in different model runs, with flooding depth and frequency homogeneous within a model run. Analyzing the effects of spatially variable flooding is a major conceptual and modeling challenge, because it would be difficult to assess the importance of these processes relative to other spatial processes. Furthermore, I attempted to assess seedling emergence from sown seeds in the field at Yazoo NWR, to derive my own empirical data and assess potential mechanisms, but the study was not successful. Not only was I unable to establish very many seed-sowing plots, but the plots I did establish failed to produce a single seedling. According to Table 3.1, these species (American elm, red maple, sweetgum) have average germination rates of 1–9%. However, my failure to observe any emergence, despite sowing several hundred seeds, suggests that in reforestation sites, real emergence rates might be more on the order of those observed by Pinder et al. (1995) for loblolly pine (*Pinus taeda*) in old fields of the southeast United States, namely 1 in 3,000 to 1 in 30,000. Such dramatic reductions in germination probability were not assessed in my sensitivity analyses, so it might be interesting to examine their consequences for community development. Even more interesting is the possibility that emergence rates might be highly variable from year to year and from species to species, another factor not addressed that might have dramatic consequences if it changes the relative proportions of seedlings of the various species that establish at a given site.

I have briefly touched on some additional model analyses and refinements that would allow assessment of both how realistic the current version of YAFSIM is and address some additional theoretical and practical questions. There are many other modeling experiments and refinements that may address additional questions or tease apart additional details and mechanisms. On the whole, however, YAFSIM, with its wind-dispersal algorithm, produces very reasonable—and reasonably accurate—predictions of spatial patterns of seed dispersal and resulting forest community development both in natural forest and reforestation sites. The exact identities of colonizing species are not so important as the general result that emerged over the many sensitivity runs and alternative scenarios: differences in dispersal ability among species have profound effects on species composition both in the near and long term because species that arrive first sequester the site from subsequent colonization.

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CURRICULUM VITAE

Timothy James Nuttle
(October 2003)

CAREER OBJECTIVE:

To become a university professor.

EDUCATION:

2003 Ph.D., Ecology, Utah State University, 3.91 GPA.
1997 M.S., Wildlife Ecology, Mississippi State University, 3.76 GPA.
1993 B.S., Wildlife Ecology & Management, Honors College, Michigan State University, withnor. 3.57 GPA.

RESEARCH EXPERIENCE:

2002-present **Postdoctoral Research Fellow,** *Institute of Ecology, Friedrich Schiller University Jena.*

Developing and testing conceptual and qualitative reasoning models of ecosystem recovery from degradation. Co-edited the book *Assembly Rules in Restoration Ecology* (Island Press). Co-organized workshop on qualitative reasoning models for stream ecosystem recovery.

1998-2002 **Doctoral Research Fellow/Research Assistant**, *Department of Biology and Ecology Center, Utah State University.*

Developed a spatially explicit computer simulation model (written in C) to investigate processes leading to spatial patterning of tree colonization in forested wetland restoration sites in the Mississippi Alluvial Valley. This is the first forest simulation model to include mechanistic algorithms for seed dispersal. The model was used to forecast likely success of restoration efforts based on initial planting regime, location of source populations of trees, wind patterns, and species characteristics such as growth, survival, and dispersal. Model development was based on a foundation of my empirical fieldwork, in cooperation with USDA Forest Service, US Fish & Wildlife Service, and National Wetlands Research Center, and published literature. Funded by the Willard Eccles Foundation, Yazoo National Wildlife Refuge, USU Ecology Center, and the USDA Forest Service Center for Bottomland Hardwoods Research.

1997-1998 **State Coordinator of Mississippi Ornithological Atlas Project, Avian Database Manager**. *Mississippi Gap Analysis Project, Mississippi Cooperative Fish & Wildlife Research Unit.*

Directed the Mississippi Ornithological Atlas Project in its inaugural year, and thus developed all protocols for winter/breeding season bird monitoring, including compilation of all handbooks, data forms, bulletins, etc. Conducted numerous workshops and one-on-one consultations throughout Mississippi to instruct volunteer birders in the more scientific procedures of data collection for the Atlas. Received a grant from the USDA Forest Service to establish a bird-monitoring program on all National Forests in Mississippi. For the Gap Analysis Project, compiled range maps and habitat data for all Mississippi birds. All projects involved extensive use and development of various GIS databases.

1994-1997 **Graduate Research Assistant**. *Department of Wildlife & Fisheries, Mississippi State University.*
Investigated bird-community response to restoration of forested wetlands in the Mississippi Alluvial Valley. Research identified ways in which restoration practices can be improved to enhance both avian conservation and development of more diverse vegetation communities in restoration sites. Research in this system lead to an invitation to write a chapter for the book *Bottomland Hardwood Ecosystems: the State of Our Understanding*. Funded by the McIntyre-Stennis Ecosystem Project of the College of Forest Resources, Mississippi State University; Yazoo National Wildlife Refuge, and Delta National Forest.

1998 **Research Assistant**. *Department of Fisheries & Wildlife, Utah State University.*
Conducted winter and breeding-season bird surveys and monitored bird nests. Participated in trapping, handling, and radiotracking mule deer and cougars.

1992-1994 **Research Aide, Wildlife**. *Department of Fisheries & Wildlife, Michigan State University.*
Participated in a broad array of research projects, under the direction of several faculty and graduate students, including analyzing small mammal community data and presenting the resulting paper at Michigan Academy of Science, compiling GIS databases of forest land cover, capturing and radio-tracking raccoons, censusing forest songbirds and surveying forest vegetation on Hiawatha National Forest (a cooperative project with the USDA Forest Service), and entering data.

1990-1992 **Research Aide, Fisheries**. *Department of Fisheries & Wildlife, Michigan State University.*
Participated in a broad array of research projects, under the direction of several faculty and graduate students, including an independent research project on microhabitat use of stream fish, laboratory analysis of energetics, sorting and identifying aquatic invertebrates, and assisting with field monitoring projects of stream fisheries. Led field research on a project to monitor stream fisheries in northern Michigan.

TEACHING EXPERIENCE:

1999 **Laboratory Instructor:** Terrestrial Ecology Laboratory, *Department of Fisheries & Wildlife, Utah State University.*
Co-instructor of course emphasizing hypothesis testing of field and laboratory analyses of terrestrial populations, communities, and ecosystems. Course culminated in students developing a small research project to test ecological hypotheses of their choosing, using data collected at a common field site.

1998 **Laboratory Instructor**: Introductory Biology Laboratory (3 sections), *Biology Department, Utah State University.*
Focused on comparative anatomy, animal diversity, and ecology. Developed all quizzes, homework, and lecture material for my sections. Participated in a project to better integrate quantitative lab exercises throughout the biology curriculum.

1998-2000 **Teaching Assistant.** *Department of Fisheries & Wildlife, Utah State University.*
Assisted faculty with: Wildlife Diversity Laboratory, Fish & Wildlife Populations, Management of Wildlife Populations, and Wildlife Law Enforcement.

1999 **Teaching Assistant Workshop**. *Utah State University.*

PUBLICATIONS:

Books:

Temperton, V. M., R. J. Hobbs, T. Nuttle, and S. Halle. 2004 (in press). *Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice.* Island Press

Peer-reviewed articles:

Nuttle, T., and J.W. Haefner. A mechanistic model for wind-dispersed seeds in heterogeneous environments: design and validation. Submitted to *Ecology.*

Nuttle, T., and J. W. Haefner. A forest dynamics model that explicitly incorporates seeds and seedlings: implications for forest restoration. Submitted to *Ecological Monographs.*

Nuttle, T., and J. W. Haefner. Thinning strategies for bottomland hardwood forests: applications of a forest simulator. In preparation for *Forest Ecology and Management.*

Temperton, V. M., R. J. Hobbs, T. Nuttle, M. Fattorini, and S. Halle. 2004 (in press). Introduction: why assembly rules are important to the field of restoration ecology. In *Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice.* Island Press.

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Nuttle, T., and L. W. Burger. 2003 (in press). Birds of bottomland hardwood restoration sites: patterns of occurrence and response to vegetation structure. In L. Fredrickson, M. Heytmeier, and R. Kaminski, eds. *Ecology and Management of Bottomland Hardwood Systems: the State of our Understanding.* Mississippi State University Press.

Nuttle, T., A. Leidolf, and L. W. Burger. 2003. Assessing the conservation value of bird communities with Partners in Flight–based ranks. *Auk* 120:541-549.

Leidolf, A., S. McDaniel, and T. Nuttle. 2002. The flora of Oktibbeha County, Mississippi. *Sida* 20(2):691-765

Hamel, P. B., D. J. Twedt, T. J. Nuttle, C. A. Woodson, F. Broerman, and J. M. Wahome. 2002. Winter bird communities in afforestation: should we speed up or slow down ecological succession? Pages 98-108 in M. M. Holland, M. L. Warren, and J. A. Stanturf, editors. *Proceedings of a conference on sustainability of wetlands and water resources: how well can riverine wetlands continue to support society into the 21st century?.* U. S. Forest Service General Technical Report SRS-50.

Nuttle, T. 1997. Densiometer bias? are we measuring the forest or the trees? *Wildlife Society Bulletin* 25(3):610-611.

Nuttle, T. and L. W. Burger. 1996. Response of breeding bird communities to restoration of hardwood bottomlands. *Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies* 50:228-236.

Published abstracts (peer reviewed):

Nuttle, T., and J. W. Haefner. 2003. A mechanistic model for wind-dispersed seeds in heterogeneous environments: design and validation. Annual Meeting of the Ecological Society of America, Savannah, Georgia.

Nuttle, T. 2003. A model of tree colonization in forested wetland restoration sites of the Mississippi Alluvial Valley. Restoration of river valleys: Annual meeting of the working group for restoration ecology of the Gesellschaft für Ökologie, Kiel, Germany.

Nuttle, T., and J. W. Haefner. 2002. Incorporating a mechanistic algorithm of seed dispersal by wind into a spatially explicit simulation model of forest dynamics. Annual Meeting of the Ecological Society of America, Tucson, Arizona.

Nuttle, T., and J. W. Haefner. 2000. Modeling restoration processes in a bottomland forest-agricultural landscape: Mississippi Alluvial Valley hardwood bottomland reforestation sites. Annual Meeting of the Ecological Society of America, Salt Lake City, Utah.

Nuttle, T., A. Leidolf, and L. W. Burger, Jr. 2000. Using Partners in Flight species concern scores to compare the conservation value of bird communities. Birds 2000: Joint Meeting of the American Ornithologists' Union, British Ornithologists' Union, and Union of Canadian Ornithologists. St. John's, Newfoundland.

Nuttle, T., F. J. Vilella, and R. B. Minnis. 1997. The Mississippi Ornithological Atlas: a statewide survey of birds. Annual Meeting of the Mississippi Chapter of the Wildlife Society. Mississippi State, Mississippi.

Nuttle, T. and L. W. Burger. 1996. Breeding bird response to afforestation of hardwood bottomlands. The Delta Conference. Memphis, Tennessee.

Nuttle, T. and L. W. Burger. 1995. Breeding avian community response to restoration of hardwood bottomlands. Midwest Fish and Wildlife Conference. Detroit, Michigan.

Nuttle, T. and L. W. Burger. 1995. Breeding bird response to hardwood bottomland restoration in the Mississippi Alluvial Valley. Second Annual Conference of The Wildlife Society. Portland, Oregon.

Nuttle, T., G. Dudderar, and S. R. Winterstein. 1994. Small mammal community response to prairie restoration. Michigan of Academy of Science, Arts, & Letters Centennial Meeting. East Lansing, Michigan.

GRANTSMANSHIP, FELLOWSHIPS, & SCHOLARSHIPS (POST-BACCALAUREATE):

2003	European Commission, Sixth Framework Programme, Specific Target Research Project "Qualitative Reasoning for Education and Decision Support: Integrated Modelling Environment for Understanding Sustainable Development and Restoration of River Ecosystems." 2.1 million Euros (in review). 3 years, 9 partner institutions.
2003	NATO Advanced Research Workshop "Qualitative Simulations in Ecology: applications to stream ecosystem restoration and recovery." 34,172 Euros (in review).
2003	European Commission, Sixth Framework Programme, Specific Target Research Project "Qualitative Reasoning for Stream Ecosystem Restoration and Recovery". 3.5 million Euros (not funded). 3 years, 15 partner institutions.
2001	US Fish & Wildlife Service, Yazoo National Wildlife Refuge. "Factors affecting the distribution of trees in real and simulated hardwood bottomland restoration sites in the Mississippi Alluvial Valley" (renewal). $4,784. 12 months.
2000	US Department of Agriculture, National Research Initiative. "Modeling restoration processes in a bottomland forest-agricultural landscape" with PI's J. W. Haefner and E. W. Schupp. $223,701 (not funded). 30 months
2000	US Fish & Wildlife Service, Yazoo National Wildlife Refuge. "Factors affecting the distribution of trees in real and simulated hardwood bottomland restoration sites in the Mississippi Alluvial Valley". $2,267. 12 months.
2000	USU Ecology Center. "Factors affecting the distribution of trees in real and simulated hardwood bottomland restoration sites" (renewal). $3,200. 12 months.
2000	USU Gay & Lesbian Diversity Scholarship. $1,000.
1999	USU Ecology Center. "Factors affecting tree colonization of natural and afforested hardwood bottomlands". $2,500. 12 months.
1998	USU College of Science, Willard F. Eccles Foundation Fellowship. $48,000. 36 months.
1997	USDA Forest Service, National Forests of Mississippi. "Monitoring avian communities of National Forests in Mississippi". $50,000. 12 months.

1995	The Wildlife Society. Travel Grant. $300.
1995	USDA Forest Service, challenge cost-share grant. "Monitoring avian communities of Delta National Forest". $500. 2 months.

SELECTED UNIVERSITY COMMITTEES AND STUDENT ORGANIZATIONS:

- USU Ecology Center, Seminar Committee, 1999-2001; chair of committee in 2000-2001.
- USU President's Diversity Board, 1999-2002
- USU Pride! Alliance (Gay, Lesbian, Bisexual Alliance), Executive Board member 1998-2002.
- Mississippi State University chapter of The Wildlife Society, 1994-1996. President in 1995-1996.
- Michigan State University, Lyman Briggs School, Student Advisory Council, 1991-1992.

LANGUAGES:

- English (mother language)
- German (good conversational and reading ability)
- French (advanced university instruction, excellent reading ability, good conversational ability)
- Spanish (advanced university instruction, excellent reading ability, good conversational ability)