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The increasing scarcity of red oaks in Mississippi River floodplain forests: Influence of the residual overstory

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Abstract

Red oaks – cherrybark oak (*Quercus pagoda* Raf.), willow oak (*Quercus phellos* L.), water oak (*Quercus nigra* L.), and Nuttall oak (*Quercus texana* Buckley; aka: *Quercus nuttallii* Palmer) – are not regrowing in Mississippi Delta river floodplain forests in the southeastern United States in sufficient numbers to sustain the former species composition and timber and wildlife values. Even if vigorous red oak reproduction becomes established, partial harvesting that does not remove the taller trees will suppress understory red oak height growth more than it will suppress height growth of such other species as sugarberry (*Celtis laevigata* Willd.), American elm (*Ulmus americana* L.), cedar elm (*Ulmus crassifolia* Nutt.), swamp dogwood (*Cornus foemina* Mill.), green ash (*Fraxinus pennsylvanica* Marshall), and sweetgum (*Liquidambar styraciflua* L.). Consequently, the red oaks in these partially harvested stands become increasingly suppressed and probably die; and there is a shift in species composition to the other species. In addition to ensuring vigorous oak reproduction, silvicultural clearcutting or rapid removal of the residual trees following shelterwood or seed tree harvesting to provide full sunlight is needed to ensure red oaks become a dominant part of these future river floodplain stands.

Keywords: River floodplain forests; *Quercus*; Red oaks; Regeneration; Silvicultural systems; Clearcutting; Shade tolerance; Bottomland forests; Hardwood forests

1. Introduction

Young red oaks may not be regrowing in sufficient numbers to sustain oak-dominated stands in many river floodplain (a.k.a. "bottomland") forests of the southeastern United States (Johnson, 1979; Janzen and Hodges, 1985; Lockhart et al., 2000). Recent studies (Loftis and McGee, 1993) are suggesting that red oaks may not be regrowing in some other areas of the United States as well; and inventory data shows a greater proportion of shade tolerant species in small diameter classes, suggesting that forests may be changing to species other than red oaks in many parts of the eastern United States (Smith and Sheffield,

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2000). If this shift away from oak forests is occurring in river floodplain hardwood forests, it could harm the wildlife depending on acorn mast, the timber income to the landowners, and the high quality hardwood timber industry, among others (Clatterbuck and Meadows, 1992).

Many factors may be contributing to this shortage of young red oaks, if in fact it is occurring: the forests have been fragmented by agricultural fields, the flooding and drainage patterns have been altered by ditches and levees, the climate has changed, wild and domestic animal populations have changed, introduced insects and diseases may have an impact, and the natural and human disturbance patterns have changed. A combination of several factors is probably contributing to the apparent scarcity of red oaks, and the challenge is to determine the most influential and proximate causes. A shortage of vigorous oak reproduction and poor subsequent growth of the vigorous reproduction that does exist have been suggested as important causes. Reproduction vigor is being studied for these river floodplain red oaks (Gardiner and Hodges, 1998; Gardiner et al., 2004), and subsequent growth has been studied in other ecosystem types by Loftis and McGee (1993). This study addresses the influence of various densities of residual trees left after harvesting on subsequent growth of young red oaks in the river floodplain forests. Residual trees are overstory and understory trees left after harvesting. The red oaks and other species which began with the last harvesting or were in the understory before harvesting are referred to as "recruiting" trees. Shade from the residual trees may hinder growth of the recruiting oaks and prevent them from growing to the overstory.

This study first determined if there are enough recruiting red oaks to replace the mature red oaks that are being harvested in floodplain forests. Then it examined the effects of residual trees on height growth of recruiting red oaks and other species. The red oaks (subgenus *Erythrobalanus*) are especially valuable and were historically abundant in these forests. The study focuses on the species cherrybark oak, willow oak, water oak, and Nuttall oak growing within the red oak/sweetgum forest type complex. The study was conducted on sites protected by levees from Mississippi river flooding in the central Yazoo-Mississippi river floodplain. Results from this study may prove to be applicable to other southeastern United States floodplain forests.

2. Background

River floodplain forests of the southeastern United States range from Virginia to Texas and contain a large number of tree species, some of which are primarily or exclusively found in this forest type. The red oak species examined in this study historically and presently are a major component of the overstory of these forests. Known as "bottomland hardwoods" (Putnam et al., 1960), these ecosystems currently contain a small area and proportion of remaining forests compared to other forest ecosystems in the eastern United States (Noss et al., 1995). The Lower Mississippi Alluvial Valley (LMAV; National Research Council, 1992) – also known as "Lower Mississippi riverine Forests" (Bailey, 1983) or "Mississippi lowland forests" (World Wildlife Fund and National Geographic Society, 2004) – originally contained a large proportion of these bottomland hardwood forests, but much of the LMAV has been converted to agriculture (Haynes et al., 1993).

The floodplain forests have historically and prehistorically been disturbed by seasonal flooding and sediment deposition (Barry, 1998; Harrison, 1951); extensive Native American and recent agricultural clearing (Moore et al., 1998; Fickle, 2001); wild, feral, and domestic animal grazing (Hamilton, 1992); and tornados, hurricanes, fires, and ice storms (Toole, 1965; Hamilton, 1992). Within the past century, artificial levees have altered the flooding and sediment deposition patterns on many floodplains. The floodplains are characterized by a frequently varying mosaic of soil types ranging from poorly drained to excessively drained, with different species characteristically growing on each soil type (Hodges, 1997). The red oaks are part of the red oak/sweetgum forest type complex and are found on ridges and well-drained flats, which are the most productive soils. Consequently, this forest type complex has been more extensively converted to agriculture than the other floodplain forest types. The small area and fragmented nature of remaining forests means that natural and human processes that occurred at larger scales to maintain the diversity of species in these forests may not be effective now. It may take careful, active management to ensure the diverse species composition – and especially the red oaks and species dependent on them – are maintained.

There is concern of an insufficient number of young red oaks to sustain the oak-dominated forests in much of the eastern United States. There are distinct parts to this concern:

- First, there is confusion over how many red oaks are needed in the initial stand to provide an overstory dominated by red oaks. Clatterbuck et al. (1985) have found that only 100–125 red oaks per ha may be needed to form a pure oak overstory in 55-year-old mixed species bottomland hardwood stands. Oliver (1978) also found that northern red oak (*Quercus rubra*) had a low mortality rate compared to associated species in mixed stands, and suggested a minimum stocking of only 150 oaks per ha in young stands to obtain a pure oak overstory of 110 oaks per ha at 60 years in southern New England. In both studies, trees of other species were found to compete with the oaks when young but fall behind and live in the understory as the stands developed. Clatterbuck and Meadows (1992) allowed greater possibility of young red oak mortality and suggested 375 red oak seedlings per ha to ensure a dominant overstory of red oaks. In contrast to pure conifer stands which regenerate with 740–2470 stems per ha of a single species, 200–375 red oaks may be needed per ha, in combination with many stems of other species, to ensure an overstory of pure red oaks (Oliver, 1978; Clatterbuck and Meadows, 1992); however, greater understanding of the survival rate and vigor of young red oaks is needed.
- Second, there is concern about obtaining red oaks in the reproduction. Red oaks can begin in old fields from seeds, but are generally believed to need first to develop as advance reproduction to compete after a disturbance in an established forest. A partial overstory is believed optimum for establishing this advance reproduction (Gardiner and Hodges, 1998).
- Third, the red oaks must grow rapidly enough to compete with their neighboring woody and herbaceous species and become part of the overstory following a disturbance that releases them from advance reproduction. Janzen and Hodges (1985) had found that releasing red oak seedlings from midstory and overstory competition did not markedly stimulate height growth during the subsequent 3 years. Johnson and Krinard (1988), however, found that bottomland red oaks developing after seed tree harvesting became dominant in mixed stands with sweetgum, river birch (*Betula nigra*), and American hornbeam (*Carpinus caroliniana*) after several decades.

Beginning in the late 19th century and still continuing in some places, selection harvesting has been practiced that leaves residual trees which shade the newly developing cohort. Early forest scientists studying bottomland hardwood silviculture advocated selection harvesting as the primary method for removing mature stems. This trend continued following recommendations by Putnam et al. (1960; Meadows and Hodges, 1997). Commercial clearcutting, in which all merchantable trees are harvested but the remaining trees are left standing, has been stressed in the past few decades and is still practiced. It also leaves residual trees that shade shorter residual trees and trees in the new cohort developing after the harvest. Silvicultural clearcutting, which entails removal of unmerchantable trees as well as the merchantable ones, has since been emphasized to ensure there are no residual trees to shade the new cohort. To provide some shade for germination and growth of the new cohort as well as reduce competition from more shade intolerant species, shelterwood and seed tree harvesting and mid-story removal have also been suggested (Gardiner and Hodges, 1998; Peairs et al., 2004); and the residual overstories have been left for varying periods of time. Different conditions may be most favorable for the establishment of vigorous red oak advance reproduction and for its subsequent growth.

Selection harvesting was consistent with management practices elsewhere and the general premise that the natural "succession" of these mixed species forests was all-aged growth of new, young trees as the older trees died or were harvested (Boyce and Oliver, 1999). The understanding of forest development has changed, and it is now recognized that trees in these and other forests generally begin following disturbances that release growing space for new trees to occupy (Oliver and Larson, 1996). A stand replacing disturbance can produce a mixed species stand where the trees are nearly identical in age but soon grow to dramatically different sizes, with some species occupying the overstory and other species occupying the understory. Species found in the overstory that are intolerant of shade will be rare in the understory. Selection harvesting or other partial disturbances allow many species to initiate from seeds, advance reproduction, and sprouts; but the taller residual trees may regrow into the above and below ground growing space, suppressing the post-disturbance cohort of trees. Trees of shade tolerant species in this suppressed cohort generally survive and grow slightly better than intolerant ones, although all trees slow in growth as the overstory shade increases. In multiple cohort stands, therefore, a tree's survival depends not just on its initial establishment, but also on its subsequent growth. A species in the understory that is more sensitive to suppression than its neighbors undergoes a negative feedback in growth; it slows in height growth as it becomes suppressed, allowing the other species to suppress it further (Oliver and Larson, 1996). Consequently, the primary representatives of the shade intolerant species following partial cutting are those remaining in the overstory from an earlier stand-replacing disturbance.

Red oaks in the floodplains and uplands of the southeastern United States and elsewhere have been found to grow to the overstory following old field abandonment or silvicultural clearcutting (Oliver, 1978; Bowling and Kellison, 1983; Clatterbuck et al., 1985; Kelty, 1986; Clatterbuck and Hodges, 1988; Kittredge, 1988; Johnson and Krinard, 1988)—especially if yellow-poplar (*Liriodendron tulipifera* L.) is absent (Loftis and McGee, 1993). When growing in this pattern, they produce high quality wood, with the other species relegated to the understory and acting as "trainers" that keep their lower boles free of limbs. It is uncertain if these oaks are also shade tolerant enough to grow into the overstory in stands subjected to partial harvesting or other partial disturbances. Intense sunlight of stand-replacing disturbances may be needed in other mixed species, highly productive forests in order for certain species to remain part of the forests. Snook (2003) suggested that bigleaf mahogany (*Swietenia macrophylla*) needs such disturbances to be maintained in mixed tropical forests in central America. Baker et al. (in press) studied an extensive stand with an overstory predominated by *Hopea oderata*, but little of this species was found in the understory in the seasonal tropical forests of western Thailand.

3. Methods

The study was divided into two parts: the "census" and the "reconstruction." The census study examined sixteen stands of various stand histories throughout the Yazoo-Mississippi river floodplain. It determined if sufficient recruiting oaks were in the stands to form pure red oak overstories, assuming these recruiting oaks would grow to the overstory.

The reconstruction study examined a subset of these stands to determine the conditions needed for the recruiting red oaks to grow to the overstory. It determined how taller trees influenced the height growth of recruiting oaks and other species in similar conditions. A third important area of study, causes of initial establishment and survival of the red oak reproduction, was not examined but is being studied by others (e.g., Gardiner and Yeiser, 1999; Lockhart et al., 2000; Gardiner et al., 2004).

3.1. Study area

Both the census and reconstruction studies were conducted in the Yazoo-Mississippi river floodplain in the state of Mississippi between Memphis, Tennessee (latitude 35N°) and Vicksburg, Mississippi (latitude approximately 32N°; Fig. 1). This floodplain is bound to the west by the Mississippi river and to the east by the Loess Bluff physiographic region of Mississippi. From Memphis, the floodplain extends southward, gradually reaching a width of 129 km before tapering to its southern terminus near Vicksburg, Mississippi, nearly 322 km from its northern most point; it covers approximately 18,400 km^2 in the state of Mississippi. The topography is nearly flat; and subtle variations in relief dictate drainage patterns, soil type, and vegetative cover. The "higher" elevations range from 64 m above sea level at Memphis to 29 m near Vicksburg. Natural drainage occurs away from the Mississippi river and towards the south and east, emptying into the Yazoo river upstream from its confluence with the Mississippi river (Gunn et al.,

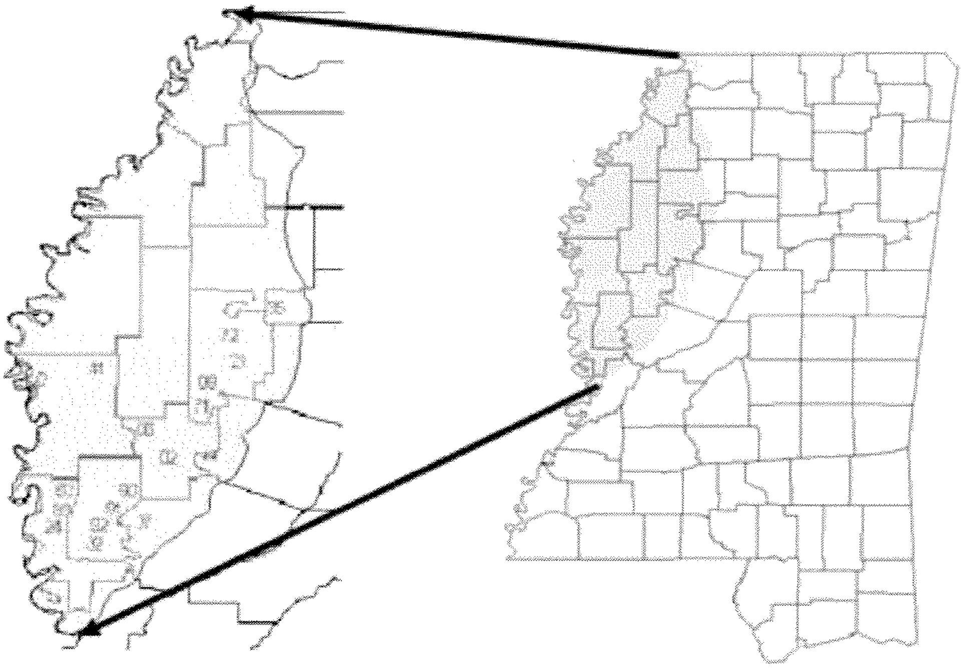

Fig. 1. The state of Mississippi, USA (right), showing counties. The Mississippi Delta study area (left), showing approximate locations of stands used.

1980). It is commonly referred to as the "Mississippi Delta," although the term "Mississippi Delta" is also used to describe Mississippi river floodplain both within and outside of the state of Mississippi. It is not a "delta" in the geologic sense but is the largest floodplain in the southeastern United States.

These floodplain forests are host to approximately 30 commercially important hardwood tree species, as well as a diverse assemblage of shrubs, wood vines, herbs, and non-commercial tree species (Carter, 1978; Gunn et al., 1980). Common overstory trees include water oak, willow oak, Nuttall oak, overcup oak (*Quercus lyrata* Walt.), American elm, green ash, sugarberry, sweetgum, sweet pecan (*Carya illinoensis* [Wangenh.] K. Koch), baldcypress (*Taxodium distichum* [L.] Richard), American sycamore (*Platanus occidentalis* L.), and eastern cottonwood (*Populus deltoides* Marshall). Cherrybark oak and cow oak (a.k.a. swamp chestnut oak; *Quercus michauxii* Nutt.) are found on some higher elevations which escaped clearing for agriculture from the south central Yazoo-Mississippi river floodplain northward.

The climate of the Yazoo-Mississippi river floodplain can be described as temperate with hot, humid summers; mild, wet winters; and a fairly even distribution of rainfall throughout the year, with slightly higher amounts during the winter and spring months. July is the warmest month, with an average daily high of 33 °C. January is the coldest month, with an average daily low of 0 °C. Average annual precipitation is approximately 1320 mm (USDA Soil Conservation Service, 1961; Remy, 1995). Until efforts were made to construct a continuous levee along the Mississippi river beginning in the 1880s, winter and spring flooding often occurred. Levee failures and resultant flooding occurred in 1927 and earlier, largely because of increasingly higher Mississippi river flood stages (Harrison, 1951). The southern portion of the floodplain was subject to backwater flooding until the 1970s and is now subject to trapped internal water; however, none of the stands included in this study were in the backwater areas.

Stands to be studied were identified across a range of forests in the portion of the Yazoo-Mississippi river floodplain protected by the Mississippi river levee.

Stands were distributed throughout the central and southern floodplain and assigned to three "zones" – North, Middle, and South – and across a range of stand histories—old field origin or different harvesting histories. Acceptable plots within the stands were on ridges and well-drained flats ideal for growth of the red oak species. Stands with acceptable plots were difficult to find because most ridges and well-drained flats were in agricultural use. As each stand was identified, permission was gained to study it. The approximate history of each stand was obtained through landowner records and field observations. The census part of this study was conducted between September 1999 and November 1999; and a subset of these stands was used for the reconstruction study, performed between January 2000 and April 2001.

The last harvest or other treatment in each stand was performed between 7 and 75 years before this study, with most stands having been treated between 15 and 40 years before this study. A variety of treatments had been done, from no action to old field abandonment. Many stands were not uniformly treated, with variable overstories retained in different parts of the stand. Stands that had been harvested by shelterwood and seed tree harvests in this study had not been followed up by subsequent removals of the residual overstory. The stands' estimated treatment histories and number of plots taken of each type (census and reconstruction) are shown in Table 1.

3.2. Census study

3.2.1. Field procedures

Potential plot centers were located on a 40 m grid with a random starting point within each stand. Plots were considered acceptable if the center was on a soil type suitable for red oak growth and there had been no alteration (e.g., logging road) that would have affected tree growth. A maximum of 20 census plots were located within each stand.

Four concentric circular subplots and one offset circular subplot were established and measured around each acceptable plot center. The diameter (DBH, measured at 1.4 m height) or height for trees less than 1.4 m tall and species were recorded for all trees within specific size ranges on each subplot, as described below:

- 0.08 ha subplot (16.1 m radius): All trees > 38.4 cm DBH.
- 0.04 ha subplot (11.3 m radius): All trees between 25.6 cm and 38.3 cm DBH.
- 0.008 ha subplot (5.1 m radius): All trees between 13.0 cm and 25.5 cm DBH.
- 0.004 ha subplot (3.6 m radius): All trees between and 0.9 m tall and 12.9 cm DBH.
- Reproduction subplot (0.0004 ha subplot, 1.13 m radius). Subplot center was located 4.9 m due West of center of the other subplots: All trees less than 0.9 m tall were measured.

Table 1
Locations and histories of stands used in the census and reconstruction parts of this study

Stand #	Location	Estimated treatment history	Treatment abbreviation	# Census plots	#Reconstruction plots
2	Central	Selection cuts 1969/1970 and 1981/1982	SEL	20	
6	Central	Selection cut 1970/1971; TSI later	SEL	18	
9	North	No record	?	20	
21	North	Shelterwood 1963, residual trees left	SW	20	
24	South	Selection cut (diameter limit) 1972/1973	SEL	20	6
32	South	Commercial clearcut 1986	CCC	20	
35	North	Seed tree 1993	ST	20	
37	South	Selection cut 1972; TSI 1976	SEL	20	
41	North	Silvicultural clearcut 1969/1970	SCC	18	15
71	North	Old field, 1941	OF	14	
72	North	All merchantable timber last cut in 1923	CCC	20	
82	South	Shelterwood 1993/1994	SW	20	13
83	South	In 1972 classified as sapling/pole stand	?	20	
90	South	Selection cut 1972?	SEL	10	
91	South	Old growth	OG	20	
92	South	Commercial clearcut 1960	CCC	20	6

3.2.2. Data analyses

Information on each plot was summarized graphically and tabularly, as described in the results. Analyses of variance, regressions, and other statistical techniques were performed using the Microsoft@ Excel 2000 statistical package.

To ensure residual, overstory oaks were not considered as part of the recruiting oaks in the census study, a means of defining "overstory" and "recruiting" oaks and other species was needed. In the silvicultural clearcut and old field stands, all trees would have arisen after the last disturbance and be considered recruiting, so there would be no residual overstory trees. For the other stands, the census data was used to detect a change in basal area distribution by diameter classes that would define the maximum diameter at which the oaks could be considered recruiting and, therefore, in the "understory." Examination of diameter growths from the reconstruction study (described below) further determined the reasonableness of this maximum diameter of oaks to be considered in the understory. The diameter distributions and diameter growths of other species were then examined to determine if the same minimum diameter could be used to assign trees of other species to the overstory or understory in the census study.

3.3. Reconstruction study

3.3.1. Field procedures

Four stands sampled in the census study and covering a range of harvesting treatments were used in the reconstruction study (Table 1). Reconstruction studies examine the past history of stands using growth rings, stem dissections, and other means to determine past growing conditions of trees (Henry and Swan, 1974; Oliver and Stephens, 1977; Oliver, 1978). Each reconstruction plot was centered at a recruiting red oak (the "plot center" red oak) that was identified by the following criteria:

- The red oak was not in the overstory at the time of the last harvest, and had begun or was released by this harvest.
- It was at least 1.4 m tall at the time of this study.
- It was at least 40 m away from any other plot center red oak.
- It was the most dominant (e.g., tallest) red oak of any surrounding red oaks that similarly began or were released by the last harvest.

Plot center red oaks in each stand were selected on transects 40 m apart beginning 40 m from a random point on the stand edge. Plot centers were selected as the first red oak found to meet these criteria. Plot center oaks were identified in each stand until a maximum of 20 were found or until no more could be found. Four concentric, circular subplots were established around each plot center oak and sampled as follows:

- 0.08 ha subplot (16.1 m radius): All trees that were at least 2/3 as tall as the tallest tree in the plot were identified by species and measured for total height and location (azimuth and distance from plot center). An increment core was taken to the tree center at 1.4 m.
- 0.04 ha subplot (11.3 m radius): All trees within this subplot which began before the treatment and which were not measured as part of the 0.08 ha subplot were identified by species, measured for location (azimuth and distance from plot center), and destructively sampled by felling and removing disks as described later.
- 0.008 ha subplot (5.1 m radius): All trees within this subplot which began after the last treatment and which were taller than the plot center oak tree, plus all red oaks which began after the last treatment, plus all trees greater than 25.6 cm diameter which had not been previously sampled were identified by species, measured for location, and destructively sampled as described for the 0.04 ha subplot.
- 0.004 ha subplot (3.6 m radius): All trees within this subplot which began after the treatment and had not been previously sampled were identified by species, measured for location, and destructively sampled as described for the 0.04 ha subplot.
- Plot center red oak: on each plot, this tree was identified by species and destructively sampled as described for the 0.04 ha acre subplot. Heights of any crooks, forks, scars, or losses of excurrent growth form were noted.

Destructively sampled (cut) trees were processed in two ways. For all parts of the tree over 5.1 cm diameter, tree sections were cut at 10.2 cm; 0.6 m, 1.4 m, and 1.8 m above the ground, and every 0.61 m thereafter. Each disk was immediately measured in four directions for bark thickness and then labeled for later measurement. When the stem first reached less than 5.1 cm in diameter, the remaining portion was cut into 1.2 m lengths for further analyses in the laboratory.

3.3.2. Laboratory procedures

Increment cores and disks were stored in a temperature controlled climate until prepared and analyzed. Preparation of the cores involved allowing time for the cores to air dry, mounting them on increment core holders, and sanding the cores to a smooth surface. Disks were similarly dried and a smooth surface for counting and/or measuring annual rings was prepared by sanding and/or routing as necessary.

To determine diameter growth, width of each annual ring was measured for each disk and increment cores taken at 1.4 m using an "Acu-dendrochronometer" and "Turbo Ringread" software developed by P. van Deusan and Kim Lee (USDA Forest Service, New Orleans, LA, USA in 1988). A file was created for each disk and core, and files from the same plot and stand were organized in DOS directories. The data were then transferred into MSExcel for Windows.

All disks were aged by ring counts. Collected stem sections (less than 5.1 cm diameter) were cut into 0.6 m lengths and the stem age at each cut was determined from ring counts. For the small terminal stems, annual growth was measured along the stems from the stem tip toward the base using bud break scars in the bark for as many years as these scars were visible.

3.3.3. Data analyses

From the disk ages and small stem height growth analyses, the height of each tree of each species for each year was determined, except for those trees sampled on the 0.08 ha subplots (where only increment cores were taken). Height growth curves of all trees in a plot were developed (Fig. 2A). Similarly, the diameter, diameter growth, and basal area of each tree at 1.4 m were calculated for each year, as shown graphically (Fig. 2B).

Stem basal area was used as a measure of the amount of competition that taller trees asserted because of the close relation of root area, foliage area, and stem basal area (Oliver and Larson, 1996). For the reconstruction study, "residual overstory" trees in stands 21, 82, and 92 (Table 1) were defined as those trees measured in the 0.08 ha subplot. Stand 41 was a silvicultural clearcut and did not contain any residual overstory trees. All trees not considered residual overstory trees were considered "recruiting" trees—trees that could potentially grow to the overstory. Note the reconstruction study used different, more precise criteria for residual overstory and recruiting trees than the census study's definitions described earlier. The total basal areas per ha of all residual overstory trees and other trees taller or shorter than each plot center oak during each year were calculated (Fig. 2C).

Height growth was used to measure understory tree vigor, since it affects how rapidly the tree will grow to the overstory—if at all. Stem breaks were common in the understory trees. To avoid confusing the height growth analyses around the times of stem breaks, height growths were eliminated for all trees during the time that its measurements appeared to be influenced by the break, as well as for 2 years following resumption of growth—to eliminate possible sprout vigor. Growths for the first 2 years above the root collar were rejected for similar reasons.

From an initial 877 height growth measures of individual years on 40 plot center oak trees, 580 measures were acceptable after measurements surrounding these breaks were eliminated. Only the acceptable height growth measures were used in subsequent analyses. Annual height growths appeared too varied to be used as a measure of vigor for the oak trees, since there was a poor correlation between annual height growths of the same tree during consecutive years (Fig. 3; $R^2 = 0.14$; square root of mean square residual = 0.167; slope = 0.35; intercept = 0.11). Consequently, 5- and 7-year running average height growths were calculated for each plot center oak using only cases where a series of acceptable measures could be found. The 5-year running average had 431 acceptable series, and the 7-year running average had 326 acceptable series. There was a close, consistent relation between the 5- and 7-year running average height growths (Fig. 4; $R^2 = 0.91$; square root of mean square residual = 0.074; slope = 0.98; intercept = 0.003), suggesting that an approximation of a tree's height growth and vigor could be obtained by

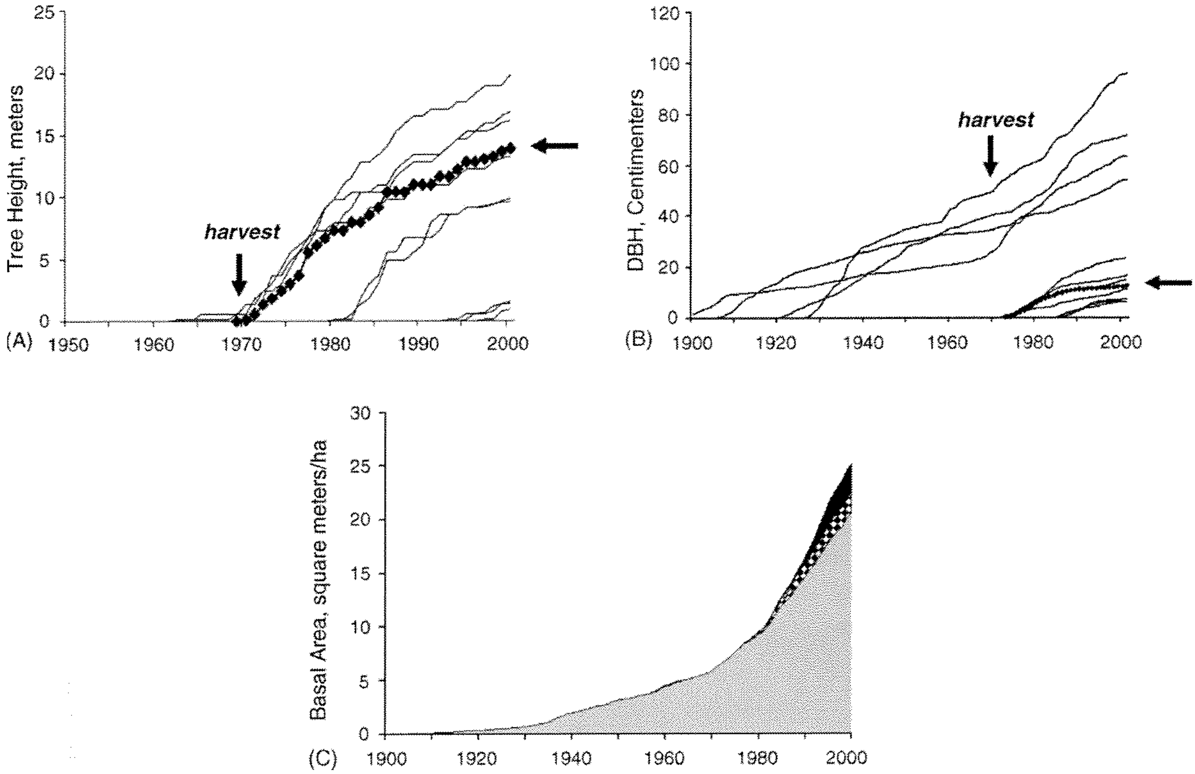

Fig. 2. Example results of reconstruction techniques for one plot in stand #24. "Harvest" indicates year of last treatment. Horizontal arrows in (A) and (B) show recruiting red oak at plot center. (A) Height growths of all trees except residual overstory trees (trees measured in 0.08 ha reconstruction subplots) in a plot in a selection harvested stand. (B) Diameter growths of all trees in a plot in a selection harvested stand. (C) Basal area growth of residual overstory trees and other trees taller and shorter than plot center red oak (gray, residual overstory BA; hatched, BA of recruiting trees taller than plot center red oak; black, BA of recruiting trees shorter than plot center red oak).

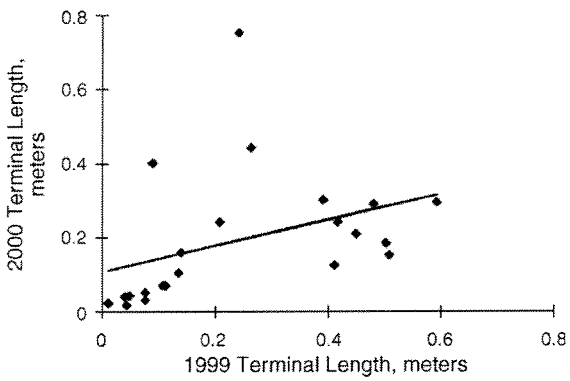

Fig. 3. Comparison of annual height growths of two consecutive years for plot center red oaks.

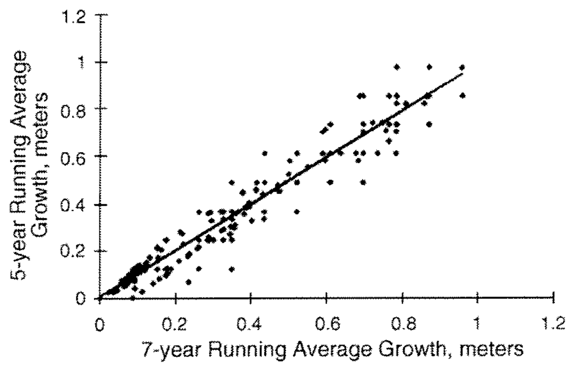

Fig. 4. Comparison of 5- and 7-year running average height growths for plot center red oaks.

these running averages. In the remaining analyses, the 5-year running average was used because it provided more data and appeared as reliable as the 7-year running average.

The same 5-year running average height growth was calculated for each "acceptable series" for all stem analyzed trees of other species shown in Tables 3 and 4, except that American elm and cedar elm were analyzed separately and the hickories (sweet pecan [*Carya illinoensis* (Wangenh.) K. Koch] and water hickory [*Carya aquatica* (Michx. F.) Nutt.]) and red maple were not analyzed because few hickory and red maple stems had been sampled in the reconstruction study.

The plot center oak height growths (5-year running average) varied from zero to nearly 1.4 m per year. To determine if competition from taller trees could be affecting height growth of these oak trees, height growth of each of these oaks at each acceptable year was compared to the total basal area of all taller trees during that year (Fig. 5A). Some of the sample points in Fig. 5A were from consecutive years from the same tree; consequently, some points were correlated. The greatest, single height growth measures for each plot center oak tree are shown as large icons in Fig. 5A, and all remaining measures are shown as small icons.

The pattern in Fig. 5A is expected, since multiple factors affect tree growth. An oak growing under optimum conditions may grow slowly if it did not arise from a vigorous seedling or was on a poor microsite. The important characteristic in Fig. 5A is the maximum growth attained by oaks at the various densities of taller trees. Three statistical analyses were tried to examine this characteristic:

- Linear and non-linear regressions;

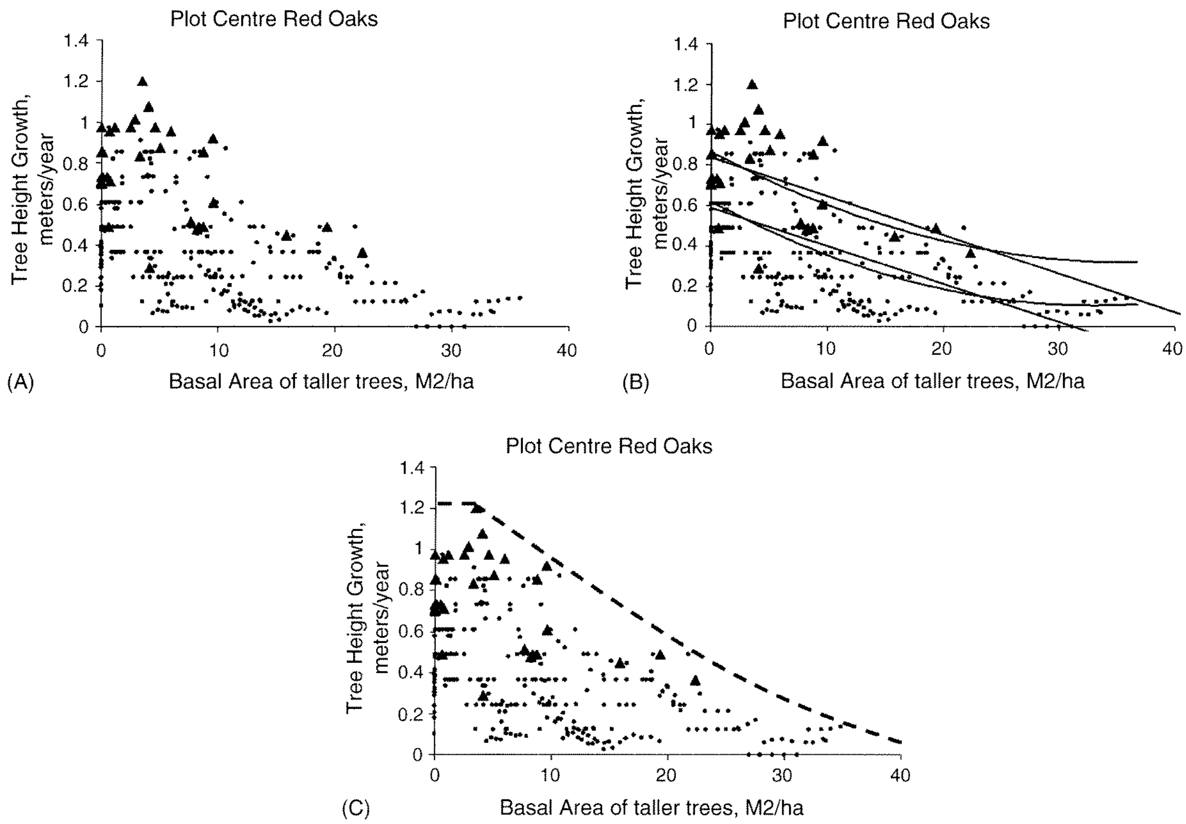

Fig. 5. Relation of 5-year running average height growth of each plot center oak and basal area of taller trees during that year. Large icons indicate measure of maximum height growth for each tree. (A) Basic data plotted. (B) Linear and non-linear regressions (bottom two lines) and linear and non-linear frontier analysis results (top two lines). (C) Hand-fitted boundary line.

- Linear and non-linear frontier analysis (Nepal et al., 1996);
- Boundary analysis (Webb, 1972).

The boundary analysis proved the most effective way to determine the maximum height growth under different densities (basal areas) of taller trees, as described later in the results. Consequently, the basal area of the residual overstory trees for each plot and each year was compared to the 5-year running average annual height growths calculated for the other species, as described earlier. Stems of these individuals were not at plot center and only the basal of the residual overstory trees on each plot were considered, so more variation would be expected in these relations than in those shown in Fig. 5; however, the results appear consistent.

4. Results

4.1. Census study

A total of 300 census plots was taken in 16 stands. Fig. 6A shows the basal area distribution by diameter class of red oaks and all trees. A change in the shape of this distribution suggested that 30.5 cm DBH was a reasonable division between overstory and understory trees to ensure overstory oaks were not considered part of the recruiting population in this census study. This diameter (30.5 cm) was further examined using reconstruction data (Fig. 6B). All red oaks not in silvicultural clearcuts (where there was no residual overstory) that were 30.5 cm DBH or larger at the time of reconstruction were at least 25 cm DBH when the last harvesting occurred. Assuming a conservative

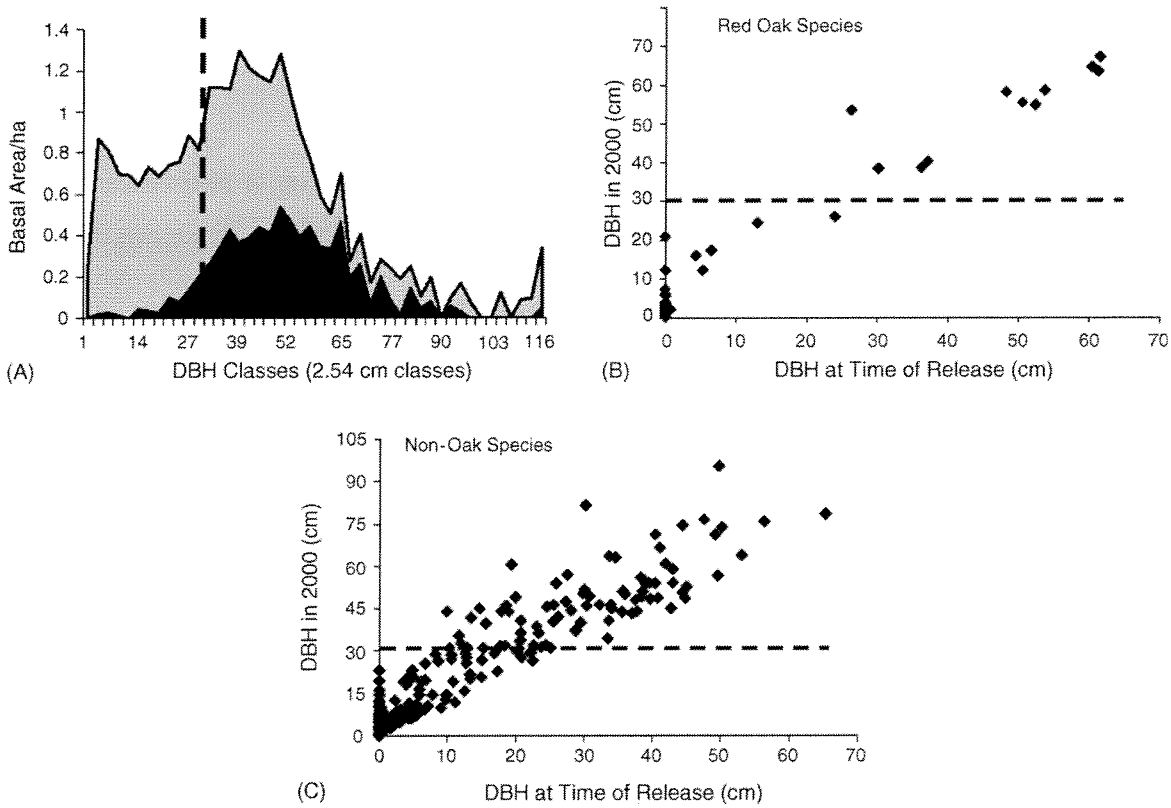

Fig. 6. (A) Basal area distribution by 2.54 cm DBH classes of all trees in all census plots (grey) and red oaks (black). Trees larger than 30.5 cm (marked by vertical line) were considered overstory trees in the census study (Tables 2–4). (B) and (C) DBH from reconstruction study of all red oaks (Fig. 2B) and all other trees (Fig. 2C) at time of reconstruction compared to their diameter at time of release. Trees larger than 30.5 cm (marked by vertical line) at time of reconstruction were considered overstory trees in the census study (Tables 2–4).

Table 2
Summary of total overstory basal area, recruiting red oak numbers, and red oak overstory basal area ranked by plots in descending order of overstory basal area

Stand	Year cut	Treatment abbreviation	Mean overstory basal area (all species)		Mean recruiting red oaks		Percent of census plots with recruiting red oak (%)	Mean overstory red oaks basal area		Percent of census plots with overstory red oaks
			m^2/ha	S.D.	Trees/ha	S.D.		m^2/ha	S.D.	
72	1923	CCC	28.6	6.9	28	79	20	12.1	8.2	85
9		?	23.3	4.6	46	76	55	16.0	6.9	100
91		OG	23.0	10.6	37	121	10	0.8	1.8	20
6	1971	SEL	22.0	7.8	64	112	33	18.1	7.7	100
21	1963	SW	21.5	6.5	16	45	25	13.0	7.6	90
2	1970/1982	SEL	20.5	5.0	61	130	35	9.5	6.3	95
24	1973	SEL	19.2	7.9	4	12	10	3.0	5.9	35
37	1972	SEL	18.9	7.7	159	390	55	11.5	7.5	100
83		?	17.6	3.5	180	166	5	1.1	2.3	25
90	1972	SEL	17.3	8.0	119	139	70	3.2	3.0	70
92	1960	CCC	14.8	7.4	83	145	35	2.8	5.3	35
32	1986	CCC	6.2	4.8	188	459	35	1.2	1.9	35
82	1994	SW	4.2	3.1	114	238	35	2.6	2.9	60
35	1993	ST	2.9	1.7	494	730	65	1.9	2.0	55
71	1941	OF	0.0	0.0	173	145	86	0.0	0.0	0
41	1970	SCC	0.0	0.0	274	322	72	0.0	0.0	0
Mean			15.0		127.4		40	6.0		57

height/diameter ratio of 60%, the trees would be at least 18 m tall, and therefore could be considered in the overstory. The same diameter (30.5 cm) also proved to be a reasonable separation between overstory and understory trees for non-oak species (Fig. 6A and C). Fig. 6C shows that 80% of the other species that were 30.5 cm DBH when examined in the reconstruction study were at least 20 cm DBH when released, and 90% were larger than 15 cm DBH. Consequently, all red oaks less than 30.5 cm DBH were considered recruiting red oaks in Table 2; all trees over 30.5 cm DBH were considered in the overstory; and all trees less than 30.5 cm DBH were considered in the understory in Tables 2–4.

Table 2 shows the average number of recruiting red oaks in each stand, ranked in descending order of overstory basal area. Table 2 also shows the average total overstory basal area, the average basal area of red oaks, and the percent of census plots containing recruiting and overstory red oaks in each stand. A total of 30 species were found in the stands. The overstory basal areas of the most predominant species in the study are shown for each stand in Table 3. The numbers of understory trees of these predominant species are shown in Table 4. Tables 3 and 4 also show the standard deviations for each species in each stand and the percent of plots containing each species.

Red oaks were the most dominant residual overstory trees (Table 3), comprising 40% of the overstory basal area; however, they were not numerous in the understory (Table 4). Elms, swamp dogwood, sugarberry, red maple, and green ash were common in the understory (Table 4). Red oaks, sweetgum, elms, and sugarberry were found in many plots. Swamp dogwood, green ash, and red maple were found in fewer plots, but were abundant where they were found (Tables 3 and 4).

A large range of total trees per ha (1532–10,170) and recruiting red oaks (0–502 per ha) were obtained. If 200–325 young red oaks per ha are needed to ensure an oak-dominated stand as described earlier, only 22% of the plots had more than the minimum 200 recruiting red oaks per ha and only 8% had more than 325 recruiting red oaks per ha. Consequently, in most cases, there were far fewer recruiting red oaks than would be needed to reform an overstory dominated by red oaks (Table 2).

The numbers of recruiting red oaks per ha were significantly different among stands (Table 4;

Table 3
Overstory basal areas and standard deviations by stands and percent of plots containing the species for the most predominant species in the census study

Stand	Year cut	Treatment	Measure	Overstory residual basal area (m^2/ha) and standard deviation								
				All species	Red oaks	Sweet-gum	All elms	All hickories	Sugar-berry	Green ash	Red maple	Swamp dogwood
72	1923	CCC	BA	28.6	12.1	11.8	0.2	0.3	0.5	0.6	0.1	0.0
			S.D.	6.9	8.2	7.6	0.5	1.2	1.4	0.9	0.6	0.0
9		?	BA	23.3	16.0	3.4	1.7	0.3	0.1	0.0	0.0	0.0
			S.D.	4.6	6.9	4.8	2.3	0.7	0.4	0.0	0.0	0.0
91		OG	BA	23.0	0.8	10.4	4.9	0.6	0.4	1.5	0.6	0.0
			S.D.	10.6	1.8	9.1	4.2	1.9	1.0	3.3	1.4	0.0
6	1971	SEL	BA	22.0	18.1	0.7	0.3	0.1	0.0	1.2	0.0	0.0
			S.D.	7.8	7.7	1.6	0.8	0.5	0.0	1.9	0.0	0.0
21	1963	SW	BA	21.5	13.0	1.5	0.3	0.4	0.1	0.7	0.4	0.0
			S.D.	6.5	7.6	1.6	0.8	0.9	0.6	1.6	0.9	0.0
2	1970/1982	SEL	BA	20.5	9.5	6.2	0.6	0.6	0.3	0.8	0.0	0.0
			S.D.	5.0	6.3	6.3	0.9	1.4	0.8	1.7	0.0	0.0
24	1973	SEL	BA	19.2	3.0	8.5	1.4	2.0	2.7	0.0	0.0	0.0
			S.D.	7.9	5.9	7.8	2.0	3.7	2.7	0.0	0.0	0.0
37	1972	SEL	BA	18.9	11.5	2.5	0.5	0.4	0.8	0.7	0.0	0.0
			S.D.	7.7	7.5	3.6	1.0	0.9	2.2	1.4	0.0	0.0
83		?	BA	17.6	1.1	9.1	0.1	5.8	0.3	0.0	0.0	0.0
			S.D.	3.5	2.3	7.1	0.5	4.0	0.9	0.0	0.0	0.0
90	1972	SEL	BA	17.3	3.2	10.1	1.3	0.2	1.4	0.3	0.2	0.0
			S.D.	8.0	3.0	9.5	1.3	0.5	2.2	0.7	0.6	0.0
92	1960	CCC	BA	14.8	2.8	3.5	2.7	0.4	1.6	2.8	0.0	0.0
			S.D.	7.4	5.3	3.5	4.7	0.8	2.6	3.7	0.0	0.0
32	1986	CCC	BA	6.2	1.2	1.6	0.0	2.0	0.5	0.2	0.1	0.0
			S.D.	4.8	1.9	1.6	0.0	2.6	1.3	0.5	0.4	0.0
82	1994	SW	BA	4.2	2.6	0.6	0.0	0.0	0.7	0.2	0.0	0.0
			S.D.	3.1	2.9	1.9	0.0	0.0	1.0	0.8	0.0	0.0
35	1993	ST	BA	2.9	1.9	0.0	0.0	0.3	0.0	0.0	0.0	0.0
			S.D.	1.7	2.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0
71	1941	OF	BA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			S.D.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
41	1970	SCC	BA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			S.D.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mean			BA	15.0	6.0	4.4	0.9	0.8	0.6	0.6	0.1	0.0
P-value				<0.0001	<0.0001	<0.000	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Percent of plots containing the species				88	57	51	23	20	18	16	3	0

$P < 0.0001$), indicating that the recruiting red oaks were not completely randomly distributed. Most stands had less than 125 recruiting red oaks per ha, and these few recruiting red oaks present were commonly not well distributed throughout most stands.

Locations of the stands within the Yazoo-Mississippi river floodplain (North, Central, or South) did not appear to have a consistent relation with the numbers or distributions of the recruiting red oaks and were not considered in further analyses.

Table 4
Understory numbers of trees and standard deviations by stands and percent of plots containing the species for the most predominant species in the census study

Stand	Year cut	Treatment	Measure	Understory number of trees (#/ha) and standard deviation								
				All species	Red oaks	Sweet-gum	All elms	All hickories	Sugar-berry	Green ash	Red maple	Swamp dogwood
72	1923	CCC	#/ha	5282	28	100	479	20	112	32	99	99
			S.D.	4113	79	193	678	83	184	79	315	442
9		?	#/ha	1533	46	91	287	12	247	49	114	222
			S.D.	704	76	168	470	55	399	172	271	367
91		OG	#/ha	1227	37	37	192	7	392	40	124	37
			S.D.	474	121	121	264	28	356	90	283	91
6	1971	SEL	#/ha	4164	64	10	2941	7	371	104	0	439
			S.D.	1933	112	35	2045	29	417	147	0	983
21	1963	SW	#/ha	1858	16	166	489	6	0	93	785	0
			S.D.	768	45	216	502	28	0	101	792	0
2	1970/1982	SEL	#/ha	1331	61	43	572	2	269	33	74	62
			S.D.	896	130	113	616	8	293	78	141	158
24	1973	SEL	#/ha	2208	4	10	356	0	698	32	74	222
			S.D.	1441	12	28	441	0	816	112	242	467
37	1972	SEL	#/ha	1913	159	15	750	44	95	25	99	173
			S.D.	847	390	42	705	122	202	86	218	290
83	?		#/ha	2267	180	203	469	114	705	6	37	420
			S.D.	1255	166	177	449	96	539	28	166	897
90	1972	SEL	#/ha	1265	119	47	25	12	482	25	25	0
			S.D.	775	139	96	78	39	665	78	78	0
92	1960	CCC	#/ha	2643	83	188	225	28	299	308	513	198
			S.D.	1216	145	293	210	110	294	589	520	248
32	1986	CCC	#/ha	5006	188	434	399	114	447	238	1164	778
			S.D.	1767	459	432	344	239	479	377	978	936
82	1994	SW	#/ha	9727	114	630	704	62	2261	582	111	3138
			S.D.	2723	238	827	667	136	2199	612	315	3174
35	1993	ST	#/ha	4164	494	124	531	25	0	593	235	1075
			S.D.	2982	730	272	686	76	0	779	464	2249
71	1941	OF	#/ha	1554	173	366	362	18	44	18	53	0
			S.D.	992	145	299	476	40	92	66	105	0
41	1970	SCC	#/ha	4073	274	0	2025	117	316	865	7	0
			S.D.	1229	322	0	1319	210	334	611	29	0
Mean			#/ha	3138	127	154	675	37	421	190	219	429
P-value				<0.0001	<0.0001	<0.000	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Percent of plots containing the species				100	40	45	70	20	59	35	27	29

There was essentially no relationship between the numbers of recruiting red oaks and either basal area of overstory red oaks ($R^2 = 0.02$; square root of mean square residual = 282.59; slope = −5.34; intercept = 138.49) or time since last harvest ($R^2 = 0.02$; square root of mean square residual = 310.10; slope = −2.26; intercept = 190.97).

The overstory basal areas were also significantly different among stands (Table 3; $P < 0.0001$). The lack of uniformity of treatments within each stand, the few stands with some treatments, and the varying times since treatments probably accounts for the wide variation within stands; however, some trends can be noted. The old field and silvicultural clearcut stands contained no residual overstory basal area, and the basal area was low in the stand treated by the seed tree method. The residual basal areas varied greatly among the shelterwood and commercial clearcut stands, probably in part because of the large variation in time since the last harvest of the stands. The residual basal areas of the selection harvested stands were consistently high. The residual basal area in the stand that apparently had not been treated (old growth) was also high; the 37 recruiting red oaks (per ha) in this stand were all concentrated in two of the twenty plots.

There was not a pattern to the stands in which each of the four red oak species were found. This lack of noticeable differences reinforces the initial decision to consider all red oak species together.

4.2. Reconstruction study

The simple linear and non-linear regressions showed poor correlations of height growth to basal area of taller trees (Fig. 5B. For linear regression, $R^2 = 0.38$; square root of mean square residual = 0.21; slope = −0.02 [S.E. = 0.014]; intercept = 0.59 [S.E. = 0.001]. For quadratic regression, intercept = 0.62 [S.E. = 0.016], BA = −0.03 [S.E. = 0.003], BA × BA = 0.000 [S.E. = 2.838E−5]). In addition, the relation is relatively unhelpful, since the concern is for maximum possible

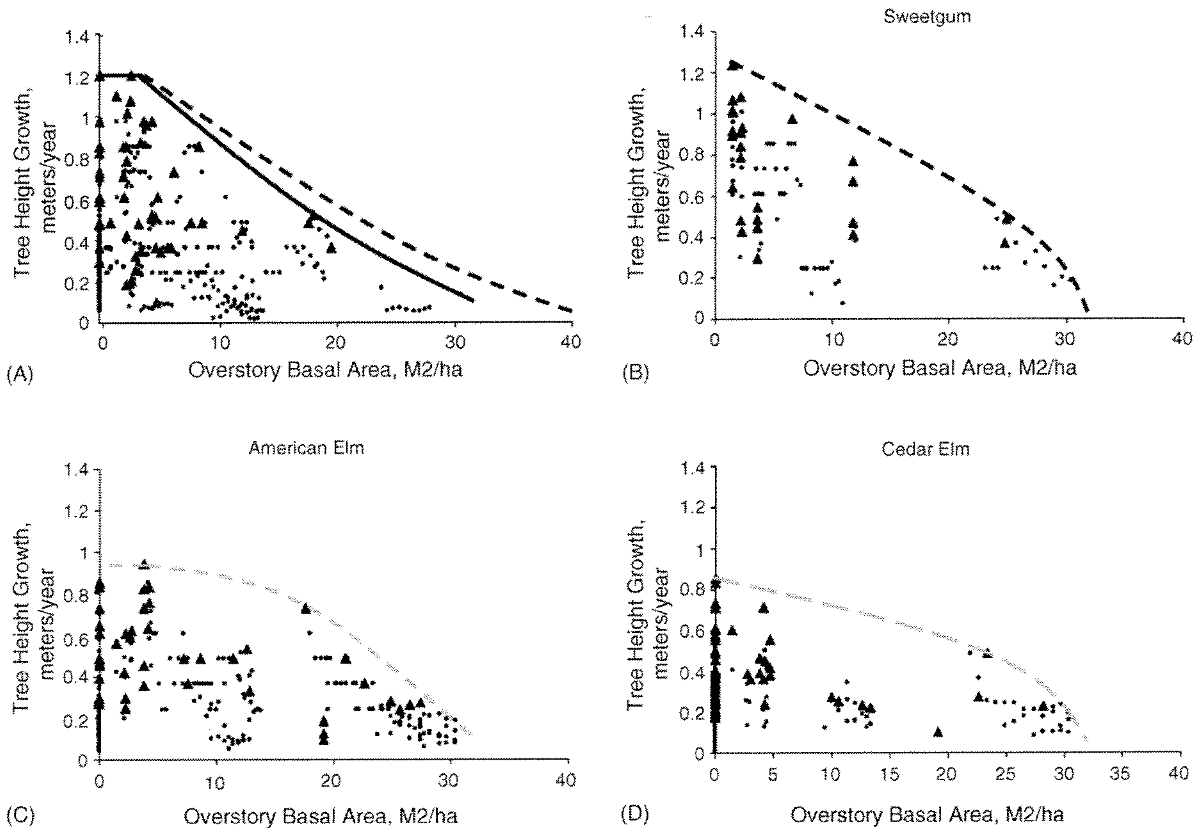

Fig. 7. Boundary line and relation of 5-year running average height growth of predominant species (Tables 3 and 4) and basal area of residual overstory trees during that year. Large icons indicate measure of maximum height growth for each plot: (A) All non-residual overstory red oaks (solid line) in the reconstruction plots. Dashed line indicates boundary line of Fig. 5 where basal area of *all* taller trees were considered on the "plot center" subset of these red oaks; (B) Sweetgum; (C) American elm; (D) Cedar elm; (E) Sugarberry; (F) Green ash; (G) Swamp dogwood.

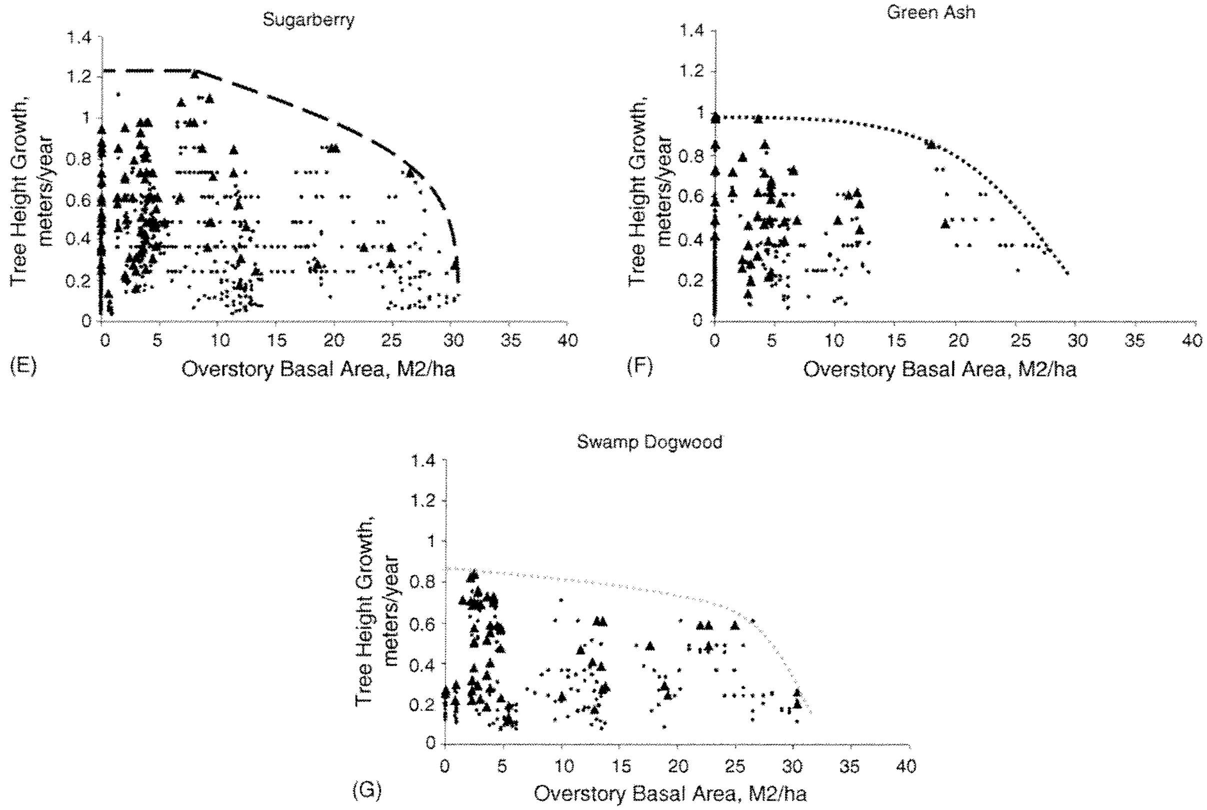

Fig. 7. (*Continued*).

growth, not average growth. The linear and non-linear frontier analyses indicate that there is a line above the simple regression line that shows a closer relation of the average maximum height growth for a given basal area (Fig. 5C; for linear stochastic frontier model, slope = −0.02 [S.E. = 0.001]; intercept = 0.84 [S.E. = 0.001]. For the quadratic stochastic frontier model, intercept = 0.86 [S.E. = 0.011], BA = −0.03 [S.E. = 0.002], BA × BA = 0.9.78E−05 [S.E. = 1.89E−5]); however, this line also does not show the maximum possible height growth at each density of taller trees. The boundary analysis, although a "hand-fit" line without statistical backup, describes the desired relation best. It has been found to be useful in interpreting other plant-environment relationships (Webb, 1972; Jarvis, 1976; Pezeshki and Hinckley, 1982).

Fig. 6A shows the relation of all recruiting red oaks to residual overstory basal area and its boundary line (solid line). This graph is different from Fig. 5 in two respects: all recruiting red oaks are considered here, not just those at plot center; and, only the basal areas of residual overstory trees are considered here, whereas, Fig. 5 considers the basal area of all trees taller than

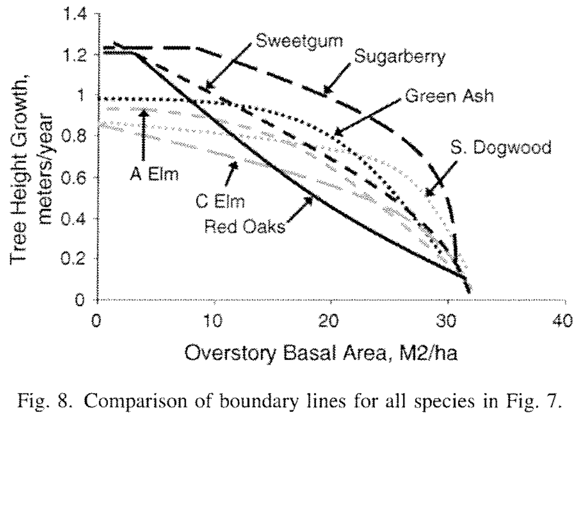

Fig. 8. Comparison of boundary lines for all species in Fig. 7.

the plot center oak during each year. For comparison, the boundary line established in Fig. 5C is shown as a dashed line in Fig. 6A.

Fig. 7B–G show the relations of height growths to residual overstory basal areas and the boundary lines for other species. Fig. 8 shows the boundary lines of all species on a single graph.

5. Discussion

The numbers of recruiting red oaks in all stands were surprisingly small. Only two stands had over 250 recruiting red oaks per ha—barely enough to meet the needed number, including mortality, to fill the overstory in a mixed species stand. There was a slight trend of stands that had less overstory having a higher number and more uniform distribution of recruiting red oaks (Table 2). Age of the stand, location within the study area, or other trends besides residual overstory density that might further explain the low and irregular distribution of recruiting red oaks could not be discerned.

The preponderance of red oaks in the residual overstories (Tables 2 and 3) reinforces the past importance of red oaks in these river floodplain forests. The weak and inverse relation between the amount of red oaks in the overstory and the number of recruiting red oaks strongly suggests that a lack of seed source is not the cause of recruiting oak scarcity.

After initial establishment, red oaks are primarily able to grow as fast as the other species studied when in full sunlight, and almost any taller trees left during the harvest will slow height growth of red oaks more than many associated species (Figs. 5–8). This shade also probably kills many young red oaks, since the slowed growth is associated with a decline in vigor and ultimately death.

A lack of vigorous red oak reproduction may also help account for the scarcity of recruiting red oaks; however, this study indicates that no red oaks will grow well in partial shade. Consequently, essentially complete removal of residual taller trees appears necessary to maintain red oaks as a significant component of the new forest. It appears necessary either to have complete removal of the residual trees following partial cuttings (shelterwood or seed tree) after oak advance reproduction is obtained, to have silvicultural clearcutting if the advance reproduction is already present, or to weed out competing species that grow faster than oaks in residual shade. Planting red oaks in silvicultural clearcuts may also be feasible where vigorous advance regeneration is not present; however, this opportunity was not studied. This study did not examine how long a residual overstory could be left (e.g., in a shelterwood) before it suppresses the understory oaks; however, the recruiting oaks in stand 82 were growing poorly beneath a shelterwood residual overstory that had been left for only 6 years.

In stands with residual trees left after harvest, the recruiting red oaks were not vigorous; and other recruiting species were more numerous and vigorous, even when many of the residual trees were red oaks. Even if it does not kill the red oaks, shade from taller residual trees will dramatically prolong the time it will take for red oaks to grow into the overstory. This shade also slows associated species, although generally not as much as the oaks. The scarcity of recruiting red oaks following harvesting that only partially removes the standing trees is probably because of several factors:

- "feedback" of shade from the residual trees causes the recruiting red oaks to grow increasingly slower in height or to die, allowing more trees of other species to surpass and suppress them;

Table 5
Relation of initial residual overstory basal area to residual overstory basal area 5, 10, 15, 20, and 25 years later calculated from the reconstruction study

T (future times) (years)	A	B	R^2	Square root of mean square residual	Observations
5	1.22	0.69	0.97	0.93	36
10	1.43	1.20	0.95	1.60	27
15	1.66	2.35	0.89	2.84	27
20	1.60	5.76	0.96	2.23	8
25	1.64	7.60	0.92	3.24	5

Equation form $\mathrm{baT} = A \times \mathrm{baH} + B$. baH: residual basal area at time of last harvest; baT: basal area at time T; A and B are coefficients.

- taller residual and recruiting trees of other species expand more rapidly than red oaks to refill the growing space made available by the harvesting; and
- other residual species in the stand become increasingly dominant because they have little commercial values and so were not harvested.

Even a few trees left after a harvest can suppress shorter red oaks, because these residual trees also increase in density (basal area) with time. To determine how rapidly the residual tree basal area increases, the relation of residual tree basal area immediately after the last treatment and the residual basal area 5, 10, 15, 20, and 25 years later was determined from the reconstruction plots (Table 5). By combining the change in residual overstory basal area over time with the relation of residual overstory basal

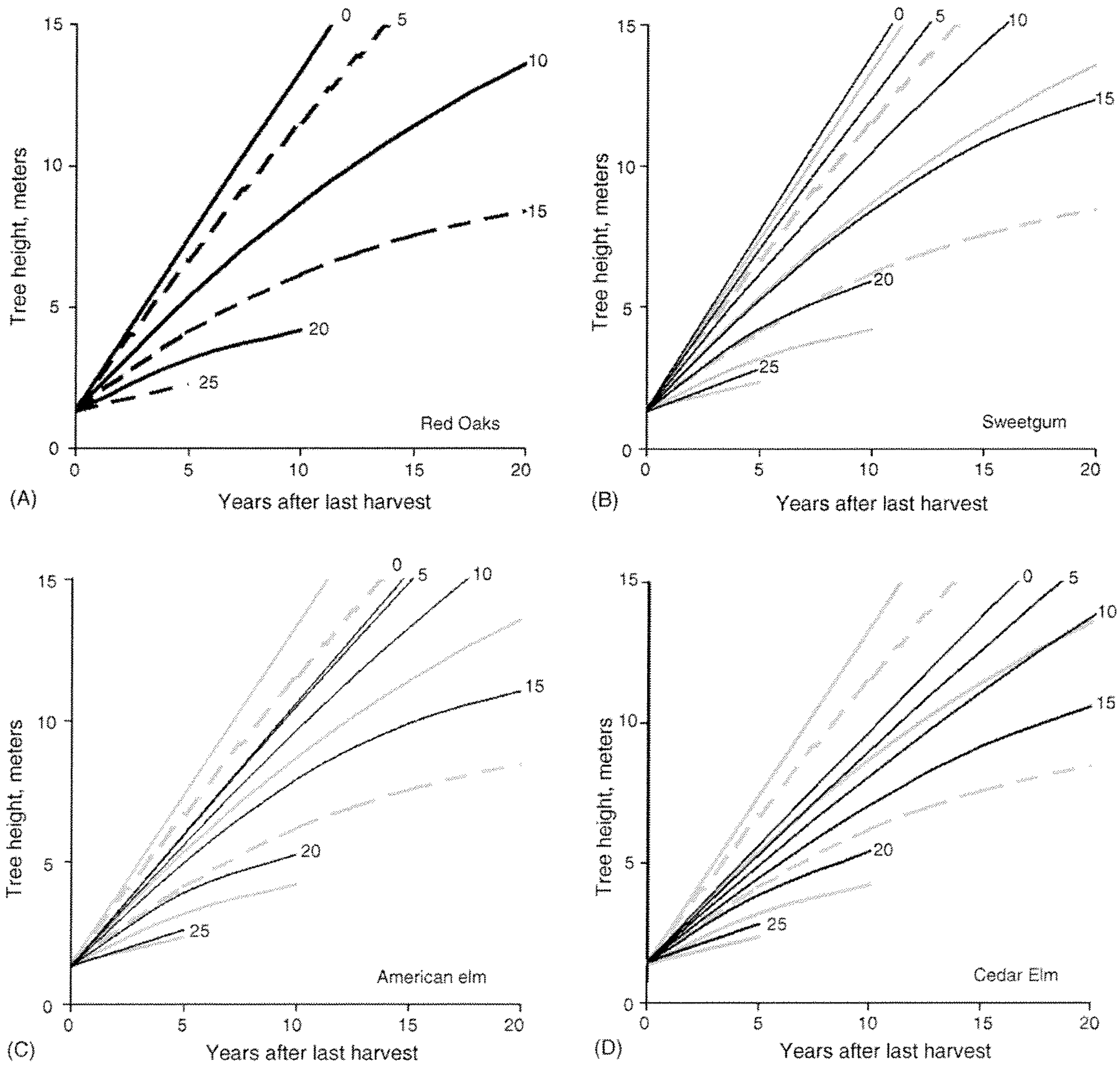

Fig. 9. Projected height growths for predominant species following harvests that leave different residual overstory basal areas, calculated from Fig. 8 and Table 5. Gray lines in background in (B) to (G) show red oak growths (Fig. 8A), to be used for comparisons. Numbers on graph indicate initial residual overstory basal areas (m^2/ha) for each line: (A) Red oaks; (B) Sweetgum; (C) American elm; (D) Cedar elm; (E) Sugarberry; (F) Green Ash; (G) Swamp dogwood.

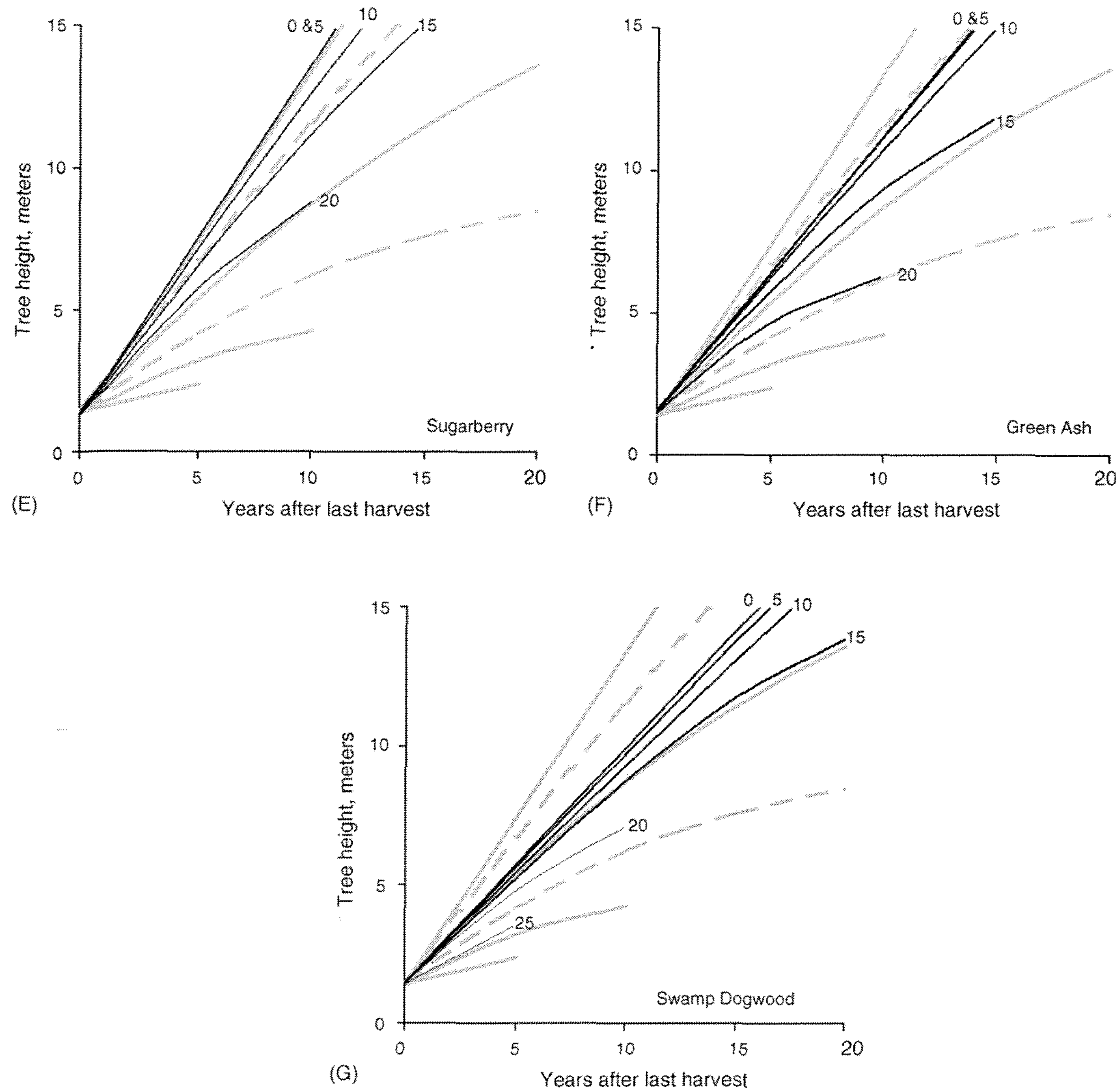

Fig. 9. (*Continued*).

area to maximum height growth (Fig. 8), the maximum potential height growths for understory trees of each species can be estimated for harvests that leave different residual overstory densities (Fig. 9).

Figs. 8 and 9 show how different species can shift height dominance and give different patterns of stratification both with different initial residual overstory densities and as these densities change with time.

For example (Fig. 9), if a residual red oak is 1.4 m tall following a harvest that leaves a residual overstory density of 15 m^2/ha of basal area, the oak will be no more than 7 m tall 15 years later. At the same time, American elm will be 10 m tall, sugarberry will be 15 m tall, and swamp dogwood and green ash will both be about 12 m tall. Alternatively, if the same red oak is released with no taller trees, it will be a maximum of 13 m tall only 10 years later, while

American elm would be 10 m tall, sugarberry would be 11 m tall, and swamp dogwood and green ash would both be about 8 m tall. This study expands the studies of species stratification that have primarily been done in stands with no residual trees (Oliver and Larson, 1996).

This study also shows that sugarberry and sweetgum can grow nearly as fast as red oaks in the open and faster in partial shade. On the other hand, red oaks have been found to overtop the sweetgums eventually when growing together without taller residual trees (Johnson and Krinard, 1988; Clatterbuck et al., 1985; Clatterbuck and Hodges, 1988). Other factors probably help give the red oaks a competitive advantage, such as stiffer branches (Oliver, 1978), different allocations of photosynthate to root and stem growth as trees mature (Moser, 1994), and differences in reproduction mechanisms.

The general patterns of overstory shade and growth are consistent with descriptions of shade tolerances for the various species (Burns and Honkala, 1990). Fig. 8 suggests that species may have two physiological mechanisms that allow them to gain a competitive advantage in different niches. These mechanisms are maximum potential height growth and sensitivity to overhead shade. For example, if the species are arrayed in a two-dimensional matrix, with one axis being height growth rate and the other axis being sensitivity to overhead shade, red oaks would be at one extreme (or corner of the matrix) of rapid height growth and high sensitivity to overhead shade. Swamp dogwood would be at the opposite extreme of slow height growth and low sensitivity to overhead shade, while American and cedar elms and green ash would be intermediate. Sugarberry would be at another "corner" of rapid height growth and low sensitivity to overhead shade, and sweetgum would be intermediate between red oaks and sugarberry—rapid height growth and intermediate sensitivity to overhead shade.

6. Conclusions

The bottomland red oaks – cherrybark oak, willow oak, water oak, and Nuttall oak – are able to grow as rapidly in height as the other tree species in riverbottom forests only when there is little or no overstory shade. Shade from a partial overstory will cause trees of all species to slow in height growth; however, red oaks will slow more than the other species, allowing the oaks to be outgrown and suppressed by the other species. Past harvesting practices such as selection harvesting, "commercial clearcuts", or seed tree or shelterwood harvesting that did not remove the residual overstory have probably contributed to the observed scarcity of red oaks growing into the overstory of formerly red oak-dominated stands in these forests.

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