NRC Research Press

ARTICLE

Effect of gap size on composition and structure of regeneration 19 years after harvest in a southeastern bottomland forest, USA

W. Henry McNab, John C. Kilgo, John I. Blake, and Stanley J. Zarnoch

Abstract: Following timber harvests in bottomland mixed-oak (*Quercus* L.) stands, desirable oak advance regeneration can be overgrown by shade-intolerant pioneer species. We investigated the effects of group selection opening size on composition of tree regeneration 19 years postharvest in an oak-dominated bottomland forest and compared results with earlier findings to evaluate development trends. In response to six opening sizes (7–40 m radii), we evaluated regeneration density and dominance of four tree species groups: conifers, hard mast, shade-intolerant hardwoods, and shade-tolerant hardwoods. Our objectives were to determine the optimum gap size for regenerating oaks and test the delayed oak dominance hypothesis, in which oaks slowly gain dominance as pioneer species undergo self-thinning. Opening size influenced conifer regeneration but minimally affected hardwoods. Hard mast species density was less than that of either intolerant or tolerant species regardless of opening size. Future stem density trends suggest increasing intolerant species and constant mast and tolerant species. Modeled future height trends suggest increasing mast species dominance over intolerant pioneers after 30 years. Our results suggest that gap-based silviculture can be used to regenerate bottomland hardwood stands with desirable species including oaks; larger gaps favor conifers but there was no optimum size to enhance oak regeneration.

Key words: dominance hypothesis, group selection, opening size, *Quercus*, self-thinning.

Résumé : Après la récolte de bois dans des peuplements mixtes de chênes (*Quercus* L.) établis sur des basses terres, la régénération préétablie du chêne que l'on souhaite conserver peut être envahie par des espèces pionnières intolérantes à l'ombre. Nous avons étudié les effets de la taille des ouvertures d'un jardinage par groupes sur la composition de la régénération des arbres 19 ans après la coupe dans une forêt des basses terres dominée par le chêne. Nous avons ensuite comparé ces résultats à ceux d'études antérieures pour évaluer les tendances de développement. En fonction de six tailles d'ouverture (rayons de 7 à 40 m), nous avons évalué la densité de la régénération et la dominance de quatre groupes d'espèces d'arbres : les conifères, les feuillus à noix, les feuillus intolérants à l'ombre et les feuillus tolérants à l'ombre. Notre objectif était de déterminer la taille optimale des ouvertures pour régénérer les chênes et de tester l'hypothèse de la dominance retardée des chênes qui stipule que les chênes deviennent lentement dominants avec le développement de l'autoéclaircie des espèces pionnières. La taille des ouvertures a influencé la régénération des conifères, mais très peu celle des feuillus. La densité des espèces à noix était inférieure à celle des espèces intolérantes et tolérantes à l'ombre, quelle que soit la taille des ouvertures. Les tendances de la variation temporelle de la densité des tiges indiquent que la densité des espèces intolérantes à l'ombre augmentera alors que celle des espèces à noix et des espèces tolérantes à l'ombre demeurera constante. Les tendances modélisées de la hauteur des arbres indiquent que la dominance des espèces à noix augmentera après 30 ans au détriment des espèces pionnières intolérantes à l'ombre. Nos résultats indiquent que la sylviculture fondée sur la création d'ouvertures peut être utilisée pour régénérer les peuplements de feuillus des basses terres avec des espèces intéressantes, notamment des chênes. Les grandes ouvertures favorisent les conifères, mais il n'y avait pas de taille optimale d'ouverture pour améliorer la régénération du chêne. [Traduit par la Rédaction]

Mots-clés : hypothèse de la dominance, jardinage par groupes, taille des ouvertures, *Quercus*, auto-éclaircie.

Introduction

Bottomland forests of the southeastern United States (US) occupy the transition zone between well-drained uplands and periodically flooded wetlands (Kellison and Young 1997). These highly productive mesic sites can support tree communities of 30 or more species of hardwoods and several species of conifers (Imm and McLeod 2005). Mature stands are multilayered, consisting of an overstory of shade-intolerant species, a midstory of shade tolerants, and an understory of advance regeneration (Meadows and Stanturf 1997). Multiple species of shade-intolerant oaks characterize the overstory of many bottomland stands, which are highly desirable for their economic and wildlife values (Kellison and Young 1997). Following large clearcut harvests, successful regeneration of oaks can

Received 23 April 2020. Accepted 10 August 2020.

W.H. McNab. USDA Forest Service, Southern Research Station, 1577 Brevard Road, Asheville, NC 28806, USA.
J.C. Kilgo. USDA Forest Service, Southern Research Station, P.O. Box 700, New Ellenton, SC 29809, USA.
J.I. Blake.* USDA Forest Service, Southern Region, Savannah River Site, New Ellenton, SC 29809, USA.
S.J. Zarnoch.* USDA Forest Service, Southern Research Station, Clemson, SC 29634, USA.

Corresponding author: W. Henry McNab (email: henry.mcnab@usda.gov).
*Retired.

be problematic because large seedlings and saplings may be lacking, which are needed to compete with faster growing pioneer species (Johnson et al. 2002). Natural regeneration of mature, multi-aged oak-dominated stands occurs in the light-enhanced environment of canopy gaps following mortality of dominant trees (Battaglia et al. 1999). Wind storms, primarily hurricanes and tornados, are sporadically recurring large-scale natural disturbances in bottomland forests (Battaglia et al. 1999). Small-scale disturbances are straight-line winds from thunderstorms and lightning strikes that can kill individual trees but seldom cause wildland fires. However, altered natural disturbance regimes during the early 20th century, particularly the cessation of frequent, low intensity wildland fire, has changed historical vegetation dynamics in oak-dominated upland (Nowacki and Abrams 2008) and bottomland forests (Gagnon 2009). Reduced recruitment of oak and hickory (*Carya* spp.) advance regeneration has long been recognized in bottomland stands (Kellison and Young 1997) and is a growing concern for sustainable management of this keystone group of hard mast species in these forests (Meadows and Stanturf 1997).

The intensity of canopy disturbance and duration of its effects altering the lower level light regime has a differential influence on the response of advance regeneration in bottomlands (Battaglia et al. 1999). Each of the 30 or more tree species likely to occur responds individually in relation to its silvical characteristics of light, moisture, and nutrient requirements needed for survival and growth (Poorter 1999). Approximately half of the tree species in southeastern bottomland forests are tolerant of shade (Imm and McLeod 2005). Tolerant species can form a dense midstory layer that reduces light needed for survival and growth of advance regeneration of intolerant species on the forest floor (Kobe et al. 1995). Although most oak species are classified as shade intolerant, juveniles can survive for several years in heavily shaded conditions of approximately 3% of full sunlight beneath mature canopies by using food reserves in the acorn and achieve potential growth at 30% (Johnson et al. 2002). In undisturbed oak stands, a recurring cycle of recently germinated seedlings and mortality of older seedlings can give the appearance of survival of intolerant oak seedlings in a heavily shaded environment (Johnson et al. 2002). Because newly established oak seedlings grow slowly in height while establishing a large taproot, it has long been known that successful regeneration of oaks following a disturbance requires large (usually older) advance regeneration (Sander and Clark 1971). Large oak saplings have sufficient carbohydrate reserves in root systems that allow quick growth response to release for capture of a canopy position in competition with more shade tolerant species (Johnson et al. 2002). In comparison, other intolerant hardwood species, classified as pioneers, are usually not present as advance regeneration in mature stands but originate as seedlings from wind dispersed seeds and can begin rapid height growth soon after germination (Whitmore 1989; Johnson and Krinard 1988). This stand initiation stage is the first of four that describes the sequential development of forests following major disturbances (Oliver 1980). Following timber harvests, rapidly growing pioneer species, such as *Liquidambar styraciflua* L. (sweetgum) and *Pinus taeda* L. (loblolly pine), are the primary oak competitors in bottomlands (Meadows and Stanturf 1997). Oak seedlings can survive and grow slowly as even-aged regeneration cohorts in recently formed openings, where pioneer species with excurrent crown structure allows admittance of filtered light within the low canopy (Lockhart et al. 2006). The growth trajectory of oak advance regeneration has variable outcomes depending on a complex interaction of environmental and biological factors (Clatterbuck and Hodges 1988). Important factors include favorable soil moisture and duration of increased light conditions following the initial and subsequent canopy disturbances, and the presence, size, and distribution of existing advance regeneration of competing species (Clatterbuck and Hodges 1988; Johnson et al. 2002).

Bottomland hardwood stands can be harvested with little detrimental effects to site quality (Stokes and Schilling 1997) and successfully regenerated with desirable commercial species by even-aged (clearcutting, shelterwood) or uneven-aged (single tree, group selection) methods (Meadows and Stanturf 1997). Clearcutting removes the entire overstory typically consisting of large shade-intolerant hardwoods and conifers, leaving smaller stems of midstory tolerant species that sprout from cut stumps or damaged root systems. Small advance oak regeneration responds slowly to release after clearcutting (Sander and Clark 1971) and can be quickly overtopped by growth of residual tolerant species and pioneer seedlings, both of which can make rapid height growth (Meadows and Stanturf 1997). Shelterwood harvests allow moderately increased light on the forest floor that is sufficient to stimulate growth of mid-tolerant oak advance regeneration but inadequate for germination and growth of intolerant pioneer species (Meadows and Stanturf 1997). Modification of light levels can be achieved by reducing basal area of the tolerant midstory and retaining an intact overstory to reduce direct light favorable for pioneer species (Cunningham et al. 2011). Attaining desirable response of advance regeneration can be variable with shelterwoods because subcanopy light levels required for physiological functions and subsequent height growth response are difficult to implement uniformly using timber harvests (Poorter 1999).

Gap-based silviculture closely mimics natural disturbance conditions (Coates and Burton 1997) and promotes the development of a diverse species composition and structure of regeneration that responds to a range of environmental conditions, particularly light. Partitioning of light in gaps creates niche conditions ranging from full light in the center to semi-shaded at edges near the unharvested forest (Kern et al. 2017). The variable light regimes within gaps thus create conditions suitable for development of a suite of species with varying shade tolerances (Dale et al. 1995). Wind-dispersed intolerant pioneer species can make best growth in the center of large openings and less at the edges (Matlack 1994). Advance regeneration of mid-tolerant and intolerant non-pioneers, such as oak and hickory, are typically near the gap edges and often on the south aspects (Dale et al. 1995). Harvest by single tree selection is generally not suitable for lasting development of advance oak regeneration because the relatively small openings quickly close from crown expansion by trees in the surrounding uncut forest (Meadows and Stanturf 1997). Group selection harvests, which create larger canopy openings by cutting multiple trees, have been more effective for regenerating mid-tolerant and intolerant species in many conifer and hardwood forest types (Kern et al. 2017).

Appropriate sizes of group selection openings for enhancing regeneration of preferred species has been a question long investigated in many forest types. However, findings are often inconclusive because a large number of interacting environmental factors affect available light and moisture (Kern et al. 2017). Relatively few results are available from group selection harvests in oak-dominated bottomland stands, particularly long-term studies when initially dense pioneer regeneration is undergoing self-thinning from mutual competition. Oliver (1980) describes self-thinning by pioneer species as the stem exclusion stage of forest development. The reduced density allows increased light to reach the smaller oaks, which can result in their increased rate of growth following an initial delay in the stand initiation stage. Also, shifts in density and dominance between pioneer species and oaks can occur because of their different inherent rates of growth with age (Clatterbuck and Hodges 1988; Lockhart et al. 2006). Shifts in dominance from pioneer species to oaks have been reported from periodic inventories of several case studies in aging clearcut bottomland stands of the Gulf Coastal Plain (Bowling and Kellison 1983; Johnson and Krinard 1988). Similar shifts of dominance between pioneer species and oaks have been reported in older group selection studies in upland mixed oak-

hardwood stands of the eastern US (Lhotka 2013). A German study has shown that changes in the light regime of aging regeneration can affect the competitive status of *Quercus robur* L. (pedunculate oak) and *Quercus petraea* (Matt.) Liebl. (sessile oak) seedlings and saplings (Anighofer et al. 2015). Observations on changing shifts in dominance are not available for group selection harvests in bottomland stands of the Atlantic Coastal Plain, where oak regeneration competes with a suite of pioneer species differing from those in the Gulf Coastal Plain. Information on shifts of species dominance with age will fill a knowledge gap for managers considering group selection harvests in bottomland oak-hardwood stands of the Atlantic Coastal Plain.

In 1994, a large multidisciplinary study of gap-based silviculture was installed in an oak-dominated bottomland forest of the Atlantic Coastal Plain (Collins and Battaglia 2008). The objectives of that study were to determine whether opening size, position within openings, vegetative competition, or mammalian herbivory influenced natural (and artificial) oak regeneration. After 10 years, it was clear that (1) herbivory did not affect oak regeneration and (2) density of seedlings was greatest around gap edges, but results were inconclusive for effects of opening sizes. Holladay et al. (2006. p. 223) observed that oaks tended to be more frequent in large gaps and "... did not become prevalent ..." until the end of their study. Collins and Battaglia (2008) also detected no clear response of 10-year-old oak regeneration to gap size in the study and recommended future inventory of the openings to evaluate shifts in competitive positions among species. Our study is a follow-up inventory at 19 years of the 1994 study openings with the same purpose of evaluating oak regeneration in relation to opening size. We also used the study as a test of the "delayed oak dominance" hypothesis (Oliver 1978) of tree species development in aging regenerated bottomland stands now entering the exclusion stage (Oliver 1980). The purpose of this paper is to present 19-year results from a re-inventory of openings in the 1994 gap study. The premise of this study in the Atlantic Coastal Plain was that relatively slowly growing oak seedlings would maintain and advance their competitive position in aging group selection openings dominated by pioneer species, as has been reported elsewhere in mixed-oak bottomland stands. Our primary objectives were to (1) determine whether species composition and structure of regeneration at 19 years varied by gap size, (2) compare our findings with similar results at 10 years to evaluate trends of development of species, and (3) determine whether the surrounding unharvested mature forest influenced composition of regeneration in gaps of different sizes. A related interest was application of the age–height model reported by Clatterbuck and Hodges (1988) to assess potential changes of growth by regeneration of *Quercus pagoda* Raf. (cherrybark oak) and *Liquidambar styraciflua*, two species that dominated the preharvest stand.

Methods

Site description

In 1994, a large-scale, multidisciplinary study was established to investigate regeneration of oak stands by the group selection method on bottomlands of the Savannah River, at the US Department of Energy's Savannah River Site in the Upper Coastal Plain of South Carolina (33.14553°N, 81.67247°W) (Fig. 1). The climate is humid subtropical with a mean annual temperature of 18 °C and annual precipitation of 1225 mm. The study area is on a terrace landform approximately 1.5 km east of the Savannah River and not subject to flooding. Topography is nearly flat with a slope gradient of <2%. Soils are poorly drained Ultisols in the Rembert series, which are strongly acidic, have a shallow water table, high organic matter in the A horizon, and high clay content in the B horizon. Tree vegetation consists of a high overstory canopy of mixed, largely shade-intolerant hardwoods with scattered conifers, a midstory of shade-tolerant hardwoods, and an understory of shrubs, tree seedlings, and saplings. Bottomland terrace stands can consist of 30 or more tree species and range in basal area from 29 to 48 $m^2 \cdot ha^{-1}$ (Imm and McLeod 2005). Wind storms, particularly hurricanes and tornados, are the primary types of disturbances. There was no indication of large-scale wind disturbance in this 90-year-old forest that had been logged around 1900. Predicted oak site index (50 years) is 34.8 m (Parresol et al. 2017).

Treatments consisted of six replications of six gap sizes (7, 10, 14, 20, 29, and 40 m radii; 0.015, 0.031, 0.062, 0.126, 0.264, and 0.503 ha). The smallest size (7 m) is approximately the area of an extended gap formed by the mortality of a mature oak in a bottomland forest (Smith and Zollner 2001). The largest size (40 m) is approximately the area of an opening with a radius equal to the height of mature, dominant trees in the study area and has been suggested as appropriate for group selection harvests for regenerating oaks in bottomland stands (Johnson et al. 2002). Prior to harvesting, total tree basal area ≥5 cm diameter at breast height (DBH; breast height = 1.37 m) averaged 33 $m^2 \cdot ha^{-1}$ with a canopy consisting mostly of *Liquidambar styraciflua*, *Quercus* spp., and *P. taeda* (Table 1). The mean distance between gaps was 64 m. Gaps were harvested in December 1994, when soil moisture content was high. Merchantable stems of cut trees were skidded through the gaps to roadside loading areas using wheeled harvesting equipment. Trees not harvested were cut near ground level and left in place. Collins and Battaglia (2008) provide additional information on the design and installation of the 1994 study, which included investigation of natural and artificial regeneration.

A second study was installed adjacent to the first in August 2000, primarily to investigate the effects of gap size on insects and birds (Champlin et al. 2009) (Fig. 1). It consisted of four replications of three gap sizes used in the 1994 study (20, 29, and 40 m radii) in a completely randomized design. Site properties and tree vegetation were similar to the 1994 study, although soil moisture was lower at the time of harvest. Herein, we compare the results of the 2000 study (age 13 years) with the trends and variables observed in the 1994 study (age 19 years) for a subset of the three largest gap sizes.

Vegetation measurements

In 1994, the initial inventory of regeneration was made using two permanent, parallel north–south transects established through each gap into the unharvested mature forest on each end. Each transect was placed 4 m on either side of the gap center to avoid fenced exclosures used for a study of herbivory. Permanent vegetation sample plots (1 m × 2 m) were established along each transect: at the center, each gap/forest edge, and in the mature forest, for a total of 5 (or 10 per plot). Seedlings (<1.37 m height) and saplings (≥1.37 m) were inventoried by species postharvest and periodically thereafter until finally after 10 growing seasons. Because gaps of the 2000 study were created to determine the influence of opening size and vegetation structure on avian use, only height by vegetation type (e.g., woody, vine) was inventoried on temporary transects at selected locations of mist capture nets (Champlin et al. 2009).

In our September 2013 inventory, we sampled tree vegetation in gaps of the 1994 and 2000 studies and the surrounding forest matrix using conventional stand inventory methods. All plots were installed along a north–south transect through the center of each gap and into the mature forest on each end. Within all gaps, either two or four fixed radius plots (3.6 m, 0.004 ha; 11.8 ft., 0.01 ac) were installed on the transect. In all gaps, two fixed radius plots were installed midway between the center and edge. In gaps ≥29 m, two additional plots were installed 5 m on each side of the center. Trees ≥0.04 cm (0.1 in.) DBH were inventoried by species in each plot and recorded by 2.54 cm (1 in.) classes. In the mature forest, which served as untreated controls, one variable radius (prism) sample plot (2.3-factor metric, 10-factor English)

Fig. 1. Maps showing location of the study area at the Savannah River Site (S.R.S.) in South Carolina, USA (inset), and distribution of various size gaps for two studies in the study area. (The maps were created using Microsoft Paint software by W.H. McNab, US Department of Agriculture, Forest Service).

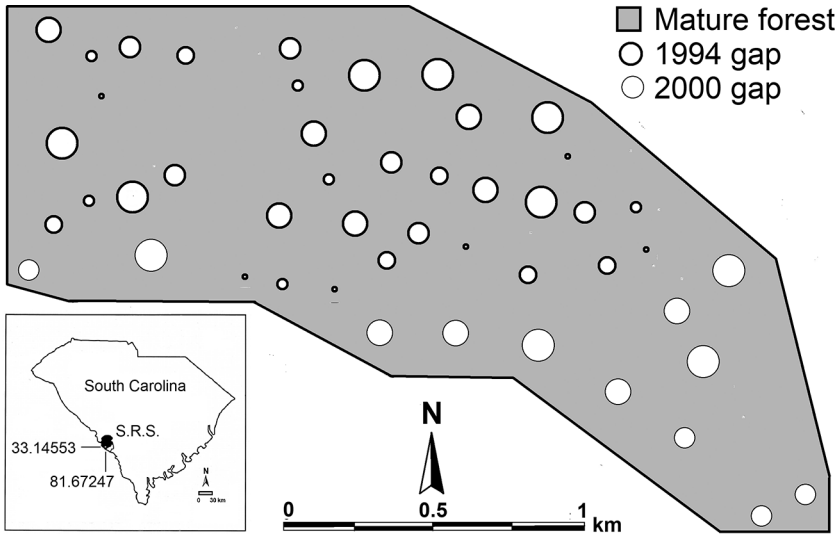


Table 1. Species groups, major and minor tree species in each group, shade tolerance class (Tol), stem density (Den.), basal area (BA), and importance value (IV) for tree species (≥5 cm diameter at breast height, 1.37 m) occurring preharvest on the 1994 study sites in a bottomland hardwood forest on the Savannah River Site, South Carolina, USA.

Species group	Major and minor tree species	Tol.	Den. (n·ha^{-1})	BA (m^2·ha^{-1})	IV (%)
Conifer	Loblolly pine (*Pinus taeda* L.)	I	19.39	4.37	15.63
	Minor species	I	0.45	0.10	0.36
Mast	Laurel oak (*Quercus laurifolia* Michx.)	I	59.49	4.47	20.94
	Cherrybark oak (*Quercus pagoda* Raf.)	I	31.60	4.28	16.88
	Swamp chestnut oak (*Quercus michauxii* Nutt.)	IM	53.78	2.83	15.27
	Hickory (*Carya* Nutt.)	IM	58.77	1.82	11.97
	Bluff oak (*Quercus austrina* Small)	I	29.96	2.11	10.12
	White oak (*Quercus alba* L.)	IM	40.80	1.41	9.36
	Willow oak (*Quercus phellos* L.)	I	11.40	2.20	8.07
	Water oak (*Quercus* nigra L.)	I	21.26	1.54	7.31
	Post oak (*Quercus stellata* Wangenh.)	IM	3.18	0.28	1.24
	Minor species	NA	5.54	0.21	1.25
Intolerant	Sweetgum (*Liquidambar styraciflua* L.)	I	171.72	3.39	31.69
	Ash (*Fraxinus* L.)	IM	53.40	0.84	9.21
	American sycamore (*Platanus occidentalis* L.)	I	9.25	0.18	1.70
	Minor species	NA	1.96	0.06	0.42
Tolerant	Red maple (*Acer rubrum* L.)	T	90.98	1.07	14.59
	Red mulberry (*Morus rubra* L.)	T	29.18	0.17	4.16
	Blackgum (*Nyssa sylvatica* Marshall)	T	16.41	0.50	3.56
	Winged elm (*Ulmus alata* Michx.)	T	17.23	0.31	3.09
	American elm (*Ulmus americana* L.)	T	15.75	0.36	3.05
	Hornbeam (*Carpinus caroliniana* Walter)	VT	19.99	0.11	2.93
	Sugarberry (*Celtis laevigata* Willd.)	T	9.62	0.21	1.84
	Persimmon (*Diospyros virginiana* L.)	VT	5.13	0.18	1.18
	American holly (*Ilex opaca* Aiton)	VT	7.88	0.03	1.07
	Minor species	NA	20.72	0.18	3.07

Note: Shade tolerance classes: I, intolerant; IM, intermediate; NA, not applicable; T, tolerant; VT, very tolerant. IV (%) = relative (%) density + relative (%) basal area for species ≥ 1.0. Minor species with individual IV < 1.0: conifer group - bald cypress (*Taxodium distichum* (L.) Rich.); mast group - pin oak (*Quercus palustris* Münchh.), southern red oak (*Quercus falcata* Michx.), water oak (*Quercus nigra* L.); intolerant group - yellow-poplar (*Liriodendron tulipifera* L.), black locust (*Robinia pseudoacacia* L.), black willow (*Salix nigra* Marshall); tolerant group - flowering dogwood (*Cornus florida* L.), loblolly bay (*Gordonia lasianthus* (L.) J. Ellis), redbud (*Cercis canadensis* L.), witch hazel (*Hamamelis virginiana* L.).

was located approximately 30 m from the gap edge at each end of the transect for inventory of trees by species. The purpose for the prism samples was to determine whether the within gap regeneration variables on a species group basis were related to those in the adjacent mature forest. Thirty-six gaps were inventoried in the 1994 study. Twelve gaps were installed in the 2000 study, but only 11 were inventoried in 2013 because one (29 m) could not be accurately located.

Table 2. Least squares means and standard errors (SE) for tree regeneration (≥0.04 cm diameter at breast height, 1.37 m) cohort attributes of density, dominance, and logistic model predicted means for frequency by species group and gap size estimated from fixed circular plots (0.00407 ha) in regenerated openings of the 1994 study 19 years after harvest in a bottomland hardwood forest at the Savannah River Site, South Carolina, USA.

	Gap sze (radius)						
Species group	7 m	10 m	14 m	20 m	29 m	40 m	*p*
Density (n·ha^{-1})							
Conifer	25.0	0.0	50.0	41.7	166.7	200.0	0.902
(SE)	(36.4)	(0.0)	(72.8)	(60.7)	(242.6)	(291.1)	
Mast	183.3	58.3	83.3	150.0	133.3	200.0	0.820
(SE)	(133.1)	(42.4)	(60.6)	(108.9)	(96.9)	(145.2)	
Intolerant	766.7	666.7	891.7	983.3	1425.0	716.7	0.115
(SE)	(152.0)	(132.2)	(176.7)	(194.8)	(282.1)	(142.1)	
Tolerant	288.3	266.7	266.7	283.3	433.3	383.3	0.820
(SE)	(89.8)	(84.5)	(84.5)	(89.8)	(137.1)	(121.3)	
Dominance (m^2·ha^{-1})							
Conifer	0.035	0.010	0.039	0.145	0.803	2.979	0.100
(SE)	(0.052)	(0.015)	(0.059)	(0.216)	(1.200)	(4.455)	
Mast	1.041	1.085	0.175	0.440	0.505	4.566	0.672
(SE)	(1.435)	(1.494)	(0.241)	(0.606)	0.695)	(6.291)	
Intolerant	13.868	20.226	30.554	45.741	45.069	27.231	0.004
(SE)	(3.098)	(4.518)	(6.825)	(10.217)	(10.067)	(6.082)	
Tolerant	6.090	4.680	3.639	1.898	5.793	5.263	0.882
(SE)	(4.54)	(3.49)	(2.71)	(1.41)	(4.32)	(3.92)	
Frequency (proportion)							
Conifer	0.093	0.112	0.143	0.201	0.320	0.502	<0.050
(SE)	(0.063)	(0.066)	(0.069)	(0.069)	(0.074)	(0.125)	
Mast	0.410	0.418	0.428	0.444	0.468	0.497	>0.050
(SE)	(0.084)	(0.074)	(0.064)	(0.056)	(0.071)	(0.113)	
Intolerant	0.906	0.947	0.975	0.993	0.999	1.000	>0.050
(SE)	(0.055)	(0.038)	0.040)	(0.024)	(0.007)	(0.001)	
Tolerant	0.819	0.813	0.805	0.792	0.772	0.746	>0.050
(SE)	(0.067)	(0.061)	(0.053)	(0.047)	(0.058)	(0.097)	

Note: The *p* values are based on type III tests of fixed effects, except for frequency where they represent whether the 95% confidence interval based on the logistic model slope parameter was significantly different from zero. Species in each group are listed in Table 1. Species group compositions: conifer group, species in *Pinus* or *Taxodium* genera; mast group, species in *Quercus* or *Carya* genera; intolerant group, species classified as intolerant or mid-tolerant of shade; tolerant group, species classified as tolerant or very tolerant of shade.

Tree species were grouped into four categories primarily by similar silvical characteristics or wildlife habitat importance: (1) The conifer group (hereinafter termed conifer) included *P. taeda* and *Taxodium distichum* (L.) Rich. (bald cypress), which are shade-intolerant, pioneer species with open crowns of needle-like foliage that allows admittance of light to lower levels within the canopy. Conifers regenerate by wind-dispersed seeds that germinate best on bare soil. (2) The hard mast group (hereinafter mast) consists of approximately 10 large overstory species of oaks (*Quercus* spp.) and hickories (*Carya* spp.) that are intolerant to mid-tolerant of shade and have high value for wildlife habitat. This group of species produces large, hard fruits (acorns, nuts) that fall beneath or near the source tree and provide fall-season food for wildlife. Fruit not immediately consumed can be dispersed up to 200 m from source trees by eastern gray squirrels (*Sciurus carolinensis* Gmelin, 1788) and cached by scatter hoarding. (3) The non-mast, shade intolerant to midtolerant (hereinafter intolerant) group of large, deciduous hardwood species are predominantly light-seeded, wind-dispersed pioneers that are early colonizers of disturbed sites and typically do not need a well-developed root system before initiating rapid height growth. Trees in this group typically produce large seed crops annually and dispersed seeds quickly lose viability in the soil seed bank (Meadows et al. 2006). (4) The shade-tolerant and very tolerant (hereinafter tolerant) species group are small to moderate size trees that can form a dense midstory and understory foliage layer that intercepts light passing through the overstory. Fruits of this group are typically berries or drupes containing one or more hard seeds surrounded by a soft mesocarp, which are consumed by wildlife and can be distributed far from the source tree. These categories are mutually exclusive and allow assignment of other species not present in the gap study area to only one group. Species in each group are listed in Table 1. Importance values, the sum of the relative density (%) and relative basal area (%) (maximum value of 200%), were used to rank each species in relation to its dominance in the preharvest tree community. We adjusted the higher level of sampling intensity in large gaps ≥29 m (four plots) to match that for small gaps ≤20 m (two plots) by taking the mean of the pair of plots on each segment of the transect. Density is the number of stems per hectare by species group. Dominance is the basal area per hectare for each species group. We computed frequency for each gap size as the proportion of sample plots that had at least one occurrence of one of the species in the respective group. We also converted density, dominance, and frequency to relative (%) metrics. Quadratic mean DBH (DBHq) was calculated from mean density and mean basal area by species group and gap size to provide a more commonly used measure of average stem sizes in stands (Curtis and Marshall 2000).

Vegetation development trends

To assess trends of species composition during early to mid-stand development we extracted relevant published tabular data reported for this study at ages 2 and 10 (Holladay et al. 2006; Collins and Battaglia 2008) and combined those metrics with our 19-year data. The trend of future heights of oaks compared with *Liquidambar*

styraciflua, the predominant intolerant species in the postharvest stand (Holladay et al. 2006), was assessed using growth models based on stand age developed for bottomland stands with similar species compositions in the Gulf Coastal Plain (Clatterbuck 1987). Mean total height of *Liquidambar styraciflua* was predicted using relationships developed by Lhotka (2012).

Statistical analysis

Because of the difference in sampling methods for density, dominance, and frequency of regeneration by species groups in the gaps (using fixed plots) and in the mature forests (using variable radius prism plots), the analyses were performed separately. This analysis was feasible only for density and dominance in the gaps and their relative counterparts in the mature forest. Frequency was not calculated for the prism plots because the effective area sampled varied depending on the diameter limiting distance relationship for each tree.

As a result of sampling two plots in each gap (or two means in large gaps) the frequency variable took on the values 0.0, 0.5, or 1.0. Therefore, we fitted a nonlinear logistic model as a function of gap size and determined significance by examining the 95% confidence interval on the slope parameter to determine whether it included zero. Density was count data and the variance exceeded the mean, so a generalized linear model was used based on the negative binomial distribution. For dominance, a logarithmic transformation was needed to ensure normality before performing an analysis of variance (ANOVA). We obtained least square means for each analysis, except frequency where we obtained the predicted mean for a gap size from the fitted logistic model. We performed pairwise comparisons with the Tukey's test, and we analyzed residuals for bias and distribution. We performed a one-way ANOVA using the untransformed values for relative density, relative dominance, and relative frequency as these were distributed normally.

We performed a one-way ANOVA on the 1994 data to determine whether species groups in the mature forest differed by gap size. Transformations were not required because the residuals were distributed normally. We then calculated Pearson correlations between the prism and the fixed plot variables for the dependent variables of density, dominance, relative density, and relative dominance by species group. If there were significant effects of gap size for the prism points or significant Pearson correlations across gaps between prism plot and fixed plot variables, we performed one-way analysis of covariance (ANCOVA) using the prism density as a covariate to increase the power and significance of the tests for gap effect for the fixed plots. All data summaries and tests were performed using SAS software (SAS Institute Inc. 2011) with probability of significance determined at the $p \leq 0.05$ level.

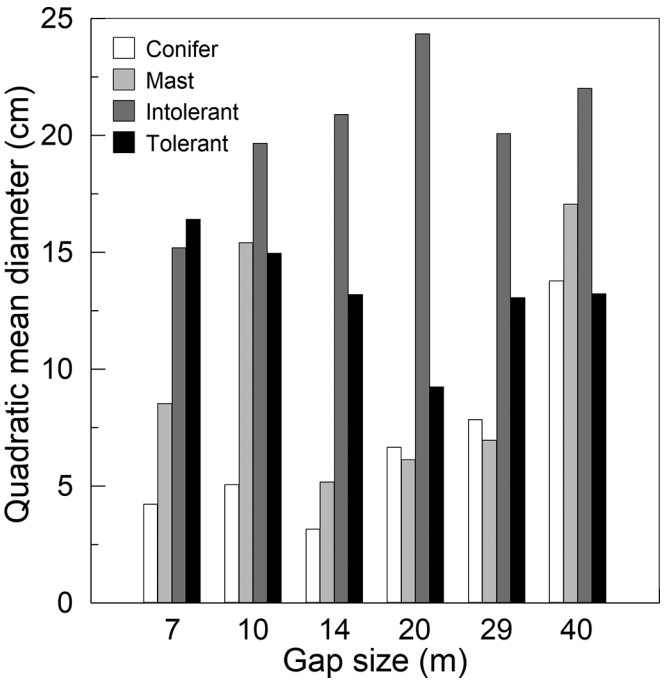
Results

1994 gap study

The gap radii treatments resulted in significant effects on dominance and frequency within the four species groups. First, dominance of the intolerant group differed significantly among gap sizes ($p = 0.004$), generally increasing with gap size through 29 m but lower in 40 m radius gaps (Table 2); results for the three relative variables were all nonsignificant and not provided). Gap size affected regeneration frequency ($p = 0.050$) only for the conifer group: as gap size increased, tree (primarily *P. taeda*) occurrence increased. Although not statistically significant, relative dominance of the intolerant group trended lower in the 7 and 10 m gaps compared with the 14, 20, and 29 m gaps, whereas the mast group trended the opposite pattern (data not shown).

Mean DBHq across all gap sizes was usually largest for intolerants and smallest for conifers (Fig. 2). With only several exceptions, mean DBHq of these two groups tended to increase with larger gap sizes. In a similar but opposite relationship, DBHq of the tolerant group decreased from gap sizes 7to 14 m and, except for smaller trees in the 20 m gaps, remained constant across larger openings. Mast DBHq was largest in 40 m gaps but varied across other sizes.

Fig. 2. Quadratic mean diameter at breast height (1.37 m) of trees (≥0.04 cm diameter at breast height) by gap size for four species groups at 19 years postharvest for the study site at the Savannah River Site, South Carolina, USA. Species group compositions: conifer, species in *Pinus* or *Taxodium* genera; mast, species in *Quercus* or *Carya* genera; intolerant, species classified as intolerant or mid-tolerant of shade; tolerant, species classified as tolerant or very tolerant of shade.



A significant association of tree densities in the mature forest with densities across all gap sizes was present only for the intolerant group that consisted primarily of wind=dispersed seeds of pioneer species ($R^2 = 0.26$; $p = 0.0008$) (Fig. 3). Although there was a significant regression relationship between the density of the intolerant hardwoods in the mature forest and the density of this group in the fixed plots, ANCOVA did not increase the power of the test of effects for the fixed radii gaps. Even when the density of this group was close to zero in the mature forest, the regeneration densities in the gaps were often >500 stems·ha^{-1} (Fig. 3). The average ratio of stem densities across all gap sizes for each group obtained from fixed plots relative to densities in the prism plots showed that the density of the conifer and intolerant groups were more than 10 times greater in the gaps than in the adjacent forest (Table 3). The equivalent average ratios of densities for the mast and tolerant groups in harvested gaps were about twice that in the mature forest.

2000 gap study

Our analysis revealed three significant results in this study. Among opening sizes, the only significant effect ($p = 0.025$) was greater densities of the tolerant species with increasing gap sizes (Table 4). Two relationships were significant between vegetation in the gaps and the mature forest. Relative density of the mast group was greater in 40 m gaps compared with smaller sizes and

Fig. 3. Relationship between mean density (n·ha^{-1}) of tree regeneration (≥0.04 cm diameter at breast height) in the intolerant species group in gaps and the mature forest at 19 years postharvest for the 1994 study at the Savannah River Site, South Carolina, USA. The intolerant group consists of species that are intolerant or mid-tolerant of shade.

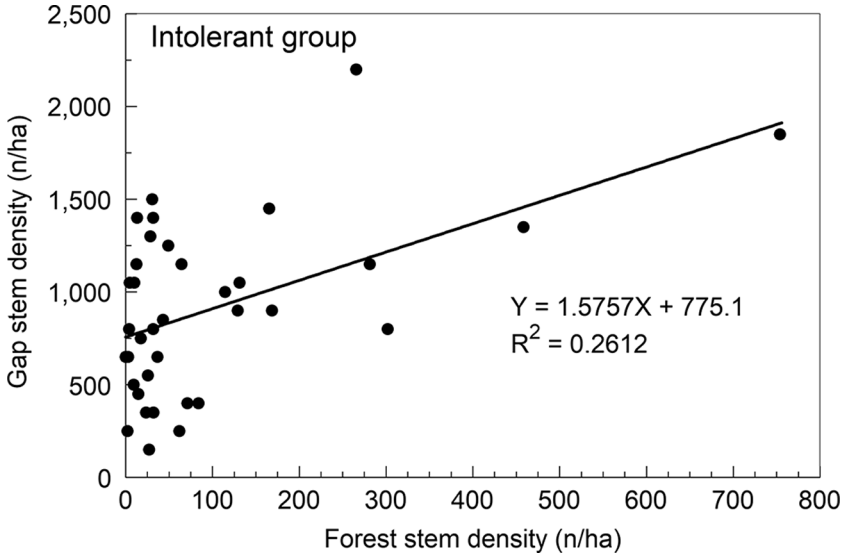
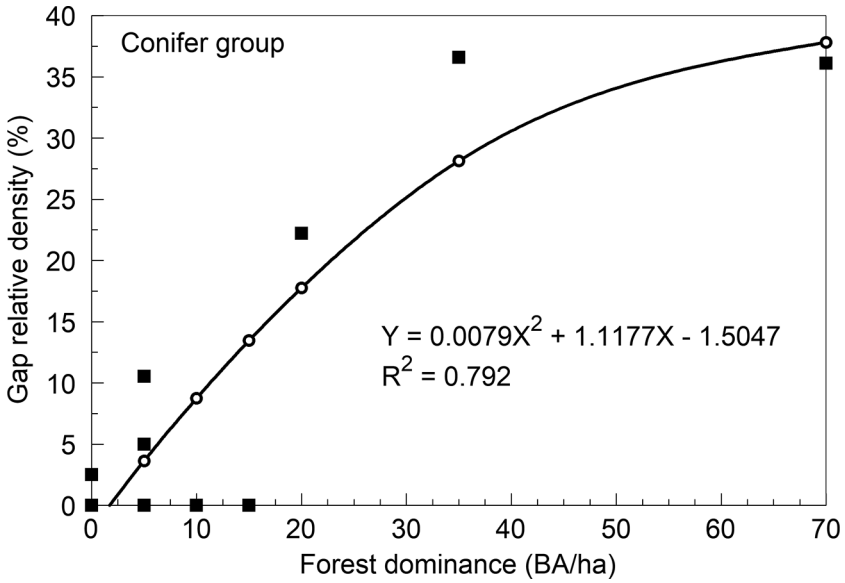


Fig. 4. Relationship between mean relative density (% of total n·ha^{-1}) of tree regeneration (≥0.04 cm diameter at breast height) in the conifer group in gaps and dominance (m^2·ha^{-1}) of the conifer group in the mature forest at 13 years postharvest for the 2000 study at the Savannah River Site, South Carolina, USA. The conifer group consists of species in *Pinus* or *Taxodium* genera. BA, basal area.



was associated (p = 0.019, data not shown) with density of that species group in the mature forest. Also, relative density of the intolerant group was greater in the 20 and 29 m gaps compared with the 40 m size and was associated (p = 0.016, data not shown) with density of this group in the prism plots. Relative density of the conifer group in gaps was associated with dominance of this group in the mature forest (p = 0.005; Fig. 4).

Comparison of 1994 and 2000 study results

There was a positive trend of conifer group frequency as gap size increased in both studies, but the relationship was significant only for regeneration in the 1994 study at 19 years (Fig. 5A). Frequency of occurrence for the mast, intolerant, and tolerant groups were not associated with gap size in either study. For the 13-year-old regeneration in the 2000 study, mean densities of the intolerant group were usually about half of those in 1994 across the same gap sizes (Tables 2 and 4). Relative dominance of the intolerant group was consistently greater in the older (1994) gaps than the 2000 gaps, but it declined in gaps of both ages as opening size increased (Fig. 5B). In contrast to the 1994 study, density and frequency of the mast group was greater in the 2000 study (Tables 2 and 4). Frequencies of occurrence of the mast species group were approximately 88% in sample plots of the 2000 study and densities were three times greater than in 1994. Relative dominance of the mast group tended to increase with gap size for studies and was consistently greater for the 13-year-old

Table 3. Ratio of tree regeneration (≥0.04 cm diameter breast at height, 1.37 m) stem density in fixed plots within gaps to stem density of trees in prism points within the mature forest for the 1994 study (age 19 years) and 2000 study (age 13 years) at the Savannah River Site, South Carolina, USA.

	Gap size (radius)						
Species group	7 m	10 m	14 m	20 m	29 m	40 m	Mean
1994 Study							
Conifer	2.2	0	7.4	3.1	23.3	36.4	12.2
Mast	3.1	0.8	0.4	0.7	1.1	3.0	2.6
Intolerant	11.4	6.6	11.1	17.1	6.3	14.1	11.1
Tolerant	1.6	3.4	1.5	1.4	4.6	0.8	2.2
2000 Study							
Conifer	NA	NA	NA	21.1	46.7	114.3	60.7
Mast	NA	NA	NA	5.4	17.0	4.3	8.9
Intolerant	NA	NA	NA	8.9	6.7	24.5	13.4
Tolerant	NA	NA	NA	0.5	2.0	9.2	3.9

Note: NA, not applicable; the 2000 study did not include gaps of these three sizes. Species in each group are listed in Table 1. Species group compositions: conifer group, species in *Pinus* or *Taxodium* genera; mast group, species in *Quercus* or *Carya* genera; intolerant group, species classified as intolerant or mid-tolerant of shade; tolerant group, species classified as tolerant or very tolerant of shade.

regeneration (Fig. 5C). The relative basal area of the mast group in the mature forest ranged between 52% and 62% for the six gap sizes in the 1994 study and between 38% and 59% for the three gap sizes in the 2000 study (data not shown).

Trends of regeneration development

The trend of density for the mast group between ages 2 and 19 years was approximately constant among all gap sizes except for the 7 m, which was positive (Fig. 6). In comparison, the trend of density for the intolerant group increased for all gap sizes between ages 10 and 19 years. The trend of density changes for the tolerant species was consistent across all gap sizes, with increases between ages 2 and 10 years and decreases from 10 to 19 years. Relative density of conifers across all gap sizes decreased between ages 2 and 10 years (from 11% to 5%) and then remained nearly constant at 6% of all trees until age 19 years (data not shown). The trends of height growth by the two species dominating the preharvest stand (Table 1), *Liquidambar styraciflua* and *Q. pagoda*, indicates a declining rate for the former species and steady or increasing rate for the latter (Fig. 7). The predicted height of *Liquidambar styraciflua* at 19 years in the 1994 study was 19.5 m, which agrees closely with a predicted value of 19.9 m for this species based on a model developed from a bottomland stand in Mississippi (Clatterbuck 1987). The height of this species for the 2000 study was 17.5 m, which was approximately 3 m taller than predicted by the model.

Discussion

Maintaining oaks after using group selection to harvest oak-dominated stands requires the presence of advance oak regeneration in the canopy gaps (Meadows and Stanturf 1997). A tenet of gap-based silviculture is that the light environment in openings of certain sizes and positions in openings (center, edge) will be more favorable for development of a focal species than its competitors (Coates and Burton 1997). One of the objectives of this 1994 study was to determine the optimum gap size of group selection openings for stocking and growth of natural oak regeneration in a bottomland oak-dominated forest of the southeastern US (Collins and Battaglia 2008). In that study, Holladay et al. (2006) observed a weak trend of increasing oak frequency and height in centers of larger gaps. Collins and Battaglia (2008) concluded that longer study time will be needed to determine a gap size most beneficial for development of slowly growing oak seedlings in competition with rapidly growing pioneer species. In our inventory of the Collins and Battaglia (2008) sample transects after 19 years, densities for the mast group ranged from 58 to 200 stems·ha^{-1} (Table 2), which was approximately twice the densities present in the surrounding forest (Table 3). There were no differences in stem density among gap sizes for the mast group. Therefore, at 19 years postharvest, we conclude that gap size has no statistically measurable effect on the regeneration of the mast group consisting of highly desirable species of *Quercus* and *Carya*. The only clear effect of gap size on regeneration was for dominance of the intolerant group, which tended to be greater in gaps of radii 20 and 29 m than in smaller or larger gap sizes. The reduced dominance of the intolerant group in the largest gaps may result from increased competition from the conifer and mast groups, both of which had greater basal areas in the 40 m gaps than in smaller gaps.

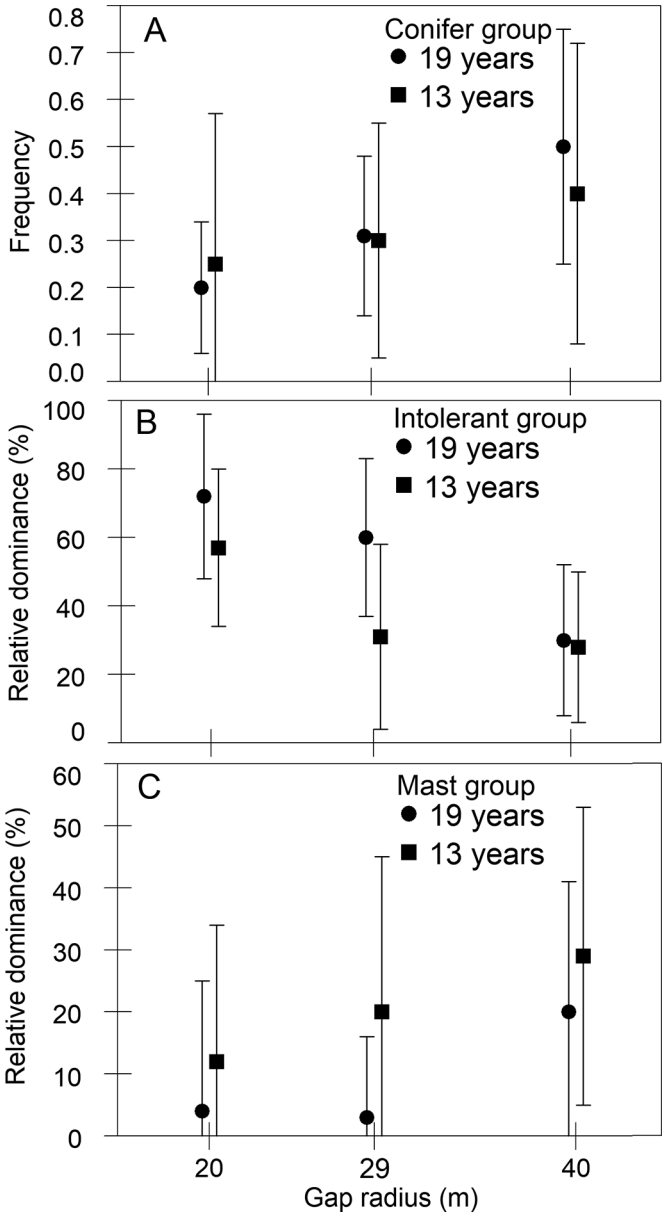
One of our interests in a follow-up inventory of the 1994 gaps was to test Oliver's (1978) hypothesis of delayed oak dominance, an objective seldom specifically proposed in other regeneration studies where oaks were a focal species (Steiner et al. 2018). We

Table 4. Least squares means and standard errors (SE) for tree regeneration (≥0.04 cm diameter at breast height, 1.37 m) cohort attributes of density and dominance and logistic model predicted means for frequency by species group and gap size estimated from fixed circular plots (0.00407 ha) in 11 regenerated openings of the 2000 study 13 years after harvest in a mature bottomland hardwood forest at the Savannah River Site, South Carolina, USA.

	Gap size (radius)			
Species group	20 m	29 m	40 m	*p*
Density (n·ha^{-1})				
Conifer	187.5	116.7	400.0	0.843
(SE)	(262.2)	(188.4)	(559.2)	
Mast	375.0	750.0	600.0	0.272
(SE)	(101.5)	(233.8)	(162.1)	
Intolerant	575.0	483.3	400.0	0.497
(SE)	(119.3)	(115.9)	(83.1)	
Tolerant	162.5	283.3	850.0	0.025
(SE)	(55.7)	(111.7)	(289.6)	
Dominance (m^2·ha^{-1})				
Conifer	0.351	1.502	0.372	0.890
(SE)	(0.76)	(3.76)	(0.81)	
Mast	2.622	9.516	8.444	0.281
(SE)	(1.5)	(6.2)	(4.8)	
Intolerant	14.021	12.687	11.450	0.932
(SE)	(5.3)	(5.6)	(4.4)	
Tolerant	1.590	5.502	5.452	0.503
(SE)	(1.3)	(5.1)	(4.4)	
Frequency (proportion)				
Conifer	0.260	0.312	0.382	>0.050
(SE)	(0.16)	(0.11)	(0.17)	
Mast	0.875	1.000	1.000	>0.050
(SE)	(0.07)	(0.08)	(0.00)	
Intolerant	0.854	0.911	0.953	>0.050
(SE)	(0.10)	(0.07)	(0.09)	
Tolerant	0.625	1.000	1.000	>0.050
(SE)	(0.11)	(0.13)	(0.00)	

Note: The *p* values are based on type III tests of fixed effects except for frequency where they represent whether the 95% confidence interval based on the logistic model slope parameter differed from zero. Species in each group are listed in Table 1. Species group compositions: conifer group, species in *Pinus* or *Taxodium* genera; mast group, species in *Quercus* or *Carya* genera; intolerant group, species classified as intolerant or mid-tolerant of shade; tolerant group, species classified as tolerant or very tolerant of shade.

Fig. 5. Mean frequency with 95% confidence intervals (95% CI) of the conifer group (A), relative dominance (95% CI) of the intolerant group (B), and relative dominance (95% CI) of the mast group (C) by three gap radii (20, 29, and 40 m) common to the 1994 (19 years of age) and 2000 (13 years of age) studies at the Savannah River Site, South Carolina, USA. Species group compositions: conifer, species in *Pinus* or *Taxodium* genera; mast, species in *Quercus* or *Carya* genera; intolerant, species classified as intolerant or mid-tolerant of shade.



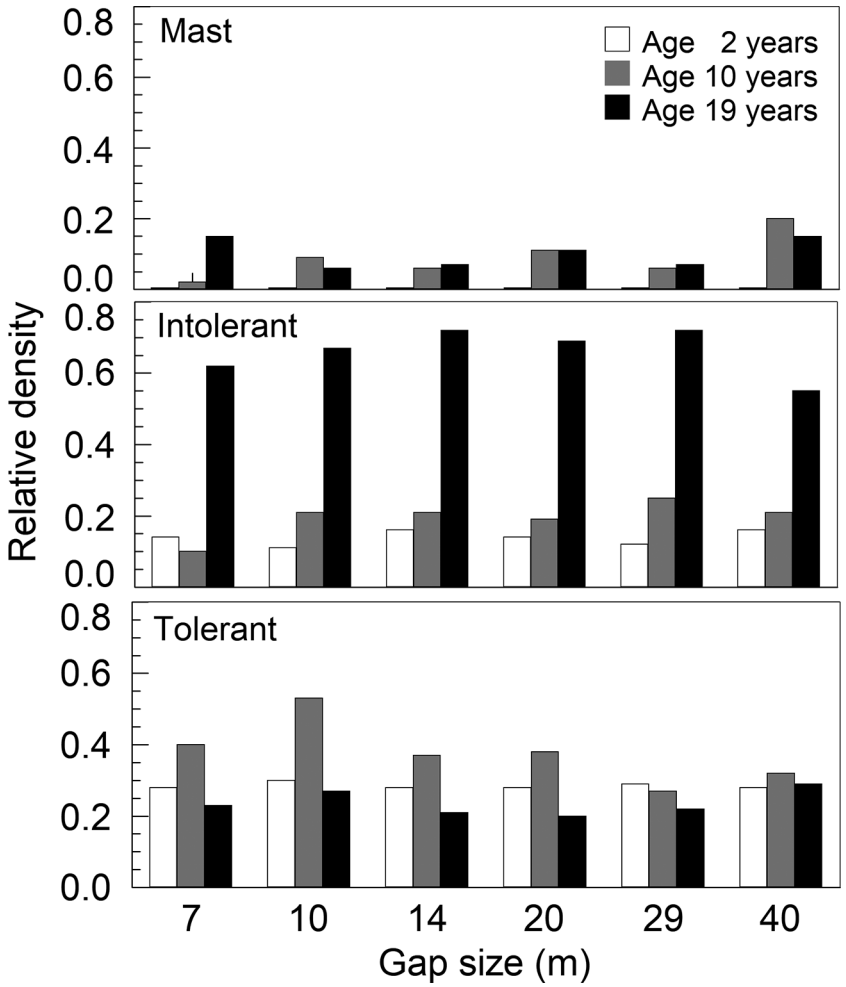
were unable to do that at stand age 19 years because self-thinning was not evident among stems in the intolerant group. Our results agree with second-decade trends of development in a bottomland stand of similar species in Mississippi (Johnson and Krinard 1988). However, the trend of steady relative density of mast species with age in our study, despite an increased density of intolerants (Fig. 6), adds tentative support for applicability of the hypothesis. Conclusive results will await a later inventory during the third or fourth decades of stand development.

Many of the largest oaks in our study at age 19 years were probably stump sprouts from well-developed root systems that are capable of rapid height growth (Gardiner and Helmig 1997). The majority of non-mast species (tolerants and intolerants) in our inventory, however, probably originated from seedlings (height $<$ 1.37 m) and saplings (height $\geq$ 1.37 m) recorded by Holladay et al. (2006) in summer 1996, two growing seasons after the openings were harvested in late fall 1994. The source of regeneration in the mast group in our inventory is not clear. Holladay et al. (2006) observed that oaks became evident 10 years after harvesting. In our inventory, therefore, trees in the mast group originated either as new seedlings several years after the gaps were harvested in late fall 1994 or were sprouts from existing advance regeneration that had been crushed by the logging equipment and were not apparent in the 1996 postharvest inventory.

Between the 1994 and 2000 studies, differences unrelated to the gap size treatments may have affected regeneration densities for the conifer and intolerant groups. The 1994 gaps were cut in December, when soil moisture was high, compared with the dry conditions for the 2000 openings harvested in mid-summer. Severe rutting of the saturated soil from logging equipment for the 1994 study likely destroyed a large proportion of conifer seeds dispersed earlier, during fall. For the 2000 study, conifer seeds were dispersed following logging on a dry seedbed that had been previously scarified by the harvesting equipment, which probably exposed mineral soil favorable for germination of *P. taeda* seeds. Wet-weather harvesting of the 1994 gaps could also have affected germination and survival of seeds for other species groups. Although herbivory can affect regeneration and species composition (Tilghman 1989), the results from other research in our gaps indicate that neither mammalian herbivory, primarily by white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) and marsh rabbits (*Sylvilagus palustris* (Bachman, 1837)) (Castleberry et al. 2000), nor herbivorous insects (Ulyshen et al. 2005) affected mast regeneration. Rooting by wild hogs (*Sus scrofa* Linnaeus, 1758) was a destructive influence on planted hardwood seedlings on a bottomland site in the vicinity of this study (Mayer et al. 2000); however, their effects on natural regeneration in our gaps were probably limited to predation of hard and soft mast. Both new and advance regeneration for the mast group in the 2000 study may have contributed to the high densities relative to the initial densities of this group in the mature forest (Table 3). It could also be possible that the higher density, dominance, and frequency of the mast group in the 2000 study compared with the 1994 study reflects unknown effects associated with season of harvesting, soil properties, acorn production, and climate between the two periods.

This study had several minor weaknesses that reduced the overall statistical strength of the results. Identification of regeneration originating from stump sprouts versus advance regeneration would have been desirable given the greater likelihood of their position in the current overstory. Sampling in proportion to gap size would have provided greater sensitivity in our analysis, but resources were not available. We inventoried small ($\leq$20 m radii) and large ($\geq$29 m radii) gaps with different sampling intensity (2 or 4 plots, respectively). Although our inventory included plots at or near the edges of small gaps, the results did not show evidence of differences in species composition or dominance in relation to gap edges at the study site, as reported by Collins and Battaglia (2008) and Holladay et al. (2006) at 10 years. Because gap edge effects on regeneration composition and stature have been well documented at younger ages in this study, our interests were primarily to detect effects of gap size on species shifts in aging stands. Lhotka (2013) inventoried total gap areas (not sample plots) to determine species shifts in older upland hardwood stands, a method that likely would have been superior to our sample plots. Although summarized species composition data were available for seedlings (height $<$ 1.37 m) (Holladay et al. 2006), lack of similar data for saplings (height $\geq$ 1.37 m) reduced our ability to make a more comprehensive analysis of trends of species shifts at older ages.

Fig. 6. Trends of current relative densities (trees·ha^{-1} ≥ 0.04 cm diameter at breast height) of the mast, intolerant, and tolerant species groups by gap size at three ages. Data for ages 2 (1996) and 10 (2004) years were extracted from plotted values in fig. 3 of Holladay et al. (2006). Species group compositions: mast, species in *Quercus* or *Carya* genera; intolerant, species classified as intolerant or mid-tolerant of shade; tolerant, species classified as tolerant or very tolerant of shade.

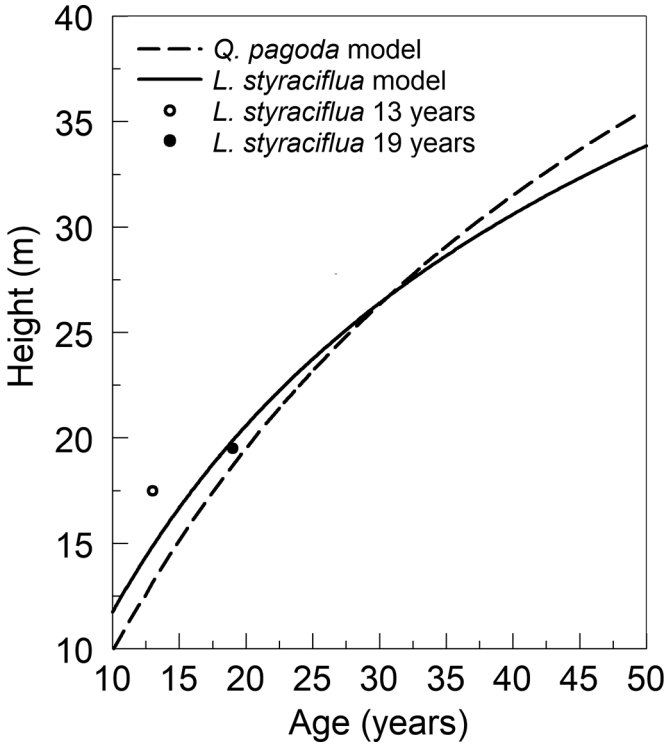


Our postharvest assessment at 19 years indicated little change in density of the mast group since age 10 years, which suggests high survival of oaks with increasing age. Oaks will likely persist as ascending midstory components in partial shade until released by a combination of natural thinning (Bowling and Kellison 1983) and reduced rate of height growth (Clatterbuck 1987) by *Liquidambar styraciflua* and other pioneer species (Fig. 7). Observations at older ages will be desirable to confirm this trend also observed in an aging mixed upland oak stand by Lhotka (2013) and predicted by the delayed oak dominance hypothesis (Oliver 1978).

Trends of stem density changes from 2 to 19 years in our study area are similar to findings reported for older bottomland stands of similar composition and could provide insight into the future development of vegetation in gaps of this study area. In agreement with findings of Johnson and Krinard (1988), earlier stem density data extracted from figures in Holladay et al. (2006) when combined with our data show trends of an increase of intolerant species and nearly constant numbers of mast and tolerant species (Fig. 6). Predicted height of *Liquidambar styraciflua* at 19 years in our study matches that reported by Clatterbuck (1987) (Fig. 7). Beyond 19 years, Johnson and Krinard (1988) report a sharp decline in density of *Liquidambar styraciflua* with nearly constant density of oaks. At a similar age, Clatterbuck and Hodges (1988) reported declining rate of height growth for *Liquidambar styraciflua* but steady rate for *Q. pagoda*, until both species were equal in height at age 25 years. For our study, height of the *Q. pagoda* is predicted to intersect with *Liquidambar styraciflua* at approximately 30 years (Fig. 7). Overall, vegetation in our study follows similar patterns of development reported for other bottomland stands in the southeastern US (Bowling and Kellison 1983) and suggests a return to the preharvest composition of an oak and hickory dominated overstory as the gaps age. We note that reports of long-term stand development by Johnson and Krinard (1988) and Clatterbuck and Hodges (1988) were made in clearcut stands, not group selection openings. Therefore, vegetation dynamics in our 40 m openings would be most likely to track their findings.

After 19 years of stand development, our inventories revealed no optimum gap size to enhance natural regeneration of oaks. Because the young regenerated openings of all sizes are now dominated by tolerant and intolerant non-oak species, a logical question is how the largely intolerant mast species gained dominance in the relatively old stand used for our study, which had originated after logging in the early 1900s. Insight on likely subsequent (post 1900) stand dynamics is available from the periodic long-term inventories of two clearcut mixed-oak bottomland

Fig. 7. Trends of future predicted heights by age for *Liquidambar styraciflua* (sweetgum) and *Quercus pagoda* (cherrybark oak) (Clatterbuck 1987) and predicted mean current height based on quadratic mean diameter at breast height (1.37 m) (Lhotka 2012) for *Liquidambar styraciflua* in the 2000 study at age 13 years and the 1994 study at age 19 years.



stands in Mississippi, which were initially dominated by tolerant and intolerant non-oak species (Bowling and Kellison 1983; Johnson and Krinard 1988). In both of those studies, stands initially dominated by rapidly growing pioneer species began self-thinning in the second and third decades after their establishment. This stem exclusion stage of stand dynamics (see Oliver 1980) was accompanied by a corresponding increase in development by a subordinate population of oaks, responding presumably to additional growing space and light. The gradually dominating oaks then maintained that canopy position until maturity. We suggest this is the development sequence for the delayed oak dominance hypothesis that is beginning to be exhibited in openings of our study where the relatively brief stand initiation stage has been completed and the much longer stem reduction stage is beginning.

Although results of this study at 19 years have not changed since the previous inventory at age 10 years when Collins and Battaglia (2008, p. 3026) stated "... there is no optimal gap size for oak regeneration ...", there are several implications for intermediate stand management by group selection with a focus on oaks. Perhaps most important, it was learned that highly desirable oaks can be regenerated in gaps ranging in radius from 7 to 40 m, which allows managers flexibility in creating opening sizes based on factors such as harvesting economics, wildlife habitat needs, and visual quality. As reported in the 10-year results from this study, we also observed that density and basal area of oak regeneration tends to be greater in larger gaps. Although not part of our study, Meadows and Stanturf (1997) suggest intermediate stand management activities, such as thinning and crop tree release, can enhance growth of focal species in group selection openings. Without active management, however, trends of height growth suggest codominance by *Q. pagoda* and other species of *Quercus* with the principal pioneer species, *Liquidambar styraciflua*, at approximately 30 years, which has been observed in other bottomland stands following timber harvests (Clatterbuck and Hodges 1988). Because the rate of natural thinning of the pioneer species will likely increase during the next decade along with continued growth of the oaks, one management strategy would be to defer crop tree release until the best candidate trees become apparent. Clatterbuck and Hodges (1988) provide additional information on management of mixed *Q. pagoda* – *Liquidambar styraciflua* stands, including recommended densities of crop trees. Lhotka (2013) reported continued self-thinning in 48-year-old openings of a group selection study in an upland mixed oak-hardwood stand, where previously subordinate oaks attained codominance with *Liriodendron tulipifera* L. (yellow-poplar) as the pioneer species. Our tentative findings based on early trends of stand development and results from older studies mentioned above are in support of the delayed oak dominance hypothesis (Oliver 1978), which proposes natural dominance by oaks in the absence of management.

The growth response similarity of oak saplings to competition from pioneer species in regenerated upland canopy gaps (Lhotka 2013) with our bottomland site suggests results from this study could be relevant for development of *Quercus* regeneration across global forest types. The slower rate of growth by oaks compared with intolerants in our study agrees with results reported by Niinemetts (1998) in mixed conifer-hardwood forests of Estonia, who reported that height growth of *Q. robur* seedlings in canopy gaps was slower than that for *Acer platanoides* L. (Norway maple) seedlings because the oaks use light resources to develop a large root system. In the subtropical evergreen forests of northeastern India, Khan and Shankar (2001) reported little effect on survival or height growth on *Quercus semiserrata* Roxb. regeneration across a light gradient in canopy gaps ranging from 28% to 90% of full sunlight. Results from their work agrees with our findings where small regeneration of the mast group receives adequate light through the canopy of the larger intolerant species for survival and slow growth. Our observations on survival and growth of the mast group in small (7 m radius) gaps are in agreement with observations by von Lupke (1998) in Germany, who observed that *Q. robur* and *Q. petraea* can be regenerated in small (8.5 to 10 m radius) canopy gaps of *Fagus sylvatica* L. (European beech) where the light environment was approximately 40% of potential. Working in Japanese forests, Yamamoto (1992) reported little or no advance regeneration of *Quercus acuta* Thunb. (Japanese evergreen oak) and *Quercus salicina* (Schottky) Koidz (Japanese willowleaf oak) in small (≤11 m radius) natural canopy gaps of deciduous, mixed-oak forests, but did not speculate on insufficient light as a possible contributing factor. In a study on river floodplains of Slovenia, Diaci et al. (2008) reported that 4-year-old seedlings of *Q. robur* averaged 15·m^{-2} across gaps ranging from 0.03to 0.40 ha, with greatest density in gaps where sunlight ranged from 10% to 20% of potential. In a meta-analysis, Kern et al. (2017) suggested that a range of gap sizes often results in successful regeneration of desired species and can address forest management goals that complement biomass production, such as harvesting economics and wildlife habitat.

Conclusions

Nineteen years after six sizes of canopy gaps were created by timber harvests in a bottomland mixed oak-hardwood forest in the Coastal Plain of South Carolina, composition and structure of tree regeneration was influenced more by differences in shade tolerance of tree species than by size of opening. Opening sizes, which ranged in radii from 7to 40 m, were dominated in stem density and basal area by rapidly growing intolerant pioneer species that were established from seeds soon after gap creation.

Stem density of hard mast species (oaks and hickories), most of which likely originated from advance regeneration, was greater in gaps than in the mature forest. Mast regeneration density was not affected by gap size, but it tended to be greater in larger gaps. Density of conifer regeneration was associated with larger gaps and higher densities of conifers in the mature forest. Previously reported 10-year results showed mast species were tallest in gap centers of all sizes and shortest in the mature forest around gaps. Predicted height growth of mast species indicates likely dominance over pioneer species at stand age of approximately 30 years. The size and distribution of advance regeneration are probably more important than opening size for enhancing establishment and development of oak regeneration in the area of our study. Overall results of this study suggest that openings of 7 m radius or greater can be regenerated with desirable species using group selection harvests in bottomland stands. Management activities that reduce density of pioneer species, such as thinning or crop tree selection, would probably increase survival and growth of mast species.

Acknowledgements

This study was conducted with funding provided by the US Department of Energy, Savannah River Operations Office through the US Department of Agriculture (USDA), Forest Service, Savannah River, under Interagency Agreement DE-AI09-00SR22188 and by the USDA, Forest Service, Southern Research Station. We are grateful to Jason Jeffcoat for field assistance, Walt Thompson for logistical assistance, and Mark Ford for reviewing an earlier draft of the manuscript. Beverly Collins provided essential information about the 1994 study design. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or US Government determination or policy.

References

Anighofer, P., Beckschafer, P., Vor, T., and Ammer, C. 2015. Regeneration patterns of European Oak species (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) in dependence of environment and neighborhood. PLoS ONE, **10**(8): e0134935. doi:10.1371/journal.pone.0134935.

Battaglia, L.L., Sharitz, R.R., and Minchin, P.R. 1999. Patterns of seedling and overstory composition along a gradient of hurricane disturbance in an old-growth bottomland hardwood community. Can. J. For. Res. **29**(1): 144–156. doi:10.1139/x98-187.

Bowling, D.R., and Kellison, R.C. 1983. Bottomland stand development following clearcutting. South. J. Appl. For. **7**(3): 110–116. doi:10.1093/sjaf/7.3.110.

Castleberry, S.B., Ford, W.M., Miller, C.V., and Smith, W.P. 2000. Influences of herbivory and canopy opening size on forest regeneration in a southern bottomland hardwood forest. For. Ecol. Manage. **131**(1–3): 57–64. doi:10.1016/S0378-1127(99)00200-5.

Champlin, T.B., Kilgo, J.C., and Moorman, C.E. 2009. Food abundance does not determine bird use of early-successional habitat. Ecology, **90**: 1586–1594. doi:10.1890/08-1190.1. PMID:19569373.

Clatterbuck, W.K. 1987. Height growth and site index curves for cherrybark oak and sweetgum in mixed, even-aged stands on the minor bottoms of central Mississippi. South. J. Appl. For. **11**(4): 219–222. doi:10.1093/sjaf/11.4.219.

Clatterbuck, W.K., and Hodges, J.D. 1988. Development of cherrybark oak and sweet gum in mixed, even-aged bottomland stands in central Mississippi, U.S.A. Can. J. For. Res. **18**(1): 12–18. doi:10.1139/x88-003.

Coates, K.D., and Burton, P.J. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. For. Ecol. Manage. **99**(3): 337–354. doi:10.1016/S0378-1127(97)00113-8.

Collins, B., and Battaglia, L.L. 2008. Oak regeneration in southeastern bottomland hardwood forest. For. Ecol. Manage. **255**(7): 3026–3034. doi:10.1016/j.foreco.2007.09.023.

Cunningham, K.K., Peairs, S.E., Ezell, A.W., Belli, K.L., and Hodges, J.D. 2011. Understory light conditions associated with partial overstory removal and midstory/understory control applications in a bottomland hardwood forest. Forests, **2**: 984–992. doi:10.3390/f2040984.

Curtis, R.O., and Marshall, D.D. 2000. Why quadratic mean diameter? West. J. Appl. For. **15**(3): 137–139. doi:10.1093/wjaf/15.3.137.

Dale, M.E., Smith, H.C., and Pearcy, J.N. 1995. Size of clearcut openings affects species composition, growth rate and stand characteristics. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, Pa. Res. Pap. NE-698.

Diaci, J., Gyoerek, N., Gliha, J., and Nagel, T.A. 2008. Response of *Quercus robur* L. seedlings to north-south asymmetry of light within gaps in floodplain forests of Slovenia. Ann. For. Sci. **65**: 105. doi:10.1051/forest:2007077.

Gagnon, P.R. 2009. Fire in floodplain forests in the southeastern USA: insights from disturbance ecology of native bamboo. Wetlands, **29**(2): 520–526. doi:10.1672/08-50.1.

Gardiner, E.S., and Helmig, L.M. 1997. Development of water oak stump sprouts under a partial overstory. New For. **14**(1): 55–62. doi:10.1023/A:1006502107495.

Holladay, C.A., Kwit, C., and Collins, B. 2006. Woody regeneration in and around aging southern bottomland hardwood forest gaps: effects of herbivory and gap size. For. Ecol. Manage. **223**(1–3): 218–225. doi:10.1016/j.foreco.2005.11.004.

Imm, D.W., and McLeod, K. W. 2005. Plant communities. *In* Ecology and management of a forested landscape: fifty years on the Savannah River Site. *Edited* by J.C. Kilgo and J.I. Blake. Island Press, Washington, D.C. pp. 106–161.

Johnson, P.S., Shifley, S.R., and Rogers, R. 2002. The ecology and silviculture of oaks. CABI Publishing, Wallingford, Oxon, U.K. 503pp.

Johnson, R.L., and Krinard, R.M. 1988. Growth and development of two sweetgum-red oak stands from origin through 29 years. South. J. Appl. For. **12**(2): 73–78. doi:10.1093/sjaf/12.2.73.

Kellison, R.C., and Young, M.J. 1997. The bottomland hardwood forest of the southern United States. For. Ecol. Manage. **90**(2–3): 101–115. doi:10.1016/S0378-1127(96)03905-9.

Kern, C.C., Burton, J.I., Raymond, P., D'Amato, W., Keeton, W.S., Royo, A.A., et al. 2017. Challenges facing gap-based silviculture and possible solutions for mesic northern forests in North America. Forestry, **90**(1): 4–17. doi:10.1093/forestry/cpw024.

Khan, M.L., and Shankar, U. 2001. Effect of seed weight, light regime and substratum microsite on germination and seedling growth of *Quercus semiserrata* Roxb. Trop. Ecol. **42**(1): 117–125.

Kobe, R.K., Pacala, S.W., Silander, J.A., Jr., and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. **5**(2): 517–532. doi:10.2307/1942040.

Lhotka, J.M. 2012. Height-diameter relationships in sweetgum (*Liquidambar styraciflua*) dominated stands. South. J. Appl. For. **36**(2): 98–106. doi:10.5849/sjaf.10-039.

Lhotka, J.M. 2013. Effect of gap size on mid-rotation stand structure and species composition in a naturally regenerated mixed broadleaf forest. New For. **44**(3): 311–325. doi:10.1007/s11056-012-9319-7.

Lockhart, B.R., Ezell, A.W., Hodges, J.D., and Clatterbuck, W.K. 2006. Using natural stand development patterns in artificial mixtures: A case study with cherrybark oak and sweetgum in east-central Mississippi, USA. For. Ecol. Manage. **222**: 202–210. doi:10.1016/j.foreco.2005.09.029.

Matlack, G.R. 1994. Vegetation dynamics of the forest edge - trends in space and successional time. J. Ecol. **82**(1): 113–123. doi:10.2307/2261391.

Mayer, J.J., Nelson, E.A., and Wike, L.D. 2000. Selective depredation of planted hardwood seedlings by wild hogs in a wetland restoration area. Ecol. Eng. **15**: S79–S85. doi:10.1016/S0925-8574(99)00074-9.

Meadows, J.S., and Stanturf, J.A. 1997. Silvicultural systems for southern bottomland hardwood forest. For. Ecol. Manage. **90**(2–3): 127–140. doi:10.1016/S0378-1127(96)03898-4.

Meadows, J.S., Bonner, F.T., and Haywood, J.D. 2006. Soil-seed bank survival in forests of the southern United States. New For. **32**: 335–345. doi:10.1007/s11056-006-9007-6.

Niinemetts, U. 1998. Growth of young trees of *Acer platanoides* and *Quercus robur* along a gap-understory continuum: interrelationships between allometry, biomass partitioning, nitrogen, and shade tolerance. Int. J. Plant Sci. **159**(2): 318–330. doi:10.1086/297553.

Nowacki, G.J., and Abrams, M.D. 2008. The demise of fire and the mesophication of forests in the eastern United States. Bioscience, **58**(2): 123–138. doi:10.1641/B580207.

Oliver, C.D. 1978. The development of northern red oak in mixed stands in central New England. Yale School of Forestry and Environmental Studies Bulletin 91, 63pp.

Oliver, C.D. 1980. Forest development in North America following major disturbances. For. Ecol. Manage. **3**: 153–168. doi:10.1016/0378-1127(80)90013-4.

Parresol, B.R., Scott, D.A., Zarnoch, S.J., Edwards, L.A., and Blake, J.I. 2017. Modeling forest site productivity using mapped geospatial attributes within a South Carolina landscape, USA. For. Ecol. Manage. **406**: 196–207. doi:10.1016/j.foreco.2017.10.006.

Poorter, L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. Funct. Ecol. **13**: 396–410. doi:10.1046/j.1365-2435.1999.00332.x.

Sander, I.L., and Clark, F.B. 1971. Reproduction of upland hardwood forests in the central states. Agric. Handb. 405. U.S. Department of Agriculture, Forest Service, Washington, D.C.

SAS Institute, Inc. 2011. SAS/STAT 9.3 User's Guide. SAS Institute Inc., Cary, N.C.

Smith, W.P., and Zollner, P.A. 2001. Seasonal habitat distribution of swamp rabbits, white-tailed deer, and small mammals in old growth and managed bottomland hardwood forests. In Bottomland hardwoods of the Mississippi Alluvial Valley: characteristics and management of natural function. *Edited by* P.B. Hamel and T. Foti. General Technical Report SRS-42. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, N.C., pp. 83–98.

Steiner, K.C., Stein, B.S., and Finley, J.C. 2018. A test of the delayed oak dominance hypothesis at mid-rotation in developing upland stands. For. Ecol. Manage. **408**: 1–8. doi:10.1016/j.foreco.2017.10.027.

Stokes, B.J., and Schilling, A. 1997. Improved harvesting systems for wet sites. For. Ecol. Manage. **90**(2–3): 155–160. doi:10.1016/S0378-1127(96)03907-2.

Tilghman, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildl. Manage. **53**(3): 524–532. doi:10.2307/3809172.

Ulyshen, M.D., Hanula, J.L., Horn, S., Kilgo, J.C., and Moorman, C.E. 2005. Herbivorous insect response to group selection cutting in a southeastern bottomland hardwood forest. Environ. Entomol. **34**(2): 395–402. doi:10.1603/0046-225X-34.2.395.

von Lupke, B. 1998. Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. For. Ecol. Manage. **106**: 19–26. doi:10.1016/S0378-1127(97)00235-1.

Whitmore, T.C. 1989. Canopy gaps and the two major groups of forest trees. Ecology, **70**(3): 536–538. doi:10.2307/1940195.

Yamamoto, S.I. 1992. Gap characteristics and gap regeneration in primary evergreen broad-leaved forests of western Japan. Bot. Mag. Tokyo, **105**: 29–45. doi:10.1007/BF02489401.