

Competition intensity varies with hardwood species identity and constrains stand-level productivity in southeastern pine–hardwood mixtures compared to loblolly pine monocultures

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Abstract

We examined the performance of sweetgum (*Liquidambar styraciflua* L.), cherrybark oak (*Quercus pagoda* Raf.), and loblolly pine (*Pinus taeda* L.) in two-species pine–hardwood mixtures (sweetgum : loblolly pine and cherrybark oak : loblolly pine) at various planting densities (1482–1976 trees per hectare (TPH)) over 23 years in northern Louisiana, USA. Species were planted in alternating rows with hardwood establishment occurring 1 year prior to loblolly pine. Mixtures were also compared to loblolly pine monocultures at a common density (1482 TPH) to assess whether mixing improved productivity. Sweetgum exerted more competitive pressure on loblolly pine than cherrybark oak. At final measurement, sweetgum survival statistically exceeded that of loblolly pine across mixture density. Moreover, sweetgum cumulative basal area and volume growth nearly tripled that of loblolly pine in balanced high-density mixtures (1976 TPH, 50 pine : 50 hardwood). In contrast, cherrybark oak basal area and volume growth did not significantly exceed loblolly pine at any density. At a common density (1482 TPH), loblolly pine monoculture cumulative basal area and volume significantly exceeded those of mixtures with sweetgum and cherrybark oak by 19% and 24%, respectively. Collectively, these results indicate that growing loblolly pine in mixture with these two species did not produce complementary interactions and negatively affected stand-level growth.

Key words: overyielding, loblolly pine, cherrybark oak, sweetgum, interspecific competition, mixed stands

Résumé

Nous avons examiné la performance du copalme d'Amérique (*Liquidambar styraciflua* L.), du chêne à feuilles en pagode (*Quercus pagoda* Raf.) et du pin à encens (*Pinus taeda* L.) dans des mélanges de pins et de feuillus à deux espèces (copalme d'Amérique : pin à encens et chêne à feuilles en pagode : pin à encens) à diverses densités de plantation (1482 à 1976 TPH) pendant 23 ans dans le nord de la Louisiane, aux États-Unis. Les espèces ont été plantées en rangs alternés, l'établissement des feuillus ayant lieu un an avant celui des pins à encens. Les mélanges ont également été comparés aux monocultures de pin à encens à une densité commune (1482 TPH) pour évaluer si le mélange améliorerait la productivité. Le copalme d'Amérique a exercé une plus grande pression concurrentielle sur le pin à encens que le chêne à feuilles en pagode. Lors de la mesure finale, la survie du copalme d'Amérique a statistiquement dépassé celle du pin à encens, quelle que soit la densité du mélange. De plus, la croissance cumulative de la zone basale et du volume du copalme d'Amérique a presque triplé par rapport à celle du pin à encens dans les mélanges équilibrés à haute densité (1976 TPH, 50 pins : 50 feuillus). En revanche, la croissance de la surface terrière et du volume du chêne à feuilles en pagode n'a pas dépassé de manière significative celle du pin à encens, quelle que soit la densité. À une densité commune (1482 TPH), la zone basale et le volume cumulés de la monoculture du pin à encens ont dépassé de manière significative ceux des mélanges avec le copalme d'Amérique et le chêne à feuilles en pagode de 19 % et 24 %, respectivement. Collectivement, ces résultats indiquent que la culture du pin à encens en mélange avec ces deux espèces n'a pas produit d'interactions complémentaires et a affecté négativement la croissance au niveau du peuplement. [Traduit par la Rédaction]

Mots-clés : rendement excessif, pin à encens, chêne à feuilles en pagode, copalme d'Amérique, compétition interspécifique, peuplements mixtes

Introduction

Maintaining productive forests is a global priority. Historically, monocultures have been established to maximize forest productivity (Rubilar et al. 2018). However, concerns over declining biodiversity, enhanced risk of species-specific pests and pathogens, and future resilience to disturbance wrought by the widescale replacement of natural stands with monocultures have created interest in establishing forests capable of provisioning a broad array of ecosystem services in addition to timber production (Messier et al. 2015; Huuskonen et al. 2021). Thus, new management strategies must balance traditional and contemporary societal demands.

Understanding local interactions within forests is critical for developing new management strategies. Neighboring trees interact in multiple ways, with the aggregate of these interactions determining the nature of the relationship (Callaway and Walker 1997; Fichtner et al. 2018). Competitive interactions occur when the survival or growth of one tree is negatively affected by its neighbor. Existing evidence generally indicates that competition within species (intraspecific competition) is more intense than competition between species (interspecific competition) (Adler et al. 2018), as a result of intraspecific similarities in resource requirements (Man and Lieffers 1999; Toigo et al. 2018), root and crown architecture (Bayer et al. 2013; Pretzsch 2014; Madsen et al. 2020), phenology (Moore et al. 2011; Lu et al. 2016), physiology (Forrester and Smith 2012; Pretzsch et al. 2012), and morphological plasticity (Dieler and Pretzsch 2013; Jucker et al. 2015). In contrast to competition, niche complementarity occurs when interactions between trees ameliorate environmental stress or reduce competition intensity (Hooper et al. 2005; Forrester and Bauhus 2016). Complementarity is typically found in stands with high degrees of diversity in size, functions, and structure, which introduces the potential for resource partitioning, facilitation, and improvements in resource use efficiency (Pretzsch et al. 2016; Forrester et al. 2017; Williams et al. 2017). Interactions between species can also vary with changes in resource availability and environmental stress (Wright et al. 2014). Thus, predicting the outcome of tree interactions across broad spatial and temporal scales remains challenging.

Establishing mixed stands is one potential strategy for reducing intraspecific competition. This approach assumes that enhanced diversity will reduce competition intensity leading to improvements in productivity and resilience. Indeed, positive relationships between species diversity, productivity, and drought resilience have been widely reported in mixed-species stands (Pequette and Messier 2011; Jactel et al. 2018; Fichtner et al. 2020). Nevertheless, the viability of this approach depends on the degree of complementarity between neighboring species. Studies reporting positive diversity–productivity relationships among temperate tree species often include at least one shade-tolerant species, which is considered important for improving canopy space partitioning and the interception of photosynthetically active radiation (Bauhus et al. 2004; Forrester and Albrecht 2014). Comparatively less is known about the compatibility of temperate tree species with moderate-to-high light demands

and how interactions between species vary with stand density (Forrester 2017; Steckel et al. 2019; Brunner and Forester 2020).

Loblolly pine (*Pinus taeda* L.) is a premiere commercial species widely grown in monoculture throughout the southeastern United States (Prestemon and Abt 2002; Fox et al. 2007). Historically, little consideration was given to growing loblolly pine in mixed stands, as hardwood species have long been considered inhibitory to loblolly pine growth (Willis et al. 2019). Existing research documenting improvements in loblolly pine growth with hardwood control early in stand development are prevalent (Phillips and Abercrombie 1987; Miller et al. 2003). However, these studies often quantified the effect of hardwood sprouts on planted pine seedlings potentially skewing neighborhood interactions toward asymmetric competition (Weiner 1990; Schwinning and Weiner 1998). Most existing studies also typically considered hardwood competition to be a generic entity rather than a density-dependent, species-specific process. The few existing studies exploring interspecific competition were conducted at density ranges representative of natural regeneration that may not represent interactions occurring in planted stands (Zutter et al. 1997; Granger and Buckley 2021). Thus, little is known about how hardwood species with varying life history traits will interact with loblolly pine in mixture at differing densities over multiple decades. For example, shade-tolerant species may be more suitable for mixing with loblolly pine at high planting densities due to their ability to persist in subcanopy positions. The benefits of mixing loblolly pine with a shade-tolerant species at high density may be further enhanced by species featuring a decurrent crown structure, which provides the opportunity for vertical stratification and crown complementarity with loblolly pine (Forrester and Albrecht 2014; Schmid and Nicklaus 2017; Bongers 2020). Yet, in stands established at low density, fast-growing, shade-intolerant species may be a viable mixing option due to their height growth potential.

To explore these questions, an experiment was established examining the survival and growth of shade-intolerant sweetgum (*Liquidambar styraciflua* L.), moderately shade tolerant cherrybark oak (*Quercus pagoda* Raf.), and shade-intolerant loblolly pine in two-species pine–hardwood mixtures at varying density for over two decades. In addition, to determine whether pine–hardwood mixtures can produce overyielding, loblolly pine survival and growth in mixtures were compared to those produced in monocultures established at the same initial density. We hypothesized that (1) loblolly pine interspecific competition with sweetgum would exceed interspecific competition with cherrybark across all mixture densities; (2) loblolly pine mixtures with cherrybark oak would have higher survival and produce more cumulative basal area growth than mixtures with sweetgum across all densities; (3) loblolly pine survival, diameter growth, and height growth in mixture would exceed those produced in monoculture; and (4) mixtures would have higher stand-level productivity than loblolly pine monocultures. The information gleaned from this study will fundamentally improve our understanding of complementarity between three prominent southeastern tree species. Moreover, from an applied perspective, the

Fig. 1. The study was conducted at the Louisiana State University Agricultural Center Hill Farm Research Station near Homer, Louisiana, United States (32.749025N, -93.04111111W). The location of site represented in the map originated from an ESRI shapefile and is in the Geographic Coordinate System, WGS 1984 projection. [Color online]



findings of this study could contribute to the development of new forest management strategies in the southeastern United States.

Materials and methods

Study site

Our study was conducted at the Louisiana State University Agricultural Center Hill Farm Research Station near Homer, Louisiana, United States (32.749025N, -93.04111111W) (Fig. 1). The regional climate at Hill Farm is classified as humid subtropical. Temperatures in the region range from 3.3–13.3 °C in January to 22.8–33.9 °C in July. The growing season in the region ranges from 219 to 276 days. Average precipitation occurs primarily in the form of rain and averages 1330 mm·year⁻¹, with droughts commonly occurring in the summer (USDA SCS 1989). Soils at Hill Farm are dominated by two soil groups: the Guyton–Ouachita complex and Darley soil series. The Guyton (fine-silty, siliceous, active, thermic Typic Glossaqualfs)–Ouachita (fine-silty, siliceous, active, thermic Fluventic Dystrudepts) complex is commonly

found in floodplains on the western Coastal Plain and features silty-loam soil texture with moderate-to-poor drainage (USDA SCS 1989). The Darley series (fine, kaolinitic, thermic Hapludult and a fine, mixed, active, thermic Aquic Hapludult) is commonly found in upland forests in the region and has a fine sandy loam texture with good drainage (USDA SCS 1989). Sweetgum and cherrybark oak site index at age 50 years was approximately 30.0 and 29.5 m, respectively (McTague et al. 2006). Site index for loblolly pine at age 50 years was approximately 34.0 m (Popham et al. 1979). Our study areas were generally flat (<2% slope) and most recently maintained as pastureland.

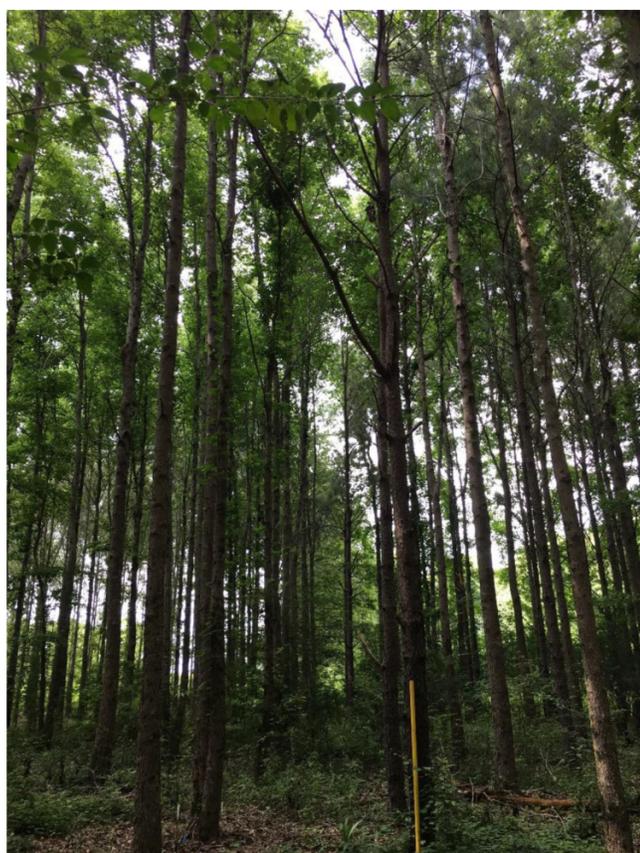
Experimental design

The study utilized a randomized complete block design, with soil type as the blocking factor. Beginning in 1997, three blocks were established across the existing soil types at Hill Farm. Within each block, we established square plots (0.031 ha), which were randomly selected for a stand type and planting density treatment combination. Stand type consisted of two-species pine–hardwood mixtures (sweet-

Table 1. The number of monoculture and mixture plots (experimental unit) at each density level.

Density	Stand type	Species	Replicates	Trees per plot
1482	Monoculture	Loblolly pine	3	113
1482	Mixture	Loblolly pine + sweetgum	6	113
1482	Mixture	Loblolly pine + cherrybark oak	6	113
1729	Mixture	Loblolly pine + sweetgum	5	113
1729	Mixture	Loblolly pine + cherrybark oak	6	113
Balanced 1976	Mixture	Loblolly pine + sweetgum	3	113
Balanced 1976	Mixture	Loblolly pine + cherrybark oak	3	113
Unbalanced 1976	Mixture	Loblolly pine + sweetgum	3	113
Unbalanced 1976	Mixture	Loblolly pine + cherrybark oak	3	113

Fig. 2. An example of a sweetgum–loblolly pine medium-density mixture 20 years after planting. For reference, the height pole leaning against the tree in the foreground was 1.5 m in length. [Color online]



gum : loblolly pine and cherrybark oak : loblolly pine) and loblolly pine monocultures. Density treatments varied by stand type. Within pine–hardwood mixtures, density treatments included low-density (1482 TPH, 50:50 pine–hardwood ratio, 3.6 m × 1.8 m spacing, six internal measurement rows), medium-density (1729 TPH, 57:43 pine–hardwood ratio, 3.3 m × 1.8 m spacing, six internal measurement rows) (Fig. 2), balanced high-density (1976 TPH, 50:50 pine–hardwood ratio, 3.3 m × 1.5 m spacing, six internal measurement rows), and unbalanced high-density (1976 TPH, 37:63

pine–hardwood ratio, 3.3 m × 1.5 m spacing, six internal measurement rows) (Table 1). Loblolly pine monocultures were established at 1482 TPH (3.6 m × 1.8 m spacing, six internal measurement rows) (Table 1). Mixtures combining sweetgum and cherrybark oak were not conducted due to land area restrictions at the study site. Plot-level replication ranged from three to six and varied by each unique stand type and density combination (Table 1). Each species was planted as a 1-year-old bareroot seedling of local genetic origin and was obtained from nurseries administered by the Louisiana Department of Agriculture and Forestry. Cherrybark oak and sweetgum were planted in 1997, while loblolly pine was planted in 1998. The mixtures were planted with even spacing between and within rows. Mixtures were established by alternating pure rows of individual species. Prior to planting, each plot was treated with glyphosate and sulfometuron methyl herbicides for competing vegetation suppression using backpack sprayers. No additional silvicultural treatments were conducted in the plots after planting.

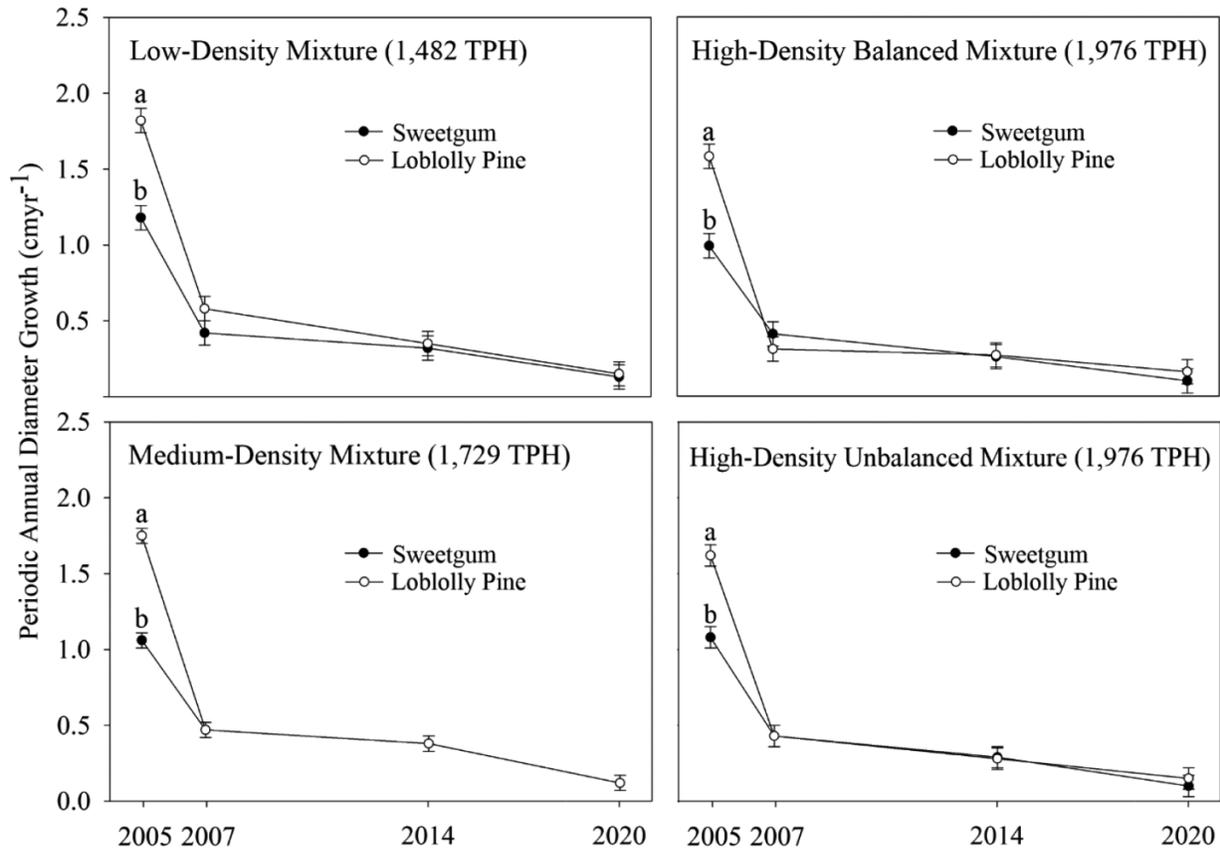
Field measurements

Within each plot, all planted trees in the interior rows were measured for survival, total height (m), and diameter at breast height (1.37 m) (cm) in the winter of 2005, 2007, 2014, and 2020. Trees in the external rows were excluded from the study to account for edge effects. By final measurement, plots contained 7–43 measurement trees. Total tree height was measured with a hypsometer to the nearest decimetre (Haglöf Vertex III, Haglöf Inc.). Tree diameter was measured with a diameter tape to the nearest millimetre. These measurements were then used to calculate basal area and total stemwood volume. Loblolly pine volume was calculated following the equations of Amateis and Burkhart (1987) for old-field loblolly pine. Sweetgum and cherrybark oak volume was determined with the equations of Matney et al. (1985). All survival and growth metrics were averaged by species at the plot level prior to statistical analyses.

Statistical methods

The primary goals of this study were to quantify the performance of individual species within pine–hardwood mixtures of varying density and to compare the performance of different mixture types (sweetgum : loblolly pine and cherrybark oak : loblolly pine). To minimize issues associated with an un-

Fig. 3. The estimated effect of mixture density over time on sweetgum and loblolly pine periodic annual diameter growth ± 1 standard error from 2005 to 2020. Sweetgum was planted in 1997, while loblolly pine was planted in 1998. Data points represent the difference in periodic annual increment between the year indicated on the x -axis and the previous measurement year. Species with different letters at each measurement interval were statistically different at $\alpha = 0.05$ (Student's t post hoc test).



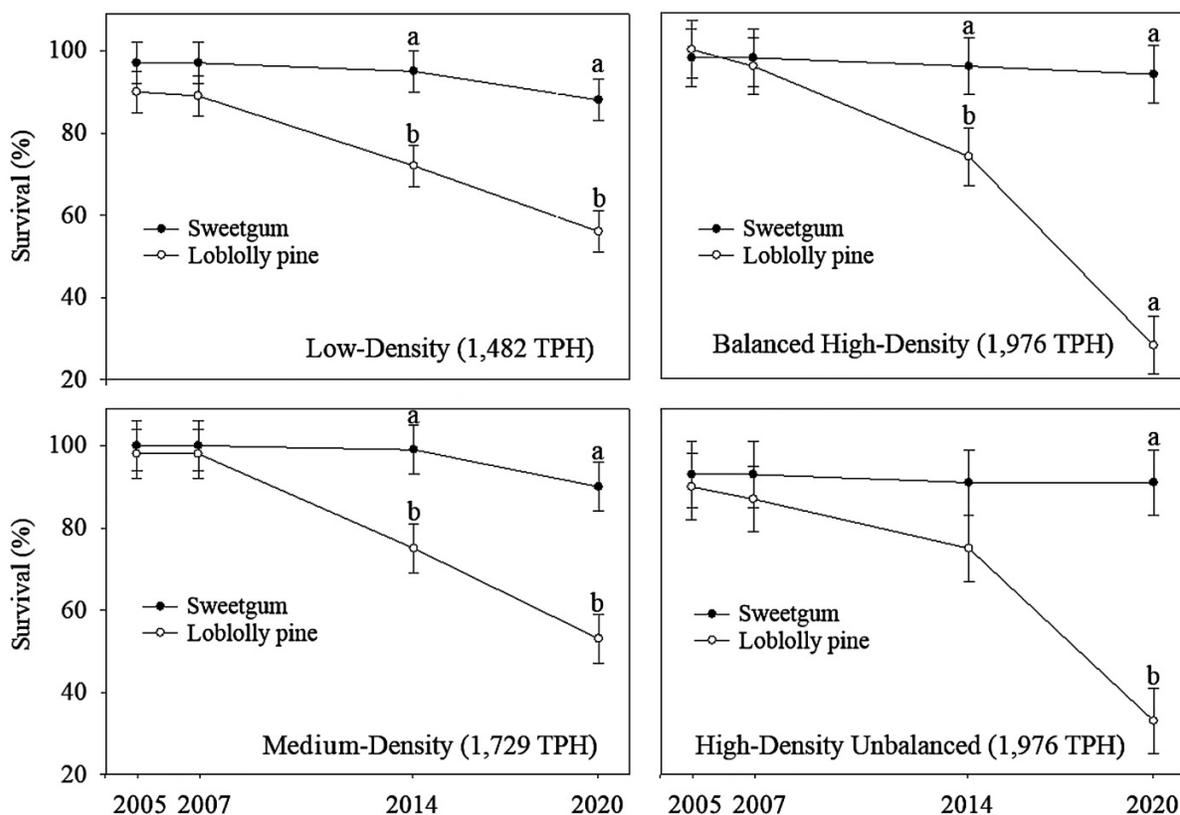
balanced experimental design, we conducted separate analyses within each density category (low, medium, balanced high, unbalanced high). In the analyses of species effects, models were further separated by mixture type within each density category.

Species effects were modeled with a repeated-measures mixed-effects analysis of variance (ANOVA). We ran separate models evaluating the survival (percentage of original surviving trees) and growth (periodic annual diameter, height, basal area, and volume) over time. The model assumed a Gaussian distribution and used an identity link function to account for overdispersion. Denominator degrees of freedom were estimated with a Kenward–Roger's approximation due to the imbalanced experimental design (Schaalje et al. 2002). The models considered species, time, and their interaction as fixed effects. Block was considered a random effect in the model. A spatial Gaussian structure was chosen to model serial correlation after examining multiple potential structures with Akaike's information criterion. Models producing significant main effects or interactions were further explored with a Student's t post hoc comparison. Significant interactions between species and time were examined at each measurement year. Differences between means were considered significant at $\alpha = 0.05$.

To compare the performance of individual mixture types within density categories, we ran a mixed-effects ANOVA using nearly identical procedures. Mixture type was considered a fixed effect in the model, while block was considered a random effect. However, in these analyses, the response variables represented cumulative survival and growth values obtained from the final stand measurements. Within each stand type, cumulative survival, height, and diameter growth were derived from the average of species' averages in the mixture. Cumulative basal area and volume growth were derived from the sum of species' averages in the mixture. Differences between stand types and species within stand types were then compared with Student's t post hoc comparisons ($\alpha = 0.05$).

A secondary objective was to compare the performance of mixtures to monocultures at a common density. Due to a lack of monocultures and mixtures with an equivalent initial density, our analysis was limited to 1482 TPH. Mixed-effects ANOVA models were used to compare loblolly pine cumulative survival, diameter growth, and height growth across low-density stand types over time. This analysis was limited to the performance of loblolly pine due to the lack of hardwood monocultures at an equivalent planting density. The models considered stand type, time, and their interaction as fixed effects. Block was considered a random effect. Significant main

Fig. 4. The estimated effect of mixture density over time on sweetgum and loblolly pine mean survival ± 1 SE from 2005 to 2020. Sweetgum was planted in 1997, while loblolly pine was planted in 1998. Species with different letters at each measurement interval were statistically different at $\alpha = 0.05$ (Student's t post hoc test).



effects and interactions were examined with Tukey's post hoc comparisons and were considered significant at $\alpha = 0.05$. We then used mixed-effect ANOVA to compare cumulative survival, diameter, height, basal area, and volume growth across low-density stand types. Mixture type was considered a fixed effect in the model, while block was considered a random effect. In these analyses, cumulative mean survival, diameter growth, and height growth were explored for loblolly pine exclusively. Cumulative basal area and volume growth represent the average of species' averages within mixture. Significant main effects were examined through Tukey's post hoc comparisons ($\alpha = 0.05$). All tests were conducted within the GLIMMIX procedure in the SAS 9.4 software (SAS Institute, Cary, NC, USA).

Results

Density effects on species dynamics over time

Low-density mixtures

Within low-density sweetgum : loblolly pine mixtures, survival and periodic annual diameter growth varied significantly between species over time (Appendix Table A1). Loblolly pine added statistically more periodic annual diameter growth than sweetgum 7 years after planting (Fig. 3);

however, sweetgum survival significantly exceeded loblolly pine over the last 13 years of the study (Fig. 4). Periodic annual height and basal area growth were similar between species and did not differ significantly over time (sweetgum: 42.00 ± 4.00 cm \cdot year $^{-1}$, loblolly pine: 46.00 ± 4.00 cm \cdot year $^{-1}$) (sweetgum: 0.50 ± 0.07 m 2 \cdot ha $^{-1}$ \cdot year $^{-1}$, loblolly pine: 0.56 ± 0.07 m 2 \cdot ha $^{-1}$ \cdot year $^{-1}$) (Appendix Table A1). At final measurement, sweetgum survival significantly exceeded that of loblolly pine, while loblolly pine produced significantly more cumulative diameter growth compared to sweetgum (Table 2).

In contrast to low-density sweetgum : loblolly pine mixtures, survival in low-density cherrybark oak : loblolly pine mixtures was similar among species and did not differ significantly over time (Appendix Table A2). Trends in periodic annual diameter growth between species varied significantly over time, as loblolly pine growth exceeded cherrybark oak over the first 9 years of the study but grew at similar rates thereafter (Appendix Table A2) (Fig. 5). Periodic annual height growth was similar between species (cherrybark oak: 42 ± 3.00 cm \cdot year $^{-1}$, loblolly pine: 48 ± 3.00 cm \cdot year $^{-1}$) and did not differ significantly over time (Appendix Table A2). Loblolly pine periodic annual basal area growth significantly exceeded that of cherrybark oak (cherrybark oak: 0.43 ± 0.07 m 2 \cdot ha $^{-1}$ \cdot year $^{-1}$, loblolly pine: 0.69 ± 0.07 m 2 \cdot ha $^{-1}$ \cdot year $^{-1}$) and did not vary statistically over

Table 2. The estimated effects of species composition and planting density on cumulative mean survival, diameter, height, basal area, and volume growth (± 1 standard error) since planting (22–23 years).

	Sweetgum	Loblolly pine
Low-density mixtures		
Survival (%)	88 (7)a	56 (7)b
Diameter (cm)	22.49 (1.06)b	26.27 (1.06)a
Height (m)	19.84 (0.70)a	20.91 (0.70)a
Basal area (m ² ·ha ⁻¹)	14.43 (1.58)a	17.89 (1.58)a
Volume (m ³ ·ha ⁻¹)	129.15 (14.21)a	152.40 (14.21)a
Medium-density mixtures		
Survival (%)	89 (8)a	52 (8)b
Diameter (cm)	22.29 (0.83)a	24.20 (0.83)a
Height (m)	19.76 (1.73)a	19.34 (1.73)a
Basal area (m ² ·ha ⁻¹)	18.24 (2.31)a	14.54 (2.31)a
Volume (m ³ ·ha ⁻¹)	163.55 (31.88)a	125.82 (31.88)a
High-density balanced mixtures		
Survival (%)	94 (8)a	28 (8)b
Diameter (cm)	18.71 (1.12)a	21.67 (1.12)a
Height (m)	18.93 (1.56)a	18.47 (1.56)a
Basal area (m ² ·ha ⁻¹)	23.77 (4.67)a	8.66 (4.67)b
Volume (m ³ ·ha ⁻¹)	215.41 (44.90)a	73.26 (44.90)b
High-density unbalanced mixtures		
Survival (%)	91 (9)a	33 (9)b
Diameter (cm)	20.15 (2.02)a	23.11 (2.02)a
Height (m)	20.16 (0.79)a	20.10 (0.79)a
Basal area (m ² ·ha ⁻¹)	25.07 (2.99)a	8.59 (2.99)b
Volume (m ³ ·ha ⁻¹)	246.43 (32.51)a	76.00 (32.51)b
	Cherrybark oak	Loblolly pine
Low-density mixtures		
Survival (%)	61 (9)a	61 (9)a
Diameter (cm)	18.25 (1.60)b	27.81 (1.60)a
Height (m)	19.06 (0.81)b	21.72 (0.81)a
Basal area (m ² ·ha ⁻¹)	9.63 (1.52)b	20.62 (1.52)a
Volume (m ³ ·ha ⁻¹)	83.50 (18.49)b	180.17 (18.49)a
Medium-density mixtures		
Survival (%)	62 (6)a	57 (6)a
Diameter (cm)	17.65 (1.47)b	26.80 (1.47)a
Height (m)	19.55 (1.26)a	21.87 (1.26)a
Basal area (m ² ·ha ⁻¹)	7.67 (1.49)b	24.71 (1.49)a
Volume (m ³ ·ha ⁻¹)	66.16 (13.85)b	206.74 (13.85)a
High-density balanced mixtures		
Survival (%)	65 (18)a	37 (18)a
Diameter (cm)	16.08 (3.13)a	23.54 (3.13)a
Height (m)	15.28 (2.37)a	18.29 (2.37)a
Basal area (m ² ·ha ⁻¹)	19.51 (9.15)a	12.63 (9.15)a
Volume (m ³ ·ha ⁻¹)	166.84 (45.79)a	108.59 (45.79)a
High-density unbalanced mixtures		
Survival (%)	66 (18)a	25 (18)b
Diameter (cm)	19.72 (1.17)a	21.51 (1.17)a

Table 2. (concluded).

Height (m)	20.25 (0.59)a	22.23 (0.59)a
Basal area (m ² ·ha ⁻¹)	23.55 (5.98)a	6.02 (5.98)a
Volume (m ³ ·ha ⁻¹)	204.15 (82.34)a	50.97 (82.34)a

Note: For each row, species' means with different letters were statistically different at $\alpha = 0.05$ (Student's *t* post hoc test).

time (Appendix Table A2). At final measurement, loblolly pine was statistically dominant in terms of cumulative mean diameter, height, basal area, and volume growth compared to cherrybark oak (Table 2).

Medium-density mixtures

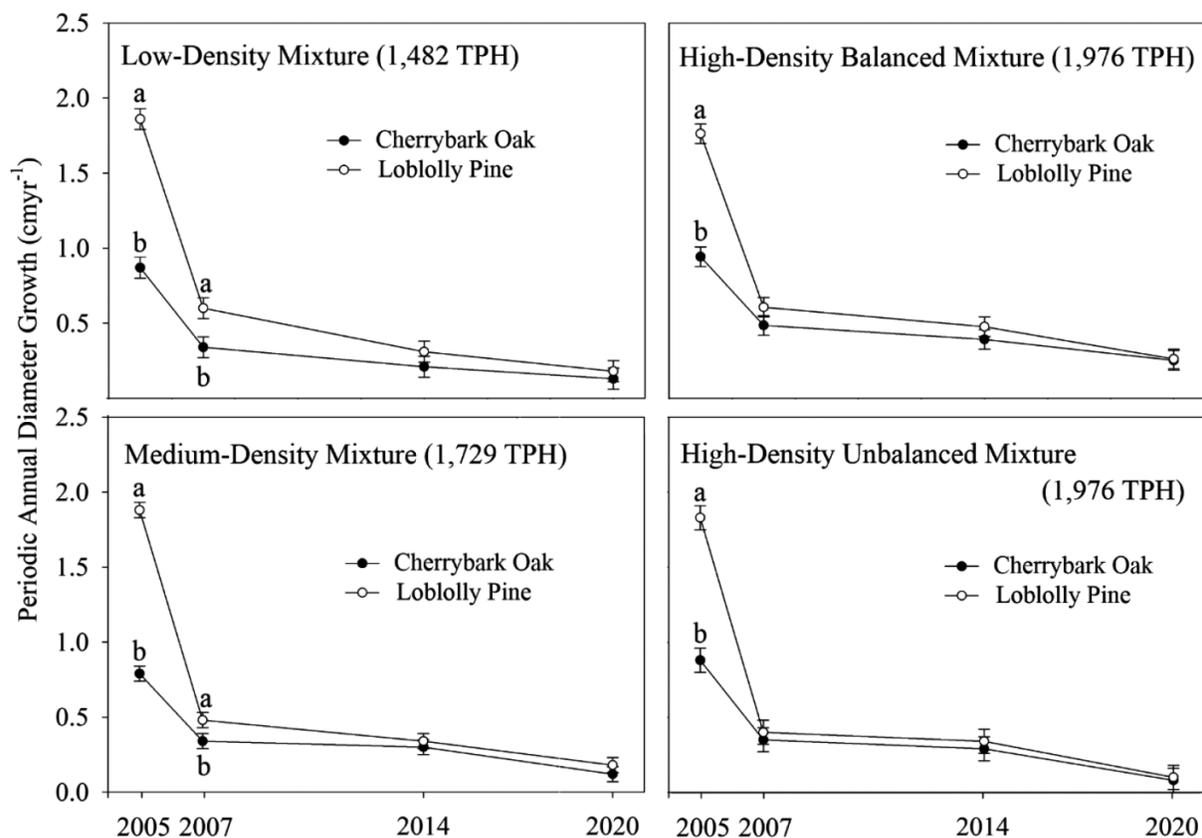
Within medium-density sweetgum : loblolly pine mixtures, survival, periodic annual diameter growth, and periodic annual basal area growth varied significantly between species over time (Appendix Table A1). Like in low-density mixtures, loblolly pine produced significantly more periodic annual diameter growth than sweetgum 7 years post-planting but survived at a significantly lower rate over the last 13 years of the study (Figs. 3 and 4). Loblolly pine periodic annual basal area growth statistically exceeded that of sweetgum 7 years after planting but was statistically surpassed over the final 6 years of the study (Appendix Table A1) (Fig. 6). Periodic annual height growth was similar between species and did not significantly differ over time (sweetgum: 43.00 ± 4.00 cm·year⁻¹, loblolly pine: 42.00 ± 4.00 cm·year⁻¹) (Appendix Table A1). At final measurement, sweetgum survival statistically exceeded that of loblolly pine (Table 2).

In contrast to medium-density mixtures with sweetgum, significant differences in survival between species did not develop in medium-density mixtures with cherrybark oak (Appendix Table A2). Loblolly pine periodic annual diameter growth statistically exceeded that of cherrybark oak over the first 9 years of the study but grew at similar rates in the subsequent 13 years (Appendix Table A2) (Fig. 5). Like medium-density mixtures with sweetgum, loblolly pine periodic annual basal area growth significantly exceeded that of cherrybark oak 9 years post-planting but was surpassed over the final 6 years of the study (Appendix Table A2) (Fig. 7). Periodic annual height growth was similar between species and did not differ statistically over time (cherrybark oak 40.00 ± 5.00 cm·year⁻¹, loblolly pine: 48.00 ± 5.00 cm·year⁻¹) (Appendix Table A2). At final measurement, loblolly pine statistically exceeded cherrybark oak in terms of cumulative diameter, basal area, and volume growth (Table 2).

Balanced high-density mixtures

Within balanced high-density sweetgum : loblolly pine mixtures, sweetgum survival significantly exceeded that of loblolly pine over the last 13 years of the experiment (Appendix Table A1) (Fig. 4). Periodic annual diameter growth between species also varied significantly over time, as loblolly pine added statistically more diameter growth than sweet-

Fig. 5. The estimated effect of mixture density over time on cherrybark oak and loblolly pine periodic annual diameter growth ± 1 standard error from 2005 to 2020. Cherrybark oak was planted in 1997, while loblolly pine was planted in 1998. Data points represent the difference in periodic annual increment between the year indicated on the x -axis and the previous measurement year. Species with different letters at each measurement interval were statistically different at $\alpha = 0.05$ (Student's t post hoc test).



gum 7 years after planting but grew at a similar rate over the subsequent 16 years (Appendix Table A1) (Fig. 3). Loblolly pine periodic annual basal area growth was also statistically higher than sweetgum 7 years after planting; however, sweetgum basal area growth statistically surpassed that of loblolly pine over the final 13 years of the study (Appendix Table A1) (Fig. 6). Sweetgum periodic annual height growth was comparable to loblolly pine and did not significantly differ over time (sweetgum: 41.00 ± 3.00 cm·year⁻¹, loblolly pine: 40.00 ± 3.00 cm·year⁻¹) (Appendix Table A1). At final measurement, sweetgum cumulative survival, basal area, and volume growth significantly exceeded those of loblolly pine (Table 2).

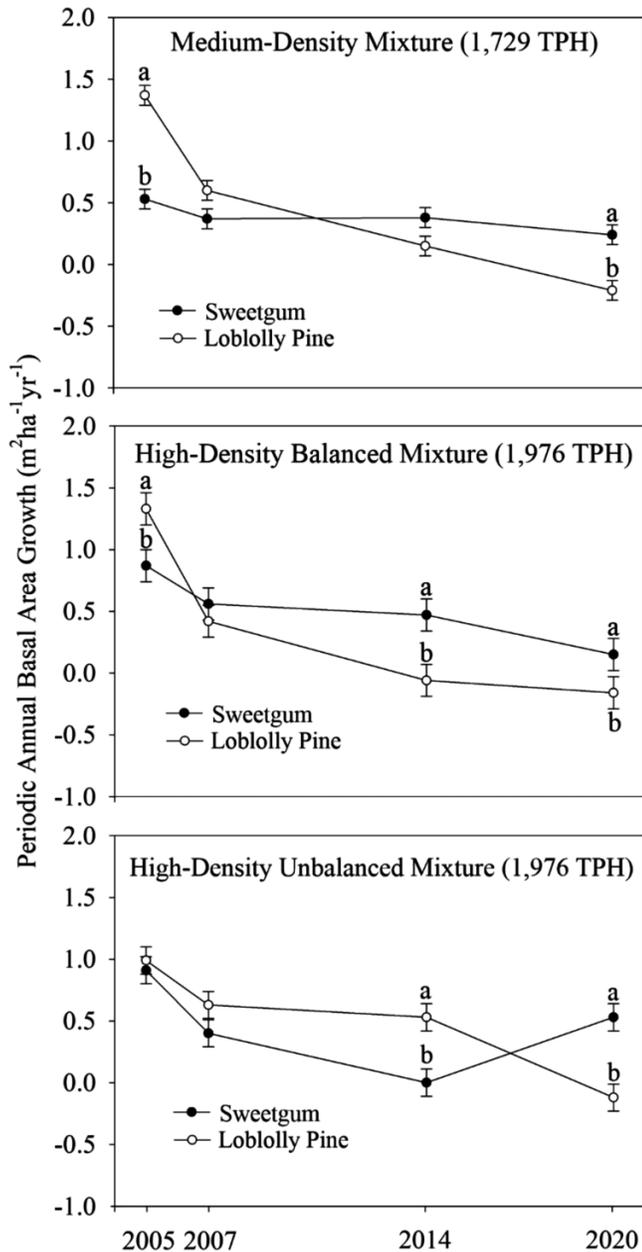
Within balanced high-density cherrybark oak : loblolly pine mixtures, survival was similar between species and did not statistically differ over time (Appendix Table A2). Loblolly pine added significantly more periodic annual diameter growth 7 years after planting, but cherrybark oak grew at a similar rate over the subsequent 16 years (Appendix Table A2) (Fig. 5). Periodic annual basal area growth followed a similar pattern, as loblolly pine statistically added more basal area growth than cherrybark oak 7 years after planting but grew at a similar rate thereafter (Appendix Table A2) (Fig. 7). Trends in periodic height growth between species were compar-

able and did not differ statistically over time (cherrybark oak: 35.00 ± 3.00 cm·year⁻¹, loblolly pine: 42 ± 3.00 cm·year⁻¹) (Appendix Table A2). At final measurement, cherrybark oak and loblolly pine cumulative survival and growth were not statistically significant (Table 2).

Unbalanced high-density mixtures

Within unbalanced high-density sweetgum : loblolly pine mixtures, significant changes in survival between species occurred over time, as sweetgum survival statistically exceeded that of loblolly pine over the last 6 years of the study (Appendix Table A1) (Fig. 4). In contrast, loblolly pine added significantly more periodic annual diameter growth than sweetgum 7 years after planting (Appendix Table A1) (Fig. 3). Trends in periodic annual basal area growth between species varied significantly over time (Appendix Table A1). Periodic annual basal area growth was statistically indistinguishable between species 9 years after planting (Fig. 6). Loblolly pine added statistically more periodic annual basal area than sweetgum over the next 7 years; however, sweetgum outproduced loblolly pine over the final 6 years of the study (Fig. 6). Periodic annual height growth was identical between species and did not significantly differ over time

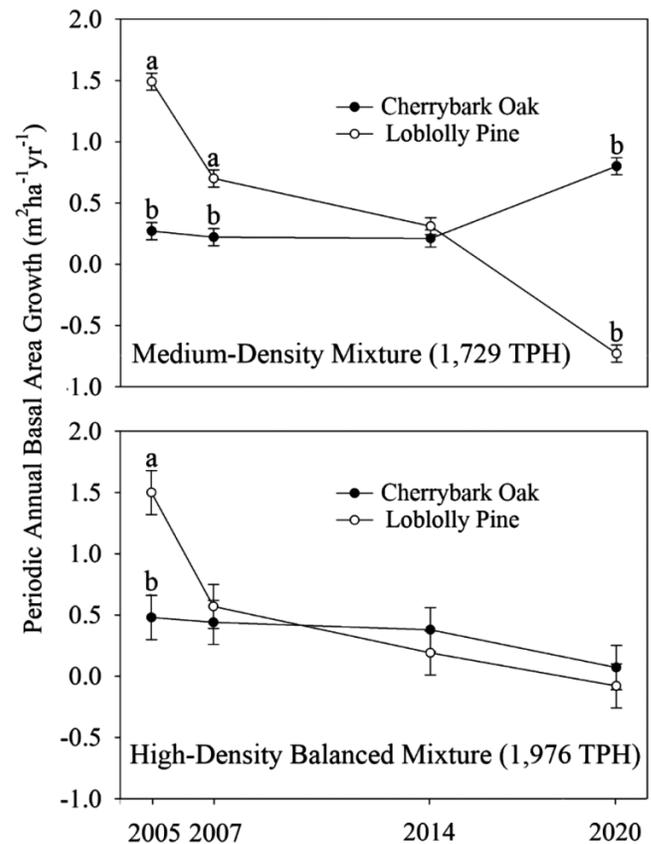
Fig. 6. The estimated effect of mixture density over time on sweetgum and loblolly pine periodic annual basal area growth ± 1 standard error from 2005 to 2020. Sweetgum was planted in 1997, while loblolly pine was planted in 1998. Data points represent the difference in periodic annual increment between the year indicated on the x -axis and the previous measurement year. Species with different letters at each measurement interval were statistically different at $\alpha = 0.05$ (Student's t post hoc test).



(43.00 \pm 2.00 cm \cdot year⁻¹) (Appendix Table A1). At final measurement, sweetgum statistically surpassed loblolly pine in terms of cumulative survival, basal area, and volume growth (Table 2).

Within unbalanced high-density cherrybark oak : loblolly pine mixtures, cherrybark oak survival statistically exceeded that of loblolly pine (Appendix Table A2). Loblolly pine pe-

Fig. 7. The estimated effect of mixture density over time on cherrybark oak and loblolly pine periodic annual basal area growth ± 1 standard error from 2005 to 2020. Cherrybark oak was planted in 1997, while loblolly pine was planted in 1998. Data points represent the difference in periodic annual increment between the year indicated on the x -axis and the previous measurement year. Species with different letters at each measurement interval were statistically different at $\alpha = 0.05$ (Student's t post hoc test).



riodic annual diameter growth statistically exceeded that of cherrybark oak 7 years after planting but progressed at a similar rate thereafter (Fig. 5). Species' periodic annual height (cherrybark oak: 48.00 \pm 3.00 cm \cdot year⁻¹, loblolly pine: 42.00 \pm 3.00 cm \cdot year⁻¹) and basal area growth (cherrybark oak: 0.48 \pm 11.00 m²ha⁻¹year⁻¹, loblolly pine: 0.33 \pm 11.00 m²ha⁻¹year⁻¹) were statistically indistinguishable and did not vary significantly over time (Appendix Table A2). At final measurement, cherrybark oak cumulative survival was statistically higher than loblolly pine (Table 2).

Mixture type cumulative performance comparisons

Mixture types were statistically indistinguishable in terms of cumulative survival and each growth metric at low, medium, and balanced high densities (Appendix Table A3 and Table 3). Within unbalanced high-density mixtures, cumulative survival in mixtures with sweetgum significantly

Table 3. The cumulative survival, diameter, height, basal area, and volume growth (± 1 standard error) of mixture types since planting (23 years).

Mixture type	Sweetgum : loblolly pine	Cherrybark oak : loblolly pine
Low-density mixtures		
Survival (%)	72 (6)a	61 (6)a
Diameter (cm)	24.34 (0.97)a	23.03 (0.97)a
Height (m)	20.57 (0.47)a	20.39 (0.47)a
Basal area ($\text{m}^2 \cdot \text{ha}^{-1}$)	32.32 (1.38)a	30.25 (1.38)a
Volume ($\text{m}^3 \cdot \text{ha}^{-1}$)	281.55 (15.00)a	263.67 (15.00)a
Medium-density mixtures		
Survival (%)	71 (5)a	60 (5)a
Diameter (cm)	23.55 (1.06)a	22.22 (0.91)a
Height (m)	19.55 (1.42)a	20.71 (1.31)a
Basal area ($\text{m}^2 \cdot \text{ha}^{-1}$)	32.78 (0.81)a	32.38 (0.74)a
Volume ($\text{m}^3 \cdot \text{ha}^{-1}$)	289.37 (12.38)a	272.90 (11.07)a
High-density balanced mixtures		
Survival (%)	61 (4)a	51 (4)a
Diameter (cm)	20.19 (1.62)a	19.81 (1.62)a
Height (m)	18.70 (0.91)a	16.77 (0.91)a
Basal area ($\text{m}^2 \cdot \text{ha}^{-1}$)	32.43 (3.85)a	32.14 (3.85)a
Volume ($\text{m}^3 \cdot \text{ha}^{-1}$)	288.67 (27.66)a	275.43 (27.66)a
High-density unbalanced mixtures		
Survival (%)	62 (3)a	46 (3)b
Diameter (cm)	21.63 (1.54)a	20.62 (1.54)a
Height (m)	20.13 (0.60)a	21.24 (0.60)a
Basal area ($\text{m}^2 \cdot \text{ha}^{-1}$)	33.66 (4.08)a	29.57 (4.08)a
Volume ($\text{m}^3 \cdot \text{ha}^{-1}$)	322.43 (35.20)a	255.12 (35.20)a

Note: For each row, mixture type means with different letters were statistically different at $\alpha = 0.05$ (Student's *t* post hoc test).

exceeded that of mixtures with cherrybark oak (Appendix Table A3 and Table 3). However, cumulative growth comparisons between unbalanced high-density mixture types were not statistically significant (Appendix Table A3 and Table 3).

Productivity in mixtures versus monoculture

Among stand types, loblolly pine periodic annual diameter growth ($75.00 \pm 3.00 \text{ cm} \cdot \text{year}^{-1}$) and periodic annual height growth ($48.00 \pm 3.00 \text{ cm}$) were highest in low-density mixtures with cherrybark oak; however, these differences exceeded those of loblolly pine in low-density mixtures with sweetgum or monoculture by less than 5%, respectively, and did not vary statistically over time (Appendix Table A4). At final measurement, loblolly pine cumulative survival, diameter, and height growth were highest in low-density mixtures with cherrybark oak but were not statistically different from other stand types (Table 4). Cumulative basal area and volume growth (all species combined) were statistically highest in monoculture (Fig. 8).

Discussion

Interspecific competition

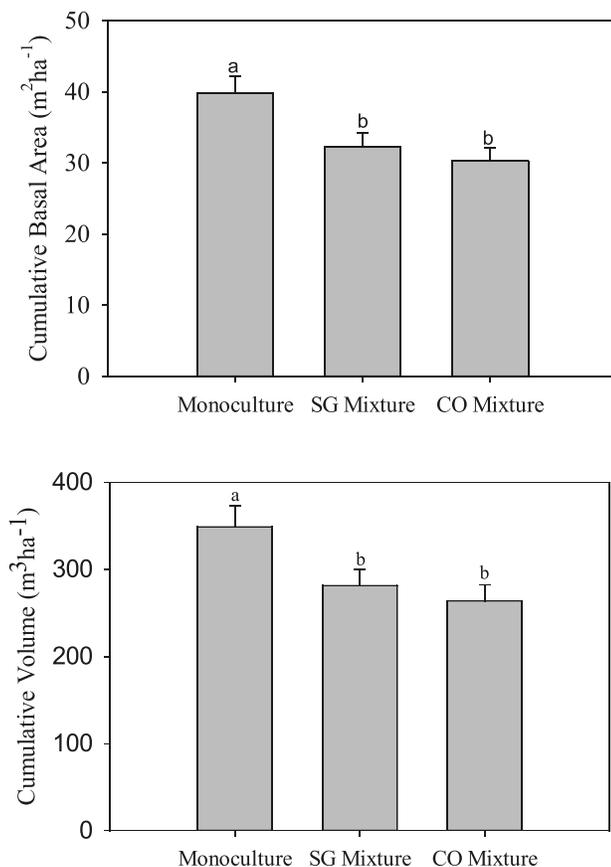
Evidence generally supports our initial hypothesis that interspecific competition with sweetgum would exceed that exerted by cherrybark oak. A key factor in the competitiveness of sweetgum was its ability to persist across planting density, as sweetgum survival never fell below 88%. In comparison, cherrybark oak cumulative survival averaged 61%–66% across mixture density. Thus, based solely on competitor density, loblolly pine encountered more competition for resources in mixtures with sweetgum than mixtures with cherrybark oak. This result also indicates that sweetgum was able to capture growing space in the main canopy, as sweetgum is less tolerant of shade than cherrybark oak (Lin et al. 2001). While limited to speculation, we suspect that two factors enhanced sweetgum survival and overall competitiveness. The first factor relates to the rich, moist edaphic conditions at Hill Farm, which likely enabled sweetgum to maximize its relatively high growth potential and compete with loblolly pine for growing space (Wenger 1952; Zutter et al. 1997; Coyle et al. 2008). Second, sweetgum has been shown to distribute its fine

Table 4. The estimated effect of low-density stand type on loblolly pine cumulative mean survival, diameter, and height growth (± 1 standard error) since planting (22–23 years).

Low-density stand type	Survival (%)	Diameter (cm)	Height (m)
Loblolly pine monoculture	54 (9)a	24.89 (1.88)a	21.12 (1.11)a
Sweetgum : loblolly pine mixture	56 (7)a	26.27 (1.06)a	20.91 (0.70)a
Cherrybark oak : loblolly pine mixture	61 (9)a	27.81 (1.60)a	21.72 (0.81)a

Note: Comparisons within mixtures are limited to the performance of loblolly pine. For each column, means with different letters were statistically different at $\alpha = 0.05$ (Tukey's post hoc test).

Fig. 8. Cumulative basal area and volume growth of low-density loblolly pine monocultures, sweetgum : loblolly pine mixtures (SG Mixture), and cherrybark oak : loblolly pine mixtures (CO Mixture) since planting (22–23 years). Mixture values represent the average productivity of both species. Bars with different letters were statistically different at $\alpha = 0.05$ (Tukey's multiple comparison post hoc test).



roots more evenly throughout the soil profile than loblolly pine, potentially easing competition for soil resources (Mou et al. 1995).

In addition to a high survival rate, sweetgum generally produced greater periodic annual height and diameter growth compared to cherrybark oak. This result is not particularly surprising considering the difference in growth strategy between species (Kormanik 1990; Krinard 1990). While sweetgum was the dominant competitor 23 years after planting, it

is important to recognize that interactions between species can change over time (Filipescu and Comeau 2007; Cavard et al. 2011; Jucker et al. 2020). For example, cherrybark oak competitiveness for growing space has been shown to exceed sweetgum within hardwood mixed plantings after two decades (Lockhart et al. 2006). Therefore, it is possible that cherrybark oak competitiveness may increase within pine-hardwood mixtures with further stand development.

Density effects on mixture performance

Stand density is another factor that can influence neighborhood interactions (Condés et al. 2013; Forester and Bauhus 2016). Though limited to the low- and balanced high-density plantings, which initially featured equal representation between species, our results demonstrate that loblolly pine basal area and volume growth were negatively affected by stand density. These results contradict the notion that shade-intolerant species gain a competitive advantage in high-density stands (Oliver et al. 1990; Garber and Maguire 2004; Maguire and Mainwaring 2021). One factor that may have contributed to this result was the early establishment of sweetgum and cherrybark oak. Early hardwood establishment likely prevented loblolly pine from gaining dominant canopy positions, resulting in direct competition for light within mixtures. The effect of planting order was likely magnified in balanced high-density mixtures where loblolly pine had less time to gain dominant canopy position before the onset of competition. Therefore, the combined effects of early hardwood establishment, increased competitive pressure, and inherent differences in growth potential between hardwood species in high-light environments could explain the patterns of loblolly pine survival in balanced high-density mixtures (Jones and McLeod 1989; Lin et al. 2001).

In contrast to the performance of loblolly pine, sweetgum and cherrybark oak basal area and volume increased with mixture density. Previous studies examining stand-level productivity have also reported positive effects of stand density on the performance of shade-tolerant species in mixture (Condés et al. 2013; Kweon and Comeau 2019). While our experimental design prevented investigation of hardwood overyielding, it seems unlikely that the presence of loblolly pine improved hardwood growth, as loblolly pine is an aggressive competitor for growing space and neither hardwood species is particularly shade tolerant (Krinard 1990; Lin et al. 2001). Moreover, loblolly pine litter quality is known to be relatively poor, suggesting that its addition to the forest floor did

not improve nutrient availability (Polyakova and Billor 2007). We suspect that a reduction in competition density, resulting from abundant loblolly pine mortality, likely accounts for the shift toward hardwood dominance within balanced high-density mixtures. The effect of loblolly pine mortality on competition was magnified by our planting design, as large segments of pine-planted rows were lost over the course of the study.

Another interesting result was the similarity in stand-level productivity between mixture types across planting density. Stand-level productivity in mixture generally increases with stand density when complementarity exists between species (Amoroso and Turnblom 2006; Brunner and Forrester 2020). In this study, hardwood productivity increased with stand density; however, improvements came at the expense of loblolly pine productivity preventing gains at the stand-level. Similar results were also reported by previous studies examining the effects of hardwood density on loblolly pine productivity early in stand development (Glover and Zutter 1993; Glover and Quicke 1999).

Low-density mixtures do not promote overyielding

Loblolly pine cumulative survival, diameter growth, and height growth were highest in low-density mixtures with cherrybark oak. Yet, in contrast to our initial prediction, none of these differences statistically exceeded loblolly pine performance in monocultures. Moreover, cumulative basal area and volume growth were significantly greater in monoculture than either mixture type, indicating a lack of complementarity between species. The lack of a competitive release or facilitation of loblolly pine within mixture is consistent with several studies, indicating that hardwood species interact competitively with loblolly pine early in stand development (Miller et al. 2003; Clabo and Clatterbuck 2015). Other studies examining loblolly pine performance report a lower maximum stand density index in mixture compared to pure stands (Woodall et al. 2005). Shelton and Murphy (1997) also reported negative effects of hardwood retention on loblolly pine basal area and volume growth in pine-hardwood mixtures post-thinning. Thus, our results generally support the current view of pine-hardwood interactions in the southeastern United States. Nevertheless, our findings contrast with several European studies reporting minimal effects of interspecific competition on Scots pine (*Pinus sylvestris* L.) survival and growth (Vallet and Perot 2016) or improvements in pine average diameter, basal area, standing volume, and volume increment when grown in mixture with oak (Steckel et al. 2019; Pretzsch et al. 2020).

Reconciling these disparate results is difficult, as numerous factors could be involved. Part of the difference may be explained by the lack of canopy stratification in low-density mixtures. Loblolly pine cumulative average height was statistically indistinguishable from either hardwood species. Thus, the advantages of a multilayered canopy for light interception are not being realized in either mixture type (Pretzsch 2014).

The development of a relatively homogenous canopy layer could be attributed to early hardwood establishment, as loblolly pine growth potential in high light exceeds that of sweetgum and cherrybark oak (Samuelson et al. 2001; Lockhart et al. 2006; Coyle et al. 2008). However, we suspect that the relative shade intolerance of each species examined in this study contributed to this result by suppressing survival beneath the canopy (Niinemets and Valladares 2006; Toigo et al. 2018). Another potentially important factor was the relatively high site quality at Hill Farms, which helped sweetgum and cherrybark oak compete with loblolly pine for growing space. The relatively rich soils may also have minimized the impact of any potential improvement in nutrient availability resulting from an increase in litter quality or decomposition in mixture (Hättenschwiler et al. 2005; Polyakova and Billor 2007; Richards et al. 2010). Indeed, the mixing effect in pine-oak mixtures has been shown to be greatest on low-quality sites (Lu et al. 2016, 2018).

Conclusions

Interactions between tree species influence the productivity of any management strategy. After 23 years, our results demonstrate that neither sweetgum nor cherrybark oak is complementary with loblolly pine at any investigated density. This result corresponds with a longstanding belief that interspecific competition overwhelms any positive interactions in pine-hardwood mixtures in the southeastern United States. It also underscores the potential importance of combining species with broad functional differences in mixture. Nevertheless, it is important to view our results within the context of some important caveats. First, sweetgum and cherrybark oak were planted 1 year before loblolly pine likely modifying competitive dynamics. Second, our experiment was conducted on a high-quality site, which increased hardwood competitiveness and potentially minimized the impacts of hardwood litter addition within mixtures. Third, production was evaluated over a limited range of planting densities. Future studies exploring mixed stand dynamics should consider investigating a more functionally diverse suite of pine-hardwood mixtures, a broader range of site qualities, and multiple planting strategies to augment the findings presented in this study.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Author contributions

JLW: performed research, analyzed data, and wrote the manuscript.

MAB: performed research and assisted with manuscript preparation.

Competing interests

The authors declare there are no competing interests.

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Appendix A

Appendix Tables A1–A4 appear on the following pages.

Table A1. Results of linear mixed models examining the main effects of species, time (2005, 2007, 2014, and 2020), and the interaction between species and time on the survival, periodic annual diameter growth, periodic annual height growth, and periodic annual basal area growth of sweetgum and loblolly pine across a gradient of pine–hardwood mixture density.

Metric	Factor	DFN	DFD	F statistic	P value
Low-density sweetgum : loblolly pine mixtures (1482 TPH)					
Survival	Species	1	48.00	23.28	<0.0001
	Time	3	48.00	7.42	0.0005
	Species × Time	3	48.00	2.87	0.0484
Mean annual diameter growth	Species	1	48.00	21.33	<0.0001
	Time	3	48.00	167.09	<0.0001
	Species × Time	3	48.00	9.88	<0.0001
Mean annual height growth	Species	1	46.07	3.96	0.0526
	Time	3	46.07	120.77	<0.0001
	Species × Time	3	46.07	1.01	0.3963
Mean annual basal area growth	Species	1	40.00	0.38	0.5429
	Time	3	40.00	19.25	<0.0001
	Species × Time	3	40.00	0.56	0.6439
Medium-density sweetgum : loblolly pine mixtures (1729 TPH)					
Survival	Species	3	29.71	14.80	<0.0001
	Time	1	29.71	24.82	<0.0001
	Species × Time	3	29.71	5.95	0.0026
Mean annual diameter growth	Species	1	24.00	19.06	0.0002
	Time	3	24.00	303.60	<0.0001
	Species × Time	3	24.00	32.06	<0.0001
Mean annual height growth	Species	1	21.88	0.40	0.5359
	Time	3	21.88	78.93	<0.0001
	Species × Time	3	21.88	0.68	0.5741
Mean annual basal area growth	Species	1	32.00	2.41	0.1305
	Time	3	32.00	40.67	<0.0001
	Species × Time	3	32.00	20.77	<0.0001
Balanced high-density sweetgum : loblolly pine mixtures (1976 TPH)					
Survival	Species	1	14.00	21.96	0.0002
	Time	3	14.00	13.97	0.0004
	Species × Time	3	14.00	10.90	0.0006
Mean annual diameter growth	Species	1	14.00	7.43	0.0149
	Time	3	14.00	144.20	<0.0001
	Species × Time	3	14.00	13.90	<0.0001
Mean annual height growth	Species	1	14.00	0.03	0.8731
	Time	3	14.00	50.51	<0.0001
	Species × Time	3	14.00	0.80	0.5161
Mean annual basal area growth	Species	1	16.00	1.91	0.1861
	Time	3	16.00	27.61	<0.0001
	Species × Time	3	16.00	5.28	0.0101
Unbalanced high-density sweetgum : loblolly pine mixtures (1976 TPH)					
Survival	Species	1	14.00	17.04	0.0010
	Time	3	14.00	7.62	0.0029
	Species × Time	3	14.00	6.67	0.0050

Table A1. (concluded).

Mean annual diameter growth	Species	1	14.00	11.80	<0.0001
	Time	3	14.00	164.30	<0.0001
	Species × Time	3	14.00	9.52	0.0011
Mean annual height growth	Species	1	14.00	0.34	0.5668
	Time	3	14.00	139.30	<0.0001
	Species × Time	3	14.00	2.78	0.0796
Mean annual basal area growth	Species	1	15.00	0.33	0.5729
	Time	3	15.00	15.63	<0.0001
	Species × Time	3	15.00	9.78	0.0008

Note: DFN, degrees of freedom numerator; DFD, degrees of freedom denominator.

Table A2. Results of linear mixed models examining the main effects of species, time (2005, 2007, 2014, and 2020), and the interaction between species and time on the survival, periodic annual diameter growth, mean annual height growth, and mean annual basal area growth of cherrybark oak and loblolly pine across a gradient of pine–hardwood mixture density.

Metric	Factor	DFN	DFD	F statistic	P value
Low-density cherrybark oak : loblolly pine mixtures (1482 TPH)					
Survival	Species	1	40.00	4.26	0.0658
	Time	3	40.00	7.67	0.0004
	Species × Time	3	40.00	1.33	0.2786
Mean annual diameter growth	Species	1	35.99	98.17	<0.0001
	Time	3	36.04	260.21	<0.0001
	Species × Time	3	35.99	40.27	<0.0001
Mean annual height growth	Species	1	38.00	2.93	0.0952
	Time	3	38.00	84.33	<0.0001
	Species × Time	3	38.00	0.44	0.4366
Mean annual basal area growth	Species	1	40.00	8.00	0.0073
	Time	3	40.00	26.38	<0.0001
	Species × Time	3	40.00	1.30	0.2891
Medium-density cherrybark oak : loblolly pine mixtures (1729 TPH)					
Survival	Species	1	40.00	0.05	0.8217
	Time	3	40.00	34.58	<0.0001
	Species × Time	3	40.00	0.87	0.4658
Mean annual diameter growth	Species	1	40.00	41.19	<0.0001
	Time	3	40.00	537.30	<0.0001
	Species × Time	3	40.00	134.37	<0.0001
Mean annual height growth	Species	1	40.00	1.71	0.1987
	Time	3	40.00	13.95	<0.0001
	Species × Time	3	40.00	0.79	0.5045
Mean annual basal area growth	Species	1	40.00	2.11	0.1542
	Time	3	40.00	50.01	<0.0001
	Species × Time	3	40.00	131.01	<0.0001
Balanced high-density cherrybark oak : loblolly pine mixtures (1976 TPH)					
Survival	Species	1	14.00	1.57	0.2301
	Time	3	14.00	2.90	0.0719
	Species × Time	3	14.00	0.80	0.5162
Mean annual diameter growth	Species	1	14.00	36.09	<0.0001
	Time	3	14.00	126.57	<0.0001
	Species × Time	3	14.00	19.29	<0.0001
Mean annual height growth	Species	1	16.00	3.10	0.0975
	Time	3	16.00	45.51	<0.0001
	Species × Time	3	16.00	0.22	0.8794
Mean annual basal area growth	Species	1	16.00	2.61	0.1259
	Time	3	16.00	11.54	0.0003
	Species × Time	3	16.00	5.15	0.0110
Unbalanced high-density cherrybark oak : loblolly pine mixtures (1976 TPH)					
Survival	Species	1	14.00	5.06	0.0388
	Time	3	14.00	6.82	0.0036
	Species × Time	3	14.00	1.92	0.1679

Table A2. (concluded).

Mean annual diameter growth	Species	1	13.09	44.48	<0.0001
	Time	3	13.08	89.75	<0.0001
	Species × Time	3	13.08	16.64	<0.0001
Mean annual height growth	Species	1	13.28	2.27	0.1556
	Time	3	13.26	38.21	<0.0001
	Species × Time	3	13.26	2.21	0.1351
Mean annual basal area growth	Species	1	15.08	1.02	0.3286
	Time	3	15.09	6.53	0.0048
	Species × Time	3	15.09	3.05	0.6100

Note: DFN, degrees of freedom numerator; DFD, degrees of freedom denominator.

Table A3. Results of linear mixed models examining the main effects of mixture type on the mean survival and cumulative diameter, height, and basal area growth within pine–hardwood mixtures of varying density.

	DFN	DFD	F statistic	P value
Low-density mixtures (1482 TPH)				
Survival	1	8	1.66	0.2337
Cumulative diameter	1	8	1.65	0.2350
Cumulative height	1	8	0.08	0.7835
Cumulative basal area	1	8	0.05	0.8354
Cumulative volume	1	8	0.01	0.9495
Medium-density mixtures (1729 TPH)				
Survival	1	7	2.72	0.1429
Cumulative diameter	1	7	0.91	0.3758
Cumulative height	1	7	0.37	0.5633
Cumulative basal area	1	7	0.14	0.7147
Cumulative volume	1	7	0.35	0.5722
Balanced high-density mixtures (1976 TPH)				
Survival	1	4	0.03	0.8766
Cumulative diameter	1	4	0.03	0.8798
Cumulative height	1	4	2.22	0.2744
Cumulative basal area	1	4	0.01	0.9401
Cumulative volume	1	4	0.01	0.921
Unbalanced high-density mixtures (1976 TPH)				
Survival	1	4	21.44	0.0436
Cumulative diameter	1	4	9.89	0.2166
Cumulative height	1	4	7.85	0.1072
Cumulative basal area	1	4	0.46	0.5682
Cumulative volume	1	4	8.91	0.0951

Note: Survival and cumulate growth account for the sum of both species in mixture. DFN, degrees of freedom numerator; DFD, degrees of freedom denominator.

Table A4. Results of linear mixed models examining the main effects of stand type, time (2005, 2007, 2014, and 2020), and the interaction between stand type and time on the survival, periodic diameter growth, and periodic height growth of loblolly pine in monoculture and pine–hardwood mixtures established at 1482 trees per hectare.

Metric	Factor	DFN	DFD	F statistic	P value
Monoculture and low-density mixtures (1482 TPH)					
Survival	Stand type	2	46	2.21	0.1213
	Time	3	46	149.59	<0.0001
	Stand type × Time	6	46	0.12	0.9941
Periodic annual diameter growth	Stand type	2	50.11	2.57	0.0867
	Time	3	50.03	801.19	<0.0001
	Stand type × Time	6	50.03	0.69	0.6547
Periodic annual height growth	Stand type	2	50.12	0.46	0.6330
	Time	3	50.04	132.91	<0.0001
	Stand type × Time	6	50.04	0.32	0.9224

Note: DFN, degrees of freedom numerator; DFD, degrees of freedom denominator.