



Canadian Journal of Forest Research

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Journal:	<i>Canadian Journal of Forest Research</i>
Manuscript ID	cjfr-2022-0125.R1
Manuscript Type:	Article
Date Submitted by the Author:	09-Aug-2022
Complete List of Authors:	Willis, John; USDA Forest Service Region 8 Blazier, Michael; University of Arkansas at Monticello
Is the invited manuscript for consideration in a Special Issue? :	Not applicable (regular submission)
Keyword:	Overyielding, Loblolly pine, Cherrybark oak, Sweetgum, Mixed stands

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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 (1,482 – 1,976 TPH) over 23-years in northern Louisiana, USA. Species were planted in alternating rows with hardwood establishment occurring one-year prior to loblolly pine. Mixtures were also compared to loblolly pine monocultures at a common density (1,482 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 (1,976 TPH, 50pine:50hardwood). In contrast, cherrybark oak basal area and volume growth did not significantly exceed loblolly pine at any density. At a common density (1,482 TPH), loblolly pine monoculture cumulative basal area and volume significantly exceeded that 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.

Keywords: Overyielding, loblolly pine, cherrybark oak, sweetgum, interspecific competition, mixed stands

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 has 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 intraspecies similarities in resource requirements (Man and Lieffers 1999, Toïgo 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 et al. 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, Williams et al. 2017, Forrester 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 towards 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 et al. 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 sub-canopy 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 mixture was compared to that 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 that 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 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 (32.749025 N, -93.04111111 W) (Figure 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 219-276 days. Average precipitation occurs primarily in the form of rain and averages 1330 mm yr⁻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 was approximately 30.0 m and 29.5 m, respectively (McTague et al. 2006). Site index for loblolly pine at age 50 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 (sweetgum: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 (1,482 TPH, 50:50 pine-hardwood ratio, 3.6 m x 1.8 m spacing, six internal measurement rows), medium-density (1,729 TPH, 57:43 pine-hardwood ratio, 3.3 m x 1.8 m spacing, six internal measurement rows) (Figure 2), balanced high-density (1,976 TPH, 50:50 pine-hardwood ratio, 3.3 m x 1.5 m spacing, six internal measurement rows), and unbalanced high-density (1,976 TPH, 37:63 pine-hardwood ratio, 3.3 m x 1.5 m spacing, six internal measurement rows) (Table 1). Loblolly pine monocultures were established at 1,482 TPH (3.6 m x 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, density combination (Table 1). Each species was planted as a one-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 decimeter (Haglöf Vertex III, Haglöf Inc.). Tree diameter was measured with a diameter tape to the nearest millimeter. 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 unbalanced 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 1,482 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 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 represents 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 SAS 9.4 software (SAS Institute, Cary, NC, United States).

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 1). Loblolly pine added statistically more periodic annual diameter growth than sweetgum seven-years after planting (Figure 3); however, sweetgum survival significantly exceeded loblolly pine over the last 13-years of the study (Figure 4). Periodic annual height and basal area growth were similar between species and did not differ significantly over time (sweetgum: $42.00 \text{ cm yr}^{-1} \pm 4.00$, loblolly pine: $46.00 \text{ cm yr}^{-1} \pm 4.00$) (sweetgum: $0.50 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1} \pm 0.07$, loblolly pine: $0.56 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1} \pm 0.07$) (Appendix 1). 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 were similar among species and did not differ significantly over time (Appendix 2). Trends in periodic annual diameter growth between species varied significantly over time, as loblolly pine growth exceeded cherrybark oak over the first nine-years of the study but grew at similar rates thereafter (Appendix 2) (Figure 5). Periodic annual height growth was similar between species (cherrybark oak: $42 \text{ cm yr}^{-1} \pm 3.00$, loblolly pine: $48 \text{ cm yr}^{-1} \pm 3.00$) and did not differ significantly over time (Appendix 2). Loblolly pine periodic annual basal area growth significantly exceeded that of cherrybark oak (cherrybark oak: $0.43 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1} \pm 0.07$, loblolly pine: $0.69 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1} \pm 0.07$) and did not vary statistically over time (Appendix 2). 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 1). Like in low-density mixtures, loblolly pine produced significantly more periodic annual diameter growth than sweetgum seven-years post-planting but survived at a significantly lower rate over the last 13-years of the study (Figures 3 & 4). Loblolly pine periodic annual basal area growth statistically exceeded that of sweetgum seven years after planting but was statistically surpassed over the final six-years of the study (Appendix 1) (Figure 6). Periodic annual height growth was similar between species and did not significantly differ over time (sweetgum: $43.00 \text{ cm yr}^{-1} \pm 4.00$, loblolly pine: $42.00 \text{ cm yr}^{-1} \pm 4.00$) (Appendix 1). 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 2). Loblolly pine periodic annual diameter growth statistically exceeded that of cherrybark oak over the first nine-years of the study but grew at similar rates in the subsequent 13-years (Appendix 2) (Figure 5). Like medium-density mixtures with sweetgum, loblolly pine periodic annual basal area growth significantly exceeded that of cherrybark oak nine-years post-planting but was surpassed over the final six-years of the study (Appendix 2) (Figure 7). Periodic annual height growth was similar between species and did not differ statistically over time (cherrybark oak $40.00 \text{ cm yr}^{-1} \pm 5.00$, loblolly pine: $48.00 \text{ cm yr}^{-1} \pm 5.00$) (Appendix 2). 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 1) (Figure 4). Periodic annual diameter growth between species also varied significantly over time, as loblolly pine added statistically more diameter growth than sweetgum seven-years after planting but grew at a similar rate over the subsequent 16-years (Appendix 1) (Figure 3). Loblolly pine periodic annual basal area growth was also statistically higher than sweetgum seven-years after planting; but sweetgum basal area growth statistically surpassed that of loblolly pine over the final 13-years of the study (Appendix 1) (Figure 6). Sweetgum periodic annual height growth was comparable to loblolly pine and did not significantly differ over time (sweetgum: $41.00 \text{ cm yr}^{-1} \pm 3.00$, loblolly pine: $40.00 \text{ cm yr}^{-1} \pm 3.00$) (Appendix 1). At final measurement, sweetgum cumulative survival, basal area, and volume growth significantly exceeded that 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 2). Loblolly pine added significantly more periodic annual diameter growth seven-years after planting, but cherrybark oak grew at a similar rate over the subsequent 16-years (Appendix 2) (Figure 5). Periodic annual basal area growth followed a similar pattern, as loblolly pine statistically added more basal area growth than cherrybark oak seven-years after planting but grew at a similar rate thereafter (Appendix 2) (Figure 7). Trends in periodic height growth between species were comparable and did not differ statistically over time (cherrybark oak: $35.00 \text{ cm yr}^{-1} \pm 3.00$, loblolly pine: $42 \text{ cm yr}^{-1} \pm 3.00$) (Appendix 2). 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 six-years of the study (Appendix 1) (Figure 4). In contrast, loblolly pine added significantly more periodic annual diameter growth than sweetgum seven-years after planting (Appendix 1) (Figure 3). Trends in periodic annual basal area growth between species varied significantly over time (Appendix 1). Periodic annual basal area growth was statistically indistinguishable between species nine-years after planting (Figure 6). Loblolly pine added statistically more periodic annual basal area than sweetgum over the next seven-years; however, sweetgum outproduced loblolly pine over the final six-years of the study (Figure 6). Periodic annual height growth was identical between species and did not significantly differ over time ($43.00 \text{ cm yr}^{-1} \pm 2.00$) (Appendix 1). 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 2). Loblolly pine periodic annual diameter growth statistically exceeded that of cherrybark oak seven-years after planting but progressed at a similar rate thereafter (Figure 5). Species' periodic annual height (cherrybark oak: $48.00 \pm 3.00 \text{ cm yr}^{-1}$, loblolly pine: $42.00 \text{ cm yr}^{-1} \pm 3.00$) and basal area growth (cherrybark oak: $0.48 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1} \pm 11.00$, loblolly pine: $0.33 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1} \pm 11.00$) were statistically indistinguishable and did not vary significantly over time (Appendix 2). 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-density (Appendix 3 & Table 3). Within unbalanced high-density mixtures, cumulative survival in mixtures with sweetgum significantly exceeded that of mixtures with cherrybark oak (Appendix 3 & Table 3). However, cumulative growth comparisons between unbalanced high-density mixture types were not statistically significant (Appendix 3 & Table 3).

Productivity in mixtures versus monoculture

Among stand types, loblolly pine periodic annual diameter growth ($75.00 \text{ cm yr}^{-1} \pm 3.00$), and periodic annual height growth ($48.00 \text{ cm} \pm 3.00$) were highest in low-density mixtures with cherrybark oak; but these differences exceeded that of loblolly pine in low-density mixtures with sweetgum or monoculture by less than five percent, respectively, and did not vary statistically over time (Appendix 4). 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 (Figure 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 percent. In comparison, cherrybark oak cumulative survival averaged 61-66 percent 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 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 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.

361

362 *Density effects on mixture performance*

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

378 In contrast to the performance of loblolly pine, sweetgum and cherrybark oak basal area
379 and volume increased with mixture density. Previous studies examining stand-level productivity
380 have also reported positive effects of stand density on the performance of shade tolerant species
381 in mixture (Condés et al. 2013, Kweon and Comeau 2019). While our experimental design
382 prevented investigation of hardwood overyielding, it seems unlikely that the presence of loblolly
383 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. 2021). 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 towards 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; but 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 monoculture. Moreover, cumulative basal area and volume growth was 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 et al. 2015). Other studies examining loblolly pine performance report a lower SDI_{max} 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 (*P. sylvestris*) 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 multi-layered 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 and Stokes 2001, Lockhart et al. 2006, Coyle et al. 2008). However, we suspect 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, Toïgo 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 are 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 one-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 density. Future studies exploring mixed stand dynamics should consider investigating a more functionally diverse suite of pine-hardwood mixtures, a broader range of site quality, and multiple planting strategies to augment the findings presented in this study.

Acknowledgements

The authors are indebted to Dr. Terry Clason for initiating this research and the numerous personnel of the Hill Farm Research Station that collected tree dimension data during this project. David Hood, Bradley Osbon, Michelle Moore, and Ryan Holbrook were especially vital in collecting data that made this paper possible. This paper was written and prepared in part by a U.S. Government employee on official time, and therefore it is in the public domain and not subject to copyright. The findings and conclusions in this publication are those of the author(s) and should not be construed to represent an official USDA, Forest Service, or United States Government determination or policy.

Competing interests statement

The authors declare there are no competing interests.

Author contributions

JLW: Performed research, analyzed data, wrote the manuscript; MAB: performed research and assisted with manuscript preparation.

Funding statement

Partial funding for this project was provided by the USDA Forest Service.

Data availability statement

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

References

- 471 Adler, P.B., Smull, D., Beard, K.H., Choi, R.T., Furniss, T., Kulmatiski, A., Meiners, J.M.,
472 Tredennick, A.T. and Veblen, K.E., 2018. Competition and coexistence in plant communities:
473 intraspecific competition is stronger than interspecific competition. *Ecology Letters*, 21(9),
474 pp.1319-1329. <https://doi.org/10.1111/ele.13098>
- 475 Amateis, R. L., and Burkhardt, H. E. 1987. Tree volume and taper of loblolly pine varies by stand
476 origin. *Southern Journal of Applied Forestry*, 11(4), pp.185-189.
477 <https://doi.org/10.1093/sjaf/11.4.185>
- 478 Amoroso, M.M. and Turnblom, E.C., 2006. Comparing productivity of pure and mixed Douglas-
479 fir and western hemlock plantations in the Pacific Northwest. *Canadian Journal of Forest*
480 *Research*, 36(6), pp.1484-1496. <https://doi.org/10.1139/x06-042>
- 481 Bauhus, J., Van Winden, A.P. and Nicotra, A.B., 2004. Aboveground interactions and
482 productivity in mixed-species plantations of *Acacia mearnsii* and *Eucalyptus globulus*. *Canadian*
483 *Journal of Forest Research*, 34(3), pp.686-694. <https://doi.org/10.1139/x03-243>
- 484 Bayer, D., Seifert, S. and Pretzsch, H., 2013. Structural crown properties of Norway spruce
485 (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in mixed versus pure stands
486 revealed by terrestrial laser scanning. *Trees*, 27(4), pp.1035-1047.
487 <https://doi.org/10.1007/s00468-013-0854-4>
- 488 Bongers, F.J., 2020. Functional-structural plant models to boost understanding of
489 complementarity in light capture and use in mixed-species forests. *Basic and Applied*
490 *Ecology*, 48, pp.92-101. <https://doi.org/10.1016/j.baae.2020.09.007>
- 491 Borders, B.E. and Bailey, R.L., 2001. Loblolly pine—pushing the limits of growth. *Southern*
492 *Journal of Applied Forestry*, 25(2), pp.69-74. <https://doi.org/10.1093/sjaf/25.2.69>

- 493 Brunner, A., & Forrester, D. I., 2020. Tree species mixture effects on stem growth vary with
494 stand density—An analysis based on individual tree responses. *Forest Ecology and*
495 *Management*, 473, 118334. <https://doi.org/10.1016/j.foreco.2020.118334>
- 496 Callaway, R.M. and Walker, L.R., 1997. Competition and facilitation: a synthetic approach to
497 interactions in plant communities. *Ecology*, 78(7), pp.1958-1965. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9658(1997)078[1958:cafasa]2.0.co;2)
498 [9658\(1997\)078\[1958:cafasa\]2.0.co;2](https://doi.org/10.1890/0012-9658(1997)078[1958:cafasa]2.0.co;2)
- 499 Cavard, X., Bergeron, Y., Chen, H.Y., Paré, D., Laganière, J. and Brassard, B., 2011.
500 Competition and facilitation between tree species change with stand
501 development. *Oikos*, 120(11), pp.1683-1695. <https://doi.org/10.1111/j.1600-0706.2011.19294.x>
- 502 Clabo, D. C., & Clatterbuck, W. K., 2015. Site preparation techniques for the establishment of
503 mixed pine-hardwood stands: 22-year results. *Forest Science*, 61(4), pp.790-799.
504 <https://doi.org/10.5849/forsci.13-617>
- 505 Condés, S., Del Rio, M. and Sterba, H., 2013. Mixing effect on volume growth of *Fagus*
506 *sylvatica* and *Pinus sylvestris* is modulated by stand density. *Forest Ecology and*
507 *Management*, 292, pp.86-95. <https://doi.org/10.1016/j.foreco.2012.12.013>
- 508 Coyle, D.R., Coleman, M.D. and Aubrey, D.P., 2008. Above-and below-ground biomass
509 accumulation, production, and distribution of sweetgum and loblolly pine grown with irrigation
510 and fertilization. *Canadian Journal of Forest Research*, 38(6), pp.1335-1348.
511 <https://doi.org/10.1139/x07-231>
- 512 Dieler, J. and Pretzsch, H., 2013. Morphological plasticity of European beech (*Fagus sylvatica*
513 L.) in pure and mixed-species stands. *Forest Ecology and Management*, 295, pp.97-108.
514 <https://doi.org/10.1016/j.foreco.2012.12.049>

- 515 Fichtner, A., Härdtle, W., Bruelheide, H., Kunz, M., Li, Y., & Von Oheimb, G. (2018).
516 Neighborhood interactions drive overyielding in mixed-species tree communities. *Nature*
517 *Communications*, 9(1), pp.1-8. <https://doi.org/10.1038/s41467-018-03529-w>
- 518 Fichtner, A., Schnabel, F., Bruelheide, H., Kunz, M., Mausolf, K., Schuldt, A., Härdtle, W. and
519 von Oheimb, G., 2020. Neighborhood diversity mitigates drought impacts on tree
520 growth. *Journal of Ecology*, 108(3), pp.865-875. <https://doi.org/10.1111/1365-2745.13353>
- 521 Filipescu, C. N., & Comeau, P. G. 2007. Competitive interactions between aspen and white
522 spruce vary with stand age in boreal mixedwoods. *Forest Ecology and Management*, 247(1-3),
523 pp.175-184. <https://doi.org/10.1016/j.foreco.2007.04.038>
- 524 Forrester, D.I. and Smith, R.G.B., 2012. Faster growth of *Eucalyptus grandis* and *Eucalyptus*
525 *pilularis* in mixed-species stands than monocultures. *Forest Ecology and Management*, 286,
526 pp.81-86. <https://doi.org/10.1016/j.foreco.2012.08.037>
- 527 Forrester, D.I., Kohnle, U., Albrecht, A.T. and Bauhus, J., 2013. Complementarity in mixed-
528 species stands of *Abies alba* and *Picea abies* varies with climate, site quality and stand
529 density. *Forest Ecology and Management*, 304, pp.233-242.
530 <https://doi.org/10.1016/j.foreco.2013.04.038>
- 531 Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species
532 forests: from pattern to process. *Forest Ecology and Management*, 312, pp.282-292.
533 <https://doi.org/10.1016/j.foreco.2013.10.003>
- 534 Forrester, D.I. and Albrecht, A.T., 2014. Light absorption and light-use efficiency in mixtures of
535 *Abies alba* and *Picea abies* along a productivity gradient. *Forest Ecology and Management*, 328,
536 pp.94-102. <https://doi.org/10.1016/j.foreco.2014.05.026>

- 537 Forrester, D.I. and Bauhus, J., 2016. A review of processes behind diversity—productivity
538 relationships in forests. *Current Forestry Reports*, 2(1), pp.45-61.
539 <https://doi.org/10.1007/s40725-016-0031-2>
- 540 Forrester, D.I., 2017. Ecological and physiological processes in mixed versus monospecific
541 stands. In *Mixed-species forests* (pp. 73-115). Springer, Berlin, Heidelberg.
542 https://doi.org/10.1007/978-3-662-54553-9_3
- 543 Forrester, D.I., Benneter, A., Bouriaud, O. and Bauhus, J., 2017. Diversity and competition
544 influence tree allometric relationships—Developing functions for mixed-species forests. *Journal*
545 *of Ecology*, 105(3), pp.761-774. <https://doi.org/10.1111/1365-2745.12704>
- 546 Fox, T.R., Jokela, E.J. and Allen, H.L., 2007. The development of pine plantation silviculture in
547 the southern United States. *Journal of Forestry*, 105(7), pp.337-347.
548 <https://doi.org/10.1093/jof/105.7.337>
- 549 Fredericksen, T.S., Sedaker, S.M. and Seiler, J.R., 1993. Interference interactions in simulated
550 pine-hardwood seedling stands. *Forest Science*, 39(2), pp.383-395. [https://doi.org/10.1139/x93-](https://doi.org/10.1139/x93-254)
551 [254](https://doi.org/10.1139/x93-254)
- 552 Garber, S.M. and Maguire, D.A., 2004. Stand productivity and development in two mixed-
553 species spacing trials in the central Oregon cascades. *Forest Science*, 50(1), pp.92-105.
554 <https://doi.org/10.1139/x04-164>
- 555 Glover, G. R., & Zutter, B. R., 1993. Loblolly pine and mixed hardwood stand dynamics for 27
556 years following chemical, mechanical, and manual site preparation. *Canadian Journal of Forest*
557 *Research*, 23(10), pp.2126-2132. <https://doi.org/10.1139/x93-265>

- 558 Glover, G., & Quicke, H., 1999. Growth response of loblolly pine, sweetgum, and water oak in a
559 pine-hardwood density study. *Canadian Journal of Forest Research*, 29(7), 968-978.
560 <https://doi.org/10.1139/x99-086>
- 561 Gonzalez de Andres, E., Seely, B., Blanco, J.A., Imbert, J.B., Lo, Y.H. and Castillo, F.J., 2017.
562 Increased complementarity in water-limited environments in Scots pine and European beech
563 mixtures under climate change. *Ecohydrology*, 10(2), p.e1810. <https://doi.org/10.1002/eco.1810>
- 564 Granger, J.J. and Buckley, D.S., 2021. Performance of white oak (*Quercus alba*) and three pine
565 species in novel multi-cropped plantations in eastern Tennessee, USA. *Forest Ecology and*
566 *Management*, 489, 119060. <https://doi.org/10.1016/j.foreco.2021.119060>
- 567 Groninger, J.W., Seiler, J.R., Zedaker, S.M. and Berrang, P.C., 1995. Effects of elevated CO₂,
568 water stress, and nitrogen level on competitive interactions of simulated loblolly pine and
569 sweetgum stands. *Canadian Journal of Forest Research*, 25(7), pp.1077-1083.
570 <https://doi.org/10.1139/x95-119>
- 571 Groninger, J.W., Seiler, J.R., Peterson, J.A. and Kreh, R.E., 1996. Growth and photosynthetic
572 responses of four Virginia Piedmont tree species to shade. *Tree Physiology*, 16(9), pp.773-778.
573 <https://doi.org/10.1093/treephys/16.9.773>
- 574 Hättenschwiler, S., Tiunov, A.V. and Scheu, S., 2005. Biodiversity and litter decomposition in
575 terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, pp.191-218.
576 <https://doi.org/10.1146/annurev.ecolsys.36.112904.151932>
- 577 Hooper, E., Legendre, P. and Condit, R., 2005. Barriers to forest regeneration of deforested and
578 abandoned land in Panama. *Journal of Applied Ecology*, 42(6), pp.1165-1174.
579 <https://doi.org/10.1111/j.1365-2664.2005.01106.x>

- 580 Huuskonen, S., Domisch, T., Finér, L., Hantula, J., Hynynen, J., Matala, J., Miina, J., Neuvonen,
581 S., Nevalainen, S., Niemistö, P. and Nikula, A., 2021. What is the potential for replacing
582 monocultures with mixed-species stands to enhance ecosystem services in boreal forests in
583 Fennoscandia? *Forest Ecology and Management*, 479, p.118558.
584 <https://doi.org/10.1016/j.foreco.2020.118558>
- 585 Jactel, H., Gritti, E.S., Drössler, L., Forrester, D.I., Mason, W.L., Morin, X., Pretzsch, H. and
586 Castagneyrol, B., 2018. Positive biodiversity–productivity relationships in forests: climate
587 matters. *Biology Letters*, 14(4), p.20170747. <https://doi.org/10.1098/rsbl.2017.0747>
- 588 Jones, R.H. and McLeod, K.W., 1989. Shade tolerance in seedlings of Chinese tallow tree,
589 American sycamore, and cherrybark oak. *Bulletin of the Torrey Botanical Club*, pp.371-377.
590 <https://doi.org/10.2307/2996627>
- 591 Jucker, T., Bouriaud, O. and Coomes, D.A., 2015. Crown plasticity enables trees to optimize
592 canopy packing in mixed-species forests. *Functional Ecology*, 29(8), pp.1078-1086.
593 <https://doi.org/10.1111/1365-2435.12428>
- 594 Jucker, T., Koricheva, J., Finér, L., Bouriaud, O., Iacopetti, G. and Coomes, D.A., 2020. Good
595 things take time—Diversity effects on tree growth shift from negative to positive during stand
596 development in boreal forests. *Journal of Ecology*, 108(6), pp. 2198-2211.
597 <https://doi.org/10.1111/1365-2745.13464/v1/review3>
- 598 Kelty, M.J., 2006. The role of species mixtures in plantation forestry. *Forest Ecology and*
599 *Management*, 233(2-3), pp.195-204. <https://doi.org/10.1016/j.foreco.2006.05.011>

- 600 Kormanik, P. 1990. *Liquidambar styraciflua*, sweetgum. In: Silvics of North America: 2.
601 Hardwoods. Burns, R.M., and B.H. Honkala, Tech. Coords. Silvics of North America, Vol. 2,
602 Hardwoods. USDA Forest Service Ag. Handbook 654, pp.644-649.
- 603 Krinard, R.M., 1990. *Quercus falcata* var. *pagodifolia* Ell. Cherrybark Oak. In: Silvics of North
604 America: 2 Hardwoods. Burns, R.M., Honkala, B.H. Tech. Coords. Silvics of North America,
605 Vol. 2, Hardwoods. USDA Forest Service Ag. Handbook 654, pp. 640–649.
- 606 Kweon, D. and Comeau, P.G., 2019. Factors influencing overyielding in young boreal
607 mixedwood stands in western Canada. *Forest Ecology and Management*, 432, pp.546-557.
608 <https://doi.org/10.1016/j.foreco.2018.09.053>
- 609 Lin, J., Harcombe, P.A. and Fulton, M.R., 2001. Characterizing shade tolerance by the
610 relationship between mortality and growth in tree saplings in a southeastern Texas
611 forest. *Canadian Journal of Forest Research*, 31(2), pp.345-349. [https://doi.org/10.1139/x00-
612 157](https://doi.org/10.1139/x00-157)
- 613 Lockhart, B.R., Ezell, A.W., Hodges, J.D. and Clatterbuck, W.K., 2006. Using natural stand
614 development patterns in artificial mixtures: A case study with cherrybark oak and sweetgum in
615 east-central Mississippi, USA. *Forest Ecology and Management*, 222(1-3), pp.202-210.
616 <https://doi.org/10.1016/j.foreco.2005.09.029>
- 617 Lu, H., Mohren, G.M., den Ouden, J., Goudiaby, V. and Sterck, F.J., 2016. Overyielding of
618 temperate mixed forests occurs in evergreen–deciduous but not in deciduous–deciduous species
619 mixtures over time in the Netherlands. *Forest Ecology and Management*, 376, pp.321-332.
620 <https://doi.org/10.1016/j.foreco.2016.06.032>

- 621 Lu, H., Condés, S., del Río, M., Goudiaby, V., den Ouden, J., Mohren, G.M., Schelhaas, M.J., de
622 Waal, R. and Sterck, F.J., 2018. Species and soil effects on overyielding of tree species mixtures
623 in the Netherlands. *Forest Ecology and Management*, 409, pp.105-118.
624 <https://doi.org/10.1016/j.foreco.2017.11.010>
- 625 Niinemets, Ü. and Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of
626 temperate northern hemisphere trees and shrubs. *Ecological monographs*, 76(4), pp.521-547.
627 [https://doi.org/10.1890/0012-9615\(2006\)076\[0521:ttsdaw\]2.0.co;2](https://doi.org/10.1890/0012-9615(2006)076[0521:ttsdaw]2.0.co;2)
- 628 Ma, Z. and Chen, H.Y., 2018. Positive species mixture effects on fine root turnover and mortality
629 in natural boreal forests. *Soil Biology and Biochemistry*, 121, pp.130-137.
630 <https://doi.org/10.1016/j.soilbio.2018.03.015>
- 631 Madsen, C., Potvin, C., Hall, J., Sinacore, K., Turner, B.L. and Schnabel, F., 2020. Coarse root
632 architecture: Neighbourhood and abiotic environmental effects on five tropical tree species
633 growing in mixtures and monocultures. *Forest Ecology and Management*, 460, p.117851.
634 <https://doi.org/10.1016/j.foreco.2019.117851>
- 635 Maguire, D.A. and Mainwaring, D.B., 2021. Effects of initial spacing and species mix on stand
636 developmental patterns in two field trials in central Oregon. *Forest Ecology and*
637 *Management*, 491, p.119153. <https://doi.org/10.1016/j.foreco.2021.119153>
- 638 Man, R. and Lieffers, V.J., 1999. Are mixtures of aspen and white spruce more productive than
639 single species stands? *The Forestry Chronicle*, 75(3), pp.505-513.
640 <https://doi.org/10.5558/tfc75505-3>

- 641 Matney, T.G., Hodges, J.D., Sullivan, A.D. and Ledbetter, J.R., 1985. Tree profile and volume
642 ratio equations for sweetgum and cherrybark oak trees. *Southern Journal of Applied*
643 *Forestry*, 9(4), pp.222-227. <https://doi.org/10.1093/sjaf/9.4.222>
- 644 McTague, J. P., Robison, D. J., O'Loughlin, O'Loughlin, J. R., Kellison, R. Development of
645 growth and yield models for southern hardwood: site index determination. Pp. 319-321. In
646 Connor, Kristina F., ed. 2006. Proceedings of the 13th biennial southern silvicultural research
647 conference. Gen. Tech. Rep. SRs-92. Asheville, NC: U.S. Department of Agriculture, Forest
648 Service, Southern Research Station. 640 p.
- 649 Messier, C., Puettmann, K., Chazdon, R., Andersson, K.P., Angers, V.A., Brotons, L., Filotas,
650 E., Tittler, R., Parrott, L. and Levin, S.A., 2015. From management to stewardship: viewing
651 forests as complex adaptive systems in an uncertain world. *Conservation Letters*, 8(5), pp.368-
652 377. <https://doi.org/10.1111/conl.12156>
- 653 Miller, J. H., Zutter, B. R., Zedaker, S. M., Edwards, M. B., & Newbold, R. A., 2003. Growth
654 and yield relative to competition for loblolly pine plantations to midrotation—a southeastern
655 United States regional study. *Southern Journal of Applied Forestry*, 27(4), pp. 237-252.
656 <https://doi.org/10.1093/sjaf/27.4.237>
- 657 Moore, G. W., Bond, B. J., & Jones, J. A. (2011). A comparison of annual transpiration and
658 productivity in monoculture and mixed-species Douglas-fir and red alder stands. *Forest Ecology*
659 *and Management*, 262(12), 2263-2270. <https://doi.org/10.1016/j.foreco.2011.08.018>
- 660 Mou, P., Jones, R.H., Mitchell, R.J. and Zutter, B., 1995. Spatial distribution of roots in
661 sweetgum and loblolly pine monocultures and relations with above-ground biomass and soil
662 nutrients. *Functional Ecology*, pp.689-699. <https://doi.org/10.2307/2390162>

- 663 Oliver, C.D., Clatterbuck, W.K. and Burkhardi, E.C., 1990. Spacing and stratification patterns of
664 cherrybark oak and American sycamore in mixed, even-aged stands in the southeastern United
665 States. *Forest Ecology and Management*, 31(1-2), pp.67-79. [https://doi.org/10.1016/0378-](https://doi.org/10.1016/0378-1127(90)90112-o)
666 [1127\(90\)90112-o](https://doi.org/10.1016/0378-1127(90)90112-o)
- 667 Paquette, A. and Messier, C., 2011. The effect of biodiversity on tree productivity: from
668 temperate to boreal forests. *Global Ecology and Biogeography*, 20(1), pp.170-180.
669 <https://doi.org/10.1111/j.1466-8238.2010.00592.x>
- 670 Phillips, D. R., & Abercrombie, J. A., 1987. Pine-hardwood mixtures—a new concept in
671 regeneration. *Southern Journal of Applied Forestry*, 11(4), pp.192-197.
672 <https://doi.org/10.1093/sjaf/11.4.192>
- 673 Polyakova, O. and Billor, N., 2007. Impact of deciduous tree species on litterfall quality,
674 decomposition rates and nutrient circulation in pine stands. *Forest Ecology and*
675 *Management*, 253(1-3), pp.11-18. <https://doi.org/10.1016/j.foreco.2007.06.049>
- 676 Popham, T. W., Feduccia, D. P., Dell, T. R., Mann Jr., W. F., Campbell, T. E. 1979. Site index
677 for loblolly pine plantations on cut-over sites in the West Gulf Coastal Plain. SO-250, Forest
678 Service, USDA, New Orleans, LA. 7 pp.
- 679 Prestemon, J. P., & Abt, R. C., 2002. Southern forest resource assessment highlights: The
680 southern timber market to 2040. *Journal of Forestry*, 100(7), pp.16-22.
- 681 Pretzsch, H., Dieler, J., Seifert, T. and Rötzer, T., 2012. Climate effects on productivity and
682 resource-use efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus*
683 *sylvatica* [L.]) in stands with different spatial mixing patterns. *Trees*, 26(4), pp.1343-1360.
684 <https://doi.org/10.1007/s00468-012-0710-y>

- 685 Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands
686 compared with monocultures. *Forest Ecology and Management*, 327, pp.251-264.
687 <https://doi.org/10.1016/j.foreco.2014.04.027>
- 688 Pretzsch, H., del Río, M., Schütze, G., Ammer, C., Annighöfer, P., Avdagic, A., Barbeito, I.,
689 Bielak, K., Brazaitis, G., Coll, L. and Drössler, L., 2016. Mixing of Scots pine (*Pinus sylvestris*
690 L.) and European beech (*Fagus sylvatica* L.) enhances structural heterogeneity, and the effect
691 increases with water availability. *Forest Ecology and Management*, 373, pp.149-166.
692 <https://doi.org/10.1016/j.foreco.2016.04.043>
- 693 Pretzsch, H. and Rais, A., 2016. Wood quality in complex forests versus even-aged
694 monocultures: review and perspectives. *Wood Science and Technology*, 50(4), pp.845-880.
695 <https://doi.org/10.1007/s00226-016-0827-z>
- 696 Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, C., Ehbrecht, M., Bielak, K., Bravo, F.,
697 Ordóñez, C., Collet, C. and Vast, F., 2020. Stand growth and structure of mixed-species and
698 monospecific stands of Scots pine (*Pinus sylvestris* L.) and oak (*Q. robur* L., *Quercus petraea*
699 (Matt.) Liebl.) analysed along a productivity gradient through Europe. *European Journal of*
700 *Forest Research*, 139(3), pp.349-367. <https://doi.org/10.1007/s10342-019-01233-y>
- 701 Richards, A.E., Forrester, D.I., Bauhus, J. and Scherer-Lorenzen, M., 2010. The influence of
702 mixed tree plantations on the nutrition of individual species: a review. *Tree Physiology*, 30(9),
703 pp.1192-1208. <https://doi.org/10.1093/treephys/tpq035>
- 704 Rothe, A. and Binkley, D., 2001. Nutritional interactions in mixed species forests: a
705 synthesis. *Canadian Journal of Forest Research*, 31(11), pp.1855-1870.
706 <https://doi.org/10.1139/x01-120>

- 707 Rubilar, R.A., Allen, H.L., Fox, T.R., Cook, R.L., Albaugh, T.J. and Campoe, O.C., 2018.
708 Advances in silviculture of intensively managed plantations. *Current Forestry Reports*, 4(1),
709 pp.23-34. <https://doi.org/10.1007/s40725-018-0072-9>
- 710 Samuelson, L., Stokes, T., Cooksey, T. and McLemore III, P., 2001. Production efficiency of
711 loblolly pine and sweetgum in response to four years of intensive management. *Tree*
712 *Physiology*, 21(6), pp.369-376. <https://doi.org/10.1093/treephys/21.6.369>
- 713
- 714 Schaalje, G.B., McBride, J.B. and Fellingham, G.W., 2002. Adequacy of approximations to
715 distributions of test statistics in complex mixed linear models. *Journal of Agricultural,*
716 *Biological, and Environmental Statistics*, 7(4), pp.512-524.
717 <https://doi.org/10.1198/108571102726>
- 718 Schmid, B. and Niklaus, P.A., 2017. Biodiversity: complementary canopies. *Nature Ecology &*
719 *Evolution*, 1(4), pp.1-2. <https://doi.org/10.1038/s41559-017-0104>
- 720 Schwinning, S. and Weiner, J., 1998. Mechanisms determining the degree of size asymmetry in
721 competition among plants. *Oecologia*, 113(4), pp.447-455.
722 <https://doi.org/10.1007/s004420050397>
- 723 Shelton, M.G. and Murphy, P.A., 1997. Growth after thinning a 35-year-old natural stand to
724 different loblolly pine and hardwood basal areas. *Southern Journal of Applied Forestry*, 21(4),
725 pp.168-174. <https://doi.org/10.1093/sjaf/21.4.168>
- 726 Steckel, M., Heym, M., Wolff, B., Reventlow, D.O.J. and Pretzsch, H., 2019. Transgressive
727 overyielding in mixed compared with monospecific Scots pine (*Pinus sylvestris* L.) and oak

- 728 (Quercus robur L., Quercus petraea (Matt.) Liebl.) stands—Productivity gains increase with
729 annual water supply. *Forest Ecology and Management*, 439, pp.81-96.
730 <https://doi.org/10.1016/j.foreco.2019.02.038>
- 731 Toïgo, M., Perot, T., Courbaud, B., Castagneyrol, B., Gégout, J.C., Longuetaud, F., Jactel, H.
732 and Vallet, P., 2018. Difference in shade tolerance drives the mixture effect on oak
733 productivity. *Journal of Ecology*, 106(3), pp.1073-1082. [https://doi.org/10.1111/1365-
734 2745.12811](https://doi.org/10.1111/1365-2745.12811)
- 735 United States Department of Agriculture, Soil Conservation Service, Soil Survey of Claiborne
736 Parish, Louisiana, United States Department of Agriculture, Washington, DC, USA 1989.
- 737 Vallet, P. and Perot, T., 2016. Tree diversity effect on dominant height in temperate
738 forest. *Forest Ecology and Management*, 381, pp.106-114.
739 <https://doi.org/10.1016/j.foreco.2016.09.024>
- 740 Weiner, J., 1990. Asymmetric competition in plant populations. *Trends in Ecology &
741 Evolution*, 5(11), pp.360-364. [https://doi.org/10.1016/0169-5347\(90\)90095-u](https://doi.org/10.1016/0169-5347(90)90095-u)
- 742 Wenger, K.F., 1952. Effect of moisture supply and soil texture on the growth of sweetgum and
743 pine seedlings. *Journal of Forestry*, 50(11), pp.862-864.
- 744 Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C. and Reich, P.B., 2017. Spatial
745 complementarity in tree crowns explains overyielding in species mixtures. *Nature Ecology &
746 Evolution*, 1(4), pp.1-7. <https://doi.org/10.1038/s41559-016-0063>

Willis, J.L., Gordon, J.S., Tanger, S., Blazier, M.A., Self, A.B. and Brodbeck, A., 2019. Managing mixed stands: Reassessing a forgotten stand type in the southeastern United States. *Forests*, 10(9), p.751. <https://doi.org/10.3390/f10090751>

Woodall, C.W., Miles, P.D. and Vissage, J.S., 2005. Determining maximum stand density index in mixed species stands for strategic-scale stocking assessments. *Forest Ecology and Management*, 216(1-3), pp.367-377. <https://doi.org/10.1016/j.foreco.2005.05.050>

Wright, A., Schnitzer, S.A. and Reich, P.B., 2014. Living close to your neighbors: the importance of both competition and facilitation in plant communities. *Ecology*, 95(8), pp.2213-2223. <https://doi.org/10.1890/13-1855.1>

Zutter, B.R., Glover, G.R., Mitchell, R.J. and Gjerstad, D.H., 1997. Response of loblolly pine and sweetgum to intra-and inter-specific competition and influence of soil organic matter. *Canadian Journal of Forest Research*, 27(12), pp.2079-2087. <https://doi.org/10.1139/x97-179>

Figure 1 – The Study was conducted at the Louisiana State University Agricultural Center Hill Farm Research Station near Homer, Louisiana, United States (32.749025 N, -93.0411111 W). The location of site represented in the map originated from an ESRI shapefile and is in the Geographic Coordinate System, WGS 1984 projection.

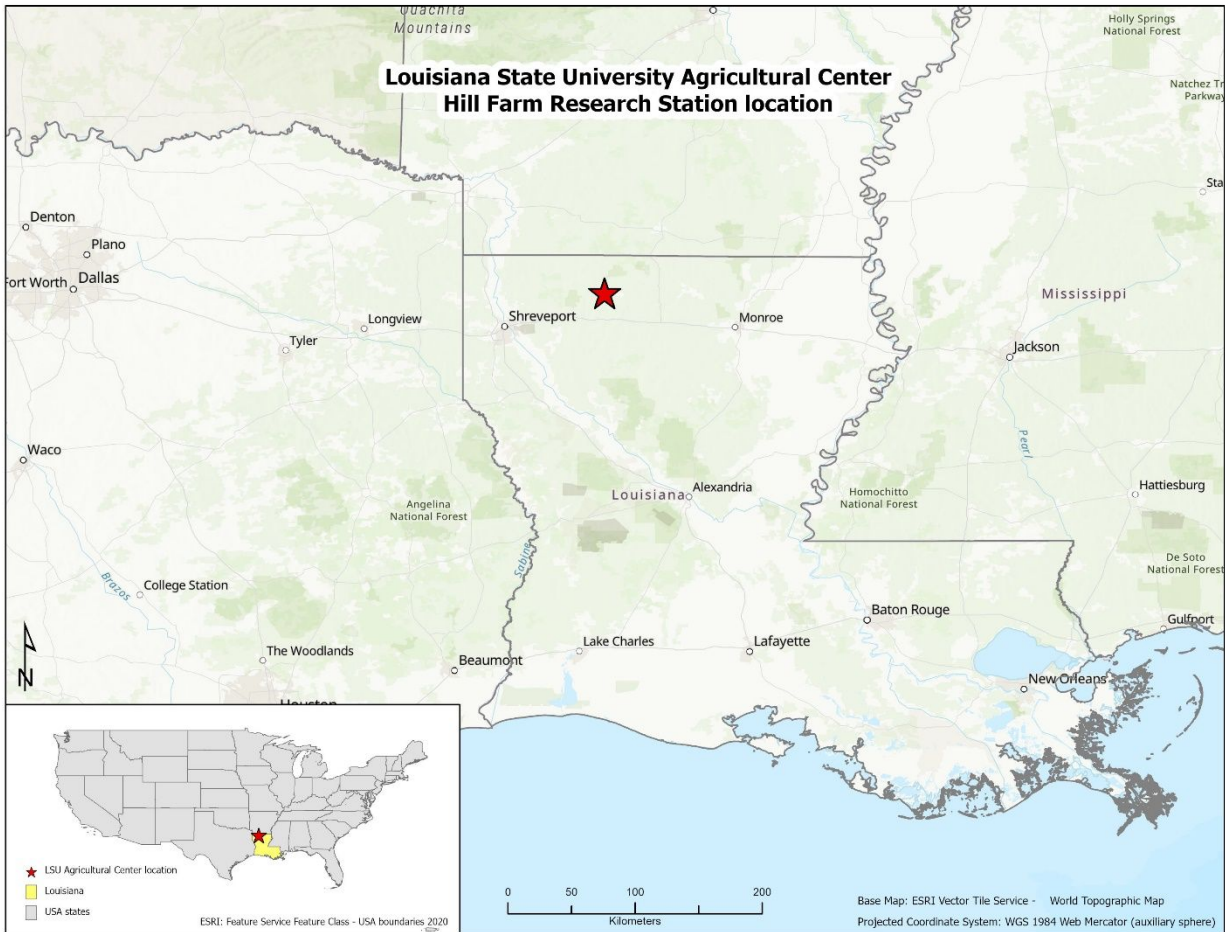


Figure 2 – An example of a sweetgum-loblolly pine medium-density mixture 20 years after planting. For reference, the height pole leaning against the tree in the foreground was 1.5 m in length.



Figure 3 – The estimated effect of mixture density over time on sweetgum and loblolly pine periodic annual diameter growth ± 1 SE from 2005-2020. Sweetgum was planted in 1997, while loblolly pine was planted in 1998. Data points represent the difference in PAI 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).

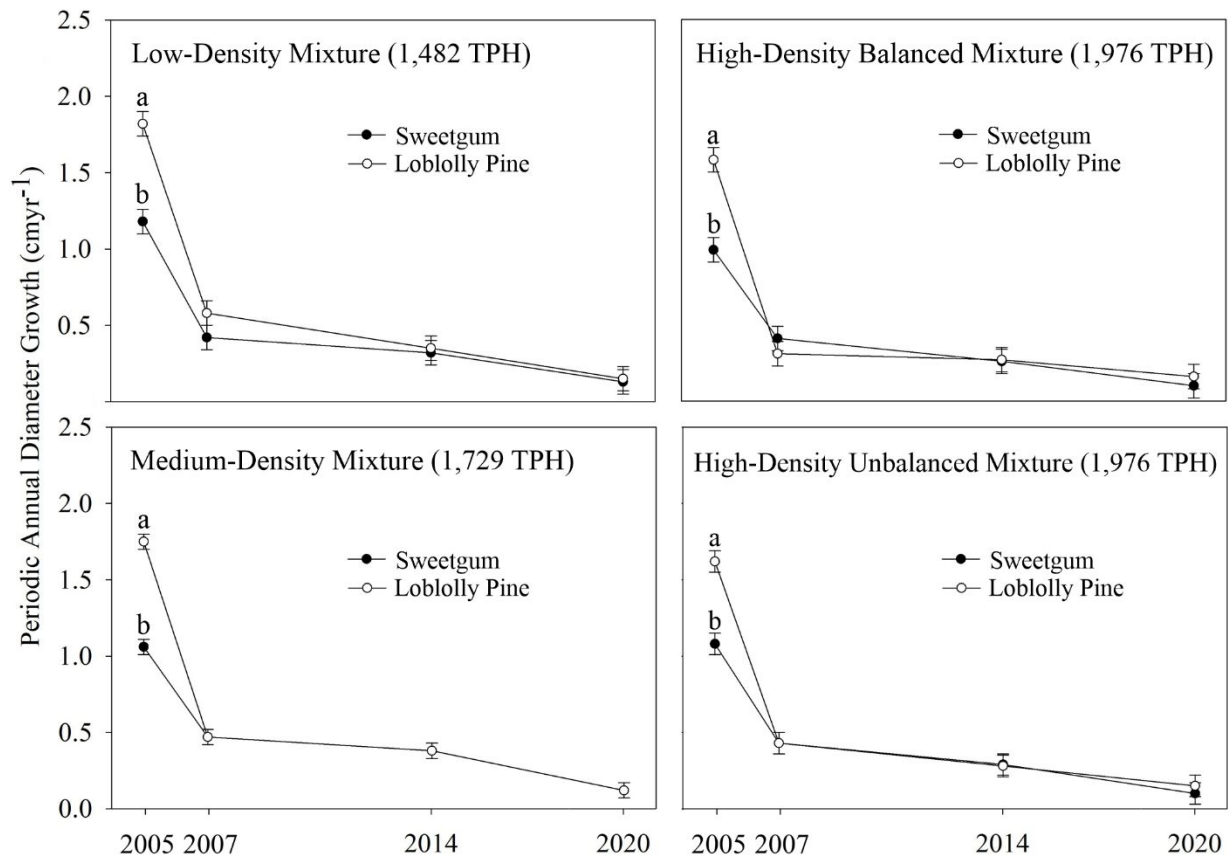


Figure 4 – The estimated effect of mixture density over time on sweetgum and loblolly pine mean survival $\pm$ 1 SE from 2005-2020. Sweetgum was planted in 1997, while loblolly pine was planted in 1998. Species with different letters at each measurement interval were statistically different at $\alpha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

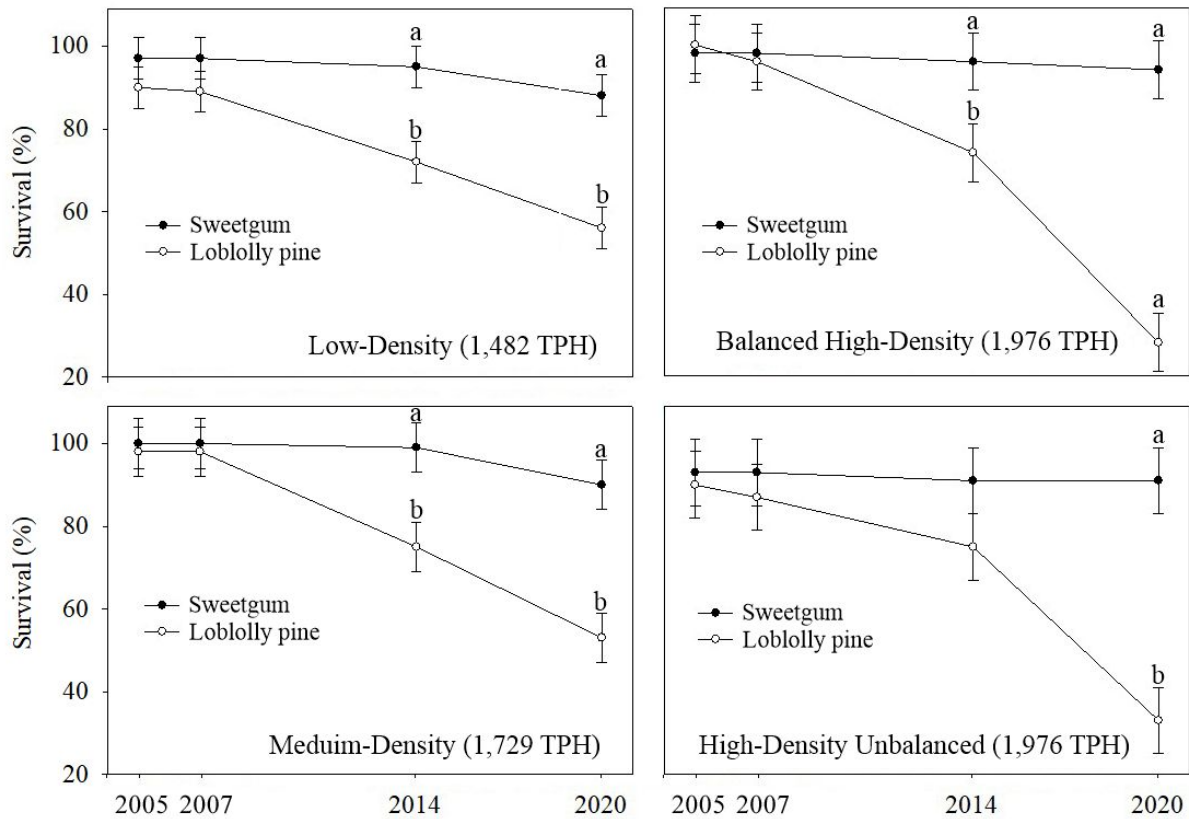


Figure 5 - The estimated effect of mixture density over time on cherrybark oak and loblolly pine periodic annual diameter growth ± 1 SE from 2005-2020. Cherrybark oak was planted in 1997, while loblolly pine was planted in 1998. Data points represent the difference in PAI between the year indicated on 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).

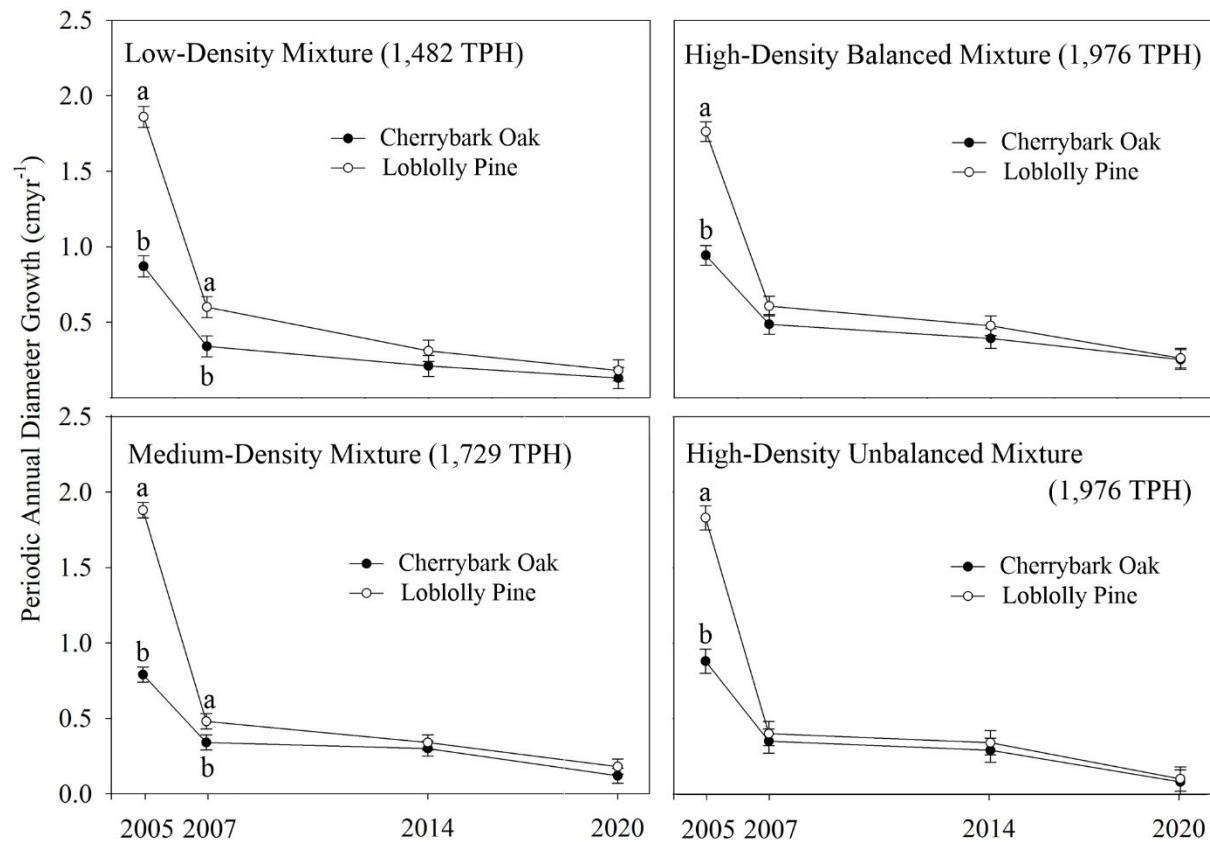


Figure 6 – The estimated effect of mixture density over time on sweetgum and loblolly pine periodic annual basal area growth ± 1 SE from 2005-2020. Sweetgum was planted in 1997, while loblolly pine was planted in 1998. Data points represent the difference in PAI between the year indicated on the x-axis 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).

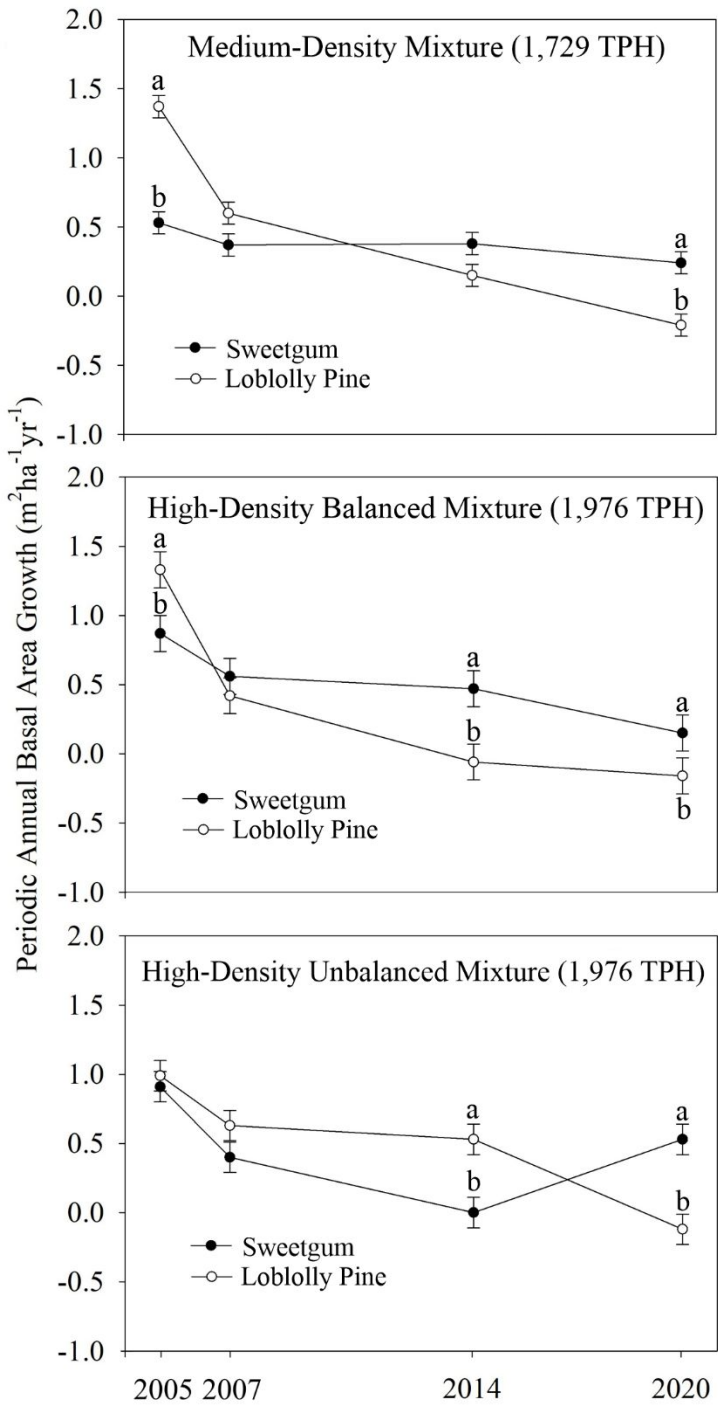


Figure 7 – The estimated effect of mixture density over time on cherrybark oak and loblolly pine periodic annual basal area growth ± 1 SE from 2005-2020. Cherrybark oak was planted in 1997, while loblolly pine was planted in 1998. Data points represent the difference in PAI between the year indicated 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).

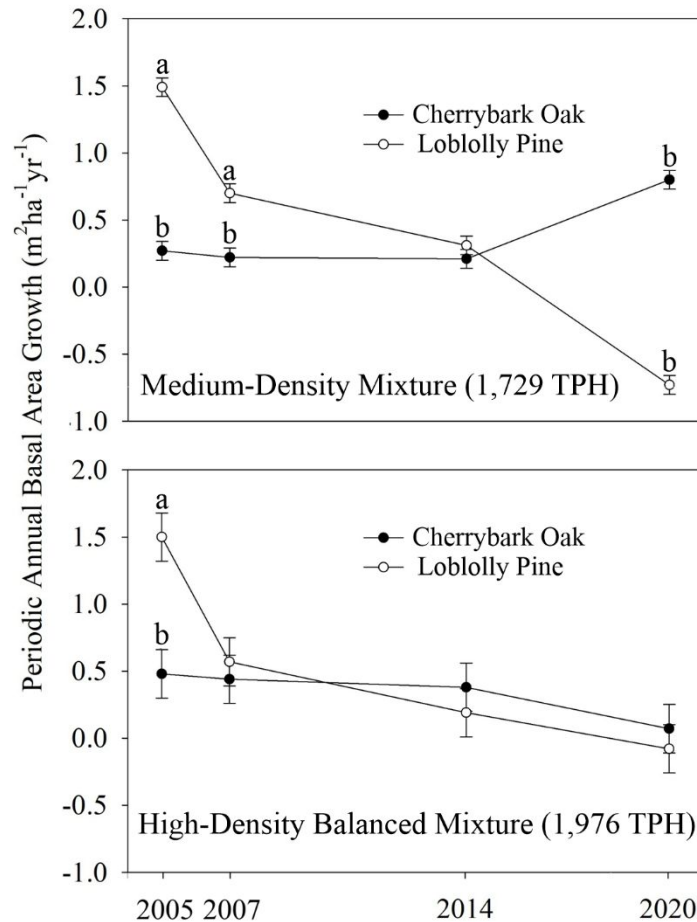


Figure 8 – Cumulative basal area and volume growth of in low-density loblolly pine monocultures, sweetgum:loblolly pine mixtures (SG Mixture), and cherrybark oak:loblolly pine mixtures (CO Mixture) since planting (22-23 years). Mixture values represent the average productivity of both species. Bars with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

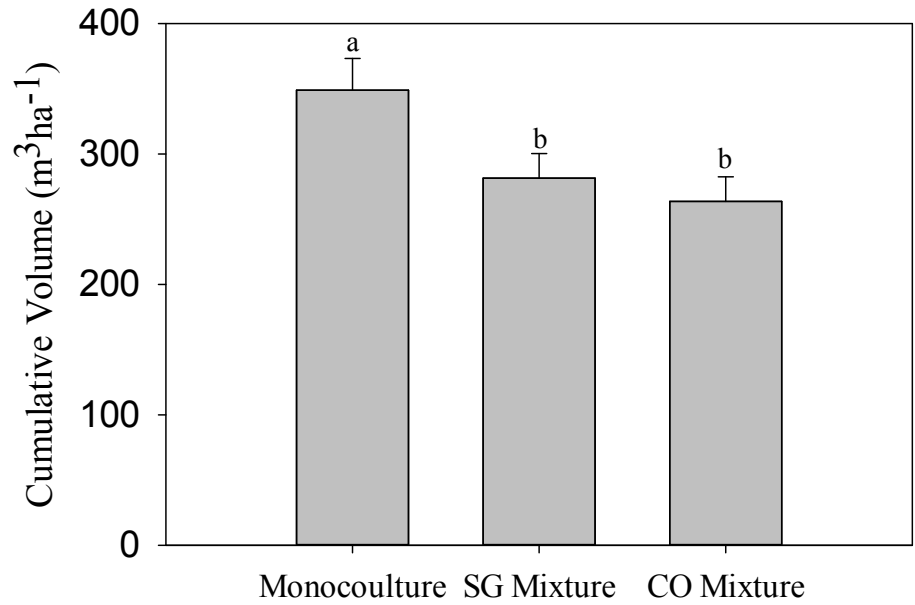
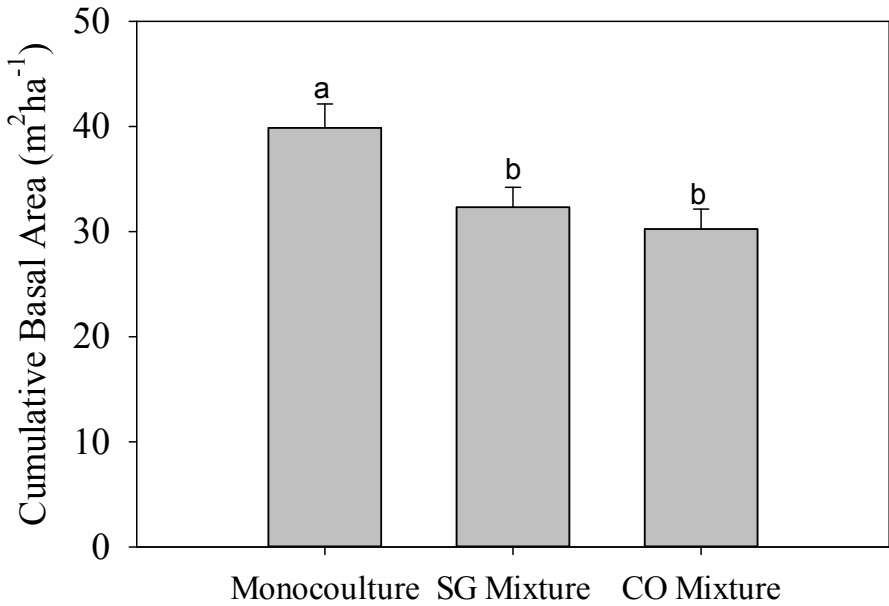


Table 1 – The number of monoculture and mixture plots (experimental unit) at each density level.

Density	Stand Type	Species	Replicates	Trees per Plot
1,482	Monoculture	Loblolly pine	3	113
1,482	Mixture	Loblolly pine + sweetgum	6	113
1,482	Mixture	Loblolly pine + cherrybark oak	6	113
1,729	Mixture	Loblolly pine + sweetgum	5	113
1,729	Mixture	Loblolly pine + cherrybark oak	6	113
Balanced 1,976	Mixture	Loblolly pine + sweetgum	3	113
Balanced 1,976	Mixture	Loblolly pine + cherrybark oak	3	113
Unbalanced 1,976	Mixture	Loblolly pine + sweetgum	3	113
Unbalanced 1,976	Mixture	Loblolly pine + cherrybark oak	3	113

Table 2 – The estimated effects of species composition and planting density on cumulative mean survival, diameter, height, basal area, and volume growth ($\pm$ 1 standard error) since planting (22-23 years). For each row, species’ means with different letters were statistically different at $\alpha = 0.05$ (student’s t post-hoc test).

Species	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
Species	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
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

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Table 3 – The cumulative survival, diameter, height, basal area, and volume growth (± 1 standard error) of mixture types since planting (23 years). For each row, mixture type means with different letters were statistically different at $\alpha = 0.05$ (student’s t post-hoc test).

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 (m ² ha ⁻¹)	32.32 (1.38)a	30.25 (1.38)a
Volume (m ³ 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 (m ² ha ⁻¹)	32.78 (0.81)a	32.38 (0.74)a
Volume (m ³ 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 (m ² ha ⁻¹)	32.43 (3.85)a	32.14 (3.85)a
Volume (m ³ 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 (m ² ha ⁻¹)	33.66 (4.08)a	29.57 (4.08)a
Volume (m ³ ha ⁻¹)	322.43 (35.20)a	255.12 (35.20)a

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). 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).

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

Appendix 1 – Results of linear mixed models examining the main effects of species, time (2005,2007,2014,2020), 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.

Low-Density Sweetgum:Loblolly Pine Mixtures (1,482 TPH)					
Metric	Factor	DFN	DFD	F-Statistic	P-Value
Survival	Species	1	48.00	23.28	<0.0001
	Time	3	48.00	7.42	0.0005
	Species x 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 x 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 x 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 x Time	3	40.00	0.56	0.6439
Medium-Density Sweetgum:Loblolly Pine Mixtures (1,729 TPH)					
	Species	3	29.71	14.80	<0.0001

Survival	Time	1	29.71	24.82	<0.0001
	Species x 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 x 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 x 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 x Time	3	32.00	20.77	<0.0001

**Balanced High-Density Sweetgum Loblolly Pine
Mixtures (1,976 TPH)**

Survival	Species	1	14.00	21.96	0.0002
	Time	3	14.00	13.97	0.0004
	Species x 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 x 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 x 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 x Time	3	16.00	5.28	0.0101

**Unbalanced High-Density Sweetgum:Loblolly Pine
Mixtures (1,976 TPH)**

Survival	Species	1	14.00	17.04	0.0010
	Time	3	14.00	7.62	0.0029
	Species x Time	3	14.00	6.67	0.0050
Mean Annual Diameter Growth	Species	1	14.00	11.80	<0.0001
	Time	3	14.00	164.30	<0.0001
	Species x 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 x 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 x Time	3	15.00	9.78	0.0008

*DFN - Degrees of freedom numerator, DFD – Degrees of freedom denominator

Appendix 2 – Results of linear mixed models examining the main effects of species, time (2005, 2007, 2014, 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.

Low-Density Cherrybark Oak:Loblolly Pine Mixtures (1,482 TPH)					
Metric	Factor	DFN	DFD	F-Statistic	P-Value
Survival	Species	1	40.00	4.26	0.0658
	Time	3	40.00	7.67	0.0004
	Species x 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 x 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 x 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 x Time	3	40.00	1.30	0.2891
Medium-Density Cherrybark Oak:Loblolly Pine Mixtures (1,729 TPH)					
Survival	Species	1	40.00	0.05	0.8217
	Time	3	40.00	34.58	<0.0001

	Species x 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 x 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 x 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 x Time	3	40.00	131.01	<0.0001
Balanced High-Density Cherrybark Oak: Loblolly Pine Mixtures (1,976 TPH)					
Survival	Species	1	14.00	1.57	0.2301
	Time	3	14.00	2.90	0.0719
	Species x 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 x 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 x Time	3	16.00	0.22	0.8794
	Species	1	16.00	2.61	0.1259

Mean Annual Basal Area Growth	Time	3	16.00	11.54	0.0003
	Species x Time	3	16.00	5.15	0.0110

**Unbalanced High-Density Cherrybark
Oak:Loblolly Pine Mixtures (1,976 TPH)**

	Species	1	14.00	5.06	0.0388
Survival	Time	3	14.00	6.82	0.0036
	Species x Time	3	14.00	1.92	0.1679
	Species	1	13.09	44.48	<0.0001
Mean Annual Diameter Growth	Time	3	13.08	89.75	<0.0001
	Species x Time	3	13.08	16.64	<0.0001
	Species	1	13.28	2.27	0.1556
Mean Annual Height Growth	Time	3	13.26	38.21	<0.0001
	Species x Time	3	13.26	2.21	0.1351
	Species	1	15.08	1.02	0.3286
Mean Annual Basal Area Growth	Time	3	15.09	6.53	0.0048
	Species x Time	3	15.09	3.05	0.6100

*DFN - Degrees of freedom numerator, DFD – Degrees of freedom denominator

Appendix 3 – 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.

Low-Density Mixtures (1,482 TPH)	DFN	DFD	F-Statistic	P-Value
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 (1,729 TPH)	DFN	DFD	F-Statistic	P-Value
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 (1,976 TPH)	DFN	DFD	F-Statistic	P-Value
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 (1,976 TPH)	DFN	DFD	F-Statistic	P-Value
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

*Survival and cumulate growth accounts for the sum of both species in mixture

*DFN - Degrees of freedom numerator, DFD – Degrees of freedom denominator

Appendix 4 – Results of linear mixed models examining the main effects of stand type, time (2005, 2007, 2014, 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 1,482 trees per hectare.

Monoculture and Low-Density Mixtures (1,482 TPH)					
Metric	Factor	DFN	DFD	F-Statistic	P-Value
Survival	Stand Type	2	46	2.21	0.1213
	Time	3	46	149.59	<0.0001
	Stand Type x 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 x 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 x Time	6	50.04	0.32	0.9224

*DFN - Degrees of freedom numerator, DFD – Degrees of freedom denominator