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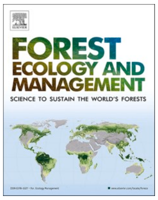

Effects of hurricane canopy gaps on longleaf pine and upland oak sapling growth

Cody A. Pope [a,b], Jeffery B. Cannon [b,*], Seth W. Bigelow [c], Ajay Sharma [a]

[a] West Florida Research and Education Center, University of Florida, Milton, FL 32583, USA
[b] The Jones Center at Ichauway, Newton, GA 39870, USA
[c] Tall Timbers Research Station and Land Conservancy, 13093 Henry Beadel Rd., Tallahassee, FL 32312, USA

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ABSTRACT

Longleaf pine forests and woodlands are an ecologically important ecosystem that once dominated much of the southeastern U.S. Frequent fire is well-known to be a driver of forest dynamics in these systems, but far less is known about how wind disturbance may reorganize plant communities. To gain a better understanding of how hurricane impacts may alter dynamics in a second-growth longleaf pine woodland, we investigated growth response of saplings from three competing upland species (*Pinus palustris, Quercus falcata, Q. margaretta*) following Hurricane Michael (2018) in southwest Georgia, United States. We used maximum likelihood to model height and radial growth of saplings as species-specific Michaelis-Menten functions of light availability and examined the effect of sapling size, soil water holding capacity, and annual precipitation using a model comparison approach. The best model for both height and radial growth included species-specific growth rates, a power function for sapling size, and an effect of 2-year lagged precipitation. Overall, we found that height growth rate increased with irradiance for all species, but asymptotic height growth rate for all species was approached at low irradiance. Rates of radial growth also increased with irradiance and were more strongly differentiated among species. Radial growth in longleaf pine and southern red oak responded most strongly to increasing irradiance. Our findings suggest that increases in light availability from hurricanes has direct effects on altering growth dynamics of saplings. Further, because stem radius is a strong predictor of survival from surface fires, hurricane damage may also have an indirect effect on sapling dynamics, by altering survival in future fires. Our results suggest that hurricanes can reinforce the dominance of longleaf pine and potentially play a role in stabilizing community structure. Understanding the effects of common disturbances like wind and fire—together and individually—can reveal important mechanisms that shape the structure and function of fire-prone ecosystems.

1. Introduction

Longleaf pine (*Pinus palustris* Mill.) woodlands frequently experience disturbance from natural events and management activities including windstorms, insect outbreaks, harvest, and prescribed burning (Ojha et al., 2020). Although the role of fire in longleaf pine woodlands has long been studied, these systems are also subjected to periodic wind events such as hurricanes (Gilliam et al., 2006; Zampieri et al., 2020). Return intervals for major hurricane events average ~ 58 years across the U.S. Gulf Coast (Keim et al., 2007), and many climate models predict that the number of major hurricanes is likely to increase in the future (Bender et al., 2010; Pielke et al., 2005). When less intense hurricanes are included, the hurricane return interval averages ~ 13 years (Keim et al., 2007). Hurricane disturbance may play a role in shaping the high structural and biological complexity of longleaf pine ecosystems (Gilliam et al., 2006; Platt and Rathbun, 1993).

Several authors have presented conceptual models to explain how open-structure and pine-dominance is maintained in longleaf pine systems through interactions among hurricane damage and prescribed fire (Gilliam et al., 2006; Myers and Van Lear, 1998; O'Brien et al., 2008). Gilliam et al. (2006) posit that hurricanes increase longleaf pine seedling establishment and recruitment which eventually produce fuel that perpetuates frequent fire and open-structure. By contrast, O'Brien et al. (2008) posit that large hurricane-caused gaps reduce fuel input, reduce

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* Corresponding author.
E-mail address: jbcannon.pubs@gmail.com (J.B. Cannon).

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fire frequency, and allow fire-sensitive vegetation to outcompete pines. Both conceptual models emphasize the role of hurricanes in shaping patterns of survival and competition of fire-sensitive seedlings from fire. Fire-susceptible individuals are conceptualized as being suppressed by a “fire trap” (*sensu* Bond and Midgley, 2000) where recurring fires repeatedly prevent recruitment of saplings by top-killing them before they are large enough to withstand fire. Canopy opening events can differentially increase growth rates among co-occurring species and alter the rate at which they reach fire-resistant sizes (Cannon et al., 2019). Both models consider the post-hurricane dynamics of pines and oaks among fire-sensitive stages (Gilliam et al., 2006; O’Brien et al., 2008), but neither considers dynamics of established saplings of longleaf pines and associated hardwood species that are large enough to escape fire. Given the increasing frequency of hurricanes, it is important to understand how species-specific responses of saplings to the particular combination of altered resource factors after hurricanes may influence successional trajectory and reorganize the sapling community (Peterson and Pickett, 1995).

Longleaf pine woodlands contain many associated hardwood species such as oaks (*Quercus* spp.) which contribute to the high biodiversity and complex functioning of longleaf pine ecosystems (Cavender-Bares et al., 2004). Oaks are considered foundation tree species that play a role in supporting high levels of plant and animal diversity (Hanberry and Nowacki, 2016; Hiers et al., 2014). Some oaks known as pyrophytic oaks have litter traits that facilitate fire (Fonda, 2001; Kane et al., 2008). Pyrophytic oaks commonly associated with longleaf pine include sand post oak (*Quercus margaretta* (Ashe) Small); turkey oak, (*Q. laevis* Walter); and southern red oak (*Quercus falcata* Michx.). Historical accounts support the presence of old-growth pyrophytic oaks in frequently burned sites dating as far back as 300 years indicating they may play an important role in longleaf pine ecosystems (Hiers et al., 2014). The presence of old-growth pyrophytic oaks demonstrates their ability to resist damage and top-kill from fire at large sizes. Unlike mesophytic oaks which can disrupt fire regimes through production of low flammability litter, pyrophytic oaks present in low productivity sites on xeric sandhills may not produce sufficient leaf area to reduce understory light availability (Hiers et al., 2014) and may facilitate longleaf pine establishment in xeric sites (Loudermilk et al., 2016).

Although longleaf pine has high wind resistance compared to co-occurring species (Hook et al., 1991; Johnsen et al., 2009; Rutledge et al., 2021; Touliatos and Roth, 1971), damage during hurricanes can be sufficient to directly and indirectly alter forest community dynamics. Studies of post-hurricane dynamics are important because surviving trees and advanced regeneration can control many aspects of post-disturbance forest dynamics (Cooper-Ellis et al., 1999; Plotkin et al., 2013). Platt and Rathbun (1993) demonstrated that hurricanes are important for recruitment in longleaf-pine dominated stands. Canopy gap creation by removal of one or more mature trees may be necessary for longleaf pine regeneration and canopy recruitment in managed woodlands with high basal area (e.g., >14 m^2/ha; Gagnon et al., 2003; McGuire et al., 2001). Liu et al. (1997) found that substantial encroachment of hardwood species, especially some mesic oak species, may occur after wind damage in mixed pine-hardwood stands. Growth rates of longleaf pine saplings often increase after canopy removal (Curtin et al., 2020; Pederson et al., 2008; Platt and Rathbun, 1993) but the same is true for competing oak saplings (Liu et al., 1997; Pecot et al., 2007). Both groups are expected to increase growth in response to increased light availability but other factors such as sapling size, precipitation, and soil texture may influence growth rate and competitive relationships among longleaf pine and associated species. However, very little information is available on how these factors may change forest dynamics following hurricanes.

Longleaf pine and associated upland oak saplings differ in their growth and life history characteristics in ways that may represent different strategies for usurping resources released after hurricanes (Batista and Platt, 2003). Growth of understory hardwoods is primarily influenced by belowground competition with mature longleaf pine trees, whereas longleaf pine seedlings are more strongly influenced by decrease in light due to shading by mature trees, and by belowground competition with herbaceous plants (Pecot et al., 2007). Following high levels of canopy removal, oak saplings respond by increasing lateral branch extension at the expense of height growth, while maintaining relatively constant radial growth (Allen and Marquis, 1970). Southern red oak, a canopy tree, is taller than the sub-canopy sand post oak at maturity and may exhibit different growth strategies following a canopy opening disturbance. Although we expect both oaks and longleaf pine to increase growth in response to canopy disturbance, there may be a canopy openness threshold at which height growth advantage switches from the more shade-tolerant oaks to longleaf pine (*i.e.*, crossover point irradiance *sensu* Sack and Grubb, 2001). In addition, southeastern oaks occupy distinct niches partly defined by gradients of soil moisture (Cavender-Bares et al., 2004; Jacqmain et al., 1998; Monk, 1968). However, the relationship of growth to soil moisture gradients in these species has received little attention.

Further research into species responses following wind disturbance and canopy recruitment initiation can inform post-storm dynamics in fire- and wind-prone longleaf pine systems. Our objectives were to (1) determine whether hurricane damage alters the growth responses of saplings of longleaf pines and two associated upland oak species; and (2) determine the extent to which effects on growth response vary based on factors such as tree size, soil texture, and precipitation. We hypothesize that height growth of longleaf pine and two associated upland oak species will increase with gap openness, but that longleaf pine height growth may benefit more from high light levels. On sites that experience similar canopy removal, saplings growing in soil with greater water holding capacity (loamy sand) may exhibit a stronger growth response compared to saplings on drier sites (sandy loam), and we expect that oak species may have a greater growth response to canopy opening events on drier sites where competition for resources with overstory trees may be greatest.

2. Methods

2.1. Study site

We conducted this study at The Jones Center at Ichauway (Fig. 1), an 11,300-ha ecological research site in southwest Georgia, USA. The site is within the Lower North American Coastal Plain with a humid subtropical climate (McNab and Avers, 1994). Elevation ranges between 27 and 61 m above sea level, with gently rolling hills that are typical of the karst topography of the Dougherty Plain physiographic region, where 10 to 20 m of weathered residuum overlay Eocene to Oligocene age limestone. The rapidly draining limestone bedrock results in a landscape with few streams although wet depressions are common (Barrie et al., 2022). Ultisols characterized by coarse-textured sandy surface horizons over fine-textured clayey sub-horizons predominate in uplands at the study site, although there are some deep sand soils (Goebel et al., 2001). The most common soil subgroup is Kandiudult.

Forest types are primarily second-growth longleaf pine woodlands (~ 12–17 m^2/ha), and a minor component of loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.) dominated woodlands are also present (~ 1700 ha). In the uplands, several species of oaks (*Quercus* spp.) co-occur which may be classified along a gradient of preference for soil moisture (Cavender-Bares et al., 2004). These species include some that are common on xeric soils: sand post oak (*Q. margaretta* (Ashe) Small), and turkey oak (*Q. laevis* Walter); some that are most common on soils of intermediate water-holding capacity: post oak (*Q. stellata* Wangenh.), and southern red oak (*Q. falcata* Michx.); and those most common on more mesic soils: laurel oak (*Q. laurifolia* Michx.), water oak (*Q. nigra* L.), and coast live oak (*Q. virginiana* L.). Most upland forested stands are managed with prescribed fire on a 2-year burn rotation.

Hurricane Michael made landfall on October 10, 2018 near Panama

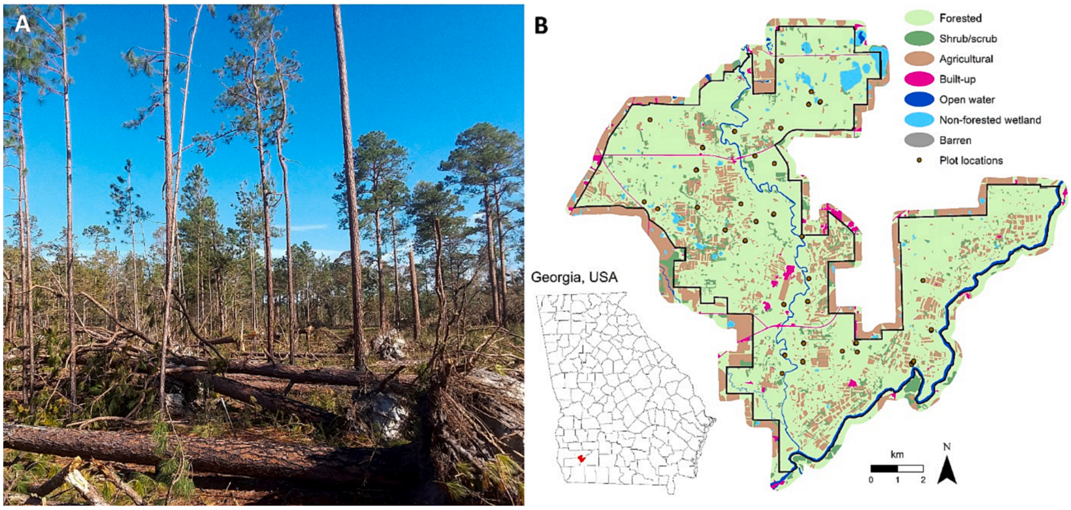

Fig. 1. (A) Photograph of heterogeneous overstory disturbance from Hurricane Michael in longleaf pine-dominated stands and (B) plot locations in the study area at the Jones Center at Ichauway, an 11,300-ha research center in southwestern Georgia USA.

City, Florida, USA (30.0°, −85.5°) as a Category 5 hurricane. Maximum sustained wind estimates of 257 km h^{-1} resulted in roughly 88 % tree mortality in some longleaf pine stands near landfall (Zampieri et al., 2020). Impacts were sustained approximately 150 km inland but were less severe. The eyewall came within 10 km of the western boundary of the study site causing mortality of ~ 16 % of trees > 10 cm dbh (diameter at breast height) (Rutledge et al., 2021). Among trees > 10 cm dbh, xeric oaks sustained higher damage than longleaf pine, and this was especially true among individuals > 30 cm dbh and on the drier soils present at the site (Rutledge et al., 2021).

2.2. Field measurements

In summer 2020, approximately 1.5 years following Hurricane Michael, we surveyed height and radial growth rates of three xeric species common in the sapling and understory tree layers including *Pinus palustris, Quercus falcata, Q. margaretta*. To select trees for the study, we identified 34 sampling areas that were ~ 0.2 ha, sustained some canopy loss as indicated by a map of hurricane damage (Fig. 2), contained saplings or understory trees ranging between 3 and 12 m in height (hereafter, saplings), and were > 15 m from a road (Fig. 1B). Though sampling areas were generally focused in areas that sustained damage, because hurricane damage was patchy throughout the site (Whelan et al., 2023), our sample includes saplings that had damage directly overhead as indicated by an increase in canopy openness and saplings with no increase in canopy openness, in roughly equal numbers. We selected saplings for study within the 34 sampling plots in the summer and autumn of 2020; ~30 % of plots contained all three species. The sample included 282 saplings comprising similar numbers of longleaf pine ($n = 99$), southern red oak ($n = 92$), and sand post oak ($n = 91$). Trees at each plot were within 50 m of one another, and we sampled ≤ 8 individuals per species at each plot. We determined sapling locations using a Nomad GPS with a Crescent A100 backpack antennae with a horizontal accuracy < 0.6 m (Hemisphere GPS, Calgary, Canada). We measured sapling diameter at breast height (dbh) with a diameter tape. We measured sapling height with a telescoping pole and a spotting scope (Celestron Regal M2 80ED); the spotting scope was used to see bud-break scars on the oaks. To reconstruct height growth in years prior to sampling, we measured heights at bud scars for the current year (2020) and two previous years to calculate the elongation of the terminal shoot (Bigelow and Canham, 2002). To reconstruct growth rate in years prior to the hurricane (2018–2020), we extracted a core from each sapling at 15 cm above root collar using an increment borer. We transported cores to the lab in paper straws, dried at 70 °C for 24 h and mounted on a board. We sanded cores with progressively finer grit then measured ring widths to 0.001 mm on a sliding stage (UniSlide, Velmex, Inc. Bloomfield New York, USA) with a microscope and measurement software (Voortech Consulting, Holderness NH, USA).

We combined soil observations at each plot with pedotransfer functions (Schapp et al., 2001) to develop a proxy for water availability. We inserted a 5 cm diameter bucket auger to 1 m in two locations at each sampling plot and examined the soil at 5 cm depth increments to determine the depth of transition from coarse- to fine-textured soil if present. Soil series was determined from United States Department of Agriculture Web Soil Survey, and soil texture of upper (A) horizons and lower kandic horizons was determined from soil series descriptions. As a proxy for soil water availability, we estimated soil water holding capacity at −15 cm hydrostatic pressure (θ_{-15}) for the upper 1 m of soil using ROSETTA pedotransfer functions (Schapp et al., 2001) applied to each horizon then weighting based on the depth of the coarse-to-fine texture transition.

To estimate canopy cover in sampling locations before and after hurricane disturbance, we used airborne lidar collected each year from 2016 to 2019 by the National Ecological Observation Network Aerial Observation Platform (NEON AOP; Kampe et al., 2010; Whelan et al., 2023). We compared estimates of canopy closure (*sensu* Jennings et al., 1999) collected using a spherical canopy densiometer from 624 circular 0.1 ha forest inventory and monitoring plots between 2016 and 2019 (Holland et al., 2019). At each plot location we calculated the proportion of lidar returns > 4 m in height from the corresponding area and year to generate a canopy closure index (*CCI*). We modeled canopy closure as a logistic function of *CCI* using the following formula:

$$Canopy\ closure = \frac{a}{1 + e^{-b(CCI - c)}}$$

where the parameters a, b, and c were fit using nonlinear least squares regression. After finding strong correlation between measured and estimated canopy closure ($r^2 = 0.609$; Fig. 2A), we used the resulting model to predict canopy closure across the study area using LiDAR collections in 2018 and 2019 (Fig. 2B-D). We converted estimated canopy closure to canopy openness ($o_c = 1 - canopy\ closure$) for growth modeling and to ease interpretation.

2.3. Statistical modeling

We used a maximum likelihood modeling approach to model how o_c, soil texture, and precipitation affected height and radial growth of

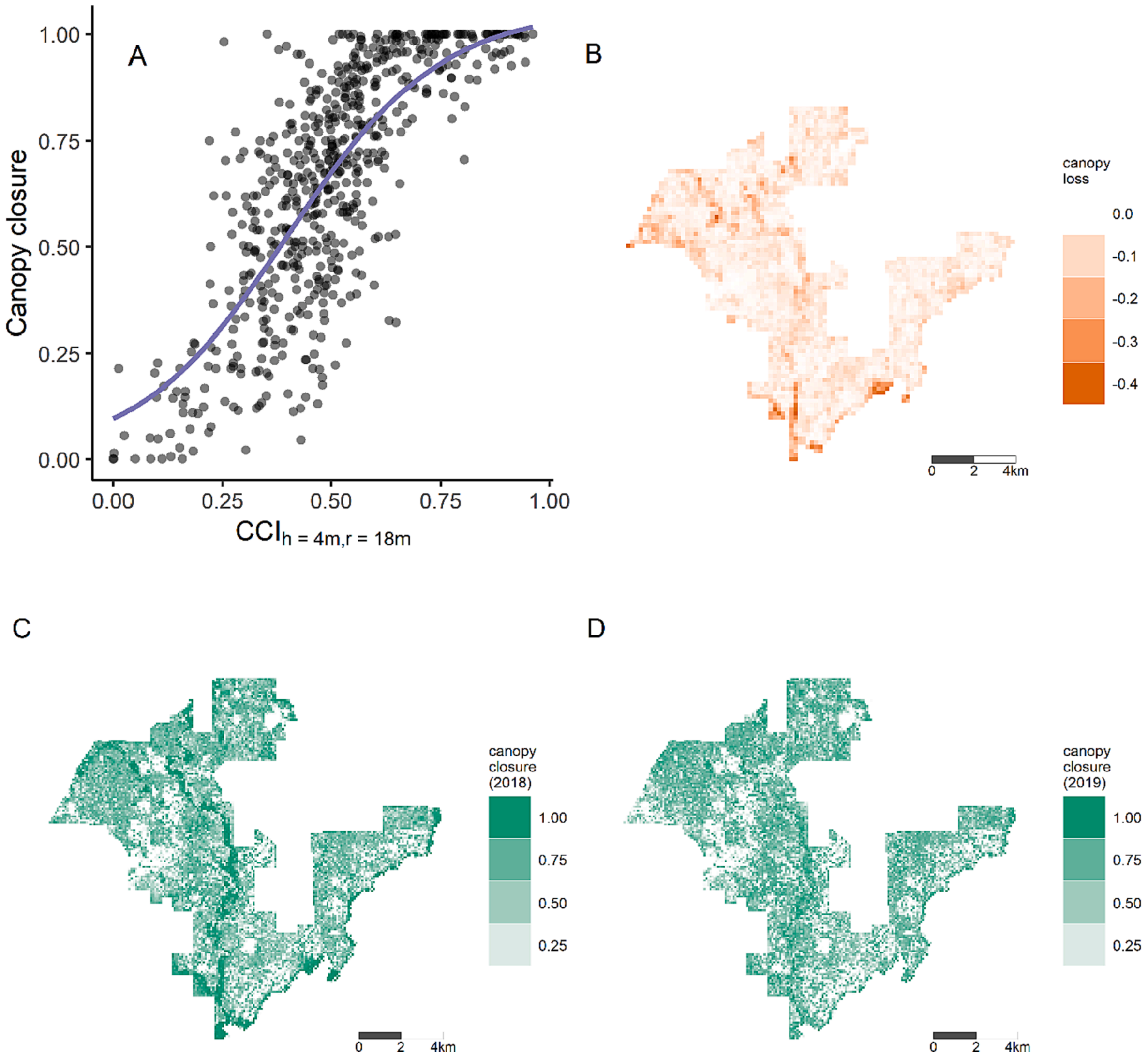

Fig. 2. (A) Relationship between canopy closure (averaged from four orthogonal canopy densiometer readings) and the aerial lidar-derived canopy cover index (CCI) defined as the proportion of lidar returns > 4 m in height in an 18 m radius (0.1 ha). $Canopy\ closure = 1.0576/(1 + e^{-5.750*(CCI-0.400)})$; $r^2 = 0.609$, RMSE = 0.1720. (B) Proportion canopy loss estimated based on the difference between (C) lidar-based estimate of canopy closure in 2018 and (D) lidar-based estimate of canopy closure in 2019.

saplings. Height growth data were available from one year before (2018) and two years after the hurricane (2019, 2020). We obtained radial growth data from tree ring measurements. Height growth is complete by early summer so the full height growth for 2020 was probably reflected in the measurements; radial growth may continue through November (Rother et al., 2018) so our measurements may have missed a small portion of the 2020 annual radial growth increment. Further, o_c data were only available for one year before and one year after the hurricane, *i.e.*, 2018 and 2019. We substituted 2019 o_c for 2020 o_c in our analysis, assuming that o_c changed little in a non-hurricane year.

We modeled height and radial growth as Michaelis-Menten functions of o_c (Bolker, 2008; Michaelis and Menten, 1913; Pacala et al., 1994). We used o_c as an index of irradiance because large size of the saplings ruled out the use of typical light measurements. The Michaelis-Menten function was

$$\Delta ht = \frac{a\ o_c}{\left(\frac{a}{s}\right) + o_c}$$

where Δht is annual height growth (m), a is a parameter for asymptotic height, and s corresponds to growth rate (*i.e.*, slope) at $o_c = 0$. The numerator of the Michaelis-Menten function was multiplied by a power function to assess sensitivity to plant size (MacFarlane and Kobe, 2006). The power function was ht^f, where f was allowed to vary from −0.5 to 0.5. We modeled the dependence of radial growth on radius in the same fashion.

We incorporated soil water holding capacity at 15 cm tension ($\theta_{\text{-}15}$) as a multiplier of the asymptote parameter, based on a normal distribution function $\exp\{-0.5[(\theta_{\text{-}15} - \theta_m)/\ \theta_v]^2\}$. The θ_m parameter corresponds to the soil moisture retention at which growth is greatest, and the θ_v parameter controls the breadth of the normal distribution. To control for variation in precipitation among years, we incorporated a site-level annual precipitation as multiplier of the asymptote parameter based on a normal function with a similar functional form, $\exp\{-0.5[(P - P_m)/ P_v]^2\}$. We scaled precipitation using m units.

To examine the effects of sapling size, soil texture, and precipitation on sapling growth rates, we developed several models for height and radial growth and compared them using Akaike's information criterion (*AIC*; Anderson and Burnham, 2002). We assembled models starting with a single a and s Michaelis-Menten parameters for the three species, then using different a and s parameters for the species, then we introduced the power function of size, and then introduced the normal functions of $\theta_{\text{-}15}$ and P. P was lagged up to two years because the response of trees, particularly height, to precipitation is often delayed (Lanner, 2017). Error was modeled with the Gamma error distribution (Bolker, 2008).We used AIC_c as the model selection criteria to ensure that the most parsimonious model was selected. We compared models using Δ_i, the difference between the AIC_c of the model in question and the best approximating model. AIC differences of < 2 indicate models with similar support; Δ_i of 4–7 indicate considerably less support, and differences > 10 indicate essentially no support from the data (Anderson and Burnham, 2002). We followed a similar process for height and diameter growth. We report adjusted R^2 (proportion of variance explained by the model beyond that explained by the simple mean) as a measure of goodness of fit.

3. Results

Among the saplings included in the study, average diameter at breast height was 5.8 ± 2.24 cm (standard deviation) for longleaf pine, 5.5 ± 2.45 cm for southern red oak and 6.1 ± 2.80 cm for sand post oak (Table 1). Average height was 6.5 ± 2.18 m for longleaf pine, 5.5 ± 1.87 m for southern red oak and 5.7 ± 1.71 m for sand post oak. Total height increased with dbh for all species, but longleaf pine had larger height at a given diameter than sand post oak, especially for larger diameter trees (Fig. 3). Canopy closure measurements from inventory plots were strongly correlated to LiDAR-derived *CCI* (Fig. 2A; $R^2 = 0.609$; RMSE = 0.172).

Overall, we found that sapling height growth rates were highest for longleaf pine, across all levels of canopy removal and at all sizes (Fig. 4A). An increase in height growth in response to decreased canopy closure was found among small saplings (1.5–4.0 m), and little or no height growth response to increased light was found among sand post oak individuals of any size (Fig. 4A). Similarly, we observed no radial growth rate increase with decreased canopy cover among sand post oak; but both longleaf pine and southern red oak showed increased radial growth rate in response to light, especially among large (60 – 160 mm dbh) individuals (Fig. 4B).

The best model for height growth included species-specific growth rates, a power function for size, and species-specific response to 2-year lagged precipitation (Fig. 5A, Table 2, $\Delta_i = 0$, $R^2 = 0.50$). In this model all three species were strongly differentiated in their asymptotic height growth rate consistent with their relative heights at maturity (*a* parameter, Table 2, Table 3). At low-o_c (<0.2), longleaf pine height growth rates quickly increased relative to the oak species as reflected by the *s* parameter although the support interval overlapped with sand post oak. All species had higher height growth at higher annual *P* (lagged by two years) as reflected in the P_m parameter. Longleaf pine had the greatest increase in growth at higher *P* as reflected by the smaller P_v parameter. The oaks did not differ in growth reduction at lower *P* as attested by overlapping parameter support intervals. Model comparisons indicated that θ_{-15} explained no variation in height growth of any species (Table 2, Table 3).

Similar to the height growth model, the best model for radial growth included species-specific growth rates and a power function for size (Fig. 5B, Table 4, $\Delta_i = 0$, $R^2 = 0.17$). Like the height growth model, the best radial growth model also included 2-year lagged precipitation, but the parameters were not species-specific. The second-best model had a $\Delta_i < 2$ and was similar to the best model but included one year lagged precipitation. Radial growth with respect to o_c differed among the tree species; asymptotic radial growth of longleaf pine and southern red oak exceeded that of sand post oak (Table 4, Table 5). Asymptotic radial growth of longleaf pine was 5.7 mm yr^{-1}, of southern red oak was 4.67 mm yr^{-1}, and of sand post oak was 2.13 mm yr^{-1}. In contrast to height growth, longleaf pine radial growth at low-o_c was less than those of the oaks. Radial growth responded positively to higher annual *P,* but the response did not differ among species. Estimated soil water retention θ_{-15} explained no variation in radial growth of any species (Table 4, Table 5).

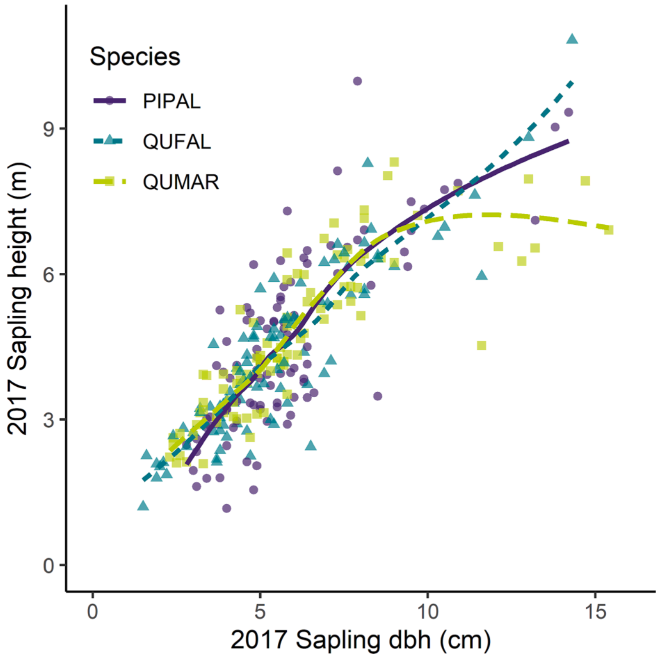

Fig. 3. Relationship between initial height and diameter at breast height (dbh) for 282 saplings included in the study distributed among three species: longleaf pine (PIPAL), southern red oak (QUFAL), and sand post oak (QUMAR). Data shown with loess smoothing function applied to each species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Hurricanes present a profound disturbance to the overstory of coastal forests—one which has the potential to alter the course of succession and reset community dynamics (Ibanez et al., 2020; Spurr, 1956). Nevertheless, our results suggest that hurricanes can reinforce the dominance of longleaf pine when adequate regeneration is available. Our results show that height growth of individual longleaf pine saplings

Table 1

Characteristics of saplings of three species sampled in longleaf pine woodland in southwest Georgia, and environmental factors: basal area of neighboring trees, canopy cover index from aerial LiDAR, soil moisture retention in upper 1 m of soil at −15 cm tension, and annual precipitation lagged by two years.

Year	Longleaf pine Height[†]	 dbh[†]	Southern red oak Height	 dbh	Sand post oak Height	 dbh	BA[‡] (m^2•ha^{-1})	CCI (m^2•m^{-2})	θ (m^3•m^{-3})	P_{-2} (mm)
2020	6.5 (2.2)	5.5 (2.5)	5.5 (1.9)	5.5 (2.5)	5.7 (1.7)	6.1 (2.8)	11.0 (5.8)	~	0.107 (0.041)	1752
2019	5.6 (2.0)	5.4 (2.1)	5.1 (1.8)	5.0 (2.4)	5.3 (1.7)	5.8 (2.8)	~	0.575 (0.157)	~	1030
2018	5.0 (1.9)	5.1 (2.0)	4.7 (1.8)	4.7 (2.4)	5.0 (1.6)	5.6 (2.8)	~	0.550 (0.152)	~	1285

[†] Height unit is m, dbh unit is cm.

[‡] BA is basal area of neighboring trees (identified with prism), CCI is canopy cover index, θ is soil moisture retention (-15 cm), and P_{-2} is precipitation lagged by two years.

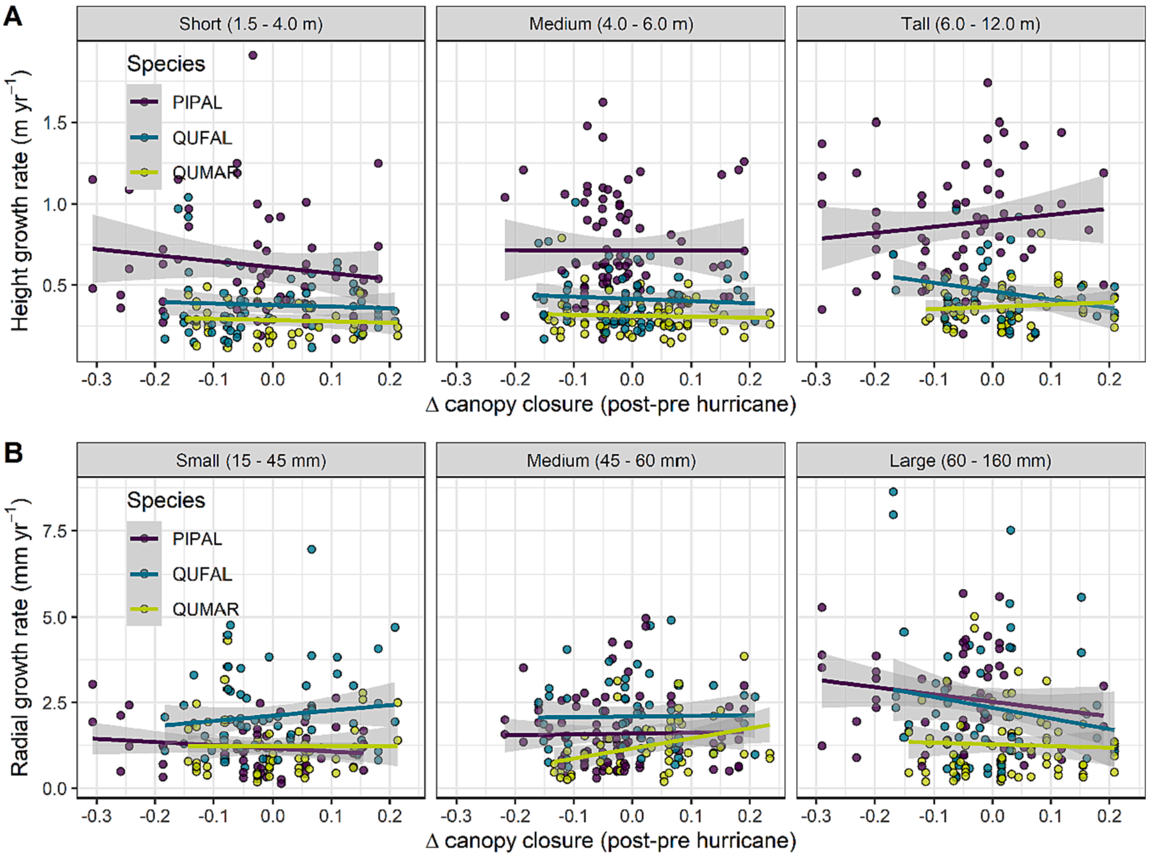

Fig. 4. (A) Height growth rate and (B) radial growth rate of saplings in the first 2- years following hurricane as a function of change in canopy closure for three sapling species. Panels in A separate saplings into three initial height classes of approximately equal sizes, and Panels in B separate saplings into three initial diameter classes of approximately equal sizes. Negative values of Δ canopy closure indicate canopy loss from (2018) Hurricane Michael. PIPAL = *P. palustris*, QUFAL = *Q. falcata*, QUMAR = *Q. margaretta.*

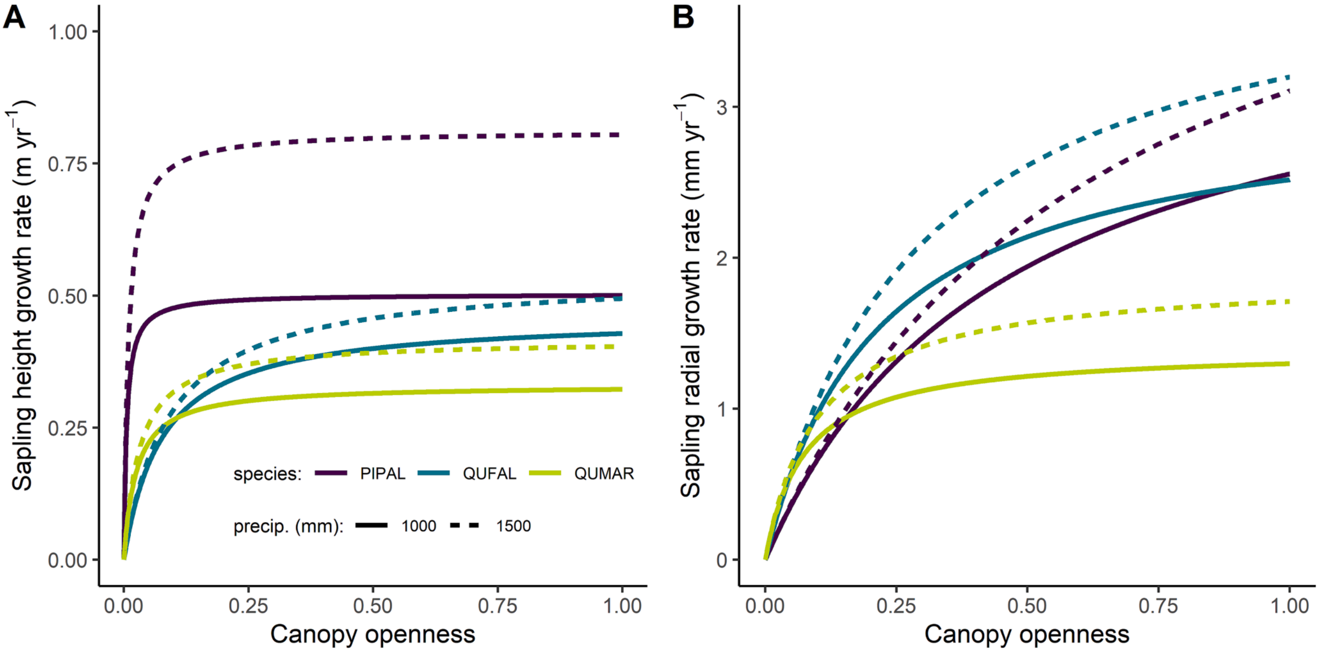

Fig. 5. (A) Modeled height growth rate (m/yr) as a function of canopy openness for three species (longleaf pine, southern red oak, and sand post oak) and two precipitation levels (1000 mm and 1500 mm) with an assumed height of 5 m. See Table 3 for model parameters. (B) Modeled radial growth rate (mm/yr) as a function of canopy openness for three species (longleaf pine, southern red oak, and sand post oak) and two precipitation levels (1000 mm and 1500 mm) with an assumed dbh of 5 cm. See Table 5 for model parameters. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Information criteria for candidate Michaelis-Menten models of height growth of juvenile trees as a function of canopy openness, species (longleaf pine, southern red oak, and sand post oak), height, soil water retention at 15 cm tension, and annual precipitation lagged by 2 years. Soil water and precipitation were incorporated in Normal functions that multiplied the Michaelis Menten asymptote parameter.

Model	K[†]	L	AIC$_c$	Δ_i	R^2
Mean	2	74.96	−145.91	489.67	0.00
Ht, MM	3	111.98	−215.92	419.66	0.08
Ht, MM$_{sp}$	8	263.53	−510.89	124.69	0.39
Ht, MM$_{sp}$, $N_{sp}(\theta_{-15})$[‡]	14	263.77	−499.04	136.54	0.38
Ht, MM$_{sp}$, $N(P_{-2})$[‡]	10	319.32	−618.73	17.21	0.49
Ht, MM$_{sp}$, $N_{sp}(P_{-2})$[‡]	14	332.05	−635.58	0.00	0.50

[†] K is number of parameters estimated for model, L is maximum log likelihood, AIC$_c$ is Akaike's information criterion adjusted for small sample size, $\boldsymbol{\Delta_i}$ is the *AIC* difference of candidate model and minimum AIC, and R^2 is variance explained by the candidate model relative to the mean.

[‡] $N_{sp}(\theta_{-15})$ is a Normal function of water retention at 15 cm of tension where 'sp' subscript indicates that parameters differed for species. $N(P_{-2})$ is a Normal function of annual precipitation with a 2-year time lag.

Table 3
Parameters for best Michaelis-Menten model of height growth of juvenile trees as a function of canopy opennness, species, height, and annual precipitation lagged by 2 years. Parameters are presented as mostly likely values with +/- 2 AICc units support interval (close to 95 % confidence interval).

Parameter[†]	Longleaf pine	Southern red oak	Sand post oak
a	0.662 (0.640–0.680)	0.395 (0.383–0.435)	0.312 (0.297–0.331)
s	63.2 (20.9–100*)	4.21 (3.62–6.97)	9.38 (5.91–26.3)
P_m	1.99 (1.97–2.00*)	1.99 (1.62–2.00*)	1.99 (1.81–2.00*)
P_v	0.885 (0.838–0.920)	1.55 (1.38–3.05)	1.28 (1.16–1.66)

[†] a indicates asymptotic height growth rate (m/yr), s indicates the increase in growth rate when canopy openness (o_c) is near zero, P_m indicates annual precipitation (m) at which growth is maximum, and P_v controls breadth of Normal function of precipitation. Parameters common to the three species are f, 0.225 (0.213–0.252) and *scale*, 0.0684 (0.0614–0.0734).

[*] Upper limit allowed.

Table 4
Information criteria for Michaelis-Menten models of radial growth of juvenile trees as a function of canopy openness, species (longleaf pine, southern red oak, and sand post oak), stem radius, soil water retention at 15 cm tension, and annual precipitation lagged by 0, 1, or 2 years. Soil water and precipitation were incorporated in Normal functions that multiplied the Michaelis Menten asymptote parameter.

Model	K	L	AIC	Δ_i	R^2
Mean	2	−1186.86	2376.37	164.13	0.00
MM$_{sp}$	7	−1153.22	2314.48	102.24	0.07
Rad.[†], MM$_{sp}$	8	−1106.55	2229.28	17.04	0.15
Rad., MM$_{sp}$, $N(\theta_{-15})$	10	−1106.19	2232.82	20.58	0.15
Rad., MM$_{sp}$, $N(P_{-2})$	10	−1095.99	2212.24	0.00	0.17
Rad., MM$_{sp}$, $N(P_{-1})$	10	−1096.42	2213.12	0.88	0.17
Rad., MM$_{sp}$ $N_{sp}(P_{-2})$	14	−1094.59	2217.70	5.46	0.17

[†] Rad. = stem radius at breast height, $N(\theta_{-15})$ is a Normal function of water retention at 15 cm of tension, N(P) is a Normal function of annual precipitation where numeric subscript indicates 0, 1 or 2 y time lag and 'sp' subscript indicates that parameters differed for species.

Table 5
Parameters (2 likelihood unit support intervals in parentheses) for best Michaelis-Menten model of radial growth of juvenile trees as a function of canopy openness, species (longleaf pine, southern red oak, and sand post oak), stem radius, and annual precipitation lagged by 2 years. The exponent for radius (f), precipitation parameters P_m and P_v, and the scale parameter for the Gamma distribution apply to all three species.

Parameter[†]	Longleaf pine	Southern red oak	Sand post oak
a	5.70 (4.97–6.62)	4.67 (4.12–4.99)	2.13 (1.97–2.37)
s	8.31 (7.48–9.22)	14.6 (12.2–16.6)	19.4 (14.2–29.5)

[†] Parameters common to the three species: f = -0.0269 (-0.0401 – −0.0153); P_m = 2 (1.90–2.00); P_v = 1.12 (0.99–1.27); *scale* = 0.648 (0.590–0.702).

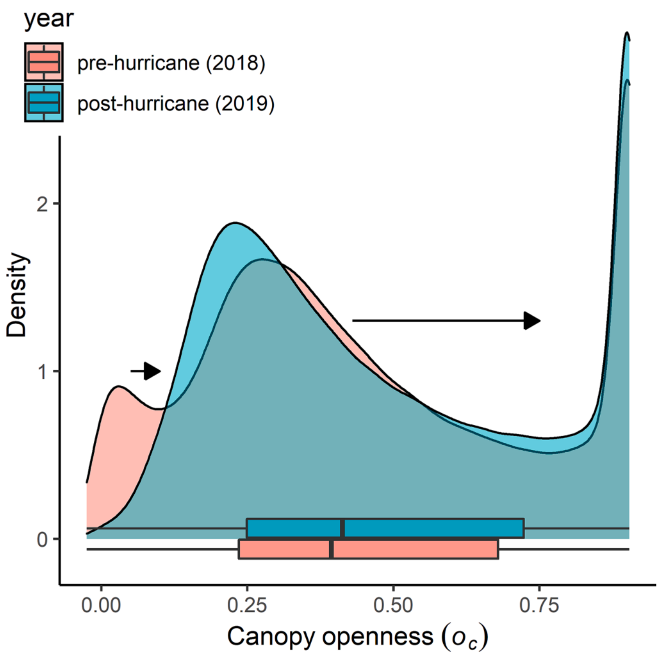

Fig. 6. Distribution of canopy openness (o_c) as predicted by aerial LiDAR prior to hurricane (2018) and after hurricane (2019) showing increase in openness especially in the ranges of 0.10 > o_c > 0.30 and o_c > 0.60.

was higher than competing oak species at all light levels, across sapling sizes, and across precipitation gradients. These results suggest that longleaf pines will continue to be the dominant tree species, and overall community structure may change little following hurricane damage. Impacts from Hurricane Michael were most evident in the most densely shaded sites (Fig. 6), and even under moderately low light longleaf pine could achieve greater height growth than the two oak species. This fact combined with the high wind resistance of overstory longleaf pine especially in dry soils (Rutledge et al., 2021) suggest that hurricanes may stabilize community structure in longleaf pine and contribute to the dominance of this species.

The Michaelis-Menten model (1913)—a saturating curve—best captured growth patterns in our study. Planted longleaf pine seedlings increase exponentially in biomass with linear increases in canopy openness at our study site (Pecot et al., 2007), but the naturally regenerated saplings in the present study were too large to still be in the exponential growth phase (Mencuccini et al., 2005). We expected increased light availability to favor longleaf pine height growth over oak species, although longleaf pine had a higher growth rate overall, height growth rates of both species were essentially fixed at o_c > 0.1. Only southern red oak continued to show increases in height growth rate beyond this threshold. Nevertheless, there was no o_c at which height growth rate of southern red oak was greater than longleaf pine. This difference in early height growth is striking given the similar stature of the species as adults; height growth ranking of the species may reverse with age because longleaf pine slows in height growth and forms a flat top as it matures (Landers and Boyer, 1999). This late-in-life presumed competitive reversal may help southern red oak achieve a co-dominant position in the canopy, but the early rapid height growth of longleaf pine is likely an important mechanism for competition against hardwoods in the post-hurricane environment assuming continuous presence of prescribed fire.

While growth rate of longleaf was highest for all levels of light, the growth rate ranking of the oak species changed with increasing light. Although the growth rate of sand post oak was higher at low light levels ($o_c < 0.15$), southern red oak growth rate exceeded that of sand post oak at higher light levels. This crossover occurred at a higher threshold ($o_c = 0.2$) when precipitation was 1500 mm yr^{-1}. (Fig. 5B) (Sack and Grubb, 2001). Hurricane damage led to an increase in microsites with o_c in the range of ~ 0.1 to 0.2 (Fig. 6). In this range, height growth rates for all species increased rapidly with only small increases in openness, especially for longleaf pine and to a lesser extent for southern red oak. Disparities in height growth rates were even larger if coupled with high precipitation (Fig. 5A).

It is common to find similar light-dependent radial growth rates among species in a community (Wright et al., 1998). In our study, light-dependent radial growth rate was similar in the two larger species and was slower in the smaller sand post oak. Radial growth rate of longleaf pine and southern red oak continued to increase with increasing light availability up to high levels of $o_{c,}$ whereas sand post oak, reached asymptotic radial growth rate at moderate light levels ($o_c \approx 0.25$). At lower light levels ($o_c < 0.20$), radial growth rate of longleaf pine was lower than both oak species. At moderate light levels ($0.20 > o_c > 0.75$), radial growth rate of longleaf pine was intermediate between post oak and southern red oak. At the highest light levels ($o_c > 0.75$), longleaf pine radial growth rate was roughly equivalent to southern red oak. Although radial growth rates were higher with higher precipitation, the patterns among species were similar regardless of precipitation (Fig. 5B). As a slow-growing species that reaches highest abundance on sub-xeric soils (Espeleta et al., 2004), sand post oak may be classified as employing a stress-tolerance strategy in the competitive – stress tolerance / ruderal (CSR) classification (Grime, 1977).

The two oak species are segregated along soil moisture and cation availability gradients (Jacqmain et al., 1998; Monk, 1968), a pattern which may be generated by differing growth performance along the gradient (Bigelow and Canham, 2002). Although we expected differences in peak growth rates along the soil texture (water retention) gradient, no sensitivity of growth to soil water retention could be seen. Lack of response may have been due to imprecise soil series classification on the soils map. Pedo-transfer functions such as the one we used to estimate water retention capacity from soil texture are a potentially powerful tool for linking soil observations to forest dynamics (Schapp et al., 2001); in hindsight the soil series maps were probably too coarse scale for the requirements of the study and direct measurements of soil texture would have been superior.

The strong differentiation in hurricane effects on radial growth rates (Fig. 5B) suggests the potential for an indirect effect of hurricane impacts on sapling dynamics in longleaf pine communities via a wind–fire interaction effect. Though longleaf pine is fire resistant at many life stages, associated hardwood species are often susceptible to fire, especially at small diameters (Hare, 1965). The pine and oaks in this study have similar radial growth rates at low light levels ($o_c < 0.25$). However, when wind disturbance increases light availability, longleaf pine and southern red oak are expected to have greater radial growth relative to sand post oak and more quickly reach size classes less vulnerable to surface fires all else being equal (e.g., fire conditions, sapling size, bark thickness, etc.). Following a surface fire, canopy gaps may continue to modify the growth and recovery even among top-killed saplings. Growth of resprouting saplings top-killed by fire can be nearly double in canopy gaps relative to saplings resprouting outside of gaps (Cannon et al., 2019). Thus, hurricanes have the potential to directly and indirectly alter sapling dynamics. Additional research on hurricane effects and interactions between wind and fire may reveal important disturbance-mediated mechanisms shaping the structure and function of longleaf pine ecosystems.

Frequent fire has long been recognized to govern community dynamics in longleaf pine ecosystems (Boyer, 1979). Frequent hurricane events in the Gulf Coastal plain are increasingly recognized as key disturbances in longleaf pine ecology (Gilliam et al., 2006; Myers and Van Lear, 1998; Rutledge et al., 2021; Zampieri et al., 2020). Research in longleaf pine has been focused on the ability of overstory gaps to influence regeneration dynamics (Brockway and Outcalt, 1998; Cannon et al., 2022; Palik et al., 2003; Palik and Pederson, 1996; Pecot et al., 2007), but these studies primarily focus on gap dynamics after harvest or small-scale natural disturbances such as lightning. Previous studies have intimated that wind disturbances such as hurricanes and other wind events play an important role in maintaining biodiversity and structural complexity in longleaf pine (Batista and Platt, 2003; Gilliam et al., 2006; Myers and Van Lear, 1998; Platt et al., 1988). However few empirical studies have examined the role that hurricanes and other wind disturbances play in the ecology of structuring longleaf pine forests and woodlands (Kleinman and Hart, 2017; Rutledge et al., 2021).

4.1. *Conclusions and management implications*

We found little evidence for any change in relative ranking of competitive ability after a tropical cyclone and its attendant shifts in resource availability (cf. Latham, 1992). Our results suggest that hurricanes and other wind disturbances may reinforce existing competitive dynamics among saplings in frequent fire ecosystems by their effects on height and radial growth rates. The rapid height growth of longleaf pine, particularly after high rainfall, contributes to the maintenance of its dominance on upland soil after wind disturbance. In the absence of other rank-reversals in competitive relationships after extensive wind damage, we conclude that windstorms reinforce/stabilize community dynamics among these species, with the all-important caveat that the frequent fire regime must continue uninterrupted.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Allen, R.H., Jr., Marquis, D.A., 1970. Effect of thinning on height and diameter growth of oak & yellow-poplar saplings. US Department of Agriculture, Forest Service, Northeastern EForest Experiment Station.

Anderson, D.R., Burnham, K.P., 2002. Avoiding Pitfalls When Using Information-Theoretic Methods. Source J. Wildl. Manag. 66, 912–918.

Barrie, C.J., Rasmussen, T.C., Tollner, E.W., Golladay, S.W., Brantley, S.T., 2022. Steady vs dynamic stream-aquifer interactions: Lower Flint River Basin, Southwest Georgia, USA. J. Hydrol. Reg. Stud. 40, 101046 https://doi.org/10.1016/j.ejrh.2022.101046.

Batista, W.B., Platt, W.J., 2003. Tree population response to hurricane disturbance: syndromes in a south-eastern USA old-growth forest. J. Ecol. 91, 197–212. https://doi.org/10.2307/3599755.

Bender, M.A., Knutson, T.R., Tuleya, R.E., Sirutis, J.J., Vecchi, G.A., Garner, S.T., Held, I. M., 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. Science 327, 454–458. https://doi.org/10.1126/science.1180568.

Bigelow, S.W., Canham, C.D., 2002. Community organization of tree species along soil gradients in a north-eastern USA forest. J. Ecol. 90, 188–200.

Bolker, B.M., 2008. Ecological Models and Data in R. Princeton University Press, Princeton, NJ.

Bond, W.J., Midgley, J.J., 2000. Ecology of sprouting in woody plants: the persistence niche. Trends Ecol. Evol. 16, 45–51. https://doi.org/10.1016/S0169-5347(00)02033-4.

Boyer, W.D., 1979. Regenerating the natural longleaf pine forest. J. For. 77, 572–575.

Brockway, D.G., Outcalt, K.W., 1998. Gap-phase regeneration in longleaf pine wiregrass ecosystems. For. Ecol. Manag. 106, 125–139. https://doi.org/10.1016/S0378-1127(97)00308-3.

Cannon, J.B., Henderson, S.K., Bailey, M.H., Peterson, C.J., 2019. Interactions between wind and fire disturbance in forests: Competing amplifying and buffering effects. For. Ecol. Manag. 436, 117–128. https://doi.org/10.1016/j.foreco.2019.01.015.

Cannon, J.B., Bigelow, S.W., Hiers, J.K., Jack, S.B., 2022. Effects of silvicultural selection treatments on spatial pattern and dynamics in a *Pinus palustris* Mill. woodland. For. Ecol. Manag. 505, 119888 https://doi.org/10.1016/j.foreco.2021.119888.

Cavender-Bares, J., Kitajima, K., Bazzaz, F.A., 2004. Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. Ecol. Monogr. 74, 635–662. https://doi.org/10.1890/03-4007.

Cooper-Ellis, S., Foster, D.R., Carlton, G., Lezberg, A., 1999. Forest response to catastrophic wind: Results from an experimental hurricane. Ecology 80, 2683–2696. https://doi.org/10.1890/0012-9658(1999)080[2683:FRTCWR]2.0.CO;2.

Curtin, P.J., Knapp, B.O., Jack, S.B., Vickers, L.A., Larsen, D.R., Guldin, J.M., 2020. Effects of overstory competition on canopy recruitment patterns of naturally regenerated longleaf pine on two site types. Can. J. For. Res. 50, 625–635. https://doi.org/10.1139/cjfr-2019-0343.

Espeleta, J.F., West, J.B., Donovan, L.A., 2004. Species-specific patterns of hydraulic lift in co-occurring adult trees and grasses in a sandhill community. Oecologia 138, 341–349. https://doi.org/10.1007/s00442-003-1460-8.

Fonda, R.W., 2001. Burning characteristics of needles from eight pine species. For. Sci. 47, 390–396.

Gagnon, J.L., Jokela, E.J., Moser, W.K., Huber, D.A., 2003. Dynamics of artificial regeneration in gaps within a longleaf pine flatwoods ecosystem. For. Ecol. Manag. 172, 133–144. https://doi.org/10.1016/S0378-1127(01)00808-8.

Gilliam, F.S., Platt, W.J., Peet, R.K., 2006. Natural disturbances and the physiognomy of pine savannas: A phenomenological model. Appl. Veg. Sci. 9, 83–96. https://doi.org/10.1658/1402-2001(2006)9[83:NDATPO]2.0.CO;2.

Goebel, P.C., Palik, B.J., Kirkman, L.K., Drew, M.B., West, L., Pederson, D.C., 2001. Forest ecosystems of a Lower Gulf Coastal Plain landscape: Multifactor classification and analysis. J. Torrey Bot. Soc. 128, 47–75. https://doi.org/10.2307/3088659.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111, 1169–1194.

Hanberry, B.B., Nowacki, G.J., 2016. Oaks were the historical foundation genus of the east-central United States. Quat. Sci. Rev. 145, 94–103. https://doi.org/10.1016/j.quascirev.2016.05.037.

Hare, R.C., 1965. Contribution of bark to fire resistance of southern trees. J. For. 63, 248–251.

Hiers, J.K., Walters, J.R., Mitchell, R.J., Varner, J.M., Conner, L.M., Blanc, L.A., Stowe, J., 2014. Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. J. Wildl. Manag. 78, 383–393. https://doi.org/10.1002/jwmg.676.

Holland, A.M., Rutledge, B.T., Jack, S.B., Stober, J.M., 2019. The longleaf pine forest: Long-term monitoring and restoration of a management dependent ecosystem. J. Nat. Conserv. 47, 38–50. https://doi.org/10.1016/j.jnc.2018.11.006.

Hook, D.D., Buford, M.A., Williams, T.M., 1991. Impact of Hurricane Hugo on the South Carolina coastal plain forest. J. Coast. Res. SI 8, 291–300.

Ibanez, T., Keppel, G., Baider, C., Birkinshaw, C., Florens, F.B.V., Laidlaw, M., Menkes, C., Parthasarathy, N., Rajkumar, M., Ratovoson, F., Rasingam, L., Reza, L., Aiba, S., Webb, E.L., Zang, R., Birnbaum, P., 2020. Tropical cyclones and island area shape species abundance distributions of local tree communities. Oikos 129, 1856–1866. https://doi.org/10.1111/oik.07501.

Jacqmain, E.I., Jones, R.H., Mitchell, R.J., 1998. Influences of frequent cool-season burning across a soil moisture gradient on oak community structure in longleaf pine ecosystems. Am. Midl. Nat. 141, 85–100. https://doi.org/10.1674/0003-0031.

Jennings, S.B., Brown, N.D., Sheil, D., 1999. Assessing forest canopies and understorey illumination: Canopy closure, canopy cover and other measures. Forestry 72, 59–73. https://doi.org/10.1093/forestry/72.1.59.

Johnsen, K.H., Butnor, J.R., Kush, J.S., Schmidtling, R.C., Nelson, C.D., 2009. Hurricane Katrina winds damaged longleaf pine less than loblolly pine. South. J. Appl. For. 33, 178–181. https://doi.org/10.1093/sjaf/33.4.178.

Kampe, T.U., Johnson, B.R., Kuester, M., Keller, M., 2010. NEON: the first continental-scale ecological observatory with airborne remote sensing of vegetation canopy biochemistry and structure. J. Appl. Remote Sens. 4, 043510 https://doi.org/10.1117/1.3361375.

Kane, J.M., Varner, J.M., Hiers, J.K., 2008. The burning characteristics of southeastern oaks: Discriminating fire facilitators from fire impeders. For. Ecol. Manag. 256, 2039–2045. https://doi.org/10.1016/J.FORECO.2008.07.039.

Keim, B.D., Muller, R.A., Stone, G.W., 2007. Spatiotemporal patterns and return periods of tropical storm and hurricane strikes from Texas to Maine. J. Clim. 20, 3498–3509. https://doi.org/10.1175/JCLI4187.1.

Kleinman, J.S., Hart, J.L., 2017. Response by vertical strata to catastrophic wind in restored *Pinus palustris* stands. J. Torrey Bot. Soc. 144, 423–438. https://doi.org/10.3159/TORREY-D-16-00046.1.

Landers, J.L., Boyer, W.D., 1999. An oldgrowth definition for upland longleaf pine and south Florida slash pine forests, woodlands and savannas (General Technical Report No. SRS-29). USDA FS Southern Research Station.

Lanner, R.M., 2017. Primordium initiation drives tree growth. Ann. For. Sci. 74, 11. https://doi.org/10.1007/s13595-016-0612-z.

Latham, R.E., 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology 73, 2129–2144.

Liu, C.X., Glitzenstein, J.S., Harcombe, P.A., Knox, R.G., 1997. Tornado and fire effects on tree species composition in a savanna in the Big Thicket National Preserve, southeast Texas. USA. For. Ecol. Manag. 91, 279–289. https://doi.org/10.1016/S0378-1127(96)03705-X.

Loudermilk, E.L., Hiers, J.K., Pokswinski, S., O'Brien, J.J., Barnett, A., Mitchell, R.J., 2016. The path back: Oaks (*Quercus* spp.) facilitate longleaf pine (*Pinus palustris*) seedling establishment in xeric sites. Ecosphere 7, 1–14. https://doi.org/10.1002/ecs2.1361.

MacFarlane, D., Kobe, R.K., 2006. Selecting models for capturing tree-size effects on growth-resource relationships. Can. J. For. Res. 36, 1695–1704. https://doi.org/10.1139/x06-054.

McGuire, J.P., Mitchell, R.J., Moser, E.B., Pecot, S.D., Gjerstad, D.H., Hedman, C.W., 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannas. Can. J. For. Res. 31, 765–778. https://doi.org/10.1139/cjfr-31-5-765.

McNab, W.H., Avers, P.E., 1994. Ecological subregions of the United States, section descriptions. United States Department of Agriculture, Forest Service, Ecosystem Management, Washington, D.C.

Mencuccini, M., Martínez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S., Michiels, B., 2005. Size-mediated ageing reduces vigour in trees. Ecol. Lett. 8, 1183–1190.

Michaelis, L., Menten, M.L., 1913. Die Kinetik der Invertinwirkung. Biochem. Ztg. 49, 333–369.

Monk, C.D., 1968. Successional and environmental relationships of the forest vegetation of north central Florida. Am. Midl. Nat. 79, 441–457. https://doi.org/10.2307/2423190.

Myers, R.K., Van Lear, D.H., 1998. Hurricane-fire interactions in coastal forests of the south: A review and hypothesis. For. Ecol. Manag. 103, 265–276. https://doi.org/10.1016/S0378-1127(97)00223-5.

O'Brien, J.J., Hiers, J.K., Callaham Jr., M.A., Mitchell, R.J., Jack, S.B., 2008. Interactions among overstory structure, seedling life-history traits, and fire in frequently burned neotropical pine forests. Ambio 37, 542–547. https://doi.org/10.1579/0044-7447-37.7.542.

Ojha, S.K., Naka, K., Dimov, L.D., 2020. Assessment of disturbances across forest inventory plots in the southeastern united states for the period 1995–2018. For. Sci. 66, 242–255. https://doi.org/10.1093/forsci/fxz072.

Pacala, S.W., Canham, C.D., Silander Jr., J.A., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. Can. J. For. Res. 24, 2172–2183. https://doi.org/10.1139/x94-280.

Palik, B., Mitchell, R.J., Pecot, S., Battaglia, M., Pu, M., Mou, P., 2003. Spatial distribution of overstory retention influences resources and growth of longleaf pine seedlings. Ecol. Appl. 13, 674–686. https://doi.org/10.1890/1051-0761(2003)013[0674:SDOORI]2.0.CO;2.

Palik, B.J., Pederson, N., 1996. Overstory mortality and canopy disturbances in longleaf pine ecosystems. Can. J. For. Res. 26, 2035–2047. https://doi.org/10.1139/x26-229.

Pecot, S.D., Mitchell, R.J., Palik, B.J., Moser, E.B., Hiers, J.K., 2007. Competitive responses of seedlings and understory plants in longleaf pine woodlands: Separating canopy influences above and below ground. Can. J. For. Res. 37, 634–648. https://doi.org/10.1139/X06-247.

Pederson, N., Varner, J.M., Palik, B.J., 2008. Canopy disturbance and tree recruitment over two centuries in a managed longleaf pine landscape. For. Ecol. Manag. 254, 85–95. https://doi.org/10.1016/j.foreco.2007.07.030.

Peterson, C.J., Pickett, S.T.A., 1995. Forest reorganization: A case study in an old-growth forest catastrophic blowdown. Ecology 76, 763–774.

Pielke, R.A., Landsea, C., Mayfield, M., Laver, J., Pasch, R., 2005. Hurricanes and global warming. Am. Meteorol. Soc. https://doi.org/10.1038/nature04477.

Platt, W., Evans, G.W., Rathbun, S.L., 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). Am. Nat. 131, 491–525.

Platt, W.J., Rathbun, S.L., 1993. Dynamics of an old-growth longleaf pine population. In: Hermann, S.M. (Ed.), Proceedings of the Tall Timbers Fire Ecology Conference, Tall Timbers Research Station, pp. 275–297.

Plotkin, A.B., Foster, D., Carlson, J., Magill, A., 2013. Survivors, not invaders, control forest development following simulated hurricane. Ecology 94, 414–423. https://doi.org/10.1890/12-0487.1.

Rother, M.T., Huffman, J.M., Harley, G.L., Platt, W.J., Jones, N., Robertson, K.M., Orzell, S.L., 2018. Cambial phenology informs tree-ring analysis of fire seasonality in Coastal Plain pine savannas. Fire Ecol. 14, 164–185. https://doi.org/10.4996/fireecology.140116418.

Rutledge, B.T., Cannon, J.B., McIntyre, R.K., Holland, A.M., Jack, S.B., 2021. Tree, stand, and landscape factors contributing to hurricane damage in a coastal plain forest: Post-hurricane assessment in a longleaf pine landscape. For. Ecol. Manag. 481, 118724 https://doi.org/10.1016/j.foreco.2020.118724.

Sack, L., Grubb, P.J., 2001. Why do species of woody seedlings change rank in relative growth rate between low and high irradiance? Funct. Ecol. 15, 145–154.

Schapp, M.G., Leij, F.J., van Genuchten, M.T., 2001. Rosetta: a computer program for estimating soil hydraulic parameters with hierarchical pedotransfer functions. J. Hydrol. 251, 163–176.

Spurr, S.H., 1956. Natural restocking of forests following the 1938 hurricane in central New England. Ecology 37, 443–451. https://doi.org/10.2307/1930166.

Touliatos, P., Roth, E., 1971. Hurricanes and trees: Ten lessons from Camille. J. For. 69, 285–289. https://doi.org/10.1093/jof/69.5.285.

Whelan, A.W., Cannon, J.B., Bigelow, S.W., Rutledge, B.T., Sánchez Meador, A.J., 2023. Improving generalized models of forest structure in complex forest types using area- and voxel-based approaches from lidar. Remote Sens. Environ. in press.

Wright, E.F., Coates, K.D., Canham, C.D., Bartemucci, P., 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. Can. J. For. Res. 28, 871–886.

Zampieri, N.E., Pau, S., Okamoto, D.K., 2020. The impact of Hurricane Michael on longleaf pine habitats in Florida. Sci. Rep. 10, 1–11. https://doi.org/10.1038/s41598-020-65436-9.