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Tropical cyclone winds and precipitation stimulate cone production in the masting species longleaf pine (*Pinus palustris*)

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Summary

- Many trees exhibit masting – where reproduction is temporally variable and synchronous over large areas. Several dominant masting species occur in tropical cyclone (TC)-prone regions, but it is unknown whether TCs correlate with mast seeding.
- We analyzed long-term data (1958–2022) to test the hypothesis that TCs influence cone production in longleaf pine (*Pinus palustris*). We integrate field observations, weather data, satellite imagery, and hurricane models to test whether TCs influence cone production via: increased precipitation; canopy density reduction; and/or mechanical stress from wind.
- Cone production was 31% higher 1 yr after hurricanes and 71% higher after 2 yr, before returning to baseline levels. Cyclone-associated precipitation was correlated with increased cone production in wet years and cone production increased after low-intensity winds ($\leq 25\ \mathrm{m\ s^{-1}}$) but not with high-intensity winds ($> 25\ \mathrm{m\ s^{-1}}$).
- Tropical cyclones may stimulate cone production via precipitation addition, but high-intensity winds may offset any gains. Our study is the first to support the direct influence of TCs on reproduction, suggesting a previously unknown environmental correlate of masting, which may occur in hurricane-prone forests world-wide.

Introduction

Many plants exhibit a reproductive phenomenon known as mast seeding where seed production is highly variable in time and synchronous over large geographic areas (Janzen, 1971; Kelly, 1994; Koenig & Knops, 2005; Pesendorfer *et al.*, 2021). Several mechanisms have been proposed to explain the adaptive significance of masting, and the pattern has been linked to satiation of seed predators, increased wind pollination efficiency, and timing reproduction for favorable establishment conditions (Kelly, 1994; Pearse *et al.*, 2016). Weather variability including temperature cues and water relations are frequently associated with seed production (Kelly *et al.*, 2013; Wion *et al.*, 2020; LaMontagne *et al.*, 2021). Reproduction in several masting species is temporally linked to climate oscillations, such as El Niño–Southern Oscillation (ENSO) which influences the variability and synchrony of masting cues (Schauber *et al.*, 2002; Fletcher, 2015; Ascoli *et al.*, 2020; Mundo *et al.*, 2021; Wion *et al.*, 2021). Studies on drivers of masting often examine correlations between reproduction and weather patterns, but far less is known about how tropical cyclones (TCs) may also contribute to observed variability in seed production.

Among environmental cues, forest disturbances such as drought and fire have been found to stimulate masting, but a recent review of global studies identified a paucity of research on whether intense winds may stimulate masting events (Vacchiano *et al.*, 2021). While fire and smoke can directly trigger hormonal signals that shift resource allocation to reproduction (Vacchiano *et al.*, 2021), few studies examine how severe wind influences seed production. Walker & Neris (1993) noted increased fruit production among shrubs following TC damage in a Puerto Rican forest and speculated that increased light enhanced fruit production. Read *et al.* (2008) examined the population structure of a monocarpic tree species *Cerberiopsis candelabra* Vieill. ex Pancher & Sébert (Apocynaceae) and suggested that cyclone damage cues mass flowering. Each of these studies suggests that canopy mortality can increase resource availability among surviving trees, but none examined additional mechanisms by which storm-stimulated seed production may occur.

Tropical cyclones (TCs) are common in the Atlantic and Pacific Oceans (Patricola *et al.*, 2022), and masting is common among several tree species that occur in forests prone to TCs, including ecologically dominant genera such as *Quercus*, *Pinus*, *Picea*, and *Nothofagus* (Table 1). Mortality from TCs affects forest dynamics in a broad range of forests across the globe (Boose *et al.*, 2001; Van Bloem *et al.*, 2006; Lee *et al.*, 2008; Altman *et al.*, 2013; Chen *et al.*, 2014; Dahal *et al.*, 2014; Zampieri *et al.*, 2020; Rutledge *et al.*, 2021; Zhang *et al.*, 2021). Because of the high global incidence of TC activity and masting, it is important to understand whether, and how, cyclones may relate to reproductive behavior in masting species.

Longleaf pine (*Pinus palustris Mill*) is a masting species well-suited to testing hypotheses of TC-stimulated seed production.

Table 1 Selected tree species associated with hurricane-prone regions and exhibiting a masting habit of seed production.

Cyclone basin	Family	Species	Native range	Masting studies
North Atlantic	Betulaceae	*Betula alleghaniensis* Britton	Eastern N. America, incl N. Atlantic coast	Houle (1999)
	Fagaceae	*Quercus alba* L.	Eastern N. America, incl Atlantic coast	Sork *et al*. (1993), Lichti *et al*. (2014), Bogdziewicz *et al*. (2018)
	Fagaceae	*Q. montana* Willd.	Eastern N. America, Appalachia	Bogdziewicz *et al*. (2018)
	Fagaceae	*Q. rubra* L.	Eastern N. America, incl. N. Atlantic coast	Sork *et al*. (1993), Liebhold *et al*. (2004), Lichti *et al*. (2014), Bogdziewicz *et al*. (2018)
	Fagaceae	*Q. velutina* Lam.	Eastern N. America, incl. mid-Atlantic coast	Sork *et al*. (1993)
	Pinaceae	*Abies balsamea* (L.) Mill.	Eastern N. America, North Atlantic coast	Houle (1999)
	Pinaceae	*Picea glauca* (Moench) Voss	N. American taiga, incl. N. Atlantic coast	Ascoli *et al*. (2020)
	Pinaceae	*Pinus palustris*	Southeastern N. America, South Atlantic and Gulf coasts	Chen *et al*. (2018), LaMontagne *et al*. (2021)
	Sapindaceae	*Acer saccharum* Marshall	Eastern N. America, N. Atlantic coast	Houle (1999)
NW Pacific	Dipterocarpaceae	*Shorea siamensis* Miq.	Southeast Asia	Marod *et al*. (2002)
	Dipterocarpaceae	Various	Various	Yasuda *et al*. (1999)
	Fagaceae	*Fagus crenata* Blume	Japan	Kon *et al*. (2005)
	Fagaceae	*Q. crispula* Blume	East Asia	Shibata *et al*. (2020)
SW Pacific	Apocynaceae	*Cerberiopsis candelabra*	New Caledonia	Read *et al*. (2008)
	Nothofagaceae	*Nothofagus* spp.	Temperate southern hemisphere	Ogden (1988), Kelly *et al*. (2008)

Ecosystems dominated by the species once spanned 370 million km^2 of the southeastern United States (Jose *et al.*, 2006) – an area that experiences hurricanes every *c.* 13 yr (Keim *et al.*, 2007). Due to land use changes and fire suppression, longleaf pine has been reduced to 5% of its historic range and is considered an endangered ecosystem (Noss *et al.*, 1995). Because of widespread interest in restoring the species, long-term records of seed production are available across its range that can reveal insights into reproduction dynamics (Brockway, 2018).

Weather variation is thought to drive mast seeding events and has been shown to impact longleaf pine cone production (Boyer, 1990; Kelly & Sork, 2002; Pearse *et al.*, 2014). Several weather factors are associated with longleaf pine cone production (Chen *et al.*, 2022). Abundant precipitation in the spring and early summer followed by a period of dryness has been linked with increased abundance of longleaf pine female strobili (Shoulders, 1967). Moderate levels of precipitation and temperature generally favor higher cone production, but the relationship between weather and cone production is generally modest and inconsistent across stands (Guo *et al.*, 2016; Chen *et al.*, 2018, 2022). Estimates of periodicity in longleaf pine cone production have ranged from 3 to 4 yr (Guo *et al.*, 2016), 5 to 7 yr (Wahlenberg, 1946), and 8 to 10 yr (Maki, 1952). Results differ somewhat depending on sites and time periods analyzed. The high variability in cone production combined with weak linkages with temperature and precipitation suggest that yet unexplored factors, such as TC occurrence, may influence cone production.

Objectives and hypotheses

We tested the primary hypothesis that TCs influence cone production in longleaf pine, contributing to high reproductive variability. Some forest managers hold this belief anecdotally, but we know of no documentation of its occurrence, nor empirical evidence supporting any specific causal mechanism. Thus, we also tested hypotheses related to specific mechanisms by which TCs influence cone production through: (1) increased precipitation; (2) canopy density reduction; and (3) mechanical damage or stress. Several of these mechanisms may concurrently alter cone production leading to a net increase, or decrease, in cones.

First, precipitation associated with TCs may increase cone production. Tropical cyclones (TCs) bring rainfall events that with record high intensity during autumn months in the Northern Hemisphere (Schwarz, 1970). Because aspects of reproduction in longleaf pine are primarily driven by weather factors (Shoulders, 1967; Boyer, 1973; Chen *et al.*, 2022), TC-associated precipitation may influence cone production depending on the amount, timing, or drought conditions that precede the storm. For example, the effect that TC-associated precipitation has on cone production may depend on soil moisture conditions or the physiological state of trees before the storm. Second, tree mortality from TCs increases resource availability (Cooper-Ellis *et al.*, 1999; McNab *et al.*, 2004) and may increase cone production among survivors. Reductions in stand density from silvicultural thinning often result in increased growth and cone production in many pine species (Krannitz & Duralia, 2004; Moreno-Fernández *et al.*, 2013; Ayari & Khouja, 2014). Additionally, thinning to a basal area of 8 m^2 ha^{-1} can increase cone production (Croker & Boyer, 1975; Brockway *et al.*, 2006). If TCs reduce competition, then cone production could increase 3 yr after overstory reduction as observed after silvicultural thinning (Croker & Boyer, 1975). Third, mechanical damage or stress from intense winds may either increase or decrease cone production. Severe winds may physically damage reproductive structures as seen following freeze events (Shoulders, 1967; Croker & Boyer, 1975; Du *et al.*, 2012). However, wind damage can also lead to minor mechanical breakage and leaf stripping or sublethal damage to the trunk (Doyle *et al*., 1995; Rutledge *et al*., 2021), which may trigger a stress response that induces cone production. A pattern of enhanced reproduction is often seen after drought stress (Lauder *et al*., 2019). Removal of live leaf area induces physiological changes in transpiration and respiration (Clinton *et al*., 2011), which has been suggested to stimulate a range of responses including increased reproduction (Lauder *et al*., 2019).

Materials and Methods

Effects of tropical cyclone occurrence on cone production

The overall approach of our study was to evaluate changes in longleaf pine (*Pinus palustris*) cone production following TCs. Long-term data on longleaf pine cone production is available at 12 longleaf pine sites distributed across the southeastern United States, including many years where sites were impacted by TCs (Fig. 1). The length of records at each site ranges from 8 to 67 yr and averages 39 yr (Supporting Information Fig. S1). At each site, annual counts of green cones were measured each spring (April and May) by USDA Forest Service scientists using ×8–10 binoculars (Fig. 1c). During spring and summer, cones have a distinctive green color, which changes to a dull brown when they reach maturity between mid-September and mid-October (Chen *et al*., 2018). We used publicly available data on cone counts as site-level averages which represented the mean number of cones per tree averaged from ≥ 10 trees at each site. Complete details on cone count methodology can be found in previous reports (Chen *et al*., 2016).

To identify years when each study site was impacted by TCs, we identified instances where a storm reached hurricane-strength winds (sustained winds $\geq 33\ \mathrm{m\,s^{-1}}$) within 50 nautical miles (92.6 km) of each site, using wind speed and location data from the National Hurricane Center best track data during the years when cone counts were collected (Fig. 1a; HURDAT2; Landsea & Franklin, 2013). Among the 56 tracks identified, we used a hurricane model to estimate wind speeds experienced from each hurricane. To estimate maximum sustained wind speeds experienced at each site, we used the HURRECON model implemented in R (Boose *et al*., 2001; Cannon, 2022). Briefly, the HURRECON model combines information on the location and wind speed of TC observations from HURDAT2 (Landsea & Franklin, 2013) and uses a lognormal function to estimate sustained wind speeds as a function of distance from the hurricane center (Boose *et al*., 2001; Cannon, 2022). The HURRECON model requires multiple wind speed measurements to estimate hurricane wind fields. These measurements are only available for TCs that reach hurricane-level winds (sustained winds $\geq 33\ \mathrm{m\,s^{-1}}$). Thus, we limited our analysis to hurricanes only. We use the term TC when discussing storms broadly and the more specific term hurricane when necessary to restrict the term to storms in our analysis. Further details of the model can be found in Boose *et al.* (2001) and Cannon *et al.* (2023). Though relatively simple, this meteorological model predicts sustained wind speeds comparable to those predicted from more complex numerical weather simulations and has been used to predict hurricane damage to forests and to characterize forest hurricane disturbance regimes in the eastern United States (Boose *et al*., 2001; Gannon & Martin, 2014; Bigelow *et al*., 2020; Cannon *et al*., 2023). Lastly, we included only events where maximum sustained winds from the cyclone were $> 10\ \mathrm{m\,s^{-1}}$ – the lowest nonzero wind speeds predicted by the model, resulting in a total of 52 unique tracks. These tracks represent 96 instances where cyclones impacted study sites (hereafter, 'events'), as some hurricane tracks affected multiple sites.

To test the hypothesis that TCs influence cone production, we assessed changes in cone production by site 1 yr before, and in the 3 yr after a hurricane event. We classified the cone record using a lag function ranging from Year 0 (before the event) to Year 3 after an event. Because cone records were consistently recorded in early spring (April and May), and no hurricanes approached a site before 31 May of any year, cone records occurring in the same year as a hurricane were classified as prestorm measurements (Year 0, baseline), and subsequent years were classified as 1- to 3-yr poststorm, correspondingly. If another hurricane reached the site during the interval, the lag function restarted at zero. In 34 of the 96 events identified, cone count data were available for both 1 yr prior and all 3 yr following a cyclone. To test the hypothesis that TCs influence cone production, we used a repeated measures ANOVA to determine whether mean cone count significantly differed in Years 0–3 following a hurricane ($n = 34$). After applying a log transformation to cone counts, we inspected for outliers using the boxplot method, checked for normality, and tested for sphericity using Mauchly's test (Mauchly, 1940), to ensure data met assumptions for using repeated measures ANOVA. We used the repeated measures ANOVA to assess for differences among lag years (0–3; within-subject effects) while accounting for differences in site-level cone production. Because of the occurrence of periodic masting events, it is possible that cone counts could, by chance, significantly differ over any arbitrarily chosen four-year period irrespective of TC occurrence. Thus, we used a repeated measures ANOVA on cone counts over 34 arbitrarily chosen periods naïve of TC occurrence as a null model for comparison with the above hurricane lag model.

Effects of precipitation supplementation on cone production

Once we established that hurricanes increase cone production, particularly in Year 2 after a hurricane, we explored three hypothetical mechanisms by which TCs might influence cone production. To test the hypothesis that precipitation associated with TCs increases cone production, we compared changes in cone counts in Year 2 following each hurricane to the associated precipitation anomaly. We also tested whether timing, or preceding drought conditions, influenced the effect that anomalous precipitation had on cone production. To estimate the amount of additional precipitation associated with each event, we calculated the precipitation anomaly ($\mathrm{PPT_A}$) as

$$\mathrm{PPT_A} = \mathrm{PPT_C} - \mathrm{PPT_T} \qquad \text{Eqn 1}$$

where $\mathrm{PPT_A}$ is anomalous precipitation (mm), $\mathrm{PPT_C}$ is 15-d precipitation in the period flanking the TC, and $\mathrm{PPT_T}$ is the typical

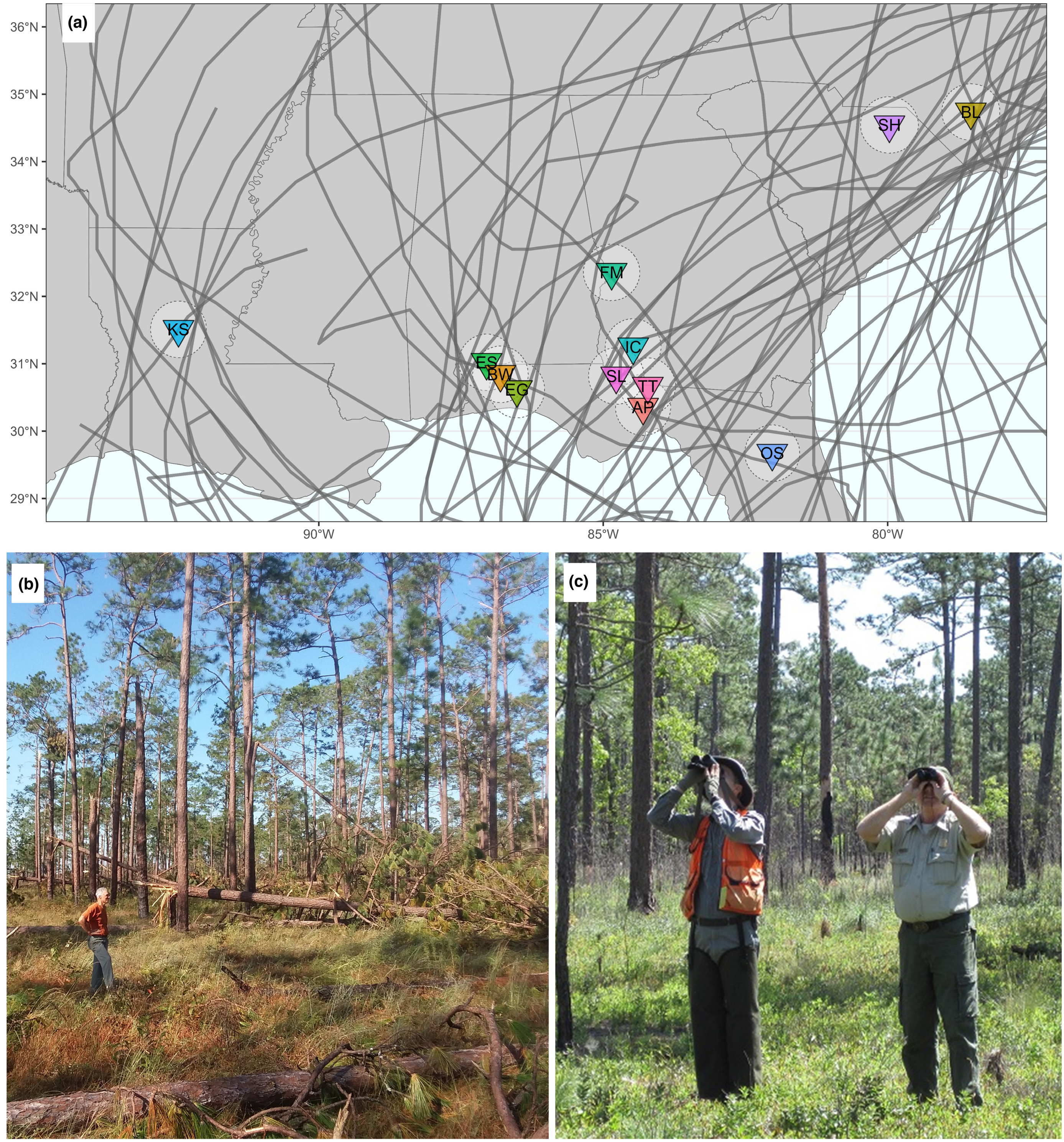

Fig. 1 Longleaf pine cone counts at 12 tropical cyclone (TC)-prone sites in the southeastern United States. (a) Tropical cyclone (TC) tracks that approached within 100 NM (92.6 km) of 12 longleaf pine study sites (triangles) between 1958 and 2020 from HURDAT2 database (Landsea & Franklin, 2013). Site abbreviations as in Table 2. (b) Portion of moderately damaged longleaf pine stand impacted by Hurricane Michael (2018) in Baker County, GA, USA. (Photo credit: The Jones Center at Ichauway, used with permission). (c) Counting longleaf pine cones on tree crowns using ×8–10 binoculars at Bladen Lakes State Forest (2015) in Bladen County, NC, USA. (Photo credit: Yoko Brockway, USDA Forest Service, used with permission).

15-d precipitation in the same period based on the mean value for years between 1981 and 2022. To calculate precipitation values, we used the PRISM daily spatial climate dataset AN81d (Daly *et al*., 2008, 2015). This dataset provides spatially continuous estimates of daily precipitation from 1981 to present across the coterminous United States at a spatial resolution of 1 km as interpolated from surface stations. We extracted daily precipitation at each site from 1981 to 2022 using Google Earth Engine (Cannon, 2023). We calculated the mean daily precipitation (Fig. S2) and averaged cumulative precipitation across a 15-d window to obtain PPT_T. To obtain PPT_C, we calculated the cumulative precipitation in the 15-d window flanking each event.

To test the hypothesis that the amount, timing, or conditions preceding TC-associated precipitation increase cone production, we modeled the change in cone production after hurricanes as a function of PPT_A and hurricane timing. We reasoned that the relationship between increased cone production and PPT_A could take one of three forms. Cone production may increase linearly with additional precipitation; cone production may increase with precipitation up to a threshold and then have no additional effect; or cone production may initially increase with precipitation and then decrease with high precipitation. Thus, we modeled cone production as: (1) a linear function; (2) a saturating function; and (3) a quadratic function of PPT_A to represent each of these possibilities. The linear model took the following form:

$$\Delta\text{cones} = \beta_0 + \beta_1 \text{PPT}_\text{A} \qquad \text{Eqn 2}$$

where Δcones is $\text{cones}_{\text{year 2}} - \text{cones}_{\text{year 0}}$ and β_0 and β_1 are fit using linear regression. The saturating model took the following form:

$$\Delta\text{cones} = (a\,\text{PPT}_\text{A})/(a\,s^{-1} + \text{PPT}_\text{A}) \qquad \text{Eqn 3}$$

where a is a parameter representing asymptotic cone production and s corresponds to the increase in cones (i.e. slope) when $\text{PPT}_\text{A} = 0$ (Michaelis & Menten, 1913; Bolker, 2008). The quadratic function allows an increase in cone production to a maximum before declining with excess precipitation and took the following form:

$$\Delta\text{cones} = \beta_0 + \beta_1\,\text{PPT}_\text{A} + \beta_2\,\text{PPT}_\text{A}^2 \qquad \text{Eqn 4}$$

where β_0, β_1, and β_2 are parameters fit using nonlinear least squares regression.

To test the hypothesis that timing of precipitation can influence cone production, we modeled cone production as a linear function of hurricane timing expressed as Julian date (timing-only model). We also modeled cone production as a linear function of precipitation timing, amount, and their interaction (Precipitation × Timing model).

To test the hypothesis that TC-associated precipitation and drought interactively influence cone production, we modeled cone production as linear function of PPT_A, Palmer Drought Severity Index (PDSI), and their interaction (Precipitation × Drought model). We obtained PDSI values 1 wk before each event using the GRIDMET drought indices dataset, which provides 5-d estimates of PDSI since 1980 (Abatzoglou, 2013) using Google Earth Engine (Cannon, 2023). Lastly, to compare models, we included an intercept-only null model and ranked all models using Akaike information criterion (AIC; Anderson & Burnham, 2002). We included only those events where data were available to calculate PPT_A (i.e. after 1981) and where cone count data were available in Years 0 and 2 for calculating Δcones ($n = 38$).

Effects of canopy density reduction on cone production

To test the hypothesis that TCs increase cone production through canopy density reduction, we examined whether changes in cone production were associated with declines in vegetation density in the area surrounding focal trees at each site. Because detailed stand information was not available over the long temporal and spatial extent of the study, we used remotely sensed vegetation indexes to capture major changes in vegetation structure. We compiled available satellite imagery between 2000 and 2013 from Landsat 7 Enhanced Thematic Mapper Plus (ETM+) and from 2014 to 2021 using Landsat 8 Operational Land Imager (OLI)/Thermal Infrared Sensor (TIRS; Fig. S3). Both imagery datasets consist of multispectral atmospherically corrected surface reflectance bands at a resolution of 30 m. We generated composite imagery for each site and year by compiling multiple scenes from each year using Google Earth Engine (Cannon, 2023). We masked pixels classified as clouds and composited imagery by selecting the median value among available imagery for each spectral band (Fig. S3). Using the composite imagery, we calculated the Normalized Difference Vegetation Index (NDVI; Soudani *et al*., 2006).

$$\text{NDVI} = \frac{\text{NIR} - \text{Red}}{\text{NIR} + \text{Red}} \qquad \text{Eqn 5}$$

We composited imagery for the winter months of each year (November–February) for all available years and sites within 50 ha (0.4 km radius). We used winter NDVI to avoid the influence of growing season growth of understory vegetation and to avoid compositing pre- and postdisturbance imagery in the same image. For each site and TC event, we calculated ΔNDVI as the $\text{NDVI}_{\text{year 2}} - \text{NDVI}_{\text{year 0}}$, and we calculated Δcones as $\text{cones}_{\text{year 2}} - \text{cones}_{\text{year 0}}$. We tested whether ΔNDVI was a significant predictor of Δcones using linear regression. We included in the analysis only those events where data were available to calculate ΔNDVI (after 2000) and where cone count data were available in Years 0 and 2 for calculating Δcones ($n = 24$).

Effects of mechanical stress or damage on cone production

To test the hypothesis that TCs may alter cone production through mechanical stress, we evaluated whether changes in cone production were related to maximum sustained wind speed experienced at each site. For each site and cyclone event, we estimated maximum sustained wind speed experienced each year using the HURRECON model. We tested whether maximum sustained wind speed was a significant predictor of Δcones using linear regression. We included in the analysis only those events where cone count data were available in Years 0 and 2 for calculating Δcones ($n = 46$).

Table 2 Mean annual cone count summary data from 12 longleaf pine (*Pinus palustris*) sites distributed across the southeastern United States.

			Cone counts (per tree yr^{-1})				Cyclones		
Site	Symbol	Record length (yr)	Mean	SD	Median	90^{th}%	Count	Frequency (yr^{-1})	Return interval (yr)
Apalachicola	AP	43	20.6	33.0	9.9	38.3	8	0.1860	5.38
Blackwater	BW	58	27.9	43.4	11.1	75.5	10	0.1724	5.80
Bladen Lakes	BL	43	24.8	36.8	9.7	91.0	11	0.2558	3.91
Eglin	EG	50	16.6	22.2	8.3	45.0	10	0.2000	5.00
Escambia	ES	67	29.0	36.1	14.8	67.1	10	0.1493	6.70
Ft Moore	FM	28	27.9	32.6	16.2	61.3	1	0.0357	28.00
Ichauway	IC	26	49.4	50.8	24.9	123.1	4	0.1538	6.50
Kisatchie	KS	55	35.0	39.6	24.3	72.7	9	0.1636	6.11
Ordway–Swisher	OS	8	6.7	10.0	1.8	17.8	2	0.2500	4.00
Sandhills	SH	54	29.1	32.5	16.8	63.7	3	0.0556	18.00
Southlands	SL	30	14.7	29.6	1.7	51.9	3	0.1000	10.00
Tall Timbers	TT	24	23.4	19.0	14.5	52.9	4	0.1667	6.00
Average			25.4	32.1	12.8	63.3	6.25	0.16	6.35

SD, standard deviation of cone counts.

Comparison among hypotheses

After finding that the maximum sustained wind speed model and Precipitation × Drought model were both good predictors of change in cone production after hurricanes, we further sought to compare these two models. Comparison of AIC values requires identical datasets, and the observations included in initial tests varied slightly depending on the availability of weather data for calculating $\mathrm{PPT_A}$ and satellite imagery for calculating NDVI. Thus, to compare among competing hypotheses, we reduced the dataset to instances where all relevant values were available and used AIC to compare among the two models ($n = 18$).

Results

Mean cone counts varied widely among sites and years (Table 2; Figs S4, S5). Study-wide mean cone counts across sites were 25 ± 32 cones per tree and ranged from 7 ± 10 to 49 ± 51 cones per tree at the Ordway–Swisher and Ichauway sites, respectively. The coefficient of variation in cone count, often used as an indicator of masting behavior, averaged 1.33 across sites and ranged from 0.81 to 2.01 (Table 2). Cone counts during mast years, defined as the site-specific 90^{th} percentile cone count, averaged 63 cones per tree and ranged from 18 to 123 cones per tree at the Ordway–Swisher and Ichauway sites, respectively (Table 2).

Cone production increased following hurricane events. After a log transformation, cone count data met assumptions of repeated measures ANOVA with no influential outliers (Fig. S6A), were normally distributed (Fig. S6B), and met the sphericity assumption with equal variance among combinations of lag years (Mauchly's $W = 0.790$, $P = 0.187$; Fig. S6C,D). We found that cyclone activity significantly increased cone production in the years following a hurricane event ($P = 0.028$). Relative to precyclone years (Year 0), we found that cone production was *c.* 31% higher one year after cyclones, 71% higher in Year 2, and returned to precyclone measurements by Year 3 (Figs 2, S7). By comparison, the repeated measures ANOVA for arbitrary (null) 4-yr periods showed no difference in cone counts among arbitrary lag years ($P = 0.417$; Fig. S8).

TCs significantly increased precipitation at affected sites and $\mathrm{PPT_A}$ averaged 107 mm in the 15-day flanking cyclone approach (Fig. 3a, $P < 0.001$). Supplemental precipitation was concentrated in days preceding storm approach and daily precipitation peaked 3–4 d before a cyclone's closest approach to a study site (Fig. 3b). $\mathrm{PPT_A}$ was highest in late September (averaging *c.* 150 mm) and was lower in summer and winter months (Fig. 3c).

Anomalous storm-associated precipitation was a good predictor of change in cone production, when considering antecedent drought conditions. Simple models of anomalous storm-associated precipitation did not improve upon the null model (Table 3). Neither the linear, quadratic, or asymptotic relationships with precipitation were good predictors of change in cone production (Fig. 4a). Similarly, neither the precipitation timing only nor precipitation and timing interactions models improved upon the null model (Table 3). We found that the precipitation × drought model was the best model of cone production ($R^2 = 0.2277$; Fig. 4b) and was significantly better than the null model according to AIC (Table 3). In this model, the effect that $\mathrm{PPT_A}$ had on cone production depended on antecedent drought conditions as measured by PDSI ($\mathrm{PPT_A} \times \mathrm{PDSI}$ interaction effect, $P = 0.006$). Hurricane-associated precipitation increased cone production during wet conditions (e.g. $\mathrm{PDSI} > 2$), but the opposite was true during dry conditions (e.g. $\mathrm{PDSI} < 0$; Fig. 4c).

TC-induced changes in NDVI were modest, with no discernable impact on cone production. Winter NDVI generally increased at all sites over the period where data were available (Fig. S9). Mean ΔNDVI following cyclone events was not significantly different from zero ($P = 0.887$; Fig. 5a), and Δcones was not significantly correlated with ΔNDVI ($R^2 = 0.014$, $P = 0.637$; Fig. 5b).

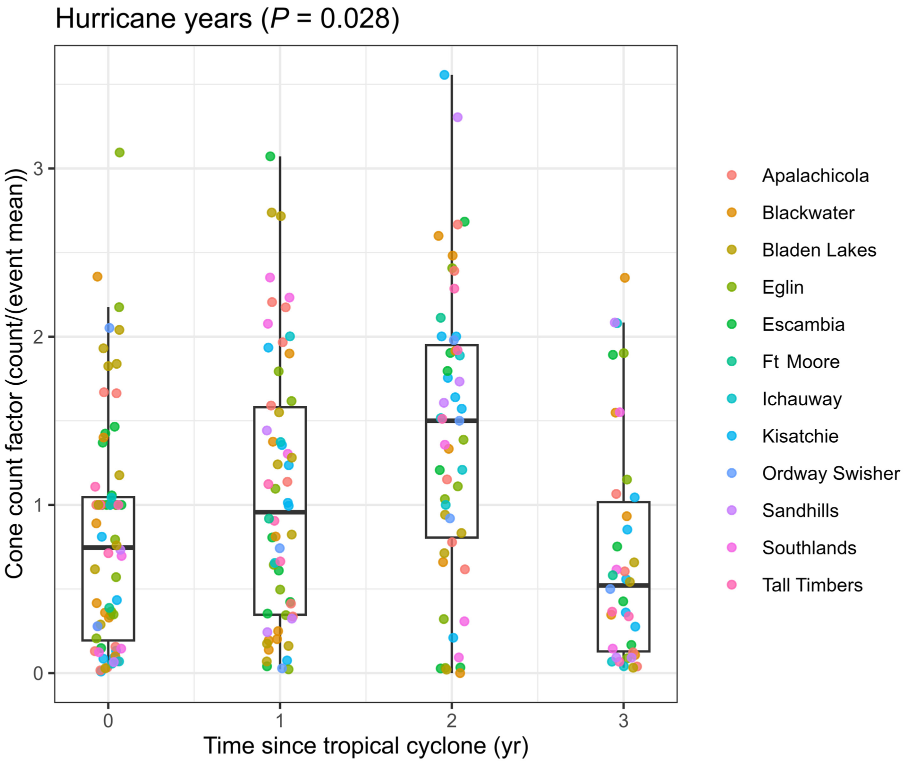

Fig. 2 Changes in longleaf pine cone count following tropical cyclones (TCs). Changes shown as count factor (cone count in a given year divided by mean over the 4-yr period) before (Year 0), and 3 yr following (Years 1–3) cyclone events at 12 longleaf pine sites in the southeastern United States. Thick horizontal line represents median, hinges represent 25th and 75th percentile, and whiskers represent 1.5× interquartile range. *P*-value represents lag effect using repeated measures ANOVA on log transformed cone counts.

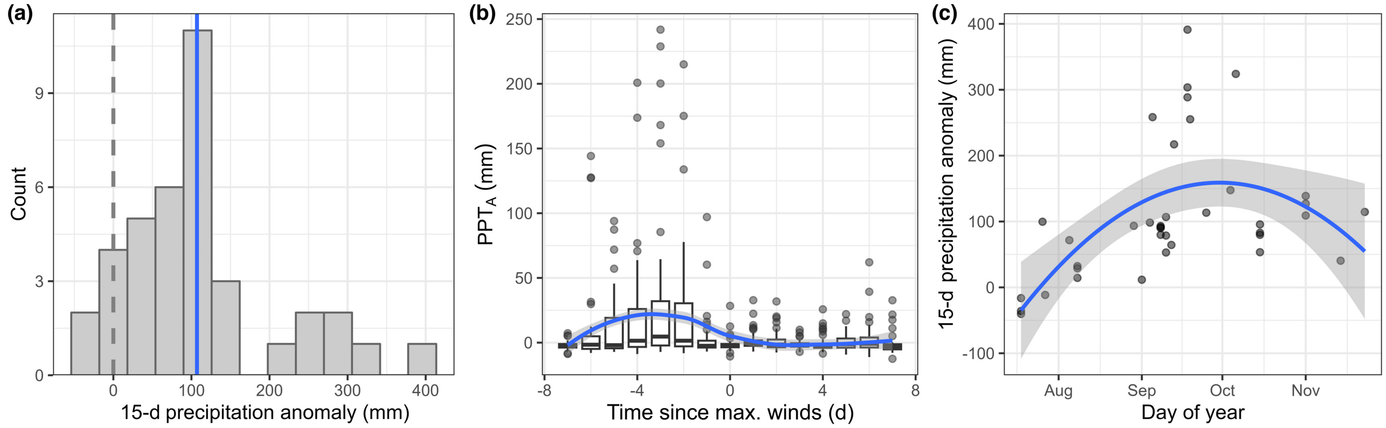

Fig. 3 Tropical cyclone (TC)-associated precipitation at study sites (a) 15-d precipitation anomaly associated with 38 cyclones occurring at 12 study sites. Blue line represents mean hurricane-associated precipitation anomaly of *c*. 107 mm and dashed line represents $x = 0$. (b) Timing of individual precipitation anomalies, indicating peak hurricane-associated precipitation occurring 3–4 d before approaching a site. Thick horizontal line represents median, hinges represent 25th and 75th percentile, and whiskers represent 1.5× interquartile range. *P*-value represents lag effect using repeated measures ANOVA. (c) Seasonal variation in 15-d precipitation anomaly illustrating higher cyclone-associated precipitation in the fall season (~October). Blues lines in (b, c) represent a loess smoothing function.

Maximum sustained wind speed significantly influenced cone production (Fig. 6). We found that Δcones significantly decreased with increasing wind speed, as predicted by the HURRECON model ($R^2 = 0.142$, $P = 0.010$).

In the reduced dataset with common observations of PPT_A, PDSI, and maximum sustained wind speeds, we found greater support for the PPT_A × drought model ($AIC_C = 196.966$), compared with the wind model ($AIC_C = 203.069$), representing a ΔAIC of 6.103.

Discussion

Our study is the first to reveal that TCs may increase reproductive output for at least 2 yr, supporting the hypothesis that TCs may simulate cone production. We found that average cone production increased 31% in the first year after a hurricane and 71% in the second year, before returning to baseline levels (Fig. 2). This consistent pattern of increased cone production is striking, in light of the high annual variability typically observed in

Table 3 Akaike Information criteria for candidate models of Δcones as a function of 15-d precipitation anomaly, precipitation timing, and/or Palmer Drought Severity Index for longleaf pine (*Pinus palustris*).

Model	K[a]	LL[a]	AIC_c[a]	ΔAICc[a]	R^2
Null	2	−207.039	418.420	5.500	0.000
Precipitation (linear)	3	−206.867	420.440	7.520	0.009
Precipitation (quadratic)	4	−205.396	420.005	7.085	0.008[b]
Precipitation (asymptotic)	3	−207.219	421.144	8.224	−0.001[b]
Timing only	3	−206.882	420.470	7.550	0.008
Precipitation × Timing	5	−204.845	421.566	8.646	0.109
Precipitation × Drought	5	−200.522	412.920	0.000	0.290

[a] K is number of parameters estimated for model, LL is maximum log likelihood, AICc is Akaike's information criterion adjusted for small sample size, and ΔAIC is the AIC differences of candidate model and minimum AIC.

[b] We report pseudo-R^2 for the nonlinear model as variance explained by the candidate model relative to the null model (McFadden's pseudo-R^2).

longleaf pine cone production (Figs S4, S5), and the fact that other authors have found that weather patterns are not consistently good predictors of cone production in the species (Chen *et al*., 2022). Long-term climate patterns such as ENSO have been linked to increased cone production in some pine species (Wion *et al*., 2021) as have discrete disturbances such as drought, fire, and frost (Ascoli *et al*., 2021). To our knowledge, this is the first demonstration that TCs may also relate to seed masting in longleaf pine.

Although we examined a single tree species with a distribution that highly overlaps TC-prone regions (Cannon *et al*., 2023), cyclone-induced masting may occur in other species. Several ecologically dominant masting tree species have native ranges that coincide with high TC activity (Table 1). Long-term seed production records (e.g. Pearse *et al*., 2017; Hacket-Pain *et al*., 2022) could be used to determine whether TC-associated masting is a widespread phenomenon. Although we found strong linkages between hurricanes and increased cone production (Fig. 2), the effect was not universal (Fig. S1). Some masting events occurred without a preceding hurricane, and not all hurricanes led to a masting event (Fig. S1). Winds from TCs add complexity to understanding patterns of seed production in masting species. Previous studies underscore that weather patterns, both long- and short-term, can be proximate drivers of seed production and provide environmental cues that stimulate masting (Pearse *et al*., 2014; Guo *et al*., 2016; Vacchiano *et al*., 2021; Wion *et al*., 2021).

We identified two potential mechanisms by which TCs may lead to increased cone production. Both TC-associated precipitation and mechanical stress from intense winds were correlated with changes in cone production. Tropical cyclone (TCs) were associated with an average of 107 mm of additional precipitation (Fig. 3a). Precipitation and its timing can play a role in longleaf pine cone production. Chen *et al*. (2018) found that cone production increased with decadal variability in precipitation and temperature. We found that cone production increased with TC-associated precipitation, but only when preceded by a wet period (Fig. 4c). Additional precipitation following drought conditions did not lead to increased cone production. This pattern may be explained if drought conditions alter the physiological state of trees or edaphic conditions. For example, prolonged drought may cause trees to allocate resources to growth or defense rather than reproduction (Trowbridge *et al*., 2021). Alternatively, the soils found in these study sites are coarsely textured and typically have high infiltration rates to deep soil layers, especially in dry conditions. Thus, drought conditions may cause TC-associated precipitation to lead to little change in soil moisture (Brady & Weil, 2014). In a study of masting in *Pinus edulis* Engelm., Wion *et al*. (2020) explored similar interactions, finding that late summer monsoonal provide precipitation during key periods of cone development and were especially influential on masting in arid regions. Conversely, our findings suggest that TC rains are associated with increased cone development only when preceded by wet conditions.

Higher cone production in Years 1 and 2 after a hurricane suggests that TC-associated precipitation may increase survival of existing conelets. The male catkins and female conelets of longleaf pine initiate in July and August and develop during subsequent months (Guo *et al*., 2016). Pollen shedding occurs around March (Boyer, 1973; Chen *et al*., 2020), but fertilization does not occur until the following spring, and maturation and dispersal occur *c*. 2.5 yr after initiation in October (Chen *et al*., 2018). Because of the prolonged development time, newly initiated catkins and conelets (*c*. 2 months old) and recently pollinated conelets (*c*. 14 months old) are both present during the period of peak TC activity (August–September). Thus, TC-associated precipitation could increase reproductive output in Year 1 by enhancing the survival of pollinated conelets and increase reproductive output in Year 2 by increasing output or persistence of new catkins and conelets.

Although it had less support than the precipitation-based model, we found cone production decreased with TC wind intensity (Fig. 6). This pattern could suggest that TC winds stimulate cone production through some mechanism (e.g. precipitation as discussed earlier) but that higher intensity wind may offset gains causing mechanical damage to developing reproductive structures. Severe freezing events can damage reproductive structures in longleaf pine and limit cone or seed production (Shoulders, 1967; Croker & Boyer, 1975; Du *et al*., 2012). Similarly, high wind intensity may damage, or remove, reproductive structures offsetting potential gains. Although less plausible, low-intensity wind itself could stimulate reproduction. Many vascular plants are known to exhibit resource allocation toward reproduction in response to stress (Takeno, 2016; Lauder *et al*., 2019). Severe wind damage can result in lethal stem breakage or uprooting of trees. However, in many instances, damage may be sublethal, resulting in broken crowns, broken branches or stripped leaves (Doyle *et al*., 1995; Rutledge *et al*., 2021). Sublethal mechanical damage from TCs may cue hormonal pathways responsible for increased reproduction. Branch girdling, for example, has long been used horticulturally to stimulate reproduction in Pinaceae seed orchards (Ebell, 1971; Bonnet-Masimbert, 1987). Most research on the influence of stress on

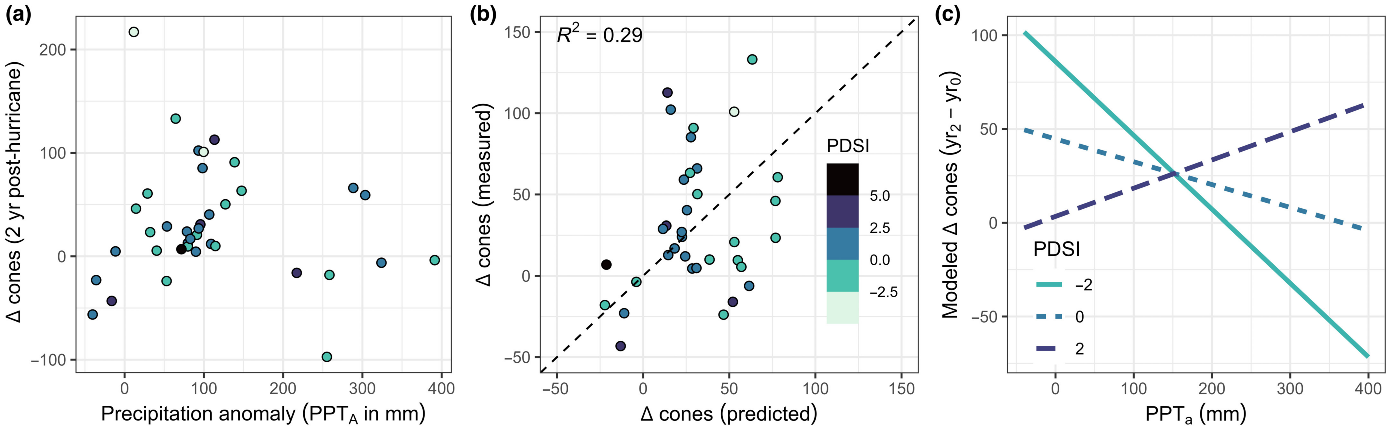

Fig. 4 Models of change in longleaf pine cone counts based on tropical cyclone (TC)-associated precipitation. (a) Simple models of precipitation anomaly ($\mathrm{PPT_A}$) were inadequate to predict change in longleaf pine cone production (Δcones). (b) A precipitation × drought model had the strongest relationship with change in longleaf pine cone production (Δcones; $R^2 = 0.2277$). Dashed line represents 1 : 1 line (c) Modeled changes in longleaf pine cone production increased with precipitation anomaly ($\mathrm{PPT_A}$) for wet conditions (Palmer Drought Severity Index, PDSI = 2), moderate conditions (PDSI = 0), and drought conditions (PDSI = −2).

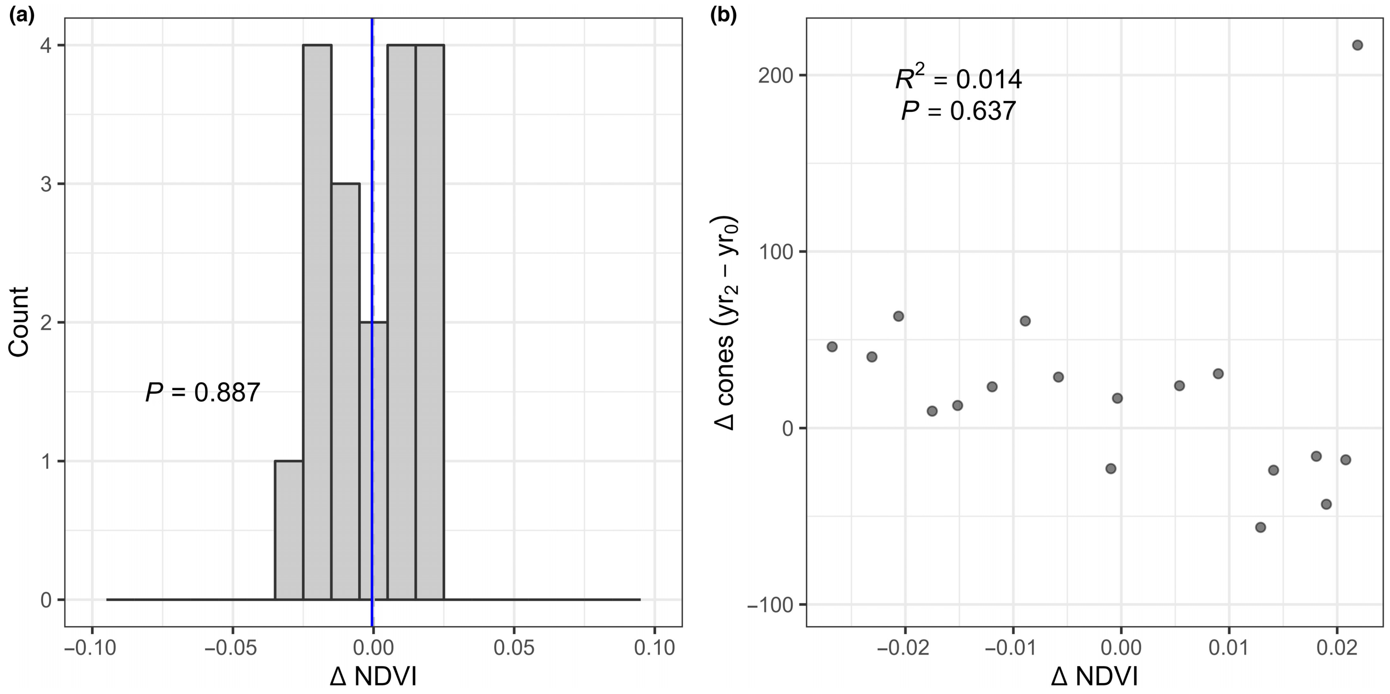

Fig. 5 Changes in vegetation index at 12 longleaf pine sites. (a) Changes in Normalized Difference Vegetation Index (NDVI) immediately before (Year 0) and after (Year 2) tropical cyclone (TC) events, indicating that ΔNDVI did not significantly differ from zero ($P = 0.225$) using a two-tailed *t*-test. (b) Relationship between ΔNDVI and Δcones for 24 cyclone events occurring 2001–2021 ($R^2 = 0.041$, $P = 0.345$).

conifer reproduction has focused on drought impacts (Thabeet *et al.*, 2009; Lauder *et al.*, 2019). Additional research on the linkages between severe wind events and tree stress response can confirm the influence of sublethal damage from TCs on reproductive output in longleaf pine and other species.

Our results also do not support the hypothesis that postcyclone increases in cone production are related to increased resource availability from tree mortality. We found no relationship between changes in vegetation abundance (as measured by NDVI) and cone production (Fig. 6). Increased reproduction resulting from decreased density should increase cone production in Year 3, but we found no such increase. This is surprising considering that other studies have found that silvicultural thinning can increase cone production in longleaf pine (Brockway *et al.*, 2006) and many other pines (Krannitz & Duralia, 2004; Moreno-Fernández *et al.*, 2013; Ayari & Khouja, 2014). Competition among mature longleaf trees in open forests is relatively small compared with earlier life stages (Rathbun & Cressie, 1994); thus, removal of neighbors may have minimal impact on resource availability and cone production in the low-density

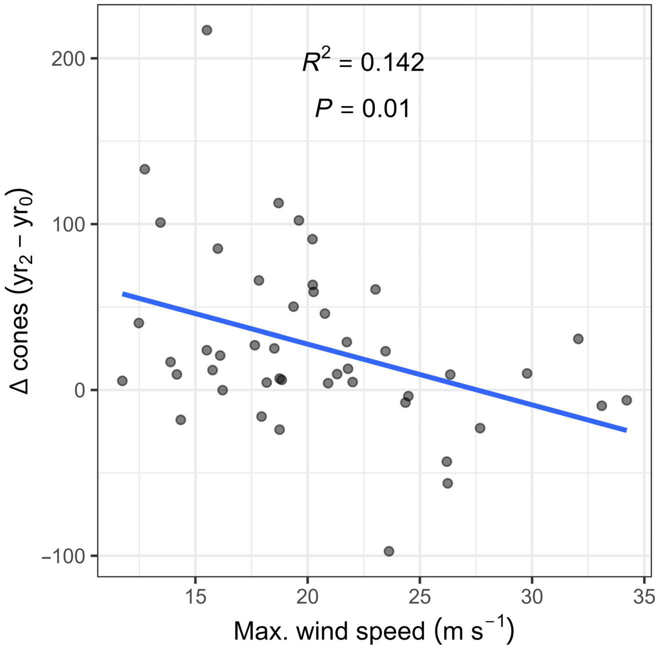

Fig. 6 Relationship between change in longleaf pine cone counts between Year 2 and Year 0 after 46 cyclone events (Δcones) and maximum sustained wind speed as predicted by HURRECON. Blue line represents best fit linear regression.

stands examined here. Competition reduction from TCs may play a larger role in cone production when cyclone impacts occur in younger, denser stands (Brockway *et al.*, 2006; Patterson & Knapp, 2016).

The hypothesized mechanisms explored in this study are well suited for experimental manipulation to confirm causality of the linkages found. For example, drought and rain conditions can be manipulated via throughfall exclusion and irrigation systems (e.g. Nepstad *et al.*, 2002; Kirkman *et al.*, 2016; Samuelson *et al.*, 2019). Mechanical stress from wind can be simulated by branch girdling (e.g. Ebell, 1971), leaf stripping (e.g. Shiels & González, 2014), and tree shakers used for seed, nut, and fruit collection (Alper *et al.*, 1976).

Several hypotheses have been advanced to explain the adaptivity of masting in tree species. One hypothesized mechanism for the evolution of masting is the environmental prediction hypothesis where the same weather cues associated with favorable establishment conditions also trigger reproduction (Payton & Brasch, 1978; Smith *et al.*, 1990; Kelly, 1994; Ascoli *et al.*, 2020; Satake *et al.*, 2021). Hurricanes may also represent a plausible mechanism by which environmental prediction may occur. While our study does not attempt to test whether TC-induced seeding is adaptive, it is informative to consider how high seed years soon after TCs may be advantageous to longleaf pine establishment. Longleaf pine seeds require bare mineral soil for germination, which is often exposed after surface fires (Brockway *et al.*, 2006). When mature trees are uprooted following wind damage, large areas of soil are exposed (*c.* 2 m^2; Sobhani *et al.*, 2014). Soil exposed from uprooted trees may provide germination sites for the increased cone and seed production following TCs, as is the case with some herbaceous plants (Beatty, 1984; Ulanova, 2000). Wind disturbance may also create barriers to fire by disrupting fuel continuity (O'Brien *et al.*, 2008; Cannon *et al.*, 2017) and providing short fire-free periods that can enhance successful regeneration (Robertson *et al.*, 2019). In addition, longleaf pine is more resistant to wind damage relative to other pine species across many soil types (Johnsen *et al.*, 2009; Rutledge *et al.*, 2021), and longleaf pine saplings respond more positively to cyclone-created gaps compared with some associated oak species (Pope *et al.*, 2023; Arko *et al.*, in press). Increased reproduction may complement other longleaf pine traits that promote resistance, resilience, and dominance of the species in the TC-prone region.

These findings highlight the key role that winds from TCs may play in shaping the ecology and evolution of species occurring in areas where TCs are common. Anthropogenic influences may warm sea surface temperatures (Elsner, 2006) and increase the proportion of severe TCs (Holland & Bruyère, 2014); thus, storm effects on reproductive behavior may become more important in coming decades. Tropical cyclone (TCs) may also interact with increases in temperature and extreme precipitation to induce cone production (Terando *et al.*, 2018). The conservation and management of naturally regenerating longleaf pine stands depends on periodic masting events for persistence. If longleaf pine or other coastal masting species experience more frequent high-severity winds (> 25 m s^{-1}), then cone production may decrease with an increased incidence of high-severity storms. However, it is important to note that high-severity storms contain only a small area of the most severe winds with a much larger footprint of low-severity winds (Boose *et al.*, 2001; Jagger & Elsner, 2006; Cannon *et al.*, 2023). Thus, despite more severe winds in some areas, climate change may increase the frequency of low-intensity winds over larger areas, leading to net increases in cone production in longleaf pine. Additional global-scale research on TCs and the mechanisms by which they alter reproductive behavior in a broad array of species can improve ecological understanding of masting phenomena and refine conservation efforts in masting species like longleaf pine.

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Competing interests

None declared.

Author contributions

JBC and BTR contributed to conceptualization, data curation, methodology, and investigation. JJP contributed to conceptualization and methodology. JLW and DGB contributed to data curation and methodology. All authors contributed to writing and revision.

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Data availability

All data used in this study were compiled from publicly available sources, including data on cone counts (Brockway, 2018; Willis & Brockway, 2022), satellite imagery (USGS, 2022), weather data (PRISM Climate Group, 2004), and hurricane data (Landsea & Franklin, 2013; Cannon, 2022). Weather and satellite imagery analyses were performed using custom scripts in Google Earth Engine available from Cannon *et al.* (2023). Hurricane wind field analyses were completed following methods in Cannon *et al.* (2023) using the R package hurrecon (Cannon, 2022; Cannon *et al.*, 2023).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Annual longleaf pine cone count records collected from 12 longleaf pine sites from 1958 to 2022.

Fig. S2 Mean daily precipitation at longleaf pine study sites from 1981 to present.

Fig. S3 Demonstration Normalized Difference Vegetation Index (NDVI) analysis using derived from Landsat 7 and Landsat 8.

Fig. S4 Summary of longleaf pine cone count records for sites across the southeastern United States.

Fig. S5 Variation in longleaf pine cone counts for 12 longleaf pine sites in study area.

Fig. S6 Visualization evaluating assumptions of repeated measures ANOVA on longleaf pine cone counts.

Fig. S7 Mean site-level longleaf pine cone counts immediately before and 3 yr following cyclone events.

Fig. S8 Mean site-level longleaf pine cone counts for 34 arbitrary 4-yr periods at 12 longleaf pine sites.

Fig. S9 Changes in winter Normalized Difference Vegetation Index (NDVI) between 2000 and 2021 at 12 longleaf pine sites.

See also the Commentary on this article by Pearse & Wion, **242**: 8–9.