

Life cycle and masting of a recovering keystone indicator species under climate fluctuation

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Abstract. Ecosystem health and sustainability, to a large degree, depend on the performance of keystone or dominant species. The role of climate on population dynamics of such species has been extensively examined, especially for health indicator species. Yet the life-cycle processes and response lags for many species could complicate efforts to detect clear climate signals. Longleaf pine (*Pinus palustris* Mill.) is such a keystone tree species in the southeastern United States that has declined in both abundance and distribution during the past century. Despite research efforts on multiple fronts, the mechanisms behind the large spatial and temporal fluctuations in cone production that affects its regeneration are largely unknown. On the basis of long-term (15–56 yr) monitoring data at 10 sites across the species' native range, we examine the spatial and temporal patterns in cone production and possible climatic effects on those patterns using the information-theoretic approach. Cone production exhibited great variation across sites and years, and long-term data revealed a weak, ca. 3 yr cycle (4 in one case) across the native range. The effects of climate were rather complex, most likely due to a mismatch between the prolonged cone-production life-cycle process and climatic fluctuation. Spatially, sites close to each other generally showed similar physical conditions and temporal trends in cone production. Across sites within longleaf pine's range, moderate climate conditions appear to promote cone production. At most sites, there was an increasing trend in cone production, but how such a trend might be linked to climate change requires further investigation.

Key words: *idiosyncrasy; life history; Moran effect; Pinus palustris; regeneration; sustainability; synchrony; time lag; wavelet analysis.*

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Introduction

The impacts of climate on population dynamics of component species can significantly affect ecosystem health and sustainability, especially when keystone species and global change are considered (Carignan and Villard 2002, Brockway et al. 2006, Lu et al. 2015). Within a growing season, shifts in phenological events for a species (e.g., flowering, seed setting) often match the seasonal environmental conditions. However, for some species with multiyear life-cycle processes, detecting climate signals can be complicated because of a temporal mismatch between regular life-history

events and the irregularity of climate fluctuations; that is, they are most likely unsynchronized (Chen et al. 2016).

Using longleaf pine (*Pinus palustris* Mill.) as an example, this study examines how the multiyear life-history cycle of a species and climate variability might jointly affect long-term cone (seed) production. Longleaf pine was formerly dominant across a broad landscape and is still a keystone species in remnant longleaf pine ecosystems (Schmidtling and Hipkins 1998). Results from this study would help fill a knowledge gap critical for ecological restoration, sustainable management and conservation of multiple resource values of longleaf pine ecosystems.

Despite an historic decline in both abundance and distribution (from exploitation, fire exclusion, and land conversion into other uses), longleaf pine remains an important species in the forest ecosystems of the

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southeastern United States (Fig. 1; Brockway et al. 2005, Oswalt et al. 2012, Chen et al. 2016). Longleaf pine forests are rich ecosystems supporting high biodiversity and high timber production, but they nearly vanished following European settlement (Brockway et al. 2005). Currently, multiple efforts are being made to restore this species within its historical native range. However, longleaf pine can be difficult to naturally regenerate because its annual seed production is often inadequate and less reliable than other southern pine species (Brockway et al. 2006). Previous research indicates that a minimum of 1,850 cones/ha is usually needed for successful natural regeneration under even-aged management, when using the shelterwood method (Boyer 1993).

Knowledge of cycles in longleaf pine cone production is very important for understanding the species' long-term population dynamics and restoration potential (Connor et al. 2014). Early studies noted that episodes of higher seed production (i.e., masting) take place only once every 5–7 yr (Wahlenberg 1946) or 8–10 yr (Maki 1952). But, such observations have not been confirmed in subsequent studies. Boyer (1998) reported large spatial and temporal variation in cone production across the 10 sites described here with a rapid increase since 1986 after 20 yr of relatively stable low levels of production. This variation in cone production is thought to be primarily driven by climate (Pederson et al. 2000, Kelly and Sork 2002, Pearse et al. 2014). However, to date, there is no confirmation of how climate variables might affect cone yield. This is mainly because of the prolonged time period between the initiation and final development of cones, which are influenced by many factors (see also Kelly et al. 2013, Pearse et al. 2014). Particularly, it is largely unknown what biotic (age, size, and life history) and physical (temperature, moisture, elevation, and soil) factors are associated with spatial and temporal variation in cone production.

The numerous plausible combinations of climate variables coupled with other interactive factors operating through the prolonged period of cone/seed production, spanning multiple critical life stages, add extraordinary complexity to detecting climate signals even from long-term observations. Longleaf pine male (catkins) and female (conelets) strobili are initiated during the growing season before buds emerge (Brockway et al. 2006) with catkins forming in July and conelets in August. However, since it takes almost 3 yr from strobili initiation to seed fall (Appendix S1: Fig. S1), climate conditions during the entire 3 yr may affect the final cone production in profound ways. In addition, the relationship of cone production with other life-history events (e.g., pollen shedding, conelet receptivity, and seed setting) is not clear.

A better understanding of the seed/cone production cycle is clearly needed to facilitate longleaf pine restoration and to ensure species sustainability through either natural regeneration (i.e., seed dispersal from trees) or

planting seedlings grown from collected longleaf pine seed. To achieve this goal, we need to explore possible effects of various climatic factors on cone production, by examining the relationships among the associated variables (e.g., annual, seasonal, monthly data) 0, 1, 2, and 3 yr prior to cone formation. In addition to the effects of climate, species life-history cycles and physical factors such as fire regime and management practices could affect cone production. For example, studies in ecosystem productivity show effects of age and fire (Ford et al. 2010), with different relative importance across species and ecosystems. That is, in early stages after fire, productivity usually increases with age and then shows less fluctuation during mature stages (e.g., Guo and Ren 2014), and in some cases, may decline when the system becomes very old.

As a keystone species, longleaf pine is an important indicator of the overall health and sustainability of forest and woodland ecosystems in the southeastern United States where it dominates. Adaptive management of such an umbrella species is likely to favor a great many other species. Here, to fill an information gap in the species' regeneration strategy critical for management of longleaf pine ecosystems, we examine the species' long-term (1958–2014) patterns in cone production such as periodicity (cycles) and trends using data collected from 10 sites across the southeastern region (Fig. 1, Table 1). We then compare the spatial similarities (synchrony) and differences in cone production of longleaf pine across its native range and through time. Finally, we examine what climate factors are correlated with the spatial and temporal variation in cone production. For example, what could have caused the large differences in cone production on sites across the range during the same year or at the same site through different years? We hypothesize that, due to the prolonged cone production cycle, the climatic conditions in the previous three seasons before cone maturation would be important factors causing premature cones to be lost because of harsh conditions during the 3 yr.

Methods

Study sites

Longleaf pine grows in a wide variety of habitats across the southeastern United States, with mean annual temperatures ranging from 16 to 23 °C, annual precipitation from 109 to 175 cm, and elevation from 0 to 600 m (Boyer 1990). At lower elevations (0–150 m), sandy, shale, limestone, and dolomitic parent materials produce soils characterized by low organic matter and relatively low fertility. In the mountains, soils are derived largely from granite, quartzite, schist, phyllite, and slate. In addition, periodic surface fire is essential for sustaining longleaf pine forests (Brockway and Lewis 1997).

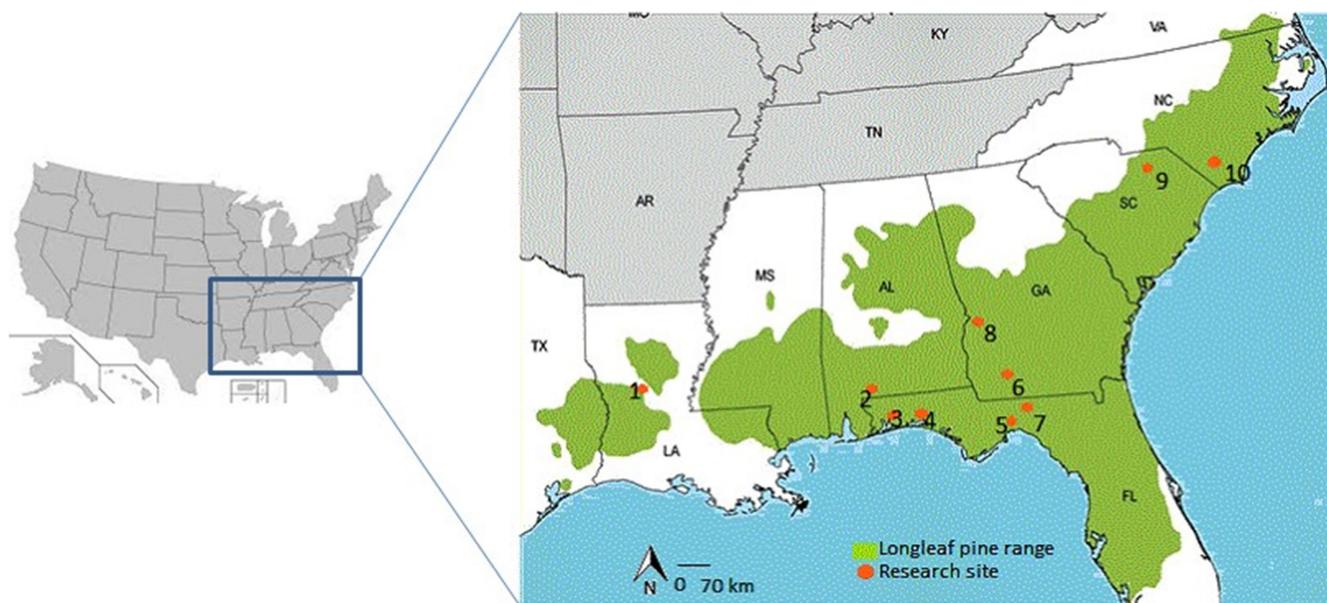


Fig. 1. Historical and present distribution of longleaf pine and locations of the long-term sampling sites across its native range in the United States. Modified from Boyer (1990). The site name and number are given in Table 1.

The long-term (1958–2014) monitoring of cone production on mature and even-aged longleaf pine trees greater than 42 yr old (Pederson et al. 2000) was initiated in 1958 at the Escambia Experimental Forest, Escambia County, Alabama. Since then, 11 sites (with elevations ranging from 0–120 m) were added to this range-wide effort spanning from North Carolina to Louisiana. Monitoring continues at 10 sites distributed among national forests in Florida and Louisiana, state forests in Florida, South Carolina and North Carolina, military bases in Florida and Georgia and privately owned lands in Florida, Georgia and Alabama (Table 1, Fig. 1).

Data collection

At least 10 mature longleaf pine trees were selected for monitoring per site. During mid-to-late April of each year, binocular (8 to 10×) counts on tree crowns were made of green cones (bearing seed for the coming October), brown cones (which shed their seed during the previous October) and unfertilized conelets (which will shed seed during October, 18 months hence). However, we only reported the green cones as the current year’s cone production (for more details about the cone counting, see Boyer 1998).

Table 1. Study sites and associated physical conditions across the native range of longleaf pine in the southeastern United States (see also Fig. 1; Appendix S1: Table S1).

Sites (State)	Lat (°N)	Long (°W)	Elev (m)	Total PPT (cm)	Mean T (°C)	Tmin (°C)	Tmax (°C)	No. cones	CV (no. cones)
1. Kisatchie (LA)	31.34	92.41	37.97	136.10	18.30	12.66	25.41	26.23	0.96
2. Escambia (AL)	31.13	87.16	51.35	152.82	18.05	11.88	25.55	33.11	1.22
3. Blackwater (FL)	30.94	86.81	51.35	152.82	18.05	11.88	25.55	26.43	1.69
4. Eglin (FL)	30.48	86.53	18.30	168.84	18.65	12.82	24.74	20.88	1.33
5. Apalachicola (FL)	30.15	85.02	3.80	131.97	18.67	13.26	26.53	14.87	1.61
6. Jones (GA)	31.22	84.48	53.30	123.34	18.35	12.42	25.03	53.51	1.52
7. Tall Timbers (FL)	30.91	85.84	16.80	141.09	19.99	13.54	26.76	27.66	0.78
8. Fort Benning (GA)	32.34	85.0	119.50	116.78	18.62	13.09	24.80	22.31	0.82
9. Sandhills (SC)	34.08	80.52	56.40	112.60	16.71	10.14	23.53	20.09	1.13
10. Bladen Lakes (NC)	34.71	78.56	31.40	125.19	13.66	9.66	23.47	26.27	1.62

Notes: Total PPT is the mean annual precipitation and Mean T, Tmin, and Tmax represent mean annual temperature, minimum and maximum annual temperature, respectively, observed during this study (1958–2014). CV is the temporal coefficient of variation in cone production (number of cones per tree per year) over the sampling years. To make all sites comparable, cone data were from 1999–2014 when all 10 sites were surveyed; see Fig. 2).

Data analysis

To examine the overall temporal trends and possible periodicities (cyclical patterns) in longleaf pine cone production, we conducted wavelet analyses (Torrence and Compo 1998). Wavelet analysis is a powerful tool that can detect cyclic or periodic patterns in population dynamics at multiple temporal scales. It visualizes the structures buried in the entire or separate observation time periods and expresses the signals in terms of scaled and translated wavelets by wavelet transforms (WTs) and wavelet multiresolution analysis (MRA) (Hubbard 1998, for a preliminary introduction of this analysis, see Dong et al. 2008). Wavelet transform allows us to manipulate features at different scales independently. For spatial patterns, we calculated spatial autocorrelation (Moran's I) to examine the similarity in physical conditions (Table 1) among the 10 sites related to distances between the sites (Liebhold et al. 2004, Koenig and Knops 2013). We also measured correlations in cone production for different populations in relation to the distances between the 10 study sites. We chose five sites with the most observations (45–56 yr; i.e., Escambia, Kisatchie, Jones, Blackwater, and Sandhills) for detailed analyses, such as wavelet analysis and climatic modeling.

The prolonged period of time needed for cones to mature following initiation (~ 3 yr) complicates efforts to determine the appropriate climatic variables to examine when discerning climatic effects on cone production (i.e., there are many combinations of annual, seasonal, and monthly data; Pederson et al. 2000). To examine the possible effects of seasonal and annual precipitation and temperature on cone production, monthly climate data were collected from a nearby weather station for each site. The climatic effects were investigated using monthly, seasonal or annual temperature and precipitation data from 0, 1, and 2 yr prior to cone maturation.

The information-theoretic approach (Burnham and Anderson 2002) was used with a multivariate general linear model to assess the effects of climate variables (monthly rain and temperature; Table 2) on longleaf pine cone production (i.e., the number of cones per tree per year). This approach allows comparisons and selection among multiple models based on the Akaike information criteria (AIC). Nine candidate models (Table 2) were ranked based on the corrected AIC_c for small sample size, the differences in AIC_c between a model and the lowest model (Δ AIC_c), and the corresponding Akaike weights (w). Preferred models are those with the smallest AIC_c and Δ AIC_c and the largest Akaike weights which represents the relative likelihood of a model with respect to those in the candidate pool.

Boyer (1973) and Brockway et al. (2006) reported that cone production is affected by the amount of annual rain during the year of strobili formation (2 yr before seed production, that is, variable L2r_{annual}; see definition in Table 2) and the July temperature during the following conelet formation year (L1t_{jul}). A model consisting

Table 2. Model name and variable specification for the nine models evaluated by the information-theoretic approach.

Model number: Model name	Variables
1: Constant	None
2: July Base	L1t _{jul} , L2r _{annual}
3: July Base + July Rain	L1t _{jul} , L2r _{annual} , L2r _{jul}
4: July Base + July Rain + Early Fall Rain	L1t _{jul} , L2r _{annual} , L2r _{jul} , L1r _{oct} , L1r _{nov}
5: July Base + July Rain + Late Fall Rain	L1t _{jul} , L2r _{annual} , L2r _{jul} , L1r _{nov} , L1r _{dec}
6: August Base	L1t _{aug} , L2r _{annual}
7: August Base + August Rain	L1t _{aug} , L2r _{annual} , L2r _{aug}
8: August Base + August Rain + Early Fall Rain	L1t _{aug} , L2r _{annual} , L2r _{aug} , L1r _{oct} , L1r _{nov}
9: August Base + August Rain + Late Fall Rain	L1t _{aug} , L2r _{annual} , L2r _{aug} , L1r _{nov} , L1r _{dec}

Notes: The "base" is a model component that consists of two variables, the annual rain two seasons previous (L2r_{annual}) and the summer temperature one year previous (L1t_{jul} or L1t_{aug}). The lag variables are defined as Lxy_{zzz} where x = number of lag years (1 or 2), y = climate variable (r = rain or t = temperature), and zzz = abbreviation for month.

of these two variables was formulated as the July Base model. In addition to this July Base model, it was hypothesized that July rain (L2r_{jul}) may also have an effect in the strobili formation year, forming the July Base + July Rain model. The effect of latitude was evaluated by postponing the effect of July rain and temperature until August, providing analogously the August Base and August Base + August Rain models. Preliminary stepwise regression models indicate a potential effect of rain during the fall of the conelet production year (i.e., between pollination and fertilization). This led to the addition of Early Fall Rain (L1r_{oct} and L1r_{nov}) and Late Fall Rain (L1r_{nov} and L1r_{dec}) effects to each of the July Base + July Rain and August Base + August Base models. In addition, the model with only the constant term was also included yielding a total of nine models for evaluation.

We also performed nonparametric Spearman rank correlation analysis to examine whether the coefficients of variation of selected climate variables are related to those of cone production during the sampling periods as described by Kelly and Sork (2002). In addition, we tested the effect of temperature differences between two previous summers on cone production as was done by Kelly et al. (2013) for many other species in New Zealand. This was performed with stepwise regression to see if differences in temperature and also precipitation between previous 1, 2, and 3 growing seasons were important for cone production.

Results

Overall trends

Cone production exhibited great variation across sites and years and lacked statistically significant synchronization

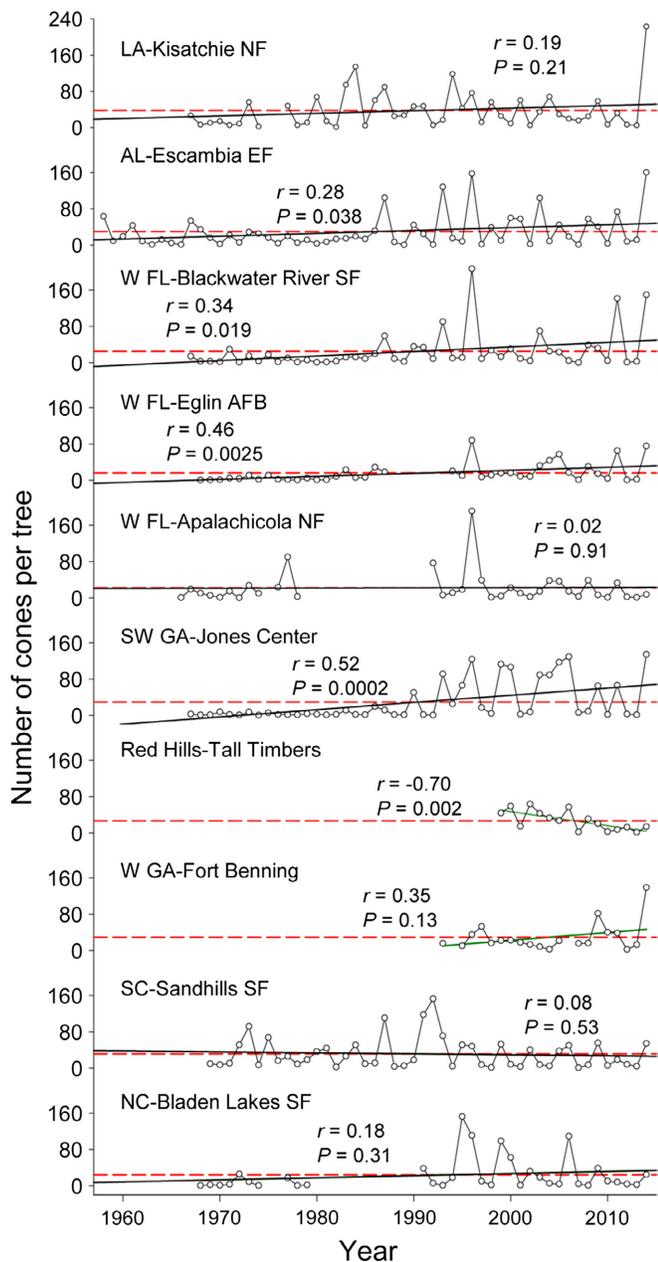


Fig. 2. Cone production of longleaf pine at all 10 sites across its native range over the sampling years. Horizontal dashed lines are means, and the solid straight lines indicate the long-term trends.

across the entire range during most years (Fig. 2). There was a slight to moderate increase through time at seven of the 10 sites, a decrease at Tall Timbers, and no clear change at Apalachicola and Sandhills (Fig. 2). Spatially, sites close to each other generally showed similar physical conditions and temporal trends in cone production. Across all sites, cone production was low in most of the observational years and very high only in a few years (e.g., Appendix S1: Fig. S2). Among the eight sites with data before and after 1980, six showed a general increase in cone production since mid-1980s (for example, at Escambia, there was a big jump in cone production between the

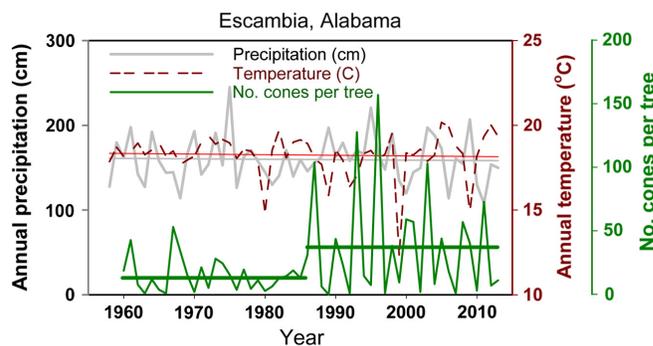


Fig. 3. Cone production of longleaf pine at the Escambia Experimental Forest, Alabama with climate data as references (cone production was divided into two parts, before and after 1986).

1960–1985 and 1986–2014 time periods, Figs. 2, 3). The largest cone crop occurred at Escambia in 1996 (115 cones per tree) and 2014 (99 cones per tree). Across all sites, we did not observe the 5–7 or 8–10 yr trend cycle in high cone production as previously reported (e.g., Wahlenberg 1946, Maki 1952), which was based on shorter term 16-year monitoring. In contrast, wavelet analyses revealed that four out of the five sites with the longest monitoring showed periodicities around 3-yr (Sandhills had a ca. 4-yr cycle; Appendix S1: Fig. S3).

Climate effects

We failed to detect a clear and consistent correlation between climate events and cone production across all the study sites. However, the sudden increase in cone production at most study sites since the mid-1980s appears to coincide with greater climatic variability, especially with temperature (Fig. 3).

Using the information-theoretic approach, we evaluated nine candidate models (Table 2) for the five sites with long-term data and ordered the models by Akaike weights (Table 3). Models with $\Delta AIC_c < 2$ are the top models for consideration, but models with ΔAIC_c between 2 and 7 also have considerable support and such models should not be dismissed (Burnham and Anderson 2002). For example, results for the Escambia site indicate that only the July Base + July Rain + Early Fall Rain model meets this criterion, which contains over 99% of the Akaike weight and is overwhelmingly the best of the nine compared. The next best model is a slight modification which represents a delay in the temperature and rain effects until August, but based on the extremely small Akaike weight, there is little support for this model (Table 3). In general, across the five sites, the models involving climate variables (i.e., rain and/or temperature) for July and August in the years when male and female strobili were formed or conelets were formed in the following years seemed to be important to cone production (see top models [$\Delta AIC_c < 2$] for each site in Table 3).

Table 3. Results from the information-theoretic approach for the five study sites across the native range of longleaf pine.

Model number: Model name	Ln(L)	K	AIC _c	ΔAIC _c	w
Escambia					
4: July Base + July Rain + Early Fall Rain	-166.316	6	346.418	0.000	0.9981
8: August Base + August Rain + Early Fall Rain	-172.586	6	358.959	12.541	0.0002
5: July Base + July Rain + Late Fall Rain	-179.743	6	373.272	26.854	0.0000
9: August Base + August Rain + Late Fall Rain	-180.022	6	373.832	27.414	0.0000
1: Constant	-188.871	1	379.819	33.401	0.0000
6: August Base	-188.607	3	383.694	37.276	0.0000
2: July Base	-188.642	3	383.763	37.345	0.0000
7: August Base + August Rain	-188.323	4	385.463	39.045	0.0000
3: July Base + July Rain	-188.470	4	385.755	39.337	0.0000
Kisatchie					
1: Constant	-155.883	1	313.860	0.000	0.4026
9: August Base + August Rain + Late Fall Rain	-150.355	6	314.920	1.060	0.2369
6: August Base	-155.050	3	316.685	2.825	0.0980
7: August Base + August Rain	-153.846	4	316.691	2.831	0.0977
2: July Base	-155.567	3	317.719	3.859	0.0585
8: August Base + August Rain + Early Fall Rain	-151.972	6	318.155	4.295	0.0470
5: July Base + July Rain + Late Fall Rain	-152.375	6	318.961	5.101	0.0314
3: July Base + July Rain	-155.423	4	319.845	5.986	0.0202
4: July Base + July Rain + Early Fall Rain	-153.793	6	321.796	7.936	0.0076
Jones					
1: Constant	-173.980	1	350.049	0.000	0.2521
9: August Base + August Rain + Late Fall Rain	-168.307	6	350.714	0.665	0.1808
6: August Base	-172.232	3	351.022	0.973	0.1550
2: July Base	-172.326	3	351.211	1.162	0.1410
5: July Base + July Rain + Late Fall Rain	-168.662	6	351.424	1.375	0.1267
7: August Base + August Rain	-171.729	4	352.411	2.362	0.0774
3: July Base + July Rain	-172.216	4	353.385	3.336	0.0476
8: August Base + August Rain + Early Fall Rain	-171.025	6	356.151	6.102	0.0119
4: July Base + July Rain + Early Fall Rain	-171.502	6	357.103	7.055	0.0074
Blackwater					
4: July Base + July Rain + Early Fall Rain	-153.719	6	321.538	0.000	0.7264
8: August Base + August Rain + Early Fall Rain	-154.696	6	323.491	1.953	0.2736
1: Constant	-170.338	1	342.765	21.226	0.0000
9: August Base + August Rain + Late Fall Rain	-164.810	6	343.719	22.181	0.0000
6: August Base	-169.144	3	344.845	23.307	0.0000
2: July Base	-169.352	3	345.263	23.724	0.0000
7: August Base + August Rain	-168.613	4	346.178	24.640	0.0000
5: July Base + July Rain + Late Fall Rain	-166.287	6	346.674	25.135	0.0000
3: July Base + July Rain	-169.335	4	347.622	26.084	0.0000
Sandhills					
2: July Base	-156.317	3	319.219	0.000	0.4170
1: Constant	-159.106	1	320.305	1.086	0.2423

(continued)

Table 3. (continued)

Model number: Model name	Ln(L)	K	AIC _c	ΔAIC _c	w
3: July Base + July Rain	-155.749	4	320.498	1.279	0.2200
6: August Base	-158.240	3	323.066	3.847	0.0609
4: July Base + July Rain + Early Fall Rain	-155.531	6	325.273	6.054	0.0202
7: August Base + August Rain	-158.240	4	325.480	6.261	0.0182
5: July Base + July Rain + Late Fall Rain	-155.667	6	325.544	6.325	0.0176
8: August Base + August Rain + Early Fall Rain	-157.786	6	329.783	10.564	0.0021
9: August Base + August Rain + Late Fall Rain	-158.084	6	330.379	11.160	0.0016

Notes: Ln(L) is the value of the maximized log-likelihood function, K is the number of parameters in the model including the intercept term, AIC_c is the Akaike information criterion corrected for small sample size, ΔAIC_c is the difference in AIC_c between a model and the lowest model, and w is the Akaike weight.

Several components consistently appear in the top candidate models with their AIC_c < 2. The July Base or August Base components (i.e., temperature in the summer before cone maturation and annual rain in the year of strobili formation) appear in all models, supporting earlier work based on field observations (Boyer 1973, Brockway et al. 2006). In addition, July rain or August rain (in the summer of strobili formation) also appears to be an important component for all models. Lastly, early fall rain or late fall rain (in the year before cone maturation) is an important component in all models, except at the Sandhills site which is located far from the other four sites (Fig. 1). These components comprise the top model for the Escambia and Blackwater River sites and the probability of this model being the best of the nine models is 0.9981 and 0.7264, respectively. At these two sites, the effects of July were convincingly more important than August, as is seen from the July variables being in the top models. In contrast to these two sites, the Kisatchie and Jones sites appear to be more sensitive to the effects of August instead of July and late fall rain instead of early fall rain. Although the best model for both of these sites was the simple constant model (Akaike weights being 0.4026 and 0.2521, respectively), there was considerable support for the August Base + August Rain + Late Fall Rain (Akaike weights being 0.2369 and 0.1808, respectively).

Our investigation into alternative variables that may have influence on cone production revealed only weak relationships. The CV of mean annual temperature was significantly correlated with the CV of cone production through time ($r = 0.62, P = 0.042$), but the means and CVs of mean annual precipitation, minimum temperature and maximum temperature were not (Appendix S1: Table S2). Stepwise regressions, using yearly difference variables defined as lag years 1–2, 1–3, and 2–3, showed that, at Escambia, differences in seasonal (April–October) temperature for lag years 2–3 and annual rain for lag years 1–2 seemed somewhat important (selected as middle candidates); for Sandhills, the difference in annual temperature for lag years 2–3 was the first variable selected. However, for Jones, the difference in seasonal rain for

lag years 1–3 was selected late, for Blackwater, the difference in seasonal temperature for lag years 2–3 and seasonal rain for lag years 1–2 was also selected late and, for Kisatchie, no difference variable was selected. Since there were no consistent patterns, we did not incorporate any of these difference variables into the information-theoretic approach for further analyses.

Spatial and temporal relationships

As expected, spatial synchrony in cone production between the sites clearly declined with distance (Fig. 4; see also Appendix S1: Table S1), probably corresponding to the reduced similarity in physical conditions with distance. However, many of the closer sites were also dissimilar to one another. In addition, contrary to within-site patterns in which cone production usually increases with precipitation (e.g., at Escambia; Table 3), across the native range of longleaf pine, sites with moderate climate conditions (i.e., mean annual precipitation and temperature) tended to have

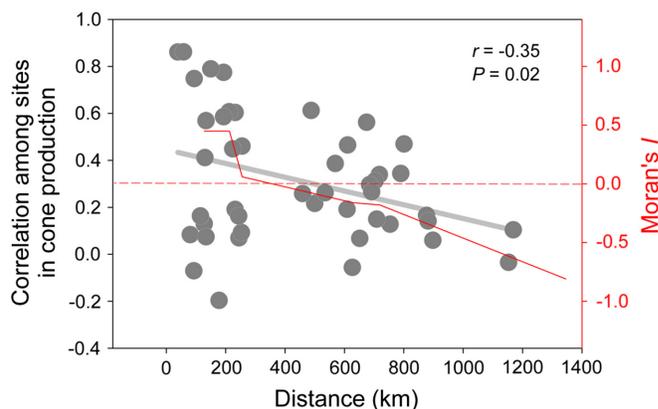


Fig. 4. Spatial synchrony measured by correlations in cone production among the 10 study sites declined with distance from each other (i.e., “Moran effect”, Peltonen et al. 2002, see also Appendix S1: Table S1). The red line represents spatial autocorrelation in physical conditions (Table 1) among the 10 study sites—sites closer to each other showed higher similarity in physical conditions (see Fig. 1, Table 1).

greater cone production, as shown by the roughly hump-shaped curves in relation to some climate variables (Fig. 5).

Discussion

Our long-term study, using longleaf pine as a keystone indicator species for longleaf pine forest health, demonstrates how life-history cycles and climate change can jointly affect seed production. It is possible that other combinations of climate variables might also have produced significant results and their underlying causes need to be explored in the future. The results from our analyses have several management implications. For example, managers may benefit by planning ahead relative to the known reproduction cycles vs. climate conditions during critical phases of cone production

(e.g., July and August). Understanding when good cone crops are likely will help managers to better mobilize the assets necessary for timely site preparation treatments needed for natural regeneration success and for cone/seed collection efforts that support longleaf pine seedling production in nurseries for artificial regeneration. In addition, despite differences among sites, the level of spatial synchrony in cone production indicates that lessons learned about the successful management and conservation practices for longleaf pine restoration and sustainability should be applicable on nearby sites.

One interesting observation of this study is the ca. 3-year cycle in cone production across longleaf pine's native range, which seems to reflect the time needed for cone production from the initiation of strobili to cone maturation. The exception to this is the Sandhills, the site located at the highest latitude, where the metabolic rate may be lower (Brown et al. 2004) and the cycle appears to be 4 yr. Thus, to achieve high cone production, longleaf pine must initiate a high number of both male and female strobili of good quality. If this does not occur, and even if the environmental conditions are highly favorable before cones mature in about 3 yr, the initial low number of strobili already sets the upper limit on final cone production. However, it is important to point out that the 3-year period only indicates cone production cycles, rather than a masting year occurring every 3 yr as the latter occurs only after cone or seed production reaches a certain level (Kelly and Sork 2002). Another intriguing result is the general increase in cone production at seven of 10 sites, especially since mid-1980s. However, we have not been able to explain this phenomenon using the annual temperature or precipitation (e.g., Fig. 3).

The spatial synchrony in cone production which declined with distance (Fig. 4; see also Appendix S1: Table S1) seems to reflect the species' responses to the reduced similarity in physical conditions with distance (the so called "Moran effect"; Moran 1953, Peltonen et al. 2002, Liebhold et al. 2004, Koenig and Knops 2013). The clear dissimilarity among many of the closer sites may also reflect the variation in other conditions such as soil and elevation. Viewing the entire longleaf pine native range, it is clear that the dynamics of cone production is very complex in both space and time, and many interactive factors are involved in controlling cone production. Our long-term comparative study across multiple sites clearly shows that each site must be treated individually as there is no general set of conditions controlling cone production among sites. Part of the reason for such idiosyncratic nature of longleaf pine could be linked to the latitudinal and altitudinal shifts in phenology across its relatively large native range (Fig. 1). That is, even in the same month, different stages of the longleaf pine life cycle are responding to temperature and precipitation across the longleaf pine's range. Although we were unable to consider several

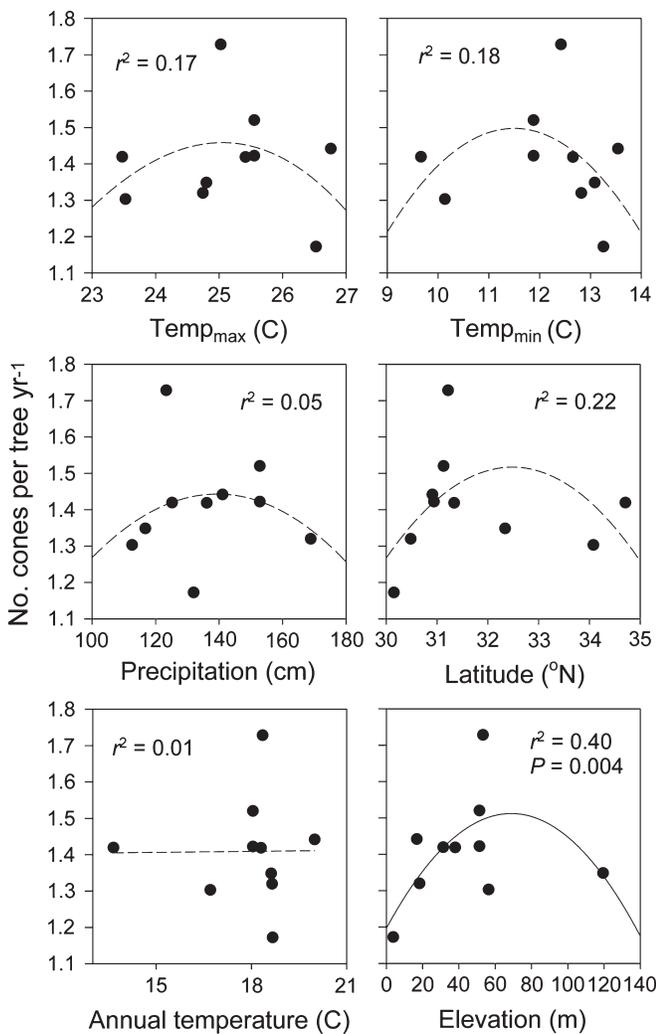


Fig. 5. Relationships of physical variables with longleaf pine cone production. Each data point represents a long-term study site. Results are based on Poisson (log-linear) regression, and dashed lines indicate insignificant relationships. The dashed curves indicate nonsignificant unimodal response curves in cone production to various physical variables.

other potentially important factors, such as fire, age, size and soil because suitable data were lacking (Deng et al. 2012), we are able to offer the following insights.

First, detecting climate effects on longleaf pine cone production has proven difficult, mainly due to the prolonged cone production process (~3 yr), the complexity in detecting influential climate variables (endless combinations and durations), and the species' possible nonlinear responses. We recognize that seasonal climate conditions corresponding to critical life-history events are more important for a species than are average annual climate data. We found that weather conditions (i.e., climate variables such as precipitation and temperature) in July–August during the years when male and female strobili are initiated or conelets were formed in the following years seemed to play a major role in controlling cone production (Table 3; Appendix S1: Fig. S1). It takes almost 3 yr for longleaf pine to generate a cone crop, from strobili formation to the setting of seeds, and many events can happen during this long process that can affect the final number of cones and seeds (Brockway et al. 2006). For example, usually fewer than half of the conelets survive to eventually form mature cones. Since climate events related to male strobili (catkins) initiation differ from those favoring female strobili (conelets), high numbers of catkins and conelets do not necessarily coincide (Shoulders 1967). The male and female strobili of longleaf pine are initiated during the growing season before buds emerge. Catkins form in July while conelets in August. The number of conelets may be related to climate conditions during the year of initiation and yet the number of cones surviving to maturity for final seed production also largely depends on the climate variations during the entire three-year period. Additionally, the switch in importance between July Base and August Base climate variables among the five study sites probably reflects the interplay between latitudinal and/or elevational gradients in the phenology of longleaf pine (Table 3; Appendix S1: Fig. S1).

Our results are not consistent with findings by Kelly et al. (2013) that the difference in temperature between two previous summers is an important cue in detecting masting. In contrast, all previous field observations indicate that, for longleaf pine, precipitation (or drought) is an important factor. This is probably because, unlike the species examined by Kelly et al. (2013) which can finish seed production in one season, longleaf pine has a prolonged period (ca. 3 yr) of seed production from initiation to maturation. This is largely because any of the critical components of cone production, such as catkin buds, cone buds, pollen, conelets or small green cones, could be lost in any season/year due to harsh environmental conditions during the 3-year period.

In general, in terms of overall climate effects across the native range of longleaf pine, sites with moderate climate conditions seem to promote somewhat higher cone production (Fig. 5). For each site, however, warmer July–August and wetter falls (October–November) seem to be

more favorable for cone production (e.g., Escambia site; Table 3). In addition, although the temperature CV is linked to CV of cone production (using log-transformed CVs; Appendix S1: Table S2), similar to observations at larger scales by Kelly and Sork (2002), it is difficult to predict the consequences, if temperature CV continues to increase along with global warming in the future.

It is puzzling why cone production suddenly began to increase during the 1980s at four of the study sites (Figs. 2, 3). Indeed, climate change may also influence masting patterns through its effects on environmental variability (Fig. 3; Koenig et al. 2015). Since the 1980s, atmospheric extremes in temperature, moisture, storms and wildfires have contributed to a multidecadal period of increased environmental variability (Ford et al. 2010). For example, at the Escambia site, the coefficient of variation (CV) of annual mean temperature was almost doubled, increasing from 0.05 during 1958–1985 to 0.09 during 1986–2014. However, there was no change in the coefficient of variation for annual mean precipitation during the two periods, which were 0.18 vs. 0.17, respectively (Fig. 3).

Second, at five of the 10 sites, cone production for longleaf pine was rarely high during 2 successive years. This could be because one year's high productivity exhausts critical resources, such as nitrogen, leading to lower production during the following year(s) even when climate conditions may still be highly favorable (Crone et al. 2009). However, unlike many plant species which finish their life cycle in one year, such a clear consecutive-year trade-off pattern may be less common in woody plants in families such as Pinaceae and Fagaceae that need multi-years to produce seeds.

Third, our study shows how the analysis of data from longer term and multisite observations can improve our understanding of cone production dynamics over previously reported patterns based on short-term or single-site studies. For example, although strong synchrony is lacking across all 10 sites, the sites close to each other generally show similar physical site conditions and temporal patterns in cone production (Appendix S1: Table S1). Also, our longer term data did not confirm the 5–7 or 8–10 yr cycle in cone production previously reported and based on shorter term observations (Boyer 1998).

Compared with earlier findings (e.g., Wahlenberg 1946, Maki 1952), the patterns in cone production are clearly scale-dependent in terms of observational time (i.e., longer term studies can reveal something new or different from short-term studies). For example, with large fluctuations in temporal cone production, using the number of standardized deviations of the annual cone production from the longer term vs. shorter term mean seed production could yield different results in classifying mast and nonmast years (LaMontagne and Boutin 2009, Moreira et al. 2014). In our case, we could use data from 1958–1985 vs. 1986–2014; both could be called “long-term” data sets. If we use the entire 56-yr data set

to define mast years, the first data set would not have a “mast year” while the second would have many mast years (Fig. 3; see also Fig. 2 for some other sites with a similar situation).

Conclusions

Cone production is a key indicator of longleaf pine regeneration and sustainability. Although climate change would affect every life stage of a species, life-history cycles, including time needed for seed production and other factors, could complicate efforts to detect clear climate signals (Brockway et al. 2006). Such complications in revealing climate effects on cone production because of species' life cycles could be a common phenomenon especially for long-lived species, since climate variation is mostly random or irregular and the species may have more or less regular life-cycle processes. Our results signal that, in addition to more sophisticated analyses of climate data, future integrated studies must identify other life-history factors such as germination (Linhart et al. 2014) and site-specific conditions such as soil characteristics, fire regimes and local management practices (Haymes and Fox 2012), which are also crucial for the natural regeneration and sustainability of longleaf pine ecosystems (Brockway and Lewis 1997, Lahoz-Monfort et al. 2014).

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