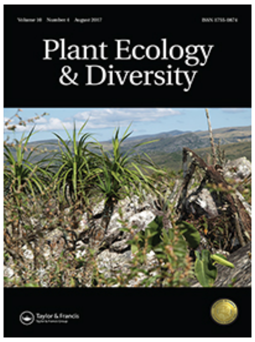

Plant Ecology & Diversity

ISSN: 1755-0874 (Print) 1755-1668 (Online) Journal homepage: http://www.tandfonline.com/loi/tped20

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**To cite this article:** Qinfeng Guo, Dale G. Brockway & Xiongwen Chen (2017) Temperature-related sex allocation shifts in a recovering keystone species, Pinus palustris, Plant Ecology & Diversity, 10:4, 303-310, DOI: 10.1080/17550874.2017.1402968

**To link to this article:** https://doi.org/10.1080/17550874.2017.1402968

*Plant Ecology & Diversity*, 2017
Vol. 10, No. 4, 303–310, https://doi.org/10.1080/17550874.2017.1402968

ARTICLE

# Temperature-related sex allocation shifts in a recovering keystone species, *Pinus palustris*

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(*Received 14 April 2017; accepted 6 November 2017*)

***Background***: The possible effects of climate change on sex allocation of a species have recently emerged as a topic of interest, relative to population sustainability via natural regeneration. Also, the universality of pollen limitation for reproduction and how climate may influence it in different taxonomic groups remain to be explored.
***Aims***: The aim of this study was to examine how climate fluctuation may affect sex allocation in *Pinus palustris*.
***Methods***: We used a long-term observational data on *P. palustris* (1957–2014), including pollen, female conelets and cone production.
***Results***: We found that, unlike cone production with its ca. 3-year cycle, (1) pollen (male) and unfertilised conelet (female) production did not exhibit any temporal cycles, (2) pollen and unfertilised conelet production showed lower variation than cone production, (3) pollen and unfertilised conelet production were positively correlated to one another and to final cone production, (4) an optimal male-to-female sex allocation ratio exists for promoting cone production and (5) sex allocation ratio was positively correlated with temperature.
***Conclusions***: Our findings shed new light on both the reproductive ecology and management of *P. palustris* ecosystems under changing climates (e.g., through alteration of pollen density and thus the resulting sex allocation).

**Keywords:** climate change; cone production; sex ratio; life cycle; longleaf pine; long-term study; pollen limitation; regeneration

## Introduction

Seed production, a key regulator of the regeneration and population dynamics for a species, often has complex relationships with multiple intrinsic (e.g., genetics, life history) and extrinsic (e.g., climate, resource availability) factors (Campbell and Halama 1993; Brockway et al. 2006; Chen, Brockway, et al. 2016; Chen et al. 2017; Patterson 2017). Biologically, seed production can be controlled by genetics, life cycle (Guo et al. 2016), sex ratio or allocation ratio (i.e., allocation of resources to male vs. female reproduction in sexual species) (Charnov 1982) and other phenomena (Rapp et al. 2013). Pollen availability (i.e., pollen density and timeliness) and sex allocation in general have also been recently considered as factors influencing each seed crop (Kelly et al. 2001; Knight et al. 2005). Manipulating the sex allocation and pollen density may have practical importance for achieving management objectives related to species conservation or stand regeneration, particularly under the potential threat of rising temperatures.

Sex allocation theory (Charlesworth and Charlesworth 1981; Charnov 1982) predicts that monoecious plants have flexible sex allocation depending on spatio-temporal changes in habitat quality (Freeman et al. 1981; Lloyd and Bawa 1984). However, to date, whether seed crops (or cone crops in the case of conifers) are limited by pollen density remains controversial (Friedman and Barrett 2009). Recent meta-analyses have indicated that pollen limitation on seed output is widespread and often severe in flowering plants (Knapp et al. 2001; Sork et al. 2002), but less common in non-flowering plants (Wagner et al. 2016), such as gymnosperms (Knight et al. 2005). Among conifers, one study in Scots pine (*Pinus sylvestris*) reported that pollen was not limiting (Robledo-Arnuncio et al. 2004), while results for whitebark pine (*Pinus albicaulis*) indicated that there was a pollen limitation (Rapp et al. 2013). Nevertheless, relative to other taxa, sex allocation has rarely been studied in monoecious (i.e., having both male and female reproductive organs growing on the same individual) wind-pollinated trees such as pines thus a major and critical information gap remains (Ne'eman et al. 2011).

In addition to the inconsistent evidence for pollen limitation, it is possible that, even for the same species, pollen limitation may occur in some years but not during other years. Also, in years with or without pollen limitation, the number of female strobili (conelets) might also be limiting, especially among wind-pollinated species (Burd and Allen 1988; Friedman and Barrett 2009). Consequently, there may be an optimal sex allocation for a species at a particular location that promotes seed production. Identifying this optimal sex allocation and the underlying mechanisms in seed production are subjects of key interest, because they ultimately determine whether

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*Corresponding author. Email: qguo@fs.fed.us the species can successfully regenerate in the future (Brockway et al. 2006).

Abundant evidence demonstrates that climate change affects plants in multiple ways, but some new studies also indicate that such effects could emerge in somewhat surprising ways (Boyer 1973; Isbell et al. 2015; Patterson 2017). Major information gaps, such as how life history traits of many plant species may be influenced by climate change and how their responses may be sex specific, remain largely unknown or difficult to address. For example, Petry et al. (2016) have found that climate change can significantly alter plant sex ratios and thus species distribution. However, the frequency and extent with which such an effect may occur among species or a particular taxonomic group remains largely unknown, more so for plants than for animals.

Longleaf pine (*Pinus palustris*), a wind-pollinated monoecious species, is a keystone and indicator species in the ecosystems in which it remains a dominant component across the southeastern United States (Chen, Guo et al. 2016). The endangered longleaf pine ecosystem, which drastically declined as a result of harvest without replacement, land-use change and fire exclusion, has been slowly recovering in recent years (Guo et al. 2016). Restoration efforts for this species have been constrained by highly variable and often low seed production, for supporting natural regeneration and production of longleaf pine seedlings in nurseries, and by a lack of critical information regarding its natural regeneration mechanisms (Brockway et al. 2006). Although fertile seeds may occur in the smaller number of cones grown on younger (at least age 9) sapling or pole-stage trees (<20 cm at dbh) (Wahlenberg 1946), substantial longleaf pine cone and seed crops are not produced until trees approach 30 years of age. The small conelets are typically pollinated during March but will not become fertilised for almost another 11 months (until a pollen tube grows from the surface of the conelet deep into its ovary) (a complete reproductive cycle of longleaf pine is available online: http://onlinelibrary.wiley.com/store/10.1002/ehs2.1226/asset/supinfo/ehs21226-sup-0001-AppendixS1.pdf). It is possible that insufficient pollen availability in this species can lead to poor cone crops and regeneration failure.

The possibility and degree of pollen limitation can be examined both spatially and temporally. However, long-term data are exceedingly rare. Using the only long-term data set on record (Figure 1), we examined the temporal fluctuation in pollen density and cone production to discern whether pollen availability was related to cone production for longleaf pine. We asked the following specific questions: (1) How do the numbers of pollen and unfertilised conelets as well as the sex allocation vary through time? (2) How is sex allocation related to cone production and is there an optimal sex allocation for cone production in longleaf pine? (3) How may climate change affect the sex allocation in longleaf pine? Answers to these questions would provide new insights relevant to basic ecology (i.e., general effects of relative male and female efforts on reproductive output) and to management of longleaf pine ecosystems.

## Materials and methods

Longleaf pine pollen data were collected for 56 years (1957–2013) at the Escambia Experimental Forest. This 1214-ha, long-term study site is located 11 km south of Brewton, Alabama, USA (31°13′N, 87°16′W; elevation: 51 m a.s.l.), and was established by the USDA Forest Service in 1947 to study the ecology and management of longleaf pine forests. When the study was established in 1957, trees at this site were about 50 years old and stands were selected because they typified low-density (less than 9.2 $m^2$ $ha^{-1}$ in basal area), second-growth longleaf pine forests. Sample trees ranged from 27 to 46 cm at dbh, with a mean diameter of 34 cm and mean height of 24 m. Climate at the site is temperate subtropical with long, hot and humid summers and a growing season exceeding 200 days. Mean daily temperatures range from 16 to 23° C and annual precipitation of 1090–1750 mm is uniformly distributed throughout the year (Boyer 1973). The soils

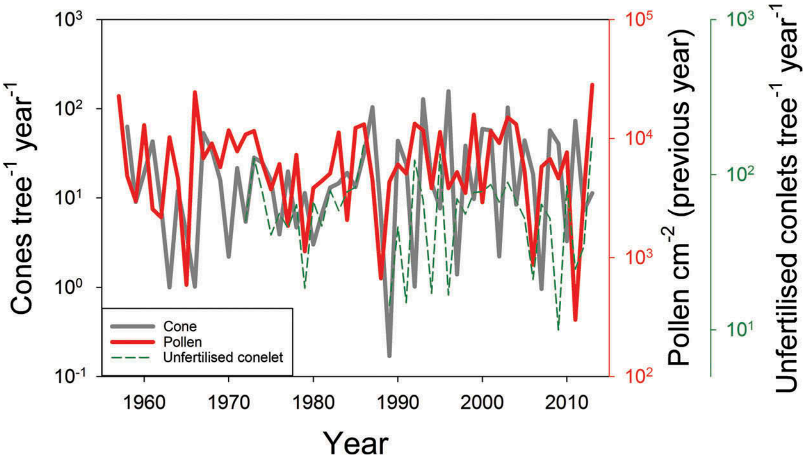

Figure 1. Temporal fluctuation of pollen density (grains $cm^{-2}$) from 1972 to 2013, unfertilised conelets per tree from 1957 to 2013 and cone production (cones per tree) for longleaf pine from 1958 to 2014 at the Escambia Experimental Forest, AL, USA.

consist predominantly of sandy loams and range from well-drained gently rolling sandy uplands to lesser areas of poorly drained stream bottoms. The understorey plant community is dominated by grasses, legumes, composites and other forbs, in association with a lesser component of shrubs and hardwood tree seedlings which are typically controlled by prescribed surface fires, applied on a 3-year cycle.

Pollen traps, consisting of dimensionally stable tape and aluminium slides with open cells for pollen to adhere to the tape (Grano 1958), were exposed in a standard weather instrument shelter during the period of pollen shedding (typically mid-February through early April). Traps were changed 3 times per week, totalling 24 traps with the time of exposure and recovery of each noted and the duration of exposure recorded. Given the overwhelming dominance of longleaf pine and absence of other sexually mature tree species near the sampling location, only the pollen of longleaf pine was found on each slide during the specific sampling period. Longleaf pine shed pollen early in the season and the pollen (55–60 μm in diameter) could be clearly distinguished from much smaller particles of aerial debris or possible pollen of other species that fell onto the traps. The density of longleaf pine pollen deposited on each trap was estimated by counting all pollen grains under each of 10 systematically distributed 100× microscope fields per trap (Boyer 1973). Pollen counts were converted to the average number of pollen grains per cm$^2$. These data were then used to establish the peak time of pollen shedding and the trends in pollen density across the multiple sampling intervals.

Unfertilised female strobili were counted each April, following pollination but before fertilisation, in the crowns of 30–70 longleaf pine trees at the site, during the period 1972–2014 (except in 1987–1988). These data provided an estimate of the potential cone crop for the following calendar year (i.e., 18 months later). Cone production for the current year was assessed on the same mature longleaf pine trees via the same procedure, by conducting visual counts from the ground using 8–10× binoculars during middle-to-late April of each year. In these tree crowns, counts were made of both green cones (bearing seeds for the following October, 6 months hence) and brown cones (which had already shed their seeds during the previous October). We used the mean number of green cones per tree as an estimate of the longleaf pine cone crop for each year (for details about the cone counting method, see Guo et al. 2016).

Since longleaf pine is a monoecious species, which produces large amounts of pollen relative to its smaller number of unfertilised conelets, its “sex allocation ratio” (i.e., pollen density/mean number of unfertilised conelets per tree) could not be 1:1. Unlike previous studies that have used some still-debated currencies, such as biomass or nutrients, to measure sex allocation (Ne’eman et al. 2011), we examined temporal patterns (e.g., cycles) of the relative abundance of pollen vs. unfertilised conelets, as well as sex allocation ratio, using wavelet analysis (Hubbard 1998; Torrence and Compo 1998). Wavelet analysis is a powerful tool that can detect cyclic or periodic patterns in time-series data at multiple scales. It can effectively reveal and visualise the structures buried in the observation time periods and reflect the signals in scaled and translated wavelets by *transformation and* multi-resolution analysis (for detailed description of this analysis, see Torrence and Compo 1998). In addition to the possible effects of climate and other physical factors, final cone production is primarily determined by the availability of male (pollen) and female unfertilised strobili. To examine the combined or interactive effects of these two key variables, we also made a cross-wavelet analysis by adopting and analysing a complex formed by pairing data of pollen and unfertilised conelets.

To examine the possible effects of climate on pollen, unfertilised conelet and cone production and sex allocation, we used weather data collected from a weather station located at the study site. The climatic effects were investigated using four selected variables: annual precipitation, annual temperature, minimum monthly temperature ($T_{\min}$, coldest month) and maximum monthly temperature ($T_{\max}$, warmest month). As pollen, unfertilised conelets and cone crops were sampled early each year, the climate data from each previous year were used as independent variables (for detailed information regarding the life cycle of longleaf pine, see Appendix S1 in Guo et al. 2016). We carried out linear regression analyses using log-transformed data and second-order regression on raw data to examine the temporal correlations among pollen, unfertilised conelet and cone production. We also conducted linear regression analyses to investigate the possible effects of the selected climate variables on these biotic variables and to sex allocation.

## Results

The production of longleaf pine pollen, unfertilised conelets and cones is described by different temporal frequency distributions for the period 1957–2014 (Figure S1). All three variables exhibited significant temporal variation, with cone production being most variable (CV = 1.22), followed by pollen (CV = 0.77) and unfertilised conelets (CV = 0.58; Figure 1). Unlike the yield for cones, the production of pollen and unfertilised conelets did not exhibit a clear 3-year cycle detected by wavelet analyses for green cone production (Figure S2). The cross-wavelet spectrum showed some level of cyclic behaviour, i.e., large covariance around 3–5 (significant) and 10–12 years (non-significant) in the bivariate time series of pollen and unfertilised conelets (which together contributed the most to final green cone production) (Figure S3).

Our long-term records revealed that both pollen and unfertilised conelets during the previous year had strong but somewhat different correlations with cone production during the following year (Figure 2, S4). The intercept and

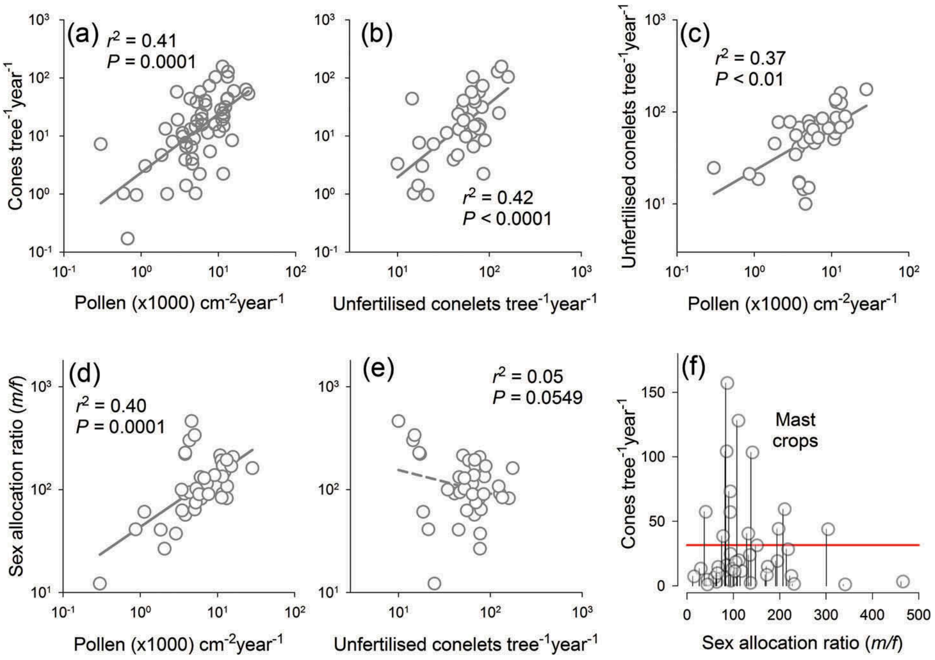

Figure 2. Top: Relationships among pollen density (previous year), unfertilised conelets (previous year) and final mature cone production at the Escambia Experimental Forest, Alabama, USA, based on log-transformed data: (a) pollen vs. cone: $r^2$ = 0.27, $P$ = 0.001; (b) unfertilised conelets vs. cone: $r^2$ = 0.48, $P$ < 0.001; (c) pollen vs. unfertilized conelets: $r^2$ = 0.56, $P$ < 0.001). Bottom: Relationships between sex allocation ratio (male-to-female) and pollen density (d), unfertilised conelets (e), and final cone production (f) of longleaf pine (1958–2014). Similar to Moreira et al. (2014), data points above the horizontal line (mean cone production during 1958–2014) in (f) represent mast crops qualitatively defined as years when a heavy cone crop is produced (Silvertown 1980).

slope of the former were −2.662 and 1.010 (isometric), respectively, whereas corresponding values of the latter were −0.601 and 1.272 (positive allometry or accelerating returns), respectively (Figure 2(a,b) based on log-transformed data; see also Figure S4a,b based on raw data). We also observed that, across the years, the two sexes (i.e., pollen and unfertilised conelets) were positively related to each other (intercept = −0.392, slope = 0.485 in Figure 2(c), and intercept = 12.429 and slope = 0.564 in Figure S4c).

Sex ratio allocation was positively related to pollen density and showed no clear relationships with unfertilised conelets (Figure 2(d,e)). There was no linear relationship between the male-to-female sex allocation ratio and cone production. In general, when the sex allocation ratio (CV through time = 0.68) was at intermediate values between 50 and 150, the large cone crops (i.e., masting) were observed (Figure 2(f)). The maximum cone production occurred when sex allocation ratio was close to 100 but very small cone crops could occur with any sex allocation ratio.

Pollen density showed positive relationships with annual, minimum ($T_{\min}$) and maximum ($T_{\max}$) temperatures (i.e., pollen limitation was more pronounced in relatively cold years), while unfertilised conelets only increased with $T_{\min}$ (Table 1). Sex allocation ratios also increased with annual, minimum ($T_{\min}$) and maximum ($T_{\max}$) temperature (Figure 3). We found no evidence that sex allocation or production of pollen, unfertilised conelets and final cones were related to annual precipitation (PPT; Table 1).

There appeared to be a trade-off in cone production during two successive years, i.e., high cone production in 1 year was most likely to be followed by low cone production in the following year. Randomisation tests (see Supporting information for detailed description of the procedure) showed that the null hypothesis of no association of cone production between any two consecutive years was rejected ($P$ = 0.001). However, no such trade-off was observed for pollen and unfertilised conelets (Figure S5).

## Discussion

The influence of climate change on sex allocation may differ between plants and animals, but the relevant information gap is much wider for the former than the latter. This is probably a result of practical difficulties (e.g., for monoecious species) and our lack of appreciation for the role of sex allocation and the ways in which it can be altered by a changing climate. Recent studies found that warmer climate favours males more in some plants (Petry et al. 2016) and animals (Ospina-Alvarez and Piferrer 2008) and the degree of such climate effects may be different among species. Although male strobili (pollen) and female strobili (unfertilised conelets) for longleaf pine were positively related to each other and to final cone production during our study, it was clear that warmer climate in the previous year disproportionally favoured more male strobili (i.e., greater pollen output), thus increase sex allocation ratio. If this finding becomes

Table 1. Results from linear regression analyses between four selected physical variables, i.e., annual precipitation (PPT), annual temperature (*T*), minimum monthly temperature ($T_{min}$) and maximum monthly temperature ($T_{max}$) in previous years, and four biotic variables, i.e., pollen density, unfertilised conelet production, cone production and sex allocation ratio at the Escambia site, AL, USA.

| Climate | Pollen grains ($cm^{-2}$ $year^{-1}$) | | | | Unfertilized conelets ($tree^{-1}$ $year^{-1}$) | | | | Cone ($tree^{-1}$ $year^{-1}$) | | | | Sex allocation ratio | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Coefficient* | *MS* | *F* | $r^2$ | *Coefficient* | *MS* | *F* | $r^2$ | *Coefficient* | *MS* | *F* | $r^2$ | *Coefficient* | *MS* | *F* | $r^2$ |
| PPT (cm) | 3.54 | 0.02 | 0.12 | 0.002 | 1.57 | 0.00 | 0.02 | 0.000 | 0.83 | 0.25 | 0.65 | 0.014 | 2.24 | 0.03 | 0.36 | 0.009 |
| *T* (°C) | −0.77 | 2.08 | 17.15 | 0.244*** | 0.20 | 0.00 | 0.03 | 0.001 | 0.09 | 0.48 | 1.75 | 0.036 | −0.98 | 0.82 | 10.93 | 0.233** |
| $T_{min}$ (°C) | 1.61 | 2.24 | 18.89 | 0.263*** | 0.19 | 0.50 | 6.34 | 0.143* | 0.09 | 0.04 | 0.09 | 0.002 | 0.86 | 0.78 | 10.31 | 0.221** |
| $T_{max}$ (°C) | −0.45 | 1.14 | 8.20 | 0.134** | 1.60 | 0.05 | 0.58 | 0.015 | 1.55 | 0.66 | 1.75 | 0.035 | −1.22 | 0.56 | 6.88 | 0.151* |

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
The data for nonphysical variables were log-transformed prior to analyses.

confirmed at other sites across its entire native range, a continuing increase in sex allocation ratio, beyond 300 from further climate warming, would reduce future cone production for this species (Figure 2(f)). Regardless, the high cone production at intermediate values of sex allocation ratio suggests that there is selection against extreme male- or female-biased allocation.

Earlier studies, using 10 years of longleaf pine data, did not report any correlation between pollen density and cone production. By contrast, our results, based on much longer term data, revealed a strong correlation between pollen density and cone production (Figure 2(a)). Many studies have provided evidence for a pollen limitation in the seed production of flowering plants, although to varying degrees (Moreira et al. 2014). Our results, from long-term observational data, indicate the presence of both a pollen and a female strobili (conelet) limitation in longleaf pine. Although how widely such a limitation is present remains to be seen in other pines or all conifers in general (Ashman et al. 2004), it is unlikely that our results were influenced by tree size (Ne'eman et al. 2011), since field sampling did not include trees younger than 50 years old (Boyer 1987). Nevertheless, the relative role of stochasticity in cone production remains to be examined in the future.

In contrast with spatial results for Scots pine (Savolainen et al. 1993) or among individual trees for whitebark pine (Rapp et al. 2013), we also observed a positive relationship (i.e., no trade-off) between the two sexes (male and female strobili) for all sampled trees across years at this long-term study site. However, our observation is consistent with Rapp et al. (2013) that when averaging over trees among years, in years of greater pollen production, there was also greater female conelet production. Although pollen density appears to limit cone production on a year-to-year basis, increasing environmental variability and climate change, such as variable temperature and moisture regimes related to periods of drought and/or tropical storms (Boyer 1973), may also be related to the more frequent heavier masting of longleaf pine since the mid-1980s (Guo et al. 2016). However, how environmental factors interact with the production and survival of female strobili and pollen and therefore lead to better cone crops remain to be tested. Also, future work needs to examine why cone production shows proportional (isometric) change with pollen density but accelerated increase with female conelet production (positive allometry).

Given the recently discovered roughly 3-year cycle in cone crops for longleaf pine (Guo et al. 2016), it is somewhat surprising that pollen and unfertilised conelets do not exhibit the 3-year cycle (Figure S2). However, even without such cycles, pollen and unfertilised conelet production and sex allocation clearly reflect climate signals related to temperature. It is important to note that, similar to cone production, pollen and unfertilised conelets are also influenced by environmental conditions, such as resource availability, pests and disease (Boyer 1973; Campbell and

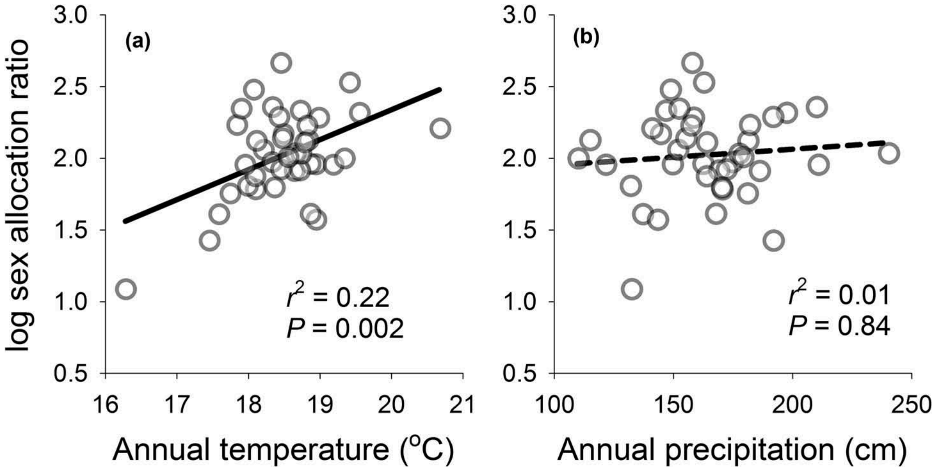

Figure 3. Male–female sex allocation ratio showed an increasing trend with mean annual temperature and precipitation, consistent with Petry et al. (2016). Higher ratios could lead to increased pollination and thus seed production which encourage plants to expand their range (e.g., at higher elevations) in response to climate change.

Halama 1993). While pollen coupling can synchronise masting in the absence of external forcing (Crone and Rapp 2014), environmental variation can also lead to synchrony through the "Moran effect" (i.e., spatial correlations in environmental stochasticity can synchronise populations.

Optimal longleaf pine green cone production occurs when the sex allocation ratio is between 50 and 150, with the best values around 100. This seems to contradict the fact that both pollen and female conelets are positively correlated with cone production. However, this could be explained by the differing positive correlations of pollen vs. unfertilised conelets with cone production, in terms of strength and shape shown in Figure 2(a vs. b) based on log-transformed data and also in raw data (Figure S4: concave downward in panel a but upward in panel b). That is, after pollen density reaches a certain level, cone production does not continue to increase, whereas cone production continues to increase at an even higher rate when the number of unfertilised conelets is high. Thus, the relative production of pollen vs. unfertilised conelets plays a key role in cone production. Meanwhile, it is equally important to note that the sex allocation ratio at the intermediate value does not always result in high cone crops as they could also produce low cone crops (Figure 2(f)). Through time, evolution has perhaps developed a mechanism in longleaf pine for physiologically balancing this ratio, in a manner similar to which trees balance their allocation of photosynthate among the various organs, principally roots, stem and leaves.

Investing too few internal resources in pollen density, as depicted in the left-hand tail of Figure 2(f), almost guarantees a failed green cone crop during the following year. However, investing too much energy and resources in the production of pollen, causing very high sex allocation ratios, also seems to result in poor green cone crops. This is likely because too much investment in pollen may result in a shortage of female conelets to receive the ample pollen that is shed. We postulated that longleaf pine reproduction might be best accomplished through an effective balance in the output of both male and female gametes, a favourable ratio and number of conelets and pollen, and a temporal coincidence during the pollination period (late February–early April). Because the female and male strobili initiate at different times during the previous summer (July and August, respectively) and develop at different rates depending on weather conditions, it is remarkable that successful cone crops occur as they do on a fairly regular basis.

Our recent studies have shown that cone production of longleaf pine has complex relationships with multiple biotic and abiotic factors, particularly because its cone production shows a 3-year cycle while climatic factors do not (Guo et al. 2016). In light of these findings, it is worth considering how sex allocation can or will be influenced by management and/or climate change, relative to promoting longleaf pine cone production for stand regeneration and species conservation. For example, consistent with a recent study by Petry et al. (2016), our results show that sex allocation ratios seem to increase with annual temperature but not with annual precipitation. However, it remains to be seen through further study, whether these findings were caused by gender-specific differences in their responses to environmental stresses and resources under varied temperature regimes (Zhang and Jiang 2002; Crone and Rapp 2014). Pollen density or the sex allocation ratio may be altered by factors such as climate warming and the internal resource balance of trees (e.g., carbohydrate reserves, nutrient status, hormone levels) (Petry et al. 2016). If pollen density or sex allocation ratio becomes too high, female conelet production could decline to levels low enough to jeopardise future longleaf pine cone crops, potentially creating management challenges to sustaining natural regeneration of this species (Boyer 1973; Patterson 2017).

Cone production for longleaf pine was rarely high during two successive years, indicating a trade-off most likely resulting from resource exhaustion when production is very high. This appears to be a carrying-over effect, similar to the patterns found for annual plants observed in the south-western deserts of the United States (Guo and Rundel 1997). Such effect is largely because 1 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 favourable (Crone and Rapp 2014).

In sum, pollen density and the resulting sex allocation in longleaf pine are apparently sensitive to climate variation, with both direct and indirect ecological and evolutionary implications (Boyer 1973). To better anticipate future climate effects on the regeneration species, further (preferably experimental) research is needed to investigate why climate warming disproportionally favours male vs. female allocations in plants, especially finding an effective approach to address this matter in the more challenging monoecious species (Petry et al. 2016). For restoration and management under changing climates and habitat fragmentation resulting from land-use change, initial planting density and tree density reduction during stand tending need to consider pollen and female strobili limitation. Given the central role of pollen density in cone and seed production for longleaf pine, a pollen limitation, which could result from increasing habitat fragmentation and uncertainties arising with climate change, could have important management implications (Sork et al. 2002). For example, during years when pollen is limiting, artificial pollination could improve pollination efficiency thus increasing cone production, even when sex ratio does not change. Although impractical in mature forests on the larger landscape scale, such a technique could be useful at smaller scale seed orchards, which produce seed essential for growing longleaf pine seedlings needed for restoration and management programmes ongoing across the region.

## Conclusions

Our long-term research found that pollen and unfertilised conelets were positively correlated to each another and to cone production in longleaf pine, *P. palustris*. An optimal male-to-female sex allocation ratio exists for promoting cone production, and sex allocation ratio was positively correlated with temperature. The high cone production at intermediate values of sex allocation ratio suggests that there is selection against extreme male- or female-biased allocation. Our findings shed new light on both the reproductive ecology and management of *P. palustris* longleaf pine ecosystems under changing climates.

## Acknowledgements

We thank many individuals who assisted with collection of the pollen and cone data and Marilyn Buford, James Barnett and Juan Arroyo for constructive comments which improved this manuscript. X. Chen was partially supported by USDA National Institute of Food and Agriculture McIntire-Stennis project 1008643.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

None.

## Supplemental data

Supplemental data for this article can be accessed here.

## Notes on contributors

Qinfeng Guo is interested in community ecology, biogeography and invasion ecology.

Dale G. Brockway is a research ecologist interested in forest ecosystem ecology, fire ecology, restoration ecology and silviculture.

Xiongwen Chen is interested in landscape ecology using field information, ecological analysis and modelling, remote sensing and GIS for basic ecological and forestry research.

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