Analyzing Patterns of Seed Production for Chinese *Torreya*

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Additional index words. climate, coefficient of variance in seed production, multiscale entropy, power laws

Abstract. Chinese *Torreya* (*Torreya grandis* cv. *Merrillii*) is an important economic tree in China, but there are limited studies on its seed production. We analyzed the patterns of historical seed production at two major sites (Zhaojiazhen and Jidongzhen) for Chinese *Torreya* from different perspectives. The results indicated that there were no 3-year or multiyear cycles in its seed production. A positive correlation existed between the average seed production and the average annual air temperature in 5 or 10 years at both study sites. There was no trend of the increasing coefficient of variance (cv) in seed production, but the cv generally increased before 1975, and became flat after that time. Frequency power law existed in seed production at both sites, but Taylor's Law existed only at Zhaojiazhen. The multiscale entropy decreased with time scales, and the patterns were similar at both sites. Our research results provide a new understanding of seed production for Chinese *Torreya*.

Chinese *Torreya* (*Torreya grandis* cv. *Merrillii*) is an important economic plant species and the main source of income for local farmers. This species is distributed in mountainous areas in southeastern China, particularly in Zhejiang, Anhui, and Fujian Provinces (Chen and Jin, 2019a; Li and Dai, 2007; Wu, 2013). The origin of the Chinese *Torreya* forest can be traced back to the late Tang Dynasty, which is more than a thousand years ago. It was developed from a quality tree species through grafting from ≈ 1500 years ago (Li and Dai, 2007). The seeds of this tree can be processed to produce nuts, which have been served as snack foods with some health effects (Chen and Chen, 2019; Chen and Jin, 2019a). The seeds have a high nutritional content, including proteins, fatty acids, carbohydrates, calcium, phosphorus, and iron (Li et al., 2005). The seeds also possess antioxidative and acute anti-inflammatory

properties (Chen et al., 2006). Currently, the nuts cost $\approx \$50$ to $\$70$ per kg. Usually, one mature Chinese *Torreya* tree can bring an income of $\approx \$5000$ from seed crops each year. Zhuji City (or County) of Zhejiang Province, which is within the central production area of Chinese *Torreya*, produces more than 1000 tons of nuts every year (Chen and Jin, 2019b). During the last years, more and more farmers have planted this tree species and produced nuts (People's Government of Shaoxing City, 2013). With the increasing demand for seeds, scientific studies on the different perspectives for the growth of Chinese *Torreya* trees and seeds, including photosynthesis, drought tolerance, and nut quality, have been conducted (Hu et al., 2018; Lin et al., 2019; Zhang et al., 2017). However, there are high variations in the seed production of Chinese *Torreya* with time. So far, few studies have been conducted to analyze the dynamics of seed production for this important tree species at a community level.

The reproduction of Chinese *Torreya* is a lengthy process. The development of male and female gametophyte starts in April and May, pollination occurs in May of the second year, but seeds become mature during September to November in the third year (Li and Dai, 2007). Then, it can be hypothesized that 3-year cycles should exist in the dynamics of seed production for Chinese *Torreya*. But because of the lengthy processes in reproduction, environmental factors, such as weather conditions, may affect the final seed

production. The crop production of Chinese *Torreya* can vary ≈ 20 -fold. The production of many seed crops is typically correlated with the weather. It is necessary to study how annual weather can affect seed production in Chinese *Torreya* (Chen and Chen, 2019). No studies were conducted for the effects of climate on seed production. For the variable tree seed production, there are several hypotheses (e.g., Kelly and Sork, 2002). The resource-matching hypothesis indicates that better environmental conditions during the growing season will later result in a more significant production of seeds. But the resource accumulation hypothesis suggests that trees need to accumulate resources for several years until a threshold is reached, and then a large production occurs, which means a large number of seeds will be produced with a certain biological periodicity despite the weather effect. Pearce et al. (2017) found that the cv in plant seed production increased over time for many masting and long-lived plants because these species with most variable seed production responded strongly to interannual differences in weather or resources. Because Chinese *Torreya* can live more than a thousand years, it is expected that its cv of seed production may increase with time. Entropy, usually related to disorder and predictability in information, is used to characterize spatial and temporal complexity in ecology (e.g., Chen et al., 2005). Chen et al. (2016) found that the cone production of longleaf pine at different sites followed a similar pattern in complexity with the increase of time scales. It is necessary to know whether the seed production of Chinese *Torreya* has the same phenomenon. Comparisons of complexity, such as entropy of seed production at local sites through time, may provide insight about seed production from a new perspective. Using or developing useful methods at local areas to characterize the emergent behavior of seed production (e.g., regime shift) for Chinese *Torreya* needs to be investigated.

Various life forms may obey a host of simple and systematic empirical scaling laws because all biological systems must transform energy and materials to support multiple life functions and structures (West, 1999). Power laws are considered as ubiquitous in nature and are broadly found in the distribution of rain droplet size, earthquakes, drainage area for rivers, and populations of cities (Bak, 1996; Gutenberg and Richter, 1956; Zipf, 1949). In statistics, a power law describes a relationship between two variables, in which a relative change in one variable results in a relative proportional change in the other variable: one varies as the power of another. Although there were fluctuations in seed production, trees were found to have reproductive consistency (Herrera et al., 1998; Koenig and Knops, 1998). Chen et al. (2017) found invariant scaling properties in cone production for longleaf pine in the southeastern United States. Thus, we may derive a hypothesis that there existed possible power laws in the seed production of Chinese *Torreya*.

Received for publication 30 Dec. 2019. Accepted for publication 13 Feb. 2020.

Published online 23 April 2020.

We thank Hangbiao Jin and Jinchang Li at Zhuji Forestry Academy for the helpful information.

This research was partially supported by the U.S. Department of Agriculture National Institute of Food and Agriculture Mc-Stennis program (1008643) and Shaoxing 330 program.

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Fig. 1. The locations of study sites in Zhejiang Province of China.

The primary goal of this study was to analyze the possible patterns in the dynamics of seed production for Chinese *Torreya*. The specific objectives were to determine 1) whether there were 3-year cycles in the dynamics of seed production; whether climate correlated with seed production; 2) whether the cv in seed production increased with time; 3) how the complexity of seed production changed with time scales; whether power laws existed in seed production. The results of this study can provide a new understanding of seed production dynamics for Chinese *Torreya*.

Material and Methods

Study sites and data. The study sites are located at Zhaojiazhen in Zhuji City and the adjacent Jidongzhen in Shaoxing City, and both are in Zhejiang Province of China (Fig. 1). This region is within the major seed production area of Chinese *Torreya*. The data were from the book by Li and Dai (2007), but further analysis of the data were lacking. The information of seed yield at different times was collected from local town agencies by the book authors because 1) the seeds were picked up and weighted by local people every year; and 2) the seeds were expensive and the yield data should be accurate. The seed production data at Zhaojiazhen were from 1971 to 2006, and the data at Jidongzhen were from 1962 to 2002. Usually, Chinese *Torreya* trees were sparsely distributed within the natural vegetation. The exact covered area of Chinese *Torreya* trees each year at these

two sites was not known; however, the change in the total area of Chinese *Torreya* was limited during these periods because the major industrial plantations were not established yet (Chen and Jin, 2019b). The covered area of Chinese *Torreya* was ≈ 3300 ha in Zhaojiazhen (Chen and Jin, 2019b) and 630 ha in Jidongzhen (Li and Dai, 2007). There were $\approx 32,000$ trees with production in Zhaojiazhen and 21,000 trees in Jidongzhen (Li and Dai, 2007). Seedlings need to grow ≈ 10 to 15 years to produce first seeds, and young trees usually have limited seed production at the beginning. Thus, it could be assumed that seed production at the two sites was unaffected by the covered area or the number of trees during that time. There were high variations in seed production, which could reach ≈ 20 - or even 40-fold at each site. The map distance between two sites in the mountainous area is only ≈ 10 km. Weather data were from local weather stations near the study sites. Beyond seed harvesting, the management practice during that time was minimal, which means nature mainly controlled the trees and forests.

Three-year cycle. If 3-year cycles existed in the yield of *Torreya* seeds, then, the yields at time $t_0, t_1, \dots, t_{n-3}$ would be correlated with the yield at $t_3, t_4, \dots, t_n$. If x -year cycles existed, then, the yields at time $t_0, t_1, \dots, t_{n-x}$ should be correlated with the yield at $t_x, t_{x+1}, \dots, t_n$.

Variation in seed production. The cv (standard deviation/mean) for seed production during different periods was calculated to facilitate comparisons between the two sites. Time periods included all time intervals

from the beginning at each site. The average and sd were calculated for each year and the decade periods (the 1970s, 1980s...2000s). For the 2000s, only data from 2000 to 2006 were included.

Power law of frequency. The quantity of seed production was sorted based on an increment of 50 tons. For example, a production level of 180 tons had the following length categories associated with it: 50, 100, 150, and 200 tons. The number of seeds produced within each group was counted. At each research site, the cumulative percentage of probability for the quantity of seed production within each group was then calculated (White et al., 2008). A figure with the logarithm of seed production in tons (m) and the logarithm of the cumulative probability (P) was produced. The power law of frequency was calculated at both Zhaojiazhen and Jidongzhen because of their long time series of seed production.

Taylor's Law. In many species, the logarithm of the variance of the density (individuals per area or volume) of populations was approximately a linear function of the logarithm of the mean density. This relationship has been known as Taylor's Law (Taylor, 1961). Taylor's Law is one of the most widely verified empirical relationships in ecology. Taylor's Law can be expressed in the following way for this study:

$$\text{Variance} = a \times \text{Mean}^b$$

with *Variance* as the variance of seed production, *Mean* as the average of seed production.

After logarithm, $\log(\text{Variance}) = \log(a) + r \times \log(\text{Mean})$. With the time increase of 1, 2 ... to n years from the time with seed production record, the scaling exponent (r) between the variance and average of seed production for Chinese *Torreya* was estimated at each site.

Multiscale entropy. A method of multiscale entropy was applied to characterize and compare the patterns of seed production in Chinese *Torreya* based on available long-term data at Zhaojiazhen and Jidongzhen. Multiscale entropy is a method broadly used for analyzing the complexity of nonlinear and nonstationary signals in finite-length time series (Chen et al., 2005). In this study, entropy is defined as the Shannon entropy

$[H_\epsilon(x)]$ of seed production at different time scales of ϵ (length of years) as the following:

$$H_\epsilon(x) = -\sum p_\epsilon(x) \text{Log} p_\epsilon(x),$$

where $H_\epsilon(x)$ is the probability (percentage) of seed production (x) at the i th year measured using samples of ϵ units in time. The time scale of ϵ includes 1, 2, ... $m/2$ or $(m-1)/2$.

The percentage at different time scales (ϵ) is calculated by the following approach:

$$p_\epsilon(y) = \frac{y_i}{\sum y_i} \times 100,$$

For details, please see the references (Chen et al., 2005, 2016). Higher values of entropy represent higher temporal evenness

of the seed production at the time scale of ϵ years.

Statistical analysis. The Spearman correlation was conducted by SAS software (Version 9.3; SAS Institute Inc., Cary, NC), such as a correlation between the multiscale entropy of seed production and time scale. The estimated slopes were compared by a t test (Sokal and Rohlf, 1981). Statistical significance was discerned at $P < 0.05$.

Results

There were fluctuations in seed production for Chinese *Torreya* at both Zhaojiazhen and Jidongzhen (Fig. 2A). However, 3-year cycles or multiyear cycles did not statistically

Fig. 2. Dynamics of seed production for Chinese *Torreya* at study sites (A) and correlation between seed production at Zhaojiazhen and Jidongzhen during overlapped time (B).

exist in the seed production for Chinese *Torreya* ($P > 0.05$). High seed production was usually followed by lower production in the successive years. There was a significant correlation in seed production between Zhaojiazhen and Jidongzhen (Fig. 2B).

The correlation between seed production of Chinese *Torreya* and annual average air temperature or precipitation was not significant at both sites (Fig. 3). However, a positive correlation existed between the average annual air temperature in 5 or 10 years, and the average seed production of Chinese *Torreya* at both sites ($P < 0.05$). The correlation between the average annual precipitation in 5 or 10 years and the average seed production was not significant at both

sites except for Zhaojiazhen at every 10 years ($y = -1.2276x + 1845.9$, $R^2 = 0.9043$, $P < 0.01$).

The cv of seed production generally increased with the time scales before 1975 (Fig. 4A and B), but after that, cv became flat. There were breaks in the cv dynamics at both Zhaojiazhen and Jidongzhen. There was no general trend of increasing cv at different decades on both sites (Fig. 4C).

Frequency power law existed in seed production for Chinese *Torreya* at both Zhaojiazhen and Jidongzhen ($P < 0.05$) (Fig. 5A and B). The power exponents were 0.5229 at Zhaojiazhen and 0.9677 at Jidongzhen, respectively. Taylor's Law existed significantly only at Zhaojiazhen, and the

relationship was not significant at Jidongzhen (Fig. 6A and B).

The multiscale entropy decreased with time scales at both Zhaojiazhen and Jidongzhen (Fig. 7A and B). There was no significant difference between the slopes of the fitting line (e.g., -1.1914 and -1.2398).

Discussion

It appeared that 3-year cycles or multiple-year cycles did not exist in seed production for Chinese *Torreya*, although biologically a completed reproduction cycle needs 3 years. The biological process determines the dynamics of seed production, but environmental stress and disturbances might affect

Fig. 3. Correlation between seed production of Chinese *Torreya* and average air temperature.

Fig. 4. Dynamics in the cv in seed production for Chinese *Torreya* at two sites (A, B), and during different decades (C).

Fig. 5. Frequency power law in seed production for Chinese *Torreya* at Zhaojiazhen (A) and Jidongzhen County (B).

this 3-year cycle in the reproduction process during the lengthy reproduction period. If trees were not healthy, the production cycle might change. However, it is observed that there existed no high seed production in two successive years at both sites.

This pattern may indicate a carry-over effect, a trade-off from resource exhaustion when seed production is high (Crone and Rapp, 2014; Guo and Rundel, 1997; Guo et al., 2016), because the high seed production exhausts some critical resources (e.g., nitrogen) that need time for trees to restore. It appears that these results support the resource accumulation hypothesis (Kelly and Sork, 2002), although the exact resources are not

known here. Spatial autocorrelation, also known as “Moran effect” (Moran, 1953), was observed in seed production for Chinese *Torreya* between Zhaojiazhen and Jidongzhen. Because this tree species lives in the mountainous area, the environmental conditions, such as soil, elevation, and microclimate, might change dramatically even within a short distance, which could affect spatial autocorrelation. More spatial data should be collected to study spatial autocorrelation in a large area.

Although the correlation between annual air temperature or precipitation (including the previous 1 or 2 years) and seed production was not significant, a positive correlation existed between average air temperature in

5 or 10 years and average seed production. The mechanism is not clear. The partial reason may be related to its lengthy reproduction processes. The increasing annual air temperature may benefit seed production in Chinese *Torreya*. But too high summer air temperature and also cold winter air temperature could both kill this species, especially for young trees (Li and Dai, 2007). Warm winters (high air temperature in January) and warm spring (high air temperature in March) were possibly correlated with high seed production at some sites (Li and Dai, 2007). The correlation between seed production and precipitation was not significant at both sites except for the negative relationship at

Fig. 6. Taylor's power laws in seed production for Chinese Torreya at Zhaojiazhen (A) and Jidongzhen (B).

Zhaojiazhen in 10-year scale. Too much precipitation (or soil water) might affect the seed production process, such as pollination. This tree species likes loam soil, and the growth of root systems needs both water and air (Li and Dai, 2007). Long-term flooding or saturation of soil water could kill trees of this species. Climate change may affect the fate of this species (Chen and Niu, 2020).

By comparing the cv of seed production at different decades, our results did not support that cv in plant seed production increased

over time (Pearse et al., 2017). This result is similar to the research on longleaf pine (Chen et al., 2018). It is understood that cv can quickly increase at the beginning and then become flat because of the fluctuation in seed production in the first several years. But it is not clear why cv trajectory suddenly changed at ≈ 1975 at both sites. The sudden high and low seed production could cause breaks in the cv trajectory. A potential explanation might be related to pollination or the decline of male trees. Local people once cut down male

trees for timber because these trees did not produce seeds (Chen and Jin, 2019a).

Frequency power laws existed in seed production for Chinese Torreya at both Zhaojiazhen and Jidongzhen. Power laws represent a holistic measure of the "pace of life" because they link to the rates of many biological activities at various hierarchical levels of organization (Bak, 1996), such as these trees must transform energy and materials to support tree structure and seed production. Also, the scaling exponents (0.5229 and

Fig. 7. Change of multiscale entropy in seed production for Chinese *Torreya* with time scales at Zhaojiazhen (A) and Jidongzhen (B).

0.9677) of these frequency power laws were quite different, and none of them followed a universal value (e.g., one-third or one-fourth). This result supports that scaling exponents of power laws can be a nonfixed value (e.g., Chen and Li, 2003; Kolokotronis et al., 2010).

Taylor's Law in seed production existed only at Zhaojiazhen, and it was not significant at Jidongzhen. Taylor's Law is considered to associate with long-range interactions among all components in a given system (Arruda-Neto et al., 2012). Because of limited information, it is not clear what occurred to the Chinese *Torreya* at Jidongzhen. The failure of Taylor's Law may reflect diseases such as parasitism or epidemic infection

(Lagrue et al., 2015). The exponent of Taylor's Law was supposed to be between 1 and 2 (Marquet et al., 2005), but it was 2.5982 at Zhaojiazhen. An exponent higher than 2 may indicate deterministic and exponential growth (Ballantyne, 2005). Some previous studies also found that the exponents were not within the proposed range (Chen et al., 2017; Cohen et al., 2012). Taylor's Law may inform our understanding of the resilience and change in Chinese *Torreya* at different sites.

The multiscale entropy of seed production for Chinese *Torreya* was not significantly different between Zhaojiazhen and Jidongzhen. The multiscale entropy could indicate

the interactions between species' biological characters and environmental processes (e.g., drought) (Chen et al., 2005). The similar dynamics of multiscale entropy at both sites might indicate that the Chinese *Torreya* ecosystems and their environmental interactions at both sites were very similar and shared some intrinsic characters of this species. This is supported by the spatial correlation in this study. The multiscale entropy of seed production in Chinese *Torreya* decreased with the time scale in this study. This suggests that seed production became more irregular with the increase of time scale. The time scale-free in the decreased multiscale entropy of seed production may

provide useful clues for predicting seed production or at least contributing to model development in the future.

Conclusions

Chinese *Torreya* is an essential economic tree species in some counties (or provinces) in China, but there are limited long-term data on seed production. It is necessary to start to record tree growth and seed production at different spatial scales (e.g., stand, village, and county) and also to establish permanent plots and set up observation at the ecosystem level. Based on the historical data at two sites in the central area of Chinese *Torreya*, some patterns in the dynamics of seed production were analyzed, and some useful information about this species could be inferred. The different results reflected the different perspectives (e.g., reproduction process and self-organization) of this tree species and its local ecosystems. Some results may provide theoretical information, and some may offer management strategies (e.g., temperature and water). Monitoring the dynamics of these indices across more sites under different environmental conditions could provide a better understanding of the responses of this species to management practices and environmental change.

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