RESEARCH ARTICLE

Decadal changes in masting behaviour of oak trees with rising temperature

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Abstract

1. Decadal changes in masting behaviour—directional changes in seed production with fluctuations on a decadal time-scale—are attracting widespread attention in the context of global climate change. However, our mechanistic understanding of the effects of climate on seed production on a decadal scale is unsatisfactory, partly because of the insufficient statistical analyses of long-term data on masting.

2. We detected decadal changes in masting behaviour in the Japanese oak *Quercus crispula* based on long-term data (38 years: 1980–2017) from the Kitakami Mountains of Japan. The moving average of seed production in a 20-year sliding window increased, whereas the coefficient of variation decreased. A wavelet power spectrum, as well as a second-order log-linear autoregressive (AR) model showed that masting intervals shortened from 3- or 4-year cycle to a 2-year cycle.

3. The moving average of seed production increased linearly as the moving average of temperature increased. Temporal variations of the two AR model coefficients as a function of temperature were well described by concave curves.

4. *Synthesis*. By conducting the statistical analyses of a long-term seed production dataset, we obtained significant evidence of decadal changes in the masting behaviour of the Japanese oak and showed that the shortening of the masting interval was associated with rising temperature. A resource allocation shift and an environmental veto were discussed as possible mechanisms underlying the decadal change.

KEYWORDS
autoregressive model, decadal change, masting, plant reproduction, *Quercus crispula*, resource allocation, time-series analyses, wavelet model

1 | INTRODUCTION

Masting—synchronous and highly variable seed production among years by a plant population (Kelly, 1994)—is widespread in long-lived species, particularly woody and wind-pollinated species (Herrera, Jordano, Guitian, & Traveset, 1998). It is a conspicuous phenomenon that has confounding impacts on ecological communities (Bisi et al., 2018; Jones, Ostfeld, Richard, Schauber, & Wolff, 1998; Kelly, Koenig, & Liebhold, 2008; Koenig & Knops, 2005; Onodera, Akimoto, Shimada, & Saitoh, 2017; Ostfeld, Jones, & Wolff, 1996). Masting causes a chain reaction by influencing the growth and

regeneration of trees, their population dynamics and the evolution of seed consumers, and it eventually affects the dynamics of the entire community (Jones et al., 1998; Koenig, Knops, Carmen, & Pearse, 2015). Masting even affects the disease risk to humans. For example, acorn masting increases the risks of people contracting hantavirus (Reil, Imholt, Eccard, & Jacob, 2015) or Lyme disease (Bogdziewicz & Szymkowiak, 2016) through increases in the populations of rodent vectors. For a deeper understanding of forest ecosystems, and for sustainable forest management planning, information about the determinants and underlying mechanisms of masting is essential (Pearse, Koenig, & Kelly, 2016; Vacchiano et al., 2018).

Decadal changes in masting behaviour—directional changes in seed production with fluctuations on a decadal timescale—are attracting widespread attention in the context of global-scale environmental change (Ascoli et al., 2017) and impacts on ecological interactions (McKone, Kelly, & Lee, 1998). Seed production of various temperate species is increasing (Allen, Hurst, Portier, & Richardson, 2014; Ascoli et al., 2017; Buechling et al., 2016; Caignard et al., 2017; Richardson et al., 2005), although decreases in seed production have also been reported (Redmond, Forcella, & Barger, 2012). A shortening of masting intervals has been observed in beeches in northern Europe (Müller-Haubold, Hertel, & Leuschner, 2015; Övergaard, Gemmel, & Karlsson, 2007), whereas a meta-analysis of world-wide datasets has shown an increase in inter-annual variation in seed production (Pearse, LaMontagne, & Koenig, 2017). Suggested causes of decadal changes in masting behaviour include global changes in, for example, climate and nitrogen deposition (Caignard et al., 2017; Övergaard et al., 2007), but Kelly et al. (2013) have reported that masting may be insensitive to gradual increases in temperature. These discrepancies in findings on masting behaviour and our understanding of its mechanism can be attributed not only to interspecific differences in the response to climate change (Koenig et al., 2016; Koenig & Knops, 2014) but also to an insufficient understanding of how climate and resources drive seed production (Pearse et al., 2016, 2017).

The effect of weather as a proximate cause of masting is of interest from at least two perspectives—resource dynamics and pollination (Allen, Millard, & Richardson, 2017; Koenig et al., 2015; Pearse, Koenig, & Knops, 2014; Richardson et al., 2005). Many studies examining resource dynamics (Bogdziewicz, Steele, Marino, & Crone, 2018; Bogdziewicz et al., 2019; Pesendorfer, Koenig, Pearse, Knops, & Funk, 2016; Satake & Bjørnstad, 2008; Schermer et al., 2019; Venner et al., 2016) have adopted the resource budget model, which assumes that plants accumulate resources each year and produce seeds once the stored resources exceed a threshold (Isagi, Sugimura, Sumida, & Ito, 1997). Recovery from resource depletion by reproduction may be faster in higher productivity environments, enabling plants to reproduce more frequently (Kelly & Sork, 2002; Satake & Bjørnstad, 2008). Moreover, Satake and Bjørnstad (2008) have shown that the input of surplus resources (net production per year) can be a determinant of local masting interval variations. This idea of a relationship between surplus resources and local masting intervals may help explain decadal changes in masting behaviour. Weather factors—particularly temperature and precipitation—are considered to be the drivers of resource

priming for reproduction because of their effects on photosynthesis and productivity in trees (e.g. Allen et al., 2014, 2017; Müller-Haubold et al., 2015; Piovesan & Adams, 2001; Richardson et al., 2005; Smaill, Clinton, Allen, & Davis, 2011). Therefore, we predicted that, in response to favourable temperatures and precipitation, trees would more frequently shift their resource allocation pattern from storage to reproduction, thus shortening the masting interval. Furthermore, an enhanced resource supply may lead to an increase in the total mass of seed produced.

However, resource dynamics alone cannot explain the population-level synchrony of seed production, which is an essential feature of masting (Crone & Rapp, 2014; Isagi et al., 1997). Flowering or pollination may be a key to that synchrony. One proposed the mechanism of synchronization is pollination efficiency, which is often referred to as pollen coupling (Isagi et al., 1997; Satake & Iwasa, 2000). However, the pollination Moran effect (Pearse et al., 2016) may be more applicable as a mechanism of synchronization in oaks (Bogdziewicz et al., 2017). In support of a pollination Moran effect, Bogdziewicz, Steele, et al. (2018) showed that pollination failures caused by environmental vetoes could synchronize the dynamics of seed production among individual trees. The environmental veto hypothesis, according to which specific weather conditions can prevent individual trees from flowering or being pollinated over a substantial area, may thus be a plausible mechanism linking masting (seed production synchrony) with climate (Bogdziewicz, Steele, et al., 2018; Pearse et al., 2016). Koenig et al. (2015) showed that low springtime temperatures caused pollination failure in the valley oak *Quercus lobata*. In turn, poor seed production due to pollination failure in a low-temperature year may contribute to the tuning of the resource dynamics of individual trees and thus to synchronization of mast years (Pesendorfer et al., 2016). Therefore, we can predict that low temperatures in spring sharpen masting in oak species.

A variety of statistical techniques have been developed for analysing the time series of cyclic fluctuations or spatial synchrony in animal populations (e.g. Bjørnstad, Falck, & Stenseth, 1995; Cazelles et al., 2008; Haydon, Stenseth, Boyce, & Greenwood, 2001; Royama, 1992), and some of these techniques have been adopted in recent studies on masting (Ascoli et al., 2017; Chen, Brockway, & Guo, 2018). Although the mast year frequency (or masting interval) has been measured as a key component of temporal variability in seed crops (Abrahamson & Layne, 2003; Allen, Mason, Richardson, & Platt, 2012; Kasprzyk, Ortyl, & Dulska-Jeż, 2014), frequency analyses are prone to bias as a result of the subjective categorization of years into mast or non-mast years. In contrast, a wavelet analysis can describe the decadal changes in population fluctuations avoiding the bias associated with a dichotomous categorization (Cazelles et al., 2008), and Ascoli et al. (2017) have introduced the wavelet analysis as a technique for investigating long-term changes in masting patterns. A second-order log-linear autoregressive (AR) model has also been used to describe the decadal changes in wildlife populations (e.g. Cornulier et al., 2013; Ims, Henden, & Killengreen, 2008). The

AR model can be used to investigate how the current population density reflects population densities during the previous 1 and 2 years. Seed production in a certain year may be determined by the interaction between the input (photosynthesis) and output (seed production) of resources in previous years; thus, the AR model may be useful for analysing inter-annual fluctuations of seed crops.

The aim of this study was to investigate the decadal changes in the masting behaviour of the Japanese oak *Quercus crispula* in relation to climate change. This deciduous tree species is a principal component of cool-temperate forests in Japan. In recent decades, atmospheric temperature and precipitation in the study area have been increasing. We therefore performed time-series analyses by using the wavelet power spectrum and an AR model for seed production in *Q. crispula* in the Kitakami Mountains of Japan, where seed production by this species has been observed for 38 years (1980–2017). Our results indicate that the masting interval shortened over this 38-year period. In addition, average number of seed production and the mass of individual seeds increased, whereas the coefficient of variation (CV) of seed production decreased. Variations in weather factors—in particular temperature—showed a good agreement with AR model results, variations of average number and CV of seed production. Then, as possible mechanisms underlying the observed decadal changes in masting behaviour, we examined both a shift in the allocation of resources and an environmental veto.

2 | MATERIALS AND METHODS

2.1 | Study species

The Japanese oak *Q. crispula* (a synonym of *Q. mongolica* var. *grosseserrata*) is a broad-leaved deciduous tree species in the family Fagaceae. It is native to East Asia and is distributed widely in Japan (Yagihashi, Matsui, Nakaya, Taoda, & Tanaka, 2003 (Figure S1). Along with *Fagus crenata*, *Q. crispula* is often dominant in cool-temperate forests, though it occasionally forms monospecific stands (Ohba, 2006). *Quercus crispula* is monoecious and anemophilous. The seeds develop slowly for about 2 months after the completion of flowering and more rapidly thereafter (Nakajima et al., 2012).

2.2 | Study site and field research

The field survey was performed in a *Q. crispula* stand at the Nakaimura research site (39°48′32″N, 141°33′27″E, 900 m a.s.l; Figure S1), which is located in a national forest in the central region of the Kitakami Mountains. Although the stand history is not known in detail, the stand age is estimated to be 135 years (Sanriku-Hokubu District Forest Office, 2016).

Since 1980, annual seed production has been monitored in a plot (35 m × 35 m; 0.12 ha) in this research site (Figure S1); it contained a total of 56 stems (467 stems/ha)—mainly *Q. crispula*—with a DBH of 28.7 ± 9.6 cm ($M \pm SD$). A grid was superimposed on the plot, and 16 seed traps were set at the grid nodes. All reproductive organs, including both seeds and cupules, that fell into the seed traps each year between mid-July and early November were collected over the 38 years from 1980 to 2017. The receiving area of each trap was 1.0 m^2 from 1980 to 1996 and 0.5 m^2 from 1997 to 2017. The data from each year were therefore converted to the number of seeds per unit area (1.0 m^2) according to the receiving area of traps. Collected seeds were classified as mature or immature and then counted. From 1987 to 1994 and from 2006 to 2014, all mature seeds collected in years when the total number of mature seeds in the 16 traps exceeded 10 were air dried and weighed.

2.3 | Analyses

2.3.1 | Annual fluctuation of seed production

The change in the masting interval was analysed by wavelet analysis, using the WAVELETCOMP package 1.1 (Roesch & Schmidbauer, 2018) in the R statistical environment (R Development Core Team, 2013). This analysis is appropriate for data with irregular time-series characteristics and is superior for quantifying the dynamics of populations with non-stationary dynamics (Cazelles et al., 2008). The significance of the wavelet power spectrum, which shows time-series changes at time *t* in the analysis period, was tested by bootstrapping with 10,000 replications. A calculation process based on Markov process-based resampling of observed values was adopted.

The AR model was also used to describe the temporal changes in the annual fluctuation of seed production. The equation for the AR model, which was originally used to describe the change in population density between year *t* and year *t* − 1 (i.e. $x_t - x_{t-1}$) as a function of density, was transformed into the following simple one (Royama, 1992):

$$x_t = \left(1 + a_1\right) x_{t-1} + a_2 x_{t-2} + \varepsilon_t,$$

where x_t represents the natural logarithm of annual seed production (the number of seeds) in year t, $x_t = \log_e(N_t)$. The coefficients $[1 + a_1]$ and a_2 represent the effects of seed production during the previous 1 and 2 years, respectively, on seed production in the current year t, and ε_t is an error term for density-independent effects in year t (independent random numbers with mean = 0).

In the AR model, sustainable cycles are represented by certain combinations of $[1 + a_1]$ and a_2. The population dynamics are cyclic if the combinations of $[1 + a_1]$ and a_2 are on the left side of the $[1 + a_1] = 0$ line or are inside the outermost convex upward curves in Figure 3c (see also Bjørnstad et al., 1995). Temporal changes in the masting interval cause a point plotted in $a_2 - [1 + a_1]$ space to be relocated over time (Figure 3c). Therefore, masting pattern changes can be traced by observing how plots of the AR model coefficients move over time.

State-space model was used to estimate the number of mature seeds and the two coefficients of the AR model. We used JAGS ver. 4.3.0 (Plummer, 2017) and the Markov Chain Monte Carlo (MCMC) method, taking measurement errors into consideration, to estimate the number of seeds per 1.0 m^2 in the 16 seed traps and the two coefficients of the AR model ($[1 + a_1]$ and a_2) governing all 16 time series. The numbers of chains and iterations were set at 3 and 50,000 respectively; the initial burn-in was set at 10,000 and thinning was set at 40 (see the JAGS code, Appendixes S3 and S5 and seed-fall data, Appendix S4). Good convergence ($\hat{R} < 1.02$) of MCMC was confirmed for the 608 estimates of the number of seeds (16 traps × 38 years; Figure S2).

Although in general a shorter time frame provides a more sensitive estimation of the variation of $[1 + a_1]$ and a_2, the estimates based on short time frames may not be robust because of the small sample size (i.e. the number of years). Therefore, to explore the characteristic length scale at which the underlying dynamics could be most clearly observed (Habeeb, Trebilco, Wotherspoon, & Johnson, 2005), we used the sliding window method and compared the results from various time frames. For example, when the window size (i.e. time frame) was set at 11 years, a_1 and a_2 were estimated for each of 28 periods (1980–1990, 1981–1991, …, 2006–2016, 2007–2017). We compared the convergence ($\hat{R}$), stability and sensitivity of the a_1 and a_2 estimates among 15 window sizes (11–25 years). Estimates of a_1 and a_2 obtained with smaller window sizes (≤13 years) showed poor convergence ($\hat{R} > 1.1$, Figure S3), whereas convergence was satisfactory with larger windows (>13 years, $\hat{R} \leq 1.006$, Figure S3). In accordance with the reduction in erratic behaviour (Figure S3), the stability, which was assessed based on the change rate of the coefficients between neighbouring years, became higher as the size of window increased (Figure S4). The stability levelled off when the window exceeded 20 years. In contrast, the sensitivity, which was represented by the range of the coefficients, decreased with the increase in the window size in general (Figure S4). However, it was stable at intermediate values when the window size ranged between 15 and 21 years (Figure S4). Considering these results, we adopted a 20-year time frame as the characteristic length scale.

In addition to $[1 + a_1]$ and a_2, the average and CV of seed production were calculated by using a 20-year sliding window. Furthermore, seed weight was compared among those years in which data were available by using Tukey–Kramer's HSD test.

2.3.2 | Weather effects on seed production

The effects of climate change on masting behaviour were analysed by examining the temperature and precipitation during the growing and flowering seasons. At the study site, *Q. crispula* blooms and develops new leaves from late May to early June, and mature seeds and leaves fall from mid-October to early November. In a cool-temperate forest located 500 km south-west of our study site, where the annual mean temperature is 7.2°C, *Q. crispula*

actively photosynthesize between June and September (Muraoka & Koizumi, 2005). The annual mean temperature at our study site is comparable to that during the 38-year study period, and it ranged between 4.4 and 7.1°C. Therefore, at our study site, we considered the growing season of *Q. crispula* to be between June and September and the flowering season to be from late May to early June.

We used meteorological data recorded at the Yabukawa Meteorological Station (39°47′00″N, 141°19′42″E, 680 m a.s.l), which is 20 km south-west of the study site. The data were downloaded from the website of the Japan Meteorological Agency (2019). The 20-year moving averages of mean temperature and precipitation during the growing season were analysed as proxies for productivity. Similarly, the 20-year moving averages of mean temperature and precipitation during the flowering season were used as those for environmental vetoes.

To explore the influence of weather factors on masting behaviour, we compared the results of three regression models (linear, quadratic and multivariate). The explanatory variables were the 20-year moving averages of temperature or precipitation, or both, in each season, and the objective variable was average seed production, its CV or one of the two AR model coefficients ($[1 + a_1]$ or a_2) in the 20-year sliding windows.

3 | RESULTS

3.1 | Annual fluctuation of seed production

The average of seed production of the 16 seed traps fluctuated widely, from 0.5 in 1988 to 117.7 in 1987 (Figure 1a); the average throughout the study period was 28.3, with a large standard deviation (31.9). During the study period, high seed production never occurred in two successive years, but successive years of low abundance were observed several times between 1980 and 2000. The interval between peak years—where a peak year is one in which seed fall was higher than in adjacent years—ranged from 2 to 4 years until 2005. Thereafter, peaks and troughs occurred alternately without exception.

The wavelet analysis revealed three different patterns of periodicity. During the first 10 years of the study period, periodicities of about 2 and 4 years exhibited high power on the wavelet spectrum, although only the 4-year cycle between 1988 and 1989 was significant. Therefore, the combined intervals of 2 and 4 years dominated in the first 10 years. From 1992 to 2002, the masting interval became shorter and a 3-year cycle dominated. After 2003, the masting interval shortened further and a 2-year cycle exhibited high power on the spectrum (Figure 1b).

The 20-year moving average of number of seed production generally increased (Figure 2). The average number of seeds exhibited a significant linear relationship with period number (Figure 2; average ≈ −1,060 + 0.547 period, adjusted R^2 = .724, $F_{1,17}$ = 48.18, $p < .0001$). Although a complete dataset of seed weight covering
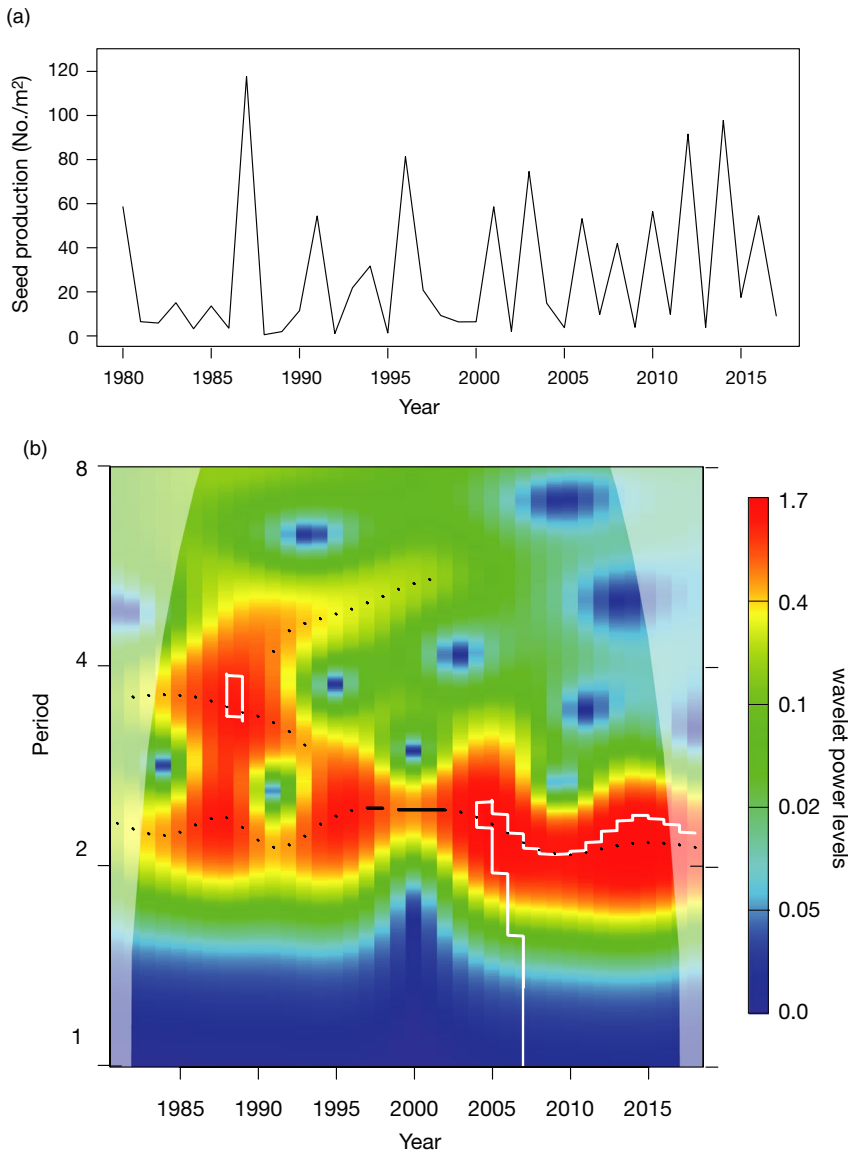
(a)

(b)

the entire study period was not available, average seed weight was significantly greater in 2010, 2012 and 2014 (1.63–2.13 g) than in any of the 9 years before 2008 (range 0.25–1.39 g) (Figure S5). Therefore, the gross weight of seeds produced (obtained by multiplying seed weight by the number of seeds) increased over time. The CV of seed production obtained in each 20-year sliding window gradually decreased from >1.4 until 1989–2008 (10th period) and thereafter stabilized at about 1.0 (Figure 2). CV showed a significant linear relationship with period number (CV ≈ 53.04–0.026 period, adjusted $R^2 = .805$, $F_{1,17} = 75.38$, $p < .0001$).

Coefficient $[1 + a_1]$ varied from −0.782 to −0.374 and a_2 varied from −0.406 to 0.250 (Figure 3a, b). The net value of a_1 was always negative, ranging from −1.782 to −1.374 (Figure 3a) and its variance was small (0.016). Because none of the 95% credible intervals included zero, the effect of a_1 was always significant. In contrast, a_2 exhibited large variation (variance = 0.040) and ranged between negative and positive values (Figure 3b). Assessment of the significance of a_2 on the basis of the 95% credible interval revealed that its effect was significantly negative

in nine periods (in the 4th and from the 6th to 13th period), significantly positive in two periods (18th and 19th) and non-significant in eight periods (1st to 3rd, 5th and 14th to 17th). The changes in both coefficients $[1 + a_1]$ and a_2 were well described by a concave approximation against period (Figure 3a, b; $[1 + a_1] \approx -0.209 + 0.004$ period^2 − 0.085 period, adjusted $R^2 = .779$, $F_{2,16} = 33.69$, $p < .0001$; $a_2 \approx -0.085 + 0.006$ period^2 − 0.098 period, adjusted $R^2 = .859$, $F_{2,16} = 55.73$, $p < .0001$). The two coefficients $[1 + a_1]$ and a_2 were also significantly correlated with each other ($r_p = .649$, $p = .003$).

When we plotted the values of each coefficient in each period in $a_2 - [1 + a_1]$ space, the first period (1980–1999) was located on the contour indicating a 3-year cycle (Figure 3c, d). The positions of the plotted points moved downward along the contour, indicating a 3-year cycle as the effect of a_2 became stronger (i.e. as a_2 became more negative). The point for 8th period (1987–2006) was the deepest under the outermost convex upward curves, indicating a robust 3-year cycle. From 10th to 13th period, the points plotted in the area indicating a 2.5-year cycle, but after 14th period (1993–2012) the points moved upward to

FIGURE 2 Changes in average seed production and its coefficient of variance (CV). Moving average (black circles) and CV (white triangles) values for the number of mature seeds produced over 38 years, obtained by using the sliding window method with a window size of 20 years
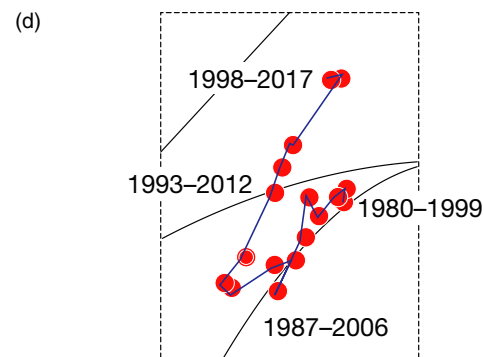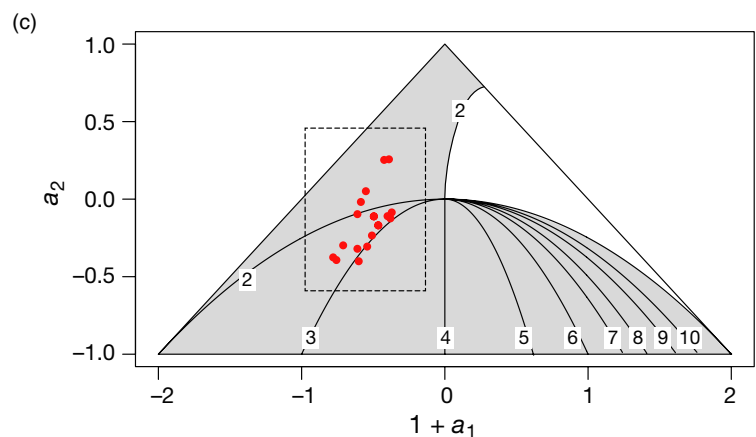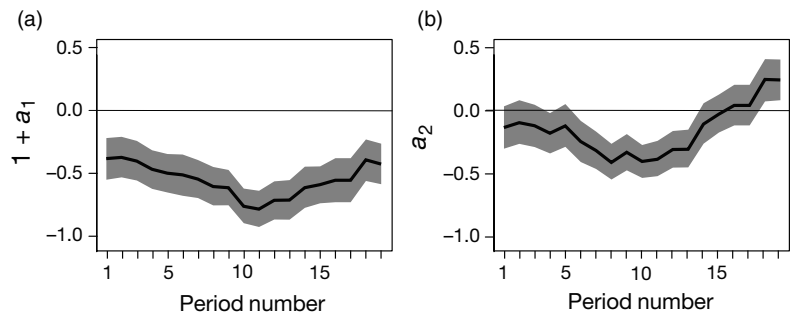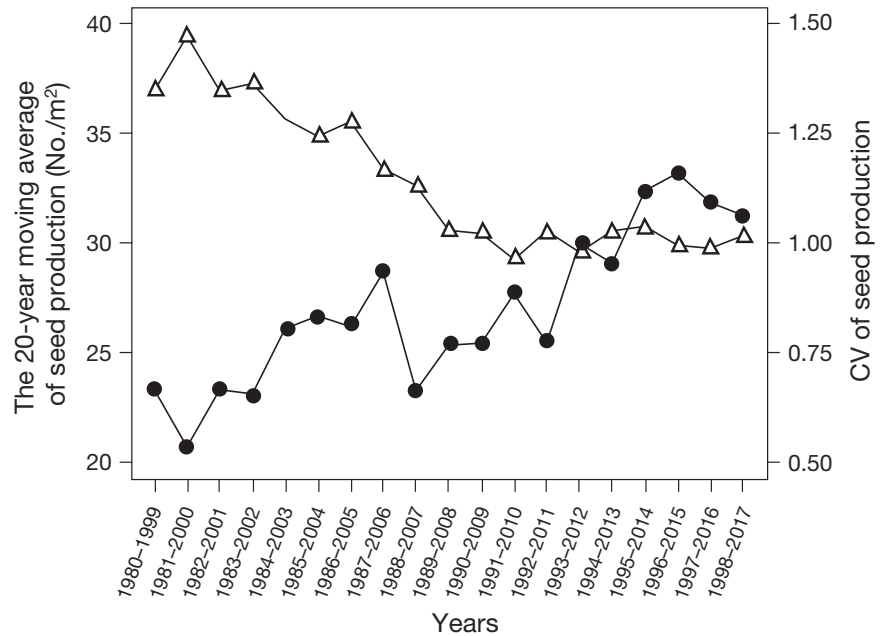
FIGURE 3 Changes in autoregressive (AR) model coefficients for observed seed production. AR model coefficients $[1 + a_1]$ and a_2 were obtained by using the sliding window method with a window of 20 years (see main text for details). (a) $[1 + a_1]$ and (b) a_2 in relation to the 19 twenty-year periods. Shading indicates the 95% credible interval. (c) Relationship between a_2 and $[1 + a_1]$ in the 19 periods were plotted on the parabola diagram of Bjørnstad et al. (1995). Shaded areas indicate coefficient combinations that produce sustainable cyclic fluctuations. Numbers on the contours indicate the length of the periodicity (year) of the cycle. Details of the behaviour of the coefficients are shown in (d). Polygonal line indicates the temporal sequence of the plotted points

FIGURE 4 Effects of temperature on seed production and autoregressive (AR) model coefficients. (a) The 20-year moving averages of seed production and (b) AR model coefficients plotted against the 20-year moving averages of mean temperature in the growing season (June–September). Regression analysis results for seed production and the AR model coefficients against the moving average of mean temperature are summarized in Tables 1 and 2 respectively

positions in the area indicating a 2-year cycle (Figure 3c,d). The upper limit of the 95% credible interval of a_2 in 8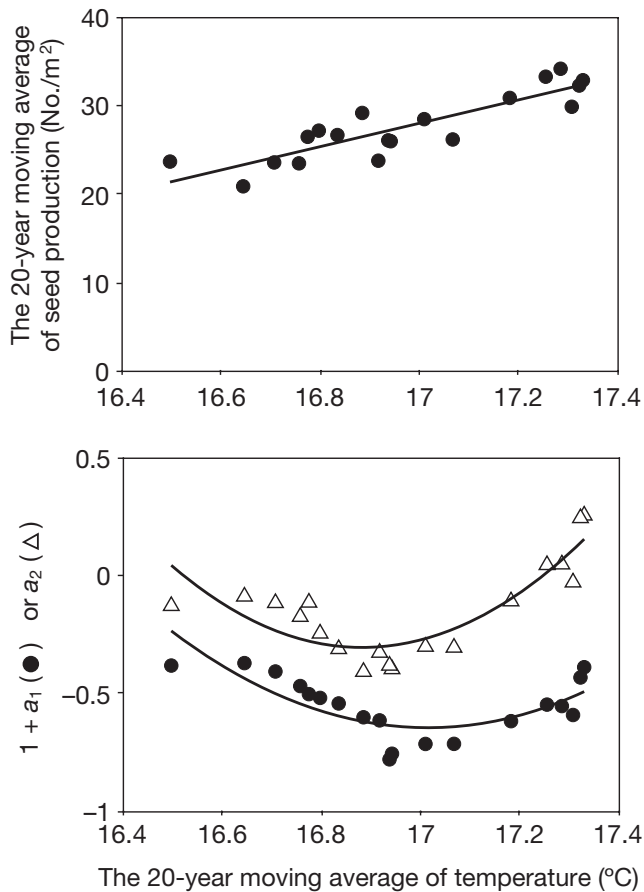th period (1987–2006) was −0.258 and the lower limit of the 95% credible interval in 15th period (1994–2013) was −0.168 (Figure 3b). In contrast, the credible interval of a_2 in 8th period did not overlap with that in later periods after 15th one. These facts indicated that the masting pattern changed significantly during the study period. Overall, the AR model results were consistent with the wavelet analysis results (see Figure 1b).

3.2 | Weather effects on seed production

In the growing season (June–September), monthly mean temperature showed a gradual upward trend, with high inter-annual fluctuation (Figure S6). Its 20-year moving averages increased monotonically with period number in all months (Figure S6; Table S1). Although monthly precipitation showed a gradual increasing trend in July and August, its moving average fluctuated more than that of temperature (Figure S6; Table S1).

The 20-year moving average of seed production showed good agreement with that of mean temperature in the growing season (Figure 4a). In the linear regression model, but not in the quadratic model, temperature had a significant positive effect on average seed production (Table 1). Similarly, precipitation had a significant positive effect on the moving average of seed production in the linear model but not in the quadratic model (Table 1). The multivariate model with two explanatory variables (temperature and precipitation) showed a significant contribution of temperature and not of precipitation (Table 1). Moreover, the moving averages of temperature and precipitation were highly correlated with each other (r_p = .847, t = 6.566, p < .0001). Therefore, we focused on the effects of temperature to the CV of seed production and masting interval. Temperature had a significant negative effect on the CV of seed production in the linear model but not on the quadratic model (Table 2). The regression of coefficient $[1 + a_1]$ against temperature was significant only in the quadratic model (Table 2; Figure 4b). Although the regression of a_2 was significant in both the linear and quadratic models, the quadratic model showed higher adjusted coefficient of determination than the linear model (Table 2; Figure 4b).

In the flowering season (late May to early June), the moving average of temperature increased monotonically, whereas that of precipitation showed a decreasing trend (Figure S6; Table S1). Temperature had a significant positive effect on seed production in the linear model but not in the quadratic model (Table S2). Similarly, precipitation had a significant negative effect on the seed production in the linear model but not in the quadratic model (Table S2). The multivariate model with the two explanatory variables (temperature and precipitation) revealed a significant contribution of temperature but not of precipitation (Table S2). Therefore, we focused on the effects of temperature even in the flowering season. Temperature also had a significant negative effect on the CV of seed production in both the linear and quadratic models (Table S3). The regression of coefficient $[1 + a_1]$ against temperature was significant in the quadratic model (Table S3), whereas the regression of coefficient a_2 against temperature was significant in both the linear and quadratic models (Table S3).

Overall, temporal variation of temperature showed similar trends between the growing and flowering seasons, and its effect on masting behaviour was similar between the two seasons. The moving averages of seed production, CV and the AR model coefficients could be described as a function of temperature in both the growing and flowering seasons. Adjusted R^2 of the linear regression models against temperature in the growing season was .751 for the moving averages of seed production (Table 2) and .728 for CV (Table 2), whereas those against temperature in the flowering season was .755 and .574 respectively (Table S2 and S3). Adjusted R^2 of the quadratic regression models against temperature in the growing season was .553 for $[1 + a_1]$ and .743 for a_2 (Table 2), whereas those against temperature in the flowering season was .484 and .596 for $[1 + a_1]$ and a_2 respectively (Table S3). Thus, overall, the regression models against temperature were better in the growing season than in the flowering season.

TABLE 1 Summary of regression model results for the relationships between seed production and weather factors in the growing season. The objective variable was the 20-year moving average of seed production. Explanatory variables were the 20-year moving average of temperature, precipitation or temperature and precipitation from June to September. Parameter estimates with the *SE*, *t*-values, *p*-values and adjusted R^2 are shown. Significant predictors (*p* < .05) are shown in bold type

	Seed production ~ intercept + temperature				
Linear model	**Estimate**	*SE*	*t*	*p*	**Adjusted R^2**
Intercept	−196.82	30.22	−6.51	**<.0001**	.751
Temperature	13.23	1.78	7.43	**<.0001**	
	Seed production ~ intercept + temperature + temperature²				
Quadratic model	**Estimate**	*SE*	*t*	*p*	**Adjusted R^2**
Intercept	2006.64	2,145.79	0.94	.3636	.752
Temperature	−246.46	252.87	−0.97	.3442	
Temperature²	7.65	7.45	1.03	.3197	
	Seed production ~ intercept + precipitation				
Linear model	**Estimate**	*SE*	*t*	*p*	**Adjusted R^2**
Intercept	−81.08	25.58	−3.17	**.0056**	.487
Precipitation	0.65	0.15	4.25	**.0005**	
	Seed production ~ intercept + precipitation + precipitation²				
Quadratic model	**Estimate**	*SE*	*t*	*p*	**Adjusted R^2**
Intercept	271.48	795.71	0.34	.7374	.461
Precipitation	−3.59	9.55	−0.38	.7123	
Precipitation²	0.013	0.03	0.44	.6635	
	Seed production ~ intercept + temperature + precipitation				
Multivariate model	**Estimate**	*SE*	*t*	*p*	**Adjusted R^2**
Intercept	−195.04	33.20	−5.87	**<.0001**	.736
Temperature	12.84	3.12	4.12	**.0001**	
Precipitation	0.03	0.19	0.15	.8799	

4 | DISCUSSION

4.1 | Decadal changes in masting behaviour

At our study site, the masting interval of *Q. crispula* shortened over time. The wavelet analysis showed that a combination of 2- and 4-year masting cycles was dominant during the first part of the study period, whereas masting transitioned to a 2-year cycle via a 3-year cycle from the middle to the latter part of the study period (Figure 1). The AR model results also showed a shortening of the masting interval from 3 to 2 years (Figure 3). Decadal changes in the masting interval may be prevalent in Fagaceae, although the patterns of change may differ among species and regions. Övergaard et al. (2007) recognized a shortening masting interval pattern in *Fagus sylvatica* in northern Europe; in Sweden it changed from 4 to 7 years between the end of the 17th century and the 1960s and then to 2.5 years in the 1970s and 2000s. In contrast, during a 20-year observation period (1966–1985) in Hokkaido, Japan, the 2-year masting cycle in *Q. crispula* became irregular and elongated (Imada, Nakai, Nakamura, Mabuchi, & Takahashi, 1990). In a very long-term (253-year) time-series analysis of *F. sylvatica*,

shorter masting intervals alternated with longer ones (Drobyshev, Niklasson, Mazerolle, & Bergeron, 2014).

In addition to the masting interval, average seed production may show temporal changes. During our study period, we observed an increasing trend in seed production (Figure 2), which was consistent with trends reported for two *Quercus* species in Europe (Caignard et al., 2017) and one *Nothofagus* species in New Zealand (Allen et al., 2014; Richardson et al., 2005) but opposite to the trend of the pinyon pine (*Pinus edulis*), which has shown a decrease in cone production in North America (Redmond et al., 2012).

Our temporal variation results are basically opposite to the seed production trends found in a meta-analysis conducted by Pearse et al. (2017). The meta-analysis showed an increase in the temporal variation represented by the CV, whereas in this study the temporal variation represented by the CV decreased. There may be an interaction between the temporal variation of seed production (CV) and the masting interval; in the studied forest, the increasing frequency of the output of stored resources (i.e. the shortening of the masting interval) during the study period may have reduced the CV of seed production by lowering the peak seed production level (Figure 1).

TABLE 2 Summary of regression model results for the relationships between temperature in the growing season and the coefficient of variation (CV) of seed production and each of the two AR model coefficients. The objective variable was CV of seed production, $[1 + a_1]$, or a_2 in 20-year sliding windows. The explanatory variable was the 20-year moving average of temperature from June to September. The parameter estimates with the SE, t-values, p-values and adjusted R^2 are shown. Significant predictors ($p < .05$) are shown in bold type

	CV ~ intercept + temperature				
Linear model	**Estimate**	**SE**	**t**	**p**	**Adjusted R^2**
Intercept	10.86	1.39	7.84	**<.0001**	.728
Temperature	−0.57	0.08	−7.02	**<.0001**	
	CV ~ intercept + temperature + temperature^2				
Quadratic model	**Estimate**	**SE**	**t**	**p**	**Adjusted R^2**
Intercept	180.56	92.28	1.96	.0681	.762
Temperature	−20.57	10.87	−1.89	.0768	
Temperature^2	0.59	0.32	1.84	.0845	
	$[1 + a_1]$ ~ intercept + temperature				
Linear model	**Estimate**	**SE**	**t**	**p**	**Adjusted R^2**
Intercept	1.50	2.02	0.75	.4664	.002
Temperature	−0.12	0.12	−1.02	.3225	
	$[1 + a_1]$ ~ intercept + temperature + temperature^2				
Quadratic model	**Estimate**	**SE**	**t**	**p**	**Adjusted R^2**
Intercept	451.86	96.08	4.70	**.0002**	.553
Temperature	−53.20	11.32	−4.70	**.0002**	
Temperature^2	1.56	0.33	4.69	**.0002**	
	a_2 ~ intercept + temperature				
Linear model	**Estimate**	**SE**	**t**	**p**	**Adjusted R^2**
Intercept	−7.18	2.77	−2.59	**.0190**	.232
Temperature	0.41	0.16	2.54	**.0213**	
	a_2 ~ intercept + temperature + temperature^2				
Quadratic model	**Estimate**	**SE**	**t**	**p**	**Adjusted R^2**
Intercept	655.09	114.00	5.83	**<.0001**	.743
Temperature	−78.81	13.43	−5.87	**<.0001**	
Temperature^2	2.33	0.40	5.90	**<.0001**	

Thus, a clearer understanding of the relationship between the seed production amount and its temporal variation may be gained by considering the effect of the masting interval.

4.2 | Mechanisms underlying the decadal changes in masting behaviour

What led to the observed decadal changes in masting behaviour in *Q. crispula*? Our results suggest that climate change—in particular, rising temperatures—may be a factor driving the decadal changes in masting. The effects of temperature have been analysed from at least from two perspectives (resource dynamics and as a cue for synchronous flowering) (Allen et al., 2017; Koenig et al., 2015; Pearse et al., 2014; Richardson et al., 2005) that

imply two possible mechanisms—a resource allocation shift and an environmental veto.

In the flowering season, temperature showed a rising trend, whereas precipitation decreased (Figure S6; Table S1). Although these changes in the weather conditions were not large, Schermer et al. (2019) pointed out that even a subtle change in weather conditions at the time of pollen release and aerial diffusion can, by making pollen limitation more likely, significantly affect reproduction of oak trees. The regression models showed that average seed production increased with rising temperature and decreasing precipitation (Tables S2, S3) and that the CV of seed production decreased with rising temperature. These results imply that warmer springtime temperatures accompanied by less precipitation may have reduced the frequency of an environmental veto of the pollination process and contributed to the higher seed production and its lower variability in the second half of the study period.

The regression models showed that the effect of temperature on average seed production in the growing season was similar to that in the flowering season (Tables 1; Table S2). In addition, in the growing season regression models, temperature well explained the CV of seed production and the variation of the AR model coefficients (Table 2; Table S3). These results suggest that changes in the resource dynamics during the growing season may exert influence on the decadal changes in masting.

Rising temperatures and a consequent surplus of resources may cause oak trees to shift their allocation of resources from storage to more frequent use. In *Q. crispula*, rising temperatures encourages photosynthesis in the canopy (Hikosaka, Nabeshima, & Hiura, 2007). Moreover, Nabeshima, Kubo, Yasue, Hiura, and Funada (2015) reported that the number and total area of earlywood vessels in tree stems of this species had increased since 1970s. These vessel changes may improve water transport efficiency and encourage the production of photosynthates and thus surplus resources. These findings support our inference that temperature in the growing season may be an indicator of surplus resources. The variations in the moving average of seed production and the AR model coefficients $[1 + a_1]$ and a_2 were well explained by that of temperature in the growing season (Figure 4). Thus, an increase in surplus resources can reasonably be interpreted as having a causal connection with the observed decadal changes in masting.

The effect of surplus resources on masting may not be straightforward. The concave curve describing the relationship between the AR model coefficient for a delayed effect (a_2) and temperature (Figure 4b) was an unexpected result. If the masting level is constant, the delayed effect of a_2 should simply become weaker (i.e. a_2 should increase) as surplus resources increase, because the stored resources consumed (converted to output) would likely be recovered quickly. In point of fact, after the 8th period (1987–2006), the values of a_2 increased linearly (Figure 3b). However, a_2 was relatively high in the earlier periods, even though the level of surplus resources may have been low. The behaviour of a_2 may reflect the interplay between the storage and output of surplus resources. The masting level varied in the study period, particularly in the earlier periods. There were two small peaks of seed production, in 1983 and 1985, separated by a short interval (2 years) (Figure 1a). Because a 2-year interval causes a_2 to increase, a_2 had become relatively high by 5th period (1984–2003), and it decreased thereafter (Figure 3b). Peak size variation, which is a key feature for obtaining a deeper understanding of decadal changes in masting behaviour, should be investigated in future studies.

As the resource depletion by seed production in the previous year is considered to be a fundamental determinant of seed production in the current year, we predicted that the effects of $[1 + a_1]$ would always be negative and stable. Although the observed values of a_1 were always significantly negative (Figure 3a), the curve describing the relationship of a_1 with temperature was also concave (Figure 4b). However, in comparison with a_2, the variation of a_1 was small and the change in masting behaviour was determined mainly

by the variation of a_2. In another deciduous oak *Quercus serrata*, the total time of carbon accumulation in seeds has been estimated to be 1.38 years (Ichie et al., 2013); therefore, carbon stored for more than one year might be used for seed production. This finding is consistent with our result that $[1 + a_1]$ was a fundamental component that always influenced seed production, and a_2 was the component that made masting behaviour variable.

Differing from Ichie et al., (2013), several studies showed that reproduction in masting species did not depend on stored carbon reserves (Hoch, Siegwolf, Keel, Körner, & Han, 2013; Igarashi, Shibata, Masaki, Tayasu, & Ichie, 2019). Reproduction in beech does not deplete stored carbohydrates, but it does change the amount of nitrogen stored (Han & Kabeya, 2017; see also Han, Kabeya, Iio, Inagaki, & Kakubari, 2013; Miyazaki et al., 2014), and masting in *F. crenata* is well explained by the interplay between stored nitrogen and climatic cues (Abe et al., 2016). However, nutrient accumulation may not have direct effects on the masting of *Q. crispula*—the target species of this study—because the seeds of this species contain only small amounts of protein (Shimada, Saitoh, Sasaki, Nishitani, & Osawa, 2006). Nitrogen may have indirect effects on seed production through bio-assimilation in *Q. crispula*, because in *Quercus* species, photosynthetic activity increases as the leaf nitrogen content increases (Takashima, Hikosaka, & Hirose, 2004). Our limited knowledge about carbohydrate–nitrogen interactions (Allen et al., 2017; Han & Kabeya, 2017) and the variation of carbon storage in relation to masting request further researches on the resource dynamics of masting.

The two possible mechanisms underlying decadal changes in masting that we examined, namely a resource allocation shift and an environmental veto, are not mutually exclusive. Inter-annual fluctuations of seed production have various aspects, including the number and mass of seeds; its variability represented by the CV; the masting interval; the peak size; and the interactions among them. Each aspect may have a different mechanism. From these aspects, testing the effects of a resource allocation shift and an environmental veto on the decadal change in masting behaviour provides us a good opportunity to identify the determinants and underlying mechanism of masting itself, because identified covariates explaining decadal changes would also be the candidate determinants of masting. To generalize our findings, it is necessary to investigate whether similar changes in masting behaviour occur in various places with different climatic features. Physiological and phenological data on seeding are also needed to further evaluate these two possible mechanisms of decadal changes in masting.

The decadal changes in masting behaviour may provoke various changes in the forest ecosystem. Solbreck and Knape (2017) showed that highly fluctuating biennial seed production can lead to predator satiation. However, biennial seed production in *Q. crispula* may reduce predator satiation. One of the major seed consumers of *Q. crispula* is curculionid weevils, which generally have a prolonged diapause of 2 years (Maeto & Ozaki, 2003). Therefore, the life cycle of the weevils might synchronize with seed production on a 2-year

cycle. The decrease in the CV of seed production may also reduce the predator satiation effect. Thus, it would be interesting to investigate how the decadal changes in masting behaviour influence seed consumers and its feedback to trees (Bogdziewicz, Marino, Bonal, Zwolak, & Steele, 2018).

Because the Japanese wood mouse *Apodemus speciosus* increases in abundance after the masting year of *Q. crispula* (Onodera et al., 2017; Saitoh et al., 2007), the shortening of the masting interval may increase the frequency of high-density years of the wood mouse. Rodents are a significant vector of tick-borne pathogens, and the short masting interval may increase the risk for zoonoses. However, several vertebrate species may be involved in the population dynamics of ticks (Ostfeld, Levi, Keesing, Oggenfuss, & Canham, 2018; Takumi, Sprong, & Hofmeester, 2019). Thus, to establish a comprehensive forest management program that includes the management of zoonosis risks, studies of decadal changes in masting behaviour in the context of community ecology should be conducted.

AUTHORS' CONTRIBUTIONS

T. Shimada conceived the ideas behind this study. M.S. designed the methodology. M.S., T.M., T. Shimada and T.Y. collected the data. T. Saitoh conducted the data analyses. T. Saitoh and M.S. wrote the initial drafts of the manuscript. All the authors critically discussed the drafts, contributed to their revision and gave final approval for publication.

DATA AVAILABILITY STATEMENT

R scripts are available in Appendix S3 and Appendix S5 of the online supporting information, and seed-fall data are available in Appendix S4 of the online supporting information. Other data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.v6wwpzgrb (Shibata, Masaki, Yagihashi, Shimada, & Saitoh, 2019). Original weather data are available from the Japan Meteorological Agency at: https://www.data.jma.go.jp/gmd/risk/obsdl/index.php.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.