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Oak masting drivers vary between populations depending on their climatic environments

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Summary

Large inter-annual variation in seed production, called masting, is very common in wind-pollinated tree populations and has profound implications for the dynamics of forest ecosystems and the epidemiology of certain human diseases¹⁻⁵. Comparing the reproductive characteristics of populations established in climatically contrasting environments would provide powerful insight into masting mechanisms, but the required data are extremely scarce. We built a database from an unprecedented fine-scale 8-year survey of 150 sessile oak trees (*Quercus petraea*) from 15 populations distributed over a broad climatic gradient, including individual recordings of annual flowering effort, fruiting rate and fruit production. While oak masting was previously considered to depend mainly on fruiting rate variations^{6,7}, we show that the female flowering effort is highly variable from year to year and explains most of the fruiting dynamics in two-thirds of the populations. What drives masting was found to differ among populations living under various climates. In soft-climate populations, the fruiting rate increases initially strongly with the flowering effort, and the intensity of masting results mainly from the flowering synchrony level between individuals. In contrast, the fruiting rate of harsh-climate populations depend mainly on spring weather, which ensures intense masting regardless of the flowering synchronization level. Our work highlights the need for jointly measuring flowering effort and fruit production to decipher the diversity of masting mechanisms among populations. Accounting for such diversity will be decisive in proposing accurate, and possibly contrasted, scenarios about future reproductive patterns of perennial plants with ongoing climate change and their numerous cascading effects.

Results & Discussion

Identifying the key mechanisms of masting and assessing their relative contribution, are among the main obstacles to overcome if we are to propose robust scenarios for the future of forest regeneration and the dynamics of associated ecosystems⁸⁻¹². Comparing the characteristics of masting between populations evolving in contrasting climatic environments should be an extremely powerful approach to achieve this goal^{13,14}, in line with in-depth studies made, for example, on leaf phenology or on tree growth¹⁵⁻¹⁸. Regarding masting, powerful investigations should quantify the flowering efforts of trees together with their annual fruit production¹⁹⁻²². Such dual monitoring should be carried out simultaneously on several populations living in contrasting climates, using the same methodology and over enough years to accurately quantify the interannual dynamics of flowering effort, fruiting rate and fruit production, and the synchrony between trees. Due to the substantial investment required to accumulate such data, studies meeting these strong requirements are extremely rare (but see^{23,24}) and are even absent in oaks, which are nevertheless very abundant and whose fruiting regime has a determining impact on forest ecosystems in the Northern Hemisphere.

In our study, based on an 8-year field survey, we quantified in a very precise and unprecedented sampling effort the annual allocation to female flowering (the number of flowers produced, hereafter called flowering effort), the fruit production (the number of fruits produced) and the fruiting rate (calculated as the number of fruits divided by the number of flowers) of 150 sessile oak trees (*Quercus petraea* Liebl. L) from 15 populations living in various climatic conditions (see methods). The flower and acorn sampling was carried out on individually monitored trees equipped with unusually large (20m²) trap nets placed under the canopy allowing accurate estimation of reproductive effort even in years with little or no fruit production²⁵. Using this unique dataset, we first assessed to what extent interannual variation of fruit production was linked to interannual variation of flowering effort.

Flowering effort, a dominant driver of oak masting. Interannual variations in the fruiting rate, due to weather-mediated variable pollination, fertilization and/or fruit ripening success, are usually considered to be the main driver of oak masting, thereby considered as a “Fruit maturation” masting^{6,7}. In that sense, a number of studies report the positive effect of spring temperatures on pollination success and/or the negative effect of summer drought on fruit maturation, depending on species²⁶⁻³². Oaks would thus contrast with many other perennial plant species where masting is highly dependent on interannual variations in flowering effort (i.e. “flowering masting”)^{6,21,33}.

If oak masting would be essentially a matter of successful transition from flower to fruit (i.e. pollination or fruit ripening after fecundation), then mast seeding events should occur in years with high fruiting rates. On the contrary, in our study, trees reaching their maximum annual fruit production concomitantly experienced a wide range of fruiting rates (from 0.1 to 0.9, Figure S2A). In addition, the trees were found to produce highly variable amounts of female flowers between years, these amounts often being very low compared to their peak production (Figure 1A). Consequently, there is a very high density of points describing low flowering effort concomitant with low fruit production, revealing the limiting effect of flower availability. When flowering effort is increased, fruit production becomes extremely variable, ranging from no fruiting to the maximum value observed. At the population level, the fruit production strongly increases, on average, with the flowering effort (Figure 1B, see Table S1), although fruiting failure was occasionally observed despite relatively high flowering effort, on average.

Of the many studies on oak masting, only a few have rigorously quantified female flowering effort and fruit production intensity, and have already revealed a statistically positive relationship between the two, even though these analyses were based on a short time series and a relatively small sampling area per tree^{34,35}. From our 8-year study on 15 distinct populations, we provide a compelling demonstration of the major contribution of flowering effort to fruit production dynamics. The way flowering effort is involved in masting may vary, however, depending on climate locations.

Variable contribution of flowering effort to fruit production dynamics among populations.

Flowering effort might have a dual effect on the dynamics of fruit production^{6,19,23,36–38}: (i) there can be a direct effect because the number of female flowers corresponds to the maximum number of fruits that can be produced each year. More indirect effect can be due to pollen coupling and limitation: in self-incompatible plant species, the flowering effort and pollen production by neighboring trees may be positively related to the pollination success and the fruiting rate, which might theoretically enhance in a non-linear way the contribution of flowering to masting³⁹.

We determined, at the population level, the part of fruit production variation explained by flowering effort (direct and indirect) then by fruiting rate, and used these statistics to place each population along a gradient from "fruit maturation masting" to "flowering masting" (see method). While it is often tempting to classify one masting species at a single location along such gradient, we found that the 15 sessile oak populations were widely distributed (Figure 2B, C). While most populations were very close to the "flowering" end of the gradient, one was found at the other extreme, and several others occupied intermediate positions.

Regardless of the flowering effort, regular exposure to unfavorable weather conditions during pollination or fruit maturation may result in frequent fruiting failure^{29–31,40–42}, which environmental effect should loosen the link between flowering and fruit production dynamics and promote stochastic fruit production dynamics^{11,43}. Therefore, we predict greater contribution of flowering to fruit production dynamics in softer climate sites. Accordingly, we show that soft-climate sites are significantly closer to the "flowering masting" end of the masting gradient than harsh-climate ones ($t = 2.776$, p value = 0.0157, $cor = 0.61$, see Figure S1).

The diversity of oak masting drivers among populations. To detect the various possible drivers of oak masting, sites were assigned to either of "soft" and "harsh" climate categories on the basis of their mean annual temperature and temperature variation within and between years (see Figure 2A and methods). Then, we analyzed in these two groups the contribution of flowering effort and spring weather to fruiting rates (Figure 3, Table S2). Finally, we computed several masting statistics (i.e. interannual variation at the population level (CV_p or PV_p), at the individual level (\overline{CV}_i or \overline{PV}_i) and the degree of synchronization between trees (Sy) applied to each of the following: flowering effort, fruiting rate and fruit production and we analyzed their relationships (Figure 4, Table S3). CV s and PV s provided qualitatively similar results (see Figure S4 and Table S4).

Our results reveal marked differences among populations regarding masting characteristics (Figure 4). We noticed, however, few differences across the populations in the averaged interannual variation of flowering effort measured at the individual tree level (\overline{CV}_i , Figure 4B,E or \overline{PV}_i , Figure S4). Although such variation is crucial to explain masting locally, it is marginally involved in explaining the differences in masting patterns between populations. Those differences are mainly explained by two key component: (i) the shape and strength of the relationships between the fruiting rate and flowering effort and spring temperatures (Figure 3) and (ii) the degree of synchrony between trees in their interannual flowering effort which is extremely variable between populations (\overline{Sy} ranging from 0.1 to 0.8, Figure 4C).

Oak masting is mainly driven by flower dynamics in soft climate locations. In those populations, the fruiting rate initially increases very strongly with flowering effort (up to ca. 3000 flowers/m² per year per tree), then the fruiting rate becomes almost independent from variations in flowering effort (Figure 3A). The fruiting rate initially close to zero is presumably driven by pollination failure at very low pollen density²³. On the contrary, the fruiting rate is only weakly related to the spring temperature (Figure 3B). These results show a high, indirect effect of flowering effort on masting (through its effect on the fruiting rate) and suggest that there is little or no spring weather veto on

fruiting rate. Moreover the masting statistics (CV_p , \overline{CV}_i , \overline{Sy}) applied to fruit production or fruiting rate do not differ significantly -or differ very little- from those quantified on flowering effort (Figure 4). This result is clearly in line with masting being mainly driven by flowering dynamics in those populations.

In the absence of a marked effect of spring weather conditions on fruiting rate, what mainly drives masting is the degree of synchronization of flowering efforts between neighboring trees, which is highly variable among soft climate populations and drives the degree of synchrony of fruiting rate and fruit production (Figure 4C). For example, at one extreme, one population has trees fully desynchronized in their flowering effort (the null value being part of the \overline{Sy} confidence interval); the fruit production is then itself poorly synchronized and masting is almost lacking (fruit production: $CV_p = 45.50\%$). These results suggest that the synchrony of annual flowering effort is a masting feature that is very sensitive to changes in climatic conditions, which echoes the reported decline in flowering synchronization in beech trees over the past decade, highlighting its impact in the context of climate change on masting pattern, tree reproductive success and even on forest regeneration^{11,21,44}.

Oak masting is driven by spring weather in harsh-climate locations. In those locations, as opposed to the soft-climate oak forests, fruiting rate is highly variable but only weakly related to flowering effort, while it is very sensitive to spring temperature (Figure 3B). Fruiting rates can then be very low, even when the trees allocate a lot in flowering, which may be due to weather conditions unfavorable to pollination. These results are in accordance with previous studies showing that high spring temperatures could either increase flower phenological synchrony between individuals^{40,41,45}, or positively affect annual airborne pollen amounts^{31,43}, which in both cases would increase cross-pollination opportunities and promote fruiting rate. More surprisingly, harsh-climate populations experienced higher fruiting rates than soft-climate populations, which occurred in the rare years when the spring temperatures were high and favorable to pollination (Figure 3B). This is related to the fact that trees are more synchronized with each other in their fruiting rate in harsh than soft climate sites (Figure 4F). These results are therefore consistent with mechanistic model predictions that frequent occurrence of unfavorable conditions contributes to increase the synchrony of reproduction between trees and increase the intensity of masting^{20,43,46-49}.

In that sense, and contrary to the soft-climate sites, the masting statistics for fruiting rate and fruit production often have higher estimates than the ones related to flowering effort at the same sites (Figure 4 and Figure S4). Moreover, the dynamics of fruit production is more synchronized, more fluctuating and less dependent on the dynamics of flowering in harsh than in soft-climate sites. In

Figure 4 and Figure S4, the y-intercepts of the regression lines are often significantly higher for the harsh than soft climate sites and their slopes are lower (see Tables S3 - S4). Finally, masting remains intense in harsh climate locations even when the trees have poorly synchronized interannual flowering dynamics.

Although the effect of spring temperatures is very strong in harsh-climate locations, half of these study populations are relatively close to the extreme "flowering masting" position on the gradient, with flowering and fruit production dynamics being tightly linked (Figure 2B,C). This suggests that climatic factors, even when efficient on the fruiting rate, should be considered as drivers of oak masting only in connection with flowering effort.

Several scenarios expected of temperate oak masting in the context of climate change. Forest tree fecundity and masting are likely to be very sensitive to climate change^{9,21,33,50,51}. As the relative weight of flowering effort and of the weather conditions influencing the fruiting rate are very variable depending on the population considered, oak masting could take very different trajectories. In soft-climate populations, what will happen for the synchrony of flowering effort between trees will be decisive, similar to what was recently documented in beech populations²¹. The decline in tree synchrony may be expected as it already occurs in one of the populations surveyed experiencing very weak masting. In harsh-climate populations, masting may be largely based on the extent to which the flower phenology will shift⁴³. If the phenology changes only marginally, an increase in spring temperatures may promote more regular conditions favorable to pollination and strongly reinforce the coupling between flowering and fruit production dynamics⁴³. Conversely, if trees start flowering earlier in the season in response to higher spring temperatures, the weather conditions at the time of pollination could remain unchanged on average, and so could the dynamics of fruit production.

Our work highlights the need to place flowering effort at the heart of oak masting mechanisms and to account for possibly diversified patterns and processes among populations of the same species, diversity that could be generalized beyond the species studied here^{13,14}. Whatever the perennial plant species considered, future studies on masting should give priority to accurately quantifying allocation in flowering, ideally considering the early stages of flower development and the allocation to sex³², and aim to identify the mechanisms underlying flowering effort (i.e., the limiting constraints and resources, the responses to signals and both hormonal and genetic basis)^{11,19,20,22,52-55}. Secondly, there is a strong need to uncover the processes governing synchronization in tree floral dynamics (Moran effect, pollen limitation or coupling^{37,56,57}), which appears extremely labile and may ultimately drive masting trajectories²¹. Finally, based on pairwise quantification of flowering and fruit production, it will be essential to weigh the impact of weather attributes on the decoupling between flowering and fruit production dynamics. In those perspectives, comparing populations settled in

contrasting environments provides unprecedented powerful investigations. Combined with a growing number of experimental approaches^{22,32,38,45,58,59}, such sound framework will enable reliable fitting of mechanistic and demographic models⁶⁰ for proposing realistic scenarios of the future of masting in the context of climate change and of its many cascading effects, including the demography and evolution of fruit consumers -insects, birds, mammals-^{3,44,61-67}, the dynamics of some human diseases^{3,68,69}, the success of forest recruitment and regeneration, and other masting-driven ecosystem services⁷⁰.

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Author contributions

Conceptualization, Program construction and management, S.V & M-C.B-V; field and biological methodology, S.V, M-C.B-V & V.B; Data collection, S.V, M-C.B-V, F.D, C.M-B, E.F; data curation, E.F, M-C.B-V; formal analysis & visualization, E.F, J-R.L; writing – original draft and editing, S.V and E.F; writing – review, M-C.B-V, J-R.L, T.C, S.D; supervision, S.V and M-C.B-V; project administration, S.V; funding acquisition, S.V.

Declaration of interests

Funding : This study was funded by the ANR Program FOREPRO (ANR-19-CE32-0008) and the program RESPOND (ANR & Lyon University).

Conflict of Interest: The authors declare that they have no conflict of interest.

Ethical approval : All applicable institutional and/or national guidelines for the care and use of animals were followed.

Consent to participate : All patients included in this study gave written informed consent to participate in this research.

Consent for publication : All patients provided written informed consent to publish the data contained within this article.

Availability of data and materials: The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability: Not applicable

Main figure titles and legends

Figure 1 : Fruit production is tightly linked to flowering effort. A : relative fruit production as a function of relative flowering effort; for each tree, fruits counted each year are divided by the maximum number of fruits it produced over the 8 year survey. Relative flowering effort is calculated the same way. **B :** Same as **A**, but each point is the annual mean value over a site. The selected models and the corresponding fitted line/curve were generated from the relative data (according to AIC criterion, see method). In the two panels, the green points correspond to the maximum annual fruiting value of each tree (**A**) or each site (**B**) over the 8-year survey. This figure is related to Table S1 (for statistical analysis), and Figure S2.

Figure 2 : The flowering effort and the fruiting rate contribute unequally to fruit production dynamics in oak populations living in soft (red) or harsh (blue) climates. A : The 15 populations surveyed were splitted in “soft” (oceanic or mediterranean) and “harsh” (semi-continental) climatic conditions according to whether average annual temperatures were mild or low, and to whether temperature was rather steady or variable both within and between years (see method). **B :** Relative contribution of flowering effort and fruiting rate to the fruit production dynamics. **C :** The sites are positioned along the “Fruit Maturation - Flowering Masting” gradient, according to their orthogonal projection on the Fruit Maturation - Flowering Axis (**B**, see method). They distribute themselves between fruit production dynamics governed exclusively by fruiting rate (0) to exclusively by flowering dynamics (1). This figure is related to Figure S1.

Figure 3 : Fruiting rate, at the crossroads between the influence of April temperatures and flowering intensity. A: Mean fruiting rate (mean fruit number/mean flowers number) as a function of the mean flowering effort per year and per site. **B:** Mean fruiting rate per year and per site as a function of mean temperature measured at each site each year in April. The red and blue dots correspond to soft and harsh climate sites, respectively. This figure is related to Table S2.

Figure 4 : Relationship between masting statistics applied to fruit production and flowering intensity (A,B,C) and to fruiting rate and flowering intensity (D,E,F). The most synthetic statistic of masting corresponds to CV_p , which reflects the degree of interannual variability in flowering effort, fruiting rate or fruiting production at the population level (**A & D**). Population-level variation (CV_p) depends on both the individual-level variability ($\overline{CV_i}$, **B & E**) and the degree of synchrony between individuals (\overline{Sy} , **C & F**). Black dotted lines correspond to the first bisector ($y = x$). Error bars are the

95% confidence intervals of the statistics computed by means of bootstrapping method. Round and star-shaped dots indicate non significant and significant departure from equality between the x and y statistics, respectively (i.e. whenever the bisector does (does not) overlap the confidence interval - see **G** for a fictional statistic S). Soft and harsh climate sites are illustrated in red and blue, respectively. Full lines are used whenever there is a significant difference in the slope and intercept between the two climatic groups; dotted lines are represented when only the intercepts are significantly different (see Table S3). This figure is related to Figures S3, S4 and to Tables S3, S4.

STAR Methods

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to the Lead Contact, Samuel Venner (samuel.venner@univ-lyon1.fr).

Materials availability

This study did not generate new unique reagents

Data and code availability

- The datasets generated during this study are available upon request to the corresponding author.
- The study did not generate code.
- Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Sessile oak (*Quercus petraea* Liebl. L) is widely distributed all over Europe from Spain to southern Scandinavia until western Russia. Sessile oak forests are largely represented in France except around the Mediterranean basin⁷¹. It is a monoecious, wind pollinated and self-incompatible species where male and female flowers both develop on the current year's shoots. Each year, male flowers develop at the base of the first leaves and begin their development at the same time as the leaves break out. The female flowers start to develop shortly after at the base of the intermediate (5th or 6th) or apical leaves of the young shoot. In France, pollination occurs from mid-April to early May while fertilization occurs several weeks later, in early July⁷². Unfertilized flowers and aborted immature fruits fall all along the reproductive period, with unfertilized flowers massively falling in July. Fruit maturation lasts until late September and the oak acorns fall mostly in October⁷².

METHOD DETAILS

Field design

The annual production of female flowers and acorns was individually monitored for 8 years (from 2013 to 2020) on 150 trees from 15 sites located throughout France. On each site, we randomly selected ten mature trees of comparable size. A 20m² fine-meshed net (4×5m shade cloth) was

stretched about 1.80m above ground at the base of each tree, to collect all the female flowers and acorns that fall from the tree. To reliably assign the reproductive items to each monitored tree, the nets were placed under the tree crowns, in a way that avoided contamination from adjacent trees. These positions were fixed for all the trees during the 8-year survey. Each year, the nets were deployed from April till late December, which safely encompassed the period when the aborted flowers and fruit fall. The net had a hole in the middle and was funnel-shaped so that the fallen items could converge toward a collecting device (80 cm in height and diameter) placed underneath. This collector was surrounded by a wooden fence and was closed with its lid to prevent seed consumption by predators (i.e. birds, rodents and ungulates). This device is, however, unable to quantify the removal of fruits by consumers while still on the tree, which could underestimate fruit production, especially in low fruit production years. Collecting device content was collected twice a year, in August and in December; trees with for which the harvest protocol was incomplete any given year (at least one harvest missing in the year) were omitted in the data set for that year.

During harvesting sessions, whenever the total plant material collected from the net of one tree exceeded 3L volume, it was weighed to the nearest decagram, together with a 3L-sample that was brought back within two days to the laboratory in an individually marked and sealed bucket. At the laboratory, the samples were naturally dried for two months, then weighed again (to the nearest 0.1mg, to estimate the number of aborted flowers (including flowers from 1mm diameter), mature fruits and total female flowers (sum of aborted flowers and mature fruits) produced per m² by each individual.

Flower and fruit variables

For each tree, we gathered the bi-annual harvests made each year (one made during summer and the other one during winter) to estimate the number of aborted flowers, acorns and total flowers produced yearly per m². The annual fruiting rate was computed for each tree by dividing the number of mature fruits (i.e., the fruit production) by the number of flowers produced (i.e., the flowering effort). To overcome inter-individual variability and for illustrative purposes, we also computed the relative flowering and fruit production (Figure 1A and B), by dividing, for each tree, its flowering effort (or fruit production) in a given year by the maximum number of flowers (or fruits) it has annually produced in the eight-year series. We also averaged individual tree data per site to account for annual flowering effort, fruit production and fruiting rate at the population scale.

Meteorological dataset

Each site was characterized for its climatic features, on the basis of a 60-year dataset (1960-2020) including the average daily temperature estimated and extracted from the SAFRAN spatially explicit database (8 x 8 km mesh size grid)⁷³.

QUANTIFICATION AND STATISTICAL ANALYSIS

Climatic group assignment

The 15 sites were initially assigned to one of two categories depending on whether they belong to oceanic or mediterranean climatic regions (“soft-climate” sites, Figure 2A, red dots) or to semi-continental regions⁷⁴ (“harsh-climate” sites, Figure 2A, blue dots). To evaluate the relevance of this partitioning, we ran a discriminant analysis (ade4 package⁷⁵) from the average temperatures estimated daily at each site using the SAFRAN spatially explicit database (8 x 8 km mesh size grid)⁷³ over a 60-year period (1960 - 2020). For each site and each year, we calculated the annual average temperature and the monthly average temperatures to measure the temperature amplitude between the warmest and coldest month within the years. We then computed for each site the mean and standard deviation of the annual temperature and of the annual temperature amplitude. The discriminant analysis allows to find a linear combination of the 4 variables so that the coordinates of sites on the discriminant axis maximize the Mahalanobis distance⁷⁶ between the two a priori defined groups. This analysis perfectly assigned the sites to their groups defined a priori (Figure S1), so that the sites assigned to the soft climate group indeed experienced both higher and less variable averaged annual temperature (Figures S1A and S1B), and lower and less variable within-year thermal amplitude (Figures S1C and S1D), than the sites assigned to the harsh climate group.

To further check the significance of our typology we used a permutation test : we repeated 10 000 times random assignment of the sites to either soft or harsh group followed by the discriminant analysis to generate the empirical distribution of the Mahalanobis distance between the two groups under the assumption of no difference in climate typology between the groups. The Mahalanobis distance observed between the a priori defined soft vs. harsh climate sites is significantly smaller than the one expected under the null hypothesis (p -value = 0.01), confirming the robustness of the typology initially proposed.

Linking flowering effort to fruit production

We tested the relation between fruit production and flowering effort at the individual level (Figure 1A) and at the population level (using population-averaged yearly flowering effort and fruit production, Figure 1B). We used mixed linear models with tree and/or population as random effects

(see Table S1). For illustrative purposes, in Figure 1, we removed the variability between trees and between populations, by computing the relative variables. The models best fitting these data, selected from AIC criterion, were linear (panel A) and $y = x/(a * x + r)$ (panel B).

Masting components

Allocation in flowering can have a dual effect on fruit production: (i) it may directly determine the maximum number of fruits that possibly develop each year and (ii) it may influence the fruiting rate and then indirectly fruit production (see main text). Considering the annual mean values at the site level, we assessed the relative contribution of flowering effort (through both their direct and indirect effects) and of fruiting rate (once accounting for the direct and indirect effect of flowering effort) to fruit production, using linear, simple and multiple regression models. In a first step, we determined the coefficient of determination (R^2 called hereafter “Flowering masting index”), from models where fruit production and flowering effort are the response and explanatory variables, respectively. In a second step, we computed the coefficient of determination (R_{Tot}^2) of the more complete model including additive effects of flowering effort and fruiting rate. The part of the variation in fruit production explained by the fruiting rate (independently of the indirect effect of flowering effort) was called hereafter “Fruit maturation masting index”, and was computed as the difference between R_{Tot}^2 and the Flowering masting index.

From the graph with axes corresponding to “Fruit maturation masting index” (the $y - axis$) versus the “Flowering masting index” ($x - axis$) (Figure 2B), we defined a synthetic “Fruit maturation-flowering masting axis”, whose equation is $y = 1 - x$. Each site with coordinates (x,y) is then orthogonally projected on this new axis, and gets a unique value between 0 (fruit production dynamics governed exclusively by fruiting rate) and 1 (fruit production dynamics controlled exclusively by flowering dynamics; Figure 2C). Using a linear regression model, we then tested the relationship between the coordinates of sites along the “Fruit maturation-flowering masting” and the “climate” gradients (Figure S1).

Fruiting rate drivers

To understand the differences between populations in the strength of the coupling between flowering and fruit production dynamics, we examined the form and strength of the link between fruiting rate and flowering effort on the one hand (Figure 3A), and mean April temperatures on the other (Figure 3B). April temperatures are indeed known to influence fruit production in temperate oaks, through their effects on pollination success³¹ and could therefore partly explain the decoupling

between flowering and fruit production dynamics. We examined these relationships using the annual mean values per site, fitting Generalized Linear Mixed Models with a binomial error and a $\log(x + 1)$ transformation for the model with flowering effort. We tested the interaction with climatic groups to test for differences between soft and harsh climate sites. Models include population as random effect (Table S2). For illustrative purposes in Figure 3 we used fruiting rate as a response variable and represented two models, one for each climatic group. The best-fitted models were selected between four proposed relation types (linear, quadratic, exponential and saturating) based on AIC criterion.

Masting statistics

We computed several statistics to describe interannual variability in Flowering effort, Fruiting rate and in Fruit production, at the individual and population levels, and their synchrony among trees within populations.

Inter-annual variability

Two statistics can be used to account for interannual variability in seed production. The coefficient of variation (CV)⁷⁷ which has been used for a long time and in many studies dealing with masting⁷⁸⁻⁸², and a more recent statistic (PV)⁸³ computed as :

$$PV(x) = \frac{2}{n(n-1)} \sum_{i=1}^{n-1} \sum_{j=i+1}^n d(x_i, x_j)$$

where $d(x_i, x_j)$ correspond to the distance (i.e the difference) between x_i and x_j .

Which of CV or PV statistics should be used has already been debated in the masting literature⁸³. While PV overcomes some mathematical difficulties encountered by the CV ⁵⁵⁻⁵⁷, this statistic has strong limitations. As it is saturating, it might be poodle efficient at discriminating between high levels of interannual variation in fruiting. Moreover, as it is based on the calculation of distances, it does not account for the difference between theoretical fruiting dynamics that would be radically different. For example, the same PV values would be expected for time series composed (i) mainly of very low fruiting and including seldom years of massive fruiting and (ii) mainly of massive fruiting with seldom years of very low fruiting.

To overcome the problems with PV described above, we first ensured that PV and CV captured the same general information (Figure S3) and provided qualitatively similar results (Figures 4 and S4).

Results with CV s were put forward in the main text, as this is a thoroughly used statistic and easier to interpret biologically. Results with PV s were also made available in supplemental information because their confidence intervals (obtained by bootstrap from 10,000 replications) are much

smaller than those of the CV s (Figure S3), so the PV statistic confers greater statistical power in our analyses (Tables S3, S4).

The coefficients of variation computed at individual (Figure 4B,E) and population scale (Figure 4A,D) were called CV_i and CV_p , respectively, while population-averaged CV_i values were noted $\overline{CV_i}$.

Synchrony

For each variable (flowering effort, fruiting rate, fruit production) and for each pair of trees within a population, we calculated the Spearman correlation coefficient to measure their synchrony (Sy). We then plot the mean of synchrony of tree pairs at the population level (\overline{Sy}), in Figure 4C and 4F.

Comparison of masting patterns

To test whether the masting statistics (CV_p , $\overline{CV_i}$, \overline{Sy}) for fruit production or fruiting rate are significantly different from those obtained with flowering effort, we calculated 95% confidence intervals of these statistics using a bootstrap approach (random sampling of values and performing 10 000 random resampling with replacement). Each point in Figure 4 then has a two-dimensional confidence interval (along the x and the y -axis). The statistics calculated for fruit production (Figure 4A to 4C) or for fruiting rate (Figure 4D to 4F) significantly departed from those associated with flowering (x -axis) if the confidence rectangle defined by the confidence intervals does not overlap the bisector line $y = x$ (black dotted line, Figure 4G). On the contrary, when the confidence rectangle does overlap with the bisector, the y statistics are considered not significantly different from the x one. See Figure S4 for results with PVs .

To test whether the relationship between flowering and fruit production (or fruiting rate) statistics differs between soft and harsh climate sites, we test the interaction between the climate group and flowering statistics, on fruit production (or fruiting rate) statistics from ANCOVAs (see Table S3 for results of CV s and Sy and Table S4 for PVs).

All statistical analyses were performed using the R free software (v.4.0.2, <http://cran.r-project.org>). Packages `boot`⁸⁴, `latex2exp`⁸⁵, `ade4`⁷⁵, `lmerTest`⁸⁶ and `fitdistrplus`⁸⁷ were used for our analysis in addition to the basic functionalities as well as packages `tmap`⁸⁸ `raster`⁸⁹ to trace map.

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