Increasing spring temperatures favor oak seed production in temperate areas

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ABSTRACT (130/150 words)
The changes in reproductive phenology (i.e. timing of flowering and fruiting) observed in recent decades demonstrate that tree reproduction has already been altered by climate change. However, understanding the impact of these changes in reproductive success and fitness remains a major challenge for ecologists. We describe here a previously unreported phenomenon: a significant increase in the reproductive effort (seed production) of temperate
oaks with increasing spring temperature, observed over the last two decades. This sensitivity of seed production to temperature was confirmed by a “space-for-time” substitution based on elevation gradients. Our findings suggest that global warming may enhance oak reproductive effort in temperate ecosystems. Nevertheless, while fitness can be enhanced by higher levels of seed production, it also depends on the frequency and synchronization of mast seeding production, which may also be influenced by climate change.

MAIN TEXT (1925/3000 words)

Forests are important for biodiversity and as a terrestrial carbon sink\(^1\), and contrasting responses to climate change have been identified. For instance, growth and survival, two of the main components of tree fitness, have been found to be substantially altered by climate change\(^2,3\). In cold and mild areas, such as boreal and temperate forests, global warming is extending tree growing seasons\(^4,5\) and promoting wood production and tree growth\(^3\), whereas, in warmer and drier areas, negative impacts on tree growth\(^6\) and survival\(^7,8\) have been observed. In addition to the reported impact on growth, and, to a lesser extent, forest dieback, we need to know how tree reproduction, one of the most important components of plant fitness, is being affected by climate change, and its likely response.

Reproduction is critical for the maintenance and demography of populations, and should therefore be assessed carefully when modeling population responses to climate change\(^9\). Seedling regeneration and survival are directly linked to variations in seed production\(^10,11\) and the assessment of changes in regeneration from seeds in response to temperature has become a major challenge. There is, therefore, an urgent need to assess the
impact of climate change on tree reproduction, to improve our understanding of the likely
effects of this phenomenon on tree population dynamics.

An impact of climate change on the timing of reproduction has been reported for
numerous organisms\textsuperscript{12,13}. Indeed, reproductive phenology is known to be sensitive to
environmental cues, such as temperature\textsuperscript{14,15}, so climate change is likely to alter the intensity
of seed production. However, the impact of climate change on reproductive effort is difficult
to quantify, particularly in forest trees, which display the synchronized, intermittent
production of large amounts of seeds. This phenomenon, commonly observed in oak species
at the population scale, is called “masting” or “mast-seeding”\textsuperscript{16,17}. Most studies of tree seed
production over long time series have focused on single sites or small numbers of sites in
limited areas. The specific features of masting have, thus, made it difficult to assess the
sensitivity of seed production to temperature. Moreover, as pointed out by Crone and Rapp\textsuperscript{18},
the large numbers of isolated studies and of weather variables tested have highlighted
contradictory correlations with seed production, even for related species. As a result, to avoid
artifacts caused by masting, the monitoring of seed production should be replicated in space
and time, in ecologically independent forests.

In this study, we analyzed extensive sets of tree reproduction data for two temperate
European white oak species (the sessile oak (\textit{Quercus petraea}) and the pedunculate oak (\textit{Q. robur})), to determine whether seed production had changed over the last two decades in
response to global warming. We monitored seed production in 28 forests of \textit{Q. petraea} and
\textit{Q. robur} distributed throughout France over a period of 14 years. In parallel, a “space-for-
time” substitution was used to quantify the temperature sensitivity of acorn production over
elevation gradients. These analyses demonstrated significant temperature-induced trends in
seed production over the last two decades, suggesting that climate change enhances oak reproductive effort in temperate ecosystems.

Results and Discussion

Temporal trend in seed production

We examined temporal changes in the seed production of two oak species across France over recent decades (1994 to 2007). We observed a significant increase over time in reproductive effort for *Q. petraea* (Figure 1a) but not for *Q. robur* (Figure 1b). On average, acorn production (M<sub>acorn</sub>) in *Q. petraea* populations increased by 19.8 kg [8.3, 31.3] per hectare per year (Table 1). A similar trend was observed for *Q. robur*, but the correlation (M<sub>acorn</sub>/Year = 14.1 kg.ha<sup>-1</sup> [-1.7, 29.8]) was not significant (Table 1). Similar positive temporal trends have been reported in a few other studies. A limited number of reports for *Pinus engelmannii*<sup>19</sup> and in *Nothofagus solandri*<sup>20,21</sup> have demonstrated temporal shifts. In these studies, the monitored populations were located at high elevations, at which reproduction appears to be more sensitive to environmental change<sup>20,21</sup>. However, in most cases, no temporal trend in fruit production, for example, was observed<sup>22,23</sup> and such trends have rarely even been sought, due to the scarcity of adequate, long-term datasets. In our study, the many populations surveyed were found in temperate lowland forests located over a large area and at an elevation of between 55 and 330 m above sea level. The mean synchrony of seed production (Spearman’s coefficient) among the populations was very low for both species (0.11 ± 0.016 for *Q. petraea* and 0.15 ± 0.052 for *Q. robur*), demonstrating the lack of synchrony between populations over this large scale (the differences in seed production dynamics between the populations monitored are shown in Supplementary Figure S1). As the
populations were independent, any temporal change in reproductive effort can be seen as a robust overall pattern rather than a local trend in a marginal population. Many studies have explored the potential drivers of plant reproduction\textsuperscript{18,24,25}, but only a few have investigated changes in reproductive effort in response to global warming, due to a general lack of statistical power\textsuperscript{26,27}. In the context of climate change, the temporal trends observed here may reflect the effects of recent warming over the last few decades. Consistent with this view, we observed a significant increase in temperature over time at the sites studied (Supplementary Figure S2), potentially sufficient to account for the positive temporal trend observed.

Reproductive effort in oak is increasing with increasing spring temperatures in temperate areas

Temperature and rainfall are routinely recorded and are considered the most relevant climatic variables driving seed production\textsuperscript{24}, but their effects seem to differ between tree species and ecosystems\textsuperscript{23}. Tree reproductive effort has been studied mostly in Mediterranean oak species and monitored mostly in Southern Europe and California\textsuperscript{28}. For most of these species, a warmer, drier summer season results in lower levels of seed production\textsuperscript{29,30}. Interestingly, the main driver appears to be water deficit rather than temperature \textit{per se}\textsuperscript{31,32}. By contrast, we found that, in both \textit{Q. petraea} and \textit{Q. robur}, seed production was positively correlated with spring temperature (Figure 2a, 2b, Table 1), which is known to have a strong effect on flowering and pollination\textsuperscript{14,15}. No study has ever reported positive temporal clines for acorn production, but positive correlations with spring temperature have been found in California for three Mediterranean oak species, \textit{Q. lobota}, \textit{Q. douglasii} and \textit{Q. kelloggii}\textsuperscript{33}, and three temperate oak species, \textit{Q. alba}, \textit{Q. rubra} and \textit{Q. velutina}\textsuperscript{17}. In our study, despite the broad distribution of the populations, the positive correlation with spring temperature
observed could be explained mostly by temperature variability over time rather than temperature variability over space (Supplementary Table 1). The trend towards an increase in seed production over time observed for both species was therefore directly correlated with the increase in spring temperature observed over the last two decades (Supplementary Figure S2). Climate change has had a negative impact on reproduction in Mediterranean oaks in Europe, but we show here that the increase in spring temperature has favored reproduction in temperate oaks.

We then examined seed production along elevation gradients in Southern France, to refine the temperature-seed production relationship. Our findings confirm the strong positive correlation between seed production and spring temperature in *Q. petraea* (Table 1). The gain in acorn production per one-degree rise along the elevation gradient ($M_{acorn}/T_{Ap-Ma}$= 334.2 kg.ha$^{-1}$) was three times greater than that along the spatio–temporal gradient ($M_{acorn}/T_{Ap-Ma}$= 111.89 kg.ha$^{-1}$). This difference may reflect differences in temperature values and gradients between the two designs. Indeed, the range of spring temperature variation was lower for the spatio-temporal gradient (6.2°C) than for the elevation gradient (10.8°C).

**What is the impact on tree fitness?**

Our observations suggest that climate change may increase the fitness of temperate oaks. An increase in seed production is beneficial to the tree, as it increases seed dispersal$^{34,35}$, thereby increasing the number of potential offspring and, consequently, their establishment. In addition, acorn mass increases with increasing temperature, by about 0.15 g per degree [0.09, 0.22] (Figure 3). This gain may increase the resistance of acorns to environmental stress (predation by insects, frost) and enhance germination$^{36,37}$. However, reproduction in many
tree species, including oaks, is characterized by masting or mast-seeding, with synchronized large-scale seed production at the population scale (Supplementary Figure S1). This process is considered to be an adaptive response to the selective pressure exerted by predators\textsuperscript{16,17}. Masting limits seed predation and promotes seed dispersal, thereby ensuring high rates of offspring survival and optimizing resource allocation to reproduction\textsuperscript{24,38}. Changes in masting associated with climate change may, therefore, have a negative impact on the fitness of tree populations.

There is an ongoing controversy about the influence of climate change on reproduction. On the one hand, climate is considered to be a cue for variations in seed production\textsuperscript{26}, and on the other, it is considered a proximal driver\textsuperscript{39,40}. Kelly et al.\textsuperscript{26} recently suggested that the difference in temperature between two consecutive years (ΔT) may act as the main signal for massive, synchronous seed production. As a gradual increase in mean temperature will not affect ΔT, these authors suggest that climate change may not affect masting. However, other studies have contested this differential-temperature hypothesis. They have shown that ΔT effects do not apply to all species\textsuperscript{23,39} and have suggested that this cue is relevant only because it combines the direct proximal effects of recent weather and the indirect effects of previous weather through previous seed set and resource limitation\textsuperscript{40,41}. For instance, Övergaard et al.\textsuperscript{42} observed, during 30 years of measurement in European beech forest (\emph{Fagus sylvatica}), an increase in the frequency of mast events directly correlated with an increase in temperature. With increasing periodicity, the temporal variability characterizing mast-seeding and enabling the trees to control predator population size\textsuperscript{24,43} might be greatly reduced\textsuperscript{27}. Low inter-annual variability in seed crops may lead to an increase in predator population size, decreasing reduce offspring survival. This paradoxical consequence of climate warming for
temperate tree reproduction highlights the need for improvements in our understanding of the proximal mechanisms underlying masting in trees, for prediction of the response of forest ecosystems to climate change.

This study focused on temperate forests dominated by deciduous oak species and cannot be extended to other forest types. However, we can compare the time and temperature trends of acorn production observed in oaks with the patterns reported for whole biomass growth in trees44,45. There is a clear congruent increase in vegetative growth and reproductive growth (our results) in Q. petraea and Q. robur in recent decades in central Europe. Such trends can be seen as two facets of the overall consequence of the same causes relating to global changes in recent decades. An increase in temperature extends the period of vegetative growth4,5 and enhances tree growth46. In addition to increasing temperature, increases in the carbon dioxide content of the atmosphere may also promote tree growth in some species, and increases in nitrogen (N) deposition have been shown to stimulate forest growth and carbon sequestration in Europe47. As reproduction in trees is also dependent on resource availability48,49, the combined effects of temperature, carbon dioxide, and nitrogen deposition may also contribute to the increase in seed production. However, the congruent pattern of vegetative and reproductive growth may be negatively affected by extreme events and disturbances, such as firestorms or the spread of insects and diseases, which may also be triggered by global changes50.

Global warming has had a positive effect on temperate oak growth. However, the response of tree reproduction to environmental changes remains unclear, mostly due to our limited understanding of masting processes. Long-term studies of reproductive investment over large areas would be required to assess the global impact of climate change on trees.
REFERENCES (50/50)


AUTHORS’ CONTRIBUTIONS:

T.C and S.D. conceived the idea for this work. T.C., C.F. and M.N. assembled the dataset and analyzed the data. T.C. and S.D. wrote the manuscript and A.K., S.V. and C.F. revised the manuscript.

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Table 1: Temperature sensitivity of reproductive efforts in oaks | Slopes of the linear mixed-effect regression between acorn production in kilograms per hectare ($M_{\text{Acorns}}$) and year (temporal gradient, ($M_{\text{Acorns}}$/Year)), and for every 100 m increase in elevation (spatial gradient, $M_{\text{Acorns}}$/Alt$_{100m}$), and the mean temperature in April and May in °C ($M_{\text{Acorns}}$/T$_{\text{Ap-Ma}}$) in both studies. The 95% credibility intervals are indicated in square brackets. Reproduction in *Quercus petraea* was monitored in both studies, whereas *Quercus robur* was monitored in the temporal gradient study only. Significant correlations are indicated in bold.

<table>
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<tr>
<th>Species</th>
<th>Temporal</th>
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<td>$M_{\text{Acorns}}$/Year</td>
<td>$M_{\text{Acorns}}$/T$_{\text{Ap-Ma}}$</td>
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<tr>
<td><em>Q. petraea</em></td>
<td>19.82 [8.3, 31.3]</td>
<td>111.89 [63.1, 146.0]</td>
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<tr>
<td><em>Q. robur</em></td>
<td>14.07 [-1.7, 29.8]</td>
<td>72.66 [19.6, 120.5]</td>
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Figure 1: Temporal variation in seed production for *Q. petraea* and *Q. robur* | Temporal variation in seed production (kg ha\(^{-1}\)) of 19 and 9 populations of *Q. petraea* (a) and *Q. robur* (b) respectively, monitored over 14 years and distributed throughout France. Each dot corresponds to the mean seed production across all populations per year (kilograms per hectare per year averaged over all sites). The slope of the regression line and its 95% credibility interval, calculated from a linear mixed-effects model [2], are given for both species, with the coefficient of determination (R\(^2\)) between model [2] and mean production.

(a) *Quercus petraea*  
\[ b = 19.82 \text{ [8.3, 31.3]} \text{ kg/ha/year} \]  
\[ p.\text{value} < 0.001 \]  
\[ R^2 = 0.28 \]

(b) *Quercus robur*  
\[ b = 14.09 \text{ [-1.7, 29.8]} \text{ kg/ha/year} \]  
\[ p.\text{value} = 0.08 \]  
\[ R^2 = 0.15 \]
Figure 2: Responses of seed production to spring temperature for both \textit{Q. petraea} and \textit{Q. robur}. Changes in acorn production per population and per year ($M_{\text{Acorns}}$) for \textit{Quercus petraea} (a) and \textit{Quercus robur} (b) according to mean spring temperature. For both species, acorn production data for all populations and all years were binned into 19 temperature classes of the same size. Mean acorn production per bin is correlated with the temperature class median. The slope of the regression line and its 95% credibility interval, calculated from a linear mixed-effects model [3], and the coefficient of determination ($R^2$) between the model [3] and the binned data are given for each species.
Figure 3: Temperature trends in seed mass for *Quercus petraea* | Trend in acorn mass (g) with mean temperature from April to November (°C) along the elevation gradient. Each dot corresponds to the mean value for acorn mass for a tree in a given year. The slope of the regression line and its 95% credibility interval, calculated from a linear mixed-effects model, and the coefficient of determination ($R^2$) are indicated. April to November corresponds to reproductive cycle length in *Quercus petraea*: from flowering to acorn release.
Materials and methods  (1241/3000 words)

Study sites

We analyzed variations in seed production for two European oak species (*Quercus petraea* and *Quercus robur*) along latitudinal and an elevation gradients. The latitudinal field survey concerned 19 *Q. petraea* populations and nine *Q. robur* populations distributed across France, for which seed production assessed during 14 years, from 1994 to 2007. Populations were distributed between latitudes of 43.2° and 50.2°N and longitudes of 0.04° and 3.7°E (Supplementary Table S2). The populations studied were mature oak stands with a mean age of 85.5 years ± 28.7 in 1994, at the start of monitoring. In each forest, acorns were collected at the population scale, in 10 5 m² litter bags, set up under the closed canopy and evenly distributed over an area of about half a hectare. Acorns were harvested twice during the fall (before and after leaf senescence). The mass of acorns produced was estimated for each population in kg ha⁻¹ through the measurement of dry mass. Daily mean, minimal and maximal temperatures (°C) and precipitation (mm) were extracted from the SAFRAN⁵¹ spatially explicit database (8 x 8 km grid) for each site.

The elevation gradient survey was set up in the French Pyrenees, along a replicated transect in two parallel valleys: Ossau and Gaves (latitude 42° 47’ N to 43° 45’ N; longitude 00° 44’ W to 00° 06’ E). Five natural mature populations of *Q. petraea* were monitored in each valley, at different elevations, from 131 m to 1630 m (Supplementary Table S3). At each site, nets were set up 1 m above the ground under the whole tree canopy, to collect all the acorns produced by an individual. In total 15, 13, 25 and 30 adult trees were monitored in 2012, 2013, 2014 and 2015, respectively. The 30 trees had a mean height of 19.2 ± 9.4 m and a mean
diameter of 37.7 ± 19.6 cm. From 2012 onwards, the organic components (leaves, branches, fruits) falling from the trees were harvested every two weeks, from the end of September until the beginning of December. For each tree, the projected area of the canopy on the ground (SC_{OBi}) was calculated by first defining the canopy center (O) and then determining the distance from O to the outer limit of the canopy (B_i), at 8 points, 45° apart (OB_{1-8}). The surface area was calculated as:

\[
SC_{OB_i} = \frac{\pi}{i} \times \sum OB_i^2 \quad [1]
\]

The harvested litters were sorted in the laboratory, and total acorn production, total dry mass and mean acorn weight per tree and per year (g) were determined. Total seed production was normalized by dividing by the total projected surface area of the tree canopy. Air temperature was measured with a data logger (HOBO Pro RH/Temp, Onset Computer Corporation, Bourne, Massachusetts, USA) at all sites. Data were recorded hourly, from January 1 2012 to December 31 2015.

**Statistical analysis**

**Temporal trend**

We evaluated the change in seed production over time separately for the two species, with a linear mixed effects model:

\[
Y_{jt} = a_\mu + b_\mu t + (a_j + b_j t) + \varepsilon_{jt} \quad [2]
\]

where \(a_\mu\) is the overall intercept and \(b_\mu\) is the overall slope of line of acorn production over time (t), \(a_j\) is the random deviation associated with population \(j\), and \(b_j\) is the population-
specific deviation in slope, and the residuals are denoted $\epsilon_{jt}$. For both species, we compared the model [2] with a simpler model not including the random deviation in slope $b_{jt}$. We then used a likelihood ratio test (the Chi-squared test) to test the hypothesis that the temporal trend observed was homogeneous among populations. As the $p$-value values obtained, 0.91 for *Quercus petraea* and 1.00 for *Quercus robur*, were greater than the significance threshold of 0.05, we did not reject the null hypothesis of a homogeneous temporal trend between populations. Moreover, slopes and confidence intervals were calculated with the simpler model (i.e. $Y_{jt} = a_{\mu} + b_{\mu}t + (a_j) + \epsilon_{jt}$).

We then evaluated the response of seed production to temperature:

$$Y_{ij\mu T} = a_{\mu} + c_{\mu}T + (a_j + c_jT) + \epsilon_{ij\mu T} [3]$$

where $c_{\mu}$ is the overall slope of the line of acorn production plotted against temperature (T) and $\epsilon_{ij\mu T}$ denotes the residuals. As before, we compared the model [3] with a simpler model lacking the random deviation of slope $c_jT$. We then used a likelihood ratio test (the Chi-squared test) to test the hypothesis that the observed correlation with temperature was homogeneous among populations. As the $p$-values obtained, 0.08 for *Q. petraea* and 0.12 for *Q. robur* were greater than the significance threshold of 0.05, we did not reject the null hypothesis that the observed correlation with temperature was homogeneous among populations.

We therefore used the simplest model [3] (i.e. $Y_{ij\mu T} = a_{\mu} + c_{\mu}T + (a_j) + \epsilon_{ij\mu T}$) to estimate the effect of temperature on seed production. For this purpose, we first compared this model with the null model (i.e. without the fixed effect of temperature $c_{\mu}T$), using the Akaike criterion and hypothesizing that temperature has no effect on seed production. This
comparison was performed for the mean temperature of each month of the year. For April, March-April and April-May for *Q. petraea* and for April, and April-May for *Q. robur*, the Akaike criterion differed significantly between the models with and without a fixed effect of temperature (Supplementary Figure S3). The Akaike criterion values were lowest for temperatures recorded during the spring months, so we estimated slopes for different spring periods (Supplementary Table S4). For *Quercus petraea*, a significant relationship was found with the temperature in April (94.8 [61.5, 128.4] kg.ha$^{-1}$), March-April (102.98 [56.6, 152.4] kg.ha$^{-1}$), April-May (111.89 [63.1, 146.1] kg.ha$^{-1}$) and May-June (41.59 [1.1, 86.1] kg.ha$^{-1}$) (values given for each one-degree increase in temperature). For English oak, a significant increase was observed only for April (54.07 [14.4, 93.7] kg.ha$^{-1}$) and April-May (72.66 [19.6, 120.5] kg.ha$^{-1}$) (values given for each one-degree increase in temperature; Table 1, Supplementary Table S4).

As spring temperature was found to have increased over the last two decades (Supplementary Figure S2) and seed production was significantly correlated with temperature (Table 1, Figure 2), we considered the observed temporal trend in seed production in both species (Table 1, Figure 1) to be due principally to the increase in temperature. However, as the populations were distributed over a large area covering a large range of temperatures, we explicitly accounted for variability due to the year and population, with the following model:

\[
Y_{ijPY} = a_\mu + b_\mu P + c_\mu Y + (a_j) + e_{ijPY} [4]
\]

where $b_\mu$ denotes the overall slope of the mean population temperature against year line (P) and $c_\mu$ is the overall slope of mean yearly temperature against population line (Y) for acorn
production and $\varepsilon_{ijPY}$ denotes the residuals. We used model [4], with the mean temperature of April-May (Supplementary Table S1).

**Trend along the elevation gradient**

We then evaluated the sensitivity of reproduction to temperature along the elevation gradients in Pyrenees:

$$Y_{ijkT} = a_\mu + c_\mu T + (p_j) + (n_{k(j)}) \varepsilon_{ijkT} \ [5]$$

where $a_\mu$ denotes the overall intercept and $c_\mu$ the overall slope of the line of acorn production against temperature ($T$), $p_j$ and $n_{k(j)}$ are the random deviations associated with population $j$ and the individuals within the population $k$ and the residuals are denoted $\varepsilon_{ijkT}$. We tested the effect of temperature over the same period as above (Table 1, Supplementary Table S4).

Finally, we also evaluated the sensitivity of acorn size to temperature along the same elevation gradient, with the same model [5].

All the linear mixed effects models were fitted by the restricted maximum likelihood (REML)$^{52}$ method in the *lme4* R package$^{53}$

**References**
