The effects of local climate on the correlation between weather and seed production differ in two species with contrasting masting habit

Michał Bogdziewicz[1], Jakub Szymkowiak[2], Marcos Fernandez-Martinez[3], Josep Peñuelas[4,5], Josep M. Espelta[5]

[1]Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Poznań, Poland
[2]Population Ecology Lab, Faculty of Biology, Adam Mickiewicz University, Poznań, Poland
[3] Centre of Excellence PLECO (Plant and Ecosystems), Department of Biology, University of Antwerp, Wilrijk, 2610, Belgium.
[4] CSIC, Global Ecology Unit, CREAF-CSIC-UAB, Bellaterra, 08193 Catalonia, Spain
[5]CREAF, Cerdanyola del Valles, 08193 Catalonia, Spain

Abstract

Many plant species present inter-annual cycles of seed production (mast seeding), with synchronized high seed production across populations in some years. Weather is believed to be centrally involved in triggering masting. The links between meteorological conditions and seeding are well-recognized for some species, but in others consistent correlates have not been found. We used a spatially extensive data set of fruit production to test the hypothesis that the influence of weather on seed production is conditioned by local climate and that this influence varies between species with different life history traits. We used two model species. European beech (*Fagus sylvatica*) that is a flowering masting species, i.e. seed production is determined by variable flower production, and sessile oak (*Quercus petrea*) that is a fruit-maturation masting species, i.e. seed production is determined by variable ripening of more constant flower production. We predicted that climate should strongly modulate the relationship between meteorological cue and fruit production in *Q. petrea*, while the relationship should be uniform in *F. sylvatica*. The influence of meteorological cue on reproduction in fruiting masting species should be strongly conditioned by local climate because the strength of environmental constraint that modulates the success of flower-to-fruit transition is likely to vary with local climatic conditions. In accordance, the meteorological cuing was consistent in *F. sylvatica*. In contrast, in *Q. petraea* the relationship between spring temperature and seed production varied among sites and was stronger in populations at colder sites. The clear difference in meteorological conditioning of seed production between the two studied species suggests the responses of masting plants to weather can be potentially systematized according to their masting habit: i.e. fruiting or flowering.

Key-words: environmental variability, mast seeding, masting, Moran effect, plant reproduction, seed production

Introduction

Masting is characterized by synchronized and highly variable levels of seed production over years within a population or a community (Kelly and Sork 2002). It is a ubiquitous reproductive strategy of plants worldwide that has major cascading effects on ecosystem functioning (Jones et al. 1998, Ascoli et al. 2015, Bogdziewicz et al. 2016, Pearse et al. 2017, Vacchiano et al. 2018). Masting is spatially synchronous, often over large portions of species distributions (Koenig and Knops 1998, Ascoli et al. 2017, Fernández-Martínez et al. 2017a, Vacchiano et al. 2017). The Moran effect (correlated environmental disturbances driving the spatial autocorrelation of ecological phenomena, cf. Koenig 1999) is a major mechanism that can account for large-scale synchrony of reproduction (Koenig and Knops 1998, Kelly and Sork 2002). Specifically, some weather signals (cues) may have large effects on reproduction because selection has favored plants that all respond to the cue in the same way, resulting in high synchrony and individual variability (Kelly et al., 2013, Pearse et al. 2016).

Consequently, the correlations between seed production and weather have often been investigated (Crawley and Long 1995, Piovesan and Adams 2001, Kon and Noda 2007, Allen et al. 2012, Koenig and Knops 2014, Fernández-Martínez et al. 2017a, Koenig et al. 2017, Vacchiano et al. 2017). Despite the large effort, consistently linking and predicting the effects of weather on seed production across species has proven to be surprisingly difficult (Crone and Rapp 2014). In particular, consistent and unequivocal links between weather and seed production have not been found in some common and widely studied genera like oaks (*Quercus* spp.), and the specific meteorological correlations vary among species, and even within species among different studies (Sork et al. 1993, Crawley and Long 1995, Lusk et al. 2007, Crone and Rapp 2014, Koenig and Knops 2014, Pérez-Ramos et al. 2015, Koenig et al. 2016). Conversely, the link is much more consistent across space and time in some other species, such as New Zealand tussock grasses (*Chionochloa* sp.) or European beech (*Fagus sylvatica*) (Piovesan and Adams 2001, Rees et al. 2002, Schauber et al. 2002, Kelly et al. 2008, 2013, Tanentzap et al. 2012, Vacchiano et al. 2017). Why the correlations between seed production and weather are consistent in some masting species, and how the irregularity in the responses of other species can be systematized, remains unclear.

The lively debate that focused on the mechanistic drivers of masting has begun to formulate a theoretical background that may allow us to resolve the puzzling relationship between weather and masting (Kelly et al. 2013, Crone and Rapp 2014, Koenig et al. 2016, Pearse et al. 2016, Pesendorfer et al. 2016, Bogdziewicz et al. 2017b, a). Specifically, masting species can be broadly divided into two groups: flowering masting species and fruit-maturation masting species (Pearse et al. 2016). Even though the division is continuous rather than dichotomous, it may be a useful concept helping us to better understand the impact of weather on plant reproduction. The annual variation in seed production in flowering masting species is largely driven by variable flowering effort (Rapp et al. 2013, Monks et al. 2016, Pearse et al. 2016, Bogdziewicz et al. 2017b). In contrast, the annual variation in flowering effort is less relevant in fruit-maturation masting species, where variation in fruit production is driven by the variable ripening of a more constant flower crop (Espelta et al. 2008, Pérez-Ramos et al. 2010, Pearse et al. 2016, Bogdziewicz et al. 2017b). The theory predicts that the level of synchrony will then depend on the nature of the weather cue and the biological sensitivity of the plant to that signal (Pearse et al. 2016). Here, we further propose that the timing of the cue (i.e. whether it happens before or after flower production) is also relevant.

In flowering masting species, selection favored sensitivity to weather signals that trigger flower initiation (Richardson et al. 2005, Smaill et al. 2011, Tanentzap et al. 2012, Kelly et al. 2013). Therefore, in these species, plants are hypersensitive to weather before flowering, and once flowers are initiated, weather is less likely to affect their reproduction (relatively to fruiting masting species). In contrast, fruit-maturation masting species are hypersensitive to weather after flowering, i.e. weather events have strongest influence on fruit production by modulating the success of fruit maturation (Espelta et al. 2008, Koenig et al. 2015, Pearse et al. 2016, Bogdziewicz et al. 2017a). Consequently, a large range of weather events can modulate the flower-to-fruit transition, making the responsiveness of the plant to particular weather event more variable. Thus, we hypothesize that in flowering masting species, the effect of weather signal on seeding should be more consistent than in fruit-maturation masting species. In the latter, the link between fruiting and weather should be strongly modulated by local conditions, because these will define the most severe factor limiting the maturation of flowers to fruits (Bogdziewicz et al. 2017a, 2018). For example, drought is the most limiting factor for *Quercus spp.* individuals in dry and dense Mediterranean forests (i.e. coppices), and seed production is strongly correlated with rainfall (Espelta et al. 2008, Pérez-Ramos et al. 2010, Fernández-Martínez et al. 2012, Bogdziewicz et al. 2017a). In contrast, water is less limiting for *Q. petraea* in temperate forests, and seed production is thus correlated with spring temperature that determines flowering synchrony and associated pollination efficiency (the phenology synchrony hypothesis; Koenig et al. 2015). Nonetheless, both constraints likely operate in both species, just with different strength (Bogdziewicz et al. 2017a). Thus, similar differences may occur within species and among sites. For example, the strength of the positive correlation between spring temperature and seed production in case of temperate oaks, could be stronger at colder sites, because these sites may have a generally lower average synchrony of flowering (due to frequent cold springs) (Pessi and Pulkkinen 1994, Zhang et al. 2014). Therefore, the positive effect of increased flowering synchrony and associated pollination efficiency should be more important for seed production. If local climate strongly determines the weather influence on reproduction in fruit-maturation masting species, it would explain the apparent inconsistency of results of past studies.

To test how the local climate modulated the meteorological cuing of seed production in two species that belong to the two contrasting masting groups described above, we analyzed data for seed production by the sessile oak (*Quercus petraea*) and European beech (*Fagus sylvatica*) at 17 and 19 sites, respectively. *Fagus sylvatica* is a flowering masting species, and *Q. petraea* is a fruit-maturation masting species (Nilsson and Wastljung 1987, Bogdziewicz et al. 2017b, Lebourgeois et al. 2018). In *F. sylvatica*, hot summers a year before seed production increase flower initiation, and seeding consequently correlates positively with the temperatures in the preceding year (Piovesan and Adams 2001, Hacket-Pain et al. 2015, Bogdziewicz et al. 2017b). This relationship is spatially conserved throughout Europe (Vacchiano et al. 2017). In contrast, acorn production in *Q. petraea* often correlates with current spring temperatures (Kasprzyk et al. 2014, Bogdziewicz et al. 2017b, Caignard et al. 2017, Lebourgeois et al. 2018). The mechanism driving masting is likely through phenology synchrony of flowering (Koenig et al. 2015). In warm springs, flowering in trees within a population is synchronized, which produces high pollination efficiency and success of flower-to-fruit maturation (Bogdziewicz et al. 2017b). Conversely, cold springs lead to desynchronized flowering and pollination failure (Koenig et al. 2012, Pesendorfer et al. 2016, Bogdziewicz et al. 2017b). However, while the link between spring temperature and seeding has been often reported, other studies did not confirm this relationship (Crawley and Long 1995, Wesołowski et al. 2015, Fernández-Martínez et al. 2017a). We hypothesize that such inconsistency is caused by variation in local climate. By considering the contrasting masting strategies of these species, we predict that the response of *F. sylvatica* to weather will be similar across climatic gradients. Specifically, warmer summers in the year preceding seed dispersal in *F. sylvatica* will be consistently positively correlated with seed production everywhere. In contrast, the strength of the correlation between spring temperature and seed production in *Q. petraea* will vary with local climate among the sampling sites. The strength of the positive correlation should be particularly stronger at colder sites.

Materials and Methods

We obtained data for seed production for *Q. petraea* and *F. sylvatica* from the ICP Forests database (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forest, operated under the United Nations Economic Commission for Europe (UNECE) Convention on Long-range Transboundary Air Pollution, http://icp-forests.net/). We used data for the carbon content of fruit provided by the same database to calculate fruit production per plot and year expressed as fruit net primary production (units of g C m^{-2} y^{-1}, i.e. average per unit of surface) (Fernández-Martínez et al. 2017a). These data included fruit production at 17 sites for *F. sylvatica* and 19 sites for *Q. petraea*. Seed production was monitored from 2002 to 2008, but the length of the time series differed slightly between the sites (see Figs. S1 and S2 for details). The following analyses were thus based on 95 site-year observations for *F. sylvatica* and 121 site-year observations for *Q. petraea*.

We extracted climatic data for our study sites from the WorldClim database. This database provides climatic data with a high spatial resolution and contains robust mean monthly climatic data derived from lengthy time series (1950–2000). We used the long-term annual temperature and precipitation means for the study sites as indicators of local climate. We extracted meteorological time series for our forests from the interpolated meteorological data of the MARS unit AGRI4CAST/JRC (http://agri4cast.jrc.ec.europa.eu/), with a resolution of 0.25 × 0.25° (latitude × longitude). This database provided monthly mean temperatures and total precipitation. We used the mean summer temperature (July-September) and mean spring temperature (April-June) for the analysis.

Statistical analysis

We calculated population-level masting metrics, including the coefficient of variation (CV), synchrony between sites (Pearson's correlation coefficients) and lag-1 temporal autocorrelation of seed production. The CV, synchrony, and their corresponding 95% confidence intervals (CIs) were calculated by bootstrap resampling with 1000 replications. To further explore the spatial synchrony, we also computed a Mantel correlograms of reproduction in both species.

We tested our predictions in two steps, each repeated for both *F. sylvatica* and *Q. petraea*. First, we tested whether the populations of the two species responded to the meteorological cues suggested by previous studies, i.e. fruit production for *F. sylvatica* would be strongly correlated with summer temperature in the year preceding seed fall. In contrast, fruit production in *Q. petraea* should be correlated (at the global, complete data-set level) with spring temperature. We built a linear mixed model, with log-transformed fruit production as a response, study site as a random intercept and meteorological variables (i.e. summer temperature for *F. sylvatica* and spring temperature for *Q. petraea*) as predictors. Second, we explored whether the links between weather and seeding were conditioned by local climate. We calculated Pearson correlations coefficients between (log-transformed) seed production and meteorological variables separately for each study site. We then used the correlation coefficients as response variables in two linear regression models, each with climatic variables, i.e. either mean annual temperature at the site or mean annual precipitation, included as an explanatory variable. We built separate models because these climatic variables were colinear ($r = 0.56$). In case of *F. sylvatica*, we also run analogous analysis but with summer temperature in year T-1 replaced by summer temperature in year T-2, as this is also frequently reported cue for that species (Piovesan and Adams 2001, Vacchiano et al. 2017, Hacket-Pain et al. 2018). Results of that analysis are given in the Online Appendix.

We used the R lme4 package for the mixed models (Bates et al. 2014). All models were fitted with Gaussian distributions and identity link functions. Model validation by graphical inspection of the residual patterns indicated normality and homoscedasticity. We calculated the R^2 for the linear models and calculated marginal R^2 (i.e. the proportion of variance explained by fixed effects) and conditional R^2 (i.e. the proportion of variance explained by fixed and random effects) for the GLMMs (Nakagawa and Schielzeth 2013, Bartoń 2014).

Results

Both species and all populations had typical masting behavior. Annual seed production was more variable in *F. sylvatica*, with site-level CV ranging from 1.36 to 2.38 (mean = 1.75). *Q. petraea* was less variable (0.80 – 2.37, mean = 1.36). The negative autocorrelation of seed production ranged from -0.77 to -0.22 (mean = -0.40) for *F. sylvatica* and from -0.49 to 0.34 (mean = -0.17) for *Q. petraea*. The among-site synchrony was 0.81 (95% CI: 0.68–0.96) for *F. sylvatica* and 0.18 (95% CI: 0.02–0.37) for *Q. petraea*. Furthermore, Mantel correlograms suggested that *F. sylvatica* seed production was consistently highly synchronized among sites at all studied distances (up to 800 km), which was not the case in *Q. petraea* (Fig. 1). Note, however, that most of the correlations were not significant (Fig. 1).

Figure 1.

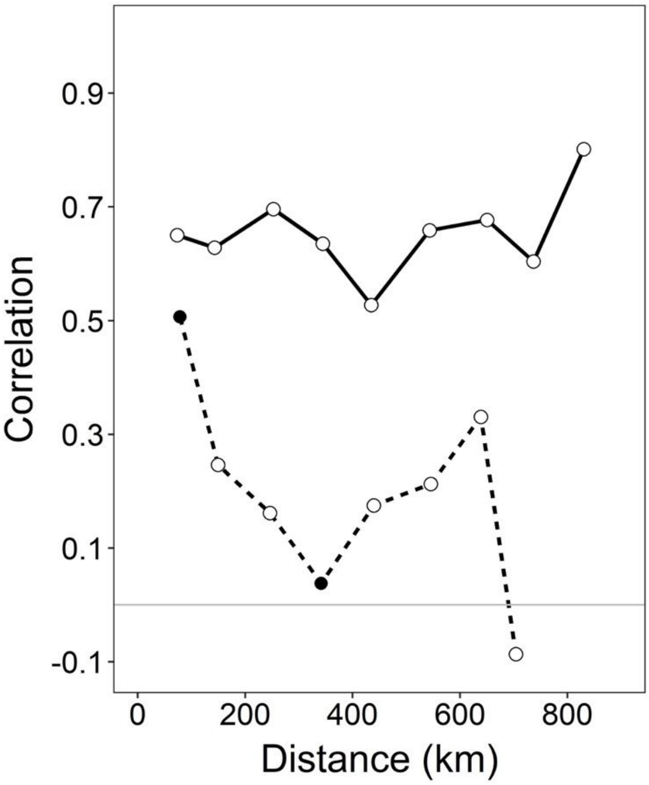

Figure 1. Mantel correlogram of seed production in *F. sylvatica* (solid line) and *Q. petraea* (dashed line). The horizontal grey line indicates 0 correlation, while filled circles indicate significant correlations.

F. sylvatica seed production was strongly correlated with summer temperatures in the year preceding seed fall ($\beta = 0.52$, 95% CI range: 0.29 – 0.72, $t = 5.48$, $p < 0.001$; Fig. 2A), in accordance with our predictions. The marginal R^2 of the model was 0.24, and the conditional R^2 was 0.31. In contrast, seed production by *Q. petraea* was positively but not significantly correlated with spring temperature ($\beta = 0.20$, 95% CI range: -0.04 – 0.45, $t = 1.63$, $p = 0.10$; Fig. 2B). The marginal R^2 of the model was 0.02, and the conditional R^2 was 0.02.

Figure 2.

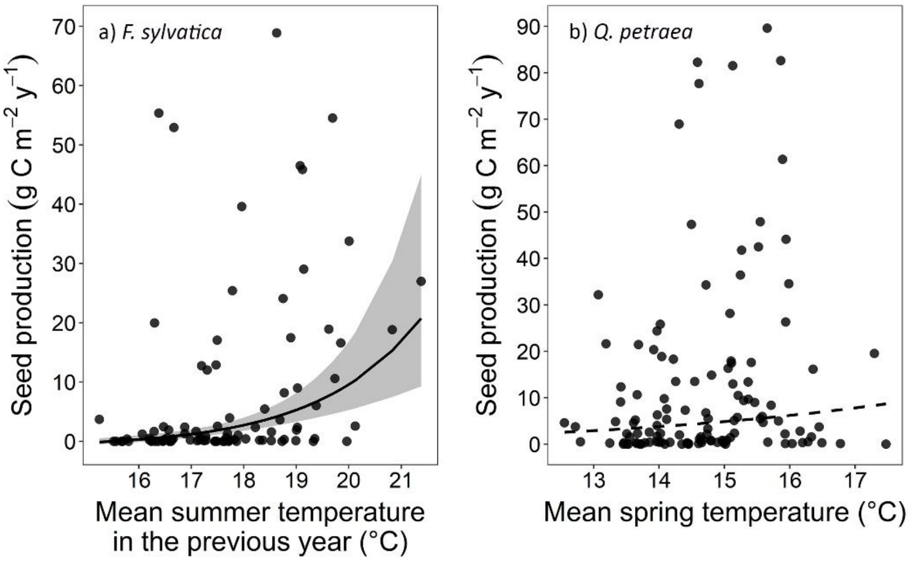

Figure 2. Relationships between a) seed production and previous summer temperature for *F. sylvatica* and b) seed production and current-year spring temperature for *Q. petraea.* The lines represent GLMM predictions, and the shaded regions represent 95% confidence intervals. The dashed line represents a nonsignificant relationship.

The response of the *F. sylvatica* but not the *Q. petraea* populations to weather was clearly consistent after the correlations between seeding and meteorological cues had been decomposed to the site level. All correlations for *F. sylvatica* were positive (range: 0.23–0.92, mean = 0.64; Fig. 3A, B), while the site-level correlation coefficients for Q. *petraea* ranged from -0.24 to 0.84 (mean = 0.24, Fig. 3C, D).

Figure 3.

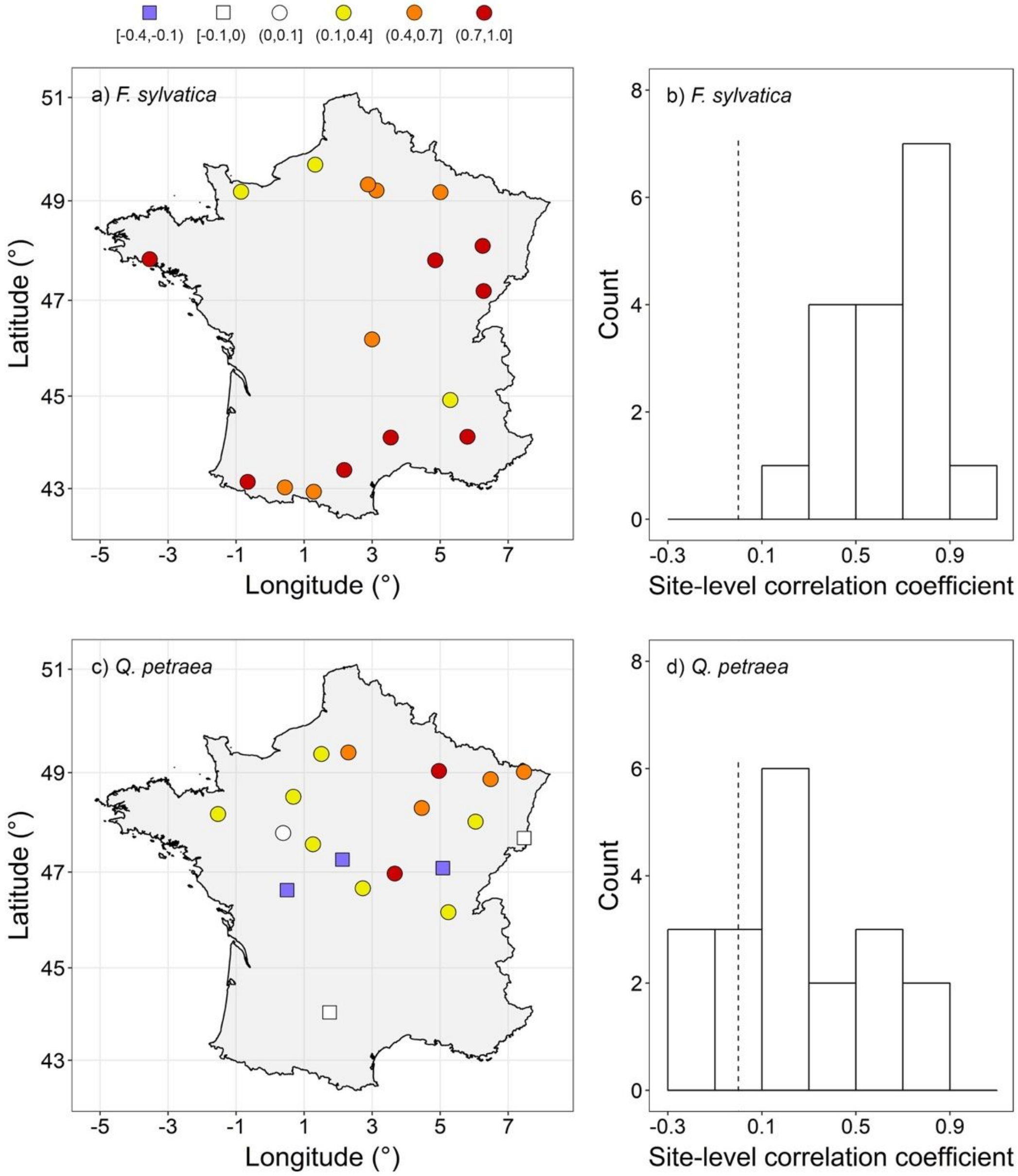

Figure 3. Spatial variation in the response of *F. sylvatica* and *Q. petraea* to meteorological cues. A) and B) site-level Pearson correlation coefficients between log-transformed fruit production and previous summer temperature for *F. sylvatica*. C) and D) site-level Pearson correlation coefficients between log-transformed fruit production and current-year spring temperature for *Q. petraea*. The vertical dashed lines in b) and d) indicate 0 correlation.

The strength of the correlation between summer temperature of the previous year and seed production for *F. sylvatica* did not differ with either the mean annual temperature of the site ($\beta = -0.01$, 95% CI range: -0.07 – 0.05, $t = -0.35$, $p = 0.73$; Fig. 4A) or the mean annual precipitation ($\beta = 0.0004$, 95% CI range: -0.0002 – 0.001, $t = 1.29$, $p = 0.22$; Fig. 4B). In contrast, the correlation between spring temperature and seed production for *Q. petraea* was weaker at sites with higher mean annual temperatures ($\beta = -0.21$, 95% CI range: -0.40 – -0.04, $t = -2.62$, $p = 0.018$; $R^2 = 0.29$; Fig. 4C) with no effects of mean annual precipitation ($\beta = -0.0002$, 95% CI range: -0.002 – 0.002, $t = -0.18$, $p = 0.86$; Fig. 4D).

Figure 4.

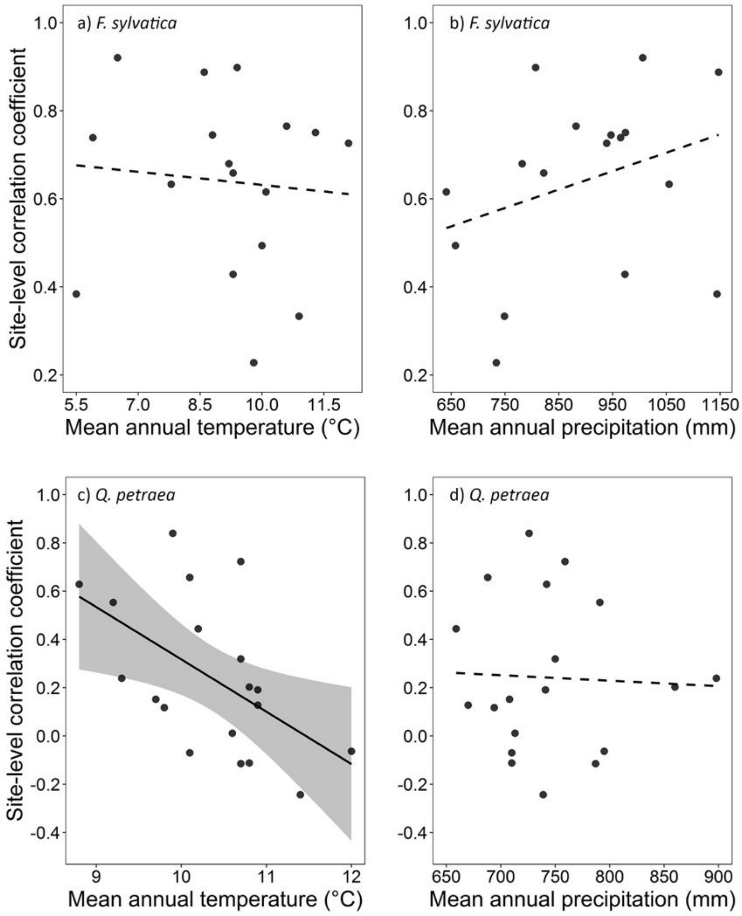

Figure 4. Relationships between the site-level Pearson correlation coefficients and mean annual temperature (A and C) and mean annual precipitation (B and C). The lines represent linear model predictions, and the shaded regions represent 95% confidence intervals. The dashed lines represent nonsignificant relationships.

Discussion

The relationship between weather and fruit production for *F. sylvatica* was consistently positive at all 19 sites studied (Figure 3A). In contrast, the relationship between spring temperature and seed production for *Q. petraea* was not significant at the whole database level. Yet, decomposition of this relationship to the site-level, hinted that it was because the relationship largely varied among sites (Figure 3C) and was stronger in populations at colder locations. While certainly further studies are warranted, our results are consistent with the prediction that the climatic modulation of the responses of flowering masting and fruit-maturation masting species to weather should be different. The flowering masting *F. sylvatica* is hypersensitive to weather cue that triggers flowering (Bogdziewicz et al. 2017b), possibly through increased expression of genes involved in floral transition (Miyazaki et al. 2014, Pearse et al. 2016). Thus, the general positive effect of temperature on flower initiation should be less susceptible to varying local climate, and therefore more uniform across sites. In contrast, the key meteorological variable in fruit-maturation masting species favors (or prevents) the transition from flower to fruit. The environmental constraint that modulates this success is likely to vary with local conditions, as we observed in *Q. petraea*.

The response of *Q. petraea* to spring temperature was stronger at colder sites. Low temperatures during flowering are associated in oaks with desynchronized flowering, because meteorological variability in microhabitats is high in cold springs, which leads to a variable onset of flowering (Koenig et al. 2015, Pesendorfer et al. 2016, Bogdziewicz et al. 2017b). The phenological mismatch among individuals within a population leads to relatively lower pollen availability for each tree and therefore lower pollination success and seed production (Koenig et al. 2012, Bogdziewicz et al. 2017b). Warm springs enhance the synchronization of flowering, allowing high pollination success and lead to high fruit production. We thus believe that this variable background synchronization of flowering (Koenig et al. 2015, Pesendorfer et al. 2016, Bogdziewicz et al. 2017b) is the mechanism responsible for the systematic among-site variation of oaks response to spring weather. The average flowering synchrony is likely lower at cold sites (Pessi and Pulkkinen 1994, Zhang et al. 2014), so pollination success would be a strong constraint on seed production. Consequently, the effect of increased spring temperature on fruits production was clear at these sites. In contrast, pollination success probably affects seed production less at warmer sites, because the synchrony of flowering is generally higher, so the correlations would be weaker. As an indirect support, pollen seasons in *Pinus sylvestris* are longer at northern sites (Pessi and Pulkkinen 1994), and were also found to be shorter at warmer sites in *Betlua sp.* (Zhang et al. 2014). Nonetheless, the opposite can also be true (e.g. Qiu et al. 2018). Thus, direct tests of that hypothesis are necessary, and can include evaluating the effects of spring temperatures and phenological synchrony on oak seeding across elevations.

Spring temperature may also condition acorn production in oaks by different mechanisms, e.g. by modulating the acorn development process (Sork et al. 1993, Koenig and Knops 2014). Spring temperature had a negative influence on seed production in 4 of the 19 populations. Trees may respond to meteorological variables in a symmetric, Gaussian-like fashion, with an optimal response (Fernández-Martínez et al. 2017b). The direction of the response (positive/negative) could then depend on the range of the meteorological variable at different sites. If the meteorological cue has a mode below the optimum in one region, then the correlation between the meteorological variable and the response at that site will be positive (Lusk et al. 2007, Fernández-Martínez et al. 2017b). Likewise, if the mode of the meteorological cue is above the optimum at a site, then the correlation between the meteorological variable and the response in that region will be negative. Our sites at which we observed the negative correlations may operate above the environmental optimum for *Q. petraea*, e.g. excessively hot springs will lead to flower abortion. *F. sylvatica* probably has a similar optimum, but it may not be as strongly modulated by local climate as for *Q. petraea* due to differences in the life-history traits discussed here. Experimental investigations of the influence of weather on flower and seed development in masting plants are rare (Kon and Noda 2007, Kelly et al. 2008, Pérez-Ramos et al. 2010), but will provide necessary insight into the mechanistic links between weather and seeding variation.

The spatial consistency in the response of *F. sylvatica* to weather explains why *F. sylvatica* populations were on average 4-times better synchronized than *Q. petraea* (0.81 vs 0.18, respectively; for similar result see Nussbaumer et al. 2016). The response of *F. sylvatica* to meteorological cues was spatially uniform, so all populations within a region fluctuated similarly in response to correlated meteorological conditions (see also Fig. 1). The synchrony of reproduction may then be easily scaled up to a continental scale, as shown in Vacchiano et al. (2017). Conversely, each population of *Q. petraea* probably responded more in accordance with its local optimum, which consequently lowered the large-scale spatial synchronization. Spatial synchrony of masting has been intensively studied (e.g. Koenig and Knops 1998, Kelly and Sork 2002, Fernández-Martínez et al. 2017, Vacchiano et al et al. 2017) but why species differ in how well they are synchronized is unclear. We propose that synchrony will differ between flowering and fruit-maturation masting species, with the former having a higher average large-scale synchrony due to spatially conserved meteorological cuing, i.e. a regional pattern more consistent with the Moran effect.

Conclusions

The clear difference in meteorological conditioning of seed production between the two species suggests that the responses of masting plants to weather can be systematized and predicted. Meteorological cues in species where annual flowering intensity is the main determinant of seed production should include variables associated with resource acquisition and flower initiation, and be generally similar across species ranges (Richardson et al. 2005, Monks et al. 2016, Vacchiano et al. 2017). Meteorological cues in fruit-maturation masting species, though, could be predicted by considering the likely key environmental constraint (so called 'veto' cf. Pearse et al. 2016, Bogdziewicz et al. 2018) to fruit maturation for the particular species and region studies. We note, however, that the differentiation between flowering and fruit-maturation masting species is not distinct but a continuum of species with more or fewer mixed strategies (Montesinos et al. 2012, Abe et al. 2016, Pearse et al. 2016). Accurate predictions will therefore need detailed information of species biology. Our research nonetheless provides new insights into the resolution of apparently inconsistent responses of plant reproduction to meteorological variation. Finally, climate appears to condition the species responses to weather stronger in fruit-maturation masting species. It indicates that these species may be more sensitive to global climate change then flowering masting species.

Acknowledgements

We thank Anonymous Reviewers for their helpful comments on the previous versions of this manuscript. MB was supported by the Polish National Science Centre grant Sonatina No. 2017/24/C/NZ8/00151. JSz was supported by the Foundation for Polish Science (FNP) scholarship "Start". MFM is a postdoctoral fellow of the Research Foundation – Flanders (FWO), and JP was supported by the European Research Council Synergy grant ERC-SyG-2013-610028 IMBALANCE-P.

Competing interest statement

Authors declare no competing interests.

Literature

Abe, T. et al. 2016. Parameterisation and validation of a resource budget model for masting using spatiotemporal flowering data of individual trees. - Ecology Letters 19: 1129–1139.

Allen, R. B. et al. 2012. Synchronicity, periodicity and bimodality in inter-annual tree seed production along an elevation gradient. - Oikos 121: 367–376.

Ascoli, D. et al. 2015. The synchronicity of masting and intermediate severity fire effects favors beech recruitment. - Forest Ecology and Management 353: 126–135.

Ascoli, D. et al. 2017. Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction. - Nature communications 8: 2205.

Bartoń, K. 2014. MuMIn: multi-model inference. R package version 1.10. 0. - See http://CRAN. R-project. org/package= MuMIn in press.

Bates, D. et al. 2014. lme4: Linear mixed-effects models using Eigen and S4. - R package version 1: 1–23.

Bogdziewicz, M. et al. 2016. How do vertebrates respond to mast seeding? - Oikos 125: 300–307.

Bogdziewicz, M. et al. 2017a. The Moran effect and environmental vetoes: phenological synchrony and drought drive seed production in a Mediterranean oak. - Proc. R. Soc. B 284: 20171784.

Bogdziewicz, M. et al. 2017b. Masting in wind-pollinated trees: system-specific roles of weather and pollination dynamics in driving seed production. - Ecology 98: 2615–2625.

Bogdziewicz M et al. 2018. Correlated seed failure as an environmental veto to synchronize reproduction of masting plants. - New Phytologist 219: 98-108.

Caignard, T. et al. 2017. Increasing spring temperatures favor oak seed production in temperate areas. - Scientific Reports 7: 8555.

Crawley, M. and Long, C. R. 1995. Alternate bearing, predator satiation and seedling recruitment in Quercus robur L. - Journal of Ecology: 683–696.

Crone, E. E. and Rapp, J. M. 2014. Resource depletion, pollen coupling, and the ecology of mast seeding. - Annals of the New York Academy of Sciences 1322: 21–34.

Espelta, J. M. et al. 2008. Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. - Ecology 89: 805–817.

Fernández-Martínez, M. et al. 2012. Masting in oaks: disentangling the effect of flowering phenology, airborne pollen load and drought. - Acta Oecologica 43: 51–59.

Fernández-Martínez, M. et al. 2017a. The North Atlantic Oscillation synchronises fruit production in western European forests. - Ecography 40: 864–874.

Fernández-Martínez, M. et al. 2017b. Nature beyond linearity: meteorological variability and Jensen’s inequality can explain mast seeding behaviour. - Frontiers in Ecology and Evolution 5: 134.

Hacket-Pain, A. J. et al. 2015. The influence of masting phenomenon on growth–climate relationships in trees: explaining the influence of previous summers’ climate on ring width. - Tree Physiology 35: 319–330.

Hacket-Pain, A. J. et al. 2018. Climatically controlled reproduction drives interannual growth variability in a temperate tree species. - Ecology Letters 21: 1833-1844.

Jones, C. G. et al. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. - Science 279: 1023–1026.

Kasprzyk, I. et al. 2014. Relationships among weather parameters, airborne pollen and seed crops of Fagus and Quercus in Poland. - Agricultural and forest meteorology 197: 111–122.

Kelly, D. and Sork, V. L. 2002. Mast seeding in perennial plants: why, how, where? - Annual Review of Ecology and Systematics 33: 427–447.

Kelly, D. et al. 2008. Mast seeding, predator satiation, and temperature cues in Chionochloa (Poaceae). - Population Ecology 50: 343–355.

Kelly, D. et al. 2013. Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. - Ecology Letters 16: 90–98.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. - Trends in Ecology & Evolution 14: 22–26.

Koenig, W. D. and Knops, J. M. 1998. Scale of mast-seeding and tree-ring growth. - Nature 396: 225.

Koenig, W. D. and Knops, J. M. 2014. Environmental correlates of acorn production by four species of Minnesota oaks. - Population Ecology 56: 63–71.

Koenig, W. D. et al. 2003. Dissecting components of population-level variation in seed production and the evolution of masting behavior. - Oikos 102: 581–591.

Koenig, W. D. et al. 2012. Stabilizing selection for within-season flowering phenology confirms pollen limitation in a wind-pollinated tree. - Journal of Ecology 100: 758–763.

Koenig, W. D. et al. 2015. What drives masting? The phenological synchrony hypothesis. - Ecology 96: 184–192.

Koenig, W. D. et al. 2016. Is the relationship between mast-seeding and weather in oaks related to their life-history or phylogeny? - Ecology 97: 2603–2615.

Koenig, W. D. et al. 2017. Drivers of synchrony of acorn production in the valley oak (*Quercus lobata*) at two spatial scales. - Ecology 98: 3056–3062.

Kon, H. and Noda, T. 2007. Experimental investigation on weather cues for mast seeding of Fagus crenata. - Ecological Research 22: 802–806.

Lebourgeois, F. et al. 2018. Assessing the roles of temperature, carbon inputs and airborne pollen as drivers of fructification in European temperate deciduous forests. - European Journal of Forest Research 137: 349–365.

Lusk, J. J. et al. 2007. Correlates of interspecific synchrony and interannual variation in seed production by deciduous trees. - Forest Ecology and Management 242: 656–670.

Monks, A. et al. 2016. Resource limitation underlying multiple masting models makes mast seeding sensitive to future climate change. - New Phytologist 210: 419–430.

Montesinos, D. et al. 2012. Masting uncoupling: mast seeding does not follow all mast flowering episodes in a dioecious juniper tree. - Oikos 121: 1725–1736.

Miyazaki, Y. et al. 2014. Nitrogen as a key regulator of flowering in Fagus crenata: understanding the physiological mechanism of masting by gene expression analysis. - Ecology Letters, 17: 1299-1309.

Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. - Methods in Ecology and Evolution 4: 133–142.

Nilsson, S. G. and Wastljung, U. 1987. Seed predation and cross-pollination in mast-seeding beech (Fagus sylvatica) patches. - Ecology 68: 260–265.

Nussbaumer, A. et al. 2016. Patterns of mast fruiting of common beech, sessile and common oak, Norway spruce and Scots pine in Central and Northern Europe. - Forest Ecology and Management 363: 237–251.

Pearse, I. S. et al. 2016. Mechanisms of mast seeding: resources, weather, cues, and selection. - New Phytologist 212: 546–562.

Pérez-Ramos, I. M. et al. 2010. Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. - Ecology 91: 3057–3068.

Pérez-Ramos, I. M. et al. 2015. Environmental drivers of mast-seeding in Mediterranean oak species: does leaf habit matter? - Journal of Ecology 103: 691–700.

Pesendorfer, M. B. et al. 2016. Individual resource limitation combined with population-wide pollen availability drives masting in the valley oak (*Quercus lobata*). - Journal of Ecology 104: 637–645.

Pessi, A.-M. and Pulkkinen, P. 1994. Temporal and spatial variation of airborne Scots pine (*Pinus sylvestris*) pollen. - Grana 33: 151–157.

Piovesan, G. and Adams, J. M. 2001. Masting behaviour in beech: linking reproduction and climatic variation. - Canadian Journal of Botany 79: 1039–1047.

Qiu, S. et al. 2018. Latitudinal pattern of flowering synchrony in an invasive wind-pollinated plant. - Proceedings of the Royal Society B: Biological Sciences, 285: 20181072.

Rapp, J. M. et al. 2013. Sex allocation, pollen limitation and masting in whitebark pine. - Journal of Ecology 101: 1345–1352.

Rees, M. et al. 2002. Snow tussocks, chaos, and the evolution of mast seeding. - The American Naturalist 160: 44–59.

Richardson, S. J. et al. 2005. Climate and net carbon availability determine temporal patterns of seed production by Nothofagus. - Ecology 86: 972–981.

Schauber, E. M. et al. 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. - Ecology 83: 1214–1225.

Smaill, S. J. et al. 2011. Climate cues and resources interact to determine seed production by a masting species. - Journal of Ecology 99: 870–877.

Sork, V. L. et al. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. - Ecology 74: 528–541.

Tanentzap, A. J. et al. 2012. Soil nutrient supply modulates temperature-induction cues in mast-seeding grasses. - Ecology 93: 462–469.

Vacchiano, G. et al. 2017. Spatial patterns and broad-scale weather cues of beech mast seeding in Europe. - New Phytologist 215: 595–608.

Vacchiano, G. et al. 2018. Reproducing reproduction: How to simulate mast seeding in forest models. - Ecological Modelling 376: 40–53.

Wesołowski, T. et al. 2015. Interannual variation in tree seed production in a primeval temperate forest: does masting prevail? - European Journal of Forest Research 134: 99–112.

Zhang, Y. et al. 2014. Climate change effect on Betula (birch) and Quercus (oak) pollen seasons in the United States. - International Journal of Biometeorology 58: 909–919.

Online Appendix. Bogdziewicz et al. The effects of local climate on the correlation between weather and seed production differ in two species with contrasting masting habit.

Figure 1S. Fruit production time series for *F. sylvatica*. Each plot represents a site.

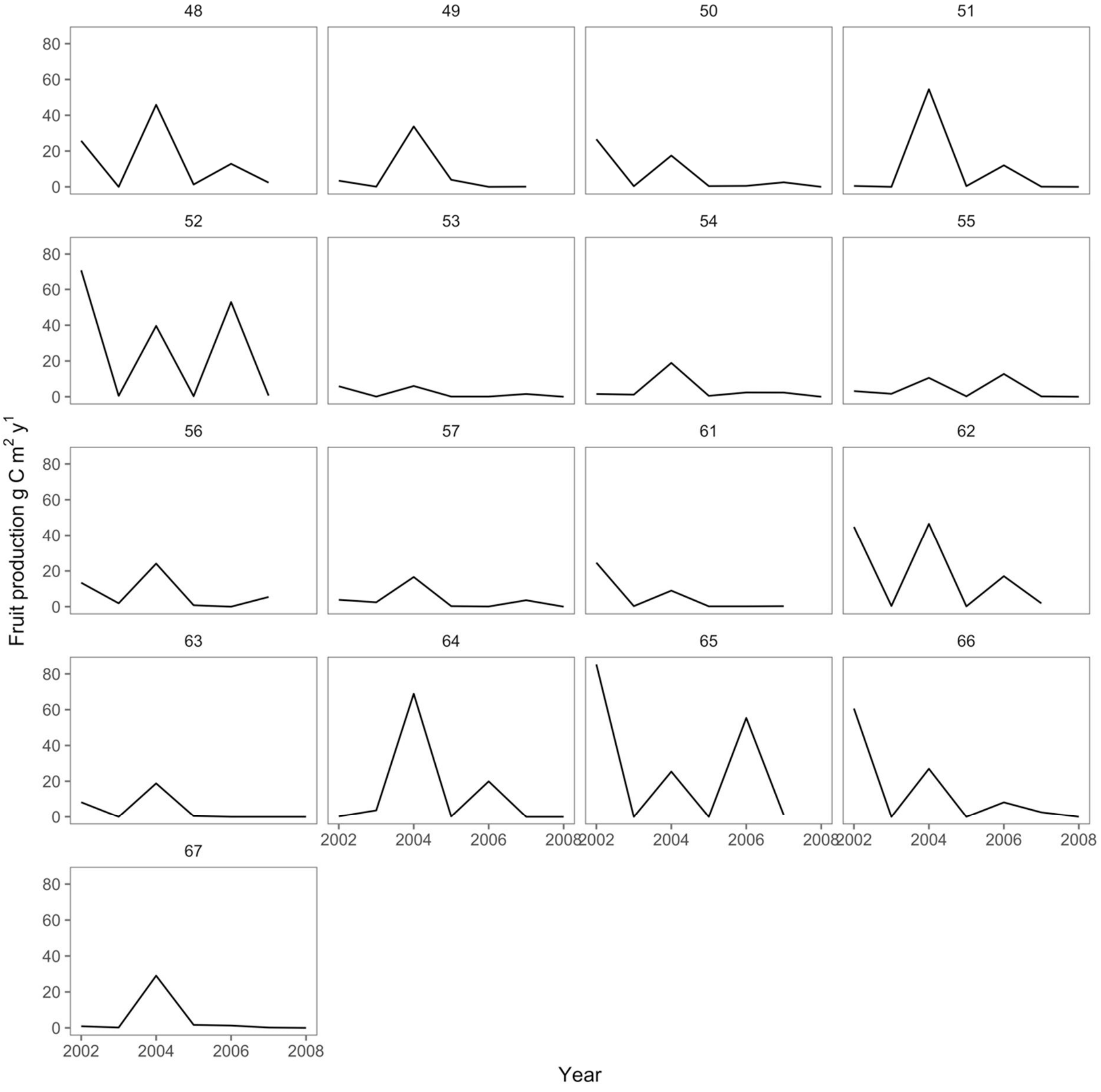

Figure 2S. Fruit production time series for *Q. petraea*. Each plot represents a site.

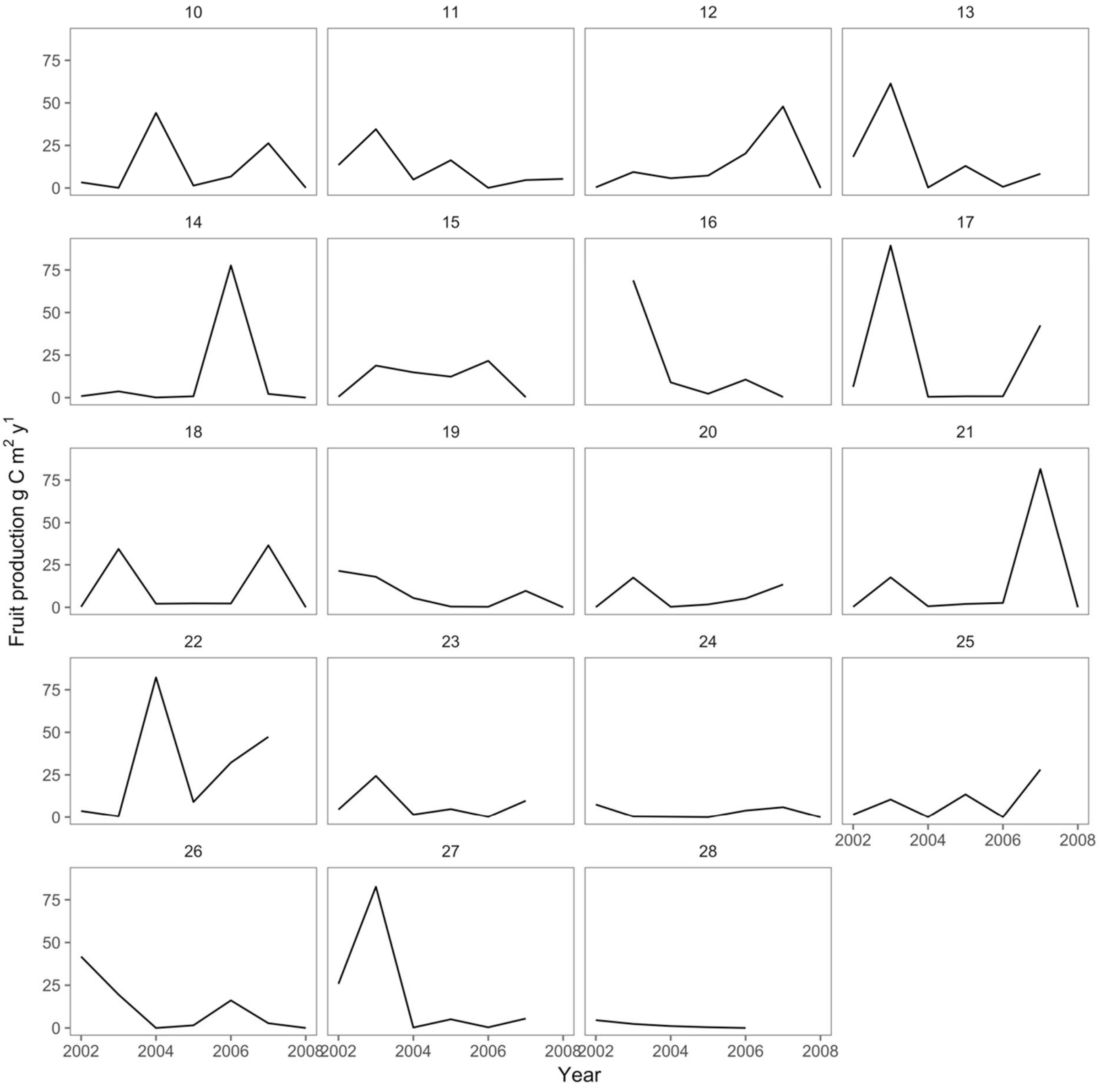

Figure S3. A) The relationship between seed production and mean summer temperature two years before seed dispersal ($\beta = -0.62$, 95% CI range: -0.82 – -0.42, $t = -6.13$, $p < 0.001$). B) Site-level Pearson correlation coefficients between log-transformed fruit production and summer temperature two years before seed dispersal. Both figures for *F. sylvatica.*