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ORIGINAL PAPER

Pollen source affects acorn production in pedunculate oak (*Quercus robur* L.)

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Abstract Acorn production in oaks (*Quercus* spp.) shows considerable inter-annual variation, known as masting. The effects of pollen sourced from trees within or outside the stand on acorn production were investigated in pedunculate oak (*Quercus robur* L.) in an ancient mixed woodland during two moderate masting years. Comparisons were made between natural pollination, hand pollinations with out-of-stand pollen, in-stand pollen or a 1:1 combination of the two pollen sources, and for bagged flowers left unpollinated. After all treatments, > 85% of the flowers or developing acorns were aborted between May and August of both years. When flowers were protected with pollen bags and no pollen added, no acorns were produced. In contrast, hand pollination with out-of-stand pollen produced the most acorns both years and significantly more than within-stand pollen or natural pollination in 2022. Hand pollination with out-of-stand or within-stand pollen provided significantly more acorns than natural pollination in 2023. In 2022, hand pollination with a 1:1 mixture of out-of-stand and within-stand pollen yielded an intermediate number of mature acorns between those for the out-of-stand and within-stand pollination treatments. The study provides clear evidence of maternal choice during acorn development in pedunculate oak and of the benefits of pollen supplementation. It also confirms that pedunculate oak is a fruit-maturation masting species; abortion of pollinated flowers and immature acorns determines a mast year (rather than the number of flowers produced) at this site.

Keywords *Quercus robur* L. · Acorns · Masting · Pedunculate oak · Pollination

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Introduction

Masting is a plant reproductive strategy characterised by large inter-annual variation in seed or flower output that is geographically synchronous (Koenig and Knops 2005). It may have evolved in anemophilous (wind-pollinated) plants as a strategy to increase pollination efficiency (Smith et al. 1990; Kelly et al. 2001). Most wind-pollinated trees, including *Quercus* species, are self-incompatible (Loveless and Hamrick 1984; Yacine and Bouras 1997; Boavida et al. 2001). Synchronous flowering and long-distance pollen flow are important to prevent compatible pollen from becoming locally limiting (Ashley 2021).

Oaks (*Quercus* spp.) are common and widespread forest trees across the northern hemisphere and considered an evolutionary success (Kremer and Hipp 2020). The two oak species *Quercus robur* L. (pedunculate oak) and *Quercus petraea* (Matt.) Liebl. (sessile oak) that are native to the United Kingdom are important umbrella species for biodiversity in the region, supporting 2300 species of birds, bryophytes,

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fungi, invertebrates, lichen and mammals (Mitchell et al. 2019). Oak forests also provide many ecosystem services including climate regulation, biomass production, water supply and purification, and flood reduction (Brockerhoff et al. 2013; Thompson et al. 2014).

Approximately 50%–70% of the gene flow in oak species comes from pollen outside the oak stands that have been studied (Dow and Ashley 1998a, b; Streiff et al. 1999; Craft and Ashley 2010; Abraham et al. 2011). The predominance of foreign parentage in oak remains consistent whether for clonal seed orchards (Buiteveld et al. 2001), naturally-regenerated stands (Dow and Ashley 1998a; Streiff et al. 1999), stands with nearby pollen sources (Dow and Ashley 1998b), or those without (Craft and Ashley 2010). Moreover, the stands in all these studies had similar areas (4 – 5 ha), but varied in having from 57 to 296 adult oak trees.

Within a stand, Dow and Ashley (1998b) found proximity to pollen sources to be less influential than traditional models predicted. Often, oak trees failed to pollinate their neighbours and instead pollinated much more distant trees; however, they found no evidence of genetic-based avoidance of within-stand pollen. Indeed, out-of-stand pollen still accounted for > 35% of all successful pollinations even within highly isolated oak stands beyond the central distribution range of the species where out-of-stand pollen had to travel > 80 km and past physical barriers (i.e., the Southern Ural Mountain Range) (Buschbom et al. 2011).

The consistent detection of acorns that were produced by out-of-stand pollen implies that the parent trees were likely to be genetically distinct, providing a distinct advantage. Genetic analysis of developing acorns can only determine the pollen source if there is a successful outcome; the failure of pollination from an incompatible source cannot be determined from the analysis of an acorn. Without studying the initial pollination event, one cannot distinguish between a higher initial foreign pollen load or later selective abortion of acorns from local pollen.

Studies of hand-pollinated flowers of Holm oak (*Quercus ilex* L.) and Japanese Jolcham oak (*Quercus serrata* Thunb. ex Murray) found slow pollen tube growth and delayed, selective abortion in self-pollinated flowers and no seed development (Yacine and Bouras 1997; Tsuruta et al. 2011). When a mixture of self and foreign pollen was used, there was a positive correlation between the number of self-pollen tubes that reached the ovule and the subsequent number of acorns that aborted (Yacine and Bouras 1997).

In many outcrossing species, self-fertilisation is avoided early on because the pollen tubes grow abnormally (Kalinganire 2000). In contrast, oak appears to have evolved a delayed self-incompatibility mechanism (Boavida et al. 2001), which could be an adaptive strategy to limit insect attacks or a mechanism to selectively abort acorns from lower-quality pollen (Tsuruta et al. 2011). The production of surplus flowers and subsequent abortion of many fertilised flowers and very early-developing acorns can enable maternal selection and increase acorn diversity (Craft et al. 2009). In oak, the resource cost of maintaining early-developing acorns is likely to be low in relation to the benefits of later maternal selection.

This study on pollen addition and limitation experiments over two years was designed to determine the effect of pollen source identity on *Q. robur* acorn development and abortion and test two hypotheses: (1) Supplemental out-of-stand pollen will lead to more acorn production; and (2) The number of acorns that develop to maturity will be greater from flowers that are pollinated by out-of-stand pollen.

Materials and methods

The experiments in 2022 and 2023 used the same eight *Q. robur* trees in Wytham Woods, Oxford, UK (latitude 51.76946° N, longitude 1.33849° W), an ancient mixed woodland dominated by broadleaved species (*Acer pseudoplatanus* L., *Betula* spp., *Fagus sylvatica* L., *Fraxinus excelsior* L., and *Quercus robur* L.) (Kirby et al. 2014). All eight trees were mature, with DBH > 50 cm and height > 15 m. Five of the eight were accessed via a canopy walkway, allowing access to the upper canopy. The remaining three trees were chosen due to abundant low branches aiding accessibility. Historical observations of additional trees at this site showed that 2022 and 2023 were moderate for acorn production (respectively, 61% and 42% the level in 2020, a mast year), and no acorns were produced in 2021. The weather in April and May (when pollination occurs at the site; data from the Met Office's Oxford weather station) was slightly warmer and drier in 2022 than in 2023, 12.18 °C and 27.85 mm precipitation *vs* 11.38 °C and 58.55 mm, respectively.

In early February of the two years, a total of 300 branches from among the eight trees were selected at random. Groups of flowers on each branch were isolated by covering with pollen bags (PBS International, Scarborough, UK). The leaves and flowers on each branch were counted in May; the leaves were used to account for differences in branch size and architecture, akin to Pearse et al. (2015). Each branch was randomly assigned to one treatment only, with a similar number of branches assigned to each treatment per tree. In 2022, five treatments were applied to isolated oak inflorescences: within-stand pollen (WSP), out-of-stand pollen (OSP), a 1:1 combination of within-stand and out-of-stand pollen (1:1), natural pollination (NAT), and no pollination (NOP; i.e., bagged flowers). In 2023, only three treatments were applied: WSP, OSP and NAT.

Pollen was collected in late April and early May each year as described by Roussel (2011), when the anthers of

the catkins had a yellow tinge, and the pollen sacs had just begun to release pollen. The out-of-stand pollen was collected from five sites across southern England: Greenham Common, Newbury [51.37702° N, 1.29067° W (the closest site, 43 km from Wytham Woods)], Whiteknights campus, Reading (51.44044° N, 0.94176° W), Corsham Court, Corsham (51.44267° N, 2.16142° W), Bannerdown Common, Bath (51.41703° N, 2.30005° W), and Southampton Common, Southampton [50.92893° N, 1.40879° W (the farthest, 93 km from Wytham Woods)]. The within-stand pollen was collected from 10 trees at Wytham Woods, but not from the eight selected for this study. Catkins were collected by hand, taking care to exclude leaves, twigs, and insects, and immediately spread on metal trays to dry for 3–4 d in a well-ventilated room at > 25 °C; then sieved to separate the pollen. Pollen was combined and mixed within either the out-of-stand or within-stand pollen sets to provide the two pollen samples and then stored at –18 °C for a short period until applied to the trees. Three subsamples of pollen from each pollen sample were used to assess viability after storage: the pollen was added to agar plates (sucrose 20%, agar 1%, boric acid 0.01% w/v in water, pH 5.5) and incubated at 30 °C. After 48 h, the Petri dishes were observed with a microscope (100 times magnification) and the proportion of germinated (pollen tube length > half the pollen grain diameter) *vs* ungerminated pollen grains in three fields of view per dish were counted.

Female flowers were deemed receptive when the stigmas became pink-red and were deployed horizontally. Each flower received two applications of pollen from a hand-pollination pump (Yardwe, China). To prevent cross contamination of pollen, a different hand-pollination pump was used for each pollen source and flowers were pollinated within the pollen bags. The 1:1 treatment was applied using a separate application from each pump (that is, one from the pump with out-of-stand pollen and one with the in-stand). The flowers remained bagged until they were no longer receptive. For the NAT treatment, bags were removed in late April to enable natural pollination. For the NOP treatment, the bags were removed on 12 May 2022, when the stigmas were no longer receptive to pollination. Acorn development on the selected branches was monitored throughout the rest of the season. Flowers and acorns were counted six times in 2022 (1, 12, and 30 May, 29 June, 3 August, 15 September) and twice in 2023 (9 May, 10 August).

All statistical analyses were performed in R version 4.1.1 (R Core Team 2021). The results were analysed separately each year using a generalised linear mixed effect model with a binomial distribution. The function glmer in the R package lme4 (Bates et al. 2024) was used to assess the effect of the pollen treatment, using flower or acorn counts as the binary response variable, treatment as a fixed effect and leaf number, branch and tree as random effects. Models were built separately for each collection date, and model assumptions were checked via diagnostic functions in the R package DHARMa (Hartig 2018). Chi-squared tests in the R package car (Fox and Wiesberg 2019) were used to identify significant differences in flower or acorn development among pollen source treatments. Where significant differences were detected, means were subjected to post hoc Tukey pairwise comparisons using the emmeans model function in the R package emmeans (Lenth 2018). The function aov in the R package stats and the base function summary (R Core Team 2021) were used to test for differences in pollen viability between the pollen treatments and the initial flower number per branch between treatments and years.

Results

The control branches, with pollen bags kept on and no pollen added (NOP), aborted their flowers (May to July counts) and produced no acorns (August and September) in 2022 (Fig. 1). Thus, the pollen bags proved to be effective in isolating flowers from environmental pollen. The number of flowers declined markedly over time in all treatments, with < 15% of total flowers developing acorns by August in either year. Differences in the initial number of flowers per 100 leaves among treatments were apparent (Fig. 2), with more in the naturally pollinated (NAT) treatment than in the within-stand pollen (WSP) treatment and more in WSP than in the out-of-stand pollen (OSP) treatment. These differences were not significant in 2022 ($F = 2.85$, df = 2, $P = 0.06$), but were so in 2023 ($F = 15.55$, df = 1, $P < 0.0001$). Acorn production on the branches in the natural pollination treatment (NAT) varied between years (Fig. 3); more flowers were produced in 2022 than 2023, with 1.84 ± 0.69 acorns per 100 leaves in 2022 and 0.89 ± 0.27 in 2023.

Pollen viability of the two pollen sources was similar (pollen grains with visible pollen tubes: OSP = (45 ± 27)%, WSP = (52 ± 4)%; $F = 1.774$, df = 1, $P = 0.2$). The effect of treatment on flower or acorn numbers was significant for every count date after the initial flower counts (Table 1). The OSP treatment yielded the most acorns per 100 leaves by the end of the season in both years (2022: 5.4 ± 1.39, 2023: 2.06 ± 0.37; Fig. 3); the difference between the numbers of acorns after the OSP and WSP treatments was significant in 2022, but not in 2023. The 1:1 mixture of out-of-stand and within-stand pollen provided the second highest number of acorns in 2022, intermediate between OSP and WSP (Fig. 3), but did not differ significantly from the number with WSP, which yielded the fewest acorns (0.89 ± 0.36 acorns per 100 leaves) or with natural pollination (NAT); nor did the number after the 1:1 treatment differ significantly from the yield with out-of-stand pollen despite the considerable difference. Within-stand pollen performed relatively better

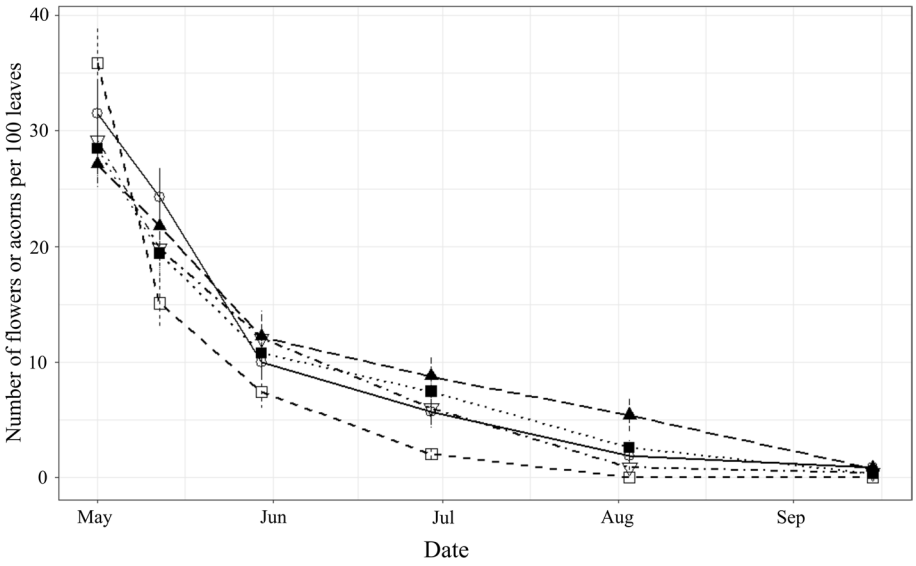

Fig. 1 Numbers of flowers or acorns per 100 leaves for a supplemental pollination experiment on branches of eight oak trees at Wytham Woods, Oxford, UK in 2022. Acorns matured by early August; earlier counts were considered flowers, whether fertilised or not, in various stages of development. The treatments in 2022 were: within-stand pollen (dot-dash line, ▽ [WSP]), out-of-stand pollen (long dash line, ▲ [OSP]), 1:1 mix of within-stand and out-of-stand pollen (dotted line, ■ [1:1]), natural pollination (solid line, ○ [NAT]), and no pollination (short dash line, □ [NOP]). Vertical lines on data points are standard errors for each treatment

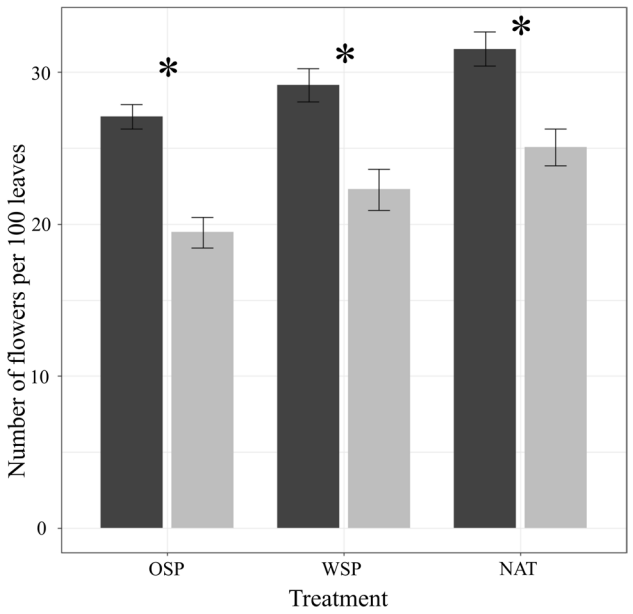

Fig. 2 Mean number of flowers in 2022 (dark grey) and 2023 (light grey) for each pollination treatment (out-of-stand pollen [OSP], within-stand pollen [WSP] and natural pollination [NAT]) for eight trees at the start of a supplemental pollination experiment at Wytham Woods, Oxford, UK on 1 May 2022 and 9 May 2023. The vertical lines are the standard error. Asterisks indicate significant differences between years ($P < 0.01$) based on post hoc Tukey pairwise comparisons

in 2023, yielding 1.59 ± 0.3 acorns for every 100 leaves, significantly more than with NAT (Fig. 3).

Discussion

This study provides experimental evidence for the selective abortion of flowers, whether fertilised or not, based on pollen source in *Q. robur* at Wytham Woods, Oxford, in 2022, but not significantly so in 2023 when natural acorn production was half of that in 2022. Hence, the source of pollen may be as important as its abundance (or limitation) to successful seed production in *Q. robur* and perhaps other masting species. Evidence of the effect of pollen limitation is also clear, with acorn set in both years increased by pollen supplementation. These findings have several consequences for the understanding of the mechanisms driving masting.

Pollen source and abortion

Many more acorns were produced from pollen outside the stand (OSP) than from within the stand (WSP) in 2022 (Fig. 3) despite a large initial number of flowers in both treatments (Fig. 1). These results suggest selective abortion of flowers that were pollinated with suboptimal pollen. Such a response is in accord with studies that report high out-of-stand pollen flow (Dow and Ashley 1998a, b; Streiff et al. 1999; Abraham et al. 2011). Maternal choice in oak has an evolutionary advantage because it removes

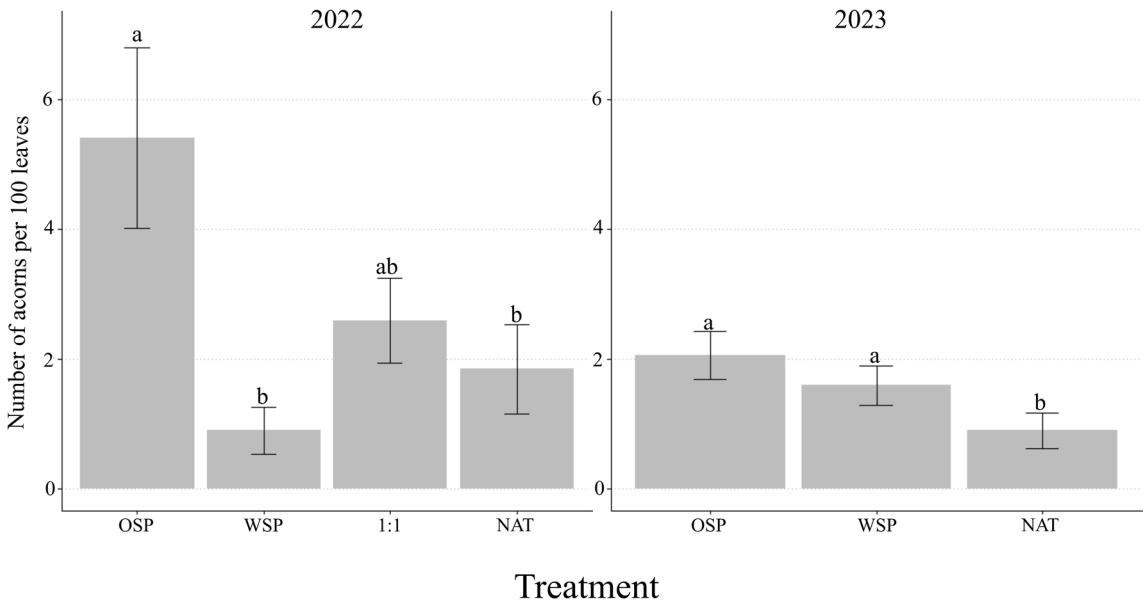

Fig. 3 Mean number of acorns per 100 leaves at peak acorn maturation (3 August 2022 or 10 August 2023) in supplemental pollination experiments on branches of eight trees at Wytham Woods, Oxford, UK in 2022 and 2023. Treatments: out-of-stand pollen (OSP), within-stand pollen (WSP), mix of half within-stand and half out-of-stand pollen (1:1), and natural pollination (NAT). The NOP treatment in 2022 resulted in no acorns (Fig. 1) and is not shown here. Only treatments OSP, WSP and NAT were applied in 2023. Vertical lines are standard errors; for ANOVA results, see Table 1. Within each year, different letters above means indicate significant differences ($P < 0.05$) in post hoc pairwise comparisons for generalised linear mixed effects model with fixed explanatory factor pollen treatment and random effects leaf number, branch and tree

Table 1 Results of Wald chi-squared tests for supplemental pollination experiments using eight oak trees at Wytham Woods, Oxford, UK on different dates in 2022 and 2023 from a series of generalised linear mixed effect models with a binomial distribution

Date		Treatment		
		χ^2	df	*P*
Year 1	12-May-22	238.13	4	< 0.0001
	30-May-22	86.25	4	< 0.0001
	29-Jun-22	135.67	4	< 0.0001
	3-Aug-22	82.22	4	< 0.0001
Year 2	10-Aug-23	24.19	2	< 0.0001

Presence of flowers or acorns is the response variable and pollen treatment is the fixed effect (within-stand pollen, out-of-stand pollen, a 1:1 mix of within-stand and out-of-stand pollen, natural pollination, and no pollination). In 2023, only treatments within-stand, out-of-stand pollen, and natural pollination were applied. The random effects leaf number, branch and tree were included in each of the models

poor-quality embryos before resources are invested in them (Stephenson 1981; Havens and Delph 1996) and expands the genetic diversity within the acorn crop. Several studies show that genetic variation in plant populations is linked to greater fitness (Leimu et al. 2006) and greater adaptability to environmental change (Hamrick 2004). Oaks produce six ovules per flower (Stairs 1964). Differential selection and abortion of ovules, depending on the pollen source, may be a method of exhibiting maternal choice (Craft et al. 2009). The results of this study suggest that maternal choice also occurs at the level of individual flowers because hand-pollinated flowers, presumably with all ovules pollinated, were aborted selectively based on pollen source.

In 2022, the 1:1 pollen treatment was the second most successful in terms of acorns produced and intermediate in value between WSP and OSP, but the number of acorns did not differ significantly from any of the other pollen addition treatments (Fig. 3). Since the 1:1 treatment resulted in acorn numbers about midway between WSP and OSP, the presence of some out-of-stand pollen may be beneficial, a possibility that is also compatible with the selective abortion of flowers pollinated with suboptimal pollen in 2022. Despite the oak flowers receiving an equal amount of pollen from outside and within the stand in the 1:1 treatment, by chance, some would have had all their ovules pollinated by the latter. The signal to abort before acorn development may have been stronger within these flowers, similar to the mechanism underlying abortion when self-pollen loads are greater (Yacine and Bouras 1997), resulting in the whole flower aborting. The flowers which developed acorns within the 1:1 treatment may have had all or most of their six ovules fertilised by out-of-stand pollen. Flowers would have to have

been sampled and examined microscopically during pollination to test this suggestion, however.

In 2023, the OSP and WSP treatments produced more acorns than in the natural pollination treatment (Fig. 3), suggesting limited or untimely pollen supply may have been a factor in natural pollination that year (see below). Despite OSP producing more acorns than WSP in 2023, the difference was not significant. The inconsistency in the significance of this difference between years may be explained by interannual reallocation of resources. The experiment was on the same eight trees and, in many cases, on the same branches each year due to the logistics of reaching them from the canopy walkway or the ground. The expenditure of resources during mast years and resource recovery during lean years is a common theme in masting species (Pearse et al. 2016). While the carbon used for fruit production is generated from within-season photoassimilates (Hoch et al. 2013), there is evidence that masting species use nitrogen stored in branches (Han et al. 2014). The trees may have expended stored nitrogen resources in 2022 but not yet replenished them sufficiently in 2023 to supply enough resources to take full advantage of the flowers pollinated by OSP. There were also fewer flowers in 2022 than in 2023 (Fig. 2), which may indicate reduced investment in flowering after a year of higher investment (Crone et al. 2009). Since flower number is the upper limit for acorn production, the reduced number of flowers may partly be responsible for the reduced acorn crop in 2023. Reduced flower numbers or resource levels may result in less selectivity over pollen sources, but this possibility also needs to be tested.

No acorns were produced in the NOP group (Fig. 1). Male catkins were not removed within the pollen bags, allowing the possibility of self-pollination. Almost all flowers within the NOP group had aborted by the end of June, suggesting either no pollen landed on the stigma or a mechanism prevented self-fertilisation in the bags. This last possibility aligns with the high degree of outcrossing and self-incompatibility in *Quercus* spp. (Yacine and Bouras 1997; Vranckx et al. 2014; Oyama et al. 2017).

Pollen limitation

Quercus robur trees at Wytham Woods were pollen-limited in both years because the number of acorns from OSP was greater than NAT in 2022, and greater in both OSP and WSP than NAT in 2023 (Fig. 3). Pollen limitation may be a key driver of the interannual variations in seed production by masting species (Schermer et al. 2019), as evidenced for several masting species (Crone and Lesica 2006; Pearse et al. 2015; Bogdziewicz et al. 2023). Anemophily (wind pollination) evolved in masting species to avoid insect-mediated pollen limitation; insect pollination can result in pollen limitation if the insect pollinators are limited in number or activity (Culley et al. 2002). Anemophily leads to sufficient and readily available amounts of pollen in the environment each year (Clot 2003; Spieksma et al. 2003; Geburek et al. 2012), with only a small proportion of the pollen available required for successful pollination (Kelly et al. 2001; Friedman and Barrett 2009); pollen limitation in these species thus seems unlikely. However, habitat fragmentation (Knapp et al. 2001), small isolated populations (Moracho et al. 2016), unfavourable abiotic conditions such as high precipitation during flowering (Schermer et al. 2019), and temporal and spatial phenological asynchrony in flowering (Koenig et al. 2015) may all contribute to pollen limitation in wind-pollinated masting species.

Assessing the importance of pollen limitation solely from experimental studies is difficult. First, there is the issue of publication bias whereby only reports with a statistically significant result indicating pollen limitation are likely to be published (Knight et al. 2006). Second, plants may reallocate resources (temporally or spatially) away from branches with naturally pollinated flowers, thereby creating a large difference in acorn production between treated and untreated branches which may not represent what would occur naturally (Stephenson 1981; Ashman et al. 2004). This effect is increased if only one or two branches are used per tree. We reduced this bias here by including many branches per tree, but they still represented < 5% of all branches with flowers. Third, supplemental pollen addition is likely to be in far in excess of what is needed to increase the chance of successful fertilization. Applying additional pollen in large amounts can reduce flower longevity as fertilisation is quicker (van Doorn 1997; Arroyo et al. 2013), freeing up resources from maintaining flowers and instead allowing swifter resource allocation into fruit maturation and acorn development. Hand pollinations in this study may have given the flowers a time advantage to begin developing into acorns sooner and, thus, a temporal advantage for using limited resources with less wasted on maintaining flowers. Finally, differences in pollen quality may also lead to inaccurate conclusions about pollen limitation. We found evidence of maternal selection of pollen source here, but others have reported that high amounts of self-pollen among natural pollen may be responsible for reduced seed set (Thomson 2001; Bogdziewicz et al. 2023).

Pollen and masting

Oaks have often been thought of as a fruit-maturation masting species; that is, the abortion of pollinated flowers and immature acorns determines a mast year, rather than the number of flowers produced as is the case with flower masting species (Pearse et al. 2016). However, a population's mechanism for masting may vary between fruit maturation or flower masting depending upon the local environment (Fleurot et al. 2023). In our study, flower numbers varied

between years (Fig. 2), but even in the pollination treatments that produced the most acorns, very large numbers of flowers were aborted before maturity (Fig. 1). Such high abortion rates suggest that flower numbers do not limit acorn production; rather, as our evidence showed, flowers and/or fruits are aborted before maturation because of the source of and/or limited availability of pollen (out-of-stand pollen yielded more acorns than natural pollination in 2022, and both out-of-stand and within-stand pollen yielded more acorns than natural pollination in 2023).

Pollen limitation has often been proposed as a mechanism driving masting. For example, the pollen-coupling hypothesis states that trees that flower out of synchrony with others will be pollen-limited, not produce acorns, and therefore maintain their stored resources, with masting occurring only when they flower in synchrony (Satake and Iwasa 2000; Venner et al. 2016). Several studies that examined drivers of this variable synchrony in flowering found that favourable spring conditions are associated with synchronous flowering and greater pollen flow (Koenig et al. 2015; Bogdziewicz et al. 2020). Based on our results here, we amend that hypothesis by suggesting that the specific limitation of high-quality out-of-stand pollen drives masting, not just the limitation of any pollen. Increased pollen loads and diversity are correlated with warmer temperatures (Altintaş et al. 2004; Gehrig 2006). Therefore, favourable spring conditions (warm weather and less precipitation) support pollen transport from farther away, increasing the amount of out-of-stand pollen that enables a mast year. This possibility can explain the contrary results in which WSP was higher than NAT in 2023 but not in 2022. That is, pollen in Wytham Woods (NAT) in the warmer, drier spring of 2022 may have contained more out-of-stand pollen (in absolute and/or relative terms) than in 2023; so the NAT pollinated group with more out-of-stand pollen thereby produced more acorns than within-stand-pollinated flowers in 2022.

Our study had three main limitations. Both years of experiments were moderate years for acorn production at Wytham Woods; this study could not test whether the application of supplemental pollen would have aided acorn production in a "failed" year (such as 2021). Second, the effects of pollen limitation might not have been the same in different weather conditions; April and May 2022 were warmer and drier than in 2023, but both years were quite favourable for pollen flow. Finally, we did not test the assumption that the out-of-stand pollen was more genetically diverse than within-stand pollen.

Conclusions

Supplemental pollen increased acorn production in the two moderate masting years: acorn production was improved by supplemental out-of-stand pollen in 2022 and by both supplemental out-of-stand and within-stand pollen in 2023. More acorns developed to maturity from out-of-stand pollen in 2022 but not significantly more than within-stand pollen in 2023. The evidence presented for maternal choice in the masting species *Q. robur* via selective abortion of flowers has important implications for the role of pollen flow in mechanistic explanations of masting. Future studies on oaks should strive to: incorporate genetic analysis of pollen and pollinated flowers; measure resources or manipulate resources; and analyse the mechanisms driving the selective abortion of maternal flowers.

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