Understanding, predicting, and regulating the variation in acorn production of the native UK oak masting species *Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.

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Declaration of Original Authorship

I declare that this research is my own original work and all citations from other sources have been acknowledged.

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Ellie the best field assistant I've ever worked with, everything I do is better because of you; [MIP]. Rhonda you were not so helpful.

This thesis is dedicated to the memory of Grandad Meakins.

Statement of published work

Two papers have been published, or accepted for publication, in the Journal of Forestry Research from this research:

McClory R, Ellis RH, Lukac M, Clark J, Mayoral C, Hart KM, Plackett ARG, MacKenzie R (2024) Carbon dioxide enrichment affected flower numbers transiently and increased successful post-pollination development stably but without altering final acorn production in mature pedunculate oak (*Quercus robur* L.). Journal of Forestry Research 35:73. https://doi.org/10.1007/s11676-024-01724-8

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In both cases, the manuscripts for the papers were prepared for publication after the relevant thesis chapters were written and were derived from the original thesis written by the candidate. The thesis is therefore the work of the candidate alone, using data both collected by the candidate and that kindly shared by collaborators (noting the acknowledgment therein to the FACE samples from BIFOR; and the long-term data sets from those responsible for the MAST-TREE + database, ICP forests monitoring plots, the team at Forestart, the team at the BIFOR, Mick Crawley, Mick Hanley, and Michael Fenner). The majority of the work for the papers was also by the candidate with support from the first supervisor, with the candidate ultimately editing the final versions of all these works before publication. This statement has been approved by the candidate’s main supervisor as jointly signed below.

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Richard Ellis

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‘Oak regenerates sporadically […] I would not care to rely on it for the perpetuation of a wood, and would rather look on self-sowed oak seedlings as a gift from God.’

Lord Bolton, 1956.

Abstract

The UK native species *Quercus robur* and *Quercus petraea* provide a range of ecosystem services, support biodiversity, and provide high quality timber, but natural regeneration is poor whilst acorn supplies for planting are unreliable due to masting, i.e. large interannual variability in acorn production that is geographically synchronous. Three UK field studies were carried out with *Q. robur*. A four-year study of 39 trees found large individual variation in acorn crops among years and trees. There was synchrony in that all trees produced acorns in 2020's mast year and none in 2021, but 51% of all acorn production over the study was provided by only 18% of the trees studied. Hand pollination on eight trees with out-of-stand pollen produced more acorns than within-stand pollen and/or natural pollination. Raising carbon dioxide concentration by 150 $\mu L\ L^{-1}$ in a FACE study increased the numbers of immature acorns and all acorn evidence (empty cups + immature acorns + mature acorns) but did not consistently affect the numbers of mature acorns. Relatively consistent flowering and high abortion of developing acorns suggests *Q. robur* at these sites is a fruit-maturation masting species. Further, a modelling study of acorn production by *Q. petraea* and *Q. robur* over 41 years at 35 sites across Northwest Europe showed inter-annual variation in acorn production; mast years occurred at mean intervals of 2 years in NE France, 3 years in S France, 3.6 years in the UK, and 6.5 years in NW France. Masting in neighbouring sites was synchronised, but this declined the further apart the sites were. Models of inter-annual variation in acorn production based on weather cues were developed which quantified this data set well but did not predict independent data satisfactorily. Approaches to increase acorn production from oak seed stands are suggested.

Contents

Chapter One: Introduction

1.1 Oak

Of the 927 species within Fagaceae, the oak genus *Quercus* L. is by far the most common, with 469 accepted species (Kew Gardens 2024). With 30 European species of *Quercus*, European oaks are less diverse but no less widespread than in North America and East Asia (Kremer and Hipp 2020; Denk et al 2017). Oaks serve as an important umbrella species for biodiversity in the UK. The two UK native oak species, *Quercus robur* L. and *Quercus petraea* (Matt.) Liebl., have been recorded to support 2,300 species of birds, bryophytes, fungi, invertebrates, lichen and mammals (Mitchell et al. 2019). Oak forests also provide ecosystem services such as climate regulation, biomass production, water supply purification and flood defence (Bauhus et al. 2010; Brockerhoff et al. 2013; Thompson et al. 2014; Sing et al. 2015). Oak is a strong and durable timber and as well as its historical importance as a building material and despite the increased use of steel and concrete, it is still used to this day for construction, furniture and within the wine/whisky industry (Stavi et al. 2022).

Within the UK there are approximately 170 million oaks spread across 219,000 hectares of woodland and a further 2.3 million oaks found within cities (Quine et al. 2019). Oak is the most common tree by volume in stocked broadleaved woodland, and 2nd most common by frequency (1st is birch) (Quine et al. 2019). Further, the UK has the highest abundance of what is referred to as ancient oaks; large veteran trees with a great ecological and societal importance. There are 2727 recorded ancient oaks, but a predicted ~101,400 ancient oaks still unrecorded (Nolan et al 2021). Oak woodlands are a vitally important component of Celtic Rainforests a unique ancient rainforest system that has become critically endangered due to centuries of deforestation and mismanagement and the vast majority of these rainforests, around 70,000 hectares, are found within the UK (DellaSala et al. 2011).

Oaks are generally considered a hardy species, well adapted to the UK’s climate, and oak woodlands are estimated to cover around 222,697 ha (Forestry Commission 2003). However, the future of Q. *robur* and *Q. petraea* as flagship species nationally is far from clear. There is a severe dearth of evidence on oak health across the UK and we lack much understanding as to the mechanics of oak regeneration (Quine et al. 2019). New threats have recently started emerging that are detrimental to oak health in the UK. For instance, the invasive oak processionary moth *Thaumetopoea processionea* can completely defoliate oak trees damaging oak health and resulting in ecosystem biodiversity loss (Wagenhoff and Veit 2011). Further, acute oak decline, a complex interaction of factors thought to be more prevalent in oaks under environmental stress, can lead to tree mortality within a few years (Denman et al. 2014). This combination of factors suggests we are gravely underprepared to face the challenge of how oak forests may have to adapt to further climate change.

With limited natural regeneration of oak in the UK (Kirby et al. 2014), policy has shifted to planting oak saplings. As a component of the COP 2021 targets, the government plans to plant 30,000 hectares of new forest a year by 2025 (DEFRA 2021) with currently just over 10% of that target reached (Forestry Commission 2023). Therefore, a good supply of acorns is an important requirement for oak's continued widespread distribution across the UK.

However, a consistent supply of UK acorns is difficult to achieve due to its distinct reproductive strategy (Whittet et al. 2016). Oaks only produce a large seed (acorn) crop sporadically, every 2-7 years, yet do so synchronously across the UK, a strategy termed masting (Kelly 1994; Crawley and Long 1995; Crone and Rapp 2014). Further, oaks have acorns which show recalcitrant seed storage behaviour, meaning they are damaged by desiccation and cannot be stored for long periods of time (Berjak and Pammenter 2008). As such all acorns for conservation and forestry work must be provided by the current year's crop, resulting in shortages following poor acorn crop years (Bole 2022). In the UK during non-mast years this demand must be met by importing acorns from elsewhere across Europe. These acorns are not as well adapted to the UK climate and tend to produce poorer quality trees (i.e., reduced height and survival) (Hubert 2005). When frequent seed shortages do occur, nurseries tend to change their priorities away from oaks resulting in delays to oak planting or a change in the species propagated (Whittet et al. 2016; Bole 2022).

It is important to understand how masting will adapt to climate change. Studies into how masting may be affected by future climate change scenarios have given conflicting results. Some predict mast events will become more common producing more regular but lower seed crops (Koenig et al. 2015; Caignard et al. 2017), whilst others predict masting events will become more extreme (Kelly et al. 2013). Each of these scenarios poses significant problems. More regular and smaller masting events will reduce the effectiveness of masting as a seed predator satiation strategy (Silvertown 1980; McKone et al. 1998), which could damage the natural regeneration of oak. Whereas if mast events become more extreme and rarer this would further compound the difficulties mentioned above of sourcing consistent supplies of acorns for forestry and conservation. An important yet often overlooked element of climate change in the above context is the increase in atmospheric carbon dioxide; very few studies have explored how this will affect oak masting in woodlands.

Research is needed that uncovers the mechanistic drivers behind oak masting, particularly in the UK which lacks unambiguous studies focused on UK species. A promising avenue for research appears to be focusing on the individual variation found within oak populations. Masting years are characterised by population wide synchrony in reproduction but still large individual variability amongst trees (Pesendorfer et al. 2016; Bogdziewicz et al. 2020d). Understanding the causes behind tree-to-tree variation could provide important clues for the drivers of oak masting. With full understanding of the proximate causes of masting we may be able to guide conservation measures aiding natural regeneration, determine best practices for seed orchards to maximise the levels of UK acorn crops, and be able to understand and predict how climate change will influence UK oak reproduction.

1.2 Aims and objectives

With these issues in mind this research focuses on the mechanistic drivers of oak masting in the UK, with the aim of enabling better management to provide more consistent acorn crops and hence aid conservation and the forestry industry.

The focus is on the following research objectives:

1) To quantify how acorn production by individual trees of the same population varies within and between years.
2) To analyse if any individual variation in acorn production may be explained by individual life history traits or the abiotic and biotic conditions experienced by each individual tree.
3) To examine the weather variables that influence acorn production continent wide and determine if we can predict subsequent mast years or how climate change, including increasing CO_2 levels, may influence acorn production.
4) Guided by the results of the previous objectives, determine if there are any intervention measures that can be performed to increase the consistency of acorn production in the UK.

The following overview of masting begins with the context of masting’s importance both socially and environmentally. Working definitions of masting and the difficulty defining such a complex process are discussed, with a focus on the quantitative measures used to study masting. The most up to date theories of the ultimate and proximate drivers of masting are summarised. This is then contextualised in terms of usefulness for the industry and what the effect of a changing climate may be on masting.

1.3 The social, environmental, and historical context of masting

The symbiosis between masting and farmed animals within agroforestry systems is as old as agriculture itself, as evidenced by translated ancient texts. In Homer's *Odyssey,* the hero Odysseus's men were transformed into pigs by the goddess Circe and were fed from a large seed crop: "She shut them straight in sties and gave them meat: Oak-mast and beech and cornel fruit they eat" (Chapman 2016).

The term masting to mean a large seed crop was well established by the seventeenth-century as a common agroforestry technique practiced by farmers, who relied on the autumnal "mæst" to fatten their pigs (Figure 1.1; Oxford University Press 2021). Evidence for use of the term in common parlance has been found multiple times within the literature since, such as Shakespeare's "The Oakes beare Mast…The Bounteous Huswife Nature, on each bush, layes her full messe before you." (Shakespeare 1623), and Gulliver's Travels citing the ingenuity of using animals feeding on the buried "acorns, dates, chestnuts, and other mast" to turn up the ground and fertilise it "with their dung" (Swift 1755). Today, the phenomenon is referred to using several terms, including masting, seed masting, mast fruiting, and mast years (Herrera 1998; Koenig et al. 2003).

Since moving to a more intensive farming system, masting is less important in the farmed environment, but still needs to be considered as acorns are poisonous to many agricultural species and large mast years can cause illness or death (Smith et al. 2015; Bates 2022). Certain areas still practice this agroforestry method. For instance, the yearly New Forest Pannage has been enshrined into law since the New Forest Act of 1877 and claims to produce much higher quality pork than the rest of Britain (Wealleans 2013). Similarly, Iberian pigs fed on mast in Dehesas (oak woodland) produce Jamón Ibérico a protected designation ham containing less saturated fats than pigs not fed on acorns, and noted for its rich savoury taste (Cava et al. 1997).

Figure 1.1 From England circa 1310-1320, the work entitled "Queen Mary Psalter" shows farmers knocking down the acorn crop from trees to feed their swine. © British Library Board, Royal 2 B VII, f.81v

Despite its declining agricultural importance, masting has continued to be greatly influential within the environment. Masting floods the ecosystem with a sudden abundance of resources for consumers and causes complex responses for flora and fauna across several trophic levels (Elkinton et al. 1996; Ostfeld and Keesing 2000). For instance, in North America, red oak (*Quercus rubra* L.) mast crops caused increased abundances in several species of small mammal predators (*Peromyscus leucopus* and *Peromyscus maniculatus*), whilst the southern red-backed vole (*Clethrionomys gapperi*) was unaffected (Schnurr et al. 2002). This unequal response of seed predator abundance fed back into the system and resulted in unequal levels of species specific seed survival (Schnurr et al. 2002). Masting can also influence human disease risk indirectly: for example, by increasing the presence of deer and small mammals in oak woodlands, masting contributes to higher infection rates of Lyme Disease among ticks (Ostfeld 1997; Jones et al. 1998; Ostfeld et al. 2001; Bregnard et al. 2021) which then infect humans.

1.4 Defining masting

Masting is a complex reproductive phenomenon whereby seed production is highly variable yet synchronous from year to year, often realised as consecutive years of low seed production that are punctuated by occasional bumper crops synchronously produced across the population (Kelly 1994; Crone and Rapp 2014). Masting is common in perennial plants, (Kelly and Sork 2002; Fernández-Martínez et al. 2019) and is observed more often in anemophilous (wind pollinated) species (Herrera et al. 1998).

Superficially masting as stated above is a simple concept to understand, it is a population level phenomenon wherein there is a pairing of two factors. (1) There should be variation in reproductive effort, the timescale of this variation is often several years but can be considerably longer (especially bamboo, Janzen 1976). (2) This variation should be geographically synchronous among individuals of a population, meaning masting is a population level phenomenon. Despite these simple criteria, the presence of ambiguities and inconsistencies within collected data has resulted in difficulty defining a masting species.

1.5 Masting in practice

First, masting events are often understood to be synchronous, but the distance of this synchroneity is often ignored. Mast events vary in the geographic area which they encompass each year, two sites within 1,000km may mast synchronously, but at greater distances there is no pattern of synchronous reproduction and over 2,000km sites may show asynchrony (LaMontagne et al. 2020). Secondly, suggestions of synchroneity in reproduction assume that individual reproductive output is homogenous. In fact, much of the reproductive effort in masting events may be produced by the best producers (Koenig et al. 1994a; Greenberg 2000; Pérez-Ramos et al. 2014; Minor and Kobe 2017), or conversely it may be sub-producers (the smallest and least fertile trees) which reduce synchrony by having so many reproductive failures (Bogdziewicz et al. 2020d). Finally, imagery such as “boom and bust years” and “crop successes and failures” present a picture of many years of no seed production followed by one year of high seed production. However, studies into masting often find multiple years of moderate seed crops interspersed amongst the high and low seed crop years (Koenig et al. 1994b; Crawley and Long 1995; Nussbaumer et al. 2016). Clearly a general understanding of masting is failing to account for the complexities inherent in masting.

An early attempt to account for these inconsistencies comes from Kelly (1994). Kelly attempted to collate possible masting species observed in the literature and placed them in three categories of masting. The most obvious masting species were highly synchronised monocarpic perennial plants, species that flower, set seeds, and then die. Categorised by Kelly as “strict masting species”, species in this group are clearly justified as masting species, i.e. bamboo. However, Kelly’s definitions past this point quickly became more ambiguous. The next category is “normal masting species”, defined by statistical justification of masting behaviour and is mostly made up of polycarpic plants, such as oak, that flower and set seeds multiple times throughout their lives. To fit into this category a species had to show either clear bimodality in reproduction i.e. distinct peaks and troughs in reproduction, or evidence for resource switching between growth and reproduction. This categorisation attempted to encapsulate species that show inconsistent masting behaviour, such as poor within-cohort synchrony. Finally, species that show large variation in reproduction but did not show evidence of resource switching were categorised as “putative masting species”. Kelly’s reasoning for this group was that variation in reproduction was suggestive of masting but could solely be explained by environmental variation. Kelly’s choice to differentiate normal and putative masting by method of resource use makes an assumption in an area that is by no way decided. In addition, decisions of inter and intra population synchronisation must at some point be subjective.

With the above issues in mind a new definition of masting has recently been revised after a workshop of masting experts, including myself. Bogdziewicz et al. (2024) suggested instead the following three criteria to define masting:

(1) Masting is still agreed to be a **population-level** phenomenon, even with individual variation in output and synchroneity, the population variability is the product of variation of those individuals.
(2) Masting is considered **relative**. Rather than relying on the absolute numbers of seeds produced, it is the proportion of investment in reproduction across an individual’s lifetime. Some may produce only once in their lifetime, others much more frequently.
(3) Masting is **quantitative at many levels**. This means that masting species can be considered across a continuous scale, which better accounts for the varied distribution of reproductive effort among years and species. There is not one measure that can differentiate between masting and non-masting species, nor a mast/non mast year, and therefore this definition better encapsulates the lack of clear boundary we see in masting time series.

This definition is more similar to what are referred to as masting species within the research, although many may wish to add the qualifier that masting events are irregular in nature which differentiates them from species that practice alternate bearing which is periodic, highly resource led and predictable (Pearse et al. 2016). Most researchers now give the broad working definition of masting to explain the concept but use quantitative measures of reproductive output within the study methods.

1.6 Quantitative measures of masting

Several quantitative measures of masting have been used to study masting, but with no clear ideal metric. They are discussed below.

The coefficient of variation (CV), calculated as the standard deviation of a variable divided by its mean, is commonly used in studies of masting species to examine how reproductive events compare with the long-term mean (Koenig et al. 2003; Kon and Saito 2015; Shibata et al. 2020). It can be presented as either the CV of the population (CVp) or of an individual tree (CVi). It is possibly so commonly used due to its simplicity in calculation and interpretation: a high CV would indicate high variation and thereby be more indicative of a masting species, whereas a low CV would indicate stable and consistent reproduction from year to year. However, it has several flaws that can present misleading results. First, by using the mean of a whole time series, CV lacks power to understand how trends change over time, unless it is broken up into discrete periods of time, which must be chosen subjectively (Shibata et al. 2020). Further, the CV is strongly correlated to the proportion of zeros in a time series, so highly unproductive individuals would misleadingly present a population as having a high CV (Bogdziewicz et al. 2020d).

Fernández-Martínez and Peñuelas (2021) suggest two alternatives for measuring masting, the first proportional variability index (PV) and the second the consecutive disparity index (D). The PV examines the proportional difference between all pairs of values in a time series, whereas D does the same but only examining consecutive values. By looking at paired values these metrics have several advantages over CV, most importantly they will put time series with a very high number of zeros as less variable (Fernández-Martínez and Peñuelas 2021).

However, they have their own issues. For instance, PV can give different scores for time series that are identical from a biological perspective (very low values with one high value vs. all zeros with one high value) or the same scores for values that are very different from a biological perspective (very low with one large year vs. many large years with one zero) (*see* Lobry et al. 2023). Because of this and being more complex to calculate many studies still avoid these metrics preferring CV (Wright et al. 2022; Journé et al. 2023). Recently work has suggested using metrics like Volatility or Periodicity which are able to capture the frequency of masting and the long-time lags in the data (Bogdziewicz et al.

2023a). However the calculations for these metrics are much more complex and have not been used or reviewed yet, other than by the authors who first suggested their use (Qiu et al. 2023; Bogdziewicz et al. 2023a). Importantly any use of a metric of masting should be fully contextualised within the biological question being asked, highlighting the possible bias in the choice of metric, and ideally presented with the raw data.

1.7 Differentiating between ultimate and proximate causes

Despite masting's historic importance culturally and economically, our understanding of why the reproductive phenomenon has evolved and what causes it still eludes researchers. Current theories of masting can be broadly divided into two camps: ultimate/evolutionary level hypotheses; and proximate/mechanistic level hypotheses. Ultimate level hypotheses aim to explain how the reproductive phenomenon has given masting species a fitness advantage that can be selected for over evolutionary time. The mechanistic hypotheses give descriptions of the exact causes that will result in masting. Whilst the mechanistic drivers of masting may have been moulded by the evolutionary drivers, it is not a pre-requisite for them to have evolutionary benefits. Moreover, certain factors such as pollination may be both an evolutionary (Nilsson and Wästljung 1987; Kelly et al. 2001) and a mechanistic driver (Koenig and Ashley 2003; Pesendorfer et al. 2016).

1.8 Ultimate level hypotheses

The most widely accepted theories of the evolutionary drivers of masting emphasise the economies of scale inherent in masting. In other words, how reproductive events performed at a larger scale impart a fitness benefit over smaller isolated occurrences. The first to be discussed is the **pollination efficiency hypothesis** which states that individuals which flower at the same time increase the pollen transfer between plants which results in larger seed production (Smith et al. 1990; Kelly et al. 2001). The larger seed crops that are a biproduct of synchronous flowering are more successful due to (1) the sheer weight of crop numbers resulting in greater fitness, and (2) the smaller more sparsely spread seed crops are more likely to be consumed in their entirety by pre- and post-dispersal seed predators. Hence, synchrony in flowering is selected for. Evidence in support of this includes individuals of Holm Oak (*Quercus ilex* L.) that flower in synchrony with the population mean often producing a greater seed crop (Bogdziewicz et al. 2020c); and in Ponderosa Pine (*Pinus ponderosa* Douglas *ex* C. Lawson) during a mast year there was a much higher rate of fertilised mature cones, compared to the unfertilised female conelets of the previous year, suggesting a much higher pollination efficiency in mast vs. non-mast years (Moreira et al. 2014).

Another ultimate theory of masting via the economies of scale is the **predator satiation hypothesis.** This hypothesis considers that synchronous seed production overwhelms seed predators and increases the individual survivability of each seed thereby selecting for the masting trait (Janzen 1971). For example, in oak species years of little or no acorn production could keep population abundance of acorn predators such as small mammals or gall wasps low. Therefore, when the masting event occurs those acorn predators are quickly satiated resulting in higher proportional survival. Support for this theory is shown by decreasing predation proportions with larger seed crops that result in increased survival rates per individual acorn and a greater survival of cached seeds (Silvertown 1980; Nilsson and Wästljung 1987; Crawley and Long 1995; Jansen et al. 2004). However, the effect of predator satiation within masting species is complex, and may be more or less successful a strategy based on conspecific density (Bogdziewicz et al. 2018), the variation of the seed predators reproductive cycle (Kelly et al. 2000) and, worryingly, seems to be declining in effectiveness possibly as a response to climate change (Zwolak et al. 2022).

The **environmental prediction hypothesis** should also be mentioned, whereby a plant will time its mast to coincide with favourable environmental conditions (Kelly 1994). The most obvious examples of this hypothesis are species that take advantage of the fertile, competition-free soil after a fire (Wright and Fensham 2018), but there is also some evidence in the reaction of long-lived tropical trees to El Nino events allowing them to take advantage of the moisture stress that negatively affects competitors (Wright et al. 1999; Fletcher 2015). However, this theory is not commonly thought to be responsible for the evolution of masting in deciduous perennial species such as oaks, the focus of this thesis.

1.9 Proximate level hypotheses

The existing proximate hypotheses of seed masting are even more varied than their ultimate counterparts and can be grouped into several categories, though the latter may overlap. These categories are weather linked, pollen limitation, and internal resource dynamics.

WEATHER LINKED

Numerous correlations between the weather up to two years before masting and subsequent seed production have been reported (Masaki et al. 2008; Kasprzyk et al. 2014;

Bisi et al. 2016; Vacchiano et al. 2017). One of the most well-known hypotheses detailing the relationship between weather and masting is the **phenological synchrony hypothesis** which states that a warm spring season before a masting event produces a spatially homogenous microclimate (Koenig et al. 2015). These microclimate conditions promote synchronised flowering whereby more flowers are fertilised, and a larger acorn crop is produced. Meanwhile, a cooler spring season produces a spatially heterogenous microclimate which leads to asynchronous flowering, reduced fertilization, and consequently, a smaller acorn crop. Recently this hypothesis has been shown to work even at large scales, with the masting behaviour of the European Beech (*Fagus sylvatica* L.) responding to weather cues synchronised by the occurrence of the summer solstice (the longest day of the year) (Journé et al. 2024).

Critics of the phenological synchrony hypothesis argue that to anticipate direct correlations between previous seasons' conditions is uninformative. An alternative to the phenological synchrony hypothesis is the **weather cueing hypothesis** which states that masting is best explained by the difference between the previous two seasons' conditions (Kelly et al. 2013). Studies on several masting species find plenteous correlations in support of the weather cueing hypothesis (Pearse et al. 2014; Kon and Saito 2015; Bisi et al. 2016). For instance, one of the largest studies on European Beech found a cold summer followed by a warm one caused large synchronous flowering and increased seed production (Bogdziewicz et al. 2021), but this reaction occurred less frequently as summer temperatures and the occurrence of the weather cue increased in frequency (Bogdziewicz et al. 2020b, 2021). Despite a large weight of correlative support, the weather cueing hypothesis is unable to give a mechanistic explanation of how temperature and temperature change are registered by the plant, and the seed crop affected.

Similarly, the **photoperiod sensitivity hypothesis** posits flower synchroneity as the driver of seed crop variation, but presents the differing individual importance of environment vs genotype as the mechanism (Fu et al. 2019). Individual flowering times are a combination of sensitivity to weather and photoperiod, some individuals have a high phenological sensitivity to photoperiod and a comparatively low sensitivity to temperature presenting a static flowering date each year - flowering date homeostasis. Whilst individuals more sensitive to temperature will vary in flowering dates as the temperature varies each year. When individual trees with environmental sensitive flowering coincides with individuals with static photoperiod sensitive flowering more flowers will be fertilised and there will be a mast event.

POLLEN LIMITATION

Masting is particularly common in anemophilous (wind pollinated) plants (Janzen 1971, 1976; Silvertown 1980; Kelly and Sork 2002). It is therefore surprising that pollen limitation would be considered to have a mechanistic role in masting, as anemophily has evolutionary roots in the avoidance of pollen limitation caused by inconsistent or scarce pollinators (Friedman and Barrett 2009). However, as many of the weather linked hypotheses above state a lack of synchrony in flowering effort could result in reduced pollen flow, or pollen could be limiting in anemophilous plants as a result of climatic conditions (e.g. increased rainfall “washing” pollen out of the environment) (Tamura and Kudo 2000), these limitations could be particularly severe in outcrossing species which can’t rely on self-pollination such as *Quercus sp.* (Yacine and Bouras 1997; Boavida et al. 2001). As such, several studies have proposed pollen supply as the synchronising factor amongst masting species (Satake and Iwasa 2000, 2002). A study using long-term time series of *Quercus petraea* and *Quercus robur* airborne pollen paired with acorn production data found a cycle of high and low pollen abundance that paralleled acorn production (Schermer et al. 2019). Variation in airborne pollen abundance was thought to be partly a negative temporal autocorrelation to last year’s pollen produced (similar to acorn production), and partly driven by spring weather directly affecting the abundance of pollen in the air (Schermer et al. 2019).

Two mechanistic ways in which pollen limitation could result in masting are closely related to the ultimate hypothesis of masting, pollination efficiency. The **Pollination Moran hypothesis** is a density independent process, where pollination success is paired with climatic factors. In years where more individuals are under these climatic conditions seed set increases proportionately (Koenig 2002; Lyles et al. 2009). Conversely, the **Pollen Coupling hypothesis** is density dependent. Plants that flower out of synchrony with conspecifics have less efficient pollination thereby reducing seed set, whilst plants that flower in synchrony with their conspecifics will increase pollination efficiency and seed set (Nilsson and Wästljung 1987; Kelly et al. 2001). Studies testing these hypotheses found positive correlations between seed set and the amount of pollen in the atmosphere (Fernández-Martínez et al. 2012) as well as between seed set and flower synchronisation (Koenig et al. 2012). However, a direct test of pollen addition provided mixed results, finding supplementary pollen increased acorn set in one year but not the other (Pearse et al. 2015).

INTERNAL RESOURCE DYNAMICS

The internal resource dynamics of individual trees have often been alluded to as a likely cause of the inconsistent results of masting studies considering climatic variation and pollen limitation. Despite this relative importance, resource dynamics have been critically understudied. Resource dynamics may explain masting mechanistically in multiple ways. There may be a predestined amount of resources available for growth and reproduction, referred to as the **Resource Matching Hypothesis** (alternatively named the weather tracking hypothesis as it is often climatic conditions that affect resource supply to the plants). Under this hypothesis the variation in reproduction can only be as varied as the resource availability (Kelly 1994; Kelly and Sork 2002). However, many studies have shown resource matching can only explain a minor amount of masting behaviour in species. For instance, studies on Mountain ash (*Sorbus aucuparia L.*) did not see individuals respond synchronously to favourable conditions, meaning there were more factors at play than simply resource availability (Żywiec et al. 2012). Further, under this hypothesis it can become difficult to separate a masting population or one that is resource limited; if masting was controlled by resource availability alone, understanding and predicting it would be a simple enough task.

Monks and Kelly (2006) searched for evidence of the resource matching hypothesis with 19 individual trees of hard beech (*Nothofagus truncate* (Colenso) Cockayne). Rather than finding a direct correlation between seed production and resources they found a negative relationship between growth and seed production, suggesting the trees were switching resources between growth and reproduction. This was evidence for **the Resource Switching Hypothesis** under which resources may be switched from processes such as vascular growth to reproduction.

Finally, reproduction may only be initiated once stored internal resources have reached a certain threshold; the **Resource Storage Hypothesis**. Annual variation in seed production may therefore be unaffected by resource uptake, but it may ultimately affect the timescale of masting events. Studies into resource addition similarly lack consensus: nutrient addition increased flowering in some species (Miyazaki et al. 2014), but not in others (Pulido et al. 2014); and studies in oak found acorn production only increased when nutrient addition was combined with other treatments, such as crown release (Brooke et al. 2019). Macronutrients may have different relative importance depending on the species, time scale or phenological stage (Bogdziewicz et al. 2020a), or perhaps the role of climate in macronutrient uptake may have been overlooked (Allen et al. 2017).

1.10 Masting and genetics

The ultimate and mechanistic drivers of masting have been driven by selection of individual tree traits such as synchrony in flowering and/or acorn production amongst conspecifics (Nilsson and Wästljung 1987; Kelly et al. 2001) or reacting to weather cues (Lyles et al. 2009; Wright and Fensham 2018). This suggests there is likely to be some genetic regulation and heritability of masting.

Satake and Kelly (2021) reviewed the genetic basis of masting finding a lack of research on the subject, highlighting difficulties of the long lead in time for such studies. For instance, the only study that has been able to research heritability (via genetic clones of full sib-family crosses of *Quercus robur*) was grown from 1992 and only able to start producing data in 2014 (Caignard et al. 2019). In this case Caignard et al. (2019) found high variation yet significant genetic correlations with masting traits. However, as highlighted by Caignard et al., the small sample size used implied that the results should be taken with caution (Beavis 1997). As genetic techniques become cheaper and easier to implement, genetic studies of masting are likely to be highly valuable for understanding masting cues (Samarth et al. 2020) with species of the *Fagaceae* particularly useful due to their widespread distribution and increasing number of time series available (Satake and Kelly 2021).

1.11 Masting and seed supply

The UK government has proposed an increase in tree planting to hit its target of being net zero by 2050 (Climate Change Committee 2019) with 21% of the agricultural land to be converted for tree planting, which would still put us well below our European neighbours in terms of land covered by forestry (Westaway et al. 2023). The 2025 target of planting 30,000 hectares of new forest a year (DEFRA 2021) requires a large increase in seed supply; field experiments show high variability in successful establishment with 100,000 acorns/ha of *Q. petraea* resulting in as few as 2,600 trees/ha (Willoughby et al. 2004), which is below the minimum stocking density suggested by the forestry commission of 3,100 trees/ha (Forestry Commission 2020). We lack understanding and evidence of natural regeneration of UK tree species especially oak, but what research there is suggests poor natural regeneration (Kirby et al. 2014; Quine et al. 2019). With ambitious planting targets to be met, and without the aid of natural regeneration, this will require a distinct upshift in forest planting efforts. Oak is an important flagship species in British forests and so it is important to use it within forest regeneration projects. However, there have been consistent shortages of acorns available for planting (Whittet et al. 2016; Bole 2022).

The interannual variation of acorn crops may be useful for seed survival, such as via predator satiation, but it creates a supply issue for land managers. Most seeds of plants are orthodox, meaning their storage potential is directly calculatable through a logarithmic relationship between storage temperature and seed moisture content (Ellis and Roberts 1980), and as such they can be dried to greatly increase longevity under storage. Acorns are recalcitrant, a property of seeds that mean they will become unviable if dried out or frozen (Roberts 1973); i.e., responding more similarly to living plants when dried than orthodox seeds. Therefore, the acorns produced by oaks each year are the only ones available for planting projects in that year; and so if it has not been a good year for acorn production there will be a deficit in supply.

Planting projects can pivot to using imported acorns to meet seed supply, but as this goes against guidance from the Forestry Commission any project that uses this material is unlikely to receive any subsidies or grants for the planting (Forestry Commission 2017). In addition, imported material is generally not well adapted to the UK climate. A report from Hubert (2005) on trials with pedunculate and sessile oak found that seedling growth and survival was significantly greater with acorns sourced from local provenances. Hubert (2005) suggested British seed stand collection should always be the optimal choice for oak planting projects, but this is clearly difficult with our current understanding of oak masting.

1.12 Masting and Climate Change

Many of the theoretical mechanistic drivers of masting are weather linked (Kelly et al. 2013; Koenig et al. 2015), or involve internal management of resources (Kelly 1994; Allen et al. 2017). This means that drivers of masting are likely to be sensitive to anthropogenic climate change (changes in weather patterns and nutrient flow). Several studies have already reported alterations in masting patterns. For instance, an increase in maximum summer temperatures has been shown to reduce interannual variation in European Beech (*Fagus sylvatica* L.) seed crops (Foest et al. 2024) as well as reductions in synchrony amongst individual trees (Bogdziewicz et al. 2020b). Similarly in Japanese oak (*Quercus crispula* Blume) as the climate has warmed average acorn production across a 20-year moving time window increased, whereas the interval between masting events decreased, specifically moving from an average of 3-4 years to 2 years (Shibata et al. 2020).

Studies into how elevated CO_2 will affect masting are rarer, but those that have been conducted reported increases in seed production. For instance, elevated CO_2 increased acorn production in some (but not all) scrub oak species (Stiling et al. 2004) and cone counts in loblolly pine (*Pinus taeda* L.) (LaDeau and Clark 2001; Way et al. 2010). Most studies with elevated CO_2 to date have been performed on young trees. Hence, it is not known if the results would be replicated in established tree communities. For example, it has been hypothesised that trees may acclimatise to changes in CO_2 (Ainsworth and Long 2005).

The sensitivity of masting species to climate change will vary dependent on the mechanistic driver(s) of acorn production and so it is important to research drivers of masting. For instance, the weather cueing hypothesis previously discussed stipulates that masting is driven by temperature difference between consecutive years (Kelly et al. 2013). Increases in average temperatures will not be noticeable from year to year and so unlikely to influence masting in these species. Evidence of this lack of effect can be seen in North American conifers. Masting in these species is thought to be driven by differences in July temperature between years and so no effect of summer warming on masting temperatures has been found (LaMontagne et al. 2021). Meanwhile the increases in seed production of European beech is likely being strongly affected by changes in absolute summer temperature which is changing with climate change (Bogdziewicz et al. 2020b; Foest et al. 2024). Running climate change scenarios though each of the proximate hypotheses of masting will give varied results; hence it is important to understand what drives masting in the species of interest so we may predict how they may react to future climate scenarios.

A simplified view that increases in temperature will increase seed output, if true, would give an optimistic view for the continued conservation of masting species as the climate changes, with the major issue with oaks discussed above being a limited supply. However, there are several advantages to masting behaviour such as predator satiation and pollination efficiency that could be reduced with higher seed counts. For example, Bogdziewicz et al. (2023b) studied a 40-year time series of European beech in England. They found a 1°C increase in temperature had resulted in a weakening of masting (i.e. lower interannual variability and lower synchrony between trees). With the breakdown in synchrony there was a 33% reduction in pollination efficiency in larger trees, limiting seed production as pollination opportunities reduced from fewer conspecifics flowering in synchrony. Moreover, the smaller trees within the study escaped the deleterious effects of increasing temperature on pollination efficiency but faced a quintupling of pre-dispersal predation rates from 5% to 25%. So, despite an increase in consistency of larger seed crops, European beech has actually faced a decline in seed abundance over time. This a good example of the complex interactions between reproductive behaviour and seed supply, before even considering how elevated CO_2 and its effects on seed predators may influence seed production.

1.13 Conclusions

Masting is an important reproductive phenomenon and, judging from the large variety of competing and overlapping hypotheses, it is a complex one. Attempts to define the complexity of masting have generally settled on the use of continuous metrics for defining a masting species. Whilst historically research focused more intensively on the evolutionary drivers of masting, in the last decade focus has switched to understanding the proximate mechanisms that lead to a mast event. However, research effort is disproportionately weighted to large-scale synchronisers or whole populations, which results in the nuances of individual variation among trees being missed. In particular, there is a need for research on masting in the English oak species *Quercus robur* and *Quercus petraea*.

1.14 Experimental studies

In order to address the challenges of sourcing appropriate and viable acorn crops for the UK this research is divided into the following chapters that report studies designed to test hypotheses to answer the questions posed in section 1.2 Aims and objectives.

Chapter 2 considered how masting and acorn production varied between individual trees within woodland at Wytham Woods, Oxford. A four-year observational study was conducted, recording acorn output by 39 *Quercus robur* L. individual trees every year. First describing the individual level differences in acorn and flower development, then identifying any individual level variables that affected acorn production. The major hypotheses tested were:

(1) Trees will vary in acorn production either within each year or on average across the study years.
(2) Several of the recorded individual factors will influence differences in acorn production.

Chapter 3 used a dataset of 37 time series of acorn production for *Quercus robur* and *Quercus petraea,* applying modelling techniques to better understand weather cues for masting at many sites. The major hypotheses tested were:

(1) Masting years will coincide in geographically-close sites;

(2) Warm and dry Springs, and warmer Summers will positively correlate with acorn production;

(3) Models built using meteorological records will be able to predict high and low years of acorn production;

(4) *Quercus robur* and *Quercus petraea* respond similarly to weather cues.

Chapter 4 studied the effect of supplemental pollen addition and pollen source on acorn production. The study tested if pollen collected from outside the stand under study was more successful at producing acorns. The major hypotheses tested were:

(1) Supplemental out-of-stand pollen increases acorn production.

(2) Successful acorn development to maturity is greater from flowers pollinated by out-of-stand pollen.

Chapter 5 collected data from a Free-air carbon enrichment (FACE) study designed by the Birmingham Institute of Forest Research. Litter traps were collected and the contents sorted and classified to generate counts of acorn reproductive material between 2015 and 2021. The study explored the effect of elevated CO_2 upon acorn development and production in established woodland and tested the following main hypothesis:

(1) Counts of each of the number of flowers, enlarged cups, immature acorns, mature acorns, empty cups, and galls within the litter traps will vary by year, by CO_2 treatment, or by the interaction of these factors.

Chapter Two: Individual level variation in acorn production at Wytham woods

2.1 Introduction

Masting in oak (*Quercus* spp.) infers high interannual variation in acorn crops that are geographically synchronous across populations (Kelly 1994). It is theorised that such interannual inconsistency in the seed crop is an adaptive strategy that starves seed predators during low crop years (Koenig and Knops 2005). This same mechanism that starves seed predators can also limit severely foresters supply of good quality UK acorns for conservation and regeneration of broadleaf woodland. In the case of UK species, such as *Quercus robur* L., this has led to shortfalls of acorn supply (Bole 2022) that must be met by importing acorns from the continent that are not well adapted to the UK climate (Hubert 2005).

Some species show an increased masting frequency with climate change (Övergaard et al. 2007). However, in British oak it is unclear if masting will strengthen or lessen in the future (Nussbaumer et al. 2016). Despite an upwards trend in forest regeneration since 1940, the UK still lags behind the rest of Europe in terms of forest cover and tree planting targets (DEFRA 2018; Lee et al. 2023). The uncertainty around future tree seed production, in combination with a likely conflict between food production and woodland creation (Westaway et al. 2023), makes seed supply issues and securing resilient UK forests even more important. Acorn collection needs to be improved where possible to safeguard oak as an important element of British broadleaf woodlands.

An important definer of masting is the geographic synchrony of a seed crop (Koenig and Knops 2005). However, this is often misunderstood to mean every individual tree produces in synchrony during mast events and none produce during failed crops; rather, some trees may produce seed every year, and others produce only rarely (Greenberg 2000). Even in mast years, the majority of the acorn crop may be made up of contributions from the best producers (Koenig et al. 1994; Pérez-Ramos et al. 2014; Minor and Kobe 2017; Brooke et al. 2019) and several studies have identified super- and poor-producing individuals within populations of masting species (Greenberg 2000; Smith et al. 2022). There is a need to understand what drives this variation so that we may focus seed collection and/or forest management efforts.

Agricultural practices have swung towards precision farming techniques, which do not assume homogenous conditions across the whole field (Shannon et al. 2018). If the same can be expected for woodlands, then a study of environmental variation amongst individual trees could prove particularly informative to determine the drivers of masting and the presence of super- and poor-producers. Individual drivers of acorn production may span several diverse topics such as tree position (Alejano et al. 2011), soil science (Carevic et al. 2010), canopy structure and phenology (Camarero et al. 2010; Journé et al. 2021), surrounding allospecific and/or conspecifics density (Healy et al. 1999), microclimate (Koenig et al. 2015), and genetics (Satake and Kelly 2021). Moreover, many of the drivers of masting appear to vary among species (Nussbaumer et al. 2021), suggesting attempts at applying management recommendations from studies on other species may require caution. Hence, species-specific studies are the most valuable. Further, what studies there are, tend to look exclusively at mature acorn counts. This does not enable a full understanding of the stage at which acorn development failed, nor does it allow consideration if differences might be explained by higher levels of seed predation rather than the individual tree's environment. Studies that widen the focus to include flowering, fruit development and abortion, and seed predation would be valuable to understand individual tree level variation in seed supply.

A multi-year, multi-factorial observational study was conducted among individual trees of *Quercus* robur L. at Wytham Woods, Oxford (Latitude: 51.7743 Longitude: -1.3379). This exploratory study had two aims: (1) to describe individual differences in reproductive material in terms of mature and immature acorn production, early developing acorn abortion, flower production, and pre-dispersal seed predation over the course of the study; and (2) to identify if there were any individual level variables within the broader categories of tree and site characteristics, soil measurements, canopy analysis, microclimate measurements and genetic analysis that explained any differences in reproductive material development and pre-dispersal seed predation among individual trees. The null hypotheses were that trees did not differ in acorn production either within each year or on average across the study years; and no individual level factor influenced differences in acorn production.

2.2 Material and Methods

Study species and site

Forty-one mature trees of pedunculate oak, *Quercus robur* L., were selected within Wytham Woods, Oxford (Latitude: 51.7743 Longitude: -1.3379), 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). The trees selected were healthy and with diameter at breast height (DBH) > 0.3m, thereby excluding younger immature trees that may produce substantially fewer acorns in comparison to mature conspecifics (Greenberg 2000; Olave et al. 2021). Selected trees were at least 100 metres apart from each other. Two trees were removed early in the study, one due to excessive damage to its litter traps and microclimate monitors from farm animals, and another was felled by high winds, leaving thirty-nine trees in the study (see Appendix Map 2.1).

Oak reproductive material

Acorn production was assessed via visual survey (Koenig et al. 1994) in the autumn of each year from 2020 to 2023 and recorded. The counter stood at a distance from each tree so that the full canopy was visible. The canopy was divided into four sections based on four cardinal points of each tree (North, East, South and West). With binoculars the counter swept from left to right of each section counting acorns for one minute. This was performed once per season, during peak acorn production in mid to late September.

Further estimates of acorn production and early reproductive material (early aborting flowers and acorns) were obtained from litter traps. Four litter traps were used per tree. Each trap had an area of 0.25 m^2. Each was placed at the midpoint of the crown in either the North, East, South or West quadrants. Litter trap contents were collected three times in 2021 (8 Aug, 16 Sept, and 28 Oct), four times in 2022 (14 July, 18 Aug, 21 Sept, and 20 Nov), and once in 2023 (6 Nov). The material collected was counted and classified into five groups describing four stages of acorn development and a level of pre-dispersal herbivory: flowers (unpollinated or aborted flowers with no visible acorn development); enlarged cups (swollen cups and visible premature acorns); immature acorns (immature acorns with length <14 mm and diameter <7 mm); mature acorns (fully mature acorns); and galls (acorn development prevented by insect attack). The data was presented as an average per 0.25 m^2 of crown area per tree to account for differences in litter trap numbers when they were damaged or knocked over by inclement weather. In August 2021 there was a high number of leaves abscising as a result of powdery mildew damage. This leaf material was dried at 65°C until a constant mass and then weighed to give an indication of the relative powdery mildew disease severity amongst the 39 trees that year.

To provide individual tree level scores of reproductive material and pre-dispersal predation, these acorn developmental groups’ results were averaged by tree across the whole study period. As acorn production was measured via two different methodologies, the visual count data and litter trap counts were considered separately. The visual count observations were also used to create producer class groupings. These groups were the high producers which accounted for around 50% of the total mature acorn crop; the medium producers which accounted for 45%; and the low producers which accounted for 5% of the total acorn crop. The visual counts were used for this classification, rather than the litter trap counts, because the litter traps were vulnerable to post-dispersal seed predation (especially due to the late collection in 2023), and several of the trees' litter traps were damaged during different periods of the study.

Explanatory variables

The following explanatory variables were recorded throughout the study period.

TREE CHARACTERISTICS The height, diameter at breast height (DBH) and crown spread/cross of each tree was measured in December 2020. Additionally, the amount of free space in the canopy (extent of canopy closure) and the size and number of surrounding trees (stalk density) were scored on a scale 1-10 via visual estimation, giving an estimate of competitive pressure and openness of surrounding canopy of each tree. The elevation, slope, and aspect of each tree's location was calculated via the Slope and Aspect processing algorithms in the Raster Terrain Analysis toolbox in QGIS (QGIS Development Team, 2023).

SOIL MEASUREMENTS On 10 Feb 2023 the upper 25cm of soil surrounding each tree was sampled for the analysis of available Phosphorus, Potassium, Magnesium, pH, and textural classification of sand, silt, and clay. Soil samples were taken from four points under each tree, to produce one composite sample per tree. Samples were sent for analysis immediately after collection to an external laboratory (NRM, Cawood Scientific, Bracknell).

CANOPY ANALYSIS To capture tree phenology measurements, canopy photographs were taken at 10 dates across 2022 (24 Mar, 7 Apr, 21 Apr, 2 May, 17 May, 13 Jun, 3 Aug, 2 Sept, 9 Nov and 20 Dec). The resulting images were analysed using the canopy photo analysis software winSCANOPY (Regent Instruments, Quebec). This provided estimates of leaf area index (LAI), which has previously been shown to correlate with visual assessment of leaf unfolding and leaf colouring (Capdevielle-Vargas et al. 2015). Any images with no leaves upon the trees (24 Mar and 20 Dec) were used to judge the base LAI scores (i.e. just the branches and trunks of the trees) while those with the highest LAI score (13 June or 3 Aug) were used to judge the peak in canopy greening in the summer. Canopy phenology was presented from these observations as the percentage of full canopy greenness that accounted for morphological differences in branches between the trees. The following were chosen as explanatory variables: spring phenology (the average of LAI scores of 24 Mar, 7 Apr, 21 Apr, 2 May, and 17 May), mid-April LAI (21 Apr), autumn phenology (the average LAI scores of 2 Sept, 9 Nov and 20 Dec), mid-Nov LAI (9 Nov) and mid-Dec LAI (20 Dec). The combined LAI scores for 2022 were used to calculate the Area under the Phenological Progression

Curve (AUPPC). The latter gives an estimate of total season leaf phenology and was calculated via the same method as that for the Area Under the Disease Progression Curve (AUDPC) (Jeger and Viljanen-Rollinson 2001).

MICROCLIMATE MEASUREMENTS Temperature records (mean, maximum and minimum) were collected using Tinytag monitors (Gemini Data Loggers, UK) attached to the trunk of each experimental tree (approx. 1.3 metres from base, on the northern side). Measurements were recorded hourly and averaged to give daily measurements for the whole study period. These daily temperatures per tree were then sorted into three periods based on oak physiology and acorn production. Budburst from 1 Mar to 15 May, acorn development from 16 May to 15 Sept, and post-acorn drop leaf senescence from 6 Oct to 31 Dec. As tree phenology can be affected by the accumulated heat experienced (Wilkinson et al. 2017), the mean daily temperature was used to calculate the warmth for each tree during each of these selected periods.

GENOME SEQUENCING Every tree had its full genome sequenced in January 2022 through a collaboration with the Darwin Tree of Life project. This identified the degree of relatedness among the trees measured using the KING method of relationship inference producing kinship coefficients. The estimated kinship coefficients can be interpreted as the following relationships: >0.354 = duplicate/monozygotic twins, 0.177 to 0.354 = 1st degree (full sibling or parent), 0.0884 to 0.177= 2nd degree (half-siblings), 0.0442 to 0.0884 = 3rd degree (first cousins), while negative values suggest the individuals are unrelated (Manichaikul et al. 2010). The paired coefficient scores were summed for each tree to give an average relatedness to the rest of the sample.

In total, 27 explanatory variables were recorded throughout the study period and applied to attempt to explain the six response variables; for a full list see Appendix table 2.1.

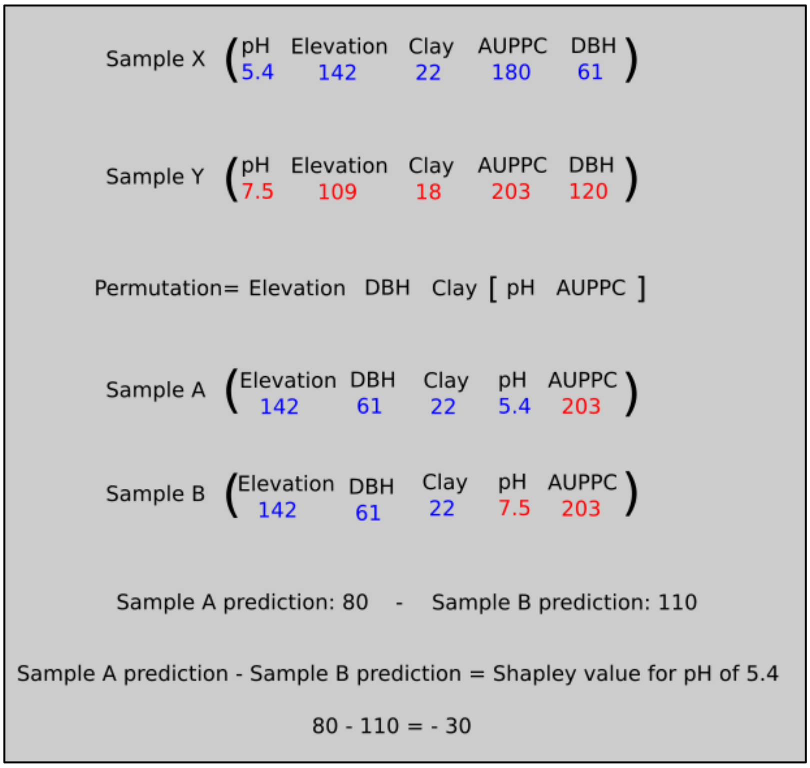
Descriptive statistics

The variables recorded were described using various functions in the package ggplot2 and descriptive statistics in R (R Core Team 2021). Additionally, each group of reproductive material and gall counts were given as percentages of the total crop to aid identification of producer groupings. The visual counts were also used to calculate coefficient of variation (CV) scores among years, giving an idea of the level of variation in acorn crop for each individual.

Statistical analysis

To detect if the explanatory variables had an effect on any stage of acorn production or pre-dispersal predation a two-stage statistical methodology was used: (1) variable selection using Random Forests and (2) variable interpretation using Generalized Linear Models. The package and function 'VSURF' was used first to deal with the high number of variables recorded (Genuer & Poggi, 2019). VSURF uses nested random forest models to select variables based on three criteria: (1) the ranking of variable importance scores generated from iterative bootstrapped samples of the data; (2) selection of variables to generate the most accurate model; and (3) selecting only those variables that lower the out of bag error (the prediction error on variable samples not selected during bootstrapping [James et al. 2021]), more than an artificial "noisy variable". For a more complete description of the VSURF methodology see Genuer and Poggi (2019) and chapter 3 of this thesis.

To aid explanation of the contribution and direction of influence for each variable to the VSURF models, the function 'Shapley' from the package *iml* (Strumbelj and Kononenko 2014) was used to calculate Shapley Values (Shapley 1953). Shapley Values are a model agnostic method of interpreting how explanatory variables affect the prediction of a black box model. The full process can be followed in the example below (Example 2.1) which explains how Shapley Values are generated for a specific explanatory variable value when predicting acorn production. First, a variable is selected to generate Shapley Values for. In this example pH was selected first, but the process will eventually select all the variables identified as important by the VSURF models. Two random samples are chosen from the dataset, called Sample X and Sample Y, and a random permutation (ordering) of the explanatory variables are generated. The first sample selected, Sample X, has a pH value of 5.4 and so we shall be calculating the influence a pH of 5.4 has on the model output. Two new samples are now created by mixing together Samples X and Sample Y. New sample A uses all the values from sample X including the pH column, it then fills the rest of the sample with remaining values from sample Y, in this example that only uses the AUPPC. Sample B is then created, which takes all the values from sample X, until just before pH, when it then selects the values from Sample Y, so in this case it takes pH and AUPPC from sample Y. Therefore, the only difference between sample A and Sample B is the pH value. Sample A and Sample B are then run through the VSURF model, Sample A gives a prediction of 80 acorns counted whereas Sample B predicts 110 acorns counted. The Shapley Value for a pH of 5.4 is simply the difference between these two predictions, in this case -30. This process is repeated hundreds of times to generate individual Shapley values for a full range of variable values. The Shapley values are then graphed to identify the effect of high or low values of each variable on the model output.



	pH	Elevation	Clay	AUPPC	DBH
Sample X	5.4	142	22	180	61
Sample Y	7.5	109	18	203	120

Permutation= Elevation DBH Clay [pH AUPPC]

	Elevation	DBH	Clay	pH	AUPPC
Sample A	142	61	22	5.4	203
Sample B	142	61	22	7.5	203

Sample A prediction: 80 - Sample B prediction: 110

Sample A prediction - Sample B prediction = Shapley value for pH of 5.4

80 - 110 = - 30

Example 2.1 Shapley value calculation for a pH of 5.4

To further aid interpretation of the explanatory variables, Generalised Linear Models were built using the variables selected from the VSURF models. The function ‘glm’ of the *stats* package (R Core Team) was used to construct each model, all with the gamma distribution and log link. Model assumptions were visually checked via the function ‘glm.diag.plots’ of the package *boot* (Canty and Ripley, 2024; Davison and Hinkley, 1997). Significance testing was performed with the ‘Anova’ function in the *car* package (Fox and Weisberg, 2019). The strong powdery mildew damage recorded in 2021 was analysed separately. The leaf abscission measurements, a proxy for powdery mildew damage, were used as the independent variable in a series of linear regression models for the dependant variables immature acorns, enlarged cups, flowers, and galls for 2021 (no mature acorns were counted in 2021).

To examine if there was an effect of tree microclimate on acorn production, using the ‘aov’ function of the package *stats*, the microclimate data was used to model each of the five acorn production classes (mature acorns, immature acorns, enlarged cups, flowers and galls), year, assigned oak phenological period, and the interactions of producer class × oak physiological period and of producer class × year. Models were built separately for maximum, minimum, mean and accumulated temperatures (i.e. total of daily mean temperature values over the phenological period of interest).

2.3 Results

Visual surveys

Wytham Woods experienced a strong mast event in 2020, followed by a complete crop failure in 2021 where not a single mature acorn was counted. The subsequent two years, 2022 and 2023, produced middling numbers of mature acorns (Figs 2.1, 2.2).

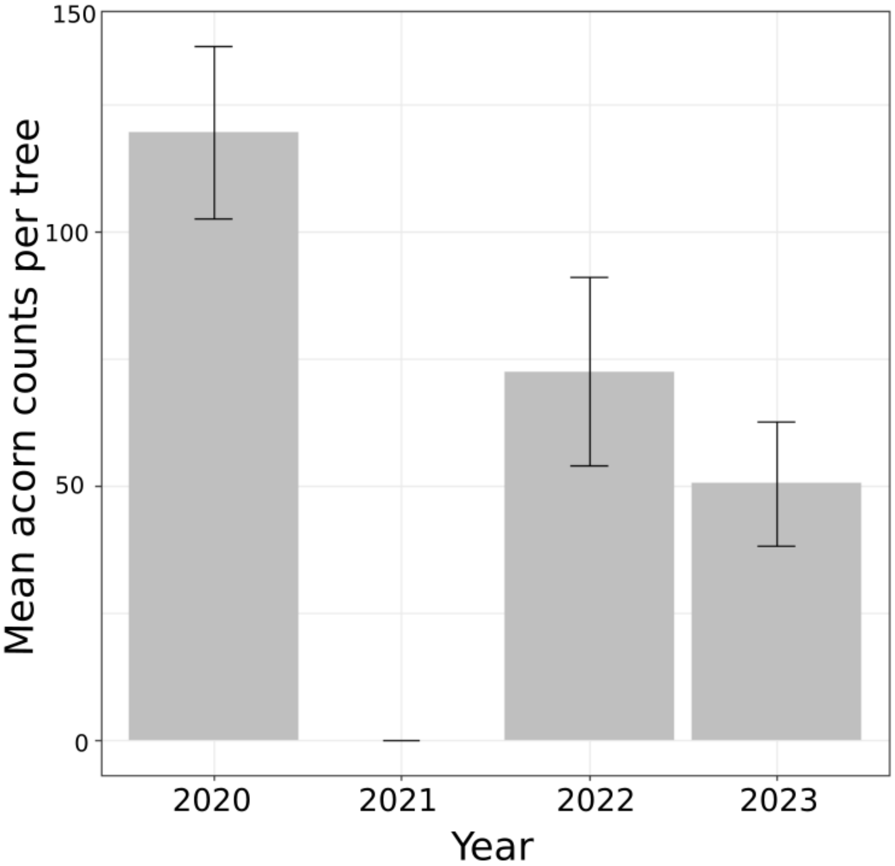


Figure 2.1 The variation in annual mature acorn production (mean of 39 oak trees ± standard error) at Wytham Woods, Oxford. Counts were made via the visual survey method (see Koenig et al., 1994). In 2021 no mature acorns were observed at Wytham Woods.

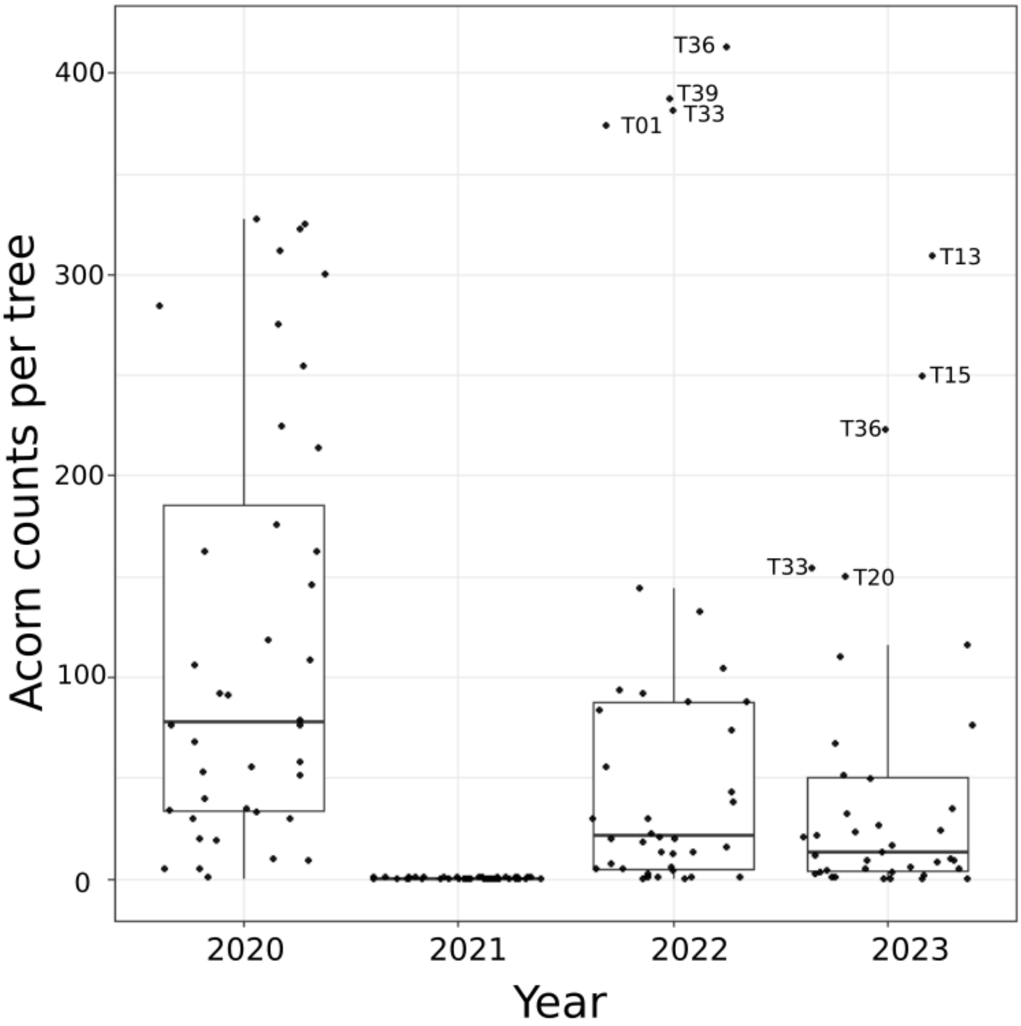


Figure 2.2 The variation in mature acorn production among 39 oak trees each year at Wytham Woods, Oxford, counted from visual survey (see Koenig et al., 1994). The vertical boxes and bars represent the minimum, 1st quartile, median, 3rd quartile, and maximum values for each year. Individual trees are represented by black dots. Outliers were detected in 2022 and 2023 and are labelled with their tree ID code.

The 2020 mast year saw large individual variation in acorn output among the 39 trees (Fig. 2.2): the minimum acorn count was 5 acorns per tree and the highest 327 (Table 2.1), and there were no outlier individual trees in 2020 (Fig. 2.2).

Table 2.1 Visual counts of acorns on 39 oak trees at Wytham Woods, Oxford, showing the number of acorns counted each year, and the percentage that each tree contributed to the total acorn crop that year. Counts are colour coded to identify super-, average- and poor-producing individuals each year and in total. Contributing >5% = green, between 0.99% and 5.0% = yellow, <1% = red. Trees italic, emboldened = acorns 2022> 2020; italic, underlined 2023>2020.

Tree	2020	%	2021	%	2022	%	2023	%	Total	%	COV
36	300	6.28%	0	na	413	14.60%	223	12.12%	936	9.91%	0.75
39	327	6.84%	0	na	387	13.68%	21	1.14%	735	7.78%	1.10
13	312	6.53%	0	na	87	3.08%	309	16.79%	708	7.49%	0.89
1	254	5.31%	0	na	373	13.19%	50	2.72%	677	7.17%	1.03
15	284	5.94%	0	na	132	4.67%	249	13.53%	665	7.04%	0.77
33	55	1.15%	0	na	381	13.47%	154	8.37%	590	6.24%	1.14
19	322	6.74%	0	na	104	3.68%	67	3.64%	493	5.22%	1.13
30	275	5.75%	0	na	144	5.09%	4	0.22%	423	4.48%	1.24
28	325	6.80%	0	na	43	1.52%	10	0.54%	378	4.00%	1.64
11	214	4.48%	0	na	88	3.11%	21	1.14%	323	3.42%	1.19
41	176	3.68%	0	na	38	1.34%	51	2.77%	265	2.80%	1.15
24	224	4.69%	0	na	29	1.03%	0	0.00%	253	2.68%	1.71
20	51	1.07%	0	na	30	1.06%	150	8.15%	231	2.44%	1.12
23	108	2.26%	0	na	12	0.42%	110	5.98%	230	2.43%	1.04
8	92	1.92%	0	na	13	0.46%	116	6.30%	221	2.34%	1.04
12	118	2.47%	0	na	94	3.32%	9	0.49%	221	2.34%	1.08
14	162	3.39%	0	na	55	1.94%	4	0.22%	221	2.34%	1.37
3	163	3.41%	0	na	6	0.21%	16	0.87%	185	1.96%	1.69
4	146	3.05%	0	na	19	0.67%	13	0.71%	178	1.88%	1.53
34	79	1.65%	0	na	74	2.62%	23	1.25%	176	1.86%	0.88
2	76	1.59%	0	na	7	0.25%	76	4.13%	159	1.68%	1.06
22	91	1.90%	0	na	21	0.74%	26	1.41%	138	1.46%	1.14
35	29	0.61%	0	na	92	3.25%	11	0.60%	132	1.40%	1.25
18	106	2.22%	0	na	2	0.07%	9	0.49%	117	1.24%	1.75
31	33	0.69%	0	na	83	2.93%	1	0.05%	117	1.24%	1.33
29	76	1.59%	0	na	22	0.78%	0	0.00%	98	1.04%	1.46
26	58	1.21%	0	na	4	0.14%	35	1.90%	97	1.03%	1.13
25	35	0.73%	0	na	18	0.64%	24	1.30%	77	0.81%	0.76
16	68	1.42%	0	na	4	0.14%	2	0.11%	74	0.78%	1.79
5	53	1.11%	0	na	0	0.00%	8	0.43%	61	0.65%	1.67
6	39	0.82%	0	na	13	0.46%	3	0.16%	55	0.58%	1.29
32	29	0.61%	0	na	19	0.67%	5	0.27%	53	0.56%	1.00
37	4	0.08%	0	na	1	0.04%	32	1.74%	37	0.39%	1.65
38	20	0.42%	0	na	15	0.53%	0	0.00%	35	0.37%	1.18
7	34	0.71%	0	na	0	0.00%	0	0.00%	34	0.36%	2.00
21	19	0.40%	0	na	0	0.00%	0	0.00%	19	0.20%	2.00
9	9	0.19%	0	na	4	0.14%	0	0.00%	13	0.14%	1.31
17	9	0.19%	0	na	1	0.04%	3	0.16%	13	0.14%	1.24
27	5	0.10%	0	na	0	0.00%	5	0.27%	10	0.11%	1.15
Tot.	4780	100%	0	na	2828	100%	1840	100%	9448	100%	Avg: 1.27

Moreover, every individual tree produced acorns in 2020 (judged by the visual survey). In contrast, no acorns were counted on any tree in 2021 by visual survey (Figs 2.1, 2.2), nor were mature acorns counted in litter traps either that year (Fig. 2.3). In 2022 acorns were counted on the majority of individual trees, but four trees had no acorns in the visual survey (Table 2.1; Trees 27, 21, 7, and 5 [in order of total production over the four years]). At the other extreme, four trees were outliers in 2022 producing the highest acorn counts of the entire study period (Fig. 2.2; Table 2.1; Trees 1, 33, 39, 36). In 2023, six trees failed to produce a single acorn (Table 2.1; Trees 9, 21, 7, 38, 29, and 24), and five high-producing outliers were found (Fig. 2.2; Trees 20, 33, 36, 15, and 13). Trees 36 and 33 were outliers due to their high acorn production in both 2022 and 2023, but of these two trees in 2020 only Tree 36 was identified as one of the highest producers; Tree 33 produced a mediocre to low number of acorns that year (Table 2.1). Overall, Tree 36 produced the greatest number of acorns over the four years (936, 201 more than the second-ranked tree) and Tree 27 the fewest (10).

Based on the visual counts, seven trees produced 50.9% of the acorns counted throughout the study (Table 2.1; Fig. 2.4; Trees 36, 39, 13, 01, 15, 33, and 19). The next 20 trees contributed just over 44% of the total crop, while the remaining 5.1% of acorns were produced by the 12 least-productive trees. Within the super-producing group, three trees (Trees 36, 13, and 15) consistently produced more than the average number of acorns each year, while seventeen trees consistently produced less than the average each year (Figure 2.5). The observation overall from the 39 trees that 2020 was a mast year and 2021 was a very lean year was not contradicted by the observations for any single tree: all the trees produced acorns in 2020 and all trees no acorns in 2021 (Table 2.1). However, some trees produced more acorns in 2022 than in 2020 (Trees 39, 1, 35, 31; Table 2.1) and a few others more in 2023 than in 2020 (Trees 20, 23, 8, 37; Table 2.1). One tree produced more acorns in each of 2022 and 2023 than in 2020 (Tree 33, Table 2.1). To compare the masting behaviour of individual trees, the coefficient of variation (CV) was calculated. This showed the population to have an average CV of 1.27 (Table 2.1). When comparing the Coefficient of Variation between producer groupings, the high producing classes had the lowest CV (0.95 ± 0.07), then the mid producer group (1.27 ± 0.06), followed by the poor producing group with the highest CV (1.42 ±0.11). A one way anova found these differences to be statistically significant $F(2,36) = 5.1$, $P < 0.05$). A Tukey post hoc test found the high producer's CV to be significantly less than the low producer's CV ($P<0.01$), with insignificant differences between the medium and poor producers ($P=0.46$) and the high and medium producers ($P=0.05$).

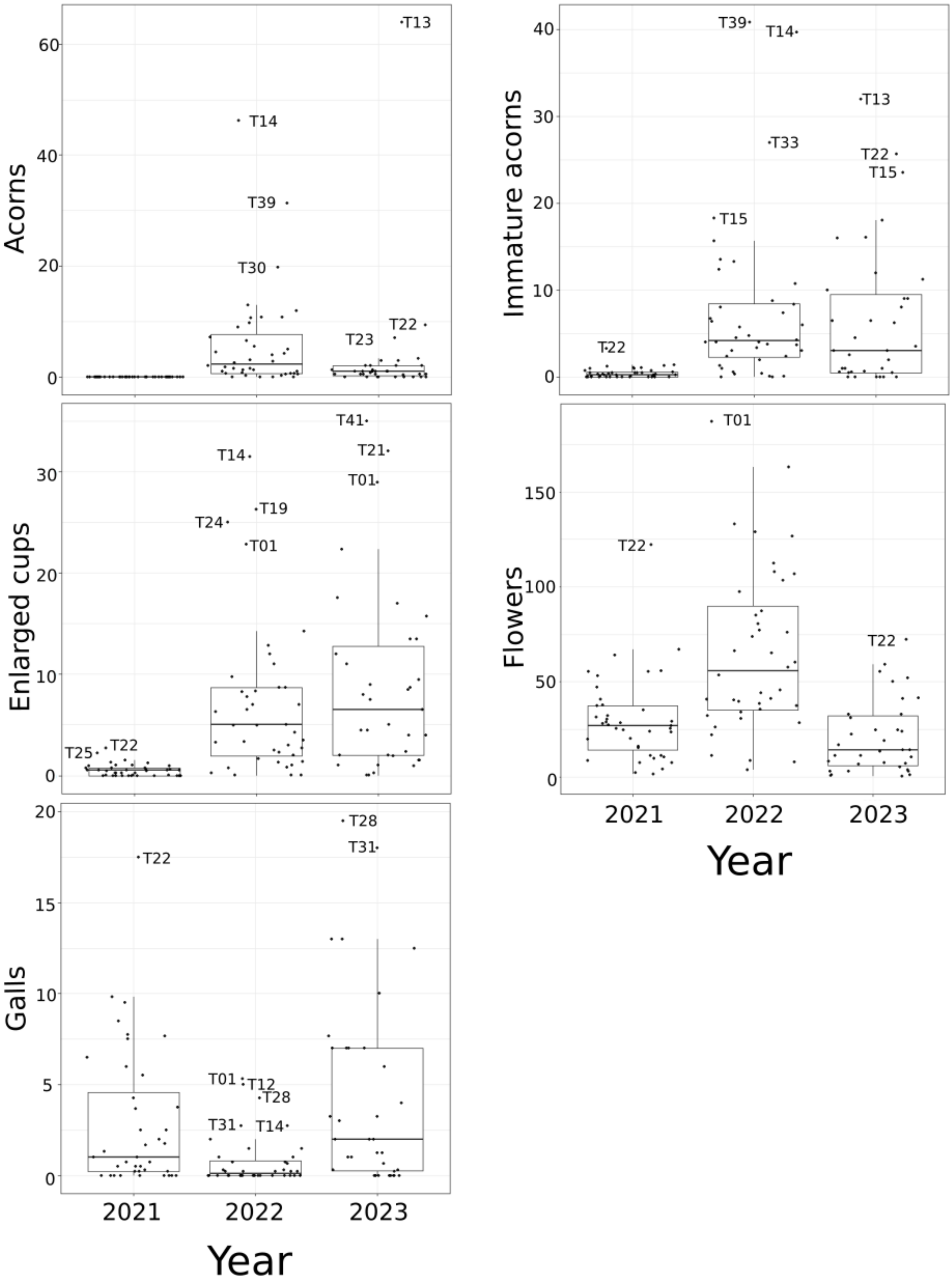


Figure 2.3 Oak reproductive material collected from litter traps underneath 40 experimental trees at Wytham Woods, Oxford, from 2021 to 2023. Each black dot represents a single tree's average for that year. Outliers were detected in each year and these trees ID code are shown.

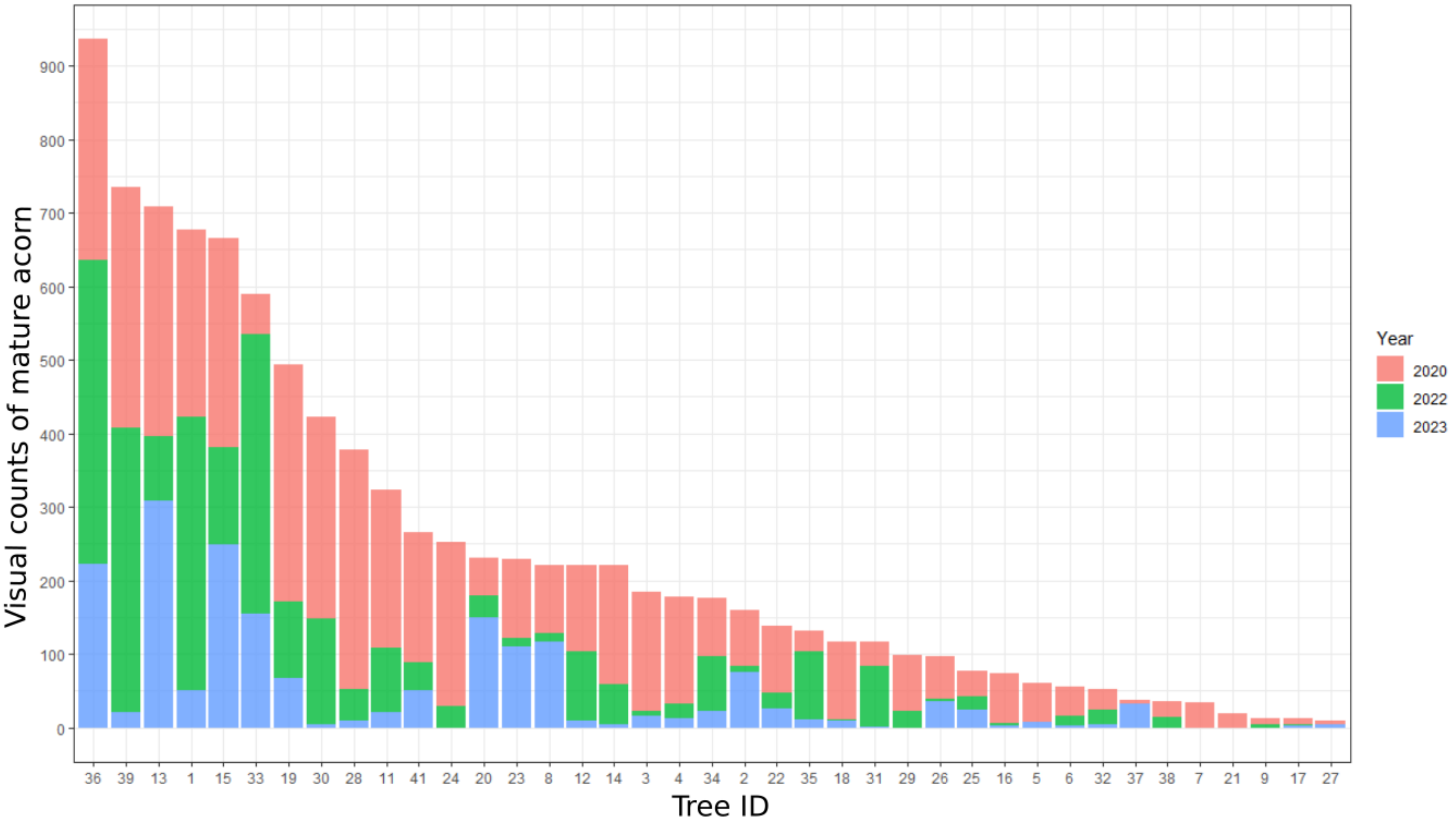


Figure 2.4 Total visual counts of acorns from 39 oak trees at Wytham, Woods, Oxford, over the years 2020-23 showing the contribution each year (the bars are colour coded to identify each year). There were no acorns collected in 2021 due to a failed crop.

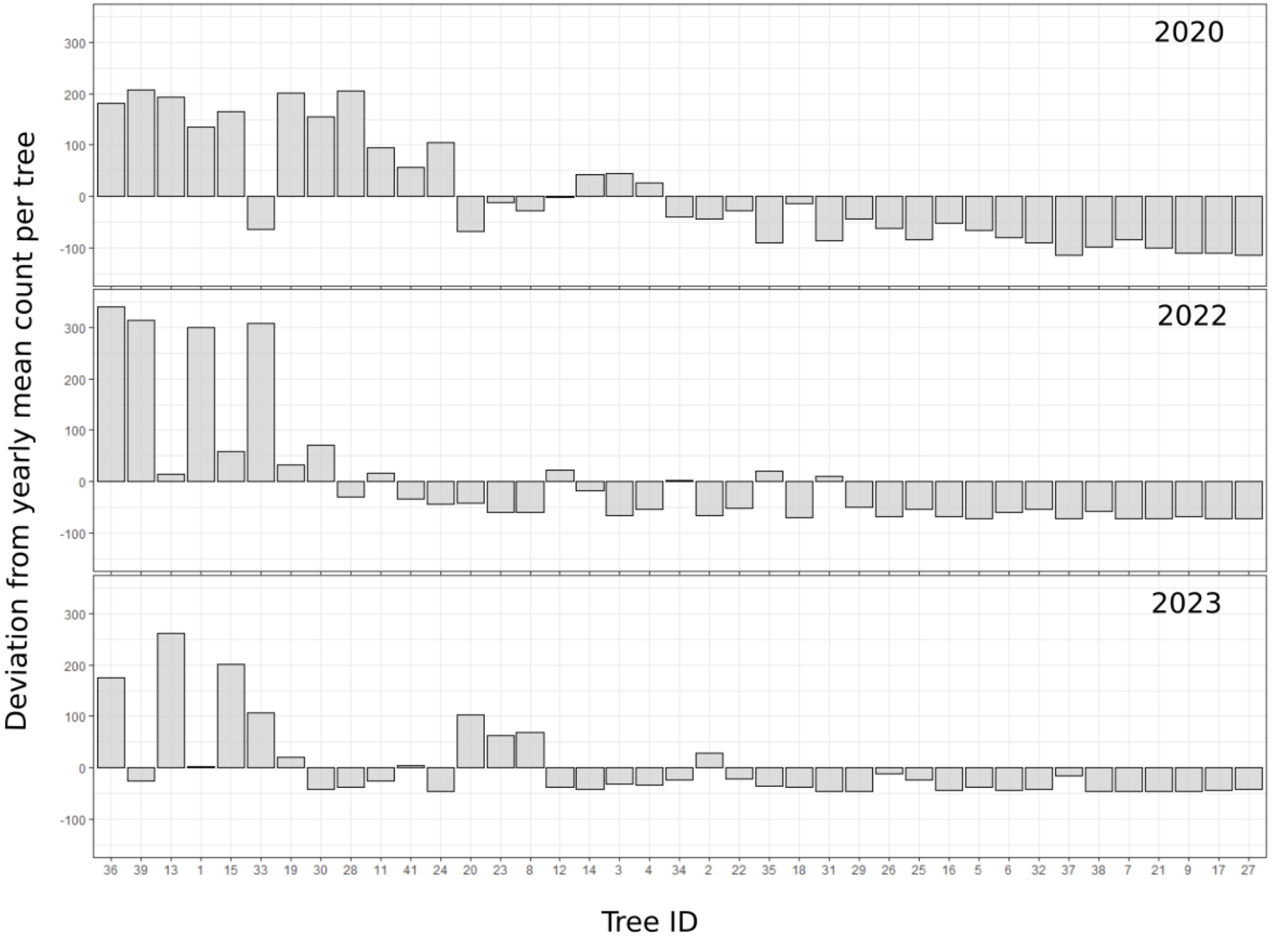


Figure 2.5 The total deviation in acorn counts for individual trees from the yearly mean acorn count for each of 39 oaks at Wytham Woods, Oxford. The x-axis is ordered by total acorn counts (Table 2.1). Year of survey is recorded on the top right of each graph. There were no acorns collected during 2021 due to a failed crop.

Litter traps

Mature acorns counted within the litter traps produced a similar pattern to the visual counts: 2021 was a failed year with no mature acorns found within the traps; 2022 and 2023 were better years with some outlier individuals producing many more acorns than the rest of the population (Fig. 2.3). Comparing the visual count and litter trap results, Trees 39 and 13 were high-producing outliers in both survey methods for 2022 and 2023, respectively. The numbers of mature acorns counted from the visual counting method and the litter traps were strongly correlated ($\tau = 0.72$, $z = 9.38$, $P < 0.0001$, Fig 2.6.), although within each year the correlation between survey methods was less strong in 2023 ($\tau = 0.43$, $z = 3.34$, $P < 0.0001$) than 2022 ($\tau = 0.70$, $z = 5.72$, $P < 0.0001$). Due to several traps becoming damaged, and suspected small mammal herbivory, the visual counts were judged to provide the best estimate of mature acorn production for individual trees at Wytham Woods, and were used to define the acorn producer classes.

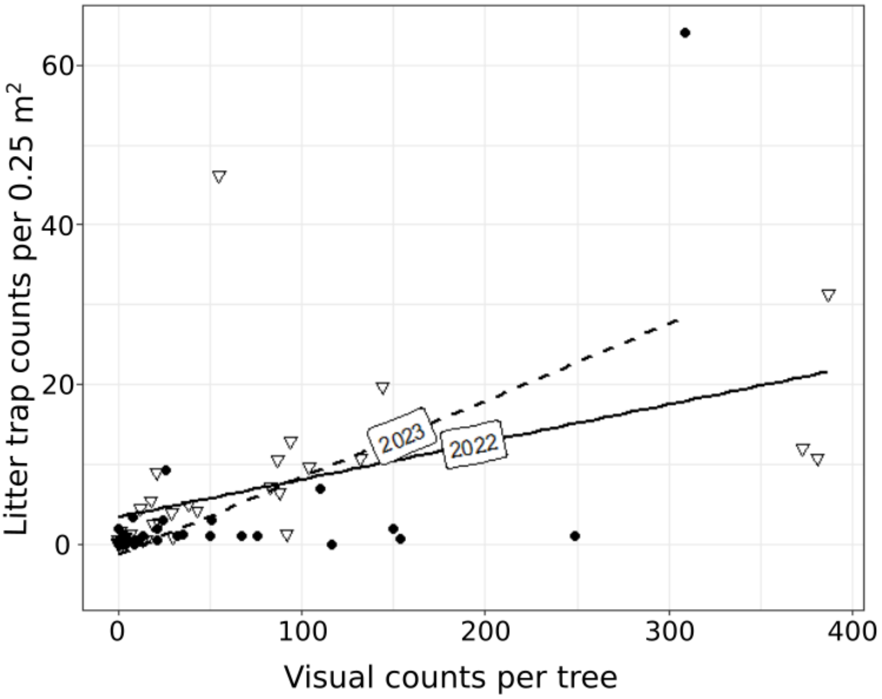


Figure 2.6 Correlation of acorn counts from visual survey and litter trap collection methods at Wytham Woods, Oxford, separated by year. Acorns counted in 2022 are shown with empty triangles and solid line and the correlation was significant (Kendall's rank correlation, $\tau = 0.70$, $z = 5.72$, $P < 0.0001$). The acorns counted in 2023 are shown by black dots and dashed line and the correlation was significant (Kendall's rank correlation, $\tau = 0.43$, $z = 3.34$, $P < 0.0001$). Litter traps were set up from 2021 onwards, but no acorns were counted via either method in 2021 due to a failed crop. Traps for trees 3, 6, 32, 34, and 36 in one or more years were knocked down by adverse weather or wildlife and so were removed from this analysis.

Whilst 2021 produced no mature acorns, the litter traps did capture some of the other reproductive material. Immature acorns and enlarged cups were present but in very low numbers in 2021, whereas considerably more flowers and galls were found (Fig. 2.3). In 2022, immature acorns and flowers produced the highest median counts of the study (i.e. more than 2021 or 2023), enlarged cups the second highest, and galls the lowest (Fig. 2.3). The highest counts of enlarged cups and galls were observed in 2023 (Fig 2.3). Several trees were consistent outliers. Tree 22 produced high numbers of flowers and immature acorns in 2021 and in 2023, and high numbers of enlarged cups and of galls in 2021 (Fig. 2.3). All of the categories of litter trap data showed a log normal, or gamma distribution, with a long tail of right skewed data, and a high number of low or zero counts of reproductive material (Fig. 2.7), as also did the visual counts of mature acorns. The decline in flower count data was less steep than for the other categories with its distribution showing a less severe right skew (Fig 2.7). The flower count data had a lesser occurrence of zeros and showed less variability, in particular between 2021 and other years (Fig 2.3).

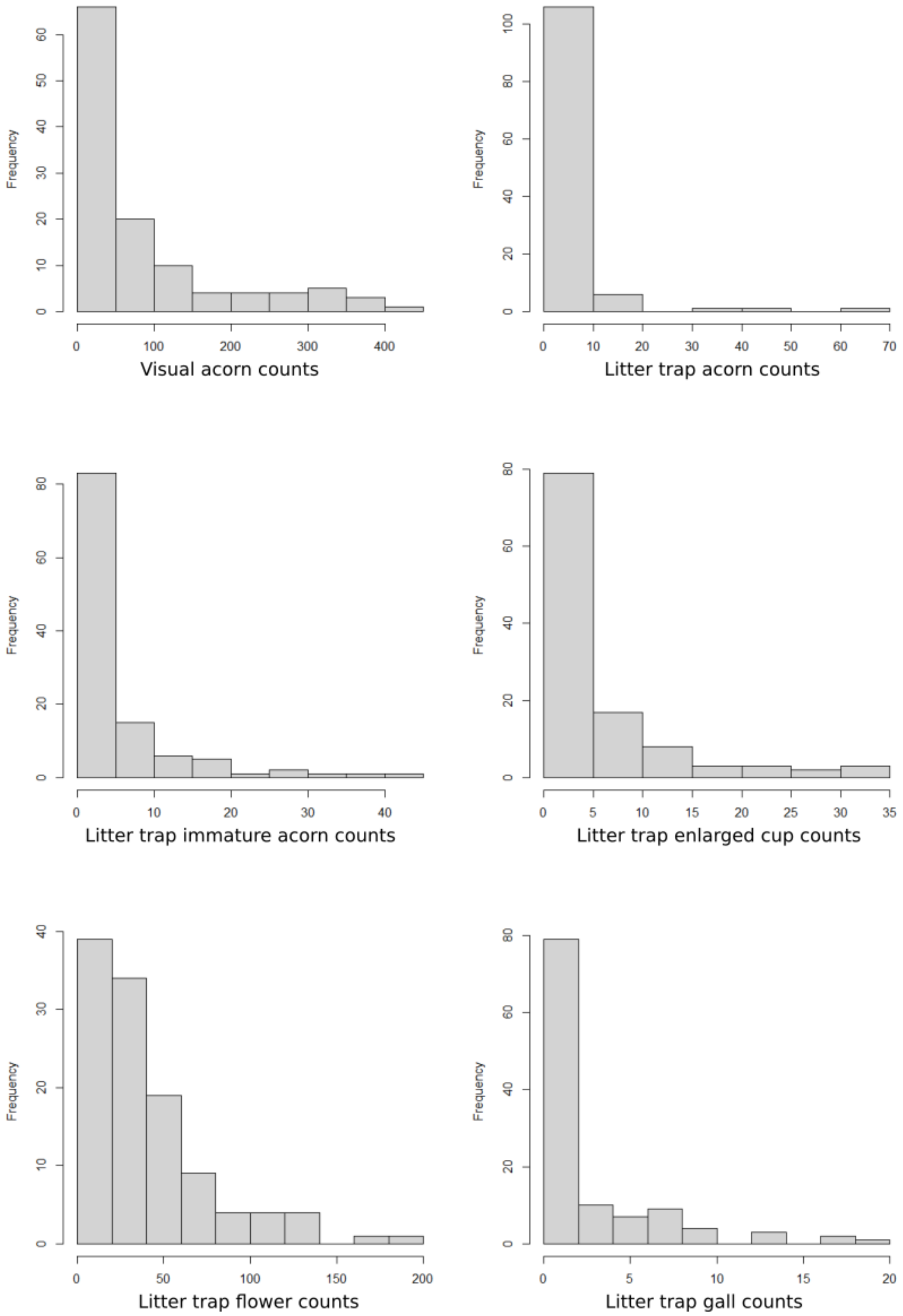


Figure 2.7 Histograms of oak reproductive material and pre-dispersal predation of 39 oaks trees at Wytham Woods, Oxford, sums of total yearly counts from 2021 to 2023 for litter trap material and 2020 to 2023 for Visual acorn counts. Acorns were counted by visual survey (top left) and from litter traps (top right)

Similar to the mature acorn counts, 50% of the immature acorns counted were produced by seven high-producing individual trees (Appendix table 2.2), with four of those individuals being super producers of both mature and immature acorns (Table 2.1 cf. Appendix table 2. 2). The pattern weakens in comparison with earlier stages of acorn development, however: the highest nine producers of enlarged cups contributed to 50% of the total number counted, but with only two also being acorn super producers (Appendix table 2.3); and twelve individuals contributed to 50% of the flower counts with only one (Tree 1) also being an acorn super producer (Appendix table 2.4). Seven trees generated the majority of the galls counted (Trees 31, 22, 1, 28, 15, 12, and 7 produced 53.1% of the galls; Appendix 5), but these heavily-attacked trees were spread quite evenly throughout the high-, medium- and low-acorn producers' groups (Appendix table 2.5).

Weather

Spring temperatures at Wytham Woods in 2021 were colder than normal, with the last ten days in April and the first ten days in May being uncharacteristically cold, with high levels of precipitation (Figs 2.8 and 2.9). There was a heatwave in summer 2022 with extremely warm temperatures in July and August, followed by a much colder December (Fig. 2.8). Examining the microclimatic conditions of individual trees, all were within ±0.5°C of the mean tree population temperature each year (Fig. 2.10). The two extreme trees in this regard were Tree 11 (average acorn production, Table 1), -0.49°C colder maximum, -0.44°C mean, and -0.4°C minimum temperatures and Tree 27 (the poorest acorn production, Table 2.1), which was +0.49°C warmer for the maximum, minimum and mean temperatures (Fig. 2.5).

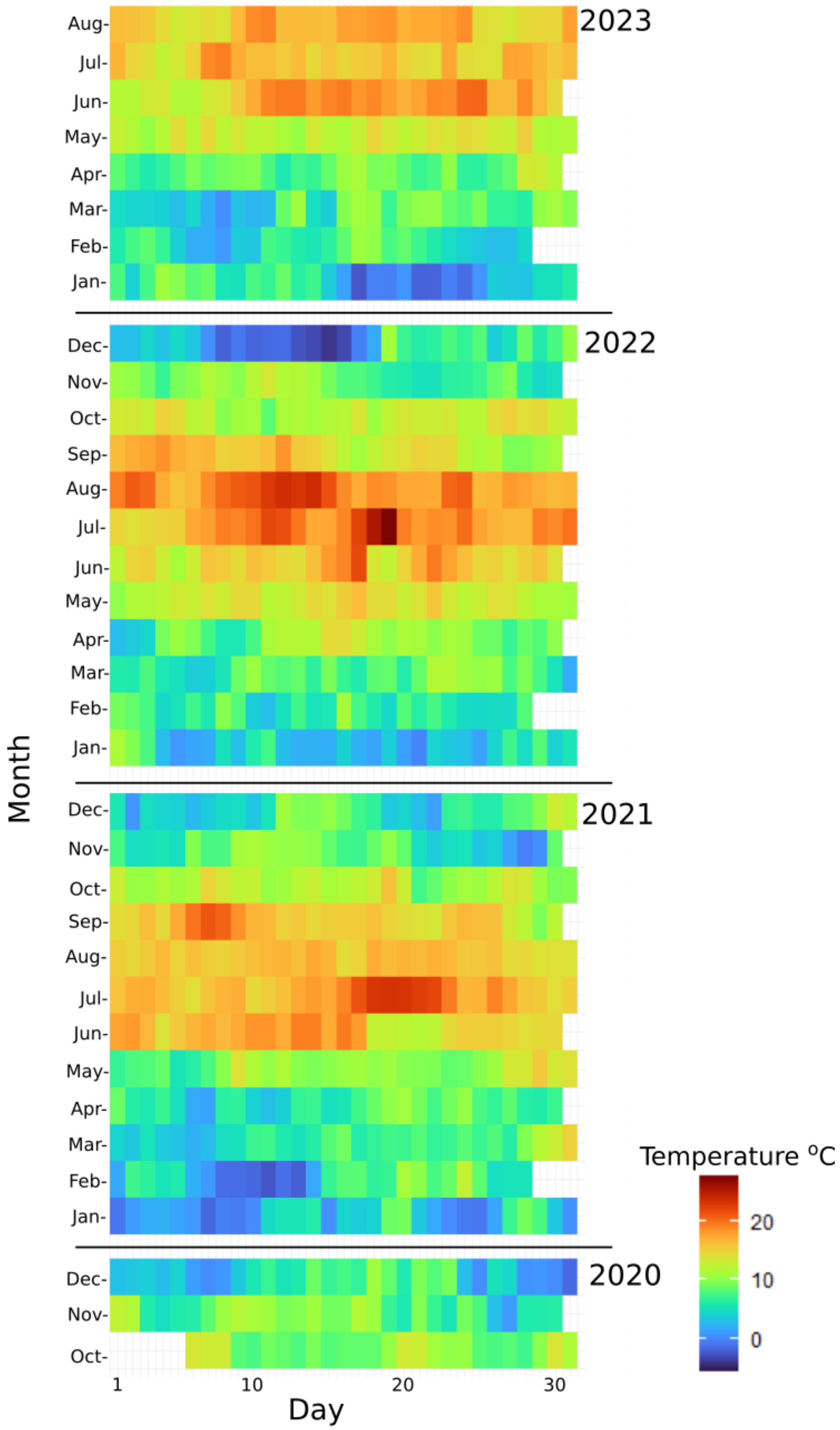


Figure 2.8 Heatmap of daily mean temperature (°C) at Wytham Woods, Oxford, 2020 to 2023. Daily mean temperatures were logged from each experimental tree and combined to provide mean values. The scale is from -5.5°C to + 28°C.

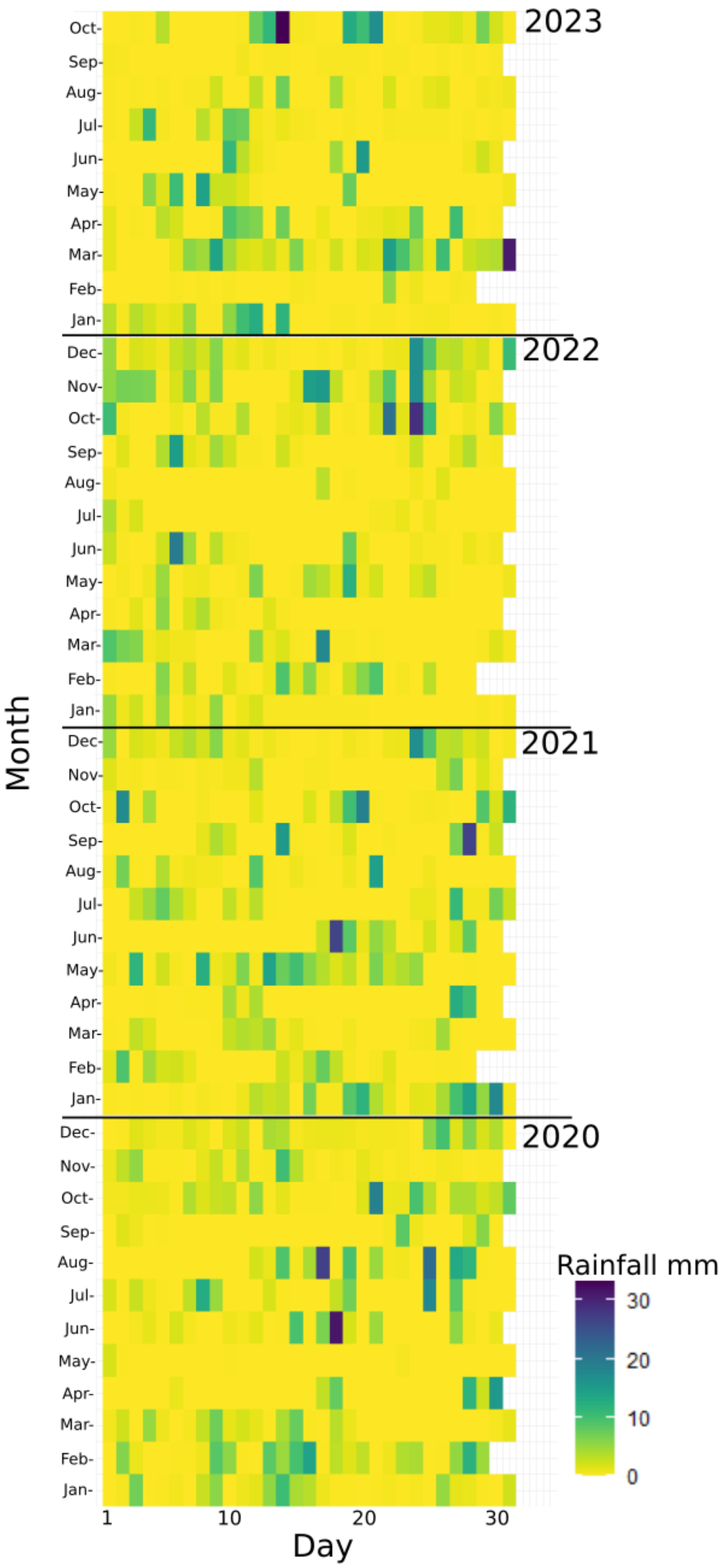


Figure 2.9 Heat maps of daily total precipitation (mm) at Wytham Woods, Oxford, from 2020 to 2023. Data is from the UK Environmental Change Network (ECN) site at Wytham. Data from Stefanie M. Schäfer and Denise Palle

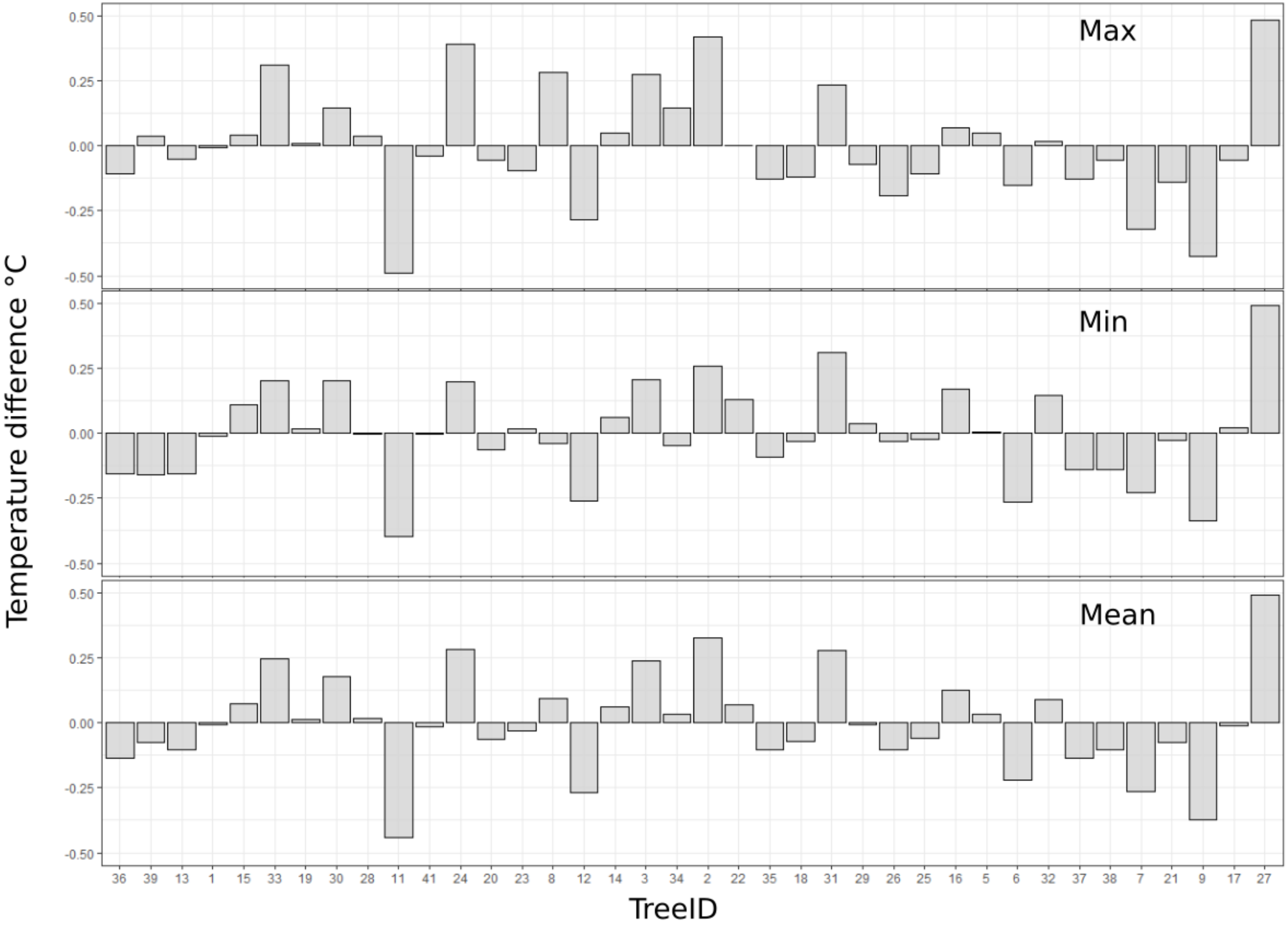


Figure 2.10 Difference of maximum, minimum and mean temperature for 39 individual oak trees at Wytham Woods, Oxford from means of the whole sample. The x-axis is ordered from high to low numbers of acorns produced from 2020-2023 [Figure 2.4].

Genomic sequencing

Almost all of the 38 trees with their full genomes sequenced were 2nd degree related, meaning they were likely to be half siblings (Table 2.2). Of the four trees that were not 2nd degree related, Tree 7 was found to be highly unrelated to all the other trees studied, Trees 11 and 35 were likely to be 1st degree related and so full siblings, and Tree 25 was a 1st degree relation to all the other trees sampled except Tree 7. Based on DBH and height measurements, as proxies for tree age, Tree 25 is unlikely to be a parent of the rest of the population, but it may be that Tree 25 was the product of all these trees' (except Tree 7) shared parent tree reproducing with another half sibling, generating a closer relationship to the rest of the population. High, medium, and low producing individual trees were found throughout the 2nd degree related cohort (Table 2.1; Table 2.2). Trees 7 and 25 were poor acorn producers and trees 11 and 35 average acorn producers.

Table 2.2 King scores from a Kinship Inference showing the degree of relatedness among 38 oak trees at Wytham Woods, Oxford. The pair-wise kinship coefficient estimates (rounded to the nearest 2 decimal places) can be interpreted as follows: >0.354 = duplicate or monozygotic twin [shaded grey], 0.177 to 0.354 = 1st degree [full sibling or parent, highlighted green], 0.0884 to 0.177= 2nd degree [half-siblings, highlighted yellow], 0.0442 to 0.0884 3rd degree [first cousins] and negative values suggest the individuals are unrelated [highlighted red] (Manichaikul et al. 2010). Trees 10 and 40 were removed from the study due to damage and Tree 33 was not included for genetic analysis due to a sampling error.

Tree	1	2	3	4	5	6	7	8	9	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	34	35	36	37	38	39	41
1		0.10	0.10	0.10	0.09	0.10	-0.23	0.12	0.11	0.10	0.11	0.10	0.10	0.10	0.10	0.10	0.12	0.10	0.10	0.10	0.10	0.10	0.10	0.20	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.11	0.10	0.11	0.10	0.11	0.10
2	0.10		0.10	0.10	0.09	0.09	-0.23	0.13	0.10	0.11	0.10	0.10	0.10	0.11	0.10	0.10	0.12	0.10	0.10	0.10	0.10	0.09	0.10	0.20	0.10	0.10	0.10	0.10	0.09	0.10	0.10	0.10	0.11	0.10	0.10	0.10	0.10	0.09
3	0.10	0.10		0.10	0.10	0.10	-0.22	0.12	0.10	0.10	0.11	0.10	0.10	0.10	0.10	0.10	0.12	0.10	0.09	0.10	0.10	0.10	0.10	0.20	0.10	0.10	0.10	0.10	0.10	0.10	0.11	0.10	0.11	0.10	0.11	0.11	0.10	0.09
4	0.10	0.10	0.10		0.16	0.11	-0.22	0.13	0.11	0.11	0.11	0.10	0.11	0.11	0.10	0.10	0.13	0.11	0.10	0.10	0.11	0.10	0.10	0.21	0.11	0.11	0.11	0.11	0.10	0.11	0.11	0.10	0.11	0.10	0.11	0.11	0.11	0.10
5	0.09	0.09	0.10	0.16		0.10	-0.23	0.12	0.11	0.10	0.10	0.09	0.10	0.10	0.10	0.10	0.12	0.10	0.10	0.10	0.10	0.10	0.10	0.20	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.11	0.09	0.10	0.10	0.10	0.10
6	0.10	0.09	0.10	0.11	0.10		-0.22	0.13	0.11	0.10	0.12	0.11	0.11	0.11	0.10	0.10	0.12	0.10	0.10	0.10	0.10	0.10	0.10	0.21	0.10	0.11	0.10	0.11	0.10	0.10	0.10	0.11	0.10	0.10	0.11	0.10	0.11	0.09
7	-0.23	-0.23	-0.22	-0.22	-0.23	-0.22		-0.18	-0.21	-0.21	-0.21	-0.22	-0.22	-0.21	-0.21	-0.22	-0.19	-0.22	-0.22	-0.22	-0.22	-0.23	-0.21	-0.05	-0.22	-0.22	-0.21	-0.22	-0.21	-0.22	-0.22	-0.21	-0.21	-0.22	-0.20	-0.21	-0.21	-0.23
8	0.12	0.13	0.12	0.13	0.12	0.13	-0.18		0.14	0.13	0.13	0.13	0.13	0.13	0.13	0.15	0.15	0.13	0.13	0.12	0.13	0.12	0.13	0.23	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.12
9	0.11	0.10	0.10	0.11	0.11	0.11	-0.21	0.14		0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.13	0.10	0.11	0.11	0.11	0.10	0.11	0.21	0.11	0.11	0.11	0.12	0.11	0.11	0.11	0.11	0.12	0.11	0.12	0.11	0.11	0.10
11	0.10	0.11	0.10	0.11	0.10	0.10	-0.21	0.13	0.11		0.11	0.11	0.11	0.11	0.11	0.11	0.12	0.11	0.10	0.11	0.11	0.10	0.10	0.21	0.10	0.11	0.11	0.11	0.10	0.11	0.10	0.11	0.18	0.11	0.11	0.11	0.10	0.10
12	0.11	0.10	0.11	0.11	0.10	0.12	-0.21	0.13	0.11	0.11		0.11	0.11	0.11	0.11	0.11	0.13	0.11	0.11	0.11	0.11	0.11	0.11	0.21	0.11	0.11	0.11	0.10	0.11	0.10	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.10
13	0.10	0.10	0.10	0.10	0.09	0.11	-0.22	0.13	0.11	0.11	0.11		0.11	0.11	0.11	0.10	0.12	0.10	0.10	0.10	0.10	0.10	0.11	0.21	0.10	0.11	0.11	0.11	0.11	0.10	0.10	0.11	0.11	0.10	0.11	0.11	0.11	0.10
14	0.10	0.10	0.10	0.11	0.10	0.11	-0.22	0.13	0.11	0.11	0.11	0.11		0.10	0.10	0.11	0.12	0.12	0.11	0.10	0.11	0.10	0.11	0.21	0.10	0.11	0.11	0.10	0.10	0.10	0.10	0.11	0.11	0.10	0.11	0.10	0.10	0.10
15	0.10	0.11	0.10	0.11	0.10	0.11	-0.21	0.13	0.11	0.11	0.11	0.11	0.10		0.10	0.11	0.13	0.11	0.11	0.10	0.11	0.10	0.11	0.21	0.10	0.12	0.11	0.11	0.11	0.10	0.11	0.11	0.12	0.11	0.12	0.11	0.11	0.10
16	0.10	0.10	0.10	0.10	0.10	0.10	-0.21	0.13	0.11	0.11	0.11	0.11	0.10	0.10		0.12	0.13	0.10	0.11	0.11	0.11	0.10	0.11	0.20	0.10	0.12	0.11	0.11	0.10	0.10	0.10	0.11	0.11	0.11	0.11	0.11	0.11	0.10
17	0.10	0.10	0.10	0.10	0.10	0.10	-0.22	0.15	0.11	0.11	0.11	0.10	0.11	0.11	0.12		0.13	0.11	0.10	0.10	0.11	0.10	0.11	0.21	0.11	0.10	0.11	0.11	0.11	0.10	0.10	0.11	0.11	0.11	0.11	0.11	0.10	0.10
18	0.12	0.12	0.12	0.13	0.12	0.12	-0.19	0.15	0.13	0.12	0.13	0.12	0.12	0.13	0.13	0.13		0.12	0.12	0.12	0.12	0.12	0.12	0.22	0.14	0.13	0.13	0.13	0.12	0.13	0.12	0.12	0.13	0.12	0.13	0.12	0.13	0.12
19	0.10	0.10	0.10	0.11	0.10	0.10	-0.22	0.13	0.10	0.11	0.11	0.10	0.12	0.11	0.10	0.11	0.12		0.10	0.10	0.11	0.10	0.11	0.21	0.10	0.11	0.11	0.11	0.10	0.10	0.10	0.10	0.12	0.11	0.11	0.11	0.11	0.10
20	0.10	0.10	0.09	0.10	0.10	0.10	-0.22	0.13	0.11	0.10	0.11	0.10	0.11	0.11	0.11	0.10	0.12	0.10		0.10	0.10	0.10	0.10	0.21	0.11	0.10	0.11	0.10	0.11	0.10	0.10	0.11	0.10	0.10	0.11	0.10	0.10	0.10
21	0.10	0.10	0.10	0.10	0.10	0.10	-0.22	0.12	0.11	0.11	0.11	0.10	0.10	0.10	0.11	0.10	0.12	0.10	0.10		0.11	0.09	0.12	0.20	0.10	0.11	0.11	0.10	0.10	0.10	0.10	0.10	0.11	0.10	0.11	0.10	0.10	0.10
22	0.10	0.10	0.10	0.11	0.10	0.10	-0.22	0.13	0.11	0.11	0.11	0.10	0.11	0.11	0.11	0.11	0.12	0.11	0.10	0.11		0.10	0.11	0.20	0.10	0.11	0.11	0.11	0.10	0.10	0.11	0.11	0.11	0.10	0.11	0.11	0.10	0.10
23	0.10	0.09	0.10	0.10	0.10	0.10	-0.23	0.12	0.10	0.10	0.11	0.10	0.10	0.10	0.10	0.10	0.12	0.10	0.10	0.09	0.10		0.11	0.20	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.11	0.10	0.10	0.11	0.10	0.10	0.10
24	0.10	0.10	0.10	0.10	0.10	0.10	-0.21	0.13	0.11	0.10	0.11	0.11	0.11	0.11	0.11	0.11	0.12	0.11	0.10	0.12	0.11	0.11		0.21	0.11	0.12	0.10	0.10	0.11	0.11	0.10	0.11	0.11	0.10	0.12	0.11	0.11	0.11
25	0.20	0.20	0.20	0.21	0.20	0.21	-0.05	0.23	0.21	0.21	0.21	0.21	0.21	0.21	0.20	0.21	0.22	0.21	0.21	0.20	0.20	0.20	0.21		0.21	0.21	0.21	0.21	0.20	0.20	0.20	0.21	0.21	0.20	0.21	0.21	0.20	0.20
26	0.10	0.10	0.10	0.11	0.10	0.10	-0.22	0.13	0.11	0.10	0.11	0.10	0.10	0.10	0.10	0.11	0.14	0.10	0.11	0.10	0.10	0.10	0.11	0.21		0.10	0.10	0.10	0.10	0.11	0.10	0.10	0.11	0.11	0.11	0.10	0.10	0.10
27	0.10	0.10	0.10	0.11	0.10	0.11	-0.22	0.13	0.11	0.11	0.11	0.11	0.11	0.12	0.12	0.10	0.13	0.11	0.10	0.11	0.11	0.10	0.12	0.21	0.10		0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.10
28	0.10	0.10	0.10	0.11	0.10	0.10	-0.21	0.13	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.13	0.11	0.11	0.11	0.11	0.10	0.10	0.21	0.10	0.11		0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.10
29	0.10	0.10	0.10	0.11	0.10	0.11	-0.22	0.13	0.12	0.11	0.10	0.11	0.10	0.11	0.11	0.11	0.13	0.11	0.10	0.10	0.11	0.10	0.10	0.21	0.10	0.11	0.11		0.11	0.10	0.11	0.11	0.11	0.10	0.12	0.11	0.11	0.10
30	0.10	0.09	0.10	0.10	0.10	0.10	-0.21	0.13	0.11	0.10	0.11	0.11	0.10	0.11	0.10	0.11	0.12	0.10	0.11	0.10	0.10	0.10	0.11	0.20	0.10	0.11	0.11	0.11		0.10	0.11	0.12	0.11	0.10	0.12	0.10	0.11	0.10
31	0.10	0.10	0.10	0.11	0.10	0.10	-0.22	0.13	0.11	0.11	0.10	0.10	0.10	0.10	0.10	0.10	0.13	0.10	0.10	0.10	0.10	0.10	0.11	0.20	0.11	0.11	0.11	0.10	0.10		0.10	0.10	0.11	0.10	0.11	0.11	0.11	0.09
32	0.10	0.10	0.11	0.11	0.10	0.10	-0.22	0.13	0.11	0.10	0.11	0.10	0.10	0.11	0.10	0.10	0.12	0.10	0.10	0.10	0.11	0.10	0.10	0.20	0.10	0.11	0.11	0.11	0.11	0.10		0.11	0.10	0.10	0.11	0.11	0.11	0.10
34	0.10	0.10	0.10	0.10	0.10	0.11	-0.21	0.13	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.12	0.10	0.11	0.10	0.11	0.11	0.11	0.21	0.10	0.11	0.11	0.11	0.12	0.10	0.11		0.11	0.10	0.12	0.11	0.10	0.10
35	0.11	0.11	0.11	0.11	0.11	0.10	-0.21	0.13	0.12	0.18	0.11	0.11	0.11	0.12	0.11	0.11	0.13	0.12	0.10	0.11	0.11	0.10	0.11	0.21	0.11	0.11	0.11	0.11	0.11	0.11	0.10	0.11		0.11	0.12	0.11	0.11	0.10
36	0.10	0.10	0.10	0.10	0.09	0.10	-0.22	0.13	0.11	0.11	0.11	0.10	0.10	0.11	0.11	0.11	0.12	0.11	0.10	0.10	0.10	0.10	0.10	0.20	0.11	0.11	0.11	0.10	0.10	0.10	0.10	0.10	0.11		0.11	0.11	0.10	0.10
37	0.11	0.10	0.11	0.11	0.10	0.11	-0.20	0.13	0.12	0.11	0.11	0.11	0.11	0.12	0.11	0.11	0.13	0.11	0.11	0.11	0.11	0.11	0.12	0.21	0.11	0.11	0.11	0.12	0.12	0.11	0.11	0.12	0.12	0.11		0.11	0.11	0.11
38	0.10	0.10	0.11	0.11	0.10	0.10	-0.21	0.13	0.11	0.11	0.11	0.11	0.10	0.11	0.11	0.11	0.12	0.11	0.10	0.10	0.11	0.10	0.11	0.21	0.10	0.11	0.11	0.11	0.10	0.11	0.11	0.11	0.11	0.11	0.11		0.11	0.10
39	0.11	0.10	0.10	0.11	0.10	0.11	-0.21	0.13	0.11	0.10	0.11	0.11	0.10	0.11	0.11	0.10	0.13	0.11	0.10	0.10	0.10	0.10	0.11	0.20	0.10	0.11	0.11	0.11	0.11	0.11	0.11	0.10	0.11	0.10	0.11	0.11		0.10
41	0.10	0.09	0.09	0.10	0.10	0.09	-0.23	0.12	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.12	0.10	0.10	0.10	0.10	0.10	0.11	0.20	0.10	0.10	0.10	0.10	0.10	0.09	0.10	0.10	0.10	0.10	0.11	0.10	0.10	

Modelling individual variation in acorn crop

The VSURF models identified between one and seven variables (and 18 overall) that influenced oak reproductive material and gall damage (Table 2.3). Each of the VSURF models fitted the data well, with R2 scores of between 0.69 and 0.89 (Fig. 2.11). Spring Phenology and Tree Height were the only variables that were selected for both mature acorn counts (visual and litter trap) and the immature acorn counts (Table 2.3). Additionally, from the Shapley Value plots, both types of mature acorn counts analyses agreed that a lower Spring Phenology score (meaning a later flowering tree) and a taller tree resulted in greater numbers of acorns produced, shown by the higher Shapley Values at higher than lower explanatory variable values respectively (Figs 2.12, 2.13). Models based on the visual count data also identified negative correlations on acorn counts against Canopy Closure and Crown Spread and found that more alkaline soils tended to produce higher numbers of acorns (Fig 2.12).

Table 2.3 Variables selected from VSURF models for different categories of reproductive material from 39 oak trees at Wytham Woods, Oxford. Variables are emboldened and underlined the first time they appear within the table. The influence of the explanatory variables on the response variables is estimated via Shapley Values shown in Figure 2.12 and 2.13.

Response Variable	Collection method	Number	Explanatory variables selected
Mature acorns	Visual survey	5	**Canopy Closure, Crown Spread, Tree Height, pH, and Spring Phenology**
Mature acorns	Litter traps	2	Tree Height, Spring Phenology
Immature acorn	Litter traps	7	Crown Spread, **Site Elevation**, Tree Height, **K, Mid-April LAI, P**, Spring Phenology
Enlarged cups	Litter traps	6	**Autumn Phenology, Clay, Mid-November LAI**, pH, **Sand, Silt**
Flowers	Litter traps	7	**Site Aspect, AUPPC***, Autumn Phenology, Mid-April LAI, **Mid-December LAI**, Mid-November LAI, **Stalk Density**
Galls	Litter traps	1	Tree Height

*AUPPC = Area under the Phenological Progression Curve

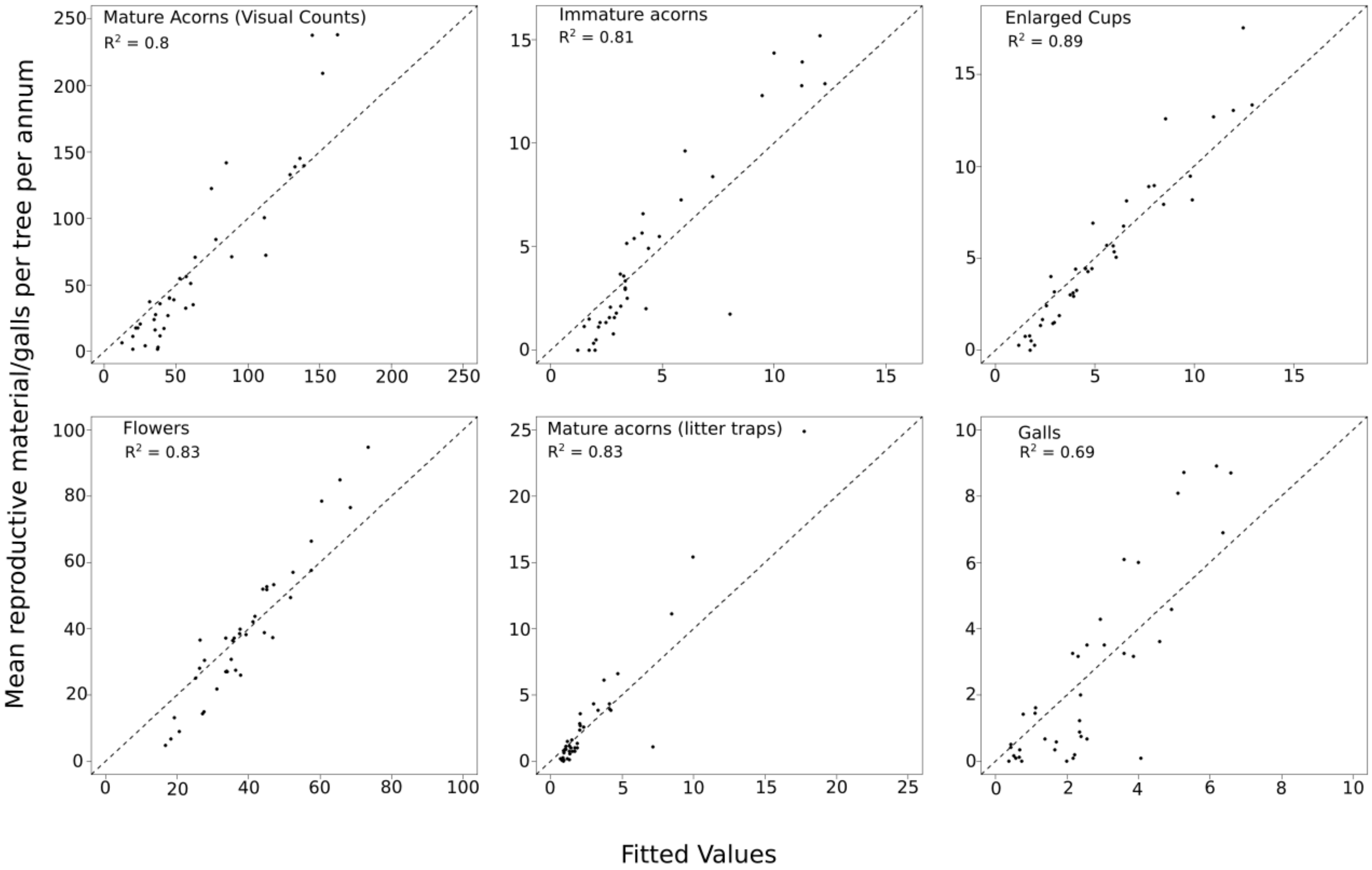


Figure 2.11 The mean reproductive material [Mature acorns, Immature acorns, Enlarged cups, Flowers] and Galls for 39 oaks trees at Wytham Woods, Oxford plotted against fitted values calculated from the VSURF models. The diagonal dotted black line shows a hypothetical perfect fit between the models fitted values and the actual mean material per tree per annum. Coefficient of determination scores (R^2) were calculated to give a score of model fit and are labelled on each graph.

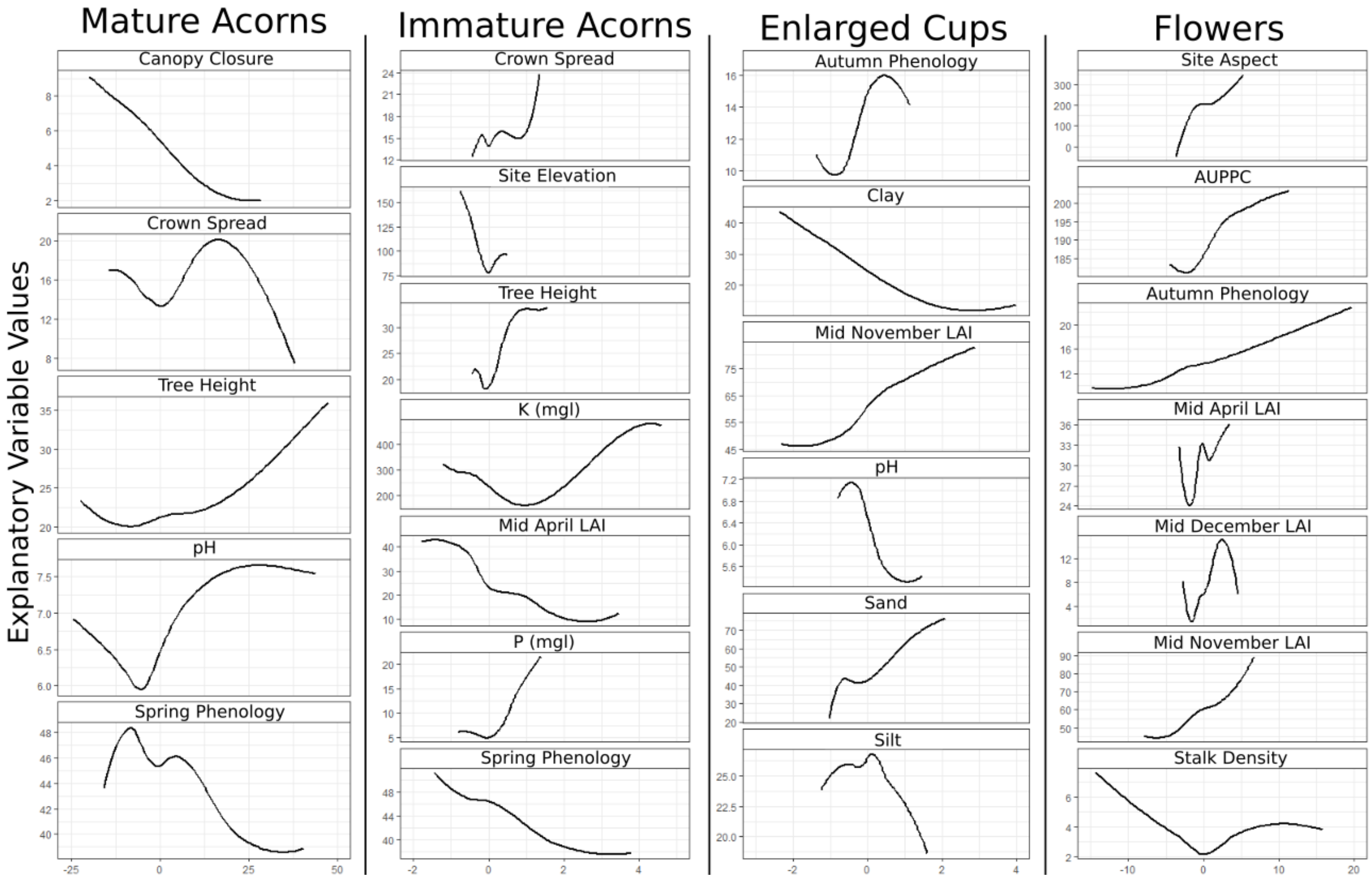


Figure 2.12 Shapley value sensitivity plots from VSURF models of reproductive material of 39 oaks at Wytham Woods. Each variable shown was selected from the corresponding random forests model (Table 2.3) for mature acorns (visual method), immature acorns, enlarged cups and flower counts (latter three from litter traps). The Shapley Value is the response in the models' predictions based on varying the explanatory variable's values. Lines have been smoothed with the function *geom_smooth* in the package 'ggplot2' via local polynomial regression, specifically LOESS (locally estimated scatterplot smoothing).

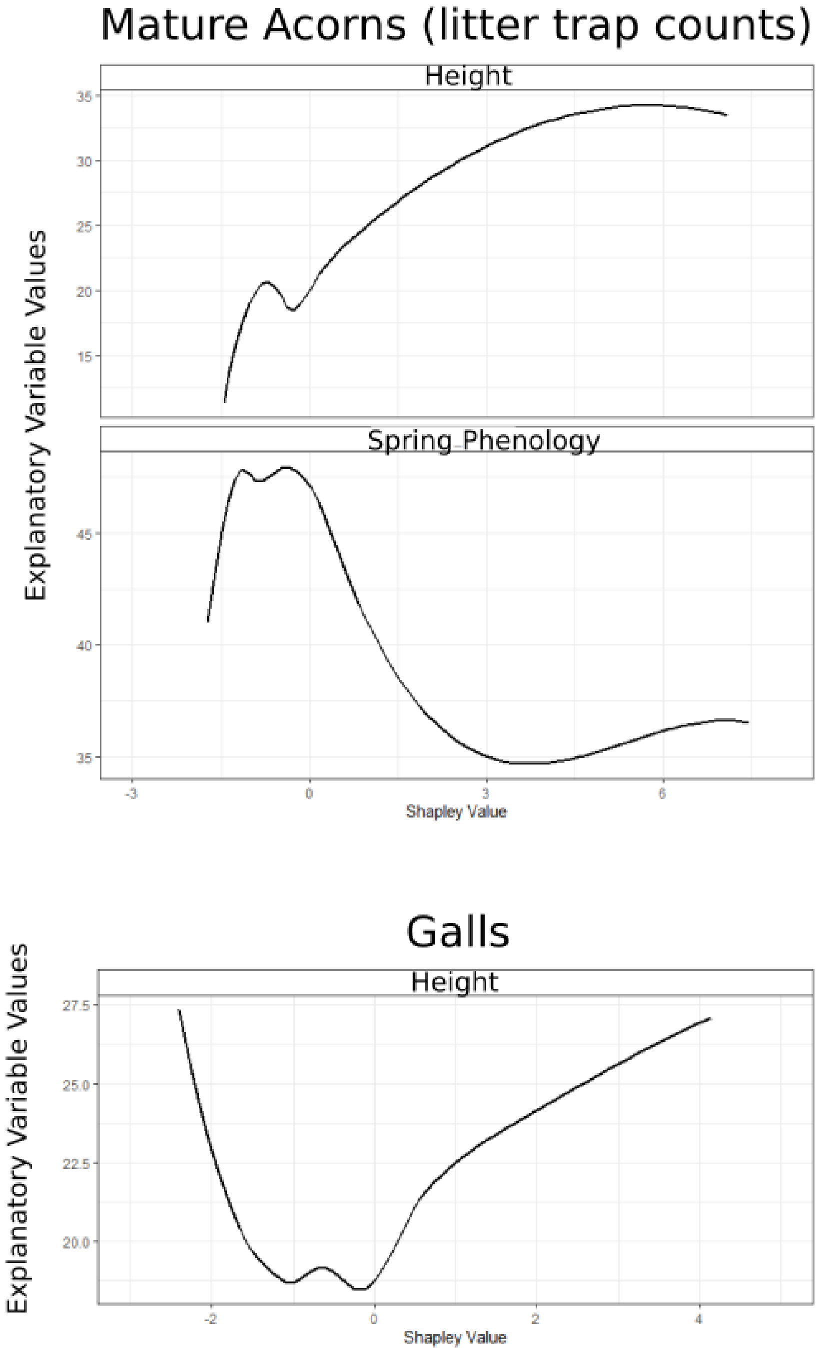


Figure 2.13 Shapley value sensitivity plots from VSURF models of reproductive material of 39 oaks at Wytham Woods. Each variable shown was selected from the corresponding random forests model (Table 2.3) for mature acorns and gall counts (both from litter traps). The Shapley Value is the response in the model’s predictions based on varying the explanatory variable’s values. Lines have been smoothed via local polynomial regression, specifically LOESS (locally estimated scatterplot smoothing).

Generalised linear models performed on the visual acorn counts and litter trap acorn counts only found Canopy Closure to be significant for the visual counts, and only Spring Phenology to be significant for the litter trap counts (Table 2.4). In each case, both GLMs agreed with the VSURF models that the acorn counts showed a negative relationship with Canopy Closure and Spring Phenology scores (Fig. 2.14).

The VSURF model for immature acorns found seven variables to be influential (Table 2.3). However, judging from the shorter range of Shapley Values observed, four of the variables (Crown Spread, Site Elevation, Tree Height, and P) where Shapley Values ranged from -1 to +1 appeared to have minimal effects on the predictions of immature acorns produced by the models (Fig. 2.12). In contrast, Mid-April LAI and Spring Phenology scores showed negative relationships with immature acorn counts, whereas K had a positive relationship with immature acorn counts (Fig. 2.12). The generalised linear models constructed with the selected explanatory variables did not find any significant relationships for the immature acorn counts, although Elevation and Spring Phenology approached significance (0.1>P>0.05, Table 2.4).

Four variables related to the soil were identified as drivers of enlarged cup counts (Table 2.3; Clay, Sand, Silt and pH), with the other two related to autumnal senescence (Table 2.3; Autumn Phenology and Mid-November LAI). When building the generalised linear models, the soil types Sand, Silt and Clay were highly correlated and so Soil Class was used within the model for enlarged cup counts in their place. The resulting model showed Soil Class and Mid-November LAI to be highly significant (Table 2.4). A higher Mid-November LAI score (i.e. later senescence in autumn) was related to a higher count of enlarged cups (Fig. 2.14). Based on a post hoc Tukey pairwise analysis within the Soil Class groupings, trees on Sandy Clay Loam soils had significantly fewer enlarged cups than on Clay Loam or Sandy Loam soils (Fig. 2.14; Table 2.5). Clay soils' enlarged cups counts were significantly lower than Sandy Loam soils, but none of the other pairings differed significantly (Fig. 2.14, Table 2.5).

The VSURF models identified seven variables important for determining flower counts within the litter traps (Table 2.3). The majority of the variables selected were related to phenology (AUPPC, Autumn Phenology, Mid-April LAI, Mid-December LAI, and Mid-November LAI). When the selected variables were used to build generalised linear models, however, not one of them was found to be a significant predictor of flower counts (Table 2.4).

Only tree height was found to be an important predictor of Gall counts within the litter traps by the VSURF models (Table 2.3). These showed an inconsistent pattern with both high and low values of tree height resulting in increases and decreases to the response variable (Fig. 2.13). The resulting generalised linear model found Tree Height to have no significant effect on gall counts (Table 2.4).

Microclimate temperature differed among years (as well as among trees, Fig. 2.5), and among the three different phenological periods within each year of course, but there was no difference in temperature among trees in the different producer classes, including no difference in microclimate temperatures between producer classes dependent on the study year or the phenological period considered (Table 2.6).

To give a measure of the relatedness of each tree to the whole sample, the paired kinship scores (Table 2.2) were summed per tree (King score of Tree 1 to Tree 2 + Tree 1 to Tree 3 + Tree 1 to Tree 4 etc…) and included in the VSURF models. The summed kinship scores were not selected as important by any of the VSURF models (Table 2.3). Despite this, the summed kinship scores were compared between producer groupings and higher-producing individual trees were slightly less related on average (High: 4.19 ±0.04; Medium: 4.29 ±0.06; Low: 4.24 ±0.04). But these differences were not significant when modelled via one-way anova (F(2,33) = 0.538, P = 0.59).

Gall counts were negatively correlated with powdery mildew damage (assessed by leaf abscission) (Table 2.7; Fig. 2.15). It was not possible to test if powdery mildew damage affected acorn production as no mature acorns were counted in 2021. No other response variable was affected by powdery mildew damage, although that on flower number approached significance (0.1>P>0.05, Table 2.7).

Table 2.4 Results of a series of ANOVAs for generalised linear models using the Gamma distribution and log link on the reproductive material and pre-dispersal predation on 39 oaks at Wytham Woods, Oxford. Estimates of *P* are given to the nearest 2 decimal places.

Visual Counts

Variable	$\chi2$	df	*P*
Canopy Closure	7.4750	1	**0.006**
Crown Spread	1.1475	1	0.28
Height	2.3696	1	0.12
pH	0.2575	1	0.61
Spring Phenology	1.3640	1	0.24

Mature Acorns (Lit. Traps)

Variable	$\chi2$	df	*P*
Height	1.2446	1	0.26
Spring Phenology	9.3327	1	**0.002**

Immature Acorns

Variable	$\chi2$	df	*P*
Elevation	3.2490	1	0.07
Height	0.2920	1	0.59
Crown Spread	0.0677	1	0.79
P	2.6287	1	0.10
K	0.0029	1	0.96
Spring Phenology	3.4365	1	0.06
Mid-April LAI	0.6547	1	0.42

Enlarged Cups

Variable	$\chi2$	df	*P*
pH	0.7369	1	0.39
Soil Class	26.4584	5	**<0.0001**
Autumn Phenology	2.1550	1	0.14
Mid-November LAI	7.6391	1	**0.006**

Flowers

Variable	$\chi2$	df	*P*
Aspect	0.11080	1	0.74
AUPPC	0.08782	1	0.77
Autumn Phenology	1.45853	1	0.23
Mid-April LAI	0.02670	1	0.87
Stalk Density	0.15583	1	0.69

Galls

Variable	$\chi2$	df	*P*
Height	0.22914	1	0.63

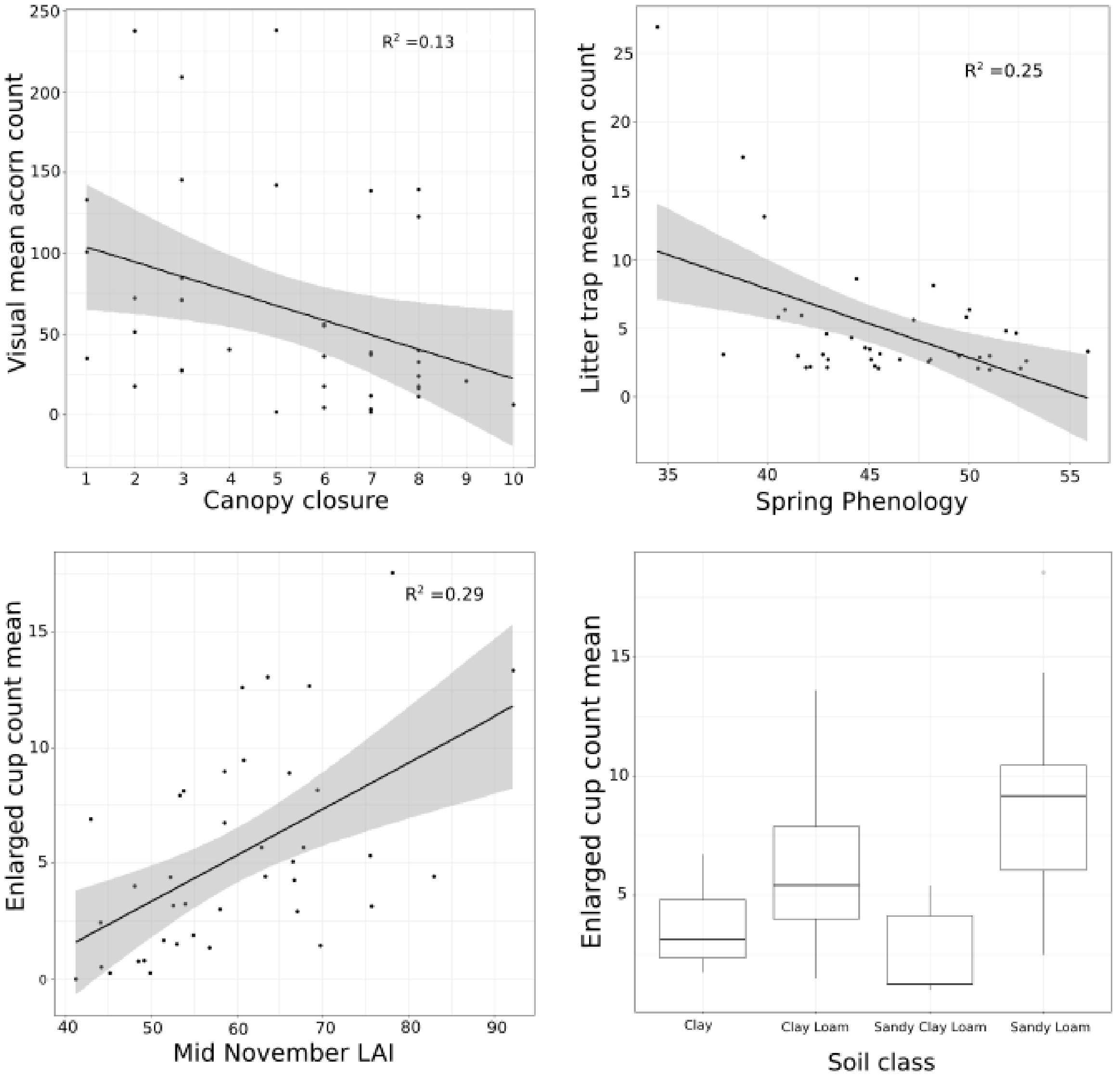


Figure 2.14 Plots of relations for significant variables from generalised linear models on reproductive material of 39 oaks at Wytham Woods, Oxford. The visual mean acorn count (top left) is given per tree per annum, whilst the other variables are per m^2 per annum collected from litter traps. The black lines on the scatter plots represent a linear model between the explanatory variable and response variable, with the shaded area representing the 95% confidence limits. The enlarged cup count mean by soil class (bottom right) gives the median enlarged cup counts, min, max and interquartile range.

Table 2.5 Tukey's all-pair comparisons of soil classes of 39 oaks at Wytham Woods, Oxford, based on their relationship with counts of enlarged cups from litter traps (see Fig. 2.14). The estimate is the logs odd ratio for the comparisons. Performed via the *glht* function of the package ‘multcomp’.

Soil Class pairings	Estimate	Std. Error	*Z*	*P*
Clay Loam - Clay	0.4012	0.2088	1.922	0.22
Sandy Clay Loam - Clay	-0.6424	0.2754	-2.333	0.09
Sandy Loam - Clay	0.6128	0.2343	2.615	**0.04**
Sandy Clay Loam – Clay Loam	-1.0435	0.2459	-4.243	**<0.001**
Sandy Loam – Clay Loam	0.2116	0.2049	1.033	0.73
Sandy Loam – Sandy Clay Loam	1.2551	0.2630	4.773	**<0.001**

Table 2.6 Results of a series of ANOVAs for linear models of microclimate temperatures of 39 oaks at Wytham Wood Oxford, with the variables acorn producer class (oaks classified as high, average or poor producers based on total acorns produced over the study period), phenological period (the phenological period of the tree classified as budburst, acorn development and post leaf drop), year and the interaction producer class × year, and producer class × phenological period. Estimates of *P* are given to the nearest 2 decimal places.

Maximum Temperature

Variable	df	Sum Sq	Mean Sq	*F*	*P*
Producer	2	64	32	2.240	0.11
Period	2	86883	43441	3020.332	**<0.0001**
Year	1	369	369	25.631	**<0.0001**
Producer × Year	2	0	0	0.007	0.99
Producer × Period	4	11	3	0.188	0.95

Minimum Temperature

Variable	df	Sum Sq	Mean Sq	F	P
Producer	2	36	18	1.246	0.288
Period	2	40073	40073	2806.947	**<0.0001**
Year	1	414	414	28.992	**<0.0001**
Producer × Year	2	0	0	0.02	0.98
Producer × Period	4	7	2	0.121	0.98

Mean Temperature

Variable	df	Sum Sq	Mean Sq	F	P
Producer	2	44	22	1.545	0.213
Period	2	82924	41462	2896.987	**<0.0001**
Year	1	399	399	27.852	**<0.0001**
Producer × Year	2	0	0	0.007	0.99
Producer × Period	4	8	1	0.134	0.97

Accumulated Mean Temperature

Variable	df	Sum Sq	Mean Sq	F	P
Producer	2	6905	3453	0.714	0.49
Period	2	438985	219492	45.408	**<0.0001**
Year	1	175455	175455	36.297	**<0.0001**
Producer × Year	2	106	53	0.055	0.99
Producer × Period	4	1173	293	0.061	0.99

Table 2.7 Results of a series of generalised linear models using the Gamma distribution and log link, determining the effect of powdery mildew infection in 2021 on the response variables within that same year. Estimates of P are given to the nearest 2 decimal places.

Variable	Estimate	Std. error	*t*	*P*
Immature Acorns	-0.007296	0.011043	-0.661	0.51
Enlarged Cups	-0.005	0.010892	-0.462	0.65
Flowers	-0.03	0.01781	-1.776	0.083
Galls	-0.06	0.02239	-2.842	**0.007**

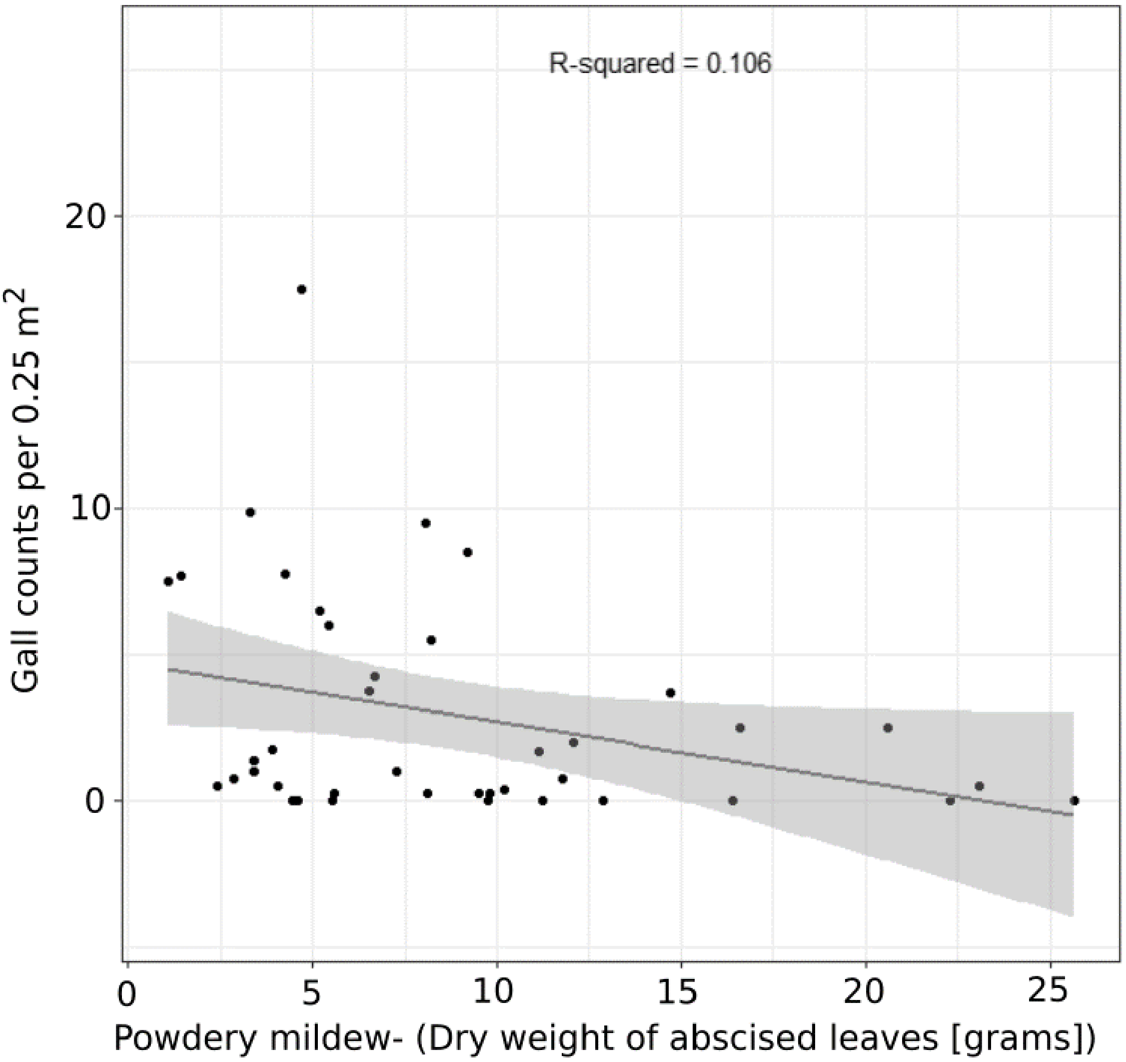


Figure 2.15 The number of galls from 39 trees at Wytham Woods, Oxford, counted per 0.25m^2 of litter trap area plotted against the dry weight of abscised leaves in these traps (used as a proxy for powdery mildew damage) during the year 2021 of the study. The black lines on the scatter plots represent a linear model between the explanatory variable and response variable ($P < 0.05$), with the shaded area representing the 95% confidence limits. The coefficient of determination (R-Squared) is labelled on the plot.

2.4 Discussion

The goal of this study was to (1) quantify individual variation in oak reproductive material and pre-dispersal herbivory at Wytham Woods, and (2) identify if any environmental or tree characteristics explained such variation. This study identified considerable variation in acorn production among the 39 trees studied, as well as among years, and highlighted possible causative relationships for both acorn production and abortion in terms of tree characteristics, soil classes, and phenology. These topics are discussed in more detail below.

High individual variation in acorn production, with several identifiable super producers

Despite its short length, this four-year study captured the interannual variation in acorn production that helps to define masting (Kelly, 1994). A large masting event at Wytham in 2020 was followed by a complete crop failure in 2021, and moderate acorn crop years in 2022 and 2023 (Fig. 2.1). This pattern of high interannual variation has been well reported in *Quercus robur* L. and oak species more generally (Sork et al. 1993; Crawley and Long 1995; Nussbaumer et al. 2016; Hanley et al. 2019). This study found a small number (7 of the 39 studied) of individual trees contributed to the majority of the total acorn crop (Table 2.1). Earlier studies that have collected masting data at the individual tree level found that super producers accounted for the majority of the seed crop (Moran and Clark 2012; Minor and Kobe 2017; Patterson 2020). At Wytham these super producing individuals appeared to produce acorns in large numbers most years (but not in 2021). By producing consistently large crops, the super producers were not responsible for much of the interannual variation in the acorn crop – although all trees failed to produce a crop in 2021. Rather, 2020's intense mast year (cf. 2022 and 2023) was caused in large part by the much greater proportion of less productive trees producing large crops in that year (Fig. 2.2; Table 2.1). In 2020 only twelve trees produced less than 1% of the total acorn crop and none failed to produce acorns (Table 2.1). It seems that masting at Wytham is not dictated by the super-producing trees but by the inclusion of the less prolific acorn producing individuals in the crop year. This agrees with previous work that identified smaller less fertile trees as responsible for interannual variation in seed crops (Bogdziewicz et al. 2020d). No small immature trees were sampled at Wytham, but nonetheless it does appear that less fertile individuals with a higher variation in fecundity could still be identified; and these trees played a large role in the pattern of masting behaviour.

The pattern of super producing individual trees appears to weaken as one compares earlier stages of acorn development, although it is still somewhat present (Table 2.1, Appendices tables 2.2, 2.3, 2.4). Importantly an individual tree producing more mature acorns may be more likely to produce more immature acorns (Table 2.1 cf. Appendix Table 2.2) and more enlarged cups (Table 2.1 cf. Appendix Table 2.3), but this is not necessarily the consequence of a higher flower count (Table 2.1 cf. Appendix Table 2.4). Until recently *Quercus robur* has been thought of as solely a fruit abortion species, meaning a high acorn crop in a mast year is determined by the number of flowers that will develop into acorns and not the number of flowers that are produced (Pearse et al. 2016). However, recent research has identified several populations of sessile oak (*Quercus petraea* Matt. Liebl.) in which acorn crops can be determined by flowering effort linked to climatic conditions (Fleurot et al. 2023). Flowering effort at Wytham is evenly spread throughout the high, medium, and low acorn production classes (Appendix Table 2.4), and even during the failed crop of 2021 there were reasonable numbers of flowers produced (Fig. 2.3, Appendix Table 2.4). This study can therefore conclude that masting in the *Quercus robur* population at Wytham is fruit maturation masting. To caveat this, a flower that goes on to develop into an acorn would not be counted as a flower within this data set, and so high acorn producers may drop fewer flowers, but the number of flowers produced is consistently much more than the number of acorns (Appendix Table 2.1 [comparing litter trap collections]), and so this discrepancy is unlikely to bias this study's findings.

To assess how individual trees showed a pattern of masting the coefficient of variation (CV) was included for each tree individually (Table 2.1). Most individuals had high CV scores of above 1, which is generally indicative of masting behaviour (Kelly 1994); and between the producer groupings, CV scores increased as average acorn counts decreased (High =0.95 ± 0.07, Mid = 1.27 ± 0.06, Poor =1.42 ±0.11 [$F(2,36) = 5.1$, $P < 0.05$]). The higher CV found within the low producing group is likely due to the high number of crop failures (zeros) recorded, and such patterns have already been seen where unproductive individuals with more crop failure years result in higher CV scores (Bogdziewicz et al. 2020b). As such CV scores should be interpreted with caution and as a supplement to the raw data not instead of it (Bogdziewicz et al. 2023a). With only four years of data this study cannot comment more on long-term variation in individual acorn production. However, the data does highlight that the apparent synchrony in masting among trees is not absolute: seven trees produced more acorns in either 2022 or 2023, and one of these (Tree 33) many more in each of 2022 and 2023 than in 2020 (Table 1). There was, however, complete synchrony among the trees in the failed crop year of 2021.

Pre-dispersal predation

Masting is purported to have evolved as a seed predator defence, whereby a failed crop will starve seed predators and so keep predator numbers low, enabling better individual seed survival the following crop year (Janzen 1971; Silvertown 1980; Kelly 1994). There are not enough years of data within this study to confirm seed predator satiation, but there was a positive trend between the previous year's mature acorns and the current year's Gall numbers: high numbers of Galls in 2021 after the 2020 mast year, followed by low numbers in 2022 after 2021's failed crop, then rebounding again in 2023 after a decent acorn crop in 2022 (Fig. 2.3). Previous research highlights the benefit of masting in reducing seed predator populations the year after a poor seed year (Yasaka et al. 2003) and thereafter greater seedling survival as the larger seed crop results in a lower percentage of seeds predated (Crawley and Long 1995; Espelta et al. 2008). Within the life cycle of the Oak Knopper Gall (*Andricus quercuscalicis* Burgsdorf) each Gall should produce one adult Gall wasp the following Spring (Stone et al. 2002). Higher Gall counts in 2021 did not result in higher Gall counts in 2022, suggesting survival rates from 2021's Galls may be lower, possibly due to smaller less nutrient rich acorns that develop during small crop years (Alejano et al. 2011) or a parallel cycle of predation/parasitism of the Gall wasps (Schonrogge et al. 1999). Some invertebrate seed predators are able to take advantage of greater seed years by increasing fecundity (Bogdziewicz et al. 2018b). This does not appear to be the case in the Gall wasp, with its effective reproduction constrained by last year's crop. It may also be that powdery mildew damage reduced resources for gall development (Fig. 2.15); this is discussed later in this discussion.

Whilst the data suggests an annual or autocorrelative effect of acorn number on pre-dispersal predation (High acorn counts in 2020 + 2022 [Fig. 2.2] preceding high gall counts in 2021 + 2023 [Fig. 2.3]), it is not so at the individual tree level. Gall attack at Wytham was concentrated on comparatively few trees; seven trees accounted for over 50% of the Galls counted throughout the study (Appendix Table 2.5). These highly-predated trees were spread equally throughout the data, and there was no relationship between Gall numbers and individual acorn production (P =0.85) suggesting satiation or starvation of Galls can only work at the community scale. This disagrees with studies on neotropical oaks that found weevils would preferably attack the higher-producing individuals (Pérez-Ramos et al. 2017). Comparison of the effects of conspecific density on predator satiation found the effectiveness of predator satiation was vastly reduced within dense oak patches (Bogdziewicz et al. 2018a). The density of oaks within Wytham Woods is likely to be low enough to starve or satiate seed predators when there is synchrony in acorn production.

Masting and weather cues

Four years data is not enough to identify weather cues of masting clearly, but this study may suggest that the very dry spring in 2020 was one possible causative factor of that masting year (Fig. 2.4). Several hypotheses posit weather conditions during flowering as important for masting (Nussbaumer et al. 2018). In contrast to 2020, 2021's failed crop was after high precipitation during flowering and low temperatures (Figs 2.3, 2.4), far from ideal conditions for pollen flow (Corden and Millington 1999) and with an increased risk of frost damage to flowers (Inouye 2000). The phenological synchrony hypothesis suggests that a mast year may be caused by a homogenous microclimate during high spring temperatures (Koenig et al. 2015). There was no significant pattern found between temperature data and the producer groupings from 2021 to 2023, and this remained so when phenological period and study year were included within the models (Table 2.6). This study therefore purports that 2021's failed crop was caused by the poor weather conditions during spring and not a lack of synchrony in flowering, and may have combined with a lack of available resources from 2020's large mast event. This study cannot determine if this would have been the case during the 2020s mast year as there was no microclimate data from that spring.

Identifying the environmental and tree characteristics affecting oak reproductive material and pre-dispersal predation

To examine the possible role of environmental variables affecting oak reproductive material production and pre-dispersal predation, 29 variables were considered within this study. Eighteen were chosen as important within at least one of the VSURF models (Table 2.3), but only four were found to have significant effects in the resulting generalised linear models (Table 2.4). This is likely because the VSURF models explain much larger variance in the data in comparison to the GLMs.

Tree characteristics

Previous research has identified several tree characteristics that can improve or hinder acorn production. For example, in white oak (*Quercus alba* L.) experimental canopy release [thinning branches] was seen to increase acorn production by 65% (Brooke et al. 2019). Similarly in red oak (*Quercus rubra* L.), stands that had been thinned produced on average 33% more acorns than unthinned stands (Healy et al. 1999). In agreement with the above, individual trees in Wytham Woods with a closed canopy produced fewer acorns than those in a less-densely packed canopy (Table 2.4; Fig. 2.12). A closed canopy can act as physical barrier to pollen flow, whereas canopy gaps allow vertical fluxes in air flow causing pollen to penetrate the canopy effectively (Di-Giovanni and Kevan 1991). For example, pollen flowed more successfully in open oak savannah canopies than in unthinned natural canopies (Sork et al. 2002). There is prior evidence that larger beech trees (*Fagus sylvatica* L.) become pollen limited even by the extent of their own crown blocking pollination of flowers by outcrossed pollen (Bogdziewicz et al. 2023b). It is likely that dense, surrounding canopies may have blocked pollination at Wytham. It is worth considering if a more open canopy is biasing the visual count data by enabling clearer views of acorns. The visual counts were significantly correlated with the litter trap counts (Fig. 2.6), however, suggesting this study observed a relationship between canopy openness and acorn production which was not an experimental artifact of the data collection procedure.

Several other explanatory variables were chosen as important by the VSURF models: crown spread, tree height, site elevation and site aspect (Table 2.3). However, none were significant within generalised linear models (Table 2.4).

Soils

Of the soil measurements recorded, the only significant effects on reproductive material were by soil classification upon enlarged cup numbers, which identified the early aborting acorns (Table 2.4). Higher clay soils negatively impacted enlarged cup counts (Figs 2.12, 2.14; Table 2.4), whereas more sandy soils increased enlarged cup counts (Figs 2.12, 2.14; Table 2.4). Populations of *Quercus robur* favour heavy, higher clay content, and moist soils (Jones 1959). Studies examining acorn production within Spanish Dehesas found acorn production increased with higher soil water content (Carevic et al. 2010) and within heavier soils, specifically loamy-clay and clay soils (Gea-Izquierdo et al. 2006 in Carbonero et al. 2014). Although there was no noticeable effect of soil class on mature acorns, it is reasonable to suggest this study may have identified individual trees in high clay soils aborting fewer acorns early on in development. Clay soils inherently maintain higher water contents than sandy soils, and this may enable better flow of soil nutrients as well as moisture, whereas sandy soils may leach nutrients more quickly, causing nutrients to become limiting during acorn development.

The VSURF models also found that less acidic soils produced more acorns and mildly fewer enlarged cups (Fig. 2.12), and higher Phosphorus-content soils increased immature acorn counts (Figure 2.12) although these findings were not significant within the generalised linear models (Table 2.4). Previous studies also found a limited impact of soil nutrients and pH on masting, with some variation among species. For instance, there was no effect of soil nutrients on mean acorn production in chestnut oak (*Quercus montana* Willd.) nor in black oak (*Quercus velutina* Lam.) (Smith et al. 2022), a limited impact on white spruce (*Picea glauca* (Moench) Voss) cone production in low production years (Leeper et al. 2020), while nitrogen fertilisation increased acorn production in red oak (*Quercus rubra* L.) (Bogdziewicz et al. 2017). Less acidic soils have been linked to higher seed productivity in Algerian oak (*Quercus canariensis* Willd.) individuals, but not in the evergreen cork oak (*Quercus suber* L.) (Pérez-Ramos et al. 2014). Clearly soil nutrients play an important role in acorn development at different stages (see Allen et al. 2017), but the complexity and transience of many soil nutrients has made it hard to study holistically. When suggesting management implications, the collective findings of these studies may therefore be to highlight the usefulness of broader soil classifications such as soil type, rather than narrow such as cation exchange capacity and soil nutrients.

Canopy Analysis

Tree phenology influenced mature acorn counts and enlarged cup counts collected in the litter traps (Fig. 2.12; Table 2.4). A higher spring phenology score [earlier-developing trees] was related to a lower acorn count (Figs 2.12, 2.13; [but not significant in GLMs, Table 2.4]), whereas a higher mid-November LAI score [later-senescing individuals] was related to a higher number of enlarged cups (Figs 2.12, 2.14; Table 2.4). Earlier-developing individual trees make a trade-off with increased canopy duration from the earlier start against the risk of late spring frosts damaging foliar tissue (Vitasse et al. 2014), flowers and immature acorns (Inouye 2000). However by beginning growth earlier the individuals have a head start in assimilating resources such as carbon through photosynthesis, which may be important for later fruit development (Hoch et al. 2013). The average *Quercus robur* leaf-out date is already quite late compared to other tree species, and the movement towards earlier budburst dates is actually reducing the risk of damaging frost events during leaf out and flowering across the UK and mainland Europe (Chamberlain et al. 2021). This suggests that earlier-developing acorns would benefit from a longer canopy duration without the downside of frost damage. However, a lack of frost damage does not guarantee optimal conditions for pollen flow and pollination; the earlier flowering phenology may be an adaptive trait of masting species, causing greater reproductive failure from variable weather conditions (Schermer et al. 2019). In which case, later flowering trees would produce more consistent and higher mean acorn crops, which is what this study found. If weather events that hinder effective pollen flow increase, such as more extreme spring precipitation (Fowler and Ekström 2009), and spring budburst dates continue to become earlier with higher temperatures (Wenden et al. 2020), we may see greater interannual variation in acorn crops.

Fertiliser experiments have shown higher nutrient availability results in an increased autumnal canopy duration (Fu et al. 2019). As such, one might expect higher Mid-November LAI individual trees to have more resources and so abort a smaller number of acorns. This is not the case, with higher Mid-November LAI individuals aborting more acorns during the enlarged cup stage of development (Figs 2.12, 2.14). This result may instead be evidence that these individual trees have put more nutrients into foliar development instead of reproduction (Pearse et al. 2016). Masting can reduce leaf size, lower foliar nitrogen content (Müller-Haubold et al. 2015), increase leaf shedding and reduce canopy duration (Camarero et al. 2010). As such, the higher number of aborted acorns is evidence for switching of resource use away from maturing acorns and instead towards sustained leaf development and woody growth.

Pre-dispersal predation and Powdery mildew infection

Of the explanatory variables recorded to help explain pre-dispersal herbivory over the full study period, only tree height was chosen as important by the VSURF models (Table 2.3), with an inconsistent effect from the sensitivity analysis (Fig. 2.13) that was not significant within the generalised linear models (Table 2.4). However, during 2021 there was an extremely high level of leaf defoliation from powdery mildew infection (*Erysiphe alphitoides* Griffon & Maubl.), which reduced Gall counts within the litter traps (Table 2.7, Fig. 2.15). Several herbivore species have been shown to avoid individuals infected with pathogens, preferring non-infected conspecifics (van Dijk et al. 2021; Gaytán et al. 2022) and infection from oak powdery mildew has been found to reduce the diversity and abundance of Gall wasps on the Aleppo oak (*Quercus infectoria* Oliv.) (Zargaran et al. 2012). As well as causing leaf shedding, powdery mildew infection reduces leaf nutrients, such as reducing carbon acquisition (Marçais and Desprez-Loustau 2014). As the oviposition and development of galls is affected by nutritional status (Stone et al. 2002), it seems likely that Gall wasps at Wytham are avoiding infected oaks. Interactions between plants, pathogens, and herbivores are incredibly complex, and further study of how these interactions may affect acorn production would be useful.

Genome sequencing

Results from the genetic analysis showed that the majority of the trees at Wytham Woods were 2nd degree relatives or half siblings (Table 2.2). The summed kinship scores were not selected as important by any of the VSURF models, nor were they significantly different between producer classes (Table 2.3; F(2,33) = 0.538, P =0.59). Pollen flow studies using paternity analysis have consistently found a higher occurrence of out-of-stand pollination than would be expected by chance alone (Buiteveld' et al. 2001; Craft and Ashley 2010; Gerber et al. 2014; Vranckx et al. 2014). Further, a recent experiment on individual trees within Wytham Woods found out-of-stand pollen to be more successful than pollen collected within Wytham (Chapter 4). As such it was assumed that relatedness would predict acorn production.

For instance, individual trees less related to the remaining oaks within the stand would have a larger amount of outcrossed pollen readily available. No such pattern was found within this study, possibly because the differences in relatedness between the individuals were minor (Table 2.2), or the level of out-of-stand pollen was already high enough within the site to make such differences meaningless.

Conclusions

Strong interannual variation in acorn production was detected that was highly variable among individual trees and independent of variation in flowering number. The results suggest that the *Quercus robur* population at Wytham Woods is a fruit maturation masting species, where the masting behaviour is characterised by variation in acorn production by the less productive individual trees. This study was unable to distinguish how microclimate, weather, or genetic relatedness may have affected individual masting success or the different acorn producer classes. But among these producer classes this analysis has highlighted several explanatory variables that may explain differences in average acorn crop, including understanding the stage of acorn development that each variable may be affecting. To summarise, this study finds that a limited number of trees contribute a large proportion of the acorn crop and a mast year occurs when less productive individual contribute to the acorn crop; and suggests that late flowering trees within an open canopy and situated on heavy clay soils produce more consistent good acorn crops at Wytham Woods.

Chapter Three: Assessment of weather as a driver to model inter-annual variation in acorn production in *Quercus robur* and *Quercus petraea*

3.1 Introduction

Mast seeding is the phenomenon of highly interannually variable but geographically synchronous production of seeds or fruits (Kelly, 1994). Common in anemophilous perennial plants (Herrera et al., 1998), it means several years of limited seed production followed by a sudden pulse of seeds produced in a single year. Although still often referred to as "mast years", difficulty differentiating between good and moderate years of seed crops makes such unambiguous definitions difficult. Instead, many now refer more generally to seed production and use metrics like the coefficient of variation or volatility to define a species as masting or not (Bogdziewicz et al., 2023a).

The resource pulses from masting species influence flora and fauna across trophic levels (Elkinton et al., 1996; Ostfeld & Keesing, 2000), ranging from regeneration of the masting species (Ascoli et al., 2015), response from animals in the ecosystem (Bogdziewicz et al., 2016), conservation of native species (King & Powell, 2011), to even impact on human-managed crops (Picard et al., 1991) and human disease risk (Clement et al., 2010; Jones et al., 1998; Ostfeld, 1997). *Quercus robur* L. and *Quercus petraea* (Matt.) Liebl. are both masting species, deciduous broad-leaved species of the Fagaceae. Both are found throughout Europe, with *Q. robur* having the broader range of the two species, stretching from Northern Portugal into Southern Fennoscandia and Russia (Caudullo et al. 2017).

Mast seeding in these oaks can be detrimental to their establishment. Poor natural regeneration of oaks in the UK (Quine et al., 2019) has meant an increase in planting efforts, with the England Trees action plan aiming to plant 30,000 hectares of new forest by 2025 (DEFRA, 2021). Unreliable production of acorns because of masting, combined with poor survival in storage (Berjak & Pammenter, 2008), has led to shortages across Europe (Bole, 2022). With better understanding of what drives masting, seed collection efforts could be improved, reducing the risk of a shortfall in acorn supply.

The evolutionary benefits of masting appear to be associated with "economies of scale", with improved pollination efficiency as a result of synchronous flowering (Kelly et al., 2001; Smith et al., 1990), higher individual survivability of seeds due to predator satiation (Janzen, 1971), and increased distance of seed dispersal by animal dispersers (Vander Wall, 2002). The direct causes of masting are not so clear. Several mechanisms have been suggested, such as internal tree resources or pollen limitation (Pearse et al., 2016). The hypotheses that overlay these two potential mechanisms concern the effects of weather. Weather can affect the uptake of tree nutrients (Allen et al., 2017), influence the full range of a tree's phenology and physiology (Buechling et al., 2016), affect pollen flow (Kasprzyk et al., 2014), and synchronise tree development within and amongst populations (Koenig et al., 2015).

Exploring the influence of weather on masting is a promising research area – as weather is a factor which affects a large geographic area simultaneously. There has been considerable interest in studying weather as a mechanistic driver, although the particular weather cues for masting often vary amongst species (Nussbaumer et al., 2016). Numerous weather cues with positive and negative influences on seed crops have been identified. These include the weather within the seed crop year (Bogdziewicz et al., 2017), that in the years preceding it (Hacket-Pain et al., 2015), and the differences between these years' weather (Vacchiano et al., 2017), as well as significant weather events such as drought (Vilà-Cabrera et al., 2014) or the north Atlantic oscillation (Fernández-Martínez et al., 2017). The strength of these correlations varies between species, however. Whereas seed production in *Fagus sylvatica* L. may have consistent weather cues, those for *Q. robur* and *Q. petraea* have varied between studies and sites (Bogdziewicz et al., 2019; Kasprzyk et al., 2014; Wesołowski et al., 2015).

The influence of weather on masting is complex, and its study requires robust statistical methods, able to consider large numbers of variables whilst also being able to differentiate between species and sites. With the poor state of conservation and seed management in *Q. robur* and *Q. petraea* a species-specific study considering the environment's effect at each development phase is required.

This chapter reports the analysis of acorn production observations across different sites in Northwest Europe over several years to attempt to create predictive models for the effect of weather on *Q. robur* and *Q. petraea* masting.

The aims of this paper are to:

(1) Assess any weather cues for masting in *Quercus robur* and/or *Quercus petraea*.
(2) Identify if a predictive model can accurately predict masting events across Europe.
(3) Assess if any weather cues differ spatially or phylogenetically.

The explicit hypotheses include:

(1) Masting years coincide in geographically-close sites;

(2) Warm and dry Springs, and warmer Summers will positively correlate with acorn production;

(3) Models built using meteorological conditions will be able to predict high and low years of acorn production;

(4) *Quercus robur* and *Quercus petraea* respond similarly to weather cues.

3.2 Materials and Methods

Acorn production

Acorn production data for *Q. robur* and *Q. petraea* from multiple sites across Northwest Europe (Tables 3.1 and 3.2) was selected for analysis. Time series of acorn production were retrieved from several sources: the MAST-TREE+ database (Hackett-pain et al. 2022), the ICP forests network, BIFoR, with additional time series provided by Mick Crawley, Mick Hanley and Michael Fenner. Site selection was based on the length of the time series (>5 years) and consistent data collection methods (specifically, stand-level recording via litter trap collection at all sites).

Acorn counts varied greatly amongst stands, years, and species. The count data was first logarithmically transformed and then standardised using the following formula for each site prior to the analyses:

$$A^{DF} = \left(\frac{A^{t}}{A^{m}} * 100\right) - 100$$

where A^{DF} = standardised acorn count difference from the mean for each year, A^{t}= log transformed acorn count for that year at that site, and A^{m} = mean log-transformed acorn count for all years at that site. Hence, the response variable A^{DF} was calculated as the log-transformed acorn count in a given year expressed as a percentage of the mean of the log-transformed acorn counts for all years at that site.

The standardised acorn count (A^{DF}) was also classified into two and three-class groupings. The two-class groups split the response variable into mast years (A^{DF} > 0%) and lean years ($A^{DF} \leq$ 0%), i.e. above or below the mean. The three-class group accounted for years of more moderate acorn production, splitting the response variable between lean years (A^{DF}< -25%), moderate years ($A^{DF} \geq$ -25% to ≤ 25%), and mast years (A^{DF}>25%).

These calculations provided one continuous response variable (A^{DF}) and two categorical response variables (2-class and 3-class) for the analyses. Previous studies have highlighted a negative autocorrelation between past and current annual seed production (Moreira et al., 2015). The response variables (A^{DF}, 2-class and 3-class), were therefore lagged for one year and this value included as the explanatory variable 'Acorn Lag'.

Site*	Country	Latitude (°N)	Longitude (°E, +; °W, -)	Coefficient of Variation	Length of time series (years)	From	To
Adtornish	UK	56.558	-5.739	1.24	6	2003	2008
Arscott	UK	52.651	-2.845	1.60	7	2014	2020
CHS 01	France	46.171	5.239	1.08	12	1996	2007
CHS 03	France	46.668	2.727	0.99	13	1995	2007
CHS 10	France	48.298	4.460	1.35	13	1995	2007
CHS 18	France	47.255	2.125	1.26	10	1996	2005
CHS 21	France	47.083	5.075	1.89	13	1995	2007
CHS 27	France	49.366	1.504	0.90	13	1995	2007
CHS 41	France	47.569	1.260	1.89	22	1996	2017
CHS 57a	France	48.872	6.484	1.51	13	1994	2007
CHS 57b	France	49.016	7.463	1.26	13	1994	2007
CHS 58	France	46.970	3.661	1.94	13	1994	2007
CHS 60	France	49.398	2.300	1.17	13	1994	2007
CHS 61	France	48.523	0.680	1.41	12	1995	2007
CHS 68	France	47.693	7.468	1.52	13	1994	2007
CHS 72	France	47.796	0.380	1.42	11	1995	2006
CHS 81	France	44.046	1.749	0.94	12	1995	2007
CHS 86	France	46.627	0.496	1.45	12	1995	2007
CHS 88	France	48.027	6.040	1.89	11	1994	2005
Grizedale	UK	54.343	-3.019	0.94	11	2000	2010
Hofstetten	Germany	47.467	7.500	1.54	9	2000	2008
La Petite Pierre	France	48.830	7.000	1.47	7	2011	2017
Newtown	UK	52.534	-3.284	1.37	7	2014	2020
Whitbourne	UK	52.216	-2.405	0.94	7	2014	2020
Average				1.4	11.375		

Table 3.1 Sites used for time series analysis of acorn production for *Quercus petraea*

*CHS = Chêne Sessile (i.e. sessile oak)

Table 3.2 Sites used for time series analysis of acorn production for *Quercus robur*

Site*	Country	Latitude (°N)	Longitude (°E, +; °W, -)	Coefficient of Variation	Length of time series (years)	From	To
Alice Holt	UK	51.183	-0.858	1.12	20	2000	2019
BIFoR(ghost)**	UK	52.800	-2.304	0.90	6	2016	2021
CHP 10	France	48.348	4.305	1.57	13	1994	2007
CHP 18	France	46.826	2.574	1.31	12	1995	2007
CHP 49	France	47.456	0.031	1.16	12	1996	2007
CHP 55	France	49.023	5.767	2.10	13	1994	2007
CHP 59	France	50.171	3.754	1.60	19	1995	2013
CHP 65	France	43.204	0.038	1.07	10	1997	2007
CHP 70	France	47.871	6.211	2.41	13	1995	2007
CHP 71	France	46.970	5.243	1.48	13	1995	2007
Newtown	UK	52.534	-3.284	1.02	7	2014	2020
Silwood Park	UK	51.400	-0.630	0.95	41	1980	2020
Southampton	UK	50.930	-1.410	1.41	26	1990	2015
Average				1.36	15.77		

*CHP = Chêne Pedunculate (i.e. pedunculate oak)

**The BIFoR (ghost) site is part of the free air carbon enrichment experiment at the Birmingham Institute of Forest Research. The ghost treatment is a control not placed under any experimental conditions, and so deemed suitable for inclusion in this study.

Weather variables

The three weather variables, daily temperature minimum, daily temperature maximum, and daily precipitation, were retrieved for each site from the European climatic database via the R package ‘easyclimate’ (Cruz-Alonso et al., 2023; Moreno & Hasenauer, 2016; Pucher 2023; Pucher and Neumann 2022). This data was used to generate ten unique weather indices (Table 3.3) for each of the 33 months before assumed acorn collection dates in September (i.e., in case of delayed effects, the weather throughout the two calendar years before acorn fall was included). Further weather indices were calculated for the periods of Winter (December, January and February), Spring (March, April and May), Summer (June, July and August), and Autumn (September, October and November) for the 33 months. The difference between the current and previous year's estimate (Δ) was also estimated for each monthly and seasonal weather observation. In addition, to capture any effect of weather in the immediate period before bud burst, the accumulated growing degree days above base temperatures of 0°C, 5°C, and 10°C were considered in three groupings: (1) January, February, and March, (2) February and March, (3) March. In total, this generated 319 weather variables to consider.

As the sites across Europe were very different, each site's latitude, longitude, and coefficient of variation (CoV) for acorn production were also included as potential explanatory variables to identify any site-specific differences in the response to weather.

Table 3.3 A list of the weather indices used to model acorn production

Variable*	Description	Units
T_{max}	Average maximum temperature recorded	°C
T_{min}	Average minimum temperature recorded	°C
T_{mean}	Average mean temperature recorded [$(T_{max} + T_{min})/2$]	°C
NRM	Maximum number of concurrent days without rain	days
Avg NR	Average number of concurrent days without rain	days
AF	Average number of days experiencing air frost	days
Rain	Total amount of rain in given period	mm
GD 0	Accumulated number of growing degree days above 0 °C	°C
GD 5	Accumulated number of growing degree days above 5 °C	°C
GD 10	Accumulated number of growing degree days above 10 °C	°C

*In the text and later tables these terms are preceded by the appropriate period (month or season); for example, Jan T_{max}

Statistical analyses

The weather variables were not fully independent, often presented collinearity, and were more numerous than the number of observations. To identify and interpret their role in determining acorn production, therefore, a mix of statistical methods was applied that either used dimension-reduction techniques or were robust to multicollinearity: (1) Partial Least Squares Regression and Discriminant Analysis (PLSR/PLS-DA), (2) Classification and Regression Trees (CART), (3) Variable Selection Using Random Forests (VSURF). In all three cases, several iterations of model fitting were carried out that included all of the nine combinations of each species alone, both species together, i.e. mixed species models, with each of the two countries alone (France and UK) and also with all three countries combined (i.e. also including the single site in Germany). The two oaks *Q. robur* and *Q. petraea* were considered together in some models of this study because there are often high rates of hybridisation between them in mixed forests (Muir et al., 2000). Moreover, similar mixing of the species groups has previously been used in other research (*see* Nussbaumer et al. 2016; Bogdziewicz et al. 2023c). The three different analytical methods, see below, were each applied to the continuous data for standardised acorn count (A^{DF}) and for the data classified in two ($A^{DF} >$ 0% or ≤ 0%) or three-classes (A^{DF}< -25%, -25% to ≤25%, or >25%).

(1) PLSR/PLS-DA

Partial Least Squares (PLS) is a guided form of dimension reduction which creates latent variables (a selection of linear combinations from the variables) and then uses least squares regression to fit the latent variable as an explanatory variable (Wold et al., 1984). Conducting a PLS analysis on a continuous variable is referred to as a Partial Least Squares Regression (PLSR) and one conducted on a categorical variable is referred to as Partial Least Squares Discriminant Analysis (PLS-DA). An important difference between this method and alternatives, such as Principal Components Regression (PCR), is that PLS creates latent variables that explain variation in both the explanatory and response variables (Geladi & Kowalski, 1986). Because PLS reduces the dimensionality of the correlated variables into latent variables, it is a robust method when faced with multicollinearity in data (Wold et al., 1984; Wondola et al., 2020) and when there are more predictors than observations (Geladi & Kowalski, 1986).

The train function in the '*caret*' package (Kuhn, 2008) in R was used to perform PLSR and PLS-DA. Variables were recorded in different units; to improve interpretation, the values of the explanatory variables were mean centred and scaled by dividing each variable by their standard deviation (Geladi & Kowalski, 1986). To interpret the explanatory variables the chosen model was then put through a measure of variable importance (VIP) using the VarImp function in the '*caret*' package (Kuhn, 2008). For PLS models the VIP orders the coefficients based on the reduction each one makes to the sum of squares across the PLS components. This generated a list of all the weather variables ordered by their estimated influence over acorn counts.

(2) CART

Classification and Regression Trees (CART) is a simple but powerful technique wherein a selection of explanatory variables is chosen best to predict the response variable (Breiman, 2017). Like a dichotomous key, the tree is organised into a root node, which then branches off into several decision nodes, ending at the leaf nodes that give the mean value of the predicted response variable based on those decisions. The initial tree often overfits the data as it finds the best root and decision nodes to predict the response variable; a pruning step is performed, which removes nodes until the best balance of model complexity and interpretability is found (Breiman et al., 1984). This pruned tree was then visualised via the 'rpart.plot' function and package (Milborrow, 2019), either as a regression tree (continuous variables) or a classification tree (discrete variables).

(3) VSURF

Variable selection using random forests (VSURF) is a dimension reduction technique using a method called Random Forests (Genuer & Poggi, 2019). This method (summarised from Genuer and Poggi 2019) has two steps:

(1) Fit multiple random forests models using a bootstrapped sample of the data. Rank variables by their variable importance scores averaged across multiple random forest runs and eliminate those of small importance.

(2) Generate two sets of variables: an interpretation set selecting the variables used to form the most accurate model from a collection of nested random forests models; and a prediction set, adding variables to nested random forest models in a stepwise manner, and only selecting those that lower the out of bag error more than adding useless “noisy” variables. The out-of-bag error is generated from comparing the prediction error on variable samples that were not selected during bootstrapping (James et al., 2021).

Random Forests are often considered black box models because their increased complexity makes them especially difficult to interpret. To aid the interpretability of the model, Shapley Values were calculated. Shapley Values are a model-agnostic method of explaining the contribution of each variable to the model’s prediction (Shapley, 1953). By rerunning predictions using the VSURF models with different assigned values to each explanatory variable, Shapley values can show how changes in the explanatory variables’ values affect the response variable.

Data partitioning, hyperparameter tuning, and evaluation of predictions

Each dataset was randomly split between a training (70%) and a testing (30%) data set. Models were trained on the training data, and hyperparameter tuning for PLS and CART models was performed via five-fold cross-validation (Cohen, 1960), with the “one SE” rule that selects the least complex model with the average cross-validated accuracy within one standard error (SE) from that in the optimal model (Hastie et al., 2001). The hyperparameters for VSURF models, the number of trees and nodes in each random forest model, were selected based on the computational power available. The predictive ability of each regression model was then evaluated using the previously unseen testing data set, generating the mean square error (MSE), root mean square error (RMSE), and mean absolute error (MAE). The normalised root mean square error (NRMSE) was also calculated by dividing the RMSE by the range of the testing data, to allow some comparison between species and models. The classification models were assessed with the test data, working out the Accuracy and Kappa scores instead (Cohen, 1960; McHugh, 2012). These metrics were also presented for the training data to show how well the model fitted the data.

3.3 Results

Acorn production

All sites showed a high coefficient of variation for acorn production (Tables 3.1 and 3.2), the coefficients varied more than twofold within each species. The irregularity in acorn production, which is a key qualifier of masting, was apparent for all sites in England (Figs 3.1, 3.2), S France (Figs 3.3, 3.4), NE France and Germany (Figs 3.5, 3.6), and NW France (Figs 3.7, 3.8). Most sites showed a large dip in acorn production in one or more years after a high year of acorn production (Figs 3.1, 3.3, 3.5, 3.7). Many sites occasionally showed multiple sequential years of poor acorn production (Fig 3.7, CHP 49: 1998 to 2002 or Fig 3.5, CHS 57a and 57b: 1994 to 1997). Sequential years of high acorn production were rare but did occasionally occur, such as 2006 and 2007 when CHP 59 produced two years in a row with acorn production more than 100% above the mean (Fig 3.5).

Geographic synchrony between sites was low when considering all sites with more than six years of overlapping time series data: the average synchrony from Spearman rank correlations in acorn production (A^{DF}) for *Q. robur* sites was ρ = 0.14 ±0.022 and for *Q. petraea* was ρ = 0.10 ±0.028. Geographic synchrony in A^{DF} decreased with greater distance between sites (Fig

3.9): synchrony in *Quercus robur* masting decreased by 0.05 /100km ($F_{1;258} = 31.65$, $R^2=0.11$, $p<0.0001$) and for *Quercus petraea* it decreased by 0.03 /100km, ($F_{1;194} = 7.94$, $R^2=0.04$, $p<0.01$) for all site pairs. When only pairings within the same contiguous land mass were considered, the decline in the synchrony of masting with greater distance was steeper (Fig 3.9): *Quercus robur* synchrony decreased by 0.09 /100km ($F_{1;194} = 54.14$, $R^2=0.22$, $p<0.0001$); and in *Quercus petraea* it also decreased by 0.09 /100km ($F_{1;173} = 32.44$, $R^2=0.16$, $p<0.0001$).

In England, there was an equal spread of high- and low-acorn producing sites within most years (Fig 3.2), other than occasional purported mast years, specifically 1995, 1997, 1999, 2006, 2011, 2013, 2015 and 2020 where all sites recorded above average acorn output. Within the UK, *Q. robur* at Southampton and Silwood Park sites showed the greatest variability in acorn production (Fig 3.1, Table 3.2); these sites also had the longest series of data. As quantified here, the inter-annual variability in acorn production in *Q. petraea* in the UK was smaller than in *Q. robur*.

In France, the two southern sites (one *Q. petraea*, one *Q. robur*) were broadly similar in variability but much less so than Southampton and Silwood Park in the UK, and synchronised in masting in some years (1997, 2000, 2002, 2004, 2006) but not synchronised in other years (Fig 3.4). A lack of synchrony was also observed in the North-eastern France sites, which didn't have any years with more than three observations where all sites were either above or below the mean output (Fig 3.6). In North-western France, 1994 and 2003 were the only years where all sites produced more than the mean acorn production (Fig 3.8); albeit 2007 was very close.

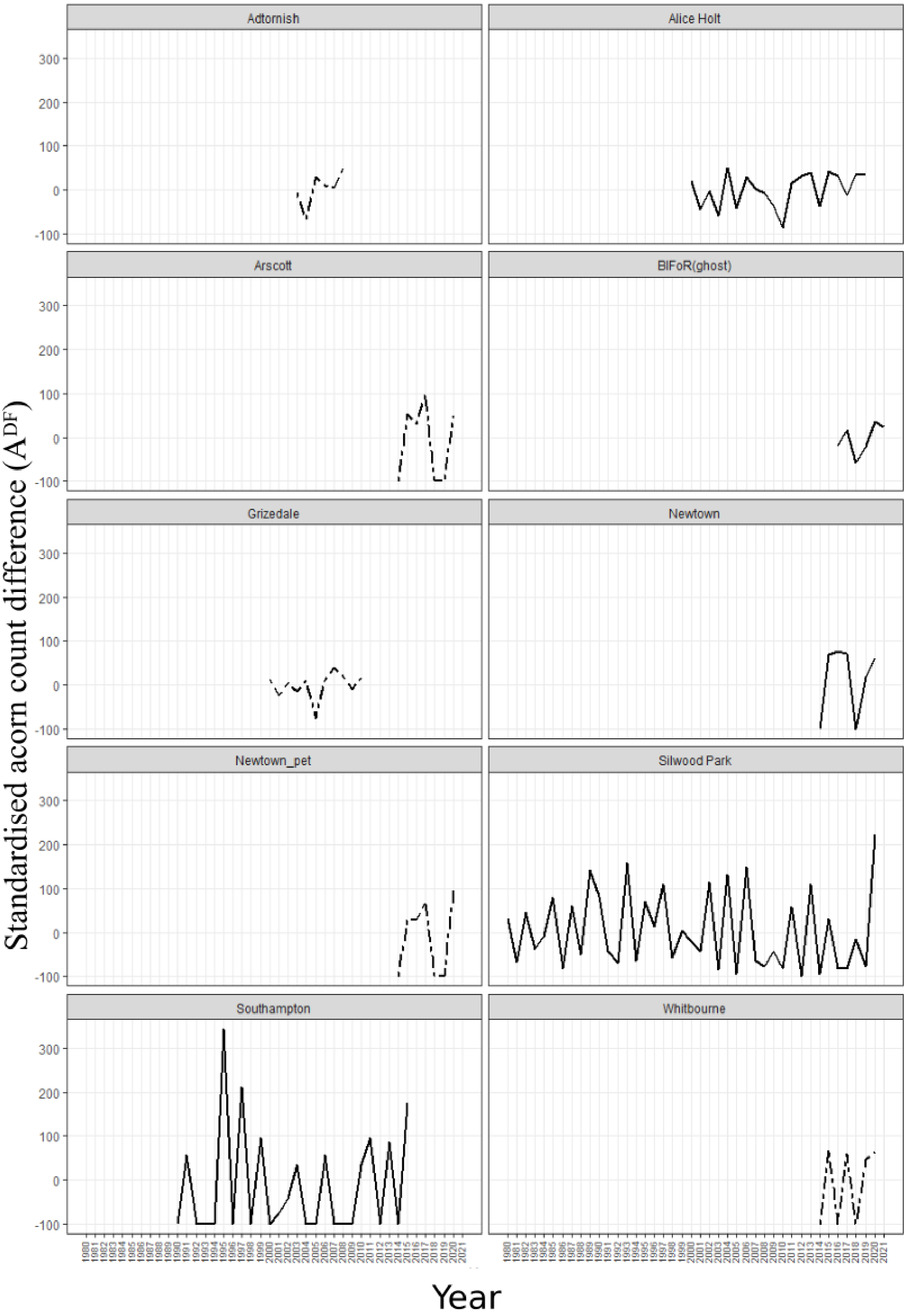


Figure 3.1 Annual recordings of acorn production presented as a difference from the mean of each site (A^{DF} = standardised acorn count difference from the mean for each year; see methods) for all the sites in the UK. All graphs are on the same scale for the X and Y axes. *Quercus petraea* is represented by a broken line and *Quercus robur* is represented by a solid line.

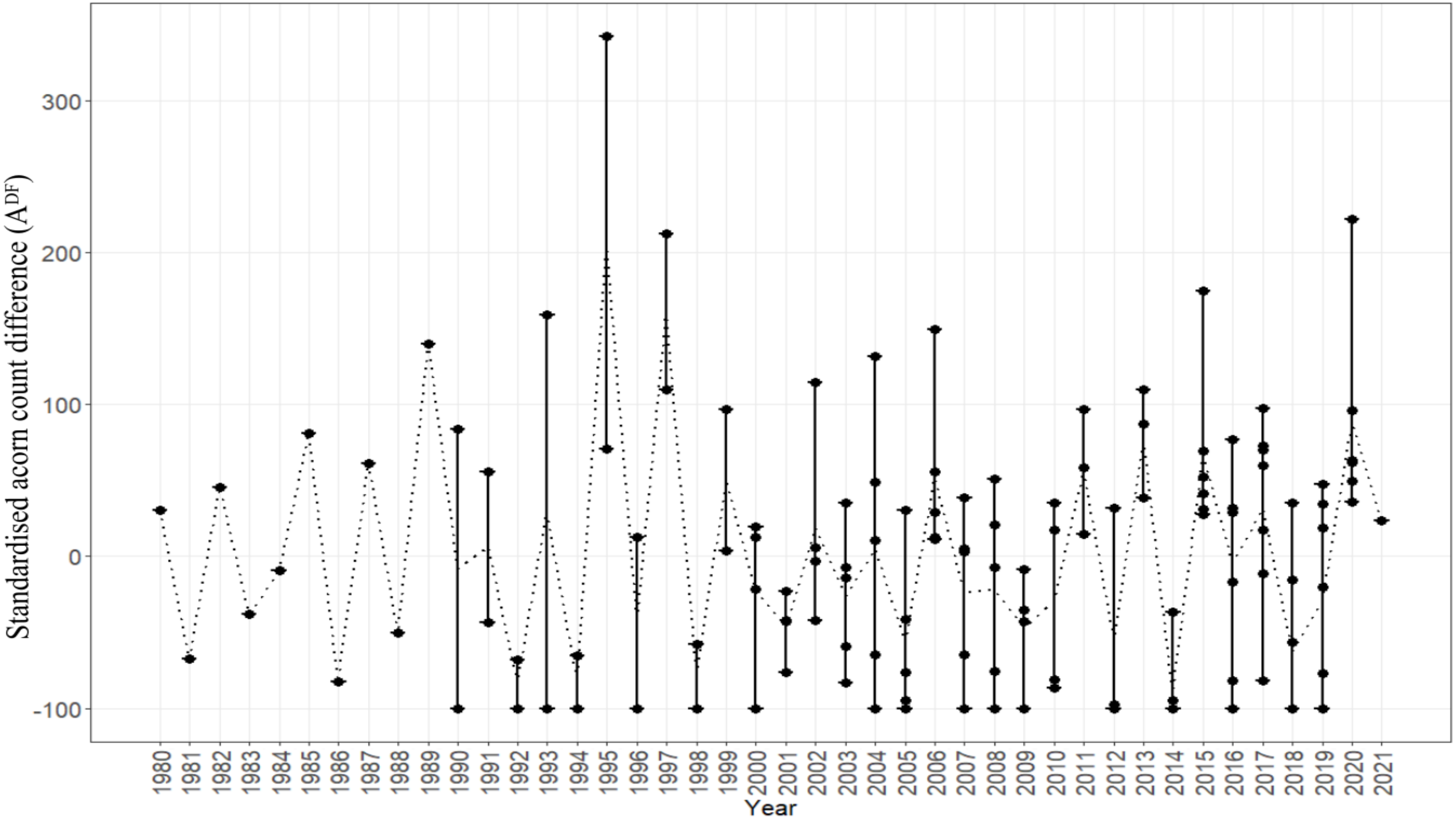


Figure 3.2 Annual recordings of acorn production (*Quercus petraea* and *Quercus robur*) presented as a difference from the mean of both species at all the sites in the UK. Each site is represented by a single symbol (●), with black vertical bars highlighting the range between the highest and lowest acorn-producing sites. In years where no vertical line is shown observations were only available at one site. The mean A^{DF} for each year, of those sites for which data is available, is shown by the dotted line. The number of sites with observations differs amongst years; no sites overlap perfectly with the same sequence of years (Tables 3.1 and 3.2).

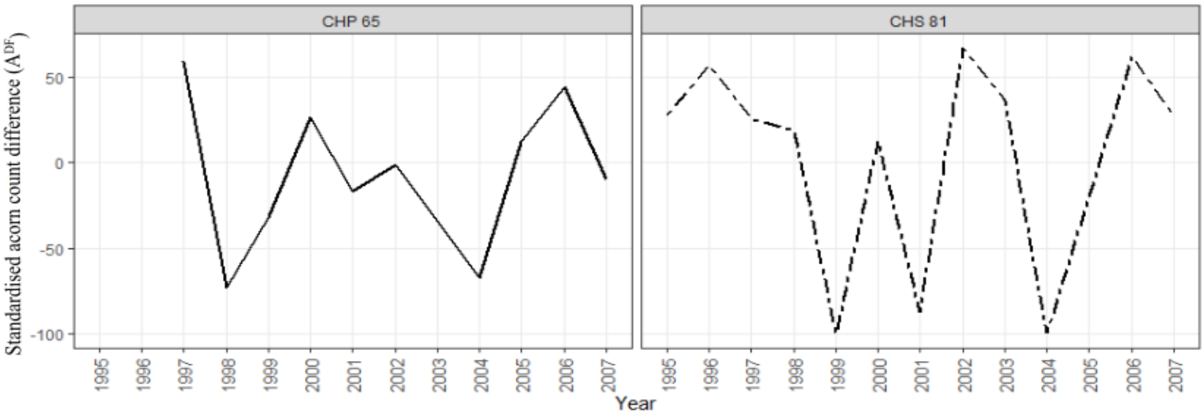


Figure 3.3 Annual recordings of acorn production presented as a difference from the mean of each site A^{DF} = standardised acorn count difference from the mean for each year; see methods) for both sites in Southern France. All graphs are on the same scale for the X and Y axis. *Quercus petraea* is represented by a broken line and *Quercus robur* is represented by a solid line.

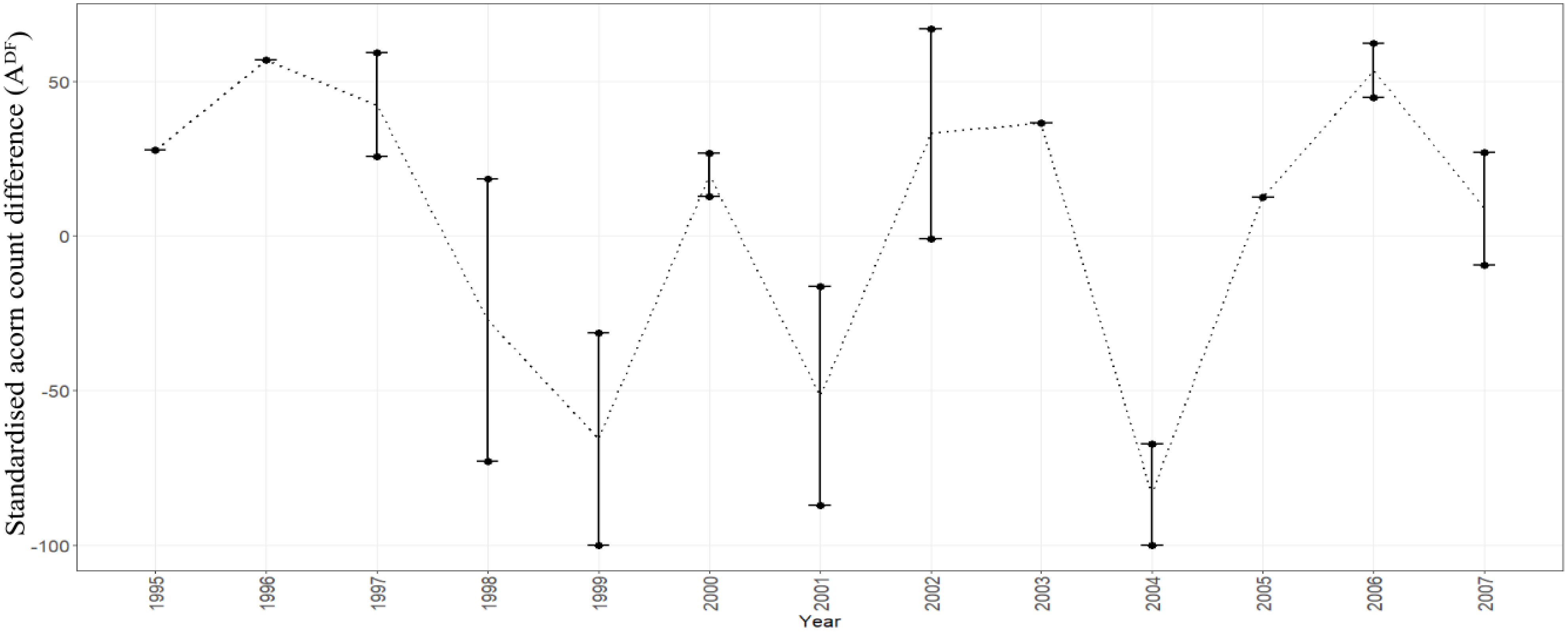


Figure 3.4 Annual recordings of acorn production (*Quercus petraea* and *Quercus robur*) presented as a difference from the mean of both species at both sites in Southern France. Each site is represented by a single symbol (●), with black vertical bars highlighting the range between the highest and lowest acorn-producing sites. In years where no vertical line is shown observations were only available at one site. The mean A^{DF} for each year, of those sites for which data is available, is shown by the dotted line. The number of sites with observations differs amongst years; no sites overlap perfectly with the same sequence of years (Tables 3.1 and 3.2).

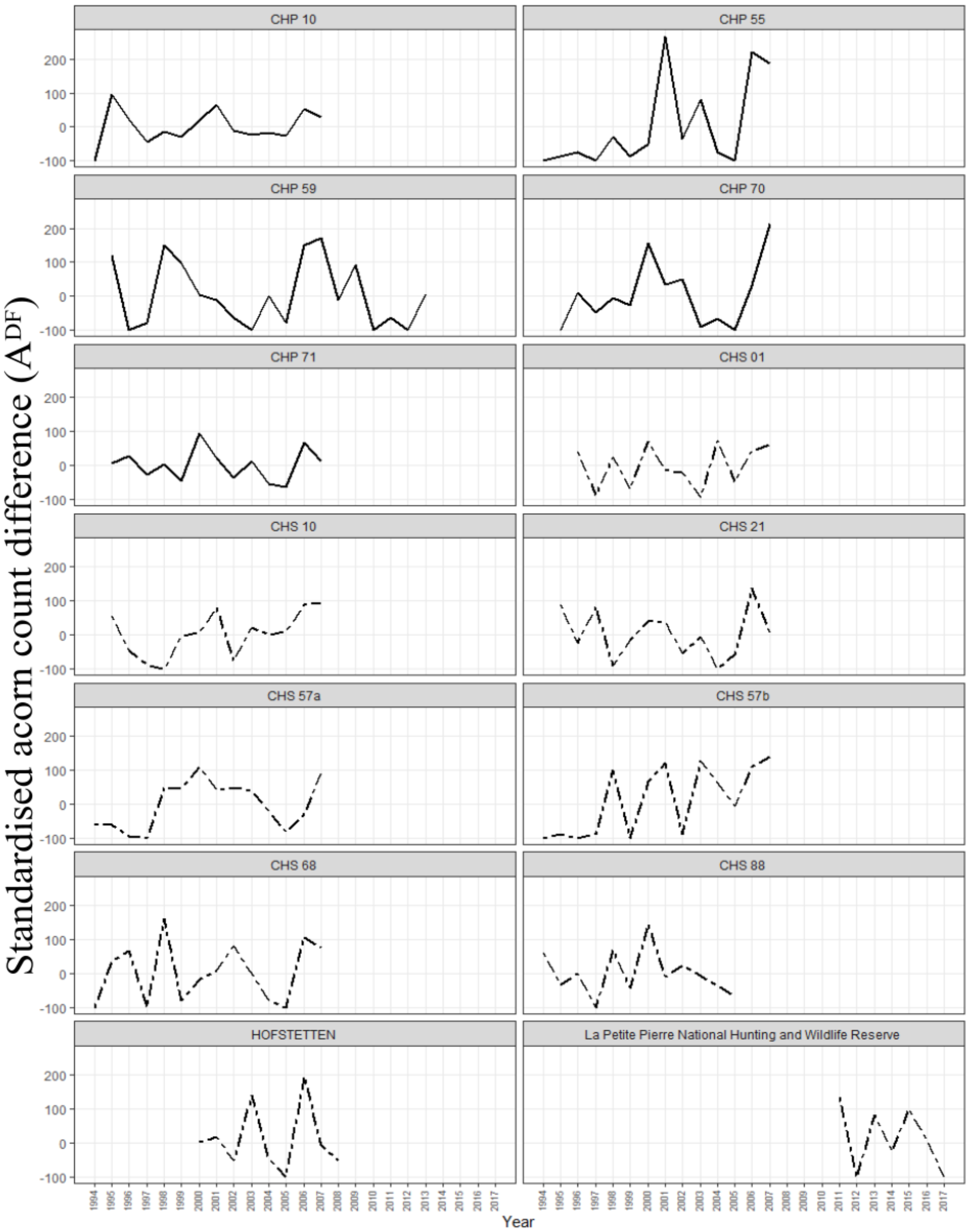


Figure 3.5 Annual recordings of acorn production presented as a difference from the mean of each site A^{DF} = standardised acorn count difference from the mean for each year; see methods) for all the sites in North-eastern France and one site (Hofstetten) in Germany. All graphs are on the same scale for the X and Y axis. *Quercus petraea* is represented by a dotted line and *Quercus robur* is represented by a solid line.

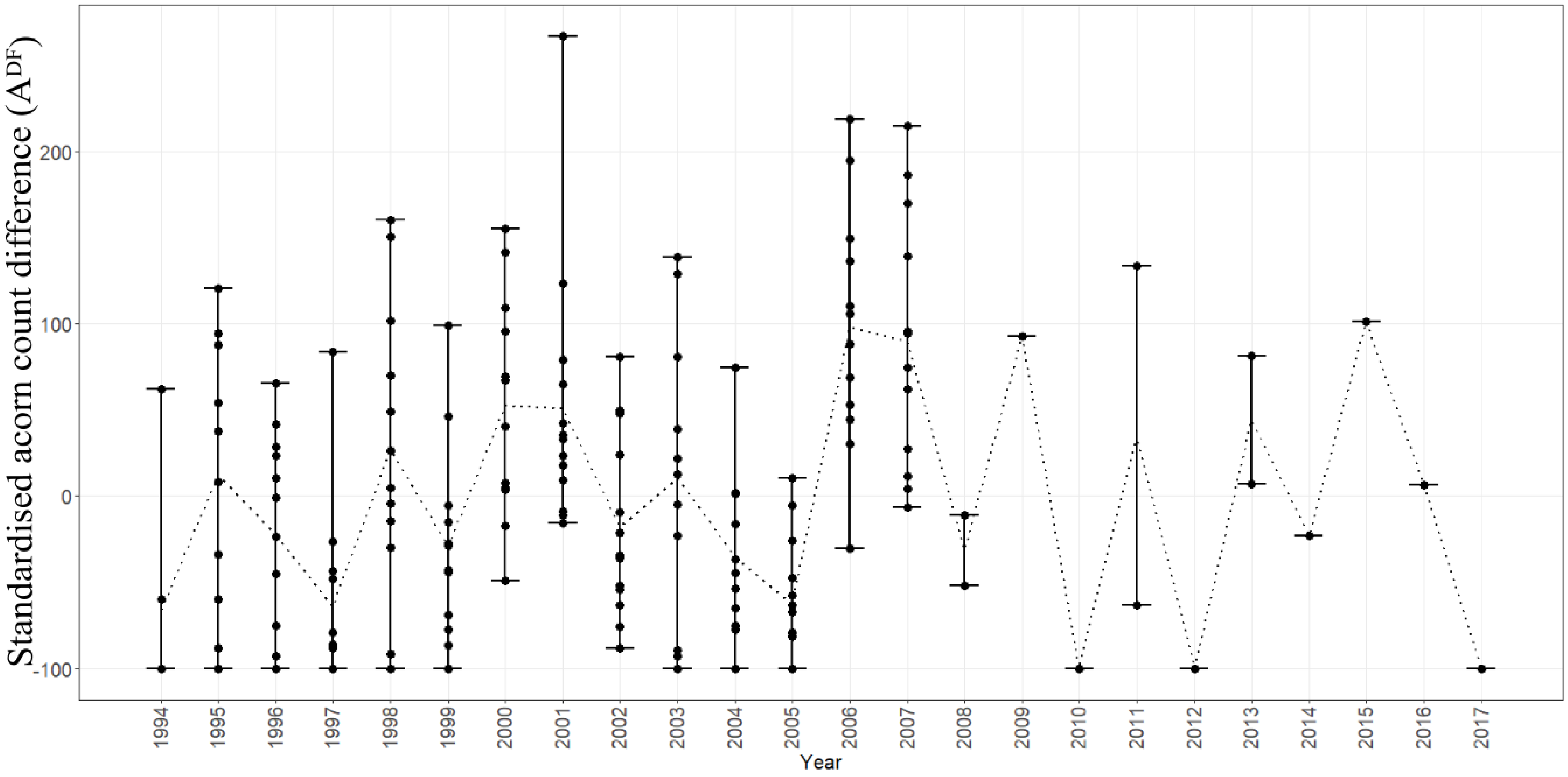


Figure 3.6 Annual recordings of acorn production (*Quercus petraea* and *Quercus robur*) presented as a difference from the mean of both species at all sites in North-eastern France and the one in Germany. Each site is represented by a single symbol (●), with black vertical bars highlighting the range between the highest and lowest acorn-producing sites. In years where no vertical line is shown observations were only available at one site. The mean A^{DF} for each year, of those sites for which data is available, is shown by the dotted line. The number of sites with observations differs amongst years; no sites overlap perfectly with the same sequence of years (Tables 3.1 and 3.2).

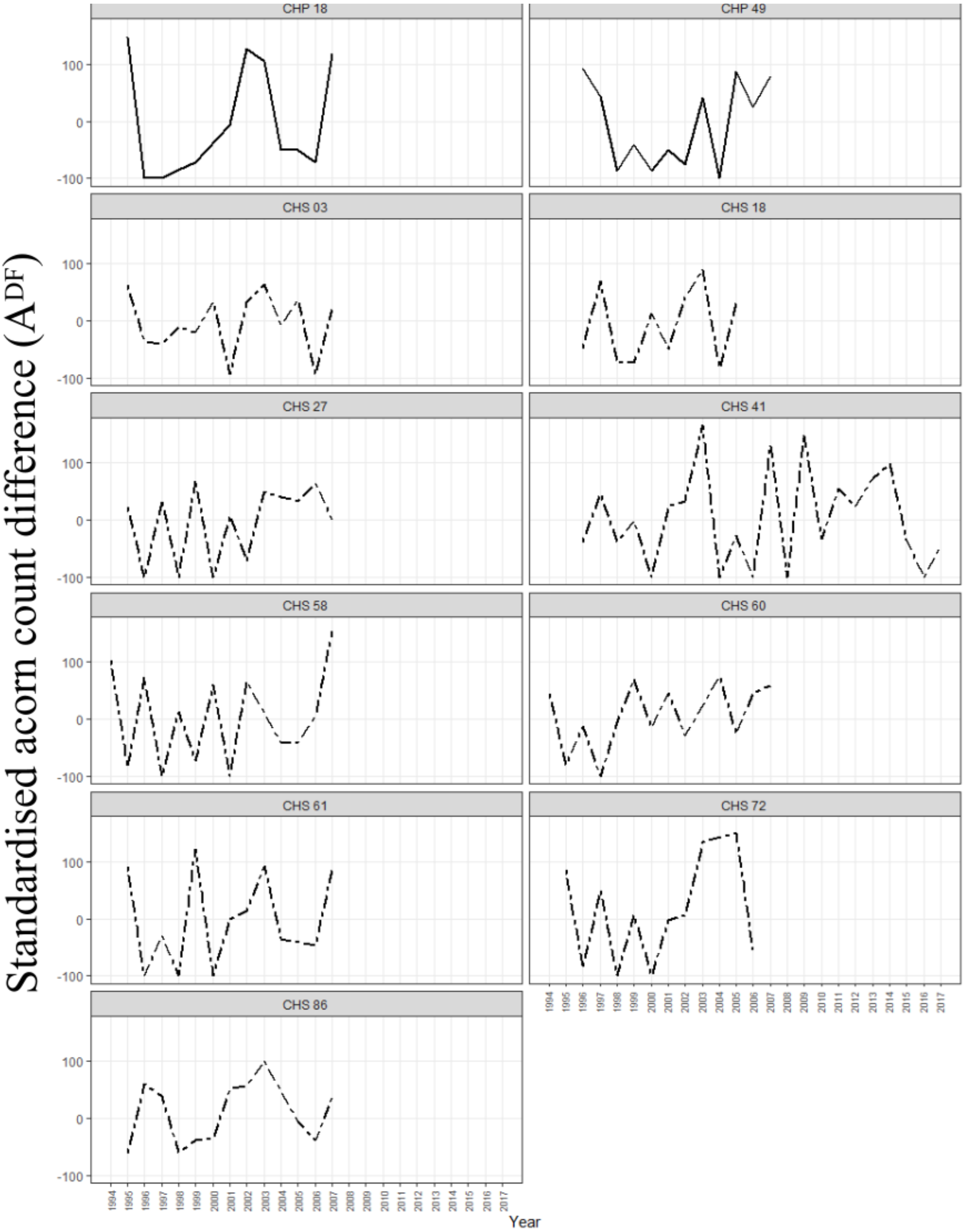


Figure 3.7 Annual recordings of acorn production presented as a difference from the mean of each site A^{DF} = standardised acorn count difference from the mean for each year; see methods) for all the sites in North-western France. All graphs are on the same scale for the X and Y axis. *Quercus petraea* is represented by a broken line and *Quercus robur* is represented by a solid line.

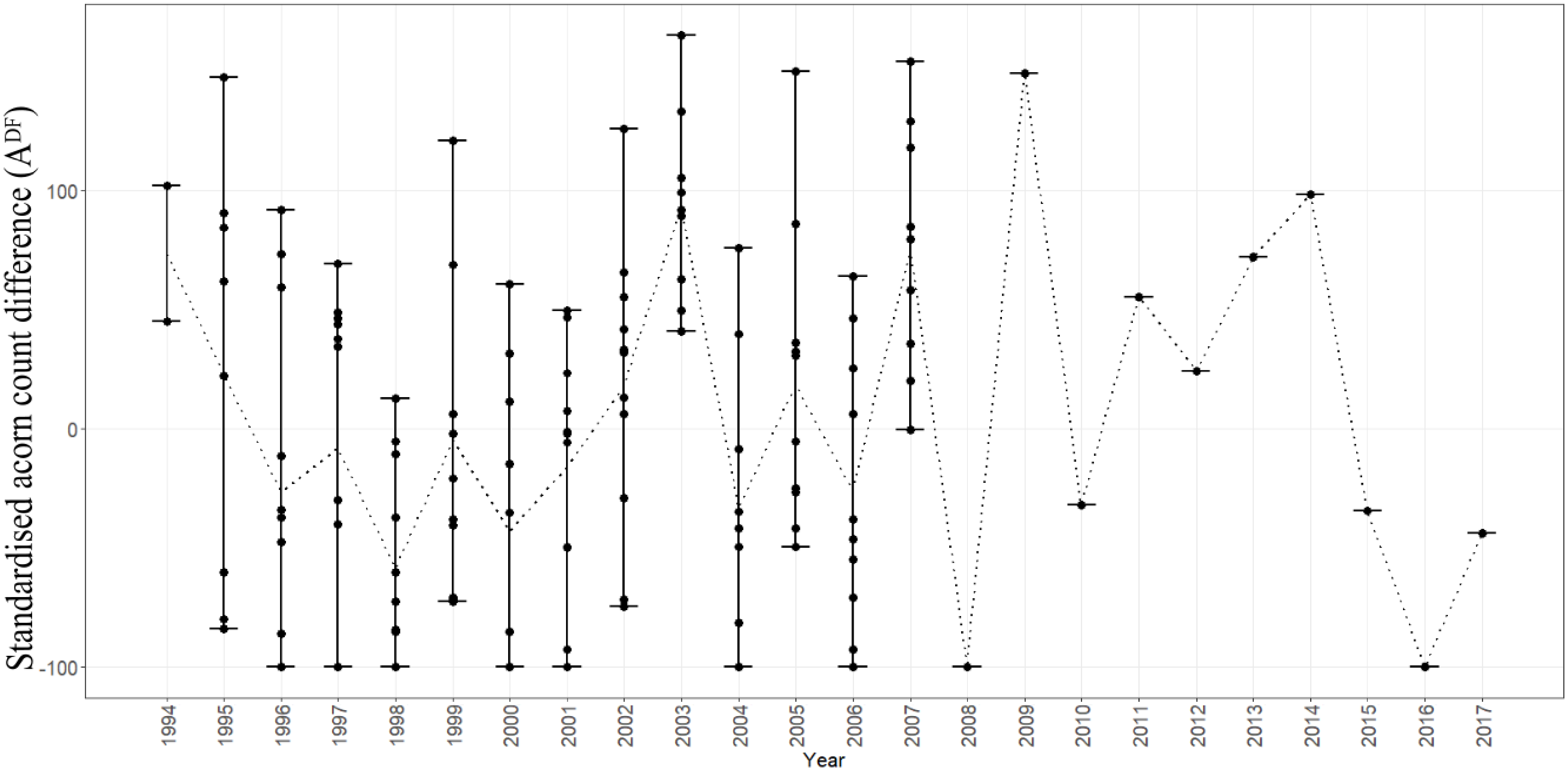


Figure 3.8 Annual recordings of acorn production (*Quercus petraea* and *Quercus robur*) presented as a difference from the mean of both species at all sites in North-western France. Each site is represented by a single symbol (●), with black vertical bars highlighting the range between the highest and lowest acorn-producing sites. In years where no vertical line is shown observations were only available at one site. The mean A^{DF} for each year, of those sites for which data is available, is shown by the dotted line. The number of sites with observations differs amongst years; no sites overlap perfectly with the same sequence of years (Tables 1 and 2).

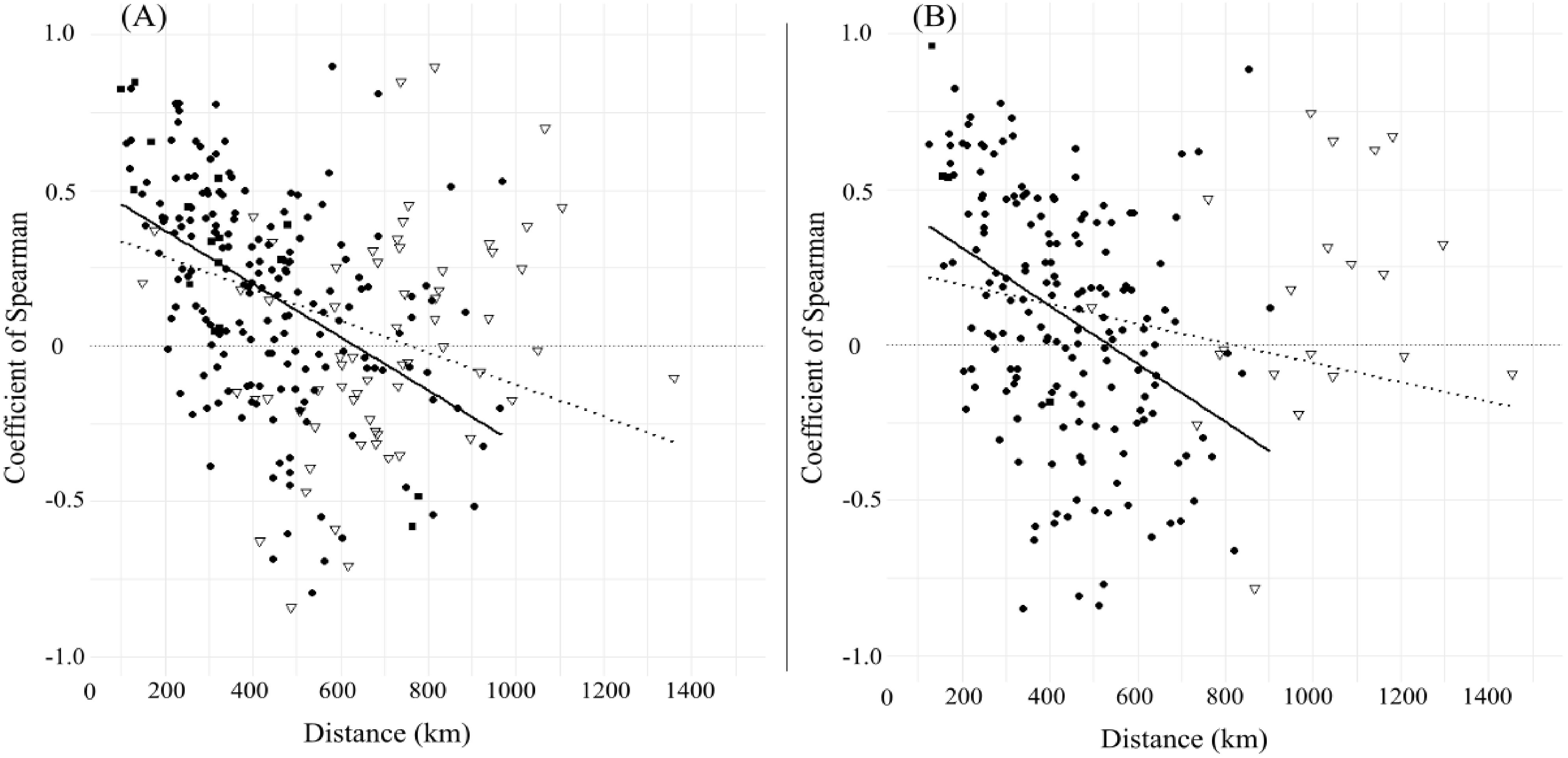


Figure 3.9 Spearman's rank correlation coefficient scores (ρ) by distance between pairs of sites for acorn production (A^{DF}) in (A) *Quercus robur* and (B) *Quercus petraea*. The symbols are for any two sites that overlap for six years or more of their time series range, with correlation tests only for the overlapping years. Symbols identify correlations within the UK (■), those within France (●), and those between the UK and France (∇). The linear models show how the degree of synchrony between sites changes with distance between sites for all sites (dotted line) and for site pairs within one country (solid line).

Model selection

Three models were ultimately selected for interpretation: all the *Q. robur* observations, all the *Q. petraea* observations, and the mixed species model (containing all *Q. robur* and *Q. petraea* observations). These models were decided upon in the following way. In the analyses, (summarised in Appendix 3.1-3.6), of the nine data groupings (each species and both species × UK, Continent (France and Germany) or all countries), the VSURF models showed better estimates for R^2, MSE and RMSE when comparing the three different types of regression models but minimal difference was detected when considering the out of sample MSE and RMSE scores (Appendix 3.1, 3.3, 3.5), nor in Accuracy and Kappa scores amongst the three different types of classification models (Appendix 3.2, 3.4, 3.6).

The initial models built included all the generated weather variables (Appendix 3.1-3.14), given that the effect of lagged acorn production likely mediated the effect of past weather variables on acorn production. A subsequent round of models was built with a simplified subset of the explanatory variables in which: (a) all weather variables before the 12 months running up to acorn fall were removed; and (b) very strongly correlated weather variables such as Tmax and Tmin were removed, keeping only Tavg instead; and (c) explanatory variables Acorn Lag, longitude, latitude and CoV were kept. These simplifications had minimal to no effect on the RMSE or MSE scores, and so as the most parsimonious method, the simplified models with continuous data only are presented for interpretation (Table 3.4). The continuous data models with the three highest number of observations were selected for presentation because (a) they were judged to be the most informative for interpreting the role of weather on masting; and (b) classifying the response variable failed to improve prediction accuracy.

PLSR

All three PLSR models fitted the training data poorly, only explaining between 17% and 27% of the variance in acorn production (Table 3.4; Fig 3.10). Neither did the models provide accurate predictions of acorn production, often making predictions that were, on average, wrong by more than 50 units (Table 3.4; Fig 3.11).

Variable importance scores (VIP) of the PLSR models were computed, and scaled as a percentage weighted importance, and the top 20 variables were ranked (Table 3.5). A non-scaled VIP score >0.8 (calculated as the weighted sum of the squared coefficients) suggests the variable makes a large contribution to the model (Wold et al., 1987). Over half of all the variables considered reached this threshold (45 for mixed species, 42 for *Q. petraea*, and 51 for *Q. robur*). Hence, variation in the weather contributed significantly and considerably to variation in acorn production across sites and years. However, a considerable number of weather variables affected acorn production.

Acorn lag (i.e., the previous year's value of A^{DF}) was the most important variable across all three models. It was by far the most important explanatory variable for the *Q. petraea* and mixed species models, whilst for *Q. robur* the difference between acorn lag's importance and the second most important variable was the smallest at 15.1% (Table 3.5). All models agreed that a dry, warm Spring (Apr Tavg, Apr Rain) was important to high acorn production, but whereas Apr Tavg had second highest importance in the *Q. petraea* and mixed species model, it was only placed 14th in the *Q. robur* model (Table 3.5). The *Q. robur* model was most driven by the negative effects of more growing degree days (Mar GD 0, Mar GD 5 etc.), higher March temperatures, and rain in April. The *Q. petraea* model highlighted positive effects of a warm previous autumn (Oct Tavg, Sep Tavg) and a wet and warm summer (Aug Rain, Jun Tavg, Rain Summer) (Table 3.5).

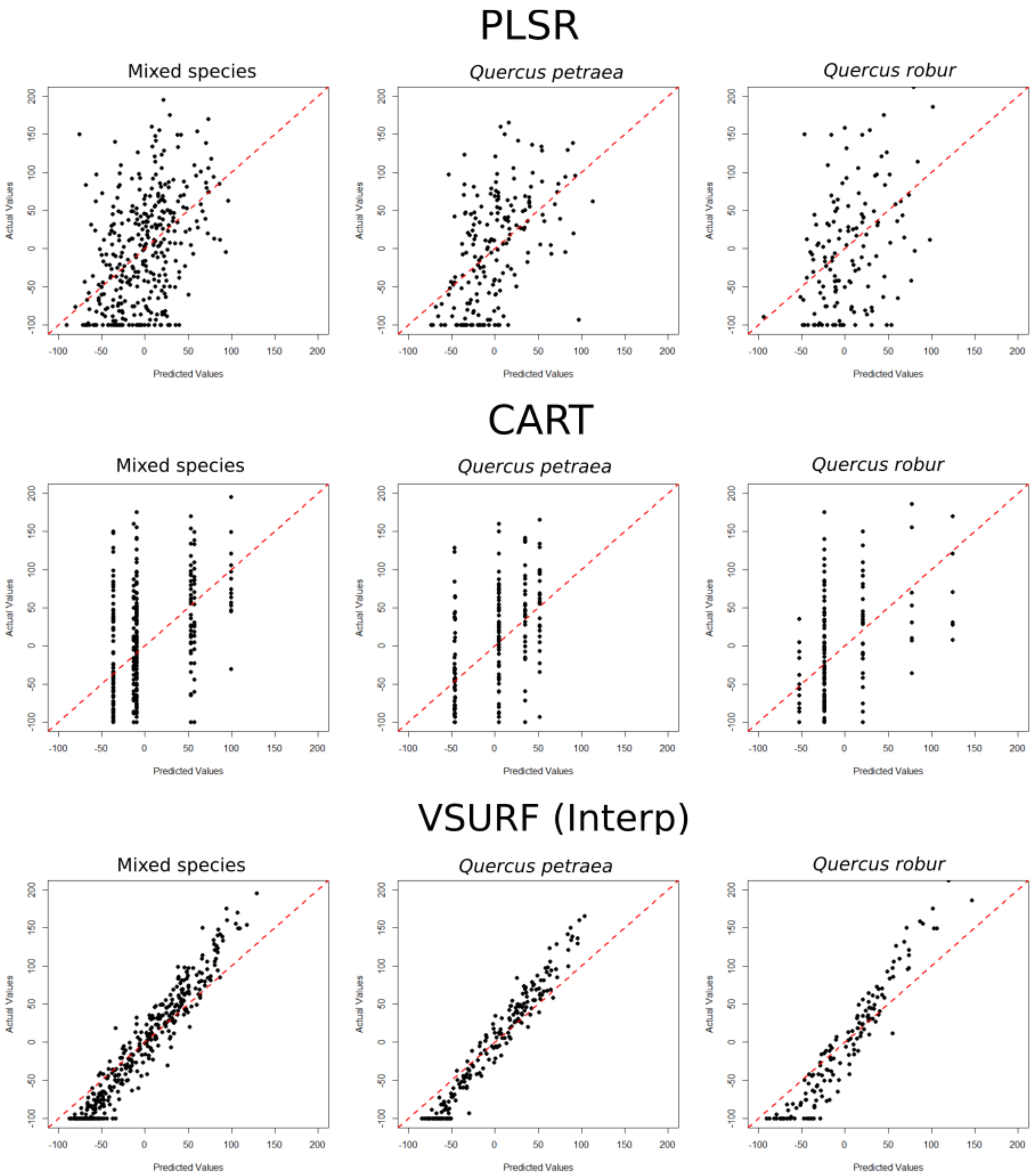


Figure 3.10 Comparison of fitted acorn production A^{DF} = standardised acorn count difference from the mean for each year; see methods) with actual values of the within sample data for the PLSR, CART and VSURF models (Table 3.5). The red broken line represents perfect agreement of fitted with actual values.

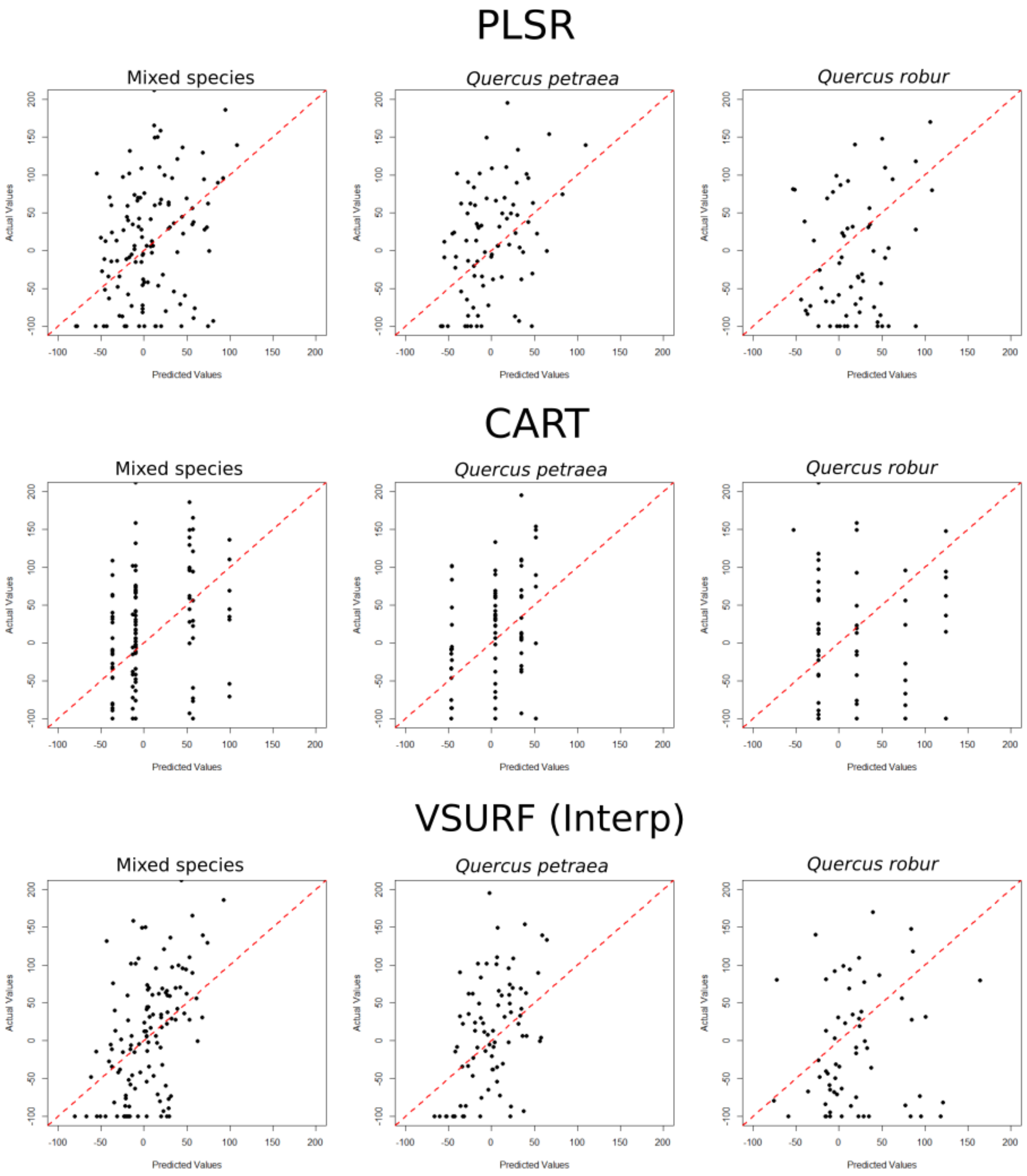


Figure 3.11 Comparison of predicted acorn production A^{DF} = standardised acorn count difference from the mean for each year; see methods) with actual values of the out of sample data for the PLSR, CART and VSURF models (Table 3.5). The red broken line represents perfect agreement of predicted with actual values.

Table 3.4 Results from fitting a series of models to quantify (training data [“In sample”]) or to predict (test data [“Out of sample”]) acorn production (standardised acorn count difference from the mean, continuous data, i.e. A^{DF}) for *Quercus petraea*, *Quercus robur,* and both species together.

Species	Method	In sample R^2	In sample MSE	In Sample RMSE	In Sample MAE	In Sample NRMSE	Out of sample MSE	Out of sample RMSE	Out of sample MAE	Out of Sample NRMSE
Mixed	PLSR	0.23	4705	68.6	54.62	0.16	5572	74.65	58.8	0.24
Q. petraea	PLSR	0.27	3691	60.76	49.00	0.23	4573	67.63	55.46	0.23
Q. robur	PLSR	0.17	5608	74.89	59.76	0.23	9601	97.98	78.56	0.22
Mixed	CART	0.23	4656	68.24	55.13	0.15	5501	74.17	60.23	0.23
Q. petraea	CART	0.25	3753	61.27	49.05	0.23	4321	65.74	54.47	0.22
Q. robur	CART	0.40	4346	65.93	53.68	0.15	11519	107.33	80.76	0.29
Mixed	VSURF- Inter.	0.87	818	28.61	22.71	0.06	4636	68.09	54.05	0.22
Q. petraea	VSURF- Inter.	0.86	695	26.37	21.64	0.10	4278	65.41	53.45	0.22
Q. robur	VSURF- Inter.	0.84	1031	32.12	25.42	0.07	7866	88.69	69.59	0.20
Mixed	VSURF- Pred.	0.85	854	29.24	23.24	0.06	5089	71.34	55.81	0.23
Q. petraea	VSURF- Pred.	0.84	797	28.23	23.51	0.11	4284	65.45	53.29	0.22
Q. robur	VSURF- Pred.	0.85	995	31.55	25.67	0.07	8082	89.90	71.00	0.20

Table 3.5. The top 20 variable importance scores (VIP) and model coefficients of three partial least squares regression (PLSR) analyses using weather variables to predict standardised acorn count difference from the mean (A^{DF}). The PLSR models for two oak species (*Quercus petraea* and *Quercus robur*) are presented separately and for both together. The number of components (latent variables) considered for each model are listed, together with the in-sample R^2, out of sample Root Mean Square Error ($_{\text{OOS}}$RMSE), and out of sample Normalised Root Mean Square Error ($_{\text{OOS}}$NRMSE). The NRMSE is calculated via the range of the response variables of each model. VIP scores are calculated as the weighted sum of the squared coefficients, ordering them based on the reduction each one makes to the sum of squares across the PLSR components and scaled from 1-100. For ease of interpretation, variables with negative coefficients are highlighted in red and those with positive coefficients are in green.

Quercus petraea			
Components	3		
R^2	0.27		
$_{\text{OOS}}$RMSE	67.62		
$_{\text{OOS}}$NRMSE	0.23		
Variable	VIP %	VIP score	Coeff
Acorn lag	100	4.1	-12.99
Apr Tavg	78.3	3.3	9.15
Feb AvgNR	59.4	2.5	7.89
Aug Rain	56.4	2.4	6.96
Oct Tavg	53.0	2.3	6.81
Apr Rain	49.1	2.2	-6.21
Sep Tavg	48.2	2.1	5.96
Jun Tavg	43.6	1.9	5.80
Dec Rain	41.7	1.9	5.69
Nov AvgNR	37.4	1.7	-4.81
Rain Summer	36.4	1.7	4.37
Tavg Spring	35.7	1.6	4.39
Dec AvgNR	30.5	1.4	-4.69
AF Feb	30.4	1.4	-3.85
Jul Rain	29.9	1.4	3.69
Jun AvgNR	29.7	1.4	-4.09
AF Mar	29.5	1.4	4.54
May NRM	29.0	1.4	-3.75
Jan AvgNR	28.4	1.4	-3.24
Mar Rain	26.8	1.3	3.59

Quercus robur			
Components	1		
R^2	0.17		
$_{\text{OOS}}$RMSE	97.98		
$_{\text{OOS}}$NRMSE	0.22		
Variable	VIP %	VIP score	Coeff
Acorn lag	100	6.4	-3.42
Mar GD 0	84.9	5.5	-3.04
AF Mar	72.9	4.7	3.0
Mar Tavg	67.7	4.4	-2.99
Mar GD 5	67.2	4.3	-2.96
Apr Rain	64.1	4.1	-2.86
Apr NRM	63.3	4.1	2.51
Jan GD 5	58.4	3.8	-2.44
Feb GD 5	53.3	3.4	-2.4
Jan Rain	51.7	3.3	-2.33
Nov AvgNR	51.2	3.3	-2.30
AvgNR Spring	51.1	3.3	2.29
Apr AvgNR	49.6	3.2	2.28
Apr Tavg	48.2	3.1	2.24
AvgNR Winter	46.3	3.0	-2.11
Jan GD 0	43.0	2.8	-2.07
Mar GD 10	39.0	2.5	-2.03
Jan GD 10	36.3	2.4	-2.00
Feb GD 10	35.8	2.3	-1.98
Aug Rain	35.3	2.3	1.98

All oak			
Components	3		
R^2	0.22		
$_{\text{OOS}}$RMSE	74.65		
$_{\text{OOS}}$NRMSE	0.24		
Variable	VIP %	VIP score	Coeff
Acorn lag	100	4.5	-13.06
Apr Tavg	64.9	3.0	6.18
Jul Tavg	57.9	2.7	7.54
AvgNR Spring	57.1	2.7	5.66
Mar Rain	52.4	2.5	7.38
Apr Rain	51.8	2.4	-4.72
AF Feb	51.6	2.4	-5.59
Oct Tavg	49.6	2.3	5.92
Aug Rain	48.5	2.3	5.96
Apr AvgNR	47.4	2.2	3.26
Sep Tavg	45.5	2.2	5.57
Apr NRM	43.5	2.1	1.78
Mar AvgNR	40.9	2.0	4.81
Nov AvgNR	40.3	1.9	-4.35
Tavg Summer	40.0	1.9	4.54
Mar GD 5	38.8	1.9	-5.41
Jun NRM	35.8	1.7	-3.99
May Tavg	34.9	1.7	4.28
AvgNR Autumn	34.7	1.7	-3.51
Tavg Spring	32.3	1.6	2.96

Pruned Regression trees (CART)

The pruned regression trees built from the three data sets (Figs 3.12, 3.13, 3.14) had similar success in fitting the training data when compared to the PLSR models (Fig 3.10), with only a higher in-sample R^2 for the *Q. robur* CART model (Table 3.4). None were better than PLSR models at accurately predicting masting on the test data (Fig 3.11), with similar out-of-sample RMSE scores for *Q. petraea* and mixed species models and higher RMSE for the *Q. robur* model (Table 3.4).

Both the *Q. petraea* and the mixed species model had April average temperature and previous acorn production as the most important nodes within the tree (Figs 3.12, 3.13), with *Q. petraea* placing some importance on a drier May and a warmer winter (Fig 3.13). The mixed species model included positive effects of a drier Spring (more days without rain) and wetter yet warmer Summer (Jul Tavg and Aug Rain) (Fig 3.12).

The *Q. robur* CART model did not find Acorn lag as one of the most important predictors, as it was not included in the pruned regression tree. Instead, the model found April rain to be the most important node (Fig 3.14), in which two scenarios led to greater acorn production: either a combination of low April rain and a warm summer; or high April rain after colder cumulative conditions from January to March (Jan GD 10) with a dry and cold March (AF Mar and Mar AvgNR).

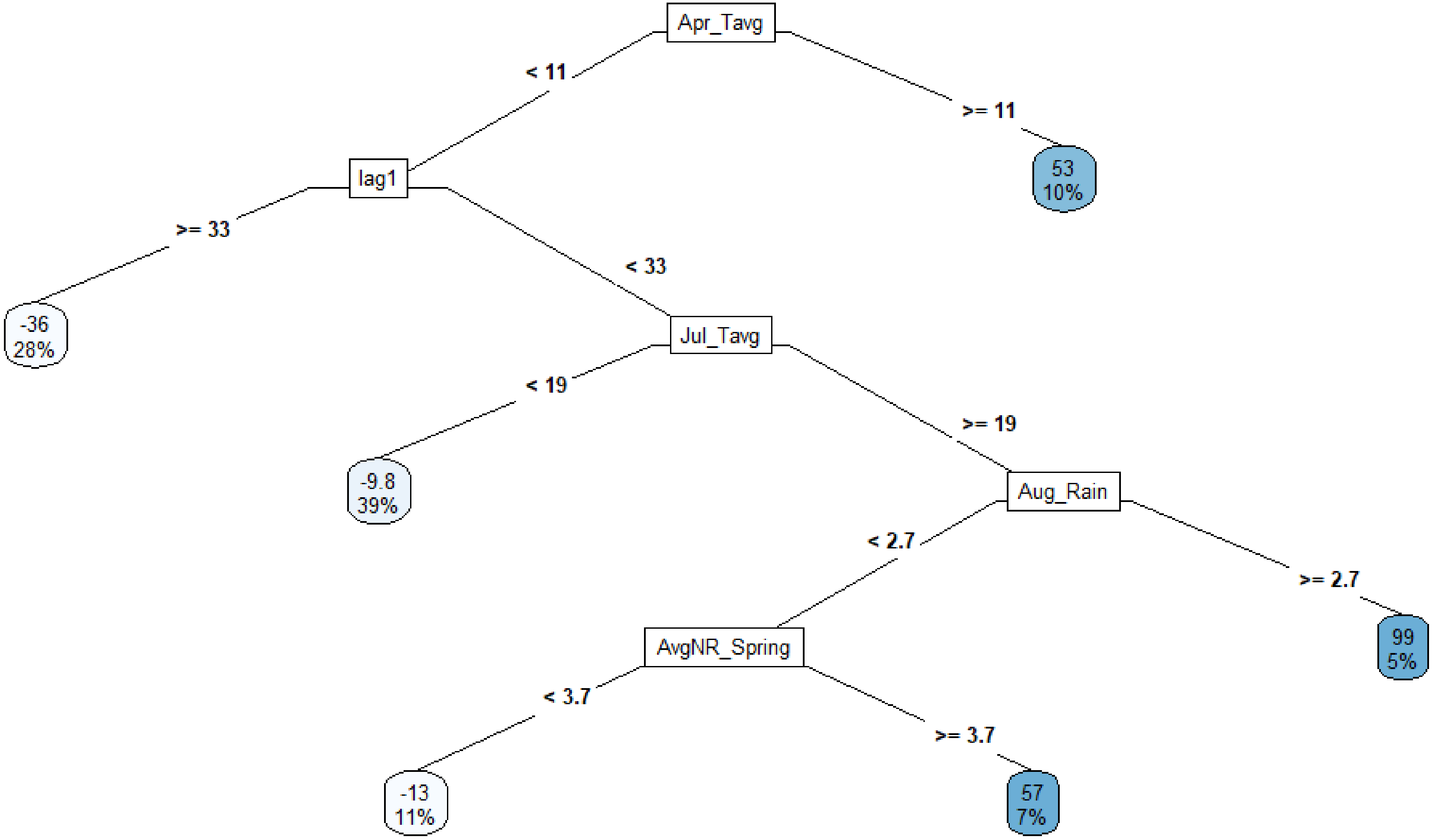


Figure 3.12. A pruned regression tree predicting acorn production in oak (*Quercus robur* and *Quercus petraea* data combined). The value splitting the nodes is shown on each branch. Each terminal node shows average difference from mean acorn production (for A^{DF}) (upper value in lozenge) and the percentage of observations from the full dataset (i.e. the percentage of the results [all years at all sites] which apply to this end branch of the tree) (lower value in lozenge). Terminal nodes are colour scaled from blue (high acorn production) to white (low acorn production). In sample R^2: 0.23, MSE: 4646, RMSE: 68.24. Out of sample RMSE: 74.17. NRMSE: 0.24

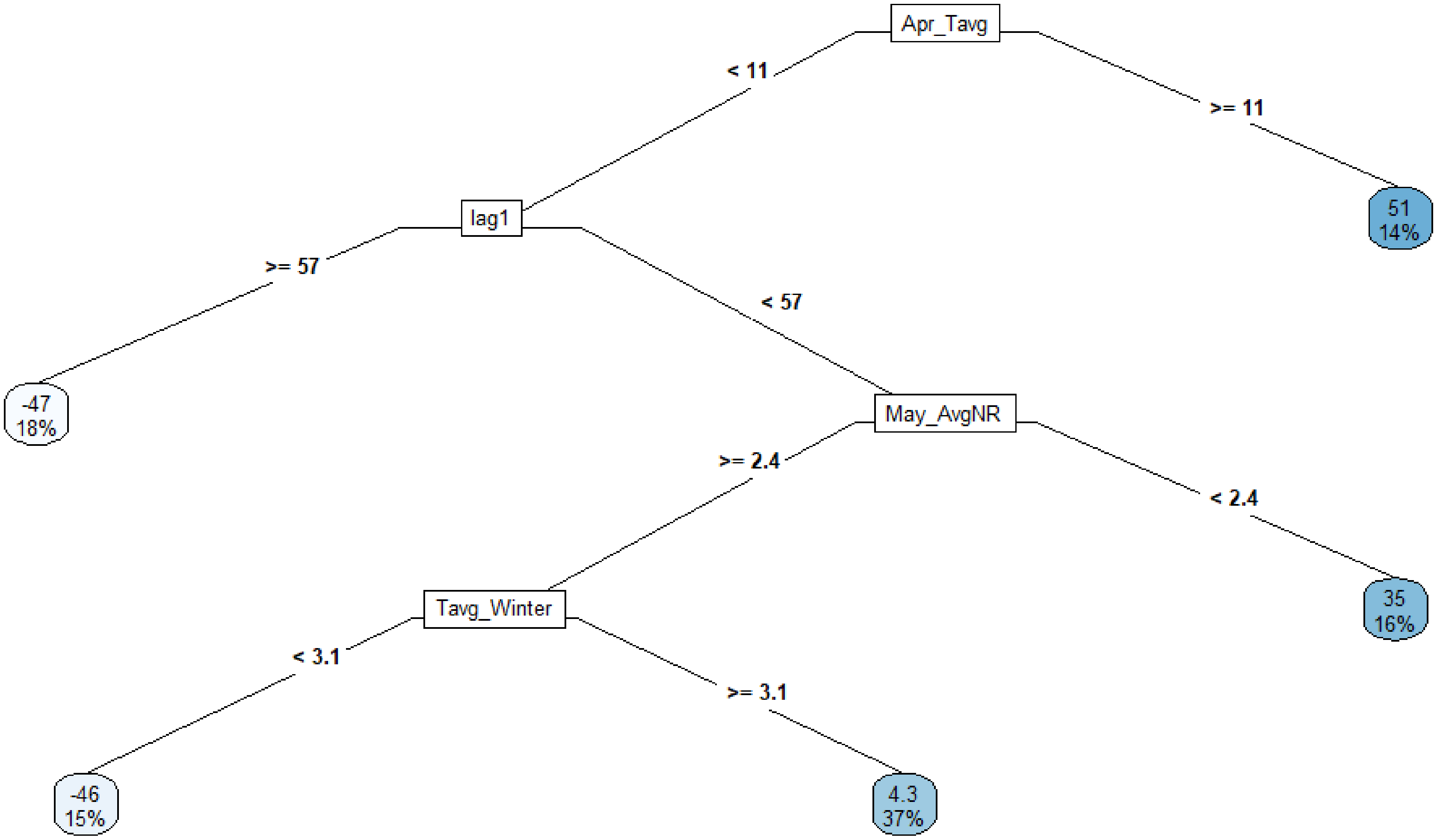


Figure 3.13. A pruned regression tree predicting acorn production in oak (*Quercus petraea*). The value splitting the nodes is shown on each branch. Each terminal node shows average difference from mean acorn production (for A^{DF}) (upper value in lozenge) and the percentage of observations from the full dataset (i.e. the percentage of the results [all years at all sites] which apply to this end branch of the tree) (lower value in lozenge). Terminal nodes are colour scaled from blue (high acorn production) to white (low acorn production). In sample R^2: 0.66, MSE: 3753, RMSE: 61.27. Out of sample RMSE: 65.74, NRMSE 0.22.

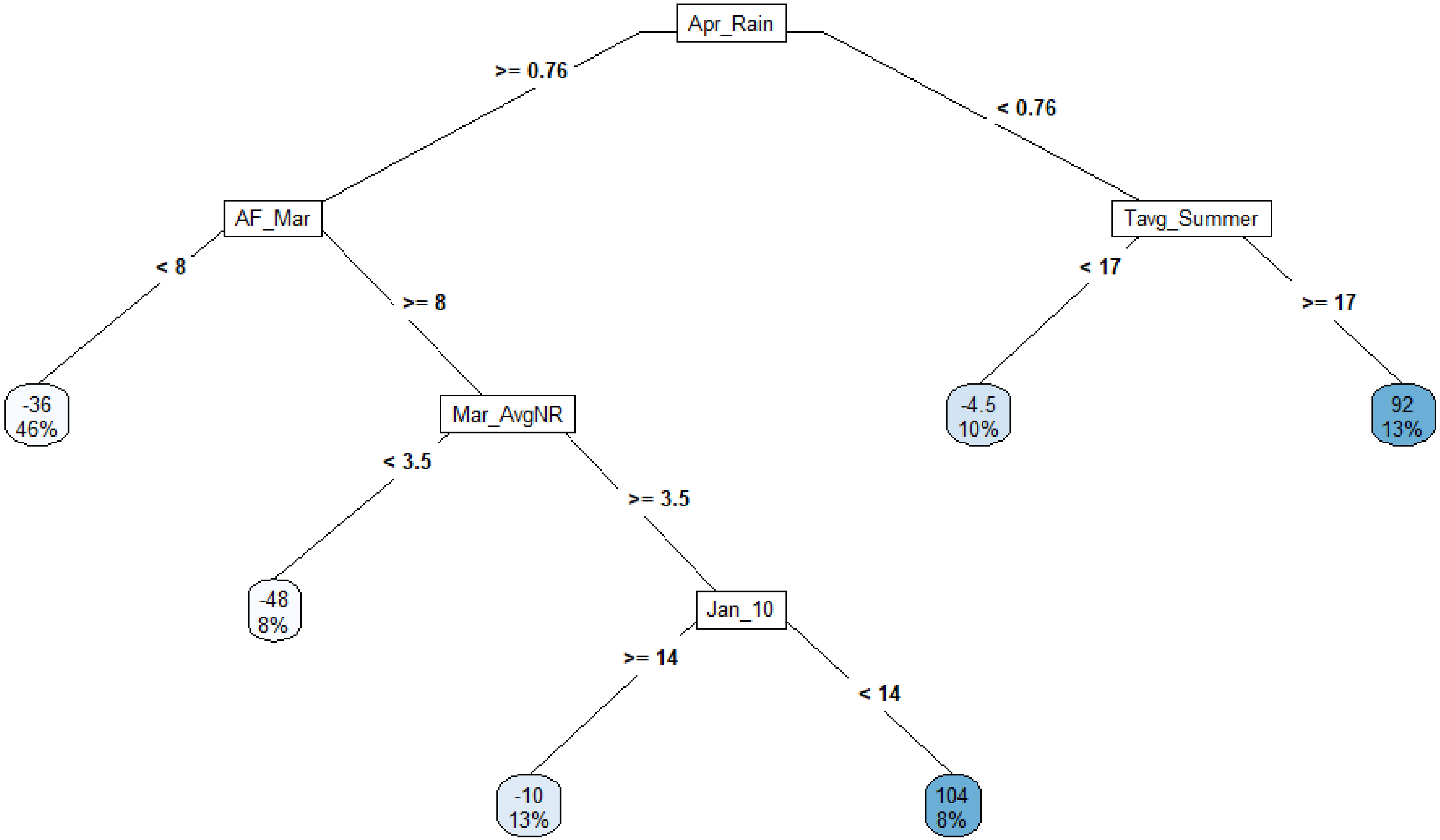


Figure 3.14 A pruned regression tree predicting acorn production in oak (*Quercus robur)*. The value splitting the nodes is shown on each branch. Each terminal node shows average difference from mean acorn production (for A^{DF}) (upper value in lozenge) and the percentage of observations from the full dataset (i.e. the percentage of the results [all years at all sites] which apply to this end branch of the tree) (lower value in lozenge). Terminal nodes are colour scaled from blue (high acorn production) to white (low acorn production). In sample R^2: 0.39, MSE: 4346, RMSE: 65. Out of sample RMSE: 107, NRMSE 0.29.

VSURF

There was minimal difference in the RMSE or MAE between the prediction, interpretation, and threshold steps, so the interpretation model was used to assess the VSURF method's performance (Table 3.4). The VSURF models fitted the training data much more closely than alternate models, with high R^2 scores of 0.87 for the mixed species; 0.86 for *Q. petraea*; and 0.84 for *Q. robur* (Table 3.4; Fig 3.10). However, the models struggled with the more extreme values, tending to underestimate the high and overestimate the low A^{DF} values (Fig 3.10).

Despite the VSURF models fitting the training data well (Fig 3.10), predictions with the test data provided high MSE, RMSE and MAE scores that were not low enough to consistently predict high or low acorn production (Fig 3.11). However, they were slightly improved over the PLSR and CART models (Table 3.4). However, when comparing the actual vs predicted values, it is hard to see any improvement of the VSURF models over the PLSR and CART models (Fig 3.11).

A site-specific VSURF model for Q. robur was built to examine this further using the longest time series available (Silwood Park). The model fitted the Silwood Park data well (Fig 3.15). When this model was applied to predict the independent data for *Quercus robur* production at the other four sites in England, it was much less successful (Fig 3.15). The VSURF method may be robust in explaining acorn production on a site-by-site basis but may not be applicable for extrapolating to multiple sites (Fig 3.15).

Returning to the full VSURF models, the more parsimonious prediction and interpretation models were chosen for presentation (Table 3.4). Five variables were selected in both the *Q. robur* and *Q. petraea* interpretation models: the average temperature in May, July, Spring, and Summer and the average number of days without rain in May (Table 3.6). In contrast, for the prediction models, only the summer average temperature and average days without rain in May were consistently chosen (Table 3.6). Acorn lag was selected within the *Q. petraea* prediction and interpretation models and the mixed species interpretation model but for neither of the *Q. robur* models. In agreement with the previous PLSR and CART models, the VSURF models for *Q. robur* found growing degree days to be much more important in influencing acorn production (Tables 3.5, 3.6; Fig 3.14).

To interpret how these variables influence acorn production, Shapley Values were calculated for each VSURF model repeated 100 times (Figs 3.16, 3.17, 3.18). Shapley values are shown on the scale of the response variable and show how the response variable may change based on the model being rerun with a different valued explanatory variable. There was complete agreement on the response direction for all explanatory variables shared between models. Acorn production showed a simple response to most explanatory variables, with high or low values of each variable showing an increase or decrease in levels of acorn production represented by higher or lower Shapley values (Figs 3.16, 3.17, 3.18).

For *Q. petraea,* by examining the effect of high or low values of the explanatory variables on the response variable, the VSURF model suggests the best order of events for high acorn production is a previous year of low acorn production and a warm previous autumn (Sep Tavg.1, Oct Tavg.1 etc), followed by a warm and dry spring (Tavg Spring, Apr Tavg, Apr AvgNR) and wet and warm summer (Tavg Summer, Jun Tavg and Aug Rain) (Fig 3.17). In comparison, for *Q. robur*, a cooler winter (represented by fewer growing degree days; Mar GD 5, Mar GD 10 etc.), followed by a warm and dry spring (May Tavg, Rain Spring and Apr NRM) and a warm summer (Tavg Summer) present the best conditions for acorn production (Fig 3.18). The VSURF model did not consider Acorn lag to be an important predictor.

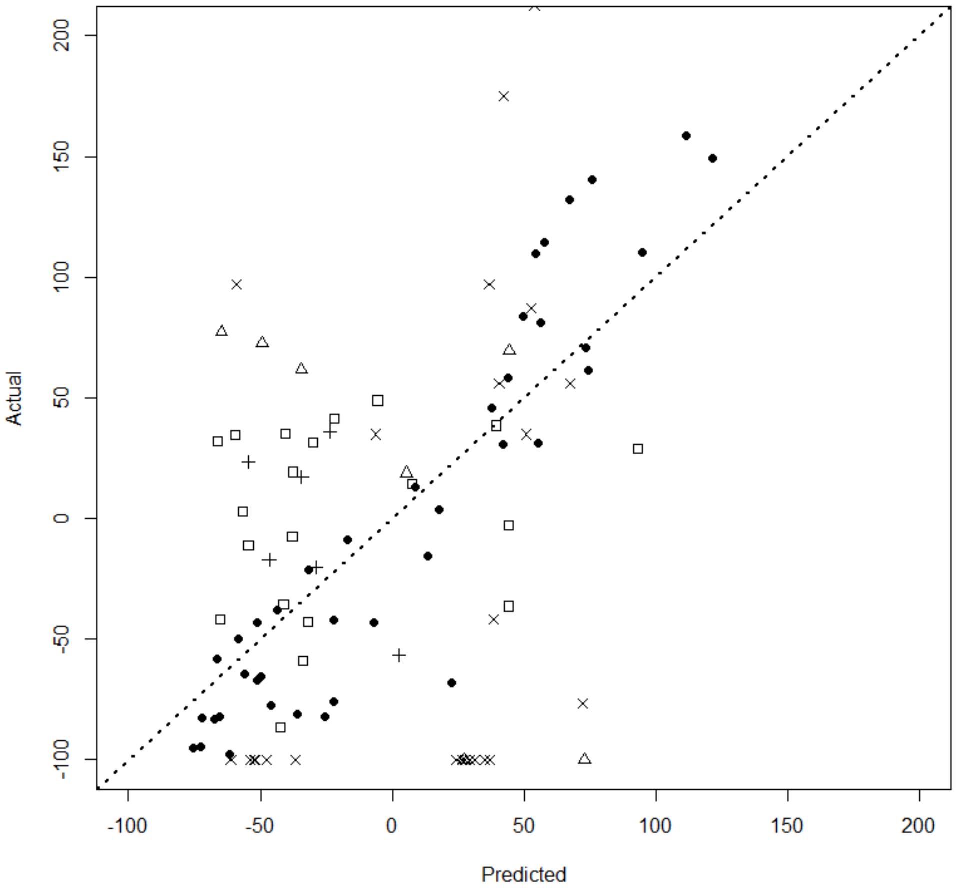


Figure 3.15 Comparison of actual values of *Q. robur* acorn production A^{DF} = standardised acorn count difference from the mean for each year; see methods) with either fitted values from a VSURF model trained with all Silwood Park data (●) or with values predicted by this model for Alice Holt (□), BIFoR (+), Newtown (Δ), or Southampton (×). (Training data (i.e., Silwood Park) : R^2 = 0.93, MSE = 931, RMSE = 30.52, MAE = 22.36; Test data: R^2 = 0.02, MSE = 8298, RMSE = 91.01, MAE = 74.48)

Table 3.6. A summary of the explanatory variables selected to build a random forest model predicting acorn production (A^{DF}) in the two oak species *Quercus robur*, *Quercus petraea* and both species considered together. Variables selection and model building was performed via the VSURF function in R. The variable for the interpretation models built embedded random forests models, starting with using the variables with the highest variable importance scores, and ending with those selected within a prior thresholding step. The smallest model with the mean out of bag error (OOB) rate below the threshold was then selected. The prediction model similarly built embedded random forest models, but instead added variables to the model in a stepwise manner, including a variable in the model if it lowered the OOB error more than a threshold. Explanatory variables selected for inclusion within a model are highlighted in green; those not included are highlighted in red.

	Quercus petraea		*Quercus robur*		Mixed species	
Variable	Inter.	Pred.	Inter.	Pred.	Inter.	Pred.
Jul Tavg	Y	N	Y	N	Y	Y
Sep Tavg	Y	Y	N	N	Y	Y
Apr Tavg	Y	Y	N	N	Y	Y
Tavg Summer	Y	Y	Y	Y	Y	Y
Apr AvgNR	N	N	Y	Y	Y	Y
AF Apr	N	N	N	N	Y	Y
Mar GD 5	N	N	Y	Y	Y	Y
Jun Tavg	Y	Y	N	N	Y	Y
Oct Tavg	Y	N	N	N	Y	N
Apr Rain	N	N	N	N	Y	N
Avg NR Spring	N	N	N	N	Y	Y
Acorn Lag	Y	Y	N	N	Y	N
Jun Avg NR	N	N	N	N	Y	N
May AvgNR	Y	Y	Y	Y	Y	Y
Tavg Spring	Y	N	Y	N	Y	N
Feb Rain	N	N	N	N	Y	Y
Aug Tavg	Y	Y	N	N	Y	N
May Tavg	Y	N	Y	N	Y	N
Feb Tavg	N	N	N	N	Y	Y
AF Nov	N	N	N	N	Y	N
Aug Rain	Y	Y	N	N	N	N
Jan Tavg	Y	N	N	N	N	N
Sep AvgNR	Y	Y	N	N	N	N
Rain Summer	Y	N	N	N	N	N
Mar GD 0	N	N	Y	Y	N	N
Mar Tavg	N	N	Y	N	N	N
Mar GD 10	N	N	Y	Y	N	N
Apr NRM	N	N	Y	Y	N	N
Feb GD 5	N	N	Y	N	N	N
Jul AvgNR	N	N	Y	Y	N	N
Apr Rain	N	N	Y	N	N	N
AF Mar	N	N	Y	N	N	N
Jan GD 5	N	N	Y	N	N	N
Rain Spring	N	N	Y	Y	N	N
Feb GD 10	N	N	Y	N	N	N
Mar AvgNR	N	N	Y	Y	N	N
Jan GD 0	N	N	Y	N	N	N
Dec Rain	N	N	Y	Y	N	N

Jan GD 10	N	N	Y	N	N	N
Mar Rain	N	N	Y	N	N	N
Jul Rain	N	N	Y	N	N	N

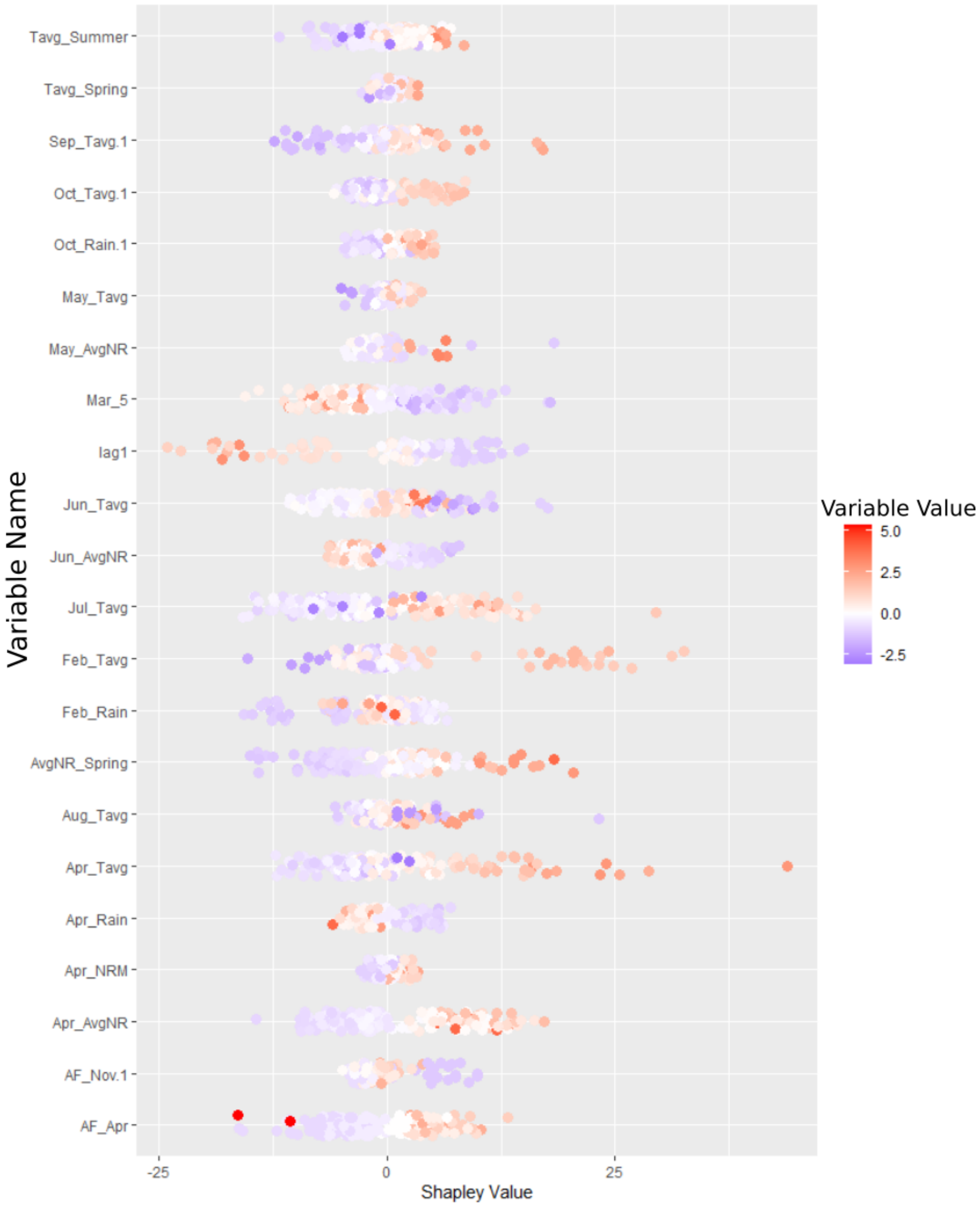


Figure 3.16. A summary of Shapley values of the VSURF model using weather variables to predict acorn production A^{DF} = standardised acorn count difference from the mean for each year; see methods) for the oak species *Quercus robur* and *Quercus petraea* considered together. Variables from the previous growing season are highlighted by ".1" (e.g. AF_Nov.1). Explanatory variable values were randomly generated 100 times each and their influence on the response variable was recorded as a Shapley Value. Shapley values are directly proportional to the change in the response variable based on change in one of the explanatory variables. The colour scale gives the value of the explanatory variable randomly selected in relation to its range. Red represents a high value of the variable and blue represents a low value of the variable. So, for instance we can see a high feature value for last year's acorn count (lag1) results in a strong negative effect on the Shapley value (a strong negative affect on this year's acorn count).

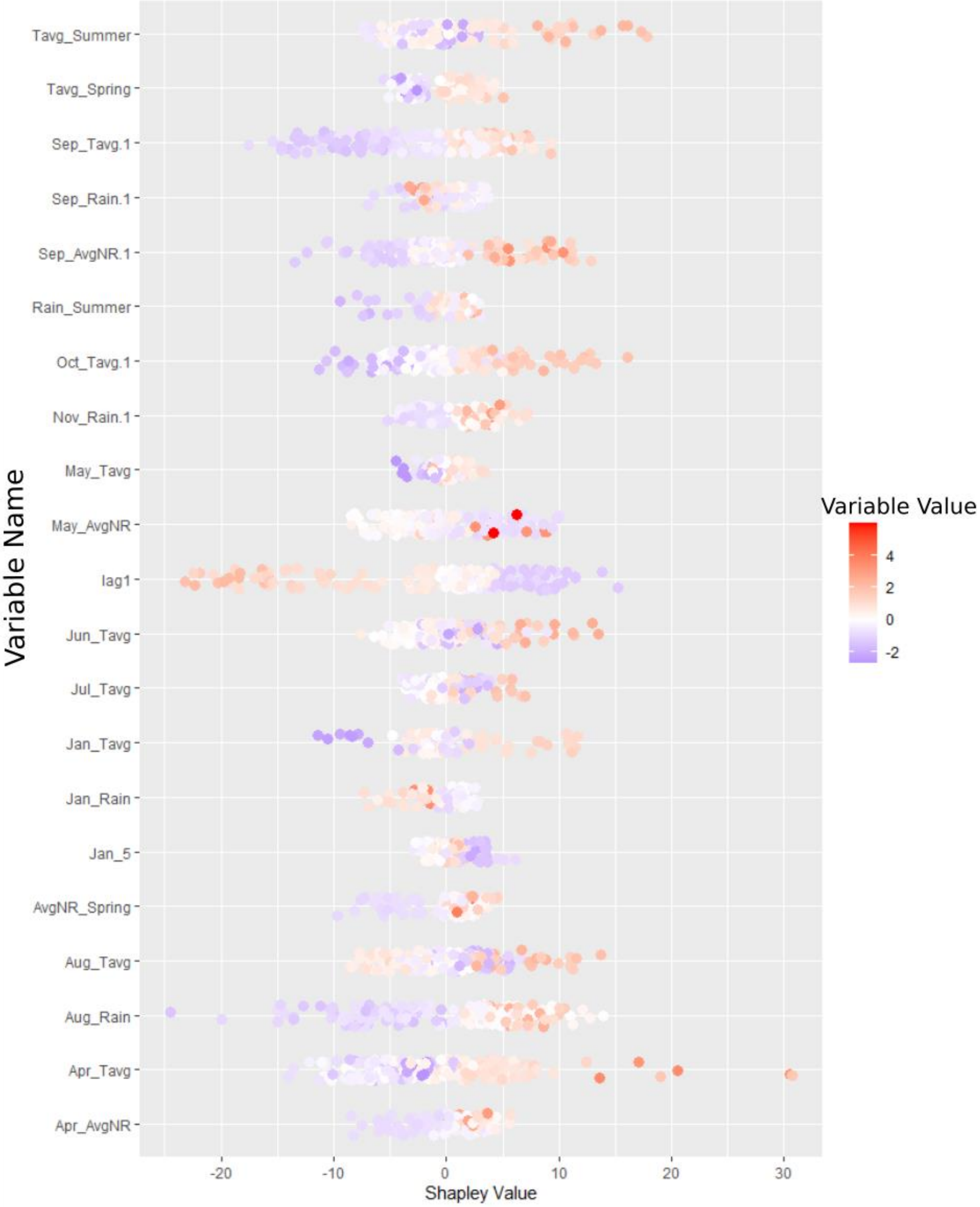


Figure 3.17 A summary of Shapley values of the VSURF model using weather variables to predict acorn production (A^{DF} = standardised acorn count difference from the mean for each year; see methods) for the oak species *Quercus petraea*. Variables from the previous growing season are highlighted by “.1” (e.g. Nov_Rain.1). Explanatory variable values were randomly generated 100 times each and their influence on the response variable was recorded as a Shapley Value. Shapley values are directly proportional to the change in the response variable based on change in one of the explanatory variables. The colour scale gives the value of the explanatory variable randomly selected in relation to its range. Red represents a high value of the variable and blue represents a low value of the variable.

Figure 3.18 A summary of Shapley values of the VSURF model using weather variables to predict acorn production A^{DF} = standardised acorn count difference from the mean for each year; see methods) for the oak species *Quercus robur*. Explanatory variable values were randomly generated 100 times each and their influence on the response variable was recorded as a Shapley Value. Shapley values are directly proportional to the change in the response variable based on change in one of the explanatory variables. The colour scale gives the value of the explanatory variable randomly selected in relation to its range. Red represents a high value of the variable and blue represents a low value of the variable.

3.4 Discussion

Considering the four hypotheses set out in the introduction, the study concludes that:

(1) Masting years coincided in geographically close sites, but this was not the case for all sites, and this synchrony broke down over larger distances;

(2) Warmer and drier conditions in Spring and warmer Summers were positively correlated with acorn production,

(3) The ability of models to predict acorn production using meteorological conditions was poor;

(4) *Quercus robur* and *Quercus petraea* responded similarly to many weather cues but with some differences as to which of the many cues was more important.

These points are considered in more detail below.

Patterns of masting and geographic synchrony

Key definitions of masting include (1) interannual variability and (2) geographic synchrony in seed production (Kelly, 1994; Kelly & Sork, 2002). This study found large interannual variability in acorn production for all sites in both *Quercus robur* and *Quercus petraea*, with large peaks in acorn production often followed by deep troughs (Figs 3.1, 3.3, 3.5, 3.7). Sequential years of high acorn production were particularly uncommon. This is in accord with the suggestion that the trees expend most of their stored resources during a mast event and need at least one year's recovery (Pesendorfer et al., 2016; Schermer et al., 2019). The rare occasions of sequential high production years may have been due to interannual variation in the individual trees producing large numbers of acorns (i.e., different trees contributed to the large numbers of acorns in each year). Data specific to individual trees across years would be needed to test this suggestion. Increased resource uptake in the year after the initial mast event would also explain this pattern, but one would expect to see a climatic cause, such as increased precipitation (Yang et al., 2008).

The inherent subjectiveness in the definition of masting makes it difficult to identify the periodicity of mast events, but high acorn production commonly occurs every 2-4 years (Figs 3.1, 3.3, 3.5, 3.7). The lack of consistent periodicity in masting is widely reported in the literature (Bogdziewicz et al., 2017; Fernández-Martínez et al., 2017) and is likely indicative of the stochasticity of weather variables, driving changes in resource uptake (Resource Matching) and conditions for efficient pollination (Pollination Moran) (Pearse et al., 2016).

In agreement with Caignard et al. (2017), there was weak synchrony in masting between sites, the strength of these correlations was influenced by distance: synchrony decreased as the distance between the sites increased (Fig 3.9). This effect may be explained by environmental heterogeneity across Europe, as well as differences in tree and stand age which have been reported to affect seed production in several masting species (Caignard et al., 2017; Genet et al., 2010; Pérez-Ramos et al., 2014; Pesendorfer et al., 2020).

Reduced synchrony the greater the distance between sites may suggest a range limit to the weather's ability to synchronise oak masting – or important differences in weather over long distances. In white spruce (*Picea spp.*), synchrony of cone masting had a limit of 1000 km and was largely asynchronous over 1500 km (LaMontagne et al., 2020). From the results of this study on *Q. robur* and *Q. petraea*, the correlation in masting appears to decline to nil (on average) after 655km for *Q. robur* and 714km in *Q. petraea* (Fig 3.9). When only considering paired sites on the same landmass, the relation between synchrony and distance was stronger; synchrony was lost after 532km for *Q. robur* and 434 km in *Q. petraea.* That the effect was stronger when removing site pairs between the UK and mainland Europe could be because of the Atlantic and Continental air masses causing differences between the UK and Continental climates. On the other hand, such considerations mean that the southern UK's weather is more like neighbouring areas of France (i.e., warm summers). At the same time, intra-landmass differences in climate are strengthened by the Maritime and Arctic winds (i.e., cooler summers and heavy rain) in the northern UK, and mountainous regions in southern mainland Europe (i.e., lower temperatures and more rain) (Joly et al., 2010).

The predictive ability of models built from weather variables

If the lack of synchrony in acorn production at sites far apart (Fig 3.9) were due to differences in their weather, then quantifying the effect of weather on acorn production might resolve site differences. Although weather accounted for some of the variations in acorn production (Fig 3.10), modelling weather variables proved rather uninformative in predicting mast years across all model types and species groups (Fig 3.11). The VSURF approach, however, was the most effective at fitting models to observations (Figs 3.10, 3.15). That consideration of the continuous response variables was more successful than the categorical variables highlights the difficulty of dichotomising datasets into mast and non-mast years (Kelly, 1994).

As the sites being studied were spread out over such a large area, there were likely phenological differences, such as different peak flowering times. This study attempted to generalise by presenting weather variables as monthly or seasonal values. However, effects on masting could be much narrower in time, with the receptivity of female flowers to pollination measured in days, not weeks (Roussel, 2011), something the models may fail to capture.

Further, the models cannot consider the internal resources within the trees. Periods of optimal conditions could be missed if a lack of stored resources results in failed fruiting. It may also be incorrect to generalize across many populations whose genetics may differ (Le Corre et al., 1997; Zanetto & Kremer, 1995). Previous studies have found interregional differences in masting cues (Nussbaumer et al., 2018), suggesting masting cues may be population specific. That a VSURF model could fit the data at one location, but that same model was unable to correctly predict masting at other sites in England is further evidence of the difficulty of generalising across sites (Fig 3.15). Despite these models' inability to predict acorn production successfully, we may cautiously use them for inference in terms of identifying the more important weather variables involved in the phenomenon of masting. In particular, the VSURF models fitted the training data well (Fig 3.10), whilst the regression trees provided by the CART models identified certain combinations of different weather variable values that led to greater probability of above average acorn production (Figs 3.12, 3.13, 3.14).

The importance of weather cues for *Quercus robur* and *Quercus petraea*

A warm and dry spring is commonly associated with a higher chance of a masting event in *Quercus robur* and *Quercus petraea* (Caignard et al., 2017; Hanley et al., 2019; Nussbaumer et al., 2018). This was also the case in this study, with the average number of days without rain in May positively correlated with acorn production (Table 3.6; Figs 3.16, 3.17. 3.18). Drier periods during peak flowering likely increase subsequent acorn production as a result of the Moran effect (Koenig, 2002), in which the trees under optimum environmental conditions have more efficient and longer distance pollen flow, whereas sub-optimal high precipitation conditions instead wash pollen out of the air (Caramiello et al., 1994; Rodríguez-Solà et al., 2022).

The average summer temperature was also positively correlated with acorn production (Table 3.6; Figs 3.16, 3.17, 3.18). This has been witnessed in *Q. robur* populations across Europe (Askeyev et al., 2005; Hanley et al., 2019). Warmer summer temperatures likely enable higher rates of photosynthesis, increasing the assimilate available for acorn development (Kelly & Sork, 2002). This is either represented by a larger biomass of acorns (Sánchez-Humanes et al., 2011) or less acorn abortion (Tsuruta et al., 2011).

What is clear from this study is the complexity of weather cues involved. The weather might be expected to influence acorn production at many different stages in development. Potentially these include, but are not limited, to flower bud formation; duration and timing of flower opening; pollen development; pollen dispersal; receptivity of the stigma to pollen; pollen germination; pollen tube growth; early acorn development (cell division and differentiation); acorn filling (assimilate deposition). Hence it is perhaps not surprising that many weather cues were identified in the analyses. The strength of the CART method of analysis is the visualisation of complex interactions. For instance, in *Q. robur* the combination of four weather factors (April Rain, Air Frost in March, No Rain days in March and Growing Degree Days from January) determined the difference between a strong mast year and a failed year (Fig 3.14). Similarly, the simplest VSURF model identified nine explanatory variables for acorn production (Table 3.6, *Q. petraea* prediction model). Hence this study may agree with other reports on the specific weather variables that affect acorn production; its main conclusion is that there is no simplistic answer to predicting acorn production accurately each year at many sites.

The lagged acorn count was considered much more influential for *Q. petraea* than *Q. robur* in this study, as shown by (1) the lesser relative importance of “Acorn Lag” for the PLSR models (Table 3.5) and (2) its complete absence as an important predictor in the VSURF or CART methods (Fig 3.14, Table 3.6). This difference between the two species has not previously been reported. It could suggest a higher reliance on stored reserves for acorn production in *Q. petraea* than in *Q. robur*, or a greater ability of *Q. robur* to recover stored reserves, making them less of a limiting factor. All of this could explain why some studies have found *Q. robur* to mast more frequently than would be expected from other masting species (Crawley & Long, 1995). Similarly, growing degree days were highlighted as important variables in all three model types for *Q. robur*, with higher growing degree days negatively affecting acorn production but not for *Q. petraea* (Tables 3.5, 3.6; Fig 3.14). Likely, the more growing degree days in the early months of the year hasten budburst, lengthening the growing season and increasing resource accumulation, but it also makes the flowers more vulnerable to spring frost, negatively affecting acorn production (Wypych et al., 2017). This pattern of a longer growing season followed by failed acorn production would also increase stored reserves and could be responsible for the weaker impact of “Acorn Lag” on *Q. robur*.

The poor fits from the models to predict independent observations in the current climate (Figs 3.11, 3.15) indicate that our quantitative understanding of the effect of weather on acorn production is not yet sufficient to predict acorn production with further climate change. It is generally believed that species that follow differential-temperature cues (the difference in weather between years) are robust to the effects of climate change, as increasing temperatures will not influence the between-year differences in temperature (Kelly et al., 2013). However, this study is in agreement with many other findings that acorn production in *Q. robur* and *Q. petraea* is affected by weather cues in the same growing season as the acorns are produced (Bogdziewicz et al., 2017; Fernández-Martínez et al., 2017; Lebourgeois et al., 2018). Drought and water stress in summer have been shown to reduce acorn production in Southern European *Quercus spp.* (Fernández-Martínez et al., 2012; Pérez-Ramos et al., 2010) we should be cautious about the effects of increased temperature on the already strained supply of *Q. robur* and *Q. petraea* seeds (Bole, 2022).

In conclusion, this modelling study has identified several important weather cues that influence acorn production and so the phenomenon of masting in *Quercus robur* and *Quercus petraea*. Although it has highlighted the considerable errors likely in attempting to predict widespread acorn production from weather records alone. Instead, next steps may entail taking these modelling methods and applying them on more detailed and temporally precise scales of single woodlands, with inclusion of additional explanatory factors such as soil nutrients, and pollen levels.

Chapter Four: Pollen source affects the success of acorn production in pedunculate oak (*Quercus robur* L.)

Abstract Acorn production in oak (*Quercus* spp.) shows considerable inter-annual variation, known as masting. The effect of pollen sourced from different trees within or outside the stand on acorn production were investigated in pedunculate oak (*Quercus robur* L.) in an ancient mixed woodland over two moderate masting years. More than 85% of the flowers or developing acorns were aborted between May and August each year in all pollination treatments. Where flowers were protected with pollen bags, no acorns were produced. In contrast, hand-pollination with out-of-stand pollen provided the greatest number of acorns in both years, 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, applying a mixture of half out-of-stand and half within-stand pollen produced an intermediate number of mature acorns between 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 where the abortion of pollinated flowers and immature acorns determines a mast year (rather than the number of flowers produced) at this site.

4.1 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 are self-incompatible (Loveless and Hamrick 1984), including *Quercus* spp. (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).

There is a consensus that around 50%-70% of the geneflow in oak species comes from pollen outside studied oak stands (Dow and Ashley 1998a, b; Streiff et al. 1999; Craft and Ashley 2010; Abraham et al. 2011). The domination 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, whilst each of these studies analysed stands of similar size (4-5 hectares), the individuals in each study varied 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 assume. Often, oak trees would fail to pollinate their nearby neighbours but pollinate much more distant trees instead. There was, however, no evidence of genetic-based avoidance of within-stand pollen (Dow and Ashley 1998b). Indeed, out-of-stand pollen still accounted for >35% of all successful pollinations even within highly-isolated oak stands beyond the species' central distribution range where out-of-stand pollen had to travel >80km and past physical barriers (i.e. the Southern Ural Mountain Range) (Buschbom et al. 2011).

The consistent detection of acorns pollinated by out-of-stand pollen implies a considerable advantage of wide crossing – i.e. with trees likely to be genetically distinct. Genetic analysis of developing acorns can only determine pollen source if there is a successful outcome, i.e. the failure of pollination from incompatible sources cannot be estimated from acorn production. Without studying initial pollination, one cannot distinguish whether there is 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 of 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 selfed-pollen tubes reaching the ovule and subsequent acorn abortion (Yacine and Bouras 1997).

Many outcrossing species prevent self-fertilisation at pollination via pollen tube growth abnormalities (Kalinganire 2000). In contrast, oak appears to have evolved a delayed self-incompatibility mechanism (Boavida et al. 2001). This 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 compared to the benefits of later maternal selection.

This study reports pollen addition and limitation experiments over two years to determine the effect of pollen source identity on *Quercus robur* L. acorn development and abortion in order to test the following hypotheses.

(1) Supplemental out-of-stand pollen increases acorn production.

(2) Successful acorn development to maturity is greater from flowers pollinated by out-of-stand pollen.

4.2 Materials and Methods

The experiment was conducted at Wytham Woods, Oxford (Lat: 51.76946°, Long: -1.33849°), 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), on the same eight *Q. robur* trees in 2022 and 2023. All eight trees were mature, with diameters at breast height >50cm and heights >15m. 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 on additional trees at this site showed that 2022 and 2023 were moderate for acorn production: 2020 was a mast year, no acorns were produced in 2021, whilst mature acorn numbers in 2022 and 2023 were 61% and 42% of those in 2020, respectively. The weather in April and May (the period 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 27.85mm precipitation compared with 11.38°C and 58.55mm, respectively.

In early February each year, a total of 300 branches on 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 numbers of leaves and flowers on each branch were counted in May; the former 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 mix of half within-stand and half out-of-stand pollen (50-50), natural pollination (NAT), and no pollination (NOP). In 2023, only three treatments were applied: WSP, OSP and NAT.

Pollen was collected in late April and early May each year, following Rousell (2011), when the anthers of the catkins had a yellow tinge, and the pollen sacs had just begun to burst releasing pollen. The out-of-stand pollen was collected from five sites across the South of England (Appendix 4.1): Greenham Common, Newbury (Lat: 51.37702°. Long: -1.29067° [the closest site, 43km from Wytham Woods]), Whiteknights campus, Reading (Lat: 51.44044° Long: -0.94176°), Corsham Court, Corsham (Lat: 51.44267°, Long: -2.16142°), Bannerdown Common, Bath (Lat: 51.41703° Long: -2.30005°), and Southampton Common, Southampton (Lat: 50.92893°, Long:-1.40879° [the furthest, 93km from Wytham Woods]). The within-stand pollen was collected from ten trees at Wytham Woods, but not the eight selected for this study. Catkins were collected by hand, taking care to exclude any leaves, twigs, or insects, and spread out on metal trays immediately to dry for 3-4 days in a well-ventilated room at above 25 °C; then sieved to separate the pollen. Pollen was combined and mixed within either the out-of-stand or within-stand sets to provide the two pollen samples and then stored at -18 °C for a short period until it was applied to the experimental trees. Three samples of pollen from each were drawn to assess viability after storage: the pollen was added to agar plates (sucrose 20%, agar 1%, boric acid 0.01%, pH adjusted to 5.5) and incubated at 30 °C. After 48 hours, the Petri dishes were observed under a microscope and the proportion of germinated (pollen tube length > half the pollen grain diameter) pollen grains in view were counted. This observation was repeated three times per Petri dish.

The female flowers were deemed receptive to pollination when the stigmas showed a pink-red inflorescence and were deployed horizontally. Each flower received two applications from a hand pollination pump (Yardwe, China). To prevent cross contamination of pollen, flowers were pollinated within the pollen bags using a different hand pollination pump for each pollen source. The 50-50 treatment received one application from each pump separately.

The pollen bags were left on whilst the flowers remained receptive to pollen, after which they were removed to avoid hindering growth. Bags were removed in late April from the NAT treatment enabling natural pollination. In the case of the NOP treatment, the bags were not removed until 12 May 2022, when the stigmas were no longer receptive to pollination. The selected branches were observed throughout the rest of the season to monitor the progress of acorn development. The presence of flowers and acorns was counted on six occasions in 2022 (1 May, 12 May, 30 May, 29 Jun, 3 Aug, 15 Sep); and twice in 2023 (9 May, 10 Aug).

All analyses were performed in R (R Core Team 2021). The experiments were analysed separately each year using a Generalised Linear Mixed Effect Model with a binomial distribution. The function '*glmer*' of the package lme4 (Bates et al. 2014) was used to assess the relationship of pollen treatment, using flower or acorn counts as the binary response variable, with the '*treatment'* category as a fixed effect and *'leaf number'*, '*branch'* and '*tree'* as the random effects. Models were built separately for each collection date, and model assumptions were checked via diagnostic functions in the package DHARMa. The Anova function from the 'car' package was used as an omnibus test to see if there was a significant difference in flower or acorn development amongst pollen source treatments. Where significant differences were detected, post-hoc Tukey pairwise comparisons were conducted via the *emmeans* model function of the 'emmeans' package. The functions '*aov*' from the package 'stats' and '*summary*' from 'base' R were used to assess if there were differences in pollen viability between the pollen treatments and the initial flower number per branch between treatments and years.

4.3 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. 4.1). 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 into acorns by August in either year. Differences in the initial numbers of flowers per 100 leaves among treatments were apparent (Fig. 4.2), 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). The branches allowed to pollinate naturally (NAT) showed inter-annual variation in acorn production (Fig. 4.3) with more acorns in 2022 than 2023; 1.84 ±0.69 acorns per 100 leaves in 2022, and 0.89 ±0.27 in 2023.

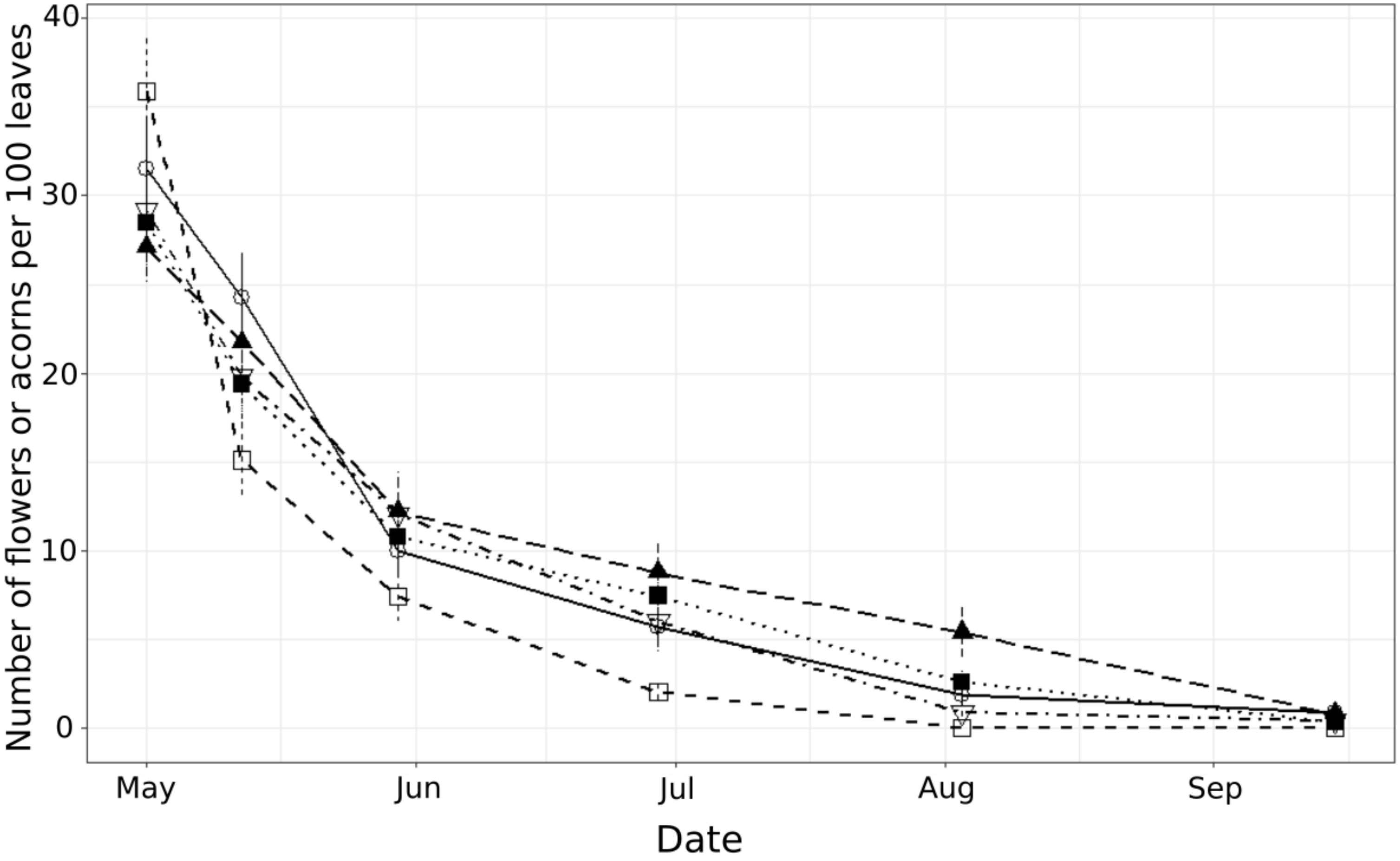


Fig. 4.1 The number of flowers or acorns per 100 leaves for a supplemental pollination experiment on branches of eight oak trees at Wytham Woods, Oxford, in 2022. Acorns matured by early August, whilst earlier counts were considered to be flowers, whether fertilised or not, in various stages of development. The treatments in 2022 were: within-stand pollen (dot-dash line, ▽ [WSP]), out-of-stand pollen (long dash line, ▲ [OSP]), a 50-50 mix of within-stand and out-of-stand pollen (dotted line, ■ [50-50]), natural pollination (solid line, ○ [NAT]), and no pollination (short dash line, □ [NOP]). The standard errors for each treatment are shown by vertical lines in the same style as lines connecting the datapoints

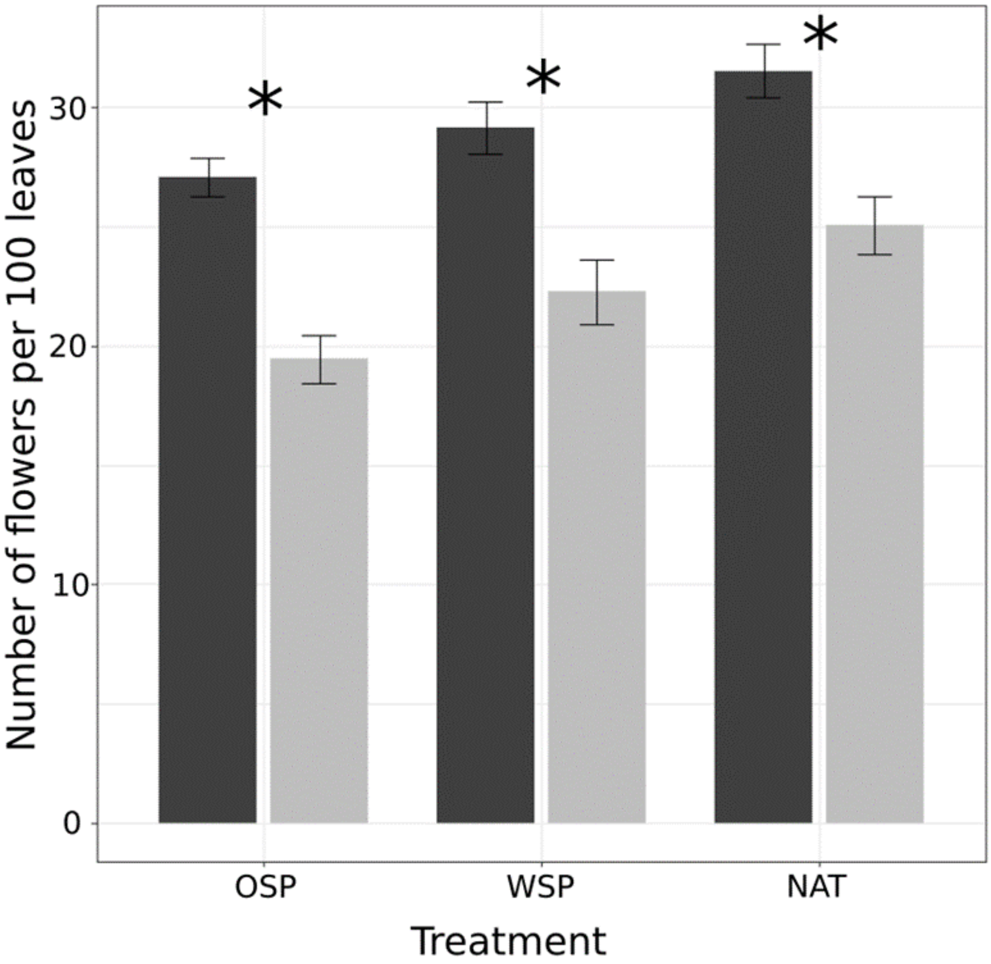


Fig. 4.2 Variation in flower counts between years (dark grey = 2022; light grey = 2023) and treatments (out-of-stand pollen [OSP], within-stand pollen [WSP] and natural pollination [NAT]), for eight trees at the start of a supplemental pollination experiment at Wytham Woods, Oxford, on 1 May 2002 and 9 May 2023. The vertical bars represent the mean number of flowers counted ± standard error. Asterisks indicate significant differences between years (*P*<0.01) from post-hoc Tukey pairwise comparisons.

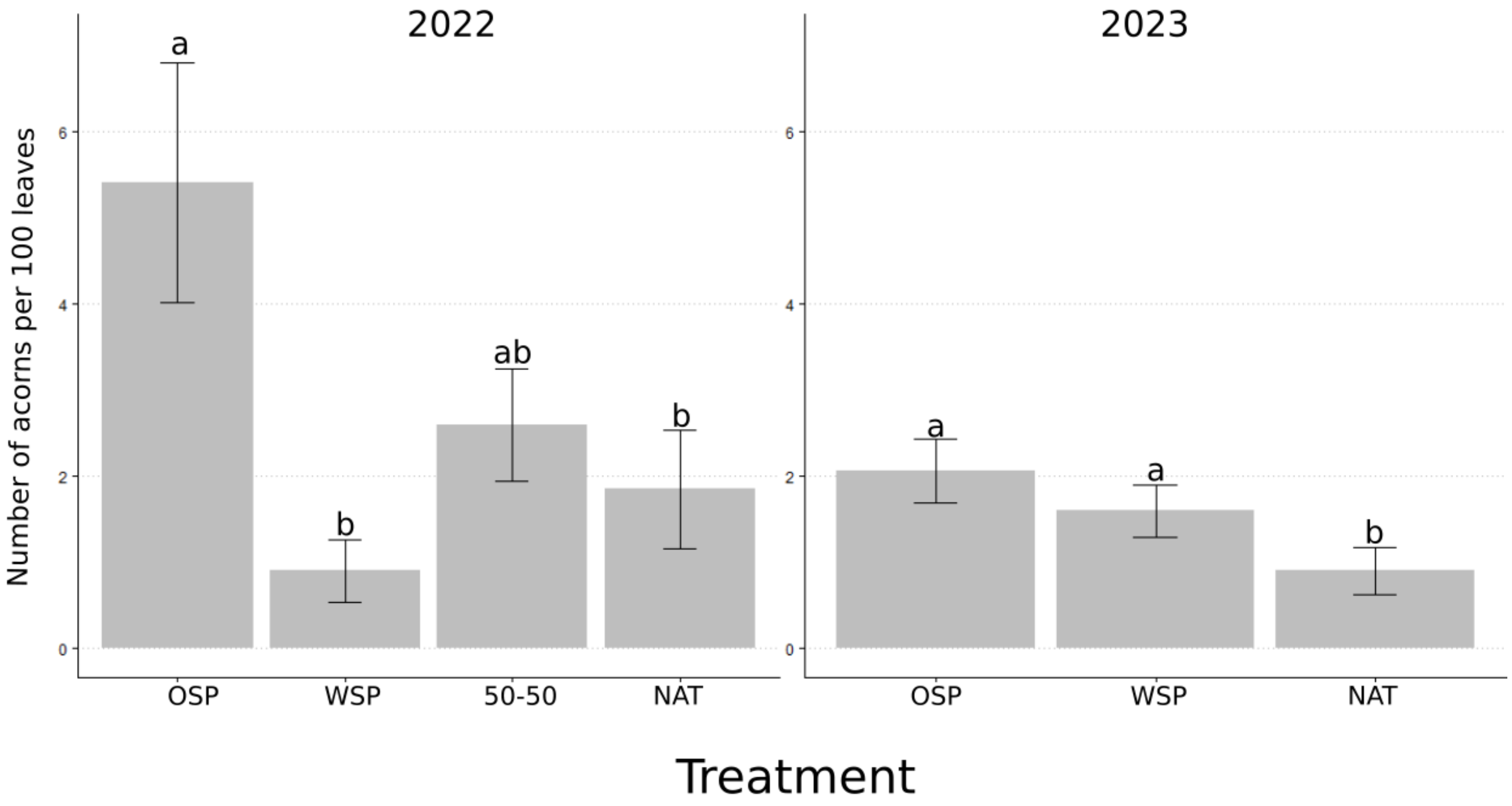


Fig. 4.3 The number of acorns per 100 leaves at peak acorn maturation point (3 Aug 2022 or 10 Aug 2023) for a supplemental pollination experiment on branches of eight trees at Wytham Woods, Oxford, in 2022 and 2023. The pollen addition or isolation treatments were out-of-stand pollen (OSP), within-stand pollen (WSP), a mix of half within-stand and half out-of-stand pollen (50-50), and natural pollination (NAT) in 2022. The NOP treatment in 2022 produced no acorns (Fig. 1) and is not shown here. Only the treatments OSP, WSP and NAT were applied in 2023. The vertical bars represent the mean ± standard error; for ANOVA see Table 1. Within each year, significant differences (*P*<0.05) of post hoc pairwise comparisons of generalised linear mixed effects model with the fixed explanatory factor pollen treatment, and the random effects' leaf number', 'branch' and 'tree', are shown via subscript lettering (a, b).

Table 4.1 Results of ANOVA tests for a supplemental pollination experiment on eight oak trees at Wytham Woods, Oxford, on different dates in 2022 and 2023 from a series of Generalised Linear Mixed Effect Models with a binomial distribution. Presence of flowers or acorns is the response variable and the pollen type applied is the fixed effect (within-stand pollen, out-of-stand pollen, a 50-50 mix of within-stand and out-of-stand pollen, natural pollination, and no pollination). In 2023 only the treatments within-stand, out-of-stand pollen, and natural pollination were investigated. The random effects' leaf number', 'branch' and 'tree' were included in each of the models.

Date	Treatment		
	$\chi 2$	df	*P*
Year 1			
12 May 2022	238.13	4	**<0.0001**
30 May 2022	86.25	4	**<0.0001**
29 Jun 2022	135.67	4	**<0.0001**
03 Aug 2022	82.22	4	**<0.0001**
Year 2			
10 Aug 2023	24.19	2	**<0.0001**

Pollen viability was very similar between the two pollen sources (pollen grains with visible pollen tube growth: 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 recording date after the initial flower counts (Table 4.1). The OSP treatment had the highest number of acorns per 100 leaves by the end of the season in both years (2022: 5.4 ±1.39, 2023: 2.06 ±0.37; Fig. 4.3); the difference between OSP and WSP treatments was significant in 2022, but not in 2023. The 50-50 mixture of out-of-stand and within-stand pollen provided the second highest proportion of acorns in 2022, intermediate between OSP and WSP (Fig. 4.3). This was not significantly more than WSP, which provided the lowest value (0.89 ±0.36 acorns per 100 leaves), or natural pollination (NAT), however; nor was the 50-50 treatment significantly less than the out-of-stand pollen treatment despite an apparent considerable difference. The within-stand pollen treatment performed relatively better in 2023, producing 1.59 ±0.3 acorns for every 100 leaves, significantly more than the NAT treatment (Fig. 4.3).

4.4 Discussion

This study provides experimental evidence for the selective abortion of flowers, whether fertilised or not, based on pollen source in *Q. robur* L. 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* L., 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 OSP than WSP in 2022 (Fig. 4.3) despite large initial numbers of flowers in both treatments (Fig. 4.1). This suggests that the trees selectively aborted flowers pollinated with sub-optimum pollen sources. 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 as it removes poor-quality embryos before resources are invested in them (Stephenson 1981; Havens and Delph 1996). It also widens 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 makes plants more adaptable 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 50-50 pollen treatment was the second most successful in terms of acorns produced and intermediate in value between WSP and OSP, but not significantly different from either or natural pollination (Fig. 4.3). Given that the 50-50 treatment resulted in acorn numbers about midway between WSP and OSP, this suggests a benefit from the presence of some out-of-stand pollen and is also compatible with the suggestion that the trees selectively aborted flowers pollinated with sub-optimum pollen sources in 2022. Despite the oak flowers receiving an even split of OSP and WSP, by chance, some would have had all their ovules pollinated by WSP. The signal to abort acorns may have been stronger within these flowers, similar to the mechanisms of aborting flowers with greater selfed pollen loads (Yacine and Bouras 1997). The successful flowers within the 50-50 treatment may have had all or most of their six ovules fertilised by OSP. Flowers would have to have been sampled during pollination to test this suggestion, however.

In 2023, flowers from the OSP and WSP treatments produced more acorns than the natural pollination treatment (Fig. 4.3), 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 inter-annual reallocation of resources. The experiment was on the same eight trees and, in many cases, the same branches each year due to the logistics of using branches within reach from the canopy walkway or ground level. 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 carbon used for fruit production is generated from within-season photo-assimilates (Hoch et al. 2013), there is evidence that masting species use nitrogen stored in the branches (Han et al. 2014). The trees may have expended stored nitrogen resources in 2022 but not replenish them sufficiently in 2023, so that they could not apply sufficient additional resources to take full advantage of the flowers pollinated by OSP. There were also fewer flowers in 2023 than in 2022 (Fig. 4.2), which may indicate reduced investment in flowering after a year of higher investment (Crone et al. 2009). Flower numbers set an upper limit for acorn production; hence, the reduced number of flowers may partly be responsible for the reduced acorn crop in 2023. Reduced flower numbers or resource levels may force less selectivity over pollen sources, but this suggestion was not tested here.

No acorns were produced in the NOP group (Fig. 4.1). Male catkins were not removed within the pollen bags, leaving the possibility of self-pollination. Almost all flowers within the NOP group had aborted by the end of June, suggesting either (a) a lack of pollen landing on the stigma or (b) a mechanism preventing self-fertilisation within the flowers in each bag. The latter would align 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 L. trees at Wytham Woods were pollen-limited in both years because OSP > NAT in 2022 and OSP and WSP> NAT in 2023 (Fig. 4.3). Pollen limitation may be a key driver of the inter-annual variation in seed production witnessed in masting species (Schermer et al. 2019). Indeed, evidence for it has already been found in several masting species (Crone and Lesica 2006; Pearse et al. 2015; Bogdziewicz et al. 2023b). 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.

It is difficult to assess the importance of pollen limitation from experimental studies fully. First, there is the issue of publication bias, wherein only the papers which find a statistically significant result of pollen limitation are likely to be published (Knight et al. 2006). Secondly, plants may reallocate resources (temporally or spatially) away from branches with naturally-pollinated flowers, thereby inflating the results of pollen limitation studies (Stephenson 1981; Ashman et al. 2004). This effect is increased if performed on only one or two branches per tree. This study reduced this bias by including many branches per tree, but they still represented only a relatively small proportion of the number of branches with flowers. Thirdly, supplemental pollen addition and natural pollination often occur during the same brief period, and the former is likely to be in excess to ensure successful pollination. This could be an issue as pollen addition can reduce flower longevity (van Doorn 1997; Arroyo et al. 2013), freeing up resources for fruit maturation and acorn development. Hand pollinating the flowers in this study may have given the flowers a time advantage to begin developing into acorns and, thus, a head start on using limited resources. Finally, conclusions from pollen limitation studies may be clouded by differences in pollen quality. There is evidence of maternal selection of pollen source in this study, whilst others have reported that high amounts of self-pollen within natural pollen may be responsible for reduced seed set (Thomson 2001; Bogdziewicz et al. 2023b).

Pollen and masting

Oaks have often been thought of as a fruit maturation masting species, wherein it is the abortion of pollinated flowers and immature acorns that 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). Flower numbers varied between years (Fig. 4.2), but even in the most successful treatments for acorn production, very large numbers of flowers were aborted before maturity (Fig. 4.1). Such high abortion rates suggest that flower numbers do not limit acorn production. Instead, the evidence in this study is that flowers and/or fruits are aborted before maturation because of the source of and/or limited availability of pollen (OSP > NAT in 2022, or OSP and WSP> NAT in 2023).

It has been proposed that pollen limitation is a mechanism driving masting. For instance, 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 these individuals with stored resources flower in synchrony (Satake and Iwasa 2000; Venner et al. 2016). Several studies examining drivers of this variable synchrony in flowering mention favourable spring conditions that allow synchronous flowering and greater pollen flow (Koenig et al. 2015; Bogdziewicz et al. 2020e). The current study presents an amendment to these hypotheses, suggesting it is not just pollen limitation (which may still be a problem in some trees) but precisely a limitation of high-quality out-of-stand 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 further away, increasing the amount of out-of-stand pollen that enables a mast year. This may have been responsible for the contrary results of WSP being higher than NAT in 2023 but not in 2022. That is, pollen available at Wytham Woods in the warmer and drier spring of 2022 may have contained more out-of-stand pollen (in absolute and/or relative terms) than in 2023 which was preferentially selected over within-stand-pollinated flowers in 2022.

There are three main limitations to this study. Both years of experiments were moderate years for acorn production at Wytham Woods; this study could not test if 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 under different weather conditions; April and May 2022 were warmer and drier than in 2023, but conditions were quite favourable for pollen flow in both years. Finally, the assumption that the out-of-stand pollen was more genetically diverse than within-stand pollen was not tested.

Conclusions

Supplemental pollen increased acorn production in this study's 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. Mature acorn development was greater with out-of-stand pollen in 2022 but not significantly greater 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 should strive to incorporate genetic analysis of pollen and pollinated flower sampling, including resource measuring or experimental alteration of resources, and analyse the mechanisms driving the selective abortion of maternal flowers in oaks.

Chapter Five: Elevated carbon dioxide and acorn production in mature pedunculate oak (*Quercus robur* L.)

Abstract Acorn production in oak (*Quercus* spp.) shows considerable inter-annual variation, known as masting, which provides a natural defence against seed predators but a highly-variable supply of acorns for uses such as in commercial tree planting each year. Anthropogenic emissions of greenhouse gases have been very widely reported to influence plant growth and seed or fruit size and quantity via the 'fertilisation effect' that leads to enhanced photosynthesis. To examine if acorn production in mature woodland communities will be affected by further increase in CO_2, the contents of litter traps from a Free Air Carbon Enrichment (FACE) experiment in deciduous woodland in central England were analysed for numbers of flowers and acorns of pedunculate oak (*Quercus robur* L.) at different stages of development and their predation levels under ambient and elevated CO_2 concentrations. Inter-annual variation in acorn numbers was considerable and cyclical between 2015 and 2021, with the greatest numbers of mature acorns in 2015, 2017, and 2020 but almost none in 2018. The numbers of flowers, enlarged cups, immature acorns, empty acorn cups, and galls in the litter traps also varied amongst years; comparatively high numbers of enlarged cups were recorded in 2018, suggesting *Q. robur* at this site is a fruit maturation masting species (i.e., the extent of abortion of pollinated flowers during acorn development affects mature acorn numbers greatly). Raising the atmospheric CO_2 concentration by 150 $\mu L\ L^{-1}$, from early 2017, increased the numbers of immature acorns, and all acorn evidence (empty cups + immature acorns + mature acorns) detected in the litter traps compared to ambient controls by 2021, but did not consistently affect the numbers of flowers, enlarged cups, empty cups, or mature acorns. The number of flowers in the elevated CO_2 plots' litter traps was greater in 2018 than 2017, one year after CO_2

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enrichment began, whereas numbers declined in ambient plots. Enrichment with CO_2 also increased the number of oak knopper galls (*Andricus quercuscalicis* Burgsdorf). This study concludes that elevated CO_2 increased the occurrence of acorns developing from flowers, but the putative benefit to mature acorn numbers may have been hidden by excessive pre- and/or post-dispersal predation. There was no evidence that elevated CO_2 altered masting behaviour.

5.1 Introduction

Cumulative net anthropogenic carbon dioxide (CO_2) emissions have amounted to 2400 ± 240 Gt since 1850, 42% of this between 1990 and 2019, raising atmospheric CO_2 concentrations to a global annual average of 410 parts per million in 2019 (IPCC 2023). These emissions together with those of other greenhouse gases increased global surface temperatures by 1.1 °C above 1850–1900 values in the period 2011–2020, with anthropogenic climate change affecting every region of our planet (IPCC 2023). Anthropogenic-induced climate change has well-reported effects and will also have future impacts on forest survival and composition (Flannigan et al. 2000; Ibáñez et al. 2006; Sturrock et al. 2011; Khaine and Woo 2015). It is also established that increased CO_2 will have a direct fertilization effect (Zhu et al. 2016; Ruehr et al. 2023). Under elevated CO_2, plants show increased photosynthetic rates and decreased CO_2 loss via photorespiration, along with a reduced stomatal conductance that results in increased water use efficiency (Drake et al. 1997; Long et al. 2004; Gardner et al. 2022a). Plants may acclimate to greater CO_2 to some extent over time, the degree of acclimation varying with temperature and leaf nitrogen content, but nonetheless a benefit to assimilate production is retained (Wheeler et al. 2004). This CO_2 fertilisation effect leads to increased plant growth (Ainsworth and Long 2005, 2021; De Graaff et al. 2006), induces alterations in plant structure (Pritchard et al. 1999), and affects reproductive outcomes by increasing flowers and seed production, although the strength of these responses vary amongst species (Jablonski et al. 2002). The literature on the effects of differences in CO_2 concentration on plants tends to rely greatly on small-scale studies of individual plants or closely-confined experiments (Wand et al. 1999; Poorter and Navas 2003). This has begun to change since the advent of Free Air Carbon Enrichment (FACE) experiments (Hendrey et al. 1999; De Graaff et al. 2006; DOE 2020), in which CO_2 levels are elevated via a method of open-air CO_2 enrichment (Ainsworth and Long 2021) within the field environment. Whilst FACE experiments have mostly agreed with prior findings of elevated CO_2 under experimental conditions in many species (Kimball et al. 2002; Long et al. 2004), the advantage of FACE is that it subjects intact ecosystem patches to elevated CO_2, so that it is testing a community response rather than the response of (often potted) plants. Hence, FACE experiments are important extensions to work on potted plants not just because of the size of trees but also because all the biotic and abiotic drivers are in play simultaneously. However, such studies with elevated CO_2 are difficult to perform on mature trees due to their large size, and so there is a need for further research on the topic.

Fruit and seed production by plants is a resource-intensive process that uses large amounts of carbohydrates derived from photosynthesis, often competing with vegetative growth (Obeso 2002). Many long-lived perennial plants employ a reproductive strategy known as "masting” defined, in part, by large inter-annual variation in flowers or seeds/fruits produced (Kelly 1994). One of several mechanistic controls of masting in oak (*Quercus* spp.) has previously been attributed to variations in the rates of fruit maturation or abortion rather than the quantity of flowers produced (Pearse et al. 2016; Hacket-Pain 2021). Recent research, however, suggests that masting species may practice different adaptive strategies of either “fruit maturation” or “flower masting”, with the prevalence of one strategy over the other dependent on the environmental conditions of the site (Fleurot et al. 2023). Masting is hypothesized to have evolved as a predator satiation strategy and may be mechanistically controlled by resource dynamics (Isagi et al. 1997; Koenig and Knops 2005). The significance of fruit production in mature communities for tree demography and the maintenance of food webs makes it important to determine the effects of elevated CO_2 on seed production in masting species empirically. An increase in baseline seed production could ultimately result in lower plant fitness if seed supply is surplus to requirement for successful propagation, preventing the herbivore limiting effects of masting's seed predator satiation - starving cycle (Bogdziewicz et al. 2020b). On the other hand, a decline in seed production may damage natural regeneration or reduce seed supply for human-managed regeneration projects (Bole 2022).

Isotope studies with several masting tree species have concluded that 100% of the carbon resources for fruiting are provided by fresh photosynthate - rather than from stored carbon resources - and so elevated CO_2 may influence tree fruiting promptly and directly (Hoch et al. 2013). Experimental evidence supports this suggestion. One of the few studies reported on this topic was performed on a plantation of 13-year-old Loblolly pine (*Pinus taeda* L.) at the Duke Forest FACE site, North Carolina, USA, in which the numbers of cones increased up to three fold in individual trees under elevated CO_2 (+ 200 $\mu L\ L^{-1}$) compared to ambient CO_2 (LaDeau and Clark 2001; Way et al. 2010). Similarly, in the Aspen FACE site in Rhinelander, Wisconsin, USA, flower numbers in 10-year-old paper birch (*Betula papyrifera* Marshall) trees grown from seedlings under elevated CO_2 (+200 $\mu L\ L^{-1}$) were increased by up to 100% and 260% in each of two years compared to the control group, while seed mass was only increased in the first year of the experiment (Darbah et al. 2008). In agreement with the above, modelling studies have linked elevated CO_2 to a stronger influence on multi-decadal increases in flowering rates in tropical species (Pau et al. 2018). Similarly, an *in situ* growth chamber study conducted on a mature scrub oak community (*Quercus myrtifolia* Willd., *Q. chapmanii* Sarg., and *Q. geminata* Small) saw increases in acorn production with elevated CO_2 (+ 325 $\mu L\ L^{-1}$) but only for the dominant species in the environment (Stiling et al. 2004). On the other hand, it has also been hypothesised that trees may acclimatise to elevated CO_2 over time, presenting down-regulation of photosynthesis (Ainsworth and Long 2005); mineral nutrients might also become limiting over the longer term (Hoch et al. 2013; Palacio et al. 2014). To date, the few FACE studies examining the effect of elevated CO_2 upon the reproductive behaviour of masting trees have been performed on comparatively young trees; < 19 years old (LaDeau and Clark 2001; Darbah et al. 2008; Way et al. 2010), but not mature communities. Exposing an established tree community to a step-change in atmospheric CO_2 is unlikely to have the same effect on propagule production as in trees grown under elevated CO_2 as juveniles. Whether the masting behaviour of mature trees - typically slower-growing and with greater internal nutrient reserves - will respond differently to elevated CO_2 or not remains unknown.

To address this question this study investigated the influence of increased atmospheric CO_2 concentration on flower and acorn production of the masting species (Askeyev et al. 2005; Wesołowski et al. 2015) pedunculate oak (*Quercus robur* L.). Reproductive material was recorded from litter traps over seven years within the Birmingham Institute of Forest Research (BIFoR) Free-Air Carbon Enrichment (FACE) facility, in which mature trees were exposed to elevated CO_2. This study tested the null hypotheses that counts of each of the number of flowers, enlarged cups, immature acorns, mature acorns, empty cups, and galls within the litter traps were unaffected by year, by CO_2 treatment, or by the interaction of these factors.

5.2 Materials and methods

Study site

The Birmingham Institute of Forest Research (BIFoR) has maintained a Free-Air Carbon Enrichment (FACE) facility at Mill Haft, Staffordshire, UK (52°48’3.6” N, 2°18’0” W) since 2015, with CO_2 treatments beginning in April 2017. Mill Haft is a 19.1 ha deciduous woodland in a temperate maritime climate; the woodland is dominated by *Q. robur* L., planted around 1850, in the upper canopy and *Corylus avellana* L. in the understorey (Hart et al. 2019; MacKenzie et al. 2021) alongside self-seeded *Acer pseudoplantanus* L. and *Crataegus monogyna* Jacq. of varying ages.

The site contains three experimental treatments divided equally across nine experimental areas, each approximately 30 m in diameter. These comprise of three ‘elevated CO_2’ arrays maintained at +150 $\mu L\ L^{-1}$ above ambient CO_2 (eCO_2), three control arrays at ambient CO_2 (aCO_2) which blow ambient air collected and redistributed from the site, and three undisturbed woodland areas (i.e., no CO_2 array infrastructure, uCO_2). The FACE arrays have operated during daylight hours throughout the growing season from initial budburst to leaf fall (early April to late October) and the CO_2 treatments since early April 2017 to the present.

There is significant spatial variability in soil volumetric water content at the site, with the undisturbed patches (uCO_2) considerably wetter than the other two treatment groups (MacKenzie et al. 2021). Soil pH and phosphate contents for the treatment arrays aCO_2 and eCO_2 (only), recorded once in 2021, were broadly similar with the aCO_2 array having slightly more phosphate but not significantly so (aCO_2: phosphate = 2.63 ±0.96 µg PO_4 P/g, pH = 4.41 ± 0.05. eCO_2: phosphate = 1.36 ± 0.48 µg PO_4 P/g, pH = 4.26 ± 0.5). For further details of the site and the long-term experiment see Hart et al. (2019).

Data collection

Three litter traps each 1 m^2 were placed within each of the nine arrays from 2015. This was changed to six litter traps of 0.25 m^2 per array from 2020 with no detectable impact on amounts per unit area (see below). The litter traps were in place all year round and their contents were collected at least once a month during acorn fall between August and October each year. The *Q. robur* reproductive material collected from litter traps from 2015 to 2021 was separated, classified, counted, and totalled within each year. The reproductive material was classified into six categories encompassing acorn development and predation: female flowers (unpollinated or aborted flowers with no visible acorn development); enlarged cups (swollen cups and visible premature acorns); immature acorns (immature acorns with length < 14 mm and diameter < 7 mm); mature acorns (fully mature acorns); empty cups (large empty acorn cups with acorns missing); and galls (acorn development prevented by insect attack). A seventh category was calculated for all evidence of acorns. This combined observations for immature and mature acorns with an estimate of seed predation (i.e., empty cups) and provided a best estimate of total acorn numbers because empty cups are often all that remains after post-dispersal seed predation (Martínez-Baroja et al. 2019). To allow comparison between years in which trap number and size differed all data was standardised to the amount of reproductive material per 1 m^2 of litter trap area. To do this, counts from litter traps of 0.25 m^2 were multiplied by four (comparable to traps of 1 m^2), and these and those of 1 m^2 were averaged by the number of litter traps in each array (n = 3 or 6) to give the average count per 1 m^2. The means for each collection date were then added to give the total amount of reproductive material produced by each array per 1 m^2 across the whole year, with three arrays in each treatment (n = 3).

Data analyses

All analyses were performed using R statistical software (R Core Team 2021). Model assumptions were tested with the *ggrplot* and *rootogram* functions in the package 'countreg' and by examining diagnostic plots from the functions *plotQQunif* and *plotResiduals* in the package 'DHARMa'. The best-fitting models were decided by comparing models' Akaike Information Criterion (AIC) scores (Akaike 1998) and by comparing models via the *vuong* function and package. After the most appropriate family of model had been determined, the selection of explanatory variables to include were decided by AIC scores. The best fits were provided by Negative Binomial Distribution models in all cases, with the explanatory variables Treatment (i.e., array type) and Year, and these are presented here.

Negative Binomial Models were built with the *glm.nb* function in the package 'MASS'. Initial models, with the factors Treatment and Year and the Treatment × Year interaction, were built separately for each of the seven categories of acorn development and predation as the response variables. The function *Anova* from the 'car' package was used as an omnibus test to see if there was a significant difference in reproductive material amongst treatments. If the default Anova (type 2) provided a significant interaction, then the model was run again as a type 3. The latter is preferred in the presence of a significant interaction (Langsrud 2003). Where significant differences were detected, post-hoc Tukey pairwise comparisons were conducted via the *emmeans* model function of the 'emmeans' package. To generate a baseline comparison, analyses of observations for the two years before the treatments began (2015 and 2016) were made. Further, as site conditions were found to be quite heterogeneous, especially of the 'undisturbed' plots with high soil volumetric water content, statistical analyses were also re-run with only the two treatments eCO_2 and aCO_2 (Appendix 5.1).

5.3 Results

All categories of *Q. robur* reproductive material counted from the litter traps showed inter-annual variation, with high synchrony among the five reproductive material groupings (Fig. 5.1). Flower counts were consistently the most abundant category, whereas the other reproductive material varied in their rank order between groupings (Fig. 5.1). The lowest year for acorn production at Mill Haft was 2018 (Fig. 5.1). This was the case for all categories of acorn development (enlarged cups, immature acorns, mature acorns), and also for empty cups. Nevertheless, large numbers of flowers (aborted flowers with no visible acorn development) were collected in that low acorn production year, and post-hoc pairwise comparisons showed that flower numbers in 2018 were not significantly different from those during the mast years in 2015 ($P = 0.99$) nor 2020 ($P = 0.54$). These results demonstrate that masting behaviour was captured at the experimental site over the study period.

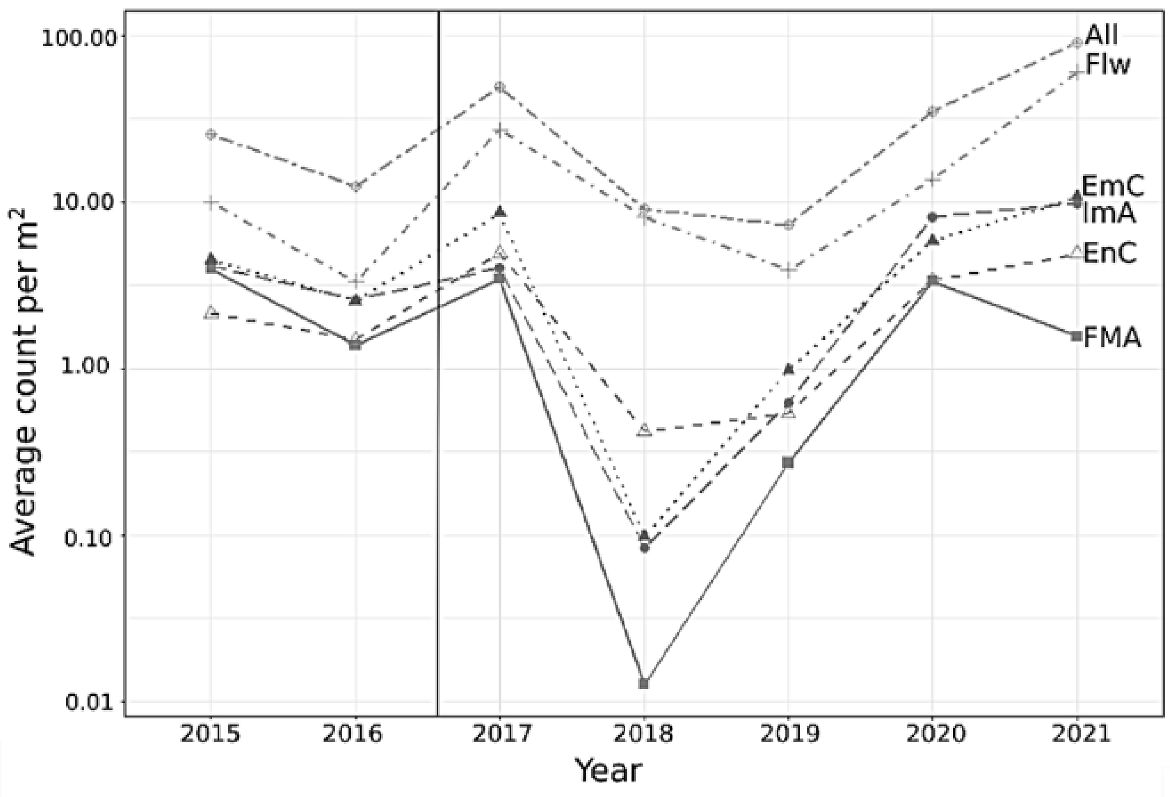

Fig. 5.1 Variation in counts (logarithmic scale) of oak reproductive material from litter traps (mean of all three CO_2 treatments) at the BIFoR FACE facility, Mill Haft, across seven years (CO_2 treatments were provided from early April 2017 [vertical solid black line]): fully mature acorns (solid line, ■, FMA), immature acorns (long-dashed line, ●, ImA), empty cups (dotted line, ▲, EmC), enlarged cups (short-dashed line, Δ, EnC), flowers (dot-dash line, +, Flw), and all the reproductive material combined (two-dash line, □, All).

To test whether greater CO_2 might either enhance, or mitigate the phenomenon of masting, the relative difference in mature acorn counts under eCO_2 and aCO_2 each year was regressed against the number in aCO_2, viz. ($\frac{eC0_2\text{-}\ aC0_2}{aC0_2} \sim aC0_2$); the argument being that if CO_2 concentration affected masting then a trend would be detected. There was no trend in this relation across these five years (*P* = 0.87); that is the relative difference between the CO_2 treatments did not vary with inter-annual variation in acorn production. Hence, masting was not affected by the differences in CO_2 concentration. Similar analyses also showed no such relation for the relative effect of eCO_2 on numbers of immature acorns (*P* = 0.74), the combined category of all evidence of acorns (*P* = 0.20), galls (*P* = 0.24), or of flowers (*P* = 0.29).

The counts of mature acorns, immature acorns, all evidence of acorns, and galls were affected significantly by the main effect of the CO_2 treatments, whereas those of empty cups, enlarged cups and flowers were not (Table 5.1). The main effect of year (2017–2021) was significant for all seven variables, with a significant treatment × year interaction for immature acorns, empty cups, all evidence of acorns, and flowers: but not any other category. From this, one concludes that CO_2 treatment had a significant effect on *Q. robur* reproduction but for four of the seven categories of reproductive material this effect varied depending upon year.

Table 5.1 Results of ANOVA tests of a series of negative binomial regressions with category of *Q. robur* reproductive material as the response variable and the explanatory variables treatment (elevated CO_2, ambient CO_2, or 'undisturbed') and year (2017-2021); significant effects are shown in bold.

Category	Treatment			Year			Treatment ×Year		
	$\chi 2$	df	*P*	$\chi 2$	df	*P*	$\chi 2$	df	*P*
Mature Acorns	9.38	2	**0.009**	70.13	4	**< 0.0001**	9.93	8	0.270
Immature Acorns	11.64	2	**0.002**	145.86	4	**< 0.0001**	17.9	8	**0.022**
Empty Cups	5.12	2	0.070	159.71	4	< 0.0001	17.21	8	**0.028**
All evidence of acorns	13.20	2	**0.001**	200.32	4	**< 0.0001**	17.05	8	**0.030**
Enlarged cups	4.67	2	0.090	48.22	4	**< 0.0001**	12.31	8	0.140
Flowers	2.40	2	0.300	152.63	4	**< 0.0001**	29.34	8	**0.0003**
Galls	10.56	2	**0.005**	44.49	4	**< 0.0001**	8.62	8	0.380

To understand the effect of elevated CO_2 on *Q. robur* reproductive behaviour and check if there was a baseline difference affecting the apparent treatment results found in Table 5.1, the mean counts of reproductive material were compared within and between each treatment for the periods before (2015–2016) and after the start of CO_2 enrichment (2017–2021). For every category of reproductive material with a significant main effect of treatment and/or interaction of treatment × year except immature acorns (Table 5.1), the 'undisturbed' (uCO_2) arrays provided the greatest number of counts throughout 2015–2021. Post hoc pairwise comparisons show the mean counts of all acorn evidence and galls to be significantly less ($P < 0.05$) in the aCO_2 treatment compared with eCO_2 and uCO_2 (Fig. 5.2). This significantly greater quantity of all acorn evidence and galls (but no difference for mature acorns and empty cups) for elevated cf. aCO_2 (Fig. 5.2) was confirmed by a re-analysis which omitted the undisturbed treatment (Appendix 5.1). Furthermore, a significant increase ($P < 0.05$) in immature acorns and in all acorn evidence was detected between the periods before and after enrichment began specifically in the eCO_2 treatment (Fig. 5.2). A significant increase ($P < 0.05$) in flower counts was also detected after the seasonal enrichment period but in both the ambient and elevated CO_2 treatments (Fig. 5.2). A significant increase ($P < 0.05$) in the number of empty cups was also detected after enrichment began, specifically under the eCO_2 treatment, but before the seasonal enrichment period began there were significantly fewer empty cups in the eCO_2 plots than in the uCO_2 and aCO_2 treatments (Appendix 5.2, Fig. 5.2). After enrichment began, however, the numbers of empty cups did not differ significantly amongst treatments ($P > 0.05$). Thus, these results suggest that enrichment with elevated CO_2 resulted in an increase in the mean number of acorns developing compared to the pre-enrichment baseline period, whereas increases in the number of flowers could not be ascribed specifically to eCO_2.

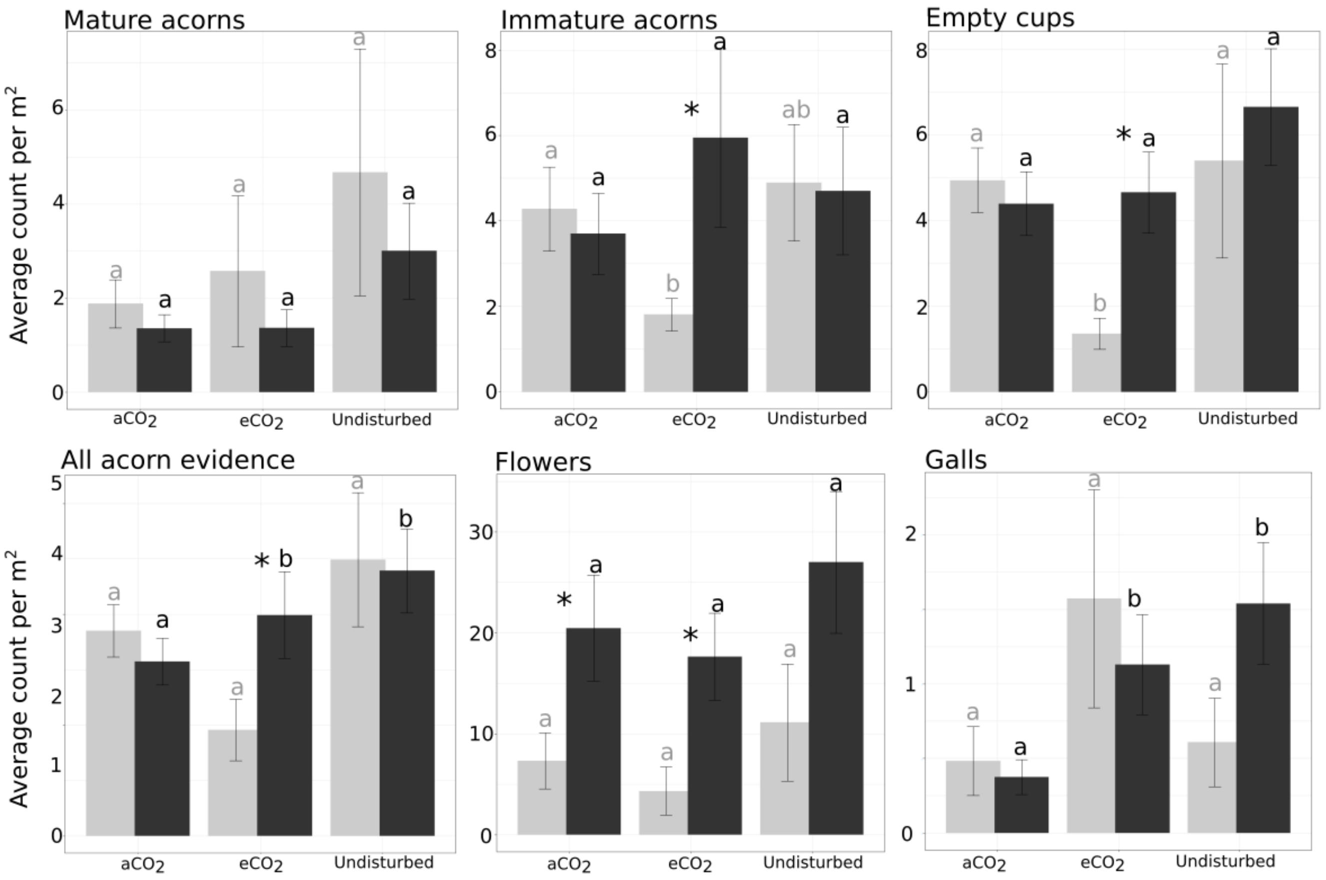

Fig. 5.2 Variation in counts of *Q. robur* reproductive material from litter traps (mean of two years pre-treatment [2015–2016/light grey] and five years post-treatment [2017–2021/dark grey]) at the BIFoR FACE study at Mill Haft for the $\mathrm{aCO_2}$, $\mathrm{eCO_2}$ or $\mathrm{uCO_2}$ treatments. The vertical bars represent the mean ± standard error. Asterisks denote significant differences ($P < 0.05$) of a post hoc pairwise comparison between the periods before and after seasonal enrichment started (i.e. 2015–2016 cf. 2017–2021) within a treatment ($\mathrm{aCO_2}$, $\mathrm{eCO_2}$ or $\mathrm{uCO_2}$). Bars labelled with different letters (a, b) denotes significant differences ($P < 0.05$) between treatment groups during the two years before seasonal enrichment (2015–2016, light grey letters) and within the period after seasonal enrichment started (2017–2021, dark grey letters).

To investigate the significant interaction between CO_2 treatment and year for several of the reproductive groups (Table 5.1), the significant differences of group means before and after enrichment began (Fig. 5.2), and how any effect of CO_2 enrichment changed, the counts for each treatment per year were analysed. Analysis showed that before enrichment began (2015 and 2016), those woodland patches destined to be subjected to eCO_2 had the lowest production of several reproductive material groups (Fig. 5.3), although the only significant pairwise comparison found was of empty cups in 2015 (aCO_2 cf. eCO_2, $P < 0.001$; eCO_2 cf. undisturbed, $P < 0.001$). By the fifth year of CO_2 enrichment (the last of the seven-year period studied, 2021), however, the elevated CO_2 treatment provided the greatest numbers for immature acorns, empty cups, and all evidence of acorns (Fig. 5.3). Although this difference was not statistically significant between any treatment with post hoc pairwise comparison within 2021 ($P = 0.64$ to 0.99), a clear trend is nevertheless visible where counts in the elevated CO_2 treatment transition from being the lowest of the three treatments (2017) to the highest (2021). Flower counts oscillated mostly in step between the treatment groups each year other than in 2018, one year after the CO_2 treatments started. In that year, flower numbers in the elevated CO_2 treatment were much greater than in 2017, whereas they decreased substantially between 2017 and 2018 in the ambient and undisturbed treatments (Fig. 5.3). Post hoc pairwise comparisons for flower numbers in 2018 showed a difference between eCO_2 and undisturbed treatments ($P < 0.05$), but not between eCO_2 and aCO_2 ($P = 0.86$). These results suggest that the significant increase in developing acorns identified across the entire period of elevated CO_2 enrichment (Fig. 5.2) is the result of a progressive effect over multiple years since enrichment began. In contrast, *Q. robur* flower production apparently demonstrated an immediate-but-transient response to elevated CO_2 enrichment in 2017–2018.

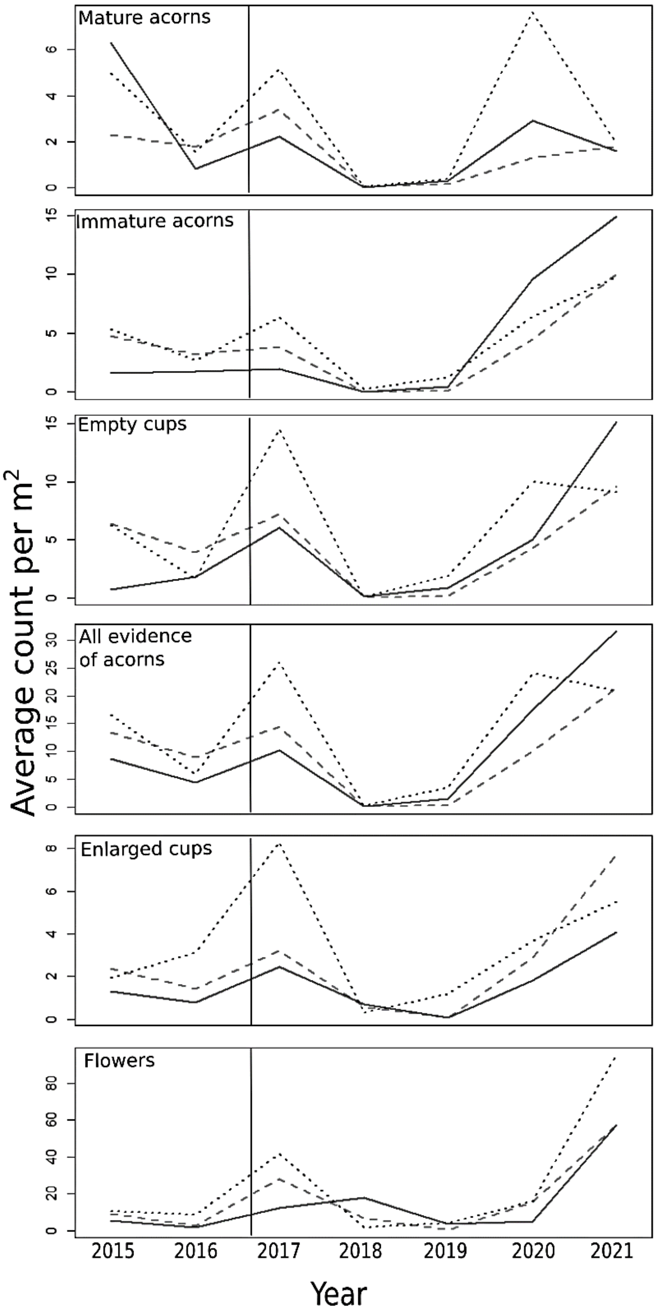

Fig. 5.3 Variation in counts of *Q. robur* reproductive material for mature acorns, immature acorns, empty cups, all evidence of acorns, enlarged cups, and flowers from litter traps at the BIFoR FACE study at Mill Haft across seven years for elevated CO_2 (solid line), ambient CO_2 (dashed line) and undisturbed plots (dotted line). The CO_2 treatments were provided from early April 2017, shown by the vertical solid black line.

5.4 Discussion

Masting

Masting is an important feature in the ecology of oak woodlands, which affects the ability of oak to regenerate naturally, and the supply of seed for tree nurseries. The counts of mature acorns and empty cups differed considerably amongst years (Table 5.1, Fig. 5.1); mature acorns were most numerous in 2015, 2017, and 2020 but almost none were collected in 2018. The inter-annual variation at Mill Haft coincided with that for acorn production at other sites across the UK, in which 2015 and 2020 gave above-average numbers of acorns and 2018 very few. This is further evidence for the masting behaviour of high inter-annual variation in acorn output that is geographically synchronous, already well reported within oak species (Kelly 1994).

Oaks are said to be a “fruit maturation” species whereby it is the abortion of flowers and underdeveloped acorns that determines the level of acorn production each year rather than the number of flowers produced (Pearse et al. 2016; Bogdziewicz et al. 2019). This has been questioned recently; whether a population practices “fruit maturation” or “flower masting” may depend upon the climatic conditions experienced (Fleurot et al. 2023). All the reproductive material counted within the litter traps represents a flower that has either aborted or developed into an acorn. This total, along with the flower numbers, remained high each year, and consistently so compared to variation in the much lower counts of other reproductive material (Fig. 5.1). Thus, non-masting years were not caused by too few flowers; indeed, the failed acorn crop of 2018 followed an average number of flowers (Fig. 5.1) which was not significantly different from flower numbers during the mast years of 2015 ($P = 0.99$) and 2020 ($P = 0.54$). On average flowers were 53% of the count of reproductive material found each year, but 89% in 2018 highlighting the influence of early flower abortion during a failed year (Fig. 5.1). Hence, inter-annual variation in flowering (Table 5.1) may set an upper limit to acorn production in any one year but not markedly affect the numbers of acorns actually produced.

This study concludes that *Q. robur* masting is affected primarily by the success of reproductive processes that occur after flowering, consistent with the fruit maturation model. This mode of masting has been linked to the maritime climate of northern UK sites (see Fleurot et al. 2023).

The patterns of variation in the counts of reproductive material across the seven years were broadly consistent between underdeveloped acorns (enlarged cups or immature acorns) and evidence of developed acorns (mature acorns or empty cups) (Fig. 5.1). In 2018, when mature acorn production failed, however, enlarged cups (the very initial stage of acorn development) was the second most numerous category of reproductive material (Fig. 5.1). In this year the number of enlarged cups was statistically indistinguishable from those during the mast year of 2015 (2015 =1.87 per m^2 vs. 2018 = 0.56 per m^2; $P = 0.48$). In contrast the counts were much reduced for mature acorns (2015 = 4.53 per m^2 vs. 2018 = 0.03 per m^2; $P < 0.001$) and empty cups (2015 = 4.42 per m^2 vs. 2018 = 0.11 per m^2; $P < 0.001$). Hence, it is likely that it is the extent of abortion of pollinated flowers early on in acorn development that determines the numbers of mature acorns produced. Fewer pollinated flowers developing acorns wastes less resources and it may be due to selective abortion of an unfavourable pollen source or may indicate limited pollen availability (Boavida et al. 2001). The early abortion of acorns in 2018 (relatively more enlarged cups to immature and mature acorns, Fig. 5.1) could also be the result of environmental factors, such as summer drought (Espelta et al. 2008) or herbivore-mediated resource limitation (Canelo et al. 2018). In this regard, 2018 and 2019 were years marked by intense defoliation and powdery mildew infection in Mill Haft (Mayoral et al. 2023), which may have also affected acorn production.

CO_2 treatment effects

Among the treatments, the undisturbed plots produced the most reproductive material overall (Fig. 5.2). The two CO_2 plots may have been limited in some way. This might have been due to lower soil nitrate or phosphate, important for early-stage flower development (Allen et al. 2017) and acorn development (Sever et al. 2023), or lower soil water (MacKenzie et al. 2021) which reduces mineral and nutrient uptake by trees (Alam 1999; Skopp et al. 1990); or more carbon might have been allocated to the roots and lower stems for increased growth or storage (Dickson and Tomlinson 1996). It is also possible that the two CO_2 treatment areas may have been stressed from the increase in activity, such as trampling, during and after the construction of the enrichment infrastructure (Komatsu et al. 2007).

There was a significant interaction between CO_2 treatment and year on flower numbers (Table 5.1, Appendix 5.1). Flower numbers were initially oscillating in synchrony between the treatment groups, however after the CO_2 treatments began the eCO_2 treatment desynchronised with both the aCO_2 and undisturbed plots, producing more flowers than the undisturbed plots during the 2018 failed crop (Fig. 3, eCO_2 / undisturbed: $P < 0.05$); although not significantly more than ambient (Fig. 3, eCO_2 / aCO_2: $P = 0.86$). Flower development uses assimilate stored in the trunk or roots (Hoch et al. 2013). Hence, flower counts may not have been expected to respond to the initial season under elevated CO_2, but greater net photosynthesis under elevated CO_2 (Gardner et al. 2022b) may have refilled stored reserves more quickly later in 2017. The higher-than-expected number of flowers in the eCO_2 plot during 2018 may be evidence of this (Fig. 5.3). After 2018, flower numbers broadly returned to synchrony among the treatments. It may be that trees under elevated CO_2 acclimatised to the increased CO_2 and/or switched the additional carbon resource from reproduction into maintenance and growth, as evidenced by the higher leaf mass per unit area (Gardner et al. 2022c) found in the eCO_2 cf. aCO_2 arrays at the site.

The undisturbed treatment produced the most mature acorns on average during the recorded period of CO_2 enrichment, with no difference between eCO_2 and aCO_2 (Fig. 5.2, Appendix 5.1). To have found no increase in mature acorn number for eCO_2 over aCO_2 is surprising as it disagrees with the results from an open-top chamber study of scrub oaks (Stiling et al. 2004) and for seeds of *Pinus taeda* L. (LaDeau and Clark 2001; Way et al. 2010). There were however higher counts of empty cups observed after CO_2 enrichment began and when all evidence of acorns is combined an increase is detected within the eCO_2 treatment (Figs. 5.2, 5.3). This suggests an increase in acorn production resultant from elevated CO_2 that is being obscured by greater acorn predation rates. Seed predators favour larger, more mature acorns (Gómez 2004). Whilst efforts are made to control the numbers of seed predators at the BIFoR FACE site (Bradwell 2022), it is clear from camera trapping that they remain present. Moreover, the litter traps used were not sealed. Hence, one likely explanation is that post-dispersal acorn predation in the litter traps reduced the counts of mature acorns, leaving behind empty cups and immature acorns; as such, counts of empty cups, immature acorns, and the composite group all acorn evidence are potentially more reliable indicators of the impact of CO_2 on acorn production in this study. The importance of predation in determining the fate of reproductive material under eCO_2 illustrates the importance of process-permitting experimental designs such as FACE in contrast to more closed systems.

There were significant interactions between treatment and year for immature acorns, empty cups, and all acorn evidence, suggesting these groups are increasing after CO_2 enrichment began (Table 5.1; Figs. 5.2, 5.3). At the start of the experiment the number of empty cups, immature acorns and all evidence of acorns were lowest in the eCO_2 plots, but post-treatment application the eCO_2 plots were producing the highest counts of these reproductive material categories (Table 5.1; Figs. 5.2, 5.3). Treatments were assigned to FACE arrays to pair aCO_2 and eCO_2 treatments as geographically close as practicable, but the variation observed in the pre-enrichment period suggests that other underlying differences remain between the aCO_2 and eCO_2 treatment arrays. The increase in these groups of reproductive material over this period might indicate an increase in post-fertilisation production of acorns under elevated CO_2. That the number of mature acorns does not increase in line with this might indicate inadequate nutrient supply to support acorn development to maturity. The numbers of immature acorns (i.e., early-aborting acorns) were greatest in the eCO_2 treatment for 2020 and 2021 (Fig. 5.3). There is, however, no evidence for nutrient limitation in leaf composition at BIFoR FACE (Gardner et al. 2022c). Moreover, post-hoc pairwise comparison showed the higher immature acorn counts in the eCO_2 plots in these years was not statistically significant, however; as the experiment continues it is worth monitoring this putative trend. If elevated CO_2 were to increase the numbers of immature acorns produced each year this might damage the management of *Q. robur* by negating the seed predator defence of masting (Bogdziewicz et al. 2020b). The higher numbers of immature acorns could provide a bridging effect between mast years, maintaining consistently higher seed predator populations that would eat higher proportions of mature acorns during the mast year.

Attacks from pre-dispersal predators, in this case exclusively oak knopper galls (*Andricus quercuscalicis* Burgsdorf), showed no significant effects of the plots on galls in the two years before the CO_2 treatments were applied (Fig. 5.2), but thereafter galls were more common in the undisturbed and eCO_2 treatments (Table 5.1, Fig. 5.2). The greater numbers of mature acorns in the undisturbed plot might explain why more galls were found (i.e., with more acorns one may expect more galls). However, the eCO_2 treatment had the lowest mature acorn count on average and yet the number of galls was three times higher than the aCO_2 treatment (Fig. 5.2). If one assumes that each gall could have developed into a mature acorn if it had not been attacked, then eCO_2 would have produced more acorns than aCO_2 on average: galls plus mature acorns were 3.43 per m^2 of litter trap under eCO_2 and 2.15 under aCO_2; and this difference would be yet greater if the numbers of immature acorn were also added (see Fig. 5.2). The higher attack rate by galls observed may thus have contributed to more acorns failing to reach maturity in the eCO_2 plots. These results suggest that the presence of more developing acorns in elevated CO_2 may be of greater benefit to seed predators than to the regeneration of the trees themselves, as noted by Bogdziewicz et al. (2020b). Moreover, higher growth under CO_2 may result in higher mortality rates in mature trees (Büntgen et al. 2019; Brienen et al. 2020). And so, the potential benefits from future increase in CO_2 may, conversely, result in fewer juvenile trees with shorter lifespans.

Elevated CO_2 has been found to increase herbivore numbers in some years (Kampichler et al. 2008), but this effect may be specific to species and functional groups because other species have shown the opposite result (Hall et al. 2005; Roberts et al. 2022). In this study the difference in the numbers of galls in the periods before and after enrichment was not statistically significant under any treatment (Fig. 5.2), agreeing with previous research at the site into herbivory per unit area of leaf on *Q. robur* (Roberts et al. 2022). Pre-enrichment counts suggest that the eCO_2 plots were already experiencing higher pre-dispersal seed predation, with two years of data giving insufficient power to pick up on this difference statistically.

Studies of this type are exceedingly rare due to the resources required to set up such large, long-duration experiments. Moreover, the requirement to build such investigations around long-established trees in mature woodlands means that the experimental sites cannot be as homogeneous as with, for example, experimental grounds with annual plants. Nonetheless, this study provides strong evidence of bottlenecks to fruit production and the ultimate fate of fruit in old temperate forest subject to predation by granivorous vertebrates. Our results suggest that the effects of elevated CO_2 on acorn production increase over time (Fig. 5.3, 'all evidence' panel) and so may be cumulative, especially as masting works on multi-year cycles. Hence it will be important to carry on the study for some years to determine if more pronounced effects emerge over time.

Conclusions

Using FACE to increase the atmospheric CO_2 concentration by 150 $\mu L\ L^{-1}$ in old, temperate deciduous woodland, had no significant direct effect on the phenomenon of masting in *Quercus robur* L., nor on the numbers of either enlarged cups or mature acorns, but it did increase significantly the numbers of empty cups, immature acorns, and all evidence of acorns. All categories of reproductive material were affected by year, with *Q. robur* at this site conforming to fruit maturation masting behaviour. This study suggest that elevated CO_2 increased the initial numbers of acorns developing, but this was not reflected by the mature acorn counts due to (1) higher load of pre-dispersal seed predation in the elevated CO_2 plots, and (2) post-dispersal seed predators taking mature acorns. This study has no evidence currently for a third possible explanation of nutrient limitations under eCO_2 preventing full acorn development. The number of immature acorns also increased under eCO_2 from being the lowest of the three treatments in the early years to the highest by the final two studied, suggesting that the effects of elevated CO_2 may be cumulative - which requires further study. Flower number was also affected by the interaction of CO_2 treatment with year, suggesting elevated CO_2 may affect the cycle of resource expenditure and storage, but in this regard the trees appeared to acclimatise to this increase in CO_2 quickly.

Chapter Six: General Discussion

6.1 Introduction

This thesis has examined the drivers of synchrony and intensity of acorn production in the English oaks *Quercus robur* and *Quercus petraea*. The literature into the science of masting, how it may have evolved and how the phenomenon has impacted the seed sourcing/forest restoration industry was reviewed within Chapter 1 of this thesis. Within Chapter 1 several gaps in our knowledge of oak masting were identified: more research was needed on understanding if and how masting synchronises between and amongst populations, there was a lack of experimental studies examining the role of pollen limitation and pollen source in high and low acorn production, and no experimental studies into how future levels of elevated CO_2 may influence acorn production and masting in the English oaks. Further, despite much research, there remains a lack of models that accurately predict masting events based on weather cues, and understanding of oak regeneration in the UK was generally poor.

With reference to these points, five studies were designed to fill our knowledge gaps of oak masting. Study 1 (Chapter 2) explored how masting and acorn production varied between individual trees within one woodland population by carrying out a four-year long survey of acorn production at Wytham Woods, Oxford. Study 2 (Chapter 3) used a novel machine learning approach to understand the weather cues for masting by pairing over 100 time series of acorn production with >300 environmental variables. Study 3 (Chapter 4) performed the first experimental study into the role of pollen source in driving acorn production over two years. Study 4 (Chapter 5) used the Birmingham Institute of Forest Research Free Air Carbon Enrichment site to explore the effect of elevated CO_2 upon oak reproductive material and pre-dispersal predation of acorns. Study 5 (Appendix 6.1) was a collaboration of the PENCAFOr COST action, determining best practices for forest regeneration (i.e. whether to sow acorns directly or to sow in a nursery and then transplant the seedling. The findings of each of these studies are discussed below, before summarising how these may help aid seed sourcing and the forestry industry and suggesting the next steps for future research.

6.2 Variation in masting and acorn production

Despite synchrony often being a key definer of masting, strong individual variation among trees was highlighted within Chapter 2. There were super-producing trees that produced good crops most years, poor producers that failed to produce more than a handful of acorns each year and a large mid-section of average producers, flitting between large and small acorn crops among years. An important finding, that mirrors others (Bogdziewicz et al. 2020d), is that a mast event occurs when these poor- to mid-productive trees contribute synchronously to a large acorn crop. In the mast year every tree produced acorns with the majority producing a record high count of the four-year study; in the following year there was completely synchrony in failed crops with, astonishingly, not a single acorn being counted. This is strong evidence for a synchronising factor that acted upon these trees, but there was no evidence of a synchronising microclimate that has been reported by other researchers (Koenig et al. 2015). Spring conditions were highlighted in Chapter 3 as important predictors of acorn production, as was the strong lag effect of the last year's acorn counts. Although only over a short time series, the data at Wytham agrees that the poor weather conditions in Spring 2021 (cold and wet) combined with the negative temporal autocorrelation from very high acorn counts in 2020 likely explain the complete crop failure of 2021.

This research was one of the few studies that examined not just acorn production, but also the earlier stages of acorn development and pre-dispersal herbivory. A similar pattern of super-, mid-, and poor-producing individual trees was seen within immature acorn counts and the early aborting enlarged cup counts but the production of flowers was much more equal across producer groups. New research had questioned a long-held belief that oaks are solely a fruit maturation masting species (Fleurot et al. 2023), meaning a mast year will be decided by the number of developing acorns that are aborted (from flower to acorn stage) rather than the number of flowers initially produced. However, within the population of *Quercus robur* at Wytham the even spread and consistently high number of flowers counted (even during the failed crop of 2021) means we can conclude that it is the abortion of developing acorns rather than initial flower counts that mechanistically cause a mast year at this site. Similarly, at the BIFoR FACE site, described in Chapter 5, consistently high flower counts suggests fruit abortion rather than flower production to be the limiting factor for acorn crops there – and possibly in the UK more widely. The evidence that flower or fruit abortion may be a key driver of masting was influential in devising the pollination study (Chapter 4).

The infrequent and interannually irregular production of acorns, reported in Chapters 2 and 3 of this thesis, as well as within the literature (Crawley and Long 1995; Nussbaumer et al. 2016), can produce a predator satiation effect where seed predators are starved in some years and overwhelmed in others (Janzen 1971). However, the strong variation in acorn production among individual trees reported in Chapter 2 may act against this effect, with consistently high acorn producers possibly maintaining greater seed predator populations able to take advantage of population wide mast crops. Despite this there was an annual autocorrelation between acorn production and gall attack at the level of the whole population at Wytham and no effect of galls preferentially attacking the higher acorn producing individual trees at Wytham (Chapter 2) nor at Mill Haft (Chapter 5). It may be that the oak populations at these sites were more numerous or dense which has been found to increase the effectiveness of predator satiation via masting (Bogdziewicz et al. 2018).

6.3 Predicting oak masting by weather cues alone

Within the literature there has been consistent evidence of geographic synchrony between populations of intraspecific masting species. The most obvious candidate for causing this synchrony are weather cues, as these tend to cover large areas and create homogenous conditions for populations. This idea has generated lots of interest in using weather cues to model masting (Vacchiano et al. 2017; Caignard et al. 2017; Nussbaumer et al. 2018), however they have so far found mixed success with the most successful models for Britain only explaining around 10% of the variance in the data used (Nussbaumer et al. 2018). Similarly, Chapter 3 of this thesis reported mixed success in modelling acorn production across NW Europe with weather cues alone.

There was agreement with the literature with regard to which are the more important weather variables. For example, spring temperature and precipitation influence acorn production and there is the strong effective of negative temporal autocorrelation (i.e. low production after a mast year) and these factors likely explain in part the very poor production in 2021 at Wytham Woods (Chapter 2). However, once the models were tested on unseen data their predictive ability was shown to be so poor as to not be considered useful. The high individual variation among trees found in oak populations (Chapter 2) could be affecting the accuracy of time series collections, as this data would be collected from litter traps and averaged for each site thereby giving the super producers an unbalanced dominance in the data, instead sampling from and modelling the more average producers may better predict mast events. Further, it is probable that individual trees of the same species can have different mechanistic drivers of masting with different weather cues, i.e. abortion of acorns was more important for *Quercus robur* in Chapters 2 and 5, but flower production was more important in some French populations (Fleurot et al. 2023).

This thesis did identify strong positive correlations in acorn production between geographically close sites (Chapter 3). This synchrony declined the further apart sites were and was absent (on average) once distances between sites had reached 655km for *Q. robur* and 714km in *Q. petraea*, and negative at greater distances. Such negative correlations with greater distances had previously been reported on a subset of the data used within this thesis (Caignard et al. 2017) and within other masting species (LaMontagne et al. 2020). When comparing sites from mainland Europe and the British Isles in Chapter 3, the negative correlation in synchrony with distance between sites was strongest when considering paired sites within the same contingent land mass. Such reduction in synchrony between geographically distant sites is further evidence for weather cue's role in masting synchrony, assuming stronger differences in weather between geographically far sites. Further, comparatively higher synchrony between the UK and mainland Europe, vs paired sites on the same contingent landmass, may be indicative of the Atlantic and Continental air masses causing similar weather conditions between Southern UK and France. But also, the likelihood of different climates and so different weather cues acting upon these populations may be an important reason as to why an overarching model to predict masting is so hard (if not impossible) to achieve.

6.4 Pollen and its role in masting

Chapter 4 reported unique experimental evidence of a maternal choice in pollen source for *Quercus robur*. Previous research has suggested a higher proportion of successful acorns coming from out of stand pollen (Dow and Ashley 1998), that is to mean pollen that comes from outside of the stand that was being studied. This was the case even in highly isolated stands where local pollen would be plentiful and out of stand pollen limited (Craft and Ashley 2010). Modelling had suggested a selective benefit of female choice (Craft et al. 2009), and as is shown in Chapters 2 and 5 oaks consistently produce many more flowers than needed, aborting flowers and immature acorns less in a mast year. Hence an experiment was designed to examine if trees were selectively aborting certain acorns based on pollen source: out of stand pollen produced more acorns than the within stand pollen. This could explain the high levels of flower and immature fruit abortion seen in Chapters 2 and 5 and could generate an alternate explanation to weather as a driver of masting, as detailed below.

Previous work purported that good spring conditions create homogenous microclimates increasing synchrony in flowering amongst trees within a population (Koenig et al. 2015). My research (Chapter 4) suggests an alternative hypothesis wherein the good spring conditions allow long-distance pollen flow, which is more successful, and so a mast event could only occur when a larger geographic area is under good spring conditions as suggested by the pollination moran effect hypothesis (Pearse et al. 2016). Chapter 2 did not report any synchrony in microclimate disagreeing with the phenological synchrony hypothesis, instead Chapter 3 highlighted several spring variables conducive to greater long distance pollen flow (dry and warm spring temperatures) which supports the idea that masting is led by weather cues enabling long-distance pollen flow. This cannot be unequivocally concluded, however, as Chapter 2 did not have microclimate measurements for the main mast year of 2020, only the more average years of 2022 and 2023.

By aborting flowers early, trees can reduce the resource load of developing poor quality embryos and maintain higher genetic diversity within the acorn crop (Stephenson 1981). Chapter 2 reported that many of the trees sampled at Wytham were half siblings. Hence, maternal choice in sexual reproduction may prevent inbreeding depression and maintain genetic diversity. Further, early abortion of flowers or developing acorns from lesser quality pollen could prevent internal resources becoming limiting; internal resources may limit acorn production, which may explain the strong negative autocorrelation between successive acorn crops (Chapters 2 and 3) and is supported by the high acorn producers growing on heavy clay soils which maintain high moisture content and aid efficient nutrient flow (Chapter 2). Chapter 3 also identified that the trees sampled at Wytham were pollen limited, giving one explanation for why open canopies with less surrounding foliage to block pollen flow produced higher acorn counts over the four years of sampling (Chapter 2).

6.5 Masting and climate change

Due to the high research costs, there are only a limited number of Free Air Carbon Enrichment sites and even fewer containing established communities of masting species. Hence the FACE experiment (Chapter 5) helps to fill an underrepresented niche in masting research. The experiment did not find evidence that elevated CO_2 altered masting cycles but did find an increase in developing acorns. An important distinction is that this increase was only evident when including all evidence of acorns (mature and immature acorn, and empty cupules), but was not evident for mature acorns alone. Despite having the lowest numbers of mature acorns produced, the elevated CO_2 plot had high predation from oak knopper galls (*Andricus quercuscalicis*). This seems to show that any increase in acorn production under elevated CO_2 may be counteracted by increased activity of seed predators. Chapter 2 found no pattern of higher acorn producing individuals facing greater seed predation. This would imply that the seed predators may have reacted to the increased CO_2 in Chapter 3. Other studies have reported increases in herbivore numbers under elevated CO_2 (Kampichler et al. 2008), but this depends on the species considered (*see* Hall et al. 2005; Roberts et al. 2022). This reinforces the view that research studying the effect on acorn production from elevated CO_2 should be considered in tandem with effects on seed predators.

Chapter 3 was unable to accurately predict masting events based on weather cues, which makes it difficult to infer how any change in weather cues from anthropogenic climate change will influence masting cycles. Despite this, several weather variables were selected from the models as particularly important for high acorn production. A reduction in the number of spring frosts but wetter springs (Kendon et al. 2021) may reduce flower damage from frost (*as in* 2021, Chapter 2) suggesting a benefit for acorn production, yet conversely wet weather in spring could reduce the long distance pollen flow which Chapter 4 suggested was beneficial for masting. Chapter 3 found wet and warm summers were linked with higher acorn production, and whilst summer temperatures have been increasing this is paired with a higher occurrence of extreme high-temperature events which are predicted to cause more summer and winter droughts in the future (Tanguy et al. 2023). Dry conditions prevent effective nutrient flow and absorption, and due to the importance of resource limitation in masting species (e.g. acorn lag effects shown in Chapters 2 and 3) it is perhaps these weather changes that will be most damaging to long-term acorn production (Monks et al. 2016). The ability of oaks to maintain higher genetic diversity through maternal choice in pollen source (Chapter 4) may, however, enable a more plastic response to many of these changes in masting's weather cues. A better understanding of the mechanistic drivers of masting and further study of self-maintenance of genetic diversity, will be vital to understanding how anthropogenic climate change will influence oaks and their role in British broadleaf woodland communities.

6.6 Natural regeneration of oak

The understanding of the health of British Oaks and their regeneration is sorely lacking (Quine et al. 2019; Kohler et al. 2020), and what data there is suggests oaks are not regenerating naturally with < 3.5% of the natural regeneration at Wytham Woods coming from oak (Kirby et al. 2014). Much of the regeneration of oaks in woodlands will therefore have to be assisted by land managers, highlighting the importance of this thesis in studying how acorn production can be improved (Chapter 2 and 4), seed crops predicted (Chapter 2 and 3), and the effect of climate change on acorn supply understood (Chapter 5). This thesis also directly studied the effectiveness of different techniques for oak reforestation. Appendix 6.1 presented the initial findings from one of 80+ sites from a collaborative COST action study assessing the effectiveness of direct seeding vs planting. The directly-seeded plots grew taller than the planted plots in both species, with no difference in stem diameter (Appendix 6.1). Direct seeding measures are cheaper to pre-growing and translocating (Palma and Laurance 2015) so if this patten holds up in the larger meta-analysis it would be reassuring for forest regeneration programmes. However, this is only one of many sites taking part in the experiment, with no data yet on the underground biomass of these seedlings. Moreover, many more considerations in terms of longer term seedling survival need to be considered.

6.7 Aiding seed sourcing

As was addressed within Chapter 1, and throughout this thesis, oak masting has created frequent shortages of acorns for planting efforts (Bole 2022). It is a particular issue for the UK where we aim to regenerate much of our historic forests but often have to rely on imported acorns that are not well adapted to the UK climate (Hubert 2005). This thesis aimed to aid consistency of acorn supply by (1) building predictive models to focus limited collection efforts efficiently and help animal conservation, (2) identify which trees produce more acorns and why, (3) suggest interventions that land managers can take to increase acorn crops.

Due to the otherwise high efforts for minimal gain, seed collectors will tend to only collect acorns during mast years, impacting not just the supply of oaks but also companion species as nurseries will choose to move focus away from oak planting ultimately delaying regeneration projects (Whittet et al. 2016). However, a predictive model for oak masting would enable collection efforts to be focussed within areas that a good crop is likely to be found, enabling collections to occur even in nationally poor years. Additionally, predicting mast years would be able to feed into the understanding of the carrying capacity of an area for at risk species such as red squirrels (Slade et al. 2020). Unfortunately, as Chapter 3 showed, a universal model to predict oak masting is difficult to achieve. This thesis was able to produce good models to explain historical results, but these models were not accurate enough to be used for prediction. However, the models did agree with much of the literature in identifying several important weather variables that often led to higher acorn production: a previous year of low acorn production, warm and dry springs, and wet and warm summers. In combination with the findings from Chapter 2 that identified high producers on heavy clay soils, these weather variables could be used in a limited way to either identify new locations for seed collections or be a deciding factor as to whether collection efforts should take place. Further, Chapter 3 showed asynchrony in acorn production at large distances, suggesting poor acorn production at one site might be a useful hint of good acorn crops at sites much further away.

What this thesis did show clearly was the large tree to tree variation in acorn production with identifiable super- and poor-producing trees (Chapter 2). This finding suggests selecting individual trees with consistently high acorn production would be helpful: in Chapter 2, half of all the acorns produced over four years were shown to come from just 18% of the trees. Selecting individual trees for their quality, termed “plus Trees”, is already a common strategy used to generate the best growing trees such as for timber production (Matthews 1956; Clark and Wilson 2005). A similar method could be used to select super acorn producers to collect acorns from consistently and even to use as parent trees for future seed source stands. Late-phenology trees were shown to be better producers of acorns (Chapter 2). Phenology is genetically led and so some of the variability in acorn production may in turn be heritable. A danger of relying on a smaller pool of trees for seed sourcing could be the genetic bottlenecking of the population (Sujii et al. 2019). However, Chapter 2 showed that naturally regenerated oak woodlands can already be highly related to each other, and so it seems likely that naturally regenerated stands are already being formed from a smaller number of super producing trees. Further, as shown in Chapter 4, a maternal choice mechanism acting on pollen source could keep populations as genetically diverse as those that are naturally regenerated.

The recalcitrant nature of acorns means their storage is not viable and seed sources must rely on yearly crops. We do not currently have an effective way of increasing acorn yield via intervention measures. Some work has been done on the addition of macronutrients to increase seed yield of masting species. For instance, Smail et al. (2011) added nitrogen to Black Beech (*Nothofagus solandri* [Hook.f.] Oerst.) and found it increased seed yield in around half of the years studied. Land managers attempting to use macronutrient addition to increase acorn numbers may likely find the extra cost of such fertilisation would quickly make seed sourcing financially unviable, especially as much more work is needed to understand the complex interactions of these transient nutrients.

Alternatively, as shown in Chapters 2 and 5, independently of the variation in seed crops trees produce large numbers of flowers each year and pollen can remain viable in storage for up to two years (Batos et al. 2012). If trees are pollen limited, which Chapter 4 suggests, then supplementing pollen during flowering could increase acorn crops, especially if that pollen is from outside of the seed stand. Pollen is cheap to collect in large quantities. Further, its addition and collection is unlikely to damage the trees collected from, as these flowers are already a “spent” resource. As oak are a wind pollinated species, pollen application may not need to be precise and pollen application has been shown to be effective in certain agricultural species (Karimi et al. 2017) with different methods shown as effective in Scots Pine (*Pinus sylvestris* L.) seed orchards (Torimaru et al. 2013). In years where conditions are suitable for flower development (i.e. not frost damaged like those in Chapter 2 during 2021), then pollen supplementation could provide a useful low cost and low effort method of increasing yearly consistency in acorn crops.

Combining all the ideas discussed in this section, a method for improving seed sourcing scored by their current applicability and confidence in the evidence are listed in the table 6.1 below.

Table 6.1 Summary of management and future research recommendations for seed stand managers.

Method	Applicability	Confidence	Suggestion
Identifying super producers for collection	This is low cost and easy to implement. It is likely seed sourcing companies already identify higher producing trees or areas anecdotally, but clear and consistent record keeping could help formalise this and give clear instructions of where is mostly likely to provide the highest number of acorns.	High	Implement immediately
Pollen (from outside the stand) addition to increase production	Pollen is freely available as a resource and its collection is unlikely to damage trees or their seed production. Labour costs may be higher and methods of effectively applying the pollen still need to be researched. But it seems a promising method to trial in the short term.	Medium	Trial
Thinning canopies around selected trees	Other research has already found canopy thinning to increase acorn production (Brooke et al. 2019) and along with the results of Chapter 2 suggests canopy thinning should be used often when managing seed orchards. It is again low cost and in natural settings could also increase the chance of seedling recruitment.	High	Implement immediately
Application of fertilisers to increase production	Although not the subject of this thesis much previous work has suggested inconsistent benefits of nutrient application. It seems unlikely that application costs will overtake the gains in yield, and it could cause issues from nutrient leeching into the surrounding environment.	High	Research more

Planting seed orchards from high yielding trees	Phenological differences are heritable and were a driver of individual acorn production (Chapter 2) suggesting planting from super producers may be a useful strategy. However, high acorn production being linked to genetics was not explicitly studied, and with super producers' dominance within the system they are likely already forming the majority individuals planted within a seed orchard.	Medium	Research more
Timing seed collections from selected weather cues	With the current issues in modelling acorn production the suggestions for weather cues may be no better than those heard anecdotally in forestry. So whilst easy to implement it is possibly not useful in it's current form and shouldn't be relied upon.	Low	Trial/research more

6.8 Recommendations for future research

An important next step for future research would be to build a predictive model on the scale of an individual woodland or seed stand. Chapter 3 showed attempts at making a predictive model based on weather variables alone and applicable to all oaks in Europe was unsuccessful. This may have been because these different sites had different weather cues for masting. By considering trees at one site there is likely to be less heterogeneity in weather cues for mast or failed acorn crops. Further, by looking at one site the study could include tree level attributes starting with those shown to be important within Chapter 2. Wytham Woods has already been surveyed in great detail for the past four years, and researched more generally for >75 years (Savill et al. 2010). Although there is no perfect length or sample size for a masting study, at least a decade of sampling of 30 to 40 trees would be the minimum needed to capture enough information to perform a holistic study (i.e. including weather/environment/genetics). Hence Wytham Woods is an obvious choice for this longer-term sampling and modelling study, with already four years completed that captured one mast and one failed year. Moreover, as each tree sampled had its full genome sequenced there is opportunity for a fuller study into the genetics of masting.

Chapter 4 was the first to give experimental evidence for the selective ability of oak trees to abort flowers or developing acorns based on pollen source. However, the two years in which the experiment took place were moderate years for acorn production, and so it is not known if this would also occur during large mast years or importantly during failed years such as 2021. Therefore, the experiment should be repeated in other years and at other sites to see if this pattern holds. Additionally logistical considerations meant that the genetic study of the pollen source and resulting acorns could not be researched. Future work could include genetic analysis of pollen and flowers to see if there is an effect of relatedness to successful acorn production. The study also added a consistent amount of pollen to each flower, but it would be useful if used as an intervention measure to increase acorn crops, to know how the effect changes or stays the same depending on pollen quantity and method of application.

More experimental work could be put into seed orchard management. Chapter 2 made suggestions into how canopy thinning could enable greater acorn production, but this advice is still somewhat vague. Studies should experiment with different intensities of canopy thinning, or explore how tree planting density influences acorn production, something that could influence oak regeneration through seed production generally. Due to the long-life cycle of oak reproduction, we are still unsure how masting will be affected by anthropogenic climate change. Chapter 5 reported one of the few sites that is studying the effects of elevated CO_2 on oak. The experiment should continue to enable better study of masting, but also research if the effects of elevated CO_2 are cumulative. Further, within this study there was a lack of data into the stored nutrients within the tree. Future work could sample roots, trunk, and branches to explore how nutrient storage is being affected by elevated CO_2 and by acorn load and relate those results to an effect on masting.

6.9 Conclusions

This thesis aimed to understand the mechanistic drivers of oak masting in the UK and suggest methods to increase the supply and sourcing of acorns adapted for the UK climate. In doing so the studies within this thesis have filled research gaps in climate changes influence on masting, as well as being the first to present experimental evidence for a maternal choice of pollen source in oaks. By modelling acorn production at the level of individual trees as well as across a continental range it has been able to make several suggestions for better management of oak trees for increased acorn production and more efficient seed sourcing. Further, several important areas for this work to continue have been highlighted such as pairing individual level and inter-population models of masting, and the further study of the genetic basis of masting, even highlighting a useful experimental stand in Wytham Woods, Oxford. Studying the long-term reproductive process of a species that lives across many human generations is a challenge, particularly in the context of a three-year PhD study, but this thesis has provided important steps that we can take now to increase oak supply as well as making suggestions of what the next generation should be working on.

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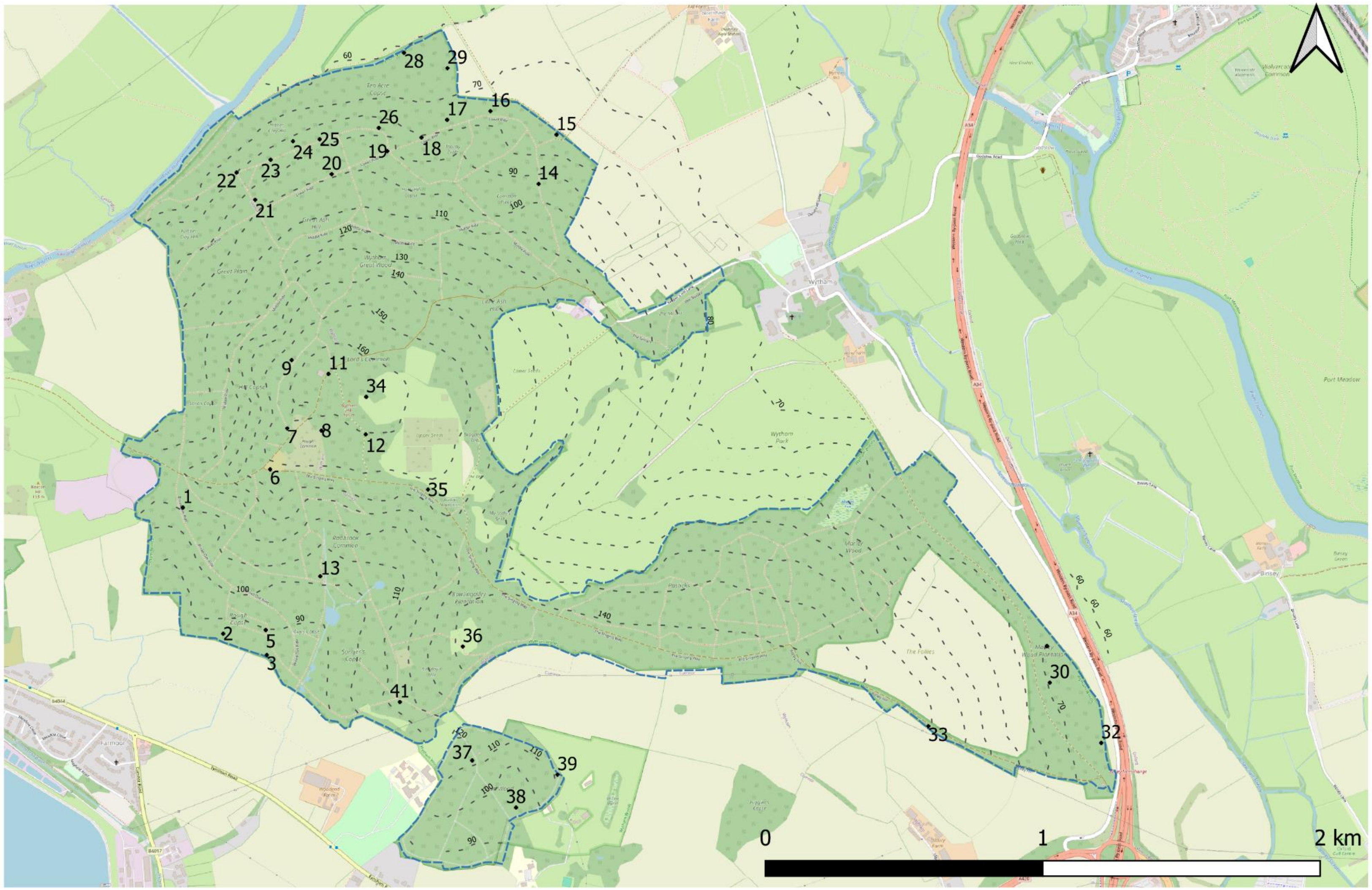


Appendix Map 2.1 A map of Wytham Woods, Oxford, showing the locations of 39 experimental trees used in this study. The extent of Wytham Woods is show by blue dashed line, the units for the black dashed contour lines are meters above sea level and the arrow on the top right of the image shows the direction of north.

Appendix table 2.1 Variables and descriptive statistics (to 2dp) of acorn production at Wytham Woods

Variable	Unit	Mean	SD	Max	Min
Response:					
Acorn Production (Visual Counts)	Avg count per tree	65.03	64.84	238	1.67
Acorn Production (Litter traps)	Count per 0.25m^2 crown area	2.96	4.76	24.89	0
Immature Acorns	Count per 0.25m^2 crown area	4.6	4.52	15.19	0
Enlarged Cups	Count per 0.25m^2 crown area	5.28	4.3	17.53	0
Flowers	Count per 0.25m^2 crown area	39.31	21.13	94.72	4.72
Galls	Count per 0.25m^2 crown area	2.54	2.8	8.92	0
Explanatory:					
Diameter at Breast height (DBH)	Centimetres	77	27.77	185.26	41.06
Tree Height	Meters	21.43	5.27	33.76	12.74
Site Elevation	Meters above sea level	103.30	32.48	162.62	59.93
Slope Aspect	Degrees	186.91	123.13	359.62	1.00
Crown Spread	Meters	14.88	3.58	24	5.50
Crown Cross	Meters	11.87	3.38	19.8	5.50
Canopy Closure	1 (Open) to 10 (Closed)	5.28	2.57	10	1
Stalk Density	1 (Open) to 10 (Closed)	3.33	1.9	7	1
pH	pH	6.49	0.82	7.8	4.6
Phosphorus	Milligram per litre (mg/l)	9.47	7.47	32.2	4.0
Potassium	Milligram per litre (mg/l)	270.6	98.02	549.0	103.0
Magnesium	Milligram per litre (mg/l)	180.9	68.36	371.0	90.0
Sand	% per composite sample	47.59	18.31	88.00	14.00
Silt	% per composite sample	25.33	7.78	41.00	8.00
Clay	% per composite sample	27.08	11.14	51.00	4.00
Spring Phenology	% peak LAI per tree	45.81	4.81	55.92	34.48
Mid-April LAI	% peak LAI per tree	29.43	14.08	58.65	1.35
Autumn Phenology	% peak LAI per tree	13.68	3.62	22.42	8.46
Mid-November LAI	% peak LAI per tree	59.69	11.64	92.12	41.25
Mid-December LAI	% peak LAI per tree	7.06	8.43	29.1	0
AUPPC	Cumulative % LAI per tree	186.5	10.28	203.0	164.6
Maximum Temp	Celsius	10.86	5.5	28.75	-5.2
Minimum Temp	Celsius	10.12	5.41	27.21	-5.8
Mean Temp	Celsius	10.48	5.45	27.33	-5.48
KING scores	Pair-wise kinship coefficients	0.1	0.08	0.34	-0.23
Soil Class	Factor	na	na	na	na

Appendix table 2.2 Immature acorn counts from litter traps, at Wytham Woods, Oxford. The table shows the values of immature acorns counted each year, averaged per individual litter trap ($0.25m^2$) and to 2dp, and the percentage that each tree contributed to the total mature acorn crop that year. Counts each year are colour coded to identify super, average and poor producing individuals. Contributing >5% = green, between 0.99% and 5.0% = yellow, <1% = red. The table is ordered by visual acorn counts [Table 1]. All traps for trees 3, 6, 32, 34, and 36, were knocked down by adverse weather or wildlife in 2023.

Tree	2021	%	2022	%	2023	%	Total	%
36	0	0.00%	3	1.00%	na	na	3	0.54%
39	0.25	1.41%	40.83	13.57%	4.5	1.92%	45.58	8.25%
13	0	0.00%	6.33	2.10%	32	13.68%	38.33	6.94%
1	0.5	2.82%	15.66	5.21%	9	3.85%	25.16	4.56%
15	1.33	7.51%	18.25	6.06%	23.5	10.05%	43.08	7.80%
33	0.33	1.88%	27	8.97%	11.25	4.81%	38.58	6.98%
19	0	0.00%	13.5	4.49%	3	1.28%	16.5	2.99%
30	1.25	7.04%	8.75	2.91%	0	0.00%	10	1.81%
28	0	0.00%	13.25	4.40%	6.5	2.78%	19.75	3.57%
11	0.25	1.41%	4	1.33%	0.5	0.21%	4.75	0.86%
41	1	5.63%	6	1.99%	10	4.28%	17	3.08%
24	0	0.00%	3.33	1.11%	0	0.00%	3.33	0.60%
20	1	5.63%	2	0.66%	1	0.43%	4	0.72%
23	0.75	4.23%	3	1.00%	18	7.70%	21.75	3.94%
8	0.5	2.82%	0.5	0.17%	6.5	2.78%	7.5	1.36%
12	0	0.00%	5.75	1.91%	0.5	0.21%	6.25	1.13%
14	0	0.00%	39.75	13.21%	2	0.86%	41.75	7.56%
3	0.25	1.41%	4	1.33%	na	na	4.25	0.77%
4	0.5	2.82%	12.33	4.10%	16	6.84%	28.83	5.22%
34	0	0.00%	7.33	2.44%	na	na	7.33	1.33%
2	0.25	1.41%	1.25	0.42%	2.5	1.07%	4	0.72%
22	3.25	18.31%	8	2.66%	25.66	10.98%	36.91	6.68%
35	1.08	6.10%	2.33	0.78%	0	0.00%	3.41	0.62%
18	1	5.63%	0.33	0.11%	1	0.43%	2.33	0.42%
31	0.5	2.82%	10.75	3.57%	3.5	1.50%	14.75	2.67%
29	0.25	1.41%	4.5	1.50%	0.5	0.21%	5.25	0.95%
26	0.25	1.41%	4.25	1.41%	6.25	2.67%	10.75	1.95%
25	0.75	4.23%	6.75	2.24%	8	3.42%	15.5	2.81%
16	0	0.00%	4.75	1.58%	0	0.00%	4.75	0.86%
5	0	0.00%	2.33	0.78%	3	1.28%	5.33	0.97%
6	0	0.00%	0	0.00%	na	na	0	0.00%
32	0	0.00%	0	0.00%	na	na	0	0.00%
37	0	0.00%	0	0.00%	9	3.85%	9	1.63%
38	0	0.00%	8.33	2.77%	0.5	0.21%	8.83	1.60%
7	0	0.00%	0	0.00%	0	0.00%	0	0.00%
21	0.5	2.82%	3.66	1.22%	12	5.13%	16.16	2.93%
9	0	0.00%	1	0.33%	0	0.00%	1	0.18%
17	1.25	7.04%	3.75	1.25%	1	0.43%	6	1.09%
27	0.5	2.82%	0.33	0.11%	0.66	0.29%	1.5	0.27%
Total	17.5	100%	296.91	100%	217.83	100%	532.25	100%

Appendix table 2.3 Enlarged cup counts from litter traps, at Wytham Woods, Oxford. The table shows the values of enlarged cups counted each year, averaged per individual litter trap (0.25m^2) and to 2dp, including the percentage that each tree contributed to the total count of enlarged cups that year. Counts each year are colour coded to identify super, average and poor producing individuals. Contributing >5% = green, between 0.99% and 5.0% = yellow, <1% = red. The table is ordered by visual acorn counts [Table 1]. All traps for trees 3, 6, 32, 34, and 36, were knocked down by adverse weather or wildlife in 2023.

Tree	2021	%	2022	%	2023	%	Total	%
36	1.25	5.98%	5	1.77%	na	na	6.25	1.01%
39	0	0.00%	8.66	3.06%	4.5	1.44%	13.16	2.14%
13	0.5	2.39%	3.33	1.18%	9	2.88%	12.83	2.08%
1	0.75	3.59%	22.83	8.07%	29	9.27%	52.58	8.53%
15	0.58	2.79%	6.25	2.21%	17.5	5.60%	24.33	3.95%
33	0	0.00%	14.25	5.04%	9.5	3.04%	23.75	3.85%
19	0.5	2.39%	26.25	9.28%	11	3.52%	37.75	6.12%
30	0.5	2.39%	7.75	2.74%	5	1.60%	13.25	2.15%
28	0	0.00%	11	3.89%	1	0.32%	12	1.95%
11	0	0.00%	5	1.77%	4.5	1.44%	9.5	1.54%
41	0.75	3.59%	3.33	1.18%	35	11.19%	39.08	6.34%
24	1.33	6.37%	25	8.84%	2	0.64%	28.33	4.60%
20	0.5	2.39%	7	2.47%	17	5.44%	24.5	3.97%
23	0.25	1.20%	4.25	1.50%	22.33	7.14%	26.83	4.35%
8	0.5	2.39%	1	0.35%	7.5	2.40%	9	1.46%
12	0.25	1.20%	6.5	2.30%	13.5	4.32%	20.25	3.28%
14	0	0.00%	31.5	11.14%	8.5	2.72%	40	6.49%
3	1	4.78%	2.75	0.97%	na	na	3.75	0.61%
4	0.25	1.20%	12.83	4.54%	4	1.28%	17.08	2.77%
34	0.5	2.39%	8.33	2.95%	na	na	8.83	1.43%
2	0.5	2.39%	0.25	0.09%	6.5	2.08%	7.25	1.18%
22	2.75	13.15%	8.25	2.92%	15.66	5.01%	26.66	4.33%
35	0.75	3.59%	7	2.47%	1	0.32%	8.75	1.42%
18	0	0.00%	0	0.00%	1.5	0.48%	1.5	0.24%
31	0	0.00%	3	1.06%	2	0.64%	5	0.81%
29	0	0.00%	8.75	3.09%	1	0.32%	9.75	1.58%
26	0	0.00%	3.5	1.24%	13.5	4.32%	17	2.76%
25	2.25	10.76%	9.75	3.45%	8.66	2.77%	20.66	3.35%
16	0.25	1.20%	2.25	0.80%	1.5	0.48%	4	0.65%
5	1	4.78%	1.33	0.47%	2	0.64%	4.33	0.70%
6	0	0.00%	0	0.00%	na	na	0	0.00%
32	0.5	2.39%	2.5	0.88%	na	na	3	0.49%
37	1.5	7.17%	1.66	0.59%	12	3.84%	15.16	2.46%
38	0	0.00%	12	4.24%	4	1.28%	16	2.60%
7	0	0.00%	0.75	0.27%	0	0.00%	0.75	0.12%
21	1	4.78%	5	1.77%	32	10.23%	38	6.16%
9	0	0.00%	0.75	0.27%	0	0.00%	0.75	0.12%
17	0	0.00%	2	0.71%	0.25	0.08%	2.25	0.36%
27	0	0.00%	0	0.00%	2.33	0.75%	2.33	0.38%
Total	20.91	100%	282.83	100%	312.75	100%	616.5	100%

Appendix table 2.4 Flower counts from litter traps, at Wytham Woods, Oxford. The table shows the values of flowers counted each year, averaged per individual litter trap (0.25m^2) and to 2dp, including the percentage that each tree contributed to the total count of flowers that year. Counts each year are colour coded to identify super, average and poor producing individuals. Contributing >5% = green, between 0.99% and 5.0% = yellow, <1% = red. The table is ordered by visual acorn counts [Table 1]. All traps for trees 3, 6, 32, 34, and 36, were knocked down by adverse weather or wildlife in 2023.

Tree	2021	%	2022	%	2023	%	Total	%
36	26.75	2.23%	126.5	4.84%	na	na	153.25	3.38%
39	7.25	0.60%	85.16	3.26%	19	2.63%	111.41	2.45%
13	25.5	2.13%	44	1.68%	50	6.92%	119.5	2.63%
1	64	5.33%	187.16	7.16%	33	4.56%	284.16	6.26%
15	23.58	1.97%	103.25	3.95%	31	4.29%	157.83	3.48%
33	9.66	0.81%	57.75	2.21%	13.5	1.87%	80.91	1.78%
19	10.25	0.85%	106.75	4.08%	14	1.94%	131	2.89%
30	24.75	2.06%	87.25	3.34%	14	1.94%	126	2.78%
28	1.5	0.13%	97.25	3.72%	11	1.52%	109.75	2.42%
11	55.5	4.63%	76	2.91%	24.5	3.39%	156	3.44%
41	32	2.67%	66.33	2.54%	11	1.52%	109.33	2.41%
24	19.67	1.64%	40.66	1.55%	5	0.69%	65.33	1.44%
20	53	4.42%	32	1.22%	7	0.97%	92	2.03%
23	28.75	2.40%	128.75	4.92%	41.66	5.76%	199.16	4.39%
8	11	0.92%	7.75	0.30%	24	3.32%	42.75	0.94%
12	37.25	3.11%	77.25	2.95%	1	0.14%	115.5	2.54%
14	2	0.17%	163	6.23%	8	1.11%	173	3.81%
3	28.5	2.38%	45.75	1.75%	na	na	74.25	1.64%
4	31.5	2.63%	80.66	3.08%	59	8.16%	171.16	3.77%
34	24	2.00%	53.66	2.05%	na	na	77.66	1.71%
2	29	2.42%	30.5	1.17%	24.5	3.39%	84	1.85%
22	122	10.17%	60.25	2.30%	72.33	10.00%	254.58	5.61%
35	37.83	3.15%	41.33	1.58%	3	0.41%	82.16	1.81%
18	15.33	1.28%	8.33	0.32%	3	0.41%	26.66	0.59%
31	25.25	2.10%	107.75	4.12%	22.5	3.11%	155.5	3.43%
29	4	0.33%	39.5	1.51%	1	0.14%	44.5	0.98%
26	27.25	2.27%	37.5	1.43%	16.75	2.32%	81.5	1.80%
25	16	1.33%	65	2.48%	10.33	1.43%	91.33	2.01%
16	40.75	3.40%	112.5	4.30%	6.5	0.90%	159.75	3.52%
5	35.33	2.95%	38.66	1.48%	3.66	0.51%	77.66	1.71%
6	28	2.33%	22	0.84%	na	na	50	1.10%
32	20	1.67%	34	1.30%	na	na	54	1.19%
37	30.25	2.52%	40.41	1.55%	41	5.67%	111.66	2.46%
38	67	5.58%	73.66	2.82%	7.5	1.04%	148.16	3.26%
7	47	3.92%	133	5.08%	55.5	7.68%	235.5	5.19%
21	55.5	4.63%	26	0.99%	33	4.56%	114.5	2.52%
9	8.5	0.71%	11	0.42%	0.5	0.07%	20	0.44%
17	11	0.92%	28.25	1.08%	0.25	0.03%	39.5	0.87%
27	7.5	0.63%	3.66	0.14%	3	0.41%	14.16	0.31%
Total	1199.66	100%	2615.75	100%	723	100%	4538.41	100%

Appendix table 2.5 Gall counts from litter traps, at Wytham Woods, Oxford. The table shows the values of Galls counted each year, averaged per individual litter trap (0.25m^2) and to 2dp, including the percentage that each tree contributed to the total count of flowers that year. Counts each year are colour coded to identify super, average and poor producing individuals. Contributing >5% = green, between 0.99% and 5.0% = yellow, <1% = red. The table is ordered by visual acorn counts [Table 1]. All traps for trees 3, 6, 32, 34, and 36, were knocked down by adverse weather or wildlife in 2023.

Tree	2021	%	2022	%	2023	%	Total	%
36	0	0.00%	0	0.00%	na	na	0	0.00%
39	0	0.00%	0	0.00%	0	0.00%	0	0.00%
13	2.5	2.16%	0	0.00%	7	4.57%	9.5	3.16%
1	7.75	6.68%	5.33	17.11%	13	8.48%	26.08	8.68%
15	7.66	6.61%	0	0.00%	13	8.48%	20.66	6.88%
33	1.33	1.15%	0.25	0.80%	3.25	2.12%	4.83	1.61%
19	0.5	0.43%	0.75	2.41%	0	0.00%	1.25	0.42%
30	0	0.00%	0.25	0.80%	0	0.00%	0.25	0.08%
28	0.5	0.43%	4.25	13.64%	19.5	12.72%	24.25	8.07%
11	0.25	0.22%	0	0.00%	0	0.00%	0.25	0.08%
41	8.5	7.33%	0.33	1.07%	2	1.31%	10.83	3.61%
24	3.66	3.16%	0.66	2.14%	0	0.00%	4.33	1.44%
20	7.5	6.47%	0	0.00%	3	1.96%	10.5	3.50%
23	0.25	0.22%	0	0.00%	2	1.31%	2.25	0.75%
8	0	0.00%	0	0.00%	1	0.65%	1	0.33%
12	0.75	0.65%	5	16.04%	12.5	8.16%	18.25	6.07%
14	0	0.00%	2.75	8.82%	7	4.57%	9.75	3.25%
3	1.75	1.51%	0	0.00%	na	na	1.75	0.58%
4	2.5	2.16%	0	0.00%	7	4.57%	9.5	3.16%
34	1	0.86%	0.33	1.07%	na	na	1.33	0.44%
2	3.75	3.23%	0	0.00%	10	6.53%	13.75	4.58%
22	17.5	15.09%	1	3.21%	7.66	5.00%	26.166	8.71%
35	9.83	8.48%	2	6.42%	1	0.65%	12.83	4.27%
18	1.66	1.44%	0	0.00%	2	1.31%	3.66	1.22%
31	6	5.17%	2.75	8.82%	18	11.75%	26.75	8.90%
29	0	0.00%	0.25	0.80%	0.25	0.16%	0.5	0.17%
26	0.5	0.43%	0	0.00%	1.25	0.82%	1.75	0.58%
25	0.25	0.22%	0	0.00%	0.33	0.22%	0.58	0.19%
16	0	0.00%	0.25	0.80%	1.25	0.82%	1.5	0.50%
5	0.33	0.29%	0	0.00%	0.66	0.44%	1	0.33%
6	5.5	4.74%	1.5	4.81%	na	na	7	2.33%
32	6.5	5.60%	0	0.00%	na	na	6.5	2.16%
37	0	0.00%	0	0.00%	0	0.00%	0	0.00%
38	2	1.72%	0	0.00%	0	0.00%	2	0.67%
7	9.5	8.19%	1.5	4.81%	7	4.57%	18	5.99%
21	1	0.86%	1	3.21%	4	2.61%	6	2.00%
9	0.25	0.22%	0	0.00%	0	0.00%	0.25	0.08%
17	0.75	0.65%	0.25	0.80%	3.25	2.12%	4.25	1.41%
27	0	0.00%	0	0.00%	0.33	0.22%	0.33	0.11%
Total	116	100%	31.16	100%	153.25	100%	300.41	100%

Appendix T3.6 Results of a series of Partial Least Squares Regression models predicting acorn production in *Quercus robur*, *Quercus petraea*, and both species together (mixed) in England, or France and Germany (Fra. & Ger.) in response to weather (see text). (Data from ten sites in England, 27 in France and one in Germany) showing how well the models fit the training or test (out of sample) data. (Response variable is A^{DF} = standardised acorn count difference from the mean for each year; see methods)

Species	Country	Method	Data	R^2	MSE	RMSE	Out of sample MSE	Out of sample RMSE
Q. robur	England	PLSR	Regression	0.41	4205	64.85	9585	97.91
Q. robur	Fra. & Ger.	PLSR	Regression	0.35	4172	64.60	6468	80.43
Q. petraea	England	PLSR	Regression	0.82	730	27.02	3411	58.41
Q. petraea	France	PLSR	Regression	0.23	4112	64.13	5143	71.72
Mixed	England	PLSR	Regression	0.46	2921	54.05	9519	97.57
Mixed	Fra. & Ger.	PLSR	Regression	0.34	3860	62.13	6057	77.83
Q. robur	Mixed	PLSR	Regression	0.24	5098	71.41	8312	91.17
Q. petraea	Mixed	PLSR	Regression	0.15	4290	65.50	5067	71.19
Mixed	Mixed	PLSR	Regression	0.32	4088	63.94	5871	76.62

Appendix 3.7 Results from a series of Partial Least Squares Discriminant Analysis predicting acorn production in *Quercus robur* and *Quercus petraea* from data in England, France/Germany and both of them considered together. (Data from 10 sites in England, 27 in France and one in Germany). The two-class group data set splits the acorn production data into below or above the mean. The three-class group data set splits acorn production relative to the mean into: Class 1 <=-25%, Class 2 >-25% <=25%, Class 3 >25%. The Accuracy scores and the Kappa scores (Cohen, 1960; McHugh, 2012) are shown, with the p-values representing the chance of the accuracy being different from the no information rate (i.e. the chance of predicting the right answer at random). Significant results are highlighted in bold.

Species	Country	Method	Class	Accuracy	Kappa	P
Q. robur	England	PLS-DA	2	0.63	0.26	0.29
			3	0.56	0.22	0.83
Q. robur	Fra. & Ger.	PLS-DA	2	0.62	0.22	0.57
			3	0.62	0.33	0.83
Q. petraea	England	PLS-DA	2	0.58	0	0.82
			3	**0.75**	**0.61**	**<0.05**
Q. petraea	France	PLS-DA	2	0.63	0.26	0.15
			3	0.53	0.18	0.90
Mixed	England	PLS-DA	2	0.64	0.28	0.08
			3	**0.64**	**0.42**	**<0.05**
Mixed	Fra. & Ger.	PLS-DA	2	0.67	0.33	0.23
			3	0.46	0.09	0.86
Q. robur	Mixed	PLS-DA	2	0.61	0.16	0.93
			3	0.51	0.14	0.92
Q. petraea	Mixed	PLS-DA	2	0.54	0.09	0.46
			3	0.5	0.2	0.92
Mixed	Mixed	PLS-DA	2	0.59	0.17	0.1
			3	0.47	0.11	0.99

Appendix 3.8 Results for a series of pruned regression trees predicting acorn production in *Quercus robur*, *Quercus petraea*, and both species together (mixed) in England, or France and Germany (Fra. & Ger.) in response to weather (see text). (Data from ten sites in England, 27 in France and one in Germany) showing how well the models fit the training or test (out of sample) data. (Response variable is A^{DF} = standardised acorn count difference from the mean for each year; see methods)

Species	Country	Method	Data	R^2	MSE	RMSE	Out of sample MSE	Out of sample RMSE
Q. robur	England	CART	Regression	0.52	3369	58.05	8122	90.13
Q. robur	Fra. & Ger.	CART	Regression	0.59	2422	49.22	8261	90.89
Q. petraea	England	CART	Regression	0.64	1482	38.51	3605	60.05
Q. petraea	France	CART	Regression	0.69	1589	39.87	5993	77.42
Mixed	England	CART	Regression	0.73	1428	37.79	8479	92.09
Mixed	Fra. & Ger	CART	Regression	0.69	1797	42.40	7220	84.97
Q. robur	Mixed	CART	Regression	0.64	2372	48.71	9689	98.44
Q. petraea	Mixed	CART	Regression	0.67	1674	40.92	7889	88.82
Mixed	Mixed	CART	Regression	0.4	3669	60.58	6219	78.86

Appendix 3.9 Results from a series of pruned classification trees predicting acorn production in *Quercus robur* and *Quercus petraea* from data in England, France/Germany and both of them considered together. (Data from 10 sites in England, 27 in France and one in Germany). The two-class group data set splits the acorn production data into below or above the mean. The three-class group data set splits acorn production relative to the mean into: Class 1 <=-25%, Class 2 >-25% <=25%, Class 3 >25%. The Accuracy scores and the Kappa scores (Cohen, 1960; McHugh, 2012) are shown, with the p-values representing the chance of the accuracy being different from the no information rate (i.e. the chance of predicting the right answer at random). Significant results are highlighted in bold.

Species	Country	Method	Class	Accuracy	Kappa	P
Q. robur	England	CART	2	0.56	0.11	0.83
			3	0.46	0.04	0.9
Q. robur	Fra. & Ger.	CART	2	0.53	0.06	0.57
			3	0.43	0.15	0.29
Q. petraea	England	CART	2	0.75	0.5	0.19
			3	0.58	0.4	0.62
Q. petraea	France	CART	2	0.56	0.15	0.73
			3	**0.56**	**0.31**	**<0.01**
Mixed	England	CART	2	0.67	0.27	0.44
			3	0.57	0.31	0.22
Mixed	Fra. & Ger.	CART	2	0.55	0.1	0.31
			3	**0.48**	**0.2**	**<0.05**
Q. robur	Mixed	CART	2	0.6	0.2	0.12
			3	0.47	0.13	0.64
Q. petraea	Mixed	CART	**2**	**0.62**	**0.24**	**<0.05**
			3	0.48	0.18	0.11
Mixed	Mixed	CART	2	0.58	0.16	0.1
			3	0.47	0.17	0.53

Appendix 3.10 Results for a series of Random Forest regression models predicting acorn production in *Quercus robur*, *Quercus petraea*, and both species together (mixed) in England, or France and Germany (Fra. & Ger.) in response to weather (see text). (Data from ten sites in England, 27 in France and one in Germany) showing how well the models fit the training or test (out of sample) data. (Response variable is A^{DF} = standardised acorn count difference from the mean for each year; see methods)

Species	Country	Method	Data	R^2	MSE	RMSE	Out of sample MSE	Out of sample RMSE
Q. robur	England	VSURF	Regression	0.84	1099	33.16	7752	88.05
Q. robur	Fra. & Ger.	VSURF	Regression	0.84	920	30.34	7424	86.17
Q. petraea	England	VSURF	Regression	0.90	378	19.47	3584	59.87
Q. petraea	France	VSURF	Regression	0.88	639	25.29	4787	69.19
Mixed	England	VSURF	Regression	0.83	857	29.28	7797	88.30
Mixed	Fra. & Ger.	VSURF	Regression	0.88	652	25.54	5793	76.11
Q. robur	Mixed	VSURF	Regression	0.84	1015	31.86	7438	86.25
Q. petraea	Mixed	VSURF	Regression	0.87	624	24.98	3996	63.22
Mixed	Mixed	VSURF	Regression	0.87	761	27.60	4701	68.57

Appendix 3.11 Results for a series of Random Forest classification models predicting acorn production in *Quercus robur* and *Quercus petraea* from data in England, France/Germany and both of them considered together. (Data from 10 sites in England, 27 in France and one in Germany). The two-class group data set splits the acorn production data into below or above the mean. The three-class group data set splits acorn production relative to the mean into: Class 1 <=-25%, Class 2 >-25% <=25%, Class 3 >25%. The Accuracy scores and the Kappa scores (Cohen, 1960; McHugh, 2012) are shown, with the p-values representing the chance of the accuracy being different from the no information rate (i.e. the chance of predicting the right answer at random). Significant results are highlighted in bold.

Species	Country	Method	Class	Accuracy	Kappa	P
Q. robur	England	VSURF	2	0.95	-0.08	0.95
			3	0.5	0.14	0.71
Q. robur	Fra. & Ger.	VSURF	2	0.63	0.24	0.3
			3	0.5	0.19	0.57
Q. petraea	England	VSURF	2	0.58	0.17	0.38
			3	0.5	0.23	0.81
Q. petraea	France	VSURF	2	0.59	0.18	0.09
			3	0.47	0.17	0.72
Mixed	England	VSURF	2	0.59	0.19	0.22
			3	0.64	0.42	0.13
Mixed	Fra. & Ger.	VSURF	2	0.63	0.26	0.24
			3	0.53	0.23	0.19
Q. robur	Mixed	VSURF	2	0.61	0.19	0.66
			3	0.58	0.26	0.35
Q. petraea	Mixed	VSURF	2	0.59	0.08	0.89
			3	0.6	0.37	0.11
Mixed	Mixed	VSURF	2	0.64	0.27	<0.05
			3	0.53	0.24	0.4

Appendix 3.7. The top 20 variable importance scores (VIP) and model coefficients of three partial least squares regression analyses using weather variables to predict standardised acorn count differences from the mean (A^{DF}). The PLSR models for two oak species (*Quercus petraea* and *Quercus robur)* are presented separately and together in the same model (All Oak). The number of components (latent variables) considered for each model are noted, as well as the in-sample Coefficient of Variation (R^2), out of sample Root Mean Square Error (RMSE) and out of sample Normalised Root Mean Square Error (NRMSE). The NRMSE is calculated via the range of the response variables of each model. Variables that have a VIP score >0.8 are judged to have a large contribution the prediction and are highlighted in bold. The VIP scores are calculated as the weighted sum of the squared coefficients, ordering them based on the reduction each one makes to the sum of squares across the PLSR components. For ease of interpretation, variables with negative coefficients are highlighted in red and those with positive coefficients are in green.

Quercus petraea		
Components considered	2	
In Sample R^2	0.15	
Out of sample RMSE	71.19	
Out of sample NRMSE	0.24	
Variable	VIP score	Coeff
Oct Tmin t-2	**1.05**	**0.97**
Apr Tmax	**0.99**	**0.99**
Apr Tavg	**0.98**	**0.98**
Oct Tavg t-2	**0.97**	**0.98**
Oct Tmax t-2	**0.84**	**0.84**
Tmin Autumn t-1	**0.81**	**0.81**
Tavg Autumn t-1	0.78	0.78
Sep Tmin t-1	0.77	0.77
Tmin Summer Δ2	0.75	0.75
Acorn Lag	0.71	-0.72
Jun Tmin	0.7	0.7
Tavg Spring	0.7	0.7
Tmax Spring Δ2	0.7	0.7
Tmax Spring	0.7	0.7
Tmax Autumn t-1	0.69	0.69
Tmin Summer Δ1	0.69	0.69
Tmin Autumn t-2	0.67	0.67

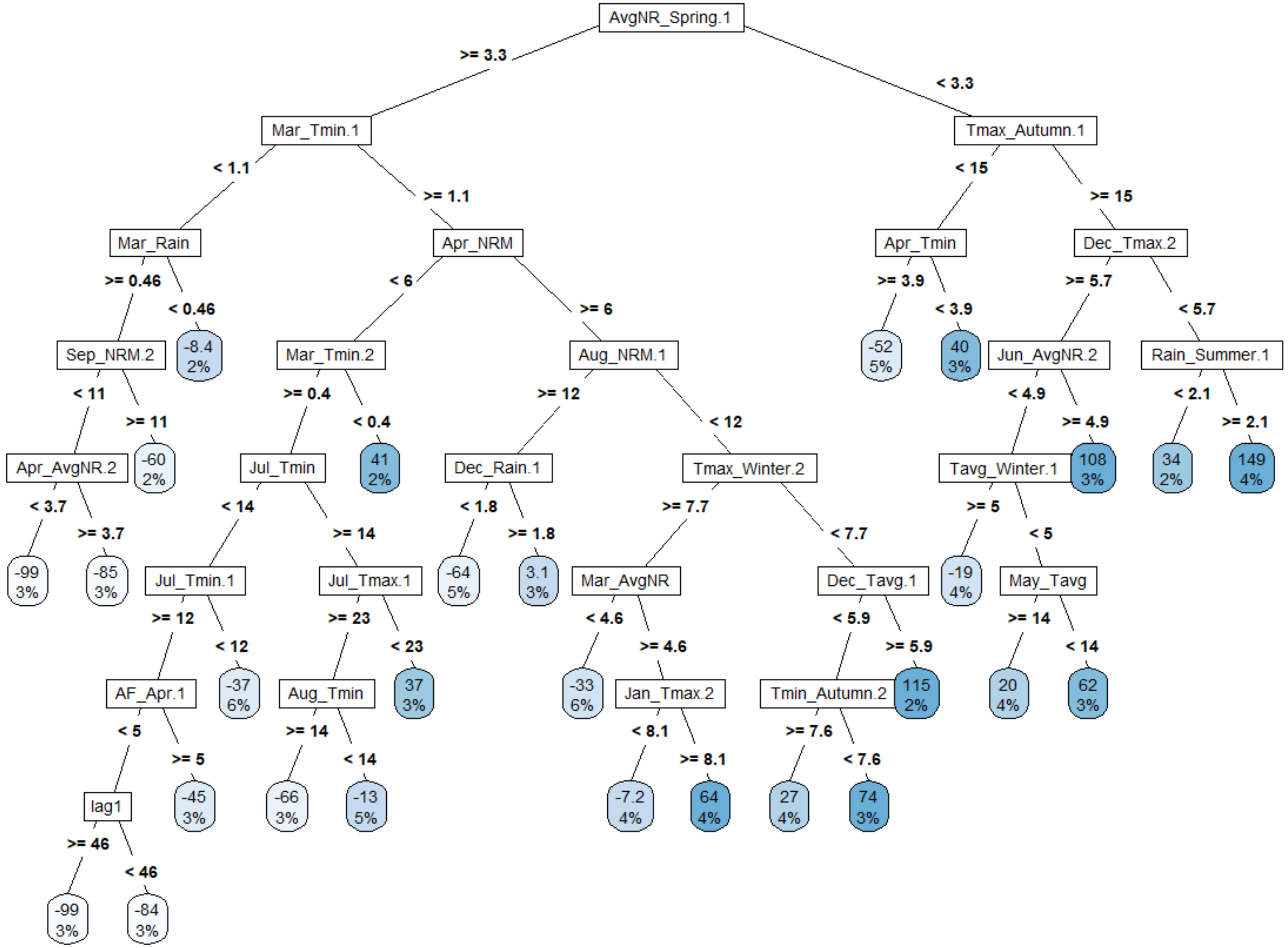
Quercus robur		
Components considered	2	
In sample R^2	0.24	
Out of sample RMSE	91.17459	
Out of sample NRMSE	0.21	
Variable	VIP score	Coeff
AvgNR Spring Δ1	**1.59**	**1.59**
Acorn Lag	**1.53**	**-1.53**
Mar Tmin t-2	**1.52**	**-1.52**
Mar Tavg t-2	**1.45**	**-1.45**
Mar Tmin	**1.4**	**-1.41**
AF Mar t-2	**1.38**	**1.38**
Mar 0	**1.36**	**-1.36**
AF Mar	**1.34**	**1.34**
Mar Tavg	**1.34**	**-1.34**
Mar 5	**1.33**	**-1.33**
AF Nov t-2	**1.3**	**1.3**
Apr Rain	**1.28**	**-1.28**
Apr Tmax	**1.27**	**1.27**
Aug Tavg t-1	**1.22**	**-1.22**
Apr Tmin t-2	**1.19**	**1.19**
Aug Tmin t-1	**1.16**	**-1.16**
Aug NRM t-1	**1.16**	**-1.16**

All oak		
Components considered	2	
In sample R^2	0.32	
Out of sample RMSE	76.62341	
Out of sample NRMSE	0.24	
Variable	VIP score	Coeff
Acorn lag	**1.46**	**-4.81**
Avg NR spring Δ1	**1.32**	**3.41**
Apr Tmin t-2	**0.94**	**2.32**
Tmin Summer Δ2	**0.94**	**2.33**
Apr Tmax	**0.92**	**2.4**
AvgNR Spring t-1	**0.92**	**-2.17**
Mar Tmin t-1	**0.91**	**2.7**
NRM Spring Δ1	**0.86**	**1.88**
NRM Spring t-1	**0.84**	**-1.83**
Apr Tavg	**0.84**	**2.17**
AvgNR Spring	**0.83**	**2.32**
Aug Rain	0.8	2.62
Tmin Summer Δ1	0.78	2.11
Tavg Summer Δ2	0.75	1.91
Jun AvgNR t-2	0.75	2.39
Apr Tavg t-2	0.75	2.17
Aug Tmin t-1	0.73	-2.15

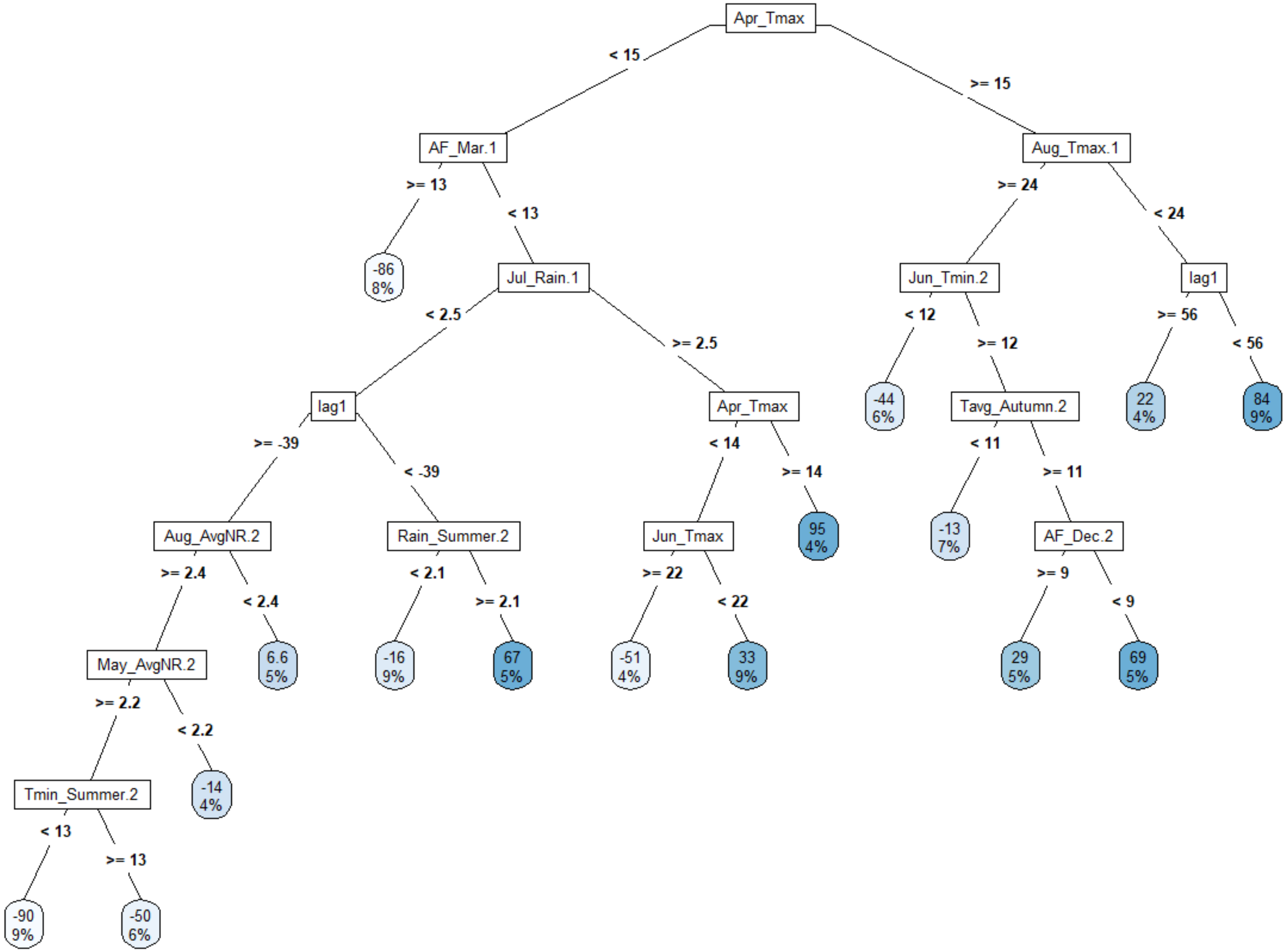
Sep Tavg t-1	0.67	0.67
NRM Spring t-1	0.66	-0.66
Apr Tmin t-2	0.66	0.66

AvgNR Spring t-1	**1.16**	**-1.16**
Aug Tmax t-1	**1.13**	**-1.13**
Apr NRM	**1.13**	**1.13**

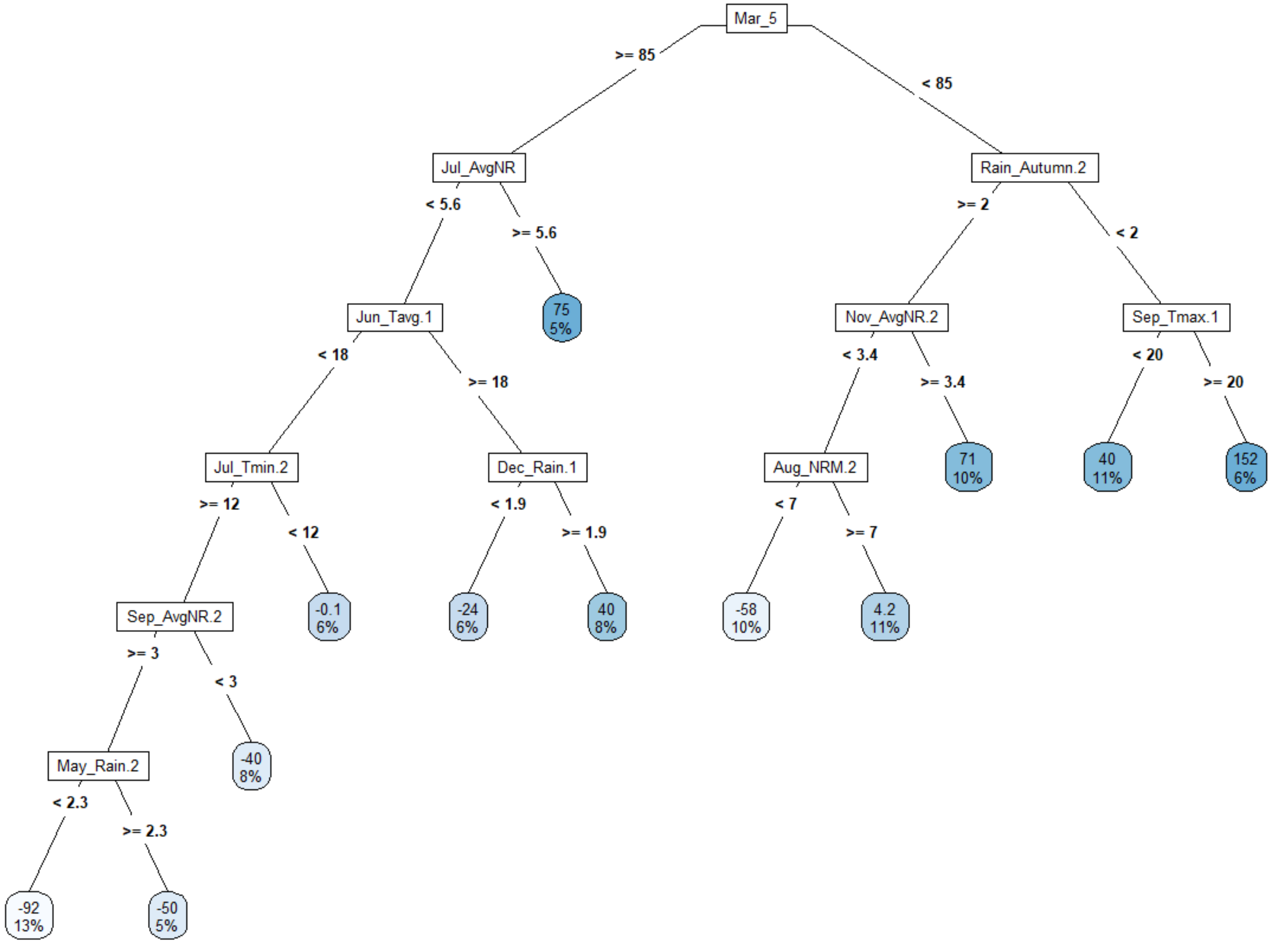
AF Mar t-1	0.72	-2.23
Tavg Summer Δ1	0.72	1.96
Apr Rain	0.72	-1.97



Appendix 3.8. A pruned regression tree predicting acorn production in the oak species *Quercus robur* and *Quercus petraea* combined. The value splitting the nodes is shown on each branch. Each lozenge shows the average of the standardised acorn count difference from the mean (A^{DF}, upper value) and the percentage of observations from the full dataset (lower value). Nodes are colour scaled from blue (high acorn production) to white (low acorn production). In sample R^2: 0.66, MSE: 2087, RMSE: 45. Out of sample RMSE: 87.



Appendix 3.9. A pruned regression tree predicting acorn production in the oak species *Quercus robur* and *Quercus petraea* combined. The value splitting the nodes is shown on each branch. Each lozenge shows the average of the standardised acorn count difference from the mean (A^{DF}, upper value) and the percentage of observations from the full dataset (lower value). Nodes are colour scaled from blue (high acorn production) to white (low acorn production). In sample R^2: 0.66, MSE: 1685, RMSE: 41. Out of sample RMSE: 87.



Appendix 3.10 A pruned regression tree predicting acorn production in the oak species *Quercus robur* and *Quercus petraea* combined. The value splitting the nodes is shown on each branch. Each lozenge shows the average of the standardised acorn count difference from the mean (A^{DF}, upper value) and the percentage of observations from the full dataset (lower value). Nodes are colour scaled from blue (high acorn production) to white (low acorn production). In sample R2: 0.64, MSE: 2372, RMSE: 49. Out of sample RMSE: 98.

Appendix 3.11. A summary of all the explanatory variables selected to build a random forest model predicting standardised acorn count differences from the mean (A^{DF}) in the two oak species *Quercus robur*, *Quercus petraea* and both species considered together. Variable selection and model building was performed via the VSURF function in R. The variable for the interpretation models built embedded random forests models, starting with using the variables with the highest variable importance scores, and ending with those selected within a prior thresholding step. The smallest model with the mean out of bag error (OOB) rate below the threshold is then selected. The prediction model, similarly builds embedded random forest models, but instead adds variables to the model in a stepwise manner, including a variable in the model if it lowers the OOB error more than a threshold. If an explanatory variable was selected for inclusion within a model it is highlighted in green, if not it is highlighted in red.

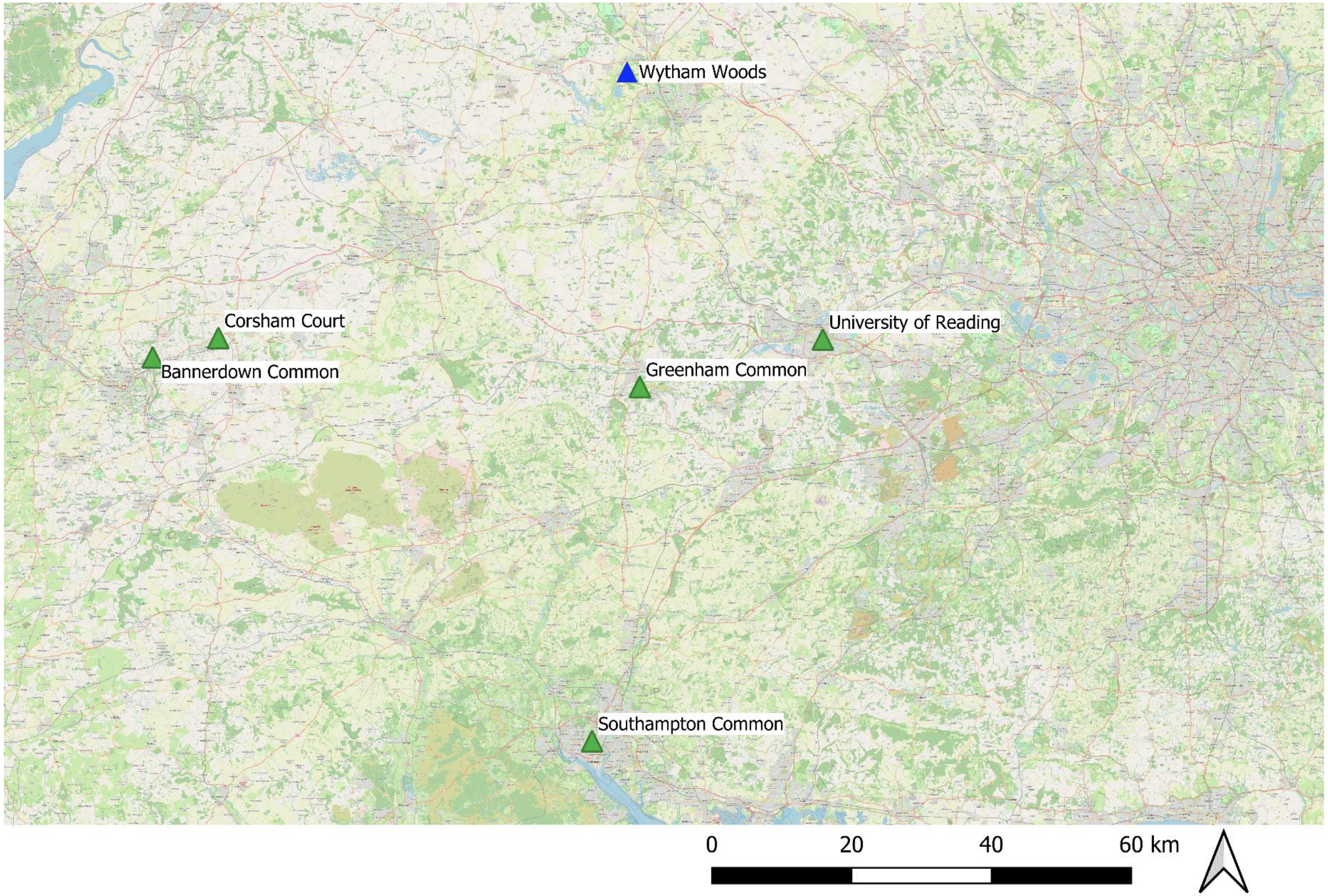
	Quercus petraea		*Quercus robur*		Mixed Species	
Variable	Inter.	Pred.	Inter.	Pred.	Inter.	Pred.
Acorn Lag	Yes	Yes	Yes	No	Yes	Yes
Apr Tmin t-2	Yes	No	Yes	No	Yes	Yes
Tmax Spring	Yes	No	Yes	Yes	Yes	No
Apr Avg NR	No	No	Yes	No	Yes	Yes
Avg NR Spring t-1	No	No	Yes	No	Yes	Yes
Jul Tavg	No	No	Yes	No	Yes	No
Jul Tmax	No	No	Yes	Yes	Yes	Yes
Mar 5	No	No	Yes	Yes	Yes	No
Mar Tavg t-2	No	No	Yes	No	Yes	Yes
Nov Tavg t-2	No	No	Yes	No	Yes	No
Nov Tmax t-2	No	No	Yes	Yes	Yes	No
NRM Spring t-1	No	No	Yes	Yes	Yes	Yes
Tavg summer	No	No	Yes	No	Yes	No
Apr Tavg	Yes	Yes	No	No	Yes	No
Apr Tmax	Yes	Yes	No	No	Yes	Yes
Jul Tavg t-1	Yes	No	No	No	Yes	No
Jul Tmax t-1	Yes	Yes	No	No	Yes	No
Mar tmin t-1	Yes	No	No	No	Yes	Yes
Oct Tmin t-2	Yes	Yes	No	No	Yes	No
Sept Tavg t-1	Yes	No	No	No	Yes	Yes
Tmin autumn t-1	Yes	Yes	No	No	Yes	Yes
AF April t-2	No	No	No	No	Yes	No
Avg NR Spring	No	No	No	No	Yes	Yes
Jan Rain t-1	No	No	No	No	Yes	No
Jul Tmin	No	No	No	No	Yes	Yes
May AvgNR t-1	No	No	No	No	Yes	Yes
Nov rain t-2	No	No	No	No	Yes	No
Nov tmin t-2	No	No	No	No	Yes	No
Oct tavg t-1	No	No	No	No	Yes	No
Oct Tmax t-1	No	No	No	No	Yes	No
Tmax Summer	No	No	No	No	Yes	Yes
Jul Tavg t-2	Yes	Yes	Yes	No	No	No
May AvgNR	Yes	No	Yes	No	No	No
AF Mar	No	No	Yes	No	No	No
Apr NRM	No	No	Yes	Yes	No	No

Apr Tavg t-1	No	No	Yes	No	No	No
Aug NRM t-1	No	No	Yes	No	No	No
Feb 10	No	No	Yes	No	No	No
Feb 5	No	No	Yes	No	No	No
Jan tmin t-2	No	No	Yes	No	No	No
Jul AvgNR	No	No	Yes	Yes	No	No
Mar 0	No	No	Yes	No	No	No
Mar 10	No	No	Yes	Yes	No	No
Mar rain t-2	No	No	Yes	No	No	No
Mar tavg	No	No	Yes	No	No	No
Mar tmax	No	No	Yes	Yes	No	No
Mar tmin	No	No	Yes	No	No	No
Mar tmin t-2	No	No	Yes	Yes	No	No
Rain Spring	No	No	Yes	Yes	No	No
Sep AvgNR t-2	No	No	Yes	No	No	No
AF Mar t-1	Yes	Yes	No	No	No	No
Apr AvgNR t-2	Yes	No	No	No	No	No
Apr NRM t-2	Yes	No	No	No	No	No
Aug Tavg	Yes	Yes	No	No	No	No
Aug Tavg t-1	Yes	No	No	No	No	No
Aug Rain	Yes	No	No	No	No	No
Aug Tmax t-1	Yes	No	No	No	No	No
Aug Tmin t-1	Yes	No	No	No	No	No
Jan tmin	Yes	Yes	No	No	No	No
Jun Tavg	Yes	No	No	No	No	No
Jun Tmin	Yes	No	No	No	No	No
Mar Tavg t-1	Yes	No	No	No	No	No
May tavg t-2	Yes	No	No	No	No	No
Oct Tavg t-2	Yes	No	No	No	No	No
Oct Tmax t-2	Yes	No	No	No	No	No
Sept Tmax t-1	Yes	No	No	No	No	No
Sept tmin t-1	Yes	No	No	No	No	No
Tavg autumn t-2	Yes	No	No	No	No	No
Tavg Spring	Yes	No	No	No	No	No
Tmax Spring t-1	Yes	Yes	No	No	No	No

Appendix 3.12. A summary of Shapley values of the VSURF model using weather variables to predict standardised acorn count differences from the mean (A^{DF}) for the oak species *Quercus robur* and *Quercus petraea* considered together. Feature values were randomly generated 100 times and then plotted. The Shapley value is given along the x axis and the feature name is given along the Y axis. The colour scale gives the value of the feature randomly selected in relation to the range of possible feature values. Red represents a high feature value and green represents a low feature value. So for instance we can see a high feature value for last year’s acorn count (lag1) results in a strong negative effect on the Shapley value (a strong negative affect on this year’s acorn count).

Appendix 3.13 A summary of Shapley values of the VSURF model using weather variables to predict standardised acorn count differences from the mean (A^{DF}) for the oak species *Quercus petraea*. Feature values were randomly generated 100 times and then plotted. The Shapley value is given along the x axis and the feature name is given along the Y axis. The colour scale gives the value of the feature randomly selected in relation to the range of possible feature values. Red represents a high feature value and green represents a low feature value.

Appendix 3.14 A summary of Shapley values of the VSURF model using weather variables to predict standardised acorn count differences from the mean (A^{DF}) for the oak species *Quercus robur*. Feature values were randomly generated 100 times and then plotted. The Shapley value is given along the x axis and the feature name is given along the Y axis. The colour scale gives the value of the feature randomly selected in relation to the range of possible feature values. Red represents a high feature value and green represents a low feature value.



Appendix 4.2. Locations of pollen collection sites used for the pollen supplementation experiment at Wytham Woods, Oxford (blue triangle). The out of stand pollen collection sites are shown by green triangles. © OpenStreetMap contributors, CC-BY-SA. *URL:* https://www.openstreetmap.org/copyright

Appendix 5.1 Results of ANOVA tests of a series of negative binomial regressions with the category of oak reproductive material as the response variable and only two (elevated and ambient CO_2) treatments over the years (2017–2021); i.e., the results of the undisturbed treatment were omitted. Significant effects are shown in bold. Each array was of 15m radius, with elevated CO_2 arrays maintained at +150 $\mu L \cdot L^{-1}$ above ambient CO_2 during the day from early April to late October. The ambient arrays were maintained at current CO_2 levels via the same infrastructure. For more details on the site and the long-term experiment see Hart et al (2019) and Mackenzie et al (2021).

Category	Treatment			Year			Treatment ×Year		
	$\chi 2$	df	*P*	$\chi 2$	df	*P*	$\chi 2$	df	*P*
Mature Acorns	0.29	1	0.59	48.36	4	**< 0.0001**	5.11	4	0.27
Immature Acorns	3.7	1	0.054	131.52	4	**< 0.0001**	6.71	4	0.15
Empty Cups	3.53	1	0.06	151.84	4	**< 0.0001**	4.15	4	0.39
All evidence of acorns	5.68	1	**< 0.05**	206.09	4	**< 0.0001**	6.36	4	0.17
Enlarged cupules	1.11	1	0.3	44.7	4	**< 0.0001**	0.91	4	0.92
Flowers	1.39	1	0.24	107.17	4	**< 0.001**	18.56	4	**< 0.001**
Galls	5.47	1	**< 0.05**	26.18	4	**< 0.0001**	0.75	4	0.95

Appendix 5.2 Results of ANOVA tests of a series of negative binomial regressions with the category of reproductive material as the response variable and the treatments elevated CO_2, ambient CO_2, or ‘undisturbed’ for the two years 2015 and 2016 (i.e., before the experimental treatments began). Significant effects are shown in bold. Each array was of 15m radius. For more details on the site and the long-term experiment see Hart et al (2019) and Mackenzie et al (2021).

Category	Treatment			Year			Treatment ×Year		
	χ2	df	*P*	*χ2*	df	*P*	*χ2*	df	*P*
Mature Acorns	0.21	2	0.89	8.29	1	**< 0.005**	3.76	2	0.15
Immature Acorns	7.79	2	**< 0.05**	1.11	1	0.29	1.18	2	0.55
Empty Cups	20.75	2	**< 0.0001**	0.17	1	0.28	8.9	2	**< 0.05**
All evidence of acorns	5.09	2	0.07	7.1	1	**< 0.01**	0.90	2	0.64
Enlarged cupules	3.37	2	0.19	0.4	1	0.52	1.34	2	0.51
Flowers	4.19	2	0.12	4.68	1	**< 0.05**	1.07	2	0.59
Galls	2.84	2	0.24	1.47	1	0.22	2.07	2	0.35

Appendix 6.1 Seeding vs Planting: A collaborative continental experiment.

I was involved with a Europe wide common garden experiment as part of the Pan-European Network for Climate Adaptive Forest Restoration and Reforestation (PEN-CAFoRR EU COST Action). The experiment is to explore the benefits/costs of direct seeding vs planting as a tool for forest regeneration. The full study protocol has been published since the start of the experiment (see Leverkus et al. 2021), but in short involves setting up a common garden experiment, with half of the individuals directly seeded and half grown in the greenhouse first then transplanted, height and stem diameter measurements were completed over several seasons. A complete evaluation will be made via a mixed effect meta-analysis upon all 80+ participants data that involves 40 institutions in 17 different countries. But the data collected at the Reading University experimental ground is briefly presented below (Fig A6.1.1). There was a significant difference in final height with seeded plots taller on average for both species (*Q. robur*: t= -2.9826, df = 56.211, p<0.01; *Q. petraea*: t= -4.377, df = 43.383, p<0.0001) but there was no difference in stem diameter (*Q. robur*: t = 0.07, df = 61.656, p=0.94; *Q. petraea*: t= -1.8033, df = 59.974, p=0.08).

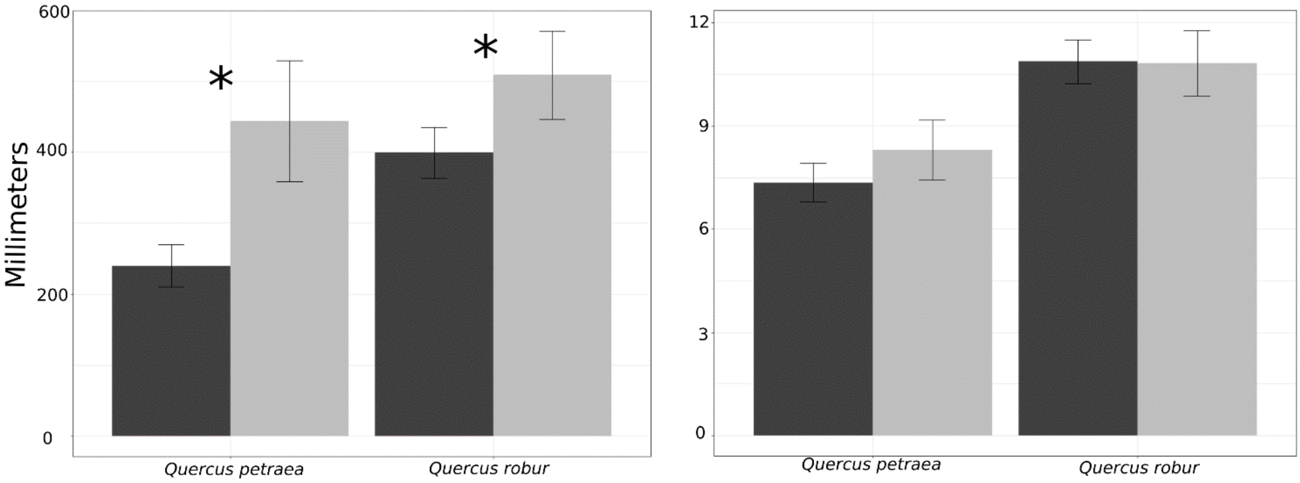


Figure 6.1.1 The variation in height (left panel) and diameter (right panel) of oak seedlings under different restoration techniques, the dark grey bars are seedlings transplanted from the greenhouse (planting group) and the light grey bars are direct seeded (seeding group). Error bars give the 95% confidence limits of each group. Asterisk show significant differences from Welch's T-tests.

Leverkus AB, Levy L, Amdivia E, Annighöfer P, De Cupyer B, Ivetic V, Lazdina D, Löf M, Villa-Salvador P (2021) Restoring oak forests through direct seeding or planting: Protocol for a continental-scale experiment. Plos One 16:e0259552.