

1 **Leaf phenology correlates with fruit production in European beech (*Fagus sylvatica*) and in**
2 **temperate oaks (*Quercus robur* and *Quercus petraea*)**

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22 #0 Supporting Information

23 **Abstract**

24 Phenology and fruit production are sensitive to climate. Variation of leaf phenology alters canopy
25 duration (an indicator of growing season length), which in turn affects forest ecosystem functioning
26 and tree productivity. However, the influence of canopy duration on tree reproduction is poorly
27 explored. In this study, we investigated if, and to what extent the canopy duration influence fruit
28 production in three major European deciduous trees, European beech (*Fagus sylvatica*) and two
29 temperate oaks (*Quercus robur* and *Quercus petraea*). We used a long-term (11 years) monitoring
30 dataset from 50 populations. In addition to the widely reported main effect of previous summer
31 temperature on fruit production in European beech, we detected a non-linear relationship between
32 current canopy duration and fruit production. For beech, intermediate canopy duration is associated
33 with highest fruit production. In oaks, fruit production was positively correlated with spring temperature
34 and current canopy duration. Total variance explained by our models is 45% and 13%, for beech and
35 oaks respectively. These results suggest contrasting effects of expected increase in canopy duration
36 on fruit production: non-linear in European beech, and positive linear in oaks.

37

38 **Keywords:** Deciduous trees, *Fagus sylvatica*, canopy duration, masting, *Quercus sp.*

39 Introduction

40 Masting or mast seeding is a plant reproductive strategy characterized by spatially
41 synchronous and highly variable seed productions (Kelly 1994). Understanding the mechanisms
42 underlying masting pattern is a major challenge as it directly impacts forest regeneration, seed
43 consumers and thus the whole forest community (Kelly and Sork 2002; Bogdziewicz et al. 2016;
44 Vacchiano et al. 2018). Flower phenology is known to be a major driver of masting. For example, the
45 variability of flower phenology and the synchrony during the period of pollination have a direct
46 influence on the intensity of fructification (Koenig et al. 2015, Bogdziewicz et al. 2020b). Growing
47 season length, referred to here as canopy duration, i.e. the period between leaf unfolding and leaf
48 senescence, might also be important for reproduction. A longer canopy duration generally results in
49 greater annual carbon assimilation (Nemani et al. 2003; Delpierre et al. 2009; Richardson et al. 2010;
50 Keenan et al. 2014; Forkel et al. 2016) and fructification in trees depends on the availability of
51 resources (Han and Kabeya 2017). In masting species, the resource investment to fruit production is
52 highly variable from year to year (Crone and Rapp 2014) and can be substantial in mast years. For
53 example, Müller-Haubold et al. (2015) showed that during a masting year, around 50% of the
54 aboveground net primary productivity in beech was allocated to reproduction whereas the allocation to
55 wood and leaves formation was reduced. According to the resource budget model of masting, plants
56 need to accumulate a threshold amount of resources to initiate reproduction (Isagi et al. 1997; Satake
57 and Iwasa 2000). If this threshold cannot be reached in the first year, then plants accumulate
58 resources over several years, which translates into intermittent fruit production by individual plants
59 (Satake and Iwasa 2000; Crone et al. 2009). Furthermore, variation in resource supply over the
60 current and past years appear to be implicated in bud initiation, flower and fruit maturation (Allen et al.
61 2017; Han and Kabeya 2017). The carbon stored during the previous year is used to fuel the
62 beginning of fruit development, and then the final stage of fruit maturation is supplied with carbon
63 assimilated during the current year (Hoch et al. 2013; Han and Kabeya 2017). Finally, due to the high
64 reproductive cost, there is a trade-off between previous and current fruit production, where a large
65 fruit production limits production in the next year (Knops et al. 2007; Pearse et al. 2016; Fernández-
66 Martínez et al. 2019). This trade-off appears to be caused by a large depletion in resources such as
67 non-structural carbohydrates in herbaceous plants (Crone et al. 2009) or by nitrogen and phosphorus
68 for woody species (Sala et al. 2012; Barringer et al. 2013; Crone and Rapp 2014; Pearse et al. 2016;
69 Allen et al. 2017; Moreira et al. 2019). Non-structural carbohydrates depletion was also found for

70 woody trees (Miyazaki et al. 2002; Ichie et al. 2005), but other studies did not find such evidence (e.g.
71 Hoch et al. 2013; Igarashi et al. 2019). As masting seems to be dependent on the accumulated
72 resources and on variability in leaf and flower phenology during the year, change in canopy duration
73 may have a direct impact on this phenomenon. Yet, apart from a few studies (Tapper 1996,
74 Nakamura et al. 2010), little attention has been directed to the likely effect of canopy duration on
75 masting.

76 The aim of this study was to investigate how canopy duration can influence reproduction,
77 in terms of fruit biomass, for three major temperate deciduous trees in Europe; European beech
78 (*Fagus sylvatica*) and temperate oaks (*Quercus petraea* and *Quercus robur*). While all these species
79 exhibit the variable and synchronized fruit production known as masting, they show contrasting
80 masting mechanisms. Consequently, these species differ in how weather affects their fruit production.
81 *Quercus petraea* and *Quercus robur* are “fruit maturation masting” species, and warm spring
82 temperatures favor flowering and pollination (Fernández-Martínez et al. 2017a; Lebourgeois et al.
83 2018; Bogdziewicz et al. 2019; Schermer et al. 2019), which in turn increase fruit production
84 (Caignard et al. 2017). After pollination, the inter-annual variation in fruit production is driven by the
85 rate of fruit abortion (Pearse et al. 2015). For *Fagus sylvatica*, previous summers’ temperatures are
86 the main driver of fruit production (Vacchiano et al. 2017; Hackett-Pain et al. 2018; Lebourgeois et al.
87 2018; Bogdziewicz et al. 2019). This period corresponds to the season of floral initiation (see Table
88 1). Unlike oak, beech is considered as a “flowering masting” species, where seed production
89 variability is largely determined by the variation in flower production and not fruit abortion (Pearse et
90 al. 2016; Bogdziewicz et al. 2017c, b). Consequently, to test the effect of canopy duration on masting,
91 we accounted for the well-established determinants of fruit production: previous summer weather for
92 European beech, current spring temperature for temperate oaks, and the negative temporal auto-
93 correlation between current and previous year for both species.

94 We hypothesised that canopy duration of the current year might affect fruit production, as
95 carbohydrates are used for fruit maturation (Hoch et al. 2013; Hoch 2015; Han and Kabeya 2017). An
96 increase of canopy duration could increase fruit biomass production, such as seed and fruit mass.
97 Therefore, we expected that canopy duration to be positively correlated to fruit biomass production.
98 The lack of relationship may indicate that fruit production is not limited by canopy duration, as has
99 previously been inferred for tree growth (Vitasse et al. 2009a; Čufar et al. 2015; Delpierre et al. 2017).
100 We also tested whether canopy duration of the previous year influence fruit production by, for

101 example, affecting the production of floral buds. Moreover, we hypothesised that long canopy duration
102 might be associated with increases in environmental stresses that might indirectly impact fruit
103 productivity. We also tested for relationships between canopy duration and the frequency of climatic
104 events, including extreme high and low temperatures and dry events (Xie et al. 2015, 2018) that could
105 impact negatively and indirectly fruit production.

106

107 **Material and Methods**

108 **Study sites and data collection**

109 We used data collected at 50 sites of the French Permanent Plot Network for the
110 Monitoring of Forest Ecosystems (RENECOFOR, Ulrich 1995). Sites are widely distributed across
111 France between latitude 50.1° and 42.9°N and longitude -3.53° and 7.71°E, covering various climatic
112 and soil conditions (Fig. 1). In total, 20 sites dominated by European beech species and 30 sites
113 dominated by two European oak species (*Quercus robur* and *Q. petraea*) were monitored. These
114 populations were mature when they started to be monitored with a mean age of 96 years (standard
115 error = 7.8) for beech and 85 year (standard error = 5.2) for oaks species in 1994. Due to the high
116 hybridization rate between the two oak species (Abadie et al. 2012), we combined and merged all
117 oaks records. The monitored plots had a size of approximately 2 ha, with a central fenced zone of 0.5
118 ha. For every site, fruit production was monitored from 1993 to 2007 and leaf phenology from 1997 to
119 2015. Because we were interested in investigating the relationship between leaf phenology and fruit
120 production, we used data from 1997 to 2007, corresponding to the overlapping period between the
121 two datasets. The litterfall was collected at the population scale with ten traps of 0.5 m², distributed
122 over the central fenced zone. Every season, the litter fallen into the traps was collected and sorted in
123 different category: leaves, branches and fruits (acorns and nuts). All compartments were dried and
124 weighed, and then divided by the total area of the trap. Fruit production was estimated in kg.ha⁻¹. Leaf
125 unfolding and leaf coloring were monitored at the population scale based on a sample of 36 trees per
126 site. Phenological stages were monitored every week during spring for leaf unfolding (from March to
127 June) and autumn for leaf coloring (from September to November) (Lebourgeois et al. 2010). Leaf
128 unfolding and leaf coloring dates (both in Julian days) were defined when 90% of sampled trees had
129 20-50% of opening buds and when 90% of sampled trees had 20-50% yellowing leaves, respectively.
130 We defined the canopy duration as the number of days between leaf unfolding and leaf coloring. We
131 extracted the closest climatic data for each of the 50 sites by using French climate station data

132 obtained from SAFRAN atmospheric re-analysis (8-km gridded spatial resolution, Vidal et al. 2010).
133 We extracted daily temperature data and summarized it for summer and spring period from the
134 closest station to each of the RENECOFOR sites: in total we extracted climate variable from 50
135 stations. We also extracted daily temperature for autumn, spring and summer and precipitation during
136 summer to define different climatic events that occurred during the canopy duration.

137

138 **Statistical analysis**

139 We first investigated how species differ in their canopy duration and fruit production. We
140 used a *t*-test to identify differences in the mean between species and an *F*-test of equality of variance
141 to test if the two species had equal variance. Next, we tested the relationships between canopy
142 duration and fruit production from 1997 to 2007 using linear mixed models (LMMs) implemented via
143 the *glmmTMB* package (Brooks et al. 2017). We built two separate models, one for beech and one for
144 oaks. In beech, we used mean maximum summer temperature (June to July) from one- and two-
145 years preceding fruit production as covariates (Vacchiano et al. 2017, Lebourgeois et al. 2018). We
146 have also explored models that included the difference between summer temperatures one- and two-
147 years preceding fruit maturation (ΔT model, cf Kelly et al. 2013). These models produced similar fit
148 and qualitatively the same results (unpublished analysis), and are thus not included here. In oaks, we
149 used mean spring temperature (April to May) from the year of fruit production (Lebourgeois et al.
150 2018; Bogdziewicz et al. 2019) as a covariate. We used log-transformed fruit production data as a
151 response variable. To allow log-transformation of zeros in fruit production we added 1 to all
152 observations. Linear and quadratic terms for both current and the previous year canopy duration, and
153 the previous year fruit production were scaled after being centered and included as fixed effects.
154 Climate covariates for beech and oaks were also scaled after centering in order to evaluate their
155 respective weights. Quadratic terms were added by computing orthogonal polynomials with the
156 function *poly()*. If the quadratic effect was not significant it was dropped from the initial model.
157 Moreover, quadratic terms were only retained in the final models if they improved the AIC model fit by
158 $\Delta AIC > 2$ (Burnham and Anderson 2002, Arnold 2010). We then calculated the marginal R^2 (i.e.
159 variance explained by fixed effects) and conditional R^2 (i.e. variance explained by both fixed and
160 random effects) (Nakagawa and Schielzeth 2013). Year and site were included as random effects in
161 these two models (i.e. one model per species). We checked for collinearity between variables using

162 variance inflation factor (VIF). All VIF values were less than two, which indicates no collinearity among
163 predictors (Zuur et al. 2009).

164 We also tested whether the frequency of extreme climate events was related to canopy
165 duration, focusing on climate events that affect tree phenology (Xie et al., 2015, 2018). We used
166 generalized linear mixed models (GLMMs) and a Poisson family. With the matching data (1997-2007)
167 and for each canopy duration, we counted the number of frost days during the spring season
168 (minimum daily temperature from April to June $< 0^{\circ}\text{C}$) and autumn season (minimum daily
169 temperature from September to October $< 0^{\circ}\text{C}$). We also calculated the number of hot days during the
170 summer season (maximum daily temperature from June to August $\geq 30^{\circ}\text{C}$) and during autumn season
171 (maximum daily temperature from September to October $\geq 30^{\circ}\text{C}$), and dry spells which corresponds
172 to the number of events without rain during 7 consecutive days. We built models with the frequency of
173 the five climate events occurring during canopy duration as the response variable and the canopy
174 duration as the explanatory variable. In total we had five models for oaks, and five models for beech.
175 We scaled and centered canopy duration (i.e. the explanatory variable) and included it as fixed effect.
176 Year and site were included as random effects in all the models. All statistics were done using the R
177 software (R Core Team 2018). We used *visreg* package to plot model predictions with partial
178 residuals (Breheny and Burchett 2017). Partial residual plots illustrate the relationship between the
179 response variable (e.g. fruit production) against an independent variable, accounting for the effects of
180 the other independent variables included in the model. Model diagnostics were run with the DHARMA
181 package (Hartig 2019). Conditional and marginal R^2 were obtained with the package *sjstats* (Lüdtke
182 2019).

183

184 **Results**

185 Fruit production (mean \pm standard deviation) was different between species with a value of
186 161.2 ± 303.7 kg/ha for beech (*t*-test, $t = -3.22$, $df = 655$, $P = 0.001$) and 246.5 ± 389.9 kg/ha for oaks,
187 with higher variations for oaks (*F*-test of equality of variances; $F_{263, 433} = 0.60$, $P < 0.001$) (Fig. 2). The
188 canopy duration estimated for beech (mean = 173.9 ± 19.8 days) was significantly shorter than the
189 canopy duration estimated for oaks (mean = 187.0 ± 18.5 days) (*t*-test, $t = -9.19$, $df = 764$, $P < 0.001$)
190 whereas the variations were similar (*F*-test of equality of variances; $F_{290, 474} = 1.15$, $P = 0.17$) (Fig. 2).

191 In beech, inter-annual variation in fruit production was positively related to temperature in
192 the previous summer ($t = 4.62$, $P < 0.0001$), negatively to the summer temperature two years before (t

193 = -5.93, $P < 0.0001$), and negatively to previous year fruit production ($t = -2.88$, $P = 0.004$, Table 2,
194 Fig. 3c). We also found that significant additional variance in fruit biomass could be explained by a
195 concave relationship between fruit production and current canopy duration (degree 1: $t = 0.38$, $P =$
196 0.7 , degree 2: $t = -2.59$, $P = 0.009$, Table 2, Fig. 3a). The quadratic terms of previous canopy duration
197 were dropped from the final model ($P = 0.22$). We did not detect a relationship between previous
198 canopy duration and fruit production ($P = 0.73$, Fig. 3b).

199 In oaks, we detected a positive correlation between spring temperature of the year and
200 fruit production ($t = 2.26$, $P = 0.02$). Previous year fruit production was negatively correlated with
201 current year fruit production ($t = -2.52$, $P = 0.011$, Table 2, Fig. 4c). Moreover, both current and
202 previous canopy duration were correlated with fruit production and explained additional variance. We
203 found a positive relationship between current canopy duration and fruit production ($t = 2.32$, $P = 0.02$,
204 Table 2, Fig. 4a), and negative relationship between fruit production and previous canopy duration (t
205 $= -2.96$, $P = 0.003$, Fig. 4b). The quadratic terms of previous ($P = 0.55$) and current canopy duration (P
206 $= 0.44$) were not significant and were dropped from the final model.

207 Finally, we observed significant correlations between relevant climate events and canopy
208 duration in all species. For beech and oaks, we found a positive relationship between the number of
209 frost days during autumn and canopy duration (beech, $t = 4.74$, $P < 0.0001$; oaks, $t = 5.04$, $P <$
210 0.0001 , Table 3) and between number of hot days during autumn and canopy duration (beech, $t =$
211 1.99 , $P = 0.046$; oaks, $t = 2.00$, $P = 0.045$, Table 3). Furthermore, for oaks we found a positive
212 relationship between frost days during spring and canopy duration ($t = 4.93$, $P < 0.0001$) and between
213 dry spells and canopy duration ($t = 2.23$, $P = 0.026$). We did not detect relationships between the
214 number of summer hot days and canopy duration for any species (Table 3).

215

216 **Discussion**

217 There is widespread evidence of enhanced carbon assimilation as a response to extended
218 canopy duration (Nemani et al. 2003; Delpierre et al. 2009; Richardson et al. 2010; Keenan et al.
219 2014; Forkel et al. 2016). However, the effects of extended canopy duration on carbon allocation,
220 including to growth and reproduction, are more controversial. For example, longer canopy duration
221 can correlate positively with tree growth (Vitasse et al. 2009a, Delpierre et al. 2017), but other studies
222 have reported no effect (Čufar et al. 2008; 2015). Few studies have investigated the effect of
223 increased canopy duration on allocation to reproduction and indicated that longer canopy duration

224 may be positively correlated with fruit production (Tapper 1996; Nakamura et al. 2010). In our study,
225 we show that once the well-documented weather cues of fruit production were accounted for (i.e.
226 previous summer temperature in beech and spring temperature in oaks), canopy duration was
227 correlated with fruit biomass production. In beech, fruit production was highest for intermediate levels
228 of canopy duration length. In turn, in oaks fruit production increased linearly with canopy duration. We
229 discuss possible mechanisms below.

230

231 **European beech**

232 We suggest that the initial increase in fruit production with canopy duration may be related
233 to increased resource assimilation, which in turn could increase total reproductive biomass. A longer
234 canopy duration may influence total fruit biomass by either increasing the number of fruits, increasing
235 the mean mass of each fruit, or both. The maximum number of fruits is determined by the number of
236 flowers, which are initiated during the previous canopy duration in response to summer temperature
237 cues (Vacchiano et al. 2017). However, Mund et al. (2020) showed that once mass flowering was
238 initiated in beech, the final fruit biomass was decreased by high precipitation conditions during
239 flowering even though Nussbaumer et al. (2020) found no effect of spring weather on beech fruit
240 production. Thus, weather conditions during fruit maturation are also important for determining final
241 fruit production, and high summer temperatures and drought conditions result in fruit abortion in
242 beech (Nussbaumer et al. 2018, 2020, Vergotti et al. 2019). Similar process may explain our results.
243 We suggest that greater plant resources associated with an extended canopy duration increase the
244 fraction of flowers that mature into fruits, increasing the total fruit biomass production. Additionally, the
245 mean mass of one fruit may also be higher in association with longer canopy duration, considering
246 that greater resource availability results in larger seed size (Espelta et al. 2009). Finally, we note that
247 unfertilized beech flowers still develop into non-viable fruits (Bogdziewicz et al. 2020). As these non-
248 viable fruits have a pericarp but no developed embryo, they have significantly lower average seed
249 mass (Hacket-Pain, unpublished data). Consequently, weather conditions during pollination in the
250 early part of the canopy duration may influence the proportion of fully-developed seeds, and thus the
251 mean seed mass.

252 We found that canopy duration was positively correlated with hot days during the autumn,
253 and was also positively correlated to autumn frost events. However, because fruit maturation is largely
254 completed by that time, this is unlikely to affect fruit production. Furthermore, longer canopy duration

255 was not associated with elevated late spring frost risk, which are known to damage beech flowers and
256 result in masting failure (Matthews 1955). These results lead us to reject our hypothesis that the
257 decrease of beech fruit production at very long canopy duration could be associated with the
258 compensatory effects of climate events (drought, heat, frosts) that occur more frequently in long
259 canopy duration.

260 The lack of correlation between the previous canopy duration and the following year fruit
261 production suggests that flower initiation is not affected by the previous year leaf phenology. This is
262 consistent with previous experimental studies that found stored carbon is used for flower and leaf
263 expansion, and was not a limiting factor for flower initiation (Hoch et al. 2013; Han and Kabeya 2017).

264

265 **Temperate Oaks**

266 Canopy duration correlated positively with fruit production in oaks. Similar to beech, this
267 result suggests that carbon availability during fruit maturation may limit reproduction in oaks. This
268 result is in accordance with previous studies, showing for example that masting episodes were
269 preceded by longer canopy duration in *Quercus ilex* (Camarero et al. 2010). A warming experiment at
270 the branch level, showed that increased canopy duration was also associated with higher acorn
271 production in *Quercus crispula* (Nakamura et al. 2010). The negative effect of the previous canopy
272 duration on current fruit production observed in Figure 4b, likely correspond to the effect of previous
273 canopy duration on previous fruit production as associated resource depletion. Indeed, previous year
274 fruit production and previous year canopy duration correlate positively in our data (log transformation
275 of previous fruit production with linear scale previous canopy duration; $t = 2.05$, $P = 0.04$).

276 In addition to canopy duration, other factors such as pollen limitation and water availability
277 may also help to explain fruit production patterns in oak species. For example, pollen limitation limits
278 oak fruit production (Koenig et al. 2012, Venner et al. 2016; Bogdziewicz et al. 2017c, b; Schermer et
279 al. 2019). Moreover, other direct climatic effects, such as drought, are also linked to episodic fruit
280 production (Pérez-Ramos et al. 2010; Lebourgeois et al. 2018). Schermer et al. (2019) demonstrated
281 that pollen dynamics was the key driver of fruit production in *Quercus petraea* and *Q. robur*, and
282 Lebourgeois et al. (2018) showed that spring temperature was important for oak fruit production for
283 the same dataset, due to its positive effects on pollination (Caignard et al. 2017; Schermer et al.
284 2020). Spring temperature during year of fruit maturation is an important determinant of fruit
285 production, but also a major determinant of leaf season (Vitasse et al. 2009c).

286 For oaks, we also found that the frequency of early frost in autumn and high autumnal
287 temperatures were associated with increased canopy duration. We also found that earlier-
288 commencing canopy duration was associated with increased occurrence of late frosts during spring,
289 which can cause major foliar damages (Vitasse et al. 2014), reduce photosynthetic activity (Zohner et
290 al. 2019), and kill flowers and developing fruits (Inouye 2000). In our study, we considered canopy
291 duration as a proxy of photosynthetic activity that influences carbohydrate accumulation. However, in
292 oaks, the development of leaves from leaf unfolding to maturation can take up to 70 days (Morecroft
293 et al. 2003). Canopy duration may not be a reliable proxy of the length of the carbon assimilation
294 period, but it could also integrate underlying mechanism such as reproductive phenology. Future
295 investigations should thus also include flux data to better estimate of carbon uptake and release.

296

297 **Reproductive cost and differences in species strategies**

298 The negative correlation in fruit production observed between current and previous year is
299 generally interpreted as a trade-off between current and future reproduction (Knops et al. 2007; Crone
300 et al. 2009; Sala et al. 2012; Santos-del-Blanco and Climent 2014; Moreira et al. 2019). A review by
301 Pearse et al. (2016) showed that carbon-based resources have a short period of residence, and are
302 unlikely to be directly linked to this trade-off, but can act as a mobile signal interacting with hormones.
303 Therefore, carbon-based resources can affect fruit production without being stored. Furthermore, oak
304 and beech differ in their reproductive strategies where growth and reproduction are negatively
305 correlated for beech but are positively correlated for oaks (Lebourgeois et al. 2018). These two
306 species, also differ in their masting habit, where oaks have a higher level of flowers abortion than
307 beech (Espelta et al. 2008; Pearse et al. 2016; Bogdziewicz et al. 2017c, b). Finally, these species
308 differ in their leaf and wood formation phenology, and their wood anatomy (Barbaroux and Breda
309 2002; Michelot et al. 2012; Vitasse and Basler 2013; Lebourgeois et al. 2018) which in turn influence
310 their resource allocation scheme. Oaks are ring porous species, thus they use stored carbohydrates
311 for earlywood vessel formation before leaf unfolding and leaf expansion. In contrast, beech is a
312 diffuse porous species. Thus, growth commences after leaf unfolding and is mainly reliant on carbon
313 assimilated in the current season (Barbaroux and Breda 2002; Michelot et al. 2012). We hypothesised
314 that our species are mainly dependent of carbohydrates assimilated during the canopy duration for
315 fruit production, but other factors limit both bud initiation and fruit maturation. For oaks, from all the
316 flowers initiated each year, only a fraction of them mature into fruits, depending on pollination success

317 (Pearse et al. 2016; Bogdziewicz et al. 2017c, b; Schermer et al. 2019), weather conditions like
318 drought or late frost limiting fruit maturation (Espelta et al. 2008; Pérez-Ramos et al. 2010), and the
319 availability of macro-nutrients other than carbohydrates (Pearse et al. 2016, Fernández-Martínez et al.
320 2019). Indeed, our statistical model that included spring temperature and canopy duration explained
321 little variance in oak. For beech, major determinants of fruit production are previous summer
322 conditions with a relatively small effect of canopy duration. Canopy duration is not the main driver of
323 fruit production, but it could be a new driver involved in masting patterns.

324

325 **Perspective and conclusion**

326 In addition to previously known cues of fruit production for beech and oaks, we show that
327 canopy duration participates in determining annual fruit production. While more research is required to
328 fully understand the mechanism(s) responsible for the observed relationships of fruit production with
329 canopy duration, we speculate that this may be related to variation in resource assimilation and
330 effects of adverse climate events (e.g. late drought, early freezing in autumn, late frosts in springs)
331 occurring at the edges of longer growing seasons. We suggest that the difference we found in the
332 relationship between canopy duration and fruit production in oaks and beech is due to different
333 strategies of carbohydrates allocation (e.g. ring porous vs diffuse porous species) and different
334 phenology (Barbaroux and Breda 2002; Michelot et al. 2012). The positive effect of current canopy
335 duration on fruit production is in accordance with a reported relationship between high levels of gross
336 primary productivity and increased fruit production (Fernández-Martínez et al. 2017b), although with
337 these data Lebourgeois et al (2018) reported no relationship between annual GPP and fruit
338 production. Recently, in a beech forest in Germany, Mund et al (2020) also confirmed the absence of
339 this relationship. An increase of canopy duration can increase exposure to climatic events, and also
340 positively impact fruit biomass production of oaks but, eventually, negatively for beech. Variation of
341 canopy duration impacts nutrient remobilization, which can make elements less available for
342 reproduction and impact fruit production. While we worked at the population scale, future research
343 should focus on individual plants, as they present considerable variation in fecundity (Davi et al. 2016;
344 Hacket-Pain et al. 2019), leaf phenology that can impact individual tree growth (Delpierre et al. 2017),
345 and age and size that impacts both mean fecundity and interannual variation of seed production
346 (Pesendorfer et al. 2020; Bogdziewicz et al. 2020b). Inter-annual and inter-individual variation of leaf

347 phenology could improve our understanding of resource allocation and variability in plant reproductive
348 patterns.

349

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358

359 **Data availability**

360 Data used are available upon request from M. Nicolas (manuel.nicolas@onf.fr) and S.
361 Macé (sebastien.mace@onf.fr).

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370 **List of Tables and Figures**

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372 **Table 1:** Summary of studies exploring factors determining fruit production in European tree species

373 based on the RENECOFOR network (which is also part of the ICP forest network, International Co-

374 operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests <[http://icp-](http://icp-forests.net/)

375 [forests.net/](http://icp-forests.net/)>).

376

Study	Species	Factors explaining variation in fruit production
Bogdziewicz et al. 2019	<i>F. sylvatica</i> , <i>Q. petraea</i>	<ul style="list-style-type: none"> - In <i>F. sylvatica</i>, positive correlation with summer temperature in the year before fruit maturation - In <i>Q. petraea</i>, positive correlation with spring temperature in the year of flower pollination
Caignard et al. 2017	<i>Q. robur</i> , <i>Q. petraea</i>	<ul style="list-style-type: none"> - Positive relation with spring temperature in the year of flower pollination (April/May). - Negative effect of aging in <i>Q. petraea</i>
Fernández-Martínez et al. 2017a	<p><i>P. nigra</i>, <i>P. sylvestris</i>, <i>P. abies</i>, <i>P. pinaster</i>, <i>A. alba</i>, <i>P. menziesii</i>, <i>F. sylvatica</i>, <i>Q. robur</i>, <i>Q. petraea</i></p>	<ul style="list-style-type: none"> - Foliar zinc and phosphorus concentration positively correlated with fruit production - High level of gross primary productivity increase fruit production
Fernández-Martínez et al. 2017b	<p><i>A. alba</i>, <i>F. sylvatica</i>, <i>P. abies</i>, <i>P. menziesii</i>, <i>Q. petraea</i>, <i>Q. robur</i></p>	<ul style="list-style-type: none"> - In <i>F. sylvatica</i> and <i>P. abies</i>, positively correlated with dry and cold autumns, with dry and warm spring and with dry summers - In <i>Q. robur</i> and <i>Q. petraea</i>, positive

		<p>relationship with warm and wet autumns (and also with wet summers and cold winters for <i>Q. robur</i>)</p> <ul style="list-style-type: none"> - In <i>P. menziesii</i>, positive correlation with cold and dry autumns, warm and wet winters and warm springs - In <i>A. alba</i>, positive correlation with dry and warm spring and negative correlation with warm and wet winters
Lebourgeois et al. 2018	<i>F. sylvatica</i> , <i>Q. robur</i> , <i>Q. petraea</i>	<p>- In <i>F. sylvatica</i>, positive correlation with summer temperature signal (Differential of June/July temperature of year₋₁ – year₋₂). Trade-off between growth and reproduction</p> <p>- In <i>Quercus</i>, positive correlation with the period of pollen emission and spring temperature (April). Positive relation between growth and reproduction</p>
Schermer et al. 2019	<i>Q. robur</i> , <i>Q. petraea</i>	- Positive correlation with amount of airborne pollen and its sensibility to spring weather
Schermer et al. 2020	<i>Q. robur</i> , <i>Q. petraea</i>	- Positive effect of spring temperature and negative effect of rainfall. Pollen release sensitive to late frost.

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380 **Table 2:** Results of linear mixed models (LMMs) for beech and oaks (including *Q. robur* and *Q.*
381 *petraea*). TmaxSummer_{n-1} for previous year maximal temperature (average June-July), and
382 TmaxSummer_{n-2} for two previous year maximal temperature (average June-July) were tested only for
383 beech. TmeanSpring_n for the mean temperature of the current year of fruit production (average April-
384 May) only for oaks. The marginal R² of the model for beech was 0.45 and the conditional value was
385 0.65. For oaks, the marginal R² was 0.13 and the conditional value was 0.28.
386

Species	Variables	Estimate	Standard error	t-value	P value
Beech	Intercept	3.22	0.32	9.97	<0.0001
	Canopy duration (current year)	0.96	2.55	0.38	0.7
	Canopy duration (current year) ²	-4.26	1.65	-2.59	0.009
	Previous year fruit production	-0.48	0.19	-2.88	0.004
	Canopy duration (previous year)	0.07	1.91	0.34	0.7
	TmaxSummer_{n-1}	1.28	2.78	4.62	<0.0001
	TmaxSummer_{n-2}	-1.53	2.82	-5.93	<0.0001
Oaks	Intercept	4.23	0.25	17.19	<0.0001
	Canopy duration (current year)	0.43	0.19	2.32	0.02
	Previous year fruit production	-0.35	0.14	-2.52	0.011
	Canopy duration	-0.55	0.18	-2.96	0.003

(previous year)

TmeanSpring_n	0.48	0.21	2.26	0.02
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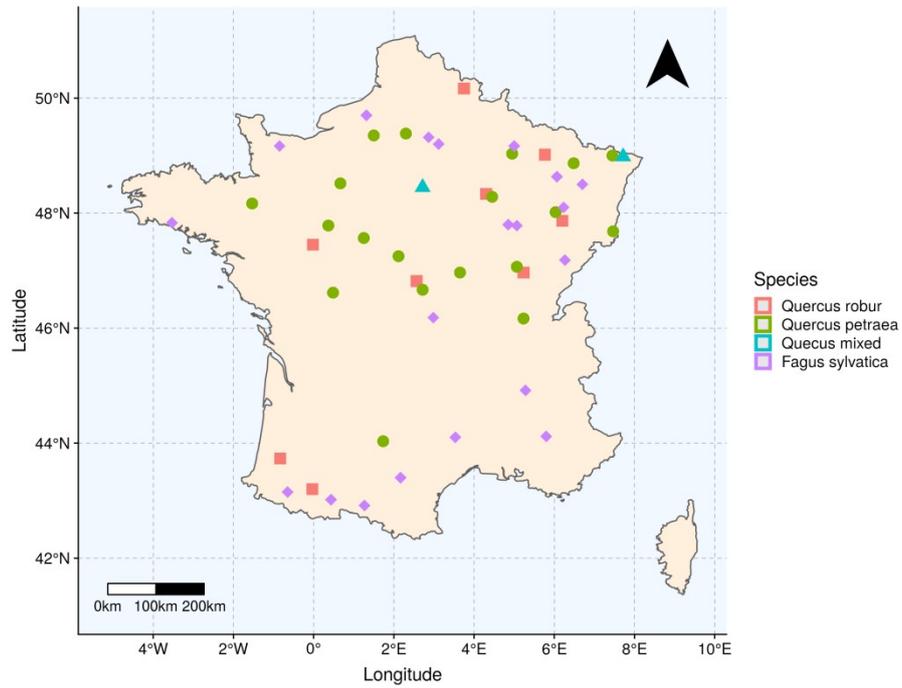
388 **Table 3:** Relationship between climatic events and canopy duration. Summary results of generalized
 389 linear mixed models (GLMMs) for beech and oaks (including *Q. robur* and *Q. petraea*) with climatic
 390 events as response variable and canopy duration as explanatory variable. A total of 10 GLMMs were
 391 used (i.e. 5 GLMMs for oaks and for beech). Level of significance are indicated with stars in the last
 392 column.

393 DS for dry spells (i.e. number of events when more than seven consecutive days without
 394 precipitation), FDspring for the number of frost days during spring season (minimal temperature from
 395 April to June < 0°C), FDautumn for the number of frost days during autumn season (minimal
 396 temperature from September to October < 0°C), HDsummer for the number of hot days during
 397 summer season (maximal temperature from June to August ≥ 30°C) and HDautumn for the number of
 398 hot days during autumn season (maximal temperature from September to October ≥ 30°C). Year and
 399 sites were included as random effects. † we incorporated an observation-level random effect to limit
 400 overdispersion.

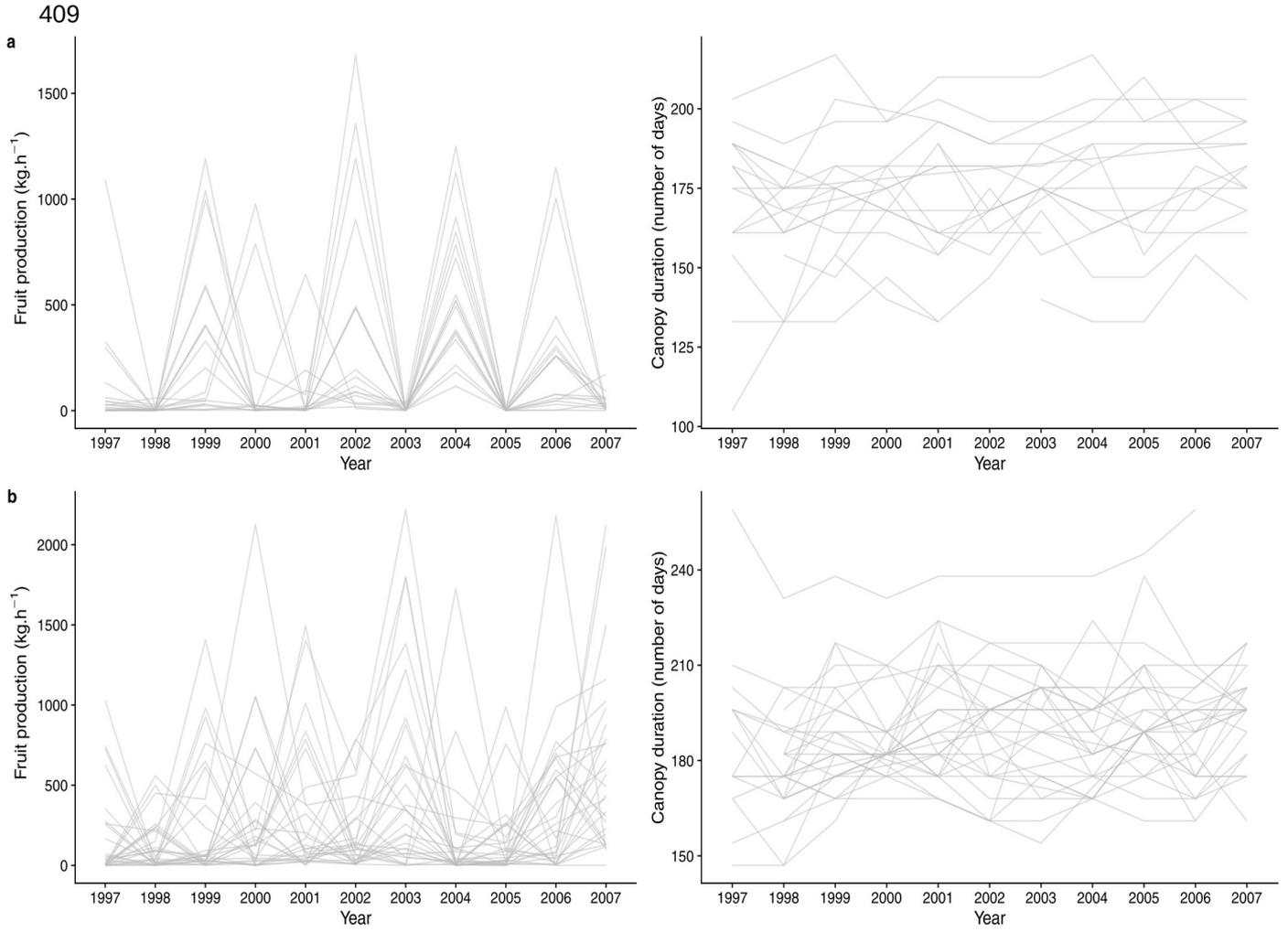
Species	Climate event (response variable)	Estimate	Standard error	t-value	P value
Beech	DS	-0.02	0.13	-0.16	0.87
	FDspring	0.67	0.56	1.20	0.22
	FDautumn†	1.17	0.24	4.74	<0.0001
	HDsummer	0.12	0.08	1.50	0.13
	HDautumn	0.79	0.39	1.99	0.046
Oaks	DS	0.21	0.097	2.23	0.026
	FDspring	0.90	0.18	4.93	<0.0001
	FDautumn†	0.93	0.18	5.04	<0.0001
	HDsummer	0.002	0.03	0.075	0.94
	HDautumn	0.31	0.16	2.00	0.045

401

402 **Figure 1:** Sites location from the RENECOFOR network. Distribution of the studied European beech
403 (*F. sylvatica*) and temperate oaks (including *Q. robur*, *Q. petraea* and mixed) populations across
404 France for a total of 50 sites.
405

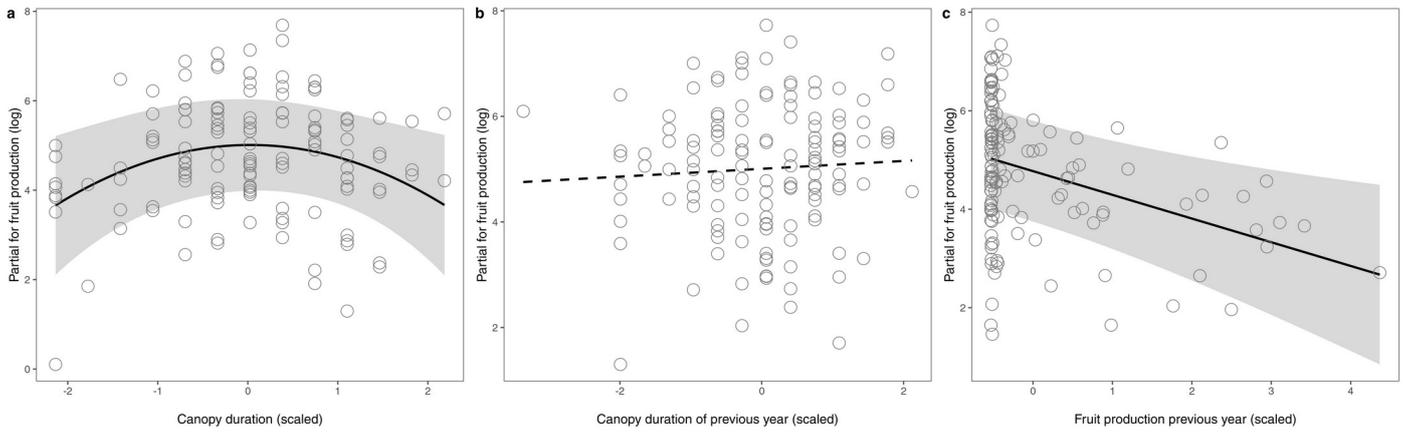


407 **Figure 2:** Fruit biomass production and canopy duration across years for a) beech (*F. sylvatica*) and
408 b) oaks (including *Q. robur*, *Q. petraea* and mixed). Each line represents one monitored stand.



410 **Figure 3:** Relationship between fruit production of beech and canopy duration (a), previous year
411 canopy duration (b), and previous year fruit production (c). Trend lines are based on LMM while
412 shaded regions correspond to 95% confidence intervals. Axis-y are given at the scale of partial
413 residuals and axis-x are scaled variables. Dashed line for non-significant relationship are presented in
414 (b).

415



417 **Figure 4:** Relationship between fruit production of oaks and canopy duration (a), previous year
418 canopy duration (b) and previous year fruit production (c). Trend lines are based on LMM while
419 shaded regions correspond to 95% confidence intervals. Axis-y are given at the scale of partial
420 residuals and axis-x are scaled variables.

421

