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Crown defoliation decreases reproduction and wood growth in a marginal European beech population

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• **Background and Aims:** Abiotic and biotic stresses related to climate change have been associated with increased crown defoliation, decreased growth and a higher risk of mortality in many forest tree species, but the impact of stresses on tree reproduction and forest regeneration remains understudied. At the dry, warm margin of species distributions, flowering, pollination and seed maturation are expected to be affected by drought, late frost and other stresses, eventually resulting in reproduction failure. Moreover, inter-individual variation in reproductive performance versus other performance traits (growth, survival) could have important consequences for population dynamics. This study investigated the relationships among individual crown defoliation, growth and reproduction in a drought-prone population of European beech, *Fagus sylvatica*.
• **Methods:** We used a spatially explicit mating model and marker-based parentage analyses to estimate effective female and male fecundities of 432 reproductive trees, which were also monitored for basal area increment and crown defoliation over 9 years.
• **Key Results:** Female and male fecundities varied markedly between individuals, more than did growth. Both female fecundity and growth decreased with increasing crown defoliation and competition, and increased with size. Moreover, the negative effect of defoliation on female fecundity was size-dependent, with a slower decline in female fecundity with increasing defoliation for the large individuals. Finally, a trade-off between growth and female fecundity was observed in response to defoliation: some large trees maintained significant female fecundity at the expense of reduced growth in response to defoliation, while some other defoliated trees maintained high growth at the expense of reduced female fecundity.
• **Conclusions:** Our results suggest that, while decreasing their growth, some large defoliated trees still contribute to reproduction through seed production and pollination. This non-coordinated decline of growth and fecundity at individual level in response to stress may compromise the evolution of stress-resistance traits at population level, and increase forest tree vulnerability.

Key words: Defoliation, drought, female and male fecundity, growth, trade-off, marginal population, Mediterranean forest, mixed effect mating model, microsatellite, parentage analyses, *Fagus sylvatica*.

INTRODUCTION

Climate and land-use changes can have major and complex effects on forest vegetation dynamics (McDowell *et al.*, 2020). Indeed, increasing episodic forest disturbances, such as windthrow or wildfire, together with land-use changes and changes in chronic drivers of forest dynamics (e.g. rising temperature, vapour pressure deficit and CO_2) lead to both compounding and antagonistic impacts that alter demographic processes of tree growth, mortality and recruitment. Many studies have focused on how global change can lead to massive forest decline (Briceño-Elizondo *et al.*, 2006; Camarero *et al.*, 2015) and tree mortality (Allen *et al.*, 2010; Adams *et al.*, 2017). However, the long-term response of forests is at least as dependent on recruitment, as the number and composition of

recruits determines the demography (Beckage *et al.*, 2005) and the adaptive potential (Hampe and Petit, 2005) of tree populations. Hence, we need more studies investigating the impacts of stresses related to climate or global change on tree reproduction and forest regeneration.

The warm and dry margins of tree species distributions are expected, and already observed, to suffer massive forest decline, driven by climate change and its consequences (Jump *et al.*, 2009; Anderegg *et al.*, 2019). Most importantly, prolonged droughts and high temperatures have been extensively associated with decreasing tree growth and forest productivity (Zhao and Running, 2010; Zimmermann *et al.*, 2015), increasing crown defoliation and leaf fall (Dobbertin, 2005; Galiano *et al.*, 2011) and higher risk of tree mortality

(Allen *et al.*, 2010; Adams *et al.*, 2017; Anderegg *et al.*, 2019). There is also an increasing concern that the advance in spring phenology currently observed in many species exposes them to a higher risk of late frost, with damaging effects on crown development (Charrier *et al.*, 2015; Bigler and Bugmann, 2018). Finally, the few existing studies monitoring tree reproduction and forest regeneration over time (i.e. the diachronic approach; see Bontemps *et al.*, 2013 for a definition) suggest that, at the rear edge of tree species' distributions, reproduction abilities are lowered by climatic stresses, in particular drought (Cecich and Sullivan, 1999; Fernández-Martínez *et al.*, 2012). However, such observational, diachronic studies are limited by the rarity of long-term reproduction-monitoring data sets (Clark *et al.*, 1999). Moreover, masting (i.e. the synchronized, intermittent production of large amounts of seeds) is common in forest trees (Pearse *et al.*, 2016), which makes the interpretation of reproduction time series challenging (Caignard *et al.*, 2017). Hence, we need complementary approaches to generalize whether climate stresses systematically decrease seed production and forest regeneration at the rear edge of tree species distribution.

Knowledge of species physiology predicts diverse, antagonistic effects of climate stress on reproductive performance. On the one hand, abiotic stresses such as droughts or late frosts are indeed expected to directly reduce plant sexual reproduction through altered reproductive phenology (i.e. the timing of flowering and fruiting), a higher risk of pollen abortion or pollination failure, a shorter seed maturation cycle and/or a higher risk of seed abortion (Hedhly *et al.*, 2009; Zinn *et al.*, 2010; Bykova *et al.*, 2012). Moreover, indirect negative effects are also expected: plant sexual reproduction can be strongly dependent on complex relationships between climate, plants and seed predators (Bogdziewicz *et al.*, 2020; Clark *et al.*, 2021). Also, by decreasing photosynthetic activity, leaf fall may reduce the amount of stored resources to invest in growth and reproduction in the next year (Obeso, 1988). On the other hand, stresses have also been hypothesized to shift patterns of resource allocation and act like a cue stimulating higher reproductive effort (Lee, 1988; Bréda *et al.*, 2006; Pulido *et al.*, 2014; Wiley *et al.*, 2017; Lauder *et al.*, 2019).

In their conifer-centred review, Lauder *et al.* (2019) proposed that trees under stress may exhibit either fight behaviour (i.e. increased allocation to survival at the expense of reproduction) or flight behaviour (i.e. increased allocation to reproduction at the expense of growth and survival). They hypothesize that flight behaviours increase as drought stress escalates the likelihood of mortality in a given location. The clearest experimental evidence of flight behaviour can be found in the literature on (fruit) tree orchards. Among the cultural practices allowing early and abundant flowering, water stress is used to enhance flower initiation in conifers, while hot, dry summers are reported to induce abundant seed crops in both conifers and broadleaved species (Meilan, 1997). Another practice relies on circumferential girdles (the removal of a swath of the bark, down to the phloem, around the entire stem), which are associated with reduced vegetative growth and increased fruiting (Bonnet-Masimbert and Webber, 2012). Finally, pruning (the reduction of crown leaf area) is also recommended to favour reproductive development while reducing vegetative growth in fruit trees (Karimi *et al.*, 2017).

This study investigates the effects of climatic stresses on sexual reproduction and growth using an observational synchronic approach, which consists in comparing the reproductive and growth performances of declining versus non-declining trees within a single population. As in Camarero *et al.* (2015), we consider crown defoliation as an indicator of stress, and analyse the relationships between crown defoliation, growth and fecundity at the inter-individual scale to first test whether defoliation leads to a decline in fecundity and growth. Moreover, by investigating the correlation between growth and fecundity in response to defoliation, we also test two alternative hypotheses. Hypothesis 1 (H1) is that crown defoliation is associated with a proportional decrease in growth and reproduction, so that the relationship between reproduction and growth does not change with increasing crown defoliation. Alternatively, hypothesis 2 (H2) holds that if defoliation or stresses act like a cue stimulating reproductive performances at the expense of reduced growth, then the relationship between reproduction and growth should change with increasing crown defoliation.

A main originality of our study is the use of a spatially explicit mating model and marker-based parentage analyses to estimate individual tree fecundity (e.g. Oddou-Muratorio *et al.*, 2018). Male and female *basic fecundities* (i.e. the numbers of pollen grains and seeds produced) have traditionally been estimated before dispersal through the resource allocated to male (i.e. biomass/number of pollen grains or staminate flowers) and female (i.e. biomass/number of ovules, seeds, ovuliferous flowers or fruits) functions. The development of marker-based approaches for parentage reconstruction has then allowed *realized reproductive successes* to be estimated from genotypes of seedlings and their potential parents, and used as a proxy of fitness (Conner *et al.*, 1996; Elle and Meagher, 2000). The next step was to combine genotypes with spatial locations of sampled individuals, through spatially explicit mating models, to disentangle the effect of fecundity from that of spatial design on reproductive success (Oddou-Muratorio *et al.*, 2005; Burczyk *et al.*, 2006; Goto *et al.*, 2006; Oddou-Muratorio and Klein, 2008; Moran and Clark, 2011). This approach avoids the spatial bias typically generated by sampling seedlings non-uniformly with respect to the positions of their parents or by the confounding effects of heterogeneous spatial distribution of mates. With this aim, dispersal is explicitly modelled using pollen and seed dispersal kernels. We used a previously developed Bayesian framework to estimate individual male and female individual *effective* fecundities (mixed-effect mating model, MEMM; Klein *et al.*, 2008; Oddou-Muratorio *et al.*, 2018). In this mating model for monoecious species, each adult individual is considered in turn as the potential father and mother of each sampled seedling. The MEMM hence estimates the *effective* amount of pollen achieving successful fertilization, and of seeds achieving successful germination.

Our study is focused on a major European tree species (the European beech, *Fagus sylvatica*), considered to be sensitive to summer drought. Beech is a monoecious, wind-dispersed species, and shows a masting behaviour triggered both by weather and plant resource status (Vacchiano *et al.*, 2017). Hacket-Pain *et al.* (2017) showed that summer droughts combined with masting years were associated with reduced growth, while growth was not reduced in mast years without summer drought, nor when summer droughts occurred during non-mast years. There is overall little evidence of a direct effect of drought on

beech seed production, except in Bréda *et al.* (2006), which reported increased seed production associated with leaf fall in high drought years, even though this relationship between crown defoliation and fruit production may not be directly causal. Our study site is a drought-prone, rear-edge natural population of *F. sylvatica* in southern France (Supplementary Data Fig. S1), where crown defoliation and mortality have been surveyed since 2003 (Petit-Cailleux *et al.*, 2020). We estimated effective female and male fecundities cumulated from 2002 to 2012. Growth over the same period was assessed through inventory data, completed by ring-width measurements. Finally, this study is based on the well-accepted hypothesis that recurrent defoliation is related to physiological stresses associated with climate change, and symptomatic of declining health in beech (Bréda *et al.*, 2006; Peñuelas and Boada, 2003). Supporting this hypothesis, a companion study on 4327 trees individually surveyed in the same population showed that crown defoliation increases the risk of mortality (Petit-Cailleux *et al.*, 2020). Moreover, simulations with a process-based physiological model indicated that the mortality rate in this population is driven by a combination of drought-related processes such as loss of hydraulic conductance or carbon reserve depletion, and late frost damages (Petit-Cailleux *et al.*, 2020).

MATERIALS AND METHODS

Study site

Located on the foothills of Eastern Pyrenees in southern France, the Massane Forest National Nature Reserve (42°28′41″N, 3°1′26″E) was created in 1973. It covers 336 ha on the highest part of the Massane valley, from 600 to 1127 m a.s.l., and is only around 5 km from the Mediterranean Sea. With a mean annual temperature of 11.95 °C and 1164.9 mm of mean annual precipitation (monitored on site since 1976 and 1960 respectively; Supplementary Data Fig. S1A), the site is under a meso-Mediterranean climate influence (*sensu* Quézel and Médail, 2003). This site is one of the European beech locations most prone to water stress (Supplementary Data Fig. S1B).

More than half of the reserve consists of an old-growth forest, where no logging operation has been performed since at least 1886. The canopy is dominated by European beech (*Fagus sylvatica*) in mixture with downy oak (*Quercus pubescens*), maples (*Acer opalus*, *A. campestris*, *A. monspessulanum*) and holly (*Ilex aquifolium*). A 10 ha fenced plot has excluded cow grazing since 1956. All trees from this protected plot have been monitored since 2002.

Adult seed–tree inventory and phenotyping

This study was conducted on two circular-shaped plots (as classically used in parentage analyses) covering 0.17 ha in total, where all the 683 live adult beeches were mapped and material was collected for genetic analyses in 2012 (red circles in Fig. 1). Although beech reproduction is mostly sexual, vegetative reproduction may occasionally occur, with the production of stump shoots resulting in multiple stems (i.e. several ramets for a single genet). In obvious cases of vegetative reproduction (i.e.

root-connected stems), we sampled only the largest ramet of each genet for genetic analyses.

Only 439 among the 683 collected beeches were included within the protected plot and monitored since 2002 (filled circles in Fig. 1). The monitoring consisted first in measuring tree size as the diameter at breast height (DBH) in 2002 and 2012, which allowed us to derive the basal area (BA = $\pi \times DBH^2/4$). Individual radial growth was measured by the basal area increment (herein BAI) between 2002 and 2012, as estimated by BAI = $\pi(DBH^2_{2012} - DBH^2_{2002})/4$.

The presence of major dead branches or foliage loss was recorded each year between 2004 and 2012 as a qualitative measure (1 = presence; 0 = absence). Note that only branch mortality of the current year is accounted for. This simple estimate of defoliation can be applied to a large number of individuals (e.g. 4327 trees in Petit-Cailleux *et al.*, 2020). Here, we used the sum of these nine annual defoliation (DEF) scores as an integrative, qualitative ordered measure. A high DEF score means that a tree either suffers recurrent defoliation or/and is not able to recover from previous defoliation.

The conspecific local density (herein $\text{Dens}_{d_{max}}$) was estimated as the number of beech neighbours found within a radius of d_{max} (see below) around each mother-tree. We also used the Martin-Ek index (Martin and Ek, 1984) to quantify the intensity of competition on a focal individual *i*. This index (herein $\text{Compet}_{d_{max}}$) accounts simultaneously for the diameter and the distance of each beech competitor *j* from the competed individual *i*:

$$\text{Compet}_{i,d_{max}} = \frac{1}{\text{DBH}_i} \sum_{j=1}^{n_{d_{max}}} \text{DBH}_j e^{\frac{-16d_{ij}}{\text{DBH}_i + \text{DBH}_j}} \qquad (1)$$

where DBH_i and DBH_j are the DBH (in centimetres) of the competed individual *i* and of competitor *j* (any adult tree of any species with $\text{DBH}_j > \text{DBH}_i$), $n_{d_{max}}$ is the total number of competitors in a given radius d_{max} (in metres) around each individual *i*, and d_{ij} is the distance between individuals *i* and *j*. We computed a total of 20 $\text{Dens}_{d_{max}}$ variables and 20 $\text{Compet}_{d_{max}}$ variables, by considering d_{max} values between 1 and 20 m with a 1-m step. The $\text{Dens}_{d_{max}}$ variables were strongly and positively correlated with each other, and so were the $\text{Compet}_{d_{max}}$ variables, but $\text{Dens}_{d_{max}}$ variables were not correlated with $\text{Compet}_{d_{max}}$ variables (Supplementary Data Fig. S2).

Offspring sampling and genotyping

To estimate adult fecundity, we sampled 365 seedlings located amidst the 683 genotyped adult beeches in 2012 (shaded quadrats in Fig. 1). Seedlings were sampled exhaustively within a selected number of quadrats at the centre of each circular plot: 165 seedlings germinated in spring 2012 (masting in 2011), and 200 seedlings germinated from spring 2011 back to spring 2001 (age was estimated using annual bud scars). Qualitative surveys indicated that masting occurred in years 2002, 2004, 2006 and 2009. In this study the two seedlings cohorts were mixed to estimate cumulative reproduction from 2001 to 2012.

The genotypes of the 683 live adult beeches and 365 seedlings were scored at a combination of 18 microsatellite loci

FIG. 1. Study site and sampling design. Red filled circles represent the 432 beech trees for which individual fecundity, growth and defoliation were assessed. Hatched squares represent the seedling patches used to estimate fecundity through parentage analyses and MEMMs. Open red circles represent the 244 beech trees outside of the protected area and included in the fecundity analyses (but not phenotyped for growth and defoliation). Grey circles and crosses represent other beeches within the protected area not included in the fecundity analyses either because they were far from sampled seedlings (circles) or because they were dead in 2012 (+). Open circles represent other species within the protected area.

(Supplementary Data Table S1). DNA extraction, PCR amplifications and genotype scoring with a MegaBACE 1000 sequencer were performed using the conditions described by Oddou-Muratorio *et al.* (2018). The total number of alleles observed in each cohort was >95 (Supplementary Data Table S1). Adult genotypes revealed seven pairs of clones among the adult beeches. We checked that these clones were always spatially clustered, and kept only one ramet for each genet in the following analyses (i.e. 676 adult beeches).

Inference of male and female relative fecundities: MEMM analyses

Male and female fecundities ($F_{\male}$ and $F_{\female}$ respectively) (F_M and F_F respectively) of each adult tree were jointly estimated with the pollen and seed dispersal kernels in a Bayesian framework (MEMM approach; Klein *et al.*, 2008; Oddou-Muratorio *et al.*, 2018). Briefly, MEMM considers that each sampled seedling originates either (1) from a mother tree located outside the study site (implying seed immigration) or (2) from a mother tree located within the study site. The latter case includes three possible origins of the fertilizing pollen: (1) pollen immigration; (2) selfing; or (3) pollination

by a male tree located within the study site. The approach bypasses parentage assignation and focuses instead on the fractional contribution of all adults, either as female or as male parent, to each seedling (see Appendix A1 for details). For instance, the probability $\pi_{S_{ij}}$ of each sampled female tree j contributing to the seedling pool at the spatial location of seedling i is modelled as:

$$\pi_{S_{ij}} = \frac{F_{\female j}\theta_s\left(d_{ij}\right)}{\sum_{l:\text{mother}} F_{\female l}\theta_s\left(d_{il}\right)} \tag{2}$$

where $F_{\female j}$ and $F_{\female l}$ are the female fecundities of mother j and l, respectively; d_{ij} and d_{il} are the distances between seedling i and mother j and l, respectively; and θ_s is the seed dispersal kernel. Both the seed and pollen dispersal kernels (θ_s and θ_p) are modelled using a power-exponential function. All the parameters of the model are estimated in a Bayesian framework (Appendix A1). Note that $F_{\female}$ (and $F_{\male}$) estimates are relative, with the average $F_{\female}$ value (or F_M value) over the entire parent population fixed to 1.

For the estimation, we accounted for typing errors at microsatellite loci, with two possible types of mistyping: in the first type, the allele read differs only by one motif repeat from the true allele with a probability P_{err1}, while in the second type the

allele read can be any allele observed at this locus with a probability P_{err2}. We considered a mixture of the two error types, with $P_{err1} = 0.01$ and $P_{err2} = 0.01$. We performed ten Markov chain Monte Carlo (MCMC) runs of 10 000 steps, each with an additional 500 first MCMC steps as burn-in, checked that the different chains converged to the same value visually, and then combined the ten chains. Individual female ($F_♀$) and male ($F_♂$) fecundities were summarized by their median value across the 100 000 iterations.

Adult subsampling for dendrochronological analysis

We selected 90 trees within the protected plot, for which we sampled cores to measure ring widths. These 90 trees were chosen to represent contrast in terms of defoliation and female fecundity (Supplementary Data Fig. S3). Cores were extracted in February 2016 at 1.30 m above ground. After sanding, cores were scanned at high resolution (1200 dpi). Boundary rings were read using CooRecorder v 9.0. Ring widths were transcribed, individual series were checked for missing rings and dating errors and mean chronologies were calculated using Cdendro 9.0 (CDendro 9.0 and CooRecorder 9.0; Cybis Elektronik & Data, Sweden). Using the sum of ring widths' increments between 2002 and 2012 (Σ_{rw}), the growth of the 90 individuals between 2002 and 2012 was estimated as: $BAI_{wood} = \pi((DBH_{2002}/2 + \Sigma_{rw})^2 - DBH^2_{2002}/4)$.

Statistical analyses of the ecological drivers of growth and fecundity

Our objective herein was to test whether defoliation significantly affected individual growth and female/male fecundity cumulated across the 2002–12 period. For each response variable independently (i.e. growth as measured by BAI and fecundity as estimated with MEMM), we considered the following initial linear model:

$$
\begin{aligned}
BAI \text{ or } F♀ \text{ or } F♂ = {} & DEF + DBH_{2002} + DBH^2_{2002} \\
& + Compet_{d_{max}} + Dens_{d_{max}} + DEF : DBH_{2002} \\
& + DEF : Compet_{d_{max}} + DEF : Dens_{d_{max}}
\end{aligned}
$$
(3)

where all the predictors are quantitative variables (Supplementary Data Table S2). Besides the target defoliation factor (DEF), this model includes one size-related factor (DBH_{2002}) and two competition-related factors ($Compet_{d_{max}}$ and $Dens_{d_{max}}$). Size and competition are considered here as 'nuisance' parameters, likely to blur the signal between defoliation, growth and reproduction. A quadratic effect of DBH_{2002} was also included, as growth and sometimes fecundity are known to be proportional to basal area. Density and the competition index can both be relevant in capturing the competition effect on growth or fecundity; moreover, their influence may vary with the distance up to which competitors are accounted for. Therefore, we first selected the best $Compet_{d_{max}}$ and the best $Dens_{d_{max}}$ terms for each response variable independently using

the model described by eqn (3) without interaction terms, and retaining the radius distance d_{max} leading to the highest coefficient of determination (R^2). Then, we included interaction terms, i.e. the three last terms in eqn (3), to investigate specific effects of defoliation depending on individual size or on the level of competition.

The model was fitted on 432 focal adult beech trees within the protected plot (Fig. 1) for which BAI was estimated from inventory data. All response variables were log-transformed to approach Gaussian distribution and to account for the higher variance associated with higher fecundity or higher growth. We visually inspected the relationship between each predictor and each response variable (Supplementary Data Fig. S4). For each response variable, we selected the most parsimonious model based on the Akaike information criterion (AIC) using the functions 'lm' and 'step' in R 3.3 (R Core Team, 2018). The residuals were visually inspected through a plot of residuals versus predicted. Interaction effects were visualized with the package 'jtools' (Long, 2020).

Collinearity resulting from correlations between predictor variables is expected to affect the statistical significance of correlated variables by increasing type-II errors (Schielzeth, 2010). To evaluate this risk, we computed variance inflation factors (VIFs) associated with each term retained in the best model with the R package 'car' (Fox and Weisberg, 2019).

Statistical analyses of the joint defoliation effects on female fecundity and growth

Our objective here was to focus on the two variables (growth and female fecundity) responding to defoliation (see the Results section) and to investigate how the relationship between these two variables varied with defoliation. We first compared the effects of defoliation on female fecundity versus growth after centring and normalizing fecundity and growth, and by using the best models fitted with eqn (3) to estimate the effect of defoliation on these transformed variables.

Then, we investigated the individual correlation between raw relative female fecundity and growth for non-defoliated trees (DEF = 0) versus defoliated trees (DEF > 0). Note that a part of these correlations may be due to variation in size and/or competition. Moreover, they do not account for the quantitative nature of DEF. To overcome these limitations, we further investigated the trade-off between growth and female fecundity using the following linear model:

$$
\begin{aligned}
F♀ = {} & BAI + DEF + DBH_{2002} + DBH^2_{2002} \\
& + Compet_{d_{max}} + Dens_{d_{max}} + DEF : BAI \\
& + DEF : DBH_{2002} + DEF : Compet_{d_{max}} \\
& + DEF : Dens_{d_{max}}
\end{aligned}
$$
(4)

where BAI and the interaction between BAI and DEF are added to the model described by eqn (3) above. A quadratic effect of DBH_{2002} was also included.

RESULTS

Patterns of covariation of defoliation, tree size and competition

Recurrent crown defoliation was overall limited in the 432 individuals, with 95 trees with a non-null DEF-value (mean = 0.37; Supplementary Data Table S2). Defoliation increased with tree size; the significant interaction between DBH_{2002} and competition (mediated by competition in a radius of 19 m) or density (mediated by density in a radius of 20 m) reflected a stronger effect of size on defoliation as competition increased (Supplementary Data Fig. S5).

Inter-individual variation in relative fecundity and growth

The distributions of relative female and male individual fecundities estimated by MEMM were strongly L-shaped (Fig. 2A). Female fecundities varied from 0.03 to 32.44 (median = 0.42, mean = 1, s.d. = 2.78), while male fecundities varied from 0.17 to 21.16 (median = 0.48, mean = 1, s.d. = 1.86). By comparison, the distributions of growth values were less L-shaped than those of fecundity (Fig. 2B). In the data set of 432 adult trees, where cumulated growth from 2002 to 2012 was estimated through inventory data, DBH radial growth varied from 0 to 4.4 cm (median = 0.45, mean = 0.60, s.d. = 0.62), while BAI varied from 0 to 581.22 cm² (median = 23.98, mean = 61.58, s.d. = 86.87).

In the subset of 90 cored trees, where cumulated growth from 2002 to 2012 was estimated through ring-width data, radial growth varied from 0.17 to 2.70 cm (median = 0.97, mean = 1.03, s.d. = 0.57), while BAI varied from 7.8 to 805.89 cm²

(median = 126.30, mean = 180.07, s.d. = 172.7). Moreover, for these 90 cored trees, the correlation between inventory-based and ring-width-based radial growth was 0.84 ($P < 0.001$), while the correlation between inventory-based and ring-width-based BAI was 0.68 ($P < 0.001$). The lower correlation for BAI values was due to the largest trees, for which inventory data generally underestimated growth (Supplementary Data Fig. S6).

Ecological drivers of fecundities and growth

Defoliation, size and competition overall explained a significant part of the variation in growth (61 %) and female fecundity (12 %), while competition alone was found to marginally explain a small part of the variation in male fecundity (<1 %). In the whole data set of 432 individuals, the most parsimonious model showed that female fecundity significantly decreased with defoliation and competition (mediated by competition in a radius of 10 m), while it increased with DBH_{2002} and density (mediated by density in a radius of 10 m; Table 1A). For instance, the 10 % of trees with the largest DBH were associated with 36 % of the total female fecundity. The 10 % of trees with the lowest competition index were associated with 27 % of the total female fecundity. Moreover, the interaction between DEF and DBH_{2002} was significant, reflecting a weaker negative effect of defoliation on female fecundity as tree size increased (Fig. 3A). By contrast, male fecundity was only marginally (and negatively) affected by competition (mediated by density in a radius of 5 m; Table 1B). Finally, growth (as measured by BAI) significantly decreased with defoliation and competition (mediated by competition in a radius of 7 m), and increased with DBH_{2002} and density (mediated by density in a radius of 10 m; Table 1C). We
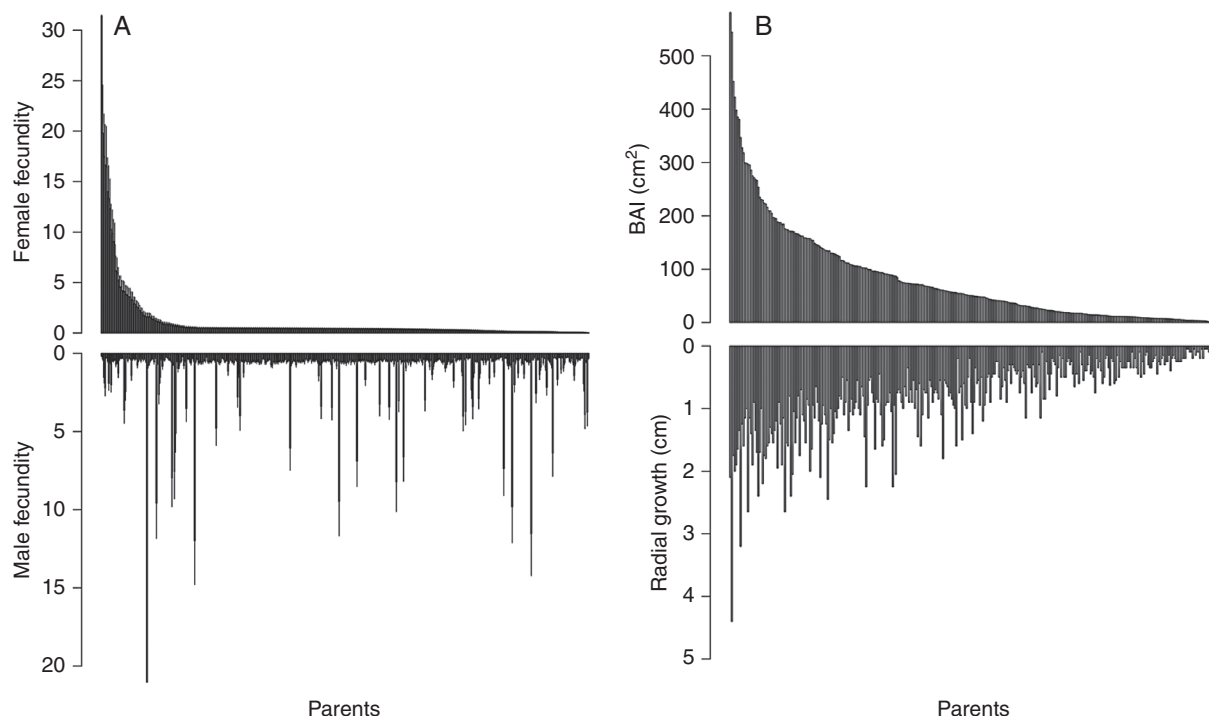

FIG. 2. Distribution of individual (A) relative female (top) and male (bottom) fecundities estimated with MEMM, and (B) absolute growth estimated by BAI (top) or radial growth (bottom) for the 432 adult trees. Parents on the *x*-axis are ranked in decreasing order of female fecundity (A) or BAI (B).

TABLE 1. *Analysis of variance table for (A) female fecundity ($F_♀$), (B) male fecundity ($F_♂$) and (C) BAI in response to ecological determinants included in eqn (3). Results of the most parsimonious model are shown: its adjusted R^2, the type-III sum of squares (SSQ) and degrees of freedom associated with each term. For each predictor, we give the estimate of its effect, the standard error and associated t and P-values. VIFs were computed with R package 'CAR'. All the response variables were log-transformed. Results are based on the whole data set of 432 individuals for $F_♀$ and $F_♂$, and on the 341 individuals with non-null BAI for BAI*

Predictor	R^2	SSQ	d.f.	Estimate	s.e.	T	*P*-value	VIF
(A) Log($F_♀$)	*0.12*						*<0.001*	
DEF		9.33	1	−0.349	0.111	−3.148	0.002	4.13
DBH_{2002}		11.97	1	0.013	0.004	3.564	<0.001	2.19
Compet10		7.9	1	−0.033	0.011	−2.896	0.004	1.43
Dens10		7.46	1	0.010	0.003	2.815	0.005	1.35
DEF:DBH_{2002}		7.28	1	0.006	0.002	2.780	0.006	4.61
Residuals		401.29	426					
(B) Log($F_♂$)	*0.004*						*0.097*	
Dens5		1.695	1	−0.01	0.01	−1.662	0.10	–
Residuals		263.854	430					
(C) log(BAI)	*0.61*						*<0.001*	
DEF		4.89	1	−0.153	0.058	−2.646	0.00853	1.05
DBH_{2002}		139.39	2	15.494	1.167	13.275	<0.001	1.21
$(DBH_{2002})^2$				−5.539	0.886	−6.251	<0.001	
Compet7		20.92	1	−0.090	0.016	−5.473	<0.001	1.27
Dens14		4.78	1	0.005	0.002	2.617	0.00927	1.16
Residuals		234.02	335					

Italic type correspond to the statistics (R^2, P) associated with the model itself.

Compet7, Compet10, Compet14, competition index within 7, 10 and 14 m, respectively; Dens5, Dens10, Dens14, number of neighbours within 5, 10 and 14m, respectively.

did not find significant interactions between defoliation and size on growth. For all fitted models, VIFs (Table 1) were all <10, ruling out any serious multicollinearity issue. Diagnostic plots confirmed the quality of the fitted models (Supplementary Data Fig. S7).

To compare the effects of defoliation on fecundity and growth, we centred and normalized female fecundity and BAI, and ran the best models for each response variable. The average decline in response to a 1-unit increase in DEF was −0.06 for female fecundity (s.e. = 0.10; measured in the standard unit of the trait) versus −0.10 for BAI (s.e. = 0.04).

Joint defoliation effects on female fecundity and growth

The raw female fecundities and BAIs were significantly and positively correlated in the 337 non-defoliated trees (ρ = 0.31, *P* < 0.001), but not in the 95 defoliated trees (ρ = 0.13, *P* = 0.2; Fig. 4).

The linear model for female fecundity including BAI as a predictor [eqn (4)] allowed us to disentangle the effects of defoliation, size and competition on the relationship between female fecundity and growth. In addition to the previous effects, a significant interaction between BAI and defoliation was detected (Table 2): female fecundity overall decreased with increasing defoliation, but this decrease was faster and stronger for trees with a higher BAI (Fig. 3B). The complex interaction between BAI, DEF and DBH_{2002} on female fecundity resulted in a defoliation-dependent trade-off between growth (as estimated by BAI) and female fecundity. The female fecundity of the non-defoliated trees (Fig. 3C, leftmost panel) increased with BAI (no trade-off), whereas the female fecundity of the most defoliated trees (Fig. 3C, rightmost panel) decreased with increasing BAI (trade-off). Moreover, the female fecundity of small trees (Supplementary Data Fig. S8, left panel) always decreased in

response to increasing defoliation, whatever their BAI, whereas the female fecundity of large trees (Supplementary Data Fig. S8, right panel) did not change in response to increasing DEF. This last result, combined with the observed trade-off between female fecundity and growth in response to defoliation (Fig. 3C, right panel), suggests that some large trees maintained high female fecundity under stressful conditions at the expense of reduced growth. Diagnostic plots confirmed the quality of the fitted models (Supplementary Data Fig. S9).

DISCUSSION

The results of our study supported the hypothesis of an overall negative effect of climatic stresses on reproduction and growth in the study beech population. Moreover, the declines in growth and fecundity in response to stress varied between individuals: some defoliated trees maintained significant female fecundity at the expense of reduced growth, while others maintained high growth at the expense of reduced female fecundity. Hypothesis H1 (a coordinated decrease in growth and reproduction in response to stress) was thus rejected. We discuss below the ecological and physiological processes underlying these patterns, and their long-term consequences for the adaptive response of the beech to water stress, before summarizing the methodological insights of our study.

Climate stress reduced and generated a trade-off between female fecundity and growth

This study is among the rare ones to bring observational evidence that increasing crown defoliation decreases individual
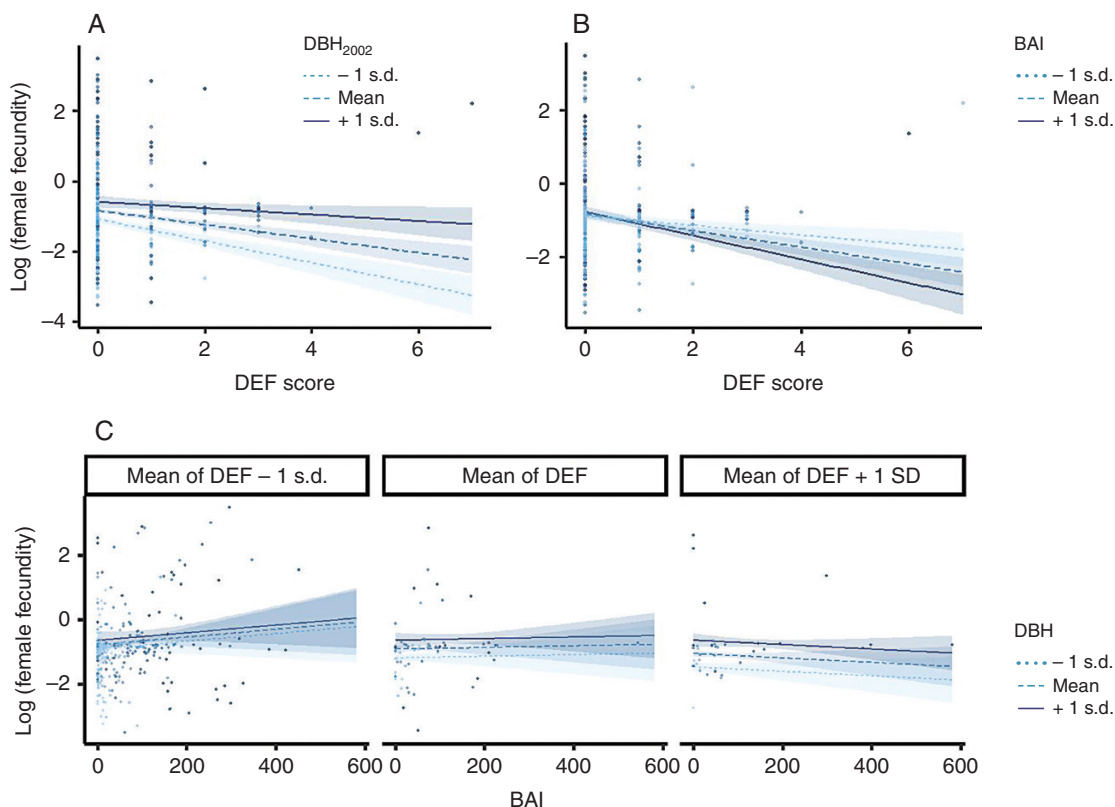
FIG. 3. Interaction plots for (A) DEF and DBH$_{2002}$ effects on female fecundity, (B) DEF and BAI effects on female fecundity, and (C) BAI, DBH$_{2002}$ and DEF effects on female fecundity. Regression lines are plotted for three values of each moderator variable, corresponding to ±1 s.d. from the mean. Confidence interval at 80 % are shown around each regression line. Points are the observations.
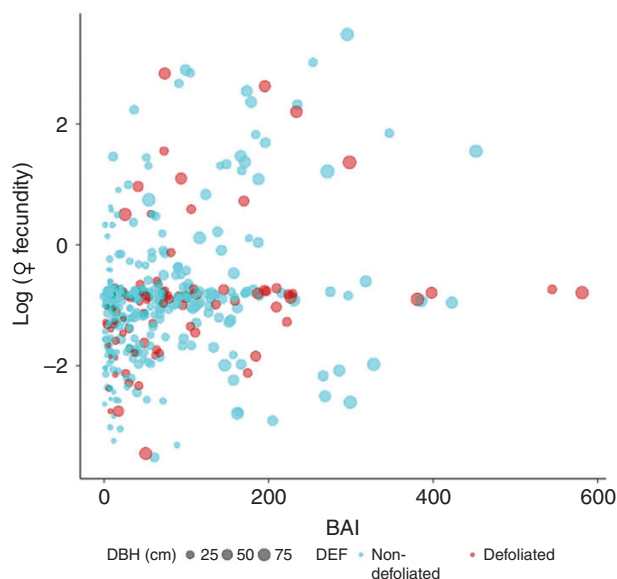

FIG. 4. Correlation between growth, measured by BAI and female fecundity plotted on a log scale. The size of the dots is proportional to tree diameter (DBH$_{2002}$). This is a scatter plot of raw data, not of model predictions.

female fecundity. This negative effect of climate stress on tree reproductive performances is consistent with the few diachronic studies based on time-series data sets, which reported a reduction over time of seed production in European Mediterranean ecosystems, attributed to increasing drought duration and severity (Cecich and Sullivan, 1999; Pérez-Ramos *et al.*, 2010). These findings are also supported by the few results available so far from experiments manipulating stresses *in situ*. For instance, by manipulating temperature during pollen dispersal and germination, Flores-Rentería *et al.* (2018) demonstrated negative impacts of high temperatures on the pollen viability of *Pinus edulis*. Bykova *et al.* (2018) showed that water deficit increases pollen abortion in *Quercus ilex*. Also in *Q. ilex*, Pérez-Ramos *et al.* (2010) showed that reduced water availability increased the rate of acorn abortion, while Sánchez-Humanes and Espelta (2011) showed that increased drought reduces acorn production. However, the mechanisms mediating climate effects on reproduction may differ strongly between species, and even between *Quercus* and *Fagus* genera (Journé *et al.*, 2021a), and we still lack studies testing how different climate variables affect the stages of the reproductive cycle of the beech.

Our results also indicated a negative effect of climate stress on tree growth, which has been reported by many previous studies (Zhao and Running, 2010; Zimmermann *et al.*, 2015). There is still some debate on the physiological processes causing radial growth variations in response to drought stress (Hayat *et al.*, 2017; Mund *et al.*, 2020). High temperatures and low precipitation undoubtedly directly affect photosynthesis and hydraulic conductance, inducing source limitations to tree growth and reproduction. However, at the same time the large number of physiological processes involved in the response

TABLE 2. *Analysis of variance table for female fecundity in response to ecological determinants included in eqn (4). Results are based on the whole data set of 432 individuals. See Table 1 legend for further explanation*

Predictor	R^2	SSQ	d.f.	Estimate	s.e.	t	P-value	VIF
	0.13						*<0.001*	
BAI		0.56	1	0.001	0.001	0.773	0.440	2.468
DEF		11.04	1	−0.384	0.112	−3.433	0.001	4.231
DBH		6.24	1	0.011	0.004	2.582	0.010	3.171
Compet10		7.49	1	−0.032	0.011	−2.828	0.005	1.444
Dens10		6.85	1	0.009	0.003	2.704	0.007	1.354
BAI:DEF		4.09	1	−0.001	0.001	−2.091	0.037	2.857
DEF:DBH		11.39	1	0.009	0.003	3.488	0.001	6.750
Residuals		397.03	424					

Italic type correspond to the statistics (R^2, P) associated with the model itself.

to drought (including meristem and cell growth rates) and the time-sequencing of physiological responses throughout successive annual cycles (with carry-over effects) result in a complex system of sink and source limitations driven by drought conditions (Mund *et al.*, 2020). In particular, growth is under direct environmental control, such as through water limitation, is not determined only by the amount of available carbon, and stops before photosynthesis with increasing drought (Eckes-Shephard *et al.*, 2021).

Another major finding of this study was the negative correlation between growth and reproduction for defoliated trees, contrasting with the positive correlation for non-defoliated trees. Several studies have tested the existence of a negative correlation between growth and reproduction at the individual level, as a signature of the possible trade-off between these functions. The key assumption underlying this trade-off is that reproduction is costly and competes with growth for resources (Obeso, 1988; Koenig and Knops, 1998; Thomas, 2011). By contrast, the absence of correlation is usually interpreted as independence between these functions in terms of the resource pool (Obeso, 1988; Knops *et al.*, 2007; Pulido *et al.*, 2014). A trade-off between growth and reproduction has already been found for beech (Hacket-Pain, 2017, 2018; Lebourgeois *et al.*, 2018). Hacket-Pain *et al.* (2017) found that masting years (i.e. years with high seed production) are negatively correlated with growth and that this trade-off is more pronounced during drought years due to resource scarcity.

These different results hence support the general idea that the correlation between reproduction and growth depends on the level of resources available (van Noordwijk and de Jong, 1986; Obeso, 1988), a trade-off being present only under limiting resources, i.e. crown defoliation in our case. Moreover, the detailed analysis of the interactions between defoliation, size and growth on female fecundity showed that those defoliated trees maintaining high female fecundity were the largest ones, suggesting that crown defoliation could shift the allocation of carbon to reproduction above a given tree size (Genet *et al.*, 2010; Thomas, 2011). Besides the literature on forest seed orchards and fruit trees orchards, one of the rare studies supporting this hypothesis is that of Wiley *et al.* (2017), who experimentally defoliated black oak, a tree species that matures its acorns over 2 years. Recovery following defoliation

was shown to involve substantial allocation shifts, with carbohydrate storage and already initiated reproduction cycles (i.e. maturation of 2-year acorns) being favoured relative to growth and new reproductive cycles (i.e. flowering and production of new 1-year acorns).

Long-term consequences for adaptive response of beech to stress

This study showed that defoliated beech trees reduce their fecundity and growth in varying proportions depending on the individual. Some trees maintained significant female fecundity at the expense of reduced growth (i.e. flight behaviour as defined by Lauder *et al.*, 2019), while other trees showed the reverse, i.e. fight behaviour, where growth is maintained at the expense of reduced female fecundity. Moreover, as male fecundity was insensitive to crown defoliation, the defoliated trees that were subject to less intra-specific competition also contributed to reproduction through male function. Hence, we can reject hypothesis H1, that the relationship between reproduction and growth does not change with increasing crown defoliation. Note, however, that the alternative hypothesis, H2 (defoliation or stresses act like a cue stimulating reproductive performances at the expense of reduced growth), was only supported for some individuals.

This response to stress could have major consequences for the short-term evolutionary dynamics of the local population. Indeed, assuming that at least some of the traits underlying vulnerability to stresses are under genetic control, we showed here that the most vulnerable individuals (those that are the most impacted by stress) still contribute to regeneration, which could lead the population to evolve traits compromising its adaptation to stress. By contrast, if the defoliated individuals showed a coordinated decrease in their growth and reproduction (H1), their potentially non-adapted genotypes could be purged more efficiently. Still, the fact that the study population is composed of a diversity of individuals that promote either growth or reproduction in response to stress could also give it an adaptive advantage in the long term, depending on the climate change scenario that will actually take place. For example, if climatic conditions become so difficult that all trees eventually decline, and that even the most 'fighting' individuals can neither grow nor survive, then the flight strategy may be the only viable one (e.g. by migrating to higher altitudes and establishing new populations).

Demonstrating that these fight and flight behaviours actually occur as adaptive strategies and deriving demo-genetic scenarios for the adaptive response of the population to stress would, however, require further investigations. The coexistence within the same population of several adaptive strategies for the allocation to reproduction versus growth in response to stress may be the rule rather than the exception (Bontemps *et al.*, 2017), and could be the result of ongoing, antagonistic selection within genetically diverse tree populations (Hampe and Petit, 2005). However, demonstrating the existence of these strategies would first require disentangling how genetic factors versus microenvironment variation (stress exposure) and ontogeny each contribute to the intra-individual variation in allocation to reproduction versus growth. Then, projections of possible evolutionary changes in response to drought stress would need to be quantitatively investigated (Hamanishi and Campbell, 2011).

Methodological insights

Our synchronic approach, comparing reproductive performances among trees with different levels of defoliation, thus usefully complements other observational, diachronic studies based on the analysis of reproduction and climate time series. However, it relies on several hypotheses, which need to be carefully evaluated. First, we assumed that crown defoliation is an indicator of higher intrinsic sensitivity to drought stresses, and/or a higher impact of drought stresses due to lower availability of resources in a heterogeneous environment. The companion study of Petit-Cailleux *et al.* (2020) supports this hypothesis. Still, our qualitative measure of defoliation suffered some limitations. Being the sum over 9 years of annual binary scores (0, no defoliation; 1, major dead branch or foliage loss), our DEF variable was likely to be informative about the recurrence of defoliation, but less informative about its intensity (in terms of percentage of the crown affected). Although out of the scope of this study, a better quantification of the intensity of defoliation would allow a more thorough investigation of the effects of defoliation on growth and reproduction.

Second, we used a spatially explicit mating model (MEMM) and marker-based parentage analyses to estimate individual fecundity, which had both advantages and drawbacks. Unlike traditional resource-based estimates of seed/pollen production, MEMM estimates of fecundity have the main advantage of integrating several processes of the regeneration loop. Indeed, being evaluated after mating, dispersal, germination and possibly early mortality preceding the sampling stage, MEMM estimates are considered as better proxies of fitness than seed/pollen biomass or numbers (Oddou-Muratorio *et al.*, 2018). Note that MEMM estimates account specifically for individual effects (either maternal or genetic) that affect survival independently on location; for instance, two trees producing the same number of seeds (same basic fecundity) but with different intrinsic quality of germination or survival, are expected to have different MEMM estimates of fecundity. By contrast, MEMM estimates are expected to be insensitive to spatial processes such as density-dependent mortality affecting seedling survival depending on their location (Klein *et al.*, 2013). Early mortality is massive in trees, and has been shown to reshuffle the reproductive success

ranking (but not the MEMM fecundity ranking) of adult oak trees, where gravity-dispersed seedlings suffer higher density-dependent mortality than seedlings dispersed over a long distance (Gerzabek *et al.*, 2017). Finally, a main drawback of the MEMM is that it estimates effective amounts of pollen or seed produced by each individual *relative* to other plants; these relative fecundities hence convey no information on the absolute contribution of defoliated or non-defoliated individuals to regeneration, and thus on the demographic impact of defoliation. Still, it should be noted that recruitment and seed production are abundant in the study site, despite its marginality and the presence of declining trees. These overall good reproduction abilities ensure that our relative measures of fecundity are not biased by overall very low recruitment.

In conclusion, this study brings new insights on the reproductive and adaptive response to stress of European beech, by investigating the inter-individual variation in the impact of stress-induced defoliation on fecundity and wood growth within a natural population at the warm, dry margin of the species' distribution. Elucidating the causal processes underlying these relationships deserves further investigation (Supplementary Data Fig. S10). In particular, accounting for the non-observed level of resource allocated to reproduction and growth would require either an estimation of this resource (e.g. Mund *et al.*, 2020) or specific methodological approaches [e.g. path analyses (Shipley, 2016) or other Bayesian tools introducing the level of resource as a latent variable (Journé *et al.*, 2021*b*)]. Our study overall stresses the need to investigate simultaneously the impact of climate change on reproduction, growth and survival, and how the inter-individual variations in these responses may affect the adaptation or maladaptation of forest tree populations in the face of climate change.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Table S1: genetic data for the adult and offspring population. Table S2: size, competition and defoliation variables measured in adult trees. Figure S1: climate characteristics of the study site. Figure S2: patterns of covariation among competition index and density. Figure S3: sampling design for the 90 cored individuals. Figure S4: preliminary check of the quality of linear models. Figure S5: effect of size and competition on defoliation. Figure S6: relationship between growth estimated from ring width and growth estimated from inventory data. Figure S7: diagnostic plot for the linear regression model described by eqn (3). Figure S8: interaction plots for DEF, BAI and DBH_{2002} effects on female fecundity. Figure S9: diagnostic plot for the linear regression model described by eqn (4). Figure S10: conceptual framework for the impacts of abiotic and biotic stresses on individual plant performance.

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DATA AVAILABILITY

The data set analysed is available online under the zenodo platform (https://doi.org/10.5281/zenodo.3516305).

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