Peer Community In
Forest & Wood Sciences

An interesting analysis of the interactions between English oaks (*Quercus robur* L.) and powdery mildew (*Erisyphe* sp.) at tree population level.

Erwin Dreyer *based on peer reviews by* ***Louis Bernier*** *and 1 anonymous reviewer*

Benoit Barrès, Cyril Dutech, Gilles Saint-Jean, Catherine Bodénès, Christian Burban, Virgil Fievet, Camille Lepoittevin, Pauline Garnier-Géré, Marie-Laure Desprez-Loustau (2024) Demographic and genetic impacts of powdery mildew in a young oak cohort. bioRxiv, ver. 2, peer-reviewed and recommended by Peer Community in Forest and Wood Sciences. `https://doi.org/10.1101/2023.06.22.546164`

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This preprint is recommended after a round of reviews by two external reviewers and the recommender and a careful revision of the initial text. The revision addressed all the the concerns raised by the reviewers and myself acting as recommender. I commend the authors for the care taken in the revision process and in addressing all concerns raised by the referees. The preprint is now in a status anabling a very positive recommendation, and I am convinced that PCI friendly journals will be keen to publish it given the quality of the contribution to Forest Pathology and Epidemiology as well as to and Forest Ecology.

Indeed, the preprint adresses an important topic in forest ecology and forest management. Powdery mildew (due to a complex of fungi species of *Erysiphe* spp.) is a very frequent pathogen affecting oaks and mainly English oak (*Quercus robur* L.), a widespread species in Western European forests which bears great ecological and economic interests (see Marçais and Desprez-Loustau, 2014, for a review). Young regenerations are mostly affected by the disease, which infects young, unfolding leaves and leads to severe reductions in photosynthesis (Hajji et al, 2009) and in some cases to tree dieback in young regenerations, and sometimes in older trees in the case of repeated infestations over several years, or combinations with defoliaitions by processionnary moths (*Thaumetopoea processionea* L.). Powdery mildew was introduced to Europe at the beginning of the

20th century and caused initially very severe damage in oak stands; currently, damage is much less prevalent, probably due to a co-evolution of the oak host and the pathogen (Desprez-Loustau and Marçais, 2019).

The present investigation adds very interesting and important information to our current knowledge of this disease, and addresses in particular the genetic variability of susceptibility to the disease among oak families and the effect of the disease on the survival of seedlings in the long run. Five main research questions were addressed: i. How does powdery mildew affect juvenile survival; ii. Is the survival rate differing among oak families? iii. Does powdery mildew infection reduce the differences of fitness among oak families? iv. Does powdery mildew impact the genetic diversity of oak populations? v. Are there significant genetic associations between some genetic loci and seedling survival? These questions are important for unerstanding the evolution of a pathosystem like the powdery mildew/English oak system and for explaining the past dynamics of this pathosystem, which resulted in a dicrease in virulence of the disease since its introduction in Europe.

The preprint reports results from a very original and solid experimental design based on the cultivation in the field of 15 oak progenies comprising 1733 indivduals over a quite long time span (9 years) and recurrent observations of growth, survival, infection intensity, ... A control group was protected against the pathogen by application of a fungicide. Moreover, a large number of individuals were genotyped, using single nucleatide polymorphism (SNP) allowing the detection of some candidate loci, and preparing future genome-wide association studies. The results are quite clear, and add very important elements to our understaning of this interesting and evolving pathosystem present in mots of the western European oak forests.

This preprint is of particular interest since such approaches, which are becoming common in cultivated crops, have only seldom been applied to natural pathosystems despite their importance for the dynamics of forest ecosystems under the increasing impact of climate change. In brief, this is an important preprint that brings a large set of new data and addresses the urgent question of epidemiology of diseases in forest ecosystems.

References:

Barrès B, Dutech C, Saint-Jean G, Bodénès C, Burban C, Fiévet V, Lepoittevin C, Garnier-Géré P, Desprez-Loustau M-L (2024) Demographic and genetic impacts of powdery mildew in a young oak cohort. bioRxiv, 2023.06.22.546164, ver. 2 peer-reviewed and recommended by Peer Community in Forest and Wood Science. `https://doi.org/10.1101/2023.06.22.546164`

Desprez-Loustau ML, Hamelin FM, Marçais B (2019) The ecological and evolutiionary trajectory of oak powdery mildew in Europe. In: Wilson K, Fenton A, Tompkins D, Wildlife Disease Ecology: Linking Theory to Data and Application. Ecological Reviews. Cambridge University Press, 978-1-107-13656-4. `https://doi.org/10.1017/9781316479964.015`

Hajji M, Dreyer E, Marçais B. (2009) Impact pf Erysiphe alphotoides on transpiration and photosynthesis in Quercus robur leaves. Eur J Plant Pathol, 125, 63-72, `https://doi.org/10.1007/s10658-009-9458-7`

Marçais B, Desprez-Loustau ML (2014) European oak powdery mildew: impact on trees, effects of environmental factors, and potential effects of climate change. Ann For Sci, 71, 633-642, `https://doi.org/10.1007/s13595-012-0252-x`

Reviews

Evaluation round #1

DOI or URL of the preprint: `https://doi.org/10.1101/2023.06.22.546164`

Version of the preprint: 1

Authors' reply, 27 March 2024

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Decision by Erwin Dreyer, posted 22 December 2023, validated 08 January 2024

Revision for the preprint by Barrès et al: Demographic and genetic impacts of powdery mildew in a young oak cohort.

This manuscript addresses the very important question of the interactions between a widely disseminated pathogen (powdery mildew, *Erysiphe alphitoides* and a related species) recently (beginning of the twentieth century) introduced in Europe and english oak (*Quercus robur*) progenies, checking for differences in mortality among genotypes and in growth trends of seedlings with respect to infection. The results are important and contribute to a clarification of the interactions, which will be quite useful for understanding the biology behind these infestations, and for the management of oak stands in their very young stage (seedlings and saplings).

Two reviewers have produced very detailed assessments of the manuscript. They were both very positive about the content, the results, and their analysis. They also converged in underlying a few shortcomings in the presentation of the methods, of the actual species of mildew, and a few further details that need revision and some attention.

At some point, I wondered, given the numerous results presented (and the frequent reference to supplementary material) whether the manuscript did not address two complementary but rather independent groups of questions: that of the interactions between fitness and powdery mildew infection (questions 1-3), and that about the genetic analysis of the sensitivity to powdery mildew (questions 4 and 5). This could have justified two different and more concise manuscripts, with a shorter and easier-to-follow presentation of the results. I very seldom make such a statement, given that most authors are rather inclined to salami publication. Anyway, the choice remains that of the authors, and it is also very positive to have a unique manuscript addressing a very complete range of questions based on a single and long-term experiment (over 10 years!) in a unique albeit quite long manuscript.

As recommender I have a few more mostly minor suggestions.

1. Like the reviewers, I would like to see the full species names (with authorities) quite early in the abstract, introduction, and possibly the title, and authorities associated with every species name at first occurrence.

2. I wondered why the data were not deposited in the French recherche.data.gouv repository, which has more interesting features for data visibility and organization than Zenodo, and is more compliant with the FAIR criteria. A switch to the former repository is not required at this stage, but I urge the authors to consider this in the future.

3. I also suggest avoiding the use of supplementary material and would recommend adding all supplementary material either to the data set (which is the case here) or as an annex associated with the main text (which would be justified for a reader not willing to search through the Zenodo database. A few figures should be available as an annex to the main text.

4. A few more details of the mode of action of the fungicide used would be helpful to guess the degree of protection provided: is it a systemic fungicide, and what is its specificity. Similarly, the procedure used to assess the degree of infection would also need some more details.

5. Please check Figure 2C: does it really represent the total height of the seedlings, or is it the annual increment? A stability of total height after year 3 at 30-50 cm would be surprising; if yes, this requires a specific comment and discussion. The answer comes later L442: the final height of the seedlings reached values from 17 to 53 cm after almost 10 years of growth. The apparent stability over time is surprising: were annual growth flushes that small? or did the tallest seedlings die over time?

6. The results of the models should be at least partly shown in the main text and not in the annex (and even less in supplementary material).

8. The caption of Figure 7 should make clear that the index is computed in the 9 different plots (6 exposed and 3 protected). Similarly, the caption of Figure 9 should provide more details and clearly identify the significant associations for people who are not familiar with Manhattan plots.

9. The first paragraph of the discussion sounds like a summary of the results; while this is relevant given the large array of complementary results, it should be made clear in the results section or significantly reduced in length. The structure of the rest of the discussion is excellent and follows the different questions raised at the end of the discussion, and I have no particular comment for the discussion which is very clear and precise.

Last but not least, I have to apologize for the long delay in producing this assessment. I had difficulties finding suitable and available reviewers and contacted close to 30 different specialists before fetching the two reviews attached below. This may be because PCI is not yet fully recognized by the scientific community as a full and reliable alternative to traditional publishing. However, the two reviewers who accepted the commitment did a very good job, and I do warmly thank them.

Reviewed by anonymous reviewer 1, 05 October 2023

This manuscript by Barres et al investigates one of the key questions in the disease ecology, how diversity is maintained in host populations. They test Janzen-Connell hypothesis using 15 oak families. They investigated the effect of powdery mildew disease on oak population structure in a multiyear experiment. The authors followed powdery mildew epidemics, host mortality and population diversity (half sib family diversity) across years in controlled field study. They also SNP genotyped the experimental plants to assess changes in heterozygosity and to perform GWAS on infection traits, height, survival, and acorn wight. They present enormous dataset and all experiments seem adequately designed and analysed.

They find that against expectations, there are no strong effect of powdery mildew infection on population structure of oak. The same fittest families survive in diseased and protected treatments.

In GWAS, the authors are able to identify multiple loci that contribute to acorn weight and some that contribute either to survival, infection or height.

This manuscript has both applied importance as it describes potential loci of interest for breeding and provides understanding on the lack of growth defense trade-off in a forest tree.

I have no major criticism, only few comments how to clarify the paper.

l. 80 it would be good to describe the causal agents of powdery mildew in the introduction somewhere more specifically. In the first mention I recommend stating the genus or species scientific name.

l. 127 to me the maternal conditions high vs low disease pressure come here as a surprise. I would recommend using a small paragraph earlier in introduction for transgenerational effects of disease. There is also a recent publication on maternal effects in powdery mildew resistance in Plantago: Höckerstedt et al. J Ecol. 2021; 109: 1439–1451. `https://doi.org/10.1111/1365-2745.13568`.

l. 141-142 Please, be more specific.

l. 144 under which stress?

l. 149 A brief description of the genetics and biology of Q. robur is needed here. E.g. is it diploid or what? What powdery mildew species might infect it? What other stresses are important in its ecology?

l. 151 Please, describe here how infected the mother trees were and for how long was that assessed? How far the mother trees were from each other? How is this species pollinated? How it is known that the seeds are half sibs?

l. 154 when and where the trees were sown? It would be good to state here the duration of the study.

l. 168 please, provide details of the annual disease scoring for each year. Was the scoring performed every year? How many times?

l.270 How the 7 % minor allele frequency threshold was chosen?

l. 671 it would be good to explain the underlying genetics of powdery mildew-oak system somewhere.

Minor

l.23 it would be good to mention also scientific name for the pathogens causing powdery mildew in the abstract.

l. 89-90 specialized feeding structures that penetrate in living cells?

l. 94 replace little with rarely

l. what kind of importance? Economic, cultural, ecological or what?

l. 97-100 this sentence is unclear and needs clarification.

l. 105-108, this sentence could be simplified.

l.113-115 could the authors place the citation to refer the study in question.

l. 339 something weird in this sentence

Fig. 5. This is very informative way of presenting the results! There seems to be error in the direction of] in the infection rate legend.

l. 591 see also Susi et al. Journal of Ecology 105, no. 5 (2017): 1399-1412.

Reviewed by **Louis Bernier**, 08 December 2023

The manuscript submitted by Barrès and colleagues describes the effect of several years of exposure to powdery mildew on the demographics and genomic diversity of a young population of Quercus robur. The latter consisted of 1,733 individuals recovered from 15 half-sib families from a single geographic area (Cestas), and exposed to natural infection by agents responsible for powdery mildew. The study is based on the same experimental set-up as the one used in previously published research on the host phenotypic response to infection (Desprez-Lousteau et al. 2014. Annals of Forest Science 71:563–573). In the new study, infection was monitored from 2009 to 2013, and survival was evaluated until the end of the 2017 growing season. In addition, an exhaustive combination of genetic /genomic analyses was carried out on close to 1,200 individuals. The authors then used phenotypic and genomic data in statistical models to estimate the role of abiotic and biotic factors in survival and identify genomic regions that might contribute to disease resistance. The authors also concluded that there was no evidence of a trade-off between host growth and defense in their pathosystem.

Globally, I am impressed by the experimental approach, diversity of analyses, and overall quality of the work. I agree with the authors that, in the population of *Q. robur* they studied, « Powdery mildew infection thus did not suppress the competitive advantage of the dominant, fast-growing families, and no evidence of a growth-defense trade-off was obtained.» While it may be argued that the nine years of growth considered in the analysis represent only a small fraction of the lifespan of a long-lived tree species, the authors have generated a large quantity of useful data on a phase of tree growth and establishment that is critical, especially with regard to exposure to powdery mildew.

I have identified a few relatively minor points which I would like the authors to address.

1. In the Discussion, the authors state that the study of a single population sampled locally may not have allowed for the detection of trade-offs between traits, and suggest that sampling across a wider spatial range might have yielded different results (L613-617). Yet, in the Introduction, the authors state that high genetic diversity is present within oak populations (L97-98; L115-116). So, if the level of genetic diversity found within the Cestas population is comparable to the average level found in populations of *Q. robur* throughout its range, the problem associated with sampling only a local population may not be so important after all. On the other hand, if the Cestas population has an unusually low level of genetic diversity, the possibility that methodological constraints prevented the detection of trade-offs

between traits becomes higher. How does the level of genetic/genomic diversity of the Cescas population compare with that of other *Q. robur* populations?

2. In their description of the experimental design, the authors state that there were two levels of exposure to powdery mildew: either Natural or Protected, with protection provided by the application of the fungicide Myclobutanil in the latter case. In their 2014 Annals of Forest Science paper based on the same experimental design, Desprez-Lousteau et al. indicate there were three levels of exposure (low, medium, and high) to powdery mildew. The low level corresponded to repeated applications of Myclobutanil. The medium level corresponded to natural inoculation, whereas the high level was obtained by blowing spores from highly sporulating leaves above the seedlings, using a portable air compression device. My understanding is that the new study included only plots with medium (Natural) and low (Protected) exposures. If this is indeed the case, I suggest mentioning this in the Materials and Methods section.
3. The identity of the causal agents of powdery mildew is not mentioned in the text, except for the mention of *Erysiphe quercicola* and *E. alphitoides* in the Keywords. I suggest including at least one sentence on the identity and specificity of the pathogens responsible for powdery mildew on *Q. robur*, as was done in the 2014 Annals of Forest Science paper.
4. The caption of Figure 3 should include information on the meaning of the small vertical green and beige/light brown bars at the top and bottom of the graph, respectively.
5. The caption of Figure 10 should include information on the acronyms for the genotypic classes C/C, T/C, and T/T. I have indicated a few typos on the annotated PDF copy of the manuscript.

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