

Interspecific and intraspecific diversity in oak powdery mildews in Europe: coevolution history and adaptation to their hosts

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Abstract *Quercus* has been reported as the genus with the largest number of attacking powdery mildews. In Europe, oak powdery mildew was rarely reported before 1907, when severe outbreaks were observed. These epidemics were attributed to the newly described species *Erysiphe alphitoides*, presumed to be of exotic origin. After the burst of interest following the emergence of the disease, research on this topic remained very limited. Interest in research was recently reactivated in response to the availability of molecular tools. This review summarizes current knowledge on the diversity of oak powdery mildews in Europe and their possible evolutionary relationships with European oaks. The most striking results are the evidence of cryptic diversity (detection in France of a lineage closely related to *Erysiphe quercicola*, previously thought to only have an Asian distribution), large host range (similarity of *E. alphitoides* and *E. quercicola* with powdery mildews of tropical plants) but also local adaptation to *Quercus robur*. These recent findings highlight the complexity of the history of oak powdery mildew in Europe and point to the question of host specialization and host jumps in the evolution of powdery mildew fungi.

Keywords *Erysiphe alphitoides* · *Erysiphe quercicola* · Host range · Local adaptation · *Phyllactinia roboris*

Introduction

Quercus has been reported as the genus with the largest number of attacking powdery mildew fungi, spanning species in various genera of the Erysiphales: *Cystotheca*, *Erysiphe* (including former *Microsphaera* and *Uncinula*), *Phyllactinia*, *Typhulochaeta*, and *Brasiliomyces* (Braun 1995). More than 50 powdery mildew species occurring in various regions of the world are listed on oaks in the Systematic Mycology and Microbiology Laboratory Fungus-Host Database (Farr and Rossman 2010). In spite of probable synonyms and overlooked cryptic species (see following), this list is indicative of the apparently strong affinity between oaks and Erysiphales. Mori et al. (2000) pointed out that one of the most basal taxa of powdery mildews, *Uncinula septata*, infects *Quercus* species, and suggested that Fagaceae might be among the earliest hosts of powdery mildews. A close evolutionary relationship between *Quercus* and powdery mildews has been suggested by several authors (Viennot-Bourgin 1966; Braun 1995; Mori et al. 2000; Takamatsu et al. 2003).

In Europe, only four powdery mildew species in three genera were listed on *Quercus* by Viennot-Bourgin (1966) and later by Braun (1995), fewer than in Asia or Northern America (Viennot-Bourgin 1966). It must be noted that Europe is relatively poor in terms of oak species diversity compared to north central America and Asia, which are considered to be centers of diversity for this genus (Nixon 2006). Moreover, as is developed in this review, the origin of oak powdery mildew species in Europe, whether autochthonous or not, is still unclear, leaving questions about their coevolution with European *Quercus* species unanswered.

After the burst of interest following the oak powdery mildew epidemics in Europe at the beginning of the 20th

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century, research on this topic remained very limited during several decades, with a very slow evolution in the state of knowledge. The advent of molecular biology in recent years has dramatically improved our ability to reveal cryptic diversity in powdery mildews, to link this diversity with morphological species and to explore their phylogenetic relationships. The availability of these new tools prompted many new studies. This review aims to summarize current knowledge on the diversity of oak powdery mildew fungi in Europe and their possible coevolutionary relationships with European oaks. We first review the diversity of species and their putative geographic origins and then introduce recent studies on local adaptation of powdery mildew fungi to oaks in Europe. Although many studies are still in progress, these recent data have already called into question several previous assumptions and open interesting directions for future research.

Interspecific diversity

Phyllactinia roboris (Gachet) S. Blumer is considered to be the most anciently recorded powdery mildew species on oaks in Europe, under the names *Erysiphe roboris* Gachet, with a first report near Bordeaux (Gachet 1832), or *Erysiphe quercus* Merat, with a first report near Paris in 1843 (Viennot-Bourgin 1966; Braun 1995). Although the disease it caused was probably not very spectacular, Viennot-Bourgin (1966) pointed out that it was quite common in the 19th century, based on numerous observations on herbaria specimens.

In 1907, another species took center stage. In that year, unprecedentedly severe disease outbreaks were observed in a few French locations as well as in the neighboring countries of Spain, Luxemburg, and the Netherlands (Hariot 1907; Foex 1941). The disease rapidly spread all over Europe in subsequent years and soon reached an almost worldwide distribution (Foex 1941). Damage in Europe was severe on several deciduous *Quercus* species, especially *Q. robur*, *Q. petraea*, and *Q. toza*. For example, Bureau (1908) mentioned that he could not find a single healthy *Quercus toza* tree during a survey in the Loire region. Damage on *Q. robur* was especially severe in coppices and lopped trees, leading to growth loss and even mortality (Griffon and Maublanc 1911; Foex 1941). This sudden outbreak and the high susceptibility of indigenous oaks strongly suggested a novel host–parasite interaction (Parker and Gilbert 2004), resulting either from the introduction of an exotic fungus (e.g., Griffon and Maublanc 1908; Raymond 1927) or from the emergence of a virulent genotype arisen from a local species (Gillot 1909; Ayres 1976). In both alternatives, the hypothesis of host shift or even host jump (Stukenbrock and McDonald 2008) was

assumed, with strains from a powdery mildew species initially nonpathogenic to native oaks in Europe becoming able to infect these new hosts. The fact that sexual fruiting bodies were observed only several years after the disease outbreak in Europe, as also reported for other introduced powdery mildew fungi, was often interpreted as a result of an adaptation to a new host (Raymond 1924, 1927). A limited number of morphological traits were available for the identification of the species causing the new epidemic, especially in the first years when only the anamorphic stage of the fungus was observed. In addition, only rough descriptions were available for reports made before 1900. However, the fungus causing the new epidemic could easily be distinguished from oldest reports, e.g., *Erysiphe roboris* or *Erysiphe quercus*, now assigned to *Phyllactinia* (Viennot-Bourgin 1949). By contrast, other species reported in the second part of the 19th century showed morphological similarities to the fungus involved in the new outbreak: *Calocladia penicillata* f. *Quercus* Pass. described in 1875 in Italy, and *Oidium quercinum* Thüm. described on *Quercus racemosa* (= *Quercus robur*) in 1877 in Portugal, and might be the first reports of the new species (Raymond 1927; Viennot-Bourgin 1966). When the teleomorphic stages were found in South-East France in 1912, Arnaud and Foex (1912) identified the newly observed species as the American *Microsphaera quercina* included in *Microsphaera alni* sensu Salmon (Salmon 1900). However, after a detailed morphological study, Griffon and Maublanc demonstrated that the species was different from all previously described species, including the American ones, and described the new species as *Microsphaera alphitoides* Griffon & Maubl. [current name: *E. alphitoides* (Griffon & Maubl.) U. Braun & S. Takam.], from a Greek word meaning “flour,” referring to the abundant white sporulation (Griffon and Maublanc 1912).

Another powdery mildew species, *Microsphaera hypophylla* Nevod. [= *M. silvatica* Vlasov; current name: *E. hypophylla* (Nevod.) U. Braun & Cunningt.], was reported on oaks in Europe after the 1950s. The species seemingly expanded westward (Viennot-Bourgin 1968), with first reports from Russia, then in Norway (Roll-Hansen 1961) and several countries of Eastern and Central Europe, e.g., Slovenia (Macek 1975a).

Finally, *Uncinula pyrenaica* Vienn.-Bourg. [now *Erysiphe pyrenaica* (Vienn.-Bourg.) U. Braun & S. Takam.] was described by Viennot-Bourgin in 1966 on *Quercus ilex* from a single location in the French Pyrenees. The species could not be retrieved thereafter and was never reported elsewhere.

The availability of new markers provided by molecular biology, especially nuclear ribosomal DNA polymorphisms (rDNA), recently allowed a better identification of species and prompted new appraisals of powdery mildew species

diversity. The phylogeny of Erysiphales was extensively revisited (Hirata and Takamatsu 1996; Takamatsu et al. 1998, 1999, 2006, 2007; Saenz and Taylor 1999; Braun and Takamatsu 2000; Cunnington et al. 2003; Takamatsu 2004; Limkaisang et al. 2005, 2006; Braun et al. 2006). In particular, molecular studies of numerous powdery mildew species in the former *Erysiphe*, *Microsphaera*, and *Uncinula* genera showed that they formed a separate, monophyletic clade, characterized by common morphological characters. The *Erysiphe* emend. genus was therefore introduced by Braun and Takamatsu (2000) for this clade, including *E. alphitoides* and *E. hypophylla*. Molecular analyses also allowed some clarifications in the definition of these species. The species previously reported as *E. alphitoides* on *Q. phillyraeoides* in Japan was shown to differ in molecular characteristics but also in morphology from true *E. alphitoides* by Limkaisang et al. (2006) and was described as *E. quercicola* S. Takam. & U. Braun by Takamatsu et al. (2007). In contrast to *E. alphitoides*, which is most commonly found in temperate areas, *E. quercicola* was assumed to be a species of subtropical to tropical distribution (Takamatsu et al. 2007). By the same time, the situation of oak powdery mildew in Europe, especially France, was reexamined using internal transcribed spacer (ITS) and intergenic spacer (IGS) regions of the nuclear

rDNA repeat unit (Mougou et al. 2008). These authors confirmed the presence of *E. alphitoides*, *E. hypophylla*, and a *Phyllactinia* sp., based on perfect homologies of the ITS sequences described for these species. However, quite unexpectedly, the ITS sequence of *E. quercicola* was also found (Fig. 1). The study of the distribution of the four ITS-based lineages in France confirmed that *E. alphitoides* was the dominant species, with a frequency of its ITS around 80% among samples; the frequency of the *E. quercicola* ITS lineage was rather high, approximately 15%, whereas others related to *Phyllactinia* and *E. hypophylla* were quite rare and mostly found in mixed infections with *E. alphitoides* (Mougou-Hamdane et al. 2010). This study further revealed no clear pattern of spatial differentiation between lineages whatever geographic scale was considered, i.e., different ITS lineages could be found in the same region, altitude, host species (mainly *Q. robur* and *Q. petraea*, but also *Q. pubescens*), tree, and even lesion. Studies based on multigene phylogenies are in progress to confirm the conspecificity of French specimens with *E. quercicola* and to test a temporal niche differentiation hypothesis between *E. alphitoides* and *E. quercicola* (Feau et al., unpublished data).

Molecular analyses not only revealed the existence of cryptic species under common symptoms but also have

Fig. 1 Phylogenetic relationships among species of the oak powdery mildew complex retrieved in Europe (in **bold**), in Asia, and on non-oak hosts. The neighbor-joining tree reconstruction was based on a Kimura two-parameter distance matrix of internal transcribed spacer (ITS) nucleotide sequences obtained from the International Nucleotide Sequence Database Collaboration database (indicated with *accession numbers*). Bootstrap values from 1,000 replicates and up to 60% are indicated at each *node* as follows: neighbor-joining bootstrap value/maximum-parsimony bootstrap value (single asterisk, the holotype for *Erysiphe quercicola*; double asterisk, the neotype for *Erysiphe alphitoides*)

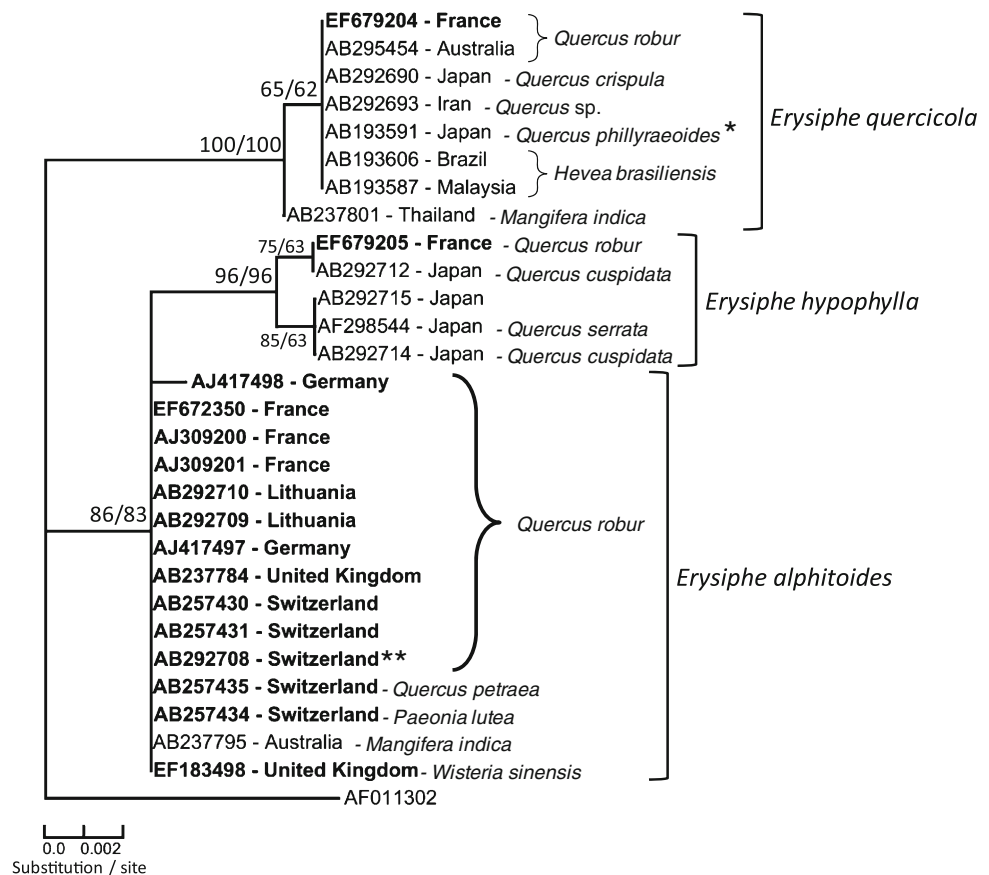


Table 1 Oak powdery mildew species reported in Europe

Species	First report	Putative origin	Comments	References ^a
<i>Phyllactinia roboris</i>	1832	Europe	Relictual?	Gachet (1832)
<i>Erysiphe alphitoides</i>	1907	Asia?	Most frequent nowadays	Hariot (1907); Griffon and Maublanc (1912)
<i>Erysiphe hypophylla</i>	1954	Asia?		Vlasov, in Roll-Hansen (1961)
<i>Erysiphe pyrenaica</i>	1966	?	One single report in France	Viennot-Bourgin (1966)
<i>Erysiphe quercicola</i>	2007	Asia?	Only the internal transcribed spacer (ITS) sequence was detected	Mougou et al. (2008); Mougou-Hamdane et al. (2010)

^a See also Viennot-Bourgin (1949); Braun (1995)

dramatically changed our view of host specificity in powdery mildews. Based on morphology and ITS sequences, *E. alphitoides* and species found on a variety of hosts, including *Paeonia* (Takamatsu et al. 2006), *Wisteria* (Henricot and Cook 2007), and *Vaccinium*, but also mango, were shown to be identical (Takamatsu et al. 2007). Similarly, *E. quercicola* was shown to be identical to the powdery mildew on *Hevea brasiliensis*, only found as the anamorph named *Oidium heveae*. Both *E. alphitoides* and *E. quercicola* thus seem to have large host ranges (Takamatsu et al. 2007). Interestingly, Boesewinkel (1980) had earlier stated the identity of *Oidium mangiferae* Berthet, causing powdery mildew of mango, and *E. alphitoides*, based on morphological similarity and successful cross-inoculations on oak and mango. He further suggested that this might give an indication in the history of *E. alphitoides* in Europe, with a possible first introduction in Portugal on exotic plants, followed by a host jump on *Quercus*.

Finally, a possible scenario emerging from all observations that could explain the presence of the different powdery mildew species in Europe is the progressive edging out of an indigenous species, *Phyllactinia roboris*, by more virulent introduced species (Table 1). Already in 1966, Viennot-Bourgin pointed out the decline of *P. roboris* concomitant with the rise of *E. alphitoides*. *Phyllactinia roboris* is considered as a relic of an almost eradicated species in several eastern European countries and has been put on the Red List in Slovakia (Macek 1975a,b; Palovcikova et al. 2009). Its exact position in the phylogenetic tree remains to be investigated because no sample from *Quercus* in Europe was included in the phylogenetic study of *Phyllactinia* spp. by Takamatsu et al. (2008). Moreover, some reports of *Phyllactinia* on *Quercus* sp. in Europe refer to *P. guttata* (Wallr.) Lév., whether in synonymy with *P. roboris* (Viennot-Bourgin 1949) or not (Braun 1995). Although their origins still remain doubtful, *E. alphitoides*, *E. hypophylla*, and *E. quercicola* are assumed to be exotic to Europe. A North American origin of *E. alphitoides* was first proposed by analogy with other introduced species, such as the grapevine powdery mildew

(Griffon and Maublanc 1908). However, the close phylogenetic relationship of this species with *E. quercicola* and *E. hypophylla*, for which an Asian origin was proposed (Takamatsu et al. 2006), rather suggests Asia as the region of origin. The three species would have been introduced at different times in Europe, with different pathways, resulting in different invasion patterns, e.g., rather eastward for *E. alphitoides* and westward for *E. hypophylla*. This scenario is still very speculative and is only supported by fragmentary observations. A phylogeographic study of the genetic diversity of the different species using intraspecific markers would be particularly interesting in this regard, by providing clues on the possible centers of diversity, hence possible centers of origin.

Intraspecific diversity

Population genetic studies based on neutral markers can give useful indications of the regime of reproduction (sexual/asexual) or dispersal patterns within a species (Milgroom and Peever 2003; Giraud et al. 2008). Studies of powdery mildew species have been hampered by difficulty in developing valuable markers in these fungi. Anonymous dominant markers such as amplified fragment length polymorphisms (AFLPs) and random amplification of polymorphic DNA (RAPDs) are potentially useful for organisms with a haploid life cycle (such as powdery mildews). These markers can generally be obtained at low cost but are difficult to interpret because of the risk of non-Mendelian inheritance, and, for biotrophic fungi, of amplifying DNA from host or hyperparasite species. In a few species, attempts to isolate more specific and polymorphic markers such as microsatellite loci were performed, but with no or very limited success (Dutech et al. 2007). Pioneering studies essentially focused on cereal powdery mildew, *Blumeria graminis* (DC.) Speer (Parks et al. 2009) and grapevine powdery mildew, *Erysiphe necator* Schwein. (Délye et al. 1997). For the latter, the European population, originating from North America, was

shown to be composed of two biotypes with limited gene flow between them (Délye et al. 1997; Brewer and Milgroom 2010). The next generation of high-throughput DNA sequencing methodologies should soon help to develop such neutral genetic markers for powdery mildews, including *E. alphitoides* and other related species found on oaks (Malausau et al., unpublished data).

Phenotypic variation within and among populations can also provide useful indications to infer evolutionary processes. As biotrophic obligate parasites, powdery mildew fungi establish intimate interactions with their hosts and are therefore expected to adapt to host resistance traits. In natural plant pathosystems, reciprocal adaptations between host and pathogen result in a coevolutionary process (Clarke and Akhkhia 2002). Although most studies of evolution of resistance or virulence in powdery mildew pathosystems are concerned with crop plants (e.g., Parks et al. 2008), a few natural pathosystems have been investigated, e.g., the groundsel powdery mildew caused by *Golovinomyces fischeri* (S. Blumer) U. Braun & R.T.A. Cook [\equiv *Golovinomyces cichoracearum* var. *fischeri* (S. Blumer) U. Braun] on *Senecio* spp. (Clarke and Akhkhia 2002) or *Podosphaera plantaginis* (Castagne) U. Braun & S. Takam. on *Plantago* (Laine 2005, 2007; Laine and Hanski 2006). The occurrence of powdery mildew fungi on the model plant *Arabidopsis thaliana* has prompted many studies on the plant side but few on pathogen populations (Adam et al. 1999; Micali et al. 2008). The *E. alphitoides*–*Quercus robur* interaction was recently investigated in two studies, in Finland and France (Roslin et al. 2007; Marçais et al. 2009, Desprez-Loustau et al. 2010a). A common objective of these studies was to test the hypothesis of a local adaptation of powdery mildew to its host. Pathogen populations, with a high and fast reproductive rate, are expected to have high evolutionary potential, especially if they combine asexual and sexual reproduction (McDonald and Linde 2002). Pathogens are thus generally expected to be locally adapted to their hosts (Morgan et al. 2005). However, local adaptation is a balance between selection and gene flow. Parasites are predicted to be locally adapted only if they migrate more than do their hosts but migration rates are not so high as to homogenize populations completely (Morgan et al. 2005; Hoeksema and Forde 2008). Even though *E. alphitoides* is not native to Europe, its introduction occurred more than 100 years ago, resulting in almost as many sexual generations and many more asexual generations, with huge population sizes. Adaptation processes could thus have taken place.

In a first study, local adaptation of *Erysiphe alphitoides* was considered at population level and targeted the “encounter” component of the interaction. The encounter refers to the conceptual framework introduced by Combes (2001) where parasite success on a potential host is

explained by the opening of two “filters”: the encounter filter and the compatibility filter. The encounter filter determines whether and to what extent the parasite can find the host. The compatibility filter determines infection and reproduction success of the parasite once it makes contact with the host. In temperate regions with strong seasonality, biotrophic foliar pathogens such as powdery mildews are expected to have adapted to their host plants for phenological synchrony to optimize the possibility of contacts leading to infections. The study by Desprez-Loustau et al. (2010a) investigated phenological synchrony (flushing-ascospore dispersal) in the *Q. robur*–*E. alphitoides* pathosystem, along an altitudinal gradient in the Pyrenees, with a high phenological variation within and between host populations. Host–pathogen phenological matching was shown to vary between and within sites at different altitudes. Moreover, common garden experiments did not give any evidence of genetic differentiation for fungal phenology among populations from different altitudes or geographic origins (Marçais et al. 2009). These data therefore did not support local adaptation of the fungus for host encounter at population level. An explanatory hypothesis was the high variation in phenology among trees at each altitude, which would rather favor fungal adaptation at a lower level, i.e., on a single tree.

In another study, local adaptation was considered at tree level, and targeted the compatibility component of the interaction. Most studies of local adaptation, especially with powdery mildews, have involved herbaceous hosts (Laine 2005, 2007). Characteristics of long-lived hosts may promote different patterns of local adaptation, e.g., at the fine scale of individual trees, as has been proposed in the deme-formation hypothesis for herbivore insects (Cobb and Whitham 1993). In addition, woody plant-parasitic genera of powdery mildews exhibit specific characteristics compared to herb-parasitic genera, which may favor the establishment and maintenance of an adapted population on a single tree. The complex morphology of appendages in woody plant-parasitic genera of powdery mildews has been suggested to be an adaptation allowing the chasmothecia to be retained on the bark of trees (Takamatsu 2004). In the case of *Erysiphe necator*, the overwintering of chasmothecia in the bark of the vines where they were formed was shown to favor their survival and the infection of adjacent emerging shoots in spring (Gadoury and Pearson 1988).

Interestingly, the study performed by Roslin et al. (2007) demonstrated both highly efficient dispersal and local adaptation at tree level in oak powdery mildew. Efficient dispersal was strongly suggested by the low spatial aggregation of mildew infection and the rapid colonization of transplanted uninfected host plants in all parts of the landscape (a 5-km² island in southwestern Finland).

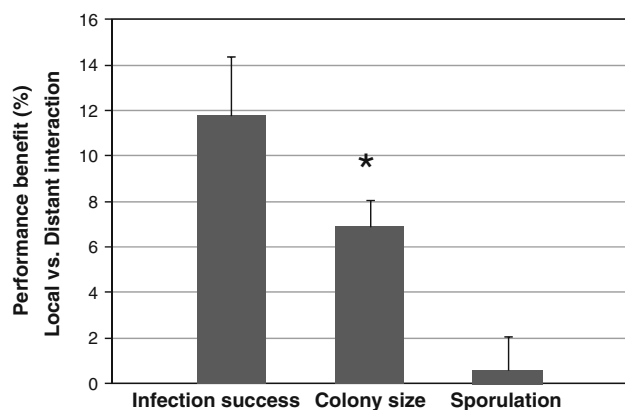


Fig. 2 Relative performance benefit of local versus distant interactions in cross-inoculations between strains of oak powdery mildew (*Erysiphe althitoides sensu lato*) and *Quercus robur* progenies (asterisk, significant difference between local and distant interactions)

On the other hand, local powdery mildew populations performed best on their original hosts: in reciprocal inoculations conducted on mature foliage, local powdery mildew populations infected a significantly higher proportion of leaves from their original host tree than from other trees. These results are consistent with those obtained by Mougou (2009) in another study performed in southwest France. Here, the performance of powdery mildew strains isolated from four trees was compared for progenies from their original host tree and progenies from distant trees in a controlled inoculation experiment. The size of powdery mildew colonies was significantly larger in the local interaction, and a similar trend was observed for infection success (Fig. 2).

These two studies suggested that local parasite populations of oak powdery mildew are shaped by complex processes involving selection pressures and gene flow, which may vary over the season.

Conclusion

Although understanding of the oak–powdery mildew interaction in Europe is still far from comprehensive, it has greatly improved in recent years and has provided interesting new insights into the biology of powdery mildews. Perhaps the most striking finding is the similarity between species thought to be specific to *Quercus*, *E. althitoides* and *E. querciola*, with species that had been described on very distantly related hosts in the tropics, e.g., *Oidium heveae* and *O. mangiferae* (Takamatsu et al. 2007). The recent reports of *E. althitoides* on *Paeonia* (Takamatsu et al. 2006) and *Wisteria* (Henricot and Cook 2007) also support the polyphagy of the species. Although these observations need to be confirmed both genetically, using

regions other than in rDNA, and biologically (e.g., cross-inoculations), they point to the interesting although difficult question of the host range and specialization in powdery mildew fungi. Although Salmon in 1900 considered powdery mildews as polyphagous fungi and used a very wide species concept, conventional wisdom has more recently held that Erysiphaceae are mostly specialized pathogens, with host ranges often limited to a single family (Braun 1995). The host matrix has often been used as a criterion included in keys for the identification of powdery mildew species (Cook et al. 1997). It must be noted that general concepts and ideas in plant pathology have been strongly influenced and even biased by observations and knowledge from crop diseases, which have been studied earlier and more intensively. The idea of strong host specialization in powdery mildews might thus be a view that emerged from these crop pathosystem studies. Indeed, the most intensively studied powdery mildew species, *Blumeria graminis*, shows a very high specialization, with distinct formae speciales causing disease on distinct host species. For example, *B. graminis* f. sp. *hordei* infects only barley and *B. graminis* f. sp. *tritici* infects only wheat. However, crop pathosystems exhibit special characteristics that make them inappropriate for generalization. In particular, they impose a very different type of selection on pathogens compared to the selection operating in more heterogeneous natural systems. By providing denser and genetically more uniform host populations, it is thought that crop domestication at the beginning of agriculture led to the emergence of more specialized pathogens (Stukenbrock and McDonald 2008). The same process is still at work at an infraspecific level, with the emergence of virulent races able to overcome resistance genes deployed over large areas (McDonald and Linde 2002). Contrastingly, the host range of oak powdery mildew appears far less host specialized than was initially thought and could be more representative of natural pathosystems. However, native plant–powdery mildew interactions can also show high specialization (Clarke and Akhkhia 2002; Laine and Hanski 2006).

High specialization and host jumping might be only apparently paradoxical. Some authors have argued that high host specificity does not exclude possibilities for host shifts/host jumps, i.e., evolutionary lability (Parker and Gilbert 2004). Indeed, host jumps and host shifts are thought to be major driving forces in powdery mildew evolution (Vági et al. 2007; Hirose et al. 2005) and have also been recognized in the evolution of rust fungi, another group of highly specialized biotrophic pathogens (Roy 2001). It seems that at least some powdery mildew fungi possess pathogenicity factors that allow them to establish a compatible parasitic relationship with allopatric plant species, e.g., upon introduction of the fungi in a new region (Vági et al. 2007); this might be one of the reasons why

powdery mildews have been reported as one of the most successful group of invasive species among fungi (Kreisel and Scholler 1994; Jones and Baker 2007; Desprez-Loustau et al. 2010b). The mechanisms underlying this ability to overcome basic resistance and, reciprocally, the host factors favoring compatibility to powdery mildew fungi have been increasingly dissected but still require further investigation (Eichmann and Hückelhoven 2008; Ridout 2009). Genome-wide studies should provide some clues to the molecular mechanisms behind variation in host range among different powdery mildew species. Population genomics approaches will further help to reconstruct patterns of selection in both time and space, leading to a more complete understanding of coevolutionary and adaptation processes, with or without a shared evolutionary history. In particular, patterns of dispersal and of genetic differentiation at different spatial scales should be explored, taking into account not only a few neutral markers but also genome-wide studies allowing testing of the hypothesis that only a few genes might be the target of a strong diversifying selection. Oak powdery mildew offers an interesting study model as a tree-parasitic powdery mildew in a naturally evolving interaction, where evolutionary patterns different from those observed in herb-parasitic powdery mildews, especially in crop plants, can be expected.

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