Biological Conservation 253 (2021) 108928

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Rethinking the natural regeneration failure of pedunculate oak: The pathogen mildew hypothesis

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ARTICLE INFO

Keywords:
Quercus robur
Lowland pedunculate oak forest
Erysiphe alphitoides
Alien invasive species
Plant-pathogen interaction
Forest dynamics

ABSTRACT

Introduced pathogen microorganisms are important drivers of ecosystem change. This paper highlights the impact of the non-native pathogen mildew multi-species complex on the natural regeneration dynamics of pedunculate oak (*Quercus robur*). Pedunculate oak is a European keystone tree species, hosting a great amount of biodiversity, but its future role in (near-)natural forests is uncertain due to the lack of natural regeneration. We reviewed historical and recent ecological, pathological and forestry literature on topics related to the impact of mildew on the success of advanced natural regeneration of pedunculate oak in (near-)natural forests. We propose a novel hypothesis, the 'pathogen mildew hypothesis', to explain the failure of natural regeneration of pedunculate oak. Mildew reduces shade tolerance and vertical growth in seedlings and saplings, so sapling vitality and competitiveness have diminished considerably since it was unintentionally introduced to Europe in the early 20th century. Due to mildew infection, pedunculate oak in many cases no longer regenerates well naturally under its own canopy. We found that forest ecologists and conservationists often overlook the impacts of this 'recent' driver, while the 'closed-forest' and 'wood-pasture' hypotheses do not adequately help the management of pedunculate oak regeneration. Nature conservation and forest management plans should thus also consider the impact of mildew in order to improve natural regeneration, promote close-to-nature management of pedunculate oak forests, and support associated diversity. More generally, nature conservation, forest ecology and close-to-nature forestry should pay greater attention to the impact of introduced non-native microorganisms on the dynamics of natural ecosystems.

1. Introduction

1.1. Alien pathogen species as drivers of natural ecosystems

Invasive alien species are among the key drivers of biodiversity loss and ecosystem change, and they attract great attention, particularly when affecting keystone and dominant species (Collinge et al., 2008; Seebens et al., 2017). Native pathogen-induced changes of forest ecosystem patterns and processes (e.g. forming gaps, killing seedlings or changing competitive relationships) are also well documented in many biomes (e.g. bark beetle infestation in coniferous forests, Castello et al., 1995; Collins et al., 2011). However, the legacy of invasive alien pathogen micro-organisms (e.g. fungal pathogens) on ecosystem dynamics has received much less attention among ecologists, foresters and nature conservationists, especially in the temperate region (Hansen, 2008). For example, alien *Phytophthora* spp. have recently been identified as a key agent in the decline of several tree species throughout the world (Hansen, 2008).

Several disciplines, especially pathology, plant physiology and forestry, have produced detailed knowledge about the effects of introduced microbial pathogens at organ and plant levels (Marçais and Desprez-Loustau, 2014; Lonsdale, 2015). However, discussion of the

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https://doi.org/10.1016/j.biocon.2020.108928
Received 29 August 2020; Received in revised form 21 November 2020; Accepted 12 December 2020
Available online 25 December 2020

consequences of pathogen infestation on natural forest dynamics often exceeds the scope of these disciplines, or only considers forest management issues (e.g. natural regeneration decline in shelterwood systems or decline of mature stands) (Thomas et al., 2002; Marçais and Desprez-Loustau, 2014).

Ecology (e.g. historical, landscape and vegetation ecology) and conservation biology – disciplines that study drivers of ecosystem change – often omit to integrate the results of less connected scientific disciplines (Molnár et al., 2020). For example, the impact of introduced invasive pathogen micro-organisms on the dynamics of natural ecosystems may be overlooked unless ecologists also interpret and integrate the results of pathology and forestry. Consequently, misconclusions may arise if the real impact of the pathogen is underestimated.

Scientific misconclusions and knowledge gaps have potentially serious consequences for conservation management (cf. Molnár et al., 2020), especially in cases concerning the loss of keystone species (Mitchell et al., 2019). A good example is the case of pedunculate oak (*Quercus robur*), which is not only a culturally and economically significant forest tree species, but also hosts a great amount of biodiversity (Mölder et al., 2019). It has been shown that 2,300 species are associated with *Q. petraea/robur* within the U.K. alone, of which 326 species are obligate associates (Mitchell et al., 2019). Losing keystone species such as pedunculate oak may have a serious impact on associated biodiversity and ecosystem functioning (Collinge et al., 2008; Mitchell et al., 2019). The future of European (near-)natural pedunculate oak forests looks bleak, due to the decline of mature/old trees in stands (Thomas et al., 2002) and unclear reasons for the lack of natural regeneration (see Sections 1.2 and 6; Bobiec et al., 2018). Based on a thorough review of recent and historical ecological, pathological and forestry literature, in this paper we posit a new hypothesis, the 'pathogen mildew hypothesis', about the natural regeneration failure of pedunculate oak forest by bringing an invasive alien microfungus into the debate.

The pathogen powdery mildew (the most common species in Europe are *Erysiphe alphitoides* and *E. quercicola*, hereafter PPM) of oak species was first reported in France in 1907 (Hariot, 1907) and subsequently spread rapidly across Europe (Kövessi, 1910; Woodward et al., 1929). Despite the rapid accumulation of knowledge among foresters in the first years after its discovery, and the persistent impact of this fungus within oak woodlands, its possible long-term consequences for (near-)natural oak forest ecosystems have not been adequately addressed in field studies dealing with forest ecology and conservation biology. Among the known studies to date on the impacts of powdery mildew on pedunculate oak regeneration success, the one with the longest timespan lasted only three years (Pap et al., 2012).

1.2. A century-old failure of natural regeneration of pedunculate oak

Pedunculate oak (*Quercus robur*) is a dominant forest-forming species throughout Europe (Eaton et al., 2016), whose present dominance in (near-)natural stands is considered to be challenged in future stands (Bobiec et al., 2018). The two main concerns for forest and conservation management are oak decline (Thomas et al., 2002) and limited advanced natural regeneration of the species (individuals above 150 cm in height and thinner than 10 cm diameter at breast height) within the forest domain (Bobiec et al., 2018; Mölder et al., 2019). We focus on the second concern, while the decline of mature pedunculate oak falls outside the scope of this paper.

The main environmental and biological factors impeding natural regeneration of pedunculate oak within the forest domain are widely debated. Two basic hypotheses exist in ecological and forestry literature (Birks, 2005), which explain the natural stand and regeneration dynamics of oak forests. According to the 'closed-forest' hypothesis (Watt, 1919; Watt, 1947), pedunculate oak is expected to regenerate naturally under its own canopy (at least to some extent) and in natural canopy gaps, but various factors were found to hinder it, for example, light availability (Watt, 1919; Von Lüpke, 1998; Čater and Batič, 2006), game browsing (Watt, 1919; Petersson et al., 2020), soil water content (Čater and Batič, 2006), competitive species (e.g. *Rubus* spp., *Pteridium aquilinum*, *Carpinus betulus*, *Fagus sylvatica*) (Harmer and Morgan, 2007; Janik et al., 2008; Jensen and Löf, 2017), and most frequently the synergistic action between damaging agents (Vadas, 1917; Watt, 1919; Bobiec et al., 2018). These factors are believed to have been driven by intensified forest management, river regulation and drainage, and increasing game populations in the 20th century.

In the second, 'wood-pasture' hypothesis, researchers question whether canopy gaps are the main site for natural regeneration (Vera, 2000; Bakker et al., 2004). Evidence (Vera, 2000; Bobiec et al., 2018) shows successful cases of regeneration in habitats having a more open structure (e.g. abandoned pastures, wood-pastures, meadows, orchards, forest edges and windthrow areas). Several authors suggest that the regeneration strategy of pedunculate oak is misinterpreted and that niches for natural regeneration must be outside present closed forests (Vera, 2000; Bakker et al., 2004; Bobiec et al., 2018). It is hypothesized that pedunculate oak-dominated forests were historically kept relatively open by traditional land-use practices, such as forest grazing, selective cutting, and low-intensity fires (Kirby and Watkins, 2015; Petersson et al., 2020). There was consequently sufficient light for oak to regenerate naturally (Vera, 2000; Bakker et al., 2004; Kirby and Watkins, 2015).

Despite the proliferation of ecological and forestry studies, as well as the numerous hypotheses of forest dynamics built on the accumulated knowledge, none provides a coherent explanation why pedunculate oak fails to produce advanced natural regeneration under the moderate shade of its own canopy throughout the whole distribution range. At the same time, these hypotheses drive the thinking of researchers and the setting of experiments.

This paper outlines the authors' perspectives on the causal agents of pedunculate oak regeneration failure and misconclusions in the prevailing hypotheses. We (i) highlight knowledge gaps in the prevailing hypotheses, (ii) proposing a complementary novel forest ecological hypothesis (the 'pathogen mildew hypothesis') explaining the failure of natural regeneration of pedunculate oak. We postulate that PPM could be a much stronger driver of limited regeneration success than previously thought, thus warranting greater attention by field ecologists, nature conservationists, and foresters dealing with close-to-nature forestry based on spontaneous regeneration (Mölder et al., 2019). In general, we stress the need for a more complex and multidisciplinary understanding of pedunculate oak forest dynamics.

2. Methods

Analysed articles were collected using the snowball method, completed with systematic database searches. First, we identified the key literature on pathology, pedunculate oak forest structure and dynamics, regeneration failure of pedunculate oak, and oak powdery mildew, from the authors' personal collections. Afterwards, the reference lists and citations of these publications were checked in order to identify further papers containing information on (i) factors influencing the regeneration dynamics of pedunculate oak seedlings and saplings, and (ii) the impacts of pathogen powdery mildew (PPM) on spontaneous regeneration and pedunculate oak forest dynamics. Additionally, articles published in Hungarian about PPM impacts were searched using the archive of the Forestry Journal (http://www.epa.hu/01100/01192 – published since 1862) and the Forestry Experiments Journal (https://adtplus.arcanum.hu/hu/collection/BME_ErdeszetiKiserletek/ – published between 1900 and 1932). In this search we used the following broad search string: 'oak' AND 'mildew' (in Hungarian). We retained only publications that contained information on pedunculate oak and its natural regeneration, in the context of mildew infestation. Historical forestry literature from different parts of the Carpathian Basin about the structure and natural regeneration dynamics of pedunculate oak forests before the introduction of PPM was identified in a similar manner to the above-mentioned sources.

The same broad search string was repeated in the Web of Science, Scopus and Google Scholar Databases. Findings were refined based on the title and abstract, to identify publications focusing on the ecology and dynamics of pedunculate oak forests, their natural regeneration, and the influence of oak powdery mildew, including its pathology, taxonomy and distribution. The reference lists and citations of these publications were also checked to identify further relevant papers. Database searches were conducted between February and March 2020. Altogether, we collected and analysed 254 papers and books in English, Hungarian, French, German, Romanian and Polish languages. All these publications were analysed by at least one of the authors. As the identified studies covered over 130 years of publication history, with major differences in their methodology, we felt that, in comparison with a more systematic method, such an approach and overview would pose a lower risk of losing information and ecological meaning.

3. The origin and emergence of PPM

Before the first mention of PPM in 1907, the occurrence of other (likely native) species of oak mildew (e.g. *Phyllactinia roboris*, *Microsphaera penicillata* f. *quercus*, *Erysiphe pyrenaica*) was reported in Europe (Woodward et al., 1929; Desprez-Loustau et al., 2019). Each species was relatively inconspicuous and never regarded as significantly damaging (Kövessi, 1910; Lonsdale, 2015; Desprez-Loustau et al., 2019). *Erysiphe alphitoides* (Griffon & Maubl.) U. Braun & S. Takam. (Braun and Takamatsu, 2000) was first proposed as a new species by Griffon and Maublanc (1912). Yet, it is not known why the alien oak mildew multi-species complex is more detrimental to oak seedlings than native species.

Recent molecular taxonomical studies provide new insight into the identity and behaviour of PPM in Europe (Fig. 2). The origin of the species causing the infection was clarified (Desprez-Loustau et al., 2017), and the factors influencing the severity of the epidemic were identified (Marçais et al., 2017), together with the geographical distribution of different PPM species and their evolutionary trajectories (Mougou-Hamdane et al., 2010; Desprez-Loustau et al., 2017, 2018).

There are two competing hypotheses regarding the origin of PPM. Morphological and fungal DNA studies show that PPM includes more than one species (e.g. *E. alphitoides*, *E. quercicola*, *E. hypophylla*), all of which possibly originated from host shifts of tropical *Erysiphe* species introduced to Europe through infected exotic host plants (probably mango; Raymond, 1927; Boesewinkel, 1980; Mougou et al., 2008; Mougou-Hamdane et al., 2010; Desprez-Loustau et al., 2017). The second explanation, that a virulent genotype arose from a local species (Kövessi, 1910; Ayres, 1976), is considered less probable (Desprez-Loustau et al., 2011, 2017). Regardless of which is right, severe outbreaks of disease throughout Europe since the early 20th century are attributed to a 'new' oak mildew species (or species complex). Among them, *E. alphitoides* is the most dominant at European scale and often appears to co-occur with *E. quercicola* (Mougou-Hamdane et al., 2010; Desprez-Loustau et al., 2017).

4. Impact of PPM on the development of oak seedlings

In the first years after germination, pedunculate oak seedlings invest energy in developing a strong taproot rather than the vertical growth of the shoot. Vertical growth is minimal (ca. 15–30 cm) during this developmental phase, and light availability is not a crucial factor. Strong vertical growth and significant light demand start 7–10 years after germination. Under favourable conditions, several shoot flushes are produced during a growing season, which can significantly advance the elongation of the sapling (Eaton et al., 2016).

PPM species infect only young, developing leaves and shoots. Thus, seedlings and saplings are susceptible to infection in spring and again in early summer, when second or third so-called 'lammas' growth develops, whereas the first growth usually escapes infection (Kövessi, 1910; Woodward et al., 1929; Hajji et al., 2009; Marçais and Desprez-Loustau, 2014).

Epidermal cells are colonized by the spores or the mycelium of PPM (Kövessi, 1910; Lonsdale, 2015). The mycelium can survive the winter in axillary buds, subsequently colonizing new shoots that develop from these buds the following spring (Marçais et al., 2009; Lonsdale, 2015). However, the main agents of infection are the spores produced by the chasmothecia (the sexual part), which survive the winter in cracks in the bark of mature trees and on the previous year's fallen leaves (Marçais et al., 2009).

After infection of young, developing leaves with PPM, various damage types were reported: (1) Severe foliar infection can lead to seedling mortality, especially when coinciding with other damage (e.g. insect defoliation, game browsing or late frost) (Vadas, 1917; Woodward et al., 1929; Lonsdale, 2015); (2) Severe shoot infection can diminish cold resistance by altering bud hardening and dormancy (Kövessi, 1910; Marçais and Desprez-Loustau, 2014); (3) PPM may parasitize nutrients from the living cells of their hosts (Hewitt and Ayres, 1976; Desprez-Loustau et al., 2014). Moreover, Lonsdale (2015) highlighted in his review that heavy infection of leaves by *E. alphitoides* can lead to a 50–70% reduction in the net assimilation rate. The direct consequence of altered nutrient uptake by PPM and the reduced carbon assimilation may lead to a significant decrease in both vertical and radial growth in seedlings (Woodward et al., 1929; Igmándy, 1972; Desprez-Loustau et al., 2014; Bert et al., 2016). Vertical growth correlates negatively with the level of infection and is significantly decreased (about 40%) compared to seedlings treated with fungicide (Igmándy, 1972); (4) Although saplings can produce up to 4–5 new shoots a year under favourable light conditions, PPM infection is more severe in these shoots, which renders them unable to compensate for diminished vertical growth (Roth, 1915; Lonsdale, 2015; Desprez-Loustau et al., 2019). Exposure to extra light and a warmer and drier microclimate (e.g. conditions in gaps and natural openings in forest-steppe forests) favour the spread of PPM over the assimilation and vertical growth of oak seedlings (Roth, 1915; Lonsdale, 2015; Newsham et al., 2000). Thus, the growth potential of the seedling is compromised during this crucial growing period.; (5) Leaf lifespan and shade-tolerance are significantly reduced by severe infection in the shade of the parent tree (Hajji et al., 2009); (6) PPM infection in young leaves results in increased transpiration and water loss (Hewitt and Ayres, 1975). Infected seedlings and saplings may thus be more light-demanding, less drought-tolerant and less competitive with the surrounding vegetation (Hajji et al., 2009; Marçais and Desprez-Loustau, 2014; Lonsdale, 2015). Considering all these impacts, PPM can seriously impede the natural regeneration of pedunculate oak, especially in shade and when competition is high (Fig. 1).

5. A knowledge gap between unexpectedly isolated disciplines

Despite the acknowledgement in taxonomical and forestry literature that this fungus most probably has a tropical origin, becoming an oak specialist in Europe in the 1900s, according to our field experience in Central and Eastern Europe, many ecologists and foresters rarely realize the alien invasive character of PPM as a key factor influencing spontaneous regeneration. Most ecological studies on oak forest dynamics and natural regeneration in Europe also fail to mention it as a possible factor influencing growth rate, mortality and regeneration success of oak individuals (e.g. Harmer and Morgan, 2007; Petersson et al., 2020). Meanwhile, in many parts of Europe, fungicides have been applied for decades to control PPM (e.g. Hobza, 2007; Pap et al., 2012; Lonsdale, 2015). While foresters realized the impact of PPM early on (e.g. decreased growth intensity of seedlings) (Fig. 2, Kövessi, 1910; Roth, 1915; Vadas, 1916), they have focused on nurseries, plantations, oak coppices, shelterwood systems and on the decline of mature trees and stands (Vadas, 1917; Woodward et al., 1929; Igmándy, 1972; Thomas et al., 2002; Pap et al., 2012; Dillen et al., 2016; Tkach et al., 2020). As

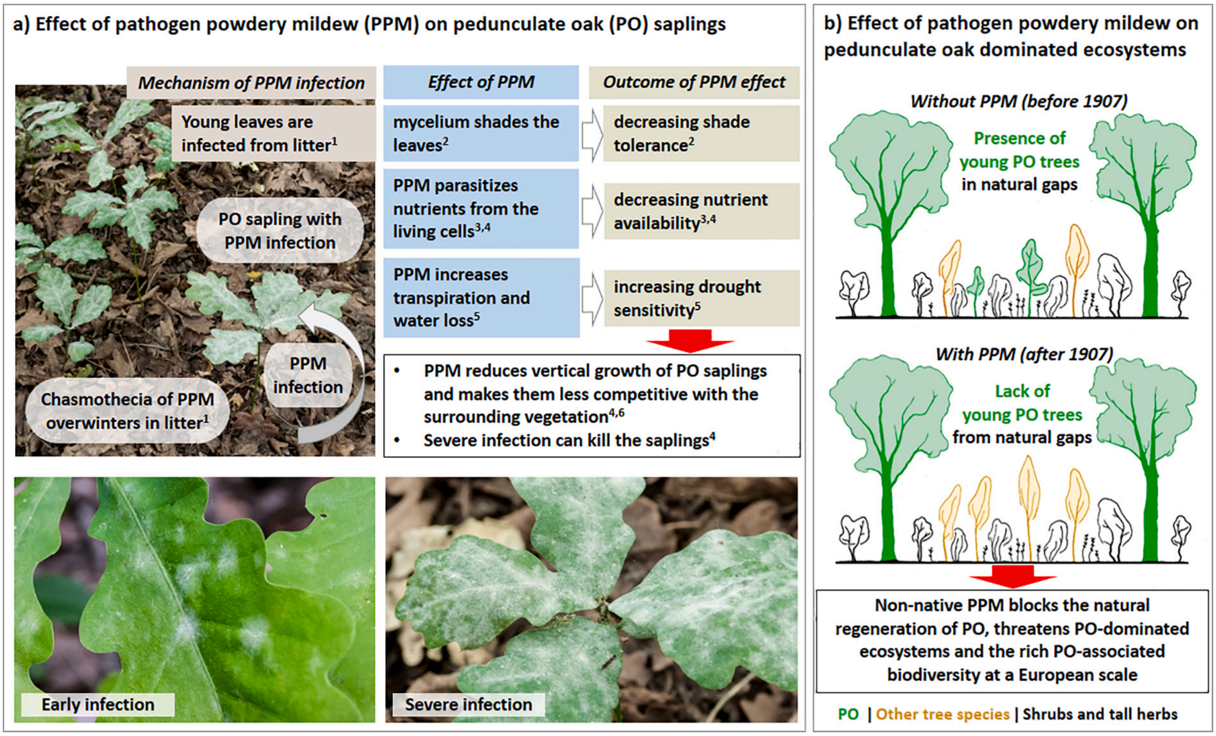

Fig. 1. The effects of pathogen powdery mildew (PPM) on pedunculate oak (PO) saplings (a) and on the dynamics and diversity of (near-)natural PO ecosystems (b). References: [1]Marçais et al., 2009; [2]Hajji et al., 2009; [3]Hewitt and Ayres, 1976; [4]Desprez-Loustau et al., 2014; [5]Hewitt and Ayres, 1975; [6]Igmándy, 1972.

silviculture and regeneration techniques of pedunculate oak in Europe have been dominated by rapid shelterwood cutting and clearfelling in the past 150 years (Kirby and Watkins, 2015), the forestry sector has largely ignored the natural regeneration dynamics of pedunculate oak in canopy gaps and under its own canopy. Consequently, the impacts of PPM on regeneration dynamics in (near-)natural forests fell beyond the scope of forestry studies. Naturally germinated seedlings have long been used in the shelterwood system, although their dynamics fundamentally differs from the regeneration occurring in natural systems due to intensive interventions aimed at enhancing the competitiveness of oak seedlings/saplings.

Few leading forest ecologists discuss the potential impact of PPM on the dynamics and regeneration of pedunculate oak. Shortly after the introduction of PPM, Watt (1919) warned foresters to take PPM into consideration when dealing with natural oak regeneration, but did not highlight the exotic origin of PPM, as evidence for this was missing at that time. Rackham (1986; see also Peterken, 2001 and Rackham, 2006) suggests that PPM may play a role in the poor shade-tolerance and regeneration of young oak saplings under canopy. '*Oak mildew may not be the trivial disease it seems. Oaks have mysteriously lost the ability, which they had until the nineteenth century, to grow easily from seed in existing wood.* (…) *The critical change could well be the introduction of mildew, which may have deprived oak of the power of surviving in shade.*' (Rackham, 1986, p. 59). Rackham's idea failed to take root in the general discussion on regeneration failure of pedunculate oak, and was even overlooked (Vera, 2000). Later, Peterken (2001) criticized Vera for ignoring Rackham's (1986) idea on PPM. None of these authors, however, provided a detailed, well-elaborated hypothesis on how PPM can induce regeneration failure of pedunculate oak and alter natural forest dynamics.

The vast majority of pathological and forestry studies focus on host-pathogen interaction, especially the impact of PPM on the growth pattern, health condition and assimilation activity of mature and young trees (Igmándy, 1972; Hewitt and Ayres, 1975; Marçais and Desprez-Loustau, 2014). A general conclusion is that natural oak regeneration is usually very dense and that regeneration success is seldom impeded by the pathogen (Marçais and Desprez-Loustau, 2014). However, these studies were carried out in laboratories, plantations, and rotation systems applying natural regeneration (e.g. shelterwood cutting). The environmental conditions in these habitats (e.g. higher seedling abundance, increased light availability and reduced competition through the removal of surrounding vegetation) differ considerably from those in closed canopy (near-)natural forests and in their gaps. The scope of these studies excluded the consequences of PPM infection on the natural forest dynamics and regeneration of pedunculate oak-dominated forests. Moreover, not a single study has been conducted in (near-)natural forests, in a well-designed complex experiment focusing on investigating the interacting impact of PPM and other factors (e.g. soil water content, browsing, light availability) on natural regeneration dynamics.

Although some ecologists have recently highlighted the impact of PPM on the growth rate and health of pedunculate oak juveniles (Palmer et al., 2004; Dillen et al., 2016; Bobiec et al., 2018), they did not integrate the impacts of PPM into the two main forest dynamics hypotheses. The 'closed-forest' and 'wood-pasture' hypotheses were posited on observations and research conducted after the fungus was introduced, so the dynamics studied may already have been substantially impacted by PPM. The reason why the impacts of PPM on pedunculate oak have been overlooked may be that many studies do not differentiate between *Quercus robur* and *Quercus petraea* (Palmer et al., 2004; Götmark et al., 2005; Bobiec et al., 2018; De Lombaerde et al., 2019; Mölder et al., 2019; Petersson et al., 2020). Pedunculate oak is assumed to be less shade tolerant (Ellenberg et al., 2001) and more susceptible to PPM than *Q. petraea* (e.g. Kövessi, 1910; Leibundgut, 1969; Ayres, 1976). The distribution area of both oak species overlaps in most parts of Europe (Eaton et al., 2016). Moreover, they often have hybrids in the same stands. It is therefore challenging to make a clear distinction between the responses of the two species to PPM.

Despite a significant body of research, knowledge gaps exist concerning: i) the impact of PPM on the natural regeneration of pedunculate oak in its (near-)natural habitats, with particular regard to growth loss, light demand, and competition with other species, and ii) the success of

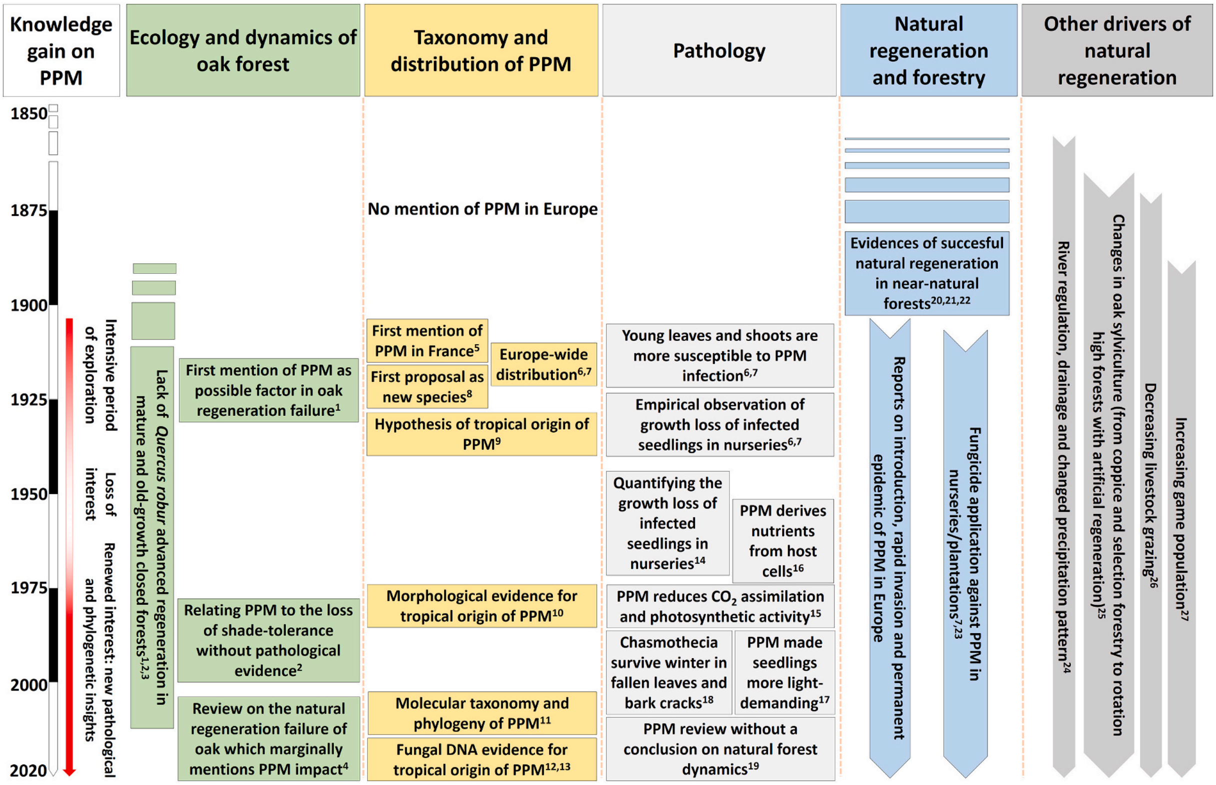

Fig. 2. The history of knowledge gain on the relationship between the pathogen oak powdery mildew (PPM) and its impact on pedunculate oak regeneration in Europe. The evidence was grouped into the main categories of scientific disciplines, marked with coloured boxes, according to their year of publication. The red arrow shows the intensity of scientific interest (based on Desprez-Loustau et al., 2019). Grey arrows in the rightmost column indicate other socio-ecological drivers regarded as important in the reviewed literature in blocking natural regeneration of pedunculate oak. The introduction of PPM coincides with the change of other strong landscape-scale drivers of natural regeneration. The figure shows that highly specialized results from different disciplines addressing PPM have not been integrated into the ecological understanding of the natural regeneration failure of pedunculate oak. Consequently, in the main hypotheses about natural oak forest dynamics and regeneration (Watt, 1919; Rackham, 1986; Vera, 2000; Bobiec et al., 2018) the impact of PPM has not been given the attention warranted by its seriousness. References in the coloured boxes: [1]Watt, 1919; [2]Rackham, 1986; [3]Bobiec, 2012; [4]Bobiec et al., 2018; [5]Hariot, 1907; [6]Kövessi, 1910; [7]Woodward et al., 1929; [8]Griffon and Maublanc, 1912; [9]Raymond, 1927; [10]Boesewinkel, 1980; [11]Braun and Takamatsu, 2000; [12]Takamatsu et al., 2007; [13]Mougou et al., 2008; [14]Igmándy, 1972; [15]Hewitt and Ayres, 1975; [16]Hewitt and Ayres, 1976; [17]Hajji et al., 2009; [18]Marçais et al., 2009; [19]Lonsdale, 2015; [20]Fekete, 1890; [21]Kozarac, 1895; [22]Kuzma, 1910; [23]Vadas, 1917; [24]Čater and Batič, 2006; [25]Kirby and Watkins, 2015; [26]Vera, 2000; [27]Milner et al., 2006. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

regeneration in canopy gaps and under its own canopy before the introduction of PPM. The main reason for these knowledge gaps may be that researchers from different scientific fields (e.g. conservation, forestry, ecology, forest pathology) conducted isolated and specialized studies. Additionally, it is difficult to find reliable and relevant data on forest conditions before the introduction of PPM.

6. Regeneration niches of pedunculate oak in forest habitats before and after the invasion of PPM

According to both recent and historical literature (Fekete, 1888; Roth, 1935; Bobiec et al., 2018; Mölder et al., 2019), advanced regeneration of pedunculate oak under its closed canopy cover is scarce, while its natural regeneration niches in forest habitats are: young closed canopy forests after clear-cuts, long-lasting canopy gaps, degraded deciduous forests, where oaks have a competitive advantage, shelterwood cutting areas, and closed pine, spruce and poplar plantations. Even in years with good masting and germination rates, seedlings grow slowly under strong shade and die within 3–5 years (Fekete, 1888; Von Lüpke, 1998). The most frequently reported drivers of death are shade casting by the overstorey, competition with understorey species, and game browsing (Götmark et al., 2005; De Lombaerde et al., 2019). Opening up the canopy is recommended as essential for saplings to develop further. However, the quantity of light needed by pedunculate oak saplings is unknown, as is its lifespan under limited light without PPM infection.

According to historical sources, in large gaps and clearcut areas oak saplings can survive in the shade of competitive species (e.g. *Fraxinus angustifolia*), outgrowing them after 15–30 years. '*After four years, the clearcut areas were left undisturbed, allowing rich vegetation to regenerate everywhere, albeit with few oaks. (…) When the dense young forest reached 10–15 years of age, oak trees grew in search of light and air, reaching the upper canopy by 20–25 years. (…) By the age of 30, the oak trees had surpassed other tree species and begun thickening their trunks.*' (Kuzma, 1910). This highlights the fact that moderate shade alone was not a factor limiting the development of advanced regeneration before the introduction of PPM.

Evidence exists that sufficient light (15–20% of full light, Von Lüpke, 1998) for survival and minimal growth of pedunculate oak saplings may be available even in relatively small canopy gaps (at least 17–20 m diameter), beneath the open canopy of deciduous forests or closed coniferous stands (Von Lüpke, 1998). Long-lasting canopy gaps are rare, however, even in unmanaged mature stands (Bobiec et al., 2018; Demeter et al., 2020). Gaps are more frequent in remnant old-growth pedunculate oak-dominated forests in the temperate forest zone and as natural openings of dry oak forests in the forest-steppe zone. Advanced regeneration is also scarce in these cases as fast-growing, shade-tolerant species (e.g. *Fagus sylvatica*, *Carpinus betulus*, *Acer campestre*) are strong competitors hindering the successful regeneration of pedunculate oak-dominated stands (Roth, 1935; Bobiec, 2012; Janik et al., 2008; Demeter et al., 2020). Higher game pressure in the gaps and natural openings may further jeopardize regeneration success (Götmark et al., 2005). However, these authors do not address whether PPM decreases the growth intensity of pedunculate oak seedlings while competition with and suppression by shade-tolerant species is strong.

Historically, irregular selective logging was successfully applied in lowland pedunculate oak-dominated forests in the Carpathian Basin. Before the introduction of PPM, a high number of established saplings could regenerate in the gaps created by traditional selective logging, provided stands were protected from grazing and browsing (Fekete, 1888). '*Forests where selective logging takes place irregularly but not excessively*, (…) *if they are not heavily grazed, assumed the form of primeval forests, or to be more precise, of selectively logged forests of shade-tolerant trees, containing regrowths of very mixed ages. Among these, for each group and each patch, 20-35-year-old oak saplings are managed by removing those trees that are older and less valuable* (…)' (Fekete, 1890). Burgsdorf (1810) also reported that pedunculate oak saplings developed well in the gaps of lowland oak-hornbeam forests in Poland. '*The best distance between parent trees is when a crown of one tree is not further than 18 feet from another oak's crown.*' (Burgsdorf, 1810).

Nowadays, selection forestry with natural regeneration is difficult or even impossible to implement in pedunculate oak forests, even under low grazing pressure (Dobrowolska, 2008; Mölder et al., 2019; Demeter et al., 2020). The canopy must be radically opened up to provide sufficient light for optimal height growth (> 0.2 ha, Von Lüpke, 1998, Čater and Batič, 2006). As PPM infection is more severe in seedlings exposed to sufficient light, the growing conditions of pedunculate oak seedlings are more unfavourable than before the introduction of PPM.

Shelterwood cutting is considered one of the most efficient and reliable ways for natural pedunculate oak regeneration (Dobrowolska, 2008; Mölder et al., 2019; Tkach et al., 2020). However, additional light also enhances the growth of competing herbaceous and woody vegetation (Löf et al., 1998; Harmer and Morgan, 2007). Thus, further site preparation measures (e.g. soil preparation, herbicides and fungicides) for ground vegetation and PPM control must be applied (Hobza, 2007; Pap et al., 2012).

Historical studies suggest that successful oak regeneration was easily achievable without such measures before the introduction of PPM. Only admixed tree species were removed and grazing was prohibited. '*In treasury-owned forests, the exclusive practice is natural regeneration, which is justified nowhere more than here* [*in Slavonia*]. (…) *Fortunately, based on local experience, pedunculate oak tends to reach, and then surpass the height of elm and ash within approximately thirty years* (…)' (Fekete, 1890). '*In these patches of young forest, while ash trees measured 3–5 metres in height, oak trees, despite perfect health, reached only 0.6–1.5 metres.*' (Kozarac, 1895).

Recent studies suggest that pedunculate oak can regenerate in conditions of moderate to heavy shade (Von Lüpke, 1998); e.g. in relatively closed, mixed Scots pine-oak (Von Lüpke, 1998; Gerzabek et al., 2017; Woziwoda et al., 2019) and Norway spruce-oak forests (Bobiec, 2012; Smit et al., 2012), and in closed-canopy poplar plantations (Lust et al., 2001; Minotta and Degioanni, 2011). Von Lüpke (1998) suggests that underneath such stands, pedunculate oak meets favourable light conditions (at least 30% of full light) for optimal growth. However, we argue that besides light conditions, the distance from mature oak/parental trees is another important factor. Several authors suggest that the probability of mildew infection and the severity of damage are lower in the case of oak saplings growing away from the parental tree canopy (Palmer et al., 2004; Dillen et al., 2016). Other studies suggest that seedlings dispersed away from their mother tree are significantly more likely to survive than non-dispersed seedlings (Harmer and Morgan, 2007; Gerzabek et al., 2017; Woziwoda et al., 2019). A possible explanation for this is that the chasmothecia of PPM overwinter in fallen leaves and in cracks in the bark of mature oak trees, from where the seedlings are infected every spring. We therefore expect pedunculate oak to have a better survival rate and height growth where mature oak trees are absent or scarce.

In summary, taking PPM impact on vertical growth into account, we argue that pedunculate oak seedlings may be more competitive with other tree species and would escape game browsing in a shorter period of time without PPM (similarly to *Quercus petraea*, *Q. cerris*, and *Fraxinus angustifolia*). Accordingly, natural regeneration of pedunculate oak would be more successful in canopy gaps and under the shelterwood system. Furthermore, regeneration is expected to be more successful further from infested parental trees, where the spore bank is smaller. All the above suggests that greater attention should be paid to PPM in understanding the failure of pedunculate oak regeneration in Europe.

It might appear oversimplified to ascribe the regeneration failure of pedunculate oak to a single driver (e.g. PPM, in our case). However, the interacting drivers emphasized in other hypotheses (e.g. increased browsing pressure, land-use changes and decreasing available soil water) seem unable to provide a coherent explanation throughout the whole distribution range of pedunculate oak. For example, in a regularly flooded old-growth and selection forest in Ukraine (Demeter et al., 2020), natural regeneration of oak is still absent despite the fact that game density is very low and groundwater availability has decreased little. However, as cited above (Fekete, 1890), before the introduction of PPM, there was 'enough' advanced regeneration in this forest.

In other cases, low water availability may have a significant impact on the shade tolerance of pedunculate oak (Sánchez-Gómez et al., 2006) and may also be a key factor triggering the decline of young oak seedlings (Čater and Batič, 2006). At the same time, interactions between other native and non-native fungal pathogens (e.g. root rot basidiomycetes or *Phytophthora* species) have also been hypothesized as possible factors in pedunculate oak seedling mortality (Marçais et al., 2011).

Whatever combinations of formerly recognized drivers of spontaneous regeneration exist in a European landscape, our review suggests that one additional key driver must be added since the beginning of the 20th century. Together with high ungulate browsing pressure, climate change (resulting in rising temperatures and altered precipitation regimes), and competitive pressure for soil water, PPM infection may be the fourth, yet unacknowledged member of an essential quartet contributing to the regeneration failure of pedunculate oak.

7. Outlook and practical implications

We have shown that an invasive alien microfungus (the alien pathogen oak powdery mildew) may have an impact on the natural regeneration of a keystone tree species of a threatened forest ecosystem that is higher than previously acknowledged, therefore ecologists and conservationists need to focus on it more.

Our newly proposed 'pathogen mildew hypothesis' argues that, as previously suggested by Rackham (1986, 2006), PPM makes pedunculate oak saplings more light-demanding and less competitive with the surrounding vegetation (Figs. 1, 2). Therefore, despite some studies mentioning its potential role, PPM may be a key factor, hitherto overlooked by ecologists and nature conservationists, responsible for blocking the natural regeneration of pedunculate oak under its own canopy throughout Europe. While much is known about the impact of PPM in nurseries and managed forests, its impact on natural dynamics is poorly understood.

Further research is required into the impact of PPM on (near-)natural forest stands, with particular focus on these research gaps:

- Height growth and natural dynamics of saplings in forest gaps with and without PPM infection,
- Differentiation between the impact of grazing/browsing, competition with surrounding vegetation, and PPM under closed canopy and in gaps of near natural forests,
- Time (in years) saplings can survive strong shade under mature oak trees (under closed pedunculate oak canopy) with and without PPM.

If the 'pathogen mildew hypothesis' is proven by field experiments, it will have serious consequences for forest ecology, invasion ecology, nature conservation management, and close-to-nature forest management. Even without rigorous testing, the 'pathogen mildew hypothesis' seems to have high explanatory power for the failure of natural pedunculate oak regeneration in (near-)natural forests. The proposed 'pathogen mildew hypothesis' complements both the 'closed-forest' and the 'wood-pasture' hypotheses. The three perspectives together may better describe the recent dynamics of (near-)natural pedunculate oak forest. More generally, ecologists should devote greater attention to the non-native nature of fungal and other microbial pathogens as key drivers of vegetation change in natural ecosystems.

Regarding practical nature conservation and close-to-nature forestry, management plans that take the PPM impact into consideration are needed for pedunculate oak-dominated forests. Close-to-nature silviculture that combines selective cutting and small canopy gaps for the regeneration of pedunculate oak-dominated forests is sporadic and regarded as complicated, due to the high light demand of young oaks and competition by shade-tolerant co-occurring tree species (Mölder et al., 2019). Our conclusions suggest that close-to-nature silviculture can be applied to lowland pedunculate oak forests if PPM is not present. This assumption is supported by historical forestry literature originating from the time before and just after the introduction of PPM. Selection forestry and different kinds of shelterwood systems were recommended as best practices for pedunculate oak forests in the 19th century (Fekete, 1888, 1890; Kozarac, 1895). Since PPM became present throughout Europe, with regard to long-term protection, the selection of resistant variants of pedunculate oak may be one of the key tasks for forestry (Leibundgut, 1969). Another proposed effective measure is to increase the diversity of admixed tree species in patches of regeneration (Vadas, 1917; Dillen et al., 2016; Field et al., 2020).

The decline of old trees and the lack of natural regeneration of pedunculate oak raise some serious questions. How will the composition and structure of (near-)natural temperate hardwood forests change in the future? Which species will occupy the niche of pedunculate oak? How will changes in composition impact the associated diversity? Answering these questions should be of high priority both for nature conservation and forest management. Many studies suggest that pedunculate oak will play a marginal role in existing (near-)natural oak dominated forests in the future (Janik et al., 2008; Bobiec, 2012; Demeter et al., 2020). Therefore, establishing native tree species (e.g. *Fraxinus excelsior*, *Tilia cordata*, *Carpinus betulus*) has been recommended to mitigate the impact of oak decline on associated biodiversity (Mitchell et al., 2019). The only sustainable option to conserve oak-associated diversity seems to be a mixture of species because none of the studied tree species supported a high enough amount of oak-associated species (Mitchell et al., 2019).

Climate change may further impact on the success of natural regeneration of pedunculate oak by favouring PPM spread and infestation. Firstly, mild winters may favour good overwintering of PPM (Marçais et al., 2017). Secondly, direct competition with other oak species having greater tolerance to drought and PPM (e.g. *Q. petraea* and *Q. cerris*) may further decrease the survival of pedunculate oak seedlings. Simultaneously, canopy damage to young and canopy trees will increase, due to more frequent defoliation by insect herbivores (Thomas et al., 2002). Frequent and/or severe defoliation of canopy trees, combined with drought, alters the microclimate and light conditions in the understorey (Csóka et al., 2015), which may favour the reproduction and spread of PPM. Extra light and the severe defoliation of young trees may lead to the development of more 'lammas shoots', which are more susceptible to PPM (Marçais and Desprez-Loustau, 2014). More infected lammas shoots will result in an increased 'spore bank' of PPM, which may further decrease the probability of seedlings escaping PPM infestation.

In conclusion, pedunculate oak and its associated diversity face an uncertain future with a high complexity of drivers. Our review shows that cooperation between foresters, nature conservation rangers, pathologists and forest ecologists may play a crucial role in improving understanding, management and protection of pedunculate oak-dominated forests, and in safeguarding the ability of this valuable ecosystem to regenerate naturally, despite PPM.

Data availability statement

Data have not been archived because this article does not use data.

CRediT authorship contribution statement

LD, ÁM and ZsM conceived the idea, LD and ZsM led the writing of the manuscript. All co-authors contributed to developing conceptual ideas and writing the manuscript. All authors gave their approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to Marcin Andrzej Kotowski for providing historical literature data on PPM and natural regeneration of pedunculate oak from modern-day Poland and Ukraine, and for Steve Kane for English editing. This research was supported by the National Research, Development and Innovation Office, Hungary [grant number NKFIH K 131837]. KÖ received further support from the Romanian Academy [grant number RO1567-IBB03/2020].

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