Powdery mildew of oak: a familiar sight with some hidden surprises

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A white, powdery covering of mildew on oak leaves is such a familiar sight that it could easily be dismissed as a normal occurrence across the UK and the rest of temperate Europe. The situation was, however, very different until the early years of the last century. Until then, powdery mildew of oak was rarely noticed in Europe, being caused by a few inconspicuous fungi and having apparently very little impact on the health of affected trees. The mildew that we know all too well today was first observed in 1907, initially in France. By 1909, it was being seen all over Europe and beyond.

Some experts of the day initially attributed the new outbreak of oak mildew to a mutation in one of the rare or inconspicuous oak mildew fungi that were already known in Europe. Their hypothesis was, however, disproved by French mycologists E. Griffon and A. Maublanc, who found that the new form of mildew was caused by a previously undescribed species, which they named *Microsphaera alphitoides* (now known as *Erisyphe alphitoides*). Evidently, this fungus had become newly established across Europe in a remarkably short time.

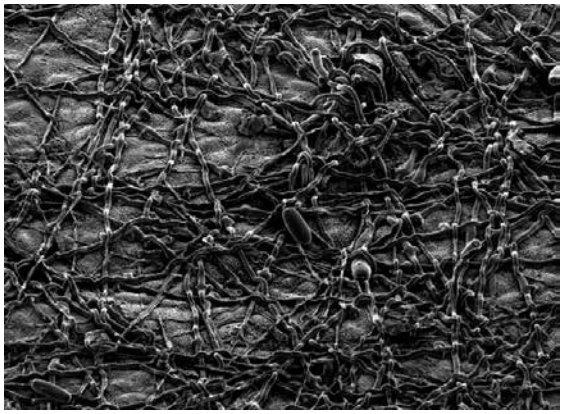
The rapid and often devastating emergence of alien invasive pests and pathogens, assisted by international trade, is now happening at an unprecedented rate. But the spread of such species from one continent to another is not entirely new, as the events of 1907–09 showed in the case of powdery mildew of oak. The mildew did not, however, prove to be as damaging as various other disease-causing fungi that human beings have unintentionally transported to new shores. Unlike the fungi that, for example, cause Dutch elm disease or blight of sweet chestnut, powdery mildew of oak has not wiped out entire tree populations.

After a few decades, oak mildew became regarded as part of the regularly occurring assemblage of leaf-inhabiting fungi, insects and other organisms, taking a share of a tree's reserves and perhaps reducing its growth rate but not seriously harming its general health. Although mildew has often been regarded as 'just another' disease of oak foliage, early observers of the disease in the UK expressed serious concern about its effects, especially on seedlings and coppice shoots, which were observed to become seriously stunted or distorted and often to die. The impact of mildew on the health of older trees was more difficult to assess but concern was expressed also about this.

General view of oak foliage, including whitish mildew-covered leaves (D. Lonsdale)

A lammas shoot of oak, showing a heavy covering of mildew. (D. Lonsdale)

After the 'double' droughts of 1975–76 and 1983–84, there were increasing signs of poor growth and, in some cases, crown dieback in oak trees across much of the UK. Eventually, the term 'oak decline' (now called chronic oak decline to distinguish it from acute oak decline) was applied to particular trees or tree populations that were showing certain signs of crown dieback, usually with a long-term trend of reduced expansion of stem diameter. Using increment cores, Brian Greig at Alice Holt Research Station found that this decline in diameter growth often dated back to the 1920s, not long after the trees concerned would have first been affected by the new form of powdery mildew.



Surface of oak leaf, showing the superficial mycelium of powdery mildew (scanning electron micrograph). (Image Syngenta, courtesy of Martin Woolner)

Other fungi were also suspected to be playing a part in chronic oak decline, such as honey fungus (*Armillaria* spp.) or the spindle-shank (*Collybia fusipes*). Also, there was *Phytophthora quercina*, a fungus-like organism that kills a proportion of the fine roots of oak trees. The latter was unrecognised until 1999, when it was discovered as a result of research on oak decline in continental Europe. But, as far as was known, these organisms had been living alongside oak trees long before the onset of the decline that had apparently begun in the 1920s. There was therefore reason to believe that one or more further factors were involved in chronic oak decline, with suspicion being focussed on pollution, changes in land use, climate change and the possible role of powdery mildew as a relative newcomer.

Oak mildew has come under increasing attention during the present century, partly because it often appears to affect trees more conspicuously than before. The mildew has always been particularly conspicuous on the leaves of 'lammas' shoots, which develop from a second and/or third flush of growth during the summer. Mildew is, however, now observed on a larger proportion of the foliage of affected trees. Also, since the 1990s, *E. alphitoides* has shown a change in its life cycle. It used to reproduce almost entirely by means of its asexual spores (conidia), which make up the white covering on the oak leaves, together with the superficial mycelium. Nowadays, the fungus also regularly forms its formerly rare sexual fruiting structures on oak leaves in the autumn. These blackish spherical structures, which can just be seen with the naked eye, are called chasmothecia (previously described as cleistothecia or perithecia). They persist on the fallen leaves into the following growing season, eventually releasing spores (ascospores), which can colonise oak leaves during the summer.

Enthusiasm for ancient and other veteran trees was burgeoning at about the time that oak mildew seemed to start affecting large trees more extensively. Before long, there were suspicions that mildew might be adversely affecting veteran oak trees, especially by heavily colonising the new shoots that grow after such trees

Close-up of mildew on oak leaves; the small, dark dots are immature sexual fruit bodies (chasmothecia). (Forestry Commission: Crown Copyright)

have been pruned with the intention of preventing life-shortening mechanical failure. There was concern also about the viability of new oak pollards, which were being created in order to maintain long-term continuity of the habitat and other values of veteran oak trees. These young oak trees might have been expected to tolerate pruning better than their veteran counterparts but there was concern about unexpected deaths amongst them after pollarding.

Early in 2013, I was commissioned by the City of London (through the good offices of Drs Helen Read and Jeremy Dagley) to prepare a review of research on powdery mildew of oak. This commission reflected the importance of old oak populations that are managed by the City at Epping Forest, Essex, together with others at Ashtead Common, Surrey and Burnham Beeches, Buckinghamshire. With kind permission from the City, I also published a paper, based on the resulting review, in the July 2015 edition of the *Arboricultural Journal*. The rest of the present article covers the main findings of the research articles that I have cited.

The research review indicated that, by regularly producing its sexual fruit bodies, *Erisyphe alphitoides* is now able to colonise an increased proportion of oak foliage. Research, mainly by Marie-Laure Desprez-Loustau, B. Marçais and their colleagues in France, has shown that the sexually produced spores of the fungus are released in summer, when they can add significantly to the likelihood of mildew becoming established on young, highly susceptible leaves. This boosts the build-up of the fungus, which would otherwise initiate infection only on a small proportion of shoots that develop from buds harbouring its overwintering mycelium.

Other research, also mainly by the same group in France, has revealed another possible reason for the apparent upsurge in the severity of oak mildew. This is the presence of another species of *Erisyphe*, known as *Erisyphe quercicola*. In the field, it looks the same as *E. alphitoides*, except that it has never been found to form sexual fruit bodies (chasmothecia) anywhere in Europe. These structures have, however, been found in a subtropical region of southern Japan, where the disease affects Ubame oak (*Quercus phillyraeoides*). The chasmothecia of the two mildews can be differentiated under a microscope, as shown by S. Takamatsu and co-workers, but the absence of chasmothecia of *E. quercicola* in Europe makes it necessary to use DNA-based methods to separate the species.

The reason why *E. quercicola* may be adding to the severity of oak mildew is that the two species tend to be at their most active in different months of the growing season, at least in France, thus potentially releasing large numbers of spores over a longer period than would be the case if only *E. alphitoides* were present. It is not yet known for certain whether *E. quercicola* occurs in the UK, as well as in France, but this seems highly likely, given the very rapid spread of the similar *E. alphitoides* across Europe in 1907–09.

As mentioned above, it has been assumed for over a hundred years that *E. alphitoides* was accidentally introduced from another continent into Europe. Before this fungus was recognised as a previously undescribed species by E. Griffon and A. Maublanc in 1912, it was initially mis-identified as a North American species, *Microsphaera quercina* (now included in *M. alni*). The idea of a North American origin was then perpetuated by the discovery of *E. alphitoides* in that continent but there is now general agreement that the latter was introduced there, as in Europe.

The first inkling of the true origin of *E. alphitoides* came with an observation in New Zealand, where this mildew occurs on introduced species of European oak. About thirty-five years ago, the

mycologist H.J. Boesewinkel noticed that microscopically identical mildews were growing on one of these oak trees and on a mango tree in a glasshouse. He suggested that the oak mildew and the mango mildew were one and the same fungus but the mildew on mango has never been known to form sexual fruit bodies (chasmothecia) and it is therefore known only by a name based on its asexual form: *Oidium mangiferae*. Many years elapsed before H.J. Boesewinkel's suggestion was corroborated by the use of DNA-based methods, again by the French research group.

It is remarkable not only that our now-familiar oak mildew *E. alphitoides* seems to have a tropical origin but also that it seems to have transferred to a very different family of plants. The same seems to be true of the 'other' oak mildew, *E. quercicola*, which appears to be more or less identical with *Oidium heveae*, a tropical mildew which affects rubber trees (*Hevea brasiliensis*). Various European and North American oak species play host to *E. alphitoides*. Some of these have been ranked for their susceptibility (in descending order) as follows: *Quercus robur*> *Q. petraea* > *Q. cerris* > *Q. borealis* > *Q. ilex*, with *Q. rubra* probably between *Q. cerris* and *Q. borealis*. The same fungus has also been found on sweet chestnut (*Castanea sativa*), beech (*Fagus sylvatica*), horse chestnut (*Aesculus hippocastanum*), a maple (*Acer* sp.) and several other hosts in various plant families.

With regard to the mango mildew becoming established on 'new' host species, it is not clear whether it needs to adapt to such hosts in order to succeed as it has done on various oak species. If so, perhaps it was introduced into Europe long before it became conspicuous. Intriguingly, the mycologist F. von Thümen found a new species of mildew *Oidium quercinum* on *Quercus racemosa* in Portugal in 1877. Over fifty years later, there was a suggestion that this fungus had been imported from Portuguese colonies, long before the new form of oak mildew emerged in 1907–09. *Oidium quercinum* is, however, generally thought not to have been the same as *E. alphitoides*.

As mentioned above, oak mildew has long been known to have particularly severe effects on seedlings and saplings. Their shoots continue to develop over a relatively long part of the growing season and thus remain highly susceptible to infection throughout the peak periods of mildew spore deposition. The resulting heavy colonisation by mildew leads to stunting, distortion and sometimes death of the affected shoots. On older trees, this kind of damage is usually confined to shoots that form during a final flush of late summer growth or that develop in response to pruning, coppicing or insect defoliation. Such shoots often become prematurely defoliated in autumn and they sometimes die back. As mentioned above, however, observations in recent years indicate that mildew now often affects the crown of trees more extensively than previously; this is partly why I was commissioned to review the literature with veteran oak trees especially in mind.

Even where mildew is not heavy enough to cause distortion, stunting or death of oak shoots, it is likely to have significant harmful effects on the tree as a whole, as shown by several research studies. Perhaps the most predictable effect is that mildewed leaves have a reduced capacity to supply the tree with the products of photosynthesis. Most of the affected leaf tissue remains alive beneath the covering of mildew but its photosynthetic efficiency is reduced. Also, some of the photosynthetic output is appropriated by the fungus.

Perhaps an even more serious effect of oak mildew, especially in hot, dry weather, is to allow uncontrolled water loss by transpiration from the leaf surface. Healthy leaves are able to control their rate of transpiration to some extent by the opening and closing of their stomata. Mildew bypasses this regulatory mechanism by the evaporation of water from the fungal mycelium. The resulting excessive water loss probably adds

Premature defoliation of oak shoots affected by mildew; this can be followed by dieback. (Forestry Commission: Crown Copyright)

A veteran pollard oak with epicormic shoots; these sustain the longevity of the tree by replacing lost branches if they are not severely affected by mildew. Survival of the tree provides continuity of decaying wood habitat, associated here with the fungus *Laetiporus sulphureus* (chicken-of-the-woods). (D. Lonsdale)

significantly to the physiological stress that hot, dry weather can induce in the entire tree. To make matters worse, oak leaves become more readily colonised by mildew as a result of strong exposure to ultraviolet light, as typically occurs in such weather. These findings may help to explain why a proportion of oak trees seem to have entered into long-term decline following drought years. With climate change leading to greater extremes of weather, the impact of oak mildew is likely to increase further.

In the management of veteran oak trees, mildew can be especially harmful to the new growth that develops after such trees are pruned in order to prevent life-shortening, structural failure. Mildew can similarly weaken or kill pre-existing epicormic shoots, which represent a veteran tree's supply of potential new branches that can develop in places where old branches have been lost or removed. As well as directly damaging the shoots of veteran oak trees, mildew can render entire trees more susceptible to drought-related stress, as mentioned above.

Another aspect of veteran tree management is the reduction of excessive shade at sites where veterans are very close to other trees. The shade-casting trees are felled or reduced in height within a certain radius of a veteran tree or group of trees in a staged process known as 'haloing'. In some instances, this may need to be done even more gradually, now that we know that mildew can exacerbate the adverse effects of sudden, unaccustomed increased exposure to strong sunlight. On the other hand, we can run into the problem of failing to 'halo' or to prune enough to safeguard the veteran tree(s) concerned. Furthermore, research has shown that mildew-induced reduction in photosynthetic efficiency is especially severe under shady conditions. Thus, the presence of mildew adds to the ever-present difficulty of finding the right balance between over-exposure and excessive shading when pruning or haloing veteran trees.

Mildew is an adverse factor in the management not only of veteran oaks but also of their younger successors. As mentioned above, mildew can harm the shoots of newly pollarded young trees and it is also a threat to the natural regeneration of oak. In the latter situation, there is a particular need to protect oak seedlings and saplings from shading by other vegetation, since mildew impairs their shade-tolerance. This should, however, probably be done gradually, in order to mitigate the adverse effects of direct sunlight on mildew-affected foliage.

In most situations, the only reasonable means of mitigating the effects of oak mildew is probably to take extra care when managing veteran oak trees and their successors. The use of fungicides, although potentially very effective, is unlikely to be practicable (or perhaps legally permissible) except in tree nurseries. Tree shelters might also provide partial protection against infection but further research would be needed to show whether this is worthwhile. Another possibility that could be explored through research is to use natural control agents; these are mainly fungi that can parasitize oak mildew, thus suppressing the formation of its spores.

When experts try to assess the risks posed by alien pathogens and pests not yet present in the UK, one of the key risk-factors is the capacity of such organisms to damage trees (and other plants) that grow in our cool-temperate climate. It is therefore sobering to find that the familiar sight of mildewed oak leaves is the result of introducing a fungus that probably originated in the tropics on an unrelated plant species. It is also rather worrying to realise that oak mildew is probably more damaging that we used to think. On the other hand, it probably does not rank very highly alongside some of the 'nasties' that are waiting to hitch a lift here through international trade.

Acknowledgment

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David Lonsdale is a founder-member of the Ancient Tree Forum, having worked for the Veteran Tree Initiative in the 1990s. After early retirement from Forest Research in 2002, he helped to represent the ATF on the drafting panels of two British Standards then under revision (BS 5837:2005 and BS 3998:2010), adding new guidance for the care of veteran trees. He also accepted the ATF's invitation to compile and edit a multi-author book on the subject. Under the title Ancient and other Veteran Trees: Further Guidance on Management, this was eventually published in 2013 as a sequel to Helen Read's Veteran Trees: a Guide to Good Management (2000). Since then, he has been involved in the international VETree educational project. Also, with a background in tree disease research, David represents the ATF at various plant health conferences and he is a member of the ATF Working Group on Pests and Diseases, among others.