THE HIBERNATION OF THE OAK MILDEW

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The oak mildew invaded Western Europa in the years 1908 and 1909. Since then this parasite, *Microsphaera alphitoides* Griff. & Maubl. (syn. *M. quercina* (Schw.) Burr.) has occurred regularly in the Netherlands on oak seedlings and oak coppice, mainly *Quercus pedunculata* Ehr. (syn. *Q. robur* L.). After the appearance of the fungus its identity and also its mode of hibernation has been amply discussed. Perithecia with ascospores were discovered by ARNAUD and FOËX (1912) in France. In the Netherlands perithecia were only occasionally observed, as their occurrence seems to depend on weather conditions during the summer months (HARTSUYKER, 1939). Besides ascospores, if present, chlamydospores on old infected leaves described by FERRARIS (1909) might be a source of infection of young leaves in spring (PETRI, 1923). However, these observations were not confirmed by other investigators.

NEGER (1911), PEGLION (1911), and somewhat later also VAN POETEREN (1912) observed hibernation of the mildew in infested buds from which malformed shoots developed in spring, stem and leaves being covered with mycelium and conidia. WOODWARD *et al.* (1929) described the way the mildew spreads: conidia from these shoots infect young healthy leaves in the neighbourhood, on which circular colonies develop. The growth of these white patches stops rather soon, probably owing to thickening of the cuticle of the ageing leaves. As has been noted by DITU *et al.* (1964) leaves are severely attacked up to the age of 20 days. A second outbreak may occur on the newly developed Lammas shoots. VAN POETEREN (1918) gave a clear description of the two periods of spread.

According to Woodward *et al.* young buds developing in the axils of mildewed leaves may contract infection when the scales are still young, soft, and loosely applied. Under such conditions the mildew "enters the bud where the mycelium may become established on the softer tissues of the scales and subsequently between the leaf initials. As the buds grow older the scales become tough, more tightly applied, and then afford complete protection from infestation". In their experiments with hundreds of heavily infected plants the authors found only a few trees to carry infected shoots in the following spring. The chance a bud will become infected seems to be extremely low.

According to VAN POETEREN (1912 and 1918) hibernation of the mycelium will take place between the scales of a small number of

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buds. GÄUMANN (1951) is of another opinion: mycelium may hibernate on the bud scales from where it may infect the underlying leaf initials at the time of budbreak in spring.

None of the investigators describing perennation in or on buds refer to their site at the stems or to the time at which they may become infected.

The purpose of our study was to make out at which time of the season which buds will have a chance to become infected.

The spread of the mildew was observed on oak coppice grown on sandy soils in the centre of the Netherlands during two seasons from spring unto autumn of 1961 and 1962. Bud development was studied mainly in 1965. Experiments were carried out with a group of 100 oaks planted in the garden of the laboratory. All oaks belonged to *Quercus pedunculata*. No fungicides were applied.

OBSERVATION ON MILDEW INFECTIONS

Every year, earlier or later in April, depending on weather conditions, bud break occurs. The spring shoots usually develop from the apical bud or the highest axillary ones of the Lammas shoots formed in the year before. If a Lammas shoot is lost, which is frequently the case, the new shoots develop from the axillary buds of the one year old spring shoots. The axes of the buds stretch slowly, scales, ligulae and leaflets expand gradually, and though individual trees develop their shoots far from simultaneously, the new shoots are full grown in the beginning of June.

In 1961 oak coppice was regularly observed over a vast area. In the first week of May about 75 heavily contaminated shoots were found on low shaded branches, as a rule not more than one per tree. They had originated from buds present on shoots formed in spring 1960 (Fig. 1a). The Lammas shoots of that year had disappeared, they had probably been heavily infected by mildew. It is known that such shoots do not survive the winter. Also Woodward *et al.* found contaminated shoots "mostly at the base of the previous year's shoots, the upper portion of which had been killed by a severe attack of mildew".

The basal parts of the stems and the leaves of the contaminated shoots were covered with mycelium and conidia. Specially the basal leaves were partly or totally malformed. Some shoots were only unilaterally infected and misshapen.

As soon as these shoots had expanded infection of the young surrounding leaves occurred, at first within a radius of about half a meter, later mildewed leaves were found in a bigger area around the source of infection. Colonies became visible when the leaves had reached a length of about one cm. They enlarged until the leaves were dark green and mature. Then further spread of mildew was not observed.

After mid-June the apical bud and sometimes also three to five axillary buds of the spring shoots suddenly started elongating, which

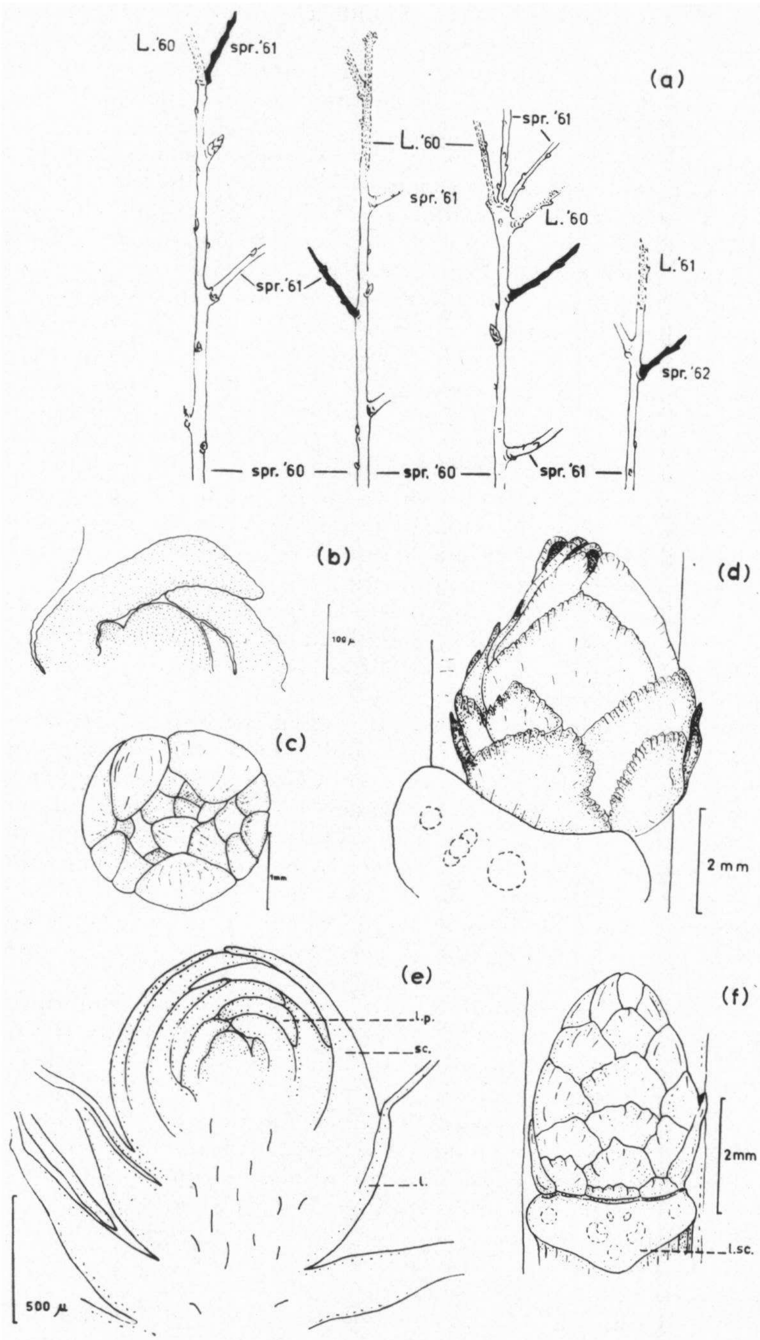
L.'60
spr.'61
(a)
spr. '61
L.'60
spr.'61
L.'60
spr.'61
L.'61
spr.'62
spr. '60
spr. '60
spr. '61
(b)
100 μ
(c)
1mm
(d)
2 mm
(e)
l.p.
sc.
l.
500 μ
(f)
2mm
l.sc.

Fig. 1.

resulted in the formation of the Lammas shoots. They could reach a length of 30 to 40 cm in about a month time, carrying a range of growing leaflets at their tips. All leaves and also the stems became readily covered with mildew. Conidia present on the leaves of the spring shoots were probably the source of contamination, for at that time the mildewed and malformed spring shoots had already shed their leaves.

The younger the leaves of the Lammas shoots were attacked the more they became malformed. At the end of August the tips with the apical buds of heavily mildewed shoots started to die off. The infection potential seemed to have reached its maximum.

Bud development and possibility of infection

More than half of the 75 heavily contaminated shoots found in spring 1961, were situated at the distal third part of the spring shoots formed in 1960, the others were situated lower. From this observation and the disappearance of the Lammas shoots it became evident that hibernation takes mainly place in the highest buds of the spring shoots and not in those of the Lammas shoots.

The question was raised at which stage the buds of the spring shoots might become infected.

Healthy, overwintered buds ready to break in spring, are somewhat conical with a length of about 2 to 5 mm. They may contain about 30 to 50 brown scales, from which the outer, shorter ones, are oldest and darkest. The younger ones partly overlap each other, while the youngest inner ones are tightly folded over the leaf initials in such a way that their margins alternate with the bases of the scales situated at the opposite side of the buds. Hairs are inserted in the margins of the about 30 to 50 scales. There may be 8 to 10 leaf initials, each with a pair of ligulae and a meristematic tissue at its base: the vegetation point of the future axillary bud. During bud break, stem

Fig. 1. a. Scheme of 4 spring shoots observed between May 16 and 19.
L: Lammas shoots.
spr.: spring shoots.
dotted: Lammas shoots dead or disappeared.
black: infected spring shoots.
b. Young flat bud developed in the axil of a leaflet of the apical bud of a spring shoot (June 29).
c. Closed spherical bud in the axil of the third leaf of a spring shoot, covered by scales and seen from above (June 26).
d. Elongated axillary bud situated on a spring shoot under two Lammas shoots (July 23).
e. Longitudinal section of a conical axillary bud of a spring shoot. The lower bracts and stipulae have been cut away; others loosened by the treatment (July 1).
sc.: scales.
l.: ligulae.
lp.: leaf primordia.
f. Conical bud on a spring shoot, situated under a Lammas shoot (October 4).
l. sc.: leaf scar.

elongation and leaf expansion, these axillary growing points split off primordia, first the initials of the future outer scales, which fully enclose the vegetation point. Buds with one to four scale initials are still flat. They are found in the axils of leaflets that have just become macroscopically visible (Fig. 1b). The younger scale and leaf initials develop in succession. In turn they are first applied to the vegetation point and then pressed towards the outside of the bud by the initial that develops next. During this process of growth the shape of the buds becomes more and more spherical. By the end of May, when the shoots are fully developed and the leaves initially present in the overwintered buds have expanded, the axillary buds of these leaves show a scala of developmental stages: the flat upper ones with a width of about ½ mm, still consisting in a vegetation point surrounded by only a few soft green scales, the basal ones with a diameter of about one mm, covered by 5 to 8 scales from which the margins begin to discolour. All buds are tightly closed, though the outer scales of the oldest ones are applied laterally only (Fig. 1c). In June all buds are covered by brown scales and they may contain 10 or more initials. The tips of the shoots show a number of ligulae, leaflets and initials from which the green tips are visible. Further development stops, however.

The question arose, whether the buds of the young spring shoots can become infected. According to Woodward *et al.* the mildew can only establish itself on very young buds with soft green scales. Only shortly after bud break are the buds in the axils of the basal leaves still in that condition, but at that time one scarcely finds mildewed shoots producing conidia. Therefore these buds may escape infection. This might also be the case with the topmost buds. Though they develop later, at the time mildewed shoots have developed, they remain protected by ligulae and growing leaflets for a long time. The scales of all buds darken rapidly after they have become exposed. The condition for contamination of soft green buds seems but seldom to be fulfilled. For that reason Woodward *et al.* consider the rapidity with which the bud scales harden to be the cause of the low percentage of bud infection. Moreover, the infection potential remains usually low at that time of the season. Still, contamination in this early stage of the epidemic should not be excluded, since development of the shoots of different trees is not simultaneous. It may occur that conidia from a full-grown infected shoot will contaminate young buds of a neighbouring tree that is less advanced in shoot development.

That mycelium might grow between the scales and the leaflets of a contaminated bud as Woodward *et al.* suggest, seems, however, unlikely in this stage. These parts cover each other and the vegetation point tightly from the very first stage of bud development. Microscopic examination never revealed mycelium of mildew at the inner side of these buds.

After the second decade of June the condition of nearly all buds changes rather suddenly. Besides the spectacular development of longer or shorter Lammas shoots from the apical and the highest buds, also the buds situated under these rapidly growing shoots start elongating, but at a much lower rate. Some may still produce new shoots as late as the end of July or in August (Fig. 1d), but the majority of the buds, however, stops growing when they have reached a length of 2 to 5 mm. Their shape becomes conical instead of spherical, which is due to the stretching of the axes, following which the outer scales become more loosely applied to each other, hardly overlapping each other. Only the inner ones do remain tightly applied to the leaf primordia (Fig. 1e and f).

In this condition the buds overwinter, and it is in these buds that the fungus might hibernate. They are exposed to clouds of conidia from the severely infected Lammas shoots on top of them.

That they may become infected was observed in August 1961, when such a bud started new growth. It gave rise to a heavily infected shoot, similar to those that develop in spring. If it had remained dormant it would probably have shown the infection after winter.

Microscopical examination of those conical buds overgrown with mildew revealed mycelium on the green or slightly discoloured superficial parts of the scales, entangled with the marginal hairs. Neither on the innerside nor on the covered parts of the scales was mycelium found.

Experiments

Only a few experiments out of many were successful. Branches were cut off just above inoculated buds in order to study a possible infection of the developing shoots, but no infection occurred. Only bringing conidia between the loosely applied scales and leaflets of the apical buds of spring shoots did result in spread of the mildew on stem and leaves of the developing Lammas shoots. If a bud had been inoculated laterally, the leaves of the Lammas shoot also showed a one sided infection. The disease symptoms did not differ from those of infected shoots in early spring.

In another experiment a young Lammas shoot with a length of 5 cm and leaflets of ½ to 1 cm on a healthy tree was inoculated in July 1961. It soon became covered with mycelium. During the following winter it died off, but in spring 1962 an infected shoot developed from a bud at the tip of the spring shoot of 1961 (Fig. 1a). Probably conidia applied to the Lammas shoot or produced on the Lammas shoot itself had contaminated this bud, in which or upon which the fungus hibernated.

Conclusion and summary

It was observed that infected spring shoots usually develop from buds situated at the highest parts of spring shoots formed in the previous year, the Lammas shoots of which had died off during winter. Therefore the development of the buds on spring shoots was studied in relation to the possibility of contamination and infection with mildew. Initially the young buds are flat, their vegetation point being surrounded by a few scales. Later, when more scales are de-

veloped, they become spherical. During the first period of the mildew epidemic infection of these buds is unlikely, since it seems impossible for mycelium to enter these tightly closed buds. Even overgrowing can hardly be expected, because the highest buds at least will remain covered by ligulae and leaflets for a long time during shoot development. Moreover, the scales harden quickly and infection potential is still low.

Contamination of the buds of the spring shoots probably occurs during the second period of the mildew activity from July until autumn, when there is an abundant production of conidia in the Lammas shoots. At that time the highest buds of the spring shoots that did not produce Lammas shoots have become conical, following a process of elongation which stops when the buds have reached a length of 2 to 5 mm. The outer scales overlap each other only partly and they become less tightly applied to the core of the bud containing the inner scales and the leaflets. Hyphae could be observed, covering the superficial, only slightly discoloured parts of the scales.

Considering the heavy spore loads present around the infected Lammas shoots, the number of outwardly contaminated buds must be high. Still hibernation occurs relatively seldom. Probably the dark brown scales of most buds are unsuitable for infection. They are mostly too tightly applied to each other to allow the fungus to reach the underlying soft green tissue. It is not impossible that mycelium settles itself on the hairs or on green parts of some bud scales, where it may remain dormant. At the time of bud break it might infect the underlying initials, as it has been assumed by Gäumann.

This way of hibernation is, however, unlikely, since the buds during their transition from spherical to conical do not show superficial green parts, and the hairs die off fairly soon. It is more likely that mycelium entangled in the hairs of bracts or even conidia might penetrate incidentally between the outer, somewhat loosened scales of some buds, where the fungus can settle itself on underlying soft tissue. Here it may hibernate, as has been suggested by Van Poeteren. It can thus be explained that infected shoots develop mainly from the highest buds of the spring shoots situated under the Lammas shoots, since it is these ones that show the greatest elongation at the end of June. In this way a unilateral infection of spring shoots can be accounted for as well as the fact that the stem and the basal leaves often show the heaviest infection: these parts are the first to become infected by mycelium present between the outer, loosened scales.

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