

Apple powdery mildew caused by *Podosphaera leucotricha*: some important features of biology and epidemiology

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Summary: In this review, some important features of biology and epidemiology are summarised for apple powdery mildew (*Podosphaera leucotricha*). In the first part of the review, the geographical distribution of the pathogen are discussed, then the morphology and taxonomy of the causal organism are described. Disease symptoms of apple powdery mildew are also shown and then host susceptibility/resistance is discussed in relation to durability of resistance. In the second part of this review, the general disease cycle of powdery mildew on apple are demonstrated and some basic features of powdery mildew epidemiology (such response of the pathogen to temperature, relative humidity, and rain as well as spore production, spore dispersal, diurnal patterns and temporal dynamics of the pathogen/disease) are also given on apple host.

Key words: geographical distribution, taxonomy, apple, powdery mildew, *Podosphaera leucotricha*, host susceptibility, disease cycle, epidemiology

Introduction

Powdery mildews are worldwide distributed pathogens on several host including horticultural crops. In spite of some exceptions, general features of the symptoms is the white epiphytic micelia that covers the plant surface. In fruit crops, one of the most known powdery mildew pathogen is *Podosphaera leucotricha*, which causes economic losses mainly on cultivated apple. In last decades, several new commercial apple cultivars were introduced that has low to moderate susceptibility to powdery mildew. Use of these cultivars decreased *P. leucotricha* infections and epidemics in most apple orchards. This resulted in less intensive control against this pathogen compared to the mid twentieth century. However, the pathogen is still well distributed worldwide and causing severe losses in most apple growing region.

The aim of this review was, first, to outline some of the biological features of apple powdery mildew, and second, to describe the disease cycle and some epidemiological features of the disease.

Geographical distribution

Powdery mildew is a worldwide distributed disease in most apple growing areas and it is an important disease in apple nurseries worldwide. It is a major disease of orchard trees in semiarid regions. Economic loss varies mainly with cultivar susceptibility and orchard management practices. The management of powdery mildew in commercial orchards can be well integrated with several other diseases

(such as apple scab) having different environmental requirements (Hickey & Yoder, 1990; Holb, 2005, 2008).

Causal organism and its morphology and taxonomy

Salmon (1900) divided *Erysiphae* into the subfamilies *Erysiphae* and *Phyllactineae*. Then Homma (1937) prepared the subfamilies *Erysiphe*, *Phyllactineae* and *Leveilluleae*. *Podosphaera* has general features from that they are commonly recognized: superficial mycelium, appendages dichotomously branched at tip, and one ascus in the fruiting bodies of chasmothecia (previously known as cleistothecia). *Podosphaera leucotricha* (Ell. Ev.) E. S. Salmon (anamorph *Oidium farinosum* Cooke), an ascomycetous heterothallic fungus, causes powdery mildew of apple and pear and quince (Hickey & Yoder, 1990). Conidia are ellipsoidal and varying in the size of 20–38 µm in diameter. Conidia often contain distinct fibrosin bodies and they are truncate and hyaline. Conidia are produced on long chains on thin mycelium. The sexual fruiting bodies, chasmothecia (cleistothecia) are subglobose and varying in the size of 75–96 µm in diameter. Sexual fruiting bodies are globose and have apical and basal appendages. The number of apical appendages are 3 to 11 per chasmothecia. They are widely spreading and their length is 3 to 7 times the diameter of the chasmothecia. The basal appendages are short-tortuous, and mostly irregularly branched. General size of an ascus within the chasmothecia is 55–70 × 44–50 µm. Their shapes are oblong to subglobose. The ascus contains eight ovate to elliptical ascospores with the size of 22–36 × 12–15 µm.

Symptoms

On apple, this fungus affects twigs, foliage, blossoms and fruits. Infected twigs often are stunted and may also die. When young leaves are infected, they tend to increase in length, but they become folded longitudinally (Ellis et al., 1981).

Infections on leaves appear first as fungal mycelium and spores on the lower surface. These lesions may spread to the upper surface and cover the entire leaf with a white mass of spores and mycelium. Infections often result in leaf curling or crinkling. Severely infected leaves are narrower than normal and folded longitudinally, or curled, crinkled, and stiff (Figure 1). These leaves become brittle, and they can fall during the summer. (Hickey & Yoder, 1990).



Figure 1: Severe infection caused by *Podosphaera leucotricha* on apple leaf showing a mass production of mycelia and conidia. (Photo by Imre Holb)

Severely infected terminals have shortened internodes and are covered with mycelium. During summer, the white fungal micelium turns brown, and may produce dark brown fruiting bodies (Figure 2). These infected shoots may survive summer but often they die before autumn. If the spring or summer infections survive then these symptoms on the woody shoots can be seen from late autumn until early spring during the dormant season (Holb, 2005; Holb & Abonyi, 2007; Figure 3). The overwintered terminals act as a source of inoculum for the coming season (Hickey & Yoder, 1990; Szentiványi & Kiss, 2003). These overwintered, infected terminal are very susceptible to winter injury and they can die during long, cold winter (above -20°C for several weeks). If they survive the winter, buds of the infected shoots start to open 5–8 days later than healthy buds (Holb et al., 2005). Apple blossoms emerging from infected buds may produce small and russeted fruit (Hickey & Yoder, 1990).

The flower parts as a part of cluster leaves can also be covered with white mycelium. The white micelial mat may cover all parts of the flower including petals, sepals, receptacles and peduncles. The petals of infected flowers are often light green and stunted. Although blossom infection is not very common, infected flower buds are more susceptible to spring frost and also often fail to set fruit (Hickey & Yoder, 1990; Holb, 2008).



Figure 2: Severely infected terminals caused by *Podosphaera leucotricha* showing a mass production of mycelia and conidia. (Photo by Imre Holb)



Figure 3: Severely infected terminals caused by *Podosphaera leucotricha* showing a mass production of mycelia and conidia. (Photo by Imre Holb)

Fruit infections are common on severely infected trees. Fruits are susceptible in the early stages in spring. Older fruit infection is seldom. Infected fruits are smaller and they surface severely russeted. Mycelia or conidia can be seen rarely on older infected fruits (Hickey & Yoder, 1990).

As it was noted *P. leucotricha* can cause symptoms on pear especially on fruit. White mycelium is visible on young fruits, but later fruit become russeted as cells die (Hickey & Yoder, 1990).

Host susceptibility and durability of resistance

Several older apple cultivars are susceptible to apple powdery mildew. According to Hickey & Yoder (1990), moderately to highly susceptible apple cultivars are Jonathan, Baldwin, Cortland, Idared, Rome Beauty, Monroe, Gravenstein, Stayman Winesap, Cox's Orange Pippin, Granny Smith, and Prima. Apple cultivars with low susceptibility are Golden Delicious, Winesap, York Imperial, Nittany and Lord Lambourbe (Hickey & Yoder, 1990).

Borovinova (1982a) studied the susceptibility of 59 apple cultivars to powdery mildew in a five-year study. It was found that all cultivars studied were infected by powdery mildew, but their infection differed greatly by cultivar susceptibility. Only cv. Kolotny was very lowly susceptible and the shoot infection was below 1%. Cultivars Linda, Gray Renette, Boiken, White winter Kalvil, Rik's Renette, Renette des grandes villes, Beforest, Jonathan, Fenuette grise, Fenuette rouge, Wellington, Jonathan type 3 and Pepin Shafran were highly susceptible to both leaf and shoot infestations (incidence was above 20%).

Borovinova (1982b) also investigated the effect of the fertilization on the powdery sensitivity of cv. Jonathan to powdery mildew. Application of N, P₂O₅ and K₂O by 100, 40, 40 mg active ingredient per 1 kg dry soil, respectively, both separately and in a combination of the three nutrient elements, increased the sensitivity of cv. Jonathan to the

powdery mildew pathogen. The greatest increase in the sensitivity was induced by the combined fertilization with N, P₂O₅ and K₂O. The fertilizer combinations prolonged the period of shoot growth and decreased the sugar content in leaves, causing higher sensitivity of trees to the powdery mildew pathogen.

Cimanowski et al. (1988) showed that cultivars Liberty, Macfree, Paulared, Priam and Priscilla can be ranked as susceptible to apple mildew. The varieties James Grieve, Prima, Redfree, Tydeman's Red were less susceptible to the disease.

According to Jeger et al. (1986), for some cultivars the association between the resistance components permitted resistance to be classified as very high (cv. Discovery), very low (cv. Golden Delicious) or intermediate (cvs. Bramley's Seedling, Suntan).

Van der Scheer (1989) also sorted apple cultivars assessing their sensitivity to powdery mildew, the highest disease incidence were found on cvs Gloster and Cox's Orange Pippin. Borovinova (1994) studied the susceptibility of scab resistant apple varieties to powdery mildew. All the evaluated varieties were susceptible to powdery mildew but to a different degree. Cultivar Moira was the most susceptible. Evaluated varieties (except for cv. Moira) do not require any special control against powdery mildew in the first 4 years after planting. Pedersen et al. (1994) studied the susceptibility of 15 apple cultivars to powdery mildew. Their results were compared with findings of other researchers, this comparison is shown in Table 1.

Cimanowski & Millikan (1970) showed that high osmotic values of cell sap are associated with resistance of apple to powdery mildew. This relationship occurs within a single variety in comparisons between young susceptible and old resistant leaves and among four clones of McIntosh having different levels of resistance.

Several study were made on powdery mildew resistance genes. Monogenic or oligogenic resistances have been identified in wild *Malus* species such as *Malus robusta* (P11),

Table 1. Comparison of powdery mildew susceptibility 15 apple cultivars (partly adopted from Pedersen et al., 1994)

Cultivar	Susceptibility to powdery mildew
'Belle de Boskoop'	Low (Mygind, 1965; Cimanowski et al., 1988; Pedersen et al., 1994)
'Bramleys Seedling'	Low (Mygind, 1963; Norton, 1981; Jeger et al., 1986; Pedersen et al., 1994)
'Cox's Orange'	Medium (Mygind, 1963; Jeger et al., 1986), high (Jeger & Butt, 1983b; Jeger & Butt, 1986; van der Scheer, 1989; Hickey & Yoder, 1990; Pedersen et al., 1994)
'Discovery'	Low (Norton, 1981; Jeger & Butt, 1983b; Jeger & Butt, 1986; Jeger et al., 1986; van der Scheer, 1989; Pedersen et al., 1994)
'Filippa'	Low (Mygind, 1963; Pedersen et al., 1994)
'Gravenstein'	Low (Norton, 1981), medium (Pedersen et al., 1994), high (Mygind, 1963; Hickey & Yoder, 1990)
'Guldborg'	Medium (Pedersen et al., 1994), high (Mygind, 1963)
'Ildrod Pigeon'	High (Norton, 1981; Pedersen et al., 1994)
'Ingrid Marie'	Low (Pedersen et al., 1994), low-medium (Mygind, 1963)
'James Grieve'	Low (Pedersen et al., 1994)
'Mutsu'	Low (Pedersen et al., 1994; Norton, 1981)
'Red Ananas'	Low (Pedersen et al., 1994)
'Skovfoged'	Medium (Pedersen et al., 1994)
'Summerred'	Medium (Pedersen et al., 1994; Norton, 1981),
'Transparente Blanche'	Medium (Pedersen et al., 1994), high (Mygind, 1963)

Malus zumi (*PI2*) and Mildew Immune Selection (MIS), or in ornamental crab apples such as White Angel (*Plw*) and the D series (*Pld*) (Knight & Alston, 1968; Dayton, 1977; Visser & Verhaegh, 1979; Korban & Dayton, 1983; Gallott et al., 1985). Selection for resistance to powdery mildew, caused by *P. leucotricha*, is based mainly on major resistance genes, which provide a high level of resistance (Lespinasse, 1983; Fischer, 1994; Krüger, 1994). However, it is also known that the use of cultivars carrying major resistance genes are able to overcome the resistance (e.g. Wolfe & McDermott, 1994; Lebeda & Zinkernagel, 2003). The resistance from *M. zumi* has been used mainly in the apple-breeding in France. Knight & Alston (1968) demonstrated that this resistance was initially considered to be the result of one dominant gene. However, additional studies have shown that it might be more complex and at least two genes are involved in the resistance (Seglias & Gessler, 1997). The source of resistance in *M. zumi* was considered to involve at least one single major resistance gene, named *PI2*. The resistance introgressed from *M. zumi* seemed to be stable under field conditions (Krüger, 1994) and in one study it stayed stable over 17 years in unsprayed orchards (Alston, 1983). Recently, an increase of susceptibility to powdery mildew was observed on apple genotypes carrying *PI2* (Caffier & Laurens, 2005). It was demonstrated by tests of pathogenicity that isolates of *P. leucotricha* sampled in this orchard were virulent to *PI2*. Authors demonstrated that additional quantitative resistance genes may influence the durability of resistance *PI2*.

Disease cycle

Disease cycle of apple powder mildew has generally two phases: first occurs at bud break on leaves, flowers and shoots, referred as the "primary infection phase" and the second occurs from these sources (by conidia) during the whole growing season and the resultant infections represent the "secondary infection phase" (Woodward, 1927).

P. leucotricha overwinters in dormant buds on apple (but not on pear) as mycelium infected during the previous growing season (Woodward, 1927; Figure 4). Overwintering potential is largely affected by temperature. Research showed that less than 5% of the infected buds are open in spring if the temperatures below $-24\text{ }^{\circ}\text{C}$ but in these temperature infected buds are also die. However, another research showed that temperatures near $-12\text{ }^{\circ}\text{C}$ can kill the *P. leucotricha* mycelium in buds and the buds can produce healthy leaves in spring. It is known that infected buds can survive temperatures

$2\text{--}10\text{ }^{\circ}\text{C}$ higher than healthy buds (Cimanowski, 1969; Covey, 1969; Butt, 1978; Jeger & Butt, 1983a).

Fruit buds probably provide the earliest source of inoculum in next spring. Infected buds are open and overwintered mycelia produce conidia on the young leaf surface which initiate the primary infections of the fungus (Figure 4). Because infected buds usually open later than healthy ones, susceptible tissue is present when the first conidia are produced. Conidia infect most parts of the trees including young leaves, shoots, flowers and fruit. These infections will provide inoculum sources for secondary disease cycles. Only young tissues are susceptible and leaves are susceptible for only a few days after they emerge (Hickey & Yoder, 1990).

It was shown that if leaves are mechanically injured, they can be infected when they are older. 96–100% relative humidity and $20\text{--}22\text{ }^{\circ}\text{C}$ are necessary for conidia germination. Germination is slow at temperatures below $4\text{--}10\text{ }^{\circ}\text{C}$ and approximately 50% after 24 hours. Conidia can not germinate in free water and/or at above $30\text{ }^{\circ}\text{C}$ air temperature (Coyier, 1968). Formation of appressoria, division of generative cells, abstriction of conidia, dissemination of conidia and germination of conidia in *Erysiphae* occur principally during the light portion of the day (Yarwood, 1934, 1957). Maturation of conidia in *P. leucotricha* is also diurnal. The highest concentration of conidia in the air occurs from late morning to early afternoon (Stephan, 1988; Xu et al., 1995). In the study by Burchill (1965), spore concentrations reached a maximum in June, thereafter a series of minor peaks occurred until the end of September. The June peak of spore release was followed approximately 2 weeks later by a rise in the incidence of new leaf infections.

Infection of buds occurs before the creation of protective shields of bud scales (Woodward, 1927; Burchill, 1958). After bud infection the mycelium does not grow and remains

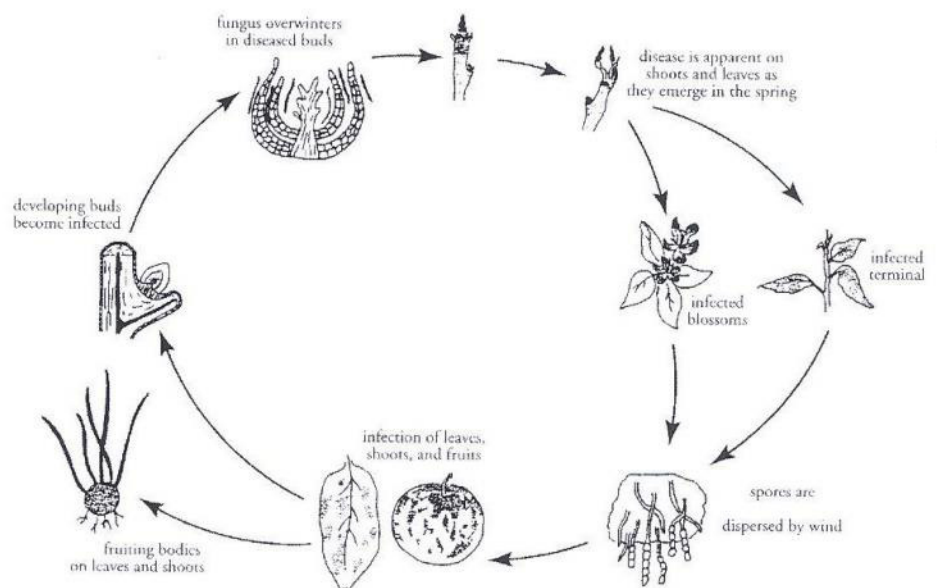


Figure 4: Disease cycle of apple powdery mildew caused by *Podosphaera leucotricha* (adopted partly from and Hickey and Yoder, 1990; Jones and Sutton, 1996; and Bessin et al., 1998)

quiescent until the following spring. Terminal buds are more likely to serve as overwintering sites for the fungus compared to lateral buds (Woodward, 1927; Burchill, 1958).

The sexual stage of *P. leucotricha* do not appear to be important in the disease cycle of apple powdery mildew (Cunningham, 1923). Inoculation of foliage with ascospores have been unsuccessful (Hickey & Yoder, 1990).

Some features of epidemiology

Powdery mildews, such as rusts, downy mildews and plasmodiophoras, have not been cultured successfully on non-living substrata and are called obligate parasites. On conventional media, such as potato dextrose agar, powdery mildew conidia may form short germ tubes, but these germ tubes soon die.

Conidia of *P. leucotricha* have failed to germinate at low relative humidity (Berwith, 1936). Germination was usually poor under most conditions tested. Perhaps germination of the fungus is rather dependent on host stimulation (Yarwood, 1957).

Factors that affect the dispersal of conidia have been studied several countries (e.g. Burchill, 1965; Cimanowski, 1969; Molnár, 1970; Butt, 1971, 1972). Spore release is generally diurnal, with a secondary peak after dark (Cimanowski, 1969; Molnár, 1970; Pady, 1972). Relative humidity, wind and rainfall have the greatest influence on spore dispersal. High relative humidity favors sporulation but not spore release. Release of conidia increases with wind speeds and rainfall is generally unfavorable for dispersal (Butt, 1971; Cimanowski, 1969; Molnár, 1970). Temperatures greater than 20 °C are favor to release of conidia (Molnár, 1970). Butt (1971, 1972) reported that high relative humidity was unfavorable and increasing wind speed was favourable for conidia dispersal. Regarding the relationship to rainfall, splash dispersal at onset on rain was characteristic of many dry air spores such as for *P. leucotricha* (Sutton & Jones, 1979). They confirmed also that warm temperatures were more favourable than low temperatures for spore dispersal. Temperature was significantly correlated positively with spore concentration. Solar radiation also had a positive influence on spore concentration. Diurnal periodicity of conidia concentration reported previously (Burchill, 1965; Cimanowski, 1969; Molnár, 1970; Pady, 1972; Sutton & Jones, 1979).

Coyier (1968) showed that very limited germination could be observed after 6 hours of incubation at 32.2 °C and less than 10% of the conidia germinated in 24 hours. Germination was highest and mycelial growth best at 21 °C. Incubation at 21 °C resulted in 71% germination in 6 hours and 88% in 24 hour. Good development of the mycelium occurred at 15.6, 21 and 26.7 °C; but best growth and greatest number of germ tubes per conidium were observed again at 21 °C (Coyier, 1968).

Cimanowski et al. (1975) studied the effect of light on the development of powdery mildew and they concluded that exposure of leaves to increased lux of light increases the photosynthetic activity, but reduces or inhibits the development of mildew.

Ellis et al. (1981) found that powdery mildew infection significantly reduced photosynthesis and transpiration of apple leaves. Photosynthesis inhibition was more severe in young infected leaves than in mature, fully expanded leaves. Nine days after inoculation, leaf area covered by mycelia was 20% for mature leaves, with no reduction of photosynthesis or transpiration. At 30 days after inoculation, 90% of the leaf was covered and percentage reduction of photosynthesis and transpiration was approx. 50%. Young infected leaves were covered by mycelia at a 90% level and their photosynthesis and transpiration were reduced 85%. Reductions in photosynthesis and transpiration were accompanied by a corresponding reduction of leaf carbohydrate content. Infected leaves did not recover from inhibition of photosynthesis and transpiration after treatment with a combination fungicide (Ellis et al., 1981).

Powdery mildew colonies were observed on both older and younger leaves by Butt & Jeger (1986). Conidiophore density was higher on younger than on older leaves, higher on the upper than on the lower leaf surface and decreased with the age of the colony. The number of conidia/conidiophore was higher on the younger leaves and on the upper surfaces and was at maximum 7–12 days after the first sign of the colony. Athors also found that the number of conidia/mm² colony was higher on lower surfaces, especially of the younger leaves.

In the study of Stephan (1988), regression analysis proved temperature to be the dominant meteorological factor influencing sporulation and spore dispersal. Spore counts increased about twofold at temperatures between 15 and 20 °C. The author noted that the night depression in the diurnal patterns of spore dispersal seems to be due to high relative humidity. Rains of greater intensity (3 mm and more) and longer duration (up to 3 hours) caused a considerable decrease of spore dispersal.

Stephan (1989) found that powdery mildew epidemic follows a sigmoid curve. The epidemic started if the daily mean of temperature were above 13 °C. The epidemic showed three distinct phases. In phase 1, the rates of disease increase were between 0.084 and 0.200 (when rate of leaf increase was greater than 0.20/day). While in phase 3, these rates declined to 0.010 when rate of leaf increase was lower than 0.10/day. Phase 2 had the characteristics between phases of 1 and 3.

Xu et al. (1995) revealed that the temporal pattern of the number of airborne conidia was similar, generally following a diurnal pattern with an afternoon peak. In each year the most important weather variables influencing the number of airborne conidia were vapour pressure deficit and rainfall.

References

- Alston, F. H. (1983): Progress in transferring mildew (*Podosphaera leucotricha*) resistance from *Malus* species to cultivated apple. IOBS WPRS Bulletin. 6: 87–95.

- Berwith, C. E. (1936):** Apple powdery mildew. *Phytopathology*. 26: 1071–1073.
- Bessin, R. T., McManus, P. S., Brown, G. R. & Strang, J. G. (1998):** Midwest tree fruit pest management handbook. Kentucky State University.
- Borovinova, M. (1982a):** Susceptibility of some apple cultivars to powdery mildew (*Podosphaera leucotricha* (Ell. et Ev. Salmon) in the region of Kyustendil. *Horticultural and Viticultural Science*. 19 (8): 50–55.
- Borovinova, M. (1982b):** The effect of the mineral fertilizers on the sensitivity of the apple cultivar Jonathan to the powdery mildew (*Podosphaera leucotricha* [Ell. et Ev.] Salmon). Reports of Second National Symposium of Plant Immunity, Plovdiv. 3: 199–206.
- Borovinova, M. (1994):** Susceptibility of 9 scab resistant apple varieties to powdery mildew [*Podosphaera leucotricha* (Ell. et Ev.) Salmon]. Fourth Symposium on Plant Immunity to Diseases and Pests. November 7–11, 1994, Dobrich. 132–135.
- Burchill, R. T. (1958):** Observations on the mode of perennation apple mildew. Ann. Rep. Long Ashton Research Station for 1957, 114. p.
- Burchill, R. T. (1965):** Seasonal fluctuations in spore concentrations of *Podosphaera leucotricha* (Ell. and Ev.) Salm. in relation to the incidence of leaf infections. *Ann. Appl. Biol.* 55: 409–415.
- Butt, D. J. (1971):** The role of the apple spray programme in the protection of fruit buds from powdery mildew. *Annals of Applied Biology*. 68: 149–157.
- Butt, D. J. (1972):** The timing of sprays for the protection of terminal buds on apple shoots from powdery mildew. *Annals of Applied Biology*. 72: 239–248.
- Butt, D. J. & Jeger, M. J. (1986):** Components of spore production in apple powdery mildew (*Podosphaera leucotricha*). *Plant Pathology*. 35: 491–497.
- Caffier, V. & Laurens, F. (2005):** Breakdown of *P12*, a major gene of resistance to apple powdery mildew, in a French experimental orchard. *Plant Pathology*. 54: 116–124.
- Cimanowski, J. (1969):** (Epidemiology of *Podosphaera leucotricha* in Poland. I. Overwintering of the fungus.) *Acta Agrobot.* 22: 253–263.
- Cimanowski, J. & Millikan, D. F. (1970):** Resistance of apple to powdery mildew and its relationship to osmotic activity of the cell sap. *Phytopathology*. 60: 1848–1849.
- Cimanowski, J., Dzieciol, W. & Kowalik, B. (1988):** Evaluation of susceptibility of 22 apple varieties to apple scab [*Venturia inaequalis* (Cooke) Aderh/ and apple powdery mildew [*Podosphaera leucotricha* (Ell. et Ev.) Salm]. *Fruit Science Reports*. 15 (2): 81–84.
- Cimanowski, J., Novacki, J. & Millikan, D. F. (1975):** Effect of light on the development of powdery mildew and on some physiological and morphological changes in apple leaf tissue. *Phytoprotection*. 56: 96–103.
- Covey, P. R. (1969):** Effect of extreme cold on the overwintering of *Podosphaera leucotricha*. *Plant Disease Reporter* 53: 710–711.
- Coyier, D. L. (1968):** Effect of temperature on germination of *Podosphaera leucotricha* conidia. *Phytopathology*. 58: 1047.
- Cunningham, G. H. (1923):** Powdery mildew: *Podosphaera leucotricha*. *New Zeal. Jour. Agr.* 26: 344–351.
- Dayton, D. F. (1977):** Genetic immunity to apple mildew incited by *Podosphaera leucotricha*. *HortScience*. 12: 225–226.
- Ellis, M. A., Ferree, D. C. & Spring, D. E. (1981):** Photosynthesis, transpiration, and carbohydrate content of apple leaves infected by *Podosphaera leucotricha*. *Phytopathology*. 71: 392–395.
- Fischer, C. (1994):** Using wild *Malus* species and apple cultivars for breeding for resistance. *Erwerbsobstbau*. 36: 208–212.
- Gallott, J. C., Lamb, R. C. & Aldwinckle, H. S. (1985):** Resistance to powdery mildew from some small-fruited *Malus* cultivars. *HortScience*. 20: 1085–1087.
- Hickey & Yoder (1990):** Powdery mildews. p. 9–10. In: Jones, A.L. and Aldwinckle, H. *Compendium of Apple and Pear Diseases*. APS Press, USA.
- Holb I. (2005):** Effect of pruning on disease incidence of apple scab and powdery mildew in integrated and organic apple production. *International Journal of Horticultural Science*. 11 (1): 57–61.
- Holb, I.J. (2008):** Diseases and pests in the flowers of fruit trees. p. 393–438. (Powdery mildew p. 414–415.) (In: Nyéki, J., Soltész, M. Szabó, Z. Morphology, biology, and fertility of flowers in temperate zone fruits.) Akadémia Kiadó, Budapest.
- Holb, I. J. & Abonyi F. (2007):** Almafalisztharmat elleni védekezés integrált és ökológiai almatermesztésben. *Növényvédelem*. 43 (6): 247–251.
- Holb I., Veisz J., Medgyessy I. & Abonyi F. (2005):** Az alma komplex ökológiai növényvédelmi technológiája. 138–144. (In: Holb I. (ed.): A gyümölcsösök és a szőlő ökológiai növényvédelme.) Mezőgazda Kiadó, Budapest 341.
- Homma, Y. (1937):** Erysiphaceae of Japan. *Jour. Fac. Agr. Hokkaido Univ.* 38: 183–461.
- Jeger, M. J. & Butt, D. J. (1983a):** The effect of weather during perennation on epidemics of apple mildew and scab. *EPPO Bull.* 13 (2): 79–85.
- Jeger, M. J. & Butt, D. J. (1983b):** Using partial resistance in the integrated control of apple powdery mildew. *Bulletin SROP, WPRS bulletin*. VI/4: 111–122.
- Jeger, M. J. & Butt, D. J. (1986):** Epidemics of apple powdery mildew (*Podosphaera leucotricha*) in a mixed orchard. *Plant Pathology*. 35: 498–505.
- Jeger, M. J., Butt, D. J. & Swait, A. A. J. (1986):** Components of resistance of apple to powdery mildew (*Podosphaera leucotricha*). *Plant Pathology*. 35: 477–490.
- Jones A. L. & Sutton, T. B. (1996):** Diseases of tree fruit in the East. Michigan State University.
- Szentiványi, O. & Kiss, L. (2003):** Overwintering of *Ampelomyces* mycoparasites on apple trees and other plants infected with powdery mildews. *Plant Pathology*. 52: 737–746.
- Knight, R. L. & Alston, F. H., (1968):** Sources of field immunity to mildew (*Podosphaera leucotricha*) in apple. *Canadian Journal of Genetics and Cytology*. 10: 294–298.
- Korban, S. S. & Dayton, D. F. (1983):** Evaluation of *Malus* germplasm for resistance to powdery mildew. *HortScience* 18: 219–220.
- Krüger, J. (1994):** Observations on different mildew sources used in apple breeding at Ahrensburg. In: Schmidt, H., Kellerhals, M., eds. *Progress in Temperate Fruit Breeding*. Dordrecht, the Netherlands, Kluwer Academic. 7–12.
- Lebeda, A. & Zinkernagel V. (2003):** Evolution and distribution of virulence in the German population of *Bremia lactucae*. *Plant Pathology*. 52: 41–51.

- Lespinasse, Y. (1983):** Amélioration du pommier par la résistance à l'oidium (*Podosphaera leucotricha*): premiers résultats concernant la virulence du champignon. In: IOBC WPRS Bulletin 6: 96–110.
- Molnár, J. (1970):** Vyskyt, koncentrácia konidii a priebeh sekundárnej infekcie múcnatky jablonovej. Orchrana Rostlin. 43: 207–214.
- Mygind, H. (1963):** Meldug med saerlig omtale of ablemeldug. Tidsshr. Planteavl. 67: 255–320.
- Mygind, H. (1965):** Undersogelse af nogle faktorer som pavir ker ablemelduggens livslob. Meldug med saerlig omtale of ablemeldug. Tidsshr. Planteavl. 69: 216–239.
- Norton, R. A. (1981):** Field susceptibility of apple cultivars to scab, *Venturia inaequalis* and powdery mildew, *Podosphaera leucotricha* in a cool, humid climate. Fruit Variety Journal 3: 2–5.
- Pady, S. M. (1972):** Spore release in powdery mildews. Phytopathology 62: 1099–1100.
- Pedersen, H. L., Christensen, J. V. & Hansen, P. (1994):** Susceptibility of 15 apple cultivars to apple scab, powdery mildew, canker and mites. Fruit Varieties Journal. 48 (2): 97–100.
- Salmon, E. S. (1900):** A monograph on the Erysiphaceae. Torrey Bot. Club. Mem. 9: 292. p.
- Seglias, N. P. & Gessler, C. (1997):** Genetics of apple powdery mildew resistance from *Malus zumi* (P12). Bulletin SROP 20: 105–109.
- Stephan, S. (1988):** Untersuchungen zu Sporulation und Sporenflug des Apfelmehltaus (*Podosphaera leucotricha* (Ell. et Ev.) Salm.) Arch. Phytopathol. Pflanzenschutz. 24 (6): 491–501.
- Stephan, S. (1989):** Untersuchungen zur Epidemiologie des Apfelmehltaus (*Podosphaera leucotricha* Ell. et Ev. (Salm.). Arch. Phytopathol. Pflanzenschutz. 25 (5): 449–458.
- Sutton, T. B. & Jones A. L. (1979):** Analysis of factors affecting dispersal of *Podosphaera leucotricha* conidia. Phytopathology. 69: 380–383.
- van der Scheer, H. A. T. (1989):** Susceptibility of apple cultivars and selections to scab and powdery mildew in The Netherlands. OILB Bulletin WPRS. XII/6: 205–211.
- Visser, T. & Verhaegh, J. J. (1979):** Resistance to powdery mildew (*Podosphaera leucotricha*) of apple seedlings growing under glasshouse and nursery conditions. Proceedings of Eucarpia Fruit Section Symposium. Tree Fruit Breeding, Angers, France, 111–120.
- Wolfe, M. S. & McDermott, J. M. (1994):** Population genetics of plant-pathogen interactions: the example of *Erysiphe graminis*-*Hordeum vulgare* pathosystem. Annual Review of Phytopathology. 32: 89–113.
- Woodward, R. C. (1927):** Studies on *Podosphaera leucotricha* (Ell. and Ev) Salm. I. The mode of perennation. Trans. Brit. Mycol. Soc. 12: 173–204.
- Xu, X. M., Butt, D. J. & Ridout, M. S. (1995):** Temporal patterns of airborne conidia of *Podosphaera leucotricha*, causal agent of apple powdery mildew. Plant Pathology. 44: 944–955.
- Yarwood, C. E. (1934):** The diurnal cycle of development of *Erysiphe polygoni*. J. Agr. Res. 52: 659–665.
- Yarwood, C. E. (1957):** Powdery mildews. The Botanical Review 23 (4): 235–300.