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Primary inoculum of *Venturia inaequalis* (Cooke) Wint. in its asexual form in apple – a review

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This review summarizes and discusses the geographical distribution, overwintering, dissemination, and management of the asexual stage of *Venturia inaequalis*, the fungal pathogen causing apple scab. The asexual overwintering of *V. inaequalis* has primarily been described as wood scab, superficial scab, or bud scab, and more rarely, it is mentioned as overwintering on infected leaves and fruits still attached to the trees. Wood scab is fungal pustules found on new and 1-year-old shoots, but it is also found on 2-year-old wood. It has been reported in many apple-growing countries throughout the world; however, most reports of wood scab being an important source of primary inoculum, as well as the most in-depth studies, are from the UK. Reports from some countries describe what is named superficial scab, which are symptomless infections of the pathogen on shoot surfaces. Overwintering of *V. inaequalis* on the inner or outer bud scales has also been reported in some countries. Infections may appear as small lesions on the bud scales, but numerous conidia have also been found in buds without symptomatic fungal tissue. The incidence and quantity of overwintering in the asexual stage are dependent on the amount of scab in the previous season, growth characteristics, and cultivar susceptibility. In orchards with limited options for fungicide control and/or in orchards with loss of scab control in the preceding season, conidia of *V. inaequalis* should not be underestimated as a source of primary inoculum.

KEYWORDS
bud scab, *Malus* × *domestica*, shoot scab, superficial scab, twig scab, wood scab

Introduction

Apple scab, caused by the ascomycete *Venturia inaequalis* (Cooke) Wint., is one of the most common diseases of apple (*Malus* × *domestica* Borkh.) worldwide. Overwintering as mycelium and conidia of *V. inaequalis* in shoots or buds is reported in many countries where apples are produced (Tables 1, 2). In 1855, Berkley in the UK was wondering why twigs of apple and pear were cracking, thus indicating the appearance of scab in the wood

(Marsh and Walker, 1932). Bagenal et al. (1925) claimed that until 1924, the only stage of *V. inaequalis* known in the UK, in which the fungus persisted through the winter, was on the 1-year-old wood of certain apple cultivars. However, no solid evidence for this statement was put forward.

Asexual overwintering of *V. inaequalis* has most commonly been described as dark pustules consisting of fungal stroma with conidial spores under the bark on twigs (Table 1). Such symptoms have been named shoot scab, twig scab, and wood scab and are designated as wood scab below. The fungus can also be symptomless as conidia or hyphae on the surface of shoots, and this is named superficial scab (Table 1). On both the inner and outer bud scales, the fungus may overwinter as visible fungal lesions or asymptomatically, both with conidia present. This is named bud scab (Table 2). Finally, shoot base scab are scab lesions expanding from the surface of 1-year-old shoots onto new emerging leaves and shoot tissues (Kennel, 1990). Leaves and non-detached fruits may stay on trees throughout winter and into the early spring and can potentially be sources of inoculum of apple scab (e.g., Young and Curtis, 1927; Shabi et al., 1981; Kennel, 1990; Washington et al., 1998; Von Diest et al., 2015), but this is not further discussed below.

Asexual overwintering as conidia in twig lesions in wood is reported also for other *Venturia* spp. (e.g., Saccas, 1944; Kienholz and Childs, 1951; Umemoto, 1992; Scherm et al., 2008). This review reports on the geographical distribution, overwintering, and dissemination of *V. inaequalis* in its asexual stage in wood and bud tissue, and briefly also on management.

Geographical distribution and importance

The occurrence of wood scab of *V. inaequalis* has been known for a long time (e.g., Cuboni, 1892; Sorauer, 1890; Stewart and Blodgett, 1899). In Europe, wood scab has especially been reported from the northwestern parts, including Ireland, Scandinavia, and the UK (Table 1). It was not detected in a survey in Finland (Hårdh, 1955). In Germany, Switzerland, and Poland, most reports describe symptomless superficial scab. In the Netherlands, it was concluded that the conidial inoculum of *V. inaequalis* from wood tissue was of minor importance (Holb et al., 2004; Holb et al., 2005). Wood scab has been reported in several states in northern regions of the USA

TABLE 1 Publications that report on *Venturia inaequalis* overwintering on apples in its asexual stage in wood pustules, and/or superficially on shoots.

Country	Reference
Australia	McAlpine, 1902; Washington et al., 1998
Belgium	Soenen et al., 1957
Canada	McCurry & Hicks, 1926; Hockey, 1953
Denmark	Weber, 1934; Weber and Jorgensen, 1953; Vang-Petersen, 1990;
France	Griffen and Maublanc, 1908; Saccas, 1944
Germany	Sorauer, 1890; Aderhold, 1900; Voges, 1907; Sorauer, 1908; Voges, 1910; Kennel, 1981a; Kennel, 1981b; Ahrens, 1985; Moosherr and Kennel, 1986; Moosherr and Kennel, 1995; Portz, 2002
India	Gupta and Lele, 1980
Ireland	McKay, 1938
Italy	Cuboni, 1892
The Netherlands	Goossens, 1934; Van der Scheer and Grabowski, 1991; Holb et al., 2004; Holb et al., 2005
New Zealand	Cunningham, 1925
Norway	Schøyen, 1907; Gjærum, 1962; Stensvand et al., 1996
Poland	Rogaś and Grabowski, 2005
Sweden	Eriksson, 1911; Olsson, 1960
South Africa	Louw, 1951
Switzerland	Müller-Thurgau, 1902; Wiesmann, 1932; Wiesmann, 1935; Siegfried et al., 1989
UK	Salmon (1906); Massee, 1910; Morse and Darrow, 1913; Bagenal et al., 1925; Moore, 1930; Marsh and Walker, 1932; Dillon Weston and Petherbridge, 1933; Preece, 1961; Swinburne, 1965; Cook, 1974; Hill, 1975; Jeger and Alston, 1986
USA	Illinois: Clinton, 1901; Maine: Morse and Darrow, 1913; Morse, 1916; Massachusetts: Nichols and Peterson, 1969; Nichols and Petersen, 1971; Montana: Morris, 1914; New Jersey: Cook and Schwarze, 1917; New York: Stewart and Blodgett, 1899; Wallace, 1913; Gloyer, 1937; Mills and Dewey, 1947; Becker, 1990; Becker and Burr, 1992; Ohio: Nichols and Peterson, 1969; Pennsylvania: Nichols and Peterson, 1969; Rhode Island: Nichols and Peterson, 1969; Washington: Lawrence, 1904

TABLE 2 Publications that report on *Venturia inaequalis* overwintering in its asexual stage in apple buds.

Country	Reference	Lesions[a]	Conidia[b]	Outer/inner bud scales[c]
Australia	Cass Smith et al., 1948; Jeffrey, 1953	+ +	+ n.d.	n.d.[d] n.d.
France	Saccas, 1944	+	+	outer, inner
Germany	Portz, 2002	+	+	**outer**, inner
Ireland	McKay, 1938	+	+	**outer**, inner
Japan	Kudo et al., 1976	+	+	outer, inner
The Netherlands	Van der Scheer and Grabowski, 1991	+	n.d.	n.d.
	Holb et al., 2004; Holb et al., 2005	-	+	outer, **inner**
South Africa	Louw, 1951	-	+	outer
	Von Diest et al., 2015	n.d.	+	inner
Sweden	Olsson, 1960	+	+	outer
UK	Salmon and Ware, 1931	+	+	outer, inner
	Hirst et al., 1955	+	-	Outer
	Dillon Weston et al., 1952	+	+	n.d.
USA, New York	Gloyer, 1937	+	+	n.d.
	Becker, 1990; Becker and Burr, 1992	+	+	outer, **inner**

[a]+/- indicates visible/not visible scab lesions.
[b]+/- indicates detection/no detection of conidia.
[c]Indicates if conidia were observed on the inner or outer bud scales; in bold if reported as most important.
[d]n.d. = no data reported.

(Table 1); however, with few exceptions (e.g., Morse and Darrow, 1913), it has not been considered important. Wood scab has been reported in Australia (McAlpine, 1902), New Zealand (Cunningham, 1925), India (Gupta and Lele, 1980), and South Africa (Louw, 1951) but as of minor importance. In a survey in Chile, wood scab was not detected (Montealegrale and González, 1982). Winter survival of *V. inaequalis* in buds has been reported in Australia, South Africa, and the USA, as well as in several countries in Europe and Asia (Table 2).

Pathogen development on shoots

Green, succulent tissue of shoots of apple trees may become infected by *V. inaequalis* (Marsh and Walker, 1932; Dillon Weston and Petherbridge, 1933; Hockey, 1953; Swinburne, 1965). Both vigorously growing terminal shoots and water sprouts (rapidly emerging shoots from dormant buds) are susceptible to wood infections (Morse and Darrow, 1913). Marsh and Walker (1932) and Swinburne (1965) in the UK and Saccas (1944) in France provided detailed descriptions and illustrations of the infection process of *V. inaequalis* in apple shoots. The fungus forms a lens-shaped parenchymatous tissue, forcing the epidermis and the cuticle apart. The epidermal cells in contact with the fungal tissue will collapse, and these cells are invaded by the fungus. New infections may take place at any time during the shoot growth, but only in the green apical regions. The time of infection determines the final position of the lesion on the shoot, i.e., early infections appear closer to the base, while later infections are further up along the shoots (Cook, 1974). In winter, the fungus may grow between the collenchyma and bark tissues to form subsidiary pustules, and this new extension of fungal growth remains covered until spring (Marsh and Walker, 1932). The fungal stroma is eventually stopped by the formation of cork barriers in the host tissue (Marsh and Walker, 1932; Saccas, 1944; Swinburne, 1965).

During late winter and early spring, the subsidiary stromata become thicker, with layers of radially arranged rows of fungal cells (Marsh and Walker, 1932; Cook, 1974). Conidiophores and conidia are formed under the bark although the bark is still unbroken. Eventually, the bark gives way to the pressure and is ruptured, and the formation of conidia begins in the central portions and spread toward the margins (Marsh and Walker, 1932). In late spring or early summer, further cork barriers are formed, and eventually, the infected tissue is sloughed off. Infections on apple shoots are predominantly found on new and 1-year-old wood (e.g., Marsh and Walker, 1932; Wiesmann, 1935; Saccas, 1944; Stensvand et al., 1996) but have been found on 2-year-old wood in early spring (Swinburne, 1965).

In the UK, the release of conidia on new shoots of cv. Cox Orange Pippin was observed from August to November, with a peak in October (Hill, 1975). There were low releases from December to February, high releases from March to May, and they ceased in June. Another study in the UK found conidia in wood pustules on 1-year-old wood from 2-3 weeks prior to bud burst, with the highest numbers in April and May (Cook, 1974).

Yet another study from the UK found the first conidia of *V. inaequalis* on wood pustules in early March (Dillon Weston and Petherbridge, 1933), and in Switzerland, conidia on wood pustules were recorded before mid-March (Müller-Thurgau, 1902). Conidia were produced in wood pustules from November to early July in Ireland but were most abundant from March to June (McKay, 1938). In Germany, the first conidia in wood pustules were found in late February and early March (Voges, 1910; Winkelmann et al., 1937). Conidia on new shoots were found in August and on 1-year-old shoots from March to September in Norway (Stensvand et al., 1996), and in France, conidia were produced in 1-year-old wood from February to April (Saccas, 1944). In New York, high numbers of conidia were observed in new infections on green shoots in July, while numbers and viability declined in October (Becker and Burr, 1992). Wood pustules of new apple shoots in Australia had conidiophores and conidia of *V. inaequalis* in early autumn (March) (Washington et al., 1998).

The viability of conidia from scab pustules of 1-year-old wood was 50 to 70% in April and May in the UK (Marsh and Walker, 1932). In Maine, high amounts of viable conidia in scab pustules were found in March and April, in the time before or around bud break (Morse and Darrow, 1913). In Norway, the viability of conidia was low in February, high in March to August, and low in September (Stensvand et al., 1996). Conidia on the surface of apple shoots in the Netherlands had a viability of less than 1.5% (Holb et al., 2004; Holb et al., 2005). In New York, very few viable conidia were found on wood in an unsprayed orchard in April (Becker and Burr, 1992).

Superficial scab on shoots

Shoot base scab is lesions appearing superficially on the surface of 1-year-old shoots and growing directly onto the new apple tissue (Kennel, 1990; Stensvand et al., 1996). However, superficial scab was described in Germany as asymptomatic scab overwintering as individual hyphae and/or conidia on the bark surface or on the trichomes (epidermal hairs) (Kennel, 1981a; Moosherr and Kennel, 1986; Moosherr and Kennel, 1995). It was speculated that the fungus could overwinter inside trichomes (Moosherr and Kennel, 1995), but this could not be confirmed by Portz (2002). In France, trichomes were also mentioned as retaining conidia of *V. inaequalis* during winter (Saccas, 1944). Superficial scab was commonly observed if trees started regrowth after summer pruning, thus providing a tissue highly susceptible to *V. inaequalis* (Kennel, 1981a; Moosherr and Kennel, 1995).

In spring, an average of 12% of the conidia would germinate from superficial scab, but occasionally, more than 50% were viable (Moosherr and Kennel, 1995). High numbers of overwintering conidia were found on apple wood in early spring in Poland, especially on trees with much scab the preceding autumn (Rogaś and Grabowski, 2005). In South Australia, no superficially overwintered conidia of *V. inaequalis* remained viable after mid-winter (Jeffrey, 1953).

Scab in apple buds

Bud scales can be infected by *V. inaequalis* when buds start to form (Saccas, 1944; Olsson, 1960), and both in Ireland (McKay, 1938) and New York (Becker, 1990), new buds were infected in July. On immature newly infected bud scales, conidiophores and conidia were formed in dark lesions, and later, a more developed stroma was developed that was mostly less than 1 mm in diameter in February (McKay, 1938). In New York, scab lesions on bud scales were up to 2 mm in diameter (Becker and Burr, 1992). The formation of stroma in bud scales in autumn and winter was also described by Salmon and Ware (1931) and Dillon Weston et al. (1952) in the UK and by Saccas (1944) in France. Both external and internal bud scales can carry mycelial stroma, and it was stated that vegetative and generative buds constituted a source of inoculum as important as wood scab (Saccas, 1944). A mean viability of conidia of 77% was found in New York just before bud break, and viability was lowest for conidia of outer bud scales (Becker and Burr, 1992). Scab lesions were found in bud scales in several apple orchards in South Australia at the time of bud burst (Jeffrey, 1953).

Both in the Netherlands and New York, viable conidia were present in buds without any apparent lesion formation (Becker and Burr, 1992; Holb et al., 2004; Holb et al., 2005). It was speculated that conidia may remain ungerminated from the previous season, or that non-visible lesions had formed. Saccas (1944) indicated that conidia of *V. inaequalis* may themselves produce a conidiophore identical to the one normally formed by the hyphae. Most conidia were found on the outer bud scales, with a mean viability of only 2%, while viability from inner bud scales was up to 11% (Holb et al., 2004; Holb et al., 2005). In South Africa, the viability of conidia of *V. inaequalis* from inner bud tissue varied from 0 to 29% (Von Diest et al., 2015).

Although conidia of *V. inaequalis* from apple buds were found in February in Ireland, the majority were produced from mid-April to June (McKay, 1938). The reason why inoculum from bud scales was present until June may be because the lowermost part of the scab-infected scales remained attached to the shoots, as described by Salmon and Ware (1931). In Japan, scab pustules were observed on overwintering outer and inner bud scales of apple, and conidia in buds were formed before the ascospores in leaf litter (Kudo et al., 1976). In Sweden, scab pustules on infested bud scales were exposed and produced conidia in April (Olsson, 1960). Indications have been provided that new leaves can be infected prior to bud break, before they emerge (Bagenal et al., 1925; Saccas, 1944; Portz, 2002).

Factors influencing overwintering in the asexual stage

Numerous authors have concluded that overwintering in the asexual stage of *V. inaequalis* on wood or in the buds is associated with high inoculum in the orchards the preceding autumn (e.g., Morse and Darrow, 1913; Soenen et al., 1957; Siegfried et al., 1989; Van der Scheer and Grabowski, 1991; Becker and Burr, 1992; Holb et al., 2004; Holb et al., 2005; Rogaś and Grabowski, 2005; Von Diest et al., 2015). It has also been speculated that specific strains of the fungus may be more aggressive on wood (Cook, 1974).

Holb et al. (2004) concluded that conidia were unlikely to overwinter on the surface of apple tissues if they were exposed to fluctuating environmental conditions as in the Netherlands. Moosherr and Kennel (1995) speculated that insufficient winter hardiness and part death of shoots that had emerged after summer pruning was a less favorable environment for superficial scab. In experiments under controlled conditions, conidia of *V. inaqualis* survived repeated temperature fluctuations around 0°C, with minor losses in viability (Portz, 2002). Another study showed minimal loss of viability of conidia if kept at -5°C for 150 days or -10°C for one month (Saccas, 1944).

The amount of trichomes may vary with the genotype and stage of development of the apple tree. It has been speculated that trichomes may be barriers preventing spores from reaching the cuticle of the shoot surface, or contrary, that trichomes may prevent drying and thus create a better environment for fungal infection (Marsh and Walker, 1932). In a study in Germany, it was concluded that dense growth of trichomes on the shoots prevents infection by *V. inaequalis* (Portz, 2002).

In older literature from the UK and Ireland, cultivars reported as susceptible to wood scab included Bramley's Seedling, Cox Orange Pippin, Egremont Russet, and Worcester Pearmain (Bagenal et al., 1925; Salmon and Ware, 1931; Marsh and Walker, 1932; Dillon Weston and Petherbridge, 1933; McKay, 1938; Preece, 1961; Swinburne, 1965), while cv. Blenheim Orange was mentioned as slightly to moderately susceptible (Salmon and Ware, 1931; Dillon Weston and Petherbridge, 1933; Preece, 1961). Cvs. Bramley's Seedling and Cox's Orange Pippin were mentioned as susceptible to wood scab also in Germany (Ahrens, 1985). In Canada and USA, cv. McIntosh was considered susceptible to wood scab (Morse and Darrow, 1913; Morris, 1914; McCurry and Hicks, 1926), as well as cv. Fameuse (Morse and Darrow, 1913). In Norway, wood scab was detected on all seven apple cultivars examined, including five with high susceptibility to scab (Gravensteiner, Lobo, Quinte, Summerred, and Vista Bella), and two with moderate to low susceptibility (Ingrid Marie and Torstein) (Stensvand et al., 1996). In Germany, Moosherr and Kennel (1995) reported that cvs. Gloster, Golden Delicious, and Jonagold frequently developed superficial scab. Medium to less susceptible cultivars were Cox Orange, James Grieve, and Jonathan, and the least susceptible was Gravensteiner. In Poland, cv. McIntosh was highly susceptible to superficial scab but was also found on cvs. Idared and Jonagold (Rogaś and Grabowski, 2005).

Control measures

Saccas (1944) suggested chemical treatments in the autumn when infections of the young twigs start to occur, as well as one or more treatments at the beginning of vegetation when overwintering conidia are released. Holb et al. (2004) indicated that a fungicide spray at bud break may protect against overwintered conidia. Marsh and Walker (1932), and Wiesmann (1935) considered that fungicide application in spring would likely not control scab in wood pustules because fungicides would only kill the outer layer of the exposed stroma, and lower portions would remain unharmed. They claimed that the prevention of new shoot infections during the summer and autumn would be more appropriate. The application of urea in autumn or spring reduced the formation of conidia in wood lesions (Cook, 1974), and the use of lime sulfur or copper compounds killed conidia and parts of the stroma in wood scab pustules of apple (Morse and Darrow, 1913; Weber, 1934).

Holb et al. (2004) found the most overwintered conidia in the upper third part of the shoots of the tree, and they, therefore, suggested pruning out that portion of the 1-year-old shoots combined with a fungicide spray at bud break. Moosherr and Kennel (1995) strongly recommended avoiding improper summer pruning since it promotes late shoot growth, thus providing a substrate for superficial scab infection.

Discussion

In reports from many apple-growing regions of the world, it has been shown that *V. inaequalis* can overwinter either as fungal stroma, inconspicuous hyphae, or conidia on apple shoot tissue and serve as sources of primary inoculum in spring. It seems evident that the asexual stage is associated with the presence of a high inoculum from the previous growing season; however, in most orchards with good scab control, primary inoculum from conidia is likely to be of minimal importance.

Historically, overwintering in scab pustules in shoots (wood scab) was frequently reported and considered more important in the UK than anywhere else. It may be speculated that predominant cultivars and the cool and wet weather during parts of the growing season when the green shoot and bud tissue is susceptible may be reasons for this. It is known that there can be significant genetic variations in strains of *V. inaequalis* within and between orchards, and among regions in a country (e.g., Xu et al., 2013; Koopman et al., 2017; Passey et al., 2017). Further speculation may thus be that the presence of specific strains of the fungus could explain a higher frequency of asexual overwintering in the UK, as indicated by Cook (1974).

Reports on wood and bud scab are commonly found in early reports when fungicide use was less intense, and at that time, the inoculum was likely higher. However, in organic production with strong restrictions on the use of chemicals or in integrated production with insufficient scab control, e.g., due to fungicide resistance, the risk of heavy scab attacks in autumn and asexual overwintering may occur. In an unsprayed research orchard in the UK, 20-50% of primary infections originated from conidia (Passey et al., 2017), clearly indicating that if scab control is lost, asexual overwintering of *V. inaequalis* may be important the following year. If overwintered conidial inoculum appears, it is ready to infect already at bud break and may cause early infections of the flower and fruit sepals and, thereby, be a source for severe fruit infections later in the season (Kennel and Moosherr, 1983; Kennel, 1987; Becker and Burr, 1992). To avoid overwintering in the asexual stage, attention must be drawn to avoid the build-up of the disease late in the season, and also following harvest, which is a time growers are often not focused on scab control.

Author contributions

RR and AS surveyed the literature, planned, and wrote the manuscript, and AV critically revised the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

Aderhold, R. (1900). Die Fusicladien unserer Obstbäume, II. *Landw. Jahrb.* 29, 541–587.

Ahrens, P. G. (1985). Die Möglichkeiten einer Bekämpfung des Apfelschorfes im Rahmen des integrieten Pflanzenschutzes. *Erwerbsobstbau* 27, 90–95.

Bagenal, N. B., Goodwin, W., Salmon, E. S., and Ware, W. M. (1925). Spraying experiments against apple scab. *J. Mineral Agric.* 32, 137–149.

Becker, C. M. (1990). Overwintering of the anamorph of *Venturia inaequalis* (*Spilocaea pomi*) in apple buds and the viability of conidia as affected by discontinuous wetting. *PhD thesis. Ithaca (NY): Cornell Univ.* 86.

Becker, C. M., and Burr, T. J. (1992). Overwintering of conidia of *Venturia inaequalis* in apple buds in New York orchards. *Plant Dis.* 76, 121–126. doi: 10.1094/PD-76-0121

Cass Smith, W. P., Harvey, H. L., and Goss, O. J. (1948). Apple scab outbreaks season 1947-48, with special reference to the introduction of the disease by infected buds on imported nursery stock. *W. Aus. J. Agric.* 25, 129–135.

Clinton, G. P. (1901). Apple scab. *Univ. Illinois Agric. Exp. Stn. Bull.* 67, 118.

Cook, R. T. A. (1974). Pustules as sources of inoculum in apple scab and their responses to chemical treatments. *Ann. Appl. Biol.* 77, 1–9. doi: 10.1111/j.1744-7348.1974.tb01381.x

Cook, M. T., and Schwarze, C. A. (1917). Apple scab on the twigs. *Phytopathology* 7, 221–222.

Cuboni, G. (1892). Sulla Forma ibernante del *Fusicladium dendriticum*. *Bull. Soc. Bot. Ital.* 1, 287–288.

Cunningham, G. H. (1925). *Fungous diseases of fruit trees in New Zealand and their remedial treatment* (Auckland, New Zealand: Brett Printing and Publishing Co.).

Dillon Weston, W. A. R., and Petherbridge, F. R. (1933). Apple and pear scab in East Anglia. *J. Pomol. Hortic. Sci.* 11, 185–198. doi: 10.1080/03683621.1933.11513417

Dillon Weston, W. A. R., Storey, I. F., and Ives, J. V. (1952). Apple scab in the Wisbech area. *Garden. Chron.* 132, 195.

Eriksson, J. (1911). Die rote Farbe der Fruchtschale und die Schorfkrankheit der Obstsorten. *Z. f. Pflanzenkrankh.* 21, 129–131.

Gjærum, H. B. (1962). Skurv på frukttrær. [In Norwegian]. *Landbruksdepartementets opplysningstjeneste Småskrift* 1/62, 8.

Gloyer, W. O. (1937). Evaluation of the Geneva experiment on scab control. *Phytopathology* 27, 129.

Goossens, J. (1934). Onderzoek naar de erste infectiebron van appel- en peerenschurft. *T. Pflantenziekten* 40, 174–176.

Griffen, E., and Maublanc, A. (1908). Note sur diverses maladies des branches du pommier. *Bull. Séances Soc. Natl. Agric.* 8.

Gupta, G. K., and Lele, V. C. (1980). Morphology, physiology and epidemiology of the apple scab fungus, *Venturia inaequalis* (Cke.) Wint., in Kashmir Valley. *Indian J. Agric. Sci.* 50, 51–60.

Hårdh, J. E. (1955). Omenarupi ja sen torjunta suomessa. [In Finnish, English summary]. *Publ. Finnish State Agric. Res. Board* 144, 43.

Hill, S. A. (1975). The importance of wood scab caused by *Venturia inaequalis* (Cke.) Wint. as a source of infection for apple leaves in spring. *Phytopathol. Z.* 82, 216–223. doi: 10.1111/j.1439-0434.1975.tb03486.x

Hirst, J. M., Storey, I. F., Ward, W. C., and Wilcox, H. J. (1955). The origin of apple scab epidemics in the Wisbech area in 1953 and 1954. *Plant Pathol.* 4, 91–96. doi: 10.1111/j.1365-3059.1955.tb00749.x

Hockey, J. F. (1953). Studies in fruit diseases IX. Apple scab. *Dept. Agric., Ottawa, Canada* 519, 1–8.

Holb, I. J., Heijne, B., and Jeger, M. J. (2004). Overwintering of conidia of *Venturia inaequalis* and the contribution to early epidemics of apple scab. *Plant Dis.* 88, 751–757. doi: 10.1094/PDIS.2004.88.7.751

Holb, I. J., Heijne, B., and Jeger, M. J. (2005). The widespread occurrence of overwintered conidial inoculum of *Venturia inaequalis* on shoots and buds in organic and integrated apple orchards across the Netherlands. *Eur. J. Plant Pathol.* 111, 157–168. doi: 10.1007/s10658-004-1883-z

Jeffrey, M. W. (1953). Preliminary investigations into the life cycle of *Venturia inaequalis* (Cooke) Wint. in South Australia. *Aust. J. Aric. Res.* 4, 415–422. doi: 10.1071/AR9530415

Jeger, M. J., and Alston, F. H. (1986). Resistance in apple to shoot infection by *Venturia inaequalis*. *Ann. Appl. Biol.* 108, 387–394. doi: 10.1111/j.1744-7348.1986.tb07660.x

Kennel, W. (1981a). Integrierte Bekämpfung des Apfelschorfes (*Venturia inaequalis*). *Erwerbsobstbau* 23, 132–135.

Kennel, W. (1981b). Zum auftreten von Schorfkonidien auf äußerlichunversehrter Rinde von Apfelzweigen. *Mitt. BBA Heft* 203, 117.

Kennel, W. (1987). Kelchblätter als erste Objekte für Apfelschorf. *Erwerbsobstbau* 29, 36–38.

Kennel, W. (1990). Die Überwinterung des Apfelschorfs. *Obstbau* 8/90, 346–347.

Kennel, W., and Moosherr, W. (1983). Kelchblattschorf, eine gefährliche aber wenig bekannte Erscheinungsform des Apfelschorfs. *Obstbau* 8/83, 470–472.

Kienholz, J. R., and Childs, L. (1951). Pear scab in Oregon. *Agric. Exp. Stn. Oregon State Coll. Corvallis Stn. Techn. Bull.* 21, 31.

Koopman, T. A., Meitz-Hopkins, J. C., Bester-van der Merwe, A. E., Tobutt, K. R., Bester, C., and Lennox, C. L. (2017). Genetic diversity and gene flow of four South African *Venturia inaequalis* (apple scab) populations. *Phytopathology* 107, 455–462. doi: 10.1094/PHYTO-07-16-0279-R

Kudo, T., Takahashi, S., and Mizuno, N. (1976). Studies on scab disease (*Venturia inaequalis* (Cooke) Winter) of apple. 1. Overwintering of apple scab fungus on the bud scales. *Bull. Akita Fruit Tree Exp. Stn.* 8, 19–29.

Lawrence, W. H. (1904). The apple scab in Western Washington. *Wash. Agric. Exp. Stn. Bull.* 64, 23.

Louw, A. J. (1951). Studies on the influence of environmental factors on the overwintering and epiphytology of apple scab [*Venturia inaequalis* (Cke.) Wint.] in the winter-rainfall area of the Cape Province. *Union S. Afr. Dep. Agric. Sci. Bull.* 310, 47.

Marsh, R. W., and Walker, M. M. (1932). The scab fungus (*Venturia inaequalis*) on apple shoots. *J. Pomol. Hortic. Sci.* 10, 71–90. doi: 10.1080/03683621.1932.11513393

Massee, G. (1910). *Diseases of cultivated plants and trees* (Duckworth & Co: London).

McAlpine, D. (1902). The apple scab fungus causing black spot of apple and pear. *Victoria Agric. Dept. J.* 1, 703–708.

McCurry, J. B., and Hicks, A. J. (1926). Sixth annual report on the prevalence of plant diseases in the Dominion of Canada. *Canada Expt. Farms, Div. Bot. Ann. Rpt., Canad. Plant Dis. Survey* 6, 1–47.

McKay, R. (1938). Conidia from infected bud-scales and adjacent wood as a main source of primary infection with the apple scab fungus *Venturia inaequalis* (Cooke) Wint. *Sci. Proc. R. Dublin Soc.* 21, 623–640.

Mills, W. D., and Dewey, J. E. (1947). Control of diseases and insects in the orchards. *Cornell Ext. Bull.* 711, 89.

Montealegrale, J. A., and González, S. M. (1982). Prospeccion de invernacion de *Fusicladium dendriticum* (Wallr.) Fckl. en ramillas de manzano durante la prima-vera de 1979 en la provincia de Valdivia, Chile. *Agro Sur.* 10, 47–48.

Moore, M. H. (1930). The incidence and control of apple scab and apple mildew at East Malling. *J. Pomol. Hortic. Sci.* 8, 283–304. doi: 10.1080/03683621.1930.11513365

Moosherr, W., and Kennel, W. (1986). Zur epidemiologischen Bedeutung von superfiziellem Zweigschorf bei Apfelbäumen. *Mitt. BBA Heft* 232, 212.

Moosherr, W., and Kennel, W. (1995). Investigations on superficial apple scab on apple shoots. *Z. Pflanzenk. Pflanzen* 102, 171–183.

Morris, H. E. (1914). A contribution to our knowledge of apple scab. *Montana Agric. Coll. Exp. Stn. Bull.* 96, 65–102.

Morse, W. J. (1916). Spraying experiments and apple diseases in 1915. *Maine Agric. Exp. Stn. Bull.* 252, 190–192. doi: 10.5962/bhl.title.86714

Morse, W. J., and Darrow, W. H. (1913). Is apple scab on young shoots a source of spring infection? *Phytopathology* 3, 265–269.

Müller-Thurgau, H. (1902). Die Schorfkrankheit der Obstbäume. *Jahresb. D. deutsch-schweizerischen Versuchsstation und Schule F. Obst. Wein- und Gartenbau Wädenswil* 9, 60–65.

Nichols, L. P., and Petersen, D. H. (1969). Occurrence of the apple scab fungus on twigs of flowering crab apples and one cultivar of commercial apple. *Plant Dis. Rep.* 53, 974.

Nichols, L. P., and Petersen, D. H. (1971). Overwintering of *Fusicladium dendriticum*, the imperfect stage of the apple scab fungus on twigs of flowering crab apples. *Plant Dis. Rep.* 55, 509–510.

Olsson, K. (1960). En inventering av gren- og knoppskorv på äpple. [In Swedish]. *Väkstskyddsnotiser Statens Växtskyddsanstalt* 23, 5–9.

Passey, T. A. J., Robinson, J. D., Shaw, M. W., and Xu, X. (2017). The relative importance of conidia and ascospores as primary inoculum of *Venturia inaequalis* in a southeast England orchard. *Plant Pathol.* 66, 1445–1451. doi: 10.1111/ppa.12686

Portz, C. (2002). *Venturia inaequalis* (Cke.) Wint. beim Apfel: Bedeutung der Konidien als Primärinokulum, Einfluss auf die Knospenentwicklung und Alternativen zum Kupfereinsatz bei der Kontrolle des Blatt- und Fruchtschorfbefalls. *PhD thesis at Hohen Landwirtschaftlichen Fakultät der Rheinischen Friedrichs-Wilhelms-Universität*, 158.

Preece, T. F. (1961). Scabbed wood on Bramley's Seedling apple. *Plant Pathol.* 10, 39–40.

Rogaś, K., and Grabowski, M. (2005). The effect of autumn infection of apple leaves on the occurrence of the conidial stage of fungus *Venturia inaequalis* (Cooke) Aderh. on one-year-old shoots. *Acta Sci. Pol. Hortorum Cultus* 4, 21–26.

Saccas, A. (1944). *Étude morphologique et biologique des Fusicladium des Eosacees* (Librairie Le François), 317.

Salmon, E. S. (1906). Apple scab or black spot. *Gard. Chron.* 40, 21–23.

Salmon, E. S., and Ware, W. M. (1931). A new fact in the life-history of the apple scab fungus. *Gard. Chron.* 89.

Scherm, H., Savelle, A. T., Boozer, R. T., and Foshee, W. G. (2008). Seasonal dynamics of conidial production potential of *Fusicladium carpophilum* on twig lesions in southeastern peach orchards. *Plant Dis.* 92, 47–50. doi: 10.1094/PDIS-92-1-0047

Schøyen, W. M. (1907). Æbleskurv. [In Norwegian]. *Fra Landbrugsdepartementet. Meddelelser fra Statsentomologen* 3, 1–4.

Shabi, E., Elisha, S., and Zelig, Y. (1981). Control of pear and apple diseases in Israel with sterol-inhibiting fungicides. *Plant Dis.* 65, 992–994. doi: 10.1094/PD-65-992

Siegfried, W., Bosshard, E., and Schüepp, H. (1989). Das Schorjahr 1988. *Schweiz. Z. Obst- und Weinbau* 125, 175–182.

Soenen, A., Aerts, R., and Porreye, W. (1957). La tavelure du pommier. *Rev. L'Agric.* 6, 681–749.

Sorauer, P. (1890). Der Grind des Apfelbaume. *Oesterr. Landwirtsch. Wochenbl.* 15, 121.

Sorauer, P. (1908). III C. Ascomycetes Pleosporaceae. *Handbuch der Pflanzenkrankheiten* 2, 249.

Stensvand, A., Amundsen, T., and Semb, L. (1996). Observations on wood scab caused by *Venturia inaequalis* and *V. pirina* in apple and pear in Norway. *Norw. J. Agr. Sci.* 10, 533–540.

Stewart, F. C., and Blodgett, F. H. (1899). A fruit disease survey of the Hudson Valley in 1899. *New York Agric. Exp. Stn. Bull.* 167, 283.

Swinburne, T. R. (1965). Apple scab infection of the young wood of Bramley's Seedling trees in Northern Ireland. *Plant Pathol.* 14, 23–25. doi: 10.1111/j.1365-3059.1965.tb00614.x

Umemoto, S. (1992). A simple method for estimating conidial numbers of Japanese pear scab in suspension. *JARQ* 26, 34–40.

Van der Scheer, H. A., and Grabowski, M. (1991). Ascosporen meestal dader van schurftinfecties in het voorjaar. *Fruitteelt* 16, 28–29.

Vang-Petersen, O. (1990). Varsling af skurv. [In Danish]. *Frugtavleren* 10/90, 301–306.

Voges, E. (1907). Über die Schorfkrankheit der Obstbäume. *Deut. Landw. Presse* 34, 276–285.

Voges, E. (1910). Die Bekämpfung des Fusicladium. *Z. f. Pflanzenkrankh.* 20, 385–393.

Von Diest, S. G., Meitz-Hopkins, J. C., MacHardy, W. E., and Lennox, C. L. (2015). Overwintering of *Venturia inaequalis* conidiospores in South African apple orchards. *IOBC/WPRS Bull.* 110, 123–124.

Wallace, H. H. (1913). Scab disease of apples. *New York Cornell Agr. Exp. Stn. Bull.* 335, 543–624.

Washington, W. S., Villalta, O. N., Ingram, J., and Bardon, D. (1998). Susceptibility of apple cultivars to apple scab and powdery mildew in Victoria, Australia. *Austral. J. Exp. Agric.* 38, 625–629. doi: 10.1071/EA98073

Weber, A. (1934). Undersøgelser over æbleskurvens (*Venturia inaequalis*) overvintring. [In Danish]. *Tidsskrift Planteavl* 40, 754–758.

Weber, A., and Jorgensen, H. A. (1953). Forsøg med bekæmpelse af æbleskurv efter løvfald samt undersøgelse over skurvens modningstid. [In Danish]. *Beretning fra Statens Forsøgsvirksomhed i Plantekultur* 469, 443–469.

Wiesmann, R. (1932). Untersuchungen über die Überwinterung des Apfelschorf – Pilzes *Fusicladium dendriticum* (Wallr.) Fckl. im toten Blatt sowie die Ausbreitung der Sommersporen (Konidien) des Apfelschorfpilzes. *Landw. Jahrb. Schweiz* 46, 619–679.

Wiesmann, R. (1935). Untersuchungen über die Bedeutung des Ascosporen (Wintersporen) und der Konidien an den schorfigen Trieben für die Entstehung der Primärinfektionen des Apfelschorfpilzes *Fusicladium dendriticum.. Landw Jahrb. Schweiz.* 49, 147–175.

Winkelmann, A., Holz, W., and Jaenichen, H. (1937). Beiträge zur Biologie und Bekämpfung des Apfelschorfes (*Fusicladium dendriticum* (Wallr.) Fckl.). III. *Zbl. für Bakt.* 96, 177–191.

Xu, X., Harvey, N., Roberts, A., and Barbara, D. (2013). Population variation of apple scab (*Venturia inaequalis*) within mixed orchards in the UK. *Europ. J. Plant Pathol.* 135, 97–104. doi: 10.1007/s10658-012-0068-4

Young, H. C., and Curtis, M. (1927). The timing of apple scab sprays. *Ohio Agric. Exp. Stn. Bull.* 403, 3–28.