

Review Article

<https://doi.org/10.20546/ijcmas.2019.801.019>

Studies on Biology and Management of Apple Scab Incited by *Venturia inaequalis*

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ABSTRACT

Apple (*Malus × domestica*) is an important fruit crop cultivated worldwide. Apple orchards are exposed to a diverse set of environmental and biological factors that affect the productivity and sustainability of the apple cultivation. Many of the efforts for apple production rely on reducing the incidence of fungal diseases, and one of the main diseases is apple scab caused by the fungus *Venturia inaequalis* (Cooke) Wint. Apple scab is the most devastating important disease of cultivated apple causing economic losses in terms of fruit quality and yield in many apple growing areas. Apple scab attacks foliage, blossoms and fruits, resulting in the defoliation of trees and making the fruits unmarketable. If the disease is not controlled effectively, more than 80 percent fruits of susceptible cultivars can be damaged. Depending on the severity of disease, 10 to 15 or even more fungicidal applications are usually needed for efficient control. The uncontrolled disease may result in almost devastation of whole crop. The main strategy used for scab control is still the frequent application of fungicides throughout the season. However, selection pressure has led to the evolution of fungicide-resistant strains of scab that represent a threat to the apple industry. Therefore, all the research work in apple growing regions will be focus on identifying and creating commercial varieties with long lasting resistance characteristics and develop alternative strategies to manage apple scab. Main strategies for effectively managing apple scab includes use of resistant cultivars, tolerant rootstock, effective control of primary and secondary infection through use of an integrated crop management system, biological control, use of biotechnological approaches that maximizes yield and quality of apple.

Keywords

Biology and
Management,
Apple scab,
Venturia inaequalis

Article Info

Accepted:
04 December 2018
Available Online:
10 January 2019

Introduction

Apple (*Malus x domestica* Borkhausen) is an important fruit species widely cultivated in the temperate regions of the world (Harris *et al.*, 20002). It ranks third in terms of production with annual production of about

84.6 million tons (FAOSTAT, 2014). Apple is a major industrial fruit and millions of people are associated with it. However like any other crop species many diseases cause huge economic losses to the growers. Usually, apples are consumed fresh or after storage for up to 6 months or even longer. It can be also

an important raw material for many fields of processing industry like juice, sauce, slices, vinegar and cider (Vejl *et al.*, 2003; Folta and Gardiner, 2009). Apple is attacked by several pathogens for example fungi, bacteria, viruses, mycoplasmas and nematodes. Among fungal diseases is the main problem for commercial apple production in temperate and humid regions. It has been reported that apple is host to over 70 infectious diseases; most of these diseases are caused by pathogenic fungi. They cause root rots, leaf blights, leaf spots, blossom blights, fruit decay, fruit spots, canker and post-harvest decay. Among the common fungal diseases, apple scab is the major fungal disease in commercial apple production in temperate and humid regions of the world (Sandskar, 2003). Apple scab is caused by *Venturia inaequalis* (Cooke) Wint. The first report on scab was published by Fries in Sweden in 1819 (Fries, 1819), but the oldest clue to the existence of scab dates from 1600, in a painting by Michelangelo Caravaggio ('The Supper at Emmaus'), held at the National Gallery, London (MacHardy *et al.*, 2001). *Venturia inaequalis* has a wide geographical range and is found in almost all region in which apples are grown commercially. However, the disease is more severe in temperate region with cool, moist climates during early spring (MacHardy, 1996). Direct infection of fruits and pedicels results in yield losses. In addition, severe leaf damage can lead to a weakened tree with reduced flower bud formation (Verma and Sharma, 1999). If the apple scab is chemically controlled losses can be minimized, but the production costs increase together with increasing health and ecological concerns (Patrascu *et al.*, 2006). A well-integrated approach is usually needed to achieve successful disease management, for example improve the environment and selection of a suitable site for the orchard, selection of resistant or tolerant rootstocks and grafts (scion) varieties, application of

fungicides and biological disease control are among the tools used to control apple scab disease (Jonsson, 2007; Dewasish and Amal, 2010). Since the late nineteenth century, apple scab has been extensively investigated, and substantial information covering all key aspects of the biology and genetics of the fungus and the epidemiology and control of the disease has been published and reviewed by Machardy (1996) and Bowen *et al.*, (2011). In contrast to the efforts devoted to investigating *Venturia inaequalis*, little work has been conducted on *Venturia* spp. affecting other fruit trees. This difference in research effort and number of publications, however, does not directly reflect the importance of the host crop worldwide. The difference might be explained by (i) minor investments in these non-apple crops, (ii) less specialized management directed at the non-apple crops, and (iii) the common use of the information developed for *Venturia inaequalis* for managing the other fruit scabs. Concerning the last point, researchers generally assume that infection of any scab fungus may occur under environmental conditions similar to those required by *Venturia inaequalis*. The Mills and Laplante's (1954) table, which is the most popular system for scheduling fungicides against apple scab, has been broadly recommended for management of pear scab (Sobreiro and Mexia, 2000; Mitcham and Elkins, 2007; Travis *et al.*, 2012; Elkins *et al.*, 2016), cherry scab (Schweizer, 1958), peach scab (Keitt, 1917; Pineau *et al.*, 1991), and loquat scab (Ramos, 2008). However, there is no clear evidence that the environmental conditions conducive for infection are similar for all of these *Venturia* species. In fact, recent studies have revealed important differences concerning the environmental requirements for infection by *F. eriobotryae* and *F. oleagineum* vs. *Venturia inaequalis* (Viruega *et al.*, 2011; Gonzalez-Dominguez *et al.*, 2013). In addition, substantial differences exist in the

ecophysiologicals and the life cycles of their hosts. Objectives of this review are: to summarize the review and simplify the use of different disease control measures in an integrated management program, and different defense mechanisms of apple to *Venturia inaequalis*.

Taxonomy

Apple scab is caused by a pathogen fungus including two different states: *Venturia inaequalis*, the perfect (sexual) or saprophytic state and *Spilochaetia pomorum* Fr., the imperfect (asexual) or parasitic state (Jamar, 2011). *Venturia inaequalis* belongs to genus *Venturia* (Lepoivre, 2003). It can be classified it to the subdivision of Ascomycota, class Loculoascomycetes, order Pleosporales and family Venturiaceae (MacHardy, 1996). *Spilochaetia pomorum* Fr. is placed in the subdivision of Deuteromycota, class Hyphomycetes, order Moniliales (Lepoivre, 2003). Basically, *Venturia inaequalis* only infects *Malus* species. It is a non-pathogen to all non *Malus* plants. However, pathogens responsible for scab on *Malus* sp. and *Pyracantha* sp. are considered as two formae speciales belonging to *Venturia inaequalis* (Cam *et al.*, 2002). Yet, while the genus *Malus* is the main host of *Venturia inaequalis*, not all *Malus* genotypes are susceptible.

Venturia inaequalis was one of the first studied ascomycetes and remains to be a practical implementation for numerous genetic studies, for example, its sexual compatibility and the heritability of pathogenicity. This is caused by similarity to other parasites that infect young living tissues without obvious damage for a long period as well as its ability to be cultivated and mate *in vitro* (Vaillancourt and Hartman, 2000). Among the characteristics that make *Venturia inaequalis* so acceptable to genetic studies include its genotype and phenotype stability for many years and large diversity in nature.

Living tissues are infected by heterothallic fungus *Venturia inaequalis* (Jha *et al.*, 2009).

Apple scab physiological races

The concept of race as a fixed genetic unit is not valid for an obligatory sexually reproducing organism. The terminology 'race' used for *Venturia inaequalis* indicate an isolate capable of infecting and sporulating on a particular host resistant to other isolates; as such it should be called physiological race as in the early literature. In other words, in the case of an obligatorily sexually reproducing pathogen like *Venturia inaequalis*, the word 'race' indicates nothing more than the presence or lack of virulence traits with respect to specific hosts on which the isolate is tested. Eight physiological races of scab are currently defined according to their virulence on 'specific host' varieties as shown in table 1. The first three of these were identified by Shay and Williams (1956) Race 1 is taken as a well sporulating isolate on popular domestic cultivars and eliciting flecks or necrotic lesions without sporulation on *Malus* clones Dolgo, R12740- 7A and Geneva (Shay and Williams, 1956). Race 2 can sporulate on 'Dolgo,' 'Geneva' and certain offspring of 'R12740-7A.' Race 3 is characterized as being able to sporulate on 'Geneva,' otherwise being the same as race 1, and race 4 differs from 1 by sporulating on those offspring of 'R12740-7A' that race 2 is not able to sporulate on. Race 5 has the ability to sporulate on carriers of the Vm resistance and can thus circumvent the resistance of *Malus micromalus*. Race 6 first appeared at Ahrensburg, in Germany, in the nineteen-eighties (Bus *et al.*, 2005). It is virulent on most of the varieties containing the Vf gene, but not on clone.

Symptoms of the disease and host range

The most visible and severe symptoms of apple scab occur on leaves and fruits. It also

visible on sepals and petals, young shoots and bud scales (Sandskar, 2003; Daniels, 2013; Turechek, 2004; Giraud *et al.*, 2011). The earliest symptoms of the apple scab are usually appearing on the underside of emerging cluster leaves. However, symptoms may first develop on the upper side of these leaves in cases where significant infection was delayed. Young lesions are velvety brown to olive green and have feathery, indistinct margins. Lesions expand with time and may coalesce with other leaf lesions. The number of lesions can vary from very few to several hundred per leaf. Young leaves with significant infection often curl, shrivel and fall from the tree. However, it is not atypical for infected leaves to remain on the tree for the entire season. The term “sheet scab” refers to the condition when the entire leaf surface is covered with the disease; when this occurs, leaves typically shrivel and fall to the ground. Eventually, fungal growth stops and the lesions develop distinct margins. The infected leaf tissue around lesions often becomes thickened and lead to bulging of the infected area and a corresponding cupping of the area underneath the leaf lesion.

Lesions on the petiole (leaf stem) extend along the length of the petiole and are similar in appearance to those on the leaf. Severe infection of the petiole typically leads to a yellowing of the infected leaf and eventual leaf drop. On the fruit, young lesions appear similar to those on leaves. Although the entire surface of the fruit is susceptible to infection, lesions often cluster around the calyx end of the fruit (Fig. 1). As lesions get older they become brown and corky and take on a “scabby” appearance. Early infections kill the expanding tissue which often results in deformed fruit. As lesions age, they typically crack and provide sites that may serve as an opening to invasion by secondary pathogens. Infections late in the season are usually not detectable until after harvest when the fruit

are in storage. This is referred to as “pin-point scab”. The term “storage scab” refers to incipient infections that were too small to see prior to fruit storage or may be the result of infections during storage that occur as a result of sporulation from older scab lesions.

Life cycle and epidemiology of apple scab

The ascomycete *Venturia inaequalis* infects members of the subfamily Maloideae, and causes the disease apple scab. *Venturia inaequalis* is a hemibiotrophic fungus. It overwinters mostly in dead fallen leaves, in which microscopic flask-formed black fruiting bodies, called pseudothecia, are formed. In the early spring, the ascospores inside pseudothecia start to mature and in suitable weather conditions, when leaves become wet after the rain, spores are forcibly ejected into the air (Sandskar, 2003; Jamar, 2011). The life cycle of *Venturia inaequalis* can be subdivided into two phases: primary or sexual phase and secondary or asexual phase (Figure 1). The primary phase mainly occurs in winter and the secondary in summer (MacHardy, 1996; Verma and Sharma, 1999). Primary phase/Sexual reproduction phase generally creates primary infection. The fungus over winters remains as pseudothecia (sexual fruiting bodies) that develop in apple leaf litter following a short phase (maximum of four weeks) of saprophytic vegetative growth after leaf abscission. As most ascomycetes, *Venturia inaequalis* is anisogamous: the sex organs are differentiated into ascogonia in the female and antheridia in the male haploid parent. Also, it is heterothallic: plasmogamy of the two gametangia can only proceed if the antheridium and the ascogonium originate from parents of opposite mating type, i.e. carry different mating type alleles on the mating type (MAT) locus. The mating type is the result of a complex interaction between the gene products encoded by the different

genes which are situated on MAT locus (Gisi *et al.*, 2002; Billiard *et al.*, 2011). The ascospores are produced in the asci which are in turn carried by the pseudothecium (Daniels, 2013). The optimal temperature for the development of ascogonia and maturation of the ascospores is 8-12° C and 16-18° C, respectively (Turechek, 2004). The primary inoculum is released by rainfall in spring within five to nine weeks and mainly consists of ascospores (Sandskar, 2003). The sexual spores have inner and outer cell wall. The outer cell wall is fragile and thin. The inner cell wall is elastic and thick that protects the ascospores from winter conditions (Jha *et al.*, 2009). The asci also have a double cell wall. The release of ascospores takes place if the inner and outer cell walls of the asci break. During rainfall, a thin water film is developed around the pseudothecia due to asci adsorb water and expand. Because of the building pressure first the outer cell wall breaks and, after some time, also the inner. The release of ascospores is mainly takes place during the day favoured by sunlight (Biggs and Stensvand 2014; Rossi *et al.*, 2001). The spores are spread up to 200 m from the source by the wind (Turechek, 2004). The primary inoculum lands on the host plant surface (inoculation) after which an infection can take place when conditions are favourable. Free moisture on the leaf surface is necessary for spore germination. Once initiated, the germination will continue as long as the relative humidity (RH) is more than 95% (Turechek, 2004). Spore germination does not guarantee infection. The further development of the fungus is dependent on the temperature, the duration of leaf wetness and the susceptibility of the plant itself and of the inoculated plant organ such as leaves vs. sepals and petals, age of the leaf. Meteorological criteria defining the duration of (leaf) wetness required for infection at different temperatures were first proposed by (Daniels, 2013), and are known as Mills'

periods. These criteria have become a standard tool, in combination with electronic weather monitoring, for identifying when conditions favourable for infection occur, so that fungicide applications can be targeted effectively. Infection risk is greatest early in the growing season when leaves and fruit are young and at their most susceptible developmental phase (Xu and Robinson, 2005). The germ tubes arising from ascospores penetrate through the cuticle not through stomata *via* an appressorium and differentiate to form sub cuticular runner hyphae. At regular intervals, from these sub cuticular hyphae, multilayered, pseudo parenchymatous structures, termed stromata, formed. Stromata are made up of laterally dividing cells and these are presumed to obtain nutrients from the sub cuticular space (Lepoivre, 2003; Jha *et al.*, 2009). Secondary phase/Asexual reproduction of *Venturia inaequalis* starts by producing conidia, these conidia responsible for secondary infection. *Spilocae apomi* is known as the conidial stage of the *Venturia inaequalis*. The conidia are olive/brown colored single-cells with width of 6-12µm and length of 12- 22µm. They are produced one after the other at the tip of hyphae termed as conidiophores. The conidia and conidiophores give a distinctive velvety exterior to the newly formed lesions of scab as mass produced on the thick mat of mycelium (Vaillancourt and Hartman, 2000). Once distributed by wind and flopping rain, conidia land on an apple blossom or fruit and leaves, and stick to the surface and germinate. The hyphae germination breaks through the cuticle and develops a new infection (Fig. 2).

The conidia of *Venturia inaequalis* are able to adhere and germinate also on non-host plants. Like in the case of ascospores, the discharging of conidia depends on temperature as well as moisture and humidity, and may develop from few days to a couple of weeks after initial leaf infection. The

favourable conditions for the development of secondary infection by conidia are wet and cool days in spring, summer and fall (Biggs and Stensvand, 2014). Many cycles of conidial production and secondary infection take place during particular growing period under the suitable weather conditions. Late infection in autumn may not be detected. But, during storage, it can affect fruits (Sandskar, 2003).

Control measures of the disease

Host plant resistance

Besides considerations such as fruit quality, productivity, ease of tree management and commercial criteria, it is also essential use varieties that are more resistant to apple scab diseases and other pest. Therefore, now a day there is more than 100 apple cultivars are released with reaction to *Venturia. inaequalis* (Table 2) (Beckerman, 2006). To reduce fungicide applications, apple breeders are currently introgressing disease resistance from wild *Malus* accessions into commercial lines. The first attempts were made 100 years ago. Genetic resistance to the apple scab pathogen was originally found in a crab apple, *Malus floribunda* 821 and therefore most of today's scab-resistant cultivars rely on a single introduction of scab resistance from *Malus floribunda* 821, referred to as Vf (Gessler and Pertot, 2012). Currently cultivars with scab resistance incorporate several dominant resistance genes, most of which are located at the Vf locus of the apple genome. Generally, in apple scab disease management, resistance breeding is the most efficient and effective method. But, this has been complicated by the presence of several races or forms of the fungus, and the fact that plants resistant to one race may be susceptible to another, because of the scab strains' ability to adapt to a specific host plant (Carisse *et al.*, 2006). So, the immunity of some species of

wild *Malus* or certain cultivated genotypes can break down if new scab races/forms appear (Benaouf and Parisi, 2000). 'Golden Delicious' is good example which was regarded as relatively scab resistant at the beginning of 20 century and has now become extremely susceptible (Carisse *et al.*, 2006). Therefore, disease management practices on scab resistant cultivars, should take into consideration the development of new strains of *Venturia inaequalis* that may be virulent on the cultivars resistant to only one strain of the pathogen (Parisi *et al.*, 1993). Commonly, apple cultivars differ greatly in regard to their resistance and susceptible level to scab. For instance, in Europe and New Zealand, over 50 scab-resistant cultivars have been released based on apple breeding programs. Redfree, Prima and Liberty are good examples of resistant cultivars (Table 2) (Lepoivre, 2003; Benaouf and Parisi, 2000; Shane, 2016) (Fig. 3).

Resistant varieties

There are a number of apple varieties that have high levels of resistance to apple scab disease (Carisse and Dewdney, 2002). Currently, there are six major genes that impart resistance to apple scab: Vf (*Malus floribunda*), Vr (Russian apple seedling), Vbj (*Malus baccata* Jackii), Vb (Hansen's *baccata*), Va (Antonovka), and Vm (*Malus micromalus* susceptible to race 5). Each of these genes, except for Vm, confer resistance to all known races of the pathogen. Nearly all resistant commercial varieties contain the Vf gene. Resistant varieties include 'Prima', 'Priscilla', 'Macfree', 'Florina', 'Liberty', 'Jonafree', and 'Pioneer' to name a few. These varieties are planted primarily in organic orchards and not widely planted in many commercial orchards. The role of cultivar susceptibility has received little attention in disease management, particularly in forecasting. The original Mills curves were

developed for the highly susceptible cultivar 'McIntosh'. Aldwinckle (Aldwinckle, 1974) ranked 51 varieties but made no attempt to adjust Mills' curves based on his findings. Olivier (1984) also ranked cultivars into susceptibility groups for the selection of an appropriate infection curve but does not seem to have verified his results to confirm his classification. Schwabe (1980) in South Africa tested commercial varieties for differences in leaf wetness required for infection and reported that all cultivars required between 3-6 hrs of wetness for ascospore infection but made no mention of the relative susceptibility of the cultivars. In a 3 year study, Ellis *et al.*, (1998) evaluated the efficacy and economics of using an inorganic (primarily sulfur) and conventional spray program to manage apple scab on the scab-resistant variety 'Liberty' and the scab-susceptible variety 'McIntosh' in Ohio. During the three year period, an average of 5 and 9 applications of fungicide were applied under the conventional program and 7 and 12.6 applications under the inorganic program on 'Liberty' and 'McIntosh', respectively. The reduction in the number of sprays on 'Liberty' was associated with the elimination of all pre-petal fall applications which are usually targeted for apple scab. This resulted in a cost savings of 73% and 57% for the inorganic and conventional, respectively, for apple scab disease management on 'Liberty' compared to 'McIntosh'. Despite the savings, apple scab resistant varieties are not widely grown as there is virtually no consumer demand for these varieties.

Structural and biochemical defence mechanisms of Apple for *Venturia inaequalis*

Both structural (cuticle) and biochemical (relative oxygen species, enzymes, defence proteins, phytoalexins, phytoanticipins, hormones, etc.) defence mechanisms have

role against apple scab disease causing pathogen. Cuticle is one of the outer structural defence mechanisms of plants. It is a protective film cover the epidermis of leaves, young shoots and other aerial plant organs without periderm (Kolattukudy, 1996). It consists of lipid and a three dimensional hydrocarbon polymer impregnated with cuticular wax Beisson *et al.*, 2012). The physical and chemical properties of cuticular waxes have role in vital functions for plants i.e. limits water loss, inhibits the growth and development of disease causing pathogens such as bacteria and fungi (Dominguez *et al.*, 2011). The pathogen *Venturia inaequalis* needs certain amount of free water on surface of leave in order to survive and the composition, the thickness and robustness of cuticle also determine the speed with which the *Venturia inaequalis* able to penetrate the host plant. Generally, the properties of the cuticle and the hydrophilicity of the leaf change during development. This would play a role in ontogenic resistance (Jha *et al.*, 2009). The role of a number of PR proteins has been demonstrated in apple scab defence. A comparative study by (Gau *et al.*, 2004) between the apoplastic protein accumulation of the Rvi6 resistant cultivar 'Remo' and the susceptible cultivar 'Elstar' found that, the apoplast is formed by the continuum of cell walls of adjacent cells as well as the extra-cellular matrix. It is important for all the plant's interaction with its environment. By means of two-dimensional gel electrophoresis (2-DE) and mass spectrometry, differences in concentration of a number of PR proteins between both cultivars (resistant and susceptible) were detected. In the susceptible cultivar 'Elstar' the number of detectable apoplastic proteins more than doubled after infection. Most of the extra proteins detected had an isoelectric point between 4 and 5 (Gau *et al.*, 2004). The concentrations of the respective PR-2, PR-3 and PR-8 proteins β -1,3-glucanase (36-40 kDa), chitinase (27-28

kDa) and endochitinase type III (27-28 kDa) are higher prior to infection in cv. 'Remo' than in 'Elstar'. After infection by *Venturia inaequalis*, the concentrations in 'Elstar' become similar to those in 'Remo'. This suggests a constitutive accumulation of these proteins only in the resistant cultivar. B-1, 3-glucanase, chitinase and endochitinase are capable to hydrolyze the fungal cell wall. The chito-oligosaccharides that are formed as a result of the endochitinase activity would induce defense mechanisms through a yet uncharacterized pathway (Paris *et al.*, 2009). A thaumatin-like protein (PR-5) is constitutively present in higher concentrations in the apoplast of the resistant cv. Remo. In the susceptible 'Elstar', the accumulation increases upon infection. Thaumatin (21 kDa) is a sweet-tasting protein and considered a prototype for a PR protein (Gau *et al.*, 2004). These authors also detected osmotin like proteins and a PR-1 protein (15-16 kDa). A possible explanation is that this protein would play a role in the recognition of the pathogen and the onset of the defence response. It would interact with pathogen's effectors and induce a non-specific, systemic resistance (Blein *et al.*, 2002). The lipid transfer protein also transfers phospholipids through membranes and would play a role in the formation of the cuticle and epicuticular wax (Diaz-Perales *et al.*, 2002). The reduced accumulation of the Mald3 gene that codes for this lipid transfer protein was confirmed by Paris *et al.*, (Paris *et al.*, 2009). The accumulation of a number of Mald1 proteins of the ribonuclease type (PR-10) is increased after infection in HcrVf2 transformed 'Gala' (Paris *et al.*, 2009). Besides, the expression of genes that code for defencing-like proteins (PR-12) is also increased after infection. Plant defences would exert their antifungal activity by altering fungal membrane permeability and by inhibiting fungal macromolecule biosynthesis (Thevissen *et al.*, 1999). Phenolic compounds of apple and their

relationship to scab resistance Phenolic compounds would play important role in the defence of apple against *Venturia inaequalis*. For instance, the elimination of phenyl alanine ammonia-lyase (PAL), a very important enzyme in the phenol synthesis signal transduction pathway, turns the resistant cv. 'Sir Prize' susceptible (Mayr *et al.*, 1997). PAL catalyzes the first step in the phenyl propanoid pathway and is therefore involved in the biosynthesis of phenolic compounds such as phenyl propanoids, flavonoids and lignin in plants. The activity of PAL is known to be induced dramatically in response to various stimuli, including pathogenic attack (MacDonald and D'Cunha, 2007). The main phenolic compounds are present in both susceptible and resistant cultivars. However, the absolute amounts and relative proportions of these compounds differ. Rvi6 cultivars generally have higher total phenol contents, as well as greater amounts of particular phenolic molecules, as compared with susceptible cultivars, even as these levels vary over the course of the season (Petkovsek *et al.*, 2009) and are influenced by cultural practices (Petkovsek *et al.*, 2010). An example of a phenolic compound that is present in higher amounts in older leaves and in resistant apple cultivars is chlorogenic acid (Petkovsek *et al.*, 2009). Not only the phenols themselves, but also their degradation products also contribute to resistance development. Phlorizin for example is the most prominent phenolic glycoside in apple and has an inhibitory action on *Venturia inaequalis* (Gosch *et al.*, 2009). It is mainly present in the cuticle and thus would influence the most critical moment in the survival of the fungus after inoculation: the germination and penetration in the subcuticular space. *Venturia inaequalis* converts phlorizin to phloretin. This compound has an antifungal action as well (MacHardy, 1996). Gessler *et al.*, (2006) concluded from the studies that it is not the

constitutive presence of phenols that causes resistance, but rather a local accumulation and transformation activated by an elicitor. Infection of apple by *Venturia inaequalis* also leads to an accumulation of flavanols in the region adjacent to the scab lesions (Mayr and Treutter, 1998). Malusfuran and derivatives of dibenzofuran are produced upon fungal attack and suppress the germination and growth of *Venturia inaequalis* (Jha *et al.*, 2009).

Cultural control methods

Standard cultural and sanitary practices are used to reduce scab infection such as leaf shredding, burning or burying leaves in the soil, and application of 5% urea (approximately 40 pounds urea in 100 gallons of water) onto leaves on the floor, which help to reduce the development of *Venturia inaequalis* (Giraud *et al.*, 2011; Ziemis, 2009). However, these inoculum reduction practices may be expensive and impractical for some commercial operations, and never fully eradicate all sources of primary inoculum (Sutton *et al.*, 2000; Merwin *et al.*, 1994). In general, to prevent spread of inoculum from crab apple trees to apple trees, crab apple trees at the edges of the apple orchard should be removed. Regular pruning is also necessary for the proper sunlight penetration and air circulation in the canopy and between trees for the prevention of scab development. Selecting sites that provide more than six hours of sunlight per day, spacing trees adequately, and following proper pruning practices to open the tree canopy can be also minimize or even prevented the disease (Beckerman, 2006a).

Pruning

To reduce apple scab, it is necessary to keep the leaves as dry as possible, in other words, to avoid planting too close together, to ventilate the canopy by pruning and to avoid

planting in wet, low-lying areas (Corroyer and Petit, 2002). Kolbe (1983) found that orchards which promote circulation of air through the rows and between the rows by means of appropriate pruning have lower levels of scab in the long term. Holb (2005) compared three pruning models (intense, moderate and none) on two very susceptible cultivars (cv. Jonagold and cv. Mutsu), two susceptible cultivars (cv. Elstar and cv. Idared) and two resistant cultivars (cv. Liberty and cv. Prima) in an organic apple orchard. He concluded, notably, that intense pruning of susceptible cultivars results in significantly less scab on the leaves and fruit as compared to other two models. Simon *et al.*, (2006) showed the favourable effects of centrifugal as training compared to conventional solaxetraining on scab control, interpreting these results as being due to better ventilation within the tree and, therefore, a microclimate which is unfavourable to scab.

Inoculum reduction

Scab over winters mainly on dead leaves fallen on the ground and these are therefore the main source of the primary inoculum that causes contamination the following spring (MacHardy *et al.*, 2001). The two main ways of discouraging the primary inoculum are (i) to reduce the mass of scabbed leaf litter and (ii) to prevent *Venturia inaequalis* developing in the litter that remains (MacHardy *et al.*, 2001). Several other studies have also shown the effects of sanitary practices such as burning or burying leaves in the soil (Gomez *et al.*, 2004), leaf shredding (Vincent *et al.*, 2004; Holb *et al.*, 2006) and a combination of shredding and using urea (Sutton *et al.*, 2000) on reducing scab inoculum. These studies found that an ascosporic inoculum reduction of between 40 and 95% and a correlated scab reduction of 45 to 85%. Collecting leaves from the ground in the inter-rows in autumn along with burying the leaves left along the row has

a positive effect in discouraging primary contamination (Gomez *et al.*, 2004). Gomez *et al.*, (2004) reported that for two consecutive years the practice of 'raking and ridging' reduced the severity of scab on the fruit by 68 to 74%, depending on the year. Burchill *et al.*, (1965) first showed that application of 5% urea to English orchards in the autumn completely suppressed ascospore production the following spring. Burchill (1968) treated Bramley's Seedling trees at two sites in Kent with a post-harvest, pre-leaf fall application of 5% urea; scab lesions on blossom-spur leaves were reduced by 59% and 46%, respectively, the following spring compared to the untreated control. Mitre *et al.*, (2012) studied the effect of applications of urea 5% after harvest but before leaf-fall, as foliar application, in order to restrict perithecial production by *Venturia inaequalis* in a commercial super intensive apple orchard situated near Cluj-Napoca, Romania. The results found that large reductions in spore production, often as high as 70 to 80%, following application of 5% urea. Spraying the surface of the leaves on the ground with urea 5% reduced primary infection by about 60%.

Fertilization

Professional fruit grower requires regular supplement of minerals to warrant fruit set and quality. Heavy nitrogen fertilization supports tree and fruit growth i.e. it is a prominent controlling tool for yield. An enhanced vegetative growth of apple trees, however, is often correlated with an increasing susceptibility to pathogens such as *Venturia inaequalis* (Leser and Treutter, 2005). This may be result of the concomitant decrease of phenolic compounds by high nitrogen uptake (Leser and Treutter, 2005), indicating that environmental conditions favouring plant growth reduce investment of carbon for defence. Kumar and Gupta (1986)

reported that a high level of potassium fertilizers increased resistance of apple tree to scab but a similar effect was not obtained with high levels of phosphorus fertilization.

Biological control methods

Biological control is the method of controlling or suppressing of plant disease by using other microorganisms (Pal and Gardener, 2006). Several studies have identified different antagonistic agent to manage *Venturia inaequalis*. Such as, *Microsphaeropsis ochracea*, which occurs naturally on dead leaves and isolated, as a good antagonist of *Venturia inaequalis* when applied in August and September resulting in a 95 to 99% reduction in spring ascospore production as compared to untreated treatments (Carisse and Rolland, 2004). This potential biological control method is not solely sufficient for management of apple scab to commercially acceptable level. Therefore, cultural and potential biological practices would have to be used in combination with a fungicide spray program (MacHardy, 1996). MacHardy (1996) identified two antagonistic fungi, *Athelia bombacina* and *Chaetomium globosum* which are potentially useful as biological control agents for *Venturia inaequalis*. *Chaetomium globosum* applied during the secondary infection season could be beneficial, it decreases the size and number of lesions, the conidial density and the conidial germ tube germination rate and elongation. Vincent *et al.*, (1986) observed a reduction in spring ascospore production of about 81 and 85% following autumn application of *Athelia bombacina* and *Microsphaeropsis ochracea*, respectively. Several studies showed that some fungi such as *Auerobasidium botrytis*, *Cladosporium* spp. and several epiphytic yeast strains from the apple tree phyllosphere are capable to inhibit *Venturia inaequalis* germination and mycelial growth

on apple tree plantlets by up to 80%. Some strains of *Trichoderma longibrachiatum* also found antagonistic towards *Venturia inaequalis*, decreasing ascospore production from naturally infected leaves (Fiss *et al.*, 2003; Palani and Lalithakumari, 1999) The earthworms, *Lumbricus terrestris* are the main natural biological agents for removing dead fallen leaves from orchard floors in winter and early spring (Holb *et al.*, 2006). In grassed-down orchards the number and weight of leaves buried are directly related to the weight of *Lumbricus terrestris* in the soil. In some orchards containing between 275 and 367 kg of *Lumbricus terrestris* per hectare, the earthworms can bury up to 184 kg of leaves per hectare, which is equivalent to 90% of the total autumn leaf fall (MacHardy, 1996). At the same time, this is a major contribution to the turnover and redistribution of organic matter in the soil.

Chemical control method

On susceptible apple cultivars, apple scab is primarily managed through the application of fungicides (Diaz-Perales *et al.*, 2002). At the end of 19th century first chemical fungicides, especially protective fungicides based on copper against pathogen *Venturia inaequalis*, were discovered. However, in some countries, the use of copper as fungicides in apple fruit is totally prohibited. These constraints drive growers to use large quantities of sulphur-based fungicides, which may have other drawbacks. Recently based on epidemiological trainings, mineral fungicides like sulfur with less toxicity were developed (Jamar, 2011). Farmers have to treat apple cultivars, which are vulnerable for scab, many times with fungicides per season (Soriano *et al.*, 2009). Also in organic apple production, applications of mineral substances like sulfur, lime sulfur, and copper salts are essential for effective scab management to preserve the resistance of cultivars and to prevent initial

infection (Daniels, 2013; Beckerman, 2009). Preventing early or initial infection of apple scab produced by ascospores is the most critical step toward successful control of later leaf and fruit infections, on which chemical control of apple scab is concentrated. Later fungicide sprays are targeted at other fungal diseases as well as against secondary infection of apple scab. The strategies of using fungicides are formed on the base of studies of apple scab epidemiology and biology throughout the years (Alaniz *et al.*, 2014; Cova *et al.*, 2015). In general, growers apply preventive and curative chemical fungicides together for good efficiency that are capable of stopping fungus development (Vaillancourt and Hartman, 2000; Chapman *et al.*, 2011). Even though, regular and well-timed fungicide sprays have proven to be the most commercially practical means of controlling scab for susceptible apple trees, but the first line of defense is to consider scab-resistant apples (Ziems, 2009) and at present, to reduce fungicide applications, enhanced strategies are developed based on a better understanding of the airborne spreading of ascospores, host foliage and fruit area, and the host defenselessness against infection. In addition, repeated application of fungicide for apple scab management result in high costs in terms of money and for the fungicide sprays and in the time dedicated to scab management. Because of increasing pressure on apple growers to reduce pesticide use and reduce production costs, while maintaining a high level of crop quality, we believe it is crucial and timely to simplify and optimize apple scab management (Gessler *et al.*, 2006). Therefore, this is indicating that researchers or growers will focus into new strategies for controlling apple scab in apple production. Generally, selection pressure has resulted in the evolution of fungicide-resistant strains of scab that represent a threat to the industry. For example, dodine was first released in 1959 to control scab, and 10 years later resistance was

first recorded (MFPMG, 2017; Szkolnik and Gilpatrick, 1969). In addition, resistance of *Venturia inaequalis* to demethylation inhibitors fungicides was documented in practice (Braun 1994). Strategies to delay the development of resistance to the different classes of fungicides under field conditions rely on restricting the number of applications per season of fungicides in each class and mixing or alternating fungicides of different classes (Lepoivre, 2003). Therefore, the use of compounds or fungicides, acting via elicitation or priming for plant defense enhancement, and the development of new, durable scab-resistant apple cultivars will most likely gain importance in future apple scab management strategies.

Integrated disease management Integrated Disease Management (IDM)

IDM is a multidisciplinary strategy for disease management that seeks to achieve long-term effectiveness, affordability, and minimal environmental disruption (Fadamiro *et al.*, 2003). IDM tactics include host plant resistance, cultural practices, biological controls and chemical application. All these

methods are used in combination and more likely to be effective to managing disease as compared to reliance on a single technique, such as calendar-based pesticide spraying (Trumble, 1998; Shumann. and D’Arcy, 2006). IDM programs for scab control usually focus on reduction of primary inoculum, or reducing fungicidal sprays using predictive models. The pathogen, *Venturia inaequalis* has high pathogenic variability and new races of the pathogen are evolved frequently.

Therefore, IDM is the most effective approach to minimize the yield losses due to scab. Malavolta and Cross (2009) stated that, IDM has made tremendous progress in terms of tree nutrition, plant protection product spraying quality, restriction on post-harvest treatments, soil management, selection and rate of application of active substances used in disease and pest control and timing of pest treatments, based on an assessment of the actual risk they pose. Pruning in combination with fungicide use has been shown to significantly reduce leaf scab because it improved spray deposition in the tree canopy (Holb, 2005).

Table.1 Physiological races of *Venturia inaequalis* (Bus *et al.*, 2005; MacHardy, 1996)

Races	Pathological characteristics on apple cultivars
Race 1	Non sporulating lesion on Dolgo, R 12740-7A (a Russian cultivar) and Geneva
Race 2	Sporulating lesions on Dolgo, Geneva and some progenies of R 12740-7A
Race 3	Sporulating lesions on Geneva, and non sporulating lesion on Dolgo, R 12740-7A
Race 4	Non sporulating lesion on Dolgo, Geneva and sporulating lesion on those progenies of R12740-7A on which race 2 isolates cannot sporulate
Race 5	Sporulating lesions on Vm R gene containing cultivars
Race 6	Sporulating lesions on Vf hybrids but cannot infect <i>Malus floribunda</i> 821 containing Vf _h R gene
Race 7	Can infect cultivars having Vf and Vf _h R gene but cannot infect Golden delicious which contains Vg gene
Race 8	Can infect Golden delicious, Royal gala, and cultivars containing Vh ₈ R gene

Table.2 List of apple cultivars reaction to apple scab

Apple cultivar	Apple scab	Apple cultivar	Apple Scab	Apple cultivar	Apple Scab	Apple cultivar	Apple Scab	Apple cultivar	Apple Scab
Adam's Permain	MR	Crimson Crisp	VR	Golden Delicious	VS	Jonamac	S	Murray	R
Akane	R	Delicious (Red)	S	Gold Rush	VR	Jonathan	S	Mutsu (Crispin)	VS
Ambrosia	VS	Dayton	VR	Granny Smith	S	Julyred	VS	Newtown Pippin	S
Ashmead's Kerne	MR	Early McIntosh	S	Gravenstein	S	Lodi	S	NJ90	MR
Baldwin	S	Empire	VS	Grimes Golden	R	Macfree	R	Northern Spy	S
Beacon	S	Enterprise	VR	Haralson	MR	Macoun	VS	Nova Easygrow	VR
Belmac	R	Florina (Querina)	R	Honey Crisp	MR	McIntosh	VS	Novamac	VR
Braeburn	S	Freedom	VR	Honey Gold	R	Melrose	VS	Nova Spy	R
Britegold	R	Fuji	S	Idared	S	Milton	S	Paula Red	R
Cameo	S	Gala	VS	Jerseymac	VS	Moira	R	Pink Lady	VS
Cortland	VS	Ginger Gold	VS	Jonagold	S	Mollies Delicious	S	Pinova (Corrail)	R
Prima	VR	Roxbury Russet	S	Starkspur Earliblaze	S	Trent	VR	Winesap	VS
Priscilla	VR	Runkel	R	Stark Splendor	S	Viking	S	Winter Banana	VS
Pristine	VR	Scarlet O'Hara	VR	Stayman	VS	Wayne	S	Wolf River	R
Puritan	S	Silken	VS	Summer red	S	Wealthy	S	Yellow Transparent	MR
Redfree	R	Sir Prize	VR	Suncrisp	MS	Wellington	S	York Imperial	S
R.I. Greening	S	Spijon	S	Sundance	VR	William's Pride	VR	Zestar	MS
Rome Beauty	VS	Stark Bounty	S						

Abbr: Where, VR=Very Resistant; VS=Very Susceptible; R= Resistant S=Susceptible; MR=Moderately Resistant and MS=Moderately Susceptible) (Jamar, 2011; Jha *et al.*, 2009; Ziems, 2009; Shane, 2016)

Figure.1 (a) Apple scab lesion in the early stage of development; (b-c) secondary scab lesions on leaves; (d-e) scab lesions on fruits; and (f) pin-point scab (Gessler *et al.*, 2006; Carisse *et al.*, 2006)

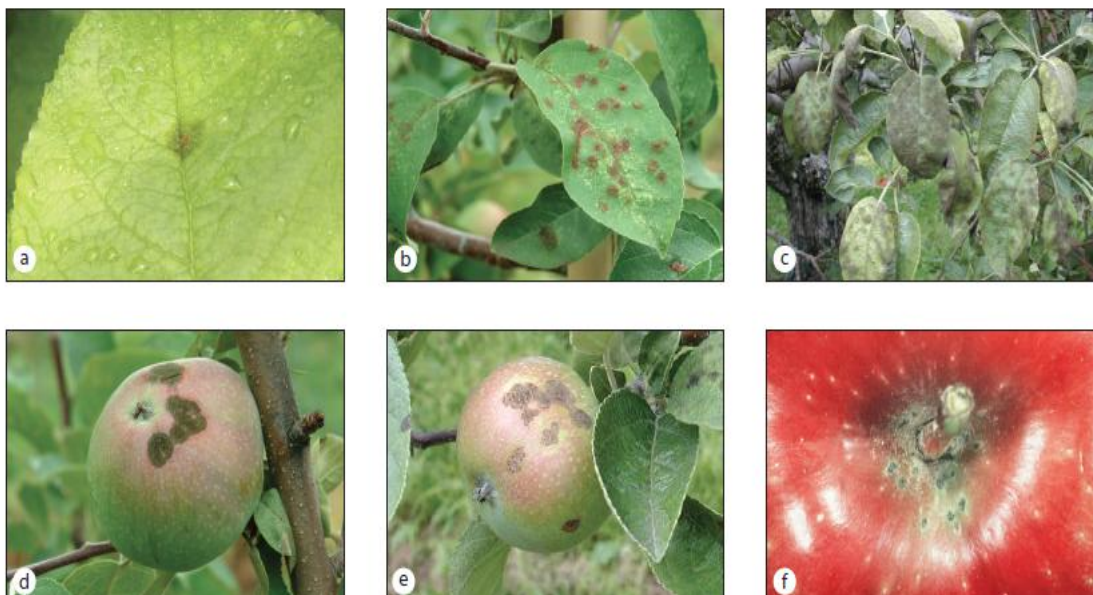


Figure.2 Apple scab disease cycle (Cornell University, NYSAES, Geneva, NY.).

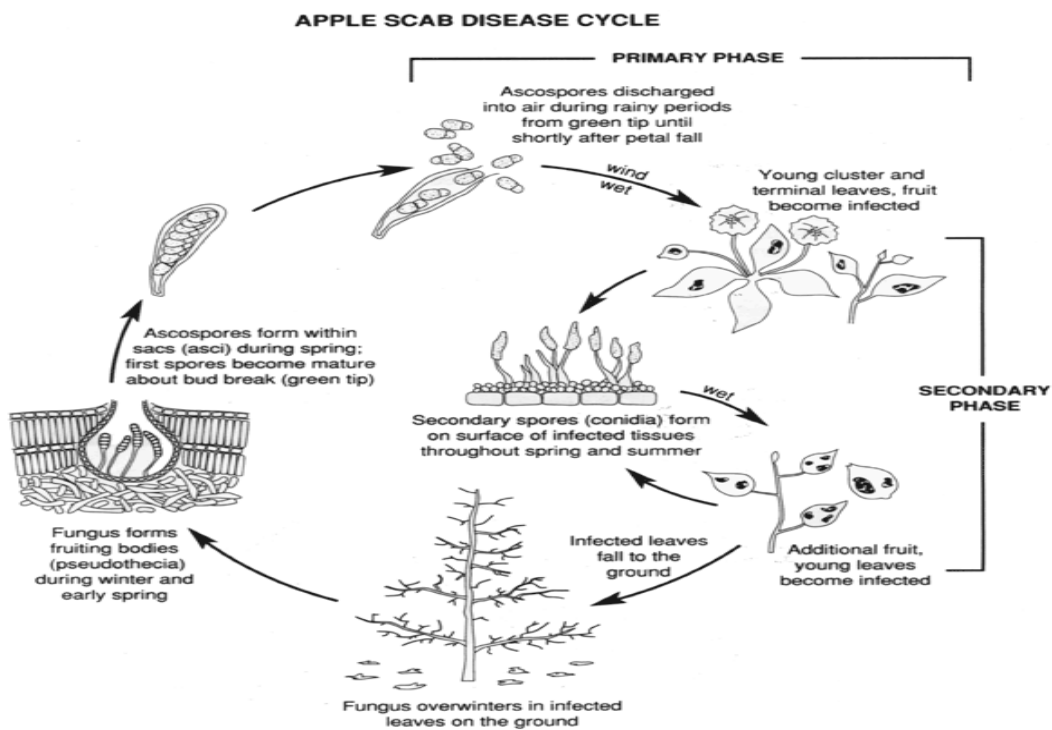
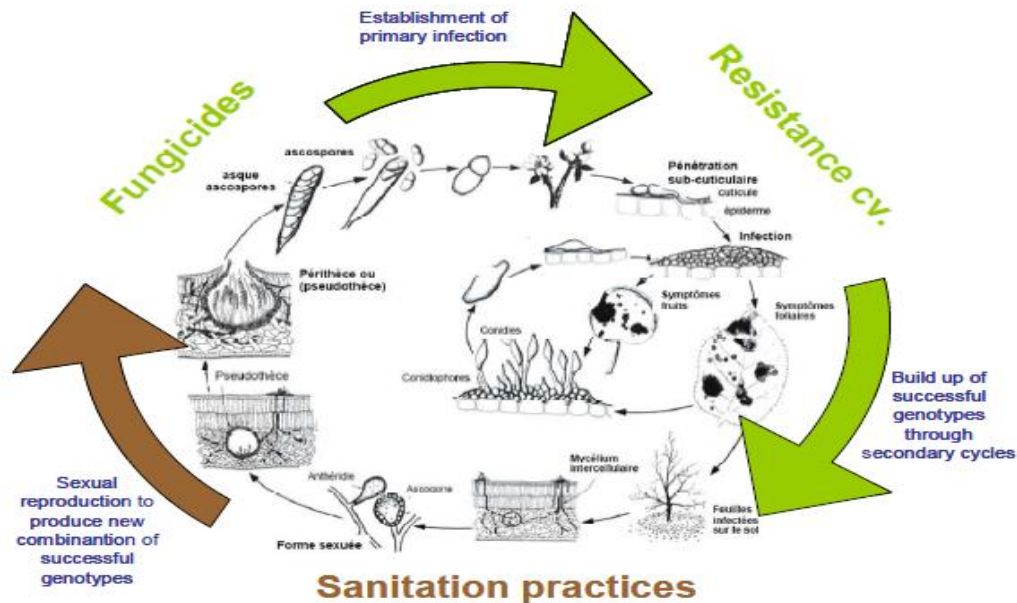


Figure.3 Three reproductive strategies and practices for controlling each reproductive strategy (Jamar, 2011)



In conclusion, apple scab is economic importance and if not managed, the disease can cause extensive losses following humid and cool weather conditions during the spring months. Direct losses result from fruit infections and indirect losses from defoliation, which can reduce tree vigour, winter hardiness, and subsequent yield. Fungicidal control is generally considered the sole economically feasible control measure against apple scab disease. However, this may change due to the high costs of new fungicides, increased fungicide resistance in populations of *Venturia inaequalis*, and increasing concerns of environmental pollution and consumers negative perceptions of fungicide use. Therefore, new strategies for development of a durable management of apple scab are clearly necessary. The use of fungicides or compounds, acting via elicitation or priming for plant defense enhancement, and the development of new, durable scab-resistant apple cultivars will most likely gain importance in future apple scab management strategies. Knowledge of the biology and variability of *Venturia*

inaequalis is also a prerequisite for breeding program aimed at obtaining durable resistance to apple scab. Further studies on ecology of *Venturia inaequalis* and its epidemiology are required to improve current disease management strategies. Both innovative and conventional approaches should be used to investigate the host-pathogen relationship between *Malus×domestica* and *Venturia inaequalis*. Intensive research on the management of apple scab using bio-agents, improved cultural practices and developing resistance varieties should be emphasized in the future to enhance the overall efficacy of both organic and conventional apple production. Generally, integrated disease management (IDM), which combines biological, resistance, cultural and chemical control strategies in a holistic way rather than using a single component strategy proved to be more effective and sustainable for apple scab disease management. Therefore, every country will give a propriety on research in order to: identify and create commercial varieties with lasting resistance characteristics, improve the effectiveness of

phyto-sanitary practices aimed at reducing the inoculum and develop knowledge of the potential of such practices in order to reduce demand for fungicides, find alternative fungicides to sulfur and copper, refine strategies and protection schemes, optimize treatment timing, improve plant protection product application techniques and develop specific cultural practices that are less favourable to the development of the disease.

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How to cite this article:

Annu, Rinku Rani and Sharma, J.R. 2019. Studies on Biology and Management of Apple Scab Incited by *Venturia inaequalis*. *Int.J.Curr.Microbiol.App.Sci*. 8(01): 162-182.
doi: <https://doi.org/10.20546/ijcmas.2019.801.019>