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Effect of dry and wet years on primary inoculum source, incubation period and conidial production of *Venturia inaequalis*

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Summary: The present study focuses on the characteristics of epidemics caused by the selected model-pathogen, *Venturia inaequalis* in relation to weather elements, with special respect to the increasing or decreasing effects of the specific weather elements. First, those weather elements are discussed which have a role in the development of scab epidemics. Subsequently, by accepting the thesis that climate change includes also weather extremes, an extremely hot and dry year (2003) and a colder year of higher than average precipitation (2004) were chosen as models. The presented examples verified that the variability of weather elements had had an undoubtable effect on the development of epidemics. The variability of weather elements manifests in the unusual behaviour of the pathogen, resulting in no or extreme disease epidemics. The extremities are well demonstrated by the fact, that in a year of drought an efficient protection can be achieved by considerably less applications than average, while in the next rainy year, the susceptible cultivar cannot be protected effectively even with such a high number of applications as is usual under humid Western-European climate conditions. It can also be noted, that the pathogen has a very good adaptability under unfavourable weather conditions. Consequently, more efficient management strategies should be developed for protection against the effects of extremities. However, it should be emphasized that it is very difficult to adapt to the variability and extremities of weather in the practice, because no long-term, accurate and reliable information is available about the variability of these elements.

Key words: *Malus x domestica* Borkh., apple scab, epidemiology, disease cycle, primary scab control

Introduction

Numerous studies examine the relationships of weather parameters and plant pathogens. Early research results have proven that there was a tight correlation between the epidemics of pathogens and weather. The most important weather parameters influencing the build-up of epidemics are temperature, precipitation, relative humidity and leaf wetness duration. In addition, the importance of wind should also be mentioned, which plays a role in the transport of the pathogens. Recent research revealed that the different weather parameters contribute to the epidemics to a different extent depending upon the lifecycle of the pathogen. Moreover, it has been proven that the precondition of epidemics is that several weather parameters reach the the threshold values at the same time. If the weather conditions are favourable for the pathogen, then infection will occure provided that a susceptible host plant is available. The continuity and regularity of the favourable conditions will result in the build-up of an epidemic. Consequently, if the weather conditions (and within this the weather parameters) change and become variable for some reason, then it will also have an effect on the epidemiological parameters. A widely discussed feature of the global climate change is the extremely variable weather of the recent years. This variability probably has an impact on the epidemics caused by plant pathogens, which may call for the development of new, more effective plant protection strategies (*Vályi* et al., 1986). The process is greatly influenced by the susceptibility or resistance of pathogens in case of apple scab (*Holb*, 2000; *Holb*, et al, 2003; *Tóth*, 2005; *Tóth & Pedryc*, 2005; *Tóth & Gracza*, 2005; *Mattisson & Nybom*, 2005).

The present study focuses on the characteristics of epidemics caused by a polycyclic pathogen, *Venturia inaequalis* in relation to weather elements. We placed special emphasis on how the variability of specific weather elements increases or decreases the epidemics. Of course, several other factors, such as heat-stress (*Kovács*, 1993), play an important role in the build-up of epidemics besides weather, however, they are not included in the objectives of the present study, therefore they are not discussed here.

Literature review

The influence of weather elements on the build-up of apple scab epidemics

In order to study the effect of the weather parameters' variability on the build-up of *Venturia inaequalis* epidemics, we should know those weather elements which have a role in the formation of epidemics. The role of weather elements differs largely in the different stages of the pathogen's lifecycle, therefore we will discuss the topic according to the main lifecycle stages: a) the period of pseudothecium and ascospore formation, b) the period between ascospore discharge and ascosporic infection, c) the period between the formation of conidia and conidial infection, d) the ascosporic and conidial infection period, e) the incubation period.

Weather elements influencing the formation of pseudothecia and ascospores

The role of weather elements becomes significant after leaf fall in the period of pseudothecia and ascospore formation (*Table 1*). Besides this, important factors can be for example leaf disease severity, the nutrient content and pH value of leaves and the type of fungicides applied in the vegetation period and the frequency of their application.

Among the weather elements, soil moisture, temperature and light have the greatest effect on the formation of pseudothecia. The development of pseudothecia is determined primarily by the moisture content of the leaves (*James & Sutton*, 1982). It has been observed that the number of abnormally developing pseudothecia increases in continuously wet leaves. However, if the leaves become wet at certain intervals, then the pseudothecia develop rapidly. For the wetting of pseudothecia, it can be enough if the relative humidity is permanently above 90%. However, *Wiesmann* (1932) noticed that the development of older pseudothecia containing asci stopped at under 60% relative humidity, while the younger (a few weeks old) pseudothecia can endure longer dry periods (even 200 days). If the infected fallen leaves reach the minimum wetness threshold value, then the pseudothecia development is dependent upon temperature (*Gadoury & MacHardy*, 1982). In the initial development of pseudothecia, the temperature of the first month after leaf fall is of determining importance. In this period, the optimum temperature requirement is between 10-15 °C. With the decrease in the autumn temperature, the development of pseudothecia gradually decreases and stops at about 4 °C. At the beginning of winter, the pseudothecia are undeveloped. In the next spring, the development starts already at 0 °C, but the more developed the pseudothecia, the higher optimum temperature they require. The optimum temperature for asci development, elongation of asci and the maturing of ascospores is 6 °C, 16 °C and 20 °C, respectively (*Louw*, 1951; *Jeger & Butt*, 1983). If the minimum leaf wetness and temperature threshold values are reached, then light has a determining role. *Hirst & Stedman* (1962) observed, that when leaves overwintered in several layers on the orchard floor, then it frequently happened that pseudothecia in the bottom layers could not develop. By the end of the 1980s, it had been clarified that a minimum daily light duration is necessary for the normal development of pseudothecia on the overwintering leaves (*MacHardy*, 1996). Pseudothecia enter the winter period in different stages of development depending upon the temperature, wetness and light conditions. During winter, the development of pseudothecia slows down considerably or stops. Very cold winter periods and dry periods without snow can result in the death or abnormal development of pseudothecia (*Tóth*, 1997; *Holb*, 2002).

Table 1 The effect of weather elements on the major developmental stages of *Venturia inaequalis*. Data summarized from the study of Holb (2002) and MacHardy (1996)

	Temperature (°C)	Moisture	Light
*Pseudothecia formation**			
Minimum	0–4	60 %	20 minutes /day
Optimum	10–15	90 %	–
Maximum	25	100 %	–
*Ascospore discharge**			
Minimum	0,5	60 %	–
Optimum	14–16	90 %	–
Maximum	32	100 %	–
*Conidial production**			
Minimum	4	60 %	–
Optimum	14–21	90 %	–
Maximum	26	100 %	–
*Infection***			
Minimum	5	9 hours dependent upon temperature	–
Optimum	16–22		–
Maximum	26	51 hours	–
*Incubation period****			
Short (<11 days)	16–22	85–100 %	–
Average (12–16 days)	9–15, 23–25	70–85 %	–
Long (>17 days)	<8, 26<	40 %	–

* Moisture given as relative humidity.
** Moisture given as leaf wetness duration.
*** Temperature and relative humidity values classified based on the length of the incubation period.

The role of weather elements in the period between ascospore discharge and infection

In spring, the ascospores formed in the mature pseudothecia are discharged and they infect the susceptible plant tissues. In this period, weather has a determining role in the formation of epidemics (*Table 1*).

Prior to ascospore discharge, ascospores can remain viable in the pseudothecia for 200 days under dry conditions (*Wiesmann*, 1932; *Louw*, 1948). However, the viability of discharged ascospores is significantly smaller, it ranges between a few hours and 20 days depending upon the environmental conditions. If the discharged ascospores are stored at 5-10 °C, then they will die after 20 days (*Boric*, 1985). Under field conditions, the discharged ascospores die quickly without moisture. According to the examinations of *Severin* (1989), the viability of ascospores reduces after a 2-hour sunny and dry period and they will not be able to germinate. The ascospores germinate between 0,5 and 32 °C and develop a germination tube (*Wiesmann*, 1932; *Boric*, 1985), however, the rate of germination tube formation significantly decreases under 11 °C and above 26 °C. *Turner* et al. (1986) examined at 2-hour intervals how the number of ascospores not germinating, developing germination tubes and developing both germination tubes and appressoria on the leaves of apple trees changed in relation to temperature. The results showed that the 14–16 °C interval is the most favourable in the above listed germination periods. In this temperature interval, the germination of ascospores starts in the first hour. After the eighth hour, the formation of germination tubes reaches the highest rate. The first germination tubes with appressoria appear already in the fifth hour and all germination tubes develop appressoria within 24 hours.

Influencing weather elements in the period between the formation of conidia and conidial infecton

Numerous weather elements have an influence on the formation of conidia. The amount of conidia is determined primarily by temperature, relative humidity and light (*Table 1*). The correlation is the tightest between temperature and conidial production. Conidia germinate at average temperatures ranging between 4 and 26 °C. The optimum temperature values range between wide limits between 14 and 21 °C. The most significant conidial production happens between 70 and 100 % relative humidity (*Stundt & Weltzien*, 1975). 90 % relative humidity is optimal for the formation of conidia. According to some studies, light also has an influence of the germination of conidia. Continuous darkness can reduce amount of conidia produced by 30 % (*Boric*, 1985). On the other hand, strong sunlight for 2–6 hours can also have a detrimental effect on the physiological processes (*Szkolnik & Hamilton*, 1960). Complex weather analyses verified that continuous light, 80–100 % relative humidity and temperature between 12–24 °C result in at least 50 % germination capacity. According to the study of *Becker & Burr* (1990), the viability of conidia under field conditions can be significantly smaller due to the variations in sunlight, wind, temperature and relative humidity. During germination and the formation of hyphae and appressoria, conidia become especially sensitive to the changes in the environmental factors. With infection, the sensitivity of the pathogen gradually decreases (*Becker & Burr*, 1990). Changes in the temperature are not lethal during germination and the formation of germination tubes, but a reduction in the relative humidity or a short dry period can result in the immediate death of germs and young hyphae.

Weather elements influencing ascosporic and conidial infections

In the case of *Venturia inaequalis*, light, temperature, relative humidity and leaf wetness duration have the strongest effect on ascosporic and conidial infections (*Keitt & Jones*, 1926; *Keitt*, 1927) (*Table 1*). The characteristics of infection greatly differ on the different plant organs (leaf or fruit). It was determined, that ascospores need continuous wetness from germination until entering the plant tissue. It was also revealed, that the lower the temperature, the longer leaf wetness duration is necessary for infection, moreover, the number of scab lesions increased with increasing leaf wetness duration. *Mills & Laplante* (1951) showed that the leaf wetness period under field conditions should be about three hours longer than under laboratory conditions. The leaf wetness durations given for weak, moderate and strong infection in the Mills table are valid for the 5–26 °C temperature interval. In addition, the table also includes the incubation periods (in days) at the different temperatures. For conidial infection, a 30 % shorter leaf wetness duration is satisfactory than for ascosporic infection. Hungarian studies also reported positive results about the application of the Mills table in the practice of plant protection. (*Sallai*, 1972; *Holb*, 2002).

Influencing weather elements during the incubation period

According to *Tomerlin & Jones* (1982), the incubation period of apple scab (from infection until the appearance of the first sporulating lesions) ranges between 9.5 and 15 days in the temperature interval of 17–24 °C. This period is determined mainly by temperature and the age of leaves, but relative humidity can also have a significant role (*Table 1*). *Keitt & Jones* (1926) found that the incubation period is the shortest (8–12 days) between 20–25 °C, however, it takes 17 days at 8 °C. According to the studies of *Tomerlin & Jones* (1982), relative humidity above 60 % reduces the length of the incubation period. On the other hand, relative humidity below 40 % significantly increases the length of the incubation period. Hyphae under the cuticle are not destroyed even at such a low relative humidity and their growth also continues, howeverm the sporulating scab lesions appear a few days and sometimes weeks later.

Materials and methods

Orchards and plant materials

Observation was made in three integrated apple orchards located at Debrecen-Pallag, Eperjeske and Nagykálló in autumn of 2002 and in the full season of 2003 and 2004. All orchards was treated to according to the European Integrated Fruit Production Guidelines (*Dickler*, 1990). In all orcards, trees were at least five years old and were maintained by regular horticultural practice. Only cv. Jonagold was assessed in all orchards. Mills infection periods (*Mills & LaPlante*, 1951) were calculated in oder to timing fungicide applications in each season and in each orchard.

Assessments

According to life cycle of apple scab, several measures were assessed in order to charactherize the year effect on scab epidemics. The assessed measures were the next: i) number of pseudothecia suitable for overwintering (%), ii) number of pseudothecia killed during overwintering (%), iii) number of overwintered pseudothecia (%), iv) PAD (potential ascospore dose) (%), v) length of the incubation period, vi) the number of conidia per unit lesion area (%), vii) viability of conidia (%), and viii) leaf incidence values in the autumn (%).

In all orchards and years, pseudothecia were counted on 100 leaves replicated four times and ont he same amount of leaves PAD was measured according to the methods of *Gadoury & MacHardy* (1986). Length of the incubation period was calucated as the days between the predicted time of infection and appearence of new symptoms. Conidia were counted on 50 newly produced lesions, replicated four times. Viablilty of conidia was tested by germinating 200 conidia on water agar for 24 hours, replicated four times. Leaf incidence was also measured at 15 October, 2003 and 31 August, 2004.

All measures was expressed as percentages of an average year measures. The average year measures were calculated as the mean of the data measured during the period of 1997-2004. This mean data was considered to be as 100 %. Measured data were analysed by analyses of variance. Means were separated by LSD t-test at P = 0.05 level.

Results and discussion

The effects of the weather elements are presented according to the major stages of the pathogen's lifecycle. In the two years, the disease could be described as follows. Based on the assessments in the season of 2002/2003 at Debrecen-Pallag, Eperjeske and Nagykálló, the integrated orchards could be protected with 5–8 spray applications against the pathogen. Assessments at the beginning of October 2003 verified that the leaf disease incidence values were between 6–24% depending on the susceptibility of the cultivar and the fruit incidence values were below 5%. At the same locations, 14–18 spray applications were not enough to ensure an appropriate protection everywhere and on every cultivar in 2003/2004 (based on the assessments on 31 August 2004). The values of leaf incidence and fruit incidence ranged between 29–73 % and 20–50 % by the end of August, depending on cultivar susceptibility.

Winter started in the first half of November 2002. Assessments carried out on the fallen infected leaves on the orchard floor revealed that less pseudothecia suitable for overwintering were formed on the leaves than in the previous years. On more than 50% of the fallen leaves, only the first steps of the sexual phase were finished and the pathogen was not ready for overwintering. During the more than 4-month long winter of 2002/2003, there were several long periods with temperatures below -15 °C. As it was mentioned earlier, the very cold winter periods and the dry periods without snow can result in the death or abnormal development of pseudothecia (*Holb,* 2002). In 2002/2003, this effect was further strengthened by the fact that the number of pseudothecia not suitable for overwintering on the fallen leaves was high (*Table* 2). Consequently, the PAD (potential ascospore dose) in the spring of 2003 was 30–60% lower than in the previous years. Accordingly, the number of ascospores per m^2 orchard floor decreased, which was verified by the data of the spore traps operated in the period of ascospore discharge. In 2003, the number of Mills infection periods necessary for the infection ranged between 14 and 16. The weather conditions were suitable for strong infection 3–5 times during the vegetation period in the orchards studied. (In an average year, the number of Mills infection periods ranges between 23 and 33 during the vegetation period.) Consequently, the build-up of epidemics was hindered. If we examine the infection periods, significant differences can be found compared to an average year. After a moderate infection in the middle of summer, the symptoms appear after 9–14 days and the brown-black lesions appear on the susceptible leaves. In the summer of 2003, the conditions were rarely suitable for infection and the incubation period was as long as 25 days in some cases. According to our data, the temperatures above 30 °C and the relative humidity values below 40 % slowed down the development of the pathogen in the plant. Moreover, the number of conidia per unit lesion area produced after the incubation period also decreased by 30–55 % compared to the values measured in 1998 and 1999. Among the conidia, there were also morphologically abnormal ones. The viability of conidia reduced by 20–45 % (*Table 2*). After the formation of conidia, there were frequent periods with strong sunlight, which resulted in a fast reduction in the viability of conidia, a fast aging and an early death of conidia. The extremely high temperature and the strong sunlight significantly hindered the summer infection by conidia and the build-up of an epidemic. Consequently, the scab disease incidence values measured in the autumn were not higher than 25 % even in the case of susceptible apple cultivars (*Table 2*).

Table 2 The effect of the years 2003 and 2004 on the development stages of *Venturia inaequalis* on a susceptible apple cultivar (Jonagold) based on the mean data assessed at Derecske, Eperjeske and Nagykálló

	Years	
Stages of the lifecycle, infection indices *	2003	2004**
Number of pseudothecia suitable for overwintering (%)	43	121
Number of pseudothecia killed during overwintering (%)	58	7
Number of overwintered pseudothecia (%)	22	125
PAD (potential ascospore dose) (%)	45	143
Number of Mills infection periods in total	15	39
Number of Mills infection periods: strong infection	4	22
Length of the incubation period (%)	180	76
The number of conidia per unit lesion area (%)	57	195
Viability of conidia (%)	67	125
Leaf incidence values in the autumn (%)***	24	73

* The mean of the data measured during the period of 1997-2004 was considered as 100 %. The values in the table are expressed as percentages of the mean data.

** All values are from assessments on 31 August 2004.

*** Leaf incidence values in % at the middle of October 2003 and at the end of August 2004.

In 2003, winter started in December after a long autumn. Because of the long autumn, there was scan infection even in October. Although leaf disease incidence was not high on the fallen leaves, the pathogen had enough time due to the long autumn to form pseudothecia suitable for overwintering (*Table 2*). In 2003/2004, the winter was not long and long periods with temperatures under -15 °C did not occur. As a result of this, more 90 % of the pseudothecia (suitable for overwintering) overwintered and started to develop rapidly in the spring of 2004 (*Table 2*). Therefore, in spite of the fact that amount of fallen infected leaves was much smaller in the autumn of 2003 compared to the previous years, the amount of PAD was not significantly smaller than in the average years (*Table 2*). Moreover, the number of ascospores trapped by the spore traps operated in the period of ascospore discharge was much higher than in the average years due to the frequent rainy periods in the spring. In 2004 (until 31 August), the number of Mills infection periods necessary for the infection ranged between 36 and 43, strong infections occurred on 19-24 occassions in the orchards studied (*Table 2*). It should be noted that such high numbers of infection periods are usually measured in the apple orchards of Western European countries (*Holb*, 2000; *Holb & Heijne*, 2001; *Holb* et al., 2003, 2004). Accordingly, the build-up of epidemics was almost not hindered at all. The characteristics of infection in the vegetation period and the related weather parameters can be characterized by two periods. One is the several-day long rainy period at the midlle and end of April interrupted only for short periods. The young fruits are the most susceptible in this period. Although the rainy period was interrupted several times, but the relative humidity was above 90 % in the hours or days of the breaks. This meant that although the germination of the discharged ascospores landed on the surface of the plant stopped, but they were not killed and their germination continued after the next rain and entered the plant through the cuticle. This series of infections could be prevented only by precisely-timed combined applications of contact and systemic fungicides sprayed with well-adjusted sprayers. Many growers did not succeed in performing this, because they could not spray at the critical periods, because of the unfavaourable soil conditions for example. The other important period was at the end of July. At this time, there was a week when it rained each day and there was a period of 80–86 hours when it was raining continuously in the studied orchards. The situation was worsened by the fact that although there were sunny periods during this week, but their length did not exceed 10 hours and the relative humidity was above 90 % even during these periods. Concerning the possibilities of infection by the pathogen, this means that the hours with relative humidity of higher than 90%/ could be added to the hours of leaf wetness duration (*Jones* et al., 1980). Consequently, the leaf wetness duration exceeded 110 hours. This is such a critical number of hours, after which not even the best systemic fungicides could prevent the development ofthe pathogen in the plant. In addition, the number of infected leaves and fruits was already high by the end of July and the average daily temperature raised quickly above 20 ºC after the rainy period, which can reduce the incubation period to 8 days. The rainy and warm summer favourable for the pathogen resulted in a severe epidemic. Consequently, the scab disease incidence exceeded even 75% on susceptible apple cultivars (*Table 2*).

Conclusions

The variability of weather had an obvious effect on the build-up of the epidemic. The extremities are well demonstrated by the fact, that in one year the protection against the pathogen could be solved by a much lower number of sprays than in average years, while in the next year, even such a high number of sprays as used under the humid conditions of Western Europe could not protect the susceptible cultivars in every orchard. It can also be stated that the pathogen has an outstanding adaptibility under unfavourable weather conditions. Although it cannot cause severe epidemics under such condutions, but in the next year it can result in a severe epidemic if the conditions are favourable. The variability of weather results in an altered epidemiological behaviour of the pathogen, meaning that the pathogen does not cause a problem or protection against it cannot be solved. These facts should be taken into consideration when setting up the protection strategies, especially if economic factors should also be considered (e.g. in mild winters, the treatment of fallen leaves with urea is advantageous and reduces the number of pseudothecia, while in cold winters, it is a waste of money; or the timing of applications in extremely dry and warm and extremely rainy years requires different decision-making). However, it should be emphasized that in the practice it is very hard to adapt to the variability and extremities of weather elements. It is even more difficult to base the decisions on that, since we do not have long-term, precise and reliable information about the variability of weather elements.

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