Potential and actual ascospore release of *Erysiphe necator* chasmothecia in Austria

M. Redl¹ · L. Sitavanc¹ · B. Spangl² · S. Steinkellner¹

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Abstract

Ascospores of grape powdery mildew (*Erysiphe necator* Schw.) play a crucial role in the disease onset in spring in many vine-growing areas. We investigated the physiological maturation of chasmothecia and the time of the first potential ascospore release in three grape-growing areas in Austria by providing standardized conditions for ascospore release in the laboratory and excluding the environmental influence for the release itself. In the overwintering season 2017/2018, the potential ascospore release started in March 2018 in all three investigated wine-growing areas, while in 2018/19, the potential ascospore release was already possible in autumn 2018. Autumn 2018 was characterized by higher temperatures than autumn 2017. We related accumulated degree days (base 8 °C) after chasmothecia formation with the time of first potential chasmothecia dehiscence and found that more than 480 degree days are necessary to reach physiological maturity of chasmothecia. Temperature significantly influenced the dynamics of the potential of ascospore release. More than 50% of the total potential of ascospore release occurred before bud break in both years. Furthermore, weather factors affecting the actual ascospore release in the field were studied. Precipitation and leaf wetness showed a significant positive correlation with ascospore release in the vineyard. In contrast to the potential release, only a small percentage of actual release in the field occurred before bud break, while 84 and 95% of total trapped ascospores were found between bud break and flowering in 2018 and 2019, respectively. Our results reveal that the potential release and actual release have to be combined to predict ascospore release in spring.

Keywords *Erysiphe necator* · Chasmothecia · Ascospores · Degree days · Leaf wetness

Introduction

Grape powdery mildew, caused by *Erysiphe necator* Schw. [syn. *Uncinula necator* (Schw.) Burr.], is one of the most important diseases in the world's grape-growing regions. The principles of the disease's development are well described. Primary infections can arise from overwintering mycelia in buds of vines (Sall and Wrysinsky 1982) or from ascospores produced in chasmothecia (Pearson and Gadoury 1987). The latter are considered as the most common

primary inoculum source in many grape-growing regions (Pearson and Gadoury 1987; Cortesi et al. 1997; Steinkellner 1998; Jailloux et al. 1999; Schneider et al. 1999; Gee et al. 2000; Grove 2004; Rossi et al. 2010; Hoffmann et al. 2012; Thiessen et al. 2018). Chasmothecia are formed on infected green tissue, especially on leaves, when two compatible mating types are available (Gadoury and Pearson 1991). In their early stages of development in late summer, they are white. Later they change their colour until they turn black at morphological maturity. At this stage, chasmothecia lose their connection to the mycelium and can be dispersed by rain events to the bark of grapevines or onto the soil (Legler et al. 2012), but many of them can remain on leaves (Cortesi et al. 1997). After overwintering, the viability rate of ascospores in chasmothecia on the soil and on leaf litter is very low. It is assumed that in many regions only those chasmothecia which overwintered in the bark can serve as a primary inoculum source (Gadoury and Pearson 1988). It is expected that the majority of ascospores are released between bud break

✉ S. Steinkellner
siegrid.steinkellner@boku.ac.at

¹ Institute of Plant Protection, University of Natural Resources and Life Sciences, Gregor-Mendel-Straße 33, A-1180 Vienna, Austria

² Institute of Statistics, University of Natural Resources and Life Sciences, Peter-Jordan-Straße 82, A-1190 Vienna, Austria

and flowering in the presence of free water (Jailloux et al. 1999), leading to infections of basal leaves in proximity to the exfoliating bark of vines (Pearson and Gadoury 1987).

After initiation of chasmothecia formation, they take up to 4 weeks to reach their morphological maturity (Gadoury and Pearson 1988). At this stage, they cannot yet dehisce in the presence of free water. Following this morphological maturity, chasmothecia have to undergo a physiological maturation process; only then ascospores can be released from chasmothecia (Gadoury et al. 2015). It is assumed that in cooler climates this process takes several months and that chasmothecia can dehisce only after an overwintering period in spring (Pearson and Gadoury 1987; Jailloux et al. 1999; Grove 2004; Moyer et al. 2014), whereas in more temperate climates the first potential ascospore release can occur even in autumn (Gee et al. 2000; Rossi et al. 2010; Thiessen et al. 2018). In previous studies, it was shown that weather factors, especially rainfalls, play a key role for the actual ascospore release in the vineyard (Gadoury and Pearson 1990; Jailloux et al. 1999; Rossi et al. 2010).

Although grapevine powdery mildew is a well-documented fungus, our knowledge on the influence of weather conditions in the field on the timing of ascospore release and their dynamics is still limited (Moyer et al. 2014), and a number of questions remain unanswered. In particular, more detailed information on both the potential and the actual ascospore release in the period from autumn to the beginning of growth in spring the following year could provide a better understanding of the inoculum status in the following season. To date, both parameters, the potential and the actual ascospore release, were not examined at the same time. Therefore, the objectives of this study were to close this gap, combining the assessment of the actual ascospore release in the field with investigations on the influence of environmental conditions on physiological maturation of chasmothecia, the dynamics of the potential ascospore release and the viability rate of ascospores in the laboratory. This information would allow more specific disease forecast models and could be very valuable for improved timing, facilitating a reduction in the use of fungicides.

Materials and methods

Study sites

The study was conducted in three different Austrian grape-growing regions in Krems (lat. 48 °25' 35.6" N; long. 15 °36' 48.8" E), Vienna (lat. 48 °17' 20.8" N; long. 16 °25' 35.2" E) and Illmitz (lat. 47 °47' 35.6" N; long. 16 °48' 33.1" E). The vineyards were planted with *Vitis vinifera* cv. Grüner Veltliner (Krems), cv. Chardonnay (Illmitz) and a mixture of 43 different cultivars (Vienna). The

distance of the vines was 2.8–3.0 m between the rows and 0.75–1.2 m within each row; the heads of the vines were 0.7–0.8 m high. All vines were hand-pruned to two canes per vine, and vertical shoot positioning was done. The vines had been planted in 1998, 2001 and 2003 at Krems, Vienna and Illmitz, respectively. The three vineyards were sprayed with fungicides against powdery mildew until BBCH 79 (majority of berries touching), considering that chasmothecia were formed on leaves from mid-August and reflecting the start of chasmothecia formation in poorly sprayed vineyards in Austria (Steinkellner and Redl 1998). A weather station (OTT Hydromet, Kempten, Germany) was positioned directly in a row in each vineyard to measure temperature, humidity and leaf wetness directly at cordon height (0.8 m), and precipitation over the canopy at 15-min intervals.

Potential ascospore release from chasmothecia

In October 2017 and 2018, leaves with clearly visible high amounts of chasmothecia were collected in the vineyards in Vienna, Krems and Illmitz. These leaves were put into plastic boxes (25 leaves/1.5 l box) filled with 750 ml of tap water and shaken intensively for 1 min. The content of the plastic boxes was then poured into a 0.4 mm sieve placed over a 0.1 mm sieve to collect chasmothecia. The chasmothecia were diluted with distilled water to obtain a suspension containing approximately 950 chasmothecia* ml⁻¹. Subsequently, 0.85 ml of the suspension was pipetted onto the centre of 9-cm-diameter filter paper discs (VWR 417, Vienna, Austria).

For studying the ascospore release in autumn, 1–3 discs (to ensure in total 35–55 chasmothecia per vineyard) with a diameter of 5 mm were punched out of each of four filter papers positioned in each vineyard. The discs from each filter paper were fixed separately with Vaseline onto the centre of a lid of a 9-cm-diameter Petri dish lined with fresh filter paper moistened with 1 ml of distilled water. In the bottom of the Petri dish, a microscope slide was fixed. The Petri dishes were carefully closed and incubated for 24 h at 25 °C to allow ascospores to be released from the chasmothecia. Afterward, the ascospores trapped on slides were stained with 1% Cotton Blue in lactoglycerol, and their number was counted using a microscope at 200-fold magnification.

For studying the potential ascospore release over the period from autumn to spring, 1,500 leaves were sampled in the vineyard in Vienna, and chasmothecia from 60 boxes were collected on filter papers as described above. The next day, after drying at room temperature, the filter paper discs were folded into quarter circles, enclosing chasmothecia, and 20 folded discs were fixed with pushpins on a wooden board (50 cm long and 15 cm wide), as described by Gee et al. (2000). Subsequently, four boards per vineyard were fixed, with the filter paper discs bearing side facing

upward, at cordon height (0.8 m above the ground) on the trellis system in 1–10 m distance from the weather stations in unsprayed plots in the vineyards at Vienna, Illmitz and Krems. Periodically (in 2–4-week intervals), four filter papers per vineyard were brought to the laboratory, prepared as described above, and the ascospore release was counted. The potential ascospore release was expressed as cumulated total released number over the whole period from October to June 2017/2018 and 2018/2019, respectively.

Actual ascospore release in the field

The actual ascospore release was studied in the vineyard in Krems. In October 2017 and 2018, filter papers containing chasmothecia from the vineyard in Vienna were prepared as described above for this purpose. Twenty filter papers each were fixed on eight wooden boards and placed in the vineyard in Krems over the winter. In the following March, the filter papers were removed from the vineyard, were cut into four quadrants and put into 0.25-l plastic boxes (16 pieces per box). The boxes were then filled with 150 ml of cold (+4 °C) distilled water and shaken vigorously for 1 min, and the quadrants were removed from the suspension. Four new filter paper discs (9 cm diameter) were folded once, and the edges were folded up to prevent runoff. The above-mentioned suspension was subdivided into four aliquots each poured in the orifice of the new filter paper discs. After drying, each disc was fixed in the gap between two surface-sterilized (0.5% sodium hypochlorite for 10 min) vine trunk sections mounted lengthwise parallel on a board. In March 2018 and 2019, respectively, four boards were fixed at cordon high (0.8 m) in a fungicide-free plot in the vineyard in Krems. A microscope slide (75 × 25 mm) coated with a mixture of 89% Vaseline and 11% paraffin was attached horizontally over each board in a distance of 2–3 cm away from the chasmothecia source to trap ascospores. The coated slides were replaced every 7 days until no more ascospores were detected on the slides for 2 weeks. The slides were stained with 1% Cotton Blue in lactoglycerol, and five transects along the long side of each slide were examined at 400-fold magnification for the presence of ascospores. The data were expressed as the cumulated percentage of released ascospores.

Viability of ascospores

For viability testing, 20 chasmothecia per filter paper (three filter papers per vineyard) were treated periodically (in 2–4-week intervals) with 0.5% (w/v) fluorescein diacetate and examined under a fluorescence microscope equipped with a fluorescein isothiocyanate (FITC) fluorescence filter, at 400-fold magnification as described by Cortesi et al. (1995).

A chasmothecium was classified as viable when at least one ascospore fluoresced.

Statistical analysis

Statistical analysis was performed using R 3.5.1 (R Core Team 2018). Mean degree days (base 8 °C), according to Moyer et al. (2014), for all three vineyards were calculated from 15 August 2017 and 2018 to the respective date of the cumulated potential of released ascospores in the seasons 2017/2018 and 2018/2019. Furthermore, analyses of the correlations (Pearson) between percentages of released ascospores during trapping periods in the field and average temperature, average relative humidity, total precipitation, sum of leaf wetness hours and sum of degree hours wetness, according to Blaeser and Weltzien (1979), in trapping periods for the vineyard in Krems in 2018 and 2019 were performed.

Results

Potential of ascospore release from chasmothecia and viability of ascospores

The ascospore release in autumn differed between both years of this study: in October 2017, chasmothecia collected from the three vineyards at Krems, Vienna and Illmitz did not release any ascospores under laboratory conditions (Table 1). In the following year, in October 2018, chasmothecia from the same locations released 1.28–12.10 ascospores per 100 chasmothecia. The viability of chasmothecia was in the range of 60–70% and 55–70% in 2017 and 2018, respectively.

In spring 2018, the starting date for ascospore release from chasmothecia overwintered on filter papers in the vineyards differed by up to 3 weeks between the three vineyards (Fig. 1). The earliest release was found for chasmothecia overwintered in Krems (10 March), followed by Illmitz (21 March,) and Vienna (31 March). In all vineyards, the highest

Table 1 Potential ascospore release (mean ± SE) and viability of chasmothecia (mean ± SE) collected from three vineyards at Krems, Vienna and Illmitz in October 2017 and 2018

Location	Number of released ascospores per 100 chasmothecia		Viability (%)	
	2017	2018	2017	2018
Krems	0.00	1.28 (± 1.28)	70 (± 0.00)	63 (± 2.55)
Vienna	0.00	3.68 (± 2.99)	60 (± 0.00)	55 (± 1.67)
Illmitz	0.00	12.10 (± 5.35)	68 (± 2.55)	70 (± 3.33)

Fig. 1 Percentage of viable chasmothecia (squares), cumulated total potential of released ascospores (dots), daily mean temperature (line) and daily precipitation (bars) at the vineyards **a** Krems, **b** Vienna, **c**

Illmitz in the chasmothecia overwintering season 2017/2018. Chasmothecia were collected at Vienna, transferred to filter papers in the laboratory and exposed in all three vineyards on 12 October 2017

ascospore release from chasmothecia was found on 24 April with 13, 7 and 3% viable chasmothecia at Krems, Vienna and Illmitz, respectively (Fig. 1). This release coincided

with an increase in mean daily temperature. The following month was characterized by a daily mean temperature in the range from 12 °C to 20 °C and several rain events

(Krems = 81 mm, Vienna = 40 mm and Illmitz = 37 mm). The last ascospore release was found on 19 June in Vienna. In the following weeks, no further ascospore release was found.

In the following overwintering season, the first ascospores were already released in autumn 2018 (Table 1). During the winter months, the number of released ascospores was very low or zero. High release rates were found between 8 March and 29 April 2019. This phase was characterized by higher daily mean temperatures than in 2018 (Figs. 1 and 2). In the following weeks, with several striking rain events, a decrease in the rate of ascospores release was determined (Fig. 2). Ascospores were detected until 9 May at Vienna and until 21 May at Krems and Illmitz. In the period of highest ascospore release (8 March–29 April 2019), the viability of chasmothecia dropped from a maximum of 53, 32 and 42% to 28, 12 and 12% at Krems, Vienna and Illmitz, respectively.

In the overwintering season 2017/2018, 4, 13 and 46% of the total potential of ascospore release were found before bud break and 96, 85 and 54% from bud break until flowering at Krems, Vienna and Illmitz, respectively. After flowering, ascospore release was found only at Vienna (2%) (Fig. 3). In 2018/2019, 42, 53 and 52% of ascospores were detected before bud break and 58, 47 and 48% from bud break until flowering at Krems, Vienna and Illmitz, respectively. No ascospores were released after flowering.

The mean temperature from mid-August to October, i.e. the period from the start of chasmothecia forming to the time when chasmothecia were examined for ascospore release, ranged from 15.7 to 16.9 °C in 2017 and from 17.2 to 18.3 °C in 2018 (Table 2). Considering both years, the humidity ranged between 71 and 79%, precipitation between 94 and 144 mm and leaf wetness between 141 and 309 h in the same period. From mid-August to October, accumulated degree days (base 8 °C) from 409 to 478 were calculated in 2017, while in 2018 between 502 and 569 degree days were counted. Computational analyses of different temperature bases (0 °C, 5 °C, 8 °C and 10 °C) showed that a base of 8 °C corresponded to the different starting dates of ascospore release in 2017/2018 and 2018/2019. From mid-August to the following March, degree days ranged between 484 and 586 in the season 2017/2018 and between 638 and 765 in 2018/2019.

Actual ascospore release in the vineyard in relation to potential release

Ascospores were observed weekly from week 14 to 21 on slides in the vineyard at Krems in spring 2018 (Fig. 4) and from week 12 to 23 (except week 13 and 15) in 2019 (Fig. 5), but the pattern of release was different. In 2019, although the potential release was at a high level from week 13 to 17 of the year, the actual release in the field was low in

this period and in 2018 the same pattern was observed. The highest numbers of ascospores (46% in 2018, 30% in 2019) were trapped in the vineyard in week 20 in 2018 at BBCH 57 (inflorescences fully developed) and in week 19 in 2019, when five leaves were unfolded (BBCH 15). In 2018, 16, 84 and 0%, and in 2019, 5, 95 and 0% of ascospore release were trapped before bud break, from bud break until flowering and after flowering, respectively (Fig. 4).

In both years, the cumulated percentage of potential ascospore release was exhausted when the maximum actual release occurred in the vineyard. In 2018, the weekly actual ascospore release was accompanied by precipitation, except in week 15, when 16 h of leaf wetness was recorded. In 2019, no ascospore release was found in weeks 13 and 15 when no rain was recorded (Figs. 4 and 5). Considering both years, precipitation from 0 to 58.0 mm per week, average humidity from 56.4 to 78.4 and leaf wetness hours from 1 to 44 were measured in ascospore trapping periods in the vineyard (data not shown). The highest ascospore release rates occurred in periods with 58 and 26 mm precipitation per week in 2018 and 2019, respectively. In weeks when actual ascospore release occurred, the weekly average temperature ranged from 8.5 to 17.9 °C and from 6.7 to 21.3 °C in 2018 and 2019, respectively. In both years, degree hours wetness between 7.2 and 569.7 were recorded during these periods.

A significant positive correlation was found between the number of actually released ascospores and the accumulated precipitation as well as the leaf wetness during the trapping periods in both years (Table 3). The degree hours of wetness were significantly correlated with the actual percentage of ascospores released in 2018, but not in 2019. In both years, neither the average relative humidity nor the temperature was significantly correlated with the amount of trapped ascospores in the vineyard.

Discussion

In this study, we investigated both the potential and the actual ascospore release of *E. necator*. The picture was different in both years of the study. In the overwintering season 2017/2018, the potential ascospore release started in March 2018 in all three investigated vineyards, while in the overwintering season 2018/2019 potential ascospore release was already possible in October 2018. For most grape-growing regions, it is assumed that ascospore release starts in spring (Pearson and Gadoury 1987; Jailloux et al. 1999; Grove 2004; Moyer et al. 2014). An ascospore release in autumn was only reported in warmer climates of southern Australia (Gee et al. 2000), northern Italy (Rossi et al. 2010) and Oregon (Thiessen et al. 2018). Our results show for the first time that chasmothecia can already release ascospores in autumn even in the cooler climates of Central Europe.

Fig. 2 Percentage of viable chasmothecia (squares), cumulated total potential of released ascospores (dots), daily mean temperature (line) and daily precipitation (bars) at the vineyards **a** Krems, **b** Vienna, **c**

Illmitz in the chasmothecia overwintering season 2018/2019. Chasmothecia were collected at Vienna, transferred to filter papers in the laboratory and exposed in all three vineyards on 8 October 2018

To our knowledge, this is the first report that in one particular region first ascospore release may occur in both spring and autumn. Gee et al. (2000) postulated that the

differences in the starting point of ascospore release are related to differences in the accumulation of degree days following initiation of chasmothecia, because in warmer

Fig. 3 Percentage of released ascospores from chasmothecia samples overwintered at Krems, Vienna and Illmitz before bud break, between bud break and flowering and after flowering

climates, like in southern Australia, ascospore release starts in autumn, while in cooler climates, like New York, it does not begin before spring the following year (Pearson and Gadoury 1987). This theory is supported by results from Italy (Rossi et al. 2010). Our data provide evidence that more than 480 degree days (base 8 °C) are needed for the start of ascospore release from chasmothecia: in the season 2017/2018, in three locations degree days from mid-August—the time of initiation of chasmothecia development in Austria (Steinkellner and Redl 1998)—to March ranged between 484 and 586, whereas in the season 2018/2019, 502–569 degree days were calculated from mid-August to October. In the overwintering season 2017/2018, potential ascospore release did not start until March the following year, but in 2018/2019 chasmothecia were able to release ascospores in October 2018 already.

Moreover, in our study the potential of ascospore release increased when temperatures (degree days) rose in spring. This is in agreement with Jailloux et al. (1998), who also

found a higher ascospore release of chasmothecia when stored at 10 °C compared to 5 °C for 170 days under dry and wet controlled conditions. Gadoury and Pearson (1990) observed a decrease in water potential of cytoplasm of chasmothecia incubated at 20 °C, but not at 4 °C.

In the present study, the potential of ascospore release was low or zero in winter 2018/2019, although ascospore release had already been found in autumn. The same dynamics of a low/zero potential of ascospore release in winter was also documented in Australia (Gee et al. 2000). One reason could be that colder temperatures in winter reduce this. Therefore, the probability of inoculum reduction due to ascospore release in winter seems to be very low in Austria, not least because optimal conditions for release like in the laboratory (25 °C and moisture) are never reached in the field in winter. Our results show that accumulated temperature is an important factor to reach physiological maturity of chasmothecia and more than 480 degree days (base 8 °C) are necessary. When chasmothecia reached their full potential of ascospore release, the viability rate of ascospores was very low (3–28%). This finding can be a reason for the low efficiency of ascosporic infections (Pearson and Gadoury 1987; Jailloux et al. 1998; Grove 2004).

In our study, chasmothecia released up to more than 50% of total potential of ascospores before bud break in both years. In many regions studied, the chasmothecia were able to dehiscence before bud break and release ascospores (Gee et al. 2000; Grove 2004; Rossi et al. 2010; Moyer et al. 2014; Holb and Füzi 2016), but a starting point after bud break was reported as well (Jailloux et al. 1999; Falacy et al. 2007). Moyer et al. (2014) found that cohorts of chasmothecia collected early and late in autumn varied in their temporal distribution of ascospore release, but not in their rate. In order to reflect the time of chasmothecia formation in commercial vineyards, we collected chasmothecia in autumn from plots that had been sprayed only until BBCH 79.

In the present study, only 16 and 5% of actual ascospores release were trapped between the start of sampling and

Table 2 Average temperature, relative humidity, total precipitation and leaf wetness hours from 15 August to 8 October 2017 and from 15 August to 12 October 2018. Degree days (base 8 °C) until October were calculated from 15 August to 8 October 2017 and

from 15 August to 12 October 2018. Degree days (base 8 °C) until March were calculated from 15 August 2017 to respective first date of ascospore release (March 2018) and from 15 August 2018 to 21 March 2019

Location	Season	Temperature (°C)	Humidity (%)	Leaf wetness (h)	Precipitation (mm)	Degree days August—October	Degree days August—March
Krems	2017/18	15.7	73.6	309.0	93.8	409	484
	2018/19	17.2	71.1	255.4	103.2	502	638
Vienna	2017/18	16.3	71.2	199.2	114.4	444	546
	2018/19	17.5	71.4	262.4	144.0	523	704
Illmitz	2017/18	16.9	79.8	141.7	99.6	478	586
	2018/19	18.3	71.4	287.2	79.8	569	765

Fig. 4 Cumulated total potential of released ascospores (dots), cumulated actually released ascospores trapped on slides (means of four replicates, squares) **a** and precipitation **b** in a vineyard at Krems in spring 2018. Trapping started in week 14 of the year, and the slides were replaced every 7 days until no ascospores were detected on slides in the field for 2 weeks (week 23 of the year). Phenological stages (BBCH scale) from (09) bud break to (65) full flowering were recorded (Lorenz et al. 1994)

Fig. 5 Cumulated total potential of released ascospores (dots), cumulated actually released ascospores trapped on slides (means of four replicates, squares) **a** and precipitation **b** in a vineyard at Krems in spring 2019. Trapping started in week 11 of the year, and the slides were replaced every 7 days until no ascospores were detected on slides in the field for 2 weeks (week 25 of the year). Phenological stages (BBCH scale) from (09) bud break to (65) full flowering were recorded (Lorenz et al. 1994)

bud break, and this was similar to vineyards in Hungary where 7% was detected during this period (Holb and Füzi 2016). In contrast, it is reported from Oregon that 87% of ascospores were trapped before bud break (Thiessen et al. 2018). In our study, most ascospores were trapped directly

in the vineyard between bud break and flowering (84 and 95% in 2018 and 2019, respectively) and no ascospores were captured after flowering. This is in contrast to Holb and Füzi (2016) who reported an ascospore release also after flowering in Hungary. Although a high percentage

Table 3 Correlation coefficients between percentages of actual released ascospores in the field and average temperature, average relative humidity, total precipitation, sum of leaf wetness hours and sum

of degree hours wetness in trapping periods (weeks 14–23 in 2018 and weeks 11–25 in 2019) at the vineyard in Krems

Season	Temperature	Humidity	Precipitation	Leaf wetness hours	Degree hours wetness
2018	−0.44	0.61	0.94*** ^a	0.88***	0.82**
2019	−0.22	0.46	0.62*	0.56*	0.33

^aThe symbols *, ** and *** indicate a significant correlation with *p* values lower than 0.05, 0.01 and 0.001, respectively

of the potential ascospore release occurred before bud break, it must be noted that this reflects the theoretical ascospore release under optimal conditions in the laboratory only. The relationship between the potential and the actual ascospore release is not consistent. We trapped only a few ascospores in the vineyard at the beginning of the trapping period in 2019, although weather conditions were favourable (high precipitation) for ascospore release; at the same time, the potential ascospore release was also low. In early spring, the cumulated percentage of potential ascospore release increased but again the actual ascospore release was low. Only after precipitation of more than 25 mm* week^{−1}, a high actual release rate was observed in the field and the potential ascospore release was exhausted. Thereafter, rainfalls did not lead to an effective ascospore release in 2019.

In our studies, precipitation and leaf wetness had a significant positive effect on the actual ascospore release, in this way confirming the results of Holb and Füzi (2016). Unlike in the study of these authors, humidity did not correlate with trapped ascospores in our study. In contrast, we trapped few ascospores only in periods with no or light rain (<2 mm), like in northern Italy (Rossi et al. 2010) and Hungary (Holb and Füzi 2016). In trapping periods with low precipitation, we always determined leaf wetness durations of more than 16 h. In contrast to the results from Hungary (Holb and Füzi 2016), humidity did not correlate with trapped ascospores in our study. During trapping periods, average temperatures of more than 6 °C were recorded, while from New York (Gadoury and Pearson 1990) and the Bordeaux region (Jailoux et al. 1999), thresholds of 4 °C and 8 °C, respectively, were reported.

In a 6-year study, Holb and Füzi (2016) detected a significant relationship between the cumulative number of trapped ascospores and leaf incidence of powdery mildew. Therefore, the probability that periods with low ascospore release—like those that we observed mainly at the beginning of the trapping period—contribute to epidemic onsets on a large scale is very unlikely. With this background, it needs to be clarified, if fungicide treatments are necessary in these periods, or if they need to be adjusted to the actual ascospore release.

All in all, our study provides information for a better prediction of ascospore release in spring. Several models for predicting ascospore release and infection are available (Gubler et al. 1999; Caffi et al. 2011, 2012; Moyer et al. 2014; Thiessen et al. 2018), and most of them are based on either the potential or the actual ascospore release. Our data indicate that the potential ascospore release combined with the actual ascospore release can improve the data basis for developing a more accurate ascospore release model. We found that temperature acts as an important factor for chasmothecia maturation and that precipitation is essential for ascospore release. Not every forecast model fits all wine-growing regions, as has been shown by testing different models at the same location in Oregon (Thiessen et al. 2018). We are confident that our results provide valuable information for developing a release model applicable in Central Europe. Furthermore, our findings might improve the timing of fungicide sprays in this way helping to reduce premature sprays in spring prior to actual ascospore release.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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