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Meteorological conditions determine the thermal-temporal position of the annual *Botrytis* bunch rot epidemic on *Vitis vinifera* L. cv. Riesling grapes

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Abstract

Aims: Under Central European climatic conditions, bunch rot caused by *Botrytis cinerea* occurs virtually every season on *Vitis vinifera* L. cv. Riesling grapes. Statistical investigations based on at least three annual disease severity assessments in 7 seasons (2007-2013) aimed at (i) simulating the disease progress and (ii) identifying meteorological conditions with predictive value for epidemics.

Methods and results: Sigmoidal regression models were used to describe the disease progress as function of thermal time. Coefficients of determination were > 0.97. The thermal time adjusted pace of the epidemic was almost constant in all seasons while the point of time when 5 % disease severity was reached varied among years. Window pane analyses showed that relatively low temperatures and wet conditions during bloom as well as relatively high temperatures and low precipitation sums around/after veraison were associated with thermal-temporally late epidemics.

Conclusions: Environmental conditions determine the timing of annual bunch rot epidemics. Analyses indicate a strong link between meteorological conditions around grape bloom (probably affecting fruit set and cluster structure) and the predisposition of the grape clusters to bunch rot.

Significance and impact of the study: The enhanced understanding of the effect of environmental conditions on the bunch rot epidemics supports growers to optimize control measures and is supposed to result in a *Botrytis* bunch rot model.

Key words: *Botrytis cinerea*, environmental conditions, thermal time, viticulture, window pane analysis

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Introduction

Bunch rot also referred to as Botrytis bunch rot or grey mould caused by *Botrytis cinerea* Pers. : Fr. (teleomorph : *Botryotinia fuckeliana* (de Bary) Whetzel) is a major fungal disease on more than 200 mainly dicotyledonous plant species (Williamson *et al.*, 2007) including grapevine (*Vitis vinifera* L.), where it causes severe economic damage worldwide (Kassemeyer and Berkelmann-Löhnertz, 2009). Besides the loss of yield, *B. cinerea* can reduce wine quality in terms of off-flavors, unstable color, oxidative damages, premature aging and difficulties in clarification (Ribéreau-Gayon, 1983 ; Smart and Robinson, 1991 ; Ky *et al.*, 2012).

B. cinerea is considered as an opportunistic pathogen infecting plant tissues primarily via wounds (Elmer and Michailides, 2007 ; Evans, 2008). Grape flowers are susceptible to infections since they represent natural apertures and provide sugars, which foster the colonization (Keller *et al.*, 2003 ; Viret *et al.*, 2004). Between fruit set and veraison, young, immature grape berries are highly resistant to *B. cinerea* (Hill *et al.*, 1981). Here, constitutive and inducible defense mechanisms (Elmer and Michailides, 2007) leading to a stop of the infection in the penetration stage (Kelloniemi *et al.*, 2015) account for a low susceptibility. Since the levels of fungistatic substances decline with maturity and micro-cracks in the berry skin occur more frequently after veraison, host defense progressively breaks down with grape maturation (Kretschmer *et al.*, 2007). Hence, infections of ripe berries are most common and destructive (Shtienberg, 2007).

Under the climatic conditions of many traditional (non-irrigated) grapegrowing regions, grape bunch rot occurs virtually every season. The time course of the *B. cinerea* disease severity was shown to be well described by logit, exponential or sigmoidal functions (Beresford *et al.*, 2006 ; Evers *et al.*, 2010 ; Hill and Beresford, 2010 ; Molitor *et al.*, 2015a). However, the starting point of bunch rot outbreaks is considered as highly unpredictable (Redl *et al.,* 2014), and forecasting the severity of bunch rot at harvest continues to represent a challenge (Evans, 2008).

Since the development of grape bunch rot on grapes cannot be suppressed completely under the climatic conditions of many viticultural regions, bunch rot control strategies primarily aim at delaying the epidemic as much as possible to take benefit of a long-lasting maturation period prior to enforced (due to the declining grape health status) harvest date (Molitor *et al.*, 2015a). In the past, control strategies were mainly based on routine applications of fungicides at pre-determined intervals (Shtienberg, 2007). Since pesticide use shall be minimized in Integrated Pest Management, excessive chemical treatments are becoming increasingly criticized and restricted (Elmer and Michailides, 2007 ; Shtienberg, 2007). A reduction of fungicide use in integrated bunch rot control strategies could be realized by (i) crop cultural measures that suppress fungal infections and spread and (ii) more targeted timing of botryticide treatments based on reliable forecast and decision support systems. For instance, the decision for botryticide applications could be guided by a warning system, which attempts to recognize weather conditions highly conductive for spore germination and to schedule fungicide applications accordingly (Shtienberg, 2007). Such efficient decision support systems for targeted control strategies need to incorporate the (potentially opponent) effects of environmental conditions in the course of the grape development on the bunch rot epidemic.

Even though it has been demonstrated that the microclimate in the cluster zone (which might be altered by canopy management measures such as leaf removal) has a distinct effect on bunch rot disease incidence and severity (English *et al.*, 1989), in-depth field data-based investigations on the impact of annual weather conditions in the different stages of grape development on the epidemics of bunch rot have not been published, yet.

Consequently, present investigations based on a long-time (7 years with three or more assessments ; 3 years with two assessments) data set on the epidemics of *B. cinerea* in the *Vitis vinifera* cultivar Riesling under cool climate conditions in Geisenheim/Germany aimed at (i) simulating the epidemic disease progress as functions of time and thermal time (summation of the physiologically effective temperature (Trudgill *et al.*, 2005) after bloom reflecting the grape phenological development) and (ii) identifying meteorological conditions with predictive value for annual grape bunch rot epidemics using window pane analysis according to Coakley and Line (1982).

Materials and methods

1. Experimental vineyard

Time series of grape bunch rot disease severity were recorded between 2004 and 2013 in the experimental vineyard “Mäuerchen M2” in Geisenheim, Germany (49.98 N, 7.95 E) on the white *Vitis vinifera* L. variety Riesling, clone Gm 239. Riesling is the most widely grown variety in Germany and one of the most widely grown varieties in Luxembourg. The

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vineyard used for the present study was planted in 1982. Vines were grafted onto 5C rootstocks and trained to a vertical shoot positioning system (two canes per vine). Cultural as well as soil management (altering open soil and grass vegetation) was performed identically in all seasons. To avoid downy and powdery mildew, background applications against those diseases were carried out on a regular basis (application intervals approximately 14 days) in all seasons. The exact records of annual background treatments are available in Supplementary Table 1 (http://oeno-one.eu/article/view/36). Fungicides with known activity against *B. cinerea* were not applied. Grape berry moth was controlled biotechnologically via mating disruption (pheromone dispensers) in all seasons.

2. Meteorological data

Meteorological data were recorded by a weather station of the German Meteorological Service (Deutscher Wetterdienst), located at a distance of approximately 100 m from the experimental vineyard. Air temperatures (measured at two meters above the ground) and precipitation sums (measured at one meter above the ground) were recorded each hour. Leaf wetness was calculated according to Hoppmann and Wittich (1997) based on hourly data of air temperatures (2 m), relative humidity (2 m), precipitation (1 m), wind speed (2.5 m) and global radiation (2.5 m).

3. Assessing *Botrytis cinerea* epidemics

Disease severity of Botrytis bunch rot caused by *B. cinerea* was assessed two (years 2004 to 2006) or three to seven times (years 2007 to 2013) per season between the start of the epidemic and harvest by examining 100 randomly selected clusters (50 on each side of the row) each in four randomized plots inside the experimental vineyard. Visually observed disease severities were classified in seven levels (0 %; 5 %; 10%; 25%; 50%; 75%; 100% disease severity). Average disease severity values were calculated based on the recorded mean disease severities of the four plots.

4. Normalization of grape phenological development

To allow time series analyses that are unbiased regarding differences in phenological plant development between seasons, assessment dates were normalized in terms of thermal time after full bloom. Thermal time is the summation of the physiologically effective temperature (Trudgill *et al.*, 2005) over time. This normalization for the cultivar Riesling was realized following the cumulative degree day approach proposed by Molitor *et al.* (2014). The model to simulate the phenological development incorporates (i) a lower threshold (base temperature), (ii) an upper threshold temperature, above which a further increase of the temperature will not accelerate plant development, and (iii) a heat threshold temperature, above which a further increase of the temperature leads to a development deceleration. This approach has been shown to enable for higher model accuracy than traditional cumulative degree day based approaches (Molitor *et al.*, 2014). To adapt this model to the variety Riesling, in the present investigations a parameterization based on 32 long-term phenological and meteorological observation data sets from Eltville (Germany; 50.03° N, 8.14° E), Veitshöchheim (Germany; 49.83° N, 9.87° E), Kindel (Germany; 49.97° N, 7.06° E) and Remich (Luxembourg; 49.54° N, 6.35° E) took place. Threshold triplets (cardinal temperatures) with best predictive fit were determined based on the normalized coefficients of variance on average of all stages as described before (Molitor *et al.*, 2014). Best adaptation on the 32 long-term phenological data sets (lowest average normalized coefficient of variation (0.7446)) was achieved using the threshold triplet 7, 18 and 24 °C. Observed average cumulative degree days ($CDD_{7;18;24}$) reaching specific BBCH stages are given in Supplementary Table 2 (http://oeno-one.eu/article/view/36).

In the following, cumulative degree days ($CDD_{7;18;24}$) after BBCH 65 represent the phenological grape development or the maturity status at a specific date (e.g., the assessment date).

5. Describing bunch rot epidemics as function of time and phenological development (thermal time)

Sigmoidal curves were fitted to the disease severity data of the years 2007 to 2013 plotted against both the days after BBCH 65 as well as the cumulative degree days $CDD_{7;18;24}$ after BBCH 65 following equation (1) using Sigma Plot 12.5 (Systat Software Inc., San Jose, CA, USA). The starting date at full bloom (BBCH 65 according to Lorenz *et al.* (1995)) was chosen since this stage was consistently noted in all seasons of observation.

$$y = \frac{100}{1 + e^{-((x - x_0)/a)}} \quad (1)$$

where y is the disease severity, x either the day after BBCH 65 or the cumulative degree day $CDD_{7;18;24}$ after BBCH 65, x_0 the inflection point of the curve and a the slope factor. For each of the 7 seasons, parameters describing the disease progress curve as

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well as their standard errors were determined. Coefficients of determination (r^2) and significance levels (p) were calculated to quantify the adaptation of the fitted curves to the observation data.

To compare the adequacy of both approaches tested (time, thermal time), average values of the slope factor as well as its coefficients of variation were computed.

The number of days after BBCH 65 as well as the cumulative degree days ($CDD_{7;18;24}$ after BBCH 65) that passed until a disease severity level of 5 % (acceptable disease severity level for high quality wines as proposed by Evers *et al.* (2010)) was reached were calculated for each year by interpolation using equation (1).

6. Effects of annual meteorological conditions on the epidemics (window pane analysis)

The impact of the following environmental variables on the bunch rot epidemics was investigated:

- daily average temperatures,

- daily precipitation sums,

- daily number of hours with leaf wetness,

- daily sum of the "Bacchus index" according to Kim *et al.* (2007).

The Bacchus index takes into account that the length of a wetness period required for the development of *B. cinerea* is depending on the temperature conditions (Kim *et al.*, 2007). Bacchus index sums (BI(d)) for every day were calculated using equation (2).

$$BI(d) = \sum_{i=1}^{24} BI(h) \text{(i)}$$

$$BI(h) = \frac{1}{84.37 - 7.238 * t + 0.1856 * t^2} \quad (2)$$

where BI(d) is the Bacchus index sum of the day d, BI(h) is the Bacchus index in the hour h; t is the mean air temperature during an hour with leaf wetness and i is the hour of the day d (Kim *et al.*, 2007).

To detect critical temporal periods during the season (relative to the date of BBCH 65), when environmental variables influence the thermal-temporal position of the epidemic, window pane analyses were conducted following the approach of Coakley and Line (1982). This method allows determining the length and the starting time of temporal windows during which average values of environmental variables are significantly correlated with plant disease levels at a specific time-point (target) such as at the end of a season (Kriss *et al.*, 2010). In the present investigation, tested time windows had widths of 5, 10, 20, 30, 50 or 100 days and windows were moved along the time frame between 50 days prior to full bloom and 125 days thereafter in daily steps. Average values of the environmental variables during each specific window ("summary environmental variables" (Kriss *et al.*, 2010)) were calculated separately for each data set. Linear correlations between each summary environmental variable and the cumulative degree day $CDD_{7;18;24}$ reaching a disease severity of 5 % (target) were calculated for each window width (5, 10, 20, 30, 50, 100 days) and each starting date. Pearson correlation coefficients (r-values) and significance levels (p-values) were determined for each summary environmental variable. Significant correlations were declared when individual p-values were below 0.05.

Results

1. Disease progress as a function of time and the thermal time

Table 1 shows the observed disease severities at the different assessment dates (expressed as calendar date, day of the year, days after BBCH 65 and cumulative degree days $CDD_{7;18;24}$ after BBCH 65).

Sigmoidal curves of the type $y = \frac{100}{1 + e^{-((x - x_0)/a)}}$, fitted the disease progress curves very precisely ($0.97 > r^2$, p£0.0148) (Figure 1). Coefficients of variance of the slope factors were 0.28 (time based approach) and 0.18 (thermal time based approach), respectively (Table 2; Table 3).

In case of the $CDD_{7;18;24}$ based approach, the slope factors ranged from 26.6 (2013) to 48.8 (2012) and the thermal-temporal position of the inflection points of the curves (x_0) from 915 (2010) to 1222 (2007) cumulative degree days $CDD_{7;18;24}$. Disease severities of 5 % were reached between 781.2 (2010) and 1104.7 (2009) cumulative degree days $CDD_{7;18;24}$ (Table 3).

2. Impact of seasonal meteorological conditions on the epidemic

Figure 2 shows the results of window pane analyses for all four summary environmental variables using the 30 day window. The results of all six tested

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Table 1 - Dates and disease severities of *Botrytis cinerea* at the different assessments in the years 2004 to 2013.

Year	Date	Day of the year (DOY)*	Days after BBCH 65	Cumulative degree day $CDD_{7;18;24}$ after BBCH 65	Disease severity
2004	01.09.	244	73	735.3	0.1
2004	12.10.	285	114	1034.6	20.6
2005	30.08.	242	74	751.2	0.1
2005	05.10.	278	110	1054.8	33.8
2006	05.09.	248	79	776.4	3.4
2006	04.10.	277	108	1055.7	95.9
2007	22.08.	234	86	850.9	0.4
2007	28.08.	240	92	914.4	0.6
2007	04.09.	247	99	975.5	3.3
2007	24.09.	267	119	1120.5	9.6
2007	09.10.	282	134	1211.5	44.4
2008	27.08.	239	81	829.9	0.2
2008	10.09.	253	95	967.9	1.7
2008	09.10.	282	124	1111.0	32.3
2009	15.09.	258	98	999.4	0.5
2009	22.09.	265	105	1074.4	6.7
2009	01.10.	274	114	1149.6	12.1
2009	08.10.	281	121	1200.0	38.0
2010	31.08.	243	70	724.2	2.2
2010	10.09.	253	80	801.0	4.1
2010	14.09.	257	84	836.4	18.6
2010	23.09.	266	93	894.1	41.7
2010	29.09.	272	99	921.4	48.2
2010	07.10.	280	107	980.5	80.8
2010	14.10.	287	114	1009.5	92.4
2011	29.08.	241	89	884.5	7.7
2011	05.09.	248	96	952.9	19.2
2011	13.09.	256	104	1034.4	60.7
2011	19.09.	262	110	1077.1	82.3
2012	05.09.	248	83	862.2	0.8
2012	12.09.	255	90	929.1	1.0
2012	18.09.	261	96	973.6	2.7
2012	25.09.	268	103	1012.7	6.8
2012	02.10.	275	110	1048.6	11.9
2012	08.10.	281	116	1080.2	20.9
2012	12.10.	285	120	1090.5	25.0
2013	09.09.	252	77	791.9	0.2
2013	16.09.	259	84	842.4	0.7
2013	23.09.	266	91	886.1	2.9
2013	30.09.	273	98	932.0	7.1
2013	08.10.	281	106	975.0	13.1
2013	14.10.	287	112	988.7	37.0
2013	21.10.	294	119	1029.1	65.7

* The 29th of February was not considered in leap years

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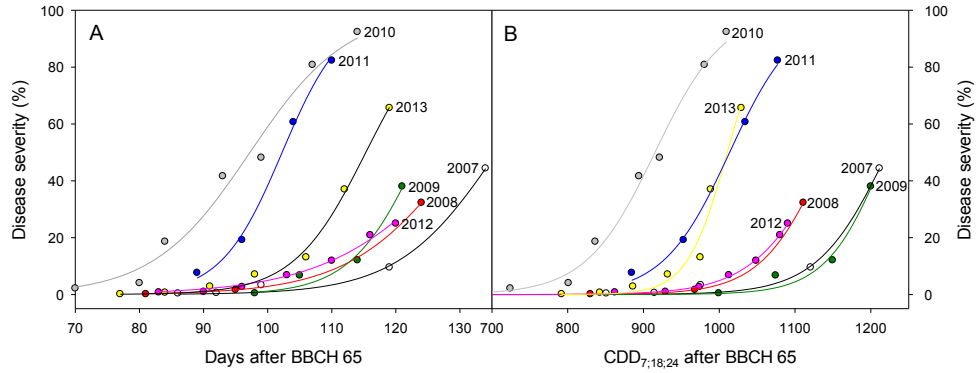


Figure 1 - Disease progress curves in the years 2007 to 2013 in Geisenheim as functions of the time (days after BBCH 65, A) or the thermal time (cumulative degree days $CDD_{7;18;24}$ after BBCH 65, B).

Table 2 - Parameters describing the disease progress curves of the type $y = \frac{100}{1+e^{-((x-x_0)/a)}}$ plotted against the time (days after BBCH 65) and calculated days after BBCH 65 reaching 5 % disease severity in the years 2007 to 2013. a = slope factor of the curve in the inflection point; x_0 = the inflection point of the curve. SE = standard error. Average and coefficient of variance (cv) of the slope factor a are given.

Year	a	SE (a)	x_0	SE (x_0)	R^2	P-value
2007	7.7	0.7	135.8	0.5	0.995	0.0001
2008	8.6	0.2	130.4	0.2	1.000	0.0037
2009	5.4	1.0	123.8	1.0	0.977	0.0113
2010	7.5	0.9	97.2	1.0	0.982	<0.0001
2011	4.8	0.3	102.2	0.3	0.997	0.0016
2012	10.5	0.7	130.9	1.1	0.991	<0.0001
2013	5.6	0.4	115.3	0.3	0.995	<0.0001
Average	7.2					
Cv	0.284					

window widths (5, 10, 20, 30, 50, 100 days) for all four summary environmental variables are given in the Supplementary Figure 1 (http://oeno-one.eu/article/view/36).

Correlation coefficients of window pane analyses are generally depicted at the end of the respective summary period (Figure 2; Supplementary Figure 1 http://oeno-one.eu/article/view/36).

Analyses (30 day window) revealed that the following summary environmental variables were significantly and **positively** (high value à late epidemic) correlated with the thermal-temporal position of the epidemic (x_5 % -value):

- summary environmental variable temperature between 75 and 84 days after BBCH 65 ;

- summary environmental variable precipitation between 9 and 10 days after BBCH 65 ;

- summary environmental variable leaf wetness between 3 and 20 as well as between 27 and 29 days after BBCH 65 ;

- summary environmental variable Bacchus index between 2 and 8, 12 and 16, 78 and 79 as well as between 90 and 91 days after BBCH 65 (Figure 2) ;

whereas the following summary environmental variables were significantly and **negatively** (low value à late epidemic) correlated with the thermal-temporal position of the epidemic (x_5 % -value):

- summary environmental variable temperature between the days 11 and 12 after BBCH 65 ;

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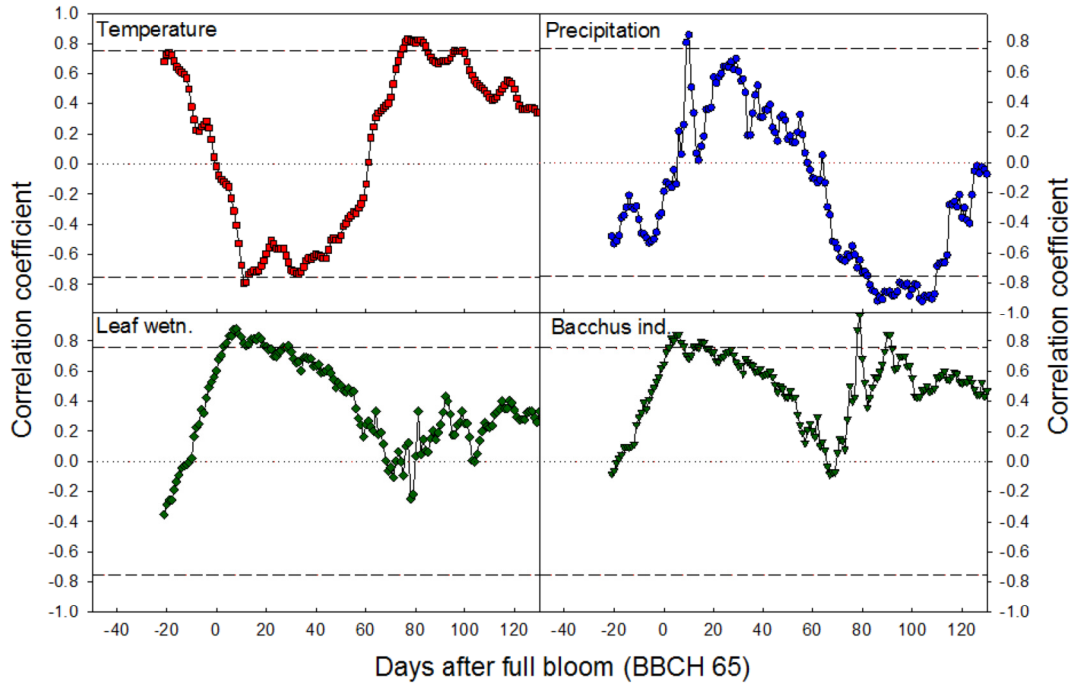


Figure 2 - Window pane analysis

Pearson correlation coefficients between the summary environmental variables (daily average temperatures (Temperature), daily precipitation sums (Precipitation), daily number of hours of leaf wetness (Leaf wetness), daily Bacchus index sums (Bacchus Index) and the cumulative degree days $CDD_{7;18;24}$ reaching a disease severity of 5 % depending on the starting date of a window (window length: 30 days). Dotted horizontal lines indicate a correlation coefficient level of 0; short dashed horizontal lines indicate the critical (positive and negative) correlation coefficients for a significance level of 0.05. Correlation coefficients between the summary environmental variables and the cumulative degree days $CDD_{7;18;24}$ reaching a disease severity of 5 % are depicted as dots at the last day of the temporal window.

Table 3 - Parameters describing the disease progress curves of the type $y = \frac{100}{1+e^{-((x-x_0)/a)}}$ plotted against the thermal time ($CDD_{7;18;24}$ after BBCH 65) and calculated values for the $CDD_{7;18;24}$ reaching 5 % disease severity as well as 95 % confidence bands in the years 2007 to 2013. a = slope factor of the curve in the inflection point; x_0 = the inflection point of the curve. SE = standard error. Average and coefficient of variance (cv) of the slope factor a are given.

Year	a	SE (a)	x_0	SE (x_0)	R^2	P-value	$CDD_{7;18;24}$ value reaching 5% disease severity		
							Predicted	Lower 95% confidence band	Upper 95% confidence band
2007	46.2	4.7	1222	3.7	0.994	<0.0001	1086	1052	1123
2008	43.0	0.9	1143	0.7	1.000	0.0028	1016	992	1039
2009	39.2	8.7	1220	8.7	0.971	0.0148	1105	1044	1161
2010	45.5	4.1	915	4.2	0.990	<0.0001	781	753	815
2011	43.8	2.8	1014	3.1	0.997	0.0014	885	851	927
2012	48.8	1.5	1145	2.2	0.999	<0.0001	1001	995	1007
2013	26.6	3.5	1011	3.5	0.972	<0.0001	932	910	959
Average	41.9								
Cv	0.176								

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- summary environmental variable precipitation between 83 and 109 days after BBCH 65 (Figure 2).

Overall (all 6 window widths), maximum correlation coefficients (positive correlations) were observed in case of the summary temperature using the 50 day window on day 96 (r= 0.9006), in case of the summary leaf wetness using the 5 day window on day -17 after BBCH 65 (r= 0.9337) and in case of the summary Bacchus index using the 30 day window on day 79 after BBCH 65 (r= 0.9444).

Overall minimum correlation coefficients (negative correlations) were observed in case of the summary precipitation using the 20 day window on day 97 after BBCH 65 (r= -0.9500) (Table 4; Supplementary Figure 1 http://oeno-one.eu/article/view/36).

Discussion

1. Disease progress curves

To describe the disease progress of *B. cinerea* different approaches were used in previous studies. Beresford *et al.* (2006) proposed logit transformed linear regressions, whereas Evers *et al.* (2010), Molitor *et al.* (2011) and Molitor *et al.* (2012) used exponential equations of the type $y= e^{a(x-x0)}$. Exponential equations, however, do not consider an upper limit, thus ignoring that disease severity values cannot exceed 100 %. Exponential regression models therefore fit epidemics well at their beginning, but cannot consider the off-levelling at later stages. Since some time courses in the present data set contained data points in the period of levelling off, the sigmoidal curve of the type $y= 100 / (1 + e^{-((x-x0)/b)})$ was chosen to simulate the disease progress following Molitor *et al.* (2015a) and Molitor *et al.* (2015b).

Under the climatic conditions of Geisenheim, the phenological development of grapes on the same calendar day strongly varies from year to year. Since thermal time is independent of the temperature regime in a specific season (Tsimba *et al.*, 2013), adequate cumulative degree day based approaches are able to describe the phenological development more reliably than calendar days. As a novelty, in the present investigation, disease progress was plotted against the thermal time after full bloom (BBCH 65) representing the phenological development of the plants.

Sigmoidal curves fitted the disease severity as a function of both the time and the thermal time very precisely ($r^2 >0.97$). The average coefficient of variance of the slope factors was 0.28 in case of the time based curves (Figure 1A), while it was 0.18 for the thermal time curves (Figure 1B). Obtained coefficients of variance are suggesting that in case of the time based approach temperature fluctuations between the seasons partly accounted for the variation of the slope factors, while in the thermal-time based approach fluctuations were generally lower. Here, slope factors ranged from 39.2 to 48.8 in 6 out of 7 seasons demonstrating the almost identical pattern of the fitted sigmoidal disease progress curves in most seasons. Only the slope factors of the year 2013 (a season with abnormally high precipitation sums in the ripening period) differed considerably from the average.

In general, the good fit of the sigmoidal disease progress curves plotted against the thermal time as well as the constant slope factors suggest that the progress of the annual disease is (under given environmental conditions) proceeding in close connection with the phenological development, which is driven by the time and the temperature. In consequence, during a defined time period the pace of the epidemic is much faster under warm than under cool temperature conditions.

On the other hand the constant slope factors indicate that other factors such as specific annual precipitation or leaf wetness conditions seem to have only a minor influence on the disease progress once the epidemic

Table 4 -Maximum (positive correlations) or minimum (negative correlations) Pearson correlation coefficients between the summary environmental variables and the cumulative degree day reaching 5 % disease severity, days after full bloom (BBCH 65), where those correlation coefficients were reached as well as temporal windows used. Years 2007 to 2013.

	Maximum or minimum correlation coefficient	Days after full bloom	Window widths
Temperature	0.9006	96	50 days
Precipitation	-0.9500	97	20 days
Leaf wetness	0.9337	-17	5 days
Bacchus index	0.9727	79	30 days

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started. This is true at least (i) under the present climatic conditions in Geisenheim located in the Rhine river valley, with frequently foggy conditions in the autumn months, and (ii) for the variety Riesling. However, it cannot be excluded that the epidemic might behave differently under different climatic conditions or in case of other cultivars, e.g. due to divergent ripening characteristics, cluster morphology or physical properties of the berry skins.

Interestingly, the good fit of the disease progress curves plotting the recorded disease severities against the thermal time representing the phenological development (expressed as cumulative degree days $CDD_{7;18;24}$) furthermore revealed that the temperature conditions that force the development of *B. cinerea* on grapes might be similar to the forcing conditions for the phenological development of *V. vinifera* cv. Riesling. The theoretical reflections that the temperature conditions and cardinal temperatures favoring plant and fungal development are largely the same merit further investigations.

2. Impact of annual environmental factors on thermal-temporal position of the epidemic

The equations of the sigmoidal progress curves obtained were used to calculate the cumulative degree day when 5 % disease severity were reached (x_5 %) in each year. The considerable variations observed in x_5 % (range from 781.2 $CDD_{7;18;24}$ in 2010 to 1104.7 $CDD_{7;18;24}$ in 2009) suggest that other factors besides physiologically efficient temperatures (as the drivers of grape phenological and maturation development) determined the thermal-temporal position of the epidemic. In other words, the present data showed that the thermal-temporal position of the annual epidemic is not directly linked to the degree of grape maturity but influenced by other factors.

In fact, window pane analyses demonstrated that meteorological conditions during different phases of the phenological development have a distinct and partially significant impact on the thermal-temporal position of the annual epidemic. Interestingly, relatively high temperatures during grape bloom (range of summary daily average temperatures on day 11 after BBCH 65 (30 day window): 16.4°C (2009) to 15.5°C (2010)) were associated with (thermal-temporal) early epidemics, while relatively high temperatures around/after veraison (range of summary daily average temperatures on day 77 after BBCH 65 (30 day window): 17.4°C (2010) to 20.6°C (2012)) were associated with a (thermal-temporally) late epidemic (Figure 2).

The close correlations observed between high precipitation sums around/after veraison (range of summary daily precipitation sums on day 86 after BBCH 65 (30 days window): 0.36 mm (2009) to 4.01 mm (2010)) and (thermal-temporally) early bunch rot epidemics are most likely explained by the combination of the known phenomena that (i) the availability of water tends to foster the development of fungal pathogens, (ii) high post-veraison water availability leads to high water uptake into the berries, which results in larger berries, compact clusters and, in consequence, a high risk of fruit cracking (Smart and Robinson, 1991; Keller *et al.*, 2003) and (iii) rain events after veraison re-activate latent infections, which often lead to direct infection of ripening berries (Evans and Emmett, 2011).

Interestingly, the present analyses furthermore pointed out that generally high temperatures, low precipitation sums, low leaf wetness and low Bacchus index values around grape bloom were significantly correlated with (thermal-temporally) early bunch rot epidemics (Supplementary Figure 1 http://oeno-one.eu/article/view/36). Hence, the meteorological conditions during this period of grape development are of considerable prognostic value. Observed correlations might be explained by direct or indirect effects of the meteorological conditions around grape bloom on the physiology of (i) either the fungus or (ii) the plant. Generally, high temperatures in combination with low precipitation and low moisture are not supposed to promote fungal development. Consequently, an accelerating influence of such conditions on the epidemic appears unlikely, suggesting that the reason might be found on the plant's side. In grapevine, the degree of fruit set and abscission (as result of the grape flowering process) is highly determined by environmental conditions (Caspari *et al.*, 1998; Vasconcelos *et al.*, 2009). Low temperatures (< 15°C) or rain during bloom can lead to excessive abscission of flowers and poor fruit set (Koblet, 1966; Keller, 2010). High fruit set is often linked to a compact cluster structure (Vasconcelos and Castagnoli, 2000). Such compact cluster structures have been repeatedly demonstrated to be closely correlated with a high predisposition of grapes to bunch rot (e.g., Hed *et al.*, 2009; Molitor *et al.*, 2012; Intrigliolo *et al.*, 2014; Tello and Ibanez, 2014; Molitor *et al.*, 2015a). The observed phenomenon (hot and dry weather conditions around grape bloom à thermal-temporally early bunch rot epidemics) is consequently assumed to be most likely explained best by the conjunction of the both well-described and scientifically undoubted relations (hot + dry flowering conditions à high fruit set, compact

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cluster structure; compact cluster structure à high predisposition to bunch rot). This conjunction of both phenomena has up to the best of our knowledge not yet been highlighted in the scientific literature.

The fact that wet conditions during grape flowering were linked to a (thermal-temporally) late epidemic might furthermore indicate that under present conditions (i) latent infections during bloom (as described as an important factor influencing the annual bunch rot epidemic in other viticultural regions, such as in Spain (Calvo-Garrido *et al.*, 2014)) are absent, or (ii) the epidemiological consequences of such latent infections are superimposed (e.g., by the strong effect of flowering weather conditions on the cluster structure and the predisposition to bunch rot).

Assuming an average temperature of 16°C in the ripening period (average September temperatures between 2000 and 2009 in Geisenheim/Germany: 15.57°C, in Remich/Luxembourg: 15.59°C), the observed difference between the thermal-temporally earliest (2010) and latest (2009) epidemic (323.6 $CDD_{7;18;24}$) corresponds to 35.9 days and the standard deviation of the mean x_5 % values of all seven seasons of 114.8 $CDD_{7;18;24}$ corresponds to 12.7 days. Compared to these inter-annual differences, the observed average beneficial epidemic delaying effects achieved by single viticultural measures such as the use of the bioregulators gibberellic acid (Evers *et al.*, 2010) (0.3 days) or prohexadione-ca (Molitor *et al.*, 2011) (2.5 days), a single application of a botryticide (active ingredient fenhexamid) (Molitor *et al.*, 2011) (2.5 days), flower debris removal (Molitor *et al.*, 2015b) (3.7 days), late first shoot topping (first shoot topping compared to first shoot topping four weeks after BBCH 68 instead of one week) (Molitor *et al.*, 2015a) (4.3 days) or cluster zone leaf removal (BBCH 71) (Molitor *et al.*, 2011) (7.3 days) are clearly inferior. Thus, as a novelty, the present investigations revealed that (under the present conditions) the observed inter-annual variations in the environmental conditions outweigh the effect on the thermal-temporal position of the epidemic that might be introduced by cultural practices. Certainly, combining efficient cultural practices (including soil and canopy management) is able to reduce the risk of early epidemics in case of adverse environmental conditions.

3. Effect of the thermal-temporal position of the bunch rot epidemic on the vintage quality

In general, wines from (thermal-temporally) late harvested grapes are often preferred in wine tastings

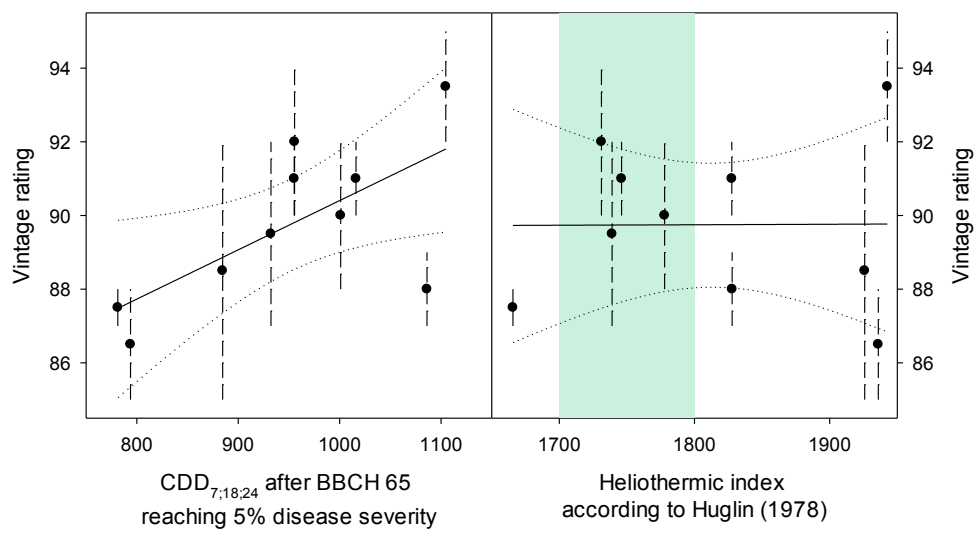


Figure 3 - Annual vintage quality ratings for white wines of the Rheingau winegrowing region in the years 2004 to 2013 according to Payne (2013; 2014) plotted against the annual thermal-temporal position of the bunch rot epidemic (cumulative degree day $CDD_{7;18;24}$ after BBCH 65 reaching 5 % disease severity) (left) as well as against the annual heliothermic index according to Huglin (1978) (right).
Dots represent average vintage ratings, vertical dashed bars the vintage rating span. Solid lines represent the linear regression curves and dotted lines the margins of the 95 % confidence bands. The green highlighted zone in the right graph shows the band of the annual heat consumption (expressed as heliothermic index according to Huglin (1978)) enabling successful cultivation of the grape cultivar Riesling according to Huglin (1978).

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(Spring, 2004) and they show a lower tendency to untypical aging defects (Schneider, 2014). This is especially the case under cool climate conditions close to climatic borders limiting viticulture. While in years with a late epidemic, grapes and, consequently, potential wine quality might benefit from a long-lasting maturation period, high bunch rot levels force grape-growers to harvest grapes at a stage of incomplete maturity in years with an early epidemic.

Consequently, it is assumed that under present Central European climatic conditions the potential wine quality of a specific vintage is determined (in case no efficient measures to control bunch rot are realized) to a major degree by the annual thermal-temporal position of the *B. cinerea* epidemic.

To broaden the data base to test this theory, we assumed that in the years 2004 to 2006 of the presented data set, where only two assessments took place, the disease severity at the data of BBCH 65 was 0 %. This assumption is based on the fact that organs (here, grape berries) which are not yet formed cannot show disease symptoms, yet. This allowed constructing the complete disease progress curves for those years and, in turn, calculating the cumulative degree days ($CDD_{7;18;24}$ after BBCH 65) that passed until a disease severity level of 5 % ($x_{5\ \%}$) was reached. Following this step, annual Gault & Millau WineGuide (Payne, 2013 ; Payne, 2014) vintage quality ratings (2004-2013 ; criteria for rating undisclosed) for white wines originating of the Rheingau winegrowing region (region where the experimental vineyard is located) were plotted against (i) the annual thermal-temporal position of the epidemic (cumulative degree day $CDD_{7;18;24}$ reaching a disease severity of 5 %) in the vineyard of the present investigations as well as (ii) the annual value of the heliothermic index according to Huglin (1978). The heliothermic index according to Huglin (1978) represents a widely use metric to describe the annual heat consumption during the vegetation period (April-September ; Northern Hemisphere) as well as the sustainability of a specific location for the successful cultivation of specific grape cultivars (Figure 3).

Analyses confirm that the average annual vintage quality rating of the Rheingau region was significantly and positively correlated with the annual thermal-temporal position of the bunch rot epidemic in the present experimental vineyard (r^2= 0.45; p= 0.03) (Figure 3). This means that vintages with a thermal-temporally early epidemic were on average perceived to be of lower quality. Possible explanations are (i) a negative sensorial impact of bunch rot (especially in early stages of grape maturity ; unripe rot) on wine quality/wine quality perception and/or (ii) an early harvest date of incompletely mature grapes enforced by a fast spread of the disease.

Interestingly, data analyses furthermore showed that no significant influence of the annual heat consumption (expressed as heliothermic index according to Huglin (1978)) and the vintage rating (r^2 < 0.0001 ; p= 0.98) could be demonstrated. These considerations suggest that under the present climatic conditions in the Rheingau region (minimum heat consumption demands for Riesling fulfilled ; i.e., heliothermic index ≥1700-1800), the impact of the thermal-temporal position of the bunch rot epidemic is more important for the wine quality than the annual heat consumption.

4. Implementation into practical applications

The following conclusions and potential applications are based on the recorded and analyzed data set originating from the cultivar Riesling under the environmental conditions of the Rheingau region. It has to be taken into account that the observed relationships between meteorological conditions and the bunch rot epidemiology might vary in case of other cultivars or deviating climatic conditions.

Interestingly, in the present analyses high values of the Bacchus index (actually foreseen as an indicator of *B. cinerea* infection probability) as well as long-lasting leaf wetness during bloom were significantly and positively correlated with thermal-temporally late epidemics (long leaf wetness à late epidemic) (Figure 2). Even in the other parts of the season (50 days prior to BBCH 65 to 125 days after BBCH 65) neither leaf wetness nor Bacchus index were in any temporal window significantly and negatively correlated with the thermal-temporal position of the epidemic. In fact, those findings raise the question if the use of leaf wetness based bunch rot models, such as the Bacchus (Kim *et al.*, 2007), the Broome (1995) or the Nair and Allen (1993) model, would be adequate to fix botryticide application dates under the present Central European conditions, since all models recommend applications in periods of long-lasting leaf wetness independent of the present susceptibility of grape berries to *B. cinerea* infections.

The virtually constant patterns and slope factors of the disease progress curves plotted against the thermal time observed in the present investigations imply that a simulation of the further disease progress is possible as soon as the disease severity

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level is assessed for the first time at an earlier stage of the epidemic (provided a minimum level of disease severity already existing; threshold to be defined). For such a simulation (of the further disease progress) for example short-term temperature forecast or local daily based long-term average temperature data might be used. Thinking one step ahead, the date reaching a defined bunch rot threshold might be simulated and for example harvest dates, harvest logistics or the chronological order of vineyards to be harvested might be predicted accordingly. In recent years, such an approach to extrapolate disease progress curves has been suggested and already implemented in the Botrytis Decision Support webpage (http://www.botrytis.co.nz/) by Hill and Beresford (2010) in New Zealand. However, Hill and Beresford (2010) did not take into account the effect of temperatures – which vary distinctively from year to year (see present investigations) and from location to location – on the disease progress.

Furthermore, the present findings that the environmental conditions around grape bloom have a distinct influence on the thermal-temporal position of the annual bunch rot epidemic could be directly implemented in the early season bunch rot protection strategy. For example, in the case that warm and dry bloom weather conditions are observed (and, consequently, compact cluster structures are, according to the presented theory, likely to occur), cultural measures leading to a loosening of the cluster structure, such as leaf removal in the cluster zone, late timing of the first shoot topping or cluster division, could be intensified. Even a short-term application of bioregulators (application date mostly around full bloom) could be considered, in case weather forecast indicates conditions supporting a high fruit set. In addition, in case of high fruit set due to optimal flowering conditions a targeted botryticide application prior to bunch closure might be scheduled. In contrast, in case weather conditions around bloom are suboptimal (leading to a poor fruit set), (i) further measures to loosen cluster structure might be omitted to avoid cumulative abscission effects (as the result of the combination of suboptimal environmental conditions and crop cultural measures reducing fruit set) and (ii) botryticide applications saved.

Based on the present investigations a model indicating the annual risk for severe bunch rot attack prior to full grape maturity as well as simulating the annual thermal-temporal position of the bunch rot epidemic is under development. More specifically, the seasonal risk classification might enable (i) a reduction of the number of botryticide applications and hence a reduction of pesticide use in years with a lower expected bunch rot risk or (ii) a higher bunch rot control efficiency due to the targeted application of botryticides in years with a high bunch rot risk.

Conclusions

Bunch rot epidemics followed sigmoidal disease progress curves with comparable slope factors each year, while the thermal-temporal position of the epidemic strongly varied between seasons. Low temperatures and wet conditions during bloom as well as high temperatures and low precipitation around/after veraison were associated with thermal-temporally late epidemics. Results indicate that the first effect might be explained by the impact of the environmental conditions during the flowering period on the fruit set and, in consequence, on the cluster structure, which is generally strongly linked to the predisposition to bunch rot. Inter-annual variations in the meteorological conditions have been observed to exhibit a stronger influence on the thermal-temporal position of the epidemic than the effects that might be introduced by cultural practices. Furthermore, the annual thermal-temporal position of the bunch rot epidemic was detected to have a significant impact on the vintage wine quality perception. The new knowledge obtained might support grape-growers' decisions concerning direct (botryticide applications) or indirect (cultural) measures to control grape bunch rot and is supposed to build the starting point for the development of a bunch rot model.

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