Physiological and Molecular Plant Pathology 114 (2021) 101626

Contents lists available at ScienceDirect

Physiological and Molecular Plant Pathology

journal homepage: www.elsevier.com/locate/pmpp

Distinct volatile signatures of bunch rot and noble rot

Tamás Dankó, Magdolna Szelényi, Tibor Janda, Béla Péter Molnár, Miklós Pogány *

Centre for Agricultural Research, H-2462 Martonvásár, Hungary

ARTICLE INFO

Keywords:
Grapevine
Gray mold
qPCR
Fungal biomass
VOCs

ABSTRACT

Bunch rot and noble rot development were simultaneously instigated on healthy *Vitis vinifera* cv. Furmint bunches collected in the Tokaj wine region in Hungary. Bunches transferred into a growth chamber with controlled temperature and humidity exhibited symptoms of the two forms of botrytization. Berries exposed to noble rot-inducing conditions gradually dehydrated and showed higher level of soluble solids but less biomass of *Botrytis cinerea* in comparison with berries subjected to bunch rot. GC-MS analysis of volatile compounds produced by the berries revealed obvious differences in the emission of odorants between bunch rot and noble rot.

1. Introduction

Noble rot and bunch rot (or gray mold) are two crucially different appearances of the interaction between grape berries and the filamentous fungus *Botrytis cinerea* (teleomorph: *Botryotinia fuckeliana*). Noble rot development is perceived as a favorable process that results shrivelled, chocolate-brown berries, enriched in exquisite aroma components. These raisin-like berries are the main sources of flavor and odor in botrytized sweet wines, such as the Sauternes of France, the Trockenbeerenauslese of Germany and the Aszú of Hungary [1,2]. Bunch rot, on the contrary, is a detrimental form of the same interaction, leading to the soft decay of berries together with intense fungal mycelium formation and unappealing taste and smell [3]. Mature grape berries are usually highly susceptible to *B. cinerea*. Immature and veraison berries, on the contrary, possess natural resistance to *B. cinerea* attributed to their greater performance in synthesizing the phytoalexin resveratrol, activating a burst of reactive oxygen intermediates and triggering salicylate-dependent defense mechanisms [4,5]. The decisive circumstance that controls the direction of the infection is humidity. Essentially, high air humidity (typically above 90%) that continues for several days supports the emergence of bunch rot, whereas lower air humidity (below 80%) favors noble rot development. Microclimate conditions ideal for abundant natural noble rot appearance more specifically include a short rainy period, followed by an extended period of sunny, warm, dry weather during daytime and cooler, misty, humid nights [6,7]. Berries affected by noble rot or bunch rot are highly distinct in their morphology, chemical composition or agricultural value. These two phenomena have been studied separately before, by analyzing berries of different red and white cultivars, using samples collected in varying wine regions and working with bunches subjected to diverse botrytization techniques (natural or artificial botrytization, using mature berries or berries in veraison stage). Furmint is the most frequently planted white grapevine cultivar in the Tokaj wine region. Here, we present results on the simultaneous, artificial induction of noble rot and bunch rot using mature Furmint grape berry material collected in a vineyard.

2. Material and methods

2.1. Biological samples and conditions of botrytization

Sixty healthy bunches of *V. vinifera* cv. Furmint were collected in Mád, Hungary in vineyard Betsek, 48°11′16″N 21°19′03″E, in mid September 2018. Half of the bunches were sprayed with *B. cinerea* strain B05.10 conidium suspension (10^5 conidia suspended in 1 ml Gamborg B5 liquid medium supplemented with 2% glucose) and bunches of the other half were sprayed only with the liquid medium lacking fungal conidia. Both inoculated and uninoculated bunches were moved to a Conviron growth chamber and were kept in closed plastic boxes for 24 h. When the 24 h incubation was over, half of the bunches (inoculated and also uninoculated ones) were removed from the boxes and were kept under noble rot-inducing conditions, the other half was left in the boxes subjected to bunch rot for one week. Noble rot-inducing growth chamber settings were as follows: Between 8 a.m. and 12 noon temperature was gradually raised from 5 °C to 20 °C, meanwhile relative humidity (RH%) was lowered from 96% to 60%. From 5 p.m. to 8 p.m. temperature got reduced from 20 °C to 10 °C, and RH% was increased from

* Corresponding author.
E-mail address: pogany.miklos@atk.hu (M. Pogány).

https://doi.org/10.1016/j.pmpp.2021.101626
Received 11 October 2020; Received in revised form 26 January 2021; Accepted 3 February 2021
Available online 10 February 2021

Fig. 1. Representative bunches of *V. vinifera* cv. Furmint after artificial botrytization carried out in a growth chamber. A) Healthy bunch, B) Furmint bunch inoculated with a suspension of 10^5/ml *B. cinerea* conidia, incubated for 1 week under gray mold-inducing conditions, C) Furmint bunch without *B. cinerea* inoculation, incubated for 1 week under noble rot-inducing conditions, D) Furmint bunch inoculated with a suspension of 10^5/ml *B. cinerea* conidia, incubated for 1 week under noble rot-inducing conditions, E) Furmint bunch without *B. cinerea* inoculation, incubated for 3 weeks under noble rot-inducing conditions, F) Furmint bunch inoculated with a suspension of 10^5/ml *B. cinerea* conidia, incubated for 3 weeks under noble rot-inducing conditions.

(caption on next column)

60% to 96%. Between 8 p.m. and 5 a.m. temperature further declined to 5 °C and RH% was kept at 96%.

2.2. Detection of total soluble solids

The Brix degree value of the juice in our healthy or botrytized berry samples was measured using a RHB0-80ATC manual refractometer (YHequipment, Shenzhen City), analyzing 6 samples for each treatment. Every sample contained the juice of two representative berries.

2.3. Assessment of B. cinerea biomass

Biomass of *B. cinerea* in the berries was assessed by detection of fungal DNA using quantitative real-time PCR. For each treatment, six samples each comprising content of two berries were analyzed in duplicate real-time PCR amplifications. Healthy berries or berries exhibiting symptoms characteristic of noble rot or bunch rot were selected for the analysis. DNA extraction was performed by a nucleic acid purification protocol described before [8] with the following modifications: tissue was ground to a fine powder in liquid nitrogen by a Retsch laboratory ball mill. Spermidine trihydrochloride and β-mercaptoethanol were eliminated from the extraction buffer and 200 mg of ground tissue was extracted with 5 ml extraction buffer in 15 ml centrifuge tubes. After precipitation of DNA in the samples with 0.1 vol 3 M NaOAc (pH 5.2) and 0.6 vol ice cold isopropanol, incubation at −80 °C for 30 min and subsequent centrifugation, the nucleic acid pellets were not dissolved in TE buffer and the following LiCl treatment was also omitted. Instead, the supernatant was removed and the DNA pellet was washed twice with ice cold 70% EtOH, centrifuged after both washing steps at 4800×*g* for 15 min at 4 °C and the supernatant was discarded after each washing step. The resulting sample DNA was air dried and then dissolved in 30 μl nuclease-free water. Following nanodrop nucleic acid quantification all samples were adjusted to a concentration of 10 ng/μl DNA. Real time qPCR amplifications were carried out in a Bio-Rad CFX96 instrument. The reaction mixture contained 7.5 μl SensiFAST SYBR No-ROX mix (Bioline Meridian Life Science Company), 2.5 μl template DNA, 0.6 μl of *B. cinerea*-specific forward and reverse primers (administered from 10 μM stock solutions) and 3.8 μl of nuclease-free ultrapure water in a 15 μl total reaction volume. Primer sequences were designed for the RNA polymerase II second largest subunit gene (*RBP2*) of *B. cinerea*: forward (5′-TTCACAGATGCAGGACGAGT-3′) and reverse (5′-ACAGTCTCTTCTTCCTCGGC-3′). Cycling parameters were as follows: initial denaturation at 95 °C for 3 min, followed by 40 cycles of 5 s at 95 °C, 10 s at 60 °C and 20 s at 72 °C. The specificity of the PCR was confirmed by melting curve analysis. A calibration curve was obtained using genomic DNA isolated from a plate of *B. cinerea* strain B05.10 cultivated on malt extract agar medium. Content of *B. cinerea* biomass was expressed as a ratio of *B. cinerea* DNA compared to total sample DNA.

2.4. Volatile collection

Bunches inoculated with *B. cinerea* and incubated under gray mold or noble rot-inducing conditions (as described before) were used. Volatile profiles were created using 4 independent noble rot and 4 gray mold

Table 1
Concentration of soluble solids in Furmint berries following various botrytization treatments leading to gray mold (bunch rot) or noble rot, with or without sprays of *B. cinerea* conidium suspension. Data show the average of 6 biological samples ± SD (each sample composed of a pool of two berries). Means marked with different letters are significantly different at P ≤ 0.01.

Healthy berries	Gray mold – uninoculated (1 week)	Gray mold – *B. cinerea* 10^5 (1 week)	Noble rot – uninoculated (1 week)	Noble rot – *B. cinerea* 10^5 (1 week)
22.52 ± 0.89[a]	20.67 ± 0.65[b]	17.77 ± 0.15[c]	24.3 ± 0.38[d]	24.67 ± 0.27[d]

samples, each sample containing two bunches. Bunches were placed into inert polyester oven bags and charcoal filtered continuous airflow was drawn through at 0.8 l min−1 using a vacuum pump (Thomas G 12/02 EB, Gardner Denver Thomas, Fürstenfeldbruck, Germany). Volatiles were collected continuously for 4 h with 5 mg active charcoal (Brechbühler AG, Schlieren, Switzerland) loaded glass column (ID. = 4 mm) [9]. Adsorbed volatiles were eluted with 150 µl of dichloromethane, and 300 ng internal standard ((Z)-Octadec-13-enal [Pherobank, Wijk bij DuurstedeThe Netherlands]) was added right after elution. The eluted volatiles were stored at −80 °C until analysis.

2.5. GC-MS analysis

Volatilomes were analyzed by GC-MS (HP Agilent 5890 GC and 5975 MS, Agilent Technologies, Palo Alto, USA) on a VF-WAXms fused silica capillary column (60 m × 0.25 mm x 0.25 µm J&W Scientific, Folsom, CA, USA). In splitless mode 3 µl sample was injected and purged for 1 min at 220 °C. Oven temperature was initially held at 50 °C for 2 min then raised to 240 °C at 8 °C min-1, and held for 10 min. The ionization voltage was 70 eV, scanning *m/z* 29–300, at 2 scans/s and the flow rate of the carrier gas (helium) was 1.0 ml/min. Compounds were tentatively identified by matching their mass spectra with those in the MS Libraries (NIST 17 and Wiley) using the software MassHunter Qualitative Navigator B.8.00. The compounds were also verified by synthetic standards (Sigma-Aldrich) and compared to published and calculated Kováts index (KI) values using C8–C20 alkanes calibration standard.

2.6. Statistics

Data for total soluble solids and *B. cinerea* biomass were statistically analyzed by one-way ANOVA and subsequent Tukey's honestly significant difference test for pairwise comparisons. Results of volatile collection were analyzed by the non-parametric Mann–Whitney *U* test. Areas of the identified peaks for each sample were determined and normalized by the internal standard area then transformed to logarithmic value. P-values of ≤0.05 were considered statistically significant.

3. Results

3.1. Simultaneous induction of bunch rot and noble rot in growth chambers with controlled temperature and humidity

Bunches of ripe, healthy Furmint grape were collected in the Tokaj wine region in a vineyard with a reputation of yielding high quality noble rot berries. They were transferred to a growth chamber programmed to imitate optimal conditions for noble rot development. Half of the bunches were sprayed with *B. cinerea* conidium suspension and bunches of the other half were sprayed with Gamborg B5 medium supplemented with 2% glucose. Both inoculated and uninoculated bunches were moved to the growth chamber and were kept in closed plastic boxes for 24 h that ensured high humidity necessary for the establishment of the infection. When the 24 h incubation was over, half of the bunches (inoculated and also uninoculated ones) were removed from the boxes and were kept under noble rot-inducing conditions, the other half was left in the boxes subjected to bunch rot. One week after the beginning of the experiment, berries kept in conditions favorable of noble rot turned dark pink and started to shrivel. Berries subjected to gray mold development showed marked mycelium growth on their surfaces (Fig. 1).

3.2. Bunch rot and noble rot distinctively affect sugar and fungal biomass levels

Soluble solids concentration, expressed in °BRIX, reliably reflects total sugar content, as most of the soluble solids in unfermented grape juice are sugars [10]. °BRIX also correlate well with the accumulation of reducing sugars in ripening Shiraz grape berries [11].

Furmint bunches incubated under gray mold-inducing conditions showed significantly lower sugar content (measured as °BRIX) in comparison with healthy berries. Noble rot development, on the other hand resulted in elevated sugar level in the juice of the berries (Table 1). BRIX values were measured 8 days after collecting the bunches in the vineyard (1 day incubation in boxes + 7 days kept in bunch rot- or noble rot-promoting environment).

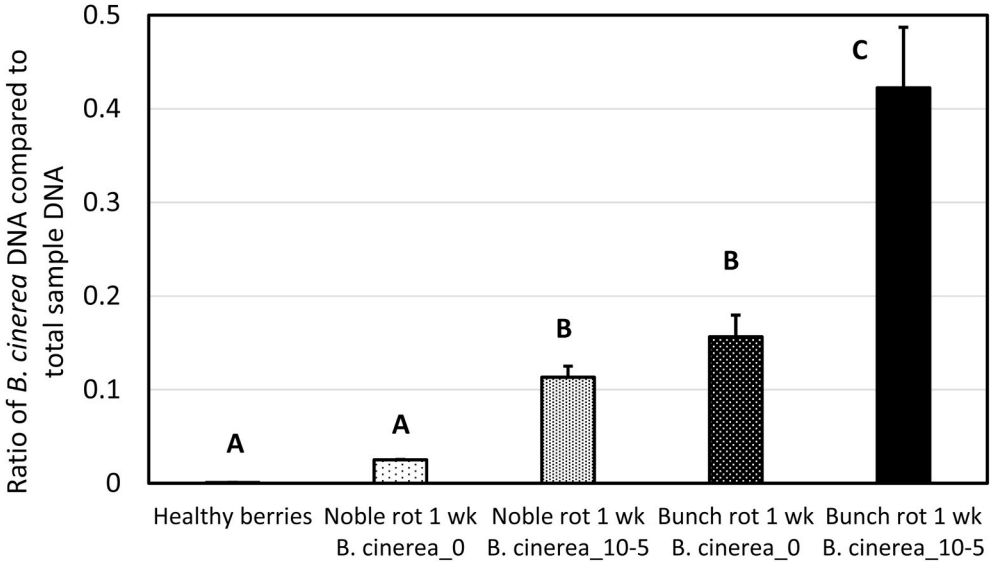

Fig. 2. Assessment of *B. cinerea* biomass in Furmint berries following botrytization treatments leading to gray mold (bunch rot) or noble rot, with or without sprays of *B. cinerea* conidium suspension. Quantitative real-time PCR amplifications were performed using DNA extracts of botrytized berry tissues and a serial dilution of pure *B. cinerea* DNA extract for calibration curve. *B. cinerea* biomass was expressed as a ratio of *B. cinerea* fungal DNA compared to the total DNA content of the samples. Bars represent mean of 6 biological samples ± SD (each sample composed of a pool of two berries). Means marked with different letters are significantly different at P ≤ 0.01.

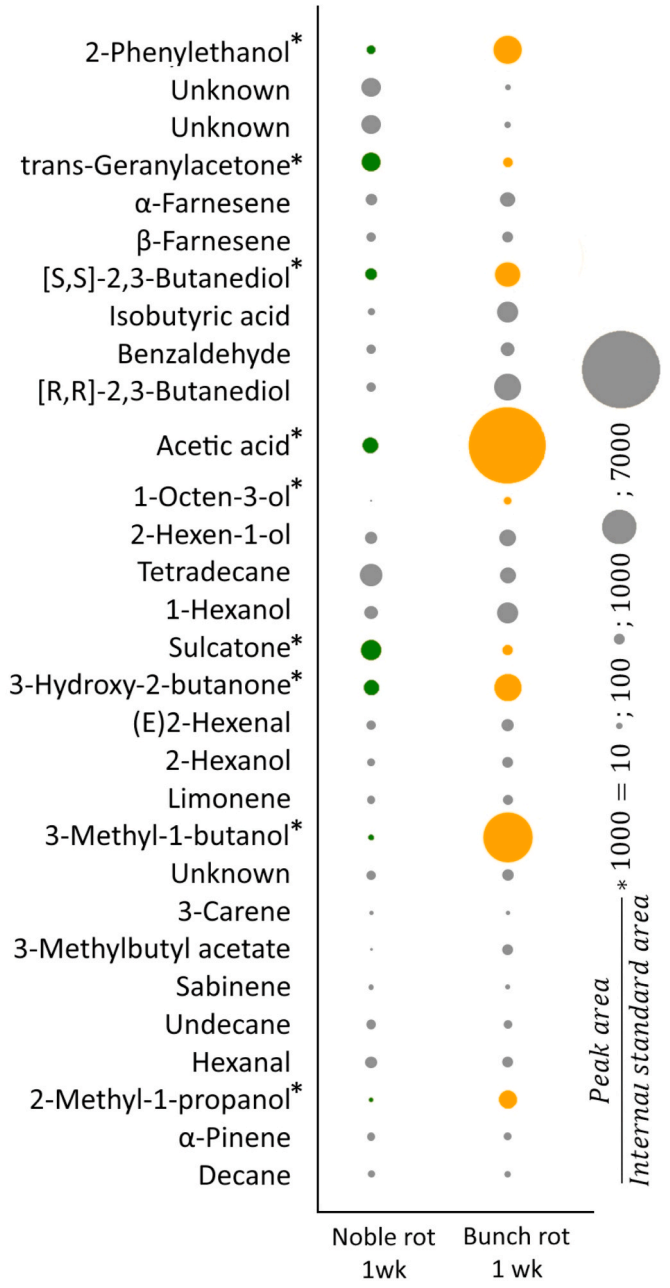

Fig. 3. Volatile organic compounds emitted by bunches of *V. vinifera* cv. Furmint incubated for one week in a growth chamber under conditions inducing either noble rot or bunch rot. Components appearing in significantly different concentration ($P \leq 0.05$) between noble rot and bunch rot samples are labelled (*). Data represent the average of 4 independent noble rot and 4 gray mold samples, each sample containing two bunches.

The biomass of *B. cinerea* was assessed by real-time PCR in healthy and botrytized berries. The proportion of *B. cinerea* DNA compared to the total DNA content of samples was calculated. The fungus was present in healthy Furmint berries with low abundance. Both noble rot and gray mold development could be associated with increased *B. cinerea* biomass in the berries, but the impact of gray mold was more robust (Fig. 2). The fungus was able to instigate infections even naturally but an external application of *B. cinerea* conidia led to more pronounced accumulation of fungal biomass.

3.3. Volatile markers of noble rot and bunch rot

We were able to quantify a total of 30 volatile components that were emitted by berries kept under noble rot- or bunch rot-inducing conditions for one week (Fig. 3.). Volatile organic compounds (VOCs) characteristic of Furmint berries subjected to noble rot development included *trans*-geranylacetone and sulcatone. VOCs enriched in the volatilome of bunch rot-affected Furmint berry samples comprised 2-phenylethanol (phenethyl alcohol), 2-methyl-1-propanol (isobutyl alcohol), 3-methyl-1-butanol (isoamyl alcohol), 1-octen-3-ol, acetic acid, 3-hydroxy-2-butanone (acetoin) and [S,S]-2,3-butanediol. Detailed results of volatile analysis (normalized peak areas) for each component are available in Supplemental Table 1.

4. Discussion

Noble rot and bunch rot are two fundamentally different manifestations of the same plant-microbe interaction. In this work, it was possible to investigate the two appearances of the *B. cinerea*-grape berry interaction side by side. Noble rot and bunch rot samples were produced in growth chambers, starting with healthy, mature bunches from identical background. Under growth chamber settings that mimicked ideal weather for noble rot we were able to receive berries showing dark, shrivelled morphology, characteristic of noble rot. Bunches incubated in high humidity, on the contrary, developed typical gray mold symptoms.

Gray mold significantly reduced sugar accumulation in the juice of the berries (monitored by °BRIX readings). Noble rot, however, resulted in an elevated sugar concentration in the must collected from crushed berries. Although *B. cinerea* oxidizes some of the sugars available in the berries but this decrease in the sugar content is masked and reversed by the effect of concentration due to shrivelling and dehydration in case of noble rot [1,6,12].

It should be noted, that in our case the base level of soluble solids concentration (°BRIX) in healthy berries at harvest was considerably lower than in typical, mature, excellent quality Furmint berries ready to be subjects of natural noble rot development. The base °BRIX level of healthy berries was only 22.52 ± 0.89. The ideal Furmint grape material for noble rot-type botrytization in the Tokaj wine region includes bunches with overripe berries possessing approximately 25 °BRIX level. Lower °BRIX level was due to our early (mid September) harvesting time. We specifically chose this time for our harvest, expecting lower natural *B. cinerea* abundance and a higher chance to collect healthy bunches without any signs of botrytization.

Accumulation of *B. cinerea* biomass assessed by real-time qPCR revealed that fungal colonization is crucial in both forms of the interaction, but it is less prominent in berries affected by noble rot. A genotype-dependent increase in *B. cinerea* biomass was revealed by real-time qPCR detection of fungal genomic DNA during ripening of gray mold-affected Trincadeira (susceptible) and Syrah (tolerant) grape berries [13].

The progression of gray mold disease in Furmint grape berries could be connected to the increased emission of VOCs 3-methyl-1-butanol (isoamyl alcohol), acetic acid, 2-phenylethanol (phenethyl alcohol), 1-octen-3-ol, 2-methyl-1-propanol (isobutanol), 3-hydroxy-2-butanone (acetoin) and [S,S]-2,3-butanediol. Enrichment of he first 5 volatiles were previously detected in must produced from *B. cinerea*-infected grape [14]. With the exception of 2-phenylethanol, which has a rose-like fragrance, they have been labelled as causes of aromatic flaws in wine [6]. Gray mold development in our experimental system was triggered by keeping the bunches in high humidity. Increased water activity, however, does not only support the growth of *B. cinerea* but also enables the multiplication of aerobic, Gram-negative *Acetobacter* species, leading to accumulation of acetic acid in the berries [6,15]. Interestingly, the addition of acetic acid to must enhances the formation of acetoin and 2,3-butanediol perhaps as a result of yeast activity [6]. Besides acetic acid, the enrichment of acetoin and 2,3-butanediol volatiles have been also

detected in our Furmint samples spoiled by gray mold. The last volatile marker of gray mold-attacked Furmint bunches, 1-octen-3-ol is a volatile characteristic of botrytized fruits and wines [16–18]. It is a crucial eight-carbon oxylipin compound produced predominantly by fungi through the enzymatic oxidation and cleavage of linoleic acid by a lipoxygenase and a hydroperoxide lyase. This volatile possesses a typical mushroom or earthy odor [3,19].

Furmint bunches subjected to noble rot induction exhibited greater emission of sulcatone and *trans*-geranylacetone in comparison with bunches exposed to bunch rot (gray mold) development. Grape juice made out of berries of four Tokaj grapevine varieties showed higher sulcatone levels after going through natural noble rot development compared to healthy, non-botrytized extracts of the same grape cultivars [20]. The decreased *trans*-geranylacetone level released by bunches upon gray mold advancement can be the result of gray mold-associated inhibition of its biosynthesis. Bunch rot was reported to suppress the formation of another geraniol derivative, geranyl acetate in the must of three different grapevine varieties [14]. Interestingly, geraniol is a known monoterpenoid with inhibitory effect on *B. cinerea* [21].

Volatile analyses on botrytized berries have been performed before using crushed samples [14,18,20]. These assays yielded a greater number of VOCs in comparison with our results. Sample collection in our case included a non-invasive technique, extracting volatile compounds directly from the gas space around intact bunches.

5. Conclusions

Simultaneous and artificial induction of bunch rot and noble rot in grape berries enabled us to compare the accumulation of *B. cinerea* biomass in these two forms of botrytization, revealing that fungal growth in berries under bunch rot-inducing conditions is more intense than in berries subjected to noble rot. In addition, several volatile components have been described before in bunch rot and noble rot in separate experimental systems. Relying on results of our side by side analysis we defined isoamyl alcohol, acetic acid, phenethyl alcohol, 1-octen-3-ol and isobutanol as VOC markers in contrasting bunch rot and noble rot.

CRediT authorship contribution statement

Tamás Dankó: Conceptualization, Investigation, Visualization, read and approved the final version of the manuscript. **Magdolna Szelényi:** Methodology, Literature search and references. read and approved the final version of the manuscript. **Tibor Janda:** Writing - review & editing, read and approved the final version of the manuscript. **Béla Péter Molnár:** Methodology, Writing - review & editing, read and approved the final version of the manuscript. **Miklós Pogány:** Conceptualization, Investigation, Writing - original draft, preparation, read and approved the final version of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors express their gratitude to Dr. Mathias Choquer (Université Lyon) for kindly sharing *B. cinerea* strain B05.10. István Szepsy (Szepsy Winery, Mád) is also greatly appreciated for his collaboration by providing the grapevine biological material used in the experiments. Gabriella Szalai (Centre for Agricultural Research, Martonvásár) is acknowledged for providing access to the growth chamber infrastructure. This work was funded by the Széchenyi 2020 programme, the European Regional Development Fund and the Hungarian Government (GINOP-2.3.2-15-2016-00061).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pmpp.2021.101626.

References

[1] I. Magyar, Botrytized wines, in: R.S. Jackson (Ed.), Advances in Food and Nutrition Research, Academic Press, Burlington, 2011, pp. 147–206.
[2] B. Blanco-Ulate, K.C.H. Amrine, T.S. Collins, R.M. Rivero, A.R. Vicente, A. Morales-Cruz, C.L. Doyle, et al., Developmental and metabolic plasticity of white-skinned grape berries in response to *Botrytis cinerea* during noble rot, Plant Physiol. 169 (2015) 2422–2443.
[3] C.C. Steel, J.W. Blackman, L.M. Schmidtke, Grapevine bunch rots: impacts on wine composition, quality, and potential procedures for the removal of wine faults, J. Agric. Food Chem. 61 (2013) 5189–5206.
[4] P. Jeandet, R. Bessis, B. Gautheron, The production of resveratrol (3,5,4′-trihydroxystilbene) by grape berries in different developmental stages, Am. J. Enol. Vitic. 42 (1991) 41–46.
[5] J. Kelloniemi, S. Trouvelot, M.-C. Héloir, A. Simon, B. Dalmais, P. Frettinger, A. Cimerman, et al., Analysis of the molecular dialogue between gray mold (*Botrytis cinerea*) and grapevine (*Vitis vinifera*) reveals a clear shift in defense mechanisms during berry ripening, Mol. Plant Microbe Interact. 28 (2015) 1167–1180.
[6] P. Ribéreau-Gayon, D. Dubourdieu, B. Donèche, A. Lovaud, The Handbook of Enology, in: The Microbiology of Wine and Vinifications, second ed. vol. 1, Wiley, Chichester, 2006.
[7] A. Vannini, G. Chilosi, *Botrytis* infection: grey mould and noble rot, in: F. Mencarelli, P. Tonutti (Eds.), Sweet, Reinforced and Fortified Wines: Grape Biochemistry, Technology and Vinification, first ed., Wiley, Chichester, 2013, pp. 159–170.
[8] K.E. Reid, N. Olsson, J. Schlosser, F. Peng, S.T. Lund, An optimized grapevine RNA isolation procedure and statistical determination of reference genes for real-time RT-PCR during berry development, BMC Plant Biol. 6 (2006) 27.
[9] B.P. Molnár, Z. Tóth, Z. Kárpáti, Synthetic blend of larval frass volatiles repel oviposition in the invasive box tree moth, *Cydalima perspectalis*, J. Pest. Sci. 90 (2017) 873–885.
[10] V. Jayasena, I. Cameron, °Brix/acid ratio as a predictor of consumer acceptability of crimson seedless table grapes, J. Food Qual. 31 (2008) 736–750.
[11] C. Davies, S.P. Robinson, Sugar accumulation in grape berries (Cloning of two putative vacuolar invertase cDNAs and their expression in grapevine tissues), Plant Physiol. 111 (1996) 275–283.
[12] B. Donèche, Botrytized wines, in: G.H. Fleet (Ed.), Wine Microbiology and Biotechnology, Harwood Academic Publishers, Chur, Switzerland, 1993, pp. 327–352.
[13] J. Coelho, M. Almeida-Trapp, D. Pimentel, F. Soares, P. Reis, C. Rego, A. Mithöfer, A.M. Fortes, The study of hormonal metabolism of Trincadeira and Syrah cultivars indicates new roles of salicylic acid, jasmonates, ABA and IAA during grape ripening and upon infection with *Botrytis cinerea*, Plant Sci. 283 (2019) 266–277.
[14] A. Lopez Pinar, D. Rauhut, E. Ruehl, A. Buettner, Effects of *Botrytis cinerea* and *Erysiphe necator* fungi on the aroma character of grape must: a comparative approach, Food Chem. 207 (2016) 251–260.
[15] J.M. Guillamón, A. Mas, Acetic acid bacteria, in: A. Carrascosa, S.R. Munoz, R. G. Garcia (Eds.), Molecular Wine Microbiology, Academic Press, London, 2011, pp. 227–255.
[16] É. Miklósy, Z. Kerényi, Comparison of the volatile aroma components in noble rotted grape berries from two different locations of the Tokaj wine district in Hungary, Anal. Chim. Acta 513 (2004) 177–181.
[17] B. Fedrizzi, E. Tosi, B. Simonato, F. Finato, M. Cipriani, G. Caramia, G. Zapparoli, Changes in wine aroma composition according to botrytized berry percentage: a preliminary study on Amarone wine, Food Technol. Biotechnol. 49 (2011) 529–535.
[18] T. Van den Driessche, J. Keulemans, A. Geeraerd, B.M. Nicolai, M.L.A.T.M. Hertog, Evaluation of fast volatile analysis for detection of *Botrytis cinerea* infections in strawberry, Food Microbiol. 32 (2012) 406–414.
[19] E. Combet, J. Henderson, D.C. Eastwood, K.S. Burton, Eight-carbon volatiles in mushrooms and fungi: properties, analysis, and biosynthesis, Mycoscience 47 (2006) 317–326.
[20] K. Furdíková, A. Machyňáková, T. Drtilová, T. Klempová, K. Ďurčanská, I. Špánik, Comparison of volatiles in noble-rotten and healthy grape berries of Tokaj, LWT - Food Sci. Technol. (Lebensmittel-Wissenschaft -Technol.) 105 (2019) 37–47.
[21] R. Tsao, T. Zhou, Antifungal activity of monoterpenoids against postharvest pathogens *Botrytis cinerea* and *Monilinia fructicola*, J. Essent. Oil Res. 12 (2000) 113–121.