Hungarian University of Agriculture and Life Sciences

Transcriptome-level response of grapevine (*Vitis vinifera*) to infection by black rot (*Guignardia bidwellii*) and fine analytic composition of infected berries

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1 BACKGROUND AND THE OBJECTIVES OF THE RESEARCH

Grapes are attacked by several fungal diseases worldwide, which can result in significant yield losses and deterioration of grape quality (Ramsdell and Milholland, 1988). Powdery mildew (*Erysiphe necator*) appeared in European viticulture in 1845, phylloxera (*Daktulosphaira vitifoliae*) in 1863, and peronospora (*Plasmopara viticola*) in 1878, and black rot (*Guignardia bidwellii*) in 1885. Grapes grown in Europe are highly susceptible to these pathogens (Töpfer et al., 2011).

Due to the lack of experience with the disease, control, and prevention options are limited and little information on resistance is available.

Resistance breeding is the general and best solution to control pathogens (Barna, 1963). European varieties are almost invariably susceptible to the disease (Demaree et al., 1937; Barrett, 1953; Hausmann et al., 2017). Most of the newly produced cultivars with a high degree of powdery mildew and Peronospora resistance are also susceptible to black rot infection. This disease can cause severe plant protection problems in organic/organic viticulture, often posing an insoluble problem, and resistance to powdery mildew should be incorporated into new innovative resistant varieties.

My primary objective was to understand the biological background of the relationship between grapevine and black rot. To do this, I planned to investigate the transcriptome-level response of grapevine to black rot. By identifying overexpressed or underexpressed genes in response to *Guignardia bidwellii* infection, we aim to aid marker development and marker-assisted selection.

Theoretical problems to be solved, scientific objectives:

- Investigate the transcriptome-level response of grapevine to black rot challenge
    - Sequencing of the whole RNA from infected and mock (control) inoculated, resistant and susceptible plants using next-generation sequencing to identify differentially expressed genes
    - Identification of genes with specific roles in the pathogen-plant relationship

Tasks to be carried out to achieve the scientific objectives:

- Set up infection experiments, carry out infections
- Preparation of whole RNA extracts of sufficient quality to generate libraries of new generation sequencing
- Development and adaptation of a pipeline for processing the sequence data
- Analysis of physiologically active compounds from infected samples:
    - Chemical composition of black rot grapes
    - Examination of the formation of certain biologically active compounds in response to black rot

2 MATERIALS AND METHODS

2.1 Artificial contamination

2.1.1 Plant material used for artificial infestation

In the pedigree of the Csillám cultivar grown in Hungary, the resistant grandparent of the Merzling cultivar with high resistance to black rot, Rayon d'Or (Seibel 4986), is included, which presumably inherited its resistance from the ancestors of *Vitis rupestris*. The Csaba pearl variety is generally susceptible to disease and promises to be a suitable susceptible control.

The Csaba pearl propagating material was collected from Balatonboglár, the Csillám canes from the premises of the Soós István Wine-growing Technical and Vocational School in Szigetcsép during the period of forced dormancy.

The plants were grown from two-bud cuttings under laboratory conditions in a 1:1 mixture of general potting soil and perlite.

2.1.2 Course of infection

Infection was carried out with a suspension of spores on a filter paper disc and the disc was left on the leaf until sampling (up to 72 hours). This allowed us to collect tissue from the same site of infection.

Plants were incubated at 27°C with 100% relative humidity and continuous leaf surface humidity maintained for 36 hours to promote infection.

The *Guignardia bidwellii* isolate used for artificial infections was provided by Dr Kálmán Zoltán Váczy from the Research Institute of Viticulture and Enology, Eger, Hungary. The concentration of the spore isolate produced was 5×105 spores/ml.

10 µl of the spore suspension was transferred to a 7 mm diameter sterile filter paper disc, and these discs were placed on the prepared grape leaves.

The infections were carried out by the half-leaf method, i.e. three discs of filter paper soaked in distilled water were placed on one half of the leaf with the spore suspension and the other half (control) with three discs of filter paper soaked in distilled water.

2.1.3 Sampling

Sampling was focused on the early steps of the infection process, and therefore, samples were taken before infection (0 h sample) and 6, 18, 36, and 72 h after infection.

The excised leaf discs were placed in microcentrifuge tubes and immediately frozen in liquid nitrogen (snap-freeze), and samples were stored at -80°C until processing.

In parallel, leaf discs from infected samples collected for RNA extraction were also placed in ethanol for fungal-specific staining with trypan blue.

2.1.4 *Guignardia bidwellii* staining with trypan blue

Grape black rot staining protocol:

Removal of chlorophyll

The leaves to be stained must be cleaned of chlorophyll to allow the study of fungal tissues in the light microscope by placing the infected leaf discs face up on filter paper in a petri dish and pipetting a 1:1 ethanol: acetic acid mixture onto them. The optimum time for purification is two days.

Staining with trypan blue

Remove the acid ethanol from the cleaned leaves and pipette 1% HCl instead, then incubate for half an hour at room temperature. During the incubation, prepare the trypan blue stain (0.5 g/l in hydrochloric acid glycerol. 25% glycerol, 0.5% HCl). The leaf discs are placed in microcentrifuge tubes, and the trypan blue stain is added and incubated for half an hour at room temperature. Aspirate the trypan blue into a collector, then pipette hydrochloric acid glycerol (25% glycerol, 0.5% HCl) onto the leaves and wash the staining background in this. After half an hour, the leaf discs are placed on a slide, 50% glycerol is dripped on top and covered with a coverslip.

The germination rate of black rot conidia tested at different time points on the pearl millet cultivars of Chilla and Chaba pearl was determined by Welsch's t-test.

2.2 RNA extraction

Samples stored at -80°C were extracted using the LiCl precipitation protocol reported by Gambino et al. (2008).

The quantity and quality of RNA extracts were checked by denaturing agarose gel electrophoresis and spectrophotometric measurements.

2.3 Total RNA sequencing

RNA sequencing was performed by UD Genomed Ltd. of the University of Debrecen. The sequencing was performed using Illumina's technology (SBS, Sequencing By Synthesis).

Sequencing libraries prepared from RNA extracts were sequenced on the IlluminaHiScanSQ platform. Quality control of raw reads was performed using FastQC software (Wingett and Andrews, 2018).

2.4 Data analysis, bioinformatics

First, all quality-filtered reads were aligned to the reference genome, and then the size of the insert was determined based on these alignments. Sequence reads were aligned to the reference genome using bwa (Li and Durbin, 2009) software, and the Picard tools (Broad Institute, 2018) package was used for the insert size statistics.

Raw counts of all sequence read that matched different gene transcripts were determined using HTSeq software (Anders et al., 2014). To identify differentially expressed genes, sequence libraries were normalized using EDASeq (Risso et al., 2011), and expression levels were analyzed using edgeR (McCarthy et al., 2012). For the GO enrichment assay, we used the ShinyGO application (GE et al. 2020).

2.5 Finomanalytical analysis of the chemical composition of black rot grapes

2.5.1 Plant material tested

Black rotten berries of six different grape varieties were analyzed. These were the resistant grape varieties Bácska, Danubius, Hibernál, Palatina, Panonija collected from Borota (Koch Winery) and Kékfrankos grape bunches collected from Villány (Koch Winery). All samples were black rotten. Only the berries with complete black rot were selected and used from the infected bunches for sample preparation. Berries picked from healthy bunches were used as control samples.

2.5.2 Methods of measurement used for the analysis of the components

The first step in the analysis of the constituents was the preparation of the black-ripened berry extract. The preparation of the extract was carried out as follows: 20 mg of the sample was blended with 60 ml of methanol (12 V/V% methanol-water mixture) and then soaked for 30 min. After centrifugation for 2 min, the supernatant was extracted with 2x50 ml of chloroform. The extract was evaporated to dryness on a rotatable bed under a vacuum. The dry residue was dissolved in 2 ml of an eluent.

Basic analytical tests

The reducing sugar content of the musts was determined by the Rebelein method according to MSZ 9479-1980. The glycerol content, malic acid content, citric acid content and lactic acid content were determined by Boehringer Mannheim enzyme assay, and the tartaric acid content by spectrophotometry according to MSZ 9489:1978.

Spectrophotometric studies

The spectrophotometric studies were performed with a MOM Spektromom 195. The total polyphenol content was measured using Folin-Ciocalteu-phenol reagent (Singleton-Rossi, 1969). Leucoanthocyanins were measured spectrophotometrically after heating with a 40:60 mixture of hydrochloric acid and butanol containing ferrous sulfate, also according to the modified method of Flanzy (1969). The catechol and epicatechin contents were measured spectrophotometrically at 500 nm in wine diluted with alcohol and reacted with sulphuric acid vanillin (Rebelein, 1965).

NMR spectroscopy

Gluconic acid, galacturonic acid, succinic acid, succinic acid, fumaric acid, and kaftaric acid were determined by the H NMR technique (Godelmann et al., 2013). H NMR spectra were recorded at 26.85°C using a Bruker AVANCE 400 spectrometer and a 400'54 ASCEND magnet system (Bruker, Karlsruhe, Germany) in proton NMR mode at a frequency of 400.13 MHz. The NMR analyses were performed by Dyagnosticum Ltd. Szerencs, Hungary.

Chromatography

The qualitative and quantitative determination of resveratrol (trans-piceid, trans-resveratrol, cis-piceid, cis-resveratrol) was carried out by high-performance liquid chromatography (HPLC) in the research laboratory of the Department of Oenology, University of Agricultural and Life Sciences, Hungary. Resveratrol was determined according to the method of Kállay and Török (1997).

The determination of the biogenic amine content by HPLC was carried out at the Department of Oenology of the Hungarian University of Agricultural and Life Sciences (Kállay and Nyitrainé Sárdy, 2003).

The ochratoxin A of the extracts was determined by high-performance liquid chromatography. The calibration curve was plotted on OTA (Sigma Aldrich, CAS Number: 303-47-9).

The data obtained were evaluated using one-factor analysis of variance and Tukey-Kramer test to determine whether there was a significant difference between the samples at the 95% confidence level.

3 RESULTS

3.1 Black rot susceptibility testing

The infestation was carried out under reproducible artificial conditions, so the difference in the germination of fungal spores between the tested varieties can only be attributed to their different susceptibility. The different growth rates of germplasm on susceptible and resistant cultivars have not been previously investigated.

3.1.1 Investigation of the relationship between grape black rot and filter paper disc infection

Microscopic examination of stained leaf discs confirmed the success of infection in all cases. The leaf discs examined under stereo microscopy at 40x and 100x magnification showed that the Csaba pearl variety found to be susceptible had fungal spores germinating at 18h post-infection and showing significant germ tube growth at 36h.

3.1.2 Germination rate of *Guignardia bidwellii* condia

Infection was successful in the Csillám variety, but the germination of fungal spores was significantly shifted in time compared to the Csaba pearl variety. In Csaba pearl, spores germinated at a significant rate of 77.8% as early as 6 hours after infection. By the 18th hour after infection, the germination percentage was already above 99%, and a significant increase in germination was observed.

3.1.3 Germ tube growth

The results obtained from the germplasm growth study showed a significant difference between the two varieties.

The length of the germ tubers 18 hours after infection on the leaves of the susceptible cultivar Csaba pearl averaged 120μm in length, while on the leaves of the resistant cultivar Csillám they averaged 40μm in length. There was evidence [t (98,9) = 11,83, p < 0,001] that the growth of *Guignardia bidwellii* germ tubers was slower on leaves of the black rot resistant cultivar Csaba pearl than on the susceptible cultivar Csaba pearl.

3.2 The RNA level response to infection in black rot

3.2.1 Results of RNA sequencing

Quality control

The program also detected overrepresented sequences in some of the samples. These are both different adaptors and unknown sequences. The blast search for unknown sequences returned the grip24 gene as a match in all cases.

Based on the quality control of the raw sequence reads, it is necessary to remove possible adaptor residues, which will improve both the unequal base distribution at the beginning of the sequence reads and the indicators for overrepresented K-meres.

3.2.2 Determination of the insert size

From the determination of the insert sizes, we can conclude that the average insert size of the libraries has a negative value, which indicates that the sequences obtained from the two sides overlap during pair-end sequencing.

3.2.3 *De novo* transcriptome construction

A *de novo* transcriptome is generated from all sequenced RNA, from which the expression level of each gene can be determined for each sample.

In addition to the 32,000 genes already known, 4,331 new putative genes were identified in the 42 pair-end RNA libraries in addition to the splice variants.

Using the *de novo* transcriptome generated using Cufflinks software (Trapnell et al., 2012) - specific and complete for our experiment - as a reference, we aligned the sequence reads to the genome and reference transcriptome using TopHat (Trapnell et al., 2012) software. The percentage of aligned reads was remarkably high (above 80%).

3.2.4 Determination of gene expression levels

Normalization to GC ratio and library size

Normalization resulted in a SeqExpressionSet library with raw read counts, normalization factors, and normalized sequence read counts. EdgeR can handle the correction values obtained as a result of EDASeq normalization.

3.2.5 Differentially expressed genes

Finally, for the normalized libraries, a list of differentially expressed genes was read out using the edgeR tool, taking into account appropriate controls, i.e. at three sampling time points, the genes that respond differently in terms of expression changes to the effect of mottle infection in susceptible and resistant varieties were determined. The statistical analysis results identify genes that respond differently at different time points to black rot infection in resistant and susceptible varieties.

Of the top 25 differentially expressed genes at the three-time points, 19 are related to oxidative stress processes and 16 genes belong to the phenylalanine ammonia-lyase or stilbene synthase genes.

Among the differentially expressed genes involved in this process, most stilbene synthases play a role at 6h post-infection.

The role of stilbene synthases decreases gradually in number during infection, with no differential expression between susceptible and resistant species at 36 h post-infection. The results indicate that oxidative processes play a predominant role at 18 h post-infection, followed by an increase in the proportion of genes of unknown function and genes related to specific stress response at 36 h.

The differentially expressed genes are generally scattered on the chromosomes, while for chromosome 16, several groups show differences together.

At the beginning of the chromosome, the group showed differential expression only in the 6 hpi samples, encompassing a cluster of phenylalanine ammonia-lyase genes.

The cluster towards the end of the chromosome showed differential expression in both 6 hpi and 18 hpi samples. In all cases, the change was negative, i.e. the magnitude of the change was smaller in the Csillám variety than in the Csaba pearl variety. The expression data indicated that the expression of the respective stilbene synthase was either lower at 0 hpi or no expression was detectable in the Csaba pearl variety. In contrast, the intensity of gene expression increased upon infection.

3.3 Testing physiologically active compounds

3.3.1 Composition of black dried grapes

To investigate the effects of black rot (*Guignardia bidwellii*), measurements were made on the composition of black rot grape berries. There was a significant difference in sugar content between the samples, except for the Bácska and Kékfrankos varieties. Glycerol is formed in the black-rot berries and, proportionally, gluconic acid, the latter in lower concentrations.

The galacturonic acid concentration in black-rot berries ranged from 0.55 to 1.36 g/kg. There was no significant difference between the Palatina, Hibernál, and Kékfrankos samples.

Malic acid was not detectable, but (+)-lactic acid was present. In the black rot berries, 0.056-01.00 g/kg (+)-lactic acid was measured, with the highest amount in the Bácska grape variety, significantly different from other samples.

Also of interest is the absence of succinic and citric acids in the berry, while the concentration of succinic and fumaric acids is significant.

The concentration of tartaric acid ranged from 8.2 to 15.9 g/kg. There were significant differences between the samples, except for Danubius, Bácska, and Kékfrankos.

Polyphenols were present in the amounts reported in the literature (Kállay, 2010), no significant differences were found between the measurements. There was a significant difference between samples except for Palatina, Panonija.

The measured values for catechin varied between 3452-5796 g/kg. There was a significant difference between samples.

The amount of epicatechin ranged from 100-1156 g/kg. There was a significant difference between the samples. For leucoanthocyanins, values ranged from 3276-5180 mg/kg. There was a significant difference between samples. Total antioxidant capacity ranged from 100.8 to 122.8 mmol/kg. The Danubius sample showed the lowest significant value.

As expected, only piceids (resveratrol glucosides) are present in grape berries. The measured trans-piceid values varied between 0.28 and 3.28 mg/kg. The significantly higher values were found in Bácska and Kékfrankos grapes.

The resveratrol concentration in the samples and vintages tested was not influenced by black rot.

The biogenic amine content of the black rot infected samples was investigated. The measured tyramine content ranged from 0.06 to 0.11 mg/kg. The serotonin content varied between 0.04 and 0.10 mg/kg. For histamine content, a range of 8.8-11.6 mg/kg was obtained. There was no significant difference between the varieties for tyramine and histamine content. The serotonin content measured in the Blue Franc sample is significantly higher than the other samples.

The biogenic amines were present at low concentrations for wine production (Kállay, 2010). However, the histamine content is significant. Compared to the chemical composition of the aszú grapes, the latter have lower histamine and stable tyramine and serotonin concentrations. In contrast, the berries that have undergone black rot have higher values.

3.3.2 Analysis of mycotoxin content in berries affected by black rot

The pathogen *Guignardia bidwellii*, which causes the black rot of grapes, does not produce mycotoxin. The experimental varieties, which do not carry resistance to black rot, are vulnerable to attack by associated toxin-producing microorganisms without adequate plant protection.

3.3.3 Mycotoxin content of berries showing symptoms of black rot

From the measurements, it can be concluded that of the innovative grape varieties tested, Hiber, Palatina, and Panonija samples did not contain ochratoxin A. Danubius contained 1.01 µg/kg, Bácska 0.93 µg/kg and Kékfrankos 1.36 µg/kg of ochratoxin A, all below the EU limit. There was no significant difference between the samples. No linear correlation was found between black rot and OTA content.

4 CONCLUSIONS AND RECOMMENDATIONS

A relatively quick method to characterize susceptibility and resistance to black rot can be to measure the length of germ tubes. In just two days, a difference in susceptibility can be detected. This can make the breeder's job considerably easier, as a rapid prediction of the plant material is obtained, whereas the slowness of the disease process means that symptoms and brown spots on the leaves can be expected to appear in about two weeks. The method can also be used for ex-situ testing of compounds that inhibit fungal germination or growth.

A total of 42 pair-end RNA libraries were sequenced from samples of control and black rot-infected, resistant, and susceptible plants at four-time points (0, 6, 18, 36 hpi) in three biological replicates. The number of qualitatively filtered sequence read pairs in each sample ranged from 5 to 30 million (0.5 to 3 billion bases). The size of the inter-sequencing gap went from -53 to 2, suggesting that the inter-sequencing length of the libraries was ideal, with 41 libraries of two-sided sequencing overlapping, with a maximum average overlap of 53 bp.

Preliminary functional analysis was described for samples taken at each time point based on simple blast annotation of the 25 most statistically supported differentially expressed genes. By evaluating the samples taken at time 0 hpi, i.e. immediately before infection, we aimed to filter out the initial differences so that any differentially expressed genes could be screened out of the candidate samples at later time points. The 25 differentially expressed genes with the highest significance level included different protein kinases and an rpm-1-like resistance gene. In general, few specific signals were detected.

Based on the analysis of differentially expressed genes, it can be assumed that the components of general resistance or PTI may play a crucial role in the resistance of the Csillám grapevine to black rot, among which the group of

stilbene synthases responsible for the production of phytoalexin-like stilbenes is of major importance. However, resistance gene-based ETI cannot be excluded.

As far as we know at present, the changes caused by black rot are negligible in terms of the nutritional values of grapes. Also in terms of undesirable compounds such as ochratoxin or histamine. Black rot produces more histamine than botrytis. It produces melatonin, tyramine, and serotonin in the berry, but these amounts are also negligible. It follows that grapes affected by black rot are qualitatively worth sorting, but they are not a problem if they do get caught.

Overall, the chemical data obtained from black rot grapes do not change the chemical composition of the wine in terms of polyphenols, biogenic amines, resveratrol, and ochratoxin.

5 NEW SCIENTIFIC ACHIEVEMENTS

1. I have developed a leaf disc infection method that ensures that the pathogen propagules are localized and highly concentrated on leaves infected with *Guignardia bidwellii*. The method also allows targeted sampling.

2. I confirmed the tolerance of the cultivar Csillám to black rot based on conidial germination and germ tube growth. Differential germplasm growth rates in susceptible and resistant cultivars have not been previously investigated.

3. I have shown that genes involved in processes related to pathogen-induced immunity (e.g. phytoalexin production) respond differently to infection in the first 36 hours after infection.

4. Based on my results, the tolerance to black rot in Csillám grapes is related to the inherently high stilbene production in the early stages of the disease process.

5. I first examined the effect of black rot on the chemical composition of the grape berry.

6. I first examined the effect of black rot on the overall fruit content and acid composition. I found that black rot berries produce glycerol and, proportionally, gluconic acid.
   I found that although malic acid, succinic acid, citric acid could not be detected, the presence of (+)-lactic acid was detectable in the samples.

Succinic acid, fumaric acid, and kaftaric acid were also detected in significant concentrations.

7. I first examined the effect of blackening on the polyphenol composition. I found that the polyphenol composition (total polyphenols, leucoanthocyanin, catechin, epicatechin) was measurable in the amounts reported in the literature. Based on my measurements, it can be concluded that the blackening effect was more likely to influence the change in catechol concentration.

8. I first examined the effect of black rot on the concentration of resveratrol (trans-piceid, trans-resveratrol, cis-piceid, cis-resveratrol), which has a positive physiological effect within the polyphenol composition. Based on my measurements, it can be concluded that the black rot affected the occurrence of piceids in the berries.

9. I first examined the effect of blackening on biogenic amines (the most important physiological compounds: tyramine, histamine, serotonin). I found that biogenic amines were present at levels consistent with previous literature. Black rot did not affect the amines I tested.

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