Differential Physiological Responses of Resistant and Susceptible Grape Cultivars to Eutypa dieback

Gabriela C. Sinclair[1], Renaud Travadon[2], Paula J. Eschen[3], Christopher Wallis[4], Kendra Baumgartner[5], Chloé E. L. Delmas[6], Joshua F. Hnizdor[1], Megan K. Bartlett[1]

[1]Department of Viticulture & Enology, University of California, One Shields Avenue, Davis, CA, 95616, USA
[2]E2S UPPA, CNRS, IPREM, Université de Pau et des Pays de l'Adour, 64000 Pau, France
[3]Department of Plant Pathology, University of California, One Shields Avenue, Davis, CA, 95616, USA
[4] United States Department of Agriculture-Agricultural Research Service, Crop Diseases, Pests and Genetics Research Unit, Parlier, CA, 93648, USA
[5] USDA-ARS, Davis, CA
[6]INRAE, BSA, ISVV, SAVE, 33882 Villenave d'Ornon, France

Highlight: Resistant 'Zinfandel' and susceptible 'Syrah' *Vitis vinifera* cultivars exhibited opposing responses in gas exchange and leaf photosynthetic biochemistry to fungal pathogen (*Eutypa lata*) infection

Abstract:*Eutypa lata* is a fungal pathogen of grapevine that causes widespread economic damage and threatens vineyard longevity worldwide. This study was initiated to further understanding of how grapevines resist *E. lata* infections, using an integrated approach combining inoculation assays in the greenhouse with physiological and biochemical measurements. Resistant 'Zinfandel' and susceptible 'Syrah' grapevines were subjected to control and inoculation treatments and assessed for gas exchange, water status, photosynthetic biochemistry, hydraulic conductivity, wood chemistry, and fungal spread (lesion length). Infection reduced leaf photochemical function and gas exchange in Zinfandel and increased these variables in Syrah ($p<0.05$). Infection produced shorter lesions in Zinfandel ($p<0.05$), suggesting that downregulating gas exchange limited pathogen spread by reducing the carbon supply to the pathogen or fungal movement in the transpiration stream. Neither cultivar upregulated wood defense compounds in response to infection, but proanthocyanidin and catechin levels were constitutively higher in Zinfandel and stilbenoid and flavonoid contents were constitutively higher in Syrah ($p<0.05$). Altogether, this study is the first to show that, counterintuitively, downregulating physiological function in response to infection improves long-term resistance to *E. lata. S*creening responses in photochemical function or gas exchange could provide a high-throughput alternative to measuring lesion lengths in assessing resistance.

Keywords: Grapevine, Grapevine Trunk Disease, Viticulture, Eutypa dieback, *Eutypa lata*, disease resistance, pathogen detection, gas exchange, photosynthesis

Introduction:

Eutypa lata, the main causal agent of Eutypa dieback of grapevine and other perennial fruit and nut crops (Rolshausen et al., 2015), is a pathogenic fungal ascomycete that reduces vineyard longevity and causes widespread economic damage to the viticultural sector (Munkvold et al. 1994, Bertsch et al. 2013, Kaplan et al. 2016, Baumgartner et al. 2019). Eutypa dieback is a major concern to growers due to the chronic nature of this disease that kills fruiting positions (Rolshausen et al. 2008). Because *E. lata* is a wood-colonizing fungus that can form long-term necrotrophic relationships, infection can eventually kill the host (Rolshausen et al. 2008). There is no cure for this complex disease, and detection is difficult, since the diagnostic foliar symptoms of Eutypa dieback may not appear until 3 to 8 years after the initial wood infection and these symptoms are not apparent consistently each year (Sosnowski et al. 2007b, Sosnowski et al. 2011; Etienne et al. 2024, Travadon et al. 2024). Eutypa dieback may also intensify in grape production areas where climate change intensifies rainfall events in the spring, potentially increasing spore production and inoculum pressure (Carter, 1991) and promoting foliar symptom expression (Sosnowski et al., 2007b). Thus, identifying and enhancing the mechanisms underlying resistance to *E. lata* will be an important approach to mitigate the economic impacts of this disease (Cardot et al. 2019).

Multiple studies have shown that grape cultivars vary in susceptibility to Eutypa dieback (Péros & Berger, 1994, Sosnowski et al. 2007a, Travadon et al. 2013, Moisy et al. 2017, Sosnowski et al. 2022, Travadon and Baumgartner 2023, Etienne et al. 2024, Travadon et al. 2024). Grapevines are pruned during the dormant season, and most Eutypa infections occur when spores colonize the pruning wounds. Susceptibility to colonization, measured as the proportion of *E. lata* recovered from pruning wounds treated with inoculum, is similar between cultivars (Chapuis & Dubos 2007). Instead, variation in susceptibility to dieback is mainly determined by the rate of pathogen spread after colonization. Susceptibility to pathogen spread is typically measured from the incidence and severity of foliar symptoms, or the length of lesions formed in the wood by pathogen spread after inoculation (Sosnowski et al. 2007a, Ramírez et al. 2018, Travadon et al. 2023). The physiological strategies that make some cultivars more effective at halting wood colonization and minimizing foliar symptoms remain unclear. Previous work has shown that infected grapevines accumulate antifungal phenolic compounds in the wood around the infection site, and that resistant cultivars – those with less wood colonization (shorter lesions) – rapidly upregulate genes related to defense compounds in response to infection (Rolshausen et al. 2008, Galarneau et al. 2021, Cardot et al. 2019). However, *E. lata* impairs multiple physiological functions, suggesting that limiting this damage would also be an important resistance mechanism. Yet, to our knowledge, no studies have tested this hypothesis by comparing physiological responses to infection in cultivars of varying susceptibility to identify new *Eutypa* resistance mechanisms.

Eutypa impairs vine physiology in multiple ways. First, *E. lata* causes soft-rot wood decay. The mycelia release hydrolytic enzymes to break down cell walls in the stem and digest the glucose-rich cell wall components, and hydroxyl radicals and other toxins to induce cell death and facilitate wood decay (Rudelle et al. 2005, Perez-Gonzalez et al. 2022). Degrading woody tissues damages the xylem and stimulates the vine to block the xylem around the infection site with tyloses, to limit pathogen spread (Rudelle et al. 2005). These processes are expected to reduce

plant hydraulic conductivity and the capacity to supply water to the canopy, as observed for the Esca fungal complex (*Phaeomoniella chlamydospora*, *Phaeoacremonium minimum*, and *Fomitiporia* sp.) (Bortolami et al. 2021). Second, fungal toxins and secondary metabolites travel to the leaves via the transpiration stream, where they are hypothesized to induce foliar symptoms (Octave et al. 2006a; Octave et al. 2009, Andolfi et al. 2011, Travadon and Baumgartner 2023). *E. lata* toxins (e.g., eutypine, eulatachromene, and benzofuran) accumulated in the leaf cytoplasm and damaged thylakoids and reduced leaf chlorophyll content (Amborabé et al. 2001, Mahoney et al. 2003, Smith et al. 2003, Mahoney et al. 2005, Octave et al. 2006, Sosnowski et al. 2007, Andolfi et al. 2011). Toxins secreted by the Esca complex reduced photosynthesis and chlorophyll fluorescence parameters (Petit et al. 2006). However, the interactions between toxins and other fungal-secreted molecules and their contribution to leaf symptom severity and cultivar susceptibility remain unclear, especially since symptom expression is often inconsistent between vintages (Sosnowski et al. 2007b, Travadon et al. 2024).

Resistant cultivars have been hypothesized to have several characteristics that limit hydraulic and photochemical damage. First, the wood chemistry of resistant cultivars may be less conducive to colonization/decay, possibly due to a host response which includes generating a high concentration of antifungal phenolic compounds (e.g., resveratrol; Galarneau et al., in press) and incorporating more lignin in the xylem (Rolshausen et al. 2008, Lambert et al. 2012, Pereira et al. 2018). Lignin increases cell wall rigidity, which can slow pathogen growth and wood decay (Pereira et al. 2018). Lesion lengths were shorter in a cultivar with higher xylem lignin content (i.e., 'Merlot' compared to 'Cabernet Sauvignon') (Rolshausen et al. 2008). Second, resistant cultivars could have more effective leaf detoxification mechanisms (Legrand et al. 2002, Andolfi et al. 2011). In resistant, but not susceptible cultivars, *E. lata* infection stimulated the leaves to rapidly upregulate many defense-related genes, including genes controlling phenolic pathways (Cardot et al. 2019). Resistant cultivars could also counteract phytotoxicity by accumulating solutes that prevent cellular damage through antioxidant activity (i.e., osmoprotectants), as part of osmotic adjustment, though this mechanism has not previously been tested (Patakas et al. 2002, Zivcak et al. 2016). Finally, photochemical and hydraulic damage could have downstream effects on gas exchange that impact pathogen spread and resistance. Impaired hydraulic or photochemical function could lead vines to close the stomata and reduce gas exchange to avoid placing additional stress on the hydraulic system or declines in water-use efficiency (Sosnowski et al. 2011, Pouzoulet et al. 2014). This response could increase susceptibility by reducing the plant carbon supply for costly defense compounds, or benefit resistance by limiting toxin and pathogen movement in the transpiration stream and the photoassimilate available to the pathogen. These competing hypotheses have not been tested. Collectively, understanding the role of these mechanisms in infection responses will offer new insights into how grapevines respond to *E. lata* and resist pathogen attack in the early stages of infection.

We conducted the first study to address how physiological responses to infection are associated with cultivar susceptibility to *E. lata* infection. We measured the effects of infection on vine physiology – including gas exchange, photochemical function, hydraulics, and osmotic adjustment – and wood-chemistry profiles for two cultivars (*Vitis vinifera* 'Zinfandel' and 'Syrah') that differ in resistance. Zinfandel has been classified as resistant (Travadon and Baumgartner, 2023) and Syrah as susceptible (Loschiavo et al. 2007, Sosnowski et al. 2007a) to Eutypa dieback based on wood lesions and leaf symptoms. These cultivars also differ in their physiology. Syrah has higher gas exchange rates than Zinfandel, whereas Zinfandel has more

negative leaf osmotic potentials, which could indicate a higher concentration of osmoprotectant compounds (Charrier et al. 2018, Gallo et al. 2021, Sinclair et al. 2024). We hypothesized that infected Zinfandel would maintain greater leaf photochemical function than infected Syrah, in part because infection would upregulate osmotic adjustment for Zinfandel. We also expected that infected Zinfandel would more strongly upregulate wood-defense compounds, which would reduce lesion spread and declines in plant hydraulic conductance compared to infected Syrah. Together, we expected this combination of lower photochemical and hydraulic damage to allow infected Zinfandel to maintain greater gas exchange than infected Syrah. For each cultivar, we compared wounded, non-inoculated controls to vines inoculated with *E. lata* isolate BX1-10, originally isolated from Bordeaux, France, which is a virulent isolate used in phenotyping for resistance to Eutypa dieback (Moisy et al. 2017, Travadon et al. 2023). We maintained vines under well-watered conditions to avoid confounding effects of drought on fungal colonization, and instead to focus on the effects of infection on host physiology. We tested whether the physiology variables, lesion length, and wood chemistry varied between the two cultivars and inoculation treatments using an integrated approach combining classic pathogenicity assays, molecular detection of the pathogen, and physiological and biochemical measurements. Altogether, we expected this study to advance our understanding of the physiological responses at the chemical, cellular, and whole-plant level that promote resistance to *E. lata* in the early stages of this chronic disease. Identifying important traits also could improve screening for disease resistance and aid the development of more resilient plant material.

Materials and Methods

Plant Material and Growth Conditions

Vitis vinifera cultivars Zinfandel and Syrah were propagated from dormant, certified disease-free cuttings in March in Davis, CA. The certification process tests for 38 diseases, including 36 viruses (https://fps.ucdavis.edu/fgr2010.cfm). The plant material was provided by the University of California, Davis Foundation Plant Services. Cuttings were callused in a dark, humidified room in containers layered with equal parts vermiculite and perlite for 2-3 weeks. Once rooted, the cuttings were planted in paper-carton inserts containing a mixture of sunshine mix, perlite, and vermiculite and allowed to establish in the same room for an additional 2 weeks. Afterwards, the plants were transitioned to an auto-controlled mist room for 2 weeks to acclimate, then transferred to a greenhouse. Plants were then transplanted to 1-gallon pots containing an agronomy mix (60:40 Agromix, perlite soil mixture) with an extended release fertilizer and well-watered to field capacity weekly until the experimental period.

Eutypa lata (isolate BX-10) Inoculation

During the winter prior to experimentation (January 6th), each cultivar was divided into two categories: Non-Inoculated Wounded (NIW) controls (N=5) and Inoculated-Wounded (INOC) (N=22-25). All plants were pruned to three buds and inoculated following procedures outlined by Travadon et al. (2013). Briefly, a 4.4-mm width × 3-mm depth injection site was created 2 cm directly below the main upper node on each vine cutting, using a 4.4-millimeter power drill to penetrate the woody stem (Travadon et al. 2023). The plants designated for the inoculated treatments were then inoculated with mycelium plugs (4.2 mm-diameter) taken from the margin offive-days old culture of *E. lata* isolate BX1-10 on Potato Dextrose Agar (PDA; PDA, Difco,

Detroit, MI). The plants designated for the NIW treatment were mock-inoculated with a sterile PDA plug of equal size. The wound was sealed with Vaseline (Unilever, Greenwich, CT) and wrapped with Parafilm (American National Can, Chicago, IL). Following inoculation, the plants were left for one week in the greenhouse to establish infection and then moved to the lathe house for 5 months. On June 10th, the plants were transferred back into the greenhouse and transplanted to 2.5 gal pots containing agronomy mix and extended-release fertilizer.

Watering Regime

Saturated weight (SW) for each pot was established by watering pots to field capacity, waiting until dripping from the bottom ceased (approximately 2 hours), then recording the weight. All pots were maintained at well-watered conditions for 2 weeks before the start of the experiment to allow for acclimatization by re-watering to SW every 3 days. During the experiment, the pots were weighed and re-watered to target weights, following the methods from Bartlett et al. (2021). Initially, pots were re-watered every Monday, Wednesday, and Friday to a target weight of 95% of SW plus half of the expected pot evapotranspiration between waterings, which was calculated from the change in pot weights during the acclimation period (Bartlett et al. 2021, Pita and Pardos, 2001). The pots were watered following this regime until August, when heat waves forced us to increase the frequency of watering to five days a week to avoid water stress. Watering treatments were maintained until September 8th, the date of the destructive harvest. During the experiment the pot surface was covered with aluminum foil to limit evaporation from the soil. Greenhouse environmental conditions (temperature, relative humidity, and VPD) were tracked throughout the experiment (Supplementary Materials Fig. S1, S2).

Gas exchange, Water Potential, and Plant Hydraulic Conductivity

We measured gas exchange on one fully expanded, mature asymptomatic leaf per vine, at positions 6-12 leaves below from the growing tip, weekly from July 8th to September 2nd with a portable gas exchange system (Li-Cor 6800 Portable Photosynthesis System, Nebraska USA). Gas exchange parameters include a fan speed of 10,000 rpm, CO_2 concentration level of 400 µmol mol^{-1}, light intensity of 1200 µmol m^{-2} s^{-1}, and VPD setpoint of 1.8 kPa. The temperature set point was approximately 30 ± 2°C at the beginning of the experiment (July) and 32 ± 2°C over the course of the hotter months of the experiment (August- September). We allowed humidity in the sample chamber to match ambient conditions.

Pre-dawn (4AM to 6AM) and midday (11AM to 4PM) stem water potentials (PDLWP and MDSWP) were measured on the same day as gas exchange on one fully expanded, mature leaf per vine using a pressure chamber (PMS Instrument; model 1505D). The leaves were acclimated in dark-adapting bags for 30 minutes prior to excision, then measured immediately or stored in humidified Whirl-Pak bags in a refrigerator for up to 3 days before measuring. Whole-plant evapotranspiration (E_{tot}) was calculated from the change in pot weight between watering intervals, normalized by the canopy area, and whole-plant hydraulic conductance (K_{plant}) was calculated as $K_{plant} = E_{tot}/(PDLWP - MDSWP)$.

Leaf Chlorophyll Concentration and Fluorescence

At two timepoints (August 12th and September 2nd) at midday, two fully expanded, asymptomatic leaves per vine from the same positions (6-12 from the growing tip) were measured for chlorophyll content using a chlorophyll concentration meter (Apogee MC-100, Utah USA). The same leaves were then dark adapted for 30 minutes inside dark-adapting bags to fully open PSII reaction centers and immediately before taking the chlorophyll fluorescence measurement placed inside a tent made of black plastic bags to limit sun exposure. The settings for determining *Fv/Fm* was outlined in the user instructions in the LICOR-6800 manual. The actinic light was turned off and the measuring beam turned on with a dark mod rate set to 50 Hz. The rectangular flash had a red target set to 8000 µmol m^{-2} s^{-1} and a duration of 1000 ms. The leaves were then excised to measure midday stem water potential.

Leaf Osmotic Potential

Leaf osmotic potentials at full turgor (π_o) were measured for each vine 6 and 8 months after inoculation (July 12th and September 6th). We sampled one asymptomatic, fully expanded leaf per vine and recut the petiole under water using a fresh razor blade. We then rehydrated the leaves overnight in tubes of DI water. Leaf hydration was standardized by beginning and ending rehydration for all leaves at the same time and storing the leaves in humidified Whirl-Pak bags in a refrigerator until measuring. We measured leaf osmotic potential following the rapid osmometer method from Bartlett et al. (2012) using a vapor pressure osmometer (Vapro 5520, Wescor, Logan, Utah, USA).

Destructive Harvest

On September 8th, canopies and shoots were excised from the main stem from all plants. Five canopies per cultivar per treatment were measured for total leaf area. The root biomass was carefully removed from the main stem, shaken to remove excess soil, and rinsed before drying in a drying oven at 114° C for a few weeks. The stem of the inoculated and non-inoculated cuttings was used to measure lesion length, pathogen recovery, and wood chemistry. We measured lesion length in the inoculated internode. The bark was scraped from their woody stems and the stem was cut lengthwise through the inoculation site to allow measuring the internal lesion length (up and down from the inoculation site) using digital calipers. One half of the stem was stored at -80°C and used for molecular detection of the pathogen. The other half of the stem was flash frozen in liquid nitrogen and kept at -80 °C for wood chemistry.

DNA-based detection of *E. lata* using qPCR

Due to low and inconsistent recovery rates of *E. lata* using culture-based methods, we adopted a DNA-based detection approach previously used for detecting the pathogen from grapevine wood (Brown et al., 2021; Baumgartner et al., 2023). This approach relies on adapting quantitative qPCR procedures (Pouzoulet et al. 2013, Pouzoulet et al. 2017) to a qualitative assay, as outlined by Brown et al. (2021). On the half stem used for pathogen detection, a 3cm section encompassing the inoculation site (1.5 cm above and below) of wood was collected for grinding. DNA was extracted from 100 mg of cryogenically ground wood tissue following tissue grinding procedures outlined by Galarneau et al. (2021). The exact DNA extraction procedure, including extraction buffers and kit used, and qPCR conditions have been detailed by Brown et al. (2021) and Baumgartner et al. (2023). After the PCR amplifications were completed, dissociation curves

were obtained. Genomic DNA from pure cultures was used as positive controls. Amplification of target DNA was based on the dissociation temperature (79.0-79.5°C for *E. lata*). Positive detections were samples crossing the threshold level by 45 cycles.

Wood Chemistry

Total phenolics and lignin content was measured using extractions methods by Wallis et al. (2012). In brief, 100 mg of cryogenically ground wood tissue was added to 500 uL of methanol (LC-MS grade, Fisher Scientific, Pittsburgh, PA, USA), vortexed, and left overnight on a shaker in a cold room (4°C). The following day, the samples were centrifuged at 10000 g for one minute, the supernatant was removed, and the previous steps were repeated to re-extract the pellet. The next day, both supernatants were combined for a final volume of 1 mL. The tubes were centrifuged briefly, and 150 uL of the supernatant was placed into 2 mL glass vials with glass inserts.

High-performance liquid chromatography (HPLC) was conducted using a Shimadzu (Columbia, MD, USA) LC-20AD based system equipped with a Supelco Ascentis C18 reverse-phase column (Millipore-Sigma, St. Louis, MO, USA) and a photodiode array detector for quantification (with peak areas obtained at 280 nm) (Wallis et al. 2012). For each sample, 50 µL were injected, and a binary gradient proceeding from 0.2% (v/v) acetic acid in water to 0.2% (v/v) acetic acid in methanol over a 40-min run (Wallis et al. 2012). Compound identification and quantification was made matching retention times with standards obtained from Millipore-Sigma, and based on previous compound identifications by Wallis et al. (2012). Levels of individual compounds within a phenolic subclassification (stilbenoids, proanthocyanidins/catechins, or other flavonoids) were summed together for analyses, as well as an overall sum of all quantified phenolic compounds.

Lignin extraction was completed using the same pellet for the phenolic extractions. All reagents were obtained from Millipore-Sigma. First, the leftover pellet was washed with 1mL ultra-pure H_2O. Then 800 µL of 2 N HCL was pipetted onto the pellet followed by 300 µL of mercaptoacetic acid. This solution was incubated at 86°C for 4 hours. Afterwards, the supernatant was discarded and the pellet was washed twice with 1mL of water. Next, 1 mL of 0.5 M NaOH was added to the sample, the supernatant and pellet were mixed then placed on a vortexer shaker overnight. The next day, the tubes were centrifuged at 10,000 g for 2 minutes and the supernatant was removed and saved at 4˚C. With the remaining pellet, 500 ul of 0.5 M NaOH was added and the vortexer shaking overnight and centrifuge steps were repeated once more. Both supernatants from the overnight steps were combined with 300 µL of concentrated HCl, vortexed, and incubated at room temperature for 4 hours. Afterwards, the supernatant samples were centrifuged for 2 min at 10000 g. The supernatant was then discarded and the remaining pellet precipitated from the supernatants combined with the 300 µL of concentrated HCl was dried overnight in a fume hood. The following day, the pellet was mixed with 1 mL of 0.5 M NaOH and allowed to rest at room temperature for 4 hours. Finally, 1 µL aliquots of this solution were diluted in 99 µL of 0.5 M NaOH and used to measure lignin absorbance at 280 nm using a microplate reader. Lignin concentrations were calculated from a standard curve spanning 0, 18, 45, 90, and 180 µg/mL.

Statistical Analysis

All analyses were performed in Rstudio (R version 4.2.2). First, Shapiro tests were performed to confirm the data were normally distributed ($p > 0.05$ for all variables). We then used Type III ANOVA to test the main and interactive effects of inoculation (Treatment), cultivar (Cultivar), number of days after inoculation (Timepoint), on stomatal conductance (*gs*), net photosynthesis (*A*), leaf transpiration (*E*), water-use efficiency (WUE), pre-dawn and midday stem water potential (PDLWP and MDSWP), and whole-plant hydraulic conductivity (K_{plant}). We included Timepoint and the interaction with Treatment as predictors to test whether inoculation effects became stronger over time. A type III ANOVA was also used to test whether differences in gas exchange were impacted by differences in soil water availability by using pre-dawn water potential PDLWP), inoculation (Treatment), cultivar (Cultivar), number of days after inoculation (Timepoint) and their interactions as predictors. We represented sampling date as a categorical variable (Date) in analyses of osmotic potential at full hydration, chlorophyll content, and maximum quantum yield of photosystem II (*Fv/Fm*), since these variables were measured twice (i.e., OSM ~ Cultivar + Treatment + Date + Cultivar · Treatment + Date · Treatment). Analyses of lesion length, root biomass, leaf canopy area, and wood chemical composition excluded time, as these variables were measured once at the end of the experiment. Differences between statistically significant effects were evaluated and further compared with post-hoc Tukey's HSD tests. We also repeated these analyses using the subset of inoculated vines where the establishment of *E. lata* was confirmed with qPCR detection and generally found the same results with no significant changes in the results for photosynthesis, chlorophyll content, *Fv/Fm*, osmotic adjustment, and wood chemistry (see Results section "Inoculation Treatments" and Supplementary Materials Tables S3- 7).

Results

Inoculation Treatments: pathogen detection, stem lesions, root biomass and canopy leaf area

Eutypa lata DNA was not detected in any of the NIW plants, indicating the absence of the pathogen in the control grapevine stems. Conversely, *E. lata* DNA was positively detected in 31 of the 42 (74%) inoculated plants, hence suggesting the successful establishment of the pathogen in inoculated plants.

We found significant effects of Cultivar (ANOVA *P*-value < 0.0001) and Treatment (ANOVA *P*-value < 0.001) on lesion length. Total lesion length was significantly higher in inoculated Syrah (35.19 ± 1.48 mm) than inoculated Zinfandel (25.13 ± 1.38 mm). Lesions were also present in NIW plants of both cultivars but were significantly smaller than those of inoculated plants (Table 1, Fig. 1) and did not test positive for *Eutypa lata* DNA.

Root biomass was not statistically different between Cultivars, Treatments, or their interactions. Conversely, total canopy leaf area was significantly different between Cultivars, with Syrah exhibiting a larger canopy area (Supplementary Table S1). Total canopy leaf area was not significantly affected by Treatment or Cultivar · Treatment interactions (ANOVA *P*-value > 0.05; Table 1).

Plant Gas Exchange, Water Status, and Hydraulics

There were significant interactive effects of Cultivar and Treatment on all gas exchange variables except water-use efficiency (WUE), including stomatal conductance (*gs*), leaf-level transpiration (*E*), and photosynthesis (*A*) (Table 2). These variables also varied significantly over the experiment, though the interaction between Timepoint and Treatment was not significant for *gs*, *A*, and *E*, indicating that the time effect was independent of inoculation treatment (Fig. 2 A, B, Supplementary Fig. S3). Conversely, for whole-plant evapotranspiration (E_{tot}), we found a significant interactive effect of Treatment x Timepoint on E_{tot} as well as significant main effects of Cultivar, Timepoint, and Treatment (Table 2, Supplementary Fig. S4 B).

Relative to non-inoculated plants, plants inoculated with the pathogen had lower photosynthesis and lower stomatal conductance in Zinfandel but higher photosynthesis and higher stomatal conductance in Syrah. Mean *gs* (averaged across timepoints) for Zinfandel was 0.064 ± 0.004 mol m^{-2} s^{-1} (mean ± standard error) for the NIW treatment and 0.046 ± 0.002 mol m^{-2} s^{-1} for the INOC treatment (Table 3)**.** Mean *A* (averaged across timepoints) for Zinfandel was 8.34 ± 0.4 µmol m^{-2} s^{-1} and 6.72 ± 0.21 µmol m^{-2} s^{-1} for the NIW and INOC treatments, respectively (Table 3). Conversely, mean *gs* and *A* were higher in the inoculated treatment for Syrah (0.055 ± 0.004 mol m^{-2} s^{-1} and 7.12 ± 0.19 µmol m^{-2} s^{-1}, respectively) than in the NIW treatment (0.047 ± 0.005 mol m^{-2} s^{-1}, 6.19 ± 0.46 µmol m^{-2} s^{-1}) (Table 2, Fig. 2 A, B).

Pre-dawn water potential (PDWP) varied significantly between cultivars (ANOVA *P*-value < 0.0001; Table 2; Fig 2C) and this was the only significant fixed effect on PDWP. There was a significant effect of PDWP on gas exchange (specifically on *gs* and E; Table 4). However, when controlling for pre-dawn water potential in our statistical model, there was still a significant Cultivar · Treatment impact on gas exchange, specifically on stomatal conductance, photosynthesis, and leaf level transpiration, indicating that this interactive effect is not just due to accidental variation in water availability (ANOVA *P*-value < 0.001; Table 4).

On the other hand, there was a significant effect of Cultivar and Treatment on midday stem water potential (ANOVA *P*-value < 0.005, Table 2). Inoculated Zinfandel and Syrah both had more negative mean midday stem water potentials than the non-inoculated controls (Fig. 2D).

Finally, there was no significant effect of any of the predictors on whole-plant hydraulic conductivity except Timepoint (Table 2) indicating that the changes in hydraulic conductivity over time are likely in response to increased water demand from canopy development and climate-related variables (Supplementary Fig. S1, S2).

Leaf Chlorophyll and Fluorescence Measurements

There was a significant interactive effect of Treatment × Date on chlorophyll content, and a significant interactive effect of Cultivar × Treatment on chlorophyll fluorescence (Table 5). Chlorophyll content and the maximum quantum yield of photosystem II (*Fv/Fm*) were higher in inoculated (14.22 ± 0.39 and 0.773 ± 0.004 µmol per m^2 of leaf, respectively) than non-inoculated (NIW) vines for Syrah (12.61 ± 0.81 and 0.758 ± 0.009 µmol m^{-2}), while chlorophyll content and *Fv/Fm* were lower in inoculated (17.49 ± 0.55 and 0.776 ± 0.004 µmol m^{-2}) than non-inoculated vines (18.0 ± 1.18 and 0.789 ± 0.007 µmol m^{-2}) for Zinfandel (Table 3, Fig. 3).

Osmotic Potential

There was no significant effect of any of the predictors on osmotic potential except Date (ANOVA *P*-value < 0.001, Table 5), indicating osmotic adjustment between the two sampling periods, but independently of the impacts of infection.

Wood Chemical Composition

Among the different fixed effects, only "Cultivar" had a significant effect on total (ANOVA *P*-value < 0.008; Table 6) or individual chemical compounds (Supplementary Table S2). Proanthocyanidin (catechins) were significantly higher in Zinfandel than Syrah (Table 7). Total stilbenoid and other flavonoid concentrations- derived from total phenolic extractions- were higher in Syrah in comparison to Zinfandel. Lignin content and overall phenolic concentrations were not significantly different between treatments or cultivars (ANOVA *P*-value > 0.2; Table 7).

Discussion

This study is the first to test how physiological responses to infection vary with resistance to *Eutypa* dieback. We found that the resistant cultivar Zinfandel downregulated physiological function in response to infection, while the susceptible cultivar Syrah maintained or even improved function, suggesting there are trade-offs between short-term performance and long-term resistance to this slow-acting disease. Zinfandel and Syrah have been classified as resistant and susceptible based on lesion spread in the wood of inoculated vines (Travadon and Baumgartner, 2023), and our findings support this classification, with infection associated with longer lesions in Syrah than Zinfandel (Fig. 1). Contrary to our hypotheses, infection was associated with greater leaf photochemical damage in Zinfandel, which would reduce photosynthetic capacity and induce stomatal closure, producing the observed declines in gas exchange (Figs. 2, 3). In contrast, photochemical function and gas exchange increased in infected Syrah, suggesting that Syrah was less sensitive to fungal toxins than Zinfandel and instead upregulated leaf photochemistry and gas exchange, potentially to improve the carbon supply for fungal defense. This strategy did not produce hydraulic damage in infected Syrah under the well-watered conditions in this study (Table 2) but may have promoted pathogen growth by increasing fungal movement in the transpiration stream or the carbon and nutrient supply to the pathogen. This strategy also did not improve the production of wood phenolic compounds, as proanthocyanidin/catechin levels were constitutively higher in Zinfandel and stilbenoid and flavonoid contents were constitutively higher in Syrah and were not upregulated in response to infection (Tables 6, 7). Altogether, these findings show that vine performance responses to infection can have counterintuitive effects on long-term resistance, with worse impacts of infection on photochemistry and gas exchange seemingly helping the resistant cultivar reduce pathogen growth and lesion spread. These findings also suggest that screening for infection responses in chlorophyll content and fluorescence or g_s could provide a high-throughput alternative to measuring lesion lengths in breeding programs for *Eutypa* resistance, although these results need to be confirmed for additional cultivars and *E. lata* isolates (Rolshausen et al. 2006, Sosnowski et al., 2022, Travadon et al., 2024). However, these findings also suggest that selecting for current physiological resistance mechanisms could limit lesion spread but produce

earlier declines in carbon gain, yield, and quality for growers. Future work should address whether selecting for alternative mechanisms (e.g., higher proanthocyanidin/catechin contents) could produce resistant cultivars that are less prone to carbon limitations.

This study is the first to compare the effects of *E. lata* on gas exchange and its photochemical and hydraulic drivers in cultivars that vary in susceptibility, and we found that infection produced opposite responses, reducing gas exchange in resistant Zinfandel and increasing gas exchange in susceptible Syrah (Tables 2, 3, Fig. 2). Previous work has shown that fungal disease can impact vine gas exchange. *E. lata* was associated with a slightly higher g_s in young vines of another susceptible variety, Grenache; *Phaeomoniella chlamydospora* (Petri disease) was associated with a higher g_s in young vines of Zinfandel, Chardonnay, and Cabernet Sauvignon; and some pathogens in the Esca complex (*P. chlamydospora*, *Phaeoacremonium minimum*, and *Fomitiporia sp*.) were associated with lower g_s in mature vines of Sauvignon blanc, Chardonnay, and Cabernet Sauvignon (Petit et al. 2006, Edwards et al. 2007b, c, Sosnowski et al. 2011, Bortolami et al. 2021, Dell'Acqua et al. 2024). All studies included a well-watered treatment, and it is unknown whether these differences were driven by pathogens, cultivars, or vine age. Here, gas exchange responses were more strongly determined by pathogen effects at a distance from the infection site, on photosynthetic biochemistry, than effects on hydraulics at the infection site. Esca induced vines to produce xylem occlusions to compartmentalize disease spread, which can impede water transport and lower hydraulic conductivity (Bortolami et al. 2019, Dell'Acqua et al. 2024). However, we did not find that hydraulic conductivity was impacted by infection (Table 2), suggesting that the lower gas exchange in Zinfandel was not used to compensate for impaired hydraulic function. This could reflect methodological differences or differences between pathogens. The previous studies examined mature vines with years-long infections, allowing more time for colonization of and damage to the vasculature (Bortolami et al. 2019, Dell'Acqua et al. 2024). Water potentials can also change over time in stored leaves (Tomasella et al. 2023), and our storage period (up to 3 days) could have contributed error to the K_{plant} measurements. Instead, leaf chlorophyll content and *Fv/Fm* were higher in inoculated than non-inoculated vines for Syrah, while *Fv/Fm* was lower in inoculated than non-inoculated vines for Zinfandel, consistent with the trends in gas exchange (Table 2, Fig. 3). Esca decreased photosynthesis and chlorophyll fluorescence parameters in symptomatic leaves (Petit et al. 2006, Bortolami et al. 2021, Dell'Acqua et al. 2024), and phytotoxic metabolites produced by *E. lata* (e.g., eutypine, eulatachromene, and benzofuran) accumulate in the leaf cytoplasm and negatively impact chlorophyll content (Mahoney et al. 2003, Smith et al. 2003). We expected Zinfandel to have better leaf detoxification strategies, such as upregulating defensive genes that help convert toxic molecules like eutypine to compounds that can be readily metabolized/tolerated, or genes involved in the phenylpropanoid pathway, which enhance antifungal defense by producing secondary metabolites that help plants perceive pathogens and aid in molecular crosstalk with plant stress hormones (Andolfi et al. 2011, Cardot et al. 2019). However, we found the opposite trend. Toxin-induced damage to the photochemical machinery could serve as a signal to close the stomata in Zinfandel (Busch 2014), while Syrah could have used earlier detection of infection or stronger detoxification to maintain carbon assimilation to support the metabolic costs of pathogen defense. Finally, plants often accumulate osmoprotectants, which reduce oxidative stress, as part of osmotic adjustment (Yin et al. 2022). Thus, we expected infection would cause plants to increase osmotic adjustment, though this has not previously been tested for grapevine trunk diseases. While osmotic adjustment occurred in both cultivars, there was no treatment

effect, suggesting that osmotic adjustment does not play a pivotal role in the defense against *E. lata* infection.

Incorporating more lignin into the xylem cell walls has been suggested to increase fungal pathogen resistance by acting as a physical barrier, deterring the spread of infection and preventing rotting by reinforcing cell walls (Shigo 1984, Rolshausen et al. 2008). *E. lata* produces enzymes that degrade lignin, but it preferentially degrades hemicellulose and pectin (Galarneau et al., 2024 in press). Consistent with this hypothesis, *E. lata* consumed more carbohydrates from grapevine cell walls than lignin, and the resistant cultivar Merlot had more lignin in the xylem than the susceptible cultivar Cabernet Sauvignon (Rolshausen et al. 2008). However, in other studies, the relationship between wood lignin and suberin content and lesion length across cultivars was inconsistent (Munkvold and Marois, 1994), highlighting the need for more assessments of defensive role of lignification against fungal pathogens. We expected to find a higher lignin content in Zinfandel than Syrah, but we found no significant differences between cultivars or with inoculation (Table 6). Differences in lignin content may become more pronounced as the vines mature and produce more woody biomass, and the vines in this study were 15 years younger than those tested by Rolshausen et al. (2008).

Phenolics are antimicrobial compounds that are typically upregulated in response to fungal infection (Wallis and Galarneau 2020), and their expression is associated with grapevine resistance to pathogens (Aziz et al. 2020). *E. lata* growth in vitro has been shown to be inhibited by multiple phenolic compounds, including gallic acid (a hydrolysable tannin), rutin (a flavanol), piceid (a stilbene), and epicatechin (a proanthocyanidin/catechin) (Galarneau et al., 2024 in press). Thus, we expected infection to increase wood phenolic content, especially in Zinfandel. We found significant cultivar differences in the content of specific categories classes of phenolic compounds – stilbenoids, proanthocyanidins/catechins, and other flavonoids – though not total overall phenolics. Zinfandel had higher concentrations of total proanthocyanidins/catechins, while Syrah had higher concentrations of stilbenoids and other flavonoids (Tables 6,7). Fungal infections have been shown to upregulate each of these phenolic classes in woody plants (Morkunas & Ratajczak 2014, Ullah et al. 2017, Galarneau et al. 2021), but we did not find any infection treatment effects on wood chemistry in this study (Tables 6, 7). Proanthocyanidins, also known as condensed tannins, are polymers of flavan-3-ols, such as catechins, that are present in the bark and heartwood. Proanthocyanins can deter pathogen growth by bonding to and thickening cell walls (Rudelle et al. 2005, Hanlin et al. 2009), and higher levels have been associated with greater resistance to fungal diseases in woody species, including greater resistance to powdery mildew in grapevine (Hanlin et al. 2009, Wang et al. 2023). Catechin also neutralized lignin-degrading enzyme activity and reduced fungal growth for other grapevine trunk disease pathogens (Gomez et al. 2016). The higher levels of proanthocyanidins in Zinfandel could account for the lower levels of other flavonoid compounds, since flavonoids are their precursors in the biosynthetic pathway and are likely being converted to proanthocyanidins at a higher rate. Stilbenoids are phytoalexins that scavenge reactive oxygen species (ROS) and have been shown to limit mycelium growth in other trunk pathogens (Amalfitano et al. 2000, Lambert et al. 2012). Flavonoids also exhibit antifungal and antioxidant properties when stimulated in response to fungal attack (Morkunas & Ratajczak 2014).

Our results suggest that a higher constitutive expression of proanthocyanidins and catechins could reduce pathogen spread and lesion length in Zinfandel. Fungal infections induce phenolic

accumulation in existing cells near infection sites to compartmentalize the pathogen, so we expected to see the inoculation treatment upregulate wood phenolics despite limited stem growth over the short (7-month) post-inoculation period. Instead, this period could have been too long to see infection induction effects. Previous studies showing induction measured wood phenolic content within 1 week to 3 months of fungal inoculation (Barry et al. 2002, Miranda et al. 2007, Lambert et al. 2012, Hammerbacher et al. 2014, Nemesio-Gorriz et al. 2016, Wallis and Galarneau 2020 and references within), while measurements in grape over a 3-month period found that the content of most phenolics peaked 2 months after *E. lata* inoculation (Galarneau et al. 2021). Phenolics could return to baseline levels as other defense mechanisms take precedence, or the growth of new tissues farther away from the infection site with lower phenolic levels could reduce the overall wood phenolic content.

To conclude, we found that resisting damage to physiological function from *E. lata* did not increase resistance to pathogen spread, contrary to our hypotheses. Syrah exhibited longer lesion lengths, but greater levels of certain wood antifungal compounds and higher gas exchange rates and photochemical function. This could indicate that Zinfandel leaves are more vulnerable to fungal toxins, but that this vulnerability protects the woody tissues by reducing transpiration and, consequently, pathogen spread and resource delivery to the pathogen. However, this study focused on two cultivars and one *E. lata* strain, and future work should confirm this response is a general mechanism for *Eutypa* resistance across more cultivars and pathogen strains. This study also focuses on responses 6 - 9 months after inoculation, and additional studies are needed to understand how short- and long-term physiological and chemical defense strategies differ. Our findings could potentially be applied in breeding for *Eutypa* resistance, since screening new plant material for infection responses in chlorophyll content and fluorescence or g_s would be faster and higher-throughput than measuring lesion length. However, our findings also suggest that current physiological resistance mechanisms are not ideal for growers, who need cultivars that can both compartmentalize infection spread and maintain enough photosynthesis to avoid reductions in yield and wine quality. Thus, future work should explore whether selecting for other resistance mechanisms, such as higher constitutive proanthocyanidin/catechin levels, could reduce dependence on downregulating gas exchange and produce cultivars that prevent lesion spread without becoming severely carbon-limited. Finally, while our study focused on these traits in well-watered conditions to isolate responses to infection, future work should incorporate multiple abiotic stressors (e.g., heat and water stress) to evaluate how resistance mechanisms interact with climate. Ultimately, understanding interactions between abiotic and biotic stress responses will advance the development of more climate- and disease-resilient grape cultivars.

Acknowledgements:

We kindly thank Stephanie Martinez for their assistance with the greenhouse experiment and taking physiological measurements.

Author Contributions:

GS: Conceptualization; GS, RT, PJE, CW, CEL, KB, and MKB: Methodology; GS: Formal analysis; GS: Writing – Original Draft; GS, RT, PJE, CW, CEL, KB, and MKB: Writing – Review & Editing; RT, PJE, and CW: Validation; JFH: Visualization; RT, PJE, KB, and MKB: Resources. GS, KB, and MKB: Funding Acquisition.

Conflict of Interest:

The authors acknowledge no known conflict of interest. Any opinion, findings, and conclusions or recommendations expressed in this material are those of the authors(s) and do not necessarily reflect the views of the National Science Foundation.

Funding: This work was supported by the Department of Viticulture and Enology at the University of California, Davis. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. (2036201).

References

Alsina, M. M., De Herralde, F., Aranda, X., & Save, R. 2007. Water relations and vulnerability to embolism are not related: experiments with eight grapevine cultivars. *Vitis / Herausgegeben Im Auftrage Der Bundesforschungsanstalt Fur Rebenzuchtung Geilweilerhof*. https://core.ac.uk/download/pdf/235691303.pdf

Amalfitano, C., Evidente, A., Surico, G., Tegli, S., Bertelli, E., & Mugnai, L. 2000. Phenols and stilbene polyphenols in the wood of esca-diseased grapevines. *Phytopathologia Mediterranea*, *39*(1), 178–183. https://doi.org/10.2307/26456544

Amborabé, B.-E., Fleurat-Lessard, P., Bonmort, J., Roustan, J.-P., & Roblin, G. 2001. Effects of eutypine, a toxin from *Eutypa lata*, on plant cell plasma membrane: Possible subsequent implication in disease development. *Plant Physiology and Biochemistry: PPB / Societe Francaise de Physiologie Vegetale*, *39*(1), 51–58. https://doi.org/10.1016/s0981-9428(00)01216-x

Andolfi, A., Mugnai, L., Luque, J., Surico, G., Cimmino, A., & Evidente, A. 2011. Phytotoxins produced by fungi associated with grapevine trunk diseases. *Toxins*, *3*(12), 1569–1605. https://doi.org/10.3390/toxins3121569

Aziz, A., Perazzolli, M., Gramaje, D., Zyprian, E. M., & Cantu, D. 2020. Editorial: Recent Advances on Grapevine-Microbe Interactions: From Signal Perception to Resistance Response. *Frontiers in Plant Science*, *11*. https://doi.org/10.3389/fpls.2020.01164

Barry, K. M., Davies, N. W., & Mohammed, C. L. 2002. Effect of season and different fungi on phenolics in response to xylem wounding and inoculation in *Eucalyptus nitens*. *Forest Pathology*, *32*(3), 163–178. https://doi.org/10.1046/j.1439-0329.2002.00281.x

Baumgartner, K., Hillis, V., Lubell, M., Norton, M. & Kaplan, J. 2019. Managing grapevine trunk diseases in California's southern San Joaquin Valley. *American Journal of Enology and Viticulture,* 70**,** 267-276.

Bednarek, P. 2012. Chemical warfare or modulators of defense responses - the function of secondary metabolites in plant immunity. *Current Opinion in Plant Biology*, *15*(4), 407–414. https://doi.org/10.1016/j.pbi.2012.03.002

Bertsch, C., Ramírez-Suero, M., Magnin-Robert, M., Larignon, P., Chong, J., Abou-Mansour, E., Spagnolo, A., Clément, C., & Fontaine, F. 2013. Grapevine trunk diseases: complex and still poorly understood. *Plant Pathology*, *62*(2), 243–265. https://doi.org/10.1111/j.1365-3059.2012.02674.x

Bortolami, G., Gambetta, G. A., Delzon, S., *et al*. 2019. Exploring the Hydraulic Failure Hypothesis of Esca Leaf Symptom Formation. *Plant Physiology*, *181*(3), 1163–1174. https://doi.org/10.1104/pp.19.00591

Bortolami, G., Gambetta, G. A., Cassan, C., Dayer, S., Farolfi, E., Ferrer, N., Gibon, Y., Jolivet, J., Lecomte, P., & Delmas, C. E. L. 2021. Grapevines under drought do not express esca leaf symptoms. *Proceedings of the National Academy of Sciences*, *118*(43). https://doi.org/10.1073/pnas.2112825118

Bota, J., Tomás, M., Flexas, J., Medrano, H., & Escalona, J. M. 2016. Differences among grapevine cultivars in their stomatal behavior and water use efficiency under progressive water stress. *Agricultural Water Management*, *164*, 91–99. https://doi.org/10.1016/j.agwat.2015.07.016

Busch, F. A. 2014. Opinion: the red-light response of stomatal movement is sensed by the redox state of the photosynthetic electron transport chain. *Photosynthesis Research*, *119*(1-2), 131–140. https://doi.org/10.1007/s11120-013-9805-6

Cardot, C., Mappa, G., La Camera, S., Gaillard, C., Vriet, C., Lecomte, P., Ferrari, G., & Coutos-Thévenot, P. 2019. Comparison of the Molecular Responses of Tolerant, Susceptible and Highly Susceptible Grapevine Cultivars During Interaction With the Pathogenic Fungus *Eutypa lata*. *Frontiers in Plant Science*, *10*, 991. https://doi.org/10.3389/fpls.2019.00991

Carter M. V. 1991. The status of *Eutypa lata* as a pathogen. Phytopathological Paper 32. Commonwealth Agricultural Bureau, International Mycological Institute, Wallingford, Oxon, England.

Chapuis, L., Richard, L., & Dubos, B. 1998. Variation in susceptibility of grapevine pruning wound to infection by Eutypa lata in south-western France. *Plant Pathology*, *47*, 463–472. https://doi.org/10.1046/J.1365-3059.1998.00258.X

Charrier, G., Delzon, S., Domec, J.-C., *et al*. 2018. Drought will not leave your glass empty: Low risk of hydraulic failure revealed by long-term drought observations in world's top wine regions. *Science Advances*, *4*(1), eaao6969. https://doi.org/10.1126/sciadv.aao6969

Czemmel, S., Galarneau, E. R., Travadon, R., McElrone, A. J., Cramer, G. R., & Baumgartner, K. 2015. Genes expressed in grapevine leaves reveal latent wood infection by the fungal pathogen *Neofusicoccum parvum*. *PloS One*, *10*(3), e0121828. https://doi.org/10.1371/journal.pone.0121828

Dell'Acqua, N., Gambetta, G. A., Delzon, S., Ferrer, N., Lamarque, L. J., Saurin, N., Theodore, P., & Delmas, C. E. L. 2024. Mechanisms of grapevine resilience to a vascular disease: investigating stem radial growth, xylem development and physiological acclimation. *Annals of Botany*, *133*(2), 321–336. https://doi.org/10.1093/aob/mcad188

Edwards, J., Salib, S., Thomson, F., & Pascoe, I. G. 2007b. The impact of *Phaeomoniella chlamydospora* infection on the grapevine's physiological response to water stress Part 1: Zinfandel. *Phytopathologia Mediterranea*.

Edwards, J., Salib, S., Thomson, F., & Pascoe, I. G. 2007c. The impact of *Phaeomoniella chlamydospora* infection on the grapevine's physiological response to water stress Part 2: Cabernet Sauvignon and Chardonnay. *Phytopathologia Mediterranea*.

Etienne Lucas, Frederic Fabre, Davide Martinetti, Elise Frank, Lucie Michel, Valerie Bonnardot, Lucia Guerin Dubrana, and Chloe EL Delmas. 2024. Exploring the role of cultivar, year and plot age in the incidence of grapevine trunk diseases: insights from 20 years of regional surveys in France. *bioRxiv*: 2024-03.

Fontaine, F., Pinto, C., Vallet, J., Clément, C., Gomes, A. C., & Spagnolo, A. 2016. The effects of grapevine trunk diseases (GTDs) on vine physiology. *European Journal of Plant Pathology / European Foundation for Plant Pathology*, *144*, 707–721.

Flexas, J., Bota, J., Escalona, J. M., Sampol, B., & Medrano, H. 2002. Effects of drought on photosynthesis in grapevines under field conditions: an evaluation of stomatal and mesophyll limitations. *Functional Plant Biology: FPB*, *29*(4), 461–471. https://doi.org/10.1071/PP01119

Galarneau, E. R. A., Lawrence, D. P., Travadon, R., & Baumgartner, K. 2019. Drought Exacerbates Botryosphaeria Dieback Symptoms in Grapevines and Confounds Host-based Molecular Markers of Infection by *Neofusicoccum parvum*. *Plant Disease*, *103*(7), 1738–1745. https://doi.org/10.1094/PDIS-09-18-1549-RE

Galarneau, E. R. A., Lawrence, D. P., Wallis, C. M., & Baumgartner, K. 2021. A comparison of the metabolomic response of grapevine to infection with ascomycete wood-infecting fungi. *Physiological and Molecular Plant Pathology*, *113*, 101596. https://doi.org/10.1016/j.pmpp.2020.101596

Galarneau ERA, Wallis CM, Baumgartner K. 2024, accepted and in print. Biochemical characterization of wood decay and metabolization of phenolic compounds by causal fungi of grapevine trunk diseases. *PLoS ONE*.

Gallo, A. E., Perez Peña, J. E., & Prieto, J. A. 2021. Mechanisms underlying photosynthetic acclimation to high temperature are different between *Vitis vinifera* cv. Syrah and Grenache. *Functional Plant Biology: FPB*, *48*(3), 342–357. https://doi.org/10.1071/FP20212

Gómez, P., Báidez, A. G., Ortuño, A., & Del Río, J. A. 2016. Grapevine xylem response to fungi involved in trunk diseases: Grapevine vascular defence. *The Annals of Applied Biology*, *169*(1), 116–124. https://doi.org/10.1111/aab.12285

Guan, P., Schmidt, F., Riemann, M., Fischer, J., Thines, E., & Nick, P. 2020. Hunting modulators of plant defence: the grapevine trunk disease fungus *Eutypa lata* secretes an

amplifier for plant basal immunity. *Journal of Experimental Botany*, *71*(12), 3710–3724. https://doi.org/10.1093/jxb/eraa152

Hammerbacher, A., Paetz, C., Wright, L. P., Fischer, T. C., Bohlmann, J., Davis, A. J., Fenning, T. M., Gershenzon, J., & Schmidt, A. 2014. Flavan-3-ols in Norway spruce: biosynthesis, accumulation, and function in response to attack by the bark beetle-associated fungus Ceratocystis polonica. *Plant Physiology*, *164*(4), 2107–2122. https://doi.org/10.1104/pp.113.232389

Hanlin, R. L., & Downey, M. O. 2009. Condensed tannin accumulation and composition in skin of Shiraz and Cabernet Sauvignon grapes during berry development. *American Journal of Enology and Viticulture*, *60*(1), 13–23. https://doi.org/10.5344/ajev.2009.60.1.13

Herms, D. A., & Mattson, W. J. 1992. The Dilemma of Plants: To Grow or Defend. *The Quarterly Review of Biology*, *67*(3), 283–335. https://doi.org/10.1086/417659

Kaplan J, Travadon R, Cooper M, Hillis V, Lubell M, Baumgartner K. 2016. Identifying economic hurdles to early adoption of preventative practices: The case of trunk diseases in California winegrape vineyards. Wine Econ Policy. 5:127-141. https://doi.org/10.1016/j.wep.2016.11.001

Khattab, I. M., Sahi, V. P., Baltenweck, R., Maia- Grondard, A., Hugueney, P., Bieler, E., & Nick, P. 2021. Ancestral chemotypes of cultivated grapevine with resistance to Botryosphaeriaceae- related dieback allocate metabolism towards bioactive stilbenes. New Phytologist, 229(2), 1133-1146. https://doi.org/10.1111/nph.16919

Lambert, C., Bisson, J., Waffo-Téguo, P., Papastamoulis, Y., Richard, T., Corio-Costet, M.-F., Mérillon, J.-M., & Cluzet, S. 2012. Phenolics and their antifungal role in grapevine wood decay: focus on the Botryosphaeriaceae family. *Journal of Agricultural and Food Chemistry*, *60*(48), 11859–11868. https://doi.org/10.1021/jf303290g

Legrand, V., Dalmayrac, S., Latché, A., Pech, J.-C., Bouzayen, M., Fallot, J., Torregrosa, L., Bouquet, A., & Roustan, J.-P. 2003. Constitutive expression of Vr-ERE gene in transformed grapevines confers enhanced resistance to eutypine, a toxin from *Eutypa lata*. *Plant Science: An International Journal of Experimental Plant Biology*, *164*(5), 809–814. https://doi.org/10.1016/S0168-9452(03)00069-4

Loschiavo A, Sosnowski M, Wicks T. 2007. Incidence of Eutypa dieback in the Adelaide Hills. Aus New Z Grapegrower Winemaker. (April volume):26-29.

Mahoney, N., Lardner, R., Molyneux, R. J., Scott, E. S., Smith, L. R., & Schoch, T. K. 200). Phenolic and heterocyclic metabolite profiles of the grapevine pathogen *Eutypa lata*. *Phytochemistry*, *64*(2), 475–484. https://doi.org/10.1016/s0031-9422(03)00337-6

Mahoney, N., Molyneux, R. J., Smith, L. R., Schoch, T. K., Rolshausen, P. E., & Gubler, W. D. 2005. Dying-arm disease in grapevines: diagnosis of infection with *Eutypa lata* by metabolite

analysis. *Journal of Agricultural and Food Chemistry*, *53*(21), 8148–8155. https://doi.org/10.1021/jf0510236

Miranda, M., Ralph, S., Mellway, R. D., White, R., Heath, M. C., Bohlmann, J., & Constabel, C. 2007. The transcriptional response of hybrid poplar (Populus trichocarpa x P. deltoides) to infection by Melampsora medusae leaf rust involves induction of flavonoid pathway genes leading to the accumulation of proanthocyanidins. *Molecular Plant-Microbe Interactions: MPMI*, *20*(7), 816–831. https://doi.org/10.1094/MPMI-20-7-0816

Moisy, C., Berger, G., Flutre, T., Le Cunff, L., & Péros, J.-P. 2017. Quantitative Assessment of Grapevine Wood Colonization by the Dieback Fungus *Eutypa lata*. *Journal of Fungi (Basel, Switzerland)*, *3*(2). https://doi.org/10.3390/jof3020021

Morkunas, I., & Ratajczak, L. 2014. The role of sugar signaling in plant defense responses against fungal pathogens. *Acta Physiologiae Plantarum / Polish Academy of Sciences, Committee of Plant Physiology Genetics and Breeding*, *36*(7), 1607–1619. https://doi.org/10.1007/s11738-014-1559-z

Munkvold, G., Duthie, J., & Marois, J. 1994. Reductions in yield and vegetative growth of grapevines due to Eutypa dieback. *Phytopathology*, *84*, 186–192. https://doi.org/10.1094/PHYTO-84-186

https://doi.org/10.1094/PD-78-0200 **Munkvold G.P., Marois J.J.** 1995. Factors associated with variation in susceptibility of grapevine pruning wounds to infection by *Eutypa lata*. *Phytopathology* 85: 249-256.

Mutawila, C., Fourie, P. H., Halleen, F., & Mostert, L. 2011. Histo-pathology study of the growth of Trichoderma harzianum, Phaeomoniella chlamydospora and Eutypa lata on grapevine pruning wounds. *Phytopathologia Mediterranea*, *50*, S46–S60. http://www.jstor.org/stable/26458710

Nemesio-Gorriz, M., Hammerbacher, A., Ihrmark, K., Källman, T., Olson, Å., Lascoux, M., Stenlid, J., Gershenzon, J., & Elfstrand, M. 2016. Different alleles of a gene encoding leucoanthocyanidin reductase (PaLAR3) influence resistance against the fungus Heterobasidion parviporum in Picea abies. *Plant Physiology*, *171*(4), 2671–2681. https://doi.org/10.1104/pp.16.00685

Patakas, A., & Noitsakis, B. 1999. Osmotic Adjustment and Partitioning of Turgor Responses to Drought in Grapevines Leaves. *American Journal of Enology and Viticulture*, *50*(1), 76–80. https://doi.org/10.5344/ajev.1999.50.1.76

Péros, J. P., Berger, G. 1994. A rapid method to assess the aggressiveness of *Eutypa lata* isolates and the susceptibility of grapevine cultivars to Eutypa dieback. *Agronomie*, *14*(8), 515–523. https://doi.org/10.1051/agro:19940804

Pereira, L., Domingues-Junior, A. P., Jansen, S., Choat, B., & Mazzafera, P. 2018. Is embolism resistance in plant xylem associated with quantity and characteristics of lignin? *Trees*, *32*(2), 349–358. https://doi.org/10.1007/s00468-017-1574-y

Perez-Gonzalez, G., Sebestyen, D., Petit, E., Jellison, J., Mugnai, L., Gelhaye, E., Lee, N., Farine, S., Bertsch, C., & Goodell, B. 2022. Oxygen radical-generating metabolites secreted by Eutypa and Esca fungal consortia: Understanding the mechanisms behind grapevine wood deterioration and pathogenesis. *Frontiers in Plant Science*, *13*, 921961. https://doi.org/10.3389/fpls.2022.921961

Petit, A.-N., Vaillant, N., Boulay, M., Clément, C., & Fontaine, F. 2006. Alteration of photosynthesis in grapevines affected by esca. *Phytopathology*, *96*(10), 1060–1066. https://doi.org/10.1094/PHYTO-96-1060

Pou, A., Medrano, H., Tomàs, M., Martorell, S., Ribas-Carbó, M., & Flexas, J. 2012. Anisohydric behaviour in grapevines results in better performance under moderate water stress and recovery than isohydric behaviour. *Plant and Soil*, *359*(1-2), 335–349. https://doi.org/10.1007/s11104-012-1206-7

Pouzoulet, J., Mailhac, N., Couderc, C., Besson, X., Daydé, J., Lummerzheim, M., & Jacques, A. 2013) A method to detect and quantify *Phaeomoniella chlamydospora* and *Phaeoacremonium aleophilum* DNA in grapevine-wood samples. *Applied Microbiology and Biotechnology*, *97*(23), 10163–10175. https://doi.org/10.1007/s00253-013-5299-6

Pouzoulet, J., Rolshausen, P. E., Schiavon, M., Bol, S., Travadon, R., Lawrence, D. P., Jacques, A. 2017. A method to detect and quantify *Eutypa lata* and *Diplodia seriata*-complex DNA in grapevine pruning wounds. *Plant Disease*, 101(8), 1470-1480.

Pouzoulet, J., Pivovaroff, A. L., Santiago, L. S., & Rolshausen, P. E. 2014. Can vessel dimension explain tolerance toward fungal vascular wilt diseases in woody plants? Lessons from Dutch elm disease and esca disease in grapevine. *Frontiers in Plant Science*, *5*, 253. https://doi.org/10.3389/fpls.2014.00253

Ramírez, M., Pérez, L. M., & Montealegre, J. R. 2018. Susceptibilidad de diferentes cultivares de vid vinífera (Vitis vinifera L.) a *Diplodia seriata* y *Diplodia mutila*. Ciencia e investigación agraria, 45(1), 93-98. repositorio.uchile.cl. https://repositorio.uchile.cl/handle/2250/151730

Rolshausen, P. E., Mahoney, N. E., Molyneux, R. J., & Gubler, W. D. 2006. A Reassessment of the Species Concept in *Eutypa lata* , the Causal Agent of Eutypa Dieback of Grapevine. *Phytopathology*®, *96*(4), 369–377. https://doi.org/10.1094/PHYTO-96-0369

Rolshausen, P. E., Greve, L. C., Labavitch, J. M., Mahoney, N. E., Molyneux, R. J., & Gubler, W. D. 2008. Pathogenesis of *Eutypa lata* in grapevine: identification of virulence

factors and biochemical characterization of cordon dieback. *Phytopathology*, *98*(2), 222–229. https://doi.org/10.1094/PHYTO-98-2-0222

Rolshausen PE, Sosnowski M, Trouillas FP, Gubler WD. 2015. Eutypa dieback, p 57-61. In: Wilcox WF, Gubler WD, Uyemoto JK (eds.). Compendium of Grape Diseases, Disorders, and Pests (2nd ed). American Phytopathological Society Press, Saint Paul, Minnesota, USA.

Rudelle, J., Octave, S., Kaid-Harche, M., Roblin, G., & Fleurat-Lessard, P. 2005. Structural modifications induced by Eutypa lata in the xylem of trunk and canes of Vitis vinifera. *Functional Plant Biology: FPB*, *32*(6), 537–547. https://doi.org/10.1071/FP05012

Shigo, A. L. 1984. Compartmentalization: A conceptual framework for understanding how trees grow and defend themselves. *Annual Review of Phytopathology*, *22*(1), 189–214. https://doi.org/10.1146/annurev.py.22.090184.001201

Sinclair, G., Galarneau, E. R., Hnizdor, J. F., McElrone, A. J., Walker, M. A., & Bartlett, M. K. 2024. Grape cultivars adapted to hotter, drier growing regions exhibit greater photosynthesis under hot conditions despite less drought-resistant leaves. *Annals of Botany*. https://doi.org/10.1093/aob/mcae032

Smith, L. R., Mahoney, N., & Molyneux, R. J. 2003. Synthesis and structure-phytotoxicity relationships of acetylenic phenols and chromene metabolites, and their analogues, from the grapevine pathogen *Eutypa lata*. *Journal of Natural Products*, *66*(2), 169–176. https://doi.org/10.1021/np020415t

Songy, A., Fernandez, O., Clément, C., Larignon, P., & Fontaine, F. 2019. Grapevine trunk diseases under thermal and water stresses. *Planta*, *249*(6), 1655–1679. https://doi.org/10.1007/s00425-019-03111-8

Sosnowski, M. R., Lardner, R., Wicks, T. J., & Scott, E. S. 2007. The Influence of Grapevine Cultivar and Isolate of *Eutypa lata* on Wood and Foliar Symptoms. *Plant Disease*, *91*(8), 924–931. https://doi.org/10.1094/PDIS-91-8-0924

Sosnowski, M. R., Shtienberg, D., Creaser, M. L., Wicks, T. J., Lardner, R., & Scott, E. S. 2007b. The influence of climate on foliar symptoms of eutypa dieback in grapevines. *Phytopathology*, *97*(10), 1284–1289. https://doi.org/10.1094/PHYTO-97-10-1284

Sosnowski, M. R., Luque, J., Loschiavo, A. P., Martos, S., Garcia-Figueres, F., Wicks, T. J., & Scott, E. S. 2011. Studies on the effect of water and temperature stress on grapevines inoculated with *Eutypa lata*. *Phytopathologia Mediterranea*, *50*, S127–S138. https://doi.org/10.2307/26458716

Sosnowski, M. R., & Ayres, M. R. 2022. Winegrape cultivars (*Vitis vinifera*) vary in susceptibility to the grapevine trunk pathogens *Eutypa lata* and *Diplodia seriata*. *Australian Journal of*. https://onlinelibrary.wiley.com/doi/abs/10.1111/ajgw.12531

Tomasella, M., Calderan, A., Mihelčič, A., Petruzzellis, F., Braidotti, R., Natale, S., Lisjak, K., Sivilotti, P., & Nardini, A. 2023. Best procedures for leaf and stem water potential

measurements in grapevine: Cultivar and water status matter. *Plants*, *12*(13). https://doi.org/10.3390/plants12132412

Travadon, R., Rolshausen, P. E., Gubler, W. D., Cadle-Davidson, L., & Baumgartner, K. 2013. Susceptibility of Cultivated and Wild *Vitis* spp. to Wood Infection by Fungal Trunk Pathogens. *Plant Disease*, *97*(12), 1529–1536. https://doi.org/10.1094/PDIS-05-13-0525-RE

Travadon, R., & Baumgartner, K. 2023. Phenotyping grapevine cultivars for resistance to Eutypa dieback. *Phytopathologia Mediterranea*. https://www.torrossa.com/gs/resourceProxy?an=5583954&publisher=FF3888#page=95

Travadon, R., Heinitz, C., & Baumgartner, K. 2024. A Field Survey of Grapevine Germplasm Susceptible to Eutypa Dieback. HortScience, 59(3), 362-370. https://doi.org/10.21273/HORTSCI17521-23

Ullah, C., Unsicker, S. B., Fellenberg, C., Constabel, C. P., Schmidt, A., Gershenzon, J., & Hammerbacher, A. 2017. Flavan-3-ols are an effective chemical defense against rust infection. *Plant Physiology*, *175*(4), 1560–1578. https://doi.org/10.1104/pp.17.00842

Wallis, C. M., Chen, J., & Civerolo, E. L. 2012. Zebra chip-diseased potato tubers are characterized by increased levels of host phenolics, amino acids, and defense-related proteins. *Physiological and Molecular Plant Pathology*, *78*, 66–72. https://doi.org/10.1016/j.pmpp.2012.02.001

Wallis, C. M., & Galarneau, E. R.-A. 2020. Phenolic Compound Induction in Plant-Microbe and Plant-Insect Interactions: A Meta-Analysis. *Frontiers in Plant Science*, *11*, 580753. https://doi.org/10.3389/fpls.2020.580753

Wang, Y., Wang, X., Fang, J., Yin, W., Yan, X., Tu, M., Liu, H., Zhang, Z., Li, Z., Gao, M., Lu, H., Wang, Y., & Wang, X. 2023. VqWRKY56 interacts with VqbZIPC22 in grapevine to promote proanthocyanidin biosynthesis and increase resistance to powdery mildew. *The New Phytologist*, *237*(5), 1856–1875. https://doi.org/10.1111/nph.18688

Yin, H., Sun, Q., Lu, X., Zhang, L., Yuan, Y., Gong, C., He, X., Ma, W., Mu, P. 2022. Identification of the glutamine synthetase (GS) gene family in four wheat species and functional analysis of Ta4D.GSe in *Arabidopsis thaliana*. *Plant Molecular Biology*, *110*(1-2), 93–106. https://doi.org/10.1007/s11103-022-01287-4

Zivcak, M., Brestic, M., & Sytar, O. 2016. Osmotic Adjustment and Plant Adaptation to Drought Stress. In M. A. Hossain, S. H. Wani, S. Bhattacharjee, D. J. Burritt, & L.-S. P. Tran (Eds.), *Drought Stress Tolerance in Plants, Vol 1: Physiology and Biochemistry* (pp. 105–143). Springer International Publishing. https://doi.org/10.1007/978-3-319-28899-4_5

Main Text Tables & Figures:

Table 1: Type III ANOVA results for variables measured once at the end of the experimental period, including lesion length, total root biomass, and canopy leaf area. (* for $p < 0.05$, ** for $p < 0.01$, *** for $p < 0.001$). NS represents non-significant results.

Predictor	**Lesion Length**	**Root biomass**	**Canopy leaf area**
Cultivar	**7e-06 *** **	0.3 NS	**1e-03 ** **
Treatment	**3e-04 *** **	0.7 NS	0.8 NS
Cultivar · Treatment	0.4 NS	0.6 NS	0.9 NS

Table 2: Type III ANOVA results for variables measured repeatedly over the experiment, including stomatal conductance (g_s), photosynthesis (A), leaf-level transpiration (E), water use efficiency (WUE), pre-dawn (PDLWP) and midday stem water potentials (MDSWP), whole-plant evapotranspiration (E_{tot}), and whole-plant hydraulic conductivity (K_{plant}). Predictor variables are Cultivar, Treatment (inoculated versus wounded controls), Timepoint (days since the start of the experiment), and their interactions (Cultivar · Treatment and Treatment · Timepoint). Asterisks represent significance (* for $p < 0.05$, ** for $p < 0.01$, *** for $p < 0.001$). NS represents non-significant results.

Predictor	g_s	A	E	**WUE**	**PDLWP**	**MDSWP**	E_{tot}	K_{plant}
Cultivar	**5e-03****	0.1 NS	**0.03***	0.4 NS	**1e-13*****	**2e-16*****	**2e-16*****	0.9 NS
Treatment	0.08 NS	**8e-03****	0.09 NS	0.4 NS	0.6 NS	**4e-03****	**0.03***	0.4 NS
Timepoint	**8e-07*****	**4e-12*****	**2e-03****	**0.01***	0.09 NS	0.06 NS	**2e-16*****	**0.03***
Cultivar · Treatment	**5e-04*****	**7e-05*****	**1e-03***	0.9 NS	0.8 NS	0.2 NS	0.2 NS	0.9 NS
Treatment · Timepoint	0.3 NS	0.07 NS	0.3 NS	0.9 NS	0.5 NS	0.3 NS	**0.01***	0.1 NS

Table 3: Cultivar and treatment means for stomatal conductance (g_s), photosynthesis (A), pre-dawn (PDLWP) and midday stem water potentials (MDSWP), whole-plant hydraulic conductivity (K_{plant}), leaf osmotic potential at full hydration (π_o), leaf chlorophyll content (Chl), quantum efficiency of photosystem II (Fv/Fm), and lesion length. Values are means +/- standard errors. Letters show Tukey HSD test results for significant main effects (ANOVA, P-value < 0.05). N = 22 – 25 for inoculated (INOC) Syrah and Zinfandel and N = 5 for non-inoculated wounded (NIW) Syrah and Zinfandel for all variables except Fv/Fm, where N = 5 for all cultivar and treatment combinations.

Treatment	g_s **(mol m^{-2} s^{-1})**	A **(µmol m^{-2} s^{-1})**	PDLWP **(MPa)**	MDSWP **(MPa)**	K_{plant} **(kg MPa^{-1} s^{-1} m^{-2})**	π_o **(MPa)**	Chl **(µmol m^{-2})**	F_v/Fm **(-)**	Lesion Length **(mm)**
Zinfandel (NIW)	0.064 ± 0.004^{a}	8.34 ± 0.40^{a}	-0.57 ± 0.02^{a}	-0.95 ± 0.06^{a}	0.0012 ± 1.4e-04 ^{a}	-1.48 ± 0.04^{a}	18.00 ± 1.18^{a}	0.789 ± 0.007^{a}	12.09 ± 1.69^{c}
Syrah (NIW)	0.047 ± 0.005^{bc}	6.19 ± 0.46^{b}	-0.66 ± 0.02^{b}	-1.14 ± 0.05^{b}	0.0011 ± 9.5e-05 ^{a}	-1.68 ± 0.14^{a}	12.61 ± 0.81^{b}	0.758 ± 0.009^{b}	16.38 ± 3.28^{bc}
Zinfandel (INOC)	0.046 ± 0.002^{c}	6.72 ± 0.21^{b}	-0.56 ±0.01^{a}	-1.14 ± 0.02^{b}	0.0010 ± 4.0e-05 ^{a}	-1.61 ± 0.04^{a}	17.49 ± 0.55^{a}	0.766 ± 0.004^{ab}	25.13 ± 1.38^{b}
Syrah (INOC)	0.055 ± 0.004^{ab}	7.12 ± 0.19^{b}	-0.65 ±0.01^{b}	-1.23 ± 0.02^{b}	0.0011 ± 4.2e-5 ^{a}	-1.65 ± 0.03^{a}	14.22 ± 0.39^{b}	0.773 ± 0.004^{ab}	35.19 ± 1.48^{a}

Table 4: Type III ANOVAs testing whether cultivar and treatment differences in gas exchange are driven by differences in pre-dawn leaf water potential (PDLWP). Symbols follow Table 2. Cultivar and treatment interaction effects remained significant for g_s, *A*, and *E* and non-significant for WUE, indicating that cultivar differences in soil water status did not explain the cultivar and treatment differences in gas exchange.

Predictor	***gs***	***A***	**E**	**WUE**
Cultivar	**0.02***	0.3 NS	0.1 NS	0.6 NS
Treatment	0.3 NS	0.4 NS	0.3 NS	0.9 NS
Timepoint	**2e-07*****	**4e-12*****	**0.001****	**0.01***
PDLWP	**6e-04*****	0.07 NS	**0.002****	0.06 NS
Cultivar · Treatment	**4e-04*****	**1e-04*****	**0.001****	1 NS
Treatment · PDLWP	0.5 NS	0.7 NS	0.5 NS	0.9 NS
Cultivar · PDLWP	0.2 NS	0.6 NS	0.4 NS	0.9 NS

Table 5: Type III ANOVA results for variables measured twice during the experiment, including leaf osmotic potential at full hydration (π_o), chlorophyll content (Chl), and the quantum efficiency of PSII (*Fv/Fm*). Since these variables were measured less often, time since the start of the experiment is represented with the categorical variable Date instead of the continuous variable Timepoint (Table 2). * for $p < 0.05$, ** for $p < 0.01$, *** for $p < 0.001$, and NS for non-significant results.

Predictor	**π_o**	**Chl**	***Fv/Fm***
Cultivar	0.5 NS	4e-06***	0.7 NS
Treatment	0.7 NS	0.01*	0.2 NS
Date	2e-05***	0.7 NS	0.9 NS
Cultivar · Treatment	0.1 NS	0.2 NS	0.02*
Treatment · Date	0.3 NS	0.01*	1 NS

Table 6: Type III ANOVA results for wood chemistry measured at the end of the experimental period. Asterisks represent significance (* for $p < 0.05$, ** for $p < 0.01$, *** for $p < 0.001$). NS represents non-significant results.

Predictor	**Lignin**	**Total Phenolics**	**Total Procyanidins/ Catechins**	**Total Stilbenoids**	**Total Flavonoids**
Cultivar	0.8 NS	0.2 NS	**6e-05*** **	**7e-03*** **	**9e-06*** **
Treatment	0.4 NS	0.8 NS	1 NS	0.4 NS	0.7 NS
Cultivar · Treatment	0.4 NS	0.9 NS	0.9 NS	1 NS	0.8 NS

Table 7. Wood chemical composition for each cultivar and treatment. Values are means +/- standard errors for lignin, total phenolics, total procyanidin and catechins, total stilbenoids, and total other flavonoid content for wood near the inoculation site. *N* = 22 - 25 for inoculated (INOC) Syrah and Zinfandel and *N* = 5 for non-inoculated wounded control (NIW) Syrah and Zinfandel. There were significant cultivar differences in chemistry, but no effects of treatment or interactive effects between treatment and cultivar. Letters show Tukey HSD test results.

Treatment	Lignin (mg g^{-1} FW)	Total Phenolics (mg g^{-1} FW)	Total Procyanidins/Catechins (mg g^{-1} FW)	Total Stilbenoids (mg g^{-1} FW)	Total Other Flavonoids (mg g^{-1} FW)
Zinfandel (NIW)	17.44 ± 0.14^{a}	31.53 ± 7.3^{a}	23.86 ± 5.94^{a}	3.07 ± 0.82^{ab}	4.57 ± 1.47^{ab}
Syrah (NIW)	17.32 ± 0.05^{a}	26.43 ± 3.8^{a}	13.36 ± 1.96^{b}	4.09 ± 0.47^{a}	8.96 ± 1.96^{a}
Zinfandel (INOC)	17.39 ± 0.04^{a}	29.33 ± 1.60^{a}	23.55 ±1.89^{a}	2.54 ± 0.23^{ab}	3.22 ± 0.29^{b}
Syrah (INOC)	17.41 ± 0.04^{a}	25.44 ± 2.07^{a}	13.56 ±0.94^{b}	3.57 ± 0.27^{a}	8.28 ± 0.95^{a}

Figure Legends

Fig 1: Internal wood lesion length of each cultivar and treatment measured in millimeters (mm). Syrah (SY) significantly had higher lesion lengths than Zinfandel (ZN) treatments. Box plots represent averages of Syrah and Zinfandel inoculated plants (INOC) (*N*=22-25) and Non-Inoculated Wounded control plants (NIW) (*N*= 5).

Fig. 2: Gas exchange, pre-dawn leaf, and midday stem water potential for each cultivar and treatment over the experimental period. The x-axis contains sampling dates: July 15th (Jul 15), August 1st (Aug 01), August 15th (Aug 15), and September 1st (Sep 01). Data points represent averages of Syrah (SY) and Zinfandel (ZN) inoculated plants (INOC) (*N*=22-25) and Non-Inoculated Wounded control plants (NIW) (*N*= 5).

Fig. 3: Panel **(A)** mean leaf chlorophyll concentration in µmol per m^2 of leaf tissue averaged for the two sampling dates (6 & 8 month's post-inoculation: August 12th (12-Aug) and September 2nd (2-Sep)) per cultivar and treatment. Bar graphs for the first sampling date represents averages of (INOC) (*N*=22-25) and Non-Inoculated Wounded control plants (NIW) (*N*= 5). Second sampling date represents averages of (INOC) (*N*=5) and Non-Inoculated Wounded control plants (NIW) (*N*= 5). Chlorophyll content significantly differed between Cultivar and Treatment. Panel (B): fluorescence values (*Fv/Fm*) taken during the same sampling date. There were significant interaction effects of cultivar and treatment on *Fv/Fm*. SY stands for Syrah and -INOC refers to the inoculated treatment group. ZN stands for Zinfandel and -INOC refers to the inoculated treatment group. The mock-inoculated control group is labeled NIW (Non-Inoculated wounded).

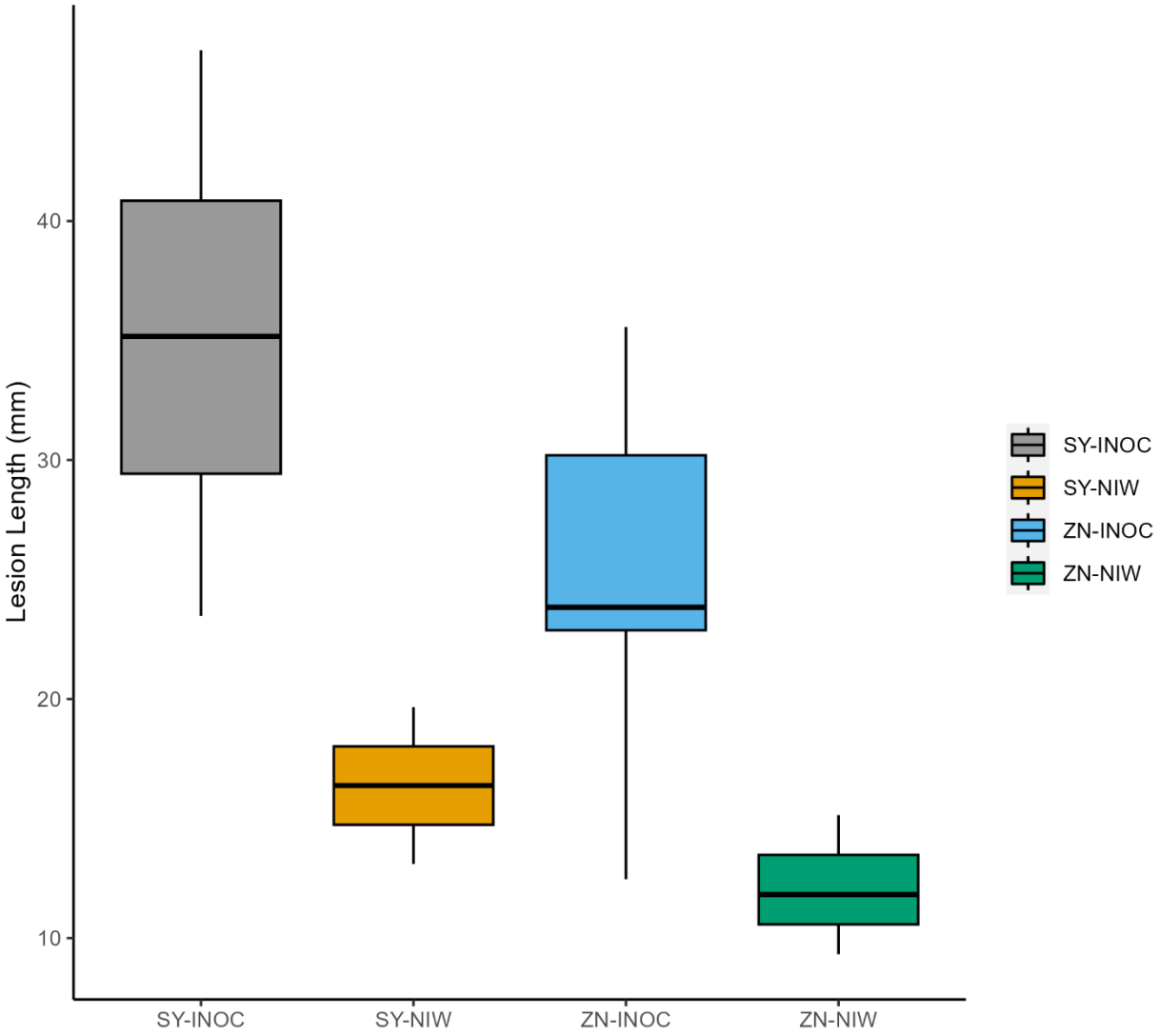

Fig 1: Internal wood lesion length of each cultivar and treatment measured in millimeters (mm). Syrah (SY) significantly had higher lesion lengths than Zinfandel (ZN) treatments. Box plots represent averages of Syrah and Zinfandel inoculated plants (INOC) (N=22-25) and Non-Inoculated Wounded control plants (NIW) (N=5).

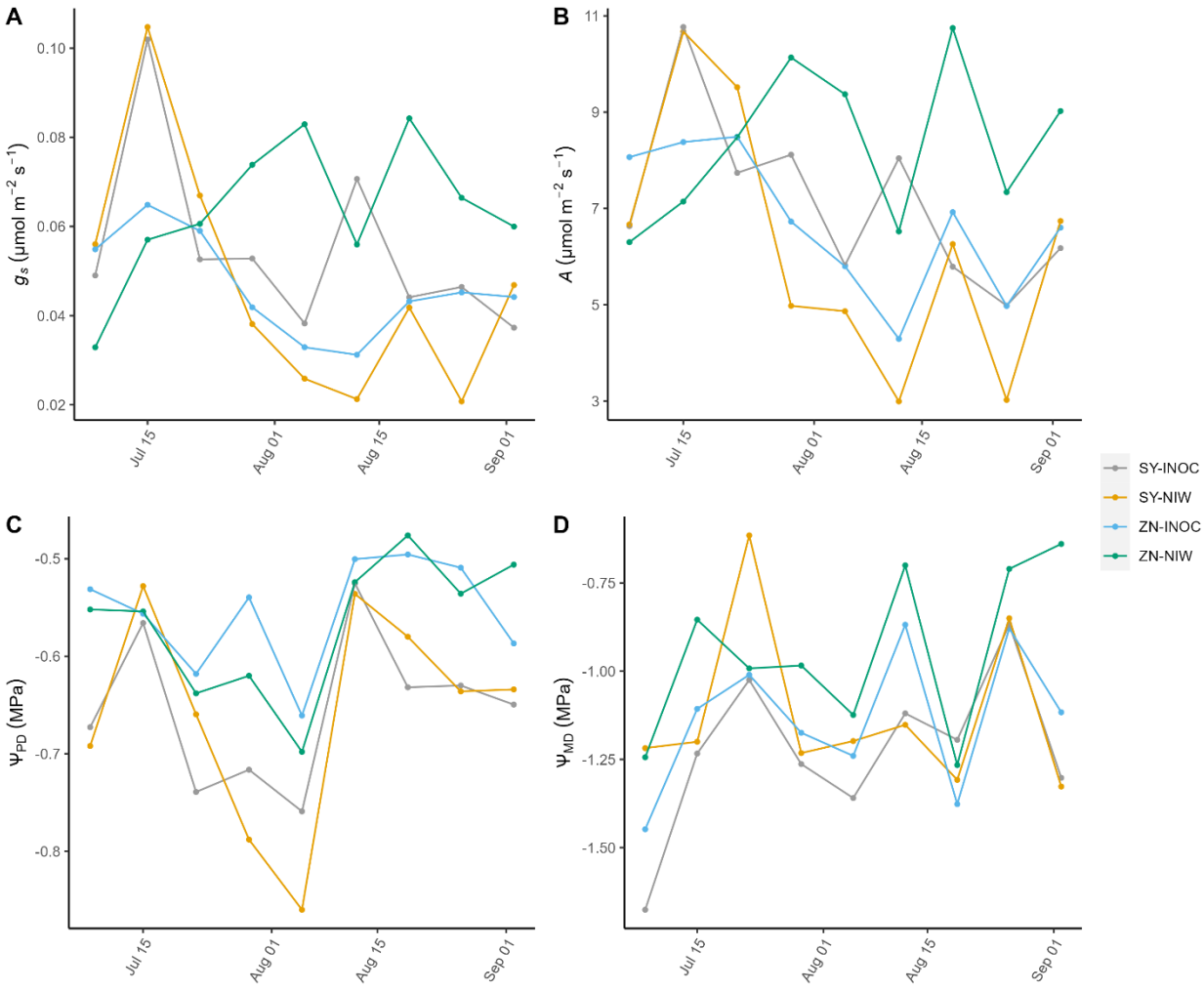

Fig 2.: Gas exchange, pre-dawn leaf, and midday stem water potential for each cultivar and treatment over the experimental period. The x-axis contains sampling dates July 15th (Jul 15), August 1st (Aug 01), August 15th (Aug 15), and September 1st (Sep 01). Data points represent averages of Syrah (SY) and Zinfandel (ZN) inoculated plants (INOC) (*N*=22-25) and Non-Inoculated Wounded (NIW) (*N*=5) plants.

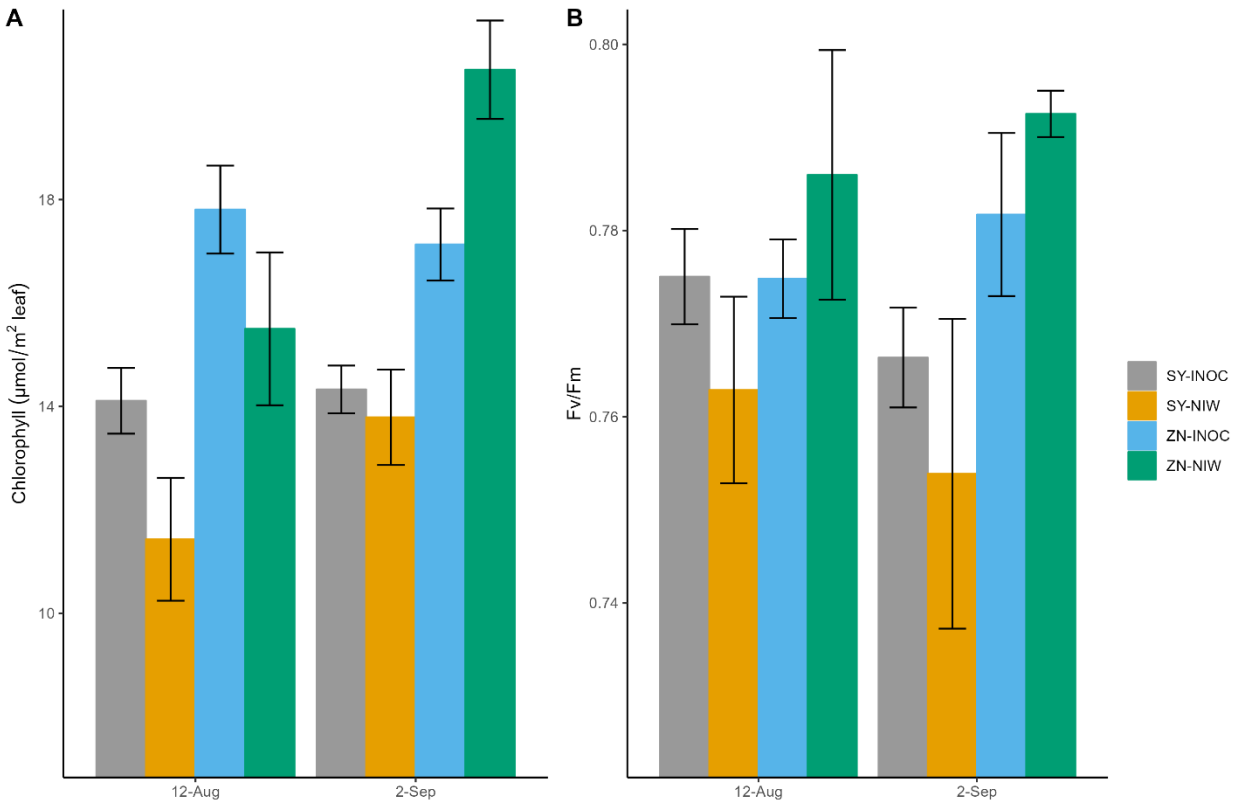

Fig 3. Panel **(A)** mean leaf chlorophyll concentration averaged per cultivar per treatment for two sampling dates 6 & 8 months post-inoculation (12 Aug. and 2 Sep). Bar graphs for 1st sampling date represent averages of inoculated (INOC) (*N=22-25*) and Non-Inoculated Wounded (NIW) (*N=5*). 2nd sampling date represents averages for INOC (*N=5*) and NIW (*N=5*). Panel (**B**): Flourescence values (*Fv/Fm*) taken during the same sampling dates. For both figures, SY=Syrah, and ZN=Zinfandel.