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SHORT COMMUNICATION

Grapevine leaf size influences canopy temperature

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ABSTRACT

Grapevine leaves have diverse shapes and sizes which are influenced by many factors including genetics, vine phytosanitary status, environment, leaf and vine age, and node position on the shoot. To determine the relationship between grapevine leaf shape or size and leaf canopy temperature, we examined five seedling populations grown in a vineyard in California, USA. The populations had one parent with compound leaves of the *Vitis piasezkii* type and a different second parent with non-compound leaves. In previous work, we had measured the shape and size of the leaves collected from these populations using 21 homologous landmarks. Here, we paired these morphological data with canopy temperature measurements made using a handheld infrared thermometer. After recording time of sampling and canopy temperature, we used a linear model between time of sampling and canopy temperature to estimate temperature residuals. Based on these residuals, we determined if the canopy temperature of each vine was cooler or warmer than expected, based on the time of sampling. We established a relationship between leaf size and canopy temperature: vines with larger leaves were cooler than expected. By contrast, leaf shape was not strongly correlated with variation in canopy temperature. Ultimately, these findings indicate that vines with larger leaves may contribute to the reduction of overall canopy temperature; however, further work is needed to determine whether this is due to variation in leaf size, differences in the openness of the canopy or other related traits.

KEYWORDS: Ampelography, grapevine, leaf morphology, canopy temperature, leaf shape, *Vitis*, infrared thermometry

INTRODUCTION

Grapevine (*Vitis* spp.) leaves have diverse shapes and sizes (Chitwood *et al*., 2014; Chitwood and Mullins, 2022), which are influenced by genetics (Chitwood *et al*., 2014; Demmings *et al*., 2019), vine phytosanitary status (Klein *et al*., 2017), environment (Chitwood *et al*., 2016b; Chitwood *et al*., 2021), leaf age, node position (Chitwood *et al*., 2016a; Chitwood *et al*., 2016b; Bryson *et al*., 2020), rootstock (Migicovsky *et al*., 2019; Harris *et al*., 2021), and many other factors.

The primary photosynthetic organ of the plant, the leaf has many characteristics that impact photosynthesis. For example, increasing stomatal density enhances leaf photosynthesis (Tanaka *et al*., 2013). Leaf colour may also impact photosynthetic rate, as shown in one study of red and green leaves, in which the green leaves had a 47 % higher maximum CO_2 assimilation rate compared to red leaves from neighbouring plants (Menzies *et al*., 2015). In addition, a larger leaf size will increase the photosynthetic potential of the plant; however, it may also have negative consequences: larger leaves with a thicker boundary layer can slow heat loss, increasing respiration at a rate greater than the increase in photosynthesis (Givnish, 1987; Westoby *et al*., 2002). Both the size of an individual leaf and the combined size of all leaves, also known as the total leaf area, may influence plant growth and health. In grapevine, the higher water demand for transpiration associated with a larger total leaf area may increase vine water stress and as a result reduce yield (Mirás-Avalos *et al*., 2017).

In addition to the temperature of individual leaves, it is important to consider canopy temperature, which we define as the average temperature taken across multiple leaves across the whole plant. Canopy temperature can be influenced by many factors, both external (environmental), such as net radiation and wind velocity, and internal (physiological), such as stomatal control of transpiration. The architecture of the canopy, which can be altered through management practices, as well as the spacing and orientation of rows, can also interact with the environment to impact the temperature of the canopy (Boissard *et al*., 1990). For example, wide row spacing, a high number of shoots per hectare, and high vine vigour all increase within-canopy shading, altering the canopy microclimate and ultimately influencing traits such as yield and fruit composition (Smart, 1985).

Canopy temperature can be measured using infrared thermometry, such as remote thermal imaging, which is non-invasive and non-destructive (Leinonen and Jones, 2004; Giménez-Gallego *et al*., 2021). Temperature can influence many developmental processes in grapevines, with higher temperatures accelerating them (e.g., the timing of budbreak, bloom and onset of fruit ripening), which is of particular concern in the face of climate change (Keller and Tarara, 2010; Parker *et al*., 2011). However, the relationship between temperature and development is not linear, and both low and high temperatures can be detrimental, limiting berry size and delaying ripening (Keller, 2020b). While ambient temperature plays a critical role, canopy temperature is also important. For example, bud temperature, rather than air temperature determines the timing of budbreak (Keller and Tarara, 2010).

In addition to the important role of temperature in vine development, it has a critical impact on vine transpiration. While transpiration increases with temperature, very high temperatures will lead to stomatal closure (Keller, 2020a). Stomatal closure due to, for example, water deficit, will also decrease photosynthesis due to decreased CO_2 availability (Chaves *et al*., 2008). Transpiration contributes to the cooling of the leaves, and by extension the canopy as a whole, and can be particularly important in sunlit leaves (Gates, 1964).

Many grapevines are irrigated and to efficiently manage water stress in both vines and other plants, the grower needs to know when water stress will begin and how much water to apply. Water status is also important in rain-fed vineyards where management practices are applied to minimise water stress. Canopy temperature can be used to assess plant water status using the crop water stress index (CWSI), which is calculated based on the difference between canopy and air temperature (Cohen *et al*., 2005). CWSI may be used in grapevines to determine the need for and effect of irrigation (Ahi *et al*., 2015). Thus, canopy temperature plays an important role in vine development and is a critical indicator of vine water status. How the shape and size of grapevine leaves interact with the environment to influence canopy temperature is poorly understood. Given that grapevine leaf shape is at least partly controlled by genetics (Chitwood *et al*., 2014; Demmings *et al*., 2019), the potential positive impact of particular leaf shapes or sizes on canopy temperature (such as keeping vine temperature low in hotter climates and reducing the need for irrigation) could be a desirable target for grapevine breeders. Based on this premise, we examined the relationship between grapevine leaf shape or size and canopy temperature.

MATERIALS AND METHODS

1. Experimental design

Leaves were sampled from seedlings of five biparental *Vitis* populations located in San Joaquin Valley, Madera County, California. As described in Migicovsky *et al*. (2022b), and copied here for convenience, the populations consisted of a total of 500 seedlings. Of these, 450 seedlings had DVIT 2876 as a parent, and the remaining 50 seedlings had DVIT 2876 as a grandparent. DVIT 2876 'Olmo b55-19' is a compound-leafed accession from the USDA-ARS National Clonal Germplasm repository, thought to have *Vitis piasezkii* Maximowicz as one of its parents (or grandparents) due to its leaf shape. Thus, all of the populations had one parent with compound leaves of the *V. piasezkii* type, and each population had a different second parent with non-compound leaves. The populations were created to examine variation in leaf lobing and the resulting progeny from each cross had a range of leaf shapes from very lobed to entire.

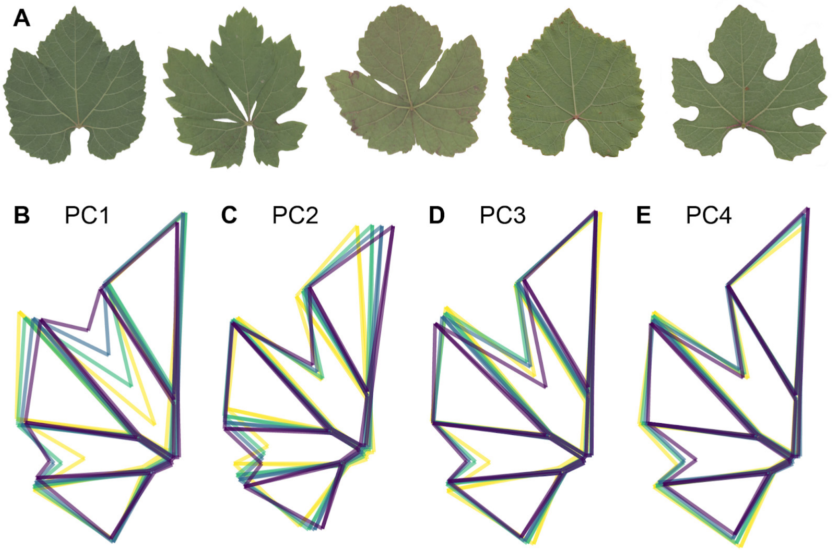

FIGURE 1. Real leaves and eigen leaves showing variation in shape across the populations sampled.

(A) A leaf from each of the five populations (Pop1 to 5 shown from left to right) showing the range of lobing present across the accessions. Given the extensive range of lobing within a population, the leaf shown is not representative of a particular population, but rather used to show the range across all populations. (B-E) For each PC quartile, a mean leaf is plotted, with the lowest PC quartile shown in yellow, increasing in colour to dark blue across quartiles. PC1 to PC4, explaining a total of 78 % of the variance in leaf shape, are shown.

Sampled populations (Figure 1A) comprised 125 individuals from a DVIT 2876 x unnamed *Vitis vinifera* selection cross (Pop1), 100 individuals from a DVIT 2876 x a different unnamed *Vitis vinifera* selection cross (Pop2), 150 individual from a DVIT 2876 x unnamed *Vitis* hybrid cross (Pop3), 75 individual from a DVIT 2876 x a different unnamed *Vitis* hybrid cross (Pop4), and 50 individuals from a seedling (DVIT 2876 x unnamed *Vitis vinifera* selection) x DVIT 3374 (*Vitis mustangensis* Buckley) cross (Pop5). The selections used in these crosses are unnamed, because they are the result of breeding crosses.

The vines were planted in 2017 with east/west row orientation. They were trained as high wire cordon (no foliage catch wire) with a west-pointing unilateral cordon, and were spur-pruned. Vine pest management corresponded to commercial standards for the region. The vines were irrigated using drip irrigation, ordinarily applied daily. Deficit irrigation was not carried out and the vines were irrigated with the aim of replacing the transpired and evaporated water.

2. Sampling

Three representative leaves, selected based on visual assessment of the vine, were collected and scanned from each vine throughout June and July in 2018, and again throughout June and July in 2019. For full details regarding leaf collection and scanning, see Migicovsky *et al*. (2022b).

Canopy temperature measurements were carried out twice in 2018 (19 July and 10 August) and 2019 (24 July and 1 August). On three of the four dates, the measurements were made from around 09:00 to 11:00, but on one date (24 July 2019) they were made from around 11:30 to 13:30. For this purpose, a handheld infrared thermometer (Extech 42515 InfraRed Thermometer) was used to measure the temperature of the canopy from the north-facing side of the vine. The Extech 42515 InfraRed Thermometer has a field of view (distance/spot) with a 13:1 ratio and can be used to make fast and non-contact measurements by holding the device and pointing it at the vine. The accuracy of the device for temperatures ranging from - 0.5 to 65 °C (31 °F to 150 °F) is ± 2.0 % rdg or ± 4.5 °F / 2.5 °C. To make canopy temperature measurements, the thermometer was scanned across the outside of the canopy by holding the device approximately 15 cm from the canopy and scanning slowly while measuring continuously. The mean canopy temperature was recorded for each vine.

In most cases, the exact time of the measurement was also recorded; however, in some cases, it was recorded every few vines. In these instances, the time of sampling was interpolated by dividing the difference in time between two measurements by the number of measurements made between those two times and adding it to the initial time.

For the purposes of this study, data were only included from vines from which canopy temperature measurements recorded at all four timepoints and at least one leaf was measured for shape in both 2018 and 2019. As a result, the total number of unique accessions across all time points used for the analyses were 388 out of the 500 vines initially planted. Of these, 375 had a total of 6 leaves measured (3 in each year) while the remaining 13 had a total of 4 or 5 leaves.

Weather data for each of the dates were downloaded from an on-site weather station, which included temperature measurements taken once per hour. Precipitation was also recorded, although there was no precipitation during the sampling days.

3. Data analysis

Image analysis of the leaf scans is fully described in Migicovsky *et al*. (2022b) and scans are available on Dryad (Migicovsky *et al*., 2022a). Briefly, leaves were analysed using 21 landmarks as previously described (Chitwood *et al*., 2016b; Chitwood *et al*., 2021; Bryson *et al*., 2020). Leaf area was calculated using the shoelace algorithm, which calculates the area of a polygon using the landmarks as vertices, following previously described methods (Chitwood *et al*., 2021). In addition, we calculated the ratio of vein to blade area of each leaf, as well as the degree of distal and proximal lobing. Following adjustment using a generalised Procrustes analysis in the shapes package in R (Dryden, 2021), principal components analysis (PCA) was performed to determine the primary sources of variation in leaf shape.

Subsequent analyses were performed in R; the code is available at the following GitHub repository: https://github.com/zoemigicovsky/grape_leaf_temp. All visualisations were performed using ggplot2 v3.3.5 (Wickham, 2016).

Although temperature measurements were made twice a year, leaves were sampled for shape analyses only once. For this study, morphometric values were averaged across measurements made on all the leaves sampled from a vine in a particular year in order to be able to link average leaf shape and size for that year with canopy temperature. In some cases, the vines included in this study had fewer than three leaves sampled; in these instances, the measurements were still averaged when more than one leaf was sampled.

Only three measurement temperatures exceeded 105 °F, and only one value was less than 64 °F, and thus, these were considered likely errors and removed from the dataset. Temperature measurements were converted from Fahrenheit to Celsius using the weather metrics version 1.2.2 package in R (Anderson and Peng, 2012) for downstream analyses.

Using the broom package in R (Robinson *et al*., 2021), a linear model was performed for each date, to determine the effect of time of sampling on canopy temperature (Equation 1):

Temperature ~ time

by extracting the residuals from this model. This approach was necessary, because ambient temperature increased throughout the period of sampling, and using residuals instead of raw temperature measurements allowed us to account for time of sampling on a particular day of sampling. Residuals from these models were used in all downstream analyses.

To perform subsequent analyses, we merged leaf morphology and area measurements from Migicovsky *et al*. (2022b) with residuals from the temperature model.

First, we performed a Type 2 Anova using the car R package v.3.0-11 (Fox and Weisberg, 2019). We used the following model (Equation 2), in which each of the principal component (PC) values are morphometric PCs calculated using the landmark data:

temperature residuals ~ population + date + PC1 + PC2 + PC3 + PC4 + PC5 + PC6 + PC7 + PC8 + PC9 + PC10 + PC11 + PC12 + PC13 + PC14 + PC15 + PC16 + PC17 + PC18 + PC19 + PC20 + ln(area) + vein to blade ratio + proximal lobing + distal lobing

Forty-two morphometric PCs estimated shape across the 21 homologous landmarks (each with an X and Y coordinate). However, only the first 20 morphometric PCs were used in the model, because cumulatively they explain 99.7 % of the variance in leaf shape. The percent variation was calculated for all terms by calculating the Sum of Squares for a particular term, divided by the Total Sum of Squares, then multiplied by 100. The results for significant terms ($p < 0.05$) were reported.

Since the highest amount of variance was explained by ln(area), scatterplots showing the relationship between ln(area) and the temperature residuals were plotted. To determine the correlation between these two measurements, a repeated measures correlation coefficient (r_{rm}) was calculated. The r_{rm} calculation accounts for the non-independence of sampling the same vines on four different days and was performed using the rmcorr R package version 0.4.5 (Bakdash and Marusich, 2021). Lastly, we used hourly weather data from an on-site weather station to calculate the average, minimum and maximum temperatures on each day of sampling.

RESULTS

In this study, we build on the findings of Migicovsky *et al*. (2022b) to explore the consequences of leaf shape variation on vine canopy temperature across 388 unique accessions resulting from five biparental crosses. Each biparental cross had one parent with compound leaves and a different second parent with non-compound leaves, thus these accessions varied primarily in terms of lobing (Figure 1) and also differed in leaf area.

The first objective of this study was to account for the time of sampling on canopy temperature, as measured using a handheld infrared thermometer. To do this, we calculated a linear model for temperature ~ time of sampling, and determined the value of each vine on a particular date, based on the residuals from that model (Figure 2). The slope of the line differed between dates, indicating that both date and time of sampling influenced canopy temperature.

After accounting for the time of sampling, we estimated whether leaf shape and size significantly influenced variation in temperature residuals. Temperature residuals were used, because they allowed us to estimate whether a vine was cooler or hotter than expected, at a given time of sampling. We performed a Type 2 Anova using Equation 2, and four factors were found to be significant ($p < 0.05$): three morphometric PCs and the natural logarithm of leaf area (Table 1). In all the cases, less than 2.5 % of the variance was explained by a given factor, with 0.5 % or less explained for the morphometric PCs. Distal lobing, the primary source of variation in shape in the populations, was not significant

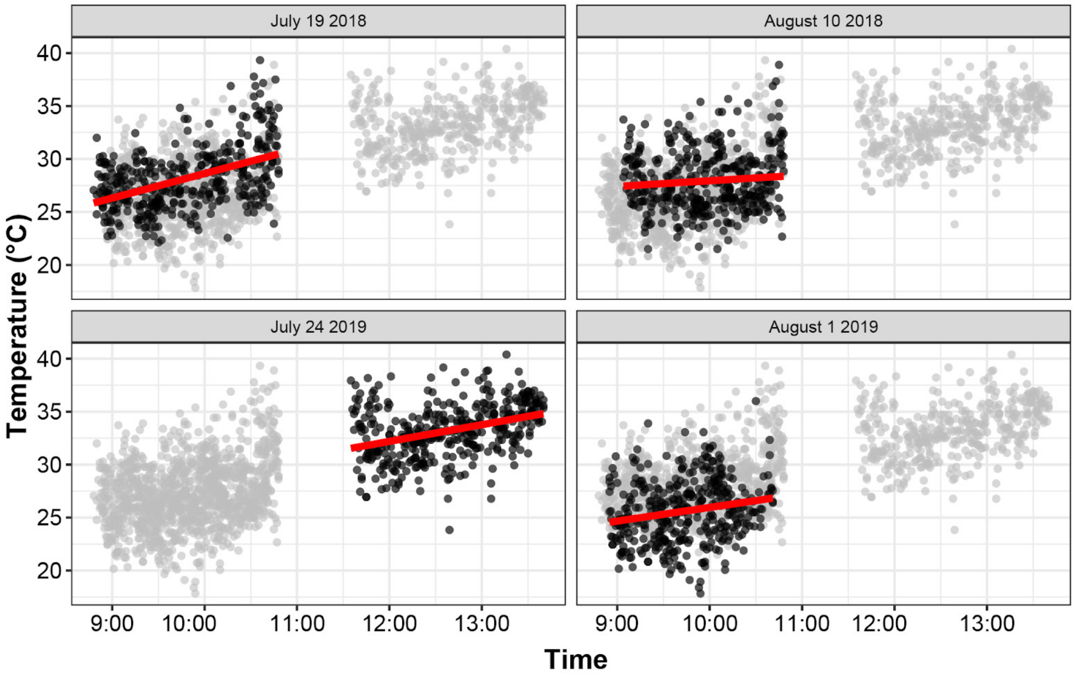

FIGURE 2. Scatterplots modeling canopy temperature vs time of sampling on each of the four dates the measurements were taken.

Each dot represents the temperature of a particular vine at a particular sampling day and time (n = 388). For each date, the measurements taken on that date are black, while the measurements from the remaining three dates are plotted in grey. The linear model for a particular date is shown using a red line.

TABLE 1. Percent variance explained by factors of interest estimated using a linear model (Equation 2) and Type 2 Anova.

	ln(area)	PC14	PC18	PC8
Variance explained of temperature residuals (%)	2.13 %	0.46 %	0.32 %	0.29 %

Only factors which explained the significant amount of variance ($p < 0.05$) are included. Significant factors are sorted left to right from most variance explained to least variance explained.

(Migicovsky *et al*., 2022b). In comparison, leaf area explained 2.13 % of the variance in temperature residuals, which was the highest amount of any significant factor. Overall, these results indicate that leaf size, and not leaf shape, had a stronger influence on the variation in canopy temperature.

Once we established a relationship between leaf area and canopy temperature, we used the repeated measures correlation coefficient to account for the non-independence of the four days of sampling and examined how the residuals from the temperature ~ time model change in response to leaf area (Figure 3). We found that leaf area and the residuals were significantly negatively correlated ($r = -0.178$, $p = 1.52 \times 10^{-12}$). This negative correlation indicates that vines with larger leaves had a canopy temperature which was cooler than expected, at a given time of sampling.

While the overall correlation is significant, this relationship was driven by the first three sampling dates. Regarding the weather data for these dates, the average temperature on the final date of sampling, 1 August 2019, was found to be cooler than the other three dates (24.6 °C in comparison to 26.9 to 28.1 °C) with the coolest max temperature value of 34.5 °C in comparison to 37.3 to 39 °C. A visual examination of the fitted temperature values, which were adjusted based on time of sampling, confirms that the canopy temperatures were lowest on 1 August 2019 (Figure 3).

DISCUSSION

On a global scale, smaller leaves are generally found at drier sites in warm regions in comparison to large-leaved species which are found in wet and hot environments. In wet and

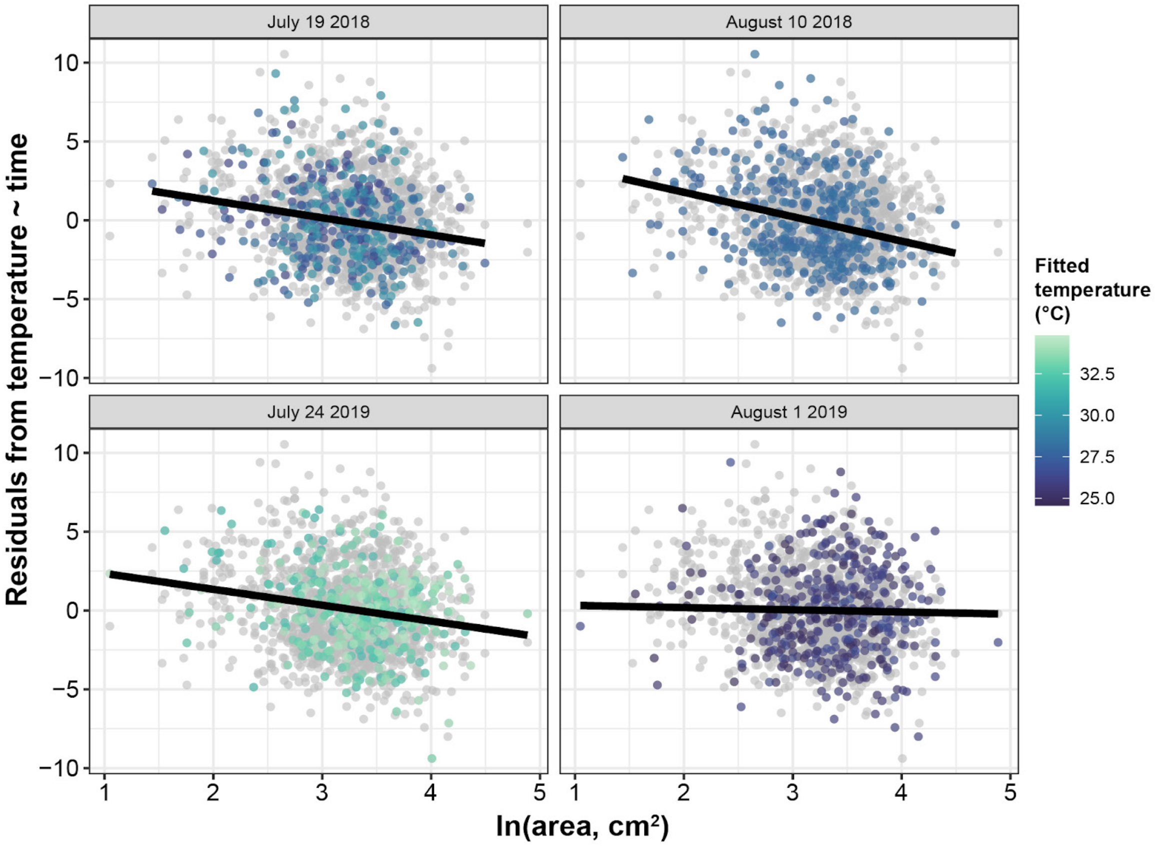

FIGURE 3. Scatterplot modeling the relationship between ln(area) and residuals from the linear model for temperature ~ time.

Each dot represents the measurement of a particular vine at a particular sampling day and time (n = 388). For each date, the measurements taken on that date are shown in the colour of the fitted temperature value, as shown in Figure 2, while the measurements from the remaining three dates are plotted in grey. The linear model for a particular date is shown using a black line, but the overall correlation was calculated using r_{rm} to account for the non-independence of the four days of sampling.

cold environments, species with smaller leaves predominate (Wright *et al*., 2017). The difference in leaf sizes based on access to water is due to the thicker boundary layer of large leaves, which makes them more reliant on transpirational water loss for cooling (Gates, 1968; Wright *et al*., 2017). In previous work, thermal imagery of 68 Proteaceae species was used to determine the effect of leaf size on leaf temperature, and temperature was found to increase significantly with leaf area (Leigh *et al*., 2016). Similarly, in another study examining the difference between canopy temperature and air temperature using trees from 18 different species in an urban environment, trees with smaller leaves had lower canopy-to-air temperature differences, indicating they remained cooler during the day than trees with larger leaves (Meier and Scherer, 2012). Both these studies provide evidence that smaller leaves are generally cooler than larger ones.

Although the climate in Madera County, California is dry and hot, vines were fully irrigated and thus water was not a limiting factor. The cooler temperature of the canopy for vines with larger leaves in our study may indicate that transpirational cooling was occurring at a higher rate, reducing the risk of high temperatures in comparison to vines with smaller leaves. In our study, the vines were fully irrigated, thus the larger leaves were not limited in terms of water, allowing more transpirational cooling to occur when necessary due to increased leaf area. This relationship seems particularly probable when considered in the context of the ambient temperatures on days of sampling: on the coolest day, 1 August 2019, the temperature was on average over 2 °C cooler, with a maximum temperature of 2.8 to 4.6 °C less than the other dates; this was the same sampling day on which no relationship between leaf size and temperature residuals was found, indicating that this trend is strongest on hotter days when the transpirational cooling benefits resulting from large leaves may be greater; by contrast, this may not occur on cooler days when the vines are under less stress from temperature. However, we did not measure transpiration rate in our study and, while temperature is known to influence the vapour pressure deficit and therefore transpiration, future work should measure transpiration rate directly.

In one study of an Australian heat wave, some vines were covered with a protective layer to reduce heating while others were exposed. In the exposed vines, transpiration increased nearly three-fold while photosynthesis decreased by 35 %, delaying ripening and causing a reduction in berry quality (Greer and Weedon, 2013). In another study, controlling canopy temperatures resulted in a significant reduction in yield for vines with the warmed temperature treatment (Greer and Weedon, 2018). These results clearly show the negative impact of excessive increases in canopy temperature. The ability to maintain a cooler canopy temperature on hot days is desirable for grape growers, and our preliminary findings indicate that this may be possible with larger leaves.

While we measured both leaf size and shape in our study, we did not measure canopy architecture, photosynthesis or water use efficiency, as the heterogeneity of individual seedling canopies is very high, which substantially complicates such observations on unreplicated seedlings. While overall reduction in canopy temperature was found to occur with larger leaves, this may not be due to leaf size, but may instead be due to differences in the openness of the canopy.. We also did not measure the distance from the ground that the temperature measurements were taken; trunk height has been shown to have an impact on temperature in previous work (De Rességuier *et al*., 2023). Our measurements were taken on the north side of the vines; therefore, while all the vines were measured on the same side using the same method, and the vines were small and unlikely to cause shading, we may have detected stronger temperature differences, if we had measured from the south side due to the direct solar radiation received. Future work should also include measurements of total leaf area to determine if vines with smaller leaves have smaller total leaf area, allowing sunlight to penetrate the canopy in comparison to vines with larger leaves and a greater total leaf area. In addition, leaf area index is a useful metric of canopy density and may be altered through management practices such as shoot thinning and leaf removal, altering light interception (Wang *et al*., 2019). As alternatives to making manual measurements of leaf area index, which is time-consuming, mobile digital devices (Orlando *et al*., 2016) or remote sensing (Illniyaz *et al*., 2022) can be used.

There are also limitations to the accuracy of handheld infrared thermometers. For example, the distance that the thermometer is held from the target may impact accuracy, and if it is held too far away, the target may include areas not of interest, or external sources of light may impact the results; it should be noted that it was not possible to quantify the magnitude of this potential source of error in our study.

Future work making use of thermal remote sensing imaging (Still *et al*., 2021) would be particularly useful in order to estimate the canopy temperature across numerous vines simultaneously, thus reducing the effects of timing and human error on the results. Indeed, thermal imaging paired with the CWSI could ultimately facilitate precision viticulture by assessing water stress and the need for irrigation; work in this area is ongoing (Tanda and Chiarabini, 2019).

CONCLUSION

This temperature study built on our previous work, in which we determined that more highly lobed leaves compensated for what would otherwise result in a reduction in leaf area by having longer veins and a higher vein to blade ratio (Migicovsky *et al*., 2022b). In this study, we determined that vines with larger leaves had cooler canopies than anticipated. Taken together, these findings indicate that it may be possible to select for large, highly lobed leaves in order to reduce canopy temperature and improve photosynthetic capacity, while still allowing light to permeate the canopy. However, due to the limitations of this work, future studies are still required in order to measure canopy density and transpiration rate in vines of differing leaf sizes and shapes. Ultimately, it may be possible for grape breeders to harness variation in grapevine leaf size for reduction in canopy temperature which would be valuable target for future cultivar improvement.

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CONFLICTS OF INTEREST

PC is employed by E. & J. Gallo Winery. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential 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.

DATA AVAILABILITY

All data and code used in this study can be found on GitHub (https://github.com/zoemigicovsky/grape_leaf_temp). All original scans used in this study are available from Dryad (Migicovsky *et al*., 2022a).

AUTHOR CONTRIBUTIONS

PC generated the seedlings and supervised the maintenance of the vineyard. ZM, JFS, PC, and DHC conceived of the initial idea for this study. ZM coordinated the research. ZM, JFS, ZH, LLK, AL, MM, and KW sampled the leaves for this study. AF, MK, AJM, PC, and DHC acquired the funding for this study and provided supervisory support. ZM performed the data analysis with input from DHC. ZM wrote the first draft of the manuscript, which all authors read, commented on, and edited.

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