Vein-to-blade ratio is an allometric indicator of leaf size and plasticity

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PREMISE: As a leaf expands, its shape dynamically changes. Previously, we documented an allometric relationship between vein and blade area in grapevine leaves. Larger leaves have a smaller ratio of primary and secondary vein area relative to blade area compared to smaller leaves. We sought to use allometry as an indicator of leaf size and plasticity.

METHODS: We measured the ratio of vein-to-blade area from the same 208 vines across four growing seasons (2013, 2015, 2016, and 2017). Matching leaves by vine and node, we analyzed the correlation between the size and shape of grapevine leaves as repeated measures with climate variables across years.

RESULTS: The proportion of leaf area occupied by vein and blade exponentially decreased and increased, respectively, during leaf expansion making their ratio a stronger indicator of leaf size than area itself. Total precipitation and leaf wetness hours of the previous year but not the current showed strong negative correlations with vein-to-blade ratio, whereas maximum air temperature from the previous year was positively correlated.

CONCLUSIONS: Our results demonstrate that vein-to-blade ratio is a strong allometric indicator of leaf size and plasticity in grapevines measured across years. Grapevine leaf primordia are initiated in buds the year before they emerge, and we found that total precipitation and maximum air temperature of the previous growing season exerted the largest statistically significant effects on leaf morphology. vein-to-blade ratio is a promising allometric indicator of relationships between leaf morphology and climate, the robustness of which should be explored further.

KEY WORDS: allometry; ampelography; grapevine; leaf morphology; leaf shape; Vitaceae; Vitis.

Correlations with climate and physiological constraints have been proposed to explain the staggering diversity of leaf shapes and sizes. Just over a century ago, large, entire leaves were first observed to predominate in the tropics, while smaller, more dissected leaves are more commonly found in temperate regions (Bailey and Sinnott, 1915, 1916). The correlation between leaf serrations and present climate conditions can be used as indicators of ancient climates (Wolfe, 1978; Wilf, 1997; Peppe et al., 2011). Beyond serration correlations, scaling relationships constrain the relationship between blade and vein area across evolution. In mature, larger leaves, primary and secondary veins are wider but with less vein density compared to smaller leaves (Sack et al., 2012). These scaling laws have implications for leaf physiology, especially with respect to leaf hydraulic conductance, that offer a framework for the relationship between form and function in leaves and possibly explain major shifts in the evolutionary history of plants (Scoffoni et al., 2011; Sack and Scoffoni, 2013).

To understand how broad patterns across plant evolution and geological time arise, ultimately, we must consider how leaves develop and how individual plants respond to the environment over a lifetime of growth. Distinguishing genetic, environmental, and interaction effects are critical to explain patterns in leaf shape and size observed from individual to global scales. Hypotheses about the mechanisms underlying plasticity in leaf shape have long been proposed (Goebel, 1908), but only careful work disentangling distinct processes—such as leaf ontogeny from the heteroblastic series—can inform us to what extent when development and how plasticity arises (Jones, 1995). Ontogenetic contingency—how the developmental program of an individual plant responds to changes in the environment during different phases of its life—can lead to disparate morphological outcomes in the same genotype or individual exposed to different environments (Diggle, 1994, 1995, 2002). Ontogenetic contingency is not important for this study with
respect to the question of whether morphological outcomes are functional or reflect developmental constraint, but rather to more precisely identify how the environment alters leaf shape in long-lived perennials from year to year (Chitwood et al., 2016a, b). Species with buds initiate organ primordia long before they emerge, presenting the opportunity to study developmental constraints related to bud packing (Edward et al., 2016) and differences in preformed and neofomed leaf shape (Spriiggs et al., 2018). Grapevines are a special case in which organ primordia are initiated the year before they emerge, allowing the influences of environment on developmental plasticity (such as cluster counts and, in this study, leaf shape and size) to be separated across years (Khanduia and Balasubrahmanyam, 1972; Srinivasan and Mullins, 1976; Vasquez and Fidelibus, 2006; Guilpart et al., 2014). As long-lived perennials often maintained in vineyards where it is easy to identify individual vines, grapevines also permit longitudinal studies of leaf shapes arising from the same vines across years.

Morphometric techniques, such as elliptical Fourier descriptors (EFDs; Kuhl and Giardina, 1982; Chitwood et al., 2014; Chitwood and Otoni, 2017) and topological data analysis (TDA; Li et al., 2018) allow comparative studies of leaf shape across large evolutionary distances (Chitwood and Sinha, 2016). The morphology of grapevine (Vitis spp.) leaves, however, uniquely allows their shape to be measured using a large number of homologous landmarks (Bookstein, 1997). Nearly all leaves in the genus Vitis, whether simple or compound, possess seven major veins with established nomenclature (OIV, 2018): a midvein (or L1), two distal veins (or superior, L2), two proximal veins (or inferior, L3), and two petiolar veins (or L4) that branch off the proximal veins forming a petiolar sinus encircling the petiolar junction. These veins also define the distal (or superior) and proximal (or inferior) sinuses of the leaf (Fig. 1). Ampelometry (“vine” + “the process of measuring”) has long recognized the homologous morphology between grapevine leaves and leveraged it for purposes of classification and identification. After the European phylloxera crisis, Louis Ravaz proposed using angles of the petiolar veins to classify new resistant rootstocks and blasty) on leaf morphology have been studied in detail previously (Chitwood et al., 2016a, b), assigned species identities are ignored for these reasons, and because the effects of species and development (both ontogeny and heteroblasty) on leaf morphology have been studied in detail previously (Chitwood et al., 2016a, b), assigned species identities are ignored in this study. Here, each of the 208 vines was treated as an individual with repeated measures in a longitudinal study across 4 years to focus on interannual plasticity.

Leaves were collected as stacks in the vineyard keeping track of shoot order and stored in labelled plastic bags with cut holes for ventilation. All leaves longer than ~1 cm starting from the tip of a single shoot were sampled. Leaves were kept in a cooler during the collection and scanned within 1–2 days. Leaves were arranged on a large format Epson Workforce DS-50000 scanner (Tokyo, Japan) in the order collected from the shoot with a ruler for scale and a small number near each leaf to indicate the node of origin. Files were named by the vine ID, followed by a sequential lowercase

![Figure 1](image-url) Vein-to-blade ratio is an allometric indicator of leaf size. (A) For each year, a single leaf from each node for each vine is sampled. Example leaves matched by node (counting from the shoot base, as these leaves are the first to emerge and most mature) from a Vitis acerifolia vine across the 4 years studied are shown. (B) Leaves from nodes 2, 4, and 6 (left to right) counting from the growing tip of a V. cinerea shoot to demonstrate exponential decreases in vein-to-blade ratio as leaves expand. On the left side of each leaf, vein (purple) and blade (green) areas calculated from homologous landmarks are shown. On the right side of the largest leaf, sinuses and lobe tips are indicated with associated ampelometric nomenclature. (C) Landmarks from the leaves in (B) but scaled to comparable areas. Note that the ratio of vein-to-blade area decreases as leaves expand. (D) Square root of blade area, (E) square root of vein area, and (F) natural logarithm of the ratio of vein-to-blade area vs. year as boxplots. (G) Scatter plot of vein-to-blade ratio vs. ln of total leaf area. The relationship is largely linear but is best explained by a fifth-order polynomial (indicated in black). (H) Fifth-order polynomial models of vein-to-blade ratio vs. ln of total leaf area for each year with 95% confidence limit bands. Median leaf area is indicated by a black line and model values of vein-to-blade ratio for each year are shown. For all panels: 2013, salmon; 2015, green; 2016, turquoise; 2017, purple.

### MATERIALS AND METHODS

#### Germplasm, sample collection, and scanning

Leaves were sampled each year from the USDA germplasm repository in Geneva, New York during the second week of June. Vines from 11 species and four hybrids were analyzed: V. riparia (67 vines), V. labrusca (32 vines), V. cinerea (25 vines), V. rupestris (24 vines), Vitis acerifolia (12 vines), V. amurensis (10 vines), V. vulpina (9 vines), V. aestivalis (6 vines), V. palmata (3 vines), V. coignetiae (2 vines), Ampelopsis glandulosa var. brevipedunculata (1 vine), V. ×andersonii (1 vine), V. ×chantinii (1 vine), V. ×do-aniana (1 vine), V. ×novae-angliae (1 vine). Additionally, 13 vines with unassigned identity (indicated as Vitis spp.) were analyzed. Previous work has genetically characterized these accessions (Klein et al., 2018). Grapevine accessions show complex hybridization and segregation in and among species, as well as large amounts of intraspecific morphological variation. For these reasons, and because the effects of species and development (both ontogeny and heteroblasty) on leaf morphology have been studied in detail previously (Chitwood et al., 2016a, b), assigned species identities are ignored in this study. Here, each of the 208 vines was treated as an individual with repeated measures in a longitudinal study across 4 years to focus on interannual plasticity.

Leaves were collected as stacks in the vineyard keeping track of shoot order and stored in labelled plastic bags with cut holes for ventilation. All leaves longer than ~1 cm starting from the tip of a single shoot were sampled. Leaves were kept in a cooler during the collection and scanned within 1–2 days. Leaves were arranged on a large format Epson Workforce DS-50000 scanner (Tokyo, Japan) in the order collected from the shoot with a ruler for scale and a small number near each leaf to indicate the node of origin. Files were named by the vine ID, followed by a sequential lowercase
letter if multiple scans were needed to accommodate the leaves of a shoot. We returned to the same vines sampled in 2013 (Chitwood et al., 2016a) and 2015 (Chitwood et al., 2016b) to again sample all leaves from a shoot in 2016 and 2017 (Fig. 1A). All original scans used in this study are available from the Dryad Digital Repository (Chitwood et al., 2020). Leaves were analyzed using 21 landmarks to measure vein width in order to determine allometric relationships between vein and blade area (Fig. 1B, C).

Landmarking

The 21 landmarks were placed by hand using the point tool in ImageJ (Abrámoff et al., 2004) as in Fig. 1C on either side of the leaf. For the 8412 leaves in this study, 176,652 landmarks were analyzed, or 353,304 values. Landmarks were placed sequentially for each leaf in a scan and saved as a text file of x and y coordinate values. Landmarks for each scan were visualized using ggplot2 (Wickham, 2016) in R (R Core Team, 2019) to detect mistakes, and if found, the landmarking was redone.

Data analysis

R scripts (R Core Team, 2019) used for analyzing the data in this study can be found at github: https://github.com/DanChitwood/grapevine_climate_allometry. All visualizations were made using ggplot2 (Wickham, 2016). For correlating leaf shape and size with climate variables without statistical artifacts, leaves were matched such that, for each year, there was exactly one leaf for each node (counting from the shoot base) from each vine (Fig. 1A). The result is that an equal number of leaves are represented for each year and that each leaf has a counterpart from the same vine and node for each other year. After matching, the number of leaves analyzed drops from 8412 leaves to 6284, and the number of vines analyzed remains 208. For calculating the number of leaves per shoot and overall shoot area, all leaves (not matched by node) from the 208 vines were used. Leaf, blade, and vein areas were calculated using landmarks as vertices of a ploygon using the shoelace algorithm, also known as Gauss’s area formula. Originally described by Meister (1769), the vertices of a polygon are cross-multiplied to calculate the area comprising a polygon and then subtracted from the surrounding polygon to find the polygon area within using the following formula (where n is the number of polygon vertices defined by x and y coordinates):

$$\frac{1}{2} \left| x_1 y_2 + x_2 y_3 + \ldots + x_{n-1} y_n + x_n y_1 - x_2 y_1 - x_3 y_2 - \ldots - x_n y_{n-1} - x_1 y_n \right| .$$

To select an appropriate allometric model, we used polynomial functions of different orders to model the natural log of the ratio of vein-to-blade area as a function of the natural log of overall area. After the second order model, decreases in the Akaike information criterion (AIC) and increases in the adjusted $R^2$ were minimal, but significant differences were still detected until the fifth order model, which was ultimately selected (Table 1).

The relationship between leaf morphology traits and climate variables was tested using the repeated measures correlation coefficient (Bland and Altman, 1995a, b) using the rmcorr package in R (Bakdash and Marusich, 2017). With exactly one leaf per vine per node per year—such that each leaf is part of a group of four across years—each of 208 vines can be treated as individuals in a longitudinal study (especially if only one node is analyzed at a time, as in Fig. 2). Correlation assumes independence of measures, yet independence is violated in repeated measures, in which multiple leaves come from the same vine across years. The repeated measures correlation coefficient (rm) accounts for this non-independence using analysis of covariance (ANCOVA) to adjust for inter-individual variability. Parallel regression lines with the same slope but varying intercepts calculate the best linear fit for each individual vine. The resulting correlation coefficient $r_{rm}$ is like a Pearson correlation coefficient except that it accounts for non-independence by evaluating the overall intra-individual association between two variables (Bakdash and Marusich, 2017).

Climate data were retrieved from the Northeast Weather Association website via Cornell University (newa.cornell.edu, retrieved 28 September 2019). Daily summaries of minimum, average, and maximum temperatures, leaf wetness hours, and precipitation were analyzed for the Geneva, New York station at latitude 42.83, longitude −77.01. The USDA Vitis germplasm collection is 4 miles away at latitude 42.89, longitude −77.01. Daily data was averaged across two periods for each growing season: “previous year” and “current year”. The previous year period is inclusive of March to November of the previous year. The current year period is inclusive of March to June of the year the leaves were harvested. The months December through February were excluded because temperatures are below freezing during this time in Geneva, New York (USA).

RESULTS

For the data set matched by vine and node (Fig. 1A), blade area varied by year, showing almost identical distributions between 2013 and 2015 and decreasing in 2016 and 2017 (Fig. 1D). Vein area varies less than blade by year (Fig. 1E), consistent with our previous work demonstrating that increases in leaf size are mostly driven by blade expansion while vein area remains more constant. As a consequence, the proportion of vein area decreases exponentially relative to blade as a leaf expands, creating an allometric relationship between vein and blade area in a leaf (Chitwood et al., 2016b). We plotted the natural log of the ratio of vein-to-blade area by year and found that it varies dramatically relative to blade or vein area alone (Fig. 1F), supported by Kruskal–Wallis rank sum test $\chi^2$ values (square root of blade area, square root of vein area, and natural log of vein-to-blade ratio area by year $\chi^2$ values equal 369.56, 83.453, and 1531.8, respectively). Vein-to-blade ratio is inversely correlated with leaf size. The relationship appears strongly linear when both vein-to-blade ratio and leaf area are natural log-transformed (Fig. 1G). However, there are nonlinear relationships at extreme leaf area values (small and large). Polynomial models of different orders were
tested to explain this allometric relationship, and a fifth order model was found to best suit the data (Table 1). Fifth order models were created for each year (Fig. 1H), showing shifts in vein-to-blade ratio between years that correspond with differences in blade area (Fig. 1D). Because the model is only approximately linear, vein-to-blade ratio intercepts at the median leaf area value were calculated to quantify the shifts between years. The median leaf area intercept for vein-to-blade ratio rank for the four years (−2.93, −2.87, −2.71, and −2.58 for 2015, 2013, 2016, and 2017, respectively; Fig. 1H) correspond to the median value ranks for blade area across the four years as well (Fig. 1D).

To determine the environmental factors most closely associated with leaf shape and size changes in individual vines across years, we correlated vein-to-blade ratio with climate variables (total precipitation, maximum air temperature, average air temperature, and minimum air temperature). Climate variables are divided between “previous year” and “current year”, representing averaged daily values from March to November of the previous year and March to June of the current year (the year of harvest), respectively. Purple, positive correlation; orange, negative correlation; light gray, coefficients with a Bonferroni-adjusted $p$ value ≥ 0.05.

FIGURE 2. Repeated measures correlation coefficient of traits with climate variables. Repeated measure correlation coefficient values ($r_{rm}$) between traits (vein-to-blade ratio by node, leaf count, and shoot area) and climate variables (total precipitation, leaf wetness hours, maximum air temperature, average air temperature, and minimum air temperature). Climate variables are divided between “previous year” and “current year”, representing averaged daily values from March to November of the previous year and March to June of the current year (the year of harvest), respectively. Purple, positive correlation; orange, negative correlation; light gray, coefficients with a Bonferroni-adjusted $p$ value ≥ 0.05.

used to predict cluster counts for the coming year (Vasquez and Fidelibus, 2006). Because we matched nodes by mature leaves counting from the base of the shoot, a large proportion of the leaves analyzed in this study were not neoformed the year of harvest and potentially influenced by the climate of the previous year in which they initiated. Considering that the buds are frozen during the winter (Londo and Kovaleski, 2017, 2019; Kovaleski et al., 2018; Kovaleski and Londo, 2019), we chose two windows over which we averaged daily climate variables: “previous year” is the average inclusive of March to November of the previous year, “current year” inclusive of March to June of the year of harvest.

Calculating the repeated measures correlation coefficient ($r_{rm}$), which uses ANCOVA to account for inter-vine variance by calculating regression lines with a common overall slope but varying intercepts, we examined how the 208 vines in this study respond to climate variables using vein-to-blade ratio (Fig. 2). The highest absolute $r_{rm}$ values were negative correlations of individual vine vein-to-blade ratio with previous year total precipitation and leaf wetness hours, which are absent for the current year. This correlation was strong and consistent across nodes for total precipitation but became stronger for leaf wetness hours for leaves farther from the base, indicating interaction with the heteroblastic series or leaf ontogeny. Correspondingly, overall leaf count and shoot area were positively correlated with previous year total precipitation and leaf wetness hours, but not for the current year. Maximum air temperature shows a similar pattern to total precipitation and leaf wetness hours, correlating with the previous year but not the current, but in the opposite direction. High maximum temperature values in the previous year correspond to high vein-to-blade ratio values and low leaf count and shoot area in the next year. Average and minimum air temperature $r_{rm}$ values follow the same trends as maximum air temperature, except show significant correlation in the current year as well.

The repeated measures correlation coefficient ($r_{rm}$) fits a regression line for each individual such that all lines have the same slope but different intercepts. To help visualize the data from Fig. 2, we plotted regression lines for each vine (and unlike Fig. 2, for all nodes together) for vein-to-blade ratio vs. climate variables for the previous and current years. Unlike $r_{rm}$, these regression lines can vary in slope and intercept for each vine and only represent a visualization to better understand the data, not a statistical test (Fig. 3). This visualization is intended to convey that behind the highly negative $r_{rm}$ values for previous year total precipitation, there is a strong trend among vines to show a negative relationship between vein-to-blade ratio and previous year total precipitation; similarly for previous year maximum air temperature, except the relationship is positive.
FIGURE 3. Data visualization of trends of the relationship of vein-to-blade ratio with climate variables of the previous and current years. Unlike the $r_m$ values in Fig. 2, these plots are only visualizations and not statistical tests, aggregate all node data together, and show regressions lines in which both slope and intercept can vary for each vine. (A) Previous year and (B) current year regression lines for each vine and each node of vein-to-blade ratio vs. average total precipitation (top) and average maximum air temperature (bottom). As indicated in the figure, previous year represents average daily climate values from March to November of the previous year, and current year represents average daily climate values from March to June of the current year. Colors for previous/current years: 2012/2013, salmon; 2014/2015, green; 2015/2016, turquoise; 2016/2017, purple.
(Fig. 3A). For the current-year total precipitation and maximum air temperature visualizations, the trends are more neutral (Fig. 3B), reflective of the corresponding non-significant $r_{an}$ values (Fig. 2).

DISCUSSION

This study has extremely high replication ($n = 208$ vines) of repeated measures of leaf shape across 4 years, perfectly balanced by node. Leveraging this replication, we asked how vein-to-blade ratio changes with respect to different climate variables across 4 years. It is important to emphasize that the large number of vines in this study and a statistical approach that accounts for repeated measures on individuals (Bland and Altman, 1995a, b; Bakdash and Marusich, 2017) provide abundant power to determine how vein-to-blade ratio commonly responds across vines to different climatic variables for the years analyzed. The strong repeated measure correlation values reported are not robustly predictive of how vines in general respond to climate. With only 4 years of climate data, the possibility of spurious relationships is high. What the results do show, unequivocally, is that vein-to-blade ratio is an allometric indicator of leaf size that changes similarly, year-to-year, across many vines. The correlations suggest that the previous year total precipitation and maximum air temperature positively and negatively, respectively, correlate with leaf size, leaf count, and shoot area in the next (Fig. 2). Given the development of grapevine leaves and inflorescences across years and the known influence of climate on leaf size and shape across geological time, our results show that vein-to-blade ratio is an important measure of the allometric relationships underlying these processes. As a ratio of two measures of leaf area that proportionally diverge in opposite directions as a leaf expands, vein-to-blade ratio is more sensitive to leaf size than just area, as it is a composite measure of allometry. Measuring how vein-to-blade ratio responds across more years and environmental conditions, and in different species, is an important next step to determine its generalizability and to untangle the contributions of plasticity to observed diversity in leaf shape and size.

That climate would alter grapevine morphology is not unanticipated. The environmental sensitivity of grapevines to climate variability is long recognized and has been measured in many ways. Several unique developmental, life history, and cultivation characteristics of grapevines lend themselves to the study of the relationship between plants and climate (Carmona et al., 2008). Records of grapevine harvest dates going back centuries exist because of the cultural importance of wine to Europeans and have been correlated with (and used to predict) past temperature anomalies (Chuine et al., 2004; Menzel et al., 2005; Meier et al., 2007). This is possible because many of the same wine grape varieties that existed centuries ago still exist today because of clonal propagation, permitting historical longitudinal analyses. Similarly, predictions of the impact of future climates on grapevine growth and wine quality have been made (Jones et al., 2005; De Orduna, 2010; Hannah et al., 2013). Because grapevines are long-lived perennials, typically harvested over longer periods than other crops, larger investments are made when choosing the location to establish a vineyard.

The long-term economic implications of climate change for grapevines and the wine industry are evident in the very data presented in this study. We can report effects of precipitation because the vineyard we sampled is not irrigated. An analysis of the effects of the historic 2016 New York drought reveals that rainfed crops in the region needed to increase their water use by 500–600% (Sweet et al., 2017). From this perspective, unlike annuals, grapevines remain a constant as the climate changes around them. Because the grapevine phenotype is a summation of past and current environmental effects, it can be leveraged to study how plants respond to climate change. However, it is also a liability to viticulture and the wine industry. Even over the short-term, the effects of climate linger longer than in annuals, and the environment of the previous year cannot be discounted when studying annual variation, yield, or crop quality in grapevines (Khandua and Balasubrahmanyam, 1972; Vasquez and Fidelibus, 2006; Guilpart et al., 2014).

The ability to calculate vein-to-blade ratio is permitted by the unique morphology of grapevine leaves, that contain a multitude of homologous landmarks found across nearly all Vitis species (Fig. 1B, C). The use of landmarks in grapevine leaves is inspired by ampelometry, a more than century-old tradition of using geometric morphometrics to quantify and classify grapevine varieties (Ravaz, 1902; Galet, 1979, 1985, 1988, 1990, 2000). Yet, despite the uniqueness of the approaches presented here to grapevines, our results have implications for the relationship between plants and climate in general. The correlation between leaf size and toothed margins with the climate has long been studied in present day and ancient plants (Bailey and Sinnott, 1915, 1916; Wolfe, 1978; Wilf, 1997; Peppe et al., 2011). For both these traits, allometry plays an important role. Leaf size is of course fundamental to allometric relationships, and the theory of its functional significance is well established (Parkhurst and Loucks, 1972). Many hypotheses have been put forward regarding the functional significance of teeth (Nicotra et al., 2011), but as vascularized extensions of the margin that are predominate in leaf primordia (Jones et al., 2013) and diminish in relative size as the leaf expands, allometry and specifically vein-to-blade ratio are predominate morphometric features. Lobes and teeth might be a developmental constraint resulting from the packing of leaves in buds (Edwards et al., 2016), as is the case for grapevine. Recently, the allometry of teeth for the grapevine leaves from the 2013 and 2015 growing season described in this study was undertaken, noting their phenotypic plasticity across years, developmental context, and the meaningfulness of measuring traits used for paleoclimate reconstructions in a living germplasm collection (Baumgartner et al., 2020). The relationship between vein and blade is a fundamental feature of all leaves, an indicator of development itself that is modulated by both evolutionary and environmental forces.

CONCLUSIONS

By tracing the movement of pinpricks arranged as a grid on a young fig leaf, Stephen Hales documented the allometric growth of leaves in 1727: “By observing the difference of the progressive and lateral motions of these points in different leaves, that were of very different lengths in proportion to their breadths” (Hales, 1727, p. 344). Here, we documented a strongly linear allometric relationship between the ratio of vein-to-blade area with grapevine leaf size. Vein-to-blade ratio in grapevine leaves varies across years more strongly than leaf size itself. Blade area expands exponentially faster than vein area, making it a sensitive indicator of leaf size and shape. Using vein-to-blade ratio as an allometric
indicator, we documented the effects of climate on grapevine leaf morphology across 208 vines of North American Vitis species in a 4-year study, showing that precipitation and maximum air temperature of the previous year affect leaf size in the next. Our results show how leaf size and shape in grapevines varies year to year through allometry similarly across vines and has implications for monitoring the relationship between plants and climate in the past, present, and future.

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AUTHOR CONTRIBUTIONS

D.H.C. and J.P.L. conceived of the project and experimental design. J.M., Z.M., and MF collected data. D.H.C. and R.V. designed statistical analyses. D.H.C. analyzed data and wrote the paper with input and editing from J.M., Z.M., M.F., R.V., and J.P.L.

DATA AVAILABILITY

The original scans of leaves used for this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.zkh189377 (Chitwood et al., 2020). All data and code used in this study can be found on github (https://github.com/DanChitwood/grapevine_climate_allometry).

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