The shapes of wine and table grape leaves: An ampelometric study inspired by the methods of Pierre Galet

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Societal Impact Statement
Leaf shapes are critical to the identification of grapevine varieties. Historically, measures of grapevine leaves were used to enforce appellation law and leaf shape is used to this day to distinguish economically important clones that genetic analyses fail to discriminate. The ampelometry (“vine” + “process of measuring”) of Pierre Galet (1921-2019), through quantitative measurements and hand-drawings, illuminated the beauty of grapevine diversity for the world. Here, mathematical methods rigorously quantifying hand-drawings of grapevine leaves are presented, with implications for how we document and preserve the stunning diversity of plants we so readily see with our eyes.

Summary
• People have an innate ability to recognize different patterns in among plants. Quantifying these differences, that we assimilate so effortlessly with our senses, is more challenging. Grapevines are a special case in which leaf shape has been critical to identify varieties correctly. The distinct morphology of grapevine leaves lends itself to the application of mathematical approaches that quantify shape.
• Here, corresponding points on every grapevine leaf (landmarks) and equidistant points between landmarks (pseudo-landmarks) were used to capture intricate, local features in grapevine leaves: the curvature of veins, lobes, and sinuses and the shapes of serrations. Using these points, averaged leaf shapes for 60 varieties of wine and table grapes were calculated that quantify shape to the same resolution as hand drawings.
• The overall morphological similarity of each variety to the other classified the leaves into two discrete groups: (i) deeply lobed and (ii) more entire—corresponding to the measurements of sinus depth put forward by the ampelographer Pierre Galet. Using the system of Galet, landmarks, and pseudo-landmarks were converted into relative distance and angle measurements. Using a high number of landmarks and pseudolandmarks increased the accuracy of predicting variety correctly, compared to using a finite number of landmarks alone.
• The ability to identify correctly a vine variety from leaf shape will have significant implications for the wine industry, from ensuring correct scion and rootstock
1 | INTRODUCTION

At a glance, differences in shape, color, and growth habit can be used to differentiate and categorize plants. The ability to measure what a plant is—its phenotype—provides an objective record of its biologically and economically relevant features that can be used for scientific or commercial applications. Leaf shape is one of the most conspicuous features of plant morphological diversity (Chitwood & Sinha, 2016). Leaf shape varies across geologic time scales with climate (Bailey & Sinnott, 1915, 1916; Peppe et al., 2011; Wilf, 1997; Wolfe, 1978), is constrained by developmental pressures (Edwards, Spriggs, Chattelet, & Donoghue, 2016), and evolves in response to environmental and physiological effects both in nature (Schmerler et al., 2012) and in agricultural systems (Rowland et al., 2020). Despite morphological diversity underlying the biological, economic, and aesthetic value of plants to humanity, quantifying shape and form remains challenging. Morphometrics is a set of diverse mathematical techniques to measure morphology. A traditional morphometric technique for measuring shape is landmark analysis (Bookstein, 1979; Gower, 1975). Landmarks are corresponding homologous points found on every sample, and pseudo-landmarks are placed between these homologous points to create more continuous representations of curves and outlines. As described below, palmate leaves such as grapevine, that have a consistent number of lobes, sinuses, and other corresponding points, are amenable to this powerful type of analysis (Chitwood, Klein, et al., 2016; Chitwood et al., 2014; Chitwood, Rundell, et al., 2016; Demmings et al., 2019; Klein et al., 2017). In the absence of landmaks, a Fourier decomposition of the outline can be used (Iwata & Ukai, 2002; Kuhl & Giardina, 1982), and the resulting harmonic series is used for statistical analysis using an Elliptical Fourier Descriptor (EFD) framework (Andres et al., 2017; Chitwood et al., 2012, 2013; Chitwood & Otoni, 2017a, 2017b). Finally, when comparing disparate leaf shapes, for example across seed plants (Li et al., 2018), neither landmark nor EFD analyses can accommodate the large amounts of shape variation, and other methods, such as Topological Data Analysis (TDA) must be used (Amézquita, Quigley, Ophelders, Munch, & Chitwood, 2020).

The leaves of grapevines are exceptional because of corresponding points found in every leaf that form a coordinate system. If possible, using landmark-based analyses are preferable to other morphometric techniques, as data points correspond to features on the leaf that can be identified intuitively (rather than abstractions, such as harmonic series or topological signatures) and interpreted within the context of leaf shape itself. Each grapevine leaf has a midvein, two distal/superior veins, two proximal/inferior veins, and two prominent veins that branch off of the proximal veins called petiolar veins (Figure 1). The major primary veins of the leaf terminate at the lobe tips. The secondary veins that branch off the primary terminate at the blade margin, forming serration patterns between consecutive branches. Using the ordered branching pattern that emerges from the primary veins defining each lobe, a hierarchy of venation and serrated teeth along the blade can be defined. The spatial correspondence between all grapevine leaves enables sophisticated morphometric approaches. These approaches have historically been used to discriminate grapevine species and varieties.

In the mid-1800s, an aphid crossed the Atlantic from North America attacking the root system of Vitis vinifera (domesticated grape) vines in France decimating the wine industry. North American grapevine species rootstocks were resistant to the pest and ultimately provided the solution to the blight that restored wine production. The rootstocks were new to European viticulturists, yet correctly identifying and selecting the correct rootstock variety was vital. The roots themselves and the grape clusters were of little use to identifying varieties, so viticulturists turned to the leaves. The field of ampelography (“vine” + “writing”), concerning the discrimination of grapevine varieties, was born and chief among its techniques was ampelometry (“vine” + “process of measuring”), a method of measuring leaf shape. Hermann Goethe (Goethe, 1876, 1878) first proposed to use the angle of the petiolar sinus to identify North American grapevine species, but Louis Ravaz expanded upon the idea and established a foundational system for quantifying the shapes of grapevine leaves in his Les vignes américaines: Porte-greffes et producteurs directs (1902). A focus on not only the angle, but the shape and contour of the petiolar sinus in hand-drawings was made. The overall shape of the leaf (reniform, orbicular, cordiform, cuneiform, or truncate) was described in terms of ratios of lengths and angles between veins, and codified into discrete groups based on ranges of values. Even the serrations were described in terms of length-to-width ratio and convex/concave shapes.

While Ravaz popularized the system of ampelometry, Pierre Galet turned it into an artform (Galet, 1979, 1985, 1988, 1990, 2000). In his works, Galet hand draws a representative leaf for each variety, a format that guides the reader’s eyes to the major veins and their relationship to the blade. Extensive information regarding the history, geography, and phenology of vines, and the appearance of the inflorescence and growing tip, in addition to descriptions of leaf hirsuteness, contour, and surface, verbally recreates the experience of encountering a vine in the reader’s mind. Like Ravaz, Galet created a discretized system of values to describe ratios of vein lengths and...
angles (the Galet formula), but also created measuring devices (the Galet ruler and protractor) to easily quantify values in the vineyard and compare to ideal values for each variety that he published. Galet, through careful observation, a quantitative mindset, detailed description, encyclopedic knowledge, hand illustration, and an artist's eye effectively transcribed the immense phenotypic variation among grapevine species into books that have since inspired and taught those who work with and love grapevines.

Others took the analysis of grapevine leaves in a more mathematical direction. The homologous coordinates in every grapevine species leaf allows even minor veins to be hierarchically accounted for. By counting teeth, where veins terminate, and measuring leaf shape, Acúrcio Rodrigues developed a method for calculating an average leaf shape (Rodrigues, 1939, 1941a, 1941b, 1952a, 1952b). María-Carmen Martínez developed the method further, and through statistically measuring numerous angles, lengths, and numbers of teeth for a variety, developed a model for reconstituting a visual representation of an average leaf (Martinez & Grenan, 1999). The method opened the door for statistical analysis of grapevine leaf morphology (Martinez, Loureiro, & Mantilla, 1995), discriminating cultivars (Gago, Santiago, et al., 2009; Santiago, Boso, Gago, & Martinez, 2009).

Another approach to measuring shape is landmarks (Bookstein, 1997): homologous x and y coordinates that are found in every leaf. Using Procrustean methods, landmarks can be superimposed through translation, rotation, scaling, and reflection minimizing the distance of all points to each other (Gower, 1975). Although landmarks capture less of the overall shape of an object, because they are finite, high levels of replication are possible. Tens of thousands of grapevine leaves have been measured using landmarks. Previous analysis of wine and table grape varieties in the USDA Wolfskill National Clonal Germplasm Repository in Winters, California (USA) used 10 landmarks along the distal and proximal lobe tips and sinuses (excluding the petiolar veins) on both sides of the leaf to measure the genetic basis of leaf shape (Chitwood et al., 2014). A set of 17 landmarks including the petiolar vein and the first major secondary branch points of the midvein, distal vein, and proximal vein on both sides of the leaf was used to explore leaf shape in a developmental and evolutionary context using wild grapevine species in the USDA Geneva, New York (USA) germplasm collection (Chitwood, Klein, et al., 2016), to find conserved loci regulating leaf shape in multiple interspecific hybrid mapping families (Demmings et al., 2019), and to document inter- and intra-species leaf shape variation between V. riparia and V. rupestris clones at the Missouri Botanical Garden, St. Louis (USA; Klein et al., 2017). A set of 21 landmarks capturing the widths of the primary veins and their major secondary branching veins for half of the leaf was used to reanalyze

**FIGURE 1** The Galet formula and Procrustean methods. (a) A scan of a Zinfandel leaf over which raw data have been plotted. Data are saved as pixel coordinates and this image is an example of overlaid data on photographs to verify tracing results (see Chitwood et al., 2020a). On the right side of the leaf landmarks (orange dots) and pseudo-landmarks (magenta lines) are plotted. Landmark + pseudo-landmarks form vectors, which are stylistically indicated as black arrows and the names of which are indicated. “p,” “d,” and “m” refer to “proximal”, “distal”, and “midvein” regions of the leaf. Along the blade, the base of each arrow and its tip indicate the beginning and end of a vector. Arrows arising from the tips of veins indicate the direction of vein vectors that originate at corresponding branch points within the leaf and terminate at the tips. On the left side of the leaf, the nomenclature of Galet is provided. Midvein, distal/superior, proximal/inferior, and petiolar veins are called L1, L2, L3, and L4 respectively. Superior and inferior sinuses are shown, as well as angles S’ and S between L1/L3 and L1/L4 respectively. A, B, and C are ratios of the lengths of L2, L3, and L4, respectively, to L1; r is the ratio of length to width; and Su and In are the distances to the petiolar junction (O) of the superior (Su) and inferior (In) sinuses divided by the length of the L2 and L3 respectively. (b) Detail of the “ds” and “ma” vectors of the distal sinus region shown as dotted and solid arrows, respectively. If the lobes of a leaf overlap, the vectors cross each other while preserving vector identity. This allows overlap in averaged leaf shape calculations and reflects the overlap seen in reality.
| Wine Variety                        | A | B | C | r  | S' | S | Su | ln  |
|-----------------------------------|---|---|---|----|----|---|----|-----|
| Chasselas cioutat                 | 0 | 4 | 6 | 3  | 6  | 9 | 5.5| 4.5 |
| Zinfandel/Primitivo               | 0 | 4 | 6 | 3  | 6  | 9 | 5.5| 4.5 |
| Gewürztraminer                    | 0 | 4 | 6 | 3  | 6  | 9 | 5.5| 4.5 |
| Burger/Monbadon                   | 0 | 4 | 6 | 3  | 6  | 9 | 5.5| 4.5 |
| Chenin blanc                      | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Sauvignon blanc                   | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Merlot noir                       | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Saint Emilion/Ugni blanc          | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Grand Noir de la Calmette         | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Olivette noire                    | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Terret gris                       | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Cinsaut                           | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Muscat blanc à Petits Grains      | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Mondeuse noire                    | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Ribier                            | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Cardinal                          | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Sémillon                          | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Mataro/Mourvèdre                  | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Muscat Hamburg                    | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Syrah                             | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Alivette blanche                  | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Almeria                           | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Clairette blanche                 | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Cornichon blanc                   | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Durif/Petite Sirah                | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Béclan                            | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Cabernet Franc                    | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Dabouki/Malaga blanc              | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Emperor                           | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Chasselas Doré                    | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Muscat of Alexandria              | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Folle blanche                     | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Italia                            | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Meunier                           | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| White Riesling                    | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Gamay Noir à Jus Blanc            | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Müller-Thurgau                    | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Cabernet Sauvignon                | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Carignane                         | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |

**Group II**

| Wine Variety                        | A | B | C | r  | S' | S | Su | ln  |
|-----------------------------------|---|---|---|----|----|---|----|-----|
| Grenache                          | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Sylvaner                          | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Perla di Csaba                    | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Trousseau                         | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Aligoté                           | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Chardonnay                        | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Colombard                         | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Aramon                            | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Sauvignon vert/Sauvignonasse      | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Perlette                          | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Thompson Seedless                 | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Calmeria                          | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Flame Tokay                       | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Alicante Bouschet                 | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Tannat                            | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Malbec                            | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Dattier                           | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Melon/Muscadet                    | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Black Corinth                     | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Pinot noir                        | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
| Traminer/Savagnin                 | 0 | 3 | 5 | 3  | 5  | 8 | 5  | 3.5 |
the USDA Geneva, New York (USA) germplasm across two years on the same vines to test for climate-induced changes in leaf shape plasticity (Chitwood et al., 2020; Chitwood, Rundell, et al., 2016).

Although insightful and permitting the analysis of thousands of leaves, a finite number of landmarks fails to capture the curves, serrations, and intricate details of grapevine leaf shape that are readily apparent. The analysis presented here captures these finer features of grapevine leaf shape by (a) maximizing the number of landmarks used and (b) capturing curves and local features (such as serrations) by using a large number of pseudo-landmarks between them. Some landmarks, such as the distal sinus, vary more between varieties than others, and should be chosen if comprehensive phenotyping is not possible. However, using a large number of landmarks + pseudo-landmarks, variety can be more accurately predicted, regardless of the method used (landmarks or angle/distance-based methods). This additional shape information can be used to better discriminate grapevine scion and rootstock varieties or among clones that cannot be distinguished genetically, preventing misplantings and ensuring fidelity in the viticulture and wine industries.

2 | MATERIALS AND METHODS

2.1 | Plant material and photography

Over 9,500 leaves from more than 1,200 wine and table grape varieties (Vitis vinifera) were collected at the USDA Wolfskill National Clonal Germplam Repository in Winters, California (USA) from May 28 through June 1, 2011. As previously described in Chitwood et al., 2014, photographs of the leaves were taken using a remote-controlled camera attached to a copy stand and placing the leaves under nonreflective glass to flatten them on top of a light box to highlight venation. A total of 4,950 photos were taken, named by vine location that serves as a key for variety identity. In the previous study, the shapes of all leaves were measured using 10 landmarks. This study examines a small subset of 60 varieties (using a replication of four leaves) in intensive detail that were also described by Pierre Galet in A Practical Ampelography (Galet, 1979, 1985). The original photographs used for this study can be found on the GitHub repository (Chitwood, 2020a). Each photo is named by its vineyard location at the USDA Wolfskill repository followed by letters if multiple images were taken for the sampled clones, which can be used to determine variety identity using the associated key.

Only 60 varieties using a replication of four are analyzed in this study, but all of the > 4,950 photos of 9,500 leaves of more than 1,200 wine and table grape varieties can be downloaded at Dryad (Chitwood, 2020b).

2.2 | Landmarking, tracing, and visual checks

24 landmarks corresponding to the tips of midvein, distal vein, and proximal vein (3 points), the distal and proximal sinuses (2 points), the petiolar junction (1 point), and the three major secondary branch points for the midvein, distal vein, and proximal vein (9 points) and their termination along the blade margin (9 points) were used. The landmarks form the framework for the rest of the points in the analysis, as they are homologous features found in every leaf. Landmarks are indicated as orange dots in Figure 1a. Between the landmarks, pseudo-landmarks were used to capture continuous curves, indicated in magenta in Figure 1a. The landmarks + pseudo-landmarks create vectors, ordered sets of spatial coordinate pixel values, with an origin and an end. Sometimes the lobes of grapevine leaves overlap. To accommodate this feature of leaves the vectors, too, can overlap (Figure 1b).

Accommodating the overlap of grapevine leaf contours is a significant ampelometric problem that has been explicitly addressed in the past using other methods than presented here (Diaz, 2017). The vectors are as follows: m, from the petiolar junction to the tip of the midvein; d from the petiolar junction to the tip of the distal vein; p from the petiolar junction to the tip of the proximal vein; p1 (the petiolar vein), d1, and m1 from the first secondary branch point of their respective primary veins to the termination of the vein at the margin; p2, d2, and m2 from the second secondary branch point of their respective primary veins to the termination of the vein at the margin; p3, d3, and m3 from the third secondary branch point of their respective primary veins to the termination of the vein at the margin; pa, da, ma along the margin from the beginning of their respective lobe to the termination of p1, d1, and m1, respectively; pb, db, mb from the termination of pa, da, and ma, respectively, to the termination of p2, d2, and m2, respectively; pc, dc, mc from the termination of pb, db, and mb, respectively, to the termination of p3, d3, and m3, respectively; pd, dd, md from the termination of pc, dc, and mc, respectively, to the tips of the proximal, distal, and midveins, respectively; ps and ds from the tip of the proximal and distal veins, respectively, to the midpoint of the proximal and distal sinus respectively. The vectors are visualized as arrows in Figure 1.

Vectors were traced by hand in ImageJ using the segmented line tool with fitted splines (Abrámoff, Magalhães, & Ram, 2004). The set of x and y coordinates for each vector were saved as individual tab-delimited.txt files named by (a) the photo ID of the leaf indicating the vineyard position of the vine it was collected from, (b) an enumerating value 1 through 4 specifying which of four leaves for the variety the data corresponds to, and (c) which vector the data file represents. These files, the raw data, are available on GitHub (Chitwood, 2020a). Tracing all data for a single leaf took approximately 15 min. Methods to automate tracing of shape data are feasible at this time and increasing the numbers of leaves.
analyzed would be impactful. However, such image processing is difficult to implement and beyond the scope of this manuscript. Because the data were traced by hand, it was important to visually verify its accuracy, especially to ensure that vector identities had been correctly recorded and formatted for subsequent analyses. Analyses were undertaken using the Python modules NumPy (Oliphant, 2006), pandas (McKinney, 2010), and Matplotlib (Hunter, 2007) to plot the data on the actual photo. The code for plotting vectors onto the original photo and visual checks for each of the 240 leaves analyzed in this study can be found on GitHub (Chitwood, 2020a).

### 2.3 Interpolation and Procrustes analysis

Once data for all 240 leaves were collected, an appropriate number of points to interpolate for each vector was determined. Procrustes analysis requires corresponding points in every sample. For the 24 homologous landmarks, this condition is already met, but for the landmarks + pseudo-landmarks, an equal number of equidistant points for each vector must be calculated. A function to retrieve the overall distance of a vector path was created using the numpy. ediff1d function (consecutive differences between elements of an array) to calculate Euclidean distance and the numpy.cumsum function (cumulative sum of an array) to calculate the cumulative distance. For each vector, its total sum distance across all leaves was calculated, as well as the overall distance for all vectors for all leaves.

The total number of landmarks + pseudo-landmarks apportioned to a vector was based on its relative total distance. The total number of landmarks + pseudo-landmarks was chosen at 6,000. This was an arbitrary decision to select a number as high as possible so that pseudo-landmarks were so close as to create approximately-continuous curves and capture local details, such as serration shape but still low enough that computationally intensive Procrustes analyses were feasible on a laptop computer. Due to rounding, the final number of landmarks + pseudo-landmarks was 5,999. With assigned numbers of points to every vector, interpolation was used to calculate equidistant pseudo-landmarks between landmarks that inclusively comprise the vector. A function was created using the scipy (Virtanen et al., 2020) interp1d function to interpolate the correct number of equidistance points for each vector. The code used to interpolate points and the interpolated points themselves can be found on GitHub (Chitwood, 2020a).

With corresponding points between all leaves, a Procrustes analysis could be performed. Generalized Procrustes Analysis (GPA) minimizes distances between corresponding points through translation, rotation, scaling, and reflection to an arbitrarily selected reference shape. The resulting mean shape for the superimposed points is calculated and becomes the new reference if the Procrustes distance to the reference does not meet a minimum threshold (Gower et al., 1975). GPA was performed using the procGPA() function from the package “shapes” (Dryden & Mardia, 2016) in R (R Core Team, 2019). GPA was first performed for the four leaves for each variety producing mean shapes and superimposed Procrustes coordinates. The Procrustes mean shape and coordinates were used for plotting. The procdist() function from “shapes” was used to calculate the Procrustes distance between each pair of mean shapes and the results saved as a pairwise distance matrix. The hclust() function in R using the “mcquitty” method was used to hierarchically cluster varieties based on the pairwise distance matrix and overall morphological similarity. The code for performing a Procrustes analysis for each variety and outputs can be found on GitHub (Chitwood, 2020a).

A GPA was also performed for all 240 leaves. The outputs include an overall Procrustes mean shape, super-imposed Procrustes coordinates for all leaves, and eigenvalues and eigenleaves (theoretical leaf shapes representing shape variation along principal component axes) from a PCA. The superimposed Procrustes coordinates of all leaves and the mean shape were plotted together. The code for the Procrustes analysis for all 240 leaves and the outputs can be found on GitHub (Chitwood, 2020a).

### 2.4 Data analysis

To calculate allometry for each line segment (the differential growth of features relative to each other in relation to organ size), distances between all points were converted to cm using the pixel to cm scale measured for each leaf. The lm() function in R was used to model the natural log of the distance from each point to the next as a function of the natural log of the overall distance for each leaf. The slopes and residuals were saved. Slope values for each point were projected onto the Procrustes mean leaf and were visualized using ggplot2 (Wickham, 2016). Importantly, because landmarks + pseudo-landmarks are equidistant from each other for each vector, the slope values within each vector for allometry calculations are nearly equal. The standard deviation of the residuals for each point was also calculated and plotted onto the mean leaf.

To calculate the statistical contribution of each landmark and pseudo-landmark to discriminating leaves by variety, the Euclidean distance of each point to the corresponding point of the mean leaf was calculated. The distance of each point to the mean was then modeled as a function of variety using the kruskal.test() function. The test statistic and p-value were saved. The p-value was adjusted using the Benjamini-Hochberg method (for multiple test adjustment), and plotted on the mean leaf.
FIGURE 4  Leaf shapes by variety. Four leaves for each variety with superimposed Procrustes coordinates (left, gray), the mean leaf (middle, magenta, and orange), and one example leaf overlaid with coordinates (right) are shown. Leaves are in the same order as presented in the hierarchical clustering in Figure 2, continued from Figure 3
Figure 5  Leaf shapes by variety. Four leaves for each variety with superimposed Procrustes coordinates (left, gray), the mean leaf (middle, magenta and orange), and one example leaf overlaid with coordinates (right) are shown. Leaves are in the same order as presented in the hierarchical clustering in Figure 2, continued from Figure 4.
FIGURE 6 Allometry and variability between varieties and their prediction. (a) Superimposed Procrustes coordinates for all leaves (gray) and overall mean leaf (magenta and orange). (b) Allometric values for each coordinate projected onto the mean Procrustes leaf. Points are colored by slope of a fitted line for the natural log of the given point to the next divided by the natural log of the overall total distance of the leaf. (c) Mean leaf with coordinates colored by the standard deviation of the residuals for each coordinate for the allometric relationship described in B. (d) Mean leaf with coordinates colored by $-\log_{10}$-values (Benjamini-Hochberg multiple test adjusted) for a Kruskal–Wallis test for the Euclidean distances of each point to the mean leaf modeled by variety. Values failing to meet the adjusted significance value of $p = .05$ are shown in gray. (e) A plot of the distance of each coordinate to the petiolar junction divided by the midvein length versus the angle of each point from the midvein (the angle defined by the tip of the midvein, the petiolar junction, and the point of interest). The mean leaf defined by angle and distance coordinates is shown in blue. (f) Three morphometric methods are compared: only landmarks (24 landmark values, orange), the Galet-inspired method (angle and distance transformation, teal), and all Procrustes points (the 5,999 landmarks + pseudo-landmarks, lavender). The overall accuracy of predicting variety using the indicated number of PCs for each method is plotted. The number of PCs that yielded the maximum accuracy ultimately used for prediction is shown (27 for only landmarks, 42 for Galet, and 54 for all Procrustes). (g) The $-\log_{10}$ value of the proportion of variance explained by each of the PCs for each of methods is shown. Again, the number of PCs used for prediction that yielded the maximum accuracy is indicated.

To predict variety from leaf shape, datasets were first converted into orthogonal components using Principal Component Analysis (PCA) with the prcomp() function in R. Transformation into orthogonal variables was a necessity before proceeding with Linear Discriminant Analysis (LDA) to avoid collinearity (a problem with the high number of landmarks + pseudo-landmarks with similar values used in this study). LDA was performed using the lda() function with the “MASS” package (Venables & Ripley, 2002). The cross-validated “leave-one-out” approach was used to predict the variety of each leaf using CV = TRUE. The confusionMatrix() function from the package caret (Kuhn, 2008) was used to calculate overall classifier statistics and estimates of accuracy from the resulting LDA model.

3 | RESULTS

3.1 | Morphological similarity, comparison to the results of Pierre Galet, and average leaf shapes

Using the pairwise Procrustes distance matrix of the overall morphological similarity of the average leaf of every variety to the other, a hierarchical clustering was performed to find groups of varieties with similar leaf shapes (Figure 2). Because the clustering reflects the minimization of the distance of 5,999 points for each variety to the other, it is difficult to interpret which features of the leaf most strongly contribute to a leaf resembling another. To help understand which shape attributes of the leaf contributed to the clustering signal, the measurements of Pierre Galet for each variety were analyzed (Galet, 1979, 1985). Each variety has values for the “Galet formula”, a method that measures the relative lengths of veins and their angles (Figure 1). The values A, B, and C measure the relative ratio of the lengths of L2, L3, and L4, respectively, to the L1. The variable $r$ is the ratio of length to width. $S'$ and $S$ are angles between the L1 and the L3 and L4 respectively. Su and In are the ratios of distances from the petiolar junction (0) to the superior and inferior sinuses, respectively, divided by the length of the L2 and L3 respectively. Ratios and angles are discretized into values 0–9 and can be measured using the Galet ruler and the Galet protractor. For ratios of primary veins A, B, and C, increasing values correspond to decreasing ratios. For length-to-width ratio $r$, increasing values correspond to increasing ratios. For angles $S'$ and $S$ increasing values correspond to increasing angles, and for measures of sinus depth Su and In, increasing values correspond to deeper sinuses. Comparing Galet formula values to hierarchical clustering, the overwhelming correspondence between the two datasets is sinus depth (Su and In; Figure 2). Excluding uniquely shaped varieties that cluster alone (Chasselas cioutat and Zinfandel/Primitivo indicated in gray because they lack Galet formula values, as well as Gewürztraminer Burger/Monbadon), two major groups of varieties arise. Group I leaves are deeply lobed and Group II leaves slightly lobed or entire.

One of the most impactful features of A Practical Ampelography (Galet, 1979, 1985) is Galet’s drawings. For each variety, Galet drew a representative leaf. While the Galet formula provided a means to quantify shape, the drawings capture the totality of information embedded in leaf shapes that we so easily take in with our eyes but defies measurement. The relationship of all angles comprising a leaf together, the curves of the primary and secondary veins, the shapes of the serrations, the shape of the petiolar sinus, and the overlap of lobes: these are features that impact the values of the Galet formula but are not fully captured by it. The drawings of Galet highlight the ampelographic features used to quantify grapevine leaves: namely, the veins and their relationship to the blade. By analyzing a high number of landmarks + pseudo-landmarks, these intricate features of grapevine leaves have been quantitatively captured. To create a statistical version of Galet’s drawings, the 5,999 coordinate values for the four leaves for each variety were superimposed and the average leaf calculated. Figures 3-5 show the superimposed Procrustes coordinates for the four leaves for each variety (left), the average leaf (middle), and one example leaf with its coordinates overlaid. Such visualization combines the best attributes of landmark-based analyses and hand drawings: the calculation of an average leaf and the visualization of variance using superimposed Procrustes coordinates adds statistical rigor that drawings lack, while the use of a high number of landmarks + pseudo-landmarks captures the continuous curves of veins and blade that a finite number of landmarks cannot.
Leaves in Figures 3-5 are displayed in the order of their clustering in Figure 2. At a glance, the deep lobing of Group I leaves in Figure 3 and Figure 4 can be compared to the more entire Group II leaves in Figure 5.

3.2 Allometry and the ability of each coordinate to discriminate varieties

In order to analyze the contributions of individual coordinates to global features of the leaf and variability between varieties, a Generalized Procrustes Analysis (GPA) was calculated for all 240 leaves. All superimposed coordinates were overlaid on the overall average leaf (Figure 6a). The mean leaf was subsequently used to project attributes of individual coordinates. Allometry (the differential growth of features in relation to organ size) was analyzed for each landmark + pseudo-landmark. Previously, we demonstrated strongly linear relationships between the natural log of primary vein area versus the natural log of blade area: smaller leaves have a higher vein-to-blade area ratio than larger leaves (Chitwood et al., 2020; Chitwood, Rundell, et al., 2016). To determine the allometric relationships for the coordinates used in this study, the natural log of the Euclidean distance of each point to the next was regressed against the overall Euclidean distance of all veins and blades. The slope for each coordinate was recorded and plotted on the mean leaf (Figure 6b). Because the distance between landmarks + pseudo-landmarks is equidistant, and because these points are apportioned between vectors on the leaf, the slope values within a vector are nearly identical. The distal/superior sinus had the largest slope values, demonstrating that relative to other segments of the leaf, the invagination of this region in deeply lobed varieties takes up a larger proportion of the overall leaf. The proximal side of the proximal/inferior sinus also has relatively high slope values. Although slight, for the mid and distal lobes, the slope is less at the tip and increases incrementally along the blade toward the base. This is consistent with the distal regions of the leaf and lobes initiating and developing before the proximal regions (Jones, Doughan, Gerrath, & Kang, 2013). To determine if there was a relationship between higher slope values and variability, the standard deviation of the residuals of the allometric regression were projected onto the mean leaf (Figure 6c). Again, the distal/superior sinus and the proximal side of the proximal/inferior sinus had the highest variability. Together, the results show that the invagination of the sinuses, especially the distal/superior sinus, across varieties is the most malleable part of the grapevine leaf contributing to variation in leaf shape.

To determine the ability of different coordinates to discriminate varieties, a Kruskal–Wallis test was used. The Euclidean distance of each coordinate to the mean leaf was calculated and modeled as a function of variety. If the replicated leaves of one or more varieties consistently varies from the mean leaf, the Kruskal–Wallis test statistic will be responsive. After multiple test adjustment, coordinates in the distal/superior sinus were found to be the most significant, especially the points in the middle of the sinus pocket (Figure 6d). The proximal/inferior sinus did not show similar variation between varieties, demonstrating that a strong allometric relationship (Figure 6b) is not necessarily indicative of variability. The mid lobe showed the least significant variation between varieties. Not only is the distal sinus an allometrically sensitive region of the leaf, but it is one of the strongest indicators of variety, consistent with the depth of sinus lobing differentiating the two main morphological groupings of grapevine leaves (Figure 2).

3.3 Comparing the ability of different morphometric methods to predict variety

The morphometric methods presented so far rely on a set of 5,999 equidistant landmarks + pseudo-landmarks that capture finer features, such as curves and serrations. Pierre Galet proposed a separate method of quantification, focusing on the ratios of lengths of lobes and relative angles between them (Figure 1). He even published idealized values for each variety (Figure 2) that could be compared with real world measurements by viticulturists using the Galet ruler and protractor. Without replication, there is no way to compare the methods of Galet to other morphometric techniques. In order to approximate the focus of Galet’s methodology on length ratios and angles, while preserving the continuous measurement of local features (such as curves and serrations) enabled by using a high number of landmarks + pseudo-landmarks, a ratio/angular transformation of the data was developed. For each coordinate 1) the ratio of its distance from the petiolar junction divided by the length of the midvein and 2) its angle from the midvein was calculated. Plotting the ratio of the distance from the petiolar junction against angle, features of the leaf are still apparent (Figure 6e). The mid lobe, as the point of comparison, lacks variability. But the farther from the mid lobe points lie, the more variation is observed. This is in part because of variation in the primary vein angles, which was a focus of the methodology of Galet and Ravaz. The petiolar vein, in particular, shows a large amount of angular variation relative to the midvein, verifying the long-term focus of ampelographers on the petiolar sinus as a source of identifying information between varieties.

With replication for three different methods (only the 24 landmarks, the Galet-inspired transformation to ratios and angles, and all 5,999 Procrustes-adjusted coordinates) the ability to predict variety from shape information can be compared. A Principal Component Analysis (PCA) was performed on all three datasets to reduce information into orthogonal components. This step was necessary to avoid the collinearity of points that are, by definition, colinear. A Linear Discriminant Analysis (LDA) was performed on increasing number of PCs using a cross-validated approach and the overall accuracy was recorded. Each method peaked in accuracy and then diminished (Figure 6f). For the only landmark method the peak in accuracy was at 27 PCs, for the Galet-inspired method 42 PCs, and for the all Procrustes coordinate method at 54 PCs. The amount of variation in the higher number PCs is miniscule.
still contain relevant information to discriminate between varieties. Plotting out the prediction from each dataset as a confusion matrix, especially for the only landmark dataset with lower accuracy, leaves tend to be most often confused within Groups I and II (Figure 7a). The increased accuracy of the Galet and all Procrustes methods is expected given the increased amount of information that is captured using a high number of landmarks + pseudo-landmarks (Figure 7b-c). The overall accuracy of the only landmarks method was estimated at 0.454 (95% confidence interval 0.390 to 0.519, \( p \)-value = \( 5.70 \times 10^{-125} \)), whereas the accuracy of the Galet method at 0.579 (95% confidence interval 0.514 to 0.642, \( p \)-value = \( 5.72 \times 10^{-179} \)) and the all Procrustes method at 0.629 (95% confidence interval 0.565 to 0.690, \( p \)-value = \( 2.04 \times 10^{-202} \)) shows that high numbers of landmarks + pseudo-landmarks—regardless of method—contributes to increased accuracy in predicting variety.

4 | DISCUSSION

Leaf shape has historical importance in grapevines. Had genotyping existed in the late 1800s, new rootstock varieties to combat phylloxera in Europe and the North American grapevine species from which they are derived would have been identified molecularly. However, molecular biology did not exist yet. To verify rootstock identity and enforce appellation laws, the earliest of ampelographers, Goethe and Ravaz, turned to the angles and shapes of the petiolar sinus. Before the concept had existed, a relationship between genotype and phenotype, based on leaf morphology, was used to enforce law and regulate trade. Pierre Galet took the concept further, extending a framework for measuring the ratios of vein length and their angles to capture overall leaf morphology, as well as cataloging shape through hand-drawings, allowing readers to appreciate the beauty of grapevine leaf diversity and its constituent features at a glance. María-Carmen Martínez examined the features of leaves in even greater detail, allowing averaged leaves to be reconstructed at the level of individual teeth along the margins and providing inspiration for landmark-based methods. Using landmarks, genetic, developmental, and environmental effects on leaf shape have been measured. Yet, the high replication that a limited number of landmarks permits misses the exquisite features of veins and blade, while drawing-based methods that holistically capture the leaf have until this point been difficult to quantify.
Using a high number of landmarks + pseudo-landmarks that capture continuous curves and intricate local features, powerful Procrustean-based methods can be used to measure leaf shape at a global level. A pairwise Procrustes distance matrix clusters leaves into two major categories: deeply lobed and more entire (Figure 2). These categories correspond to Pierre Galet’s measurements of sinus depth, showing that this feature especially is diagnostic of variety, even when varieties are measured on different continents and decades later. Calculating the Procrustean mean shape is a way to summarize drawings quantifying underlying replication, preserving local and global features to represent the ideal leaf for each variety without having to pick any particular individual one as an example (Figures 3-5). The distal/superior sinus contributes disproportionately to the variation in leaf shape that discriminates varieties, both through alometry and the conspicuous placement of the distal/superior sinus pocket (Figure 6a-d). The focus of Galet on the ratios of vein lengths and relative angles can be used to transform continuous coordinates while preserving the overall morphology of leaves (Figure 6e). Both the Galet-inspired transformation to ratios and angles and using all Procrustes-adjusted coordinates gives comparable overall accuracies of 0.579 and 0.629 respectively (Figure 6f-G, Figure 7). Both methods outperform using only 24 landmarks with an accuracy of 0.454, showing that the use of a high number of landmarks + pseudo-landmarks (and less the framework within which they are analyzed) leads to higher prediction rates through capturing intricate features of the leaf. Some of these landmarks (such as the distal sinuses) contribute more to the discrimination of grapevine varieties than others, but using all landmarks together significantly increases prediction accuracy. Although automated methods to trace vectors are beyond the scope of this manuscript, with the correct application of computer vision, they are feasible. Automating the extraction of high numbers of shape features from simple scans of grapevine leaves not only has implications for more comprehensively modeling phenotype as a function of genotype, but practically as well, to correctly identify rootstock and scion varieties and avoid costly misplantings.

The leaves of grapevines lend themselves to mathematical analysis and have served as artistic inspiration for as long as grapevines have been cultivated (Gago et al., 2014; Gago, Santiago, et al., 2009). But the measurement of leaf shape has continuing, economic repercussions to this day in the wine industry, valued globally at USD $302 billion in 2017 and projected to grow to $423 billion by the end of 2023 (Zion Market Research, 2018). Underpinning the success of the wine industry are varieties and rootstocks and scion varieties and avoid costly misplantings (Galet, 1979; Morton, 2019). Among clones, the selection of which is imperative for optimizing cultivation in different locales and conditions (Torregrosa et al., 2011), at best genotyping can be used for identification of some clones within a variety (Riaz, Garrison, Dangl, Boursiquot, & Meredith, 2002; Ye et al., 1998) and at worse they are genetically indistinguishable. In these cases, subtle phenotypic features of clones are used for identification, the shape of leaves among the principal ampelographic tools available (Martínez, Boursiquot, et al., 1997; Martínez, Grenan, et al., 1997). The ability to recognize by eye or quantify genetic variation in leaf shape can be extended to development (Bryson et al., 2020; Chitwood, Klein, et al., 2016), disease (Klein et al., 2017), herbicide damage (Morton, 2019), and responses to climate change (Baumgartner, Donahoo, Chitwood, & Peppe, 2020; Chitwood et al., 2020; Chitwood, Rundell, et al., 2016). The shape of a leaf is a narrative of its history. Quantifying shape and creating predictive models formalizes what ampelographers have done by eye for centuries, providing a way to scrutinize leaf morphology for the underlying factors that sculpt it. The morphometric methods described here maximize the features available to analyze within the grapevine leaf, approaching the predictive limits of shape analysis.

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