OENO One
VINE AND WINE OPEN ACCESS JOURNAL
By IVES International Viticulture & Enology Society

DOI: https://doi.org/10.20870/oeno-one.2022.56.3.3796

OPEN ACCESS

ORIGINAL RESEARCH ARTICLE

Whole-vine resources modify within-vine relationships between growth parameters and metabolites in *Vitis vinifera* L. cv. Cabernet-Sauvignon

Joanne Margaret Bennett Wisdom[1,2*] and John Anthony Considine[2]

[1] The University of Western Australia, The School of Agriculture and Environment, Perth, 6009, Western Australia, Australia
[2] The University of Western Australia, The Institute of Agriculture, Perth, 6009, Western Australia, Australia

*correspondence:
joanne.wisdom@uwa.edu.au

Associate editor:
Stefanos Koundouras

Received:
22 June 2020

Accepted:
26 July 2022

Published:
3 August 2022

This article is published under the **Creative Commons licence** (CC BY 4.0).

Use of all or part of the content of this article must mention the authors, the year of publication, the title, the name of the journal, the volume, the pages and the DOI in compliance with the information given above.

ABSTRACT

Fruit ripening on a perennial tree or vine is typically asynchronous and rarely investigated. In commerce, this is problematic as it impairs sampling to meet commercial maturity and quality standards at harvest. For grapevines, understanding within-grapevine variability in berry maturity will benefit precision management and harvest planning. It is accepted that variation in maturity is approximately equally allocated at the within- and between-vine scale. However, the mechanistic and ecological factors that cause functional variance are poorly understood and rarely documented.

This study aimed to identify structural and spatial within-vine attributes associated with berry composition at harvest related to available resources from the whole grapevine. Vegetative and reproductive biomass attributes within- and between-vines were analysed for cv. Cabernet-Sauvignon trained as a cordon, spur-pruned system using a Smart-Dyson trellis in a 'New World' industrial-scale vineyard. The vines were located in northern Margaret River, Western Australia. Variability in soluble solids, anthocyanins and phenolics were analysed for clusters and corresponding canopy characteristics.

Berry size was the best predictor of variance in maturity among sugar, anthocyanins and phenolics composition within individual vines. Smaller stems or fruit had greater variation in maturity than larger stems or fruit. However, the relationship between whole plant biomass and fruit maturity interacted at different scales; the first report for grapevines. Including different vine-biomass scales helped explain the heteroscedasticity observed when the individual vine effect was excluded from the analysis. These findings suggest that high vigour grapevines could benefit from differential management, regardless of harvest index. Furthermore, these findings may help explain the diversity of response to treatment effects such as cluster or leaf thinning reported previously for perennial fruit.

KEYWORDS: Resource allocation, carbohydrate partitioning, berry composition, vine-to-vine variance, within-vine variance, *Vitis vinifera*, grapevine growth

INTRODUCTION

Fruit ripening in grapevine is asynchronous within an individual vine and varies widely between vines within a management unit. Variation within the grapevine is commonly as large as that between grapevines (Carbonneau *et al*., 1991; Lefort *et al*., 1979; Pagay and Cheng, 2010; Rankine *et al*., 1962; Wisdom, 2018). Varieties with a propensity for high leaf biomass, such as Cabernet-Sauvignon, are more likely to exhibit internal variation in maturity (Wisdom *et al*., 2020). However, functional relationships between vegetative structures and fruit are rarely considered within- or between-vines. The allocation or partitioning of resources will likely differ depending on stored metabolites, yet this phenomenon is under-researched in grapevines (Zufferey *et al.,* 2012). Modelling the ripening processes within a grapevine is challenging because many analogous activities co-occur (Dai *et al*., 2011). Thus, understanding ripening patterns within a grapevine should improve our understanding of grapevine physiology and ultimately grapevine management.

Partitioning of resources among organs within a grapevine reflects the biophysics of the underlying processes: synthesis and utilisation, and processes driving the flow from source to sink. Grapevine is likely similar to willow (*Salix babilonica*) and the vast majority of woody trees that rely on mass flow in phloem vessels that are connected symplastically from source mesophyll to sink in vegetative organs and which possess open minor veins in source leaves (Gamalei, 1989; Rennie and Turgeon, 2009; Turgeon and Medville, 1998). The ripening grape berry differs however, changing from symplastic unloading to apoplastic at véraison (Zhang *et al*., 2006). While this differentiation of process directs solutes preferentially to the berry, scale and spatial influences are likely to impact partitioning of solutes between organs within an individual vine, together with temporal influences likely to impact variation in the onset of véraison within and between clusters.

Assimilate accumulation is determined by three confounding characteristics of the vine (de Cortázar-Atauri *et al*., 2009). First, the capacity to provide assimilates, which —as with annual plants—depends on leaf size and number (Winkler, 1958), but is supplemented by the translocation from reserves especially during the period from bud burst to anthesis (Clingeleffer and Krake, 1992; Coombe, 1987; Hardie and Considine, 1976). Second, the efficiency or rate of metabolite production in leaves: orientation, light intensity, exposure, temperature and stomatal aperture (García de Cortázar-Atauri *et al*., 2005; Poni *et al*., 1994; Reshef *et al.*, 2019). Third, competition between permanent storage organs and growth influences the assimilate pathway (Dai *et al*., 2010; Zhu *et al.*, 2019). Specifically, sugar accumulation depends on available carbohydrates and the duration of fruit ripening, whereas anthocyanins (and therefore likely phenolics) are affected by climatic conditions and canopy structural effects that influence the light environment and drive metabolic processes (Dai *et al.*, 2010; Rienth *et al.*, 2021; Shahood *et al.*, 2020).

Distal shoot dominance may be responsible for ripening trends related to distance from the crown in cane-pruned systems (Belvini *et al*., 1978; Carbonneau *et al*., 1991), explained by morphology management and its association with acrotonic growth. However, the direction of the trend is not always consistent; thus, inferences made from studies on cane-pruned vines should not be extrapolated to spur-pruned vines (Belvini *et al*., 1978; Carbonneau *et al*., 1991; Lefort *et al*., 1979; Wisdom *et al.*, 2020). Spur-pruned systems exhibit reduced positional trends and greater synchronicity of shoot ontogeny than Guyot or head (cane)-pruned vines. However, there remains significant unexplained internal variation in maturity (Wisdom *et al.*, 2020).

Much attention has been given to the individual vine concerning exposed leaf area and carbon allocation to fruit (Bobeica *et al.,* 2015; Chorti *et al*., 2010; Kliewer and Antcliff, 1970; Šuklje *et al.*, 2013), but little to individual shoot effects. It is asserted that leaves adjacent to the grape cluster are the primary source of assimilates (Hale and Weaver, 1962), particularly early in the growing season (Poni *et al.*, 2004). The effect on cluster size indicates that individual shoot characteristics are a likely determinant of metabolite allocation to the attached cluster(s) (Caspari *et al*., 1998; Eltom *et al*., 2013; Joubert *et al*., 2016). Interesting observations have been made on fruiting cuttings; however, in the field, there is limited information on the comparative contributions of the components used to model ripening in the whole vine at the within-vine level (Morales *et al*., 2016).

Surprisingly few studies have compared the impact of *in situ*, intact, differential vine biomass from similarly managed vines on vine and fruit behaviour; that is, unadulterated in-field vines with differing vegetative biomass (colloquially vigour) due to external factors such as soil type. This may be due to smaller management units that have minimised whole-vine variability through experience. However, greater variability in biomass may be more common in industrial vineyards with larger plantings and management units that suit larger vineyard operations and mechanical equipment. In some regions of the United States of America, New Zealand and Australia, whole-vine vegetative biomass can considerably affect reproductive biomass and photosynthetic behaviour, resulting in variable sugar, acidity, colour, phenolics, yield and ripeness (Cortell *et al*., 2007; King *et al*., 2014; Song *et al*., 2014). Such measures have subsequently informed the development of canopy ideals or 'ideotypes' (Donald, 1962; Kliewer and Dokoozlian, 2005; Smart and Robinson, 1991).

In this study, we used statistical models of increasing complexity to assess fruit composition on individual stems to provide insight into biomass and architectural parameters and how they interact to influence berry composition at harvest. We use the insight gained to evaluate contemporary indices of vine management: harvest index and leaf area models.

MATERIALS AND METHODS

1. Study site

Samples for this study were collected from Jindong Estates vineyard in the Jindong subregion (33°45'S, 115°14'E) of the Greater Margaret River Wine Region, Western Australia. The climatology is Mediterranean (Gladstones, 1999). Soils were either medium brown sandy loam to loam over sandy clay loam and brown clay loam over grey or yellow-brown medium clay (no inclination or elevation). The irrigated *V. vinifera* L. cv. Cabernet-Sauvignon vines (WA clone, own rootstock) were planted in 1998 in north-south rows. Vines were spur pruned to two nodes and unilaterally cordon-trained, trellised to a Smart-Dyson trellis, where approximately 30-40 % shoots originating from the same cordon are left to hang (Smart and Robinson, 1991). Data were collected in the 2003-2004 vintage. Vines were spaced approximately 2 m apart in rows approximately 3 m apart. Standard vineyard operations of trimming and thinning were excluded from the experimental sites. Whole-vine canopy statistics are summarised in Table 1.

2. Leaf area analysis

Leaf area per stem was estimated using a linear equation relating leaf area to stem diameter using pipe theory as the basis (Vertessy *et al.*, 1995). Leaf area was determined for 64 stems across three vines using a Li-Cor LI-3100C® Leaf Area Meter (Nebraska, USA). Stem diameter was calculated using digital Vernier callipers on the same stems at the middle of the second clear node using the equation for an ellipse. A linear regression was calculated between actual leaf area and stem diameter as $y = 14.68x + 172.80$ ($R^2 = 0.63$). The leaf area for all remaining stems with known stem diameters measured in the field at the same time point was estimated in this way (Note: the equation is site-and variety-specific). This methodology allows for the development of a model for non-destructive measurement of stem leaf area. For clarity of nomenclature, 'stem' refers to the vegetative anatomy of the grapevine (season growth) and 'shoot' refers to whole-of-season growth, including vegetative and reproductive anatomy.

3. Harvest

Thirty clusters were picked by hand from each of nine vines (2004). If a vine yielded more than 30 clusters, then 30 clusters were selected at random from evenly spaced positions along the cordon, taking care to avoid operator bias in choosing cluster position and exposure. If there were less than 30 clusters, all clusters were collected, and appropriate statistical measures used (such as Games-Howell pairwise comparisons). The length of the vine's cordon was measured from the beginning to the end of the permanently trellised cordon (± 0.01 m).

The remaining clusters on each vine were counted, weighed, and used to calculate total vine fruit biomass. Sample collection was as close to harvest as possible and determined by the operating viticultural company to meet harvesting schedule requirements. All clusters were hand-harvested into labelled zip-lock plastic bags and cooled in batches as practical. The samples were kept in a cool room overnight and transported to the laboratory the following day for freezing (-20 °C). Individual stem weights were recorded (± 0.01 g).

4. Fruit analysis

Clusters were thawed and gently warmed over warm water to release any precipitated tartrates (Fowles, 1992). Each cluster was weighed (± 0.001 kg) then crushed in the bag, so the juice maintained contact with skin, stalks, and seeds (debris) immediately prior to analysis. Clusters were hand-pressed to extract juice. The debris was allowed to settle, and the supernatant used for analysis. The sugar concentration of the clear juice sample was measured as degrees Brix (°Bx), referred to as °Brix, grams of sucrose equivalent per 100 g of solution, with a digital refractometer (Atago PR32® Japan). Anthocyanins and phenolics were determined spectrophotometrically (Iland *et al.*, 2000). A subsample of 20 berries per cluster was used to estimate the average berry mass of each cluster.

5. Data analysis

Data analysis was carried out using Microsoft Excel®, Addinsoft XLSTAT® and the R statistical environment (Addinsoft, 2016; R Core Team, 2016). Damaged samples were excluded from analysis. The Dixon test for outliers at 5 % significance was used to exclude outliers later in the maturity analyses (sugar, acid, colour and phenolics).

TABLE 1. Winegrape canopy descriptive statistics.

Statistic	Number of observations	Minimum	Maximum	Mean	Standard deviation
Vegetative biomass (vigour) (leaf area m^2 $vine^{-1}$)	9	3.22	11.73	6.09	2.87
Reproductive biomass (yield) (fruit weight kg $vine^{-1}$)	9	1.77	10.67	6.37	3.18
Vine balance (leaf area: fruit weight cm^2 g^{-1})	9	6.57	19.20	10.87	4.02
Canopy density (stems m^{-1})	9	15.06	30.82	23.38	5.63

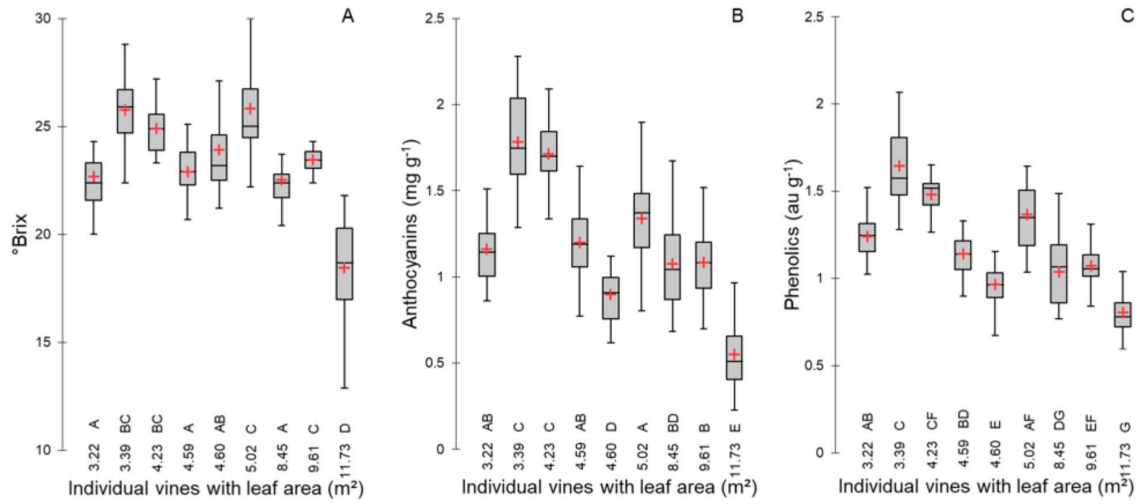


FIGURE 1. Box plots of grape maturity data °Brix (A), anthocyanins (mg g^{-1} berry) (B) and phenolics (absolute units g^{-1} berry) (C). One box per vine. Red crosses (+) are mean maturity values, black central horizontal bars are medians, and black lower and upper limits of the box are the first and third quartiles, respectively. Pairwise comparison post hoc test (Games-Howell) results by maturity parameter with a confidence interval of 95 % are indicated by different letters denoting significant difference. Mean vegetative biomass (leaf area) is presented adjacent to the x axis, and vines are ordered accordingly.

RESULTS

1. Univariate analysis

The maturity data per whole vine used for all subsequent analyses are summarised in Figure 1. The box plots highlight the spread of the individual cluster maturity data around the mean and the spread between individual vines. The whole-vine maturity trend by leaf area is generally negative, but values increase at first and then decrease as leaf area increased (respective R^2 and p-values for °Brix (0.27, 0.148), anthocyanins (mg g^{-1} berry) (0.47, 0.042) and phenolics (absolute units g^{-1} berry) (0.45, 0.049). The range of values within an individual vine is approximately equivalent to between vines with leaf areas less than ~10.00 m^2.

2. Bivariate analysis

The interrelationships for all sampled shoots for all vines are displayed as a matrix of bi-plots, correlations and fits (linear) of the relationships between the maturity variables and stem and fruit descriptors (Figure 2). The diagonal cells display the variable name code and a histogram; those below the diagonal, a bivariate scatter plot with a linear fit; and those above the diagonal present the Pearson coefficients of determination (R^2) and their statistical significance.

Berry count (BeCl) was predictive of cluster mass (ClM), and stem mass (StM) was predictive of both (BeCl and ClM). Similarly, anthocyanins (Antho) were predictive of phenolics (Pheno) and vice versa. Sugar accumulation (°Brix) correlated with phenolic and anthocyanin concentrations, but the distributions were unique, though near normal; anthocyanins had the greatest variance and °Brix the least. Tests showed multi-collinearity between ClM and BeCl and maturity indicators with variance inflation factors of 39.3 and 33.7, respectively. From this point on, the number of berries per cluster was excluded from further model building.

°Brix displayed no clear relationship with any of the measured parameters. While generally skewed to the left, anthocyanins and phenolics tended to be negatively related to the correlate: cluster, berry or stem mass, for example. The reproductive parameters of berry count, berry mass and cluster mass generally increased with stem leaf area.

The vine descriptors were skewed to the left: stem mass, cluster mass and °Brix were statistically correlated with shoot position but accounted for a low fraction of variance (< 5 %). Stem mass and leaf area were skewed strongly to the left, and while the two were correlated statistically, the correlation only accounted for about 10 % of the variation, *i.e.* the two were largely independent despite appearing correlated. The remaining variables and relationships displayed a high degree of heteroscedasticity, indicating either no or a complex relationship (Figure 2). The Breusch-Pagan test for heteroscedasticity was used to verify these observations by determining whether the error variance from the regression depended on the independent variable values (Table 2). Unequal variability was evident, particularly for position and reproductive predictor variables in °Brix, all predictor variables in anthocyanins, and all phenolics variables except for position. The model could not be improved by transformation or weighted least-squares estimation.

3. Multiple regression

Bivariate analysis is useful for data exploration and to describe the relationships between discrete independent variables, yet it has limitations when multiple parameters interact. Thus, a multivariate approach was adopted using partial least-squares (PLS) regression to rank the contribution of individual

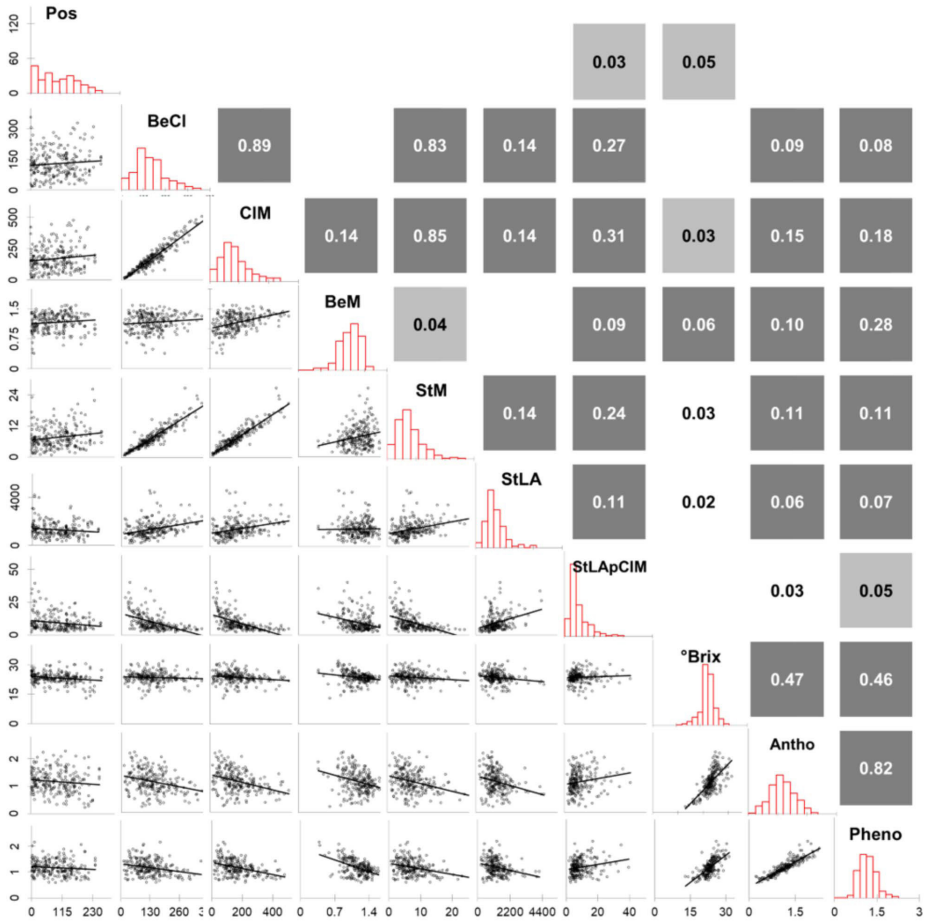


FIGURE 2. Scatterplot matrix of individual plant growth variables and grape maturity indicators within a grapevine, with bivariate scatterplots with fitted linear regression line (below diagonal), frequency histogram overlays (on diagonal), Pearson's coefficients of determination (R2) (above diagonal) and coefficient statistical significance indicated by text and colour (absent > 0.05, black text white background < 0.05, black text grey background < 0.01, white text dark grey background < 0.001). Pos, distance from permanent cordon origin (cm); BeCl, number of berries per cluster; ClM, mass of whole cluster (g); BeM, average individual berry mass per cluster (g); StM, mass of stem (g); StLA, leaf area per stem (cm^2); StLApClM, stem leaf area per corresponding mass of cluster (cm^2 g^{-1}); Sug, sugar concentration as °Brix; Antho, anthocyanins (mg g^{-1} berry); Pheno, phenolics (absolute units g^{-1} berry).

TABLE 2. Breusch-Pagan (BP) test for heteroscedasticity where H0 = homoscedasticity using Chi-square for three grape maturity indicators, sugar concentration as °Brix, anthocyanins (mg g^{-1} berry) and phenolics (absolute units g^{-1} berry), from individual vegetative and reproductive plant growth components within a grapevine. The table relates to data in Figure 2.

Maturity indicator (dependent variable)	Test statistic	Pos	ClM	BeM	StM	StLA
°Brix	BP	11.13	3.68	36.71	NS	NS
	p-value	< 0.001	0.05	< 0.001		
Anthocyanins	BP	6.86	13.42	23.19	5.79	12.30
	p-value	< 0.01	< 0.001	< 0.001	< 0.05	< 0.001
Phenolics	BP	NS	16.71	39.78	6.56	6.59
	p-value		< 0.001	< 0.001	0.01	0.01

Sugar as total soluble solids (°Brix); Colour as anthocyanins (mg g^{-1} fruit); Flavonoids as phenolics (absolute units g^{-1} berry); Pos, position along cordon measured as distance from head of vine (permanent cordon-trained) (cm); ClM, mass of whole cluster (g); BeM, average individual berry mass per cluster (g); StM, mass of stem (g); StLA, leaf area per stem (cm^2); NS, not significant.

grapevine shoot components to explaining variability in the individual grape cluster maturity (Figure 3). Additionally, PLS was used to assist in parameter number reduction and to minimise the collinear influence of the reproductive and vegetative components of the model (identified in Figure 2).

Q^2 cumulative model strength (highest value) was used to select the number of components (Components 1 to 4 = 0.155, 0.178, 0.161, 0.157), which is similar to R^2 as an estimate of the strength of the least-squares fit but derived from the test set; it also ranges from 0 to 1 but is relatively independent of the number of fitted variables. The lines in the correlation map exhibit the direction and strength of the relationship between the predictors and the response variables in three-dimensional space (only two presented, Figure 3A).

Clear relationships between predictor and indicator variables emerged from this approach. Strong clustering is apparent with the three compositional attributes of maturity, which were negatively related to the biomass variables: BeM and StLA (PLS t1, Figure 3A). The strength of the contribution made by each predictor variable is shown by the variable importance of the projection (VIP) value (Figure 3B). Berry mass was the strongest predictor for each maturity indicator. The model is untrustworthy if the confidence interval falls below reference line; for example, for stem leaf area (StLA), the ratio of stem leaf area to cluster mass (StLApClM), and shoot distance from the crown or start of the crodon (Pos) (Figure 3B).

4. Analysis of covariance

It is apparent from the values presented in Figure 1 that the observed maturity values partly depended on the whole-vine leaf area. Hence, the individual vine was added to the model, and individual vine growth predictors were explored as covariates with the maturity indicator variables through analysis of covariance (Table 3). All ANOVAs were verified with the Welch statistic as a robust test of equality of means. No effects were noted.

The effect of the whole vine as a covariate was greatest in the model of each maturity parameter, indicated by a higher whole-vine Fisher's F value than the shoot growth parameter (Table 3). The vine effects were important and additive for cluster mass and stem mass, as indicated by the significant effect of vine on the model but with no significant interaction (Table 3). However, statistically significant interactions were observed when considering individual berry mass and stem leaf area. In all instances, no interaction was expected if the differences were solely due to a temporal factor; for example, if the harvest was staged to ensure all fruit was harvested at a similar maturity. To simplify interpretation, and to place the analysis in a framework more relevant to populations of vines and vineyard management, vines were then grouped according to two popular indices describing canopy characteristics.

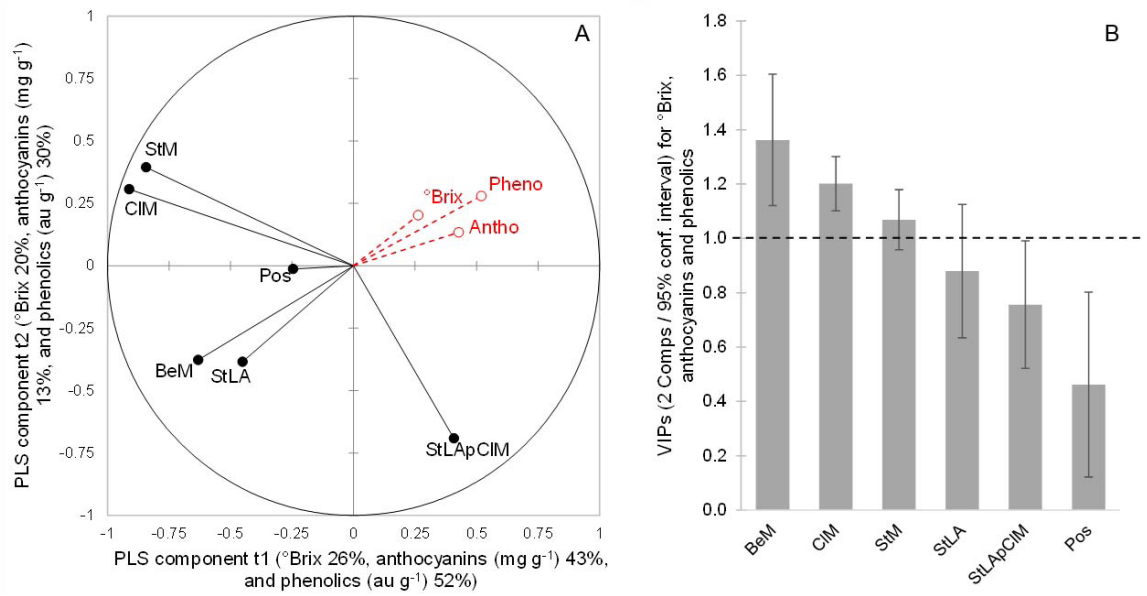


FIGURE 3. Correlation map by partial least-squares regression visualising the first two components of the correlations between Xs and the components, and Ys and the components for grape maturity parameters from individual stem vegetative and reproductive plant growth components within a grapevine (A). Variable importance in the projection (VIP) bar graph with a 95 % confidence interval with reference line (black dashed) (B). Maturity indicators (dependent variable Ys) in red dashed line and open circle: °Brix; Antho, anthocyanins (mg g^{-1} berry); Pheno, phenolics (absolute units g^{-1} berry). Plant growth maturity predictors (independent variables Xs) in black line and closed circle: BeM, average individual berry mass per cluster (g); ClM, mass of whole cluster (g); StLA, leaf area per stem (cm^2); StM, mass of stem (g); StLApClM, stem leaf area per corresponding mass of cluster (cm^2 g^{-1}). Goodness of fit (R^2) A = 0.13, B = 0.20, C = 0.36.

TABLE 3. Analysis of covariance (ANCOVA) for grape maturity indicators: sugar concentration as °Brix; anthocyanins (mg g^{-1} berry); phenolics (absolute units g^{-1} berry), against individual plant growth parameters within grapevines by, and including interactions with, whole individual vines as a factor. Vines significantly differed (P > F < 0.001) for all maturity indicators. Vine factor alone accounted for 58, 53 and 50 % of the variability in °Brix, anthocyanins and phenolics, respectively. Equation fitted was $y = a + bx + cz + dxz$, where 'x' is the vine, 'z' is cluster mass, berry mass, stem mass or leaf area, respectively, and 'y' is the predicted maturity variable.

Plant growth parameter	Maturity indicator	Model goodness of fit (R^2)	Model Fisher's F	Model p-value	Whole vine		Stem plant growth parameter		Stem x vine interaction	
					Fisher's F	p-value	Fisher's F	p-value	Fisher's F	p-value
Cluster mass (g)	°Brix	0.56	18.03	< 0.001	8.93	< 0.001	–	NS	–	NS
	Anthocyanins	0.75	36.73	< 0.001	26.54	< 0.001	18.45	< 0.001	–	NS
	Phenolics	0.73	33.55	< 0.001	30.58	< 0.001	18.15	< 0.001	–	NS
Average individual berry mass per cluster (g)	°Brix	0.64	24.88	< 0.001	15.63	0.00	9.51	< 0.001	5.06	< 0.001
	Anthocyanins	0.70	32.49	< 0.001	4.37	0.04	2.71	0.01	1.29	0.25
	Phenolics	0.76	42.48	< 0.001	40.12	< 0.001	6.89	< 0.001	2.47	0.01
Stem mass (g)	°Brix	0.56	18.13	< 0.001	8.25	< 0.001	–	NS	–	NS
	Anthocyanins	0.72	35.63	< 0.001	17.56	< 0.001	16.70	< 0.001	–	NS
	Phenolics	0.68	29.53	< 0.001	9.85	0.00	12.17	< 0.001	–	NS
Stem leaf area (cm^2)	°Brix	0.59	19.94	< 0.001	10.72	< 0.001	–	NS	2.38	0.02
	Anthocyanins	0.71	33.41	< 0.001	–	NS	19.66	< 0.001	2.57	0.01
	Phenolics	0.69	30.16	< 0.001	–	NS	12.91	< 0.001	2.88	0.00

NS = not significant.

TABLE 4. Winegrape canopy indices and their impact on berry composition as °Brix, anthocyanins (mg g^{-1} berry) and phenolics (absolute units g^{-1} berry) at maturity.

Canopy index	Maturity indicator	Goodness of fit (Adjusted R^2)	p-value (Model)	Vine index class means and pairwise comparisons		
				Low	Ideal	High
Vine leaf area	°Brix	0.41	< 0.001	24.40 a	23.70 a	18.45 b
	Anthocyanins	0.50	< 0.001	1.54 a	1.12 b	0.55 c
	Phenolics	0.45	< 0.001	1.45 a	1.12 b	0.80 c
Vine harvest index	°Brix	0.35	< 0.001	23.70 a	20.26 b	25.33 c
	Anthocyanins	0.51	< 0.001	1.12 a	0.81 b	1.75 c
	Phenolics	0.40	< 0.001	1.12 a	0.99 b	1.56 c

Leaf area is ideal leaf area according to Kliewer and Dokoozlian (2005) for single upright canopy (Low < 2 m^2 m^{-1}, Ideal 2–5 m^2 m^{-1}, High > 5 m^2 m^{-1}); Harvest index (leaf biomass and fruit biomass of whole vine cm^2 g^{-1}) according to Smart and Robinson (1991) (Low < 10 cm^2 g^{-1}, Ideal 10-14 cm^2 g^{-1}, High > 14 cm^2 g^{-1}). NS = not significant. Pairwise comparison groups indicated by lowercase a, b and c adjacent to LS mean, different letters indicate significant differences according to Games-Howell test.

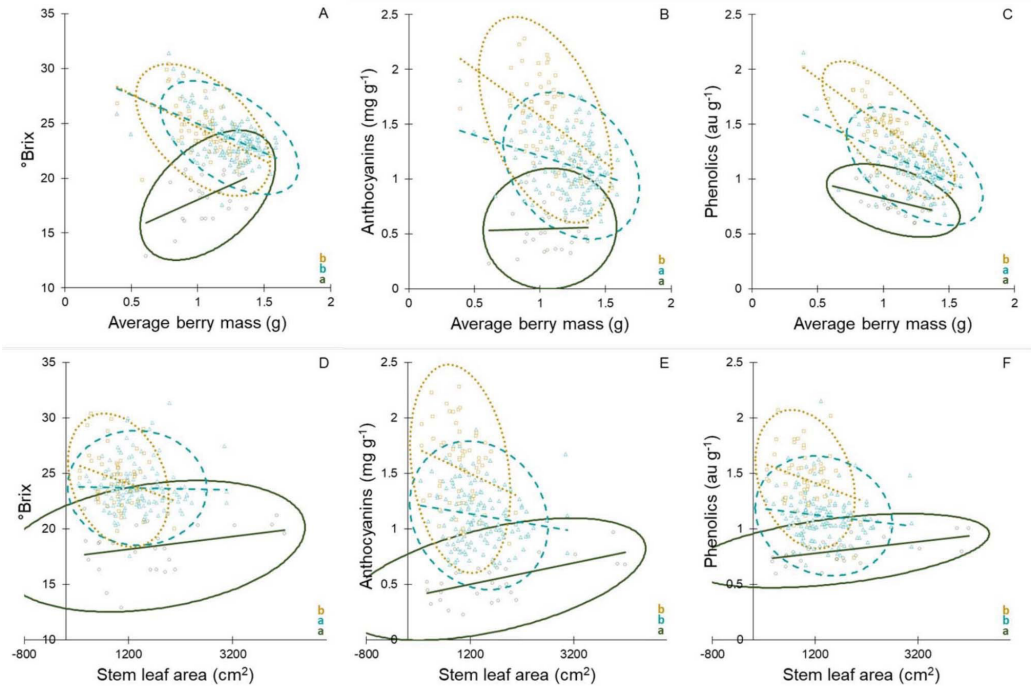
5. Canopy descriptor models

Predictability of maturity by two common indices that describe winegrape canopy characteristics—harvest index (Ravaz, 1906), also known as leaf area:fruit weight ratio (Smart *et al.*, 1988), and leaf biomass (area) (Candar *et al.*, 2020)—showed a moderate goodness of fit (Table 4). The first index is ideal 'vine leaf area' and for an upright canopy is defined as: Low < 2 m^2 m^{-1}, Ideal 2–5 m^2 m^{-1} and High > 5 m^2 m^{-1} (Kliewer and Dokoozlian, 2005). The second index is ideal 'vine harvest index' (leaf area to fruit biomass of the whole vine cm^2 g^{-1}) and is defined as: Low < 10 cm^2 g^{-1}, Ideal 10–14 cm^2 g^{-1} and High > 14 cm^2 g^{-1} (Smart and Robinson, 1991).

The trends in the maturity ranking within each index contrast strongly (Table 4), and pairwise comparisons indicate significant differences between each class within each index across all maturity indicators. For the vine leaf area model, the trend in mean from Low to High was strongly negative (-25 % for °Brix, -60 % for anthocyanin content and -45 % for phenolics). Whereas for the vine harvest index model, the trends were non-linear, with the minima at the 'ideal' level. The High harvest index class had the highest predicted values for °Brix, anthocyanins and phenolic composition. The vine leaf area index was the best predictor of maturity of the two indices, as indicated by the greater Fisher's F values, and was selected for further analysis.

TABLE 5. Analysis of covariance (ANCOVA) for grape maturity indicators including sugar concentration—°Brix, anthocyanins (mg g^{-1} berry) and phenolics (absolute units g^{-1} berry)—against individual stem size variables—berry mass (average individual berry mass per cluster (g)) and leaf area (shoot leaf area (cm^2))—within grapevines by, and including interactions with, vine leaf area (whole-vine leaf biomass (cm^2)). The table relates to data in Figure 4.

Shoot size variables	Maturity indicator	Model goodness of fit (R^2)	Model p-value	Vine leaf area		Shoot size variable		Interaction	
				Fisher's F	p-value	Fisher's F	p-value	Fisher's F	p-value
Berry mass	°Brix	0.56	< 0.001	32.23	< 0.001	5.90	0.02	14.92	< 0.001
	Anthocyanins	0.56	< 0.001	15.37	< 0.001	11.83	0.00	4.32	0.01
	Phenolics	0.64	< 0.001	15.79	< 0.001	58.49	< 0.001	4.62	0.01
Leaf area	°Brix	0.44	< 0.001	76.95	< 0.001	10.62	0.001	3.95	0.02
	Anthocyanins	0.53	< 0.001	102.65	< 0.001	32.76	< 0.001	5.47	0.01
	Phenolics	0.48	< 0.001	82.41	< 0.001	31.14	< 0.001	4.57	0.01



Legend:
leaf area per vine Low ··· □ < 2 m² m^{-1}, Ideal ----- △ 2–5 m² m^{-1}, High —— ○ > 5 m² m^{-1}.

FIGURE 4. Bivariate correlation confidence ellipses (foreground) and scatter plots (background) (confidence interval 95 % Chi-Square) of three grape maturity indicators °Brix (A, D), anthocyanins (mg g^{-1} berry) (B, E), and phenolics (absolute units g^{-1} berry) (C, F), against average individual berry mass per cluster (g) (A–C) and individual stem leaf area (cm^2) (D–F) within a grapevine, by whole-vine leaf area groups. Grouped according to Kliewer and Dokoozlian (2005) for single upright canopy, data points, whole-vine leaf area groups and regression trend line indicated by shape and line style (see legend). Comparison of slopes (ANCOVA) indicated by letters on each subplot (respectively low, ideal, high) where those with the same letter do not statistically differ at $P < 0.05$. Determination coefficient (R^2) for °Brix, anthocyanins and phenolics respectively: Models A–C Low = 0.26, 0.21, 0.50; Ideal = 0.28, 0.08, 0.28; High = 0.22, 0.00, 0.19, Models E–F Low = 0.08 0.00, 0.08; Ideal = 0.05, 0.02, 0.25; High = 0.07, 0.02, 0.21. All significant except high vigour anthocyanins. See Table 5 for the analysis of covariance.

Analysis of covariance was undertaken using the berry and stem size predictors, with whole-vine leaf area across all maturity indicators (Table 5). Berry size and stem leaf area size were selected because they showed interactions between the parameters and the individual, whole-vine covariate and a strong goodness of fit (Table 3). All models were statistically significant, with vine biomass the strongest predictor except for berry phenolic content, where berry mass was the strongest predictor (Table 5). The models are shown in Figure 4.

The trend in slope for the relationships between °Brix and both individual berry mass and leaf area per stem depended

TABLE 6. Summary of the linear regression model goodness of fit values (Pearson's R^2) for best models of individual vegetative and reproductive plant growth components with maturity indicators: °Brix, anthocyanins (mg g^{-1} berry) and phenolics (absolute units g^{-1} berry).

Model components	°Brix	Anthocyanins	Phenolics
Bivariate within-vine: berry mass (Figure 2)	0.06	0.10	0.28
Multivariate all data (Figure 3)	0.12	0.20	0.34
Bivariate whole-vine: Berry mass and individual whole-vine covariate	0.64	0.70	0.76
ANCOVA: Berry mass and vine leaf area covariate (Figure 4)	0.56	0.56	0.64

on the leaf area class of the vine: from strongly negative for low leaf area vines to nil or even positive for high leaf area vines depending on the composition component assessed (°Brix, anthocyanins or phenolics) (Figure 4). Note that high leaf area class vines had lower maturity levels than the low leaf area class vines.

While the slopes depicted in Figure 4 are consistent with the information provided in Table 4, an important degree of interaction is not apparent in the previous analysis. Generally, the value of the dependent variable (°Brix, anthocyanin or phenolics) decreased as the predictor stem leaf area or individual berry mass increased. However, while the slope decreased with whole-vine leaf biomass, strong interactions are associated with average individual berry mass, especially for °Brix and anthocyanin content. Comparatively low vine leaf area significantly influenced the relationship between berry mass anthocyanins and phenolics. The inverse occurred for the relationship between stem mass and maturity indicators. Adding other within-vine plant growth predictors decreased the fit of the analysis of covariance model (data not presented: °Brix 5.5 %, anthocyanins 1.3 % and phenolics 1.0 %). Thus, there was no added value in adopting multiple independent variables to the model beyond berry size.

6. All models summary

Table 6 summarises the strength of goodness of fit for the key models evaluated. It allows for easy comparison and demonstrates that the models with whole-vine covariates best explain the variability in the dependent variables (°Brix, anthocyanins and phenolics). In summary, the whole vine does matter; however, something to do with vine physiology or its location affects the level of maturity attained that is not captured by the two most popular grapevine canopy characteristics (leaf area and leaf area to fruit weight ratio). When considering within-vine variation, whole-vine leaf area and individual shoot berry mass together describe the most variability in maturity.

DISCUSSION

Smaller grapevines produced fruit with higher intensity of composition than larger grapevines. Smaller berries exaggerated this trend. While such observations are not new at the whole-vine scale, the novelty of this study is evidence of these trends at the within-vine scale. The solute concentration of berries at maturity typically varies inversely with their size (Barbagallo *et al*., 2011; Considine, 2004; Dreier *et al*., 1998; Gray, 2002; Roby *et al*., 2004). Conversely, this relationship did not hold for vines with much greater vegetative biomass, where larger berries had higher sugar contents, or the maturity progression of sugar with anthocyanin and phenolic development becomes uncoupled. These relationships represent the interplay of the biophysical factors driving source – sink relationships in grapevines. In the context of a viticulture environment where water, sunlight and temperature do not limit grapevine growth, our modelling informs the management of large grapevine canopies such as those found in industrial-scale viticulture.

We demonstrated that leaf area as an estimate of whole-vine vegetative biomass best represent the characteristics of reproductive organs, as opposed to harvest index, harvest mass, or internal spatial location (*c.f.* Bravdo *et al*., 1984; Carbonneau *et al*., 1991; Chapman *et al*., 2004; Kliewer and Dokoozlian, 2005; Lefort *et al*., 1979). The observed trends from low to high leaf biomass diverge from the 'ideals' presented in the literature but are consistent with the concept that high vegetative biomass delays or impedes maturity. The harvest index trend, which appears to intuitively offer a standard way of matching traditional to industrial viticultural systems, failed to show the anticipated trends: the berry composition values were lowest for the 'ideal' values suggested by Smart and Robinson (1991). Clearly, matching theory to field observation remains a challenge.

Bivariate analysis of berry composition with shoot growth parameters did not help dissect the importance of these maturity determinants. The single most important factor contributing to the scatter of values in the bivariate analysis was the individual vine, particularly the leaf area of the individual vine. This analysis helped elucidate the observed heteroscedasticity from the bivariate analysis with shoot growth parameters. This also showed that the mass of the reproductive organ, the berry, was the single most important predictor of its composition, though leaf area of individual stems within a vine also exerted a significant influence. Together, these parameters largely determined the observed within-vine variance of fruit composition: °Brix, colour (anthocyanin content) and phenolics concentration. There were complex relationships between °Brix and anthocyanins and phenolics (secondary metabolites), representing the quality potential of berries for wine production (Downey *et al*., 2006; Ough and Singleton, 1968).

The solute concentration of berries at maturity typically varies inversely with their size (Barbagallo *et al*., 2011; Considine, 2004; Dreier *et al*., 1998; Gray, 2002; Roby *et al*., 2004). However, the data presented here showed that size alone did not account for the values found. A novel finding from this study was that the sugar concentration of high biomass vines tended to increase as berry mass increased. Temporal influences seem unlikely because the slopes vary in direction rather than intercept (*i.e.* and interactive effect Figure 4). It has been proposed that high vegetative biomass vines allocate resources preferentially to shoot and root growth (Hale and Weaver, 1962); however, larger fruit may be more competitive in certain circumstances, as reported for peach (Marini and Sowers, 1994) and grapes (Ollat and Gaudillere, 1998). This response is likely to relate to the biology and physics of the phloem acting as the conduit, as well as the energetics of the apoplastic unloading in the pericarp. Surface area–volume trends have been thought to influence the mass–concentration relationship (Greer and Rogiers, 2009) but recent research suggests that such a relationship may only become apparent once loading has ended (Savoi *et al*., 2021) and therefore internal spatial factors may underpin the general relationship. This leaves the relationship observed in high biomass vine enigmatic and open to further study.

Canopy geometry factors such as shading likely interacted with our measures. While this was not assessed here, its importance is well understood for anthocyanins. Anthocyanins and phenolics are strongly influenced by vegetative biomass and microclimate, and then post véraison more strongly by climatic conditions post-véraison, especially light intensity and temperature (Azuma *et al*., 2012; Bergqvist *et al*., 2001; Guidoni *et al*., 2008). It is unclear whether the impact of vegetative biomass on this biosynthetic pathway occurs through changes in metabolite availability and/or changes in microclimate. Shading influences biosynthesis directly through the phytochrome system (Matus *et al.*, 2009; Sun *et al.*, 2017) and indirectly through an effect on berry temperature (Costa *et al.*, 2020; Tarara *et al*., 2008). Temperature also affects other maturity parameters, such as acid and sugar accumulation (Brandt *et al.*, 2019; Rienth *et al.*, 2021). A recent study suggested that limited carbon supply promotes carbohydrate accumulation in berries at the expense of secondary metabolites (Bobeica *et al*., 2015). Our results support the concept that high vegetative biomass conditions can delay the accumulation of anthocyanins and phenolic polymerisation. The influence of berry size on the relationship to maturity parameters in this study was highly significant, which suggests a competitive aspect to these processes (see also Gray and Coombe, 2009; Trought *et al*., 2017).

A limitation to interpreting our observations is that we harvested on a single date, so the fruit was not necessarily all mature. However, leaf area manipulation studies have similar limitations. Thus, the matter is more complicated than the leaf area/fruit weight model assumes and perhaps accounts for the relatively poor performance of the harvest index model in this study. It should be noted that we partitioned variation across space rather than time. Season, management and clonal variabilities could influence vegetative vine biomass, but we present comparative data across one year because spatial variability does not change with these contributing factors.

Lateral growth increases with increasing growth rate, particularly in highly vegetative vines (Keller *et al*., 2015). As growth slows post-anthesis, reducing vegetative competition in general, increased growth of sylleptic lateral shoots may provide an alternative competitive sink for vines with high vegetative biomass such as those in this study (Filippetti *et al*., 2013; Santesteban *et al*., 2017; Song *et al*., 2014). Three factors - early shoot growth vigour, degree of partitioning to storage organs and lateral shoot growth - may help us understand the disparity in the reported relationships between berry size and maturity (Casassa *et al*., 2016; Ferrer *et al*., 2014).

CONCLUSION

This study identified a previously unrecorded phenomenon in grapevines where shoot-to-shoot variation in berry mass and its relationship with berry composition changes with whole-vine biomass. Thus, biomass management at the whole-vine scale may affect metabolite partitioning and thus fruit composition within vines. Present management indices that have been developed to predict ideal fruit composition at harvest, direct agronomic practice (such as cluster thinning) to low yield per hectare. In locations with the potential for high vine biomass, such as those with non-limiting conditions (abundant water, warmth and light) found commonly in new-world industrial-style agriculture, such practices may exacerbate the high vegetative state, with excess carbohydrates redirected to leaf growth with negative consequences for quality.

The functional relationship between vegetative and reproductive organs in grapevines must be examined in the context of other factors influencing the dynamics of berry development, such as light penetration and water availability. Our study represents a 'natural' experiment, with the grapevine population exhibiting a range of vegetative biomass in the field rather than experimentally manipulated to achieve this result. Future studies could be based on contemporary understanding of the nature of source – sink relationships in the grapevine. How sugars are not loaded into phloem vessels but diffuse from mesophyll cytosol to phloem vessel, undergo mass flow and then follow a diffusion pathway to sink cytosol is critical to understanding source – sink relationships in the grapevine (Turgeon and Medville, 1998; van Bel, 2003), as is the switch to apoplastic unloading in the pericarp of the berry at véraison (Zhang *et al*., 2006).

In contrast to expectations, large berries can be competitive sinks for carbohydrates when canopies are large. Consequently, management practices that encourage larger berries (*e.g.* increased light penetration before anthesis) may be beneficial when resources and growing conditions

are not limiting. Ubiquitous generalisations, such as cluster thinning to achieve 'vine balance', may be problematic if the whole viticultural system and contributing factors to fruit development are not considered. This experiment demonstrated how high leaf area and large average berry size per cluster can delay maturity. For grapevines with low or ideal vegetative biomass grown in warm conditions, management practices that encourage smaller berries rather than fewer clusters are desired (Clingeleffer *et al.*, 2002).

ACKNOWLEDGEMENTS

This work was supported by an Australian Government Research Training Program scholarship [scholarship # LP034319] and a collaborative fund from Evans & Tate Ltd and The University of Western Australia and the Australian Grape and Wine Council Project [grant # 39141100]. We thank Evans and Tate Winery for additional funds and access to vineyards and labs. Thanks to the UWA School of Agriculture and Environment and Greg Cawthray for technical assistance.

REFERENCES

Addinsoft (2016). *Xlstat V. 2016.02.27444*. Data analysis and statistics software for Microsoft Excel. Paris, France.

Azuma, A., Yakushiji, H., Koshita, Y., & Kobayashi, S. (2012). Flavonoid biosynthesis-related genes in grape skin are differentially regulated by temperature and light conditions. *Planta*, *236*, 1067–1080. https://doi.org/10.1007/s00425-012-1650-x

Barbagallo, M., Guidoni, S., & Hunter, J. (2011). Berry size and qualitative characteristics of *Vitis vinifera* L. cv. Syrah. *South African Journal of Enology and Viticulture*, *32*, 129–136.

Belvini, P., Dalla Costa, L., & Scienza, A. (1978). A sampling technique for the control of grape maturing, also in relation to genetic improvement. *Vignevini*, *5*, 35–38.

Bergqvist, J., Dokoozlian, N. K., & Ebisuda, N. (2001). Sunlight exposure and temperature effects on berry growth and composition of Cabernet-Sauvignon and Grenache in the Central San Joaquin Valley of California. *American Journal of Enology and Viticulture*, *52*, 1–7.

Bobeica, N., Poni, S., Hilbert, G., Renaud, C., Gomès, E., Delrot, S., & Dai, Z. (2015). Differential responses of sugar, organic acids and anthocyanins to source-sink modulation in Cabernet-Sauvignon and Sangiovese grapevines. *Frontiers in Plant Science*, *6*, 1–14. https://doi.org/10.3389/fpls.2015.00382

Brandt, M., Scheidweiler, M., Rauhut, D., Patz, C. D, Will, F., Zorn, H., & Stoll, M. (2019). The influence of temperature and solar radiation on phenols in berry skin and maturity parameters of *Vitis vinifera* L. cv. Riesling. *OENO One*, *53*(2). https://doi.org/10.20870/oeno-one.2019.53.2.2424

Bravdo, B., Hepner, Y., Loinger, C., Cohen, S., & Tabacman, H. (1984). Effect of crop level on growth, yield and wine quality of a high yielding Carignane vineyard. *American Journal of Enology and Viticulture*, *35*, 247–252.

Candar, S., Bahar, E., & Korkutal, I. (2020). Impacts of leaf area on the physiological activity and berry maturation of Merlot (*Vitis vinifera* L.). *Applied Ecology and Environmental Research*, *18*, 1523–1538. https://doi.org/10.15666/aeer/1801_15231538

Carbonneau, A., Moueix, A., Leclair, N., & Renoux, J. L. (1991). A proposed berry sampling method based on analysis of maturation heterogeneity on a plant. *Journal International des Sciences de la Vigne et du Vin*, *64*, 679–690.

Casassa, L.F., Larsen, R.C., & Harbertson, J. F. (2016). Effects of vineyard and winemaking practices impacting berry size on evolution of phenolics during winemaking. *American Journal of Enology and Viticulture*, *67*, 257–268. https://doi.org/10.5344/ajev.2016.15105

Caspari, H. W., Lang, A., & Alspach, P. (1998). Effects of girdling and leaf removal on fruit set and vegetative growth in grape. *American Journal of Enology and Viticulture*, *49*, 359–366.

Chapman, D. M., Matthews, M. A., & Guinard, J-X. (2004). Sensory attributes of Cabernet-Sauvignon wines made from vines with different crop yields. *American Journal of Enology and Viticulture*, 55:325-334.

Chorti, E., Guidoni, S., Ferrandino, A., & Novello, V. (2010). Effect of different cluster sunlight exposure levels on ripening and anthocyanin accumulation in Nebbiolo grapes. *American Journal of Enology and Viticulture*, *61*, 23–30.

Clingeleffer, P., & Krake, L. (1992). Responses of Cabernet Franc grapevines to minimal pruning and virus infection. *American Journal of Enology and Viticulture*, *43*, 31–37.

Clingeleffer, P. R., Krstic, M. P., & Welsh, M. A (2002). Effect of post-set, crop control on yield and wine quality of Shiraz. In R. Blair (Ed.), *Proceedings 11th Wine Industry Technical Conference* (pp. 84–86), Adelaide.

Considine, J. A. (2004). Grapevine productivity and yield components: A case study using field vines of Zante currant. *Australian Journal of Grape Wine Research*, *10*, 108–115. https://doi.org/10.1111/j.1755-0238.2004.tb00013.x

Coombe, B. (1987). Distribution of solutes within the developing grape berry in relation to its morphology. *American Journal of Enology and Viticulture*, *38*, 120–127.

Cortell, J. M., Halbleib, M., Gallagher, A. V., Righetti, T. L., & Kennedy, J. A. (2007). Influence of vine vigour on grape (*Vitis vinifera* L. cv. Pinot Noir) anthocyanins. 1. Anthocyanin concentration and composition in fruit. *Journal of Agricultural and Food Chemistry*, *55*, 6575–6584.

Costa, C., Graça, A., Fontes, N., Teixeira, M., Gerós, H., & Santos, J. A. (2020). The interplay between atmospheric conditions and grape berry quality parameters in Portugal. *Applied Sciences*, *10*, 4943–4965. https://doi.org/10.3390/app10144943

Dai, Z., Ollat, N., Gomès, E., Decroocq, S., Tandonnet, J-P., Bordenave, L., Pieri, P., Hilbert, G., Kappel, C., & van Leeuwen, C. (2011). Ecophysiological, genetic, and molecular causes of variation in grape berry weight and composition: A review. *American Journal of Enology and Viticulture*, *62*, 413–425. https://doi.org/10.5344/ajev.2011.10116

Dai, Z., Vivin, P., Barrieu, F., Ollat, N., & Delrot, S. (2010). Physiological and modelling approaches to understand water and carbon fluxes during grape berry growth and quality development: a review. *Australian Journal of Grape Wine Research*, *16*, 70–85. https://doi.org/10.1111/j.1755-0238.2009.00071.x

de Cortázar-Atauri, I. G., Brisson, N., Ollat, N., Jacquet, O., & Payan, J. C. (2009). Asynchronous dynamics of grapevine (*Vitis vinifera*) maturation: experimental study for a modelling approach. *Journal International des Sciences de la Vigne et du Vin*, 43, 83–97.

Donald, C. (1962). In search of yield. *The Journal of the Australian Institute of Agricultural Science*, *28*, 171–178.

Downey, M. O., Dokoozlian, N. K., & Krstic, M. P. (2006). Cultural practice and environmental impacts on the flavonoid composition of grapes and wine: a review of recent research. *American Journal of Enology and Viticulture*, *57*, 257–268.

Dreier, L. P., Hunter, J. J., & Ruffner, H. P. (1998). Invertase activity, grape berry development and cell compartmentation. *Plant Physiology and Biochemistry*, *36*, 865–872. https://doi.org/10.1016/S0981-9428(99)80004-7

Eltom, M., Trought, M., & Winefield, C. (2013). The effects of cane girdling before budbreak on shoot growth, leaf area and carbohydrate content of *Vitis vinifera* L. Sauvignon Blanc grapevines. *Functional Plant Biology*, *40*, 749–757. https://doi.org/10.1071/FP12278

Ferrer, M., Echeverría, G., & Carbonneau, A. (2014). Effect of berry weight and its components on the contents of sugars and anthocyanins of three varieties of *Vitis vinifera* L. under different water supply conditions. *South African Journal of Enology and Viticulture*, *35*, 103–113.

Filippetti, I., Allegro, G., Valentini, G., Pastore, C., Colucci, E., & Intrieri, C. (2013). Influence of vigour on vine performance and berry composition of cv. Sangiovese (*Vitis vinifera* L.). *Journal International des Sciences de la Vigne et du Vin*, *47*, 21–33.

Fowles, G. (1992). Acids in grapes and wines: A review. *Journal of Wine Research*, *3*, 25–41. https://doi.org/10.1080/09571269208717912

Gamalei, Y. (1989). Structure and function of leaf minor veins in trees and herbs. *Trees*, *3, 96-110*. https://doi.org/10.1007/BF00191540

García de Cortázar-Atauri, I., Cordova, C., & Pinto, M. (2005). Canopy structure and photosynthesis modelling of grapevines (*Vitis vinifera* L. cv. Sultana) grown on an overhead (parronal) trellis system in Chile. *Australian Journal of Grape Wine Research*, *11*, 328–338.

Gladstones, J. (1999). *Viticulture and Environment.* Winetitles.

Gray, J., & Coombe, B. (2009). Variation in Shiraz berry size originates before fruitset but harvest is a point of resynchronisation for berry development after flowering. *Australian Journal of Grape Wine Research*, *15*, 156–165. https://doi.org/10.1111/j.1755-0238.2009.00047.x

Gray, J. D. (2002). *The basis of variation in the size and composition of grape berries*. [Doctoral thesis, University of Adelaide].

Greer, D. H., & Rogiers, S. Y. (2009). Water flux of *Vitis vinifera* L. cv. Shiraz bunches throughout development and in relation to late-season weight loss. *American Journal of Enology and Viticulture*, *60*, 155–163.

Guidoni, S., Ferrandino, A., & Novello, V. (2008). Effects of seasonal and agronomical practices on skin anthocyanin profile of Nebbiolo grapes. *American Journal of Enology and Viticulture*, *59*, 22–29.

Hale, C. R., & Weaver, R. J. (1962). The effect of developmental stage on direction of translocation of photosynthate in *Vitis vinifera. Hilgardia*, *33*, 89–131. https://doi.org/10.3733/hilg.v33n03p039

Hardie, W., & Considine, J. A. (1976). Response of grapes to water-deficit stress in particular stages of development. *American Journal of Enology and Viticulture*, *27*, 55–61.

Iland, P., Ewart, A., Sitters, J., Markides, A., & Bruer, N. (2000). *Techniques for Chemical Analysis and Quality Monitoring during Winemaking.* Patrick Iland Wine Promotions.

Joubert, C., Young, P. R., Eyeghe-Bickong, H. A., & Vivier, M. A (2016). Field-grown grapevine berries use carotenoids and the associated xanthophyll cycles to acclimate to UV exposure differentially in high and low light (shade) conditions. *Frontiers in Plant Science*, *7*, 786. https://doi.org/10.3389/fpls.2016.00786

Keller, M., Deyermond, L. S., & Bondada, B. R. (2015). Plant hydraulic conductance adapts to shoot number but limits shoot vigour in grapevines. *Functional Plant Bioliogy*, *42*, 366–375. https://doi.org/10.1071/FP14206

King, P. D., Smart, R. E., & McClellan, D. J. (2014). Within-vineyard variability in vine vegetative growth, yield, and fruit and wine composition of Cabernet-Sauvignon in Hawke's Bay, New Zealand. *Australian Journal of Grape Wine Research*, *20*, 234–246. https://doi.org/10.1111/ajgw.12080

Kliewer, W. M., & Antcliff, A. (1970). Influence of defoliation, leaf darkening, and cluster shading on the growth and composition of Sultana grapes. *American Journal of Enology and Viticulture*, 21, 26–36.

Kliewer, W. M., & Dokoozlian, N. K. (2005). Leaf area/crop weight ratios of grapevines: influence on fruit composition and wine quality. *American Journal of Enology and Viticulture*, *56*, 170–181.

Lefort, P., Schaffer, A., Bisson, J., Becker, P., & Immele, A. (1979). Variations in the maturity of bunches of grapes in relation to their position on the vine. The investigation of a sampling method. *Vitis*, *18*, 291–300.

Marini, R., & Sowers, D. (1994). Peach fruit weight is influenced by crop density and fruiting shoot length but not position on the shoot. *Journal of the American Society for Horticultural* Science, *119*, 180–184. https://doi.org/10.21273/JASHS.119.2.180

Matus, J. T, Loyola, R., Vega, A., Peña-Neira, A., Bordeu, E., Arce-Johnson, P., & Alcalde, J. A. (2009). Post-veraison sunlight exposure induces MYB-mediated transcriptional regulation of anthocyanin and flavonol synthesis in berry skins of *Vitis vinifera*. *Journal of Experimental Botany, 60*, 853–867. https://doi.org/10.1093/jxb/ern336

Morales, F., Antolín, M. C., Aranjuelo, I., Goicoechea, N., & Pascual, I. (2016). From vineyards to controlled environments in grapevine research: investigating responses to climate change scenarios using fruit-bearing cuttings. *Theoretical and Experimental Plant Physiology*, *28*, 171–191. https://doi.org/10.1007/s40626-016-0065-7

Ollat, N., & Gaudillere, J. (1998). The effect of limiting leaf area during stage I of berry growth on development and composition of berries of *Vitis vinifera* L. cv. Cabernet-Sauvignon. *American Journal of Enology and Viticulture*, 49, 251–258.

Ough, C., & Singleton, V. (1968). Wine quality prediction from juice Brix/acid ratio and associated compositional changes for 'White Riesling' and 'Cabernet-Sauvignon'. *American Journal of Enology and Viticulture*, *19*, 129–138.

Pagay, V., & Cheng, L. (2010). Variability in berry maturation of Concord and Cabernet franc in a cool climate. *American Journal of Enology and Viticulture*, *61*, 61–67.

Poni, S., Bernizzoni, F., Briola, G., & Cenni, A. (2004). Effects of early leaf removal on cluster morphology, shoot efficiency and grape quality in two *Vitis vinifera* cultivars. *Acta Horticultura*, *689*, 217–226.

Poni, S., Intrieri, C., & Silvestroni, O. (1994). Interactions of leaf age, fruiting, and exogenous cytokinins in Sangiovese grapevines under non-irrigated conditions. I. Gas exchange. *American Journal of Enology and Viticulture*, *45*, 71–78.

R Core Team (2016). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rankine, B. C., Cellier, K., & Boehm, E. W. (1962). Studies on grape variability and field sampling. *American Journal of Enology and Viticulture*, *13*, 58–72.

Ravaz, L. (1906). Influence des opérations culturales sur la végétation de la vigne. *Annals Ecole Nationale d'Agriculture de Montpellier, VI-I,* 1–41.

Rennie, E. A., & Turgeon, R. (2009). A comprehensive picture of phloem loading strategies. *In Proceedings of the National Academy of Sciences of the United States of America, 106,* 14162–14167. https://doi.org/10.1073/pnas.0902279106

Reshef, N., Fait, A., & Agam, N. (2019). Grape berry position affects the diurnal dynamics of its metabolic profile. *Plant Cell and Environment*, *42*, 1897–1912. https://doi.org/10.1111/pce.13522

Rienth, M., Vigneron, N., Darriet, P., Sweetman, C., Burbidge, C., Bonghi, C., Walker, R. P., Famiani, F., & Castellarin, S. D. (2021). Grape berry secondary metabolites and their modulation by abiotic factors in a climate change scenario – A review. *Frontiers in Plant Science*, *12*, 262. https://doi.org/10.3389/fpls.2021.643258

Roby, G., Harbertson, J. F., Adams, D. A., & Matthews, M. A. (2004). Berry size and vine water deficits as factors in winegrape composition: anthocyanins and tannins. *Australian Journal of Grape Wine Research*, *10*, 100–107. https://doi.org/10.1111/j.1755-0238.2004.tb00012.x

Santesteban, L. G., Miranda, C., Urrestarazu, J., Loidi, M., & Royo, J. B. (2017). Severe trimming and enhanced competition of laterals as a tool to delay ripening in Tempranillo vineyards under semiarid conditions.*OENO One*, *51*(2), 191–203. https://doi.org/10.20870/oeno-one.2017.51.2.1583

Savoi, S., Torregrosa, L., & Romieu, C. (2021). Transcripts switched off at the stop of phloem unloading highlight the energy efficiency of sugar import in the ripening *V. vinifera* fruit. *Horticulture Research, 8*, 1-15. https://doi.org/10.1038/s41438-021-00628-6

Shahood, R., Torregrosa, L., Savoi, S., & Romieu, C. (2020). First quantitative assessment of growth, sugar accumulation and malate breakdown in a single ripening berry. *OENO One*, 54, 1077–1092. https://doi.org/10.20870/oeno-one.2020.54.4.3787

Smart, R., & Robinson, M. (1991). *Sunlight into wine: A handbook for winegrape canopy management.* Winetitles.

Smart, R. E., Smith, S. M., & Winchester, R. V. (1988). Light Quality and Quantity Effects on Fruit Ripening for Cabernet-Sauvignon. *American Journal of Enology and Viticulture*, *39*, 250–258.

Song, J., Smart, R. E., Dambergs, R. G., Sparrow, A. M., Wells, R. B., Wang, H., & Qian, M. C. (2014). Pinot Noir wine composition from different vine vigour zones classified by remote imaging technology. *Food Chemistry*, *153*, 52–59. https://doi.org/10.1016/j.foodchem.2013.12.037

Šuklje, K., Česnik, H. B., Janeš, L., Kmecl, V., Vanzo, A., Deloire, A., Sivilotti, P., & Lisjak, K. (2013). The effect of leaf area to yield ratio on secondary metabolites in grapes and wines of *Vitis vinifera* L. cv. Sauvignon blanc. *OENO One*, *47*, 83–97. https://doi.org/10.20870/oeno-one.2013.47.2.1546

Sun, R. Z., Cheng, G., Li, Q., He, Y. N., Wang, Y., Lan, Y. B., Li, S. Y., Zhu, Y. R., Song, W. F., Zhang, X., & Cui, X. D. (2017). Light-induced variation in phenolic compounds in Cabernet-Sauvignon grapes (*Vitis vinifera* L.) involves extensive transcriptome reprogramming of biosynthetic enzymes, transcription factors, and phytohormonal regulators. *Frontiers in Plant Science*, *8*, 547.

Tarara, J. M, Lee, J., Spayd, S. E., & Scagel, C. F. (2008). Berry temperature and solar radiation alter acylation, proportion, and concentration of anthocyanin in Merlot grapes. *American Journal of Enology and Viticulture*, *59*, 235–247.

Trought, M. C., Naylor, A. P., & Frampton, C. (2017). Effect of row orientation, trellis type, shoot and bunch position on the variability of Sauvignon Blanc (*Vitis vinifera* L.) juice composition. *Australian Journal of Grape Wine Research*, *23*, 240–250. https://doi.org/10.1111/ajgw.12275

Turgeon, R., & Medville, R. (1998). The absence of phloem loading in willow leaves. *In Proceedings of the National Academy of Sciences of the United States of America, 95,* 12055–12060. https://doi.org/10.1073/pnas.95.20.12055

van Bel, A. J. (2003). The phloem, a miracle of ingenuity. *Plant, Cell & Environment, 26,* 125–149. https://doi.org/10.1046/j.1365-3040.2003.00963.x

Vertessy, R. A, Benyon, R. G, O'Sullivan, S. K., & Gribben, P. R (1995). Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiology*, *15*, 559–567. https://doi.org/10.1093/treephys/15.9.559

Winkler, A. (1958). The relation of leaf area and climate to vine performance and grape quality. *American Journal of Enology and Viticulture*, *9*, 10–23.

Wisdom, J. (2018). *Modelling Fruit Composition within the Grapevine Canopy*. [Doctoral thesis, The University of Western Australia].

Wisdom, J. M, Stuckey, A. W., & Considine, J. A. (2020). Hierarchical modelling partitions variation in vineyard fruit maturity for optimal sampling. *Australian Journal of Grape Wine Research*, *26*, 148–157. https://doi.org/10.1111/ajgw.12426

Zhang, X. Y., Wang, X. L., Wang, X. F., Xia, G.H., Pan, Q. H., Fan, R.C., Wu, F. Q., Yu, X. C., & Zhang, D. P. (2006). A shift of phloem unloading from symplasmic to apoplasmic pathway is involved in developmental onset of ripening in grape berry. *Plant Physiology, 142,* 220–232. https://doi.org/10.1104/pp.106.081430

Zhu, J., Génard, M., Poni, S., Gambetta, G. A., Vivin, P., Vercambre, G., Trought, M. C., Ollat, N., Delrot, S., & Dai, Z. (2019). Modelling grape growth in relation to whole-plant carbon and water fluxes. *Journal of Experimental Botany*, *70*, 2505–2521. https://doi.org/10.1093/jxb/ery367

Zufferey, V., Murisier, F., Vivin, P., Belcher, S., Lorenzini, F., Spring, J. L., & Viret, O. (2012). Carbohydrate reserves in grapevine (*Vitis vinifera* L. 'Chasselas'): The influence of the leaf to fruit ratio. *Vitis, 51,* 103-110.