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Manipulating the leaf area to fruit mass ratio alters the synchrony of total soluble solids accumulation and titratable acidity of grape berries

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Abstract

Background and Aims: This study investigated: (i) the importance of changing the leaf area: fruit mass ratio (LA : FM) by crop removal and/or shoot trimming on total soluble solids (TSS) concentration and content, pH, titratable acidity (TA) and berry mass; (ii) the extent to which changes in LA : FM ratio altered the synchrony TSS : TA ratio; and (iii) whether the responses were consistent for Pinot Noir and Sauvignon Blanc.

Methods and Results: Vertical shoot positioned–trained vines were trimmed shortly after fruitset or at veraison to six or 12 main leaves per shoot and crop thinned by removing 0, 50 or 75% of the bunches. TSS and pH, TA and fresh berry mass were measured weekly from pre-veraison to harvest.

TSS concentration accumulation in berries was slowed with shoot trimming and accelerated by crop removal, with crop removal having a greater effect. Trimming shoots at fruitset in combination with no crop removal resulted in the greatest delay in veraison (the start of TSS accumulation) and slowest rate of TSS accumulation. TSS content mirrored TSS concentration for LA : FM manipulations at fruitset but fewer differences were detected for LA : FM changes at veraison. In contrast, TA and pH were largely unaffected.

Conclusions: Changes to the LA : FM ratio via crop removal or shoot trimming modified berry TSS accumulation but not TA. Such desynchronisation was consistent for both cultivars.

Significance of the Study: Crop and/or leaf removal represent valuable means to manipulate the time to achieve target fruit TSS concentration and TA. The similar responses of the two cultivars indicate that LA : FM manipulation could potentially have common responses for different cultivars. The desynchronisation of berry components highlights the need to consider each berry component individually and in a dynamic manner by sampling throughout the ripening phase.

Keywords: crop removal, cultivar, leaf area, synchrony, titratable acidity, total soluble solids

Introduction

Grapevine development (phenology), particularly from dormancy to flowering, is largely determined by temperature (Pouget 1967, Winkler et al. 1974, Moncur et al. 1989). After flowering, factors other than temperature may have an increasingly important influence on grape development and maturity, particularly when carbohydrate source–sink partitioning of the grapevine is affected. For example, the leaf area to fruit mass ratio (LA : FM) is one source–sink relationship that can be manipulated by management practices. Leaf area (source) can be reduced through shoot trimming or leaf removal. Crop removal can be used to reduce the number of grapevine bunches, and consequently, total FM (sink). Reducing LA by trimming shoots and/or leaf removal has been shown to delay the onset of maturation (Ollat and Gaudillere 1998, Petrie et al. 2000a, Poni and Giachino 2000, Parker et al. 2014a,b) and to lower TSS concentration in the berries at harvest (Ollat and Gaudillere 1998, Petrie et al. 2000a, Poni and Giachino 2000, Kliewer and Dokoozlian 2005, Nuzzo and Matthews 2006, Stoll et al. 2011).

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When crop removal, however, is used to manipulate the LA : FM ratio, the results are varied. Crop removal post-flowering/post-fruitset increased TSS accumulation (Guidoni et al. 2002, Kliewer and Dokoozlian 2005, Nuzzo and Matthews 2006, Petrie and Clingeleffer 2006), and a small effect was also observed when crop was removed pre-flowering and under high shoot density (Naor et al. 2002). Conversely, no effect was found when bunches were removed from shoots not arising from count nodes 1 month post-flowering or at veraison (Keller et al. 2005). These inconsistent responses may be explained by the fact that while LA is the predominant source of photosynthates to the grapevine, bunches are only one of several competing sinks, such as developing shoots, roots and carbohydrate storage pools in the trunk and root system. Nevertheless, the extent by which thinning and/or reduction in LA alter the source– sink ratio in grapevines and subsequently change TSS accumulation rates post-veraison is still unclear, as they largely depend on the degree and timing of crop removal and/or leaf reduction. Reducing LA may in part be compensated by an increase in photosynthesis rate per unit LA (Hunter and Visser 1988, Candolfi-Vasconcelos and Koblet 1991, Petrie et al. 2000b, 2003). The rate of TSS accumulation in berries, however, may be affected if the increase in photosynthetic rate is insufficient to compensate for the reduced LA.

Despite the importance of managing the LA : FM ratio to manipulate the maturation of grapes, the mechanisms that lead to the change in harvest date and berry composition at harvest are poorly understood. Although it has been observed that the onset of ripening may be delayed and the rate of TSS accumulation from veraison is slower when LA : FM ratios are reduced, few studies have examined the relative importance of altering the onset versus the rates in determining the observed differences at harvest. For example, later ripening may be caused by a delay in the onset of maturation (Parker et al. 2014b) and/or slower TSS accumulation. Understanding the relative importance of the mechanisms that lead to an earlier or later harvest is important as it provides a method to shift the time of development and maturity processes. This information is potentially important to counteract the effects of advanced phenology in response to increased temperature due to climate change (Duchêne and Schneider 2005, Jones et al. 2005, Webb et al. 2007, Petrie and Sadras 2008, Duchêne et al. 2010) or conversely to enable a target TSS concentration to be reached in marginal environments with cooler climates. In addition, a better comprehension of how LA : FM ratio manipulation affects other key berry components (e.g. pH, TA and berry mass) in different grapevine cultivars is essential to describe the extent to which fruit maturity models can be developed at a species rather than a cultivar level.

To understand better these aspects of grapevine response to manipulation of the LA : FM ratio, this study investigated: (i) the rate of TSS accumulation of Pinot Noir and Sauvignon Blanc at a similar LA : FM ratio; (ii) the response of these two cultivars to manipulation of the LA : FM ratio by crop removal and/or reduction in the LA via shoot trimming; and (iii) the extent to which the timing of LA : FM ratio manipulation influenced the changes in TSS concentration and content, pH and TA of the fruit and berry mass. In combination with a previous publication on the effect of LA : FM ratio on the time of veraison (Parker et al. 2014b), our results provide insights into the relative importance of influencing the onset of TSS accumulation versus the rate of TSS accumulation in response to source–sink manipulation and whether the responses are similar between cultivars at the same location.

Materials and methods

Experimental site

The trial was conducted in the seasons 2009/10 and 2010/11 in a commercial vineyard in the Wairau Valley, Marlborough, New Zealand (41°32′S, 173°51′E). At this site, the accumulated degree days in 2010/11 were greater than that in 2009/10 early in the season (approximately until mid-late December) after which point the accumulated degree days increased similarly between seasons (Figure 1). Further meteorological information for Marlborough, New Zealand is available at the Marlborough Research Centre website (http://www.mrc.org.nz/).

A previous paper (Parker et al. 2014b) provides full details of the experimental layout. In summary, two adjacent rows of the *Vitis vinifera* L. cultivars Sauvignon Blanc (clone MS, rootstock Richter 110) and Pinot Noir (clone 777, rootstock 101-14MGt) were used in this trial in 2009/10 and two further adjacent rows were used for each cultivar in 2010/11. Both cultivars were of similar age (Sauvignon Blanc was planted in 1997, Pinot Noir in 1998). Rows were orientated +15° from north, in a north to south direction; vines were planted 1.8 m within the row, the row spacing was 3.0 m, and vines were trickle irrigated per standard practices at the site.

Leaf and crop removal treatments are described in full in Parker et al. (2014b). In summary, the LA : FM ratio was manipulated shortly after fruitset, approximately 3.5 weeks after flowering at stage 31 on the modified Eichhorn–Lorenz (E-L) scale (Coombe 1995), or at veraison where all the shoots on the vines were trimmed to 12 or 6 main leaves (counting from the basal leaf up the shoot). To achieve 50% crop removal, all bunches (apical and basal whole bunches) were removed on alternate shoots along the cane; for 75% crop removal, all bunches from three of every four shoots along the cane were removed. Lateral shoots were removed at fruitset and bi-weekly thereafter until harvest.

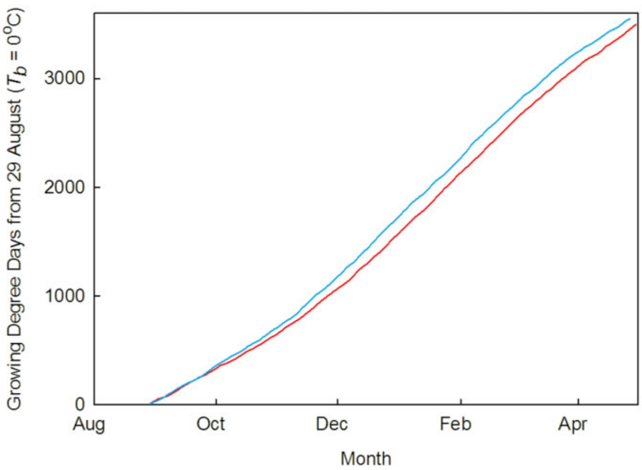

Figure 1. Growing degrees days calculated using the parameters of the Grapevine Flowering Veraison model [Parker et al. (2011)], the sum of the average of daily minimum and maximum temperature from 29 August with a base temperature T_b = 0°C] in 2009/10 (—) and 2010/11 (—). Differences between the thermal summation (2009/10 season values subtracted from the 2010/11 season values) around flowering, veraison and harvest were: 133 degree days (on 15 December), 160 degree days (on 15 February) and 116 degree days (on 15 April). See Parker et al. (2014b) for further details on exact flowering and veraison dates.

Experimental design

In 2009/10, a two (time of treatment) × two (cultivar) × three (crop removal) × two (main leaf number per shoot) factorial design randomised within the cultivar was used with four blocks (four replicates per treatment per cultivar). Blocks were designated by trunk circumference size taken as the average of the circumference 10 cm below the head of the vine and 10 cm above the graft union. Each replicate corresponded to one vineyard bay with three adjacent vines. The LA : FM ratio was adjusted on whole vines in six ways: (i) 12 main leaves per shoot, 100% crop retained on the vine; (ii) 12 main leaves per shoot, 50% of the crop removed; (iii) 12 main leaves per shoot and 75% of the crop removed; (iv) six main leaves per shoot and 100% crop retained on the vine; (v) six main leaves per shoot and 50% of the crop removed; and (vi) six main leaves per shoot and 75% of the crop removed. The design enabled comparisons of similar LA : FM ratios obtained by different leaf or fruit removal treatments (same ratio, 6 leaves and 50% crop with 12 leaves and full crop; 6 leaves and 75% crop with 12 leaves and 50% crop).

In 2010/11, a two (cultivar) × two (crop removal) × two (main leaf number per shoot) block design was used, randomised within each cultivar, with two blocks that were designated by trunk circumference size as before (two replicates per treatment per cultivar in each block). Treatments (i), (ii), (iv) and (v) of the 2009/10 experiment were repeated in 2010/11 to confirm trends observed in that season.

Leaf area estimation and harvest measures

In 2009/10, harvest date was 8 April (day of the year, DOY 96) for Pinot Noir and 15 April (DOY 105) for Sauvignon Blanc (Table 1). In 2010/11, Pinot Noir was harvested on 30 March (DOY 89) and Sauvignon Blanc on 6 April (DOY 96) (Table 1). At harvest, plots were hand harvested, and bunches were counted and weighed.

Full details of the vine management and LA estimation are published in Parker et al. (2014b). Briefly, leaves were removed at harvest from between the trunks of the second and third vines in each replicate and weighed. A random subsample of 100 leaves was then weighed and the area measured using a LiCOR 3100 LA metre (LiCOR Inc., Lincoln, NE, USA). The total LA was calculated from the correlation between leaf mass (LM) and LA.

Fruit development and berry composition measurements

Thirty berries were randomly sampled from both sides of the canopy on a weekly basis from each plot from pre-veraison (ca. 5°Brix) until harvest. Total berry mass for each 30-berry sample was measured, and then berry samples were crushed by hand in polythene bags and coarsely filtered. The following measurements were made on the berry juice: total soluble solids (TSS) (°Brix) determined by refractometry with an Atago Pocket PAL-1 Refractometer (Atago Co., Ltd, Tokyo, Japan); titratable acidity (TA) by end point titration (tartaric equivalents in g/L) using 0.1 mol NaOH to pH 8.4 at 20°C with a Mettler Toledo DL 50 Graphix titrator [Mettler Toledo (Schweiz) GmbH, Greifensee, Switzerland]; and pH using a Metrohm 744 pH metre (Metrohm AG, Herisau, Switzerland).

Modelling and statistical analysis

The exponential three-parameter growth function curve (Equation 1) was fitted to each replicate to TSS accumulation data greater than 5°Brix (which corresponds to the start of rapid TSS accumulation)

$$y = a + br^x \quad (1)$$

where a is the y asymptote (in °Brix), $b < 0$, $0 < r < 1$ and x is the DOY.

The following measures were interpolated from the curve fits:

- duration of TSS accumulation that was comparable across all curve fits, measured as the number of days to go from the onset of maturation [8°Brix as described in Parker et al. (2012, 2014b)], up to the lowest TSS concentration that was measured at harvest for one experimental unit across both cultivars, all treatments and both seasons (14.2°Brix); and
- average rates of TSS accumulation (increase in TSS/day) calculated over the same period as the duration for TSS accumulation.

From the curve fits, the difference in the number of days to reach a target TSS concentration of 21°Brix was also interpolated or extrapolated. The time to a threshold concentration of 21°Brix for treatments applied at fruitset was not assessed in either season because in both years, three out of four of the six-leaves full-crop treatments for Sauvignon Blanc had

Table 1. Berry diameter, date and days after flowering at the manipulation of grapevine leaf area to fruit mass ratio at fruitset and veraison.

	LA : FM ratio manipulation at fruitset†				LA : FM ratio manipulation at veraison‡	
	Pinot Noir		Sauvignon Blanc		Pinot Noir	Sauvignon Blanc
	2009/10	2010/11	2009/10	2010/11	2009/10	2009/11
Berry diameter (mm)	6.64	7.73	6.25	8.37	NA	NA
Proportion veraison (%)§	NA	NA	NA	NA	51	57
Date of manipulation	5 January (5)¶	29 December (363)	14 January (14)	5 January (5)	17 February (48)	1 March (60)
Days after 50% flowering	23	25	23	27	66	69

†Corresponds to stage 31 on the modified Eichhorn–Lorenz (E-L) scale. ‡Corresponds to approximately 50% veraison as assessed by proportion (%) of colour change in the field for Pinot Noir (stage 35 on the modified E-L scale) and softness (%) of a 30-berry sample for Sauvignon Blanc (stage 34 on the modified E-L scale). §The proportion veraison (%) corresponds to the average value across all 12-leaves 100% crop treatments for each cultivar. ¶Values in brackets are day of the year. LA : FM, leaf area to fruit mass ratio; NA, not applicable.

an upper asymptote (a value in $y = a + br^x$) fitted for the exponential response that was less than the tested target TSS concentration of 21°Brix. Berry TSS content (per berry) was calculated from the average berry fresh mass (g) and the corresponding TSS.

The relative importance of main effects (crop removal, main leaf number, cultivar and time of treatment) was analysed by ANOVA using Genstat 12 (VSN International Ltd, Hemel Hempstead, England), and the proportion (%) total sum of squares and significance of main effects were compared. Mean separations were analysed by the Fisher's unprotected least significant difference (LSD) method at the 5% level of significance. Interpolated rates and durations were analysed for TSS accumulation; for pH, TA, fresh berry mass, and TSS content each time point was assessed. Relationships between TSS concentration, pH and TA were evaluated for each combination of main leaf number and crop removal. Means plots presented in figures were plotted using Sigmaplot 12 (Systat Software, Inc., San Jose, CA, USA).

Results

Response of cultivars to manipulation of leaf area to fruit mass ratio

The date at which fruit reached any particular TSS was generally delayed when the LA : FM ratio was reduced at fruitset (Figure 2). The rate and time to go from 8 to 14.2°Brix for TSS accumulation (duration) were similar at the equivalent ratios (6 leaves and 50% crop with 12-leaves and full-crop treatment; 6 leaves and 75% crop with 12 leaves and 50% crop treatment) and similar between cultivars (Table 2).

In 2009/10 when the LA : FM ratio was manipulated at veraison, the rate of TSS accumulation from 8 to 14.2°Brix was similar to that observed when treatments were applied at fruitset (Tables 2,3). Where vines were severely source limited, however, (six leaves and full crop), the anticipated time for Sauvignon Blanc to reach 21°Brix was delayed compared with the same treatment for Pinot Noir (Table 3).

Both crop removal and leaf removal influenced the rate and duration from 8 to 14.2°Brix ($P < 0.001$), although crop removal had a greater effect (greater proportion of total sum of squares, for example total sum of squares for rates: fruitset 2009/10, 48% crop removal, 29% leaf removal; 2010/11 40% crop removal, 36% leaf removal; veraison 2009/10, 34% crop removal, 28% leaf removal) (Figure 2, Tables 2,3).

Unlike TSS, the changes in TA, pH and fresh berry mass were largely unaffected by the LA : FM ratio for either cultivar (Figures 3–5). The only differences observed that related to the LA : FM ratio for TA, pH or berry mass were: (i) in 2010/11, for the LA : FM manipulation at fruitset, TA in the six-leaves full-crop treatment was less than that in all other treatments for both cultivars early in the maturation phase during the first three to four sampling time points (Figure 3e,f); (ii) pH was lower in the Sauvignon Blanc 12-leaves full-crop treatment than in the two 12-leaves thinned treatments for LA : FM ratio manipulation at fruitset in 2009/10 (Figure 4); and (iii) the average fresh berry mass was reduced with reduced main leaf number (Figure 5) for LA : FM ratio manipulation at fruitset – the 6-leaves average berry mass was lower than that of the 12-leaves ($P < 0.05$) on most days including harvest in both seasons for both cultivars (except Pinot Noir in 2009/10, Figure 5a).

Total soluble solids content per berry mirrored the results of TSS concentration when the LA : FM was reduced at fruitset in both seasons (Figure 6 compared with Figure 2). Although similar ratios often overlapped, there was a greater separation of TSS content with respect to leaf number than for TSS concentration. When the LA : FM ratio was manipulated at veraison, and the relative differences in TSS content (Figure 6d) mirrored that of TSS concentration for Sauvignon Blanc, both leaf number and crop removal were important main effects ($P < 0.05$); for Pinot Noir although TSS concentration differed (Figure 2) there were few measurable differences in TSS content at any time point (Figure 6c).

Given that there was no difference in TA or pH at any particular TSS concentration, the TA was lower when the main leaf number was reduced or there was no crop removal (Figure 7). There was a consistent relationship between pH and TA irrespective of the LA : FM ratio for all times of treatments, seasons and cultivars (Figure 8).

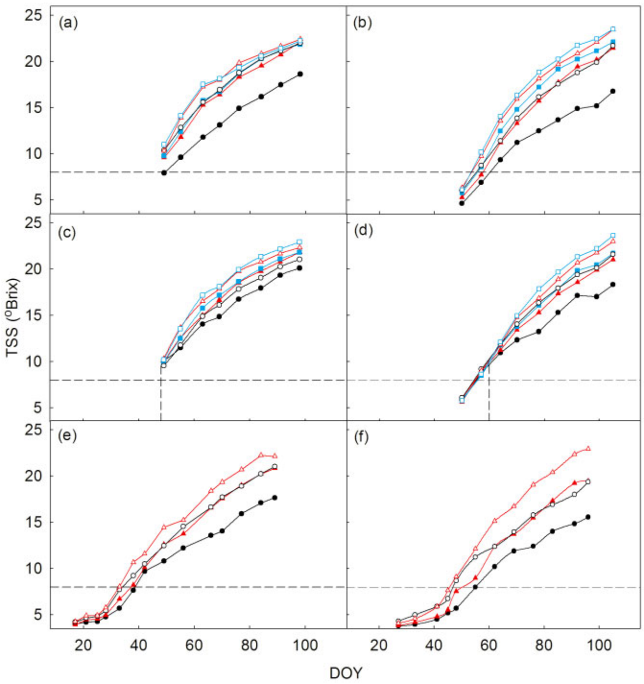

Figure 2. Effect of leaf area to fruit mass (LA : FM) ratio on total soluble solids accumulation (TSS) over time [day of the year (DOY)] in grapes for (a) Pinot Noir, LA : FM ratio altered at fruitset in 2009/10; (b) Sauvignon Blanc, LA : FM ratio altered at fruitset 2009/10; (c) Pinot Noir, LA : FM ratio altered at veraison in 2009/10; (d) Sauvignon Blanc, LA : FM ratio altered at veraison in 2009/10; (e) Pinot Noir, LA : FM ratio altered at fruitset in 2010/11; and (f) Sauvignon Blanc, LA : FM ratio altered at fruitset in 2010/11. Treatments: six main leaves per shoot and no crop removed (●); six main leaves per shoot and 50% crop removed (▲); six main leaves per shoot and 75% crop removed (■); 12 main leaves per shoot and no crop removed (○); 12 main leaves per shoot and 50% crop removed (△); and 12 main leaves per shoot and 75% crop removed (□). Vertical dashed lines (- -) indicate the time at which the LA : FM ratio manipulation was applied at veraison and the horizontal dashed lines (- -) indicate the DOY when 8°Brix was reached.

Berry composition and leaf area to fruit mass ratio at harvest

Crop removal had a greater effect than leaf number on harvest TSS (38 and 22% of total sum of squares, $P < 0.001$) with an important interaction (25% of total sum of squares, $P < 0.001$) (Tables 4,5). The interaction of reduced leaf number in combination with a high yield (low crop removal) resulted in the greatest reduction in harvest TSS accumulation for both times of

Table 2. Effect of main leaf number and crop removal treatments applied at fruitset on the accumulation of grape total soluble solids.

Cultivar	Main leaf number per shoot†	Proportion of crop removed (%)‡	Duration 8–14.2°Brix (days)§		Rate for 8–14.2 °Brix§	
			2009/10	2010/11	2009/10	2010/11
Pinot Noir	6	0	24.2c	28.2c	0.257a	0.222a
	6	50	15.4ab	19.6b	0.407bc	0.317bc
	6	75	13.7ab	NA	0.453cd	NA
	12	0	14.9ab	20.6b	0.420bc	0.301b
	12	50	10.7a	18.1ab	0.587f	0.344c
	12	75	11.4a	NA	0.552ef	NA
Sauvignon Blanc	6	0	29.8c	32.4c	0.229a	0.199a
	6	50	15.6ab	19.7b	0.404bc	0.316bc
	6	75	14.1ab	NA	0.44c	NA
	12	0	17.8b	19.8b	0.357b	0.317bc
	12	50	13.1ab	14.9a	0.475cde	0.416d
	12	75	11.7a	NA	0.532de	NA
LSD	–	–	5.68	4.24	0.081	0.040

Means within columns followed by different letters are significantly different from each other at $P < 0.05$ by Fisher's unprotected Least Significant Differences test (LSD). †Shoots were trimmed to the specified number of main leaves and laterals were removed. ‡Removal of a proportion of bunches relative to the control (0% crop removal). §Duration from 8 to 14.2°Brix as determined from exponential curve fits to each replicate where $y = a + br^x$, where x is the day of the year of measurement and all other parameters are fitted; 8°Brix was defined as a start point for maturation, and 14.2°Brix was the lowest measured °Brix value across all replicates at harvest (including veraison treatments). NA, not applicable.

Table 3. Effect of main leaf number and crop removal treatments applied at veraison in 2009/10 on the accumulation of grape total soluble solids.

Cultivar	Main leaf number per shoot†	Proportion of crop removed (%)‡	Date of 21°Brix	Duration 8–14.2°Brix (days)§	Rate for 8–14.2°Brix§	Duration 8–21°Brix (days)§
Pinot Noir	6	0	14 April cde (104)¶	22.6ef	0.281ab	61.3d
	6	50	2 April abcd (92)	15.6bcd	0.403cde	47.1abc
	6	75	31 March ab (90)	13.7abc	0.467ef	44.5abc
	12	0	9 April bcde (99)	15.8bcd	0.393cde	53.2cd
	12	50	26 March a (85)	11.7ab	0.534fg	39.7ab
	12	75	22 March a (81)	11.0a	0.570g	35.8a
Sauvignon Blanc	6	0	27 May f (147)	24.9f	0.261a	91.5e
	6	50	15 April e (105)	18.6de	0.336bc	50.6bcd
	6	75	11 April bcde (101)	16.5cd	0.377cd	46.5abc
	12	0	14 April de (104)	17.1cd	0.376cd	50.2bcd
	12	50	4 April abcde (94)	14.3abc	0.434de	39.1ab
	12	75	1 April abc (91)	13.7abc	0.453e	36.6a
LSD	–	–	6.36	4.17	0.075	6.25

Means within columns followed by different letters are significantly different from each other at $P < 0.05$ by Fisher's unprotected Least Significant Differences test (LSD). †Shoots were trimmed to the specified number of main leaves and laterals were removed. ‡Removal of a proportion of bunches relative to the control (0% crop removal). §Duration from 8 to 14.2°Brix and 8 to 21°Brix as determined from exponential curve fits to each replicate where $y = a + br^x$, where x is the DOY of measurement and all other parameters are fitted; 8°Brix was defined as a start point for maturation and 14.2°Brix was the lowest measured °Brix value across all replicates at harvest (including veraison treatments). ¶Values in brackets are day of the year.

LA : FM ratio manipulation (Tables 4,5). The two crop removal treatments resulted in TSS concentration at harvest higher than that for the 100% crop treatments for all 6-leaves treatments and most 12-leaves treatments, but the two crop removal treatments were not different to one another (Tables 4,5).

Harvest TSS concentration was the same among equivalent ratios at both times of LA : FM ratio manipulation for both seasons for all comparisons (Tables 4,5). There were few detectable differences in TA or pH at harvest for either time of LA : FM ratio manipulation (fruitset and veraison) for either cultivar

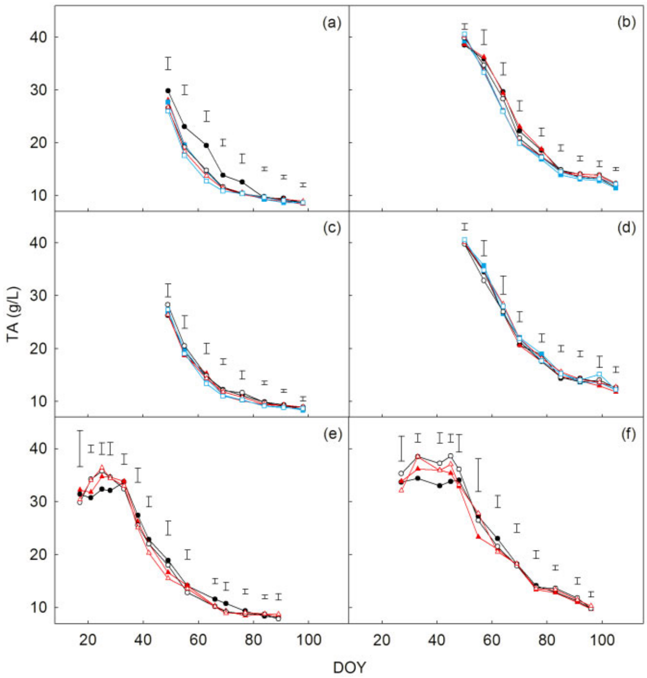

Figure 3. Effect of leaf area to fruit mass (LA : FM) ratio on grape titratable acidity (TA) over time [day of the year (DOY)] for (a) Pinot Noir, LA : FM ratio altered at fruitset in 2009/10; (b) Sauvignon Blanc, LA : FM ratio altered at fruitset 2009/10; (c) Pinot Noir, LA : FM ratio altered at veraison in 2009/10; (d) Sauvignon Blanc, LA : FM ratio altered at veraison in 2009/10; (e) Pinot Noir, LA : FM ratio altered at fruitset in 2010/11; and (f) Sauvignon Blanc, LA : FM ratio altered at fruitset in 2010/11. Treatments: six main leaves per shoot and no crop removed (●); six main leaves per shoot and 50% crop removed (▲); six main leaves per shoot and 75% crop removed (■); 12 main leaves per shoot and no crop removed (○); 12 main leaves per shoot and 50% crop removed (△); and 12 main leaves per shoot and 75% crop removed (□). Vertical bars at each time point represent least significant differences (LSD) for Fisher's unprotected LSD ($P < 0.05$).

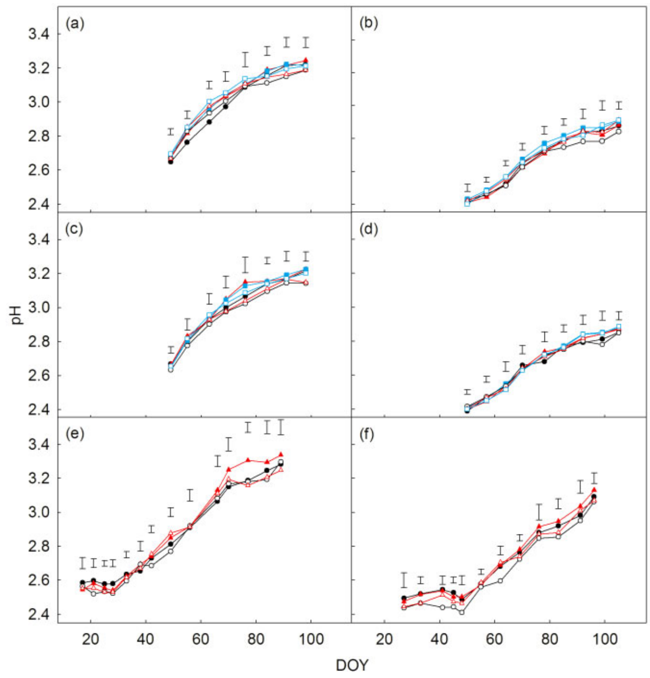

Figure 4. Effect of leaf area to fruit mass (LA : FM) ratio on grape pH over time [day of the year, (DOY)] for (a) Pinot Noir, LA : FM ratio altered at fruitset in 2009/10; (b) Sauvignon Blanc, LA : FM ratio altered at fruitset in 2009/10; (c) Pinot Noir, LA : FM ratio altered at veraison in 2009/10; (d) Sauvignon Blanc, LA : FM ratio altered at veraison in 2009/10; (e) Pinot Noir, LA : FM ratio altered at fruitset in 2010/11; and (f) Sauvignon Blanc, LA : FM ratio altered at fruitset in 2010/11. Treatments: six main leaves per shoot and no crop removed (●); six main leaves per shoot and 50% crop removed (▲); six main leaves per shoot and 75% crop removed (■); 12 main leaves per shoot and no crop removed (○); 12 main leaves per shoot and 50% crop removed (△); and 12 main leaves per shoot and 75% crop removed (□). Vertical bars at each time point represent least significant differences (LSD) for Fisher's unprotected LSD ($P < 0.05$).

(Tables 4,5). The yield and LA : FM ratio of both cultivars were similar at equivalent thinning and trimming treatments (Table 6).

Discussion

Manipulation of leaf area to fruit mass ratio influences onset and rate of total soluble solids accumulation

Removal of sinks (fruit) early in the season at fruitset or at veraison resulted in the same increase in the rate of TSS accumulation with few differences between cultivars (Tables 2,3). The magnitude of difference, however, in TSS concentration at harvest when sinks were removed at either time was less than when the source (leaf) was removed as well by shoot trimming, whereby the six-leaves full-crop treatments always resulted in the lowest TSS concentration at harvest (Tables 4,5). The greatest reduction in TSS rates for the source-limited treatment of six-leaves full crop was therefore a result of a combined effect of delaying onset (Parker et al. 2014b) and slowing TSS accumulation. The delay of this onset indicated the lack of source compensation during the flowering to veraison period. The smaller influence of crop removal during this period (Parker et al. 2014b) also indicated that fruits as sinks were not competing with leaf development and metabolism for carbohydrate resources. If this were the case, crop removal would have resulted in allocation of carbohydrates to leaves, which would have negated the delay caused by leaf removal. It does not exclude, however, the possibility that other competing sinks could contribute to the observed delay of veraison under low source conditions.

When the source–sink relationship was manipulated at veraison, which removed the possible confounding effect of changes in the time of veraison or fruit development, both leaf removal and crop removal altered TSS accumulation. The slower rate of TSS accumulation caused by reduced LA (source-limiting conditions in the case of six leaves and full crop) was counteracted by crop removal; this reduced the duration from 8 to 14.2°Brix and increased the rate of TSS accumulation. As a result, the rate of TSS accumulation of the 6-leaves 50% crop removal treatment was similar to that of the 12-leaves full-crop treatment (Table 3). This would suggest either that other sinks have little effect on TSS accumulation in the maturation phase, even under source-limited conditions, or that there is potentially some source compensation under source-limited conditions. In other research, photosynthesis rates increased at the whole-vine level when LA was reduced via trimming or removal of apical leaves (Petrie et al. 2000b, 2003) to compensate for the source limitation. As a result, any initial difference in carbohydrate production was compensated for shortly after leaf removal. In our study, however, reduced TSS accumulation for the six-leaves full-crop treatment

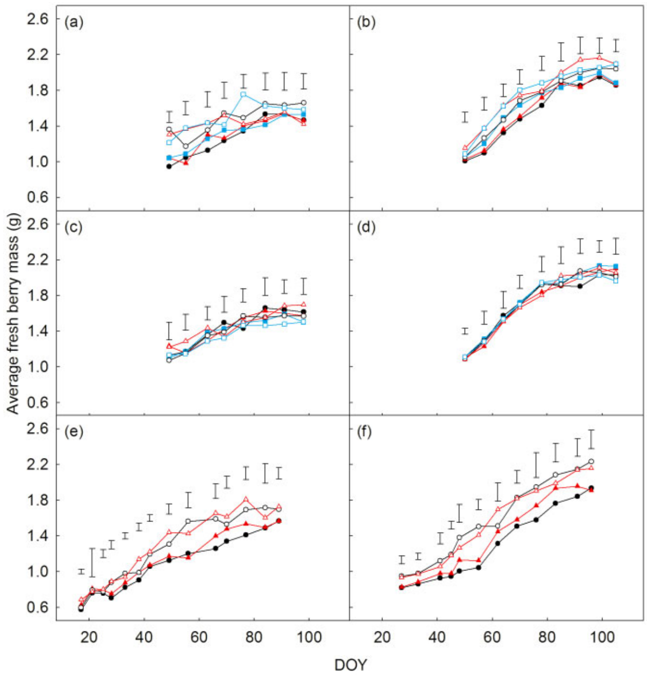

Figure 5. Effect of leaf area to fruit mass (LA : FM) ratio on the average grape fresh berry mass over time [day of the year (DOY)] for (a) Pinot Noir, LA : FM ratio altered at fruitset in 2009/10; (b) Sauvignon Blanc, LA : FM ratio altered at fruitset 2009/10; (c) Pinot Noir, LA : FM ratio altered at veraison in 2009/10; (d) Sauvignon Blanc, LA : FM ratio altered at veraison in 2009/10; (e) Pinot Noir, LA : FM ratio altered at fruitset in 2010/11; and (f) Sauvignon Blanc, LA : FM ratio altered at fruitset in 2010/11. Treatments: six main leaves per shoot and no crop removed (●); six main leaves per shoot and 50% crop removed (▲); six main leaves per shoot and 75% crop removed (■); 12 main leaves per shoot and no crop removed (○); 12 main leaves per shoot and 50% crop removed (△); and 12 main leaves per shoot and 75% crop removed (□). Vertical bars at each time point represent least significant differences (LSD) for Fisher's unprotected LSD ($P < 0.05$).

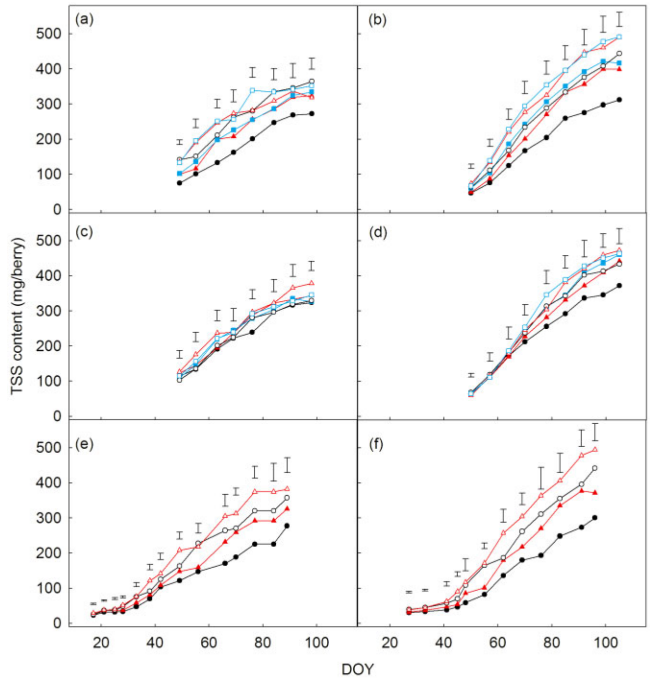

Figure 6. Effect of leaf area to fruit mass (LA : FM) ratio on the average fresh total soluble solids (TSS) content) over time [day of the year (DOY)] for (a) Pinot Noir, LA : FM ratio altered at fruitset in 2009/10; (b) Sauvignon Blanc, LA : FM ratio altered at fruitset 2009/10; (c) Pinot Noir, LA : FM ratio altered at veraison in 2009/10; (d) Sauvignon Blanc, LA : FM ratio altered at veraison in 2009/10; (e) Pinot Noir, LA : FM ratio altered at fruitset in 2010/11; and (f) Sauvignon Blanc, LA : FM ratio altered at fruitset in 2010/11. Treatments: six main leaves per shoot and no crop removed (●); six main leaves per shoot and 50% crop removed (▲); six main leaves per shoot and 75% crop removed (■); 12 main leaves per shoot and no crop removed (○); 12 main leaves per shoot and 50% crop removed (△); and 12 main leaves per shoot and 75% crop removed (□). Vertical bars at each time point represent least significant differences (LSD) for Fisher's unprotected LSD ($P < 0.05$).

indicated that there was insufficient source compensation (remobilisation or activity) for the reduced LA at high sink demand (Figure 2, Tables 2,3). Furthermore, the number of days to reach a target of 21°Brix was often heavily extrapolated from the curve fits (see Figure 2c,d and Table 3) and therefore did not correspond to a plausible or realistic DOY; these values, however, illustrate the impossibility of reaching that target under the source-limited conditions tested here.

Duchêne et al. (2012) suggested that the rate of TSS accumulation is affected by temperature. The time of veraison and the ripening phase are later for Sauvignon Blanc than for Pinot Noir, and it could therefore be anticipated that the rate of TSS accumulation for Sauvignon Blanc vines may be confounded by lower temperature and shorter day length during ripening. Although Sauvignon Blanc had a lower LA : FM ratio and a later development when compared with that of Pinot Noir, these factors had little effect between the cultivars on the TSS accumulation (when comparing rates between the two cultivars for the same treatments) (Tables 2, 3). The only difference was it took longer to reach a target of 21°Brix for Sauvignon Blanc vines compared with those of Pinot Noir when vines were trimmed to six leaves at veraison (Table 3).

Reduced LA caused a reduction in berry mass for both times of LA : FM manipulation; this trend is in agreement with previous findings (Ollat and Gaudillere 1998, Parker et al. 2014a). Ollat and Gaudillere (1998) attributed the reduced berry size in response to leaf removal, to restricted assimilate supply during the first growth period in berry development: fresh and dry mass accumulation was reduced and source-limited vines entered the lag phase early compared with vines with high source levels (even though they displayed a subsequent delay in the onset of ripening). Here, for LA : FM manipulation at fruitset, the difference in TSS content mirrored that of TSS concentration, although the main effect of LA became more prominent (Figure 6), reflecting the difference in fresh berry mass as a result of reduced source size (Figure 5). Early rates of TSS accumulation at the same level of maturity (8–14.2°Brix) were slower for reduced source size, indicating not only sink size, but also TSS import rates were affected by reduced LA (Tables 2,3). In agreement with this, when crop was removed at fruitset, the fresh berry mass increased even when veraison was not advanced (Figure 5). The rate of increase in TSS concentration was faster when crop was removed compared with no crop removal (Table 2); therefore, the increase in TSS content may be due to one or both factors: increased source supply resulting in increased berry size or faster TSS accumulation rates (import).

For Sauvignon Blanc where the LA : FM manipulation occurred at veraison, the TSS content in general mirrored TSS concentration (Figure 2 compared with Figure 6). Given that there were fewer differences in fresh berry mass due

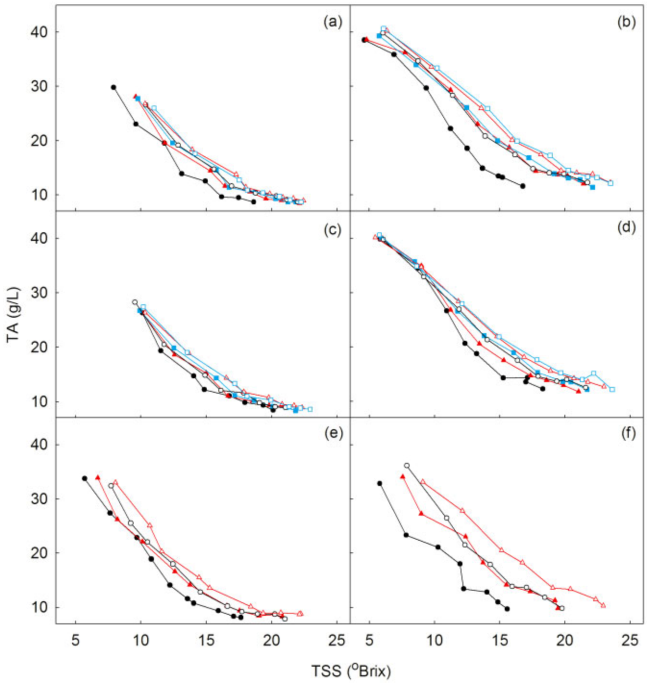

Figure 7. Effect of leaf area to fruit mass (LA : FM) ratio on the relationship between grape total soluble solids (TSS) accumulation and titratable acidity (TA) for (a) Pinot Noir, LA : FM ratio altered at fruitset in 2009/10; (b) Sauvignon Blanc, LA : FM ratio altered at fruitset 2009/10; (c) Pinot Noir, LA : FM ratio altered at veraison in 2009/10; (d) Sauvignon Blanc, LA : FM ratio altered at veraison in 2009/10; (e) Pinot Noir, LA : FM ratio altered at fruitset in 2010/11; and (f) Sauvignon Blanc, LA : FM ratio altered at fruitset in 2010/11. Treatments: six main leaves per shoot and no crop removed (●); six main leaves per shoot and 50% crop removed (▲); six main leaves per shoot and 75% crop removed (■); 12 main leaves per shoot and no crop removed (○); 12 main leaves per shoot and 50% crop removed (△); and 12 main leaves per shoot and 75% crop removed (□).

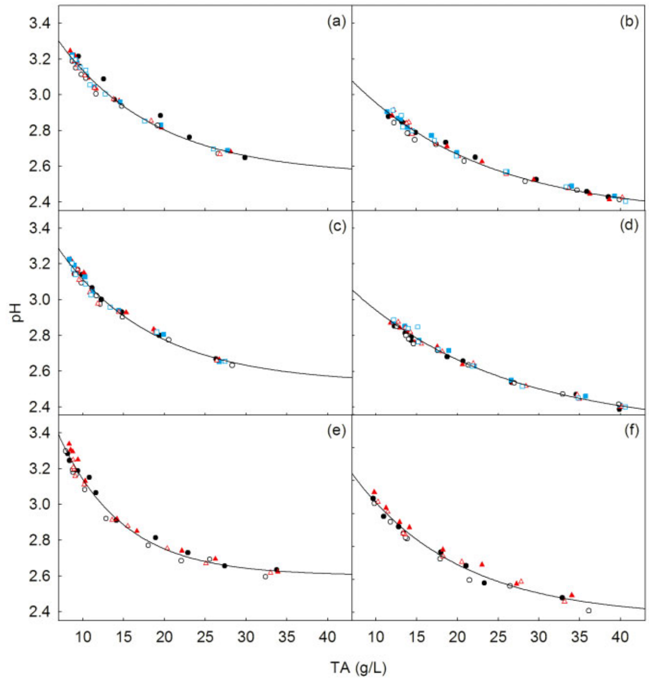

Figure 8. Effect of leaf area to fruit mass (LA : FM) ratio on the relationship between grape titratable acidity (TA) and pH for (a) Pinot Noir, LA : FM ratio altered at fruitset in 2009/10 ($R^2 = 0.98$, $y = 2.55 + 1.35\ (0.92^x)$); (b) Sauvignon Blanc, LA : FM ratio altered at fruitset 2009/10 ($R^2 = 0.98$, $y = 2.32 + 1.17\ (0.94^x)$); (c) Pinot Noir, LA : FM ratio altered at veraison in 2009/10 ($R^2 = 0.98$, $y = 2.53 + 1.39\ (0.92^x)$); (d) Sauvignon Blanc, LA : FM ratio altered at veraison in 2009/10 ($R^2 = 0.99$, $y = 2.27 + 1.14\ (0.95^x)$); (e) Pinot Noir, LA : FM ratio altered at fruitset in 2010/11 ($R^2 = 0.98$, $y = 2.6 + 1.93\ (0.88^x)$); (f) Sauvignon Blanc, LA : FM ratio altered at fruitset in 2010/11($R^2 = 0.97$, $y = 2.37 + 1.52\ (0.93^x)$). Treatments: six main leaves per shoot and no crop removed (●); six main leaves per shoot and 50% crop removed (▲); six main leaves per shoot and 75% crop removed (■); 12 main leaves per shoot and no crop removed (○); 12 main leaves per shoot and 50% crop removed (△); and 12 main leaves per shoot and 75% crop removed (□).

to source limitation (Figure 5), the TSS content difference between 6-leaf and 12-leaf treatments was less pronounced (Figure 6). For LA : FM manipulation at veraison for Pinot Noir, there were few differences in TSS content, most likely reflecting the lack of difference in average fresh berry mass (which were variable) (Figure 5). Further work would be necessary on a per berry basis to see if TSS content differences could be observed for Pinot Noir.

A consistent leaf cover in the fruiting zone is maintained when shoots are trimmed as opposed to when leaves are removed in the fruiting zone. Therefore, the shoot-trimming treatments minimised the confounding effects of fruit exposure on fruit development. Laterals were removed in this study, however, to allow a precise control over leaf number and consequently LA. The relative contribution of laterals on the time of veraison and maturity warrants further investigation.

In this current study, the yields were similar between Pinot Noir and Sauvignon Blanc irrespective of the use of different rootstock (Table 6). Nuzzo and Matthews (2006) found that when investigating the role of rootstock and crop level, reduced soluble solids was related to crop level and not rootstock. Yield parameters can be influenced by rootstock choice, although there has been little effect observed of rootstock on maturation parameters, such as TSS and/or TA (Walker et al. 2000, Nuzzo and Matthews 2006, Di Filippo and Vila 2011, Harbertson and Keller 2011, Keller et al. 2012). Rootstocks still may need to be considered in future work concerning a greater range of berry components or if yield difference is substantial between different rootstocks as illustrated in Jones et al. (2009).

The influence of leaf area to fruit mass ratio on other maturation parameters

A reduced LA : FM ratio decreased TSS without altering TA or pH; therefore, it is possible to delay TSS accumulation to reach a target concentration without all other berry components also being delayed (Figures 7,8). The TSS : TA ratio, which can be used as a maturity index, changed in the presence of a higher yield, where TA was lower relative to the target TSS, indicating that this relationship can be desynchronised (Figures 2,3,7). This highlights the need to understand the repercussions of altering the LA : FM ratio to increase potential yield: even if target TSS are met, the balance between berry components in the berry is offset by such manipulations.

Photosynthetic activity was not measured for the LA : FM ratio treatments tested, but the results indicated that a reduced source size had no effect on the TA (Figure 3 and Tables 4,5). Although tartaric and malic acids, which contribute over 90% of the total TA in grape berries (Coombe and Dry 1992), are dependent on photosynthesis for their formation (via different biochemical pathways), a lack of photosynthesis is not generally

Table 4. Effect of main leaf number and crop removal treatments at fruitset and veraison in 2009/10 on the total soluble solids, titratable acidity and pH of grapes at harvest.

Timing of LA : FM ratio manipulation	Main leaf number per shoot†	Proportion of crop removed (%)‡	TSS (°Brix)		TA (g tartrate/L)		pH	
			Pinot Noir	Sauvignon Blanc	Pinot Noir	Sauvignon Blanc	Pinot Noir	Sauvignon Blanc
Fruitset	6	0	18.6a	16.8a	8.65a	11.6ab	3.22bc	2.88abc
	6	50	22.1de	21.4c	8.44a	12.0abcd	3.25c	2.88abc
	6	75	21.9cd	22.1cde	8.65a	11.4a	3.22bc	2.91c
	12	0	22.0cde	21.7cd	8.69a	12.3bcd	3.19ab	2.84a
	12	50	22.4de	23.5ef	8.93a	12.2abcd	3.19ab	2.91c
	12	75	22.3de	23.5ef	8.66a	12.1abcd	3.21bc	2.91c
Veraison	6	0	20.1b	18.3b	8.48a	12.3bcd	3.22bc	2.85ab
	6	50	21.8cd	21.0c	8.47a	11.8abc	3.23bc	2.87abc
	6	75	21.8cd	21.7cd	8.36a	12.2abcd	3.23bc	2.88abc
	12	0	21.1bc	21.6cd	8.94a	12.6cd	3.14a	2.85ab
	12	50	22.3de	23.0def	8.97a	12.7d	3.15a	2.88abc
	12	75	23.0e	23.6f	8.65a	12.2abcd	3.20bc	2.89bc
LSD	–	–	1.01	1.48	0.73	0.858	0.052	0.043

Means within columns followed by different letters are significantly different from each other at $P < 0.05$ by Fisher's unprotected Least Significant Differences test (LSD). †Shoots were trimmed to the specified number of main leaves and laterals were removed. ‡Removal of a proportion of bunches relative to the control (0% crop removal). LA : FM, leaf area to fruit mass ratio; NA, not applicable; TA, titratable acidity; TSS, total soluble solids.

Table 5. Effect of main leaf number and crop removal treatments at fruitset in 2010/11 harvest values for grape total soluble solids, titratable acidity and pH of grapes at harvest.

Main leaf number per shoot†	Proportion of crop removed (%)‡	TSS (°Brix)		TA (g tartrate/L)		pH	
		Pinot Noir	Sauvignon Blanc	Pinot Noir	Sauvignon Blanc	Pinot Noir	Sauvignon Blanc
6	0	17.7a	15.6a	8.13a	9.82a	3.28ab	3.09ab
6	50	20.8b	19.5b	8.31a	9.70a	3.34b	3.13b
12	0	21.0b	19.8b	7.86a	9.85a	3.30ab	3.06a
12	50	22.1b	23.0c	8.76a	10.28a	3.25a	3.07ab
LSD	–	1.39	1.67	1.22	0.954	0.087	0.062

Means within columns followed by different letters are significantly different from each other at $P < 0.05$ by Fisher's unprotected Least Significant Differences test (LSD). †Shoots were trimmed to the specified number of main leaves and laterals were removed. ‡Removal of a proportion of bunches relative to the control (0% crop removal). LA : FM, leaf area to fruit mass ratio; NA, not applicable; TA, titratable acidity; TSS, total soluble solids.

limiting to TA (Jackson and Lombard 1993). This could explain why no difference in TA was detected here.

Kliewer (1973) showed that TA and malic acid must concentration were negatively correlated with temperature; the possibility that differences in malic acid concentration could occur under the different source levels tested here cannot be excluded. If there were a difference found in other studies, it would be important to determine whether this is due to the shift in timing of TSS accumulation relative to little change in the timing of change in acid concentration, or whether fruit exposure or source limitations were having an effect.

Pinot Noir generally had a pH value at harvest 0.2–0.4 greater than that of Sauvignon Blanc (Tables 4,5), confirming previous studies that have shown that pH as a measure at maturity is strongly cultivar dependent (van Leeuwen et al. 2004). Further analysis of TA and pH at each time point indicated that the response curve over time was also not affected by the LA : FM ratio (Figure 8). In practice, if the date of harvest was altered, the effect of LA : FM ratio manipulation on TA or pH would not need to be anticipated, only that in response to the change of date.

Other berry components important for winemaking also need to be considered in future work to understand the effect of the LA : FM ratio for a given cultivar and whether the berry components respond in a way similar to each other at the same LA : FM ratio or are desynchronised; these include anthocyanins, thiol precursors, phenolic substances and amino acids.

Implications for modelling phenology and maturation

The method and time of LA : FM ratio manipulation, which alter the source–sink balance, define the relationship between the LA : FM ratio and berry component development and

Table 6. Effect of cultivar, main leaf number per shoot and crop removal at fruitset and veraison on grapevine yield and leaf parameters.

Cultivar	Main leaf number per shoot†	Proportion of crop removed (%)‡	Yield (kg/m)			LA : FM (m^2/kg)		
			Fruitset		Veraison	Fruitset		Veraison
			2009/10	2010/11	2009/10	2009/10	2010/11	2009/10
Pinot Noir	6	0	4.10f	5.65b	4.02c	0.29a	0.28a	0.29a
	6	50	1.93bcde	2.84a	2.29b	0.54ab	0.40bc	0.55abc
	6	75	1.16a	–	1.30a	0.98bc	–	0.91d
	12	0	3.82f	5.96b	4.36c	0.45a	0.40bc	0.46ab
	12	50	1.98cde	3.82a	2.44b	0.99cd	0.72d	0.96d
	12	75	1.34ab	–	1.21a	1.85e	–	1.75e
Sauvignon Blanc	6	0	3.97f	5.21b	4.22c	0.27a	0.25ab	0.29a
	6	50	2.24de	3.04a	2.53b	0.54ab	0.49c	0.46ab
	6	75	1.54abc	–	1.62a	0.80bc	–	0.78cd
	12	0	4.34f	5.97b	4.07c	0.51a	0.46c	0.58bc
	12	50	2.34e	3.38a	2.42b	1.06cd	0.91e	1.01d
	12	75	1.64abcd	–	1.47a	1.24d	–	1.60e
LSD	–	–	0.610	1.049	0.570	0.277	0.179	0.271

Means within columns followed by different letters are significantly different from each other at $P < 0.05$ by Fisher's unprotected Least Significant Differences test (LSD).†Shoots were trimmed to the specified number of main leaves and laterals were removed.‡Removal of a proportion of bunches relative to the control (0% crop removal).LA : FM, leaf area to fruit mass ratio.

harvest composition for a given cultivar. Kliewer and Dokoozlian (2005) suggested an LA : FM ratio of 0.8–1.2 m^2/kg as a target to ensure a target berry composition was achieved without source or sink constraint. The results presented here also show that when and how this ratio is manipulated are of importance, which would need to be considered when modelling phenology and maturation. The shifts in the time of development and maturity as a result of LA : FM ratio manipulation offer a potential way to alter the time of phenological stages and the maturation phase in response to increased temperature or increased CO_2 concentration; these management changes could therefore offer one solution to counter the effects of climate change. Sadras and Petrie (2011a,b) have highlighted the importance of understanding if the onset of maturation, maturation rates or both are altered in response to temperature increase; using historical data, they found that when modelling maturity in response to increased temperature the onset of maturation rather than the rate of TSS accumulation is changed. We have found that in response to LA : FM ratio manipulation, both components need to be considered for modelling TSS accumulation. Therefore, thermal time can be helpful in predicting veraison and the onset of maturation (Caffarra and Eccel 2010, Duchêne et al. 2010, Parker et al. 2011), and it is possible that an optimal combination of LA : FM ratio and thermal time of veraison for a given cultivar could be determined and incorporated in a temperature-driven modelling framework. Interrelationships between different berry components important for target composition would also need further consideration in this context if LA : FM ratio manipulation was to be used as a tool to counter climate change effects on advancing development and maturity.

Conclusions

The time of veraison, the time to reach target TSS concentration and the rate of TSS accumulation were influenced by manipulation of the LA : FM ratio. Leaf removal via trimming represents a way to shift the timing of maturity, whereas both leaf removal and crop removal represent ways to manipulate TSS accumulation during berry maturation without affecting the other berry components of TA or pH.

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References

Caffarra, A. and Eccel, E. (2010) Increasing the robustness of phenological models for *Vitis vinifera* cv. Chardonnay. International Journal of Biometeorology **54**, 255–267.

Candolfi-Vasconcelos, M.C. and Koblet, W. (1991) Influence of partial defoliation on gas-exchange parameters and chlorophyll content of field-grown grapevines – mechanisms and limitations of the compensation capacity. Vitis **30**, 129–141.

Coombe, B.G. (1995) Adoption of a system for identifying grapevine growth stages. Australian Journal of Grape and Wine Research **1**, 104–110.

Coombe, B.G. and Dry, P.R. (1992) Viticulture. Volume 1. Resources (Winetitles: Adelaide, SA, Australia) p. 376.

Di Filippo, M. and Vila, H. (2011) Influence of different rootstocks on the vegetative and reproductive performance of *Vitis vinifera* L. Malbec under irrigated conditions. Journal International des Sciences de la Vigne et du Vin **45**, 75–84.

Duchêne, E. and Schneider, C. (2005) Grapevine and climatic changes: a glance at the situation in Alsace. Agronomy for Sustainable Development **25**, 93–99.

Duchêne, E., Huard, F., Dumas, V., Schneider, C. and Merdinoglu, D. (2010) The challenge of adapting grapevine varieties to climate change. Climate Research **41**, 193–204.
Duchêne, E., Dumas, V., Jaegli, N. and Merdinoglu, D. (2012) Deciphering the ability of different grapevine genotypes to accumulate sugar in berries. Australian Journal of Grape and Wine Research **18**, 319–328.
Guidoni, S., Allara, P. and Schubert, A. (2002) Effect of cluster thinning on berry skin anthocyanin composition of *Vitis vinifera* cv. Nebbiolo. American Journal of Enology and Viticulture **53**, 224–226.
Harbertson, J.F. and Keller, M. (2011) Rootstock effects on deficit-irrigated winegrapes in a dry climate: grape and wine composition. American Journal of Enology and Viticulture **63**, 40–48.
Hunter, J.J. and Visser, J.H. (1988) The effect of partial defoliation, leaf position and developmental stage of the vine on the photosynthetic activity of *Vitis vinifera* L. cv. Cabernet Sauvignon. South African Journal for Enology and Viticulture **9**, 9–15.
Jackson, D.I. and Lombard, P.B. (1993) Environmental and management-practices affecting grape composition and wine quality – a review. American Journal of Enology and Viticulture **44**, 409–430.
Jones, G.V., White, M.A., Cooper, O.R. and Storchmann, K. (2005) Climate change and global wine quality. Climatic Change **73**, 319–343.
Jones, T.H., Cullis, B.R., Clingeleffer, P.R. and Rühl, E.H. (2009) Effects of novel hybrid and traditional rootstocks on vigour and yield components of Shiraz grapevines. Australian Journal of Grape and Wine Research **15**, 284–292.
Keller, M., Mills, L.J., Wample, R.L. and Spayd, S.E. (2005) Cluster thinning effects on three deficit-irrigated *Vitis vinifera* cultivars. American Journal of Enology and Viticulture **56**, 91–103.
Keller, M., Mills, L.J. and Harbertson, J.F. (2012) Rootstock effects on deficit-irrigated winegrapes in a dry climate: vigor, yield formation, and fruit ripening. American Journal of Enology and Viticulture **63**, 29–39.
Kliewer, W.M. (1973) Berry composition of *Vitis vinifera* cultivars as influenced by photo-temperatures and nycto-temperatures during maturation. Journal of the American Society for Horticultural Science **98**, 153–159.
Kliewer, W.M. and 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.
Moncur, M.W., Rattigan, K., Mackenzie, D.H. and McIntyre, G.N. (1989) Base temperatures for budbreak and leaf appearance of grapevines. American Journal of Enology and Viticulture **40**, 21–26.
Naor, A., Gal, Y. and Bravdo, B. (2002) Shoot and cluster thinning influence vegetative growth, fruit yield, and wine quality of 'Sauvignon Blanc' grapevines. Journal of the American Society for Horticultural Science **127**, 628–634.
Nuzzo, V. and Matthews, M.A. (2006) Response of fruit growth and ripening to crop level in dry-farmed Cabernet Sauvignon on four rootstocks. American Journal of Enology and Viticulture **57**, 314–324.
Ollat, N. and Gaudillere, J.P. (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.
Parker, A.K. (2012) Modelling phenology and maturation of the grapevine *Vitis vinifera* L.: varietal differences and the role of leaf area to fruit weight ratio manipulations. PhD Thesis, Lincoln University, Lincoln, New Zealand.
Parker, A.K., Garcia de Cortázar-Atauri, I., van Leeuwen, C. and Chuine, I. (2011) General phenological model to characterise the timing of flowering and veraison of *Vitis vinifera* L. Australian Journal of Grape and Wine Research **17**, 206–216.
Parker, A.K., Trought, M.C.T., Hofmann, R.W., McLachlan, A.R.G. and van Leeuwen, C. (2014a) The influence of two methods of crop removal at different leaf areas on maturation of Sauvignon blanc (*Vitis vinifera* L.). Journal International des Sciences de la Vigne et du Vin **48**, 43–50.
Parker, A.K., Hofmann, R.W., van Leeuwen, C., McLachlan, A.R.G. and Trought, M.C.T. (2014b) Leaf area to fruit mass ratio determines the time of veraison in Sauvignon Blanc and Pinot Noir grapevines. Australian Journal of Grape and Wine Research **20**, 422–431.
Petrie, P.R. and Clingeleffer, P.R. (2006) Crop thinning (hand versus mechanical), grape maturity and anthocyanin concentration: outcomes from irrigated Cabernet Sauvignon (*Vitis vinifera* L.) in a warm climate. Australian Journal of Grape and Wine Research **12**, 21–29.
Petrie, P.R. and Sadras, V.O. (2008) Advancement of grapevine maturity in Australia between 1993 and 2006: putative causes, magnitude of trends and viticultural consequences. Australian Journal of Grape and Wine Research **14**, 33–45.
Petrie, P.R., Trought, M.C.T. and Howell, G.S. (2000a) Fruit composition and ripening of Pinot Noir (*Vitis vinifera* L.) in relation to leaf area. Australian Journal of Grape and Wine Research **6**, 46–51.
Petrie, P.R., Trought, M.C.T. and Howell, G.S. (2000b) Influence of leaf ageing, leaf area and crop load on photosynthesis, stomatal conductance and senescence of grapevine (*Vitis vinifera* L. cv. Pinot Noir) leaves. Vitis **39**, 31–36.
Petrie, P.R., Trought, M.C.T., Howell, G.S. and Buchan, G.D. (2003) The effect of leaf removal and canopy height on whole-vine gas exchange and fruit development of *Vitis vinifera* L. Sauvignon Blanc. Functional Plant Biology **30**, 711–717.
Poni, S. and Giachino, E. (2000) Growth, photosynthesis and cropping of potted grapevines (*Vitis vinifera* L. cv. Cabernet Sauvignon) in relation to shoot trimming. Australian Journal of Grape and Wine Research **6**, 216–226.
Pouget, R. (1967) Méthode d'appréciation de l'évolution physiologique des bourgeons pendant la phase de pre-débourrement: application à l'étude comparée du debourrement de la vigne. Vitis **6**, 294–302.
Sadras, V.O. and Petrie, P.R. (2011a) Quantifying the onset, rate and duration of sugar accumulation in berries from commercial vineyards in contrasting climates of Australia. Australian Journal of Grape and Wine Research **17**, 190–198.
Sadras, V.O. and Petrie, P.R. (2011b) Climate shifts in south-eastern Australia: early maturity of Chardonnay, Shiraz and Cabernet Sauvignon is associated with early onset rather than faster ripening. Australian Journal of Grape and Wine Research **17**, 199–205.
Stoll, M., Scheidweiler, M., Lafontaine, M. and Schultz, H.R. (2011) Possibilities to reduce the velocity of berry maturation through various leaf area to fruit ratio modifications in *Vitis vinifera* L. Riesling. Progrès Agricoles et Viticole **127**, 68–71.
van Leeuwen, C., Friant, P., Chone, X., Tregoat, O., Koundouras, S. and Dubourdieu, D. (2004) Influence of climate, soil, and cultivar on terroir. American Journal of Enology and Viticulture **55**, 207–217.
Walker, R.R., Read, P.E. and Blackmore, D.H. (2000) Rootstock and salinity effects on rates of berry maturation, ion accumulation and colour development in Shiraz grapes. Australian Journal of Grape and Wine Research **6**, 227–239.
Webb, L.B., Whetton, P.H. and Barlow, E.W.R. (2007) Modelled impact of future climate change on the phenology of winegrapes in Australia. Australian Journal of Grape and Wine Research **13**, 165–175.
Winkler, A.J., Cook, J.A., Kliewer, W.M. and Lider, L.A. (1974) General viticulture (University of California Press: Berkley, CA, USA) p. 710.

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