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Effects of canopy management practices on grapevine bud fruitfulness

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ABSTRACT

Background and aims: Bud fruitfulness is a key component of grapevine reproductive performance as it determines crop production for the following growing season. While canopy microclimate can impact bud fruitfulness, the effects of canopy management practices on bud fruitfulness are not well known. The objective of this study was to investigate the effects of common canopy management practices on bud fruitfulness and the relationships with shoot growth capacity, bud microclimate and bud carbohydrate level.
Methods and results: Different canopy management practices, (shoot thinning, bunch thinning, leaf removal and lighter pruning) were applied to Semillon and Shiraz grapevines (*Vitis vinifera* L.). Light interception at the bud zone was measured after canopy management practices were applied. Bud fruitfulness at dormancy was assessed using bud dissection analysis. The number and size of inflorescence primordia, and the incidence of primary bud necrosis were recorded. The results were correlated with measurements of shoot growth capacity and carbohydrate content of buds and canes.
Conclusions: Bud fruitfulness was mostly influenced by bud light interception, while the size of inflorescence primordia was positively correlated with shoot growth capacity and the carbohydrate level of buds. By altering canopy microclimate, canopy management practices can be used to manipulate bud fruitfulness and potentially bunch size.
Significance and impact of the study: This study provides novel information on the impact of canopy management on grapevine bud fruitfulness and the size of inflorescence primordia. These findings can be used to make more informed vineyard management decisions for better yield control.

KEYWORDS

inflorescence primordia, primary bud necrosis, bud dissection, microclimate, yield prediction

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INTRODUCTION

In grapevine, bud fruitfulness is defined as the formation of inflorescence primordia (IP) in mature latent buds (Srinivasan and Mullins, 1981; Dry, 2000). The number and size of IP play a key role in yield variation as they form the potential yield for the next season (May and Antcliff, 1973; Dry, 2000; Sánchez and Dokoozlian, 2005). It is well established that the main components of grapevine yield are bunch number per vine and berry number per bunch, which together can account for about 90 % of seasonal yield variation (Clingeleffer *et al.*, 2001; Guilpart *et al.*, 2014). Actual fruitfulness (number of bunches per shoot) can be predicted early on by counting the number of IP in compound buds (Williams, 2000; Rawnsley and Collins, 2005). The branching level of IP (indicated by its size) determines flower number on an inflorescence after budburst (Dunn and Martin, 2007; Guilpart *et al.*, 2014) and relates to potential bunch weight (Dry, 2000).

A grapevine compound bud is normally composed of one large primary latent bud and two or more small secondary latent buds (Pratt, 1974). Primary bud necrosis (PBN) is a physiological disorder that results in the death of the primary bud during bud initiation (Morrison and Iodi, 1990; Dry and Coombe, 1994; Collins *et al.*, 2006). In Australia, Shiraz was found to be the variety most susceptible to PBN and it has been linked to low yields in some vineyards (Dry and Coombe, 1994; Rawnsley and Collins, 2005). PBN can reduce bud fruitfulness as the secondary buds, which enlarge and burst to compensate for the loss of the primary bud, are normally less fruitful (Dry, 2000; Rawnsley and Collins, 2005; Kavoosi *et al.*, 2012). The reduction in bunch number and decrease in bunch weight has been reported in shoots arising from secondary buds when PBN occurred (Dry and Coombe, 1994). Bud dissection analysis involves recording the number and size of IP and the incidence of PBN before or during grapevine dormancy. It can be conducted as early as 10 months before harvest (Antcliff and Webster, 1955) and is useful for early yield prediction (Rawnsley and Collins, 2005).

Bud fruitfulness varies depending on variety, rootstock, node position and shoot orientation (May and Cellier, 1973; Cox *et al.*, 2012; Noyce *et al.*, 2016). A series of exogenous and endogenous factors influencing bud fruitfulness have been summarised by Li-Mallet *et al.* (2016). Briefly, environmental factors, such as air temperature, light intensity, mineral nutrition, and water and nitrogen supply, have an impact on the formation of IP. Also, the interaction of endogenous hormones, such as gibberellins and cytokinins, can regulate the initiation and development of IP (Srinivasan and Mullins, 1980; Li-Mallet *et al.*, 2016) and occurrence of PBN (Collins and Rawnsley, 2008). Grapevine capacity and vigour are often measured by cane length, internode length and diameter, as well as shoot growth rate (Wolf and Warren, 1995; Rawnsley and Collins, 2005). It is generally considered that excessive vigour is the main reason for a high incidence of PBN (Dry and Coombe, 1994; Rawnsley and Collins, 2005). In addition, the carbohydrate status during budburst can influence bud fruitfulness as the actively growing shoot tips, young leaves and inflorescences strongly compete for carbohydrate reserves with the compound bud (Buttrose, 1966; Candolfi-Vasconcelos and Koblet, 1990). Hence, IP initiation and differentiation can be suppressed by limited carbon reserves.

Canopy management plays a key role in commercial vineyards for seasonally sustainable production. A number of practices are used with the aim of improving canopy structure in order to optimise total photosynthesis, reach a balance between vegetative and reproductive growth, and ensure fruit obtains sufficient exposure to sunlight (Smart and Robinson, 1991; Coombe and Dry, 1992). Canopy management can be used to manipulate canopy microclimate factors, such as light intensity and temperature; both of which are positively correlated to the formation of IP in late spring (Buttrose, 1969; Dry, 2000; Sánchez and Dokoozlian, 2005). Bud fruitfulness may be improved by light as a result of its effect on photosynthesis, and subsequent carbohydrate availability, or its direct effect on the bud itself (Vasconcelos *et al.*, 2009; Li-Mallet *et al.*, 2016).

Fruitfulness can be manipulated by carrying out canopy management (Dry, 2000). Reynolds *et al.* (1994) carried out shoot thinning at three shoot densities (16, 26 and 36 shoots per metre of row) and found that the lowest shoot density resulted in highest bunch number per shoot. However, severe shoot thinning (up to 85 % of shoots removed) resulted in increased vigour of the remaining shoots and increased incidence of PBN (Dry and Coombe, 1994; Dry, 2000). Ames *et al.* (2016) also found that improved light

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conditions resulting from shoot thinning did not increase bud fruitfulness. Light pruning, such as when double nodes are left (Morris *et al.*, 1983) or 25 % more nodes are retained (Zabadal *et al.*, 2002), has resulted in reduced node fruitfulness. Meanwhile, leaf removal in the bunch zone at fruit set has been shown to increase light intensity in the renewal area and to increase bunch number per shoot and berry number per bunch for the following season (Dry, 2000). Conversely, other studies on leaf removal have reported no carry-over effects on bud fruitfulness for the next season (Percival *et al.*, 1994; Intrieri *et al.*, 2008; Palliotti *et al.*, 2012; Intrigliolo *et al.*, 2014). A study by Sánchez and Dokoozlian (2005) investigated the effect of bud microclimate on bud fruitfulness by setting up discrete light exposure levels through pruning and shoot positioning. It was found that shoot light exposure, rather than light interception by individual buds, had a significant impact on IP number and size (Sánchez and Dokoozlian, 2005). This implies that higher photoassimilatory capacity and subsequent carbohydrates levels may be important in IP induction and differentiation.

Research has been conducted worldwide to determine how canopy management practices affect vine growth and fruit quality. However, to our knowledge, little research has been conducted on the effects of canopy management on bud fruitfulness, especially the branching level of inflorescence primordia. This study aimed to investigate how the common canopy management practicesof shoot thinning, bunch thinning, leaf removal and lighter pruning influence bud fruitfulness of Semillon and Shiraz (*Vitis vinifera* L.).

MATERIALS AND METHODS

1. Experimental sites

The experiment was carried out in the Coombe vineyard on the Waite Campus of the University of Adelaide, South Australia (34°58' S; 138°38' E). The climate of the region is classified as hot, dry, and moderately maritime (Smart and Dry, 1980). Both Semillon (clone SA 32) and Shiraz (clone BVRC12) vines were planted on their own roots in 1991, and trained using a bilateral spur pruned cordon with the shoots vertically positioned. Row spacing and vine spacing were 3.0 m and 1.8 m respectively, with rows oriented north/south. The vineyard was irrigated with in-line drippers at a spacing of 0.6 m and discharging at 2.0 L/h. The soil for this site is described as Dr2.23, a hard pedal red duplex soil (Litchfield, 1951).

2. Experimental design and treatments

Five canopy management treatments were carried out on the same Semillon and Shiraz vines annually. The details of the treatments are shown in Table 1. For Semillon, the following treatments were applied for four growing seasons (2014/15, 2015/16, 2016/17 and 2017/18): control (C), bunch thinning (BT), shoot thinning (ST), leaf removal (LR) and lighter pruning (double nodes, DN). Each treatment was replicated three times in blocks of three panels with each panel containing three vines. Measurements were conducted on the middle vine of each panel. The data for this study was collected in the seasons 2015/16, 2016/17 and 2017/18. Treatments for Shiraz vines included C, BT, ST and LR, which were conducted in the same way as for Semillon, and another type of leaf removal (LR-B) (Table 1). The treatments were applied on Shiraz for two

TABLE 1. Canopy management treatments applied to the Semillon and Shiraz varieties in the Coombe vineyard of the University of Adelaide.

Canopy management treatment	Description of treatment	Variety
Control (C)	No manipulation was conducted on the canopy.	Semillon; Shiraz
Bunch thinning (BT)	50 % of total number of bunches were removed just after veraison (E-L stage 35) (Coombe, 1995).	Semillon; Shiraz
Shoot thinning (ST)	50 % of total number of shoots were removed at E-L stage 15-17 (Coombe, 1995).	Semillon; Shiraz
Leaf removal (LR)	30 % of leaves were removed in the middle third of the canopy at veraison (E-L stage 35) (Coombe, 1995).	Semillon; Shiraz
Leaf removal at bunch zone (LR-B)	4-5 leaves per shoot were removed on the eastern side of the canopy in the fruit zone at veraison (E-L stage 35) (Coombe, 1995).	Shiraz
Lighter pruning (double nodes, DN)	Double the number of nodes were left on the vine at winter pruning by leaving two2-node spurs at each spur position.	Semillon

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growing seasons (2016/17 and 2017/18), with each treatment containing nine replicates. For both varieties, four shoots were randomly labelled on each vine in the early spring of the season. Measurements of light microclimate, shoot growth capacity and bud fruitfulness were conducted on labelled shoots.

3. Microclimate measures

Bud light microclimate was assessed by calculating light interception (%) at the bud zone on labelled shoots. Both ambient and bud zone light intensity were measured via photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) using a Sunfleck PAR ceptometer (Decagon Devices, Pullman, WA, USA). The bud zone readings were taken by the top sensor of the ceptometer that was placed in the bud zone. The ambient readings were taken outside and adjacent to the surface of the canopy, with the sensors facing upward in a zenith angle. The light interception (%) was calculated as:

The light measurements were taken on clear days after the application of treatments for both seasons. For season one (2016/17), the time of measurement was solar noon (at 13:30). In season two (2017/18), measurements were taken at three time points: morning (at 10:00), solar noon (at 13:30) and afternoon (at 16:30). The sensors on the ceptometer faced upwards with the zenith angle of the sun at each time point.

4. Shoot growth capacity and bud fruitfulness assessment

The labelled canes were collected from the vines of each treatment after leaf fall. Each cane was weighed and then cut to retain the basal and first four nodes. This section of the cane was also weighed. Cane diameter (mm) was measured at the mid-point of second and third nodes, and internode length (cm) of the same two nodes was taken using callipers. The canes were then placed in sealed plastic bags with a moistened paper towel and stored at 4 °C until bud dissection (Rawnsley and Collins, 2005).

For bud fruitfulness assessment, compound buds at nodes one to four were dissected using a razor blade to make transverse cuts perpendicular to the bud axes in the middle of the buds (Rawnsley and Collins, 2005). The bud was then observed under a light microscope at 25x magnification (Model EZ4 W, Leica, Heerbrugg, Switzerland). The number of IP in the primary bud and occurrence of PBN of each compound bud was recorded. If the primary bud was necrotic, the largest secondary bud was assessed instead. PBN incidence was expressed as a percentage of all buds dissected for each treatment. Images of dissections were taken using the Leica AirLab App, and the cross-sectional area of IP was measured on the images using software Image J (NIH, USA). For Semillon, the measurements of shoot growth capacity were only conducted in seasons 2016/17 and 2017/18, and bud fruitfulness assessment in season 2015/16 was only conducted on the first two nodes.

5. Carbohydrate measures

Three samples of canes (spurs) and buds (leaf and stem tissue from budburst) were collected in each panel of Semillon after budburst in season 2017/18. All samples were kept on dry ice until storage in a -80 °C freezer and then freeze dried (Alpha 2-4 LSC; John Morris Scientific, Adelaide, Australia). Bud tissues and cane tissues were separated and ground in an electrical mill (Model A11, IKA, Germany) for carbohydrate analysis. Carbohydrate measurement was performed according to Edwards *et al.* (2011). 5 mg of each sample was weighed and stored in a tube as a subsample. Soluble sugars were extracted using 80 % aqueous ethanol and measured by carrying out an Anthrone assay (Edwards *et al.*, 2011). The absorbance was read at 600 nm using a spectrophotometer (Multiskan Spectrum, model 00300011, Thermo Electron Corporation, Vantaa, Finland) and the content was determined from a fructose standard curve. Starch concentration was determined with a commercial enzyme assay kit (Total starch assay kit, Megazyme, Ireland). The absorbance was read at 505 nm and the content was determined using a glucose standard curve.

6. Statistical analysis

Statistical analysis was performed using one-way analysis of variance (ANOVA) to assess whether there were any significant differences between the results of treatments for bud fruitfulness, defined as IP number and IP area. Least significant difference (LSD) was applied at the 5 % level ($p<0.05$) for *post hoc* tests. Pearson correlation was used to assess relationships between bud fruitfulness and shoot growth capacity, bud zone light interception and bud

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carbohydrate content. All statistical analyses were performed using SPSS Statistics 24 (IBM, Chicago, IL, USA).

RESULTS

1. Bud fruitfulness

The results of bud fruitfulness of Semillon for each treatment in three growing seasons (2015/16, 2016/17 and 2017/18) are summarised in Table 2 and Supplementary Table S1. Means of IP number and area, PBN incidence from each node position, and averages for nodes one to two and nodes one to four are shown respectively. In general, IP number and area were higher in ST. IP number at nodes two to four and the two average values were increased significantly by ST in season 2016/17, as were node two in season 2015/16 and node three in season 2017/18 (Table 2 and Supplementary Table S1). The number of IP did not show much response to the other treatments, only decreases in node one by BT in season 2015/16 and by DN in 2016/17, and node four was increased by BT in season 2016/17.

IP areas were significantly enlarged by ST at each node position and the averages in all seasons except node one in season 2015/16. In season 2016/17, IP area at node three was enlarged significantly by BT and LR, as were the two averages. The incidence of PBN did not show a consistent response to the treatments, while it was noticeable that in all of three seasons the highest PBN incidence at node two was caused by BT. In addition, the incidence of PBN in nodes one and two for all the treatments was higher in 2017/18 than the former two seasons, especially at node one where it ranged from 42 to 55 %.

Compared with Semillon, PBN incidence in Shiraz was higher in both seasons and resulted in lower bud fruitfulness, especially for season 2016/17 (Table 3 and Supplementary Table S2). For all the treatments, the average incidence of PBN of the first two nodes ranged from 44 to 60 % in both seasons, with an even higher incidence in node one (54 to 72 % in season 2016/17 and 47 to 74 % in season 2017/18, Supplementary Table S2). However, there was no consistent pattern with canopy management

TABLE 2. Results of Semillon bud fruitfulness in response to different canopy management treatments for three seasons.

Measurement	Season	Treatments[a]					Significance[b]
		C	BT	DN	LR	ST	
IP[c] Number average (first 2 nodes)	2015/16	1.90	1.73	1.86	1.88	1.98	ns
	2016/17	1.77 ab	1.71 ab	1.59 a	1.72 ab	1.88 b	*
	2017/18	1.56	1.39	1.56	1.60	1.63	ns
IP Number average (first 4 nodes)	2015/16	-	-	-	-	-	-
	2016/17	1.74 a	1.81 ab	1.66 a	1.73 a	1.94 b	**
	2017/18	1.61	1.58	1.64	1.66	1.78	ns
IP area average (first 2 nodes) (mm^2)	2015/16	0.062 a	0.059 a	0.065 ab	0.062 a	0.068 b	*
	2016/17	0.048 a	0.053 bc	0.049 ab	0.053 bc	0.057 c	**
	2017/18	0.048 a	0.047 a	0.045 a	0.047 a	0.060 b	***
IP area average (first 4 nodes) (mm^2)	2015/16	-	-	-	-	-	-
	2016/17	0.049 a	0.055 b	0.049 a	0.054 b	0.061 c	***
	2017/18	0.050 a	0.051 a	0.047 a	0.050 a	0.064 b	***
PBN[d] (%) average (first 2 nodes)	2015/16	1.70	11.70	5.40	3.30	1.70	-
	2016/17	0.00	5.80	8.30	6.90	8.80	-
	2017/18	22.86	26.39	29.03	26.67	30.65	-
PBN (%) average (first 4 nodes)	2015/16	-	-	-	-	-	-
	2016/17	2.88	4.35	5.59	6.94	5.88	-
	2017/18	12.86	14.6	17.75	15.00	16.94	-

[a]Treatments: C, control; BT, bunch thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning. Means with different letters within rows are significantly different using the LSD test at 5 % level.
[b]*, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively; ns: not significant.
[c]IP, inflorescence primordia.

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treatments, as seen with Semillon. IP number was significantly higher in ST at node two and the averages in season 2017/18, but not in season 2016/17. IP number was also increased significantly by LR-B at node three in season 2016/17, and by BT at node two in season 2017/18. IP area was influenced only by ST, with significant increases in node two to four in season 2016/17 and in node three in season 2017/18, and increases in two averages for both seasons. LR did not significantly impact IP number or area.

Since the incidence of PBN was considerably higher in Shiraz, average IP areas of the treatments were compared separately within primary buds and secondary buds. The results are shown in Table 4. IP area of primary buds of nodes one to four were higher when ST was applied. The treatments did not significantly affect IP area of secondary buds in both seasons.

2. Shoot growth capacity

In seasons 2016/17 and 2017/18, total cane weight, cane weight of the first four nodes, internode lengths between nodes two and three,

TABLE 3. Results of Shiraz bud fruitfulness in response to different canopy management treatments for two seasons.

Measurement	Season	Treatments[a]					Significance[b]
		C	BT	LR-B	LR	ST	
IP[c] Number average (first 2 nodes)	2016/17	1.17	1.09	1.17	1.32	1.19	ns
	2017/18	1.36 a	1.64 b	1.42 ab	1.43 ab	1.65 b	*
IP Number average (first 4 nodes)	2016/17	1.20 ab	1.08 a	1.42 b	1.30 ab	1.33 b	*
	2017/18	1.54 a	1.68 ab	1.52 a	1.61 ab	1.78 b	*
IP area average (first 2 nodes) (mm^2)	2016/17	0.051 a	0.048 a	0.047 a	0.053 ab	0.058 b	**
	2017/18	0.059 a	0.059 a	0.060 a	0.059 a	0.067 b	*
IP area average (first 4 nodes) (mm^2)	2016/17	0.050 a	0.051 a	0.052 a	0.052 a	0.062 b	**
	2017/18	0.065 a	0.065 a	0.062 a	0.064 a	0.072 b	*
PBN[d] (%) average (first 2 nodes)	2016/17	50.00	56.52	59.15	48.61	55.56	-
	2017/18	51.70	45.60	48.50	51.50	43.50	-
PBN (%) average (first 4 nodes)	2016/17	55.47	56.83	48.95	53.85	52.45	-
	2017/18	36.70	34.60	40.20	36.00	32.30	-

[a]Treatments: C, control; BT, bunch thinning; LR-B, leaf removal at bunch zone; LR, leaf removal; ST, shoot thinning. Means with different letters within rows are significantly different using the LSD test at 5 % level.
[b]*, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively; ns: not significant.
[c]IP, inflorescence primordia. [d]PBN, primary bud necrosis.The confidence intervals given for the estimated parameters corresponding to a 10 % quasi-invariance region of the least-square sum.

TABLE 4. Average of inflorescence primordia area for different bud types of Shiraz.

Measurement	Season	Bud type	Treatments[a]					Significance[b]
			C	BT	LR-B	LR	ST	
IP[c] area average (first 2 nodes) (mm^2)	2016/17	Primary	0.051 a	0.050 a	0.053 a	0.058 ab	0.064 b	**
		Secondary	0.045	0.043	0.038	0.039	0.044	ns
	2017/18	Primary	0.066	0.066	0.065	0.065	0.073	ns
		Secondary	0.052	0.050	0.053	0.050	0.051	ns
IP area average (first 4 nodes) (mm^2)	2016/17	Primary	0.054 a	0.057 a	0.059 a	0.058 a	0.073 b	*
		Secondary	0.039	0.042	0.040	0.043	0.041	ns
	2017/18	Primary	0.068 a	0.068 a	0.067 a	0.069 a	0.077 b	**
		Secondary	0.052	0.052	0.050	0.050	0.053	ns

[a]Treatments: C, control; BT, bunch thinning; LR-B, leaf removal at bunch zone; LR, leaf removal; ST, shoot thinning. Means with different letters within rows are significantly different using the LSD test at 5 % level.
[b]*, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively; ns: not significant. [c]IP, inflorescence primordia.

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TABLE 5. Means of Semillon shoot growth capacity parameters in response to different canopy management treatments for two seasons.

Measurement	Season	Treatments					Significance[b]
		C	BT	DN	LR	ST	
Whole cane weight (g)	2016/17	67.71 ab	71.28 ab	57.47 a	74.56 ab	86.31 b	*
	2017/18	45.26 a	54.31 ab	46.12 a	41.11 a	68.29 b	**
Cane weight (first 4 nodes) (g)	2016/17	13.88 a	14.07 a	11.71 a	14.12 a	16.78 b	**
	2017/18	13.67 a	14.63 a	13.10 a	13.36 a	17.73 b	*
Internode length	2016/17	4.28 a	4.17 a	3.66 b	3.94 ab	4.11 a	*
between 2nd and 3rd nodes (cm)	2017/18	5.25	4.81	5.15	5.15	5.23	ns
Internode diameter	2016/17	8.20 a	8.14 a	7.67 a	8.26 a	8.94 b	*
between 2nd and 3rd nodes (mm)	2017/18	7.25 a	7.71 ab	7.12 a	7.18 a	8.36 b	**

[a]Treatments: C, control; BT, bunch thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning.
Means with different letters within rows are significantly different using the LSD test at 5 % level.
[b]*, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively; ns: not significant.

TABLE 6. Means of Shiraz shoot growth capacity parameters in response to different canopy management treatments for two seasons.

Measurement	Season	Treatments[a]					Significance[b]
		C	BT	LR-B	LR	ST	
Whole cane weight (g)	2016/17	141.91ab	106.58c	109.18c	124.22bc	153.20a	**
	2017/18	113.77	116.48	108.32	96.24	130.21	ns
Cane weight (first 4 nodes) (g)	2016/17	20.60ab	19.47a	20.17ab	23.52ab	24.53b	*
	2017/18	25.78	27.29	28.34	26.57	27.82	ns
Internode length	2016/17	6.06	5.67	6.08	5.96	5.75	ns
between 2nd and 3rd nodes (cm)	2017/18	7.83	7.66	8.27	7.85	7.52	ns
Internode diameter	2016/17	8.82ab	8.69ab	8.63a	8.75ab	9.24b	*
between 2nd and 3rd nodes (mm)	2017/18	8.39	8.86	8.97	8.62	8.79	ns

[a]Treatments: C, control; BT, bunch thinning; LR-B, leaf removal at bunch zone; LR, leaf removal; ST, shoot thinning.
Means with different letters within rows are significantly different using the LSD test at 5 % level.
[b]*, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively; ns: not significant.

and the cane diameter between nodes two and three were measured as indicators of shoot growth capacity (Tables 5 and 6). For Semillon, all parameters, apart from internode length, increased with ST in both seasons. When DN was applied, only the internode length was affected (decreased) in season 2016/17. In Shiraz, the canopy management treatments had less influence on the shoot growth capacity parameters (Table 6) than in Semillon. Only the whole cane weight decreased with LR-B in season 2016/17. The highest whole cane weight for two seasons, and four-nodes cane weight and internode diameter for season 2016/17 were found in ST.

3. Light interception at bud zone

The results of light interception at the bud zone in season 2016/17 for both varieties are shown in Figure 1A-B. For Semillon, ST and BT significantly increased bud light interception after application (Figure 1A). For Shiraz (Figure 1B), bud light interception was increased by LR-B, while ST did not show any effects in season 2016/17. In season 2017/18 (Figure 1C-H), ST increased bud light interception for both varieties immediately after application; however, the effects gradually diminished and no differences were observed in the last measurement in Semillon (Figure 1C,E and G) and the last two measurements in Shiraz (Figure 1D,F and H). LR also significantly increased bud

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light interception in Semillon at midday (13:30) (Figure 1E). In Shiraz, LR-B increased bud light interception significantly at 10:00 (Figure 1D) and 13:30 (Figure 1F), while LR increased light at 16:30 (Figure 1H). Interestingly, bud light interception in BT treatment of Shiraz was also found to be significantly higher in the first measurement at 16:30 (Figure 1H), when BT had not yet been conducted on the vines, hence the higher light interception in BT was a result of coincidence rather than the treatment.

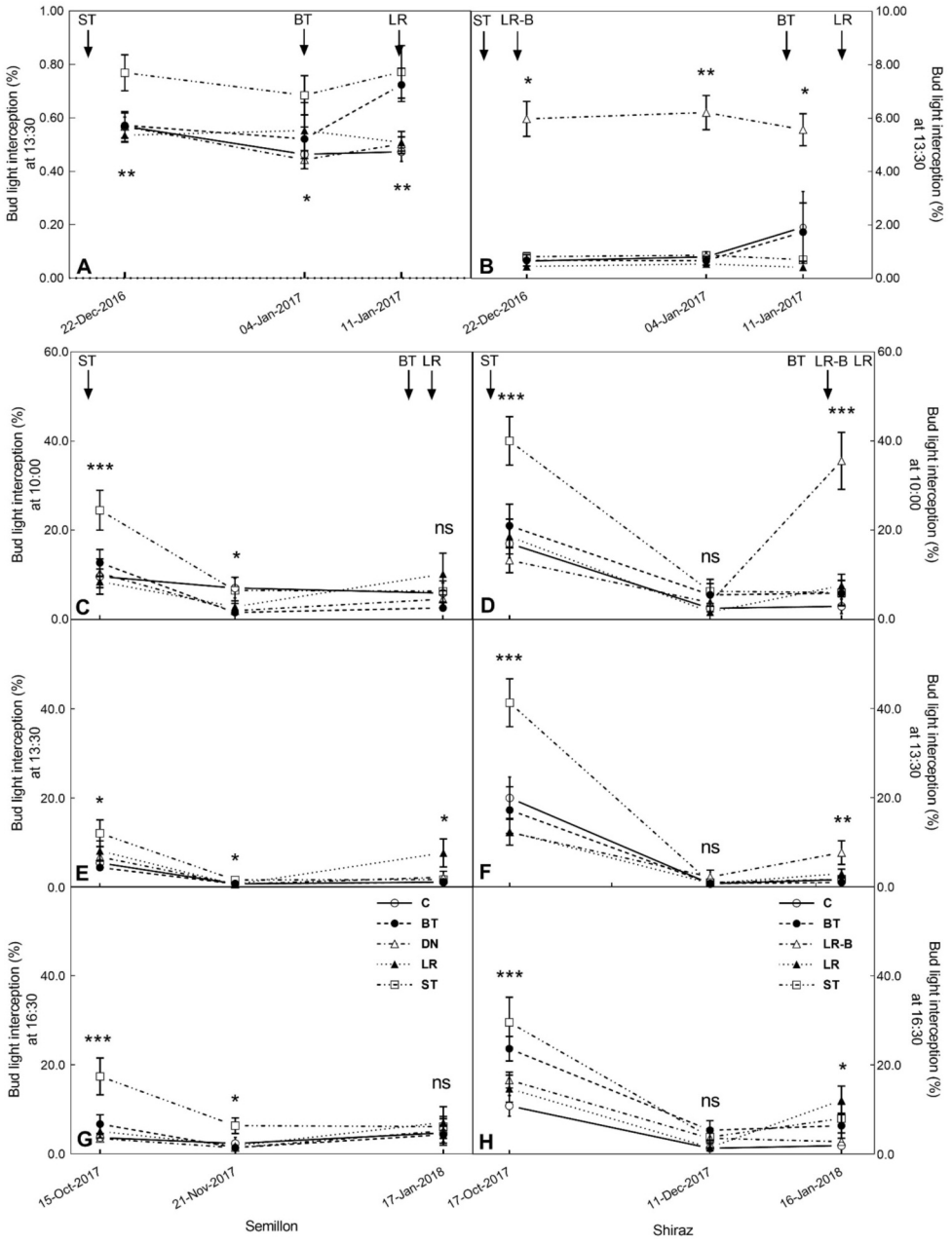


FIGURE 1. Effects of different canopy management treatments on light interception at bud zone of Semillon (A, at 13:30) and Shiraz (B, 13:3) for season 2016/17, and light interception at bud zone of Semillon (C, at 10:00; E, at 13:30; G, at 16:30) and Shiraz (D, at 10:00; F, at 13:30; H, at 16:30) for season 2017/18.

C, control; BT, bunch thinning; DN, double nodes; LR-B, leaf removal at bunch zone; LR, leaf removal at middle third canopy; ST, shoot thinning. The time of the application of the treatments are indicated by arrows. *, and ** indicate significance at $p \leq 0.05$ and 0.01 respectively, ns: not significant, using the LSD test at 5 % level.

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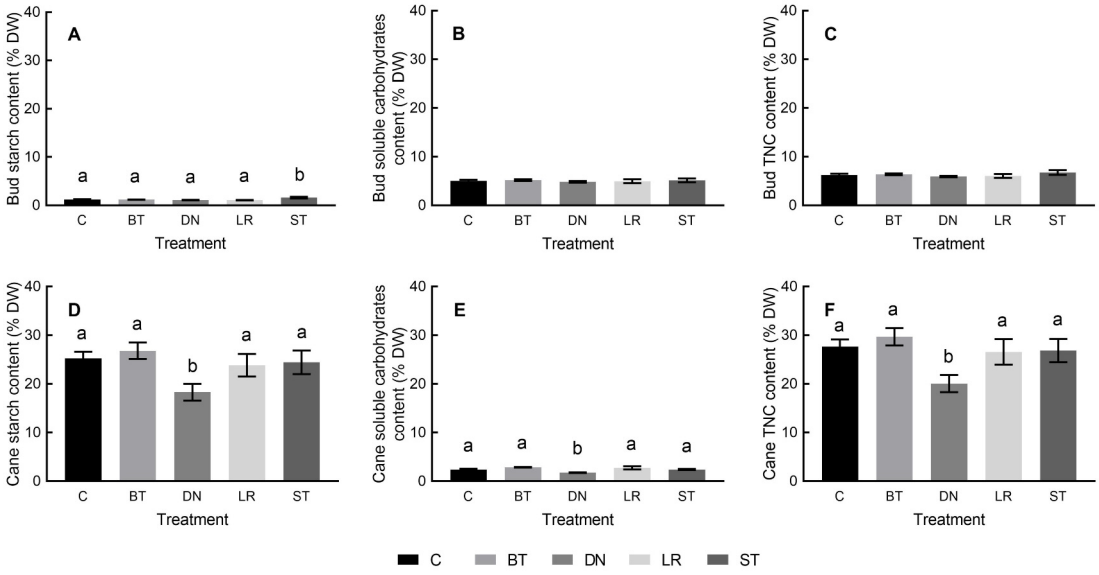


FIGURE 2. Effects of different canopy management treatments on Semillon carbohydrate contents of bud (A, bud starch content; B, bud soluble carbohydrate content; C, bud TNC content) and cane (D, cane starch content; E, cane soluble carbohydrate content; F, cane TNC content) for season 2017/18.

4. Carbohydrate content and its correlations with bud fruitfulness

Carbohydrate content was measured separately for buds and cane samples in all the treatments of Semillon in season 2017/18. The results of each sample were expressed as a percentage dry weight (% DW) of starch, soluble carbohydrates and total non-structural carbohydrate (TNC), respectively (Figure 2). Bud carbohydrate content was only influenced by ST, with an increase in bud starch content (Figure 2A). Both starch and soluble carbohydrates in canes were significantly lower in DN (Figure 2D-E). The other treatments did not show an effect on the carbohydrate content.

The correlations between each carbohydrate content parameter and bud fruitfulness are summarised in Supplementary Table S3. No correlations were found between IP number and carbohydrate content. In contrast, the average IP area (nodes one to two) was positively correlated with bud starch content and bud TNC, and average IP area average (nodes one to four) was correlated with bud TNC. The carbohydrate content in the canes, although influenced by DN, was not related to bud fruitfulness.

DISCUSSION

Bud dissection analysis can be a useful tool for early yield prediction, as the IP assessed within compound buds have the potential to develop into bunches in the following season (Dry, 2000). The conditions during the initiation and differentiation of IP in the current season can influence bud fruitfulness and potential yield (Watt *et al.*, 2008; Li-Mallet *et al.*, 2016). In this study, bud fruitfulness - comprising IP number and area - was determined by bud dissection analysis and was found to be influenced by canopy management practices, which also had effects on light microclimate, shoot growth capacity and bud carbohydrate level.

Among the treatments, ST in particular had the strongest effects on bud fruitfulness, especially on IP size for both Semillon and Shiraz (Tables 2 and 3). Previous research has shown that the number and size of IP are positively related to light exposure during bud initiation and differentiation (Buttrose, 1969; Dry, 2000; Sánchez and Dokoozlian, 2005). In the current study, the significant increase in IP number upon application of ST to Semillon may be attributed to the increase in light interception at the bud zone, as shown by the light interception measurements performed during spring in both seasons (Figures 1). Similarly, the IP number of

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Semillon was also increased by BT in season 2016/17, although only at node four (Supplementary Table S1), and a significant increase in bud light interception was also measured in BT in the same season (Figure 1A). Meanwhile, in season 2017/18, neither IP number nor bud light interception changed when BT was applied. This supports the idea that BT increases IP number by affecting the light conditions in the bud zone. BT improved bud fruitfulness considerably less than ST. This could be due to the different levels of change in microclimate, and also to the application stage of ST being E-L stage 15-17, which was much earlier in the season than BT (after veraison, E-L stage 35). The impact of bud light interception on IP number was also shown for Shiraz. ST increased light interception at the bud zone (Figures 1D, F and H) and increased IP number of Shiraz in season 2017/18 (Table 3), but not in season 2016/17. The higher bud light interception found in BT in 2017/18 (Figure 1H) may also have led to a higher number of IP in node two of Shiraz (Supplementary Table S2). Bud light interception was also increased by LR in both varieties (Figure 1E and H), and by LR-B in Shiraz (Figures 1D and F) in season 2017/18, however this had no effect on IP number. This lack of effect when LR was applied is in agreement with previous studies (Percival *et al.*, 1994; Palliotti *et al.*, 2012; Intrigliolo *et al.*, 2014). Intrieri *et al.* (2008) suggested that the expected positive effect of leaf removal on bud fruitfulness due to the improvement in light microclimate can be offset by negative effects on bud initiation due to source limitation.

IP area was significantly greater when ST was applied in both varieties and seasons and it was positively correlated with the measurements of shoot growth capacity. LR, LR-B and BT did not change shoot growth capacity; this is not surprising as these treatments were applied around veraison, well after the period of rapid period of shoot growth. The results of separate analyses for IP area in primary buds and secondary buds (Table 4) showed that secondary buds remained unaffected by canopy management treatments. This is in accordance with previous findings by Sánchez and Dokoozlian (2005), who used diameter summation to indicate IP size and found that secondary buds were not changed by different light exposure levels.

The carbohydrate content of buds and canes was affected by ST and DN (Figure 2). Bud starch content was significantly higher in ST treatments and was positively correlated with IP area. As the carbohydrate measurement was conducted at budburst in the season following that in which the practices were applied, this indicates a carry-over effect of ST on carbohydrate level and bud fruitfulness in the next season. Carbohydrate levels in canes were not influenced by ST and were lower in DN (Figure 2). At budburst, compound bud initiation is sensitive to the carbohydrate reserve status, as the other sink organs (actively growing shoots and leaves) are competing with the buds (Buttrose, 1966; Candolfi-Vasconcelos and Koblet, 1990). DN significantly lowered both starch and soluble sugars in canes, while bud fruitfulness was not decreased accordingly. This suggests that in the current study, the amount of carbohydrate reserves stored in canes of DN were enough to support bud initiation, and thus bud fruitfulness was not limited by DN. This is also supported by the lack of correlation between IP number and cane carbohydrate content (Supplementary Table S3). In contrast, the positive correlation between IP area and bud starch content and bud TNC (Supplementary Table S3) indicates that the IP branching level can be increased by higher bud carbohydrate level.

Overall, Shiraz had high PBN incidence in both seasons (around 50 % in the first two nodes) (Table 3), which is in line with previous research reporting that Shiraz is the most susceptible variety to PBN in Australia (Dry and Coombe, 1994; Rawnsley and Collins, 2005). In Semillon, PBN incidence was much higher in season 2017/18 than the two previous seasons (Table 2 and Supplementary Table S1). As expected, the incidence of PBN was negatively related to IP number. For instance, in node one of Semillon, BT in season 2015/16 and DN in season 2017/18 had significantly lower IP numbers (Supplementary Table S1). Both of the treatments also induced a higher incidence of PBN in the same season compared with other treatments. The relatively lower IP number of ST in node one of Semillon for seasons 2016/17 and 2017/18 can also be due to the high incidence of PBN, which was 17.6 % and 51.61 % respectively (Supplementary Table S1).

A high incidence of PBN is generally considered to be correlated with excessive shoot growth and canopy shading (May, 1965; Dry and Coombe,

1994; Collins and Rawnsley, 2004). However, in our study, PBN did not respond to the applied canopy management treatments in a consistent way in both seasons and for both varieties. Despite shoot growth capacity being highest in ST, the incidence of PBN was not, occuring randomly among all the treatments. This suggests that the incidence of PBN may be related to other factors that need further investigation.

CONCLUSIONS

Canopy management practices are normally used to optimise crop yield and quality in vineyards. The initiation and development of inflorescence primordia take place concurrently with the development of the crop in the current season. Hence the application of canopy management should be carefully considered as it may not only influence production in the current season, but it could also have a carry-over effect on the potential yield components for the next season. The results of this study demonstrated that grapevine bud fruitfulness, which determines yield potential for the next growing season, can be affected by canopy management practices. Shoot thinning significantly increased both the number and the cross-sectional area of the inflorescence primordia through modifications of bud microclimate, shoot growth capacity and carbohydrate content. Light interception at the bud zone was positively correlated to the number of inflorescence primordia, while the area of inflorescence primordia was more correlated to bud carbohydrate level. Lighter pruning by retaining double the number of nodes on vines decreased carbohydrate reserves in canes, but did not lower bud fruitfulness. The incidence of primary bud necrosis can reduce bud fruitfulness by decreasing the number of inflorescence primordia; however, it did not show a consistent pattern of response to canopy management practices.

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REFERENCES

Ames ZR., Olmstead M., Sims C. and Darnell R., 2016. Effect of shoot and cluster thinning on vine performance, fruit and wine quality of «Blanc Du Bois». *Journal of the American Pomological Society*, 70, 2-15.

Antcliff A. and Webster W., 1955. Studies on the sultana vine. I. Fruit bud distribution and bud burst with reference to forecasting potential crop. *Australian Journal of Agricultural Research*, 6, 565-588. doi:10.1071/AR9550565

Buttrose M., 1966. Use of carbohydrate reserves during growth from cuttings of grape vine. *Australian Journal of Biological Sciences,* 19, 247-256. doi:10.1071/BI9660247

Buttrose MS., 1969. Fruitfulness in grapevines: effects of light intensity and temperature. *Botanical Gazette,* 130, 166-173. doi:10.1086/336486

Candolfi-Vasconcelos MC. and Koblet W., 1990. Yield, fruit quality, bud fertility and starch reserves of the wood as a function of leaf removal in *Vitis vinifera* - Evidence of compensation and stress recovering. *Vitis*, 29, 199-221.

Clingeleffer P.R., Martin S., Krstic M. and Dunn G.M., 2001. Crop development, crop estimation and crop control to secure quality and production of major wine grape varieties: a national approach. Final report to Grape and Wine Research & Development Corporation. CSIRO, Merbein, Australia.

Collins C., Coles R., Conran J. and Rawnsley B., 2006. The progression of primary bud necrosis in the grapevine cv. Shiraz (*Vitis vinifera* L.): a histological analysis. *Vitis,* 45, 57-62.

Collins C. and Rawnsley B., 2004. National survey reveals primary bud necrosis is widespread. *Australian and New Zealand Grapegrower and Winemaker,* 485, 46-49.

Collins C. and Rawnsley B., 2008. Effect of gibberellic acid and paclobutrazol on the incidence of primary bud necrosis in cv. Shiraz (*Vitis vinifera* L.). *American Journal of Enology and Viticulture*, 59, 83-87.

Coombe BG. and Dry PR., 1992. Viticulture. Volume 2. *Practices. Winetitles.* Underdale, SA, Australia.

Cox CM., Favero AC., Dry PR., McCarthy MG. and Collins C., 2012. Rootstock effects on primary bud necrosis, bud fertility and carbohydrate storage in Shiraz. *American Journal of Enology and Viticulture*, 63, 277-283. doi:10.5344/ajev.2012.11012

Dry PR., 2000. Canopy management for fruitfulness. *Australian Journal of Grape and Wine Research*, 6, 109-115. doi:10.1111/j.1755-0238.2000.tb00168.x

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Dry PR. and Coombe BG., 1994. Primary bud-axis necrosis of grapevines. I. Natural incidence and correlation with vigour. *Journal of Grapevine Research*, 33, 225.

Dunn GM. and Martin SR., 2007. A functional association in *Vitis vinifera* L. cv. Cabernet-Sauvignon between the extent of primary branching and the number of flowers formed per inflorescence. *Australian Journal of Grape and Wine Research*, 13, 95-100. doi:10.1111/j.1755-0238.2007.tb00239.x

Edwards EJ., Downie AF. and Clingeleffer PR., 2011. A simple microplate assay to quantify nonstructural carbohydrates of grapevine tissues. *American Journal of Enology and Viticulture*, 62, 133-137. doi:10.5344/ajev.2010.10051

Guilpart N., Metay A. and Gary C., 2014. Grapevine bud fertility and number of berries per bunch are determined by water and nitrogen stress around flowering in the previous year. *European Journal of Agronomy*, 54, 9-20. doi:10.1016/j.eja.2013.11.002

Intrieri C., Filippetti I., Allegro G., Centinari M. and Poni S., 2008. Early defoliation (hand vs mechanical) for improved crop control and grape composition in Sangiovese (*Vitis vinifera* L.). *Australian Journal of Grape and Wine Research*, 14, 25-32. doi:10.1111/j.1755-0238.2008.00004.x

Intrigliolo D.S., Llacer E., Revert J., Esteve M.D., Climent M.D., Palau D. and Gomez I., 2014. Early defoliation reduces cluster compactness and improves grape composition in Mandó, an autochthonous cultivar of *Vitis vinifera* from southeastern Spain. *Scientia Horticulturae*, 167, 71-75. doi:10.1016/j.scienta.2013.12.036

Kavoosi B., Eshghi S., Tafazoli E., Rahemi M. and Emam Y., 2012. Primary bud necrosis (PBN) as affected by cane diameter, node position and sampling date in grapevine (*Vitis vinifera* L. 'Askari'). *Acta Horticulturae*, 931, 453-460. doi:10.17660/ActaHortic.2012.931.54

Li-Mallet A., Rabot A. and Geny L., 2016. Factors controlling inflorescence primordia formation of grapevine: their role in latent bud fruitfulness? A review. *Botany*, 94, 147-163. doi:10.1139/cjb-2015-0108

Litchfield WH., 1951. Soil survey of the Waite Agricultural Research Institute. CSIRO, Australian Division of Soils, Adelaide, Australia.

May P., 1965. Reducing inflorescence formation by shading individual Sultana buds. *Australian Journal of Biological Sciences*, 18, 463-474. doi:10.1071/BI9650463

May P. and Antcliff A., 1973. The fruitfulness of grape buds: I. Measuring bud fruitfulness on forced single node cuttings. *Annales de l'amélioration des plantes* , 23, 1-12.

May P. and Cellier K., 1973. Fruitfulness of grape buds. II. The variability in bud fruitfulness in ten cultivars over four seasons. *Annales de l'Amélioration des Plantes*, 23, 13-26.

Morris J., Spayd S. and Cawthon D., 1983. Effects of irrigation, pruning severity and nitrogen levels on yield and juice quality of Concord grapes. *American Journal of Enology and Viticulture*, 34, 229-233.

Morrison J.C. and Iodi M., 1990. The development of primary bud necrosis in Thompson Seedless and Flame Seedless grapevines. *Vitis*, 29, 133-144.

Noyce P.W., Harper J.D., Steel C.C. and Wood R.M., 2016. A new description and rate of development of inflorescence primordia over a full season in *Vitis vinifera* L. cv. Chardonnay. *American Journal of Enology and Viticulture*, 67, 86-93. doi:10.5344/ajev.2015.14050

Palliotti A., Gardi T., Berrios JG., Civardi S. and Poni S., 2012. Early source limitation as a tool for yield control and wine quality improvement in a high-yielding red *Vitis vinifera* L. cultivar. *Scientia Horticulturae*, 145, 10-16. doi:10.1016/j.scienta.2012.07.019

Percival DC., Fisher KH. and Sullivan JA., 1994. Use of fruit zone leaf removal with *Vitis vinifera* L. cv. Riesling grapevines. I. effects on canopy structure, microclimate, bud survival, shoot density, and vine vigor. *American Journal of Enology and Viticulture*, 45, 123-132.

Pratt C., 1974. Vegetative anatomy of cultivated grapes - A review. *American Journal of Enology and Viticulture*, 25, 131-150.

Rawnsley B. and Collins C., 2005. Improving vineyard productivity through assessment of bud fruitfulness and bud necrosis. South Australian Research and Development Institute (SARDI), Adelaide, Australia.

Reynolds A., Edwards C., Wardle D., Webster D. and Dever M., 1994. Shoot density affects 'Riesling' grapevines I. Vine performance. *Journal of the American Society for Horticultural Science*, 119, 874-880. doi:10.21273/JASHS.119.5.874

Sánchez LA. and Dokoozlian NK., 2005. Bud microclimate and fruitfulness in *Vitis vinifera* L. *American Journal of Enology and Viticulture*, 56, 319-329.

Smart R. and Dry P., 1980. A climatic classification for Australian viticultural regions. *The Australian Grapegrower & Winemaker*, 196, 8,10,16.

Smart R. and Robinson M., 1991. Sunlight into wine: a handbook for winegrape canopy management. Winetitles, Underdale, SA, Australia.

Srinivasan C. and Mullins M.G., 1980. Effects of temperature and growth-regulators on formation of anlagen, tendrils and inflorescences in *Vitis*-

vinifera L. *Annals of Botany*, 45, 439-446. doi:10.1093/oxfordjournals.aob.a085842

Srinivasan C. and Mullins MG., 1981. Physiology of flowering in the grapevine - A review. *American Journal of Enology and Viticulture*, 32, 47-63.

Vasconcelos MC., Greven M., Winefield CS., Trought MCT. and Raw V., 2009. The flowering process of *Vitis vinifera*: a review. *American Journal of Enology and Viticulture*, 60, 411-434.

Watt A., Dunn G., May P., Crawford S. and Barlow E., 2008. Development of inflorescence primordia in *Vitis vinifera* L. cv. Chardonnay from hot and cool climates. *Australian Journal of Grape and Wine Research*, 14, 46-53. doi:10.1111/j.1755-0238.2008.00006.x

Williams LE., 2000. Bud development and fruitfulness of grapevines. *Raisin Production Manual.* Christensen LP. (Ed), 24-29.

Wolf T.K. and Warren M.K., 1995. Shoot growth rate and density affect bud necrosis of 'Riesling' grapevines. *Journal of the American Society for Horticultural Science*, 120, 989-996. doi:10.21273/JASHS.120.6.989

Zabadal T.J., Vanee G, Dittmer T. and Ledebuhr R., 2002. Evaluation of strategies for pruning and crop control of Concord grapevines in southwest Michigan. *American Journal of Enology and Viticulture*, 53, 204-209.

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