



# Evaluating sources of variability in inflorescence number, flower number and the progression of flowering in Sauvignon blanc using a Bayesian modelling framework

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## ABSTRACT

The time of flowering is key to understanding the development of grapevines. Flowering coincides with inflorescence initiation and fruit set, important determinants of yield. This research aimed to determine between and within-vine variability in 4-cane-pruned Sauvignon blanc inflorescence number per shoot, number of flowers per inflorescence and flowering progression using an objective method of assessing flowering via image capture and statistical analysis using a Bayesian modelling framework. The inflorescence number and number of flowers per inflorescence were measured by taking images over the flowering period. Flowering progression was assessed by counting open and closed flowers for each image over two seasons. An ordinal multinomial generalised linear mixed-effects model (GLMM) was fitted for inflorescence number, a Poisson GLMM for flower counts and a binomial GLMM for flowering progression. All the models were fitted and interpreted within a Bayesian modelling framework. Shoots arising from cane node one had lower numbers of inflorescences compared to those at nodes 3, 5 and 7, which were similar. The number of flowers per inflorescence was greater for basal inflorescences on a shoot than apical ones. Flowering was earlier, by two weeks, and faster in 2017/18 when compared to 2018/19 reflecting seasonal temperature differences. The time and duration of flowering varied at each inflorescence position along the cane. While basal inflorescences flowered later and apical earlier at lower insertion points on the shoot, the variability in flowering at each position on the vine dominated the date and duration of flowering.

This is the first study using a Bayesian modelling framework to assess variability inflorescence presence and flower number, as well as flowering progression via objective quantification of open and closed flower counts rather than the more subjective method of visual estimation in the field or via cuttings. Although flower number differed for apical and basal bunches, little difference in timing and progression of flowering by these categories was observed. The node insertion point along a shoot was more important. Overall, the results indicate individual inflorescence variation and season are the key factors driving flowering variability and are most likely to impact fruit set and yield.

**KEYWORDS:** grapevine, phenology, inflorescence, flower number, flowering, Bayesian modelling, yield

## INTRODUCTION

Flowering is a key phenological stage monitored for understanding the development of grapevines during the season and for yield component formation. Seasonal differences in the time of grapevine flowering are known and flowering is often predicted using the thermal time (a key driver of vine development) from a fixed date or a prior phenological stage until 50 % flowering is reached (Huglin, 1978; Webb *et al.*, 2007; García de Cortázar-Atauri *et al.*, 2010, Parker *et al.*, 2011; Parker *et al.*, 2013; García de Cortázar-Atauri *et al.*, 2017; Morales-Castilla *et al.*, 2020; Prats-Llinas *et al.*, 2020). Differences in the timing of flowering (and other phenological stages) also occur among cultivars that also enables growers to consider using cultivar diversity to adapt to climate change, by choosing later developing cultivars (Parker *et al.*, 2013; García de Cortázar-Atauri *et al.*, 2017; van Leeuwen *et al.*, 2019b; Morales-Castilla *et al.*, 2020; Parker *et al.*, 2020).

Flowering is typically monitored by visual observation in the field (García de Cortázar-Atauri *et al.*, 2017; Destrac-Irvine *et al.*, 2019; van Leeuwen *et al.*, 2019a). However, monitoring flowering in the vineyard can be subjective and several factors may influence the outcome for determining 50 % flowering: the number of vines observed, the position of vines within a vineyard and the frequency, accuracy and consistency of observer(s), as well as the scale used for determining flowering (for example scoring on a numeric scale such as 1–10, designating an absolute percentage value, or assigning percentage values in ‘bins’ such as each 10 %). These factors may lead to differences in determining the time of flowering, our ability to predict flowering or utilise the information from the flowering period in models. While flower number has been successfully counted manually (May, 2000; Poni *et al.*, 2006), or using image processing techniques and/or automated counting systems (Diago *et al.*, 2014; Aquino *et al.*, 2015a; Aquino *et al.*, 2015b; Millan *et al.*, 2017; Liu *et al.*, 2018; Tello *et al.*, 2020), no studies to date have counted open and closed flowers on inflorescences to objectively score the percentage flowering as a method of flowering assessment to evaluate flowering variability, which is the method employed in this current study.

Flowering between vineyards, within a vineyard and within a vine can be variable and is an important consideration in vineyard management. Therefore, if vast differences in the timing of flowering occur, this could lead to yield variation (Trought *et al.*, 2017) or differences in the duration and the time to target sugar concentrations (Eltom *et al.*, 2017). Phenological models which take into account temperature and can be used to describe variation in the time of 50 % flowering within and between vineyards, regions and countries of differing climate influences (Parker *et al.*, 2013; Verdugo-Vásquez *et al.*, 2019; de Ressaúier *et al.*, 2020; Morales-Castilla *et al.*, 2020). There is less of an understanding of the variability of flowering within a vine and how this may affect our assessment of 50 % flowering

and the duration of flowering and its consequences for fruit set and yield. Trought *et al.* (2017) demonstrated that distal shoots on the cane flowered on average, up to 2.5 days earlier than shoots proximal to the head of the vine, likewise that basal inflorescences flowered up to on average, 1.8 days earlier than apical inflorescences on the shoot. Just as importantly though, they also demonstrated that there was great variability in percentage flowering, from 4 to 96 %, among individual inflorescences early in the season on a given day of observation. This highlights despite within-vine mean trends being determined, flowering itself among inflorescences may be highly variable. Eltom *et al.* (2017) also found that basal inflorescences flower earlier than apical ones, as well as inner arms of inflorescences flowering earlier than outer arms, indicating that there are also important within-inflorescence patterns of flowering. The study by Trought *et al.* (2017) used an 8-point scale to assess flowering and Eltom *et al.* (2017) visually assessed percentages in-field. The exact counting of the number of open and closed flowers on individual inflorescences was not carried out at the various positions in the vine. This proceeding research did not specifically look at individual shoot positions along a cane (shoots were classed into broad groupings of proximal, middle and distal for example in Trought *et al.*, 2017) or node insertion points of inflorescences up shoot. So, while these studies indicate sources and the importance of within-vine variability in flowering, it also presents an opportunity to complete a more detailed analysis of the within vine flowering variability by using objective, exact counts of open and closed flowers from images and considering specific shoot and node insertion locations of inflorescences that are monitored.

The duration of flowering is also of interest because this can influence the flowering to fruit set process, as temperatures and radiation intensity prior, during and post-flowering can influence the success of pollination, germination, pollen tube growth for fertilisation and seed and berry weight (Staudt, 1982; Ebadi *et al.*, 1996; Friend, 2005; Trought, 2005). Consequently, the duration of the flowering period and the temperatures characteristics prior, during and post-flowering have been successfully implemented in yield predictions models (Trought, 2005; Zhu *et al.*, 2020). Understanding the variability in flowering duration and how this may influence within block yield variability among vines is therefore important to capture when monitoring flowering.

Inflorescence number per shoot and flower number can also influence final yield. Prior research has already demonstrated that inflorescence number varies by node position along a cane and with cultivar (May and Cellier, 1973; Huglin and Balthazard, 1975), and that basal bunches have more flowers than apical bunches irrespective of cultivar (May and Cellier, 1973; Huglin and Balthazard, 1975; Eltom *et al.*, 2017), although it appears that the number of berries per bunch is not different between apical and basal bunches within a season for a given cultivar (the percentage fruit set is reduced on basal bunches relative to apical bunches, Eltom *et al.*, 2017; Trought *et al.*, 2017).

The pattern of inflorescence number per shoot has not been characterised for Sauvignon blanc and there is an opportunity to investigate the relationship of the node insertion point of inflorescences up a shoot with the time and duration of flowering.

Most of the above-cited research has used more ‘classical’ maximum likelihood estimation (MLE) methods applied to ANOVA and regression, or simply exploratory data analysis to investigate sources of variability inflorescence number, flower number and the progression of flowering. However, a Bayesian approach is becoming more and more commonly used in natural sciences due to its ability to combine prior information, such as experts’ opinions and results of previous studies, with the newly collected data, and its flexible approach to modelling. When using binary and binomial logistic or Poisson Generalised Linear Models, necessary when modelling proportions and counts respectively, it also avoids the potential technical problem of complete separation encountered in classical maximum likelihood estimation. Warton and Hui (2011) explain why the use of the binomial logistic model is recommended over the use of linear regression when modelling proportions (which is what percentage flowering represents). The Bayesian approach also works well with fitting a mixed-effects model adjusting for repeated measures or other hierarchy within data, especially in cases of unbalanced design, which is common when characterising inflorescence presence and number of inflorescences per various shoot positions within a vine in the field (i.e., not all shoots exhibit the same number of inflorescences or locations).

The objective of this research was to determine how variability in Sauvignon blanc flowering is associated with the following vine structures: individual vines, canes on vines, shoot positions along canes, inflorescence positions on shoot (basal or apical, or node insertion points up a shoot), using an objective method of assessing flowering via image capture, and statistical analysis via a Bayesian modelling framework. The position and number of inflorescences on the different shoots along the canes was also evaluated; the number of flowers per inflorescence was also evaluated for any underlying relationship with regard to the different vine structures.

## MATERIALS AND METHODS

### 1. Experimental site and vine management

The experiment was conducted over two growing seasons in the teaching and research vineyard at Lincoln University, Canterbury, New Zealand (43°38’49”S, 172°27’28”E) in a row of *Vitis vinifera* L., four-caned pruned vertically shoot positioned (VSP) Sauvignon blanc vines (clone MS, rootstock SO<sub>4</sub>). The vines were planted in 1996, with the selected row orientated in a north-south direction, and between vine spacing of 1.6 m and vineyard row spacing of 2.5 m. Vines were pruned to 10 nodes per cane with two renewal spurs. Canes were wrapped to fruiting wires at a height of 900 and 1000 mm from the soil surface, with four canes attached to

each wire (lower and upper canes), two facing in the north direction, two in the south direction. Shoots were thinned pre-flowering so that only one shoot per node was retained.

### 2. Experimental design

The row was divided into 12 blocks and one vine per block was randomly selected. Nine vines were initially selected from these initial 12 vines (three vines were eliminated to growth issues) for this experiment, of which image data was successfully captured for eight vines in 2017/2018 resulting in 287 counts from 89 inflorescences. In 2018/2019 data was collected for three of the eight vines from the previous season (138 counts on 37 individual inflorescences).

South-facing canes on the vine were chosen, as it is assumed that these can also represent the north-facing half of the vine (assuming equivalent responses for both directions of the vine and therefore between the south and north-facing canes). Both the upper and lower south-facing canes were tagged and monitored for the presence of inflorescences, as the microclimate of these canes may differ (the lower cane shoots grow into the fruiting zone of the upper cane in the 4-cane VSP configuration). For each vine, shoots 1, 3, 5 and 7 (1 = shoot closest to the head of the vine) along the lower and upper south-facing canes were tagged to investigate the responses at node positions relative to the head of the vine. Where there was a missing shoot/flag shoot/shoot without an inflorescence at the designated positions, this was replaced by another shoot randomly selected along the same cane for flower counts and flowering progression measurements. The count values 89 inflorescences (2017/2018) on 37 individual inflorescences (2018/19) are the sum of the naturally occurring presence of one, two, or three inflorescences at each node monitored across all vines in each year. The 287 and 138 counts of individual images/flowering scores for 2017/2018 and 2018/19, respectively, are a function of the number of inflorescences multiplied by the dates of image capture, for images from 0 to the first instance of 100 % flowering.

Flowering variability was investigated between vines, upper and lower canes, shoot position (along the cane with position one denoting the shoot most proximal to the head of the vine), inflorescence position (basal or apical relative to the cane) and node insertion point of the inflorescence up the shoot (with node one being the first fully separated node from the cane). Node insertion points were recorded for the 2017/18 season only (77 inflorescences in total).

### 3. Flowering observations and counts

Detailed flowering progression was monitored via image capture: photos were taken approximately bi-weekly from pre-flowering to bunch closure. A standardised background was placed behind the inflorescence when the image was taken, where the grid provided a standardised scale and visually distinct background and the QR code corresponded to each vine/cane/shoot/inflorescence identity (alongside this information also annotated in full on the background, Figure 1A).

Open and closed flowers were identified manually from the photographs: flowers were considered as open when the base of the cap was detached, whether it had fallen off or not (Destrac-Irvine *et al.*, 2019) and were identified based on this characteristic, or a clearly identifiable pistil (where the cap had fallen off) (Figure 1A). While automated systems have been developed to count the total number of flowers on an inflorescence (Diago *et al.*, 2014; Aquino *et al.*, 2015a; Aquino *et al.*, 2015b; Millan *et al.*, 2017; Liu *et al.*, 2018; Tello *et al.*, 2020), flowers were manually labelled in our experiments using Krita 4.2.9 (Krita Foundation and KDE, Germany), to identify the subtle differences between flowers with the cap intact or detached; open flowers were labelled with red dots and closed flowers were labelled with blue dots (Figure 1B). Labels were placed to avoid overlap so all dots could be accurately counted. These dots were added as an overlay to the original image (a completely separate image of exactly the same size as the original), so the overlay only contained dots (Figure 1B). The “label connect components” function of the Scipy library (used in the Python programming language, USA) was used to extract each individual dot, whereby all dots were automatically classified from their colour channel alone and counted as open or closed.

Within an image, if a flower was obscured by flowers in the first layer of the image, it was not possible to label it open or closed, and therefore it was necessary to be excluded from the count. Furthermore, any image containing blurred sections that compromised the count were eliminated, likewise, all images post-100 % flowering were eliminated.

#### 4. Temperature

Daily maximum and minimum temperatures were sourced from the Lincoln University meteorological station. Accumulated mean daily temperatures from August 29 were used to estimate Sauvignon blanc 50 % flowering, using the Grapevine, Flowering, Veraison (GFV) model (Parker *et al.*, 2011).

#### 5. Bayesian models

##### 5.1. Number of inflorescences

An ordinal multinomial regression model was fitted to test for the possible effects of vine, cane, shoot and inflorescence position (apical versus basal). The number of inflorescences per shoot was treated as an ordinal categorical variables with the categories 0 for blind bud/flag shoot/shoot with no inflorescence, 1 for 1 inflorescence and 2 for 2 or more inflorescences.

##### 5.2. Number of flowers per inflorescence

The observed number of flowers for each inflorescence was evaluated as the maximum observed number of flowers for that inflorescence over the study period. For each season, we compared the model accounting for vine, cane, shoot and inflorescence position (basal or apical), and vine and shoot variability (full model) to the model accounting only for cane and inflorescence position, the model accounting only for the vine and shoot variability and, finally, the null model, which did not account for any of the above effects (the null model).



A.



B.



C.

**FIGURE 1.** A. Image of inflorescence as captured in the field, B. Image of an inflorescence annotated for open (red dots) and closed (blue dots) flowers, C. Overlay of labelled flowers (dots) based on the image of the inflorescence used to count the open and closed flowers.

1-5-2 in Figures 1A and B refers to the lower cane (cane 1), the fifth shoot along the cane counting from the head of the vine outwards (shoot 5) and the apical inflorescence (1 = basal inflorescence, 2 = apical inflorescence). The QR code was unique for each individual inflorescence.

The number of flowers was modelled using the Poisson GLMM as Poisson distribution is typically used for modelling counts. For this,  $y_i$  was the number of berries observed on the inflorescence  $i$ . We can assume that this number follows a Poisson distribution:

$$y_i \sim \text{Pois}(\mu_i),$$

where  $\mu_i$  is the expected number of flowers. This Poisson intensity parameter itself is modelled as follows:

$$\log(\mu_i) = \beta_0 + \beta_1 * \text{cane}_i + \beta_2 * \text{inflorescence}_i + \beta_{12} * \text{cane}_i * \text{inflorescence}_i + \gamma * \text{date}_i + \varepsilon_{\text{vine}_i}^{(\text{vine})} + \varepsilon_{\text{shoot}_i}^{(\text{shoot})} + \varepsilon_{\text{id}_i}^{(\text{id})}$$

where  $\text{cane}_i = 0, 1$  for the lower and upper canes, respectively, and  $\text{inflorescence}_i = 0, 1$  for the basal and apical inflorescence, respectively. Normal priors were assumed for both, random and fixed effects as follows:

$$\begin{aligned} \beta_0, \beta_1, \beta_2, \beta_{12} &\sim N(0, 10^{-8}), \\ \varepsilon_{\text{vine}_i}^{(\text{vine})} &\sim N(0, \tau_{\text{vine}}), \\ \varepsilon_{\text{shoot}_i}^{(\text{shoot})} &\sim N(0, \tau_{\text{shoot}}), \\ \varepsilon_{\text{id}_i}^{(\text{id})} &\sim N(0, \tau_{\text{id}}). \end{aligned}$$

Note, that the second parameter in the Normal distribution notation is the precision (inverse variance). They, in turn, were given non-informative gamma priors:

$$\tau_{\text{vine}}, \tau_{\text{shoot}}, \tau_{\text{id}} \sim \text{Gamma}(0.01, 0.01).$$

### 5.3. Flowering progression

Flowering progression (from zero to all open flowers) was assumed to follow a logistic curve. The following three models were fitted:

- 1) The model with the effects of cane, inflorescence position, as well as vine, shoot and the inflorescence-specific random effect to account for repeated measures (full model)
- 2) The model with vine shoot and inflorescence-specific random effect but not cane or inflorescence position (random effects only-model)
- 3) The model with inflorescence-specific random effect only (null model).

Binomial GLMM was used where  $y_i$  was the number of opened flowers and  $n_i$  be the total number of flowers (opened and closed) observed on the inflorescence  $i$ . We can assume that the number of opened flowers follows a binomial distribution:

$$y_i \sim \text{Bin}(p_i, n_i),$$

where  $n_i$  is the total number of flowers and  $p_i$  is the expected proportion of opened flowers. The proportion itself is modelled as follows:

$$\logit(p_i) = \beta_0 + \beta_1 * \text{cane}_i + \beta_2 * \text{inflorescence}_i + \beta_{12} * \text{cane}_i * \text{inflorescence}_i + \gamma * \text{date}_i + \varepsilon_{\text{vine}_i}^{(\text{vine})} + \varepsilon_{\text{shoot}_i}^{(\text{shoot})} + \varepsilon_{\text{id}_i}^{(\text{id})}$$

where  $\text{cane}_i = 0, 1$  for the lower and upper cane, respectively, and  $\text{inflorescence}_i = 0, 1$  for the basal and apical inflorescence, respectively. The priors were as in the Poisson GLM. Note that the link function

$$\text{logit}(z) = \log\left(\frac{z}{1-z}\right).$$

is commonly used for proportion transformations. Furthermore, because  $\text{logit}(0.50) = 0$ , to find the time when 50 % of flowers on a particular cane and inflorescence position are expected to be opened, one can solve the linear equation above to obtain:

$$t_{50\%} = \frac{-(\beta_0 + \beta_1 * \text{cane} + \beta_2 * \text{inflorescence} + \beta_{12} * \text{cane} * \text{inflorescence})}{\gamma}$$

To test the influence of node insertion point (node position of the inflorescence up a shoot, counting the first separated node from the cane as node 1) on the growth trajectory, we have fitted the models with and without accounting for node insertion point to the smaller subset of the 2017/2018 data for which the information was available.

### 5.4. Model comparisons

The models for the number of flowers (Section 5.1.) and flowering progression (Section 5.2.) were compared using the deviance information criterion (DIC) to evaluate model complexity and fit (Spiegelhalter *et al.*, 2002). The smaller DIC corresponds to the better model, and a difference of at least three indicates sufficient statistical evidence to choose the more complex model. Bayesian posterior probabilities, the so-called Bayesian  $p$ -values, were used to report the posterior probability of the truth of a certain statement given the data (the greater  $p$ -values indicate greater statistical support for a given statement). The posterior distributions were summarised via posterior means and the 95 % central credible intervals (CI).

In the absence of prior information, we have used so-called vague or non-informative priors. WinBUGS software (Lunn *et al.*, 2000) was used for Bayesian estimation, and statistical software R (R Core Team, 2013), specifically the R2WinBUGS package (Sturtz *et al.*, 2005) was used for pre- and post-processing. For more details on the code please read the Supplementary material.

A total of 50,000 iterations were run after the burn-in of 1000 with thinning after every five. The resulting posterior sample of 1000 was used for inference. Convergence was visually assessed.

## RESULTS

### 1. Number of inflorescences per shoot

The best model for the number of inflorescences per shoot was found not to include cane indicating the lack of statistical evidence for the difference between canes (Table 1). The probability of having a node position without an inflorescence (i.e., blind bud/flag shoot, or shoot without inflorescence) was greater at node 1 (closest to the head of the vine) than other shoot positions further away (shoots 3, 5 and 7) ( $p = 0.906$ ).

There were no directional trends observed for an increased/decreased probability of shoots with one ( $p = 0.044$ ) or two inflorescences ( $p = 0.232$ ) as shoot position increased. Overall differences among shoot positions 3, 5 and 7 were less pronounced than those with shoot 1 (Figure 2).

**TABLE 1.** Deviance Information Criterion (DICs) for the Bayesian ordinal categorical Generalized Linear Models fitted to explain the differences in the number of inflorescences per shoot.

Model	2017/2018 <sup>1</sup>
Cane, vine and shoot position	132.865
Cane and vine, no shoot position	139.019
Cane and shoot position, no vine	145.824
Shoot position and vine, no cane	<b>130.594</b>
Shoot position only	141.952
Intercept-only (Null model)	144.302

<sup>1</sup>The smallest DIC for the best model is in bold.

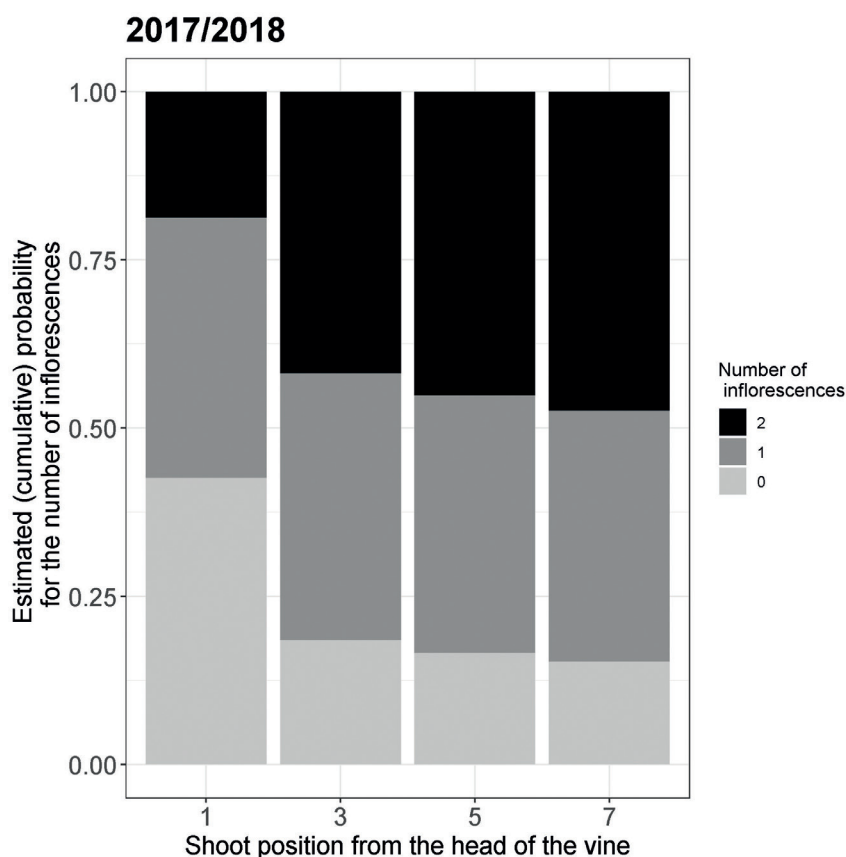
## 2. Number of flowers per inflorescence

The observed mean and median number of flowers for each inflorescence (Table 2) indicated differences between apical and basal inflorescences as well as canes which was supported by the model results: for both seasons, the model accounting

for cane and inflorescence position was only marginally better than the other three models, implying no statistical effect of any of the considered factors on the flower counts (Table 3; posterior estimated means and the corresponding 95 % credible intervals are shown in Figure 3). Specific differences observed were in 2017/2018, basal inflorescences on a shoot on the lower cane had 50 % higher counts than the apical inflorescences on shoots found on the upper cane with no other notable differences among canes or inflorescence positions (Figure 2). However, in 2018/2019 there were no differences between the modelled mean counts for different cane and inflorescence positions, with larger credible intervals, likely due to fewer vines being measured in this season (Figure 3).

## 3. Flowering progression

The null model (inflorescence-specific random effects only) was the best, indicating the lack of evidence for the effects of cane, inflorescence position and the variation among vines and shoots on flowering progression (Table 4). However, for both seasons, there was a wide range of dates at which different inflorescences reached 50 % flowering (Figure 4A and B) indicating that the time taken for all inflorescences to go through 50 % flowering was highly variable and occurred over several weeks.



**FIGURE 2.** The proportion of inflorescences corresponding to zero, one or two or more inflorescences at each shoot position along the cane relative as estimated via a Bayesian model (adjusted for variation among vines). Shoot 1 = shoot closest to the head and shoot 7 = furthest from the head of the vine.

**TABLE 2.** The observed mean, median and standard deviation of flowers per inflorescence for each cane and inflorescence position (basal or apical).

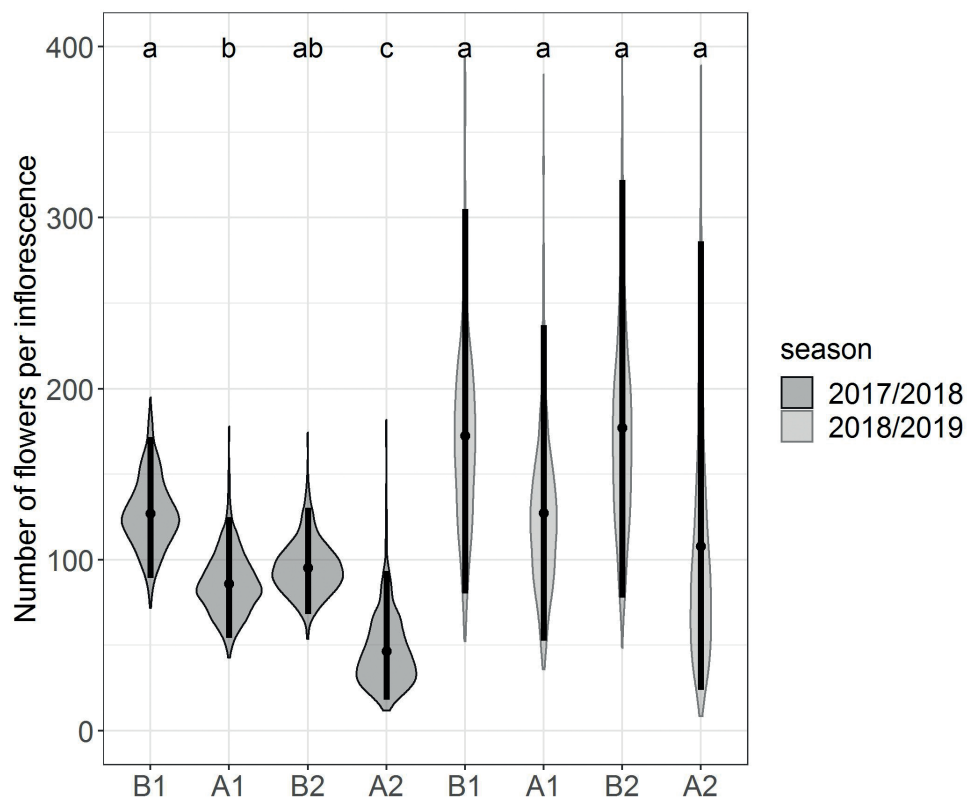
	Inflorescence position	mean	median	standard deviation
2017/2018				
Lower cane	Basal	138.5	135.0	47.1
	Apical	98.0	113.0	42.3
Upper cane	Basal	108.0	117.0	41.7
	Apical	83.3	77.5	57.1
2018/2019				
Lower cane	Basal	186.8	186.0	24.6
	Apical	149.4	162.0	56.7
Upper cane	Basal	191.6	187.5	43.5
	Apical	112.0	109.0	67.5

**TABLE 3.** Deviance Information Criterion (DICs) for the Bayesian Poisson Generalized Linear Models fitted to explain the number of flowers per inflorescence.

	2017/2018 <sup>1,2</sup>	2018/2019 <sup>2</sup>
Cane, inflorescence position, vine and shoot (Full model)	749.667	326.461
Vine and shoot	750.268	326.567
Cane and inflorescence position model	<b>748.735</b>	<b>326.268</b>
Null model	749.563	326.501

<sup>1</sup> The comparison is within each season not between seasons.

<sup>2</sup> The smallest DIC for the best model is in bold.



**FIGURE 3.** Posterior distributions (violin plots), posterior means and 95 % Credible Intervals (points and segments) for the average number of flowers per inflorescence. B and A refer to basal and apical inflorescences on lower (1) and upper (2) canes, respectively. For any two groups within the same season with the posterior estimated mean counts  $\mu_1$  and  $\mu_2$ , there is a shared letter  $0.025 < \Pr(\mu_1 > \mu_2 | \text{data}) < 0.975$ , i.e., there is no evidence of difference.

The progression through flowering differed by season with the odds of flowering estimated to increase 2.51-fold per day in 2017/2018 (95 % CI: 2.44–2.57) and 1.71-fold per day in 2018/2019 (95 % CI: 1.68–1.73) (Figure 5A and B, faster rate/greater slope in 2017/2018). When considering the average population timing for the 50 % flowering, it was estimated earlier at 9 Dec (95 % CI 8–10 Dec) in the

2017/2018 season compared with 23 Dec in the 2018/2019 season (95 % CI 22–24 Dec) (Figure 5A and B).

In 2017/2018, the model was also fitted with and without considering the node insertion point up the shoot of each inflorescence and it was found that the model with nodes was significantly better than the one without ( $\Delta DIC = 32.19$ ). There was approximately a two-day difference in the

**TABLE 4.** Deviance Information Criterion (DICs) for the Bayesian Poisson Generalized Linear Models fitted and parameter estimates for the Generalized Linear Model fitted to explain the differences in flowering progression.

Model		2017/2018 <sup>1,2</sup>	2018/2019 <sup>2</sup>		
Cane, inflorescence position, vine, shoot and inflorescence-specific random effects (full model)		2803.18	1225.52		
Vine, shoot, inflorescences-specific random effects (random-effects only model)		2802.56	1227.20		
Inflorescence-specific random effects only (null model)		2801.24	1226.38		
Parameters <sup>3</sup>	Mean <sup>4</sup>	sd	Credible intervals <sup>5</sup>		
			2.50 %	50 %	97.50 %
<b>2017/2018</b>					
$\beta_0$	-2.53	0.729	-3.720	-2.597	-1.029
$\gamma$	0.919	0.012	0.895	0.918	0.943
$\beta_1$ (cane)	0.556	0.856	-1.198	0.583	2.133
$\beta_2$ (inflorescence)	-1.110	0.915	-2.858	-1.100	0.790
$\beta_{12}$ (cane * inflorescence)	-2.246	1.699	-5.557	-2.247	1.099
sd.vine	0.788	0.566	0.106	0.674	2.140
sd.shoot	0.828	0.584	0.100	0.732	2.289
sd.id <sup>6</sup>	<b>3.682</b>	0.339	3.110	3.660	4.390
<b>2018/2019</b>					
$\beta_0$	-7.210	0.715	-8.737	-7.186	-5.849
$\gamma$	0.534	0.009	0.516	0.534	0.553
$\beta_1$ (cane)	1.977	0.935	0.287	1.958	3.726
$\beta_2$ (inflorescence)	-0.894	0.787	-2.414	-0.909	0.689
$\beta_{12}$ (cane * inflorescence)	-1.146	1.259	-4.154	-1.053	0.997
sd.vine	0.714	0.894	0.084	0.454	2.741
sd.shoot	0.484	0.412	0.080	0.358	1.648
sd.id <sup>6</sup>	<b>2.074</b>	0.316	1.577	2.033	2.782

<sup>1</sup> The comparison is within each season not between seasons.

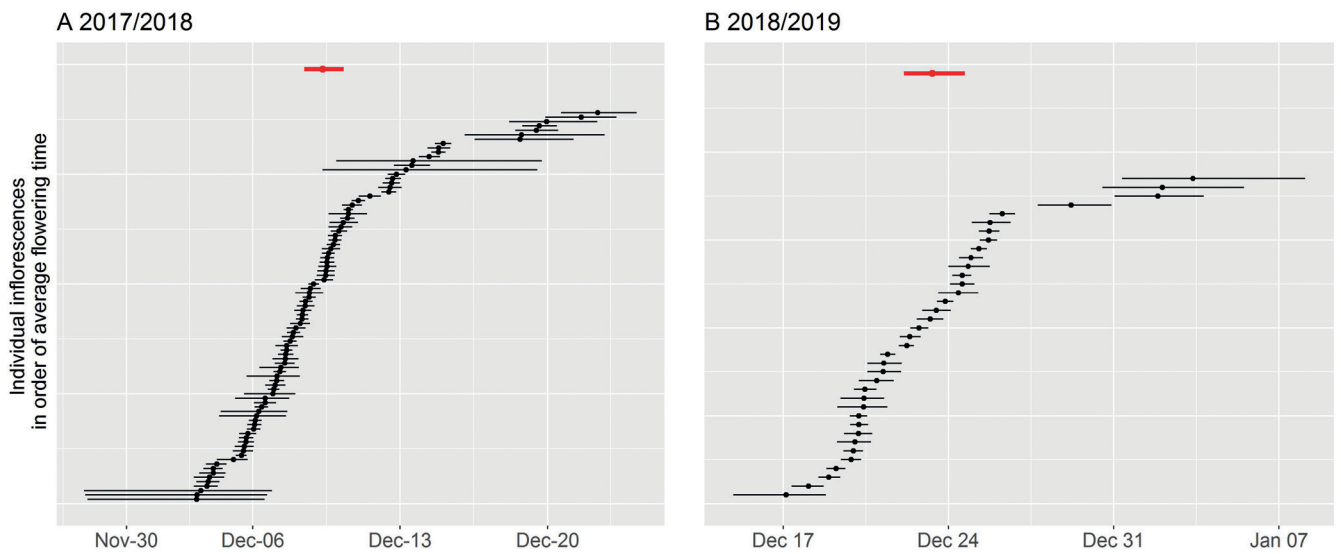
<sup>2</sup> The null model was the best models as there was no decrease in DIC with the other models (difference of 3 or less between the null model and others).

<sup>3</sup>  $\beta_0$  = intercept,  $\gamma$  = relative change in odds of flowering per day, sd = standard deviation, where sd.vine/ sd.shoot/ sd.id provides standard deviation of random effects of the model.

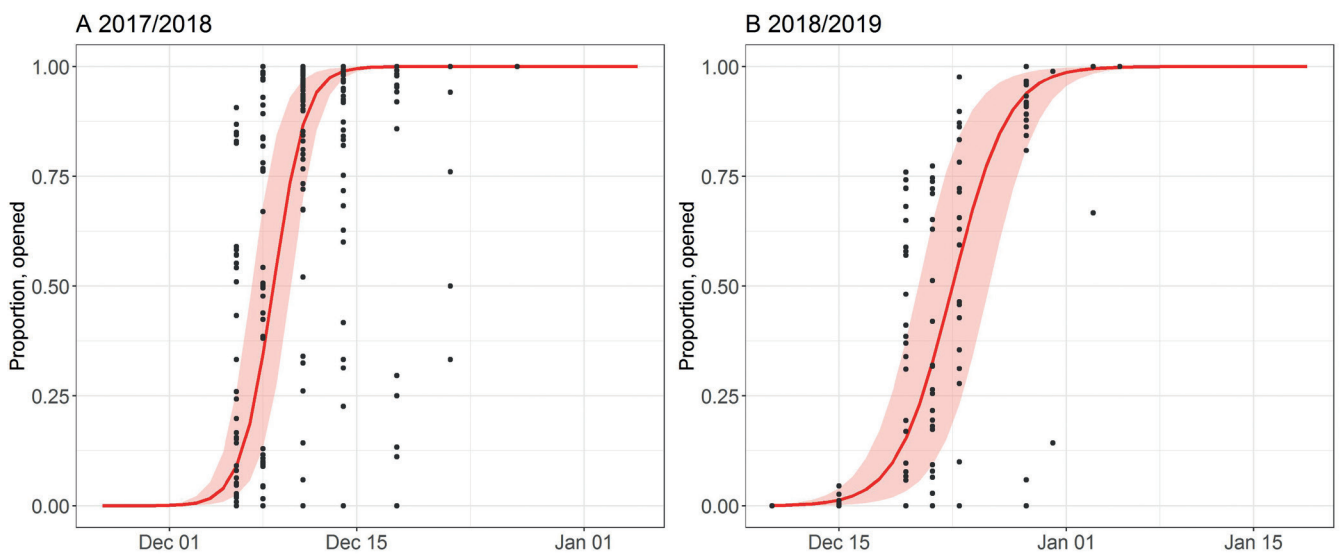
<sup>4</sup> Positive co-efficient indicate flowering is earlier, negative co-efficient correspond to later flowering compared to the average timing. For example, a negative co-efficient (mean) for  $\beta_2$  corresponds to the timing of 50 % flowering of the apical inflorescence id delayed relative to the timing of 50 % flowering of the basal inflorescence; a negative co-efficient for  $\beta_{12}$  corresponds to a delay in apical bunches on the upper cane being delayed relative to apical bunches on the lower cane.

<sup>5</sup> The credible intervals contain 95 % of the posterior probability mass for each parameter. If they include zero, there is no sufficient statistical evidence for a non-zero effect.

<sup>6</sup> Greatest variation among individual inflorescences (highlighted in bold).



**FIGURE 4.** The posterior mean estimated date at which individual inflorescences reach 50 % flowering as determined by logistic curve fits of data to individual inflorescence open and closed flower counts. Bars are 95 % credible intervals for the date of 50 % flowering for each inflorescence. The inflorescences have been ordered by the posterior estimated mean date of reaching 50 % flowering. The posterior estimated population mean is depicted in red. A. 2017/2018 season. B. 2018/2019 season.

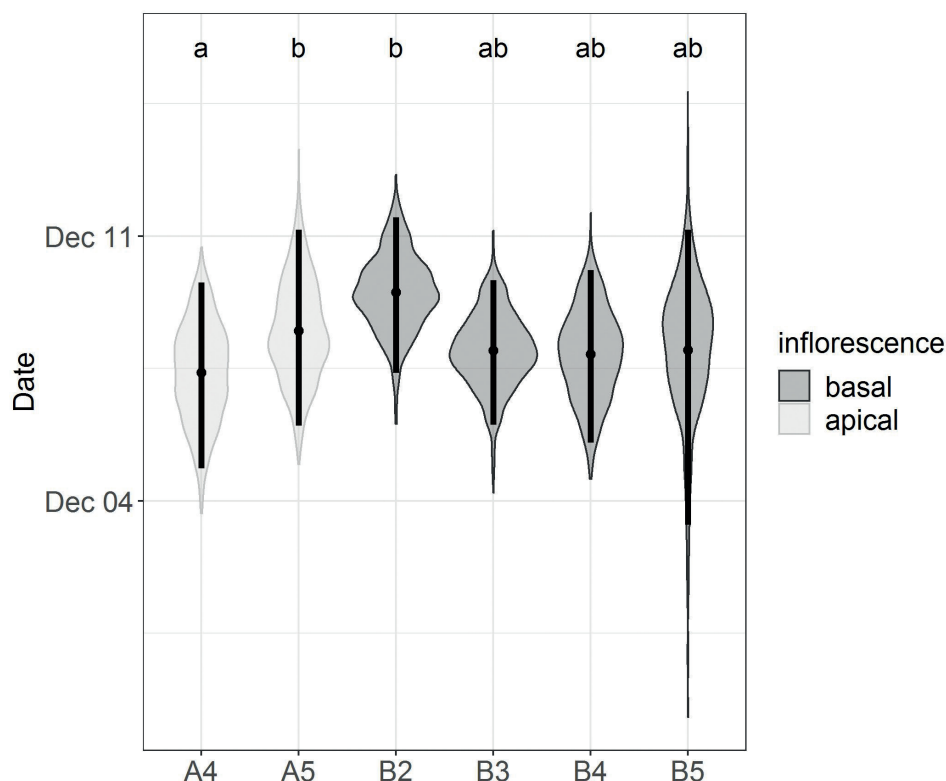


**FIGURE 5.** Proportion of open flower for individual images (dots) on different days during the progression of flowering. The population average is depicted in red. A. 2017/2018 season. B. 2018/2019 season.

average 50 % flowering date for node insertion point 3 (the earliest) and node insertion point 5 (the latest) (Figure 6). Often, where the inflorescence was at a higher insertion point, there was naturally no apical inflorescence on the same shoot (47 % of the shoots with basal inflorescences below the 4th node insertion point has apical shoots, but only 20 % of those with basal inflorescences at or above the 4th node insertion point did).

The timing and duration of flowering reflected the temperature differences in the two seasons. The accumulated

degree days (base 0 °C) calculated from 29 August indicated that the spring of 2017 was warmer than the average (2016 to 2020) accumulating 1715 degrees by 31 December, compared to 1558 degrees in 2018. Using the GFV model (Parker *et al.*, 2011) the estimated dates of 50 % flowering were 7 and 14 December in 2017 and 2018 respectively (Figure S1). Despite the earlier flowering in 2017, the mean daily temperature over the 5 to 95 % flowering period (5 to 12 December) was higher (20.5 °C), when compared to 2018 (17 to 31 December) 16.6 °C.



**FIGURE 6.** Posterior distribution (violin plots), posterior means and 95 % Credible Intervals (points and segments) for the expected date of 50 % flowering for basal (B) and apical (A) inflorescences on cane 1, at insertion points 2–5. For any two groups with the estimated timing  $t_{50\%,1}$  and  $t_{50\%,2}$ , there is a shared letter if  $0.025 < Pr(t_{50\%,1} > t_{50\%,2} \vee data) < 0.975$ , i.e., there is no evidence of difference. Note that apical bunches only existed at node insertion points 4 and 5.

## DISCUSSION

### 1. Variability in inflorescence position, size and flowering progression

May and Cellier (1973) and Huglin and Balthazard (1975) reported differences among cultivars (note: the cultivars investigated did not include Sauvignon blanc) in their pattern of inflorescence expression at different shoot positions along a cane, specifically indicating low basal bud fruitfulness (fewer inflorescences at shoot positions close to the head of the vine), a trend towards increased inflorescences as shoot position increased, but slowly declining again at higher shoot numbers for many cultivars. There were some differences in the number of inflorescences and the patterns by cultivar indicating the importance of understanding the genetic component of this phenomenon. Prior studies including these two, indicate that the presence or absence of an inflorescence primordia is determined the season prior to its expression, and this is determined by temperature, carbohydrate availability, light and associated plant growth regulators (for detailed reviews on this refer to Vasconcelos *et al.*, 2009 and Li-Mallet *et al.*, 2016), although a lack of carbohydrate availability at bud burst may result in inflorescence abortion (Eltom *et al.*, 2013). The timing of inflorescence initiation has been shown to depend on the position of bud on the shoot (and therefore along the resulting cane) (Vasconcelos *et al.*, 2009; Eltom *et al.*, 2014). Given that Sauvignon blanc is considered

an early-mid cultivar for phenology (Parker *et al.*, 2013), a genetic component may have contributed to poor bud fruitfulness at shoot position one, but it is also plausible that the conditions at the time of inflorescence primordia formation at position one in the two seasons were cool, favouring the absence of an inflorescence. Interestingly at the other positions (3, 5 and 7), there were either one or two inflorescences per shoot and little differences among these positions similar to that observed by Eltom *et al.* (2014), indicating either little environmental differences at the time of development and/or a genetically determined frequency relatively consistent across these positions. Future research could consider the same measurements in a warmer climate to determine if the extent of the genetic versus environmental basis for low basal bud fruitfulness. Nonetheless, the results highlight that basal bud fruitfulness is a key source of variability for the yield component of inflorescence number per shoot for Sauvignon blanc when considering cane-pruned vines in the climate where this research was conducted, and the importance to characterise this for different cultivars, climates and pruning systems.

When flower number per inflorescence was counted using our objective assessment method and analysed by the Bayesian model, our results indicated more flowers on basal inflorescences than apical inflorescences supporting prior findings (Huglin and Balthazard, 1975; Eltom *et al.*, 2017; Trought *et al.*, 2017).

As flower primordia develop pre-budburst until a few weeks prior to flowering (Dunn and Martin, 2000; Dunn and Martin, 2007; Petrie and Clingeleffer, 2005; Keller *et al.*, 2010), it is plausible that micro-climate/photosynthetic differences during this period may have contributed to the measured difference of more flowers on basal inflorescences on the lower cane compared with the apical inflorescences on the upper cane in 2017/2018. It has been demonstrated that flower number and temperature combined influence fruit set (Ebadi *et al.*, 1995). A full understanding of factors determining the number of flowers on an inflorescence has still to be elucidated. The number of flowers is the product of the number of branches on the inflorescence and the number of flowers on those branches. The majority of first-order branching appears to be completed by the onset of bud dormancy (May, 2000; Eltom *et al.*, 2017), although Jones *et al.* (2009) reported that Pinot noir inflorescence primordia increased in size and branch number between the onset and end of the dormancy period. It is not yet known how branching is controlling inflorescence size and flower number (Vasconcelos *et al.*, 2009), however, increasing the temperature shortly before budburst reduced inflorescence flower number (Eltom *et al.*, 2017) suggesting flower initials are developing at this time. Differences in the timing of branch and flower initiation in the developing inflorescences may explain the lack of consistency when relating inflorescence primary branch number to inflorescence flower number. May (2004) indicated that branch number per inflorescence is not a good indicator of flower number; however, Dunn and Martin (2007) subsequently found an association between primary branching and the number of flowers per inflorescence. Understanding the relationship between branching and flower number as well as the influence of cultivar, microclimate and training system warrants further investigation in the future. When considering the importance of flower number for yield formation, increased flower numbers do not correspond to increased berry number, where greater flower numbers have been associated with reduced percentage fruit set within a given season (Huglin and Balthazard, 1975; Keller *et al.*, 2010; Eltom *et al.*, 2017). This indicates a self-regulation of fruit set across all inflorescences on a vine in response to seasonal conditions. Furthermore, no association has been found between the number of berries per bunch with regard to the node insertion point up a shoot within a season (Eltom *et al.*, 2017). Therefore, although we observed differences between apical and basal inflorescences, the implications of differences in flower number for yield variability require an understanding of the flowering variability at the block, vine, cultivar and within vine level whereby environmental factors at the time of flowering may influence fruit set and yield.

Eltom *et al.* (2017) and Trought *et al.* (2017) demonstrated that the duration from 50 % flowering to target sugar concentrations and berry weights differed depending on the timing of flowering; understanding the sources of this variation is important for yield formation and reaching desired quality targets. Our research demonstrated that there were the greatest differences in the rate of flowering

progression between the seasons and that the greatest source of variability in flowering within a season was associated with individual inflorescences more so than between vine differences or within vine position effects. While there were some measured differences in timing as a result of node insertion point up shoot, the number of day's difference here was a lot less than the day's difference among the difference inflorescences within a vine to reach 50 % flowering. Given the importance of temperature during the flowering period for germination and fertilisation (Staudt, 1982), this means that fruit set could be highly variable among inflorescences within a vineyard block irrespective of where they occur within a vine. Within a vine, Eltom *et al.* (2017) also observed that duration from 50 % flowering to target sugar concentrations was greater for outer versus inner arms on inflorescences, rather than the inflorescences at set shoot positions themselves. So while we have demonstrated that at the whole inflorescence level there is a greater degree of variability associated with inflorescences alone rather than their position, the common method of assessing flowering for whole inflorescences may mask some important within-vine variability that would influence the time of maturity and potentially yield at harvest.

## 2. Implications for phenology monitoring and yield predictions

The collection of more accurate and representative data for vineyard blocks is becoming increasingly important to understand the consequences of climate change on phenology and yield and for the development of phenology and yield models. The great variability in flowering progression between seasons and among inflorescences within a season indicate that to accurately track flowering, it would be important to sample intensively throughout a block, rather than rely on tracking one or two shoots per vines, or a few neighbouring individual vines to determine flowering, although it is recognised this may not be feasible in a commercial context. However, research by Bramley and Hamilton (2004), Bramley (2005), Trought and Bramley (2011), Verdugo-Vásquez *et al.* (2016) and Bramley *et al.* (2019) demonstrate that through precision viticulture techniques, it is possible to sample within a block and implement the method of kriging to interpolate estimates of un-sampled sites within the block; these approaches can be used for characterising phenology and yield. This represents a potential way to determine approaches to monitor phenology and yield at the block level. Bramley & Hamilton (2004) and Bramley (2005) also demonstrated that yield has a spatial structure and that sampling can be improved if completed with information about the spatial structure of variation, notably soil property differences. Therefore, suitable phenology monitoring by sub-plots within a block would need to be considered for adequate implementation in the kriging methodology context. Verdugo-Vásquez *et al.* (2019) also developed a spatio-temporal model of within-field phenology, representing another potential avenue to determine sampling size and location. When considering the within vine variability in flowering progression, this may still be important for maturity as demonstrated by

Eltom *et al.* (2017) and Trought *et al.* (2017) but potentially a lesser contributor than general variation among inflorescences and between seasons. However, our research indicates that a range of inflorescence positions in the canopy (determined by node insertion points up a shoot) should be captured when monitoring phenology and yield. Furthermore, distinct patterns in inflorescence number per shoot for cane pruned vines were observed, indicating for this particular yield component it would be important to ensure that any monitoring captures this. Keller *et al.* (2010) demonstrate that as flower number increases, fruit set decreases and Eltom *et al.* (2017) demonstrated that inflorescences with different flower numbers, often converged to the same berry number within a site and within a season. Therefore, while we observed some differences in patterns of flower number per inflorescence associated with vine structures of cane or inflorescence position (basal or apical), the true implications of this are unknown for yield formation. Further research is warranted to model the flowering to fruit set process for these factors.

The method used for monitoring phenology was counting open and closed flowers from images and this is the first report of detailed analysis of flowering progression by this method. While this has enabled an objective and detailed approach to assessing flowering progression it does present some limitations: the image capture may not always maintain the exact angle of photo for each point in a time series, especially as overall growth can alter the position of the inflorescence between one day and the next (leading to potential differences in total flower number per inflorescence); it is time-consuming to manually count open and closed flowers in each image; not all images are useable due to operator error with image capture (resulting in blurry images); it requires two people to capture the image (one to hold a background/position leaves away from the inflorescence so the image can be captured). For this study, we have assumed that the proportion of open and closed flowers visible within the image is a suitable estimation of the flowering progression. However, one potential limitation is that more compact inflorescences, where there are several layers of flowers, may have been underestimated in the overall flower counts due to the flowers in the first layer of the photo obscuring or partially obscuring those in subsequent layers, or subsequent layers being out of focus. This is one limitation of the image capture process, although the human eye may also miss these flowers in the field for similar reasons.

While blurry images, time and personnel may be difficult to overcome, the future opportunity exists to investigate the ability to automate the processing of images via models or artificial intelligence. This could extend beyond flowering to berry counts and berry size analysis for yield predictions.

### 3. Application of the Bayesian modelling framework

Fifteen years ago, Ellison (2004) explained the philosophy behind Bayesian inference and expressed the opinion that the popularity of the Bayesian approach among ecologists may be hindered by computational difficulties

and the lack of user-friendly software. Although these difficulties still exist, the Bayesian approach is gaining ground. Examples of recent applications of the Bayesian approach include modelling seed germination (Popova *et al.*, 2016; Moltchanova *et al.*, 2020); plant physiology (Ogle and Barber, 2008; Mora *et al.*, 2016) and conservation biology (Wade, 2000). The data collected in this study represents what is observed in the field, rather than selecting shoots with pre-determined numbers of inflorescences (e.g., Trought *et al.*, 2017) or using cutting techniques to investigate the phenomenon of interest (e.g., May and Cellier, 1973). While all represent valid methods, the measurements made here reflect the *in-situ* variability that exists within a vineyard. As a result, the representation of inflorescences at different vine structures was not equal across vines, shoots and inflorescence positions, leading to an unbalanced dataset. The monitoring of flowering repeated measures over time on the inflorescences of interest also represents a repeated measurement data collection. Consequently, the Bayesian approach employed here, worked well to deal with fitting a mixed effect model with repeated measures and hierarchy within the data and unbalanced design as a result of measuring specific within vine structures. Therefore, the approach used to analyse the variability in this study is another example of applying a Bayesian modelling framework to investigate variability in biology. It should be noted that the Bayesian approach is especially useful in dealing with logistic regression as it does not suffer from the consequences of complete separation. In addition, the interpretation of Bayesian P-values as “the probability that a statement/hypothesis is true given the evidence/data” is much more intuitive than the definition of a classical p-value (i.e., probability of observing something at least as extreme as the data given that the null hypothesis is true) and allows one to interrogate the model in a natural and flexible way. Having successfully implemented this type of analysis to understand variability in inflorescence number, flower number and flowering progression, it could be envisaged a similar approach could be used for other phenological stages of interest (e.g. veraison), the degree of fruit set, or yield. The method could also be applied to investigate trends in inflorescence position, flower number and flowering progression for different cultivars as well as Sauvignon blanc in different climates or terroirs. To make our methods more accessible we have also attached the code for the models which can be run using the freely available WinBUGS software (Lunn *et al.*, 2000).

## CONCLUSIONS

Using objective counting of open and closed flowers in images of grapevine inflorescences, and a Bayesian modelling framework, sources of between and within vine variability in inflorescence number per shoot position along a cane, flower number per inflorescence and the progression of flowering could be evaluated for 4-cane pruned Sauvignon blanc vines. The most proximal shoot position closest to the head of the vine had low bud fruitfulness for cane-pruned Sauvignon blanc.

Flower number per inflorescence was greater for basal compared to apical inflorescences, but this was not always detectable in different seasons. Flowering progression varied the most by season and the individual trajectory of each individual inflorescence, rather than in a prescribed pattern relating to the vine, cane or shoot position in the vine, or basal or apical position up a shoot; however, there was some association with earlier flowering of inflorescences at lower nodes numbers on a shoot. These findings highlight the importance of adapting observation methods to reflect these trends for monitoring flowering and yield development in the grapevine.

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