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Quantifying the seasonal variations in grapevine yield components based on pre- and post-flowering weather conditions

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ABSTRACT

Seasonal differences in weather conditions cause marked variation in grapevine yield. However, quantitative relationships between various yield components and climatic factors at field scales are still lacking. By using a long-term field trial, we quantified the correlation between weather conditions during the key development stages and the yield components of *Vitis vinifera* L. Sauvignon blanc growing under cool-climate conditions. A long-term phenology and yield monitoring trial using both two-cane and four-cane trained vertically shoot positioned (VSP) Sauvignon blanc vines was established in four vineyards in Marlborough, New Zealand in 2004. Phenology, bunch number, berry mass, yield and meteorology records were collated. A multivariable mixed linear model was used to assess the relationship between various yield components and weather conditions. The critical periods for each yield component and weather factor were optimised based on the maximum likelihood returned from the mixed linear model. The optimised critical periods of temperature for all yield components occurred mainly before 50 % flowering either in the previous season (during inflorescence initiation) and the current season, indicating the importance of the pre-flowering period on yield formation. Out of all weather factors, maximum daily temperature had the largest effect on bunch number and overall yield and strongly influenced berry number and bunch mass. Rainfall near flowering time had a negative effect on berry mass and bunch mass, but post-flowering rainfall had a strong positive effect. The statistical model explained 60 to 85 percent of the seasonal variations in bunch number, berry number, berry and bunch mass and yield per vine.

KEYWORDS

grapevine yield, bunch number, berry number, berry mass, seasonal variations

Supplementary data can be downloaded through: https://oeno-one.eu/article/view/2926

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INTRODUCTION

Seasonal or inter-seasonal factors, especially temperature, radiation and water status, have pronounced effects on the fruitfulness and overall yield of grapevine (Buttrose, 1969b; Buttrose, 1974). Maintaining stable yields from year to year is essential for achieving a consistent fruit quality and supply, which are crucial within the context of increasing competition in the international market (Kliewer and Dokoozlian, 2005; Trought, 2000).

Grapevine initiate inflorescence primordia in the summer of the year prior to that in which they flower (Figure 1). This enables us to anticipate potential yield early in the season (Perold, 1927), allowing adjustments of crop load to be made during winter pruning and after fruit set. In this study, we use long-term field experimental data to investigate the relationship between weather conditions and yield.

Yield per hectare is the product of vines per hectare, shoots per vine, inflorescences per shoot, berry number per bunch and berry mass. Grapevines may generally form up to four inflorescences on a shoot (Watt, 2010). An undifferentiated mass of cells (anlagen, potential bunches for the following season) develop in the basal node approximately 15 days before bloom, with approximately 12 expanded leaves on the shoot (Swanepoel and Archer, 1988; Watt, 2010; Watt *et al.*, 2008). This process progresses along the developing shoot as further leaves appear (Vasconcelos *et al.* 2009). Whether or not anlagen become inflorescence or tendril primordia will depend on temperature and radiation conditions around the bud at the time differentiation takes place (Buttrose, 1969a, 1969b, 1970). High radiation intensities or temperatures during initiation will encourage inflorescence primordia development, while shaded or cool conditions will lead to tendril formation (Buttrose, 1970; Sanchez and Dokoozlian, 2005; Trought, 2005). In addition to

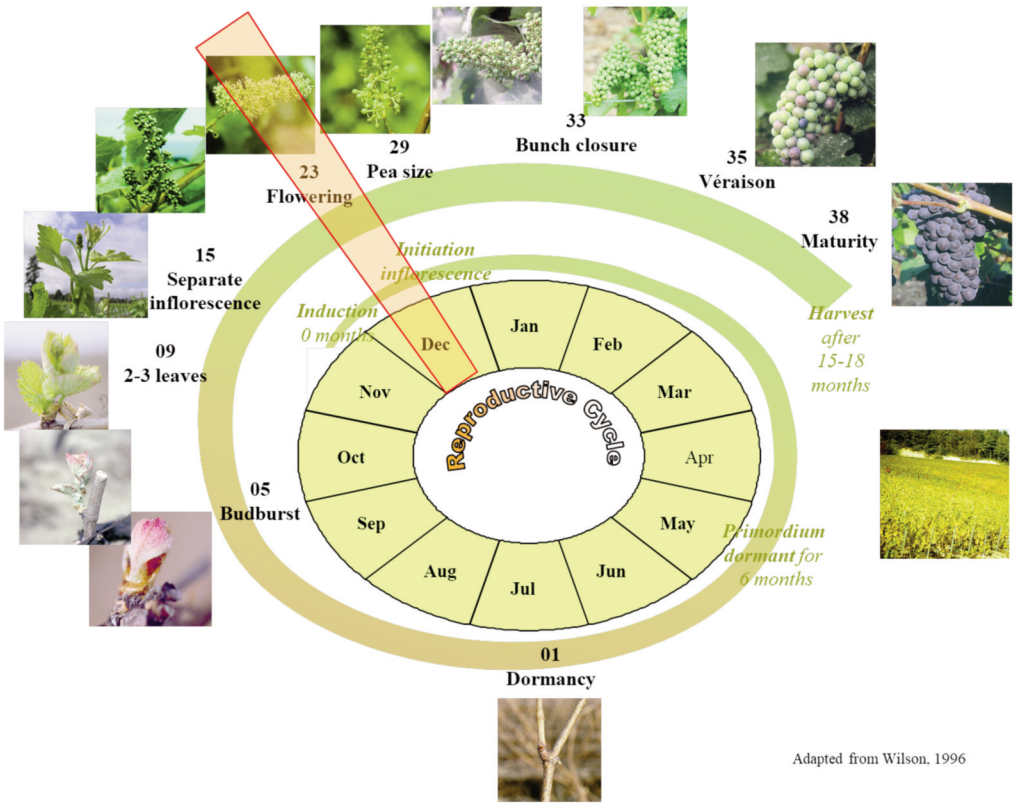


FIGURE 1. The reproductive cycle of a grapevine under southern hemisphere conditions.
The reproductive cycle starts at the time of induction and ends at harvest,
which occurs about 15-18 months after induction.
The numbers before the phenology stage represent the Modified E-L system code for growth stages (Coombe, 1995a). The idea of using a circle to represent the reproductive cycle was adapted from Wilson (1996). A figure detailing the yield formation processes is provided in Supplementary Figure S1.

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bud fruitfulness, temperature can influence the primary branching of inflorescence primordia, which can account for 51 to 81 % of the flower number per inflorescence the following season (Dunn and Martin, 2007). In this paper, we use 'inflorescence' to refer to the fruit bearing part of the vine that has not set berries and 'bunch' to refer to the fruit bearing part of the vine that has set berries.

Berry number per bunch is the product of flowers per inflorescence and percentage of flowers that set fruit. Cool temperatures shortly before budburst can increase the total flower number per shoot (Eltom *et al.*, 2017). However, cold weather after budburst may prevent the formation of individual flowers (Buttrose and Hale, 1973). Fruit set (or the proportion of flowers that are retained as berries) represents a change-over from the static condition of the fully developed flower to the rapidly growing condition of the young fruit (Coombe, 1962). Both low and high temperature can affect fruit set in grapevines. Pre-flowering low temperatures can disrupt both the formation and function of ovules and pollen during flowering. Likewise, exposure to temperatures of 15 or 40 °C in Pinot noir and Carignane can significantly lower fruit set (Kliewer, 1977). Temperatures below 15°C and above 32 °C are considered detrimental. However, no strong relationships between daily assessments of temperature at cap fall and berry set or berry development were found by Friend (2005), who suggests that light intensity (due to its impact on current photo-assimilate supply) may be a more valid environmental index than temperature.

Berry fresh mass is strongly linked with seed dry weight, while berry dry weight is more strongly influenced by leaf area to fruit number ratio (Friend *et al.*, 2009; Petrie *et al.*, 2000). The variation in total seed dry weight is related to changes in the extent of ovule fertilisation, which is related to the environmental and plant conditions before and after flowering (Ebadi *et al.*, 1996; Friend *et al.*, 2009). Pre-flowering or immediate post flowering low temperatures can slow pollen tube growth or disrupt ovule and seed development in Chardonnay (Ebadi *et al.*, 1996; Staudt, 1982). However, no strong relationship between daily temperature at cap fall and berry weight in Merlot was found by Friend (2005), who suggested that radiation intensity (correlated with current carbohydrates supply) may be a more valid environmental index than temperature.

Despite the importance of grapevine yield on various viticultural and winemaking practices, little effort has been made to predict yield (Dunn and Martin, 2007; Trought, 2005). Santos *et al.* (2011) have developed a multivariate linear regression model of grapevine yield (1986-2008) in response to monthly mean temperatures and monthly precipitation totals from March to June for the Demarcated Region of Douro in northeast Portugal. Bock *et al.* (2013) have analysed the correlation between long-term (1805–2010) grapevine yield records in Lower Franconia, Germany at the mean May-August temperature and sugar content at the mean April-August temperature. However, they did not consider the physiological basis of the grapevine yield formation, nor the effects of weather events during key developmental stages on yield. Furthermore, current plant growth models predict grapevine yield as a fraction of total dry matter produced during the berry growth period divided by the berry water content (Faluomi, 2017; Fraga *et al.*, 2016), using a source-sink carbon allocation approach. Thus, there is an urgent need to include the variations in shoot, bunch and berry number in plant models in order to make reliable yield predictions.

This study aimed to quantify the relationships between various yield components and climatic conditions during critical periods using a long-term field experiment of *Vitis vinifera* L. Sauvignon blanc. Sauvignon blanc was chosen as it is the main variety grown in New Zealand, representing 61 % of the total production area and 80 % of the yield (New Zealand Winegrowers, 2018). About 90 % of Sauvignon blanc in New Zealand is grown in Marlborough, which is considered to be a cool climate grape growing region (Jackson and Cherry, 1988; Jon *et al.*, 2012) and which contributes to the production of grapes with distinctive flavours. We aimed to answer the following questions (Figure S1): 1) what are the correlations between each yield component and different weather factors? (e.g., maximum or minimum temperature and radiation) 2) Is there a dominant weather factor? 3) What are the critical periods that determine each yield component? 4) Can we explain the variations in different yield components based on weather conditions during critical periods?

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MATERIALS AND METHODS

1. Experiment

Starting in 2004, data regarding phenology (budburst, flowering and fruit development) and yield per vine, bunch number (from which bunch mass was calculated) and berry mass (from which berry number per bunch was calculated) were collected from Sauvignon blanc vines in four commercial vineyards in Marlborough. Vines planted in rows 2.4 m apart and 1.8 m within each row were cane pruned and trained using vertical shoot positioning (VSP). The lowest fruiting wire was 90 cm from the ground and the top fruiting wire was 110 cm. Foliage wires were used to maintain a tight VSP canopy. Vines were either two-cane or four-cane pruned by the authors, retaining 20 or 40 buds respectively. This helped separate out the seasonal differences in yield from the management effects mainly caused by the buds retained after pruning. Active canopy management was practised throughout the growing seasons, including wire-lifting, canopy trimming and leaf plucking after flowering and before véraison. Vines were trickle irrigated, the timing and volumes determined by the vineyard manager. Pest and diseases were managed using industry protocols (www.nzwine.com/swnz/).

Data were collected from eight replicate plots of four vines (four in recent two seasons), planted between vineyard posts (bays), in each vineyard. Trunk diameters were measured on all vines in eight rows of the vineyards and plots were chosen to represent average size vines. The four chosen vineyards are spread across the predominant vineyard area of Marlborough, namely Upper Brancott (UB) [41.56569 S; 173.85154 E], Western Wairau (WW) [41.51113 S; 173.77012 E], Seaview Awatere (SA) [41.62863 S; 174.12950 E] and Central Rapaura (CR) [41.47617 S; 173.88981 E]. The current dataset contains 15 seasons (2004-2005 to 2018-2019) of phenology and 12 seasons of yield component records (except CR which has records of 15 seasons) for two-cane pruned Sauvignon blanc and 5 seasons of phenology and 13 seasons of yield component records for four-cane pruned Sauvignon blanc (see detailed history records in Supplementary Method S1). One additional vineyard with four seasons (2014-2015 to 2017-2018) of phenology and yield component records for three-cane pruned vines was added, namely Glasneven in the Canterbury region [43.10592 S; 172.74163 E].

Meteorological stations on or close to each site were used to examine the relationship between weather conditions and yield components. Four Marlborough stations were located between 0.1 and 2 km from the observation rows, namely UB [41.54248 S; 173.84736 E], WW [41.51343 S; 173.75983 E], SA [41.62959 S; 174.13096 E] and CR [41.49137 S, 173.8891 E]. Data were available from HortPlus NZ LTD. One National Institute of Water and Atmospheric Research (NIWA) station (Agent Number 26607, 43.06861 S, 172.65346 E) was used for the Waipara observation and was located 8 km from the observation rows. The meteorological stations complied with World Meteorological Organisation specifications, which require weather instruments to be sited in an open area away from buildings and shelter. The temperature and rainfall instruments were calibrated annually and data were downloaded and checked weekly. All stations recorded maximum and minimum daily temperature, rainfall and relative humidity. Radiation was not recorded in UB and CR stations. The radiation records from Blenheim central meteorology station (NIWA Agent Number 12430, 41.49722 S, 173.96292 E) were used for those two sites.

The recorded mean annual rainfall between 2002 and 2019 was 684 mm for UB, 910 mm for WW, 610 mm for SA and 723 mm for CR. The annual Penman evapotranspiration demand was 1022.6 mm according to records from the Blenheim meteorology station. The soil profile texture was loam originating from alluvium for UB and WW, silty loam originating from loess for SA and silty loam over sandy loam originating from alluvium for CR. The soil profile available water ranged from 80 mm to 140 mm per meter across sites and locations within the sites. Seasonal irrigation (mainly during summer) was between 200 mm to 450 mm. Predawn leaf water potential varied from -0.1 to -0.4 MPa during the growing season based on one of our irrigation trials (unpublished). The maximum leaf area per vine was about 7 m^2 for two-cane pruned vines and 10 m^2 for four-cane pruned vines. The yield per vine was about 5 kg for two-cane pruned vines and 7 kg for four-cane pruned vines with significant variations among years and sites.

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Flowering progression was estimated visually, twice a week, from late November through to late December (depending on the season) by assessing each of the inflorescences on all of the shoots arising from one cane in each bay (i.e., four canes per vineyard). The proportion of opened flowers per inflorescence was recorded in 5 % increments.

A random 32-berry sample was collected weekly from eight different bunches across all canes in each of the eight or four monitored bays. Berry sample collection started shortly before véraison and continued until harvest, to determine the berry mass and total soluble solids. A threshold soluble solids concentration of 8 °Brix was used as an alternate measure of the mid-point (50 %) of véraison, which was interpolated/extrapolated from soluble solids accumulation data (Parker *et al.*, 2014).

At harvest, eight monitored bays (four in recent two seasons) were hand harvested. All bunches were counted and weighed from each bay. Bunches with severe botrytis infection (>10 % visually assessed) were counted and weighed separately. The average bunch number per vine was calculated from the total number of bunches harvested from the four vines in the bay. Average bunch number per vine included bunches from the shoots along the canes (count shoots), as well as bunches on shoots arising from quiescent buds (non-count shoots) from the vine's head and trunk. Average bunch mass in this study was calculated based on bunches with less than 10 % botrytis infection. Berry numbers per bunch were estimated based on the average bunch mass and mean berry mass determined by the 32-berry sample at harvest. In order to exclude the effects of botrytis infection on observed yield, final yield was calculated as the average bunch mass × total bunch number × mean berry mass. On average, the calculated yield excluding botrytis infection was 1.7 % higher than the direct yield measurement.

During the analyses, berry number per bunch and berry mass of different treatments were grouped. There was a tendency for the berry mass in two-cane pruned vines to be slightly higher than that in four-cane pruned vines during the berry development. However, this difference was not consistent between sites and seasons and was also affected by the time of harvest. Four-cane pruned vines were normally harvested one or two weeks later than two-cane pruned vines. The Glasneven vineyard and data were only used for assessing the berry number per bunch, berry mass and bunch mass; the data were excluded from the analysis of yield per vine as it was three-cane pruned.

2. Analysis procedures

We hypothesised that bunch number per vine was determined by the weather conditions during the flowering periods of the previous season (inflorescence initiation) and berry number was determined by the weather conditions around flowering of the current season based on previous studies (Buttrose, 1970, 1974; May, 2000; Vasconcelos *et al.*, 2009). We further hypothesised that potential berry mass is determined by the environmental and plant conditions during flowering and fruit set period of the current season, while potential berry size is affected by radiation, leaf area to fruit number ratio, water status, etc., between fruit set and harvest. Thus weather conditions during three periods (flowering periods in the previous season (inflorescence initiation), flowering periods of the current season and post flowering periods, but before véraison of the current season) were analysed in more detail than during other periods (see detailed descriptions below). Other periods (e.g., before and after budburst of the current season and post véraison) were also explored, but they showed little effect and were therefore not reported.

In summary, the effects of mean daily temperature (Tmean, °C), daily maximum temperature (Tmax, °C), daily minimum temperature (Tmin, °C), radiation intensity (Ra, MJ day^{-1}), cumulative rainfall around flowering (RainTotFlow, mm) and number of rainfall days around flowering (RainDay) in the previous season (denoted by Ini after the factor; e.g., TmaxIni) and in the current season (denoted by adding Flow; e.g., TmeanFlow) on different yield components were tested. In addition, the effects of rainfall, vapour pressure deficit, potential transpiration and the difference between potential transpiration and rainfall after flowering - but before véraison in the current season (noted by Ver, e.g. RainTotVer) - were also tested. The effects of each weather factor were tested on all yield components: bunch number per vine, berry number per bunch, berry mass, bunch mass and yield per vine.

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An optimisation procedure was developed to find the critical period which would give the maximum likelihood between a certain weather factor during that period and the yield component in question (see the overall analysis procedure in Figure S2). The procedure used the recorded 50 % flowering (or 50 % véraison) time as input and tried to optimise two parameters that defined the period: one parameter defined the time before flowering and the other one defined the time after flowering (Eq. 1). The concept of thermal day was used to standardise the periods in different years with different temperatures (Eq. 2 and 3).

$$T_i = f(Temp, FL_{season-1}, TD_{backward}, TD_{forward}) \quad \text{Eq. 1}$$

$$f_T = \frac{2(T_a - T_{min})^{\alpha}(T_{opt} - T_{min})^{\alpha} - (T_a - T_{min})^{2\alpha}}{(T_{opt} - T_{min})^{2\alpha}} \quad T_{min} \le T \le T_{max} \quad \text{Eq. 2}$$

$$\alpha = \ln 2 \Big/ \ln[(T_{max} - T_{min})/(T_{opt} - T_{min})] \quad \text{Eq. 3}$$

T_i is the average max, min or mean daily temperature of the period defined by flowering time in the previous season ($FL_{season-1}$) minus and $FL_{season-1}$ plus . Thermal day (td) is the sum of thermal time units calculated using a temperature response curve (Eq. 2). f_T is the thermal time unit for a day with daily mean temperature T_{mean}. For seasonal accumulated thermal days td was summed from July 1st. T_{min} is the minimum temperature for growth, which is assumed to be 0 °C for the period before budburst and 4 °C for the growth after budburst (García de Cortázar-Atauri *et al.*, 2010). T_{opt} is the optimal temperature for growth, which is assumed to be 22 °C for the period before budburst and 28 °C for the growth after budburst. T_{max} is the maximum temperature beyond which no growth will occur, which is assumed to be 40 °C for the whole period. One thermal day in our calculation corresponds to 1.04 actual days if the mean daily temperature is 25 °C and to 1.56 actual days if the mean daily temperature is 18 °C.

A wide exploration of the parameter values that defined the periods was initially carried out to find the most plausible periods for fine optimisation (Figure S3). The package DEoptim (Ardia *et al.*, 2011) in R (R Development Core Team, 2019) was used for conducting the optimisation in parallel, thus improving the speed of optimisation. A critical period was optimised for each factor. The critical periods for two-cane and four-cane treatments were checked separately at first. As they did not practically differ from each other, a single critical period for each factor was optimised for the whole dataset simultaneously. The optimised periods for each factor on different yield components are shown in Supplementary Table S1.

The linear mixed-effects model (lmer) from the R package of 'lme4' (Bates *et al.*, 2014) was used to assess the relationship between different weather factors and yield component, as well as to assess maximum likelihood during optimisation (Eq. 4). Vineyard was included as a random intercept factor in the regression. Random slopes were not included, as they rapidly decreased the degrees of freedom of the model.

$$BerryNumT_{mean,flow} * RainTot_{flow} + T_{max,ini} + (1 \vee Vineyard) \quad \text{Eq. 4}$$

The ~ sign is the notation for the formula in R. The plus sign in the equation means that interaction between those two factors was not included; star (*) sign means interaction was included.

Maximum likelihood was returned by the basic R function logLik with restricted maximum likelihood (REML) equal to false; e.g., logLik(mod, REML=F). The REML was set to false, because we wanted to compare models with different fixed effects using likelihood ratio test and ANOVA (analysis of variance) test and the REML method was more used for estimating random effects (Hui *et al.*, 2019). The package lmerTest developed by Kuznetsova *et al.* (2017) was used to obtain the p-value of each factor.

The potential bias of parameter estimated by the mixed linear model caused by the year and site was evaluated by the bootstrap method using the function bootMer in the 'lme4' package (Bates *et al.*, 2014). Bootstrap is a general approach to statistical inference based on building a sampling distribution for a statistic by resampling repeatedly from the data at hand. The bias and standard error of the parameter from the true value estimated by the boot method were reported (Supplementary Table S2).

3. Model selection

The correlation between each yield component and weather conditions was first analysed with the R package of PerformanceAnalytics (Peterson *et al.*, 2018) to obtain an overview of the correlations. Afterwards, the combinations of different factors in the linear mixed model for improving prediction performance were tested,

resulting in a large number of models. Model selection was based on log-likelihood, R squared (R^2) and Akaike information criterion AIC (Sakamoto *et al.*, 1986). AIC rates model in terms of parsimony and efficiency, where the lowest value is associated with the best model.

$$AIC = -2 * loglikelihood + k * N_p \quad \text{Eq. 5}$$

Where N_p represents the number of parameters in the fitted model, k = 2 for the usual AIC, or k = log(n) (n being the number of observations) for the so-called BIC. A revised R^2 for the linear mixed-effects model was calculated using the r.squaredGLMM function in the R package of MuMIn (Bartoń, 2018). This function returns a marginal R^2 for the fixed effects and a

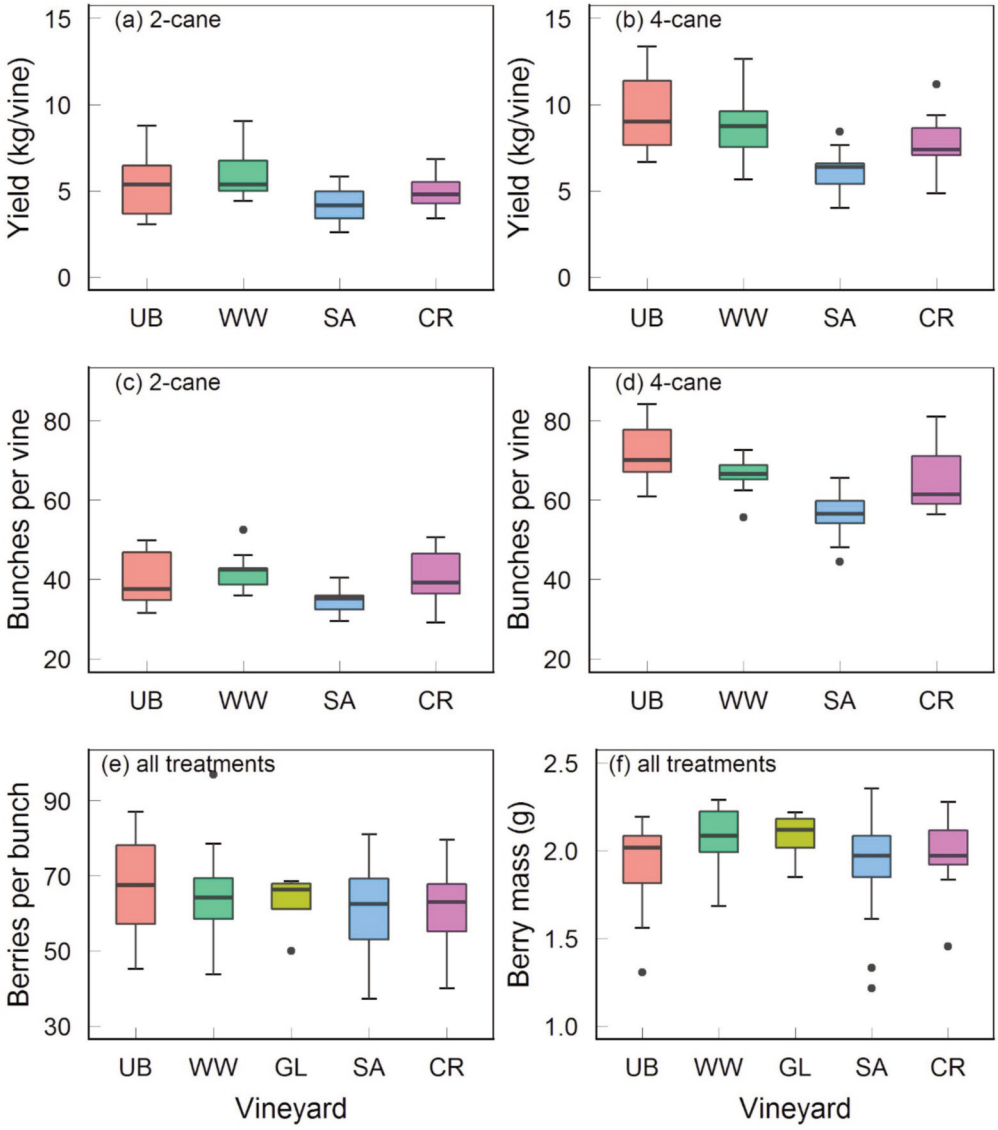


FIGURE 2. Sauvignon blanc grapevine yield (a and b), bunch number per vine (b and d) for two-cane (a and c) and four-cane (b and d) pruned vines and mean berry number per bunch (e) and berry mass (f) for all treatments.

UB represents Upper Brancott, WW represents Western Wairau, SA represents Seaview Awatere and CR represents Central Rapaura in Marlborough region, GL represents Glasneven in Canterbury region. GL vineyard is trained with three canes per vine. The other four vineyards have both two-cane and four-cane pruned vines. Only four years of data were obtained for the GL vineyards, while for the other four vineyards more than 12 years of observations were carried out for both treatments. Mean berry number per bunch and berry mass were combined for different treatments as no differences were found between treatments. Note: The bold black line in each box represents the median value for each vineyard. The middle "box" represents the middle 50 % of scores for the group, ranging from lower (25 percent, Q1) to upper (75 percent, Q3) quartile. Upper whisker represents the range to Q3 + 1.5 * IQR and lower whisker represents the range to Q1 – 1.5 * IQR where IQR equals to Q3 – Q1, the box length.

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conditional R^2 of the entire model including both fixed and random effects.

When there were two or more factors in the regression, the contribution of all factors were first checked and only the factors with a significant contribution were retained. Afterwards, the interaction term between all the factors was checked. The criteria for including the interaction were: 1) the interaction term has significant contribution; we accepted that the main factor would become non-significant after introducing the interaction term and 2) the model with the interaction term improves significantly compared to the model without the interaction term (ANOVA test).

When the best model differed between treatments, we first checked the best model in each treatment to see whether all the factors were significant. If one factor was significant in one treatment and not in another, we tended to include this factor to increase the stability of the model performance under different conditions. A list of all tested models and their regression results for bunch number per vine is shown in Supplementary Table S3; berry number per bunch is shown in Supplementary Table S4; berry mass is shown in Supplementary Table S5; bunch mass is shown in Supplementary Table S6; yield per vine is shown in Supplementary Table S7. The relationships between each yield component with the highest correlation factors are shown in separate figures. It should be noted that the final selected model only represent the highest model parsimony and efficiency. It may not include all the factors that would affect the yield Nonlinear response functions (e.g., logistic responses) were also tested. However, we could not justify the nonlinear response in our dataset.

RESULTS

1. Overview of the yield components

The mean yield across sites and years for two-cane pruned vines was 5.1 ± 0.21 (standard error) kg per vine and for four-cane pruned vines it was 7.9 ± 0.30 kg per vine (Figure 2 a, b). UB and WW were the highest yielding sites of the four sites and SA was the lowest yielding site in both two-cane and four-cane treatments. Of all the sites, UB had the highest variation in vine yield between years.

The mean bunch number per vine for two-cane pruned vines was 39.3 ± 0.8 per vine and for four-cane pruned vines it was 64.7 ± 1.2 per vine (Figure 2 c, d). Mean berry number per bunch across sites and years was 63.4 ± 1.1 (Figure 2e) and mean berry mass was 1.99 ± 0.02 g (Figure 2f).

2. Bunch number

When tested with a single factor for four-cane-pruned Sauvignon blanc vines, mean Tmax during the inflorescence initiation period (TmaxIni) gave the highest correlation with bunch number per vine (correlation index R = 0.77, Figure 3), followed by TmeanIni (R = 0.52), RadIni (R = 0.30), TminIni (R = 0.26) and RainTotIni (R = -0.18). Adding TminIni into the regression between TmaxIni and bunch number per vine did not improve the regression, indicating TmaxIni had a dominant effect on inflorescence initiation. Adding RadIni into the regression improved the overall R^2 and log-likelihood under both two- and four-cane conditions (Table S3). The interaction between TmaxIni, RadIni and RainTotIni were not significant. Thus TmaxIni + RadIni was chosen for the prediction of bunch number per vine.

Mean bunch number per vine increased linearly with the TmaxIni (Figure 4). On average, a one degree increase in temperature in TmaxIni was associated with a 2.87 bunch increase in two-cane pruned vines and a 4.6 bunch increase in four-cane pruned vines. The optimised period for TmaxIni was 15.9 td before 50 % flowering until 1.27 td after 50 % flowering and the optimised period for RadIni was 10.4 td before 50 % flowering until 0.14 td after 50 % flowering (Table 1), indicating that the critical period affecting bunch number per vine was mainly before 50 % flowering.

3. Berry number per bunch

Tmean around the flowering period (TmeanFlow) gave the highest correlation with berry number per bunch (R = 0.74, Figure 5a and Figure S4) when only one factor was considered, followed by TmaxFlow (R = 0.71), TminFlow (R = 0.48), RainTotFlow (R = -0.47) and TmaxIni (R = 0.29) and RadFlow (R = 0.22). Combining TmaxIni or RainTotFlow with Tmean improved the overall regression (Table S4). The best model was TmeanFlow * RainTotFlow + TmaxIni, which had the lowest AIC value and an overall R^2 of 0.75. Berry number per bunch decreased with the amounts of cumulative rainfall around the flowering period (Figure 5b). However,

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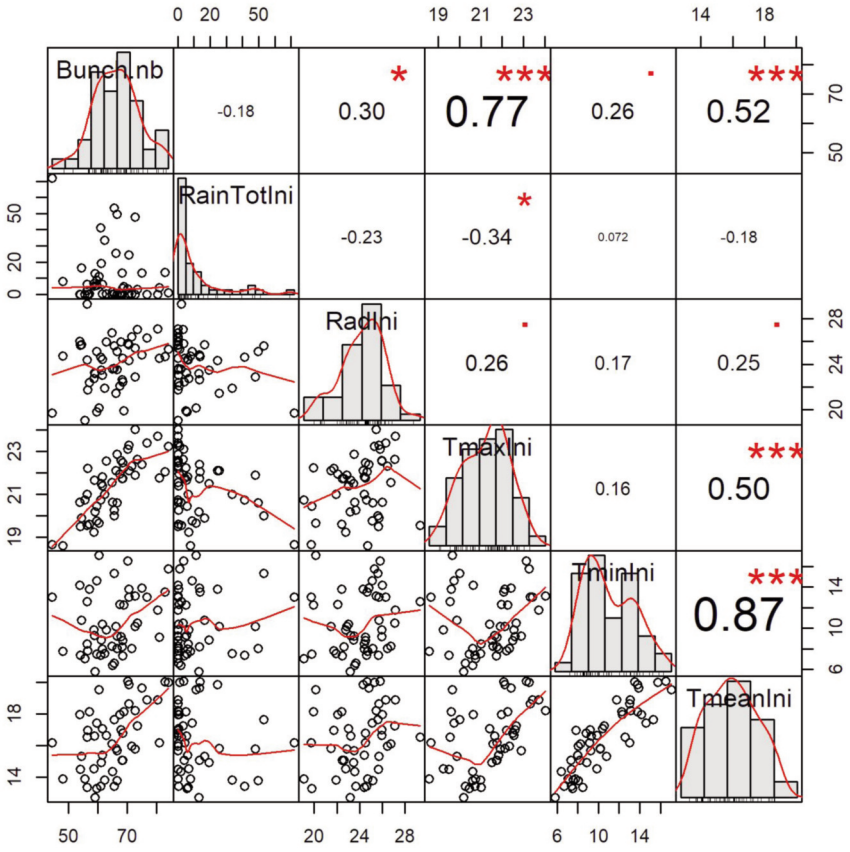


FIGURE 3. The correlation between mean bunch per vine of a four-cane-pruned Sauvignon blanc vine with sum of rainfall, mean daily radiation (MJ day^{-1}), mean maximum daily temperature (°C), mean minimum daily temperature (°C) and mean daily temperature (°C) during the inflorescence initiation period.

The distribution of each variable is shown on the diagonal. To the right of the diagonal, the values of the correlation between each factor pair plus the significance level as stars are shown. Each significance level is associated with a symbol based on p-values: 0.001 (***), 0.01 (**), 0.05 (*), 0.1 (.). To the left of the diagonal, the bivariate scatter plots with a fitted loess line are displayed. The first row and column show the correlation between bunch number per vine and climatic factor in question. Plots were made with the R package of PerformanceAnalytics (Peterson *et al.*, 2018).

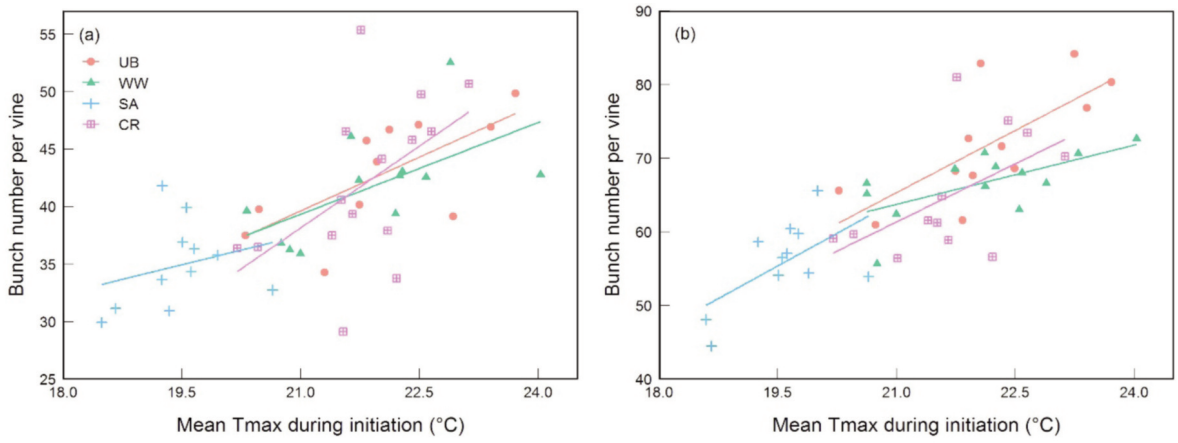


FIGURE 4. The correlation between mean maximum temperature during inflorescence initiation and mean bunch number per vine at harvest for two-cane (a) and four-cane (b) pruned Sauvignon blanc vines.

Lines are the linear regression for each vineyard region without random factors. The actual relationship could be nonlinear. UB represents Upper Brancott, WW represents Western Wairau, SA represents Seaview Awatere and CR represents Central Rapaura in the Marlborough region. Note: SA is in the Awatere Valley, which is significantly cooler and windier than the other three sites.

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TABLE 1. Selected prediction model for different yield components and the optimised periods for the factors that were included in the selected model.

Yield component	Factors[1]	TD backward[2]	TD forward	Fixed effects[3]	Random effects
Bunch number per vine (#)	TmaxIni	15.90	1.27	2-Cane: -34.48+2.87*TmaxIni+0.58*RadIni	0
	RadIni	10.42	0.14	4-Cane: -43.43+4.60*TmaxIni+0.42*RadIni	UB = 1.06; WW = -0.38; SA = -0.26; CP = -0.42
Berry number per bunch (#)	TmeanFlow	7.08	0.02	-44.3+3.18*TmeanFlow-0.83*RainTotFlow+2.58*TmaxIni+0.047*TmeanFlow*RainTotFlow	UB = 3.80; WW = 0.26; SA = 1.61; CR =-3.69; GL=-1.95
	RainTotFlow	10.50	2.69		
	TmaxIni	7.92	30.37		
Berry mass (gram)	TmeanFlow	10.02	1.17	1.4 -1.65e-2*TmeanFlow -1.67e-2 *RainTotFlow + 3.8e-2 * RadFlow+2.33e-2 * RainTotVer+9.87e-4 * TmeanFlow*RainTotFlow – 8.98e-4 * RadFlow*RainTotVer	UB = -1e-2; WW = 2e-2; SA = -1e-2; CR = 3e-3; GL = -1e-3
	RainTotFlow	13.42	2.92		
	RadFlow	11.37	11.42		
	RainTotVer	24.78	-13.10		
Bunch mass (gram)	TmeanFlow	8.49	0.17	47.23+6.42*TmeanFlow-2.88 * RainTotFlow -0.09* Et0_RainTotVer + 0.17 * TmeanFlow * RainTotFlow	UB = 9.6; WW = 4.36; SA = -5.84 ; CR = -6.19; GL = -1.92
	RainTotFlow	10.50	2.72		
	Et0_RainTotVer	27.60	-13.58		
Yield (kg/per vine)	TmaxIni	8.13	12.78	2-Cane: -13.55 + 0.2*TmaxIni + 0.34* RadIni + 0.33 * TmaxFlow - 9.6e-3 * Et0_RainTotVer	0
	RadIni	8.12	12.77		
	TmaxFlow	8.49	2.46	4-Cane: -28.24 + 0.37*TmaxIni + 0.30* RadIni + 0.92 * TmaxFlow + 4.6e-3* Et0_RainTotVer	UB = 0.07; WW = -0.02; SA = 0.01; CR = -0.06;
	Et0_RainTotVer	27.83	-13.57		

[1]Ini in each factor denotes the period during inflorescence initiation. The calculation for Ini uses flowering time of the previous season as the reference point. Flow denotes the period during the flowering time of the current season, using flowering time as the reference point. Ver denotes the post flowering and pre-véraison period of the current season, using time of véraison as the reference point.
[2]TD backward refers to the thermal days before the reference point. TD forward refers to the thermal days after the reference point.
[3]When applying the fitted equations, the biological limits of bunch number per bud, berry number per bunch and berry mass need to be considered.

Tmean and RainTotFlow had a positive interaction on berry number.

The period that gave the highest correlation between berry number per bunch and Tmean was from 7.08 td before 50 % flowering to 0.02 td after 50 % flowering, while the highest correlation with RainTot was for the period from 10.5 td before 50 % flowering to 2.69 td after 50 % flowering (Table 1). A close check of the response of R^2 to changes in the value of forward td showed that R^2 reached the peak when forward td was around 0 and then decreased when forward td further increased (Figure S3), indicating that berry number per bunch was more sensitive to temperature conditions before 50 % flowering.

4. Berry mass

TmeanFlow and RainTotVer had strong effects on berry mass (Figure 6 and Figure S5), followed by TmaxFlow (R = 0.55) and RainTotFlow (R = -0.55), Et0_RainVer (R = -0.48), RadFlow (R = 0.44) and Tmin (R = 0.34). The best model for predicting berry mass was TmeanFlow * RainTotFlow + RadFlow * RainTotVer (R^2 = 0.68) with all the interactions being significant.

RainTotFlow had a strong negative effect on berry mass, while RainTotVer had a strong positive effect, indicating the sensitivity of berry mass to changes in rainfall events during different development stages. The period that gave the highest negative correlation between

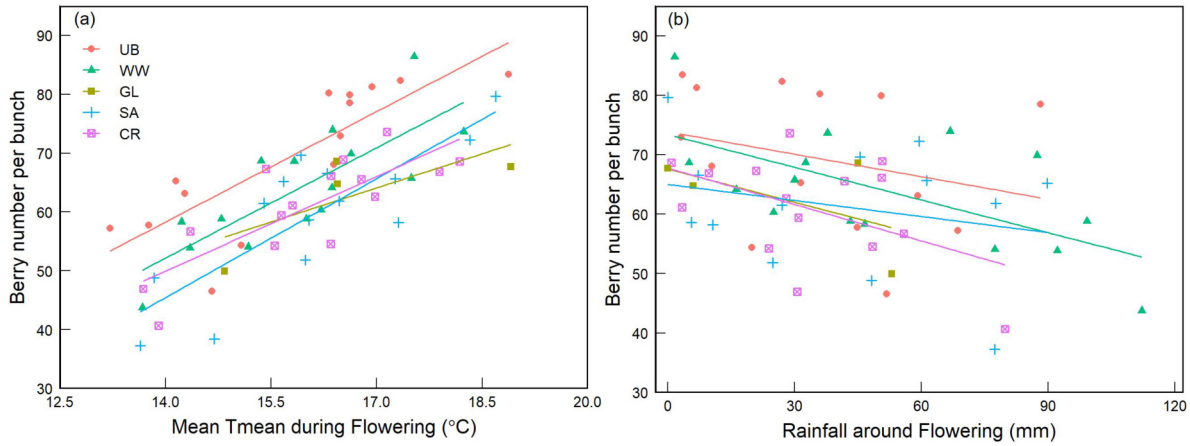


FIGURE 5. The correlation between mean temperature (a) and total rainfall (b) around the flowering period with mean berry number per bunch of Sauvignon blanc at harvest.
Lines are the linear regression for each vineyard without random factors. The actual relationship could be nonlinear. UB represents Upper Brancott, WW represents Western Wairau, SA represents Seaview Awatere and CR represents Central Rapaura in the Marlborough region, GL represents Glasneven in the Canterbury region.

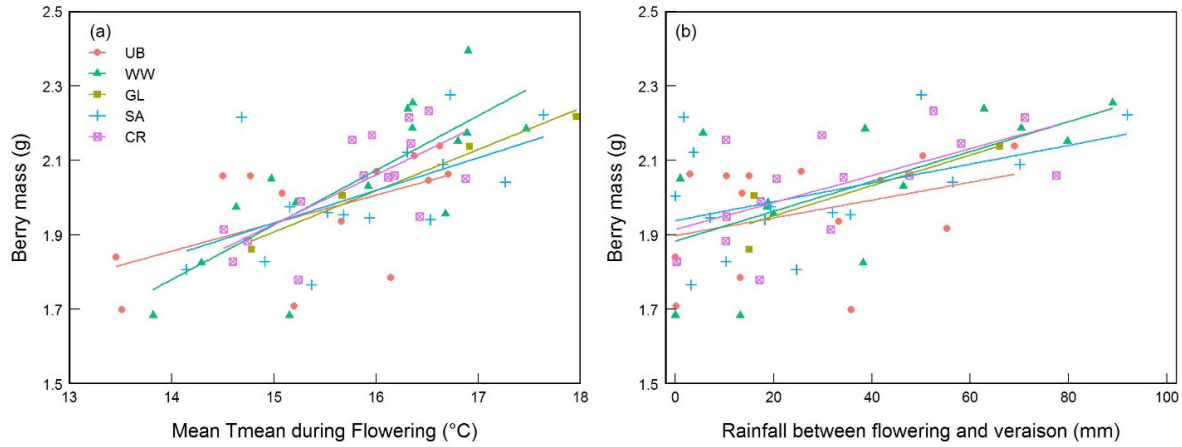


FIGURE 6. The correlation between mean daily temperature around flowering period (a) and total rainfall between flowering and véraison (b) with mean berry mass of Sauvignon blanc at harvest.
Lines are the linear regression for each vineyard without random factors. The actual relationship could be nonlinear. UB represents Upper Brancott, WW represents Western Wairau, SA represents Seaview Awatere, CR represents Central Rapaura in the Marlborough region and GL represents Glasneven in the Canterbury region.

RainTotFlow and berry mass was from 13.4 td before 50 % flowering until 2.9 td after 50 % flowering, while the highest positive correlation for RainTotVer was from 24.8 td to 13.1 before véraison (Table 1). On average, there were 40 td from 50 % flowering to véraison.

5. Bunch mass

Similar to berry mass, temperature, radiation and post flowering rainfall had positive effects on bunch mass, while rainfall around flowering showed negative effects (Figure 7 and Figure S6). However, the correlation between bunch mass and TmeanFlow (R = 0.78) was much stronger than for berry mass (R = 0.59). The best model for predicting bunch mass was TmeanFlow * RainTotFlow + ET0_RainTotVer with an overall R^2 of 0.83.

6. Yield per vine

Among all the factors, TmaxFlow (R = 0.71) and TmaxIni (0.56) stood out with the highest correlation with yield per vine (Figure S7). Despite the fact that all the vines were irrigated, yield per vine still negatively correlated with potential water deficit (ET0 minus RainTotVer). RadIni also had a marginal positive contribution on yield per vine. These four factors constitute the final model for predicting yield per vine.

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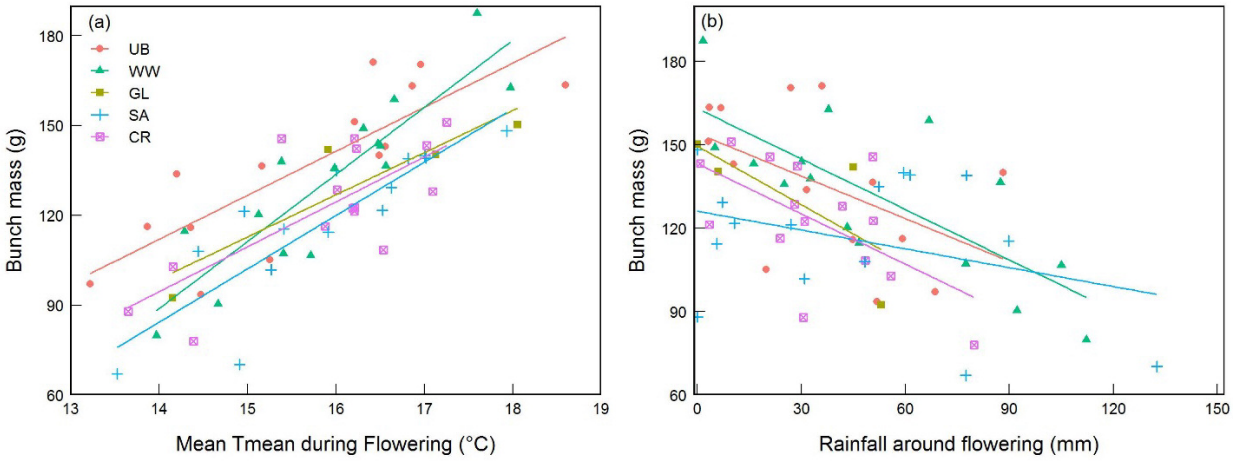


FIGURE 7. The correlation between mean daily temperature around flowering period (a) and total rainfall around flowering (b) with mean bunch mass of Sauvignon blanc at harvest.
Lines are linear regression for each vineyard without random factors. The actual relationship could be nonlinear. UB represents Upper Brancott, WW represents Western Wairau, SA represents Seaview Awatere, CR represents Central Rapaura in Marlborough region and GL represents Glasneven in Canterbury region.

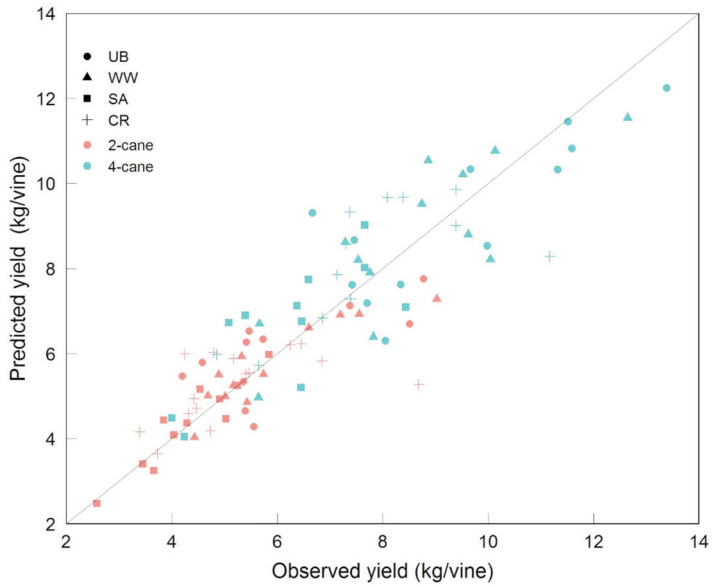


Figure 8. The relationship between seasonal observed yield per vine and predicted yields (calculated from the predicted bunch number per vine, berry number per bunch and berry mass). Individual vineyards [upper Brancott ●, west Wairau ▲, Seaview Awatere ■ and Central Rapaura +]. Orange symbols are two-cane and green four-cane pruned vines. The slope of the linear mixed regression without intercept was 0.9 and R^2 was 0.8.

The final yield - calculated by multiplying the estimated bunch number per vine, berry number per bunch and berry mass determined by weather conditions at critical periods - corresponded well with the observed yield for both two-cane and four-cane pruned vines (Figure 8). The slope between predicted yield and observed yield was 0.9 (estimated by linear mixed effects model) and explained 80 percent of the total variance. Similar results for R^2 were obtained by the direct yield estimation (Figure S8, R^2 = 0.81) and by bunch number times bunch mass (Figure S9, R^2 = 0.79).

DISCUSSION

Using data from a long-term yield monitoring experiment with meteorology data, this study quantified the relationship between grapevine

yield components (bunch number per vine, berry number per bunch, berry mass, bunch mass and yield per vine) and weather conditions during critical periods of grapevine development. Among all the weather factors, temperature was shown to have the strongest effects on all yield components. Rainfall near flowering time proved to have a negative effect, while post flowering rainfall had positive effects on berry mass, bunch mass and overall yield. Radiation had a moderate effect under our experimental conditions. We further show that weather conditions before 50 % flowering have stronger effects than post flowering weather conditions on berry number per bunch of the current season and bunch number per vine in the following season (Table 1). For instance, the optimised critical periods of temperature for berry number, berry mass and bunch mass all mainly occurred before 50 % flowering of the current season and for bunch number they mainly occurred before 50 % flowering of the previous season.

1. Maximum daily temperature

Our data indicated that maximum daily temperature had a dominant effect on bunch number and overall yield (Figure 1 and Table 2) and that it was one of the most influential factors regarding berry number and bunch mass, although it was sometimes surpassed by mean temperature. Buttrose (1969a) showed that the fruitfulness of *Vitis vinifera* L. Muscat Gordo Blanco buds was related to maximum temperature (rather than to temperature summation) when maintained for about four hours under growth chamber conditions. This was probably because high temperature stimulates cytokinin production and encourages greater inflorescence primordia development, which happens within a few hours (Buttrose, 1970). In contrast, low temperature led to a production of gibberellins and increased tendril formation (Jackson, 2008; Mullins *et al.*, 1992).

Regarding berry number and berry mass, the correlation index of TmeanFlow slightly surpassed that of TmaxFlow, indicating that minimum temperature may also play a role (Figure S4 and S5). However, when considering the whole yield, the correlation of both TmaxFlow and TmaxIni was higher than that of TmeanFlow, revealing the importance of Tmax in the overall yield formation. A positive effect of TmaxIni was also found on berry number per bunch. This was likely due to the positive effects of temperature on primary branch initiation prior to buds entering dormancy in the previous season, while primary branching was strongly correlated with flower number per inflorescence (Dunn and Martin, 2007).

2. The critical periods

Weather events during critical developmental periods that affect bunch number and berry number per bunch have a strong influence on yield. For grapevine, flowering and inflorescence initiation are critical periods, as weather conditions during these periods not only affect the current season's berry number and berry mass, but also greatly affect the following season's bunch number per vine.

Flower development, which determines the number of bunches (inflorescences) and berries in grapevine, involves three main steps: (1) formation of anlagen or uncommitted primordia, (2) differentiation of anlagen when forming inflorescence or tendril primordia and (3) differentiation of flowers. For the number of bunches per vine, our estimated critical period for TmaxIni was 15.9 td before 50 % flowering until 1.27 td after 50 % flowering. The start of the critical period is in agreement with the findings of Bennett (2002) and Swanepoel and Archer (1988), who showed that induction and initiation of anlagen generally start approximately 20 days before 50 % flowering at the basal two nodes on Chardonnay and Chenin blanc. The initiation of the first anlage continues acropetally on all nodes and takes about two days at one node for Chenin blanc in South Africa (Swanepoel and Archer, 1988). The initiation and differentiation of second anlage starts when the differentiation of the first anlage is completed. This whole process continues on all nodes till véraison, which is about 65 days after 50 % flowering (Bennett, 2002; Swanepoel and Archer, 1988).

The end of our estimated critical period (1.27 td after 50 % flowering) roughly corresponds to the end of initiation of the first anlage at the 10th node according to the diagram in Vasconcelos *et al.* (2009). Ten being the number of nodes we laid down during winter pruning. The end of the estimated critical period was much earlier than the end of second anlage differentiation process which was ~45 days after 50 % flowering at the 10th node (Vasconcelos *et al.*, 2009). We suspect that the period when the initiation of first anlage

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occurs is the most sensitive period for determining the bunch number per vine and weather conditions during this period will have more impact than the weather conditions which follow it. We further hypothesised that weather conditions during the initiation phase could greatly influence whether the anlage or uncommitted primordia will become inflorescence or tendril. The success of the initiation of the first anlage and its node position on the apical primordium could have carry-on effects on the initiation and differentiation of subsequent anlage. However, the fact that the fact that the initiation of the second anlage happens in warmer conditions (middle of summer) in our climate could have reduced its sensitivity and thus was not picked up by the optimization procedure.

For berry number per bunch, we found the critical period for TmeanFlow was 7.08 td before 50 % flowering till 0.02 td after 50 % flowering. This supports the findings by Ebadi *et al.* (1996), who found fruit set was reduced by exposing the vine to a lower temperature regime for one week in Chardonnay and Shiraz at E-L 15 (when inflorescence comprised single flowers in compact groups) or E-L 17 (when inflorescence comprised separate single flowers) (Coombe, 1995b). They further examined the seed characteristics of Chardonnay and found total number of seeds per berry was not affected, but lower temperature resulted in greater proportions of floater seeds. They further concluded that low temperature before flowering would negatively affect the structure of the ovules and the function of the pollen, seed development and reduce the number of cells and mass of the pericarp (Ebadi *et al.*, 1996; Ebadi *et al.*, 1995).

3. Rainfall around flowering and after flowering

Rainfall near flowering time was found to have a negative effect on berry number and berry mass, while rainfall after flowering was found to have a positive effect on berry mass and overall yield. Rain during the flowering period can physically inhibit pollination and fertilisation (Mullins *et al.*, 1992). Rain can also result in the failure of flower caps to be shed which will reduce fertilisation and thus fruit set (Keller, 2015). The negative effects of rain before flowering on berry number and berry mass were also confounded by reduction in radiation and temperature on rainy days (Figure 3); in overcast conditions , leaf photosynthesis will not proceed at optimal rates which could limit carbohydrate supply to the inflorescence (Friend, 2005). After flowering and fruit set, good soil moisture conditions can promote water uptake and berry development (Ojeda *et al.*, 2001; Pagay *et al.*, 2015). The positive effects of rainfall on berry and bunch mass after flowering for trickle irrigated vines as in this study (Table 1) suggest the vines could still experience some water stress. This could be because the inter row still has low soil water content under trickle irrigation. For non-irrigation practices with water-stressed plants, berry and bunch mass were generally more affected by rainfall.

A big variation in berry mass under conditions with low cumulative rainfall around flowering was found (Figure 6). This could be due to: 1) RainTotFlow not being the only factor determining berry mass; a strong interaction between TmeanFlow and RainTotFlow was also found and high temperature with high rainfall was certainly less harmful than the combination of low temperature and high rainfall, 2) a variation between seasons in the amount of irrigation applied and soil water conditions prior to the calculation of cumulated rainfall and 3) the distribution of rain events: continuous light rain would have more negative effects on berry mass than short and heavy bursts of rain.

4. Limitations of the current study

Radiation was found to only have a moderate effect on bunch number, berry number and final yield. This could be because 1) the variation of radiation intensity at the bud level may have been low due to the dense canopy, despite the changeable overall exterior radiation and 2) the overall radiation intensity under our field conditions was relatively high and was thus not the main limiting factor. Unfortunately, we did not record the pruning weight and cane diameter in each season and we were therefore unable to link the variation in radiation intensity during each season with the actual biomass production, which is an indication of plant carbon status.

Bunches from non-counted buds (quiescent buds) were not separated from the counted buds on canes at harvest. Bunches from quiescent buds account for approximately 15 % of total bunches (unpublished data). This may have added noise in the correlations between bunch number per vine and climate variables due to the

fact that these bunches developed fully during the year of harvest. In addition, due to limited data on flower number, we could not quantify the effects of temperature before budburst on flower number and the effects of weather conditions on fruit set, although this could be inferred by berry number and berry mass.

We show that an increase of one degree in both TmaxIni and TmaxFlow is associated with an increase of 0.53 kg per vine in two-cane pruned vines and an increase of 1.29 kg per vine in four-cane pruned vines, assuming other factors remain the same (Table 1). Extrapolation beyond the temperature range found in the current study is not warranted. For instance, no clear yield trends were found on Shiraz in Barossa Valley Australia by increasing daytime ambient temperature (1.8 to 4.1 °C) for 2 to 3 weeks during a single phenological window (Sadras and Soar, 2009; Victor *et al.*, 2017). This was likely linked to the background temperature. The mean daily maximum temperature in Barossa Valley in January was 30.5 °C (source: weatherzone.com.au), which was about 8 °C higher than Marlborough (Chappell, 2016).

Furthermore, direct application of the positive relationship between temperature and yield when evaluating the effects of global warming on yield is not encouraged. Warming will likely advance phenology in such a way that temperature conditions during the key periods for initiation and fruit set may not be much different to those being currently experienced. Such an advance in phenology could also occur with a reduction in radiation intensity at flowering, as flowering currently occurs about 10 days before the summer solstice in Marlborough conditions. Thus, a following step would be to integrate the effects of weather conditions on bunch number per vine, berry number per bunch and berry mass into a processed-based plant model for assessing any changes in phenology, as well as the effects of carbon assimilation on berry sugar accumulation, in order to evaluate the effects of climate change on grapevine yield.

CONCLUSION

We quantified the correlation between grapevine yield components and weather conditions during key developmental stages (e.g., flowering) by carrying out a long-term phenology and yield monitoring trial. We found daily maximum temperature played a critical role in inflorescence initiation, while both daily maximum and minimum temperature played essential roles in berry number and berry mass. Radiation and rainfall account for extra variation in yield components besides temperature. Incorporating the correlations between yield components and weather conditions into plant models will likely improve our yield prediction for grapevine.

SUPPLEMENTARY INFORMATION

The following Additional Supplementary Data can be found in the online version of this article on the publisher's web-site:

Method S1. Vineyard monitoring history.

Table S1. The optimised critical periods of each weather factor for bunch number per plant, berry number per bunch, mean berry mass, bunch mass and yield per vine

Table S2. The potential bias and standard error of parameter estimated by the mixed linear model caused by the year and site as evaluated by the bootstrap method.

Table S3. List of all models tested for bunch number per plant and weather conditions.

Table S4. List of all models tested for berry number per bunch and weather conditions.

Table S5. List of all models tested for berry mass and weather conditions.

Table S6. List of all models tested between bunch mass and weather conditions.

Table S7. List of all models tested between yield per vine and weather conditions.

Figure S1. Reproductive sequence of different grapevine yield components and the potential influence of weather conditions on each yield component at different development stages.

Figure S2 Illustration of the analysing procedure.

Figure S3. The change of R2 values of the linear regression between mean daily maximum temperature during flowering and berry number per bunch of a Sauvignon blanc vine in response to the parameters that defines the period for calculating the mean daily maximum temperature.

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Figure S4. The correlation between mean berry number per bunch with different weather factors

Figure S5. The correlation between mean berry mass with the different weather factors.

Figure S6. The correlation between mean bunch mass with different weather factors

Figure S7. The correlation between mean yield per vine with different weather factors.

Figure S8. The relationship between seasonal observed yield per vine and predicted yields (calculated directly by weather conditions around critical period).

Figure S9. The relationship between seasonal observed yield per vine and predicted yields yield (calculated from the predicted bunch number per plant × bunch mass).

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