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# Effects of cane- and spur-retained node numbers on the pre-flowering vegetative growth of cane-pruned Sauvignon blanc

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## ABSTRACT

In established vineyards, node number retention at winter pruning is the first step to achieving and maintaining vine balance. Balanced vines exhibit timely and quasi-uniform 100 percent budburst. To understand how vine capacity and balance are expressed before flowering, mature Sauvignon blanc vines were pruned according to a 5 [total node numbers on canes: 10, 20, 30, 40, 50] x 3 [total node numbers on spurs: 1, 2, 3] factorial design in one site, and in two other sites according to a 5 [total node numbers on canes: 10, 20, 30, 40, 50] x 2 [total node numbers on spurs: 1, 2] factorial design. Two spurs of one, two or three nodes each were retained on either side of the vine. The number of canes laid down per vine was one, two, three and four canes each of 10 nodes for the 10-, 20-, 30- and 40-node treatments, and four canes averaging 12.5 nodes for the 50-node treatment. The budburst percentage was calculated on the whole vine, canes, and spurs. Blind nodes, count shoots, non-count shoots and double shoots were counted and mapped along canes and spurs. Many non-count shoots were measured on the vine head of 10-node vines (29.5 ± 3.0 shoots, $p < 0.001$), compared to 50-node vines (2.8 ± 1.9 shoots, $p < 0.001$). 50-node vines had an overall budburst of 100 %, despite having the highest number of blind nodes (7.6 ± 0.3 nodes, $p < 0.001$). These were mainly located at the canes' proximal sections relative to the vine head and were likely caused by correlative inhibition and primary bud necrosis. Cane budburst provided a more accurate assessment of the vine response to node loading than vine budburst. The number of double shoots was not associated with the vine node load, as they appeared on both low-node and high-node vines. Three-node spurs developed more blind nodes than one-node and two-node spurs ($p < 0.001$). Based on the findings of this research, we recommend a composite metric (cane percent budburst, cane blind node count and head shoot count) to assess vine capacity and balance between budburst and flowering, and the practice of retaining one- or two-node spurs at cane pruning is also justified.

**KEYWORDS:** blind node, budburst, correlative inhibition, development, double shoot, vine balance

## INTRODUCTION

Retaining the requisite number of nodes after pruning is one of the most cost-effective means of achieving an equilibrium between vegetative and reproductive growth (Greven *et al*., 2014; Keller and Mills, 2007; Berkey *et al*., 2011). This equilibrium or balance is necessary for sustained quality grape and wine production (Jones *et al*., 2018; Trought and Bramley, 2011). Grapevines respond to low node loads by producing more shoots than the total number of retained nodes on canes and spurs, resulting in a vine budburst of 100 % or higher (Huglin and Schneider, 1998; Tassie and Freeman, 1992; Winkler *et al*., 1974). Retaining fewer nodes incentivises the development of more than one primordial bud per node, resulting not only in bud burst on all count nodes (nodes intentionally retained as future growing points), but also, in some instances, in double-shoots or multiple shoots arising from a single node (Keller, 2015; Tassie and Freeman, 1992). These extra shoots are referred to as non-count shoots. Additional non-count shoots also arise from quiescent buds within the head of the vine, or on the trunk (Huglin and Schneider, 1998). Conversely, retaining excessive node numbers generally leads to fewer shoots than the total number of retained nodes (less than 100 % budburst) and greater numbers of blind nodes (also termed "blind buds" in the literature). For example, a vine budburst of 115–120 % was reported on Sauvignon blanc grapevines cane-pruned to 24 nodes compared with 85–92 % on 72-node vines (Greven *et al*., 2014). Likewise, reducing retained node number from 50 to 30 nodes increased the budburst of Pinot Gris, Pinot Noir and Sauvignon by approximately 5 % (Zamboni *et al*., 1996).

The location, distribution and proportion of blind nodes is generally reported on frost damaged vines or on dormant vines. Howell and Wolpert (1978) observed the presence of blind nodes on the cane's middle section of frost-damaged vines in spring. Other authors have reported blind nodes on the middle section of canes of high-node load vines in winter (Benismail *et al*., 2007; Greven *et al*., 2014; Tomasi *et al*., 2007). Blind nodes appearing at the proximal section to the head of long canes have been ascribed to correlative inhibition (i.e., distal nodes bursting buds and growing faster than proximal buds to the head which remain dormant) (Galet, 2000; Keller, 2015).

The proportion and distribution of blind nodes along canes and spurs is especially critical for the management of cane-pruned vines. Blind nodes at the proximal section of fruiting canes can drastically limit the number of candidate dormant shoots to retain at winter cane pruning to form fruiting canes or renewal spurs (Epee *et al*., 2022). As fewer dormant shoots are available in the cane's proximal sections, they are selected farther away from the head leading to a suboptimal use of the available vine space within the row and thus reducing productivity. Blind nodes located in the middle or distal section of the trunk of the fruiting canes may lead to gaps in the canopy, resulting in insufficient light interception and poor vine performance. Therefore, understanding where and why blind nodes occur on the vine is crucial for the long- and short-term success of winter cane pruning and vineyard productivity. Moreover, although the presence of double shoots is usually associated with high vine vigour, which can be induced by low node load, their numbers and location along canes have not been investigated.

It has been observed that on cane pruned grapevines, budburst and early shoot growth is irregular, with budburst beginning on nodes at the most distal positions to the vine head, resulting in vigorous and rapidly growing shoots at distal positions compared to shoots located in the middle or proximal positions to the head (Galet, 2000; Keller, 2015; Tassie and Freeman, 1992). This phenomenon – known as correlative inhibition – is frequently reported in viticulture manuals (Galet, 2000; Jackson, 2014; Keller, 2015). Correlative inhibition is initiated well before dormancy when the shoot apex exerts apical dominance over subtending axillary buds of the actively growing shoot (Faust *et al*., 1997). This inhibition follows a gradient which is carried over into winter, manifesting itself at budburst with terminal buds breaking dormancy first and growing faster and more vigorously than the rest (Saure, 1985). The extent to which cane and spur nodes express correlative inhibition immediately following winter rest when subjected to different node numbers is unreported. The most recent published research on Sauvignon blanc vegetative growth and phenological response to increasing node loads focused on the response at the scale of the whole vine, and not on within-vine changes in growth along canes, spurs and the vine head (Greven *et al*., 2014; Greven *et al*., 2015). Research by Greven *et al*. (2014) Greven *et al*. (2015) was conducted on young vines aged three years at the start of the experiment. With more carbohydrate reserves in canes, trunk and roots, mature vines pruned to lower node numbers may offset the deleterious effects of correlative inhibition, resulting in more uniform budburst and shoot growth.

Understanding the physiological changes pruning induces on mature grapevines, such as the development and distribution of double shoots, blind nodes and percent budburst, are crucial for minimising within-vine shoot growth variability and promoting adequate dormant shoot selection at pruning, thus ensuring sustained grapevine management and productivity. A previous study on the characterisation of dormant shoot attributes found that changing the node number affects the attributes of retained dormant shoots at cane pruning (Epee *et al*., 2022). The objectives of this research were therefore to examine the effects of the number of nodes retained on canes and spurs at pre-flowering on: (i) the budburst percentage on the whole vine, canes and spurs, (ii) the number and distribution of double shoots, non-count shoots and blind nodes along canes and spurs, and (iii) early shoot growth (pre-flowering) along canes and spurs on mature grapevines at three different sites. It was hypothesised that: low-node vines will respond differently to high-node vines, with the latter having a lower budburst percentage, fewer double shoots and more blind nodes with a distinct distribution along canes and spurs.

## MATERIALS AND METHODS

### 1. Sites description

The research was conducted in two commercial vineyard blocks, one in Awatere Valley, Marlborough, New Zealand (GPS: 41°39'43.3"S, 173°59'59.9"E; masl: 140 m), and the other in Waipara, Canterbury, New Zealand (GPS: 43°06'17.4"S 172°42'26.1"E; masl: < 100 m). Across all three sites, the rows and vines were selected based on their vigour (weak vines rejected), age (replants avoided) and health condition (disease and pest free).

Awatere Valley: Site 1 and Site 2. A detailed description of the Awatere Valley vineyard block, including trellis systems, grapevines genotypes, vineyard management and prevailing weather conditions during the experiment, is given in a previous paper (Epee *et al*., 2022). Briefly, the block was established in 2008 and planted with *Vitis vinifera* cv. Sauvignon blanc clone BDX316 grafted on rootstock 101-14 Mgt with rows oriented north-south 2400 mm apart and with 1800 mm in-row vine spacing. Vines were trained to a vertical shoot positioned (VSP) system with three canes carrying on average 36 nodes (on average 12 nodes each) and two spurs carrying two nodes each. The bottom and top fruiting wires were, respectively, 1000 and 1250 mm from the soil surface on the same vertical plane, and the canopy was restrained to approximately 300 mm wide using movable foliage wires. The canopy was trimmed to a height of 2200 mm three times during the growing season from December to February. The yearly average temperature, GDDs (Growing Degree Days) and total annual rainfall in 2019 were 13.2 °C, 1212.4 °C and 211.4 mm and in 2020 12.9 °C, 1220.8 °C and 558.8 mm respectively (Harvest Electronics Ltd, 2021). At the start of the experiment in winter 2019, 75 vines were selected at the northern end of a 350-vine row, hereafter referred to as Site 1. They had, on average, 61.2 ± 0.04 mm trunk diameter, 29.1 ± 0.02 dormant shoots per vine, 1137 ± 3.0 g cane weight per vine (one-year-old wood) and 1434 ± 3.6 g total pruning weight per vine (one-year and two-year-old wood). Node load treatments were applied on these vines in both 2019 and 2020.

In 2020, 50 new vines were selected in the middle part of the row, hereafter referred to as Site 2. Site 2 represented a seasonal repeat of the 2019 experiment at Site 1, which excluded the carry-over effect of the previous year's pruning treatments. These vines had, on average, 62.2 ± 1.2 mm trunk diameter, 30.4 ± 0.06 dormant shoots per vine, 1118 ± 3.7 g cane weight per vine, and 1395 ± 4.3 g total pruning weight per vine.

Waipara vineyard block: Site 3. A vineyard block in Waipara was selected as Site 3 in 2020. It was established in 2006 and planted with *Vitis vinifera* cv Sauvignon blanc clone BDX317 grafted onto rootstock Schwarzmann. Vines were trained to a vertical-shoot-positioned (VSP) system with four canes carrying on average 48 count nodes for the whole vine (on average 12 nodes per cane) and two-node spurs on either side of the vine trunk. Rows were oriented north-south 2400 mm apart with an in-row vine spacing of 2000 mm. Fruiting wires were 900 and 1250 mm from the soil surface, and the canopy restrained to approximately 300 mm wide using movable foliage wires. The canopy was trimmed to a height of 2200 mm three times during the growing season from December to February. The vines were managed in accordance with sustainable winegrowing standards (New Zealand Wine, 2020) and drip-irrigated when appropriate. Yearly average temperature, GDDs and total annual rainfall were 12.4 °C, 1265.2 °C and 527.6 mm in 2020 (Harvest Electronics Ltd, 2021). Selected vines at this site were more vigorous than the Awatere valley sites. They had, on average, 57.7 ± 0.04 mm trunk diameter, 32.7 ± 0.06 dormant shoots per vine and 1369 ± 3.2 g canes weight per vine and 1740 ± 3.4 g total pruning weight per vine at the start of the experiment in winter 2020.

### 2. Experimental design and measurements

#### 2.1. Awatere Valley: Site 1 and Site 2.

In 2019 at Site 1, vines were pruned according to a 5 (cane node load) x 3 (spur node number) factorial design. The number of canes was set to one, two, three and four each of 10 nodes for N10 to N40 treatments, and four canes averaging 12.5 nodes for N50 treatments. Spur node number was set at one, two and three nodes per spur (on two spurs per vine). Each treatment was replicated five times to give a total of 75 experimental units (vines). The factorial design generated 15 total vine node load treatments (i.e., cane node load plus spur node number) ranging from 12 to 56 nodes at Site 1 and from 14 to 56 nodes at Site 2 and Site 3, as presented in Table S1. Cane and spur nodes were counted starting 10 mm from the junction of the cane/spur with the perennial wood, clearly distinguishing basal nodes from the first separate node at position one. Budburst occurred on 22 October 2019 and was determ ined when the first green tip was visible on over 50 % of vines. Fifteen days following budburst at growth stage EL 9 – two to three separate leaves (Modified Eichhorn and Lorenz grapevine growth stages (Coombe, 1995)) - the number and node position of count shoots, blind node, double shoots, basal shoots and flag shoots (or mal-formed shoots) on canes, spurs and vine head were mapped and recorded.

Blind node number was obtained by counting all count nodes that failed to burst bud. To determine where blind nodes and double shoots occurred, each cane was divided into four cane sections from its point of attachment on the vine head (cane origin) to its extremity (cane tip). Part one (the proximal section to the head – P1) contained nodes one to three, with node one being the closest to the cane origin and head of the vine; part two (the first middle section – P2) included nodes four to six; part three (the second middle section – P3) corresponded to nodes seven to nine; and finally, part four (the distal section – P4) contained nodes 10 to 13. This division was made to account for the differential growth response of these cane sections (Howell and Wolpert, 1978; Keller, 2015; Galet, 2000; Tassie and Freeman, 1992). The vine percent budburst was calculated 15 days after the start of budburst (on 5 November 2019) by dividing the total number of shoots on the vine by the vine node load (cane and spur count nodes) (Tassie and Freeman, 1992).

Vines were then shoot-thinned to their respective node treatments by removing all non-count shoots (i.e., shoots on the vine head, double shoots, and basal shoots) to channel the vine's resources exclusively on count shoots. Cane and spur percent budburst were obtained by dividing the total number of shoots on canes and spurs by their respective count nodes. The following winter, the same node treatments were applied to the same vines as the previous winter and the same measurements were repeated. Budburst occurred earlier (21 September 2020) and developmental stages at each node position on all canes and spurs of each vine were assessed using the Modified E-L system (Coombe, 1995) on 5 October 2020.

In winter 2020 at Site 2, 50 vines were selected and pruned for a 5 (cane node load) x 2 (spur node number) factorial experiment, with five replicates and with the same five node loads as at Site 1, in combination with two node numbers for spurs (two and three node spurs). The factorial design resulted in 10 total vine node load treatments (Table S1). The same measurements were collected as for Site 1.

Waipara site, Site 3. Fifty vines were selected along a south/north-oriented 550-vine row and pruned in winter 2020 with the same node treatments as Awatere Site 2. Measurements were the same as at the Awatere sites, except that budburst was also monitored on four dates at regular intervals from 24 September to 8 October 2020.

### 3. Statistical Analyses

All measured variables (count shoots, double shoots, basal shoots, blind nodes, growth stage and percent budburst) were compared using the Analysis of Variance (ANOVA) and the protected Fisher's Least Significant Difference Test (LSD). Before running ANOVA, Levene's test was conducted to check the homogeneity of variances and the Shapiro-Wilk test was applied to check data were normally distributed. The ANOVA assumptions were met for all measured variables and the interaction between cane node load and spur node numbers was not significant; consequently, only the main effects were analysed. The significance for all tests was defined at $p < 0.05$. Data was analysed in RStudio Version 4.0.5 (R Core Team, 2021). The following R packages were used: dplyr (Wickham *et al*., 2021), ggpubr (Kassambara, 2020), agricolae (Mendiburu, 2020), Rmisc (Hope, 2013) and Car (Fox and Weisberg, 2019).

## RESULTS

### 1. Effect of increasing node numbers on vine, cane and spur budburst

The vine budburst percentage significantly increased with decreasing cane node loads and total node load across all three sites (Table 1; Figure S1). At Site 1 in spring 2019, all treatments had a vine budburst well above 100 %, with N10 vines recording the highest and N50 vines the lowest percentages ($p < 0.001$) (Table 1). The following spring (2020) at Site 1, the vine budburst percentage dropped significantly across all treatments ($p < 0.001$), and the trend of vine budburst decreasing with increasing node numbers was the same as in the previous spring (2019). The general trend described for Site 1 of the vine budburst percentage decreasing with increasing node numbers was similar to that of Site 2 and Site 3 in 2020 (Table 1).

The budburst percentage on canes decreased with increasing node numbers, being significantly high on N10 vines but low on N50 (Table 2). The reduction in the vine budburst observed at Site 1 between 2019 and 2020 was also reflected in the cane budburst. Contrary to vine budburst that was always greater than 100 % regardless of the node treatments and sites, cane budburst was always below 100 % on N50 vines, and in the 2020 spring none of the treatments reached 100 % at Site 1 and Site 2 (Table 2). At Site 3, the cane budburst was statistically similar for all node treatments. The very high vine budburst measured on N10 vines was caused by the great number of non-count shoots on the vine head, and the cane budburst of around 100 % on those same N10 vines was the result of the very small number of blind nodes that appeared on canes, as will be discussed below.

**TABLE 1.** Effects of cane node load on the vine budburst percentage.

| Cane node loads | Site 1 Season 2019 | Site1 Season 2020 | Site 2 Season 2020 | Site 3 Season 2020 | *p*-value |
|---|---|---|---|---|---|
| | Vine budburst percentage (%)* | | | | |
| N10 | 262 ± 18 a\|A | 232 ± 15 a\|B | 211 ± 23 a | 310 ± 19 a | < 0.05 |
| N20 | 182 ± 8.2 b\|A | 155 ± 6.2 b\|B | 141 ± 7.2 b | 152 ± 15 b | < 0.01 |
| N30 | 141 ± 5.0 c\|A | 123 ± 5.7 c\|B | 118 ± 4.3 bc | 120 ± 9.0 bc | < 0.01 |
| N40 | 124 ± 4.7 cd\|A | 110 ± 2.7 c\|B | 101 ± 2.5 c | 120 ± 4.2 bc | < 0.01 |
| N50 | 114 ± 4.2 d\|A | 105 ± 2.5 c\|A | 104 ± 1.6 c | 104 ± 5.3 c | ns |
| *p*-value | < 0.001 | < 0.001 | < 0.001 | < 0.001 | |

N10, N20, N30, N40, and N50 refer to total node number on vine canes (N) equal to 10, 20, 30, 40 and 50 nodes respectively. Values are mean ± standard error of the Mean of 15 vines at Site 1 and 10 vines at Site 2 and 3. Means sharing the same lowercase letter in a column (cane node load comparison) or the same uppercase letter in a row (2019 and 2020 seasons comparison at Site 1) are not significantly different (Fisher's protected LSD test, $p \leq 0.05$).

* The vine budburst percentage was calculated by dividing the total number of buds that burst on all vine parts (cane, spur, head and trunk) by the total number of count nodes on canes and spurs.

**TABLE 2.** Effects of cane node load and spur node number on cane and spur percentage budburst.

| Cane node loads | Site 1 Season 2019 | Site 1 Season 2020 | Site 2 Season 2020 | Site 3 Season 2020 | *p*-value |
|---|---|---|---|---|---|
| | | Cane budburst percentage (%) * | | | |
| N10 | 119 ± 1.0 a\|A | 96 ± 1.8 a\|B | 90 ± 2.7 a | 107 ± 5.1 a | < 0.05 |
| N20 | 106 ± 4.0 ab\|A | 94 ± 2.1 ab\|B | 87 ± 3 ab | 108 ± 3.3 a | < 0.01 |
| N30 | 98 ± 4.0 bc\|A | 90 ± 2.2 bc\|B | 86 ± 0.8 ab | 106 ± 2.2 a | < 0.01 |
| N40 | 95 ± 3.0 bc\|A | 87 ± 1.7 c\|B | 86 ± 0.8 ab | 105 ± 1.7 a | < 0.01 |
| N50 | 90 ± 2.0 c\|A | 86 ± 1.5 c\|A | 81 ± 1.8 b | 98.6 ± 2.2 a | ns |
| *p*-value | < 0.01 | < 0.001 | < 0.05 | ns | |
| Spur node number | | Spur budburst percentage ( %) # | | | |
| S1 | 224 ± 12 a\|A | 200 ± 14 a\|B | - | - | < 0.01 |
| S2 | 130 ± 10 b\|A | 113 ± 3.5 b\|B | 109 ± 3.6 a | 128 ± 6.5 a | < 0.01 |
| S3 | 108 ± 6 b\|A | 102 ± 2.7 b\|B | 105 ± 2.5 a | 87.9 ± 6.6 b | < 0.05 |
| *p*-value | < 0.001 | < 0.001 | ns | < 0.001 | |

N10, N20, N30, N40, and N50 refer to total node number on vine canes (N) equal to 10, 20, 30, 40 and 50 nodes respectively and S1 = spurs with one node, S2 = spurs with 2 nodes, S3= spurs with 3 nodes. For cane node load treatments, values are mean ± standard error of the Mean of 15 vines at Site 1 and 10 vines at Site 2 and 3. For Spur node number treatments, values are mean ± standard error of the Mean of 25 vines at all three sites. Means sharing the same lowercase letter in a column (cane node loads or spur node load comparison) or the same uppercase letter in a row (2019 and 2020 seasons comparison at Site 1) are not significantly different (Fisher's protected LSD test, $p \leq 0.05$).

* The cane budburst percentage was calculated by dividing the total number of buds that burst on the canes by their count nodes. # The spur budburst percentage was calculated by dividing the total number of buds that burst on spurs by their count nodes.

**TABLE 3.** Percentage budburst on canes and spurs measured at Site 3 on four dates at regular intervals.

| Cane node loads | 24 Sept. 2020 | 28 Sept. 2020 | 2 Oct. 2020 | 8 Oct. 2020 |
|---|---|---|---|---|
| | | Cane budburst percentage (%)* | | |
| N10 | 5.0 ± 3.4 a | 33.3 ± 5.7 a | 78.8 ± 4.7 a | 107 ± 5.1 a |
| N20 | 2.5 ± 2.5 a | 37.1 ± 4.1 a | 74.2 ± 5.4 a | 108 ± 3.3 a |
| N30 | 6.0 ± 2.2 a | 38.4 ± 3.8 a | 79.8 ± 3.7 a | 106 ± 2.2 a |
| N40 | 3.2 ± 1.7 a | 38.6 ± 4.0 a | 75.0 ± 2.1 a | 105 ± 1.7 a |
| N50 | 2.2 ± 0.8 a | 32.1 ± 4.1 a | 69.7 ± 3.9 a | 98.6 ± 2.2 a |
| *p*-value | ns | ns | ns | ns |
| Spur node numbers | | Spur budburst percentage ( %) # | | |
| S2 | 10 ± 3.5 a | 44 ± 6.1 a | 89 ± 2.9 a | 128 ± 6.5 a |
| S3 | 8.6 ± 3.3 a | 48 ± 5.2 a | 78 ± 3.4 b | 87.9 ± 6.6 b |
| *p*-value | ns | ns | < 0.05 | < 0.001 |

N10, N20, N30, N40, and N50 refer to total node number on vine canes equals 10, 20, 30, 40 and 50 nodes respectively and S2 = spurs with 2 nodes, S3= spurs with 3 nodes. For cane node load treatments, values are mean ± standard error of the Mean of 15 vines at Site 1 and 10 vines at Site 2 and 3. For Spur node number treatments, values are mean ± standard error of the Mean of 25 vines at all three sites. Means sharing the same letter in a column are not significantly different (Fisher's protected LSD test, $p \leq 0.05$).

* The cane budburst percentage was calculated by dividing the total number of buds that burst on the canes by their count nodes. # The spur budburst percentage was calculated by dividing the total number of buds that burst on spurs by their count nodes.

The budburst on spurs also increased with decreasing spur node numbers and always exceeded 100 %, except at Site 3 for three-node spurs (Table 2). At Site 1 for instance, one-node spurs had the highest percentage (224 ± 12 %) and three-node spurs the lowest (108 ± 6 %) ($p < 0.001$; Table 2). As with the vine budburst, the budburst on spurs dropped significantly in 2020 across all three spur treatments ($p < 0.01$). The very high budburst observed on one-node spurs was caused by non-count shoots on spur basal nodes. At Site 3, all node treatments were not significantly different in their cane budburst percentage for all four dates ($p > 0.05$) (Table 3). However, two-node spurs had a greater budburst percentage than three-node spurs on date 3 (2 Oct.) and date 4 (8 Oct.) ($p < 0.001$; Table 3).

**TABLE 4.** Cane node load and site effect on blind nodes, double shoots and shoots on the vine head.

| Cane node loads | Site 1 Season 2019 | Site 1 Season 2020 | Site 2 Season 2020 | Site 3 Season 2020 | *p*-value |
|---|---|---|---|---|---|
| | | Average number of cane blind nodes per vine | | | |
| N10 | 1.0 ± 0.2 d\|A | 1.1 ± 0.2 d\|A | 0.9 ± 0.2 d | 1.0 ± 0.2 c | ns |
| N20 | 2.0 ± 0.3 cd\|A | 1.8 ± 0.3 d\|A | 2.4 ± 0.6 c | 2.0 ± 0.4 c | ns |
| N30 | 2.6 ± 0.3 bc\|B | 3.6 ± 0.5 c\|A | 4.2 ± 0.2 b | 2.3 ± 0.5 c | < 0.05 |
| N40 | 3.4 ± 0.4 b\|B | 5.5 ± 0.5 b\|A | 7.2 ± 0.7 a | 4.5 ± 0.5 b | < 0.01 |
| N50 | 6.6 ± 0.6 a\|B | 7.6 ± 0.3 a\|A | 7.6 ± 0.3 a | 6.3 ± 0.6 a | < 0.05 |
| *p*-value | < 0.001 | < 0.001 | < 0.001 | < 0.001 | |
| | | Average number of cane double shoots per vine | | | |
| N10 | 0.6 ± 0.3 b\|A | 0.7 ± 0.2 a\|A | 0.0 ± 0.0 b | 0.8 ± 0.5 b | ns |
| N20 | 1.1 ± 0.4 ab\|A | 0.7 ± 0.3 a\|A | 0.0 ± 0.0 b | 1.7 ± 0.7 ab | ns |
| N30 | 1.4 ± 0.3 a\|AB | 0.7 ± 0.3 a\|BC | 0.4 ± 0.1 b | 2.1 ± 0.5 ab | < 0.05 |
| N40 | 1.7 ± 0.6 a\|AB | 0.7 ± 0.2 a\|B | 0.5 ± 0.2 b | 2.5 ± 0.6 ab | < 0.05 |
| N50 | 1.7 ± 0.5 a\|A | 0.9 ± 0.2 a\|A | 1.1 ± 0.3 a | 2.6 ± 0.7 ab | ns |
| *p*-value | < 0.05 | ns | < 0.01 | < 0.05 | |
| | | Average number of shoots per vine head | | | |
| N10 | 13.5 ± 1.7 a\|B | 17.8 ± 1.8 a\|B | 16.8 ± 3.2 a | 29.5 ± 3.0 a | ns |
| N20 | 13.8 ± 1.5 ab\|A | 14.1 ± 1.7 a\|A | 12.5 ± 1.8 ab | 11.3 ± 3.5 b | ns |
| N30 | 10.6 ± 1.1 abc\|A | 10.0 ± 1.2 b\|A | 10.5 ± 1.4 b | 6.1 ± 3.1 bc | ns |
| N40 | 9.3 ± 1.6 bc\|A | 8.8 ± 0.7 b\|A | 7.3 ± 1.1 b | 6.8 ± 1.8 bc | ns |
| N50 | 9.1 ± 1.2 b\|B | 8.1 ± 0.8 b\|B | 9.4 ± 0.9 b | 2.8 ± 1.9 c | ns |
| *p*-value | < 0.05 | < 0.001 | < 0.01 | < 0.001 | |

N10, N20, N30, N40, and N50 refer to total node number on vine canes (N) equal to 10, 20, 30, 40 and 50 nodes respectively. Values are mean ± Standard Error of the Mean of 15 vines at Site 1 and 10 vines at Site 2 and 3. Means sharing the same lower case letter in a column (cane node loads comparison) or the same upper case letter in a row (seasons and sites comparison) are not significantly different (Fisher's protected LSD test, $p \leq 0.05$).

When the total vine node load was considered, the trends observed on the vine budburst and cane budburst percentage were confirmed, with V12 to V16 vines having the highest percentages and V52 to V56 the lowest (Figure S1 and S2).

## 2. Number and distribution of blind nodes, double shoots and head shoots

The average number of blind nodes at all three sites increased with increasing cane node loads ($p < 0.001$; Table 4; Figure S3 and Figure S4). In 2019 at Site 1 for instance, the number of blind nodes rose from 1.0 ± 0.2 on N10 vines to 6.6 ± 0.6 on N50 vines ($p < 0.001$), and this rising trend was maintained the following season across all three sites. Interestingly, despite having the highest number of blind nodes, N50 vines also achieved a vine budburst greater than 100 % (Table 1), because these vines also produced a reasonable number of non-count shoots on the vine head (Table 4). These head shoots, together with some double shoots on canes, compensated for the blind nodes, resulting in a high vine budburst percentage. For cane budburst, however, non-count shoots (mainly from double shoots) were not able to compensate for the blind nodes, and as a result the cane budburst was always below 100 % on N50 vines (Table 2 and Table 4).

At Site 1, between the 2019 and 2020 seasons, the average number of blind nodes per vine rose significantly for N30, N40 and N50 vines (from 2.6 ± 0.3, 3.4 ± 0.4 and 6.6 ± 0.6 up to 3.6 ± 0.5, 5.5 ± 0.5 and 7.6 ± 0.3 respectively). This increase in the number of blind nodes explains why the vine budburst and cane budburst decreased for these vines, given that their average number of head shoots and double shoots remained fairly stable over the same period (Table 4). Blind nodes were present on all four cane parts but with greater numbers at proximal parts and the least at distal parts regardless of sites, seasons and node loads (Figure 1). The middle sections had similar, intermediate numbers of blind nodes.

In spring 2019 at Site 1, double shoots were more frequent on high-node vines (N40 and N50; 1.7 ± 0.5 and 1.7 ± 0.6 double shoots respectively) than on low-node vines (N10; 0.6 ± 0.3 double shoots, $p < 0.05$) (Table 4; Figure S5 and S6). In contrast, the average number of shoots on the vine head was the highest on low-node vines (N10 and N20; 13.5 ± 1.7 and 13.8 ± 1.5 respectively) and the lowest on high-node vines (N50, 9.1 ± 1.2) (Table 4; Figures S7 and S8). This high number of head shoots also explains the higher budburst percentage of low-node vines, despite them having fewer double shoots.

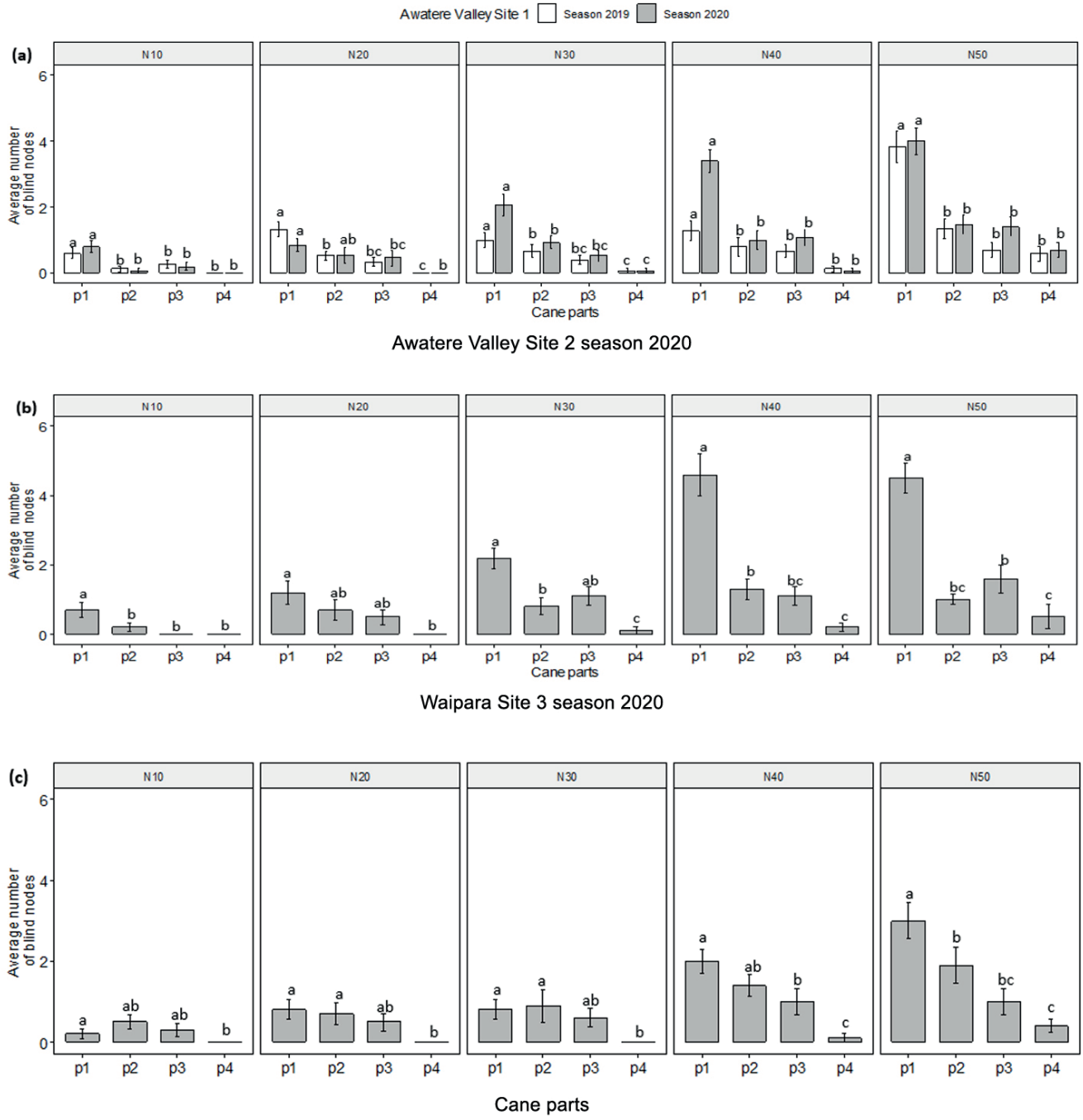



**FIGURE 1.** Blind nodes distribution along canes at Site 1 in the 2019 and 2020 season (a), Site 2 in the 2020 season (b), and Site 3 in the 2020 season (c).

N10, N20, N30, N40, and N50 refer to total node number on vine canes (N) equal to 10, 20, 30, 40 and 50 nodes respectively and p1, p2, p3 and p4 to the cane's Proximal, First middle, Second middle and Distal parts relative to the head of the vine. Points and bars represent mean ± standard error of the mean of 15 vines for Site 1 and 10 vines for Site 2 and Site 3. Means sharing the same letter across cane sections over one season are not significantly different (Fisher's protected LSD test, $p \leq 0.05$).

In the spring of 2020, all vines had statistically the same number of double shoots ($p > 0.05$). However, the pattern of shoots on the vine head remained the same, with low-node vines growing more shoots on the head than high-node vines ($p < 0.001$). At Site 2, the number of double shoots was also higher on 50-node vines compared with the other node load treatments ($p < 0.01$; Table 4). At Site 3, apart from 10-node vines which grew the lowest number of double shoots (0.8 ± 0.5), all the other node load treatments had a statistically similar number of double shoots (Table 4). However, the trend noted at Site 1 in 2019 and Site 2 in 2020 was the same at Site 3, with 50-node vines having more double shoots than 10-node vines. Unlike blind nodes that followed a distinct distribution along canes, there was no clear pattern in the distribution of double shoots along canes, as they tended to occur at all positions along the canes (Figure S9).

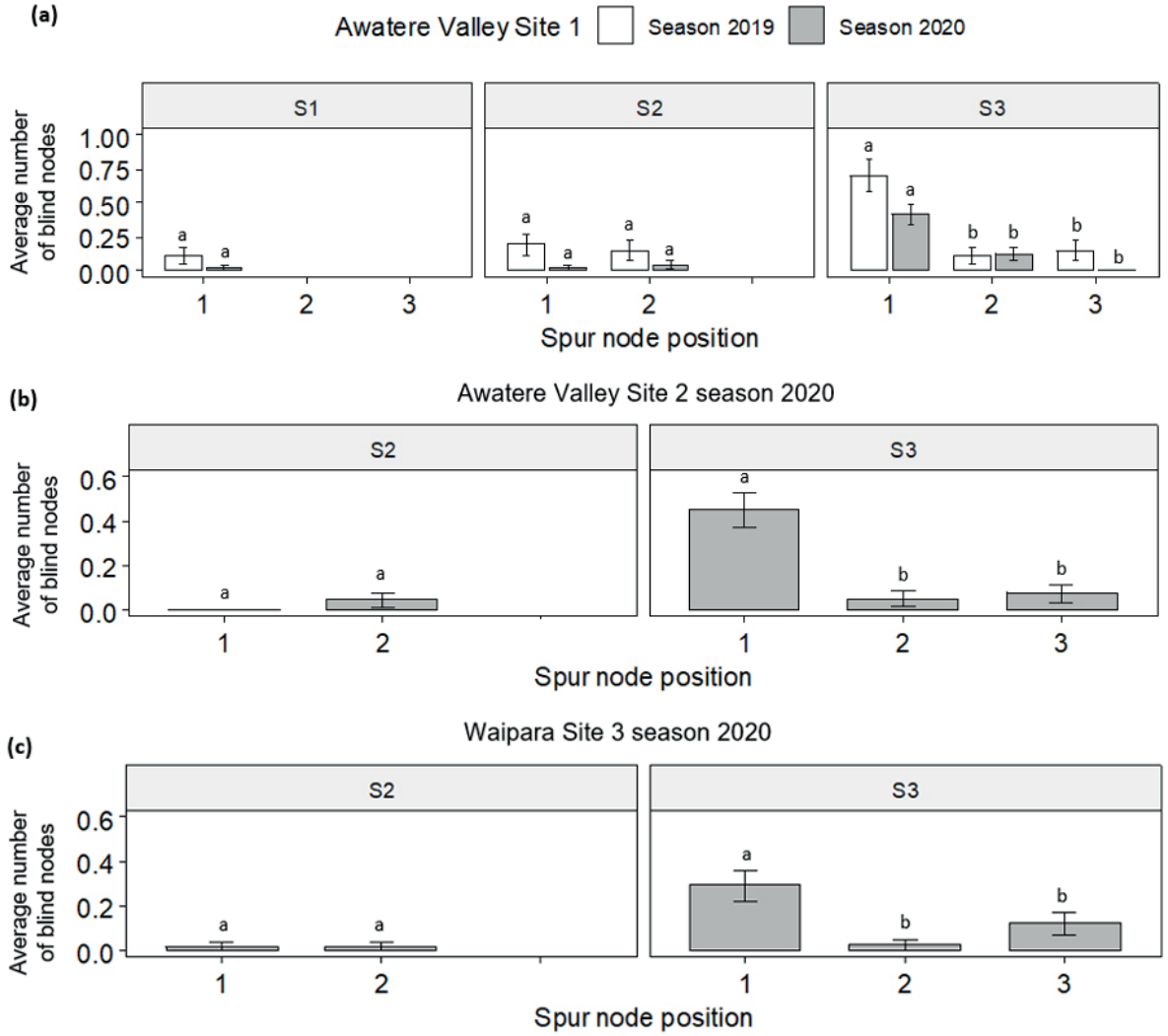



**FIGURE 2.** Effects of spur node number on the number of spur blind nodes and their distribution along spur at Site 1 (a), Site 2 (b), and Site 3 (c) over two growing seasons 2019 and 2020.

S1 = spurs with one node, S2 = spurs with 2 nodes, S3 = spurs with 3 nodes and 1, 2 and 3 to spur node positions from proximal to distal. Points and bars represent mean ± Standard error of the mean with n = 25 vines per treatment for Site 1 and n = 10 vines per spur node treatment for Site 2 and 3. Means sharing the same letter across node positions over one season are not significantly different (Fisher's protected LSD test, $p \leq 0.05$).

**TABLE 5.** Effects of Spur node number on spur blind nodes and spur basal shoots.

| Spur node numbers | Site 1 Season 2019 | Site 1 Season 2020 | Site 2 Season 2020 | Site 3 Season 2020 |
|---|---|---|---|---|
| | Average number of spur blind nodes | | | |
| S1 | 0.12 ± 0.001 b | 0.25 ± 0.001 b | - | - |
| S2 | 0.35 ± 0.001 b | 0.85 ± 0.001 a | 0.10 ± 0.001 b | 0.12 ± 0.001 b |
| S3 | 1.0 ± 0.1 a | 0.88 ± 0.1 a | 0.84 ± 0.1 a | 1.04 ± 0.2 a |
| *p*-value | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| | Average number of spur basal shoots | | | |
| S1 | 2.2 ± 0.1 a | 1.8 ± 0.2 a | - | - |
| S2 | 1.2 ± 0.3 b | 0.5 ± 0.1 b | 0.4 ± 0.1 a | 1.1 ± 0.2 a |
| S3 | 0.5 ± 0.1 c | 0.1 ± 0.001 c | 0.2 ± 0.1 a | 0.2 ± 0.1 b |
| *p*-value | < 0.001 | < 0.001 | ns | < 0.001 |

S1 = spurs with one node, S2 = spurs with 2 nodes, S3 = spurs with 3 nodes. Values represent mean ± Standard error of the Mean of 25 vines at all three sites. Means sharing the same letter in a column are not significantly different (Fisher's protected LSD test, $p \leq 0.05$).

At all three sites, there were greater numbers of blind nodes on three-node spurs than on two- and one-node spurs (Figure 2; Table 5). At Site 1 in both 2019 and 2020, one- and two-node spurs had similar but fewer blind nodes than three-node spurs ($p < 0.001$) and at Sites 2 and 3, three-node spurs had more blind node than two-node spurs ($p < 0.001$). As with Site 1, at Sites 2 and 3, three-node spurs also had more blind nodes than two-node spurs ($p < 0.001$; Table 5). These blind nodes explain why the budburst of three-node spurs was generally lower compared with one-node spurs (Table 2). However, the basal shoots compensated for these blind nodes so that the budburst was generally around 100 % (Table 2 and Table 5). At Site 3, the budburst on three-node spurs was always below 100 %, because there were not only more blind nodes but also fewer basal shoots to offset them.

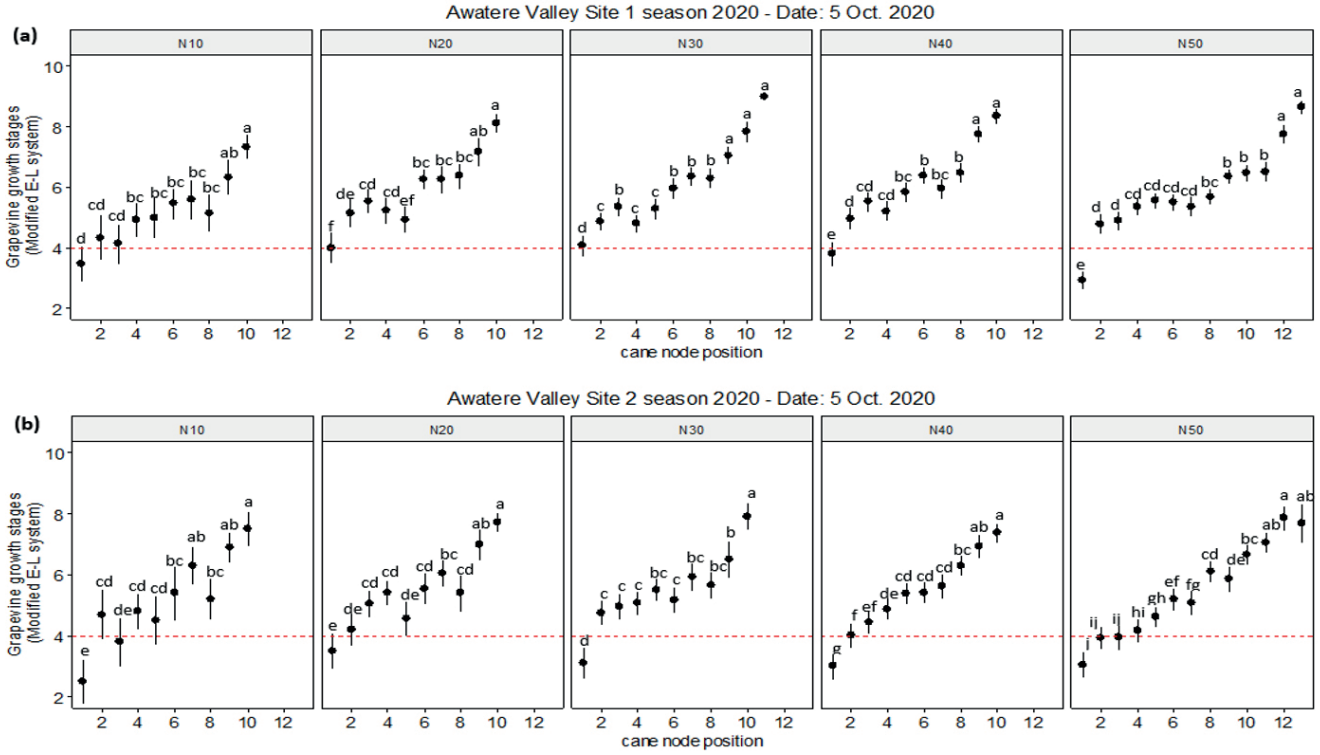



**FIGURE 3.** Leaf appearance along canes on 5 October 2020 at Site 1 (a) and Site 2 (b).

N10, N20, N30, N40, and N50 refer to the total node load on vine's canes being equal to 10, 20, 30, 40 and 50 nodes respectively. Points represent mean ± standard error of the mean with n = 15 vines at Site 1 and n = 10 vines at Site 2. Means sharing the same letter are not significantly different (Fisher's protected LSD test, $p \leq 0.05$).

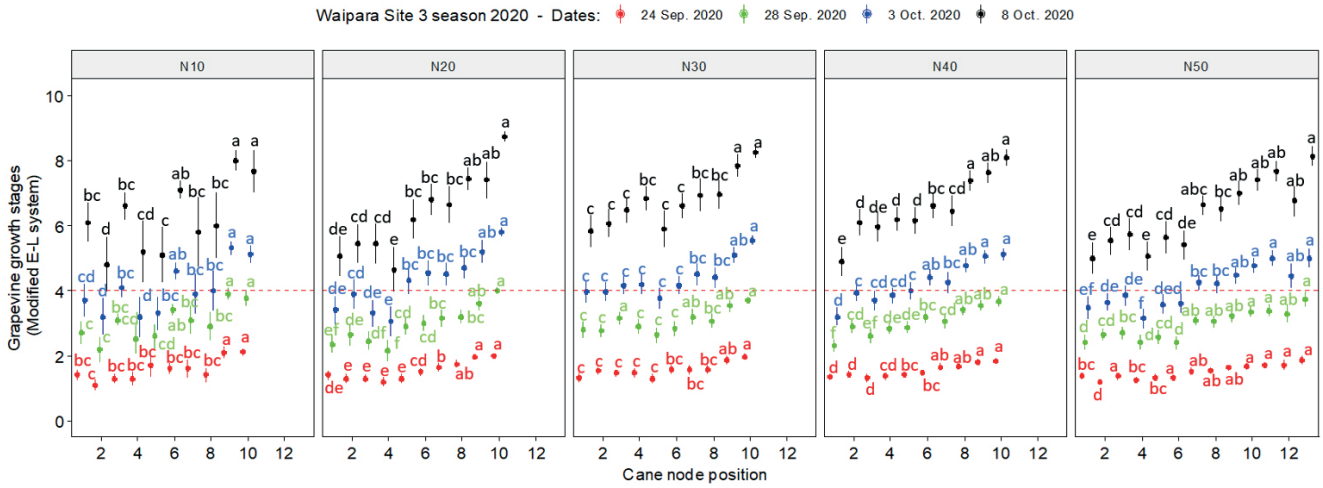



**FIGURE 4.** Leaf appearance along canes on four dates: 24 and 28 September and 3 and 8 October 2020 at Site 3.

N10, N20, N30, N40, and N50 refer to the total node load on vine canes being equal to 10, 20, 30, 40 and 50 nodes respectively. Points represent mean ± standard error of the mean with n = 10 vines for each cane node treatment. For a given date means sharing the same letter are not significantly different (Fisher's protected LSD test, $p \leq 0.05$).

### 3. Shoot developmental stages of canes and spurs

The average leaf appearance on shoots on 5 October 2020 at Site 1 was statistically similar on all vine node loads, except on 10-node vines, which were one EL unit behind compared to the other vines ($p < 0.01$; Table S2). At Site 2 and Site 3, there were no differences among all five cane node loads (Table S2). At Site 3, where leaf appearance was monitored from 24 September to 8 October 2020, there were no differences in the number of leaves per shoot among node loads over that period (Figure S10a).

The average leaf appearance on spurs at Site 1 was significantly more advanced on one-node and two-node spurs compared with three-node spurs ($p < 0.01$), but at Site 2, there was no significant difference between two-node and three-node spurs (Table S2). Similarly, at Site 3, there was no significant difference between two-node and three-node spurs from 24 to 28 September 2020 (Figure S2 b). However, from 3 October 2020 (Site 3), two-node spurs were growing faster than three-node spurs and by 8 October they were respectively at EL 7 and EL 6. (Figure S10 b; Table S2).

At Site 1 and Site 2, and regardless of cane node loads, shoots at the distal cane section (last nodes of the cane or terminal nodes) were at a more advanced leaf appearance stage than shoots at the proximal and middle cane sections ($p < 0.01$; Figure 3 a, b). Even at Site 3, the difference in leaf appearance stage between proximal and distal shoots was significant from 24 September to 8 October 2020 ($p < 0.01$; Figure 4).

As with the canes, the number of leaves at Site 1 and Site 2 was significantly higher on spur terminal shoots (node position 2 for two-node spurs and node position 3 for three-node spurs) than on proximal shoots (spur node position 1) (Figure 5 a, b). At Site 3, from 24 September 2020 to 8 October 2020, terminal shoots were significantly more advanced in the EL stages than proximal shoots for both spur node numbers ($p < 0.01$) (Figure 5 c).

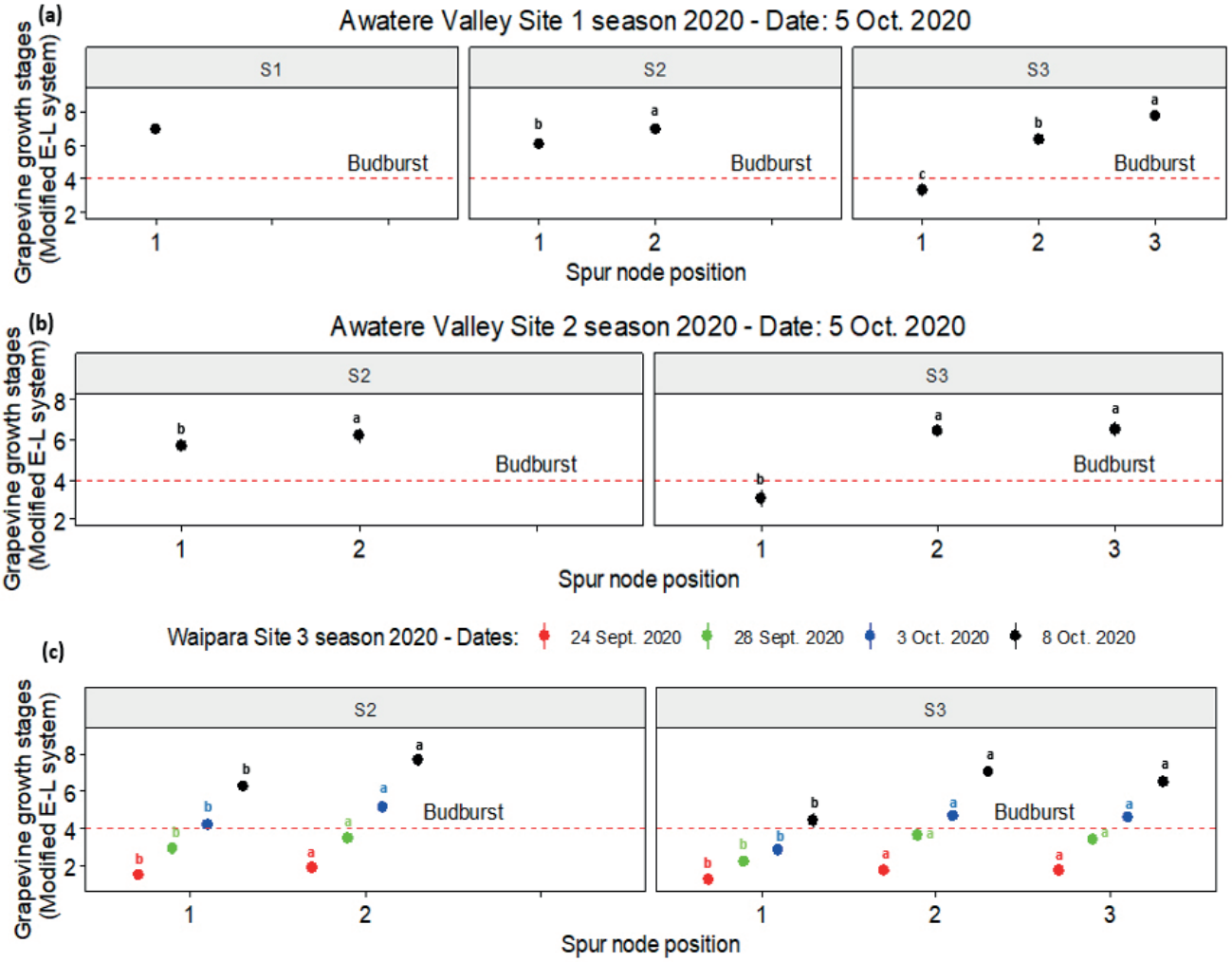



**FIGURE 5.** Leaf appearance along spurs on 5 October 2020 at Site 1 (a) and Site 2 (b), and on four dates: 24 and 28 September and 3 and 8 October 2020 at Site 3 (c).

S1 = spurs with one node, S2 = spurs with 2 nodes, S3 = spurs with 3 nodes and 1, 2 and 3 mean spur node positions from proximal to distal. Points and bars represent mean ± standard error of the mean with n = 25 vines per treatment for Site 1 and n = 10 vines per spur node treatment for Site 2 and 3. For a given date means sharing the same letter are not significantly different (Fisher's protected LSD test, $p \leq 0.05$).

# DISCUSSION

## 1. Budburst percentage and vine capacity

A vine budburst percentage at or around 100 % is often an indication that a vine has been pruned to its capacity, with higher values suggesting that the vine had potential to support more growth, and lower values the opposite scenario (i.e., potential to support less growth) (Huglin and Schneider, 1998; Tassie and Freeman, 1992; Winkler *et al*., 1974). Although all vines had a vine budburst greater than 100 %, the very high budburst percentage of 10-node vines (> 200 %) was a clear indication that they were pruned to well below their capacity, and thus could carry more count nodes and count shoots (Table 1). Fifty-node vines also had a vine budburst percentage greater than 100 %, yet these vines showed additional signs of having been pruned above their capacity, such as more blind nodes and a low cane budburst percentage (Table 4). Interestingly, the cane budburst of high-node vines was well below 100 %, indicating that some retained nodes failed to break dormancy, whereas on low-node vines the cane percent budburst was around 100 %, indicating fewer to no blind node (Table 2 and Table 4). An in-depth analysis of published data confirms this conclusion. For instance, Kurtural *et al*. (2006) have published data showing that the vine budburst percentage on 20-, 30- and 45-node vines was always above 100 %, whereas their cane budburst percentage was 115 %, 93 % and 84 % respectively, pointing to the fact that cane budburst better reflects the number of count nodes that burst bud than vine budburst percentage. Since non-count shoots, which usually appear on the vine head and on spur basal nodes, can easily offset the number of blind nodes, measuring solely vine budburst percentage may provide an incomplete picture of the vine capacity and balance at the beginning of the growing season. Thus, a composite metric that includes vine budburst percentage and blind node count could be recommended to give a better picture of the vine capacity and balance at budburst.

Previous literature reports that the higher budburst percentage observed on severely pruned vines is caused by double shoots and latent buds bursting, producing water shoots and suckers (Coombe and Dry, 2001; Galet, 2000; Huglin and Schneider, 1998; Keller, 2015; Winkler *et al*., 1974). The relative contribution of these different shoots (double shoots, head shoots, trunk shoots, cane basal shoots and spur basal shoots) to the high budburst percentage of severely pruned vines was previously unknown. This study has characterised this positional growth with low-node vines, regardless of sites and seasons, as having more shoots on the vine head than on any other parts (Table 4). Although some double shoots (on average less than one per vine) and some basal shoots (no more than two per vine) developed, the main contributor to the high percent budburst on low-node vines was shoots on the vine head. The head of mature vines contains many latent buds, mainly originating from basal nodes of dormant shoots pruned in previous winters. Latent buds may break dormancy whenever the vine's carbohydrate reserves enable it to support more growth than retained nodes (Bennett *et al*., 2005; Coombe and Dry, 2001; Keller, 2015; Winkler *et al*., 1974). However, latent buds located on the head of low-node vines appeared to burst bud more readily than the secondary, tertiary buds of the compound bud inside count nodes, and the latent buds located elsewhere on the vine (trunk, canes and spurs basal buds). These results negate previously reported suggestions of grapevines responding to severe pruning by producing more double shoots (Keller, 2015; Tassie and Freeman, 1992).

The dormancy of the secondary and tertiary bud of the compound bud is controlled not by vine vigour (higher carbohydrate reserves induced by low node numbers or severe pruning) but rather by chilling duration and phytohormones, such as Abscisic Acid (Düring and Bachmann, 1975; Field *et al*., 2021; Vergara *et al*., 2017). When the chilling duration of Sauvignon blanc was increased (by up to 414 days in controlled growth chambers), all three buds of the compound bud broke dormancy while the concentration of Abscisic Acid declined, resulting in double and triple shoots (Field *et al*., 2021). It was not possible to ascribe with certainty the presence of the few double shoots observed in this study to chilling temperature duration or Abscisic acid concentrations, as these variables were not measured. However, since the number of double shoots tended to be slightly higher on high node vines, this could suggest that high concentrations of carbohydrate reserves (induced by low node number) and the development of double shoots might not be highly interrelated.

## 2. Blind nodes and correlative inhibition

Blind nodes were conspicuous on high node vines and were mainly located at the cane proximal part to the vine head (Table 4, Figure 1). A blind node contains one or more buds that failed to burst, either because they developed inside the canopy under shaded conditions or because the vine lacked sufficient carbohydrates to stimulate growth (Bennett *et al*., 2005; Jackson, 1997; Perez and Kliewer, 1990). Some authors have observed that blind nodes are mainly located in the middle section of the cane of dormant grapevines in winter (Benismail *et al*., 2007; Greven *et al*., 2014; Tomasi *et al*., 2007). In the present study, blind nodes appeared in the mid-cane section, but not as many as in the proximal section. This may have been caused by shoots in the mid-cane section failing to develop properly, resulting in small shoots which ultimately die forming blind nodes. Such blind nodes usually form later in the season. Although some malformed shoots developed (flag shoots) on some nodes, these were not considered to be blind nodes as long as the malformed shoots were still alive and actively growing. Therefore, blind nodes appearing earlier in the growing season as a result of high node loading follow a different distribution pattern to blind nodes forming later in the season, which result from premature growth termination.

The formation of blind nodes at the proximal part to the head of fruiting canes of high-node vines can be caused by correlative inhibition. Correlative inhibition and apical dominance are two intimately connected phenomena.

Correlative inhibition is expressed in spring when distal nodes break dormancy first and grow more vigorous shoots than middle and proximal nodes (Galet, 2000; Keller, 2015; Tassie and Freeman, 1992), whereas apical dominance takes place the preceding summer during active shoot growth (Faust *et al*., 1997; Domagalska and Leyser, 2011; Thimann *et al*., 1934). Correlative inhibition is initiated when the shoot apex exerts apical dominance over subtending axillary buds through the production of auxin (indole-3-acetic acid), which is transported down the stem keeping them dormant (Faust *et al*., 1997; Domagalska and Leyser, 2011; Thimann *et al*., 1934). This dominance follows a gradient – usually stronger on lower buds and weaker on upper buds (near the shoot apex or terminal buds) – which is carried over into winter, manifesting itself at budburst with terminal buds (located in the distal section of the head of the fruiting cane) and requiring less chilling to break dormancy (Saure, 1985). Although it is accepted that both apical dominance and correlative inhibition are controlled mainly by growth substances (auxins), Champagnat (1989) argued that competition for nutrients also plays a part. With terminal buds breaking dormancy earlier they start acting as strong sinks for water, nutrients, and growth regulators (Guern and Usciati, 1976; Mcloughlin *et al*., 2011), at the expense of proximal buds, preventing them from bursting bud or developing properly.

The effect of node loading in the expression of correlative inhibition on New Zealand Sauvignon blanc grapevines had not been considered before. The most recently published research on Sauvignon blanc response to increasing node loads focused on long-term response at the scale of the whole vine; it reported the presence of blind nodes in the middle section of canes, but did not address the within-vine changes in growth along canes, spurs and the vine head (Greven *et al*., 2014; Greven *et al*., 2015). Our results showed that increasing node load can exacerbate the effects of correlative inhibition from the first season of node treatment, resulting in an increased number of blind nodes in the proximal portion of the fruiting cane. In spring, carbohydrates tend to be transported in priority towards stronger sinks, such as the more actively growing distal shoots, to the detriment of weaker sinks (i.e., the proximal buds), thus preventing them from bursting bud (Collins *et al*., 2006; Vaillant-Gaveau *et al*., 2011; Zapata *et al.*, 2004). Reducing the node load (10- to 20-node vines), on the other hand, mitigated the effect of correlative inhibition by allowing nearly all buds to burst, as there was relatively less competition for nutrients. However, this reduced competition did not eliminate the irregularity of shoot growth along the cane (Figure 3), which increased in magnitude as the season progressed (Figure 4). Correlative inhibition was also present on three-node spurs with more blind nodes appearing at the first node position (Figure 2). This agrees with the findings of Mcloughlin *et al*. (2011): on mechanically pruned Cabernet sauvignon, the first node of three-node spurs remained dormant, whereas one-node and two-node spurs burst buds at all node positions.

Between 2019 and 2020 (Site 1), the number of blind nodes rose significantly on high node vines possibly due to the conjunction of correlative inhibition and bud necrosis. Bud necrosis is a physiological disorder characterised by the abortion and death of buds developing inside a compound bud within each node (Lavee *et al*., 1981; Wolf and Warren, 1995). Various stresses, such as canopy shading, excessive shoot vigour, high gibberellin levels and low carbohydrates, have been associated with bud necrosis (Dry and Coombe, 1994; May, 1961; Perez and Kliewer, 1990; Vasudevan *et al*., 1998; Ziv *et al*., 1981). Although carbohydrate reserves and bud viability assessment were not conducted, it could be hypothesised that source restriction (low overwintering carbohydrate reserves and leaf area) contributed to the increased number of blind nodes at Site 1 in the second spring. Since carbohydrates (stored and from leaf photosynthesis) tend to be transported to stronger sinks (such as the actively developing shoot apex, grape bunches and roots) to the detriment of weaker sinks, such as developing shoot primordia (Bennett *et al*., 2005; Collins *et al*., 2006; Vaillant-Gaveau *et al*., 2011; Zapata *et al.*, 2004), it is possible that primordial shoot formation was impaired, resulting in bud abortion the following spring with more blind nodes at budburst.

The location of blind nodes at the proximal section to the head of fruiting canes could have serious consequences for the management of cane-pruned vines. At winter pruning, the dormant shoots that form fruiting canes and renewal spurs are selected from the shoots located near or on the vine head (Epee *et al*., 2022). In a four-cane pruning system, the appearance of blind nodes in the cane's proximal section may drastically limit the options available when choosing which fruiting canes to lay, as well as renewal spurs. This situation can be further compounded, if very few shoots of adequate vigour are present on the head, as was the case on high-node vines in the present study (Table 4). This may lead to suboptimal selections of retained dormant shoots. When they occur on the first node of spurs, blind nodes may contribute over time to an outward growth of the head. Therefore, setting the right node number on canes and spurs not only ensures optimal budburst and shoot growth but also contributes to a better dormant shoot selection at pruning, and controls vine shape and size.

Increasing cane node load had little or no effect on the start of budburst and its progression over the first two weeks following budburst (Figure S10 a; Table 3). This result confirms similar observations reported on young vines by Greven *et al*. (2015). Despite a potentially higher source/sink ratio, low-node vines broke dormancy and went through their early developmental stages as fast as high-node vines; this suggests that the timing of budburst and leaf appearance rates in the first two weeks post-budburst are independent of source (stored carbohydrate reserves in permanent vine's parts) and sink size (number of buds retained). Instead, the timing of budburst is dependent on a conjunction of other factors, such as soil temperature, moisture, rootstock and bud temperature (Currle *et al*., 1983; Eltom *et al*., 2017; Keller and Tarara, 2010; Moncur *et al*., 1989; Oliveira, 1998).

When comparing individual nodes on canes and spurs, there were strong differences in leaf appearance stages among node positions, with distal buds bursting earlier and developing faster than buds in proximal node positions (Figure 3 and Figure 5). As already discussed, this was caused by correlative inhibition. The consequences of correlative inhibition are non-uniform budburst and shoot growth along the cane. The variability observed in shoot growth became more pronounced over time regardless of node loading. Thus, even appropriate node loading cannot offset the negative effects of correlative inhibition on cane-pruned vines. Therefore, existing methods, such as cane cracking, bending/arching or the application of hydrogen cyanimide could be used to control correlative inhibition (Huglin and Schneider, 1998; Iland *et al*., 2011; Jackson, 2014).

## CONCLUSION

The response mechanism of mature Sauvignon blanc grapevines to increasing node loads in the first two weeks following winter rest is complex. Vines responded to lower node loading by developing a large number of non-count shoots on the head, resulting in the vine budburst percentage reaching 1.5 to three times the optimal threshold of 100 %. Higher node loading inhibited shoot development, resulting in more blind nodes on canes, particularly at proximal positions of the head, and fewer shoots, if any, on the vine head. There were no changes to double shoots in response to the higher node loads. The imbalance caused by lower node loads was well captured by the vine budburst percentage. On the other hand, the imbalance resulting from higher node loads was poorly captured by the vine budburst percentage alone, because non-count shoots may have masked the presence of blind nodes. Cane percent budburst, together with blind node and non-count shoot measurements, provided a more accurate assessment of vine response to node loading and balance status. Vines responded to high node loads by producing more blind nodes, which were mostly located at the proximal section of the cane. The presence of double shoots was not in itself a sign of vine imbalance. Three-node spurs developed more blind nodes than one-node and two-node spurs. Cane node loads had no significant effect on the start of budburst and its progression during the first two weeks following budburst at vine scale. However, budburst along the canes and spurs started at the most distal node. This research enhances our understanding of within-grapevine physiological response to increased node number, and identifies a composite metric (cane percent budburst, cane blind node, head shoot count) for monitoring grapevine vegetative growth, capacity and balance at pre-flowering. It also justifies the practice of retaining one-node or two-node spurs at winter cane pruning.

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## REFERENCES

Benismail, M. C., Bennaouar, M., & Elmribti, A. (2007). Effect of bud load and canopy management on growth and yield components of grape cv. "Cardinal" under mild climatic conditions of Agadir area of Morocco. *Acta Horticulturae, 754*, 197-204. https://doi.org/10.17660/ActaHortic.2007.754.25

Bennett, J., Jarvis, P, Creasy, G. L., & Trought, M. C. T. (2005). Influence of defoliation on overwintering carbohydrate reserves, return bloom, and yield of mature Chardonnay grapevines. *American Journal of Enology and Viticulture, 56*, 386-393. https://doi.org/10.5344/ajev.2005.56.4.386

Berkey, T. G., Mansfield, A. K, Lerch, S. D., Meyers, J. M., & Vanden Heuvel, J. E. (2011). Crop load adjustment in 'Seyval Blanc' winegrape: Impacts on yield components, fruit composition, consumer wine preferences, and economics of production. *HortTechnology, 21*(5), 593-598. https://doi.org/10.21273/horttech.21.5.593

Champagnat, P. (1989). Rest and activity in vegetative buds of trees. *Annales Des Sciences Forestières, 46* (Supplement), 9-26. https://doi.org/10.1051/forest:19890501

Collins, C., Coles, R., Conran, J. G., & Rawnsley, B. R. (2006). The progression of primary bud necrosis in the grapevine cv. Shiraz (*Vitis vinifera* L.): A histological analysis. *Vitis - Journal of Grapevine Research, 45*, 57–62.

Coombe, B.G. (1995). Adoption of a system for identifying grapevine growth stages. *Australian Journal of Grape and Wine Research, 1*, 104-110. https://doi.org/10.1111/j.1755-0238.1995.tb00086.x

Coombe, B. G., & Dry, P. R. (2001). *Viticulture, vol. 2*. Practices, seventh ed. Winetitles, Adelaide, Australia.

Currle, O., Bauer, O., Hofacker, W., Schumann, F., & Frisch, W. (1983). *Biology of the vine*. Neustadt an der Weinstrasse. Meininger, Germany.

Domagalska, M.A., & Leyser, O. (2011). Signal integration in the control of shoot branching. *Nature Reviews Molecular Cell Biology, 12*(4), 211–221. https://doi.org/10.1038/nrm3088

Dry, P. R., & Coombe, B. G. (1994). Primary bud-axis necrosis of grapevines. I. Natural incidence and correlation with vigor. *Vitis - Journal of Grapevine Research, 33*, 225-230.

Düring, H., & Bachmann, O. (1975). Abscisic acid analysis in *Vitis vinifera* in the period of endogenous bud dormancy by high pressure liquid chromatography. *Physiol. Plant. 34*, 201-203. https://doi.org/10.1111/j.1399-3054.1975.tb03821.x

Eltom, M., Trought, M. C. T., Agnew, R., Parker, A., & Winefield, C. S. (2017). Pre-budburst temperature influences the inner and outer arm morphology, phenology, flower number, fruitset, TSS accumulation and variability of *Vitis vinifera* L. Sauvignon blanc bunches. *Australian Journal of Grape and Wine Research 23*, 280-286. https://doi.org/10.1111/ajgw.12260

Epee, M. P. T., Schelezki, O., Parker, A., Trought, M. C. T, Werner, A, Hofmann, R., Almond, P., & Fourie, J. (2022). Characterising retained dormant shoot attributes to support automated cane pruning on Vitis vinifera L. cv. Sauvignon blanc. *Australian Journal of Grape and Wine Research 28* (3), 508-520. https://doi.org/10.1111/ajgw.12555

Faust, M., Erez, A., Rowland, L.J., Wang, S.Y., & Norman, H.A. (1997). Bud dormancy in perennial fruit trees: physiological basis for dormancy induction, maintenance and release. *HortScience, 32*, 623– 629. https://doi.org/10.21273/HORTSCI.32.4.623

Field, S. K., Smith, J. P., Greer, D. H., Neil Emery, R. J., Farrow, S., & Holzapfel, B. P. (2021). Secondary and tertiary budbreak release is enhanced by extended dormancy chilling in "Shiraz" grapevines. *Vitis – Journal of Grapevine Research, 60* (1), 29–33. https://doi.org/10.5073/vitis.2021.60.29-33

Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression, Third Edition*. Thousand Oaks CA: Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Galet, P. (2000). *General Viticulture* (J. Smith, Trans.). Oenoplurimedia, Chaintre, France.

Greven, M. M., Bennett, J. S., & Neal, S. M. (2014). Influence of retained node number on Sauvignon blanc grapevine vegetative growth and yield. *Australian Journal of Grape and Wine Research, 20*(2), 263-271. https://doi.org/10.1111/ajgw.12074

Greven, M. M., Neal, S. M., Hall, A. J, & Bennett, J. S. (2015). Influence of retained node number on Sauvignon blanc grapevine phenology in a cool climate. *Australian Journal of Grape and Wine Research, 21*(2), 290-301. https://doi.org/10.1111/ajgw.12122

Guern, J., & Usciati, M. (1976). Essai de reponse a huit questions concernant la regulation de la croissance des bourgeons axillaires de Cicer arietinum L. In : *Etudes de Biologie vegetale*, CNRS, Gif-sur-Yvette, pp. 191-207.

Hope, R. M. (2013). *Rmisc: Ryan Miscellaneous. R package version 1.5*. https://CRAN.R-project.org/package=Rmisc

Howell, G. S., & Wolpert, J. A. (1978). Nodes per cane, primary bud phenology, and spring freeze damage to Concord grapevines. A preliminary note. *American Journal of Enology and Viticulture, 29*, 229-232.

Huglin, P., & Schneider, C. (1998). *Biologie et Ecologie de la Vigne* (2nd ed.). Paris: Lavoisier.

Harvest Electronics Ltd (2021). *Harvest website*. https://live.harvest.com

Iland, P., Dry, P., Proffitt, T. & Tyerman, S. (2011). *The Grapevine: From the Science to the Practice of Growing Vines for Wine*. Patrick Iland Wine Promotions, Adelaide, Australia

Jackson, D. (1997). *Monographs in Cool Climate Viticulture - 1: Pruning and Training*. Lincoln University Press.

Jackson, R. S. (2014). Vineyard Practice. In: *Wine Science* (pp. 96-203). Elsevier. https://doi.org/10.1016/B978-0-12-381468-5.00004-X

Jones, J. E., Kerslake, F. L., Dambergs, R. G., & Close, D. C. (2018). Spur pruning leads to distinctly different phenolic profiles of base sparkling wines than cane pruning. *Vitis - Journal of Grapevine Research, 57*(3), 103-109. https://doi.org/10.5073/vitis.2018.57.103-109

Kassambara, A. (2020). ggpubr: 'ggplot2' Based Publication Ready Plots. *R package version 0.4.0*. https://CRAN.R-project.org/package=ggpubr

Keller, M., & Mills, L. J. (2007). Effect of pruning on recovery and productivity of cold-injured Merlot grapevines. *American Journal of Enology and Viticulture, 58*, 351 357.

Keller, M., & Tarara, J. M. (2010). Warm spring temperatures induce persistent season-long changes in shoot development in grapevines. *Annals of Botany, 106* (1), 131-141. https://doi.org/10.1093/aob/mcq091

Keller, M. (2015) Phenology and growth cycle. *The Science of Grapevines. 2d ed* (Elsevier Inc.: London, UK) pp. 67-99. https://doi.org/10.1016/B978-0-12-419987-3.00002-9

Kurtural, S. K., Dami, I. E., & Taylor, B. H. (2006). Effects of pruning and cluster thinning on yield and fruit composition of "Chambourcin" grapevines. *HortTechnology, 16* (2), 233-240. https://doi.org/10.21273/horttech.16.2.0233

Lavee, S., Melamud, H., Ziv, M., & Bernstein, Z. (1981). Necrosis in grapevine buds (*Vitis vinifera* cv. Queen of the Vineyard). I. Relation to vigour. *Vitis - Journal of Grapevine Research, 14* (20), 8–14.

May, P. (1961). The value of an estimate of fruiting potential in the Sultana. *Vitis - Journal of Grapevine Research, 3*, 15-26.

Mcloughlin, S. J., Petrie, P. R., & Dry, P. R. (2011). Impact of node position and bearer length on the yield components in mechanically pruned Cabernet Sauvignon (*Vitis vinifera* L.). *Australian Journal of Grape and Wine Research, 17* (2), 129–135. https://doi.org/10.1111/j.1755-0238.2011.00126.x

Mendiburu, F. (2020). agricolae: Statistical Procedures for Agricultural Research. *R package version 1.3-3*. https://CRAN.R-project.org/package=agricolae

Moncur, M. W., Rattigan, K., Mackenzie, D. H., & Mc Intyre, G. N. (1989). Base temperatures for budbreak and leaf appearance of grapevines. *American Journal of Enology and Viticulture, 40*, 21-26.

New Zealand Wine (2020). New Zealand Wine website. https://www.nzwine.com/media/6650/sustainable-winegrowing-new-zealand-standards.pdf

Oliveira, M. (1998). Calculation of budbreak and flowering base temperatures for *Vitis vinifera* cv. Touriga Francesa in the Douro Region of Portugal. *American Journal of Enology and Viticulture, 49*, 74-78.

Perez, J., & Kliewer, W. M. (1990). Effect of shading on bud necrosis and bud fruitfulness of Thompson Seedless grapevines. *American Journal of Enology and Viticulture, 41*, 168-175.

R Core Team (2021). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. https://www.R-project.org/

Saure, M. (1985). Dormancy release in deciduous fruit trees. *Horticultural Review, 7*, 239–300. https://doi.org/10.1002/9781118060735.ch6

Tassie, E., & Freeman, B.M. (1992) Pruning. Coombe, B.G. and Dry, P.R. eds. *Viticulture, Volume 2 - Practices. 2d ed* (Winetitles: Adelaide, SA, Australia) pp. 85- 103.

Thimann, K.V., Skoog, F., & Kerckhoff, W.G. (1934). On the inhibition of bud development and other functions of growth substance in Vicia faba. *Proceedings of the Royal Society B: Biological Sciences, 114(*798), 317–339. https://doi.org/10.1098/rspb.1934.0010

Tomasi, D., Pascarella, G., Sivilotti, P., Gardiman, M., & Pitacco, A. (2007). Grape bud burst: thermal heat requirement and bud antagonism. *Acta Hortic., 754*, 205-212 https://doi.org/10.17660/ActaHortic.2007.754.26

Trought, M. C. T., & Bramley, R. G. V. (2011). Vineyard variability in Marlborough, New Zealand: Characterising spatial and temporal changes in fruit composition and juice quality in the vineyard. *Australian Journal of Grape and Wine Research, 17*(1), 72-78. https://doi.org/10.1111/j.1755-0238.2010.00119.x

Vasudevan, L., Wolf, T. K., Welbaum, G. G., & Wisniewski, M. E. (1998). Reductions in bud carbohydrates are associated with grapevine bud necrosis. *Vitis - Journal of Grapevine Research, 37*, 189–190.

Vaillant-Gaveau, N., Maillard, P., Wojnarowiez, G., Gross, P., Clement, C., & Fontaine, F. (2011) Inflorescence of grapevine (*Vitis vinifera* L.): a high ability to distribute its own assimilates. *Journal of Experimental Botany, 62* (12), 4183–4190. https://doi.org/10.1093/jxb/err121

Vergara, R., Noriega, X., Aravena, K., Prieto, H., & Pérez, F. J. (2017). ABA represses the expression of cell cycle genes and may modulate the development of endodormancy in grapevine buds. *Front. Plant Sci. 8*, 812. https://doi.org/10.3389/fpls.2017.00812

Wickham, H., François, R., Henry, L., & Müller, K. (2021). dplyr: A Grammar of Data Manipulation. R package version 1.0.5. https://CRAN.R-project.org/package=dplyr. https://doi.org/10.1007/978-1-4842-6876-6_1

Winkler, A. J., Cook, J. A., Kliewer, W. M., & Lider, L. A. (1974). *General Viticulture*. University of California Press, Berkeley, CA. https://doi.org/10.1097/00010694-197512000-00012

Wolf, T. K., & Warren, M. K. (1995) Shoot growth rate and density affect bud necrosis of 'Riesling' grapevines. *Journal of the American Pomological Society. 54*, 34-43. https://doi.org/10.21273/JASHS.120.6.989

Zamboni, M., Bavaresco, L., & Komjanc, R. (1996). Influence of bud number on growth, yield, grape and wine quality of 'Pinot Gris', 'Pinot Noir' and 'Sauvignon' (*Vitis Vinifera* L.). *Acta Hortic. 427*, 411-420. https://doi.org/10.17660/ActaHortic.1996.427.48

Zapata, C., Deleens, E., Chaillou, S., & Magne, C. (2004) Partitioning and mobilization of starch and N reserves in grapevine (*Vitis vinifera* L.). *Journal of Plant Physiology 161*(9), 1031–1040. https://doi.org/10.1016/j.jplph.2003.11.009

Ziv, M. M., Bernstein, Z., & Lavee, S. (1981). Necrosis in grapevine buds (*Vitis vinifera* cv. Queen of the Vineyard). II. Effect of gibberellic acid (GA3) application. *Vitis - Journal of Grapevine Research, 20*, 105-114