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**Influence of canopy management on grapevine reproductive
performance**

By

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Influence of canopy management on grapevine reproductive performance

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Abstract

Grapevine reproduction is an intricate process that extends over two growing seasons. There is an overlap of two reproductive cycles; while the shoots are growing and inflorescences are developing into bunches for the first cycle (season one), the compound buds at the axil of lateral leaves are developing the potential crop for the next reproduction cycle (season two). The conditions of the first season not only influence reproductive growth of the current year, but also affect bud fruitfulness and hence potential yield for the following year.

Canopy management practices play a vital role in commercial vineyards. A range of techniques have been developed and widely applied on grapevine canopies to achieve a desired yield and fruit quality. Grapevine reproductive performance response to different canopy management practices varies as source-sink relationship and microclimate are manipulated at different levels. Therefore a better understanding of vegetative and reproductive development in relation to the practices is imperative for sustainable production in vineyards. The aim of this thesis was to investigate the effects of different canopy management practices on the reproductive performance of two winegrape varieties, Semillon and Shiraz (*Vitis vinifera* L.).

Five commonly used canopy management treatments including bunch thinning, shoot thinning, leaf removal at the bunch zone and at the middle third part of shoots, and leaving more buds after light winter pruning were applied on vines grown under field conditions. Canopy architecture was assessed by measuring leaf area index and canopy porosity. Light microclimate was measured as light interception at the whole canopy level and bud renewal zone. Reproductive performance was comprised of yield components (bunch number per vine, berry number per bunch and berry weight), bunch architecture (bunch length, width and compactness), berry uniformity and berry maturity during ripening. Bud fruitfulness was assessed using bud dissection analysis to record the number and area of inflorescence primordia and incidence of primary bud necrosis. Other measurements included shoot vigour parameters and carbohydrate contents of buds and canes.

Results showed that grapevine reproductive performance was influenced by canopy management practices at different levels. Specifically, shoot thinning had the strongest effects on yield components, bunch architecture and bud fruitfulness through a greater modification of canopy architecture and light interception. Berry weight, berry number and bunch weight were significantly increased by shoot thinning. Leaf area index was decreased and canopy porosity and light interception were increased by shoot thinning and leaf removal. The number of inflorescence primordia was increased in the two treatments when an increase in the bud light microclimate was measured. Berry ripening was positively affected by shoot thinning and bunch thinning, while leaf removal and light pruning delayed the process. Leaf removal had relatively minor impact on reproductive parameters, while shoot thinning and bunch thinning showed compensation effects in yield components and bunch architecture, and light pruning decreased berry weight. In addition, bunch compactness was found to be increased by shoot thinning and was correlated with bunch rot (*Botrytis cinerea*) incidence for Semillon.

This study improved our understanding of the role of canopy management practices on reproductive performance of grapevine, particularly for bunch architecture and bud fruitfulness. These insights may be used by practitioners to make more informed vineyard management decisions when manipulating yield.

Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

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Xiaoyi Wang

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Date

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Abbreviations

| | |
|-----------------|-------------------------------------|
| ANOVA | Analysis of Variance |
| BC | Bunch compactness |
| BT | Bunch thinning |
| C | Control |
| cm | Centimetre |
| cm ³ | Centimetre cube |
| cv | Cultivar |
| DN | Double nodes |
| DW | Dry weight |
| GDD | Growing degree days |
| E-L stages | Eichhorn-Lorenz stages |
| IP | Inflorescence primordia |
| LAI | Leaf area index |
| Li | Light interception |
| LGO | Live green ovary |
| LR | Leaf removal |
| LR-B | Leaf removal at bunch zone |
| LSD | Least significant difference |
| mg | Milligram |
| mm | Millimetre |
| mm ² | Millimetre squared |
| MI | Millerandage index |
| PAR | Photosynthetically active radiation |
| PBN | Primary bud necrosis |
| <i>P</i> -value | Probability |
| SAM | Shoot apical meristem |
| ST | Shoot thinning |
| TA | Titrateable acidity |
| TNC | Total non-structural carbohydrate |
| TSS | Total soluble solids |
| °C | Degree Celsius |
| % | Percent |

Chapter 1: Introduction

1.1 General introduction

Grapevine canopy refers to the above ground part of the vine, including shoots, fruits, trunk and cordon or canes (Smart and Robinson 1991). Canopy management practices are widely adopted in commercial vineyards to improve final yield and/or crop quality. These practices are aimed to optimize fruit development and help wineries to maintain production and achieve a targeted wine style. Different techniques of canopy management have been developed and employed to alter the vine vigour and canopy microclimate (Smart 1985, Vasconcelos and Castagnoli 2000). These manipulations lead to different outcomes in yield parameters and berry composition (Smart 1985). Due to the complexity of grapevine physiology, these practices can change vine structure, vigour and source-sink relationship at different levels, hence the effects on reproductive performance can vary to a large extent. Therefore, a thorough understanding of the effects of different canopy management practices on grapevine is necessary for the wine industry.

Commonly used canopy management techniques include dormant pruning, shoot positioning, shoot thinning, leaf removal, bunch thinning, and trellising (Smart and Robinson 1991). These practices influence vine physiology at different levels by altering a series of canopy microclimate factors, including light quantity and quality, aeration, evaporation rate, air temperature and humidity (Smart 1985, Dry 2000). Intensive research has been conducted worldwide to investigate the effect of canopy management practices on vine growth and fruit development (Shaulis and May 1971, Minden and Philipson 1982, Kliewer and Smart 1989, Dry 2000, Naor et al. 2002, Morris et al. 2004, Poni et al. 2013). While these studies confirmed that canopy management is a useful tool that allows grape growers to improve grape and wine quality, it also showed a lack of uniformity of response across different grape varieties, vineyard sites and climate. The timing and intensity of the applied practices can vary the response on grapevines.

Grapevine reproduction is an intricate process that extends over two seasons. It starts from floral induction within buds in the first year, and further development in the

second year until berry maturity (Iland et al. 2011). Reproductive performance refers to different aspects of inflorescence and bunch development, including flower number per inflorescence, fruitset (%), yield components (berry size, berry number per bunch, total bunch number and total yield), bunch architecture (bunch length, bunch width and bunch compactness), and berry variation, measured using indices such as the millerandage index (Dry et al. 2010). Bud fruitfulness is defined as the formation of inflorescence primordia (IP) in mature latent buds (Srinivasan and Mullins 1981, Dry 2000). The number and size of IP play a key role in yield variation (May 2000, Williams 2000, Sánchez and Dokoozlian 2005). The initiation and development of IP takes place concurrently with the development of the crop in the current season, which is the overlap of two reproductive cycles. Hence it is more complicated to impose canopy management on grapevines, as the manipulation does not only influence fruit production in the current season, but may also have a carry-over effect on the potential yield components for next season.

Canopy architecture is determined by the amount, distribution and size of the shoots, leaves and fruit of a vine, and is influenced by canopy management practices. It interacts with the aboveground climate and results in a particular canopy microclimate (Smart 1985). The most influential microclimate factors that affect reproductive performance are temperature and light (Smart 1985, Kliewer and Smart 1989, Dry 2000). Berry size and composition is largely dependent on total photosynthesis, which is determined by the total leaf area and light interception by the canopy (Kliewer and Dokoozlian 2005). Other studies have also found that bud fruitfulness is strongly influenced by the light environment of the renewal zone in the early stages of the growing season (Dry 2000, Williams 2000, Sánchez and Dokoozlian 2005). Therefore, by investigating the manipulation of canopy microclimate by cultural practices, we aim to better understand the effects of different canopy management practices on grapevine reproductive performance. A large proportion of previous research has investigated and elucidated how canopy management treatments affect yield components and fruit quality, however, the impact of these treatments on bunch architecture and bud fruitfulness, especially on the size of inflorescence primordia, is not well known.

1.2 Project aims

The aims of this study were to:

- i) determine how different canopy management practices impact bunch architecture and yield components of Semillon and Shiraz;
- ii) determine how different canopy management treatments change canopy architecture, light interception, and bud carbohydrate levels;
- iii) determine how canopy management practices affect bud fruitfulness, including number and size of inflorescence primordia, and occurrence of primary bud necrosis.

1.3 Linking statement

The research in this thesis is presented in five chapters, including two prepared manuscripts intended for publication.

- Chapter 1 comprises the general introduction of the research and project objectives.
- Chapter 2 is a review of the literature related to grapevine growth cycle, canopy management techniques, and the use of bud fruitfulness for early yield prediction. A summary of the literature is presented at the end of the chapter.
- Chapter 3 investigates the effects of different canopy management treatments on canopy architecture, vine microclimate, yield components, bunch architecture, berry variation and berry maturity for two varieties, Semillon and Shiraz.
- Chapter 4 examines how grapevine bud fruitfulness is influenced by canopy management treatments, including number and size of inflorescence primordia (IP) and occurrence of primary bud necrosis (PBN).
- Chapter 5 is a general conclusion of this research project. The effects of canopy management treatments on reproductive performance of Semillon and Shiraz are summarized. The significance of the results of this project is discussed and remaining questions and future directions of related research suggested.

Chapter 2: Literature Review

2.1 Reproductive growth cycle of the grapevine

The reproductive growth cycle of a grapevine spans two seasons and lasts approximately 15-18 months (Wilson and Trought 1995). It starts with inflorescence induction, initiation and formation in the first season, and flowering and fruitset, berry formation and berry ripening in the second season (Srinivasan and Mullins 1981, May 2004, Iland et al. 2011). The reproductive growth cycle is illustrated in Figure 2.1 (Coombe and Iland 2004, Carmona et al. 2008). There is an overlap of two reproductive cycles in year two, that is, while the inflorescence is developing into flowers and then berries for the current season, a compound bud at the axil of a lateral leaf on the same shoot is developing for next season's crop.

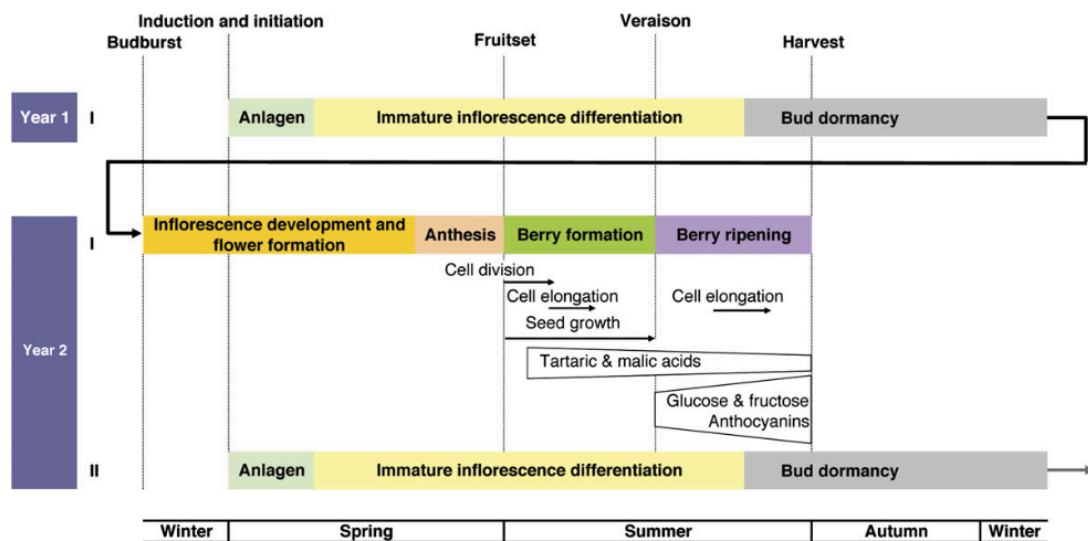


Figure 2.1 Schematic diagram of the grapevine developmental reproductive cycle (Coombe and Iland 2004, Carmona et al. 2008)

2.1.1 Bud development

In the first season, the grapevine buds develop in the axil of a leaf or bract on developing shoots (Pratt 1971, Vasconcelos et al. 2009). A bud complex comprises a lateral bud (or prompt bud) and a compound bud, which is also referred to as the latent or dormant bud (Pratt 1971, Morrison 1991, Mullins et al. 1992, Gerrath 1993, Boss et al. 2003, Vasconcelos et al. 2009). The transverse section of a bud complex is depicted in Figure 2.2. The lateral bud forms axillary to a leaf on the main shoot. It

may burst in the current season and develop into a lateral shoot, become necrotic or remain dormant (Mullins et al. 1992, May 2000, Williams 2000). The lateral shoots are typically unfruitful and may fail to lignify and thus fall off during autumn or winter, while they may occasionally have small and late-ripening bunches as a 'second crop' (Goffinet 1991, Keller 2015a). Lateral shoot development can be induced by canopy management practices such as topping or trimming of the main shoot (Iland et al. 2011).

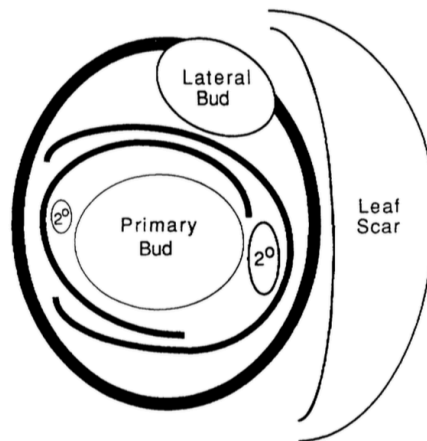


Figure 2.2 Transverse section of axillary bud complex in grapevine (Morrison 1991). Comprised of a lateral bud and a compound bud (one primary bud and two secondary buds 2°).

The compound bud is formed axillary to the basal prophyll of the lateral bud or shoot (Srinivasan and Mullins 1981, Keller 2015a). It is normally composed of three buds: one large primary and two small secondary latent buds (Figure 2.2) (Morrison 1991). The bud complex hierarchy has been described by Morrison (1991). The lateral bud is defined as the true axillary bud or the first-order bud, the primary bud is the second-order bud and the secondary buds are third-order buds in relation to the main shoot (Pratt 1974, Morrison 1991). The compound bud initiates around two to three weeks after the formation of the subtending prophyll in the lateral bud and three to four weeks before the expansion of the shoot that would bear buds, depending on the environment and variety (Morrison 1991).

As the compound bud develops, the apical meristem produces two types of lateral meristems, one for leaf production and the other for inflorescence and tendril production (Carmona et al. 2007). The formation of the uncommitted primordia, the anlagen, from the apex of the bud is the earliest indication of reproductive growth in

grapevine (Williams 2000). The anlagen can develop into inflorescence primordia, tendril primordia or intermediate primordia, regulated by internal and external factors (Barnard and Thomas 1933, Boss et al. 2003). Depending on the variety, after eight to twelve leaf primordia, one to three inflorescence primordia and several tendril primordia are formed, the bud finishes its first season's development and enters into dormancy (Srinivasan and Mullins 1981, Keller 2015b). Budburst starts in the spring of the second year. Generally only the primary buds grow into shoots and the secondary buds remain dormant (May 2004, Keller 2015b). When the primary bud is damaged or dies, the secondary buds can compensate for this loss and develop instead, but the shoots are normally small and less fruitful compared with the primary bud (Pratt 1971, Goffinet 1991, Mullins et al. 1992, Dry and Coombe 1994).

2.1.2 Inflorescence differentiation, flowering and fruitset

In the second season, branching of inflorescence primordia inside the compound bud resumes two to three weeks before budburst and continues throughout budburst (May 2000, Williams 2000, Vasconcelos et al. 2009). The initiation and development of flower parts occurs simultaneously in all parts of the inflorescence primordia (Mullins et al. 1992, Keller 2015b). Flower initials are formed, starting with the traces of calyx and followed by other parts in the order of corolla, stamens and the pistil (Pratt 1971, Srinivasan and Mullins 1980, Swanepoel and Archer 1988, Vasconcelos et al. 2009, Keller 2015b). The structure of the inflorescence is generally considered as a conical panicle characterized by multiple branching (May 2004, Vasconcelos et al. 2009). Once the inflorescences have been differentiated and the individual flowers have formed, the upper limit of potential yield has been set by the flower numbers, as the final yield will be determined by the number of individual flowers that set fruit and the extent that the individual berries develop (Dunn and Martin 2000).

Flowering occurs when the floral parts are fully developed, which is normally within eight weeks of budburst (Jackson 2008). The precise timing of flowering is dependent on weather conditions, varietal characteristics and climate type (Srinivasan and Mullins 1981, Mullins et al. 1992). It starts with the calyptra (cap) being shed from the flower, exposing the anthers and pistil (also known as capfall) (Swanepoel and Archer 1988, Iland et al. 2011). Pollen grains are released from anthers and land on

the stigma, germinate and produce a pollen tube (Boss et al. 2003, May 2004, Vasconcelos et al. 2009). The pollen tube, which carries two fused sperm cells, grows through the stigma, style and central part of the ovary towards the ovule (Iland et al. 2011, Keller 2015b). The process of pollination also has been reported to finish before anthesis (May 2004). Flowering for an individual inflorescence often lasts five to eight days, and can be delayed by cold and rainy weather (May 2004, Vasconcelos et al. 2009, Keller 2015b).

The pollen tube enters the embryo sac and releases the sperm cells. Fertilization happens in the ovule with the fusion of sperm cell and egg cell and results in the zygote, which then develops into the embryo and leads to fruitset (Keller 2015b). After fertilization, the ovule develops into a seed and the ovary wall develops into the pericarp (skin and flesh) of berry (Pratt 1971, May 2004). Fruitset is successful when a single flower develops into a single berry, however, only a proportion (20 - 50 %) of flowers complete fruitset (Mullins et al. 1992, Iland et al. 2011, Keller 2015b). There are four types of fruitset for grapevines (Winkler et al. 1974):

- a) seeded, where berries develop with normal pollination and fertilization resulting in functional seeds;
- b) stenospermocarpic (seedless), where berries develop with pollination and fertilization but seeds get aborted later in development;
- c) stimulative parthenocarpic (seedless), where berries develop with pollination but without fertilization, and berries are formed due to the stimulus from the pistil and pollen tubes (May 2004); and
- d) vegetative parthenocarpy (seedless), where berries develop without pollination and fertilization, and berries are formed from ovaries with a defective embryo sac (Stout 1936).

The berries that result from the different types of fruitset can be classified into three groups: normal seeded berries (hen berries, that contains one to four mature seeds), seedless berries (chicken berries, sometimes contains seed traces), and live green ovaries (LGO, shot berries) (Dry and Coombe 2004, May 2004, Jackson 2008, Collins and Dry 2009). Seeded berries normally make the greatest contribution to the proportion of all berries in a bunch (May 2004). The seedless berries are smaller in size but still undergo veraison and ripen normally at harvest. The LGOs remain very

small, green and hard and contribute less than 1% to the bunch weight (May 2004, Collins and Dry 2009). The relative proportion of seeded, seedless berries and LGOs on a bunch is indicative of grapevine reproductive performance. Millerandage index (MI) can be used to quantify the proportion of seedless berries and LGOs in a bunch (Collins and Dry 2009, Lohitnavy et al. 2010).

2.1.3 Berry growth

Regardless of the type of fruitset, berry growth follows a double sigmoid pattern (Coombe 1972, Coombe 1992, Mullins et al. 1992, Jackson 2008). It is comprised of two phases, berry formation and berry ripening (Figure 2.3) (Coombe and McCarthy 2000, Kennedy 2002, Dry and Coombe 2004). Berry formation is the phase when berry structure and tissue are initiated and berry ripening is mainly the accumulation of sugar and development of flavour compounds (Dry and Coombe 2004, Iland et al. 2011). Berry growth is also commonly classified into three distinct stages:

Stage 1: Rapid growth (40-60 days)

This stage is characterized by a rapid increase in berry size due to cell division and some expansion (Nitsch et al. 1960, Mullins et al. 1992). The berry remains hard and green. Organic acid accumulation, which is commonly measured as titratable acidity, and sugar level stays constant (Mullins et al. 1992, Coombe and McCarthy 2000). There is little development of the embryo at this stage (Nitsch et al. 1960, Mullins et al. 1992).

Stage 2: Lag phase (7 to 40 days)

During the lag phase there is slow or no enlargement in berry size, however, the embryo development is rapid (Pratt 1971, Mullins et al. 1992). The berries remain hard and green. The weight of seeds and titratable acidity reach the maximum at the end of this period (Ristic and Iland 2005, Adams 2006, Keller 2015b). The lag phase may be less distinct in seedless berries than in seeded berries (Nitsch et al. 1960, Iwahori et al. 1968). The length of this phase is related to whether the variety is early or late ripening (Mullins et al. 1992, Dry and Coombe 2004).

Stage 3: Resumed growth and maturation (35 to 55 days)

This stage starts with the onset of veraison. It is marked by colour change and softening of the pericarp (Coombe 1992). Rapid berry growth resumes due to cell expansion (Mullins et al. 1992) and the berries reach maximum size at this stage. Ripening is associated with the accumulation of glucose and fructose in the pericarp, a decrease in the concentration of acids, loss of chlorophyll from the skin and accumulation of anthocyanins (in black grape varieties), and acquisition of aroma compounds (Coombe 1992, Mullins et al. 1992, Dry and Coombe 2004, Jackson 2008, Keller 2015b).

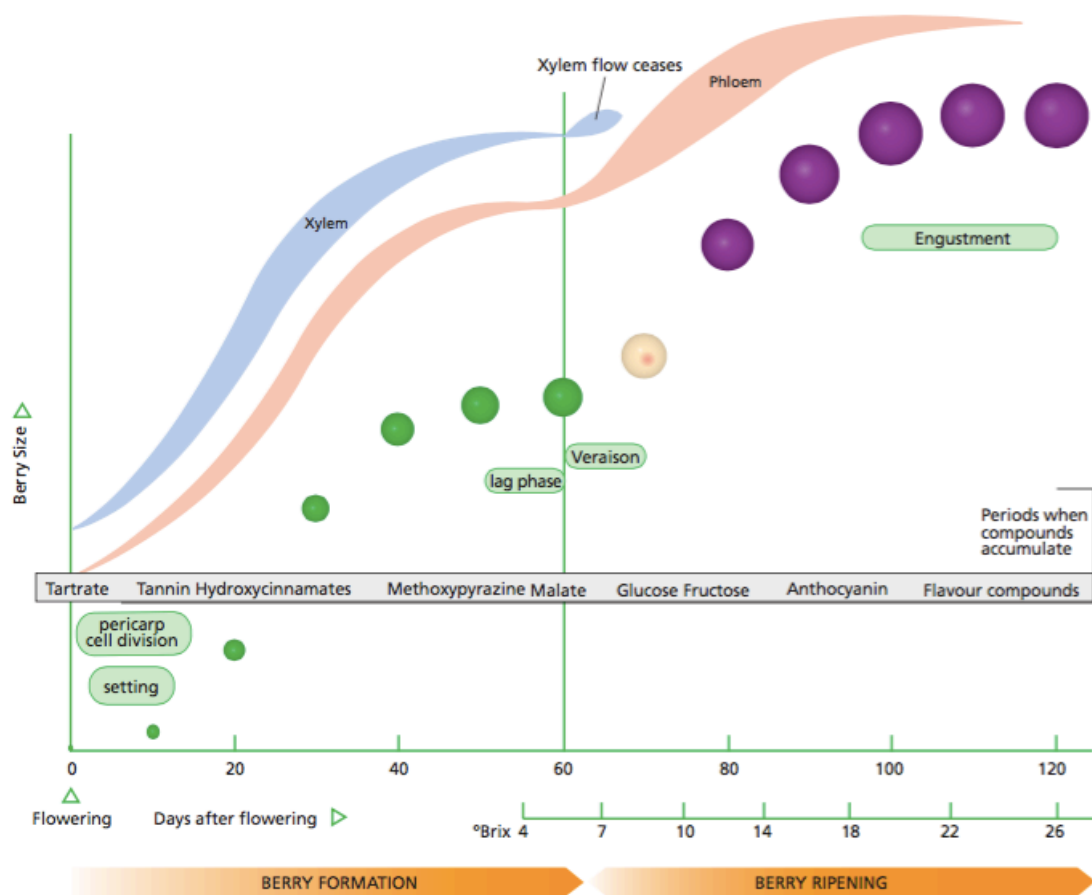


Figure 2.3 Grape berry development and ripening (Kennedy 2002). Relative size and colour of berries are illustrated at 10-day intervals showing the two successive sigmoidal growth phases, berry formation and berry ripening. Key development stages and accumulation of major solutes are shown.

In some situations, towards the end of the ripening phase, berry shrivel may take place due to transpirational water loss (McCarthy 1997, McCarthy and Coombe 1999, Coombe and Iland 2004, Fuentes et al. 2010). This is occasionally termed as the fourth stage, the berry shrinkage stage (Jackson 2008, Iland et al. 2011). Both physical and chemical changes take place during this stage. Berries soften and berry

composition is affected by shrivel and thus berry ripeness, influencing wine style and quality (McCarthy and Coombe 1999, Coombe and McCarthy 2000). The final berry size is determined largely by the grape variety, and also controlled by climatic conditions (both macro- and microclimate) and vineyard management such as irrigation, nutrient status, and canopy management practices (Coombe and Dry 1992, Mullins et al. 1992).

2.2 Vine balance and canopy microclimate

2.2.1 Vine balance and source-sink relationship

Achieving vine balance is critical for maintaining productive and healthy vines (Cloete et al. 2006, Vance 2012). According to Gladstones (1992), vine balance is achieved when vegetative and reproductive growth are in equilibrium and consistent with high quality fruit. Excessive vine vigour can be detrimental to yield and fruit quality because of the increased canopy density and shading (May 1965, Rojas-Lara and Morrison 1989, Dokoozlian and Kliewer 1996), and reallocation of resources to vegetative rather than reproductive organs (Wolf 2002). On the other hand, over-cropping can limit canopy growth and lower fruit quality by producing unripe fruit due to a lack of photo-assimilation (Kliewer and Weaver 1971, Bravdo et al. 1985, Smart and Robinson 1991, Poni et al. 1994b). Balancing the leaf area-fruit ratio can improve the canopy microclimate, increase photosynthetic efficiency and promote fruit maturation (Jackson 2008).

The relationship between sources and sinks and translocation of carbon and nutrient between them are essential for vine balance (Carbonneau 1995). In grapevine, source is used to indicate organs that produce, store and export carbon and nutrient, and sinks are the organs where the resources are transported to (Iland et al. 2011, Keller 2015c). A tissue or organ can be a source or sink depending on the stage of growth. In the early phenological stages, shoot growth and flower development are mainly dependent on reserves from the woody parts including canes, cordons, trunks and roots (Zapata et al. 2004, Jackson 2008, Smith and Holzappel 2009). Young leaves become a source when they reach about 30% of their full size and start to export photosynthates. Inflorescences are not strong sinks until fruitset when shoot growth

rates start to slow (Jackson 2008, Keller 2015c). As inflorescences and bunches develop, they become strong sinks and compete for photo-assimilates with actively growing shoot tips and developing compound buds and thus influence the potential crop for next year (Candolfi-Vasconcelos and Koblet 1990, Williams 1996, Iland et al. 2011). When resources are limited, the development of inflorescence primordia can be suppressed resulting in a lower number and less branching of the inflorescence in next season and hence a yield reduction (Williams 2000, Bennett et al. 2005, Li-Mallet et al. 2016, Noyce et al. 2016b). In the late phenological stages, the woody parts of the vine gradually become important sinks and replenish storage reserves in trunks and roots (Loescher et al. 1990, Candolfi-Vasconcelos et al. 1994, Keller 2015c).

Source-sink ratio can be manipulated by canopy management to redirect resources and improve vine growth and fruit ripening (Holzapfel et al. 2010). For instance, leaf removal is used to reduce the source strength in excessively vigorous canopies, however, the photosynthesis of the remaining leaves was found to increase (Buttrose 1966a, Hunter and Visser 1988, Poni et al. 2006). In contrast, inflorescence or bunch removal is used to decrease the number of sinks and can result in assimilate surplus and stimulate vegetative growth such as lateral shoots (Petrie et al. 2000b, Pallas et al. 2008, Keller 2015c). The remaining fruit can also compensate in size when bunch removal is conducted early in the season (Keller 2015c). The extent of the compensation for sources or sinks is uncertain and closely related to intensity and timing of the canopy manipulation.

2.2.2 Canopy microclimate and canopy architecture

Canopy microclimate refers to the environmental conditions within the immediate vicinity of leaves and fruit (Smart et al. 1985). It is largely dependent on the density and architecture of the canopy and its interaction with the aboveground climate and can be modified by cultural practices (Smart 1985, Smart and Robinson 1991, Schultz 1995, Dry 2000). Canopy architecture affects berry development and maturation by changing the amount of exposed leaf surface area and hence photosynthetic capacity of the canopy (Smart 1974, Carbonneau 1995, Schultz 1995) and by directly influencing the microclimate of the fruit (Smart 1985, Intrieri 1986, Reynolds and

Wardle 1989, Reynolds et al. 1995). In addition, the microclimate at the bud zone greatly influences bud fruitfulness and hence potential yield for next year (Dry 2000, Sánchez and Dokoozlian 2005). Leaf area index (LAI) and canopy porosity are two indices that are widely used to describe canopy architecture. LAI is defined as the projected area of leaf tissue per unit ground surface area (Watson 1947) and canopy porosity indicates canopy gaps that allow sunlight penetration and air circulation (Diago et al. 2016).

Due to attenuation by the leaves, shoots and fruit, different microclimatic factors can be varied between and within the canopy. The main components of the microclimate include temperature, sunlight (both quality and quantity), humidity, wind speed and evaporation (Smart 1985). Light intensity and temperature are the two most important factors for vine growth and berry ripening (Price et al. 1995, Matese et al. 2012, Hulands et al. 2013). The humidity, wind speed and evaporation can indirectly influence fruit quality by favouring or controlling the incidence of pests and diseases (Smart 1985, Thomas et al. 1988).

Light interception by the canopy is directly affected by the distribution of leaf and non-leaf surfaces of a vine as only about 6% of photosynthetically active radiation (PAR, the 400-700 nm wavelength spectrum) can be transmitted by a leaf (Smart 1987). Consequently, the photosynthetic efficiency and vine productivity is influenced by the canopy density and architecture (Dokoozlian and Hirschfeldt 1995, Schultz 1995). Shading has adverse effects on berry composition, such as lower sugar, higher acidity and potassium and reduced phenolics and anthocyanins (Smart 1985, Dokoozlian and Kliewer 1996, Haselgrove et al. 2000, Downey et al. 2006). Excessive sunlight exposure at the fruit zone can cause sunburn in berries (Greer and La Borde 2006, Hulands et al. 2013). Shading at the renewal zone is associated with low bud fruitfulness, bud break, fruitset and berry size (Buttrose 1969, Shaulis and Smart 1974, Dry 2000).

2.3 Grapevine bud fruitfulness

2.3.1 Bud fruitfulness and yield prediction

Reproductive development and yield formation of grapevine starts with floral initiation in a compound bud and occurs over two successive seasons (Williams 2000). A compound bud normally contains one primary and two secondary latent buds, with each of them being able to give rise to a shoot in the coming season (Goffinet 1991, Keller 2015a). However, the secondary buds normally remain dormant and do not develop unless the primary bud is damaged from spring frost, insect damage or primary bud necrosis (PBN) (Pratt 1971, Rawnsley and Collins 2005). Bud fruitfulness refers to the formation of inflorescence primordia (IP) in mature latent buds and a compound bud is considered fruitful when it contains one or more IP (Antcliff and Webster 1955, Srinivasan and Mullins 1981, Dry 2000). Actual fruitfulness, which is measured by the number of bunches per shoot, can be determined in the preceding season by a fairly common tool used in the grape production, bud dissection analysis (Rawnsley and Collins 2005, Sánchez and Dokoozlian 2005).

Unpredictable seasonal variations of grapevine yield continue to cause major economic problems in the Australian wine industry (Clingeffer et al. 2001, Anderson and Aryal 2015). Early yield prediction is important for successful yield regulation to prevent under- and over-cropping and optimize the final yield for the desired wine quality target (Dunn 2010, De La Fuente et al. 2015). Winegrowers could better schedule harvesting, processing, fermentation and storage through accurate yield prediction, and hence increase labour and production efficiencies.

It is well established that the main component of grapevine yield is the bunch number per vine, which accounts for approximately 60% of seasonal yield variation (Clingeffer et al. 2001, Guilpart et al. 2014). The other two yield components are berry number per bunch and average berry weight, accounting for about 30% and 10% of annual yield formation, respectively (Clingeffer et al. 2001, Dunn and Martin 2007). Bunch number is determined by bud fruitfulness, the number of buds retained (pruning level) on a vine and the percentage of budburst (Dry 2000). Berry

number per bunch is influenced by the branching level of IP (Morrison 1991, Dunn and Martin 2007) and percentage of fruitset (Dry and Coombe 2004). Therefore, the upper limit of around 90% of the potential yield, comprised of bunch number (60%) and maximum berry number per bunch (30%), can be affected by bud development in the early stage of the previous season (Guilpart et al. 2014). Hence assessing bud fruitfulness, which can be conducted 10 months before harvest (Antcliff and Webster 1955), is helpful for early yield prediction.

Bud dissection analysis can be performed on dormant buds where the IP formation is completed, which is usually after leaf fall in the first season and before bud break in the second season (Dry 2000). After making a transverse cut of the compound bud, bud fruitfulness is assessed by recording the number of IP and the occurrence of PBN within the primary bud using a light microscope (Rawnsley and Collins 2005). IP number in secondary buds is recorded instead when the primary bud is necrotic. With the information from bud dissection analysis, winegrowers can modify their pruning techniques and other canopy management strategies to optimize grapevine yield and quality for the upcoming season.

2.3.3 Formation of inflorescence primordia

The process of IP formation includes floral induction, IP initiation and differentiation in the first season, and further development before budburst in the second season (Srinivasan and Mullins 1981, Vasconcelos et al. 2009, Iland et al. 2011). Figure 2.4 illustrates the formation of IP in two continuous seasons (Srinivasan and Mullins 1981, Dunn and Martin 2007). Most of the branching happens before buds enter dormancy in the first season (Scholefield and Wann 1975, Srinivasan and Mullins 1981, Swanepoel and Archer 1988), and branching at a finer scale continues around budburst and terminates in the formation of individual flowers (Dunn and Martin 2007).

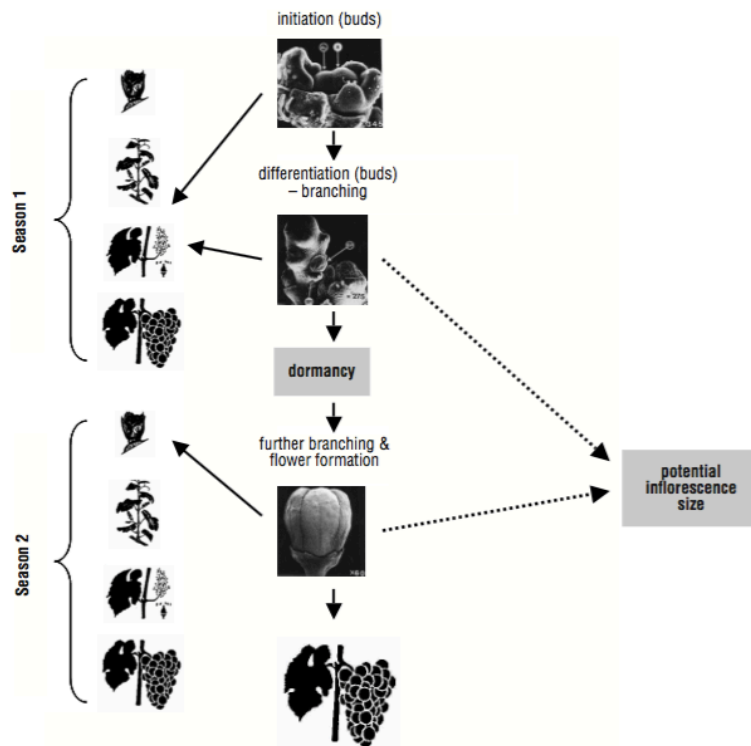


Figure 2.4 Illustration of the key stages of inflorescence primordia (IP) formation (Srinivasan and Mullins 1981, Dunn and Martin 2007).

The timing of IP initiation varies according to varieties, climate type, pruning techniques and bud location. It ranges between two and six weeks after budburst (Vasconcelos et al. 2009). Normally there are two IP formed in the primary bud, and occasionally one or three (Pool et al. 1978, May 2000, Sánchez and Dokoozlian 2005, Noyce et al. 2016a). Srinivasan and Mullins (1981) described a comprehensive flowering process from stage 0 to 11. Noyce et al. (2015) identified different IP stages using new methods and gave more detailed and new descriptions of stage 1-7, which is summarized in Table 1.

Table 1. A summary of developmental features of inflorescence primordia (IP) at stage 0 to 7 (Noyce et al. 2015)

| IP stage | Growing stage features |
|----------|--|
| 1 | Apex of Shoot apical meristem (SAM) is bilobed equally into SAM and anlage. |
| 2 | Anlage is separated from SAM and is rounded. |
| 3 | The outer edge of anlage is surrounded by a collar-like bract. |
| 4 | Anlage forms into two arms, with inner arm larger and longer than outer arm. |
| 5a | Outer arm is unbranched and covered by a bract, while inner arm has two to four branches. |
| 5b | Outer arm is still unbranched and covered by a bract. Inner arm is much larger with many branches. |
| 6 | Outer arm starts branching. |
| 7 | Both outer arm and inner arm branch extensively. There is a distinct gap between two arms. |

After three to eight leaf primordia are formed along the latent primary bud axis (Pratt 1971), the first IP is presented in stage 1 as the initiation of anlage occurs, which can be observed as early as 54 days after budburst. Anlagen can be distinguished from leaf primordia during bud dissection as the anlagen are detached from the apex from stage 2. Anlagen grow quickly up to stage 5b, which is about 76 days post-budburst (Noyce et al. 2016a). The anlagen then differentiate into IP, with an inner arm being the main body and a much smaller outer arm known as a shoulder or wing. Growth continues slowly until stage 7, which is around 236 days after budburst, when its appearance is similar to a bunch of berries (Noyce et al. 2016a). Recent studies showed that IP continues developing at stage 7 during dormancy in season one and prior to budburst in season two (Jones et al. 2009, Noyce et al. 2015).

2.3.4 Primary bud necrosis

PBN is defined as a physiological disorder that results in the death of the primary bud within the compound bud (Lavee 1987, Morrison and Iodi 1990, Dry and Coombe 1994, Rawnsley and Collins 2005, Vasudevan et al. 2015). When PBN occurs, the secondary buds in the compound bud may stay healthy and burst, but produce smaller bunches (approximately 30% of primary shoots) or potentially no fruit, hence causing yield loss (Pool et al. 1978, Wolf and Warren 1995, Rawnsley and Collins 2005, Kavooosi et al. 2012). Bud necrosis can also occur in secondary buds (Naito et al. 1986, Vasudevan et al. 1998, Collins et al. 2006).

The incidence and severity of PBN is normally assessed by bud dissection, as a bud with PBN shows no visual difference compared to a healthy compound bud (Dry 2000, Rawnsley and Collins 2005). The appearance of PBN is characterized by compressed and distorted cells with irregular cell walls (Collins et al. 2006) (Figure 2.5). The pattern of PBN can be variable and is not limited to a specific area of the bud (Morrison and Iodi 1990). When the level of PBN is severe, the entire compound bud will be brown to black in colour with little or no healthy green tissue. The timing of PBN occurrence varies among different cultivars and can be observed as early as 20 days after bloom (Morrison and Iodi 1990, Collins et al. 2006) and the incidence of PBN continues to increase throughout the season, therefore it is recommended to assess bud fruitfulness as close to pruning as possible (Rawnsley and Collins 2005, Kavooosi et al. 2012) in order to more accurately determine pruning levels for the season to achieve a targeted yield.



Figure 2.5 Assessing primary bud necrosis (PBN) by bud dissection technique under a light microscope (Rawnsley and Collins 2005). Cross sections of (A) a healthy compound bud, (B) a compound bud with PBN and (C) a compound bud with necrosis in both primary and secondary buds.

Excessive vigour is suggested to be the main reason for the high incidence of PBN (Lavee 1987, Wolf and Cook 1992, Rawnsley and Collins 2005, Kavooosi et al. 2012). Other factors, such as high level of soil nitrogen, canopy shading, high concentration of the growth hormone gibberellic acid, severe pruning, and excessive irrigation, have been associated with the severe levels of PBN (May 1961, Ziv et al. 1981, Lavee 1987, Perez and Kliewer 1990, Dry 2000, Guilpart et al. 2014, Vasudevan et al. 2015). Vasudevan et al. (2015) suggested that the reduction of carbohydrate reserve or starch in the bud could also lead to a high occurrence of PBN. Canopy management

such as shoot thinning and positioning can reduce the incidence of PBN due to a reduction in shading and increased light interception (Perez and Kliewer 1990, Dry 2000). However, severe shoot thinning could increase PBN incidence since the shoot vigour can also be increased (Dry and Coombe 1994). Therefore, canopy management needs to be considered carefully to create an optimal canopy microclimate.

2.3.5 Factors influencing bud fruitfulness

The development of IP in compound buds is affected by a series of environmental and non-environmental factors during the process over the two seasons (Dunn 2005). The environmental factors include air temperature, light intensity, nutrient availability, and water supply (Buttrose 1969, Srinivasan et al. 1972, Buttrose 1974b, Eltom et al. 2014, Li-Mallet et al. 2016). Non-environmental factors include node position and direction, rootstock, pruning strategies and canopy management (May 1966, Smart and Robinson 1991, May 2000, Iland et al. 2011). The initiation and development of IP are also regulated by the interaction of endogenous hormones; gibberellins and cytokinins (Srinivasan and Mullins 1980, Mullins et al. 1992).

Canopy management can influence development of IP mainly through changing the light environment of the renewal zone, which has a positive correlation with IP number and size and hence bud fruitfulness (Kliewer and Smart 1989, Smart and Robinson 1991, Zabadal and Dittmer 1998, Dry 2000, Sánchez and Dokoozlian 2005). Bud fruitfulness may be improved by light through its effect on photosynthesis and subsequent carbohydrate availability or through a direct effect on the bud itself (Vasconcelos et al. 2009, Li-Mallet et al. 2016). Shoot placement can also be modified by trellis-training to affect the development of IP, with vertical shoots resulting in more IP than horizontal shoots (May 1966).

The level of carbohydrate status during budburst stage can have an impact on the extent of IP development for next season's crop (May 1965, Buttrose 1966b, Smith and Holzapfel 2009). The carbohydrate reserves in canes, cordons, roots and trunk are stored in the preceding season and utilized for the development of new shoots in early spring (Winkler et al. 1974, Bennett et al. 2005). At this stage, these woody organs are source and the compound buds are sinks for carbon and nutrients (Dry and Coombe

2004, Keller 2015c). Nevertheless, the bud is a weak sink compared with other sinks such as actively growing shoot tips, young leaves and inflorescences (Candolfi-Vasconcelos and Koblet 1990), hence the IP initiation and differentiation can be suppressed by limiting carbon reserves.

The influence of light on bud fruitfulness has been studied by comparing duration of solar radiation sourced from weather station and by applying illumination or shading on vines (Baldwin 1964, May 1965, Buttrose 1969, Perez and Kliewer 1990, Sánchez and Dokoozlian 2005). The results showed that there is a direct correlation of light intensity and bud fruitfulness and the effect of light is independent of temperature (Buttrose 1974a). Fruitfulness was reduced in response to shading, especially applied at late spring (Smart et al. 1982, Morgan et al. 1985). In contrast, both number and size of IP in the primary bud increased in proportion to light intensity (Buttrose 1969). However, for secondary buds, fruitfulness is only improved in number and the size remained small under the light treatment (Buttrose 1969). It was also found that shoot exposure has a significant effect on bud fruitfulness, while light interception at the bud zone is not correlated with its particular fruitfulness, indicating an increased photosynthetic capacity of the exposed shoots improves fruitfulness (Kliewer 1982, Sánchez and Dokoozlian 2005).

2.4 Bunch architecture and Botrytis

2.4.1 Inflorescence/Bunch architecture

Botanically, the grapevine inflorescence is regarded as a panicle (Pratt 1971). The architecture or morphology of an inflorescence and the subsequent bunch are characterized by its conical structure due to multiple branching (Lebon et al. 2008, Vasconcelos et al. 2009). Bunch architecture varies among different varieties and can be an important phenotypic trait for grapevine breeding (This et al. 2006). The inflorescence/bunch architecture is influenced by: IP development that determines branching level (Li-Mallet et al. 2016); fruitset that affects final number of berries in the bunch (May 2004); the elongation of the rachis; and berry growth (May 2000, Tello et al. 2015).

The visual volume of grape bunch can be estimated as the morphological volume of a standard cone, where length is the maximum bunch length, and radius is half of the widest bunch width (Shavrukov et al. 2003). The bunch openness or compactness can be measured by the difference of actual volume and visual volume of the bunch as it represents the free space between berries (Shavrukov et al. 2003). Different morphological parameters that determine bunch architecture have been studied for their importance for the variation of bunch compactness (Vail and Marois 1991, Valdés-Gómez et al. 2008, Molitor et al. 2012, Palliotti et al. 2012, Tello et al. 2015). A study by Tello et al. (2015) found that two most influencing factors are total berry number and length of the first ramification of the rachis. In contrast, Shavrukov et al. (2003) found that rachis internode length is a major parameter determining bunch compactness and it is mostly associated with cell expansion, rather than cell division, in the loose bunch varieties.

2.4.2 Bunch compactness and bunch rot

Bunch compactness, also known as bunch density, refers to the distribution of berries inside a bunch and the portion of free space between berries (Tello and Ibáñez 2018). Structural components of a bunch that define bunch compactness include the number and size of berries (Poni et al. 2008, Vartholomaïou et al. 2008), bunch length (Molitor et al. 2012, Tello et al. 2015), pedicel length (Sarooshi 1977) and bunch weight (Valdés-Gómez et al. 2008).

Bunch compactness has been considered an important parameter of grapevine as it closely relates to disease control (Marois et al. 1986, Jackson and Lombard 1993, Hed et al. 2009, Tello et al. 2015). Compact bunches tend to have higher susceptibility of diseases such as botrytis bunch rot, which is caused by the fungus *Botrytis cinerea* (Vail and Marois 1991, Hed et al. 2009, Intrigliolo et al. 2014). The high disease susceptibility of compact bunches is due to poor air circulation and sun exposure of the inner parts of the bunch (Vail and Marois 1991, Molitor et al. 2012), the physical damage from contact of berries (Hed et al. 2009), inefficiency of chemical spraying (Molitor et al. 2012) and the formation of micro-cracks in the cuticle (Becker and Knoche 2012). For berry composition, the interior berries within the compact bunch may not receive enough solar irradiation to achieve an adequate phenolic maturity,

resulting in a heterogeneous ripeness of the bunch (Vail and Marois 1991, Figueiredo-González et al. 2013, Tello and Ibáñez 2018).

Botrytis bunch rot can substantially lower harvest yield, reduce the quality of the final wines and cause economic damage (Schildberger et al. 2011, Tello and Ibáñez 2018). Yield loss can be caused by rotting inflorescences or by rotting and desiccation of berries (Emmett and Nair 1991). Moreover, *Botrytis cinerea* can adversely influence berry composition, fermentation, protein stability of wine and increase oxidative breakdown of red wines by laccase activity (Somers 1984).

Canopy management such as early shading and leaf removal has been used to reduce bunch compactness (Poni et al. 2004, Lohitnavy et al. 2010, Sabbatini and Howell 2010, Intrigliolo et al. 2014, Basile et al. 2015). Other treatments that could lead to a reduction of botrytis bunch rot by reducing bunch compactness include the application of gibberellic acid at flowering (Weaver et al. 1962) and bunch thinning (Barbetti 1980). However, a yield reduction is caused by these treatments as fruitset or bunch number is decreased (Shavrukov et al. 2003). This needs to be taken into account when applying canopy management practices in the vineyard.

2.5 Canopy management

Grapevine canopy refers to the above ground parts of a vine that comprises shoots, leaves, fruits, cordon or canes, and trunk (Smart and Robinson 1991). Canopy management involves a range of techniques including dormant pruning, trellis-training systems, shoot positioning, shoot orientation, shoot trimming, leaf removal, bunch removal, control of shoot number and spacing, and control of shoot vigour (Smart and Robinson 1991, Dry 2000, Vasconcelos and Castagnoli 2000). These techniques result in an altered amount or position of leaves, shoots and fruit of grapevines to achieve a desired arrangement (Iland et al. 2011). Canopy management can be beneficial to grapevines and improve canopy structure and microclimate (Smart et al. 1990, Vasconcelos and Castagnoli 2000), control vine vigour and capacity (Bravdo et al. 1985), and alter the balance between vegetative and reproductive growth (Bravdo et al. 1984, Reynolds et al. 1995). The effect of canopy management is not limited to the current season but will cyclically influence future

seasons as well. The ultimate aims of grapevine canopy management are to optimize yield, improve fruit quality, decrease pests and diseases, and facilitate other vineyard operations (Kliewer 1982, Smart et al. 1990, Coombe and Dry 1992).

2.5.1 Winter pruning

Pruning is defined as the removal of vegetative parts of a vine including living shoots, canes and leaves (Winkler et al. 1974). Winter pruning is conducted during dormancy and it sets the potential yield, shoot number and density, and canopy shape and size for the next growing season. It is the most important practice in the annual cycle as it is often the sole means of adjusting the crop production level and it determines the manageable structure of the vine (Zabadal et al. 2002, Khamis et al. 2017). Manual pruning is the most labour-consuming and expensive vineyard management practice after harvest (Coombe and Dry 1992, Clingeleffer 1993). The aim of pruning is to retain the appropriate number and density of buds and achieve a balance between yield and vegetative growth in the following season (Partridge 1925, Winkler et al. 1974, Jackson and Lombard 1993).

Cane pruning and spur pruning are two common types of winter pruning. Cane pruning is preferable for varieties that have low fruitfulness in the basal buds, which are the fruiting units of spur-pruned vines. Cane pruning utilises long bearers (canes) of about 8 - 20 nodes and is sometimes accompanied by two-node replacement spurs (Coombe and Dry 1992). For spur pruning two-node spurs are more commonly the bearing units. At pruning, the distal node and shoot is removed and the shoot at the proximal node is retained to become the new two-node spur (Coombe and Dry 1992). Bud numbers can also be increased by leaving more than two nodes in spur pruning, such as long spurs (four to six nodes) that has been successfully used in Sultana (May et al. 1982).

The level of pruning influences canopy architecture and vine vigour (Clingeleffer 1993, Miller et al. 1993, Miller et al. 1996a). Severe pruning can result in vigorous growth to compensate for the reduced number of shoots per vine (Smart et al. 1990, Downton and Grant 1992), while light pruning can reduce vine vigour because of a greater number of shoots (Winkler et al. 1974, Weaver 1976). The pruning level also affects grapevine reproductive performance in a manner similar to vegetative growth.

Severe pruning reduces yield by reducing retaining bud number (Shaulis and Oberle 1948, Kimball and Shaulis 1958) but bunch weight, berry number per bunch and berry weight are increased (Sommer and Clingeffer 1993). Conversely, light pruning increases yield through an increased bunch number but bunches are smaller and less compact (Reynolds et al. 1994b, Ashley 2004), with reduced bunch weight, less berry number per bunch and reduced berry weight (Kimball and Shaulis 1958, Smart et al. 1982, Miller et al. 1996b, Bindon et al. 2008). The reduced bunch and berry weight may be due to increased partitioning of carbohydrates between more reproductive sinks. However, in the future seasons lightly pruned vines may yield less than severely pruned vines (Morris et al. 1984, Howell et al. 1987). This is because light pruning leads to a greater shoot number and can cause a denser canopy (Winkler 1958, Sommer and Clingeffer 1996, Smithyman et al. 1997, Miller and Howell 1998). Consequently, bud fruitfulness is reduced as the result of poor light penetration into the canopy and/or photoassimilate distribution (May et al. 1969, Koblet et al. 1994, Petrie et al. 2000b). Pruning level also has an impact on berry ripening. For example, delayed maturity and reduced sugar levels in berries were found in minimally pruned Chancellor vines due to increased yield levels (Reynolds and Wardle 2001).

2.5.2 Shoot thinning

While winter pruning is the primary tool used by grape growers to maintain vine structure, canopy architecture and regulate crop level, shoot thinning refines the ratio of leaves to fruits for a better balance between vegetative and reproductive growth. It is considered that high shoot density will lead to excessive leaf and bunch shading (Iland et al. 2011). Shoot thinning can be an effective mean of controlling shoot numbers and spacing. It reduces the canopy density and improves the microclimate resulting in greater exposure of shoots and bunches to sunlight (Smart and Robinson 1991, Coombe and Dry 1992). Other benefits of shoot thinning include maintaining vine shape, keeping consistency in fruit production and quality, and facilitating other vineyard operations such as spraying and thus reducing pests and diseases (Hoare 2009). On the down side, shoot thinning normally results in some yield loss because bunches are lost when shoots are removed, but this can be avoided or mitigated by selectively removing the shoots that are not or less fruitful (Iland et al. 2011). Shoot

thinning also helps to avoid short shoots that produce an under-ripe crop, since they have a low leaf area to fruit ratio (Smart and Robinson 1991).

Shoot thinning has an impact on vegetative growth, but the timing is critical for the effects (Reynolds et al. 2005). When applied early in the season such as around flowering, the removal of shoots reduces competition between shoots within the vine for carbohydrate reserves and nutrients when leaves are not fully capable of photosynthesizing to support the shoot growth (Keller 2015c). In this regard, shoot thinning often leads to compensatory growth of the remaining shoots. Severe shoot removal can also induce growth of lateral shoots. It was reported by Bernizzoni et al. (2011) that the total leaf area per vine is similar in thinned and non-thinned vines. However, the high vigour caused by shoot thinning can result in problems with reallocation of resources to vegetative rather than reproductive growth (Archer and Strauss 1990, Perez and Kliewer 1990) and bud productivity due to shading (Wolf 2002). Severe shoot thinning could also increase the incidence of PBN and hence lower bud fruitfulness (Dry 2000).

In terms of yield components, results have been found that shoot thinning collectively increased bunch weight, berry weight and berry number but yield was overall reduced due to lower bunch numbers (Morris et al. 2004, Sun et al. 2011, Sun et al. 2012, Jogaiah et al. 2013). Conversely, Reynolds et al. (2005) observed that shoot thinning had relatively minor impacts on yield components and Naor et al. (2002) reported that the number of shoots per vine did not influence berry weight.

Shoot thinning also affects berry maturity rate and composition by laying the foundation for the fruit zone microclimate during ripening, especially with regard to light interception. Reynolds et al. (1996) found that vines with 10 to 15 shoots per metre had fruit with higher total soluble solids (TSS), anthocyanins, pH and titratable acidity (TA) compared to higher shoot densities where shading likely contributed to lower fruit quality. Reduced TA and increased TSS were also found by Naor et al. (2002) and Reynolds et al. (2005). However, Morris et al. (2004) reported that shoot thinning did not affect TSS, pH, or TA.

2.5.3 Bunch thinning

Bunch thinning is a practice used to precisely regulate yield and reduce crop load in order to improve fruit maturity and quality through increasing the leaf area to fruit ratio (Weaver and McCune 1960, Intrigliolo and Castel 2011, Santesteban et al. 2011). It can be conducted from pre-flowering (thinning of inflorescence) to veraison, normally by eliminating the distal bunch/inflorescence on the shoot (Wolpert et al. 1983). In commercial vineyards it is most commonly done around veraison, when it is able to estimate final yield and visually assess the bunch colour and morphology. The unfavourable bunches that with berries underdeveloped or unevenly developed can be removed to decrease the variability within the fruit.

The impact of bunch thinning on vegetative and reproductive growth depends on the intensity and timing of the practice. When applied early in the season (before veraison), shoot growth can be stimulated due to less competition from bunches that serve as sinks for carbohydrates and nutrients (Fisher et al. 1977, Poni et al. 1993, Naor et al. 2002). However, in a study by Smithyman et al. (1998) there was no influence of bunch thinning on leaf area, pruning weight or shoot development when applied during anthesis. When bunches are removed late in the season (around veraison), the effect on vegetative growth is minor or nil (Freeman et al. 1979, Reynolds et al. 1994a, Valdés et al. 2009), but fruit ripening can be accelerated indicated by increasing TSS (Palliotti and Cartechini 1998, Keller et al. 2004, Nuzzo and Matthews 2006, Reynolds et al. 2007, Preszler et al. 2013).

In regard to reproductive performance, bud fertility and bud cold hardiness is unaffected (Palliotti and Cartechini 1998, Preszler et al. 2013), and fruitset can be improved by inflorescence removal through increasing available reserves to the remaining flowers (Smithyman et al. 1998, Lebon et al. 2008) and increased pollen viability (Winkler 1958). Yield loss by bunch thinning is not proportional to the thinning intensity as the individual berry weight can be compensated to significantly increase bunch weight (Reynolds et al. 1994b, Reynolds et al. 2007, Sun et al. 2012, Gil et al. 2013). Conversely, other studies did not show evidence of berry weight increase regardless of timing of application of the treatment (Guidoni et al. 2002, Keller et al. 2005, Reynolds et al. 2005, Santesteban et al. 2011, Preszler et al. 2013).

Contrasting results have been found by studies investigating the effect of bunch thinning on fruit and wine composition. Generally, anthocyanins and polyphenols are increased (Palliotti and Cartechini 1998, Keller et al. 2005, Nuzzo and Matthews 2006) and also total nitrogen and terpenes (Palliotti and Cartechini 1998, Reynolds et al. 2007), but results can be variable for pH and TA (Nuzzo and Matthews 2006, Intrigliolo and Castel 2011, Preszler et al. 2013).

2.5.4 Leaf removal

Leaf removal is used often for high-density canopies. It is generally imposed around the fruiting zone in order to improve light exposure and air circulation for better fruit composition, improving spray penetration and coverage, and reducing the risk of disease (Smart 1985, Arnold and Bledsoe 1990, Hunter et al. 1991, Reynolds et al. 1996, Staff et al. 1997, Poni et al. 2006, Iland et al. 2011). Specific outcomes of leaf removal depend on the timing and severity, as well as varieties, rootstock and climate (Bledsoe et al. 1988, Candolfi-Vasconcelos et al. 1994, Poni et al. 2006, Bavaresco et al. 2008, Tardaguila et al. 2008).

Leaf removal is associated with the modification of the source-sink relationship. Early defoliation such as applied before flowering reduces the leaf area available for photo-assimilation (Candolfi-Vasconcelos et al. 1994, Petrie et al. 2000a, Howell 2001) and can cause a carbohydrate shortage for berry development (Palliotti et al. 2011). At this stage the basal leaves are the main source for flowering and fruitset, their removal could lead to less compact bunches with fewer and smaller berries (Bledsoe et al. 1988, Poni et al. 2004, Poni et al. 2006, Intrieri et al. 2008, Diago et al. 2010, Lohitnavy et al. 2010). Therefore, this approach could potentially be very useful in high-yielding situations and for grape varieties characterized by large, excessively compact bunches which increase the risk of *Botrytis* bunch rot, and it can also avoid the need for bunch thinning later in the season (Poni et al. 2006).

Although the growth of lateral foliage can be simulated and the function of the remaining leaves can be enhanced by leaf removal (Hunter and Visser 1988, Candolfi-Vasconcelos and Koblet 1991, Petrie et al. 2000a, Poni et al. 2008), the treatment may have a negative effect on vine growth and reproductive performance

(May et al. 1969, Kliewer and Antcliff 1970, Hunter and Visser 1990, Petrie et al. 2003). The lack of carbohydrates from early leaf removal can affect crop production in the subsequent year through an adverse impact on bud initiation and development that leads to lower fruitfulness (Bennett et al. 2005, Smith and Holzzapfel 2009, Basile et al. 2015, Noyce et al. 2016b). In contrast, late defoliation (around veraison) has less effect on yield components (Bledsoe et al. 1988, Hunter and Visser 1990, Smithyman et al. 1998, Vasconcelos and Castagnoli 2000, Frioni et al. 2017) and bud fruitfulness (Koblet 1986, Zoecklein et al. 1992).

Leaf removal around veraison can affect primary and secondary metabolite synthesis in berries (Hunter and Visser 1988, Zoecklein et al. 1992, Zoecklein et al. 1998). Modified bunch microclimate by leaf removal is largely attributed to increased berry temperature and quantity and quality of light (Smart et al. 1988, Dokoozlian and Kliewer 1995, Dokoozlian and Kliewer 1996). Berry composition can be influenced such as increasing sugar level and flavonoids, decreasing malic acid concentration, and increasing anthocyanins in red grape varieties (Kliewer and Lider 1968, Zoecklein et al. 1992, Percival et al. 1994, Reynolds et al. 1994b, Zoecklein et al. 1998, Haselgrove et al. 2000, Poni et al. 2006). However, berry quality and colour can decrease with greater exposure leading to higher temperatures and light intensity, in some cases leading to sunburn in hot climate (Tarara et al. 2008, Chorti et al. 2010, Sabbatini and Howell 2010, Ristic et al. 2013). In this regard applying leaf removal needs to be considered carefully in hot, dry and sunny regions.

Besides the bunch zone, leaf removal has also been conducted at other positions such as the upper canopy or from lateral shoots (Poni et al. 2013, Caccavello et al. 2017). The positions of leaves in the canopy can affect leaf age and exposure to light, and hence determine their photosynthetic efficiency (Hunter and Visser 1988, Candolfi-Vasconcelos and Koblet 1991, Poni et al. 1994a, Poni and Giachino 2000). At later stages in the season, bunch zone leaves are the oldest and can be less effective at photosynthesizing than mid-canopy leaves or leaves on lateral shoots (Hunter and Visser 1988, Poni et al. 1994a, Petrie et al. 2000a). Removal of mid-canopy leaves has been used to delay berry ripening (Palliotti et al. 2013, Poni et al. 2013).

2.6 Summary

A typical trait of grapevine's reproduction system, as with other perennial woody species, is that it requires two consecutive seasons for fruit production (Keller 2015b). One reproductive growth cycle comprises bud initiation and development, flower and inflorescence development, flowering, fruitset, and berry development (Mullins et al. 1992, Iland et al. 2011). The growth and development of a grapevine is regulated by the genetic, environmental and cultural factors. Canopy management is the most direct human intervention in the vineyard and it plays a key role in wine grape cultivation for seasonally sustainable production. It includes a series of techniques that have been developed with an aim of improving canopy structure to optimize total photosynthesis, reach a balance between vegetative and reproductive growth, and obtain sufficient sunlight exposure of fruit (Kliewer and Smart 1989, Smart and Robinson 1991, Vasconcelos and Castagnoli 2000).

Research has been conducted around the world's viticulture regions to determine how canopy management practices affect vine growth and fruit quality, but results vary considerably between locations due to soil type, climate, season and other environmental conditions. The timing and intensity of applied practices, along with differences in varieties and vine age, can also vary the response of grapevines to a large extent. There are still many unknowns for the applicability and validity of these practices to grapevine reproductive performance including yield components and bunch architecture. Particularly, the impact on bud fruitfulness, which we know is impacted by microclimate (Dry 2000, Sánchez and Dokoozlian 2005), has not been well studied in terms of commonly adopted practices including light pruning, shoot thinning, leaf removal and bunch removal. Moreover, the application of canopy management techniques in Australia can be expensive, especially when conducted by hand. An increase in grape and wine quality to a certain level is expected to justify the application of the practices. It is therefore essential for the wine industry to have a solid understanding of the effects of different canopy management practices on reproductive performance of grapevines.

Chapter 3: Prepared Manuscript:

Influence of Canopy Management Practices on Canopy Architecture and Reproductive Performance of Semillon and Shiraz Grapevines in a Hot Climate

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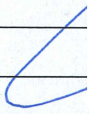
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Short title: Canopy Management Effects on Reproductive Performance

Influence of Canopy Management Practices on Canopy Architecture and Reproductive Performance of Semillon and Shiraz Grapevines in a Hot Climate

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Abstract: Canopy management practices are used to improve canopy structure and microclimate which can influence reproductive development. In this study the influence of different canopy management practices: cluster thinning, leaf removal, shoot thinning and light pruning on reproductive performance was studied for the varieties Semillon and Shiraz grown under field conditions in a hot climate in South Australia. Canopy architecture, canopy light interception and reproductive parameters for different management practices were measured. Results showed that some of the applied practices modified canopy architecture, affected reproductive performance and the berry ripening process. Specifically, shoot thinning and leaf removal decreased leaf area index (LAI) and increased canopy porosity and light interception. Berry ripening was advanced by cluster thinning and shoot thinning, while leaf removal and light pruning delayed the process. For reproductive parameters, leaf removal had a relatively minor impact; shoot thinning and cluster thinning increased cluster volume; and light pruning decreased berry weight. In addition, cluster compactness was found to be increased by shoot thinning and was positively correlated with bunch rot (*Botrytis cinerea*) incidence in Semillon.

Key words: leaf area index (LAI), microclimate, yield components, berry maturation, cluster architecture

Introduction

Canopy management practices are widely adopted in commercial vineyards to optimize vine productivity. A range of techniques, such as dormant pruning, shoot positioning, shoot thinning, leaf removal, cluster thinning, and trellising are used to achieve a balance between vegetative growth and reproductive performance, and hence improve final yield and/or crop quality (Smart and Robinson 1991, Vasconcelos and Castagnoli 2000). These practices change vine vigor and influence vine physiology by altering the source-sink ratio as well as

canopy microclimate (light quantity and quality, aeration, air temperature and humidity) (Smart 1985). Given the complexity of grapevine physiology, the reproductive performance response to different cultural practices can vary to a large extent. Canopy management therefore needs to be applied with thorough consideration to reach targeted yield and/or quality while minimizing cost (Hunter 2000). Therefore, understanding the effect of different practices on grapevine reproduction is essential.

Canopy management practices alter the distribution and amount of leaves and shoots to optimize the surrounding conditions of clusters for better yield and fruit composition (Smart 1985). One of the most significant microclimate parameters that affect cluster development is light interception within the canopy (Dokoozlian and Kliewer 1996) and it has been studied for decades by researchers particularly in regards to the influence on yield components and wine quality (Smart 1985, Frioni et al. 2017). Fruit quality is influenced by microclimate as berries which develop in shaded and exposed canopy conditions have different fruit composition, such as total soluble solids (TSS, Brix), pH and titratable acidity (TA) (Haselgrove et al. 2000, Downey et al. 2006, Jogaiah et al. 2013).

Previous research has been conducted on the effects of canopy management practices on yield components with varying results. Light pruning generally increased yield to a certain point (Smart et al. 1982) and it was found to decrease berry size (Bindon et al. 2008). Shoot thinning collectively increased cluster weight, berry weight and berry number but reduced yield by a decrease in cluster number (Sun et al. 2012, Jogaiah et al. 2013). Conversely, Reynolds et al. (2005) observed that shoot thinning had relatively minor impacts on yield components and Naor et al. (2002) reported that the number of shoots per vine did not influence berry weight. Cluster removal was found to lower yield, while increasing cluster weight and berry number (Sun et al. 2012, Gil et al. 2013). Berry weight was reported to increase in some studies (Sun et al. 2012, Gil et al. 2013), but not in others (Santesteban et al. 2011). Leaf removal led to smaller, less compact clusters with fewer berries when applied early in the season (Lohitnavy et al. 2010, Intrigliolo et al. 2014). However, it was also found to have no influence on yield components when applied four weeks after bloom or at veraison (Vasconcelos and Castagnoli 2000, Frioni et al. 2017).

Cluster compactness is another key reproductive character of grapevines as it influences wine composition (Molitor et al. 2012) and is particularly important for disease control (Hed et al. 2009, Tello et al. 2015). Compact clusters tend to have higher susceptibility to diseases such as Botrytis bunch rot, which is caused by the fungus *Botrytis cinerea*, which can lead to reductions in quality and yield (Hed et al. 2009, Molitor et al. 2012, Intrigliolo et al. 2014).

Different parameters that determine cluster architecture have been studied for their influence on cluster compactness (Molitor et al. 2012, Tello et al. 2015). A study by Tello et al. (2015) found that the two most important parameters are the total berry number and the length of the first ramification of the rachis. Canopy management techniques such as early shading and leaf removal have been used to reduce cluster compactness (Lohitnavy et al. 2010, Intrigliolo et al. 2014, Basile et al. 2015). However, there is little information on whether canopy management practices increase cluster compactness as an undesirable outcome while other benefits of the practices are achieved.

In this study, common canopy management practices, including double nodes (light pruning), shoot thinning, leaf removal and cluster thinning, were applied to Semillon and Shiraz. The study aimed to investigate and compare the effects of these practices on canopy architecture and microclimate, yield components, cluster architecture and berry maturity.

Materials and Methods

Experimental design and treatments

The experiment was conducted in the Coombe vineyard at the Waite Campus of The University of Adelaide, South Australia (34°58' S; 138°38' E). Both Semillon (clone SA 32) and Shiraz (clone BVRC12) were planted in 1991. All vines are own-rooted, trained to a bilateral spur pruned cordon with the shoots vertically positioned. Vine spacing and row spacing is 1.8 m and 3.0 m respectively, with rows oriented north/south. The vineyard was irrigated with in-line drippers at a spacing of 0.6m and discharging at 2.0 L/h. The climate is classified as hot, and arid, moderately maritime (Smart and Dry 1980). The soil for this site is described as Dr2.23, a hard pedal red duplex soil (Litchfield 1951). Rainfall and temperature data during the growing seasons was obtained from the Kent Town (South Australia) weather station, located 5.5km from the experimental site (Australian Government Bureau of Meteorology, <http://www.bom.gov.au/climate/data/>). Heat accumulation was expressed as growing degree days (GDD) calculated with a base temperature of 10°C and a maximum mean temperature of 19°C (Gladstones 2011).

Five canopy management treatments were applied to Semillon grapevines for four growing seasons (2014/15, 2015/16, 2016/17 and 2017/18). The treatments were: 1) control (C), where no manipulation was conducted on the canopy; 2) double nodes (DN), which was applied at winter pruning by leaving two, two-node spurs at each spur position rather than one, as it is normally the case; 3) shoot thinning (ST), where 50% of the total number of shoots were

removed at E-L stage 15-17 (Coombe 1995); 4) cluster thinning (BT), by removing 50% of the total number of clusters at veraison (E-L stage 35) (Coombe 1995); and 5) leaf removal (LR), which was conducted at veraison (E-L stage 35) (Coombe 1995), by removing leaves from the middle third of the canopy according to Palliotti et al. 2013. Each treatment was replicated three times in blocks of three panels with each panel containing three vines. Measurements were conducted in the middle vine of each panel (nine vines were measured for each treatment). The data for this study was collected in the 2016/17 and 2017/18 growing seasons.

For Shiraz, five canopy management treatments were imposed on vines that were randomly distributed in the vineyard for two growing seasons (2016/17 and 2017/18). Each treatment contained nine replicates. The treatments were C, BT, LR and ST, which were conducted in the same way as described for Semillon. A different type of leaf removal (LR-B) was applied at veraison (E-L stage 35) (Coombe 1995) by removing 4-5 leaves on each shoot at the cluster zone. Only leaves on the east side of canopy were removed to prevent excessive exposure of grape clusters in the afternoon on the western side of the canopy.

Canopy architecture and light interception measures

Two canopy architecture parameters, leaf area index (LAI) and canopy porosity were measured using the cover photography method (Fuentes et al. 2014). Images were taken using an iPad 4 (Apple Inc., Cupertino, CA, USA) and analyzed using the VitiCanopy App, which is described by De Bei et al. (2016). For both seasons, measures were taken before and after the application of treatments for both varieties, except for the DN treatment, which was applied to Semillon during winter pruning.

Light interception was measured as the percentage of ambient light intensity intercepted by the canopy. Photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured inside and outside of the canopy using a Sunfleck PAR ceptometer (Decagon Devices, Pullman, WA, USA). The readings inside the canopy were taken directly above the cordon, within the cluster zone and parallel to the vine row. The ambient readings were taken outside and adjacent to the surface of the canopy, with the sensors facing upward in a zenith angle. The light interception (Li , %) was calculated as follows:

$$Li = \frac{PAR \text{ inside canopy}}{PAR \text{ ambient}} \times 100$$

Light measurements were taken on sunny days after the application of treatments for both seasons. The time of the measurement was at solar noon (1330 hr) for season one. In season two, three time points were assessed: morning (1000 hr), solar noon (1330 hr) and afternoon (1630 hr). The sensors on the ceptometer were faced towards the sun in a zenith angle at each time point.

Maturity measures

Berry maturity was measured weekly from veraison (E-L stage 35) (Coombe 1995) until harvest for both varieties. For each measurement, 50 berries per replicate and per treatment were randomly sampled. After measuring berry weight, the berries samples were crushed by hand in plastic bags to extract the juice. The juice was then centrifuged at 5000 rpm for five minutes (Hettich Universal, Germany) and used for the measurements of total soluble solids (TSS, Brix), pH and titratable acidity (TA, g/L). TSS was determined using a digital refractometer (BRX-242 Erma inc. Tokyo, Japan). TA and pH were determined by an autotitrator (G20S, Mettler-Toledo, Switzerland). Harvest was carried out when TSS reached approximately 21 Brix for Semillon and 26 Brix for Shiraz, based on typical commercial harvest levels.

Reproductive measures

At E-L stage 18-19 (Coombe 1995) four shoots per vine were randomly chosen and labeled. At harvest, grape clusters were collected from the labeled shoots and frozen at -20°C for further assessment. The cordon length of each vine was measured and total cluster number and yield for each vine were recorded and then calculated on a per meter basis.

Cluster weight, cluster length (recorded as distance from the uppermost to the lowest berry of the cluster (OIV 2009) and cluster width (recorded as maximum distance between the lateral berries (OIV 2009) were measured for the frozen cluster samples. All berries were then excised from the pedicel, rachis was weighed and the number of seeded berries, seedless berries (determined by dissection) and live green ovaries (LGOs) were counted respectively for each cluster. Millerandage Index (MI) (Collins and Dry 2009) was used to measure the proportion of seedless berries and LGOs as follows:

$$MI = 10 - \left(\frac{\text{no. of seeded berries per bunch} \times 10}{\text{no. of seeded berries per bunch} + \text{no. of seedless berries per bunch} + \text{no. of LGOs per bunch}} \right)$$

The morphological volume of each cluster was estimated as the volume of a cone (Shavrukov et al. 2004) using the following formula:

$$Volume = \frac{1}{3} \pi \times \left(\frac{width}{2} \right)^2 \times length$$

Other parameters were calculated as:

Total berry no. per bunch = no. of seeded berries per bunch + no. of seedless berries per bunch

$$Berry\ weight = \left(\frac{bunch\ weight - rachis\ weight}{total\ berry\ no.\ per\ bunch} \right)$$

Cluster compactness (BC) was assessed using two indices: BC1 (Basile et al. 2015) and BC2. BC2 is a novel index for cluster compactness and represents the density of berries in a cluster. These indices were calculated as follows:

$$BC1 = \frac{total\ no.\ of\ berries\ per\ bunch}{main\ rachis\ length}$$

$$BC2 = \frac{total\ no.\ of\ berries\ per\ bunch}{bunch\ volume}$$

For Semillon, the incidence of Botrytis on the clusters was observed in season one. The incidence was recorded as the percentage of infected clusters relative to all clusters collected for each replicate in each treatment.

Statistical analysis

Statistical analysis was performed using one-way and two-way analysis of variance (ANOVA) to assess whether there were significant differences between treatments for each reproductive parameter. Least significant difference (LSD) was applied at the 5% level ($p < 0.05$) for *post hoc* tests to assess differences between treatments. Pearson correlation was used to assess the relationship between cluster Botrytis incidence and cluster compactness (BC1 and BC2) for Semillon. All statistical analyses were performed using SPSS Statistics 24 (IBM, Chicago, IL, USA).

Results

Weather conditions

Weather conditions for the experimental vineyard during the two growing seasons (October to April) are summarized in Figure 1 and compared with the long-term average (previous 30 years). The 2016/17 was a wet season with the monthly rainfall being higher than long-term average, especially in October and December, which were 81mm and 86.8 mm respectively, compared to 40mm and 28.3mm for the long-term average. On the contrary, season 2017/18 was hotter and drier. Noticeably, from January to March, which was the period of veraison to harvest, the rainfall in 2017/18 was much less than the long-term average (Figure 1). As such the GDD were lower in 2016/17 (1771) compared to the long-term average (1805), while season 2017/18 had higher GDD (1856).

Effect of canopy management on canopy architecture

In both seasons, canopy architecture was assessed after the canopy management practices were applied, which are indicated by arrows in Figures 2 and 3. As expected, LAI gradually increased and the canopy porosity decreased during the growing season. Shoot trimming was conducted on all vines in each season around veraison as a routine vineyard practice to control vigor and its effects on canopy architecture are evident in the last time points of Figures 2 and 3 where LAI decreased and canopy porosity increased. Except for DN (applied at pruning), ST was the earliest treatment to be applied in season (E-L stage 15-17) and it reduced the LAI significantly for both varieties compared with C. However, the difference between ST and C decreased with the progressing of the growing season in both seasons (Figures 2 and 3), and no significant difference was found in LAI on Semillon after veraison in season 2017/18 (Figure 2C). Canopy porosity increased significantly after the ST treatment, however, no difference was observed after veraison for both varieties. LR and LR-B significantly decreases LAI only on Semillon in 2017/18 (Figure 2C) and on Shiraz in 2016/17 (Figure 3A). LR influenced canopy porosity only in Shiraz in season 2016/17 (Figure 3B). BT and DN did not impact canopy architecture, although for DN, there was a trend of higher LAI and lower canopy porosity in Semillon (Figure 2).

Effect of canopy management on light interception

For Semillon, ST and LR increased light interception significantly (Figure 4A). However, the increase in light caused by ST diminished by the last measurement, which was after veraison. Similarly, in Shiraz, ST, LR-B and LR also increased light interception after application and

no effect of ST and LR-B was observed at the last measurement (Figure 4B). DN and BT did not influence the light interception when measured during the season.

The results of the assessment of light interception for season 2017/18 are shown in Figure 5. ST showed the strongest effect on both Semillon and Shiraz at all time points. LR slightly increased light interception at 1330 hr for both varieties and at 1630 hr for Semillon. In Shiraz, LR-B also increased the canopy light condition at 1000 hr and 1330 hr (Figure 5D and E). This was as expected since LR-B was only applied on the eastern side, hence did not influence the afternoon light interception. No effect of DN and BT treatments were demonstrated in this season.

Effect of canopy management on berry maturation

For Semillon (Figure 6), berry weight and TSS were impacted most by BT. Compared with C, the growth of berries and sugar accumulation was accelerated by BT from veraison in season 2016/17, along with a reduction in TA. In the second season, BT had the same effect on TSS, had a greater berry weight, and increased pH significantly three weeks after veraison. ST showed similar but less influence on berry weight with a slight increase, and no impact on TSS, TA or pH. In season 2017/18, there was no significant effect of ST on berry maturation, but berry weight was slightly greater. Conversely, DN and LR were shown to slow down berry maturity. In both seasons, DN lowered TSS and berry weight, and LR reduced TSS. TA was increased by DN and LR, and pH was decreased by LR in season 2016/17. However, both of the treatments did not affect acidity in season 2017/18.

In Shiraz (Figure 7), BT showed similar but less effects on berry maturity than Semillon. TSS was significantly increased by BT, while berry weight was not influenced in both seasons. Additionally, BT lowered TA in season one and increased pH for both seasons. Unlike for Semillon, ST did not show much effect on maturity of Shiraz in both seasons. Both types of leaf removal had no influence on berry weight. On the other hand, LR-B lowered TSS in season one, and LR decreased TSS in both seasons. Leaf removal did not impact berry acidity significantly. The inconsistency shown in berry weight and pH in the last few measurements could be due to the rainfall during this period.

Effect of canopy management on reproductive performance

The results of reproductive measurements of Semillon in two seasons are summarized in Tables 1 and 2. Overall, the reproductive parameters were least affected by LR, which increased berry weight and MI in season 2016/17 (Table 1) and had no influence for all

parameters in season 2017/18 (Table 2). BT was the only treatment that significantly affected yield, reducing it by 40.5% in season 2016/17 and 31.9% in season 2017/18. Berry weight was increased by BT and hence so was cluster weight. Cluster architecture was modified by BT with clusters being longer in both seasons and having a larger volume in season 2017/18. Unexpectedly, ST did not lower the yield for both seasons, although 50% of shoots were removed at an early stage of the season and significantly lowered cluster number. Cluster weight was largely increased by ST through higher berry weight and berry number. For cluster architecture, cluster length was increased in the first season and both length and width were increased by ST in the second season, which led to a substantial increase in cluster volume. Contrary to BT and ST, DN increased cluster number per meter of cordon and slightly lowered cluster weight in both seasons. In season one, cluster volume was decreased with a shorter cluster width, and in season two there was no significant effect on cluster architecture measures.

In general, the effects of the treatments on the reproductive performance of Shiraz (Tables 3 and 4) were less pronounced than Semillon. Both types of leaf removal (LR-B and LR) did not impact significantly on the reproductive parameters and only changed the MI in season 2016/17. BT lowered cluster number and yield in both seasons and caused less yield reduction in season two (37.8%) than season one (52.7%). Cluster weight was not influenced by BT in season 2016/17 but was significantly increased in season 2017/18. For ST, cluster number was decreased by 39.7% in season one and 29.2% in season two, whereas yield was only reduced in season one, as in season two cluster weight was increased by ST and hence did not lower yield. There was no significant effect of treatments on cluster architecture in season 2016/17, and in season 2017/18 only ST increased cluster volume.

When assessing cluster compactness, no difference was observed among treatments on Shiraz in season 2016/17, and in season 2017/18 BC1 was increased by ST. The effects on cluster compactness of Semillon were larger. BC2 was increased by DN in both seasons. ST increased cluster compactness with higher BC1 and BC2 in season one, and higher BC1 in season two. Botrytis bunch rot was found in Semillon in season 2016/17. The incidence of cluster Botrytis (%) was calculated for each treatment as shown in Table 5. Compared with C, Botrytis bunch rot incidence was found to be much lower in BT (reduced by 36.1%), and higher in ST (increased by 19.9%). In the case of LR, it decreased the incidence of Botrytis bunch rot by 21%. The incidence of Botrytis bunch rot from season 2016/17 was plotted against both cluster compactness indices for each replicate of the treatments (Figure 8). Significant coefficients of correlation and of determination ($r = 0.8$; $R^2 = 0.64$ respectively) were found for the relationship between BC2 and the incidence of Botrytis bunch rot (%),

whereas no correlation was observed between BC1 and the incidence of Botrytis bunch rot ($R^2 = 0.02$).

Discussion

Canopy management practices are employed in commercial vineyards in order to benefit wine quality and/or yield through modifying the vine vigor and canopy microclimate (Smart 1985, Vasconcelos and Castagnoli 2000). The main objective of this study was to investigate how these practices influence the reproductive performance of grapevines. By altering the amount of leaves, shoots or clusters, the canopy management practices directly changed canopy architecture and vine microclimate. Reproductive performance, subsequently, was influenced by these changes and resulted in differences in berry maturity, yield components, cluster architecture and berry uniformity.

The canopies of both Semillon and Shiraz were more vigorous in season 2016/17 compared to 2017/18, supported by higher LAI and lower canopy porosity in the first season (Figures 2 and 3). This could be related to the variance of rainfall and temperature between the two seasons; the large amount of rainfall in season 2016/17 (Figure 1) may have led to the higher vine vigor observed in this season. For both seasons, the canopy management practices had significantly different effects on canopy architecture. However, the effects of ST on LAI and canopy porosity on Semillon diminished gradually as the season progressed and disappeared around veraison, indicating that there was a compensation effect on the growth of the leaves on the vines. This could be due to a larger leaf area on the remaining shoots or lateral shoot development. Previous research has found an increase in mean shoot leaf area after shoot removal (Naor et al. 2002, Reynolds et al. 2005). Conversely, there was no significant effect on canopy architecture by DN, which doubled the amount of shoots per vine but only slightly increased LAI and decreased canopy porosity. This could be attributed to less leaf area per shoot, which was observed by Myers et al. (2008), who reported a lower leaf area per shoot in vines with high shoot density compared to those with a low shoot density.

As shoots/leaves were removed from vines by ST and leaf removal, the canopy density was reduced and porosity was increased which allowed more sunlight penetration into the canopy. It is well established that in grapevine, fruit yield and composition depend largely upon the canopy light environment (Smart 1985, Dokoozlian and Kliewer 1996). Sunlight exposed berries tend to have higher total soluble solids and lower acidity than shaded berries (Jogaiah et al. 2013). However, in this study, both types of leaf removal were found to lower TSS in the berries, although canopy porosity and the light interception in the fruit zone were

increased. This suggests that other factors, such as the source-sink relationships, may have more influence on berry maturity than a change in the microclimate as presented in this study. Palliotti et al. (2013) and Frioni et al. (2017) also reported a slower TSS increase when leaf removal was applied at veraison, and suggested that this may be due to a lower photosynthetic leaf area caused by this treatment.

In Semillon, ST and BT advanced berry maturation, reflected by higher berry weight and faster sugar accumulation (Figure 6). This is in agreement with previous studies that investigated shoot thinning and cluster thinning applied at veraison (Naor et al. 2002, Reynolds et al. 2005, Sun et al. 2012, Gil et al. 2013). The source-sink relationship is known to play an important role in fruit composition (Kliewer and Dokoozlian 2005). A higher source-sink ratio (leaf/fruit) was found to speed up the accumulation of metabolites in berries (Frioni et al. 2017). As discussed above, ST induced higher LAI for individual shoots in Semillon, and hence increased the source-sink ratio. Likewise, BT doubled the source-sink ratio by removing half the amount of clusters on the shoots. The reduction in the number of sinks allows greater allocation of assimilates and reserves to the remaining fruit on the vines (Naor et al. 2002), hence BT led to higher berry weight and higher sugar content for both varieties in this study. On the other hand, DN delayed the berry ripening process by slowing down the sugar accumulation and increasing berry acidity (Figure 6). This response can be attributed to lower leaf/fruit ratio caused by light pruning (Naor et al. 2002, Bindon et al. 2008, Frioni et al. 2017). Even though the number of clusters was increased by leaving double amount of nodes (potential shoots) per vine (Tables 1 and 2), the DN treatment had very little effect on LAI and canopy porosity (Figure 2).

The yield components and cluster architecture under the canopy management treatments in the current study showed consistent results in most of the parameters in the two seasons (Tables 1-4). BT and ST reduced the number of clusters as expected but at the same time both treatments resulted in greater cluster weights, suggesting a compensation effect. Similar results were also reported in previous studies (Sun et al. 2012, Gil et al. 2013, Jogaiah et al. 2013). The increase in cluster weight by BT in the current study was achieved through higher berry weight, whereas ST not only increased individual berry weight, but also increased average berry number per cluster. Interestingly, the compensation effect of ST was large enough that statistically this treatment had the same yield as the control in Semillon for both seasons and in Shiraz for season 2017/18. The significant increase in berry number suggests that fruit set was improved by ST when applied before flowering, as the remaining carbohydrate reserves in the roots and trunk of vines were directed to fewer inflorescences.

This is supported by Vasconcelos and Castagnoli (2000), who found that treatments that increase carbohydrate availability to inflorescence could increase fruit set.

For both seasons, DN significantly increased cluster number but had no influence on yield (Tables 1 and 2), which is contrary to previous studies that found an increase in yield by light pruning (Smart et al. 1982). Berry weight was decreased by DN, which was also observed by Bindon et al. (2008). LR increased MI of Semillon in season 2016/17 but had no influence in season 2017/18. The value of MI quantifies the level of seedless berries and LGOs in all berries of a cluster (Collins and Dry 2009). In this study, there were no consistent changes in MI by the treatments in the two seasons, suggesting that the success of pollination and fertilization in a cluster relates more to factors other than canopy management.

The cluster volume of Semillon demonstrated the same trend as cluster weight with each treatment. It was increased by BT and ST, and decreased by DN. Cluster compactness, similarly, was increased by ST, and expressed a higher BC1 in both seasons. BT also increased BC1 in the second season and both ST and BT did not change BC2. It is interesting to find that DN increased BC2 for both seasons, but did not change BC1. The two cluster compactness indices produced different results. The incidence of Botrytis bunch rot is well known to closely relate to cluster compactness (Hed et al. 2009, Intrigliolo et al. 2014). The significant correlation between BC2 and the incidence of Botrytis bunch rot found in this study (Figure 8) suggests that BC2 may be a more reliable index to estimate cluster compactness. However, there was no Botrytis bunch rot found in season two, therefore further investigation is required.

It is particularly noteworthy that in this study the canopy management treatments had more impact on reproductive performance of Semillon than on Shiraz. The fact that the treatments had been imposed on Semillon vines for four seasons, while Shiraz vines were treated for only two seasons, may suggest that there is a carry-over effect of the treatments. It was also demonstrated that in the case of Shiraz, the treatments had greater effect on yield components and cluster architecture in season two than season one.

Despite the very different climatic conditions of the two seasons, the canopy management treatments had an effect on canopy architecture and significantly altered the source-sink relationship. Although the light interception of the canopy was changed by the treatments, it did not serve as a limiting factor for berry maturity and had no significant impact on reproductive performance. This is attributable to the climate of Adelaide, South Australia, where the mean January temperature is over 23°C and can be classified as a hot to very hot

climate according to Smart and Dry (1980). Canopy management practices that improve vine microclimate, such as shoot thinning and leaf removal, are more beneficial in cool viticulture regions where achieving optimal ripening can be challenging (Frioni et al. 2017).

Conclusion

In the two-year study, the canopy management practices effectively manipulated reproductive parameters of Semillon and Shiraz. Among the treatments, shoot thinning and leaf removal significantly altered grapevine canopy architecture by modifying leaf area and canopy porosity, and changed vine microclimate by increasing light interception. However, the source-sink (leaf/fruit) relationship seemed to be more functional than microclimate factors in regulating berry maturity in the hot climate situation. Cluster thinning and shoot thinning can lead to early ripening through the advancement of berry growth and sugar accumulation, whilst leaf removal and increasing the number of nodes at pruning (light pruning) delayed the harvest maturity. In addition, when cluster thinning and shoot thinning were applied, the expected yield differences were either not present or minimal, suggesting that the vine compensates through an increase in berry number and weight. The extent of this compensation increased when the same treatments were continuously applied for four seasons suggesting that there may be carry-over effects between seasons. Among all the treatments, shoot thinning had the greatest impact on cluster compactness and induced the highest incidence of Botrytis bunch rot for Semillon. Our results confirm findings from previous studies about the influence of canopy management practices on grapevine reproductive performance, and present novel information on their influence on cluster architecture.

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Tables

Table 1. Means of reproductive parameters of Semillon in response to different canopy management treatments (2016/17).

Table 2. Means of reproductive parameters of Semillon in response to different canopy management treatments (2017/18).

Table 3. Means of reproductive parameters of Shiraz in response to different canopy management treatments (2016/17).

Table 4. Means of reproductive parameters of Shiraz in response to different canopy management treatments (2017/18).

Table 5. Incidence of Semillon botrytis bunch rot for different canopy management treatments.

Table 1 Means of reproductive parameters of Semillon in response to different canopy management treatments (2016/17)

| Reproductive Measurements | Treatments ^a | | | | | Sig. ^b |
|--------------------------------------|-------------------------|----------|---------|----------|---------|-------------------|
| | C | BT | DN | LR | ST | |
| Yield per meter of cordon (kg) | 7.9 a | 4.7 b | 8.6 a | 7.0 a | 6.8 a | ** |
| Cluster no. per meter of cordon | 38.1 b | 18.0 c | 53.7 a | 32.1 b | 20.3 c | *** |
| Cluster no. per shoot | 2.06 a | 1.35 b | 2.00 a | 2.00 a | 2.18 a | *** |
| Cluster weight (g) | 288.2 bc | 364.4 a | 245.9 c | 302.1 b | 372.7 a | *** |
| Berry weight (g) | 1.43 c | 1.75 a | 1.36 c | 1.58 b | 1.58 b | *** |
| Average seed no. | 1.99 a | 1.98 a | 1.79 b | 1.95 a | 1.99 a | *** |
| No. of seeded berries per cluster | 163.0 b | 170.6 b | 149.0 b | 154.2 b | 201.1 a | *** |
| No. of seedless berries per cluster | 26.1 | 24.6 | 22.7 | 28.6 | 28.1 | ns |
| No. of LGOs ^c per cluster | 11.5 bc | 18.6 a | 10.3 c | 14.8 ab | 11.4 bc | ** |
| Total berry No. per cluster | 189.1 b | 195.2 b | 171.7 b | 182.8 b | 229.2 a | *** |
| MI ^d | 1.78 bc | 2.03 ab | 1.73 bc | 2.11 a | 1.59 c | *** |
| Cluster length (cm) | 15.0 b | 16.3 a | 14.4 b | 15.0 b | 16.1 a | *** |
| Cluster width (cm) | 10.3a | 10.4a | 9.4b | 10.0ab | 10.6a | ** |
| Cluster volume (cm ³) | 445.0 ab | 493.5 ab | 366.7 c | 419.7 bc | 508.4 a | ** |
| BC1 ^e | 12.42 b | 11.76 b | 11.63 b | 11.90 b | 14.00 a | ** |
| BC2 ^e | 0.47 b | 0.44 b | 0.52 a | 0.46 b | 0.49 ab | * |

^aTreatments: C, control; BT, cluster thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning.

Means with different letters within rows are significantly different by LSD test at 5% level.

^b*, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively. ns: not significant.

^cLGOs, live green ovaries.

^dMI, Millerandage Index.

^eBC1, cluster compactness index 1; BC2, cluster compactness index 2.

Table 2 Means of reproductive parameters of Semillon in response to different canopy management treatments (2017/18)

| Reproductive Measurements | Treatments ^a | | | | | Sig. ^b |
|--------------------------------------|-------------------------|---------|---------|---------|----------|-------------------|
| | C | BT | DN | LR | ST | |
| Yield per meter of cordon (kg) | 6.9 a | 4.7 b | 6.3 a | 5.3 ab | 6.4 a | * |
| Cluster no. per meter of cordon | 36.5 b | 22.0 c | 46.5 a | 36.8 b | 19.7 c | *** |
| Cluster no. per shoot | 1.89 ab | 1.94 a | 1.74 b | 1.97 a | 1.97 a | * |
| Cluster weight (g) | 177.9 b | 244.5 a | 168.0 b | 181.9 b | 281.4 a | *** |
| Berry weight (g) | 1.34 bc | 1.46 a | 1.30 c | 1.37 b | 1.55 a | *** |
| Average seed no. | 1.94 b | 1.86 bc | 1.79 c | 1.82 bc | 2.11 a | *** |
| No. of seeded berries per cluster | 108.3 b | 140.2 a | 104.3 b | 106.2 b | 150.6 a | *** |
| No. of seedless berries per cluster | 18.6 b | 20.8 ab | 15.2 b | 19.7 b | 26.9 a | * |
| No. of LGOs ^c per cluster | 10.6 ab | 12.6 a | 8.8 b | 10.0 b | 10.1 b | * |
| Total berry No. per cluster | 126.9 b | 160.9 a | 122.7 b | 125.9 b | 177.5 a | *** |
| MI ^d | 2.02 | 1.96 | 1.87 | 2.11 | 1.81 | ns |
| Cluster length (cm) | 12.5 b | 14.0 a | 11.7 b | 12.5 b | 13.9 a | *** |
| Cluster width (cm) | 9.0 bc | 9.7 ab | 8.5 b | 9.0 bc | 10.1 a | ** |
| Cluster volume (cm ³) | 297.2 b | 381.5 a | 267.5 b | 296.2 b | 409.4 a | *** |
| BC1 ^e | 9.64 c | 11.14 b | 9.97 bc | 9.52 c | 12.26 ab | *** |
| BC2 ^e | 0.44 b | 0.48 b | 0.62 a | 0.50 b | 0.46 b | *** |

^aTreatments: C, control; BT, cluster thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning.

Means with different letters within rows are significantly different by LSD test at 5% level.

^b*, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively. ns: not significant.

^cLGOs, live green ovaries.

^dMI, Millerandage Index.

^eBC1, cluster compactness index 1; BC2, cluster compactness index 2.

Table 3 Means of reproductive parameters of Shiraz in response to different canopy management treatments (2016/17)

| Reproductive Measurements | Treatments ^a | | | | | Sig. ^b |
|--------------------------------------|-------------------------|--------|--------|--------|---------|-------------------|
| | C | BT | LR-B | LR | ST | |
| Yield per meter of cordon (kg) | 5.5 a | 2.6 b | 5.7 a | 6.0 a | 3.8 b | *** |
| Cluster no. per meter of cordon | 29.7 a | 15.8 b | 28.9 a | 31.8 a | 17.9 b | *** |
| Cluster no. per shoot | 2.09 a | 1.26 b | 2.03 a | 2.06 a | 2.06 a | *** |
| Cluster weight (g) | 250.4 | 283.0 | 277.7 | 252.6 | 277.7 | ns |
| Berry weight (g) | 1.52 b | 2.28 a | 1.56 b | 1.43 b | 1.59 b | ** |
| Average seed no. | 1.75 b | 1.98 a | 1.80 b | 1.96 a | 1.99 a | *** |
| No. of seeded berries per cluster | 153.4 | 171.1 | 172.0 | 165.6 | 165.1 | ns |
| No. of seedless berries per cluster | 4.97 | 3.24 | 3.38 | 3.20 | 4.74 | ns |
| No. of LGOs ^c per cluster | 74.8 a | 77.0 a | 56.9 b | 58.1 b | 65.0 ab | * |
| Total berry No. per cluster | 158.4 | 174.3 | 175.33 | 168.7 | 169.8 | ns |
| MI ^d | 3.39 a | 3.24 b | 2.57 b | 2.76 b | 2.89 b | ** |
| Cluster length (cm) | 16.4 | 17.6 | 17.5 | 17.4 | 17.2 | ns |
| Cluster width (cm) | 9.7 | 10.1 | 9.9 | 9.6 | 9.4 | ns |
| Cluster volume (cm ³) | 455.3 | 535.3 | 504.1 | 464.7 | 450.0 | ns |
| BC1 ^e | 9.37 | 9.69 | 9.92 | 9.59 | 9.67 | ns |
| BC2 ^e | 0.44 | 0.40 | 0.45 | 0.44 | 0.47 | ns |

^aTreatments: C, control; BT, cluster thinning; LR-B, leaf removal at cluster zone; LR, leaf removal at middle third canopy; ST, shoot thinning. Means with different letters within rows are significantly different by LSD test at 5% level.

^b*, **, and *** indicate significance at $p \leq 0.05$, 0.01 , and 0.001 , respectively. ns: not significant.

^cLGOs, live green ovaries.

^dMI, Millerandage Index.

^eBC1, cluster compactness index 1; BC2, cluster compactness index 2.

Table 4 Means of reproductive parameters of Shiraz in response to different canopy management treatments (2017/18)

| Reproductive Measurements | Treatments ^a | | | | | Sig. ^b |
|--------------------------------------|-------------------------|----------|----------|----------|---------|-------------------|
| | C | BT | LR-B | LR | ST | |
| Yield per meter of cordon (kg) | 3.7 a | 2.3 b | 3.4 a | 2.8 ab | 2.8 ab | * |
| Cluster no. per meter of cordon | 28.1 a | 16.3 c | 24.3 ab | 21.9 abc | 19.9 bc | * |
| Cluster no. per shoot | 1.84 b | 1.97 ab | 2.00 ab | 2.00 ab | 2.06 a | * |
| Cluster weight (g) | 150.6 b | 179.8 a | 154.1 ab | 152.0 b | 180.5 a | * |
| Berry weight (g) | 1.36 | 1.41 | 1.34 | 1.31 | 1.39 | ns |
| Average seed no. | 1.86 | 1.90 | 1.86 | 1.91 | 1.95 | ns |
| No. of seeded berries per cluster | 100.9 | 118.7 | 102.9 | 106.0 | 111.2 | ns |
| No. of seedless berries per cluster | 4.1 b | 4.5 b | 7.3 b | 5.5 b | 17.4 a | *** |
| No. of LGOs ^c per cluster | 7.9 b | 7.8 b | 7.0 b | 8.5 b | 13.1 a | *** |
| Total berry No. per cluster | 104.9 b | 123.3 ab | 110.2 ab | 111.5 ab | 128.6 a | * |
| MI ^d | 1.18 b | 0.95 b | 1.18 b | 1.18 b | 2.07 a | *** |
| Cluster length (cm) | 15.3 | 16.2 | 15.1 | 15.3 | 15.3 | ns |
| Cluster width (cm) | 8.4 | 8.6 | 8.4 | 8.6 | 9.0 | ns |
| Cluster volume (cm ³) | 305.0 b | 356.4 ab | 318.8 b | 315.8 b | 396.9 a | * |
| BC1 ^e | 6.67 b | 7.42 ab | 7.00 b | 7.08 ab | 7.90 a | * |
| BC2 ^e | 0.37 | 0.41 | 0.41 | 0.38 | 0.42 | ns |

^aTreatments: C, control; BT, cluster thinning; LR-B, leaf removal at cluster zone; LR, leaf removal at middle third canopy; ST, shoot thinning. Means with different letters within rows are significantly different by LSD test at 5% level.

^b*, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively. ns: not significant.

^cLGOs, live green ovaries.

^dMI, Millerandage Index.

^eBC1, cluster compactness index 1; BC2, cluster compactness index 2.

| Table 5 Incidence of Semillon botrytis bunch rot for different canopy management treatments | | | | | |
|--|-------|------|-------|-------|-------|
| Treatments ^a | C | BT | DN | LR | ST |
| Bunch Botrytis incidence (%) | 13.04 | 8.33 | 13.43 | 10.29 | 15.63 |

^aTreatments: C, control; BT, cluster thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning.

Figures

Figure 1. Weather conditions for experimental vineyard in season 2016/17 and 2017/18, compared with the long-term average (previous 30 years). Monthly average temperature (°C) and rainfall (mm) were calculated from October to April.

Figure 2. Effects of different canopy management treatments (C, control; BT, cluster thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning) on Semillon canopy architecture (LAI, leaf area index; and canopy porosity) for season 2016/17 (**A** and **B**, respectively) and season 2017/18 (**C** and **D**, respectively). The time of the application of the treatments are indicated by arrows. *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

Figure 3. Effects of different canopy management treatments (C, control; BT, cluster thinning; LR-B, leaf removal at cluster zone; LR, leaf removal at middle third canopy; ST, shoot thinning) on Shiraz canopy architecture (LAI, leaf area index; and canopy porosity) for season 2016/17 (**A** and **B**, respectively) and season 2017/18 (**C** and **D**, respectively). The time of the application of the treatments are indicated by arrows. *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

Figure 4. Effects of different canopy management treatments (C, control; BT, cluster thinning; DN, double nodes; LR-B, leaf removal at cluster zone; LR, leaf removal at middle third canopy; ST, shoot thinning) on canopy light interception of Semillon (**A**) and Shiraz (**B**) for season 2016/17. The time of the application of the treatments are indicated by arrows. *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

Figure 5. Effects of different canopy management treatments (C, control; BT, cluster thinning; DN, double nodes; LR-B, leaf removal at cluster zone; LR, leaf removal at middle third canopy; ST, shoot thinning) on canopy LI (light interception) of Semillon (**A**, at 1000hr; **B**, at 1330 hr; **C**, at 1630 hr) and Shiraz (**D**, at 1000hr; **E**, at 1330 hr; **F**, at 1630 hr) for season 2017/18. The time of the application of the treatments are indicated by arrows. *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

Figure 6. Effects of different canopy management treatments (C, control; BT, cluster thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning) berry maturity (TSS, total soluble solids; BW, berry weight; TA, total acidity; and pH) of Semillon for season 2016/17 (**A**, **B**, **C**, and **D**) and season 2017/18 (**E**, **F**, **G** and **H**). *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

Figure 7. Effects of different canopy management treatments (C, control; BT, cluster thinning; LR-B, leaf removal at cluster zone; LR, leaf removal at middle third canopy; ST, shoot thinning) on berry maturity (TSS, total soluble solids; BW, berry weight; TA, total acidity; and pH) of Shiraz for season 2016/17 (**A**, **B**, **C**, and **D**) and season 2017/18 (**E**, **F**, **G** and **H**). *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

Figure 8. Correlation of Botrytis bunch rot incidence with BC1 (**A**) and BC2 (**B**) for Semillon in season 2016/17. BC1: cluster compactness index 1, calculated as ratio between the total number of berries per cluster and main rachis length (cm); BC2: cluster compactness index 2, calculated as ratio between the total number of berries per cluster and cluster volume (cm³); *: correlation is significant at $p \leq 0.05$.

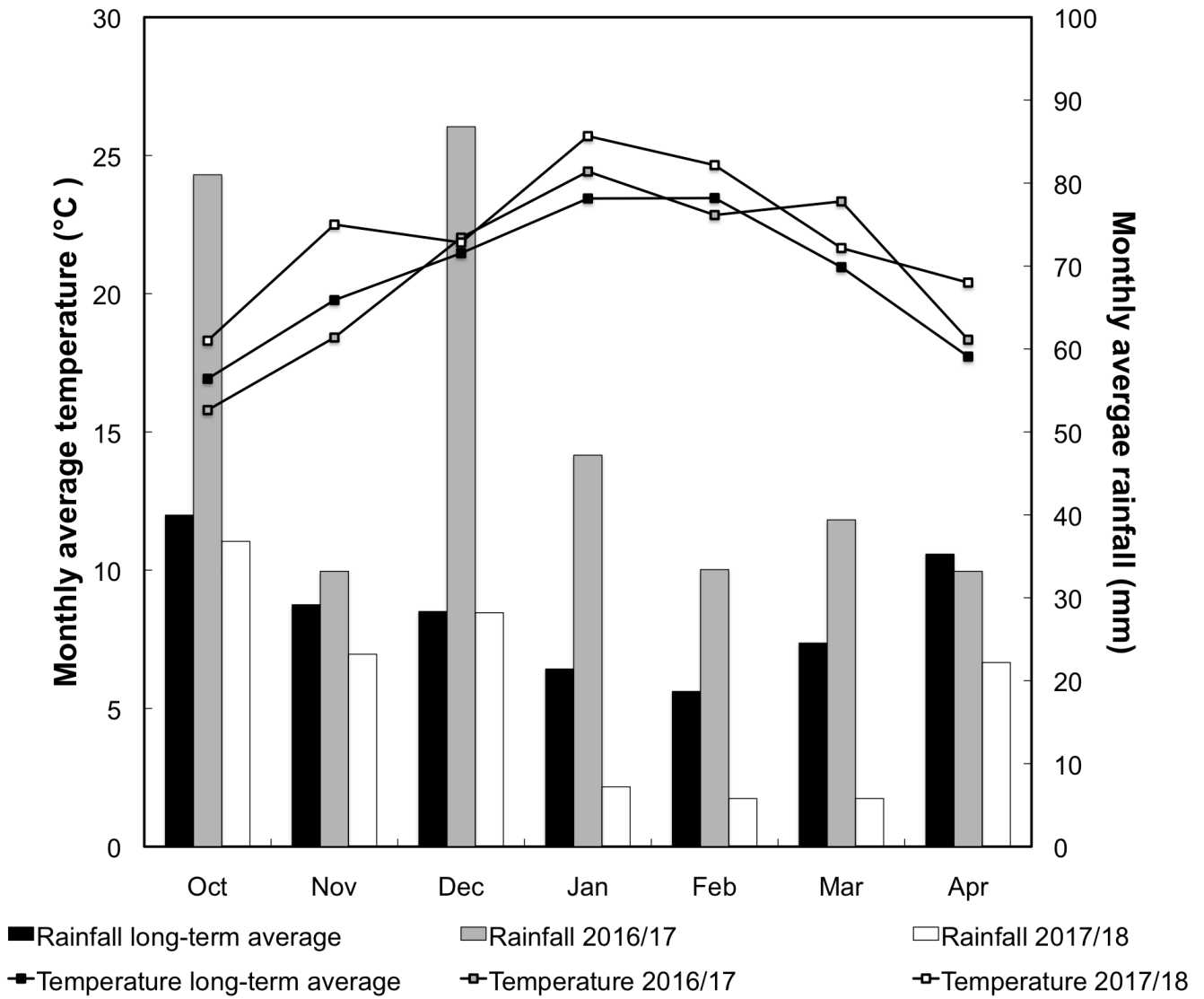


Figure 1 Weather conditions for experimental vineyard in season 2016/17 and 2017/18, compared with the long-term average (previous 30 years). Monthly average temperature (°C) and rainfall (mm) were calculated from October to April.

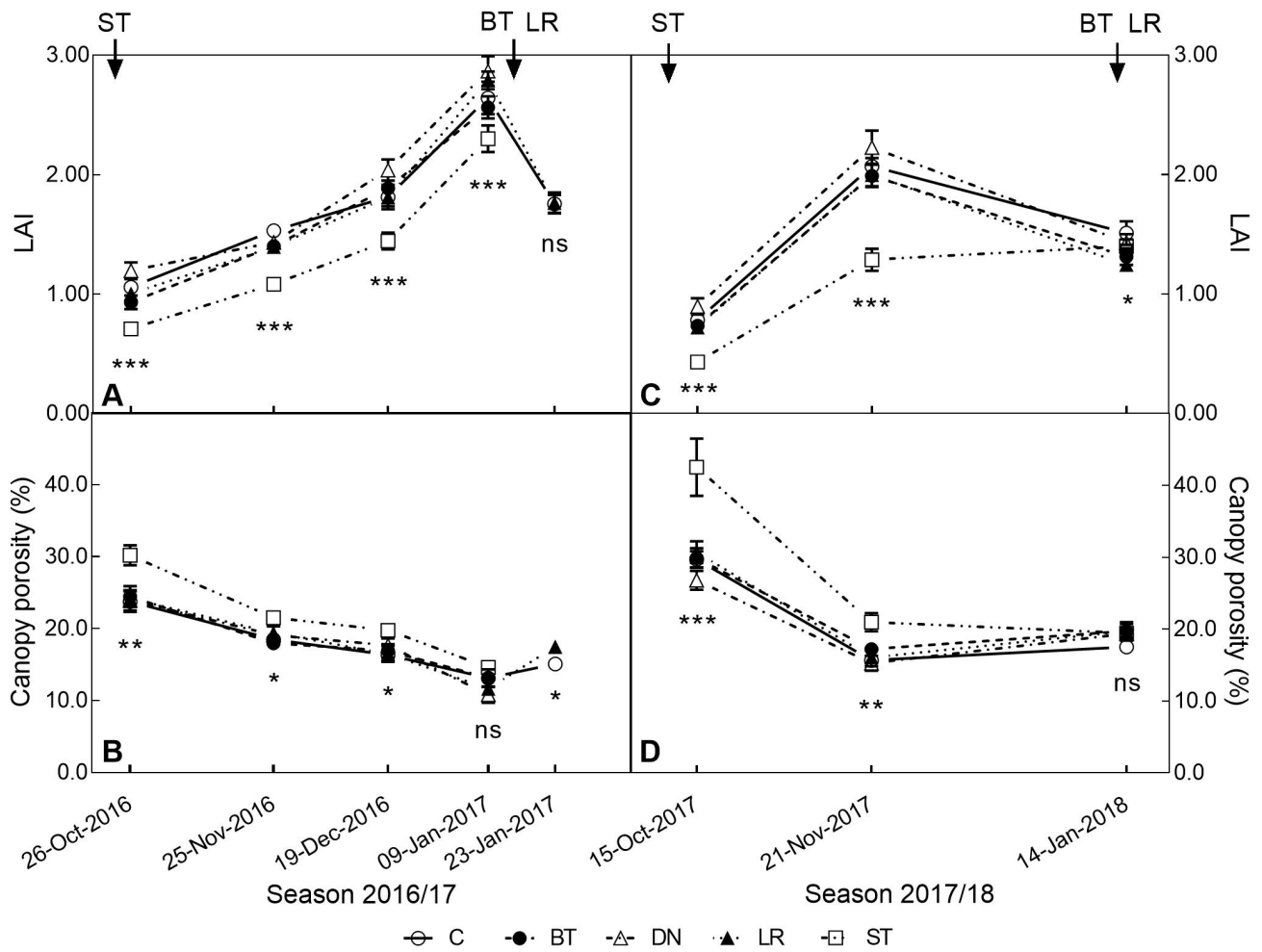


Figure 2 Effects of different canopy management treatments (C, control; BT, cluster thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning) on Semillon canopy architecture (LAI, leaf area index; and canopy porosity) for season 2016/17 (**A** and **B**, respectively) and season 2017/18 (**C** and **D**, respectively). The time of the application of the treatments are indicated by arrows. *, **, and *** indicate significance at $p \leq 0.05$, 0.01 , and 0.001 , respectively, ns: not significant, by LSD test at 5% level.

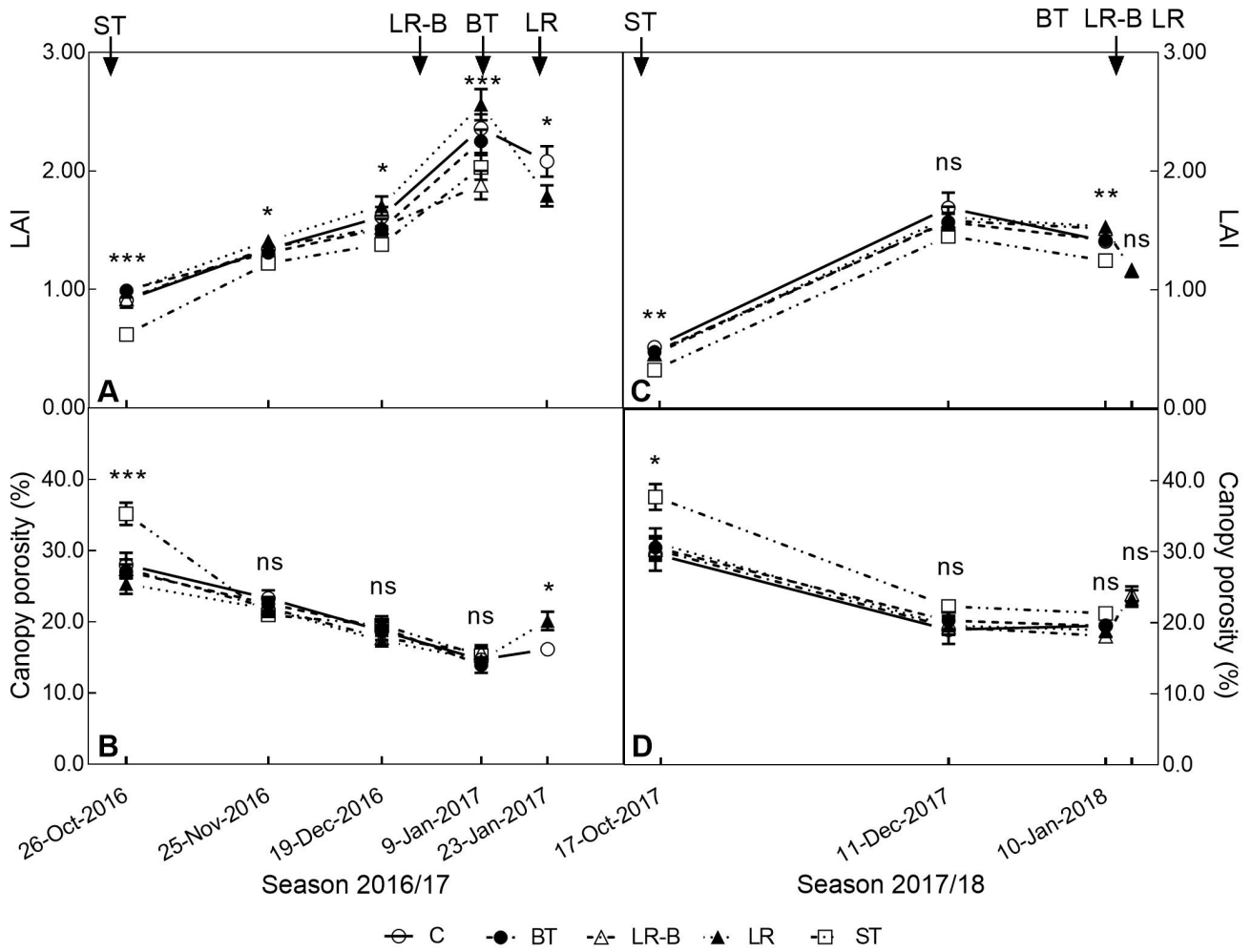


Figure 3 Effects of different canopy management treatments (C, control; BT, cluster thinning; LR-B, leaf removal at cluster zone; LR, leaf removal at middle third canopy; ST, shoot thinning) on Shiraz canopy architecture (LAI, leaf area index; and canopy porosity) for season 2016/17 (**A** and **B**, respectively) and season 2017/18 (**C** and **D**, respectively). The time of the application of the treatments are indicated by arrows. *, **, and *** indicate significance at $p \leq 0.05$, 0.01 , and 0.001 , respectively, ns: not significant, by LSD test at 5% level.

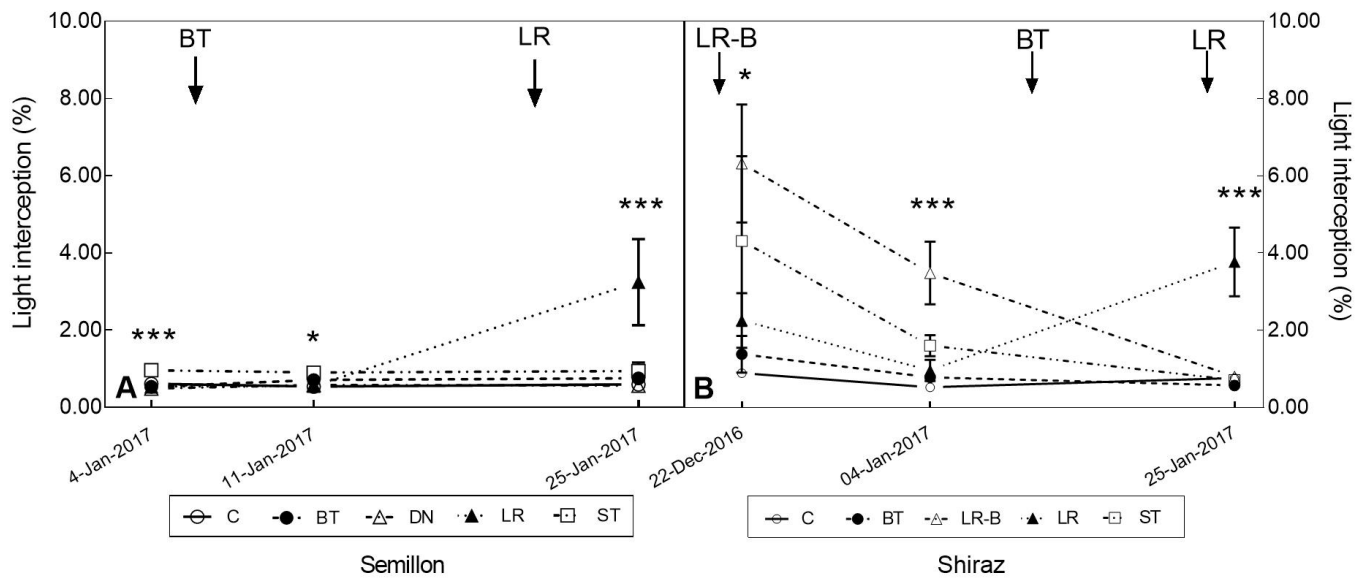


Figure 4 Effects of different canopy management treatments (C, control; BT, cluster thinning; DN, double nodes; LR-B, leaf removal at cluster zone; LR, leaf removal at middle third canopy; ST, shoot thinning) on canopy light interception of Semillon (**A**) and Shiraz (**B**) for season 2016/17. The time of the application of the treatments are indicated by arrows. *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

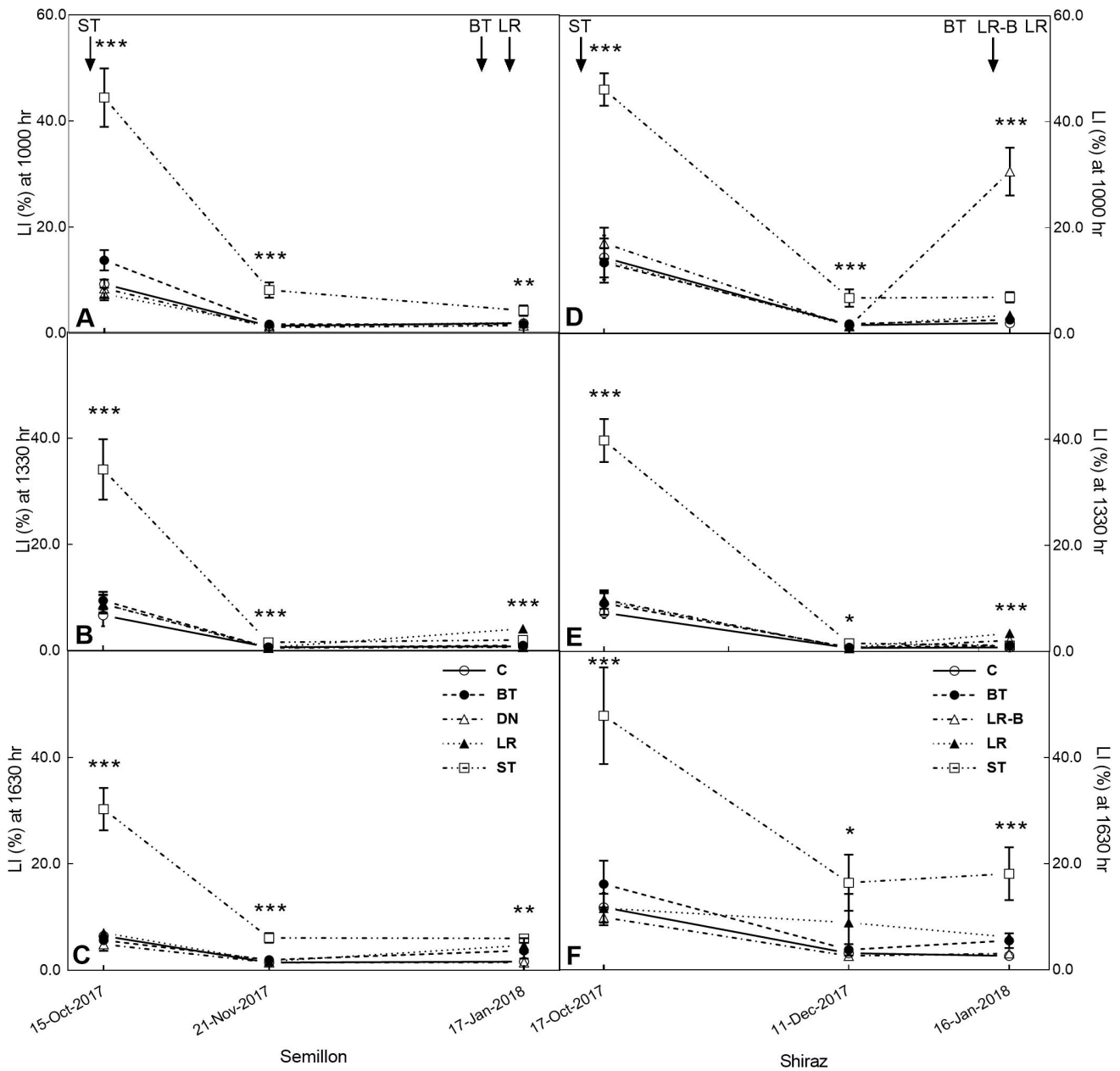


Figure 5 Effects of different canopy management treatments (C, control; BT, cluster thinning; DN, double nodes; LR-B, leaf removal at cluster zone; LR, leaf removal at middle third canopy; ST, shoot thinning) on canopy LI (light interception) of Semillon (**A**, at 1000hr; **B**, at 1330 hr; **C**, at 1630 hr) and Shiraz (**D**, at 1000hr; **E**, at 1330 hr; **F**, at 1630 hr) for season 2017/18. The time of the application of the treatments are indicated by arrows. *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

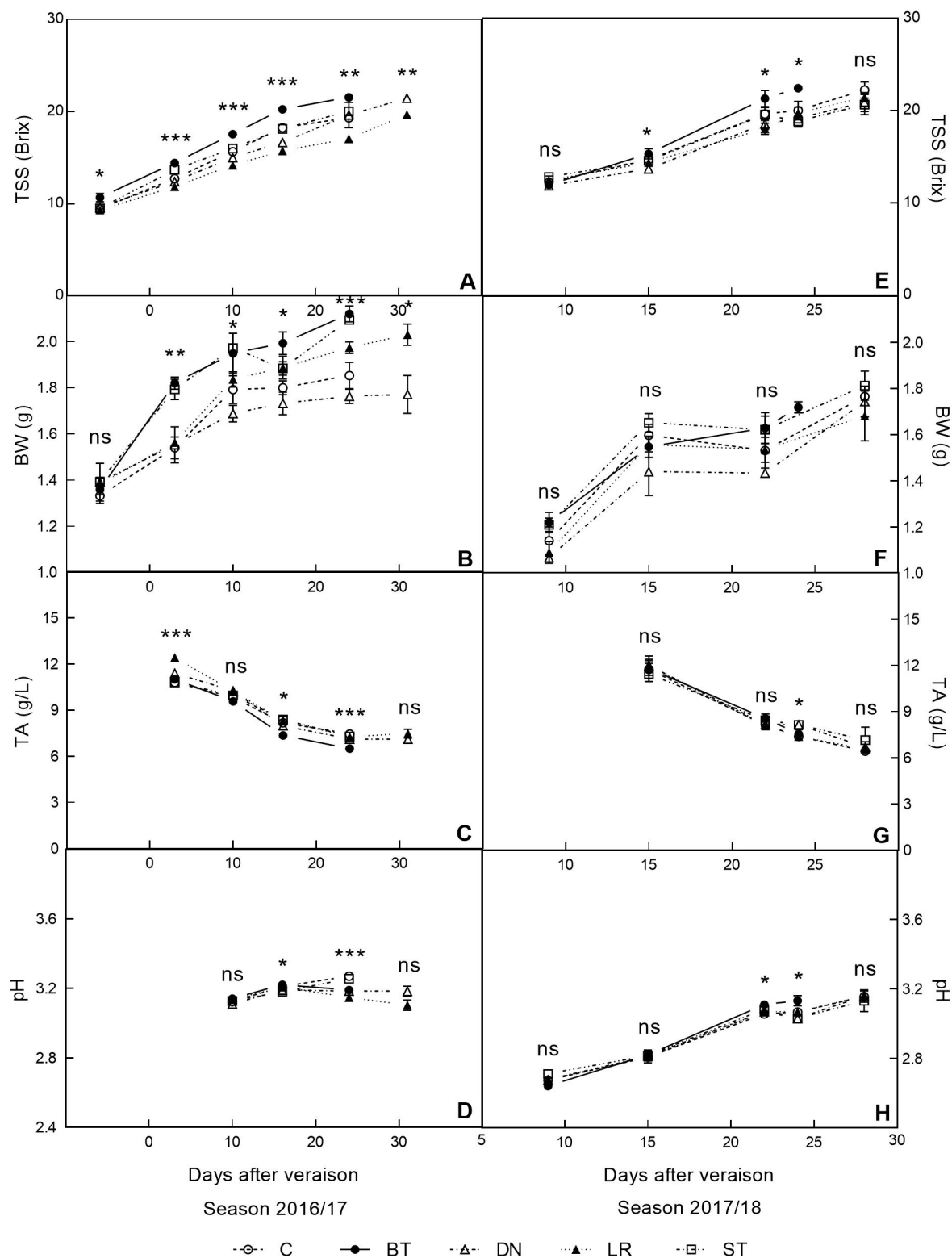


Figure 6 Effects of different canopy management treatments (C, control; BT, cluster thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning) berry maturity (TSS, total soluble solids; BW, berry weight; TA, total acidity; and pH) of Semillon for season 2016/17 (A, B, C, and D) and season 2017/18 (E, F, G and H). *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

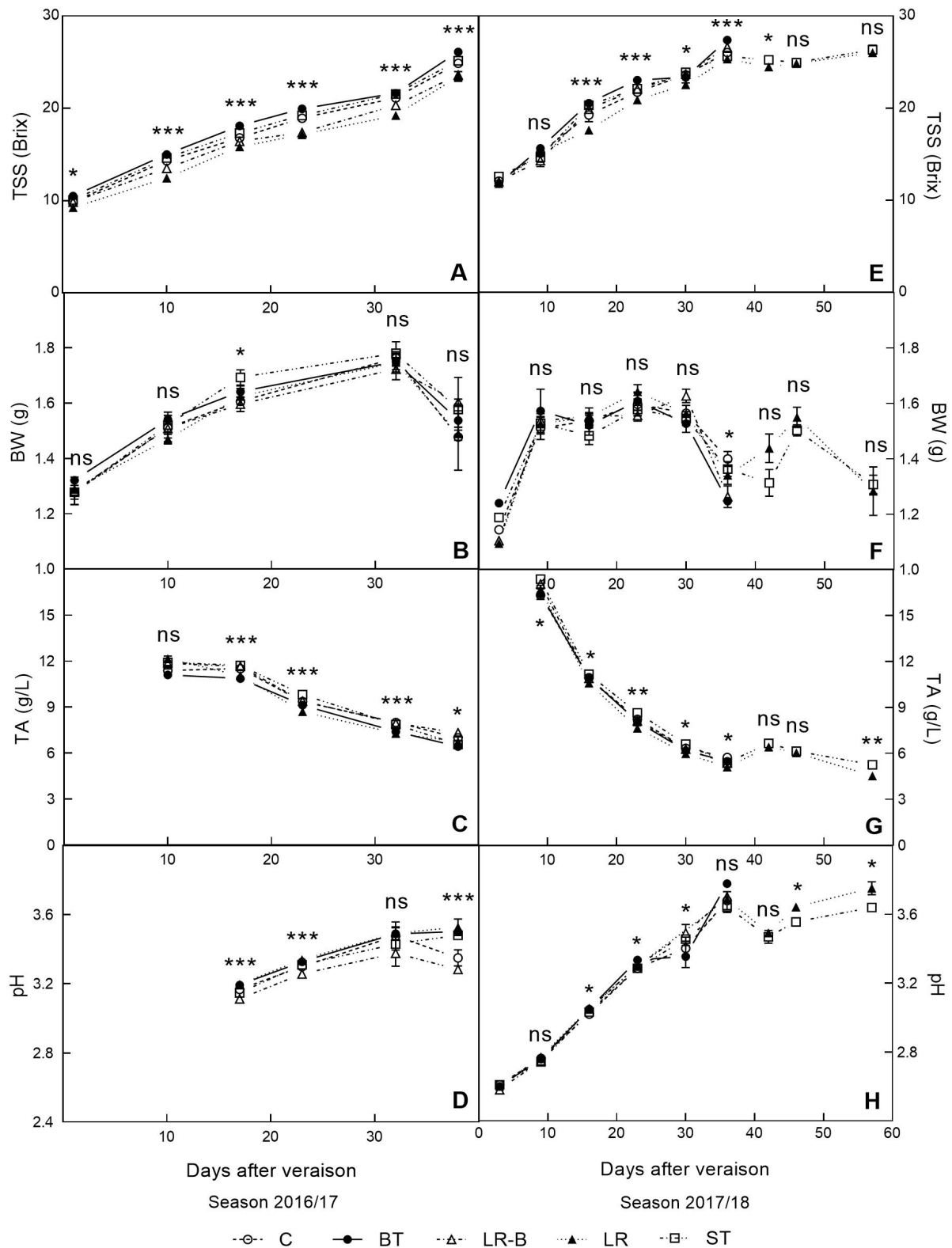


Figure 7 Effects of different canopy management treatments (C, control; BT, cluster thinning; LR-B, leaf removal at cluster zone; LR, leaf removal at middle third canopy; ST, shoot thinning) on berry maturity (TSS, total soluble solids; BW, berry weight; TA, total acidity; and pH) of Shiraz for season 2016/17 (A, B, C, and D) and season 2017/18 (E, F, G and H). *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

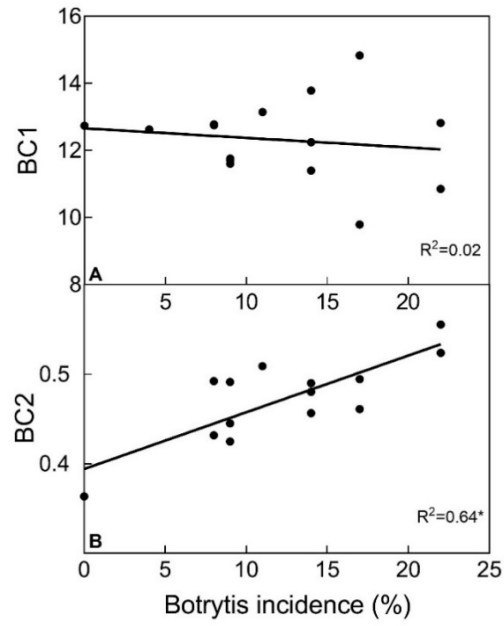


Figure 8 Correlation of Botrytis bunch rot incidence with BC1 (**A**) and BC2 (**B**) for Semillon in season 2016/17. BC1: cluster compactness index 1, calculated as ratio between the total number of berries per cluster and main rachis length (cm); BC2: cluster compactness index 2, calculated as ratio between the total number of berries per cluster and cluster volume (cm³); *: correlation is significant at $p \leq 0.05$.


Chapter 4: Prepared Manuscript:

Effects of Canopy Management Treatments on Grapevine Bud Fruitfulness

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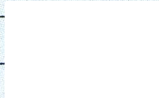
Principal Author


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| Contribution to the Paper | Performed measurements on all samples, interpreted data and wrote manuscript. | | |
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By signing the Statement of Authorship, each author certifies that:
 the candidate's stated contribution to the publication is accurate (as detailed above);
 permission is granted for the candidate to include the publication in the thesis; and
 the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Short title: Canopy Management and Bud fruitfulness

Effects of Canopy Management Practices on Grapevine Bud Fruitfulness

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Abstract

Background and Aims: Bud fruitfulness is a key component of reproductive performance of grapevine as it determines crop production for the following growing season. Canopy microclimate can impact on bud fruitfulness, however, the effects of canopy management practices on bud fruitfulness are not well known. The objective of this study was to investigate the effect of common canopy management practices on bud fruitfulness, and the relationships with vine vigour, bud microclimate and bud carbohydrate level.

Methods and Results: Different canopy management practices including shoot thinning, bunch thinning, leaf removal and lighter pruning were imposed on Semillon and Shiraz grapevines (*Vitis vinifera* L.). Light interception at the bud zone was measured after canopy management practices were applied. Bud fertility at dormancy was assessed using bud dissection analysis. The number and size of inflorescence primordia, and the incidence of primary bud necrosis were recorded. The results were correlated with measurement of shoot vigour and carbohydrate content of buds and canes.

Conclusions: Bud fruitfulness was influenced most by bud light interception, while the size of inflorescence primordia was positively correlated with shoot vigour and the carbohydrate level of bud. Through altering canopy microclimate, canopy management practices can be used to manipulate bud fruitfulness and potentially bunch size.

Significance of the Study: This study provides novel information on the impact of canopy management on grapevine bud fruitfulness and the size of inflorescence primordia. These findings can be used to make more informed vineyard management decisions for better yield control.

Keywords: *inflorescence primordia, primary bud necrosis, bud dissection, microclimate, yield prediction*

Introduction

In grapevine, bud fruitfulness is defined as the formation of inflorescence primordia (IP) in mature latent buds (Srinivasan and Mullins 1981, Dry 2000). The number and size of IP play a key role in yield variation as they form the potential yield for the next season (May and Antcliff 1973, Dry 2000, Sánchez and Dokoozlian 2005). It is well established that the main components of grapevine yield are bunch number per vine and berry number per bunch, which together account for about 90% of seasonal yield variation (Clingeffer et al. 2001, Guilpart et al. 2014). Actual fruitfulness; the number of bunches per shoot, can be predicted

early by counting the number of IP in compound buds (Williams 2000, Rawnsley and Collins 2005). The branching level of IP, that is indicated by its size, determines the flower number on an inflorescence after budburst (Dunn and Martin 2007, Guilpart et al. 2014) and relates to potential bunch weight (Dry 2000).

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

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

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

Fruitfulness can be manipulated by canopy management (Dry 2000). Shoot thinning was found to reduce shoot density and increase bunch number per shoot (Reynolds et al. 1994a). However, severe shoot thinning resulted in increased vigour of the remaining shoots and increased incidence of PBN (Dry and Coombe 1994, Dry 2000). It was also found by Ames et al. (2016) that improved light conditions by shoot thinning did not increase bud fruitfulness. Light pruning such as leaving double nodes (Morris et al. 1983) and 25% more retained nodes (Zabadal et al. 2002) resulted in reduced node fruitfulness. While leaf removal in the bunch zone has been shown to increase light intensity at the renewal area and increase bunch number per shoot and berry number per bunch (Dry 2000). However, other studies on leaf removal reported no carry-over effects on bud fruitfulness for the next season (Percival et al. 1994, Intriери et al. 2008, Palliotti et al. 2012, Intrigliolo et al. 2014). A study by Sánchez and Dokoozlian (2005) investigated the effect of bud microclimate on bud fruitfulness by setting up discrete light exposure levels through pruning and shoot positioning. It was found that shoot light exposure, rather than light interception by individual buds, had a significant impact on IP number and size (Sánchez and Dokoozlian 2005). This implies that higher photoassimilatory capacity and subsequent carbohydrates levels may be important in IP induction and differentiation.

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

Materials and Methods

Experimental sites

The experiment was carried out in the Coombe vineyard of the Waite Campus, University of Adelaide, South Australia (34°58' S; 138°38' E). The region is classified as a hot and dry, moderately maritime climate (Smart and Dry 1980). Both Semillon (clone SA 32) and Shiraz (clone BVRC12) vines were planted on own roots in 1991, trained to a bilateral spur pruned cordon with the shoots vertically positioned. Row spacing and vine spacing were 3.0m and 1.8m, respectively, with rows oriented north/south.

Experimental design and treatments

Five canopy management treatments were imposed on Semillon and Shiraz. The details of the treatments are shown in Table 1. For Semillon, treatments including control (C), bunch thinning (BT), shoot thinning (ST), leaf removal (LR) and lighter pruning (double nodes, DN) were applied for four growing seasons (2014/15, 2015/16, 2016/17 and 2017/18). Each treatment was replicated three times in blocks of three panels with each panel containing three vines. Measurements were conducted in the middle vine of each panel. The data for this study was collected in the seasons 2015/16, 2016/17 and 2017/18. Treatments for Shiraz vines include C, BT, ST and LR, which were conducted in the same way as for Semillon, and another type of leaf removal (LR-B) (Table 1). The treatments were applied on Shiraz for two growing seasons (2016/17 and 2017/18), with each treatment containing nine replicates. For both varieties, four shoots were randomly labelled on each vine in the early spring of the season. Measurements of light microclimate, shoot vigour and bud fruitfulness were conducted on labelled shoots.

Microclimate measures

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

$$Li = \frac{PAR \text{ at bud zone}}{PAR \text{ ambient}} \times 100$$

The light measurements were taken on sunny days after the application of treatments for both seasons. For season one (2016/17) the time of measurement was at solar noon (1330 hr). In season two (2017/18), three time points were assessed: morning (1000 hr), solar noon (1330 hr) and afternoon (1630 hr). The sensors on the ceptometer were faced upward with the zenith angle of the sun at each time point.

Shoot vigour and bud fertility assessment

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

Compound buds at nodes one to four were dissected using a razor blade to make transverse cuts perpendicular to the bud axes in the middle of the buds (Rawnsley and Collins 2005). The bud was then observed under a light microscope at 25x magnification (Model EZ4 W, Leica, Heerbrugg, Switzerland). The number of IP in the primary bud and occurrence of PBN of each compound bud was recorded. If the primary bud was necrotic, the largest secondary bud was assessed instead. PBN incidence was expressed as a percentage of all buds dissected for each treatment. Images of dissections were taken using the Leica AirLab App and the cross-sectional area of IP was measured on the images using software Image J (NIH, USA).

For Semillon, the vigour measurements were only conducted in seasons 2016/17 and 2017/18, and bud fruitfulness assessment in season 2015/16 was only conducted on the first two nodes.

Carbohydrate measures

Three samples of canes (spurs) and buds (leaf and stem tissue from budburst) were collected in each panel of Semillon after budburst in season 2017/18. All samples were kept on dry ice until storage in a -80°C freezer and then freeze dried (Alpha 2-4 LSC; John Morris Scientific, Adelaide, Australia). Bud tissues and wood tissues were separated and ground in an electrical

mill (Model A11, IKA, Germany) for carbohydrate analysis. Carbohydrate measurement was performed according to Edwards et al. (2011). For each sample 5mg was weighed and stored in a tube as a subsample. Soluble sugars were extracted using 80% aqueous ethanol and measured by Anthrone assay (Edwards et al. 2011). The absorbance was read at 600nm using a spectrophotometer (Multiskan Spectrum, model 00300011, Thermo Electron Corporation, Vantaa, Finland) and the content was determined from a fructose standard curve. Starch concentration was determined with a commercial enzyme assay kit (Total starch assay kit, Megazyme, Ireland). The absorbance was read at 505nm and the content was determined using a glucose standard curve.

Statistical analysis

Statistical analysis was performed using one-way analysis of variance (ANOVA) to assess whether there were significant differences between treatments for bud fruitfulness results including IP number and area. Least significant difference (LSD) was applied at the 5% level ($p < 0.05$) for *post hoc* tests. Pearson correlation was used to assess relationships between bud fruitfulness and shoot vigour, bud zone light interception and bud carbohydrate content. All statistical analyses were performed using SPSS Statistics 24 (IBM, Chicago, IL, USA).

Results

Bud fertility

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

Significantly larger IP areas were found in each node position and averages of nodes in all seasons except node one when ST was applied in season 2015/16. In season 2016/17, average IP area at node three was enlarged significantly by BT and LR, and so were the two averages. The incidence of PBN did not show a consistent response to the treatments, while it was

noticeable that in all of three seasons, the highest PBN incidence at node two was caused by BT. In addition, the incidence of PBN in nodes one and two for all the treatments was higher in 2017/18 than the former two seasons, especially at node one where it ranged from 42% to 55%.

Compared with Semillon, PBN incidence in Shiraz was higher in both seasons and resulted in lower bud fruitfulness, especially for season 2016/17 (Table 3). For all the treatments, the average incidence of PBN of the first two nodes ranged from 44% to 60% in both seasons, with an even higher incidence in node one (54% to 72% in season 2016/17 and 47% to 74% in season 2017/18). However, there was no consistent pattern with canopy management treatments, as seen with Semillon. IP number was significantly higher in node two and the averages of first two nodes and first four nodes when ST was applied in season 2017/18, but not in season 2016/17. The IP number was also increased significantly by LR-B at node three in season 2016/17 and by BT at node two in season 2017/18. IP area was influenced only by ST, with significant increases in node two to four in season 2016/17 and in node three in season 2017/18, and increases in two averages for both seasons. LR did not significantly impact on IP number or area.

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

Shoot vigour and its correlations with bud fruitfulness

In seasons 2016/17 and 2017/18, total cane weight, cane weight of the first four nodes, internode lengths between nodes two and three and the cane diameter between nodes two and three were measured as indicators of shoot vigour (Tables 5 and 6). For Semillon, all parameters apart from internode length increased with ST in both seasons. When BT was applied, only the internode length was affected (decreased) and only in 2016/17. The correlations between bud fruitfulness (IP number and area) and shoot vigour parameters of each treatment in Semillon are shown in Figure 1 (season 2016/17) and Figure 2 (season 2017/18). In season 2016/17, shoot vigour measurements showed higher correlations with IP number, rather than with IP area. The correlations between: the whole cane weight and IP number average (first two nodes); four-nodes cane weight and two IP number averages; and internode diameter and IP number average (first two nodes) were significant. The IP area (nodes one to four) only showed a significant correlation with the whole cane weight. In

season 2017/18, shoot vigour measurements showed higher correlations with IP area (Figure 2). The average IP area (nodes one and two) was correlated with four-nodes cane weight and internode diameter, and average IP area (nodes one to four) was correlated with whole cane weight, four-nodes cane weight and internode diameter.

In Shiraz the canopy management treatments had less influence on the shoot vigour parameters (Table 6) than in Semillon. Only the whole cane weight decreased with LR-B in season 2016/17. The highest whole cane weight for two seasons, and four-nodes cane weight and internode diameter for season 2016/17 were found in ST. The correlations between shoot vigour and bud fertility of Shiraz are shown in Figures 3 and 4. In season 2016/17, average IP area significantly correlated with cane weight and internode diameter measurements (Figure 3). The average IP area was also significantly correlated with whole cane weight in season 2017/18 (Figure 4).

Light interception at bud zone

The results of the light interception at the bud zone in season 2016/17 for both varieties are shown in Figure 5. For Semillon, ST and BT significantly increased bud light interception after application (Figure 5A). In Shiraz (Figure 5B), bud light interception was increased by LR-B, while ST did not show any effect. In season 2017/18 (Figure 6), ST increased bud light interception for both varieties immediately after application, however, the effects gradually diminished and no differences were observed in the last measurement in Semillon (Figures 6A-C) and the last two measurements in Shiraz (Figures 6D-F). LR also significantly increased bud light interception in Semillon at midday (1330 hr) (Figure 6B). In Shiraz, LR-B increased bud light interception significantly at 1000 hr (Figure 6D) and 1330 hr (Figure 6E), while LR increased light at 1630 hr (Figure 6F). Interestingly, bud light interception in BT treatment of Shiraz was also found to be significantly higher in the first measurement at 1630 hr (Figure 6F), when BT had not yet been conducted on the vines, hence the higher light interception in BT was by coincidence rather than by the treatment.

Carbohydrate content and its correlations with bud fruitfulness

Carbohydrate content was measured separately for buds and cane samples in all the treatments of Semillon in season 2017/18. The results of each sample were expressed as a percentage dry weight (% DW) of starch, soluble carbohydrates and total non-structural carbohydrate (TNC), respectively (Figure 7). Bud carbohydrate content was only influenced by ST, with an increase in bud starch content (Figure 7A). Both starch and soluble

carbohydrates in canes were significantly lower in DN. The other treatments did not show an effect on the carbohydrate content.

The correlations between each carbohydrate content parameter and bud fertility are summarized in Table 7. No correlations were found between IP number and carbohydrate content. In contrast, the average IP area (nodes one to two) was positively correlated with bud starch content and bud TNC, and average IP area average (nodes one to four) was correlated with bud TNC. The carbohydrate content in the canes, although influenced by DN, was not related to bud fertility.

Discussion

Bud dissection analysis can be a useful tool for early yield prediction as the IP assessed within compound buds have the potential to develop into bunches in the following season (Dry 2000). The conditions during the initiation and differentiation of IP in the current season can influence bud fruitfulness and potential yield (Watt et al. 2008, Li-Mallet et al. 2016). In this study, bud fruitfulness including IP number and area was determined by bud dissection analysis and it was found to be influenced by canopy management practices.

Among the treatments, ST in particular had the strongest effects on bud fertility especially on the IP size for both Semillon and Shiraz (Tables 2 and 3). Previously research has shown that the number and size of IP are positively related to light exposure during bud initiation and differentiation (Buttrose 1969, Dry 2000, Sánchez and Dokoozlian 2005). In the current study, the significant increase in IP number when ST was applied in Semillon may be attributed to the increase in light interception at the bud zone, as shown by light interception measurements performed during spring in both seasons (Figures 5 and 6). Similarly, the IP number of Semillon was also increased by BT in season 2016/17, although only at node four, and a significant increase in bud light interception was also measured in BT in the same season (Figure 5A). While in season 2017/18, neither the IP number nor the bud light interception changed when BT was applied. This supports the idea that BT increased the IP number by affecting the light conditions in the bud zone. The impact of bud light interception on the IP number was also shown in Shiraz. ST increased light interception at the bud zone (Figures 6D, E and F) as well as the IP number of Shiraz in season 2017/18 (Table 3) but not in season 2016/17. The higher bud light interception found in BT in 2017/18 (Figure 6F) may also have led to higher number of IP in node two of Shiraz. Bud light interception was also increased by LR in both varieties (Figure 6B and 6F), and by LR-B in Shiraz (Figures 6D and E) in season 2017/18, however this had no effects on the IP number. This lack of effect when

LR was applied is in agreement with previous studies (Percival et al. 1994, Palliotti et al. 2012, Intrigliolo et al. 2014). Intrieri et al. (2008) suggested that the expected positive effect of leaf removal on bud fruitfulness due to the improvement in light microclimate can be offset by negative effects on bud initiation due to source limitation.

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

The carbohydrate content of buds and canes measured after budburst was affected by ST and DN (Figure 7). Bud starch content was significantly higher in ST treatments and was positively correlated with IP area. This indicates a carry-over effect of ST on bud fruitfulness in the next season. Carbohydrate levels in canes were not influenced by ST and were lower in DN (Figure 7). At budburst, compound bud initiation is sensitive to the carbohydrate reserve status as the other sink organs (actively growing shoots and leaves) are competing with the buds (Buttrose 1966b, Candolfi-Vasconcelos and Koblet 1990). DN significantly lowered both starch and soluble sugar in canes while bud fruitfulness was not decreased accordingly. This suggests that in the current study, the amount of carbohydrate reserves stored in canes of DN were enough to support bud initiation and thus bud fruitfulness was not limited by DN.

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

A high incidence of PBN is generally considered to be correlated with excessive shoot growth and canopy shading (May 1965, Dry and Coombe 1994, Collins and Rawnsley 2004). However, in our study, PBN did not respond to the applied canopy management treatments in a consistent way in both seasons and for both varieties. Despite shoot vigour being highest in ST, the incidence of PBN were not and rather occurred randomly among all the treatments. This suggests that the incidence of PBN may be related to other factors that need further investigation.

Conclusions

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

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Tables

Table 1. Canopy management treatments on grapevines.

Table 2. Semillon bud fruitfulness results in response to different canopy management treatments for three seasons.

Table 3. Shiraz bud fruitfulness results in response to different canopy management treatments for two seasons.

Table 4. Shiraz IP area average for different bud types.

Table 5. Means of Semillon shoot vigour parameters in response to different canopy management treatments for two seasons.

Table 6. Means of Shiraz shoot vigour parameters in response to different canopy management treatments for two seasons.

Table 7. Correlation coefficients between Semillon bud fruitfulness parameters and carbohydrate content in season 2017/18.

Table 1 Canopy management treatments on grapevines

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

Table 2 Semillon bud fruitfulness results in response to different canopy management treatments for three seasons

| Measurement | Season | Treatments ^a | | | | | Significance ^b |
|---|---------|-------------------------|----------|----------|----------|---------|---------------------------|
| | | C | BT | DN | LR | ST | |
| IP ^c Number node 1 | 2015/16 | 1.93 a | 1.60 b | 1.72 a | 1.77 a | 1.77 a | * |
| | 2016/17 | 1.76 a | 1.70 ab | 1.40 b | 1.69 ab | 1.76 a | * |
| | 2017/18 | 1.35 | 1.19 | 1.34 | 1.43 | 1.50 | ns |
| IP Number node 2 | 2015/16 | 1.87 a | 1.87 a | 1.90 a | 2.00 ab | 2.13 b | * |
| | 2016/17 | 1.76 a | 1.73 a | 1.77 ab | 1.75 a | 2.00 b | * |
| | 2017/18 | 1.76 | 1.58 | 1.77 | 1.77 | 1.75 | ns |
| IP Number node 3 | 2015/16 | - | - | - | - | - | - |
| | 2016/17 | 1.74 ab | 1.85 ab | 1.66 a | 1.67 a | 1.91 b | * |
| | 2017/18 | 1.59 a | 1.78 ab | 1.69 a | 1.71 a | 1.94 b | * |
| IP Number node 4 | 2015/16 | - | - | - | - | - | - |
| | 2016/17 | 1.71 a | 1.97 bc | 1.83 ab | 1.81 ab | 2.09 c | * |
| | 2017/18 | 1.74 | 1.75 | 1.74 | 1.71 | 1.94 | ns |
| IP Number average (first 2 nodes) | 2015/16 | 1.90 | 1.73 | 1.86 | 1.88 | 1.98 | ns |
| | 2016/17 | 1.77 ab | 1.71 ab | 1.59 a | 1.72 ab | 1.88 b | * |
| | 2017/18 | 1.56 | 1.39 | 1.56 | 1.60 | 1.63 | ns |
| IP Number average (first 4 nodes) | 2015/16 | - | - | - | - | - | - |
| | 2016/17 | 1.74 a | 1.81 ab | 1.66 a | 1.73 a | 1.94 b | ** |
| | 2017/18 | 1.61 | 1.58 | 1.64 | 1.66 | 1.78 | ns |
| IP Area Node 1 (mm ²) | 2015/16 | 0.062 | 0.056 | 0.066 | 0.059 | 0.068 | ns |
| | 2016/17 | 0.048 ab | 0.054 bc | 0.046 a | 0.052 b | 0.056 c | ** |
| | 2017/18 | 0.046 ab | 0.046 ab | 0.042 a | 0.043 b | 0.057 c | *** |
| IP Area Node 2 (mm ²) | 2015/16 | 0.063 a | 0.062 a | 0.064 ab | 0.064 ab | 0.070 b | * |
| | 2016/17 | 0.048 a | 0.053 ab | 0.052 a | 0.052 a | 0.057 b | ** |
| | 2017/18 | 0.051 a | 0.048 a | 0.048 a | 0.048 a | 0.062 b | *** |
| IP Area Node 3 (mm ²) | 2015/16 | - | - | - | - | - | - |
| | 2016/17 | 0.048 a | 0.055 b | 0.046 a | 0.054 b | 0.061 c | *** |
| | 2017/18 | 0.049 a | 0.049 a | 0.048 a | 0.050 a | 0.065 b | *** |
| IP Area Node 4 (mm ²) | 2015/16 | - | - | - | - | - | - |
| | 2016/17 | 0.054 ab | 0.059 b | 0.053 a | 0.059 b | 0.069 c | *** |
| | 2017/18 | 0.057 ab | 0.058 b | 0.050 a | 0.055 ab | 0.070 c | *** |
| IP area average (first 2 nodes) (mm ²) | 2015/16 | 0.062 a | 0.059 a | 0.065 ab | 0.062 a | 0.068 b | * |
| | 2016/17 | 0.048 a | 0.053 bc | 0.049 ab | 0.053 bc | 0.057 c | ** |
| | 2017/18 | 0.048 a | 0.047 a | 0.045 a | 0.047 a | 0.060 b | *** |
| IP area average (first 4 nodes) (mm ²) | 2015/16 | - | - | - | - | - | - |
| | 2016/17 | 0.049 a | 0.055 b | 0.049 a | 0.054 b | 0.061 c | *** |
| | 2017/18 | 0.050 a | 0.051 a | 0.047 a | 0.050 a | 0.064 b | *** |
| PBN ^d (%) node 1 | 2015/16 | 0.00 | 13.33 | 7.47 | 6.67 | 3.33 | - |
| | 2016/17 | 0.00 | 5.71 | 13.89 | 8.33 | 17.6 | - |
| | 2017/18 | 42.86 | 41.67 | 54.84 | 43.33 | 51.61 | - |
| PBN (%) node 2 | 2015/16 | 3.33 | 10.00 | 3.33 | 0.00 | 0.00 | - |
| | 2016/17 | 0 | 5.88 | 2.78 | 5.56 | 0 | - |
| | 2017/18 | 2.86 | 11.11 | 3.23 | 10.00 | 9.68 | - |
| PBN (%) node 3 | 2015/16 | - | - | - | - | - | - |
| | 2016/17 | 2.86 | 2.94 | 2.78 | 2.78 | 2.94 | - |
| | 2017/18 | 2.86 | 0.00 | 9.68 | 3.33 | 3.23 | - |
| PBN (%) node 4 | 2015/16 | - | - | - | - | - | - |
| | 2016/17 | 8.82 | 2.86 | 2.86 | 11.1 | 2.94 | - |
| | 2017/18 | 2.86 | 5.56 | 3.23 | 3.33 | 3.23 | - |
| PBN (%) average (first 2 nodes) | 2015/16 | 1.70 | 11.70 | 5.40 | 3.30 | 1.70 | - |
| | 2016/17 | 0.00 | 5.80 | 8.30 | 6.90 | 8.80 | - |
| | 2017/18 | 22.86 | 26.39 | 29.03 | 26.67 | 30.65 | - |
| PBN (%) average (first 4 nodes) | 2015/16 | - | - | - | - | - | - |
| | 2016/17 | 2.88 | 4.35 | 5.59 | 6.94 | 5.88 | - |
| | 2017/18 | 12.86 | 14.6 | 17.75 | 15.00 | 16.94 | - |

^aTreatments: C, control; BT, bunch thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning. Means with different letters within rows are significantly different by LSD test at 5% level.

^b*, **, and *** indicate significance at $p \leq 0.05$, 0.01 , and 0.001 , respectively; ns: not significant.

^cIP, inflorescence primordia.

^dPBN, primary bud necrosis.

Table 3 Shiraz bud fruitfulness results in response to different canopy management treatments for two seasons

| Measurement | Season | Treatments ^a | | | | | Significance ^b |
|---|---------|-------------------------|----------|----------|----------|---------|---------------------------|
| | | C | BT | LR-B | LR | ST | |
| IP ^c Number node 1 | 2016/17 | 0.84 | 1.09 | 1.08 | 1.25 | 1.14 | ns |
| | 2017/18 | 1.57 | 1.64 | 1.35 | 1.32 | 1.43 | ns |
| IP Number node 2 | 2016/17 | 1.50 | 1.12 | 1.23 | 1.39 | 1.25 | ns |
| | 2017/18 | 1.14 a | 1.64 b | 1.48 ab | 1.53 ab | 1.87 b | * |
| IP Number node 3 | 2016/17 | 1.16 a | 1.17 a | 1.64 b | 1.31 ab | 1.33 ab | * |
| | 2017/18 | 1.75 | 1.67 | 1.81 | 1.68 | 1.77 | ns |
| IP Number node 4 | 2016/17 | 1.31 abc | 0.94 c | 1.71 a | 1.25 bc | 1.63 ab | ** |
| | 2017/18 | 1.68 ab | 1.79 ab | 1.45 a | 1.91 b | 2.03 b | * |
| IP Number average (first 2 nodes) | 2016/17 | 1.17 | 1.09 | 1.17 | 1.32 | 1.19 | ns |
| | 2017/18 | 1.36 a | 1.64 b | 1.42 ab | 1.43 ab | 1.65 b | * |
| IP Number average (first 4 nodes) | 2016/17 | 1.20 ab | 1.08 a | 1.42 b | 1.30 ab | 1.33 b | * |
| | 2017/18 | 1.54 a | 1.68 ab | 1.52 a | 1.61 ab | 1.78 b | * |
| IP Area Node 1 (mm ²) | 2016/17 | 0.050 | 0.047 | 0.042 | 0.048 | 0.052 | ns |
| | 2017/18 | 0.054 | 0.055 | 0.056 | 0.053 | 0.057 | ns |
| IP Area Node 2 (mm ²) | 2016/17 | 0.051 a | 0.051 a | 0.052 a | 0.055 ab | 0.062 b | * |
| | 2017/18 | 0.068 | 0.063 | 0.066 | 0.065 | 0.074 | ns |
| IP Area Node 3 (mm ²) | 2016/17 | 0.049 a | 0.054 ab | 0.052 ab | 0.053 ab | 0.059 b | * |
| | 2017/18 | 0.067 a | 0.066 a | 0.062 a | 0.066 a | 0.077 b | * |
| IP Area Node 4 (mm ²) | 2016/17 | 0.047 a | 0.057 ab | 0.057 ab | 0.057 ab | 0.076 b | * |
| | 2017/18 | 0.073 | 0.073 | 0.069 | 0.070 | 0.079 | ns |
| IP area average (first 2 nodes) (mm ²) | 2016/17 | 0.051 a | 0.048 a | 0.047 a | 0.053 ab | 0.058 b | ** |
| | 2017/18 | 0.059 a | 0.059 a | 0.060 a | 0.059 a | 0.067 b | * |
| IP area average (first 4 nodes) (mm ²) | 2016/17 | 0.050 a | 0.051 a | 0.052 a | 0.052 a | 0.062 b | ** |
| | 2017/18 | 0.065 a | 0.065 a | 0.062 a | 0.064 a | 0.072 b | * |
| PBN ^d (%) node 1 | 2016/17 | 71.88 | 54.29 | 69.44 | 61.11 | 61.11 | - |
| | 2017/18 | 46.70 | 58.80 | 69.70 | 73.50 | 67.70 | - |
| PBN (%) node 2 | 2016/17 | 28.13 | 58.82 | 48.57 | 36.11 | 50.00 | - |
| | 2017/18 | 56.70 | 32.40 | 27.30 | 29.40 | 19.40 | - |
| PBN (%) node 3 | 2016/17 | 59.38 | 48.57 | 38.89 | 57.14 | 52.78 | - |
| | 2017/18 | 23.30 | 23.50 | 27.30 | 26.50 | 22.60 | - |
| PBN (%) node 4 | 2016/17 | 62.50 | 65.71 | 38.89 | 61.11 | 45.71 | - |
| | 2017/18 | 20.00 | 23.50 | 36.40 | 14.70 | 19.40 | - |
| PBN (%) average (first 2 nodes) | 2016/17 | 50.00 | 56.52 | 59.15 | 48.61 | 55.56 | - |
| | 2017/18 | 51.70 | 45.60 | 48.50 | 51.50 | 43.50 | - |
| PBN (%) average (first 4 nodes) | 2016/17 | 55.47 | 56.83 | 48.95 | 53.85 | 52.45 | - |
| | 2017/18 | 36.70 | 34.60 | 40.20 | 36.00 | 32.30 | - |

^aTreatments: C, control; BT, bunch thinning; LR-B, leaf removal at bunch zone; LR, leaf removal; ST, shoot thinning.

Means with different letters within rows are significantly different by LSD test at 5% level.

^b*, **, and *** indicate significance at $p \leq 0.05$, 0.01 , and 0.001 , respectively; ns: not significant.

^cIP, inflorescence primordia.

^dPBN, primary bud necrosis.

Table 4 Shiraz IP area average for different bud types

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

^aTreatments: C, control; BT, bunch thinning; LR-B, leaf removal at bunch zone; LR, leaf removal; ST, shoot thinning. Means with different letters within rows are significantly different by LSD test at 5% level.

^b*, **, and *** indicate significance at $p \leq 0.05$, 0.01 , and 0.001 , respectively; ns: not significant.

^cIP, inflorescence primordia.

Table 5 Means of Semillon shoot vigour parameters in response to different canopy management treatments for two seasons

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

^aTreatments: C, control; BT, bunch thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning. Means with different letters within rows are significantly different by LSD test at 5% level.

^b*, **, and *** indicate significance at $p \leq 0.05$, 0.01 , and 0.001 , respectively; ns: not significant.

Table 6 Means of Shiraz shoot vigour parameters in response to different canopy management treatments for two seasons

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

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

Table 7 Correlation coefficients between Semillon bud fruitfulness parameters and carbohydrate content in season 2017/18

| Measurements | IP ^a Number average (first 2 nodes) | IP Number average (first 4 nodes) | IP area average (first 2 nodes) (mm ²) | IP area average (first 4 nodes) (mm ²) |
|---|--|--------------------------------------|---|---|
| Bud starch content (% DW ^b) | 0.321 | 0.775 | 0.968 ** | 0.974 |
| Bud soluble sugar content (% DW) | -0.404 | 0.147 | 0.542 | 0.616 |
| Bud TNC ^c content (% DW) | 0.037 | 0.583 | 0.886 * | 0.923 * |
| Cane starch content (% DW) | -0.393 | -0.131 | 0.282 | 0.339 |
| Cane soluble sugar content (% DW) | -0.385 | -0.168 | 0.102 | 0.163 |
| Cane TNC content (% DW) | -0.396 | -0.137 | 0.264 | 0.322 |

^aIP, inflorescence primordia.

^bDW, dry weight.

^cTNC, total non-structural carbohydrate.

* and ** indicate significance at $p \leq 0.05$ and 0.01 , respectively.

Figures

Figure 1. Correlations between Semillon bud fruitfulness and shoot vigour parameters based on average of each treatment in season 2016/17. IP: inflorescence primordia; * indicates correlation is significant at $p \leq 0.05$.

Figure 2. Correlations between Semillon bud fruitfulness and shoot vigour parameters based on average of each treatment in season 2017/18. IP: inflorescence primordia; * and ** indicate correlation is significant at $p \leq 0.05$ and 0.01, respectively.

Figure 3. Correlations between Shiraz bud fruitfulness and shoot vigour parameters based on average of each treatment in season 2016/17. IP: inflorescence primordia; * indicates correlation is significant at $p \leq 0.05$.

Figure 4. Correlations between Shiraz bud fruitfulness and shoot vigour parameters based on average of each treatment in season 2017/18. IP: inflorescence primordia; * indicates correlation is significant at $p \leq 0.05$.

Figure 5. Effects of different canopy management treatments (C, control; BT, bunch thinning; DN, double nodes; LR-B, leaf removal at bunch zone; LR, leaf removal at middle third canopy; ST, shoot thinning) on light interception at bud zone of Semillon (**A**) and Shiraz (**B**) for season 2016/17. The time of the application of the treatments are indicated by arrows. *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

Figure 6. Effects of different canopy management treatments (C, control; BT, bunch thinning; DN, double nodes; LR-B, leaf removal at bunch zone; LR, leaf removal at middle third canopy; ST, shoot thinning) on light interception at bud zone of Semillon (**A**, at 1000hr; **B**, at 1330 hr; **C**, at 1630 hr) and Shiraz (**D**, at 1000hr; **E**, at 1330 hr; **F**, at 1630 hr) for season 2017/18. The time of the application of the treatments are indicated by arrows. *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

Figure 7. Effects of different canopy management treatments (C, control; BT, bunch thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning) on Semillon carbohydrate contents of bud (**A**, bud starch content; **B**, bud soluble carbohydrate content; **C**, bud TNC content) and cane (**D**, cane starch content; **E**, cane soluble carbohydrate content; **F**, cane TNC content) for season 2017/18. DW, dry weight. TNC, total non-structural carbohydrate. Bars with different letters are significantly different by LSD test at 5% level.

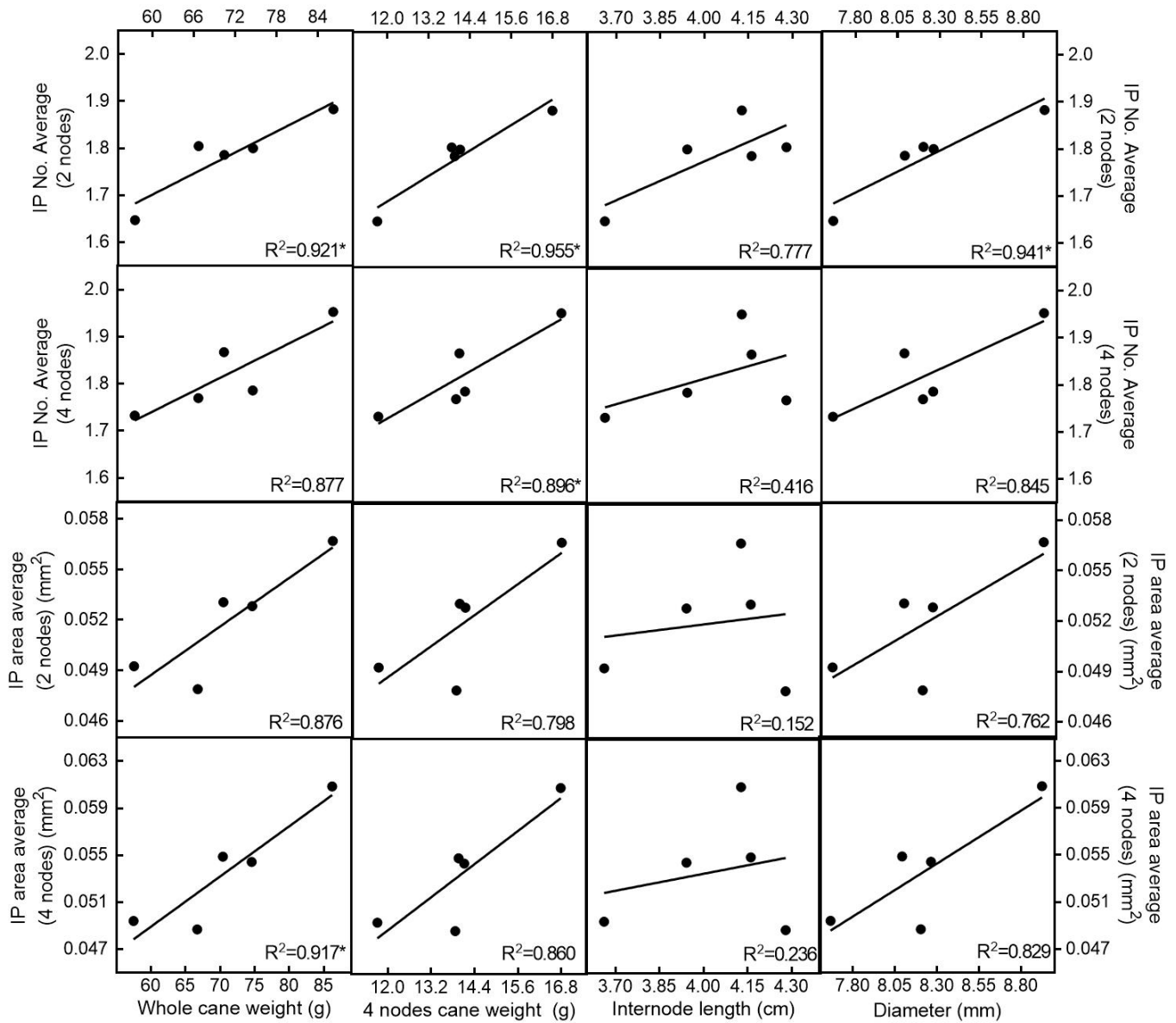


Figure 1 Correlations between Semillon bud fruitfulness and shoot vigour parameters based on average of each treatment in season 2016/17. IP: inflorescence primordia; * indicates correlation is significant at $p \leq 0.05$.

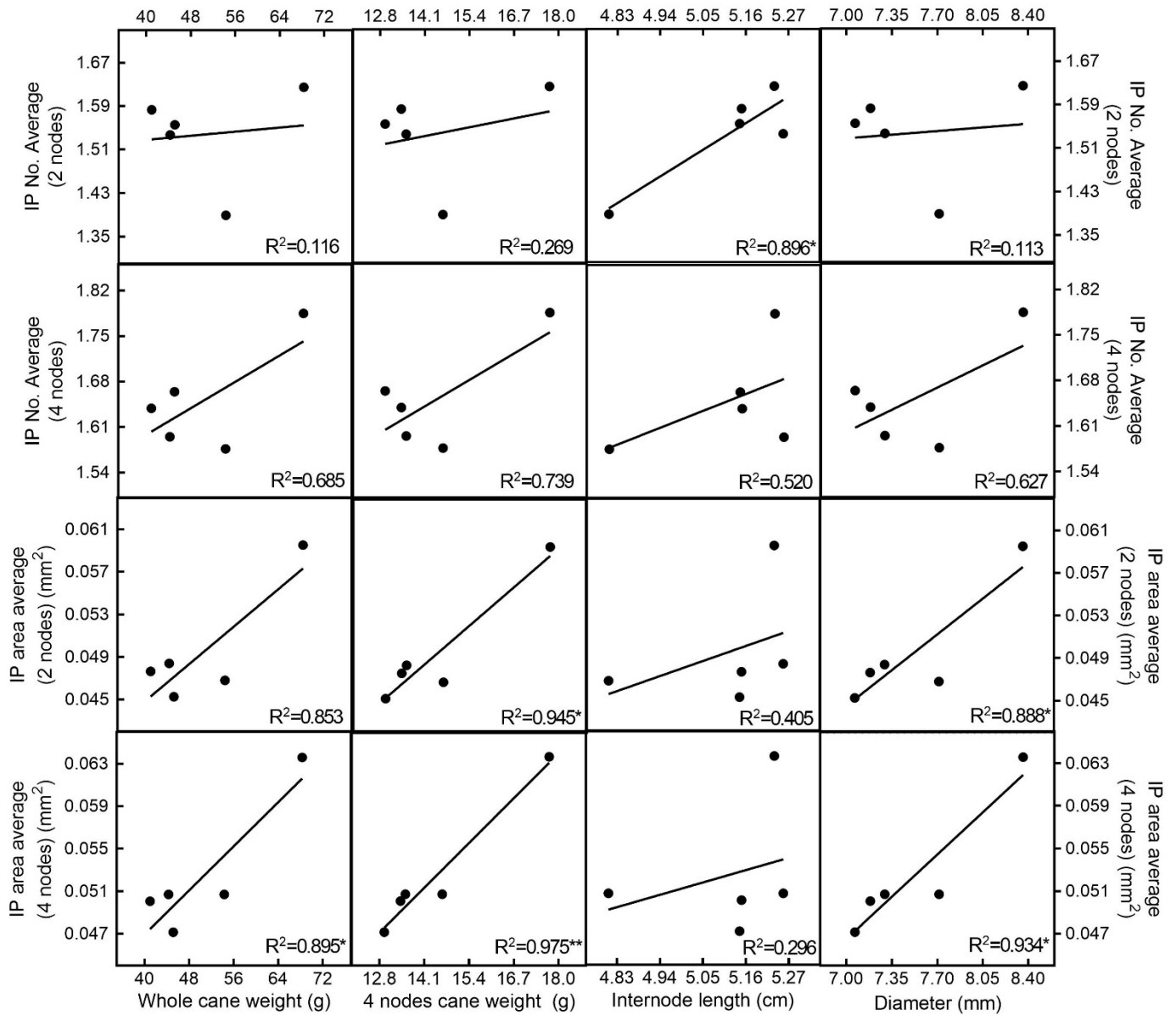


Figure 2 Correlations between Semillon bud fruitfulness and shoot vigour parameters based on average of each treatment in season 2017/18. IP: inflorescence primordia; * and ** indicate correlation is significant at $p \leq 0.05$ and 0.01 , respectively.

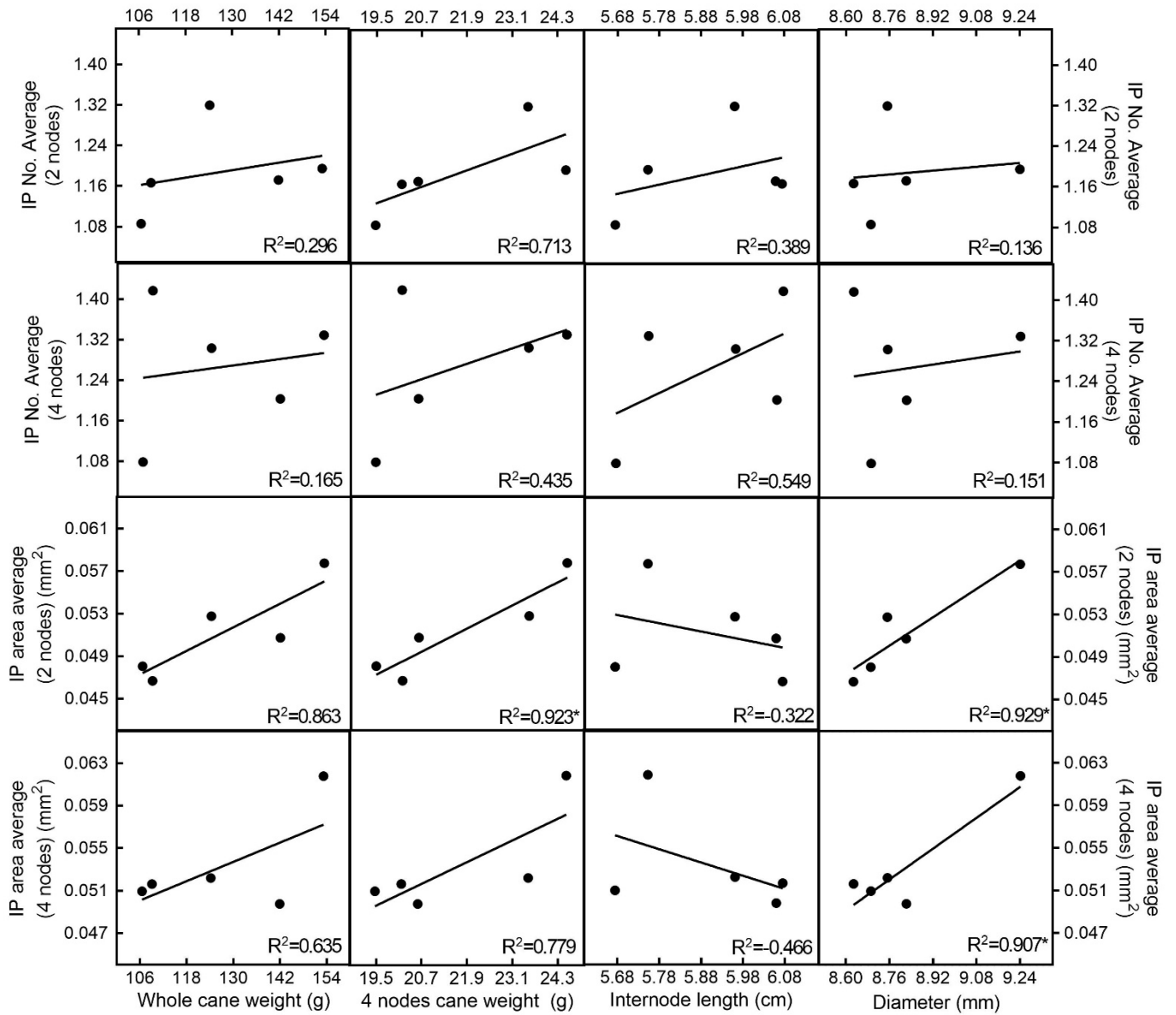


Figure 3 Correlations between Shiraz bud fruitfulness and shoot vigour parameters based on average of each treatment in season 2016/17. IP: inflorescence primordia; * indicates correlation is significant at $p \leq 0.05$.

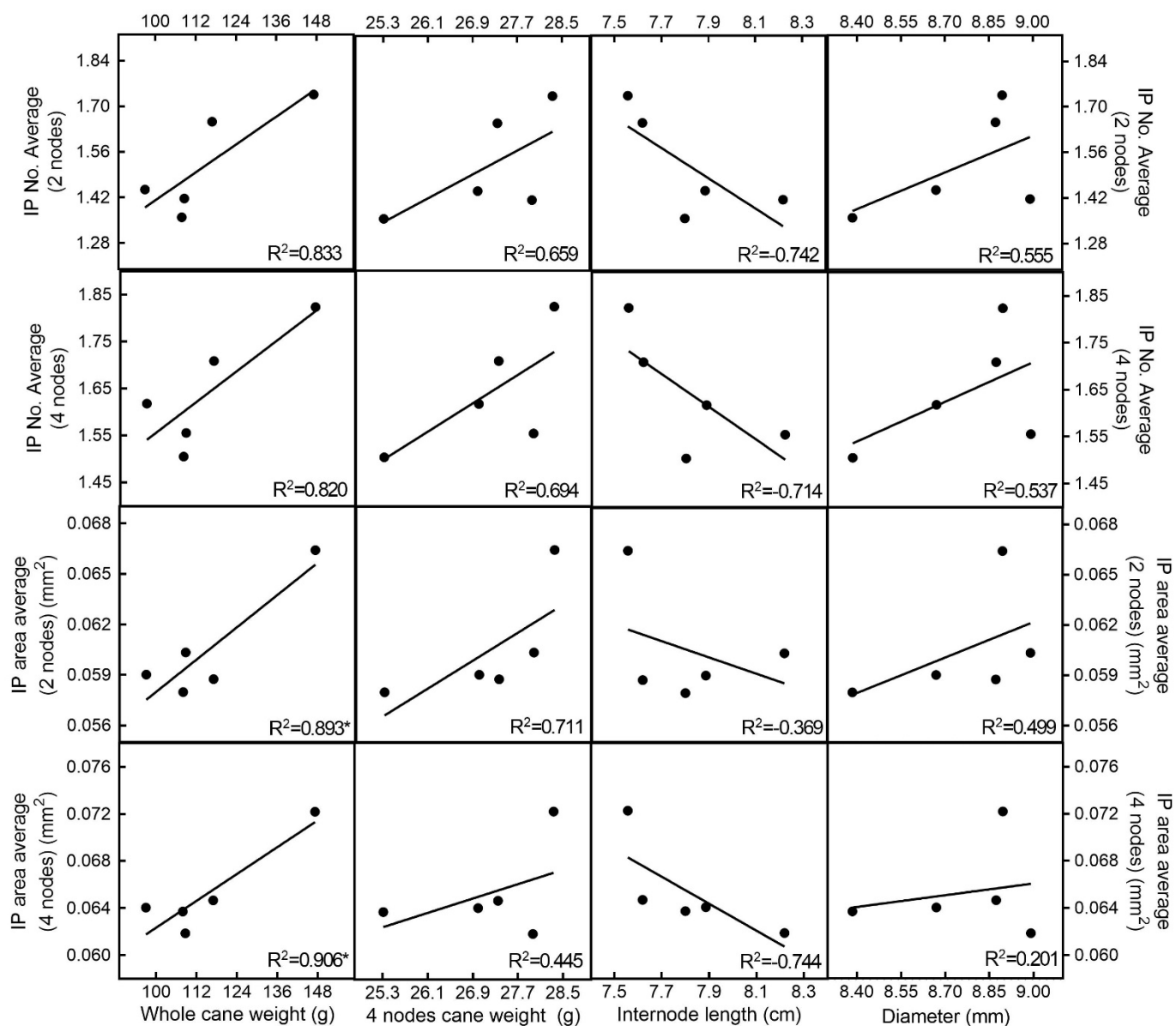


Figure 4 Correlations between Shiraz bud fruitfulness and shoot vigour parameters based on average of each treatment in season 2017/18. IP: inflorescence primordia; * indicates correlation is significant at $p \leq 0.05$.

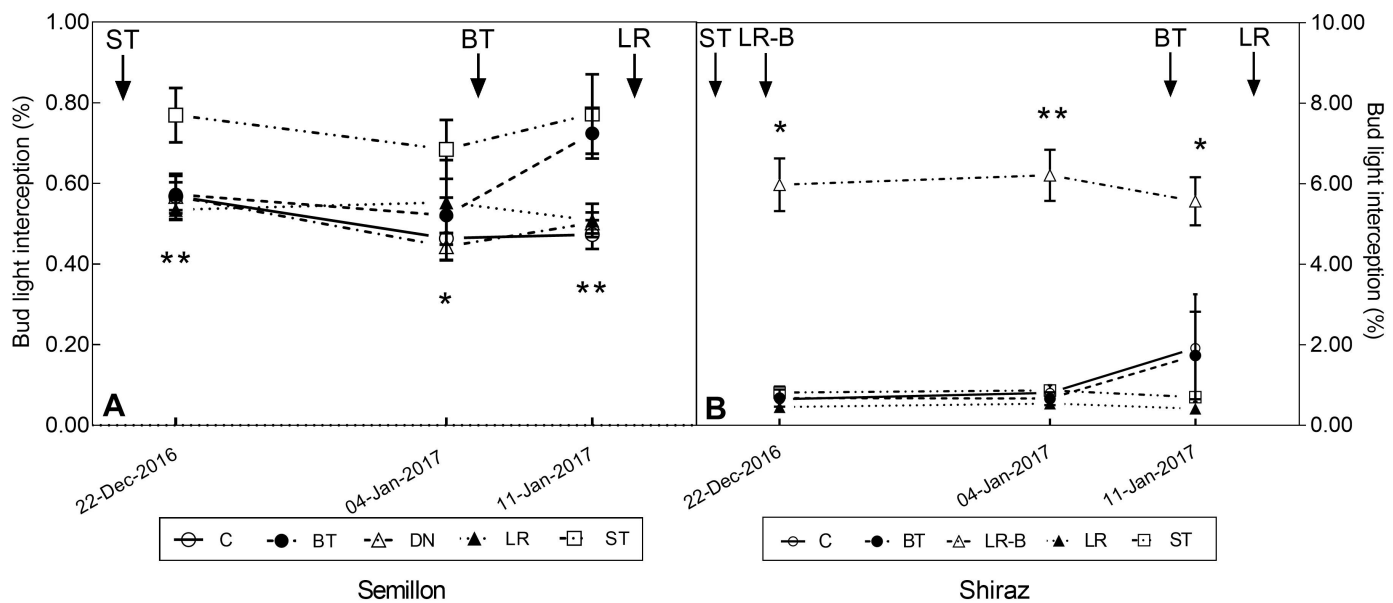


Figure 5 Effects of different canopy management treatments (C, control; BT, bunch thinning; DN, double nodes; LR-B, leaf removal at bunch zone; LR, leaf removal at middle third canopy; ST, shoot thinning) on light interception at bud zone of Semillon (**A**) and Shiraz (**B**) for season 2016/17. The time of the application of the treatments are indicated by arrows. *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

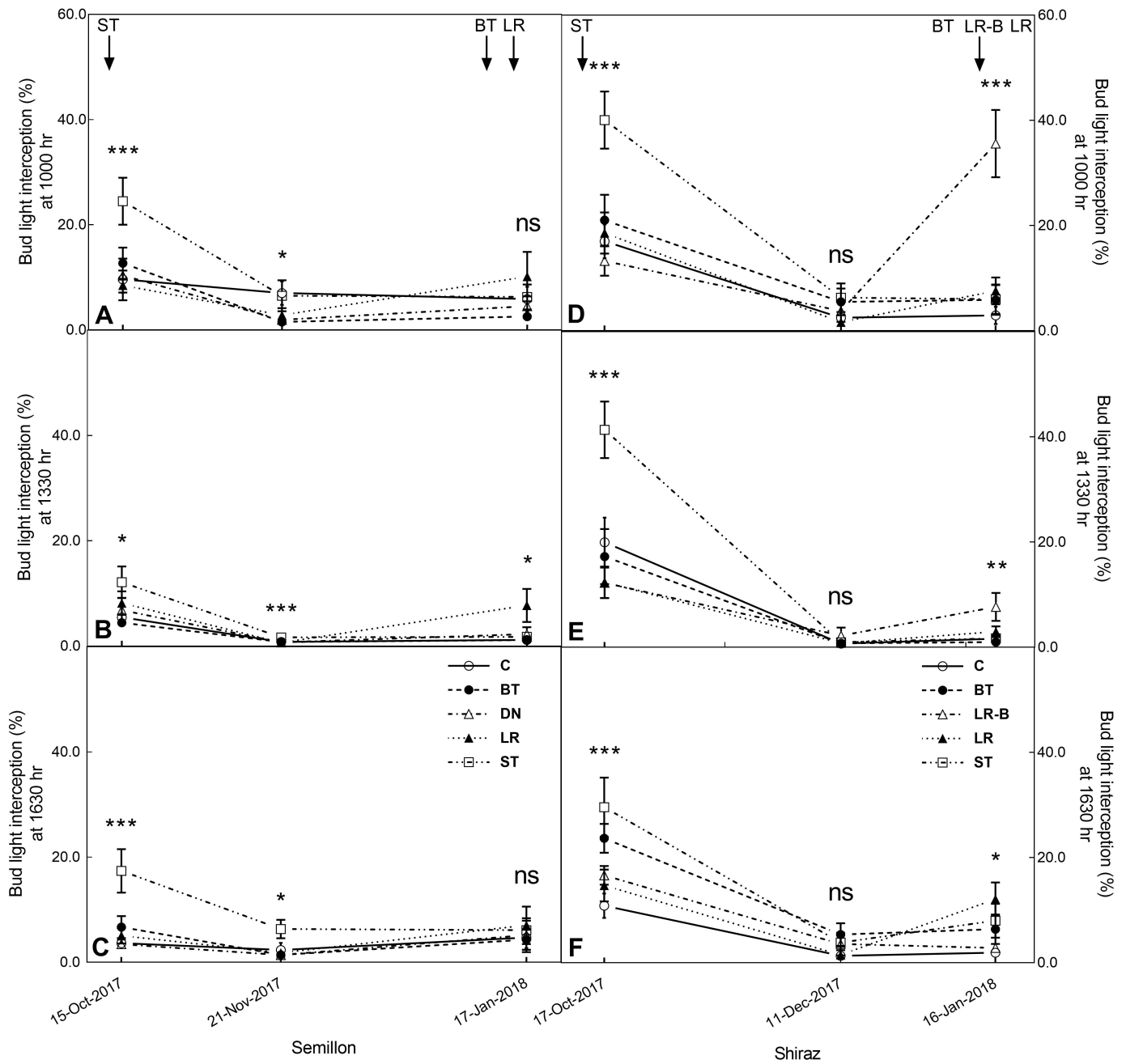


Figure 6 Effects of different canopy management treatments (C, control; BT, bunch thinning; DN, double nodes; LR-B, leaf removal at bunch zone; LR, leaf removal at middle third canopy; ST, shoot thinning) on light interception at bud zone of Semillon (**A**, at 1000hr; **B**, at 1330 hr; **C**, at 1630 hr) and Shiraz (**D**, at 1000hr; **E**, at 1330 hr; **F**, at 1630 hr) for season 2017/18. The time of the application of the treatments are indicated by arrows. *, **, and *** indicate significance at $p \leq 0.05$, 0.01, and 0.001, respectively, ns: not significant, by LSD test at 5% level.

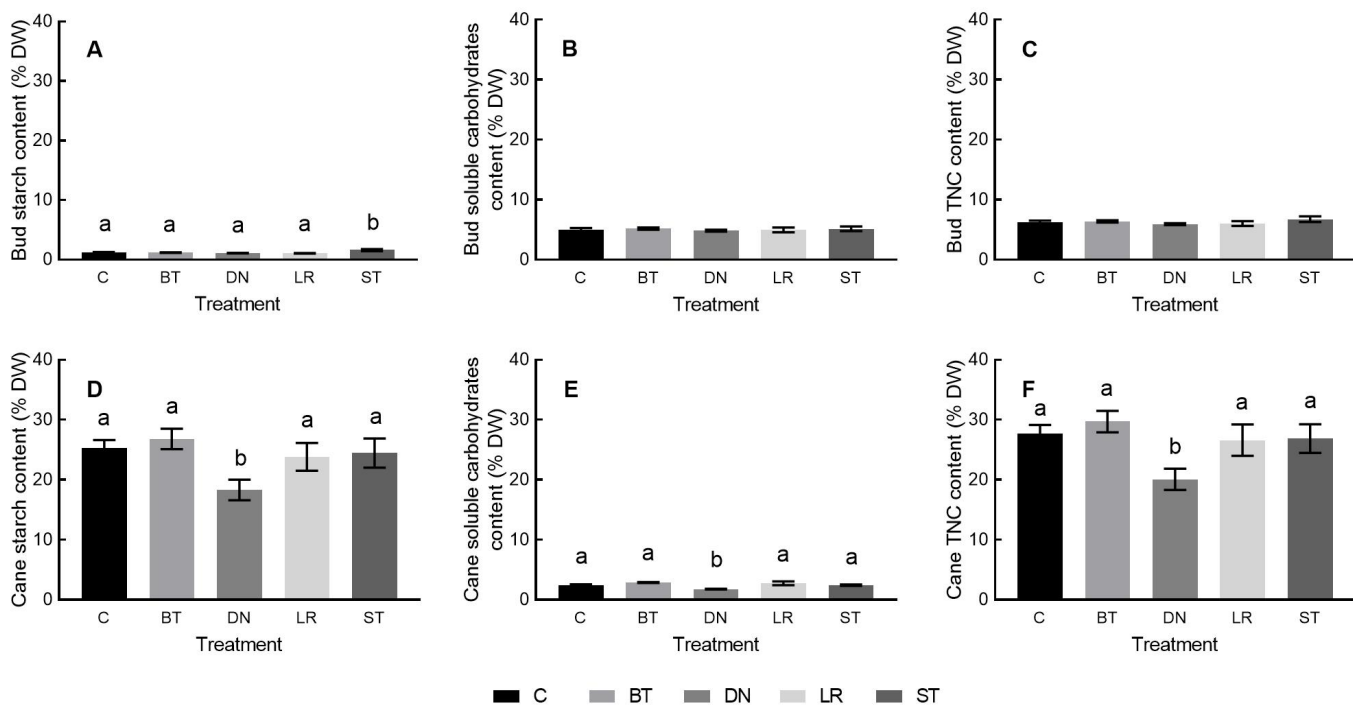


Figure 7 Effects of different canopy management treatments (C, control; BT, bunch thinning; DN, double nodes; LR, leaf removal; ST, shoot thinning) on Semillon carbohydrate contents of bud (**A**, bud starch content; **B**, bud soluble carbohydrate content; **C**, bud TNC content) and cane (**D**, cane starch content; **E**, cane soluble carbohydrate content; **F**, cane TNC content) for season 2017/18. DW, dry weight. TNC, total non-structural carbohydrate. Bars with different letters are significantly different by LSD test at 5% level.

Chapter 5: General Conclusion and Future Directions

Findings from this thesis suggest that canopy management practices can be useful to manipulate yield components, bunch architecture and berry maturity. In addition, bud fruitfulness, which determines the yield potential for the following season, can also be influenced by the practices. Certain practices were more effective at manipulating vine performance than others and careful consideration should be made when choosing and applying canopy management practices for their impact on reproductive performance in both current and future seasons.

Shoot thinning effectively changed the canopy architecture. Light interception at the cordon level and at the bud zone were both significantly increased after the application. The large increase in light interception led to an improvement in bud fruitfulness with a higher number of inflorescence primordia within the compound buds. Leaf area index was lowered by shoot thinning. However, the shoots and leaves retained showed a compensation effect and no statistically significant differences on canopy architecture by shoot thinning were found after veraison. The compensation in vegetative growth was reflected by results of shoot vigour measurement. The cane weight and internode diameter between nodes two and three were significantly increased by shoot thinning, as well as the starch content of buds. The shoot vigour, as well as carbohydrate content in buds, were both positively correlated with the size of inflorescence primordia, which was also largely increased by shoot thinning.

Shoot thinning and bunch thinning both advanced berry ripening through increasing the source-sink ratio, resulting in higher berry weight and faster sugar accumulation. In terms of yield components, the two practices both lowered bunch number as expected, but at the same time increased berry weight and bunch weight. Shoot thinning also increased berry number per bunch. The compensation effect in shoot thinning in both berry number and berry weight was great enough to lead to the same yield as the control. Additionally, shoot thinning had the greatest impact on bunch architecture among all the treatments. Bunch compactness was increased and the highest incidence of *Botrytis* bunch rot was induced by shoot thinning for Semillon.

Leaf removal at veraison decreased leaf area index and increased light interception both within the canopy and at the bud zone. Delayed berry ripening with lower TSS was found in both leaf removal at the fruit zone and when applied to the middle third part of shoots. Both types of leaf removal did not exhibit an influence on yield components for the two varieties. For bud fruitfulness, although the number of inflorescence primordia remained unaffected, the size was enlarged significantly by leaf removal in Semillon.

Light pruning was conducted by leaving double the amount of nodes (potential shoots) at winter pruning, however, the leaf area index did not change significantly and little effect on canopy porosity and light interception was found. As for yield components, bunch number was significantly higher but the total yield remained the same as the control due to the significantly lower berry weight and bunch weight of the light pruning. The carbohydrate content of canes was decreased by light pruning in both starch and soluble carbohydrate. However, bud fruitfulness was unaffected.

In this study, there were no consistent results in berry uniformity, measured by Millerandage index (Collins and Dry 2009), and primary bud necrosis incidence in response to the canopy management practices. However, the climate conditions of the two seasons of the project were very different. The season 2016/17 was wet with the monthly rainfall being higher than the long-term average, while season 2017/18 was much drier and hotter. As demonstrated by large differences between the two seasons, berry uniformity and incidence of primary bud necrosis may be more influenced by the seasonal weather or other factors. In addition, although bud fruitfulness was thought to be largely impacted by the light microclimate and shoot vigour as described in Chapter four, we cannot with certainty rule out the influence of other seasonal influences, such as rainfall and temperature. Further experimentation is required to determine how the interaction of canopy management and seasonal variance affect grapevine reproductive performance. Other factors that would influence primary bud necrosis such as plant hormones are also worth investigating in future.

The incidence of Botrytis bunch rot in Semillon was observed only in one season in this study, as well as the measurement of carbohydrate content in buds and canes.

Future experiments for additional seasons to improve our understanding would include how the two bunch compactness indices used in this study are correlated with the incidence of Botrytis bunch rot and how the carbohydrate content influences bud fruitfulness both at the whole grapevine and the bud levels.

In this study, the effects of canopy management practices on the size of inflorescence primordia that described in Chapter four and the final bunch weight at harvest (described in Chapter three) was similar where by larger IP area also resulted in larger bunch weight. Future studies are also suggested to look into the relationship between the results of bud dissection analysis and actual bunch architecture and yield components in the following season. A better understanding of the relationship between the size of inflorescence primordia and the actual bunch size may be helpful to increase the accuracy of early yield prediction.

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Appendix

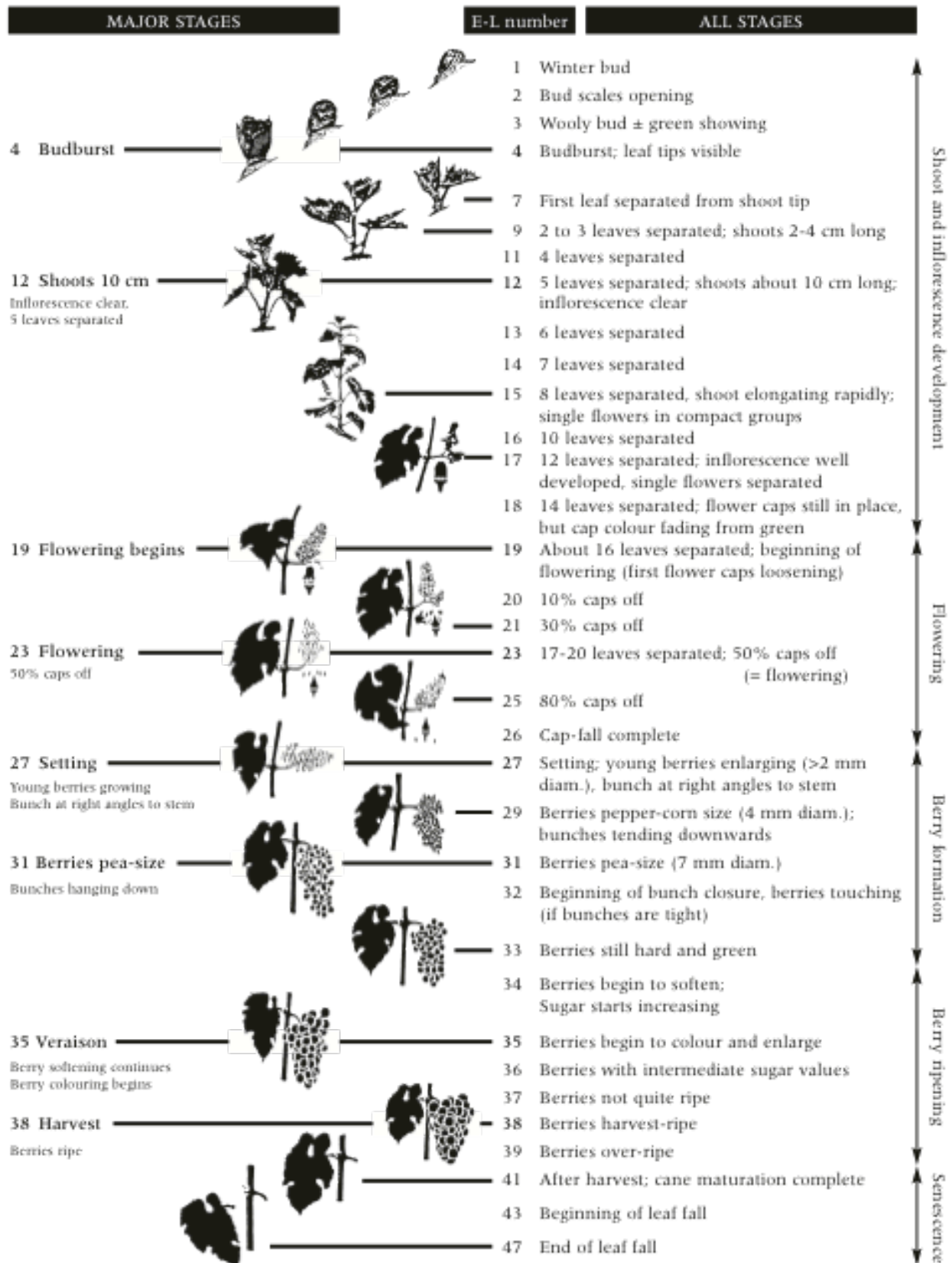


Figure. The modified Eichhorn-Lorenz stages (Coombe 1995).