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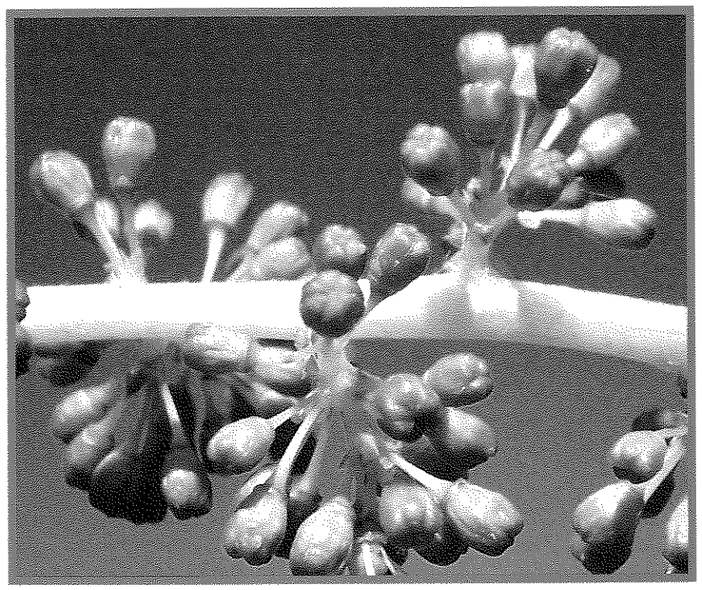

SEMINAR

Transforming Flowers to Fruit

Proceedings of a seminar held in Mildura, Victoria, 29 July 2005

Australian Society
of Viticulture and
Oenology Inc.

PROCEEDINGS

ASVO SEMINAR

Transforming Flowers to Fruit

Mildura Arts Centre, Mildura Victoria
Friday, 29 July 2005

edited by
Kerry de Garis, Christopher Dundon, Russell Johnstone and Steve Partridge

compiled by
Val Rechner

The ASVO gratefully acknowledges the support of this seminar by the Grape and Wine Research Development Corporation.

Australian Government
Grape and Wine Research and Development Corporation

Australian Society of Viticulture and Oenology
GPO Box 582
Adelaide SA 5001
Australia
www.asvo.com.au

ISBN 0 9587086 8 1

Produced for ASVO by Michael Major Media
Printed by Openbook Print, Adelaide

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Genes involved in grapevine flowering

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Introduction

Plants adapt their flowering time to the environment in which they grow for successful reproduction. A multitude of signals are involved in the induction, evocation and initiation of flowering. Molecular and genetic studies on annual model plants are identifying and characterising a growing number of genes involved in the flowering process. Current knowledge points to a complex regulatory mechanism that is in operation, and this system mediates the transmission of environmental and developmental cues to the shoot apex where they programme the vegetative meristem to undergo the transition to flowering. The environmental and developmental cues switch on genes that are involved in flowering time control and they activate the inflorescence and floral meristem identity genes, which in turn switch on the floral organ identity genes that cause the development of floral organs such as sepals, petals, stamens and the gynoecium, and flowers are formed (Figure 1).

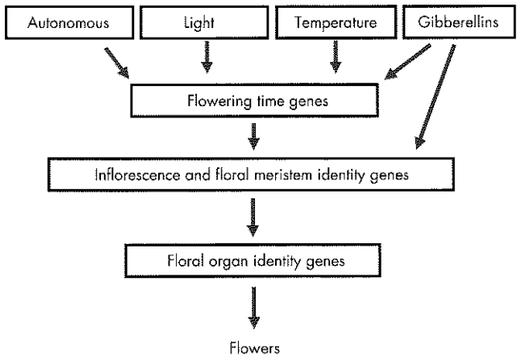

Figure 1. Flowering pathways

The flowering process in grapevine

Flowering in grapevine (*Vitis vinifera* L.) and the development of grapevine flowers differ significantly from annual species in having distinct juvenile and adult periods. Although closely linked to the transition from one to the other, time to flowering usually requires years. Unlike annual plants where the main vegetative meristem is switched to a reproductive mode, in grapevine vegetative and reproductive meristems develop on the same shoot (Boss et al. 2003). During grapevine shoot development the shoot apical meristem produces both leaf primordia and a meristematic p rotuberance called an uncommitted primordium or anlagen (Figure 2) in a regular pattern (Boss and Thomas 2002). When uncommitted primordia are formed in latent buds (second order buds in the axils of leaves) they have the potential to develop into inflorescences and when they are formed on rapidly elongating shoots, they usually develop into tendrils. In latent buds of vinifera cultivars the first uncommitted primordia are formed opposite to two of every three leaf primordia after the formation of three to eight leaves. Depending on the cultivar and environmental conditions, the first one to three uncommitted primordia formed in latent buds undergo repeated branching and form into immature inflorescences before the buds enter dormancy and the immature inflorescences survive winter in a quiescent state. Budburst occurs in the following spring and then the immature inflorescences continue differentiation to form floral organs to produce flowers.

An important aspect of grapevine development based on several lines of evidence is that grapevine tendrils and inflorescences are considered homologous structures (Boss and Thomas 2000). After seed germination, the grapevine shoot elongates and after the production of six to ten juvenile leaves by the apical meristem, the plant enters adult development and the first tendrils are formed. The production of the first uncommitted primordium, which in this case develops into a tendril, indicates that the plant now has

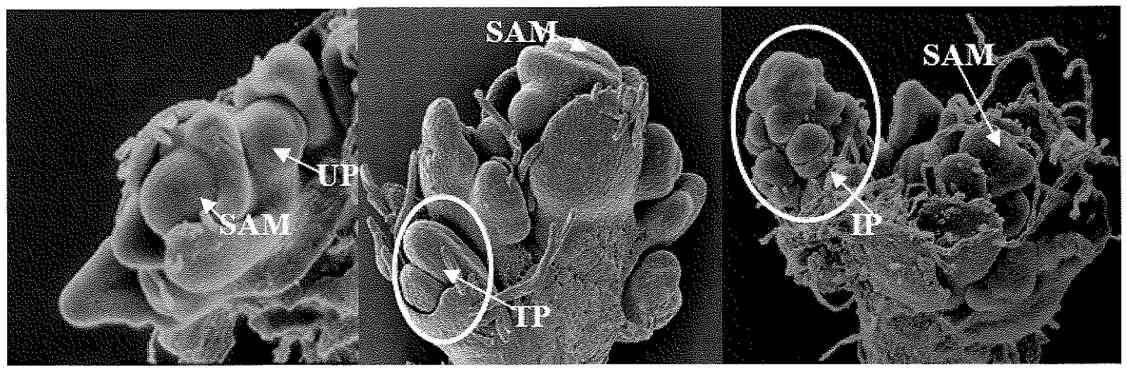

Figure 2. Electron scanning microscopy of dissected grapevine buds showing shoot apical meristem (SAM), uncommitted primordium (UP), tendril primordium (TP) and inflorescence primordium (IP)

the potential to form inflorescences. But the plant does not flower until latent buds are formed and a favourable environment exists. It is suggested that the floral stimulus is repressed in actively growing vines and that a major influence on grapevine flowering is a signal that inhibits the differentiation of uncommitted primordia into inflorescences on developing shoots (Boss et al. 2003). In the slow growing latent buds in the leaf axils, this repression is lifted and allows the production of inflorescences from uncommitted primordia.

Thus uncommitted primordia are vital to the development of the inflorescence and to the architecture of the plant. Identification of the signals that determine whether an uncommitted primordium will differentiate into an inflorescence or a tendril may enable the manipulation of fruitfulness and bunch number. If we can understand how the uncommitted primordia themselves are made, we may be able to alter the architecture of the plant, and reduce inputs into the vineyard management of grapevine (Boss et al. 2003).

Towards a grapevine flowering model

To fully understand how the flowering process is regulated in grapevine, it is essential to isolate and characterize the genes involved in flowering from grapevine and relate the expression of these genes to actual morphological development in plants. It is also important to track the progress of floral development in parallel with the expression patterns of these genes and the environmental conditions. This could in turn lead to the development of a grapevine flowering model which could help to predict time of flowering and yields more accurately. Through selected manipulation of this signaling network it may even be possible to promote or inhibit flowering. Several genes that show that they have key roles in the flowering process have now been isolated from grapevine by our group at CSIRO Plant Industry and the grapevine flowering model is being developed. These genes fall into the categories of flowering time genes, inflorescence and floral meristem identity genes and floral organ identity genes.

Figure 3. The Pinot L1 mutant produces inflorescences and berries down the length of the shoot and no tendrils

Flowering time genes in grapevine: From the analysis of a mutant grapevine that has an altered floral induction phenotype, evidence has arisen that GAs (gibberellins) are major inhibitors of inflorescence formation in grapevine (Boss and Thomas 2002), which is quite contradictory to what has been observed in the model annual plant Arabidopsis. The mutant was identified when plants were generated from the L1 and L2 cell layers of Pinot Meunier which is a periclinal chimaera of Pinot Noir (Franks et al. 2002). Those from the L1 cell layer were dwarfed and produced inflorescences down the length of the shoot without forming any tendrils (Figure 3). Large increases in bioactive GAs (GA_1 and GA_4) were observed in the dwarf plants indicating a reduced ability to respond to GAs. Genetic studies showed that this was because of a point mutation on a gene that was involved in GA signal transduction impairing the response of the plant to GAs. This gene, named *VvGAI* was the first gene involved in flowering time control to be isolated from grapevine. Three other genes have also now been isolated. Flowering time mutants are reported to display their major effects on the duration of vegetative development, whereas mutations in floral meristem identity genes are found to disrupt floral development. Therefore, flowering time genes are often assumed to act before floral meristem identity genes and to lead to their activation (Pineiro and Coupland 1998).

Floral meristem identity genes in grapevine: In recent years, a significant understanding has been gained regarding the molecular mechanisms of floral determination and the differentiation of floral organs. The two plants in which the most progress has been made in this direction are *Arabidopsis* and snapdragon (*Antirrhinum majus*). In both these plants, flowering is a two-step process in which firstly the vegetative (V) meristems are transformed into inflorescence (I) meristems, and then the inflorescence meristems produce floral (F) meristems in the axils of bracts (Fosket 1994). *TERMINAL FLOWER1* (*TFL1*), *LEAFY* (*LFY*), *APETALA1* (*AP1*) and *FRUITFULL* (*FUL*) are key meristem identity genes in *Arabidopsis* involved in the transition to flowering, inflorescence formation, and plant and inflorescence architecture. *TFL1* acts as

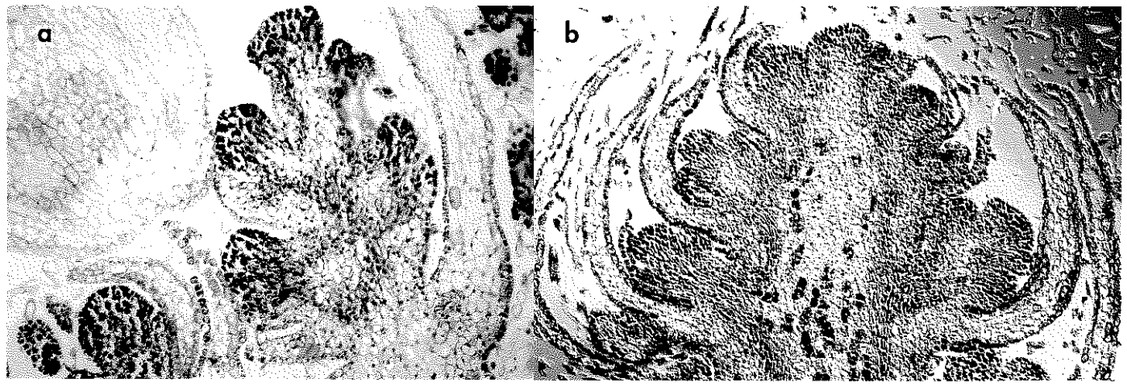

Figure 4. Sections through latent buds of grapevine at the first leaf stage show the genes *VvLFY* (a) and *VvMADS6* (b) are active in the developing inflorescence. Areas of expression are indicated by purple-blue colouration which is restricted to developing floral meristems and not to other tissues such as the bracts

a repressor of floral meristem formation acting antagonistically to *LFY* and acts as an inflorescence meristem identity gene maintaining the vegetative state of the inflorescence apex. *LFY* is involved in switching the vegetative meristem to the reproductive mode. *AP1* is the gene of floral commitment and is involved in the development of floral meristems. *FUL* acts redundantly with *AP1* in specification of floral meristems and also is involved in the normal development of fruit. Homologues of all these genes have now been isolated from grapevine by our group at CSIRO. Using the technique of *in situ* hybridisation showing in which tissues of the plant the gene is active (Figures 4a, b) and other expression studies, the roles of these genes as grapevine floral meristem identity genes could be further confirmed. When the grapevine *TFL1* gene was put into tobacco and *Arabidopsis* plants, it caused delayed flowering showing that grapevine *TFL1* is a repressor of flowering and functions like the *Arabidopsis TFL1* (Boss and Thomas, unpublished data). Characterisation of *VFL*, the *LFY* homologue in grapevine (Carmona et al. 2002), showed that it was expressed over the two seasons of inflorescence development. However, it was observed that it was not only expressed in floral meristems, but also in vegetative meristematic tissues such as leaf primordia and immature leaves, suggesting that in grapevine the gene has a more general role.

Floral organ identity genes in grapevine: As mentioned earlier, floral organ identity genes are important for the normal development of the floral whorls, and determining the genetic cause of the development of the reproductive floral organs especially would lead to a better understanding of floral development, fertilisation and fruitset. Grapevine genes belonging to this category (*VvMADS1* to *VvMADS5* and *VvMADS9*) have now been isolated and sequenced. Gene expression analyses of these genes show that they may be involved in the formation of floral organs such as petals, stamens and the ovary. Among these organ identity genes, *VvMADS5* and *VvMADS9* stand out. *VvMADS5* is highly expressed in developing seeds and could be detected at lower levels in both pre- and postveraison berries (Boss et al. 2002). Its homology with genes of known function from other species and its pattern of expression suggest that *VvMADS5* influences carpel (ovary) and ovule development and may be useful for studying dioecy in *Vitis* species, or to alter ovule and seed development in grapevine for the production of seedless grapes. *VvMADS9* is a gene which is involved in petal and stamen development. In grapevine also, its expression was detected on these two whorls. Studies in apple (Yao et al. 2001) have shown that a similar gene also has a role in the production of seedless fruit and further work may reveal if the grapevine gene has a role in producing seedless grapes.

Future research

Quite a number of the key genes involved in grapevine flowering have now been isolated to build the initial framework of a model, although there are more genes to be cloned to make the model complete. Future advances in our understanding of grapevine flowering and fruitfulness will depend on integrating gene research with physiological and biochemical studies at the cell, organ and whole-plant level (Boss et al. 2003).

If we wish to model yield development quantitatively we need to investigate closely how the environment/climate modulates the effectiveness of the genes in this genetic network. Key genes that are sensitive to environmental conditions will need to be identified through molecular techniques such as Gene chips, and this may in turn lead to better predictors of yield and genetic solutions where plants are less sensitive to environmental conditions and produce more consistent yields from year to year.

Acknowledgement

This work was supported in part by the Commonwealth Cooperative Research Centre Program, and specifically the Cooperative Research Centre for Viticulture (CRCV) and the Grape and Wine Research and Development Cooperation (GWRDC). We also wish to thank Don Mackenzie for technical assistance.

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Grapevine growth and reproduction: an overview

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The industry issue

Substantial year-to-year variation in winegrape yields (e.g. Figure 1) and fruit composition create major problems for the Australian wine industry, resulting in economic losses and frustration for viticulturist and winemaker alike.

The causes of this seasonal variation are complicated and driven by the interaction of a number of biotic and abiotic factors, principally weather, soil properties, pests and disease, and vineyard management practices.

The inability to accurately forecast yield can have significant effects on both grower and winery cash flow and budgeting process, harvest intake logistics, tank space allocation, oak management, investment strategies for future assets and marketing strategies for domestic and export markets. They may also be associated with variations in fruit composition and subsequent wine quality, which jeopardises the ability to meet customer preferences.

The cycle of yield development

In order to understand the causes of this temporal variation in yield, it is important for viticulturists and winemakers to have a detailed understanding of vegetative growth and reproduction in grapevines. This paper presents an overview of reproduction in grapevines with particular emphasis on critical stages of development.

1. Induction and initiation

In contrast to the visible vegetative growth, which occurs over a season, reproduction in the grapevine spans consecutive seasons beginning some 14 or more months prior to harvest with the induction and initiation of inflorescence primordia. The exact timing of initiation is dependant on the variety of grape, the growing region (accumulated heat units) and the node position along the growing shoot.

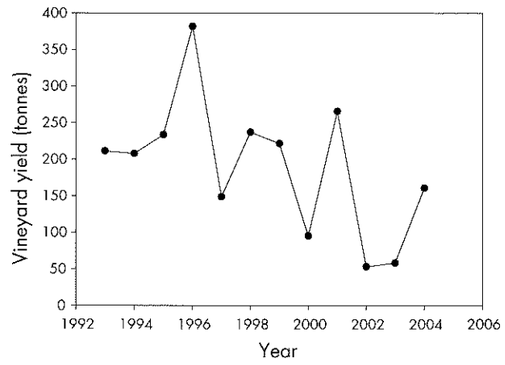

Figure 1. An example of seasonal variation in tonnage from a Cabernet Sauvignon vineyard located in Coonawarra, South Australia. The percent coefficient of variation (%CV) is 49.3% between seasons

Flower buds begin to develop in between leaf primordia of latent buds that are situated in the axils of every leaf on a young green shoot during the late spring and early summer period prior to entering dormancy (May 2004). The first visible sign of initiation is the formation of an extra-lateral meristematic structure called an 'anlage' during spring (Figure 2).

Anlagen initiation takes place in basal buds on a shoot at around the time of, or just prior to flowering and progresses up the shoot. Anlagen may develop into three types of primordia, namely inflorescence primordia, transition forms between inflorescence and tendril primordia, and tendril primordia (Barnard 1932; Barnard and Thomas 1933). Studies in controlled-environment conditions (Buttrose 1974), and in the field (Lavee et al. 1967) have demonstrated that floral induction occurs well before the initiation and presence of anlagen. This work suggested that Muscat of Alexandria and Sultana buds are sensitive to environmental stimuli 20 and 18 days respectively before the appearance of anlage.

The anlage first forms a bract primordia, then divides into an 'inner' and 'outer' arm. The inner arm, and often the outer arm, may differentiate branch initials before the bud enters dormancy (Barnard and Thomas 1933).

2. Differentiation

Light microscopy (Barnard 1932; Barnard and Thomas 1933) and scanning electron microscopy studies (Srinivasan and Mullins 1981) of developing buds demonstrate that anlagen which undergo extensive branching prior to dormancy form inflorescences, while those that possess only two or three branches prior to dormancy tend to form tendrils (Clingeleffer 2001). Anlagen which have been directed to develop as inflorescences will undergo repeated

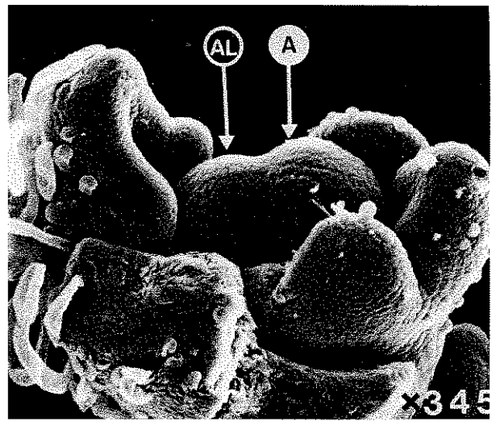

Figure 2. Section of the apex (A) to form the anlage (AL). The anlage is opposite the youngest leaf primordium. Srinivasan and Mullins 1981. AJEV 32(1). Copyright ©1981 by ASEV. Reprinted by permission

branching to form a conical structure composed of many rounded branch primordia (Srinivasan and Mullins 1981; Figure 3).

A fully developed inflorescence primordium takes the bunch-like appearance, in which each berry-like branch primordium is a protuberance of undifferentiated meristematic tissue (Srinivasan and Mullins 1981; Figure 4). There is evidence which suggests that the amount of branching occurring in the inflorescence primordia prior to the onset of dormancy positively influences potential inflorescence size expressed as flowers per inflorescence in the following spring (see Dunn in these proceedings).

The initiation and subsequent differentiation of bunches in buds is a critical control point in determining the yield potential of grapevines. Clingeleffer (2001) demonstrated that bunch number alone could typically explain 60-70% of the annual variation in yield. Therefore, in our efforts to stabilise yield between seasons, it is important to understand quantitatively how the environment and vineyard management practices combine to influence initiation and differentiation within latent buds. Baldwin (1964) identified a relationship between the percentage of fruitful buds (those containing inflorescence primordia) at node positions 4, 9 and 14 on dormant canes and the hours of sunshine and daily maximum temperatures above 29°C in a 20 day period between mid-November to mid-December in the previous season for Sultana. There is still only limited knowledge of the timing and the weather conditions affecting the formation of inflorescence primordia in Australia's major winegrape varieties (Chardonnay, Shiraz and Cabernet Sauvignon).

3. Dormancy

There is little development within the bud during the dormant period between the onset of dormancy in autumn and winter until early-mid August (in Mildura, Victoria; May 1964). This was verified by Scholefield and Ward (1975), who demonstrated using scanning electron microscopy that Sultana buds were structurally similar between 6 May and 3 August.

4. Budburst and floral development

It is widely accepted that further branching and the differentiation of individual flowers and floral parts occur during budburst. Therefore, conditions and management practices, such as pruning, which affects the extent (%) and nature (which buds burst) of budburst, can exert a profound influence on yield development. Percentage budburst on a vine is a function of the retained node number and the amount of stored carbohydrate in the perennial parts of the vine which can be mobilised in spring for growth (often referred to as 'capacity' of the vine). However, it is still unclear which buds will burst on a grapevine, especially in situations where a high number of nodes per vine are retained after pruning. Antcliff and Webster (1956) speculate that the more fruitful buds are the ones that burst in these situations, due to them acting as stronger sinks for assimilate,

Pouget (1981) found that substantially more flowers were formed on inflorescences in Cabernet Sauvignon and Merlot vines grown at 12°C compared with vines grown at 25°C (130% more for Cabernet Sauvignon and 29% higher for Merlot). Pouget (1981) speculated that the lower temperature regime favoured inflorescence growth by disadvantaging shoot growth. May (1987) proposed another theory based on higher temperatures causing a cytokinin enhanced enlargement of the early formed flowers, which in turn, inhibited the formation of other flowers on the inflorescence. Whatever the mechanism, it is clear that temperature conditions at budburst can have a major impact on the branching and differentiation of inflorescences prior to flowering. However, May (2004), suggested that the temperature conditions at budburst in Australian vineyards are unlikely to be sufficiently high to lead to reduced flower numbers per inflorescence in most years.

5. Flowering, fertilisation and fruitset

Flowering, fertilisation and fruitset is a critical period of yield development in grapevines, where a proportion of flowers will successfully set and become berries. Fruitset for grapevines can range between 0 and 40%, but commonly is between 20 and 30% (Mullins et al. 1992). The percentage fruitset is dependent on variety of grape, weather conditions at the time of flowering and fertilisation, crop load (carbohydrate balance), nutritional status and vineyard management practice.

To release pollen, the calyptra, or 'cap' must be shed. The stamens then move away from the pistil and the anthers rapidly dehisce. Both 'cap' removal and anther dehiscence are influenced by temperature and humidity (including rainfall) (Winkler et al. 1974). Below 15°C, few flowers shed their caps, but as the temperature approaches 18-20°C cap fall intensifies (Winkler et al. 1974).

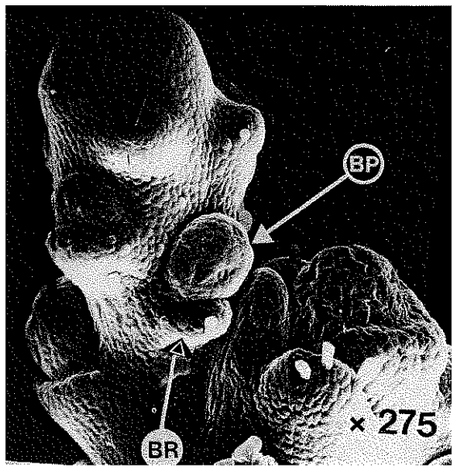

Figure 3. Growth of the main axis of the inflorescence primordium to form several branch primordium (BP) and bract primordium (BR). Srinivasan and Mullins 1981. AJEV 32(1). Copyright ©1981 by ASEV. Reprinted by permission

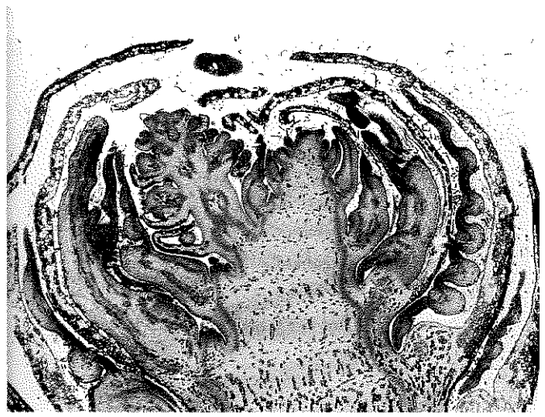

Figure 4. Longitudinal section through a Sultana bud showing the grape-like bunch primordium – August 1929. Slide prepared by C. Barnard, photographed in April 1956 by E. Lawton, CSIRO Merbein, Victoria. Reproduced with permission from Possingham et al. 1990

Poor fruitset can occur in all grape varieties, and is more prevalent in cooler grapegrowing regions. Some cultivars, e.g. Merlot, are particularly sensitive to cold weather around the time of flowering. Low temperatures interfere with the differentiation of flower primordia, leading to defective reproductive structures and fewer flowers per bud and poor fruitset (Ebadi et al. 1995). A special case of poor fruitset is called millerandage, or 'hen' (large berries) and 'chickens' (small berries). Certain cultivars and clones, such as Chardonnay and Merlot appear to be more susceptible to millerandage than other grape cultivars.

Poor fruitset has also been historically linked to poor boron and zinc nutrition (Bessis et al. 2000), but more recently there have been reports linking poor fruitset in Merlot to molybdenum (Williams and Bartlett 2002).

While flowering, fertilisation and fruitset is a critical stage of grapevine growth and development, it should be noted that in most years, berries per bunch explains only 20-30% of the annual variation in grapevine yield (Clingeleffer 2001). Again, it is important to note, that recent statistical studies have shown that the most important determinant of yield is bunch number per vine, which typically accounts for approximately 60-70% of the year-to-year variation in yield.

6. Berry Growth

In seeded grape cultivars, berry growth is initiated by pollination and subsequent fertilisation. Flowers that fail to fertilise, shrivel and die (Mullins et al. 1992). Berry growth typically follows a double sigmoidal growth pattern (Mullins et al. 1992). This can be divided into three arbitrary stages;

Stage 1 – The initial phase of rapid berry growth, characterised by the growth of the seed and pericarp. There is little development of the embryo (Mullins et al. 1992). During this stage, the majority of the cell division occurs within the berry. Berries also accumulate organic acids and are still green and hard.

Stage 2 – The 'lag' phase, characterised by slow growth of the pericarp and by the maturation of the seeds within the berry (Mullins et al. 1992). The berry remains green and hard during this phase, which may last between 7-40 days depending on cultivar and growing region (Mullins et al. 1992).

Stage 3 – This stage is marked by the onset of berry softening, berry ripening and by colour change in pigmented varieties. The stage at which anthocyanin pigments appear in the skins of red or black grape cultivars is known as 'veraison'. In this stage rapid berry growth resumes, due solely to cell expansion (Mullins et al. 1992).

Berry size is greatly influenced by the number and dry weight of seeds per berry (Clingeleffer 2001). It is also greatly influenced by irrigation management (McCarthy 2000). While berry growth is important it typically only explains approximately 10% of the year-to-year variation in vineyard yield (Clingeleffer 2001).

Summary

The cycle of yield development in grapevines extends over two growing seasons and typically is in excess of 14 months from initiation through to harvest (Figure 5).

There are a number of critical control points during reproduction and these include;

- *inflorescence initiation and differentiation* – this is the most important step in the determination of yield potential in grapevines. Bunch number per vine explains 60-70% of the annual variation in yield and the weather conditions influencing the processes are broadly understood, however, the timing bud initiation and the weather events controlling the conversion of the vegetative apex into the reproductive structure are not well understood in Australia's major winegrape varieties and growing regions.

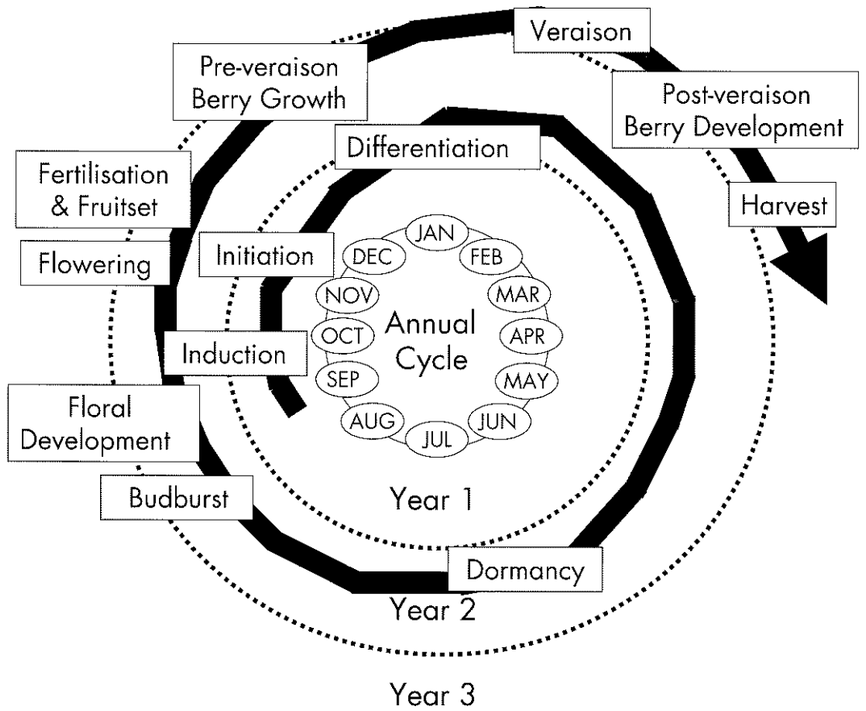

Figure 5. A summary of the cycle of yield development in grapevines from induction (Year 1) through to harvest (Year 3) (Adapted from Wilson 1996)

- *budburst and floral development* – knowing which buds will burst and the weather conditions experienced during the early floral branching and differentiation can also have a major influence on the yield potential of grapevines.
- *flowering and fruitset* – the number of berries per bunch typically explains around 20 to 30% of the total annual variation in yield. The weather conditions around this stage of development can have a major influence on the success of these flowering and fertilisation processes. Grapevines are also sensitive to nutrient disorders, water status and pest and disease pressures at this stage of development.

A grapevine has the ability to self regulate its yield to a limited degree, most likely through effects on carbohydrate balance within the vine. This plasticity allows the vine to regulate percentage bud burst, fruitset and berry growth effectively.

Acknowledgments

The authors would like to thank the Australian Society of Viticulture and Oenology for allowing us the opportunity to present at this important seminar. The ongoing financial contribution of the Grape and Wine Research and Development Corporation is gratefully acknowledged. Also, the financial contributions of the Victorian Department of Primary Industries and CSIRO Plant Industry are also gratefully acknowledged.

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Factors that control flower formation in grapevines

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Introduction

Grapevines, like most other spring-flowering perennials, commence forming their flower buds during the preceding season. Flower buds begin to develop in axils of leaf primordia of primary latent buds during late spring and summer before entering a period of dormancy. During winter these dormant buds are covered by a protective layer of hairs and enclosed within a scale. In the following season, flowers are formed during a short period spanning bud burst. The formation of inflorescence primordia (flower buds) determines the potential number of bunches that the vine will carry, while the number of flowers formed on an inflorescence primordium determines the potential number of berries that may be set on that bunch. Hence, gaining an improved understanding of the physiology of flower formation remains a pursuit of considerable economic importance as well as one of intellectual interest.

Flower formation in grapevines follows three well-defined steps:

- Anlagen, or uncommitted primordia, are formed in the apices of latent buds on shoots of the current season;
- These specialised meristematic structures may differentiate inflorescence primordia; and,
- Individual flowers are formed on inflorescence primordia (Perold 1927, Barnard 1932, Barnard and Thomas 1933).

For grapevines grown in temperate climates, steps 1 and 2 are usually completed during the previous season. Individual flowers, on the other hand, are not formed until during budburst in the current season (Barnard 1932, Synder 1933, Winkler and Shemsettin, 1937, Srinivasan and Mullins 1981, Scholefield and Ward 1975). The reproductive biology of grapevines has been reviewed from a variety of aspects. For instance, Pratt (1971) presented a detailed and comprehensive review of the reproductive anatomy of grapes while Buttrose (1974a) reviewed what was known about the effect of climatic factors (mainly light and temperature) on inflorescence initiation. More recently, Srinivasan and Mullins (1981) reviewed the physiology of flowering in grapevines, placing particular emphasis on the controlling role of phytohormones. Here flower formation is revisited with the aim of synthesising these and other, often disparate, treatments of the subject. For each step of flower formation in turn, our state of knowledge on its control with particular emphasis on the effects of the environment and viticultural management will be reviewed. Then, areas that warrant further attention within the context of the current research and development environment will be described.

Developmental morphology

Flower formation in grapevines involves a long multi-step process. The first visible sign of the evocation of flowering is the initiation, during spring, by the apical meristem of an extra-lateral meristematic structure called the 'anlage'. The anlage, a term introduced by Barnard (1932) first forms a bract primordia, then divides into an 'inner' and 'outer' arm. The inner arm, and often the outer arm, may differentiate branch initials before the bud enters dormancy. After dormancy, and during budburst of the following season, further branching takes place, terminating in the formation of individual flowers. Overall, the process determines potential yield, first by exerting a coarse control over potential bunch number, and then by exerting a finer control over flowers per bunch (bunch size).

Anlagen initiation takes place in basal buds around the time of flowering and progresses up the shoot. Anlagen may become tendrils (as is the case with all anlagen formed on actively growing shoots), inflorescences, shoots (rare) or even transitional forms between all three. Studies in controlled-environment growth cabinets (Buttrose 1974a) and in the field (Lavee et al. 1967) have demonstrated that 'floral' induction occurs well before the initiation of anlagen. For the cultivars Muscat of Alexandria and Sultana the time interval is 20 d and 18 d, respectively. It remains intriguing that the meristem would be sensitive to floral stimuli well before the appearance of anlage. It may be that conditions during this stage of development affect the competence (size or status) of the meristem to respond to floral stimuli.

Light microscope (Barnard 1932, Barnard and Thomas 1933) and scanning electron microscope studies (Srinivasan and Mullins 1981) of developing latent buds demonstrate that anlagen which undergo extensive branching prior to dormancy form inflorescences while those that possess only two or three branches form tendrils. This would suggest that the extent of branching prior to dormancy controls potential inflorescence development. There is no evidence to challenge the long-held opinion of Barnard and Thomas (1933) that "the extent of the growth of an inflorescence during this period (mid-August to budburst) is largely dependent upon the stage of development it had reached at the end of the previous season (prior to dormancy)". Thus, quantitatively, flowering seems to be irreversibly evoked during the early stages of ontogeny.

This is consistent with the observation that the yield component bunch number tends to drive fluctuating yield in vineyards (Clingeleffer et al. 2004, Martin 2004) shown graphically in Figure 1.

It is possible to stabilise yield by altering the severity of pruning in response to an assessment of bud fertility, and thus yield

potential, during dormancy (see Dunn et al. 2005). This is a type of pruning that is 'informed' by a knowledge of bud fertility. Along with assessing bud fertility one also needs to be able to predict the extent of budburst and quantify compensation in yield components in response to retaining more or less buds.

For vines that are pruned by hand, it is possible to leave more or less buds by either altering the number and length of retained spurs or the length and number of retained canes. However, many vineyards are now mechanically pruned and it is extremely difficult for pruners to target pre-determined bud numbers. Current research aims to alter the severity of mechanical pruning to manage fluctuating fertility based on modelling the number and distribution of retained buds after mechanical pruning. The model is used to set the height and width of pruning saw cuts.

Tendrils and inflorescences are considered to be homologous structures (Morrison 1991) since they are derived from the same meristematic structure, and because it is possible to convert one structure to another (Srinivasan and Mullins 1981) and intermediate forms are common in the vineyard. Evidence for growth substances playing a controlling role in flower formation is strong. Srinivasan and Mullins (1979, 1980) demonstrated that the repeated exogenous application of cytokinin to shoot apices induced inflorescence formation in the place of tendril formation. Thus, cytokinins are probably involved in the early differentiation of anlagen. Interestingly, applying cytokinins to young tendrils also transformed them into inflorescences. That young tendrils are still able to form flowers indicates that they may be modified inflorescence primordia, which are being inhibited from differentiating floral meristems. Also, isolated tendrils cultured *in vitro* with cytokinins underwent repeated branching and grew into inflorescences and inflorescence-like structures (Srinivasan and Mullins 1978). The exogenous application of gibberellins, on the other hand, turned inflorescences into tendrils and tendril-like structures (Mullins 1968). Culturing excised inflorescence primordia of Pinot Noir and Chardonnay with gibberellin alone led to the formation of shoots and tendrils (Yahyaoui et al., 1998). Interestingly, application of the growth retardant chlormequat inhibits anlagen formation but promotes the formation of inflorescence primordia from anlagen (Mullins et al. 1992). These results led Srinivasan and Mullins (1981) to propose a simple model for the transition of the vegetative apex to an inflorescence based on variations in endogenous cytokinins, gibberellins and inhibitors whose effect is mimicked by synthetic growth retardants such as chlormequat.

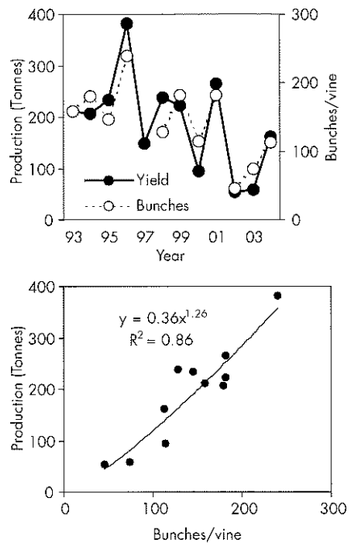

Figure 1. Patterns of yield variation over time in a commercial block of Cabernet Sauvignon at Coonawarra

Obvious differences in the distribution (on shoots) and number of inflorescences exist between genotypes. As discussed earlier tendrils and inflorescences are closely related. They derive from the same 'uncommitted primordia', intermediate forms are common in the vineyard and the transition from tendril to inflorescence and *vice versa* can be induced through the exogenous application of plant hormones. Boss and Thomas (2000) suggest that the close relationship between tendrils and inflorescences indicates a control step at the gene level, which controls the differentiation of anlagen down one or the other pathway. In the plants *Arabidopsis* and *Antirrhinum* models that describe the genetic control of flower formation have been constructed. These models incorporate a complex set of regulatory processes involved in the transition of shoot meristem > inflorescence meristem > indeterminate floral meristem > determinate floral meristem (Ma 1998). Ma (1998) suggests that these models will inevitably increase in complexity through the identification of many other genes that must be involved (for grapevines, see Sreekantan et al. in these proceedings).

To summarise, flower formation in grapevines is a complex and, in some ways, a poorly understood process. The complexity of the process is increased by the imposition of dormancy between the ontogenetic development of anlagen and the formation of individual flowers at budburst. However, the picture that emerges shows the reproductive behaviour of the plant to be characterised by astonishing plasticity. The critical stages appear to be:

- **induction** of anlagen,
- **initiation and early differentiation (branching)** during spring
- further branching terminating in the formation of individual flowers at **budburst**

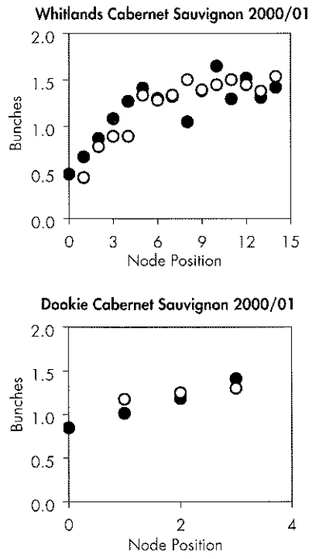

Figure 2. A comparison of estimates of fertility based on dissecting dormant latent buds during winter (μ) with observed node fertility measured six weeks after budburst (λ) for Cabernet Sauvignon at Dookie and at Whitlands. Vines at Dookie were pruned to three bud spurs while those at Whitlands were cane-pruned (from Dunn et al. 2001)

Environmental effects

High temperatures promote inflorescence formation in grapevines. This has been demonstrated in controlled-environment studies (Buttrose 1969a,b,c) and in field studies that have correlated temperature conditions during bud development with the subsequent formation of flower clusters (Alleweldt 1963, Baldwin 1964) or flowers (Palma and Jackson 1981) in the following season.

Cultivars differ in temperature requirements for inflorescence primordia formation (Buttrose 1970a, Srinivasan and Mullins 1981) and these differences seem to reflect differences in the climates of geographical origin. For instance, the 'cooler climate' cultivar Riesling will initiate inflorescence primordia at 20°C while the 'warmer climate' Muscat of Alexandria requires a temperature of at least 25°C (Buttrose 1970a) for initiation. Irrespective of the differences between cultivars, however, the temperatures required for maximum inflorescence primordia formation are higher than the temperature required for maximum dry matter production (Buttrose 1968). Thus, the mechanisms by which temperature controls dry matter production may differ from those that control inflorescence primordia formation.

Effects of temperature on induction and initiation

A perennial problem with field experiments that attempt to elucidate plant responses to environmental variables is that environmental variables are often confounded. For instance, high temperature coincides with a high number of sunshine hours or cloudiness tends to increase relative humidity. In an attempt to separate the effects of temperature and light on inflorescence primordia formation from each other as well as from other environmental factors, Buttrose (1969a,b,c, 1970a) conducted a series of studies in controlled-environment growth cabinets. By dissecting latent buds 13 weeks after budburst on small potted vines, he was able to show that temperature significantly affected the formation of inflorescence primordia. For the cultivar Muscat of Alexandria, latent buds on vines growing at 20°C formed no inflorescence primordia, while buds on vines growing at the optimum temperature of 35°C averaged 1.6 inflorescence primordia (Buttrose 1969a). By changing temperature conditions during development, he was able to deduce that the period of optimum sensitivity to induction was some three weeks prior to the initiation of anlagen (Buttrose 1969b, 1974a). Sensitivity to temperature was negligible before the separation of the node from the apex maximum at the time the node was separating from the apex, and then progressively declined becoming negligible when the node was about 10 positions below the apex. A pulse of only four hrs (day or night) of high temperature was required to maximise inflorescence primordia formation.

Thus, the induction of the vegetative apex to differentiate an inflorescence occurs long before the first visible signs of its formation. The strong relationship between size of basal leaf primordia and inflorescence number and size (May 1964, Buttrose 1970b) led Buttrose (1974a) to speculate that it is the way in which basal leaf primordia develop that influences floral induction. He suggested that basal leaf primordia must be of a certain size and adequately illuminated for the maximum development of inflorescence primordia. Thornley (1975), discussing floral transition in general, suggested that changes in the size of the vegetative apex could lead to reproductive growth. Palma and Jackson (1981) described a highly significant ($P < 0.01$) correlation between temperature on the day when the node was 3 node positions below the apex and the average number of flowers on that shoot in the following seasons for the cultivars Chasselas Doré, Pinot Noir and White Reisling. Although they did not report the number of clusters per shoot, they suggest that their results provide support for a very early, very specific effect of temperature on inflorescence primordia formation.

It is difficult, however, to reconcile optimum temperatures for inflorescence primordia formation defined by controlled-environment studies (Buttrose 1974a) with field observations. For example, the optimum temperature for inflorescence primordia formation in the cultivar Shiraz is 30°C (Buttrose 1970a), and if the period of maximum sensitivity to temperature is as the node is just separating from the apex, then this would coincide with budburst for spur-pruned vines. In the Yarra Valley at this time of year four hours of continuous 30°C+ during a 24-hour period seems unlikely. However, spur-pruned Shiraz vines produce many two-cluster shoots. It is likely that grapevine buds experience higher than ambient temperatures during the day. A theoretical analysis of the energy balance of apple buds and blossoms coupled with actual measurements (Landsberg et al. 1974) showed that apple bud temperatures could be up to 5°C higher than ambient temperatures on clear sunny days.

Effects of temperature on differentiation (branching) prior to dormancy

Baldwin (1964) described a significant ($P < 0.01$) relationship between percentage of fruitful buds (those containing an inflorescence primordia) at nodes position 4, 9 and 14 on dormant canes of Sultana and hours of bright sunshine and daily maximum temperatures above 29°C in a 20 d period in the previous November ($r^2 = 75\%$). In contrast to the very early period of optimum temperature sensitivity defined by Buttrose (1970a, 1974a), this period is much later. In fact, primary branching of anlagen would be taking place (Srinivasan and Mullins 1981, Swanepoel and Archer, 1988). Certainly, Srinivasan and Mullins (1981) reckoned that the control of inflorescence formation in grapevines 'hinged' on the control of branching of anlagen. It is possible, therefore, that while the induction of anlagen is dependent on temperatures at an earlier stage, their potential to become inflorescences is influenced by light and temperature conditions during the early branching stage. Cytokinins, which are known to regulate reproduction generally (Kinet et al. 1993), may be important regulators of this process. They are known to act as a mitotic stimulus, decrease cell membrane permeability and promote branching, and are mainly synthesised in root tips. Warm temperatures in the root zone at this time may increase cytokinin synthesis and transport and, thereby, promote the branching of inflorescence primordia.

Effects of temperature on differentiation (branching) during budburst

Those few studies that relate conditions during budburst to inflorescence development have all used small, modified plants or cuttings grown in glasshouses or growth cabinets. In one study, Pouget (1981) subjected small, experimental vines (cvs Cabernet Sauvignon and Merlot) to 12°C and 25°C during budburst. Substantially more flowers were formed on inflorescences of the vines held at 12°C (130% more for Cabernet Sauvignon and 29% more for Merlot). However, this was offset by an increased number of bunches per shoot (from 1.32 to 1.72 in Cabernet Sauvignon and from 1.73 to 2.25 in Merlot) at the higher temperature. Ezzili (1993) confirmed Pouget's observation that lower temperatures during budburst increased the number of flowers per inflorescence for two other *Vitis vinifera* varieties, namely Cardinal and Alicante Grenache.

Kliewer (1975) studied the effects of soil temperature on budburst in an effort to explain poor and often patchy budburst in

cooler grapegrowing regions in California. He exposed the roots of three-year-old Cabernet Sauvignon vines, grown in pots and pruned to two 10-node canes, to temperatures ranging from 11°C to 35°C while keeping air temperature constant at 20°C. Although he did not assess flower number, he reported that increased root temperatures substantially (60.2% across the entire temperature range) and significantly reduced the number of berries per bunch. Together, these studies suggest that temperature, probably in the root zone, may exert partial control over inflorescence differentiation at budburst. Pouget (1981) speculated that the effect of temperature on flower number was due to its effect on the growth of the developing shoot in relationship to inflorescence differentiation. Higher temperatures, he suggested, lead to the rapid growth of vegetative organs of the developing shoot which increases the 'speed' of budburst and, consequently, fewer flowers are formed. Lower temperatures, on the other hand, slow the growth of vegetative organs, which slows the 'speed' of budburst allowing inflorescence differentiation to occur over a longer period of time. Although there is often a strong correlation between changes in plastochron and flowering, it is generally considered not to be a causative relationship. May (1987) proposed an alternative hypothesis, suggesting a role for cytokinins, which are promoted at higher temperatures. He proposed that higher temperatures cause a 'cytokinin enhanced' enlargement of the early produced flowers which, in turn, inhibit the formation of other flowers.

By delaying pruning, Dunn and Martin (2000) were able to expose bursting shoots of 13-year-old Cabernet Sauvignon vines to a range of temperature conditions in the field. They showed that there were highly significant ($P < 0.05$) but very weak ($r^2 = 4\%$) associations between daily mean soil and maximum air temperatures and flowers per cluster. As temperature gradually increased over time, however, it was not possible to separate any potential effect of temperature from any effects of time itself. In any case, as budburst is a process that is mainly under the control of temperature, it is difficult to envisage practical techniques that would lead to large temperature differences during budburst in the vineyard. Also, any increase in flower number may be offset by a decrease in bunch number (Pouget 1981) and/or poorer budburst (Kliewer 1975). Of perhaps more importance was that the position of the cluster relative to other clusters (i.e. upper, lower or only) explained more than 26% of the variation in flowers per cluster (Figure 1). Furthermore, mean flowers per cluster was significantly ($P < 0.05$) and substantially (97%) higher on two-cluster shoots than single cluster shoots, suggesting that conditions during the previous spring that favour the initiation and/or differentiation of uncommitted primordia also pre-condition clusters to have more flowers (Figure 3). This is supported by work that shows that much of the seasonal variation in weight per bunch can be detected before flowering by counting either flowers or first order branches on inflorescences (Dunn and Martin 2003).

This would also help explain the observation that weight per bunch is positively correlated with bunches per vine in Cabernet Sauvignon and Chardonnay but not Shiraz (Martin 2004, Figure 4). The lack of association between bunch number and bunch size in Shiraz fits with some findings of Buttrose (1970a, Figure 5) concerning the effect of temperatures during formation of inflorescence primordia in buds in the season prior to the season of harvest. In growth cabinet experiments he found that both the number of primordia per bud and the weight per primordium in small Riesling vines increased in response to temperature to an optimum at 30°C and then decreased at higher temperatures, whereas in Shiraz the number of primordia per bud was still increasing at 35°C but there was no clear trend in the relationship of the weight per primordium to temperature in the range from 20°C to 35°C.

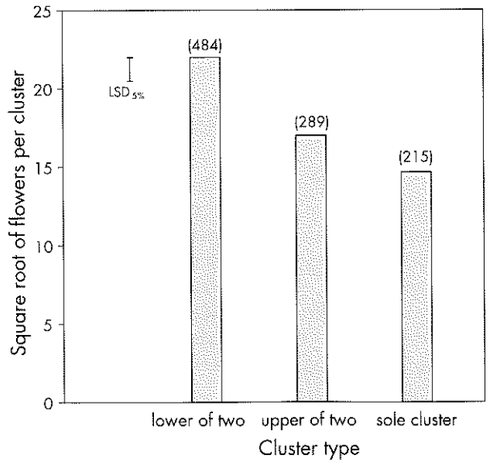

Figure 3. Effect of the relationship of sampled clusters to other clusters on the same shoot on square root of flowers per cluster in *Vitis vinifera* var. Cabernet Sauvignon. Flower clusters were separated into three types: (i) lower clusters on two-cluster shoots, (ii) upper clusters on two-cluster shoots and (iii) sole clusters on single-cluster shoots. The numbers presented in parentheses are back transformed treatment means (reproduced with permission from Dunn and Martin 2000)

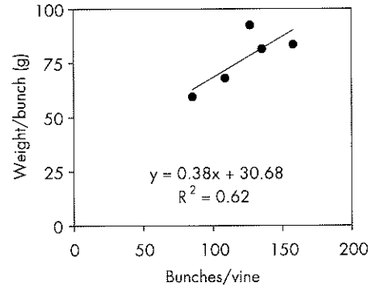

Figure 4. Relationships of seasonal weight per vine and weight per bunch to bunches per vine for Chardonnay in a rootstock trial at Wahgunyah under constant management conditions (reproduced with permission from Martin 2004)

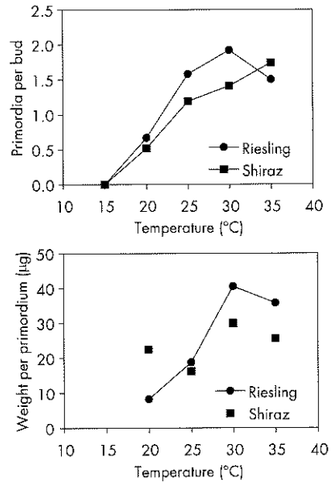

Figure 5. Effect of temperature on bunch primordia per bud for the basal 12 buds and mean weight of the most basal bunch primordium in bud 10 on shoots of vines after 13 weeks in growth cabinets (after Buttrose 1970a, reproduced with permission from Martin 2004)

Light

Light affects vegetative production directly as well as patterns of plant development. Plants respond to changes in spectral composition ('light quality'), radiant energy ('light quantity') and the periodicity (day length) of light.

Shading reduces the formation of inflorescence primordia in grapevines. This has been demonstrated through shading vines as well as individual buds in the field (May and Antcliff 1963, May 1965, Hopping 1977, Perez and Kliewer 1990) and in controlled-environment studies (Buttrose 1974a). In growth cabinet studies, both the number and size of inflorescence primordia increased with increasing light intensity (Buttrose 1969a), while increasing photosynthetic photon flux densities (PPFD) increased berries per bunch in the following season (Morgan et al. 1985). In the field, vertical shoots are more fruitful than horizontal shoots (May 1966) and natural shade profiles within canopies have been related to reduced node fertility (May et al. 1976, Smart et al. 1982a, b). For Sultana, the effect of light appears to be one of quantity rather than quality as R:FR does not significantly affect inflorescence primordia formation (May 1965). Similarly Morgan et al. (1985) showed that altering R:FR ratios did not significantly ($P>0.05$) affect node fertility of Muller Thurgau grapevines. However, these authors suggested that although there was no significant effect ($P>0.05$) of reducing R:FR ratios on node fertility there was a consistent trend for reductions in node fertility indicating a quantitative role for phytochrome in the control of flowering. Although inflorescence induction in *Vitis vinifera* cultivars is not sensitive to photoperiod, long days, in comparison to short days, increased the number of inflorescence primordia per bud for some cultivars (Buttrose 1969b, Buttrose 1974).

The timing of maximum sensitivity has been studied for Sultana. Shading (70% shade) had its greatest effect over a four-week period during late spring (May and Antcliff 1963). Earlier and later shading did not significantly reduce the number of inflorescence. Shading for the first two weeks or the last two weeks of the sensitive period did not reduce inflorescence numbers either. It may be that uncommitted primordia remain sensitive to light intensity for a period longer than two weeks. Also, shading buds directly, rather than the subtending leaves, was shown to reduce inflorescence formation (May 1965).

As with responses to temperature, the intensity of light required for optimum inflorescence primordia formation varies between cultivars and species. Sultana requires more than 30% full sunlight for maximum inflorescence primordia formation, Riesling requires just 10% full sunlight and node fertility of Muller Thurgau was reduced at one-third or less of full sunlight (Morgan et al. 1985). Although grapevines have evolved in forest habitats they are restricted to the outer, more sunlit areas of canopies. Thus, it is not surprising that their leaves display none of the typical photosynthetic characteristics of shade tolerant plants (Kriedemann 1968), such as low light saturation of photosynthesis.

Light and primary-axis bud necrosis

Low light levels have also been implicated in primary bud-axis necrosis (PBN), a condition which may lead to reduced fertility and lower yield. This condition was first reported by Berstein (1973, printed in Hebrew and cited in Lavee et al. 1981) who reported that the grapevines Dattier de Beirout and Queen of Vineyard were among the most sensitive cultivars and that lower buds were more affected than buds higher up the cane. Other susceptible varieties include Sultana, Flame Seedless, Riesling and Shiraz. PBN incidence is highest at basal nodes (Lavee et al. 1981, Dry and Coombe 1994) and the condition has been linked to canopy shading (Perez and Kliewer 1990), high shoot vigour (Lavee et al. 1981, Dry and Coombe 1994) and high levels of soil nitrogen (Kliewer et al. 1994). The promotive effects of exogenous applications of gibberellic acid (Ziv et al. 1992) on PBN, which also increase vegetative vigour in grapevines (Weaver and McCune 1961), suggest a causal role for endogenous gibberellin levels (Lavee 1987).

Morrison and Iodi (1990) investigated the development of PBN in Thompson Seedless grapevines and provided a detailed histological description of the disorder. When primary buds died earlier in the season accessory buds expanded to fill the space. However, when primary buds died later in the season accessory buds remained small. Therefore it might be that the timing of necroses is important in terms of 'bursting potential'. They also found that although shading was correlated with PBN in susceptible vineyards neither shading or GA application could induce necrosis in a vineyard with low incidence of the disorder. The timing of GA application may be important though. Ziv et al. (1981) showed that GA only increased bud necrosis if it was applied before or soon after bloom; applications made well after bloom were ineffective. Morrison and Iodi sprayed 9 and 17 days after bloom, which may have been outside the sensitive period.

Dry and Coombe (1994) reported that in Australia the most sensitive cvs were Shiraz (among the seeded) and Sultana (among the unseeded). Incidence of the disorder was lower in Australia compared to Israel, Japan, Chile and USA. At a vineyard level PBN was correlated with vineyard vigour and at a shoot level PBN was correlated with indices of shoot vigour (cane diameter, total number of lateral shoots, % nodes with lateral shoots). In an experiment (Dry and Coombe 1994), shoot thinning (65% removal 10 days after flowering) substantially increased PBN (16% to 65%) despite a significant improvement in the light environment. Thus, the effect of increased vigour of shoot thinned vines seemed to outweigh any positive effect of improving the light environment around basal buds. Like Morrison and Iodi (1990), Dry and Coombe (1994) suggest that "shading is not a major cause of PBN and that any association between shading and PBN is an indirect consequence of the poor light environment within the canopies of vigorous vines". Further work is required to quantify the effects of PBN on vineyard productivity.

Water stress

Water stress can also reduce inflorescence formation in latent buds. Controlled-environment studies have shown that the number and size of inflorescence primordia are reduced by water stress (Buttrose 1974b). In certain instances, however, mild water stress can improve inflorescence primordia development (Smart et al. 1974). It may be that mild water stress limits vegetative growth during initiation, leading to a better-lit canopy and improving initiation and differentiation of anlagen. There are reports of frost, hail and water-logging reducing inflorescence primordia formation (May 1961).

Cultural factors

Some of the preceding sections have emphasised the important influence of light and temperature during critical periods in the previous season on flower formation in grapevines. Of these two, it is more difficult to modify temperature within grapevine canopies. Thus, it is not surprising that cultural methods to modify or enhance fruitfulness have concentrated on improving the light environment. Dry (2000) recently reviewed this area.

Although there have been many experiments on the effect of trellis and training systems on vine yield, many of these have not

measured yield components so it is difficult to determine whether budburst, shoots per vine, bunches per shoot or bunches per node are affected (Dry 2000). From the research done though, it seems that only when the canopy is divided is there an increase in node fertility. This is generally attributed to improving the light environment within the canopy (Dry 2000). Although there is still some debate as to whether improvements are due to the light incident on the bud itself or the subtending leaf blade. Also, the height of the renewal zone strongly influences yield (May et al. 1976). Yield differences can be substantial (Shaulis and Smart 1974, May et al. 1976) and are strongly related to light intensity measured in the fruiting zone (Smart et al. 1990). The yield components budburst, bunches per shoot, berries per bunch and weight per berry are all affected, explaining the substantial yield improvements, which may be as high as threefold.

There have been many studies on leaf removal in the fruiting zone but by and large these have concentrated on effects on fruit development and fruit composition in the current season. Fortunately some researchers have extended these studies to include measurements of yield components in the following season. On the surface these studies seem to suggest equivocal results, with vine response being variable and ranging from nil effect to a positive effect on fruitfulness in the following season. On one hand, Howell et al. (1994) and Zoecklein et al. (1992) demonstrated no effect of shoot removal on fruitfulness (bunches per shoot) in the following season for cvs Pinot Noir, Riesling and Chardonnay; while, on the other hand, Kliewer and Smart (1989) showed that leaf removal had a positive effect on fruitfulness in the following season for Sauvignon Blanc, although the effects on bunches per shoot were less important than those on budburst (increased shoots per node) and flower number (increased flowers per cluster). However, when these papers are examined more closely important differences emerge. For instance, the timing of defoliation differed. In the experiments reported by Howell et al. (1994) and Zoecklein et al. (1992) leaves were removed mid-way between set and veraison and two to three weeks after bloom respectively, whereas in the experiment reported in Kliewer and Smart (1989) leaves were removed at fruit set. We know from May and Antcliff (1963) that the timing of shading for affecting fruitfulness is critical. They found that only if shade was applied during a four-week period in late spring (roughly coinciding with flowering) was fruitfulness reduced. It is likely that in the experiments of Howell et al. (1994) and Zoecklein et al. (1992) leaves were removed after this period. Also, the vines were pruned to 2- to 5-bud spurs or short 7-node canes. The experiments described in Antcliff and May (1963) were done on much longer canes. We know that flower differentiation begins in the basal nodes and continues distally up the cane (Swanepoel and Archer, 1988), thus the critical period for these lower nodes is likely to be earlier again.

Shoot thinning can improve yield (Shaulis and May 1971, Shaulis 1982). Shoot thinning (approx 50%) had a small but significant effect on bunch numbers per shoot for Riesling (Reynolds et al. 1994) and removing 8 to 10 leaves from the crown reduced PBN in Sultana (Perez and Kliewer 1990). However, severe shoot thinning (65%) increased PBN (Dry and Coombe 1994). Thus, it seems that the severity of thinning is important in determining the balance between an improved light environment within the canopy and any detrimental effects of increased vigour. Also, like leaf removal, the timing of shoot thinning in relation to the initiation and differentiation of anlagen is likely to determine any effects on fruitfulness in the following season.

For a discussion of the effects of a range of treatments designed to alter carbohydrate accumulation and storage on both inflorescence number and inflorescence size, see the paper by Jason Smith in these proceedings.

Conclusions

As a general rule, it seems that a combination of adequate light and exposure to high temperatures is required for maximum inflorescence initiation and differentiation in grapevines.

There are now many lines of evidence that point to the importance of conditions (including temperature and light) leading up to the initiation and differentiation of anlagen in determining yield. These include the growth cabinet studies of Buttrose, empirical field studies of Baldwin, some of the field experimentation of Antcliff, May and others, and the finding (Dunn and Martin 2000) that conditions which are conducive to initiation of anlagen also seem to pre-dispose inflorescences to form more flowers (bunch size). Therefore, there is an urgent need to describe the time-course of induction and initiation for our major wine grape varieties in a range of climatic regions and to link these processes to well defined phenological stages. This information is also required for the sensible imposition of treatments in experiments and for testing the usefulness of weather data for predicting yield potential or, retrospectively, to understand previous patterns of seasonal yield variation.

If conditions preceding and during floral initiation simultaneously promote both inflorescence and flower numbers, then an excellent opportunity to manipulate yield potential exists. It may be possible to manipulate both inflorescence number and flowers per inflorescence by actions prior to or during critical periods of the development of anlagen. For this potential to be realised, these critical periods need to be defined, the most important determining factors need to be identified, and commercially viable ways of controlling them need to be developed. This is a field of research and development that has the potential to deliver very large benefits to the grape and wine industries with regard to both predicting and controlling crop development.

In summary, these windows of sensitivity to environmental cues present opportunities to influence the formation of yield potential (Figure 6). Each of these developmental stages requires plant resources to drive the molecular processes of cell division and cell enlargement. However, this is often occurring at a time when competition for these resources from other sinks is high. Shoot growth, flowering, berry set and berry growth all place demands on available photosynthates. Identifying the genes that control fruitfulness and flowering may help us to understand how grapevines

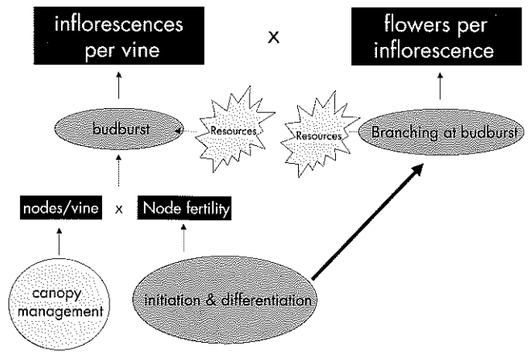

Figure 6. Potential yield at budburst is the product of inflorescences per vine and flowers per inflorescence

allocate limited resources to uncommitted primordia thus switching their developmental path towards the formation of tendrils or inflorescences. Further advances in understanding the flowering response of the grapevine are likely to come from the integration of plant physiology, biochemical studies and plant genetics.

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Effect of diseases on flowering and fruitset

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Introduction

While many fungi have a significant effect on the flowering and fruitset of grapes, only *Botrytis cinerea*, *Plasmopara viticola* (downy mildew), *Colletotrichum* sp. and possibly *Guignardia bidwellii* (black rot) and *Greeneria uvicola* (bitter rot) directly infect grapevine flowers. Other diseases, including those caused by *Erysiphe necator* var *necator* (powdery mildew – formerly *Uncinula necator*) and *Elsinoe ampelina* (black spot) will cause death of inflorescences and young clusters, reduce fruitset or affect the grape quality. Fungal infection may also cause damage to the vine, which affects future bunch development. For example, severe infections of downy or powdery mildew will cause defoliation which may affect the acquisition of carbohydrate reserves and nutrient reabsorption from leaves and reduce the crop load in the subsequent year (May 2004).

A range of common saprophytic fungi (e.g. *Alternaria, Penicillium, Aspergillus, Rhizopus* and *Cladosporium*) can be isolated from flowers clusters (Barbetti 1980, Wicks unpublished data), but the effect of these on flowering and fruitset are not yet known. Barbetti (1980) found no correlation between the fungi identified on flowers and those found in bunch rots at harvest.

The effect of applying fungicides to manage diseases in grapevines is still under investigation. Studies have shown that some fungicides can have an inhibitory effect on pollen germination (Nikolov et al. 1999, Wicks & Bartlett unpublished data), and research is currently being undertaken to determine whether the effect on pollen viability has a corresponding effect on fruitset.

This report outlines some of the main pathogens and diseases that affect the flowering and fruitset of grapevines.

Botrytis cinerea (Botrytis bunch rot)

Botrytis cinerea has a very wide host range. It over-winters in the vineyard on infected trash, lives in the bark of vines and is found on midrow crops and vegetation surrounding vineyards (Cole et al. 2004). Inflorescences infected before flowering develop a soft brown rot that produces a fluffy grey spore mass in high humidity. The affected parts then dry out and usually fall off. Infected flowers are usually symptomless, however some necrosis of stamens and sporulation of the fungus can be seen with microscopic examination (Nair & Hill 1992) and infected necrotic flowers may abort (Keller et al. 2003). Infection by *Botrytis* during flowering rarely results in death of flowers and usually causes a latent infection, where the young developing berries show no symptoms until after veraison.

There have been many studies of the infection process of *Botrytis* in grapevines: how and where the fungus infects the flower, the growth of the fungus after infection and the effect of chemicals produced by the plant either to help or hinder infection. Studies have shown that the main point of infection in grape flowers is in the channel-like gap (receptacle) at the top of the calyx after 'capfall' (Figure 1) (Viret et al. 2004). The fungus is restricted to the receptacle area in young berries and only spreads through the rest of the berry during ripening (Keller et al. 2003). This is due partly to high stilbene concentration in young berries (Bavaresco et al. 1997). Stilbene is a phytoalexin associated with resistance of grapevines to *B. cinerea*, and the concentration of this compound decreases as the berries ripen, allowing the infection to spread. Many other compounds may also be involved in either supporting or inhibiting this infection process. Keller (2003) noted that the high susceptibility of grape flowers could also be due to low levels of 'constitutive phenolic compounds, particularly in the receptacle area'.

Plasmopara viticola (downy mildew)

This disease can develop on all green parts of the vines. *P. viticola* over-winters mainly as oospores, surviving in old leaf tissue and in the surface layers of moist soil. The oospores germinate in water in spring, producing sporangium, from where the zoospores are dispersed by rain splash. Germ tubes of the zoospores penetrate the host via stomata (Langcake and Lovell 1980), however it has been reported that infection can occur through the flower stigmas (Lafon & Bulit 1981). Inflorescences are often infected before cap fall, and with continued humidity a white downy spore mass can be seen over the whole inflorescence before it withers. Infection around bloom can cause significant crop loss. When inoculated before the opening of the florets, inflorescences started shedding flowers 14 days after inoculation, with 90% of the infected flowers shed after 34 days (Srinivasan and Jeyarajan 1976).

Berries are highly susceptible to infection until two weeks post-bloom, when berries are 2-3 mm in diameter (Kennelly et al. 2001). However, the pedicel may still become diseased until at least four weeks after bloom and cause berry death. Infected berries will turn purple, shrivel and often fall from the cluster.

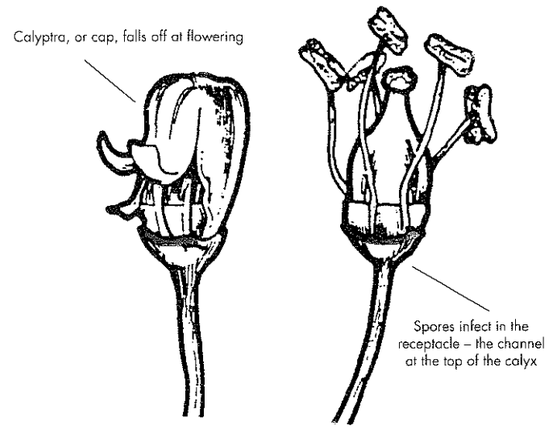

Figure 1. Botrytis infection of grape flowers at full bloom

If untreated, downy mildew can also cause significant defoliation. This may affect the acquisition of carbohydrate reserves and nutrient reabsorption from leaves, which can reduce the crop load in the subsequent year (May 2004)

Colletotrichum sp.

Colletotrichum acutatum is known to cause significant disease in grapevines, particularly when wet humid conditions at flowering and harvest occur. Infected berries will drop and have a characteristic bitter taint (Melksham et al. 2002).

C. acutatum has successfully been isolated from flowers, although studies of infection pathways have not been undertaken (C. Steel pers comm). However, since the same fungus is known to infect flowers of oranges (Zulfiqar et al. 1996), it is assumed that the same could be true for grapevines. As the berries can only be directly infected after veraison, it is thought that the infection pathway is similar to that of *Botrytis*.

C. gloeosporioides causes a disease known as ripe rot. As with *C. acutatum*, the symptoms do not appear on the fruit until near harvest. Daykin and Milholland (1984) found that the fungus penetrated the cuticle and remained latent until the fruit was ripe. No flower inoculations were undertaken in this work, but as Zulfiqur (1996) found that *C. gloeosporioides* did not infect orange flower where *C. acutatum* did, it is possible that no flower infection occurs with this species in grapevines either.

Guignardia bidwellii (black rot)

Black rot of grape occurs sporadically in Australia. In humid production regions it can lead to significant losses if not managed. Rain in spring causes release of ascospores from the mummified fruit and all green parts of the vine can become infected given the right conditions. Leaf lesions usually occur first, and these become the primary infection source for the developing clusters. When a berry becomes infected, it turns dark brown and black pycnidia develop on its surface. Infected berries shrivel and mummify.

Studies by Hoffman et al. (2002) showed that flowers with the cap intact were unlikely to become infected, but that Chardonnay and Riesling clusters were highly susceptible to infection from 50% bloom to until four to five weeks later. Therefore it is likely that flowers play a role in the infection process. However, unlike *Botrytis* and *Colletotrichum*, symptoms were observed on green berries as early as two weeks after infection.

Greeneria uvicola (bitter rot)

A disease of ripe fruit, berries taste bitter and detach easily. Bitter rot can cause significant drop of all sizes of berries (Kummuang et al. 1996), while berries that stay on the vine shrivel and become firmly attached, mummifying and providing an inoculum source for the following year. The fungus invades dead tissue in the pedicels after flowering, and remains latent until the berry reaches maturity.

Other diseases affecting grapevine bunches

Erysiphe necator var necator (powdery mildew – formerly *Uncinula necator*)

Powdery mildew, like downy mildew, affects the green parts of the vine. Clusters can become infected around bloom, causing crop loss and poor fruit set, but there is little evidence that the flowers themselves are infected. Berries of some varieties (including cvs Chardonnay and Riesling) become less susceptible to infection by two weeks after bloom, with very little infection occurring by four weeks after bloom (Gadoury et al. 2003). Infected grapes initially have a white to grey powdery appearance from the mass of conidia on the surface of the berries. Infected berries harden and remain small, often splitting and allowing entry of bunch rotting fungi.

Powdery mildew infection on leaves can also cause significant defoliation if untreated, affecting the following year's crop load as previously mentioned.

Elsinoe ampelina (black spot)

Black spot (also called bird's eye spot and anthracnose) is worst in warm humid climates, requiring free water for infection. While it does not appear to infect the flowers directly, it prefers young green tissue and causes severe necrotic lesions on bunch stems. This results in girdling and shrivelling of bunches with a resultant crop loss.

Phomopsis viticola

Phomopsis, like black spot, requires rain and humid weather early in the season to infect the young green tissue in the vines. When heavily infected, the stem of the shoots and cluster can be girdled and break, causing crop loss. In addition, infected shoots are less productive and are more prone to damage by frost and when pruning. Infection can advance from the pedicel into the berries, although this symptom is not often seen in Australia.

Australian grapevine yellows

Australian grapevine yellows is caused by a phytoplasma. It was first reported in 1976 in Australia and commonly occurs in Chardonnay and Riesling. Young bunches, individual berries or clusters of berries shrivel and die from flowering onwards.

Eutypa lata (Eutypa dieback or Dying arm)

E. lata infects vines through wounds. It is a slow-moving pathogen, producing a toxin that causes shoots to become stunted, deformed and chlorotic. Bunches from these affected shoots may be smaller, with poor set and uneven berry size. On severely affected shoots, flowers can abort and clusters shrivel.

Viruses

Several viruses can have a significant effect on grape bunches. Fanleaf virus, spread by a nematode (*Xiphinema index*) causes poor fruitset, fewer and smaller bunches with aborted berries. Leafroll virus affects fruitset with development of 'hen and chicken' berries and can cause a reduction in flavour compounds and hence wine quality.

Exotic diseases

Several diseases not yet seen in Australia also have a significant effect on bunches. Pierce's disease, caused by the bacteria *Xylella fastidiosa* and spread by xylem feeding insects, causes bunch shrivelling and raisining. Rotbrenner, caused by the fungus *Pseudopezicula tracheiphila*, attacks the pedicels of inflorescences before or after bloom, causing them to rot and dry out.

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Nutrition and its role in flowering/fruitset

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Introduction

The scheme of events from floral initiation to fruitset as outlined by May (2004) provides a useful framework for this paper. Dr May recognises the following events:

- Floral initiation (which occurs in the spring previous to the current crop)
- Inflorescence branching
- Flower formation
- Flowering
- Fruitset
  - Set achieved and berry development proceeds normally
  - *Millerandage* or 'hens and chickens' (arising either as a consequence of limited fertilisation and fruitset or failure of berries to develop to their normal size)
  - *Couloure* representing a condition where set is not achieved and the bunch fails to develop.

This paper will focus most on the floral initiation and fruitset stages of development. For the sake of completeness it is considered that disorders occurring later in the season and resulting in failure of the bunch to develop properly (e.g. bunch stem necrosis) should also be included in our discussions.

Relationships have been shown or inferred between the availability of mineral nutrients and some of these processes. On re-reading some of the older literature, it is clear that the data required to ascribe direct effects absolutely to a particular nutrient may not have been collected as precisely as would be desired, but the conclusions are usually supported by reasonable observations or inferences.

It is probably helpful to try to separate the effects into those that are indirect (i.e. affect some aspect of vine performance which in turn impacts on fruitfulness in some way or other) and those that are direct (through a direct effect on a physiological or developmental process).

Indirect effects of mineral nutrition on grapevine fruitfulness

Nitrogen

The most widely recognised influence on the cropping potential of grapevines is from nitrogen supply.

Where nitrogen is deficient, vine vigour is reduced and overall cropping potential is also reduced, probably both as a result of fewer fruiting positions and from an effect on the fruitfulness of the individual buds. However, before this devigoration occur, it seems that reducing the N supply may increase the fruitfulness of the vines. As nitrogen supply increases vine vigour increases, and bunch numbers decrease. These phenomena are illustrated by some data of Baldwin (1966) who, by manipulating cultural practices, achieved vines of low, medium and high N status as measured by the concentration of N in the leaves. (Table 1)

It is generally believed that this reduction in fruitfulness with increasing nitrogen is a manifestation of shading on individual buds deep within the canopy. Note that by the third season the vines had declined in vigour and were not capable of carrying as many bunches as the vines that continued to receive nitrogen. May and Antcliff (1963) studied this effect again in Sultana in Sunraysia and their data can be summarised as shown in Table 2.

In this experiment the percentage of fruitful buds was reduced by properly timed application of shade (during the initiation period mentioned earlier). The effect of shade at this time on subsequent bunch weight is also interesting. This was because there were fewer berries in each bunch.

In recent years there has been increased recognition of the phenomenon of the failure of primary buds to develop. Secondary buds may take over, but shoots that develop from the secondary bud often have lower fruitfulness (bunch number per shoot) than the shoots which develop from the primary bud (see, for example, Dry 2000, Rawnsley 2003). It seems possible that this disorder is also related at least in part to oversupply of nitrogen indirectly through an effect on shoot vigour.

Excessive supply of nitrogen is suspected to be involved in more specific effects on fruit set which will be discussed later.

Phosphorus

Shortage of phosphorus may have indirect effects on grape fruitfulness and productivity, even though the deficiency is not often seen. For example, Skinner, Matthews and Carlson (1987) working in California have shown that increasing the phosphorus status of vines growing on deficient sites leads to increased vine vigour and increased yields. These authors were able to show an increase in berry weight, but did not report other components of yield. Later in this discussion a specific effect of P on fruit set will be discussed.

Table 1. Bunch numbers per 3 vine plot (after Baldwin 1966)

	Year of harvest		
Nitrogen status	1957	1958	1959
Low	113	186	108
Medium	121	146	131
High	125	135	126
LSD at 5%	23.1	30.6	20

Table 2. Effect of artificial shade on fruitfulness of Sultana (after May and Antcliff 1963)

Treatment	Fruitful buds		Mean bunch weight (g)
	%	Angle	
Control	62.1	52.0	398
Single mosquito net (two months)	57.3	49.2	320
Double mosquito net (two months)	53.9	47.2	353
Hessian (two months)	**27.7**	31.8	**233**
Hessian (October only)	75.9	60.6	**265**
Hessian (November only)	**32.1**	34.5	**241**
LSD at 5%		17.45	93

Bold indicates statistically significant effect

Potassium

Severe potassium deficiency has been reported to lead to reduced vigour and smaller bunches which fail to ripen satisfactorily (e.g. Christensen 1976). It is not clear whether the smaller bunches have their origin as early as bud initiation or later in the development of the bunches. An indirect effect via vine health and 'capacity' seems most likely.

Direct effects of mineral nutrition

The most well known effects of mineral nutrients on the flowering and fruit set process are those of the micronutrients zinc and boron and more recently molybdenum (at least in Merlot) and the macronutrient phosphorus.

Zinc

Pioneering work on the effect of zinc deficiency on fruitset was in fact done in Australia. In its severest form zinc deficiency has a powerful effect on the appearance of grapevines leading to stunted shoot growth and distorted and characteristically mottled leaves. It is also known to have an effect on fruitset at sub-symptomal concentrations in the vine. As an example the following data (Table 3) are taken from a relatively early paper by Alexander and Woodham (1964) where excessive application of phosphorus fertiliser in a field experiment at Red Cliffs had led to zinc unavailability to the vines.

Zinc deficiency affects both fruitset and berry development. In zinc deficient vines bunches are straggly, with fewer normal berries than in healthy vines. Smaller berries have fewer seeds than normal berries. The shot berries in some cases fail to ripen and remain hard and green. Under May's scheme zinc deficiency induces *millerandage*.

The early work with zinc in Australia and California was based upon swabbing the cut surfaces of spurs immediately after pruning with high concentration solutions of zinc sulfate. It is now more usual to apply foliar sprays of zinc salts at relatively low concentrations. In Australia foliar sprays of zinc sulfate (which is soluble) and zinc oxide (which is not) are both used to insure against sub-symptomal zinc deficiency. These are applied 10 to 14 days before flowering is expected.

Zinc deficiency can be expected in Australia's more alkaline soils, (as zinc availability is reduced under high pH soil conditions) in areas with sandy soils, and in the presence of high soil phosphorus (e.g. where heavy dressings of superphosphate are applied to the soil prior to planting or over the life of a vineyard). Petiole analysis can be helpful in diagnosing zinc deficiency.

Boron

Boron deficiency is also recognised as leading to reduced fruitset and a 'hen and chicken' disorder (both *couloure* and *millerandage*). This has been shown to be caused by abnormal pollen tube germination and growth and failure of the pollen to fertilise the ovule. In the case of boron deficiency the 'shot' berries are flattened and may be leaden in colour. The German plant physiologist Gärtel made a comprehensive study of the disorder in the Mosel region (Gärtel 1974). There are many other symptoms of boron deficiency in grapevines which show up on the tendrils, leaves and shoots (e.g. see Hayes 1989).

As an example of the sort of responses that can be expected from boron treatment, the following data (Table 4) are taken from vineyard trials in California reported by Skinner and Bedolla (1989).

Boron can be supplied to grapevines either as foliar sprays or as soil treatment. Soil treatments must be applied in the late summer or autumn to allow the boron to move into the rootzone prior to the commencement of growth in the next season. Foliar sprays are applied in the period between budburst and flowering to the current season's early shoot growth.

Petiole tests for boron can be helpful in understanding the risk of deficiency. Boron is unique amongst mineral nutrients in being required at low levels, and leading to toxicity at higher concentrations in the vines, and for this reason treatments should only be used where a clear need has been demonstrated.

Phosphorus

Earlier in this paper phosphorus was noted as having an indirect role on fruitfulness and vine yield. Data from a long term fertiliser trial at Nuriootpa suggested a direct effect of phosphorus on fruitset in Shiraz vines. The following data are taken from Tulloch and Harris (1970). There was no obvious effect of P on vigour, in contrast to the Californian data mentioned earlier, as the vines were pruned to vigour and similar numbers of canes were left on treated and untreated vines by the pruners.

Australian growers almost invariably will supplement a vineyard soil with P fertiliser before planting and monitor grapevine P status using petiole tests to check when top up applications are required. Personal experience shows that the petiole P tests work well.

Phosphorus fertiliser is usually banded along the vine rows to ensure that fixation sites in the surface soil are saturated and some P moves deeper into the active part of the rootzone.

Molybdenum

The role of molybdenum in the fruitset behaviour of the variety Merlot will be discussed separately in these proceedings by Longbottom et al. Williams et al. (2005) showed that molybdenum foliar sprays reduced *millerandage* and substantially increased the number of seeded berries in Merlot where molybdenum supply was limited. Subsequently, Longbottom, Dry, and Sedgley (2004) have shown that molybdenum is required for proper pollen tube growth in this variety in some situations.

Examples of mineral nutrients that appear to be involved in fruit set and development in some situations

There are a few examples of disorders affecting fruit set or subsequent bunch maturation that have at some time been associated with aspects of the mineral nutrition of the grapevine.

The most serious problems seen in Australia are early bunch stem necrosis (most often seen in the cool climate parts of Australia) and the form of bunch stem necrosis that occurs after veraison (particularly a problem in Cabernet Sauvignon in some districts).

Table 3. Effect of zinc treatment on yield of dried sultanas (kg dried vine fruit/3-vine plot) at Red Cliffs, Victoria[a] (from Alexander and Woodham 1964)

Treatment	1959	1960	1961	1962	1963
No zinc[b]	14.0	14.3	18.8	19.1	12.3
Zinc	15.3*	16.7*	18.6	21.9*	14.1*

[a]Vines in this vineyard showed no obvious zinc deficiency symptoms.
[b]Data taken from the set of treatments applied to plots that had received superphosphate.
*Indicate the zinc treated vines are significantly different (p=0.05) from control vines

Table 4. Effect of boron foliar sprays on vine boron status, bunch weight and yield in cane pruned Pinot Noir after Skinner and Bedolla (1989)

Treatment (weeks after budburst)	Blade B concentration (mg per kg)	Bunch weight (g)	Yield (kg per vine)
Control	32	30.5±6.5	2.1±0.4
0 and 4	104	57.4±10.9	3.1±0.7
2 and 4	103	58.4±5.4	5.0±1.2
4 weeks	67	55.0±8.0	4.2±1.0

Early bunch stem necrosis

This disorder fits May's description of *coulure* and in its most severe form vines fail to carry any crop at all. In other cases only a few berries form on each bunch. It seems clear that weather conditions (particularly cold) have a lot to do with the development of this disorder, but various aspects of nitrogen metabolism have also been implicated, including excessive ammonium present in the vine (e.g. Jordan et al. 1991).

Late bunch stem necrosis

This physiological disorder is recognised in most grapegrowing regions around the world. The rachis of the bunch collapses prior to harvest maturity and the berries shrivel and, in some varieties, shatter. No single cause has been found that consistently explains its occurrence. For example, in parts of Europe its occurrence has been related to a localised shortage of magnesium or perturbed K:(Ca+Mg) ratio; in California high ammonium ion levels in the tissue have been implicated. In Australia no consistent nutritional causal factor could be identified in a major research program (Holzapfel and Coombe 1996), even though magnesium sprays had positive effects in some situations (e.g. greenhouse-grown grapes). It seems likely that weather is involved in the development of the disorder. A plant hormone might be involved. A recent paper from the United States suggests that nitrogen might act as a either a promoter or an inhibitor of the disorder, depending on the N status of the vines in the first place (Capps and Woolf 2000).

Diagnosis

Mineral nutrient deficiencies and excesses can most appropriately be confirmed using the tools of visual observation and tissue analysis, or both. The effects on fruit set of phosphorus, zinc, boron and molybdenum all can occur in the absence of well defined deficiency symptoms, so visual diagnosis is not effective except in cases of severe deficiency. There are some helpful photographs of the symptoms of deficiency of each of these nutrients in Magarey et al. (1999) and Nicholas (2004). Petiole analysis for some nutrients works well (eg standards reprinted in Nicholas 2004). Even though plant analysis standards for N are not as precise as many growers would like, when used in combination with visual observations on vine vegetative growth (vigour), it is relatively easy to see when N supply is too low or too high.

Treatment

Managing vineyard vigour where nitrogen supply is greater than required is the most difficult scenario to deal with, and growers and their advisers who deal with vineyards in the higher rainfall regions of Australia will be familiar with this problem. Use of cover crops to compete with the vines for nitrogen has been suggested as one approach.

Shortages of phosphorus and potassium can be dealt with by proper use of P and K fertilisers. P is usually banded to the vine rows at relatively heavy rates to ensure that saturation of fixing sites in the upper layers of the soil occurs and some P can move into the active rootzone. Potassium can be applied similarly, but it is easier to apply via fertigation in drip irrigation systems.

The micronutrients zinc, boron and molybdenum are best dealt with using foliar sprays properly targeted to the period a few weeks before flowering is expected.

Afterthoughts

In the face of a constant barrage of advertising of what are claimed to be 'magic' fertiliser products, we should frequently remind ourselves that mineral nutrition of the vines will only lead to problems in fruitfulness and fruit set if the availability of the particular nutrient is sufficiently low to limit one or more specific physiological processes within the vine; or out of balance to the extent that it affects vine growth and in turn leads to developmental problems. We should also remind ourselves that the impact of weather on the flowering and fruiting physiology of the vine can be much more important that nutritional effects.

Our objectives should be to:

- grow a well-balanced vine;
- understand if there is something about the soil in the vineyard that is likely to influence the availability of a particular nutrient and take account of that in our management program; and
- use the available monitoring tools such as petiole testing and visual observation to continually check that we are achieving this end.

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Molybdenum and fruitset of Merlot

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Introduction

Molybdenum (Mo) is a micronutrient essential to the growth of plants. However, apart from its role in the reduction of nitrogen, little is known about the function of molybdenum in higher plants (Agarwala et al. 1979). In other crop species, such as Maize, flowering and fruitset has been affected by Mo-deficiency due to its effects on structural development of the flowers and flower parts, and the timing of flowering (Agarwala et al. 1979). Abnormal seed formation and reduced yield have also been associated with Mo-deficiency in Maize (Vunkova-Radeva et al. 1988, Yu et al. 1999).

Early experiments with Mo on grapevines reported positive yield effects, however, it is unclear which components of yield were affected (Hatle and Miculka 1971, Veliksar 1977, Misa 1977, Strakhov and Chazova 1981, Staudt and Kassemeyer 1981).

In Australia, molybdenum was first reported to increase yield of Merlot vines when two spring applications of sodium molybdate ($Na_2MoO_4.2H_2O$) were applied to the foliage of own-rooted Merlot vines in the Adelaide Hills, South Australia (Williams et al. 2003). Mo sprays consistently improved yield when applied to Mo-deficient vines (suggested deficiency range is 0.05-0.09 mg/kg in the petioles at 80% flowering).

The increase in yield was primarily a function of increased mean berry weight brought about by a reduced incidence of millerandage or 'hen and chicken' (Williams et al. 2004).

This was consistent with the findings of Gridley (2003), who also suggested that high levels of Mo might be detrimental to yield. These preliminary studies highlighted the need for further research into the mechanisms by which Mo affects yield of Merlot.

In the 2003-04 and 2004-05 seasons, experiments were conducted on own-rooted Merlot (D3V14) vines in commercial vineyards in the Adelaide Hills (Hills) and at McLaren Vale to elucidate the mechanisms by which Mo affects yield of Merlot and to assess and monitor for high Mo effects on both growth and yield.

Materials and methods

Spray treatments

The experiments used a completely randomised design with seven replicates. In the Hills the sprays were applied in the 2003-04 season only, while at McLaren Vale the vines were sprayed in both seasons. In the second season, a new experimental block was established at McLaren Vale to determine any differences between vines that were treated in two successive years ('Old' block) and for one year only ('New' block).

Each spray was applied to the vines twice in spring, once when the shoots had reached approximately 10cm in length and again approximately one week later following the method of Gridley (2003). The control spray treatment was a water spray only. Rate 1 (0.101g $Na_2MoO_4.2H_2O$ per vine) was determined using the 300g/ha rate used by Gridley (2003) and calculating the application rate on a per vine basis. Rate 2 (0.202g per vine) represented a two-fold increase in concentration of Rate 1.

Tissue nutrient analysis

The level of Mo in the vines was monitored by measuring the concentration of Mo in the shoot tips and petioles at approximately 80% flowering. Waite Analytical Services performed all nutritional analyses.

Pollen and pollen tube observations

Pollen vitality

Pollen vitality was assessed on pollen collected from the field at 80% flowering. Pollen samples were stained with fluorescin diacetate (FDA) and observed under a compound microscope with UV illumination. Fluorescing pollen grains were deemed to contain living tissue and thus potentially capable of germinating (Pinney and Polito 1990).

Pollen tube observations

Individually marked flowers were collected from the field four days after opening and placed directly into a fixative solution for a minimum of two hours. Samples were then prepared for fluorescence microscopy using modified procedures of Martin (1959) and Sedgley (1979).

Yield components

Fruitset

Percent fruitset was determined by directly relating flower number per inflorescence to the resultant berry number per bunch and calculated using the following formula:

$$\% \text{ fruitset} = (\text{no. berries per bunch} / \text{no. flowers per bunch}) \times 100$$

Flower number was determined by catching the shed calyptra of each inflorescence into a mesh bag. Close to ripeness the bunches were harvested and the total number of berries on each bunch was counted excluding the live green ovaries still attached to the rachis.

Berry weight

The berries from each bunch were removed from the rachis and weighed. The total weight of all the berries on a bunch was divided by the number of berries per bunch to give the average berry weight.

Bunches per vine

Close to commercial harvest the number of bunches per vine was counted.

Total yield per vine

Five basal bunches and five distal bunches from two-inflorescence shoots were randomly selected from each vine. These bunches were weighed and an average bunch weight determined to represent the average weight of all the bunches on the vine. This value was multiplied by the number of bunches per vine to give the total yield per vine.

Seed number

Several bunches were selected from the bagged bunches and all berries from those bunches were dissected and the seeds removed. The total number of seeds per bunch was divided by the number of berries per bunch to give the mean number of seeds per berry.

Results and discussion

In all cases where Mo was applied to the vines its presence was validated by the results of the tissue analysis. In 2003-04 the concentration of Mo in the petioles of the Rate 1 and 2 treatments in the Hills was approximately 75 and 150 times that found in the petioles of the control treatment. The magnitude of the response in the shoot tips was not as great, however the corresponding increase observed with the Mo treatment confirms that the Mo did penetrate the tissue and was mobile within the vines. In the second year when none of the vines in the Hills were sprayed, the petiolar Mo concentration from all treatments dropped back to a level similar to that of the control vines in the first season. The petiolar Mo concentration in the control vines was considered adequate in both seasons according to the standards suggested by Williams et al. (2004).

At McLaren Vale a similar pattern of Mo accumulation in both the petioles and shoot tips was observed in response to the Mo sprays. However, in both seasons the petiolar Mo concentration in the control vines was within the suggested deficiency range.

Flower observations and yield components measured in the Hills in both seasons failed to show any significant differences between treatments. At McLaren Vale Mo sprays applied to Mo-deficient vines improved yield two-fold in 2003-04 and by approximately 40% in 2004-05. The Mo sprays had no effect on pollen vitality, however it did affect both the percentage of ovaries with at least one penetrated ovule and the number of ovules that were penetrated. This gave more seeds per berry, heavier berries in 2003-04 (2004-05 data unavailable) and significantly improved fruitset in both years. Fruitset was the primary contributor to the overall increase in yield in all cases. Bunch number per vine was not affected either in the season that the Mo was applied nor did it affect bunch initiation in the vines that were treated in two consecutive seasons (Table 1).

Applying the higher dose of Mo did not give any further beneficial effects compared to Rate 1, nor did it have any detrimental effects on yield. However, in the spring following Mo application vines exhibited delayed budburst compared to the control vines.

Molybdenum appears to be affecting yield of own-rooted Merlot vines via its effect on pollen tube growth, however the mechanism remains unclear. It is possible that like Mo-deficient Maize, Merlot pollen may be morphologically different thereby affecting its ability to germinate. Another possibility is that Mo-deficiency in Merlot affects the development of the ovules. Previous work has found that structural aberrations of the ovules, such as those found after exposure to cold temperatures, attract fewer pollen tubes (Ebadi et al. 1995). An alternative cause of poor pollen tube growth may be adverse conditions within the stylar canal. Each of these possibilities will be examined in more detail in the 2005-06 season.

Conclusion

Applying Mo to Mo-deficient Merlot vines can give beneficial yield effects that are predominantly a function of improved fruitset. The negative effect on fruitset appears to be via the impediment of pollen tube growth. Applying high levels of Mo does not appear to have any detrimental effects on yield in the season that it is applied, however, it has been associated with delayed budburst in the following season.

Table 1. Factors affected by Mo-deficiency on own-rooted Merlot vines at McLaren Vale

	2003-04	2004-05
Pollen vitality	×	×
# Penetrated ovules per ovary	✓	✓
% Ovaries with >/= 1 penetrated ovule	✓	✓
Seeds / berry	✓	–
Total yield / vine	✓	✓
# Bunches / vine	×	×
Bunch weight	✓	✓
% Fruitset	✓	✓
Berry weight	✓	×

Acknowledgments

We would like to thank the Adelaide Hills Wine Region Inc. for their financial support of this project and Nepenthe Viticulture and the Hardy Wine Company for the use of their vineyards. We also acknowledge Dr Robert Hallon for translating the foreign language manuscripts referred to in this paper.

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Fruitset – possible implications on wine quality

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Prologue

'Mareschlchi has carefully compiled the observations recorded on the weather and the size of the grape crops during the period 1855-1907 for the region around Monferrato in North-Western Italy, and concludes that the big crop is always obtained when the preceding year has been fairly warm and dry. A dry and mild (not cool) spring allows the young shoots and their eyes (sic. Buds) to develop well and ripens the wood well, with the result that the following crop will be heavy if it is not destroyed by hail and diseases, or if the previous crop had not already been a very big one……..

According to Mareschalchi, we can, with fair accuracy, predict the size of the crop, even before the vines begin budding, by taking into account the weather conditions (heat and rainfall) during the preceding twelve months, and the size of the preceding crop' (Perold 1927)

Introduction

When the cork is pulled, or the cap unscrewed from a bottle of wine and the contents evaluated, the culmination of considerable effort is experienced. The humble *Saccharomyces* yeast, the ebullient winemaker, the grapevine, the sun, the rain and of course the dedicated viticulturist have all had a part to play. However, it is generally accepted that the wine style will reflect the flavour and aroma compounds in the harvested fruit, br ought to fruition during the winemaking process.

While the changes in fruit composition can be described in a general form (e.g. sugars, pH, monoterpenes and thiol precursors increase, while acidity and methoxypyrazine fall), the relative concentrations vary, often reflecting changes in the fruit development during a particular season. These in turn occur as a result of differences in seasonal development, particularly at specific phenological stages of vine development. However, given that the winemaker wishes to make a consistent style of wine between seasons, it is important that the 'target' fruit composition also remains consistent between seasons. Understanding and managing these differences between seasons are particularly important in marginal cool climates, where small changes in temperature can have a large influence on vine development and fruit composition.

Impact of yield on fruit ripeness and quality

Anecdotal evidence suggests that high yield results in inferior wine, while low yield leads to quality. Unfortunately this relationship has seldom been rigorously tested. Most investigations on the influence of yield on wine sensory characters have relied on fruit thinning (e.g. Bravdo et al. 1985; Reynolds et al. 1996) and may have been harvested on the same date at different Brix levels (Cordner and Ough 1978). Sinton et al. (1978) and Gray et al. (1994) published relationships that indicate that while excessive yields generally result in inferior wine, the reverse is not necessarily true and low yields may or may not result in quality. Recently Chapman et al. (2004) reported that when harvested at a similar Brix, Cabernet Sauvignon cropped at low levels produced higher herbaceous character than vines with high crop, and that early vine manipulation was necessary to alter fruit development. In practice, achieving an optimum yield to match the environment, and producing a vine in which the yield and vegetative growth are in balance is central to good viticulture.

One of the challenges in quantifying and understanding the yield quality relationship is the impact time has on fruit composition. On a particular site in any season, the date on which a particular ripeness (for example a target Brix) is achieved will largely depend on crop load. Thus comparing wines from vines harvested on a particular date (and hence ripeness) is of limited value, and modifying harvest date so fruit is of a similar ripeness would appear more appropriate and closer to commercial practice. Unfortunately, higher yields result in a later harvest date which in cool climates puts fruit at greater risk due to leaf senescence and adverse weather events, in particular autumn frost. Thus anticipating the potential yield in any season is critical to managing wine quality.

Seasonal changes in fruit yield

Grapevines are perennial plants. The yield at the end of a particular season is the culmination of events that have occurred in at least the preceding 18 months and possibly longer and is the product of a number of components:

- Shoots per hectare
- Inflorescences per shoot
- Flowers per inflorescence
- Fruitset
- Berry weight

Shoots per hectare reflect the vineyard design (e.g. vine spacing, training, uniformity of bud break, etc.). Of these only bud break and subsequent shoot development are likely to vary between seasons, probably reflecting the over-wintering carbohydrate and nutrient reserves in the vine, which in turn potentially reflect the cropping level in the previous season.

National average yields of New Zealand Sauvignon Blanc have varied approximately two fold and Chardonnay three fold between 1990 and 2004 (Figure 1). The year-to-year differences suggests

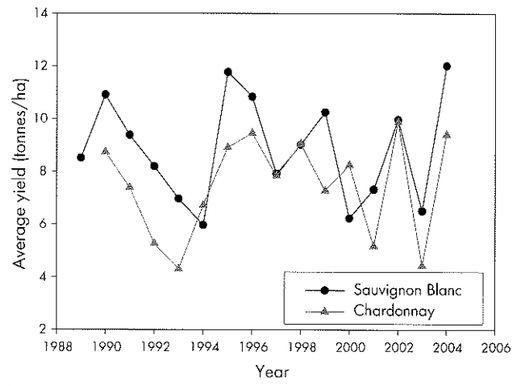

Figure 1. Average New Zealand Sauvignon Blanc and Chardonnay yields (national yield/producing vineyard area). Data sourced from NZ Winegrowers Annual Report

that much of this variation can be attributed to weather events occurring at critical times during the season. In some cases these may be catastrophic events, such as frosts in 2003, however, in other seasons, more subtle events are likely to be the cause.

Of particular importance in a cool climate are the temperatures during the initiation of inflorescence primordia and flowering. As these events occur at approximatelyw the same time of year (late spring) (Figure 2), temperatures at this time can influence both the current and subsequent season.

Temperatures at bunch initiation

Inflorescence induction starts early in the spring, with the formation of an uncommitted primordium opposite a leaf primordium on the developing shoot of a latent bud. Once formed, the primordium will, depending on environmental conditions (in particular light and temperature), develop into either an inflorescence or tendril (Srinivasan and Mullins 1981). Cool conditions, which favour gibberellin synthesis, promote vegetative growth and favour tendril differentiation. In contrast, warm conditions promote cytokinin accumulation, favouring inflorescence differentiation (Jackson 2000). The induction and subsequent differentiation of the basal inflorescence of Chenin Blanc was reported to start in basal buds when shoots have approximately 12 leaves, about 12 days before the onset of flowering (Swanepoel and Archer 1998). Once complete (approximately 10 days after the onset of flowering) the second inflorescence on the same bud undergoes the same process. It can be anticipated that the onset of inflorescence development in adjacent buds on a shoot will commence sequentially along the developing shoot, probably reflecting the emergence of new leaves at the apex.

The impact of temperatures on the differentiation of the uncommitted bud during initiation has been described by McGregor (2000) who monitored inflorescence number per shoot on spur-pruned, own rooted Chardonnay in California (Figure 3a). He described a strong linear correlation with average bunch number per shoot increasing by 0.22 per degree centigrade.

Temperatures at flowering

Flowering generally commences (depending on the variety and temperatures) 8 to 10 weeks after bud break. It commences on the primary (lower) inflorescences of the shoot arising from apical buds of cane pruned vines, with the secondary inflorescence starting some two to four days later. Inflorescences on shoots arising from basal buds on the cordon (closer to the head of the vine) begin some four to six days after the equivalent inflorescence on the apical shoot (Naylor 2001). Flowering in Marlborough Sauvignon Blanc appears to take between 10 and 25 days, largely depending on temperatures at this time.

In addition to influencing the duration of flowering, temperatures also influence the success of fertilization. Under average weather conditions, flowers start to open shortly after dawn, reaching a maximum between 07:00 and 09:00 and finish at midday (Staudt 1999). Once pollen is deposited on the stigma, the pollen grain swells, with pollen tube growth rate being a reflection of temperature (Staudt 1982). Pollen tube growth is limited to about 18 to 24 hours (Figure 4a), suggesting that it is the average temperature immediately post pollination that will determine whether or not an individual flower will be fertilized.

Using the data presented by Staudt, it is possible to estimate the maximum pollen tube length at any temperature (Figure 4b). Over a temperature range of 10 to 28 °C, maximum tube length increased by 13 µm per degree centigrade (Kheun and Trought unpublished data). This possibly suggests that the size of the flower (distance from stigma to ovary) may influence the likelihood of fertilization and where the mean daily temperature is cooler only small flowers will be fertilized.

The impact of mean daily temperature over the flowering period was studied by McGregor (2000). Average cluster weight of Chardonnay from 1983 to 1999 exhibited a sigmoid response to flowering temperature (Figure 3b).

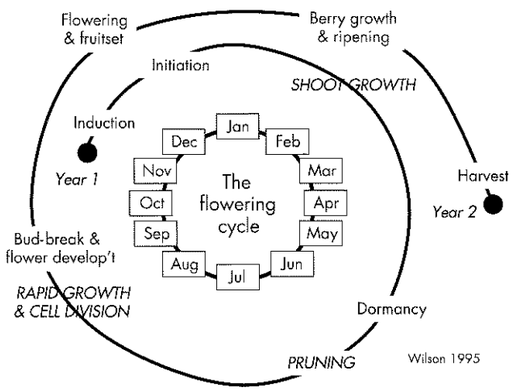

Figure 2. Time line of flowering and fruiting cycle in New Zealand vineyards

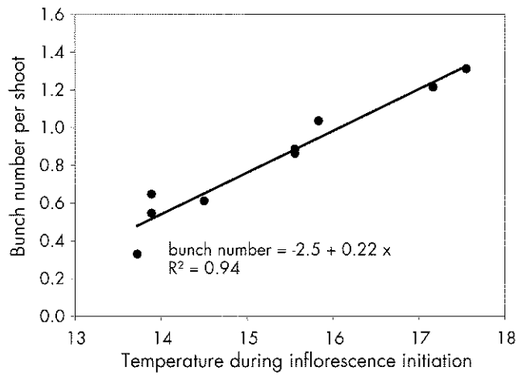

Figure 3a. Influence of initiation temperature on Chardonnay bunch number per shoot (McGregor 2000)

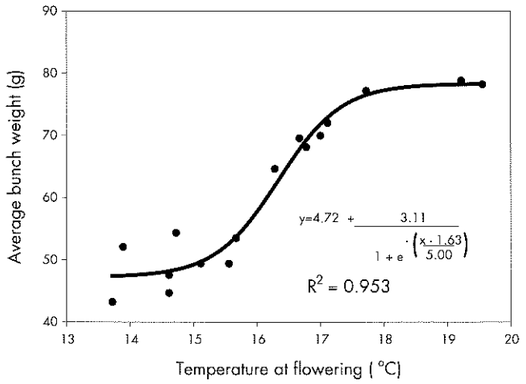

Figure 3b. Influence of mean daily temperature on average bunch weight of Chardonnay (McGregor 2000)

The sigmoid relationship between bunch weight and temperature during flowering suggests that an increase in average temperature from 15.5 to 17.5 °C resulted in an increase in average bunch weight of 60% from 50 to 80 g.

Using meteorological data to predict grapevine yield

Growing degree days (GDD) and related approaches have been widely used to assess the suitability of a particular site for grape production (Winkler 1974; Jackson 1998; Gladstones 1992). While these approaches can be used to compare long-term averages, temperatures at specific phenological stages of vine development can have a major impact on subsequent vine development. By comparing the current GDD accumulation with historical data (the long-term average) and relating these to the particular stage of vine development, the impact of short-term changes in weather can be predicted.

For example Figure 5a shows the accumulated GDD for 1999-2000 and 2003-2004 in Marlborough, New Zealand. The total seasonal accumulated GDD for both seasons was similar, yet the average yield of mature Sauvignon Blanc vines in 2000 were amongst the lowest on record, while those of 2004 were the highest. Normalizing the data to the long-term mean (Figure 5b) emphasizes the short-term temperature differences in the two seasons. In 2000, the spring was warmer than average, and by late November accumulated GDD were nearly 80 GDD ahead of the long-term average. This suggests that flowering was earlier than average. However, a particularly cold December and January meant that by late January the accumulated GDD were now 50 GDD behind average. This cold period coincided with flowering, and largely caused the low yield. In contrast, in 2003-04, data suggests that the onset of flowering was later than average, but a warm flowering (reflected in the rapid increase in accumulated GDD during December and January) resulted in an excellent fruitset and high yields.

Using temperatures during initiation and flowering, a grapevine yield prediction model has been developed for Sauvignon Blanc in Marlborough. Extensive plantings of Sauvignon Blanc in Marlborough are a reasonably recent phenomena. Average grape yields from 1996 to 2004 of 10 mature vineyards on the Wairau Plains, Marlborough were used to provide yield data. The vineyards were all 4-cane, VSP-pruned vines planted at 1.8 m within row and 3.0 m between row spacing and commercially managed to a high standard. A stepwise, multiple regression technique was used to develop a relationship between actual and predicted vine yields, adjusting the start and finish of the initiation and flowering dates until the line of best fit (highest correlation coefficient) was achieved.

The best fit between actual and estimated yield (R^2 0.92) (Figure 6) was achieved using an average GDD over the initiation period from 11 December to 17 January and a flowering period of 9 December to 9 January, and the estimated yield was described by:

Estimated Yield (t/ha) =
(2.728*initiation temperature) + (2.918*flowering temperature) – 29.48

The 2003 season was excluded from the analysis as the particularly low yield in that year was associated with a severe frost in the Marlborough region in November. It should be emphasized

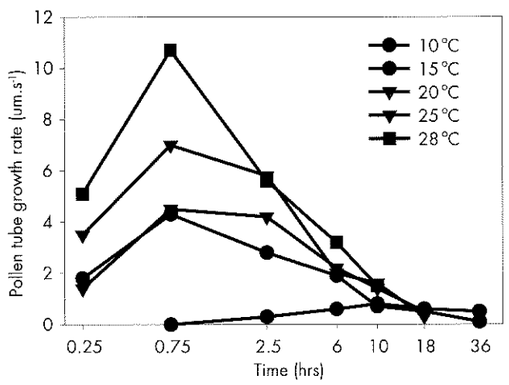

Figure 4a. Influence of temperature on pollen tube growth rate (Staudt 1982)

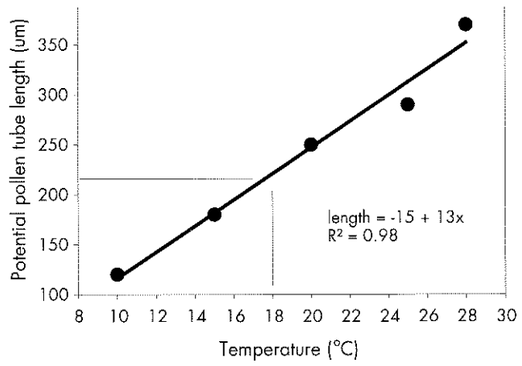

Figure 4b. Influence of temperature on potential pollen tube length. (Kheun and Trought unpublished data, adapted from Staudt 1982)

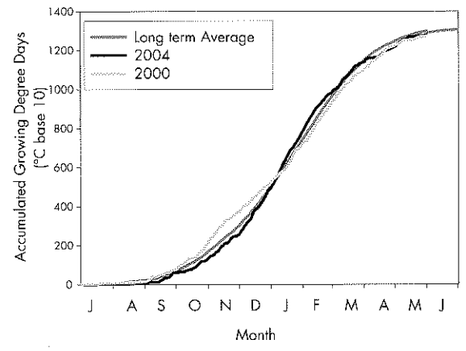

Figure 5a. Accumulated growing degree days – Marlborough Research Centre 1999-2000 and 2003-2004 growing seasons

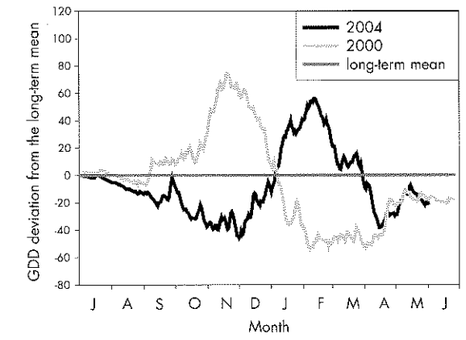

Figure 5b. Growing degree day deviation from the long-term mean – Marlborough Research Centre

that the model relates to the vineyards under consideration and the absolute yield values may vary where vine spacing and management practices alter.

Extending the yield analysis back to 1988 (Figure 7) provides an estimate of the long-term average Sauvignon Blanc yield in Marlborough (10.64 t/ha) from these vineyards, and demonstrates the seasonal differences that may be anticipated. The impact of cool seasons in 1993 and 1994 associated with the Mt Pinatubo eruption in the Philippines is clearly apparent, together with the expected yield loss from the spring frost in 2003.

The range and relative importance of initiation and flowering temperatures in determining yield is demonstrated in Table 1. The above average yields of 1999 and 2002 reflected the above average initiation and flowering temperatures, while low yields in 1993, 2000 and 2005 were a reflection of below average flowering temperatures. Data suggests that the 2001 harvest was saved by the exceptionally warm flowering, as initiation temperature was the coldest over the 18-year period. Using the model the forthcoming season's data would suggest that yields in 2006 are likely to be less than average, but as in previous years, events over flowering will determine the final outcome.

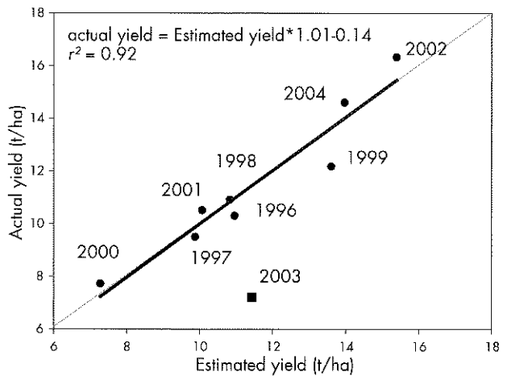

Figure 6. Estimation of Sauvignon Blanc yield using growing degree days at initiation and flowering (A spring frost in 2003 caused low yields in this season and this data was excluded from the regression)

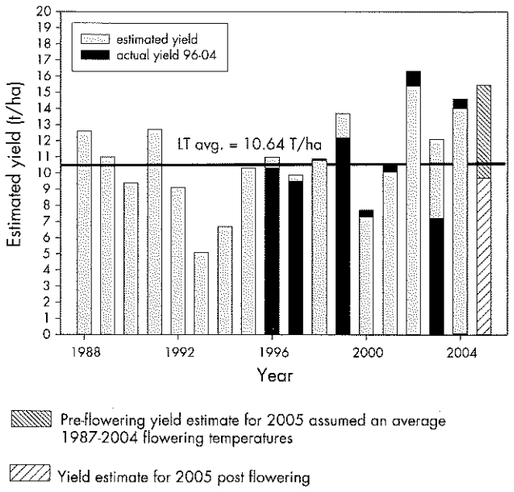

Figure 7. Yield variation of Marlborough Sauvignon Blanc 1988 – 2005

Table 1. Seasonal GDD during the estimated initiation and flowering periods of Sauvignon Blanc in Marlborough

Year of harvest	Average daily GDD over initiation (11 Dec-17 Jan) (18 months prior to harvest)	Average daily GDD over flowering (9 Dec-9 Jan) (4 months prior to harvest)
1996	6.8	7.5
1997	7.8	6.2
1998	6.2	8.0
1999	7.8	7.5
2000	8.1	5.0
2001	5.2	8.7
2002	8.6	7.3
2003	7.7	7.0
2004	7.0	8.4
Average 1988-2005	7.2	6.9

Table 2. Effect of grapevine training system on yield components on 26 April 2005

Pruning Treatment			Yield* (kg/vine)		Trunk carbohydrate concentration (August 2004)		
Trt	2003-4	2004-5	Yield 2004	Yield 2005	Starch	Soluble sugar	Total carbohydrate (glucose equivalent)
1	4 cane	4 cane	10.9 a	7.5 b	5.32	15.1	20.4
2	4 cane	2 cane		4.3 c			
3	2 cane	2 cane	6.1 b	4.8 c	9.23	13.5	22.4
4	2 cane	4 cane		9.9 a			
	P				*0.008*	*0.002*	*0.003*

*Means within the same column with the same letter are not significantly different at LSD P ≤ 0.05

Using meteorological data to predict wine quality

In addition to influencing fruitset, weather conditions at flowering may also influence flowering duration. Flowering can occur over a period from two days to 2-3 weeks, largely reflecting the temperature with warmer temperatures resulting in a compressed flowering (Howell personal comm.). The consequence of flowering duration on final fruit composition still has to be determined, but it can be anticipated that a longer flowering may result in greater variation in fruit composition (at a berry level) at harvest and a higher range of flavours in the fruit (Figure 8). This is particularly important where herbaceous character, associated with less ripe fruit, may dominate the flavour and aroma profile of the wine.

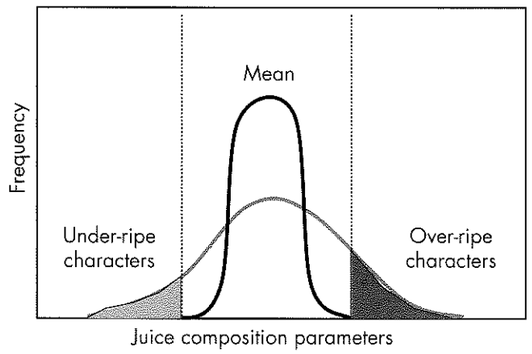

Figure 8. The potential impact of fruit variability on flavour spectrum of wine

Influence of previous season cropping on grapevine yield

While temperatures during inflorescence initiation and flowering appear to explain most of the seasonal differences in Sauvignon Blanc yield, over-wintering carbohydrate reserves may also affect production. Initial shoot growth largely depends on carbohydrates stored in the vine from the previous season (Perez and Kliewer 1990) and these reserves may be influenced by crop level. Following high crops, reserves may be depleted resulting in poor bud break and uneven shoot development. Potentially this results in low yields, which in turn results in high carbohydrate reserves, good bud break and high crops in the subsequent season. The consequence is that vines may exhibit biennial cropping.

To investigate this further, trials have been initiated to investigate the influence of crop level and over-wintering reserves on following season's production in Marlborough. Sauvignon Blanc vines are traditionally pruned using a 4-cane VSP system with 50 to 60 buds being retained after pruning. The impact of changing the pruning from 4-cane to 2-cane on yield, pruning weight and trunk carbohydrate reserves was investigated and some preliminary results are presented.

In the first season (2003-2004) 2-cane pruned vines produced 56% of the yield of 4-cane vines in 2004 (compare treatments 1 and 3, Table 2), and resulted in a significant increase in winter starch and total carbohydrate concentrations. In the second season (2004-2005) the 2-cane vines produced 64% of the 4-cane pruned vines. Converting the vines back from 2-cane to 4-cane at the end of 2003-2004 (treatment 4, Table 2) doubled the yield when compared to vines that had been 2-caned throughout and resulted in a 32% increase in yield over vines that had been 4-cane pruned throughout.

No significant differences in berry or bunch weight were recorded (data not given), and the increase in yield was a reflection of higher bud break on the 4-cane pruned vines. In contrast, yield of the 2-cane pruned vines was unaffected by crop level in the previous season, suggesting that the reserves in the vine was not limiting subsequent shoot development. The data suggests that the crop level in the previous season was having a carry over effect, particularly were an excessive number of buds are retained post pruning, and this was independent of any temperature effects at initiation or flowering.

Summary: Impact of fruitset on wine quality

Recent research (Chapman et al. 2004) questions the adage that to produce high quality wines, low yields are essential and there is still much to know about the impact of fruitset and vine yield on wine quality. Fruitset influences potential yield, which in turn will influence the time and probability of achieving a particular fruit ripeness. This will influence the balance of the various flavour and aroma components in the fruit that will be expressed in the wine. Secondly temperatures at flowering will influence the duration of flowering, and may influence the variability in fruit composition around the mean at harvest. The extent to which this affects wine quality probably depends on the variety being considered, but a small proportion of unripe, herbaceous fruit in the sample may have a disproportionate effect on the quality of wines such as Pinot Noir and Cabernet Sauvignon, where herbaceous character is considered unpleasant. Conversely it may be seen to be a positive attribute in Sauvignon Blanc.

Acknowledgements

To Charles McGregor who, after the 2000 5th International Symposium on Cool Climate Viticulture and Oenology, provided the data for Figures 3a and 3b. The assistance of Jeff Bennett for technical assistance with the vine training experiment and carbohydrate analyses. Rob Agnew for providing the meteorological data and together with Joanne Brady made useful comments on this manuscript. The cooperation of the staff of Villa Maria Estate Ltd with the field research is also appreciated.

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Management options to fruitset

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Introduction

The aim of all viticultural management is to achieve sound grapes with the desired flavours and characteristics, at an economic level. Vineyard management prior to fruitset should aim to achieve successful inflorescence development and fruitset for the current year. as well as achieving for the following year good bud and therefore inflorescence primordia initiation.

Management options will vary from site to site, with climatic factors, soil characteristics and viticultural philosophies all impacting management decisions.

Management of stored and available nutrients, soil moisture, pests and diseases is imperative, however these issues are intertwined with climatic factors that together can make or break the winegrower.

Vineyard viability is a function of final yield and price received for the grapes versus operating costs, within the constraints of the environmental conditions of the site. Final yield is determined by the number of berries per vine and their final harvest weight. The number of berries per vine is a function of fruitset while the weight of the berries is largely determined by either explicit (e.g. irrigation) or passive (e.g. rainfall) management practices. The impact of management practices on fruit set and therefore the harvest yield, is of economic importance to the wine producer.

Quantifying fruitset

There is only one way to quantify fruitset, which is an accurate per cent of conversion of flowers into berries. This can be determined by counting the immature flowers before flowering and counting the number of berries retained post fruitset. This is a very difficult and time consuming task and many people have devised different systems to complete this operation, however all have the problem that their systems rely on a small sample of each block within the vineyard. This may not accurately represent the actual fruitset within each block or the entire vineyard.

The use of long-term averages as representation for flower number per bunch can also be inaccurate as the variability of the actual flower number per inflorescence is very large, both within a season and between seasons. Unless data on flower numbers has been collected for many years to provide a reference, it will not indicate if fruitset has been good, average or poor. One figure of per cent fruitset that has been suggested as normal is 50% (Bessis 1993 from May 2004).

Final yield estimation as an indication of fruitset

Calculating the expected final yield per vine is one method that can indicate if yield is adequate (but will not give any real indication of fruitset). This can be achieved by weighing bunches at a pre-determined time post fruitset (say 21 days) and multiplying this by the increase in average berry weight from this time to harvest (determined from previous seasons) and the bunch numbers per vine. Using this figure will tell you if your vines are carrying more, average or less crop than you economically require.

Is a winegrape grower interested in fruitset *per se*, or in economic yield?

As a winegrape grower there is a problem with both measuring fruitset directly and also with final yield estimation: when you finally have all the data available to act on, it is too late to do anything to either improve fruitset or to improve harvest yield. Pro-active prediction of a poor (or good) season is very difficult using these quantifying techniques.

A guarantee of final harvest yield?

To guarantee final harvest yield the number of inflorescences at budburst must be adequate and these inflorescences must remain fully intact up to flowering. Adequate flowering must then occur and the crop maintained until harvest.

Problems in maintaining inflorescences to flowering

Outbreaks of controllable diseases such as powdery mildew (*Erisyphe necator*) and downy mildew (*Plasmopara viticola*) have resulted in inflorescence loss or aborted flowering of up to 100%. Spring botrytis affecting shoots can also lead to significant losses of inflorescences. Black spot (*Elsinoe ampelina*) and phomopsis (*Phomopsis viticola*) can cause entire shoot loss and damage to developing inflorescences.

Pests such as the European earwig (*Forficula auricularia*) can be both detrimental, by causing leaf and inflorescence damage early in the season and beneficial, by attacking larval and pupal forms of pathogenic insects later in the season. Control using non-selective approaches requires serious consideration.

Weather events such as frost and hail can have devastating consequences on final harvest yield, by damaging shoots and inflorescences. Site selection to minimise hail and appropriate control measures for frost should be used where appropriate.

Grapevine stress associated with sudden high temperatures and low soil moisture has been associated with inflorescence drop (May 2004) but is unlikely to pose problems in most Australian vineyards due to adequate levels of soil moisture maintained via rainfall or irrigation. However if soil moisture is not monitored closely throughout this period and during flowering, then an impact on final harvest yield should be expected.

Grapevine nutrition

Nutrition has a large role to play in affecting fruit set. Too little of one nutrient (zinc, boron or molybdenum) or too much of another (especially nitrogen) can change the physiological behaviour of the grapevine and may have dire consequences on final harvest weight. Timely and accurate nutrient levels must be assessed each year and acted upon both for the current season and for the following season. Many winegrape growers still use a prescriptive approach based on information from past years or from other growers in the area. Unfortunately, this may lead to over application of certain trace elements that may have toxic effects on the grapevine (boron) or may cause an additional and unnecessary financial cost.

Analysis of petioles/leaf tissue is cost effective and can lead to corrective action if required. The results of analysis from petiole samples taken at flowering (which has been the standard timing for many years) are often not available for two weeks or more. When the results are received by the winegrape grower, flowering has finished and little corrective action can be taken to alter the concentration of nutrients and affect the current season's fruitset. However, the results can be used as a guide for the following season and to maintain grapevine health during the development and ripening stages of the season.

A better option may be to use leaf tissue analysis about one month prior to historical flowering dates. The winegrower can then act on the results to adjust the levels of nutrient that may affect fruit set in the current year. Further leaf tissue analysis undertaken during the development and ripening stages of the current season can provide information for corrective action required to optimise the development and differentiation of buds and the ripening processes for the following year.

Generally, foliar applications of trace elements, especially zinc and boron are more cost effective than soil applications. The plant response is rapid, application can be timed to the period when the grapevine requires the element, there is less off-target application and the nutrient is not leached through the soil during irrigation or rain events over the course of the season. Most foliar elements can be applied in conjunction with foliar fungicides, so the additional cost of application is minimal. Long-term corrections to nutrient availability can be made by correcting soil imbalances and then fine tuning deficiencies via foliar or fertigation application.

Environmental conditions

The implications of physical ailments that effect fruit set are well understood Pest and disease control, nutrition and soil moisture can generally be corrected however weather conditions also affect flowering and fruitset.

Adverse temperature is commonly agreed to have detrimental effects on fruit set. Temperatures below 15°C and those above 32°C are strongly associated with poor fruitset. Strong wind at flowering has also been implicated and if associated with cold temperatures, can be catastrophic.

Short-term control options

Vigour control

During grapevine growth there is a hierarchy for the proportioning of assimilates to each plant part. Generally the growing shoot tips are stronger sinks than inflorescences and ripening bunches, which are stronger sinks than storage structures (trunk and root system).

In a vigorously growing shoot tip there is a greater use of assimilates created by photosynthesis than in the less vigorous shoots; thus there are fewer assimilates available to the inflorescences for flowering and for bud differentiation. In vigorous situations the per cent fruitset is often poor, increasing the amount of shoot and leaf growth which in turn increases the shading of developing buds. This reduces bud fruitfulness for the following season and a vicious cycle of ever reducing yield and ever increasing vigour occurs.

In such situations re-working of the grapevine or the trellis may provide beneficial results. This reworking may involve re-caning (in traditionally spur-pruned vineyards), leaving more buds (either as longer spurs, finger and thumbs or double-canes), and/or opening the canopy to reduce shading effects, promoting bud differentiation for the following season.

In traditional currant production the practice of cincturing the trunk has lead to increased fruitset. Cincturing is the process of cutting about two-thirds of the way around the grapevine trunk, or a shoot, to interrupt the flow of sap in the phloem tissue. Frisch (1991 from May 2004) indicated that cincturing increased fruitset in seeded varieties but can be only recommended in cases where poor fruitset can be predicted with some certainty, as the process is undertaken prior to fruitset.

Another option is the removal of the growing tips during flowering. This reduces the draw of assimilates to the growing tip, and allows the assimilates to be used to promote fruitset. However May (2004) states "*…Shoot tip removal has proven successful in increasing* per cent *fruitset under favourable weather conditions but only when done during the period of cap fall, not before and not after. No information has come to hand to determine whether tipping will also be effective when weather conditions for fruitset are unfavourable…*"

It is known that early season vigour is strongly related to stored carbohydrate reserves in the grapevine from the previous season. Much of this stored carbohydrate is laid down during the period from harvest to leaf fall. Removal of leaves soon after harvest can reduce this storage of carbohydrate and can negatively impact on the following seasons harvest yield (Smith et al. 2004). Where vigour is excessive and fruitset is poor, post-harvest leaf removal or pruning to reduce the impacts of vigour may, in certain situations, increase fruitset.

Where vigour is inadequate, a similar cycle of deterioration to that described above can occur. Poor health may lead to poor fruitset and poor health will lead to poor bud differentiation; decreasing yields each year. Poor grapevine health can be a function of inadequate nutrition, badly managed disease control/viral infection and/or poor soil health. Poor plant health can be rectified, although the process may take some years.

Long-term control options

Site selection and establishment

Original site selection is of paramount importance when establishing a new vineyard and will have the biggest influence on the vineyard's long-term economic success or failure. Climatic data for the site should be analysed in respect to occurrence of frost and hail, period of ripening and disease pressure. Analysis of the data in relation to the timing of flowering and the period from budburst to flowering to determine the likelihood of poor fruitset and economic loss, is often overlooked.

Consistent economic failure of a vineyard due to poor fruitset may indicate poor initial site selection. If temperature can be implicated in poor fruitset on these sites, there is little that can be done (some people have tried importing large quantities of rocks to accumulate solar radiation to re-radiate during the night, thus increasing average temperatures, but this has not been economically successful, so far). If periods of high wind run during flowering occur, wind breaks may be a sound investment.

Rootstock selection

Once the site characteristics have been determined, appropriate varieties/clones and rootstocks should be selected that will perform well within these constraints. If good fruitset is doubtful, the use of Schwarzmann, Teleki 5C, 101- 14 MGT and Couderc 3309 (Cirami 1998) should be considered but their use will also depend on the other characteristics of the site. For example, in a vigorous environment Couderc 3309 has been found to significantly reduce fruitset (Wolf and Pool 1988).

Frequency of loss

Economically we can reduce the impact of poor fruitset, by

including a yearly estimation of crop loss due to poor fruitset in long-term budgets. Using long term yield data to determine the probability of poor fruitset, plus the severity of the expected loss due to poor fruitset, a numerical value of economic loss can be determined. With this value in the budget, the long-term feasibility of the project can be assessed and owners/managers can at least be prepared to manage this loss should it occur.

If the frequency of poor fruitset is high then site selection or varietal/rootstock selection may be a significant contributor to poor performance. In this situation a full review of the vineyard should be undertaken and its long-term feasibility determined.

If the frequency of poor fruitset is low or sporadic there may be no requirement to change management in the future, as changes to improve fruitset may result in higher economic cost in good seasons by removing grapes to meet the required cropping levels (either imposed by wineries/winemakers, or to ripen the grapes successfully).

There may also be significant increases in disease risk from bunch rots as

- Better fruitset leads to more berries;
- More berries leads to tighter bunches and heavier bunches;
- Tighter bunches increases potential for disease;
- Heavier bunches gives higher yield (which may or may not be beneficial). How does this relate to increased disease risk?

Economics of good fruitset

Management of yield is no longer a 'prune-and-forget' task, with the wineries taking all that is produced. Most wineries now recommend cropping levels, realistic or not, that the winegrower must meet. Achievement of the required cropping levels involves pruning tasks throughout the season. Tasks such as foliage management, shoot thinning and crop thinning, all have some impact on final yield.

Unfortunately if fruitset is poor, the economic viability of the project may be questionable, especially if this occurrence is frequent. However, if yields are too high, additional economic cost must be incurred to remove grapes, which may also threaten the economic viability of the project.

With most winemakers pushing the 'lower yield equals better quality' barrow, some may question whether fruitset should be improved, particularly if we are going to remove bunches only to satisfy the winemaker. The simple answer is that poor fruitset is generally a product of poor condition during flowering, which often leads to increased flowering time. This in turn leads to greater variability in the size and level of ripeness of berries, the uniformity of bunches and if grapevine uniformity is low, to a differential in overall grapevine performance. As quality is inversely proportional to variability, increasing fruitset should lead to better winegrape quality.

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Water stress at flowering and effects on yield

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Introduction

A search of the grape literature reveals a considerable number of reports of the effect of water deficit on berry development and ripening, however, there are few reports on the effect of water deficit specifically during the flowering—setting period. Is this a result of the general acceptance that the avoidance of water deficit or stress during *Vitis vinifera* flowering is critical and not worthy of investigation? In contrast, the influence of rootzone available soil water at flowering on cereals is well documented (Figure 1). Water deficit at germination reduces the number of plants/m^2, while during the vegetative stage deficit will reduce the number of grain heads per plant and if it continues, the number of kernels per head. Water deficit around flowering will also reduce the number of kernels per head and also final kernel size in a similar manner to which water deficit after flowering in grape berries will reduce final berry size. A similar understanding exists for a range of other annual crops and for some, complex mathematical models have been developed to describe the relationship between evapotranspiration deficit and plant behaviour (see examples cited in Deficit Irrigation Practices, FAO Water Reports 22, 2002). Most annual crops exhibit a high sensitivity to water deficit at flowering with effects manifesting as reduced yield caused by, for example, smaller or fewer seeds, reduced boll or tuber size.

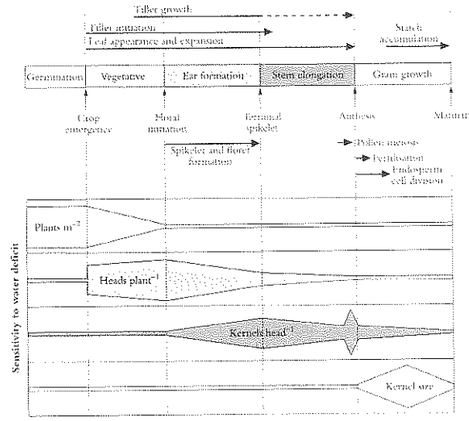

Figure 1. A schematic representation of the major developmental phases of a cereal plant. Band widths represent relative sensitivity to water deficit. (Reproduced from "Plants in Action" Eds: Brian Atwell, Paul Kriedemann & Colin Turnbull, Macmillan Education Australia, Melbourne, 1999 664 pp.)

Water stress at flowering in *Vitis vinifera*

Hardie and Considine (1976) investigated the effects of severe water stress on fruiting, container grown Cabernet Franc vines, including water deficit during the flowering—setting period. Withholding water for a 22-day period commencing at flowering resulted in a significant reduction in berry volume and weight, the number of berries per cluster, cluster weight and clusters per vine (Figure 2). Yield per vine of deficit-irrigated vines was about 6% of well-irrigated vines, highlighting the critical importance of avoiding water stress during flowering if an economic yield is to be achieved. The loss in yield reported by Hardie and Considine (1976) was accentuated by the severe water deficits that could be imposed on container-grown vines in a free draining soil with a low water holding capacity and Myburg (2003) demonstrated that with vines in the field with a larger more exploratory root system, and greater soil water reserves, comparative yield losses could not be

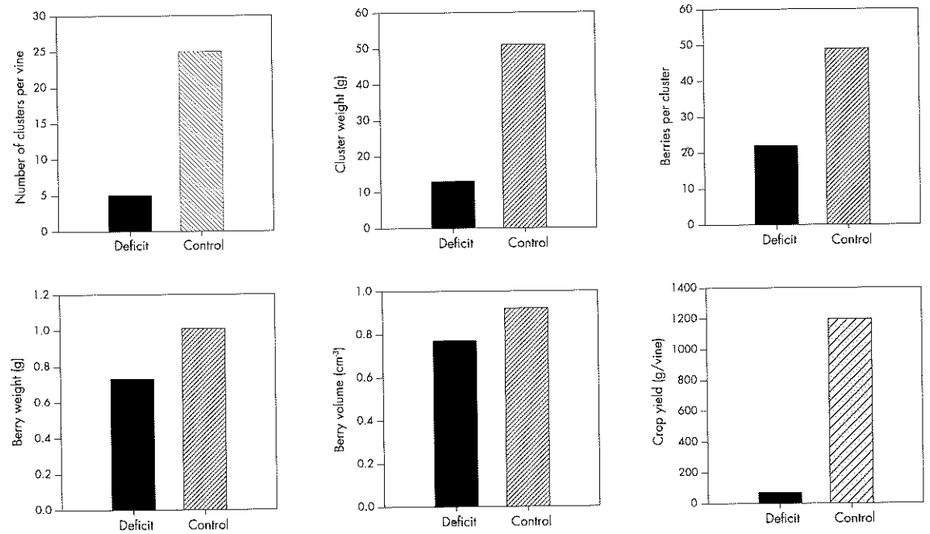

Figure 2. Yield components of well irrigated container grown Cabernet Franc grapevines and of vines subjected to 22 days of water deficit commencing at flowering. Data redrawn from Hardie & Considine (1976)

induced. Withholding micro-sprinkler irrigation on mature, field-grown Sultanina vines for a period of about three weeks prior to, and including flowering, did not result in any significant loss in yield or vegetative growth. There was a tendency for smaller berries and reduced bunch weight and a visual observation of increased berry loss on deficit vines after flowering that resulted in a 15% loss in yield compared to non-deficit vines.

Two factors may have contributed to minimising the effect of water deficit during flowering in the Myburg experiment:

i) The rootzone was near field capacity at the commencement of the deficit period and was only -0.070 MPa at the end of the treatment period, only slightly drier than suggested critical values required for the control of vegetative growth and yield.
ii) The steady decline in soil water availability during the deficit period may have provided sufficient 'buffering' through greater root exploration or adaptation.

Although less than the 94% loss in yield reported by Hardie & Considine (1976), such loss in yield would have an economic impact and indicates that the generally accepted practice of maintaining rootzone soil water close to field capacity during the flowering–setting period will ensure maximum berry set.

In the SA Riverland, field-grown Shiraz vines exhibited crop loss when the rootzone soil available water fell below the refill line at flowering and continued to decline during the flowering–setting period. At harvest, there were about nine fewer berries per bunch (Table 1) compared with well-irrigated vines. In this experiment, deficit-irrigated vines were not re-irrigated until veraison by which time berry size was also less than well irrigated vines; however, if berry weight had not been reduced there could have been a 2.4 T/ha loss in crop at harvest solely due to fewer berries per bunch. The actual loss in yield through the combination of fewer and smaller berries was about 20% compared to well irrigated vines. In previous seasons when soil water content did not fall below the refill line during the flowering and setting period there was no reduction in the number of berries per bunch. This highlights the need to accurately define the irrigation refill line for each soil type being irrigated.

Van Rooyen et al (1980), in a series of mathematically determined experimental treatments conducted in 16m^3 drainage lysimeters each containing two Waltham Cross grapevines grafted onto Jacquez rootstock, concluded that to ensure maximum yield, the soil matrix potential should not be more negative than about 5 kPa during Phase I of berry growth and no more than about 27 kPa during Phase II. These values are surprisingly low, as 5 kPa in some soils could indicate potential water logged conditions, however, these values were derived from surface contours of yield and not imposed soil water status. Although derived, these results support the recommendation that soil water status should be high during the flowering–setting period if maximum berry set is to be achieved and not less than the irrigation refill line.

Table 1. Effects of water deficit at flowering on yield components of Shiraz vines in the SA Riverland

	Irrigated	Deficit
Berries per bunch	68	59
Bunches per vine	166	164
Berry wt (g) at harvest	1.2	
Fruit wt/vine (kg)	13.5	11.6
Yield (T/Ha)	16.9	14.5

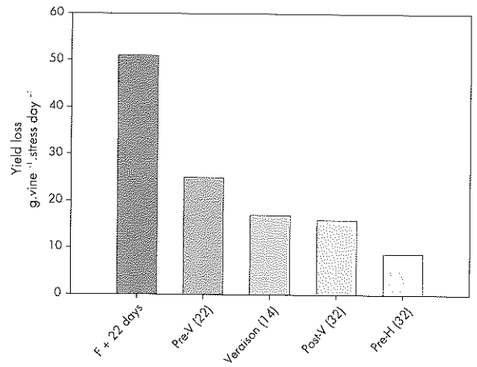

Figure 3. Yield loss (g/vine) per day of water stress for five deficit treatments imposed on potted Cabernet Franc vines. Number in brackets indicates the number of days of water deficit imposed either at flowering (F), pre veraison (Pre-V), veraison, post veraison (Post-V) or pre-harvest (Pre-H). Redrawn from Hardie & Considine (1976)

Berry developmental sensitivity to water deficit

Hardie and Considine (1976) reported that the flowering–setting period was the most sensitive period for yield loss and was about twice as sensitive to loss in berry weight per day of stress compared with the period before veraison (Figure 3) and about six times more sensitive than the period before harvest when berries were moderately resistant to stress.

McCarthy (2000) reported a similar sensitivity to water deficit during four periods of Shiraz berry development with the period after flowering being the most sensitive to soil water deficit (Figure 4).

Water deficit applied either before or after veraison resulted in a similar loss in berry weight per unit of water stress. Water deficit prior to harvest did not cause any apparent loss in berry weight, however, the intrinsic nature of ripening Shiraz berries to lose weight during the latter stages of ripening (McCarthy 1999) probably masked any treatment effect.

Although some of the periods of water deficit induced on Sultanina vines (Myburgh 2003) were too short to have significant effects, water deficit during the early stages of berry development tended to have more negative effects on yield than when water deficit was applied later in the season during berry ripening. Reduced cell division is generally attributed to be the cause of increased sensitivity of berries to water deficit post-flowering.

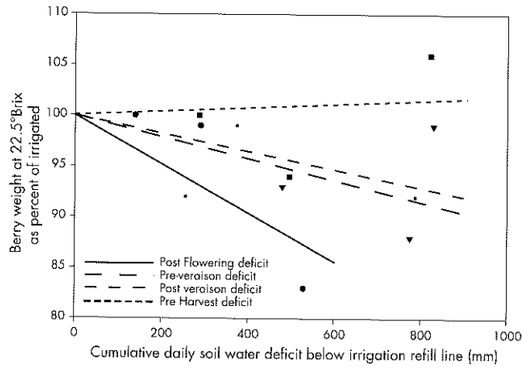

Figure 4. Relationship between cumulative daily soil water deficit (mm) below refill line and berry weight at 22.5°Brix as percent of fully irrigated for post flowering, pre- and post veraison and pre-harvest water deficit treatments.
Data points for each treatment are the calculated soil water deficit and berry weight for three consecutive seasons. In the absence of any deficit, berry weight of all treatments was assumed to be equal to fully irrigated

Pre-flowering water deficit

In regions with inadequate spring rainfall, irrigation is recommended to maintain the soil profile in a well-watered state to encourage vegetative growth (e.g. Hardie and Martin 1989) and this is generally the case in Australia. Few studies have however been conducted to examine the effects of soil water deficit during the budburst to flowering period on yield although the applicability of RDI during this growth stage is of increasing interest. In many regions, spring rainfall will minimise the effects of RDI between budburst and flowering, however, in districts where irrigation is normally applied after budburst the use of Regulated Deficit Irrigation (RDI) to control excessive early season vegetative growth and interactions with bunch development should be investigated. McCarthy (unpubl.) demonstrated a non-significant response to irrigation between budburst and flowering in the Barossa Valley, except under the extreme conditions of the 1982-83 drought when autumn–winter rainfall was much below long term average. The yield of unirrigated vines at harvest in March 1983 was less than half that of previous seasons (Figure 5) resulting from fewer bunches per vine due to poorer budburst and smaller berries. Surprisingly there were significantly more berries per bunch at harvest suggesting a compensatory response to the reduced bunch number per vine.

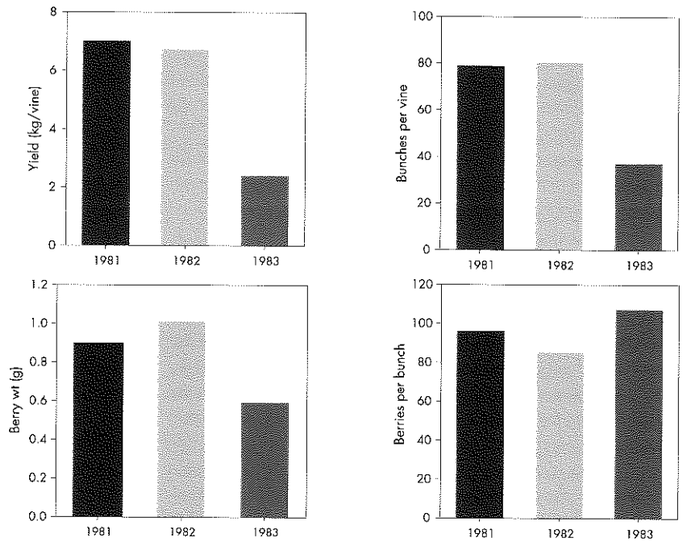

Figure 5. Components of yield of unirrigated Shiraz vines in the Barossa Valley for three seasons including the 1982-83 drought

Conclusions

The industry-wide practice of minimising soil water deficit during the flowering–setting period is supported by research outcomes both nationally and internationally over many years and the effects of water deficit in the early stages of berry expansion are the basis of Regulated Deficit Irrigation practices. While maintaining high levels of soil-available water during the flowering–setting period will contribute to ensuring a high percentage of flowers developing into berries, other factors such as temperature extremes are also critical. In high summer rainfall regions where bunch rots can often be problematical, vineyard operators perhaps need to consider whether berry set could be reduced in a controlled manner using water deficit to produce a more open structured bunch which is less susceptible to disease.

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The role of carbohydrates in the grapevine growth cycle

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Introduction

Grapevines, like all other plants, depend on a supply of carbohydrates to support vegetative growth and reproductive development. These carbohydrates are produced by the leaves and other green tissue through photosynthesis, and are either translocated for immediate use, or stored as starch or sugar reserves in the perennial parts of the vine. Studies of carbohydrate metabolism in grapevines date back many years (e.g. Winkler 1929), and these have provided us with a reasonable understanding of how the levels of carbohydrate reserves change during the season. Likewise, there has been considerable research looking at how environmental conditions and varietal differences are likely to impact on photosynthesis and the supply of carbohydrates to the vine. More recently this has extended to measurements of whole-vine photosynthesis (Petrie et al. 2003, Perez-Pena and Tarara 2004), which provides an ideal method for determining how trellis type, or management practices such as leaf removal or irrigation alters the whole-vine capacity to produce carbohydrates. In the future, combining whole-vine assimilation with detailed measurements of carbohydrate reserves may provide a more complete picture of how crop load, management and environmental factors influence carbohydrate dynamics during the season.

For the present, however, the aim of this paper is simply to provide an overview of carbohydrate production and storage within the grapevine, and discuss factors that influence both seasonal dynamics, and the amount of reserves stored before leaf-fall. It will also address the influence of carbohydrate reserves on reproductive development, and discuss the potential for managing reserve accumulation as a method for regulating vegetative growth and yield in the following season.

Carbohydrates and vine reserves

The name carbohydrate, or 'carbon hydrate', is a general term used to describe a range of sugars or saccharides that have an approximate composition of one carbon for every water molecule. The basic units of carbohydrates are called monosaccharides, with two common examples being glucose and fructose (which are also the main sugars in grape berries). Carbohydrates made up of two or more of these basic units are referred to as polysaccharides. This can range from sucrose, which is made from one glucose and one fructose molecule, to carbohydrates made up of thousands of individual sugar molecules. Sucrose is important in plants because it is the main form of carbohydrate transported through the phloem. Larger polysaccharides such as cellulose and starch, which are both made up from glucose molecules, also play an important role in plants. Cellulose is one of the main components of cell walls, and is crucial for maintaining the strength and structure of the plant. Starch has a slightly different chemical structure which enables the plant to store it in the form of small granules in living cells, but then break it back down into glucose if a supply of carbohydrates is required elsewhere in the plant. Because starch and sugars can be re-used by the plant they are often described as 'non-structural' carbohydrates. In contrast, cellulose cannot be converted back to glucose by plants, and is regarded as a structural carbohydrate.

The main non-structural carbohydrates found in grapevines are glucose, fructose, sucrose (which collectively represent the soluble sugar fraction) and starch, which is insoluble in water and has to be first converted into glucose by enzymes before it can be used by the plant. Collectively, these provide a measure of the amount of carbohydrate reserves available to the vine. However, in most studies the amounts of starch and sugars are analysed separately, so carbohydrate reserve levels are often expressed as a starch and soluble sugar fraction. On a concentration basis, the amount of soluble sugars in grapevine wood can range from about 2 to 15% of the dry weight. Soluble sugars in the roots can vary between 2 and 10% of the dry weight. The range of starch concentrations in the wood and canes is similar to that of soluble sugars, and will range between 2 and 18%. In contrast, roots are able to store much higher concentrations of starch, with young roots in turn able to store higher concentrations of starch than old roots. This can make representative sample collection more difficult than for wood or canes, but in work with Semillon, Shiraz and Chardonnay, root starch concentrations have been found in the range of 4 to 45% of the root dry weight.

Within the vine, soluble sugars are involved in a wide range of processes, and at any one time could be found in cell vacuoles, taking part in metabolic reactions, or being transported through the phloem. Therefore, depending on when samples are collected and which tissue is used, it is harder to distinguish what sugars might be available as reserves and what are essential to maintain basic physiological processes. In contrast, starch is specifically a storage form of carbohydrate which plants produce when they have an excess of carbohydrates, and then re-use later when an additional source of carbohydrates is required. In grapevines, starch is mainly found in the amyloplasts of xylem and phloem parenchyma cells. These are living cells and the most common cell type in plants. A useful property of starch is that it will stain a dark blue or purple colour when mixed with iodine, so it is easy to see where starch is being stored if a section is cut through part of the vine and stained with a mixture of iodine and potassium iodide. In both above ground parts of the vine (Figure 1) and roots (Figure 2), starch deposits are most apparent in the rays which span the water conducting xylem tissue and phloem. In Figure 2b, which is a section cut along the length of the root, the magnification is sufficient to see starch granules in the radial parenchyma cells of the xylem rays, and in the axial parenchyma cells adjacent to the water conducting xylem vessels.

Sink-source relations and vine balance

Plants produce most of their carbohydrates through photosynthesis in the green chloroplast-containing mesophyll cells of the leaves. In this process, light energy from the sun is used to combine carbon dioxide from the atmosphere with water to form molecules that are subsequently converted into carbohydrates. Although other green plant parts such as stems or pre-véraison fruit in grapevines are also

capable of photosynthesis, their contribution is very small relative to the leaves. The conversion of carbon dioxide into carbohydrates by plants is often referred to as carbon assimilation, and gives a direct indication of capacity for growth when determined at the whole plant level. As an example, measurements of leaf area and photosynthesis of spur pruned Riesling suggest that the vines were capable of assimilating 30.7g of carbon per day at harvest (Downton and Grant 1992). Carbon makes up about 44% of plant dry weight, so assuming that there are no other losses, this would convert to a dry weight gain in the form of carbohydrates of around 70g per day.

There are many processes in the grapevine that compete for these carbohydrates as they are produced by photosynthesis. Of most interest to grapegrowers is the competition between shoot growth and fruit development, but root growth, nutrient uptake and even the transport of sucrose through the phloem all require energy from the carbohydrates produced from photosynthesis. In studies of plant physiology, the term 'sink' is used to describe a part of the plant that are net importers of carbohydrates. In contrast, parts of the plant that are net exporters of carbohydrates are known as a 'source'. Vine balance is a term widely used in viticulture to describe the relationship between canopy growth and crop load, and this is effectively a measure of the relationship between the main source (leaves) and the main sink (fruit) of the grapevine during the ripening period. However, at any stage during the season, the capacity of a vine to store carbohydrate reserves means that the perennial structure can also act as a sink or a source depending on whether it is mobilizing or storing carbohydrate reserves. Reserves will be used when the demand for carbohydrates cannot be met by photosynthesis, and stored when there is an excess supply. This is an important point, as it means that the amount of carbohydrate reserves stored will be strongly influenced by crop load, climate, and management factors that impact on whole-vine assimilation.

Carbohydrates during the growth cycle

Bleeding sap provides the first visual indication that carbohydrate reserve mobilization has commenced in spring. It contains approximately 120 mg/L of sugar, of which the majority is glucose and fructose (Glad et al. 1992; Campbell and Strother 1996). It is thought that these sugars are loaded into the xylem by parenchyma cells in direct contact with xylem vessels (which can be seen in Figure 2b), which in turn leads to an influx of water from the roots to re-fill xylem vessels after winter. They may also provide a source of carbohydrates to the developing bud before the full reactivation of the sugar transporting phloem tissue occurs in spring. Following bud-break reserves are progressively mobilized to support new shoot growth, with the maximum demand occurring around the eight-leaf stage (Yang and Hori 1979). The shoot and tip and developing leaves are a strong sink for carbohydrates, and initially all carbohydrate transport is towards the shoot tip (Hale and Weaver 1962). However, once a leaf reaches about 50% of mature size it becomes self-sufficient, and will start exporting carbohydrates. Initially these also go towards the shoot tip, but as further leaves separate from the tip, the direction of transport switches towards the base of the vine. Somewhere between the ten-leaf stage and flowering the canopy becomes self-sufficient, and will start replenishing the carbohydrates that were used following bud-break.

Storage of reserves appears to continue after flowering, but as the berries develop the fruit becomes an increasingly strong sink for carbohydrates. The ability of the vine to continue replenishing reserves during the ripening period will therefore be strongly influenced by crop load. Carbohydrate reserves can also be mobilized during the season to assist with fruit ripening, so a heavy crop load may not only prevent any new storage of reserves, but also continue to deplete existing reserves. However, while it may be tempting to calculate what Baumé increase might be possible if all the reserves were transported to the fruit, it is not likely to be that simple. Experiments with radioactively labelled reserves, which allow carbohydrate movement around the plant to be followed over time, suggest that carbohydrates will not move from reserves to the fruit in the last few weeks before harvest (Candolfi-Vasconcelos et al. 1994). Although the reason for this is not known, it is reasonable to assume that vines have evolved mechanisms to ensure that enough carbohydrates are stored to support growth in the following spring. From the vine's perspective, the priority is to ripen the fruit sufficiently to produce viable seeds, and not to keep accumulating sugar until an optimum level is reached for making wine. However, from a viticultural perspective, it would be interesting to know if there really is a switch in priority from fruit ripening to reserve replenishment and whether this varies from season to season, or with management practice.

In experiments with Semillon in the Riverina, we have found carbohydrate reserves can be completely replenished by harvest in lower yielding vines. However, under heavy crop loads the post-harvest period becomes increasingly important. This is particularly emphasized for root reserves, which appear to have a lower priority than above ground parts of the vine. The length of the post-harvest period, and the ability of the vine to maintain photosynthesis rates (adequate water supply, nutrition, etc.) can therefore influence the amount of carbohydrates stored. Our work indicates that five or six weeks would be required to fully replenish reserves of high yielding vines that have not recovered prior to harvest. We have also investigated the impact that machine harvester damage may have on reserve accumulation, and found that reducing the leaf area by half had a minimal impact on reserve replenishment providing the remaining leaves were healthy.

Role of carbohydrate reserve on shoot and reproductive development

The amount of carbohydrates stored in the vine can have a significant influence on shoot growth and canopy development in spring. The initial effect of low reserves appears to be a reduction in shoot diameter rather than shoot length (Bennett et al. 2002). However, if vine reserves are depleted over several successive seasons, then shoot diameter, shoot growth rates, leaf appearance rates and lateral development are all reduced (Smith and Holzapfel unpublished data). In experiments with Semillon no significant effect of reserve level on the date of bud-break or the percentage bud-break was found, although it is possible that other varieties may respond differently. Interestingly, growth rates of the shoots on high and low reserve vines were the same in the initial weeks following bud-break before the shoots on the low reserve vines slowed about midway between bud-break and flowering. This corresponds to the period of maximum reserve demand suggested from studies with radioactively labelled reserves (Yang and Hori 1979). After this point, shoot growth recovered, and by flowering shoot growth rates on the low reserve vines were the same as vines with high carbohydrate reserves. However, canopy development of the low reserve vines did not 'catch up' with the high reserve vines, and the pruning weights of high reserve vines were more than double that of the low reserve vines at the end of the season.

The availability of carbohydrates is known to be important for several key stages of reproductive development, but the extent to which carbohydrates from reserves can supplement those from

current photosynthesis is less clear. Floral differentiation occurs soon after bud-break, so if there is any influence of carbohydrate supply on flower numbers, then any contribution from photosynthesis would obviously be limited at this point. There are many other factors likely to impact on flower numbers (as reviewed by May 2004), but the amount of carbohydrate reserves in the vine does appear to have a significant influence. Flower number per inflorescence increased from approximately 130 to 275 between Chardonnay vines with low and high reserves (Bennett et al. 2002). A similar effect was observed with Semillon vines in the Riverina, with average flower numbers ranging from 234 to 317 for vines starting the season with low or high carbohydrate reserves respectively (Smith and Holzapfel 2003). In other vineyards where lower yields or reduced water availability made it more difficult to alter the amount of reserve accumulation, less variation in flower numbers was also observed.

During fruitset, and the initiation of bunch primordia for the next season's crop, there are numerous strong sinks in the vine competing for carbohydrates. At fruitset, there is the growing shoot tip and the perennial structure of the vine which may be starting to replenish reserves and the inflorescence has little capacity to compete with the sinks (Hale and Weaver 1962). Shoot tipping to eliminate competition with the shoot tip can therefore provide a practical method of increasing carbohydrate availability to improve fruitset. Alternatively, girdling to prevent transport of carbohydrates through the phloem may temporarily remove the competition from reserve storage or carbohydrate use by the rest of the vine. It has been suggested that the susceptibility of Merlot to poor fruitset is related to its continued dependence on reserves at flowering particularly if reserve levels are low (Zapata et al. 2004). The success of any girdling operation may therefore depend on whether the perennial structure is using or supplying carbohydrates at the time of flowering. As the initiation of inflorescence primordia occurs progressively during the season, the supply of carbohydrates to the bud may be influenced by competition with growing shoots and ripening bunches. It may also be influenced by canopy density or weather conditions that change bud exposure, or the photosynthesis of leaves adjacent to the bud (e.g. Perez and Kliewer 1990; Sánchez and Dokoozlian 2005). At present, there is limited information on the contribution of reserves to bud-fruitfulness.

In the same study that examined flower numbers on Semillon vines in the Riverina, bud-fruitfulness was also found to be lower in vines with reduced carbohydrate reserves (Smith and Holzapfel 2003). However, if reserve levels were reduced sufficiently to slow shoot growth rates and reduce canopy density, the improved exposure of the basal buds or their leaves appeared to offset the effect of the low reserve levels on bud-fruitfulness. There was a general trend for fruitset to be increased by high reserves and

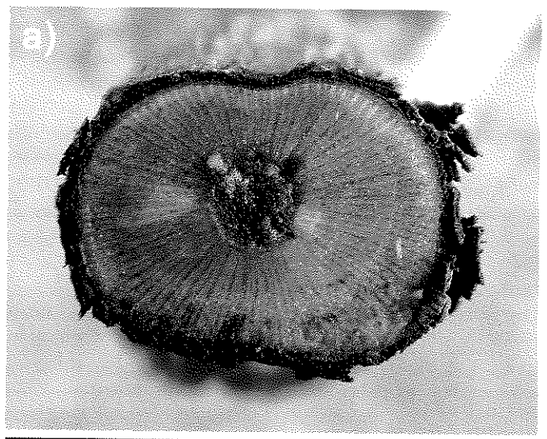

Figure 1. Cross-sections of a Chardonnay spur (a), and cane (b), collected at leaf-fall and stained with iodine to show areas of starch storage in blue. In both cases the highest concentrations are seen in the xylem rays (xr), with lower amounts in the phloem (p) and parenchyma cells between the xylem rays

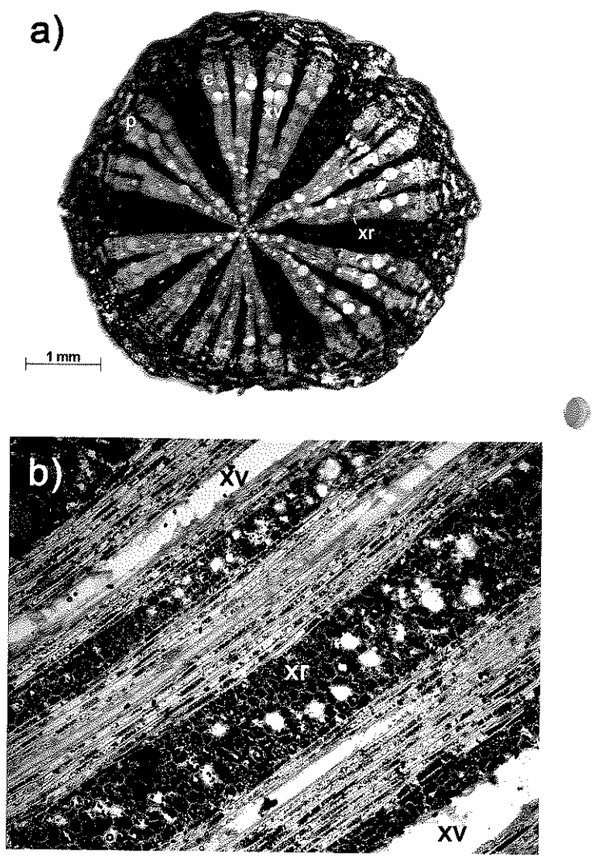

Figure 2. Cross section of a Chardonnay root at leaf-fall showing areas of starch storage in blue (a). Starch storage is most evident in the parenchyma cells of the phloem (p) and xylem rays (xr) which are continuous across the cambium (c). The lower picture (b) shows a tangential section through several xylem rays with sufficient magnification to see starch grains stored within individual cells. Water transporting xylem vessels (xv) can be seen in both images

decreased by low reserves. These maximum differences induced in set ranged between 6 and 12% within vineyards, although there was high variability between the measured bunches. However, the combined effect of reserves on flower number and fruitset meant that bunch weights were significantly influenced by the carbohydrate reserve status of the vine at the start of the season. Overall, by reducing vine reserve levels, average yields were reduced from 21.1 to 11.7 kg per vine, and increasing reserves increased average yields to 29.2 kg vine. The effect on pruning weights, due to differences in shoot growth rates, diameter and lateral development, were of similar magnitude. Consequently, vine balance was not altered by the carbohydrate reserve status of the vine.

Some practical implications and considerations

The interactions between carbohydrate production and use by grapevines are complex, and there are many factors that may influence the amount of carbohydrate reserves stored in the vine before leaf-fall. Carbohydrate reserves are also not the sole factor determining vine productivity, with nutrition, water supply and weather conditions all able to influence vine growth and reproductive development during the season. It is probable that nutrient reserves (which have received less research attention to date) are as equally important as carbohydrate reserves. However, based on the results of some of the research presented in this paper, the carbohydrate reserve status of the vine does appear to have a significant influence on vegetative growth and yield in the following season. This raises several questions about what levels of reserves are typically seen in commercial vineyards, whether a test for reserves would be a useful tool for yield regulation, and how reserve accumulation might be managed in the vineyard.

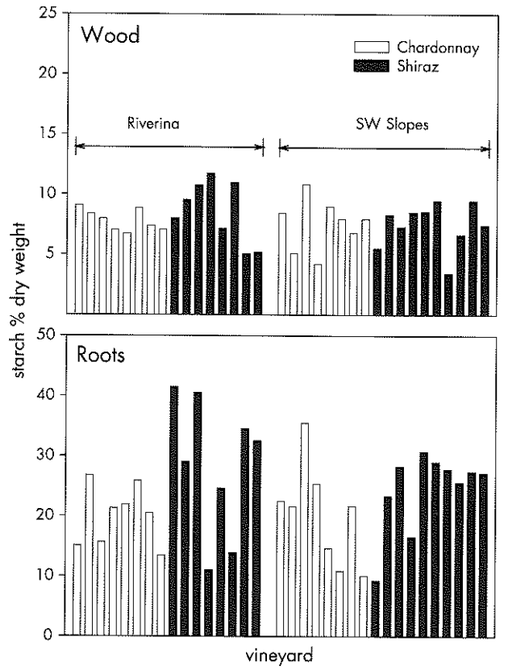

Figure 3. Variability in starch concentrations in the wood (combined cordon and trunk sample) and roots of 34 Chardonnay and Shiraz vineyards prior to pruning in winter 2005. The SW Slopes represents vineyards surveyed near Wagga Wagga, Gundagai, Young and Tumbarumba

Reserve variability: Prior to pruning in 2005 a survey of 34 Shiraz and Chardonnay vineyards in the Riverina, Gundagai, Hilltops and Tumbarumba grapegrowing regions of NSW was conducted as part of a new Grape and Wine Research & Development Corporation funded project (Figure 3). Roots, wood and canes were collected at five locations within each block to assess the variability both within and between vineyards. Only starch analysis on combined samples from each block has been completed to date, so we don't yet have information on within-vineyard variation. However, between vineyards, starch concentration in the wood ranged from 3.4 to 11.7% of dry weight, with a median value of 8.0%. Starch concentration in the roots ranged from 9.1 to 41.4% with a median value of 23.9%. No major differences between regions or varieties were observed, with vines from the cool climate Tumbarumba region accumulating similar starch concentration to the hot climate Riverina vineyards.

Testing carbohydrate reserve levels: Analysis of carbohydrates is relatively easy, so there are no difficulties in determining the concentrations of carbohydrate reserves in grapevine tissue. However, a significant limitation to such a test is that it does not take into account the size of the vine, and provides no information on the total amount of reserves stored in the vine. Using the example above, a spur-pruned vine from Tumbarumba may have significantly less biomass than a large hedge-pruned vine in the Riverina. Therefore, while the reserve concentration may be the same, the total amount of reserve may be very different. Another issue is determining what part of the vine will provide the best sample to indicate likely effects on productivity in the following season. Within single vineyards a reasonable correlation with the starch concentration of the wood at pruning and bunch weights in the following season (due to the

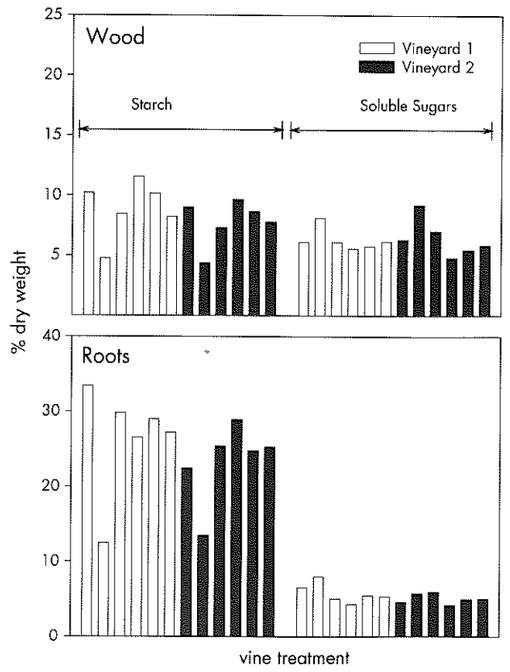

Figure 4. Starch and soluble sugar concentrations of two Semillon vineyards at pruning 2002 after the application of a range of treatments designed to alter reserve storage during the post-harvest periods of 2001 and 2002. In each group of 6 bars the treatments were: control, complete defoliation at harvest, simulated machine harvester damage, early harvest (4-5 weeks prior to commercial harvest), juice spray on leaves, and 50% leaf removal