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 into 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 (Lavce 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)”.

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.

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

**Figure 2.** A comparison of estimates of fertility based on dissecting dormant latent buds during winter (JJ) with observed node fertility measured six weeks after budburst (JJ) 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 (r² = 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.

Kliever (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 (r² = 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 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 Kliever 1990) and in controlled-environment studies (Buttrose 1974a). In growth chamber 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 phytoschoe 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 Beirut 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 Kliever 1990), high shoot vigour (Lavee et al. 1981, Dry and Coombe 1994) and high levels of soil nitrogen (Kliever 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 (Shaullis 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, Kliever 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 Kliever 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 (Shaullis and May 1971, Shaullis 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 Kliever 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

![Diagram](image.png)
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.

References


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