The Flowering Process of *Vitis vinifera*: A Review

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Abstract: The flowering of *Vitis vinifera* spreads over two seasons. Tendrils and inflorescences have a common origin known as anlage or uncommitted primordia. The fate of the uncommitted primordia depends on the cytokinin-gibberellin balance, with cytokinins promoting transition to flowering and gibberellins inhibiting it. High temperature and high light are induction stimuli for flowering. Neither photoperiod nor vernalization is very relevant for flowering induction. Inflorescence primordia development in latent buds stops after the formation of secondary and tertiary branches, approximately one month before shoot periderm formation. Buds resume growth after dormancy, with further branching of inflorescences before differentiation of individual flowers. Warm weather at budburst favors further inflorescence differentiation, resulting in more clusters per shoot, while cool weather favors differentiation of more flowers per clusters and fewer clusters per shoot. Environment and cultural practices influence flowering, either directly or indirectly via their impact on photosynthesis and nutrient availability. Cultural practices encouraging light penetration into the canopy favor flower initiation, while practices resulting in shading have a detrimental impact. Flower formation occurs through a series of sequential steps under hormone-mediated genetic control. The first genetic change involves the switch from the vegetative to the floral state, in response to different environmental and developmental signals, through the activity of floral-meristem identity genes. Second, the floral meristem is patterned into the whorls of organ primordia through the activity of floral-organ identity genes. Third, the floral-organ identity genes activate downstream effectors that specify the various tissues which constitute the different floral structures. The flowers are hermaphroditic and most are self-pollinated but cross-pollination also occurs. Fertilization is hindered by cool rainy weather and favored by warm dry weather.

Key words: variability, carbohydrates, nutrition, growth regulators, water relations, genetic control

Flower formation in grapevines is complex and is greatly influenced by the environment and viticultural practices. This review was undertaken to survey what is currently known on the flowering process with the view of identifying genetic, environmental, and cultural factors that can contribute to its variability. Critical stages of flower formation appear to be induction, initiation, and early differentiation during season one and differentiation at budburst during season two. Despite numerous studies on the influence of environmental and cultural factors on flower development, the process remains poorly understood. Seasonal variation contributes to enormous variations in yield and quality, in particular in cool-climate viticulture. Compared with 16 crops analyzed over a 58-year period, grapevine was found to have by far the highest seasonal variation in yield (32.5%), nearly twice that of the next closest crop (edible grain legumes and flax with 18.5% annual variation) (Chloupek et al. 2004). Analyses of a range of medium- and long-term yield data sets for a wide range of cultivars grown in a diverse range of climates (from cool to hot) consistently show that clusters per vine explains 60 to 70% of the seasonal variation in vine yield (Clingeleffer et al. 2001). Yield fluctuations are less sensitive to variations in berries per cluster (~30%) and berry size (~10%) (Clingeleffer et al. 2001).

Many cultural practices have been designed to improve fruit yield and quality, with considerable work on the impacts of these practices on fruit and wine composition. In general, viticultural practices aimed at producing more but smaller, less compact clusters without altering cropping potential are considered positive for fruit composition (May 2000). Uniformity or synchrony of development is perceived as advantageous for fruit composition, while variability is often viewed as undesirable. The flowering process in grapevines spreads over two seasons (Figure 1) and the interactions among genotype, environment, and management practices give rise to considerable variability, resulting in a range of cluster architectures and asynchronous development of individual flowers within a bunch, individual clusters within a shoot, within a vine, and within a vineyard block. This variability will then be reflected in the resulting population of berries used for winemaking. In this review we will attempt to catalog the sources of variability in the flowering process of cultivated *Vitis vinifera*. We will not discuss the fate of the berry after fertilization, and we will build on the extensive reviews already published on this

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subject (Boss et al. 2003, Boss and Thomas 2000, Carmona et al. 2007b, 2008, Gerrath 1993, Lebon et al. 2008, May 2000, 2004, Meneghetti et al. 2006, Pratt 1971, Srinivasan and Mullins 1981).

Anatomy of the Bud

The morphological nature of the shoot system of grapevines has been interpreted as either sympodial (Alleweldt 1963, Alleweldt and Balkema 1965, Snyder 1933) or monopodial (Morrison 1991, Pratt 1971, 1974, Srinivasan and Mullins 1976, Tucker and Hoefert 1968). A recent study showed that variation in shoot growth habit within the Vitaceae family exists and that *V. vinifera* grows monopodially (Gerrath and Posluszny 2007).

Each shoot node potentially can develop an axillary bud complex, consisting of four buds: a lateral bud (prompt, or first order axillary) positioned on the dorsal side of the shoot, and a three-member compound bud (latent bud) which is positioned ventrally (Figure 2) (Boss et al. 2003, Carmona et al. 2008, Gerrath 1993, Morrison 1991, Pratt 1971, 1974, 1979). The compound bud typically possesses three buds of unequal development stages: primary, secondary, and tertiary (Figure 3). The primary bud of the compound bud develops in the axil of the bract produced by the lateral bud. Secondary and tertiary buds develop in the axils of the bracts produced by the primary and secondary buds, respectively.

During grapevine shoot development the shoot apical meristem (SAM) produces both leaf primordia and a meristematic structure referred to as *anlage* (from the German word for primordium or more precisely, uncommitted primordium), in a regular pattern (Boss et al. 2003, Boss and Thomas 2002, Gerrath 1993, Pratt 1971, Srinivasan and Mullins 1981). The uncommitted primordium will differentiate into an extra-axillary structure, the nature of which will depend on the plant development stage and environment in which the primordium is formed. When uncommitted primordia are formed within latent buds, they can develop into inflorescence primordia. However, when uncommitted primordia are formed on rapidly growing shoots, they usually develop into tendrils (Boss et al. 2003, Boss and Thomas 2002).

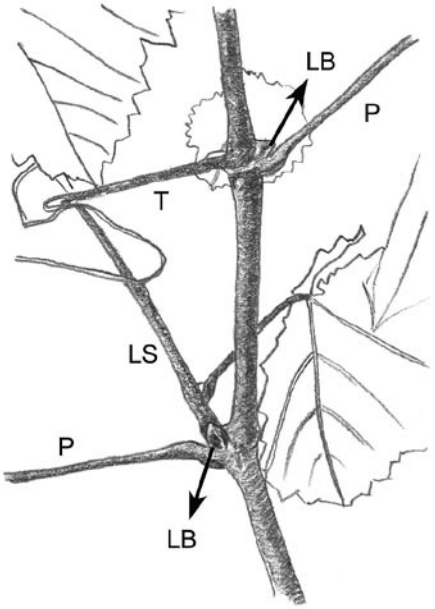

Figure 2 Location of lateral shoot and compound latent bud in a Pinot noir grapevine shoot. LS, lateral shoot; LB, latent bud; T, tendril; P, leaf petiole (drawing by Marc Greven).

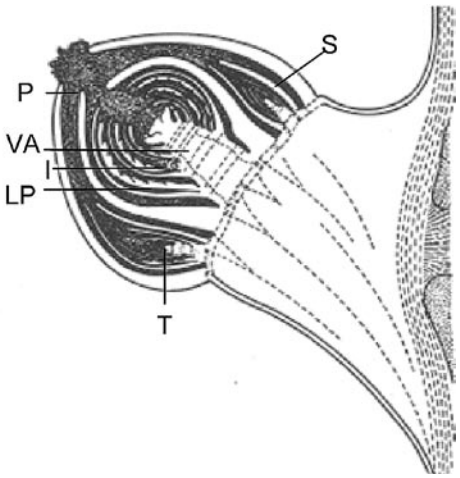

Figure 3 Compound grapevine bud immediately before budburst. P, primary bud; S, secondary bud; T, tertiary bud; LP, leaf primordium; I, inflorescence primordium; VA, vegetative axis (from Sartorius 1937).

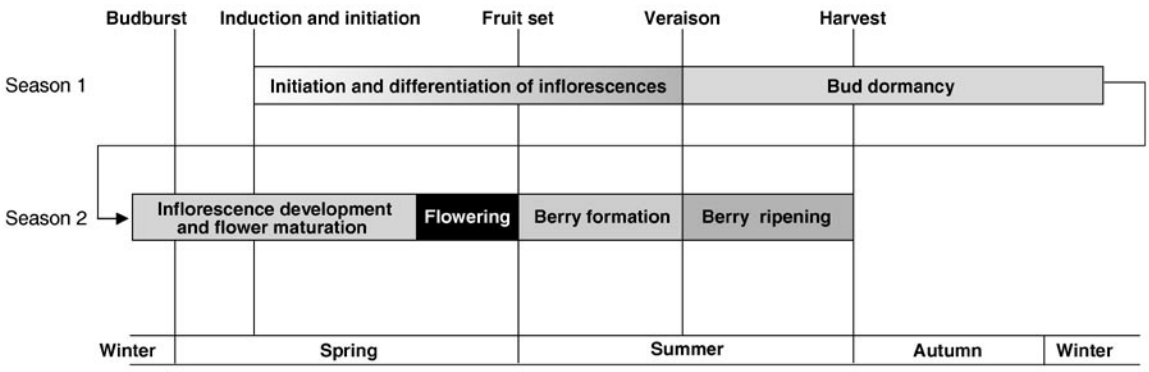

Figure 1 The two-season grapevine reproductive developmental cycle (Carmona 2008) (after Combe and Iland 2004; reprinted by permission).

The uncommitted primordium appears identical during its initiation and early development regardless of its fate, but it will mature into an inflorescence, a tendril, or an intermediate structure. There is a distinct, three-node modular construction to the shoots typical of *V. vinifera,* in which the SAM produces a series of two consecutive nodes containing opposed leaf primordia and lateral meristems (N1 and N2 in the French literature) alternating with one node bearing a solitary leaf primordium (N0) (Carbonneau 1976, Gerrath et al. 2001, Huglin and Schneider 1998).

While the lateral bud can develop into a shoot in the year it is produced, depending on environmental condition and genetic factors, the latent bud will burst and grow 9 to 12 months after the initial development. All three buds within the compound latent bud remain dormant during the growing season in which they form, unless they are stimulated by severe pruning. The primary bud is the most developed and forms 6 to 9 nodes (Pratt 1971), with usually inflorescence primordia opposite the fourth to the sixth leaf, and tendril primordia opposite subsequent leaves before becoming dormant during the summer. Huglin (1958) showed that the number of nodes developed predormancy varied from five to six at the base buds of the cane, reaching a maximum of nine in the middle part of the cane, and decreasing slightly toward the tip. Secondary latent buds are formed in the axils of the first two basal prophylls of the primary bud. These do not normally go on to form shoots in the following season except where there is some damage to the primary latent bud before budburst (e.g., primary bud-axis necrosis or mite damage) or when the primary shoot itself is damaged after budburst by frost or hail.

The Flowering Process: First Season

In brief, flower development in the grapevine involves three main steps: (1) formation of anlagen or uncommitted primordia; (2) differentiation of anlagen to form inflorescence primordia; and (3) differentiation of flowers. In temperate climates and under normal growing conditions, the time of initiation and rate of development of a flower cluster depend on the position of the winter bud on the cane (Alleweldt and Balkema 1965, Alleweldt and Ilter 1969, Barnard 1932, Barnard and Thomas 1933, Cheema et al. 1996b, Swanepoel and Archer 1988), the position of the inflorescence on the condensed shoot within the bud (Buttrose 1969, Cheema et al. 1996b, Snyder 1933, Swanepoel and Archer 1988), and the cultivar (Alleweldt and Ilter 1969). These localized variations in timing and extent of differentiation will be discussed in detail in the following sections.

After a short vegetative period, where three to five leaf primordia are developed, the SAM produces the first lateral meristem (uncommitted primordium or anlage), a club-shaped structure opposite the youngest leaf primordium (May 1964). This structure is slightly shorter and rounder than the leaf primordium. The SAM will continue to grow, alternating formation of leaf primordia with lateral meristems in a rhythmic fashion. Depending on the cultivar and environmental conditions, the first one to three uncommitted primordia formed on the shoots in latent buds will undergo repeated branching and will develop into an immature inflorescence (Pratt 1971, Srinivasan and Mullins 1976, 1981).

Timing of initiation and differentiation of inflorescences. For Riesling and Aris cultivars in Germany, anlage start developing 5 to 7 weeks after budburst (Alleweldt and Ilter 1969), coinciding with the period of maximum shoot growth. Depending on the cultivar, the number of leaves in the main shoot at the onset of induction ranged between 11 and 22 unfolded leaves. Swanepoel and Archer (1988) reported that initiation of anlage in Chenin blanc basal buds started 12 to 15 days before bloom, at which time the shoot had 12 expanded leaves. Initiation and differentiation of the first and second inflorescence primordia in each bud at the two basal nodes was complete at 25 days after bloom. Three weeks were required between initiation of the first and the second anlagen in a bud. The second anlage was initiated immediately after the differentiation of the first (Swanepoel and Archer 1988). For Merlot in Bordeaux, initiation started 6 weeks after budburst (Carolus 1970). For Syrah in southern France (Montpellier), initiation started on basal buds (buds in positions 3, 6, and 9) five weeks after budburst and two weeks before the onset of anthesis and proceeded in an acropetal gradient (Cheema et al. 1996b), following a pattern similar to that reported for Chenin blanc (Swanepoel and Archer 1988) (Figure 4). In Australia, Chardonnay anlagen initiation in latent buds at node position 4 commenced 4 weeks after budburst (corresponding to ~4 weeks before anthesis) and 6 weeks after budburst (~6 weeks before flowering), depending whether they were grown in a hot or a cool climate, respectively (Watt et al. 2008). In Riesling (bud positions 2 to 6) in New York, anlagen were initiated when the shoot had 13 flat leaves (15 nodes), that is, 12 days before bloom (Pratt 1979).

Inflorescence primordia formation. The further development of the anlagen starts with the formation of a bract (Winkler and Shemsettin 1937). The anlage then divides into two unequal parts, called arms. Two-branched anlagen have the potential to produce inflorescence primordia, tendril primordia, or shoot primordia. The larger adaxial part (nearer to the apex) is the inner arm and the smaller abaxial part adjoining the bract is the outer arm (Pratt 1971, Srinivasan and Mullins 1976).

Inflorescence primordia are formed by extensive branching of the anlage (Srinivasan and Mullins 1981). The inner arm divides and produces several globular branch primordia (Scholefield and Ward 1975), which give rise to the main body of the inflorescence. Branching of the outer arm is less extensive and it develops into the lowest branch of the inflorescence (May 1964). The branch primordia of the inner and outer arms give rise to branch primordia of the second and third order, each of which is subtended by a bract (Srinivasan and Mullins 1981). The degree of branching of the inner arm gradually decreases in an acropetal direction, which gives the inflorescence primordium a conical shape

(Srinivasan and Mullins 1981). After the formation of one to three inflorescence primordia (depending on the cultivar), the latent bud enters into dormancy (Pratt 1971). For Merlot in Bordeaux, buds of nodes 3, 7, and 14 ceased apical growth when they had 8, 9 and 10 leaf primordia, respectively (Carolus 1970). Apical growth in latent buds of Carignan at Montpellier ceased after the eighth leaf primordium (Nigond 1967) and in those of Sultana in the Murray Valley, Australia, after the tenth leaf primordium was initiated (May 1964). By examining single-node cuttings of Merlot in Bordeaux, Pouget (1963) found that dormancy development begins at the basal nodes of the shoots. Dormancy develops over a period of 2 to 3 weeks in all the latent buds within the shoot system of a vine. This period coincides with the time when the color of the shoots changes from green to yellowish-brown, and when the initiation of new nodes at the shoot apex ceases. Shoot maturation (*aoûtement* in French, periderm formation) up to node 14 was completed by late August (northern hemisphere), thus the primordial shoot of the latent bud ceased development approximately one month before periderm appeared (Pouget 1963).

Early reports indicated that calyx primordia appeared in the inflorescence primordia of the latent buds at the end of summer (Agaoglu 1971, Alleweldt 1966, Alleweldt and Balkema 1965, Alleweldt and Ilter 1969). However, later studies with scanning electron microscopy all agree that flower parts only differentiate after resumption of growth in the spring (Bernard and Chaliès 1987, Carolus 1970, Cheema et al. 1996a, Morrison 1991, Scholefield and Ward 1975, Srinivasan and Mullins 1976, Swanepoel and Archer 1988, Watt et al. 2008). The presence of bracts subtending each branch primordium could have led to this interpretation in light microscope studies (Swanepoel and Archer 1988, Watt et al. 2008).

During the following spring, when the environmental conditions permit, bud growth resumes. The relative importance of branching prior to dormancy, compared with differentiation during budburst, in controlling potential inflorescence size and flower numbers is poorly understood. According to Tourmeau (1976), in the winter bud, secondary branching is well differentiated but tertiary branching, when present, is only rudimentary. Approximately one week before budbreak, the meristems at the tip of each branch (winter meristems) resume activity. Some meristems will immediately develop flowers while others undergo a short vegetative period during which one or more bracts form. The meristems that will develop into flowers are formed in the axil of each of these bracts (Tourmeau 1976). Frequently, during budbreak, an additional branch is added to each winter meristem and three to eight lateral meristems arranged as a dichasium will form. Initiation of all flower primordia occurs in a very short period of less than two weeks (Tourmeau 1976). Not all meristems that will form flowers are present in the dormant bud, and therefore attempts to predict yield based on dissecting buds during winter or forcing dormant buds under a controlled environment are not meaningful, unless the branching pattern of the meristems is preprogrammed in the bud (Tourmeau 1976). Flower meristems sequentially form sepal, common petal-stamen, and carpel primordia, which will differentiate in the corresponding flower organs (Gerrath 1993, Pratt 1971, Srinivasan and Mullins 1981).

Variability in level of differentiation. Anlagen that undergo extensive branching before dormancy form inflorescences, while those that possess only two or three branches are thought to form tendrils. Within the compound latent bud, the buds axillary to the two basal prophylls on the primary bud also develop a few nodes and undergo dormancy.

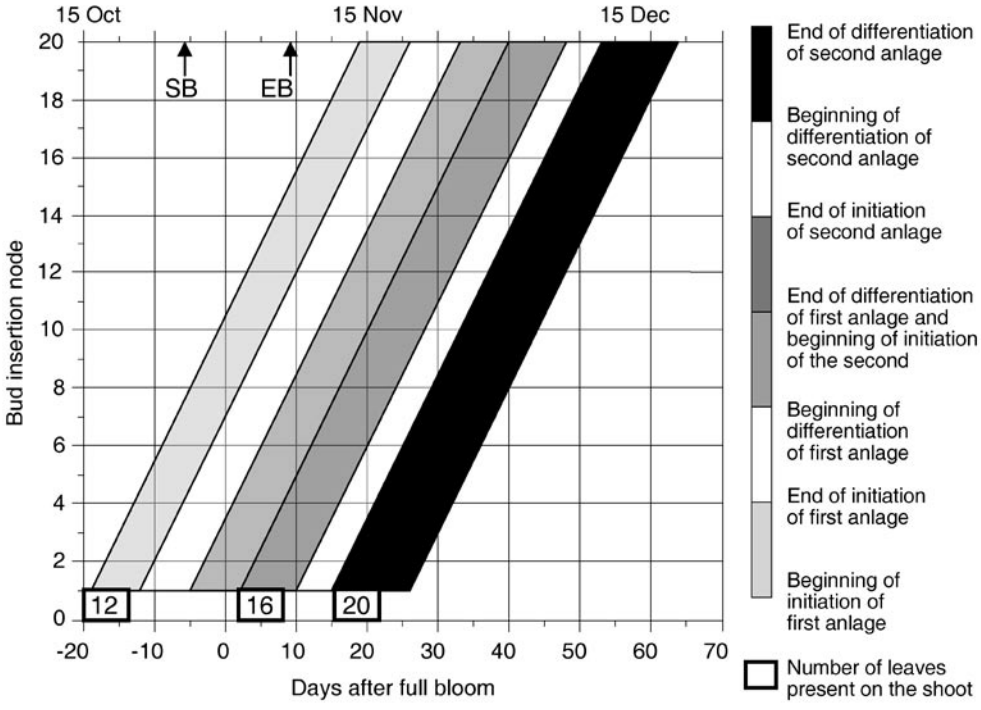

Figure 4 Representation of inflorescence formation in *Vitis vinifera* L. Chenin blanc in South Africa (based on data from Swanepoel and Archer 1988). SB: start of bloom; EB: end of bloom. Budburst was indicated as occurring in September and veraison in January. It is likely that the two-day interval between the initiation of anlage in two successive buds shortens as temperatures increase during the season.

The secondary bud usually bears inflorescences, although the tertiary usually bears none (Pratt 1971).

Earlier anlage initiation leads to earlier primary branching and hence the start of inflorescence primordia development. The level of inflorescence differentiation in the primary axis of the latent bud decreases in an acropetal gradient (Cheema et al. 1996a). However, according to May (2004), the branch number per inflorescence is not a good indicator for flower number.

Bud fertility along the cane increases from the base to the middle and decreases again toward the tip (Huglin and Schneider 1998). Cane vigor is an important factor in bud fertility. A common anecdote in European viticulture is that for optimal fertility, cane diameter should be equivalent to a cigarette or pencil size. In a multiyear survey of Pinot noir grown in the Willamette Valley, Oregon, an average cane weight at pruning of 45 g maximized the number of flowers per node (number of inflorescences per node multiplied by the number of flowers per inflorescence) the following season (M.C. Vasconcelos, unpublished data, 1999). For the cultivars Riesling, Auxerrois, and Pinot gris, a close relationship was found between cane diameter and bud fertility (number of inflorescences per shoot) (Huglin 1958). A similar relationship has been found in Sauvignon blanc, where inflorescence number per shoot decreased as cane diameter decreased from ~10 mm (M. Trought, unpublished data, 2006). Excess vigor has been associated with poor bud fertility (Carbonneau and Casteran 1979).

The inflorescences of cane-pruned vines have more branches, presumably because a higher proportion of the bunches come from more distal node positions of the canes; these contain larger inflorescence primordia than the basal two nodes present on spurs (May and Cellier 1973). At the scale of the shoot axis, the level of differentiation follows an acropetal gradient where the distal inflorescences are less differentiated than the proximal. Within the inflorescence, the outer branch or wing is less developed than the main branch. Within the main axis of the inflorescence, the development of individual flowers is not synchronous: the level of differentiation of the basal part is superior to the distal part. Within the floral group (dichasium), the terminal flower develops first, then the lateral ones develop, and the basal-most develop last (Cheema et al. 1996a).

Induction stimuli: Internal regulation. *Growth regulators.* It has been proposed that the requirement for a specific balance of hormones for flower formation is readily applicable to woody perennials (Zeevaart 1976). In grapevine, inflorescence formation is regulated at two levels: formation of anlagen and differentiation of anlagen. Gibberellin (GA) and cytokinin are the principal regulators of flowering. Gibberellin is necessary for the formation of inflorescence axes (initiation of anlagen) and the growth of inflorescence axes (two-branched stage of the anlagen). Gibberellins are inhibitors of flowering in many fruit species, but the role of GA in flowering in grapevines varies with the stage of development of the latent bud. At an early stage, GA is a promoter of flowering because anlagen formation is a GA-requiring process. Later, by promoting vegetative growth, GA acts as an inhibitor of flowering because it directs the anlagen to form tendrils. Applications of the growth-retardant chlormequat to anlage or tendrils favors inflorescence formation, possibly from its role in enhancing of cytokinin production and/or inhibiting GA synthesis in grapevines (Mullins et al. 1992b). A grapevine dwarf mutant derived from the L1 meristematic layer of the champagne cultivar Pinot Meunier produces inflorescences along the length of the shoot where tendrils are normally formed (Boss and Thomas 2000). The mutated gene associated with the phenotype is a homologue of the *Arabidopsis* gene *GA INSENSITIVE* (*GAI*). The conversion of tendrils to inflorescences in the mutant demonstrates that the grapevine tendril is a modified inflorescence inhibited from completing floral development by GA (Boss and Thomas 2000). The hormonal control of anlage, tendril, and inflorescence formation in the grapevine is shown (Figure 5).

Cytokinins are implicated in the control of many aspects of reproduction in the grapevine. Flower formation is a cytokinin-controlled process (Mullins et al. 1992b, Srinivasan and Mullins 1978, 1979, 1980a). It is generally assumed that cytokinins present in developing buds early in the season are derived from roots (Mullins et al. 1992b). The xylem sap (bleeding sap in the spring) of the grapevine contains high cytokinin activity during budburst and flowering (Nitsch and Nitsch 1965, Skene and Kerridge 1967). A recent study showed that bud cytokinin content tended to be higher in spurs than canes (Lombard et al. 2006). However, levels of xylem cytokinin in long- (cane)-pruned Sultana, Sunred

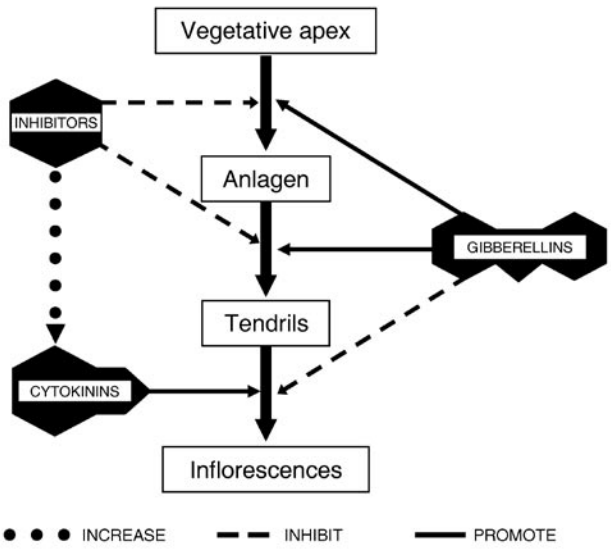

Figure 5 Hypothetical scheme for the hormonal control of anlage, tendril, and inflorescence formation in the grapevine (*Vitis vinifera* L.) summarizing in vitro experiments using excized tissues treated with growth regulators. The postulated inhibitors in this scheme are endogenous compounds, which mimic the effects of the synthetic growth retardant, chlormequat, i.e., inhibition of gibberellin biosynthesis and promotion of cytokinin biosynthesis. For simplicity, anlage that have produced a bract and two branches (inner arm and outer arm) are referred to as tendrils. (Reproduced from Srinivasan and Mullins 1981; reprinted by permission of the publisher.)

Seedless, and Alphonse Lavalée canes were significantly higher than in short-pruned spurs. The authors postulated that in longer canes more cytokinin is available for reproductive development. Evidence from grafting experiments with mutants of the legume pea (*Pisum sativum*) suggests that the transport of cytokinins from the roots is regulated by signals from the shoot (Beveridge et al. 1997), which would explain the higher levels of cytokinin in cane- versus spur-pruned vines. Physiologically, branching is regulated by a complex interplay of hormones, including auxin, cytokinin, and an unidentified root-derived signal. Auxin transported polarly from the apical bud suppresses the growth of axillary buds (Kieber 2006). In contrast, cytokinin stimulates cell division activity and outgrowth when applied directly to the axillary buds of many species, and cytokinin overproducing mutants tend to be bushy (Kieber 2006). It was recently demonstrated in lateral buds that auxin inhibits the expression of a subset of isopentenyltransferase (IPT) genes that encode the enzyme catalyzing the first committed step of cytokinin biosynthesis, thus providing a mechanistic link between these two hormones in regulating bud growth. This result and other data suggest that cytokinins responsible for axillary bud growth may be synthesized in the bud itself, not transported from the root (Kieber 2006).

Carbohydrates. During development, latent buds receive carbohydrates from leaves on the same side of the shoot (Hale and Weaver 1962). They are a weak sink for carbohydrates relative to the developing flower and fruit clusters and much weaker than the growing shoot tip (Hale and Weaver 1962). Buds only import carbon directed basipetally, from leaves that export bi-directionally or downward (Hale and Weaver 1962). Significant downward movement of labeled carbohydrates does not occur until the 10-leaf stage (Yang and Hori 1980), while the beginning of anlage initiation occurs at the 12-leaf stage (Swanepoel and Archer 1988). No investment into new reproductive growth is made until the new shoot reaches independency from the parent vine.

A number of studies relate bud fertility to carbohydrate reserve replenishment during the previous season (Bennett et al. 2005, Candolfi-Vasconcelos and Koblet 1990, Duchêne et al. 2003a, Duchêne et al. 2003b, Howell et al. 1994, Keller and Koblet 1995a, Mansfield and Howell 1981). A reduction in photosynthesis during anthesis and shortly after has the most negative impact on bud fertility (number of inflorescences per bud) (Candolfi-Vasconcelos and Koblet 1990). Unlike other perennial crops, in grapevine there is no evidence for competition between initiation and differentiation of inflorescences for the following season and the development of flowers and fruit set for the current season (Antcliff and Webster 1955, Huglin 1958), but there is ample evidence for competition between vegetative growth and the flowering process (Vasconcelos and Castagnoli 2000). Conditions that are favorable for inflorescence initiation and differentiation are also favorable for flowering and fruit set (Candolfi-Vasconcelos 1990). However, reduced shoot vigor caused by overcropping will result in lower bud fertility (Murisier 1996).

Environmental factors. Environmental factors promoting flowering in grapevine do not correspond with the major factors inducing flowering in herbaceous plants, such as photoperiod and vernalization for cruciferae and cereal species (Carmona et al. 2008). In this way, neither photoperiod nor vernalization is very relevant for flowering induction, but short-term exposures to high temperature and high light intensity have been shown to promote grapevine flowering (Buttrose 1974a, Mullins et al. 1992b). A combination of warm temperature, sufficient illumination of the bud, and absence of stress are required for optimum initiation (Buttrose 1970, Dunn and Martin 2000, Kliewer 1975, Moncur et al. 1989, Petrie and Clingeleffer 2005, Zelleke and Kliewer 1979). Environmental factors are thought to exert their influence on flowering by modifying the internal chemical composition of the plant, particularly the balance of endogenous hormones and also via their impact on vine photosynthesis.

Light. Antcliff and Webster (1955) were the first to suggest a possible connection between light intensity and fruitfulness (number of clusters per shoot) of buds in Sultana grapevines. Light and temperature may have a synergistic effect on bud fruitfulness, and evidence suggests that they are both key factors in flower induction in grapevines.

Light may influence fruitfulness through its effect on photosynthesis and carbohydrate availability or through a direct effect on the bud itself. Research in the past 50 years on the effects of light used several approaches, including use of growth cabinets with varying light levels and photoperiod, night interruptions, field manipulations of vine and bud microclimate by shading vines, shading individual shoots, the renewal zone of the shoots, and individual buds. Most of the research was conducted on Sultana, a cultivar known for fruitfulness problems. Sufficient evidence has been gathered over the years to substantiate Antcliff and Webster's initial hypothesis that light was involved in determining bud fruitfulness (Buttrose 1969, Dry 2000, Kliewer 1982, Lavee et al. 1967, May 1965, May and Antcliff 1963, Perez and Kliewer 1990, Petrie and Clingeleffer 2005, Sommer et al. 2000). Studies manipulating canopy permeability to light through changes in the irrigation regime (Carbonneau and Casteran 1979, Caspari et al. 1996, Greven et al. 2005, Loveys et al. 2000) or canopy management (Kliewer 1982, Reynolds et al. 1995, 1996, Shaulis and Smart 1974) often reported parallel changes in fruit yield. Shaulis and Smart (1974) reported that leaves of interior shoots are inferior in photosynthesis or net assimilation rate because of lower light levels and absence of leaf heating. Leaves also have a shorter life because of premature and shade-induced chlorosis and abscission. They also reported that buds of the canopy interior are inferior in survival of winter cold; shoot production from primary and secondary buds; cluster primordia initiation and development; and shoot and grape production by basal buds. They associated the high variability of light interception among canes in the same vine to the high variability in yield per cane the following year and found that light environment

was closely associated with percent budburst, clusters per shoot, and berries per cluster.

Most studies seem to agree that to optimize bud fertility it is important that adequate light reaches the renewal zone (Buttrose 1974a, May 1965, Sanchez and Dokoozlian 2005). Shading individual buds depresses fruitfulness (Hopping 1977, Koblet 1985, May 1965, May et al. 1976). Measurements for the cultivar Concord suggest that the leaf subtending the bud is the receptor of the light stimulus (Smart et al. 1982a). Reducing shoot crowding in the vineyard improves the radiation microclimate and yield is increased (Shaulis et al. 1966, Shaulis and May 1971, Smart 1985). External buds are much more fruitful than buds inside the canopy because of excessive shading closer to the head of the vine (May et al. 1976, Morgan et al. 1985). It appears that light availability in late spring is critical for flower induction; shading at this time has a greater effect on fruitfulness of latent buds than earlier or later in the season (Srinivasan and Mullins 1981). This coincides with the period when anlagen are being initiated and differentiated in the buds that will be retained at pruning the following season (Figure 4). Where daily total photosynthetic photo flux density (PPFD) was reduced to one-third or less of incident PPFD, fruitfulness was markedly reduced (Morgan et al. 1985).

Using a controlled environment and comparing *V. vinifera* cultivars Sultana, Muscat of Alexandria, Riesling, Shiraz, and Ohanez, Buttrose (1970) concluded that all cultivars may perform well with high temperature and high light intensity, but fewer (e.g., Riesling) may be able to perform satisfactorily with low temperature and low light intensity. Sanchez and Dokoozlian (2005) also reported large differences in light sensitivity between cultivars, with Sultana and Cabernet Sauvignon reaching maximum fruitfulness at just one-third of full sunlight, while in Flame Seedless and Chardonnay fruitfulness increased with increasing available light. Unfortunately, the authors did not indicate whether varietal differences were correlated with respective canopy densities. Sommer et al. (2000) found that Sultana grafted to a vigorous rootstock always had a lower fruitfulness than own-rooted Sultana, suggesting that it was mainly related to the higher canopy density of the grafted vines.

In rootstock studies using Pinot noir, Pinot gris, Chardonnay, and Merlot as scions grafted to 10 different rootstocks, there was no rootstock effect on number of flowers per inflorescence or percent fruit set (Shaffer 2002). Although rootstocks affected bud fertility, this effect was no longer significant when pruning weight was used as covariate (M.C. Vasconcelos, unpublished data, 2002), indicating that rootstocks affect fruitfulness through changes in scion vigor. The number of inflorescences per bud have been reported to decrease in horizontal or downward growing shoots, compared with upward-growing shoots (Alleweldt and Ilter 1969, May 1966), but elsewhere no effect of shoot orientation on fruitfulness was shown (Kliewer et al. 1989).

Since the original pioneering work of Shaulis with Concord grapes in New York in the early 1960s (Shaulis et al. (1966), showing the beneficial effects of splitting a canopy into two separate vertical curtains of foliage on increasing budbreak, bud fruitfulness, and crop yields, similar influences of canopy division have been demonstrated with *vinifera* grape cultivars (Baldini 1982, Carbonneau et al. 1978, Kasimatis et al. 1975, May et al. 1973, 1976). The improvement in crop yields per node by canopy division has been shown to be mainly due to improvement of the solar radiation environment in the vicinity of the nodes that become the fruiting wood for the following season (Smart et al. 1982b). There is agreement that modification of the light microclimate in the bud renewal area is mainly responsible for the improvement in budbreak, bud fruitfulness, and higher crop yields. Doubling the canopy length per meter of row—that is, training to a double curtain—has generally increased crop yields by 30 to 90% in several *vinifera* cultivars (Baldini 1982, Carbonneau et al. 1978, May and Cellier 1973, May et al. 1976, Shaulis and May 1971, Shaulis and Smart 1974). Light exposure is more important for fruitfulness than direction of shoot growth.

Temperature. The events that have a main influence on yield occur about 12 months before flowering during the initiation stage of the inflorescence primordia. In a review on the importance of the influence of temperature and light on fruitfulness, Buttrose (1974a) considered temperature as the dominant factor for inflorescence primordia formation, with the critical period for susceptibility to the high temperature response being the three weeks before the formation of anlagen by the SAM of latent buds (Buttrose 1969, 1970). Srinivasan and Mullins (1981) suggested that it was not essential to have continuous high temperatures but that a pulse of only four to five hours of high temperature was sufficient to induce a maximum number of inflorescence primordia. For optimum initiation during season 1, it has been shown that temperatures need to be above 20°C, although there are some differences among cultivars of different geographical origins (Buttrose 1970, Dunn and Martin 2000, Kasimatis et al. 1975, Moncur et al. 1989, Petrie and Clingeleffer 2005, Zelleke and Kliewer 1979). Temperatures of 20°C were high enough for the cool-climate cultivar Rhine Riesling and also for Shiraz to initiate inflorescences, but Muscat of Alexandria required a temperature of 25 to 28°C (Buttrose 1970, Srinivasan and Mullins 1981).

In general, American hybrids such as Delaware produce inflorescences at temperatures of 21 to 22°C (Srinivasan and Mullins 1981). A high temperature pulse is essential for the initiation of the second and third inflorescence in many cultivars, including cool-climate cultivars (Srinivasan and Mullins 1981). Sultana and Ohanez were less fruitful than most other cultivars investigated but were more responsive to changes in temperature (Buttrose 1970). Temperatures below 20°C increased tendril production (Buttrose 1970). Using regression analyses of long-term temperature and fruitfulness records, Durquety et al. (1982) found that the critical period for inflorescence formation in Petit Manseng was between 6 and 25 June (coincident with flowering). When mean temperatures during this period were higher

than 24°C, the maximum number of inflorescences was produced the following season; when they were 14 to 15°C or below, no inflorescences were produced. MacGregor (2000) monitoring Chardonnay vines over eight years, described a strong linear relationship between temperature at initiation and bunches per shoot in the following season, with bunch number increasing 0.22 bunches per shoot per degree centigrade over an average initiation temperature range of 13.8 to 17.5°C.

The onset and speed of budbreak is determined by temperature. May (1964) reported that the temperature before the day of budbreak was more important than the temperature on the day itself. He observed an 8-day delayed budbreak at 15°C compared with budbreak at 27°C, with no difference in the weight or structure of the inflorescence primordia at the time of budbreak of single-node cuttings of Sultana. Using controlled environment, Pouget (1981) was able to change the number of inflorescences per shoot and number of flowers per inflorescence by manipulating temperatures shortly before and shortly after budbreak. He reported that at 12°C the number of inflorescences was significantly lower than at 25°C in both Merlot and Cabernet Sauvignon grapes, but the flower number per inflorescence was significantly higher. The net result was an 18% higher flower number in Merlot and 75% in Cabernet Sauvignon at the lower temperature of 12°C. Similarly, Ezzili (1993), forcing cuttings of Alicante Grenache and Cardinal in growth cabinets, reported a decrease in flower number per inflorescence at 28°C compared with 12°C, because of the failure of a number of primordia at the higher temperature to develop past the calyx cup stage. Reduced flower numbers per inflorescence at higher temperatures during budburst in field experiments have been reported (Dunn and Martin 2000, Petrie and Clingeleffer 2005). Shading buds before budburst (and lowering their temperature) increased the number of flowers present (Petrie and Clingeleffer 2005). A greater sensitivity of the developing inflorescences to temperature during the period before budburst was found compared with after budburst. It was suggested that temperature at budburst may also influence flower size and subsequent berry weight. Flower size immediately before anthesis was reduced by management systems that also reduced berry size (Petrie and Clingeleffer 2005). Therefore, environmental conditions at budburst could have an impact on final harvest by influencing both flower number and flower size. Variation in flower number would set a limit to potential berry number, while variation in flower size would contribute to variation in final berry size.

Water status. Vine water status influences bud fertility either directly by the amount of water available for biosynthetic processes occurring during cell division and cell enlargement or indirectly via its effect on vine photosynthesis (Loveys and Kriedeman 1973), nutrient uptake, and microclimate surrounding the bud (Dry and Loveys 1998). It is difficult to separate the effect of water stress on bud fertility from its effect on the light environment of the renewal zone. Water deficit may impair shoot growth (Vaadia and Kasimatis 1961) to a point where differentiation of inflorescence primordia may be affected (Buttrose 1974a). Excess irrigation may promote unwarranted shoot growth to a point where light levels in the renewal zone limit bud differentiation (Carbonneau and Casteran 1979). Bud fruitfulness or yield per bud depends on the number of clusters initiated during the previous season, the number of flowers developed early in the spring, the number of berries set, and the size of individual berries. Most studies indicate that early water deficits are more inhibitory for bud fruitfulness than late season deficits (Matthews and Anderson 1989, Myburgh 2003). Early-season water stress affects both cell division and cell enlargement in the developing berry, thus decreasing berry size (Matthews and Anderson 1989). Persistent water stress depresses the fruitfulness of latent buds through a reduction of the number and size of inflorescence primordia (Alleweldt and Hofaecker 1975, Buttrose 1974b, Winkler et al. 1974).

Water stress may affect flower induction indirectly by changing the plant hormonal balance (Srinivasan and Mullins 1978, 1979, 1980b). Water stress affects xylem transport of cytokinin (Livne and Vaadia 1972) and increases the abscisic acid levels in leaves and stems (Düring and Alleweldt 1973, Loveys and Kriedeman 1973). Moreover, external factors that promote flowering in grapes, such as short-term exposure to high temperature, high light intensity, and optimum levels of soil moisture and macronutrients, also promote cytokinin biosynthesis in plants (Atkin et al. 1973, Jako 1976, Menary and Staden 1976, Skene and Kerridge 1967, Wareing and Thompson 1976, Yoshida and Oritani 1979). Conversely, factors that depress flower formation, such as low light intensity, low temperature, and water stress, have an inhibitory effect on endogenous cytokinin production (Itai and Vaadia 1965, Livne and Vaadia 1972). It is often difficult to interpret the relationship between water stress and fruitfulness of latent buds because of the complexity of these interactions.

Winter rainfall in most nonirrigated vineyards ensures that sufficient water is available to vines through to and including flowering, which is generally the case in Australia (McCarthy 2005) and in New Zealand on the heavier soils. The free-draining soils in Marlborough, New Zealand, often need irrigation at flowering to avoid water stress (Greven et al. 2005). Water deficit during budbreak has been reported to reduce vegetative growth and caused poor and uneven budbreak (Van Zyl 1984, Wample 1997).

Severe water stress applied to container-grown vines of Cabernet franc reduced yield by 94% because of reduced berries per cluster and berry weight (Hardie and Considine 1976). Greater yield losses occur as a result of water deficit during early stages of berry development compared with deficits later in the season (Hardie and Considine 1976, McCarthy 2005, Myburgh 2003). Matthews and Anderson (1989) found that while there were yield losses one year into their water deficit trial with Cabernet Sauvignon, the losses could be explained by large differences in yield caused by berry growth. In the second year of the trial,

the control vines had as much as 100% higher yields than vines in any of the reduced irrigation treatments, which was attributed to a combination of the high sensitivity of cluster initiation (fewer clusters) and flower development (fewer berries) to water deficits. They concluded that high water status throughout the season was essential for high fruitfulness, but only if other environmental factors were conducive to fruitfulness.

Bud fruitfulness and nutrition. Most studies on the mineral nutrition of grapes have been concerned with vine vigor, berry development, and wine composition, and there are few reports on the effects of mineral nutrition on flower formation. An adequate supply of nitrogen (N) is necessary for inflorescence primordium formation and for the differentiation of flowers (Alleweldt and Ilter 1969). Size of inflorescence primordia is generally little affected by N nutrition (Srinivasan et al. 1972), but an increase in the number of inflorescence primordia following N application is found when the initial N status of the vine is low (Baldwin 1966). Alleweldt and Ilter (1969) showed that increasing N fertilization increased the number of inflorescences per bud and flower number per inflorescence. An overapplication of N, however, decreased the number of inflorescences differentiated but not the number of flowers per inflorescence. In agreement, Keller et al. (1995) reported a depression in bud fertility in Müller-Thurgau in response to N deficiency as well as to N excess. Application of N can result in a reduction in fruitfulness, in particular if the vines are already well provided with N. Excessive N application was found to increase vegetative growth and reduce fruit production (Chang and Kliewer 1991, Christensen et al. 1994, Saini and Singh 1975). Although it is not explicitly discussed, decreased fruit production was probably the result of the poor light microclimate in the vigorous canopies, depressing inflorescence primordia initiation. Moreover, increased vegetative growth and resulting shading of the canopy was suggested to cause bud necrosis and reduced fruitfulness in Sultana (Perez and Kliewer 1990) and in Cabernet franc (Smart et al. 1990).

Optimum phosphorus (P) nutrition promoted bud fruitfulness (Skinner and Matthews 1989), and phosphate deficiency is detrimental to the maintenance of initiated inflorescence primordia (Skinner and Matthews 1989). Low N, high P, and water stress are the factors associated with high fertility in Sultana vines (Baldwin 1966). Studies with radioactive P indicated a preferential accumulation of P in actively growing shoot tips and in young buds that subsequently became fruitful (Rao et al. 1971).

There have been several suggestions for a role for potassium (K) in inflorescence formation in the grapevine. Potassium is implicated in enzyme activation and carbohydrate mobilization in grapes (Bouard 1968). Soil application of K in K-deficient vineyards in Michigan and in the Niagara Peninsula caused a marked increase in the fruitfulness of latent buds of Concord (Larsen 1963). Similar effects of K nutrition were found in Sultana vines in California (Christensen 1975). Potassium application increased the fruitfulness and yield by 45% in the first year and 156% in the second year. This high increase in yield may have been related to the larger size of inflorescence primordia that are produced by latent buds of K-fertilized vines (Srinivasan et al. 1972). The positive response of vines to K may be related to the fact that grapevines use the soil-applied K for growth and bud development rather than the K stored in the cane (Obbink et al. 1973). Optimum levels of N, P, and K are associated with maximum cytokinin production by grape roots (Srinivasan and Mullins 1981).

Flowering disorders before anthesis. *Primary bud necrosis.* The low fertility of basal nodes of vigorous vines with dense canopies is often attributed to the poor light environment of the renewal zone; however, this may be caused by a high incidence of primary bud necrosis (PBN) at basal nodes rather than reduced fruitfulness (Dry 2000). Primary bud necrosis is a physiological disorder of grapevines characterized by an abortion and subsequent drying of the primary bud within a developing compound bud (Vasudevan 1997). It may go unrecognized or be mistaken for low temperature injury unless buds are examined in the fall (autumn). One way of recognizing shoots from secondary and tertiary buds is their plane of phyllotaxy, which departs by ~90° from that of the primary shoot (M.C. Vasconcelos, unpublished data, 2009).

Primary bud necrosis may be an important source of yield variability, since shoots of surviving buds may produce an apparently normal canopy, but the crop can be significantly reduced because of the loss of the more fruitful primary buds. By altering the proportion of primary to secondary buds bursting, PBN alters the balance between vegetative and reproductive growth. Cultivars reported to be susceptible to this disorder include Queen of the Vineyard (Lavee 1987), Kyoho (Naito et al. 1986), Flame Seedless (Morrison and Iodi 1990), Riesling (Wolf and Warren 1995), Viognier (Wolf and Cook 1994), Shiraz (Collins et al. 2006, Dry and Coombe 1994), and Sultana (Morrison and Iodi 1990, Perez and Kliewer 1990). High shoot vigor (Dry and Coombe 1994, Lavee et al. 1981), high levels of soil nitrogen (Kliewer et al. 1994), canopy shading (Perez and Kliewer 1990, Wolf and Cook 1992), exogenous application of GA (Collins and Rawnsley 2008, Lavee 1987, Naito et al. 1986, Ziv et al. 1981), excessive irrigation (Kliewer et al. 1994), and low carbohydrate levels within the bud (Vasudevan et al. 1998b) have all been shown to increase PBN. Applications of the growth retardants such as paclobutrazol and succinic acid-2,2-dimethylhydrazide (SADH) have been reported to reduce the rate of shoot growth and the level of PBN (Collins and Rawnsley 2008, Naito et al. 1986, Wolf and Warren 1995). Climatic and cultural conditions that favor excessive shoot vigor and induce low fruitfulness also favor a high incidence of PBN (Lavee et al. 1981, Perez and Kliewer 1990). The incidence of PBN is highest at basal nodes (Dry and Coombe 1994, Lavee et al. 1981, Morrison and Iodi 1990, Perez and Kliewer 1990). No effect of essential nutrient deficiency could be related to PBN (Vasudevan 1997). The disorder occurs independently

of the differentiation level of the inflorescence primordia (Perez and Kliewer 1990). Retaining or removing subtending leaves, lateral shoots, or clusters from individual buds does not influence PBN (Perez and Kliewer 1990). Anatomical observations showed that the onset of the disorder occurs 20 days after bloom in Israel (Lavee et al. 1981), 3 to 6 weeks after bloom in the San Joaquin Valley (Morrison and Iodi 1990), and 15 days after bloom in Virginia (Vasudevan et al. 1998a). In many grapevine cultivars, as in many other deciduous species, application of GA during the previous growing season will delay and even completely inhibit bud opening in the following growing season (Eris and Çelik 1981, Iwasaki and Weaver 1977, Lavee and May 1997, Weaver 1959). Indeed there are many reports that in many but not all cultivars, GA applications during flowering in one season led to complete failure of buds to burst in the next one. PBN symptoms have been reproduced by exogenous applications of GA soon after flowering, before the onset of predormancy (Uys and Blommaert 1974, Ziv et al. 1981). Such applications of GA have caused the primary axis inside the bud to elongate rapidly and subsequently abscise (Lavee and May 1997). Furthermore, vigorous shoots with splits in the nodal eye due to the death of the primary axis had considerably higher levels of endogenous GA than moderately growing shoots with healthy buds (Dry and Coombe 1994, Lavee 1987).

Reversion of differentiation. Although most studies assume that reduced fertility is due to poor differentiation of inflorescence primordia, some reports indicate that abortion of predeveloped primordia is possible. Skinner and Matthews (1989) indicated that more cluster primordia are initiated in a season than are maintained in the subsequent season in potted Carignan and that maintenance of initiated primordia was dependent upon adequate phosphorus supply. Matthews and Anderson (1989) reported a decrease in the number of flowers per cluster in response to water stress and hypothesized that the branching of the anlagen is sensitive to vine water status, in particular to early season deficit. Culturing excised inflorescence primordia of Pinot noir and Chardonnay with gibberellin led to the formation of shoots and tendrils (Yahyaoui et al. 1998), indicating that it is possible to reverse reproductive structures to the vegetative stage.

In Pinot noir inflorescences, the first branch originating from the first division of the anlage (outer arm) is either well developed, forming a "wing" or "shoulder," or it degenerates and abscises, leaving a swelling in the peduncle with a visible scar. It is unknown what causes the abscision of the first branch, and the extent of its occurrence varies from season to season and with the Pinot noir clone (M.C. Vasconcelos, unpublished data, 2008). This phenomenon has been observed in many cultivars.

Filage or verrankung. *Filage* is the term used to express the reversion of the inflorescence to a tendril. It is the abortion of the flowers before anthesis. The flowers stop growing and abscise at the layer forming at the base of the pedicel. The result is a branched tendril that may still bear some rudimentary flowers at the tip, which do not open. This phenomenon occurs two weeks before anthesis when the rachis is extending rapidly on vigorous shoots and at high temperatures (Champagnol 1984). It only occurs in cultivars with large cluster size. In Algeria it is often reported on cultivars Ahmeur bou Ahmeur, Sultana, and Italia in the hot and fertile production areas of the Mitidja, but does not occur in higher regions such as Médéa (1000 m). In southern France, it has been observed on Cardinal and Alphonse Lavallée grown in hot, poorly ventilated greenhouses (Champagnol 1984). The term *filage* or *verrankung* is also used when inflorescences only have a few flowers because of poor differentiation the previous season caused by unfavorable conditions, namely cool temperatures (Alleweldt 1963, Durquety et al. 1982, May 1964).

Inflorescence necrosis. Inflorescence necrosis (IN), also known as early bunch stem necrosis (EBSN), is another disorder of grapes with some features similar to grape PBN. Inflorescence necrosis is characterized by the development of necrosis in flowers, pedicels, and in some instances peduncle tissue of clusters (Gu et al. 1996, Jackson and Coombe 1988, Keller and Koblet 1995b, Lombard et al. 1993). The causes of IN, as for PBN, are not clear. It has been shown that water or nutrient stress before flowering increased IN incidence (Jackson 1991, Jackson and Coombe 1988). Both calcium chloride and diammonium phosphate were found to increase IN. The cations calcium and ammonium were thought to be the causal agents (Jackson and Coombe 1988). Nitrogen metabolism, and especially ammonium toxicity, is implicated in the development of IN symptoms (Jordan et al. 1991). Low nitrogen availability during bloom has been reported to increase IN incidence in Cabernet Sauvignon (Keller and Hrazdina 1996) but not in Müller-Thurgau grapevines (Keller and Koblet 1994, 1996). Among several nitrogen fertilizer formulations, only NH_4^+ ions were involved in the development of IN (Gu et al. 1994). Jordan (1989) found a positive relationship of ammonium ion uptake and the severity of IN. However, Keller and Koblet (1994) were unable to confirm such a relationship, and instead suggested that the excessive amounts of ammonia may have been from increased glutamate dehydrogenase activity because of the remobilization of carbohydrates during periods of reduced carbohydrate availability. When insufficient carbohydrates from photosynthesis are available, vines use glutamate as a source of carbon, releasing ammonium, which causes IN (Keller and Koblet 1994, 1995b).

The Flowering Process: Second Season

Flower development and morphology. The conversion from inflorescence primordium to the inflorescence resumes as shoot development begins in the spring. Branching of the inflorescence primordia continues 12 to 15 days after the beginning of budbreak for Grenache and Carignan (Bernard and Chaliès 1987).

Shortly before and during budbreak, flower initials are formed and flower parts become distinct. First the traces of the calyx appear, followed by the petals, stigma, and

finally the pistil (Pratt 1971). The structure of the inflorescence has been well described (May 2004) and is generally considered to be a conical panicle characterized by multiple branching. Secondary branching along the rachis (the central axis of the inflorescence) and further tertiary branching results in a complex floral structure, terminating in triplets of grape flowers—the dichasium. The differentiation rhythm depends on conditions such as flower position on the branches of the bunch, the nutrient supply, and the expression of the sexual organs. Each grape flower is comprised of sepals, petals, stamens, and carpels, arranged in concentric rings or whorls from the outside to the inside. Five sepals, which form the calyx, are at the base of the flower and protect the rest of the flower parts in the early stages of development. Five petals form to provide a protective layer over the reproductive organs by growing up through the calyx ring. The petals are joined together by epidermal cells and form the calyptra or cap. When flower development is completed with mature pollen and the embryo sac, the basal part of the petals develop the abscission tissue (Sartorius 1926, Meryanian 1951, Pratt 1971, Kozma 2003). The abscission layer is first formed a few days before the eve of bloom, under one of the petals, and then it spreads to the neighboring petals. In those cells, starch is accumulated abundantly (Kozma 2003).

The androecium is comprised of five stamens, which form opposite the petals. Each stamen has a long filament, at the end of which is a bilocular anther which contains four pollen sacs. The anther wall is comprised of three tissues, an outer epidermis, a thick endothecium, and a tapetum, a tissue characterized by varying numbers of nuclei per cell. Meiosis in the primary mother cell results in four haploid microspores, which remain in a cavity—the anther locule—where they are sustained by a nutrient fluid. This fluid is formed by the degeneration of the tapetum, which is present up to the time of pollen release. At dehiscence the endothecium detaches from the inner wall to the center of the anther. Pollen is 25 to 30 µm long and 12 to 15 µm wide. Fertile pollen is barrel shaped and nonfertile pollen is oblong (Oberle 1938).

The pistil or gynoecium is initiated after the stamens (Gerrath 1993) on the central floral disc. The inner gynoecium wall develops into the septum, which is the central canal of the style through which the pollen tube will grow (Cholet et al. 2002). The ovary is the enlarged area at the base of the style and it has two compartments, the locules, each of which has two anatropous ovules (Figure 6). The ovules are separated from each other by the septum. Each ovule has an embryo sac with a haploid egg and diploid polar nuclei. The ovary acts to protect the ovules from desiccation and physical injury. Egg development of the ovary closely follows that of the pollen in the anthers. For Grenache and Carignan in southern France, pollen meiosis occurs 24 days (six weeks after the beginning of budburst) or 17 days before the beginning of anthesis, respectively. Ovule meioses occurs eight days or four days after pollen meiosis for Grenache and Carigan, respectively (Bernard and Chaliès 1987).

With the formation of the abscission tissue, the petals turn pale yellow-green, and the transport of nutrients through vascular bundles ceases. In the three to four days before bloom, the petals are easily detached from the axis; earlier it was difficult to tear them apart. Meanwhile the disk starts to swell. On the morning of bloom, the rising temperature and the drying air desiccate the upper, less supplied part of the petals sticking together at their tips. The tension developed between the outer, dry and inner, turgid cell layers first detaches one of the petals and subsequently, in some 20- to 30-second intervals, the next petals; thus the whole calyptra becomes separated as cap. The abscission is helped by the swollen discs (lower and upper discs or nectaries) (Baranov 1946, Kozma 2003). When the filaments elongate, the petals separate from the base of the flower, to lift upward, releasing the stamens (Figure 7).

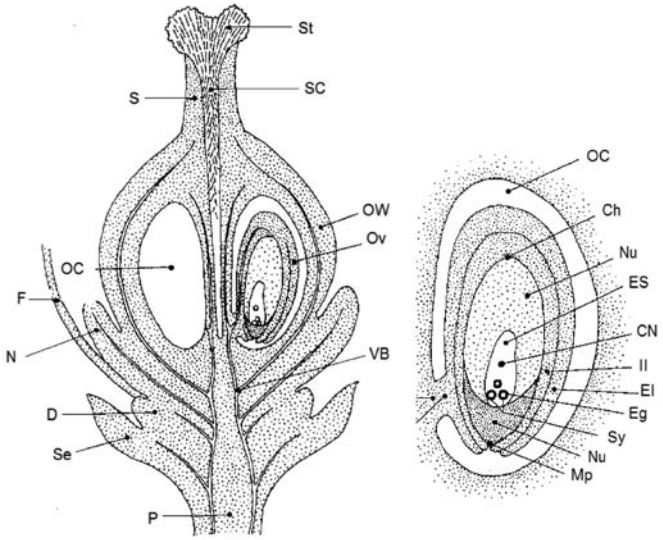

Figure 6 Detail of *Vitis vinifera* flower. OC, ovary cavity; Ch, chalaza; Nu, nucellus; ES, embryo sac; CN, central nucleus of embryo sac; II, internal integument; EI, external integument; Eg, egg cell; Sy, synergid; Nu, nucellus and epidermal cap; Mp, micropyle; Fu, funicle; Pl, placenta; St, stigma; SC, stylar Canal; S, style; OW, ovary wall; Ov, ovule; F, filament; N, nectary; VB, vascular bundle; D, discus; Se, sepal; P, peduncle. (Modified from Kozma 2003; reprinted by permission of the publisher.)

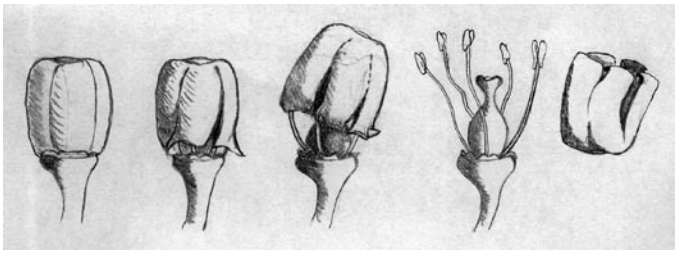

Figure 7 Sequence of events during capfall in grapevine flowers. Flowers develop an abscission tissue at the base of the corolla where the petals sticking together as a cap at the tip are shed explosively. The force of tissue tension builds up with changes in turgidity between outer and inner cell layers of petals and with the sudden elongation of the stamina (Kozma 2003) (drawing by Marc Greven).

The shedding of the calyptra is called capfall. After that, the elongation of stamina astride at an angle of 45° acts like a sling by releasing the calyptra. Immediately after the ejection of the calyptra, the anthers burst and release the pollen. In "star" flowers, in which the petals separate first at the top, disturbances in development are associated with anthers that do not open (indehiscent) and sterile pollen (Longbottom et al. 2004b, Pratt 1971).

Different theories regarding grapevine pollination, varying from insect pollination to obligatory wind pollinated to self-pollination, have been proposed over the years (Pratt 1971). The most recent views are that self-pollination is important and often happens before capfall (cleistogamy) and that cross-pollination also occurs and often results in better seed set in the berries. Staudt (1999) reported that 25 to 35% of Müller-Thurgau and Pinot noir pollen had already started pollen tube growth at the time of capfall. In contrast, Heazlewood and Wilson (2004) could find no evidence of pollen tube growth until after capfall. Cleistogamy does not appear in all cultivars, where mechanisms may be present inside the cap to prevent it (Meneghetti et al. 2006). These mechanisms include covering the stigma by the cap and situating the anthers well beneath the stigma (Lombardo et al. 1983).

Flower types. Flower morphology has been extensively reviewed by (Oberle 1938, Pratt 1971, Gerrath 1993, Meneghetti et al. 2006). Grape flowers are of three rather sharply defined types: functionally hermaphroditic, functionally pistillate, and functionally staminate. All types are morphologically hermaphroditic, however, in that flowers of each class have full complements of stamens and pistil. Unisexualism has resulted from abortion of either the male or female sexual elements in the typical bisexual type. Abortion of the sexual elements occurs during a late stage of their development and always after meiosis (Oberle 1938). The perfect-flowered form has the normal complement of five erect stamens surrounding a stout bottle-shaped pistil. The pistillate flowered form has the typical number of stamens surrounding the pistil, but the former members are recurved to a position below the base of the ovary (Oberle 1938). The recurved stamens of pistillate flowers have sporogenous tissue and produce abundant pollen, which, however, is nonviable, and pollination can only be successful if pollen from another vine is used. Cultivated grape varieties of *Vitis vinifera* L. usually have hermaphrodite flowers; only a few have functionally female flowers, including Maccabéo, François noir, Malvoisie (Bouard 1980), Naparo, Ohanes (Borrego et al. 1990), Bicane, Picolit, Lambrusco di Sorbara, and Moscato rosa (Meneghetti et al. 2006).

Sequence of events during flower opening. In central Europe, grape flowering follows a diurnal rhythm, with opening starting between 0600 and 0800 hr, accelerating until ~1000 hr, slowing down and stopping by midday, followed by a minor wave of flowering between 1500 and 1600 hr, and no flowering during the night (Sartorius 1926, Kozma 1950, 2003, Meryanian 1951, Constantinescu et al. 1952). Induced periodicity has been reported (Sartorius 1926, Kozma 1950), whereby the temperature of one day influences the flowering intensity the next day.

As early as in 1951, it was demonstrated that the later blooming racemes of a given cultivar were more intense; furthermore, during the second half of bloom time, the opening of flowers gradually shifted to the early morning hours (Meryanian 1951). The most intensive bloom was experienced at 25 to 35°C. A fast increase in temperature and a drop of relative humidity during the morning hours shortened and intensified the flowering period. This diurnal trend may in part be a function of vine water status and inflorescence turgor. Pratt (1971) ascribed the release of the calyptra to changes in the turgor of the interlocking cells. In case of moist and inclement weather, the anther will burst before the elimination of the cap. One to 60 minutes are needed to burst and release the pollen. The opening of the pollen sacs (anther locules) is caused by rapid loss of water in the walls of the anthers. Once pollen grains have landed on the stigma, they start to swell. Considine and Knox (1979) provide a detailed description of the development of the grape pistil. In summary, the style is short and stigmatic exudate gives the stigma a wet appearance when receptive at anthesis. The stickiness of the stigmatic fluid and roughness of the pollen enables the pollen to adhere to the stigma (Faegri and Iverson 1964, Faegri and Pijl 1979). The pollen tube grows through the papillae of the stigma to the stylar tissues and down to the ovules where it enters the nucellus and wall of the embryo to fertilize the egg cell. Pollen tubes grow away from oxygen toward moisture (Proctor and Yeo 1973).

A sugary solution produced in the stigma appears to be required for the growth of the pollen tube (Mullins et al. 1992). A germ tube grows from the pollen grain into the style toward the ovule. This is thought to generate a stimulus, causing the germinative nucleus in the pollen grain to divide into two sperm nuclei (Rajasekaran and Mullins 1985). Once the pollen tube reaches the ovule, a sperm nucleus moves down the tube to fuse and fertilize the egg nucleus. The other sperm nucleus fuses with the two polar nuclei. The fertilized egg nucleus forms the embryo for the development of the seed. As there are usually four ovules, two in each carpel, a berry can potentially have four seeds, each fertilized from a different pollen grain. Seedlessness can occur in different ways, but pollen grain germination is an essential part of the development of berries (Bouquet and Danglot 1996, Mullins et al. 1992). Flowers that undergo pollination and no fertilization form small live green ovaries (Friend and Trought 2007). Fertilization enables further berry development and the ovary wall turns into the skin and flesh of the berry. Two or three days are required after the pollen grains lands on the stigma for fertilization to be complete. Pollen grains are viable for only a few days after release from the anther (Faegri and Pijl 1979). In general, the water content of pollen grains varies between 15 and 35% (Dumas et al. 1983) and pollen viability is reduced by exposure to ultraviolet light and/or desiccation.

The transfer of pollen to the stigma induces a number of physiological changes.

Variation in flowering. Differences in the duration of flowering can be ascribed to two predominant causes. The first is differences in the development stages of the individual flowers in the vineyard. The causes of variation in flowering can arise at any time during the development of the flower in response to environmental factors up to shortly before the day of anthesis, and may in part be genetic (McIntyre et al. 1982), reflecting differences in bunch number and/or flower number per bunch. The differences within and between vines in the vineyard may be compressed or extended by weather, in particular temperature and rainfall at the time of flowering (Galet 2000). Flowering generally takes longer if weather conditions are cold and wet (Winkler et al. 1974).

Under favorable conditions individual clusters will bloom for 4 to 8 days, cultivars over 8 to 14 days. The first to bloom are the proximal racemes of the more distally located shoots on last year's growth, followed by the more proximally located shoots and the more distally inserted inflorescences (Manaresi 1957). Larger inflorescences generally bloom earlier than smaller ones. The first and last part of bloom tend to be much more prolonged than the short main period of bloom, when 60 to 70% of the flowers open. Flowering usually begins in the basal inflorescences of a shoot and progresses upward. The progress of flowering within the inflorescence appears to vary with cultivar (Castelli and Pisani 1985). Within the triplets of grape flowers (dichasium), the central "king" flower is larger than the central-lateral flowers on either side, which are in turn larger than the lateral-lateral flowers (Ebadi et al. 1995a), although marked variation in flower size has been observed at each position. The larger, terminal flower opens before the smaller lateral flowers (May 1987) and average flower size tends to decrease during the flowering period (Friend et al. 2003). This negative relationship between flower size and date of flowering has been observed in other horticultural crops such as boysenberry (Trought 1983) and apple (Feree et al. 2001, Westwood et al. 1967). However, given the complexity of the grape inflorescence, it is difficult to attribute the time of flowering to size and/or position. One study found no acropetal development on the inflorescence (Friend et al. 2003). In contrast, an earlier study found grape flowers open first at the base of the inflorescence (Winkler et al. 1974), while a third study found flowers on the first two primary branches and the tip of the inflorescence open later than those of all the other branches along the inflorescence (May 1987). Shoot position and bunch location on that shoot in the developing canopy influences flowering progression. Inflorescences on shoots of Sauvignon blanc vines arising from the end of canes flowered earlier than those in the midcane, and in turn the basal positions of canes and basal bunches on the shoots flowered earlier than apical bunches on the same shoots (Naylor 2001). These differences in development largely reflect the differences in the phenology of the vine.

At a vine level, soil type and training system can influence the timing of flowering. Sauvignon blanc vines growing in a single vineyard had significantly different flowering dates depending on soil texture (Trought et al. 2008). Vines growing on stony soils flowered 4 to 5 days earlier than vines in close proximity on deep silts. The earlier flowering was partly ascribed to the warmer 30-cm soil temperature of the stony soil. The warmer soils potentially enhance root activity, in particular carbohydrate remobilization to the shoot.

Similarly vine training can influence flowering date. The low vine stocks on south-facing slopes (northern hemisphere) finish bloom earlier, and higher growing trellises on the plains with heavy and cold soils show prolonged blooming (Kozma 2003). Sauvignon blanc vines trained using a two-cane vertical shoot-positioning system flowered ahead of equivalent four-cane pruned vines (Agnew et al. 2006).

The synchrony between the onset of flowering and the rate of internode development of vines in the spring has been described (Pratt and Coombe 1978). Vines flowered once shoots had developed 16 to 19 visible internodes, regardless of site, cultivar, or cultural practice, with vine vigor causing the greatest variation between vines. It is conceivable that the onset of flowering is triggered by the availability of photosynthates. Reserve mobilization continues until shortly before anthesis, depending on cultivar (Yang and Hori 1980, Zapata et al. 2003) and the transition to flowering coincides with variations in sugar concentrations in the developing shoot (Lebon et al. 2004). Photosynthesis by the inflorescence is an important source of sugars (Leyhe and Blanke 1989), suggesting that inflorescence exposure to light during development may influence the phenological development of different inflorescences within the grapevine canopy. Differences in photosynthetic rates of leaves and inflorescences and consequential sugar availability may play important roles, regulating gene expression and stress responses at flowering (Lebon et al. 2008).

Flowering and temperature. Considerable differences in optimum temperatures for flowering are reported depending on grapegrowing region and cultivar. While some cultivars start flowering when temperatures reach 16 to 17°C, warmer temperatures between 20 and 30°C are required for optimal flowering (Kozma 2003, May 2004, Winkler et al. 1974). The combination of excessive temperature and low humidity (below 45%) is harmful for normal blooming. Under rainy conditions the cap cannot open and often remains attached to the top of the pistil, resulting in in poor pollination (Kozma 2003, May 2004).

For dehiscence to occur, it is essential that anthers can dry out. Warm and fairly dry conditions are therefore important. However, when conditions are too dry and windy, the stigma will dry out and pollen cannot stick to it. For optimal pollen tube growth, it is also imperative that temperatures are high enough to allow for a speedy penetration of the style in order to reach the micropyle. Unfavorable weather extends the flowering period. In regions with high precipitation, such as Minho in Portugal, flowering time

can be as long as 32 days (Cunha et al. 2003). Spells with continuous rain and temperatures below 15°C cause washing of the airborne pollen, hinder opening of the flower cap, and cause agglomeration of the pollen grains (Cristofolini and Gottardini 2000, Cunha et al. 2003, Fornaciari et al. 1998), resulting in poor fruit set and yield. Rain before and during bloom can prevent the release of calyptras, causing flowers to drop without opening (Koblet 1966).

Besselat and Cour (1990), using a pollen trap, demonstrated marked differences in pollen dispersion duration when comparing the 1982, 1987, and 1989 flowering periods. Timing of flowering is cultivar-dependent and also depends on the weather. Warm, sunny days favor aerial pollen dispersal.

Optimum rates of pollen germination occur at 27 to 28°C (Rajasekaran and Mullins 1985, Staudt 1982) and pollen grains germinate within 30 minutes of pollination. Submitting inflorescences to cold temperatures (10°C or 13°C) shortly before and at the beginning of flowering caused a nearly complete loss of pollen germinability. Pollen was most sensitive to cold temperatures at the onset of germination. Before and after this period, cold temperatures delayed anthesis and the progress of flowering, but did not reduce substantially pollen germinability. In contrast, Staudt (1982) reported that pollen grains can withstand temperatures as low as 2°C for up to four days without injury, with growth returning to normal when grains are returned to 28°C.

Little research has studied the timing of capfall of individual flowers. Fitting a logistic curve to flowering progression, Friend (2005) investigated the influence of temperature and rain on the deviation in capfall from the predicted values. He suggested that temperatures below 15°C delayed flowering by two days, and that an increase in capfall above the predicted level could be observed once temperatures returned to above 15°C. This suggests that flower development is progressing and short-term disruptions to flower maturity are accumulated and released once weather conditions return to an acceptable level. Low temperatures near flowering can also adversely affect ovule development. One week of cold temperatures (12°C day/9°C night), starting two days before anthesis, resulted in ~30% reduction in Chardonnay and Shiraz flower size (Ebadi et al. 1995b). It also resulted in a significant decrease in pollen germination and pollen tube growth, with Chardonnay appearing to be more sensitive to the low temperature treatment than Shiraz.

The growth rate of the tube is temperature sensitive (Staudt 1982) and ceases after 18 to 24 hr, suggesting that the average temperature immediately postpollination will determine whether a flower will be fertilized. Using the data presented by Staudt (1982) it is possible to estimate the maximum potential pollen tube length at any temperature (L. Kheun and M. Trought, unpublished data, 1998). Over the temperature range 10 to 28°C, the maximum tube length increased 13 µm per degree centigrade, suggesting that the size of the flower (the distance from the stigma to the ovary) may influence the likelihood of fertilization (Trought 2005). MacGregor (2000) described a sigmoid relationship of Chardonnay bunch weight when the daily temperature over flowering ranged from 13.8 to 19.6°C. An increase in temperature from 15.5 to 17.5°C resulted in an increase in average bunch weight of ~60% (from 48 to 78 g).

With flowering within a cluster potentially spread over one week and flowers within a vineyard spread over two to three weeks, temperatures under which individual flowers are opening, being pollinated, and being fertilized can vary within a wide range. Thus, there is high variability in the success of flowering within a cluster, a vine, and vineyard.

Carbohydrate availability and flowering. The timing and duration of flowering may be influenced by availability of stored and current photosynthates. A degree of bienniality on vine yield is often observed in vineyards, and Perold (1927) noted that vineyard yields may be lower than expected if the yield in the previous season was high. This suggests that carbohydrate reserves in the trunks and roots of vines may have an important role in determining yield potential of vines.

Root- and trunk-stored photosynthates are used by the vine in the spring to develop new shoots and the new canopy. Shoot growth rate is influenced by the relative balance of retained node number after pruning (and the subsequent number of shoots that develop) and the carbohydrate reserves. Inadequate reserves and/or excessive shoot numbers result in slower shoot development. Using defoliation treatments, researchers manipulated the overwintering reserves of Chardonnay vines (Bennett et al. 2005). The lower carbohydrate reserves resulted in slower shoot development, fewer inflorescences per shoot, fewer flowers per inflorescence, and reduced vine yield. Likewise, increasing the overwintering starch reserves of the trunk by reducing vine yield resulted in a 25% increase in vine yield by increasing bunch numbers per vine in the following season (Trought 2005), independent of any temperature effects at initiation or flowering.

The extent to which these differences in bunch number and vine yields are a direct influence of reserves or an indirect effect on shoot diameter is unclear. Recent research (M. Trought and J. Bennett, unpublished data, 2006) has indicated that bunch number per shoot is related to the diameter of the cane or spur retained after pruning, which is in turn affected by vine vigor.

Influence of carbohydrates on success of flowering and fruit set. Vines appear to flower shortly after the time the canopy changes from being a net importer of carbon (largely supplied from carbohydrate reserves in the trunk and roots) to being a net exporter (Yang et al. 1980), although the timing of the transition relative to flowering appears to be cultivar specific (Zapata et al. 2004). Despite the coincidence, like many phenological events, whether or not the change in the role of the canopy induces the onset of flowering does not appear to have been tested. However, in any event, flowering occurs when carbohydrate reserves in the permanent structure are at a minimum and the final yield

appears dependent on the vine leaf area in the three weeks from bloom (Candolfi-Vasconcelos and Koblet 1990).

Flower abscission occurs naturally in vineyards and depends on the cultivar and flower number on the inflorescence (Huglin and Schneider 1998). An inverse relationship was found between the number of flowers per cluster and percent fruit set, and researchers concluded that even after the number of clusters and flowers were determined, fruit set provided an additional opportunity to regulate the crop, by adjusting it to the available resources (Vasconcelos and Castagnoli 2000). Flower clusters are weak sinks for assimilates (Hale and Weaver 1962, Koblet 1969) and growing vegetative tips compete with inflorescences for carbon. Fruit set can be improved by timely removal of competing growing tips from the main shoot and from developing lateral shoots (Candolfi-Vasconcelos and Koblet 1990, Vasconcelos and Castagnoli 2000). While carbohydrate supply to the inflorescence may come from reserves and/or photosynthesis by leaves and/or the inflorescence itself, researchers concluded that the leaf is the main source of photoassimilates for the developing inflorescence (Lebon et al. 2005). Stress at flowering may result in very high rates of flower abscission (80% in Gewürztraminer) (Huglin and Schneider 1998). The degree of abscission appears to be related to the sugar (particularly sucrose) concentration in the inflorescence shortly after anthesis (Aziz 2003) and inversely related to the polyamine concentration in the inflorescence. The exogenous application of spermadine before flowering increased the soluble sugar content of the inflorescence, but reduced the amino acid concentrations of leaves and inflorescences and inhibited fruitlet abscission.

Vine defoliation at or slightly before bloom causes poor fruit set and abortion of fruitlets (Candolfi-Vasconcelos and Koblet 1990, Coombe 1959). In contrast, treatments that increase carbohydrate availability to the inflorescence such as girdling (Caspari et al. 1998), topping the shoot, and reducing shoot growth through the application of the growth retardant Cycocel, will increase fruit set.

The influence of retranslocation of reserves and/or competition from leaves on fruit set of Sauvignon blanc has been examined (Caspari et al. 1998). The authors studied fruit set by girdling and removing leaves. Girdling without leaf removal increased fruit set by 67%. Increasing the extent of leaf removal on girdled shoots progressively decreased fruit set. The nongirdled defoliated shoots managed to use reserves from the parent vine and had fruit set equivalent to the fully leafed, nongirdled control. Under restricted photosynthetic supply, shoot import from the permanent structure was shown to occur well past the 10-leaf stage (Candolfi-Vasconcelos et al. 1994), considered as the normal transition point from heterotrophic to autotrophic carbon supply (Yang and Hori 1980).

Nutrition and flowering. Potentially one of the most complex interactions determining fruitfulness of grapevines is nutrition. An imbalance in nutrient supply may have a direct or an indirect effect on fertilization. Nitrogen is widely recognized as having an influence on the cropping potential of the vine. Where vines are low in nitrogen, vigor may be reduced. While this may result in reduced bunch numbers per vine (Baldwin 1966), the lower shading of buds within the canopy may result in higher fruitfulness. The axis of the flower style provides the pathway for pollen tubes to grow into the ovary tissue (Okamoto et al. 2001). More pollen tubes were observed to penetrate the ovary when treatments, such as the development of less vigorous shoots, increased the cross-sectional area of the pistil of the flower (Okamoto et al. 2001), and pollen tube growth into the ovary was somewhat inhibited by nitrogen fertilizer applications.

Excessive vigor is generally associated with poor fruit set. However, addition of nitrogen to nitrogen-starved vines increased seeds/berry and fruit set (Ewart and Kliewer 1977). Amiri and Fallahi (2007), working with *V. vinifera* Qermez Bidaneh table grapes in Iran, reported increases in fruitfulness after applications of nitrogen alone or combined with potassium (K) or magnesium (Mg). They also reported increased fruit set in response to these treatments.

Molybdenum (Mo) is important in nitrogen nutrition of vines and has recently been suggested as a primary cause of millerandage in Merlot vines (Longbottom et al. 2004a, Williams et al. 2004). It is thought that Mo directly affects the development of reproductive structures. Molybdenum is necessary for successful pollen tube growth, ovule penetration, and fertilization (Longbottom et al. 2004a). Application of Mo resulted in improved seed set and in some years increased yield of berries by as much as 500% (Williams et al. 2004). Coulure can be overcome by the foliar application of sodium molybdate before flowering or the grafting of vines to rootstocks such as 140 Ruggeri (Kaiser et al. 2005).

Zinc deficiency affects fruit set and berry development. Zinc deficiency can be induced by excessive applications of phosphorus (Alexander and Woodham 1964) or high pH soils, and deficiency can be prevented by foliar sprays applied during bloom.

Molecular Control of Flowering in Grapevine

Floral development. Analyses of genes controlling flowering have been carried out primarily in *Arabidopsis* mutants and rapid progress has been made in elucidating the molecular and genetic mechanisms involved in floral transition and subsequent flower development. Several excellent reviews of the topic have been recently published (Carmona et al. 2008, Dennis and Peacock 2007, Winefield and Jordan 2006, Zeevaart 2008).

Flower formation occurs through a series of sequential steps under strict genetic control (Meneghetti et al. 2006). The first genetic change involves the switch from the vegetative to the floral state, in response to different environmental and developmental signals, through the activity of floral meristem identity genes. Second, the floral meristem is patterned into the whorls of organ primordia through the activity of floral-organ identity genes. Third, the floral organ

identity genes activate downstream effectors that specify the various tissues that constitute the different floral structures (Krizek and Fletcher 2005). Although the evolutionary conservation of the mechanisms underlying flower development is well known (Boss et al. 2004, Jack 2004), an understanding of the molecular basis of grapevine flower development is just at its beginning.

The organogenesis of the flower is strictly controlled via the antagonistic and overlapping function of a number of transcriptional factors that act to activate and repress the formation of the floral organs in specific whorls of the flower. A complete review of the current understanding of this topic in model plants is beyond the scope of this review, and only those genes relevant to grapevines have been included here. The reader is encouraged to consult the suggested reviews for a background to this expansive topic (Gibson 2005, Irish 2008, Kramer and Hall 2005, Krizek and Fletcher 2005, Krizek 2006, Sablowski 2007).

In addition to the publications that review this topic in model plant species, there have been several excellent reviews published recently on flowering and flowering genes that have been isolated and partially characterized in grapevine (Boss et al. 2003, Carmona et al. 2007b, 2008, Lebon et al. 2008). It must be noted that studies of floral initiation and development at the molecular level are not complete and that genes identified still remain to be functionally characterized. Because of the long life cycle of grapevine, it is difficult to generate transgenic plants and mutants or or to analyze naturally occurring genetic variants (Carmona et al. 2008).

Floral induction. At this time, there is no clear evidence in grapevines of the classic floral initiation pathways, such as the photoperiod or vernalization pathways described in model systems like *Arabidopsis* (Carmona et al. 2008). Although homologous genes to those identified in model dicotyledons or monocotyledons can be found within the grapevine genome, presently there is no clear indication of their functions within grapevines. The majority of the current investigations have to date focused on the floral integrators and floral meristem identity genes (Boss et al. 2006, Calonje et al. 2004, Carmona et al. 2002, Joly et al. 2004, Sreekantan and Thomas 2006).

Three members of the *SUPRESSOR OF CONSTANS1/AGAMOUS LIKE 20* (*SOC1*/*AGL20*) MADS box gene subfamily in grapevine have been identified from mining of the grape genome data (Carmona et al. 2008). At this time, only one of these, *V. vinifera MADS8* (*VvMADS8),* has been characterized (Sreekantan and Thomas 2006). The expression pattern of this gene in grapevine is consistent with a role in floral initiation, being very high during the early stages of inflorescence development. Its expression decreases through the remainder of floral development and it is not found to be expressed in mature flower or fruit. Functional characterization of this gene has been limited to overexpression of this gene in wild-type *Arabidopsis*, where *VvMADS8* accelerates flowering, supporting the theory that this gene has a similar function to the *Arabidopsis* gene.

The floral signal integrator *FLOWERING LOCUS T* (*FT*) has also been characterized in grapevine (Boss et al. 2006, Carmona et al. 2007a, Sreekantan and Thomas 2006). Investigations of the grapevine whole genome sequence have identified six possible *TERMINAL FLOWER1-FT (TFL1-FT)* homologues. Five of these have been recently characterized and can be grouped into three major clades: FT, MFT (*MOTHER OF FT AND TFL1*), and TFL1 (Carmona et al. 2007a). The most likely *FT* orthologue, *VvFT*, is associated with seasonal floral induction in latent buds and with the development of inflorescences, flowers, and fruits (Carmona et al. 2007a, Sreekantan and Thomas 2006). In addition, overexpression of *VvFT* in transgenic *Arabidopsis* causes similar effects as *FT* (Kardailsky et al. 1999, Kobayashi et al. 1999), further substantiating that this gene is the *FT* orthologue. The three subfamily members that show the highest homology to *TFL1*—*VvTFL1A*, *B,* and *C*—are expressed in latent buds and during the initial stages of inflorescence development, but not during flower development in the flowering season (Carmona et al. 2007a). Overexpression in *Arabidopsis* of the nearest homologue to *TFL1*, *VvTFL1A*, results in delay in flowering and the initiation of flower meristems, which in turn results in the formation of a complex inflorescence that contains multiple co-inflorescences (Boss et al. 2006, Carmona et al. 2007a). This supports a potential role in the maintenance of meristem indeterminacy. While functional characterization of these genes in heterologous systems supports a conserved role in flowering, in vivo characterization of function through loss of function analyses and/or overexpression analyses remains to be done.

Floral meristem identity. Both *LEAFY* (*LFY*) and *APETALA1 (AP1)* grape orthologues (*VFL* and *VAP1*, respectively) have been cloned and characterized in much the same manner as described above for the *SOC1*/*FT* orthologues. Dealing first with *VFL*, the grape orthologue of *LFY*, in situ hybridization analyses have localized *VFL* expression patterns to the anlage before any commitment to the floral developmental program (Boss et al. 2006, Carmona et al. 2002, Joly et al. 2004). This pattern of expression is strongly repressed if the primordium commits to a tendril developmental fate and is conversely hugely upregulated upon conversion to a floral developmental fate. *VFL* expression reaches a peak in the floral meristems that develop in bursting buds in the following spring. *VFL* is also expressed in the petal and stamen primordia, with this expression declining as these organs develop. It has also been noted that *VFL* is expressed in leaf primordia and leaf margins, indicating a role in maintaining cell proliferation in specific leaf tissues. Similar roles for *LFY*-like genes in pea (*UNIFOLIATA*) and tomato (*FALSIFLORA*) have been identified, where these genes are required for the generation of correctly formed compound leaves and leaflets, respectively (Carmona et al. 2008, Gourlay et al. 2000, Hofer et al. 1997, Molinero Rosales et al. 1999).

Homologues of the *Arabidopsis AP1* and *FRUITFULL (FUL)* genes have also been identified in grapevine and

have been labeled *VAP1* and *VFUL-L* (Calonje et al. 2004). Both genes are expressed very early in the uncommitted lateral meristem. During flower development, *VFUL-L* transcripts are restricted to the central part of young flower meristems and, later, to the prospective carpel-forming region, which is consistent with a role of this gene in floral transition and carpel and fruit development. *VFUL-L* and *VAP1* expression has not been detected in vegetative organs such as leaves or roots (Calonje et al. 2004). The expression patterns of *VAP1* suggest that it may play a role in flowering transition and flower development. However, its lack of expression in sepal primordia does not support its role as an A-function gene in grapevine. Moreover, the high expression of *VFUL-L* and *VAP1* in developing tendrils suggests that both genes could have been recruited for the regulation of tendril development in the Vitaceae. Alternatively, their expression throughout tendril development could be considered as a remnant expression related to the evolution of these climbing organs from inflorescences (Carmona et al. 2008).

Floral organ identity. The specification of floral organ identity and development is controlled by a complex genetic regulatory network that acts in a coordinated fashion through a set of promotive and antagonistic iterations to allow the formation of organs in the correct order. This model, having been developed in model plant species, has become known as the ABC model of flowering and has been recently modified to the A, B, C, D, and E model (Krizek 2006). A-function genes are involved in the specification of sepals, while B-function genes are involved in the specification of petals and stamens. So far, three *V. vinifera* homologues of the B-function genes *PISTILATA/PI*, *Tomato MADS-box gene 6/TM6*, and *APETALLA3/AP3* have been identified: *VvMADS9*/*VvPI*, *VvAP3,* and *VvTM6* (Sreekantan et al. 2006, Poupin et al. 2007). Although these genes belong to the same genetic class, they act in different periods and/or tissues during reproductive organ development. All three genes are expressed in petals and stamens but *VvTM6* is also expressed in carpels (Poupin et al. 2007). *VvPI* and *VvAP3* transcripts are restricted almost exclusively to inflorescences (Sreekantan et al. 2006, Poupin et al. 2007), although *VvPI* has also been detected at low levels in leaves and roots (Poupin et al. 2007). *VvTM6* expresses throughout the plant, with higher levels in flowers and berries. *VvPI* expression increases during pollen maturation and decreases between the events of pollination and fertilization, before capfall, while *VvTM6* is expressed in the last stage of anther development (Poupin et al. 2007).

The C-function gene *AGAMOUS* (*AG*) is required in *Arabidopsis* for the specification of carpels and stamens. *AG,* together with the D-function genes such as *SEED STICK* (*STK/AGL11*), *SHATTERPROOF1* (*SHP1*), and *SHATTERPROOF2* (*SHP2*), are required to specify ovule identity. These D-function genes have also been implicated in the regulation of fruit development (Pinyopich et al. 2003). Several genes from grapevine have been identified that may correspond to the AG subfamily of genes (Boss et al. 2001). Among these, *VvMADS1* shares the highest degree of similarity with *SHP1/2*. This gene was found to be expressed in the inner two whorls of the flower and during berry development. In later work, overexpressing this gene in *Arabidopsis* resulted in altered sepal morphology (Boss et al. 2003). These data cannot resolve the classification of *VvMADS1* as either an *AG* or a *SHP1/2* orthologue (Carmona et al. 2008). A further member of this MADS box family, *VvMADS5,* shows homology with *STK*/*AGL11* and is expressed in the mature carpels, developing seeds, and preas well as postveraison fruit (Boss et al. 2002), indicating that this gene may be the orthologue of *STK*/*AGL11.*

E-function genes have only recently been characterized, because of the high degree of genetic redundancy and overlapping functionality, making genetic analysis of their functions very difficult. In grapevine, orthologues of *SEPALLATA1-4* (*SEP1-4*) have been identified. *VvMADS2* and *4* have been shown to have a high degree of sequence similarity to *SEPALLATA1* and *2* (*SEP1/2*), respectively (Boss et al. 2002). These two genes are expressed during early inflorescence development until anthesis and can be detected in the inner whorls of the flower. *VvMADS4* is also expressed during berry development. Finally, *VvMADS3* exhibits a high degree of sequence similarity to the *Arabidopsis* genes *AGL6* and *AGL13*, with an expression pattern that closely resembles that observed for *AGL6* (Boss et al. 2002). *AGL6* in *Arabidopsis* appears to have a function in both the development of flowers and vegetative organs (Alvarez-Buylla et al. 2000).

The recent generation of the first-draft sequence of the *V. vinifera* genome (Jaillón et al. 2007, Velasco et al. 2007) offered the possibility of genomewide analysis of some of the genes involved in the flowering process. Two recent publications have used bioinformatic approaches to mine the *V. vinifera* genome sequence in order to fully characterize the MIKC^c-type MADS-box gene family that plays a central role in the control of floral development in plants (Poupin et al. 2007, Díaz-Riquelme et al. 2009). The grape MADS-box homologues were identified and isolated using direct mining of data sets and PCR-based methodologies. The sequences were aligned and organized into phylogenetic groupings based on relatedness to genes of known function from model plant species. Patterns of gene expression where then determined and used to assist in predicting in vivo function of the particular gene with respect to extensive knowledge of homologous genes in other plant species. From these analyses, the gene family is predicted to be in the order of 38 members, which resolved into 10 major clades grouping 13 subfamilies (Díaz-Riquelme et al. 2009). All groupings saw the *Vitis* sequences grouping, with high levels of confidence, with their *Arabidopsis* counterparts. Lending support to the currently held view of a high level of functional conservation between the *Vitis* genes and functionally characterized homologues from other species, gene-expression patterns were also seen to be conserved among the majority of the 38 member gene family. Undoubtedly, while conservation of gene sequence

and expression patterns exists, it is clear that significant differences are also evident. How these differences contribute to floral processes in this species is subject to in-depth functional analyses.

It is clear from these types of study that the full genome sequence represents a resource of great importance. Prior to its release, a global appreciation of the complexity of such gene families was nearly impossible. While the difficulties associated with genetic analysis in grapevine have in the past limited functional analyses, the information presented in large-scale genomic studies provides an unprecedented opportunity to begin rigorously studying the in vivo function of individual genes involved in flowering in this species. These studies will shed much light on the conservation and differentiation of function of genes predicted to be involved in floral development that leads to the unique phenology of flowering in grapevine.

Conclusion

The flowering of *Vitis vinifera* spreads over two seasons. The numerous variables affecting each step of the flowering process throughout the 12-month period between induction and anthesis result in a high variability within the bunch, the vine, and therefore the vineyard block. From the point of view of production, there are some important gaps in our current knowledge: a better understanding of factors affecting the number and the length of the main and minor branches of inflorescence primordia is needed to support yield forecasting and disease prevention. Indirectly, understanding how to change cluster architecture would be a valuable tool to manipulate fruit secondary metabolite composition.

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