4

Bud Development and Fruitfulness of Grapevines

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The clusters on the grapevine that make up the current season's crop began to form (*differentiate*) the preceding growing season in the compound bud (Figure 4.1). Therefore, the maximum number of clusters per vine (and thus the potential yield) is determined during the previous year. By looking at what researchers have discovered about bud development and the potential fruitfulness of grapevines, along with some specific information on 'Thompson Seedless' grapevines grown in the San Joaquin Valley, we can get a good idea of how various environmental factors and cultural practices influence the formation of cluster primordia in the buds of grapevines.

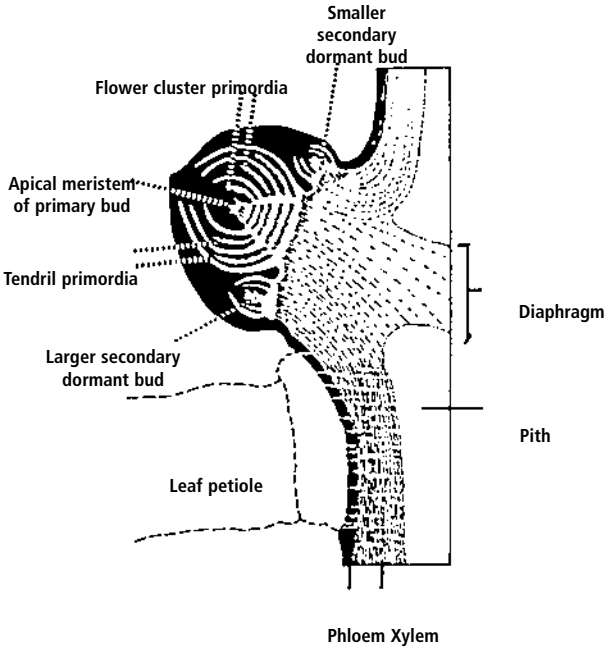

Figure 4.1 Cross-section through a dormant grapevine compound bud showing leaf, cluster, and tendril primordia (relative position of the lateral bud or shoot is not shown)

BUD AND CLUSTER DEVELOPMENT

Bud development. As shoots grow during the growing season, buds form in the axil of the leaf (at the base of the petiole). The first bud to form in the leaf axil is the *lateral bud.* This bud grows during that first growing season into a *lateral shoot*. The lateral shoot may fail to lignify and thus fall from the vine during autumn or winter, or it may lignify and remain on the vine into dormancy. If the bud does not grow in that first season it will die.

The first leaf of the lateral bud is reduced to a *prophyll,* a modified leaf that does not look like the other leaves one normally sees along the shoot. An additional bud formed in the axil of this prophyll is called the *compound bud.* The compound bud develops slowly, and depending upon the grapevine variety this bud may produce 10 to 12 leaf primordia before going dormant. It will also produce from one to three cluster primordia during that time, depending upon variety. At the base of this bud, several bracts form before the first leaf primordium appears. Like the prophyll, these bracts are also modified leaves. Second and third buds will form in the axils of these bracts, the *secondary* and *tertiary buds*. The compound bud, then, contains three individual buds.

The primary, secondary, and tertiary buds are enclosed by the basal bract or prophyll of the lateral bud or shoot. Together, these structures constitute the prominent compound bud (*eye*) one sees on mature canes at a node. Though referred to in the singular as the *latent bud,* it is in fact a compound bud, with each component bud located in the leaf axil of another. At first sight the compound or fruit bud may appear to be axillary to the cane of the primary shoot, but it is actually a basal appendage of the lateral bud or shoot. The compound bud and lateral bud or shoot are very closely associated; vascular tissue (the xylem vessels) from young compound buds lead directly to the lateral bud.

Inflorescence (cluster) differentiation. The formation of clusters for next year's crop begins concurrently with the formation of leaf primordia within the compound bud. Depending on the grapevine variety, the primary bud within the compound bud produces three or four leaf primordia and then divides into two equal or almost equal parts. The part opposite the youngest leaf primordium is the *anlage* (plural, *anlagen*). The formation of anlagen from the apex of the bud is the earliest indication of reproductive growth in the grapevine, and can be regarded as an indicator that the inflorescence (cluster) axis has begun to form. Anlagen appear first on the basal buds of the shoot, and then more and more toward the apex of the shoot as the growing season progresses. The continued development of each anlage starts with its division into two unequal parts, the larger *inner arm* and the smaller *outer arm*. The inner arm will give rise to the main body (*rachis*) of the cluster, while the outer arm will give rise to either a wing or a large branch at the top of the cluster. Other branches along the inner arm will form, and these will become lateral branches along the rachis. A fully developed cluster primordium within the bud looks rather like a bunch of grapes, in which each berrylike branch primordium is a mass of undifferentiated tissue. After one to three cluster primordia form, additional leaf primordia form and the bud enters dormancy. A fully developed compound bud is shown in Figure 4.1.

Flower differentiation. The differentiation of flowers on the cluster primordium begins after the dormant compound buds are activated in the spring. The branch primordium divides many times, ultimately producing the flower initials. This process begins before the bud starts to grow. After budbreak, the flowers continue their development until the time of *anthesis* (bloom).

Regulation of reproductive development. The crucial stage in the reproductive development of the grapevine comes when the anlage divides to form two branches. This is because the anlagen have the potential to produce either cluster primordia or tendril primordia. The first stage is a coarse control and involves the formation of the anlagen. The second stage is a finer level of control and involves the switching of the two-branched anlage into either the cluster or the tendril pathway. Sunlight and temperature have the greatest potential to regulate the differentiation of anlagen into either cluster or tendril primordia. High-intensity light on the bud and high temperatures favor the formation of cluster primordia. This is one reason to select "sun canes" when pruning 'Thompson Seedless' grapevines: they are more fruitful than canes that grow in the shade, under the vine's canopy. Cultural practices also influence the differentiation of cluster primordia. Mineral nutrition and vine water status are the two main cultural factors that influence the differentiation of cluster primordia on grapevines.

The internal regulation of cluster primordia development is the result of the interaction of at least two plant hormones. Gibberellic acid (GA) and cytokinin play roles in this differentiation. GA is involved in both anlage formation and the determination of the direction of anlage development. At an early stage of anlagen differentiation, GA promotes flowering because it favors anlage formation. Later, GA inhibits flowering because it directs the anlagen to form tendrils. Cytokinins induce the grapevine to form inflorescences from anlagen and from young tendrils. In addition, flower formation is a cytokinin-controlled process. The xylem sap (bleeding sap) of the grapevine contains high cytokinin levels during budbreak and flowering. Cytokinins influence the promotion of fruit set in grape. Cluster and flower differentiation probably are regulated by the relative proportions of both of these hormones within the bud at the time of differentiation.

Bud dormancy. The compound buds of grapevines are inhibited from growing during their development by both internal and external factors. The first phase of bud dormancy occurs during the initial development of the compound bud, while the primary shoots of the grapevine are green and actively growing. This stage of dormancy has been referred to as *conditional* (or *correlative*) dormancy. Compound buds will not grow as long as the apex of the primary shoot on which they are located is intact or growing. If the primary shoot is severed above a node position and all lateral shoots are removed along the remaining portion of the shoot, the compound bud will become activated and grow.

The next phase of bud dormancy is called *organic* (or *deep*) dormancy. It should be pointed out that these phases of bud dormancy are not necessarily separated from one another. Organic dormancy develops in the compound buds as canes mature during mid- to late summer and early autumn. During this phase, the removal of the apex of the primary shoot and the lateral shoots as described above will not induce growth of the compound bud. In addition, cuttings of canes taken during this phase and forced to grow, under favorable conditions, will take more than 70 days to sprout. The final phase of bud dormancy is *enforced* dormancy (or *rest*). Cuttings taken during this phase grow rapidly in favorable conditions. This phase comes toward the end of winter. Apparently, low temperatures normally keep the buds from developing at this time.

The regulation of bud dormancy in grapevines is not fully understood. Apparently, growing shoot tips produce a substance or substances that inhibit the

growth of the compound bud during conditional dormancy. This may be related to something called *correlative inhibition,* one aspect of apical dominance in higher plants. Organic dormancy probably is also controlled by internal factors. This phase of dormancy appears to be regulated by the interaction between growth promoters and inhibitors. Plant hormones most commonly associated with growth promotion are gibberellic acid and cytokinin, while those associated with inhibition are abscisic acid and ethylene. Grape buds are released from organic dormancy through exposure to cold, measured as a specific quantity of chilling units (like heat units [degree-days], but the amount of time buds are exposed to temperatures below a certain maximum). While no exact minimum chilling requirements have been established for grapevines, the accumulation of 400 hours at or below 37.4°F (3°C) under laboratory conditions was sufficient to achieve commercially acceptable levels of budbreak for the variety 'Perlette.' Chemicals can also be used to overcome organic dormancy and thus promote budbreak in areas where winter chilling is insufficient, such as in the Coachella Valley or tropical regions. The chemical used in most of those areas is hydrogen cyanamide (H_2CN_2). Hydrogen cyanamide has little effect on maximum observed budbreak, budbreak uniformity, or date of fruit maturity in the San Joaquin Valley, where the winter chilling is sufficient most years.

REPRODUCTIVE DEVELOPMENT OF 'THOMPSON SEEDLESS'

Time of cluster differentiation. For 'Thompson Seedless' grapevines, cluster differentiation within the compound bud begins around bloomtime, while the formation of cluster primordia along the 15-node shoot continues almost until fruit harvest (Figure 4.2). This is equivalent to approximately 3,150 degree-days (DD) Fahrenheit (base = 50°F) (1,750 DD Celsius [base = 10°C]) after budbreak. During the growing season, cluster differentiation in 'Thompson Seedless' buds begins at bud positions 4 to 9 (Figure 4.3). Cluster differentiation at bud positions 13 through 15 did not commence in 1993 until June 14 (day 165 of the calendar year).

It is interesting to note that cluster differentiation in the three basal buds did not begin until after cluster differentiation had begun in buds further along the cane. Potential bud fruitfulness along 'Thompson Seedless' canes is greatest at bud positions 7 to 13, regardless of vineyard cultural practices (Table 4.1). Fertility in the basal three buds is less than half that found at nodes 7 to 13. There also appears to be a slight decrease in bud fruitfulness at positions 14 and 15. Actual bud fertility along the canes of 'Thompson Seedless' has been demonstrated before with results similar to those shown in Table 4.1, but the potential for bud fruitfulness as it relates to bud position must be established if we are to predict actual bud fruitfulness on the basis of bud dissections.

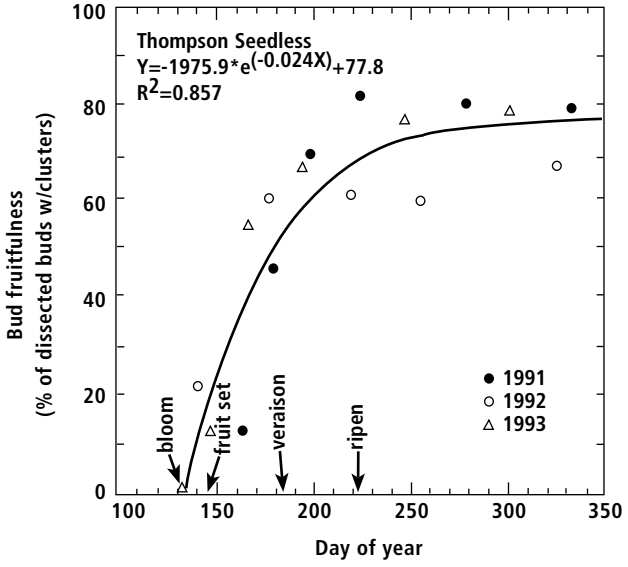

Figure 4.2 Timing of cluster differentiation in the primary bud along a 15-node shoot of 'Thompson Seedless.' Each data point is the mean of at least 10 individual shoots. Dates of bloom, fruit set, and veraison are approximate.

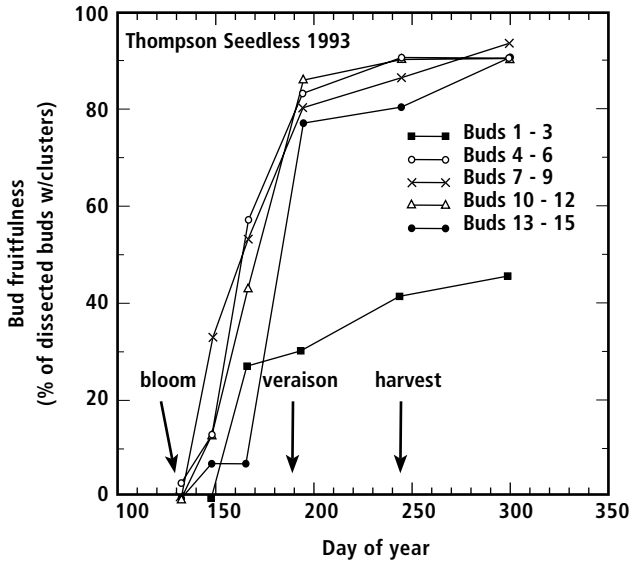

Figure 4.3 Timing of cluster differentiation as a function of bud position for 'Thompson Seedless' grapevines during the 1993 growing season. Each value is the mean of three bud positions. Bud position 1 is the basal-most node position on the shoot.

Table 4.1 Potential bud fruitfulness as a function of bud position along the canes of 'Thompson Seedless' grapevines grown at the Kearney Agricultural Center (data were collected in November or December of 1991, 1992, and 1993*)

Bud position	Vineyard A	Vineyard B_a	Vineyard B_b
	live buds w/cluster (%)†		
1	25	24	14
2	26	17	14
3	42	19	28
4	61	46	53
5	75	65	67
6	81	73	74
7	95	65	91
8	91	90	92
9	93	89	79
10	88	79	82
11	95	86	87
12	82	83	86
13	93	85	82
14	89	73	82
15	88	76	67

*Vineyard A was flood irrigated and pruned to six canes each year. Vineyard B_a was drip irrigated at full ET and pruned to six canes in 1991 and 1992, and eight canes in 1993. Vineyard B_b was drip irrigated at 20% of full ET. Pruningpattern was similar to that of Vineyard B_a.

†Each value is the mean of at least 20 individual buds dissected each year and then averaged across three years.

Seasonal variation in bud fruitfulness. Buds of four grape varieties grown in close proximity at the Kearney Agricultural Center were dissected in November or December for four years to determine potential bud fruitfulness. Based on the data from these studies, one can determine the yearly variation of potential fruitfulness across varieties. The data indicate that potential fruitfulness varied by as much as 25 percent from one year to the next, with the amount of variability dependent on variety (Table 4.2). Since the yearly variation in potential bud fruitfulness was independent of variety (i.e., bud fertility for all varieties were generally high one year and low the next), climatic factors were identified as probable causes for the variations.

Correlations made in Australia indicate that the two climatic factors most closely related to bud fruitfulness for 'Thompson Seedless' grapevines are the hours of bright sunshine and the sum of daily maximum temperatures between 82° and 90°F (27.8° and 32.2°C) during three weeks. This three-week period started just before the first observation of cluster primordia in the buds. Based on the data shown in Figure 4.2, this period would correspond to the second, third, and fourth weeks in May for 'Thompson Seedless' grapevines grown in the San Joaquin Valley. Solar radiation values and the number of days between 82° and 90°F (27.8° and 32.2°C) during that period were less in 1991 than in 1992 (7 days compared to 16 days for the temperature values). The bud fruitfulness values observed the following years, 1992, and 1993, would lend support to the observations reported from Australia. These two climatic factors followed similar patterns in 1989 and 1990, however, and in that case bud fruitfulness was less for all varieties in 1990 than in 1991. These results indicate that further study is needed before we can identify definite relationships between environmental factors and cluster differentiation.

Table 4.2 Potential bud fruitfulness of four grape varieties grown at the Kearney Agricultural Center over a 4-year period (data were collected in either November or December of each year)

	Variety			
Year	'Perlette'	'Flame Seedless'	'Ruby Seedless'	'Thompson Seedless'
	*live buds w/cluster (%)**			
1990	72	80	—†	68
1991	82	93	98	79
1992	63	68	85	67
1993	69	73	84	79

*Each value is the mean of the four basal buds on at least 30 spurs for the spur-pruned cultivars and 20 canes for 'Thompson Seedless.'

†Data not collected

Effects of irrigation amounts on bud fruitfulness. Probably the single most important cultural practice affecting bud fruitfulness of 'Thompson Seedless' grapevines is irrigation. The irrigation practices used during the previous growing season can affect this season's crop by influencing bud fruitfulness and viability. Contrary to popular belief, severe water deficits have no adverse effect on bud viability (Table 4.3). In fact, the rate of bud death (*necrosis*) increases as the amount of applied water increases. There appears to be an optimum irrigation amount that maximizes cluster differentiation or potential fruitfulness for the following year. In studies conducted at the Kearney Agricultural Center, water application amounts between 60 and 80 percent of full ET maximized bud fruitfulness (Table 4.3). These results indicate the harmful effects overirrigation has on the potential 'Thompson Seedless' crop. This practice results in both lowered cluster differentiation and greater bud mortality.

The mechanism by which irrigation management affects cluster differentiation may actually be indirect. As noted, the light environment around the bud affects cluster differentiation: greater amounts of light favor cluster formation over tendril formation. Too much irrigation produces large, dense canopies and a shaded canopy that is not conducive to cluster differentiation. Conversely, deficit irrigation results in a less-dense canopy where more light reaches the developing buds. A situation similar to overirrigation may also arise in vineyards where nitrogen fertility is high, resulting in a dense canopy and low bud fruitfulness.

Table 4.3 The percentage of live buds and potential fruitfulness of those buds on canes from 'Thompson Seedless' grapevines grown at the Kearney Agricultural Center (vines were irrigated at various fractions of vineyard ET, and data were collected over a 4-year period*)

	Irrigation treatment (% ET)-			
	0.2	0.6	1.0	1.4
Percentage of dissected buds that are alive	99	94	88	81
Percentage of live buds with clusters	68	71	62	58

*The numbers of canes retained after pruning in 1990, 1991, 1992, and 1993 were 4, 6, 6, and 8 per vine, respectively. Buds were dissected in either November or December of each year.

Irrigation treatments consisted of water applications at 20%, 60%, 100%, and 140% of full vineyard evapotranspiration (ET). ET was determined with a weighing lysimeter.

Correlation between potential and actual bud fertility. To determine potential bud fruitfulness, you can dissect buds while the vine is dormant. This information helps a grower determine how much wood to leave on the vine at pruning. Potential bud fruitfulness (determined via bud dissections) explained more than 90 percent of the variations in actual bud fruitfulness (determined by counting clusters when 'Thompson Seedless' shoots grown at the Kearney Agricultural Center were 18 inches [45.5 cm] long). However, bud dissections could only explain about 50 percent of the variations in actual bud fruitfulness for 'Thompson Seedless' grapevines grown in the Coachella Valley. Researchers in Australia have concluded that, while examining dormant buds is a valuable guide for growers of 'Thompson Seedless' grapevines, it does not yield reliable estimates of the final crop.

Another factor that needs to be addressed is the bud sampling technique and the number of buds examined. Studies conducted at the Kearney Agricultural Center determined that 10 to 15 canes sampled from an individual treatment on 'Thompson Seedless' vineyard are sufficient for a reliable estimate. A random selection of canes (taken from the head of the vine or from renewal spurs) within the vineyard or sampling at standard locations (e.g., one cane from the fifth vine in every third row) has been used with success. Regardless of the sampling technique, you should attempt to sample the same vines each year.

Dissecting every bud on a 15-bud cane is very time consuming. The relationship between entire-cane bud dissections and the dissection of alternate buds, buds 1, 4, 9, and 13, and buds 4, 9, and 13 are shown in Figure 4.4. All three methods of predicting entire-cane bud fruitfulness correlated well with bud fruitfulness as determined by dissection of every bud. As expected, the dissection of alternate buds had the highest coef-

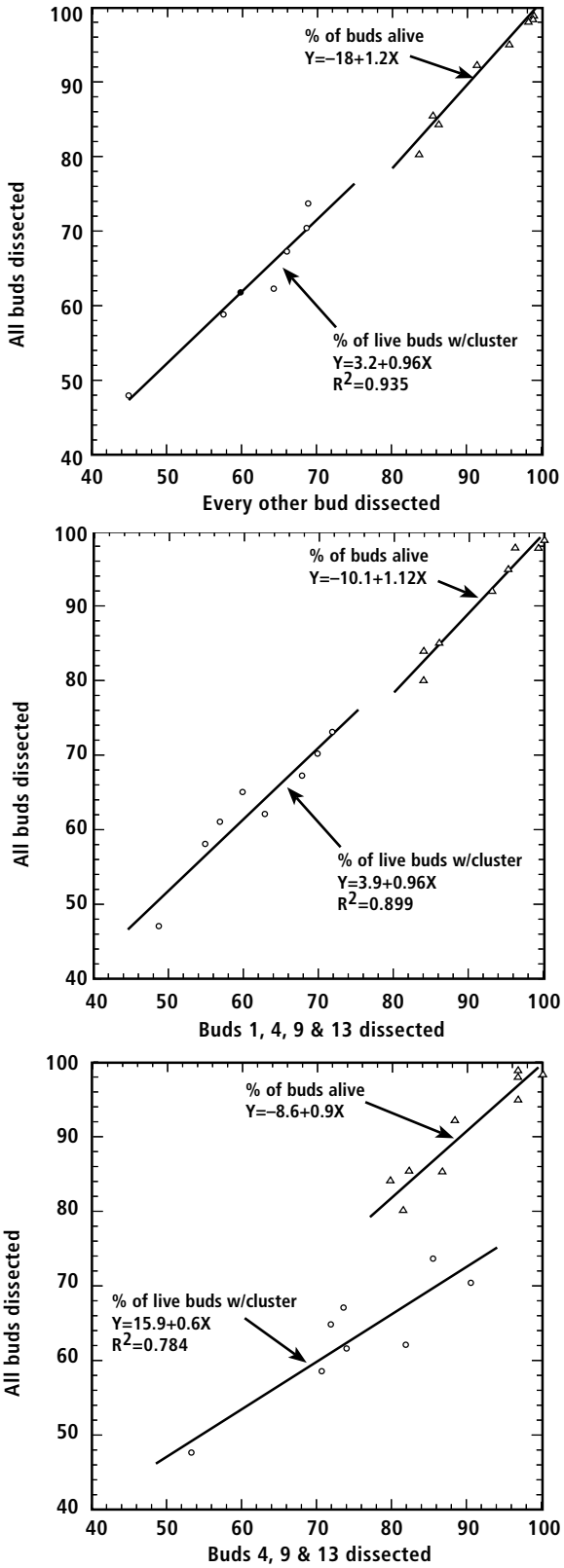

Fig 4.4 The relationship between subsampling buds at various positions along a 15-node 'Thompson Seedless' cane and the dissection of all buds on the cane. Correlations were made between the percentage of buds that were alive when dissected and the percentage of those live buds that had cluster primordia. Each data point is the mean of data from at least ten individual canes.

ficient of determination (R^2), followed by dissection of buds 1, 4, 9, and 13. It appears that at least four buds (at node positions 1, 4, 9, and 13) must be dissected in order to accurately predict bud fruitfulness of the entire cane. By restricting the number of buds sampled along the cane, you can have time to sample more canes in the vineyard and possibly increase your overall accuracy for predicting potential bud fruitfulness within your vineyard.

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