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Fruit-bud differentiation in grapevine *(Vitis vinifera)* : a review

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Abstract

Grapevine (*Vitis vinifera* L.) reproductive development extends over two growing seasons (vegetative cycles) for complete formation of inflorescences and clusters, and reproductive cycle (development of a cluster). The process of induction and floral differentiation, which leads to creation of reproductive structures within dormant buds, is intricate and occurs in three distinct stages: formation of anlagen, inflorescence primordia, and flowers. This sequence of stages involves morphological, biochemical, and physiological changes, all influenced by a range of environmental and internal factors. The review describes the morphology and physiology of fruit-bud differentiation, as well as discusses the main abiotic and biotic factors involved.

Key words: Bud differentiation, Grapevine, Inflorescence primordia, Potential yield

Grape (*Vitis vinifera* L.) is a major important fruit crop of our country, especially in the peninsular region, where its vines are pruned twice a year. In April, vines are pruned to encourage shoot growth, cane development, fruit-bud formation, and reserve storage in the cane. In October, shoots are pruned to promote fruiting for a more yield. The number of bunches on a vine indicates its yield, which is determined by fruitfulness of the canes. Yield is influenced by the number of flower clusters per unit area and average weight of clusters. The fruitfulness of the canes is determined after back pruning, the yield being reliant on cultural practices carried out between April and September. Thus, a fruiting cane is considered the unit of production.

The productivity refers to grapevine's inherent ability to produce the maximum yield, which varies across different varieties. There is often a significant gap between vine's potential productivity and actual yield, which can be improved through various cultural practices such as crop regulation, use of growth regulators, training, canopy management, and pest and disease management.

Bud development

As shoots develop throughout the growing season, buds appear in the leaf axil (at the base of the petiole). The initial bud to form in the leaf axil is the lateral bud, which grows into a lateral shoot during the first growing season. This lateral shoot may either fail to lignify and drop off the vine in autumn or winter, or it may lignify and stay on vine through dormancy. If the bud does not grow in the first season, it dies. The first leaf of lateral bud is reduced to a prophyll, a modified leaf that differs from the typical leaves along the shoot. A second bud forms in the axil of this prophyll, known as the compound bud. The compound bud develops gradually, depending on grapevine variety, it may produce 10 - 12 leaf primordia before entering into dormancy. It can also generate one to three cluster primordia during this time, again depending on variety. Several bracts, which are modified leaves, form at the base of this bud before the first leaf primordium appears. Secondary and tertiary buds develop in axils of these bracts. Therefore, compound bud contains three distinct buds. The primary, secondary, and tertiary buds are surrounded by basal bract or prophyll of lateral bud or shoot. Together, these elements form the prominent compound bud (eye) found on mature canes at a node. Although commonly called the latent bud in singular form, it is a compound bud, with each individual bud situated in the leaf axil of another. While compound or fruit bud may seem to be located in the axil of the cane from the primary shoot, it is actually a basal extension of the lateral bud or shoot. The compound bud and lateral bud or shoot are closely linked, with vascular tissue (xylem vessels) from the young compound buds connecting directly to the lateral bud.

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Flowering

The formation of inflorescence and flowers involves three well-defined stages:

Formation of anlagen: Anlagen are club-shaped meristematic protuberances which arises from the apices of latent bud. Anlagen are uncommitted primordia which may be directed to from inflorescence primordia, tendril primordia or shoot primordia. Formation of anlagen is also referred to as inflorescence initiation or inflorescence axis formation.

Formation of inflorescence primordia: Anlagen which have been directed to develop as inflorescences undergo repeated branching to form a conical structure composed of many rounded branch primordia.

Formation of flowers: Differentiation of inflorescence primordia to form the individual flowers.

Grapevine bud fruitfulness

Bud fruitfulness refers to potential of a bud to produce an inflorescence, often quantified by number of inflorescence primordia per bud. Bud fertility, typically assessed by number of bunches or fruit weight per node, provides a more practical measure of productivity (Dry, 2000). Bud fertility varies in latent buds based on their position on the cane: it increases from the base to the middle and then decreases toward the apex. Improper bud development during the growth cycle accounts for 60% of the seasonal yield variation in vineyards. A critical point in grapevine reproductive development occurs when the anlage splits into two parts (inner and outer), determining whether they will produce inflorescence or tendril primordia (Dunn and Martin, 2007). Earlier initiation of anlage results in earlier primary branching and the start of inflorescence primordium development.

The degree of inflorescence primordium differentiation in the primary axis of a latent bud follows an acropetal gradient (Li-Mallet *et al.*, 2016; Cheema *et al.*, 1996). Understanding the regulation of inflorescence initiation and differentiation is key to controlling bud fruitfulness and grapevine yield. These processes are influenced by numerous environmental factors, e.g. temperature, light, and water status and internal factors such as sugar and mineral nutrition, their metabolism, hormones, and gene regulation. Environmental factors, which are the main contributors to yield variability are difficult to control. They affect not only the initiation and differentiation of inflorescence primordia but also the plants overall physiological functions, including nutrient assimilation, metabolism, and hormonal balance.

Factors affecting fruit-bud differentiations

Environmental factors

Numerous studies have been conducted on the effects of environmental conditions on inflorescence, flower formation, and grapevine fruitfulness (Clingeleffer *et al.*, 2001; Sánchez and Dokoozlian 2005; Carmona *et al.*, 2008; Al-Obeed *et al.*, 2010; Guilpart *et al.*, 2014; Somkuwar *et al.*, 2014). Induction of inflorescences in grapevine is not sensitive to vernalization, which is usually involved in flower formation in herbaceous plants (Carmona *et al.*, 2008). Although the effect of photoperiod is not well understood, short-term exposure of grapevine to high temperature and high light intensity can promote grapefruit fruitfulness.

Temperature

Many reports have indicated that inflorescence primordia formation requires high temperatures (Dunn and Martin 2000; Petrie and Clingeleffer 2005). There is correlation between the temperature during the initiation stage of the inflorescence primordia and number of inflorescences appearing on the shoot (Guilpart *et al.*, 2014). In the temperate region, the fruit bud differentiation take place in next year on current season's growth whereas it happens during the period of 30-60 days after foundation pruning (back pruning) on current season's growth in peninsular India. Temperature appears to be more favorable than light for fruitfulness of Thompson Seedless bud or higher light intensities than 3600 ft. candles above 35°C could be favorable for fruitfulness of the bud (Somkuwar, 2005).

According to Chadha and Shikhamany (1999), the critical level of temperature and light for bud fruitfulness in Thompson Seedless is 35°C and 3600 ft candles respectively. Buttrose (1969) noted that in a temperature controlled environment with different varieties (Almeria, Muscat of Alexandria, Riesling, Syrah, and Thompson Seedless) have shown that the optimum temperature interval for formation of inflorescence varies from 20 to 35°C. At temperatures below 20°C tendrils are formed, reducing the growth and yield. On the other hand, temperatures above 30 °C for at least 4 - 5 hr per day should be sufficient to induce a maximum number of inflorescence (Srinivasan and Mullins, 1980).

Various authors have demonstrated opposite effects, with a decrease in bud fruitfulness under high temperatures. Sharma *et al.*, (2018) noted that as temperature increases more than 40°C during bud fruitfulness will lead to delayed and erratic bud sprouts and also reduces the fruit bud differentiation. High temperature negatively affects plant growth and survival and hence crop yield. According to Pouget (1981), higher temperatures lead to rapid growth of vegetative organs in the developing shoot, which increases the speed of bud break and consequently fewer flowers are formed.

The mechanism by which temperature affects the initiation of inflorescences remains unclear, although some hypotheses have been proposed. The influence of temperature on the biosynthesis of gibberellins (GAs) and cytokinins (CKs) is one of the possible explanations. May (1987) suggested that higher temperature may increase cytokinins levels in precocious flowers, thereby inhibiting the formation of other flowers. Temperatures ranging from 25°C to 35°C promote cytokinins biosynthesis, which is known to stimulate inflorescence differentiation (Jackson, 2014). Low temperatures (20°C) promote

GA biosynthesis, which promotes vegetative growth and reduces nutrient accumulation. The influence of temperature on biochemical processes such as photosynthesis, enzymatic activity, and respiratory activity has also been hypothesized (Taiz, 2006; Keller, 2015). The optimal temperature range for photosynthesis varies between 25°C and 30°C depending on the variety and phenology. Temperatures above 35°C negatively affect photosynthesis as the stomata begin to close (Somkuwar *et al.,* 2018; Monteiro *et al.,* 2021).

Light

In herbaceous plants, different light characteristics such as light quality, light intensity, and photoperiod influence the number of inflorescences, flower induction, and differentiation. Unlike herbaceous plants, there was no significant effect of red: far-red ratio on grapevine bud fruitfulness in terms of light quality (Sommer *et al.*, 2000). Light intensity is essential factor for initiation and differentiation of dormant bud (Buttrose, 1969; Dry, 2000; Vasconcelos *et al.*, 2009). Correlation between light intensity and fruitfulness (number of inflorescences per shoot) of buds in Sultana grapevine was first time noted by Antcliff and May (1961). Increases in number of inflorescence primordia with light intensity under controlled climatic condition was reported by Buttrose (1969) and Sanchez and Dokoozlian (2005).

Light may have an influence on fruitfulness through its effect on photosynthesis and carbohydrate availability, or it may have a direct effect on the bud fruitfulness. Lebon *et al.*, (2008) observed decease in emergence of primary and secondary bud due to low light intensity which reduces the amount of photoassimilates and limiting the carbohydrates supplies to emerging bud. Kriedman and Smart (1971) found that light intensity required for maximum photosynthesis in Thompson Seedless ranges from 2500 to 5000 ft candles. If the light intensity is more than 5000 ft candles, leaf loses its chlorophyll by photo oxidation. Depending on the cultivar or species, the sensitivity of bud fruitfulness to light exposure is different. The effects of photoperiod on the initiation and differentiation of inflorescence primordia are unclear; however, in some varieties, the number of inflorescence primordia appears to be greater on long days than on short days (Vasconcelos *et al.*, 2009)

Water condition

Water status affects bud fruitfulness indirectly through altering plant hormone balance, mineral nutrition, microclimate around the bud, and vine photosynthesis (carbohydrate production). Directly, it affects bud fruitfulness through the amount of water available for the biosynthetic processes occurring during cell division and enlargement (Williams, 2000; Jackson, 2014; Li Mallet *et al.*, 2016). Water deficiency and excessive water are two characteristics of water status that have a major impact on the fruitfulness of dormant buds during the growing season. An increase in bud fruitfulness is a result of enhanced inflorescence differentiation conditions, especially due to an adequate water availability.

On the other hand, when there is water stress, inflorescence size and number are significantly impacted. When water is limited, photosynthesis decreases and may hinders the production of sufficient carbohydrates for inflorescence development. Reducing canopy density under moderate water stress can boost bud fruitfulness by raising light exposure, predominantly in the renewal zone. Water stress leads to an imbalance in xylem sap hormones, resulting in a decrease in cytokinins and an increase in abscisic acid, which negatively affects differentiation. Stomatal closure, induced by elevated ABA, hinders photosynthesis in response to water stress. The differentiation of inflorescences is also sensitive to the combined effects of nitrogen deficiency and water stress (Osakabe *et al.*, 2014; Guilpart *et al.*, 2014).

Rainfall

The rainfall in grape growing area has direct impact on the fruitfulness. A rain during the stage of fruit bud differentiation (40 - 60 days after back pruning) is not favorable for grape since the excessive shoot growth hamper the initiation of floral primordial. The only alternative will be to adjust the pruning time in such a way that the rainy season will not coincide with the important growth stage like fruit bud differentiation (Somkuwar, 2005).

Relative humidity

For the grape to grow and develop, it needs a warm and dry climate. As a result, highly humid conditions are not conducive to any stage of vine growth and fruitfulness. Bud differentiation takes place between May and June if the vines are pruned in April, during which a dry atmosphere with low relative humidity prevails. Therefore, after back-pruning, the high humidity problem is not a constraint. However, rainfall in combination with high humidity during foundation pruning may delay bud break and increase the risk of diseases.

Nutrient availability

The significance of nutrition in determining vine productivity is well-established. Proper quantity of macronutrients (nitrogen, phosphorus, and potassium) are essential for maximum floral induction, differentiation, and fruitfulness. Phosphorus plays a crucial role in flowering by synthesizing proteins and nucleic acids favorable for inflorescence development. This process influences carbon dioxide absorption, cell membrane establishment, and the relocation of essential structures. Energy storage and transfer are influenced by its role as well (Adam Jacobs, 2002) 30 days after pruning, phosphorous application enhances bud fruitfulness. Zinc like phosphorus is essential during fruit bud differentiation, contributing to increased RNA synthesis and ultimately, fruitfulness. As per Rao and Srinivasan (1971), the rate of RNA syntheses and ratio of RNA/ DNA was higher in fruitful buds.

Nitrogen is vital for constructing amino acids used in building structural proteins and enzymes, as well as facilitating all biochemical reactions. Chlorophyll and hormones share a common constituent (Keller, 2015). Following nitrogen application, low nitrogen grapevines generated more inflorescences and flowers. About 30-60 days after pruning, avoid using nitrogenous fertilizer to prevent excess cane growth. For the first 30 days after pruning, nitrogen is vital for producing new growth structures in plants. Application of excess nitrogen during this phase hinders flower bud initiation by promoting vegetative growth and casting a shading effect. Potassium plays a vital role in enzyme activation, photosynthesis, and efficient plant water management. Applying K to the soil increased the fruitfulness of Thompson Seedless grapes.

Other factors

Canopy management

Efficient canopy management practices significantly contribute to seasonal sustainability in commercial vineyards. A number of practices are used to improve canopy structure for optimal photosynthesis, balance vegetative and reproductive growth, and ensure sufficient sunlight exposure (Smart and Robinson, 1991; Coombe and Dry, 1994). Proper canopy management practices enhance the late spring microclimate, promoting inflorescence primordia formation by increasing light intensity and temperature (Buttrose, 1969; Dry, 2000; Sánchez and Dokoozlian, 2005). Bud fruitfulness may be improved by light as a result of its effect on photosynthesis and subsequent carbohydrate production or a direct effect on the bud itself (Vasconcelos *et al.*, 2009; Li-Mallet *et al.*, 2016). Any lapses during the critical stages of growth may lead to barrenness of the vine. Therefor number of shoots, its orientation, partial defoliation, tipping and use of growth retardants are some of the important considerations need to be followed in the canopy management.

Number of shoots/vine

After back pruning, approximately 70-80 shoots sprout on each vine. If all the shoots are allowed to grow, there will be competition for nutrients, water, and sunlight. The fruitfulness of the bud depends on exposure to sunlight during the bud differentiation stage. Excess shoots create the shading effect, thus reducing photosynthetic activity. The leaves of such shoots become yellow and drop down leading to immature canes. Such canes do not contain fruitful buds; hence, they are removed at the time of fruit pruning. To avoid green canes during the maturity stage, shoot thinning is recommended at the 4–5 leaf stage after back pruning. This helps to avoid crowding of shoots, proper aeration and maximum sunlight harvest for bud differentiation. This type of canopy also avoids the incidence of diseases. For export markets, cane density should be 0.7 canes/sq. ft areas during the periods of back pruning and one cane for domestic markets.

Shoot vigor

The growth arising from the sprouted bud is called shoot. The shoot growth is by cell division and cell elongation. Increases in the shoot length per day is termed as rate of shoot growth. The shoot grows faster during the first 30 days of back pruning. This period is called as grand growth period. Vigor of the shoot or the rate of growth is considered more when the time required to produce an extra leaf is less (Shikhamany, 1999). During the grand period of growth, the rate of shoot growth on the renewal spurs is more than that on the fruiting canes. The duration of shoot growth also varies with the variety and the climatic condition prevailing in the area. During the grand growth period, if the growth is not controlled, there will be an increase in internodal distance and shoot length. Vigorous shoot growth led to reduced fruitfulness that results in fillage i.e. conversion of fruitful bud into tendril.

Position of shoot (horizontal vs. vertical)

Shoot orientation should be in such a way that each bud on shoot gets maximum available sunlight. Training grapes to trellis such as Geneva Double Curtain (GDC), Y-trellis and Tatura result in open canopies with diagonal shoot orientation to harvest more sunlight by individual buds on the shoot. Beside the foliar density, the angle of the shoot with the horizontal surface influences the light interception. Long and thin shoot bend by its own weight narrowing the angle while the short and thick shoot tend to be erect increasing the angle and thereby more light interception in the canopy. The vertically grown shoot is exposed to the full sunlight uniformly. (Somkuwar and Ramteke, 2008) studied effect of shoot orientation on fruitfulness in Thompson Seedless and reported that high bud fruitfulness in vertically oriented shoot due to maximum chlorophyll content in leaves. On the other hand, horizontally positioned shoots will not receive the light equally for bud differentiation and its maturity.

Cane thickness

There is a positive correlation of fruitfulness with cane diameter and position of shoot on the training system (Somkuwar and Ramteke, 2008). The thick cane at the beginning becomes erect and thus helps in receiving the required sunlight uniformly on every bud of the shoot. With the increases in the cane thickness, the bud size increases but the time taken for bud sprouting also increases. More than the size of the cane, the quality of cane is also important for bud fruitfulness.

Training system

Training system plays an important role in the fruitfulness and substantially enhances productivity. The position of shoot is determined by the training system. May training systems have been developed in the past and others are being developed to adopt vine growth to the climate and cultural conditions. Studies indicate that upward growing shoots are normally more fruitful than the downward shoots. The trellis system has a critical role in the canopy management principles, the training system must allow a uniformly distributed canopy with sufficient sunlight penetration for the continued production of healthy and equally ripened grapes of high quality (Smart, 1982; Smart *et al*., 1990; Hunter, 1999).

Bower system

In India, grapevines are commonly trained using the low-cost bower (Pandal) system. This system creates challenges for cultural operations. In this system, where the canopy is horizontal, more secondary shoots with their attached shoots are retained. The excessive foliage in the vine canopy limits the amount of sunlight it intercepts. Inadequate light negatively impacts both bud productivity and shoot maturity by inducing early leaf drop. The system promotes a favorable microclimate for the growth of fungal diseases such as downy mildew.

Flat roof gable

In this training system, the canopy is trained vertically and therefore there is a scope to harvest maximum sunlight by individual shoot uniformly. The percentage of mature and fruitful canes are always more than the bower trained vines. Cultural practices are also easy in this system. Proper aeration in the vine canopy prevent disease spread.

Table 1: Comparison of fruitful canes in bower and flat roof gable system of training

Character	Bower	FRG
No. of canes/vine	More	Less
Canopy architecture	Vertical	Vertical
Percent green shoots	More	Less
Percent mature shoots	Less	More
Percent fruitful canes/vine	Less	More

Kniffin system

A vertical trellis with horizontal wires is used for grapevine training, allowing for effective vine support and canopy management. In the Modified Kniffin system, optimal vine support and improved airflow lead to enhanced bud development and fruitfulness. Pruning and training are necessary for optimal fruit production and to prevent overcrowding.

Rootstocks

The introduction of rootstocks in grape cultivation is of recent origin. The increasing problem of soil salinity and drought felt the need of rootstock. The rootstock has the potential to sustain under adverse situation and manipulation of vine growth and production. Rootstocks play an important role in maintaining equilibrium between growth and yield. Increase in yield is mainly due to increase in fruitfulness of the vine under given set of condition. Direct effect of rootstocks on fruit bud differentiation and consequently on yield is attributed to the capacity of rootstock to synthesize the cytokinins. It is well known fact that cytokinins are synthesized in roots and high cytokinin/gibberellins ratio was found to be favorable for fruit bud formation. Somkuwar *et al*., (2006) noted that bud fruitfulness in relation to different rootstock showed that the variety Thompson Seedless grafted on 110-R rootstock produced more fruitful canes than other rootstocks.

CONCLUSION

Current environmental conditions significantly influence inflorescence initiation, differentiation, and bud fertility, accounting for approximately 60% of total crop yield variation. Temperature, light, and water status significantly impact the physiological function of a vine from budbreak to bloom. A healthy grapevine requires optimal biosynthesis, energy storage, and mineral absorption, especially for bud and inflorescence development. The regulatory mechanisms of bud fruitfulness in response to both exogenous and endogenous factors are not well understood. The application of plant growth regulator promoted inflorescence initiation, differentiation, and development. Both high and low concentrations elicit adverse effects. The stage of bud development influences the adverse effects of PGR. The regulation of bud differentiation is not well understood in terms of PGR and PGR balance. More research is needed to understand the mechanism behind inflorescence initiation and differentiation using a combination of various approaches. Because early yield estimation based on bud fruitfulness is a useful tool for viticulturists.

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