Grapes 101

What Happens from Véraison to Harvest?

By Raquel Kallas & Tim Martinson

Grapes at véraison. Photo by Tim Martinson.

For vines, grapes are a vehicle to spread DNA with so that they may perpetuate the species and colonize new locations. Co-evolution of grapes alongside birds and mammals has resulted in a mutually beneficial exchange. Animals receive a nutritious and delicious fruit snack as 'payment' for dispersing the digestion-resistant seeds within, and the seeds, effectively transported away from the parent vine, are conveniently deposited in fertilizer after passing through animals' guts. Charles Darwin said as much in the *Origin of Species*: "[fruits'] beauty serves merely as a guide to birds and beasts in order that the fruit may be devoured and the manured seeds disseminated."

Véraison heralds the start of the ripening process, which is brought about by the expression and repression of hundreds of thousands of genes. At this time, berries begin their transformation from hard, green, and bitter, with enamel-stripping acidity, to aromatic, sweet, attractively colored, and pleasantly acidic. The development of grapes from fertilized flowers to ripened fruit is a complex physical and chemical process. Here, we will focus on the final stage of development: the transition from véraison to ripeness.

The Three Stages of Berry Growth. The growth rate of a grape berry is the shape of a double sigmoid curve (Figure 1). This curve can be broken down into three stages of growth:

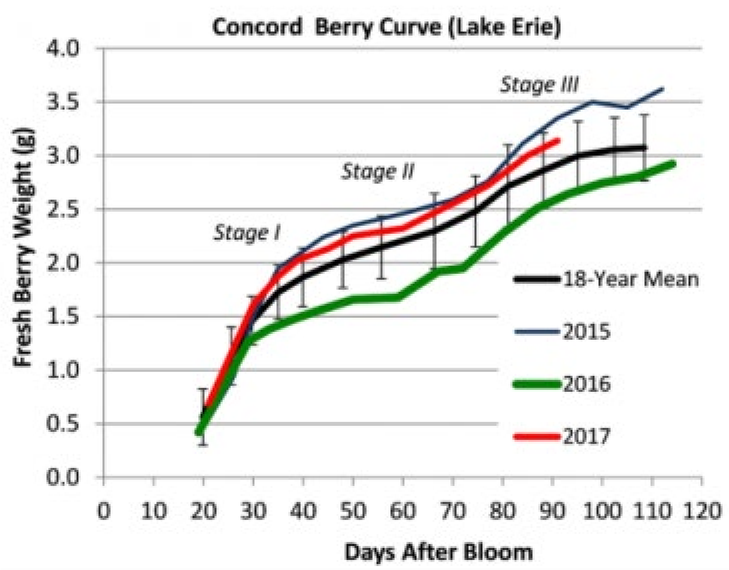

Figure 1. Berry growth curve for Concord grapes, showing the 'double sigmoid' curve encompassing three stages of growth (courtesy of Terry Bates)

- Stage I, or the *cell division phase*, is when the berry undergoes rapid cell division, accumulates acids (primarily tartaric and malic), and ultimately achieves half of its final weight and size.
- Stage II, or the *lag phase* is when berry growth pauses, and the primary focus is on seed growth and chemical signaling to prepare the berry for softening and expansion in the next stage. The duration of the lag phase is variety-specific – varieties with long lag phases tend to be later ripening, while varieties with relatively shorter lag phases ripen earlier.
- Stage III, or *véraison to harvest*, is characterized by cell expansion in the berries and a transition from photosynthetic activity to heterotrophic metabolic activity as the berries change color at véraison.In other words, the berries go from being a partial "source" to a large "sink". This sets the stage for accumulation of sugars, proteins, anthocyanins, tannins, and flavor and aroma compounds, and metabolism of acids and an increase in pH. The entire process is brought about by the expression and repression of hundreds of thousands of genes.The changes during this time heavily influence the final quality and composition of the fruit at harvest.

So *what are the changes that take place during the stage III transition from a green, bitter, acidic, unappetizing marble, to a sweet, soft, palatable, and delicious ripe berry?*

Berries soften and skin becomes elastic. Softening of the pulp is due to disassembly of the mesocarp (pulp) cell walls, so that the walls are loose and able to expand. Positive turgor pressure drops more than tenfold before and during stage III, due to accumulation of sugars and other solutes, resulting in increased softness. Simultaneously, the elasticity of the skin increases in preparation for berry expansion. Additionally, the wax on the skin changes its composition to become more resistant to evaporation.

Berries expand. Expansion is made possible due to the pulp softening and skin elasticity. Berry expansion is primarily driven by imports of water into the mesocarp vacuoles (storage compartments in the cell), which take up the vast majority of space in the cells at this time. Water is the number one player in ripening, and a berry will be 75-80% water by the time of harvest, but less if over-ripened.

Grapes at véraison. Photo by Tim Martinson.

Sugar accumulates. At véraison, xylem flow into the berry drops off, and phloem becomes the primary transport avenue into the berry during stage III. The phloem brings in amino acids (for synthesis of phenolics) and carbon in the form of sucrose into the vacuoles. In most V. *vinifera* cultivars, sucrose is broken down and stored as glucose and fructose, while hybrids and natives retain some sucrose. The sugar accumulated during this time determines the resulting alcohol concentration in the wine.

Acid changes. pH increases and titratable acidity decreases during stage III. Together, tartaric and malic acids account for 90% of the acid in grapes. Tartaric acid is accumulated and synthesized by the berries at the start of stage I and ceases roughly halfway through. There is usually no loss of tartaric acid during stage III, but breakdown can occur at temperatures over 30° C. In contrast, significant quantities of malic acid are metabolized as a source of energy for the berry during stage III, with around 2-3 g/L left by harvest (more or less depending on environment and variety).

Phenolic compounds, including those that cause color change, are formed. Flavonoids, a group of polyphenols in grapes, are largely in flux during the ripening process. Within the flavonoids are 3 classes: flavonols, flavan-3-ols (tannins), and anthocyanins.

- *Flavonols* are found in the skin of grape berries where they act as sunscreen (quercetin is an example, and the most abundant flavonol in white grapes). Flavonol accumulation begins during the first part of the cell division phase (stage I), then generally pauses until after véraison (stage III). Flavonol concentrations are highest a few weeks after véraison.
- *Flavan-3-ols are tannins*, and their concentrations are highest in the seeds followed by the skins, while the pulp has only a small amount. The synthesis of tannins in the skins and seeds finishes during the first few weeks of stage III, and remains constant or decreases slightly until harvest. During this time, the seeds turn brown during due to oxidation of tannins on the seed coat.
- *Anthocyanin synthesis* occurs exclusively during stage III. These red, purple, and blue-pigmented compounds are responsible for the various colors and hues in the skin (and the pulp in the case of teinturier varieties) of red grapes. Color change at véraison occurs due to the simultaneous breakdown of chlorophyll and accumulation of anthocyanins. Variety largely determines the types of anthocyanins present, while environmental factors during stage III influence the quantity. Environmental factors that affect anthocyanin quantities include temperature and light exposure, an increase of both being beneficial until a threshold when they become detrimental. For example, temperatures above 35-37° C have been found to diminish anthocyanin accumulation – this is not typically a concern for growers in the northeast US. White grapes do not produce anthocyanins; their change in color from opaque bright green to various translucent greens, yellows, and golds is due to the breakdown of chlorophyll and exposure of underlying carotenoids.

Flavor and aroma compounds and precursors develop. The saying "good wine is made in the vineyard" undoubtedly has its basis in the development of the flavor and aroma compounds and precursors in the fruit. All else equal, these are arguably the most important players in determining quality and expressing the typicity of a wine. Stage III is a critical time for some compounds, while the presence and abundance of others is not influenced during the ripening period.

- *Monoterpenes accumulate.* Monoterpenes, a group within the larger family of terpenes, are an example of a class of compounds that rapidly accumulate at the end of stage III. Notable monoterpenes that are characteristic of Muscat grape varieties include linalool and geraniol, which contribute coriander seed and rose aromas to the grapes and wines. Both free and glycosylated (bound to a sugar) monoterpenes have been observed to increase a few weeks after véraison, reaching their highest concentrations just as sugar accumulation slows or even past when it stops.

- *Methoxypyrazines decrease***.** Green, herbaceous vegetable aromas in wines are caused by a group of compounds known as methoxypyrazines. It has been repeatedly demonstrated that methoxypyrazines, specifically the aromatically distinctive 2-methoxy-3-isobutylpyrazine (IBMP), accumulate from fruit set to bunch closure (stage I). After véraison, the concentration of IBMP decreases as berry maturity progresses, but the final concentration is correlated with the concentration that was accumulated during stage I. Therefore, IBMP at harvest is predetermined by the amount of light exposure in the fruiting zone during stage I (increased UV exposure decreases IBMP accumulation), and remains unaffected by any management techniques implemented after véraison.

Conclusion. Véraison to harvest is a time of elaborate changes within grape berries, while they become chemically and physically perfected to appeal to mobile seed dispersers like us. Sugar, organic acids, polyphenols, aroma and flavor compounds, and berry size and softness are all in flux during stage III, and all contribute in some way to the final fruit quality and composition.

Literature Cited

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