DOI: https://doi.org/10.20870/oeno-one.2026.60.3.9979

OPEN ACCESS

ENOLOGY REVIEW ARTICLES

Insights into grape seed evolution throughout maturation and its contribution to wine: A comprehensive review

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Article number: 9979

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Associate editor: Fernando Zamora

Received: 16 March 2026

Accepted: 30 July 2026

Published: 9 September 2026

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ABSTRACT

Grape seeds are often less considered in winemaking than grape skins or pulp. Although their role in red wine vinification is well established, grape seeds remain an understudied component of the berry. Seed polyphenolic maturity is often considered an important criterion for determining the optimal harvest date in red winemaking. In practice, however, the actual impact of seed maturity on tannin composition remains debated, particularly when compared with the influence of winemaking practices. Traditionally examined mainly for their flavanols and their contribution to wine astringency and structure, grape seeds in fact contain a much wider diversity of compounds than flavanols or polyphenols, and the contribution of these other constituents to wine quality is still relatively poorly understood. This review examines the development of grape seeds from their formation in the berry to their use in winemaking, from structural evolution to their contribution to wine composition, with a particular focus on often overlooked seed-derived compounds.

KEYWORDS: *Vitis*, grapeberry, grape seed, winemaking, wine

INTRODUCTION

Grape seeds are an important part of the grape, the most cultivated fruit crop globally, with over 77 million tons of grapes produced in 2019, according to FAO. Most of this production is intended for wine production. In red wine production (43 % of total wine production in 2021, according to OIV), grape seeds play a crucial role that will be described in this review. Often disregarded compared with the grape berry (skin, pulp), grape seeds are studied mainly as a source of polyphenols (which explains the focus of scientific studies on these molecules, especially flavanols). Outside of wine production, grapes are consumed directly as table grapes. In this context, the inherently bitter and astringent nature of grape seeds is considered a defect, leading to the selection and breeding of many seedless table grape varieties.

The term grape seed refers to the seeds of fruits in the genus *Vitis,* which encompasses more than 70 species (Wan *et al.*, 2008), each with potentially specific characteristics. Not all of these species are used for winemaking; approximately 10 are involved, either directly or indirectly (*e.g.*, crossbreeds, rootstock). The most studied species is *Vitis vinifera*, which is the most commonly cultivated species. However, other species such as *Vitis lambrusca* (native to North America and a main supplier of rootstock for European vines), *Vitis rotundifolia*, *Vitis riparia*, and *Vitis coignetiae* are locally cultivated (North America, Asia, etc.) and are sometimes fairly well described in the literature. A common challenge is the absence of species mentions in some articles, which cite only the grape variety. Because a variety may derive from a species or a cross, this absence often complicates comparisons between datasets, as species-specific characteristics may be transmitted through crossbreeding. Furthermore, the term "grape seed" is used indiscriminately for seeds from both pomace and those extracted directly from the plant. Seeds from pomace, particularly red or *rosé*, have undergone significant transformation due to alcoholic fermentation and prolonged contact with other berry compartments. White pomace seeds, however, may have only experienced prolonged air exposure. The sample source (berry or pomace) can greatly influence grape seed composition. During winemaking, some compounds are extracted from the seed, while the seed absorbs others from the wine. All these differing parameters will be taken into account throughout this review. This review examines physiological changes in grape seeds from formation to maturity and the molecules of grape seeds across two aspects: their variation during maturation and their role in winemaking. It will also highlight how winemaking practices and viticulture decisions can influence the impact of grape seeds on wine.

1. FROM OVULE TO MATURITY: THE PHYSIOLOGICAL JOURNEY OF GRAPE SEEDS

Grape seed evolution, from formation to the end of maturation, can be divided into two main phases: development and maturation, which correspond to the analogous phases of the whole fruit cycle (illustrated in Figure 1).

There are numerous names in the literature for the different layers of grape seeds. To maintain consistency and avoid confusion in this review, we will adopt the nomenclature proposed by Cadot *et al*. (2006) as illustrated in Figure 2.

The formation of a viable grape seed is induced by fertilisation of the ovule. However, apomixis (development of viable seeds in the absence of fertilisation) has been observed in *Vitis vinifera* (Costantini *et al*., 2021; Negrul, 1934). This observation may be supported by the presence of the APOLLO gene in *Vitis vinifera*, which has been linked to apomixis (Corral *et al*., 2013).

1.1. Formation of the seed and the rapid development of the seed coat

If at least one seed develops completely within the berry, the berry will develop normally, even if other ovules have produced aborted, empty seeds (lacking endosperm, referred to as "floaters" because they float in water (Ebadi *et al*., 1996)) or no seeds at all. This explains variability in the number of seeds per berry, and this number directly influences berry size. Indeed, a greater number of developed seeds correlates with a greater berry mass (Cawthon & Morris, 1982; Ribéreau-Gayon *et al*., 2012).

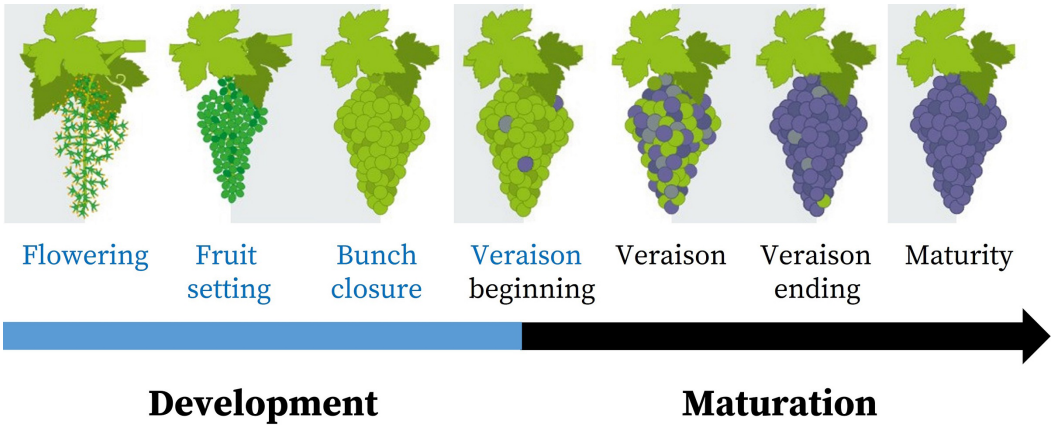

FIGURE 1. Grape cycle from formation to the end of maturation. *Modified from BASF technical documentation.*

Finally, it is possible to obtain grape berries without seeds. So-called "seedless" varieties fall into two categories: (i) berries of normal size that contain seeds, but these seeds have developed abnormally, resulting in a soft or small structure (*e.g.*, Sultanina, Thompson Seedless) or (ii) small berries that contain no seeds and are produced via parthenocarpy (*e.g.*, Corinth) (Stout, 1936). Parthenocarpy can also be induced by applying gibberellins to varieties that typically develop seeds, resulting in berries with aborted seeds (Pratt & Shaulis, 1961) due to the degeneration of the embryo sacs (Watanabe, 1963). These seedless varieties are highly sought after for table grape cultivation (where the seeds are a defect), explaining the recent increase in studies on seedless grapes and the mechanisms associated with parthenocarpy in *Vitis* (Bai *et al*., 2022; Cui *et al*., 2024; Li *et al*., 2024).

Following fertilisation, intense meristematic activity localised in the chalaza, near the raphe, and in certain parts of the outer tegument drives significant structural changes in the seed. This process transforms the ovule's ellipsoidal shape into a mature seed, which possesses a structure highly characteristic of the Vitaceae family. The development and mature structure of the seed coat are relatively similar across the genera *Ampelocissus, Cayratia, Cissus, Leea, Tetrastigma,* and *Vitis*, all members of the Vitaceae family, with variations mainly observed in seed shape (Figure 3), the number of invaginations (Figure 3), and seed coat thickness (Periasamy, 1962).

Focusing solely on the seed of *Vitis vinifera*, strong meristematic activity localised in the funicle, chalaza, raphe, and outer seed coat modulates its final structure.

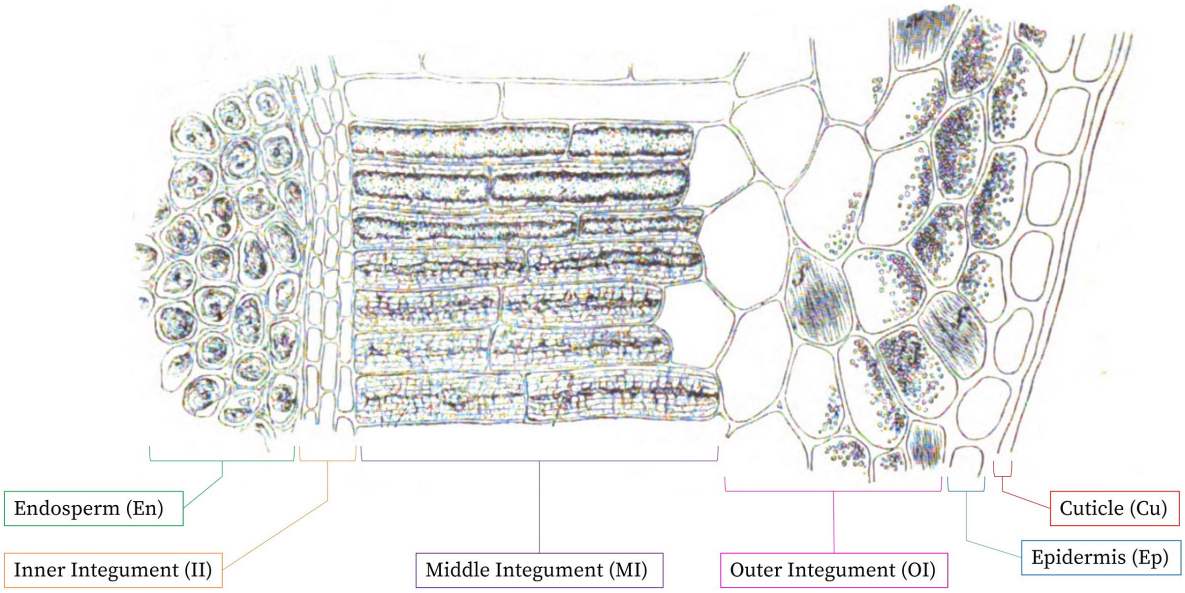

FIGURE 2. Mature grape seed structure separated into six layers from exterior to interior of the seed: cuticle, epidermis, outer integument, middle integument, inner integument, and endosperm. *Modified from Portele (Portele, 1883).*

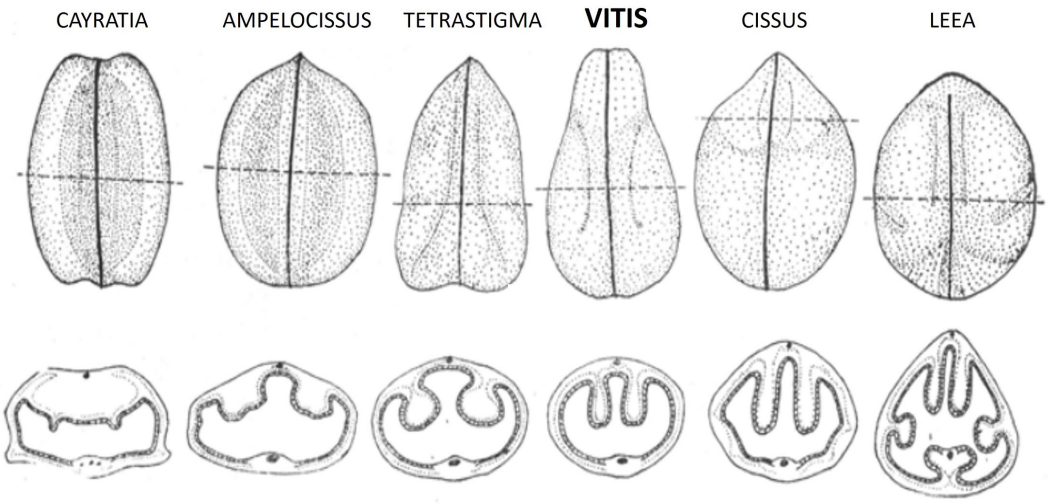

FIGURE 3. Representation of the structure of mature seeds in different genera of the Vitaceae. The top row represents the ventral view of the mature seed, and the bottom row represents the transversal cut (along the broken line in the top row) of the mature seed. *Modified from Periasamy (Periasamy, 1962).*

These structural changes occur quite early in development. For instance, there is a peak of mitosis in the outer tegument (ovule) at 20–25 Days After Flowering (DAF), with an absence of cell division from 45 DAF onwards. This period also corresponds to the moment when the location of the chalaza changes from the tip of the seed (Figure 4.1) to its dorsal side (Figure 4.2), effectively increasing the size of the basal end (formerly the chalazal end) of the seed.

The significant growth of the outer tegument will have several consequences. First, there is an overall increase in its thickness, alongside more localised changes. These include the elongation and thickening of the outer integument at the embryonic end, which forms the seed beak (Figure 4.2B). On either side of the raphe and opposite the chalaza (opposite its transverse limits), the middle integument will form fossettes (Figure 4.2A) by invagination into the nucellus. The middle integument is thickest at the beak and thinnest at the dimples, and its cells undergo lignification (formation of the hard layer). This lignification process is directly related to the seed's hardness, which changes from soft (no lignification) at fruit set to hard (lignified cells) during veraison (Cadot *et al*., 2006; Letaief *et al*., 2013; Ristic & Iland, 2005). The inner integument initially follows the growth of the nucellus, maintaining three well-defined cell layers. Subsequently, as the nucellus is replaced by the endosperm, the central layer of the inner tegument becomes crushed (Cadot *et al*., 2006; Periasamy, 1962). The final, mature structure of the seed is attained around veraison and does not change during the subsequent ripening process.

1.2. The lignin lock-down: hardness as a misleading marker of final ripeness

Among the structural changes that occur in grape seeds during development and ripening, the change in hardness is empirically observable and directly measurable. Despite this, only a few articles have been published on the subject, some comparing different grape varieties at maturity (Letaief *et al*., 2008; Verma *et al*., 2014) and others focusing on its evolution during ripening (Letaief *et al*., 2013; Yim *et al*., 2020). In the article published by Verma *et al*. 2014, the compared grape varieties were classified into three categories based on seed development (seeded, soft-seeded, and seedless). The objective of this study was to confirm whether hardness could be a useful criterion for breeding programs aimed at obtaining seedless varieties. The article highlights significant variations in hardness depending on the grape variety, with generally lower hardness levels for soft-seeded and seedless varieties. However, some seedless varieties exhibited higher hardness values than seeded varieties. Furthermore, the categorisation of varieties could be questionable (*e.g.*, grape seed average mass of 33.6 mg in seedless varieties and 14.9 mg in seeded varieties), making it difficult to draw firm conclusions on the potential use of hardness as a variety selection criterion. Letaief *et al*. (2008) compared seven Italian red grape varieties over two vintages, using three measures of hardness (break force, break energy, and stiffness). This work highlighted considerable variability between different grape varieties and between vintages for the same varieties regarding seed hardness. This variability suggests that selecting grape varieties based on this single parameter would be challenging, as the vintage greatly influences the hardness value.

The other two articles examine the evolution of seed hardness during ripening. Letaief *et al*. (2013) aimed to determine the potential of hardness as a marker of seed ripeness. This study demonstrates that hardness increases, following a logarithmic curve across both vintages tested. However, since the changes in hardness occur mainly during veraison, and the difference in hardness tends to be limited around the grape harvest date, the utility of hardness as a commercial maturity marker is greatly restricted. The second article (Yim *et al*., 2020) also shows an increase in hardness with ripening and demonstrated a link between this increase and a higher amount of lignin in the seed, along with a higher expression of the gene related to lignin biosynthesis. This link between

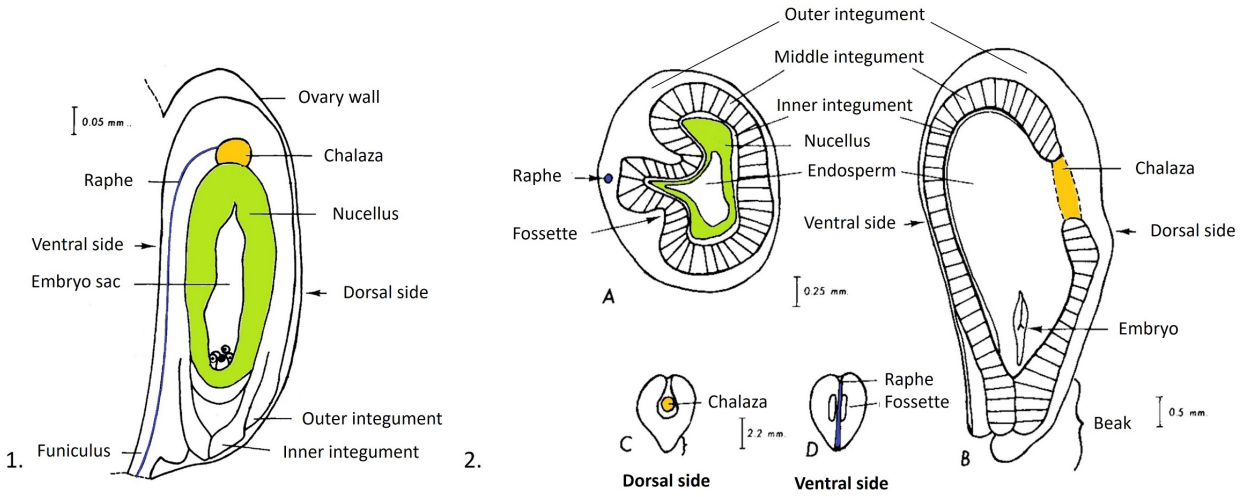

FIGURE 4. 1. Diagram of the longitudinal section of an anatropous ovule of 'Concord' grape at bloom. 2. Grape seeds. (A) Transverse section of seed above the level of the embryo about 4 weeks after pollination. (B) Longitudinal section of a mature 'Concord' seed. (C, D) Surface view of 'Concord' seeds. *Modified from (Pratt, 1971).*

seed hardness and lignin was also supported by microscopic observations (Cadot *et al*., 2006) and the significant amount of lignin in the seed (44 %) (Moldes *et al*., 2003). Changes in seed hardness are still poorly understood, and many questions remain, particularly regarding the understanding of lignification processes in seeds.

1.3. The browning enigma: chlorophyll loss, oxidation, and the quest for a perfect brown

Another physical change that grape seeds undergo during ripening is a change in colour. Simply put, the grape seed is green at bunch closure and evolves toward a brown colour during maturation. In viticulture, the grape seeds' colour is commonly used as an empirical indicator of ripeness (Ristic & Iland, 2005). However, the underlying mechanisms for this colour change are not yet fully understood. Two hypotheses, likely complementary, exist to explain these colour changes. (i) The oxidation of flavanols (Kennedy *et al*., 2000a), which will be detailed in the section dedicated to flavanols; and (ii) a colour change directly due to lignin (Cadot *et al*., 2006). Most studies on seed flavanols have focused on their oxidation, which has been extensively explored, but so far, no analysis has established a causal link between flavanol oxidation and seed colour change. The hypothesis regarding lignin has received less attention and warrants further investigation.

Furthermore, the use of colour as a maturity criterion has its limitations. Visual inspection is problematic due to a strong user bias. Additionally, near maturity, the seed is brown, and small changes in this colour are difficult for the human eye to perceive. Another challenge is the non-uniformity of the seed's colour across its surface, with significant differences between the dorsal and ventral parts of the seed (Fredes *et al*., 2017). This study also highlighted the importance of the green colour in seed maturity, noting that the brown colour appears well before harvest maturity (Fredes *et al*., 2017; Fredes & Mora, 2017; Ristic & Iland, 2005) and the disappearance of green on certain parts of the seed seems to correlate fairly well with maturity. Some authors empirically associate this green colour with very astringent flavanols (Rousseau & Delteil, 2000), though no correlation has been established. Moreover, with climate change, traces of green are becoming increasingly common on ripe seeds.

There is currently no definitive analysis explaining the disappearance of this green colour, but it is likely due to the degradation of chlorophyll in the seed. Chlorophyll presence was confirmed before veraison (Breia *et al*., 2013), and its degradation products could also contribute to browning (Heaton & Marangoni, 1996). Another challenge with colour scales is the grape variety, as significant differences in seed appearance exist depending on the variety (Bonhomme *et al*., 2021; Elagamey *et al*., 2013). It is difficult to ignore these varietal colour differences (*e.g*., Syrah seeds are yellow at certain stages of maturity, a colour not observed in Merlot seeds). To minimise these biases, colorimetric approaches using scanners have been tested on seeds (Ferrer-Gallego *et al*., 2010; Rabot, 2017; Rodríguez-Pulido *et al*., 2012; Rodríguez-Pulido *et al*., 2022; Zuñiga *et al*., 2014). These approaches have shown that while colour variation during ripening correlates with variation in flavanol concentration, this correlation holds true only for the period from grape closure to the end of veraison. Due to the stabilisation of browning as maturity approaches (Fredes *et al*., 2017; Rodríguez-Pulido *et al*., 2012), using grape seed browning as the sole indicator of maturity does not appear to be the most appropriate approach.

This should be applied in practical viticulture, particularly in determining the harvest date, which is often delayed when grape seeds are not considered to have reached a certain level of colour maturity (complete browning).

2. OENOLOGICAL SIGNIFICANCE: FLAVANOL DYNAMICS AND WINE IMPACT

Given the significant proportion of viticulture dedicated to wine (the rest being dedicated to table grapes, with several seedless varieties), most analyses conducted on grape seeds are performed on samples harvested at oenological maturity. The strong link between grape seeds and wine also influences the nature of the compounds studied in seeds. For example, there is an abundance of resources on the seed flavanols, as flavanols from seeds account for approximately 50 % of the total grape-derived tannins in red wine. This important link is reflected in numerous articles on known seed compounds found in wine (flavanols), but more limited resources on other molecular families whose oenological interest is less obvious or has not yet been demonstrated. In this second part, we will focus on grape seed molecules with potential oenological interest, examining both flavanols and other seed molecules that may have an oenological impact.

2.1. Tannin tension: declining content, stable profile, and the dominance of extraction

The most studied family of molecules in grape seeds is the flavanol family (flavan-3-ols), specifically flavan-3-ol monomers (catechin, epicatechin, epigallocatechin, and epicatechin-3-O-gallate), as well as their oligomers and polymers called proanthocyanidins or condensed tannins.

Seed flavanols are often referred to as tannins, which is a misleading term. In oenology, the term "tannin" is frequently used in a broader sense. It encompasses both grape-derived proanthocyanidins and other classes of tannins, such as hydrolysable tannins (*e.g.*, ellagitannins and gallotannins) from various botanical origins. These hydrolysable tannins may be present in wine as a result of oak barrel ageing or through the addition of commercial oenological tannins derived from non-grape sources, such as oak, chestnut, or nut gall.

Flavanols can be categorised by their degree of polymerisation (DP): monomers (DP 1), oligomers (DP 2-7, often called proanthocyanidins or PAs), and polymers (DP > 7). In seeds and, by extension, wine, the quantity of monomers is much lower than that of PA's (Rousserie *et al*., 2020).

Flavanol glucosides are typically considered a separate category rather than being classified solely by the number of flavan-3-ol monomer units. Extensive review articles already cover seed flavanols (Padilla-González *et al*., 2022; Rousserie *et al*., 2019; Unusan, 2020), including pharmaceutical properties and/or synthesis mechanisms. Therefore, this review will focus mainly on their chemical nature, evolution during ripening, and impact on wine.

2.1.1 Principal flavan-3-ol monomers

There are three main flavan-3-ol monomers in grape seeds: catechin, epicatechin, and epicatechin-3-O-gallate. More precisely, these are (+) catechin and (-) epicatechin, which are epimers. The (+) and (-) signs refer to the enantiomeric forms found in the seeds (Figure 5). It has already been established that the seeds contain only these two forms (Rockenbach *et al*., 2012), which are also the two forms most commonly found in nature (Aron & Kennedy, 2008). Because it is difficult to differentiate between enantiomers, most articles mentioning flavan-3-ol monomers do not specify the enantiomer's nature, but it can be inferred that they will always be (+) catechin and (-) epicatechin. The same applies to the galloylated form (gallic acid) of epicatechin, which will always be (-) epicatechin-3-O-gallate. Catechin and epicatechin monomers can also be found in grape skin but in much lower proportion than in seed (Chira *et al*., 2009).

2.1.2 Other flavan-3-ol monomers

Other flavan-3-ol monomers are present in the seed but in much smaller proportions and are therefore much less well characterised.

One such monomer, epigallocatechin (EGC), is mainly found in the skin but is occasionally reported in the seed (Kim *et al*., 2006; Popov *et al*., 2017; Sica *et al*., 2018). Many authors attribute the presence of EGC to poor separation of the seed from the skin (Mattivi *et al*., 2009; Santos-Buelga *et al*., 1995; Unusan, 2020). Even without suggesting sample preparation errors, as mentioned in the introduction, the lack of information on the origin of the seeds is a problem in two of the three articles that reported EGC, which were carried out on commercial seed extracts (Sica *et al*., 2018) and commercial seeds (Kim *et al*., 2006). Since the seeds used were recovered after vinification, and they had prolonged contact with the skin, this could explain the presence of EGC in seeds. In the case of Popov (Popov *et al*., 2017), the seeds do not appear to come from pomace, and while it is possible that small amounts of EGC are present in the seed, the quantities reported in the article were higher than those of epicatechin-3-O-gallate in two vintages and 36 grape varieties, including some extensively studied like Pinot noir.

However, other studies have not found EGC (Fuleki & Ricardo da Silva, 1997; Harbertson *et al*., 2002; Mattivi *et al*., 2009) in the seeds of this same grape variety (Mattivi *et al*., 2009) and even quantified EGC in the skin of this grape variety using the same HPLC method, making it unlikely they would have missed it in the seeds. In light of these results, the data obtained by Popov (Popov *et al*., 2017) can be questioned, and it can be concluded that seeds (before vinification) contain little to no EGC.

Another flavan-3-ol monomer found in grape seeds is epicatechin vanillate, which was recently discovered in grape seeds and certain red wines (Ma *et al*., 2018). Epicatechin vanillate was identified in Merlot and Cabernet seeds but not in red wines from the Bordeaux vineyards. However, it was found in red wines from China's Ningxia region. As this compound has only been described in a single article, many questions remain unanswered, such as its sensory impact, the conditions under which it is extracted (since it is not systematically found in wine), and its possible presence in flavanol oligomers or polymers. Other flavan-3-ol monomers likely exist in the seed but have not yet been identified.

2.1.3 Oligomers and polymers

Proanthocyanidins (PAs) are molecules formed from multiple flavan-3-ol monomer units. They are named according to their degree of polymerisation (DP): dimers, trimers, tetramers, pentamers, etc., and the presence or absence of epicatechin-3-O-gallate units (galloylated or not). In grape

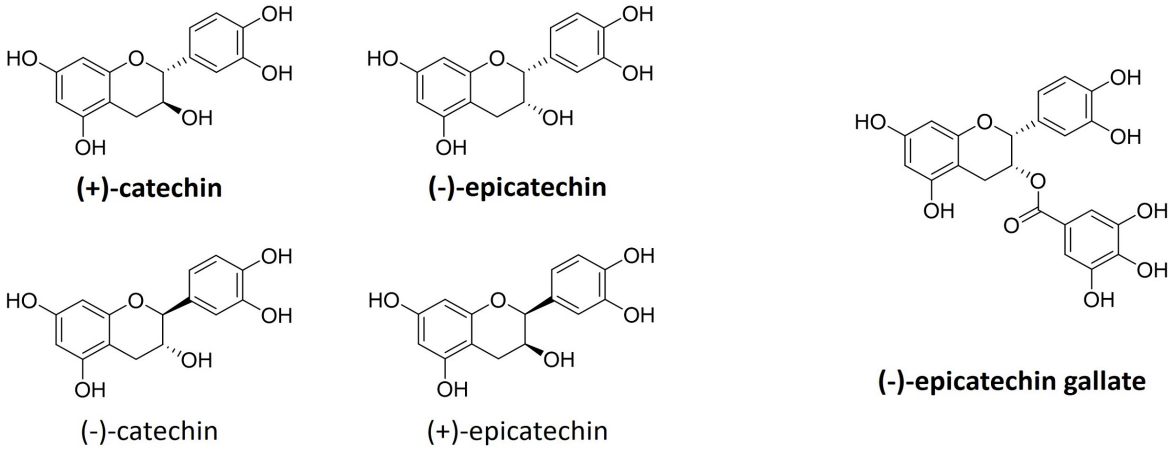

FIGURE 5. Epimers, enantiomers, and galloylated form of catechin. The one named in bold corresponds to the monomer most found in grapeseed.

seeds, the largest formally confirmed proanthocyanidins are heptamers, which have been found in grape seed extract (Gabetta *et al*., 2000). Among the PAs, 17 dimers, 16 trimers, and 1 tetramer have been formally identified, with many others not yet fully resolved (Padilla-González *et al*., 2022). These numbers do not include proanthocyanidin glucosides, which are considered separately. To analyse the proanthocyanidins in the seed, three main options exist:

- a. Direct analysis: Using separation techniques or specific polymer analysis techniques (Gabetta *et al*., 2000; Rockenbach *et al*., 2012), which provide information on the size of the polymers but only partial information on the constituent units.
- b. Depolymerisation: Techniques such as thiolysis (Rigaud *et al*., 1991) or phloroglucinolysis (Kennedy & Jones, 2001) result in the loss of precise information on the PA size, but provide more information on the nature of the constituent units and, partially, their position in the polymer (elongation or terminal unit). Calculating the mean degree of polymerisation (mDP) provides information on the overall degree of polymerisation of the sample. Depolymerisation also allows for the determination of the percentage of galloylation (%G), which is the percentage of epicatechin-3-O-gallate in the proanthocyanidins. mDP and %G are commonly used to describe proanthocyanidin structure (Chira *et al*., 2009).
- c. Spectrophotometric approaches include, for example, the Bate-Smith method, based on acid-catalysed heating of wine samples.

Other methods often determine tannin content (*e.g.*, methylcellulose precipitation assay) or total polyphenols (*e.g.*, spectrophotometric measurement at 280 nm), but these methods are not specific to proanthocyanidins.

Proanthocyanidins are also present in grape skins. Although seed and skin proanthocyanidins belong to the same molecular family, several differences exist between them. The most reliable comparison is obtained from studies analysing both tissues sampled at the same place and time. The mDP tends to be higher in skins (up to 48.8) than in seeds (up to 8.8), and %G is generally lower in skins than in seeds (Chira *et al*., 2009). Although these trends are consistently observed across varieties, vintages, and plots, proanthocyanidins exhibit substantial variability, which will be discussed in detail in the following section.

2.1.4 Maturation and variability

The ratio between flavan-3-ol monomers and different PAs is highly variable and depends on many factors, such as grape variety, climatic conditions, and vintage (Chira *et al*., 2009; Santos-Buelga *et al*., 1995). For instance, total monomer quantity in Merlot seeds from the same Bordeaux vineyard varied significantly between vintages: 12 mg/g in 2006 and 24 mg/g in 2007. There is also significant variability between plots (from 6 mg/g of seeds to 17 mg/g of seeds in 2006) and depending on the grape variety (Cabernet-Sauvignon: 14 mg/g seeds in 2006 and 28 mg/g seeds in 2007). The vintage-dependent variations tend to be more marked than variety-dependent ones, and importantly, they often follow the same trend (monomer quantities doubled between 2006 and 2007 for both varieties) (Chira *et al*., 2009).

The mechanisms behind these differences are not yet fully understood, and it is difficult to confirm observed trends without experiments that control for all parameters. Such experiments are challenging to set up, particularly when controlling for meteorological factors (sunshine, temperature, etc.) (Gouot *et al*., 2019). Nevertheless, some conclusions can be drawn. For example, irrigation (if applied during development) increases the flavanol concentration in the seed (Casassa *et al*., 2016; Chorti *et al*., 2016). Another crucial factor is the species. While all species of the genus *Vitis* are referred to as vines, significant differences exist between species in terms of seed flavanol composition (Liang *et al*., 2012), which may also explain some of the differences between grape varieties.

When looking at varietal differences, Pinot noir is known for having a high flavanol content (Fuleki & Ricardo da Silva, 1997; Mattivi *et al*., 2009) and was the grape variety with the highest polyphenol content in a study of 91 grape varieties from 17 different *Vitis* species (Liang *et al*., 2012). Some varieties exhibit a great seed flavanol variation depending on the vintage, while others do not (Núñez *et al*., 2006). At present, no clear differences have been established between white and red grape varieties. Although not all parameters influencing flavanols in grape seeds are known, their importance in the wine industry has allowed for the accumulation of extensive data, establishing the effects of certain cultural practices and genetic differences.

The evolution of flavanol quantities during development and maturation has been extensively studied, as controlling the tannin profile of a wine is a major objective in red wine production. Most studies observed an increase in the quantity of flavanols until veraison, followed by a sharp decline, and then a more moderate decline or a stabilisation until maturity (De Freitas *et al*., 2000; Kennedy *et al*., 2000a; Kennedy *et al*., 2000b; Rousserie, 2019).

The reasons for this decline in concentration are not yet fully characterised, but many studies have addressed the subject: (i) there is a halt or sharp decrease in monomer production, reflected in the observed decline in the expression of genes linked to their formation (Bogs *et al*., 2005; Bogs *et al*., 2006; Bogs *et al*., 2007; Rousserie *et al*., 2019). However, since there is also a (less pronounced) decrease in PAs concentration, the decrease in monomer is not solely related to polymerisation reactions. (ii) On the other hand, a frequently proposed hypothesis is the oxidation of these molecules (Kennedy *et al*., 2000a; Kennedy *et al*., 2000b), which was measured by Kennedy (Kennedy *et al*., 2000b) using electron paramagnetic resonance (EPR). However, this technique only measures the difference in the presence of radicals (ROS, NOS) (Kohno, 2010) and is not specific to radicals potentially formed by proanthocyanidins. In addition, Kennedy's analysis was performed on the solid part

of the seed (after rapid delipidification), and this difference in signal could be partially explained by mechanisms related to lignin formation (Denness *et al*., 2011; Wang *et al*., 2021), given that the changes observed in EPR correlate fairly well with the increase in seed hardness.

Therefore, currently, no studies exist that directly compare the appearance of oxidised proanthocyanidins during ripening with the general evolution of flavanols. This makes it difficult to determine whether oxidation alone is responsible for these changes or if other mechanisms are at work. Such a study would be necessary given the significant variations in flavanol quantities and distribution depending on the conditions described above. Nevertheless, the study of flavanol oxidation remains complex because several reactions are likely to take place. Kennedy (Kennedy *et al*., 2000a), for example, mention several forms of oxidation: oxidation into oligomers and oxidized polymers, which are currently the most studied forms of oxidation (De Freitas *et al*., 2000; Deshaies *et al*., 2022; Guyot *et al*., 1996; Leontieş *et al*., 2017) but remain only partially characterized; Oxidation with carbohydrates (glucides), which is supported by an increase in flavanol glucosides during ripening (Zerbib *et al*., 2018b; Zerbib *et al*., 2018c) or oxidation with proteins, an hypothesis that has not yet been verified in grape seeds although protein-flavanols interactions are known to exist (Watrelot & Norton, 2020).

Although not all the mechanisms behind the decrease in flavanol content during ripening are known, this remains an important indicator of grape seed maturity and is widely used in the wine industry. However, the use of this criterion to assess seed maturity may be questioned, as flavanol levels tend to stabilise in the seed around the time of harvest (Kennedy *et al*., 2000a; Rousserie *et al.,* 2020).

2.1.5 Extractability and impact on wine

Unlike the skin, whose percentage of the berry's mass varies little depending on the vintage or *terroir*, the mass of seeds per berry exhibits high variability influenced by these factors. Seed mass is determined by both the number of seeds per berry and the average weight of individual seeds, both of which are highly variable parameters (Daulta & Chauhan, 1984; Hardie & Aggenbach, 1996; Sabir, 2014). The proportion of grape seed in the must will greatly influence the quantity of seed flavanols found in wine. To better characterise the seed's contribution to wine flavanols, several studies have carried out micro-vinification with and without seeds (Bautista-Ortín *et al*., 2014; Gombau *et al*., 2020; Rousserie *et al*., 2020), in addition to another study using seed addition (Pascual *et al*., 2016). All have confirmed the importance of the seed's contribution to wine flavanols. Most of the flavanols in wine come from the seeds (around 50–60 %). Even if it is well established that flavanols from skins are extracted earlier and more rapidly than those from seeds, the ratio between flavanols from the skin and the seed (89:11) (Kennedy, 2008) means that the seeds remain an important contributor to the grape-derived tannic component of red wines.

Moreover, the flavanols in the seed and skin are different, with larger proanthocyanidins found in the skin and a higher proportion of monomers in the seed. It is therefore possible to influence the wine's tannic profile by controlling the extraction of flavanols from the seed and the skin (which differ, with a preference for skin-derived PAs in young wines and more seed-derived PAs in ageing wines (Kennedy, 2008)). Since a large proportion of skin flavanols are extracted relatively easily during vinification, it is often easier to limit or increase the extraction of seed flavanols to achieve the desired tannic balance. Numerous parameters influence the extractability of compounds, some of which are difficult or impossible to modify through oenological practices, such as the size of the molecules, their location in the seed, or their interactions with must solids (Bindon *et al*., 2017). But others can be controlled by the winemaker and influence the seed flavanols extraction. For example, the progressive formation of ethanol during alcoholic fermentation plays a key role in modulating this process. Increasing ethanol concentrations enhance the permeability of seed tissues, facilitating the extraction of flavanol compounds from seeds during the later stages of fermentation. Flavanol extraction can be further increased through post-fermentation maceration. Ethanol concentration is not the only parameter influencing flavanol extraction; a brief overview of these factors and the associated winemaking techniques are presented in Table 1.

Other winemaking practices, such as pulsed electric fields or ultrasound (López *et al*., 2008; Boussetta *et al*., 2013), can also influence flavanol extraction; however, their effect on seeds have not yet been studied. Seed flavanols are primarily recognised for two organoleptic properties: bitterness and

TABLE 1. Different parameters and techniques to influence seed flavanols extraction during winemaking.

Parameters	Techniques	References
Temperature	Cold maceration	(Busse-Valverde *et al.*, 2010, Busse-Valverde *et al.*, 2011)
	Hot maceration	(Orbanić *et al.*, 2023)
Degree of crushing	Crushing	(Cerpa-Calderón & Kennedy, 2008)
Tissue permeability	Enzymes	(Bautista-Ortín *et al.*, 2013; Castro-López *et al.*, 2016)
Solid/liquid phase ratio	Bleeding	(Orbanić *et al.*, 2023)
Quantities of seed	Seed removal	(Bautista-Ortín *et al.*, 2014; Canals *et al.*, 2008; Jagatić Korenika *et al.*, 2023; Lee *et al.*, 2008)
Maceration duration and timing	Pre- or post-fermentation maceration	(Casassa *et al.*, 2016; Hernández-Jiménez *et al.*, 2012; Lisov *et al.*, 2023; Ruiz-Rodríguez *et al.*, 2021)

astringency. Flavanol astringency is primarily attributed to their interaction with salivary proteins, whereas their bitterness is linked to the activation of various bitter taste receptors. Both the bitterness and astringency of flavanols are known to be influenced by their size and composition. For example, it is well established that the percentage of galloylation of seed proanthocyanidins (*i.e.*, the proportion of (−)-epicatechin-3-O-gallate units) can increase the perception of astringency, while proanthocyanidins with a lower mean degree of polymerization (mDP), as well as flavan-3-ol monomers, are more strongly associated with bitterness perception (Ma *et al*., 2014; Ma *et al*., 2016; Soares *et al*., 2017; Watrelot & Norton, 2020). Beyond their sensory impact, seed flavanols contribute to wine colour stabilisation through interaction with anthocyanins, either by forming new pigments (Ma *et al*., 2014; Zeng, 2015) or through copigmentation, with epicatechin being a more effective copigment than catechin (Freitas *et al*., 2017), and flavan-3-ol monomers being more effective than dimers (Guo *et al*., 2026). After extraction, the evolution of proanthocyanidins is complex: new compounds such as crown proanthocyanidin can form (Zeng *et al*., 2019), but overall, proanthocyanidin levels tend to decrease during wine ageing (Chira *et al*., 2012). Furthermore, a less-known but equally important role from an oenological perspective is the impact of flavanols on aroma release (Gabler *et al*., 2024; Lorrain *et al*., 2013; Muñoz González *et al*., 2021). Specifically, a reduction in the perception of certain aromas has been observed in the presence of flavanols (Muñoz González *et al*., 2021). While the exact mechanisms of interaction between these compounds are not yet fully defined, their existence has been proven. One common oenological input, seed tannins (flavanols extracted from the seed), can be used in wine-making. They are typically added during the ageing phase given their relatively high cost compared to quebracho-type tannins (proanthocyanidins), which are preferred during vinification. They are valued for their colour-stabilising properties or for reinforcing the tannic structure of a wine.

2.2. Flavanol glycosides: A new class of flavanols

In 2012, a new class of flavanols, flavanol glycosides, were found in grape seed and wine. These molecules will be classified and described in the subsequent paragraphs. We differentiate the various flavanol glycosides by grouping them into families based on the number of flavan-3-ol monomer units (monomer, dimer, etc.) and the number of glucose units (monoglycosides, diglycosides, etc.) that compose them. Flavanol glycosides can thus be divided into four main categories. Two correspond to flavan-3-ol monomers that differ in the number of glucose units: monoglycosides (MMGs) and diglycosides (MDGs). The other two correspond to flavan-3-ol dimers, also differing in the number of glucose units: dimer monoglycosides (DMGs), dimer diglycosides (DDGs). Other potential polymers with either more than three glucose units or more than three flavan-3-ol monomer units have not yet been described but might exist.

2.2.1 MMGs

Several MMGs have been found in grape seeds and wine (Delcambre & Saucier, 2012; Pérez-Navarro *et al*., 2019a; Zerbib *et al*., 2018c), making them the most thoroughly characterised family of flavanol glycosides. Their evolution was studied during ripening in Merlot seeds and skin. A significant increase in monoglycoside monomers in seeds was observed during ripening (Zerbib *et al*., 2018b; Zerbib *et al*., 2018c), suggesting these molecules could be a potential marker of seed ripeness. Some of these monomers are also found in the wine from this grape variety. Notably, all the mono-glucoside monomers were found exclusively in the seed and were absent from the skin at harvest (with only trace amounts observed earlier during ripening). Only two molecules (monoglycoside monomers) had their structure fully resolved by NMR, (+)-catechin-4′-O-β-glucoside (Figure 6A) and (+)-catechin-7-O-β-glucoside (Figure 6B).

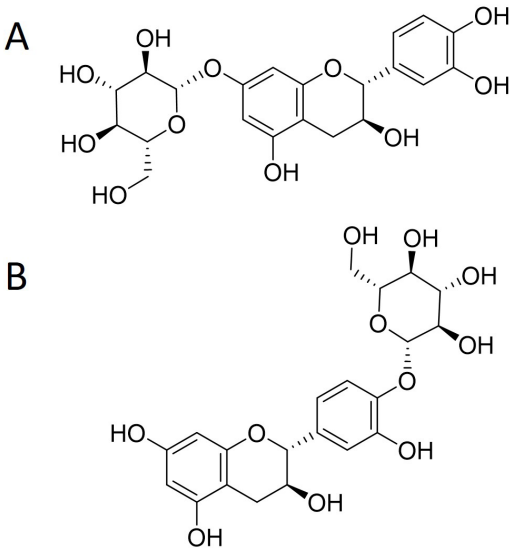

FIGURE 6. A. (+)-catechin-7-O-β-glucoside. B. (+)-catechin-4′-O-β-glucoside.

The remaining MMGs have been only partially identified via their fragmentation spectra and are therefore not fully characterised. The presence of epigallocatechin glucosides in the seed has been highlighted in two articles (Delcambre & Saucier, 2012; Pérez-Navarro *et al*., 2019a); however, another study (Zerbib *et al*., 2018c) specifically investigated these molecules and did not detect them. Given that the quantity of epigallocatechin in the seed is very low, or even zero, and considering that the balance between different flavan-3-ol monomers is highly dependent on climate, vintage, plot, and grape variety, drawing a firm conclusion about the presence or absence of these molecules remains difficult. Further analysis, specifically structural resolution (NMR), is required to confirm their existence.

Several isomers of epicatechin-3-O-gallate monoglucoside have also been found in the seed (Delcambre & Saucier, 2012; Pérez-Navarro *et al*., 2019a), which is unsurprising given the concentration of epicatechin-3-O-gallate in the seed. However, their structure remains only partially resolved, as these molecules have solely been studied by mass spectrometry. It is therefore possible that some of these isomers are actually a catechin where a gallic acid glucoside has substituted for an OH, which is plausible since the presence of gallic acid glucoside in the seed has been confirmed (Cretin *et al*. 2019). As for epigallocatechin monoglycoside, current mass spectrometry studies should be complemented by structural resolution using NMR to draw clear conclusions.

2.2.2 Other flavanol glycosides

Although MMGs are the most widely studied flavanol glycosides, the family of flavanol glycosides found in grape seeds is much more diverse. Almost all of the flavanol glycosides discovered to date are either present in both the seed and the skin, or only in the seed (Zerbib *et al*., 2018b). DMGs are found in both tissues, and their evolution during ripening is much less pronounced than that of monomers (Zerbib *et al*., 2018c). However, certain isomers appear to be specific to the seed. MDGs are also found in both seeds and skins, but mainly in seeds according to Pérez-Navarro (Pérez-Navarro *et al*., 2019a) or exclusively in seeds according to Zerbib (Zerbib *et al*., 2018b). While their evolution during ripening has been assessed, no clear trends emerged from the analysis (Zerbib *et al*., 2018b). Regarding DDGs, only four isomers have been discovered to date (three specific to grape seed and a fourth observed in wine). However, given the discovery of 12 DMG isomers (Zerbib *et al*., 2018a), many others are likely to exist. Overall, the majority of flavanol glycosides are found in the seed, and numerous isomers (mainly due to the different positions that hexose can occupy) exist. Since these molecules were only recently identified in seeds and wine (Delcambre & Saucier, 2012), they remain relatively unknown regarding their formation mechanisms in the berry, their diversity (especially the potential epicatechin-3-O-gallate glycoside, which has yet to be studied) and their role in wine.

2.2.3 Maturation and variability

Although flavanol glycosides remain relatively understudied in grapes, some information is available regarding their variability among varieties and their evolution during maturation (Zerbib *et al*., 2018b; Zerbib *et al*., 2018c). Concerning varietal variability, only red grape varieties have been investigated (Tannat, Merlot, Syrah), and differences have been observed. The concentration of flavanol glycosides varies depending on variety, and this variation depends on the specific class of flavanol glycoside. For example, at maturity, Merlot seeds contain more DMGs than Tannat and Syrah seeds but fewer MMGs than Tannat seeds, indicating that the balance among flavanol glycoside types can differ between varieties within the same vintage (Zerbib *et al*., 2018b). Regarding their evolution during maturation, conclusions remain difficult, particularly due to a strong vintage effect. In Merlot, the most studied variety, the 2015 vintage showed a marked increase in MMGs and relative stability in DMGs during maturation (Zerbib *et al*., 2018c). In contrast, for the same variety in 2017 (considering the same period from late July to maturity), a slight increase in MMGs and a marked increase in DMGs were observed (Zerbib *et al*., 2018b). For DMGs and DDGs, their low concentration in seed prevents the establishment of clear trends regarding maturation or varietal effects (Zerbib *et al*., 2018b). The combined effects of vintage and variety, along with limited sampling points around harvest, make it difficult to define a clear pattern of evolution during maturation.

Nevertheless, an overall increase during maturation has been observed. Although further studies are needed, flavanol glycosides appear to be a promising market for grape seed maturity. This relationship should also be investigated in connection with flavanol oxidation as discussed earlier.

2.2.4 Extractability and impact on wine

The kinetics of flavanol glycoside extraction during alcoholic fermentation were studied on MMGs, DMGs, MDGs, and DDGs. The extraction of these compounds follows relatively similar kinetics. It begins with a sharp increase upon the appearance of alcohol in the must (onset of AF), followed by a stabilisation toward the end of AF. Finally, a decrease in concentration is observed in wines after pressing. This decrease is probably due either to the formation of new molecules in the wine or to fixation on the solid particles during pressing. Nevertheless, differences exist between the compound families. The extraction of glycosylated monomers (MMGs and MDGs) begins before the appearance of alcohol (approximately 20 % of the maximum reached at the end of AF is extracted before the start of AF). In contrast, DMG extraction is very limited before alcohol appears (less than 10 % of the total at the end of AF) and completely null for DDGs (Zerbib *et al*., 2018a). These data are crucial because a better characterisation of the organoleptic qualities of each family will eventually allow winemakers to modulate the extraction of specific families, for instance by adjusting pre-fermentation or post-fermentation maceration, to fine-tune the ratio of these molecules. Other winemaking techniques that influence proanthocyanidin extraction (*e.g.*, pulsed electric field, enzymes or maceration temperature) may also affect flavanol glycoside extraction; however, further research is needed to characterise this potential effect. Furthermore, the fact that the concentration of these compounds changes with skin and seed maturity could also provide a means to modulate their presence in wine.

The study of these compounds is therefore important both for understanding the contribution of grape seeds to wine and for assessing the potential organoleptic qualities they could impart. Previous research on flavanol monoglycosides and cocoa highlighted a potential reduction in bitterness after adding a flavanol monoglycoside (Stark & Hofmann, 2006). A sensory characterisation of the different isomers within

each family could thus offer insights into how to compensate for bitterness in red wines, which is sometimes perceived as a fault. However, since these molecules have only recently been identified in wine (Delcambre & Saucier, 2012), little is known about how they evolve in wine during maturation and ageing. Further research is needed to understand their influence on wine fully.

3. BEYOND FLAVANOLS: AN OFTEN NEGLECTED DIVERSITY OF COMPOUNDS

3.1. Other phenolic compounds: A disregarded contribution to wine

Although grapeseed flavanols are the most extensively studied molecules in grapeseed due to their role in vinification, many other phenolic compounds are also present in grape seeds. One major analytical challenge stems from the use of seeds originating from pomace. Analyses of seeds at the end of the winemaking process frequently reveal compounds from the skin, which is expected since seeds often turn reddish in red wine due to interaction with the must. This can also happen if the seeds have not been thoroughly cleaned before analysis, leading to the pulp being analysed as a part of the seed. One way to verify seed cleanliness, or to confirm whether they came from the pomace (in red wine; in white wine, this is not a problem because pressing occurs before AF and maceration), is to test for anthocyanins. The detection of anthocyanins indicates that the extract contained pulp or skin or was derived from the pomace, as seeds naturally do not contain anthocyanins.

It is, therefore, difficult to confidently assign all molecules found in pomace seed analyses as originating strictly from grape seeds. Moreover, some studies rely solely on mass spectrometry and UV analyses without comparison against standards, which can be particularly problematic for isomers or molecules with similar molecular masses. While this issue is becoming less prevalent with increasingly accurate technologies, without comparison with a standard or structural resolution via NMR for molecules not commercially available, the presence of a molecule cannot be confirmed. Consequently, only molecules identified by comparison with a standard and derived from seeds not obtained from pomace will be considered here. Table 2 lists the species and quantification, if performed, of molecules identified by comparison with a standard.

Ellagic acid and its derivatives have been identified in *Vitis rotundifolia* seeds (Sandhu & Gu, 2010; Wei *et al*., 2017) as well as in the juice and wine produced from this species (Talcott & Lee, 2002). Sandhu (Sandhu & Gu, 2010) describes this presence as unique in the *Vitis* genus, specifically noting that this molecule is absent in *Vitis vinifera*. However, Prodanov (Prodanov *et al*., 2013) and Pasini (Pasini *et al*., 2019) found ellagic acid (confirmed with a standard) and other ellagic acid-derived molecules (hypothetical, based on mass spectrometry) in *Vitis vinifera*, though the consensus remains that these molecules are typically absent. To definitively resolve the question of ellagic acid, a larger-scale trial encompassing numerous grape varieties from different *Vitis* species would be necessary. As for ellagic acid derivatives, specifically ellagic acid hexoside, its presence cannot be confirmed in either *Vitis rotundifolia* or *Vitis vinifera* without comparison with standards. This suggests that the attribution of these peaks to ellagic acid hexosides may be incorrect, especially if relying solely on retention times and produced ions, as quercetin-3-glucoside (found in the seed) could also fit the ion profile. Pasini (Pasini *et al*., 2019) quantified this molecule using a non-standard technique based on the equivalent terms of another molecule, which is not always reliable. Pasini found a quantity of Ellagic acid hexoside 15 times higher than that of gallic acid. Without comparison to a standard to identify these molecules (ellagic acid hexoside, quercetin pentoside, etc.), they cannot be confidently identified or quantified.

Methyl gallate has only been formally identified in grape seeds in one study (Prodanov *et al*., 2013). Given that it is a common molecule in plants (Liang *et al*., 2023) and considering the abundance of gallic acid in grape seeds, its presence is not surprising. Moreover, in another study (Estrella *et al*., 2011), although not formally identified, this molecule was analysed in seeds harvested at different dates during ripening. It appeared to emerge 3 to 4 weeks before ripeness, decreased until harvest, and was absent one week after ripeness. These results, though requiring confirmation due to the lack of a standard and measurement on a limited sample, suggest that methyl gallate could serve as a marker of ripeness.

The study of phenolic compounds in grape seeds has historically focused mainly on flavanols, often neglecting other phenolics like compounds derived from gallic acid (gallic acid glucosides, ellagic acid, etc.) or quercetin.

Further research on these compounds is essential, particularly as they may be present in wine, could serve as potential markers of maturation, and may possess interesting pharmaceutical properties (*e.g.*, antioxidant activity).

3.1.1 Extractability and impact on wine

Gallic acid is the phenolic compound (excluding flavanols) that is the most extracted from seeds during winemaking. Red wine typically contains approximately 70 mg/L of gallic acid, and while the skin also contains this compound (Yilmaz & Toledo, 2004), the seeds remain its primary source. In terms of organoleptic properties, gallic acid contributes to the astringency of wines (Sterneder *et al*., 2021), colour stability (Wu *et al*., 2024), and, depending on its concentration, the release of aromas (Niu *et al*., 2024), although this last property has not been characterised in wine. Additionally, gallic acid is partially converted into ethyl gallate (the ethyl form of gallic acid) during vinification. This molecule is present in red wine (Ginjom *et al*., 2011; Monagas *et al*., 2005) but has not yet been extensively characterised sensorially in wine. It is, however, recognised for its antioxidant activity and bitterness (Hayashi *et al*., 2013).

TABLE 2. Reported phenolics in *Vitis* species seed with their species and variety of origin, and their potential quantification (S: of seed, B: of berry, GSE: of grape seed extract).

Molecule	Species	Quantification	References
Phenolic acids			
Protocatechuic acid	*Vitis vinifera*, white grape	7.5–11.9 µg/g S	(Garcia-Jares *et al.*, 2015)
	Vitis vinifera, white grape	0–4.8 µg/g B	(Rodríguez Montealegre *et al.*, 2006)
	Vitis vinifera, Red grape	3.3–8.7 µg/g B	
	Vitis vinifera (cv. Malvar)	-	(Prodanov *et al.*, 2013)
Protocatechuic aldehyde	*Vitis vinifera* (cv. Malvar)	-	(Prodanov *et al.*, 2013)
Caftaric acid	*Vitis vinifera*, white grape	11.8–40.4 µg/g S	(Garcia-Jares *et al.*, 2015)
Gallic acid	*Vitis vinifera*, white grapes	135–829 µg/g S	(Garcia-Jares *et al.*, 2015)
	Vitis vinifera, red grapes	6.8–9 µg/g B	(Rodríguez Montealegre *et al.*, 2006)
	Vitis rotundifolia (cv. Noble)	-	(Sandhu & Gu, 2010)
	Vitis vinifera (cv. Malvar)	-	(Prodanov *et al.*, 2013)
	Vitis vinifera pomace seed extract (cv. Chardonnay)	1516.1–1,788.7 µg/g GSE	(Pasini *et al.*, 2019)
	Vitis vinifera pomace seed extract (cv. Pignoletto)	832–1,490 µg/g GSE	
Methyl gallate	*Vitis vinifera* (cv. Malvar)	-	(Prodanov *et al.*, 2013)
Gallotannins			
Penta-O-galloyl-glucose	*Vitis rotundifolia* (cv. Noble, Alachua, Carlos, Fry, Granny Val)	511.7–3,190.5 µg/g S	(Wei *et al.*, 2017) (Figure S1)
Gallic acid glucoside	*Vitis vinifera* (cv Merlot and Cabernet)	410.6 µg/g GSE	(Cretin, 2016)
Ellagitannins			
Ellagic acid	*Vitis rotundifolia* (cv. Noble)	-	(Sandhu & Gu, 2010)
	Vitis rotundifolia (cv. Noble, Alachua, Carlos, Fry, Granny Val)	95.8–1,806.2 µg/g S	(Wei *et al.*, 2017) (Figure S1)
	Vitis vinifera (cv. Malvar)	-	(Prodanov *et al.*, 2013)
	Vitis vinifera pomace seed extract (cv. Chardonnay)	1102.4–1,401.7 µg/g GSE	(Pasini *et al.*, 2019)
	Vitis vinifera pomace seed extract (cv. Pignoletto)	-	
Quercetin and quercetin glycosides			
Quercetin	*Vitis vinifera* pomace seed extract (cv. Chardonnay)	85.0–177.5 µg/g GSE	(Pasini *et al.*, 2019)
	Vitis vinifera pomace seed extract (cv. Pignoletto)	10.3–98.8 µg/g GSE	
Quercetin-3-glucoside	*Vitis vinifera*, white grape	3.5–13.6 µg/g S	(Garcia-Jares *et al.*, 2015)
Quercetin-3-glucuronide	*Vitis vinifera*, white grape	1.9–3.3 µg/g S	(Garcia-Jares *et al.*, 2015)
Quercetin-3-rutinoside	*Vitis vinifera*, white grape	0.4–33.3 µg/g S	(Garcia-Jares *et al.*, 2015)
	Commercial GSE	-	(Sica *et al.*, 2018)
Quercetin-3-rhamnoside	*Vitis rotundifolia* (cv. Noble)	-	(Sandhu & Gu, 2010)

Among gallic acid derivatives, we also find gallic acid glucoside (Gallic-4-O-β-glucopyranoside acid), which is mainly found in the seeds: 95 % seeds, 4 % skins, and 1 % pulp (Cretin *et al*., 2019). This compound, which contributes to the sweet flavour of wine, can be found in red wine in concentrations ranging from 0 to 1,030 µg/L, with an average of around 80 µg/L. Since the detection threshold for this compound has not yet been established, its true impact on wine is difficult to estimate. While the presence of ellagic acid, ellagitannins, and gallotannins in *Vitis vinifera* grape seeds remains uncertain, if they are indeed present and extractable, their sensory properties should be similar to those found in wine from *Vitis rotundifolia* (the only *Vitis* species used in the wine industry where the presence of ellagic acid and its derivatives is confirmed).

Quercetin and some of these hexoses may be implicated in the headaches associated with red wine consumption (Devi *et al*., 2023). Although most quercetin hexosides originate from the skin (Rodríguez Montealegre *et al*., 2006), further study of the isomers found in the seeds could reveal molecules with a potentially greater or lesser propensity to cause headaches. Investigating the extractability of these compounds, whether they are located in the seeds or the skin, could potentially lead to methods for modulating this negative effect in red wine. Another interesting phenolic compound found in red wine and potentially sourced from the seeds is protocatechuic acid (Robbins & Bean, 2004; Rodríguez-Delgado *et al*., 2002). Protocatechuic acid is present in both the seeds and the skins, with quantities 3 to 5 times higher in the seeds (Rodríguez Montealegre *et al*., 2006). However, the lack of information on the seed or skin extraction rate makes it difficult to estimate the grape seed's actual contribution. Protocatechuic acid is used in the food industry as a flavour enhancer and has a phenolic odour (Kakkar & Bais, 2014), and could therefore contribute to the organoleptic qualities of wine. Overall, non-flavanol phenolic compounds derived from seeds are understudied in wine and warrant further investigation.

Until this point, only the polyphenolic diversity of grapeseed was discussed, but polyphenols only represent a small part of the diversity of secondary metabolites that can be found in grapeseed (Figure 7).

These non-polyphenolic molecules are present in grape seed and may contribute to wine properties. However, for many of these compounds, although their function and their presence in grape seeds are known, no studies have evaluated their extractability, which limits the ability to assess the actual impact of grape seeds on wine. Nevertheless, these molecules are briefly described below, as their role in winemaking and their presence in grape seeds have been demonstrated.

3.2. The seeds' secret reserve: lipids, the cuticle, and fueling fermentation

Grape seeds are also an important source of fatty acids, as shown by their use in oil production. Mature grape seeds (after vinification, since seeds from the pomace are used for oil extraction) generally contain between 14 and 20 % fatty acids in *Vitis vinifera* and up to 25 % in *Vitis riparia* seeds (Cherrad & Lavaud, 1993). The main fatty acids in grape seeds are linoleic, oleic, palmitic, and stearic acids (Pérez-Navarro *et al*., 2019b; Rubio *et al*., 2009; Sherman *et al*., 2023; Yalcin *et al*., 2016). Their relative proportions vary considerably, but linoleic acid is consistently the most abundant fatty acid in the seed.

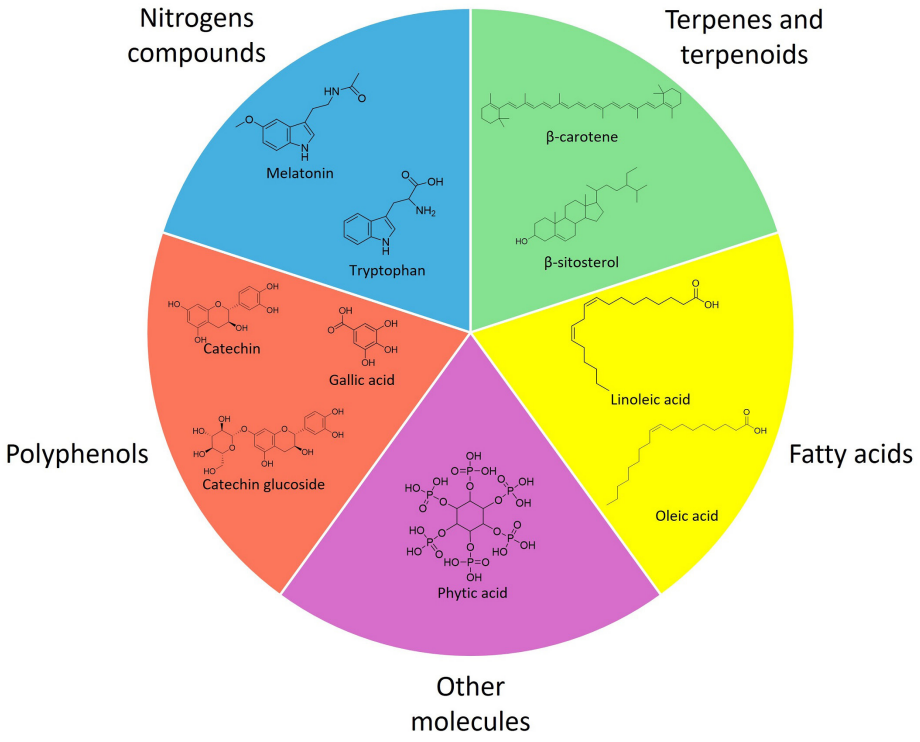

FIGURE 7. Classic plant secondary metabolite category, illustrated with molecules found in grape seed.

During ripening, the fatty acid profile changes. Sherman (Sherman *et al*., 2023) reports a marked increase in linoleic acid between underripe and ripe berries in Pinot noir seeds (around a two-fold increase) and a less pronounced increase in Sauvignon blanc seeds, along with a sharp rise in stearic and palmitic acids. In contrast, Rubio (Rubio *et al*., 2009), who followed seed development from fruit set to maturity, did not observe major changes in linoleic acid content, except for a slight decrease between fruit set and the beginning of veraison, which was also observed for palmitic acid, whereas oleic acid and stearic acid increased over the same period. This study also reported a pronounced variation in free fatty acids (*i.e.*, not in triglyceride form) between fruit set and veraison (approximately a six-fold increase), suggesting that the seed reaches its mature lipid profile at veraison (Rubio *et al*., 2009). The same authors also described the sterol composition of grape seeds and its evolution during ripening, identifying beta-sitosterol, stigmasterol, and campesterol as the main sterols (Rubio *et al*., 2009). Çakir (Çakir *et al*., 2023) obtained results consistent with those of Rubio, with stable linoleic acid and an increase in oleic acid. However, given the limited number of studies and the likely variability associated with vintage, cultivar, and site, it is difficult to draw firm conclusions about the evolution of fatty acids in grape seeds during ripening. This topic warrants further investigation, as the fatty acid composition of grape seeds may influence the qualities of grape seed oil.

3.2.1 Extractability and impact on wine

During red wine production, extraction of oil from the seeds is undesirable, although it may occur if excessive pressure is applied during pressing. In addition to the fatty acids stored in the endosperm of the seed (the oil reserve), the seed also contains fatty acids in its cuticle. The cuticle is the outermost layer of the seed and is therefore in direct contact with the must and wine during maceration and fermentation. The composition of the grape seed cuticle has not yet been characterised, but its overall composition can be inferred from studies on the cuticle of other seeds (Oshima *et al*., 2024; Yeats & Rose, 2013), which show that it is mainly composed of wax and cutin.

Waxes consist of a mixture of compounds derived mainly from very long-chain fatty acids and other lipophilic molecules (Yeats & Rose, 2013). Cuticle, in contrast, is a lipid polymer composed of hydroxylated and esterified fatty acids, glycerol, and minor constituents (Yeats & Rose, 2013). The seed is not the only part of the berry surrounded by a cuticle; the skin also has one. While the cuticle of the seed remains undescribed, the berry skin is much better known for its role as a host for microorganisms involved in winemaking (*Saccharomyces cerevisiae*, lactic acid bacteria, etc.) and as a source of fatty acids (oleic and oleanolic acid) that promote yeast growth during vinification (Ribéreau-Gayon *et al*., 2012). Given the relatively conserved composition of the cuticle across plant species, the seed cuticle may likewise act as a source of fatty acids that enhance yeast growth.

The potential role of grape seeds as a source of fatty acids deserves further investigation, particularly in comparison with other known sources of fatty acids after AF, such as lees resulting from autolysis (Fornairon-Bonnefond *et al*., 2002).

3.3. Chelators, phosphorus, and ferric haze: phytic acid's role as a wine stabiliser

Phytic acid (myo-inositol hexaphosphoric acid) is present in grapes (Trela & He, 2012) and in wine (Iwuozor, 2019). In grapes, phytic acid is mainly located in the seeds and accounts for 80 % of total mass per grape, with values ranging from 14.6 to 23.4 mg per gram of grape at veraison and from 6.9 to 9.8 mg per gram of grape at maturity (Trela & He, 2012). These values are consistent with the fact that phytic acid occurs in high amounts in many seeds (Graf, 1983). Phytic acid is an inositol phosphate, more precisely a myo-inositol ring in which each hydroxyl group is monophosphorylated. It can be used by *Saccharomyces* as a phosphorus source (Mikulski & Kłosowski, 2017), thereby releasing myo-inositol, a molecule also found in wine. However, this indirect contribution of myo-inositol via *Saccharomyces* metabolism should be interpreted with caution, since myo-inositol is lower in red wine than in white wine (Evers *et al*., 2021), and myo-inositol is also consumed by yeast during alcoholic fermentation. Phytic acid is present in wine, but in relatively low concentrations (Iwuozor, 2019). It remains a molecule of oenological interest because it can chelate certain metals, such as iron (Trela, 2010), which may cause instability or defects in wine at specific concentration ranges. A derivative, calcium phytate, is used as an oenological additive to treat ferric case (iron haze) by precipitating iron ions.

Phytic acid therefore appears as a molecule that could serve both as a maturity marker in grape seeds and as a factor influencing wine composition. However, given the limited available data on this molecule, comprehensive monitoring during maturation and investigation of its potential extractability in the wine matrix are necessary to draw clear conclusions.

3.4. The aroma factory: tracking C_{13}-norisoprenoid precursors in the seed

Carotenoids are well known as important aroma precursors in oenology. Berry skin is currently considered the main source of carotenoids, followed by the pulp (Razungles *et al*., 1988). The contribution of seeds to carotenoids in must has not been evaluated, although their presence in seeds has been demonstrated (Assumpcao *et al*., 2015). The principal carotenoids identified in seeds, beta-carotene and lutein, are precursors of norisoprenoids, in particular C_{13}-norisoprenoids, which are recognised contributors to wine aroma (Mendes-Pinto, 2009). One of these C_{13}-norisoprenoids, beta-ionone, derived from beta-carotene (Mendes-Pinto, 2009) and potentially lutein (Sánchez-Contreras *et al*., 2000), is associated with violet aromas and is more typical of red wines and may therefore point to grape seed as a possible precursor source. However, no studies have yet investigated seeds as a potential source of carotenoids during winemaking.

Carotenoids may also influence seed colour and are associated with seed maturation (Gebregziabher *et al*., 2022). Although this has not yet been established in grape seeds, carotenoids could serve as important maturity markers and may help explain variation in seed colour among grape varieties.

3.5. Amino acids, melatonin, and the need for a complete characterization of grape seed

Other grape seed constituents may also be relevant for winemaking. Amino acids identified in grape seeds (Prodanov *et al*., 2013; Sica *et al*., 2018) can influence the organoleptic properties of wine (Nandorfy *et al*., 2022) and serve as a nitrogen source for yeasts. Sugary compounds present in wine have also been detected in grape seeds (Cretin *et al*., 2019), including glycosylated hormones, and the hormonal content of grape seeds appears to be substantial (Yao *et al*., 2022), suggesting that additional related compounds may be present. Grape seeds also contain melatonin (Gao *et al*., 2024; Meng, 2017; Vitalini *et al*., 2011; Zhang *et al*., 2022), which is found in wine and may act as an aroma precursor. Despite its demonstrated presence in grape seeds (Ribalta-Pizarro *et al*., 2023), alpha-tocopherol has not yet been confirmed in red wine: in an HPLC-UV study on Armenian red wine, alpha-tocopherol levels were below the sensitivity threshold of 0.1 mg/L (Grigoryan *et al*., 2024), which does not rule out its presence, and more sensitive massspectrometrybased methods would be needed to confirm or refute its occurrence in wine.

The contribution of grape seeds to wine is often assessed by focusing exclusively on their polyphenolic fraction, leaving many questions open regarding other seed-derived wine constituents. Some studies have explored alternative uses and the potential uses of grape seeds in oenology. For example, grape seed powder has been proposed as a replacement for bentonite for wine clarification (Romanini *et al*., 2021), and other work has investigated the use of grape seed extract (GSE) as an oenological additive (Cliff *et al*., 2012).

CONCLUSIONS

This review shows that grape maturity considered by winegrowers is often oenological maturity, or, more precisely, phenolic maturity, since only flavanols (monomers, oligomers, and polymers) are usually taken into account. Yes, from an anatomical point of view, grape seeds reach physiological maturity (germination capacity) by the end of veraison, and most anatomical changes occur before this stage.

In addition, the available data indicate that flavanol concentrations tend to vary only slightly around harvest. If only these compounds are considered, seed maturity per se has limited or negligible impact on the wine composition compared with change through vintages and the differences in extractability of grape seed compounds associated with winemaking practices.

However, as highlighted in this review, the concentration of other molecules, such as the flavanols glucosides, changes substantially around harvest. The key issue is therefore to determine the actual impact on wine of those compounds whose levels are significantly modified by ripening near harvest and to interpret this in relation to other maturity criteria used to determine harvest date (technological maturity, skin maturity). This may lead to assigning less weight to seed maturity and placing more emphasis on oenological practices. Finally, the emergence of new winemaking techniques or the revival of older ones, such as orange wines (Buican *et al*., 2023), which are white wines produced with skin and seed maceration, raises new questions regarding the contribution of grape seeds to this wine style.

ACKNOWLEDGEMENTS

The authors thank the Denis Dubourdieu Chair and the foundation of Bordeaux University for their support.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

FUNDING

This work was supported by Grants from the Denis Dubourdieu Chair (University of Bordeaux).

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