

What do we know about grapevine bunch compactness?

A state-of-the-art review

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Abstract

Bunch compactness (or density) is a grapevine specific trait that affects the commercial quality and sanitary status of wine and tablegrapes. Compact bunches are more susceptible to diverse pests and diseases such as *Botrytis* bunch rot and their berries ripen more heterogeneously, causing important economic losses through a reduction in crop yield and grape and wine quality. Bunch compactness is determined by the fraction of the morphological volume of the bunch that is filled by berries, but this simple definition contrasts sharply with the difficulty to measure it. While there are several objective and quantitative methods available to measure bunch compactness, the lack of a consistent approach between researchers makes comparing measurements difficult. The complexity of bunch compactness initially arises from the several bunch and berry traits that influence it, and from the distinct effects that these traits may cause in different cultivars. In addition to this genetic effect, diverse environmental signals impact on bunch compactness by affecting those primary factors that contribute to the solid component of the bunch (berry number, berry size) or to its spatial arrangement (rachis architecture). Last, several viticultural approaches, including agronomic techniques and growth regulators, have also proven to affect bunch compactness in different ways. This review aims to discuss present knowledge about this relevant grapevine trait.

Keywords: *Botrytis bunch rot, bunch architecture, inflorescence development, rachis architecture, Vitis vinifera L.*

What do we mean by bunch compactness?

Bunch compactness is also called bunch density or, alluding to the opposite attribute, bunch openness and it refers to the way that berries are arranged in the bunch and to the portion of free space they leave. Thus, loose bunches present many holes in its structure because a significant fraction of their morphological volume is not filled by berries. On the contrary, compact bunches can develop into almost solid bodies as berries grow, which can even deform due to the lack of space between berries. In other words, bunch compactness links the morphological volume of the bunch to its solid component. The morphological volume depends on a series of bunch architecture factors, while the solid component is mainly determined by the number of berries and their individual volume, which will be discussed later.

Figure 1 shows the different sections that can be identified in the grapevine inflorescence/bunch architecture. The stalk is the structural support of the grapevine inflorescence (and subsequent bunch). It contains multiple vascular bundles, which form the pathway for water and nutrient supply from the vine to individual flowers (and berries) (Theiler and Coombe 1985, Gourieroux et al. 2016). The stalk is divided into the peduncle and the rachis (Figure 1). The peduncle [also called hypoclade or paraclade (Pratt 1971)]

comprises the part of the stalk between the shoot and the first branch point of the inflorescence. In the rachis, a main axis and one or more orders of lateral branches are distinguished; primary branches tend to decrease in length from top (the portion of the bunch closest to the peduncle) to tip (the furthest section of the bunch with respect to the vine shoot), giving bunches their typical conical shape (Dunn and Martin 2007). Ultimate (normally secondary or tertiary) branches end in flower- (or berry-) bearing pedicels (Figure 1) (Correa et al. 2014, Gourieroux et al. 2016). In addition, some cultivars present a lateral wing (also called outer arm or shoulder) (May 2000) which is differentiated from the main bunch already in the bud during the first growing season (Srinivasan and Mullins 1981). The lateral wing may have different morphologies, from a highly branched bunch-like structure rivalling the main bunch in size, to just a tendril with no flowers/berries (Carmona et al. 2008, Eltom et al. 2017).

The solid component of the bunch is defined by berry number and size. The final number of berries in the bunch depends on the number of flowers per inflorescence and the fruitset rate (Carmona et al. 2008), variables that are interconnected through an inverse correlation (May 2004). After fruitset, berry development follows a double-sigmoidal pattern with two major stages of growth (berry formation and berry ripening, phases I and III, respectively) separated by a lag period of slow or no growth (phase II) (Coombe and McCarthy 2000, Robinson and Davies 2000). These two major growth stages largely define the final berry size.

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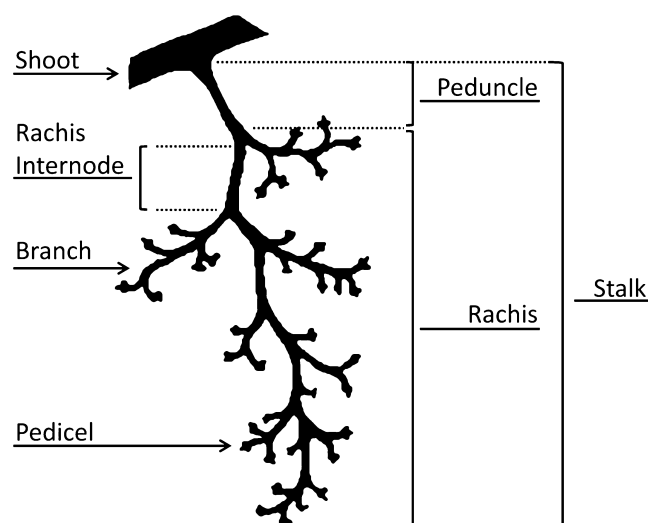


Figure 1. Schematic diagram showing the main sections of a grapevine bunch at harvest time after removing the berries.

Why is bunch compactness important?

Bunch compactness is becoming a key target for grapevine cultural management and for genetic improvement of table- and winegrapes (Wei et al. 2002, Ibáñez et al. 2015). The use by viticulturists of different cultural practices to reduce bunch compactness is becoming more common, while the existence of natural variation for the trait, both at intra- and inter-cultivar level (Vail et al. 1998, Blaich et al. 2007, Alonso-Villaverde et al. 2008, Tello et al. 2015) allows their use in clonal selection and breeding programs. The reason for such importance lies in the relevance and wide range of consequences of compactness. This trait affects disease susceptibility, berry ripening and other characteristics of grapes, as described below.

Bunch compactness is related to susceptibility to pests and diseases

The spatial arrangement of berries in compact bunches may alter some of their physical and physiological properties, contributing to their greater susceptibility to pests and diseases. Berries are in close contact in compact bunches, restricting the development of the protective waxy cuticle (Marois et al. 1986, Rosenquist and Morrison 1989, Commenil et al. 1997, Gabler et al. 2003, Kretschmer et al. 2007) and weakening its barrier function in pathogen defence against rot-inducing organisms (Herzog et al. 2015). The inner part of compact bunches is exposed to higher water vapour concentration and extended periods of surface wetness, increasing their susceptibility to microcracking and, therefore, to bunch rots (Gabler et al. 2003, Becker and Knoche 2012). In fact, the pressure exerted by growing berries during berry ripening may cause berry cracking and the leakage of juice in compact bunches, providing free water and nutrients for conidia germination and mould development (Marois et al. 1986), which might rapidly spread due to berry-to-berry contact until the entire bunch is rotted (Hed et al. 2009). Such outbreaks can be increased by retention of senescent flower debris, such as necrotic flower caps, filaments, anthers and aborted unfertilised ovaries, in the inner parts of compact bunches, because it serves as an inoculum for the infection of sound berries (Wolf et al. 1997, Molitor et al. 2015b, Jaspers et al. 2016). The dense distribution of the berries in compact bunches also restricts airflow,

which increases the internal temperature and humidity in the bunch (Igounet et al. 1995), making the bunch environment more prone for the development of different organisms (Vail and Marois 1991, Vail et al. 1998). Such tight distribution also jeopardises the exposure of individual berries to sun radiation (Vail and Marois 1991). It has been suggested that sun UV radiation generates thicker (Martínez-Lüscher et al. 2014) and waxier (Rosenquist and Morrison 1989, Percival et al. 1993) skins in exposed berries, and it also promotes the biosynthesis of resveratrol in berry skins, a phytoalexin related to resistance to moulds (Jeandet et al. 1991). These effects triggered by UV increase the natural protective function of berry skin against disease agents. Besides, fungicide spraying efficacy is reduced in compact bunches, eventually becoming limited to the outer parts of bunches (Hed et al. 2011).

These reasons explain why compact bunches show a higher development of bunch diseases causing relevant reductions in crop yield and quality (Ribéreau-Gayon 1983, Elmer and Michailides 2007, Ky et al. 2012). Thus, bunch compactness is considered one of the major factors affecting the epidemiology of *Botrytis cinerea* Pers. ex. Fr. (Vail and Marois 1991, Vail et al. 1998, Alonso-Villaverde et al. 2008, Hed et al. 2009), and many works demonstrate the strong link between the bunch structure and the final disease severity (Hed et al. 2009, 2011, Molitor et al. 2012b, 2015a). *Botrytis* bunch rot outbreaks cause large economic loss for the grape and wine industry by the direct reduction of yield and quality (Coertze and Holz 2002, Cadle-Davidson 2008, Ky et al. 2012). This effect is obvious in the case of tablegrapes, but *Botrytis* bunch rot also reduces the quality of wines by generating off-flavours, oxidative damage, premature ageing and difficulties in clarification during the winemaking process (Ribéreau-Gayon 1983), so rotten bunches are often rejected in the wine industry. As a consequence of its importance, most of the fungicides specifically targeted against *B. cinerea* are intended for wine- and table-grape growers, and the cost for the control of *Botrytis* damage is a major cause of profit reduction in many vineyards, as has been reported in Australia (about A\$52 million/year), Chile (US\$22.4 million/year) and South Africa (SA Rand 25 million/year) (Dean et al. 2012).

A positive relationship also exists between bunch compactness and the infestation rate of *Lobesia botrana* (Fermaud 1998), the European grapevine moth, which is one of the major pests in vineyards, causing substantial damage to crop yield by the larval feeding of grape berries (Fermaud 1998, Ioratti et al. 2011). For example, Moschos (2006) estimated that the carpophagous generation of the European grapevine moth was capable of reducing the yield of a vineyard of the wine cultivar Savvatiano in Greece by 27%. Larvae of *L. botrana* also increase the severity of grey mould on grapes, acting as a vector for the berry-to-berry transport of viable conidia (Fermaud and Le Menn 1989, 1992).

Moreover, Leong et al. (2006) reported a major incidence of the ochratoxigenic fungi *Aspergillus* spp. in compact bunches, and Latorre et al. (2011) pointed out that the humid and warm microclimate of tight bunches may also stimulate the incidence of *Cladosporium* spp. and the consequent development of Cladosporium rot.

In addition to these direct effects on fruit and wine composition, high pest or disease levels in the vineyard (particularly bunch rot) may force growers to harvest grapes at a stage of incomplete maturity, also affecting the final composition of grapes, musts and wines (Molitor et al. 2016).

Bunch compactness impacts ripening rate and berry composition

Berries do not receive the same solar radiation in the sunlight-exposed and in the shaded sides of the berry, the bunch or the vine, and this affects berry ripening and berry composition (Pieri et al. 2016). In compact bunches heterogeneity increases because they bear more inner berries that receive little direct solar radiation (Vail and Marois 1991). Much research has discussed the relationship of solar radiation with relevant parameters for winemaking, including juice pH and TA, sugar and organic acid variation, amino acids, anthocyanin and flavonol accumulation, and the synthesis of tannins, stilbenes, terpenes, carotenoids and methoxy-pyrazines [see Pieri et al. (2016) and references therein]. Part of the solar radiation effects is caused by UV radiation, which is an environmental signal that directly triggers different metabolic pathways resulting in the synthesis and accumulation of secondary metabolites in the skin and the pulp of ripening berries (Alonso et al. 2016). These effects have been observed in different transcriptomic studies which have shown that sunlight exposure can modulate the expression of a series of transcription factors, such as MYB and bHLH transcription factors, that activate anthocyanin and flavonol biosynthesis pathways, promoting their accumulation in the skin of berries (Matus et al. 2009, Carbonell-Bejerano et al. 2014). Another part of the solar radiation effect is related to temperature (Bergqvist et al. 2002), because individual berries heat more in compact than in loose bunches (Smart and Sinclair 1976), probably due to an inefficient aeration, that also impacts berry metabolism rate.

Bunch compactness affects specific attributes of tablegrapes and raisins

Market acceptance of tablegrapes relies on several properties, including sensory attributes (e.g. berry texture and flavour) and chemical composition (i.e. concentration of sugars and acids), but the first impression is based only on berry and bunch visual attributes, including bunch compactness (Piazzolla et al. 2016). Thus, the tablegrape consumer demands bunches with an optimal appearance, globally determined by the size, shape and colour of the berries, the colour of the rachis, and the shape, size, compactness and physical conditions of the bunch (Wei et al. 2002, Reisch et al. 2012, Dragincic et al. 2015, Zhou et al. 2015). Moreover, some of the practices used in the fruit industry, such as fruit washing, handling or transportation, are hindered if grape bunches are too compact (Nelson et al. 1970, Sepahi 1980). In the specific case of raisins, the required water loss from fresh berries is less efficient as bunch compactness increases (Christensen 2000).

How is bunch compactness evaluated?

There are several methods that have been used to evaluate bunch compactness, from subjective visual systems to novel image-based approaches, but the lack of a consistent approach between researchers makes comparison of measurements difficult.

Subjective methods

Bunch compactness is traditionally evaluated by visual and qualitative methods that classify grapevine bunches into predefined categories according to their general appearance. The most commonly used method to evaluate this trait is

the Organisation Internationale de la Vigne et du Vin (OIV) descriptor code 204 for bunch density (Organisation Internationale de la Vigne et du Vin 2007), which is equivalent to descriptor 33 in the International Union for the Protection of New Varieties of Plants (UPOV) list and descriptor 6.2.3 in the International Plant Genetic Resources Institute (IPGRI, now Bioversity International) list. This descriptor classifies bunches into five categories by considering the mobility of the berries and the visibility of the pedicels: very loose (notation 1); loose (3); medium (5); compact (7) and very compact (9). Alternatively, other visual scales with a varying number of predefined categories have been proposed (Table 1). Roberto et al. (2015) shortened the OIV descriptor code to a three-category scale, a similar approach to those used by Kasimatis et al. (1971), Miele et al. (1978) and Ristic et al. (2016). Another visual scale proposes to classify bunches into four categories of growing value of compactness (El-Banna and Weaver 1978), and other studies propose different five-category ratings (Christodoulou et al. 1967, Hopping 1975, Firoozabady and Olmo 1987). An extended six-point scale considering berry mobility and bunch gaps has also been defined (Zabadal and Dittmer 1998).

The application of these visual scales can be simple and cost-saving, and the viticulture sector finds these rapid and non-destructive systems useful. Nonetheless, its application needs trained evaluators and entails great subjectivity, which hinders its subsequent use in some studies that require an objective and continuous variable. Although subjectivity can be reduced with a panel of judges, they may provide only categorical data with limited analytical usefulness for certain studies and statistical approaches. There is a general agreement on the extreme values of the scales proposed (very compact and very loose categories); however, there is a great disparity in the intermediate values. As an example, and using the five-point scales previously indicated, the intermediate category may represent a bunch 'with the most desirable degree of looseness' (Christodoulou et al. 1967), a 'moderately loose' bunch (Hopping 1975) a 'well-filled' bunch (Firoozabady and Olmo 1987) or a 'medium' bunch (Organisation Internationale de la Vigne et du Vin 2007). Obviously, it increases the difficulty of meta-analyses aimed to compare the results obtained by different researchers.

Indirect measurement of bunch compactness using related traits

Given that there are certain characteristics of the bunch that vary with compactness, their variation may also be used for the indirect estimation of the trait. Compact bunches are less flexible than loose ones, and this feature has been used for the indirect quantification of the trait. As an example, Ipach et al. (2005) developed the so-called 'density index', which has been applied in different studies (Evers et al. 2010, Molitor et al. 2011b, 2012b, 2015a). According to this method, bunches are classified in one of five categories considering the proximity between berries and the bending of the stem: (i) very loose (no berry contact; bending of the stem to 90° possible); (ii) loose (berry contact; bending of the stem up to 45–90° possible); (iii) dense (berries still flexible; bending of the stem up to 10–45° possible); (iv) compact (berries not flexible; bending of the stem up to 10° possible); and (v) very compact (berries not flexible; bending of the stem not possible) (Ipach et al. 2005, Evers

Table 1. Visual descriptors reported for evaluation of bunch compactness.

No. categories	Categories	Reference
3	1, Very loose; 2, moderately compact; 3, very compact	Kasimatis et al. (1971)
3	1, Very tight; 2, loose; 3, very loose	Miele et al. (1978)
3	1, Very loose; 2, medium loose; 3, very compact	Roberto et al. (2015)
3	1, Compact; 2, moderate; 3, loose	Ristic et al. (2016)
4	1, Very loose; 2, moderately loose; 3, well filled; 4, compact	El-Banna and Weaver (1978)
5	1, Bunches excessively loose; 2, bunches very loose; 3, most desirable degree of looseness; 4, bunches somewhat compact; 5, bunches excessively compact	Christodoulou et al. (1967)
5	1, Excessively loose; 2, loose; 3, moderately loose; 4, slightly loose; 5, tightly compacted	Hopping (1975)
5	1, Ragged; 2, loose; 3, well-filled; 4, compact; 5, very compact	Firoozabady and Olmo (1987)
5	1, Very loose; 3, loose; 5, medium; 7, dense; 9, very dense	Organisation Internationale de la Vigne et du Vin (2007)
6	1, Rigid, unable to move berries on bunch; 2, some movement of berries; 3, able to manually separate berries; 4, loose, occasional berries not touching others; 5, uniformly loose with many berries not touching each other, able to see some gaps through the bunch; 6, large holes or gaps visible in the bunch	Zabadal and Dittmer (1998)

et al. 2010). Similarly, Schildberger et al. (2011) proposed the 'bending index', using a five-point scale for bunch classification: 1, firm; 2, flexible; 3, bending up to a maximum of 45°; 4, bending up to a maximum of 90°; and 5, bending above 90°. Although both indexes are based on a continuous indirect attribute of the bunch related to bunch compactness, the categorisation stage provides an ordinal value of the trait.

Inter-berry spacing is another characteristic of the bunch that varies with compactness, with loose bunches having more space between berries than the compact ones. This attribute has also been used for the indirect evaluation of bunch compactness, by determining the distance existing between two randomly chosen berries through the insertion of wedges in the inter-berry space (Zabadal and Dittmer 1992, 1998). Vail and Marois (1989) followed a similar approach, and proposed the use of a firmness tester to measure the force required to separate two contiguous berries by a distance of 2 mm, as another attempt to measure bunch compactness in a quantitative way. This method has been applied for the measurement of this trait in both intra-cultivar (Vail et al. 1998) and multi-cultivar studies (Vail and Marois 1991).

Other indirect measurements aim to determine how much space in the morphological volume is not actually filled by berries (Sepahi 1980, Ferreira and Marais 1987, Shavrukov et al. 2004). The actual volume of the bunch solid elements may be easily measured by the immersion of the bunch in a bucket filled with water and determining the amount of water displaced, following Archimedes' principle (Sepahi 1980, Shavrukov et al. 2004, Tello and Ibáñez 2014). Nevertheless, the determination of the morphological volume is more complex, especially in loose bunches, because any modification in the natural arrangement of the berries will modify it. Several methods for its calculation have been proposed, including the moulding of the bunch once their empty holes are filled with melted paraffin (Sepahi 1980), the packing of bunches in plastic bags in which the air is removed by suction to force the plastic film to fit the bunch (Ferreira and Marais 1987) and the use of self-adherent plastic films to wrap grapevine bunches (Tello and Ibáñez 2014). Shavrukov et al. (2004) used a different approach, and estimated the morphological volume of the

bunch assimilating it to a perfect cone where length is the maximum bunch length, and radius is half of the widest bunch width. Nonetheless, this method only provides a rough estimation because it does not take into account irregularities that may appear all along the bunch, and it is not applicable to bunches with other shapes (i.e. cylindrical or funnel shaped bunches). In this regard, different novel approaches based on the analysis of two-dimensional (2D) and three-dimensional (3D) images have been recently assayed for the automated reconstruction of grape bunch architecture (Herrero-Huerta et al. 2015, Ivorra et al. 2015, Schöler and Steinhage 2015, Tello et al. 2016a, Yuan et al. 2016), which are expected to allow the precise and objective measurement of bunch morphological volume.

Objective methods

Bunch compactness indexes. Considering that visual descriptors for bunch compactness do not provide continuous and objective values, alternative indexes of bunch compactness based on bunch quantitative variables have been proposed. The number of berries divided by the bunch (or rachis) length is the most typical objective estimator for evaluation of bunch compactness, and it has been used in numerous studies (Vail and Marois 1991, Pommer et al. 1996, Hed et al. 2009, 2011, Bavaresco et al. 2010, Fawzi et al. 2010, Sabbatini and Howell 2010, Abd El-Razek et al. 2011, Palliotti et al. 2011, 2012, Kotseridis et al. 2012). Likewise, different modifications of this basic ratio have been proposed; among them, the replacement of berry number by bunch mass (faster to obtain) has been widely used (Ferraud 1998, Ifoulis and Savopoulou-Soultani 2004, Sternad-Lemut et al. 2015). Other studies also employed this basic ratio, but using different bunch sections. Thus, Christodoulou et al. (1967) calculated bunch compactness as the number of berries per centimetre of rachis considering only the second and third branches of the bunch, Dokoozlian and Peacock (2001) considered the four first branches, and Lynn and Jensen (1966) all bunch branches. Valdés-Gómez et al. (2008) calculated two compactness indexes by dividing either the number of berries per bunch or the bunch mass by the sum of length of the rachis and of its first branch, and Intrieri et al. (2013) evaluated bunch compactness as the ratio of bunch mass and the sum of

bunch length and all bunch branches. Agreeing with the initial definition of bunch compactness, these indexes combine variables highly related to the solid component of the bunch (number of berries per bunch or bunch mass) with other variables related to the morphology of the bunch (by using rachis architecture variables, like rachis or branch length).

These indexes are based on simple metrics that do not require complex devices, so they arise as interesting methods to quantify bunch compactness within the genetic framework for which they were designed (usually a single cultivar). However, their use in other cases may be uncertain because different bunch morphologies can be found in this species. Tello and Ibáñez (2014) tested several of these objective indexes using a highly diverse sample of bunches of different table- and winegrape cultivars, and some of them, such as the number of berries divided by the bunch length (Pommer et al. 1996), were of little value in that multi-cultivar framework. As a result, a set of alternative compactness indexes (CI) was proposed, and three of them (named CI-12, CI-18 and CI-19) were remarkable for their greater correlation with the visual value of reference. The indexes CI-18 and CI-19 are based on the combination of six bunch metrics, indicating the large number of factors involved in the determination of bunch compactness. In contrast, the other selected index (CI-12) is defined by the ratio of bunch mass (g) to bunch length squared (cm^2); it requires a measure of only two bunch features, and it is proposed as the simplest way to obtain an objective and quantitative value of compactness. This index has proven to be helpful to quantify differences between different cultivars (Fernandez et al. 2014, Zdunic et al. 2015) and between clones of a single cultivar (Döring et al. 2015).

Use of novel phenotyping tools. Novel technologies may provide new solutions to old issues. Recent studies have assayed the application of automated systems for the evaluation of bunch compactness through diverse image analysis techniques. Kicherer et al. (2014) evaluated this trait in a F1-population analysing bunch images taken under controlled conditions and defining a novel compactness ratio calculated from the difference between the area of the bounding box (bunch length \times bunch width) and the visible area of the bunch. Cubero et al. (2015) also estimated this trait through the automatic analysis of RGB images of bunches from different grapevine cultivars. The applied algorithm allowed the determination of relevant bunch compactness-related variables, such as the proportion of pixels in the image corresponding to berries, rachis and holes, and a series of calculated variables related to the shape of the bunch, such as roundness, compactness shape factor and aspect ratio. These traits were subsequently used to construct a mathematical model that showed a capability of 85.3% for trait prediction. Using the same set of bunches, Ivorra et al. (2015) measured through stereo vision a series of 3D bunch architecture-related descriptors, for example concavity measure, intersection between berries and number of berries per area, to estimate bunch compactness, and build a mathematical model with a predictive value of 80.0%. In another recent study with cv. Riesling, Schöler and Steinhage (2015) have proposed the complete 3D reconstruction of grape bunch architecture through the direct scanning of the bunch before and after removing all the berries, which could lead to the accurate measurement of bunch compactness. Tello et al. (2016a) evaluated 2D image analysis and 3D scanning technologies, and

constructed a mathematical model based on two bunch compactness-related attributes (visibility of rachis and holes, and compaction of the berries) that can be automatically measured by 2D computer vision. According to the authors, it allowed the accurate and fast quantification of bunch compactness in a set of highly diverse bunches.

These examples indicate that the novel and automatic phenotyping methods can be used to obtain highly valuable information on grapevine bunch architecture and compactness. In this light, novel image-based technologies allow the quantification of different variables related to bunch architecture and highly correlated to visual bunch compactness that cannot be accurately assessed by traditional methods, such as the area of the bunch image covered by the berries, holes and rachis ($\tau_b = -0.672$; $P \leq 0.01$) (Cubero et al. 2015, Tello et al. 2016a), and the concavity of the bunch ($\tau_b = -0.710$; $P \leq 0.01$) and the intersection between berries ($\tau_b = -0.569$; $P \leq 0.01$) (Ivorra et al. 2015). The future of phenotyping lies in these approaches, but most of these methods are still at a preliminary stage of development and require further research. On the one hand, they have to be tested with a larger range of cultivars and clones with different bunch morphologies, as well as under less controlled (e.g. field) conditions, to determine their possible application. In addition, these methods require specifically-trained staff for experimental design, image acquisition, mathematical modelling and algorithm development, at least to set the protocols. Thus, depending on the aims and scope (research, breeding, tablegrapes, wineries), their economic feasibility may be limited. Once protocols have been set, for either a single or for several cultivars, a computer vision system could be implemented to rapidly work automatically in sorting tables of tablegrapes and in wineries for the classification of bunches prior to winemaking, as it is used in other fruits (Blasco et al. 2009).

Which factors affect bunch compactness?

Bunch compactness has an inherited component that comes from the genetic determination of different attributes related to inflorescence and bunch architecture and growth. These genetic factors can be shaped to some extent by environmental signals, and they can be adjusted in the field by different management strategies.

Genetic factors affecting bunch compactness

Inflorescence and bunch architecture. Differences in bunch compactness have been attributed to different structural elements of the grapevine bunch [see Tello et al. (2015) and references therein]. In a recent study, Tello et al. (2015) analysed the genetic variability of bunch compactness through the evaluation of 125 table- and winegrape cultivars in three consecutive seasons. Analysis of the results showed that the main components determining bunch compactness in a multi-cultivar framework are the length of bunch main axes (rachis architecture), the number of berries per bunch and, to a lesser extent, berry size.

Rachis architecture is highly variable between cultivars, as has been indicated for the length of the rachis, the length of primary branches and the degree of rachis branching (Shavrukov et al. 2004, Tello et al. 2015). For instance, Shavrukov et al. (2004) identified inflorescence length (in particular rachis internode length) as the major trait responsible for the difference in bunch architecture between two compact (Chardonnay and Riesling) and two loose

(Exotic and Sultana) cultivars. According to these authors, the difference in internode length was more attributable to a difference in cell size rather than in cell number.

There is also a wide range of diversity for berry number between grapevine cultivars (Dry et al. 2010, Tello et al. 2016b). Flower number and fruitset rate are under the control of complex genetic networks and are also affected by the environment, which hinders the genetic analysis of grape berry number (Fanizza et al. 2005, Tello et al. 2016b). Recently, it has been suggested that fruitset differences between three cultivars, Shiraz, Merlot and Cabernet Sauvignon, are attributable to differences in pollen viability and in the concentration of diverse amines (e.g. diaminopropane and phenylethylamine) in flowers, which can inhibit pollen tube growth and therefore interrupt the normal fertilisation process (Baby et al. 2016).

Numerous genetic (and environmental) factors affect the final size of grape berries, including specific pre-flowering flower features and multiple post-pollination events [for a review see Dai et al. (2011)]. Houel et al. (2013) analysed the genetic variability of berry size in 304 table- and wine-grape genotypes, and reported a 23-fold variation between the berry volume at ripeness for the cultivar with the smallest (cv. Domina, 0.5 cm³) and the largest (cv. Barlinka, 11.5 cm³) berries. Following this work, cell division (before and after flowering) and cell expansion (after flowering) are the major determinants of berry size variation at a multi-cultivar level.

Inflorescence and bunch development. Processes involved in the initiation of grapevine inflorescence and development have been widely reviewed (Pratt 1971, Srinivasan and Mullins 1981, Carmona et al. 2007, 2008, Lebon et al. 2008, Vasconcelos et al. 2009), therefore only a short overview is presented here. In temperate climates and under normal growing conditions, the grapevine reproductive cycle extends over two consecutive seasons separated by a period of dormancy. Inflorescence primordia differentiation from lateral meristems (anlagen) occurs during spring and summer in the first season, and primary branches are distinguished in buds before they enter dormancy (Srinivasan and Mullins 1981). The degree of branching decreases acropetally within the developing bud, and will have an influence on the degree of branching that can occur at the start of season two and on the future number of flowers in the inflorescence (Dunn and Martin 2007). During the second season, secondary and tertiary branching starts during budswell before budburst, ending in the flower initiation or formation of floral primordia in small groups, normally three (Dunn and Martin 2007, Carmona et al. 2008, Eltom et al. 2017). Major differences in the rachis elongation rate between cultivars have been described during the period of inflorescence development prior to flowering time, whereas little growth exists after flowering (Coombe 1995, Shavrukov et al. 2004). In the inflorescence, flower differentiation (floral organogenesis) starts after budburst and ends with the formation of the pistil about 2 weeks before flowering (May 2004). The number of flowers per inflorescence is highly variable, being influenced by environmental, genetic and cultural factors (Dry et al. 2010, Eltom et al. 2017). In addition, strong differences can be appreciated in the diverse branches of the inflorescence at flowering, with final branches presenting the lowest number of flowers (Dunn and Martin 2007). There is also a range of diversity along the inflorescences of the shoot, with basal

inflorescences tending to show the highest number of flowers and declining in the more distal ones (May 2004).

The final number of berries in the bunch is mainly established during fruitset, 1 or 2 weeks after flowering, as in the grapevine a delayed drop usually does not happen (May 2004). The proportion of flowers converting into berries (fruitset rate) greatly depends on the number of flowers in the inflorescence (May 2004, Eltom et al. 2017), and large differences exist for both between cultivars (Dry et al. 2010).

Igounet et al. (1995) monitored the development of bunches of the wine cultivar Syrah during the maturation process, and identified three phases in the evolution of bunch compactness: a first phase characterised by a slight increment of bunch compactness; an intermediate phase of rapid increase of bunch compactness (bunch closure); and a final phase of stabilisation of bunch compactness where a slight decline may appear. The development of models able to predict the final bunch compactness in each season would be helpful to anticipate decisions on viticultural management practices or treatments. Those models should include variables defined at early stages of inflorescence/bunch development to have such a predictive capacity. Besides, further research on diverse wine- and tablegrape cultivars differing in their compactness is necessary to determine whether the three-phase model proposed by Igounet et al. (1995) is cultivar-independent, or whether cultivar-specific models are required in each case.

Environmental and viticultural factors influence bunch compactness and its main components

Different environmental conditions and viticulture practices influence bunch compactness and its main components. Natural conditions or events, for example soil, sunlight, rain, and hail and human practices, for example leaf removal and use of growth regulators, during key periods within the two consecutive growing seasons needed for yield formation, strongly affect inflorescence development and bunch architecture (Carmona et al. 2008).

Environmental parameters affecting bunch architecture.

There are many studies on the effects of diverse environmental factors on inflorescence formation and potential grapevine fruitfulness [for a recent review see Li-Mallet et al. (2016) and references therein], but only few studies deal with their effect on important factors defining final bunch architecture. It is generally accepted that a combination of sufficient light intensity, short-term exposure to high temperature and absence of water and nutrition stresses is required for an optimum inflorescence initiation (Li-Mallet et al. 2016). These factors also greatly influence other critical processes (e.g. the date of budburst and the growth rate of the inflorescence) that have a major effect on bunch architecture and compactness (Carmona et al. 2008). This section will focus on some environmental parameters affecting bunch architecture and/or compactness, and will not consider meteorological one-off events, such as hail, spring frost or strong winds.

Sunlight and temperature. The close link between temperature and sunlight exposure (Bergqvist et al. 2002) makes it difficult to separate the direct and indirect effects on bunch and berry traits in field experiments. Nonetheless, it has been suggested that both factors are independent

critical signals for inflorescence induction and differentiation during season one and for inflorescence development during season two (Srinivasan and Mullins 1981, Carmona et al. 2008, Li-Mallet et al. 2016).

Sunlight

Some of the effects of light on inflorescence induction, differentiation and development have been recently reviewed by Li-Mallet et al. (2016). Several effects may be distinguished, depending on if the light gathering/shading occurs in the bud, in the berry or in the whole vine. The illumination of buds is strongly associated with the proportion of budburst, and the number of bunches per shoot and of berries per bunch. As an example, Hopping (1977) indicated that artificial shading of field-grown Palomino axillary buds during season one (from 15 days after flowering until leaf fall) decreases budburst, the number of fruitful shoots, and the yield per cane in season two. In fact, it is often observed that illuminated buds outside the canopy of field-grown vines are more fruitful than those located inside of it (May et al. 1976, Perez and Kliewer 1990), probably through its effect on photosynthesis and carbohydrate supplying (Vasconcelos et al. 2009, Li-Mallet et al. 2016) and/or through a direct effect of shading in the bud itself, which may cause bud necrosis resulting in 'blind buds' or 'split buds' (Perez and Kliewer 1990). Petrie and Clingeleffer (2005) studied bunch architecture using a series of plastic mini-chambers to alter the level of photosynthetically active radiation and temperature on buds shortly before and after budburst. They reported that light appeared to have little effect on bunch components other than that caused by temperature (lower temperature increased both flower number and inflorescence length), although shading treatment prior to budburst increased flower number by approximately 13%.

Rojas-Lara and Morrison (1989) found that sunlight stimulates berry growth, and the mass of Pinot Noir, Cabernet Sauvignon and Reliance berries is reduced if bunches are shaded during stages I and II or I, II and III of berry development (Gao and Cahoon 1994, Dokoozlian and Kliewer 1996). Differences in berry size are suggested to be a consequence of the repression of diverse light-mediated effects on cell division and/or expansion resulting from sunlight deprivation during the initial stages of berry growth, including effects on fruit photosynthesis and carbon metabolism. Additionally, it has been suggested that those effects cannot be reversed even if berries are exposed to light during the final stage (III) of berry development (Dokoozlian and Kliewer 1996).

Last, vine shading might also have an effect on bunch architecture, as it causes a reduction in vine photosynthesis and potential over-wintering reserves. Vine carbohydrate reserves influence inflorescence number and flower number per inflorescence in the following season (Bennett et al. 2005, Eltom et al. 2015). Sánchez and Dokoozlian (2005) observed that a reduced sunlight exposure of shoots significantly decreased inflorescence dry mass in the subsequent season, especially in cv. Thompson Seedless. Ferree et al. (2001) and Domingos et al. (2016b) have indicated that shading can reduce fruitset rate in different grapevine cultivars, which generates a loosening effect of the bunch at harvest time.

Temperature

Temperature is another factor suggested to influence bunch architecture, and high temperature during budburst can

significantly reduce flower number in different cultivars (Buttrose and Hale 1973, Pouget 1981, Ezzili 1993, Dunn and Martin 2000, Petrie and Clingeleffer 2005). Interestingly, Eltom et al. (2017) have indicated that the later heating of buds before budburst can accelerate budburst and decrease flower number per inflorescence, but increase fruitset and bunch mass in cv. Sauvignon Blanc. It has been hypothesised that high temperature can accelerate the vegetative growth phase, reducing the inflorescence differentiation stage to a shorter period of time, giving rise to a lower number of individual flowers (Pouget 1981). It could translate at harvest time into a lower berry number and a lower value of bunch compactness, but, as mentioned above, there is a compensating effect between flower number and berry set rate (May 2004, Eltom et al. 2017).

In contrast, high temperature during the flowering to berry set period can also affect grapevine reproductive performance. It has been suggested that heat stress during reproductive development reduces ovule fertility (Kliewer 1977), and pollen viability and germination capacity (Pereira et al. 2014), factors that compromise successful fruitset. As an example, Kliewer (1977) found that a temperature over 35°C during the flowering to berry set period decreased the proportion of berry set in Pinot Noir and Carignane vines.

Last, berry size is also sensitive to heat stress (Radler 1965, Kliewer 1977, Matsui et al. 1986). It has been indicated that high temperature during phase I of berry development might reduce cell division (Kliewer 1977) and cell expansion (Keller 2010b) rates, which ultimately reduce berry dimension. Nonetheless, important varietal differences have been reported, and Greer and Weston (2010) observed that berries of cv. Sémillon, overheated at fruitset time, presented a similar size to those of the Control, and only those overheated at veraison showed a reduced berry size.

Water and nutritional status. Water deficit affects grapevine yield components, including factors involved in bunch architecture determination, such as fruitset (berry number) and berry size (Hardie and Considine 1976, Matthews and Anderson 1989, McCarthy 1997, Ojeda et al. 2001, Myburgh 2003, Salón et al. 2005, Shellie 2006, Intrigliolo et al. 2012, Kidman et al. 2014). A great genetic variability in tolerance to water stress can be found in the grapevine, not only between different cultivars but also between clones (Bota et al. 2001, Tortosa et al. 2016), and the response of grapevines to water stress (mainly through its effect on photosynthesis performance) depends both on the duration and timing of the deficit. It has been recently suggested that water and nitrogen deficits during season one can affect the development of the inflorescence primordia in two cultivars (cvs Aranel and Shiraz), giving rise to bunches with a significantly lower number of berries (Guilpart et al. 2014). Following this work, grapevine water status in season one is a more limiting factor than nitrogen concentration, explaining between 23% (for Aranel) and 38% (for Shiraz) of variance for berry number in season two. Interestingly, Matthews and Anderson (1989) found that water deficit during the first weeks after flowering (early water deficit) in season one can result in a significantly lower number of individual flowers in season two in cv. Cabernet Franc. Water deficit also affects the development of the current season's fruit, and diverse studies indicate its negative effect on the berry set rate of different cultivars (Hardie and Considine

1976, Korkutal et al. 2011), which may result in a lower number of berries at harvest time.

Different studies indicate that water deficit reduces berry size. In general, these reports indicate that berry size is more sensitive to early than to late water deficits (McCarthy 1997, Niculcea et al. 2014). It has been suggested that early water deficit affects the potential berry growth by hindering cell division processes, which leads to a reduced cell number per berry (Matthews et al. 1987, McCarthy 1997). In contrast, Ojeda et al. (2001) concluded that early water deficit did not affect the cell division process in Syrah. According to these authors, berry size reduction was exclusively caused by a decrease of pericarp volume, suggesting that early water stress can modify the structural properties of the cell components and cell wall extensibility, which limits the subsequent enlargement of pericarp cells and compromises potential berry size. Water deficit after veraison (late water deficit) also reduces berry mass (Hardie and Considine 1976, Matthews et al. 1987, Myburgh 2003, Bucchetti et al. 2011), mostly because of a reduced growth of berry mesocarp tissues. In fact, limiting water input at certain stages of development is a common practice to limit berry size and bunch compactness, which in turn improve berry composition and diminish the incidence of bunch rots (Kennedy et al. 2002, Roby and Matthews 2004, Valdés-Gómez et al. 2008, Clingeffer 2010, Bucchetti et al. 2011, Intrigliolo et al. 2012).

Optimum nutritional status is an important feature to achieve maximum yield and targeted fruit characteristics, and fertilisation is needed whenever the soil cannot provide nutrients enough to ensure it. Nitrogen (N) is the most important macro-nutrient for the optimum growth of vines, playing direct and indirect effects on vegetative growth. A low N level may affect the composition of grapes and juice, and it is critical for the synthesis of compounds that provide wines certain attributes commonly aimed for, such as greater colour intensity or capacity for ageing (Hilbert et al. 2003, Mundy 2008), so accurate and effective fertilisation programs are needed to optimise vineyard efficiency. To our knowledge, few studies have related grapevine nutritional status and bunch architecture, in spite of its relevance in practical viticulture. Low N availability during season one limits N reserves needed for optimum inflorescence development in season two, and it has been suggested that low plant N reserves can reduce fruitset ratio in cv. Grenache, which affects the final number of berries per bunch (Duchêne et al. 2001). In a study to evaluate short-term responses to N supply in cv. Müller-Thurgau, Keller et al. (2001) observed that fertilisation generated more compact bunches due to an increase of both berry number (because of a higher fruitset rate) and berry size, which favoured the appearance of Botrytis bunch rot. A similar effect was seen for Aranel, where high N supplementation resulted in dense canopies with more compact and heavy bunches that correlated positively to disease incidence (Valdés-Gómez et al. 2008). In contrast, Abd El-Razek et al. (2011) reported that the size of cv. Crimson Seedless berries was the only yield component affected by N fertilisation, while berry number and bunch compactness were unaffected. In contrast, excessive N fertilisation can lead to dense canopies that hinder sunlight irradiation, varying photosynthesis efficiency and thus carbon availability for optimum bunch development. In addition, it may also alter critical microclimate factors, such as canopy temperature, humidity, wind speed and evaporation, which might have indirect effects on bunch architecture and fungal disease

incidence (Mundy 2008). Thus, the management of vineyard N needs an adapted and balanced plan to optimise vegetative growth without compromising berry and juice composition.

Besides, other macronutrients (phosphorus and potassium) and different micronutrients (e.g. boron, zinc and molybdenum) have been shown to affect grapevine reproductive performance, which may modify bunch architecture and compactness (May 2004, Keller 2010a, Li-Mallet et al. 2016). As an example, insufficient zinc can inhibit pollen formation and, therefore, pollination (Keller 2010a). Similarly, boron is required for pollen germination and pollen tube growth, so it is essential for the ovule fertilisation process (Alva et al. 2015). Deficiency of any of these nutrients may lead to reproductive disorders, resulting in an abnormally high rate of flower fall (coulture) and/or to the development of tiny and seedless berries (millerandage), leading to low fruitset rates and looser bunches (Keller 2010a).

Viticulture management strategies affecting bunch compactness. In view of the relevance of bunch compactness to practical viticulture, different strategies have been pursued to produce loose bunches in compact cultivars. Viticulture practices aimed to loosen bunches have focused on decreasing berry number, berry size and/or increasing bunch axes length to generate a more open architecture (Figure 2).

Agronomic control of bunch compactness. Among the different agronomic strategies capable of modifying bunch compactness, the modulation of source-sink balance is one of the most common practices. Fruitset rate is significantly reduced by inadequate available photosynthates at flowering (Caspari et al. 1998, Lebon et al. 2008). Although carbohydrate supply to the developing inflorescence might come from plant reserves and/or inflorescence photosynthesis, it is generally accepted that the main source of photoassimilates for the successful development of the inflorescence is leaf photosynthesis (Lebon et al. 2008, Vaillant-Gaveau et al. 2011), especially of the inflorescence-adjacent basal leaves of the same shoot (Motomura 1993, Caspari et al. 1998). Leaf removal, anti-transpirants and canopy shading (Table 2) have all been shown to reduce fruitset when applied pre-flowering or at full-flowering.

Leaf removal at pre-flowering or full-flowering typically reduces bunch compactness by affecting the number of berries, through the effect on fruitset (Table 2). Nonetheless, their effectiveness depends on a combination of other factors, including genotype and treatment severity (Molitor et al. 2011a, Acimovic et al. 2016). Too severe treatments can be effective, but they can affect the replenishment of plant reserves for the initiation and differentiation of inflorescence primordia, compromising next year's vine performance and future crop yield (Sabbatini and Howell 2010). In addition, the removal of a high number of leaves can cause an excessive bunch exposure that may lead to undesirable berry sunburn and to a decrease in must TA and an increase in must pH, which may impact wine composition (Poni et al. 2008, Intrigliolo et al. 2014, Sternad-Lemut et al. 2015, Sivilotti et al. 2016). In a recent report, Acimovic et al. (2016) found that the removal of leaves from six to eight basal nodes can be an appropriate practice for Pinot Noir to regulate fruitset and bunch compactness with no adverse effect on bud fruitfulness or vine performance the following year. In contrast, the effect of post-flowering leaf

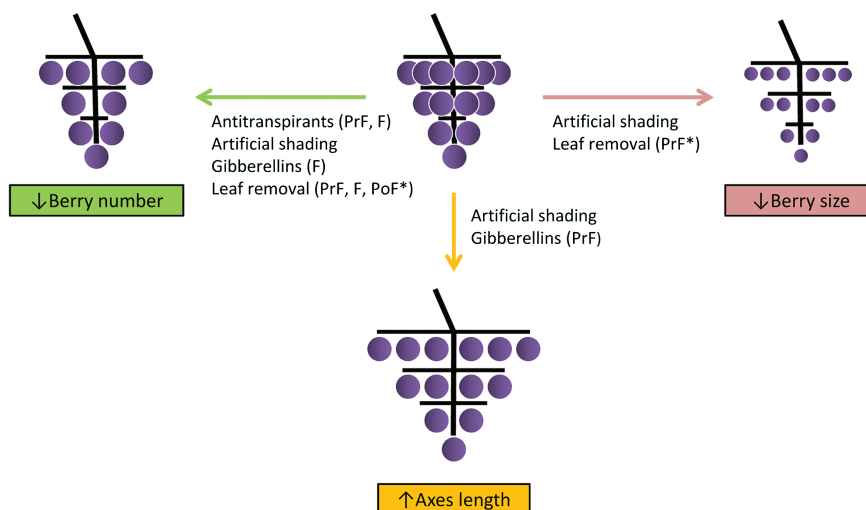


Figure 2. Schematic representation of the main viticultural strategies to reduce bunch compactness by reducing berry number (←), berry size (→) or increasing axes length (↓). F, flowering; PoF, post-flowering; PrF, pre-flowering. *Indicates inconsistent results between grapevine cultivars.

removal on bunch architecture appears to be cultivar-dependent (Table 2).

Leaf photosynthetic activity can be also interrupted by alternative and innovative systems, including the use of leaf anti-transpirants and artificial shading. Oily substances used as leaf anti-transpirants, such as paraffin and pinus oils, occlude the stomata of leaves, hinder their transpiration and influence carbon dioxide absorption, which ultimately hamper the photosynthetic activity of leaves (Palliotti et al. 2010, Hanni et al. 2013, Gatti et al. 2016). Their application at pre-flowering and full-flowering reduces the mobilisation of carbohydrates to developing inflorescences, which promotes flower drop and reduces berry number and bunch compactness (Table 2). In a study with cv. Sangiovese, Intrieri et al. (2013) reported that the pre-flowering application of the anti-transpirant Pinolene on the first eight basal main and lateral shoot leaves generated looser bunches due to the reduction in the number of berries (−32%) compared to that of the Control. Similarly, Hanni et al. (2013) observed a lower berry number and proportion of compact bunches and rot severity, after the application of two anti-transpirants (UFO and Vapor Gard) to the entire leaf canopy at full flowering in two cultivars, Pinot Gris and Pinot Blanc. In contrast, berry size, fruitset, bunch compactness and rot incidence were not significantly modified after the pre-flowering, pre-veraison or pre-flowering + pre-veraison application of Vapor Gard to the whole canopy in cv. Barbera (Gatti et al. 2016). Accordingly, additional research is needed to test the effect of different anti-transpirants in different grapevine cultivars to improve bunch architecture without impairing grape composition.

Recent studies show that artificial shading can be an efficient method to generate loose bunches (Table 2). Basile et al. (2015) observed that fruitset, berry number and compactness of cv. Aglianico bunches were significantly reduced by the early use (from flowering to full fruitset) of shade covers capable of reducing incident light by 50–90%. In a study with three seedless tablegrape cultivars, Sugraone, Crimson Seedless and Thompson Seedless, Domingos et al. (2016b) also reported the loosening effect of artificial early shading by increasing berry drop. Additionally, shade-promoted thinning induced a decrease in berry mass and diameter compared to that of untreated vines (Domingos et al. 2016b), which may

also contribute to a bunch loosening effect. From a molecular perspective, Domingos et al. (2015) suggested that shading treatments can induce flower abscission in the seeded cv. Black Magic by reducing leaf net photosynthetic rate, which induces significant metabolic alterations, including global carbohydrates starvation and an increase of oxidative stress signals that leads to flower drop. This phenomenon has also been observed in Thompson Seedless, where shade imposition promoted flower abscission via nutritional stress mainly associated with sugar-, ethylene- and auxin-responsive pathways (Domingos et al. 2016a).

Other crop management practices that have been applied to generate loose bunches include crop load management, the use of alternative pruning systems and diverse rootstocks (Ferreira and Marais 1987, Zabada and Dittmer 1998, Weyand and Schultz 2006, Archer and van Schalkwyk 2007), shoot trimming (Bondada et al. 2016), late first shoot topping (Molitor et al. 2015a), bunch thinning (Tardáguila et al. 2008, Gatti et al. 2014) and berry or bunch sections thinning (Molitor et al. 2012b, Roberto et al. 2015) (Table 2). Regarding the latter, the removal of approximately 60% of berries when they are between 7 and 18 mm in diameter is proposed as a more efficient strategy to reduce bunch compactness than flower thinning for the tablegrape cv. BRS Victoria, as the removal of flowers generates the appearance of too loose bunches with an unacceptable commercial value (Roberto et al. 2015). Accordingly, the direct removal of dense parts in the middle of compact grape bunches (grape bunch division) of winegrape cvs Pinot Gris and Riesling at pea-size has also been suggested as an efficient tool to optimise bunch architecture and grape and wine composition (Molitor et al. 2012b).

Chemical control: use of plant growth regulators. Several plant growth regulators have been experimentally applied to evaluate their effect on crop yield and on bunch and grape targeted attributes. The effects of gibberellins on different table- and winegrape cultivars have been extensively reported (Table 3), and they are widely used in tablegrape production. Gibberellins act as endogenous growth regulators on major aspects of plant growth and development and, in practical agriculture, they are successfully used in diverse

Table 2. Effect of agronomic treatments on bunch compactness.

Treatment	Cultivar	Application timing	Effect on bunch compactness†	Other effects on bunch architecture	Notes	Reference
Anti-transpirant	Sangiovese	PrF	↓	↓ Berry number	Use of Pinolene	Intrieri et al. (2013)
Anti-transpirant	Barbera	PrF, PrV and PrF + PrV	None	None	Use of Vapor Gard (pinus oil)	Gatti et al. (2016)
Anti-transpirant	Pinot Blanc	F	↓	↓ Berry number	Use of UFO (paraffin oil) or Vapor Gard (pinus oil)	Hanni et al. (2013)
Anti-transpirant	Pinot Gris	F	↓	↓ Berry number	Use of UFO (paraffin oil) or Vapor Gard (pinus oil)	Hanni et al. (2013)
Berry-bunch thinning	BRS Victoria	BPS	↓	↓ Berry number	Manual removal of berries	Roberto et al. (2015)
Manual bunch division	Pinot Gris	PoF	↓	Rearrangement of bunch morphology	Manual removal of berries	Molitor et al. (2012b)
Manual bunch division	Riesling	PoF	↓	Rearrangement of bunch morphology	Manual removal of berries	Molitor et al. (2012b)
Bunch thinning	Grenache	PoF	↓	↓ Berry number	Mechanical thinning	Tardáguila et al. (2008)
Bunch thinning	Orrugo	PoF	None	None	Manual removal 50% crop load	Gatti et al. (2014)
Bunch thinning	Tempranillo	PoF	↓	↓ Berry number	Mechanical thinning	Tardáguila et al. (2008)
Crop load	Chenin Blanc	-	None	No effect	12 and 25 buds/kg cane mass per vine	Ferreira and Marais (1987)
Leaf removal	Carignan	PrF	↓	↓ Berry number	Mechanical defoliation	Tardáguila et al. (2010)
Leaf removal	Cilieglio	PrF	↓	↓ Berry number, ↓ Berry size	Manual removal of all basal leaves	Pallotti et al. (2012)
Leaf removal	Graciano	PrF	↓	↓ Berry number	Mechanical defoliation	Tardáguila et al. (2010)
Leaf removal	Mandó	PrF	↓	↓ Fruitset, ↓ Berry number	Manual removal of leaf area of first eight basal nodes	Intrigliolo et al. (2014)
Leaf removal	Merlot	PrF	↓	↓ Berry number	Manual removal of five to six first basal leaves	Sivilotti et al. (2016)
Leaf removal	Orrugo	PrF	↓	↓ Berry number	Manual removal of leaf area of first six basal nodes	Gatti et al. (2014)
Leaf removal	Pinot Noir	PrF	↓	↓ Berry number	Manual removal of four to six first basal leaves	Sternad-Lemut et al. (2015)
Leaf removal	Sangiovese	PrF	↓	↓ Berry number	Manual removal six first basal leaves	Poni et al. (2006)
Leaf removal	Sangiovese	PrF	↓	↓ Fruitset, ↓ Berry number	Mechanical and manual removal six first basal leaves	Intrieri et al. (2008)
Leaf removal	Sangiovese	PrF	↓	↓ Fruitset, ↓ Berry number	Manual removal six first basal leaves	Poni et al. (2008)
Leaf removal	Sangiovese	PrF	↓	↓ Berry number, ↓ Berry size	Manual removal of all basal leaves	Pallotti et al. (2011)
Leaf removal	Sangiovese	PrF	↓	↓ Fruitset	Manual removal of primary leaves	Gatti et al. (2012)
Leaf removal	Sangiovese	PrF	↓	↓ Berry number	Manual removal of leaf area of first eight basal nodes	Intrieri et al. (2013)
Leaf removal	Tempranillo	PrF	↓	↓ Berry number	Mechanical defoliation	Tardáguila et al. (2012)
Leaf removal	Trebbiano	PrF	↓	↓ Berry number	Manual removal six first basal leaves	Poni et al. (2006)
Leaf removal	Vignoles	PrF	↓	↓ Fruitset	Manual removal four to six first basal leaves	Sabbatini and Howell (2010)
Leaf removal	Auxerrois	F	↓	Not reported	Manual removal of primary and lateral leaves (bunch-zone)	Molitor et al. (2011a)
Leaf removal	Mandó	F	↓	↓ Fruitset, ↓ Berry number	Manual removal of leaf area of first eight basal nodes	Intrigliolo et al. (2014)
Leaf removal	Pinot Gris	F	↓	Not reported	Manual removal of primary and lateral leaves (bunch-zone)	Molitor et al. (2011a)
Leaf removal	Pinot Noir	F	↓	↓ Fruitset, ↓ Berry number	Manual removal of leaf area of first ten basal nodes	Acimovic et al. (2016)
Leaf removal	Riesling	F	None	Not reported	Manual removal of primary and lateral leaves (bunch-zone)	Molitor et al. (2011a)
Leaf removal	Sauvignon Blanc	F	↓	↓ Berry number	Manual removal of primary and lateral leaves (bunch-zone)	Molitor et al. (2011a)
Leaf removal	Cabernet Sauvignon	PoF	None	None	Manual removal of leaf area of first six basal nodes	Kotseridis et al. (2012)
Leaf removal	Mandó	PoF	↓	↓ Fruitset, ↓ Berry number	Manual removal of leaf area of first eight basal nodes	Intrigliolo et al. (2014)
Leaf removal	Merlot	PoF	↓	↓ Berry number	Manual removal of leaf area of first six basal nodes	Kotseridis et al. (2012)
Leaf removal	Merlot	PoF	None	None	Manual removal five to six first basal leaves	Sivilotti et al. (2016)
Leaf removal	Orrugo	PoF	None	None	Manual removal of leaf area of first six basal nodes	Gatti et al. (2014)
Leaf removal	Sangiovese	PoF	None	None	Manual removal of leaf area of first six basal nodes	Kotseridis et al. (2012)
Leaf removal	Tempranillo	PoF	↓	↓ Berry number, ↓ Berry size	Mechanical defoliation	Tardáguila et al. (2012)

(Continues)

Table 2. Continued

Treatment	Cultivar	Application timing	Effect on bunch compactness†	Other effects on bunch architecture	Notes	Reference
Pruning system	Cabernet Sauvignon	-	↓	Not reported	Hand, mechanical, minimal and no pruning system.	Archer and van Schalkwyk (2007)
Pruning system	Chardonnay	-	↓	Not reported	Effect seen on non-pruned vines	Zabada and Dittmer (1998)
Pruning system	Chenin Blanc	-	None	None	Mid-wire cordon (MWC), Umbrella-Knifin training (UK) and combined MWC/UK pruning system	Ferreira and Marais (1987)
Rootstock	Chenin Blanc	-	↓	Not reported	Cane-pruning and spur-pruning system	Ferreira and Marais (1987)
Shoot trimming	Sangiovese	PoV	↓	↓ Berry size	Ramsey, 99 Richter, 110 Richter, 101–14 Mgt and Jacquez rootstocks	Bondada et al. (2016)
Vine shading	Aglianico	F	↓	↓ Berry number	Shoot trimming to ten nodes	Basile et al. (2015)
Vine shading	Black Magic	F	↓	↓ Berry number, ↓ Berry size	Use of whole-canopy artificial shading (50–90% reduction of ambient light)	Domingos et al. (2015)
Vine shading	Crimson Seedless	F	↓	↓ Berry number, ↓ Berry size	Use of whole-canopy artificial shading (90% reduction of ambient light)	Domingos et al. (2016b)
Vine shading	Sugraone	F	↓	↓ Berry number, ↓ Berry size	Use of whole-canopy artificial shading (90–100% reduction of ambient light)	Domingos et al. (2016b)
Vine shading	Thompson Seedless	F	↓	↓ Berry number, ↓ Berry size	Use of whole-canopy artificial shading (90–100% reduction of ambient light)	Domingos et al. (2016b)

†↓ indicates significant reduction of bunch compactness. BPS, berries pea size; F, flowering; PoF, post-flowering; PrF, pre-flowering; PoV, post-veraison; PrV, pre-veraison.

crop species to improve plant growth and specific traits (Gianfagna 1995, Rademacher 2015).

Early studies in viticulture indicated the potential use of gibberellins in grape production to increase crop yield, to enhance grape composition, to hasten flowering and ripening times, and to generate loose bunches in tight cultivars (Weaver 1960). Those initial studies already indicated that their efficiency depends on numerous factors, including cultivar, timing and dosage of application. Weaver et al. (1962) reported that tight bunches of wine cvs Carignane, Tinta Madeira and Zinfandel were loosened by the pre-flowering application of gibberellins (Table 3), and greatly decreased the incidence of rots without markedly affecting crop yield. More intensive studies on three cultivars, Thompson Seedless, Zinfandel and Sauvignon Blanc, indicated that the ‘loosening effect’ was caused by the elongation of the main axes of the bunch (Weaver and McCune 1962, Miele et al. 1978, Molitor et al. 2012a) (Table 3). This elongating effect was in agreement with other studies with seeded and seedless cultivars (Dass and Randhawa 1968, Considine and Coombe 1972). Correa et al. (2014) observed similar results in a Ruby Seedless × Sultanina progeny and described a complex genetic basis in response to gibberellic acid application. Besides, Miele et al. (1978) reported an additional effect of the pre-flowering application of gibberellins on Zinfandel, which caused a decrease in berry number and berry size (Table 3), contributing to the loose aspect of the bunches. Nonetheless, the use of gibberellins at pre-flowering has been related to some undesirable side effects in the subsequent seasons, such as a reduction in the number of inflorescences per shoot, that compromise future crop yield (Molitor et al. 2012a).

The application of gibberellins at full-flowering has been shown to be an effective strategy to reduce the rate of fruitset (and berry number and bunch compactness) in both seeded (Hopping 1975, Evers et al. 2010, Hed et al. 2011, 2015) and seedless cultivars (Christodoulou et al. 1966, 1968, Lynn and Jensen 1966, Mosesian and Nelson 1968, Miele et al. 1978, Dokoozian and Peacock 2001). Recently, Domingos et al. (2016a) suggested that flower abscission in Thompson Seedless inflorescences promoted by the application of gibberellins at flowering time requires energy production and stimulation of global metabolism. In any case, cultivar and dosage of application are factors that greatly affect the efficiency of the treatment (Hopping 1975, Hed et al. 2011). In some cultivars, such gibberellins-mediated berry thinning has been reported to be too excessive, causing a large number of shot berries (Blaha 1963, Lynn and Jensen 1966, Kasimatis et al. 1971, Hed et al. 2015), which reduces crop yield to an unsustainable level.

Post-flowering application of gibberellins had the opposite effect: it increased compactness of Thompson Seedless bunches, by increasing berry size (El-Banna and Weaver 1978). In fact, application of gibberellins at early stages of berry development is a common practice in viticulture to increase fruit size and economic value of seedless grapes (Kasimatis et al. 1971, Singh et al. 1978, Lu 1996, Zabada and Dittmer 2000, Casanova et al. 2009). In stenospermocarpic cultivars (most of the seedless commercial grapes), ovule fertilisation and embryo formation is followed early by seed development abortion, so that only seed traces are found in the ripe berry. Consequently, seeds (the primary natural source of gibberellins for fruit development) produce gibberellins only prior to abortion (Pérez et al. 2000), and an exogenous application is usually needed to reach a commercially-acceptable berry size. A recent transcriptomic analysis of cv. Centennial Seedless berries treated with

gibberellins after flowering suggests that the treatment triggers temporal and multi-level cross talk, generating changes in the integrated hormone signalling network, and modifying the expression of terminal cell-wall enzymes that promote cell enlargement processes (Chai et al. 2014).

Beyond gibberellins, other growth regulators have been applied to loosen compact bunches (Table 3). Application of prohexadione-calcium (3-oxido-4-propionyl-5-oxo-3-cyclohexene-carboxylate) formulations at full flowering has been shown as an effective strategy to reduce bunch compactness in diverse seeded winegrape cultivars (Molitor et al. 2011b, Schildberger et al. 2011). Prohexadione-calcium inhibits the biosynthesis of growth active gibberellins (GA_1), causing an accumulation of its inactive direct precursor (GA_{20}) (Evans et al. 1999). This disturbance in the proportion between active and inactive gibberellins has been suggested to

promote flower or berry abortion (Molitor et al. 2011b), potentially reducing berry number and, consequently, bunch compactness. Interestingly, Schildberger et al. (2011) indicated that prohexadione-calcium also generated a reduction in berry size. Other growth regulators assayed to modify bunch architecture are forchlorfenuron [N-(2-chloro-4-pyridinyl)-N-phenylurea, CPPU] and ethephon (2-chloroethylphosphate acid) (Table 3). Forchlorfenuron is a synthetic cytokinin-like regulator that, at low concentration, may promote berry set and development, increasing berry number and size (Zabada and Bukovac 2006). Nonetheless, its efficiency is cultivar-dependent: Zabada and Bukovac (2006) found that berry size and bunch compactness could be increased in the CPPU-sensitive cvs Himrod and Vanessa, whereas no significant effect was recorded in the CPPU-insensitive cvs Lakemont Seedless, Concord and Niagara.

Table 3. Effect of plant growth regulators on bunch compactness.

Treatment	Cultivar	Application timing	Effect on bunch compactness†	Effect on bunch architecture	Reference
CPPU (5–15 mg/L)	Concord	B4	None	No effect	Zabada and Bukovac (2006)
CPPU (5–15 mg/L)	Himrod	B4	↑	↑ Berry size	Zabada and Bukovac (2006)
CPPU (5–15 mg/L)	Lakemont Seedless	B4	None	No effect	Zabada and Bukovac (2006)
CPPU (5–15 mg/L)	Niagara	B4	None	No effect	Zabada and Bukovac (2006)
CPPU (5–15 mg/L)	Vanessa	B4	↑	↑ Berry size, ↑ Berry number	Zabada and Bukovac (2006)
Ethephon (100–500 mg/L)	Thompson Seedless	V	None	No effect	El-Banna and Weaver (1978)
Gibberellins (1–5 mg/L)	Carignane	PrF	↓	Not reported	Weaver et al. (1962)
Gibberellins (Gibb3, 10 mg/L)	Sauvignon Blanc	PrF	↓	↑ Bunch length	Molitor et al. (2012a)
Gibberellins	Thompson Seedless	PrF	↓	↑ Bunch length	Weaver and McCune (1962)
Gibberellins (1–5 mg/L)	Tinta Madeira	PrF	↓	Not reported	Weaver et al. (1962)
Gibberellins (1–5 mg/L)	Zinfandel	PrF	↓	Not reported	Weaver et al. (1962)
Gibberellins (5–50 mg/L)	Zinfandel	PrF	↓	↓ Fruitset, ↓ Berry size, ↑ Bunch length, ↑ Pedicel length	Miele et al. (1978)
Gibberellins (Pro-Gibb, 5–25 mg/L)	Chardonnay	F	↓	↓ Fruitset	Hed et al. (2011)
Gibberellins (Pro-Gibb, 10–25 mg/L)	Chardonnay	F	↓	↓ Berry number	Hed et al. (2015)
Gibberellins (Pro-Gibb, 2.5–25 g/ha)	Crimson Seedless	F	↓	↓ Fruitset	Dokoozlian and Peacock (2001)
Gibberellins (Gibb3, 800 L/ha)	Pinot Noir	F	↓	↓ Fruitset	Evers et al. (2010)
Gibberellins (5–40 mg/L)	Seibel 5455	F	↓	↓ Fruitset	Hopping (1975)
Gibberellins	Sultanina	F	↓	↑ Pedicel length	Sarooshi (1977)
Gibberellins (10–20 mg/L)	Thompson Seedless	F	↓	↓ Berry number	Lynn and Jensen (1966)
Gibberellins (20 mg/L)	Thompson Seedless	F	↓	↓ Berry number	Christodoulou et al. (1968)
Gibberellins (5–25 mg/L)	Thompson Seedless	F	↓	↓ Berry number	Mosesian and Nelson (1968)
Gibberellins (KGA ₃ , 15–25 mg/L)	Thompson Seedless	F	↓	↓ Fruitset	Miele et al. (1978)
Gibberellins (Pro-Gibb, 5–40 mg/L)	Vignoles	F	↓	↓ Fruitset	Hed et al. (2011)
Gibberellins (KGA ₃ , 5–50 mg/L)	Thompson Seedless	PoF	↑	↑ Berry size	El-Banna and Weaver (1978)
Prohexadione-Ca (Regalis, 1.5 kg/ha)	Grüner Veltliner	F	↓	↓ Berry size	Schildberger et al. (2011)
Prohexadione-Ca (Regalis, 1.5 kg/ha)	Pinot Blanc	F	↓	Not reported	Molitor et al. (2011b)
Prohexadione-Ca (Regalis, 1.5 kg/ha)	Pinot Gris	F	↓	Not reported	Molitor et al. (2011b)

†↓ Indicates significant reduction of bunch compactness; ↑ indicates significant increase of bunch compactness. B4, berries 4 mm; F, flowering; PoF, post-flowering; PrF, pre-flowering; V, veraison.

Lastly, ethephon has been used to stimulate spontaneous abscission of mature grape berries (Rizzuti et al. 2015, Ferrara et al. 2016) and, together with abscisic acid, to improve the colour of red grapes (Leão et al. 2015). El-Banna and Weaver (1978) evaluated the effect of ethephon in the compactness of Thompson Seedless bunches, but they found no significant modification after its use. Thus, further research is required to evaluate the impact of these compounds before recommending their use.

Conclusion and perspectives

Grapegrowers intend to produce the maximum crop yield which is compatible with the desired attributes and with the minimum inputs. That goal is difficult to achieve in the case of grapevine cultivars producing compact bunches because, in general, they are more susceptible to the pathogens of major economic importance in viticulture, and their tight architecture jeopardises the homogeneous ripening of the individual berries. Grapegrowers have then to use different strategies, such as pesticide treatments and management practices, to minimise these negative effects. Nevertheless, they normally entail additional production costs and, in some cases, collateral effects. So, a better understanding of the structure of this trait in terms of its components is needed to provide alternative solutions. In this regard, obtaining high quality phenotypic data is essential, and more studies are required both in narrow (intra-cultivar) and in wide (multi-cultivar) genetic frameworks under different environmental conditions to reveal the variation existing for the main factors involved in the compaction of the berries along the rachis.

A closely related challenge is to develop an objective methodology to assess variation in bunch compactness that can be standardised for wide use. In contrast to available subjective scales that provide categorical data, it is essential to develop and validate quantitative and reliable systems for trait evaluation, which will be useful for both vine growers and the scientific community in grapevine genetics studies and breeding activities. To this effect, the application of novel image-based tools is expected to open new possibilities in the phenotyping of bunch architecture. Nonetheless, experimental setup, image acquisition and data analysis need to be adequately developed and converted into easy-to-use systems to become a reality for the viticulture industry and for laboratories lacking highly experienced staff and dedicated equipment.

Little is known about the genetic basis and molecular mechanisms of bunch compactness. Recent linkage mapping (Correa et al. 2014) and association mapping (Tello et al. 2016b) studies have suggested the likely involvement of some genes on the determination of bunch architecture, but they need further research to test their functionality and phenotypic effect by means of specific gene-directed studies. Although these genes are interesting candidates, they might be single pieces of a highly complex puzzle. In this regard, novel -omics (genomics, transcriptomics, proteomics, metabolomics) approaches arise as powerful tools to understand natural variation in cultivated species (Van Emon 2016). They will allow the discovery and intensive analysis of the genes and metabolic pathways determining bunch architecture, and will expand the scope from the study of single genes, individual proteins or specific compounds to the study of the whole grapevine genome, transcriptome, proteome and metabolome. For this work, the reducing cost of the Next Generation Sequencing (NGS) technologies will allow the massive genotyping of genetic variants or,

ultimately, the whole sequencing of many grapevine cultivars. This information (together with phenotypic data) will provide an invaluable resource to identify candidate genes and polymorphisms with a likely role in bunch architecture and bunch compactness determination (He et al. 2014).

Last, more information on the effect of different environmental conditions on bunch architecture and compactness is needed, especially under projected climate scenarios. Climate change is expected to have important impacts on worldwide viticulture, and viticulturists will face new challenges derived from the joint effect of higher temperature, water stress, CO₂ and solar radiation (Fraga et al. 2013, Hannah et al. 2013). Accordingly, understanding the effect of these factors on bunch architecture is of paramount relevance both for practical viticulture and for breeding new cultivars or selecting new clones more adapted to drought and heat. Current available information about the way that changes in temperature, light intensity and water and nutrition status might affect bunch architecture and compactness is still scarce and further research is needed to ascertain their relevance. In practice, it is impossible to control all the environmental factors that affect the determination of bunch compactness, but novel agricultural practices might aid to overcome the negative effects derived from climate change. Within the different agronomic techniques and compounds outlined in this review, early leaf removal and artificial shading have shown the most promising results for bunch loosening. Combined with the application of low doses of plant growth regulators at specific growth stages, these methods can provide efficient and more environment-friendly solutions to the use of synthetic fungicides to control bunch rots in susceptible grape cultivars, leading to more cost-effective grape production systems to fulfil global market demand for sustainable products.

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