

Multicultural and multivariate study of the natural variation for grapevine bunch compactness

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Abstract

Background and Aims: Grapevine bunch compactness is an important trait with impact on fruit quality, mainly affecting the susceptibility to bunch rot. Many and different variables have been reported to have a significant influence on the variation of bunch compactness in particular cultivars, but little is known about the role of such variables in a wider framework. The aim of this work was to identify and weight the features responsible for the natural variation in bunch compactness in a large and diverse grapevine collection.

Methods and Results: Different statistical tests were sequentially applied to select the determining variables most influencing bunch compactness. Significant and low correlation was obtained for most of the variables studied for three consecutive seasons, confirming the multifactorial nature of this trait. Multivariate analyses indicated that there are three groups of variables with a significant influence on bunch compactness. Two groups, represented by the total number of berries per bunch and by the length of the first ramification of the bunch, are major factors responsible for the trait variation, whereas berry dimensions have a secondary role.

Conclusions: Bunch compactness is defined by the difference between its morphological (apparent) volume and its actual (solid) volume. The results showed that the actual volume is mainly determined by the total number of berries, whereas the morphological volume also depends on its spatial arrangement, determined by the architecture of the rachis.

Significance of the Study: This is the first multiyear study of bunch compactness at a multicultural level, and it has allowed the selection and weighting of the main variables affecting the trait. These variables are suitable targets to study the underlying genetics of the trait.

Keywords: *bunch architecture, bunch density, bunch morphology, linear discriminant analysis, Vitis vinifera L.*

Introduction

Grapevine (*Vitis vinifera* L.) is a fruit crop of great economic importance worldwide. In its 2013 report, the Organisation Internationale de la Vigne et du Vin (OIV) estimated that more than 7.5 million ha are dedicated to grapevine cultivation around the world, with Spain, France, Italy, China, Turkey and the USA being the major vine-growing countries (Organisation Internationale de la Vigne et du Vin 2013). Grapes are mainly produced for winemaking, followed by consumption as fresh fruit and raisins.

Bunch compactness has significant implications in the commercial quality and sanitary status of grapes, and it is an important trait in clonal selection and grape-breeding activities (Reisch et al. 2012). Loose bunches show a minor incidence of important grape pests and diseases, such as *Botrytis cinerea* (Vail and Marois 1991, Vail et al. 1998, Valdés-Gómez et al. 2008, Hed et al. 2009), *Lobesia botrana* (Fermaud 1998, Ioratti et al. 2011) and *Aspergillus* spp. (Leong et al. 2006). This fact has been explained by the combined effect of an increased inner airflow and lower humidity, an improved coverage by fungicide spraying, and/or by showing less physical damage caused by berry-to-berry contact (Hed et al. 2011, Molitor et al. 2012b) that may cause the appearance of microscopic cracks in the grape berry cuticle (Becker and Knoche 2012). In addition, compact

bunches have more inner berries than loose bunches (Vail and Marois 1991), which may lead to an inadequate sun irradiation, affecting the phenolic ripeness of the bunch (Figueiredo-González et al. 2013). The composition of phenolic substances of grapes at harvest time, especially the concentration of anthocyanins and tannins, is significant to the final quality of wine, because it influences key sensory properties, such as colour, aroma, astringency and bitterness (Pinelo et al. 2006). In contrast, the tablegrape market demands loose grape bunches of reasonable size and homogenous shape (Wei et al. 2002, Reisch et al. 2012, Río-Segade et al. 2013), and the fruit industry also prefers loose bunches because compact bunches are more vulnerable to pressure stresses that appear during normal handling of fresh grapes (Nelson et al. 1970). Moreover, water loss from fresh berries to produce raisins is slower as bunch compactness increases (Christensen 2000), requiring longer drying times and/or more energy.

Consequently, numerous treatments have been tested to reduce bunch compactness in both wine and table cultivars, including the use of gibberellins (Vartholomaïou et al. 2008, Evers et al. 2010, Hed et al. 2011, Molitor et al. 2012a), prohexadione-calcium (Lo Giudice et al. 2004, Vartholomaïou et al. 2008, Schildberger et al. 2011), forchlorfenuron [N-(2-chloro-4-pyridinyl)-N'-phenyl-Urea (CPPU)] (Zabada and

Bukovac 2006) and other innovative products (Abd-Allah et al. 2013, Hanni et al. 2013), as well as cultural practices, such as leaf removal (Evers et al. 2010, Sabbatini and Howell 2010, Kotseridis et al. 2012, Palliotti et al. 2012, Tardáguila et al. 2012, Intrigliolo et al. 2014), bunch thinning (Tardáguila et al. 2012) and alternative vine management systems (Zabadal and Dittmer 1998, Archer and van Schalkwyk 2007, Molitor et al. 2012b). Many of these strategies also affect the final number of berries in the bunch, producing a reduction of crop yield.

The grapevine inflorescence (or bunch) is botanically considered a panicle (Pratt 1971). Its structure has been fully described (May 2000, Lebon et al. 2008, Vasconcelos et al. 2009), and it is morphologically characterised by its conical structure because of its multiple and progressive branching. The morphology of grapevine inflorescences varies widely between cultivars, representing a substantial reservoir of diversity for important traits (This et al. 2011). Inflorescence morphogenesis occurs in two stages, separated by a dormant period. The first stage – in latent buds during the first season – comprises important processes such as the development of the inflorescence meristem and the differentiation of the primary branches. The second stage occurs after dormancy (second season) and includes the elongation of the rachis and branches and the differentiation of secondary and tertiary branches, ending in the formation of floral meristems and finally individual flowers (Dunn and Martin 2007, Carmona et al. 2008, Tahyaoui et al. 2008). The number of flowers formed per inflorescence, together with the rate of pollination and transformation of flowers into berries (fruitset rate), determine the final number of berries in the bunch. After fruitset, individual berries start to grow, and their size at ripening can vary considerably between cultivars (Houel et al. 2013). All these processes determine the final morphology and shape of the bunch and may contribute to bunch compactness.

Bunch compactness, in terms of morphology, is defined by the difference between the solid volume of the berries and the rachis (actual volume) and the tridimensional volume occupied by the bunch (morphological volume) (Sepahi 1980, Shavrukov et al. 2004). Many different structural elements of the grapevine bunch have been reported by different authors as key factors defining bunch compactness. Studies of clones or in plants of a single cultivar subjected to different treatments for the loosening of the bunch have identified the number of berries (Poni et al. 2008, Vartholomaiou et al. 2008, Palliotti et al. 2012), their individual size (Alonso-Villaverde et al. 2008, Schildberger et al. 2011, Palliotti et al. 2012), the bunch length (Molitor et al. 2012a), the pedicel length (Sarooshi 1977) and the bunch mass (Vail et al. 1998, Valdés-Gómez et al. 2008) as the key factors in the variation of bunch compactness. The last factor was also highlighted by Vail and Marois (1991) in a work with four grapevine cultivars with different bunch morphology (Barbera, Cabernet Sauvignon, Colombard and Semillon). Shavrukov et al. (2004) also studied four cultivars (Exotic, Sultana, Riesling and Chardonnay) and identified the total length of the inflorescence, and specifically the internode length of the inflorescence rachis as the major trait responsible for the variability in bunch compactness.

Thus, several in-depth surveys have attempted to identify and determine the significance of variables involved in bunch compactness using a limited set of cultivars, but little is known about the role of such variables in a much wider and more diverse sample. Accordingly, the aim of this survey was to identify, in a multicultural framework, which morpho-agronomic variables make the largest and most stable contribution to the definition of bunch compactness. To achieve this goal, a large

and diverse sample of grapevine cultivars was studied during three consecutive seasons.

Materials and methods

Plant material

Grapevine cultivars. In this study, a set of 125 grapevine accessions, corresponding to 118 different cultivars, was chosen to represent a high proportion of the bunch compactness and bunch morphology variability that is naturally present in the grapevine (Table 1). In some cases, different accessions of the same cultivar were used, and they appear with the same cultivar name and different accession number in Table 1. These accessions belong to the ICVV Grapevine Collection (ESP-217) and are maintained in duplicate at two experimental plots: Finca Valdegón (Agoncillo, La Rioja, Spain) and Finca La Grajera (Logroño, La Rioja, Spain). Plants at Finca Valdegón are between 20 and 30 years old and were used in the 2011 and 2012 seasons. Vines at Finca La Grajera were planted in 2009 from scions taken at Finca Valdegón and were used in 2013. All plants considered in this work were maintained in the same way within each experimental plot and year, following standard agronomical management conditions in terms of grafting, pruning system and disease control.

Tempranillo clones. Four clones of the cv. Tempranillo were chosen from the clone collection maintained at the private breeding nursery of Viveros Provedo (Logroño, La Rioja, Spain). Two clones with compact bunches (RJ-51 and VP-2) and two clones with loose bunches (VP-11 and VP-25) were selected to validate the results obtained in the multicultural study. Plants were maintained under standard cultural practices.

Characterisation of grape bunches

Morphological characterisation was done in three consecutive years (2011, 2012 and 2013) on bunches collected at their proper harvest time [modified E-L stage 38; Coombe (1995)]. In general, 10 similar bunches were selected per cultivar and year (Table 1) and were taken from at least three plants. During the 3 years, 3162 bunches (1040 in 2011, 1145 in 2012 and 977 in 2013) were collected and evaluated, and each bunch was treated and analysed independently. For winged bunches, only the primary bunch, according to the OIV descriptor N° 206 (Organisation Internationale de la Vigne et du Vin 2007), was considered. The 24 morpho-agronomic variables studied in this work are described in Table 2, and they were classified a priori in one of four categories: plant (e.g. number of shoots per plant), bunch (e.g. bunch mass), berry (e.g. berry length) and fruitfulness (e.g. number of berries per bunch). When available, definitions or recommendations included in the OIV descriptors were followed for the morphological description, but quantitative data were taken (Organisation Internationale de la Vigne et du Vin 2007). Bunch density or compactness was scored according to the ordinal OIV descriptor N° 204 (Organisation Internationale de la Vigne et du Vin 2007), using a scale from 1 to 9, where 1 means ‘very loose’ (berries in grouped formation, many visible pedicels), 3 ‘loose’ (single berries with some visible pedicels), 5 ‘medium’ (densely distributed berries, pedicels not visible), 7 ‘dense’ (berries not readily movable) and 9 ‘very dense’ (berries out of shape). A panel of four judges was trained in the use of this descriptor, and their mode value was considered in this study. In case of a tie, a fifth judge was asked for their evaluation. Bunch and berry mass was determined using a scale (Blauscal AC-5000, Gram Precision, Barcelona, Spain), whereas bunch and berry dimension was measured with rulers

Table 1. List of the grapevine accessions (n = 125), corresponding to 118 different cultivars, sampled for this study.

Accession number	Cultivar name [†]	No. of bunches			Main use [‡]	Grape skin colour [§]
		2011	2012	2013		
ESP217-5056	Afus Ali [¶]	10	10	10	W/T	Green yellow
ESP217-5000	Airén [¶]	n.i.	10	n.i.	W/T	Green yellow
ESP217-5100	Airén [¶]	10	10	10	W/T	Green yellow
ESP217-5179	Alarije [¶]	10	10	10	W	Green yellow
ESP217-5003	Albillo de Madrid [¶]	n.i.	10	n.i.	W/T	Green yellow
ESP217-5094	Alcañón [¶]	10	10	10	W	Green yellow
ESP217-5005	Aledo [¶]	10	10	10	T	Green yellow
ESP217-5001	Alfrocheiro [¶]	10	10	9	W	Blue black
ESP217-5008	Alicante Henri Bouschet [¶]	10	10	10	W	Blue black
ESP217-5009	Aligote [¶]	10	10	10	W	Green yellow
ESP217-5006	Alphonse Lavallee [¶]	10	10	10	W/T/R	Dark red violet
ESP217-5029	Alvarelhao [¶]	10	10	10	W	Blue black
ESP217-5002	Alvarinho [¶]	10	10	10	W	Green yellow
ESP217-5125	Aramon Noir [¶]	10	10	10	W/T	Blue black
ESP217-5015	Aubun [¶]	10	10	10	W	Blue black
ESP217-5016	Auxerrois [¶]	10	10	n.i.	W	Green yellow
ESP217-5022	Barbera Nera [¶]	10	10	10	W	Blue black
ESP217-5034	Beba [¶]	10	10	10	W/T	Green yellow
ESP217-5206	Beba [¶]	n.i.	9	n.i.	W/T	Green yellow
ESP217-5036	Beba Roja [¶]	10	10	10	W/T	Red
ESP217-5027	Bobal [¶]	10	10	n.i.	W	Blue black
ESP217-5148	Bouschet Petit [¶]	10	10	10	W	Blue black
ESP217-5030	Cabernet Franc [¶]	10	n.i.	10	W	Blue black
ESP217-5031	Cabernet Sauvignon [¶]	10	10	10	W	Blue black
ESP217-5032	Caiño Tinto [¶]	10	10	10	W	Blue black
ESP217-5037	Cardinal [¶]	n.i.	10	n.i.	W/T	Red
ESP217-5038	Carnelian	10	10	9	W	Blue black
ESP217-5144	Castelao [¶]	10	10	10	W	Blue black
ESP217-5021	Cayetana Blanca [¶]	10	n.i.	10	W/T	Green yellow
ESP217-5043	Centurión	10	10	10	W	Blue black
ESP217-5045	Chardonnay Blanc [¶]	10	10	10	W	Green yellow
ESP217-5046	Chasselas Blanc [¶]	10	10	10	W/T	Green yellow
ESP217-5050	Cinsaut [¶]	10	10	10	W/T	Blue black
ESP217-5051	Clairette Blanche [¶]	10	20	10	W/T	Green yellow
ESP217-5074	Colombard [¶]	10	10	10	W/T	Green yellow
ESP217-5054	Cornichon Blanc	10	10	10	W/T	Green yellow
ESP217-5149	Cornichon Blanc [¶]	10	10	n.i.	W/T	Green yellow
ESP217-5099	Cot [¶]	10	10	10	W/T	Blue black
ESP217-5158	Cuelga [¶]	10	10	10	W	Green yellow
ESP217-5156	Danugue [¶]	10	10	10	W/T	Blue black
ESP217-5057	Delight [¶]	10	10	n.i.	T	Green yellow
ESP217-5113	Derechero de Muniesa [¶]	10	10	n.i.	W/T	Blue black
ESP217-5059	Dominga [¶]	10	10	6	W/T	Green yellow
ESP217-5084	Doña Blanca [¶]	10	10	10	W/T	Green yellow
ESP217-5049	Doradilla [¶]	n.i.	10	10	W/T	Green yellow
ESP217-5063	Espadeiro	n.i.	10	10	W	Blue black
ESP217-5087	Flot Rouge [¶]	10	10	10	W	Blue black
ESP217-5068	Fogoneau [¶]	10	10	10	W	Blue black
ESP217-5070	Folle Blanche [¶]	10	10	10	W	Green yellow
ESP217-5072	Forcallat Tinta [¶]	10	10	10	W	Blue black
ESP217-5076	Gamay Noir [¶]	n.i.	10	10	W	Blue black
ESP217-5077	Garganega [¶]	10	10	10	W/T	Green yellow
ESP217-5123	Garnacha [¶]	10	n.i.	n.i.	W	Grey
ESP217-5082	Garrido Fino [¶]	10	10	10	W/T	Green yellow
ESP217-5142	Graciano [¶]	10	10	10	W	Blue black
ESP217-5190	Graciano [¶]	n.i.	10	n.i.	W	Blue black
ESP217-5060	Imperial Napoleón [¶]	10	8	10	T	Red
ESP217-5092	Italia [¶]	10	10	n.i.	W/T	Green yellow
ESP217-5093	Jacquez [¶]	10	10	10	W	Blue black
ESP217-5132	Listán Negro [¶]	10	n.i.	10	W	Blue black
ESP217-5114	Listán Prieto [¶]	10	10	10	W	Blue black
ESP217-5098	Loureiro Blanco [¶]	10	10	10	W	Green yellow
ESP217-5064	Mantuo [¶]	10	10	10	W/T	Green yellow
ESP217-5014	Marufo [¶]	10	10	n.i.	W/T	Blue black
ESP217-5107	Maturana Blanca [¶]	10	10	10	W	Green yellow

Table 1. (continued)

Accession number	Cultivar name [†]	No. of bunches			Main use [‡]	Grape skin colour [§]
		2011	2012	2013		
ESP217-5110	Mencía [¶]	10	10	10	W	Blue black
ESP217-5111	Merlot Noir [¶]	10	10	10	W	Blue black
ESP217-5112	Merseguera [¶]	10	10	10	W	Green yellow
ESP217-5134	Mollar Cano [¶]	10	10	10	W/T	Blue black
ESP217-5116	Monastrell [¶]	10	10	10	W/T	Blue black
ESP217-5117	Moravia Agria [¶]	10	n.i.	n.i.	W	Blue black
ESP217-5119	Morio Muskat [¶]	n.i.	10	10	W	Green yellow
ESP217-5095	Moristel [¶]	10	10	10	W	Blue black
ESP217-5129	Muscat a Petits Grains Blancs [¶]	10	n.i.	n.i.	W/T	Green yellow
ESP217-5120	Muscat Hamburg [¶]	10	10	10	W/T	Green yellow
ESP217-5121	Muscat Hamburg [¶]	n.i.	8	n.i.	W/T	Green yellow
ESP217-5130	Muscat Ottonel [¶]	10	10	10	W/T	Green yellow
ESP217-5131	Naparo [¶]	10	10	n.i.	T	Red
ESP217-5133	Negral	10	10	10	W	Blue black
ESP217-5136	Ondarrabi Beltza [¶]	10	10	10	W/T	Blue black
ESP217-5137	Palomino Fino [¶]	10	10	10	W/T	Green yellow
ESP217-5138	Paraíso	10	10	10	T	Green yellow
ESP217-5106	Pardillo [¶]	10	10	10	W	Green yellow
ESP217-5141	Parellada [¶]	10	10	10	W	Green yellow
ESP217-5143	Pedro Ximenes [¶]	10	10	10	W	Green yellow
ESP217-5151	Pinot Meunier [¶]	n.i.	10	n.i.	W	Blue black
ESP217-5152	Pinot Noir [¶]	10	10	10	W	Blue black
ESP217-5155	Planta Fina [¶]	10	n.i.	10	W/T	Green yellow
ESP217-5157	Planta Nova [¶]	10	10	5	W/T	Green yellow
ESP217-5209	Puesto Mayor [¶]	n.i.	10	8	W	Blue black
ESP217-5159	Quiebratinajas [¶]	10	10	10	T	Red
ESP217-5047	Rey [¶]	10	10	10	W/T	Green yellow
ESP217-5104	Rey [¶]	10	10	8	W/T	Green yellow
ESP217-5165	Riesling Weiss [¶]	10	10	10	W	Green yellow
ESP217-5167	Rubired [¶]	n.i.	10	10	W/T	Blue black
ESP217-5168	Ruby Cabernet [¶]	10	10	7	W/T	Blue black
ESP217-5169	Ruby Seedless [¶]	10	10	9	T	Rose
ESP217-5172	Sangiovese [¶]	10	10	10	W	Blue black
ESP217-5173	Sauvignon Blanc [¶]	10	n.i.	10	W	Green yellow
ESP217-5083	Savagnin (=Traminer) [¶]	n.i.	10	10	W	Green yellow
ESP217-5202	Schiava Grossa [¶]	10	n.i.	10	W/T	Blue black
ESP217-5174	Semillón [¶]	10	10	10	W	Green yellow
ESP217-5181	Silvaner Gruen [¶]	10	10	8	W	Green yellow
ESP217-5180	Sumoll [¶]	10	10	n.i.	W	Blue black
ESP217-5182	Syrah [¶]	10	10	10	W	Blue black
ESP217-5197	Syrah [¶]	n.i.	10	n.i.	W	Blue black
ESP217-5183	Tempranillo [¶]	n.i.	10	n.i.	W/T	Blue black
ESP217-5184	Tempranillo Blanco [¶]	10	10	n.i.	W/T	Green yellow
ESP217-5073	Tinto Velasco [¶]	n.i.	10	10	W	Blue black
ESP217-5194	Torrontés	10	10	10	W	Green yellow
ESP217-5198	Trajadura [¶]	10	10	10	W	Green yellow
ESP217-5203	Trebbiano Toscano [¶]	n.i.	10	10	W	Green yellow
ESP217-5028	Trepat [¶]	10	10	10	W	Dark red violet
ESP217-5108	Trousseau Noir [¶]	10	n.i.	8	W	Dark red violet
ESP217-5205	Valdiguie [¶]	10	10	10	W	Blue black
ESP217-5035	Valenci Tinto [¶]	n.i.	10	10	W/T	Blue black
ESP217-5207	Valenci Tinto [¶]	10	10	10	W/T	Blue black
ESP217-5061	Verdejo Blanco [¶]	10	10	n.i.	W	Green yellow
ESP217-5208	Verdejo de Salamanca [¶]	10	10	n.i.	W	Green yellow
ESP217-5211	Verdill [¶]	n.i.	10	n.i.	W	Green yellow
ESP217-5212	Vermentino [¶]	n.i.	10	10	W/T	Green yellow
ESP217-5058	Vijriega Común [¶]	10	10	10	W	Green yellow
ESP217-5177	Vinhao [¶]	10	10	10	W	Blue black
ESP217-5218	Xarello [¶]	10	n.i.	10	W	Green yellow
ESP217-5147	Zalema [¶]	10	10	10	W	Green yellow

[†]When possible, prime name according to the *Vitis* International Variety Catalogue (VIVC) is used (<http://www.vivc.de>). [‡]W, Wine grape; T, Table grape; R, Raisins (according to VIVC database). [§]Evaluated according to the Organisation Internationale de la Vigne et du Vin descriptor N° 225 (Organisation Internationale de la Vigne et du Vin 2007). [¶]Genetic identity confirmed by means of simple sequence repeat/single nucleotide polymorphism analyses (data not shown). n.i., not included in the year of study.

Table 2. Morpho-agronomic descriptors evaluated in this work and their corresponding variable codes.

Name	Cat.†	Code	Description	Reference
Compactness	Bu	Comp	Visual compactness of the bunch	OIV N° 204‡
First ramification length	Bu	1RmLe	Length of the first ramification of the rachis (mm)	–
Second ramification length	Bu	2RmLe	Length of the second ramification of the rachis (mm)	–
Actual bunch volume	Bu	AcBuVo	Actual (solid) volume of the bunch (mL)	–
Bunch length	Bu	BuLe	Distance from the uppermost to the lowest berry of the bunch (cm)	OIV N° 202‡
Bunch mass	Bu	BuWe	Mass of the bunch (g)	–
Bunch width	Bu	BuWi	Maximum distance between the lateral berries of the bunch (cm)	OIV N° 203‡
Morphological bunch volume	Bu	MBuVo	Apparent volume of the bunch (mL)	Modified from Ferreira and Marais (1987)
Pedicle length	Bu	PdiLe	Mean value of 15 measurements: distance from insertion to ramification (mm)	OIV N° 238‡
Peduncle length	Bu	PduLe	Distance from insertion point on the shoot to the first ramification of the bunch (mm)	OIV N° 206‡
Rachis mass	Bu	RaWe	Mass of the rachis (g)	–
Ramifications per bunch	Bu	RmBu	Number of ramifications of the bunch	–
Berries volume	Bu	ToBeVo	Total volume of all the berries of the bunch (mL)	–
Berries mass	Bu	ToBeWe	Total mass of all the berries of the bunch (g)	–
Seeds per berry	Ff	SBe	Mean value of the number of seeds of 15 berries	–
Berries per bunch	Ff	ToBeBu	Total number of berries of the bunch	–
Berry length	Be	BeLe	Mean value of the length of 15 non-deformed berries (mm)	OIV N° 220‡
Berry volume	Be	BeVo	Mean value of all the berries of the bunch: ToBeVo/ToBeBu (mL)	–
Berry mass	Be	BeWe	Mean value of all the berries of the bunch: ToBeWe/ToBeBu (g)	–
Berry width	Be	BeWi	Mean value of the width of 15 non-deformed berries (mm)	OIV N° 221‡
Bunch order	Pl	BuO	Order number of the bunch in its shoot	–
Fertility index	Pl	FI	Average number of bunches per shoot: ToBuP/ToShP	–
Bunches per plant	Pl	ToBuP	Total number of bunches in the plant	–
Shoots per plant	Pl	ToShP	Total number of shoots in the plant	–

†Variable category: Bu, bunch; Ff, fruitfulness; Be, berry; Pl, plant. ‡Organisation Internationale de la Vigne et du Vin (2007).

or digital callipers (CD-15DCX, Mitutoyo, Kawasaki, Japan). Bunch volume was determined by immersion in a bucket filled with water and by weighing the displaced water, as suggested by Sepahi (1980). For the determination of the morphological volume, bunches were wrapped with a self-adherent plastic film, modifying the procedure used by Ferreira and Marais (1987). In this process, the natural shape and morphology of the bunches were maintained as far as possible. The volume of all the berries was determined by their immersion in a graduated cylinder partially filled with a known amount of water and measuring the volume or mass of the displaced water. The Tempranillo clones (10 bunches per clone) were characterised by the same procedure, but during only one season (2012).

Statistical analysis

The experimental data obtained for the three seasons were independently analysed and consisted of 1040 observations in 2011, 1145 in 2012 and 977 in 2013. Different statistical analyses were used to determine the relationship between bunch compactness and the morpho-agronomic traits measured. All calculations were done using SPSS v. 21.0 (IBM, Chicago, IL, USA), unless otherwise stated.

Correlation analysis. Bivariate correlations between the morpho-agronomic traits included in this work were estimated using Kendall's τ_b coefficients, as recommended by Khamis (2008), because the main variable under study, which is bunch compactness, was evaluated using an ordinal descriptor.

Coefficient significance was considered at three levels ($P \leq 0.001$, 0.01 and 0.05).

Analysis of variance. Variables affecting bunch compactness may be expected to have significantly different means in the several compactness classes, at least in the extreme ones. To evaluate it, the mean for each variable was calculated in each of the five groups of compactness (1, 3, 5, 7 and 9), and then compared, determining whether any of them differed significantly from each other by using an appropriate post-hoc test. First, the homoscedasticity of the data was checked (i.e. the homogeneity of variance) using the Levene's test with a threshold of 0.05. Then, ANOVA was employed in those cases where the homogeneity of variance could be assessed; otherwise, the alternative tests of Welsh and Brown–Forsythe were used. When ANOVA or Welsh and Brown–Forsythe tests were statistically significant ($P \leq 0.05$), the differences among groups were tested with Fisher's Least Significant Difference (LSD) or Games–Howell's post-hoc tests, respectively. Results were considered statistically significant if $P \leq 0.05$.

Variables that did not show a statistically significant difference among any of the five groups of compactness for 2 or more years were not considered further as they were thought to provide no discriminant information.

Principal component analysis. A principal component analysis (PCA) with Varimax rotation was performed in order to identify the underlying relationships between selected variables,

as well as to evaluate the stability of the data structure during the 3 years of study. Bartlett’s test of sphericity and the Kaiser–Meyer–Olkin (KMO) test were calculated to assess the suitability of the data to PCA (Pérez 2004, Sreejesh et al. 2014). A parallel analysis by Monte Carlo simulation was performed, using the software developed by Watkins (2006) to determine the number of components to retain, rejecting those whose eigenvalues were higher in the simulated analysis than in the real data test.

Linear discriminant analysis. Linear discriminant analyses (LDA) were done to explore the predictive ability of previously selected independent variables on the categorical dependent variable (bunch compactness). The proportion of the variance explained was evaluated according to Wilks’ λ , which provides information about the proportion of total variability not explained by the variables included in the model (Burns and Burns 2008).

As not all variables contribute significantly to the classification, the stepwise forward–backward procedure was chosen in some cases to check which variables had the largest discrimination power. This procedure includes or excludes variables in the discriminant functions based on their effect on the Wilks’ λ and on their significance, measured by a suitable F test. In this case, default critical values of Wilks’ λ with an F -value of 3.84 for variable entry and 2.71 for removal were applied, which correspond to a confidence level of 90% (Blanco-Gomis et al. 1998). Besides, a priori class probability proportional to the number of individuals in each class was used.

This analysis also provides the proportion of samples correctly classified, by directly comparing the predicted values determined by the canonical functions with those experimentally established by the visual panel. Likewise, the prediction capacity of the discriminant models was studied by leave-one-out cross-validation. In this process, one observation is extracted from the whole sample, which is used as a validation sample in the model obtained from the remaining observations. This process is repeated n times, n being the number of observations, so all samples are used once as validation samples.

To further validate the discriminant models obtained, data of the four clones of Tempranillo (2012) were projected on the discriminant functions obtained for 2011, 2012 and 2013 to assess if these functions were able to predict correctly the compactness of these samples. One-way ANOVA with Fisher’s LSD post-hoc test was applied to the scores given by each function to each observation to determine if the loose clones could be differentiated from the compact ones. Results were considered statistically significant at $P \leq 0.01$.

Results

Correlation analysis

The univariate relationships between the morpho-agronomic traits included in this work were tested by a correlation analysis. The correlation matrices obtained for 2011, 2012 and 2013 based on Kendall’s τ_b coefficients showed a similar pattern in the 3 years (Figure 1). Most variables correlated significantly (above the diagonals in Figure 1), especially with 2013 data. As expected, variables belonging to the same category (Table 2) showed the highest values of correlation. In this sense, variables related to general dimensions of the bunch (AcBuVo, BuWe, MBuVo, RaWe, ToBeVo and ToBeWe), individual features related to the size of the berry (BeLe, BeVo, BeWe and BeWi) and the length of the primary ramifications of the bunch

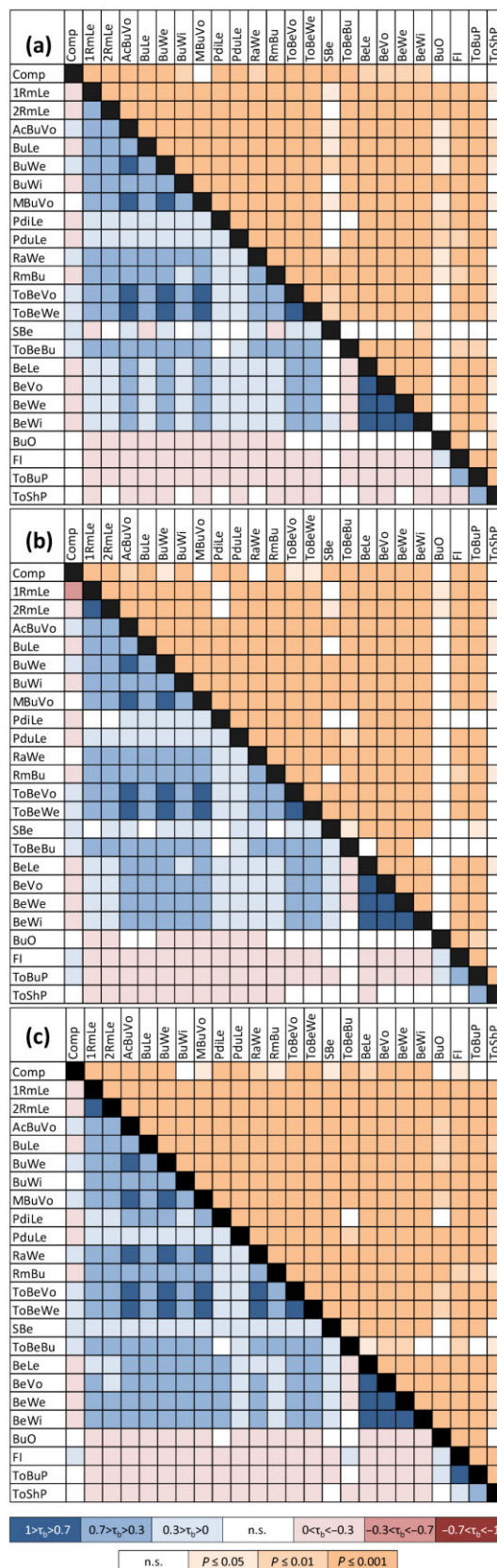


Figure 1. Correlation maps obtained for (a) 2011, (b) 2012 and (c) 2013 based on Kendall’s τ_b coefficients (below diagonal) obtained between the 24 morpho-agronomic variables included in this study. P -values are shown above diagonal. Colour codes for the value of the correlation and its significance are shown in the adjacent colour bar. Variables are coded according to Table 2.

(1RmLe and 2RmLe) showed a high coefficient of correlation during the 3 years of the study ($|\tau_b| \geq 0.700$).

Bunch compactness correlated significantly with most of the variables included in this study, although low correlation coefficients were observed (Figure 1). Moreover, correlation directions (indicated by the sign of the correlation coefficient) were consistent for the 3 years of the study, which confirms the positive or negative relationship of the traits evaluated with bunch compactness. In 2011, the total number of berries (ToBeBu) obtained the highest significant absolute value of correlation with compactness ($\tau_b = 0.223$, $P \leq 0.001$), and it also obtained significant ($P \leq 0.001$) correlation coefficients in 2012 (0.190) and in 2013 (0.281). In 2012, the variable with the highest absolute value of correlation was the length of the first ramification (1RmLe, $\tau_b = -0.309$, $P \leq 0.001$). In 2011 and 2013, this variable also correlated with bunch compactness with coefficients of -0.215 and -0.191 , respectively ($P \leq 0.001$). In 2013, the highest absolute correlation value was obtained for the variable length of pedicels (PdiLe, $\tau_b = -0.299$, $P \leq 0.001$). This variable correlated with bunch compactness with coefficients of -0.174 and -0.116 in 2011 and 2012, respectively ($P \leq 0.001$). In contrast, the correlation coefficients obtained for plant variables (BuO, FI, ToBuP and ToShP) with bunch compactness were either non-significant or had low values during the 3 years evaluated (Figure 1).

Analysis of variance

The capacity of the variables considered in this work to discriminate among the different classes of compactness was assessed using one-way ANOVAs or Welsh and Brown–Forsythe tests, as described in Materials and methods. Results of the post-hoc Fisher's LSD or Games–Howell pairwise comparison tests are shown in Table S1. A significant difference was found for the means between some of the classes of compactness in at least two of the three seasons for all the variables included in the study, except for the plant variables. In this sense, the order of the bunch in the shoot (BuO) did not obtain any significant difference in any of the 3 years evaluated, showing its lack of discriminant capacity. The number of berries of the bunch (ToBeBu), however, obtained a significant difference between the mean values for almost all the groups of compactness during the three seasons evaluated, as it occurred with the length of the primary ramifications of the bunch (1RmLe and 2RmLe). So, these variables showed a high discriminant power. On the basis of these results, the four plant variables (BuO, FI, ToBuP and ToShP), were discarded for the following analyses.

Principal component analysis

Principal component analysis was applied separately to 2011, 2012 and 2013 data to gather information about the interrelationships among the 19 remaining variables. The suitability of the data for these analyses was previously assessed by means of Bartlett's test of sphericity and the KMO test (Pérez 2004). Their results supported the factorability of the data for the three seasons evaluated, because the Bartlett's test was statistically significant ($P \leq 0.001$), indicating that the variables are correlated enough to provide a reasonable basis for PCA, and the KMO test exceeded the recommended value of 0.7 (Sreejesh et al. 2014) (0.866, 0.875 and 0.886 for 2011, 2012 and 2013, respectively), also indicating that the data sets are suitable for factoring. Parallel analysis by Monte Carlo simulation revealed the presence of three principal components (PCs) with eigenvalues exceeding those obtained from matrices of simulated data of the same dimensions than those employed in this

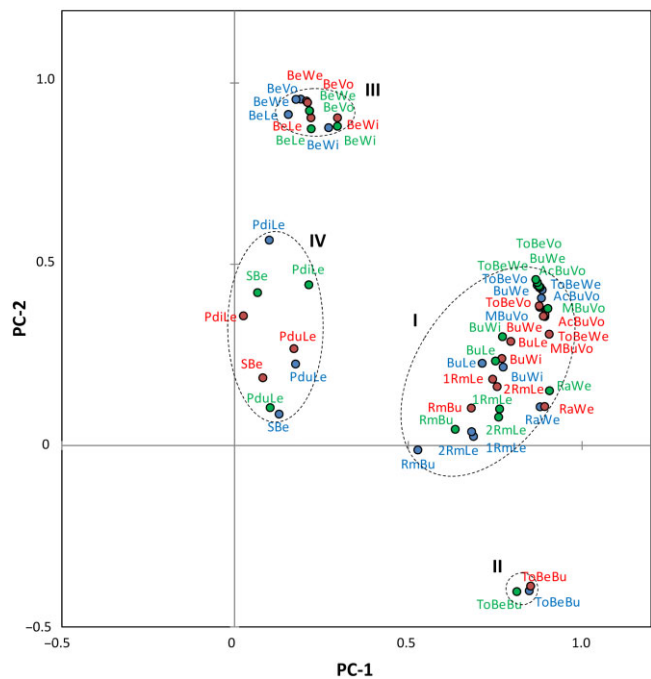


Figure 2. Varimax rotated loadings of the first (PC-1) and second (PC-2) principal components of the 19 morpho-agronomic variables evaluated obtained for 2011 (■), 2012 (■) and 2013 (■). PC-1 explains 42.4, 44.8 and 43.9%, respectively, of the variance for 2011, 2012 and 2013 data. PC-2 explains 25.6, 24.8 and 26.0% of the variance for 2011, 2012 and 2013. Variables are coded according to Table 2. PC, principal component.

work (19 variables and 1040, 1145 and 977 observations for 2011, 2012 and 2013, respectively). These three PCs explain 75.2% (2011), 76.6% (2012) and 80.1% (2013) of the total variance of the data. To aid in the interpretation of these components, Varimax rotation was undertaken, and loadings of the 19 variables in the three retained PCs were analysed. The first principal component (PC-1) explained 42.4, 44.8 and 43.9% of the variance for 2011, 2012 and 2013 data, respectively. It was highly related to bunch variables (1RmLe, 2RmLe, AcBuVo, BuLe, BuWe, BuWi, MBuVo, RaWe, RmBu, ToBeVo and ToBeWe) and the number of berries per bunch (ToBeBu) in the 3 years considered. The second principal component (PC-2) explained 25.6 (2011), 24.8 (2012) and 26.0% (2013) of the variance, and it was strongly related to berry variables (BeLe, BeVo, BeWe and BeWi). The third principal component (PC-3) was associated with the number of seeds per berry (SBe) in 2011 and 2012, whereas in 2013, it was linked to the length of the peduncle (PduLe) and the length of the pedicels (PdiLe).

Figure 2 shows the PC-1 and PC-2 loadings obtained for the 19 variables in the three seasons. A similar distribution of the variables can be observed in the bi-dimensional plot when comparing 2011, 2012 and 2013 data, in spite of the different climate conditions observed in the La Rioja region during those years (Table S2) and of the different experimental plots used. Four clusters can be easily differentiated: cluster I includes variables related to the bunch (1RmLe, 2RmLe, AcBuVo, BuLe, BuWe, BuWi, MBuVo, RaWe, RmBu, ToBeVo and ToBeWe); cluster II is exclusive for the number of berries of the bunch (ToBeBu); cluster III is related to the dimensions of the berry (BeLe, BeVo, BeWe and BeWi); and cluster IV includes the number of seeds per berry (SBe), the length of the pedicels (PdiLe) and the length of the peduncle (PduLe).

Table 3. Explained variance and classification results obtained by means of different linear discriminant analyses for 2011, 2012 and 2013. Variables are coded according to Table 2.

Model variables	Explained variance (%) [†]			Bunches correctly predicted (%)			Bunches correctly predicted by leave-one-out cross-validation (%)		
	2011	2012	2013	2011	2012	2013	2011	2012	2013
1RmLe, BeWe ^{‡§¶} , BuLe, BuWe, BuWi ^{‡¶} , PdiLe [§] , PduLe ^{‡¶} , RmBu [¶] , SBe [§] , ToBeBu	57.8	57.9	63.2	89.2	94.5	93.2	88.9	94.3	93.1
1RmLe, BeWe, BuLe, BuWi ^{‡¶} , PdiLe [§] , PduLe ^{‡¶} , RmBu [¶] , SBe, ToBeBu	55.3	55.2	57.0	89.0	91.1	89.6	88.0	91.0	89.4
1RmLe, BeWe, ToBeBu	42.8	45.2	47.2	85.7	88.6	87.4	85.7	88.4	87.2
1RmLe, ToBeBu	41.1	43.7	44.4	83.5	87.4	83.6	83.5	87.2	83.6
1RmLe, BeWe	11.7	22.1	12.4	68.7	71.9	70.3	68.5	71.6	70.1
BeWe, ToBeBu	8.7	10.7	15.7	72.6	63.1	71.8	72.3	62.8	71.5

[†]According to Wilks' λ . [‡]Variable excluded in 2011 by stepwise linear discriminant analysis (LDA). [§]Variable excluded in 2012 by stepwise LDA. [¶]Variable excluded in 2013 by stepwise LDA.

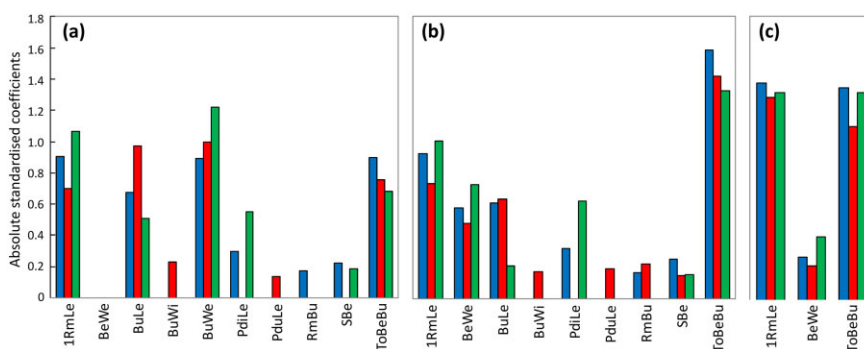


Figure 3. Absolute standardised coefficients of different morpho-agronomic variables obtained for 2011 (■), 2012 (■) and 2013 (■) data by stepwise linear discriminant analysis considering (a) 10, (b) 9 and (c) 3 variables. Variables are coded according to Table 2.

Linear discriminant analysis

The next step for the selection of the main determinants of bunch compactness and their relative importance was carried out through a stepwise LDA. Linear discriminant analysis provided canonical functions capable of classifying the observations according to the visual score of compactness on the basis of the different morpho-agronomical features considered in this work. A previous selection of the variables included in such analysis was done to avoid problems of multicollinearity between variables, which may cause an incorrect classification of some individuals on the basis of the released discriminant functions. As stated before, some variables showed a large coefficient of correlation ($|\tau_{ij}| \geq 0.700$), so only one variable was chosen to represent each group of variables (Figure 1). Thus, the variable BeWe was selected from the group formed by the variables BeLe, BeVo, BeWe and BeWi, and the variable 1RmLe was chosen from the group formed by the variables 1RmLe and 2RmLe. Likewise, the variable BuWe was chosen from the group formed by the variables AcBuVo, BuWe, MBuVo, RaWe, ToBeVo and ToBeWe, because its implication in bunch compactness had been previously reported (Vail and Marois 1991, Vail et al. 1998, Valdés-Gómez et al. 2008). Then, a stepwise LDA was performed with a set of 10 variables (1RmLe, BeWe, BuLe, BuWe, BuWi, PduLe, PdiLe, RmBu, SBe and ToBeBu) for 2011, 2012 and 2013 data. Moreover, in order to better evaluate the direction of maximum variance of compactness, the stepwise LDA was done considering only two classes of bunch compactness: (i) one comprising those observations with a visual score

value of 1 and 3 (Loose class); and (ii) one with those observations with a given value of 7 or 9 (Compact class). Observations with a medium value of compactness were not included in the calculation because of their intermediate score, which may interfere in the correct calculation of the discriminant functions. So, a stepwise LDA was done on the basis of 608 observations in 2011 (216 loose and 392 compact bunches), 675 observations in 2012 (406 loose and 269 compact bunches) and 558 observations in 2013 (220 loose and 338 compact bunches).

As only two categories of compactness were considered, only one significant discriminant function was released in 2011, 2012 and 2013. According to Wilks' λ , the models explain 57.8, 57.9 and 63.2% of the variation in the grouping variable (bunch compactness) for 2011, 2012 and 2013, respectively (Table 3). The absolute values of the standardised coefficients of the 10 variables for such functions are shown in Figure 3a. Stepwise LDA discarded the variables BeWe, BuWi and PduLe in 2011, BeWe, PdiLe, RmBu and SBe in 2012 and BeWe, BuWi, PduLe and RmBu in 2013 as they did not improve the discriminant capacity given by the other selected variables. The discriminant functions obtained for 2011, 2012 and 2013 were able to correctly classify 89.2, 94.5 and 93.2% of the observations in the two previously defined classes of compactness, respectively. The use of leave-one-out cross-validations rendered similar results: 88.9, 94.3 and 93.1% of bunches were properly classified (Table 3).

Stepwise LDA selects the most important variables, discarding those whose discriminant ability is redundant and/or less

relevant (Burns and Burns 2008). Consequently, those morpho-anagronomic variables that were consistently retained in the analyses of the 2011, 2012 and 2013 data arise as the best set of predictors. In this sense, the bunch mass (BuWe), the length of the first ramification of the rachis (1RmLe), the bunch length (BuLe) and the number of berries per bunch (ToBeBu) are the most discriminating variables for categorisation of bunch compactness (Figure 3a). Moreover, they obtained high and similar absolute standardised coefficients in the discriminant functions over the years. Among them, the variables 1RmLe, BuLe and ToBeBu may be considered as primary and independent variables, whereas BuWe is a derived variable, and essentially arises from the number of berries of the bunch and its average mass (Dunn and Martin 2007).

Consequently, stepwise LDA was repeated excluding BuWe. According to Wilks' λ , models with the nine remaining variables were capable to explain slightly lower variation for bunch compactness than that explained in the previous analysis (Table 3). In the same way, the proportion of bunches correctly classified (both directly and in the leave-one-out cross-validation processes) was also slightly lower. According to the absolute values of the standardised coefficients obtained for these variables in the functions (Figure 3b), the elimination of the variable BuWe from the analysis produced an important increment in the predictive capacity of the related variable ToBeBu, indicating that part of its predictive capacity was occluded by the first one. The elimination of BuWe also allowed the emergence of the discriminating power of the variable BeWe, revealing its role in the definition of the bunch compactness.

Linear discriminant analysis was then repeated considering only the three variables with the highest and most stable absolute standardised coefficients: 1RmLe, BeWe and ToBeBu (Figure 3c). This selection agreed with the results obtained by means of PCA: 1RmLe is found in cluster I, ToBeBu in cluster II and BeWe in cluster III (Figure 2). Wilks' λ of the discriminant functions indicate that these reduced models are able to explain between 12.7% (2012) and 16.0% (2013) less variation of bunch compactness than the best discriminant functions with 10 variables, but they were still able to correctly classify 85.7, 88.6 and 87.4% of the bunches. Leave-one-out cross-validation of the discriminant model obtained similar results (Table 3). Attending to the standardised coefficients obtained per each variable (Figure 3c), the role of the variables ToBeBu and 1RmLe is predominant over the variable BeWe.

This LDA based on three variables was also performed considering 2011, 2012 and 2013 data as a whole. This model was able to explain 46.4% of the variance of the dependent variable, classifying adequately 87.3 and 87.2% of the data (by direct and leave-one-out cross-validations processes, respectively). These values are similar to those obtained when considering the three seasons independently (Table 3). Likewise, the variables ToBeBu and 1RmLe obtained considerably higher absolute standardised coefficients than the variable BeWe (Figure S1).

To further estimate the relative weight of each of the three selected variables in the discriminant functions, three additional non-stepwise LDAs were done for the data from each season. In each of these LDAs, one of the three variables was excluded to check their individual effect by examining the reduction in the proportion of variance explained by the model and the accuracy in the bunch classification (Table 3). Thus, the extraction of the variable related to the size of the berries of the bunch (BeWe) caused a small decrease in the explained variance of the model (-1.7, -1.5 and -2.8% for 2011, 2012 and 2013 data, respectively), suggesting that its non-redundant contribution to the

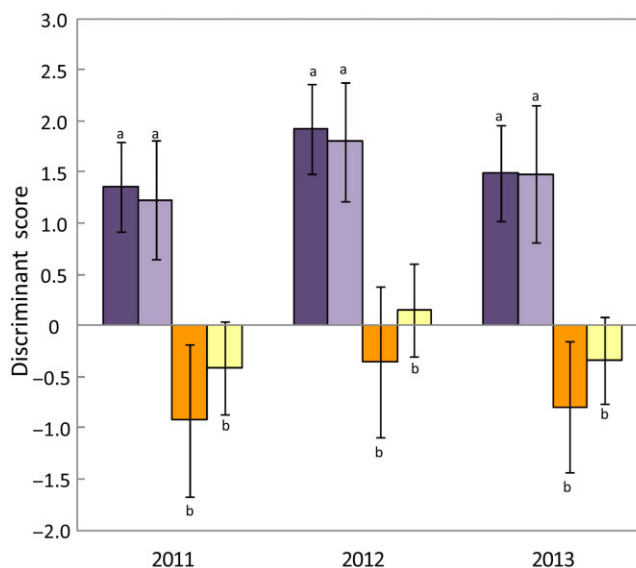


Figure 4. Discriminant scores of compactness obtained for four clones of Tempranillo [RJ-51 (■), VP-2 (■), VP-11 (■) and VP-25 (■)] on the basis of the discriminant functions obtained in 2011, 2012 and 2013 considering the variables: length of the first ramification of the rachis (1RmLe), Berry mass (BeWe) and Number of berries per bunch (ToBeBu). Each column represents mean value; bars show standard deviation. Different lowercase letters indicate a significant difference among clones according to Fisher's Least Significant Difference post-hoc tests ($P \leq 0.01$).

multivariate model is quite low. On the contrary, the extraction of the variables 1RmLe and ToBeBu caused pronounced drops in the amount of explained variance: -34.1, -34.5 and -31.5% for the former and -31.1, -23.1 and -34.8% for the latter (data for 2011, 2012 and 2013, respectively), indicating their leading roles for discriminating grapevine bunches according to their compactness.

External validation: an essay on loose and compact clones of Tempranillo

Finally, data of the clones of Tempranillo obtained in 2012 from a different plot were projected on the discriminant functions obtained for the three selected variables in 2011, 2012 and 2013, to determine their prediction capacity. First, Kendall's τ_b coefficients were calculated between the discriminant scores obtained for each observation using the discriminant functions and the mode value of compactness given by the visual evaluation panel. Highly significant ($P \leq 0.001$) correlation values were obtained for the three seasons evaluated: τ_b : 0.667, 0.667 and 0.658 for 2011, 2012 and 2013, respectively. Moreover, one-way ANOVA with Fisher's LSD post-hoc test was calculated for the scores given for the discriminant functions to each observation, using the clone as a grouping variable. In the 3 years studied, loose clones (VP-11 and VP-25) were found to be different ($P \leq 0.01$) from the compact clones (RJ-51 and VP-2), whereas VP-11 could not be significantly differentiated from VP-25, nor RJ-51 from VP-2 (Figure 4). Similar ANOVA and Fisher's LSD post-hoc results were obtained when the canonical function obtained with the whole data (2011 + 2012 + 2013) was used: whereas compact and loose clones could be statistically differentiated, VP-11 and VP-25 clones (loose) were statistically indistinguishable, as happened with RJ-51 and VP-2 (compact) (data not shown).

Discussion

The determination of the main factors having major influence on bunch compactness is essential, because this trait has a large impact on grape quality. Previous descriptive studies of this topic have been done either in grapevine clones differing in their bunch compactness (Alonso-Villaverde et al. 2008), in plants of the same cultivar subjected to different cultural or chemical treatments focused to obtain looser bunches (Sarooshi 1977, Vail et al. 1998, Poni et al. 2008, Valdés-Gómez et al. 2008, Vartholomaïou et al. 2008, Schildberger et al. 2011, Molitor et al. 2012a, Palliotti et al. 2012, Intrigliolo et al. 2014), or in a small number of cultivars (Vail and Marois 1991, Shavrukov et al. 2004). It is clear that different variables may have a significant influence on the variation of bunch compactness in particular cases, but a study aiming to discover the genetic determinants affecting this trait requires a wider framework. Thus, the goal of this work was to determine the major features affecting bunch compactness at the species level, through the evaluation of the variability that is naturally present in the cultivated grapevine. For that, a large number of bunches belonging to diverse table and wine grape cultivars has been evaluated, and many variables that were thought to have some relevance on this trait were considered.

Evaluation of bunch compactness is complicated: it cannot be precisely determined like other traits, such as bunch mass or the number of berries, and there is no reliable, objective and quantitative way for its measurement. In this work, the commonly accepted visual OIV descriptor N° 204 has been used as a reference, but it is not objective or quantitative. Thus, it was not expected to find models based on quantitative data capable of explaining a high proportion of bunch compactness variation defined in terms of this visual descriptor. As expected, our results indicate that bunch compactness is a multifactorial trait, because it correlated significantly with most of the morpho-agronomic variables evaluated (Figure 1). This multifactorial nature was supported by the low values of direct correlation observed, where no trait stood out from the rest. Thus, considering globally a large diverse sample of bunches, correlation analyses showed that this trait is the result of the interaction of many individual characteristics of the bunch, whose combination generate a major or minor compaction of the berries along the rachis. These relationships were stable over time, in spite of the different factors considered in this work (season weather, plot, age of the plants). Accordingly, PCA revealed that the interrelationships of the variables considered in this work and the distribution of the variance of the data were similar in 2011, 2012 and 2013 (Figure 2). In this sense, the two first PCs explained a similar proportion of the variance, and they correlated with the same variables during the 3 years considered. The first PC is associated with bunch characteristics, whereas the second PC is more related to berry dimension variables.

To elucidate how the variables examined affected bunch compactness globally, stepwise LDAs were performed in parallel for 2011, 2012 and 2013 data after the selection of independent variables and the grouping of the bunches into two compactness classes (Compact and Loose). The large value of unexplained variance obtained (42.2, 42.1 and 36.8% in 2011, 2012 and 2013, respectively) indicates that visual bunch compactness is dependent on other factors that were not included in the analysis and/or on non-linear relationship between the variables studied, apart from the already mentioned limitations linked to the use of the OIV descriptor as reference. These analyses revealed that a reduced number of variables are mainly involved in the definition of bunch compactness. Bunch mass arose as the most relevant variable to explain variation in bunch compact-

ness (Figure 3a), as stated previously by Vail and Marois (1991), Vail et al. (1998) and Valdés-Gómez et al. (2008). Nonetheless, the extraction of this variable of the models revealed that most of its effect is a consequence of its relationship to the number of berries of the bunch and their dimensions. Subsequent analyses showed that three characteristics of the bunch are the most discriminant in the categorisation of compactness: the number of berries per bunch, the length of the ramifications of the bunch and the dimensions of the berry. Discriminant functions based on these three variables were applied to independent data from a set of four clones of Tempranillo. The functions were capable of significantly differentiating the two clones presenting loose bunches from the two clones with compact bunches (Figure 4), confirming the main role of the selected variables in the definition of this trait.

When the relative importance of the three selected variables is examined, the absolute values of the standardised coefficients of the LDA analyses clearly indicate that the number of berries per bunch and the length of the ramifications are the more discriminant factors, whereas the dimensions of the berry appear to play a minor role in the definition of this trait in a multicultural framework. The three non-stepwise LDAs calculated by extracting one of the three selected variables fully supported those observations, as the extraction of both the number of berries per bunch and the length of the first ramification of the bunch caused a significant reduction of explained variance (in average, -29.7 and -33.4% of variance for ToBeBu and 1RmLe, respectively). The combined leading role of these two variables in the compactness of the bunch was already reported and discussed by Hed et al. (2009) in a study of loose and compact bunches of the interspecific hybrid Vignoles, and the combined variable 'number of berries per cm of rachis' is a common estimator of this trait (Pommer et al. 1996, Fermaud 1998, Valdés-Gómez et al. 2008, Hed et al. 2009). In contrast, the elimination of the variable BeWe of the multivariate model only caused small losses of explained variance (-2.0% in average), confirming its minor discriminant power.

The compactness of a bunch is defined by the difference existing between its actual volume and its morphological volume. Thus, the closer these volumes are, the more compact is the bunch (Sepahi 1980, Shavrukov et al. 2004). The actual bunch volume is mainly determined by the volume of the berries (the volume of the rachis is much less important), which is a consequence of the number of berries of the bunch and their average size. According to our results, the number of berries per bunch plays a leading role in bunch compactness, having a positive relationship with this trait. Different authors (Poni et al. 2008, Vartholomaïou et al. 2008, Palliotti et al. 2012, Tardáguila et al. 2012, Abd-Allah et al. 2013) have highlighted the positive association between the number of berries per bunch and the bunch compactness of different cultivars, and our results support such an idea in a wider framework, as a high number of berries may reduce the free space that potentially could appear in the morphological volume of the bunch. Berry number depends on the number of flowers present in the inflorescence and on the proportion that sets successfully and is retained until harvest (Dunn and Martin 2007). That is, cultivars with a low number of flowers per inflorescence and/or reduced fruitset will produce fewer berries per bunch and, according to our results, looser bunches.

Berry size has been proposed as an important factor in the definition of bunch compactness in studies developed in a single cultivar. Thus, Schildberger et al. (2011) reported that the application of prohexadione-calcium (an inhibitor of gibberellin biosynthesis) to Grüner Veltliner bunches promotes looser

structures because of the production of smaller berries. Alonso-Villaverde et al. (2008) also reported the small size of the berry as the main factor responsible for the loose bunches found in a selected individual from a set of 14 Albariño clones grown under the same conditions. Interestingly, berry variables correlated negatively with bunch compactness in 2011, 2012 and 2013 (Figure 1). This initially unexpected negative relationship might be the result of the joint analysis of table- and winegrape cultivars carried out in this work because both types of cultivar have different genetic origins and have undergone different processes of selection (This et al. 2006). Historically, tablegrape selection and breeding has focused on cultivars with large berries packed in loose and attractive clusters, whereas winegrape selection was more interested in must-related traits (e.g. yield and juiciness) and other quality parameters (This et al. 2006), and often, the selection inadvertently ended with cultivars with small and more compact bunches, with smaller berries (Reisch et al. 2012). To test if the joint analysis of table- and winegrapes could have caused the negative correlation between berry size and bunch compactness, additional analyses were performed, separating the cultivars into two groups according to their commercial use: wine vs table and multipurpose (Table 1). This division led to lower (or non-significant) correlation coefficients between berry variables and bunch compactness and was only positive for berry length in the group of wine cultivars in 2011 and 2012 (data not shown). Multivariate analysis results were similar in the two subgroups and also similar to the whole group (Figure S2), indicating that the findings of this work are independent of the genetic origin of the cultivars used, and thus are valid at a species level.

A relationship between seed number/mass and berry dimensions is generally accepted. Recently, Houel et al. (2013) studied the genetic variability of berry size in the grapevine by evaluating 304 table- and winegrape genotypes and observed that this trait is not clearly influenced by the number of seeds (and seed mass) of the berry. This fact was supported by the different quantitative trait loci found for berry mass and seed traits, which suggest that both traits are not completely associated (Doligez et al. 2013). This lack of absolute association was also observed in our work, and large and small berries were indistinctly found with a high and low number of seeds. As discussed above, this fact can be explained as a consequence of the diverse grapevine cultivars considered, whose features may be the result of different domestication and selection processes (This et al. 2006, Reisch et al. 2012). Interestingly, positive correlation values were found between the number of seeds per berry and bunch compactness during the 3 years of study, although values were low (Figure 1). Moreover, this variable was retained by stepwise LDA (in 2011, 2012 and 2013), indicating that it provides some predictive power to the discriminant function released (Figure 3b). Bayo-Canha et al. (2012) found that the number of seeds was the only characteristic correlating significantly with bunch compactness within a list of 22 agronomic traits studied in a Monastrell \times Syrah progeny. This might be due to a link between number of seeds and pollination and fruit set success, but in our data, the significant correlation between number of seeds per berry and number of berries per bunch was low (2011 and 2013) or did not exist (2012) (Figure 1).

In contrast, our results showed that the length of the main axes of the bunch plays an important role in bunch compactness, having a negative relationship with this trait, that is loose bunches used to have long stems. It can be explained by their implication in the morphological volume of the bunch and in the arrangement of the berries in the rachis: the elongation of

the main structural axes of the bunch produces a higher morphological volume, without significantly increasing the actual bunch volume, allowing the berries to be more sparsely distributed along the rachis, or, in other words, there are less berries per centimetre of rachis. Shavrukov et al. (2004) considered the morphological volume of the grapevine bunch as a cone, the volume of which is defined by the main axes of its architecture [$V_{\text{cone}} = (\pi r^2 l)/3$]. In this regard, an increment in the width of the bunch (defined as $2r$) would have a greater effect in its morphological volume than an increment in its length (l). Among other structural characteristics, the width of the bunch depends on the length of the primary ramifications, supporting the significant relationship found between this variable and the compactness of the bunch. Accordingly, it is widely known that gibberellin sprays loosen bunches through the elongation of the stems (Weaver et al. 1962, Molitor et al. 2012a). The genetic control of the length of the ramifications of the bunch has been studied in the Reiterated Reproductive Meristems somatic variant of cultivar Carignan (Fernandez et al. 2010). The bunches of this mutant have great width and length, as well as a large number of ramifications and berries, conferring them a looser appearance than that of the wild type. This abnormal pattern was mainly associated to a mutation in the gene *VvTFL1A* (orthologous to *Arabidopsis* TERMINAL FLOWER 1, *TFL1*), the expression of which plays an important role in the establishment of the structure of the inflorescence and, consequently, on bunch size, shape and compactness. Recently, the genetic variation of different attributes of the architecture of the rachis have been analysed by Correa et al. (2014) in a segregating progeny derived from the crossing of two tablegrape cultivars (Ruby Seedless \times Sultanina). The high heritability found for some of the traits analysed in such progeny (for example length of the rachis, number of ramifications of the bunch and length of the first ramifications of the rachis), together with the important role found in our work for those bunch attributes indicate that bunch compactness can be included as a target trait in breeding programs, both through traditional approaches or by marker-assisted selection (Reisch et al. 2012), once its genetic basis was known.

It is also interesting to note that some variables expected to be important factors in determining bunch compactness have not stood out in this multicultural study, including some that proved to be main causal factors in different studies. In this sense, pedicel length has been proposed as an important feature for the determination of bunch compactness in some cultivars. Short pedicels have been associated with the formation of compact bunches, by attaching the berries tightly against each other all along the rachis (Gabler et al. 2003). Accordingly, treatments based on the application of gibberellic acid have been shown to generate longer pedicels, contributing to looser bunches (Sarooshi 1977). In our work, the length of the pedicel correlated significantly and negatively with bunch compactness (Figure 1), supporting this idea. Nonetheless, stepwise LDA revealed that its relevance in a multicultural framework is low, and it was even excluded in 2012 analysis (Figure 3).

Last, some plant variables were evaluated in this work (Table 2) as they were thought to have some influences on bunch compactness. Different crop cultural techniques have been assayed to improve this trait, mainly through the modification of crop load or by hindering the photosynthetic activity of leaves. These techniques have been associated with variations in bunch architecture by producing important changes in the source-to-sink balance of the vine (Edson et al. 1993, Hanni et al. 2013). Nonetheless, we found only low significant correlations between bunch compactness and the variables related to

the fertility of the plant (2012 and 2013) and the number of bunches of the plant (2012) (Figure 1), reflecting a lack of influence on this trait in a multicultural framework. This finding was supported by ANOVA or Welsh and Brown–Forsythe tests, which generally showed that the different classes of compactness were not significantly different for these variables (Table S1).

Conclusions

This work has evaluated the influence of different morpho-agronomic variables in the determination of bunch compactness in a multicultural framework, through the study of a large and diverse sample of bunches of wine- and tablegrape cultivars. No variable has shown a large direct influence on compactness, and PCA grouped all of them into four clusters. Two variables from different groups, total number of berries and length of the first ramification, have been identified as the major factors affecting bunch compactness, followed to a lesser extent by the dimensions of the berry. The difference between the actual and morphological volume of a bunch defines its compactness. Although the number of berries (and their individual dimensions) directly determines the actual volume of the bunch, the morphological volume depends, in addition, on the tridimensional structure formed by the main axes of the bunch. According to our results, the study of the highlighted variables appears as the most appropriate way to unravel the genetic determinism that defines this complex trait.

Acknowledgements

This work was supported by the Spanish MINECO (AGL2010-15694). Mr Javier Tello acknowledges the MINECO for his predoctoral fellowship (BES-2011-047041). The authors acknowledge CIDA (Government of La Rioja) for maintaining and providing material from Finca Valdegón and Finca La Grajera, and Viveros Provedo (especially Ignacio Provedo) for providing material of Tempranillo clones used in this work.

References

- Abd-Allah, A.S.E., Abd El-Razek, E., Abdalla, M.A. and Saleh, M.M.S. (2013) Effects of spraying lemongrass extract at full bloom on yield and fruit quality of 'Flame seedless' grape. *Journal of Applied Sciences Research* **9**, 1244–1248.
- Alonso-Villaverde, V., Boso, S., Santiago, J.L., Gago, P. and Martínez, M.C. (2008) Relationship between susceptibility to *Botrytis* bunch rot and grape cluster morphology in the *Vitis vinifera* L. cultivar Albariño. *International Journal of Fruit Science* **8**, 251–265.
- Archer, E. and van Schalkwyk, D. (2007) The effect of alternative pruning methods on the viticultural and oenological performance of some wine grape varieties. *South African Journal of Enology and Viticulture* **28**, 107–139.
- Bayo-Canha, A., Fernández-Fernández, J.I., Martínez-Cutillas, A. and Ruiz-García, L. (2012) Phenotypic segregation and relationships of agronomic traits in Monastrell × Syrah wine grape progeny. *Euphytica* **186**, 393–407.
- Becker, T. and Knoche, M. (2012) Water induces microcracks in the grape berry cuticle. *Vitis* **51**, 141–142.
- Blanco-Gomis, D., Herrero-Sánchez, I. and Mangas-Alonso, J.J. (1998) Characterisation of apple cider cultivars by chemometric techniques using data from high-performance liquid chromatography and flow-injection analysis. *The Analyst* **123**, 1187–1191.
- Burns, R. and Burns, R. (2008) Discriminant analysis. Burns, R. and Burns, R., eds. *Business research methods and statistics using SPSS: Extension chapters on advances techniques* (Sage Publications Ltd: Los Angeles, CA, USA) pp. 589–608.
- Carmona, M.J., Chaib, J., Martínez-Zapater, J.M. and Thomas, M.R. (2008) A molecular genetic perspective of reproductive development in grapevine. *Journal of Experimental Botany* **59**, 2579–2596.
- Christensen, L.P. (2000) Growth regulators. Christensen, L.P., ed. *Raisin production manual* (University of California, Agriculture & Natural Resources: Oakland, CA, USA) pp. 139–142.
- Coombe, B.G. (1995) Adoption of a system for identifying grapevine growth stages. *Australian Journal of Grape and Wine Research* **1**, 104–110.
- Correa, J., Mamani, M., Muñoz-Espinoza, C., Laborie, D., Muñoz, C., Pinto, M. and Hinrichsen, P. (2014) Heritability and identification of QTLs and underlying candidate genes associated with the architecture of the grapevine cluster (*Vitis vinifera* L.). *Theoretical and Applied Genetics* **127**, 1143–1162.
- Doligez, A., Bertrand, Y., Farnos, M., Grolier, M., Romieu, C., Esnault, F., Dias, S., Berger, G., François, P., Pons, T., Ortigosa, P., Roux, C., Houel, C., Laucou, V., Bacilieri, R., Peros, J.-P. and This, P. (2013) New stable QTLs for berry weight do not colocalize with QTLs for seed traits in cultivated grapevine (*Vitis vinifera* L.). *BMC Plant Biology* **13**, 1–16.
- Dunn, G.M. and Martin, S.R. (2007) A functional association in *Vitis vinifera* L. cv. Cabernet Sauvignon between the extent of primary branching and the number of flowers formed per inflorescence. *Australian Journal of Grape and Wine Research* **13**, 95–100.
- Edson, C.E., Howell, G.S. and Flore, J.A. (1993) Influence of crop load on photosynthesis and dry matter partitioning of Seyval grapevines: I. Single leaf and whole vine response pre- and post-harvest. *American Journal of Enology and Viticulture* **44**, 139–147.
- Evers, D., Molitor, D., Rothmeier, M., Behr, M., Fischer, S. and Hoffmann, L. (2010) Efficiency of different strategies for the control of grey mold on grapes including gibberellic acid (GIBB3), leaf removal and/or botrycide treatments. *Journal International des Sciences de la Vigne et du Vin* **44**, 151–159.
- Fermaud, M. (1998) Cultivar susceptibility of grape berry clusters to larvae of *Lobesia botrana* (Lepidoptera: Tortricidae). *Journal of Economic Entomology* **91**, 974–980.
- Fernandez, L., Torregrosa, L., Segura, V., Bouquet, A. and Martínez-Zapater, J.M. (2010) Transposon-induced gene activation as a mechanism generating cluster shape somatic variation in grapevine. *The Plant Journal* **61**, 545–557.
- Ferreira, J.H.S. and Marais, P.G. (1987) Effect of rootstock cultivar, pruning method and crop load on *Botrytis cinerea* rot of *Vitis vinifera* cv. Chenin blanc grapes. *South African Journal of Enology and Viticulture* **8**, 41–44.
- Figueiredo-González, M., Cancho-Grande, B., Boso, S., Santiago, J.L., Martínez, M.C. and Simal-Gándara, J. (2013) Evolution of flavonoids in Moratón berries taken from both bunch halves. *Food Chemistry* **138**, 1868–1877.
- Gabler, M.F., Smilanick, J.L., Mansour, M., Ramming, D.W. and Mackey, B.E. (2003) Correlations of morphological, anatomical, and chemical features of grape berries with resistance to *Botrytis cinerea*. *Phytopathology* **93**, 1263–1273.
- Hanni, E., Lardschneider, E. and Kelderer, M. (2013) Alternatives to the use of gibberellins for bunch thinning and bunch compactness reduction on grapevine. First international workshop on vineyard mechanization and grape and wine quality; 27–29 June 2012; Piacenza, Italy. *Acta Horticulturae* **978**, 335–345.
- Hed, B., Ngugi, H.K. and Travis, J.W. (2009) Relationship between cluster compactness and bunch rot in Vignoles grapes. *Plant Disease* **93**, 1195–1201.
- Hed, B., Ngugi, H.K. and Travis, J.W. (2011) Use of gibberellic acid for management of bunch rot on Chardonnay and Vignoles grape. *Plant Disease* **95**, 269–278.
- Houel, C., Martin-Magniette, M.L., Nicolas, S.D., Lacombe, T., Le Cunff, L., Franck, D., Torregrosa, L., Conejero, G., Lalet, S., This, P. and Adam-Blondon, A.F. (2013) Genetic variability of berry size in the grapevine (*Vitis vinifera* L.). *Australian Journal of Grape and Wine Research* **19**, 208–220.
- Intrigliolo, D.S., Llacer, E., Revert, J., Esteve, M.D., Climent, M.D., Palau, D. and Gómez, I. (2014) Early defoliation reduces cluster compactness and improves grape composition in Mandó, an autochthonous cultivar of *Vitis vinifera* from southeastern Spain. *Scientia Horticulturae* **167**, 71–75.
- Ioratti, C., Anfora, G., Tasin, M., De Cristofaro, A., Witzgall, P. and Lucchi, A. (2011) Chemical ecology and management of *Lobesia botrana* (Lepidoptera: Tortricidae). *Journal of Economic Entomology* **104**, 1125–1137.
- Khamis, H.J. (2008) Measures of association: how to choose? *Journal of Diagnostic Medical Sonography* **24**, 155–162.
- Kotseridis, Y., Georgiou, A., Tikos, P., Kallithrana, S. and Koundouras, S. (2012) Effects of severity of post-flowering leaf removal on berry growth and composition of three red *Vitis vinifera* L. cultivars grown under semi-arid conditions. *Journal of Agricultural and Food Chemistry* **60**, 6000–6010.

- Lebon, G., Wojnarowicz, G., Holzapfel, B., Fontaine, F., Vaillant-Gaveau, N. and Clement, C. (2008) Sugars and flowering in the grapevine (*Vitis vinifera* L.). *Journal of Experimental Botany* **59**, 2565–2578.
- Leong, S.L., Hocking, A.D., Pitt, J.I., Kazi, B.A., Emmett, R.W. and Scott, E.S. (2006) Australian research on ochratoxigenic fungi and ochratoxin A. *International Journal of Food Microbiology* **111**, S10–S17.
- Lo Giudice, D., Wolf, T.K. and Zoecklein, B.W. (2004) Effects of prohexadione-calcium on grape yield components and fruit and wine composition. *American Journal of Enology and Viticulture* **55**, 73–83.
- May, P. (2000) From bud to berry, with special reference to inflorescence and bunch morphology in *Vitis vinifera* L. *Australian Journal of Grape and Wine Research* **6**, 82–98.
- Molitor, D., Behr, M., Hoffman, L. and Evers, D. (2012a) Benefits and drawbacks of pre-bloom applications of gibberellic acid (GA3) for stem elongation in Sauvignon blanc. *South African Journal of Enology and Viticulture* **33**, 198–202.
- Molitor, D., Behr, M., Hoffman, L. and Evers, D. (2012b) Impact of grape cluster division on cluster morphology and bunch rot epidemic. *American Journal of Enology and Viticulture* **63**, 508–514.
- Nelson, K.E., Ahmedullah, M. and Mitchell, F.G. (1970) Effect of container and packing methods on injury and transpiration of table grapes. *American Journal of Enology and Viticulture* **21**, 101–108.
- Organisation Internationale de la Vigne et du Vin (2007) OIV descriptor list for grape varieties and *Vitis* species (Organisation Internationale de la Vigne et du Vin: Paris, France).
- Organisation Internationale de la Vigne et du Vin (2013) Statistical report on world vitiviniculture. Proceedings of the 36th World Congress of Vine and Wine; 2–7 June 2013; Bucharest, Romania (International Organisation of Vine and Wine: Paris, France).
- Pallioti, A., Gardi, T., Berrios, J.G., Civardi, S. and Poni, S. (2012) Early source limitation as a tool for yield control and wine quality improvement in a high-yielding red *Vitis vinifera* L. cultivar. *Scientia Horticulturae* **145**, 10–16.
- Pérez, C. (2004) Análisis factorial. Pérez, C., ed. *Técnicas de análisis multivariante de datos* (Pearson Educación, S.A.: Madrid, Spain) pp. 155–192.
- Pinelo, M., Arnous, A. and Meyer, A.S. (2006) Upgrading of grape skins: significance of plant cell-wall structural components and extraction techniques for phenol release. *Trends in Food Science & Technology* **17**, 579–590.
- Pommer, C.V., Pires, J.P., Terra, M.M. and Passos, R.S. (1996) Streptomycin-induced seedlessness in the grape cultivar Rubi (Italia Red). *American Journal of Enology and Viticulture* **47**, 340–342.
- Poni, S., Bernizzoni, F. and Civardi, S. (2008) The effect of early leaf removal on whole-canopy gas exchange and vine performance of *Vitis vinifera* L. ‘Sangiovese’. *Vitis* **47**, 1–6.
- Pratt, C. (1971) Reproductive anatomy in cultivated grapes. A review. *American Journal of Enology and Viticulture* **22**, 92–109.
- Reisch, B.I., Owens, C.L. and Cousins, P.S. (2012) Grape. Badenes, M.L. and Byrne, D.H., eds. *Handbook of plant breeding: fruit breeding* (Springer: New York, NY, USA) pp. 225–262.
- Río-Segade, S., Giacosa, S., de Palma, L., Novello, V., Torchio, E., Gerbi, V. and Rolle, L. (2013) Effect of the cluster heterogeneity on mechanical properties, chromatic indices and chemical composition of Italia table grape berries (*Vitis vinifera* L.) sorted by flotation. *International Journal of Food Science and Technology* **48**, 103–113.
- Sabbatini, P. and Howell, G.S. (2010) Effects of early defoliation on yield, fruit composition, and harvest season cluster rot complex of grapevines. *Hortscience: A Publication of the American Society for Horticultural Science* **45**, 1804–1808.
- Sarooshi, R.A. (1977) Some effects of girdling, gibberellic acid sprays, bunch thinning and trimming on the sultana. *Australian Journal of Experimental Agriculture and Animal Husbandry* **17**, 700–704.
- Schildberger, B., Faltis, C., Arnold, M. and Eder, R. (2011) Effects of prohexadione-calcium on grape cluster architecture and susceptibility to bunch rot (*Botrytis cinerea*) in cv. Grüner Veltliner. *Journal of Plant Pathology* **93**, 33–37.
- Sepahi, A. (1980) Estimating cluster compactness in Yaghouti grapes. *Vitis* **19**, 81–90.
- Shavrukov, Y.N., Dry, I.B. and Thomas, M.R. (2004) Inflorescence and bunch architecture development in *Vitis vinifera* L. *Australian Journal of Grape and Wine Research* **10**, 116–124.
- Sreejesh, S., Mohapatra, S. and Anusree, M.R. (2014) Exploratory factor and principal component analysis. Sreejesh, S., Mohapatra, S. and Anusree, M.R., eds. *Business research methods: an applied orientation* (Springer: New York, NY, USA) pp. 207–228.
- Tahaoui, T., Barbier, M. and Bessis, R. (2008) *In vitro* morphogenesis of grapevine (*Vitis vinifera* L.) inflorescence primordia, cvs Pinot Noir and Chardonnay. *Australian Journal of Grape and Wine Research* **4**, 111–120.
- Tardáguila, J., Blanco, J.A., Poni, S. and Diago, M.P. (2012) Mechanical yield regulation in winegrapes: comparison of early defoliation and crop thinning. *Australian Journal of Grape and Wine Research* **18**, 344–352.
- This, P., Lacombe, T. and Thomas, M.R. (2006) Historical origins and genetic diversity of wine grapes. *Trends in Genetics* **22**, 511–519.
- This, P., Martínez-Zapater, J.M., Péros, J.P. and Lacombe, T. (2011) Natural variation in *Vitis*. Adam-Blondon, A.F., Martínez-Zapater, J.M. and Kole, C., eds. *Genetics, genomics and breeding of grapes* (Science Publishers: Clemson, SC, USA) pp. 30–67.
- Vail, M.E. and Marois, J.J. (1991) Grape cluster architecture and the susceptibility of berries to *Botrytis cinerea*. *Phytopathology* **81**, 188–191.
- Vail, M.E., Wolpert, J.A., Gubler, W.D. and Rademacher, M.R. (1998) Effect of cluster tightness on botrytis bunch rot in six Chardonnay clones. *Plant Disease* **82**, 107–109.
- Valdés-Gómez, H., Fermaud, M., Roudet, J., Calonne, A. and Gary, C. (2008) Grey mould incidence is reduced on grapevines with lower vegetative and reproductive growth. *Crop Protection* **27**, 1174–1186.
- Vartholomaiou, A.N., Navrozidis, E.I., Payne, C.C. and Salpiggidis, G.A. (2008) Agronomic techniques to control *Lobesia botrana*. *Phytoparasitica* **36**, 264–271.
- Vasconcelos, M.C., Greven, M., Winefield, C.S., Trought, M.C.T. and Raw, V. (2009) The flowering process of *Vitis vinifera*: a review. *American Journal of Enology and Viticulture* **60**, 411–434.
- Watkins, M.W. (2006) Determining parallel analysis criteria. *Journal of Modern Applied Statistical Methods* **5**, 344–346.
- Weaver, R.J., Kasimatis, A.N. and McCune, S.B. (1962) Studies with gibberellin on wine grapes to decrease bunch rot. *American Journal of Enology and Viticulture* **13**, 78–82.
- Wei, X., Sykes, S.R. and Clingeleffer, P.R. (2002) An investigation to estimate genetic parameters in CSIRO’s table grape breeding program. 2. Quality characteristics. *Euphytica* **128**, 343–351.
- Zabadal, T.J. and Bukovac, M.J. (2006) Effect of CPPU on fruit development of selected seedless and seeded grape cultivars. *Hortscience: A Publication of the American Society for Horticultural Science* **41**, 154–157.
- Zabadal, T.J. and Dittmer, T.W. (1998) Vine management systems affect yield, fruit quality, cluster compactness, and fruit rot of ‘Chardonnay’ grape. *Hortscience: A Publication of the American Society for Horticultural Science* **33**, 806–809.

Manuscript received: 31 March 2013

Revised manuscript received: 10 July 2014

Accepted: 11 August 2014

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site: <http://onlinelibrary.wiley.com/doi/10.1111/ajgw.12121/abstract>

Figure S1. Absolute standardised coefficients obtained by a linear discriminant analysis based on three selected variables and considering 2011, 2012 and 2013 data as a whole. Variables are coded according to Table 2.

Figure S2. Absolute standardised coefficients obtained by a linear discriminant analysis based on three selected variables for 2011 (■, ■, ■), 2012 (■, ■, ■) and 2013 (■, ■, ■) data, considering the whole set of cultivars (W + T) (■, ■, ■), and the subgroups of wine (W) (■, ■, ■) and table (and multipurpose) (T) (■, ■, ■) cultivars. Variables are coded according to Table 2.

Table S1. Fisher’s LSD (green background) or Games–Howell’s (blue background) results obtained for each variable when comparing two different groups of compactness (Compactness 1 vs Compactness 2). Variables are coded according to Table 2.

Table S2. Climate conditions over 2011, 2012 and 2013. Data were obtained from La Rioja Government website (<http://www.larioja.org/siar>).