Vitis **60**,85–91 (2021) DOI: 10.5073/vitis.2021.60.85-91

Effects of genotype and environmental conditions on grapevine (*Vitis vinifera* L.) shoot morphology

D. G. Dinu[1)], D. Bianchi[2)], L. Mamasakhlisashvili[3)], C. Quarta[4)], L. Brancadoro[2)], D. Maghradze[5)], M. Cardinale[1)] and L. Rustioni[1)]

[1)] Department of Biological and Environmental Sciences and Technologies, University of Salento, Lecce, Italy
[2)] Department of Agricultural and Environmental Sciences, University of Milan, Milan, Italy
[3)] Scientific-Research Center of Agriculture, Tbilisi, Georgia
[4)] Tenute Eméra di Claudio Quarta Vignaiolo, Taranto, Italy
[5)] Caucasus International University, Faculty of Viticulture – Winemaking, Tbilisi, Georgia

Summary

Grapevine shoot morphology is widely studied for both ampelography and growing adaptation to environmental stresses. However, few is known concerning the relative contribution and interactions of the genotype and of the growing conditions to the vegetative growth. In this work, seven grapevine cultivars were studied in three geographically distant ampelographic collections to maximize the genotype and environment differences among samples. Phytomers were studied concerning the leaf area and the stem and petiole diameters and lengths. These measurements allowed the calculation of derivative parameters to describe the proportions among elements. Despite most of the studied parameters significantly discriminated both factors (cultivar and growing conditions), it was possible to identify, for each one of them, the most promising parameters based on their relative variance explanation. In fact, a negative correlation was observed between the roles of genotype and environment among the studied parameters. The low interaction effect suggested a stability in the plant behaviors, confirming the possibility to use vegetative descriptions for both cultivar discrimination and growing conditions. Future studies will be performed to develop specific indexes based on the phenotypical variability of shoot morphology described here.

K e y w o r d s : phytomer; leaf area; petiole; stem; vegetative growth; Georgian grapevine cultivars; phenotyping; smart measurement; adaptation strategies.

Introduction

Grape cultivars have been described since the birth of the Mediterranean culture by ancient Greeks and Romans, such as Theophrastus (375-297), Vergilius (70-19), Pliny and Columella, although the descriptions were in many aspects incomplete (Vršič 2012). In the last centuries, the Ampelography - the description and classification of grapevine species and cultivars based on morphology - became a scientific discipline of viticulture, and detailed descriptions were produced by different authors (e.g. Clemente 1807, Nicoleano 1900, Viala and Vermorel 1901-1910, Galet 1975). Nowadays, the characters for ampelographic descriptions have been conventionally defined by the scientific community and most of them concerns the vegetative growth (OIV 2001, Muñoz-Organero *et al.* 2010). To convert the subjective visual observations, that require a lot of experience by the operators, into objective measurements, ampelometry was developed and is now widely used (Santiago *et al.* 2005, Soldavini *et al.* 2009, Laiadi *et al.* 2013, Labagnara *et al.* 2018). Ampelometry is mainly based on leaf description, underlying the importance of this organ in the cultivar classification, due to the recognized stability of the leaf growth within the same genotype.

On the other side, it is well known that the growing conditions influence the plant canopy. It has been demonstrated that different environmental factors affect the plant vegetative growth. For example, the role of water has been investigated showing an inhibition effect of drought in different grapevine cultivars (Schultz and Matthews 1988, Pellegrino *et al.* 2005, Hardie and Martin 2008). Soil and air temperatures can affect the growth of both stems and leaves (Woodham and Alexander 1966, Buttrose 1968, Kliewer and Lider 1970, Kliever 1975). Concerning light, not only the quantity, but also the spectrum (e.g. red:far-red ratio) can modify the organs' elongation (Buttrose 1968, Morgan *et al.* 1985). Keller *et al.* (1998) found that both low-light conditions and high nitrogen availability stimulate vegetative growth. The same environmental factors were studied by Grechi *et al.* (2007), highlighting the effect of the growing conditions in the plant organ biomass allocation. The importance of nitrogen availability on the vegetative growth is well known: a deficiency in this element can cause a reduction of 45 % of the lamina area expansion (Metay *et al.* 2014). Many mineral deficiencies cause variations in the plant appearance (Rustioni *et al.* 2018). Moreover, plants are integrated with and strongly influenced by the associated microbiome (the reason why the term "holobiont" was coined; Vandenkoornhuyse *et al.* 2015). This

Correspondence to: Dr. M. Cardinale, Università del Salento, Dipartimento di Scienze e Tecnologie Biologiche ed Ambientali, Centro Ecotekne, via Provinciale Monteroni, 73100 Lecce, Italy. E-mail: massimiliano.cardinale@unisalento.it

represents another integral and very important part of the environmental influence over the plant development and fitness (Berg *et al.* 2016), including the phenotype, as demonstrated by the effect of the so-called Plant Growth Promoting Bacteria (PGPB) known also for *Vitis vinifera* (Barka *et al.* 2006, Gasser *et al.* 2012).

The above-mentioned examples find applications in the potential use of vegetation indexes to support decisions for a precise and sustainable vineyard management. These technologies are already spreading among winegrowers (Hardie and Martin 2008, Hatfield *et al.* 2008, Taskos *et al.* 2015). However, despite the large body of literature concerning the effects of the genotype or of the growing conditions on the plant vegetation, few is known concerning their relative contribution and interactions in the grapevine phenotyping. Therefore, the aim of this work was to assess the respective roles of the genotype and of the growing conditions on several morphological parameters of seven grapevine cultivars grown in three different sites. The quantification of the interaction effects indicates the stability of those parameters, which gives an indication of the cultivar plasticity among growing conditions. It is worth to notice that, in this work, with the term "growing conditions" we intend a combination of environmental and anthropogenic factors. The main purpose of this study is the identification of the most promising parameters to be used for future development of accessible indexes to support winegrowers' decisions regarding vineyard management.

Material and Methods

Experimental design: The experiment was carried out in June 2020, in three very different ampelographic collections. Two of them are in different Italian wine regions – Oltrepò Pavese and Salento – and one is sited in Jighaura – Georgia.

The Oltrepò Pavese collection (FAO INSTCODE: ITA035) is located in the region Lombardy in the north of Italy (Latitude 44.97, Longitude 9.08, Elevation 144 m a.s.l.). The vineyard is planted on a hilly terrace with a slight east exposition (row direction SE-NW), with a typical clay soil. Plants are spaced 2.5 m (interrow) and 1 m (intrarow), with a plant density of about 4000 plants·ha^{-1}. Vines are trained at classic Guyot system; soil is managed with a natural grass cover and the vineyard does not have an irrigation system.

The Salento vineyard is a private collection situated in the region Apulia in the south of Italy (Latitude 40.35, Longitude 17.40, Elevation 25 m a.s.l.). The vineyard is planted in a plain area, characterized by a sandy loam calcareous soil. Plants are spaced 2.2 m (interrow) and 0.9 m (intrarow), with a plant density of about 5000 plants·ha^{-1}. Vines are trained at classic spur cordon; soil is managed by tillage and the vineyard is equipped with an irrigation system.

The Jighaura collection (FAO INSTCODE: GEO038) is sited in Georgia (Latitude 41.55, Longitude 44.46, Elevation 585 m a.s.l.). The vineyard is planted in a plain area, with a typical alluvial carbonated deep soil, with middle and heavy clay texture, and high skeleton. The soil is managed with natural grass cover. The vineyard is equipped by a drip irrigation system. Plants are spaced by 2.35 m (interrow) and 1.25 m (intrarow), with a plant density of about 3,400 plants·ha^{-1}. The training system is a double cane without spur. Jighaura's collection rows of vineyard are directed from west to east, because of the wind direction.

In each collection, the same seven cultivars were considered, namely 'Shavkapito', 'Rkatsiteli', 'Ojaleshi', 'Alexandrouli', 'Gorula', 'Mgaloblishvili' and 'Aladasturi' - all of Georgian origin. For each cultivar, a total of 27 phytomers were described (3 plants, 3 shoots/plant, 3 phytomers/shoot). The plant and shoot selection was based on the visual observation of the vines: the most healthy and vigorous ones were chosen in each collection. Concerning the phytomers, the 3rd, 4th and 5th nodes were always considered. This choice was made based on the recommendations of IPGRI, UPOV and OIV (1997), that indicate the middle third of the shoot as the most stable within the same genotype and, thus, a low variability should be expected due to different growing conditions. Furthermore, the development of the basal part of the shoot is strongly influenced by the bud preformation and the availability of reserves in the initial phenological phases (Zapata *et al.* 2004). It means that a major contribution of the *terroir* (not limited to the specific moment of shoot growth during the season, but also in relation to the general plant life) should be expected.

Morphological parameters: Phytomer morphology was described concerning the green surfaces and their proportions (Fig. S1). The selection of the variables was guided by the intention to propose those that are objective, numerical, easy to be measured, and that do not need expensive equipment. Internodal stems were measured directly on the plants, while leaves (with their petioles) were detached to facilitate the data recording. The length and diameter of internodal stems and petioles were measured using a ruler and an electronic caliper, respectively (diameter was measured in the middle point of the stem or the petiole). Leaf area was measured with the smartphone app 'Easy Leaf Area Free' (Easlon and Bloom 2014) (Fig. S2). These direct records were also used to calculate derivative variables for each phytomer. In total, 16 variables were considered, 5 direct measurements [Leaf area, Stem length, Stem diameter, Petiole length, Petiole diameter] and 9 indirect variables [Total area of the phytomer, Petiole length/Petiole diameter ratio, Stem length/Stem diameter ratio, Stem area, Petiole area, Leaf area/Petiole area ratio, Stem area/Petiole area ratio, Leaf area/Stem area ratio, Leaf area (% with respect to the total green surface), Stem area (% with respect to the total green surface), Petiole area (% with respect to the total green surface)]. The areas of petiole and phytomers were calculated mathematically (circumference x length).

Statistical analyses: All statistical analyses were done in SPSS (IBM Corporation, Armonk, US). Variables (direct and derivative) were checked for normality of distribution using the Shapiro-Wilk test. A Principal Component Analysis (PCA) was performed on all direct and derivative variables. The relative contributions to the total observed variance of the factors "Site", "Cultivar", "Internode", as well as of the respective interactions, was calculated as the percentage of the ANOVA mean of squares of each factor with respect to the sum of the mean of squares

of all factors (including the error). The relative contributions of the factors Site, Cultivar and Internode were compared each other by Pearson moment correlation. The significance of the factors "Site" and "Cultivar" on all variables, as well as on the four main PCA functions, was tested by ANOVA and Duncan Post-hoc analysis (at $p < 0.05$). Beta-error was controlled, and it was always equal to zero (analysis power = 1). The effect size was assessed by partial-η^2. Final figures were assembled using ImageJ2 (Rueden *et al.* 2017) and the online image editor Photopea (available at www.photopea.com).

Results

The Principal Component Analysis produced 4 functions with eigenvalues higher than 1, explaining, respectively, 34.9 %, 31.3 %, 16.5 % and 4.9 % of the total observed variance. The first function was mainly related to direct measurements: total phytomer, leaf, stem and petiole areas, stem length and petiole diameter. The second function instead was mainly related to the proportions among phytomer elements (leaf and stem percentage of the total area). The third function was strongly related to the petiole morphology (petiole length, percentage of petiole area and petiole area, ratios among stem/petiole and leaf/petiole areas). The fourth function was related to the stem and petiole proportions (both length/diameter ratios) and to the stem diameter (Tab. S1).

PCA ordination of morphological data differentiated the cultivars on the first principal component based mainly on the size of individual elements (Fig. 1A-B): 'Shavkapito' and 'Rkatsiteli' had small vegetation, 'Ojaleshi', 'Alexandrouli' and 'Gorula' were intermediate, 'Mgaloblishvili' and 'Aladasturi' were the biggest ones (Fig. 1B). The 2nd, 3rd and 4th functions significantly discriminated the cultivars as well (Fig. 1C-E), corroborating the important role of the genotype in the plant morphology. However, function 1 showed a large effect size (partial-$\eta^2 = 0.435$) when tested by ANOVA, while other functions showed a medium effect size (partial-$\eta^2 = 0.11$-0.12). All individual variables were significantly influenced by the cultivar (Fig. S3).

Cultivation sites (*i.e.* the environmental conditions, vineyard management, etc.) also significantly affected the plant morphology (Fig. 2A). Functions 1 and 4 showed a gradient coherent with the latitude of the study sites: from south to north, Salento, Jighaura and Oltrepò Pavese (Fig. 2B, E). However, only function 4 discriminated all three experimental sites, while function 1 only revealed significantly smaller phytomers in Salento. Functions 2 and 3 discriminated the Continents: Jighaura showed significantly lower scores with respect to the Italian records (Fig. 2C-D). It is worth to notice that functions 2 and 4 were the most discriminant and that they were both related to derivative variables (the proportions among the different elements considered in the phytomer description; Tab. S1). In fact, functions 2 and 4 showed a large effect size (partial-$\eta^2 = 0.215$ and 0.216, respectively) (Fig. 2 C, E), while the effect size of function 1 and 3 were respectively small and medium-small (partial-$\eta^2 = 0.042$ and 0.074, respectively) (Fig. 2 B, D). All individual variables were significantly influenced by the site, except petiole diameter (Fig. S4).

Fig. 3 reports the variance explanation by experimental site, cultivar, internode and interactions among factors. Considering the relative low differences among plants and shoots, these factors were not included in this analysis and, thus, their variability fall in the unexplained variance. In the graph, interactions have been merged, but extensive data are reported in Tab. S2. The average of all considered parameters

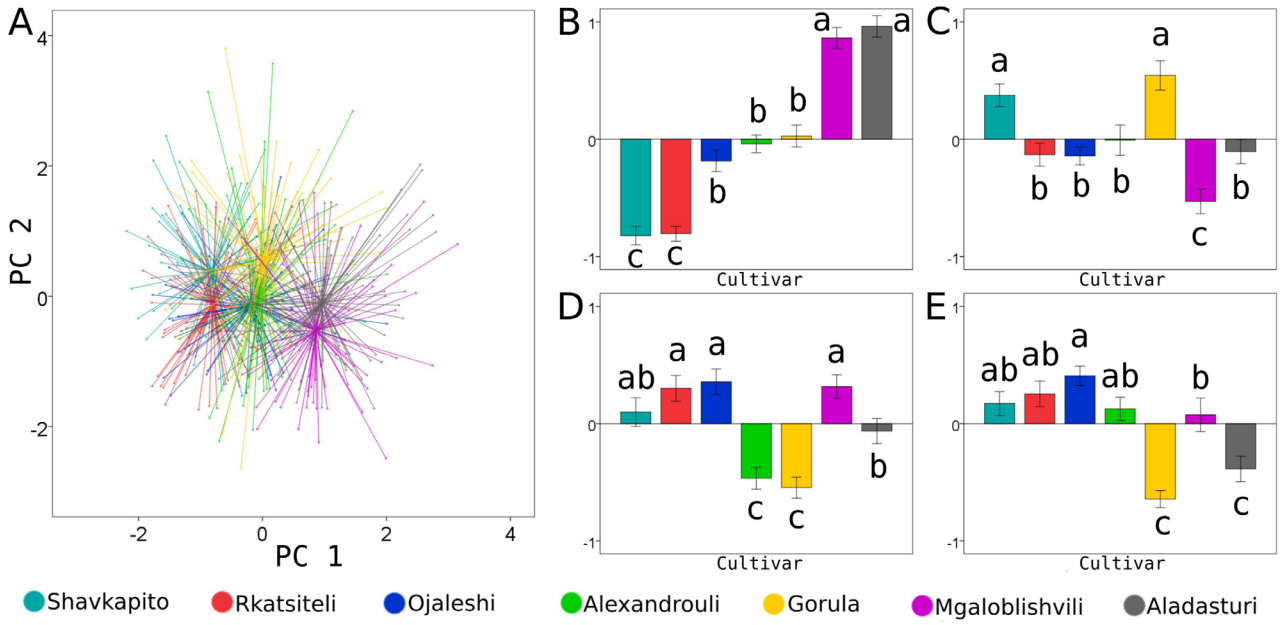

Fig. 1: (**A**) Principal Component Analysis (PCA) of 16 morphological parameters, ordering the samples according to the grapevine cultivar. The first and the second PCA-functions were used to build the plot. (**B-E**) Contribution of the four main PCA functions to the discrimination between cultivars. Different letters above the bars represent significantly different means (Duncan's Post-hoc test, $p = 0.05$). Colors indicate the cultivars according to the legend. Details concerning the matrix of the four main Principal Component functions are reported in Tab. S1.

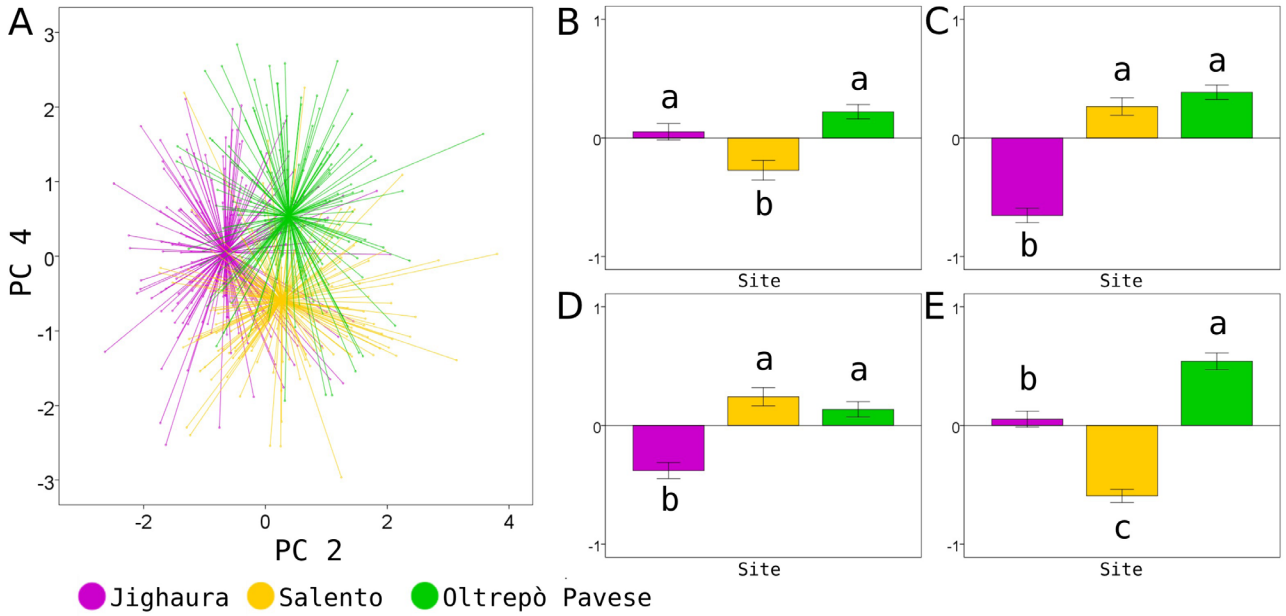

Fig. 2: (**A**) Principal Component Analysis (PCA) of 16 morphological parameters, ordering the samples according to the experimental sites. The second and the fourth PCA-functions were used to build the plot. (**B-E**) Contribution of the four main PCA functions to the discrimination between sites. Different letters above the bars represent significantly different means (Duncan's Post-hoc test, $p = 0.05$). Colors indicate the sites according to the legend. Details concerning the matrix of the four main Principal Component functions are reported in Tab. S1.

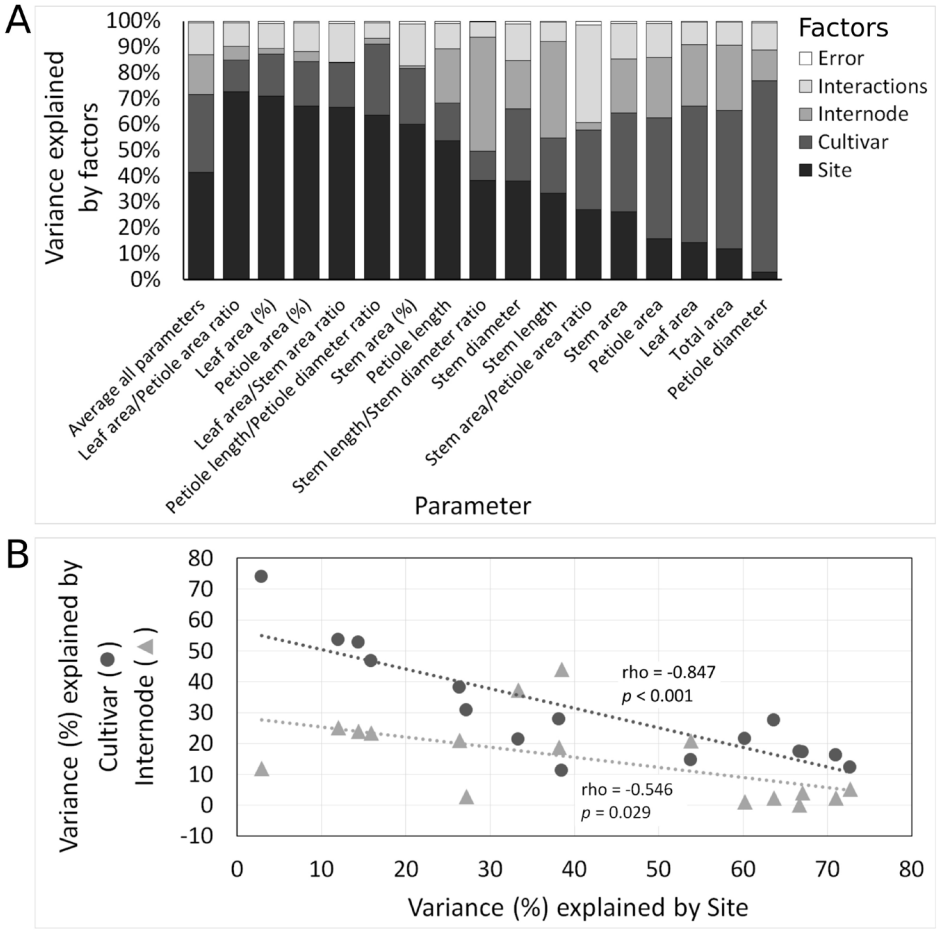

Fig. 3: (**A**) Contribution of experimental factors and their cumulative interactions to the observed variance among all parameters tested, calculated as the percentage of the ANOVA mean of squares of each factor with respect to the sum of the mean of squares of all factors (including the error). The average of all parameters is also shown (first bar). (**B**) Correlation between the relative contributions of the factors Site, Cultivar and Internode to the observed variance. Person moment correlation rho and *p* values are also shown on the graph.

indicated a variance explanation of 41.5 %, 30.2 %, 15.3 % and 12.3 % due to experimental site, cultivar, internode and interactions, respectively (Fig. 3A). Only 0.7 % of the variance remained unexplained (error). Fig. 3A shows the parameters ordered according to the variance explained by site (decreasing). A strong indirect correlation ($p < 0.001$) between contribution of genotype (cultivar) and environment (site) to the phenotype definition was observed (Fig. 3B). This result was corroborated by the correlations of the effect sizes calculated on the two factors (Pearson rho = -0.641, $p = 0.008$ - Fig. S5). Interestingly, the main factor of variability of the direct measurements (e.g. petiole diameter, total surface, leaf area, etc.) was the cultivar, indicating a strong and stable genetic control of these parameters (Fig. 3A; Fig. 5). On the other side, derivative parameters, *i.e.* the ones that describe variations in the proportions among the considered elements (e.g. Leaf area/Petiole area ratio, percentages of area distribution, etc.), varied mainly in relation to the environmental conditions, indicating a plasticity of the phenotype depending on the growing context.

Discussion

In this work, we tested the feasibility of plant morphological parameters to be used as indicators of growing conditions or cultivar classification. To do this, we assessed the relative contribution of the experimental factors (site, cultivar and internode) to the total variance of 16 direct and derivative morphological parameters of seven grapevine cultivars grown in three different sites (two in Italy, Europe, and one in Georgia, Western Asia). We found out that direct variables were mainly influenced by the genotype, while several derivative variables were more dependent from the sites: we propose that the latter could be further studied for use as indexes to measure how the plant responds to the surrounding environmental conditions.

The experimental sites were intentionally selected to maximize the differences in the plant growing conditions (weather, soil, vineyard management, etc.). In parallel, the seven genotypes were chosen, among those available in the three experimental sites, based on their morphological differences. Furthermore, these cultivars originated from different Georgian wine regions: 'Rkatsiteli' (B) – Kakheti, 'Ojaleshi' (N) – Samegrelo, 'Alexandrouli' (N) – Racha, 'Mgaloblishvili' (N) – Imereti, 'Aladasturi' (N) – Guria, 'Gorula' (B) and 'Shavkapito'(N)– Kartli (Ketskhoveli *et al.* 1960, Tsertsvadze 1989). This fact suggests that these varieties underwent different selective pressures by local farmers, which likely resulted in an increased genetic variability among them. Moreover, being Georgia a primary domestication center of cultivated grapevines, Georgian varieties have been shown to have a high intraspecific genetic variability (De Lorenzis *et al.* 2015), resulting in an interesting phenotypic variability (Maghradze *et al.* 2014, Abashidze *et al.* 2015)

Plant morphology appeared to be strongly defined by genotype, especially concerning the general size appearance of the plant (Fig. 1). It is worth to notice that the cultivar recognition has been based on the description of the plant morphology for centuries and, despite the increased importance of molecular markers, it maintains a fundamental role in the varietal classification. In ampelography, the observation of vegetative organs is mandatory focusing on the tips, young and mature leaves, shoots, clusters, berries, etc. (OIV 2001, Muñoz-Organero *et al.* 2010). However, the visual observation can often suffer of the objectivity of the evaluation and, thus, despite its major and undisputed importance in the plant classification, inaccuracies can happen, also due to the limited number of descriptor categories and the difficulties to perform statistical analyses on this kind of visual records. For example, the ampelographic descriptions of the studied cultivars report the bigness of the mature leaves as follow: 'Mgaloblishvili', 'Aladasturi' and 'Gorula' - large; 'Rkatsiteli' - medium-large; 'Ojaleshi', 'Alexandrouli' and 'Shavkapito' - medium size (Tsertsvadze, 2012). However, our results indicate (Fig. S3) that cultivars are grouped as follow: 'Rkatsiteli' and 'Shavkapito' – smaller; 'Gorula', 'Ojaleshi' and 'Alexandrouli' – medium; 'Mgaloblishvili' and 'Aladasturi' – larger sized leaves. Moreover, notably, very stable values of leaf areas were recorded among genotypes, as demonstrated by the small standard error bars of Fig. S3. Despite these (yet not huge) discrepancies with the literature data of visual description, we argue that our precise measurements are more reliable due to the quantitative and objective nature of the records. Moreover, this approach is more modern, and takes advantage of digital technologies already available for free. Thus, in the next future, this kind of measurements will also likely support the cultivar classification and the ampelographic description. With this regard, it is worth noticing that petiole diameter (a parameter never considered in the cultivar classification until now) resulted to be the most representative and stable variable for cultivar discrimination, independently from the growing conditions (Fig. S3 and S4). This evidence should encourage further studies in this direction.

It is well known that the phenotype is the result of the genotype, the environmental conditions, and their interactions (Rustioni *et al.* 2019). Many studies deal with the effects of the growing conditions on the grape production quantity and quality (Poni *et al.* 2018) or the plant phenology (Rustioni *et al.* 2014). However, considering morphology, a dominant effect is usually ascribed to the genotype, as demonstrated by the broad use of ampelography and ampelometry (Labagnara *et al.* 2018, Laiadi *et al.* 2013, OIV, 2001, Muñoz-Organero *et al.* 2010, Santiago *et al.* 2005). Generally, it is accepted that the plants undergo long-term morphological adaptations to cope with environmental constrains during their evolution; however, short-term morphological adaptation strategies to the surrounding environment also exist. Our results indicate that the growing conditions strongly and significantly affect the grapevine morphology. This is not surprising if we think about the roles of the light or of the nitrogen availability or of the plant water status or of the biotic interactions with the microbiome (Pellegrino *et al.* 2005, Schultz and Matthews 1988, Hardie and Martin 2008, Woodham and Alexander 1966, Kliever 1975, Kliewer and Lider 1970, Buttrose 1968, Morgan

et al. 1985, Keller *et al.* 1998, Grechi *et al.* 2005, Metay *et al.* 2014, Berg *et al.* 2016) on plants. Of course, the plant response to the environment is guided by the genetic information, but we found that some morphological characters are quite coherent among genotypes in different environments (low variance explanation related to the interaction; Tab. S2), indicating a stability in the adaptations mechanisms among different cultivars. In particular, we found that derivative parameters (especially proportions between elements) are those mainly influenced by the environment. This is coherent with the results of Pellegrino *et al.* (2005) who observed that morphological composite indicators are best descriptors of water deficit for grapevine. Although Schultz and Matthews (1988) showed that all shoot elements responded similarly to water stress, their work was based on one cultivar only, while in our study the analysis of seven different cultivars likely highlighted the dominant role of the genotype over the environment on the general development of individual elements.

Although the availability of an ampelographic collection network allowed the comparison of the same cultivars in different growing conditions, this preliminary work does not permit to confirm a cause-effect outcome. Moreover, our observational and explorative study does not allow a breakdown of the individual environmental factors responsible for the variance observed. Future dedicated studies, which experimentally separate the environmental factors, will be necessary to determine their actual role on the phenotype modulation in grapevine: when these will be unraveled, it will be possible to develop easily measurable indexes to assess the plant response to the different growing conditions. This will help the farmers and the policy makers to take decisions both in the long term (for example, deciding which cultivar is more suitable to be planted on a certain site, or to assess strategies to face climate change) and in the short term (for example, deciding whether to irrigate or not, or which fertilizer is needed in that growing phase). Our selection of simple, low-cost, and objective measurements of parameters able to discriminate the phenotypes based on plant morphology represents a promising tool, easily available to everybody, for future research and application in viticulture.

Acknowledgements

We thank T. Maghradze (Caucasus International University, Georgia) for contribution to the experimental work.

References

Abashidze, E.; Mdinaradze, I.; Chipashvili, R.; Vashakidze, L.; Maghradze, D.; Rustioni, L.; Failla, O.; 2015: Evaluation of eno-carpological traits in Georgian grapevine varieties from Skra germplasm repository. Vitis **54**, 151-154. DOI: https://doi.org/10.5073/vitis.2015.54.special-issue.151-154

Barka, E. A.; Nowak, J.; Clément, C.; 2006: Enhancement of chilling resistance of inoculated grapevine plantlets with a plant growth-promoting rhizobacterium, *Burkholderia phytofirmans* strain PsJN. Appl. Environ. Microbiol. **72**, 7246-7252. DOI: https://doi.org/10.1128/AEM.01047-06

Berg, G.; Rybakova, D.; Grube, M.; Köberl, M.; 2016: The plant microbiome explored: implications for experimental botany. J. Exp. Bot. **67**, 995-1002. DOI: https://doi.org/10.1093/jxb/erv466

Buttrose, M. S.; 1968: Some effects of light intensity and temperature on dry weight and shoot growth of grape-vine. Ann. Bot. **32**, 753-765. DOI: https://doi.org/10.1093/oxfordjournals.aob.a084247

Clemente S. de R.; 1807: Ensayo Sobre las Variedades de la Vid Comun que Vegetan en Andalucia. Madrid: Imprenta de Villalpando.

De Lorenzis, G.; Chipashvili, R.; Failla, O.; Maghradze, D.; 2015: Study of genetic variability in *Vitis vinifera* L. germplasm by high-throughput *Vitis*18kSNP array: the case of Georgian genetic resources. BMC Plant Biol. **15**, 154. DOI: https://doi.org/10.1186/s12870-015-0510-9

Easlon H. M.; Bloom A.; 2014: Easy leaf area: automated digital image analysis for rapid and accurate measurement of leaf area. Applic. Plant Sci. **2**, 1400033. DOI: https://doi.org/10.3732/apps.1400033

Galet, P.; 1975: Cépages et Vignoble de France. C. Dehan: Montpellier.

Gasser, F.; Cardinale, M.; Schildberger, B.; Berg, G.; 2012: Biocontrol of *Botrytis cinerea* by successful introduction of *Pantoea ananatis* in the grapevine phyllosphere. Int. J. Wine Res. **4**, 53-63. DOI: https://doi.org/10.2147/IJWR.S31339

Grechi, I. P. H. V.; Vivin, P.; Hilbert, G.; Milin, S.; Robert, T.; Gaudillère, J. P.; 2007: Effect of light and nitrogen supply on internal C:N balance and control of root-to-shoot biomass allocation in grapevine. Environmental and Experimental Botany 59: 139-149. doi: 10.1016/j.envexpbot.2005.11.002

Hardie W. J.; Martin S. R.; 2008: Shoot growth on de-fruited grapevines: a physiological indicator for irrigation scheduling. Aust. J. Grape Wine Res. **6**, 52-58. DOI: https://doi.org/10.1111/j.1755-0238.2000.tb00162.x

Hatfield J. L.; Gitelson A. A.; Schepers J. S.; Walthall C. L.; 2008: Application of spectral remote sensing for agronomic decisions. Agron. J. **100**, 117-131. DOI: https://doi.org/10.2134/agronj2006.0370c

IPGRI, UPOV, OIV; 1997: Descriptors for Grapevine (*Vitis* spp.). International Union for the Protection of New Varieties of Plants, Geneva, Switzerland/Office International de la Vigne et du Vin, Paris, France/International Plant Genetic Resources Institute, Rome, Italy (https://www.bioversityinternational.org/e-library/publications/detail/descriptors-for-grapevine-vitis-spp/).

Keller M.; Arnink K. J.; Hrazdina G.; 1998: Interaction of nitrogen availability during bloom and light intensity during veraison. I. Effects on grapevine growth, fruit development, and ripening. Am. J. Enol. Vitic. **49**, 333-340 (https://www.ajevonline.org/content/49/3/333).

Ketskhoveli, N.; Ramishvili, M.; Tabidze, D.; 1960: Ampelograohy of Georgia. Georgian Academy of Sciences Publishing. Tbilisi, Georgia. (in Georgian and Russian)

Kliewer, W. M.; 1975: Effect of root temperature on budbreak, shoot growth, and fruit-set of 'Cabernet Sauvignon' grapevines. Am. J. Enol. Vitic. **2**, 82-89 (https://www.ajevonline.org/content/26/2/82).

Kliewer, W. M.; Lider, L. A.; 1970: Effects of day temperature and light intensity on growth and composition of *Vitis vinifera* L. fruit. J. Am. Soc. Hortic. Sci. **6**, 766-769.

Labagnara, T.; Bergamini, C.; Caputo, A. R.; Cirigliano, P.; 2018: *Vitis vinifera* L. germplasm diversity: a genetic and ampelometric study in ancient vineyards in the South of Basilicata region (Italy). Vitis **57**, 1-8. DOI: https://doi.org/10.5073/vitis.2018.57.1-8

Laiadi, Z.; Bencharif, S.; Lakhrif, Z.; Bentchikou, M. M.; Mohand-Larbi, R.; 2013: First ampelometric study of autochthonous grapevines in Algeria: Germplasm collection of Mascara. Vitis **52**, 21-27. DOI: https://doi.org/10.5073/vitis.2013.52.21-27

Maghradze, D.; Vashakidze, L.; Abashidze, E.; Chipashvili, R.; Mdinaradze, I.; Failla, O.; Rustioni, L.; De Lorenzis, G.; Scienza, A.; Maul, E.; 2014: Multidisciplinary study of traditional grape cultivars from Kartli province of Georgia (the Caucasus region) and activities for their preservation. Acta Hortic. **1032**, 235-242. DOI: https://doi.org/10.17660/ActaHortic.2014.1032.33

Metay, A.; Magnier, J.; Guilpart, N.; Christophe, A.; 2014: Nitrogen supply controls vegetative growth, biomass and nitrogen allocation for grapevine (cv. Shiraz) grown in pots. Funct. Plant Biol. **42**, 105-114. DOI: https://doi.org/10.1071/FP14062

Morgan, D. C.; Stanley, C. J.; Warrington, I. J.; 1985: The effects of simulated daylight and shade-light on vegetative and reproductive

growth in kiwifruit and grapevine. J. Hortic. Sci. **60**, 473-484. DOI: https://doi.org/10.1080/14620316.1985.11515654

Muñoz-Organero, G.; Gaforio, L.; García-Muñoz, S.; Cabello, F.; 2010: Manual for standarization of *Vitis* descriptors. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA).

Nicoleano, G. N.; 1900: Introduction à l'Ampélographie Roumaine. Impr. eDreptateae, Bucharest.

OIV; 2001: OIV Descriptor List for Grape Varieties and *Vitis* Species, 2nd ed. O I V (Off. Int. Vigne Vin), Paris, France.

Pellegrino, A.; Lebon, E.; Simonneau, T.; Wery, J.; 2005: Towards a simple indicator of water stress in grapevine (*Vitis vinifera* L.) based on the differential sensitivities of vegetative growth components. Aust. J. Grape Wine Res. **11**, 306-315. DOI: https://doi.org/10.1111/j.1755-0238.2005.tb00030.x

Poni, S.; Gatti, M.; Palliotti, A.; Dai, Z.; Duchêne, E.; Truong, T. T.; Ferrara, G.; Matarrese, A. M. S.; Gallotta, A.; Bellincontro, A.; Mencarelli, F.; Tombesi, S.; 2018: Grapevine quality: a multiple choice issue. Scientia Hortic. **234**, 445-462. DOI: https://doi.org/10.1016/j.scienta.2017.12.035

Rueden, C. T.; Schindelin, J.; Hiner, M. C.; DeZonia, B. E.; Walter, A. E.; Arena, E. T.; Eliceiri, K. W.; 2017: ImageJ2: ImageJ for the next generation of scientific image data. BMC Bioinform. **18**, 529. DOI: https://doi.org/10.1186/s12859-017-1934-z

Rustioni, L.; Cola, G.; Fiori, S.; Faill a, O.; Bacilieri, R.; Maul, E.; Eiras Dias, J. E.; Brazão, J.; Kocsis, L.; Lorenzini, F.; Maghradze, D.; Chipashvili, R.; Maletic, E.; Preiner, D.; Molitor, D.; Moljukina, N.; Muñoz-Organero, G.; Musayev, M.; Nikolaou, N.; Risovanna, V.; Ruisa, S.; Salimov, V.; Savin, G.; Cornea, V.; Savvides, S.; Schneider, A.; Skala, O.; Ujmajuridze, L.; 2014: Application of standard methods for the grapevine (*Vitis vinifera* L.) phenotypic diversity exploration: phenological traits. Acta Hortic. **1032**, 253-260. DOI: https://doi.org/10.17660/ActaHortic.2014.1032.35

Rustioni, L.; Cola, G.; Maghradze, D.; Abashidze, E.; Argiriou, A.; Aroutiounian, R.; Brazão, L.; Chipashvili, R.; Cocco, M.; Cornea, V.; Dejeu, L.; Eiras Dias, J. E.; Goryslavets, S.; Ibáñez, J.; Kocsis, L.; Lorenzini, F.; Maletic, E.; Mamasakhlisashvili, L.; Margaryan, K.; Maul, E.; Mdinaradze, I.; Melyan, G.; Michailidou, S.; Molitor, D.; Montemayor, M. I.; Muñoz-Organero, G.; Nebish, A.; Nemeth, G.; Nikolaou, N.; Popescu, C. F.; Preiner, D.; Raimondi, S.; Risovannaya, V.; Savin, G.; Savvides, S.; Schneider, A.; Schwander, F.; Spring, J. L.; Ujmajuridze, L.; Zioziou, E.; Failla, O.; Bacilieri, R.; 2019: Description of the *Vitis vinifera* L. phenotypic variability in enocarpological traits by a Euro-Asiatic collaborative network among ampelographic collections. Vitis **58**, 37-46. DOI: https://doi.org/10.5073/vitis.2019.58.37-46

Rustioni, L.; Grossi, D.; Brancadoro, L.; Failla, O.; 2018: Iron, magnesium, nitrogen and potassium deficiency symptom discrimination by reflectance spectroscopy in grapevine leaves. Sci. Hortic. **241**, 152-159. DOI: https://doi.org/10.1016/j.scienta.2018.06.097

Santiago, J. L.; Boso, S.; Martín, J. P.; Ortiz, J. M.; Martínez, M. C.; 2005: Characterisation and identification of grapevine cultivars (*Vitis vinifera* L.) from northwestern Spain using microsatellite markers and ampelometric methods. Vitis **44**, 67-72.

Schultz, H. R.; Matthews, M. A.; 1988: Vegetative growth distribution during water deficits in *Vitis vinifera* L. Aust. J.Plant Physiol. **15**, 641-656. DOI: https://doi.org/10.1071/PP9880641

Soldavini, C.; Schneider A.; Stefanini, M.; Dallaserra, M.; Policarpo, M.; 2009: Superampelo – a software for ampelometric and ampelographic descriptions in *Vitis*. Acta Hortic. **827**, 253-257. DOI: https://doi.org/10.17660/ActaHortic.2009.827.43

Taskos, D. G.; Koundouras, S.; Stamatiadis, S; Zioziou, E.; Nikolaou, N.; Karakioulakis, K.; Theodorou, N.; 2015: Using active canopy sensors and chlorophyll meters to estimate grapevine nitrogen status and productivity. Precision Agric 16, 77-98. DOI: https://doi.org/10.1007/s11119-014-9363-8

Tsertsvadze, N.; 1989: Sakartvelos kulturuli vazis klasifikatsia (Classification of Georgian cultivated grapevine). Sabchota Sakartvelo, Tbilisi (in Georgian).

Tsertsvadze, N.; 2012: Georgia: native varieties of grapevine. In: D. Maghradze, L. Rustioni, J. Turok, A. Scienza, O. Failla (Eds): Caucasus and Northern Black Sea Region Ampelography. Vitis, Siebeldingen, Germany. DOI: https://doi.org/10.5073/vitis.2012.51.special-issue.3-481

Vandenkoornhuyse, P.; Quaiser, A.; Duhamel, M.; Le Van, A.; Dufresne, A.; 2015: The importance of the microbiome of the plant holobiont. New Phytol. **206**, 1196-1206. DOI: https://doi.org/10.1111/nph.13312

Viala, P.; Vermorel, V.; 1901-1910: Traité general de viticulture: ampélographie. Paris.

Vršič, S.; 2012: An overwiew of ampelographic research and modifications of grapevine assortment. Agricultura **9** (Suppl. 1), 11-20.

Woodham, R. C.; Alexander, M. C. E.; 1966: The effect of root temperature on development of small fruiting Sultana vines. Vitis **5**, 345-350. DOI: https://doi.org/10.5073/vitis.1966.5.345-350

Zapata, C.; Deléens, E.; Chaillou, S.; Magné, C.; 2004: Partitioning and mobilization of starch and N reserves in grapevine (*Vitis vinifera* L.). J. Plant Physiol. 161, 1031-1040. DOI: https://doi.org/10.1016/j.jplph.2003.11.009

Received July 8, 2020
Accepted February 1, 2021