Increasing our knowledge on grapevines physiology to increase yield, quality and sustainably

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EDITORIAL

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Scandinavia is not (yet) a famous wine-producing area, but the Scandinavian Plant Physiology Society offered me the opportunity to highlight some of the recent scientific contributions on grapevines published in *Physiologia Plantarum*. I first would like to apologize to many colleagues who published important contributions in the field and I did not cite. The aim of this short communication was to take some examples in the literature to present to scientific wine lovers, but also the ones who like grape juice and table grapes or raisins, which topics grapevine scientists are studying to increase our knowledge in grapevine physiology that could at the end help winegrowers to increase yield, quality and sustainability.

Even if the storytelling around domestication is so interesting (Badouin et al., 2020; Terral et al., 2010), for the purpose of this article, we should remember that *Vitis vinifera* is the most cultivated one. Several thousand varieties have been listed (Galet, 2015).

Grape is an important crop with high economic value for several countries, from the old European producing ones to the modern ones (North and South America, South Africa, Australia, New Zealand) and the coming one (China).

Some specificities should be remembered to understand the complexity of grape production and research; within these, we can cite (1) a wide range of yields (from 15 to 200 hl/Ha), (2) a not-fully understood, and even defined, quality linked to the notion of terroir, (3) growth at the same place since 200 years precluding crop rotations, (4) in most cultivated vineyards, the presence of grafted plants that were not introduced for yield or quality but for disease resistance (phyloxera), (5) a strong diversity in agropedoclimatic growth conditions, (6) an important development of organic and esoteric biodynamic culture, (7) an important spreading of wood diseases such as eutypiosis and esca, and (8) slow and low plant breeding outputs because of a reactionary attitude of both producers and consumers.

Like most crops, vineyards are facing biotic and biotic stresses. Although drought has been studied for a long time, climate change has induced an increase in the studies dealing with temperature, light quality and intensity and CO_2. Unfortunately, *Vitis vinifera* is very sensitive to several pathogens, the two most important being downy and powdery mildew, but other ones are also problematic in more specific areas such as trunk disease, black rot, *Xylella fastidiosa*. The combinatorial effects of these stresses cannot be predicted from the study of each stress studied alone (Bouain et al., 2019). A recent and counter-intuitive demonstration is the absence of drought effects on esca development (Bortolami et al., 2021).

Although it was claimed above that new grapevine varieties are rare and infrequent, two exceptions should not be forgotten: disease (mildew)-resistant varieties and the use of genetic as a research tool. Besides, some historical varieties from interspecific crosses are resistant to downy and powdery mildew (Jacquez, Clinton, Maréchal Foch), new breeding programs are developed to create new resistant varieties with properties closer to the international varieties. Several new varieties are available for the producer, even in conservative countries. Other breeding programs take into account climate changes adaptation (Bigard et al., 2020).

1 | WATER USE EFFICIENCY AND DROUGHT

Grapevine is often cultivated in drought areas. The efficacity to use water to produce a defined biomass can be defined at different levels and take different names: Water Use Efficiency (WUE) or Transpiration Efficiency. The importance of such parameters lies in the link between water loss and CO_2 fixation through the stomatal pores. The regulation of stomatal aperture has been studied in different conditions and varieties. Daytime regulation is well-documented, whereas the role of nighttime transpiration has been demonstrated only recently (Coupel-Ledru et al., 2016).

Several studies were performed to compare the variability in WUE between different cultivars, for example, by comparing (near) isohydric (Grenache) and (near)anisohydric cultivars (Syrah) (Coupel-Ledru et al., 2016). Buesa et al. (2021) studied the intracultivar genetic diversity using 13 Grenache genotypes (both red and white) under field conditions over three seasons. They demonstrate that three parameters (intrinsic WUE, crop WUE, and $\delta^{13}C$) are reliable indicators to select drought-resistant genotypes.

While it is expected that the growing conditions are important to study the effect of water availability of the different (eco)physiological parameters, it is also important to quantify the drawbacks that can occur. The effect of the container's volume on the plant response to drought has been studied by comparing several parameters on plants grown in 7 or 20 L pots (Herrera et al., 2021). Before drought (46 days), the number of leaves and average leaf area were the same between plants grown in containers of different volume, but differences in xylem vessel anatomy have been identified. Furthermore, the plant response to drought is different. But what should be clarified is the origin of the difference. Is the stress sensed by the plant different or is the plant anatomy at the beginning of the stress different? Indeed, differences in nutrient availability could induce anatomy differences.

Besides the importance of the development stage where the drought stress occurs, the effect of the speed of the stress should also be taken into account. Morabito et al. (2022) compared fast-developing drought to slow-developing drought on stress response and recovery. They demonstrate that Grenache, usually described as a near-isohydric cultivar, can behave as a near-anisohydric cultivar when the stress is slowly applied.

2 | PRIMARY AND SECONDARY METABOLISM

One important berry component is the sugar content. Sugar is made from CO_2 in the source (the mature leaves) and transported to the sink: berries, young leaves, roots/trunks.

Combinatorial stress application is necessary because plant response cannot be inferred from their response to a single stress. The three parameters that will change in the coming years, namely, CO_2, temperature and water availability, have been studied in two Tempranillo cultivars (Kizildeniz et al., 2021): CO_2 and temperature effect are cultivar- and combinatorial dependent. Photosynthetic acclimation is observed under long-term exposition to elevated CO_2.

The relationships between photosynthesis, carbohydrate metabolism and expression of sugar-related genes in differentially light-exposed leaves (East/West/Sun/Shade) of Malbec cultivar were studied (Dayer et al., 2021). East, West and Sun leaves exported sugars. Shade leaves accumulated starch and sugars, but the origin of these carbohydrates is unknown since the photosynthetic activity of these leaves is negligible.

Carbon balance calculation needs to take into account carbon inputs and outputs. These parameters have been quantified in leaves in a plethora of conditions, but fruit respiration has been far less considered. Hernández-Montes et al. (2020) studied this in fields conditions over two seasons at different stages in irrigated and nonirrigated Tempranillo and Grenache vineyards. Cluster respiration decrease during development. Tempranillo loss more carbon than Grenache.

What is so (the most?) important in the berry intended to wine production? The amount and characteristics of the secondary metabolites. The biosynthetic gene expression regulation, characterization and quantification of the different metabolites are under study. Del-Castillo-Alonso et al. (2021) studied the effect of UV radiation on different physiological parameters and could demonstrate that ambient UVs increase flavonol contents and expression of flavonol synthase and chalcone synthase, with UV-B having a stronger effect than UV-A.

3 | PATHOGENS

Grapevine trunk diseases (Esca, Black Dead Arm, Eutypa, …) are developing in Europe since the ban of sodium arsenite in 2003. Yield loss can be as much as 20%. Leaf metabolite fingerprints have been performed on two different clones of Trousseau, an esca-susceptible cultivar (Moret et al., 2021). A clone- and year-dependent metabolic response is demonstrated. Furthermore, comparison with data obtained on Chardonnay (Moret et al., 2018) did not allow identifying esca-specific metabolic fingerprints.

The nonproteinaceous amino-acid β-aminobutyric acid (BABA) is a priming defense elicitor known to induce broad-spectrum disease resistance. It activates the expression of several defense-related genes as PR-proteins and phytoalexin biosynthesis genes. A transcription factor (VvWRKY18) is identified as a BABA-priming regulator (Wang et al., 2021). VvWRYK18 interacts with VvNPR1 and activates the transcription of Stilbene Synthase genes.

Using specific organisms to negatively control phytopathogens is a biocontrol strategy developed in vineyards. Besides different seaweed, *Trichoderma spp*., soil fungi, are used and their mechanisms of action are partially understood. Lazazzara et al. (2021) studied the Volatile Organic Compounds (VOCs) profile of three Trichoderma strains and identified 31 compounds. They tested on leaf discs five of the identified VOCs against downy mildew, callose deposition and hypersensitive response and two of them on gene expression. All VOCs tested act as biofungicides against downy mildew.

4 | MINERAL NUTRITION

Climate change is also affecting grapevine mineral nutrition. If we take into account only two major nutrients, potassium and nitrate, a strong effect on berry quality can be expected. For potassium, its increase in berries is correlated with a decrease in acidity, often a source of low-quality wines. Potassium flux in the plant is affected by climate changes and leads to an increase in berry potassium concentration (Monder et al., 2021). Nitrogen is involved in the growth, development and synthesis of aromatic secondary metabolites. Furthermore, berry nitrogen (YAN, Yeast assimilable nitrogen) content is important for the fermentation process. Nitrogen availability, uptake, and metabolism affect berry nitrogen composition. The effects of agropedoclimatic condition on N nutrition have been recently reviewed (Verdenal et al., 2021). Mineral nutrition should be studied as an inclusive process taking into account interaction between nutrients (Bouain et al., 2019) as well as all the other abiotic and biotic factors.

5 | TECHNICAL ADVANCES

A technic that was first developed for research purposes is isotopic discrimination. Several physiological processes discriminate between the two stable carbon isotopes, ^{12}C and ^{13}C (Farquhar et al., 1989). The ratio between the two isotopes can be represented as the $\delta^{13}C$. The use of this $\delta^{13}C$ on grapevine samples was reported in this journal in 1977 (Marco et al., 1977) and was later demonstrated to be a good proxy of the summer grapevine water status (Gaudillère et al., 2002). This parameter is now quantified in routine by the oenology laboratory for the winemakers.

OMICS approaches have been used in a lot of studies to understand plant responses to the environment and plant development. Figueiredo et al. (2021) developed a protocol to prepare samples of leaves apoplast, which were used to perform proteomic and metabolomic analyses. nanoLC-MS/MS and FT-ICR-MS identified 700 proteins and 514 metabolites.

The ones who have eaten berries from the same cluster have observed that they do not all have the same taste. In spite of that, "representative" sampling is still performed. Recently, a thousand berries were collected and berry weight, sugar import and malate breakdown were quantified (Shahood et al., 2020). Kinetic analysis allowed us to build an improved model of berry growth and ripening. Should we go smaller in the analysis using the trendy single-cell approach?

6 | CONCLUSION

A number of challenges are faced by producers and scientists to cope with climate change. Being already cultivated in semi-arid areas, an increase in drought will not be fully counteracted by practice management such as irrigation or architectural forms (Deloire et al., 2022). Exploiting natural diversity (Wolkovich et al., 2018) and developing breeding strategies (Bigard et al., 2020) are required. Our understanding of abiotic stress effects due to climate change on different grape varieties was recently reviewed (Carvalho & Amâncio, 2019). The cultivar-dependent resilience to heatwaves (up to 47°C in France in June 2019) should be studied because it cannot be predicted from response to other stress. For example, Carignan, a cultivar known to be drought-resistant or drought-adapted, is the one that was the more heat-sensitive. Whatever the stresses, recurrence is increasingly occurring and effects on plant development and yield have been observed. The cumulative effects of stress over the years are a challenge that should be tackled.

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