Climate change impacts: a multi-stress issue

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Abstract

With the aim of producing premium wines, it is admitted that moderate environmental stresses may contribute to the accumulation of key compounds in grapes. However, the ongoing climate change, with the appearance of more limiting conditions of production, is a major concern for the wine industry. Will it be possible to maintain the vineyards in place, to preserve the current grape varieties and ultimately wine typicality? In this context, the question of the responses and adaptation of grapevine to abiotic stresses becomes a major scientific issue to tackle. An abiotic stress can be defined as the effect of a specific physical or chemical factor (temperature, availability of water and minerals, light, etc.) which reduces growth, and for a crop such as grapevine, yield, fruit composition and life-span of the plants. Water stress is a major factor, but a systemic vision is essential. In natural environments, a single factor is rarely limiting, and plants have to deal with a combination of constraints, as for example heat and drought, both in time and at a given time. In addition plants, including grapevine, have central mechanisms to deal with stresses, such as redox regulatory pathways, that play an important role in adaptation and survival. Here we review the most recent studies regarding the grapevine responses to a combination of environmental constraints and the underlying regulatory pathways, which may be helpful to design more adapted solutions to cope with climate change.

Introduction

According to the last IPCC report (2021), the scale of recent changes, across the climate system as a whole, are unprecedented over many centuries to many thousands of years. Each of the last four decades has been successively warmer than any decade it since 1850. The increase of global surface temperature has reached, in average, 1°C during the 2001-2020 period in comparison to 1850-1900, with increases over land reaching in average 1.6°C. The growing season has on average lengthened by up to 2 days per decade since the 1950s in the Northern Hemisphere. Projections for the future foresee that temperature should continue to increase for all scenarii of GHG emission and could reach +3.3°C to +5.7°C under the most pessimistic scenario. With increasing global warming, many other climatic parameters will be affected in frequency and intensity. Very wet and very dry weather events and seasons will become more frequent, but projections in precipitation remain uncertain. It is also projected that every region will face more concurrent and multiple changes in climatic impact-drivers, with the number of drivers affected increasing with global warming intensity, with all regions experiencing changes in at least 5 drivers and 50% in at least 15 drivers, as reported by Mora et al. (2018) which showed that the world population could exposed to at least three climatic hazards in the same location by 2100, having major consequences, among others on agriculture and food production systems.
As humans, ecosystems and plants are facing an increasing number of stressors, including abiotic and biotic ones. The probability that plants will be subjected to a multifactorial stress combination, simultaneously or sequentially, is indeed gradually increasing (Zandalinas et al., 2021a). Recent studies performed on soil properties, plant-microbiome interactions and various plants show that interactions between stressors could be synergetic, antagonist or additive, and that global effects can be hardly deduced from individual stress studies (Rillig et al., 2021; Zandalinas et al., 2022). An abiotic stress can be defined as the effect of a specific physical or chemical factor (temperature, availability of water and minerals, light, etc.) which reduces growth, and for a crop such as grapevine, the yield, the composition of the fruits and the longevity of the plants (Ollat et al., 2019). Primary environmental stresses usually lead to physiological secondary stresses, such as osmotic and oxidative stresses (Carvalho and Amâncio, 2019). Adaptive mechanisms such as escape, avoidance, tolerance and

resistance drive the capacity of an organism to overcome that environmental constraint. These adaptive mechanisms can be constitutive. They can also be triggered in response to the stressors, according to the concept of plasticity (Ollat et al., 2019).

Grapevine does not differ from other plants in terms of interactions with environmental stressors. Being a perennial plant, cumulative impacts over several growing seasons should also be considered. Projections of agro-climatic indices over the XXIst century show that depending on the region, climatic scenario and varieties, climatic constraints as drought, heat waves, extreme temperature may increasingly affect the entire developmental cycle of grapevine (Garcia de Cortazar-Atauri et al., 2017), with for example stressors as drought occurring at unusual stages as budburst. However, grapevine is originating and is frequently grown in limiting environments where several stresses interacts (high light and temperature, drought, low soil nutrients status etc…). Consequently it is likely that is has developed specific mechanisms of adaptation. Investigating these mechanisms may be highly useful to design strategies to maintain the sustainability of vineyards in regions where climate change endanger the suitability to grow grapes (Bernardo et al., 2018).

Plant responses to multifactorial stress combination

Responses of plants to environmental stresses are usually analysed for one single factor or a limited number of factors. However several recent reviews point out that responses to a combination of stresses are often not additive and plants should prioritize, or blend responses or adopt completely new strategies (Rivero et al., 2022). Therefore central physiological mechanisms such as photosynthesis, stomatal regulation, water- and nutrient-use efficiency and reproductive processes should be targeted when dissecting the multi-stress effects and developing of more climate-resilient crops. Interactions with high CO_2 should also be taken into account. Studies performed on the plant model *Arabidopsis thaliana* showed that different stresses applied individually may have a negligible effect on plant growth and survival. However the combination of these stresses has a much detrimental effect on the same traits, which is quite critical for adaptation to global changes. At the molecular level, the expression of a low number of genes was commonly enhanced or suppressed in response to all combinations of stresses, but the majority of genes differentially expressed were unique for a specific combination. Commonly enhanced expressed genes were involved in the regulation of transcription, redox control, stress responses and ABA, and repressed genes in amino-acid and carbohydrate metabolism, heme-binding and redox activities. A high representation of ROS-, iron and other stress hormone-response genes such as ABA, jasmonic acid (JA), ethylene (ET) and salicylic acid (SA). In addition even when common genes were differently expressed for different stresses when applied individually, the response became more complex when stresses were applied in combination, with the number of unique genes differentially expressed increasing with the number of combined stressors. Genetic analyses performed on different species confirm the specificity of responses to multi-stresses (Rivero et al., 2022). Genes involved in ABA signalling, basal thermos-tolerance and iron-sulfur and ROS regulation, appear to be central for multi-stress responses (Zandalinas et al., 2021b). At the metabolic level, primary metabolites such as GABA, secondary metabolites and hormones are targets for improving plant tolerance in the context of climate change (Zandalinas et al., 2022).

What about grapevine

Among the large diversity of grape varieties, those grown in Mediterranean areas are often subject to multiple and combined stresses, such as extreme temperatures, high radiation levels, strong winds, long periods of water deficit combined with mineral stresses, especially in summer (Tzortzakis et al., 2020). There is little doubt that these grape varieties are characterized by specific physiological properties (phenology, maintenance of vital functions) which allow them to produce grapes of the composition required in highly restrictive climatic situations which will be more frequent in the context of climate change. Intravarietal diversity may also be a source of variability for adaptation (Carvalho et al., 2020; Neethling et al., 2022).

Studies on the effects of combined stress in grapevine are not very numerous (Gomès et al., 2021). For most of them, they relate to the interactions between water deficit and high temperatures (Edwards et al., 2011; Zarrouk et al., 2016; Tzortzakis et al. 2020), but some address the interactions between water deficit and salinity (Cramer et al., 2007), high temperature and salinity (Dunlevy et al., 2022), as well as radiation, heat and water deficit (Carvalho et al., 2016). Overall, studies carried out at leaf level show that water deficit always has the greatest impact on the leaf physiology and that worsen the effect of a one-off thermal extreme while the combination of the two may generate different responses.

Among these studies, some analyze the effect of these abiotic factors in combination with high CO_2 levels, in order to mimic the effects of climate change (Martinez-Luscher et al., 2015; Edwards et al., 2017; Arrizabalaga-Arriazu et al., 2021). In such conditions with elevated CO_2 content (400 ppm in comparison to 650-700 ppm) and an average temperature of 2 to 4°C above the control, high temperatures consistently increase developmental rates and hasten phenology. These non-stressful temperatures have few effects on leaf physiology unless they are combined to high CO_2, regardless the experiments were performed in the field or under fruiting cuttings in controlled environments. Under the combination of high CO_2 and high temperatures, carbon assimilation is enhanced (Arrizabalaga-Arriazu et al., 2020), phenology shift increases (Martinez-Lüscher et al., 2016a) and water use is reduced (Edwards et al., 2017). The combination of elevated CO_2 and high temperature accelerate ripening, increasing sugar content, lowering acidity and reducing slightly berry amino acid content during the ripening period. Elevated CO_2 appears also to limit the decoupling effect of high temperature between anthocyanin and sugar accumulation (Martinez-Lüscher et al., 2016b; Arrizabalaga-Arriazu et al., 2020). UVB radiation has a similar antagonist effect (Martinez-Lüscher et al., 2016b). Gene expression analyses are in agreement with the measured impacts, with master genes from the phenylpropanoid pathway such as *UFGT* and the transcription factor *MybA1* differentially expressed depending on the applied treatments (Martinez-Luscher et al., 2016b).

While a mild water deficit is known to hasten ripening, experiments on fruiting cuttings combining climate change conditions (elevated CO_2 and high temperature) with drought show that water limitation has the main effect, regardless of the other treatments. Combined to the other climate change conditions, ripening is delayed, amino acid content is increased and, anthocyanin content as well as the ratio between anthocyanin and sugar is decreased (Arrizabalaga-Arriazu et al., 2021). In all these experiments performed on fruiting cuttings, varieties and clones appear to interact strongly with the abiotic effects.

Studies on the interactions between abiotic and biotic stresses are even less numerous (Songy et al., 2019) although they are of major importance in the context of climate change. For example, Bortolami et al., (2021) demonstrated that drought prevent the expression of esca symptoms in grapevine leaves suggesting that transpiration is a key mechanism driving esca-symptoms and drought could interfere with pathogenicity and plant defences.

However most of these experiments are carried out at the leaf or fruit scale on simplified experimental systems under controlled conditions. Results are not always easy to compare and to extrapolate to field conditions. It is necessary to take into account that from one study to the other conditions of application of the abiotic constraints can change. Duration and intensity of stresses should be considered with caution, for example the effects of moderately temperatures (30-35°C) will be quite different compared to the effects of extreme values (>40°C).

The underlying mechanisms of stress integration in grapevine

Carvalho and Amâncio (2019) displays similarities among responses to abiotic stresses in grapevine, pointing out central mechanisms, such as carbon assimilation, stomata closure, energy use, oxidative and secondary metabolism, as well as hormonal regulation, Traits, such as photosynthetic activity, stomatal conductance, surface leaf temperature, electrolyte leakage, photochemical efficiency of PhotosystemII, accumulation of anti-oxidative metabolites such as ascorbate and glutathione or osmoprotectants as proline, and the shift between primary to secondary metabolism should be systematically and widely investigated in combined abiotic stresses studies. Comparing two Portuguese varieties Touriga Nacional and Trincadeira, Carvalho et al. (2016) show that Touriga Nacional was able to keep its stomata open under light and heat stresses facilitating heat dissipation, while Trincadeira was not, indicating that the first one was more adapted to warm regions that the latter, as long as irrigation is provided. Drought responses were always distinct from those of the other abiotic stresses. Another varietal comparison between Chardonnay and Xynisteri, a chypriot variety, reported that they responded differently to drought and heat stress, activating their leaf antioxidative metabolism at different duration of stresses (Tzortzakis et al., 2020). Xynisteri also displayed less leaf damages than Chardonnay.

Some candidate genes from the Heat shock protein (HSP) family and transcription factors from Zinc-finger protein transcription factors (ZFP-TFs), WRKY, Ethylene response factors (ERFs) and Nam-Like protein (NAC), together with other differentially expressed genes from an initial multi-stress experiment with two varieties were used to design a qPCR array dedicated to analyse field situations and profile varieties as sensitive or tolerant to abiotic stresses (Rocheta et al., 2016; Carvalho et al., 2017, Carvalho et al., 2020). These studies allow the characterization of different responses across varieties, the complexity of responses when several stresses are combined, but also that vineyard scenarios are difficult to compare to controlled condition experiments.

Conclusions

This short review emphasizes that climate change impacts on grapevine performances is a multi-stress issue. Investigations to provide technical solutions such as viticultural and soil management practices and the use of better- adapted varieties should seriously take this fact into account. As shown on model species, impacts of combined stresses can be much more damaging than single stress taken independently and global responses appear to be somehow unique for each stress combination. Overall drought appears to have a major impact, surpassing other stresses. Consequently more studies should be undertaken combining several stresses, including when possible elevated CO_2, as it was shown to mitigate heat and drought responses. Traits enabling to characterize these complex responses should be systematically phenotyped in genotype x environment studies, including rootstock experiments. Doing so could provide better advises for plant material selection. Collaborative studies across climatic gradients should be promoted for such studies.

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