Optimizing stomatal traits for future climates

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Abstract

Stomatal traits directly regulate plant gas exchange, water stress, and temperature, making these traits a promising target to adapt grapevines to climate change. However, the most beneficial trait values are unknown. We used a functional-structural plant model (HydroShoot) to quantify the impacts of the maximum stomatal conductance (g_{max}) and leaf water potential threshold for 50% stomatal closure ($g_s\ \Psi_{50}$) on grapevine performance under historical and future climatic conditions for premium and hot American wine regions. Future conditions (2079-99) were predicted from global climate models, assuming high emissions (RCP 8.5). For both regions and climate scenarios, compared to mean trait values, water-spending traits (i.e., a high g_{max} or highly negative $g_s\ \Psi_{50}$) had negligible benefits for carbon gain and evaporative cooling, but strongly exacerbated vine water stress. Conversely, water-saving traits (i.e., a low g_{max} or high $g_s\ \Psi_{50}$) reduced transpiration and water stress, but also the carbon supply for ripening. Overall, selecting for water-saving stomatal traits could improve water-use efficiency and protect yield and quality from severe water stress, but future work is needed to compare these benefits to the consequences of minor declines in carbon gain for fruit production.

Introduction

Climate change is expected to increase growing season temperature and evaporative demand in many wine regions worldwide over the next century (Hannah et al., 2013). Greater evaporative demand increases vine transpiration and water stress, which can reduce yield and berry quality. Thus, selecting grapevines for traits that mitigate the impacts of water stress on vine performance is an important strategy to adapt viticulture to future conditions. However, physiology traits can have complex, nonlinear effects on plant performance, making it difficult to determine the trait values to target through breeding or genetic engineering (Vivin et al., 2017). Thus, we conducted the first study applying a functional-structural plant model to quantify the impacts of variation in water relations traits on grapevine performance under the future conditions projected for economically important wine regions.

We focused here on traits characterizing stomatal responses to water stress, which mechanistically determine vine gas exchange, water status, and heat balance. Under dry conditions, plants face a trade-off between closing the stomata to avoid water stress and conserve soil water, and keeping the stomata open for photosynthesis and evaporative cooling of the foliage (Chaves et al., 2016). Dry ecosystems have generally selected woody species for traits that maintain greater gas exchange under water stress (Bartlett et al., 2016). However, in crop systems, where competition for water is largely eliminated, traits that reduced stomatal conductance (g_s) and extended soil water availability longer into the growing season improved yield during drought (Sinclair et al., 2010). We compared the impacts of these opposing stomatal strategies on vine performance by parameterizing a plant model with traits defined from relationships between g_s and leaf water potential (Ψ_L), including g_{max}, the maximum stomatal conductance, and $g_s\ \Psi_{50}$, the water potential threshold for 50% stomatal closure. A higher g_{max} increases the maximum rate of photosynthesis and evaporative cooling, while a less negative $g_s\ \Psi_{50}$ increases stomatal sensitivity to water stress and limits declines in Ψ_L and soil moisture.

We used a functional-structural plant model developed to calculate water, carbon, and energy fluxes for complex grapevine canopies (HydroShoot). HydroShoot uses a spatially explicit representation of grapevine architecture to scale from leaf to canopy gas exchange (Albasha et al., 2019). HydroShoot integrates a hydraulics module, which calculates water potential for each plant segment (e.g., shoot, petiole), with an energy budget and a gas exchange module, which calculate irradiance, temperature, and gas exchange for each leaf. A soil module calculates soil water potential from canopy transpiration. The model uses digitized vine architecture, traits, meteorological variables, and soil properties as inputs and calculates the plant and soil variables at an hourly timescale. We parameterized HydroShoot for two California regions to capture different sections of the American wine industry. Napa Valley is a premium region, with an optimal climate for wine quality, while the southern San Joaquin Valley (SJV) is the hottest and highest-producing California wine region. We used meteorological data and global climate model projections to define historical and future climatic conditions for both regions, and supplied these parameterizations to HydroShoot to evaluate the impacts on vine gas exchange (i.e., cumulative transpiration (ΣE) and net carbon gain (ΣA_{net})), water status (i.e., minimum shoot water potential, Ψ_{min}), and heat stress (i.e., maximum leaf temperature, $T_{L,max}$).

Materials and methods

We collected historical climate data from two weather stations in the California Irrigation Management Information System network (CIMIS, https://cimis.water.ca.gov/). The Oakville station (38.43N, 122.41W) represents the premium Napa Valley region and the Fresno State station (36.82N, 119.74W) represents the hot southern San Joaquin Valley. We used hourly measurements for the HydroShoot input variables air temperature (T_{air}, °C), relative humidity (*RH*, %), windspeed (u, m s^{-1}), and solar radiation (*Rg*, W m^{-2}) from the earliest 20-year period available for both stations (1990 – 2010). We averaged values across years to produce a representative trajectory of hourly climate conditions. We focused on the month after veraison (Jul 30 – Aug 30 for Oakville and Jul 11 – Aug 11 for Fresno) to make computational time tractable while capturing the period of the growing season with the hottest, driest conditions and the least canopy growth, since HydroShoot assumes canopy size is constant.

We compiled global climate model (GCM) projections at each location from Cal-Adapt (https://cal-adapt.org/). We focused on the four priority GCMs for California (CanESM2, CNRM-CM5, HadGEM2-ES, MIROC5), which capture the range of temperature and precipitation changes across the 32 models compared in the Coupled Model Intercomparison Project (Pierce et al., 2018). The first three models represent average, cooler/wetter, and warmer/drier scenarios, respectively, and MIROC5 represents the most distinct scenario from those three. We used a high emissions scenario (RCP 8.5). Projections were LOCA downscaled to 1/16° resolution. We extracted daily minimum and maximum T_{air} and *RH* and mean daily *Rg* and u from 2079 – 99 and averaged values across years and models to generate a trajectory of daily climate conditions. We fitted empirical relationships between daily and hourly values for the historical data to downscale the climate projections.

We parameterized HydroShoot with the 5th, 50th, and 95th percentile g_{max} and g_s Ψ_{50} values compiled from the literature for 21 winegrape cultivars (g_{max} = 148, 426, and 531 mmol m^{-2} s^{-1} and g_s Ψ_{50} = -1.54, -1.27, and -0.85 MPa) with field-grown vines monitored for g_s and Ψ_L over the growing season (Bartlett & Sinclair 2021). Five trait parameterizations (i.e., the three g_{max} values with mean g_s Ψ_{50} and vice versa) were combined with four site and climate scenarios. We used a spur-pruned vertical shoot-positioned canopy architecture, which was digitized with LiDAR from a field-grown Syrah vine (43.62N, 3.88E) at veraison (Albasha et al., 2019). Both sites were parameterized with the same soil type (clay loam), rooting depth (1.8 m), and irrigation schedule (weekly at 60% replacement). Other parameters follow Albasha et al., 2019. We compared each trait parameterization to the mean trait values by calculating the percent difference in ΣE, ΣA_{net}, Ψ_{min}, and $T_{L,ma}$.

Results and discussion

Compared to the mean stomatal traits, the traits that would increase gas exchange (i.e., g_{max} = 531 mmol m^{-2} s^{-1} or g_s Ψ_{50} = -1.54 MPa) made grapevine performance worse, and these effects were similar for historical and future conditions in both regions (Fig. 1). Under historical conditions, shifting from mean to water-spending stomatal traits strongly increased cumulative transpiration (ΣE), by 12 – 17% in Napa and 11 – 14% in the SJV, respectively, and reduced minimum shoot water potentials (Ψ_{min}), by 10 – 15% and 11 – 18%, while inducing negligible increases in cumulative C gain (ΣA_{net}, 2 – 3% at both sites) and maximum leaf temperature ($T_{L,max}$, 0 – 2% at both sites). The water-spending simulations depleted soil water more quickly, exacerbating plant water stress and causing canopy temperature to converge on similar values as the mean simulations over time. Climate change negatively impacted performance at both sites. For the mean stomatal traits, warming increased ΣE by

37% in Napa and 12% in the SJV and $T_{L,max}$ by 13% and 22%, and reduced ΣA_{net} by 24% and 35% and Ψ_{min} by 32 and 4%, respectively. However, compared to the mean trait values, under future conditions the water-spending traits increased ΣE by 12 – 13% in Napa and 8 – 10% in the SJV, reduced Ψ_{min} by 10 – 15% and 7 – 14%, respectively, and caused small changes in ΣA_{net} (2% and -1 to -4%) and $T_{L,max}$ (0 – 3% at both sites).
Conversely, the water-saving stomatal traits (i.e., g_{max} = 148 mmol m^{-2} s^{-1} or g_s Ψ_{50} = -0.87 MPa) reduced transpiration, water stress, and carbon gain compared to the mean trait values, and these effects were also similar between regions and climate scenarios (Fig. 1). Under historical conditions, these traits reduced ΣE by 20 – 41% in Napa and 23 – 31% in the SJV, ΣA_{net} by 6 – 14% and 10 – 12%, and Ψ_{min} by 22 – 25% and 24%, respectively, and produced negligible increases in $T_{L,max}$ (0 – 1% at both sites). Under future conditions, the water-saving traits reduced ΣE by 22 – 35% in Napa and 22 – 28% in the SJV, ΣA_{net} by 9 – 13% and 11 – 16%, and Ψ_{min} by 20 – 23% and 22 - 23%, respectively, and produced negligible increases in $T_{L,max}$ (-1 – 2% at both sites), compared to the mean trait values.
Altogether, these findings suggest that selecting for water-saving stomatal traits is a promising strategy to adapt grapevines to climate change. Under extreme warming, these traits produced strong reductions in transpiration and water stress (i.e., 20 – 35%) and minor declines in carbon gain (i.e., 9 – 16%) compared to mean trait values (Fig. 1). These traits could benefit growers by reducing irrigation demand and mitigating the impacts of climate change on yield and quality. Reducing wilting and leaf shedding helps protect the fruit from excess light exposure, which heats the clusters and reduces yield, by dehydrating the fruit, and quality, by accelerating the degradation of acids and anthocyanins (Martínez-Lüscher et al., 2020; Webb et al., 2010). Water stress can also accelerate sugar accumulation and produce overly alcoholic, 'flabby' wines, suggesting these traits could also improve quality by preventing excessive sugar accumulation (Alston et al., 2018). However, these traits would reduce yield and quality, instead, if declines in carbon gain prevent the fruit from reaching target sugar concentrations. This is especially a concern in high-production regions, which can require up to ten-fold higher yields than premium regions to be profitable. More work is needed to determine how the stomatal traits impact ripening. Genetic engineering could provide a promising approach to test these impacts, by altering the stomatal traits with minimal changes to the genes directly regulating berry development. Using these techniques to develop new winegrape varieties could also potentially increase sustainability with minimal changes to wine quality and sensory characteristics.

Conclusion

Overall, our findings suggest that breeding or engineering grapevines to shift stomatal traits to more water-saving values would improve water-use efficiency and avoid the detrimental effects of severe water stress on yield and quality. These traits were favorable under historical and future climatic conditions in both hot and premium growing regions, providing a simple phenotypic target for cultivar improvement that could benefit growers now and later, even if warming is less severe than the high-emissions (RCP 8.5) projections. However, more work is needed to evaluate whether the benefits for water savings outweigh the consequences of minor declines in carbon gain for ripening, especially for high-production wine regions. Finally, these findings also suggest functional-structural plant models are an important tool to design grapevine physiology for future conditions.

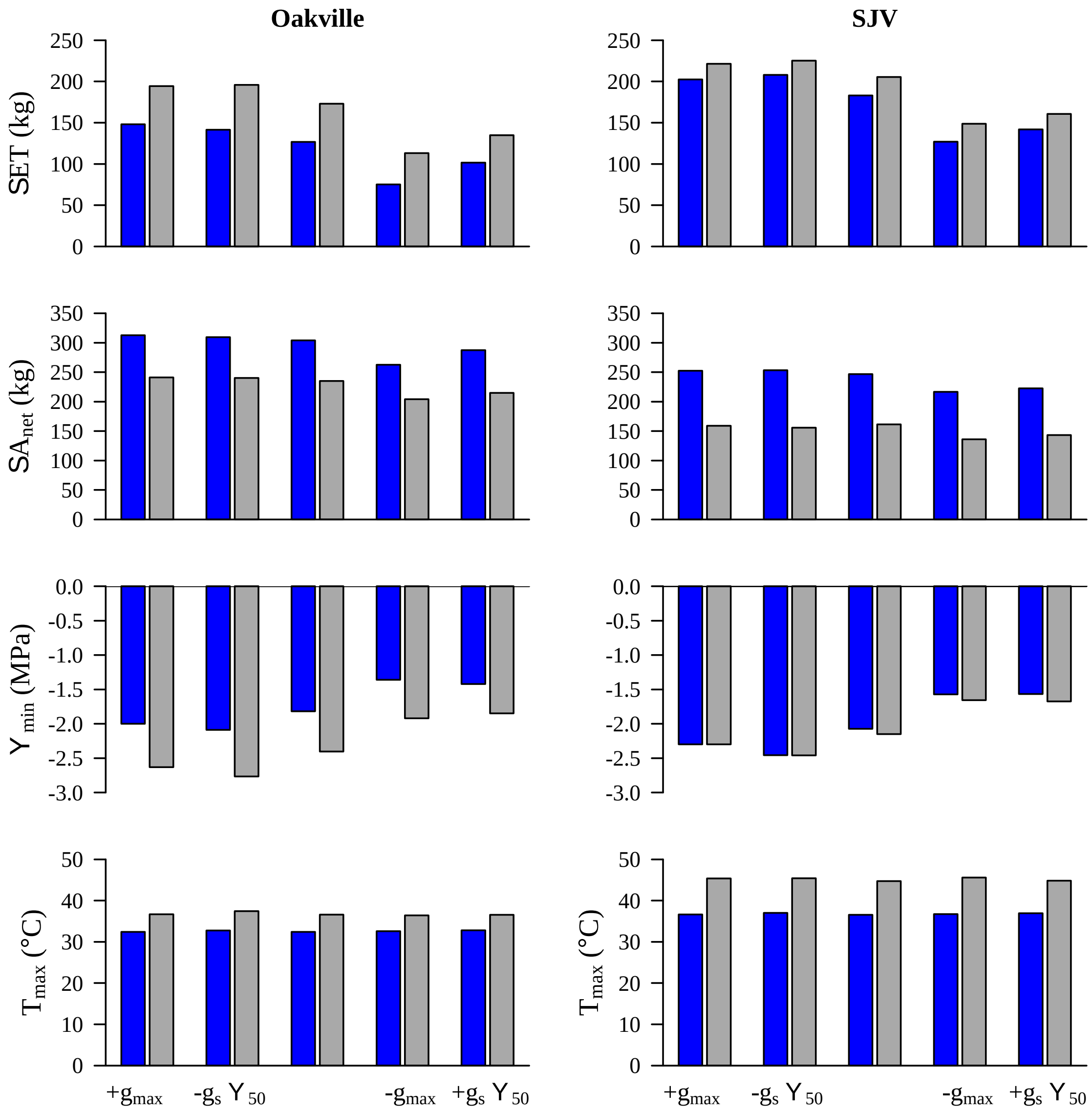

Figure 1. Predicted impacts of the stomatal traits on vine performance. Modeled cumulative whole-plant transpiration (ΣET) and net carbon gain (ΣA_{net}) and minimum shoot water potential (Ψ_{min}) and maximum leaf temperature ($T_{L,max}$) over the simulation period. Blue bars indicate historical climate and gray bars indicate projected (RCP 8.5) climate scenarios. For each panel, middle bars indicate the mean stomatal trait values, left bars indicate water-spending trait values (i.e., a higher g_{max} and more negative g_s Ψ_{50}), and right bars indicate water-saving trait values (i.e., a lower g_{max} and less negative g_s Ψ_{50}).

References

Albasha, R., Fournier, C., Pradal, C., Chelle, M., Prieto, J. A., Louarn, G., Simonneau, T., & Lebon, E. (2019). HydroShoot: A functional-structural plant model for simulating hydraulic structure, gas and energy exchange dynamics of complex plant canopies under water deficit—application to grapevine (Vitis vinifera). *In Silico Plants*, *1*(1). https://doi.org/10.1093/insilicoplants/diz007

Alston, J. M., Fuller, K. B., Lapsley, J. T., & Soleas, G. (2018). Too Much of a Good Thing? Causes and Consequences of Increases in Sugar Content of California Wine Grapes. In O. Ashenfelter, O. Gergaud, K. Storchmann, & W. Ziemba, *World Scientific Handbook in Financial Economics Series* (Vol. 1, pp. 135–163). WORLD SCIENTIFIC. https://doi.org/10.1142/9789813232747_0006

Bartlett, M. K., Klein, T., Jansen, S., Choat, B., & Sack, L. (2016). The correlations and sequence of plant stomatal, hydraulic, and wilting responses to drought. *Proceedings of the National Academy of Sciences*, *113*(46), 13098–13103. https://doi.org/10.1073/pnas.1604088113

Chaves, M. M., Costa, J. M., Zarrouk, O., Pinheiro, C., Lopes, C. M., & Pereira, J. S. (2016). Controlling stomatal aperture in semi-arid regions—The dilemma of saving water or being cool? *Plant Science*, *251*, 54–64. https://doi.org/10.1016/j.plantsci.2016.06.015

Hannah, L., Roehrdanz, P. R., Ikegami, M., Shepard, A. V., Shaw, M. R., Tabor, G., Zhi, L., Marquet, P. A., & Hijmans, R. J. (2013). Climate change, wine, and conservation. *Proceedings of the National Academy of Sciences*, *110*(17), 6907–6912. https://doi.org/10.1073/pnas.1210127110

Martínez-Lüscher, J., Chen, C. C. L., Brillante, L., & Kurtural, S. K. (2020). Mitigating Heat Wave and Exposure Damage to “Cabernet Sauvignon” Wine Grape With Partial Shading Under Two Irrigation Amounts. *Frontiers in Plant Science*, *11*, 579192. https://doi.org/10.3389/fpls.2020.579192

Pierce, D. W., Kalansky, J. F., & Cayan, D. R. (2018). Climate, Drought, and Sea Level Rise Scenarios for the Fourth California Climate Assessment. *California's Fourth Climate Change Assessment, California Energy Commission*, *CNRA-CEC-2018-006*.

Sinclair, T. R., Messina, C. D., Beatty, A., & Samples, M. (2010). Assessment across the United States of the Benefits of Altered Soybean Drought Traits. *Agronomy Journal*, *102*(2), 475–482. https://doi.org/10.2134/agronj2009.0195

Vivin, P., Lebon, É., Dai, Z., Duchêne, E., Marguerit, E., García de Cortázar-Atauri, I., Zhu, J., Simonneau, T., Van Leeuwen, C., Delrot, S., & Ollat, N. (2017). Combining ecophysiological models and genetic analysis: A promising way to dissect complex adaptive traits in grapevine. *OENO One*, *51*(2), 181–189. https://doi.org/10.20870/oeno-one.2016.0.0.1588

Webb, L., Whiting, J., Watt, A., Hill, T., Wigg, F., Dunn, G., Needs, S., & Barlow, E. W. R. (2010). Managing Grapevines through Severe Heat: A Survey of Growers after the 2009 Summer Heatwave in South-eastern Australia. *Journal of Wine Research*, *21*(2–3), 147–165. https://doi.org/10.1080/09571264.2010.530106