

Quantifying soil-grapevine hydraulics from plant to field scale

Louis Delval

Louvain-la-Neuve, Octobre 2024

*Thèse présentée en vue de l'obtention du grade de docteur en
sciences agronomiques et ingénierie biologique*

Earth and Life Institute

Université catholique de Louvain

Thesis examining board

Supervisors:	Prof. Mathieu Javaux Prof. François Jonard
President of the jury:	Prof. Marnik Vanclooster
Members of the jury:	Prof. Bruno Delvaux Prof. Xavier Draye Prof. Cornelis van Leeuwen Prof. Jan Vanderborght

,

Acknowledgements

Durant ces quatre années de thèse, j'ai eu la chance de rencontrer et de collaborer avec des personnes tout autant intéressantes qu'intéressées, tout autant passionnantes que passionnées, permettant de rendre les innombrables échanges aussi riches que marquants. Je tiens évidemment à remercier en premier lieu mon promoteur, Prof. Mathieu Javaux. Il y a cinq ans, au début de mon mémoire, je pense que nous nous sommes tous les deux lancés tête baissée vers un sujet que nous connaissions peu (surtout moi) : la vigne. Corrige-moi si je me trompe. Après toutes ces réunions, tous ces défis et ces objectifs que nous nous sommes fixés, mais surtout après avoir pris beaucoup de recul, je pense que nous pouvons être fiers du travail accompli. Je te remercie évidemment pour toutes ces discussions et ces corrections qui ont permis de faire avancer ma thèse dans le bon sens, mais je te remercie surtout de m'avoir laissé la liberté de prendre ma thèse en main du début à la fin. Je te remercie de m'avoir donné les opportunités d'aller à Vienne, Zürich et Madrid. Et merci aussi de m'avoir offert l'occasion de publier un papier dans Nature. Je remercie également mon promoteur Prof. François Jonard, qui a accepté sans hésiter, dès le début, de faire partie de cette aventure doctorale. Merci François de m'avoir permis de prendre un peu de hauteur... grâce à tes drones.

Je tiens également à remercier les membres de mon jury. Tout d'abord un grand merci à Prof. Bruno Delvaux, sans qui cette thèse n'aurait sans doute pas vu le jour. Merci Bruno d'avoir été cette personne qui a lié la viticulture belge à la recherche scientifique. Je garderai toujours en tête ces journées de terrain, à creuser des fosses durant mon mémoire, et votre capacité impressionnante à estimer la composition texturale d'un sol avec la bouche. Cela a été un honneur pour moi de travailler avec vous. Je n'oublie pas que

nous devons publier un papier ensemble, contenant toutes les connaissances acquises sur le terroir belge durant toutes ces années. Thanks also to Prof. Jan Vanderborght for all the time you invested in modelling grapevine hydraulics with me. Modelling was the part of my thesis that I dreaded the most, and you were a precious help in producing some great results, for which I am very grateful. Je remercie Prof. Kees van Leeuwen d'avoir montré beaucoup d'intérêt pour ma recherche dès le début de ma thèse (et même dès la fin de mon mémoire). Je me souviens très bien de notre première réunion ensemble, votre enthousiasme m'a donné la confiance nécessaire pour me lancer dans cette thèse et à confirmer mon envie d'en découvrir plus sur la vigne. Merci à Prof. Xavier Draye d'avoir accepté de faire partie de mon jury. Nos échanges ont été plus rares, mais toujours intéressants. Merci à Prof. Marnik Vanclooster d'avoir accepté de présider ce jury de thèse.

Je remercie particulièrement Sophie Wautier, Dimitri Vander Heyden et Vincent Dienst du Domaine W, ainsi que Germano Prior et Romain Jacob du vignoble du Château de Bousval, pour m'avoir accueilli dans leur vignoble pour que je puisse réaliser toutes les expériences de cette thèse. Quand je parlais des personnes passionnantes et passionnées au début de ces remerciements, c'est d'abord vous qui me venez à l'esprit. Merci de m'avoir laissé la liberté de récolter mes nombreuses données. Vous faites un magnifique travail, c'est très inspirant.

Je ne suis pas seul à m'être sali les mains avec le sol des vignobles. Je remercie infiniment Sébastien François qui a toujours été disponible pour préparer et installer/désinstaller ces nombreuses sondes sur le terrain, et pour régler les problèmes techniques en urgence. Toute ton aide m'a permis de collecter des données de qualité et a grandement contribué à l'avancement de cette thèse. Je te souhaite pleins de beaux voyages. Merci également à Olivier Lebbe et Arnaud Willems pour leur aide précieuse dans l'analyse de

mes nombreux échantillons de sol. Merci énormément à Jasmine De Wulf et Sabine Finné pour votre sympathie et votre empathie, et pour avoir répondu à mes innombrables questions administratives.

I would also like to thank Jordan Bates for his availability and all the work he did with the drones. You travelled a lot of miles to help me collect a lot of data, and I'm very grateful. I always admire passionate people. Your passion for drones is a beautiful thing to see, and I hope you keep it for a long time to come.

I also thank the TECH4AGRO group at ICA-CSIC in Madrid. Special thanks to Benjamin Mary for our collaboration, which I'm sure will result in some great papers. It's always a pleasure to work and talk with you. Thank you for welcoming me to Madrid, I loved the month I spent there, and I can see myself returning very soon. Thanks also to Héctor, Vicente, Miguel and Irene for integrating me into your lab as if I'd already been there for months. I felt at home straight away. I sincerely hope that our paths will cross again soon.

Je tiens à remercier tous les étudiants qui ont réalisé leur mémoire de fin d'étude sur la vigne. Merci à Romain Setton, Romain Jacob, Justine Rutten, Adrien Panagiotopoulos, Oliver Claessens et Arthur Sillis. Je vous souhaite pleine réussite dans tous vos projets.

Je remercie infiniment ma famille et mes ami·es. Je suis extrêmement reconnaissant pour tout le soutien que vous m'avez apporté, et qui m'a permis d'aller au bout de cette thèse. Vous m'avez donné le courage et la détermination de continuer quand j'en manquais. Sans vous, il est certain que je ne serais pas en train d'écrire ces lignes. Vous êtes ce qu'il y a de plus cher à mes yeux et je suis conscient de la chance que j'ai de vous avoir à mes côtés.

Andrea, je ne sais pas combien de mercis il faudrait pour exprimer à quel point je veux te remercier (je ne vais pas tous les écrire parce que je ne veux pas que ma thèse fasse plus de 1000 pages (c'est pas écolo)). Je souhaite à tout le monde de trouver un-e umami dans sa vie. Je souhaite à tout le monde de trouver une personne avec qui on peut partager, avec qui on peut communiquer, avec qui on peut créer des souvenirs, avec qui on peut s'émerveiller, avec qui on peut être soi-même. Au moment où j'écris ces lignes, tu recommences une thèse. Je te souhaite toute la réussite du monde dans ce nouveau chapitre de ta vie, et compte sur moi pour t'aider à l'écrire.

Louis

Contents

1	Introduction	1
1.1	Grapevine in the context of climate change	1
1.2	Water deficit in viticulture	3
1.3	Soil-grapevine hydraulics	4
1.3.1	Soil-grapevine hydraulic continuum	6
1.3.2	Hydraulic control in grapevine	10
1.3.3	Differences in water use strategies between grapevine cultivars	14
1.3.4	Soil-root interactions: the hidden face.....	15
2	Objectives	21
3	Grapevine transpiration control is soil texture specific	25
3.1	Introduction	26
3.2	Methodology	30
3.2.1	Study areas	30
3.2.2	Soil, grapevine and weather characterization	31
3.2.3	Hydraulic measurements	36
3.2.4	Statistical analyses and fitting relations ...	39
3.3	Results	40

3.3.1	Water potentials and transpiration evolution	40
3.3.2	Hydraulic conductances	44
3.3.3	Relation between relative stomatal conductance, soil and stem water potential	47
3.3.4	Relation between belowground and stem hydraulic conductance with soil and stem water potential	48
3.3.5	Relation between relative stomatal conductance and belowground hydraulic conductance	50
3.4	Discussion	51
3.4.1	Transpiration control is induced by belowground hydraulics in drought conditions.....	52
3.4.2	Differences between $\Psi_{\text{soil_eff}}$ and $\Psi_{\text{stem_PD}}$ during drought	56
3.5	Conclusion and perspectives	59
3.6	Supplementary material	61
3.6.1	Supplementary figures	61
3.6.2	Supplementary tables	72

4 Combination of plant and soil water potential monitoring and modelling demonstrates soil-root hydraulic disconnection during drought 75

4.1	Introduction	76
4.2	Methodology	82
4.2.1	Subplots description	82
4.2.2	Soil and plant hydraulic measurements ...	83
4.2.3	Model description	84
4.2.4	Model parameterization, initial and boundary conditions	85
4.3	Results	96

4.3.1	Comparison between measured and simulated bulk soil and stem water potentials	96
4.3.2	Root water uptake	103
4.3.3	Rhizosphere hydraulic conductance	105
4.4	Discussion	107
4.5	Conclusion and perspectives	112
4.6	Supplementary material	114
4.6.1	Supplementary figures	114
4.6.2	Supplementary tables	120
4.7	Appendix	122

5 Mapping field-scale grapevine leaf water potential with very-high-resolution UAS multispectral, thermal and LiDAR data 129

5.1	Introduction	130
5.2	Methodology	134
5.2.1	Site descriptions	134
5.2.2	Meteorological conditions	137
5.2.3	Data acquisition and processing	138
5.2.4	Pure grapevine pixels extraction	141
5.2.5	Generation and extraction of UAS-based variables	144
5.2.6	Leaf water potential prediction	145
5.2.7	Relations between leaf water potential and environmental factors	148
5.3	Results	150
5.3.1	In situ measurements of leaf water potential and relationship with UAS-based VIs	150
5.3.2	Predicting leaf water potential based on multiple linear regression model	154
5.3.3	Leaf water potential mapping	158

5.3.4	Environmental factors influencing spatial distribution of leaf water potential	161
5.4	Discussion	164
5.4.1	Leaf water potential prediction with a combination of multispectral, thermal and LiDAR UAS-data	165
5.4.2	Intra-field variability of grapevine leaf water potential	168
5.5	Conclusion and perspectives	172
5.6	Supplementary material	174
5.6.1	Supplementary figures	174
5.6.2	Supplementary tables	185

6 **Conclusions & Outlooks** **189**

6.1	Research contributions	189
6.2	Research perspectives	192
6.2.1	Grapevine root system responses to drought	193
6.2.2	Grapevine-grass interactions	195
6.2.3	Grapevine-microbiome interactions	197
6.2.4	Influence on wine quality and typicity	199

General bibliography 201

List of figures

1.1	Time evolution of the area devoted for viticulture and wine production in Belgium between 2007 and 2023	3
1.2	Water flow in the soil-grapevine-atmosphere continuum ...	9
1.3	Sequence and thresholds of grapevine responses to its water status	13
2.1	Flowchart showing the link between the research objectives	24
3.1	Soil profiles, water holding capacity and 1D grapevine fine root density up to 2 m	33
3.2	Set-up for automatic monitoring of soil and vine water status	37
3.3	Time series of soil water potential, actual transpiration, stem and leaf water potential	43
3.4	Time series of T_{act}/T_{pot} (relative stomatal conductance) ...	45
3.5	Time series of belowground hydraulic conductance and stem hydraulic conductance	46
3.6	Relationships between Ψ_{soil} and T_{act}/T_{pot} and between Ψ_{stem} and T_{act}/T_{pot}	48
3.7	Relationships between Ψ_{soil} and K_{below} , Ψ_{stem} and K_{below} , Ψ_{soil} and K_{stem} and Ψ_{stem} and K_{stem}	49
3.8	Relationships between K_{below} and T_{act}/T_{pot}	51
S.3.1	Delineation of soil profile horizons, their unsaturated hydraulic properties (water retention and hydraulic conductivity curves) and their textural class	64
S.3.2	2D grapevine fine root density up to 2 m depth	65
S.3.3	Times series of leaf area index (LAI) and cultural coefficient (K_c)	66
S.3.4	Cumulated precipitation, cumulated reference evapotranspiration, hourly mean temperature and daily mean temperature during the measurement campaign	67
S.3.5	Time series of soil water potential, actual transpiration, stem water potential, relative stomatal conductance and belowground hydraulic conductance in 2023 in CBa	68

S.3.6	Time series of stem water potential and transpiration of each replicate	69
S.3.7	Comparison between Ψ_{stem} and Ψ_{leaf}	70
S.3.8	Comparison between $\Psi_{\text{soil_eff}}$ and $\Psi_{\text{stem_PD}}$	71
4.1	Scheme of serial connection of belowground hydraulic conductances; shape of water potential as a function of distance of root xylem in the rhizosphere and within the root	95
4.2	Measured and simulated bulk soil water potential time series	98
4.3	Measured and simulated stem water potential and predawn water potential	99
4.4	Comparison between observed and simulated stem and predawn water potential	100
4.5	Simulated time cumulated root water uptake by soil horizons	104
4.6	Time series of rhizosphere hydraulic conductance and root system hydraulic conductance	105
4.7	Time series of rhizosphere hydraulic conductance in the different soil horizons	106
S.4.1	Soil profile and root density for the simulations	114
S.4.2	Daily precipitation	115
S.4.3	Simulated water sink at 10 cm, 40 cm and 100 cm depth	116
S.4.4	Spatial and temporal distribution of the sink term	117
S.4.5	Simulated cumulated water sink in the S1 and S2 horizons of the sandy subplot	118
S.4.6	Time series of rhizosphere hydraulic conductance in the S1 and S2 horizons of the sandy subplot	119
A.4.1	Results for which the soil-root hydraulic disconnection is related to the root hydraulic conductance in the sandy subplot	127
A.4.2	Results for which the soil-root hydraulic disconnection is related to the root hydraulic conductance in the loamy subplot	128
5.1	Location of both vineyards; edaphic conditions in both vineyards; locations of leaf water potential and volumetric soil water content in both vineyards	136
5.2	Process of segmenting grapevine pixels from inter-row pixels to generate a pure grapevine mask	143

5.3	Measurements of leaf water potential	152
5.4	Correlations (Pearson's ρ) between measured Ψ_{leaf} and each vegetation index	153
5.5	R^2 and RMSE obtained by comparing measured and predicted Ψ_{leaf} . Relations between measured and predicted Ψ_{leaf}	157
5.6	Maps of predicted Ψ_{leaf} and maps of the 95 % confidence interval on predicted Ψ_{leaf} ; Relation between predicted Ψ_{leaf} and the uncertainty	160
5.7	Boxplots indicating the median, quartiles, minimum and maximum of the spatial distribution of Ψ_{leaf} ; Relation between median predicted Ψ_{leaf} and the range of predicted Ψ_{leaf}	161
5.8	R^2 of the linear relation between predicted Ψ_{leaf} and elevation, slope, water holding capacity and averaged soil hydraulic conductivity	163
5.9	Relation between median predicted Ψ_{leaf} and the linear combination of SPEI and VPD; Relation between the range of predicted Ψ_{leaf} and the linear combination of SPEI and VPD	164
S.5.1	Evolution of soil water content profile down to 105 cm depth	174
S.5.2	Univariable relation between measured Ψ_{leaf} and the different VIs	178
S.5.3	Spearman's ρ quantifying the non-linear relation correlation between measured Ψ_{leaf} and each VI; Absolute difference between Pearson's ρ and Spearman's ρ	179
S.5.4	Relation between measured Ψ_{leaf} and predicted Ψ_{leaf} with random forest model, principal component regression model and stepwise regression model	180
S.5.5	Partial regression plots of each predictor variable on the prediction of Ψ_{leaf} for the model 1	181
S.5.6	Partial regression plots of each predictor variable on the prediction of Ψ_{leaf} for the model 2	182
S.5.7	Partial regression plots of each predictor variable on the prediction of Ψ_{leaf} for the model 3	183

S.5.8	R^2 and RMSE obtained by comparing measured Ψ_{leaf} and predicted Ψ_{leaf} with random forest, principal component regression and stepwise regression	184
-------	--	-----

List of tables

3.1	Leaf area index (LAI) at DOY 208 and DOY 250 in 2022	35
S.3.1	p-value of the ANCOVA to assess statistical differences in the relationships between hydraulic variables	72
S.3.2	Value, uncertainty and p-value on the coefficients of the linear regression between Ψ_{leaf} and Ψ_{stem} , between K_{stem} and Ψ_{soil} , and between K_{stem} and Ψ_{stem}	73
4.1	Unimodal van Genuchten hydraulic parameters of each soil horizon of the two subplots	83
4.2	Initial bulk soil water potential used for the simulations...	87
4.3	Setups for each simulation scenario	93
4.4	Statistical analysed of comparisons between simulated and measured soil, stem and predawn water potential for each simulation scenario in the sandy subplot	101
4.5	Statistical analysed of comparisons between simulated and measured soil, stem and predawn water potential for each simulation scenario in the loamy subplot	102
S.4.1	Sensitivity analysis to find the water potential Threshold at the soil-root interface	120
S.4.2	Sensitivity analysis to find the root depth	121
5.1	Meteorological conditions during each flight campaign ..	138
5.2	Availability of UAS data (multispectral, thermal and LiDAR) for each flight campaigns in both vineyard	140
5.3	Unimodal van Genuchten hydraulic parameters of the loamy soil and the sandy subsoil at the Château de Bousval vineyard	150
5.4	Median, minimum and maximum leaf water potential measured during each UAS flight	151
5.5	Vegetation index, spectral band or structural features, and regression weights and intercept used in the different multiple linear regression models to predict Ψ_{leaf}	156
S.5.1	List of vegetation indices, spectral bands and structural features used to predict Ψ_{leaf}	185

S.5.2	Variance Inflation Factor (VIF) to assess the collinearity between the predictor variables in the model 1	188
S.5.3	Variance Inflation Factor (VIF) to assess the collinearity between the predictor variables in the model 2	188
S.5.4	Variance Inflation Factor (VIF) to assess the collinearity between the predictor variables in the model 3	188

1. Introduction

1.1. Grapevine in the context of climate change

Grapevines (*Vitis vinifera*) hold substantial cultural significance and rank as the world's third most valuable horticultural crop (Alston and Sambucci, 2019). Grapevine, part of the Vitaceae family, produces grape, botanically a berry. More than 7 million hectares of the Earth's surface are dedicated to grape production, distributed in more than 90 countries for various purposes, including wine, distilled liquors, juice, table grapes, and raisin production (FAO-OIV, 2023). Due to its global socioeconomic importance, the environmental diversity of producing regions, and extensive research spanning from genomic to production practices, grapevine has emerged as a model perennial fruit crop species (Gambetta et al., 2020a). The domestication and cultivation of *Vitis vinifera* began 8000 years ago in the Near East, then spread to Greece 4000 years ago. A thousand years later, grapevine was cultivated in Italy, brought by the Greeks, and then in Portugal, Spain and South of France. After that and up to the Middle Age, grapevine have been implanted in the North of Europe. In Belgium, grapevines first appeared around the 9th century. In the 14th century, each Belgian city had its own vineyard. From the 17th century, the Belgian viticultural area began to decline sharply, mainly due to the growing popularity of beer, but the middle of the 20th century saw the revival of Belgian viticulture. Today, more than 10000 varieties (i.e. cultivars) believed to exist in the world, conferring a wide range of characteristics to wines produced throughout Europe, Asia, Northern America, Southern America, South Africa, New Zealand and Australia (Grassi and De Lorenzis, 2021). Grapevines are historically cultivated between latitudes 4° and 51° in the Northern Hemisphere and between latitudes 6° and 45° in the Southern Hemisphere, across a large diversity of climates (Jones and Schultz,

1. Introduction

2016). Moreover, grapevines are cultivated on a very wide range of soils, from gravelly sands to clays. Nowadays, most of cultivated grapevines are grafted onto a huge diversity of rootstocks derived from American genotypes (Delrot et al., 2020), ensuring adaptation to diverse biotic (e.g. soil-borne pests) and abiotic stress (e.g. water deficit, oxygen deficiency, salinity, etc.). Taken together, in addition to vineyard management practices of the winegrower, the interactions between the plant material (cultivar and rootstock), the climate and the soil confer sensory attributes and typicity of a wine, referred as *terroir* (Van Leeuwen et al., 2018).

Wine-growing regions worldwide have recently experienced severe and frequent droughts and heat waves, such as those in Australia in 2009, in California in 2015, and in France in 2019, leading to substantial economic losses in wine production (Lamarque et al., 2023). Today, climate change is causing these environments to become hotter and drier, increasing the frequency and severity of droughts (Pörtner et al., 2022). In addition, precipitation patterns are expected to be altered, potentially leading to increased frequency, severity and duration of drought events (Costa et al., 2016). These changes pose a significant threat to grape productivity and quality, and increases the risk of grapevine dieback (Dayer et al., 2022). Given the observed and projected climate changes, there is growing concern about how viticultural suitability will vary across different regions and over time (Jones and Schultz, 2016). Maintaining high and consistent grape quality under drought conditions and/or stricter water conservation policies is a major challenge for the sustainability of viticultural systems (Lamarque et al., 2023). Europe is the leading producer of premium wine worldwide, with Spain, France, Italy and Germany contributing to half of the global wine production (OIV, 2022). Europe emerges as an especially responsive area to climate changes, particularly during the growing season, leading to changes in grapevine phenology (Santos et al., 2020) and fruit composition in terms of sugar, acidity and aroma contents (Gambetta and Kurtural, 2021; van Leeuwen and Darriet, 2016). Projection results suggest that wine grapes in southern Europe will be negatively affected by future more frequent

drought stress during the growing season (Malheiro et al., 2010). The suitability of the most renowned wine-producing regions are at risk, leading to a shift from currently suitable wine-growing areas to new ones (Moriendo et al., 2013). Climate changes are causing the northward extension of the European viticultural landscape up to 57°N (Fraga et al., 2016), and new countries are showing rapid growth in the area dedicated to vineyards (Nesbitt et al., 2016). For example, in Belgium, where more than 130 cultivars are cultivated (SPF Economie, 2024), the wine sector is consistently growing in size with more than ten-times extension of the surface area devoted to the cultivation of grapevines over the last fifteen years (Figure 1.1), and is likely to reach 1000 ha by 2025 (Doutreloup et al., 2022).

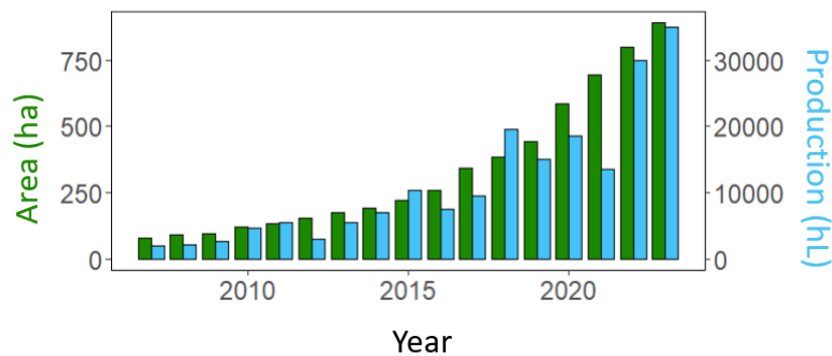


Figure 1.1 – Time evolution of the area devoted for viticulture (in green) and wine production (in blue) in Belgium between 2007 and 2023 (adapted from SPF Economie (2024)).

1.2. Water deficit in viticulture

Water availability is a crucial factor for determining plant survival and productivity in both agricultural and ecological context. In addition to

1. Introduction

air temperature (Zarrouk et al., 2016), water use and grapevine water status are known to be key factors for yield, grape composition and wine quality (Van Leeuwen et al., 2009a). Water deficits influence vine growth and decrease yield, but can improve grape and wine composition unless the deficits are severe (Chaves et al., 2010). Too much water for the plant may promote excessive vigour, leading to shaded canopies, which negatively affect grapevine phenology. This can result in lower bud break, delayed maturity, and ultimately poor fruit and wine quality (Pickering and Wheeler, 2006). Mild-to-moderate water deficits are therefore often considered beneficial in vineyards (Herrera et al., 2015). However, many wine regions are expected to become too warm and dry, which threatens high-quality wine production as well as the future of vineyards (Vivin et al., 2017). More frequent droughts could lead to more frequent severe water stress periods, caused by reduced water supply and/or excessive evaporative demand, leading to soil water deficit (Volaire, 2018). To achieve sustainable grape production, grapevines should tolerate drought periods over both short and long terms. This means they should be capable of annual quality production while avoiding drought-induced mortality over the years (Gambetta, 2016). Understanding how grapevine responds to increasingly severe and sustained droughts is therefore crucial for advising the wine industry on which varieties and/or environmental conditions are best adapted to increased drought risk (Lamarque et al., 2023). To address the critical issue of grapevine adaptation to water stress, soil-plant hydraulic processes can be seen as the cornerstone of the physiological responses involved in plant tolerance to drought (Choat et al., 2012).

1.3. Soil-grapevine hydraulics

Grapevines respond to water stress through a range of physiological, cellular and molecular mechanisms that collectively lead to drought

tolerance and/or avoidance (Delzon, 2015), in order to protect the plant against more severe damage such as cavitation, leaf shedding and/or plant mortality (Dayer et al., 2020; Hochberg et al., 2017b). To characterize drought tolerance or avoidance in grapevine, many studies focused on physiological aspects such as stomatal regulation (Gambetta et al., 2020a). For example, reduced maximum transpiration rate (Sinclair et al., 2005) early stomatal closure (Martin-StPaul et al., 2017) have been proposed as traits of drought avoidance. Stomata are considered direct responsible of optimizing the trade-off between carbon gain and water loss in plants (Rogiers et al., 2012). Water flows from the soil to the atmosphere through the plant xylem network, according to the cohesion-tension theory (Tyree and Zimmermann, 2002). This flow is driven by the more negative water potentials (Ψ) in the leaf tissues, where water is transpired into the atmosphere through stomata. As grapevine water potentials decrease (become more negative), water may enter a metastable state, increasing the risk of embolism. To mitigate this risk and prevent hydraulic failure, plants have developed safety mechanisms, such as stomatal closure, which is one of the first physiological responses to drought stress with growth cessation (Chaves et al., 2010), and helps to maintain higher (less negative) water potentials, delaying the onset of embolism (Anderegg et al., 2017; Tyree and Sperry, 1989). The closing and opening of stomata regulate the gas exchanges involved in photosynthesis. Even minor adjustments in stomatal conductance can significantly impact water loss through transpiration. Consequently, changes in the transpiration rate, due to stomatal control, affect the driving force of water flow, which is the gradient of water potential between the soil and the leaves (Wankmüller and Carminati, 2024). The sensitivity of stomata to drought is generally seen as grapevine variety specific, since most of the studies compared different cultivars planted in a common garden (Levin et al., 2019; Martorell et al., 2015; Pou et al., 2012; Tamayo et al., 2023). However, it is now well-accepted that the environment surrounding the plant shapes its hydraulic behaviour (i.e. stomatal control), and therefore its drought tolerance (Carminati and Javaux, 2020). Rare studies highlighted the influence of the edaphic properties on the stomatal conductance of grapevines (Lavoie-Lamoureux et al., 2017; Tramontini et al., 2013a). It is still unclear to

1. Introduction

what extent regulation of grapevine water use results from the genotype, as traditionally thought, or from environmental factors (Charrier et al., 2018). Because of the lingering questions surrounding the viticultural sustainability, a mechanistic understanding of the differences in drought tolerance and stomatal control of grapevine, in different environments, is needed. Numerous gaps remain in our understanding of how climatic and edaphic factors truly affect the stomatal control and drought tolerance of grapevine, making it challenging to effectively address future climate challenges. Soil-plant hydraulics offers both explanatory and predictive value for understanding and forecasting the physiological mechanisms driving the resilience of grapevine to drought.

1.3.1. Soil-grapevine hydraulic continuum

Given the interdependence between water potential, hydraulic conductance, and water flow regulation, the supply-demand framework provides a valuable perspective for understanding the transpiration process (Carminati and Javaux, 2020; Cowan, 1965; Sperry and Love, 2015; Wankmüller and Carminati, 2024). This framework underscores the interactions between both atmospheric evaporative demand and soil water supply to determine the hydraulic limits of plant transpiration. Integrating these concepts of water demand and supply has enhanced the quantitative understanding of plant (not just grapevine) gas exchange through soil-plant hydraulics (Anderegg et al., 2018; Sabot et al., 2020; Wolf et al., 2016). On its journey from the soil to the atmosphere, the water flow traverses several key hydraulic compartments (Figure 1.2), that may limit the water supply to grapevines.

1. The *bulk soil* hydraulic properties determine how the water is retained (water retention curve) and is conducted (hydraulic conductivity curve) in the soil for a given water potential. Under wet soil conditions, water flows easily between soil layers and towards the roots. The drying out of the soil leads to more negative soil water potential and consequently to significant decline in soil hydraulic conductivity. The extent of the decrease in soil water content and soil hydraulic conductivity, for a given reduction in soil water potential, largely depends on soil texture and structure.
2. Between the bulk soil and the soil-root interface, the unsaturated soil hydraulic conductivity multiplied by the water potential gradient scales the water flow in the *rhizosphere*, which is critical to sustain transpiration rate. During soil drying due to root water uptake, the water potential in the rhizosphere decreases, leading to a drop of hydraulic conductivity which could restrict root water uptake and could prevent evaporative demand from being met (Carminati and Javaux, 2020; de Jong van Lier et al., 2006; Gardner, 1960; Passioura, 1980; Schroeder et al., 2007).
3. The roots are in contact with the soil at the *soil-root interface*. Soil-root hydraulic contact is function of soil type, root type and root age (Nye, 1994). As the soil dries out, a loss of contact and a hydraulic discontinuity between the soil and the roots may occur, severely limiting or even inhibiting water flow at the soil-root interface (Carminati et al., 2013; Duddek et al., 2023).
4. The water absorbed by the *roots* passes through multiple cell layers in the radial pathway (epidermis, cortex and endodermis) before reaching the stele (Couvreur et al., 2018; Steudle and Peterson, 1998). This radial flow is considered to represent a great resistance in the roots (Frensch and Steudle, 1989; Steudle and Peterson, 1998; Timlin et al., 2008), up to 95 % of the whole-plant hydraulic resistance (Rodriguez-Dominguez and Brodribb, 2020). The radial transport of water can take place through a combination of apoplastic (i.e. external to the plasma membrane, within cell walls and intercellular spaces), symplastic (i.e. a continuum of cytoplasm interconnected by

1. Introduction

plasmodesmata, excluding vacuoles) and transcellular (i.e. crossing membranes) pathways (Steudle, 2000a; Steudle and Peterson, 1998). At the endodermis, the apoplastic pathway in plant root system is obstructed by a suberin band known as the ‘Casparian band’. This hydrophobic barrier inhibits the water flow through the apoplast, compelling water to traverse the cell-to-cell pathways (i.e. symplastic or transcellular pathways) (Cuneo et al., 2021). The radial hydraulic characteristics of *Vitis* root system undergo changes during meristem development (elongation, maturation, secondary growth zones). These changes are attributed to the development of suberized apoplastic barriers in the endodermis and exodermis (mid- to long-term processes), as well as the regulation of aquaporins (short-term processes) (Barrios-Masias et al., 2015; Gambetta et al., 2013; Vandeleur et al., 2009). Researchers consistently observe a reduction in radial root hydraulic conductivity under drought conditions (Cuneo et al., 2016, 2021; Nobel and Cui, 1992; North et al., 2004; Trifilo et al., 2004), that may function as a mechanism to prevent water flow from the root to the soil while soil dries out (Aroca et al., 2012).

5. Water then flows axially through *xylem* vessels (from the roots to the leaves, through the stem), which confer a high hydraulic conductance to the plant. As axial hydraulic conductance of grapevine is usually high (Baert et al., 2015), it does not affect much the overall plant hydraulic conductance except when *xylem* cavitation occurs (Tardieu et al., 2018). Yet, recent research suggests that grapevine operates within a hydraulic safety margin, meaning that *xylem* embolism occurs at more negative water potential ($\Psi_{\text{stem}} < -1.3$ MPa) than those generally observed for stomatal closure ($\Psi_{\text{stem}} < -1$ MPa) (Charrier et al., 2016, 2018; Gambetta et al., 2020a; Sorek et al., 2021).
6. Water leaves *xylem* vessels and flows through outside-*xylem* living leaf tissues, i.e. the *mesophyll*. This part of the pathway is relatively short but can confer high resistance to water flow (Flexas et al., 2002). A recent study suggested that the decline in grapevine leaf hydraulic conductance during drought is

dominated by outside-xylem tissues, but not by xylem cavitation (Albuquerque et al., 2020).

7. Water reaches *stomata*, where transpiration and gas exchanges occur.

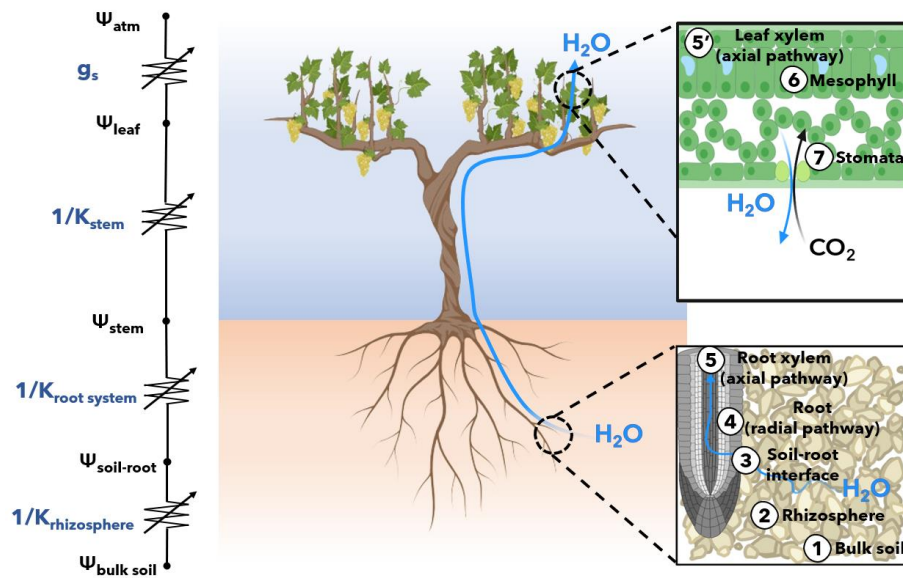


Figure 1.2 – Water flow traverses several key hydraulic compartments in the soil-grapevine-atmosphere continuum (SPAC). The water flow is driven by a gradient of water potential (Ψ) and regulated by a series of variable hydraulic conductances K (or resistances, their inverse). There is therefore an interdependence between water potentials, hydraulics conductances and water flow regulation. Variations in leaf water potential can lead to significant changes in stomatal conductance (g_s) and regulate transpiration. Conversely, alterations in transpiration rate caused by stomatal movements significantly impact the driving force of water flow in the soil-grapevine system, determined by the water potential differences between the soil and the leaves (figure adapted from Wankmüller and Carminati (2024), and created with BioRender.com).

1. Introduction

All of these hydraulic compartments contribute to the leaf water status, to which stomata respond as leaf water potential decreases due to low soil-root interface water potential (low soil water supply), high vapor pressure deficit (high atmospheric evaporative demand), and loss of hydraulic conductance (Wankmüller and Carminati, 2024). Despite our understanding of how the water flows, is driven and can be limited in the soil-grapevine-atmosphere continuum, the mechanisms that drive stomatal regulation are still obscure.

1.3.2. Hydraulic control in grapevine

In grapevine, studies suggest that both hydraulic and chemical signals influence stomatal regulation (Figure 1.3), though the relative contributions of these mechanisms remain unclear (Peccoux et al., 2018; Tombesi et al., 2015). Changes of soil-plant hydraulic conductance affect guard cell turgor and therefore stomatal conductance (Gambetta et al., 2020a). The plant hormone abscisic acid (ABA) is the most prominent biochemical factor in stomatal regulation, known for its direct impact on stomata conductance at the guard cell level (Nakashima and Yamaguchi-Shinozaki, 2013). Soil drying triggers an increase of ABA biosynthesis in the roots. Subsequently, ABA is transported via the xylem vessels to the leaves (Tardieu and Simonneau, 1998). ABA synthesis also occurs within the leaves (Christmann et al., 2007), where hydraulic and chemical signals induce the production of foliar ABA in response to water deficit (Mittler and Blumwald, 2015). Other molecular messengers also play a role in the stomatal regulation (Boneh et al., 2012; Munemasa et al., 2015). The interplay between hydraulic and biochemical mechanisms in stomatal regulation is intertwined, making the distinction between them difficult, both in theory and in practice (Gambetta et al., 2020a). However, research on grapevines indicates that ABA levels rise only when stomatal conductance drops to very low levels ($< 50 \text{ mmol.m}^{-2}.\text{s}^{-1}$), suggesting

that early stomatal closure is not driven by ABA (Degu et al., 2019; Hochberg et al., 2013), but by passive hydraulic mechanisms (Tombesi et al., 2015). ABA seems to restrict leaf gas exchange over longer term, preventing the recovery of stomatal aperture after rewatering, to prioritize embolism repair after severe drought stress (Tombesi et al., 2015). Xylem embolisms have been widely studied on laboratory and thought to trigger stomatal closure in grapevines and to limit water flow in the soil-grapevine-atmosphere continuum (Alsina et al., 2007; Choat et al., 2010; McElrone et al., 2012). Widespread embolism can result in leaf shedding and potentially lead to grapevine mortality. However, on-field grapevines generally maintain water potentials within a safe margin ($\Psi_{\text{stem}} > -1.5$ MPa) in which xylem cavitation or turgor loss is rare (Charrier et al., 2018). In potted grapevines, studies have shown that complete stomatal closure happened prior to leaf wilting and 0.3 MPa before the onset of cavitation (Dayer et al., 2020; Hochberg et al., 2017b). The gap between these events is even more striking when considering their timing: full stomatal closure occurred three days before cavitation began. These studies assumed that stomatal regulation likely prevents cavitation in vineyard conditions, even under drought stress. Moreover, it has been shown that the stem water potential for which 50 % of stomata are closed (Ψ_{50}) is a seasonal plastic trait in grapevines, adjusting in coordination with other hydraulic traits (e.g. water potential at turgor loss point Ψ_{TLP}) to more negative values as the growing season advances (Sorek et al., 2021). This seasonal hydraulic plasticity seems to be a predetermined strategy of the plant and is due to seasonal accumulation of solutes that allow to maintain turgor in stomata guard cells (Bartlett et al., 2014), resulting in higher stomatal conductance for a given water potential at the end of the season, compared to the start (Herrera et al., 2022). This adjustment enables the grapevine to maintain gas exchange late in the growing season. It has also been demonstrated that xylem embolism resistance shifts seasonally in coordination with Ψ_{50} and Ψ_{TLP} , supporting the hypothesis that the safety margin is maintained throughout the growing season in the field, with 0.4 MPa buffer between stomatal closure and the onset of cavitation. Grapevine vulnerability to xylem cavitation is therefore relatively constant throughout the growing season. In most vineyards, a 0.4 MPa drop in water potential (safety margin), takes several weeks,

1. Introduction

and it is even slower if stomata are closed. During the gradual dehydration under field conditions, grapevines have sufficient time to adapt and adjust their hydraulic properties accordingly, making xylem cavitation extremely rare in real-field conditions. However, in some conditions, e.g. very high atmospheric evaporative demand, or rapid and sharp drop of water potential close to the roots, fast changes in grapevine water potential could outpace the plant acclimation rate, potentially leading to cavitation even in vineyards (Sorek et al., 2021). Nevertheless, grapevine exhibits other conservative mechanisms, such as hydraulic vulnerability segmentation between the leaves and the stem, that are also important for the perennity of the plant (Bartlett and Sinclair, 2021; Gambetta et al., 2020a). This segmentation means that annual organs, such as leaves, are more susceptible to embolism than the perennial organs like stem. As the water potential becomes more and more negative, petioles and leaves experience embolism first, leading to the interruption of the water column that connects leaves to the upstream perennial organs, and protecting them against cavitation (Charrier et al., 2016; Hochberg et al., 2017b; Tyree and Ewers, 1991). Stomatal regulation and hydraulic safety margin, as well as hydraulic vulnerability segmentation in case of xylem embolism, are important traits for longevity and long-term productivity, in perennial crops under drought (Gambetta et al., 2020a).

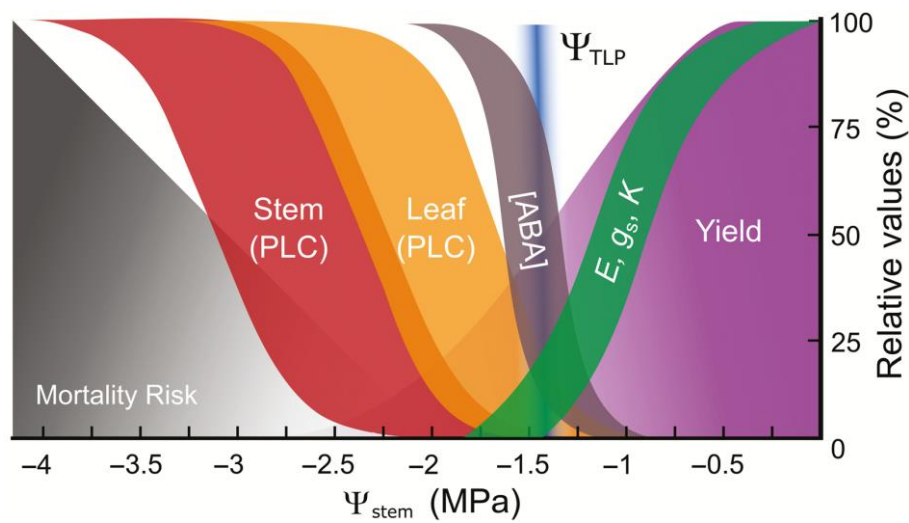


Figure 1.3 – Sequence and thresholds of grapevine responses to its water status, here quantified by the stem water potential (Ψ_{stem}). In situ grapevine usually operates within a secure range of water potentials (green zone, $\Psi_{stem} > -1.5$ MPa). Abscissic acid (ABA) levels only rise significantly after stomata have largely closed (black zone). When Ψ_{stem} drops below -1.6 MPa, grapevines can experience cavitation in the xylem vessels, measured as the percentage loss of conductivity (PLC). Grapevine exhibits hydraulic vulnerability segmentation, where leaves (orange zone) are more prone to embolism than perennial organs like stem (red zone). Embolisms in the leaves safeguard perennial tissues from severe water stress that could cause embolism. Extensive embolism can result in grapevine mortality (grey zone) (figure from Gambetta et al. (2020)).

1.3.3. Differences in water use strategies between grapevine cultivars

The sensitivity of stomatal control and grapevine water potential under water deficit conditions is traditionally seen as variety-specific, categorizing grapevine varieties as either isohydric or anisohydric (Scharwies et al., 2016), as this terminology was introduced for grapevines by Schultz (2003). Isohydric varieties finely regulate their stomatal conductance and maintain a relatively high and constant stem water potential over a wide range of vapor pressure deficit (VPD) and/or soil water potential. For anisohydric varieties, transpiration is not as tightly regulated by stomatal closure and stem water potential decreases with drought and/or high evaporative demand (Meinzer et al., 2016; Pou et al., 2012). Grapevines are known for having varieties that supposedly display contrasting iso/anisohydric behaviours. However, individual grapevine varieties can exhibit inconsistent responses across different studies. Determining a definitive behaviour in stomatal and water potential regulation for grapevines is problematic (Chaves et al., 2010). If iso/anisohydric behaviour were genetically fixed, each variety would consistently exhibit the same behaviour regardless of growing conditions. Approaches that determine drought resistance in grapevine by relying solely on phenotyping differences in stomatal regulation are insufficient, and a more integrative outlook is needed (Charrier et al., 2018). Recently, Hochberg et al. (2018) argued that the terms iso- and anisohydric should be abandoned, primarily because environmental factors are at least as influential as genetic factors. This means that the prediction of grapevine hydraulic behaviour is impossible without considering environmental conditions (Hochberg et al., 2018; Villalobos-González et al., 2019). Beyond the direct impact of environmental factors on the soil-plant hydraulics, such as soil hydraulic conductivity or VPD, different environmental exposures can shape grapevine hydraulic properties (Lovisolo et al., 2010). Traits like Ψ_{50} , Ψ_{TLP} , and hydraulic architecture exhibit high environmental plasticity (Hochberg et al., 2015; Martorell et al., 2015; Munitz et al., 2018). This plasticity means that comparisons of cultivars under

varying conditions may not always lead to consistent hydraulic behaviour. Such variability may explain the differing behaviours observed for a same variety across different studies (Charrier et al., 2018; Chaves et al., 2010; Gambetta et al., 2020a; Lavoie-Lamoureux et al., 2017). This does not diminish the findings of various authors who have identified significant hydraulic differences between cultivars under similar conditions (Schultz, 2003; Soar et al., 2006b). Rather, it highlights the dominant role of the environment in shaping these differences, often outweighing genetic factors.

1.3.4. Soil-root interactions: the hidden face

Grapevine aboveground hydraulic processes have been widely studied, while the belowground hydraulic processes, and their impact on stomatal control, are much less understood. However, an array of individual traits has been identified as crucial for grapevine drought adaptation, in both the aboveground part of the soil-grapevine system, as mentioned previously, but also in the belowground part (Simonneau et al., 2017). The root system is known to play a major role in grapevine tolerance to drought by absorbing the water in response to transpiration demand. As mentioned previously, nowadays grapevines are predominantly grafted onto rootstocks derived from American genotypes. Rootstocks offer resistance to external biotic factors and abiotic stresses, while affecting the ecophysiological responses of the scion (Cookson et al., 2019; Ollat et al., 2015; Soar et al., 2006a; Tramontini et al., 2013b). In the belowground part of the soil-grapevine system, greater attention has been given to studying how the rootstock genotype influences root water uptake and scion gas exchange, focusing on the inherent characteristics of the rootstock (Alsina et al., 2011; Cookson et al., 2019; Gambetta et al., 2013; Ollat et al., 2015; Peccoux et al., 2018). These different rootstock genotypes have been shown to differentially influence the water consumption of the plant (Marguerit

1. Introduction

et al., 2012; Ollat et al., 2015). For instance, rootstock genotype has a big impact on root density (i.e. root number by volume of soil) (Peccoux et al., 2018), that directly impacts the amount of water the plant can take up. Another example is that varying ABA concentrations, produced by drying root cells, were found in the xylem sap of the same scion grafted onto different rootstocks. These variations were linked to the chemical signals involved in grapevine stomatal control (Soar et al., 2006a). The root system architecture (i.e. the spatial distribution of the root system) is determinant in soil-grapevine hydraulics (Tron et al., 2015). Variation in root hydraulic conductance among rootstocks have been documented (Herralde et al., 2006; Tramontini et al., 2013b), yet these differences may be attributed more to the overall size and architecture of the root system rather than distinct individual root properties (Alsina et al., 2011). The root system architecture is also linked to rootstock susceptibility to embolism (Lovisolo et al., 2008), as well as aquaporin contribution to water flow during water stress (Gambetta et al., 2012), but a recent meta-analysis showed that the onset of xylem embolism is around Ψ_{root} of -1.8 MPa for a large range of rootstock genotypes (Lamarque et al., 2023), which is significantly lower than the onset of stomatal closure ($\Psi_{\text{stem}} < -1$ MPa) generally observed in a wide range of grapevine cultivars (Albuquerque et al., 2020; Gambetta et al., 2020a; Gowdy et al., 2022), suggesting that xylem rootstock embolisms do not trigger stomatal closure. However, the integrity of the radial water flow path in grapevine roots can be affected at less negative Ψ_{root} . Roots are hypothesized to act like electrical fuses, hydraulically disconnecting to the soil when subjected to drought conditions (Duddek et al., 2023; Jackson et al., 2000). Cuneo et al. (2016) demonstrated that in water deficit conditions, the development of cortical lacunae and the collapse of root cortex tissue reduce the radial hydraulic conductance in grapevine roots, leading to root shrinkage and to the formation of air gaps between the roots and surrounding soil. These cortical lacunae started forming under mild drought stress in fine roots ($\Psi_{\text{root}} = -0.6$ MPa), but not in coarse suberized roots (Cuneo et al., 2016). Soil-root air gaps formations, due to root and/or soil shrinkage (North and Nobel, 1997; Veen et al., 1992), seem to be a consequence and not a cause of limiting water flow from soil to roots (Faiz and Weatherley, 1982), but are expected to be the limiting factor controlling water uptake, for a

wide range of water potential, when they are present (Carminati et al., 2009). In the past, researchers have traditionally viewed soil-root air gaps as detrimental to soil-plant water relations. However, these air-filled gaps will insulate roots from the surrounding soil. In dry soil conditions, this may reduce water loss from roots to soil (North and Nobel, 1997). Gap formation around roots might be an effective strategy for plants to isolate parts of the root system exposed to dry soil, while younger roots continue to grow in wetter soil horizons (Carminati et al., 2013; Couvreur et al., 2014). While the presence of soil-root air gaps has recently started to be documented for grapevine (Cuneo et al., 2016, 2021), the effect of these gaps on root water uptake and grapevine water status is not well understood and is still an open question. The scarcity of studies on the effects of gaps on water flow is largely due to the challenge of simultaneously measuring gap dynamics, soil water potential, soil-root interface water potential, soil hydraulic conductivity and xylem water potential at the necessary spatial resolution (Carminati et al., 2013).

It is well-known that grapevines develop deep and dense root systems, and that the architecture of the root system is more influenced by soil type than by the rootstock genotype (Smart et al., 2006). For example, some studies showed that a same rootstock genotype developed deeper root system in a sandy soil compared to a loamy soil (Nagarajah, 1987; Ollat et al., 2015). The temporal development of the root system is driven by the heterogeneous distribution of water in the soil, which can be itself influenced by the texture distribution of a soil profile, root distribution and water uptake dynamics (Comas et al., 2010; Tron et al., 2015). Root development exhibits high plasticity, with typical allocation of carbohydrates towards root growth at the expense of shoot and canopy development in coarse-textured soils and under dry conditions, allowing the plant to enhance soil exploration for water uptake while diminishing transpiration (Cramer et al., 2013; Simonneau et al., 2017). Soil type therefore plays a major role on soil-grapevine hydraulics thanks to its intrinsic hydraulic properties given by texture and structure on the one hand, and by interacting with the canopy and root system development on the other hand. While the role of soil

1. Introduction

properties is recognized as crucial for the drought tolerance of grapevine, the impact of soil on root water uptake and hydraulic behaviour of grapevine is rarely documented and quantified in viticultural literature (Lovisolo et al., 2016). Lavoie-Lamoureux et al. (2017) highlighted that transpiration rate and stomatal conductance are lower in coarse-textured soils than in fine-textured soils, for a same variety at the same leaf water potential. Tramontini et al. (2013a) showed, on Shiraz and Cabernet Sauvignon, that the relation between stomatal conductance and stem water potential is significantly influenced by the hydraulic properties of the soil they were grown, the impact of the soil properties being as substantial as the differences between the cultivars themselves. The same authors reported opposite results one year later, with no significant differences in leaf gas exchange parameters of grapevines grown in two soil types with different water holding capacity (Tramontini et al., 2014). Same conclusions were drawn by Leibar et al. (2015). However, studies of Tramontini et al. (2014) and Leibar et al. (2015) were conducted in potted and young grapevines, while Tramontini et al. (2013a) was led on field-grown grapevines in well-established vineyards. On a recent review, Lavoie-Lamoureux et al. (2017) underscored the effect of methodological factors on grapevine hydraulic behaviour. Potted grapevines exhibited lower stomatal conductance compared to those grown in the field. This discrepancy may be attributed to the age of the grapevines and the extent of root system development, limited by the volume of the pot. Younger plants with limited root surface are more prone to severe water stress and might exhibit more isohydric behaviour compared to older, well-rooted plants, contributing to the intra-cultivar hydraulic variabilities (Charrier et al., 2018; Chouzouri and Schultz, 2005; Schultz, 2003). Moreover, potted grapevines are exposed to more rapid water stress application (typically in 4 to 10 days), not representative to slow and gradual water deficit experienced by field-grown grapevines, leading to different plant responses (Medrano et al., 2002). Although most of the studies about grapevine hydraulic response to drought were conducted under controlled conditions using potted plants (Charrier et al., 2018; Dayer et al., 2020; Hochberg et al., 2016, 2017b; Simonneau et al., 2017; Tramontini et al., 2014), extrapolating conclusions from fast-drying pot experiments to field-grown

grapevines could lead to misleading interpretations (Herrera et al., 2022), due to the limiting projection of the edaphic conditions of a real vineyard (Tramontini et al., 2014). Our understanding on grapevine hydraulics in the field remains limited, particularly due to the difficulty to access and quantify belowground hydraulics of the soil-grapevine system (Fichtl et al., 2023; Ollat et al., 2017). The interrelationships between aboveground and belowground hydraulics of *in situ* soil-grapevine systems are challenging to predict, and how they are involved in stomatal control remains to be fully elucidated (Gambetta et al., 2020a; Lovisolo et al., 2016). To fill this gap of knowledge is a crucial step towards addressing practical issues, such as winemakers' uncertainties related to climate change.

Discussions of iso/anisohydric seldom address the specific biophysical constraints of soil-plant hydraulics, particularly those imposed by the belowground environment of the plant (Hochberg et al., 2018; Javaux and Carminati, 2021; Kannenberg et al., 2022). Contrary to the binary classification of iso/anisohydric behaviour, Hochberg et al. (2018) proposed that it represents a spectrum of plant-environment interactions rather than a straightforward hydraulic trait of the plant. Grapevine hydraulic behaviour should be an adaptive response of integrative hydraulic mechanisms that depend on the interactions between the plant (rootstock and cultivar), edaphic conditions and climatic conditions. Consequently, hydraulic plasticity should manifest as varying iso/anisohydric behaviours within a same grapevine cultivar, as it has already been observed (Charrier et al., 2018; Chaves et al., 2010; Gambetta et al., 2020a; Lavoie-Lamoureux et al., 2017). It is essential to define and understand grapevine water use strategies and to link them to the biophysical constraints of soil-grapevine hydraulics. These constraints arise from dynamic interactions between the grapevine and its environment (Hochberg et al., 2018). In particular, the complex relationship between belowground hydraulics and grapevine water use needs to be thoroughly explored to understand how transpiration control and environment-dependent hydraulics interact in real-field conditions. Grapevine water use strategies are influenced by soil-plant hydraulics, specifically by the component of the soil-grapevine system

1. Introduction

(the soil, the root, the stem or the leaf) that experiences the most significant absolute drop in conductance. Rather than xylem vulnerability, it is the loss of soil conductance that may play a critical role of declining leaf water potential, inducing stomatal closure and restricting water flow during drought, as the rhizosphere hydraulic conductance falls below that of the plant (Carminati and Javaux, 2020). The rhizosphere has dynamic and complex characteristics that are not understood sufficiently at present. These considerations must be investigated to enhance our capacity to understand *in situ* grapevine water needs in different environments, particularly different edaphic conditions, and more precisely evaluate the risks posed by future climate change.

2. Objectives

The overarching goal of this PhD thesis is to understand the intricate control of soil-grapevine hydraulics on grapevine water potential, transpiration rate and water use strategies of *in situ* grapevine. A particular focus is put on the role of belowground properties and hydraulics as a constraint on water fluxes, as we believe that belowground hydraulics plays a significant role on the trigger of stomatal closure, and on transpiration and water potential control, at the plant and field scale. We assume that these soil-root water relations are soil texture dependent.

Three research objectives (RO) are defined: (1) to understand the role of the belowground (soil + root system) and aboveground (stem) parts of the soil-grapevine system on the transpiration control of *in situ* grapevine during drought for different edaphic conditions, (2) to understand how the rhizosphere hydraulic conductance controls root water uptake and stem water potential at the plant scale, in different soil types considering the complexity and heterogeneity of soil properties in real field conditions, and (3) to assess the impact of the edaphic, topographic and climatic conditions on the spatial distribution of grapevine water status at the vineyard scale. Their interdependencies are shown in Figure 2.1.

RO.1 – What are the roles of belowground (soil and root system) and aboveground (stem) hydraulics on the transpiration control of in situ grapevine?

2. Objectives

In Chapter 3 of this thesis, we will devise an integrative approach to exhaustively characterize the hydraulic response of *in situ* grapevine, in different soil types during drought. As recently highlighted by Novick et al. (2022), simultaneous monitoring of bulk soil water potential ($\Psi_{\text{bulk soil}}$), stem water potential (Ψ_{stem}), leaf water potential (Ψ_{leaf}) and potential and actual transpiration rates (T_{pot} and T_{act}), in real-field conditions, would improve our knowledge on the role of belowground and aboveground hydraulics on the transpiration control of vegetation to water deficit conditions. We will investigate the practicality of implementing *in situ* a simultaneous monitoring system using tensiometers, psychrometers, pressure chamber, sap flow sensors and weather station to respectively monitor $\Psi_{\text{bulk soil}}$, Ψ_{stem} , Ψ_{leaf} , T_{act} and T_{pot} , and to quantify the evolution of belowground (soil + root system) and aboveground (stem) hydraulics and their impact on transpiration control of grapevine during drought

RO.2 – How does rhizosphere hydraulic conductance controls root water uptake and stem water potential at the grapevine scale?

In Chapter 4, we will aim to understand the role of rhizosphere and root hydraulic properties on root water uptake and stem water potential, considering the heterogeneity of soil properties in real field conditions. Thanks to a macroscopic physically-based model, including rhizosphere and root system hydraulic properties, we will accurately quantify the evolution of the rhizosphere hydraulic conductance and compare it to root system hydraulic conductance, for soil-grapevine systems in different edaphic conditions. We will validate the model by comparing measured (Chapter 3) and simulated bulk soil and stem water potentials.

RO.3 – How edaphic, topographic and climatic conditions influence the spatial distribution of grapevine leaf water potential at the vineyard scale?

While Chapters 3 and 4 will be devoted to understanding the role of aboveground (stem) and belowground (soil + root system) hydraulics on the control of root water uptake, stem water potential and transpiration, Chapter 5 will focus on experimentally quantify the heterogeneity of grapevine leaf water potential, in an accurate way at the vineyard scale. We will evaluate the capabilities of unmanned aerial systems equipped with multispectral, thermal and LiDAR sensors to spatially monitor leaf water potential. We will assess the impact of edaphic, topographic and climatic conditions on leaf water potential spatial distribution within vineyards, during a dry and a wet viticultural season.

Each chapter of this thesis is tailored to each research objective. The first research question, answered in Chapter 3 (field experiments at the plant scale), will lay out the foundations for the second research question, answered in Chapter 4 (modelling at the plant scale). The mechanistic knowledge obtained in Chapters 3 and 4 will allow to understand and interpret experimental observations at the field scale, presented in Chapter 5 (Figure 2.1).

2. Objectives

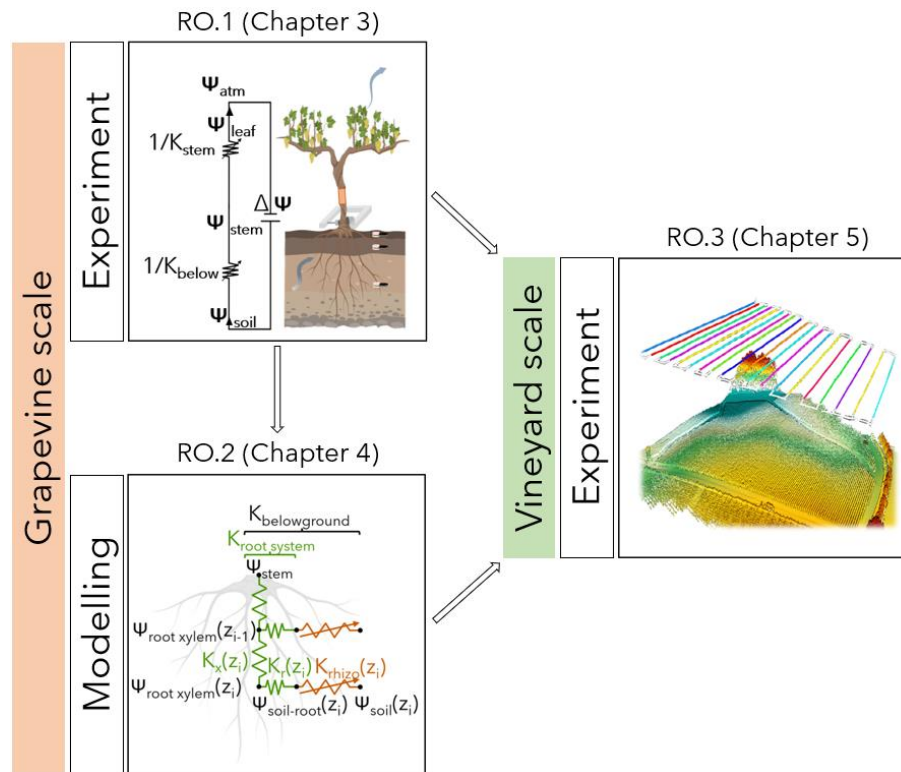


Figure 2.1 – Flowchart showing the links between the research objectives (RO) allowing us to understand how belowground properties and hydraulics influence grapevine hydraulics at the plant and field scales. **RO.1:** Role of belowground (soil + root system) and aboveground (stem) on transpiration control; **RO.2:** Role of rhizosphere and root hydraulic properties on root water uptake and stem water potential; **RO.3:** Influence of edaphic, topographic and climatic conditions on the spatial distribution of leaf water potential.

3. Grapevine transpiration control is soil texture specific

This chapter is based on the article:

Delval, L., Jonard, F., Javaux, M. Simultaneous *in situ* monitoring of belowground, stem and relative stomatal hydraulic conductances of grapevine demonstrates a soil texture specific transpiration control, in revision in OENO One.

ABSTRACT

Assessing the interrelationships between belowground, stem and stomatal hydraulics, under various edaphic conditions, is essential to enhance understanding of how grapevine (*Vitis vinifera*) responds to drought. This work aimed to quantify and compare belowground and stem hydraulic conductances of the soil-plant system, on *Vitis vinifera* cv. Chardonnay, to evaluate their coordination with the transpiration control during drought. We simultaneously monitored soil water potential, stem water potential, leaf water potential, actual transpiration and atmospheric demand to quantify the evolution of belowground, stem and relative stomatal hydraulic conductances. By comparing stomatal regulation and soil-grapevine system conductance, we assessed their coordination. Stomatal response was triggered by a decrease of belowground hydraulic conductance, but not by xylem

3. Grapevine transpiration control is soil texture specific

cavitation in the stem. Although the relation between stomatal conductance and soil water potential is soil texture specific, with stomata started to close at less negative soil water potential in sand than in loam, the onset of stomatal closure was at equivalent belowground hydraulic conductance, independently of the soil texture. These findings prove that *in situ* grapevines coordinate short-term hydraulic mechanisms (e.g. stomatal regulation) and longer-term growth (e.g. root:shoot ratio). These belowground and aboveground adjustments are therefore soil texture specific.

3.1. Introduction

Water flow through the soil-plant-atmosphere continuum (SPAC) is driven by a gradient of water potential and regulated by a series of variable hydraulic conductances (or resistances, their inverse). It is widely acknowledged that plants continually adjust to variable atmospheric and soil conditions by modifying the hydraulic conductances of key elements both below- and aboveground of the SPAC (Abdalla et al., 2021). However, our mechanistic understanding of these hydraulic adjustments remains elusive. On a short timescale, stomatal opening and closing regulate the transpiration rate of plants that in turn affects the difference between leaf and soil water potential. This safety mechanism allows the plant to operate at less negative water potentials, thereby delaying the formation of embolisms to avoid mortality, for example when the plant is in water deficit (Anderegg et al., 2017; Draye et al., 2010). It has been shown that stomatal regulation is linked to hydraulic and/or chemical (e.g. abscisic acid) signals. However, the extent to which these underlying mechanisms interact and vary among species and environmental conditions is still a subject of debate (Hochberg et al., 2018; Tardieu, 2016).

Stomatal control has been broadly studied in relation to xylem cavitation, especially to xylem vulnerability on the aboveground part (canopy) of the SPAC (Anderegg et al., 2017; Bartlett et al., 2016; Henry et al., 2019; Martin-StPaul et al., 2017; Sperry and Love, 2015; Wolf et al., 2016). However, other hydraulic constraints arise along the SPAC prior to xylem cavitation (Albuquerque et al., 2020; Corso et al., 2020; Scoffoni et al., 2017), especially in the belowground part (Abdalla et al., 2022; Koehler et al., 2022; Rodriguez-Dominguez and Brodribb, 2020). The simultaneous quantification of these above- (i.e. stem, canopy) and belowground (i.e. soil, root system) hydraulic conductances is rare and their evolution with time, in relation with stomatal conductance, would allow better understanding how biophysical constraints in the SPAC affect plant hydraulics (Novick et al., 2022). In wet soils, the soil hydraulic conductivity is typically much higher than that of roots, and water flow is primarily governed by root hydraulic conductivity (Draye et al., 2010; Passioura, 1980; Zarebanadkouki et al., 2013). As the soil dries out, the soil water potential decreases, resulting in a significant reduction in soil hydraulic conductivity, particularly in the vicinity of the roots. This soil limitation can restrict root water extraction and may limit the supply of water for transpiration (Carminati and Javaux, 2020; de Jong van Lier et al., 2006; Gardner, 1960; Passioura, 1980). The loss of soil hydraulic conductance results in large gradients in soil water potential close to the roots, leading to a significant decrease in leaf water potential, and to a large difference between soil and leaf water potential to sustain a certain transpiration. Consequently, the relationship between stomatal control and leaf water potential should be specific to the soil and root characteristics (Carminati and Javaux, 2020). The soil texture determines soil hydraulic properties, thereby influences plant hydraulics and response to drought conditions (Cai et al., 2022; Javaux and Carminati, 2021). Recent studies investigated the hypothesis that the soil rather than the xylem vulnerability has a dominant role on stomatal closure on tomato (Abdalla et al., 2021, 2022), maize (Cai et al., 2022; Koehler et al., 2022; Nguyen et al., 2024) and olive trees (Rodriguez-Dominguez and Brodribb, 2020). However, these studies are based on well-controlled laboratory experiments, exposed to rapid water stress application, not representative to slow and gradual water

3. Grapevine transpiration control is soil texture specific

deficit experienced by *in situ* plants. It is still unclear if these results obtained on these mentioned studies, under laboratory conditions, can be generalized to field conditions and other species (Wankmüller and Carminati, 2024).

Grapevines (*Vitis vinifera* L.) stand as one of the world's most widely cultivated and economically significant fruit crops (Yang et al., 2023). Water use and grapevine water status are very important in viticulture, since it has a huge impact on fruit composition and wine quality (Gambetta et al., 2020a; Matthews and Anderson, 1988; Van Leeuwen et al., 2009a). Previously, grapevine water use and stomatal control were regarded as a plant-specific strategy, categorizing grapevine cultivars as either (near-)isohydric or (near-)aniso-hydric (Schultz, 2003). However, depending on the study and the environmental conditions, a same vine variety may be considered iso- or aniso-hydric (Hochberg et al., 2013; Tamayo et al., 2023; Tramontini et al., 2014). This is also in line with soil hydraulic model predictions (Javaux and Carminati, 2021). Rootstock-scion combinations can contribute to the variability of the hydraulic behaviour of same cultivar, due to the intrinsic rooting patterns and hydraulic properties of a rootstock (Coupel-Ledru et al., 2014; Vandeleur et al., 2009). Recent studies emphasize that environmental parameters play a significant role in the transpiration limitation of grapevines, and that the whole soil-rootstock-variety system contribute to the complex hydraulic dynamics across grapevine cultivars (Hochberg et al., 2018; Lavoie-Lamoureux et al., 2017). However, the influence of soil type on grapevine hydraulics is scarcely documented in the scientific literature (Lovisolo et al., 2016). Xylem embolisms has been extensively studied on grapevine and thought to trigger stomatal closure (Alsina et al., 2007; Choat et al., 2010; McElrone et al., 2012). Yet, recent studies that simultaneously measured stomatal conductance and grapevine water potential showed that grapevine stomata closed at less negative water potentials (< -1 MPa; Albuquerque et al., 2020; Gowdy et al., 2022; Herrera et al., 2022; Morabito et al., 2021) than those at which xylem cavitation was observed in the leaf (< -1.2 MPa; Albuquerque et al., 2020; Hochberg et al., 2017), in the stem (< -1.3 MPa; Alsina et al., 2007; Charrier et

al., 2016; Lovisolo et al., 2010; McElrone et al., 2012), and the roots (< -1.8 MPa in fine roots and < -3.5 MPa in coarse roots; Cuneo et al., 2016; Lamarque et al., 2023), suggesting that xylem embolism is not the driving mechanism triggering stomatal closure in grapevines. Several studies showed the influence of soil type on soil-root interactions and grapevine water status. In a recent meta-analysis on different cultivars, Lavoie-Lamoureux et al. (2017) highlighted that for a same variety and for a same leaf water potential, the stomatal conductance and transpiration rate are lower in coarse-textured soils than in fine-textured soils. Tramontini et al. (2013) conducted statistical analysis on grapevine water potentials and gas exchanges and showed the predominance of the soil effect, while cultivar effect was subordinate. Finally, it has been shown that soil texture influences the growth of root system, with deeper but less dense root systems in sandy soils compared to loamy soils for a same rootstock (Nagarajah, 1987; Ollat et al., 2015). This also directly impacts the belowground hydraulic conductance of the soil-grapevine system. Nevertheless, none of these studies quantified the evolution of the aboveground and belowground hydraulics conductances and their relationship with transpiration control. Our comprehension of soil-plant hydraulics in field conditions is still limited, primarily because of the challenges in accessing and quantifying belowground hydraulics (Fichtl et al., 2023). The interactions between stomatal, stem and belowground hydraulics *in situ* are difficult to predict, and their role in transpiration control is not yet fully understood.

The objective of this work is to explore how the belowground (soil and roots) and aboveground (stem) parts of soil-plant system are involved on the transpiration control of *in situ* grapevine during drought, for different edaphic conditions. We aim to investigate how *in situ* grapevines respond to declining soil moisture across contrasting soil textures from a hydraulic perspective. We hypothesize that transpiration limitation during drought is significantly impacted by the belowground hydraulic properties and is therefore soil texture specific.

3.2. Methodology

3.2.1. Study areas

This study was conducted on 4 subplots located in two non-irrigated Belgian vineyards (2 subplots per vineyard), grassed in the inter-rows: *Château de Bousval* and *Domaine W*. At the *Château de Bousval* (CB) vineyard (Genappe, Belgium, 50°36'45.0"N 4°31'19.6"E), the subplots were located on an east-facing field of Chardonnay grafted on 3309C rootstock and planted in 2014 with vertical shoot positioning, a 1.6 m inter-row and a 0.8 m inter-cep. The average slope is 6 %. At the *Domaine W* (DW) vineyard (Tubize, Belgium, 50°41'19.4"N 4°09'36.9"E), the measurements were carried out on Chardonnay grafted on 101-14Mgt rootstock, in a plain field, with rows running north-south. The vines were planted in 2016 with vertical shoot positioning, a 2.2 m inter-row and a 1 m inter-cep. The average annual temperatures are 10.5 °C and 10.8 °C, and the average annual precipitations are 874.6 mm and 820.6 mm, for CB and DW vineyards respectively (Belgian Royal Institute of Meteorology, IRM). Both vineyards are equipped with weather stations providing hourly data of precipitation (P) and reference evapotranspiration (ET₀) calculated from the FAO Penman-Monteith method (Allen et al., 1998).

These vineyards were selected due to their similar pedogenesis but contrasted layering. At the CB vineyard, the soil is made of a silty loam top layer overlying a sandy subsoil, but the depth of the interface between these two layers changes within the plot reaching more than 2 m at the lowermost side of the parcel due to an accumulation of loamy colluviums, while being around 0.3 m at the upper part. Two subplots were selected in this vineyard: one with grapevines planted on the

shallow silty loam soil layer (≈ 0.3 m - CBa) and one on a deep silty loam soil (> 2 m - CBb) (Figure 3.1a). In the DW vineyard, we also worked on two subplots (Figure 3.1b). Grapevines were selected in the northern part of the field, characterized by a silty loam soil on the first 125 cm and a silty clay loam soil thereafter (DWa). The southern part is defined by a silty loam soil on the whole profile (DWb). According to the Belgian soil classification, DWa has a silty soil with good natural drainage and DWb a loamy soil with poor to very poor natural drainage.

3.2.2. Soil, grapevine and weather characterization

Soil properties

At each subplot, a 2 m deep pit was dug in April 2022 to evaluate the distribution of the soil physico-chemical properties. The walls of the pits ran parallel to the rows, at 10 cm from the grapevines. In each soil profile, disturbed samples were collected from each horizon to determine their textural class (Robinson, 1933). Undisturbed soil samples of 250 cm³ collected on stainless steel cylinders in each horizon were used to measure the soil hydraulic properties (Figure S.3.1) by Hyprop (METER Group, Inc., Pullman, WA, USA) evaporation method (Bezerra-Coelho et al., 2018). The soil water content at the permanent wilting point (pF 4.2) was measured by pressure plate (Ridley and Burland, 1993). Hyprop-fit software was used to optimize the parameters of the Mualem-van Genuchten equation of the water retention and hydraulic conductivity functions (van Genuchten, 1980).

In the CBa subplot, grapevines are planted on a shallow loamy soil of 50 cm (horizon Ap) that surmounts a sandy subsoil composed of recurring layers with characteristic colors. The basic color of the sandy

3. Grapevine transpiration control is soil texture specific

material is yellow and contains iron in the form of glauconia, which is an association of clay minerals. The alteration of the glauconia and the individualization of iron in the form of iron oxides give the sandy substrate a reddish color at several depths. The pale-yellow (S1) and red strata (S2) result from the leaching of iron and its accumulation in layers called iron crusts. The hydraulic properties of these iron crusts are significantly different than those of the yellowish layers. Their water holding capacity (WHC) is $0.08 \text{ cm}^3_{\text{water}}.\text{cm}^{-3}_{\text{soil}}$, while it is almost null in the yellow sand. The WHC of CBa is 107 mm on a 2 m soil profile. CBb subplot is composed of three silty loam horizons over at least 2 m (Ap 0-48 cm; Bw1 49-80 cm, Bw2 80-200 cm) and has a WHC of 421 mm at this depth. DWb also consists of 3 silty loam layers (Ap1 0-11 cm; Ap2 11-90 cm; Bw 90-200 cm) and has 499 mm of WHC on 2 m depth. Finally, the first three horizons of DWa are silty loam soil (Ap1 0-10 cm; Ap2 10-40 cm; Bw1 40-125 cm) and the last horizon is composed of silty clay loam (Bw2 125-200 cm). The WHC of this subplot is 383 mm to a depth of 2 m. The detailed pedological description of each soil profile is illustrated in Figure S.3.1.

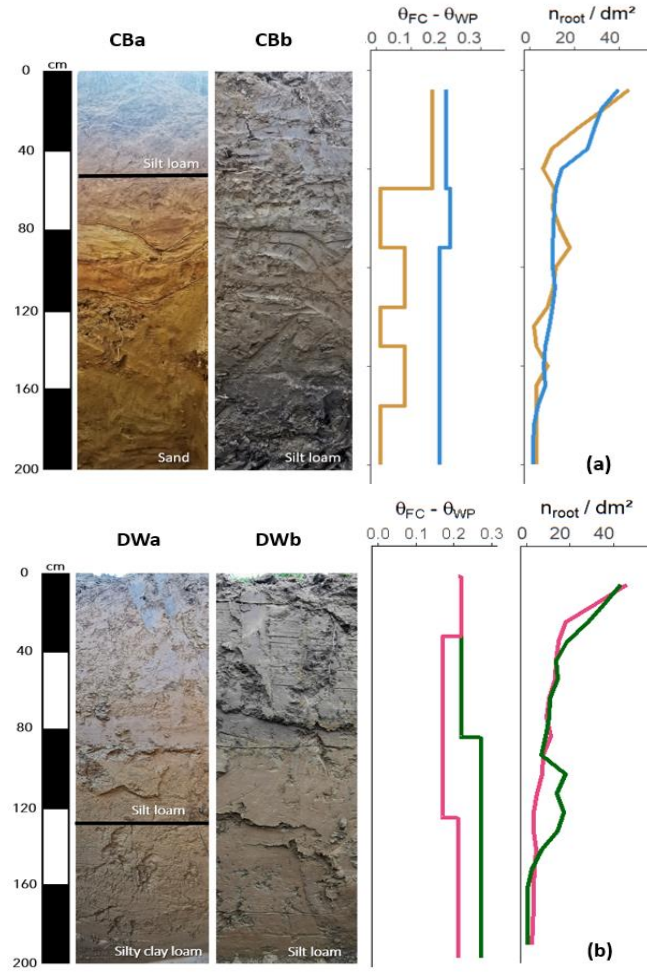


Figure 3.1 - Soil profiles, water holding capacity ($\theta_{FC} - \theta_{WP}$ in cm^3_{water}/cm^3_{soil}) and 1D grapevine fine root density up to 2 m deep for the subplots in (a) the Château de Bousval (CB) vineyard (brown and blue lines correspond to the subplots CBa and CBb respectively) and (b) the Domaine W (DW) vineyard (pink and green lines correspond to the subplots DWa and DWb respectively).

3. Grapevine transpiration control is soil texture specific

Grapevine characterization

The quantitative analysis of root distributions in the different subplots was carried out using the trench profile method (Böhm, 1979). In the 2 m deep soil pit dug in April 2022, a grid with 10 x 10 cm² cells was set against the pit wall, parallel to the vine rows at 10 cm from the vine trunk. Root impacts were mapped and counted within each cell. Large roots (diameter > 1 mm) were counted separately from the fine roots ($\leq$ 1 mm) (Perry et al., 1983). Only fine roots ($\leq$ 1 mm) were considered in this study. The distinction between vine and grass roots in the pit was made based on color (i.e. the grass roots were white and the vine roots were dark). To obtain the 1D fine root density ($n_{\text{root}}/\text{dm}^2$) in the profile for each soil layer (10 cm by 10 cm), we averaged the number of fine root impacts in each layer by the total area of the layer. In each subplot, fine root density tends to decrease with depth, and reach at least 2 m-depth (Figure 3.1). Although the number of observed fine roots were low in the bottom of the profile, as we always observed at least one fine root impact at 2 m (Figure S.3.2), it is possible that roots went even deeper.

Leaf area index (LAI) of grapevines was measured (LP-80, METER Group, Inc., Pullman, WA, USA) at two different dates, at the beginning (close to the veraison, DOY 208) and end (close to the harvest, DOY 250) of the measurement period, to assess its evolution over this period (Table 3.1). As grapevines were not thinned out or pruned during the experimental period, the observed evolution of LAI is only due to vegetative growth/senescence. We linearly interpolated LAI between these two dates (Figure S.3.3) since the vegetative growth of grapevine stopped a few days before the veraison (Reynier, 2011).

Table 3.1 – Leaf area index (LAI) at DOY 208 and DOY 250 (2022) in each subplot.

	CBa	CBb	DWa	DWb
DOY 208	1.38	1.83	1.68	1.92
DOY 250	1.27	1.51	1.36	1.52

Weather conditions

The summer of 2022 was marked by an exceptional drought in Belgium. The hydraulic measurements took place between 27 July 2022 (DOY 209 – start of the veraison) and 05 September 2022 (DOY 248 - harvest). During this period, the total rainfall (P) was only 22.2 mm and 11.4 mm in CB and DW vineyards respectively (Figure S.3.4), corresponding to a rainfall anomaly of -108 mm and -117.6 mm, compared to the period between 1991 and 2020. The cumulative reference evapotranspiration (ET_0) exceeded the total rainfall and was 160.3 mm at CB and 151.8 mm at DW. The water deficit ($ET_0 - P$), which refers to the standardized precipitation evapotranspiration index (Vicente-Serrano et al., 2010), amounted to 138.1 mm at CB and 140.4 mm at DW. The summer was also very hot, with maximum daily temperature of 27°C on average in both vineyards, which is 4 to 5°C higher than the seasonal norm. In both vineyards, temperature fluctuations between day and night were significant, on average 14.9 ± 4.9 °C at CB and 16.46 ± 5.1 °C at DW. To compare ET_0 and actual transpiration (T_{act}) per plant, we divided ET_0 given in $\text{cm} \cdot \text{s}^{-1}$ by plant density [cm^{-2}] to get ET_0 in $\text{cm}^3 \cdot \text{s}^{-1}$.

3. Grapevine transpiration control is soil texture specific

3.2.3. Hydraulic measurements

Soil and plant hydraulic measurements

Teros21 pF-meters (METER Group, Inc., Pullman, WA, USA) were installed vertically at 10 cm, 40 cm and 100 cm depth to monitor the soil water potential ($\Psi_{\text{bulk soil}}$ [MPa]). These sensors measure bulk soil dielectric permittivity, which is converted into water content, which finally is transformed into a potential based on the sensor's moisture characteristic curve. The range of measurement of these sensors are from 0 to -100 MPa (Walthert and Schleppi, 2018). In each subplot, one sensor per depth was inserted under the grapevines (no horizontal distance between the plant and the sensors) to measure the variation in soil matric potential linked to water uptake. We interpolated the soil water potential down to 1 m-depth with the classical trapezoidal method (Haverkamp et al., 1984). To extrapolate the soil water potential to the bottom of the soil profile, we considered $\Psi_{\text{bulk soil}}$ measured at 1 m depth as constant below (therefore constant between 1 m and 2 m depth).

Three plants per subplot were equipped with a stem psychrometer (PSY1, ICT International, Armidale, NSW, Australia) and a sap flow sensor (Dynagage, Dynamax Inc., Houston, TX, USA) to monitor respectively the collar stem water potential (Ψ_{stem} [MPa]) and the sap flow of the plants (assumed as being the transpiration rate T_{act} [$\text{cm}^3 \cdot \text{s}^{-1}$]). The measurements took place between 27 July 2022 (DOY 209 - end of the vegetative growing period and start of the veraison) and 05 September 2022 (DOY 248 - harvest). Since we observed that grapevines of the CBa subplot were stressed since the start of the measurements in 2022, we also took hydraulic measurements during a wet period in 2023 (between DOY 208 and DOY 243), in order to extend the range of soil and plant water potential, and transpiration observed for grapevines of this subplot. $\Psi_{\text{bulk soil}}$, Ψ_{stem} and T_{act}

measurements were logged in a datalogger (CR1000X, Campbell scientific Inc., Logan, UT, USA) (Figure 3.2).

While $\Psi_{\text{bulk soil}}$ and Ψ_{stem} were recorded every hour, sap flow measurement initial temporal resolution was 2 minutes, subsequently averaged per hour. In addition to continuous data, punctual measurements of leaf water potential (Ψ_{leaf}) were conducted regularly, at midday (between 12pm and 2pm) over the season with a pressure chamber (670 Pressure Chamber, PMS Instrument Company), on mature and healthy leaves bagged on both plastic sheet and aluminum foil at least 45 minutes before the measurements (Choné et al., 2001). Three to five leaves were measured per record.

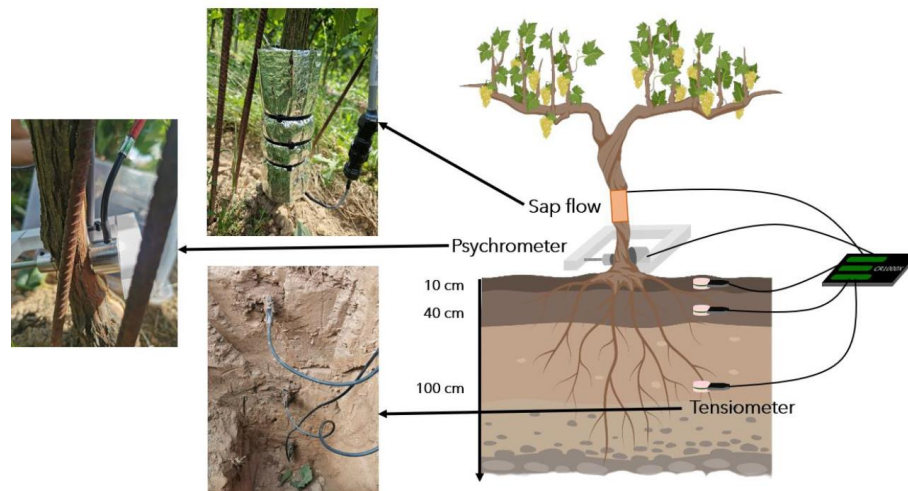


Figure 3.2 - Set-up for automatic monitoring of soil and grapevine water status. Soil matric potential (Teros21) is measured at three different depths (10 cm, 40 cm and 100 cm) and plant transpiration and stem water potential are monitored with sap flow sensors (Dynagage) and stem psychrometers (PSY1). All these sensors are logged to a CR1000X datalogger that collects the hourly data.

3. Grapevine transpiration control is soil texture specific

Estimates of hydraulic conductances

The belowground hydraulic conductance (K_{below} [$\text{cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$]), which includes the bulk soil hydraulic conductance, the soil-root interface hydraulic conductance and the root system hydraulic conductance, was calculated by analogy to Ohm's law thanks to the transpiration rate and the difference between Ψ_{stem} and Ψ_{soil} (Tsuda and Tyree, 2000) measured simultaneously:

$$K_{\text{below}}(t) = - \frac{T_{\text{act}}(t)}{\Psi_{\text{stem}}(t) - \Psi_{\text{soil}}(t)} \quad (3.1)$$

where the soil water potential (Ψ_{soil}) of the profile is the effective soil water potential felt by the plant. This soil water potential could be calculated by averaging the $\Psi_{\text{bulk soil}}$ measured at the 3 depths (down to 2 m depth), weighted by the 1D root density ($\Psi_{\text{soil}} = \Psi_{\text{soil_eff}}$) (Couvreur et al., 2012). Alternatively, this effective root-felt water potential can be inferred from the stem predawn water potential $\Psi_{\text{stem_PD}}$ assuming that soil-root interface is equilibrated with plant when $T_{\text{act}}=0$, during night ($\Psi_{\text{soil}} = \Psi_{\text{stem_PD}}$). The choice of optimal Ψ_{soil} is discussed later, in the results section. In the same way, the stem hydraulic conductance (K_{stem} [$\text{cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$]), which is the hydraulic conductance between the collar and the petiole, was calculated with the difference between Ψ_{leaf} and Ψ_{stem} , and T_{act} measured at the same moment:

$$K_{\text{stem}}(t) = - \frac{T_{\text{act}}(t)}{\Psi_{\text{leaf}}(t) - \Psi_{\text{stem}}(t)} \quad (3.2)$$

In this study, we did not measure stomatal conductance directly. Instead, we calculated a relative stomatal conductance based on the ratio between actual and potential transpiration rates $T_{\text{act}}/T_{\text{pot}}$ (Cai et al.,

2018; Jarvis and McNaughton, 1986; Koehler et al., 2022; Shaozhong et al., 2000; Shen et al., 2002). For this, the cultural coefficient K_c was calculated with the K_c -LAI relationship for grapevines described by Netzer et al., (2009) as it has already been used and validated for grapevines trained onto vertical shoot positioning (Munitz et al., 2020):

$$K_c = 0.028 * LAI^2 + 0.355 * LAI + 0.077 \quad (3.3)$$

Since LAI and K_c are grapevine-specific in our case, and do not contain inter-row information, we calculated the potential transpiration (T_{pot}) as the product between K_c and ET_0 .

3.2.4. Statistical analyses and fitting relations

We used a non-linear function, according to Muchow and Sinclair (1991), to elucidate the relations among the measured hydraulics variables (equation 3.4). For example, the relation $K_{below}(\Psi_{soil})$ was fitted with the following function:

$$K_{below} = \frac{c}{1 + \exp\left(\frac{\Psi_{soil} + a}{b}\right)}, \quad (3.4)$$

with a , b and c the fitting parameters, which rely on the measured data. Equation 3.4 was also used to fit and described the relations between T_{act}/T_{pot} and Ψ_{soil} , T_{act}/T_{pot} and Ψ_{stem} , K_{below} and Ψ_{stem} , K_{stem} and Ψ_{soil} (for CBa), K_{stem} and Ψ_{stem} (for CBa), and T_{act}/T_{pot} and K_{below} . For the subplots CBb, DWa and DWb, the relations between K_{stem} and Ψ_{soil} , and

3. Grapevine transpiration control is soil texture specific

between K_{stem} and Ψ_{soil} , were better predicted by a simple linear regression, as follows:

$$K_{stem} = a \times \Psi_{soil} + b, \quad (3.5)$$

with a and b the fitting parameters. We also assessed the statistical significance of the different relationships between the hydraulic variables with analysis of covariance (ANCOVA). We conducted these statistical analyses on the different subplots, to evaluate the impact of soil type on the different relations between hydraulic variables. We assumed that the variables exhibited approximate linear relationships for these statistical analyses (Table S.3.1). Relations between different hydraulic variables were considered statistically different for p-values less than 0.05.

3.3. Results

3.3.1. Water potentials and transpiration evolution

Soil water potential

In Figure 3.3a-d, we can see that, during the experimental period in 2022, CBa has the driest soil (more negative Ψ_{soil_eff} among the four subplots). The observed Ψ_{soil_eff} over the experimental period ranged between -0.83 and -1.09 MPa for this subplot but between -0.37 and -0.66 MPa in CBb. We can also observe that Ψ_{soil_eff} is highly dynamic in CBa. In dry soils, due to the shape of retention curve, a small

variation in water content causes a large variation of water potential. At DW vineyard, $\Psi_{\text{soil_eff}}$ of DWa decreased from -0.22 MPa to -0.67 MPa over the measurement period, while it varied between -0.19 MPa and -0.87 MPa in DWb. The soil in DWa was slightly drier than in DWb during the first two weeks, but the soil of DWb became drier after that. For each subplot, the soil was drier at the surface than at depth. Soil water potential typically decreased over time due to grapevine water uptake. Due to a higher grapevine root density at the surface, the soil dried out more quickly in the shallow horizons than in the deep ones, to reach values between -1.5 MPa and -2 MPa. At the surface, the decrease in soil water content is also due to the inter-row grass water uptake. This perennial-herbaceous association therefore also contributes to the faster drying of the surface horizons (Celette et al., 2005). During the wet period of 2023, between DOY 208 and DOY 243, $\Psi_{\text{soil_eff}}$ of the CBa subplot remained high throughout the period, varying between -0.02 MPa and -0.18 MPa (Figure S.3.5a).

It is interesting to note that, in 2022 during dry conditions, $\Psi_{\text{soil_eff}}$ is always lower (more negative) than $\Psi_{\text{stem_PD}}$, which is the stem water potential at night when transpiration should be null, and which should be equilibrated with $\Psi_{\text{soil_eff}}$. Several reasons could explain this difference, like the uncertainties on the depth of the root system or the method to interpolate or extrapolate $\Psi_{\text{bulk soil}}$ along the soil profile. This could underestimate $\Psi_{\text{soil_eff}}$, explaining why it is always lower than $\Psi_{\text{stem_PD}}$. To minimize the errors due to the different hypotheses in the estimation of $\Psi_{\text{soil_eff}}$, we will consider $\Psi_{\text{stem_PD}}$ as Ψ_{soil} for the following analyses and in the K_{below} calculation (equation 3.1). In 2023, during wet conditions, we observed similar values by comparing $\Psi_{\text{soil_eff}}$ and $\Psi_{\text{stem_PD}}$ in the CBa subplot (Figure S.3.5a).

3. Grapevine transpiration control is soil texture specific

Transpiration, stem and leaf water potential

In each subplot, three plants have been equipped with psychrometers and sap flow sensors. For both transpiration (T_{act}) and stem water potential (Ψ_{stem}), the replicates were extremely consistent, with a standard deviation of $0.0065 \text{ cm}^3 \cdot \text{s}^{-1}$ for T_{act} and of 0.05 MPa for Ψ_{stem} (Figure S.3.6). The results presented here are therefore the mean Ψ_{stem} and T_{act} of the three replicates for each subplot. Figure 3.3e-h show the evolution of hourly T_{act} measured with sap flow gauges installed at the trunk of grapevines over the experimental period in 2022. Grapevines transpired 73 L of water in CBa, 232 L in CBb, 203 L in DWa and 340 L in DWb over the measurements campaign. Grapevines start to transpire after dawn. The daily amplitude is much higher and variable for vines planted in fine-textured soil (CBb, DWa and DWb) than in sandy soil (CBa). The averaged daily peak sap flow measured during the experimental period was $0.16 \text{ cm}^3 \cdot \text{s}^{-1}$ in CBb, $0.11 \text{ cm}^3 \cdot \text{s}^{-1}$ in DWa and $0.21 \text{ cm}^3 \cdot \text{s}^{-1}$ in DWb, but only $0.04 \text{ cm}^3 \cdot \text{s}^{-1}$ in CBa. Ψ_{stem} was hourly monitored with psychrometers. Ψ_{stem} showed a diurnal pattern (Figure 3.3i-l), with minimum values corresponding to the time at which T_{pot} is maximum in each subplot. The maximum values of Ψ_{stem} are between 3am and 6am and correspond to the predawn water potential (Ψ_{stem_PD}). For the time at which T_{pot} is maximal (around midday), the average daily Ψ_{stem} observed over the experimental period were -1.05 MPa , -0.79 MPa , -0.71 MPa and -0.67 MPa for CBa, CBb, DWa and DWb respectively. In each subplot, Ψ_{leaf} followed the same time dynamic than Ψ_{stem} over the experimental period. The relationship between Ψ_{leaf} and Ψ_{stem} remained linear over the season and the slopes of the linear regressions between the two variables are statistically not different to 1 for these subplots (Figure S.3.7). This proved the reliability of Ψ_{stem} measured by psychrometers.

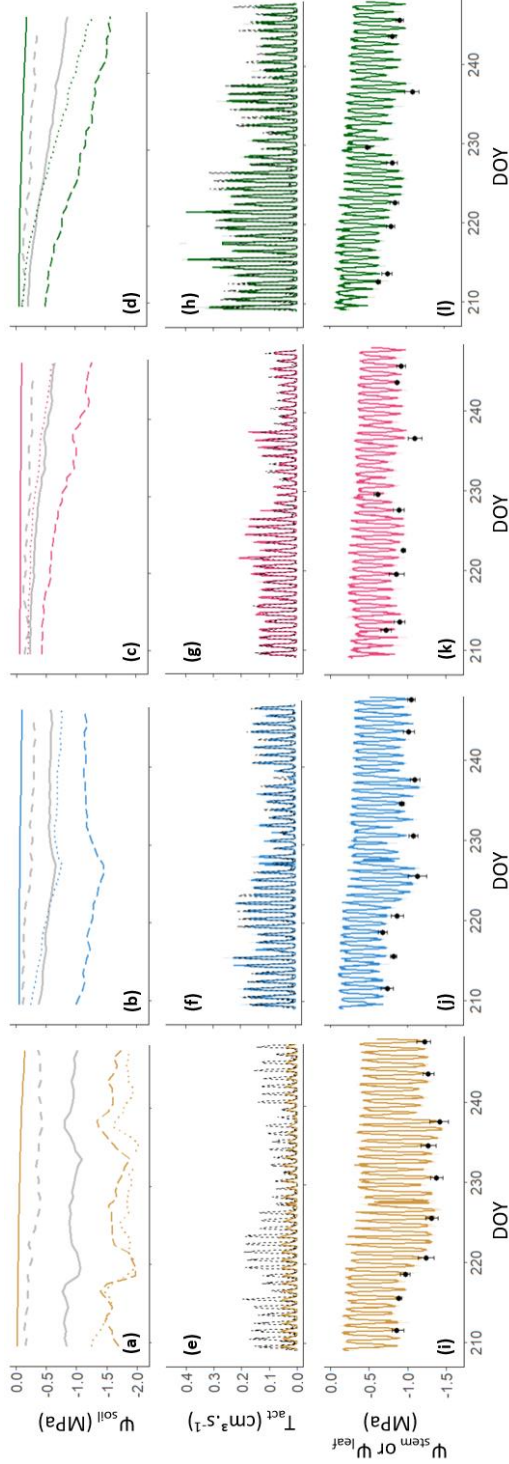


Figure 3.3 - Time series of soil water potential Ψ_{soil} (a, b, c, d), actual transpiration T_{act} (e, f, g, h) and stem (Ψ_{stem} - colored lines) and leaf (Ψ_{leaf} - black points) water potential (i, j, k, l) over the experimental period in CBa (brown) (a, e, i), CBB (blue) (b, f, j), DWa (pink) (c, g, k) and DWb (green) (d, h, l). In (a), (b), (c) and (d), the dashed colored lines, dotted colored lines and full colored lines correspond respectively to the bulk soil water potentials $\Psi_{\text{bulk soil}}$ at depths of 10 cm, 40 cm and 100 cm; the full grey lines are the root-effective soil water potentials $\Psi_{\text{soil_eff}}$, and the dashed grey lines are the predawn water potentials $\Psi_{\text{stem_PD}}$. In (e), (f), (g) and (h), the dashed black lines correspond to the potential evapotranspiration T_{pot} . In (i), (j), (k) and (l), the full colored lines are the Ψ_{stem} time series and the black points correspond to the average (error bars are the standard deviation) of Ψ_{leaf} measured punctually. The times series of T_{act} and Ψ_{stem} are an average of the 3 replicates.

3. Grapevine transpiration control is soil texture specific

3.3.2. Hydraulic conductances

Relative stomatal conductance

We used the ratio between T_{act} and T_{pot} (at peak T_{pot}) as a proxy for the relative stomatal conductance, and therefore quantify the water stress (Cai et al., 2018; Jarvis and McNaughton, 1986; Koehler et al., 2022; Shaozhong et al., 2000; Shen et al., 2002). In 2022, in CBb, DWa and DWb, we observed that T_{act}/T_{pot} slightly decreased over time, as shown in Figure 3.4, meaning that the transpiration is slightly limited by stomata at the end of the experimental period ($0.6 > T_{act}/T_{pot} > 1$). For CBa, on the other hand, T_{act}/T_{pot} had completely different values and was around 0.5 at the start of the measurement period in 2022, and around 0.25 at the end. These low value of T_{act}/T_{pot} , in CBa, present throughout the experimental period of 2022, suggest that these plants were stressed during the whole period. The stomata are partially closed during the day and limit the transpiration of the plants, which explains the limited T_{act} measured in CBa. Transpiration of grapevines was therefore significantly constrained in sandy soil due to stomatal closure, during drought conditions. During the wet period in 2023, T_{act}/T_{pot} of the CBa subplot was always close to 1 over the whole period (Figure S.3.5d). Stomata of these grapevines are therefore fully opened during this period. Measurements collected in 2023 in the CBa subplot were therefore useful to observe very different grapevine water status in this subplot for the following analyses.

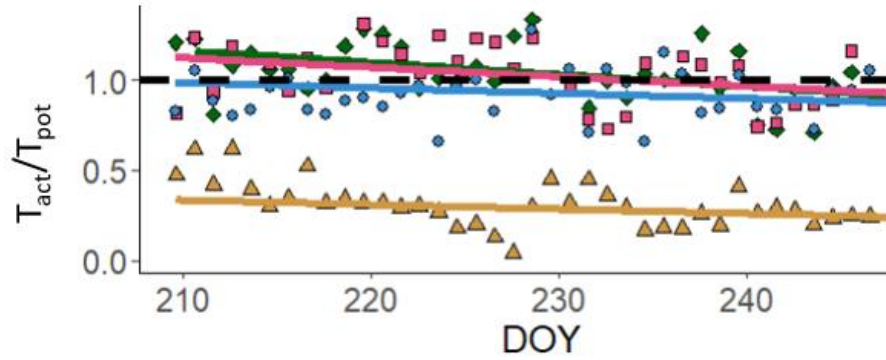


Figure 3.4 – Time series of T_{act}/T_{pot} (relative stomatal conductance) throughout the experimental period. The brown triangles and line, blue circles and line, pink squares and line, and green diamonds and line correspond respectively to the study areas CbA, CbB, DWa and DWb. Only one value of T_{act}/T_{pot} is represented per day, corresponding to the daily peak of T_{pot} . Each colored line is a linear regression of T_{act}/T_{pot} over time. The slopes of these linear regressions are slightly different from 0 ($0.01 < p\text{-value} < 0.05$), in all cases. The dotted black line is $T_{act}/T_{pot} = 1$.

Belowground and stem hydraulic conductance

Belowground hydraulic conductance (K_{below}), calculated with equation 3.1, decreased throughout the experimental period in 2022 (Figure 3.5). At the daily peak of T_{pot} (around midday) K_{below} varied between 0.39 and 0.09 $\text{cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$ in CbB, between 0.45 and 0.09 $\text{cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$ in DWa and between 0.48 and 0.11 $\text{cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$ in DWb. K_{below} was significantly lower in CbA over the whole experimental period in 2022, varying between 0.08 and 0.02 $\text{cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$, which is therefore always lower than in the other subplots. In 2023, we measured a relatively constant K_{below} of $0.26 \pm 0.04 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$ over the wet period in CbA (Figure S.3.5e), which is greater than any K_{below} measured in 2022 in

3. Grapevine transpiration control is soil texture specific

this subplot. We also punctually calculated the stem hydraulic conductance (K_{stem}) with equation 3.2. K_{stem} was relatively constant for the fine-textured subplots (CBb, DWa and DWb) over the whole experimental period (Figure 3.5). K_{stem} was $2.20 \pm 0.08 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$ in CBb, $1.16 \pm 0.09 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$ in DWa and $2.26 \pm 0.18 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$ in DWb. In CBa, K_{stem} was first relatively constant ($1.02 \pm 0.09 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$) then dropped to $0.19 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$ at DOY 237, and finally increased again to reach a value of $0.79 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$ at the end of the experimental period. In each subplot, K_{stem} was 9 to 30 times greater than K_{below} in CBa, 5 to 20 times greater in CBb, 3 to 10 times greater in DWa and 5 to 12 times greater in DWb.

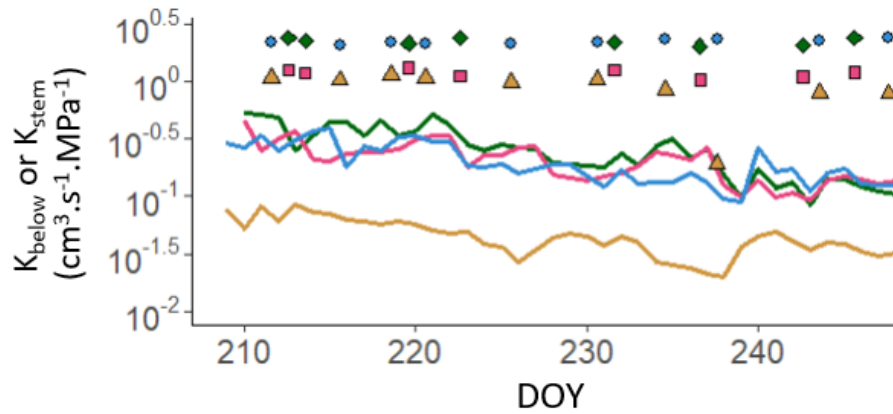


Figure 3.5 – Time series of belowground hydraulic conductance K_{below} (lines) and of stem hydraulic conductance K_{stem} (points) over the experimental period in CBa (brown line and triangles), CBb (blue line and circles), DWa (pink line and squares) and DWb (green line and diamonds). Only one value of K_{below} is represented per day, corresponding to the daily peak of T_{pot} .

3.3.3. Relation between relative stomatal conductance, soil and stem water potential

Figure 3.6 shows the relationships between Ψ_{soil} (estimated based on $\Psi_{\text{stem_PD}}$) and $T_{\text{act}}/T_{\text{pot}}$, and between Ψ_{stem} and $T_{\text{act}}/T_{\text{pot}}$. These illustrate how stomatal regulation was affected by soil and stem water potentials. These relationships are statistically similar between the subplots CBb, DWa and DWb (p-value > 0.05; Table S.3.1); data of these subplots were therefore assembled for the analyses. The observed reductions in relative stomatal conductance ($T_{\text{act}}/T_{\text{pot}}$) as Ψ_{soil} and Ψ_{stem} decreased fit well with the empirical equations (equation 3.4), particularly for the sandy subplot (CBa). Significant differences between the soil textures became apparent as the soil dried out. When comparing coarse-textured soil (CBa) and fine-textured soils (CBb, DWa and DWb), the decline of $T_{\text{act}}/T_{\text{pot}}$ happened at less negative Ψ_{soil} for CBa ($\Psi_{\text{soil}} = -0.10$ MPa) than for the other subplots ($\Psi_{\text{soil}} = -0.30$ MPa) (Figure 3.6a). The confidence interval of the observations and empirical predictions do not overlap between the fine-textured (CBb, DWa and DWb) and coarse-textured (CBa) soils, particularly for lower Ψ_{soil} . This suggests that grapevine stomatal response to soil drying was significantly impacted by soil texture. The relationship between Ψ_{stem} and $T_{\text{act}}/T_{\text{pot}}$ was also greatly impacted by soil textures. As with the relationship between $T_{\text{act}}/T_{\text{pot}}$ and Ψ_{soil} , the statistical analysis revealed that the relationship between $T_{\text{act}}/T_{\text{pot}}$ and Ψ_{stem} is significantly influenced by the soil texture, with significant differences (p-value < 0.001 – Table S.3.1) between the fine-textured subplots (CBb, DWa and DWb) and the coarse-textured subplot (CBa). There was no difference between the three fine-textured subplots (p-value > 0.05). In CBa, $T_{\text{act}}/T_{\text{pot}}$ started to decrease when Ψ_{stem} was around -0.50 MPa, while it decreased at $\Psi_{\text{stem}} \approx -1.00$ MPa in the loamy subplots (CBb, DWa and DWb) (Figure 3.6b).

3. Grapevine transpiration control is soil texture specific

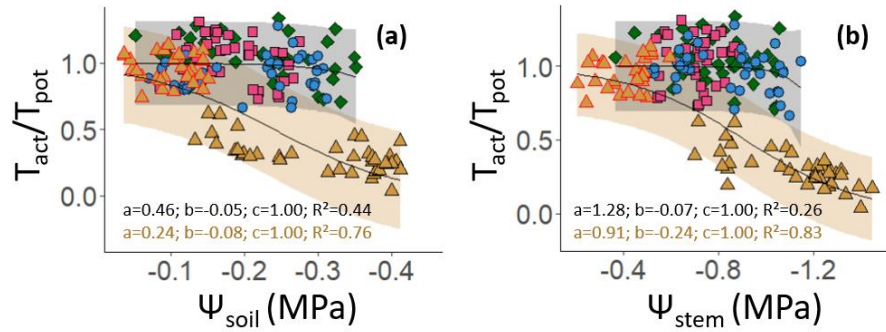


Figure 3.6 – Relationships between (a) Ψ_{soil} and T_{act}/T_{pot} and (b) Ψ_{stem} and T_{act}/T_{pot} . The brown triangles, blue circles, pink squares and green diamonds correspond respectively to the subplots CBa, CBb, DWa and DWb. The brown triangles surrounded in red are data collected in 2023 in CBa. The relationships were fitted with 95% functional prediction intervals (shaded area). The fitted parameters (a, b and c) in equation 3.4 and the fitting coefficient (R^2) are given in the plots. Points corresponding to CBb, DWa and DWb have been assembled to predict the relationships between T_{act}/T_{pot} with Ψ_{soil} and Ψ_{stem} since these relationships are not different between these subplots (p-value > 0.05 – Table S.3.1). Ψ_{soil} is equivalent to Ψ_{stem_PD} .

3.3.4. Relation between belowground and stem hydraulic conductance with soil and stem water potential

Relation between K_{below} and Ψ_{soil} was well described by equation 3.4 and was significantly affected by soil texture. Subplots CBb, DWa and DWb showed similar relations (p-value > 0.05; Table S.3.1), but CBa showed a statistically different relationship (p-value < 0.001). In wet soil conditions, K_{below} was relatively stable across fine-textured (CBb,

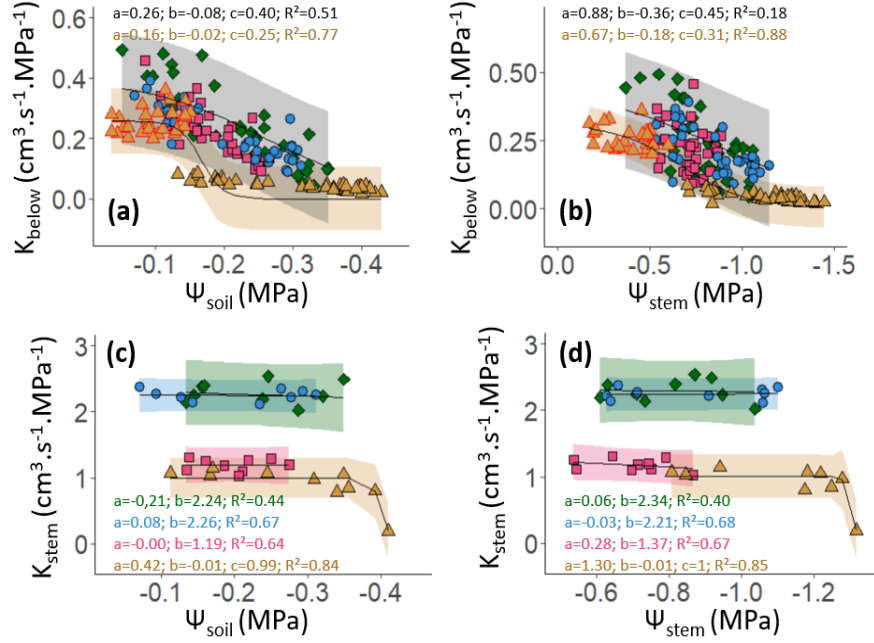


Figure 3.7 – Relationships between (a) Ψ_{soil} and K_{below} , (b) Ψ_{stem} and K_{below} , (c) Ψ_{soil} and K_{stem} and (d) Ψ_{stem} and K_{stem} . The brown triangles, blue circles, pink squares and green diamonds correspond respectively to the subplots CBA, CBb, DWa and DWb. The brown triangles surrounded in red are data collected in 2023 in CBA. The relationships were fitted with 95% functional prediction intervals (shaded area). The fitted parameters (a , b and c in equation 3.4; a and b in equation 3.5) and the fitting coefficient (R^2) are given in the points. In (a) and (b), points corresponding to CBb, DWa and DWb have been assembled to predict the relationships between K_{below} and Ψ_{soil} , and between K_{below} and Ψ_{stem} , since these relationships are not different between these subplots (p -value > 0.05 – Table S.3.1). In (c) and (d), the relations between K_{stem} and Ψ_{soil} , and K_{stem} and Ψ_{stem} , are better predicted by a simple linear regression (equation 3.5) for CBb, DWa and DWb subplots. The slopes of these linear regressions are not statistically different from 0 (Table S.3.2). Ψ_{soil} is equivalent to $\Psi_{\text{stem_PD}}$.

DWa, DWb; $K_{\text{below}} = 0.40 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$) and coarse-textured soils (CBA; $K_{\text{below}} = 0.25 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$). In each case, K_{below} decreased as the soil dried out (Figure 3.7a), with a sharper decline in the sandy subplot

3. Grapevine transpiration control is soil texture specific

(CBa) than in the loamy subplots (CBb, DWa and DWb). Ψ_{stem} also decreased with K_{below} (Figure 3.7b). However the confidence interval of the measurements and predictions overlap, the relation between K_{below} and Ψ_{stem} was less significantly different (compared to other relations) between subplots ($0.01 < p\text{-value} < 0.05$; Table S.3.1), particularly by comparing the loamy subplots (CBb, DWa and DWb) with the sandy subplot (CBa), and the decline was similar in coarse-textured and fine-textured soils. Stem hydraulic conductance (K_{stem}) was constant in CBb, DWa and DWb despite the drying out of the soil. The slopes of the linear regressions between Ψ_{soil} and K_{stem} of these subplots are not statistically different from 0 (Figure 3.7c and Table S.3.2). For CBa, K_{stem} remained constant ($1.02 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$) until Ψ_{soil} was -0.39 MPa and then dropped to $0.19 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$ (Figure 3.7c). The lowest value of K_{stem} was measured when Ψ_{stem} was -1.32 MPa (Figure 3.7d). The decrease of K_{stem} in CBa could be due to xylem cavitation between the collar and the petioles. This value corresponds to the one measured by Lamarque et al., (2023), who started to observe embolism on Chardonnay stem at $\Psi_{\text{stem}} = -1.3 \text{ MPa}$. Since K_{stem} remained constant in CBb, DWa and DWb, this suggests that there was not xylem cavitation for grapevines in these subplots.

3.3.5. Relation between relative stomatal conductance and belowground hydraulic conductance

The relation between the relative stomatal conductance ($T_{\text{act}}/T_{\text{pot}}$) and K_{below} was well characterized by equation 3.4 in the different soil types. The relations were statistically similar ($p\text{-value} > 0.05$; Table S.3.1) in the fine-textured subplots (CBb, DWa, and DWb), but different ($p\text{-value} < 0.001$) for the sandy subplot (CBa). Although we observed a sharper decline of $T_{\text{act}}/T_{\text{pot}}$ in sandy subplot (CBa) than in loamy ones (CBb, DWa and DWb), the stomatal closure was triggered at the same K_{below} for each subplot, around $0.17 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$ (Figure 3.8).

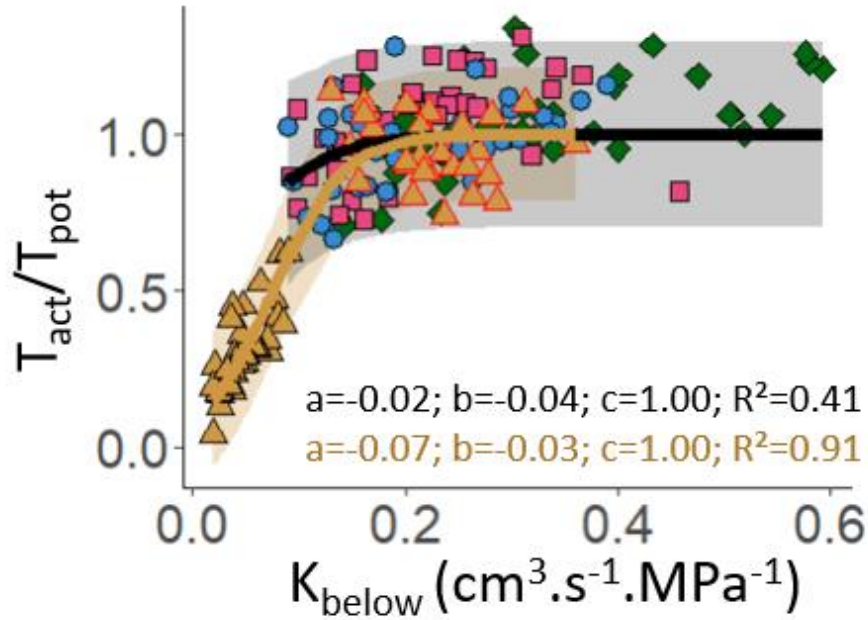


Figure 3.8 – Relationships between K_{below} and T_{act}/T_{pot} . The brown triangles, blue circles, pink squares and green diamonds correspond respectively to the subplots CBa, CBb, DWa and DWb. The brown triangles surrounded in red are data collected in 2023. The relationships were fitted (brown line for CBa, black line for CBb, DWa and DWb) with 95% functional prediction intervals (shaded area). The fitted parameters (a , b and c in equation 3.4) and the fitting coefficient (R^2) are given in the points. Points corresponding to CBb, DWa and DWb have been assembled to predict the relation between K_{below} and T_{act}/T_{pot} since this relationship is not statistically different between these subplots (p -value > 0.05 – Table S.3.1).

3.4. Discussion

The interplay between stem and belowground hydraulics is complex and their exact roles in regulating transpiration for *in situ* plants are still not fully comprehended. To assess *in situ* soil-grapevine water relations

3. Grapevine transpiration control is soil texture specific

during drought, we measured and quantified simultaneously the relative stomatal conductance, stem hydraulic conductance, and belowground hydraulic conductance on grapevines planted on different soil types. In the subsequent section, we discuss the dominant role of belowground hydraulics on grapevine transpiration control.

3.4.1. Transpiration control is induced by belowground hydraulics in drought conditions

Our comprehension of the hydraulic interactions between the soil and the plants was still limited *in situ*, particularly due to the difficulty to accurately quantify belowground hydraulics in the field (Fichtl et al., 2023). By simultaneously measuring the relative stomatal conductance, the stem hydraulic conductance and the belowground hydraulic conductance of soil-grapevine systems in different edaphic conditions, we present in this study experimental evidence that, during drought, the stomatal regulation of *in situ* grapevines is mainly governed by belowground hydraulics (i.e. soil and root hydraulics), instead of aboveground hydraulics (i.e. stem xylem cavitation). The results substantiated our hypothesis that grapevine hydraulic responses varied to varying soil texture and hydraulic properties. In this study, while grapevines were of the same variety (Chardonnay), had deep root systems and experienced same meteorological conditions, we observed different transpiration rates and relative stomatal conductance depending whether the grapevines were planted on coarse-textured (CBa) or fine-textured soils (CBb, DWa and DWb). While all plants had the same canopy variety (Chardonnay), the downregulation of T_{act} occurred at contrasted soil water potential. This stomatal downregulation occurred at more negative soil matric potential in loamy subplot (CBb, DWa and DWb; $\Psi_{soil} = -0.30$ MPa) than in sand (CBa; $\Psi_{soil} = -0.10$ MPa). Moreover, a steeper drop in stomatal conductance was observed in coarse-textured soil compared to fine-

textured ones (Figure 3.6). By fitting the relation between K_{below} and the relative stomatal conductance ($T_{\text{act}}/T_{\text{pot}}$), we observed that the stomatal closure was triggered at the same K_{below} for each subplot and each soil texture (Figure 3.8; $K_{\text{below}} = 0.17 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$). This finding proves that *in situ* grapevines coordinate mechanisms between plant hydraulic status (e.g. stomatal regulation) and longer-term growth. It has been demonstrated that the decrease of shoot:root ratio is a mid-to-long term adaptive mechanism to drought by decreasing transpiration (less canopy surface) and increasing belowground conductance (more root surface) (Carminati and Javaux, 2020). In this study, we measured lower LAI (Table 3.1), which is directly proportional to the total canopy area of grapevines (Vitali et al., 2013), in the sandy subplot than in loamy subplots. By dividing T_{act} by T_{pot} , this allowed to eliminate the effect of the canopy surface on the transpiration rate, since LAI was used to calculate K_c (equation 3.3), which was used to calculate T_{pot} . Therefore, the fact that $T_{\text{act}}/T_{\text{pot}}$ started to decrease at the same K_{below} , independently of the soil texture, showed that the plant also adjusts its root system to the soil texture. While we measured root system depth in each subplot down to 2 m, we can hypothesize that the root system is deeper in CBa than in the other subplots. Other studies observed the influence of soil texture on root system growth, with deeper root systems in sandy than in loamy soil for a same variety and same rootstock (Nagarajah, 1987; Ollat et al., 2015). Moreover, during drought conditions, we observed a bigger difference between $\Psi_{\text{soil_eff}}$ and $\Psi_{\text{stem_PD}}$ in the sandy subplot (CBa) than in the loamy subplots (CBb, DWa and DWb), suggesting that grapevine in the sandy subplot have a longer root system than in the loamy subplots, exploring deeper and wetter soil horizons. This statement is discussed in more detail in the next section. All these observations bolster the fact that grapevines adapt their shoot:root ratio to the soil texture. They adapt their structure to match the fine equilibrium between the atmospheric water demand (e.g. by adapting the canopy surface) and the soil water offer (e.g. by adapting the root system architecture), which lead to onset of stomatal closure at the same K_{below} , irrespective of soil texture. These belowground and aboveground adjustments, which are considered crucial responses and significant adaptive strategies against drought (Alsina et al., 2011), should therefore be soil texture specific. For

3. Grapevine transpiration control is soil texture specific

example, grapevines planted in a sandy soil will relatively invest more carbon into root growth than into canopy growth, compared to grapevines planted in a loamy soil.

We quantified and showed that, during a drought period, the hydraulic conductance between the collar stem and the leaves (K_{stem}) was always significantly greater than the hydraulic conductance between the soil and the collar stem (K_{below}) in each subplot. K_{below} was therefore the limiting factor for the total conductance of the SPAC, since the component in the SPAC with the lowest conductance exerts the greatest control on the overall system conductance (Draye et al., 2010). Moreover, K_{stem} was constant over the whole drought period in the loamy subplots (CBb, DWa and DWb), indicating that there was no xylem cavitation in these subplots. While we can assume that we observed xylem cavitation in the sandy subplot (CBa) by measuring a decrease of K_{stem} , the lower relative stomatal conductance (lower $T_{\text{act}}/T_{\text{pot}}$) in this subplot was measured before this drop of K_{stem} . Therefore, our results showed that stomatal closure was not triggered by stem xylem cavitation for *in situ* grapevines. This is in line with the study of Alsina et al. (2007), which measured that Chardonnay lost 50 % of stem hydraulic conductance due to embolism for a stem water potential of -2.27 MPa. We never measured such a low Ψ_{stem} . They suggested that xylem cavitation was therefore not responsible of stomatal closure of Chardonnay. Other studies claimed that the limitation of transpiration in grapevine due to stomatal closure was not the result of xylem cavitation or to decline in leaf hydraulic conductance in other grape varieties (Hochberg et al., 2017a; Charrier et al., 2018; Albuquerque et al., 2020; Corso et al., 2020).

Recent works, conducted under controlled laboratory conditions, emphasize the role of belowground hydraulics in triggering stomatal closure during drought, including changes in the hydraulic conductance of roots, soil, and their interface. The literature suggests that a decrease in soil matric potential induces stomatal closure, resulting in a reduction in transpiration rate (Abdalla et al., 2022; Carminati and Javaux, 2020;

Koehler et al., 2022; Rodriguez-Dominguez and Brodribb, 2020). Both soil water potential and soil hydraulic conductivity are recognized as key factors influencing water supply to the root system. In wet soils, root hydraulic conductivity mainly controls water flow in the belowground part of the soil-grapevine system, but as the soil dries out, its hydraulic conductivity drops significantly, limiting the water flow towards the soil-root interface and leading to a decrease in maximum transpiration rate as the plant cannot meet evaporative demand (Gardner, 1960; Passioura, 1980). Cai et al. (2022) observed that, during soil drying, the decline in soil hydraulic conductivity led to a steep and nonlinear reduction in soil matric potential at the soil-root interface, with greater reduction in sandy soils compared to loamy soils. In sandy soil, a small reduction in matric potential implies a much larger decrease of hydraulic conductivity compared to loamy soil (Figure S.3.1). This more rapid decline in soil hydraulic conductivity implies that the soil is more rapidly limiting (at less negative soil water potential), triggering earlier stomatal closure. This is consistent with our results, for which T_{act}/T_{pot} started to decrease at a less negative Ψ_{soil} in CBa. This also explains the steeper decrease of T_{act}/T_{pot} in this subplot. Stomatal control of *in situ* grapevine during drought is therefore soil texture specific. Stomatal regulation is amplified in sandy profile as compared to finer texture profile within the same grape variety. Recently, a mechanistic soil-plant hydraulic model predicted that stomata close when the soil water potential around the roots decreases more rapidly than the increase in transpiration in drying soil, preventing further decreases in water potential at the soil-root interface and protecting the plant against early xylem embolism (Carminati and Javaux, 2020). This model therefore predicted that the downregulation of transpiration differs between soil textures, which is consistent with our results.

The decrease of K_{below} and stomatal closure could also be due to xylem cavitation in the root system. However, root xylem embolism was observed at water potential of -1.8 MPa in fine roots and -3.5 MPa in coarse roots (Cuneo et al., 2016). We never observed such low plant water potentials, it is thus reasonable to say that there was little or no

3. Grapevine transpiration control is soil texture specific

cavitation in the root xylem in our case. However, these values are certainly rootstock specific (Cuneo et al., 2021; Lamarque et al., 2023). Given the great similarity of the rootstocks used in this study, it seems normal to see no effect of rootstock on the hydraulic behavior of Chardonnay. Moreover, statistical analysis conducted on the main ecophysiological parameters, including water potentials and gas exchanges, revealed that the soil effect outweighed the plant effect (Tramontini et al., 2014; Van Leeuwen et al., 2018). However, it would be interesting to study the effect of the soil-rootstock combination for rootstocks with very contrasting characteristics, since it has already been shown that rootstock controls the grapevine hydraulic response of water stress in a same soil type (Tramontini et al., 2013b). For example, the comparison between a short and a long root system would be interesting, as we could expect that long root systems limit the drop of water potential at the soil-root interface compared to a short root system (Abdalla et al., 2022), and therefore impact stomatal control of *in situ* plants.

3.4.2. Difference between $\Psi_{\text{soil_eff}}$ and $\Psi_{\text{stem_PD}}$ during drought

The predawn water potential ($\Psi_{\text{stem_PD}}$) is an indicator used in viticulture to quantify the water status of the plant and the soil (Choné et al., 2001; Gaudillère et al., 2002; Tosin et al., 2021). In fact, it has been shown that $\Psi_{\text{stem_PD}}$ should be, in principle, equal to $\Psi_{\text{soil_eff}}$ when transpiration is null (Hinckley et al., 1978, Couvreur, 2013). In this study, when conditions are dry, we always measured a greater (less negative) $\Psi_{\text{stem_PD}}$ than the $\Psi_{\text{soil_eff}}$, for each subplot and during the whole experimental period (Figure 3.3). The gap became wider as the soil dried out (Figure S.3.8). In theory, plants do not transpire at predawn hours. Several studies have shown that a disequilibrium between $\Psi_{\text{soil_eff}}$ and $\Psi_{\text{stem_PD}}$ might exist due to a non-equilibrium between bulk soil and

soil root interface and/or to night-time transpiration, even low, reducing $\Psi_{\text{stem_PD}}$ and disconnecting it from $\Psi_{\text{soil_eff}}$ (Donovan et al., 2001; Groenvelde et al., 2023; Kangur et al., 2017). In this work, we observed the opposite. Améglio et al. (1999) already observed that $\Psi_{\text{stem_PD}}$ tended to equilibrate with the water potential of the most humid soil zones rather than with $\Psi_{\text{soil_eff}}$, and therefore $\Psi_{\text{stem_PD}}$ was greater (less negative) than $\Psi_{\text{soil_eff}}$. Root density measurements were taken to a depth of 2 m, corresponding to the depth of the pits. In each subplot, we counted root impacts up to 2 m depth (Figure S.3.2). As a result, the root system of grapevines may be more than 2 m deep, exploring soil layers with higher water potential. By converting $\Psi_{\text{soil_eff}}$ in water content with the water retention curves (Figure S.3.1), we observed, throughout the experimental period in 2022, a variation of 51 L, 136 L, 165 L and 303 L on the 2 m soil profile, on CBa, CBb, DWa and DWb respectively. However, on the same period, the grapevines transpired 73 L of water in CBa, 232 L in CBb, 203 L in DWa and 340 L in DWb. Thus, there is a difference of 22 L, 96 L, 38 L and 37 L respectively in CBa, CBb, DWa and DWb. The plants therefore transpired more water than was lost over 2 m of soil, in each subplot. Given the value of soil hydraulic conductance at the suction level observed in this study, capillary rise cannot explain the large difference between transpiration and variation of soil water content. By considering the same $\Psi_{\text{bulk soil}}$ between 1 m and 2 m depth, we calculated a capillary rise of 4.5 L, 1.4 L, 4.6 L and 2.9 L over the experimental period. This suggests that grapevines take up water from a depth of over 2 m, and therefore have a longer root system than measured. The difference between $\Psi_{\text{soil_eff}}$ and $\Psi_{\text{stem_PD}}$ is significantly greater for CBa (sandy soil), compared to the other subplots. Several studies have shown that root proliferation are deeper in coarse-textured soils compared to fine-textured soils (Nagarajah, 1987; Van Leeuwen et al., 2004a; Lovisolo et al., 2016). It is therefore possible that the root system of grapevines in CBa is deeper than those in CBb, DWa and DWb, explaining the biggest difference in the sandy subplot.

Since the $\Psi_{\text{bulk soil}}$ was measured down to 1 m, $\Psi_{\text{soil_eff}}$ was calculated by considering a constant $\Psi_{\text{bulk soil}}$ between 1 m and 2 m depth. However,

3. Grapevine transpiration control is soil texture specific

it is generally observed that $\Psi_{\text{bulk soil}}$ increases with depth (Domec et al., 2012; Ewers et al., 2000; Sperry et al., 1998). Moreover, given the low root density at depth, this may be underestimated with the trench profile method (Vansteenkiste et al., 2014), thus underestimating the contribution of root density and $\Psi_{\text{bulk soil}}$ between 1 m and 2 m in the calculation of $\Psi_{\text{soil_eff}}$.

Furthermore, it has been shown that in dry soil conditions, roots shrink and lose contact with the soil as gaps formed between the roots and the soil (Carminati et al., 2009). Since the soil surface in each subplot is very dry, soil-root air gaps may have formed in these horizons, where root density is also higher. As a result, the roots, even if less dense, only feel the wettest horizons of the soil (Couvreur et al., 2014), contributing to the fact that the $\Psi_{\text{stem_PD}}$ is greater (less negative) than $\Psi_{\text{soil_eff}}$. These assumptions of deeper root systems (> 2 m) and soil-root air gap formation in dry horizons allow the plant to not reach very negative water potential (Zheng et al., 2019) and could explain why *in situ* grapevines remained within a safe margin range of water potential (> -1.5 MPa) (Charrier et al., 2018; Gambetta et al., 2020a). All these reasons justify the use of $\Psi_{\text{stem_PD}}$ instead of $\Psi_{\text{soil_eff}}$ as Ψ_{soil} in the different analyses and in the calculation of K_{below} .

It would be interesting to observe variations in soil water potential, due to water uptake, at greater depths during drought. Deep root systems are difficult to quantify, and observation methods are often destructive and limited in depth. Currently, other reliable methods to detect deep roots are used, such as water isotope quantification (Savi et al., 2018) or 3D soil tomography (Zhu et al., 2014). However, knowledge of root distribution alone is not enough, as we know that water uptake is rarely uniform along the root system (Mapfumo et al., 1994). Functional-structural root soil models integrate the nonuniformity of root and soil properties (Javaux et al., 2008), but the distribution of radial and axial hydraulic conductivities along the root system must be known, which is difficult to measure under *in situ* conditions. Electrical methods such as mise-à-la-masse method are promising for good quantification of

root structure and functioning, particularly for the active root density in the ground (Mary et al., 2018), but future developments are needed to get more accurate and reliable results with this method.

3.5. Conclusion and perspectives

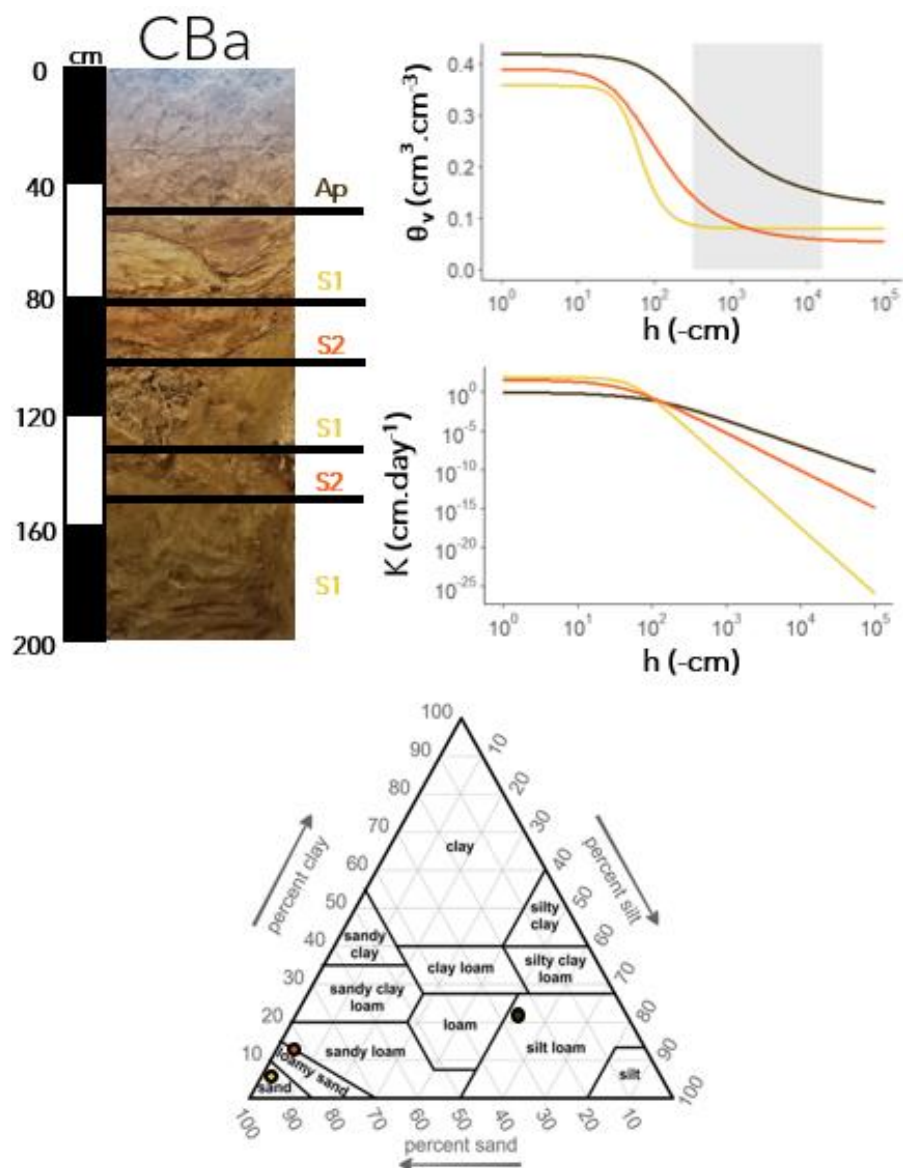
To investigate how belowground and stem hydraulics are involved on the transpiration regulation of *in situ* grapevine, we simultaneously quantified the relative stomatal conductance, stem hydraulic conductance and belowground hydraulic conductance of grapevine planted in different soil types during drought. Taken together, these concomitant measurements demonstrated that stomatal response of grapevine was triggered by a decrease of belowground hydraulic conductance, but not by xylem cavitation in the stem. Although we found that the relation between relative stomatal conductance and soil water potential of *in situ* grapevine is soil texture specific, with stomata started to close at less negative soil water potential in sandy ($\Psi_{\text{soil}} = -0.10$ MPa) than in loamy soil ($\Psi_{\text{soil}} = -0.20$ MPa), we observed that the onset of stomatal closure was triggered at the same K_{below} ($0.17 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$), independently of the soil texture. These findings show that *in situ* plants coordinate short-term hydraulic mechanisms (e.g. stomatal regulation) and longer-term growth (e.g. shoot:root ratio). These short- and long-term adjustments of *in situ* plants are crucial and significant adaptive strategies against drought conditions, and are therefore soil texture specific. Considering the dynamic properties of the rhizosphere is essential and critical for a comprehensive understanding of soil-plant hydraulic dynamics, to enhance predictions of how *in situ* plants respond to climate for different edaphic conditions. Simultaneous measurements of meteorological conditions, soil and plant water potentials, transpiration rates and root architecture can be used in physically based soil-plant hydraulic model (Vanderborght et al., 2023) to reveal the relative importance of bulk soil, soil-root interface, soil-

3. Grapevine transpiration control is soil texture specific

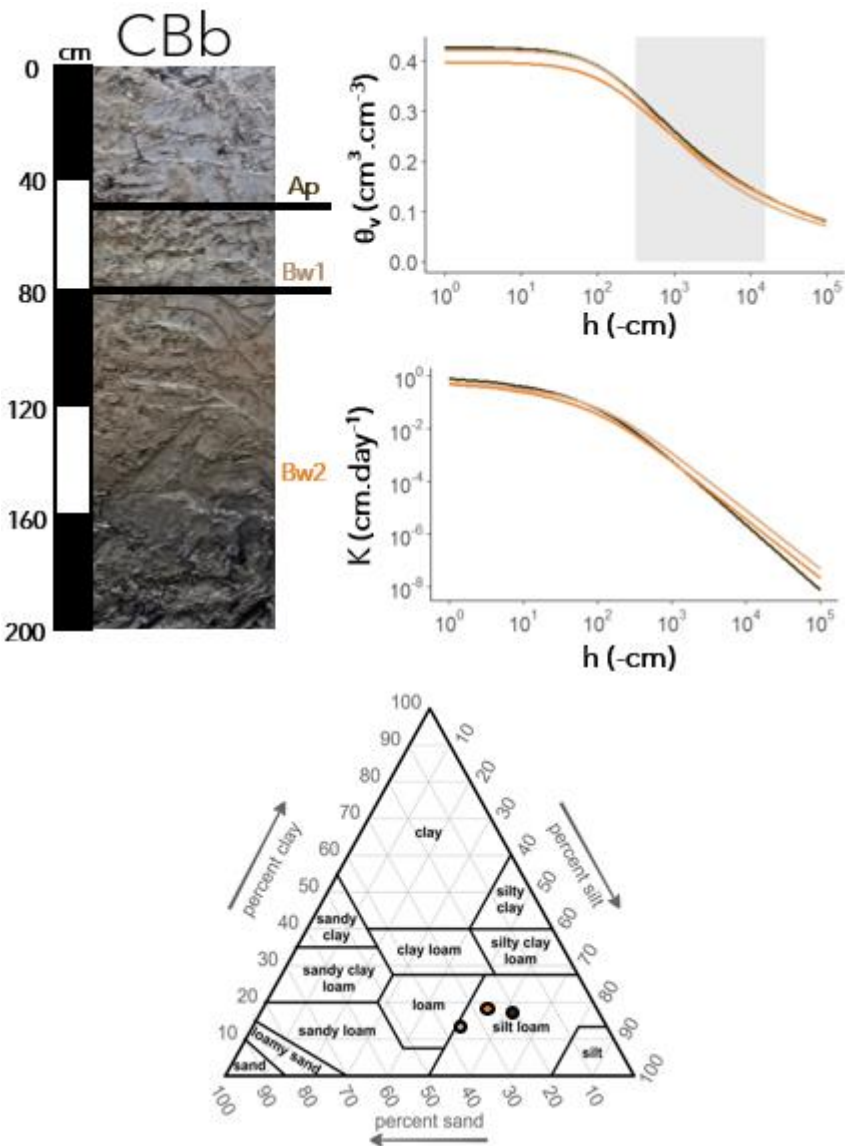
root air gaps, root and xylem vulnerability to the hydraulic operation of *in situ* grapevines. Further investigations must be done in this sense to gain a mechanistic understanding of the hydraulic functioning of complex soil-grapevine systems.

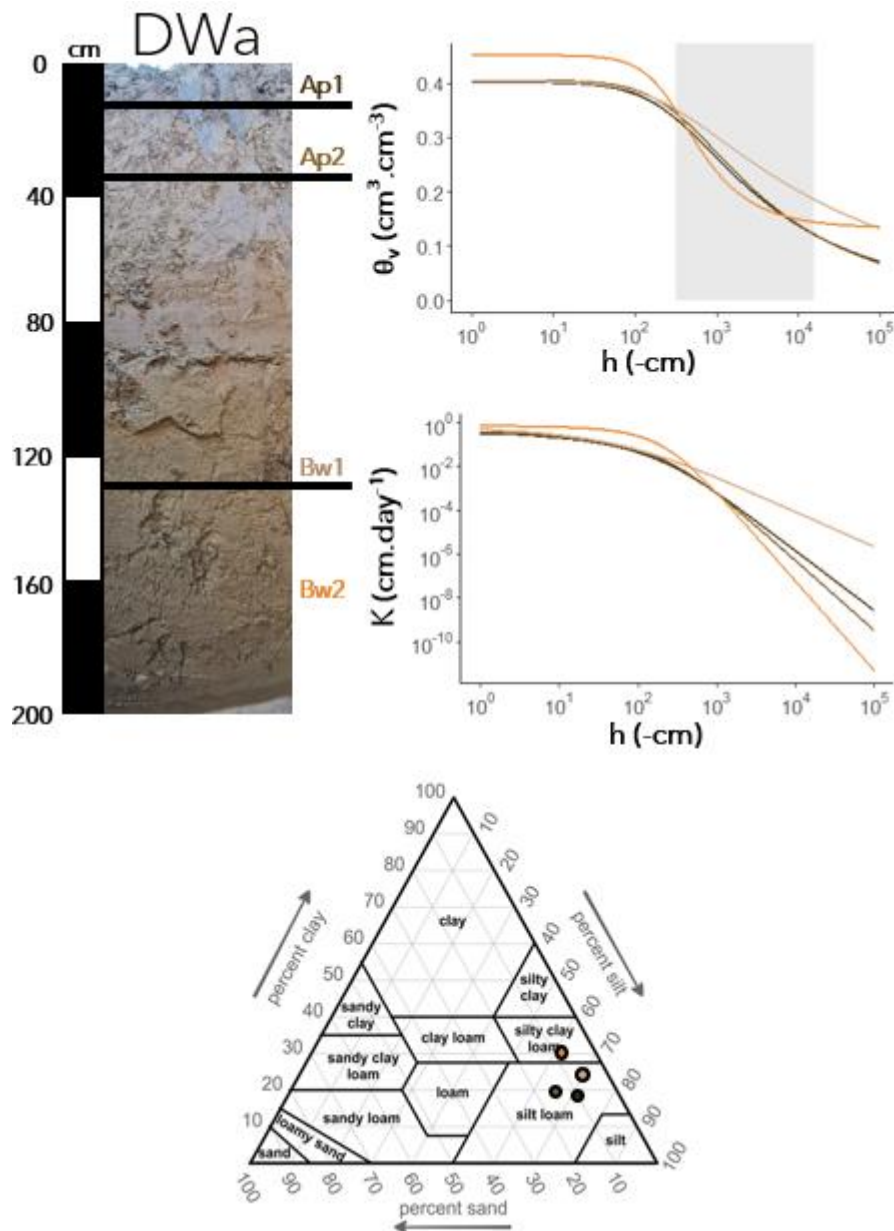
3.6. Supplementary material

3.6.1. Supplementary figures



3. Grapevine transpiration control is soil texture specific





3. Grapevine transpiration control is soil texture specific

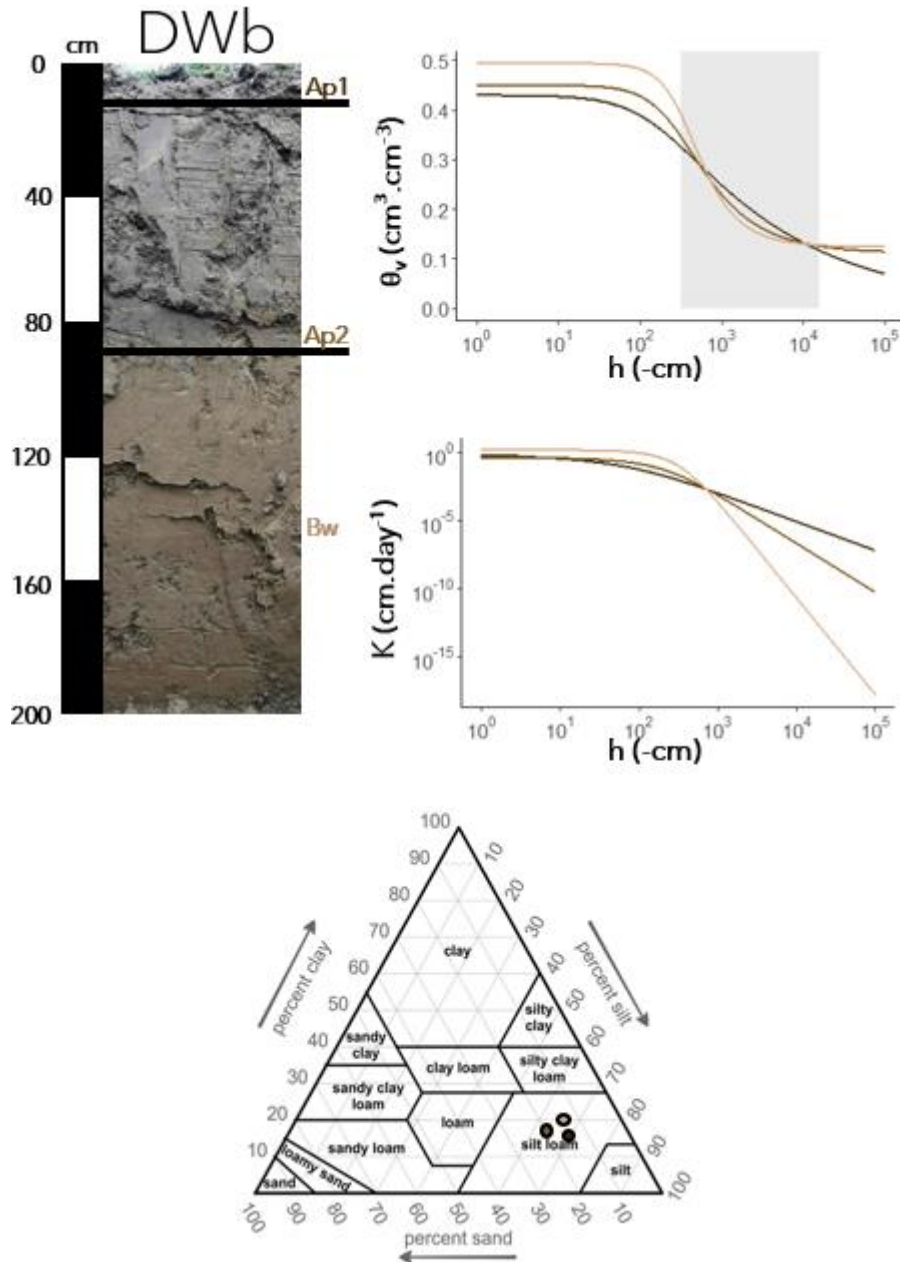


Figure S.3.1 – Delineation of soil profile horizons, their unsaturated hydraulic properties (water retention curve and hydraulic conductivity curve) and their textural class for each subplot.

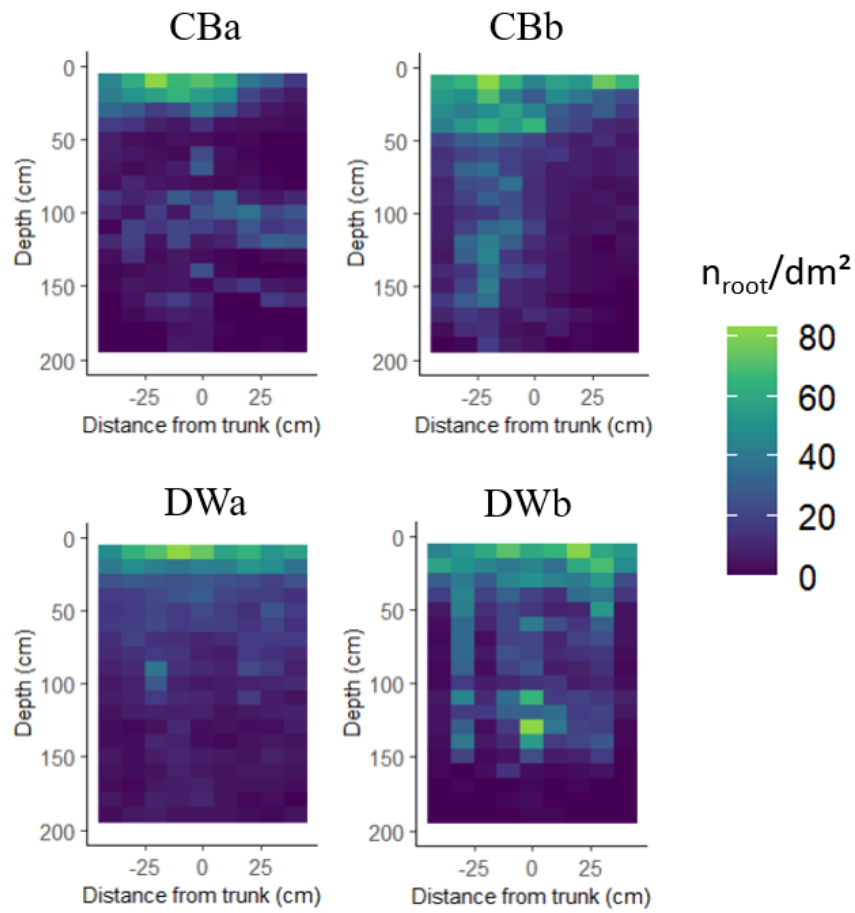


Figure S.3.2 – 2D grapevine fine root density up to 2 m deep in each subplot.

3. Grapevine transpiration control is soil texture specific

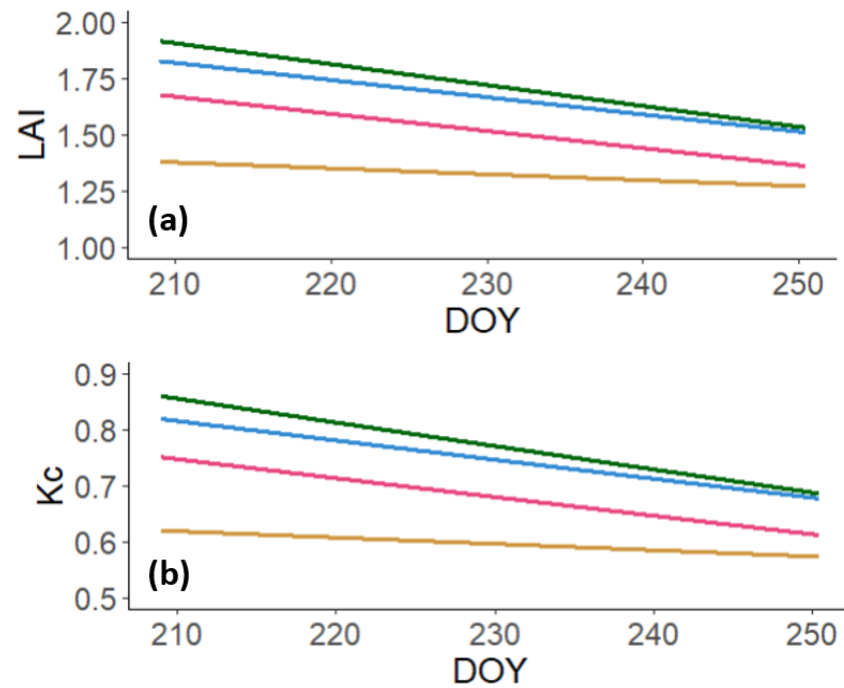


Figure S.3.3 – **(a)** Time series of leaf area index (LAI) in each subplot. The LAI was measured the DOY 208 and DOY 250. LAI is linearly interpolated between these two dates. **(b)** Time series of cultural coefficient (Kc) estimated with the Kc-LAI relationship described by Netzer et al., (2009). The brown, blue, pink and green lines correspond respectively to the subplots CBa, CBb, DWa and DWb.

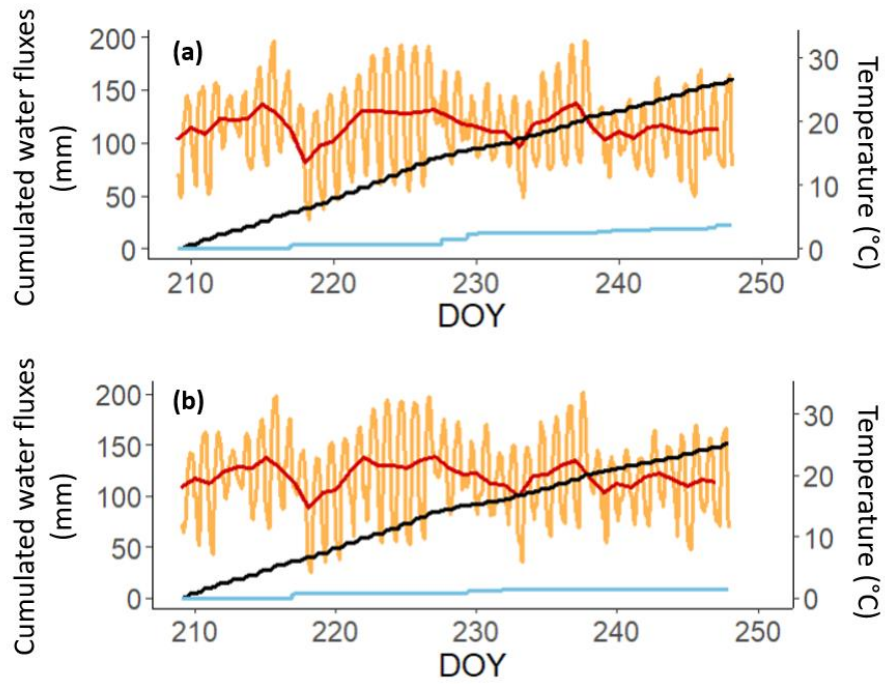


Figure S.3.4 – Cumulated precipitation (mm, blue), cumulated reference evapotranspiration (mm, black), hourly mean temperature (°C, orange) and daily mean temperature (°C, red) during the measurement campaign at (a) CB and (b) DW vineyards.

3. Grapevine transpiration control is soil texture specific

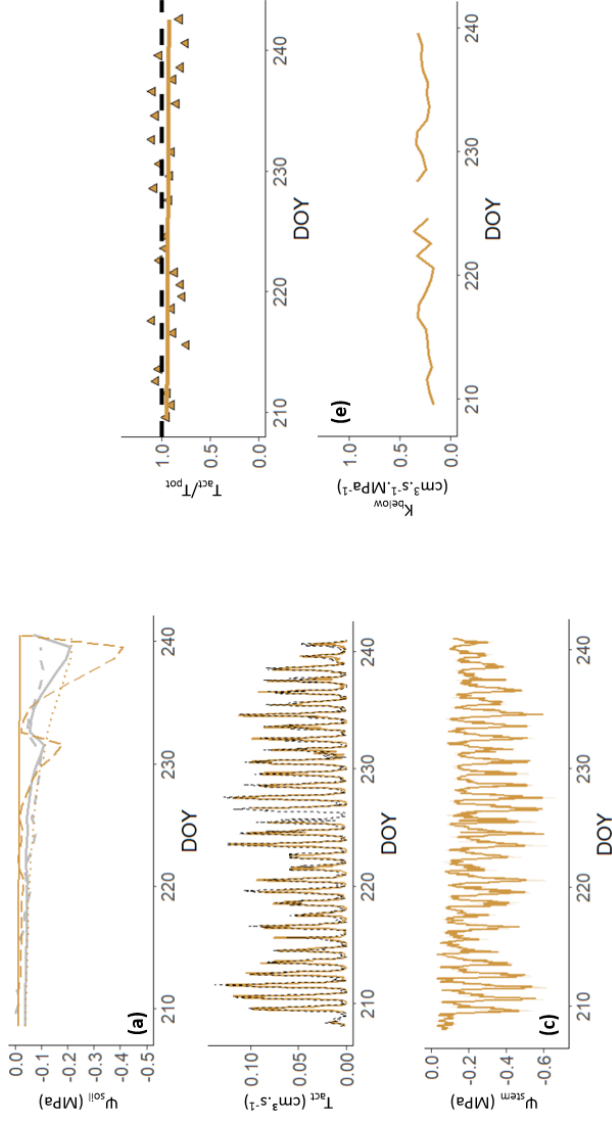


Figure S.3.5 – Time series of (a) soil water potential Ψ_{soil} , (b) actual transpiration T_{act} , (c) collar water potential, (d) $T_{\text{act}}/T_{\text{pot}}$ and (e) belowground hydraulic conductance K_{below} over the 2023 wet experimental period in the CBa subplot. In (a), the dashed brown line and full brown line correspond respectively to the bulk soil water potentials $\Psi_{\text{bulk soil}}$ at depths of 10 cm, 40 cm and 100 cm; the full grey line is the root-effective soil water potential $\Psi_{\text{soil eff}}$ and the dashed grey line is the predawn water potential $\Psi_{\text{stem PD}}$. In (d) and (e), only one value is represented per day, corresponding to the daily peak of T_{pot} . In (d), the dotted black line is $T_{\text{act}}/T_{\text{pot}} = 1$; the brown full line is the linear regression of $T_{\text{act}}/T_{\text{pot}}$ over time. The slope of this linear regression is not different from 0 (p -value > 0.05).

3.6. Supplementary material

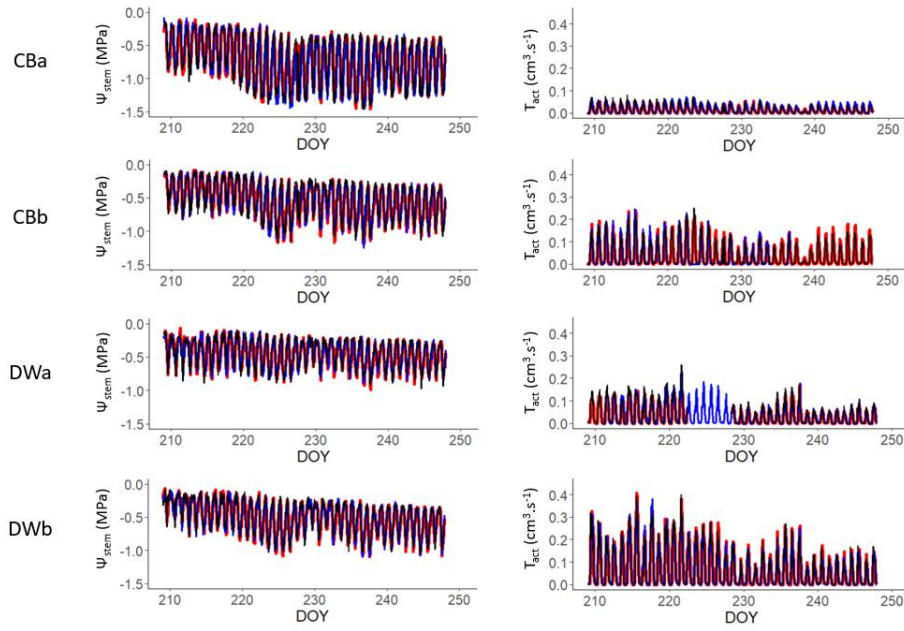


Figure S.3.6 – Time series of stem water potential (Ψ_{stem} – column left) and transpiration (T_{act} – column right) for each of the three replicates in the different subplots. Each color (red, blue or black) corresponds to one of the three replicates of the subplot.

3. Grapevine transpiration control is soil texture specific

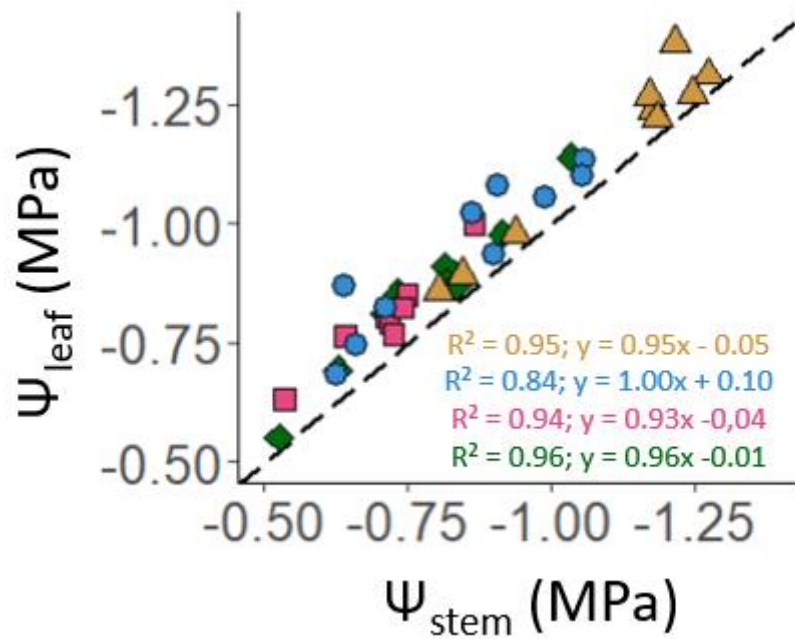


Figure S.3.7 - Comparison between Ψ_{stem} and Ψ_{leaf} measured regularly over the experimental period. Each point corresponds to each measurement taken at the same time for both water potentials. The brown triangles, blue circles, pink squares and green diamonds correspond respectively to the study areas CBa, CBb, DWa and DWb. The dashed black line is the 1:1 line. The slopes of each linear regression are not statistically different to 1 ($p\text{-value} > 0.05$; Table S.3.2).

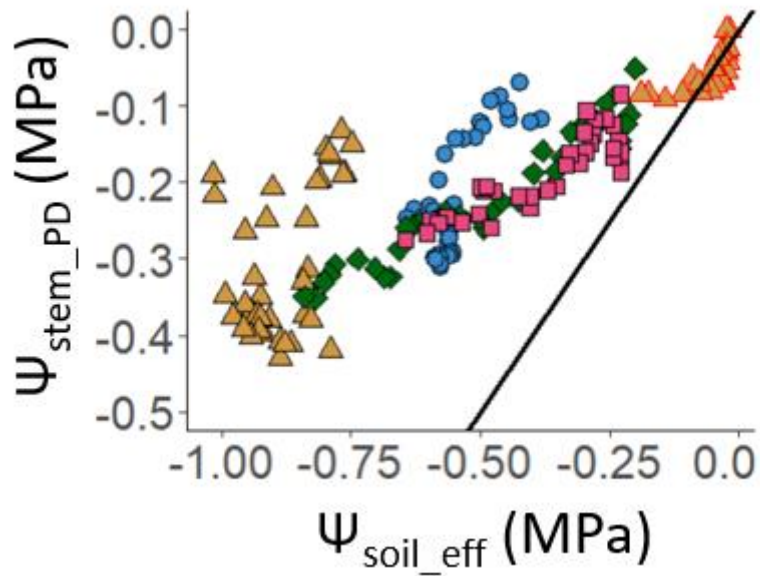


Figure S.3.8 – Comparison between $\Psi_{\text{soil_eff}}$ and $\Psi_{\text{stem_PD}}$. Each point corresponds to one day of the measurement period; the $\Psi_{\text{soil_eff}}$ and $\Psi_{\text{stem_PD}}$ compared was measured at the same time, i.e. at night when grapevine transpiration is null. The brown triangles, blue circles, pink squares and green diamonds correspond respectively to the study areas CBa, CBb, DWa and DWb. The brown triangles surrounded in red are data collected in 2023. The full black line is the 1:1 line.

3. Grapevine transpiration control is soil texture specific

3.6.2. Supplementary tables

*Table S.3.1 – p-value of the analysis of covariance (ANCOVA) to assess statistical differences in the relationships between hydraulic variables, by assessing each subplot two by two (p-value < 0.001***; p-value < 0.01**; p-value < 0.05*).*

Relationship	CBa x CBb	CBa x DWa	CBa x DWb	CBb x DWa	CBb x DWb	DWa x DWb
$T_{act}/T_{pot}(\Psi_{soil})$	< 0.001***	< 0.001***	< 0.001***	0.08	0.21	0.16
$T_{act}/T_{pot}(\Psi_{stem})$	< 0.001***	< 0.001***	< 0.001***	0.07	0.16	0.13
$K_{below}(\Psi_{soil})$	< 0.001***	< 0.001***	< 0.001***	0.24	0.09	0.07
$K_{below}(\Psi_{stem})$	0.011*	0.018*	< 0.01**	0.08	0.10	0.06
$K_{stem}(\Psi_{soil})$	< 0.001***	< 0.001***	< 0.001***	< 0.001***	0.042*	< 0.001***
$K_{stem}(\Psi_{stem})$	< 0.001***	< 0.001***	< 0.001***	< 0.001***	0.028*	< 0.001***
$K_{below}(T_{act}/T_{pot})$	< 0.001***	< 0.001***	< 0.001***	0.17	0.23	0.15

3.6. Supplementary material

Table S.3.2 – Value, uncertainty and *p*-value on the coefficients of the linear regression between Ψ_{leaf} and Ψ_{stem} , between K_{stem} and Ψ_{soil} , and between K_{stem} and Ψ_{stem} (*p*-value < 0.001***; *p*-value < 0.01**; *p*-value < 0.05*).

		Linear regression coefficient (y=a*x+b)					
		a			b		
Relationship	Subplot	Value	Uncertainty	<i>p</i> -value	Value	Uncertainty	<i>p</i> -value
$\Psi_{leaf}(\Psi_{stem})$	CBa	0.95	0.06	0.33	-0.05	0.06	0.49
	CBb	1	0.14	0.11	0.10	0.13	0.47
	DWa	0.93	0.07	0.06	-0.04	0.05	0.44
	DWb	0.96	0.06	0.12	-0.01	0.05	0.80
$K_{stem}(\Psi_{soil})$	CBb	0.08	0.35	0.82	2.26	0.07	<0.001***
	DWa	-0.001	0.76	0.99	1.19	0.15	<0.001***
	DWb	-0.21	0.78	0.79	2.24	0.18	<0.001***
$K_{stem}(\Psi_{stem})$	CBb	-0.03	0.16	0.85	2.21	0.14	<0.001***
	DWa	0.28	0.31	0.90	1.37	0.22	<0.001***
	DWb	0.06	0.43	0.13	2.34	0.35	<0.001***

4. Combination of plant and soil water potential monitoring and modelling demonstrates soil-root hydraulic disconnection during drought

This chapter is based on the article:

Delval, L., Vanderborght, J., Javaux, M. Combination of plant and soil water potential monitoring and modelling demonstrates soil-root hydraulic disconnection during drought, in revision in Plant and Soil.

ABSTRACT

Water is heterogeneously distributed in the root zone, notably due to the vertical heterogeneity of soil properties in real field conditions. At a smaller scale, water absorption by roots generates a radial water potential gradient around root segments. The influence of rhizosphere properties is garnering increasing attention, since it impacts this gradient, root water uptake and plant water status. Finally, at the scale of the thin contact between the soil and roots, the hydraulic continuity could be lost at the soil-root interface in dry conditions. This study

4. Soil-root hydraulic disconnection during drought

aimed to understand how these multiscale heterogeneities affect grapevine (*Vitis vinifera* cv. Chardonnay) root water uptake and water potential. Using a physically-based model, implementing rhizosphere and root system hydraulic properties, and loss of soil-root hydraulic continuity in dry soil conditions, we quantified belowground hydraulic conductances and their impact on grapevine root water uptake and water potential in different soil types. Soil-root hydraulic disconnection prevented the plant from feeling the dry shallowest soil horizons, and moved water uptake towards deeper wet soil horizons avoiding very negative stem water potentials. The main belowground hydraulic bottleneck of soil-plant system during drought is soil-texture dependent, with the rhizosphere limiting root water uptake in the sandy subplot, and the root system in the loamy subplot. By highlighting the key roles of rhizosphere hydraulics, root hydraulics and hydraulic disconnection on root water uptake and plant water status, in different edaphic conditions, this study enhanced our mechanistic understanding on soil-root water relations in soil water limited conditions.

4.1. Introduction

In viticulture, it is well known that soil and plant water deficit conditions can improve the quality of the wine produced (Costa et al., 2016; Van Leeuwen et al., 2009a; Yang et al., 2023). Despite being recognized as a key determinant of terroir expression in wine production, the soil is not extensively studied regarding its influence on root water uptake (RWU) in viticultural literature (Lovisol et al., 2016). Better understanding grapevine reactions and soil-root interactions to soil water limitation, under various edaphic conditions, might help to manage vineyards under changing climate conditions.

On its pathway between bulk soil and leaves, water flow is driven by gradients of water potential and crosses a series of hydraulic conductances (or resistances, their inverse). Most of these hydraulic conductances change with water potential and generate (non-)linear relations between water potential differences and fluxes in the soil-plant-atmosphere continuum (SPAC). Quantifying these conductances and how they change under drought is essential to better understand how they affect plant water status.

Similar to many plants, belowground processes in grapevines are much less understood than aboveground processes (de Herralde et al., 2010). Xylem embolisms have been widely studied in grapevines and thought to trigger stomatal closure and limit water flow in the SPAC (Alsina et al., 2007; Choat et al., 2010; McElrone et al., 2012). Yet, recent studies emphasized the dominant role of belowground conductance loss, instead of stem xylem cavitation, on the onset of stomatal closure of grapevines, and the soil texture specificity of the stomatal downregulation (Lavoie-Lamoureux et al., 2017; Lovisolo et al., 2016). Stomata start to close at less negative soil water potential in coarse-texture soil than in fine-texture soil during drought, as shown in Chapter 3. However, few studies described the origin and development of belowground hydraulic conductances of grapevines, and how they affect the distribution of RWU and grapevine water status. Gambetta et al. (2013) studied the aquaporin expression and quantified the root radial conductance along the root, showing that the root tip is 14-fold more conductive than the suberized secondary growth zone. The root tip predominate water uptake, but as older suberized portions could constitute a great proportion of the total root system, they could also supply potential for water uptake, as suberized roots are not completely sealed. Vandeleur et al. (2009) reported an up- or down-regulation of root aquaporin activity of *Vitis vinifera* in drought conditions, depending on the variety, and influencing the drought tolerance of a grape cultivar. Alsina et al. (2011) compared changes in whole root system conductance for drought-sensitive and drought-tolerant rootstock and showed deep root proliferation during a dry period for the drought-tolerant root system. Cuneo et al. (2016, 2021) showed that soil

4. Soil-root hydraulic disconnection during drought

water deficit conditions induced the formation of cortical lacunae in grapevine roots, significantly compromising the integrity of the radial water flow path in dry soil horizons. None of these studies focused on the interactions and distribution of soil-root hydraulic conductances and their dynamics during a drought period. Work is still needed to understand the factors limiting water uptake by grapevine roots in dry soil conditions and how they influence grapevine water status (Cuneo et al., 2021).

In situ RWU and belowground hydraulics monitoring is challenging due to the high heterogeneity of soil properties within a soil profile and uncertainties of root distribution in real field conditions. Work focusing on the influence of soil on plant water transport is often limited to well-controlled laboratory experiments (Mary et al., 2023; Wankmüller and Carminati, 2024) and most studies investigating RWU have been conducted on herbaceous species (Gambetta et al., 2013). Moreover, despite the evidence of rhizosphere specific behaviour (Cai et al., 2022), most studies on RWU still neglect it (Carminati et al., 2010). In this study, we defined the rhizosphere as the zone around root segments where RWU generates radially symmetric flow and hydraulic gradient fields. Recently, the impact of rhizosphere traits on RWU is garnering increasing attention (Vanderborght et al., 2023), since it has been observed that RWU led to a steep decline in hydraulic conductivity at the soil-root interface (de Jong van Lier et al., 2013, 2006). A recent soil-plant mechanistic model suggests that radial hydraulic conductances from the rhizosphere to the root are the primary constraints on water transport during drought (Carminati and Javaux, 2020). However, these belowground processes, that have a strong influence on whole-grapevine hydraulic dynamics, as shown in Chapter 3, are still rarely studied. It is still not known whether grapevine roots and/or rhizosphere constitute the main hydraulic bottleneck during drought (Figure 4.1a). Grapevines are typically known for their extended root systems which should prevent stress. However, rhizosphere hydraulic conductance might limit the uptake when roots are sparsely distributed, and the soil is dry. How this rhizosphere conductance develops with time, in soil-grapevine systems, has not

been investigated yet. In this sense, modelling RWU of grapevine and its partitioning over depth is useful and crucial to fill this knowledge (de Jong van Lier et al., 2013), which is essential in adapting viticulture to climatic change (Dayer et al., 2022; Gambetta et al., 2020a). RWU models have scarcely been applied on grapevine, or on other woody species (García-Tejera et al., 2017), and were used to simulate the soil water content dynamics in a vineyard (Zhou et al., 2007; Qingyun Zhou et al., 2008), but these studies do not focus on how the hydraulic conductances between the bulk soil and the stem collar are distributed. Quantification of the distribution of belowground hydraulic conductances of soil-grapevine system has not yet been addressed. This knowledge is fundamental to understand how they affect grapevine water status.

Recently, a macroscopic RWU, that combines a root system hydraulic model and a soil water flow model while accounting for rhizosphere hydraulic gradients around root segments, has been developed by Vanderborght et al. (2023). The model captures the interaction effects between root and soil water distributions, as well as the interplay between root and soil hydraulic properties on RWU distributions and plant water potentials. They applied their model on maize and showed that the consideration of the rhizosphere conductance, compared with no consideration, resulted in an earlier reduction of RWU during a drought period and this preserving water that could be later extracted by the plant. This also led to a better plant water status with higher nighttime plant water potentials (Vanderborght et al., 2023). To our knowledge, this kind of model has never been applied on grapevines.

In Chapter 3, we experimentally showed that stomatal response of *in situ* grapevine was triggered by a decrease of belowground (rhizosphere + root system) hydraulic conductance, but not by xylem cavitation in the stem. Despite that stomatal response to soil water potential was soil texture specific, we showed for the first time on *in situ* perennial plants, that the onset of stomatal closure was at the same belowground hydraulic conductance, independent of the soil texture, proving that *in*

4. Soil-root hydraulic disconnection during drought

situ grapevines coordinate short-term hydraulic mechanisms (e.g. stomatal regulation) and longer-term growth (e.g. root:shoot ratio). However, we hypothesized, without physical evidence, that this decrease in belowground hydraulic conductance was mainly due to a decrease in hydraulic conductance in the rhizosphere, but not to cavitation in the root xylem. Another limitation of this study is that it did not reveal the importance of rhizosphere and root system hydraulic conductances on RWU during drought, and how they are distributed, for grapevines planted on complex heterogeneous soils. We also observed, in Chapter 3, a disequilibrium between the root-effective soil water potential ($\Psi_{\text{soil_eff}}$ – equation 4.1) and the predawn water potential ($\Psi_{\text{stem_PD}}$ which is the stem water potential just before dawn), which should be equal in principle (Hinckley et al., 1978). $\Psi_{\text{soil_eff}}$ is calculated from the local bulk soil water potential $\Psi_{\text{bulk soil}}(z)$ [L] and the standard uptake fraction ($\text{SUF}(z)$ [-]) using:

$$\Psi_{\text{soil_eff}} = \sum_z \text{SUF}(z) \cdot \Psi_{\text{bulk soil}}(z), \quad (4.1)$$

with $\text{SUF}(z)$ being the normalized root length density (RLD) at depth z (Jorda et al., 2022):

$$\text{SUF}(z) = \frac{\text{RLD}(z)}{\int_0^{L_r} \text{RLD}(z) dz} \Delta z. \quad (4.2)$$

Equation 4.1 is valid when there the rhizosphere hydraulic resistance is null. We measured, in Chapter 3, a greater (less negative) $\Psi_{\text{stem_PD}}$ than $\Psi_{\text{soil_eff}}$ and the differences became larger as the soil dried out. In wet soil conditions, several studies have shown that, due to a non-equilibrium between bulk soil and soil-root interface and/or to night-time transpiration, a disequilibrium between $\Psi_{\text{stem_PD}}$ and $\Psi_{\text{soil_eff}}$ might exist, with $\Psi_{\text{stem_PD}}$ lower (more negative) than $\Psi_{\text{soil_eff}}$ (Groenvelde et

al., 2023; Kangur et al., 2017). We therefore observed the opposite in dry soil conditions, and hypothesized that this disequilibrium ($\Psi_{\text{stem_PD}} > \Psi_{\text{soil_eff}}$) was due to a longer root system than measured on the field, that was in contact with wetter soil in deeper soil layers, as we measured root systems down to 2 m depth (corresponding to the depth of the pits used to observe the root systems). It could also be explained by a loss of contact and a hydraulic discontinuity between the soil and the roots in very dry soils (e.g. due to soil and/or root shrinkage forming soil-root air gaps) (Carminati et al., 2013; Cuneo et al., 2016). As a result, the roots only felt the wettest soil horizons, contributing to a larger (less negative) $\Psi_{\text{stem_PD}}$ than $\Psi_{\text{soil_eff}}$ (Couvreur et al., 2014). These hypothesis are in line with the observations of Améglio et al. (1999) who showed that $\Psi_{\text{stem_PD}}$ tended to equilibrate with the water potential of the most humid soil zones rather than with $\Psi_{\text{soil_eff}}$. However, these assumptions still need to be demonstrated. Finally, Vanderborght et al. (2023) showed that the consideration of the rhizosphere conductances allowed the plant water potential to bounce back and to exceed bulk soil water potentials at nighttime. This led to the discrepancy between $\Psi_{\text{stem_PD}}$ than $\Psi_{\text{soil_eff}}$.

The objective of this study is to investigate the impact of rhizosphere and root hydraulics on root water uptake and stem water potential of *in situ* grapevines planted in two different soil types during drought, considering the complexity and heterogeneity of soil properties in real field conditions. We used a macroscopic physically-based model, including rhizosphere and root system conductances (Vanderborght et al., 2023) to represent the soil-grapevine systems and to quantify their belowground hydraulic conductances and their evolution. We validated this model by comparing measured and simulated bulk soil and plant water potentials.

4.2. Methodology

4.2.1. Subplots description

This study was conducted in the *Château de Bousval* vineyard (Genappe, Belgium, 50°36'45.0"N 4°31'19.6"E), on a field of *Vitis vinifera* cv. Chardonnay grafted on 3309C rootstock. The grapevines were planted with vertical shoot positioning, a 1.6 m inter-row and a 0.8 m inter-cep. The vineyard is characterized by great intra-plot variability in terms of soil type, offering contrasting water conditions within the field. The soil is constituted of a loamy top layer overlaying a sandy soil, but the depth of the interface between these two textures changes within the field, with a gradient from up to downhill, reaching more than 2 m at the downhill of the plot, while being around 0.3 m at the uphill part. We worked on two subplots in this vineyard: one on the uphill and one on the downhill. The first subplot will be called *sandy subplot* and is therefore composed of a sandy soil, which is made of recurring layers of pure sand (horizons S1) and iron crusts (horizons S2) and is surmounted by a shallow loamy horizon. The second subplot will be called *loamy subplot* and is composed of loamy horizons throughout the soil profile (Figure S.4.1). The root impact profile (Böhm, 1979), to obtain the root density (that we assumed equivalent to the root length density in this study as we considered root tip to be predominant in water uptake (Gambetta et al., 2013)), and the soil unsaturated hydraulic properties were well characterized down to a depth of 2 m, thanks to pits dug down to 2 m depth in each subplot. The soil hydraulic properties were measured by Hyprop (METER Group Inc., Pullman, WA, USA) evaporation method (Bezerra-Coelho et al., 2018). The soil water content at the permanent wilting point (pF 4.2) was measured by pressure plate (Ridley and Burland, 1993). Hyprop-fit software was used to optimize the unsaturated hydraulic parameters of van Genuchten-Mualem (1980), for each soil horizon (Table 4.1).

The vineyard is equipped with a weather station providing data of precipitation (Figure S.4.2) and reference evapotranspiration calculated from the FAO Penman-Monteith method (Allen et al., 1998).

Table 4.1 – Unimodal van Genuchten hydraulic parameters of each soil horizon of the two subplots.

		θ_{sat}	θ_{res}	n	α	K_{sat}	τ
		$\text{cm}^3.\text{cm}^{-3}$	$\text{cm}^3.\text{cm}^{-3}$	-	cm^{-1}	$\text{cm}.\text{day}^{-1}$	-
Sandy subplot	Ap	0.419	0.117	1.483	0.00669	1.12	0.701
	S1	0.358	0.08	3.11	0.0182	72	1.039
	S2	0.39	0.053	1.728	0.019	40	1.848
Loamy subplot	Ap	0.427	0	1.257	0.00626	1.46	-0.169
	Bw1	0.422	0.019	1.323	0.00519	0.791	-1.363
	Bw2	0.398	0	1.243	0.0063	0.968	-1.054

4.2.2. Soil and plant hydraulic measurements

For each subplot, bulk soil water potential ($\Psi_{\text{bulk soil}}$), stem collar water potential (Ψ_{stem}) and transpiration rates (T_{act}) of grapevines were measured and recorded every hour during 36 days in summer 2022 (between DOY 209 – start of the veraison – and DOY 245 – harvest), which was marked by an exceptional drought in Belgium. The $\Psi_{\text{bulk soil}}$ were monitored by soil water potential sensors (Teros21, METER Group, Inc., Pullman, WA, USA) installed at 10 cm, 40 cm and 100 cm under the grapevines to measure the variation in soil matric potential linked to water uptake. The Ψ_{stem} was measured by stem psychrometers

4. Soil-root hydraulic disconnection during drought

(PSY1, ICT International, Armidale, NSW, Australia) installed at the stem collar of the plant, and transpiration rate was measured with sap flow sensors (Dynagage, Dynamax Inc., Houston, TX, USA).

4.2.3. Model description

The water fluxes, hydraulic conductances and water potentials in the belowground part of the soil-grapevine system were simulated with a macroscopic soil-plant water flow model explicitly combining bulk soil, rhizosphere and root hydraulics, which is thoroughly explained in Vanderborght et al. (2023). A root water uptake (RWU) module, simulating RWU through a 1D root-soil hydraulic network, is implementing in a Matlab code using the algorithm of the SWAP model (van Dam and Feddes, 2000), which solves the 1D Richards equation employing an implicit finite difference scheme. The sink term during a time step is explicitly and iteratively calculated using the water potential distribution at the start of the time step. This sink term, which represents the RWU, was simulated according to Couvreur et al. (2012). In their method the volume of water taken up by the root at each depth ($S(z) [T^{-1}]$) is calculated as:

$$S(z)\Delta z = K_{rs} \cdot (\Psi_{SRI_{eff}} - \Psi_{stem}) \cdot SUF(z) + K_{rs} \cdot (\Psi_{SRI}(z) - \Psi_{SRI_{eff}}) \cdot SUF(z) \quad (4.3)$$

where Δz is the thickness of a soil layer, K_{rs} is the root system conductance [T^{-1}], $\Psi_{SRI_{eff}}$ [L] is the effective water potential that is felt by the root system, Ψ_{stem} is the water potential at the plant stem collar [L], $\Psi_{SRI}(z)$ [L] is the local water potential at the soil-root interface and $SUF(z)$ [-] is the standard uptake fraction, or the relative water uptake

at the depth z for a homogeneous soil water potential (the sum of these standard fractions is one by definition). All Ψ terms are total head (including gravity). The first term of the equation 4.3 describes RWU under uniform soil water potential distribution, whereas the second term describes compensatory RWU that arises heterogeneous soil water potential profile (Couvreur et al., 2012). A positive sink ($S>0$) indicates water flowing from the soil to the roots, while a negative sink ($S<0$) signifies that water is released by the roots to the soil. The soil water potential sensed by the root system is linked to the local water potential at the soil-root interface at each depth z , $\Psi_{SRI}(z)$, as:

$$\Psi_{SRI_{eff}} = \sum_z SUF(z) \cdot \Psi_{SRI}(z) \quad (4.4)$$

The maximum depth is equivalent to the depth of the root system L_r . The model includes rhizosphere hydraulic conductance, between the bulk soil and the soil-root interface (Vanderborght et al., 2023). In dry soils, when conductances to water flow toward root segments are low, significant water potential gradients are formed between the bulk soil and the soil-root interface. This necessitates the consideration of an additional ‘rhizosphere conductance’ (K_{rhizo}). The parameterization and calculation of the K_{below} is explained below, in the model parameterization section.

4.2.4. Model parameterization, initial and boundary conditions

4. Soil-root hydraulic disconnection during drought

Soil parameterization, initial and boundary conditions

A vertical spatial discretization of 1 cm was used. At the soil surface, we imposed a flux boundary condition corresponding to the potential evaporation (E_P [$L\ T^{-1}$]) or to the precipitation inputs. At the bottom boundary, a free drainage boundary condition was applied. We used the Beer Lambert law (equation 4.5), described in Ritchie (1972), to calculate E_P based on the potential evapotranspiration (ET_P), a light extinction coefficient (k_{light}) set to 0.498 (de Cortázar et al., 2005) and a leaf area index (LAI) measured with a LP-80 (METER Group, Inc., Pullman, WA, USA). At the start (DOY 209) and end (DOY 245) of the measurement and simulation period, LAI was respectively 1.38 and 1.28 in the sandy subplot, and 1.83 and 1.55 in the loamy subplot. We linearly interpolated LAI between these two dates.

$$\frac{E_P}{ET_P} = e^{-k_{light} LAI} \quad (4.5)$$

The $\Psi_{bulk\ soil}$ measured at the three different depths (10 cm, 40 cm and 100 cm) were used as initial $\Psi_{bulk\ soil}$ for the simulations. Thus, the soil is very dry at the surface from the start of the simulations. We assumed that the soil potential gradient is linear between 0 cm and 10 cm, and that $\Psi_{bulk\ soil}$ is -0.01 MPa at the bottom of the soil profile (Table 4.2), which is 1 m below the root system depth (depending on the subplot and the scenario). Finally, we assumed that the unsaturated soil hydraulic properties in the rhizosphere are equivalent to those of the bulk soil (Table 4.1), meaning that we did not consider the impact of roots on soil hydraulic properties in the rhizosphere. Only the influence of RWU on water potential gradients in the rhizosphere was taken into consideration (Vanderborght et al., 2023).

Table 4.2 – Initial bulk soil water potentials at the soil surface, bottom of the soil profile and at three depths (10 cm, 40 cm and 100 cm) used for the simulations of the two subplots.

Depth	z = 0 cm	z = 10 cm	z = 40 cm	z = 100 cm	Bottom of soil profile
Sandy subplot	-1.572 MPa	-1.571 MPa	-1.112 MPa	-0.029 MPa	-0.010 MPa
Loamy subplot	-1.175 MPa	-1.174 MPa	-0.296 MPa	-0.047 MPa	-0.010 MPa

Root system hydraulic properties parameterization

In the hydraulic model, grapevines are represented by a SUF profile (equation 4.2) and by a root system conductance (K_{rs}), as proposed by Couvreur et al. (2012) and Vanderborght et al. (2021). K_{rs} can be decomposed (Figure 4.1a) in axial conductance (K_x) and radial conductance (K_r):

$$\frac{1}{K_{rs}} = \frac{1}{K_r} + \frac{1}{K_x} \quad (4.6)$$

Since K_x is a hundred to a thousand times greater than K_r of grapevine (Baert et al., 2015), we assumed that K_x did not constraint water flow in the root system, and we can neglect it. K_{rs} is therefore equal to K_r . K_{rs} was estimated by using the field hydraulic measurements in each subplot. We calculated it thanks to the simultaneous measurements of Ψ_{soil} , Ψ_{stem} and transpiration, in wet soil conditions. In these conditions, the soil hydraulic conductance does not limit water flow, which is governed by K_{rs} (Draye et al., 2010). We calculated a K_{rs} 4.04×10^{-6} hour⁻¹

4. Soil-root hydraulic disconnection during drought

¹ in the sandy subplot and a K_{rs} of $7.86 \times 10^{-6} \text{ hour}^{-1}$ in the loamy subplot. The K_r profile is estimated proportionally to the SUF as:

$$K_r(z) = \text{SUF}(z) \times K_{rs}, \quad (4.7)$$

with intrinsic radial conductance k_r [T^{-1}] of the root tissues as

$$k_r(z) = \frac{K_r(z)}{2\pi \times \text{RLD}(z) \times r_{\text{root}}(z)}, \quad (4.8)$$

with r_{root} the radius of the roots that we assumed to be 0.5 mm for all roots, since we only considered fine roots ($< 1 \text{ mm}$) which constitute 96 % of the root density of the root systems in each subplot in this study. This is in line with other studies that showed that most of the grapevine roots have a radius between 0.5 mm and 1 mm (Cislaghi et al., 2017). Root radius of 1 mm has also been tested, but it did not change significantly the results obtained.

Rhizosphere hydraulic conductance parameterization

The soil-root conductance at depth z , $K_{\text{soil-root}}(z)$ [$\text{L}^2 \text{ T}^{-1}$] (Figure 4.1a), is defined as

$$K_{\text{soil-root}}(z) = \frac{S(z)}{\Psi_{\text{bulk soil}}(z) - \Psi_x(z)}, \quad (4.9)$$

with $\Psi_x(z)$ is the xylem water potential at depth z , and can be calculated from rhizosphere hydraulic conductance (K_{rhizo}) and K_r that are in series (Figure 4.1a) as

$$K_{soil-root}(h_{bulk\ soil}, h_{SRI}) = \frac{K_{rhizo} \times K_r}{K_{rhizo} + K_r}. \quad (4.10)$$

K_r is defined in equation 4.7 and K_{rhizo} is calculated using the root length density (RLD) at depth z , the geometry factor B at depth z that accounts for the radial flow and the variation of the soil conductivity with distance from the soil-root interface (de Jong van Lier et al., 2008), and the integrals of the soil hydraulic conductivity-pressure head relationship, $K(h)$, known as matrix flux potentials (Raats, 1970), for bulk soil ($h_{bulk\ soil}$) and soil root interface (h_{SRI}):

$$K_{rhizo}(z) = 2\pi \times RLD(z) \times B(z) \times \bar{k}_{rhizo}(h_{bulk\ soil}, h_{SRI}), \quad (4.11)$$

$$\bar{k}_{rhizo}(h_{bulk\ soil}, h_{SRI}) = \frac{\int_{-\infty}^{h_{bulk\ soil}(z)} K(h)dh - \int_{-\infty}^{h_{SRI}(z)} K(h)dh}{h_{bulk\ soil}(z) - h_{SRI}(z)}, \quad (4.12)$$

$$B(z) = \frac{2(\rho(z)^2 - 1)}{1 - (0.53\rho(z))^2 + 2\rho^2(\ln(\rho(z)) + \ln(0.53))}, \quad (4.13)$$

$$\rho(z) = \frac{r_{rhizo}(z)}{r_{root}(z)}, \quad (4.14)$$

$$r_{rhizo}(z) = \frac{1}{\sqrt{\pi \times RLD(z)}}, \quad (4.15)$$

4. Soil-root hydraulic disconnection during drought

where $\bar{k}_{rhizo}$ [$L T^{-1}$] is an effective conductivity of the rhizosphere zone that corresponds with an average of the soil hydraulic conductivity K [$L T^{-1}$] in the rhizosphere. $\bar{k}_{rhizo}$ represents the average of K when the pressure head varies between the pressure head at the soil-root interface (h_{SRI}) and the pressure head in the bulk soil ($h_{bulk\ soil}$). Pressure head h is the difference between Ψ (equivalent to total head) and the gravity head (equivalent to the depth z). Combining the above equations, we obtain for $K_{soil-root}$:

$$K_{soil-root}(h_{bulk\ soil}, h_{SRI}) = \frac{2\pi \times RLD \times r_{root} \times B \times k_r \times \bar{k}_{rhizo}(h_{bulk\ soil}, h_{SRI})}{r_{root} \times k_r + B \times \bar{k}_{rhizo}(h_{bulk\ soil}, h_{SRI})}. \quad (4.16)$$

Hydraulic disconnection between the soil and the roots

It has been shown that with soil dehydration, hydraulic disconnection would create a loss of contact between the soil and the roots, and annihilating the water movement from the soil to the roots in dry soil horizons (Cuneo et al., 2016). In this study, we considered that there was a hydraulic disconnection between the soil and the root when the bulk soil water potential ($\Psi_{bulk\ soil}$) and/or the xylem water potential (Ψ_x) reached the threshold of -0.8 MPa. This threshold comes from a sensitivity analysis where different threshold values were tested (Table S.4.1). The threshold of -0.8 MPa gave the best results by comparing measured and simulated bulk soil and stem water potential. This threshold value is in line with other studies which observed that fine roots started to shrink, leading to soil-root air gaps formation, at a Ψ_x around -0.8 MPa (Cuneo et al., 2016; Duddek et al., 2023). We related the loss of soil-root contact to the rhizosphere conductance. At a depth z , when $\Psi_{bulk\ soil}$ and Ψ_x are below the threshold of -0.8 MPa, we considered that K_{rhizo} (equation 4.11) is null and that the root xylem water potential is equal to the stem collar water potential (Ψ_{stem}) (Figure 4.1c). For $\Psi_{bulk\ soil}$ larger than the threshold and Ψ_x is smaller than the

threshold, we considered that the soil-root interface water potential at the soil side is equal to the threshold, and is smaller than the threshold at the root side (Figure 4.1d). For $\Psi_{\text{bulk soil}}$ smaller than the threshold and Ψ_x is larger than the threshold, water flows from the root to the soil, and the water potential at the root side of the interface is equal to the threshold, but is smaller than the threshold at the soil side (Figure 4.1e). Solving the flow and water potentials in the network necessitates addressing a set of nonlinear equations, which cannot be resolved directly but instead require an iterative approach. A pseudo code, with the different calculation steps, explaining how the algorithm works to find Ψ_{stem} , Ψ_{SRI} and $\mathbf{Q}$ (here Ψ_{SRI} and $\mathbf{Q}$ are vectors so are in bold), and including the hydraulic disconnection between the soil and the roots, is given in Appendix 4.1.

We also tested to relate the soil-root hydraulic disconnection to the root hydraulic conductance, by imposing a null $K_r(z)$ when Ψ_{SRI} is below the threshold of -0.8 MPa. This approach implies to recalculate a K_r and a SUF profiles at each iteration. Due to the similar results (see the Appendix 4.2 of the Supplementary materials) and in order to avoid assumptions about root hydraulic properties, we only present, in the main text, the results for which the hydraulic disconnection is related to soil processes.

Plant boundary conditions

We used the averaged sap flow [$\text{L}^3 \text{T}^{-1}$] time series measured by sap flow sensors as plant stem collar boundary condition. Sap flow was divided by the area [L^2] of vineyard ground attributable to each grapevine (i.e. row spacing x grapevine spacing) to give canopy transpiration flux T_{act} [L T^{-1}]. The aim is therefore to simulate the Ψ_{stem} time series measured in the field. We set a critical Ψ_{stem} ($\Psi_{\text{stem,crit}}$) lower than the minimum Ψ_{stem} observed in the field ($\Psi_{\text{stem,min}} = -1.45 \text{ MPa}$) at $\Psi_{\text{stem,crit}} = -2 \text{ MPa}$. If the simulated Ψ_{stem} is above the $\Psi_{\text{stem,crit}}$, the simulated transpiration rate (T_{sim}) is equal to the measured transpiration

4. Soil-root hydraulic disconnection during drought

(T_{act}). When the Ψ_{stem} reached $\Psi_{stem,crit}$, the Ψ_{stem} is kept constant, and T_{sim} is equal to the supply from the soil:

$$\begin{aligned} K_{rs} \cdot (\Psi_{srieff} - \Psi_{stem}) &= T_{sim} = T_{act} & \text{when } \Psi_{stem} > \Psi_{stem,crit}, \\ K_{rs} \cdot (\Psi_{srieff} - \Psi_{stem,crit}) &= T_{sim} < T_{act} & \text{when } \Psi_{stem} \leq \Psi_{stem,crit}. \end{aligned} \quad (4.17)$$

Setup of simulation scenarios

In the field, root density and soil hydraulic properties were measured on vertical profiles down to 2 m depths, corresponding to the depth of the pits dug to observe belowground properties of the soil-grapevine systems in both subplots. As mentioned in the introduction (Section 4.1), we hypothesized that grapevines might have a longer root system than measured ($L_r > 2$ m), that could explain the disequilibrium observed between the root effective soil water potential (Ψ_{soil_eff}) and the predawn water potential (Ψ_{stem_PD}). This difference could also be due to a loss of hydraulic continuity between the soil and the roots in dry soil horizons (e.g. soil-root air gaps). Finally, this could also emerge from the difference between the bulk soil water potentials and the soil-root interface water potentials at night, as proposed by Vanderborght et al. (2023). To test these hypotheses, we implemented four simulation scenarios per subplot (Table 4.3). Simulation scenarios 1 and 2 consisted of simulating a grapevine with a root system of 2 m depth ($L_r = 2$ m) in the sandy and loamy subplots respectively, and simulation scenarios 3 and 4 used a deeper root system (L_r is 3 m and 2.5 m for the sandy and loamy subplots respectively – Table S.4.2). These four simulations did not include the formation of soil-root air gaps (hydraulic disconnection) in dry soils. Simulation scenarios 5 to 8 used respectively the same plants and soils as simulation scenarios 1 to 4, but including a hydraulic disconnection in dry soil horizons (Appendix 4.1). The different scenarios are resumed in Table 4.3. To extend the soil depth beyond 2 m depth (scenarios 3, 4, 7 and 8), we assumed that soil horizons follow the same pattern as observed in the sandy subplot

(alternating between pure sand horizons and iron crusts). In the loamy subplot, hydraulic properties measured at 2 m depth were used below this depth (Figure S.4.1). To extend the root system below 2 m depth, we assumed that root density remained constant at depth and was equal to the root density measured at 2 m depth for the loamy subplot. We did not exactly use the same assumption for the sandy subplot, since we observed four times more roots in the iron crusts than in the pure sand (Figure S.4.1). Therefore, this ratio was used to extend the root system of this subplot. A sensitivity analysis was carried out to find the root depth at which the measured and simulated data could be matched, for scenarios for which $L_r > 2$ m. A 3 m root system was used for the sandy subplot, and a 2.5 m root system for the loamy subplot (Table S.4.2). We assumed that the root system did not grow during the simulation period. To select the best scenarios, we compared observed and simulated $\Psi_{\text{bulk soil}}$ (at 10 cm, 40 cm and 100 cm depth) and simulated Ψ_{stem} . We used the R^2 and RMSE of the linear regression, and the p-value of a Wilcoxon test to assess the significance of the difference between simulated and observed data.

Table 4.3 – Setups for each simulation scenario

Scenario	Subplot	Root system depth (L_r)	Soil-root air gaps included
1	Sandy	2 m	No
2	Loamy	2 m	No
3	Sandy	3 m	No
4	Loamy	2.5 m	No
5	Sandy	2 m	Yes
6	Loamy	2 m	Yes
7	Sandy	3 m	Yes
8	Loamy	2.5 m	Yes

4. Soil-root hydraulic disconnection during drought

Simulation outputs

The hydraulic model simulated, at each depth z , $\Psi_{\text{bulk soil}}(z)$, $\Psi_{\text{SRI}}(z)$ and $S(z)$, and also simulated Ψ_{stem} . We calculated the time cumulated amount of water absorbed by the plant throughout the simulation period S_{cum} [L]:

$$S_{\text{cum}} = \int_{t=0}^{t=\text{end}} \left[\int_{z_{\text{top}}}^{z_{\text{bottom}}} S(z) dz \right] dt, \quad (4.18)$$

with z_{top} and z_{bottom} are the top and bottom depth of the soil profile or a soil horizon. By using this equation 4.18 on the whole soil profile, we calculate the total amount of water transpired by the plant throughout the simulation period ($S_{\text{cum}} = T_{\text{sim_cum}}$). The effective rhizosphere hydraulic conductance ($K_{\text{rhizo_eff}}$), at each time interval t , was calculated with the following equation:

$$K_{\text{rhizo_eff}}(t) = - \frac{T_{\text{sim}}(t)}{\left[\sum_z \frac{Kr(z,t)}{\sum_z Kr(z,t)} \cdot \Psi_{\text{SRI}}(z,t) \right] - \left[\sum_z \frac{K_{\text{soil-root}}(z,t)}{\sum_z K_{\text{soil-root}}(z,t)} \cdot \Psi_{\text{bulk soil}}(z,t) \right]} \quad (4.19)$$

$K_{\text{rhizo_eff}}$ was calculated from the transpiration rate, and the difference between an effective soil-root interface water potential for which the weighing factors per depth z were calculated based on Kr (equation 4.7) and an effective bulk soil water potential for which the weighing factors per depth z were calculated based on $K_{\text{soil-root}}$ (equation 4.9). The calculation of the effective bulk soil water potential in this way (right term of the denominator of equation 4.9), allowed to consider the presence of soil-root air gaps, and therefore to consider how they affect $K_{\text{rhizo_eff}}$.

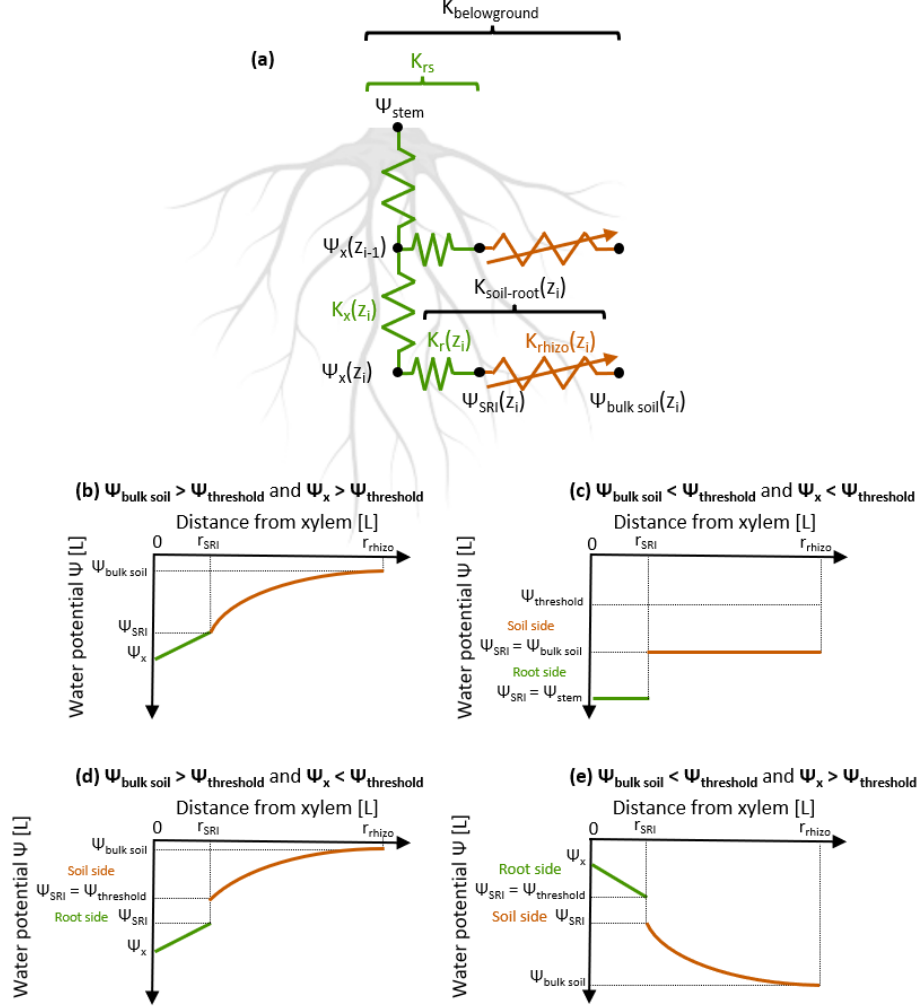


Figure 4.1 – (a) Scheme of serial connection of belowground hydraulic conductances ($K_{\text{belowground}}$). $K_{\text{belowground}}$ are constituted by the rhizosphere hydraulic conductance (K_{rhizo} in brown) between the bulk soil ($\Psi_{\text{bulk soil}}$) and the soil-root interface (Ψ_{SRI}) and by the root system hydraulic conductance (K_{rs} in green), which can be decomposed in radial (K_r) and axial (K_x) conductances, between the soil-root interface (Ψ_{SRI}) and the stem collar (Ψ_{stem}). In this study, we considered that K_x is negligible. (b, c, d and e) Shape of water potential Ψ as a function of distance of root xylem (subscript x) in the rhizosphere (in brown) and within the root (radial part, in green). In (b) there is no hydraulic disconnection between the soil and the roots ($\Psi_{\text{bulk soil}}$ and Ψ_x are larger than $\Psi_{\text{threshold}}$ of -0.8 MPa). In (c) there is a hydraulic disconnection between the soil and the roots ($\Psi_{\text{bulk soil}}$ and Ψ_x are lower than $\Psi_{\text{threshold}}$); in this case we considered no water flow in the soil and in the roots. In (d) $\Psi_{\text{bulk soil}}$ is larger than $\Psi_{\text{threshold}}$ but Ψ_x is smaller; in this case water flows from the soil to the root and we considered a hydraulic disconnection at the soil-root interface. In (e), $\Psi_{\text{bulk soil}}$ is smaller than $\Psi_{\text{threshold}}$ but Ψ_x is larger; in this case water flows from the root to the soil and we considered a hydraulic disconnection at the soil-root interface. All Ψ are total head, including gravity.

4.3. Results

4.3.1. Comparison between measured and simulated bulk soil and stem water potentials

Figure 4.2 shows the measured and simulated bulk soil water potential ($\Psi_{\text{bulk soil}}$) at three different depths (10 cm, 40 cm and 100 cm) for the eight different scenarios (four scenarios per subplot). Figure 4.3 and Figure 4.4 show measured and simulated stem collar water potential (Ψ_{stem}) and predawn water potential ($\Psi_{\text{stem_PD}}$) for the same eight scenarios.

A deeper root system enables the plant to maintain higher (less negative) Ψ_{stem} (Figures 4.3 and 4.4 – scenarios 3 and 4). However, the root system extension is not sufficient for the simulated Ψ_{stem} to match the measured Ψ_{stem} (p-value > 0.05 – Tables 4.4 and 4.5). It is necessary to include a hydraulic break between the soil and the roots in dry soil horizons, for simulation and observations to agree (scenarios 7 and 8). Moreover, by omitting the formation of soil-root air gaps (scenarios 1 to 4), $\Psi_{\text{bulk soil}}$ is not properly simulated (Figure 4.2a-d). A lot of hydraulic redistribution is simulated when there is no hydraulic disconnection in dry soil horizons. At the start of the simulation, since the soil is much drier in the shallow than in the deeper horizons, and root density is much higher close to the soil surface, compensation rewets the first horizon of the soil (second term of equation 4.3). In other words, more water is released by the roots to the soil, up to DOY 218 in both subplots (Figure S.4.3a-d), increasing the $\Psi_{\text{bulk soil}}$ (less negative water potentials). This is the case at 10 cm and 40 cm depth in the sandy subplot, and at 10 cm depth in the loamy subplot. Due to this compensation, the simulated $\Psi_{\text{bulk soil}}$ is less negative than the measured $\Psi_{\text{bulk soil}}$ (Figure 4.2a-d). The inclusion of hydraulic break between the

soil and the roots (scenario 5 to 8) severely limits the root water uptake or the release of water into the soil (Figure S.4.3e-h). As a result, there is less or no rewetting of the soil (excepted in the first few centimetres of the soil (Figure S.4.4)), and the simulated $\Psi_{\text{bulk soil}}$ keeps very negative values during the whole simulation, consistent with the measured $\Psi_{\text{bulk soil}}$ for the shallow part of the soil (Figure 4.2e-h). For a root system of 2 m depth (scenarios 5 and 6), the simulated $\Psi_{\text{bulk soil}}$ are drier than the measured $\Psi_{\text{bulk soil}}$ at 100 cm depth for the sandy and loamy subplots (Figure 4.2e,f). However, they are statistically similar (p-value > 0.05 – Tables 4.4 and 4.5) for a deeper root system (scenarios 7 and 8 - Figure 4.2g,h), due to less water being absorbed at these depths (Figure S.4.3e-h).

By including the formation of hydraulic disconnection between the soil and roots in dry soil horizons, the simulated Ψ_{stem} is maintained at values corresponding to those measured in the field, throughout the measurement and simulation period (Figure 4.3c,d and Figure 4.4a,b). Similarly, the simulated $\Psi_{\text{stem_PD}}$ is also consistent with the measured $\Psi_{\text{stem_PD}}$ when there is a hydraulic disconnection between the soil and the roots in dry surface horizons (Figure 4.3e,f and Figure 4.4c,d). In addition to the hydraulic disconnection, the compensation in the first few centimetres of the soil (Figure S.4.4) allowed to keep relatively greater (less negative) Ψ_{SRI} , contributing to the maintain of higher Ψ_{stem} . The R^2 increases and the RMSE decreases when the root system is extended beyond a depth of 2 m, as well as when the formation of soil-root air gaps is included in the simulations. Furthermore, only the 3 m (sandy subplot) and 2.5 m (loamy subplot) root system scenarios, with the formation of soil-root air gaps (scenarios 7 and 8), show that the distributions of Ψ_{stem} and $\Psi_{\text{stem_PD}}$ are statistically equivalent (p-value > 0.05 – Tables 4.4 and 4.5). For this reason, in the remainder of this study, only the results of scenarios 7 and 8 are presented.

4. Soil-root hydraulic disconnection during drought

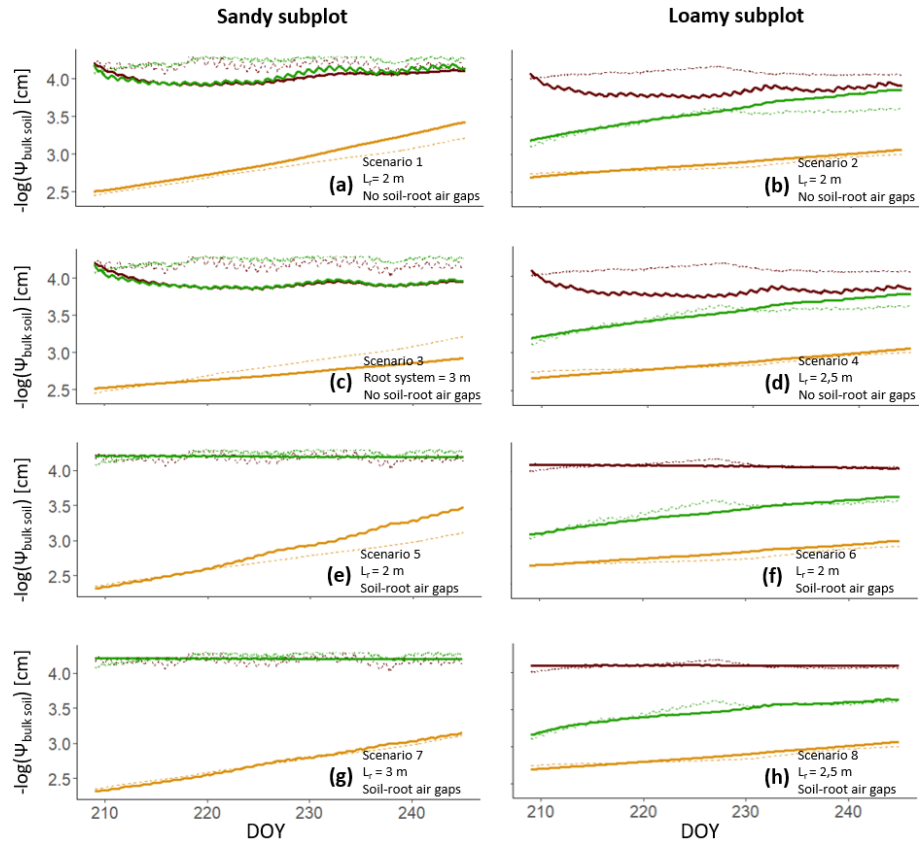


Figure 4.2 – Measured (dashed lines) and simulated (full lines) bulk soil water potential at 10 cm (brown), 40 cm (green) and 100 cm (orange) depth for each scenario in the sandy subplot (left column) and the loamy subplot (right column).

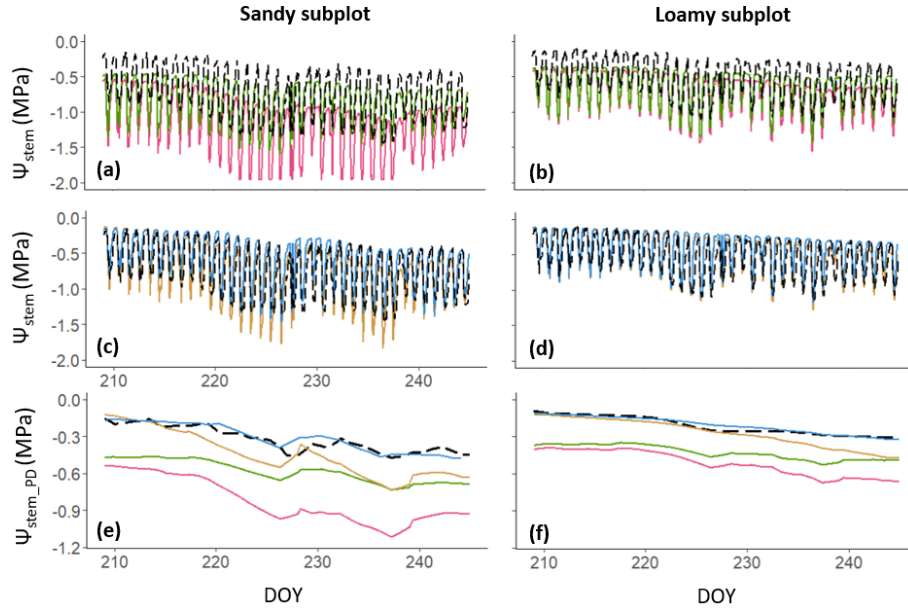


Figure 4.3 – (a-d) Measured (dashed black lines) and simulated (coloured full lines) stem collar water potential (Ψ_{stem}) time series; (e,f) measured (dashed black lines) and simulated (coloured full lines) predawn water potential (Ψ_{stem_PD}) times series for the sandy subplot (left column) and the loamy subplot (right column). Figures (a) and (b) correspond to simulation of Ψ_{stem} without formation or soil-root air gaps in dry soils (scenarios 1 to 4), while figures (c) and (d) correspond to simulation of Ψ_{stem} with formation of soil-root air gaps in dry soils (scenarios 5 to 8). For each figure, the pink lines correspond to a grapevine with a root system of 2 m without formation of soil-root air gaps (scenarios 1 and 2); the green lines to a plant with a deeper root system (3 m and 2.5 m for the sandy and loamy subplots respectively) without formation of soil-root air gaps (scenarios 3 and 4); the brown lines to a grapevine with a root system of 2 m with formation of soil-root air gaps (scenarios 5 and 6); and the blue lines to a plant with a deeper root system (3 m and 2.5 m for the sandy and loamy subplots respectively) with formation of soil-root air gaps (scenarios 7 and 8).

4. Soil-root hydraulic disconnection during drought

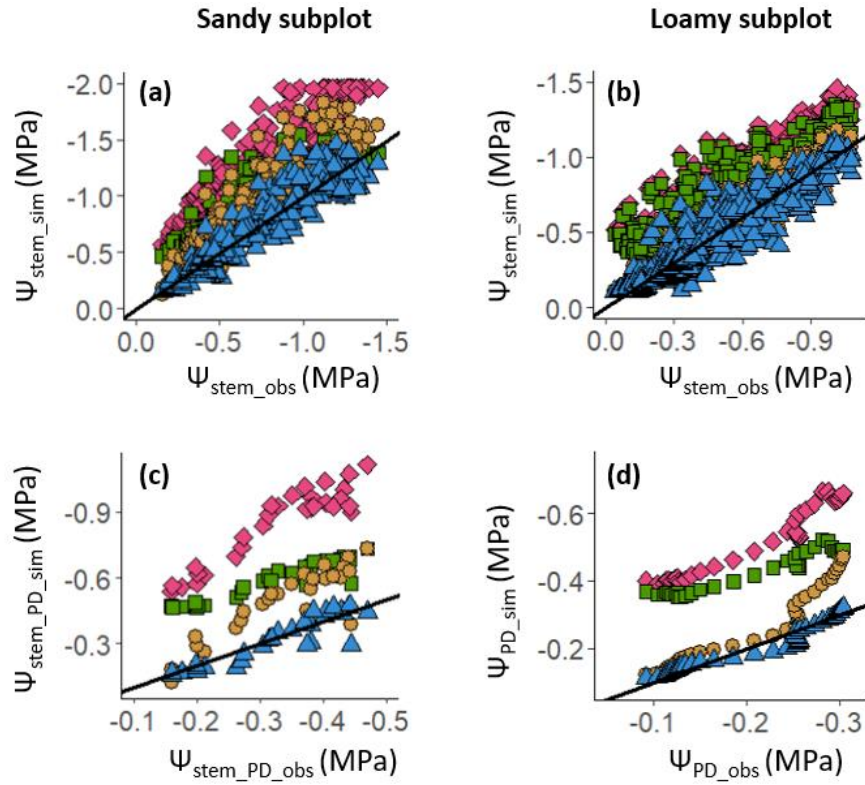


Figure 4.4 – (a,b) Comparison between observed (Ψ_{stem_obs}) and simulated (Ψ_{stem_sim}) stem collar water potential; (c,d) comparison between observed ($\Psi_{stem_PD_obs}$) and simulated ($\Psi_{stem_PD_sim}$) predawn water potential for the sandy subplot (left column) and the loamy subplot (right column). For each figure, the pink diamonds correspond to a grapevine with a root system of 2 m without formation of soil-root air gaps (scenarios 1 and 2); the green squares to a plant with a deeper root system (3 m and 2.5 m for the sandy and loamy subplots respectively) without formation of soil-root air gaps (scenarios 3 and 4); the brown circles to a grapevine with a root system of 2 m with formation of soil-root air gaps (scenarios 5 and 6); and the blue triangles to a plant with a deeper root system (3 m and 2.5 m for the sandy and loamy subplots respectively) with formation of soil-root air gaps (scenarios 7 and 8). The full black lines are the 1:1 lines.

4.3. Results

Table 4.4 – Statistical analyses of comparisons between the simulated and measured $\Psi_{\text{bulk soil}}$, Ψ_{stem} and $\Psi_{\text{stem_PD}}$ for the scenarios with varying root system depth (L_r) and accounting for hydraulic disconnection between the soil and the roots (air gaps) in the sandy subplot. The R^2 and RMSE are the statistical analyses of the respective linear regressions. The p -values are derived from the Wilcoxon test to assess the significance of the difference between the distribution of measured and simulated data. Data are considered significantly different for a p -value < 0.01 . P -values greater than 0.05 are highlighted in green.

	Sandy subplot				
		Scenario 1	Scenario 3	Scenario 5	Scenario 7
$\Psi_{\text{bulk soil 10 cm}}$	R^2	$4*10^{-3}$	$4*10^{-3}$	0.04	0.34
	RMSE	0.09	0.08	0.07	0.05
	P -value	0	0	$5.82*10^{-6}$	$6.91*10^{-3}$
$\Psi_{\text{bulk soil 40 cm}}$	R^2	0.04	0.04	0.46	0.46
	RMSE	0.08	0.08	0.05	0.06
	P -value	0	0	$2.64*10^{-8}$	$1.51*10^{-4}$
$\Psi_{\text{bulk soil 100 cm}}$	R^2	0.99	0.99	0.99	0.99
	RMSE	0.07	0.09	0.11	0.04
	P -value	$4.47*10^{-16}$	$1.19*10^{-27}$	$1*10^{-3}$	0.77
Ψ_{stem}	R^2	0.56	0.68	0.82	0.89
	RMSE	0.29	0.28	0.19	0.12
	P -value	$1.85*10^{-72}$	$1.17*10^{-28}$	$2.59*10^{-8}$	0.84
$\Psi_{\text{stem_PD}}$	R^2	0.75	0.76	0.83	0.87
	RMSE	0.14	0.15	0.08	0.04
	P -value	$1.34*10^{-21}$	$4.06*10^{-19}$	$9*10^{-3}$	0.93

4. Soil-root hydraulic disconnection during drought

Table 4.5 – Statistical analyses of comparisons between the simulated and measured $\Psi_{\text{bulk soil}}$, Ψ_{stem} and $\Psi_{\text{stem_PD}}$ for the scenarios with varying root system depth (L_r) and accounting for hydraulic disconnection between the soil and the roots (air gaps) in the loamy subplot. The R^2 and RMSE are the statistical analyses of the respective linear regressions. The p -values are derived from the Wilcoxon test to assess the significance of the difference between the distribution of measured and simulated data. Data are considered significantly different for a p -value < 0.01. P -values greater than 0.05 are highlighted in green. P -values between 0.01 and 0.05 are highlighted in yellow.

		Loamy subplot			
		Scenario 2	Scenario 4	Scenario 6	Scenario 8
$\Psi_{\text{bulk soil 10 cm}}$	R^2	0.06	0.06	0.04	0.36
	RMSE	0.10	0.09	0.07	0.04
	P -value	0	0	7.64×10^{-5}	1.20×10^{-2}
$\Psi_{\text{bulk soil 40 cm}}$	R^2	0.79	0.80	0.80	0.83
	RMSE	0.09	0.08	0.07	0.06
	P -value	9.82×10^{-19}	9.33×10^{-6}	2.04×10^{-14}	0.03
$\Psi_{\text{bulk soil 100 cm}}$	R^2	0.93	0.94	0.95	0.94
	RMSE	0.03	0.04	0.06	0.04
	P -value	0.02	1×10^{-4}	2.05×10^{-28}	0.05
Ψ_{stem}	R^2	0.72	0.75	0.86	0.87
	RMSE	0.21	0.20	0.10	0.09
	P -value	1.69×10^{-50}	1.21×10^{-31}	8.00×10^{-3}	0.95
$\Psi_{\text{stem_PD}}$	R^2	0.41	0.68	0.81	0.95
	RMSE	0.15	0.15	0.03	0.02
	P -value	6.77×10^{-27}	4.91×10^{-24}	0.015	0.86

4.3.2. Root water uptake

Figure 4.5 displays the time cumulated RWU (S_{cum}) throughout the simulation period, for both subplots. A decreasing S_{cum} ($S < 0$) indicate water release to the soil, whereas an increasing S_{cum} ($S > 0$) correspond to water uptake by the roots. In both subplots, most of the water absorbed by roots comes from deep soil horizons, since hydraulic discontinuities between the soil and the roots, in the dry shallower horizons, limit RWU in these horizons (Figure S.4.4). Similar observations have been made in other perennial species such as *Quercus alba* and *Symphoricarpos orbiculatus* (Asbjornsen et al., 2008). Despite having lower root densities compared to the upper compartment, the deeper soil layers are the primary water supply zone during drought. In the sandy subplot, most of the water was absorbed in the ferrous horizons of the sandy subsoil (horizons S2, red line). In total, at the end of the simulation, 13.68 mm and 30.17 mm of water were taken up in the S1 and S2 horizons respectively (Figure 4.5a). Interestingly, looking horizon by horizon in the sandy subplot (Figure S.4.5), we can see that, at the end of the simulation, the plant has taken more water in the deeper S1 and S2 horizons, compared with the shallower S1 and S2 horizons, excepted for the first S2 layer (81-95 cm), where root density is larger. This is because more superficial S1 and S2 horizons are drier. The water potential and hydraulic conductance of these drier horizons are therefore lower, which limits RWU (Figures S4.4 and S4.5). Similarly, this explains why the plants absorb more water in S2 horizons than in S1 horizons. For example, 0.07 mm and 8.99 mm has been taken up in the first S1 horizon (51-80 cm) and S2 horizon (81-95 cm). The $\Psi_{bulk\ soil}$ in these two layers has varied, on average, from -0.07 MPa and -0.12 MPa in the S1 horizon, and from -0.03 MPa to -0.40 MPa in the S2 horizon during the simulation. This means that the hydraulic conductivity of the soil varied from $8.09 \cdot 10^{-9} \text{ cm.day}^{-1}$ to $9.15 \cdot 10^{-11} \text{ cm.day}^{-1}$ in the S1 layer (51-80 cm), and from $1.67 \cdot 10^{-3} \text{ cm.day}^{-1}$ to $5.75 \cdot 10^{-9} \text{ cm.day}^{-1}$ in the S2 layer (81-95 cm). The bulk soil is still a hundred times more water conductive in the layer S2 than in the layer

4. Soil-root hydraulic disconnection during drought

S1, despite a lower water potential. In the layers S1, a small decrease of water potential implies a large decrease of hydraulic conductivity.

In the loamy subplot, 78 % of the water transpired by the plant has been taken up in the last horizon (Bw2 – 81-250 cm) (Figure 4.5b), even though the root system is less dense at depth. In both subplots, since we started the simulation with a very dry soil at the soil surface, the water uptake in the first horizon (horizon Ap in both subplots) is limited. Only 4.06 mm and 4.48 mm has been absorbed in this first horizon, in the sandy and loamy subplots respectively.

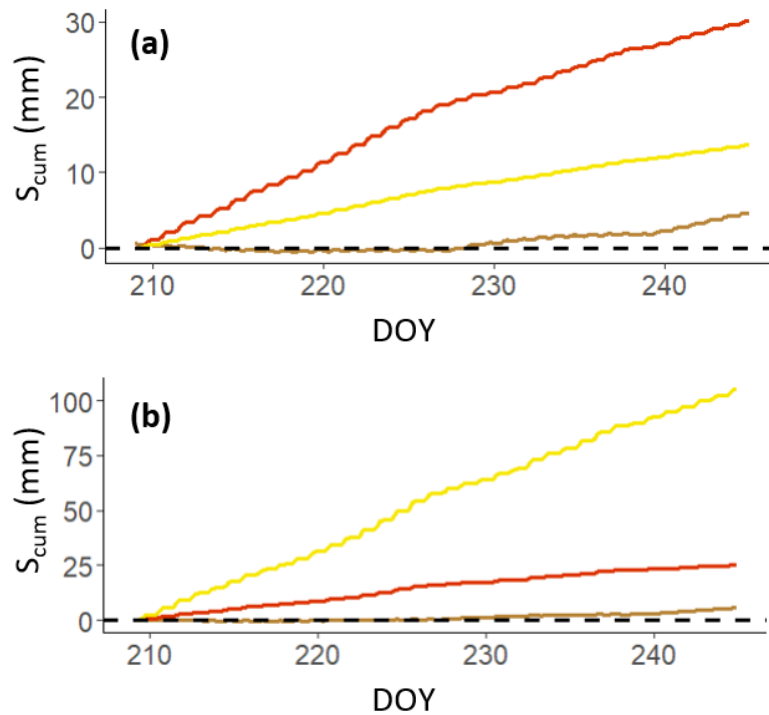


Figure 4.5 – Simulated time cumulated root water uptake (S_{cum}) by soil horizons in (a) the sandy subplot and (b) the loamy subplot. In (a), the brown line corresponds to the Ap horizon, yellow line to the sum of all S1 horizons and red line to the sum of all S2 horizons. In (b), the brown line corresponds to the Ap horizon, red line to the Bw1 horizon and yellow line to the Bw2 horizon. The dashed black lines correspond to $S_{cum} = 0$.

4.3.3. Rhizosphere hydraulic conductance

Figure 4.6 shows the evolution of the effective rhizosphere hydraulic conductance (K_{rhizo_eff} – equation 4.19) at midday (daily peak of transpiration), compared to the root system hydraulic conductance (K_{rs}) in both subplots. In the sandy subplot, K_{rhizo_eff} was greater than K_{rs} until DOY 219, then decreased until the end of the simulation, as the soil became drier (Figure 4.6a). However, K_{rhizo_eff} was always larger than K_{rs} for the loamy subplot (Figure 4.6b). K_{rhizo_eff} of the loamy subplot was ten times higher than K_{rhizo_eff} of the sandy subplot. Thus, we can affirm that in the sandy subplot, water uptake was mainly limited by the rhizosphere, while it was the conductance of the root system that limited water uptake in the loamy subplot.

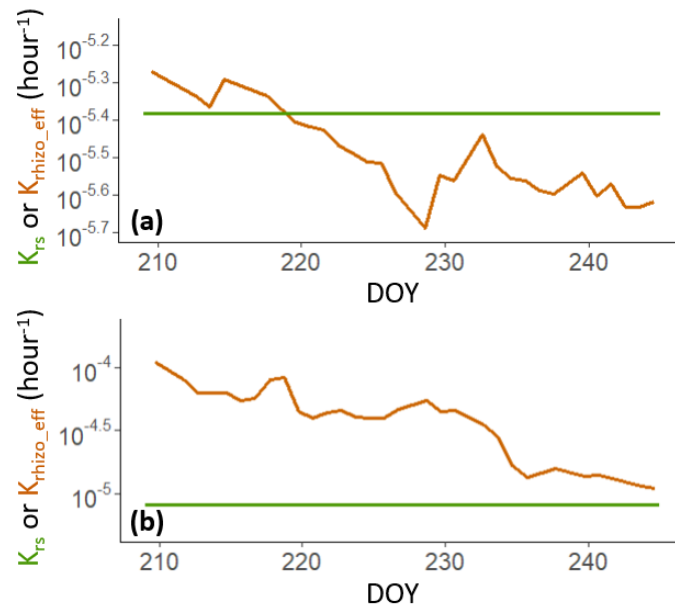


Figure 4.6 – Time series of midday effective rhizosphere hydraulic conductance (K_{rhizo_eff} - brown lines) and root system hydraulic conductance (K_{rs} - green lines) for the (a) sandy subplot and (b) loamy subplot.

4. Soil-root hydraulic disconnection during drought

In the same way as equation 4.19, we also calculated the evolution of K_{rhizo_eff} in each soil horizon of each subplot, thanks to the difference between an effective soil-root interface water potential and an effective bulk soil water potential in each horizon, and the total amount of water taken up in this same horizon. Figure 4.7 shows the evolution of K_{rhizo_eff} in each horizon at midday, compared to K_{rs} . In the sandy subplot, the S1 horizons were less conductive than the root system, with K_{rhizo_eff} of S1 horizons was ten to hundred times lower than K_{rs} (Figure 4.7a). K_{rhizo_eff} was ten times lower in the drier, more superficial S1 horizons than in the deeper, wetter S1 horizons (Figure S.4.6). On the other hand, in S2 horizons, K_{rhizo_eff} decreased over the course of the simulation but remained higher than K_{rs} . In the loamy subplot, K_{rhizo_eff} of horizons Bw1 and Bw2 decreased over the simulation period, as the soil dried out due to water uptake, but was always greater than K_{rs} (Figure 4.7b). In both subplots, K_{rhizo_eff} of horizon Ap was always lower than K_{rs} , due to the formation of soil-root air gaps in these dry soil horizons.

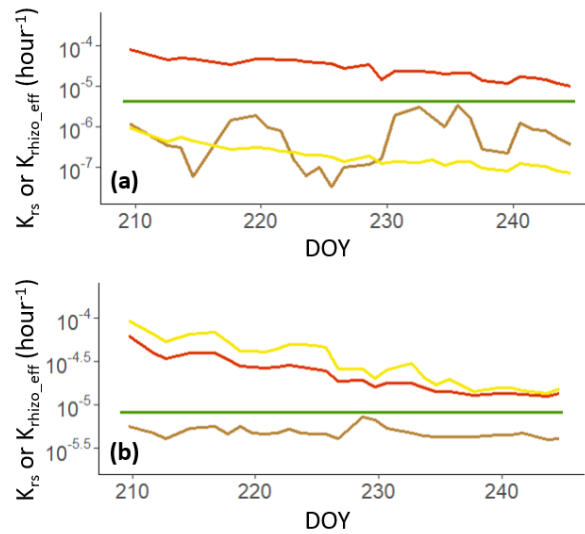


Figure 4.7 – Times series of midday effective rhizosphere hydraulic conductance (K_{rhizo_eff}) in the different soil horizons of the (a) sandy subplot and (b) loamy subplot. In (a), the full brown line corresponds to the Ap horizon, yellow line to all S1 horizons and red line to all S2 horizons. In (b), the full brown line corresponds to the Ap horizon, red line to the Bw1 horizon and yellow line to the Bw2 horizon. In both figures, the green lines correspond to the respective root system hydraulic conductance (K_{rs}).

4.4. Discussion

In this study, we used a model that links root system hydraulics and rhizosphere hydraulics, and that includes hydraulic disconnection between soil and roots in dry soils, to estimate the distribution and evolution of hydraulic conductances of belowground soil-grapevine systems in different soil types during drought. The objective was to understand how RWU may be affected by the local dynamisms of hydraulic conductances between the bulk soil and the plant stem collar.

By comparing observed and simulated $\Psi_{\text{bulk soil}}$ and Ψ_{stem} , we obtained similar values when we included, in our model, a hydraulic discontinuity (e.g. soil-root air gaps) in the rhizosphere. These soil-root air gaps enable the plant to maintain relatively high (less negative) Ψ_{stem} levels. This hydraulic disconnection between the soil and the roots in dry soil horizons can be seen as an “avoidance” strategy (Tardieu, 2011) that allows the grapevines not to feel driest soil horizons and results in an increased Ψ_{stem} (Couvreur et al., 2014), which is therefore more impacted by the wettest zones of the soil in field conditions (Richter, 1997; Schmidhalter, 1997). The hydraulic disconnection also prevents water loss to the drying soil, as observed by Nobel and Cui (1992). The formation of soil-root air gaps has already been observed in other old and recent studies, for different species (Carminati et al., 2013; Duddek et al., 2023; Faiz and Weatherley, 1982; Nye, 1994), and it has been shown that it significantly limits the water fluxes between the soil and the roots by greatly decreasing the hydraulic conductance in these zone (Zur et al., 1982).

In this work, we related the hydraulic discontinuity between the soil and the roots to the rhizosphere conductance. However, other processes may relate the hydraulic disconnection to root hydraulic conductance. The precise locations and sequence of physiological events that cause soil-root dysfunction remain largely elusive (Cuneo et al., 2021). Roots

4. Soil-root hydraulic disconnection during drought

are theorized to function like electrical fuses, hydraulically disconnecting when exposed to drought conditions (Duddek et al., 2023; Jackson et al., 2000). Cuneo et al. (2016) showed that cortical lacunae and the collapse of root cortex tissue during drought affect the grapevine root radial hydraulic conductance, and lead to root shrinkage and to the formation of gap between the soil and the roots. We also investigated this approach in a simple way by considering that the root hydraulic conductance K_r became null in dry soil horizons after reaching a threshold ($K_r(z) = 0$ when $\Psi_{SRI} < -0.8$ MPa). Given the similar results that the approach presented in this study, considering that hydraulic disconnection is a rhizosphere process, we decided to not present these results in the main text, but they are available in the Appendix 2 of the Supplementary materials.

The poor quantitative understanding of rhizosphere hydrophobicity or root shrinkage, in soil-grapevine systems, justify the simple representations of hydraulic disconnection between the soil and the roots used in this work. We considered a loss of contact between soil and roots when $\Psi_{\text{bulk soil}}$ and Ψ_x fell below a fixed threshold of -0.8 MPa., and a recovered contact if $\Psi_{\text{bulk soil}}$ and/or Ψ_x rise above this threshold, regardless of soil type, or of root type and age. However, it has been observed that there is a vertical gradient in gap formation around the tap root, characterized by larger gaps at the basal part and smaller gaps towards the apical part. Gaps originated near the root collar, losing contact with the soil before reaching the apical part of the tap root (Carminati et al., 2013). It has also been shown that the proportion of root disconnected from the soil varies depending on the type and age of the roots, and on the soil type (Nye, 1994). However, this has been studied on species other than grapevines. Further investigations need to be made into the relationship between the proportion of gap formation between soil and roots, soil type, root type and their age. This would demand a considerable increase of the model complexity. Cuneo et al. (2016) found that cortical lacunae, that could lead to root shrinkage and formation of gap between soil and roots, appeared first in the fine roots, and then in coarse and older roots. However, only fine roots (< 1 mm – Perry et al., 1983), which constitute

96 % of the root density of the root systems in each subplot, has been considered in this study.

Another type of processes potentially impacting soil-root hydraulics is aquaporin activity (Steudle, 2000b). Aquaporin regulation has been shown to radically impact root radial hydraulic conductance, due to the presence of the “Caspian band” (impermeable layer of cell walls) on the pathway between soil and root xylem, forcing water to cross cell membranes through aquaporins (Barrowclough et al., 2000). These changes in conductance can be relatively rapid and reversible. Like soil-root air gaps, aquaporin activity also hydraulically disconnect the soil and the roots, and avoid water to be released from the roots to the soil (Vandeleur et al., 2009). However, it is hard to find a common response to root aquaporin expression under drought conditions in grapevines (Aroca et al., 2012). For example, Vandeleur et al. (2009) showed a down-regulation of aquaporin activity in drought conditions for a near-isohydric grape variety, and an up-regulation for a near-anisohydric cultivar. The rootstock also influences aquaporin expression, with drought-tolerant rootstocks showing greater aquaporin activity than drought-sensitive rootstocks (Gambetta et al., 2012), such as 3309C used in this study. Hydraulic disconnection between the soil and the roots could also be caused by suberin and lignin depositions, restricting or inhibiting the apoplastic water flow (Aroca et al., 2012). In grapevines, it has been shown that water deficit conditions promote root suberization (Barrios-Masias et al., 2015; Vandeleur et al., 2009). Root xylem cavitation could also affect belowground hydraulics. However, xylem cavitation in grapevines were observed at root water potentials of -1.8 MPa in fine roots and -3.5 MPa in coarse roots (Cuneo et al., 2016), for different rootstocks (Lamarque et al., 2023). We never observed such low water potentials in this study and therefore hypothesized that there was no root xylem cavitation. Moreover, Cuneo et al. (2016) also found that the xylem stays largely functional in grapevine roots even when cortical lacunae have formed, permitting the xylem to remain largely hydraulically conductive. Additional processes, such as the change of root mucilage property toward hydrophobicity in drought conditions, could also decreased hydraulic

4. Soil-root hydraulic disconnection during drought

conductance between the soil and roots (Carminati and Vetterlein, 2012). Further works should be done to better understand the influence of all these mechanisms, impacting rhizosphere and root hydraulics, on water uptake by grapevine roots, for different rootstocks and soil types. We need to ascertain which mechanisms, and which signals (hydraulics or chemicals) are responsible for belowground hydraulic dynamics during drought stress for grapevines. Although the dynamics and magnitude of these processes are still unclear, the factors impacting soil-root hydraulics in drought conditions, such as soil-root contact or root aquaporin activity, respond simultaneously rather than independently (Lei et al., 2023).

It must also be noted that we considered the water uptake in the soil profile by a nongrowing root system. In this study, root hydraulic properties are fixed throughout the whole simulation period. However, they could change due to growth of new roots or/and regrowth from the distal meristem of roots already present (Jackson et al., 2000). Alsina et al. (2011) showed that drought-sensitive rootstocks, such as 3309C used in this study, kept a more constant root hydraulic conductance between June and September (between fruit setting and harvest), during a drought, compared to a drought-tolerant rootstock. They explained that the change of root hydraulic conductance for the drought-tolerant rootstock was due to root growth during the drought period, with roots exploring new deep wet soil horizons. In this study, we therefore hypothesized that root growth during the simulated period did not play a major role in the dynamics and distribution of belowground hydraulics, but further works are needed to valid this assumption. A root system that extends into deeper and wetter soil layers may experience a more heterogeneous water distribution in its root zone, resulting in a greater soil-root system conductance compared to a static root system that uniformly dries out the root zone (Alsina et al., 2007; Vanderborght et al., 2023). Our understanding of grapevine rootstock architecture in the field remains limited due to the challenges associated with accessing the root system of the vine (Fichtl et al., 2023). Knowledge about root morphology and root development grown *in situ*, and their relationship with grapevine performance in established vineyards, root growth

plasticity, root growth dynamics and water uptake capacity is particularly limited (Cuneo et al., 2021; Ollat et al., 2017). Root growth models describe the progression of root growth over time, frequently in relation to factors such as water availability or nutrient levels (Fichtl et al., 2023). Further progress can be made by extending our RWU model by integrating it with a dynamic crop growth model, similar to the approach in Nguyen et al. (2020) and Nguyen et al. (2022). This coupling would allow for a better exploration of relationships and feedbacks between RWU, root development, crop growth and their interactions with the rhizosphere (Soualiou et al., 2021; Vanderborght et al., 2023). Additional experiments are required to assess how root growth of grapevines affects water uptake, for different rootstocks and in different soil types, and to understand how it integrates with other responses described above.

In Chapter 3, we showed that the actual transpiration flux was downregulated by stomatal closure for grapevines planted on the sandy subplot, at less negative soil water potential compared to the loamy subplot. This downregulation was sharper in the sandy than in the loamy subplot. This stomatal response was triggered by a decrease in belowground hydraulic conductance and not by xylem cavitation in the stem. However, we did not manage to show how the belowground hydraulic conductances (rhizosphere and root system) were distributed and evolved over time. In this work, we showed that the rhizosphere hydraulic conductance in the sandy subplot became significantly lower than the root system hydraulic conductance during the simulation, but we observed the opposite in the loamy subplot (Figure 4.6). In both subplots, the formation of soil-root air gaps decreased considerably the rhizosphere hydraulic conductance in the dry surface horizons (horizon Ap), becoming lower than the root system hydraulic conductance (Figure 4.7). On the sandy subplot, the rhizosphere conductance of pure S1 sand horizons was also lower than that of the root system. RWU was therefore mainly limited by rhizosphere hydraulic conductance in the S1 horizons. Nye (1994) already observed that, except in dry sandy soil, the main resistance to water inflow lies in the root tissues. Cai et al. (2022) observed that, during soil drying, the decline in soil hydraulic

4. Soil-root hydraulic disconnection during drought

conductivity led to a steep reduction in soil matric potential at the soil-root interface, with greater reduction in sandy soils compared to loamy soils. In dry coarse-texture soils, a small reduction in water potential implies a large decrease in hydraulic conductivity (Nobel and Cui, 1992). This more rapid decrease in soil hydraulic conductivity implies that the sandy soil is more rapidly limiting, triggering earlier and sharper stomatal closure (Carminati and Javaux, 2020). The presence of S1 sandy horizons could therefore explain limited stomatal conductance of grapevines in the sandy subplot, which limited grapevine transpiration compared to the loamy subplot.

4.5. Conclusion and perspectives

To investigate the origin, distribution and dynamics of belowground hydraulic conductances of grapevines planted on different soil type with varying horizons, soil-grapevine hydrodynamics was simulated in 1-D. The objective was to understand how belowground hydraulics between the soil and the grapevine stem collar affects RWU in different soil types. We validated our model by comparing measured and simulated soil and plant water potential, and showed that the consideration of root system longer than 2 m and the loss of hydraulic contact between soil and roots in dry shallower horizons were needed to match the observations with the simulations. These conditions allowed the plant to not reach very negative stem water potential that could lead to xylem cavitation. Moreover, soil-root hydraulic disconnection limited RWU in the shallower dry soil horizons of both subplots, leading to a shift of water uptake fraction toward deeper wet zones of the soil. Overall, in the sandy subplot, RWU was mainly limited by the rhizosphere ($K_{\text{rhizo_eff}} < K_{\text{rs}}$), while it was the conductance of the root system that limited water uptake in the loamy subplot ($K_{\text{rhizo_eff}} > K_{\text{rs}}$). The very low $K_{\text{rhizo_eff}}$ of the sandy subplot was mainly due to a large decrease of $K_{\text{rhizo_eff}}$ in the pure sand horizons (S1), with these horizons were a

hundred times less water conductive than the root system, and to hydraulic disconnection between the soil and the roots in the dry surface horizon. Several mechanisms such as soil-root air gaps, aquaporin activity, root suberization, root xylem cavitation or root growth, could participate in the hydraulic disconnection or reconnection between soil and roots in dry soils, and therefore in the dynamics of belowground hydraulics. Further investigations are needed to understand how these processes concomitantly work and affect belowground hydraulics during drought. Our model could also be coupled to models that consider aboveground hydraulics (Janott et al., 2011) or chemical signals for stomatal regulation (Huber et al., 2014) or aquaporin activity (Dodd et al., 2010), and that need estimations of stem and/or soil water potentials. These couplings would allow investigating how hydraulic and chemical signalling simultaneously affect grapevine hydraulic dynamics.

4.6. Supplementary material

4.6.1. Supplementary figures

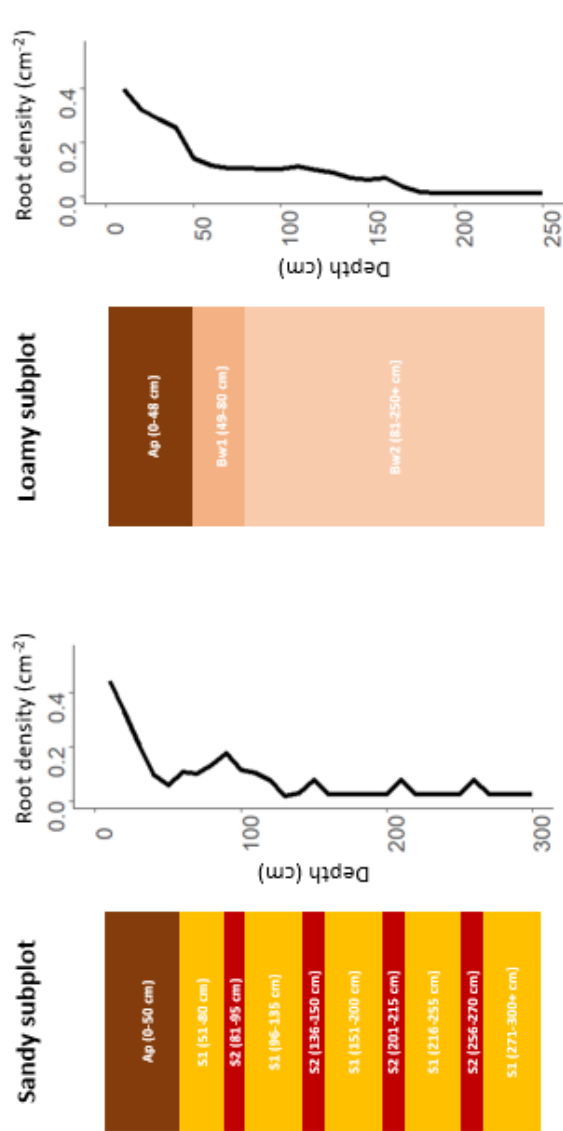


Figure S.4.1 – Soil profile horizon delineation of each subplot and root density used for the simulations.

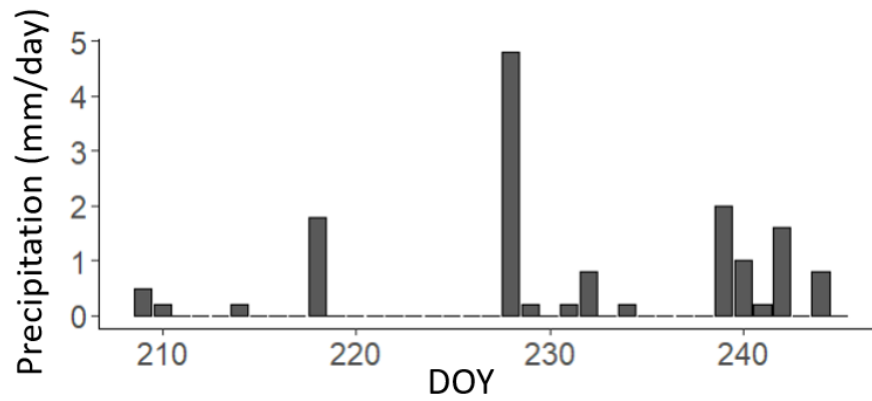


Figure S.4.2 – Daily precipitation measured by a weather station in the vineyard during the measurement campaign, between DOY 209 and DOY 245 in 2022.

4. Soil-root hydraulic disconnection during drought

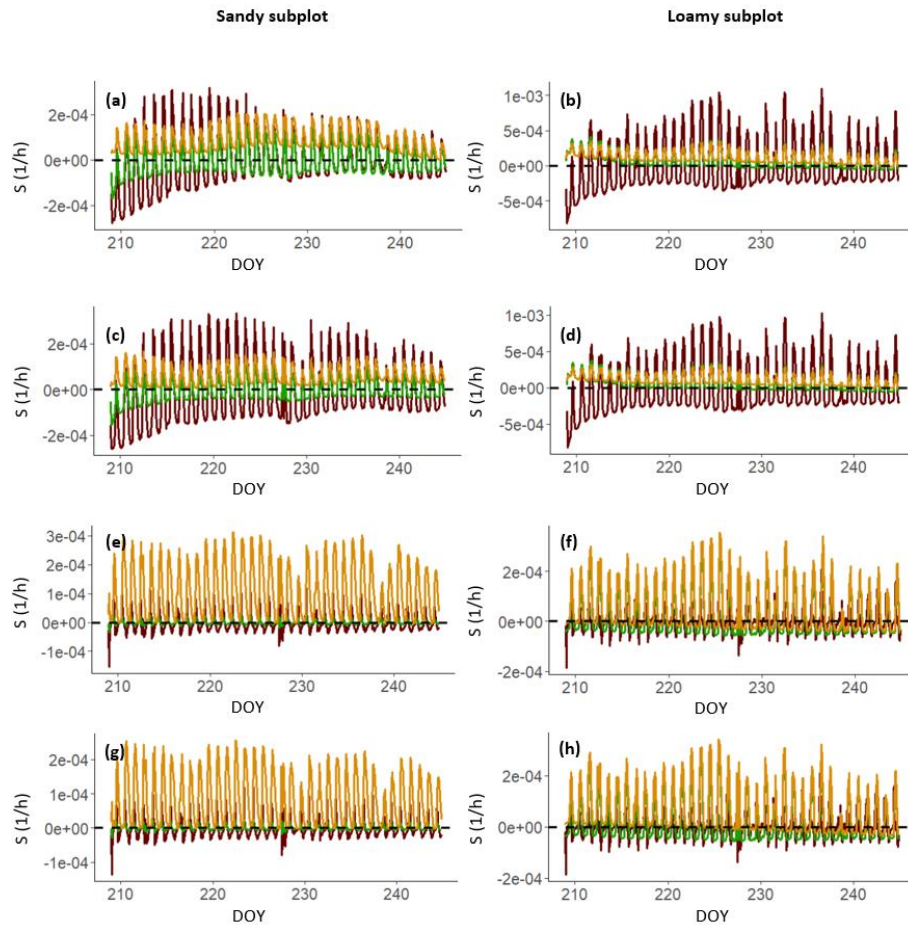


Figure S.4.3 – Simulated water sink (S) at 10 cm (brown line), 40 cm (green line) and 100 cm (orange line) depth. (a) and (b) correspond to a grapevine with a root system of 2 m depth, without formation of soil-root air gaps (scenarios 1 and 2); (c) and (d) correspond to a grapevine with a root system of 3 m and 2.5 m depth respectively, without formation of soil-root air gaps (scenarios 3 and 4); (e) and (f) correspond to a grapevine with a root system of 2 m depth, with formation of soil-root air gaps (scenarios 5 and 6); (g) and (h) correspond to a grapevine with a root system of 3 m and 2.5 m depth respectively, with formation of soil-root air gaps (scenarios 7 and 8).

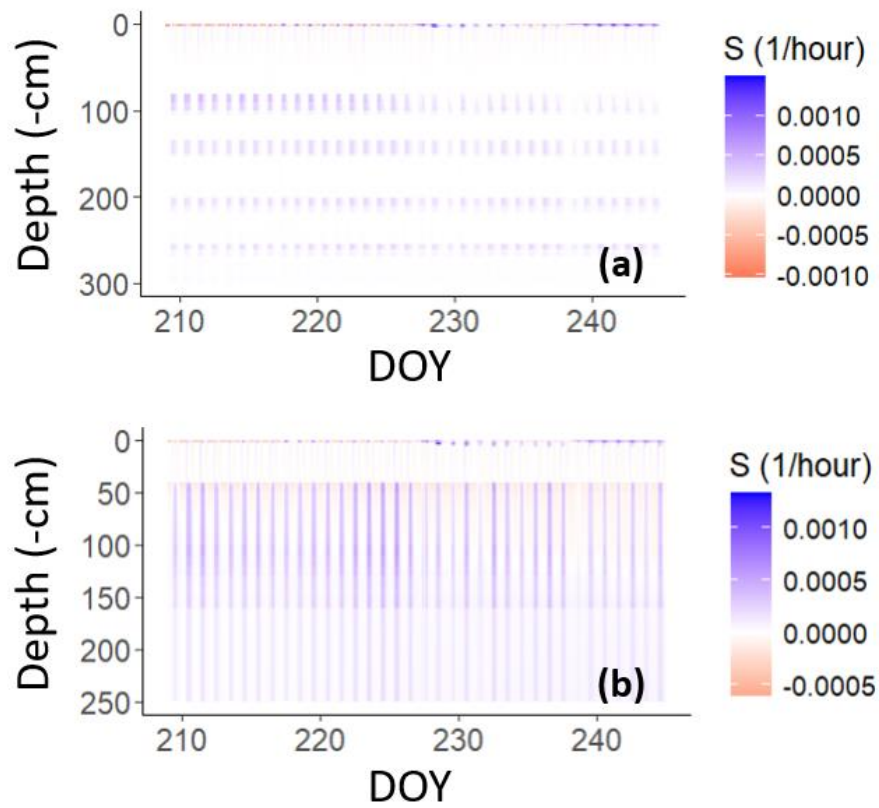


Figure S.4.4 – Spatial and temporal distribution of the sink term (S) over the simulated period, in the (a) sandy subplot and (b) the loamy subplot.

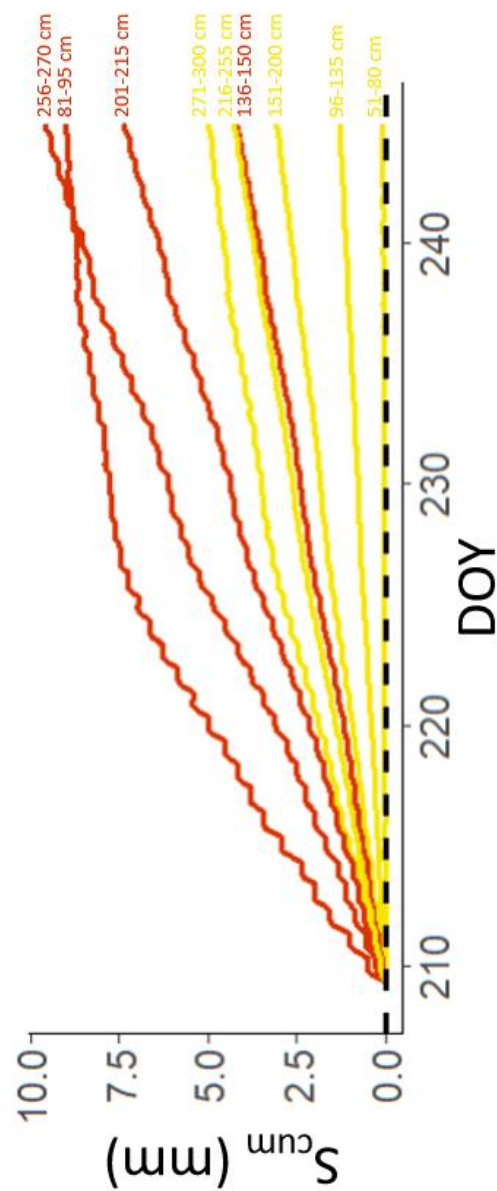


Figure S.4.5 – Simulated cumulated water sink (S_{cum}) in the different horizons S1 (yellow lines) and S2 (red lines) horizons of the sandy subplot.

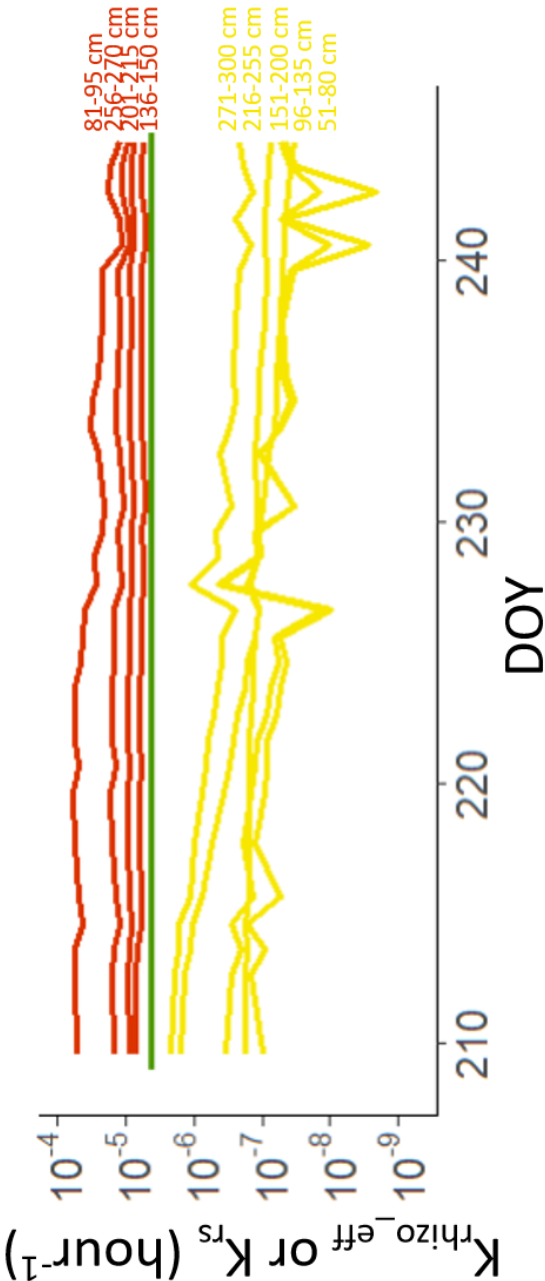


Figure S.4.6 – Times series of midday (peak of daily transpiration) effective rhizosphere hydraulic conductance (K_{rhizo_eff}) in the different horizons S1 (yellow lines) and S2 (red lines) horizons of the sandy subplot. The green line is the root system hydraulic conductance (K_{rs}).

4. Soil-root hydraulic disconnection during drought

4.6.2. Supplementary tables

Table S.4.1 – Sensitivity analysis to find the water potential threshold at the soil-root interface (Ψ_{SRI}) at which there is a loss of contact between soil and root. The values presented are the p -values of the Wilcoxon statistical tests comparing the corresponding measured and simulated data. We selected the Ψ_{SRI} threshold for which the p -value was highest (highlighted in green). The root systems are fixed at 3 m depth for the sandy subplot, and 2.5 m depth for the loamy subplot.

Ψ_{SRI}		-0.5 MPa	-0.6 MPa	-0.7 MPa	-0.8 MPa	-0.9 MPa	-1 MPa
Sandy subplot	Ψ_{stem}	$3 \cdot 10^{-4}$	$3 \cdot 10^{-4}$	$2 \cdot 10^{-3}$	0.84	0.09	0.09
	Ψ_{PD}	$1.95 \cdot 10^{-6}$	$9.5 \cdot 10^{-4}$	0.12	0.93	0.32	0.41
Loamy subplot	Ψ_{stem}	$4 \cdot 10^{-3}$	0.021	0.029	0.95	0.15	0.12
	Ψ_{PD}	$2.51 \cdot 10^{-5}$	$1.36 \cdot 10^{-3}$	0.15	0.86	0.34	0.04

Table S.4.2 – Sensitivity analysis to find the root depth. The values presented are the p -values of the Wilcoxon statistical tests comparing the corresponding measured and simulated data. We selected the root depth (L_r) for which the p -value was highest (highlighted in green). The threshold at which the soil-root air gaps are formed is fixed at -0.8 MPa.

L_r		2 m	2.10 m	2.20 m	2.30 m	2.40 m	2.50 m	2.60 m	2.70 m	2.80 m	2.90 m	3 m	3.10 m
Sandy subplot	ψ_{stem}	$2.6 \cdot 10^{-8}$	$2 \cdot 10^{-4}$	$5 \cdot 10^{-4}$	0.01	0.06	0.61	0.09	0.21	$3.4 \cdot 10^{-5}$	$4 \cdot 10^{-5}$	0.72	0.63
	ψ_{PD}	$9 \cdot 10^{-3}$	$4 \cdot 10^{-3}$	$7 \cdot 10^{-3}$	0.02	0.03	0.12	0.05	0.09	0.01	0.03	0.99	0.82
Loamy subplot	ψ_{stem}	0.01	0.06	0.24	0.57	0.94	0.95	0.39	0.16				
	ψ_{PD}	0.01	0.06	0.18	0.44	0.82	0.86	0.43	0.21				

4.7. Appendix

Appendix 4.1 - Pseudo code of the root water uptake function, considering a hydraulic disconnection between the soil and the roots in dry soil horizons ($h_{\text{threshold}} = -8000 \text{ cm}$)

1. Start with the j^{th} estimate of the soil-root interface water potential vector Ψ_{SRI}^j and calculate Ψ_{stem} , $\mathbf{Q}$ ($[\text{L}^3 \text{ T}^{-1}]$ is the vector of flow rates to root nodes), and Ψ_x . The initial estimate of Ψ_{SRI}^0 can be either the bulk soil water potential ($\Psi_{\text{bulk soil}}$) or the Ψ_{SRI} from the previous step.

$$\Psi_{\text{SRI}_{eff}}^j = \mathbf{SUF}^T * \Psi_{\text{SRI}}^j,$$

$$\Psi_{\text{stem}}^j = \max\left(\Psi_{\text{stem},\text{lim}}, \Psi_{\text{SRI}_{eff}}^j - \frac{T_p}{K_{rs}}\right),$$

$$\begin{aligned} \mathbf{Q}^j = & K_{rs} * \mathbf{SUF} * \left(\Psi_{\text{SRI}_{eff}}^j - \Psi_{\text{stem}}^j\right) + K_{rs} * \mathbf{SUF} \\ & * \left(\Psi_{\text{SRI}}^j - \Psi_{\text{SRI}_{eff}}^j\right), \end{aligned}$$

$$\Psi_x^j = \Psi_{\text{SRI}}^j - \mathbf{Q}^j * \mathbf{K}_r^{-1}. \quad (\text{A4.1})$$

2. Update Ψ_{SRI}^j and obtain Ψ_{SRI}^{j+1} :

If $\Psi_{\text{bulk soil}}^{j+1}[i] - z[i] < h_{\text{threshold}}$ and $\Psi_x^{j+1}[i] - z[i] < h_{\text{threshold}}$

$$Q^{j+1}[i] = 0,$$

$$\Psi_{SRI}^{j+1}[i] = \Psi_{\text{stem}}. \quad (A4.2)$$

Elseif for $i = 1$ to $i = \text{length } \Psi_{SRI}$

solve

$$\Psi_{SRI}^{j+1}[i] = 0 \quad (A4.3)$$

(solve can be any non-linear solver that solves the above equation for $\Psi_{SRI}^{j+1}[i]$)

If $\Psi_{SRI}^{j+1}[i] - z[i] < h_{\text{threshold}}$ and $\Psi_x^j[i] < \Psi_{SRI}^j[i]$ (water flows from the soil to the root)

$$Q^{j+1}[i] = 2\pi * l_{\text{root}}[i] * B[i] * \bar{k}_{rhizo}(\max(h_{bs}[i], h_{\text{threshold}}), \max(\Psi_{SRI}^{j+1}[i] - z[i], h_{\text{threshold}})) * (h_{bs}[i] - h_{\text{threshold}}),$$

$$\Psi_{SRI}^{j+1}[i] = \Psi_x^j[i] + \frac{Q^{j+1}[i]}{K_r[i]}. \quad (A4.4)$$

4. Soil-root hydraulic disconnection during drought

Elseif $\Psi_{SRI}^{j+1}[i] - z[i] < h_{threshold}$ and $\Psi_x^j[i] > \Psi_{SRI}^j[i]$ (water flows from the root to the soil)

$$Q^{j+1}[i] = 2\pi * l_{root}[i] * r_{root}[i] * k_r[i] * (h_{threshold} - (\Psi_x^j[i] - z[i])),$$

$$\Psi_{SRI}^{j+1}[i] = h_{threshold} + z[i]. \quad (A4.5)$$

3. Update Ψ_{collar} , $\mathbf{Q}$, and Ψ_{xylem} in equation A4.1.
4. Check for convergence and repeat, if necessary, the iteration loop.

Appendix 4.2 – Results for which the soil-root hydraulic disconnection is related to the root hydraulic conductance

To relate the formation of soil-root air gaps to root hydraulics, we considered that there was a total loss of contact between the soil and the roots when the soil-root water potential (Ψ_{SRI}) reached the threshold of -0.8 MPa. This means that $K_r(z)$ is null when the Ψ_{SRI} at the depth z is less than this threshold. This approach implies that at each time iteration, SUF and K_r profiles are recalculated, as proposed by (Couvreur et al., 2014):

$$SUF(z) = \frac{K_r(z)}{\sum_z K_r(z)}, \quad (A4.6)$$

with:

$$\begin{aligned} K_r(z) &= 0 && \text{when } \max(\Psi_{SRI}(z), \Psi_{stem}) < -0.8 \text{ MPa}, \\ K_r(z) &= K_r(z)_{init} && \text{when } \max(\Psi_{SRI}(z), \Psi_{stem}) \geq -0.8 \text{ MPa}. \end{aligned} \quad (A4.7)$$

We tested two different approaches: a first one which is reversible, meaning that the contact is restored between the soil and the roots at night and/or when the soil is rewetted, and second one for which soil-root air gaps are irreversible, except when the soil is rewetted by precipitation, allowing growth of new roots and reestablishment of root hydraulic properties (and soil-root contact) in the first few centimetres of the soil (Cuneo et al., 2016; Huck et al., 1970). For the reversible approach, we hypothesized that at a depth z for which there is a gap between the soil and the roots, the xylem water potential in the roots is

4. Soil-root hydraulic disconnection during drought

equal to Ψ_{stem} . Since at night, the Ψ_{stem} is above the threshold of -0.8 MPa, the contact is reformed between the soil and the roots. We also tested an irreversible approach, since Cuneo et al. (2016) showed that cortical lacunae irreversibly damage the root structure and root hydraulic conductance did not recover after rewatering, except if new roots are formed from the distal meristem of roots already present (Cuneo et al., 2021). Since the results are similar for both approaches, and also compared to the approach for which root-air gaps are related to the rhizosphere (elaborated in the main document of this study), we invite the reader to refer to the main document for the interpretations of the figures A4.1 and A4.2.

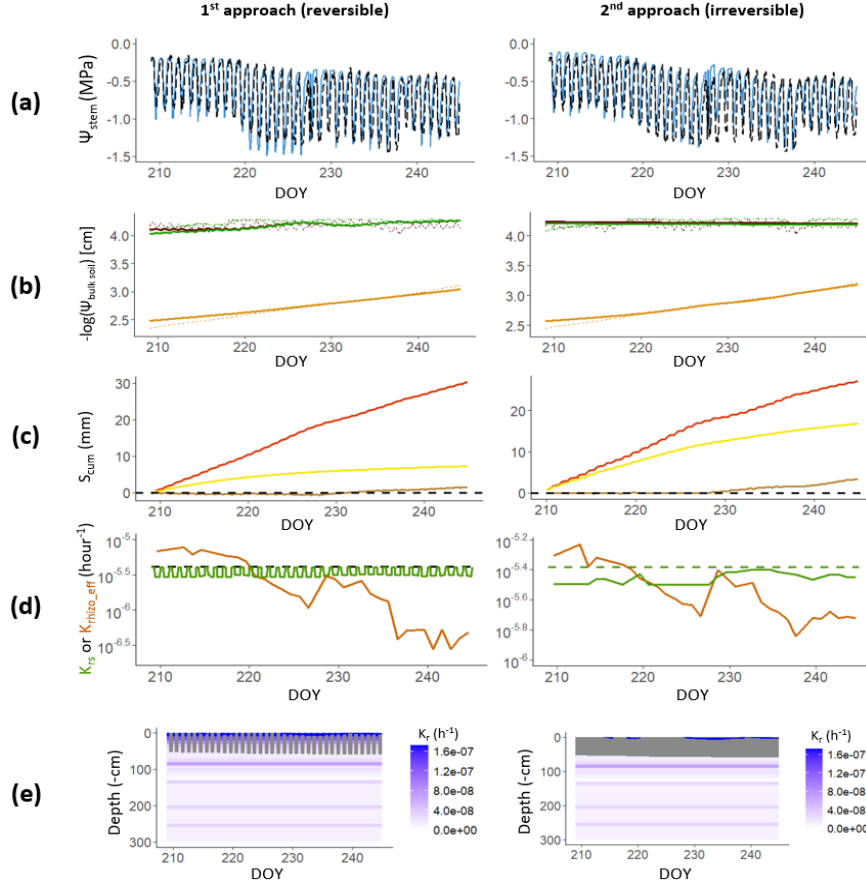


Figure A.4.1 – These graphs relate to the sandy subplot. **(a)** Measured (dashed black lines) and simulated (blue full lines) Ψ_{stem} times series. **(b)** Measured (dashed lines) and simulated (full lines) $\Psi_{bulk\ soil}$ at 10 cm (brown), 40 cm (green) and 100 cm (orange) depth. **(c)** Simulated time cumulated root water uptake (S_{cum}) by soil horizons. The brown lines correspond to the Ap horizon, yellow lines to the sum of all S1 horizons and red lines to the sum of all S2 horizons. The dashed black lines correspond to $S_{cum} = 0$. **(d)** Time series of midday effective rhizosphere hydraulic conductance (K_{rhizo_eff} - brown lines) and root system hydraulic conductance (K_{rs} - green lines). The full green lines are K_{rs} considering the formation of soil-root air gaps in dry soil horizons (root radial conductance is null at these depths). The dashed green lines are K_{rs} measured for a plant in a wet soil, for which there is full contact between the soil and the root system, corresponding to $K_{rs} = 4.04 \times 10^{-6} \text{ hour}^{-1}$. **(e)** Time evolution of root radial conductance (K_r). Zones in grey are areas where there is a loss of contact between the soil and the roots. In these grey zones, K_r is null.

4. Soil-root hydraulic disconnection during drought

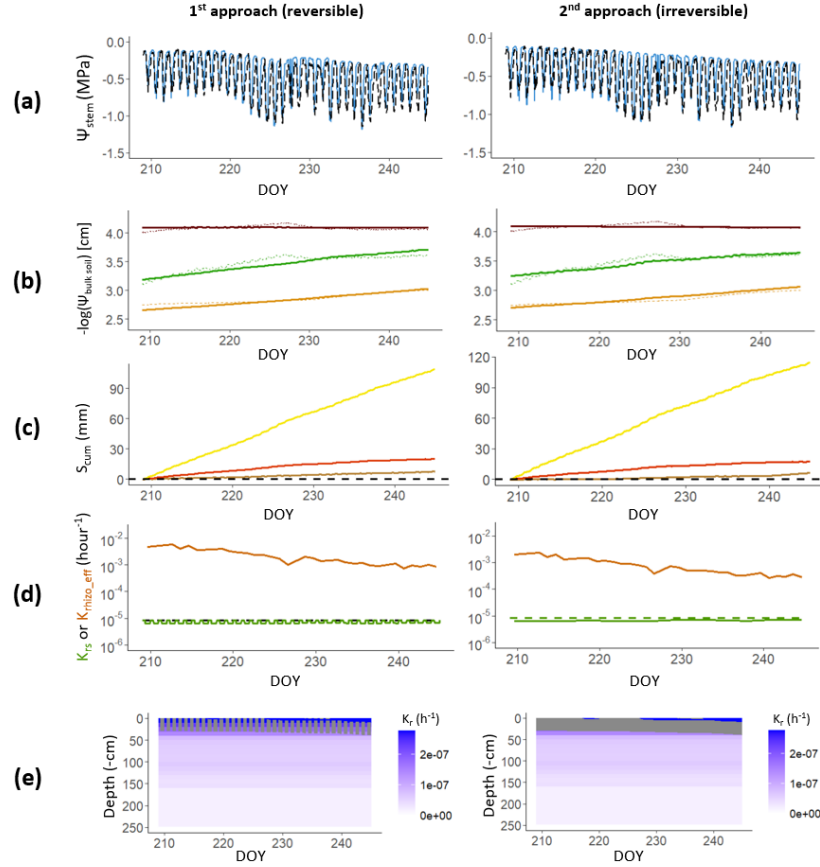


Figure A.4.2 – These graphs relate to the loamy subplot. **(a)** Measured (dashed black lines) and simulated (blue full lines) Ψ_{stem} times series. **(b)** Measured (dashed lines) and simulated (full lines) $\Psi_{bulk\ soil}$ at 10 cm (brown), 40 cm (green) and 100 cm (orange) depth. **(c)** Simulated time cumulated root water uptake (S_{cum}) by soil horizons. The brown lines correspond to the Ap horizon, yellow lines to the Bw1 horizon and red lines to Bw2 horizons. The dashed black lines correspond to $S_{cum} = 0$. **(d)** Time series of midday effective rhizosphere hydraulic conductance (K_{rhizo_eff} - brown lines) and root system hydraulic conductance (K_{rs} - green lines). The full green lines are K_{rs} considering the formation of soil-root air gaps in dry soil horizons (root radial conductance is null at these depths). The dashed green lines are K_{rs} measured for a plant in a wet soil, for which there is full contact between the soil and the root system, corresponding to $K_{rs} = 8.26 \times 10^{-6}$ hour⁻¹. **(e)** Time evolution of root radial conductance (K_r). Zones in grey are areas where there is a loss of contact between the soil and the roots. In these grey zones, K_r is null.

5. Mapping field-scale grapevine leaf water potential with very-high-resolution UAS multispectral, thermal and LiDAR data

This chapter is based on the article:

Delval, L., Bates, J., Jonard, F., Javaux, M. Field heterogeneity of soil texture controls leaf water potential spatial distribution in non-irrigated vineyards, in revision in *Biogeosciences*.

ABSTRACT

Grapevine water status exhibits substantial variability even within a single vineyard. Understanding how edaphic, topographic and climatic conditions impact grapevine water status heterogeneity at the field scale, in non-irrigated vineyards, is essential for winemakers as it significantly influences wine quality. This study aimed to quantify the spatial distribution of grapevine (*Vitis vinifera* cv. Chardonnay) leaf water potential (Ψ_{leaf}) within vineyards and to assess the influence of soil properties heterogeneity, topography and weather on this intra-field

5. Mapping grapevine leaf water potential with UAS data

variability, in two non-irrigated vineyards during two viticultural seasons. By combining multilinearly vegetation indices from very-high spatial resolution multispectral, thermal and LiDAR imageries collected with unmanned aerial systems, we efficiently and robustly captured the spatial distribution of Ψ_{leaf} across both vineyards, at different dates. Our results demonstrated that in non-irrigated vineyards, the spatial distribution of Ψ_{leaf} was mainly governed by the within-vineyard soil hydraulic conductivity heterogeneity (R^2 up to 0.86), and was particularly marked when the evaporative demand and the soil water deficit increased, since the range of Ψ_{leaf} was greater, up to 0.73 MPa, in these conditions. However, topographic attributes (elevation and slope) were less related to grapevine Ψ_{leaf} variability. These findings show that soil properties within-field spatial distribution and weather conditions are the primary factors governing Ψ_{leaf} heterogeneity observed in non-irrigated vineyards, and their effects are concomitants.

5.1. Introduction

Accurately quantifying grapevine water status is crucial for winemakers as it significantly impacts wine quality (Dry and Loveys, 1999; Van Leeuwen et al., 2009b). Detailed spatial information on grapevine water status can be particularly useful for providing guidelines on viticultural management to optimize grape production. This is especially important in the context of climate change, which poses crucial challenges for fresh water use in viticulture (Gambetta et al., 2020b). Many authors have demonstrated that grapevine water status exhibits substantial variability even within a single field, particularly when significant water restriction is found (Acevedo-Opazo et al., 2010; Brillante et al., 2017a; Tisseyre et al., 2005). Measuring leaf and/or stem water potential is an effective method to assess grapevine water status (Choné et al., 2001) but accurate measurements of leaf and stem water

potentials are usually achieved on single plants using a Scholander pressure bomb (Scholander et al., 1965) or with psychrometers. Several authors reported high magnitude of variation of leaf water potential over the viticultural season (e.g. 1.6 MPa in Ojeda et al. (2005)) and at the within field level (e.g. 1.2 MPa in Ojeda et al. (2005); 0.7 MPa in Brillante et al. (2017a)). Yet, these methods are time-consuming and labour-intensive and are therefore not effective to capture instantaneously within-field heterogeneity of grapevine water status (Romero et al., 2018), particularly under heterogeneous soil and microclimatic conditions generally observed in a vineyard.

Remote sensing technological advances give good opportunities for time- and cost-efficient detection of spatial and temporal variability of plant water status (Acevedo-Opazo et al., 2008). Particularly, unmanned aerial systems (UAS) are useful tools to assist precision viticulture thanks to high spatial resolution imagery, allowing differentiation of row and inter-row information. UAS can transport different sensors to measure and estimate plant traits, e.g., canopy area, biomass, leaf pigment concentration or grapevine water status, through vegetation indices (VIs) (Baluja et al., 2012; Poblete et al., 2017; Romero et al., 2018; Serrano et al., 2010; Zarco-Tejada et al., 2013). Most of the sensors used in precision viticulture are multispectral sensors, allowing to calculate VIs based on the visible (red, green, blue), red-edge and near infrared (NIR) reflectance of plants (Ferro and Catania, 2023). Several studies found low to moderate correlations between multispectral VIs and grapevine leaf water potential, with maximum R^2 ranging between 0.4 and 0.5 (Baluja et al., 2012; Espinoza et al., 2017; Romero et al., 2018; Tang et al., 2022). VIs based on NIR and red-edge bands are better correlated with grapevine water potential as they are greatly affected by leaf structure and chlorophyll content, both being considered as indicators of grapevine water status (Penuelas et al., 1997; Rapaport et al., 2015). Recently, machine learning models (i.e., random forest) have been applied to combine multispectral information from grapevines and predict grapevine water potential. These models performed better (R^2 around 0.85) than using single multispectral VIs (Poblete et al., 2017; Romero et al., 2018), however,

5. Mapping grapevine leaf water potential with UAS data

there was a significant loss of predictive power between calibration and validation (R^2 decreased and RMSE increased significantly) (Tang et al., 2022). Nevertheless, the combination of several VIs to predict grapevine water status is more efficient since each VI can bring complementary information (Xue and Su, 2017).

In dry conditions, grapevine closes stomata, limiting transpiration but preventing it from reaching excessively negative water potentials that could lead to xylem cavitation and death (Gambetta et al., 2020b). Once stomata are closed and transpiration is restrained, leaves temperature increases (Costa et al., 2010). Canopy temperature can therefore potentially be used to develop index giving information on stomatal conductance and leaf water potential (Jones et al., 2002). Thermal VIs such as crop water stress index (Idso et al., 1981) has shown moderate (but better than multispectral VIs) correlations with grapevine water potential, with a R^2 of 0.55 (Romero et al., 2018). Some studies even showed a significant correlation, with R^2 around 0.8, between leaf water potential and crop water stress index in Mediterranean vineyards (Bellvert et al., 2014; Möller et al., 2007). Thermal sensors are not as used as multispectral sensors in precision viticulture (Ferro and Catania, 2023). These sensors are generally more expensive and subjected to less straightforward calibration (Berni et al., 2009). Thermal data processing is less simple than multispectral data but complementary information obtained by multispectral and thermal sensors could improve the ability to remotely monitor grapevine leaf water potential (Tang et al., 2022).

The use of laser scanning sensors (Light Detection and Ranging - LiDAR) for estimating biophysical parameters of vineyard canopy is still relatively uncommon compared to other available sensors (Ferro and Catania, 2023). Point clouds obtained from LiDAR sensors are suitable for detecting structural features of grapevine such as canopy height, canopy width or even leaf area index (Bates et al., 2021; Comba et al., 2018). These structural features reflect the result of cumulative water potential of grapevine, and could therefore contain information on grapevine water status (Baluja et al., 2012). As a result, the

combination of multispectral, thermal and LiDAR (structural) data obtained from different sensors onboard unmanned aerial vehicles could potentially be used to improve the mapping of grapevine leaf water potential within a vineyard.

In addition to the value of remotely monitoring grapevine leaf water potential in an accurate way through UAS, it is also interesting to study which factors spatially determine leaf water potential at the vineyard scale. Several studies tried to assess the influence of irrigation management on grapevine water status with UAS platforms (De Bei et al., 2011; Bellvert et al., 2012, 2015; Espinoza et al., 2017; Möller et al., 2007). However, most of these studies were conducted on vineyards with homogeneous edaphic conditions, but different irrigation treatments. It remains unclear how robust these water status mapping approaches are when applied across vineyards with varying edaphic and meteorological conditions (Helman et al., 2018). Few studies evaluated how spatialized information of grapevine water status give us information about how environmental heterogeneity within a vineyard affects the distribution of grapevine water potential (Brillante et al., 2017a). It is known that the soil and the climate mainly affect grapevine water potential, and their effects are concomitant (Van Leeuwen et al., 2004b). The soil, through its texture and its ability to retain and conduct water, determines the water supply to the root system. Soil depth, texture, structure and percentage of coarse elements, also affect the growth of the root system and therefore the available water for the plant (Van Leeuwen et al., 2018). Grapevine water status is also affected by the vapor pressure deficit (VPD, corresponding to the atmospheric evaporative demand), which depends on temperature and air humidity (Soar et al., 2006b). Grapevine should therefore find an equilibrium between water supply, in the soil, and water demand, in the atmosphere, by regulating its water potential and stomatal conductance, to maintain gas exchanges for photosynthesis, while preventing excessive negative water potential leading to xylem cavitation (Gambetta et al., 2020b). Topographic attributes, such as slope and elevation, can also impact grapevine performance (Bramley et al., 2011; Karn et al., 2024). On the one hand, this influence is indirect since topography control the

5. Mapping grapevine leaf water potential with UAS data

redistribution of soil particles within the vineyard and therefore creates soil texture spatial heterogeneity (Fraga et al., 2014). On the other hand, topography can directly influence grapevine water status through its impact on water drainage and runoff, sunlight exposure and temperature variations within the vineyard (Brillante et al., 2017a; Karn et al., 2024). These effects foster microenvironments within a vineyard that could affect grapevine water status (Rabia et al., 2022).

In this study, we aimed to quantify the spatial distribution of grapevine leaf water potential within vineyards and assess the impact of edaphic, topographic and climatic conditions on this intra-field heterogeneity. We evaluated the capabilities of UAS equipped with multispectral, thermal and LiDAR sensors to monitor grapevine leaf water potential, on two non-irrigated vineyards, during two viticultural seasons.

5.2. Methodology

5.2.1. Site descriptions

This study was conducted on two non-irrigated Belgian vineyards, grassed in the inter-rows, namely the *Château de Bousval* vineyard and the *Domaine W* vineyard (Figure 5.1a). At the *Château de Bousval* vineyard (Genappe, Belgium, 50°36'45.0"N 4°31'19.6"E), we focused on an east-facing plot of Chardonnay grafted on 3309C rootstock, planted in 2014 with vertical shoot positioning, 1.6 m inter-row and 0.8 m inter-cep. The field rises between 110 m and 125 m above sea level (Figure 5.1b), and the average slope is 6 %. At the *Domaine W* vineyard (Tubize, Belgium, 50°41'19.4"N 4°09'36.9"E), two Chardonnay plain fields grafted on 101-14Mgt rootstock were selected for this study,

rising between 52 m and 54 m above sea level (Figure 5.1g), with rows oriented north-south. The grapevines were planted in 2016 with vertical shoot positioning, a 2.2 m inter-row and 1 m inter-cep.

In the *Château de Bousval* vineyard, the soil is made of a loamy top layer overlying a sandy subsoil, but the depth of the interface between these two layers changes within the plot, reaching more than 3 m at the lowermost side (east side) of the field, due to an accumulation of loamy colluviums. At the upper part (west side) of the field, the loamy layer is around 0.4 m depth. We know, on the whole field, the depth of the interface between the interface between the loam and the sand (Figure 5.1c). Moreover, in this vineyard, we also know that grapevine roots reach a depth of at least 2.5 m on the whole field (Chapter 4). In the *Domaine W* vineyard, the soil heterogeneity is less marked in terms of soil texture. The north-western part of the field is defined by a silty loam soil on the first horizons of the profile and silty clay loam soil thereafter. The south-eastern part is defined by a silty loam soil on the whole profile (Figure 5.1h). These differences in terms of soil texture have only been observed in a single location in each subplot. Therefore, unlike Bousval, the depth of the interface between silty loam soil and silty clay loam soil is not accurately known on the whole field. A stream runs adjacent to the southeast parcel, raising the water table in this area within the reach of the roots. Root depth on this vineyard is at least 2 m everywhere in the field (Chapter 3).

5. Mapping grapevine leaf water potential with UAS data

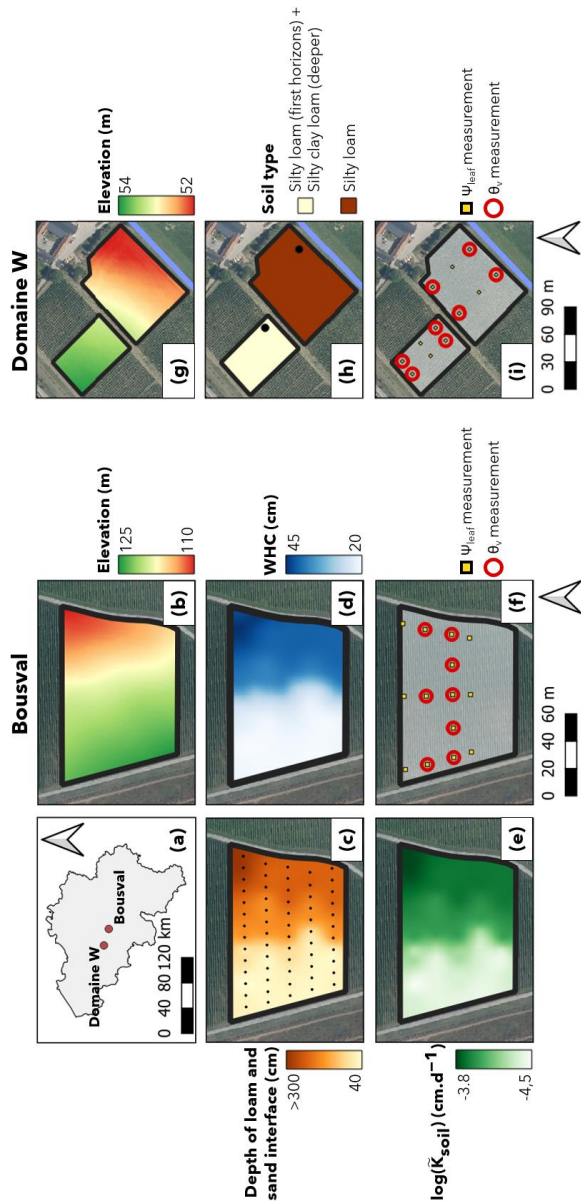


Figure 5.1 – (a) Location of the vineyards in Belgium. (b-f) Topographic attributes, edaphic properties and location of measurements in the Château de Bousval vineyard: (b) Elevation; (c) Kriged map of the depth of the interface between the loamy soil and the sandy subsoil (the black points are locations of soil samples used to determine the depth of the interface in situ and used for kriging); (d) Water holding capacity (WHC) on 2.5 m depth (equation 5.6); (e) Averaged soil hydraulic conductivity ($\bar{K}_{soil}$) on 2.5 m depth (equation 5.7); (f) Locations of the leaf water potential (Ψ_{leaf_meas}) and volumetric water content (θ_v) profile measurements. (g-i) Topographic attributes, edaphic properties and location of measurements in the Domaine W vineyard: (g) Elevation; (h) Soil type (the black points are locations of soil samples to determine soil type in situ); (i) Locations of the leaf water potential (Ψ_{leaf_meas}) and volumetric water content (θ_v) profile measurements. In (g), (h) and (i), the blue line is a stream adjacent to the south-eastern plot.

5.2.2. Meteorological conditions

Both vineyards are equipped with weather stations providing hourly meteorological data. The meteorological conditions during each flight are provided in Table 5.1. The atmospheric conditions and the evaporative demand are characterized with the vapor pressure deficit (VPD). The daily water deficit, which refers to the standardized precipitation evapotranspiration index (SPEI - Vicente-Serrano et al., 2010), is calculated as follows:

$$SPEI = \sum_i (P_i - ET_{0i}), \quad (5.1)$$

with $i = 1$ corresponds to the 1st of April of the respective year (budburst of grapevines), P_i the daily precipitation, and ET_{0i} the daily reference evapotranspiration. The more negative the SPEI, the greater the water deficit. ET_0 is calculated from the FAO Penman-Monteith method (Allen et al., 1998). Despite relatively similar air temperatures and VPDs during the 2022 and 2023 flights, 2022 was a drier year than 2023. The SPEI for any date in 2022 is significantly more negative than that for any date in 2023 in both vineyards (Table 5.1), indicating drier conditions in 2022 than in 2023.

5. Mapping grapevine leaf water potential with UAS data

Table 5.1 – Meteorological conditions during each flight campaign

	Bousval			Domaine W		
Date	<i>Air temperature (°C)</i>	<i>VPD (kPa)</i>	<i>SPEI (mm)</i>	<i>Air temperature (°C)</i>	<i>VPD (kPa)</i>	<i>SPEI (mm)</i>
27/07/22	18.9	1.02	-273.9			
10/08/22	28.3	1.95	-334.6	28.9	1.89	-276.2
31/08/22	22.5	1.15	-411.3	23	1.32	-340.2
20/07/23	20.9	1.02	-193.0	21	1.2	-193.8
10/08/23	23.1	1.53	-197.4			
06/09/23	27.9	2.17	-223.6	29.9	2.08	-236.9

5.2.3. Data acquisition and processing

Unmanned aircraft systems (UAS) data acquisition took place during the vine growth period in 2022 and 2023. Three flight campaigns were carried out in 2022 and three in 2023, for a total of six flight campaigns. Data were acquired before the veraison (27/07/22 and 20/07/23), at the start of the veraison (10/08/22 and 10/08/23) and just before harvest (31/08/22 and 06/09/23). Flights started around 12:00 (UTC +2) at Bousval and around 13:30 (UTC +2) at Domaine W. Three sensors were used in this study, a Micasense RedEdge-M multispectral sensor (Micasense Inc., Seattle, WA, USA), a FLIR Vue Pro R thermal camera (FLIR Systems, Wilsonville, OR, USA) and a YellowScan Surveyor LiDAR (YellowScan, Saint-Clément-De-Rivière, France), mounted on a DJI Matrice 600 (SZ DJI Technology Co Ltd., Shenzhen, China). The Micasense RedEdge-M is a five narrowband multispectral camera, capturing blue (465-485 nm), green (550-570 nm), red (663-673 nm), red-edge (712-722 nm) and NIR (820-860 nm) wavelengths of the

electromagnetic spectrum. Just before and after each flight, the Micasense RedEdge-M sensor was calibrated thanks to a reflectance panel to ensure accurate and consistent reflectance measurements, enabling reliable comparisons of data captured under varying light conditions and at different times. Images were acquired to ensure approximately 90 % forward and lateral overlap. To process the multispectral imagery, orthomosaics were first created for each band of the sensor, using Pix4D (Pix4D, Lausanne, Switzerland). Ground control points (GCP) were used for georeferencing.

The FLIR Vue Pro R is a radiometric thermal sensor that captured longwave infrared radiation in the 7.5-13.5 μm range. This sensor needs radiometric calibration parameters such as emissivity of the canopy, air temperature and humidity to capture accurately the surface temperature. Thermal imagery was also processed using Pix4D. The same GCPs as for multispectral imagery were used, enabling georeferencing consistent with multispectral data.

The LiDAR system, operating with a wavelength of 903 nm, is composed of a Velodyne LiDAR puck, onboard computer, Inertial Measuring Units (IMU), and Global Navigation Satellite System (GNSS) receiver. Ranging data are provided by the LiDAR puck. The IMU measured the variations in attitude and orientation, and the GNSS provided positioning. To process the LiDAR data, YellowScan's CloudStation software was used to align the flight strips for georeferencing and to apply corrections through GNSS offset (lever-arms), sensor-angle (boresight), and GNSS post-processing with precise position techniques (Bates et al., 2021).

Multispectral and thermal sensors were mounted on the same DJI Matrice 600 and data were collected at the exact same time. The LiDAR data were collected directly after the multispectral and thermal data. Multispectral and thermal flights were conducted at an altitude of 100 m above ground level and at a flight speed of 6 m.s^{-1} , yielding flight

5. Mapping grapevine leaf water potential with UAS data

durations of approximately 7 minutes, and resulting in a native pixel resolution of 7 cm for multispectral and thermal data. For the LiDAR flight, the UAS maintained an altitude of 50 m aboveground, with a ground speed of 5 m.s⁻¹, giving a spatial resolution of 16 cm for LiDAR data. Due to technical issues, there is no thermal data at Bousval the 27/07/22 and 31/08/22, no multispectral data at Domaine W the 10/08/22, and no multispectral, thermal and LiDAR data at Domaine W the 27/07/22 and 10/08/23 (Table 5.2).

Table 5.2 – Availability of the UAS data (multispectral M, Thermal T and LiDAR L) during the six flight campaigns in the two vineyards.

	Bousval			Domaine W		
Date	<i>M</i>	<i>T</i>	<i>L</i>	<i>M</i>	<i>T</i>	<i>L</i>
27/07/22	Yes	No	Yes	No	No	No
10/08/22	Yes	Yes	Yes	No	Yes	Yes
31/08/22	Yes	No	Yes	Yes	Yes	Yes
20/07/23	Yes	Yes	Yes	Yes	Yes	Yes
10/08/23	Yes	Yes	Yes	No	No	No
06/09/23	Yes	Yes	Yes	Yes	Yes	Yes

At the same time as collecting UAS data, we measured grapevine leaf water potential ($\Psi_{\text{leaf_meas}}$) on various 2x2 m² zones homogeneously distributed across the fields, using a Scholander pressure bomb (670 Pressure Chamber, PMS Instrument Company). The $\Psi_{\text{leaf_meas}}$ was measured on fourteen 2x2 m² zones at Bousval (Figure 5.1f), and on twelve 2x2 m² zones at Domaine W (Figure 5.1i). For each sampled grapevine, $\Psi_{\text{leaf_meas}}$ were recorded on three to five mature leaves, covered by an aluminium zip bag 45 minutes before the measurement. In addition, the soil water content profile to a depth of 105 cm (every 15 cm) was also measured in eight measurement zones in each vineyard (Figure 5.1f and Figure 5.1i) , before each flight, with a TRIME-FM3

time domain reflectometry combined with access T3 tube (IMKO GmbH, Ettlingen, Germany).

5.2.4. Pure grapevine pixels extraction

The fine spatial resolution of the UAS data makes it possible to distinguish rows and inter-rows. We used the k-means algorithm to generate a binary mask that distinguishes pure vine canopy pixels from inter-row soil and grass pixels. The k-means algorithm determined the optimal thresholding value to maximize the between-class variance and minimize the within-class variance (MacQueen, 1967). K-means algorithm has already shown good ability to extract pure vine pixels based on multispectral vegetation indices (Cinat et al., 2019). This segmentation enables the computation of vegetation indices on grapevine only and facilitates the derivation of Ψ_{leaf} prediction model specifically focused on the grapevine itself. The workflow of the segmentation method used in this study is illustrated in Figure 5.2. The algorithm was performed using RStudio (RStudio Team, 2022). The method consists of six steps, and was performed for each date, generating a mask per date:

- 1) The initial step was to use the canopy height, derived from the LiDAR data, to get a first raw distinction between rows and inter-rows. We derived the height of the canopy (canopy height model CHM) thanks to the difference between the Digital Surface Model (DSM) and the Digital Terrain Model (DTM): $\text{CHM} = \text{DSM} - \text{DTM}$. We considered that grapevine rows are represented by every pixel greater than 1 m. This step allowed to remove a large part of pixels representing inter-rows.

5. Mapping grapevine leaf water potential with UAS data

- 2) Due to a coarser spatial resolution of LiDAR data, we used multispectral data to get a finer separation and be sure that we extracted only pure grapevine pixels. We identified the most relevant spectral bands capable of distinguishing between vineyard rows and inter-row vegetation to choose a proper vegetation index for the mask creation. The Modified Soil Adjusted Vegetation Index (MSAVI), suggested by Qi et al. (1994), was selected due to its incorporation of the red and NIR bands known for their sensitivity to vegetation density, and its ability to minimise soil brightness influences in sparse crops (Binte Mostafiz et al., 2021). We applied the mask obtained in step 1 on the MSAVI raster.
- 3) We subdivided the new MSAVI raster into smaller areas (rectangles of 10 m x 1.5 m). By reducing the area in which the k-means algorithm was applied, the non-vine pixels in that area exhibited greater similarity, allowing the algorithm to better discriminate between grapevine and grass pixels.
- 4) The k-means algorithm was then applied in each rectangle. The number of clusters was set to three to distinguish among the three classes identifiable within the rectangles: pure grapevine pixels, mixed pixels, pure grass pixels.
- 5) Following the algorithm execution, only the class with the highest mean value of MSAVI was retained, aiming to automatically extract grapevine class. This class was expected to have the highest MSAVI value since it represents the class with highest biomass density.
- 6) Finally, the outputs of the algorithm were combined to create a unified shapefile, representing a binary mask that isolates pure grapevine canopy pixels across the field. This mask was

subsequently utilized to filter out non-vine or mixed pixels from UAS data, and only the remaining grapevine pixels were used for further analysis.

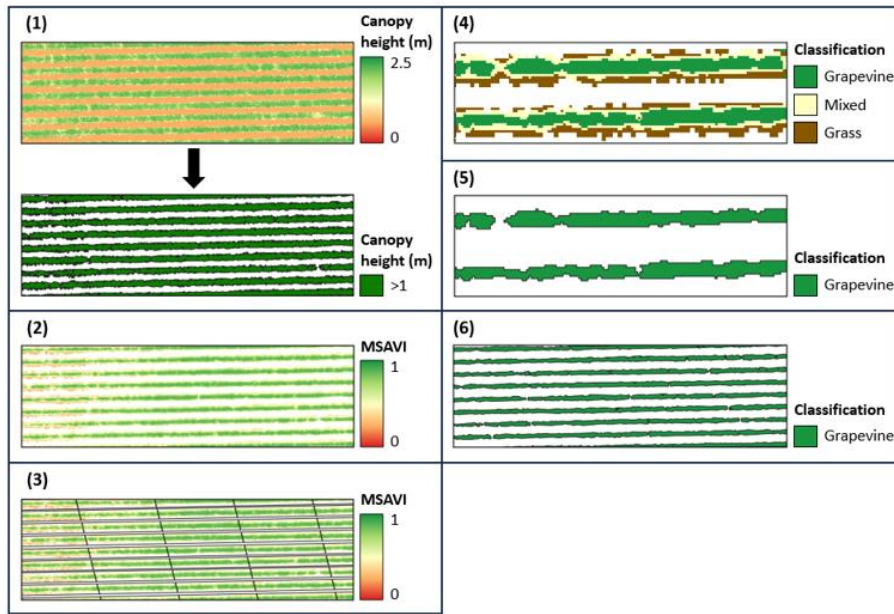


Figure 5.2 – Process of segmenting grapevine pixels from inter-row pixels to generate a pure grapevine mask. **(1)** First row distinction between rows (>1 m) and inter-rows (<1 m) using the canopy height derived from the LiDAR data; **(2)** Application of the raw grapevine mask obtained in (1) on the Modified Soil Adjusted Vegetation Index (MSAVI) raster; **(3)** Subdivision of the new MSAVI raster into smaller areas; **(4)** Application of k-means algorithm in each rectangle. The number of clusters was set to three (pure grapevine, mixed, pure grass); **(5)** Selection of pure grapevine pixels, based on the clustering obtained with the k-means algorithm; **(6)** Creation of a unique mask to extract pure grapevine pixels from each raster of vegetation indices.

5.2.5. Generation and extraction of UAS-based variables

We calculated multiple widely used multispectral vegetation indices (VIs), exploiting different band combinations. The multispectral VIs used in this study were obtained from the review of Giovos et al. (2021). 43 multispectral VIs were retained in this study, as they constitute the most frequently used to monitor and estimate vine water stress and delineation of management zones in viticulture. We also exploited the specific red, blue, green, NIR and red-edge bands alone. The complete list of all the indices and how they are calculated can be found in Table S.5.1. In addition, we calculated thermal VIs, namely the canopy surface temperature (CST [°C]) and the difference between CST and air temperature ($dT = CST - T_a$ [°C]). The Crop Water Stress Index (CWSI) was also computed using the simplified formula suggested by Jones (1992):

$$CWSI = \frac{CST - T_{wet}}{T_{dry} - T_{wet}}. \quad (5.2)$$

Two different CWSI were derived:

- (a) CWSIa: T_{dry} (dry bulb temperature) and T_{wet} (wet bulb temperature) were measured during the UAS surveys by a meteorological station installed on each vineyard.
- (b) CWSIb: T_{dry} and T_{wet} were derived from the pure canopy pixels and were respectively considered as CST_{max} and CST_{min} .

Structural features of the grapevines were derived from the LiDAR data. We derived the height of the canopy (CH) thanks to the difference between the DSM and the DTM as explained before. We also derived the leaf area index (LAI) with the LiDAR method developed by Bates et al. (2021). From the LiDAR data, we also derived the elevation and the slopes of the different vineyards, but these parameters were not used to predict Ψ_{leaf} since they do not vary over time. However, they were used to interpret the spatial distribution of Ψ_{leaf} .

After applying the binary mask to isolate pure vine pixels on each index map described above, we extracted the averages of the index values within the 2x2 m² zones defined before for the grapevine leaf water potential measurements (Figure 5.1f and Figure 5.1i).

5.2.6. Leaf water potential prediction

As a preliminary step, we examined the univariable relationships between *in situ* $\Psi_{\text{leaf_meas}}$ and the different VIs, based on Pearson's coefficient (Pearson's ρ), to account for linear relations, and based on Spearman's coefficient (Spearman's ρ), to account for monotonic relations. Pearson's ρ quantifies the strength and direction of a linear relationship, while Spearman's ρ is valuable for detecting and quantifying associations when non-linear relationships are assumed. We therefore compared Pearson's ρ and Spearman's ρ to evaluate if the relation between $\Psi_{\text{leaf_meas}}$ and a VI was linear or not. These analyses enable us to assess the capability of simple remotely sensed VIs to evaluate Ψ_{leaf} . All in-situ measurement data points (n=132; 6x14 at Bousval and 4x12 at Domaine W) across all vineyards and days, were used for a comprehensive analysis.

5. Mapping grapevine leaf water potential with UAS data

We then used the stepwise regression method to develop a multiple linear regression model to predict leaf water potentials ($\Psi_{\text{leaf_pred}}$) based on a multiple linear combination of the VIs presented previously (equation 5.3). We also predicted an uncertainty, quantified by the confidence interval of 95 % on $\Psi_{\text{leaf_pred}}$ ($IC_{0.95}^{\Psi_{\text{leaf}}}$). Stepwise regression is a step-by-step iterative construction of a linear regression model that involves the selection of independent variables to be used in a final model (Wilkinson, 1979). Stepwise regression can be achieved either by trying out one independent variable at a time and including it in the regression model if it is statistically significant (forward selection), or by including all independent variables in the model and eliminating those that are not statistically significant (backward elimination). A combination of both methods is also possible and was used in this study (bidirectional elimination). This method used the Akaike Information Criterion to add or remove VIs from the multiple linear regression model, minimizing the number of predictor variables but keeping a high predictive power (Akaike, 1974). Stepwise regression models were implemented in RStudio (RStudio Team, 2022), using respectively the *stats* package.

$$\Psi_{\text{leaf_pred}} = \beta_1 \times VI_1 + \beta_2 \times VI_2 + \dots + \beta_n \times VI_n + \alpha, \quad (5.3)$$

with β_i the regression weights (or beta coefficients) and α the intercept. β_i can be interpreted as the average effect on the predicted variable ($\Psi_{\text{leaf_pred}}$) of a one unit increase in VI_i , holding all other predictors fixed. We applied this method on different combinations of VIs and single bands to predict Ψ_{leaf} . We tested a total of seven data combinations: (1) multispectral only (M), (2) thermal only (T), (3) LiDAR only (L), (4) multispectral and thermal (M+T), (5) multispectral and LiDAR (M+L), (6) thermal and LiDAR (T+L), and (7) multispectral, thermal and LiDAR (M+T+L).

For each date, we randomly selected 70 % of the data to train the different models and 30 % to validate them. The data used for

calibration and validation were the same for each model. We evaluated the performance of the models thanks to the coefficient of determination (R^2) and the root mean squared error (RMSE). The model with the best performance was then employed to predict the Ψ_{leaf} over the fields for each flight.

We then verified the reliability of the model. To evaluate that there is no redundancy and similar information in the multiple linear regression model, we used the Variance Inflation Factor (VIF). The VIF assesses if a predictor variable is collinear with the other predictor variables (multicollinearity) in the multiple linear regression model, which could degrade the precision of an estimate, and reduce the reliability and the robustness of the model (Allen, 1997). VIF less than 5 indicates a low correlation between a predictor variable and the other ones, VIF between 5 and 10 indicates a moderate correlation, and VIF greater than 10 indicates a high correlation (James et al., 2021). VIF was computed using the *car* package in RStudio. We also used partial regression plots to show the effect of a predictor variable on the prediction of Ψ_{leaf} , after considering the effects of the other predictor variables. If the slope of the linear regression in a partial regression plot is significantly different from 0 (p-value < 0.001), then it justifies the presence of a predictor variable in the multiple linear model (Moya-Laraño and Corcobado, 2008). The correlation (R^2) of the linear model in a partial regression plot allows to quantify the unique relationship between the predicted variable (Ψ_{leaf}) and a predictor variable (VI) while controlling the effects of the other variables. The higher the R^2 , the greater the influence of the predictive factor (VI) on the predicted variable (Ψ_{leaf}) (Q. Zhou et al., 2008).

We carried out unpaired Wilcoxon tests to statistically compare if the median of the $\Psi_{\text{leaf_pred}}$ are significantly different (p-value < 0.05) or not (p-value > 0.05) between dates and vineyards. We performed the Wilcoxon test using the *stats* package (v4.1.1) of the R Statistical Software (v4.0.4) (RStudio Team, 2022).

5.2.7. Relations between leaf water potential and environmental factors

To understand how environmental conditions influence spatial distribution of $\Psi_{\text{leaf_pred}}$, we analyzed the relations between the linear combination of VPD and SPEI (Table 5.1), and the median $\Psi_{\text{leaf_pred}}$ ($\Psi_{\text{leaf_pred_median}}$) (equation 5.4), and between the linear combination of VPD and SPEI, and the distribution of $\Psi_{\text{leaf_pred}}$ ($\Psi_{\text{leaf_pred_max}} - \Psi_{\text{leaf_pred_min}}$) (equation 5.5).

$$\Psi_{\text{leaf_pred_median}} = a \times \text{SPEI} + b \times \text{VPD} + c, \quad (5.4)$$

$$\Psi_{\text{leaf_pred_max}} - \Psi_{\text{leaf_pred_min}} = a \times \text{SPEI} + b \times \text{VPD} + c. \quad (5.5)$$

with a and b the regression coefficients, and c the intercept. We applied analysis of covariance (ANCOVA) on to assess if these relations are vineyard-specific or not. Relations were considered statistically different for p -values less than 0.05. For each date, we also quantified the correlation between $\Psi_{\text{leaf_pred}}$ and the elevation, and $\Psi_{\text{leaf_pred}}$ and the slope. At Bousval, since we accurately know the depth of interface between the loamy soil and the sandy subsoil (Figure 5.1c), we also quantified the correlation between Ψ_{leaf} and the water holding capacity (WHC – equation 5.6), and between Ψ_{leaf} and an arithmetic averaged soil hydraulic conductivity ($\tilde{K}_{\text{soil}}$ – equation 5.7), corresponding to a normalized matric flux potential between field capacity and permanent wilting point. We used the coefficient of determination R^2 as we supposed that these relations are linear. For these relations, we assumed that grapevines have a uniform root depth of 2.5 m throughout the vineyard. We also assumed, in this study, that the soil unsaturated hydraulic properties of the loamy and sandy soils are the same everywhere in the field. The soil hydraulic properties were

measured by Hyprop (METER Group Inc., Pullman, WA, USA) evaporation method (Bezerra-Coelho et al., 2018). The soil water content at the permanent wilting point (pF 4.2) was measured by pressure plate (Ridley and Burland, 1993). Hyprop-fit software was used to optimize the unsaturated hydraulic parameters of van Genuchten-Mualem (1980), for each soil texture (Table 5.3). Everywhere in the Bousval vineyard, we calculated the WHC [cm] (Figure 5.1d) and $\tilde{K}_{soil}$ [cm.d⁻¹] (Figure 5.1e) for a depth of 2.5 m thanks to the following equations:

$$WHC = \left[z_{LS} * \left(\theta(h_{FC_loam}) - \theta(h_{PWP}) \right) \right]_{loam} + \left[(250 - z_{LS}) * \left(\theta(h_{FC_sand}) - \theta(h_{PWP}) \right) \right]_{sand} \quad (5.6)$$

with z_{LS} [cm] the depth of the interface between the loamy soil and the sandy subsoil, $\theta(h)$ the water content [cm³.cm⁻³] at the suction h [cm] of the respective soil texture, h_{FC_loam} and h_{FC_sand} the suction at the field capacity for the loamy and sandy soil respectively (in this study we assumed that $h_{FC_loam} = -300$ cm and $h_{FC_sand} = -100$ cm, based on the study of Twarakavi et al. (2009) which showed that the suction at the field capacity is soil texture dependent) and h_{PWP} the suction at the permanent wilting point (in this study we assumed that $h_{PWP} = -15000$ cm for each soil texture).

$$\tilde{K}_{soil} = \left[\frac{z_{LS}}{250} * \frac{\int_{h_{FC_loam}}^{h_{PWP}} K(h) dh}{h_{FC_loam} - h_{PWP}} \right]_{loam} + \left[\frac{(250 - z_{LS})}{250} * \frac{\int_{h_{FC_sand}}^{h_{PWP}} K(h) dh}{h_{FC_sand} - h_{PWP}} \right]_{sand} \quad (5.7)$$

5. Mapping grapevine leaf water potential with UAS data

with $K(h)$ the soil hydraulic conductivity [cm.d^{-1}] at the suction h [cm]. By calculating WHC and $\tilde{K}_{\text{soil}}$ with equations 5.6 and 5.7 respectively, we consider the presence and the thickness of different soil layers with distinctive texture. We chose the suction at field capacity and at permanent wilting point as upper and lower limits, since they are generally considered to determine available and usable soil water for plants (Horne and Scotter, 2016).

Table 5.3 – Unimodal van Genuchten hydraulic parameters of the loamy soil and the sandy subsoil at the Château de Bousval.

	θ_{sat} $\text{cm}^3.\text{cm}^{-3}$	θ_{res} $\text{cm}^3.\text{cm}^{-3}$	n -	α cm^{-1}	K_{sat} cm.day^{-1}	τ -
Loam	0.419	0.117	1.483	0.00669	1.12	0.701
Sand	0.358	0.08	3.11	0.0182	72	1.039

5.3. Results

5.3.1. In situ measurements of leaf water potential and relationship with UAS-based VIs

Ψ_{leaf} was measured ($\Psi_{\text{leaf_meas}}$) at the same time as the collection of UAS data, at different dates in 2022 and 2023, with a Scholander pressure bomb (Figure 5.3). We measured a lower median leaf water potential ($\Psi_{\text{leaf_meas_median}}$ more negative) in 2022 than in 2023 in both vineyards, linked to warmer and drier conditions (Table 5.1). Moreover, in each vineyard, the soil was drier in 2022 than in 2023 (Figure S.5.1). For a same date, we also measured a slightly lower $\Psi_{\text{leaf_meas_median}}$ at Bousval compared to Domaine W, except on 20/07/23 (Table 5.4). We observed

a greater $\Psi_{\text{leaf_meas}}$ heterogeneity ($\Psi_{\text{leaf_meas_max}} - \Psi_{\text{leaf_meas_min}}$) at Bousval compared to Domaine W. This heterogeneity is even more marked in 2022, when conditions were hot and dry. At Bousval, at each date, the minimum $\Psi_{\text{leaf_meas}}$ was measured at the upper part (west side) of the parcel, where the loamy soil is shallower, while the maximum $\Psi_{\text{leaf_meas}}$ were measured at the lowermost side (east side) (Figure 5.3a), where the loamy soil is deeper. At Domaine W, there is less $\Psi_{\text{leaf_meas}}$ heterogeneity, but we generally measured a lower $\Psi_{\text{leaf_meas}}$ (more negative) in the north-western plot than in the south-eastern plot (Figure 5.3b).

Table 5.4 – Median leaf water potential ($\Psi_{\text{leaf_meas_median}}$), maximum ($\Psi_{\text{leaf_meas_max}}$) and minimum ($\Psi_{\text{leaf_meas_min}}$) leaf water potentials (all in MPa) measured in the two vineyards during each UAS flight.

	Bousval (n=14 by date)			Domaine W (n=12 by date)		
	$\Psi_{\text{leaf_meas_median}}$	$\Psi_{\text{leaf_meas_max}}$	$\Psi_{\text{leaf_meas_min}}$	$\Psi_{\text{leaf_meas_median}}$	$\Psi_{\text{leaf_meas_max}}$	$\Psi_{\text{leaf_meas_min}}$
27/07/22	-0.73	-0.45	-1.00			
10/08/22	-0.82	-0.48	-1.15	-0.80	-0.70	-0.95
31/08/22	-0.74	-0.49	-1	-0.71	-0.55	-0.83
20/07/23	-0.54	-0.42	-0.60	-0.63	-0.53	-0.70
10/08/23	-0.69	-0.50	-0.9			
06/09/23	-0.72	-0.49	-0.95	-0.70	-0.55	-0.90

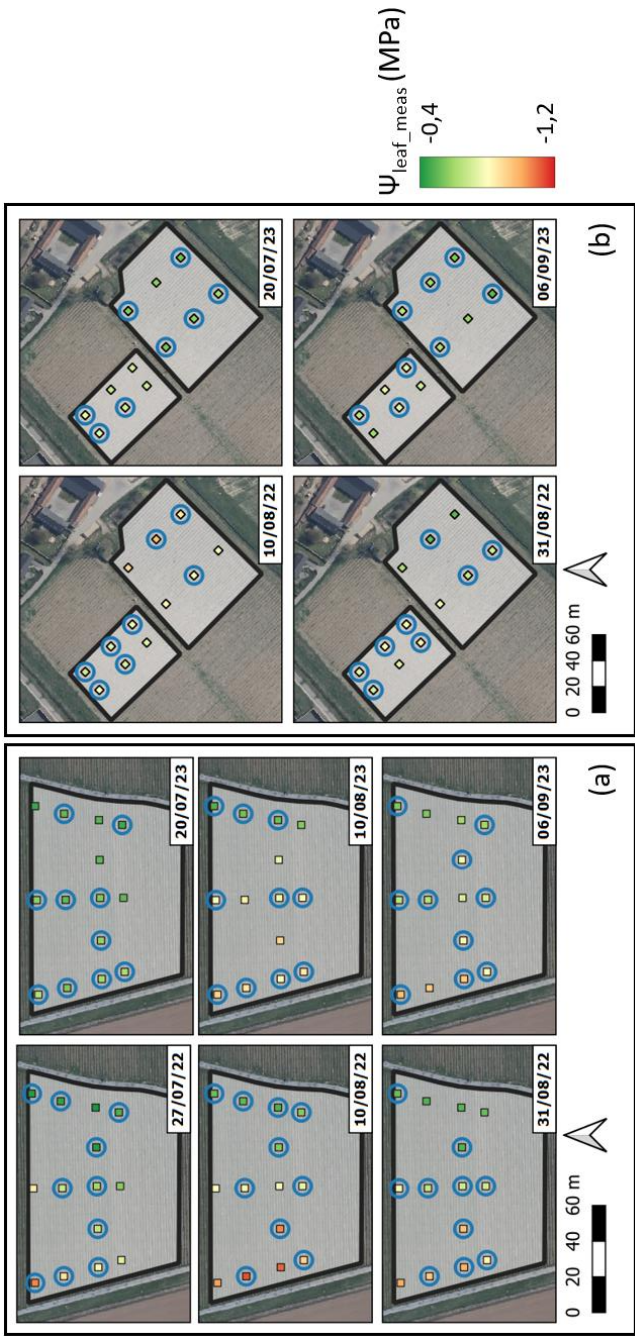


Figure 5.3 – Leaf water potential measured ($\Psi_{\text{leaf_meas}}$) with a Scholander pressure bomb in (a) 14 zones at the Château de Bousval vineyard and (b) 12 zones at the Domaine W vineyard, at the same time of UAS flights. Points surrounded in blue have been used for the calibration of the multiple linear regression models.

By examining the univariable relationships between $\Psi_{\text{leaf_meas}}$ and the different VIs, including both vineyards and all dates (Figure S.5.2), we found that the correlation (Pearson's ρ) between $\Psi_{\text{leaf_meas}}$ and VIs are low to moderate, ranging from $\rho = -0.61$ to $\rho = 0.63$ (Figure 5.4). We found a maximum ρ of 0.63 between $\Psi_{\text{leaf_meas}}$ and Chlorophyll Red-Edge (CLRededge). The second-best ρ was found with Normalized Difference Red Edge Index NDRE ($\rho = 0.62$). These two VIs are the only ones, considered in this study, to contain both NIR and red-edge bands, which have been shown to be strongly correlated with the chlorophyll content of grapevines and therefore influenced by the water

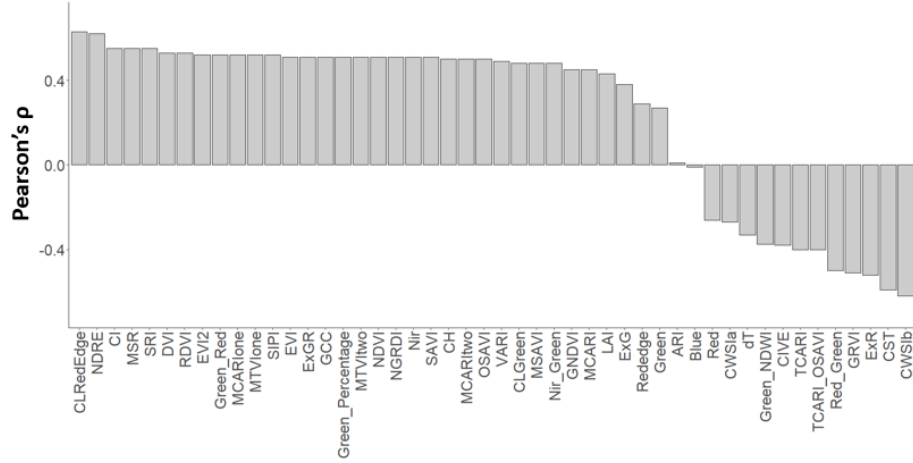


Figure 5.4 – Pearson's coefficient (Pearson's ρ) quantifying the linear correlation between measured Ψ_{leaf} ($\Psi_{\text{leaf_meas}}$) and each vegetation index (VI), by taking all the measurements in both vineyards and at all dates.

status (Laroche-Pinel et al., 2021b; Tang et al., 2022). However, in our case, these ρ values indicate a moderate correlation of these VIs with $\Psi_{\text{leaf_meas}}$. The third best correlation was found with the thermal index CWSIb, with a Pearson's ρ of -0.61. All others VIs have a lower correlation with $\Psi_{\text{leaf_meas}}$, with ρ ranging between 0.55 and -0.59. This suggests that single VIs cannot accurately predict Ψ_{leaf} in the investigated vineyards and more complex approaches, such as multiple linear regression models, are needed to better estimate Ψ_{leaf} . It is

interesting to note that for all indices, the Pearson's ρ (linear relation – Figure 5.4) is larger than the Spearman's ρ (non-linear relation – Figure S.5.3). Linear relations between $\Psi_{\text{leaf_meas}}$ and VI have therefore a higher predictive power than non-linear relations (Rebekić et al., 2015), justifying the use of partial linear regression (and not non-linear), to construct a multiple linear regression and predict Ψ_{leaf} .

5.3.2. Predicting leaf water potential based on multiple linear regression model

In response to the limited correlations obtained from simple linear regressions between $\Psi_{\text{leaf_meas}}$ and VIs, we explored multiple linear regression models to better predict Ψ_{leaf} (Figure S.5.4). We used the stepwise regression method to minimize the number of VIs in the multiple regression, and to keep the most significative to predict Ψ_{leaf} . Figure 5.5a and Figure 5.5b show respectively the R^2 and RMSE obtained by comparing measured Ψ_{leaf} ($\Psi_{\text{leaf_meas}}$) and predicted Ψ_{leaf} ($\Psi_{\text{leaf_pred}}$), for the datasets used for calibration (70 % of the data) and validation (30 % of the data), and for the seven data combinations (see *Methodology* section). The models showed a high consistency between the calibration and validation datasets, with small differences in terms of R^2 and RMSE. This showed a great robustness of these models. For example, the model using multispectral, thermal and LiDAR data to predict $\Psi_{\text{leaf_pred}}$ (Figure 5.5c) has a $R^2 = 0.80$ and $R^2 = 0.78$ for the calibration and validation respectively, and a RMSE = 0.07 MPa and RMSE = 0.08 MPa for the same respective datasets. It is interesting to note that R^2 and RMSE respectively increase and decrease by adding information from different sensors to the model. For example, the predictive power of the model containing multispectral and thermal data is greater than the predictive power of the model constructed with multispectral data only. The best multiple linear model was the one containing information from all sensors, i.e., multispectral, thermal, and

LiDAR data. We therefore used this model (model 1 in Table 5.5; Figure 5.5c) to predict $\Psi_{\text{leaf_pred}}$ at Bousval the 10/08/22, 20/07/23, 10/08/23 and 06/09/23, and at Domaine W the 31/08/22, 20/07/23 and 06/09/23. Due to the technical problems not being able to obtain data from all sensors for certain dates (Table 5.2), we predicted $\Psi_{\text{leaf_pred}}$ at Bousval the 27/07/22 and 31/08/22 by using the multiple linear model combining multispectral and LiDAR data (model 2 in Table 5.5 Figure 5.5d); we used the multiple linear model combining thermal and LiDAR (model 3 in Table 5.5; Figure 5.5e) to predict $\Psi_{\text{leaf_pred}}$ at Domaine W the 10/08/22. Models 2 and 3 in Table 5.5 are the most robust and have the best R^2 and RMSE for the data available at the respective dates and vineyards (Figure 5.5a,b). In each model, the confidence interval on $\Psi_{\text{leaf_pred}}$ increase with decreasing $\Psi_{\text{leaf_pred}}$ (more negative $\Psi_{\text{leaf_pred}}$). The model 1, combining multispectral, thermal and LiDAR data (Figure 5.5c), has the lowest uncertainty on the prediction of $\Psi_{\text{leaf_pred}}$, with a 95 % confidence interval ($CI_{0.95}$) varying between 0.14 MPa (when $\Psi_{\text{leaf_pred}}$ is high) and 0.28 MPa (when $\Psi_{\text{leaf_pred}}$ is low). This is not surprising since this model has the highest predictive power (R^2). Model 2 (Figure 5.5d), combining multispectral and thermal data, shows a lower uncertainty ($0.18 \text{ MPa} < CI_{0.95} < 0.36 \text{ MPa}$) than the model 3 (Figure 5.5e), combining thermal and LiDAR data ($0.20 < CI_{0.95} < 0.40$).

It is interesting to note that in models 2 and 3 (Table 5.5), we retrieved the same VIs (CLRedEdge, CWSIb), spectral bands (blue) and structural features (canopy height CH) used to predict $\Psi_{\text{leaf_pred}}$ in the model 1, showing consistency in the parameters used to estimate grapevine $\Psi_{\text{leaf_pred}}$. Multicollinearity between the predictors was controlled by calculating the Variance Inflation Factor (VIF). For each model, the VIFs were lower than 5 for each VI (Table S.5.2 to Table S.5.4), suggesting low multicollinearity between them and enforcing the reliability of each model (James et al., 2021). This absence of multicollinearity between VIs shows that each predictor variable provides significant additional information in the prediction of $\Psi_{\text{leaf_pred}}$. This is confirmed by the partial regression plots (Figures S.5.5 to S5.7), showing that each VI used in each model has a significant influence on

5. Mapping grapevine leaf water potential with UAS data

the prediction of $\Psi_{\text{leaf_pred}}$ (p-value < 0.05). In the model 1, accounting for multispectral, thermal and LiDAR data, the partial correlations (R^2) showed that the CLRedEdge and the CWSIb have the most significant influence on the prediction of Ψ_{leaf} ($R^2 = 0.49$ and $R^2 = 0.56$ respectively), while the blue band ($R^2 = 0.21$) and the canopy height ($R^2 = 0.13$) have less impact (Figure S.5.5). For the model 2 accounting for the multispectral and LiDAR data, CLRedEdge is also the VI influencing the most the prediction of $\Psi_{\text{leaf_pred}}$ ($R^2 = 0.47$), while the other VIs have less impact ($R^2 < 0.30$) (Figure S.5.6). CWSIb influenced the most $\Psi_{\text{leaf_pred}}$ ($R^2 = 0.37$) for the model 3 accounting for the thermal and LiDAR data (Figure S.5.7). Regardless of the model, the VIs with the greatest influence on $\Psi_{\text{leaf_pred}}$ are therefore the same (CLRedEdge and/or CWSIb). There is therefore a high consistency in the VIs, and in the explanatory power of each VI, for the prediction of $\Psi_{\text{leaf_pred}}$.

*Table 5.5 – Vegetation index (VI), spectral bands or structural features, and regression weights (β_i) and intercept (α) used in the different multiple linear regression models (equation 5.3) to predict Ψ_{leaf} ($\Psi_{\text{leaf_pred}}$). $CI_{0.95}$ are 95 % confidence interval on the β_i and α of each model; the p-value shows the significance of the variable (β_i or α) in the model assuming that all other variables exist in the model (significance: p-value < 0.001***; p-value < 0.01**; p-value < 0.05*). Model 1 was constructed based on a combination of multispectral (M), thermal (T) and LiDAR (L) data; Model 2 was constructed based on a combination of multispectral (M) and LiDAR (L) data; Model 3 was constructed based on thermal (T) and LiDAR (L) data. The equations for calculating the VIs contained in each model are given in Table S.5.1.*

		Vegetation index (VI), spectral bands or structural feature								Intercept α
		CLRedEdge	CWSIb	Blue	CH	RedEdge	ARI	GNDVI	CST	
Model 1 (M+T+L)	β_i	0.27	-0.49	8.40	0.28	0	0	0	0	-1.55
	$CI_{0.95}$	[0.18;0.36]	[-0.63;-0.34]	[4.46;12.35]	[0.11;0.44]	0	0	0	0	[-1.87;-1.23]
	p-value	<0.001***	<0.001***	<0.001***	0.006**	/	/	/	/	<0.001***
Model 2 (M+L)	β_i	0.81	0	6.78	0.38	1.49	0.02	-3.32	0	-0.77
	$CI_{0.95}$	[0.63;0.98]	0	[3.19;10.36]	[0.22;0.54]	[0.88;2.11]	[0.01;0.03]	[-4.47;-2.17]	0	[-1.43;-0.12]
	p-value	<0.001***	/	0.04*	<0.001***	<0.001***	0.015*	<0.001***	/	0.04*
Model 3 (T+L)	β_i	0	-0.28	0	0.38	0	0	0	-0.011	-0.94
	$CI_{0.95}$	0	[-0.51;-0.05]	0	[0.22;0.54]	0	0	0	[-0.017;-0.005]	[-1.20;-0.68]
	p-value	/	0.04*	/	<0.001***	/	/	/	0.002**	<0.001***

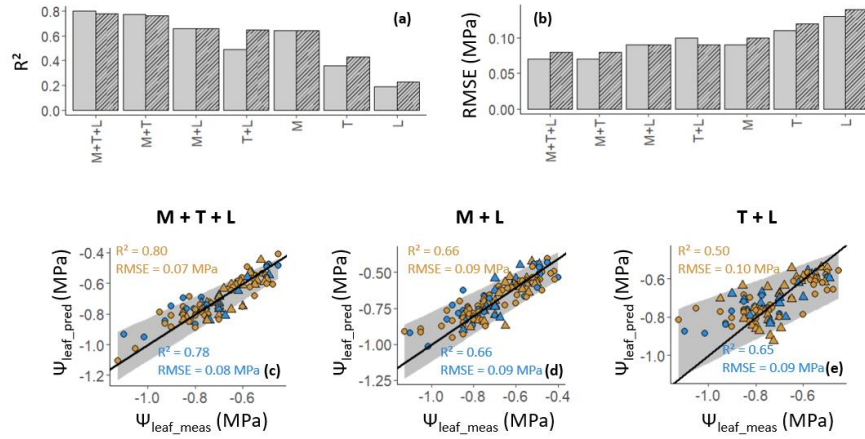


Figure 5.5 – (a) R^2 and (b) RMSE obtained by comparing measured Ψ_{leaf} (Ψ_{leaf_meas}) and predicted Ψ_{leaf} (Ψ_{leaf_pred}) by multiple linear models, for the different data combinations. The full bars correspond to the calibration dataset (70 % of the data), while the hatched bars correspond to the validation dataset (30 % of the data). (c, d, e) Relations between Ψ_{leaf_meas} and Ψ_{leaf_pred} for the three multiple linear models used in this study. The relationships were fitted with 95% confidence intervals ($CI_{0.95}^{\Psi_{leaf}}$ – shaded area). The circles and triangles correspond respectively to the Château de Bousval and the Domaine W vineyards. The brown and blue points correspond respectively to the calibration and validation datasets. The full black lines are the 1:1 line. The relation in (c) was used to predict Ψ_{leaf} at Bousval the 10/08/22, 20/07/23, 10/08/23 and 06/09/23, and at Domaine W the 31/08/22, 20/07/23 and 06/09/23, by using multispectral (M), thermal (T) and LiDAR (L) data; the relation in (d) was used to predict Ψ_{leaf} at Bousval the 27/07/22 and 31/08/22, by using multispectral (M) and LiDAR (L) data; the relation in (e) was used to predict Ψ_{leaf} at Domaine W the 10/08/22, by using thermal (T) and LiDAR (L) data.

5.3.3. Leaf water potential mapping

$\Psi_{\text{leaf_pred}}$ maps (Figure 5.6a), predicted with multiple regression model obtained with the stepwise regression method, showed a relatively constant pattern over time in both vineyards. At the Bousval vineyard, we observed more negative $\Psi_{\text{leaf_pred}}$ in the eastern part of the plot. In the Domaine W vineyard, $\Psi_{\text{leaf_pred}}$ was lower in the north-western plot than in the south-eastern plot. The spatial heterogeneity of $\Psi_{\text{leaf_pred}}$ is much larger at Bousval than at Domaine W, particularly during the drought conditions in 2022 (Figure 5.7a). For example, the 10/08/22 which was the driest day (Table 5.1), $\Psi_{\text{leaf_pred}}$ was distributed between -0.52 MPa and -1.25 MPa at Bousval, but between -0.70 MPa and -0.97 MPa at Domaine W. Although the ranges of $\Psi_{\text{leaf_pred}}$ are different, for a same date, the median $\Psi_{\text{leaf_pred}}$ ($\Psi_{\text{leaf_pred_median}}$) are similar (p-value < 0.05) in both vineyards, excepted for the 20/07/23 for which $\Psi_{\text{leaf_pred_median}}$ was slightly greater at Bousval ($\Psi_{\text{leaf_pred_median}} = -0.50$ MPa at Bousval; $\Psi_{\text{leaf_pred_median}} = -0.54$ MPa at Domaine W). Regarding the temporal dynamics, at Bousval $\Psi_{\text{leaf_pred}}$ decreased between 27/07/22 ($\Psi_{\text{leaf_pred_median}} = -0.74$ MPa) and 10/08/22 ($\Psi_{\text{leaf_pred_median}} = -0.84$ MPa), then re-increased the 31/08/22 ($\Psi_{\text{leaf_pred_median}} = -0.76$ MPa). We observed similar temporal dynamics at Domaine W, with a re-increase of $\Psi_{\text{leaf_pred}}$ between the 10/08/22 ($\Psi_{\text{leaf_pred_median}} = -0.83$ MPa) and 31/08/22 ($\Psi_{\text{leaf_pred_median}} = -0.75$ MPa). At Bousval, $\Psi_{\text{leaf_pred_median}}$ are similar (p-value < 0.05) the 27/07/22 and 10/08/22. In 2023, $\Psi_{\text{leaf_pred}}$ decreased over the season, with $\Psi_{\text{leaf_pred_median}}$ was -0.50 MPa and -0.54 MPa the 20/07/23 at Bousval and Domaine W respectively, and was -0.74 MPa and -0.73 MPa the 06/09/23 in the same respective vineyards. In both vineyard we observed similar $\Psi_{\text{leaf_pred_median}}$ for the last date of 2022 and the last date of 2023 (Figure 5.7a).

The uncertainty on $\Psi_{\text{leaf_pred}}$ ($CI_{0.95}^{\Psi_{\text{leaf_pred}}}$), quantified by the 95 % confidence interval on the prediction (Figure 5.6b) follows the same spatial pattern than predicted $\Psi_{\text{leaf_pred}}$ (Figure 5.6a), with greater

uncertainty when $\Psi_{\text{leaf_pred}}$ is more negative. The uncertainty seems also particularly affected by the model used (Table 5.5) to estimate $\Psi_{\text{leaf_pred}}$ (Figure 5.6c). $\Psi_{\text{leaf_pred}}$ at Domaine W the 10/08/22 shows the greatest uncertainty with a median value of 0.28 MPa. This is not surprising since the model used to predict $\Psi_{\text{leaf_pred}}$ at this date (model 3 in Table 5.5 only considers thermal and LiDAR data, and is the one showing the lowest predictive power (R^2) and the greatest uncertainty (Figure 5.5e). For the same date at Bousval, and for a same $\Psi_{\text{leaf_pred_median}}$ (Figure 5.7a), the uncertainty is significantly lower (median $\text{CI}_{0.95}^{\Psi_{\text{leaf_pred}}} = 0.22$ MPa – Figure 5.6c), since we used the model involving multispectral, thermal and LiDAR data to estimate $\Psi_{\text{leaf_pred}}$ (model 1 in Table 5.5), which is the one showing the highest predictive power (R^2) and the lowest uncertainty (Figure 5.5c). $\Psi_{\text{leaf_pred}}$ predicted with the model involving multispectral and LiDAR data (model 2 in Table 5.5) shows the second greater uncertainty, with a median value of 0.26 MPa at Bousval the 27/07/22 and 31/08/22. In both vineyards, the lowest uncertainty was the 20/07/23 (median $\text{CI}_{0.95}^{\Psi_{\text{leaf_pred}}} = 0.17$ MPa), for which we also predicted the highest Ψ_{leaf} .

There is a high correlation between $\Psi_{\text{leaf_pred_median}}$ and the range of $\Psi_{\text{leaf_pred}}$ ($\Psi_{\text{leaf_pred_max}} - \Psi_{\text{leaf_pred_min}}$) with a $R^2 = 0.97$ at Bousval, and $R^2 = 0.94$ at Domaine W (Figure 5.7b). The range of $\Psi_{\text{leaf_pred}}$ increased when $\Psi_{\text{leaf_pred_median}}$ decreased. These relations are vineyard-specific (p-value of ANCOVA test is lower than 0.05). The slope of the linear relation between $\Psi_{\text{leaf_pred_median}}$ and distribution of $\Psi_{\text{leaf_pred}}$ is significantly greater at Bousval (slope = -1.38) than at Domaine W (slope = -0.31).

5. Mapping grapevine leaf water potential with UAS data

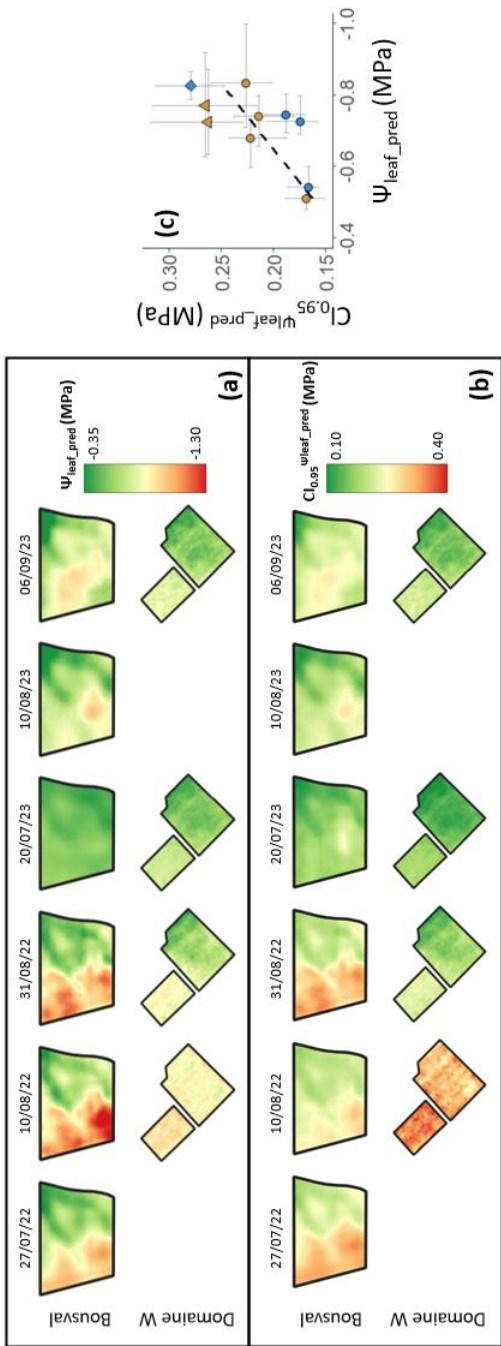


Figure 5.6 – (a) Maps of $\Psi_{\text{leaf_pred}}$ predicted ($\Psi_{\text{leaf_pred}}$) with multiple linear regression model in both vineyards. (b) Maps of uncertainty on $\Psi_{\text{leaf_pred}}$, quantified by the 95 % confidence interval on the prediction ($CI_{0.95}^{\Psi_{\text{leaf_pred}}}$). In (a) and (b) the first line of maps corresponds to the Château de Bousval vineyard, and the second line of maps to the Domaine W vineyard. $\Psi_{\text{leaf_pred}}$ at Bousval the 10/08/22, 20/07/23, 10/08/23 and 06/09/23 was predicted with the model involving multispectral, thermal and LiDAR data (model 1 in Table 5.5); $\Psi_{\text{leaf_pred}}$ at Bousval the 27/07/22 and 31/08/22 was predicted with the model involving multispectral and LiDAR data (model 2 in Table 5.5); $\Psi_{\text{leaf_pred}}$ at Domaine W the 10/08/22 was predicted with the model involving thermal and LiDAR data (model 3 in Table 5.5). (c) Relation between $\Psi_{\text{leaf_pred}}$ and $CI_{0.95}^{\Psi_{\text{leaf_pred}}}$. The points correspond to the median, and the horizontal and vertical bars show respectively the quartiles around $\Psi_{\text{leaf_pred}}$ and $CI_{0.95}^{\Psi_{\text{leaf_pred}}}$. The brown and blue points correspond respectively to the Château de Bousval and Domaine W vineyards. The circles correspond to the model involving multispectral, thermal and LiDAR data (model 1 in Table 5.5); the triangles correspond to the model involving multispectral and LiDAR data (model 2 in Table 5.5); the diamonds correspond to the model involving thermal and LiDAR data (model 3 in Table 5.5). The dashed black line is the linear regression; the slope of this regression is different from 0 ($p\text{-value} < 0.001$).

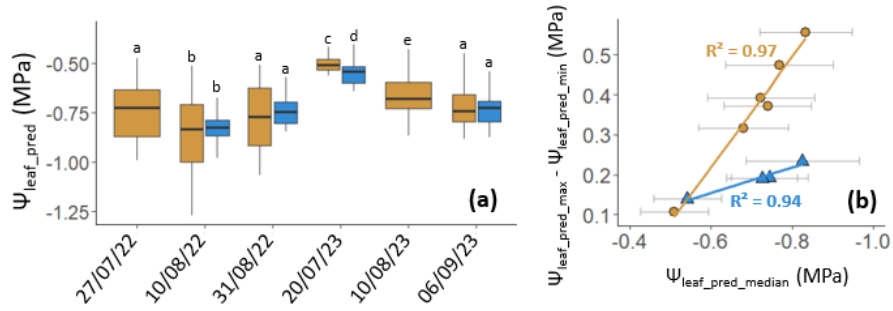


Figure 5.7 – **(a)** Boxplots indicating the median and quartiles, minimum and maximum of the spatial distribution of the predicted Ψ_{leaf} ($\Psi_{\text{leaf_pred}}$). Brown and blue boxplots correspond respectively to the distributions at the Château de Bousval vineyard and at the Domaine W vineyard. The letters above each boxplot are the results of the Wilcoxon tests; a same letter indicate a statistically similar ($p\text{-value} > 0.05$) median. **(b)** Relation between the median $\Psi_{\text{leaf_pred}}$ ($\Psi_{\text{leaf_pred_median}}$) and the distribution of $\Psi_{\text{leaf_pred}}$ ($\Psi_{\text{leaf_pred_max}} - \Psi_{\text{leaf_pred_min}}$). The horizontal bars are the median $CI_{0.95}^{\Psi_{\text{leaf_pred}}}$ (median uncertainty) on $\Psi_{\text{leaf_pred_median}}$. The brown circles correspond to the Château de Bousval vineyard and the blue triangles to the Domaine W vineyard. The brown lines are the linear regressions on the brown circles; the blue lines are the linear regressions on the blue circles.

5.3.4. Environmental factors influencing spatial distribution of leaf water potential

At Bousval, $\Psi_{\text{leaf_pred}}$ was the most correlated with the averaged soil hydraulic conductivity on 2.5 m depth $\tilde{K}_{\text{soil}}$ (Figure 5.8). The correlation was better in 2022 than in 2023, with the best correlation the 10/08/22 ($R^2 = 0.86$), the driest day (Table 5.1). Soil hydraulic conductivity has

5. Mapping grapevine leaf water potential with UAS data

therefore a great influence on the spatial distribution of $\Psi_{\text{leaf_pred}}$, particularly when the conditions are dry. The water holding capacity on 2.5 m depth (WHC) is less correlated with $\Psi_{\text{leaf_pred}}$, however we also find the best correlation the 10/08/22 ($R^2 = 0.72$). At Bousval, the elevation was moderately correlated with $\Psi_{\text{leaf_pred}}$, particularly in 2022 (e.g. $R^2 = 0.42$ the 10/08/22). This is not surprising since the interface between the loamy and sandy soil horizons is shallower in the upper part of the parcel (western part) and deeper in the lower part due to an accumulation of loamy colluviums (Figure 5.1c). However, the correlation between $\Psi_{\text{leaf_pred}}$ and elevation is lower than the correlation between $\Psi_{\text{leaf_pred}}$ and $\tilde{K}_{\text{soil}}$, and between $\Psi_{\text{leaf_pred}}$ and WHC, showing that soil properties have a greater influence on the spatial distribution of $\Psi_{\text{leaf_pred}}$ than the elevation. The slope showed the lowest correlation with $\Psi_{\text{leaf_pred}}$ (maximum $R^2 = 0.15$ the 31/08/22). It is interesting to note that the 20/07/23, the correlation between $\Psi_{\text{leaf_pred}}$ and all topographic and soil properties is low (e.g. $R^2 = 0.27$ between $\Psi_{\text{leaf_pred}}$ and $\tilde{K}_{\text{soil}}$). At Domaine W, the slope and elevation showed a low correlation with $\Psi_{\text{leaf_pred}}$. The maximum R^2 between $\Psi_{\text{leaf_pred}}$ and slope was 0.09, and was 0.24 between $\Psi_{\text{leaf_pred}}$ and elevation both the 20/07/23. These low correlations are not surprising since this vineyard is almost flat (Figure 5.1g).

As shown in Figure 5.7b, the slope of the linear relation between $\Psi_{\text{leaf_pred_median}}$ and distribution of $\Psi_{\text{leaf_pred}}$ is significantly greater at Bousval than at Domaine W, showing that environmental conditions at Bousval are much more heterogeneous (i.e. heterogeneity of soil properties), which is reflected in a larger range of distribution of Ψ_{leaf} , particularly when conditions are drier. In this study, we quantified the water deficit thanks to the standardized precipitation evapotranspiration index (SPEI – equation 5.1). More negative SPEI indicates a greater water deficit. We also used VPD to characterize the atmospheric conditions and quantify the evaporative demand. $\Psi_{\text{leaf_pred_median}}$ is highly correlated ($R^2 = 0.82$) with the linear combination of SPEI and VPD (Figure 5.9a). Interestingly, this relation is not vineyard specific (p-value of ANCOVA test is greater than 0.05). $\Psi_{\text{leaf_pred_median}}$ is positively correlated with SPEI (regression coefficient a in equation 5.4

is 0.001) and negatively correlated with VPD (regression coefficient b in equation 5.4 is -0.13). This means that $\Psi_{\text{leaf_pred_median}}$ decreases when SPEI decreases and when VPD increases. In other words, the median Ψ_{leaf} in a vineyard is more negative for greater water deficit (SPEI) and evaporative demand (VPD). The distribution of $\Psi_{\text{leaf_pred}}$ ($\Psi_{\text{leaf_pred_max}} - \Psi_{\text{leaf_pred_min}}$) is also correlated ($R^2 = 0.54$) with the linear combination of SPEI and VPD (Figure 5.9b). This relation, unlike the one with $\Psi_{\text{leaf_pred_median}}$, is vineyard-specific (p-value of ANCOVA test is lower than 0.05). The distribution of $\Psi_{\text{leaf_pred}}$ is negatively correlated with SPEI (regression coefficient a in equation 5.5 is -0.001) and positively correlated with VPD (regression coefficient b in equation 5.5 is 0.08). This means that the range of distribution of $\Psi_{\text{leaf_pred}}$ increases when SPEI decreases and VPD increases. In other words, in a vineyard, the spatial heterogeneity of Ψ_{leaf} is more important for greater water deficit (SPEI) and evaporative demand (VPD).

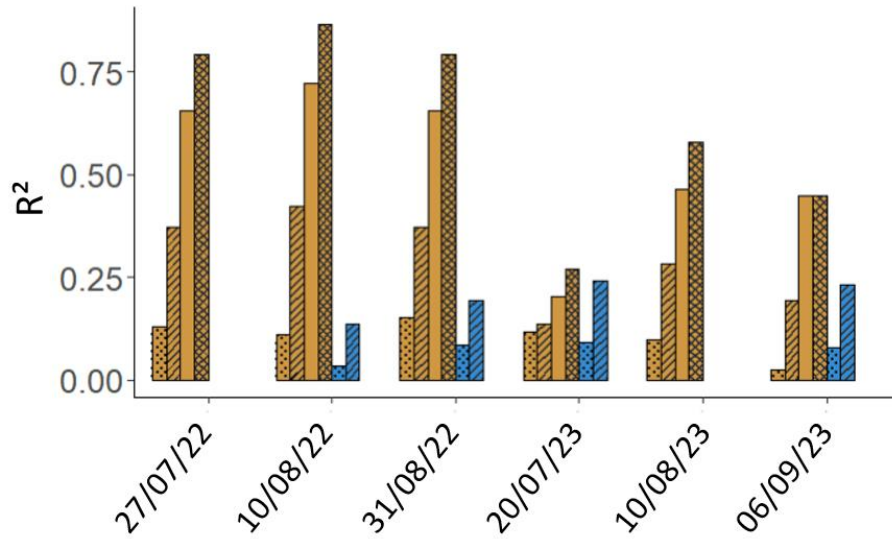


Figure 5.8 – Coefficient of determination (R^2) of the linear relation between predicted Ψ_{leaf} ($\Psi_{\text{leaf_pred}}$) and elevation (pointed bars), between $\Psi_{\text{leaf_pred}}$ and slope (hatched bars), between $\Psi_{\text{leaf_pred}}$ and the water holding capacity on 2.5 m (WHC – only at the Château de Bousval vineyard – empty bars), and between $\Psi_{\text{leaf_pred}}$ and the averaged soil hydraulic conductivity ($\tilde{K}_{\text{soil}}$ – only at the Château de Bousval vineyard – cross-hatched bars). The brown and blue bars correspond respectively to the Château de Bousval and Domaine W vineyards.

5. Mapping grapevine leaf water potential with UAS data

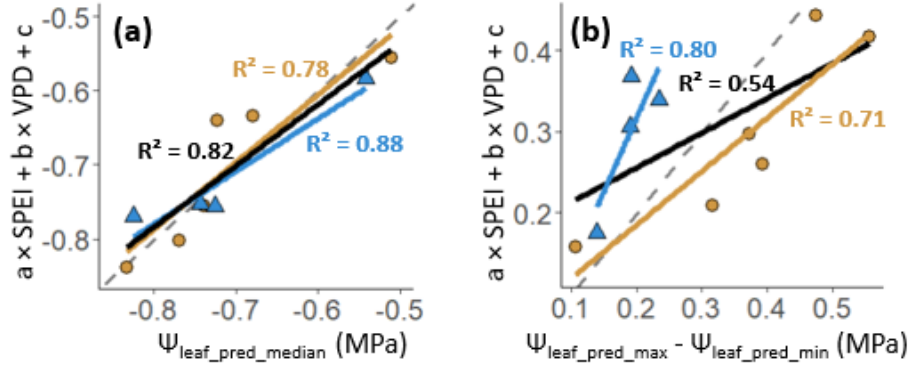


Figure 5.9 – **(a)** Relation between median $\Psi_{\text{leaf_pred}}$ ($\Psi_{\text{leaf_pred_median}}$) and the linear combination of SPEI and VPD (equation 5.4 – $\Psi_{\text{leaf_pred_median}} = 0.001 \times \text{SPEI} - 0.13 \times \text{VPD} - 0.26$). **(b)** Relation between the distribution of $\Psi_{\text{leaf_pred}}$ ($\Psi_{\text{leaf_pred_max}} - \Psi_{\text{leaf_pred_min}}$) and the linear combination of SPEI and VPD (equation 5.5 – $\Psi_{\text{leaf_pred_max}} - \Psi_{\text{leaf_pred_min}} = -0.001 \times \text{SPEI} + 0.08 \times \text{VPD} - 0.17$). In each subplot, the brown circles correspond to the Château de Bousval vineyard and the blue triangles to the Domaine W vineyard. The brown lines are the linear regressions on the brown circles; the blue lines are the linear regressions on the blue triangles; the black lines are the linear regressions on all points; the dashed grey lines are the 1:1 lines.

5.4. Discussion

In this study, we attempted to map grapevine leaf water potential (Ψ_{leaf}) intra-field heterogeneity, to assess the impact of topographic, edaphic and climatic conditions on the spatial distribution of Ψ_{leaf} . Our study demonstrated that multilinear combination of multispectral VIs, thermal VIs and structural features from LiDAR data, collected with UAS collecting high-spatial resolution imagery, is efficient ($R^2 = 0.80$ and $\text{RMSE} = 0.07$ MPa for the calibration; $R^2 = 0.78$ and $\text{RMSE} = 0.08$ MPa for the validation) to capture the spatial distribution of grapevine

Ψ_{leaf} across different vineyards during two viticultural seasons. We showed that the heterogeneity of edaphic conditions has the greatest influence on the spatial heterogeneity of Ψ_{leaf} , particularly when the water deficit and evaporative demand increase.

5.4.1. Leaf water potential prediction with a combination of multispectral, thermal and LiDAR UAS-data

We used the stepwise regression method to find the best multilinear regression to predict Ψ_{leaf} with several UAS-based multispectral VIs, thermal VIs and structural features (LiDAR) measured on grapevines (Wilkinson, 1979). The univariable linear relation between measured Ψ_{leaf} and VIs (Pearson's $\rho >$ Spearman's ρ – Figure S.5.3b) justifies the use of this statistical method to better predict Ψ_{leaf} . However, other statistical methods could also be used to predict Ψ_{leaf} , such as principal component regression (PCR) or random forest. To support our approach (stepwise regression), we also implemented the PCR and random forest methods (Figure S.5.4). However, while the random forest models gave the highest R^2 and lowest RMSE for the calibration dataset, there was a great loss of predictive power when we validated the model (R^2 decreased and RMSE increased). This showed some evidence of model overfitting, affecting the robustness of the model constructed with the random forest. Generally, the R^2 and RMSE were respectively higher and lower for the stepwise regression model compared to the PCR model. The stepwise regression method showed therefore more robustness than the random forest method when we validated models, and a better predictive power compared to PCR (Figure S.5.8). Other studies using random forest or artificial neural networks to predict Ψ_{leaf} with UAS-based multispectral VIs lost predictive power when they validated their model, showing that the model structure was overfitted (Poblete et al., 2017; Romero et al., 2018; Tang et al., 2022). Our

5. Mapping grapevine leaf water potential with UAS data

analysis highlighted the importance of incorporating multispectral, thermal and LiDAR data to improve the prediction of Ψ_{leaf} . The use of data from different sensors also makes it possible to limit the uncertainty on Ψ_{leaf} (Figure 5.5). Tang et al. (2022) already mentioned that data combination from multiple sensors acquiring data in different regions of the electromagnetic spectrum will allow mapping Ψ_{leaf} with more accuracy. In our model, the multispectral VI CLRedEdge (calculated based on the NIR and red-edge bands), the reflectance in the blue band, the thermal VI CWSIb, and the canopy height (CH) all significantly influence Ψ_{leaf} and are used in the multilinear regression to predict it (model 1 in Table 5.5). It is interesting to note that these indices, bands and features are also used in the models for which only multispectral and LiDAR data (model 2 in Table 5.5), or thermal and LiDAR data (model 3 in Table 5.5) are used to predict Ψ_{leaf} . Although they are not significantly correlated with measured Ψ_{leaf} when taken one by one (Figure 5.4), information contained in these indices is complementary and their combinations enables Ψ_{leaf} to be predicted with high predictive power (e.g. $R^2 = 0.80$ and $\text{RMSE} = 0.07$ MPa for calibration, and $R^2 = 0.78$ and $\text{RMSE} = 0.08$ MPa for validation, for model 1). It is not required to discard VIs which are not directly correlated with Ψ_{leaf} , since multilinear modelling techniques can identify the patterns in the data and assign individual weights to inputs, allowing multilinear models to fit accordingly (Romero et al., 2018). NIR and red-edge spectral regions, used to calculate CLRedEdge, have already been investigated to predict vegetation water potential (Giovos et al., 2021; Pôças et al., 2015; Soubry et al., 2017; Zygielbaum et al., 2009). Although these bands, and derived VIs, are commonly associated with plant structural traits (e.g., biomass, vigour), red-edge region is often used as a reference to detect chlorophyll content on vegetation (Clevers and Gitelson, 2013; Gamon and Surfus, 1999; Rallo et al., 2014). Plant water status is indicative and closely related to chlorophyll content, as changes in this pigment content induce changes in leaf spectral properties in the red-edge region (Carter and Knapp, 2001). NIR electromagnetic region has also been shown to be affected by leaf structure and leaf water content of grapevine (De Bei et al., 2011; Marañón et al., 2023; Tardaguila et al., 2017). VIs calculated based on NIR and red-edge bands, such as CLRedEdge, have good

potential to quantify grapevine water potential (Becker et al., 2020; Giovos et al., 2021). Additionally, bands in the visible domain, such as the blue band, can provide valuable information about plant water status, as pigment contents and composition govern reflectance in this domain (Gamon et al., 1992; Moya et al., 2004) and are related to processes associated with grapevine water status (Zarco-Tejada et al., 2013). Blue wavelengths are strongly absorbed by carotenoids (carotenes and xanthophylls). These pigments, and their proportion, also serve as indicators of plant water status (Gitelson et al., 2006). Moreover, the blue reflectance enable atmospheric corrections and allow for a more linear relationship with vegetation status (Gitelson et al., 2002). Thermal VIs, also provide information on grapevine water status. Strong relationships have been found between CWSI and stomatal conductance of grapevine (Pagay and Kidman, 2019; Pou et al., 2014), which is directly linked (non-linearly) to Ψ_{leaf} . During drought, grapevines close stomata to prevent the plant from reaching excessively negative water potentials leading to xylem cavitation (Gambetta et al., 2020b). Canopy height (CH), retrieved with LiDAR point clouds, is also used to predict Ψ_{leaf} . García-Tejera et al. (2021) showed that changes in plant canopy structure, including canopy height and width, influence the water flow between the soil and the atmosphere, thereby affecting Ψ_{leaf} . Thermal remote sensing metrics provide short term information on grapevine water status, such as Ψ_{leaf} or stomatal conductance variations (Acevedo-Opazo et al., 2010; Santesteban et al., 2017), while multispectral VIs and structural features (LiDAR) reveal mid-to-long-term water status effect on grapevine structure and traits like leaf pigment content (Baluja et al., 2012; Zarco-Tejada et al., 2013). The three approaches (multispectral, thermal and LiDAR) therefore provide complementary information and their multilinear combinations, through VIs and structural features, allow the accurate and robust assessment of intra-field variability of grapevine leaf water potential, thanks to high-spatial resolution sensors mounted on UAS.

Other sensors could also be tested and used to spatially monitor grapevine Ψ_{leaf} . Adding information from more and narrower spectral

5. Mapping grapevine leaf water potential with UAS data

bands, collected with hyperspectral sensors, could improve the capability to remotely monitor grapevine Ψ_{leaf} (Pôças et al., 2015; Tang et al., 2022). Studies using hyperspectral sensors to measure plant water potential generally get higher correlations than studies using multispectral sensors (Pôças et al., 2015; Rodríguez-Pérez et al., 2007; Zarco-Tejada et al., 2013). For example, the photochemical reflectance index (PRI, calculated with spectral reflectance at 545 nm and 567 nm) is a good indicator (R^2 between 0.5 and 0.6) of crop water status (Stagakis et al., 2012; Suárez et al., 2008). Zarco-Tejada et al. (2013) even obtained a better correlation ($R^2 = 0.82$) in vineyards by combining PRI with other hyperspectral VIs, such as the renormalized difference vegetation index (RDVI, based on reflectance at 700 nm and 761 nm) and the ratio R_{700}/R_{670} (based on reflectance at 670 nm and 700 nm), highlighting that the combination of several VIs brings complementary information to better estimate leaf water potential of grapevine. Short-wave infrared (SWIR) data (1000-2200 nm) also has a good potential to monitor grapevine water status, since this spectral range contains the water absorption bands (Laroche-Pinel et al., 2021a). VIs calculated with SWIR bands, such as the normalized drought water index (NDWI) (Gao, 1996), showed good correlations ($R^2 = 0.58$) with grapevine Ψ_{leaf} (Caruso and Palai, 2023).

5.4.2. Intra-field variability of grapevine leaf water potential

We observed a good stability in Ψ_{leaf} pattern for each date, in both vineyards (Figure 5.6a). At the Domaine W vineyard, the spatial heterogeneity of Ψ_{leaf} is less marked than at the Bousval vineyard. For example, the 10/08/22 (driest day), although median Ψ_{leaf} was similar in both vineyards, range of distribution of Ψ_{leaf} was 0.73 MPa at Bousval, but only 0.27 MPa at Domaine W. The magnitude of variation Ψ_{leaf} at the within field level predicted at Bousval is consistent with

other studies. Brillante et al. (2017a) also observed a difference of 0.70 MPa between maximum and minimum Ψ_{leaf} within a vineyard in California. They hypothesized, without directly proving it, that this variability was due to the short distance differences of soil properties in the vineyard. Tang et al. (2022) observed a spatial variability up to 0.67 MPa, but this was due to differences in irrigation treatment in a vineyard with gravelly loam soil. At Bousval, the spatial distribution of Ψ_{leaf} is highly correlated (Figure 5.8 – R^2 up to 0.86) with an averaged soil hydraulic conductivity $\bar{K}_{\text{soil}}$. In this vineyard, Ψ_{leaf} was significantly more negative in the eastern part of the plot, where the interface between the loamy soil and the sandy subsoil is more superficial, compared to the western part where the loamy soil is clearly deeper. In Chapter 3, we showed that grapevine water potential is significantly influenced by the soil texture. It is well known that the soil water potential around the roots affects Ψ_{leaf} , since the difference between both water potentials is the driving force for transpiration (Tyree and Zimmermann, 2002). The soil water potential in the vicinity of the roots decreases as the plant takes up water, resulting in a significant loss of soil hydraulic conductivity around the roots (Cai et al., 2022). This reduction of hydraulic conductivity generates large gradients in soil water potential at the vicinity of the roots, leading to a significant drop of Ψ_{leaf} to support a slight increase in transpiration (Carminati and Javaux, 2020). The soil texture determines soil hydraulic properties, thereby influencing grapevine hydraulics (Lavoie-Lamoureux et al., 2017; Tramontini et al., 2013a). Therefore, in a sandy soil, the decline in soil hydraulic conductivity around the roots is sharper than in a fine-textured soil, leading to a significantly greater reduction of water potential at the soil-root interface, which directly impacts Ψ_{leaf} which also decreases more rapidly (Cai et al., 2022). In soil-water limited conditions, such as in 2022 (Figure S.5.1), we can assume that soil hydraulic conductivity drop is larger in the western part of the Bousval vineyard, where most of the grapevine roots are found in the sandy subsoil (Chapter 3), leading to a greater drop of soil-root interface water potential and consequently to a larger decline of Ψ_{leaf} . We can therefore affirm that in a non-irrigated vineyard, the edaphic heterogeneity (i.e. in terms of soil hydraulic conductivity) governs the spatial heterogeneity (and patterns) of grapevine Ψ_{leaf} , particularly during

5. Mapping grapevine leaf water potential with UAS data

drought. At the Domaine W vineyard, we always predicted more negative Ψ_{leaf} in the north-west parcel than in the south-east plot. We observed, but only in a single location in each subplot, that the north-west parcel is made of a silty loam soil on the first horizons and silty clay loam soil thereafter, while the south-east parcel is composed by a silty loam soil on the whole profile (Figure 5.1h). Although the vertical distribution of soil texture is not accurately known in the whole field, we could assume that this spatial difference of soil properties has an influence on the spatial heterogeneity of Ψ_{leaf} , since other factors such as the elevation ($R^2 = 0.24$) and the slope ($R^2 = 0.09$) have low correlation with the spatial distribution of Ψ_{leaf} (Figure 5.8). However, other studies comparing loamy and loamy clay soils showed only a moderate effect on grapevine Ψ_{leaf} (Brillante et al., 2017b), explaining the lower range of Ψ_{leaf} observed in this vineyard. Other factors could potentially influence the spatial distribution of Ψ_{leaf} at the Domaine W. For example, in this vineyard, the level of the water table is higher in the south-eastern parcel, due to the stream running parallel to the plot. It has been observed that this water table reach the roots, and water consumed by the grapevines is therefore certainly replaced by vertical soil-water movements (capillary rises) (Van Leeuwen et al., 2018). The presence of a water table within the reach of the roots prevent or mitigate decrease of Ψ_{leaf} (Tramontini et al., 2013a). Further investigations should be done to better understand the spatial heterogeneity of Ψ_{leaf} in the Domaine W vineyard.

We showed that the linear combination of SPEI and VPD was correlated with the median ($\Psi_{\text{leaf_median}} - R^2 = 0.82$) and the range ($\Psi_{\text{leaf_max}} - \Psi_{\text{leaf_min}} - R^2 = 0.54$) of leaf water potential (Figure 5.9). In a vineyard, the $\Psi_{\text{leaf_median}}$ is more negative when the water deficit and the evaporative demand is greater (i.e. respectively when SPEI is lower and VPD is higher). Interestingly, we showed that this relation was independent of the vineyard (p-value > 0.05). The range of Ψ_{leaf} is more important for greater water deficit and evaporative demand. This relation was vineyard-dependent (p-value < 0.05). While the edaphic heterogeneity can explain the Ψ_{leaf} spatial heterogeneity observed within a vineyard, the median and range of Ψ_{leaf} are particularly affected

by the weather conditions (i.e. evaporative demand) and the intensity of water deficit. When evaporative demand and/or water deficit are greater, the spatial heterogeneity of Ψ_{leaf} is particularly marked, and follows $\tilde{K}_{\text{soil}}$ intra-field patterns. Therefore, weather conditions also have a great influence on the temporal variability of Ψ_{leaf} (Brillante et al., 2017a). The impact of weather conditions on Ψ_{leaf} can explain why we observed a re-increase of $\Psi_{\text{leaf_median}}$ between the 10/08/22 and 31/08/22 in both vineyards, since VPD on 10/08/22 was significantly higher than VPD on 31/08/22. Plants exposed to a higher evaporative demand experience a greater loss in water potential at the soil-root interface, resulting in more negative Ψ_{leaf} . Conversely, for grapevines exposed to lower VPD, the drop in Ψ_{leaf} is more limited since the water potential at the soil-root interface is higher (Cai et al., 2022; Carminati and Javaux, 2020). Spatial soil properties distribution, weather conditions and intensity of water deficit mainly influence grapevine leaf water potential heterogeneity, and the median and range of Ψ_{leaf} observed in non-irrigated vineyards, and their effects are concomitants (Van Leeuwen et al., 2018).

It is interesting to note that the 20/07/23, Ψ_{leaf} is relatively homogeneous within both vineyards and its distribution ($\Psi_{\text{leaf_max}} - \Psi_{\text{leaf_min}}$) is therefore low (Figure 5.7a). At Bousval, Ψ_{leaf} was still slightly lower in the western part of the parcel, but the difference was significantly less marked compared to the other dates (Figure 5.6). Same observations can be made at Domaine W, with slightly more negative Ψ_{leaf} in the north-western plot, but a less marked variability compared to other dates. The 20/07/23, the soil was the wettest ever measured for this study (Figure S.5.1), as well as the water deficit (SPEI) and the evaporative demand was the lowest among all dates (Table 5.1). In non-limiting soil conditions, water flow is primarily governed by plant hydraulic conductance, instead of soil hydraulic conductivity, even in sandy soils (Draye et al., 2010; Passioura, 1980). Therefore, plant hydraulic conductance mainly affects leaf water potential distribution in these conditions. Although it is well-known that edaphic conditions influence grapevine hydraulic conductance (Tramontini et al., 2013a), notably through their impact on xylem (Hochberg et al., 2015), root

5. Mapping grapevine leaf water potential with UAS data

(Ollat et al., 2015) and canopy (Pereyra et al., 2023) architecture, we can assume that the within-field grapevine hydraulic conductance is significantly less heterogeneous than within-field soil hydraulic conductivity. This is not surprising since in this study, for a given vineyard, we only worked on one cultivar-rootstock combination. Although some studies highlighted the predominance of the soil effect on grapevine water potential (Taylor et al., 2010; Tramontini et al., 2013a), it would be interesting to carry out research to understand how, within a same vineyard with different cultivar-rootstock combinations, this affects the range of within-field Ψ_{leaf} .

Other studies showed that topographic attributes, such as slope and elevation, could also impact grapevine performance (Bramley et al., 2011; Karn et al., 2024). In this study, we only observed a maximum $R^2 = 0.13$ and $R^2 = 0.54$ respectively between Ψ_{leaf} and slope, and between Ψ_{leaf} and elevation. This is consistent with Brillante et al. (2017a) who showed that slope and elevation differences are less significantly related to grapevine water status heterogeneity in vineyards with moderate or no slope, which is the case in the present study. It has been shown that topographic attributes have a real influence on grapevines for vineyards with steep slopes (Brillante et al., 2017b).

5.5. Conclusion and perspectives

We aimed to accurately map the grapevine leaf water potential (Ψ_{leaf}) and assess the impact of edaphic, topographic and climatic conditions on the Ψ_{leaf} intra-field heterogeneity, within two non-irrigated vineyards with deep heterogeneous soils in terms of soil texture, and with moderate or no slope, during two viticultural seasons. We combined UAS-based multispectral, thermal and LiDAR data to spatially predict grapevine Ψ_{leaf} . The data provided by different sensors acquiring data

in different regions of the electromagnetic spectrum brought complementary information on grapevine water status and allowed the development of a robust and high-predictive power model ($R^2 = 0.80$ and $RMSE = 0.07$ MPa for the calibration; $R^2 = 0.78$ and $RMSE = 0.08$ MPa for the validation) to estimate grapevine Ψ_{leaf} in both vineyards and during both years. While thermal VIs (e.g. CWSI) provide short term information, such as Ψ_{leaf} variations, multispectral (e.g. CLRedEdge and blue reflectance band) and LiDAR (from which we can derived grapevine structural features) data are associated to mid-to-long term water status effect on grapevine structure (e.g. canopy height) and traits like leaf pigment content. Our results provided evidence that in these non-irrigated vineyards, grapevine water status was highly variable within a vineyard, up to 0.73 MPa. This spatial distribution of Ψ_{leaf} was mainly governed by the within-vineyard soil hydraulic conductivity heterogeneity, and was particularly marked when the evaporative demand and the water deficit were greater, since the range of Ψ_{leaf} increased in these conditions. Knowledge of spatial variability of grapevine water status, through grapevine Ψ_{leaf} , could help winegrowers to accurately optimize the viticultural management during the different phenological stages of the grapevine. Although promising, our results are limited to one grapevine cultivar (cv. Chardonnay) and two vineyards. To further improve the robustness and reliability of the method used in this study, additional UAS observations should be done to represent a broader range of cultivars, rootstocks, management systems and environmental conditions, to examine how other viticultural factors may affect grapevine Ψ_{leaf} spatial heterogeneity in different conditions. Moreover, accurate spatialized information of grapevine Ψ_{leaf} could be used in functional-structural grapevine models (Yang et al., 2023) to predict berry growth and quality (i.e. sugar content) and its variation at the field scale.

5.6. Supplementary material

5.6.1. Supplementary figures

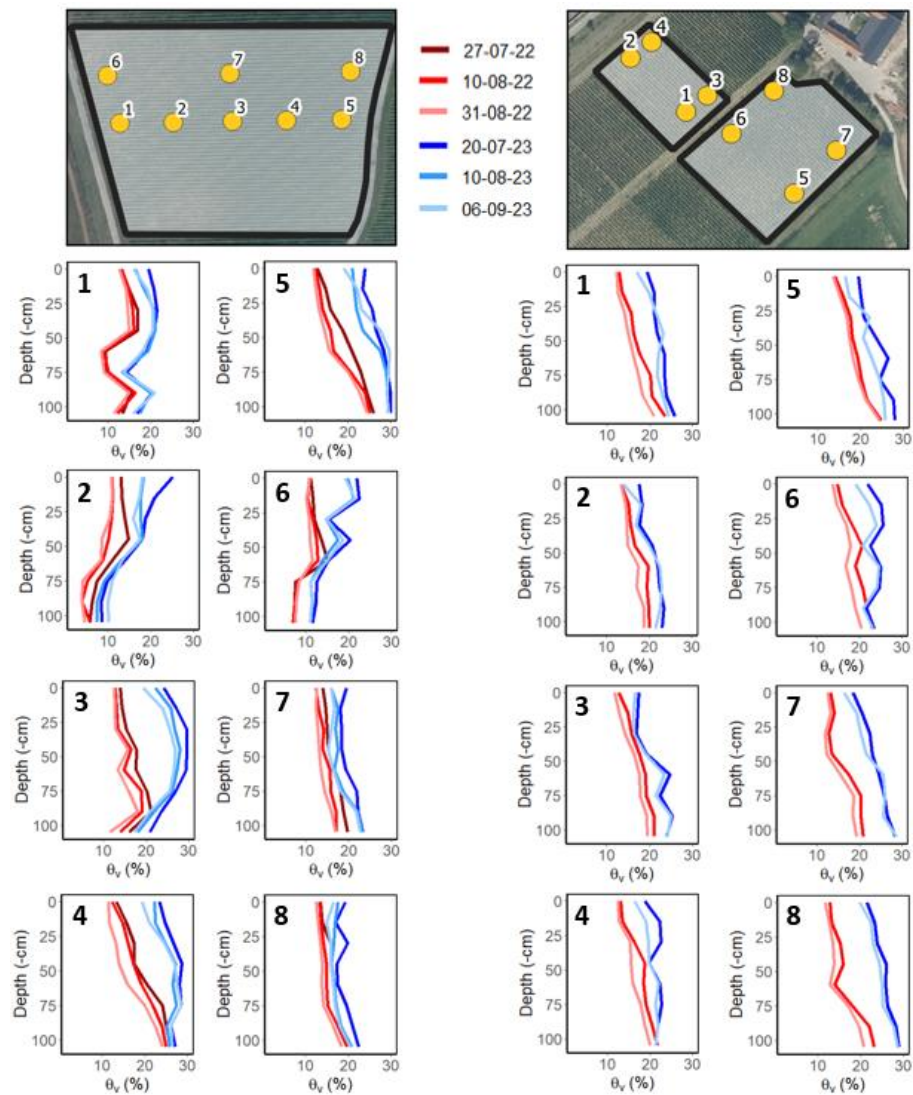
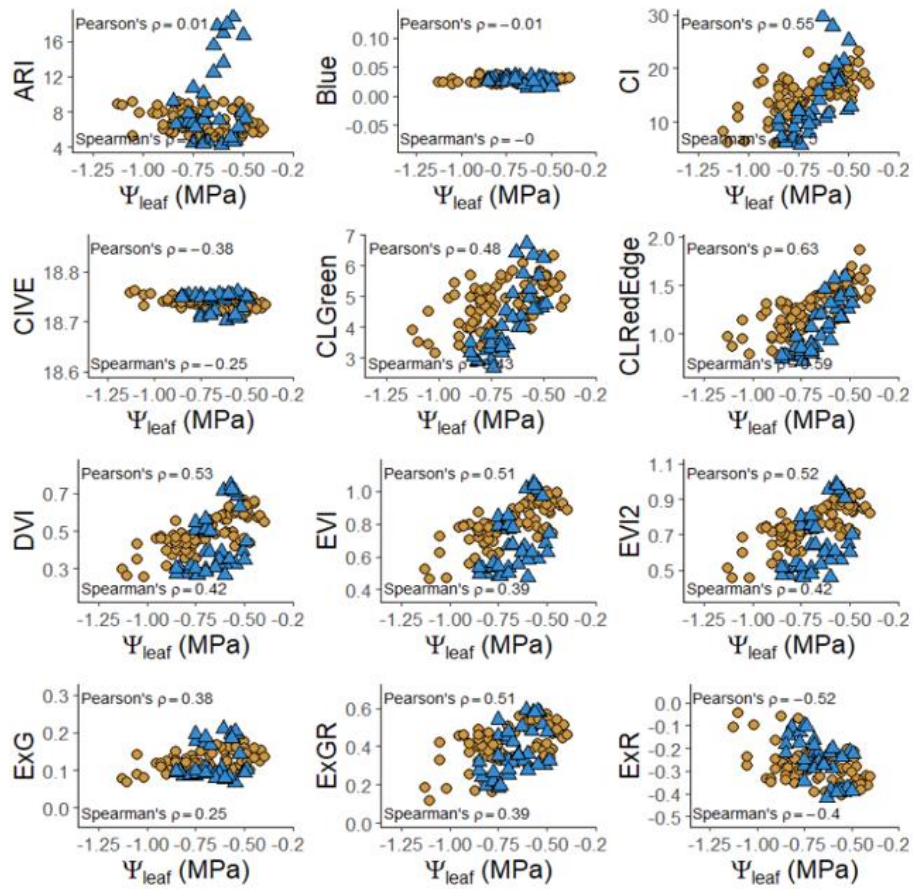
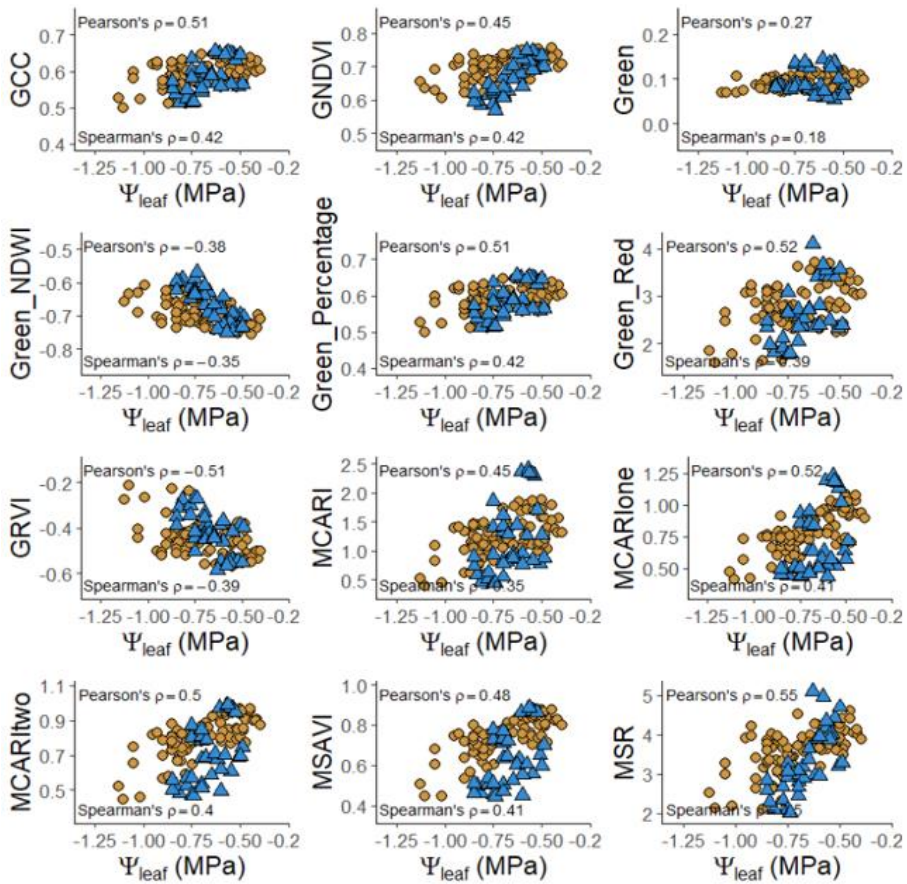


Figure S.5.1 – Evolution of soil water content (θ_v) profile down to 105 cm depth, measured just before each UAS flight at different locations (yellow points) in both vineyards.

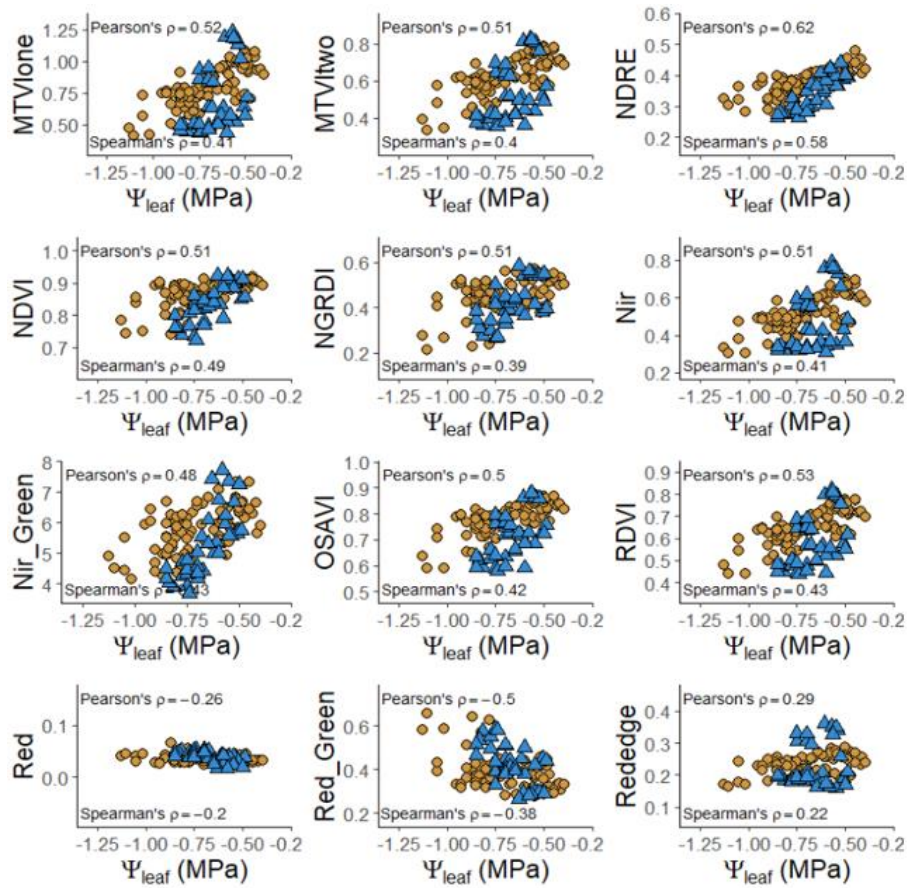
5.6. Supplementary material



5. Mapping grapevine leaf water potential with UAS data



5.6. Supplementary material



5. Mapping grapevine leaf water potential with UAS data

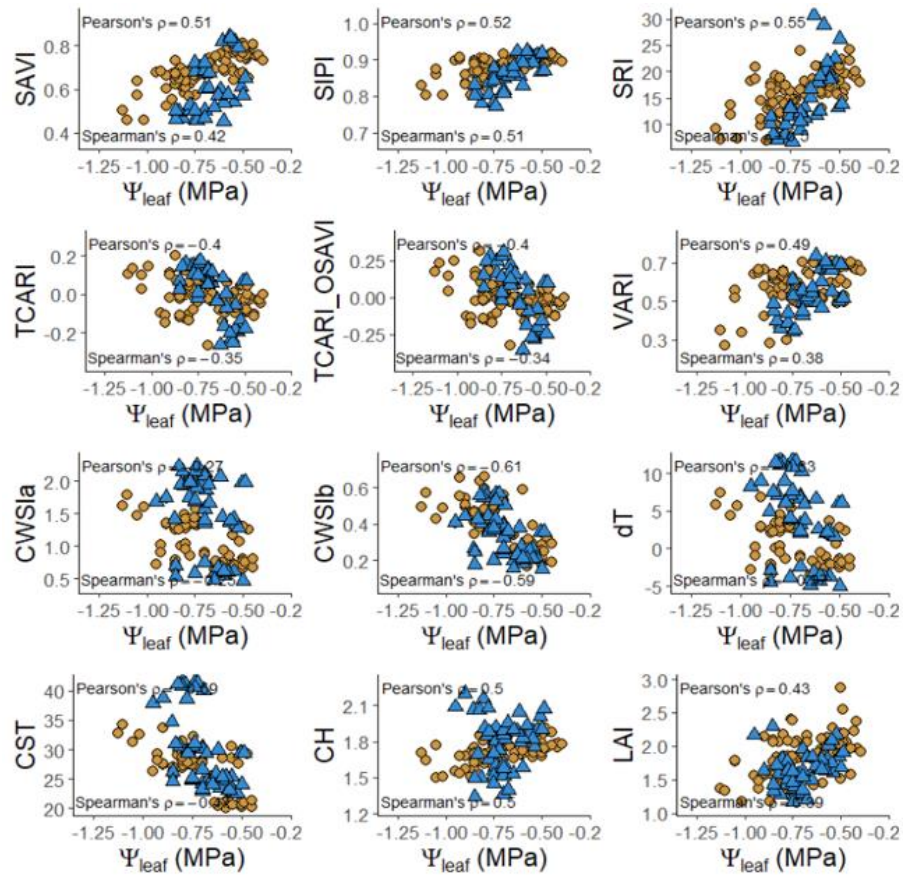


Figure S.5.2 – Univariable relation between measured Ψ_{leaf} and the different VIs. The Pearson's and Spearman's coefficients (ρ), on all points together, are shown in the plots. Brown circles correspond to data from Château de Bousval vineyard; blue triangles correspond to data from Domaine W vineyard.

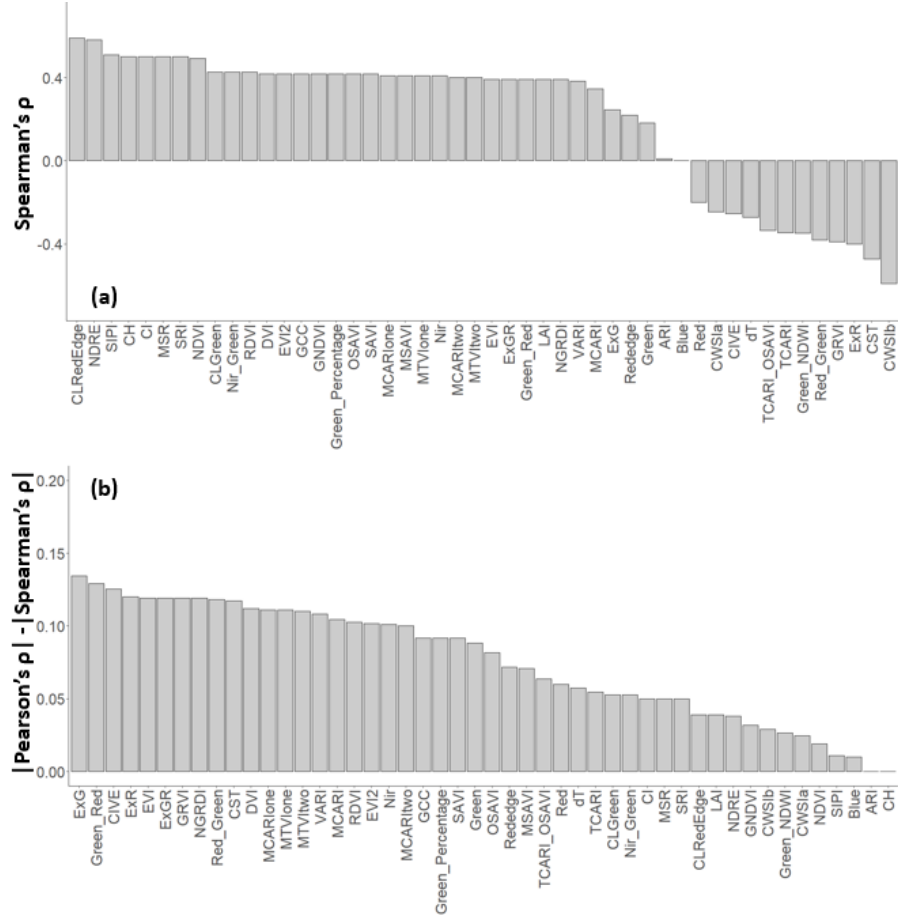


Figure S.5.3 – **(a)** Spearman's coefficient (Spearman's ρ) quantifying the non-linear correlation between measured Ψ_{leaf} and each vegetation index (VI), by taking all the measurements in both vineyards and at all dates. **(b)** Difference between the absolute values of Pearson's ρ and Spearman's ρ .

5. Mapping grapevine leaf water potential with UAS data

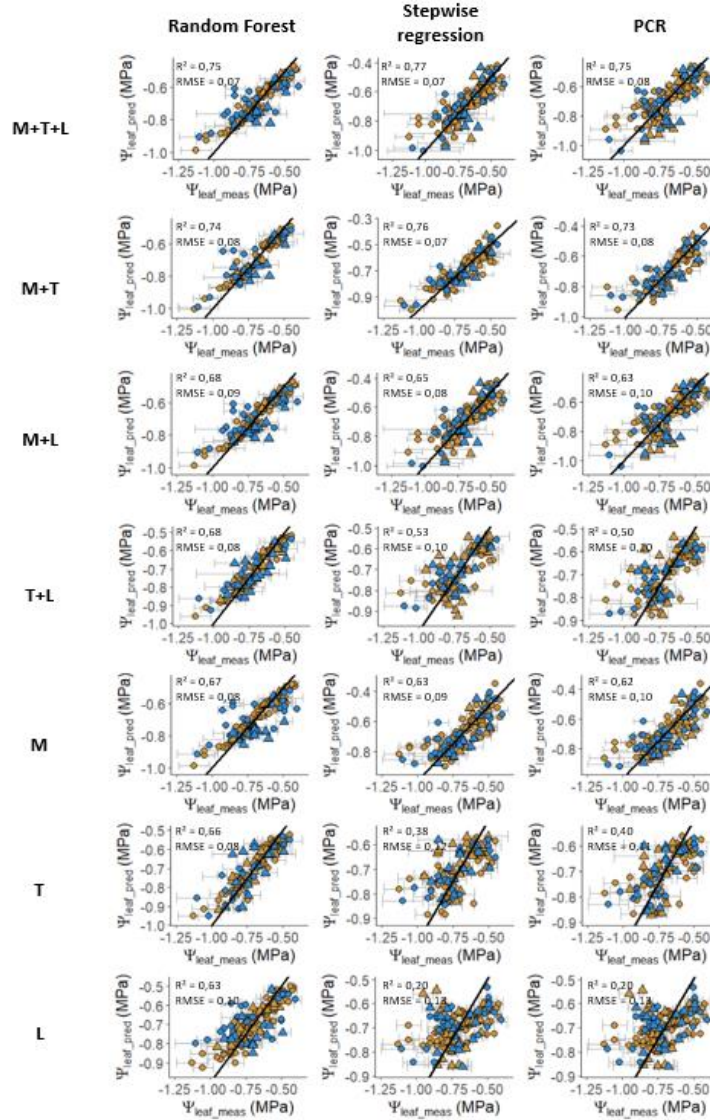


Figure S.5.4 – Relation between leaf water potential measured ($\Psi_{\text{leaf_meas}}$ – x-axis) and predicted ($\Psi_{\text{leaf_pred}}$ – y-axis) with random forest model (left column), stepwise regression model (middle column) and principal component regression model (PCR – right column), for the different UAS data combinations of multispectral (M), thermal (T) and LiDAR (L) data. Blue and brown points are respectively data from Château de Bousval and Domaine W vineyards. Circles and triangles are respectively data used for the calibration and validation of the models. Horizontal grey lines are the standard deviation of $\Psi_{\text{leaf_meas}}$. The black lines are the 1:1 line. R^2 and RMSE are calculated taking account to all points.

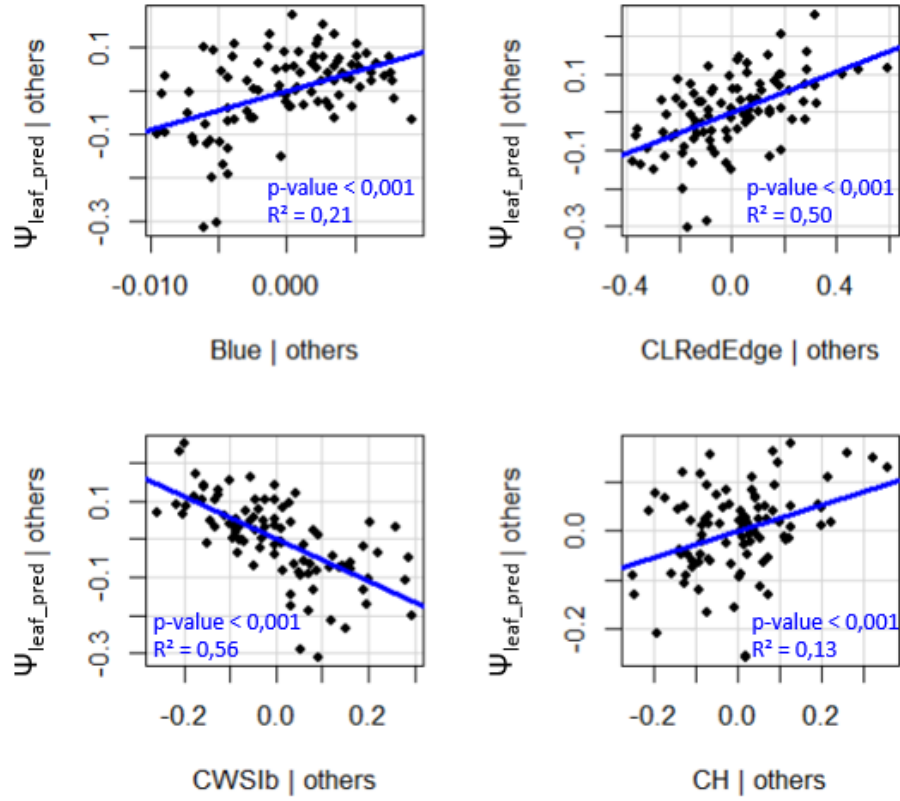


Figure S.5.5 – Partial regression plots of each predictor variable on the prediction of Ψ_{leaf} , for the model 1 $\Psi_{leaf_pred} = -1.55 + 0.27*CLRedEdge - 0.49*CWSIb + 8.40*Blue + 0.27*CH$ (multispectral, thermal and LiDAR data). The $p\text{-value} < 0.001$ signifies that the slope of the linear regression (blue line) is significantly different from 0.

5. Mapping grapevine leaf water potential with UAS data

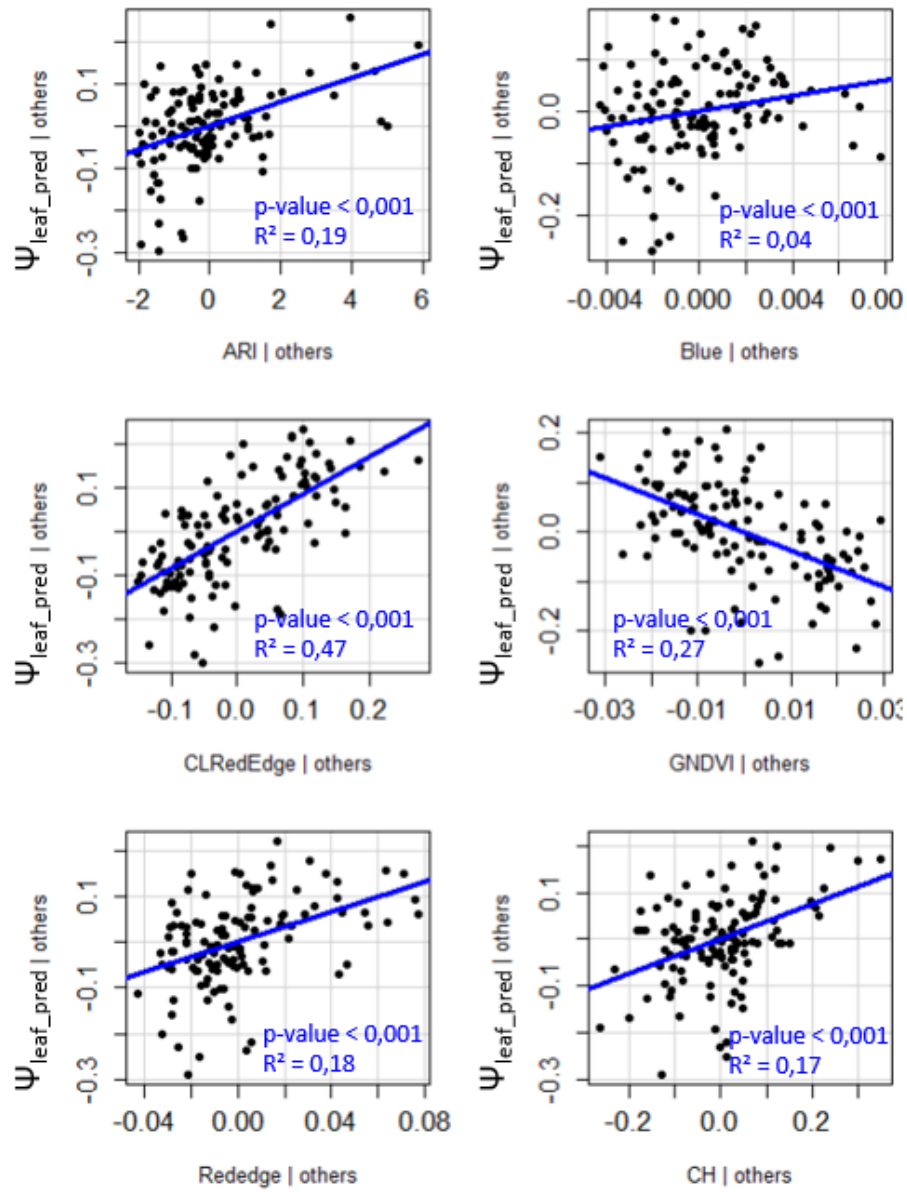


Figure S.5.6 – Partial regression plots of each predictor variable on the prediction of Ψ_{leaf} for the model 2 $\Psi_{\text{leaf_pred}} = -0.77 + 0.81 \cdot \text{CLRedEdge} + 6.78 \cdot \text{Blue} + 0.38 \cdot \text{CH} + 1.49 \cdot \text{RedEdge} + 0.02 \cdot \text{ARI} - 3.32 \cdot \text{GNDVI}$ (multispectral and LiDAR data). The p-value < 0.001 signifies that the slope of the linear regression (blue line) is significantly different from 0.

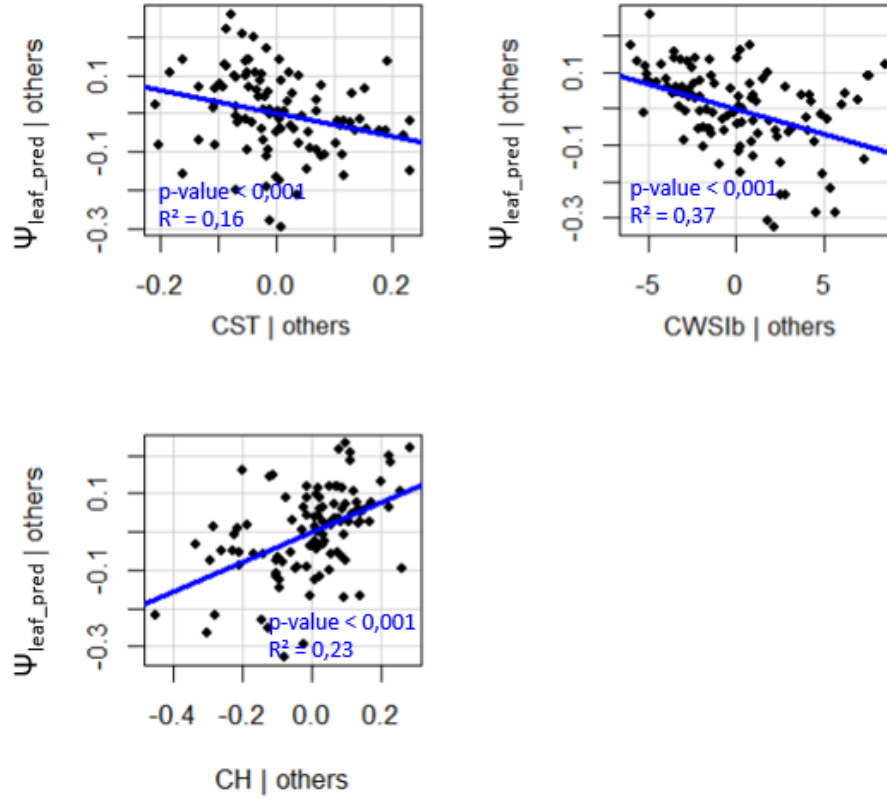


Figure S.5.7 – Partial regression plots of each predictor variable on the prediction of Ψ_{leaf} , for the model 3 $\Psi_{leaf_pred} = -0.94 - 0.28 \cdot CWSIb + 0.38 \cdot CH - 0.01 \cdot CST$ (thermal and LiDAR data). The $p\text{-value} < 0.001$ signifies that the slope of the linear regression (blue line) is significantly different from 0.

5. Mapping grapevine leaf water potential with UAS data

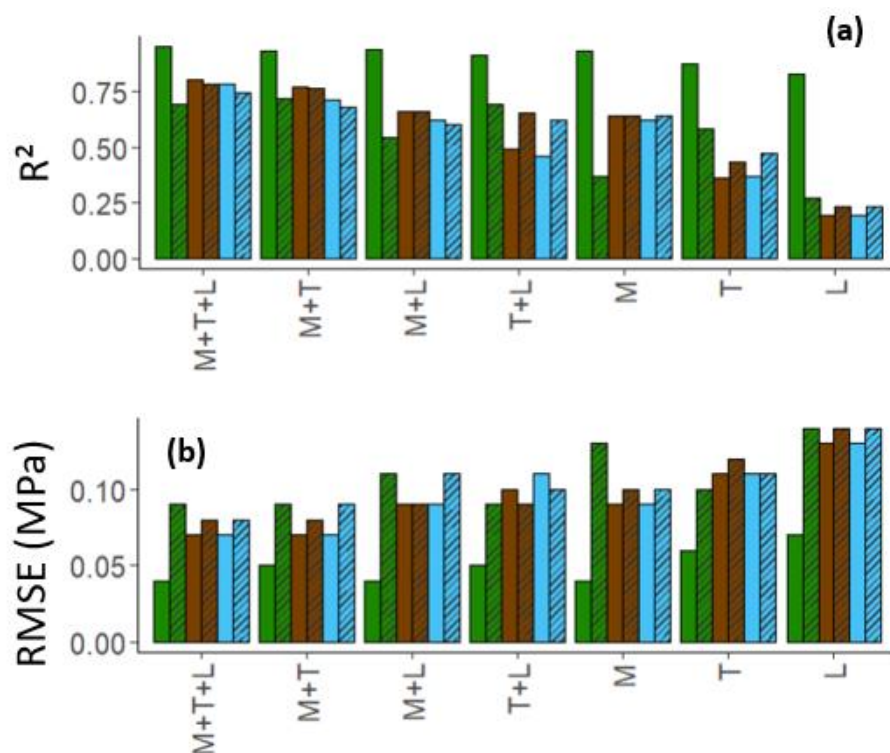


Figure S.5.8 – (a) R^2 and (b) RMSE obtained by comparing measured Ψ_{leaf} ($\Psi_{\text{leaf_meas}}$) and predicted Ψ_{leaf} ($\Psi_{\text{leaf_pred}}$) with different multiple linear regression models, for the different data combinations. The green bars correspond to the random forest model, the brown bars to the stepwise regression model, and the blue bars to the principal component regression model. The full bars correspond to the calibration dataset (70 % of the data), while the hatched bars correspond to the validation dataset (30 % of the data).

5.6.2. Supplementary tables

Table S.5.1 – List of vegetation indices (VIs), spectral bands and structural features used in this study to predict Ψ_{leaf} .

Vegetation index (VI), band or structural feature	Full name	Formula
Red	Red band	-
Green	Green band	-
Blue	Blue band	-
RedEdge	Red-edge band	-
NIR	Near infrared band	-
ARI	Anthocyanin Reflectance Index	$1/\text{green} - 1/\text{rededge}$
CI	Chlorophyll Index	$(\text{nir}/\text{red})-1$
CIVE	Color Index of Vegetation Extraction	$0.441*\text{red} - 0.811*\text{green} + 0.385*\text{blue} + 18.78745$
CLGreen	Chlorophyll index green	$(\text{nir}/\text{green})-1$
CLRedEdge	Chlorophyll index rededge	$(\text{nir}/\text{rededge})-1$
DVI	Difference Vegetation Index	$\text{nir}-\text{red}$
EVI	Enhanced Vegetation Index	$(2.5*(\text{nir}-\text{red})) / (\text{nir}+6*\text{red}-7.5*\text{blue}+1)$
EVI2	Enhanced Vegetation Index 2	$(2.5*(\text{nir}-\text{red})) / (\text{nir}+2.5*\text{red}+1)$
ExG	Excess Green Vegetation Index	$2*\text{green}-\text{red}-\text{blue}$
ExGR	-	$\text{ExG}-\text{ExR}$

5. Mapping grapevine leaf water potential with UAS data

ExR	Excess Red Vegetation Index	$(1.4 \cdot \text{red} - \text{green}) / (\text{red} + \text{green} + \text{blue})$
GCC	Green chromatic coordinates	$\text{Green} / (\text{red} + \text{green} + \text{blue})$
GNDVI	Green Normalized Difference Vegetation Index	$(\text{nir} - \text{green}) / (\text{nir} + \text{green})$
GRVI	Green-Red Vegetation Index	$(\text{red} - \text{green}) / (\text{red} + \text{green})$
Green NDVI	Green Normalized Difference Vegetation Index	$(\text{green} - \text{nir}) / (\text{green} + \text{nir})$
Green Percentage	Green Percentage	$\text{Green} / (\text{green} + \text{red} + \text{blue})$
Green/red	Green/red	$\text{Green} / \text{red}$
MCARI	Modified Chlorophyll Absorption Ratio Index	$((\text{rededge} - \text{red}) - 0.2 \cdot (\text{rededge} - \text{green})) \cdot (\text{rededge} / \text{rd})$
MCARIone	-	$1.2 \cdot (2.5 \cdot (\text{nir} - \text{red}) - 1.3 \cdot (\text{nir} - \text{green}))$
MCARItwo	-	$\frac{1.5 \cdot (2.5 \cdot (\text{nir} - \text{red}) - 1.3 \cdot (\text{nir} - \text{green}))}{\sqrt{(2 \cdot \text{nir} + 1)^2 - (6 \cdot \text{nir} - 5 \cdot \sqrt{\text{red}} - 0.5)}}$
MSAVI	Modified Soil Adjusted Vegetation Index	$0.5 \cdot (2 \cdot \text{nir} + 1 - \sqrt{(2 \cdot \text{nir} + 1)^2 - 8 \cdot (\text{nir} - \text{red})})$
MSR	Modified Simple Ratio	$\frac{\frac{\text{nir}}{\text{red}} - 1}{\sqrt{\frac{\text{nir}}{\text{red}} - 1}}$
MTVIone	Modified Triangular Vegetation Index one	$1.2 \cdot (1.2 \cdot (\text{nir} - \text{green}) - 2.5 \cdot (\text{red} - \text{green}))$
MTVItwo	Modified Triangular Vegetation Index two	$\frac{1.2 \cdot (1.2 \cdot (\text{nir} - \text{green}) - 2.5 \cdot (\text{red} - \text{green}))}{\sqrt{(2 \cdot \text{nir} + 1)^2 - (6 \cdot \text{nir} - 5 \cdot \sqrt{\text{red}} - 0.5)}}$
NDRE	Normalized Difference Red Edge	$(\text{nir} - \text{rededge}) / (\text{nir} + \text{rededge})$

5.6. Supplementary material

NDVI	Normalized Difference Vegetation Index	$(nir-red)/(nir+red)$
NGRDI	Normalized Green-Red Difference Index	$(green-red)/(green+red)$
Nir/green	Nir/green	Nir/green
OSAVI	Optimized Soil-Adjusted Vegetation Index	$(1.16/(nir-red))*nir+red+0.16$
RDVI	Renormalized Difference Vegetation Index	$\frac{nir-red}{\sqrt{nir+red}}$
Red/green	Red/green	Red/green
SRI	Simple ratio index	Nir/red
SAVI	Soil-Adjusted Vegetation Index	$((nir-red)/(nir+red+0.5))*1.5$
SIPI	Structure Insensitive Pigment Index	$(nir-blue)/(nir+red)$
TCARI	Transformed Chlorophyll Absorption Reflectance Index	$3*((rededge-red)-0.2*(rededge-green))*(rededge/green))$
TCARI/OSAVI	-	TCARI/OSAVI
VARI	Visible Atmospherically Resistant Index	$(green-red)/(green+red-blue)$
CWSIa	Crop water stress index a	$\frac{CST - T_{wet}}{T_{dry} - T_{wet}}$
CWSIb	Crop water stress index b	$\frac{CST - CST_{max}}{CST_{max} - CST_{min}}$
dT	Difference of temperature	CST – air temperature
CST	Canopy surface temperature	-
CH	Canopy height	-
LAI	Leaf area index	-

5. Mapping grapevine leaf water potential with UAS data

Table S.5.2 – Variance Inflation Factor (VIF) to assess the collinearity between the predictor variables in the model 1 $\Psi_{leaf_pred} = -1.55 + 0.27*CLRedEdge - 0.49*CWSIb + 8.40*Blue + 0.27*CH$ (multispectral, thermal and LiDAR data).

Predictor variable	CH	CLRedEdge	CWSIb	Blue
VIF	1.67	1.78	1.17	1.30

Table S.5.3 – Variance Inflation Factor (VIF) to assess the collinearity between the predictor variables in the model 2 $\Psi_{leaf_pred} = -0.77 + 0.81*CLRedEdge + 6.78*Blue + 0.38*CH + 1.49*RedEdge + 0.02*ARI - 3.32*GNDVI$ (multispectral and LiDAR data).

Predictor variable	CH	RedEdge	ARI	Blue	CLRedEdge	GNDVI
VIF	1.73	2.86	3.63	3.75	4.49	4.08

Table S.5.4 – Variance Inflation Factor (VIF) to assess the collinearity between the predictor variables in the model 3 $\Psi_{leaf_pred} = -0.94 - 0.28*CWSIb + 0.38*CH - 0.01*CST$ (thermal and LiDAR data).

Predictor variable	CH	CWSIb	CST
VIF	1.41	2.21	2.43

6. Conclusions & Outlooks

6.1. Research contributions

The general objective of the thesis was to advance the understanding of how soil-grapevine hydraulics control transpiration rate, water potential and root water uptake of *in situ* grapevines. Particularly, the thesis thoroughly explored the role of the belowground side of the soil-grapevine system as a constraint of water fluxes. We hypothesized that belowground hydraulics plays a significant role on the trigger of stomatal closure and on water potential control, at the grapevine and the vineyard scale. We believed that soil-root water relations are soil texture specific. For this thesis, we defined three research objectives (RO) to enhance our capacity to understand *in situ* grapevine hydraulic response and water uptake during drought in different environments, particularly different edaphic conditions. We conducted our research on two Belgian vineyards, planted with *Vitis vinifera* cv. Chardonnay. These grapevines grow in deep soils with contrasting subsoil textures, with no mechanical constraints (e.g. no stony load), which have allowed the growth of deep root systems.

RO.1 – What are the roles of belowground (soil and root system) and aboveground (stem) hydraulics on the transpiration control of in situ grapevine?

In the terroir conditions mentioned above, in Chapter 3 we quantified and investigated how belowground and stem hydraulics are involved

6. Conclusion & Outlook

and coordinated with the transpiration regulation of grapevine. Combining monitoring of relative stomatal conductance, belowground hydraulic conductance and stem hydraulic conductance demonstrated that stomatal closure of grapevine was triggered by a decrease of belowground hydraulic conductance, and not by xylem cavitation in the stem. Although the relation between stomatal conductance and soil water potential was soil texture specific, with stomatal regulation happened at less negative soil water potential in coarse-textured ($\Psi_{\text{soil}} = -0.10$ MPa) than in fine-textured soils ($\Psi_{\text{soil}} = -0.20$ MPa), we measured that stomatal closure was triggered at the same belowground hydraulic conductance ($K_{\text{below}} = 0.17 \text{ cm}^3 \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$), independently of the soil texture. These original findings prove that *in situ* grapevines coordinate short-term hydraulic mechanisms (e.g. stomatal regulation) and longer-term growth (e.g. shoot:root ratio).

RO.2 – How does rhizosphere hydraulic conductance controls root water uptake and stem water potential at the grapevine scale?

After proving the main role of belowground hydraulics on grapevine stomatal control, in the Chapter 4, we zoomed on this part of the soil-grapevine system to explore how rhizosphere and root system hydraulic conductances vary and affect root water uptake in different soil types at the plant scale. By combining measured and simulated soil and plant water potentials, we demonstrated that the soil and the roots are hydraulically disconnected in dry soil horizons, allowing a shift of water uptake toward deeper wet zones of the soil. Moreover, during drought, even for well-established grapevine with long root system, the rhizosphere hydraulic conductance decreased and became lower than the root system conductance ($K_{\text{rhizo_eff}} < K_{\text{rs}}$), limiting root water uptake in coarse-textured soil. In fine-textured soil, although the rhizosphere hydraulic conductance also decreased during drought, it remained greater than the root system conductance ($K_{\text{rhizo_eff}} > K_{\text{rs}}$), the latter being the main limiting factor of root water uptake in these edaphic

conditions. For the first time, by using a biophysical model that explicitly represents the series of hydraulic conductances between the bulk soil and the collar stem, and integrating hydraulic disconnection in dry soil horizons, we demonstrated the absolute contribution of the rhizosphere and the root system hydraulics on root water uptake of *in situ* grapevines planted in contrasted soil types. Belowground-related hydraulic processes are complex and their implications, notably on the transpiration control (Chapter 3 – RO.1) and root water uptake (Chapter 4 – RO.2) of grapevine, are therefore soil texture dependent.

RO.3 – How edaphic, topographic and climatic conditions influence the spatial distribution of grapevine leaf water potential at the vineyard scale?

Finally, in Chapter 5 we accurately mapped grapevine leaf water potential thanks to high-spatial resolution multispectral, thermal and LiDAR data, and assessed the impact of edaphic, topographic and climatic conditions on water potential intra-field heterogeneity. Our results provided evidence that grapevine water status can be highly variable in non-irrigated vineyards for which soils are deep, heterogeneous in terms of texture, and slope is moderate. The spatial distribution of leaf water potential was mainly governed by the within-vineyard soil hydraulic conductivity heterogeneity (edaphic conditions), and was particularly marked when the evaporative demand and the water deficit were greater (climatic conditions), since the range of leaf water potential increased in these conditions. For a vineyard with great soil hydraulic conductivity heterogeneity, the range of leaf water potential was 0.73 MPa for the driest climatic conditions. These findings are in line with those of Chapters 3 (RO.1) and 4 (RO.2), showing the major impact of soil texture, particularly at the vicinity of the roots, on grapevine water potential.

These findings – i.e. (1) the soil texture specific coordination between short-term hydraulic mechanisms and longer-term growth; (2) the contrasted role of rhizosphere and root system hydraulics on root water uptake in various soil texture; (3) the major role of intra-field edaphic heterogeneity on the spatial distribution of grapevine water potential – enhance our capacity to understand *in situ* grapevine water relations with its environment, particularly for various edaphic conditions. Rhizosphere hydraulic conductance, soil-root air gaps and root distribution play a critical role in predicting and understanding grapevine water potential and transpiration reduction, as well as grapevine root water uptake vertical distribution. A comprehensive investigation into the interrelationship between belowground hydraulics and plant water use was essential to reveal how grapevine hydraulic behaviour and environment-dependent hydraulics drive and respond to one another. Addressing these gaps in knowledge was required to accurately assess the risks associated with future climate change, particularly with the increased frequency of droughts. By studying the intricate details of soil-grapevine water relations to drought stress, this thesis could help winemakers to find answers to the uncertainties due to climate change, and therefore to ensure better adaptation to changing climatic conditions and to improve overall vineyard resilience.

6.2. Research perspectives

This thesis highlights the role of the soil and its properties on soil-grapevine water relations. We are aware that viticulture is a complex art, in which many other factors are involved, in an important way, on the water relations between the plant and its environment. In the following sections, we discuss and propose research perspectives that,

in addition to the findings of this thesis, would provide an even deeper understanding of the water relations between the grapevine and its environment.

6.2.1. Grapevine root system responses to drought

We highlighted, in Chapter 4, the hydraulic disconnection between the soil and the roots in dry soil horizons, and related it to soil processes. However, this hydraulic disconnection could also be related to numerous root processes (for a simple representation, see Appendix A4.2 in Chapter 4), since it is well known that grapevine can react flexibly to drought by modifying root system hydraulics. The role of roots in drought involves establishing a hydraulic environment that enables the plant to optimize water use under critical conditions. Drought-tolerant plants adapt to drought conditions by modifying the morphology and metabolism of their roots. Multiple examples could be proposed: on a short-time scale (seconds) aquaporin regulation has been shown to radically impact root radial conductance (Gambetta et al., 2012, 2013; Vandeleur et al., 2009); on mid- to long-time scales (hours to days) root growth (Alsina et al., 2011), root cortical lacunae formation (Cuneo et al., 2016, 2021) or root suberization (Barrios-Masias et al., 2015), also drastically affect grapevine root hydraulic conductance. Further research is needed to better understand how these different mechanisms related to root hydraulics, in addition to rhizosphere hydraulic processes studied in this thesis, simultaneously affect soil-grapevine water relations during drought, in different environments. Although the dynamics and magnitude of these processes remain unclear taken together, we could expect that they tend to interact concomitantly rather than independently.

6. Conclusion & Outlook

Other processes, that have never or few been studied on grapevines, could also affect root system hydraulics during drought. For example, roots can modify soil structure, and therefore soil hydraulic properties, through root mucilage (Carminati and Vetterlein, 2013). Root mucilage facilitates water extraction from dry soils by moderating water potential decline and enhancing xylem water potential (Alahmad et al., 2019). Additionally, its water-repellent properties enable the absorption of rainwater before it evaporates (Naveed et al., 2017). How grapevine root mucilage affects soil-grapevine water relations is still an open question that needs to be addressed.

Recently, grapevine root system architecture development is gaining interest (Fichtl et al., 2023). There is a clear lack of knowledge on spatio-temporal root system development and its interactions with environment. However, understanding root system performance, for different rootstocks in various environment, is of great interest in a changing climate. Processes influencing root system architecture, such as hydrotropism (Dietrich et al., 2017), hydropatterning (Giehl and von Wirén, 2018), root hairs (Carminati et al., 2017) or xerobranching (Orman-Ligeza et al., 2018), have rarely or never been investigated for grapevines, while it is well-known that they improve water flow and its uptake (Mohammadi Alagoz et al., 2023). Although we have not gone any further in understanding these processes for grapevines, we measured more grapevine roots in ferrous horizons compared to the pure sandy horizons at the *Château de Bousval* vineyard (see Chapters 3 and 4). These observations certainly proved that *in situ* grapevines guide its root growth towards water (hydrotropism), in addition to densifying its root system in these more hydraulically advantageous soil zones (hydropatterning). Despite the difficulty to access root systems of grapevine in real-field conditions, further research is needed to explore how these processes affect soil-grapevine water relations, especially during drought and in different environments.

6.2.2. Grapevine-grass interactions

Root ecology deals on the dynamics of roots in relation to soil properties, as we studied in this thesis, but also in relation with roots from other plant species or microbes. In this thesis, while we worked on vineyards with grass in the inter-rows, we have given little thought to the impact of the presence of this grass on grapevine hydraulics. Cropping systems significantly influence root development and soil-root hydraulic properties, particularly in diverse cropping systems, such as grapevine-grass systems. While, the effect of cover cropping on the aboveground vegetative part of perennial crops has been extensively studied (Atucha et al., 2011; Hatch et al., 2011; Merwin and Stiles, 1994), the competitive belowground interactions between herbaceous species and grapevine crops remain less understood (Atucha et al., 2013; Guerra and Steenwerth, 2012). Research is needed to understand the significant variation and complexity in hydraulic responses of grapevine crops under different groundcover management systems and soil types interactions, to gain a mechanistic comprehension of how these belowground interactions between fruit crops and cover crops influence grapevine performance. Hatch et al. (2011) identified water competition as the main factor leading to reduced annual vegetative growth in grapevines coexisting with a permanent understory grass, in a humid climate vineyard. Some studies indicate that fruit crop root systems adapt by altering their root distribution when in competition with cover crops, moving away from the upper soil horizons occupied by grass roots and extending towards deeper soil layers (Atucha et al., 2013; Centinari et al., 2016). However, the age of the woody species likely influences their root competitive response. For instance, studies on grapevines with an understory grass were conducted during the initial years of cover crop and/or grapevine crop establishment (Atucha et al., 2013; Centinari et al., 2016; Hatch et al., 2011). Further investigations should be carried out to understand how water dynamics of grapevine-grass systems evolve when the main crop and/or cover crop are well established, like in this thesis, and how this affects soil-grapevine hydraulics. Research investigating belowground hydraulics

6. Conclusion & Outlook

of grapevine systems rarely integrates root interactions between species and competition of water resources. On other mixed crop systems (e.g. pearl millet with rice), Izumi et al. (2018) showed that water absorbed by deep roots of pearl millet was utilized by rice, indicating that mixed cropping can better withstand drought stress through hydraulic lift, which releases water in the upper soil layer. Although we could expect that grass (short root system) would benefit more from this hydraulic lift than grapevines (long root system) in a grapevine-grass system, it would be interesting to study how this influences soil-grapevine water relations. We could also expect, and this should be further investigated, that the extent of hydraulic interactions between grapevine and herbaceous vegetation is highly context-dependent and is influenced by multiple factors, such as growth stage of the grapevine and herbaceous species, weather conditions and soil properties (Klodd et al., 2016). Grapevine-grass interactions could also be studied at the field scale, thanks to energy balance model that could improve evapotranspiration partitioning in vineyards (Burchard-Levine et al., 2022a). Simultaneously quantifying grapevine transpiration, cover crop transpiration and soil evaporation would also improve our understanding of soil-grapevine relations, in such complex systems such as vineyards with grass between rows. Remote sensing, in particular thermal imagery as used in Chapter 5, together with Surface Energy Balance (SEB) models, appears as an operational and low-cost method for providing spatially distributed estimates of evapotranspiration (Anderson et al., 2021; Gerhards et al., 2019). Recently, the extension of classical SEB to two (vegetation and soil) to three (overstory vegetation, understory vegetation and soil) sources energy balance improves evapotranspiration partitioning (Burchard-Levine et al., 2022b). Recent studies highlighted that the annual transpiration contribution of the cover crop is not negligible, with a contribution on average to around 30 % of daily evapotranspiration. However, this contribution is highly variable within the year, with a lower contribution (0-10 % of daily evapotranspiration) during summer months (Burchard-Levine et al., 2022a). However, these SEB models have been applied in Mediterranean vineyards, for which grass is generally already dead by summer, and with homogenous edaphic conditions. How evapotranspiration is partitioned in vineyards in

temperate climates, where grass is present and functional all year round, and with various edaphic conditions, has never been investigated. We could expect that, even during summer, the cover crop contribution to total water fluxes is not negligible and therefore has a great impact on grapevine hydraulics throughout the wine-growing season, and that this contribution is soil texture dependent.

6.2.3. Grapevine-microbiome interactions

In addition to grapevine-grass hydraulic interactions, some studies highlighted the beneficial interconnections between grapevine roots and bacteria, or with fungi (i.e. mycorrhiza), contributing to alleviate drought stress (Rolli et al., 2015; Trouvelot et al., 2015). Interest for the “microbial terroir” is relatively recent. Endophytic microbiome has been shown to colonize grapevine rhizosphere (Compant et al., 2011). Root associated endophytic bacterial communities enhance plant ability to extract water (Azarbad et al., 2018). Therefore, the beneficial microbiome associated with grapevine roots can help alleviate plant stress through various mechanisms (Hayat et al., 2010; Mapelli et al., 2013). Specifically, microbes with multiple plant growth-promoting traits can enhance grapevine responses to water stress, particularly under field conditions (Rolli et al., 2015). Nevertheless, our understanding of the role of root-associated microbes in belowground water relations of grapevine remains limited, particularly since we could expect that these associations are bacterial type, rootstock and soil-specific. In addition to endophytic bacteria, arbuscular mycorrhizal fungi (AMF) can also form symbiotic associations with grapevine roots (Trouvelot et al., 2015). Arbuscular mycorrhizal symbiosis is likely the most prevalent and beneficial interaction between plants and microorganisms (Parniske, 2008). Mycorrhiza has been widely studied on other species than grapevine and this symbiosis shows that it improves water transfer pathways in roots. Recently, several studies

6. Conclusion & Outlook

have reported enhanced root hydraulic conductivity due to AMF symbiosis in maize (Quiroga et al., 2020) and tomato (Abdalla and Ahmed, 2021). Research on mycorrhiza has demonstrated that water apoplast flow increases under water deficit conditions in maize (Bárzana et al., 2012). These AMF-induced changes in root hydraulic conductance were linked to variations in aquaporin activity (Ruiz-Lozano and Aroca, 2017). Water relations between grapevines and AMF has rarely been studied, but investigating the impact of AMF on grapevine hydraulics and on their terroir contribution is crucial, as they constitute a direct link between soil and roots. Given the high diversity of soil-rootstock-cultivar combinations in viticulture, it is not surprising that the impact of mycorrhiza on grapevine water status is still not fully understood (Trouvelot et al., 2015). Schreiner et al. (2007) and Donkó et al. (2014) showed that in water deficit conditions, the frequency of arbuscules increased and fine root production decreased in grapevines, compared to water comfort conditions. This suggests that grapevines compensated for the lower density of fine roots by enhancing mycorrhizal symbiosis. Moreover, in arbuscular mycorrhiza-colonized grapevines, the stomatal conductance, transpiration rate and xylem conductance increased compared to non-colonized grapevines, improving drought tolerance (Rooyen et al., 2004). However, the mechanisms linked to mycorrhiza that improve grapevine hydraulics are still unclear. We could assume that these AMF colonizations are fungi type, rootstock and soil-specific. Further research needs to be carried out to improve our understanding of the mechanisms involved in grapevine-AMF relations that impact soil-grapevine hydraulics.

In the future, all these ecological aspects, including grapevine root interactions with herbaceous species, endophytic bacteria or arbuscular mycorrhizal fungi, contributing and impacting grapevine drought tolerance, should be studied and considered. How they are involved and interact in different environmental conditions (e.g. edaphic conditions, climatic conditions, etc.) is still a widely open question for soil-grapevine systems. There is a growing interest among winegrowers and the scientific community in understanding the potential ecosystem services that these ecological interactions, in addition to soil-root

interactions studied in this thesis, can offer for grapevine hydraulic behaviour and drought tolerance. This knowledge, that should be addressed in the future, is crucial for adapting grapevine to climate change and advancing sustainable viticulture practices.

6.2.4. Influence on wine quality and typicity

Numerous studies have explored the impact of soil on grape ripening and overall wine quality (Morlat and Bodin, 2006; Renouf et al., 2010; Van Leeuwen et al., 2018), given that grapevine water status, which influences wine aromatic typicity, is significantly impacted by the type of soil on which the plant grows, as demonstrated in this thesis. For example, under water deficit conditions, soil texture has been shown to influence sensory attributes of Chardonnay in Canadian vineyards. Wines from sandy soil tended to exhibit floral and melon aromas and flavours, while those from fine-textured soils were noted for stronger vegetal, earthy and citrus aromas (Reynolds et al., 2013). Although soil plays a role in the aromatic composition of berries and the resulting wine, other factors are also of considerable importance in determining quality. Aromatic characteristics and typicity of the wines produced in a region, or in a vineyard, come from a unique combination of weather, soil properties, altitude, plant material, solar radiation and viticultural practices (Gambetta et al., 2014); in other words from a unique *terroir*. The primary drivers of *terroir* expression are air temperature, solar radiation, grapevine water status and grapevine nitrogen levels. Once these elements are thoroughly characterized, wine aroma profiles could be predicted based on published data from the literature (Van Leeuwen et al., 2020), but the interplay between environmental factors (climate and soil), plant material (variety and rootstock) and management practices is so complex that these predictions could be tricky. This complexity is reflected in the variability of aromas found in a same grape variety. For example, although aroma structure of Chardonnay is

6. Conclusion & Outlook

less known (Van Leeuwen et al., 2020), over 240 different aromatic compounds have been identified in various Chardonnay wines (Gambetta et al., 2014). This illustrates the incredible influence of geographical origin, vintage, and viticultural and oenological practices on wine quality and typicity. In Belgium, country in which this thesis was carried out, there is still a long way to go before we understand how Belgian terroir defines Belgian wine typicity. Belgium counts more than 130 grape varieties (traditional and interspecific) grown on its territory, grafted on dozens of different rootstocks (SPF Economie, 2024). Moreover, Belgium has a wide diversity of soil types on which are planted grapevines, from shallow stony clay soils (e.g. *Domaine du Chenoy*) to limestone and chalk soils (e.g. *Vignoble des Agaises* or *Domaine du Chant d'Éole*), passing through sandy soils (e.g. *Château de Bousval* vineyard), deep loamy soil (e.g. *Domaine W*) and many more soil types. Belgium has a unique and complex soil classification system and has the most detailed soil map in the world (scale 1:20000). The methodology used in this thesis to quantify and understand the hydraulic behaviour of grapevines needs to be applied to other grape varieties and soil types. It would be very interesting to combine these hydraulic measurements with chemical analyses of must and wines, to understand the influence of soil (and terroir in general) on the quality and typicity of Belgian wines. Belgian winemakers are aware of the textural heterogeneity of the soils in their vineyards and make the most of it. For example, at the *Château de Bousval* vineyard, the Chardonnay field, studied in this thesis (Chapter 5), is harvested in two parts between the top (sandy soil) and the bottom (loamy soil) of the field, to vinify the musts separately. Musts from the loamy zone give wines with aromas of rhubarb and grapefruit, while wines from the sandy zone have flavours of pineapple and passion fruit. The presence and intensity of these aromas may, however, depend on the vintage. The great textural diversity of Belgian wine-growing soils must be seen as a quality, enabling the production of high-quality wines every year, despite the meteorological uncertainties linked to climate change, particularly in terms of precipitation.

General bibliography

Abdalla, M., Ahmed, M.A., 2021. Arbuscular Mycorrhiza Symbiosis Enhances Water Status and Soil-Plant Hydraulic Conductance Under Drought. *Front. Plant Sci.* 12.

Abdalla, M., Ahmed, M.A., Cai, G., Wankmüller, F., Schwartz, N., Litig, O., Javaux, M., Carminati, A., 2022. Stomatal closure during water deficit is controlled by below-ground hydraulics. *Ann. Bot.* 129, 161–170. <https://doi.org/10.1093/aob/mcab141>

Abdalla, M., Carminati, A., Cai, G., Javaux, M., Ahmed, M.A., 2021. Stomatal closure of tomato under drought is driven by an increase in soil–root hydraulic resistance. *Plant Cell Environ.* 44, 425–431. <https://doi.org/10.1111/pce.13939>

Acevedo-Opazo, C., Tisseyre, B., Guillaume, S., Ojeda, H., 2008. The potential of high spatial resolution information to define within-vineyard zones related to vine water status. *Precis. Agric.* 9, 285–302. <https://doi.org/10.1007/s11119-008-9073-1>

Acevedo-Opazo, C., Tisseyre, B., Ojeda, H., Guillaume, S., 2010. Spatial extrapolation of the vine (*Vitis vinifera* L.) water status: a first step towards a spatial prediction model. *Irrig. Sci.* 28, 143–155. <https://doi.org/10.1007/s00271-009-0170-3>

Akaike, H., 1974. A new look at the statistical model identification. *IEEE Trans. Autom. Control* 19, 716–723. <https://doi.org/10.1109/TAC.1974.1100705>

Alahmad, S., El Hassouni, K., Bassi, F.M., Dinglasan, E., Youssef, C., Quarry, G., Aksoy, A., Mazzucotelli, E., Juhász, A., Able, J.A., Christopher, J., Voss-Fels, K.P., Hickey, L.T., 2019. A Major Root Architecture QTL Responding to Water Limitation in Durum Wheat. *Front. Plant Sci.* 10. <https://doi.org/10.3389/fpls.2019.00436>

Albuquerque, C., Scoffoni, C., Brodersen, C.R., Buckley, T.N., Sack, L., McElrone, A.J., 2020. Coordinated decline of leaf hydraulic and stomatal conductances under drought is not linked to leaf xylem embolism for different grapevine cultivars. *J. Exp. Bot.* 71, 7286–7300. <https://doi.org/10.1093/jxb/eraa392>

Allen, P., 1997. *Understanding Regression Analysis*. Springer US, Boston, MA. <https://doi.org/10.1007/b102242>

Allen, R., Pereira, L., Smith, M., Raes, D., 1998. Crop evapotranspiration-Guidelines for computing crop water requirements-FAO Irrigation and drainage paper 56.

Alsina, M.M., Herralde, F. de, Aranda, X., Savé, R., Biel, C.C., 2007. Water relations and vulnerability to embolism are not related: Experiments with eight grapevine cultivars. *VITIS - J. Grapevine Res.* 46, 1–1. <https://doi.org/10.5073/vitis.2007.46.1-6>

Alsina, M.M., Smart, D.R., Bauerle, T., de Herralde, F., Biel, C., Stockert, C., Negron, C., Save, R., 2011. Seasonal changes of whole root system conductance by a drought-tolerant grape root system. *J. Exp. Bot.* 62, 99–109. <https://doi.org/10.1093/jxb/erq247>

Alston, J.M., Sambucci, O., 2019. Grapes in the World Economy, in: Cantu, D., Walker, M.A. (Eds.), *The Grape Genome*. Springer International Publishing, Cham, pp. 1–24. https://doi.org/10.1007/978-3-030-18601-2_1

Améglio, T., Archer, P., Cohen, M., Valancogne, C., Daudet, F., Dayau, S., Cruiziat, P., 1999. Significance and limits in the use of predawn leaf water potential for tree irrigation. *Plant Soil* 207, 155–167. <https://doi.org/10.1023/A:1026415302759>

Anderegg, W.R.L., Konings, A.G., Trugman, A.T., Yu, K., Bowling, D.R., Gabbitas, R., Karp, D.S., Pacala, S., Sperry, J.S., Sulman, B.N., Zenes, N., 2018. Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature* 561, 538–541. <https://doi.org/10.1038/s41586-018-0539-7>

Anderegg, W.R.L., Wolf, A., Arango-Velez, A., Choat, B., Chmura, D.J., Jansen, S., Kolb, T., Li, S., Meinzer, F., Pita, P., Dios, V.R. de,

Sperry, J.S., Wolfe, B.T., Pacala, S., 2017. Plant water potential improves prediction of empirical stomatal models. *PLOS ONE* 12, e0185481. <https://doi.org/10.1371/journal.pone.0185481>

Anderson, M.C., Yang, Yang, Xue, J., Knipper, K.R., Yang, Yun, Gao, F., Hain, C.R., Kustas, W.P., Cawse-Nicholson, K., Hulley, G., Fisher, J.B., Alfieri, J.G., Meyers, T.P., Prueger, J., Baldocchi, D.D., Rey-Sanchez, C., 2021. Interoperability of ECOSTRESS and Landsat for mapping evapotranspiration time series at sub-field scales. *Remote Sens. Environ.* 252, 112189. <https://doi.org/10.1016/j.rse.2020.112189>

Aroca, R., Porcel, R., Ruiz-Lozano, J.M., 2012. Regulation of root water uptake under abiotic stress conditions. *J. Exp. Bot.* 63, 43–57. <https://doi.org/10.1093/jxb/err266>

Asbjornsen, H., Shepherd, G., Helmers, M., Mora, G., 2008. Seasonal patterns in depth of water uptake under contrasting annual and perennial systems in the Corn Belt Region of the Midwestern U.S. *Plant Soil* 308, 69–92. <https://doi.org/10.1007/s11104-008-9607-3>

Atucha, A., Merwin, I.A., Brown, M.G., 2011. Long-term Effects of Four Groundcover Management Systems in an Apple Orchard. <https://doi.org/10.21273/HORTSCI.46.8.1176>

Atucha, A., Merwin, I.A., Brown, M.G., Gardiazabal, F., Mena, F., Adiazola, C., Goebel, M., Bauerle, T., 2013. Root distribution and demography in an avocado (*Persea americana*) orchard under groundcover management systems. *Funct. Plant Biol. FPB* 40, 507–515. <https://doi.org/10.1071/FP12317>

Azarbad, H., Constant, P., Giard-Laliberté, C., Bainard, L.D., Yergeau, E., 2018. Water stress history and wheat genotype modulate rhizosphere microbial response to drought. *Soil Biol. Biochem.* 126, 228–236. <https://doi.org/10.1016/j.soilbio.2018.08.017>

Baert, A., De Schepper, V., Steppe, K., 2015. Variable hydraulic resistances and their impact on plant drought response modelling. *Tree Physiol.* 35, 439–449. <https://doi.org/10.1093/treephys/tpu078>

Baluja, J., Diago, M.P., Balda, P., Zorer, R., Meggio, F., Morales, F., Tardaguila, J., 2012. Assessment of vineyard water status variability by

thermal and multispectral imagery using an unmanned aerial vehicle (UAV). *Irrig. Sci.* 30, 511–522. <https://doi.org/10.1007/s00271-012-0382-9>

Barrios-Masias, F.H., Knipfer, T., McElrone, A.J., 2015. Differential responses of grapevine rootstocks to water stress are associated with adjustments in fine root hydraulic physiology and suberization. *J. Exp. Bot.* 66, 6069–6078. <https://doi.org/10.1093/jxb/erv324>

Barrowclough, D.E., Peterson, C.A., Steudle, E., 2000. Radial hydraulic conductivity along developing onion roots. *J. Exp. Bot.* 51, 547–557. <https://doi.org/10.1093/jexbot/51.344.547>

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. *Proc. Natl. Acad. Sci.* 113, 13098–13103. <https://doi.org/10.1073/pnas.1604088113>

Bartlett, M.K., Sinclair, G., 2021. Temperature and evaporative demand drive variation in stomatal and hydraulic traits across grape cultivars. *J. Exp. Bot.* 72, 1995–2009. <https://doi.org/10.1093/jxb/eraa577>

Bartlett, M.K., Zhang, Y., Kreidler, N., Sun, S., Ardy, R., Cao, K., Sack, L., 2014. Global analysis of plasticity in turgor loss point, a key drought tolerance trait. *Ecol. Lett.* 17, 1580–1590. <https://doi.org/10.1111/ele.12374>

Bárzana, G., Aroca, R., Paz, J.A., Chaumont, F., Martinez-Ballesta, M.C., Carvajal, M., Ruiz-Lozano, J.M., 2012. Arbuscular mycorrhizal symbiosis increases relative apoplastic water flow in roots of the host plant under both well-watered and drought stress conditions. *Ann. Bot.* 109, 1009–1017. <https://doi.org/10.1093/aob/mcs007>

Bates, J.S., Montzka, C., Schmidt, M., Jonard, F., 2021. Estimating Canopy Density Parameters Time-Series for Winter Wheat Using UAS Mounted LiDAR. *Remote Sens.* 13, 710. <https://doi.org/10.3390/rs13040710>

Becker, T., Nelsen, T.S., Leinfelder-Miles, M., Lundy, M.E., 2020. Differentiating between Nitrogen and Water Deficiency in Irrigated

Maize Using a UAV-Based Multi-Spectral Camera. *Agronomy* 10, 1671. <https://doi.org/10.3390/agronomy10111671>

Bellvert, J., Marsal, J., Girona, J., Zarco-Tejada, P.J., 2015. Seasonal evolution of crop water stress index in grapevine varieties determined with high-resolution remote sensing thermal imagery. *Irrig. Sci.* 33, 81–93. <https://doi.org/10.1007/s00271-014-0456-y>

Bellvert, J., Marsal, J., Mata, M., Girona, J., 2012. Identifying irrigation zones across a 7.5-ha ‘Pinot noir’ vineyard based on the variability of vine water status and multispectral images. *Irrig. Sci.* 30, 499–509. <https://doi.org/10.1007/s00271-012-0380-y>

Bellvert, J., Zarco-Tejada, P.J., Girona, J., Fereres, E., 2014. Mapping crop water stress index in a ‘Pinot-noir’ vineyard: comparing ground measurements with thermal remote sensing imagery from an unmanned aerial vehicle. *Precis. Agric.* 15, 361–376. <https://doi.org/10.1007/s11119-013-9334-5>

Berni, J.A.J., Zarco-Tejada, P.J., Suarez, L., Fereres, E., 2009. Thermal and Narrowband Multispectral Remote Sensing for Vegetation Monitoring From an Unmanned Aerial Vehicle. *IEEE Trans. Geosci. Remote Sens.* 47, 722–738. <https://doi.org/10.1109/TGRS.2008.2010457>

Bezerra-Coelho, C.R., Zhuang, L., Barbosa, M.C., Soto, M.A., Genuchten, M.T. van, 2018. Further tests of the HYPROP evaporation method for estimating the unsaturated soil hydraulic properties. *J. Hydrol. Hydromech.* 66, 161–169. <https://doi.org/10.1515/johh-2017-0046>

Binte Mostafiz, R., Noguchi, R., Ahamed, T., 2021. Agricultural Land Suitability Assessment Using Satellite Remote Sensing-Derived Soil-Vegetation Indices. *Land* 10, 223. <https://doi.org/10.3390/land10020223>

Böhm, W., 1979. *Methods of Studying Root Systems*, Ecological Studies. Springer Berlin Heidelberg, Berlin, Heidelberg. <https://doi.org/10.1007/978-3-642-67282-8>

- Boneh, U., Biton, I., Zheng, C., Schwartz, A., Ben-Ari, G., 2012. Characterization of potential ABA receptors in *Vitis vinifera*. *Plant Cell Rep.* 31, 311–321. <https://doi.org/10.1007/s00299-011-1166-z>
- Bramley, R.G.V., Ouzman, J., Boss, P.K., 2011. Variation in vine vigour, grape yield and vineyard soils and topography as indicators of variation in the chemical composition of grapes, wine and wine sensory attributes: Vineyard variation in wines, grapes and soils. *Aust. J. Grape Wine Res.* 17, 217–229. <https://doi.org/10.1111/j.1755-0238.2011.00136.x>
- Brillante, L., Martínez-Luscher, J., Yu, R., Plank, C.M., Sanchez, L., Bates, T.L., Breneman, C., Oberholster, A., Kurtural, S.K., 2017a. Assessing Spatial Variability of Grape Skin Flavonoids at the Vineyard Scale Based on Plant Water Status Mapping. *J. Agric. Food Chem.* 65, 5255–5265. <https://doi.org/10.1021/acs.jafc.7b01749>
- Brillante, L., Mathieu, O., Lévêque, J., van Leeuwen, C., Bois, B., 2017b. Water status and must composition in grapevine cv.Chardonnay with different soils and topography and a mini meta-analysis of the $\delta^{13}\text{C}$ /water potentials correlation. *J. Sci. Food Agric.* 98. <https://doi.org/10.1002/jsfa.8516>
- Burchard-Levine, V., Nieto, H., Kustas, W.P., Gao, F., Alfieri, J.G., Prueger, J.H., Hipps, L.E., Bambach-Ortiz, N., McElrone, A.J., Castro, S.J., Alsina, M.M., McKee, L.G., Zahn, E., Bou-Zeid, E., Dokoozlian, N., 2022a. Application of a remote-sensing three-source energy balance model to improve evapotranspiration partitioning in vineyards. *Irrig. Sci.* 40, 593–608. <https://doi.org/10.1007/s00271-022-00787-x>
- Burchard-Levine, V., Nieto, H., Riaño, D., Kustas, W.P., Migliavacca, M., El-Madany, T.S., Nelson, J.A., Andreu, A., Carrara, A., Beringer, J., Baldocchi, D., Martín, M.P., 2022b. A remote sensing-based three-source energy balance model to improve global estimations of evapotranspiration in semi-arid tree-grass ecosystems. *Glob. Change Biol.* 28, 1493–1515. <https://doi.org/10.1111/gcb.16002>
- Cai, G., König, M., Carminati, A., Abdalla, M., Javaux, M., Wankmüller, F., Ahmed, M.A., 2022. Transpiration response to soil

drying and vapor pressure deficit is soil texture specific. *Plant Soil*. <https://doi.org/10.1007/s11104-022-05818-2>

Cai, G., Vanderborght, J., Couvreur, V., Mboh, C.M., Vereecken, H., 2018. Parameterization of Root Water Uptake Models Considering Dynamic Root Distributions and Water Uptake Compensation. *Vadose Zone J.* 17, 160125. <https://doi.org/10.2136/vzj2016.12.0125>

Carminati, A., Javaux, M., 2020. Soil Rather Than Xylem Vulnerability Controls Stomatal Response to Drought. *Trends Plant Sci.* 25, 868–880. <https://doi.org/10.1016/j.tplants.2020.04.003>

Carminati, A., Moradi, A.B., Vetterlein, D., Vontobel, P., Lehmann, E., Weller, U., Vogel, H.-J., Oswald, S.E., 2010. Dynamics of soil water content in the rhizosphere. *Plant Soil* 332, 163–176. <https://doi.org/10.1007/s11104-010-0283-8>

Carminati, A., Passioura, J.B., Zarebanadkouki, M., Ahmed, M.A., Ryan, P.R., Watt, M., Delhaize, E., 2017. Root hairs enable high transpiration rates in drying soils. *New Phytol.* 216, 771–781.

Carminati, A., Vetterlein, D., 2013. Plasticity of rhizosphere hydraulic properties as a key for efficient utilization of scarce resources. *Ann. Bot.* 112, 277–290. <https://doi.org/10.1093/aob/mcs262>

Carminati, A., Vetterlein, D., 2012. Plasticity of rhizosphere hydraulic properties as a key for efficient utilization of scarce resources. *Ann. Bot.* <https://doi.org/10.1093/aob/mcs262>

Carminati, A., Vetterlein, D., Koebernick, N., Blaser, S., Weller, U., Vogel, H.-J., 2013. Do roots mind the gap? *Plant Soil* 367, 651–661. <https://doi.org/10.1007/s11104-012-1496-9>

Carminati, A., Vetterlein, D., Weller, U., Vogel, H.-J., Oswald, S.E., 2009. When Roots Lose Contact. *Vadose Zone J.* 8, 805–809. <https://doi.org/10.2136/vzj2008.0147>

Carter, G.A., Knapp, A.K., 2001. Leaf optical properties in higher plants: linking spectral characteristics to stress and chlorophyll concentration. *Am. J. Bot.* 88, 677–684.

- Caruso, G., Palai, G., 2023. Assessing grapevine water status using Sentinel-2 images. *Italus Hortus* 30, 70. <https://doi.org/10.26353/j.itahort/2023.3.7079>
- Celette, F., Wery, J., Chantelot, E., Celette, J., Gary, C., 2005. Belowground Interactions in a Vine (*Vitis vinifera* L.)-tall Fescue (*Festuca arundinacea* Shreb.) Intercropping System: Water Relations and Growth. *Plant Soil* 276, 205–217. <https://doi.org/10.1007/s11104-005-4415-5>
- Centinari, M., Vanden Heuvel, J. e., Goebel, M., Smith, M. s., Bauerle, T. l., 2016. Root-zone management practices impact above and belowground growth in Cabernet Franc grapevines. *Aust. J. Grape Wine Res.* 22, 137–148. <https://doi.org/10.1111/ajgw.12162>
- Charrier, G., Delzon, S., Domec, J.-C., Zhang, L., Delmas, C.E.L., Merlin, I., Corso, D., King, A., Ojeda, H., Ollat, N., Prieto, J.A., Scholach, T., Skinner, P., van Leeuwen, C., Gambetta, G.A., 2018. Drought will not leave your glass empty: Low risk of hydraulic failure revealed by long-term drought observations in world's top wine regions. *Sci. Adv.* 4, eaao6969. <https://doi.org/10.1126/sciadv.aao6969>
- Charrier, G., Torres-Ruiz, J.M., Badel, E., Burlett, R., Choat, B., Cochard, H., Delmas, C.E.L., Domec, J.-C., Jansen, S., King, A., Lenoir, N., Martin-StPaul, N., Gambetta, G.A., Delzon, S., 2016. Evidence for Hydraulic Vulnerability Segmentation and Lack of Xylem Refilling under Tension. *Plant Physiol.* 172, 1657–1668. <https://doi.org/10.1104/pp.16.01079>
- Chaves, M.M., Zarrouk, O., Francisco, R., Costa, J.M., Santos, T., Regalado, A.P., Rodrigues, M.L., Lopes, C.M., 2010. Grapevine under deficit irrigation: hints from physiological and molecular data. *Ann. Bot.* 105, 661–676. <https://doi.org/10.1093/aob/mcq030>
- Choat, B., Drayton, W.M., Brodersen, C., Matthews, M.A., Shackel, K.A., Wada, H., Mcelrone, A.J., 2010. Measurement of vulnerability to water stress-induced cavitation in grapevine: a comparison of four techniques applied to a long-vesseled species. *Plant Cell Environ.* 33, 1502–1512. <https://doi.org/10.1111/j.1365-3040.2010.02160.x>

- Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martinez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491, 752–+. <https://doi.org/10.1038/nature11688>
- Choné, X., Van Leeuwen, C., Dubourdieu, D., Gaudillère, J.P., 2001. Stem Water Potential is a Sensitive Indicator of Grapevine Water Status. *Ann. Bot.* 87, 477–483. <https://doi.org/10.1006/anbo.2000.1361>
- Chouzouri, A., Schultz, H.R., 2005. HYDRAULIC ANATOMY, CAVITATION SUSCEPTIBILITY AND GAS-EXCHANGE OF SEVERAL GRAPEVINE CULTIVARS OF DIFFERENT GEOGRAPHIC ORIGIN. *Acta Hortic.* 325–332. <https://doi.org/10.17660/ActaHortic.2005.689.38>
- Christmann, A., Weiler, E.W., Steudle, E., Grill, E., 2007. A hydraulic signal in root-to-shoot signalling of water shortage. *Plant J. Cell Mol. Biol.* 52, 167–174. <https://doi.org/10.1111/j.1365-313X.2007.03234.x>
- Cinat, P., Di Gennaro, S.F., Berton, A., Matese, A., 2019. Comparison of Unsupervised Algorithms for Vineyard Canopy Segmentation from UAV Multispectral Images. *Remote Sens.* 11, 1023. <https://doi.org/10.3390/rs11091023>
- Cislaghi, A., Bordoni, M., Meisina, C., Bischetti, G.B., 2017. Soil reinforcement provided by the root system of grapevines: Quantification and spatial variability. *Ecol. Eng., Soil Bio- and Eco-Engineering: The Use of Vegetation to Improve Slope Stability - Proceedings of the Fourth International Conference* 109, 169–185. <https://doi.org/10.1016/j.ecoleng.2017.04.034>
- Clevers, J.G.P.W., Gitelson, A.A., 2013. Remote estimation of crop and grass chlorophyll and nitrogen content using red-edge bands on Sentinel-2 and -3. *Int. J. Appl. Earth Obs. Geoinformation* 23, 344–351. <https://doi.org/10.1016/j.jag.2012.10.008>

- Comas, L. h., Bauerle, T. l., Eissenstat, D. m., 2010. Biological and environmental factors controlling root dynamics and function: effects of root ageing and soil moisture. *Aust. J. Grape Wine Res.* 16, 131–137. <https://doi.org/10.1111/j.1755-0238.2009.00078.x>
- Comba, L., Biglia, A., Ricauda Aimonino, D., Gay, P., 2018. Unsupervised detection of vineyards by 3D point-cloud UAV photogrammetry for precision agriculture. *Comput. Electron. Agric.* 155, 84–95. <https://doi.org/10.1016/j.compag.2018.10.005>
- Compant, S., Mitter, B., Colli, J., Gangl, H., Sessitsch, A., 2011. Endophytes of Grapevine Flowers, Berries, and Seeds: Identification of Cultivable Bacteria, Comparison with Other Plant Parts, and Visualization of Niches of Colonization. *Microb. Ecol.* 62, 188–97. <https://doi.org/10.1007/s00248-011-9883-y>
- Cookson, S.J., Prodhomme, D., Chambaud, C., Hévin, C., Valls Fonayet, J., Hilbert, G., Trossat-Magnin, C., Richard, T., Bortolami, G., Gambetta, G.A., Brocard, L., Ollat, N., 2019. Understanding scion-rootstock interactions at the graft interface of grapevine. *Acta Hortic.* 369–374. <https://doi.org/10.17660/ActaHortic.2019.1248.53>
- Corso, D., Delzon, S., Lamarque, L.J., Cochard, H., Torres-Ruiz, J.M., King, A., Brodribb, T., 2020. Neither xylem collapse, cavitation, or changing leaf conductance drive stomatal closure in wheat. *Plant Cell Environ.* 43, 854–865. <https://doi.org/10.1111/pce.13722>
- Costa, J.M., Grant, O.M., Chaves, M.M., 2010. Use of Thermal Imaging in Viticulture: Current Application and Future Prospects, in: Delrot, S., Medrano, H., Or, E., Bavaresco, L., Grando, S. (Eds.), *Methodologies and Results in Grapevine Research*. Springer Netherlands, Dordrecht, pp. 135–150. https://doi.org/10.1007/978-90-481-9283-0_10
- Costa, J.M., Vaz, M., Escalona, J., Egipto, R., Lopes, C., Medrano, H., Chaves, M.M., 2016. Modern viticulture in southern Europe: Vulnerabilities and strategies for adaptation to water scarcity. *Agric. Water Manag.*, Enhancing plant water use efficiency to meet future food production 164, 5–18. <https://doi.org/10.1016/j.agwat.2015.08.021>

- Coupel-Ledru, A., Lebon, É., Christophe, A., Doligez, A., Cabrera-Bosquet, L., Péchier, P., Hamard, P., This, P., Simonneau, T., 2014. Genetic variation in a grapevine progeny (*Vitis vinifera* L. cvs Grenache×Syrah) reveals inconsistencies between maintenance of daytime leaf water potential and response of transpiration rate under drought. *J. Exp. Bot.* 65, 6205–6218. <https://doi.org/10.1093/jxb/eru228>
- Couvreur, V., Faget, M., Lobet, G., Javaux, M., Chaumont, F., Draye, X., 2018. Going with the Flow: Multiscale Insights into the Composite Nature of Water Transport in Roots. *Plant Physiol.* 178, 1689–1703. <https://doi.org/10.1104/pp.18.01006>
- Couvreur, V., Vanderborght, J., Draye, X., Javaux, M., 2014. Dynamic aspects of soil water availability for isohydric plants: Focus on root hydraulic resistances. *Water Resour. Res.* 50, 8891–8906. <https://doi.org/10.1002/2014WR015608>
- Couvreur, V., Vanderborght, J., Javaux, M., 2012. A simple three-dimensional macroscopic root water uptake model based on the hydraulic architecture approach. *Hydrol. Earth Syst. Sci.* 16, 2957–2971. <https://doi.org/10.5194/hess-16-2957-2012>
- Cowan, I.R., 1965. Transport of water in the soil-plant-atmosphere system. *J. Appl. Ecol.* 2, 221–239.
- Cramer, G.R., Van Sluyter, S.C., Hopper, D.W., Pascovici, D., Keighley, T., Haynes, P.A., 2013. Proteomic analysis indicates massive changes in metabolism prior to the inhibition of growth and photosynthesis of grapevine (*Vitis vinifera* L.) in response to water deficit. *BMC Plant Biol.* 13, 49. <https://doi.org/10.1186/1471-2229-13-49>
- Cuneo, I.F., Barrios-Masias, F., Knipfer, T., Uretsky, J., Reyes, C., Lenain, P., Brodersen, C.R., Walker, M.A., McElrone, A.J., 2021. Differences in grapevine rootstock sensitivity and recovery from drought are linked to fine root cortical lacunae and root tip function. *New Phytol.* 229, 272–283. <https://doi.org/10.1111/nph.16542>
- Cuneo, I.F., Knipfer, T., Brodersen, C.R., McElrone, A.J., 2016. Mechanical Failure of Fine Root Cortical Cells Initiates Plant Hydraulic

Decline during Drought. *Plant Physiol.* 172, 1669–1678. <https://doi.org/10.1104/pp.16.00923>

Dayer, S., Herrera, J.C., Dai, Z., Burlett, R., Lamarque, L.J., Delzon, S., Bortolami, G., Cochard, H., Gambetta, G.A., 2020. The sequence and thresholds of leaf hydraulic traits underlying grapevine varietal differences in drought tolerance. *J. Exp. Bot.* 71, 4333–4344. <https://doi.org/10.1093/jxb/eraa186>

Dayer, S., Lamarque, L.J., Burlett, R., Bortolami, G., Delzon, S., Herrera, J.C., Cochard, H., Gambetta, G.A., 2022. Model-assisted ideotyping reveals trait syndromes to adapt viticulture to a drier climate. *Plant Physiol.* 190, 1673–1686. <https://doi.org/10.1093/plphys/kiac361>

De Bei, R., Cozzolino, D., Sullivan, W., Cynkar, W., Fuentes, S., Damberg, R., Pech, J., Tyerman, S., 2011. Non-destructive measurement of grapevine water potential using near infrared spectroscopy. *Aust. J. Grape Wine Res.* 17, 62–71. <https://doi.org/10.1111/j.1755-0238.2010.00117.x>

de CORTÁZAR, V.G., Córdova, C., Pinto, M., 2005. Canopy structure and photosynthesis modelling of grapevines (*Vitis vinifera* L. cv. Sultana) grown on an overhead (parronal) trellis system in Chile. *Aust. J. Grape Wine Res.* 11, 328–338. <https://doi.org/10.1111/j.1755-0238.2005.tb00032.x>

de Herralde, F., Savé, R., Aranda, X., Biel, C., 2010. Grapevine Roots and Soil Environment: Growth, Distribution and Function, in: Delrot, S., Medrano, H., Or, E., Bavaresco, L., Grando, S. (Eds.), *Methodologies and Results in Grapevine Research*. Springer Netherlands, Dordrecht, pp. 1–20. https://doi.org/10.1007/978-90-481-9283-0_1

de Jong van Lier, Q., Metselaar, K., van Dam, J.C., 2006. Root Water Extraction and Limiting Soil Hydraulic Conditions Estimated by Numerical Simulation. *Vadose Zone J.* 5, 1264–1277. <https://doi.org/10.2136/vzj2006.0056>

de Jong van Lier, Q., van Dam, J.C., Durigon, A., dos Santos, M.A., Metselaar, K., 2013. Modeling Water Potentials and Flows in the Soil–

Plant System Comparing Hydraulic Resistances and Transpiration Reduction Functions. *Vadose Zone J.* 12, vzj2013.02.0039. <https://doi.org/10.2136/vzj2013.02.0039>

de Jong van Lier, Q., van Dam, J.C., Metselaar, K., de Jong, R., Duijnisveld, W.H.M., 2008. Macroscopic Root Water Uptake Distribution Using a Matric Flux Potential Approach. *Vadose Zone J.* 7, 1065. <https://doi.org/10.2136/vzj2007.0083>

Degu, A., Hochberg, U., Wong, D.C.J., Alberti, G., Lazarovitch, N., Peterlunger, E., Castellarin, S.D., Herrera, J.C., Fait, A., 2019. Swift metabolite changes and leaf shedding are milestones in the acclimation process of grapevine under prolonged water stress. *BMC Plant Biol.* 19, 69. <https://doi.org/10.1186/s12870-019-1652-y>

Delrot, S., Grimplet, J., Carbonell-Bejerano, P., Schwandner, A., Bert, P.-F., Bavaresco, L., Costa, L.D., Di Gaspero, G., Duchêne, E., Hausmann, L., Malnoy, M., Morgante, M., Ollat, N., Pecile, M., Vezzulli, S., 2020. Genetic and Genomic Approaches for Adaptation of Grapevine to Climate Change, in: Kole, C. (Ed.), *Genomic Designing of Climate-Smart Fruit Crops*. Springer International Publishing, Cham, pp. 157–270. https://doi.org/10.1007/978-3-319-97946-5_7

Delzon, S., 2015. New insight into leaf drought tolerance. *Funct. Ecol.* 29, 1247–1249. <https://doi.org/10.1111/1365-2435.12500>

Dietrich, D., Pang, L., Kobayashi, A., Fozard, J.A., Boudolf, V., Bhosale, R., Antoni, R., Nguyen, T., Hiratsuka, S., Fujii, N., Miyazawa, Y., Bae, T.-W., Wells, D.M., Owen, M.R., Band, L.R., Dyson, R.J., Jensen, O.E., King, J.R., Tracy, S.R., Sturrock, C.J., Mooney, S.J., Roberts, J.A., Bhalerao, R.P., Dinneny, J.R., Rodriguez, P.L., Nagatani, A., Hosokawa, Y., Baskin, T.I., Pridmore, T.P., De Veylder, L., Takahashi, H., Bennett, M.J., 2017. Root hydrotropism is controlled via a cortex-specific growth mechanism. *Nat. Plants* 3, 17057. <https://doi.org/10.1038/nplants.2017.57>

Dodd, I.C., Egea, G., Watts, C.W., Whalley, W.R., 2010. Root water potential integrates discrete soil physical properties to influence ABA signalling during partial rootzone drying. *J. Exp. Bot.* 61, 3543–3551. <https://doi.org/10.1093/jxb/erq195>

Domec, J.-C., Ogée, J., Noormets, A., Jouangy, J., Gavazzi, M., Treasure, E., Sun, G., McNulty, S.G., King, J.S., 2012. Interactive effects of nocturnal transpiration and climate change on the root hydraulic redistribution and carbon and water budgets of southern United States pine plantations. *Tree Physiol.* 32, 707–723. <https://doi.org/10.1093/treephys/tps018>

Donkó, Á., Zanathy, G., Erős-Honti, Z., Villangó, S., Bisztray, G., 2014. Changes of mycorrhizal colonization along moist gradient in a vineyard of Eger (Hungary). *Agric. Environ.* 6, 13–23. <https://doi.org/10.2478/ausae-2014-0008>

Donovan, L., Linton, M., Richards, J., 2001. Predawn plant water potential does not necessarily equilibrate with soil water potential under well-watered conditions. *Oecologia* 129, 328–335. <https://doi.org/10.1007/s004420100738>

Doutreloup, S., Bois, B., Pohl, B., Zito, S., Richard, Y., 2022. Climatic comparison between Belgium, Champagne, Alsace, Jura and Bourgogne for wine production using the regional model MAR. *OENO One* 56, 1–17. <https://doi.org/10.20870/oeno-one.2022.56.3.5356>

Draye, X., Kim, Y., Lobet, G., Javaux, M., 2010. Model-assisted integration of physiological and environmental constraints affecting the dynamic and spatial patterns of root water uptake from soils. *J. Exp. Bot.* 61, 2145–2155. <https://doi.org/10.1093/jxb/erq077>

Dry, P.R., Loveys, B.R., 1999. Grapevine shoot growth and stomatal conductance are reduced when part of the root system is dried. *VITIS - J. Grapevine Res.* 38, 151–151. <https://doi.org/10.5073/vitis.1999.38.151-156>

Duddek, P., Ahmed, M.A., Javaux, M., Vanderborght, J., Lovric, G., King, A., Carminati, A., 2023. The effect of root hairs on root water uptake is determined by root–soil contact and root hair shrinkage. *New Phytol.* n/a. <https://doi.org/10.1111/nph.19144>

Espinoza, C.Z., Khot, L.R., Sankaran, S., Jacoby, P.W., 2017. High Resolution Multispectral and Thermal Remote Sensing-Based Water

Stress Assessment in Subsurface Irrigated Grapevines. *Remote Sens.* 9, 961. <https://doi.org/10.3390/rs9090961>

Ewers, B.E., Oren, R., Sperry, J.S., 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. *Plant Cell Environ.* 23, 1055–1066. <https://doi.org/10.1046/j.1365-3040.2000.00625.x>

Faiz, S.M.A., Weatherley, P.E., 1982. Root Contraction in Transpiring Plants. *New Phytol.* 92, 333–343. <https://doi.org/10.1111/j.1469-8137.1982.tb03391.x>

FAO-OIV, 2023. Table and Dried Grapes: World data available | OIV [WWW Document]. URL <https://www.oiv.int/table-and-dried-grapes-world-data-available> (accessed 6.6.24).

Ferro, M.V., Catania, P., 2023. Technologies and Innovative Methods for Precision Viticulture: A Comprehensive Review. *Horticulturae* 9, 399. <https://doi.org/10.3390/horticulturae9030399>

Fichtl, L., Hofmann, M., Kahlen, K., Voss-Fels, K.P., Cast, C.S., Ollat, N., Vivin, P., Loose, S., Nsibi, M., Schmid, J., Strack, T., Schultz, H.R., Smith, J., Friedel, M., 2023. Towards grapevine root architectural models to adapt viticulture to drought. *Front. Plant Sci.* 14.

Flexas, J., Bota, J., Escalona, J.M., Sampol, B., Medrano, H., 2002. Effects of drought on photosynthesis in grapevines under field conditions: an evaluation of stomatal and mesophyll limitations. *Funct. Plant Biol.* 29, 461–471. <https://doi.org/10.1071/pp01119>

Fraga, H., García de Cortázar Atauri, I., Malheiro, A.C., Santos, J.A., 2016. Modelling climate change impacts on viticultural yield, phenology and stress conditions in Europe. *Glob. Change Biol.* 22, 3774–3788. <https://doi.org/10.1111/gcb.13382>

Fraga, H., Malheiro, A.C., Moutinho-Pereira, J., Cardoso, R.M., Soares, P.M.M., Cancela, J.J., Pinto, J.G., Santos, J.A., 2014. Integrated Analysis of Climate, Soil, Topography and Vegetative Growth in Iberian Viticultural Regions. *PLOS ONE* 9, e108078. <https://doi.org/10.1371/journal.pone.0108078>

Frensch, J., Steudle, E., 1989. Axial and Radial Hydraulic Resistance to Roots of Maize (*Zea mays* L.) 1. *Plant Physiol.* 91, 719–726.

Gambetta, G.A., 2016. Water Stress and Grape Physiology in the Context of Global Climate Change. *J. Wine Econ.* 11, 168–180. <https://doi.org/10.1017/jwe.2015.16>

Gambetta, G.A., Fei, J., Rost, T.L., Knipfer, T., Matthews, M.A., Shackel, K.A., Walker, M.A., McElrone, A.J., 2013. Water Uptake along the Length of Grapevine Fine Roots: Developmental Anatomy, Tissue-Specific Aquaporin Expression, and Pathways of Water Transport. *Plant Physiol.* 163, 1254–1265. <https://doi.org/10.1104/pp.113.221283>

Gambetta, G.A., Herrera, J.C., Dayer, S., Feng, Q., Hochberg, U., Castellarin, S.D., 2020a. The physiology of drought stress in grapevine: towards an integrative definition of drought tolerance. *J. Exp. Bot.* 71, 4658–4676. <https://doi.org/10.1093/jxb/eraa245>

Gambetta, G.A., Herrera, J.C., Dayer, S., Feng, Q., Hochberg, U., Castellarin, S.D., 2020b. The physiology of drought stress in grapevine: towards an integrative definition of drought tolerance. *J. Exp. Bot.* 71, 4658–4676. <https://doi.org/10.1093/jxb/eraa245>

Gambetta, G.A., Kurtural, S.K., 2021. Global warming and wine quality: are we close to the tipping point? *OENO One* 55, 353–361. <https://doi.org/10.20870/oeno-one.2021.55.3.4774>

Gambetta, G.A., Manuck, C.M., Drucker, S.T., Shaghasi, T., Fort, K., Matthews, M.A., Walker, M.A., McElrone, A.J., 2012. The relationship between root hydraulics and scion vigour across *Vitis* rootstocks: what role do root aquaporins play? *J. Exp. Bot.* 63, 6445–6455. <https://doi.org/10.1093/jxb/ers312>

Gambetta, J.M., Bastian, S.E.P., Cozzolino, D., Jeffery, D.W., 2014. Factors Influencing the Aroma Composition of Chardonnay Wines. *J. Agric. Food Chem.* 62, 6512–6534. <https://doi.org/10.1021/jf501945s>

Gamon, J.A., Peñuelas, J., Field, C.B., 1992. A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency.

Remote Sens. Environ. 41, 35–44. [https://doi.org/10.1016/0034-4257\(92\)90059-S](https://doi.org/10.1016/0034-4257(92)90059-S)

Gamon, J.A., Surfus, J.S., 1999. Assessing leaf pigment content and activity with a reflectometer. *New Phytol.* 143, 105–117. <https://doi.org/10.1046/j.1469-8137.1999.00424.x>

Gao, B., 1996. NDWI—A normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sens. Environ.* 58, 257–266. [https://doi.org/10.1016/S0034-4257\(96\)00067-3](https://doi.org/10.1016/S0034-4257(96)00067-3)

García-Tejera, O., López-Bernal, Á., Orgaz, F., Testi, L., Villalobos, F.J., 2021. The pitfalls of water potential for irrigation scheduling. *Agric. Water Manag.* 243, 106522. <https://doi.org/10.1016/j.agwat.2020.106522>

García-Tejera, O., López-Bernal, Á., Testi, L., Villalobos, F.J., 2017. A soil-plant-atmosphere continuum (SPAC) model for simulating tree transpiration with a soil multi-compartment solution. *Plant Soil* 412, 215–233. <https://doi.org/10.1007/s11104-016-3049-0>

Gardner, W.R., 1960. Dynamic Aspects of Water Availability to Plants. *Soil Sci.* 89, 63–73.

Gaudillère, J.-P., Choné, X., Van Leeuwen, C., Trégoat, O., 2002. The assessment of vine water and nitrogen uptake by means of physiological indicators influence on vine development and berry potential (*Vitis vinifera* L. cv Merlot, 2000, Bordeaux). *OENO One* 36, 133. <https://doi.org/10.20870/oenone.2002.36.3.967>

Gerhards, M., Schlerf, M., Mallick, K., Udelhoven, T., 2019. Challenges and Future Perspectives of Multi-/Hyperspectral Thermal Infrared Remote Sensing for Crop Water-Stress Detection: A Review. *Remote Sens.* 11, 1240. <https://doi.org/10.3390/rs11101240>

Giehl, R.F.H., von Wirén, N., 2018. Hydropatterning—how roots test the waters. *Science* 362, 1358–1359. <https://doi.org/10.1126/science.aav9375>

Giovas, R., Tassopoulos, D., Kalivas, D., Lougkos, N., Priovolou, A., 2021. Remote Sensing Vegetation Indices in Viticulture: A Critical

Review. Agriculture 11, 457.
<https://doi.org/10.3390/agriculture11050457>

Gitelson, A.A., Kaufman, Y.J., Stark, R., Rundquist, D., 2002. Novel algorithms for remote estimation of vegetation fraction. *Remote Sens. Environ.* 80, 76–87. [https://doi.org/10.1016/S0034-4257\(01\)00289-9](https://doi.org/10.1016/S0034-4257(01)00289-9)

Gitelson, A.A., Keydan, G.P., Merzlyak, M.N., 2006. Three-band model for noninvasive estimation of chlorophyll, carotenoids, and anthocyanin contents in higher plant leaves. *Geophys. Res. Lett.* 33. <https://doi.org/10.1029/2006GL026457>

Gowdy, M., Suter, B., Pieri, P., Marguerit, E., Irvine, A.D., Gambetta, G., Leeuwen, C. van, 2022. Variety-specific response of bulk stomatal conductance of grapevine canopies to changes in net radiation, atmospheric demand, and drought stress.: This article is published in cooperation with Terclim 2022 (XIVth International Terroir Congress and 2nd ClimWine Symposium), 3-8 July 2022, Bordeaux, France. *OENO One* 56, 205–222. <https://doi.org/10.20870/oenone.2022.56.2.5435>

Grassi, F., De Lorenzis, G., 2021. Back to the Origins: Background and Perspectives of Grapevine Domestication. *Int. J. Mol. Sci.* 22, 4518. <https://doi.org/10.3390/ijms22094518>

Groenveld, T., Obiero, C., Yu, Y., Flury, M., Keller, M., 2023. Predawn leaf water potential of grapevines is not necessarily a good proxy for soil moisture. *BMC Plant Biol.* 23, 369. <https://doi.org/10.1186/s12870-023-04378-6>

Guerra, B., Steenwerth, K., 2012. Influence of Floor Management Technique on Grapevine Growth, Disease Pressure, and Juice and Wine Composition: A Review. *Am. J. Enol. Vitic.* 63, 149–164. <https://doi.org/10.5344/ajev.2011.10001>

Hatch, T.A., Hickey, C.C., Wolf, T.K., 2011. Cover Crop, Rootstock, and Root Restriction Regulate Vegetative Growth of Cabernet Sauvignon in a Humid Environment. *Am. J. Enol. Vitic.* 62, 298–311. <https://doi.org/10.5344/ajev.2011.11001>

Haverkamp, R., Vauclin, M., Vachaud, G., 1984. ERROR ANALYSIS IN ESTIMATING SOIL WATER CONTENT FROM NEUTRON PROBE MEASUREMENTS: 1. LOCAL STANDPOINT. *Soil Sci.* 137, 78.

Hayat, R., Ali, S., Amara, U., Khalid, R., Ahmed, I., 2010. Soil beneficial bacteria and their role in plant growth promotion: A Review. *Ann. Microbiol.* 60, 579–598. <https://doi.org/10.1007/s13213-010-0117-1>

Helman, D., Bahat, I., Netzer, Y., Ben-Gal, A., Alchanatis, V., Peeters, A., Cohen, Y., 2018. Using Time Series of High-Resolution Planet Satellite Images to Monitor Grapevine Stem Water Potential in Commercial Vineyards. *Remote Sens.* 10, 1615. <https://doi.org/10.3390/rs10101615>

Henry, C., John, G.P., Pan, R., Bartlett, M.K., Fletcher, L.R., Scoffoni, C., Sack, L., 2019. A stomatal safety-efficiency trade-off constrains responses to leaf dehydration. *Nat. Commun.* 10, 3398. <https://doi.org/10.1038/s41467-019-11006-1>

Herralde, F. de, Alsina, M. del M., Aranda, X., Savé, R., Biel, C., 2006. Effects of rootstock and irrigation regime on hydraulic architecture of *Vitis vinifera* L. Cv. Tempranillo. *OENO One* 40, 133–139. <https://doi.org/10.20870/oeno-one.2006.40.3.868>

Herrera, J. c., Bucchetti, B., Sabbatini, P., Comuzzo, P., Zulini, L., Vecchione, A., Peterlunger, E., Castellarin, S. d., 2015. Effect of water deficit and severe shoot trimming on the composition of *Vitis vinifera* L. Merlot grapes and wines. *Aust. J. Grape Wine Res.* 21, 254–265. <https://doi.org/10.1111/ajgw.12143>

Herrera, J.C., Calderan, A., Gambetta, G.A., Peterlunger, E., Forneck, A., Sivilotti, P., Cochard, H., Hochberg, U., 2022. Stomatal responses in grapevine become increasingly more tolerant to low water potentials throughout the growing season. *Plant J.* 109, 804–815. <https://doi.org/10.1111/tpj.15591>

Hinckley, T.M., Lassoie, J.P., Running, S.W., 1978. Temporal and Spatial Variations in the Water Status of Forest Trees. *For. Sci.* 24, a0001-z0001. <https://doi.org/10.1093/forestscience/24.s1.a0001>

Hochberg, U., Bonel, A.G., David-Schwartz, R., Degu, A., Fait, A., Cochard, H., Peterlunger, E., Herrera, J.C., 2017a. Grapevine acclimation to water deficit: the adjustment of stomatal and hydraulic conductance differs from petiole embolism vulnerability. *Planta* 245, 1091–1104. <https://doi.org/10.1007/s00425-017-2662-3>

Hochberg, U., Degu, A., Fait, A., Rachmilevitch, S., 2013. Near isohydric grapevine cultivar displays higher photosynthetic efficiency and photorespiration rates under drought stress as compared with near anisohydric grapevine cultivar. *Physiol. Plant.* 147, 443–452. <https://doi.org/10.1111/j.1399-3054.2012.01671.x>

Hochberg, U., Degu, A., Gendler, T., Fait, A., Rachmilevitch, S., 2015. The variability in the xylem architecture of grapevine petiole and its contribution to hydraulic differences. *Funct. Plant Biol.* FPB 42, 357–365. <https://doi.org/10.1071/FP14167>

Hochberg, U., Herrera, J.C., Cochard, H., Badel, E., 2016. Short-time xylem relaxation results in reliable quantification of embolism in grapevine petioles and sheds new light on their hydraulic strategy. *Tree Physiol.* 36, 748–755. <https://doi.org/10.1093/treephys/tpv145>

Hochberg, U., Rockwell, F.E., Holbrook, N.M., Cochard, H., 2018. Iso/Anisohydry: A Plant–Environment Interaction Rather Than a Simple Hydraulic Trait. *Trends Plant Sci.* 23, 112–120. <https://doi.org/10.1016/j.tplants.2017.11.002>

Hochberg, U., Windt, C.W., Ponomarenko, A., Zhang, Y.-J., Gersony, J., Rockwell, F.E., Holbrook, N.M., 2017b. Stomatal Closure, Basal Leaf Embolism, and Shedding Protect the Hydraulic Integrity of Grape Stems. *Plant Physiol.* 174, 764–775. <https://doi.org/10.1104/pp.16.01816>

Hochberg, U., Windt, C.W., Ponomarenko, A., Zhang, Y.-J., Gersony, J., Rockwell, F.E., Holbrook, N.M., 2017c. Stomatal Closure, Basal Leaf Embolism, and Shedding Protect the Hydraulic Integrity of Grape

Stems. Plant Physiol. 174, 764–775.
<https://doi.org/10.1104/pp.16.01816>

Horne, D.J., Scotter, D.R., 2016. The available water holding capacity of soils under pasture. *Agric. Water Manag.* 177, 165–171.
<https://doi.org/10.1016/j.agwat.2016.07.012>

Huber, K., Vanderborght, J., Javaux, M., Schröder, N., Dodd, I.C., Vereecken, H., 2014. Modelling the impact of heterogeneous rootzone water distribution on the regulation of transpiration by hormone transport and/or hydraulic pressures. *Plant Soil* 384, 93–112.
<https://doi.org/10.1007/s11104-014-2188-4>

Huck, M.G., Klepper, B., Taylor, H.M., 1970. Diurnal Variations in Root Diameter. *Plant Physiol.* 45, 529–530.
<https://doi.org/10.1104/pp.45.4.529>

Idso, S.B., Jackson, R.D., Pinter, P.J., Reginato, R.J., Hatfield, J.L., 1981. Normalizing the stress-degree-day parameter for environmental variability. *Agric. Meteorol.* 24, 45–55. [https://doi.org/10.1016/0002-1571\(81\)90032-7](https://doi.org/10.1016/0002-1571(81)90032-7)

Izumi, Y., Okaichi, S., Awala, S.K., Kawato, Y., Watanabe, Y., Yamane, K., Iijima, M., 2018. Water supply from pearl millet by hydraulic lift can mitigate drought stress and improve productivity of rice by the close mixed planting. *Plant Prod. Sci.* 21, 8–15.
<https://doi.org/10.1080/1343943X.2018.1428494>

Jackson, R.B., Sperry, J.S., Dawson, T.E., 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends Plant Sci.* 5, 482–488.

James, G., Witten, D., Hastie, T., Tibshirani, R., 2021. An Introduction to Statistical Learning: with Applications in R, Springer Texts in Statistics. Springer US, New York, NY. <https://doi.org/10.1007/978-1-0716-1418-1>

Janott, M., Gayler, S., Gessler, A., Javaux, M., Klier, C., Priesack, E., 2011. A one-dimensional model of water flow in soil-plant systems based on plant architecture. *Plant Soil* 341, 233–256.
<https://doi.org/10.1007/s11104-010-0639-0>

- Jarvis, P.G., McNaughton, K.G., 1986. Stomatal Control of Transpiration: Scaling Up from Leaf to Region, in: MacFadyen, A., Ford, E.D. (Eds.), *Advances in Ecological Research*. Academic Press, pp. 1–49. [https://doi.org/10.1016/S0065-2504\(08\)60119-1](https://doi.org/10.1016/S0065-2504(08)60119-1)
- Javaux, M., Carminati, A., 2021. Soil hydraulics affect the degree of isohydricity. *Plant Physiol.* 186, 1378–1381. <https://doi.org/10.1093/plphys/kiab154>
- Javaux, M., Schröder, T., Vanderborght, J., Vereecken, H., 2008. Use of a Three-Dimensional Detailed Modeling Approach for Predicting Root Water Uptake. *Vadose Zone J.* 7, 1079–1088. <https://doi.org/10.2136/vzj2007.0115>
- Jones, G., Schultz, H., 2016. Climate change and emerging cool climate wine regions.
- Jones, H., 1992. *Plants and Microclimate*.
- Jones, H.G., Stoll, M., Santos, T., Sousa, C. de, Chaves, M.M., Grant, O.M., 2002. Use of infrared thermography for monitoring stomatal closure in the field: application to grapevine. *J. Exp. Bot.* 53, 2249–2260. <https://doi.org/10.1093/jxb/erf083>
- Jorda, H., Ahmed, M.A., Javaux, M., Carminati, A., Duddek, P., Vetterlein, D., Vanderborght, J., 2022. Field scale plant water relation of maize (*Zea mays*) under drought – impact of root hairs and soil texture. *Plant Soil* 478, 59–84. <https://doi.org/10.1007/s11104-022-05685-x>
- Kangur, O., Kupper, P., Sellin, A., 2017. Predawn disequilibrium between soil and plant water potentials in light of climate trends predicted for northern Europe. *Reg. Environ. Change* 17, 2159–2168. <https://doi.org/10.1007/s10113-017-1183-8>
- Kannenbergh, S.A., Guo, J.S., Novick, K.A., Anderegg, W.R.L., Feng, X., Kennedy, D., Konings, A.G., Martínez-Vilalta, J., Matheny, A.M., 2022. Opportunities, challenges and pitfalls in characterizing plant water-use strategies. *Funct. Ecol.* 36, 24–37. <https://doi.org/10.1111/1365-2435.13945>

- Karn, R., Hillin, D., Helwi, P., Scheiner, J., Guo, W., 2024. Assessing grapevine vigor as affected by soil physicochemical properties and topographic attributes for precision vineyard management. *Sci. Hortic.* 328, 112857. <https://doi.org/10.1016/j.scienta.2024.112857>
- Klodd, A.E., Eissenstat, D.M., Wolf, T.K., Centinari, M., 2016. Coping with cover crop competition in mature grapevines. *Plant Soil* 400, 391–402. <https://doi.org/10.1007/s11104-015-2748-2>
- Koehler, T., Moser, D.S., Botezatu, Á., Murugesan, T., Kaliamoorthy, S., Zarebanadkouki, M., Bienert, M.D., Bienert, G.P., Carminati, A., Kholová, J., Ahmed, M., 2022. Going underground: soil hydraulic properties impacting maize responsiveness to water deficit. *Plant Soil* 478, 43–58. <https://doi.org/10.1007/s11104-022-05656-2>
- Lamarque, L.J., Delmas, C.E.L., Charrier, G., Burlett, R., Dell’Acqua, N., Pouzoulet, J., Gambetta, G.A., Delzon, S., 2023. Quantifying the grapevine xylem embolism resistance spectrum to identify varieties and regions at risk in a future dry climate. *Sci. Rep.* 13, 7724. <https://doi.org/10.1038/s41598-023-34224-6>
- Laroche-Pinel, E., Albughdadi, M., Duthoit, S., Chéret, V., Rousseau, J., Clenet, H., 2021a. Understanding Vine Hyperspectral Signature through Different Irrigation Plans: A First Step to Monitor Vineyard Water Status. *Remote Sens.* 13, 536. <https://doi.org/10.3390/rs13030536>
- Laroche-Pinel, E., Duthoit, S., Albughdadi, M., Costard, A., Rousseau, J., Chéret, V., Clenet, H., 2021b. Towards Vine Water Status Monitoring on a Large Scale Using Sentinel-2 Images. *Remote Sens.* <https://doi.org/10.3390/rs13091837>
- Lavoie-Lamoureux, A., Sacco, D., Risse, P.-A., Lovisolo, C., 2017. Factors influencing stomatal conductance in response to water availability in grapevine: a meta-analysis. *Physiol. Plant.* 159, 468–482. <https://doi.org/10.1111/ppl.12530>
- Lei, G., Zeng, W., Huu Nguyen, T., Zeng, J., Chen, H., Kumar Srivastava, A., Gaiser, T., Wu, J., Huang, J., 2023. Relating soil-root hydraulic resistance variation to stomatal regulation in soil-plant water

transport modeling. *J. Hydrol.* 617, 128879.
<https://doi.org/10.1016/j.jhydrol.2022.128879>

Leibar, U., Aizpurua, A., Unamunzaga, O., Pascual, I., Morales, F., 2015. How will climate change influence grapevine cv. Tempranillo photosynthesis under different soil textures? *Photosynth. Res.* 124, 199–215. <https://doi.org/10.1007/s11120-015-0120-2>

Levin, A.D., Williams, L.E., Matthews, M.A., Levin, A.D., Williams, L.E., Matthews, M.A., 2019. A continuum of stomatal responses to water deficits among 17 wine grape cultivars (*Vitis vinifera*). *Funct. Plant Biol.* 47, 11–25. <https://doi.org/10.1071/FP19073>

Lovisolo, C., Lavoie-Lamoureux, A., Tramontini, S., Ferrandino, A., 2016. Grapevine adaptations to water stress: new perspectives about soil/plant interactions. *Theor. Exp. Plant Physiol.* 28. <https://doi.org/10.1007/s40626-016-0057-7>

Lovisolo, C., Perrone, I., Carrá, A., Ferrandino, A., Flexas, J., Medrano, H., Schubert, A., 2010. Drought-induced changes in development and function of grapevine (*Vitis* spp.) organs and in their hydraulic and non-hydraulic interactions at the whole-plant level: a physiological and molecular update. <https://doi.org/10.1071/FP09191>

Lovisolo, C., Tramontini, S., Flexas, J., Schubert, A., 2008. Mercurial inhibition of root hydraulic conductance in *Vitis* spp. rootstocks under water stress. *Environ. Exp. Bot.* 63, 178–182. <https://doi.org/10.1016/j.envexpbot.2007.11.005>

MacQueen, J., 1967. Some methods for classification and analysis of multivariate observations. *Proc. Fifth Berkeley Symp. Math. Stat. Probab.* Vol. 1 Stat. 5.1, 281–298.

Malheiro, A., Santos, J., Fraga, H., Pinto, J., 2010. Climate change scenarios applied to viticultural zoning in Europe. *Clim. Res.* 43, 163–177. <https://doi.org/10.3354/cr00918>

Mapelli, F., Marasco, R., Rolli, E., Barbato, M., Cherif, H., Guesmi, A., Ouzari, I., Daffonchio, D., Borin, S., 2013. Potential for Plant Growth Promotion of Rhizobacteria Associated with *Salicornia* Growing in

Tunisian Hypersaline Soils. *BioMed Res. Int.* 2013, 248078.
<https://doi.org/10.1155/2013/248078>

Mapfumo, E., Aspinall, D., Hancock, T.W., 1994. Growth and Development of Roots of Grapevine (*Vitis vinifera* L.) in Relation to Water Uptake from Soil. *Ann. Bot.* 74, 75–85.
<https://doi.org/10.1006/anbo.1994.1096>

Marañón, M., Fernández-Novales, J., Tardaguila, J., Gutiérrez, S., Diago, M.P., 2023. NIR attribute selection for the development of vineyard water status predictive models. *Biosyst. Eng.* 229, 167–178.
<https://doi.org/10.1016/j.biosystemseng.2023.04.001>

Marguerit, E., Brendel, O., Lebon, E., Van Leeuwen, C., Ollat, N., 2012. Rootstock control of scion transpiration and its acclimation to water deficit are controlled by different genes. *New Phytol.* 194, 416–429.
<https://doi.org/10.1111/j.1469-8137.2012.04059.x>

Martin-StPaul, N., Delzon, S., Cochard, H., 2017. Plant resistance to drought depends on timely stomatal closure. *Ecol. Lett.* 20, 1437–1447.
<https://doi.org/10.1111/ele.12851>

Martorell, S., Diaz-Espejo, A., Tomàs, M., Pou, A., El Aou-ouad, H., Escalona, J.M., Vadell, J., Ribas-Carbó, M., Flexas, J., Medrano, H., 2015. Differences in water-use-efficiency between two *Vitis vinifera* cultivars (Grenache and Tempranillo) explained by the combined response of stomata to hydraulic and chemical signals during water stress. *Agric. Water Manag.* 156, 1–9.
<https://doi.org/10.1016/j.agwat.2015.03.011>

Mary, B., Iván, V., Meggio, F., Peruzzo, L., Blanchy, G., Chou, C., Ruperti, B., Wu, Y., Cassiani, G., 2023. Imaging of the electrical activity in the root zone under limited-water-availability stress: a laboratory study for *Vitis vinifera*. *Biogeosciences* 20, 4625–4650.
<https://doi.org/10.5194/bg-20-4625-2023>

Mary, B., Peruzzo, L., Boaga, J., Schmutz, M., Wu, Y., Hubbard, S.S., Cassiani, G., 2018. Small-scale characterization of vine plant root water uptake via 3-D electrical resistivity tomography and mise-à-la-masse

method. Hydrol. Earth Syst. Sci. 22, 5427–5444.
<https://doi.org/10.5194/hess-22-5427-2018>

Matthews, M., Anderson, M., 1988. Fruit Ripening in *Vitis vinifera* L.: Responses to Seasonal Water Deficits. *Am J Enol Vitic* 39, 313–320.
<https://doi.org/10.5344/ajev.1988.39.4.313>

McElrone, A.J., Brodersen, C.R., Alsina, M.M., Drayton, W.M., Matthews, M.A., Shackel, K.A., Wada, H., Zufferey, V., Choat, B., 2012. Centrifuge technique consistently overestimates vulnerability to water stress-induced cavitation in grapevines as confirmed with high-resolution computed tomography. *New Phytol.* 196, 661–665.
<https://doi.org/10.1111/j.1469-8137.2012.04244.x>

Medrano, H., Escalona, J.M., Bota, J., Gulias, J., Flexas, J., 2002. Regulation of Photosynthesis of C3 Plants in Response to Progressive Drought: Stomatal Conductance as a Reference Parameter. *Ann. Bot.* 89, 895–905. <https://doi.org/10.1093/aob/mcf079>

Meinzer, F.C., Woodruff, D.R., Marias, D.E., Smith, D.D., McCulloh, K.A., Howard, A.R., Magedman, A.L., 2016. Mapping ‘hydroscares’ along the iso- to anisohydric continuum of stomatal regulation of plant water status. *Ecol. Lett.* 19, 1343–1352.
<https://doi.org/10.1111/ele.12670>

Merwin, I.A., Stiles, W.C., 1994. Orchard Groundcover Management Impacts on Apple Tree Growth and Yield, and Nutrient Availability and Uptake. <https://doi.org/10.21273/JASHS.119.2.209>

Mittler, R., Blumwald, E., 2015. The roles of ROS and ABA in systemic acquired acclimation. *Plant Cell* 27, 64–70.
<https://doi.org/10.1105/tpc.114.133090>

Mohammadi Alagoz, S., Zahra, N., Hajiaghaei Kamrani, M., Asgari Lajayer, B., Nobaharan, K., Astatkie, T., Siddique, K.H.M., Farooq, M., 2023. Role of Root Hydraulics in Plant Drought Tolerance. *J. Plant Growth Regul.* 42, 6228–6243. <https://doi.org/10.1007/s00344-022-10807-x>

Möller, M., Alchanatis, V., Cohen, Y., Meron, M., Tsipris, J., Naor, A., Ostrovsky, V., Sprintsin, M., Cohen, S., 2007. Use of thermal and

visible imagery for estimating crop water status of irrigated grapevine*. *J. Exp. Bot.* 58, 827–838. <https://doi.org/10.1093/jxb/erl115>

Morabito, C., Orozco, J., Tonel, G., Cavalletto, S., Meloni, G.R., Schubert, A., Gullino, M., Zwieniecki, M., Secchi, F., 2021. Do the ends justify the means? Impact of drought progression rate on stress response and recovery in *Vitis vinifera*. *Physiol. Plant.* 174. <https://doi.org/10.1111/ppl.13590>

Moriondo, M., Jones, G.V., Bois, B., Dibari, C., Ferrise, R., Trombi, G., Bindi, M., 2013. Projected shifts of wine regions in response to climate change. *Clim. Change* 119, 825–839. <https://doi.org/10.1007/s10584-013-0739-y>

Morlat, R., Bodin, F., 2006. Characterization of Viticultural Terroirs using a Simple Field Model Based on Soil Depth – II. Validation of the Grape Yield and Berry Quality in the Anjou Vineyard (France). *Plant Soil* 281, 55–69. <https://doi.org/10.1007/s11104-005-3769-z>

Moya, I., Camenen, L., Evain, S., Goulas, Y., Cerovic, Z.G., Latouche, G., Flexas, J., Ounis, A., 2004. A new instrument for passive remote sensing: 1. Measurements of sunlight-induced chlorophyll fluorescence. *Remote Sens. Environ.* 91, 186–197. <https://doi.org/10.1016/j.rse.2004.02.012>

Moya-Laraño, J., Corcobado, G., 2008. Plotting partial correlation and regression in ecological studies. *Web Ecol.* 8, 35–46. <https://doi.org/10.5194/we-8-35-2008>

Muchow, R.C., Sinclair, T.R., 1991. Water Deficit Effects on Maize Yields Modeled under Current and “Greenhouse” Climates. *Agron. J.* 83, 1052–1059. <https://doi.org/10.2134/agronj1991.00021962008300060023x>

Munemasa, S., Hauser, F., Park, J., Waadt, R., Brandt, B., Schroeder, J.I., 2015. Mechanisms of abscisic acid-mediated control of stomatal aperture. *Curr. Opin. Plant Biol.* 28, 154–162. <https://doi.org/10.1016/j.pbi.2015.10.010>

Munitz, S., Netzer, Y., Shtein, I., Schwartz, A., 2018. Water availability dynamics have long-term effects on mature stem structure in *Vitis*

vinifera. Am. J. Bot. 105, 1443–1452.
<https://doi.org/10.1002/ajb2.1148>

Munitz, S., Schwartz, A., Netzer, Y., 2020. Effect of timing of irrigation initiation on vegetative growth, physiology and yield parameters in Cabernet Sauvignon grapevines. *Aust. J. Grape Wine Res.* 26, 220–232.
<https://doi.org/10.1111/ajgw.12435>

Nagarajah, S., 1987. Effects of Soil Texture on the Rooting Patterns of Thompson Seedless Vines on Own Roots and on Ramsey Rootstock in Irrigated Vineyards. *Am. J. Enol. Vitic.* 38, 54–59.
<https://doi.org/10.5344/ajev.1987.38.1.54>

Nakashima, K., Yamaguchi-Shinozaki, K., 2013. ABA signaling in stress-response and seed development. *Plant Cell Rep.* 32, 959–970.
<https://doi.org/10.1007/s00299-013-1418-1>

Naveed, M., Brown, L.K., Raffan, A.C., George, T.S., Bengough, A.G., Roose, T., Sinclair, I., Koebernick, N., Cooper, L., Hackett, C.A., Hallett, P.D., 2017. Plant exudates may stabilize or weaken soil depending on species, origin and time. *Eur. J. Soil Sci.* 68, 806–816.
<https://doi.org/10.1111/ejss.12487>

Nesbitt, A., Kemp, B., Steele, C., Lovett, A., Dorling, S., 2016. Impact of recent climate change and weather variability on the viability of UK viticulture – combining weather and climate records with producers’ perspectives. *Aust. J. Grape Wine Res.* 22, 324–335.
<https://doi.org/10.1111/ajgw.12215>

Netzer, Y., Yao, C., Shenker, M., Bravdo, B.-A., Schwartz, A., 2009. Water use and the development of seasonal crop coefficients for Superior Seedless grapevines trained to an open-gable trellis system. *Irrig. Sci.* 27, 109–120. <https://doi.org/10.1007/s00271-008-0124-1>

Nguyen, T.H., Gaiser, T., Vanderborght, J., Schnepf, A., Bauer, F., Klotzsche, A., Lärm, L., Hüging, H., Ewert, F., 2024. Responses of field-grown maize to different soil types, water regimes, and contrasting vapor pressure deficit. *EGUsphere* 1–53.
<https://doi.org/10.5194/egusphere-2023-2967>

Nguyen, T.H., Langensiepen, M., Hueging, H., Gaiser, T., Seidel, S.J., Ewert, F., 2022. Expansion and evaluation of two coupled root–shoot models in simulating CO₂ and H₂O fluxes and growth of maize. *Vadose Zone J.* 21, e20181. <https://doi.org/10.1002/vzj2.20181>

Nguyen, T.H., Langensiepen, M., Vanderborght, J., Hüging, H., Mboh, C.M., Ewert, F., 2020. Comparison of root water uptake models in simulating CO₂ and H₂O fluxes and growth of wheat. *Hydrol. Earth Syst. Sci.* 24, 4943–4969. <https://doi.org/10.5194/hess-24-4943-2020>

Nobel, P.S., Cui, M., 1992. Hydraulic Conductances of the Soil, the Root–Soil Air Gap, and the Root: Changes for Desert Succulents in Drying Soil. *J. Exp. Bot.* 43, 319–326.

North, G.B., Martre, P., Nobel, P.S., 2004. Aquaporins account for variations in hydraulic conductance for metabolically active root regions of *Agave deserti* in wet, dry, and rewetted soil. *Plant Cell Environ.* 27, 219–228.

North, G.B., Nobel, P.S., 1997. Root-soil contact for the desert succulent *Agave deserti* in wet and drying soil. *New Phytol.* 135, 21–29. <https://doi.org/10.1046/j.1469-8137.1997.00620.x>

Novick, K.A., Ficklin, D.L., Baldocchi, D., Davis, K.J., Ghezzehei, T.A., Konings, A.G., MacBean, N., Raoult, N., Scott, R.L., Shi, Y., Sulman, B.N., Wood, J.D., 2022. Confronting the water potential information gap. *Nat. Geosci.* 15, 158–164. <https://doi.org/10.1038/s41561-022-00909-2>

Nye, P.H., 1994. The Effect of Root Shrinkage on Soil Water Inflow. *Philos. Trans. Biol. Sci.* 345, 395–402.

OIV, 2022. State of the World Vine and Wine Sector in 2022.

Ojeda, H., Carrillo, N., Deis, L., Tisseyre, B., Heywang, M., Carbonneau, A., 2005. Precision viticulture and water status II: Quantitative and qualitative performance of different within field zones, defined from water potential mapping. *Proc. 14th GESCO Congr.* 741–748.

Ollat, N., Cookson, S.J., Lauvergeat, V., Marguerit, E., Barrieu, F., Gambetta, G., Goutouly, J.-P., Tandonnet, J.-P., Vivin, P., Delrot, S., 2017. Grapevine roots: the dark side. *Acta Hort.* 213–226. <https://doi.org/10.17660/ActaHortic.2017.1188.28>

Ollat, N., Peccoux, A., Papura, D., Esmenjaud, D., Marguerit, E., Tandonnet, J.-P., Bordenave, L., Cookson, S. j., Barrieu, F., Rossdeutsch, L., Lecourt, J., Lauvergeat, V., Vivin, P., Bert, P.-F., Delrot, S., 2015. Rootstocks as a component of adaptation to environment, in: *Grapevine in a Changing Environment*. John Wiley & Sons, Ltd, pp. 68–108. <https://doi.org/10.1002/9781118735985.ch4>

Orman-Ligeza, B., Morris, E.C., Parizot, B., Lavigne, T., Babé, A., Ligeza, A., Klein, S., Sturrock, C., Xuan, W., Novák, O., Ljung, K., Fernandez, M.A., Rodriguez, P.L., Dodd, I.C., De Smet, I., Chaumont, F., Batoko, H., Périlleux, C., Lynch, J.P., Bennett, M.J., Beeckman, T., Draye, X., 2018. The Xerobranching Response Represses Lateral Root Formation When Roots Are Not in Contact with Water. *Curr. Biol.* 28, 3165–3173.e5. <https://doi.org/10.1016/j.cub.2018.07.074>

Pagay, V., Kidman, C.M., 2019. Evaluating Remotely-Sensed Grapevine (*Vitis vinifera* L.) Water Stress Responses Across a Viticultural Region. *Agronomy* 9, 682. <https://doi.org/10.3390/agronomy9110682>

Parniske, M., 2008. Arbuscular mycorrhiza: the mother of plant root endosymbioses. *Nat. Rev. Microbiol.* 6, 763–775. <https://doi.org/10.1038/nrmicro1987>

Passioura, J., 1980. The Transport of Water from Soil to Shoot in Wheat Seedlings. *J. Exp. Bot.* 31. <https://doi.org/10.1093/jxb/31.1.333>

Peccoux, A., Loveys, B., Zhu, J., Gambetta, G.A., Delrot, S., Vivin, P., Schultz, H.R., Ollat, N., Dai, Z., 2018. Dissecting the rootstock control of scion transpiration using model-assisted analyses in grapevine. *Tree Physiol.* 38, 1026–1040. <https://doi.org/10.1093/treephys/tpx153>

Penuelas, J., Pinol, J., Ogaya, R., Filella, I., 1997. Estimation of plant water concentration by the reflectance Water Index WI (R900/R970).

Int. J. Remote Sens. 18, 2869–2875.
<https://doi.org/10.1080/014311697217396>

Pereyra, G., Pellegrino, A., Ferrer, M., Gaudin, R., 2023. How soil and climate variability within a vineyard can affect the heterogeneity of grapevine vigour and production. *OENO One* 57, 297–313.
<https://doi.org/10.20870/oenone.2023.57.3.7498>

Perry, R.L., Lyda, S.D., Bowen, H.H., 1983. Root distribution of four *Vitis* cultivars. *Plant Soil* 71, 63–74.

Pickering, G., Wheeler, S., 2006. The effects of soil management techniques on grape and wine quality. pp. 195–208.

Poblete, T., Ortega-Farías, S., Moreno, M.A., Bardeen, M., 2017. Artificial Neural Network to Predict Vine Water Status Spatial Variability Using Multispectral Information Obtained from an Unmanned Aerial Vehicle (UAV). *Sensors* 17, 2488.
<https://doi.org/10.3390/s17112488>

Pôças, I., Rodrigues, A., Gonçalves, S., Costa, P.M., Gonçalves, I., Pereira, L.S., Cunha, M., 2015. Predicting Grapevine Water Status Based on Hyperspectral Reflectance Vegetation Indices. *Remote Sens.* 7, 16460–16479. <https://doi.org/10.3390/rs71215835>

Pörtner, H.O., Roberts, D.C., Poloczanska, E.S., Mintenbeck, K., Tignor, M., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., 2022. IPCC, 2022: summary for policymakers, in: Pörtner, H.O., Roberts, D.C., Poloczanska, E.S., Mintenbeck, K., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., Rama, B. (Eds.), . Cambridge University Press, Cambridge, UK and New York, NY, US, pp. 3–33.

Pou, A., Diago, M.P., Medrano, H., Baluja, J., Tardaguila, J., 2014. Validation of thermal indices for water status identification in grapevine. *Agric. Water Manag.* 134, 60–72.
<https://doi.org/10.1016/j.agwat.2013.11.010>

Pou, A., Medrano, H., Tomàs, M., Martorell, S., Ribas-Carbó, M., Flexas, J., 2012. Anisohydric behaviour in grapevines results in better performance under moderate water stress and recovery than isohydric

behaviour. *Plant Soil* 359, 335–349. <https://doi.org/10.1007/s11104-012-1206-7>

Qi, J., Chehbouni, A., Huete, A.R., Kerr, Y.H., Sorooshian, S., 1994. A modified soil adjusted vegetation index. *Remote Sens. Environ.* 48, 119–126. [https://doi.org/10.1016/0034-4257\(94\)90134-1](https://doi.org/10.1016/0034-4257(94)90134-1)

Quiroga, G., Erice, G., Aroca, R., Zamarreño, Á.M., García-Mina, J.M., Ruiz-Lozano, J.M., 2020. Radial water transport in arbuscular mycorrhizal maize plants under drought stress conditions is affected by indole-acetic acid (IAA) application. *J. Plant Physiol.* 246–247, 153115. <https://doi.org/10.1016/j.jplph.2020.153115>

Raats, P. a. C., 1970. Steady Infiltration from Line Sources and Furrows. *Soil Sci. Soc. Am. J.* 34, 709–714. <https://doi.org/10.2136/sssaj1970.03615995003400050015x>

Rabia, A.H., Neupane, J., Lin, Z., Lewis, K., Cao, G., Guo, W., 2022. Chapter Four - Principles and applications of topography in precision agriculture, in: Sparks, D.L. (Ed.), *Advances in Agronomy*. Academic Press, pp. 143–189. <https://doi.org/10.1016/bs.agron.2021.08.005>

Rallo, G., Minacapilli, M., Ciruolo, G., Provenzano, G., 2014. Detecting crop water status in mature olive groves using vegetation spectral measurements. *Biosyst. Eng., Special Issue: Irrigated Agriculture: Water Resources Management for a Sustainable Environment* 128, 52–68. <https://doi.org/10.1016/j.biosystemseng.2014.08.012>

Rapaport, T., Hochberg, U., Shoshany, M., Karnieli, A., Rachmilevitch, S., 2015. Combining leaf physiology, hyperspectral imaging and partial least squares-regression (PLS-R) for grapevine water status assessment. *ISPRS J. Photogramm. Remote Sens.* 109, 88–97. <https://doi.org/10.1016/j.isprsjprs.2015.09.003>

Rebekić, A., Lončarić, Z., Petrović, S., Marić, S., 2015. Pearson's or Spearman's correlation coefficient - Which one to use? *Poljoprivreda* 21, 47–54. <https://doi.org/10.18047/poljo.21.2.8>

Renouf, V., Trégoat, O., Roby, J.-P., Van Leeuwen, C., 2010. Soils, rootstocks and grapevine varieties in prestigious Bordeaux vineyards

and their impact on yield and quality. *OENO One* 44, 127.
<https://doi.org/10.20870/oenone.2010.44.3.1471>

Reynier, A., 2011. *Manuel de viticulture: Guide technique du viticulteur*. Lavoisier.

Reynolds, A.G., Taylor, G., de Savigny, C., 2013. Defining Niagara Terroir by Chemical and Sensory Analysis of Chardonnay Wines from Various Soil Textures and Vine Sizes. *Am. J. Enol. Vitic.* 64, 180–194.
<https://doi.org/10.5344/ajev.2013.12092>

Richter, H., 1997. Water relations of plants in the field: some comments on the measurement of selected parameters. *J. Exp. Bot.* 48, 1–7.
<https://doi.org/10.1093/jxb/48.1.1>

Ridley, A.M., Burland, J.B., 1993. A new instrument for the measurement of soil moisture suction. *Géotechnique* 43, 321–324.
<https://doi.org/10.1680/geot.1993.43.2.321>

Ritchie, J.T., 1972. Model for predicting evaporation from a row crop with incomplete cover. *Water Resour. Res.* 8, 1204–1213.
<https://doi.org/10.1029/WR008i005p01204>

Robinson, G.W., 1933. Soils. Their Origin, Constitution, and Classification. *Soil Sci.* 35, 171.

Rodriguez-Dominguez, C.M., Brodribb, T.J., 2020. Declining root water transport drives stomatal closure in olive under moderate water stress. *New Phytol.* 225, 126–134. <https://doi.org/10.1111/nph.16177>

Rodríguez-Pérez, J.R., Riaño, D., Carlisle, E., Ustin, S., Smart, D.R., 2007. Evaluation of Hyperspectral Reflectance Indexes to Detect Grapevine Water Status in Vineyards. *Am. J. Enol. Vitic.* 58, 302–317.
<https://doi.org/10.5344/ajev.2007.58.3.302>

Rogiers, S.Y., Greer, D.H., Hatfield, J.M., Hutton, R.J., Clarke, S.J., Hutchinson, P.A., Somers, A., 2012. Stomatal response of an anisohydric grapevine cultivar to evaporative demand, available soil moisture and abscisic acid. *Tree Physiol.* 32, 249–261.
<https://doi.org/10.1093/treephys/tpr131>

Rolli, E., Marasco, R., Vigani, G., Ettoumi, B., Mapelli, F., Deangelis, M.L., Gandolfi, C., Casati, E., Previtali, F., Gerbino, R., Pierotti Cei, F., Borin, S., Sorlini, C., Zocchi, G., Daffonchio, D., 2015. Improved plant resistance to drought is promoted by the root-associated microbiome as a water stress-dependent trait. *Environ. Microbiol.* 17, 316–331. <https://doi.org/10.1111/1462-2920.12439>

Romero, M., Luo, Y., Su, B., Fuentes, S., 2018. Vineyard water status estimation using multispectral imagery from an UAV platform and machine learning algorithms for irrigation scheduling management. *Comput. Electron. Agric.* 147, 109–117. <https://doi.org/10.1016/j.compag.2018.02.013>

Rooyen, M. van, Valentine, A., Archer, E., 2004. Arbuscular Mycorrhizal Colonisation Modifies the Water Relations of Young Transplanted Grapevines (*Vitis*). *South Afr. J. Enol. Vitic.* 25, 37–42. <https://doi.org/10.21548/25-2-2137>

RStudio Team, 2022. RStudio: Integrated Development for R. RStudio, PBC, Boston.

Ruiz-Lozano, J.M., Aroca, R., 2017. Plant Aquaporins and Mycorrhizae: Their Regulation and Involvement in Plant Physiology and Performance, in: Chaumont, F., Tyerman, S.D. (Eds.), *Plant Aquaporins: From Transport to Signaling*. Springer International Publishing, Cham, pp. 333–353. https://doi.org/10.1007/978-3-319-49395-4_15

Sabot, M.E.B., Kauwe, M.G.D., Pitman, A.J., Medlyn, B.E., Verhoef, A., Ukkola, A.M., Abramowitz, G., 2020. Plant profit maximization improves predictions of European forest responses to drought. *New Phytol.* 226, 1638–1655. <https://doi.org/10.1111/nph.16376>

Santesteban, L.G., Di Gennaro, S.F., Herrero-Langreo, A., Miranda, C., Royo, J.B., Matese, A., 2017. High-resolution UAV-based thermal imaging to estimate the instantaneous and seasonal variability of plant water status within a vineyard. *Agric. Water Manag., Special Issue: Advances on ICTs for Water Management in Agriculture* 183, 49–59. <https://doi.org/10.1016/j.agwat.2016.08.026>

Santos, J.A., Fraga, H., Malheiro, A.C., Moutinho-Pereira, J., Dinis, L.-T., Correia, C., Moriondo, M., Leolini, L., Dibari, C., Costafreda-Aumedes, S., Kartschall, T., Menz, C., Molitor, D., Junk, J., Beyer, M., Schultz, H.R., 2020. A Review of the Potential Climate Change Impacts and Adaptation Options for European Viticulture. *Appl. Sci.* 10, 3092. <https://doi.org/10.3390/app10093092>

Savi, T., Petruzzellis, F., Martellos, S., Stenni, B., Dal Borgo, A., Zini, L., Lisjak, K., Nardini, A., 2018. Vineyard water relations in a karstic area: deep roots and irrigation management. *Agric. Ecosyst. Environ.* 263, 53–59. <https://doi.org/10.1016/j.agee.2018.05.009>

Scharwies, J.D., Tyerman, S.D., Scharwies, J.D., Tyerman, S.D., 2016. Comparison of isohydric and anisohydric *Vitis vinifera* L. cultivars reveals a fine balance between hydraulic resistances, driving forces and transpiration in ripening berries. *Funct. Plant Biol.* 44, 324–338. <https://doi.org/10.1071/FP16010>

Schmidhalter, U., 1997. The gradient between pre-dawn rhizoplane and bulk soil matric potentials, and its relation to the pre-dawn root and leaf water potentials of four species. *Plant Cell Environ.* 20, 953–960. <https://doi.org/10.1046/j.1365-3040.1997.d01-136.x>

Scholander, P.F., Bradstreet, E.D., Hemmingsen, E.A., Hammel, H.T., 1965. Sap Pressure in Vascular Plants. *Science* 148, 339–346. <https://doi.org/10.1126/science.148.3668.339>

Schreiner, R.P., Tarara, J.M., Smithyman, R.P., 2007. Deficit irrigation promotes arbuscular colonization of fine roots by mycorrhizal fungi in grapevines (*Vitis vinifera* L.) in an arid climate. *Mycorrhiza* 17, 551–562. <https://doi.org/10.1007/s00572-007-0128-3>

Schroeder, T., Javaux, M., Vanderborght, J., Vereecken, H., 2007. Comment on “Root water extraction and limiting soil hydraulic conditions estimated by numerical simulation.” *Vadose Zone J.* 6, 524–526. <https://doi.org/10.2136/vzj2007.0036>

Schultz, H.R., 2003. Differences in hydraulic architecture account for near-isohydric and anisohydric behaviour of two field-grown *Vitis*

vinifera L. cultivars during drought. *Plant Cell Environ.* 26, 1393–1405. <https://doi.org/10.1046/j.1365-3040.2003.01064.x>

Scoffoni, C., Albuquerque, C., Brodersen, C.R., Townes, S.V., John, G.P., Bartlett, M.K., Buckley, T.N., McElrone, A.J., Sack, L., 2017. Outside-Xylem Vulnerability, Not Xylem Embolism, Controls Leaf Hydraulic Decline during Dehydration. *Plant Physiol.* 173, 1197–1210. <https://doi.org/10.1104/pp.16.01643>

Serrano, L., González-Flor, C., Gorchs, G., 2010. Assessing vineyard water status using the reflectance based Water Index. *Agric. Ecosyst. Environ.* 139, 490–499. <https://doi.org/10.1016/j.agee.2010.09.007>

Shaozhong, K., Huanjie, C., Jianhua, Z., 2000. Estimation of maize evapotranspiration under water deficits in a semiarid region. *Agric. Water Manag.* 43, 1–14. [https://doi.org/10.1016/S0378-3774\(99\)00063-3](https://doi.org/10.1016/S0378-3774(99)00063-3)

Shen, Y., Kondoh, A., Tang, C., Zhang, Y., Chen, J., Li, W., Sakura, Y., Liu, C., Tanaka, T., Shimada, J., 2002. Measurement and analysis of evapotranspiration and surface conductance of a wheat canopy. *Hydrol. Process.* 16, 2173–2187. <https://doi.org/10.1002/hyp.1149>

Simonneau, T., Lebon, E., Coupel-Ledru, A., Marguerit, E., Rossdeutsch, L., Ollat, N., 2017. Adapting plant material to face water stress in vineyards: which physiological targets for an optimal control of plant water status? *OENO One* 51, 167–179. <https://doi.org/10.20870/oeno-one.2017.51.2.1870>

Sinclair, T.R., Hammer, G.L., Oosterom, E.J. van, Sinclair, T.R., Hammer, G.L., Oosterom, E.J. van, 2005. Potential yield and water-use efficiency benefits in sorghum from limited maximum transpiration rate. *Funct. Plant Biol.* 32, 945–952. <https://doi.org/10.1071/FP05047>

Smart, D.R., Schwass, E., Lakso, A., Morano, L., 2006. Grapevine Rooting Patterns: A Comprehensive Analysis and a Review. *Am. J. Enol. Vitic.* 57, 89–104. <https://doi.org/10.5344/ajev.2006.57.1.89>

Soar, C. j., Dry, P. r., Loveys, B. r., 2006a. Scion photosynthesis and leaf gas exchange in *Vitis vinifera* L. cv. Shiraz: Mediation of rootstock

effects via xylem sap ABA. *Aust. J. Grape Wine Res.* 12, 82–96.
<https://doi.org/10.1111/j.1755-0238.2006.tb00047.x>

Soar, C. j., Speirs, J., Maffei, S. m., Penrose, A. b., Mccarthy, M. g., Loveys, B. r., 2006b. Grape vine varieties Shiraz and Grenache differ in their stomatal response to VPD: apparent links with ABA physiology and gene expression in leaf tissue. *Aust. J. Grape Wine Res.* 12, 2–12.
<https://doi.org/10.1111/j.1755-0238.2006.tb00038.x>

Sorek, Y., Greenstein, S., Netzer, Y., Shtein, I., Jansen, S., Hochberg, U., 2021. An increase in xylem embolism resistance of grapevine leaves during the growing season is coordinated with stomatal regulation, turgor loss point and intervessel pit membranes. *New Phytol.* 229, 1955–1969. <https://doi.org/10.1111/nph.17025>

Soualiou, S., Wang, Z., Sun, W., de Reffye, P., Collins, B., Louarn, G., Song, Y., 2021. Functional–Structural Plant Models Mission in Advancing Crop Science: Opportunities and Prospects. *Front. Plant Sci.* 12.

Soubry, I., Patias, P., Tsioukas, V., 2017. Monitoring vineyards with UAV and multi-sensors for the assessment of water stress and grape maturity. *J. Unmanned Veh. Syst.* 5, 37–50.
<https://doi.org/10.1139/juvs-2016-0024>

Sperry, J.S., Adler, F.R., Campbell, G.S., Comstock, J.P., 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant Cell Environ.* 21, 347–359.
<https://doi.org/10.1046/j.1365-3040.1998.00287.x>

Sperry, J.S., Love, D.M., 2015. What plant hydraulics can tell us about responses to climate-change droughts. *New Phytol.* 207, 14–27.
<https://doi.org/10.1111/nph.13354>

SPF Economie, 2024. La viticulture belge en chiffres.

Stagakis, S., González-Dugo, V., Cid, P., Guillén-Climent, M.L., Zarco-Tejada, P.J., 2012. Monitoring water stress and fruit quality in an orange orchard under regulated deficit irrigation using narrow-band structural and physiological remote sensing indices. *ISPRS J. Photogramm.*

Remote Sens. 71, 47–61.
<https://doi.org/10.1016/j.isprsjprs.2012.05.003>

Steudle, E., 2000a. Water uptake by roots: effects of water deficit. *J. Exp. Bot.* 51, 1531–1542. <https://doi.org/10.1093/jexbot/51.350.1531>

Steudle, E., 2000b. Water uptake by roots: effects of water deficit. *J. Exp. Bot.* 51, 1531–1542. <https://doi.org/10.1093/jexbot/51.350.1531>

Steudle, E., Peterson, C.A., 1998. How does water get through roots? *J. Exp. Bot.* 49, 775–788. <https://doi.org/10.1093/jexbot/49.322.775>

Suárez, L., Zarco-Tejada, P.J., Sepulcre-Cantó, G., Pérez-Priego, O., Miller, J.R., Jiménez-Muñoz, J.C., Sobrino, J., 2008. Assessing canopy PRI for water stress detection with diurnal airborne imagery. *Remote Sens. Environ., Soil Moisture Experiments 2004 (SMEX04) Special Issue* 112, 560–575. <https://doi.org/10.1016/j.rse.2007.05.009>

Tamayo, M., Sepúlveda, L., Guequen, E.P., Saavedra, P., Pedreschi, R., Cáceres-Mella, A., Alvaro, J.E., Cuneo, I.F., 2023. Hydric Behavior: Insights into Primary Metabolites in Leaves and Roots of Cabernet Sauvignon and Grenache Grapevine Varieties under Drought Stress. *Horticulturae* 9, 566. <https://doi.org/10.3390/horticulturae9050566>

Tang, Z., Jin, Y., Alsina, M.M., McElrone, A.J., Bambach, N., Kustas, W.P., 2022. Vine water status mapping with multispectral UAV imagery and machine learning. *Irrig. Sci.* 40, 715–730. <https://doi.org/10.1007/s00271-022-00788-w>

Tardaguila, J., Fernández-Novales, J., Gutiérrez, S., Diago, M.P., 2017. Non-destructive assessment of grapevine water status in the field using a portable NIR spectrophotometer. *J. Sci. Food Agric.* 97, 3772–3780. <https://doi.org/10.1002/jsfa.8241>

Tardieu, F., 2016. Too many partners in root-shoot signals. Does hydraulics qualify as the only signal that feeds back over time for reliable stomatal control? *New Phytol.* 212, 802–804. <https://doi.org/10.1111/nph.14292>

- Tardieu, F., 2011. Any trait or trait-related allele can confer drought tolerance: Just design the right drought scenario. *J. Exp. Bot.* 63, 25–31. <https://doi.org/10.1093/jxb/err269>
- Tardieu, F., Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *J. Exp. Bot.* 49, 419–432. https://doi.org/10.1093/jxb/49.Special_Issue.419
- Tardieu, F., Simonneau, T., Muller, B., 2018. The Physiological Basis of Drought Tolerance in Crop Plants: A Scenario-Dependent Probabilistic Approach. *Annu. Rev. Plant Biol.* 69, 733–759. <https://doi.org/10.1146/annurev-arplant-042817-040218>
- Taylor, J. a., Acevedo-Opazo, C., Ojeda, H., Tisseyre, B., 2010. Identification and significance of sources of spatial variation in grapevine water status. *Aust. J. Grape Wine Res.* 16, 218–226. <https://doi.org/10.1111/j.1755-0238.2009.00066.x>
- Timlin, D., Bunce, J., Fleisher, D., Reddy, V.R., Yang, Y., Kim, S.-H., Saseendran, S. a, Quebedeaux, B., 2008. Simulation of the Effects of Limited Water on Photosynthesis and Transpiration in Field Crops: Can We Advance Our Modeling Approaches?, in: *Response of Crops to Limited Water*. John Wiley & Sons, Ltd, pp. 105–143. <https://doi.org/10.2134/advagricsystmodel1.c4>
- Tisseyre, B., Ojeda, H., Carillo, N., Deis, L., Heywang, M., 2005. Precision Viticulture and Water Status : Mapping the Predawn Water Potential to Define within Vineyard Zones. *Proc. 14th GESCO Congr.*
- Tombesi, S., Nardini, A., Frioni, T., Socolini, M., Zadra, C., Farinelli, D., Poni, S., Palliotti, A., 2015. Stomatal closure is induced by hydraulic signals and maintained by ABA in drought-stressed grapevine. *Sci. Rep.* 5, 12449. <https://doi.org/10.1038/srep12449>
- Tosin, R., Pôças, I., Novo, H., Teixeira, J., Fontes, N., Graça, A., Cunha, M., 2021. Assessing predawn leaf water potential based on hyperspectral data and pigment's concentration of *Vitis vinifera* L. in the Douro Wine Region. *Sci. Hortic.* 278, 109860. <https://doi.org/10.1016/j.scienta.2020.109860>

- Tramontini, S., Döring, J., Vitali, M., Ferrandino, A., Stoll, M., Lovisolo, C., 2014. Soil water-holding capacity mediates hydraulic and hormonal signals of near-isohydric and near-anisohydric *Vitis* cultivars in potted grapevines. *Funct. Plant Biol.* 41, 1119. <https://doi.org/10.1071/FP13263>
- Tramontini, S., van Leeuwen, C., Domec, J.-C., Destrac-Irvine, A., Basteau, C., Vitali, M., Mosbach-Schulz, O., Lovisolo, C., 2013a. Impact of soil texture and water availability on the hydraulic control of plant and grape-berry development. *Plant Soil* 368, 215–230. <https://doi.org/10.1007/s11104-012-1507-x>
- Tramontini, S., Vitali, M., Centonini, L., Schubert, A., Lovisolo, C., 2013b. Rootstock control of scion response to water stress in grapevine. *Environ. Exp. Bot.* 93, 20–26. <https://doi.org/10.1016/j.envexpbot.2013.04.001>
- Trifilo, P., Raimondo, F., Nardini, A., Lo Gullo, M.A., Salleo, S., 2004. Drought resistance of *Ailanthus altissima*: root hydraulics and water relations. *Tree Physiol.* 24, 107–114. <https://doi.org/10.1093/treephys/24.1.107>
- Tron, S., Bodner, G., Laio, F., Ridolfi, L., Leitner, D., 2015. Can diversity in root architecture explain plant water use efficiency? A modeling study. *Ecol. Model.* 312, 200–210. <https://doi.org/10.1016/j.ecolmodel.2015.05.028>
- Trouvelot, S., Bonneau, L., Redecker, D., van Tuinen, D., Adrian, M., Wipf, D., 2015. Arbuscular mycorrhiza symbiosis in viticulture: a review. *Agron. Sustain. Dev.* 35, 1449–1467. <https://doi.org/10.1007/s13593-015-0329-7>
- Tsuda, M., Tyree, M.T., 2000. Plant hydraulic conductance measured by the high pressure flow meter in crop plants. *J. Exp. Bot.* 51, 823–828. <https://doi.org/10.1093/jexbot/51.345.823>
- Twarakavi, N.K.C., Sakai, M., Šimůnek, J., 2009. An objective analysis of the dynamic nature of field capacity. *Water Resour. Res.* 45. <https://doi.org/10.1029/2009WR007944>

Tyree, M.T., Ewers, F.W., 1991. The hydraulic architecture of trees and other woody plants. *New Phytol.* 119, 345–360. <https://doi.org/10.1111/j.1469-8137.1991.tb00035.x>

Tyree, M.T., Sperry, J.S., 1989. Vulnerability of Xylem to Cavitation and Embolism. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 40, 19–36. <https://doi.org/10.1146/annurev.pp.40.060189.000315>

Tyree, M.T., Zimmermann, M.H., 2002. The Cohesion-Tension Theory of Sap Ascent, in: Tyree, M.T., Zimmermann, M.H. (Eds.), *Xylem Structure and the Ascent of Sap*, Springer Series in Wood Science. Springer, Berlin, Heidelberg, pp. 49–88. https://doi.org/10.1007/978-3-662-04931-0_3

van Dam, J.C., Feddes, R.A., 2000. Numerical simulation of infiltration, evaporation and shallow groundwater levels with the Richards equation. *J. Hydrol.* 233, 72–85. [https://doi.org/10.1016/S0022-1694\(00\)00227-4](https://doi.org/10.1016/S0022-1694(00)00227-4)

van Genuchten, M.Th., 1980. A Closed-form Equation for Predicting the Hydraulic Conductivity of Unsaturated Soils. *Soil Sci. Soc. Am. J.* 44, 892–898. <https://doi.org/10.2136/sssaj1980.03615995004400050002x>

Van Leeuwen, C., Barbe, J.-C., Darriet, P., Geffroy, O., Gomès, E., Guillaumie, S., Helwi, P., Laboyrie, J., Lytra, G., Le Menn, N., Marchand, S., Picard, M., Pons, A., Schüttler, A., Thibon, C., 2020. Recent advancements in understanding the terroir effect on aromas in grapes and wines: This article is published in cooperation with the XIIIth International Terroir Congress November 17-18 2020, Adelaide, Australia. Guests editors: Cassandra Collins and Roberta De Bei. *OENO One* 54. <https://doi.org/10.20870/oeno-one.2020.54.4.3983>

van Leeuwen, C., Darriet, P., 2016. The Impact of Climate Change on Viticulture and Wine Quality. *J. Wine Econ.* 11, 150–167. <https://doi.org/10.1017/jwe.2015.21>

Van Leeuwen, C., Friant, P., Choné, X., Tregoat, O., Koundouras, S., Dubourdieu, D., 2004a. Influence of Climate, Soil, and Cultivar on Terroir. *Am. J. Enol. Vitic.* 55, 207–217.

Van Leeuwen, C., Friant, P., Choné, X., Tregoat, O., Koundouras, S., Dubourdieu, D., 2004b. Influence of Climate, Soil, and Cultivar on Terroir. *Am. J. Enol. Vitic.* 55, 207–217. <https://doi.org/10.5344/ajev.2004.55.3.207>

Van Leeuwen, C., Roby, J.-P., Rességuier, L. de, 2018. Soil-related terroir factors: a review. *OENO One* 52, 173–188. <https://doi.org/10.20870/oeno-one.2018.52.2.2208>

Van Leeuwen, C., Trégoat, O., Choné, X., Bois, B., Pernet, D., Gaudillère, J.-P., 2009a. Vine water status is a key factor in grape ripening and vintage quality for red Bordeaux wine. How can it be assessed for vineyard management purposes? *OENO One* 43, 121. <https://doi.org/10.20870/oeno-one.2009.43.3.798>

Van Leeuwen, C., Trégoat, O., Choné, X., Bois, B., Pernet, D., Gaudillère, J.-P., 2009b. Vine water status is a key factor in grape ripening and vintage quality for red Bordeaux wine. How can it be assessed for vineyard management purposes? *OENO One* 43, 121. <https://doi.org/10.20870/oeno-one.2009.43.3.798>

Vandeleur, R.K., Mayo, G., Shelden, M.C., Gilliam, M., Kaiser, B.N., Tyerman, S.D., 2009. The Role of Plasma Membrane Intrinsic Protein Aquaporins in Water Transport through Roots: Diurnal and Drought Stress Responses Reveal Different Strategies between Isohydric and Anisohydric Cultivars of Grapevine. *Plant Physiol.* 149, 445–460. <https://doi.org/10.1104/pp.108.128645>

Vanderborght, J., Couvreur, V., Meunier, F., Schnepf, A., Vereecken, H., Bouda, M., Javaux, M., 2021. From hydraulic root architecture models to macroscopic representations of root hydraulics in soil water flow and land surface models. *Hydrol. Earth Syst. Sci.* 25, 4835–4860. <https://doi.org/10.5194/hess-25-4835-2021>

Vanderborght, J., Leitner, D., Schnepf, A., Couvreur, V., Vereecken, H., Javaux, M., 2023. Combining root and soil hydraulics in macroscopic representations of root water uptake. *Vadose Zone J.* n/a, e20273. <https://doi.org/10.1002/vzj2.20273>

Vansteenkiste, J., Van Loon, J., Garré, S., Pagès, L., Schrevens, E., Diels, J., 2014. Estimating the parameters of a 3-D root distribution function from root observations with the trench profile method: case study with simulated and field-observed root data. *Plant Soil* 375, 75–88. <https://doi.org/10.1007/s11104-013-1942-3>

Veen, B., Vannoordwijk, M., Dewilligen, P., Boone, F., Kooistra, M., 1992. Root-Soil Contact of Maize, as Measured by a Thin-Section Technique .3. Effects on Shoot Growth, Nitrate and Water-Uptake Efficiency. *Plant Soil* 139, 131–138. <https://doi.org/10.1007/BF00012850>

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. *J. Clim.* 23, 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>

Villalobos-González, L., Muñoz-Araya, M., Franck, N., Pastenes, C., 2019. Controversies in Midday Water Potential Regulation and Stomatal Behavior Might Result From the Environment, Genotype, and/or Rootstock: Evidence From Carménère and Syrah Grapevine Varieties. *Front. Plant Sci.* 10.

Vitali, M., Tamagnone, M., Iacona, T.L., Lovisolo, C., 2013. Measurement of grapevine canopy leaf area by using an ultrasonic-based method. *OENO One* 47, 183–189. <https://doi.org/10.20870/oeno-one.2013.47.3.1553>

Vivin, P., Lebon, É., Dai, Z., Duchêne, E., Marguerit, E., Cortázar-Atauri, I.G. de, Zhu, J., Simonneau, T., Leeuwen, C. van, Delrot, S., Ollat, N., 2017. Combining ecophysiological models and genetic analysis: a promising way to dissect complex adaptive traits in grapevine. *OENO One* 51, 181–189. <https://doi.org/10.20870/oeno-one.2017.51.2.1588>

Volaire, F., 2018. A unified framework of plant adaptive strategies to drought: Crossing scales and disciplines. *Glob. Change Biol.* 24, 2929–2938. <https://doi.org/10.1111/gcb.14062>

Walther, L., Schleppi, P., 2018. Equations to compensate for the temperature effect on readings from dielectric Decagon MPS-2 and MPS-6 water potential sensors in soils. *J. Plant Nutr. Soil Sci.* 181, 749–759. <https://doi.org/10.1002/jpln.201700620>

Wankmüller, F.J.P., Carminati, A., 2024. Soil Hydraulic Constraints on Stomatal Regulation of Plant Gas Exchange, in: Lüttge, U., Cánovas, F.M., Risueño, M.-C., Leuschner, C., Pretzsch, H. (Eds.), *Progress in Botany Vol. 84, Progress in Botany*. Springer Nature Switzerland, Cham, pp. 327–350. https://doi.org/10.1007/124_2023_68

Wilkinson, L., 1979. Tests of significance in stepwise regression. *Psychol. Bull.* 86, 168–174. <https://doi.org/10.1037/0033-2909.86.1.168>

Wolf, A., Anderegg, W.R.L., Pacala, S.W., 2016. Optimal stomatal behavior with competition for water and risk of hydraulic impairment. *Proc. Natl. Acad. Sci.* 113, E7222–E7230. <https://doi.org/10.1073/pnas.1615144113>

Xue, J., Su, B., 2017. Significant Remote Sensing Vegetation Indices: A Review of Developments and Applications. *J. Sens.* 2017, e1353691. <https://doi.org/10.1155/2017/1353691>

Yang, W., Zhu, J., van Leeuwen, C., Dai, Z., Gambetta, G.A., 2023. GrapevineXL reliably predicts multi-annual dynamics of vine water status, berry growth, and sugar accumulation in vineyards. *Hortic. Res.* 10, uhad071. <https://doi.org/10.1093/hr/uhad071>

Zarco-Tejada, P.J., González-Dugo, V., Williams, L.E., Suárez, L., Berni, J.A.J., Goldhamer, D., Fereres, E., 2013. A PRI-based water stress index combining structural and chlorophyll effects: Assessment using diurnal narrow-band airborne imagery and the CWSI thermal index. *Remote Sens. Environ.* 138, 38–50. <https://doi.org/10.1016/j.rse.2013.07.024>

Zarebanadkouki, M., Kim, Y.X., Carminati, A., 2013. Where do roots take up water? Neutron radiography of water flow into the roots of transpiring plants growing in soil. *New Phytol.* 199, 1034–1044. <https://doi.org/10.1111/nph.12330>

Zarrouk, O., Brunetti, C., Egipto, R., Pinheiro, C., Genebra, T., Gori, A., Lopes, C.M., Tattini, M., Chaves, M.M., 2016. Grape Ripening Is Regulated by Deficit Irrigation/Elevated Temperatures According to Cluster Position in the Canopy. *Front. Plant Sci.* 7. <https://doi.org/10.3389/fpls.2016.01640>

Zheng, X.-J., Xu, G.-Q., Li, Y., Wu, X., 2019. Deepening Rooting Depths Improve Plant Water and Carbon Status of a Xeric Tree during Summer Drought. *Forests* 10, 592. <https://doi.org/10.3390/f10070592>

Zhou, Q., Chan, C.W., Tontiwachiwuthikul, P., 2008. Regression Analysis Study on the Carbon Dioxide Capture Process. *Ind. Eng. Chem. Res.* 47, 4937–4943. <https://doi.org/10.1021/ie701747f>

Zhou, Qingyun, Kang, S., Li, F., Zhang, L., 2008. Comparison of dynamic and static APRI-models to simulate soil water dynamics in a vineyard over the growing season under alternate partial root-zone drip irrigation. *Agric. Water Manag.* 95, 767–775. <https://doi.org/10.1016/j.agwat.2008.01.018>

Zhou, Q., Kang, S., Zhang, L., Li, F., 2007. Comparison of APRI and Hydrus-2D models to simulate soil water dynamics in a vineyard under alternate partial root zone drip irrigation. *Plant Soil* 291, 211–223. <https://doi.org/10.1007/s11104-006-9187-z>

Zhu, S., Huang, C., Su, Y., Sato, M., 2014. 3D Ground Penetrating Radar to Detect Tree Roots and Estimate Root Biomass in the Field. *Remote Sens.* 6, 5754–5773. <https://doi.org/10.3390/rs6065754>

Zur, B., Jones, J.W., Boote, K.J., Hammond, L.C., 1982. Total Resistance to Water Flow in Field Soybeans: II. Limiting Soil Moisture1. *Agron. J.* 74, 99–105. <https://doi.org/10.2134/agronj1982.00021962007400010026x>

Zygielbaum, A.I., Gitelson, A.A., Arkebauer, T.J., Rundquist, D.C., 2009. Non-destructive detection of water stress and estimation of relative water content in maize. *Geophys. Res. Lett.* 36. <https://doi.org/10.1029/2009GL038906>

